Instytut Paleobiologii Polskiej Akademii Nauk

Origin and early diversification of higher Caenogastropoda (Neogastropoda, Tonnoidea, and Cypraeidae)

Pochodzenie i wczesna dywersyfikacja wyższych caenogastropodów (neogastropodów, tonnoidów i cypreidów)

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STRESZCZENIE

Neogastropoda stanowią jedną z najliczniejszych i najbardziej zróżnicowanych grup ślimaków morskich, charakteryzujące się szerokim zakresem strategii drapieżniczych, przy czym niektóre gatunki są również padlinożercami. Pochodzenie i wczesna ewolucja neogastropodów w mezozoiku były dotychczas słabo poznane, głównie z powodu fragmentarycznego zapisu kopalnego oraz rozproszenia danych w licznych regionalnych pracach taksonomicznych. Niniejsza praca przedstawia kompleksową syntezę światowych wystąpień kredowych neogastropodów i ich mezozoicznych przodków, integrując rewizję taksonomiczną wybranych grup, szczegółową analizę morfologiczną oraz interpretację paleoekologiczną, i przedstawia nowy schemat relacji między ‘wyższymi Caenogastropoda’ we wczesnym mezozoiku.

Rewizja wymarłych rodzin Maturifusidae, Pseudotritoniidae i Purpurinidae, tradycyjnie uważanych za potencjalne grupy macierzyste lub siostrzane do Neogastropoda, wykazała, że stanowią one trzy odrębne, bliżej nie spokrewnione grupy caenogastropodów, a każda z nich charakteryzuje się inną morfologią protokonchy. Zasięg stratygraficzny rodzaju *Purpurina* (Purpurinidae) został wydłużony do późnego triasu, wskazując na wcześniejszą dywersyfikację grupy niż dotychczas sądzono. Ponadto, purpurinidy prawdopodobnie rozdzieliły się już w jurze na dwie linie ewolucyjne – jedna prowadząca w kierunku neogastropodów, a druga w kierunku tonnoidów.

Skład taksonomiczny Colombellinidae, rodziny o niejasnej pozycji w obrębie ‘wyższych caenogastropodów’, został zrewidowany i ograniczony do rodzajów *Colombellina* i *Zittelia*. Szczegółowa analiza morfologii muszli *Zittelia* ujawnia stopniowe zmiany w stopniu konwolutności i cechach apertury (jej wydłużeniu oraz rozszerzeniu wargi kolumelarnej) zmierzające w kierunku morfologii znanej z Cypraeoidea. Zmiany te trwające od oksfordu do tytonu–walanżynu wspierają interpretację rodzaju *Zittelia* jako macierzystego lub siostrzanego dla cypreidów. Obecność bruzdy infrakolumelarnej u niektórych współczesnych cypreidów, interpretowanej jako homologicznej do zatoczki abapikalnej (ang. *abapical sinuosity*) diagnostycznej dla *Zittelia,* dodatkowo wzmacnia to powiązanie filogenetyczne i sugeruje, że odgałęzienie cypreidów od colombellinidów nastąpiło nie później niż w środkowej–późnej jurze.

Dane paleoekologiczne wskazują, że colombellinidy były ograniczone do nerytycznych facji węglanowych w północno-zachodniej części Oceanu Tetydy. Ich niska liczebność i wysoka endemiczność mogą odzwierciedlać drapieżny tryb życia. Współwystępowanie *Zittelia* i najwcześniejszych cypreidów w górnej jurze–najniższej kredzie Sycylii sugeruje, że rafy późnej jury i związane z nimi facje okołorafowe stanowiły centra dywersyfikacji colombellinidów i prawdopodobne obszary pojawienia się wczesnych cypreidów.

Odkrycie wczesnego neogastropoda z rodziny Vasidae, *Fimbrivasum bulgaricum* sp. nov., wykazuje, że neogastropody zaczęły różnicować się znacznie wcześniej niż dotąd sądzono, tzn. już we wczesnej wczesnej kredzie, podważając hipotezę o powstaniu i natychmiastowej radiacji w środkowej kredzie i wskazuje na wydłużoną fazę kryptyczną różnicowania o niskiej gęstości zarówno osobniczej jak i taksonomicznej. To odkrycie udokumentowało również najwcześniejsze wystąpienia niektórych cech funkcjonalnych u Neogastropoda, takich jak zgrubienia osiowe (ang. *varices*) i ząb wargowy (ang. *labral tooth*).

W trakcie całej kredy neogastropody przeszły gwałtowną radiację, prowadzącą do pojawienia się wszystkich głównych kladów (nadrodzin) do końca tego okresu oraz osiągnięcia różnorodności obejmującej 20 rodzin i 159 rodzajów o zasięgu globalnym. Duża liczba opisanych gatunków sugeruje, że ewolucja neogastropodów przebiegała przede wszystkim na poziomie gatunkowym, przy stopniowej akumulacji taksonów wyższej rangi. Choć wiele rodzajów wymarło na granicy K/Pg, część przetrwała, co wskazuje, że osiągnęły one już pewien poziom odporności ekologicznej i elastyczności ewolucyjnej, umożliwiający im odbudowę i ponowną radiację we wczesnym kenozoiku. Wzorce różnorodności rodzajowej ściśle korelują się z głównymi wydarzeniami klimatycznymi, przy czym sukces ewolucyjny neogastropodów może być interpretowany jako efekt współdziałania czynników klimatycznych, biologicznych i ekologicznych.

ABSTRACT

Neogastropoda represent one of the most abundant and diverse groups of predominantly marine gastropods, characterised by a wide range of hunting strategies, with some taxa also adopting a scavenging mode of life. The origin and early evolutionary history of neogastropods during the Mesozoic have remained poorly understood, largely due to the fragmented nature of the fossil record and the dispersion of relevant data across numerous regional taxonomic studies. This research presents a comprehensive synthesis of worldwide occurrences of Cretaceous neogastropods and their Mesozoic ancestors, integrating taxonomic revision of selected taxa, detailed morphological analysis, and palaeoecological interpretation. It also provides a revised framework for relationships among higher Caenogastropoda during the early Mesozoic.

A revision of the extinct families Maturifusidae, Pseudotritoniidae, and Purpurinidae, traditionally regarded as potential stem or sister groups of neogastropods, demonstrates that each of them represents a separate group, primarily distinguishable by protoconch morphology. The stratigraphical range of purpurinid *Purpurina* has been extended back to the Late Triassic, indicating an earlier diversification of the group than previously assumed. Furthermore, purpurinids are inferred to have diverged into two evolutionary lineages by the Jurassic, one potentially leading towards neogastropods and the other towards tonnoids.

The taxonomic composition of Colombellinidae, a group of uncertain taxonomic position within the higher caenogastropods, is revised and restricted to the genera *Colombellina* and *Zittelia*. Detailed analysis of *Zittelia* shell morphology reveals a gradual transition from the Oxfordian to the Tithonian–Valanginian leading towards Cypraeoidea, and expressed by enlargement of the last whorl, elongation of the aperture, and expansion of the columellar lip. It supports the interpretation of *Zittelia* as a stem or sister group of cypraeoids. The presence of an infracolumellar groove in some recent cypraeoids, interpreted as homologous to the anterior sinuosity diagnostic of *Zittelia*, further reinforces this phylogenetic connection and suggests that the divergence of cypraeoids from colombellinids occurred no later than the Middle–Late Jurassic.

Palaeoecological data indicate that colombellinids were restricted to neritic carbonate facies in the north-western part of the Tethys Ocean. Their low abundance and high endemism may reflect a carnivorous mode of life. The co-occurrence of *Zittelia* and the earliest cypraeoids in the Upper Jurassic–lowermost Cretaceous of Sicily suggests that Late Jurassic reefs and associated peri-reefal facies served as centres of diversification for colombellinids and as probable sites of emergence of early cypraeoids.

The discovery of the early neogastropod *Fimbrivasum bulgaricum* sp. nov. (Vasidae) demonstrates that neogastropods started to diversify much earlier than previously assumed, i.e.

already in the early Early Cretaceous, challenging the hypothesis of mid-Cretaceous emergence and immediate radiation, revealing a prolonged cryptic phase characterised by low individuals density and low taxonomic diversity. This finding also documented the earliest occurrences of certain functional traits in Neogastropoda, such as varices and a labral tooth.

Throughout the Cretaceous, neogastropods underwent significant radiation, resulting in the establishment of all major clades (superfamilies) by the end of the period and reaching a diversity of 20 families and 159 genera with a global distribution. The large number of described species may suggests that evolution of Neogastropoda proceeded primarily at the species level, with a gradual accumulation of higher taxa. Although many genera became extinct at the K/Pg boundary, a portion of Cretaceous taxa survived, indicating that they had already attained a degree of ecological resilience and evolutionary flexibility that enabled them to recover and radiate again in the early Cenozoic. Patterns of generic diversity closely correlate with major climatic events, although neogastropod evolutionary success is best explained as the outcome of interacting climatic, biological, and ecological factors.

INTRODUCTION

Gastropod shells are common fossils throughout the Phanerozoic with the earliest undisputed representatives of the class documented from the Cambrian (Lendzion 1977, Yochelson and Nuelle 1985, Gunderson 1993, Frýda et al. 2008, Pinilla et al. 2008, Qiang et al. 2023). During Permian/Triassic extinction event gastropods have been seriously decimated and after the Triassic rebound (Nützel 2005a, b, Payne 2005), they significantly diversified with the occurrence of several major groups in the later Mesozoic (Bandel 1993, Kaim 2004, Neubauer 2024). In the Cenozoic times, particularly in the Neogene, gastropods reached their greatest abundance and morphological diversity, continuing to flourish today. Their great adaptability has led them to be found in almost every environment on Earth: marine, freshwater, and terrestrial. In terms of their diversity, they are surpassed only by insects (Ponder and Lindberg 2020). One of the most significant mass extinctions at the end of the Cretaceous led to the disappearance of many marine invertebrates, including ammonites, rudists, and inoceramids, which also affected gastropods and resulted in the extinction of a considerable number of genera (162 according to Ruban 2013). Nevertheless, a range of gastropod taxa survived, thus providing insight into the evolutionary development of the class. However, the emergence and evolution of some gastropod groups is not well understood due to numerous convergences in shell morphology (e.g., Bakayeva et al. submitted). Additionally, due to their aragonitic mineralogy, gastropod shells are poorly preserved in environments with low potential for fossilization of skeletal aragonite.

An example of a group with poorly constrained origin are neogastropods, which constitute one of the most successful and diverse groups of marine molluscs, comprising approximately one-quarter of all living gastropod species (Ponder and Lindberg 2020). They are widespread, predominantly marine, and play an important role as benthic predators and scavengers. Many of the recent neogastropods, e.g. members of Conoidea Fleming, 1822 (the cone snails), produce venom and prey on invertebrate benthos as well as smaller demersal fish (James et al. 2024 and references therein). Their venom can be fatal even to humans and it is currently being investigated for medical purposes (Gao et al. 2017, Gorson and Holford 2016). Other neogastropods lack venom, but possess a long proboscis used to drill into the shells of other invertebrates, injecting enzymes into the prey's body cavity to facilitate its dissolution prior to ingestion, or employ the outer edge of the aperture to pry open the valves of bivalves (Dietl et al. 2010 and references therein). The largest living shelled snail—*Syrinx aruanus* (Linnaeus, 1758) measuring up to 90 cm long and weighing up to 18 kg—also belongs to the neogastropod family Turbinellidae Swainson, 1835, and preys on large polychaete worms of the family Acoetidae Kinberg, 1856, which can reach up to 1 m in length (Taylor and Glover 2003). These

examples represent just a small part of highly diverse predatory feeding strategies of neogastropods. The hunting innovations of the representatives of the group are considered a crucial factor in their rapid radiation in the mid-Cretaceous (Taylor et al. 1980, Modica and Holford 2010). This rapid evolution is a classic example of adaptive radiation driven by the adoption of a carnivorous lifestyle that has occurred presumably in the mid-Cretaceous and persists to the present day (e.g., Wenz 1939, 1940, Taylor et al. 1980, Ponder and Lindberg 1997, Modica and Holford 2010).

According to the most recent classification (Bouchet et al., 2017), the order Neogastropoda Wenz, 1938, is placed within the superorder Latrogastropoda Riedel, 2000, established to denote a group of "higher Caenogastropoda" (Riedel, 2000) within the subclass Caenogastropoda Cox, 1960. In addition to Neogastropoda, Latrogastropoda includes a paraphyletic clade with Colombellinidae Fischer, 1884, Calyptraeoidea Lamarck, 1809, Cypraeoidea Rafinesque, 1815, Ficoidea Meek, 1864, Stromboidea Rafinesque, 1815, Tonnoidea Suter, 1913 (1825), and Xenophoroidea Troschel, 1852 (i.e. more or less corresponding to Neomesogastropoda Bandel, 1991). In the molecular phylogeny of Osca et al. (2015), the higher caenogastropods (= Latrogastropoda) form a monophyletic group. The putative stem groups of Neogastropoda (Maturifusidae Gründel, 2001, Pseudotritoniidae Golikov & Starobogatov, 1987 and Purpurinidae Zittel, 1895) are also considered to belong to the order, whereas crown neogastropods are all recognised superfamilies included within the order.

The main morphological characteristics that distinguish representatives of Neogastropoda from other fossil gastropods are: (i) protoconch morphology and (ii) the presence of a siphonal canal or notch and some additional apertural elaborations. These diagnostic features served as the basis for allocating them into a separate monophyletic group – the order Neogastropoda, which according to Bouchet et al. (2017) comprises 58 families distributed across eight superfamilies and 11 families unassigned to superfamily (Table 6.1). This classification differs significantly from the previous nomenclator by Bouchet and Rocroi (2005), in which Neogastropoda included 31 families grouped in six superfamilies and six families unassigned to superfamily. These changes highlight the dynamics in the research on the phylogeny and taxonomy of Neogastropoda, especially regarding their fossil representatives. The increase in the number of families not assigned to superfamilies in the latest classification (Bouchet et al. 2017) resulted largely from the inclusion of some families into the order Neogastropoda, which were previously assigned to other higher gastropod taxa or had unclear systematic position.

The monophyly of Neogastropoda, as well as its place in the classification of Gastropoda, is confirmed by molecular studies of recent species (e.g., Cunha et al. 2009, Osca et al. 2015, Lemarcis et al. 2022). Recent molecular studies show that neogastropods are a clade of the siphonostome members of Caenogastropoda (Hypsogastropoda Ponder & Lindberg, 1997), which also include members of the superfamilies Tonnoidea, Stromboidea, and Cypraeoidea as most closely related groups with Tonnoidea proposed as the closest sister group to Neogastropoda (Cunha et al. 2009). Cancellariidae Forbes & Hanley, 1851, has also been proposed as a sister group to the remaining Neogastropoda or to the Ficoidea–Tonnoidea clade (Cunha et al. 2009, Fedosov et al. 2024). Relationships among neogastropod superfamilies remain rather flexible, but recent molecular studies are gradually enhancing our understanding of these relationships (Lemarcis et al. 2022, Fedosov et al. 2024). However, in fossils, such studies are more challenging, as they rely solely on shell morphology, particularly on larval shell (protoconch) characters, which are crucial for familial identification but are rarely preserved in fossils and not always documented in recent taxa.

The main **goal** of this study is to verify previous hypotheses concerning the origin of Neogastropoda and to propose a revised phylogenetic scheme for the relationships among stem and sister groups of higher caenogastropods, including Neogastropoda, Tonnoidea, and Cypraeidae. In addition, the study aims to evaluate the taxonomic diversity and distribution of neogastropods throughout the Cretaceous, with a particular focus on the Early Cretaceous, in order to identify their earliest occurrences and to reconstruct the patterns of their initial radiation and subsequent diversification.

To achieve this goal, the following **objectives** were undertaken:

i) identification of the earliest occurrences of neogastropods and revision of the families Maturifusidae, Pseudotritoniidae, and Purpurinidae, previously proposed as potential stem and/or sister groups of Neogastropoda;

ii) a comprehensive revision of all genera previously assigned to Colombellinidae, in order to assess its potential phylogenetic relationships with Purpurinidae and Cypraeoidea;

iii) analysis of well preserved Cretaceous gastropod materials from Barremian (Bulgaria), Cenomanian (India), and Campanian–Maastrichtian (United States), including the description of new taxa and the documentation of the earliest occurrences of functional traits, such as varices and a labral tooth;

iv) the revision of published data on Mesozoic neogastropod genera documented to date and compilation of a comprehensive taxonomy database;

iv) a global synthesis of the Cretaceous fossil record of Neogastropoda in order to provide new insights into the early evolutionary history and diversification patterns of the group.

Material and methods. This study is based on published data and the examination of gastropod collections from several institutions, including the Institute of Paleobiology of the Polish Academy of Sciences (Warsaw, Poland), the State Museum of Natural History of the National Academy of Sciences of Ukraine (Lviv, Ukraine), the National Museum of Natural History of Bulgarian Academy of Sciences (Sofia, Bulgaria), the Bavarian State Collection for Palaeontology and Geology (Munich, Germany), and the Geological Survey of India (Kolkata, India).

The new material was collected during fieldworks in the Triassic St Cassian Formation (Dolomites, Italy) and in the Cretaceous Coon Creek Formation (Tennessee and Mississippi, USA). The samples were hand-picked from the surface outcrops in the field. Bulk samples were also collected and subsequently washed through sieves (mesh size 0.375 mm) in the laboratory of the Institute of Paleobiology PAS. All fossil remains were picked from the resulting residues, and gastropod specimens were separated. Then specimens belonging to the taxa in question were selected and studied. Traditional conchological analysis was employed. Shell morphology was investigated using a binocular Olympus and a scanning electron microscope Philips XL20 at the Institute of Paleobiology PAS. Small specimens (<10–12 mm) were photographed using SEM in the Electron Microscopy and Electron Microprobe Laboratory of the same institute, whereas larger specimens (>10–12 mm) were coated with ammonium chloride and photographed in its photographic laboratory.

The higher-level classification follows Bouchet et al. (2017). Conchological terminology in the descriptions is based on the glossaries of Cox (1960) and Arnold (1965).

SUMMARY

The dissertation consists of six topical chapters, with five (Chapters I–V) corresponding to a published and submitted (Chapters V) papers, and one (Chapter VI) comprising a manuscript in preparation for subsequent submission to a journal. The chapters are arranged in ascending order according to the phylogeny of the respective taxa that are studied therein.

In **Chapter I,** the previous hypotheses concerning the origin of Neogastropoda are addressed, and the representatives of three extinct families that have been proposed as potential neogastropod stem groups: Maturifusidae, Pseudotritoniidae, and Purpurinidae, are analysed. Their morphological characteristics, especially the differences in protoconch morphology, strongly suggest that they should all be considered as separate clades, despite their synonymization in the recent systematic nomenclators (Bouchet and Rocroi 2005; Bouchet et al. 2017). The taxonomic status and composition of each family were reviewed and accordingly revised. The results suggest that during the Jurassic, purpurinids were divided into two groups: one, represented by *Khetella*, could be considered as the ancestor of Tonnoidea, while the other, represented by *Fossacerithium*, can be interpreted as the ancestor of Neogastropoda. Maturifusidae most likely went extinct without direct descendants, whereas the relation of Pseudotritoniidae to the neogastropod lineage remains uncertain (Bakayeva et al. 2024).

In **Chapter II** the taxonomy of the family Colombellinidae is revised. Based on a comprehensive review of all described species, the family is restricted to only two genera: *Colombellina* d'Orbigny, 1842, and *Zittelia* Gemmellaro, 1869. One new species, *Colombellina crassigranulata* sp. nov., is described from the Upper Jurassic of Bulgaria. In addition, a new genus, *Wadeina* gen. nov., is described from the Upper Cretaceous (Campanian) of Tennessee, USA, the type species of whichwas previously included in Colombellinidae but here re-assigned to the family Personidae (Tonnoidea). The distribution of the family and associated facies indicate a preference for neritic marine carbonate environments, while their low abundance may indicate a carnivorous mode of life. A comparison of Colombellinidae to Tonnoidea, Cypraeoidea, and Purpurinidae sheds a new light on the phylogenetic relationships of these groups and supports the interpretation of Colombellinidae as a stem or sister group of Cypraeoidea. This study contributes to a refined systematics of Jurassic–Cretaceous gastropods and provides new evidence for the early diversification of higher Caenogastropoda (Bakayeva et al. 2026).

Chapter III presents a comprehensive revision of the extinct genus *Zittelia* (Colombellinidae) and clarifies its diagnostic features. In contrast to members of the Cypraeidae, whose shells are convolute, the spire of *Zittelia* remains elevated. The chapter argues that species of *Zittelia* share morphological affinities with *Colombellina*, the type genus of Colombellinidae,

and are closely related to early Cypraeidae. 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 Cypraeidae is the type species of *Zittelia*, *Z. cypraeaeformis* Gemmellaro, 1869, which possesses a broadly expanded columellar lip and a low spire. The occurrence of *Zittelia* is restricted to peri-Tethyan shallow marine carbonate facies. It is hypothesized that 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 the origin of Cypraeoidea (Bakayeva et al. 2025).

Chapter IV focuses on the earliest record of Cypraeoidea and examines their evolutionary relationships with Colombellinidae. The results indicate that cypraeoids are closely related to, and possibly represent the sister group of coeval Colombellinidae, which share a narrow, elongate aperture but are not convolute. The recognition of the origin of Cypraeoidea with the new genus *Coffeacypraea*, together with an analysis of the diversification of Colombellinidae during the Middle–Late Jurassic, considerably enhances our understanding of the Mesozoic–Cenozoic radiation of Caenogastropoda. Both taxa represent higher Caenogastropoda (Neomesogastropoda sensu Bandel (1991) and Latrogastropoda sensu Riedel (2000)). At approximately the same time, the family Purpurinidae is most likely to have given rise to Neogastropoda (Bakayeva et al. 2024). Consequently, the Middle to Late Jurassic should be regarded as a pivotal time in the evolution of Caenogastropoda, one of the most diverse animal clades (Nützel et al. 2025).

Chapter V contains a report of a single record of a neogastropod from the Barremian (Early Cretaceous) known to date and provides new insights into the early evolution of the group. A new species, *Fimbrivasum bulgaricum* sp. nov. is hereby interpreted as a member of Vasidae, based on preserved protoconch and a shell morphology with prominent ornamentation and characteristic columellar folds. The specimen also exhibits the earliest occurrences of some functional traits in Neogastropoda, such as varices and a labral tooth. This finding suggests much earlier origin of the family Vasidae than previously believed, dating it as at least the Barremian, and indicates that neogastropod diversification was well underway in the earliest Cretaceous. A critical review of the earliest records of living neogastropod superfamilies and their diversification in the Cretaceous presented in this chapter reveals a notable incongruence between the fossil record and the molecular phylogeny in the current state of knowledge, highlighting both the poor fossil record of the group outside of Europe and the United States of

America and the challenges identifications of early members of particular clades (Bakayeva et al. submitted).

In **Chapter VI**, all available evidence on the Cretaceous Neogastropoda has been compiled and analysed. Ten neogastropod families and at least 20 genera are documented for the Early Cretaceous. The earliest record is represented by a juvenile shell assigned to the Buccinoidea from the Valanginian of Poland by Kaim (2004) and some additional taxa from Switzerland depicted in an archival monograph by Pictet and Campiche (1861–1864), followed by a member of Vasidae from the Barremian of Bulgaria (Bakayeva et al. submitted). A notable increase in diversity is observed in the Albian, with the first appearance of 19 genera. Among these, 15 species of Neogastropoda from Madagascar constitute the most diverse Early Cretaceous assemblage. Additional records from the Albian of Mexico, England, and Austria further support this trend of increasing diversity. During the Late Cretaceous, neogastropods became widespread, with 20 families and 159 genera documented worldwide. While the majority of Cretaceous genera went extinct at the Cretaceous/Paleogene (K/Pg) boundary, 26 genera representing 12 families survived. This research reveals a significant radiation of Neogastropoda in the late Early Cretaceous, with the Albian as a key period in the evolutionary history of the group. The increasing taxonomic richness towards the Late Cretaceous, followed by partial survival across the K/Pg boundary (compare Hansen 2019, Vellekoop et al. 2020), suggests that the group had already achieved broad ecological and evolutionary success by the end of the Mesozoic.

The **Conclusions** contain the main findings of the dissertation and summarise the key results and their significance.

CHAPTER I

An elusive ancestry of Neogastropoda: a potential of Maturifusidae, Pseudotritoniidae, and Purpurinidae as the stem groups*

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ABSTRACT

Notwithstanding considerable efforts and new data on gastropod evolution collected in the recent decades, the origin of Neogastropoda remains still elusive. In this contribution we compare and discuss members of three extinct families previously proposed as possible neogastropod stem groups, i.e., Maturifusidae Gründel, 2001, Pseudotritoniidae Golikov & Starobogatov, 1987, and Purpurinidae Zittel, 1895. Their morphological characteristics,

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especially the differences in protoconch morphology, strongly suggest that they should all be considered as separate clades. The taxonomic status and the composition of each family is here reviewed and accordingly revised. *Angularia kittli* n. sp. is introduced from the Carnian (Late Triassic) of the St. Cassian Formation (Italy).

It differs from its congeners in having a more pronounced axial ornamentation, which makes it similar to *Fossacerithium* Gerasimov, 1992 from the Jurassic. However, the protoconch of the new species is unknown and therefore its taxonomic position is tentative. An evolutionary lineage from the oldest known purpurinid species of genera *Khetella* Beisel, 1977 and *Cretadmete* Blagovetshenskiy & Shumilkin, 2006 to the recent tonnoids is proposed. We conclude that in the Jurassic, purpurinids were divided into two groups. One of them, represented by *Khetella*, could be considered as the ancestor of Tonnoidea, while the other, represented by *Fossacerithium*, can be interpreted as the ancestor of Neogastropoda. Maturifusidae most likely went extinct without direct descendants. The relation of Pseudotritoniidae to the neogastropod lineage remains uncertain.

Key words: Neogastropoda, Tonnoidea, Mesozoic, taxonomy, evolution, morphology, protoconch, larval shell, phylogeny, new combination, new species.

RÉSUMÉ

L’origine introuvable des Néogastéropodes : le potentiel des Maturifusidae, Pseudotritoniidae et Purpurinidae comme groupessouches.

Malgré des efforts considérables et de nouvelles données sur l’évolution des gastéropodes obtenues dans les dernières décennies, l’origine des Néogastéropodes reste difficile à cerner. Dans cette contribution nous comparons et discutons les membres des trois familles éteintes proposées auparavant comme groupessouches des Néogastéropodes : Maturifusidae Gründel, 2001, Pseudotritoniidae Golikov & Starobogatov, 1987 et Purpurinidae Zittel, 1895. Leurs caractères morphologiques, en particulier les morphologies différentes des protoconques, suggèrent fortement qu’ils doivent être considérés comme clades séparés. Nous passons en revue la composition de chaque famille, et nous présentons une révision taxonomique. Nous décrivons *Angularia kittli* n. sp., une nouvelle espèce du Carnien (Trias supérieur) de la formation de San Cassian ; elle diffère des autres représentants du même genre par une ornementation axiale plus prononcée, ce en quoi elle ressemble aux *Fossacerithium* Gerasimov, 1992 jurassiques. Toutefois, nous ne connaissons pas la protoconque de cette nouvelle espèce, c’est pourquoi ses relations phylogénétiques restent hypothétiques. Nous proposons la lignée évolutive conduisant des plus anciens purpurinidés, appartenant aux *Khetella* Beisel, 1977 et *Cretadmete* Blagovetshenskiy & Shumilkin, 2006, aux tonnoïdes contemporains. Nous concluons que, dans

le Jurassique, il a existé deux groupes des purpurinidés : l'un, représenté par *Khetella*, pourrait être considéré comme l'ancêtre des Tonnoidea; l'autre, représenté par *Fossacerithium*, pourrait être interprété comme l'ancêtre des Néogastéropodes. Les Maturifusidés se sont éteints, le plus probablement sans descendance. La relation des Pesudotritoniidés à la lignée des Néogastéropodes n'est pas certaine.

Mots clés: Néogastéropodes, Tonnoidea, Mésozoïque, taxonomie, évolution, morphologie, protoconque, coquille larvaire, phylogénie, combinaison nouvelle, espèce nouvelle.

INTRODUCTION

Gastropods are the most successful and diverse class of molluscs occurring in the majority of environments reflecting their great evolutionary success (e.g. Ponder et al. 2020). They also display a rich fossil record throughout the Phanerozoic. The early evolutionary history of many gastropod groups, however, is difficult to decipher since the shells of gastropods are commonly poorly preserved due to their prevailing aragonite mineralogy and numerous convergences in morphology. One of these groups is Neogastropoda – the most successful and highly diversified modern group of gastropods consisting of 17 105 living species (according to Encyclopedia of life https://eol.org/pages/2447) – nearly one-fourth of all gastropods. Their rapid evolution is a classic example of an adaptive radiation based on the adoption of a carnivorous life style that has occurred mainly since the mid-Cretaceous and persists until today (e.g. Wenz 1939, 1940; Taylor et al. 1980; Ponder & Lindberg 1997; Modica & Holford 2010). Neogastropods are active predators (also scavengers and some ectoparasites) and their hunting innovations are considered a crucial factor in their rapid radiation in the mid-Cretaceous (Taylor et al. 1980; Modica & Holford 2010). The monophyly of the group based on the phylogenetic analysis of morphological characters (e.g. Ponder & Linberg 1997; Ponder et al. 2008) was confirmed also by molecular data (Cunha et al. 2009; Osca et al. 2015; Lemarcis et al. 2022), according to which neogastropods are nested in Hypsogastropoda (sensu Ponder & Linberg 1997; see also Bouchet et al. 2017) and belong to "siphonate" caenogastropods, which also contain Tonnoidea Suter, 1913 (1825), Stromboidea Rafinesque, 1815 and Cypraeoidea Rafinesque, 1815 as more distant relatives. Tonnoidea is also proposed as the closest living sister group to Neogastropoda (see Cunha et al. 2009 for details).

According to the classification of Bouchet et al. (2017), the order Neogastropoda includes 58 families in eight superfamilies and 11 families unassigned to superfamily. This classification

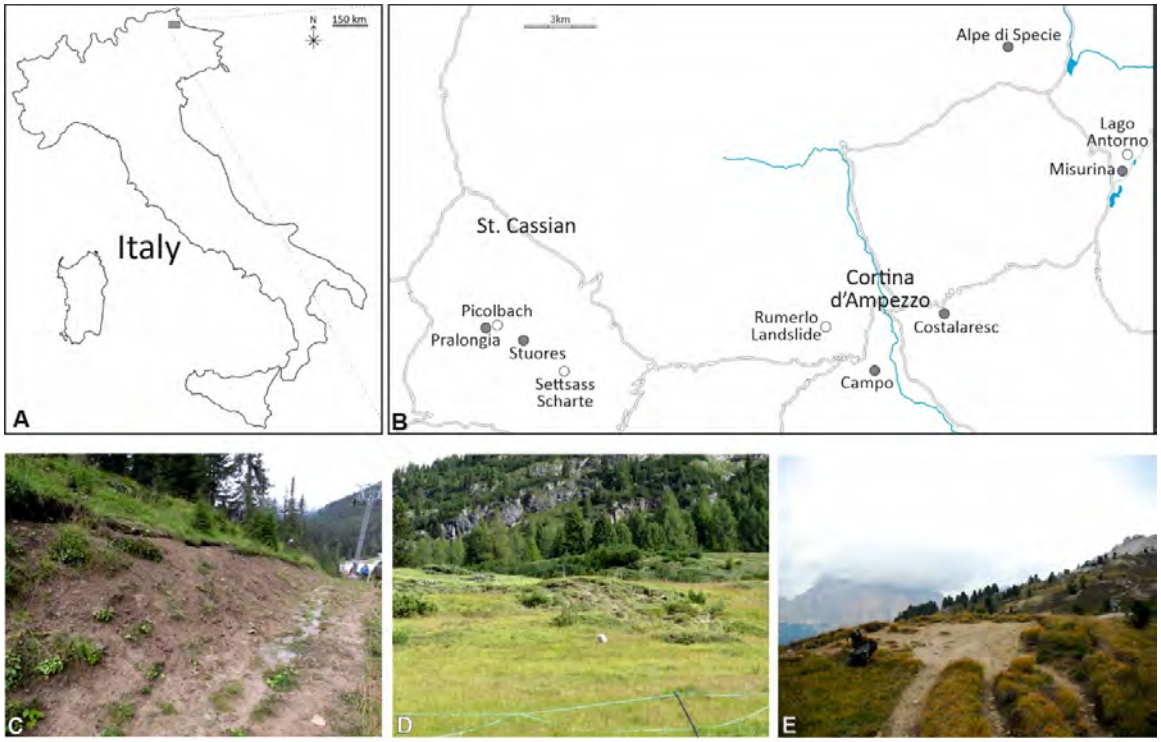

Fig. 1.1. — A, B, Location of the sampling localities in South Tyrol, Northeastern Italy (B) and their position on the map of Italy (A); localities, where specimens (see Table 1.1) were found, are marked in grey; C–E , examples of sample locations: C, Misurina Skilift; D, Alpe di Specie; E, Stuores.

differs significantly from the previous nomenclator by Bouchet & Rocroi (2005), where Neogastropoda comprise of 31 families grouped in six superfamilies and six families unassigned to superfamily. These changes highlight the dynamics in the research on the phylogeny and taxonomy of Neogastropoda, especially regarding their fossil representatives. The increase of the number of families not assigned to superfamilies in the newest classification (Bouchet et al. 2017) resulted largely from the inclusion of some families into the order Neogastropoda, which were previously assigned to other higher gastropod taxa or had unclear systematic position. The identification of the neogastropod stem group in the fossil record is challenging since it is based solely on comparative shell morphology of extinct taxa. Three families – Purpurinidae Zittel, 1895, Pseudotritoniidae Golikov & Starobogatov, 1987 and Maturifusidae Gründel, 2001 – were proposed so far as possible neogastropod stem groups (Taylor et al. 1980; Szabó 1983; Bandel 1993; Riedel 2000; Kaim 2004). Ponder (1973) also discussed Palaeozoic Subulitidae (Soleniscidae) as possible ancestors. The shells of most living neogastropods are fusiform with a pronounced anterior siphonal canal and also posterior canal or notches. Reticulate teleoconch ornaments are very common. One could expect that potential ancestors also display this type of shell morphology. The larval shells of living neogastropods are rather large and the size of the hatchings is also large when compared to those of "lower caenogastropods" such as cerithiids or

littorinids (Bandel 1975; see Nützel 2014: 486, fig. 8). The mutual relationships of Purpurinidae, Pseudotritoniidae and Maturifusidae including possible synonymy of the Triassic Pseudotritoniidae and Jurassic Maturifusidae was a matter of debate in the last decade, but remained largely unresolved due to differences in the aperture morphology and teleoconch ornamentation as well as a lack of information on protoconchs of the type species of respective type genera (Nützel 2010; Szabó 2011; Nützel & Gründel 2015; see also the Historical Background and Discussion chapters for details). In the early accounts, Purpurinidae were proposed to be ancestors of Neogastropoda (Taylor et al. 1980) or Tonnoidea (Bandel 1993), while some other authors considered Maturifusidae as better candidates (Riedel 2000; Kaim 2004). In the first version of the gastropod nomeclator (Bouchet & Rocroi 2005) Pseudotritoniidae were synonymized with Purpurinidae and located in the superfamily Littorinoidea, while in the second edition (Bouchet et al. 2017) both families are placed in Neogastropoda (not assigned to any superfamilies) as separate entities and the Maturifusidae are synonymized with Pseudotritoniidae – Maturifusidae were not assigned to any superfamily among Hypsogastropoda by Bouchet & Rocroi (2005).

This paper aims at summarizing previous studies on alleged ancestral groups of Neogastropoda in an attempt to shed some new light on problematic aspects in each of the families discussed herein. We also present new materials from the Upper Triassic (Carnian) of the St. Cassian Formation (Dolomites, Italy) and Upper Cretaceous (Campanian) of Coon Creek (Tennessee, United States), which provide additional insights for the systematics and mutual relations of the discussed groups.

MATERIAL AND METHODS

The new Triassic material under this study was collected during two fieldtrips to the Dolomites (Italy) in 2018 and 2020 respectively. The samples were collected from the following

Table 1.1. — Type specimens (asterisked) and new material from the St. Cassian Formation (Dolomites, Italy) discussed in this paper.

Locality	Species	Number of specimens
Alpe di Specie	*Purpurina macrostoma* (Klttl, 1894)	14
Campo	*Purpurina macrostoma*	1
Costalaresc	*Angularia pleurotomaria* (Münster, 1841)	6
Misurina	*Angularia subpleurotomaria* (Münster, 1841)	3
Misurina Skillft	*Angularia pleurotomaria*	1
Pralongia	*Angularia subpleurotomaria*	1
Stuores	*Angularia pleurotomaria*	1
Stuores	**Pseudoscalites elegantissimus* von Klipstein, 1892 (*in* Kittl 1892)	1
St. Cassian formation, probably Stuores	**Angularia subpleurotomaria*	3
St. Cassian formation, probably Stuores	**Angularia pleurotomaria*	1
St. Cassian	**Pseudotritonium venustum* (Münster, 1841)	1
St. Cassian	**Pseudotritonium laubei* (Kittl, 1894)	1

localities: Lago Antorno, Misurina Skilift, Alpe di Specie, Settsass Scharte, Stuores Meadows, Picolbach, Pralongia, Costalaresc, and Rumerlo (Fig. 1.1). Additional material came from collection efforts of AN and AK in 2010. The samples were handpicked from the surface outcrops in the field as well as bulk samples were collected and then washed on the sieves (0.375 mm mesh size) in the laboratory of the Institute of Paleobiology PAS. All fossil remains were picked out from the resulting residues and gastropod specimens were separated. Then specimens belonging to the families in question (Maturifusidae, Pseudotritoniidae, Purpurinidae) were selected and studied. 13 shells of interest were found in the material collected in 2018-2020 and 14 shells came from previous field campaigns (Table 1.1). The specimens collected in 2018-2020 were documented on SEM at the Institute of Paleobiology PAS. Additional unpublished material was used for line drawings of *Maturifusus* Szabó, 1983 (Callovian, Middle Jurassic of Łuków, Poland) and of *Paladmete* Gardner, 1916 (Campanian, Upper Cretaceous of Coon Creek, Tennessee, United States). A new specimen of *Astandes densatus* Wade, 1917, the type species of *Astandes* Wade, 1917 has been recovered from a bulk sample collected in the type locality of Coon Creek Formation during the fieldwork in 2022.

To identify relationships between the taxa in question and analyse their affinities we performed an extensive survey of the available literature.

Institutional abbreviations

GBA	Geologische Bundesanstalt, Vienna;
MNHN	French National Museum of Natural History, Paris;
MPRZ	Rinaldo Zardini Paleontological Museum in Cortina d'Ampezzo;
NHMW	Natural History Museum, Vienna;
PZO	Naturmuseum Südtirol, Bozen;
SNSBBSPG	Bavarian State Collection for Palaeontology and Geology, Munich;
ZPAL	Institute of Paleobiology, Polish Academy of Sciences, Warsaw.

HISTORICAL BACKGROUND

MATURIFUSIDAE

Szabó (1983: 44) placed the new genus *Maturifusus* in the family Buccinidae based on a comparison to similar Pleistocene to Recent species of *Plicifusus* Dall, 1902. Apart from the type species, *M. densicostatus* Szabó, 1983, Szabó (1983: 44) also included *Fusus piettei* Hébert & Deslongchamps, 1860 in the genus and noted that the generic assignment of other Mesozoic fusiform species is pending further investigations. The first description of the protoconch morphology – including embryonic whorl sculpture with distinct tubercles – was provided by Gründel (2001: 74), who also erected the monogeneric family Maturifusidae and noted that the genus *Maturifusus* is quite isolated from other, well investigated Jurassic gastropods, and its connections to younger genera are unclear. Subsequent studies showed that the distinct tubercles

on the embryonic whorl are easily altered post-mortem (Guzhov 2004; Kaim 2004) since initial shells are usually recrystallized and/or corroded, therefore such micro-ornaments are usually not preserved in fossil gastropod specimens (Nützel 2014).

Gründel (2001) established the new monogeneric family Maturifusidae based on the genus *Maturifusus* without enlisting the species belonging to the genus (apart from the type species). However, several species were already described by Schröder (1995), Gründel (1998, 1999, 2001), Nützel & Erwin (2004) (Table 1.2) and two revisions have been published by Kaim (2004) and Guzhov (2004). Kaim (2004) synonymized *Maturifusus* with Late Cretaceous *Astandes* and attributed *Astandes* to the family Maturifusidae. Furthermore, Kaim (2004) argued that the protoconchs of *Maturifusus* (his *Astandes*) somewhat resemble those of some Buccinidae and suggested it could be an ancestral group for neogastropods. He reviewed previously described species and placed *M. montagi* Gründel, 1998 in the synonymy with *A. conspicuus* (Eichwald, 1868). Also, he expressed doubts about the allocation of *M. ticurelatus* (Gründel, 2001) *and M. keyserlingianus* (Rouillier, 1846) into separate species as *M. conspicuus* has a wide range of intraspecific variability (Kaim 2004: 104).

Guzhov (2004) included thirteen species in *Maturifusus* and described one new species (see Table 1.2). While discussing the composition of Maturifusidae he included also two other genera into the family: *Rhynchocerithium* Cossmann, 1906 and *Khetella* Beisel, 1977 (Guzhov 2004: 483). In the discussion of the genus *Rhynchocerithium* he noted that the number of species and the taxonomic position of the genus are only tentatively accepted, because its teleoconch morphology is typical for members of Cryptaulacidae Gründel, 1976 (Cerithiimorpha), while protoconch and aperture resemble those of the family Maturifusidae (Guzhov 2004: 531). Conversely, Kaim (2004) placed *Rhynchocerithium* into Cerithiidae Fleming, 1822 citing the cerithiid-like protoconch and early teleoconch of the type species illustrated by Gründel (1997). The genus *Khetella* was primarily attributed to Columbellariidae Zittel, 1895 (junior synonym of Colombellinidae Fischer, 1884) by Beisel (1977) and then questionably to Buccinidae by Blagovetshenskiy & Shumilkin (2006). The protoconch of the Siberian *Khetella bojarkae* Beisel, 1977, illustrated for the first time by Kaim & Beisel (2005: 44), is similar to that of purpurinids, and therefore these authors suggested that the genus belongs to Purpurinidae. The attribution of *Maturifusus* to Purpurinidae was also proposed by Bandel (1993, 2006) based on an alleged similarity in protoconch morphology.

Another genus commonly attributed to the family Maturifusidae is *Astandes* (Fig. 1.2), which is known exclusively from the Late Cretaceous (CampanianMaastrichtian) of the United

Table 1.2. — Species attributed to Maturifusus Szabó, 1983 or Astandes Wade, 1917 and their revised taxonomic position.

According to publication				Taxonomic position herein
		Distribution		
Reference	Species name as in original reference	Age	Locality	
***Maturifusus* Szabó, 1983**				
Szabó 1983: 44	*Maturifusus densicostatus* Szabó, 1983	Middle Jurassic	Bakony Mts, Hungary	*Maturifusus*
	Fusus piettei Hébert & Deslongchamps, 1860	Jurassic (Oxfordian)	Montreuil-Bellay, France	?*Maturifusus*
Gerasimov 1955: 195	*Brachytrema keyserlingiana* (Rouillier, 1846)	Jurassic (Oxfordian)	Moscow region, Russia	*Maturifusus*
	Brachytrema incerta (d'Orbigny, 1845)	Jurassic (Kimmeridgian-Tithonian)	Moscow region, Russia	?*Khetella*
	Brachytrema kostromense Gerasimov, 1955	Jurassic (Callovian)	Kostroma region, Russia	*Maturifusus*
Gründel 1977: 190	*Maturifusus* sp. 1	Jurassic (Bathonian)	Kłęby, Poland	*Maturifusus*
Yamnichenko 1987: 125	*Fusus caseus* Yamnichenko, 1987	Jurassic (upper Bajocian)	Kharkiv and Dniepr regions, Ukraine	*Maturifusus*
	Fusus crassus Yamnichenko, 1987			
Schröder 1995: 40	*Maturifusus szaboi* Schröder, 1995	Jurassic (Aalenian)	Hambühren, Germany	*Maturifusus*
	Fusus piettei	Jurassic (Oxfordian)	Montreuil-Bellay, France	?*Maturifusus*
	Fusus bernouillensis (Loriol) (*Fusus* sp. ined. aff. *Bernouilensis* Lor. sp. *in* Andreae 1887)	Jurassic (Hettangian, Sinemurian)	Bernouil, France	?Aporrhaidae
	Alaria alternans Terquem & Jourdy, 1869	Jurassic (Bathonian)	Clapes, France	?Aporrhaidae
Gründel 1998: 17	*Maturifusus montagi* Gründel, 1998	Jurassic (Oxfordian)	Rogätz, Germany	*Maturifusus*
Gründel 1999: 644	*Maturifusus grimmensis* Gründel, 1999	Jurassic (Pliensbachian-Toarcian)	Western Pomerania, Germany	*Maturifusus*
Gründel 2001: 75	*Maturifusus ticurelatus* Gründel, 2001	Jurassic (Bathonian)	Kłęby, Poland	*Maturifusus*
Kiel 2001: 89	*Maturifusus*? sp.	Cretaceous (Campanian)	Torallola, Spain	?Aporrhaidae
Nützel & Erwin 2004: 391	*Maturifusus*? *siphonatus* Nützel & Erwin, 2004	Triassic (upper Norian)	Wallowa Terrane, Idaho, United States	?Triphoroidea
Guzhov 2004: 391	*Maturifusus caseus* (Yamnichenko, 1987)	Jurassic (upper Bajocian)	Kharkiv and Dniepr regions, Ukraine	*Maturifusus*
	Maturifusus conspiquus (Eichwald, 1868)	Jurassic (Oxfordian, ?lower Kimmeridgian)	European Russia, Germany	*Maturifusus*
	Maturifusus densicostatus Szabó, 1983	Middle Jurassic	Bakony Mts, Hungary	*Maturifusus*
	Maturifusus grimmensis Gründel, 1999	Jurassic (upper Pliensbachian)	Germany	*Maturifusus*
	Maturifusus keyserlingianus (Rouillier, 1846)	Jurassic (Oxfordian-lower Kimmeridgian)	European Russia	*Maturifusus*
	Maturifusus kostromenis (Gerasimov, 1955)	Jurassic (lower Callovian-middle Oxfordian)	European Russia	*Maturifusus*
	Maturifusus mosquensis Guzhov, 2004	Jurassic (upper Tithonian)	European Russia	*Purpurina*
	Maturifusus piettei (Hebert & Deslongchamps, 1860)	Jurassic (Callovian)	France	?*Maturifusus*
	Maturifusus piquus (Beisel, 1983)	Jurassic (upper Kimmeridgian)	northern Siberia, Russia	*Cretadmete*
	Maturifusus purpuriniformis (Conti, 1982)	Jurassic (lower Bajocian)	Italy	*Purpurina*
	Maturifusus szaboi Schröder, 1993	Jurassic (upper Aalenian)	Germany	*Maturifusus*
	?*Maturifusus nassoides* (Eudes-Deslongchamps, 1842)	Jurassic (Bajocian)	France	?*Maturifusus*
	?*Maturifusus zeisei* (Wollemann, 1903)	Cretaceous (Aptian-Albian)	Germany	?*Maturifusus*
Gründel 2005: 79	*Maturifusus conspicuous* (Eichwald, 1868)	Jurassic (upper Callovian)	Saratov region, Russia	*Maturifusus*
Blagovetschenskiy & Shumilkin 2006: 147	*Cretadmete neglecta* Blagovetshenskiy & Shumilkin, 2006	Cretaceous (upper Hauterivian)	Ulyanovsk Region, Russia	*Cretadmete*
	Cretadmete gracillima (Wollemann, 1903)	Cretaceous (Aptian-Albian)	Northern Germany	*Cretadmete*
	Cretadmete kostromensis (Gerasimov, 1955)	Jurassic (middle Callovian, Upper Oxfordian-lower Kimmeridgian)	Volga River Region, northern Siberia, Russia	*Maturifusus*
	Cretadmete piccua (Beisel, 1983)	Jurassic-Cretaceous (Kimmeridgian-Valanginian)	northern Siberia, Russia	*Cretadmete*

According to publication				Taxonomic position herein
Reference	Species name as in original reference	Distribution		
		Age	Locality	
	Cretadmete? *conspicua* (Eichwald,1868)	Jurassic (middle-upper Oxfordian)	central regions of Russia	*Maturifusus*
	Cretadmete? *keyserlingiana* (Rouillier, 1846)	Jurassic (Oxfordian-lower Kimmeridgian)	Russian Platform, Russia	*Maturifusus*
Gründel 2007: 86	*Maturifusus grimmensis* Gründel, 1999	Jurassic (Pliensbachian)	Usedom Depression, Germany	*Maturifusus*
Nützel & Gründel 2015: 75	*Maturifusus grimmensis*	Jurassic (upper Pliensbachian)	Franconia, Germany	*Maturifusus*
***Astandes* Wade, 1917**				
Wade 1917: 298	*Astandes densatus* Wade, 1917	Cretaceous (Campanian)	Tennesse, United States	*Astandes*
Wade 1926: 157	*Astandes densatus*	Cretaceous (Campanian)	Tennesse, United States	*Astandes*
Sohl 1960: 298	*Astandes densatus*	Cretaceous (Campanian)	Tennessee, United States	*Astandes*
Sohl 1967: 24	*Astandes densatus*	Cretaceous (Campanian)	Wyoming, Montana, Colorado, Tennessee, United States	*Astandes*
Beisel 1983: 76	*Astandes kostromensis* (Gerasimov, 1955)	Jurassic (Upper Oxfordian-lower Kimmeridgian)	Siberia, Russia	*Cretadmete* (only the material of Beisel 1983)
	Astandes piccuus	Jurassic-Cretaceous (Kimmeridgian-Valanginian)	Siberia, Russia	*Cretadmete*
Gerasimov 1992: 95	*Astandes conspiccus* (Eichwald, 1868)	Jurassic (Oxfordian)	Russian Platform, Russia	*Maturifusus*
	Astandes keyserlingianus (Rouillier, 1846)	Jurassic (Oxfordian, Kimmeridgian)	Russion Platform, Russia	*Maturifusus*
	Astandes kostromensis (Gerasimov, 1955)	Jurassic (Callovian, Oxfordian, Kimmeridgian)	Russion Platform, Siberia, Russia	*Maturifusus*
Dockery 1993: 71	*Cerithioderma nodosa* Dockery, 1993	Cretaceous (Campanian)	Mississippi, United States	*Astandes*
Kaim 2004: 102	*Astandes conspicuus* (Eichwald, 1868)	Jurassic (Callovian-Oxfordian)	Russia and Poland	*Maturifusus*
	Astandes kostromensis (Gerasimov, 1955)	Jurassic (Callovian)	Siberia, Russia, and Poland	*Maturifusus*
	Astandes ticurelatus (Gründel, 2001)	Jurassic (Bathonian)	Poland and Germany	*Maturifusus*
Kaim 2008: 168	*Astandes conspicuus* (Eichwald, 1868)	Jurassic (Callovian)	Łuków, Poland	*Maturifusus*
	Astandes kostromensis (Gerasimov, 1955)	Jurassic (Callovian)	Łuków, Poland	*Maturifusus*
Kaim 2012: 373	*Astandes ticurelatus* (Gründel, 2001)	Jurassic (Bathonian)	Gnaszyn, Poland	*Maturifusus*
Bandel & Dockery 2012: 98	*Astandes nodosus* (Dockery, 1993)	Cretaceous (Campanian)	Mississippi, United States	*Astandes*

States (Colorado, Mississippi, Montana, Tennessee, Wyoming) (Wade 1917, 1926; Sohl 1960, 1967) and consists of only two described species: the type species, *A. densatus* Wade, 1917, and *A. nodosus* (Dockery, 1993) (Dockery 1993; Bandel & Dockery 2012). While describing the new genus, Wade (1917) proposed to include two other species known from the Upper Cretaceous of Europe: *Triton cretaceum* Müller, 1851 (Müller 1851: 47, pl. 5, fig. 2; Holzapfel 18871888: 113, pl. 10, figs 57) and the closely related form *Tritonium cf. cretaceum* Müller, 1851 (Kaunhowen 1897: 77, pl. 9, 13, fig. 4, 12). However, none of these species were later revised in the context of their attribution to the genus *Astandes* apart from the straight forward inclusion of *T. cretaceum* to *Astandes* (without any comment) by Pietzonka et al. (2023).

Bandel (2006) suggested that *Astandes* might be related to Pyrifusidae based on protoconch morphology, but later he placed it in Trichotropidae Gray, 1850 (junior synonym of

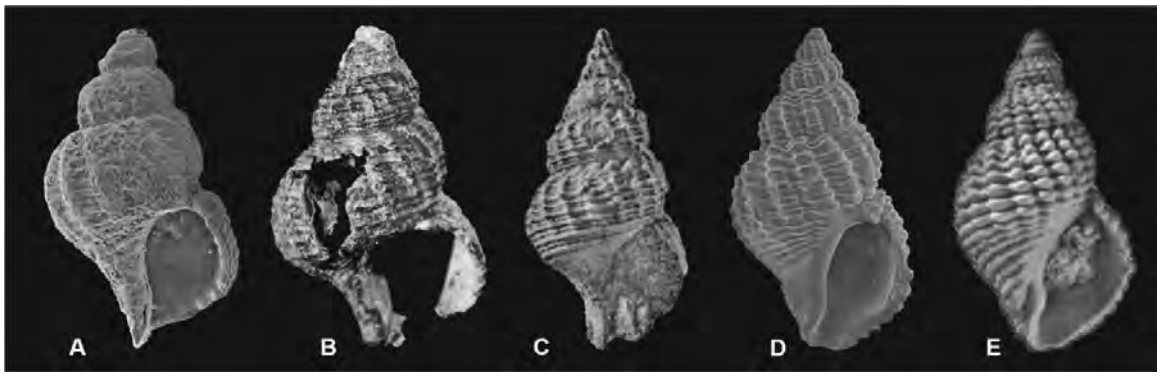

Fig. 1.2. — Selected species of *Astandes* Wade, 1917 and *Maturifusus* Szabó, 1983: A, *Astandes densatus* Wade, 1917 from Coon Creek, Tennessee, United States, upper Campanian (Upper Cretaceous); ZPAL Ga. 21/1; B, *Astandes densatus* from the Ripley Formation, Tennessee, United States, upper Campanian (Upper Cretaceous). Holotype USNM 32944. Current state of the holotype; C, *Maturifusus densicostatus* Szabo, 1983 from Bakony Mts., Somhegy: condensed Subfurcatum and Garantiana zones, Middle Jurassic. This specimen was figured by Szabó (1983: pl. 3, fig. 14); holotype J 10141; D, *Maturifusus conspicuus* (Eichwald, 1868) from Łuków (block in glacial drift), Podlasie, Poland, Callovian (Middle Jurassic). This specimen was figured by Kaim (2004: fig. 83C1); MZ VIII Mg 4227/7; E, *Maturifusus keyserlingianus* (Rouillier, 1846) from the town of Shchurovo (Zarech'e District), Russia, middle Oxfordian (Upper Jurassic). This specimen was figured by Guzhov (2004: pl. 7, fig. 5A); GMM, no. 12/38. Credits: B, photo courtesy of Anders Warén. Scale bars: 2 mm.

Capulidae Fleming, 1822) (Bandel & Dockery 2012) arguing that *Astandes* and *Maturifusus* differ in the protoconch morphology despite their similarity in teleoconch morphology. Bandel & Dockery (2012) also noted that the protoconch of *Astandes* is similar in shape and size to that of the genus *Undoriptera* Guzhov, 2014 (family Aporrhaidae Gray, 1850), but its ornamentation is different (Bandel 2016).

PSEUDOTRITONIIDAE

The family was erected by Golikov & Starobogatov (1987) as a subfamily of the family Cerithiidae and it is monogeneric to date. In the original diagnosis, the family is characterized by "axial ornamentation strongly predominating over the spiral one" (Golikov & Starobogatov 1987). Type species of *Pseudotritonium* Wenz, 1940 has been described from the Carnian (Upper Triassic) of the St. Cassian Formation in Italy as *Scalaria venusta* Münster, 1841 (Münster 1841: 103, pl. 10, fig. 28). Münster's specimen was later illustrated by Kittl (1894: pl. 11, fig. 3), and then selected by Nützel (2010: 17, fig. 4) as the lectotype (Fig. 1.3B). Laube (1868) remarked the rarity of specimens of *Scalaria venusta* and differences from other members of *Scalaria* Lamarck, 1801 (today *Epitonium* Röding, 1798), which would have allowed diagnosing a separate genus, but the poor preservation of the material deterred him from doing so. He also described two new species, *Fasciolaria avena* Laube, 1868 and *Fasciolaria karreri* Laube, 1868, which Kittl (1894) later attributed to the new genus *Palaeotriton* Kittl, 1894 (Kittl 1894: 236) in

addition to two other new species, *P. laubei* Kittl, 1894 and *Palaeotriton macrostoma* Kittl, 1894. Kittl (1894) also assumed that *Palaeotriton* might be a descendant of the Pseudomelaniidae R. Hoernes, 1884 as well as some other siphonostome gastropods (not listed) suggesting that his *Paleotriton* (now *Pseudotritonium*) belongs to Neogastropoda and placed the entire group into the family Fusidae (historically a catch all for buccinoid gastropods). Moreover, Kittl (1894) synonymized also *Cerithium*(?) *ventricosum* Klipstein, 1845 (Klipstein 1845: 182, pl. 11, fig. 34) and *Fasciolaria karreri* Laube, 1868 with *P. venustum*. Additionally, he highlighted the conspicuous similarity between *P. venustum*, *P. laubei*, and *P. macrostoma*, noting that their main distinction lies solely in the number of axial ribs. However, to ascertain whether these taxa can be synonymized or if they are distinct species, "new, well-preserved material is required" (Kittl 1894: 236). The new material collected in the Dolomites indicates that these similarities noted by Kittl (1894) might be only superficial – at least in the case of *P. macrostoma* and *P. venustum* (see below).

Cossmann (1906: 205) placed *Palaeotriton* in Purpurinidae with some doubts, noting its similarity to nassariid *Nassa* Lamarck, 1799 on the one hand and to the capulid *Cerithioderma* Conrad, 1860 on the other. He also discussed Kittl's (1894: pl. 11, figs 69) picture of *P. macrostoma*, which indicates the thickening of a peristome and, probably, a holostomous aperture. Later Wenz (1940) replaced *Palaeotriton* – a junior homonym of *Palaeotriton* Fitzinger, 1837 (Amphibia) – with the new name *Pseudotritonium* (Wenz 1940: 732) and assigned it, with hesitation, to the subfamily Paracerithiinae Cossmann, 1906 of the family Procerithiidae Cossmann, 1906.

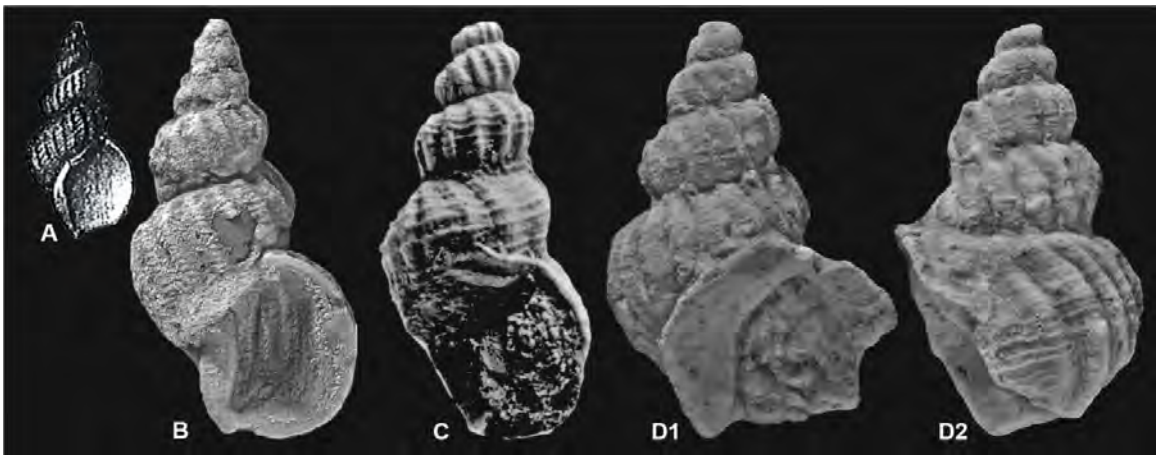

Fig. 1.3. — *Pseudotritonium* Wenz, 1940 species from the St. Cassian Formation (Triassic), South Tyrol, Italy: A, *Pseudotritonium venustum* (Münster, 1841) figured by Münster (1841: pl. 10, fig. 28); B, *Pseudotritonium venustum*, lectotype, SNSBBSPG AS VII 1871, selected from Münster's collection by Nützel (2010: fig. 4); C, *Pseudotritonium laubei* (Kittl, 1894) from Alpe di Specie figured by Zardini (1978: pl. 38, fig. 10), MPRZ No 3909 SL; D, *Pseudotritonium laubei*, holotype, NHMW: Kittl 1894: 238, 9(20)/10: D1, aperture view; D2, lateral view. Scale bars: 2 mm.

Haas (1953) doubtfully assigned to *Pseudotritonium* several specimens from the Late Triassic of Peru (not reviewed by Ferrari 2015 in her partial revision of Haas' (1953) material) noting their dissimilarity to other members of Procerithiidae investigated in his paper. Comparing them with other species of *Pseudotritonium*, he concluded that they are most similar to *P. macrostoma* from the St. Cassian Formation (Kittl 1894), which in our opinion is closer to Purpurinidae than to Pseudotritoniidae judging from its shell outline and ornamentation. Zardini (1978: 54) introduced the new species, *Pseudotritonium milierensis* Zardini, 1978, based on a well-preserved shell and noted its similarity to *P. avena*. He also described *P. macrostoma*, *P. laubei* and *P. venustum* without attributing the genus to any particular family.

Pieroni et al. (2021) discussed the similarity of Pseudotritonium to Ederazyga Pieroni, Monari & Todd, 2021 of the family Zygopleuridae Wenz, 1938. The differences in teleoconch sculpture are particularly diagnostic: Pseudotritonium has prosocline axial ribs, whereas Ederazyga is characterized by opisthocline ribs.

PURPURINIDAE

Partial revision of the family has been provided by Guzhov (2004) and more comprehensive revision is pending. Here, we address in detail only those genera that do not fit to the concept of Guzhov (2004).

Purpurina d'Orbigny, 1850

The genus include numerous species that never been revised since their initial description. As a result, the systematic composition of this genus is pending a thorough revision in a separate paper.

Angularia Koken, 1892

The genus was established by Koken (1892) who placed it in Loxonematidae Koken, 1889 and simultaneously proposed that it is a probable predecessor of *Purpurina*. Wöhrmann & Koken (1892) included three species into *Angularia*: *Turbo subpleurotomarius* Münster, 1841, *Turbo pleurotomarius* Münster, 1841, and *A. marginata* Wöhrmann & Koken, 1892 (Wöhrmann & Koken 1892: 198, pl. 14, fig. 3). Laube (1868) assigned *T. subpleurotomarius*, from the St. Cassian Formation, to *Loxonema* Phillips, 1841 (Laube 1868: 66, pl. 24, fig. 23) and introduced *Loxonema latescalata* Laube, 1868. Kittl (1892) placed the latter species into synonymy of *Purpurina pleurotomaria* (Münster, 1841) along with the type species of *Angularia*, i.e., *Purpurina subpleurotomaria* (Münster, 1841) (Kittl 1892: 6365), and discussed the differences between these two species. However, the specimen attributed by Kittl (1892) to *Purpurina*

pleurotomaria differs from the original description by Münster (1841: pl. 12, fig. 23) and represents a new species of *Angularia* described below (see below for remarks to clarifying the differences between these two species). He also introduced *Purpurina vaceki* Kittl, 1892, which in our opinion may indeed belong to *Purpurina*. Later, Kittl (1894) attributed one more new species to the genus, i.e., *Purpurina loxonemoides* (Kittl, 1894) (Kittl 1894: 251, pl. 8, fig. 4), which, however, differs significantly from all other members of the Purpurinidae due to its narrow elongated shell and very small size and most likely represents zygopleuroids or even cimids.

The oldest so far known records of A. pleurotomaria (Münster, 1841) and *A. subpleurotomaria* (Münster, 1841) have been reported by Broili (1907) from the Ladinian (Middle Triassic) of the Pachycardientuffe in South Tyrol (Italy). Cossmann (1909: 3) designated *Turbo subpleurotomarius* Münster, 1841 as the type species of *Angularia* and placed the genus into the family Purpurinidae. Wenz (1939) followed this interpretation. Kutassy (1927, 1937) described two new species of the genus: *A. multinodosa* Kutassy, 1937 and *A. plicata* (Kutassy, 1927) and one variety *A. plicata* var. *raricostata* Kutassy, 1937, from the Triassic near Budapest, Hungary. Zardini (1978) assigned *A. pleurotomaria* and *A. subpleurotomaria* to *Purpurina* and described an additional new species, P. costata Zardini, 1978, from the St. Cassian Formation.

Bandel (1993, pl. 14, fig. 4) was the first to illustrate the protoconch of the Triassic purpurinid in detail (identified as Angularia subpleurotomaria but actually A. pleurotomaria). He noted that these protoconchs display a sinusigera at its terminus, so they can be compared to protoconchs of neogastropods, even though the small dimensions resemble those of Littorinoidea Children, 1834, Rissooidea Gray, 1847 and Stromboidea Rafinesque, 1815 (Bandel 1993: 26).

Nützel & SenowbariDaryan (1999) identified a NorianRhaetian specimen from central Iran as Angularia sp. However, due to the poor preservation of this specimen, a more precise identification was not possible (Nützel & Senowbari-Daryan 1999: 107, pl. 3, fig. 10). Subsequently, the stratigraphic range of the genus has been expanded by the introduction of a new species, A. rectecostata Nützel & Erwin, 2004 from the Late Triassic of United States (Wallowa Terrane, Idaho) (Nützel & Erwin 2004). Later, Gründel (2010) assigned Natica subangulata d'Orbigny, 1850 to Angularia, which differs significantly from the type species of Angularia in several aspects and in our opinion it is closer to Purpuroidea Lycett, 1848 of Littorinimorpha than to Purpurinidae.

The controversy regarding the validity of the genus name (homonymy with a bryozoan taxon) was resolved by Nützel et al. (2022) and the name Angularia for the genus was confirmed. Also, a new species, A. corallina from the latest Triassic of Austria, was added to the genus (Nützel et al. 2022).

Cretadmete Blagovetshenskiy & Shumilkin, 2006

The genus has been classified by Blagovetshenskiy & Shumilkin (2006) in the family Admetidae and later placed in Purpurinidae by Kaim et al. (2017). Except for the type species, *C. neglecta* (Fig. 1.4), Blagovetshenskiy & Shumilkin (2006) included five more species into the genus: *C. gracillima* (Wollemann, 1903), *C. kostromensis* (Gerasimov, 1955), *C. piccua* (Beisel, 1983), *C.*? *conspicua* (Eichwald, 1868), and *C.*? *keyserlingiana* (Rouillier, 1846). Kaim et al. (2017) described additional species of *Cretadmete* from the upper Tithonian (Upper Jurassic) of Svalbard, however, because of the fragmentary preservation they left it in open nomenclature.

Fossacerithium Gerasimov, 1992

This taxon was initially established by Gerasimov (1992) as a subgenus. For additional remarks, refer to the genus description below.

Khetella Beisel, 1977

The genus was erected by Beisel (1977) with *Khetella bojarkae* Beisel, 1977 as type species. However, Beisel (1977) indicated that the most common and widely distributed species of *Khetella* is *Buccinum incertum* d'Orbigny, 1845 (d'Orbigny in Murchison et al. 1845) from the Upper JurassicLower Cretaceous of Eastern Europe (Fig. 1.5). Beisel (1977) placed the genus into the family Columbellariidae (junior synonym of Colombellinidae) based on its characteristic shell shape with complicated morphology of the aperture including anterior and posterior canals. He noted that species of Columbellariidae from the northern regions have a simplified aperture morphology which lacks a posterior canal, and that the Siberian species, *K. bojarkae* (Beisel 1977), has an even more simplified morphology: a considerably weakened spiral ornament, which is indeed very characteristic to members of the Columbellariidae. He also noted that *Khetella* differs from *Colombellina* in having a simplified morphology of the aperture that lacks a posterior canal. Other than the type species *K. bojarkae*, Beisel (1977) included four other species into this genus: *K. brunsvicensis* (Wollemann, 1900), *K. incerta* (d'Orbigny, 1845), *K. septentrionalis* (Tullberg, 1881), *K.* ?*gaultica* (d'Orbigny, 1842). In a later publication he added a fifth species, K. ventrosa Beisel, 1983.

Guzhov (2004: 526) placed *Khetella* in family Maturifusidae and mentioned twelve species, including four newly described species: *K. formosifomis*, *K. glasunovi*, *K. gradata*, and *K. makaryevensis*. Except for the species already listed by Beisel (1977, 1983), he included also *Fusus formosus* Eichwald, 1868, *Purpurina hypermeces* Cossmann, 1913 and *Fusus*? *liasicus* Dumortier, 1874.

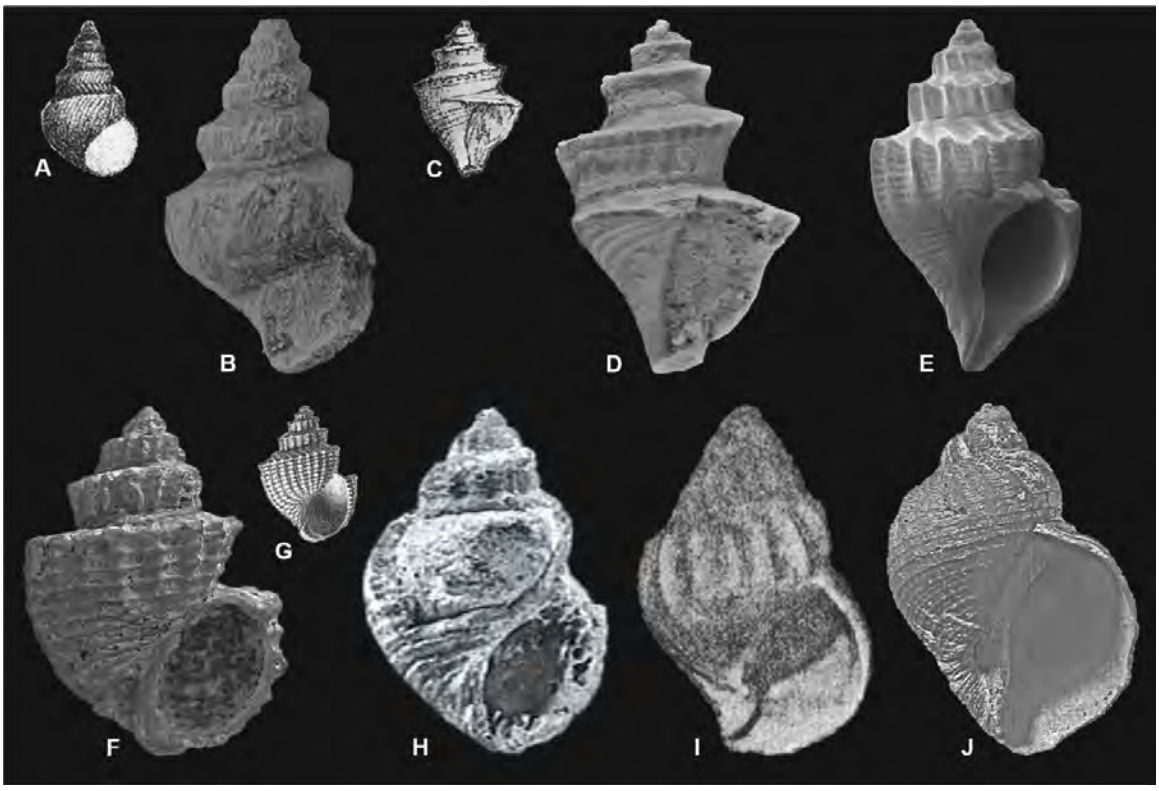

Fig. 1.4. — Type species of purpurinid genera: A, *Angularia subpleurotomaria* (Münster, 1841) from South Tyrol (Italy), St. Cassian Formation, Carnian (Upper Triassic). This specimen was figured by Münster (1841: pl. 12, fig. 24); B, *Angularia subpleurotomaria* from Costalaresc, South Tyrol (Italy), St. Cassian Formation, Carnian (Upper Triassic). Lectotype, SNSBBSPG AS VII 1800, height 8.6 mm, width 5.3 mm; C, *Pseudoscalites elegantissimus* von Klipstein, 1892 (in Kittl 1892) from Stuores (Italy), St. Cassian Formation as was figured by Kittl (1892: pl. 6, fig. 12); D, Pseudoscalites elegantissimus from Stuores, St. Cassian Formation (Triassic). Lectotype, GBA 1894/005/0007, height 16.3 mm; E, Fossacerithium formosum (Eichwald, 1868) from Łuków (block in glacial drift) (Podlasie, Poland), Callovian (Middle Jurassic). This specimen was figured by Kaim (2004: 108, fig. 87A1); MZ VIII Mg 4230/3; F, Purpurina bellona d'Orbigny, 1850 from St. Vigor (Calvados), France, Bajocian. The photograph was made by Andrzej Kaim in 2004 in the De Vibraye collection of Typotheque in the Muséum national d'Histoire naturelle; Syntypes, MNHN R.53; G, Purpurina bellona from France, Jurassic as was figured by d'Orbigny (1850: pl. 331, fig. 2); H, Purpurina bellona from Calvados, France, Bajocian (Jurassic). This specimen was figured by Fischer & Weber (1997: pl. 23, fig. 26a, b); neotype, no. IPMR.9158; I, Khetella bojarkae Beisel, 1977 from the bank of the Left Boyarka River, Russia (north of Central Siberia), lower Kimmeridgian (Jurassic). This specimen was figured by Beisel (1977: fig. 1a); holotype, N 553/260; J, Cretadmete neglecta Blagovetshenskiy & Shumilkin, 2006 from the town of Slantsevyi Rudnik, Ulyanovsk Region, Russia, upper Hauterivian, Decheni Zone (Lower Cretaceous). This specimen was figured by Blagovetshenskiy & Shumilkin (2006: pl. 6, fig. 1a); holotype, UKM, no. 155/1. Scale bars: B, DF, HJ, 2 mm; A, C, G, size not given.

An emended diagnosis of the genus *Khetella* was published by Kaim & Beisel (2005: 43) who also illustrated for the first time the protoconch of the Siberian *Khetella bojarkae* Beisel, 1977 (Kaim & Beisel 2005: 44, fig. 2). Based on characters of the protoconchs, these authors assigned the genus to the Purpurinidae, and furthermore suggested that the group might be a stem group of Neogastropoda (Kaim & Beisel 2005: 61). When Blagovetshenskiy & Shumilkin (2006) emended the diagnosis of *Khetella* – apparently unaware of the contribution of Kaim &

Beisel (2005) – they placed it provisionally in the family Buccinidae and extended the genus composition given by Beisel (1977, 1983) to fourteen species. They left the interpretation of the species included by Guzhov (2004) into *Khetella* without any remarks or discussions.

Pseudoscalites Kittl, 1892

The genus was established by Kittl (1892) with the type species *P. elegantissimus* von Klipstein, 1892 (in Kittl 1892) (Fig. 1.4D herein). An additional species, *P. cochlea* (Münster, 1841) from the St. Cassian Formation), has been identified by Karapunar & Nützel (2021). Dominici et al. (2024) described the species *P. karapunari* from the Middle Triassic of the South Alps (Northern Italy).

SYSTEMATIC PALEONTOLOGY

Order NEOGASTROPODA Wenz, 1938

Family Maturifusidae Gründel, 2001

Type genus. — *Maturifusus* Szabó, 1983.

Diagnosis. — As for genus (monogeneric family).

Range. — Jurassic (PliensbachianKimmeridgian).

Genus *Maturifusus* Szabó, 1983

Type species. — *Maturifusus densicostatus* Szabó, 1983; by original designation. Jurassic (upper Bajocian), Hungary.

Emended diagnosis. — Shell fusiform; protoconch large (approx. 1.5 mm high), high conical with about 4.5 whorls; embryonic shell of about one whorl and sculptured with distinct tubercles; larval shell with two strong spiral ribs and terminates with a sinusigera; teleoconch whorls convex with strong prosocline axial ribs and spiral cords; in the intersections of axial and spiral ornaments tubercles may occur; aperture oval with a distinct anterior canal.

Species included. — *Maturifusus densicostatus* Szabó, 1983, *M. conspicuus* (Eichwald, 1868) (senior synonym of *M. montagi* Gründel, 1998 according to Kaim, 2004), *M. caseus* (Yamnichenko, 1987) (senior synonym of *Fusus crassus* (Yamnichenko, 1987) according to Guzhov, 2004), *M. grimmensis* Gründel, 1999, *M. keyserlingianus* (Rouillier, 1846), *M. kostromensis* (Gerasimov, 1955), *M. szaboi* Schröder, 1995, *M. ticurelatus* Gründel, 2001 (formal name for *Maturifusus* sp. 1 of Gründel, 1977).

Species *M.*? *nassoides* (EudesDeslongchamps, 1842), *M.*? *piettei* (Hebert & Deslongchamps, 1860) and *M.*? *zeisei* (Wollemann, 1903) can be attributed to *Maturifusus*

pending a revision of the original material. Also, specimens illustrated by Guzhov (2004: pl. 8, figs 11, 12) as *Khetella formosa* (Eichwald, 1868) should in our opinion be assigned to a new species of *Maturifusus*. This, however, needs specimenbased revision that is not feasible at this time.

Range. — Jurassic (PliensbachianKimmeridgian).

Remarks. — A shell fragment from the Campanian of Spain (Torallola) with preserved apical part and only one teleoconch whorl was identified by Kiel (2001) as *Maturifusus*? sp. (Kiel 2001: 90, pl. 25, fig. 1) due to possessing the protoconch sculptured with two spiral ribs, characteristic for this genus. Their position—lose to adapical and abapical suture of protoconch whorls—differs from those in *Maturifusus* sensu stricto. Actually, the abapical spiral may be an element of subsutural shelf and may have resulted from the diagenetic shell deformation. Morphological characteristics of the shell fragment suggest that it may belong to the Aporrhaidae rather than to Maturifusidae.

Maturifusus? *siphonatus* Nützel & Erwin 2004 from the Triassic (early late Norian) of United States (the Wallowa Terrane, Idaho) is characterized by very distinct siphonal canal and due to that feature it has been attributed to *Maturifusus* by Nützel & Erwin (2004: 391), with some doubts though. It differs, however, significantly from other members of Maturifusidae in general shell outline (more turreted than fusiform), height of the last whorl, which is separated from the base by a rib, and a narrow aperture. Taking the characters above into consideration we conclude that *Maturifusus*? *siphonatus* may belong to cerithioideans or triphoroideans (e.g. reminiscent of Jurassic species of Cosmocerithium) rather than to Maturifusidae. Nützel & Erwin (2004) compared it also to *Pseudotritonium*, which seems to be questionable as the type species of *Pseudotritonium* has a siphonal notch (and not a canal) and the other morphological characteristics also differ significantly.

The protoconch of the type species of *Astandes* was described as small, smooth and trochoid (Wade 1917: 298, pl. 17, figs 7, 8; Wade 1926: 157, pl. 54, figs 19, 20). However, the current state of holotype preservation deteriorated considerably since its original illustration does not allow for a more precise investigation of the protoconch (Fig. 1.2B). Subsequent efforts to collect this species have been unsuccessful (Sohl 1960, 1967) and the species appears to be extremely rare even at its type locality. Our extensive sampling in 2022 in the type locality resulted in a single specimen with corroded protoconch, but partially preserved aperture (Fig. 1.2A). The protoconch of another species of this genus—*A. nodosus*—has been described in detail by Dockery (1993), Bandel (2006), and Bandel & Dockery (2012) and remains the only source of information on the protoconch morphology in *Astandes*. Based on this protoconch, Bandel (2006) and Bandel & Dockery (2012, 2016) included *Astandes* into Trichotropidae, a family now synonymized with the Capulidae (Bouchet et al. 2017). The specimen of *Astandes*

densatus (Fig. 1.2A) we collected in the Coon Creek type locality is very similar to maturifusids in all aspects except for the dentate outer lip of the aperture, a feature never observed in Maturifusidae, but present in the Colombellinidae and several other tonnoideans and neogastropods. Its protoconch morphology and ornamentation remains unknown.

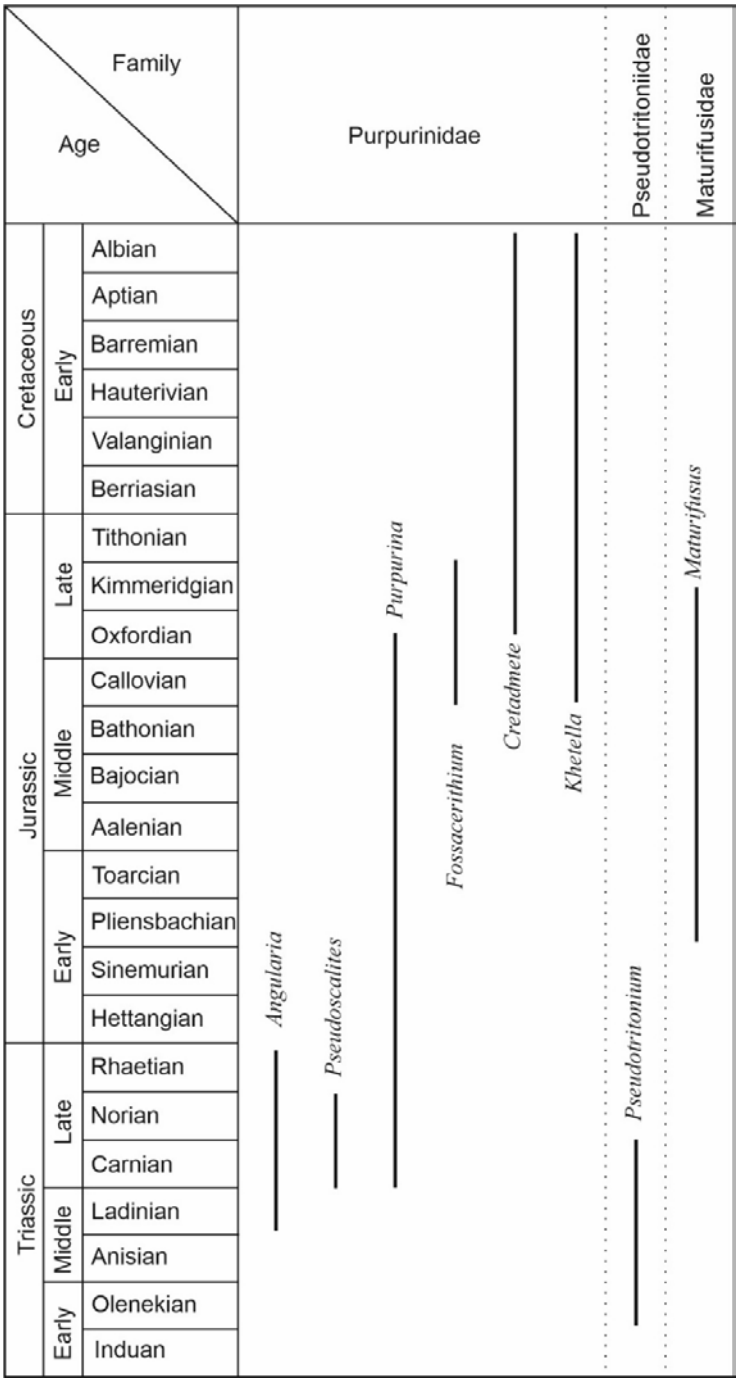

Fig. 1.5. — Stratigraphical distribution of the families Purpurinidae Zittel, 1895, Pseudotritoniidae Golikov & Starobogatov, 1987 and Maturifusidae Gründel, 2001.

Beisel (1983) and Gerasimov (1992) included some Late Jurassic and Early Cretaceous species from Siberia (Russia) into *Astandes* and placed the genus in the Trichotropidae (junior synonym of Capulidae). *Astandes kostromensis* (Gerasimov, 1955) and *A. piccuus* Beisel, 1983 recognised by Beisel (1983) were later included in *Cretadmete* by Blagovetshenskiy & Shumilkin (2006: 147). According to Beisel's description (Beisel 1983: 76, pl. 4, fig. 2), it can be assumed that two of his specimens identified as *A. kostromensis* actually belong to an unidentified species of *Cretadmete* (Table 1.2) due to protoconch morphology (without two spiral ribs) and fine spiral ornamentation, while *A. kostromensis* of Gerasimov (1955) belongs to *Maturifusus*. Also, all species identified by Gerasimov (1992) as species of *Astandes*: *A. conspiccus* (Eichwald, 1868), *A. keyerlingianus* (Rouillier, 1846), and *A. kostromensis* (Gerasimov, 1955) (Gerasimov 1992: 96) should be included into *Maturifusus*.

The type species of *Maturifusus*, *M. densicostatus*, is ornamented by spiral cords and spiral threads running inbetween, which occur in the adapical part of the older whorls (Fig. 1.2C). This character, however, has never been observed in any other species of *Maturifusus* – the strong spiral cords occur without any secondary sculpture elements (Beisel 1983; Gerasimov 1992; Guzhov 2004; Kaim 2004) (Fig. 1.2D, E). This character and lack of the protoconch put a serious doubt at the identity and composition of the genus. Protoconchs of species included in *Maturifusus* depicted in Gründel (1977, 1998, 1999, 2001, 2007), Yamnichenko (1987), Schröder (1995), Kaim (2004, 2012), Guzhov (2004), and Nützel & Gründel (2015) differ strongly from those known from *Astandes nodosus* (Dockery 1993; Bandel & Dockery 2012) in shape and ornamentation though the protoconch of *A. densatus*, the type species of *Astandes*, is yet unknown.

Family Pseudotritoniidae Golikov & Starobogatov, 1987

Type genus. — *Pseudotritonium* Wenz, 1940.

Diagnosis. — As for genus (monogeneric family).

Range. — Triassic (OlenekianCarnian).

Genus *Pseudotritonium* Wenz, 1940

Type species. — *Scalaria venusta* Münster, 1841; by typification of replaced name. Triassic (Carnian), Italy.

Emended diagnosis. — Shell fusiform; protoconch highly conical multispiral with abrupt transition to teleoconch; larval whorls convex and ornamented with faint oblique threads; teleoconch whorls convex with opisthocline axial ribs which are crossed by numerous finer spiral lirae; aperture wide, D-shaped; it seems to be siphonostomous.

Species included. — *Pseudotritonium venustum* (Münster, 1841), *P. laubei* (Kittl, 1894), *P. milierensis* Zardini, 1978, *P. sciaphosterum* (Batten & Stokes, 1986) and possibly *P. avena* (Laube, 1868).

Range. — Triassic (OlenekianCarnian).

Remarks — Only a few species of *Pseudotritonium* are known so far. They are rare and almost all of them occur exclusively in the deposits of the Upper Triassic of the St. Cassian Formation (Dolomites, Italy). The only species described outside this formation is *P. sciaphosterum* (Batten & Stokes, 1986), which was described from the Lower Triassic Moenkopi Formation (San Rafael Swell, Utah, United States) (Batten & Stokes 1986; Nützel 2010) and has preserved protoconchs.

In the following, species of *Pseudotritonium* are discussed:

Pseudotritonium venustum (Münster, 1841). — Kittl (1894) mentioned three specimens in total, including the original specimen from Münster's collection (Münster 1841). He also included in *P. venustum* one more shell described as *P. karreri* by Laube (1868). The species description by Zardini (1978) was based on eight specimens; however, their identification appears to be questionable since he apparently misidentified his specimens (see remarks to *P. laubei*). Our recent collection efforts in the St. Cassian Formation have failed to yield new specimens of this species.

Pseudotritonium? *avena* (Laube, 1868). — Kittl (1894: 238, pl. 11, fig. 11) discovered a single specimen in Laube's collection. Upon comparison with the specimen figured by Laube (1868: 4, pl. 21, fig. 2), Kittl noted that the characteristics are accurate, except for the presence of columellar folds, which were not mentioned in Laube's description. Kittl (1894) included *P.*? *avena* into the genus with doubts due to eroded shell and the limited number of specimens.

Pseudotritonium karreri (Laube, 1868). — Synonymized with *P. venustus* by Kittl (1894).

Pseudotritonium laubei (Kittl, 1894). — Laube (1868) identified one specimen as *P. venustum*, which later Kittl interpreted as a new species *Pseudotritonium laubei* (Kittl, 1894: 238, pl. 11, fig. 11; Fig. 1.3D herein). After comparing this specimen (Fig. 1.3D) to the lectotype of *P. venustum* (Fig. 1.3B) and to the specimen illustrated and identified by Zardini as *P. venustum* (Zardini 1978: 54, pl. 38, fig. 10; Fig. 1.3C herein), we conclude that they belong to two distinct species. They differ in ornamentation, where *P. laubei* has spiral cords of two orders and *P. venustum* displays spiral cords of only one order. Moreover, the inner lip of *P. laubei* is wide, while in *P. venustum* it is rather narrow. Zardini's specimen appears to have a damaged inner

lip, what could have inclined him to identify it as *P. venustum*. Otherwise, the shell shape of these two species is very similar and they are very difficult to tell apart when the preservation is imperfect.

Pseudotritonium macrostoma (Kittl, 1894). — This species is the most abundant among the species previously included in *Pseudotritonium*. Kittl (1894) listed nine specimens and Zardini (1978) mentioned 42 specimens. We identified 14 specimens of *P. macrostoma* in our collection (Table 1.1). Based on morphological characters we reassigned this species to *Purpurina* (see below).

Pseudotritonium milierensis Zardini, 1978. — Only one well preserved specimen is known. While comparing it with *P. avena*, Zardini (1978) noted their similarity in shell outlines. In our opinion *P. milierensis* differs from *P. avena* in having more numerous and thinner axial ribs.

Pseudotritonium sciaphosterum (Batten & Stokes, 1986). — Twenty five specimens were studied by Batten & Stokes (1986). Nützel (2010) identified one additional topotypical juvenile specimen with wellpreserved protoconch.

Family Purpurinidae Zittel, 1895

Type genus. — *Purpurina* d'Orbigny, 1850.

Emended diagnosis. — Shell robust, inflated, commonly with an adapical angulation of the whorl face; protoconch obtusely conical with smooth convex whorls and clearly visible demarcation between protoconch and teleoconch and a thickened apertural margin; shell sculptured with axial ribs and spiral cords; body whorl large; aperture large oval holostomous or siphonostomous.

Genera included. — *Purpurina* d'Orbigny, 1850, *Angularia* Koken, 1892, *Cretadmete* Blagovetshenskiy & Shumilkin, 2006, *Fossacerithium* Gerasimov, 1992, *Khetella* Beisel, 1977, *Pseudoscalites* Kittl, 1892.

Range. — Middle Triassic (Ladinian) to Early Cretaceous (Albian).

Remarks. — Purpurinidae is the most diverse family among possible neogastropod ancestors. Almost thirty genera were assigned to the family when they were first described (Table 1.3). Most of them differ significantly from *Purpurina* in shell shape and other morphological characteristics and were subsequently relocated to other higher gastropod taxa. Partial revision of the family composition has been provided by Guzhov (2004), but in our opinion, it requires further work since not all genera he attributed to the family actually belong to Purpurinidae.

Genus *Purpurina* d'Orbigny, 1850

Type species. — *Purpurina elegantula* d'Orbigny, 1850; by subsequent designation by Bouchet et al. 2017. Jurassic, France.

Diagnosis. — Shell moderately large to medium sized; spire short; whorls more or less broad, angulated with adapical ramp; below angulation, whorl weakly convex and ornamented with numerous axial and spiral ribs; body whorl very large; base rounded with predominant spiral sculpture; aperture large, ovate; outer lip almost even up to angulation; thin inner lip covers umbilical chink (from Kaim 2004 emended from Wenz 1939).

Range. — Late Triassic (Carnian) to Late Jurassic (Oxfordian).

Remarks — The genus *Purpurina* was established by d'Orbigny (1850) without the designation of its type species. Subsequently Bouchet et al. (2017) designated *Purpurina elegantula* d'Orbigny, 1850 as the type species. The genus is rich in species and many of them have never been revised (Kaim 2004: 107). Guzhov (2004) introduced *Globipurpurina* as subgenus of *Purpurina* (Guzhov 2004: 514, a subdivision not followed here) and assigned 23 species to the genus. In that composition, the genus as well as its systematic position is pending careful revision. Here, we address only the Triassic species of *Purpurina*: *P. macrostoma* n. comb.

Table 1.3. — List of genera which were classified as Purpurinidae Zittel, 1895 when first described. Genera included in the family by Guzhov (2004) are asterisked. Genera that are retained in the family in this work are marked by bold face.

Genus	Revised family position	Type species		
		Name	Age	Locality
Andangularia Haas, 1953	Zygopleuridae	*Pseudoscalites subarmatus* Jaworski, 1923	Triassic	Peru
Angularia* Koken, 1892	**Purpurinidae**	*Turbo subpleurotomarius* Münster, 1841	Triassic (Carnian)	South Tyrol, Italy
Aristerostrophia Broili, 1907	Zygopleuridae	*Angularia gracilis* Broili, 1907	Triassic (Ladinian)	South Tyrol, Italy
Cimoliocentrum Cossmann, 1908	Cryptaulacidae	*Centrogonia cureti* Cossmann, 1900	Cretaceous (Barremian)	France
Coronatica Blanckenhorn, 1927	Ampullariidae	*Neritopsis ornata* Fraas, 1878	Cretaceous	Syria
Cretadmete Blagovetshenskiy & Shumilkin, 2006	**Purpurinidae**	*Cretadmete neglecta* Blagovetshenskiy & Shumilkin, 2006	Cretaceous (upper Hauterivian)	Russia
Cyclobathmus Knight, 1940	Microdomatidae	*Trepospira haworthi* Beede, 1907	Permian	United States
*Eucycloidea** Hudleston, 1887	Eucyclidae	*Turbo bianor* d'Orbigny, 1850	Jurassic	France
*Globipurpurina** subgen. Guzhov, 2004	Purpurinidae	*Purpurina sowerbyi* Waagen, 1866	Jurassic (lower Bajocian)	Germany
Gonioconcha Bonarelli, 1921	Eucyclidae	*Gonioconcha spinata* Bonarelli, 1921	Triassic	Argentina
Hesperidina Dubar, 1948	Vetigastropoda	*Hesperidina striolata* Dubar, 1948	Jurassic (Pliensbachian)	Morocco
Khetella Beisel, 1977	**Purpurinidae**	*Khetella bojarkae* Beisel, 1977	Jurassic (Kimmeridgian-Berriasian)	Siberia, Russia
Kittlia Cossmann, 1909	Prostyliferidae	*Natica pleurotomoides* Wissmann, 1841	Triassic	South Tyrol, Italy
Leviathania Pchelintsev, 1927	Leviathanlidae	*Natica leviathan* Pictet & Campiche, 1863	Cretaceous	Switzerland
*Moerkeia** J.Bohm, 1895	Strombidae	*Angularia praefecta* Kittl, 1894	Triassic	Italy
Nortonia Wilson, 1889	Eucyclidae	*Turbo patroclus* d'Orbigny, 1850	Jurassic	France
Ochetochilus Cossmann, 1899	Vetigastropoda?	*Ochetochilus subvaricosus* Cossmann, 1899	Jurassic (Bathonian-Callovian)	France
Parangularia Kutassy, 1934	Turbinidae	*Purpuroidea hungarica* Kutassy, 1932	Triassic	Hungary
Propemurchisonia de Gregorio, 1930	? Ptenoglossa	*Propemurchisonia giulianensis* de Gregorio, 1930	Jurassic	Italy
Pseudalaria Hudleston, 1888	Mathildidae	*Turritella unicarinata* Deslongchamps, 1842	Jurassic	British Isles
Pseudoscalites* Kittl, 1892	**Purpurinidae**	*Pseudoscalites elegantissimus* Kittl, 1892	Triassic (lower Carnian)	South Tyrol, Italy
*Ptychostoma** Laube, 1868	Prostyliferidae	*Natica pleurotomoides* Wissmann, 1841	Triassic	South Tyrol, Italy
Purpurina* d'Orbigny, 1850	**Purpurinidae**	*Purpurina elegantula* d'Orbigny, 1850	Jurassic	France
Purpuroidea Lycett, 1848	Littorinoidea	*Purpura moreausia* Buvignier, 1843	Jurassic	British Isles
Silberlingiella Frýda & Blodgett, 2003	Eustomatidae	*Silberlingiella ornata* Frýda & Blodgett, 2003	Triassic	Nevada, United States
*Tretospira** Koken, 1892	Littorinidae	*Melania multistriata* Wöhrmann, 1889	Triassic	South Tyrol, Italy
Tuberleviathania Golivinova & Korotkov, 1986	Leviathaniidae	*Leviathania gerassimovi* Pchelintsev, 1926	Cretaceous	Caucasus
Werfenella Nützel, 2005	Paraturbinidae	*Turbo rectecostatus* Hauer, 1851	Triassic (Olenekian)	South Tyrol, Italy

Purpurina macrostoma (Kittl, 1894) n. comb.

(Fig. 1.6)

Palaeotriton macrostoma Kittl, 1894: 237, pl. 11, figs 69.

Scalaria venusta – Laube 1868: 47, pl. 23, fig. 3, not Münster 1841 that is *Pseudotritonium venustum* (Münster,1841).

Material examined. — Italy • 14 shells; South Tyrol, Alpe di Specie; PZO 16378, 16379, 16380, 16381, 16382, 16383, 16384, 16385, 16386, 16387, MPRZ 2021 1061, 2021 1062, 2021 1063, 2021 1064 • 1 shell; South Tyrol, Campo; MPRZ 2021 1060.

Range. — Late Triassic of Tyrol (Italy).

Description. — Shell coneshaped, fusiform, last whorl higher than spire; protoconch heliciform, small, mammilated, consists of 2.5 preserved whorls with corroded surface of the apex as well as demarcation between the protoconch and teleoconch; teleoconch consists of more than three convex whorls separated by incised suture; large last whorl with height about two thirds of the shell height; strong, broad, rounded prosocline axial ribs, c. 11-14 per whorls, crossed by spiral cords of two orders; the number of axial ribs increases during shell growth; ribs approximately as wide as interspaces; spiral cords cross axial ribs without nodular thickening at intersections; whole shell surface covered by strengthened growth lines; spiral cords slightly nodular when intersecting strengthened growth lines; aperture broken; columella slightly curved; base weakly convex with evenly rounded transition to whorl face.

Remarks. — Kittl (1894) attributed this species to *Palaeotriton* (replaced later by *Pseudotritonium*) and discussed its similarity to *P. venustum* (Münster, 1841), from which *P. macrostoma* n. comb. differs in shell outline and spiral ornamentation of two orders of strength. Zardini (1978: 54, pl. 38, figs 1, 2) identified some of his specimens as *Pseudotritonium macrostoma*, which differ from Kittl's (1894) type material in shell outline. Some specimens identified by Zardini (1978) as *P. laubei* better agree with the characteristics of *Purpurina macrostoma* n. comb. The protoconch morphology shown herein for the first time allows us to attribute this species to Purpurinidae.

Genus *Angularia* Koken, 1892

Type species. — *Turbo subpleurotomarius* Münster, 1841, by subsequent designation by Cossmann, 1909. Carnian (Triassic), South Tyrol (Italy).

Emended diagnosis. — Shell with high, narrow spire and angulated whorls; the protoconch obtusely conical and comprises approximately three smooth whorls; the demarcation between

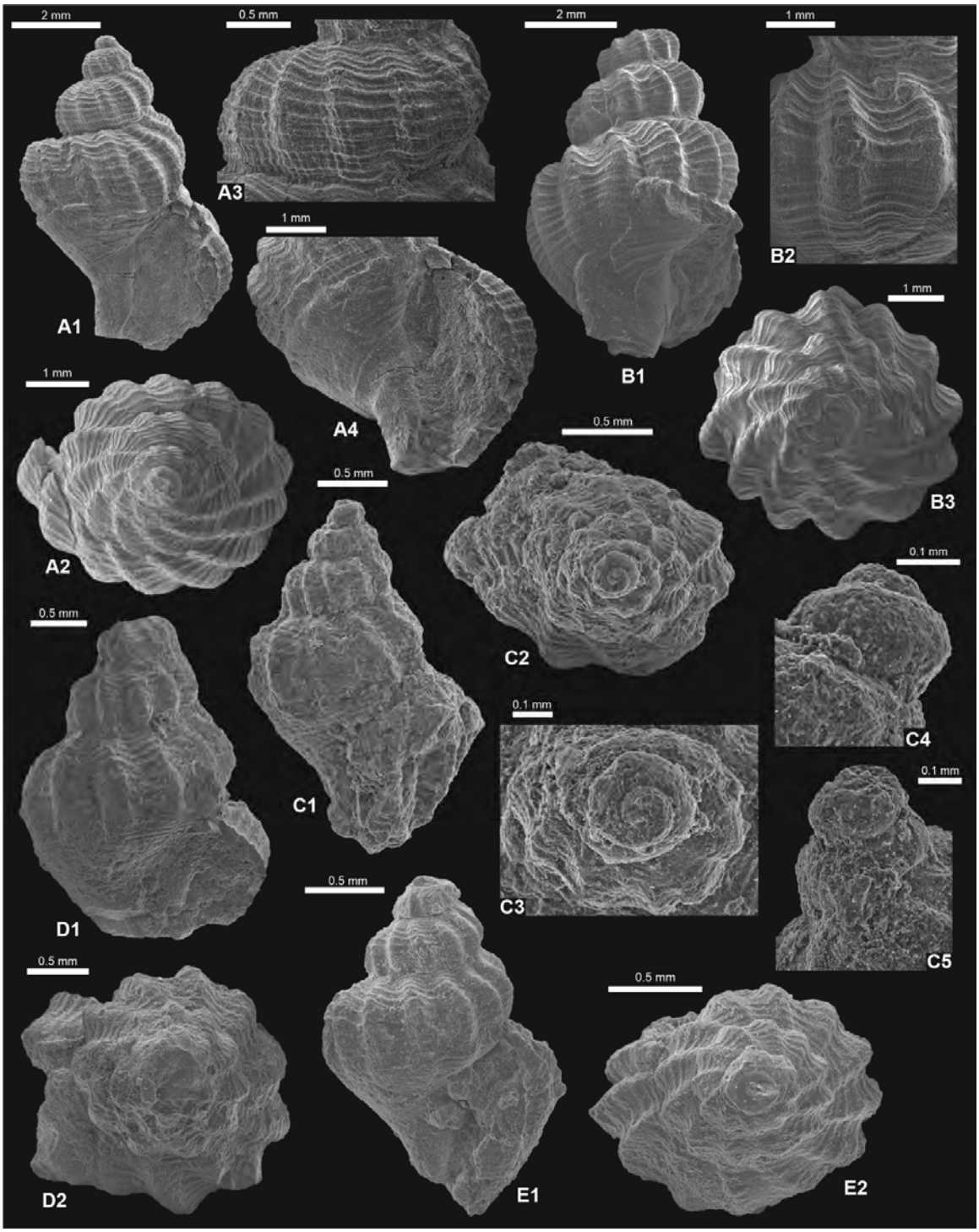

Fig. 1.6. — *Purpurina macrostoma* (Kittl, 1894) n. comb. from the Carnian of Alpe di Specie (South Tyrol, Italy): A, PZO 16381: A1, apertural view; A2, apical view; A3, lateral view, detail of ornamentation; A4, oblique basal view; B, PZO 16383: B1, lateral view; B2, lateral view, detail of ornamentation; B3, apical view; C, PZO 16382: C1, apertural view; C2, apical view; C3, apical view, detail of early whorls; C4, C5, lateral view, detail of early whorls; D, PZO 16386: D1, apertural view; D2, apical view; E, PZO 16387: E1, apertural view; E2, apical view. Scale bars: A1, B1, 2 mm; A2, A3, C1, C2, D1-E2, 0.5 mm; A4, B2, B3, 1 mm; C3-C5, 0.1 mm.

the protoconch and the teleoconch is clearly visible with thickened apertural margin; shell surface ornamented with fine and strengthened curved growth lines of different thickness and density and fine spiral lirae; last whorl large; aperture broad; peristome thickened.

Species included. — *Angularia subpleurotomaria* (Münster, 1841), *A. pleurotomaria* (Münster, 1841), *A. marginata* Wöhrmann & Koken, 1892, *A. multinodosa* Kutassy, 1937, *A. plicata* (Kutassy, 1927), *A. costata* (Zardini, 1978), *A. rectecostata* Nützel & Erwin, 2004, *A. corallina* Nützel, Nose, Hautmann & Hochleitner, 2022 and described herein *Angularia kittli* n. sp.

Range. — Triassic (LadinianRhaetian).

Remarks. — The larval shell of *Angularia* is shown here in detail based on well-preserved specimens from Costalaresc. It confirms the observations made by Bandel (1993, 1994) who pointed out that the protoconch of *Angularia* resembles those of Neogastropoda in morphology but it is much smaller. The small size of the first whorl reported herein, and the number of the protoconch whorls (Nützel 2014) clearly suggest that the species of *Angularia* from the St. Cassian Formation had planktotrophic larval development.

Angularia subpleurotomaria (Münster, 1841)

(Figs 1.4A, B; 1.7B; 1.9A)

Turbo subpleurotomarius Münster, 1841: 115, pl. 12, fig. 24.

Melania latescalata – Klipstein 1845: 190, pl. 12, fig. 29.

Loxonema subpleurotomaria – Laube 1868: 66, pl. 24, fig. 23.

Purpurina subpleurotomaria – Kittl 1892: 64, pl. 6, figs 69. — Zardini 1978: 31, pl. 14, fig. 3.

Angularia (Purpurina) subpleurotomaria – Broili 1907: 106, pl. 6, figs 31, 32.

Angularia subpleurotomaria – Cossmann 1909: 3, textfig. 1.

Non *Angularia subpleurotomaria* – Bandel 1993: pl. 5, figs 3, 4, pl. 14, figs 2, 4; 1994: 139, pl. 5, fig. 17.

?*Angularia subpleurotomaria* – Bandel 2016: 159.

Material examined. — Italy • 7 specimens; South Tyrol; Cassian beds, probably Stuores; lectotype SNSBBSPG AS VII 1800 (designated herein); 2 paralectotypes; SNSBBSPG AS VII 1801a, 1801b (designated herein) • 3 shells; South Tyrol; Misurina; PZO 16388, 16389, 16390 • 1 shell; South Tyrol; Pralongia; PZO 16391.

Range. — LadinianCarnian (MiddleLate Triassic) of Italy (Dolomites).

Description. — Shell cone-shaped, moderately high-spired with gradate spire; protoconch obtusely conical and consists of about three smooth whorls, the demarcation between the protoconch and the teleoconch is clearly visible with thickened apertural margin; teleoconch consists of seven

angulated whorls separated by incised suture; angulation in the upper third of the whorls; shell surface concave above angulation (ramp) and slightly convex below; a spiral cord situated on the ramp close to the adapical suture; shell surface ornamented with fine and strengthened growth lines of different thickness and density; lectotype with numerous densely spaced axial ribs that become weaker during ontogeny and eventually appear as strengthened growth lines; aperture oval with thickened outer and inner lips and broad, rounded anterior outlet; pseudumbilicus partly covered by columellar lip; base distinctly convex with evenly rounded transition to whorl face.

Remarks. — Shell ornamentation varies from delicate, represented by fine growth lines, to pronounced with strengthened growth lines that may be caused by the differences in the age of individuals, their preservation as well as intraspecific variability. *Angularia subpleurotomaria* differs from *A. pleurotomaria* in having a more slender shell and finer ornamentation.

The species was described as closely related to *A. pleurotomaria* which differ only in ornamentation (Münster 1841: 114, 115, pl. 12, figs 23, 24). Wöhrmann & Koken (1892: 198) noted that although both species are present in the collection from Schlern, they are difficult to separate, and transitional forms are present too. Nevertheless the material at our disposal displays a clear distinction between these two species.

Angularia pleurotomaria (Münster, 1841)

(Figs 1.7A, C; 1.8A, B; 1.9B; Table 1.4)

Turbo pleurotomarius Münster, 1841: 114, pl. 12, fig. 23.

Purpurina pleurotomaria – Kittl 1892: 63, non pl. 6, figs 35. — Zardini 1978: 31, pl. 14, fig. 2.

Angularia subpleurotomaria – Bandel 1993: pl. 5, figs 3, 4, pl. 14, figs 2, 4. — Bandel 1994: 139, pl. 5, fig. 17.

Material examined. — Italy • 1 specimen; South Tyrol; Cassian beds, probably Stuores; lectotype SNSBBSPG AS VII 1799 • 6 shells; South Tyrol; Costalaresc; PZO 16372, 16373, 16374, 16375, 16376, 16377 • 1 shell; South Tyrol; Stuores; PZO 16393 • 1 shell; South Tyrol; Misurina Skilift; PZO 16392.

Range. — LadinianCarnian (MiddleLate Triassic) of Italy (Dolomites).

Description. — Shell cone-shaped, moderately high-spired; protoconch obtusely conical, consisting of 2.7-3.0 whorls, 0.33-0.34 mm wide, 0.31-0.37 mm high (excluding base, measured from abapical suture); diameter of first whorl 0.11-0.12 mm; protoconch whorls smooth, convex; demarcation between protoconch and teleoconch abrupt at sinusigera, clearly visible due to thickened opisthocyrt apertural margin; teleoconch consists of 5-7 angulated whorls separated

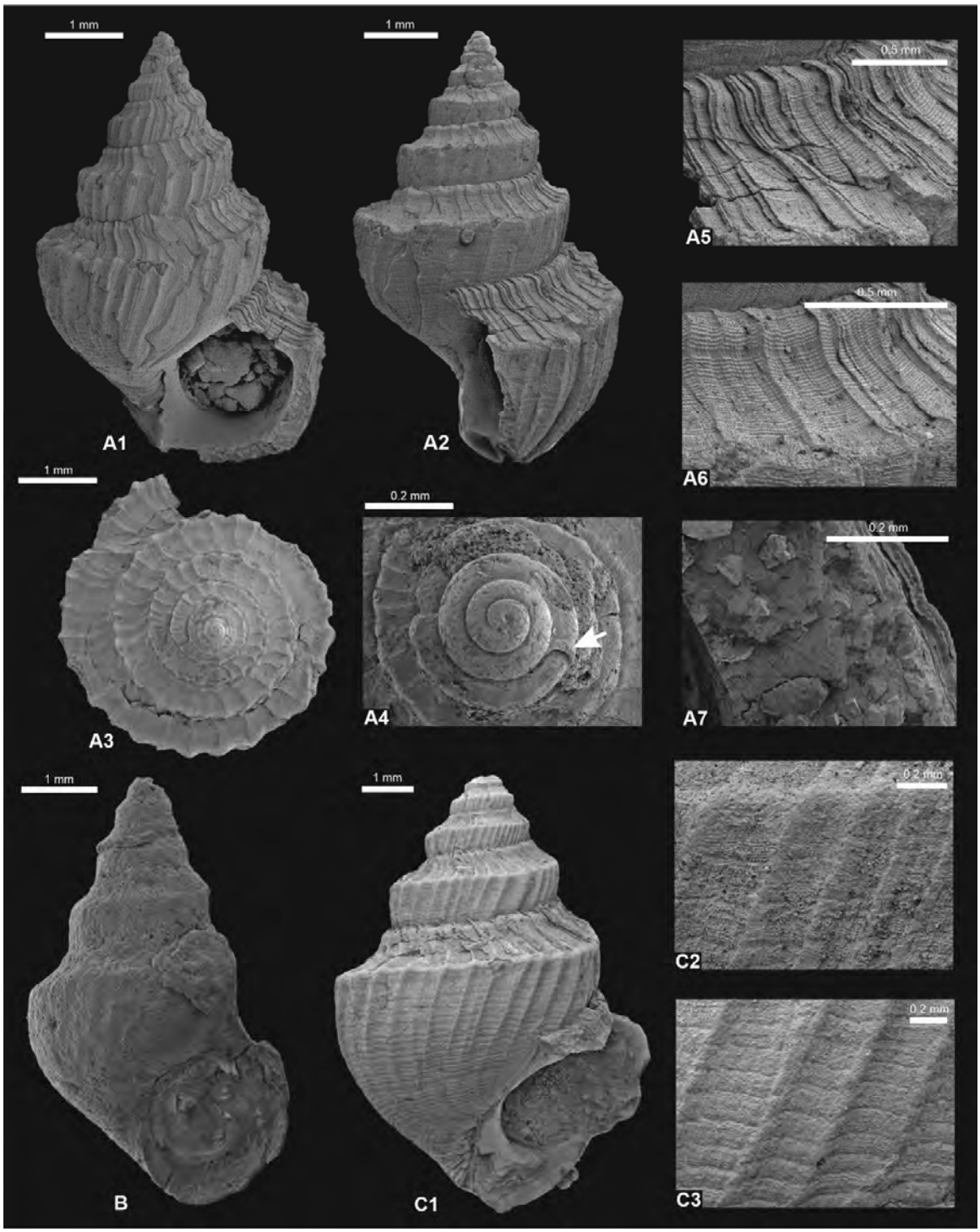

Fig. 1.7. — Two closely related species of *Angularia* Koken, 1892 from the St. Cassian Formation, Carnian (Late Triassic): A, C, *Angularia pleurotomaria* (Münster, 1841) from Costalaresc, South Tyrol (Italy): A, PZO 16374: A1, apertural view; A2, lateral view; A3, apical view; A4, detail apical view of early whorls, arrow indicates protoconch margin; A5, A6, detail of ornamentation; A7, crossed lamellar shell structure; C, PZO 16375: C1, apertural view; C2, C3, detail of ornamentation; B, *Angularia subpleurotomaria* (Münster, 1841) from Misurina, South Tyrol (Italy), PZO 16392. Scale bars: A1A3, B, C1, 1 mm; A4, A7, C2, C3, 0.2 mm; A5, A6, 0.5 mm.

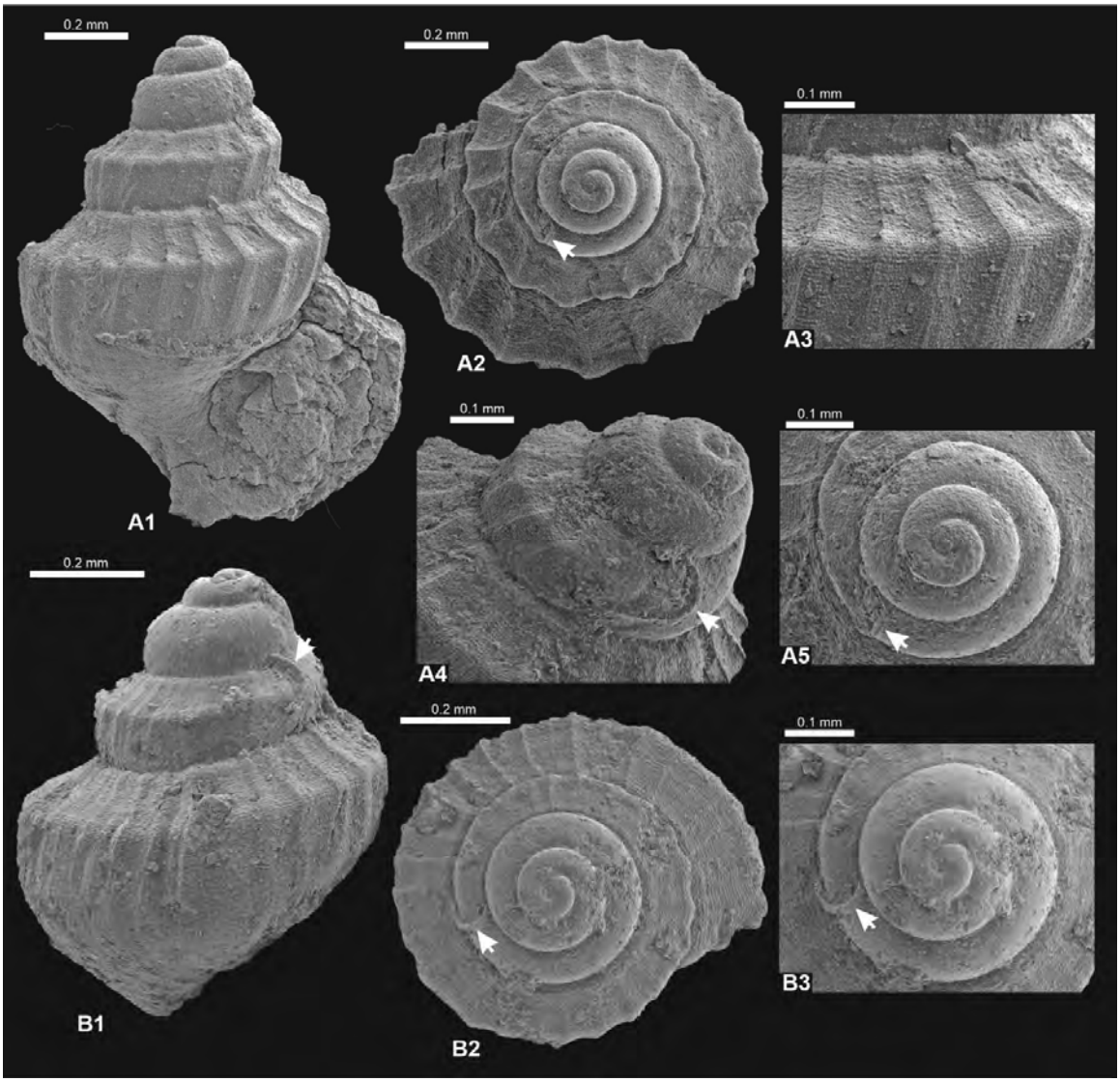

Fig. 1.8. — Juvenile shells of *Angularia pleurotomaria* (Münster, 1841) from the St. Cassian Formation, Carnian (Late Triassic), Costalaresc, South Tyrol (Italy): A, PZO 16376; A1, apertural view; A2, apical view; A3, detail of ornamentation; A4, detail view of early whorls; A5, detail apical view; B, PZO 16377, B1 lateral view; B2, apical view; B3, detail apical view of early whorls. Arrows indicate protoconch margin. Scale bars: A1, A2, B1, B2, 0.2 mm; A3A5, B3, 0.1 mm.

by incised suture; angulation situated in the upper third of the whorls; shell surface concave above angulation and slightly convex below; on the ramp close to the adapical suture a spiral cord situated; shell surface ornamented with somewhat irregular axial ribs and numerous fine granulated spiral lirae forming a microornament; abapical portion of the whorls ornamented with spiral grooves; aperture broken; pseudumbilicus partly covered by columellar lip; base weakly convex with grooves and evenly rounded transition to whorl face.

Remarks. — Kittl (1892) indicated an average of 20-24 axial ribs per whorl for this species. However, in his figure only about 14 ribs are present on the last whorl (Kittl 1892: pl. 6, figs 35).

Therefore, the description refers to *Angularia pleurotomaria*, whereas the figure shows the new species *A. kittli* n. sp. For differences with the latter see below.

Table 1.4. — Protoconch measurements of *Angularia pleurotomaria* (Münster, 1841) (mm). Abbreviations: DFW, diameter of the first whorl; DPC, diameter of protoconch; HPC, height of protoconch; WPC, number of protoconch whorls.

SEM number	WPC	HPC	DPC	DFW
PZO 16372	2.7	0.33	0.33	0.12
PZO 16373	2.9	0.31	0.33	0.11
PZO 16377 (Fig. 8B)	2.9	0.32	0.34	0.11
PZO 16376 (Fig. 8A)	3.0	0.37	0.34	0.11

Angularia kittli n. sp.

(Fig. 1.9C, D)

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?*Loxonema latescalata* – Laube 1868: 65, pl. 24, fig. 21.

Purpurina pleurotomaria – Kittl 1892: pl. 6, figs 35.

?*Angularia (Purpurina) pleurotomaria* – Broili 1907: 106, pl. 9, fig. 33.

Purpurina pleurotomaria – Zardini 1978: 31, pl. 14, fig. 1; non fig. 2 that is true *Angularia pleurotomaria* (Münster).

Material examined. — Holotype. Italy • South Tyrol; Rumerlo; Carnian; Late Triassic; MPRZ No 1271 RZ, illustrated in Zardini (1978: pl. 14, fig. 1).

Diagnosis. — Shell cone-shaped, moderately high-spired, with gradate spire; teleoconch consists of at least five angulated whorls separated by incised suture; angulation situated in the upper third of the whorls; spiral cord situated close to the adapical suture; shell surface ornamented with strong, regularly spaced axial ribs crossed by spiral cords; aperture oval; pseudumbilicus partly covered by columellar lip; base weakly convex with evenly rounded transition to whorl face.

Type locality. — Italy, South Tyrol, Rumerlo.

Derivation of the name. — In honour of Ernst Kittl (1854–1913).

Range. — Carnian (Late Triassic) of Italy (Dolomites).

Description. — Shell cone-shaped, moderately high-spired, with gradate spire; protoconch not preserved; teleoconch consists of five angulated whorls separated by incised suture; angulation situated in the upper third of the whorls; shell surface concave above angulation (ramp) and slightly convex below; on the ramp close to the adapical suture a spiral cord situated; shell surface ornamented with strong, regularly spaced axial ribs crossed by spiral cords; the number

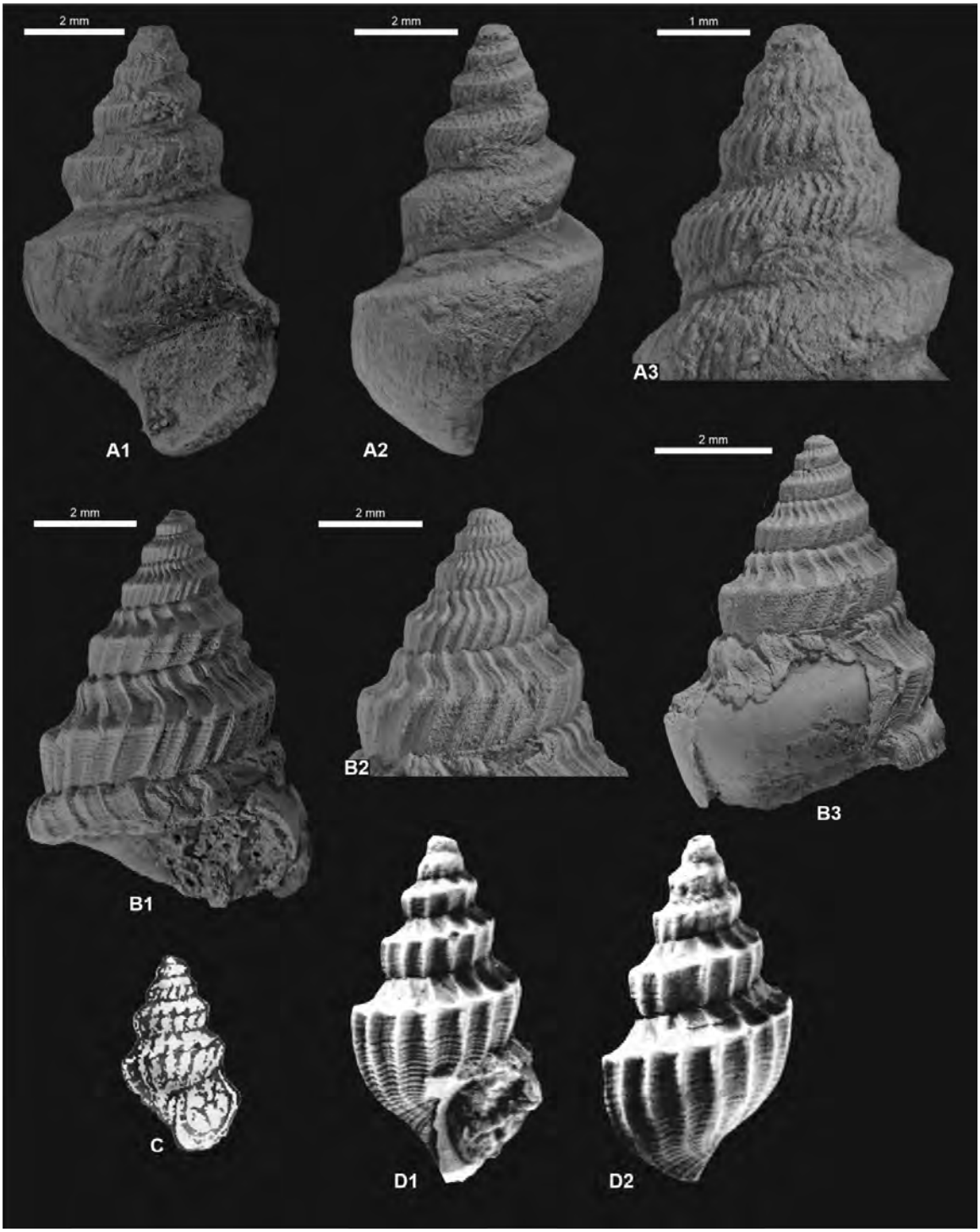

Fig. 1.9. — *Angularia* Koken, 1892 species from the St. Cassian Formation, Carnian (Late Triassic): A, *Angularia subpleurotomaria* (Münster, 1841) from Cassian beds, probably Stuores. Lectotype, SNSBBSPG AS VII 1800: A1, apertural view; A2, lateral view; A3, detail view of early whorls; B, *Angularia pleurotomaria* (Münster, 1841) from Cassian beds, probably Stuores. Lectotype, SNSBBSPG AS VII 1799: B1, apertural view; B2, detail view of early whorls; B3, lateral view; C, *Angularia kittli* n. sp. after original figure by Kittl (1892: pl. 6, fig. 3); D, specimen figured by Zardini (1978: pl. 14, fig. 1), holotype, MPRZ No 1271 RZ: D1, apertural view; D2, lateral view. Scale bars: A1, A2, B1-B3, D, 2 mm; A3, 1 mm; C, size not given.

of axial ribs increases during the shell growth; aperture oval; pseudumbilicus partly covered by columellar lip; base weakly convex with evenly rounded transition to whorl face.

Remarks. — *Angularia kittli* n. sp. differs from *A. pleurotomaria* in displaying fewer axial ribs per whorl and in having spiral cords instead of grooves, while it differs from *A. subpleurotomaria* in having stronger axial ribs and distinct spiral ornamentation. *Angularia kittli* n. sp. differs from *Fossacerithium formosum* (Eichwald, 1868) in having thinner axial ribs and also their opisthocline direction (instead of prosocline in *F. formosum*). *A. kittli* n. sp. posesses also more spiral cords below the ramp, and a holostomatous aperture.

This species has been previously identified by Zardini (1978) as *Purpurina pleurotomaria* and according to him, it is quite common in the St. Cassian Formation – he lists more than 350 specimens.

Genus *Cretadmete* Blagovetshenskiy & Shumilkin, 2006

Type species. — *Cretadmete neglecta* Blagovetshenskiy & Shumilkin, 2006, by origanl designation. Decheni Zone, Upper Hauterivian (Cretaceous), Slantsevyi Rudnik (Russia, Ulyanovsk Region).

Diagnosis. — Shell small, fusiform; protoconch smooth, consisting of 2.5-3.0 convex whorls, separated from teleoconch by prominent commissure followed by convex whorls with distinct ornamentation; spiral ornamentation consists of numerous, narrow, somewhat flattened costulae; axial ornamentation consists of low, fairly wide, rounded costae, which vary in number from 14 to 25 on last whorl; axial costae bend more sharply in upper part of last whorl and flatten below; aperture semilunar; siphonal canal not separated from apertural margin (after Blagovetshenskiy & Shumilkin 2006).

Species included. — *Cretadmete piccua* (Beisel, 1983) and *C. gracillima* (Wollemann, 1903).

Range. — Late Jurassic (Late Oxfordian) to Early Cretaceous (Albian).

Remarks. — *C.*? *conspicua*, *C.*? *keyserlingiana* and *C. kostromensi*s included into *Cretadmete* by Blagovetshenskiy & Shumilkin (2006) should be rather placed in *Maturifusus*. These species have more elongated apertures and their ornamentation is more similar to that of *Maturifusus*. Two specimens described as *Astandes kostromensis* by Beisel (1983: 76) have a “large protoconch with 2.5 smooth convex whorls” and besides, they differ significantly from the holotype as reported by Gerasimov (1955: 196). We consider these two specimens to belong to a new species of *Cretadmete*, which simultaneously constitutes the oldest record of the genus (upper Oxfordian).

Genus *Fossacerithium* Gerasimov, 1992

Type species. — *Fusus formosus* Eichwald, 1868, by original designation. Oxfordian (Jurassic), Russia.

Emended diagnosis. — Shell fusiform; whorls angulated with adapical ramp; protoconch smooth, obtusely conical; the demarcation between the protoconch and the teleoconch is clearly visible, with a thickened apertural margin; shell surface ornamented with strong, wide axial ribs and weaker spiral cords; last whorl large; aperture oval with well pronounced anterior channel; columellar lip with callus covering umbilical area.

Species included. — *Fossacerithium formosum* (Eichwald, 1868) and *F. hypermeces* (Cossmann, 1913).

Range. — Jurassic (CallovianKimmeridgian).

Remarks. — Gerasimov (1992) erected the subgenus *Fossacerithium* for the Early Jurassic members of the genus *Paracerithium* (within the family Procerithiidae) with *Fusus formosus* Eichwald, 1868 as its type species, that he previously included in *Purpurina* (Gerasimov 1955: 179, pl. 39, fig. 12). Gerasimov (1992) provided only a brief characterisation of the new subgenus, which is, however, diagnostic enough to establish a new taxon. Since the type species of *Fossacerithium* differs significantly from the type species of *Paracerithium*, we accord full genus status to *Fossacerithium* and provide a more detailed emended diagnosis. The main character distinguishing *Fossacerithium* from *Paracerithium* is a very long siphonal canal, while species of *Paracerithium* have drop-shaped apertures reminiscent of Middle Jurassic rissoids, e.g. *Buvignieria* Cossmann, 1921 (compare Kaim 2004 for *Buvignieria* and Hikuroa & Kaim 2007 for *Paracerithium*). In addition to the type species, Gerasimov (1992) also included *Paracerithium (Fossacerithium) procerum* (Gerasimov 1992: 88). The latter is most likely a cerithiid, while *Paracerithium (Fossacerithium) formosum* belongs to purpurinids according to shell characteristics, including a large smooth, obtuse conical protoconch that is typical of this family (Kaim 2004: fig. 87). *Fossacerithium* differs from *Purpurina* in having an ellipsoidal peristome with well pronounced anterior channel and wide columellar lip with a callus covering its umbilical area. It differs from *Khetella* in shell outline, namely in having an angulation in the adapical portion of the whorls, a stronger spiral ornamentation and in the shape of the aperture.

Fossacerithium formosum (Eichwald, 1868)

(Fig. 1.4E)

Fusus formosus Eichwald, 1868: 946, pl. 31, fig. 7.

Fusus minutus – Rouillier & Fahrenkohl 1849: 377, pl. 50, fig. 94 (non *Fusus minutus* Roemer 1836: 140).

Purpurina formosa – Gerasimov 1955: 179, pl. 39, fig. 12. — Kaim 2004: 108, fig. 87. — Kaim 2008: fig. 3h.

Paracerithium (Fossacerithium) formosum – Gerasimov 1992: 87, pl. 24, figs 15, 10.

?*Khetella formosiformis* Guzhov 2004: 526, pl. 8, figs 58.

?*Khetella formosa* – Guzhov 2004: 526, pl. 8, fig. 9.

Khetella formosa – Guzhov 2004: 526, pl. 9, fig. 1.

Description and emended diagnosis. — See Kaim (2004).

Range. — Middle to Late Jurassic of Russia and Poland.

Remarks. — Guzhov (2004: 524, pl. 8, fig. 8a) illustrated only one specimen of this species in apertural view with its aperture is eroded, so we attribute his material to the species with some doubt because the morphology of the aperture (oval with well pronounced anterior channel) is the main diagnostic character. On the other hand, the elongated body whorl, shell outline and inclined ramp strongly suggest that the specimen illustrated by Guzhov (2004) belongs to *Fossacerithium*.

Kaim (2004: 108) transferred the species to *Purpurina* stating that it differs significantly from the type species of *Paracerithium*, *P. acanthocolpum* Cossmann, 1902; the latter having much more slender shell, an angulation of the whorl instead of a subsutural ramp and a D-shaped peristome (compare Cossmann 1906; Gründel 1997; Hikuroa & Kaim 2007). He also abandoned the subgeneric name of *Fossacerithium* Gerasimov 1992, which we reinstate here as a full genus within the Purpurinidae.

Genus *Khetella* Beisel, 1977

Type species. — *Khetella bojarkae* Beisel, 1977, by original designation. Late Kimmeridgian (Jurassic), Levaja Bojarka River, northern part of Central Siberian Plateau, Russia.

Emended diagnosis. — Shell conical with weakly convex whorls; protoconch smooth and lowspired; demarcation between protoconch and teleoconch clearly visible; ornamentation consists predominantly of axial ribs; axial ribs sharply angulated in upper part of whorls forming distinct ramp and resulting in gradation of whorls; aperture D-shaped with anterior siphonal notch (compiled from Kaim & Beisel 2005 and Blagovetshenskiy & Shumilkin 2006).

Species included. — *Khetella bojarkae* Beisel, 1977, *K. incerta* (d'Orbigny, 1845), *K. makaryevensis* (Guzhov, 2004), *K. septentrionalis* (Tullberg, 1881), *K. ventrosa* Beisel, 1983, and *Khetella* sp. of Kaim & Beisel (2005) – the latter may represent a fully grown individual of *K. ventrosa* or a new undescribed species.

Range. — Late Jurassic (Callovian) to Early Cretaceous (Albian).

Remarks. — *Buccinum incertum* (d'Orbigny, 1845) depicted by Glazunova (1973: figs 15, 7) differs from the type species, *K. bojarkae,* in the smaller size and in having less pronounced spiral ribs (Beisel 1977). These differences could reflect intraspecific variability or preservation – the size difference of individuals could also be ecophenotypical. According to Beisel's definition (1983: 75, pl.3, figs 1617, 20), *K. ventrosa* is very similar to *K. incerta* in Glazunova's (1973) description and differs only in having a fine spiral ornamentation. This difference may be a result of imperfect preservation of the shell surface in Glazunova's (1973) materials of *K. incerta*. The new species variation of *K. incerta* var. *plana* described by Glazunova (1973: 81, pl. 43, fig. 6) cannot be attributed to the same genus as *K. incerta* according to its set of characters (most of all the elongated shell shape) and is reminiscent of some Cretaceous epitoniids (e.g. *Confusiscala* de Boury, 1909). The name itself is not available according to ICZN Code Art. 45.6.3.

Another species that can be included in *Khetella* is *Buccinum septentrionale* Tullberg, 1881 from the Late Jurassic (Oxfordian–Kimmeridgian) of Novaya Zemlya, Russia. Although its aperture is unknown, the ornamentation and gross shell morphology is typical of *Khetella* as already indicated by Guzhov (2004).

Khetella brunsvicensis (Wollemann, 1900: 174, pl. 8, figs 11, 12), included in *Khetella* by Beisel (1977), should be assigned to the genus *Purpurina* due to the distinct spiral ornamentation and its aperture morphology without distinct anterior channel. *K.* ?*gaultica* (d'Orbigny, 1842) that Beisel (1977, 1983) assigned to *Khetella* is based on a shell fragment of the last whorl (d'Orbigny 18421843: pl. 233, figs 1, 2), which Kollmann (2005) identified as *Cosnia gaultina* (d'Orbigny, 1842) (Kollmann 2005: 152, pl. 11, fig. 6) and placed into the family Buccinidae. This specimen, however, is so fragmentary and poorly preserved that we refrain from discussing its generic or even familial position; it should be treated as a nomen dubium.

We assign the specimens illustrated by Guzhov (2004: pl. 8, figs 11, 12) and identified as *Khetella formosa*, to the family Maturifusidae because of their protoconch morphology (with two spiral ribs); they most likely belong to an undescribed new species. We think, that *Purpurina hypermeces* should be attributed to *Fossacerithium*, whereas *K. formosiformis* (Guzhov 2004: pl. 8, figs 59) should be placed in synonymy with *Fossacerithium formosum* based on protoconch morphology, ramp characters, shell shape and ornamentation. The separation of the new species *K. glasunovi* (Guzhov 2004: 530, pl. 8, figs 59) that was based on Glazunova's material attributed by her to *Buccinum incertum* (Glazunova 1973: 80, pl. 43, figs 17) is rather doubtful. *K. gradata* (Guzhov 2004: pl. 9, fig. 10a) should be assigned to the genus *Maturifusus* because of its gross

shell morphology and possessing two spirals on the protoconch. *Fusus liasicus*, judging from the figure of Dumortier (1874: 163, pl. 37, fig. 11), possibly also belongs to *Maturifusus*.

The majority of species added by Blagovetshenskiy & Shumilkin (2006), based on illustrations from old monographs, most likely do not belong to the *Khetella* and require a detailed restudy. Blagovetshenskiy & Shumilkin (2006: 145, pl. 5, figs 14) also described a new species of *K. trautscholdi* and included to its synonymy the same taxa that were included by Guzhov (2004: 530) in the description of his new species of *K. glasunovi*. It seems therefore that *K. trautscholdi* should fall into the synonymy of *K. glasunovi*. This synonymization, however, should await a comprehensive review of entire material described by Glazunova (1973), Guzhov (2004), and Blagovetshenskiy & Shumilkin (2006) and its comparison to the type species of Beisel (1977).

Genus *Pseudoscalites* Kittl, 1892

Type species. — *Pseudoscalites elegantissimus* Klipstein, 1892 (in Kittl 1892), by original designation. Carnian (Triassic), South Tyrol (Italy).

Emended diagnosis. — Shell fusiform with elevated, gradate spire; whorls concave with pronounced angulation and carina; spiral ornamentation predominates over the axial; aperture broad with anterior and posterior canals.

Species included. — *Pseudoscalites elegantissimus* Klipstein, 1892 (in Kittl 1892), *P. cochlea* (Münster, 1841), *P. karapunari* Dominici, Danise & Tintori, 2024.

Range. — Triassic (LadinianNorian).

Remarks. — Haas (1953) attributed two specimens from the Late Triassic Pucara Group (Central Peru) to the genus, but they are more reminiscent of Eucyclidae. Nützel & Erwin (2004) described *Pseudoscalites* cf. *elegantissimus* from Wallowa Terrane (Idaho, United States) and noted that their specimens are almost identical to the specimen illustrated by Bandel (1994: pl. 5, fig. 10). It is worth mentioning, that the specimen from Tyrol is three times smaller than material from Idaho and it remains uncertain whether it is of evolutionary or ecophenotypical importance.

DISCUSSION

In the first edition of the gastropod nomenclator by Bouchet & Rocroi (2005) Pseudotritoniidae were synonymized with Purpurinidae and placed in Littorinoidea, while Maturifusidae were placed in the Hypsogastropoda whithout allocation to any superfamily. In the second edition by Bouchet et al. (2017) Maturifusidae are synonymized with Pseudotritoniidae, while Purpurinidae are kept separately; both unassigned to any superfamily among Neogastropoda. It shows that the relationships between all these families have been in a

state of flux in the last decades. One of the major obstacles for a clarification of the early evolution of Neogastropoda is the lack of data on the protoconch morphology of type species of type genera because this knowledge is crucial for the analysis of the higher level gastropod phylogeny (e.g. Thiriot-Quiévreux 1972; Rodriguez Babio & Thiriot-Quiévreux 1974). The mentioned families are extinct, so the identification of their relationships is based solely on comparative shell morphology. Various scenarios for the origin of Neogastropoda have been proposed, including a rather unlikely direct descent from Vetigastropoda or from Paleozoic siphonostomatous subulitids (Ponder 1973).

Certain members, such as the genus *Soleniscus* Meek & Worthen, 1861 or *Strobeus* de Koninck, 1881, of the heterogenous essentially Paleozoic caenogastropod group Subulitoidea (Nützel et al. 2000) resemble the neogastropod ground pattern in having a siphonal canal and a fusiform shell shape. *Soleniscus* is wide spread in the Late Paleozoic and has a relatively large (> 1 mm), smooth conical larval shell (Nützel & Pan 2005). However *Soleniscus* has a smooth shell and lacks an angulation of the teleoconch whorls. Soleniscidae survived the end Permian mass extinction but probably became extinct within the Early Triassic (Nützel 2005; Kaim et al. 2013) and it is unclear whether this family has later Mesozoic descendants.

In the last two decades, knowledge on the protoconch morphology of the members of the Mesozoic families Maturifusidae, Pseudotritoniidae, and Purpurinidae has increased significantly (Guzhov 2004; Kaim 2004; Nützel 2010), nevertheless, as outlined, the protoconchs of type species of potential ancestral neogastropod genera still remain unknown. However, differences between the known purpurinid and maturifusid types of protoconch are quite well constrained (see Figs 10; 11). All species of the monogeneric family Maturifusidae have highly conical multispiral protoconchs with convex whorls and two spiral ribs, one of which is situated near the abapical suture and the other above the middle part of the whorls. They display also an abrupt transition to the teleoconch (Figs 10D; 11). These characteristics may connect maturifusids to neogastropods, most of which have an abrupt transition to the teleoconch and highly conical multispiral protoconchs (Figs 10AC; 11). Also, the large size of the larval shell (1 mm height in the Early Jurassic *M. grimmensis*, see e.g. Nützel & Gründel 2015) suggests a relation to neogastropods since the larval shells of extant Neogastropoda are large. An affinity of maturifusids to modern buccinids (Neogastropoda) has been discussed by Szabó (1983) and Riedel (2000) identified *Maturifusus* as derived caenogastropods. However, members of Maturifusidae differ by their gradate protoconchs ornamented with two strong spiral ribs, while neogastropod protoconchs usually have rounded whorls and a smooth or weakly ornamented shell surface. At the same time, maturifusid protoconchs are notably larger than the protoconchs

of other Triassic and Jurassic caenogastropods, including cerithiids, which have similarly strong spirals on protoconchs.

The members of Purpurinidae have obtusely conical protoconchs with smooth convex whorls and clearly visible demarcation between protoconch and teleoconch expressed by thickened apertural margin. These characteristics connect the Triassic genus Angularia with Jurassic Purpurina (Figs 7; 8; 10E, F), whose protoconchs have been documented to date (Bandel 1993; Guzhov 2004; Kaim 2004).

Purpurinid protoconchs increased significantly in size (approximately four times) between the Triassic and Jurassic (see Fig. 1.10E, F). Extremely large sizes of Mesozoic (Jurassic) purpurinid protoconchs (Fig. 1.10E) may indicate that they are related to Cenozoic tonnoids (compare Craig et al. 2020; Fig. 1.11 herein). Molecular data have revealed a close relationship between Tonnoidea and Neogastropoda or even postulated inclusion of tonnoids to neogastropods (Osca et al. 2015; Harasewych et al. 2024) in a comparatively basal position, either alone or as a sister group of Volutidae or Cancellariidae (Cunha et al. 2009). This molecular evidence may support the earlier suggestions regarding their common origin (e.g. Haszprunar 1988). Thus, if ancestors of tonnoids are purpurinids, then maturifusids – should they be accepted as neogastropod ancestors – also have to be related to purpurinids with the common ancestor in the Triassic. Such an ancestor has not yet been reported so far.

Another possibility is that maturifusids are a group not closely related to Purpurinidae, and went extinct without direct descendants. In such a scenario both, tonnoids and neogastropods, could have evolved from purpurinids, with tonnoids separated from them in the Jurassic, perhaps in the Callovian. The comparison of *Khetella* (the oldest record known from the Early Callovian) and *Cretadmete* (Oxfordian–Albian) with alleged cancellariid *Paladmete* (described from the Upper Cretaceous by Sohl (1964) and Bandel & Dockery (2016)) and tonnoids (described from the Upper Cretaceous by Dockery (1993 and Eocene by Craig et al. (2020) and Recent (Bouchet & Warén 1993)) may support this assumption.

According to the current state of knowledge, the closest fossil relative to the hypothetical ancestor of neogastropods is *Fossacerithium* because it possesses a large protoconch and a well-developed anterior channel. The Jurassic *Fossacerithium formosum* is superficially similar in gross shell morphology to the Triassic *Angularia kittli* n. sp., but the latter lacks the derived character of the aperture (distinct anterior channel), which may have developed later in Jurassic forms. Regrettably, the protoconch of *Angularia kittli* n. sp. is unknown to date, therefore further collection effort is needed to substantiate its relations to the Jurassic *Fossacerithium*. Nevertheless, it can be assumed that purpurinids were divided into two groups in the Jurassic at the latest. One of these groups could be considered as the stem-group for Tonnoidea (*Khetella*

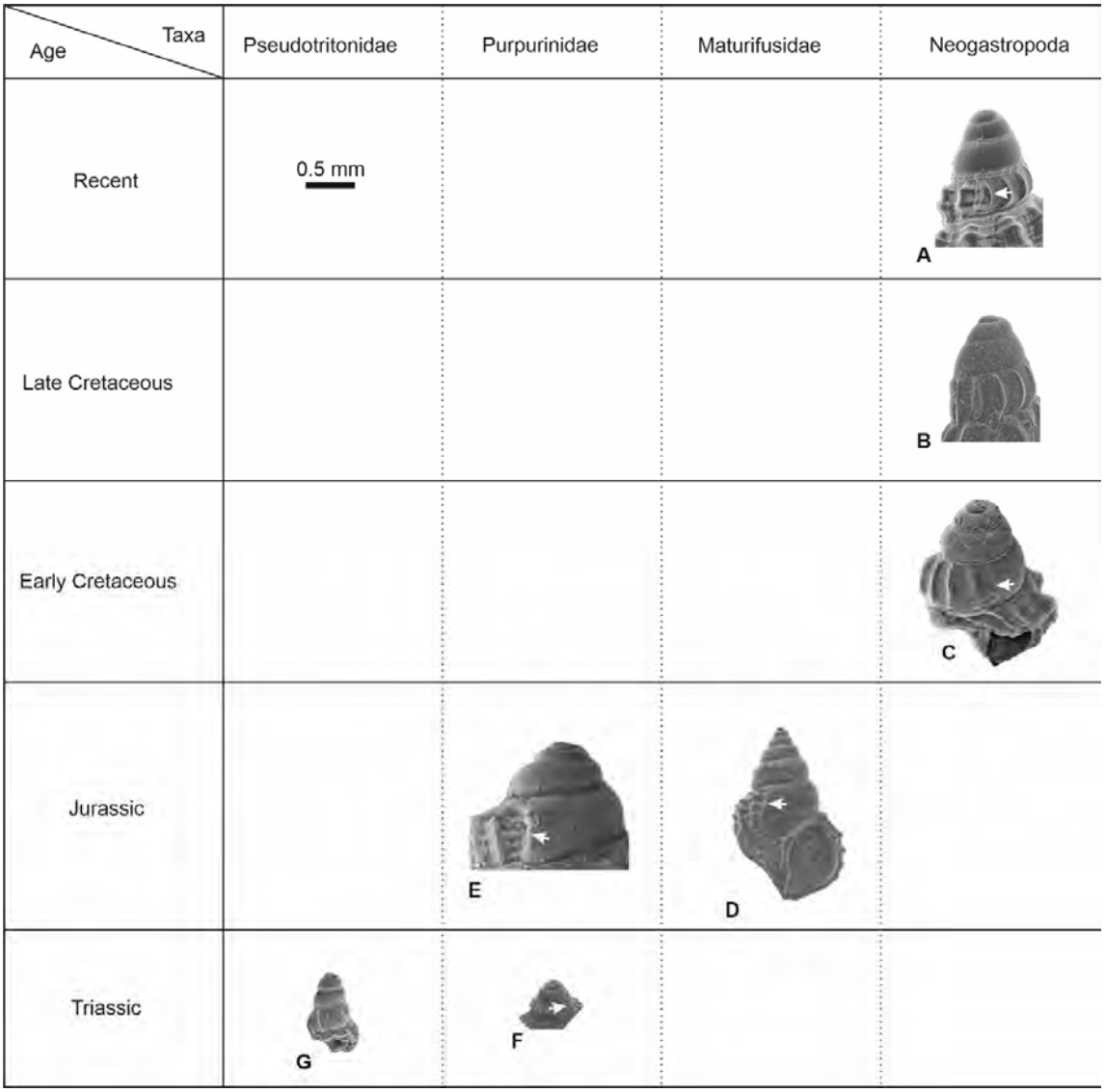

Fig. 1.10. — Comparison of protoconchs and their sizes of some neogastropod taxa and members of other families, which were proposed as neogastropod ancestors: A, the fasciolariid *Latirus rugosissimus* (Locard, 1897), North Atlantic, Recent (Kaim 2004: fig. 82B); B, the pholidotomid *Paleopsephaea* sp., G28202, Tamil Nandu, India, middle Cenomanian (Late Cretaceous); C, Muricoidea gen. et sp. indet., Poland, Valanginian (Early Cretaceous) (Kaim 2004: fig. 82A); D, maturifusid *Maturifusus conspicuus* (Eichwald, 1868), ZPAL Ga. 9/325, Poland, Callovian (Middle Jurassic); E, *Fossacerithium formosus* (Eichwald, 1868), Poland, Callovian (Middle Jurassic) (Kaim 2004: fig. 87B3); F, *Angularia pleurotomaria* (Münster, 1841), PZO 16376, South Tyrol (Italy), Carnian (Late Triassic); G, *Pseudotritonium sciaphosterum* (Batten & Stokes, 1986), Utah (United States), Early Triassic (Nützel 2010: fig. 5.2b). Arrows indicate protoconch margin. All figures are given at the same scale. Scale bar: 0.5 mm.

and *Cretadmete*), while the other (*Fossacerithium*) could be seen as an ancestral form of Neogastropoda.

The protoconch of the type species of *Pseudotritonium*, the type genus of Pseudotritoniidae, is unknown. However, the protoconch of the Early Triassic species *Pseudotritonium sciaphosterum* from the Moenkopi Formation of Utah (United States) is known

(Nützel 2010; Fig. 1.11 herein). This species resembles *P. venustum* in gross shell morphology and cancellate teleoconch ornament. Nevertheless, the protoconch of *P. sciaphosterum* appears to be more similar to that of some recent Triphoroidea (for instance as in the cerithiopsid Zaclys as depicted by Nützel 1998: pl. 2, fig. C) than to possible fossil ancestors of neogastropods or to their recent members. The protoconch of *P. sciaphosterum* is small (according to Nützel 1998 ca. three whorls 0.44 mm high and 0.27 mm wide). So, if both species of *Pseudotritonium* indeed belong to the same genus and/or family (that can be verified only if the protoconch of the type species will be found), evidence for a close relationship to the neogastropod lineage would be meager. It may also be speculated that heterobathy is observed here, where the larval stage exhibits plesiomorphic characteristics of an ancestral group, and the postmetamorphosis stage is apomorphic. Thus, the finding of the protoconch of *P. sciaphosterum* has added more controversy, because its morphology differs from those of members of the other families discussed earlier as well as from protoconchs of neogastropods.

In addition to their protoconch morphology (Fig. 1.11), the families in question differ from each other also in teleoconch characteristics. For instance, in the case of Maturifusidae the aperture is axially elongated with a rather long anterior canal (Fig. 1.2D, E), while Pseudotritoniidae have a wider aperture with a siphonal notch (Fig. 1.3). Members of Purpurinidae have a large, ovate holostomatous aperture in *Purpurina*. In *Khetella* and *Cretadmete*, the aperture is siphonostomatous with a short anterior channel and in *Fossacerithium* the anterior channel is well pronounced (Fig. 1.4).

Members of the families in question display also very uneven stratigraphic and geographic distribution. The majority of the Triassic records of Pseudotritoniidae and Purpurinidae come from the St. Cassian Formation which is result of the exceptional preservation of molluscs in these deposits, especially of small gastropods (see Roden et al. 2020). An exception is the oldest record of Pseudotritoniidae from the Early Triassic (Olenekian) of Utah (United States) (Batten & Stokes 1986; Nützel 2010). The oldest members of Purpurinidae were found in the Ladinian (Middle Triassic) and the last occurrence is known from the Albian (Early Cretaceous). Maturifusids appeared in the Early Jurassic (Late Pliensbachian) (Gründel 1999; Nützel & Gründel 2015; Schulbert & Nützel 2013) and became extinct by the end of the Late Jurassic, since the youngest record is known from the Early Kimmeridgian (Guzhov 2004). In addition to their uneven distribution, the number of their findings, even from rich tropical faunas like the one from the St. Cassian Formation, is extremely small. This could suggest, that they could have been top predators, what could explain their infrequent occurrence.

Therefore, based on the differences in shell morphology, especially on the aforementioned differences in protoconch morphology (Fig. 1.11), we consider all three families – Maturifusidae, Pseudotritoniidae, and Purpurinidae – as separate clades.

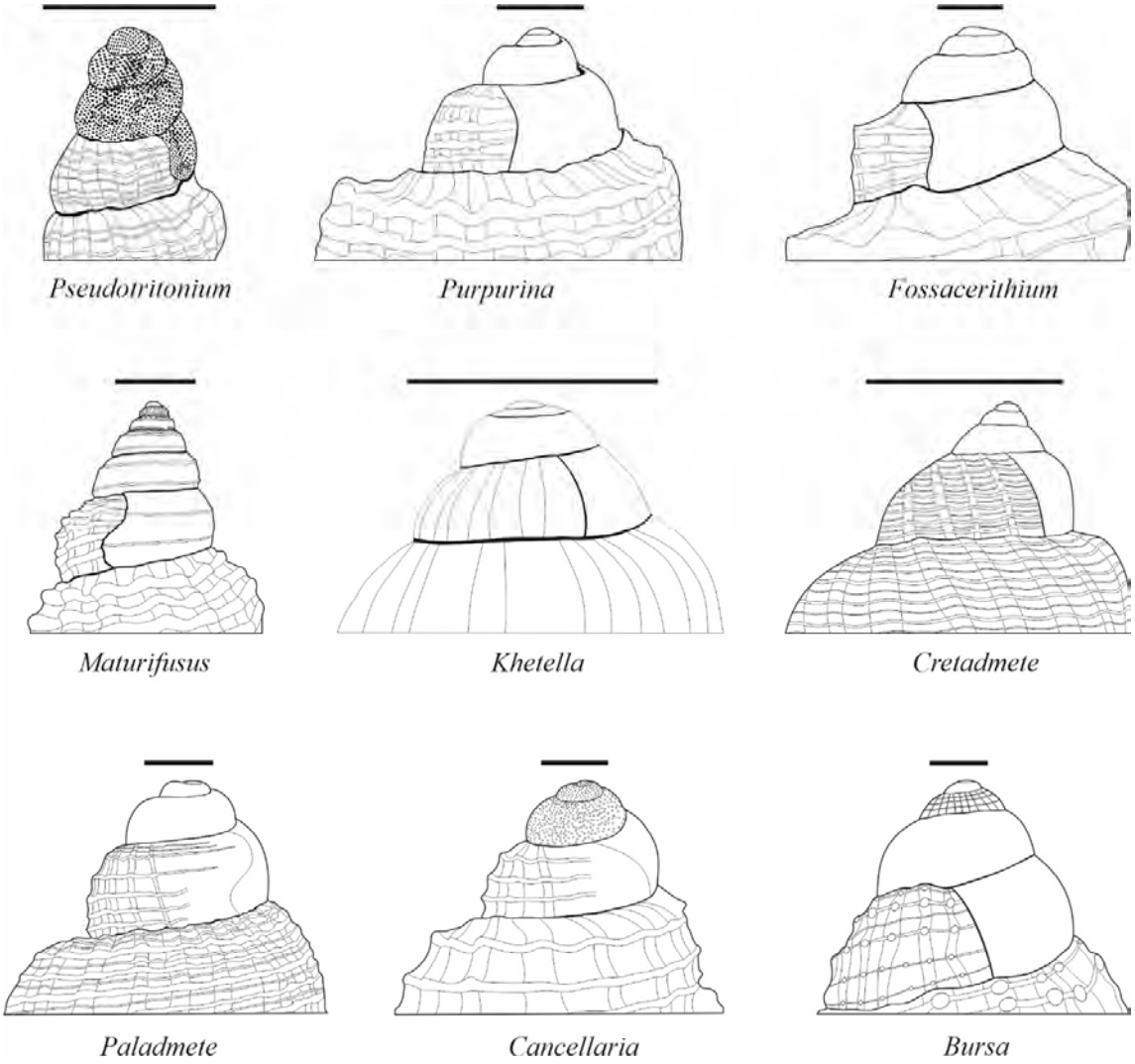

Fig. 1.11. — Main features of protoconch and early teleoconch in Pseudotritoniidae Golikov & Starobogatov, 1987, Maturifusidae Gründel, 2001, Purpurinidae Zittel, 1895, and crown Neogastropoda (Cancelariidae Forbes & Hanley, 1851) and Tonnoidea Suter, 1913 (1825) (Bursidae Thiele, 1925). Pseudotritonium Wenz, 1940 represented by P. sciaphosterum (Batten & Stokes, 1986) based on Nützel (2010) and unpublished photos. Purpurina d'Orbigny, 1850 based on P. coronata Hébert & EudesDeslongchamps, 1860 from Kaim (2004). Fossacerithium Gerasimov, 1992 based on F. formosum (Eichwald, 1868) from Kaim (2004). Maturifusus Szabó, 1983 based on unpublished photos of M. ticurelatus Gründel, 2001 from the Callovian of Łuków, Poland. Khetella Beisel, 1977 based on K. bojarkae Beisel, 1977 from Kaim & Beisel (2005). Cretadmete Blagovetshenskiy & Shumilkin, 2006 based on C. neglecta Blagovetshenskiy & Shumilkin, 2006 from Blagovetshenskiy & Shumilkin (2006). Paladmete Gardner, 1916 based on unpublished photos of P. laevis Sohl, 1964 from the Campanian of Coon Creek, United States. Cancellaria Lamarck, 1799 based on C. corrosa Reeve, 1856 from Petit & Harasewych (2013). Bursa Röding, 1798 based on B. granularis (Röding, 1798) from Sanders et al. (2017). Scale bars: 0.5 mm.

CONCLUSIONS

Three extinct families considered herein – Maturifusidae, Pseudotritoniidae, and Purpurinidae – differ in taxonomic richness, stratigraphic distribution and morphological characteristics, especially in the protoconch morphology, which is crucial for the identification of high level taxa. We conclude, that all three should be kept as separate clades.

The generic composition of each family has been reviewed. The monogeneric family Maturifusidae ranges from Early to Late Jurassic (Pliensbachian–Kimmeridgian) and is represented by the following species: *Maturifusus densicostatus, M. conspicuus, M. caseus, M. grimmensis, M. keyserlingianus, M. kostromensis, M. szaboi, M. ticurelatus, M.*? *nassoides, M.*? *piettei* and *M.*? *zeisei*. The monogeneric family Pseudotritoniidae ranges from Early to Late Triassic (Olenekian–Carnian) and includes species: *Pseudotritonium venustum*, P. laubei, *P. milierensis, P. sciaphosterum* and *P.*? *avena*. The family Purpurinidae ranges from Middle Triassic (Ladinian) to Early Cretaceous (Albian) and includes the following genera: *Angularia, Cretadmete, Fossacerithium, Khetella, Pseudoscalites,* and *Purpurina*. The genus Angularia includes the following Middle to Late Triassic (LadinianRhaetian) species: *A. subpleurotomaria, A. pleurotomaria, A. marginata, A. multinodosa, A. plicata, A. costata, A. rectecostata, A. corallina,* and *A. kittli* n. sp. The genus *Cretadmete* is represented by three Late Jurassic (Oxfordian) to Early Cretaceous (Albian) species: *C. neglecta, C. gracillima,* and *C. piccua*. Two species, namely *F. formosum* and *F. hypermeces,* should be attributed to the genus *Fossacerithium,* which ranges from Middle to Late Jurassic (CallovianKimmeridgian). Genus *Khetella* ranges from Middle Jurassic (Callovian) to Early Cretaceous (Albian) and includes *K. bojarkae, K. incerta, K. makaryevensis, K. septentrionalis* and *K. ventrosa*. The genus *Pseudoscalites* is represented by three Middle to Late Triassic (LadinianNorian) species: *P. elegantissimus, P. cochlea,* and *P. karapunari*. The species composition of *Purpurina* is not revised here as it requires further detailed study of this speciesrich genus and will be published elsewhere.

Angularia kittli n. sp. is described from the St. Cassian Formation and compared to other congeners found in the same formation, i.e., *A. subpleurotomaria* and *A. pleurotomaria*. The new species differs from the others in having a more pronounced axial ornamentation, which makes it similar to *Fossacerithium* from the Jurassic. However, the protoconch of *Angularia kittli* n. sp. is unknown, so that conclusions about its affinity requires confirmation by new specimens.

Fossacerithium, which originally was included into Procerithiidae by Gerasimov (1992), is confirmed to represent Purpurinidae.

Paleotriton macrostoma Kittl, 1894 from the Carnian (Late Triassic) of St. Cassian Formation classified so far as a species of *Pseudotritonium*, is reinterpreted here according to protoconch morphology and shell outline as the oldest record of *Purpurina* sensu stricto.

The morphological similarity between Jurassic purpurinids and recent tonnoids is suggestive of an evolutionary connection from the oldest species of *Khetella* and *Cretadmete* to the recent tonnoids, with the intermediate species of *Paladmete* from the Upper Cretaceous (Sohl 1964; Bandel & Dockery 2016) on the one hand and a number of tonnoid species from the Upper Cretaceous (Dockery 1993) and Eocene (Craig et al. 2020) on the other hand.

We also conclude that in the Jurassic, purpurinids were already divided into two groups. One of them, represented by *Khetella*, lead to Tonnoidea, while the other branch represented by *Fossacerithium*, could lead to Neogastropoda – a hypothesis, to be tested by future studies.

CHAPTER II

At the dawn of higher caenogastropods—the importance of colombellinid gastropods in deciphering the origin of Tonnoidea and Cypraeidae*

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ABSTRACT

Colombellinidae is an extinct family of marine gastropods occurring in carbonate facies from the Middle Jurassic to the lowermost Upper Cretaceous, primarily in Europe and rarely in Asia. Members of the family are characterized by thick, oval shells with a narrow aperture bearing anterior and posterior canals, a thickened peristome, and a denticulate outer lip. Colombellinids share several shell characters with representatives of Cypraeoidea, including a narrow, elongated aperture, but unlike cypraeids their shells are not convolute. Based on a comprehensive revision of all described species, the taxonomy of Colombellinidae is clarified and the family is restricted to only two genera: *Colombellina* d'Orbigny, 1842, and *Zittelia* Gemmellaro, 1869. One new species, *Colombellina crassigranulata* sp. nov., from the Upper Jurassic of Bulgaria, and one new genus, *Wadeina* gen. nov., from the Upper Cretaceous (Campanian) of Tennessee, USA—with a type species previously included in Colombellinidae but here assigned to the family Personidae (Tonnoidea)—are described. The distribution of the family and associated facies indicate a preference for shallow marine carbonate environments, while their low abundance may indicate a carnivorous mode of life. A comparison of Colombellinidae with Tonnoidea, Cypraeoidea, and Purpurinidae sheds a new light on the phylogenetic relationships of these groups and supports the interpretation of Colombellinidae as a stem or sister group of Cypraeoidea. This study contributes to a refined systematics of Jurassic–Cretaceous gastropods and provides new evidence for the early diversification of higher caenogastropods.

Key words: Colombellinidae, Jurassic–Cretaceous, taxonomy, phylogeny, reef ecosystems, palaeobiogeography.

INTRODUCTION

Colombellinidae Fischer, 1884, is an extinct family of gastropods occurring in Jurassic and Cretaceous calcareous sediments (Fig. 2.1), where their thick shells are frequently relatively well preserved. Colombellinids captured the attention of researchers in the mid-19th century due to their unusual morphology, displaying robust ornamentation and elongate siphonate apertures, as well as their similarity to neogastropods, stromboids, and tonnoids. Initially the family was considered as relatives of living Columbellidae Swainson, 1840 (Deshayes, 1853; Rolle, 1861; Pictet & Campiche, 1861–1864; Stoliczka 1867–1868), an extremely diverse family of small-sized, mostly epibenthic marine gastropods distributed worldwide, being most abundant in the tropics and with a Neogene fossil record. The placement of Columbellidae within Buccinoidea Rafinesque, 1815, and its monophyly, is supported by molecular data (Osca *et al.* 2015, deMaintenon & Strong, 2022).

Several different scenarios for the origin of the Colombellinidae were proposed in the past. The relationship of the Jurassic colombellinid genus *Zittelia* Gemmellaro, 1869, with Recent cypraeids was discussed by Sayn (1932). Taylor *et al.* (1980) included Colombellinidae in the Cassoidea (= Tonnoidea Suter, 1913 (1825)) and postulated their emergence from the Stromboidea Rafinesque, 1815, during the Jurassic. Colombellinidae were included in Stromboidea by Bouchet & Rocroi (2005) in the first edition of the gastropod nomenclator. Kollmann (2009: p. 60) disagreed with such a relationships of Colombellinidae, arguing that the origin of the family "is not known and the connection with the modern Stromboidea is not evident". Taylor & Morris (1988) considered Colombellinidae as the stem group of Cypraeoidea Rafinesque, 1815, and Tonnoidea, and as a close relatives of Purpurinidae Zittel, 1895. They also stated that the group is most closely related to Neogastropoda Wenz, 1938 (Taylor & Morris, 1988). Subsequently, Collombellinidae were placed among taxa of uncertain position within Latrogastropoda Riedel, 2000, in the second edition of the gastropod nomenclator by Bouchet *et al.* (2017). Uncertainties regarding the systematic position of the group are primarily caused by the lack of data on their protoconch morphology and the general rarity of group in the Jurassic and Cretaceous fossil record. Ponder and Lindberg (2020: p. 680) regard Colombellinidae as an "unplaced family" and noted that it was previously included in Stromboidea.

The aim of this contribution is to provide a revision of the family Colombellinidae, pending since the monograph of Wenz (1940). As a part of it, we re-figure and present re-descriptions of type material of Guirand & Ogérien (1865) and Zittel (1873) from the Upper Jurassic–Lower Cretaceous of France and Czechia, as well as a single colombellinid specimen from Stoliczka's collection from the Cretaceous (Cenomanian) of India (Stoliczka, 1867–1868).

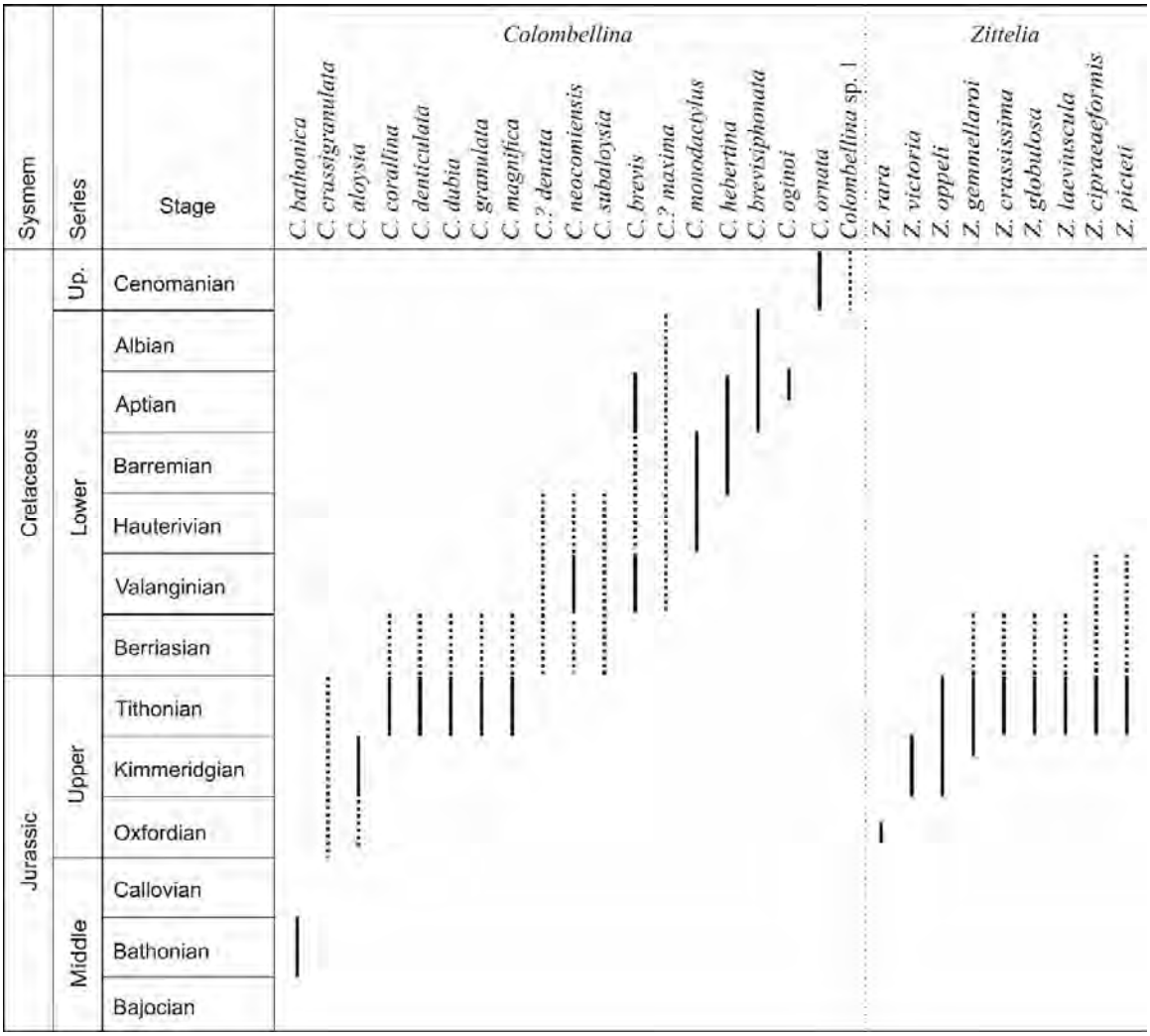

Fig. 2.1. — Stratigraphic ranges of the species of Colombellinidae. Solid lines indicate well constrained taxa ranges, while dashed lines are poorly constrained ranges.

We also present new materials from the Upper Jurassic (Tithonian) of Czechia, Upper Jurassic–Lower Cretaceous (Barremian–Aptian) of Bulgaria, and Upper Cretaceous (Campanian) of Tennessee, USA (Table 2.1). A comprehensive revision of the genus *Zittelia* is presented in a separate paper (Bakayeva *et al.* 2025). The new materials, along with the examination of the type materials, provide additional insights for the systematics and mutual relations of the taxa discussed herein.

Abbreviations:
GIYU – Geological Institute, Faculty of Education. Yokohama National University, Yokohama, Japan
GMH – Institute of Geology and Mineralogy, Faculty of Science at Hokkaido University, Sapporo, Japan
GSI – Geological Survey of India in Kolkata, India
MDC – Museum of Confluences in Lyon, France
MNHN LPMP – Muséum national d'Histoire naturelle, Laboratoire de Paléontologie, Paris, France
NMNHS – National Museum of Natural History, Bulgarian Academy of Sciences in Sofia, Bulgaria
SNSB-BSPG – Bavarian State Collection for Palaeontology and Geology in Munich, Germany

USNM – National Museum of Natural History, Department of Paleobiology, Smithsonian Institution, Washington DC, USA
VSB – Prof. Pošepný's Geological Pavilion, VSB – Technical University of Ostrava, Czechia
ZPAL – Institute of Paleobiology, Polish Academy of Sciences in Warsaw, Poland
H – shell height
H_{lw} –height of last whorl
W – shell width
W_{pr} – width of protoconch
SA – spire angle

MATERIALS AND METHODS

Colombellinidae have been described from several areas, with most records coming from Europe (Fig. 2.2). Two species have been reported from Japan (Nagao, 1934; Kase, 1984), and one, in open nomenclature, from India (Stoliczka, 1867–1868). Some species from North America have also been previously included into this family (Wade, 1926; Sohl; 1960, Dockery, 1993; Bandel & Dockery 2012).

This study is based on materials from archival collections stored at the Bavarian State Collection for Palaeontology and Geology in Munich, Germany (11 specimens from the Hohenegger collection studied by Zittel (1873) and one from the Wetzler collection), Museum of Confluences in Lyon, France (3 specimens from Guirand & Ogérien's collection), Prof. Pošepný's Geological Pavilion, VSB – Technical University, Ostrava, Czechia (2 specimens from PS collection), National Museum of Natural History, Bulgarian Academy of Sciences,

Fig. 2.2. — Spatial distribution of Colombellinidae. Material revised or studied herein is marked with asterisks.

Sofia, Bulgaria (3 specimens: one collected by R. Popov from the Barremian, one collected by B. Krumov from the Late Jurassic, and one collected by G. Shishkov from the Aptian), and

materials of Ferdinand Stoliczka, stored at the Geological Survey of India, Kolkata, India (one specimen, revisited in 2023 by S.B. and A.K.). Additional materials used come from the collections of Institute of Paleobiology, Polish Academy of Sciences, Warsaw, Poland (2 specimens), acquired during 2022 excavations in the type locality of Coon Creek Formation in Tennessee, USA (Table 2.1). We also reviewed all species within the family described so far.

Table 2.1. — New or revisited material discussed in the paper. Revisited type series are asterisked.

Stratigraphy	Locality	Species	Number of specimens	Specimen status and number
Upper Jurassic	Leskovets/Kopanitsa, Bulgaria	*Colombellina crassigranulata* sp. n.	1	NMNHS-20680 (holotype)
Kimmeridgian	Valfin, France	*Colombellina aloysia* Guirand & Ogérien, 1865*	3	MDC 20014048/1 (lectotype), 20014048/2, 3
Tithonian	Kotouč Quarry, Štramberk, Czechia	*Colombellina corallina* (von Quenstedt, 1852)	2	VSB GP 101101, 101102
Tithonian–Berriasian	Štramberk, Czechia	*Colombellina denticulata* (Zittel, 1873)*	4	SNSB-BSPG AS III 889, 890 (lectotype), 891, 892
		Colombellina dubia (Zittel, 1873)*	2	SNSB-BSPG AS III 893 (lectotype), 894
		Colombellina magnifica (Zittel, 1873)*	1	SNSB-BSPG AS III 888
	Koňákov (*Koniakau*), Czechia	*Colombellina denticulata* (Zittel, 1873)*	1	SNSB-BSPG AS III 908
		Colombellina granulata (Zittel, 1873)*	1	SNSB-BSPG AS III 895 (lectotype)
	Chotěbuz (Kotzobenz in Zittel 1873), Czechia	*Colombellina* sp. 2*	2	SNSB-BSPG AS III 911, 912
Middle Neocomian	Breiterberg, close to Bad Haslach, Germany	*Colombellina*? *maxima* de Loriol, 1861	1	SNSB-BSPG 1867 XII 530
Barremian	Veliko Tarnovo, Bulgaria	*Colombellina monodactylus* (Deshayes, 1842)	1	NMNHS-12538
Aptian	Veliko Tarnovo, Bulgaria	*Colombellina brevis* Pictet &Campiche, 1864	1	NMNHS-2780
Cenomanian	near Odiyam (Odium), Ootatoor (=Uttattur) group, India	*Colombellina* sp. 1*	1	GSI-577
Campanian	Coon Creek, USA	*Wadeina americana* (Wade, 1926)	2	ZPAL Ga.21/3, 4

The specimens from NMNHS, and VSB collections were coated with ammonium chloride and photographed in the photo laboratory of the Institute of Paleobiology PAS. SNSB-BSPG specimens were also coated with ammonium chloride and photographed by Katharina Peter (Bremen) in the course of an internship at SNSB-BSPG. MDC specimens were photographed by Didier Berthet using a Sony Alpha 7RV camera equipped with a 24×36 mm full-frame sensor and macro extension tubes (10 mm and 16 mm, depending on the specimen). The specimens from ZPAL collections were photographed with SEM in the Electron Microscopy and Electron Microprobe Laboratory of the Institute of Paleobiology PAS. GSI specimen was photographed by using a Nikon D-200 and a copy stand Kaiser RS 2 XA.

The preservation of shells varies depending on the lithological composition of the sediments. Thick collombellinid shells with robust ornamentation are well preserved in mixed siliciclastic-carbonate sediments. In sediments with a higher carbonate content, mainly moulds can be preserved e.g., de Loriol's material (de Loriol, 1861). Most specimens described herein have shells preserved by calcite-replacements of original aragonite, with some specimens from Zittel's (1873) material and the Indian specimen preserved as internal moulds.

HISTORICAL BACKGROUND

The taxonomic history of the family Colombellinidae is marked by a significant confusion, particularly due to the several spelling errors in the family and type genus names. During the long history of debate on its systematic position, the family Colombellinidae has been proposed to belong to several higher rank taxa ranging from Stromboidea to Buccinidae and Tonnoidea. Below, we provide a historical overview of the family Colombellinidae and discuss some colombellinid and colombellinid-like gastropods that have historically been associated with this group (Table 2.2).

Colombellinidae

The family Colombellinidae (= Columbellinidae in his spelling) was established by Fischer (1884: p. 657, text in brackets added by us), who noted that "this small family includes only fossils, which show affinities with Tritonidae on one hand, and Strombidae on the other, but not with Columbellidae [Swainson, 1840], despite the similarity in shape between the genus *Columbellina* [= *Colombellina* d'Orbigny, 1842] and *Columbella harpiformis* Sowerby [1832]. The posterior sinus of Columbellinidae [= Colombellinidae] is sometimes very oblique and resembles the sinus of *Pentadactylus* (*Ricinula* Lamarck [1816]) or some *Ranella* [Lamarck, 1816]. The aperture has some resemblance to that of *Persona* [Montfort, 1810 = *Distorsio* Röding, 1798]". Fisher included the following genera into the family: *Colombellina* d'Orbigny,

1842, *Columbellaria* Rolle, 1861, *Zittelia* Gemmellaro, 1869, *Petersia* Gemmellaro, 1869, and ?*Alariopsis* Gemmellaro, 1878. Later, Zittel (1895: p. 346) excluded *Alariopsis* from the family. Subsequently, Cossmann (1901, p. 230) designated the type species of *Colombellina*, *Columbellaria*, and *Zittelia* and simultaneously excluded these genera from the family Columbellidae, supporting Fischer's (1884) opinion on the systematic position of Colombellinidae between *Ranella* Lamarck, 1816, and *Cassis* Scopoli, 1777 i.e., within the tonnoideans. However, Cossmann (1904) soon changed his earlier opinion suggesting a placement "after winged shells and before cerithids", i.e., between aporrhaids and cerithiids. He excluded *Petersia* from the family Colombellinidae, leaving *Colombellina* (with subgenera *Columbellaria* and *Zittelia*), *Alariopsis*, and *Pterodonda* within it.

Wenz (1940: p. 926) considered Colombellinidae to be "the starting point" for Cypraeoidea and Tonnoidea, suggesting that *Zittelia* may have been the ancestral group of Cypraeoidea. Wenz's systematic review (1940) remains the most recent classification of the family Colombellinidae to date. The same generic composition of the family was reiterated by Pchelintsev & Korobkov (1960).

Colombellina d'Orbigny, 1842

The genus *Colombellina* was established by d'Orbigny (1842: p. 346) within the family Buccinidae Rafinesque, 1815. D'Orbigny (1842) provided the following diagnosis of *Colombellina*: "a thick, inflated oval shell with a narrow, curved aperture, often constricted in the middle, and a deep anterior part without a canal; the posterior part features an outwardly expanded canal; the outer lip is notably thickened in the middle; the columellar margin is also significantly thickened externally". The type species of *Colombellina* d'Orbigny, 1842, was originally described from the Hauterivian of France by Deshayes (*in* Leymerie 1842) as *Rostellaria monodactylus* and was intially placed within Aporrhaidae Gray, 1850. Later Deshayes (1853) placed it in *Columbella* Lamarck, 1799 (Buccinoidea Rafinesque, 1815) (Table 2.2). Geinitz (1845–1846) placed *Columbellina*, an unjustified emendation of *Colombellina* (d'Orbigny, 1842), within the family Buccinidae and compared it with *Columbella*, noting that its distribution is limited to the Cretaceous (Geinitz, 1845–1846: p. 377).

In his diagnosis of *Colombellina*, d'Orbigny (1842) included two species into the genus: *C. monodactylus* (Deshayes in Leymerie, 1842) and his new species *C. ornata* d'Orbigny, 1842. The shell morphology of both species was not accurately depicted in d'Orbigny's figures. Especially the length of the parietal canal seems to be much exaggerated (Kollmann, 2005: pl. 17, figs 4, 5). d'Orbigny (1842) also noted that the species of *Colombellina* rarely occur in the

Table 2.2. — List of species, which were originally or once included within Colombellinidae

Taxa name according to original description	Revised taxonomic name	Age	Location	Reference
	Colombellina crassigranulata sp. n.	Late Jurassic	Bulgaria	herein
Columbellaria bathonica Cossmann, 1899	*Colombellina bathonica* (Cossmann, 1899)	Bathonian	France	Cossmann 1899, 1913
Columbellaria Aloysia (Guirand et Ogérien)	*Colombellina aloysia* Guirand & Ogérien, 1865	Oxfordian?	Switzerland	de Loriol 1890
Columbellaria rara Gründel *et al*., 2022	*Zittelia rara* (Gründel *et al*., 2022)	middle Oxfordian	Switzerland	Gründel *et al*. 2022
Columbellina corallina Quenst.	*Colombellina corallina* (von Quenstedt, 1852)	Kimmeridgian	France	Etallon 1859
Columbellina Oppeli Et.	*Zittelia oppeli* (Etallon, 1859)			Etallon 1859
Columbellina Sofia (Guirand et Ogérien)	*Zittelia oppeli* (Etallon, 1859)			Guirand & Ogérien 1865, Ogérien 1867
Columbellina Victoria (Guirand et Ogérien)	*Zittelia victoria* (Guirand & Ogérien, 1865)			Guirand & Ogérien 1865, Ogérien 1867
Columbellina Aloysia (Guirand et Ogérien)	*Colombellina aloysia* (Guirand & Ogérien, 1865)			Guirand & Ogérien 1865, Ogérien 1867
Columbellaria Aloysia (Guirand et Ogérien)	*Colombellina aloysia* (Guirand & Ogérien, 1865)			de Loriol 1886-1888
Zittelia Victoria Guirand et Ogérien	*Zittelia victoria* (Guirand & Ogérien, 1865)			de Loriol 1886-1888
Zittelia Oppeli (Etallon)	*Zittelia oppeli* (Etallon, 1859)			de Loriol 1886-1888
Zittelia Victoria Guirand et Ogérien	*Zittelia victoria* (Guirand & Ogérien, 1865)			de Loriol 1886-1888
Columbellina (Columbellaria) Aloysia (Guir. et Ogér.)	*Colombellina aloysia* (Guirand & Ogérien, 1865)			Cossmann 1904, 1913
Columbellina (Zittelia) Oppeli (Etallon)	*Zittelia oppeli* (Etallon, 1859)			Cossmann 1904, 1913
Columbellina (Zittelia) Victoria (Guir. et Ogér.)	*Zittelia victoria* (Guirand & Ogérien, 1865)			Cossmann 1904, 1913
Columbellaria corallina (Quenstedt, 1852), *Columbellaria* sp. 1	*Zittelia gemmellaroi* Zittel, 1873	late Kimmeridgian	Germany	Gründel 2017, Gründel *et al.* 2019, Gründel & Nützel 2024
Columbellaria cf. *corallina* (Quenstedt, 1852)	*Zittelia gemmellaroi* Zittel, 1873	Kimmeridgian	Germany	Werner *et al.* 2017

Cassis corallina	*Colombellina corallina* (von Quenstedt, 1852)	Tithonian	Germany	Quenstedt 1852, 1858, 1884
Columbellaria corallina Quenstedt sp.	*Colombellina corallina* (von Quenstedt, 1852)			Brösamlen 1909
Zittelia globosa Brösamlen	*Zittelia globosa* Brösamlen, 1909			Brösamlen 1909
Colombellina corallina Quenstedt	*Colombellina corallina* (von Quenstedt, 1852)			Cossmann 1913
Columbellaria denticulata Zittel	*Colombellina denticulata* Zittel, 1873	Tithonian	France	Roman 1897
Zittelia Picteti Gemmellaro	*Zittelia picteti* Gemmellaro, 1869			Roman 1897
Zittelia oppeli (Et.)	*Zittelia oppeli* (Etallon, 1859)			Joukowsky, Favre 1913
Zittelia picteti G. Gemm.	*Zittelia picteti* Gemmellaro, 1869			Joukowsky, Favre 1913
Columbellaria denticulata Zittel	? *Colombellina denticulata* Zittel, 1873			Tsan-hsun 1931
Zittelia picteti Gemmellaro	? *Zittelia picteti* Gemmellaro, 1869			Tsan-hsun 1931
Columbellaria corallina Quenstedt sp.	*Colombellina corallina* (von Quenstedt, 1852)	Tithonian-Berriasian	Czechia and Poland	Rolle 1861
	Colombellina corallina (von Quenstedt, 1852)			herein
Zittelia crassissima Zitt.	*Zittelia crassissima* Zittel, 1873			Zittel 1873
Zittelia globulosa Zitt.	*Zittelia globulosa* Zittel, 1873			Zittel 1873
Columbellaria granulata Zitt.	*Colombellina granulata* (Zittel, 1873)			Zittel 1873
Zittelia Gemmellaroi Zitt.	*Zittelia picteti* Gemmellaro, 1869			Zittel 1873
Zittelia Picteti Gemm.	*Zittelia picteti* Gemmellaro, 1869	Tithonian-Valanginian	Sicily, Italy	Gemmellaro 1869
Zittelia cipraeaeformis Gemm.	*Zittelia cipraeaeformis* Gemmellaro, 1869			Gemmellaro 1869
Columbellaria denticulata Zitt.	*Colombellina denticulata* (Zittel, 1873)	Jurassic – Neocomian	Czechia	Zittel 1873
Columbellaria dubia Zitt.	*Colombellina dubia* (Zittel, 1873)			Zittel 1873
Columbellaria magnifica Zitt.	*Colombellina magnifica* (Zittel, 1873)			Zittel 1873
Colombellina maxima de Loriol, 1861	*Colombellina*? *maxima* de Loriol, 1861	Lower Cretaceous	Switzerland and France	Pictet & Campiche 1861-1864

Colombellina dentata Loriol, 1861	*Colombellina dentata* Loriol, 1861			de Loriol 1861
Fusus neocomiensis d'Orbigny	*Colombellina neocomiensis* (d'Orbigny, 1842)			de Loriol 1861
Colombellaria subaloysia Nov. sp.	*Colombellina subaloysia* (Péron, 1899)	Neocomian	France	Péron 1899
Columbellina neocomiensis d'Orbigny (sub Fusus)	*Colombellina neocomiensis* (d'Orbigny, 1842)			Péron 1899
Columbellina subaloysia Peron	*Colombellina subaloysia* Péron, 1899			Cossmann 1904
Columbellina brevis Pictet et Campiche	*Colombellina brevis* Pictet et Campiche, 1864	Valanginian	Switzerland	Pictet & Campiche 1861-1864
Columbellina neocomiensis Pictet et Campiche	*Colombellina neocomiensis* (d'Orbigny, 1842)			Pictet & Campiche 1861-1864
Colombellina maxima de Loriol, 1861	*Colombellina*? *maxima* de Loriol, 1861	Valanginian – Hauterivian	Austria	Kollmann 2002
Rostellaria monodactylus Desh.	*Colombellina monodactylus* (Deshayes, 1842)	Hauterivien	France	Deshayes in Leymerie 1842
Columbella monodactylus Desh.	*Colombellina monodactylus* (Deshayes, 1842)			Deshayes 1853
Colombellina monodactylus d'Orbigny	*Colombellina monodactylus* (Deshayes, 1842)			d'Orbigny 1842, Kollmann 2005
Fusus neocomiensis d'Orbigny, 1842	*Colombellina neocomiensis* (d'Orbigny, 1842)			d'Orbigny 1842, Kollmann 2005
Colombellina monodactylus Deshayes (sub Rostellaria)	*Colombellina monodactylus* (Deshayes, 1842)		France, Belgium	Péron 1899
Colombellina maxima de Loriol, 1861	*Colombellina*? *maxima* de Loriol, 1861	Barremian	France	de Loriol 1861
Zittelia gymna n. sp.	*Liocarenus*? *gymna* (Cossmann, 1916)			Cossmann 1916, Gründel & Kollmann 2013
Columbellina obsoleta n. sp.	Aporrhaidae?			Cossmann 1916
Colombellinidae gen. et sp. indet.	Neogastropoda?			Gründel & Kollmann 2013
	Colombellina monodactylus (Deshayes, 1842)		Bulgaria	herein

Columbellina Hebertina de Loriol	*Colombellina hebertina* de Loriol, 1866	Barremian – Aptian	France	de Loriol 1866
Zittelia drumensis (nov. sp.)	*Zittelia drumensis* Sayn, 1932			Sayn 1932
Columbellaria cf. *subaloysia* Peron	*Colombellina* cf. *subaloysia* Péron, 1899			Sayn 1932
Columbellina brevisiphonata nov. sp.	*Colombellina brevisiphonata* Nagao, 1934	Aptian – Albian	Japan	Nagao 1934, Hayami & Kase 1977, Kase 1984
	Colombellina brevis Pictet et Campiche, 1864	Aptian	Bulgaria	herein
Columbellina Verneuili nov. sp.	Aporrhaidae		Spain	Cossmann 1904
Colombellina (Colombellina) oginoi Kase, sp. nov.	*Colombellina oginoi* Kase, 1984		Japan	Kase 1984
Columbellina Dupini d'Orb.	*Iscafusus dupinianus* (d'Orbigny, 1842)	Albian	Crimea	Pchelintsev 1927
Columbellina fusiformis nov. sp	Fasciolariidae		Egypt	Douvillé 1916
Pterodonta sp.	Incertae sedis	Albian – Cenomanian	Austria	Kollmann 1978
Colombellina ornata d'Orbigny	*Colombellina ornata* d'Orbigny, 1842	Cenomanian	France	d'Orbigny 1842, Kollmann 2005
Columbellaria cf. *tuberculosa* (Binkhorst, 1861)	*Colombellina ornata* d'Orbigny, 1842		Germany	Kiel & Bandel 2004
Columbellina sp.	*Colombellina* sp.		Southern India	Stoliczka 1867, herein
Pterodonta deffisi Thomas & Peron, 1889	Tylostomatidae		Jordan	Berndt 2004
Pterodonta cf. *subinflata* Coquand, 1862	Tylostomatidae			Berndt 2004
Pterodonticeras germeri Blanckenhorn, 1927	Incertae sedis			Berndt 2004
Columbellina fusiformis Douville, 1916	Aporrhaidae?			Berndt 2004
Pterodonta deffisi Thomas & Peron, 1889	Tylostomatidae		Egypt	Mekawy 2007
Columbellina (Columbellina) fusiformis Douville, 1916	Non Colombellinidae			Mekawy 2007
Colombellina sp.	Incertae sedis		Western Ukraine, Moldova	Bakayeva 2011, Plamadeala 1999
Pterodonta elongata d'Orbigny, 1842	*Eopterodonta elongata* (d'Orbigny, 1842)		Serbia	Ayoub-Hannaa *et al.* 2015
Pterodonta inflata d'Orbigny, 1842	*Eopterodonta inflata* (d'Orbigny, 1842)			Ayoub-Hannaa *et al.* 2015

Columbellina fusiformis Douville, 1916	Fasciolariidae	Cenomanian – Turonian	Egypt	Ayoub-Hannaa & Fürsich 2011
Colombellina contorta Sowerby	*Pugnellus contortus* (Sowerby, 1846)	Senonian	SE India	d'Orbigny 1850
Colombellina uncata Forbes	*Pugnellus uncatus* Forbes, 1846			d'Orbigny 1850
Columbellina americana Wade sp. n.	*Wadeina americana* (Wade, 1926)	Campanian		Wade 1926, Sohl 1960, Bandel & Dockery 2012, herein
Colombellina cancellata n. sp.	*Neocolombellina cancellata* (Dockery, 1993)		SE USA	Dockery 1993, Bandel & Dockery 2012
Sassia carlea n. sp.	*Neocolombellina carlea* (Dockery, 1993)			Dockery 1993, Bandel & Dockery 2012
Columbellaria laevicostata sp. n.	Non Colombellinidae		Poland	Abdel-Gawad 1986
'Colombellaria' (sic!) sp. (A) *'Columbellaria'* sp. (B)	Non Colombellinidae		Germany	Pietzonka *et al.* 2024
Pterodonta ovata d'Orbigny, 1842	*Eopterodonta ovata* (d'Orbigny, 1842)	Maastrichtian		
Pterodonta deffisi Thomas e Peron	Tylostomatidae		Libia	Rossi Ronchetti 1959
Pterodonticeras dutrugei (Coquand)	Aporrhaidae?			
Columbellaria tuberculosa Binkhorst sp.	Neogastropoda		Germany	Kaunhowen 1897
Columbellaria granulata nov. sp.	Non Colombellinidae			
Columbellaria tuberculosa (Binkhorst, 1861)	Non Colombellinidae		Poland	Abdel-Gawad 1986
Columbellaria cf. *granulata* Kaunhowen, 1897	Non Colombellinidae			
Columbellaria tuberculosa (Binkhorst, 1861)	Neogastropoda		Western Ukraine	Bakayeva 2011
Columbellaria tuberculosa (Binkhorst, 1861)	Non Colombellinidae		Belgium	Hansen 2019

Cretaceous. He transfered two more species from the Senonian of India into the genus: *C. contorta* (Forbes, 1846) and *C. uncata* (Forbes, 1846), initially placed within *Strombus* Linnaeus, 1758. Later, these species were re-described by Stoliczka (1867–1868) and included into the stromboid genus *Pugnellus* Conrad, 1860.

De Loriol (1861) added two new species to *Colombellina*—*C. dentata* de Loriol, 1861 and *C. maxima* de Loriol, 1861—from the Neocomian of Mont Salève, France. However, the specimens used for the establishment of these species are preserved as internal moulds, so their attribution to the genus is questionable and requires revision of the original material. De Loriol (1866) subsequently added *C. hebertina* to *Colombellina*.

Pictet (1855; 1853–1857) primarily listed only the species of *Colombellina* documented earlier from the Cretaceous by d'Orbigny (1842). In a subsequent publication (Pictet & Campiche, 1861–1864) two new species—*Colombellina brevis* and *C. neocomiensis*—and one previously known—*C. maxima*—were re-described. Pictet & Campiche (1861–1864) also provided a list of Cretaceous species of *Colombellina*, which included four Neocomian (*C. brevis, C. maxima, C. monodactylus, C. neocomiensis*), one Cenomanian (*C. ornata*) and two Senonian species (*C. contorta, C. uncata*). Pictet & Campiche (1861–1864) shared Rolle's (1861) view on the relation of *Colombellina* with recent *Columbella* and its placement within Buccinidae. They also observed that in some species of *Colombellina*, a true anterior canal closely resembles that of muricid gastropods. The morphology of this canal was therefore interpreted as subjected to large intrageneric variability allowing for placing *Colombellina* to another family. Pictet & Campiche (1861–1864) noted a resemblance of species of *Colombellina* to those of the Ranellidae Gray, 1854 (Tonnoidea), due to the presence of the parietal canal, which is more elongated in the species of *Colombellina* than in ranellids, and to the presence of varices in some species (Pictet & Campiche, 1861–1864: p. 665).

Three new Kimmeridgian (Upper Jurassic) species of *Colombellina—C. aloysia, C. sofia,* and *C. victoria*—were described from France by Guirand & Ogérien (1865). This material was subsequently re-described by de Loriol (1886–1888) and de Loriol & Koby (1890), and has also been examined in our study on *Zittelia* (Table 2.1; Bakayeva *et al.* 2025).

Stoliczka (1867–1868) placed *Colombellina* within Columbellidae (Buccinoidea), discussing the relationship of the family with other taxa and noting that Cretaceous species are most closely allied to some tropical modern forms due to their long posterior canal. He found one specimen he attributed to *Colombellina*, but due to its poor preservation, described it in open nomenclature (Stoliczka 1867–1868: p. 139, pl. 12, fig. 1). The material of Stoliczka was re-investigated by A.K. and S.B. in 2023, and is re-figured herein (see below). This species appears to be the first and only specimen of Colombellinidae known from India so far.

Péron (1899) provided descriptions of two previously known species of *Colombellina* from the Neocomian of France—*C. monodactylus* and *C. neocomiensis*. The quantity and preservation of the material allowed him to assert that *Colombellina neocomiensis* and *Fusus*

neocomiensis are the same species, thereby resolving the uncertainty regarding their identity previously discussed by Pictet & Campiche (1861–1864).

Cossmann (1904) added a new species to *Colombellina—C. verneuili* from the Aptian of Spain, which almost certainly is an aporrhaid, showing similarity to the *Columbellina* (sic!) *fusiformis* described later by Douvillé (1916) and likely belonging to the same genus. Cossmann (1904) questioned the presence of convincing characteristics to distinguish the genera *Columbellaria* and *Zittelia* as separate taxa and therefore assigned them as subgenera of the genus *Colombellina*. Subsequently Cossmann (1913) noted that *Colombellina* sensu stricto was recorded only from the Lower Cretaceous, while *Columbellaria* and *Zittelia* occur in the Upper Jurassic. He re-described (Cossmann, 1913) previously known Jurassic species of *Colombellina—C. (Columbellaria) bathonica, C. (Columbellaria) corallina, C. (Columbellaria) aloysia, C. (Zittelia) oppeli*, and *C. (Zittelia) victoria*. Cossmann (1916) described a new species from the Lower Cretaceous (Barremian) of Orgon, France, *Colombellina obsoleta*, which resembles the earlier described *C. verneuili* (Cossmann 1904) and most likely is an aporrhaid. It is interesting to note that in the later work Cossmann (1916) did not adhere to his previously proposed (Cossmann, 1913) taxonomy of *Colombellina*, which featured a division into subgenera, including *Columbellaria* and *Zittelia* as subgenera of *Colombellina*.

Wenz (1940) disagreed with Cossmann's (1904) assertion regarding the placement of *Zittelia* as a subgenus within *Colombellina*. Instead, he classified only *Columbellaria* as a subgenus within *Colombellina*, while *Zittelia* was reinstated as separate genus along with *Alariopsis*, *Pterodonta*, and *Pterodonticeras* within Colombellinidae, although for the latter two with reservations. Some authors (Rossi Ronchetti, 1959; Kollmann, 1978; Berndt, 2004) identified *Pterodonta* and *Pterodonticeras* as colombellinids, despite Wenz's (1940) reservations about their systematic position and the notable differences in shell shape, particularly in the morphology of the aperture. Recently, Pacaud (2023) proposed a replacement name for *Pterodonta* d'Orbigny, 1842 (preoccupied)—*Eopterodonta*—and justified placing the genus within Tylostomatidae Stoliczka, 1868–1868 (Campaniloidea Douvillé, 1904).

Pchelintsev (1927) described *Colombellina dupini* from the Albian of Balaklava (Crimea, Ukraine) based on two internal moulds. Moreover, this name is an unjustified emendation of *Fusus dupinianus* d'Orbigny, 1842. According to Kollmann (2005: p. 145) this species belongs to his new genus *Iscafusus* within Fasciolariidae Gray, 1853 (Neogastropoda).

Nagao (1934) described *Colombellina brevisiphonata* from the Aptian (Lower Cretaceous) of Honshu (Japan). The same specimen (pers. comm. with Tomoki Kase in 2024) was subsequently re-described by Kase (1984), who also recorded an additional new species, *C. oginoi* Kase, 1984.

Kollmann (2002) recorded *Colombellina maxima* de Loriol, 1861, from the Valanginian–Hauterivian (Lower Cretaceous) of Haslach (Vorarlberg, Austria). One of the specimens described by Kollmann (2002), housed in the collection of the SNSB-BSPG, has also been re-examined in the present study (see below). Unlike the material described by de Loriol (1861) and Pictet & Campiche (1861–1864), the specimens of Kollmann (2002: pl. 2, figs 23, 24) have preserved shells with some visible spiral striation. However, the detailed morphology of the aperture and the ornamentation of the spire are not preserved, making the assignment of the species to *Colombellina*, and even to the family Colombellinidae, rather uncertain.

In North America, *Colombellina* and similar gastropods were documented only in the Upper Cretaceous. Wade (1926) described a new species—*Columbellina* (sic!) *americana*—from the Campanian of Tennessee. Sohl (1960) questionably left *C. americana* in *Colombellina*, noting that it is more similar to *Columbellaria* due to the shorter posterior canal. Later, Dockery (1993) described *Colombellina cancellata*, also from the Campanian of Mississippi. This species was later designated as the type species of the new genus *Neocolombellina* established by Bandel & Dockery (2012: p. 102) and assigned to the family Colombellinidae. In addition to the type species, they included two further species in the genus: *N. americana* (Wade, 1926) and *N. carlea* (Dockery, 1993). However, Riedel (2000) noted that Dockery's (1993) suggestion of a systematic relationship of *C. cancellata* to colombellinids is unclear and that even the knowledge of its protoconch does not facilitate a clarification because it is "seemingly uncharacteristic" (Riedel, 2000: p. 167). Bandel & Dockery (2016: p. 51) returned to the combination *Colombellina americana* and remarked that *C. cancellata* "resembles a sculptured *Erato* [Eratoidae Gill, 1871] in shape".

Columbellaria Rolle, 1861

Genus *Columbellaria* was erected by Rolle (1861), based on a single species, *C. corallina* (Quenstedt, 1852), which was described from Upper Jurassic shallow water carbonate deposits of Nattheim, Germany, and Štramberk, Czechia. Shortly before, this species was ascribed by Étallon (1859) to the genus *Colombellina*, erroneously adopting the spelling of the genus as *Columbellina*, as previously used by Geinitz (1845–1846). This incorrect spelling was later followed by several other authors (Rolle, 1861; Pictet & Campiche, 1861–1864; Guirand & Ogérien, 1865; Stoliczka, 1867–1868; de Loriol, 1866; Zittel, 1873, 1903; Péron, 1899; Cossmann, 1901, 1904, 1913; Douvillé, 1916; Wade, 1926; Pchelintsev, 1927; Nagao, 1934; Ayoub-Hannaa & Fürsich, 2011; Berndt, 2004). De Loriol (1886–1888) compared three specimens from the Étallon (1859) collection, identified as *C. corallina*, with *C. aloysia* from

the Guirand & Ogérien (1865) collection. He concluded that these specimens represent the same species—*C. aloysia*. The current repository of the Étallon (1859) collection remains unknown.

Rolle (1861) justified changing the genus name of *Colombellina* (d'Orbigny 1842), replacing it with *Columbellina* and sought to organize previously described species by discussing the relationships between *Columbella*, *Colombellina*, and *Columbellaria*. He regarded these genera as closely related based on morphological similarities, particularly in the aperture characters. Rolle (1861: p. 269) proposed that the lineage of Colombellinidae leads, from *Columbellaria corallina* as the oldest Jurassic taxon through the Cretaceous *Colombellina*, to the recent *Columbella*. He attributed the absence of transitional forms in the Oligocene and Eocene to the incompleteness of the fossil record. However, Quenstedt (1884: p. 685) expressed the opinion that the type species of *Columbellaria, Cassis corallina,* bears a closer resemblance to Tonnoidea and stated that its grouping with *Columbella* by Rolle (1861) was not wrong.

Zittel (1873) compared members of *Colombellina*, *Columbellaria*, and *Zittelia*, noting both their similarities and differences. He considered Rolle's (1861) justification for establishing the genus *Columbellaria* to be unclear and presented his own interpretation of species classification within these genera. Additionally, Zittel (1873) described four new species of *Columbellaria—C. magnifica*, *C. denticulata*, *C. dubia*, and *C. granulata*—from the Tithonian–Berriasian of Štramberk, Czechia. The Hohenegger collection studied by Zittel (1873) is housed in the Bavarian State Collection for Palaeontology and Geology in Munich, Germany.

Subsequently, Péron (1899) described a new species of *Columbellaria—C. subaloysia*—recorded from the Neocomian of Volvent, France.

Cossmann (1899) documented the oldest known species of Colombellinidae, *Columbellaria bathonica*, from the Bathonian of Saint-Gaultier, Indre, France.

Brösamlen (1909) provided a renewed description of *Columbellaria corallina*, which he considered, following Quenstedt (1884), as the possible earliest ancestor of Cassidae Latreille, 1825. Tsan-hsun (1931) recorded *Columbellaria denticulata* Zittel, 1873, from southern France although the available images do not provide a view of the aperture, and the descriptions also lack any information about the morphology of the aperture. *Columbellaria* cf. *subaloysia* was documented as well from the Barremian–Aptian (Urgonian) limestones of the surroundings of Barcelonne, France by Sayn (1932).

Kiel & Bandel (2004) identified *Columbellaria* cf. *tuberculosa* (Binkhorst, 1861) from the Cenomanian (Upper Cretaceous) of the Kassenberg quarry (Mühlheim, Germany).

Gründel *et al.* (2019) synonymized *Zittelia* with *Columbellaria. Gründel et al. (2022)* described a new species, *Columbellaria rara*, from the middle Oxfordian coral-reef limestones of St-Ursanne, Switzerland, which we assign to *Zittelia* (Bakayeva *et al.* 2025). Additionally,

Gründel *et al.* (2019) and Gründel & Nützel (2024) identified as *Columbellaria* several specimens from the Kimmeridgian of Saal near Kelheim (Bavaria, Germany), which we also assigned to *Zittelia* (Bakayeva *et al.* 2025).

Several species from the Campanian–Maastrichtian (Upper Cretaceous) of Europe have been assigned to the genus *Columbellaria*, including *C. tuberculosa* (Binkhorst, 1861), *C. granulata* Kaunhowen, 1897, and *C. laevicostata* Abdel-Gawad, 1986 (Table 2.2). Binkhorst (1861) originally included *C. tuberculosa* in *Pyrula* Lamarck, 1799—unaccepted name of *Ficus* Röding, 1798, a genus that is currently placed in Ficidae Meek, 1864 (1840). Kaunhowen (1897: p. 78) transferred this species to *Columbellaria* and classified it within the family Columbellidae. He illustrated the aperture of *C. tuberculosa* with a thickened peristome and folds on the outer and columellar lips (Kaunhowen, 1897: pl. 9, fig. 7, 8). *Columbellaria granulata* was illustrated by Kaunhowen (1897: pl. 9, fig. 5, 6) with only the outer lip preserved, which also exhibits folds. However, all these species are based on materials consisting mostly of composite moulds with aperture features rarely preserved, thus their revision is pending.

Cypraea Linnaeus, 1758

Sayn (1932) discovered shells similar to modern *Cypraea* from the Barremian–Albian (Lower Cretaceous) limestones in the surroundings of Barcelonne (France), which he used to describe a new species—*Cypraea antiqua*. He considered this species to be the earliest known member of *Cypraea*, although the oldest record of cypraeids dates back to the Tithonian–Valanginian of Sicily, Italy, as documented by Di Stefano (1882) and reviewed by Nützel *et al.* (2025). Sayn (1932) discussed possible common origin of *Cypraea* and *Colombellina*. He noted particular similarity to the species of *Zittelia* noting some degree of similarity of its ventral side to *Cypraea*. Sayn (1932) also observed certain differences between *C. antiqua* and the type species of *Cypraea*, *C. tigris* Linnaeaus, 1752. Consequently, he proposed a new generic name *Palaeocypraea* (Sayn, 1932: p. 30), unaware that the name was a homonym and had previously been assigned to a group of Paleocene species by Schilder (1928). The relationship of *C. antiqua* with recent members of *Cypraea* as well as with *Palaeocypraea* is pending a careful revision.

Other taxa

Some other gastropods identified as colombellinids were documented from the Cretaceous by Abdel-Gawad (1986), Bakayeva (2011), Hansen (2019), and Pietzonka *et al.* (2024). They differ greatly from the type species in shell shape and ornamentation and do not belong to Colombellinidae.

SYSTEMATIC PALAEONTOLOGY

Superorder Latrogastropoda F. Riedel, 2000

Taxa of Uncertain Position

Family Colombellinidae Fischer, 1884 (= Columbellariidae Zittel, 1895;

= Zitteliidae Schilder, 1936)

Type genus: *Colombellina* d'Orbigny, 1842

Emended diagnosis. Thick oval shell with low spire ornamented with spirals and axial ribs; last whorl large, inflated; peristome siphonostomatous, thickened; aperture narrow, elongated and curved with anterior and posterior canals; columellar lip with plaits or notch; outer lip denticulate with thickened edge.

Genera included. Colombellina d'Orbigny, 1842, and *Zittelia* Gemmellaro, 1869.

Remarks. As outlined in the historical background above, the family name (and its type species) was commonly misspelled by replacement of the second letter 'o' with 'u', thus replacing Colombellinidae with Columbellinidae, that was previously discussed by Riedel (2000). This confusion was caused initially by Geinitz (1845–1846) and later by Rolle (1861), who unjustifiably emended d'Orbigny's (1842) name *Colombellina* to *Columbellina*. We assume that it was due to the superficial similarity of *Colombellina* and *Columbella* and the initial inclusion of both genera within buccinids. In some cases, the type species of *Colombellina* was even included in *Columbella* (e.g. Deshayes, 1853). Here we follow the spelling of the family name and its authorship as given in Bouchet *et al.* (2017).

The family was established by Fischer (1884: p. 657) and originally spelled Columbellinidae, reflecting an unjustified emendation of the name of the type genus *Colombellina* d'Orbigny, 1842. Fischer (1884) included in Columbellinidae fossil gastropods with "thick generally cancellate shell, rough, subvaricose, tuberous; very narrow aperture; short anterior canal; posterior canal oblique, more or less long; thick outer lip; columella callous" and denied their relationship with *Columbella*.

Zittel (1895: p. 346) also provided the family diagnosis, indicating Fischer (1884) as the author of the family Columbellariidae, though Fischer (1884) had actually established the family Columbellinidae. Thus, the authorship of Columbellariidae should be attributed to Zittel (1895) (see Bouchet *et al.* 2017: p. 74).

Diagnoses of the family also were provided by Cossmann (1904), Wenz (1940) and Bandel (2007). Cossmann (1904) fixed the incorrect family name as Columbellinidae after Fischer (1884) and fixed type species for the genera *Colombellina, Columbellaria,* and *Zittelia* (Cossmann, 1901), and later also for other genera he included into the family (Cossmann, 1904).

The correct spelling of the family as Colombellinidae was first presented by Wenz (1940) who included the following genera into the family: *Colombellina* d'Orbigny, 1842 (with *Columbellaria* Rolle, 1861 as subgenus), *Zittelia* Gemmellaro, 1869, *Alariopsis* Gemmellaro, 1878, *Pterodonta* d'Orbigny, 1842, and ?*Pterodonticeras* Blanckenhorn, 1927. Wenz's (1940) work is the latest exhaustive review of the family to date. However, an unjustified emendation of the spelling of the type genus as *Columbellina* rather than *Colombellina* occasionally appears in the subsequent literature (Berndt, 2004; Ayoub-Hannaa & Fürsich, 2011).

We argue below that only two genera, *Colombellina* d'Orbigny, 1842, and *Zittelia* Gemmellaro, 1869, should be retained in the family Colombellinidae. Other genera included into this family by both Fischer (1884) and Wenz (1940) do not correspond to the diagnosis of the family, particularly in respect to the characteristic aperture morphology.

Stratigraphic and geographic occurrence. Bathonian (Middle Jurassic) – Cenomanian (Late Cretaceous) of Euroasia (Italy, France, Switzerland, Austria, Belgium, Germany, Bulgaria, Czechia, Poland, India, and Japan).

Genus *Colombellina* d'Orbigny, 1842 (= *Columbellaria* Rolle, 1861)

Type species. *Rostellaria monodactylus* Deshayes *in* Leymerie, 1842; subsequent designation, Cossmann, 1901, Cretaceous, France.

Emended diagnosis. Thick oval shell with low spire, ornamented with spiral cords and axial ribs; last whorl large and inflated, with axial ribs either disappearing towards aperture or completely absent; peristome siphonostomatous, thickened; aperture narrow and curved; anterior canal weakly developed; posterior canal elongated; columellar lip with folds, expanded, which can be either tightly adjacent to the last whorl or retreat from edge, often allowing the ornament of the last whorl to be visible through it; outer lip denticulate with a thickened edge and bent outward.

Species included. Colombellina monodactylus (Deshayes *in* Leymerie, 1842), *C. aloysia* Guirand & Ogérien, 1865, *C. bathonica* (Cossmann, 1899), *C. brevis* Pictet & Campiche, 1864, *C. brevisiphonata* Nagao, 1934, *C. corallina* (von Quenstedt, 1852), *C. crassigranulata* sp. n., *C. denticulata* (Zittel, 1873), *C. dubia* (Zittel, 1873), *C. granulata* (Zittel, 1873), *C. hebertina* de Loriol, 1866, *C. magnifica* (Zittel, 1873), *C. neocomiensis* (d'Orbigny, 1842), *C. oginoi* Kase, 1984, *C. ornata* d'Orbigny, 1842, *C. subaloysia* (Péron, 1899), *Colombellina* sp. 1 sensu Stoliczka, 1867–1868, *Colombellina* sp. 2 sensu Zittel, 1873. Species *C.*? *dentata* de Loriol, 1861 and *C*? *maxima* de Loriol, 1861 can be attributed to *Colombellina*, however, the original material is pending a revision.

Remarks. Rolle (1861) erected a new genus, *Columbellaria*, noting its similarity to *Colombellina* and its possible relations to *Columbella*. Apparently, the main reason for distinguishing this new

taxon was the stratigraphic difference, as d'Orbigny (1842) described *Colombellina* from the Early Cretaceous (Neocomian), while Rolle's (1861) material was from the Jurassic. After analysing all available published material and type species of these two genera, we failed to find any diagnostic characters differentiating them, and *Columbellaria* Rolle, 1861, should be treated as a junior subjective synonym of *Colombellina* d'Orbigny, 1842.

Stratigraphic and geographic occurrence. Bathonian (Middle Jurassic) – Cenomanian (Upper Cretaceous of France, Switzerland, Austria, Belgium, Germany, Bulgaria, Czechia, Poland, India, and Japan.

Colombellina monodactylus (Deshayes *in* Leymerie, 1842)

Figure 2.3

1842 *Rostellaria monodactylus* Deshayes *in* Leymerie, p. 14, pl. 17, fig. 15.

1842 *Colombellina monodactylus* d'Orb.; d'Orbigny p. 347, pl. 226, figs 2–5.

1850 *Colombellina monodactylus* d'Orb.; d'Orbigny p. 72.

1853 *Columbella monodactylus* Deshayes; Deshayes, p. 73, pl. 120, fig. 14.

1855 *Columbellina monodactylus* Deshayes; Pictet, p. 248, pl. 66, fig. 18.

1899 *Colombellina monodactylus* Deshayes (sub *Rostellaria*); Péron, p. 140.

1940 *Colombellina* (*Colombellina*) *monodactylus* d'Orb.; Wenz, p. 926, fig. 2711.

2005 *Colombellina monodactylus* (Deshayes *in* Leymerie, 1842); Kollmann, p. 151, pl. 17, fig. 4.

Holotype. Pl. 17, fig. 15 in Leymerie (1842).

Material. One specimen (NMNHS-12538) from the Barremian (Lower Cretaceous) of Veliko Tarnovo, Bulgaria.

Description. Shell partly preserved, thick, oval, relatively high-spired; apex not preserved; teleoconch consists of 3.5 convex whorls increasing rapidly in size and separated by moderately

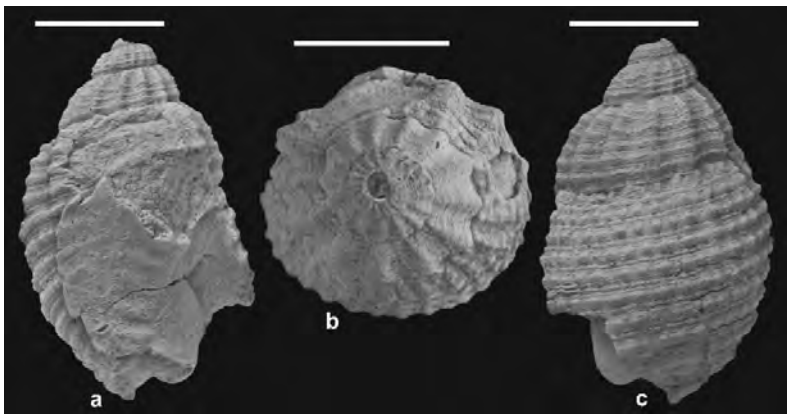

Fig. 2.3. — *Colombellina monodactylus* (Deshayes *in* Leymerie, 1842) from the Barremian; Veliko Tarnovo, Bulgaria. A–C, NMNHS-12538. A, apertural view, B, apical view, C, abapertural view. Scale bars represent 5 mm.

incised suture; shell surface sculptured by strong, opisthocline, round axial ribs (14 on the penultimate whorl), which reach sutures; axial ribs covered by nodose spiral cords of different thickness; last whorl large, partly preserved, with height of about four-fifths of shell height; the ornamentation on the last whorl differs from that on the spire—the spirals become more massive, with one or more thinner spirals occurring in the interspaces, while the axial ribs become less pronounced and gradually change into rows of rounded nodes, numbering five with two smaller adapical rows; the nodes on the rows situated at a distance slightly larger than their diameter; the nodose spirals occur in the interspaces between the rows and their number increases abapically; ornamentation of the base same as on last whorl; aperture and outer lip broken; inner lip not complete in parietal part and strongly spread over the base with five wide folds on the preserved part of the lip.

Measurements (mm):

Specimen number	H	W	SA
NMNHS-12538	12.7	9.3	70°

Remarks. Colombellina monodactylus, the type species of the genus *Colombellina*, is known from the Neocomian of France (Leymerie, 1842; d'Orbigny, 1842; Kollmann, 2005). The species is represented by a single specimen in the Bulgarian materials. Although not perfectly preserved, it exhibits the strong spread of the inner lip over the base, as well as the characteristic shell outline and ornamentation, which are diagnostic for this species. The specimen shows folds on the inner lip that are not visible on the figures of Deshayes (Deshayes *in* Leymerie, 1842; Deshayes, 1853) and d'Orbigny (1842) but are reported in the original species description (Deshayes *in* Leymerie, 1842: p.14). In his revision of d'Orbigny's collection, Kollmann (2005) figured only the lateral view of the specimen and noted that labral edge is thick with an indeterminate number of denticles inside.

The species differs from *C. ornata* (d'Orbigny, 1842; Kollmann, 2005) in having less convex and higher whorls and a nodose ornamentation of the last whorl.

Deshayes (*in* Leymerie, 1842; Deshayes, 1853) did not specify the number of studied specimens (we presume he had only one), and d'Orbigny (1842) stated that the species occurs rarely. It is also unknown how many specimens were examined by Pictet (1855) and Péron (1899). Kollmann (2005) noted that the specimen described by Deshayes (*in* Leymerie, 1842) was not found and should be considered lost. Additionally, Kollmann (2005: p. 151) designated a lectotype for this species (n°EM-30440-1) out of five more or less complete specimens from Dupin's collection, which was also cited by d'Orbigny (1842).

Stratigraphic and geographic occurrence. Hauterivian of Marolles-sous-Lignières, Aube, St-Sauveur and Leugny et Gy-l'Evêque, France and Fontenoy, Belgium; Barremian of Veliko Tarnovo, Bulgaria.

Colombellina aloysia Guirand & Ogérien, 1865

Figure 2.4

1859 *Columbellina corallina* Étallon, p. 119 (non von Quenstedt, 1852).

*1865 *Columbellina* (sic!) *Aloysia* (Guirand et Ogérien); Guirand & Ogérien, p. 387, text-figs. 36, 37.

1867 *Columbellina Aloysia* (Guirand et Ogérien); Ogérien, p. 593, figs. 207, 208.

1873 *Columbellaria Aloysia* Guirand & Ogérien; Zittel, p. 202.

1886 *Columbellaria Aloysia* (Guirand et Ogérien), Zittel; de Loriol, p. 61, pl. 3, figs. 16, 17.

? 1890 *Columbellaria Aloysia* Guirand; de Loriol & Koby, p. 168, pl. 18, fig. 10.

1904 *Columbellina* (*Collumbelaria*) *Aloysia* (Guir. et Ogér.); Cossmann, pl. 7, figs. 10, 11.

1913 *Columbellina* (*Collumbellaria*) *Aloysia* Guirard et Ogérien; Cossmann, p. 35, text-fig. 12.

Lectotype. MDC 20014048/1.

Material. Three specimens (lectotype MDC 20014048/1, designated herein, and MDC 20014048/2, 3) from the Kimmeridgian (Upper Jurassic) of Valfin, France.

Description. Shell thick, oval; spire distinctly elevated, gradate, with more or less pronounced angulation; apex not preserved; teleoconch consists of at least 6 convex whorls separated by incised suture; shell surface sculptured by orthocline axial ribs numbering 13 on the penultimate whorl; axial ribs covered by nodose spiral cords of different thickness; a larger nodose spiral cord occurs in the middle of the spire whorls (at angulation) along with a single subsutural adapical and a single abapical cord; last whorl large, with height of about three-fourths of shell height; last whorl ornamented with 14 spiral cords and numerous thinner axial ribs, with nodes at their intersections; interspaces between the spiral cords exceed their thickness; nodes oval in shape, axially elongated and situated at a distance almost equal to their diameter; base also ornamented with spirals, while the nodes become ribs; peristome siphonostomatous and thickened; aperture narrow and S-shaped; anterior canal narrow; posterior canal elongated, expanding outward; columellar lip thickened by callus spreading over base, with 7 denticles and an irregular thickened edge which does not fit tightly to the base; outer lip denticulate, with a thickened edge and bent outward.

Remarks. This species closely resembles *C. corallina*, from which it differs in having a more convex last whorl, a more curved, S-shaped aperture, as well as narrower and more elongated posterior canal.

Measurements (mm):

Specimen number	H	W	SA
Lectotype MDC 20014048/1	24.9	15.8	56°
MDC 20014048/2	27.5	15.2	55°
MDC 20014048/3	33.9	20.6	57°

In the original description, Guirand & Ogérien (1865) depicted three columellar folds, while the inner part of the outer lip was figured as smooth, i.e., without any denticles. The subsequent description and illustration of the same speciments by de Loriol (1886–1888) correspond more closely to the actual material; however, one specimen was depicted without a columellar lip (de Loriol, 1886–1888: pl. 3, fig. 17), which is present in the actual specimen.

De Loriol (1886–1888) revised Guirand & Ogérien (1865) specimen and three specimens from Étalon's collection which Étallon (1859) identified as *Columbellina* (sic!) *corallina.* All these specimens were collected from the Kimmeridgian (Upper Jurassic) of Valfin, France. Later, de Loriol (1890) documented another partially preserved specimen of *C. aloysia* from the Oxfordian of Saint-Ursanne, Switzerland. Cossmann (1913) identified this specimen as *C. corallina*, but it remains unclear whether he examined it directly or relied on the description by de Loriol (1890). We consider this determination to be rather doubtful due to the poor preservation; therefore, we have indicated its stratigraphic range from the Oxfordian as poorly constrained (Fig. 2.1).

Cossmann (1904, 1913) re-described *C. aloysia* based on the specimen from Guirand & Ogérien (1865) collection. However, the dimensions of this specimen are somewhat different (height 33 mm and width 20 mm instead of 27 and 18 mm respectively in the original description), and they also do not match our measurements.

Guirand & Ogérien (1865) originally placed this species in *Columbellina*, which is an incorrect spelling of *Colombellina* and therefore the combination *Colombellina aloysia* Guirand & Ogérien, 1865, is used herein without authors and year in parentheses (ICZN 1999, Art. 51.3.1.).

Stratigraphic and geographic occurrence. ?Oxfordian of Saint-Ursanne, Switzerland; Kimmeridgian of Valfin, France.

Colombellina bathonica (Cossmann, 1899)

Figure 2.5C

1899 *Columbellaria bathonica* Cossmann, p. 552, pl. 15, fig. 22, pl. 17, fig. 13.

1913 *Columbellina (Columbellaria)* Cossmann; Cossmann, p. 34, text-fig. 11.

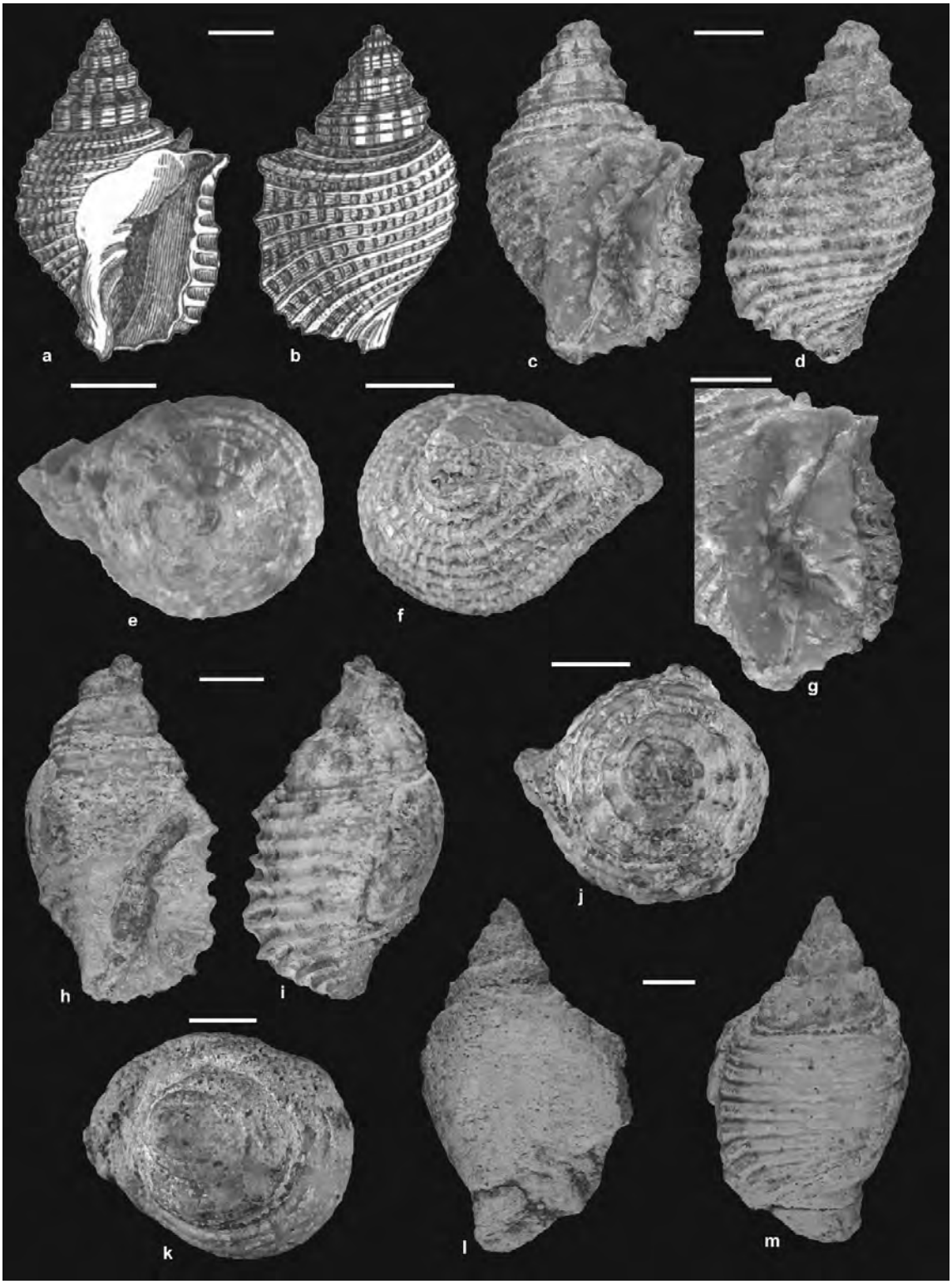

Fig. 2.4. — *Colombellina aloysia* Guirand & Ogérien, 1865 from the Kimmeridgian; Valfin, France. A–B, As figured by Guirand & Ogérien, 1865 (1865: 387, figs. 36, 37). C–G, lectotype MDC 20014048/1, designated herein; we assume that this specimen was also figured by Loriol (1886–1888: pl. 3, fig. 16), as its size and shape correspond to the illustration, although no number is inscribed on the specimen. C, apertural view, D, abapertural view, E, apical view, F, basal view, G, close apertural view. H–J, MDC 20014048/2; this specimen was also figured by Loriol (1886–1888: pl. 3, fig. 17), as the number 17 is inscribed on the shell. H, apertural view, I, abapertural view, J, apical view. K–M, MDC 20014048/3. K, apical view, L, apertural view, M, abapertural view. Scale bars represent 5 mm. For A–B an approximate scale bar is added.

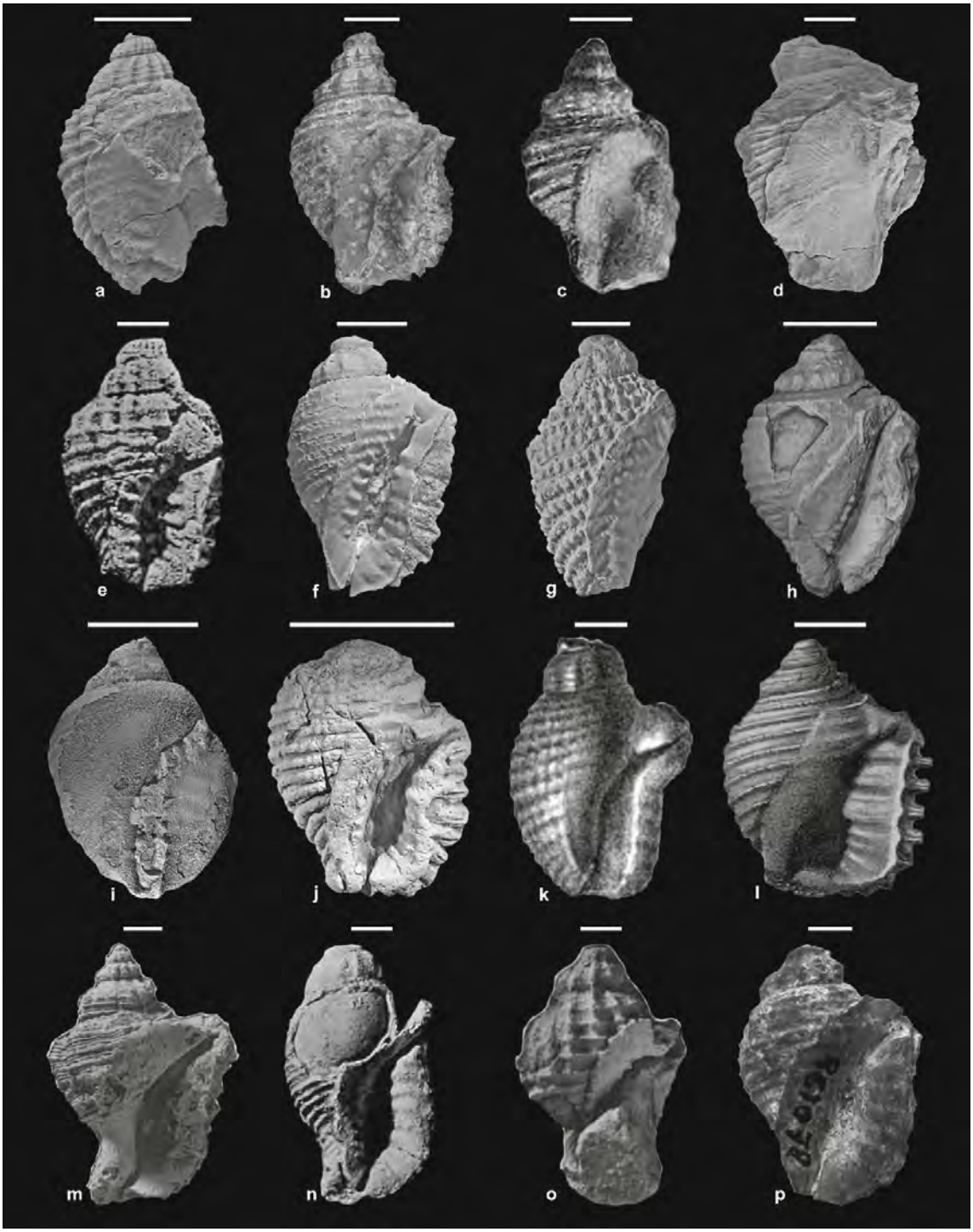

Fig. 2.5. — Species of *Colombellina*. A, *C. monodactylus* (Deshayes *in* Leymerie, 1842) from the Barremian; Veliko Tarnovo, Bulgaria; NMNHS-12538. B, *C. aloysia* Guirand & Ogérien, 1865 from the Kimmeridgian; Valfin, France; lectotype MDC 20014048/1. C, *C. bathonica* (Cossmann, 1899) from the Bathonian; Saint-Gaultier, France; specimen figured by Cossmann (1899: pl. 15, fig. 22), likely the one that was sold at the beginning of the 20th century. D, *C. brevis* Pictet & Campiche, 1864 from the Aptian; Veliko Tarnovo, Bulgaria; NMNHS-2780. E, *C. brevisiphonata* Nagao, 1934 from the Aptian–Albian; Miyako area, Japan; lectotype GMH 7086 designated by Hanzawa et al. (1961: 150) and figured by Kase (1984: pl. 23, fig. 13). F, *C. corallina* (von Quenstedt, 1852) from the Tithonian; Kotouč Quarry near Štramberk, Czechia; VSB GP101101. G, *C. crassigranulata* sp. n. from the Upper Jurassic; Leskovets/Kopanitsa, Bulgaria; holotype NMNHS-20680. H, *C. denticulata* (Zittel, 1873) from the Tithonian–Berriasian; Štramberk, Czechia; lectotype SNSB-BSPG AS III 890. I, *C. dubia* (Zittel, 1873) from the Tithonian–Berriasian; Štramberk, Czechia; lectotype SNSB-BSPG AS III 893. J, *C. granulata*

(Zittel, 1873) from the Tithonian–Berriasian; Koňákov, Czechia; lectotype SNSB-BSPG AS III 895. K, *C. hebertina* de Loriol, 1866 from the Barremian–Aptian; Essert, France; figured by de Loriol specimen (1866: pl. B, fig. 16). L, *C. magnifica* (Zittel, 1873) from the Tithonian; Štramberk, Czechia; figured by Zittel specimen (1873: pl. 40, fig. 4a, b). M, *C. neocomiensis* (d'Orbigny, 1842) from the Hauterivian; Gy-l'Evêque, France; specimen LPMP-R61077-2, figured by Kollmann (2005: pl. 17, fig. 2). N, *C. oginoi* Kase, 1984 from the upper Aptian; Miyako area, Japan; holotype GIYU-122, figured by Kase (1984: pl. 23, fig. 14). O, *C. ornata* d'Orbigny, 1842 from the Cenomanian; Cassis, France; neotype LPMP-B17561, figured by Kollmann (2005: pl. 17, fig. 5). P, *C. subaloysia* (Péron, 1899) from the Neocomian; Volvent, France; holotype MNHN R61078 from www.stromboidea.de (Wieneke *et al.* 2018). All species are presented in apertural view. Scale bars represent 5 mm.

Holotype. Pl. 15, fig. 22 and pl. 17, fig. 13 in Cossmann (1899); topotype: MNHN LPMP no. 1501 (coll. Cossman).

Remarks. Cossmann (1899, 1913) did not specify the number of specimens in his original description. According to the data continuously moderated by Wieneke *et al.* in their webpage (Wieneke *et al.* last modified: May 24, 2018), there were two specimens of the species, one of which (the most complete) was sold at the beginning of the 20th century (the information is taken from the web page stromboidea.de (Wieneke *et al.* 2018)).

Stratigraphic and geographic occurrence. Bathonian of Saint-Gaultier, Indre, France.

Colombellina brevis Pictet & Campiche, 1864

Figure 2.6

1864 *Columbellina* (sic!) *brevis* Pictet & Campiche 1861–1864, p. 667, pl. 96, figs. 6–7.

Holotype. Pl. 96, figs. 6–7 in Pictet & Campiche (1861–1864).

Material. One specimen (NMNHS-2780) from the Aptian (Lower Cretaceous) of Veliko Tarnovo, Bulgaria.

Description. Shell fragment of two incomplete whorls and partly eroded shell surface; whorls convex, separated by incised suture; shell surface sculptured by orthocline, strong and round axial ribs (about ten) covered by nodose spiral cords of two orders; axial ribs do not reach sutures; two stronger spiral cords occur in the middle part of whorls, where axial ribs become stronger too; row of round nodes with sharp tops situated close to adapical suture, the distance between them approximately equal to their diameter; aperture and outer lip broken; callus of inner lip spread over base with irregular thickened edge.

Measurements (mm):

Specimen number	H	W
NMNHS-2780	27.5	20.1

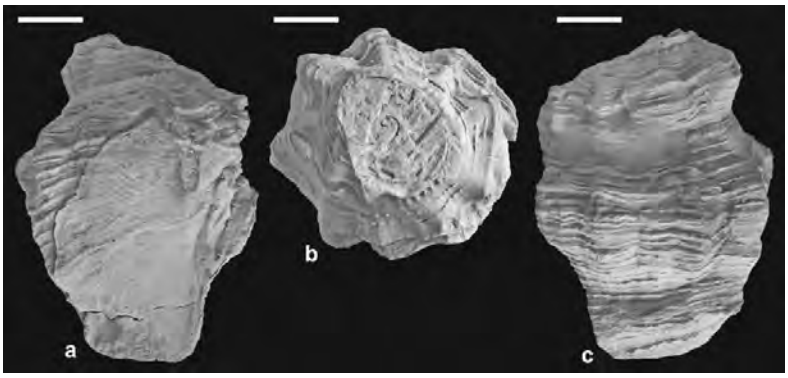

Fig. 2.6. *Colombellina brevis* Pictet & Campiche, 1864, from the Aptian; Veliko Tarnovo, Bulgaria. A–C, NMNHS-2780. A, apertural view, B, apical view, C, abapertural view. Scale bars represent 5 mm.

Remarks. The specimen NMNHS-2780, although partially preserved, displays shape and ornamentation matching that of *C. brevis* described from the Valanginian of Sainte-Croix, Switzerland, by Pictet & Campiche (1861–1864). It differs from *C. neocomiensis* Pictet & Campiche, 1861, which is similarly ornamented, in having a wider last whorl, a difference already noted by Pictet & Campiche (1861–1864). *Colombellina brevis* differs from *C.*? *maxima* de Loriol, 1861, in having a wider shell and richer spiral ornamentation.

Pictet & Campiche (1861–1864) originally placed this species in *Columbellina*, which is an incorrect spelling of *Colombellina* and therefore the combination *Colombellina brevis* Pictet & Campiche, 1861, is used herein without authors and year in parentheses (ICZN 1999, Art. 51.3.1.).

The species was previously recorded only from the Valanginian of Sainte-Croix, Switzerland; however, the number of specimens was not specified, with only a note that they ‘are not rare’ (Pictet & Campiche, 1861–1864: p. 668).

Stratigraphic and geographic occurrence. Valanginian of Sainte-Croix, Switzerland and Aptian of Veliko Tarnovo, Bulgaria.

Colombellina brevisiphonata Nagao, 1934

Figure 2.5E

1934 *Columbellina* (sic!) *brevisiphonata* Nagao, p. 260, pl. 39, fig. 6.

1977 *Colombellina (Columbellaria) brevisiphonata* Nagao; Hayami & Kase, p. 59, pl. 7, fig. 3.

1984 *Colombellina (Collumbellaria) brevisiphonata* Nagao; Kase, p. 147, pl. 23, fig. 13.

Lectotype. GMH 7086 (Hanzawa et al., 1961: 150).

Remarks. Nagao (1934) did not specify the number of specimens in his original description. According to Kase (1984: p. 147), Nagao’s collection originally contained two specimens; however, the whereabouts of the second specimen remain unknown (Hayami & Kase, 1977).

Nagao (1934) originally placed this species in *Columbellina*, a name we consider an incorrect spelling of *Colombellina* and therefore the combination *Colombellina brevisiphonata* Nagao, 1934, is used herein without authors and year in parentheses (ICZN 1999, Art. 51.3.1.).

Stratigraphic and geographic occurrence. Aptian–Albian of Hiraiga Formation, Haipe, Miyako area, Honshu, northeastern Japan.

Colombellina corallina (Quenstedt, 1852)

Figure 2.7

1852 *Cassis corallina* Quenstedt, p. 435, pl. 35, fig. 1.

1858 *Cassis corallina* Quenstedt; Quenstedt, p. 775, pl. 95, fig. 21.

Non 1859 *Columbellina corallina* Et.; Étallon, p. 119 (= *Colombellina aloysia* Guirand & Ogérien, 1865).

1861 *Columbellaria corallina* Quenstedt sp.; Rolle, p. 261, fig. 1.

1884 *Cassis corallina* Quenstedt; Quenstedt, p. 684, pl. 212, figs. 59–63.

1903 *Columbellaria corallina* Quenstedt; Zittel, p. 374, fig. 914.

1909 *Columbellaria corallina* Quenstedt; Brösamlen, p. 316, pl. 22, figs. 37–38.

1913 *Columbellina (Columbellaria) corallina* (Quenstedt); Cossmann, p. 35, pl. 2, fig. 45–47.

1940 *Colombellina (Columbellaria) corallina* (Quenstedt); Wenz, p. 926, fig. 2712.

1997 *Columbellina* (*Columbellaria*) *corallina* (Quenstedt, 1852); Hägele, p. 106, fig. on p. 108, upper left, pl. 11, fig. 5.

Non 2017 *Columbellaria corallina* (Quenstedt, 1852); Gründel, p. 32, pl. 13, fig. A.

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

Non 2019 *Columbellaria* cf. *corallina* (Quenstedt, 1852); Gründel *et al.*, p. 133, pl. 9, figs. 11–17.

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

Holotype. Pl. 35, fig. 1 in Quenstedt (1852).

Material. Two specimens (VSB GP101101, 101102) from the Tithonian (from the upper lower Tithonian to the basal upper Tithonian) of Kotouč Quarry (locality 4 in Vašíček and Skupien (2016)) near Štramberk, Czechia.

Description. Shell thick, oval, relatively high-spired; apex not preserved; spire distinctly elevateted, gradate with angulation at mid-whorl of whorl face, rounded in penultimate whorl; teleoconch in the more completely preserved specimen consists of five convex whorls separated by incised suture; spire whorls sculptured by strong, wide, round axial ribs (12 on the penultimate

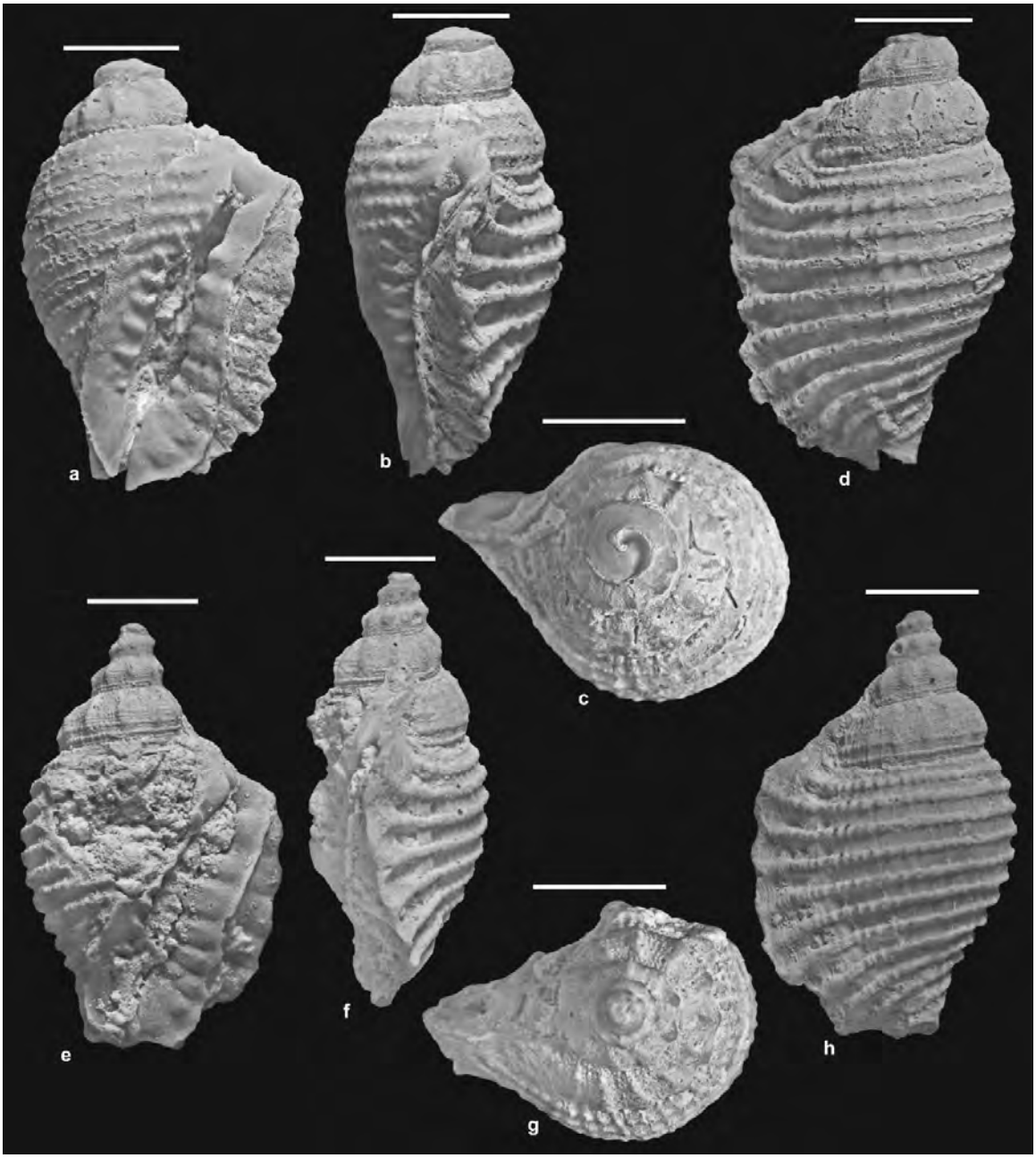

Fig. 2.7. — *Colombellina corallina* (von Quenstedt, 1852) from the Tithonian; Kotouč Quarry near Štramberk, Czechia. A–D, VSB GP101101, A, apertural view, B, lateral view of thickened edge of outer lip, C, apical view, D, abapertural view. E–H, VSB GP101102, E, apertural view, F, lateral view of thickened edge of outer lip, G, apical view, H, abapertural view. Scale bars represent 5 mm.

whorl), which reach sutures and are most prominent in the middle part of whorls; axial ribs covered by nodose spiral cords of different thickness and orders; last whorl large, of about three-fourths of shell height; ornamentation on last whorl differs from that on spire – strong axial ribs absent, as well as spiral cords of the second order in the interspaces between the ribs of the first order; spiral cords (ca. 12–13) are wide and nodose, with distance between them only slightly greater than their width, forming small wing-like expansions of outer lip; one smaller tuberculate

spiral cord located close to adapical suture; surface of last whorl densely covered with thin growth lines, which, unlike spire whorls, do not form nodules when intersected with very thin spiral threads; peristome siphonostomatous and thickened; aperture narrow, oblique and slightly curved; anterior canal narrow; posterior canal elongated, expanding outward; columellar lip thickened by callus spreading over base, with nine massive denticles; callus with an irregular thickened edge, which is not tightly adherent to base; adapical part of the columellar lip ornamented similarly to last whorl, underlying ornament is showing through the lip layer; outer lip denticulate with a thickened edge, bent outward.

Measurements (mm):

Specimen number	H	W	SA
VSB GP101101	18.7	11.9	55°
VSB GP101102	19.3	12.2	54°

Remarks. Besides the denticles, there are separate nodes on the columellar lip of *C. corallina*, which were also observed in a new species, *C. crassigranulata* sp. n., described below, and which were not documented before.

C. corallina differs from *C. aloysia* by its more elongated shell outline, a larger last whorl, and less curved aperture. It differs from *C. subaloysia* Péron, 1899, by a more elongated last whorl, a higher spire, and differences in ornamentation.

Quenstedt (1852, 1858) did not specify the number of studied specimens. From his later work (Quenstedt, 1884), we can assume that he had at least five specimens in total, all of which were illustrated. Three specimens identified as *C. corallina* by Étallon (1859) from the Kimmeridgian of Valfin, France were reviewed by Loriol (1886–1888), who compared them with the type specimen of *C. aloysia* and concluded that they are identical. The number of specimens examined by Rolle (1861) is unknown. Brösamlen (1909) examined 19 silicified specimens from Nattheim, Germany. One specimen of *C. corallina* from Péron's collection in the National Museum of Natural History in Paris was identified by Cossmann (1913).

It should be noted that the illustrations in Quenstedt (1852, 1884) differ from those in Quenstedt (1858), depicting a comparatively narrower shell, which may represent either intraspecific variability or a different species.

Stratigraphic and geographic occurrence. Tithonian of Nattheim, Württemberg, Gemany; Tithonian–Berriasian of Štramberk, Czechia.

Colombellina crassigranulata sp. n.

Figure 2.8

LSID: urn:lsid:zoobank.org:act:3547AB81-2F8E-46BC-89FDA589D73864CE

Etymology. In reference to its coarse nodose ornamentation.

Type material. Holotype, NMNHS-20680, from the Upper Jurassic of Leskovets/Kopanitsa, Bulgaria.

Type horizon & locality. Upper Jurassic of Leskovets/Kopanitsa, Bulgaria.

Diagnosis. Shell thick, oval, ornamented with axial and spiral ribs forming nodes at the intersections. Last whorl large, with strong spiral cords and thin axial ribs. Columellar lip thickened by callus and provided with massive denticles.

Description. Shell partly preserved, thick, oval, relatively high-spired; apex not preserved; preserved part of teleoconch consists of three convex whorls increasing rapidly in size and separated by moderately incised suture; ornamentation of two preserved whorls of spire consists of round axial ribs (12 on the penultimate whorl) covered by spirals bearing spirally elongated nodes at the intersections; one smaller spiral tuberculate cord is located close to adapical suture; last whorl large, with height of about four-fifths of shell height; ornamentation of the last whorl differs from that of the spire and it is sculptured by about 11 regularly spaced, strong spirals and thin axial ribs; round nodules developed at the intersections of the axial cords and spiral ribs; aperture broken; columellar lip thickened by callus which spread over base, with about ten massive denticles and an irregular thickened edge, which does not adhere tightly to the base; in the adapical part of the columellar lip, there are three round nodes in the interspaces between the denticles.

Measurements (mm):

Specimen number	H	W	SA
Holotype NMNHS-20680	21.3	12.2	52°

Remarks. The shell is partially preserved, missing the apex, and the last whorl is partially destroyed in the apertural part. Despite its incompleteness, the characters of the shell outline and of columellar lip allow to attribute the specimen to the genus *Colombellina*. The well-preserved characters of the ornament are different from those of the other known species of *Colombellina* and allow to establish a new species.

The new species differs from *C. corallina* in its ornamentation, specifically in having larger nodules on the last whorl, shorter distances between spiral rows, and differences in the morphology of the columellar lip. Compared to *C. subaloysia*, it has a narrower and less convex

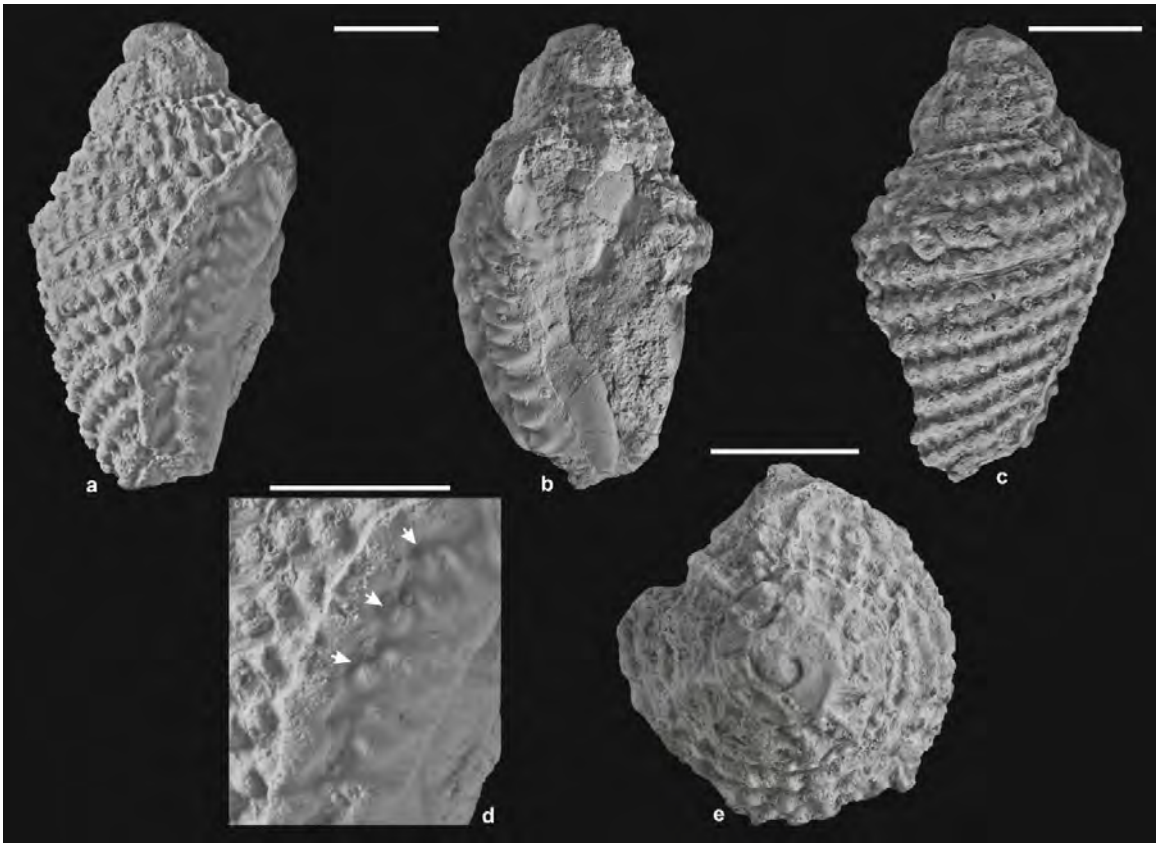

Fig. 2.8. — *Colombellina crassigranulata* sp. n. from the Upper Jurassic; Leskovets/Kopanitsa, Bulgaria. A–E, NMNHS-20680, holotype. A, lateral view, B, apertural view, C, abapertural view, D, detail view of the adapical part of the columellar lip, arrows indicate round nodules in the interspaces between the teeth, E, apical view. Scale bars represent 5 mm.

last whorl, higher spire whorls, and larger nodules on the spirals of the last whorl. The new species also differs from *C. aloysia* in having ~~a~~ narrower last whorl and spire whorls, in the absence of a prominent keel in the middle of the spire whorls, and in bearing larger nodules on the spirals of the last whorl. It differs from *C. monodactylus* by the shell outline, ornamentation of the last whorl without axial ribs in the adapical third, and the morphology of the columellar lip. *C. bathonica* has a concave middle part of the last whorl, between ramp and base and smaller tubercles on the spiral rows, while *C. ornata* exhibits a reticulate ornamentation and an almost globular last whorl.

Colombellina crassigranulata sp. n. differs from *C. brevisiphonata* by having higher spire whorls, a less convex last whorl, and the absence of axial ribs in the adapical part of the last whorl. It differs from *C. hebertina* and *C. oginoi* in overall shell shape and the nodose ornamentation of the last whorl. Both *C. brevis* and *C. neocomiensis* show differently shaped last whorl with a keel in the adapical third, while *C. dubia* exhibits an almost globular last whorl. *C. denticulata* is distinguished by its more convex last whorl and a greater number of axial ribs on the spire whorls. *C. magnifica* differs in having a more rounded last whorl and greater spacing

between the spiral rows of nodes on the last whorl. *Colombellina granulata* also exhibits a more rounded last whorl and axially elongated nodules of spiral cords on the last whorl.

Stratigraphic and geographic occurrence. Upper Jurassic of Leskovets/Kopanitsa, Bulgaria.

Colombellina denticulata (Zittel, 1873)

Figure 2.9

*1873 *Columbellaria denticulata* Zittel, p. 204, pl. 40, fig. 6–7.

1897 *Columbellaria denticulata* Zittel; Roman, p. 287, pl.2, fig. 5, 5a (non 4, 4a).

?1931 *Zittelia denticulata* Zittel; Tsan-hsun, p. 37, pl. 3, fig. 2.

Lectotype. SNSB-BSPG AS III 890.

Material. Five specimens from the Tithonian–Berriasian of Czechia: four from Štramberk (lectotype SNSB-BSPG AS III 890, designated herein, SNSB-BSPG AS III 889, 891, 892) and one from Koňákov (SNSB-BSPG AS III 908).

Description. Shell thick, oval, relatively high-spired; apex not preserved; spire elevated, gradate with median angulation; last whorl evenly rounded; teleoconch in more completely preserved specimens consists of four to five whorls separated by incised suture; spire whorls sculptured by strong axial ribs (14–16 on the penultimate whorl), which are most prominent just below the middle of the whorls, where they carry a keel; axial ribs covered by nodose spiral cords; last whorl large, of about two-thirds of shell height; ornamentation of last whorl differs from that on spire in the absence of axial ribs; it bears ca. 13–15 nodose spiral cords with interspaces almost twice their width; spiral cords turn into small wing-like expansions of the outer lip; one smaller nodose spiral cord occurs close to adapical suture; surface of last whorl densely covered with thin growth lines, which form nodules when intersected with spiral cords; peristome siphonostomatous and thickened; aperture narrow and almost straight anteriorly, slightly curved posteriorly; anterior canal narrow; posterior canal elongated and expanding outward; columellar lip thickened by callus spreading over base, with at least 9 denticles and an irregular thickened edge; outer lip denticulate, with a thickened edge and bent outward.

Measurements (mm):

Specimen number	H	W	SA
SNSB-BSPG AS III 889	32.0	27.1	78°
Lectotype SNSB-BSPG AS III 890	28.2	19.3	80°
SNSB-BSPG AS III 891	28.0	17.5	60°
SNSB-BSPG AS III 892	23.7	18.6	82°
SNSB-BSPG AS III 908	25.6	18.5	79°

Remarks. Spiral cords on the spire are more prominent on the keel and below it, possibly due to shell preservation.

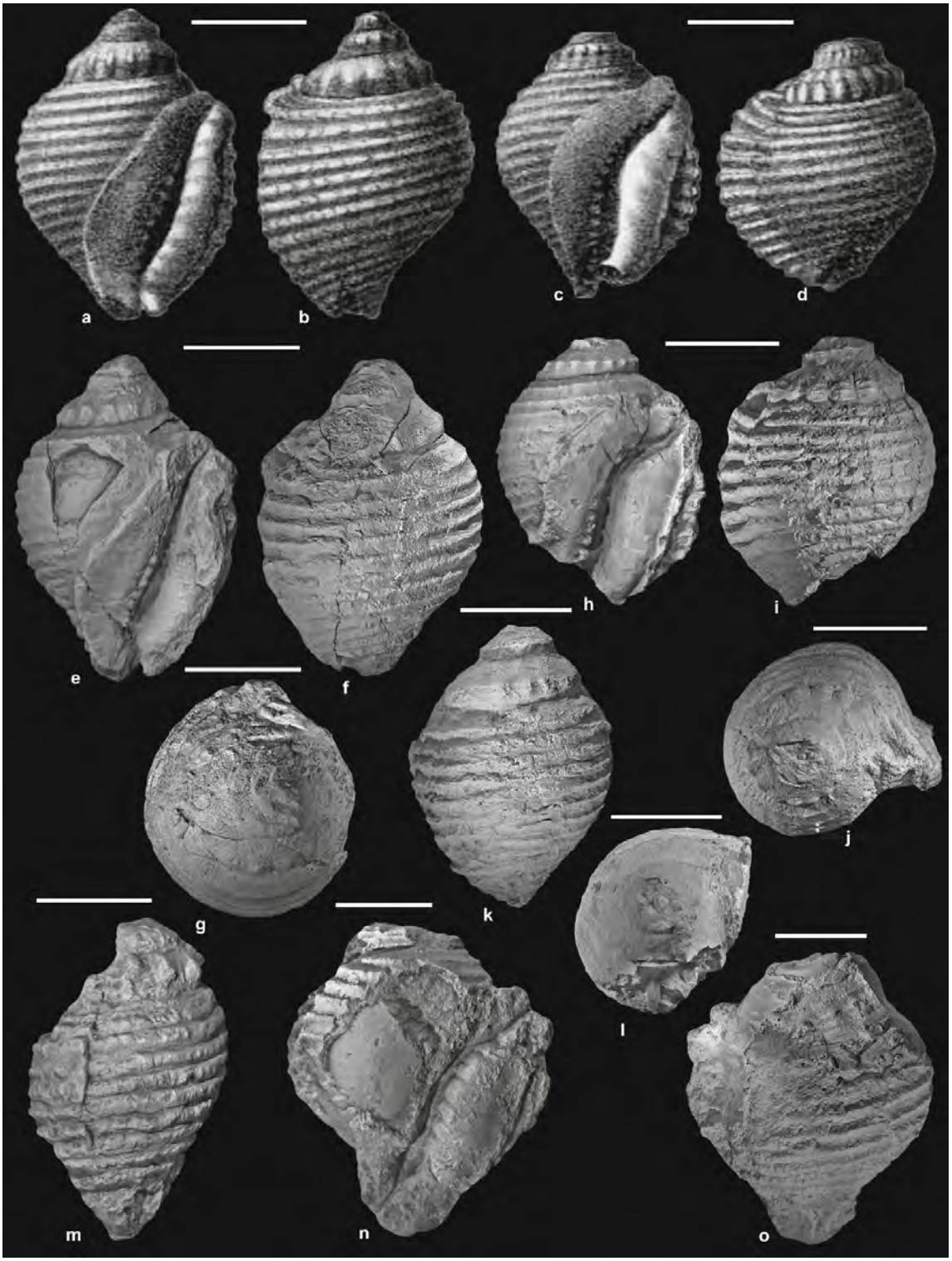

Fig. 2.9. — *Colombellina denticulata* (Zittel, 1873) from the Tithonian–Berriasian; Štramberk, Czechia. A–D, figured by Zittel specimens (1873: pl. 40, figs. 6a, b, 7a, b), A, fig. 6a, B, fig. 6b, C, fig. 7b, D, fig. 7a. E–G, lectotype SNSB-BSPG AS III 890, designated herein, it can be assumed that this specimen was figured by Zittel (1873) (A–B herein), E, apertural view, F, abapertural view, G, apical view. H–J, SNSB-BSPG AS III 892, it can be assumed that this specimen was figured by Zittel 1873 (C–D herein), H, apertural view, I, abapertural view, J, apical view. K–L, SNSB-BSPG AS III 908, K, abapertural view, L, apical view. M, SNSB-BSPG AS III 891, abapertural view. N–O, SNSB-BSPG AS III 889, from the Tithonian; Koňákov, Czechia. N, apertural view, O, abapertural view. Scale bars represent 10 mm. For A–D an approximate scale bars are added.

Zittel (1873) studied six specimens, five of which we examined from the Hohenegger collection, stored at the Bavarian State Collection for Palaeontology and Geology in Munich, Germany. The number of specimens, coming from Murles, France, examined by Roman (1897) is unknown. Tsan-hsun (1931) studied two specimens from the same locality.

Stratigraphic and geographic occurrence. Tithonian–Berriasian of Štramberk and Koňákov (both Czechia); Tithonian of Murles (France).

Colombellina dubia (Zittel, 1873)

Figure 2.10

*1873 *Columbellaria dubia* Zittel, p. 204, pl. 40, fig. 8.

Lectotype. SNSB-BSPG AS III 893.

Material. Two specimens from the Tithonian–Berriasian of Štramberk, Czechia (lectotype SNSB-BSPG AS III 893, designated herein, SNSB-BSPG AS III 894).

Description. Shell oval, relatively high-spired; apex not preserved; spire elevated, gradate with median angulation; last whorl evenly rounded; teleoconch consists of four preserved whorls separated by incised suture; spire whorls sculptured by strong axial ribs (about ten on the penultimate whorl); axial ribs covered by spiral cords with a keel in the middle part of the whorls; last whorl large, of about three-fourths of shell height; last whorl ornamented with ca. 11–12 nodose spiral cords and broad interspaces between them; one smaller nodose spiral cord occurs close to the adapical suture; peristome siphonostomatous and thickened; aperture narrow and curved in adapical part; anterior and posterior canals present; columellar lip eroded, with denticles; outer lip denticulate with a thickened edge.

Measurements (mm):

Specimen number	H	W	SA
Lectotype SNSB-BSPG AS III 893	23.9	17.4	68°
SNSB-BSPG AS III 894	22.4	15.5	70°

Remarks. We examed two specimens from the Hohenegger collection studied by Zittel (1873) housed at the Bavarian State Collection for Palaeontology and Geology in Munich, Germany, although six were mentioned in the original description. One of these is an eroded shell, and the other is an internal mould. Zittel (1873) observed that *C. dubia* exhibits a high similarity to *C. denticulata*, and differs from the latter in lacking denticles on the columellar lip. However, the columellar lip of *C. dubia* does bear denticles, as evidenced by their imprints preserved in the abapical part of the aperture of the specimen SNSB-BSPG AS III 893 (Fig. 2.10C). *Colombellina*

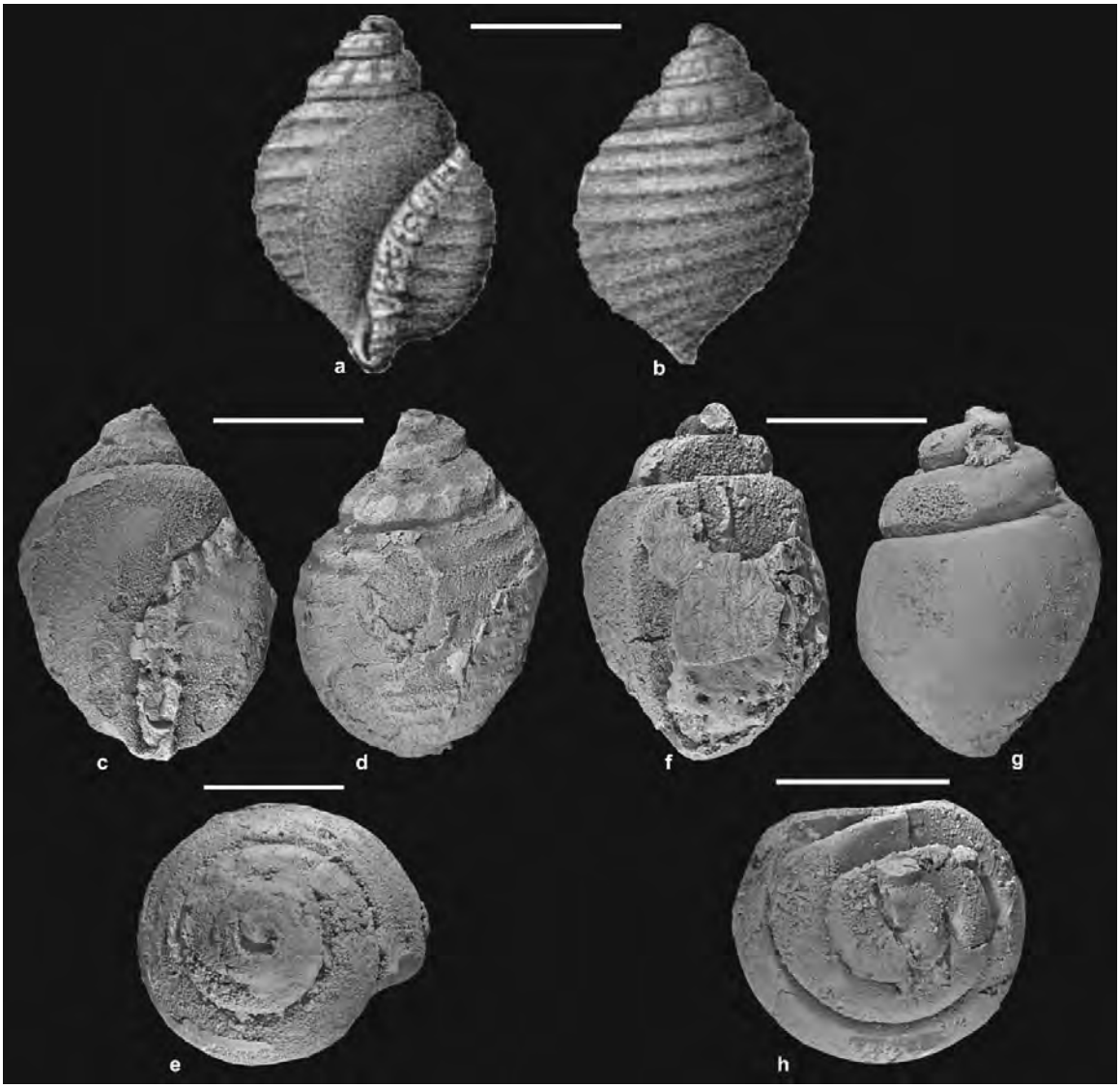

Fig. 2.10. — *Colombellina dubia* (Zittel, 1873) from the Tithonian–Berriasian; Štramberk, Czechia. A–B, Figured by Zittel specimen (1873: pl. 40, fig. 8a, b). C–E, lectotype SNSB-BSPG AS III 893, designated herein, it can be assumed that this specimen was figured by Zittel 1873 (A–B herein), C, apertural view, D, abapertural view, E, apical view. F–H, SNSB-BSPG AS III 894, F, apertural view, G, abapertural view, H, apical view. Scale bars represent 10 mm. For A–B an approximate scale bar is added.

dubia differs from *C. denticulata* in having higher spire whorls and fewer spiral cords on the last whorl, with broader interspaces between them. It is important to note that the species was established based on incomplete shells and moulds with partially preserved diagnostic characters. Although it is possible that better-preserved material could support synonymy with *C. denticulata*, we retain the original taxonomic assignment proposed by Zittel (1873).

Stratigraphic and geographic occurrence. Tithonian–Berriasian of Štramberk, Chotěbuz (Kotzobendz) (Czechia), Wilamowice (Willamowitz) (Poland).

Colombellina granulata (Zittel, 1873)

Figure 2.11

*1873 *Columbellaria granulata* Zittel, p. 205, pl. 40, fig. 9.

Lectotype. SNSB-BSPG AS III 895.

Material. One specimen from the Upper Jurassic–Neocomian of Koňákov, Czechia (lectotype SNSB-BSPG AS III 895, designated herein).

Description. Shell thick, oval; apex and most of spire whorls not preserved; teleoconch consists of two preserved whorls separated by incised suture; spire whorls sculptured by strong axial ribs and spiral cords; last whorl large, ornamented with 12 strong, nodose spiral cords; nodules on the cords densely spaced and axially elongated; interspaces between spiral cords narrower than width of cords; peristome siphonostomatous and thickened; aperture narrow, slightly expanded in the abapical part; anterior canal narrow; posterior canal elongated, expanding outward; columellar lip thickened by callus spreading over base, with denticles and an irregular thickened edge; outer lip denticulate with a thickened edge and bent outward.

Measurements (mm):

Specimen number	H	W
Lectotype SNSB-BSPG AS III 895	15.6	13.0

Remarks. Zittel (1873) studied two specimens and we examined one of those present at the Bavarian State Collection for Palaeontology and Geology in Munich, Germany. Due to the state of shell preservation, we can only assume the presence of a subsutural cord near the adapical suture. This species differs from *C. crassigranulata* sp. nov., which shows a similar ornamentation of the last whorl, in its more inflated shell shape, smaller denticles on the columellar lip, and axially elongated nodules, whereas in *C. crassigranulata* sp. nov. they are round.

Stratigraphic and geographic occurrence. Upper Jurassic–Neocomian of Štramberk and Koňákov, Czechia.

Colombellina hebertina de Loriol, 1866

Figure 2.5K

1866 *Columbellina* (sic!) *Hebertina* Loriol, p. 71, pl. B, fig. 16.

Holotype. Pl. B, fig. 16 in de Loriol (1866).

Remarks. De Loriol (1866) stated that the species is rare, without specifying the number of specimens examined. He believed that this species is intermediate between *Colombellina*

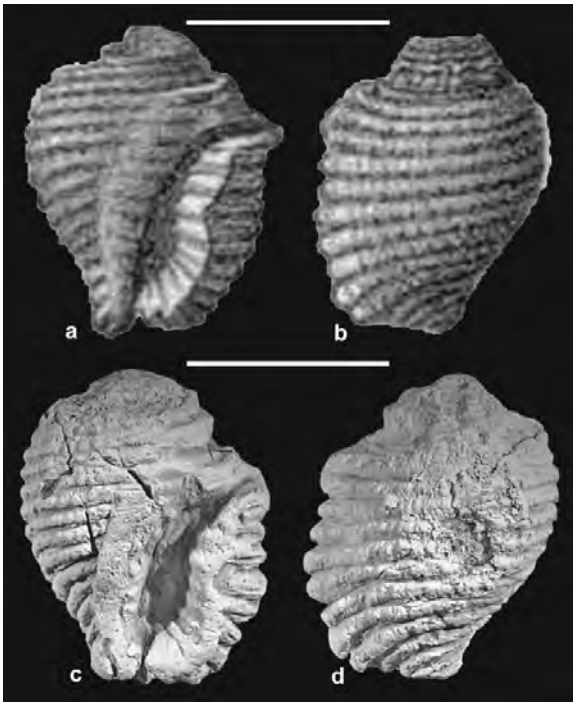

Fig. 2.11. — *Colombellina granulata* (Zittel, 1873) from the Tithonian–Berriasian; Koňákov, Czechia. A–B, Figured by Zittel specimen (1873: pl. 40, fig. 9a, b). C–D, lectotype SNSB-BSPG AS III 895, designated herein, it can be assumed that this specimen was figured by Zittel 1873 (A–B herein), C, apertural view, D, abapertural view. Scale bars represent 10 mm. For A–B an approximate scale bar is added.

monodactylus and *Colombellina ornata*. Zittel (1873) placed this species in the genus *Columbellaria*.

De Loriol (1866) originally placed this species in *Columbellina*, a name we consider an incorrect spelling of *Colombellina* and therefore the combination *Colombellina hebertina* de Loriol, 1866, is used herein without authors and year in parentheses (ICZN 1999, Art. 51.3.1.).

Stratigraphic and geographic occurrence. Barremian–Aptian of Essert (France).

Colombellina magnifica (Zittel, 1873)

Figure 2.12

*1873 *Columbellaria magnifica* Zittel, p. 203, pl. 40, fig. 4.

Holotype. Pl. 40, fig. 4 in Zittel (1873).

Material. One specimen from the Upper Jurassic–Neocomian of Koňákov, Czechia (SNSB-BSPG AS III 888).

Description. Shell thick, oval; apex and most spire whorls not preserved; teleoconch consists of 2 preserved whorls separated by incised suture; large last whorl is ornamented with 11 nodose spiral cords, with interspaces approximately one and a half times wider than cords; peristome siphonostomatous and thickened; aperture narrow, slightly expanded in the abapical part; anterior canal not preserved; posterior canal elongated, expanding outward; columellar lip not preserved; outer lip denticulate with a thickened edge and bent outward, strongly expanding.

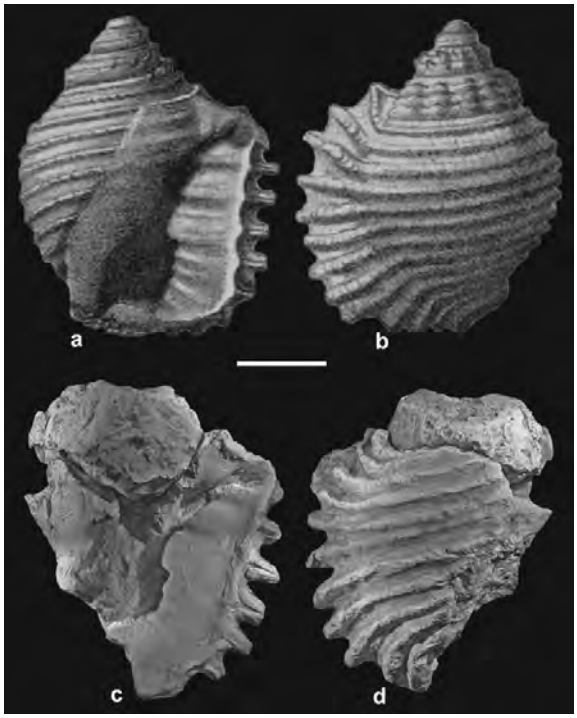

Fig. 12. — *Colombellina magnifica* Zittel, 1873 from the Tithonian; Štramberk, Czechia. A–B, Figured by Zittel specimen (1873: pl. 40, fig. 4a, b). C–D, SNSB-BSPG AS III 888, syntype from the Hohenegger collection described by Zittel (1873). C, aperture view with partly preserved aperture, D, lateral view. Scale bar represents 10 mm, for A–B the scale bar is an approximate.

Measurements (mm):

Specimen number	H_{lw}	W
SNSB-BSPG AS III 888	36.0	29.1

Remarks. We examined one partially preserved specimen from the Hohenegger collection studied by Zittel (1873) at the Bavarian State Collection for Palaeontology and Geology in Munich, Germany. Zittel (1873) studied three specimens. This species stands out among other species of *Colombellina* due to its larger size (Fig. 2.13). Given the poor preservation of the specimen, we refrained from designating a lectotype.

Stratigraphic and geographic occurrence. Upper Jurassic–Neocomian of Štramberk (Czechia).

Colombellina neocomiensis (d'Orbigny, 1842)

Figure 2.5M

1842 *Fusus neocomiensis* d'Orbigny, p. 331, pl. 222, fig. 1.

1861 *Fusus neocomiensis* d'Orbigny; de Loriol, p. 47, pl. 5, figs. 7, 8.

1861 *Columbellina neocomiensis*, Pictet & Campiche; Pictet & Campiche, p. 665, pl. 96, figs. 4, 5.

1899 *Columbellina neocomiensis* d'Orbigny (*sub Fusus*); Péron, p. 141, pl. 4, fig. 11.

2005 *Columbellina neocomiensis* (d'Orbigny); Kollmann, p. 143–144, pl. 17, figs. 1–3.

Lectotype. MNHN LPMP-B14490-1.

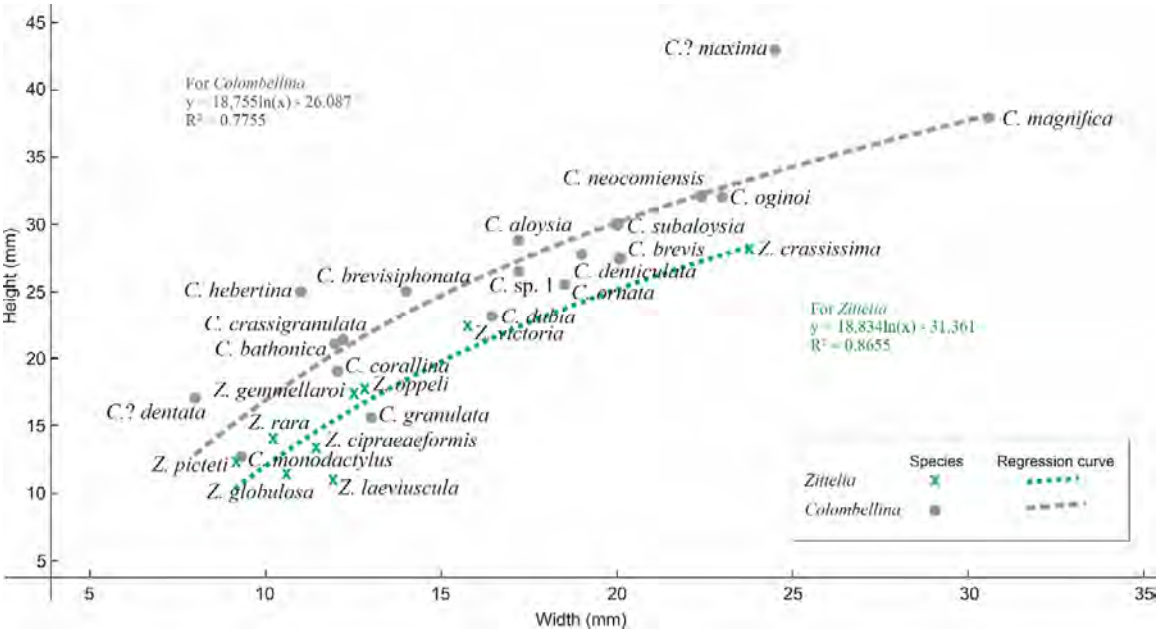

Fig. 2.13. — Size comparison of *Zittelia* and *Colombellina* with regression curves for each genus. Each point represents the mean of all specimens of a separate species.

Remarks. D'Orbigny (1842) did not specify the number of studied specimens. Kollmann (2005) noted that the type specimen figured by d'Orbigny (1842) could not be found. However, six internal moulds are stored in d'Orbigny's collection at MNHN in Paris, two of them with shell fragments preserved (Kollmann, 2005: p. 144). Kollmann also notes that his figured specimen is a lectotype from the d'Orbigny collection (MNHN LPMP-B14490-1). De Loriol (1861) stated that the species is quite common. Pictet & Campiche (1861–1864) did not specify number of studied specimens, noting that the species is not rare in the Neocomian. Péron (1899) also mentioned that the species is quite common.

Stratigraphic and geographic occurrence. Valanginian of Sainte-Croix, Locle, Switzerland, Neocomian of Marolles-sous-Lignières, La Varappe, d'Auxerre, Métairie Foudriat, and Gy-l'Evêque, France.

Colombellina oginoi Kase, 1984

Figure 2.5N

1984 *Colombellina (Colombellina) oginoi* Kase, p. 146, pl. 23, fig. 14.

Holotype. GIYU-122.

Remarks. Kase (1984) examined a single specimen.

Stratigraphic and geographic occurrence. Upper Aptian of Haipe, Miyako area, Iwate Prefecture, Honshu, Japan.

Colombellina ornata d'Orbigny, 1842

Figure 2.5O

1842 *Colombellina ornata* d'Orbigny, p. 348, pl. 226 , figs. 6, 7.

1855 *Columbellina ornata* d'Orbigny; Pictet, p. 248, pl. 66, fig. 19.

1884 *Columbellina ornata* A. d'Orbigny; Fischer, p. 657, fig. 409.

2004 *Columbellaria* cf. *tuberculosa* (Binkhorst, 1861); Kiel & Bandel, p. 121, figs. 7O, P.

2005 *Colombellina ornata* d'Orbigny; Kollmann, p. 152, pl. 17, fig. 5.

Neotype. LPMP-B17561.

Remarks. Only one specimen represents the species in d'Orbigny's collection, which Kollmann (2005) designated as the neotype (LPMP-B17561).

Kiel & Bandel (2004) described a colombellinid species based on six specimens from Kassenberg quarry, Germany. They identified them as *Columbellaria* cf. *tuberculosa* with some doubt due to the higher spire compared to the type material described by Kaunhowen (1897: p. 79, pl. 9, figs 7-8). In our opinion, the shell outline and inner lip morphology of the figured specimen correspond to *C. ornata*, whereas the non-reticulate ornamentation of the last whorl can be due to its defective preservation.

Stratigraphic and geographic occurrence. Cenomanian of Cassis, France, and Kassenberg quarry in Mühlheim, Germany.

Colombellina subaloysia (Péron, 1899)

Figure 2.5P

1899 *Colombellaria subaloysia* Péron, p. 144, pl. 4, fig. 12.

1904 *Columbellina subaloysia* Peron; Cossmann, p. 109, pl. 7, figs. 8, 9.

Holotype. Pl. 4, fig. 12 in Péron (1899).

Remarks. Péron (1899) studied two specimens, and it is likely that Cossmann (1904) illustrated one of them. Notably, Péron (1899) did not mention the presence of denticles on the columellar lip. Photographs of the type material are displayed in www.stromboidea.de (Wieneke *et al.* 2018).

Stratigraphic and geographic occurrence. Neocomian of Volvent, France.

Colombellina sp. 1

Figure 2.14

*1867 *Columbellina* (sic!) sp.; Stoliczka, p. 139, pl. 12, fig. 1.

Material. One specimen (GSI-577) from Cenomanian? (Upper Cretaceous) Ootatoor (=Uttattur) Group near Odium, India.

Description. Preserved fragment of three whorls with a dissolved outer layer of the shell surface and a broken half of the last whorl; whorls convex, separated by an incised suture; ornamentation of shell surface unknown; a weakly expressed trace of a cord situated in the middle part of the penultimate whorl is visible and could be the place where the axial ribs became thickest. Judging from cast, aperture narrow, curved and with anterior canal; outer lip thickened with folds, traces of which are preserved on the outer side of the outer lip; traces of folds visible on the columellar part; traces of varices occur on the surface of the last whorl close to the aperture, which can indicate the place of thickening of the outer lip.

Measurements (mm):

Specimen number	H	W	SA
GSI-577	26.5	17.2	62°

Remarks. Stoliczka (1867–1868) indicated preservation of this specimen as a cast noting the absence of any surface ornamentation on it. Consequently, he classified it as *Colombellina* due to aperture characters leaving the species name in open nomenclature. We consider this specimen

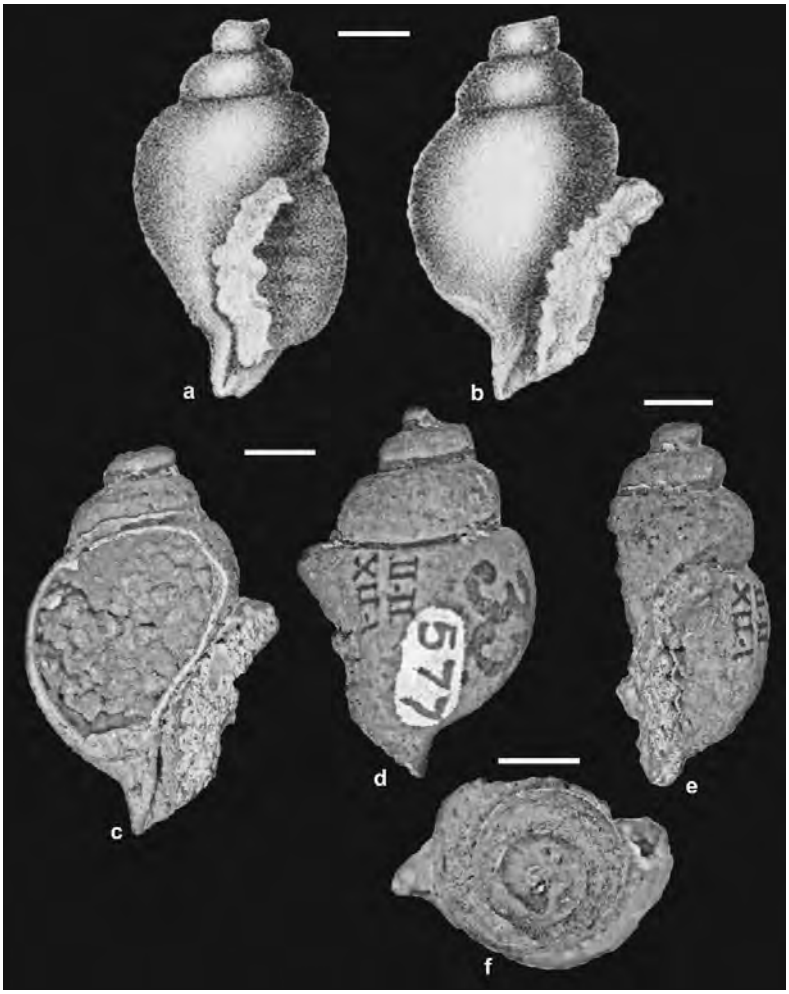

Fig. 2.14. — *Colombellina* sp. 1 from Cenomanian (Upper Cretaceous) Ootatoor (Uttattur) Group; near Odium, southern India. A–B, Figured by Stoliczka specimen (1867: pl. 12, fig. 5, 5a). C–F, Stoliczka collection in Geological Survey of India, No GSI-577. C, aperture view, D, abapertural view, E, lateral view, showing traces of folds on the outer side of the thickened outer lip, F, apical view. Scale bars represent 5 mm. For A–B an approximate scale bar is added.

undoubtedly belonging to the genus *Colombellina*, but its preservation does not allow a species-level identification.

A detailed provenance of this specimen is unknown. The area around Odiyam (Odium) in Tamil Nadu was mapped by Watkinson *et al.* (2007) as exposing Karai Shale ranging from Albian to Turonian in age. The GSI collection data indicated that the specimen is Cenomanian in age, although we use this information with caution, pending more data on the origin of the specimen.

Colombellina sp. 2

Figure 2.15

*1873 *Columbellaria* sp. Zittel, pl. 40, fig. 5.

Material. Two specimens from the Tithonian–Berriasian of Chotěbuz (Kotzobenz in Zittel 1873), Czechia (SNSB-BSPG AS III 911, 912).

Description. Shell with 1.5 whorls preserved; last whorl large and oval, ornamented with ca. 13 nodose spiral cords; interspaces between spiral cords wider in adapical part; peristome siphonostomatous; aperture narrow with anterior and posterior canals; morphology of lips unknown.

Measurements (mm):

Specimen number	H_{lw}	W
SNSB-BSPG AS III 911	26.2	23.3
SNSB-BSPG AS III 912	24.4	22.1

Remarks. Two specimens from the SNSB-BSPG collection described by Zittel (1873) are assigned to *Colombellina* sp. 2, but their poor preservation—one being a mould and the other a fragment of an eroded shell—prevents a more precise identification.

Colombellina? *dentata* de Loriol, 1861

Figure 2.16 A–C

1861 *Colombellina dentata* de Loriol, p. 49, pl. 5, figs. 5, 6.

Remarks. De Loriol (1861) did not indicate the number of examined specimens, noting that this species is rare. One of the specimens figured by him was from the Pictet collection. In the description, de Loriol (1861) also noted that the axial ribs are nodose and the outer lip has traces of four folds. We assigned this species to the genus *Colombellina* with some reservations since the species is represented only by composite moulds with only partly preserved generic characters.

Stratigraphic and geographic occurrence. Neocomian of La Varappe, France.

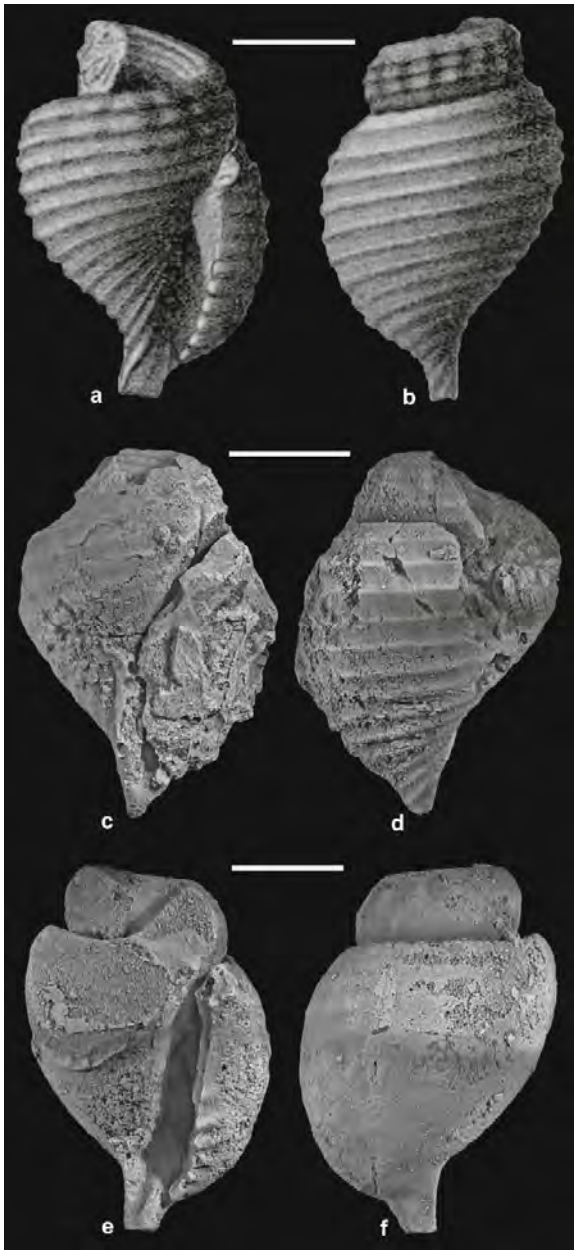

Fig. 2.15. — *Colombellina* sp. 2 from the Tithonian; Chotěbuz (Kotzobenz), Czechia. A–B, Figured by Zittel specimen (1873: pl. 40, fig. 5a, b). C–D, SNSB-BSPG AS III 912, C apertural view, D, abapertural view. E–F, SNSB-BSPG AS III 911. E, apertural view, F, abapertural view. It can be hypothesised that these specimens were utilised by Zittel (1873) for the creating a compiled figure (A–B herein). Scale bars represent 10 mm. For A–B an approximate scale

Colombellina? maxima de Loriol, 1861

Figure 2.16 D–F

1861 *Colombellina maxima* de Loriol, p. 48, pl. 5, figs. 2–4.

1864 *Columbellina maxima* de Loriol; Pictet & Campiche, p. 669, pl. 96, fig. 8, 10, pl. 97, fig. 1.

2002 *Colombellina maxima* de Loriol; Kollmann, p. 45, pl. 2, figs. 23, 24.

Material. One specimen from the middle Neocomian of Breiterberg, close to Bad Haslach, Austria (SNSB-BSPG 1867 XII 530).

Description. Shell fusiform; apex not preserved; spire distinctly elevated, gradate; teleoconch consists of 4 preserved whorls separated by incised suture; spire whorls angulated and sculptured

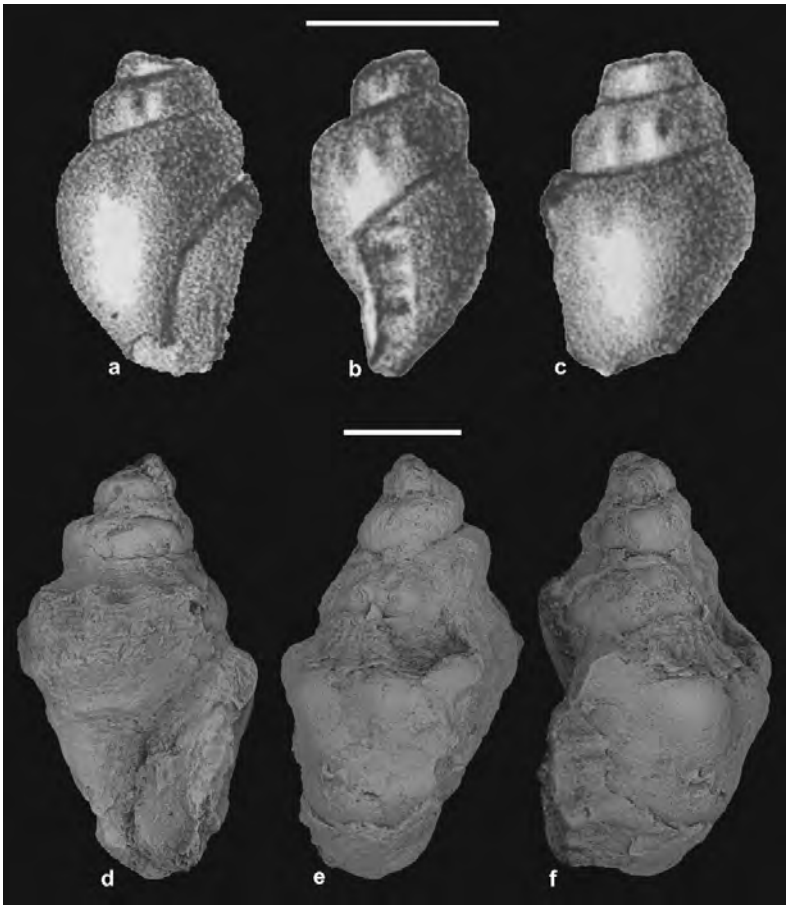

Fig. 2.16. — A–C, *Colombellina*? *dentata* de Loriol, 1861 from the Neocomian; La Varappe, France, specimen figured by de Loriol (1861: pl. 5, figs 5, 6), A, apertural view, B, lateral view, C, abapertural view. D–F, *Colombellina*? *maxima* de Loriol, 1861 from the middle Neocomian; Breiterberg, close to Bad Haslach, Germany; SNSB-BSPG 1867 XII 530, D, apertural view, E, abapertural view, F, lateral view. This specimen was also figured by Kollmann (2002: pl. 2, fig. 24). Scale bars represent 10 mm.

by strong prosocline axial ribs; last whorl large, ornamented with fine spiral cords of two orders and ca. 9 strong axial ribs, which become more prominent in the adapical third with pronounced nodes at shoulder; two strong spiral cords occur below shoulder, extending onto outer part of the flared outer lip; aperture narrow, with anterior and posterior canals.

Measurements (mm):

Specimen number	H	W	SA
SNSB-BSPG 1867 XII 530	36.2	20.2	50°

Remarks. De Loriol (1861) noted that the species is rare. He illustrated three specimens, one of which was from the collection of Pictet. Pictet & Campiche (1861–1864) did not specify the number of studied specimens, but they indicated collections from different researchers, who collected *C*? *maxima* from five localities. Kollmann (2002) examined three specimens, one of which—housed at the Bavarian State Collection for Palaeontology and Geology in Munich, Germany—was also studied by us and is illustrated herein (Fig. 2.15) (the same specimen was illustrated by Kollmann, 2002: pl. 2, figs. 23, 24). De Loriol (1861) and other researchers examined only internal moulds of this species. The specimen we investigated has a partially

preserved shell. Since the aperture morphology remains poorly known, we assign this species to *Colombellina* with some reservation.

Stratigraphic and geographic occurrence. Lower Cretaceous of Mont Salève (Suisse) and Mauremont, France, and Sainte-Croix, Landeron, Russille near Orbe, and Bôle near Boudry, Switzerland (Sainte-Croix, Landeron, Russille near Orbe, Bôle near Boudry), upper Valanginian–basal lower Hauterivian of Breiterberg and Bad Haslach, Austria.

Superfamily Tonnoidea Suter, 1913 (1825)

Family Personidae Gray, 1854

Genus *Wadeina* nov.

Type species. *Colombellina americana* Wade, 1926; Tennessee, USA, upper Campanian (Upper Cretaceous).

LSID: urn:lsid:zoobank.org:act:3F54A8D1-EA55-4459-8A74-72E8B44AB8A5

Etymology. In honour of Bruce Wade (1889–1973) for his contribution into study of Late Cretaceous gastropods and other molluscs from USA localities.

Diagnosis. Thick, oval shell with low spire, ornamented with broad, nodose spiral cords and axial ribs; protoconch obtusely conical; last whorl large and inflated; peristome siphonostomatous and thickened; columella with folds; aperture oval with deep curved short anterior canal and short posterior canal; columellar lip expanded, plicato-dentate, spreading out onto the last whorl; outer lip armoured, denticulate, with a thickened edge and bent outward.

Species included. Type species only.

Remarks. The genus is represented by a single species so far, whose shell shape and aperture morphology clearly distinguish it from other Upper Cretaceous gastropods. Although only partly preserved in the examined specimens, the protoconch still allows comparison with members of the family Personidae due to its obtusely conical shape with convex whorls (see also Kronenberg, 1994; Beu, 1998). The expanded and thickened peristome and plicato-dentate lips also indicate an attribution to Personidae. However, the varices typical in Tonnoidea in *Wadeina* are represented only by a varicose outer lip.

Wadeina gen. n. differs from *Colombellina* by its wider oval aperture, with a parietal canal that is almost perpendicular to the shell axis, does not extend to the penultimate whorl, and does not notch the peristome. *Wadeina* also possesses three columellar folds and has an inner lip that is not closely adjacent to the last whorl, and has a thickened edge. Additionally, the

ornamentation of *Wadeina* comprise thick nodose spiral cords instead of rows of nodes on the last whorl as in *Colombellina*.

Stratigraphic and geographic occurrence. Campanian of Tennessee and Mississippi, USA.

Wadeina americana (Wade, 1926)

Figures 2.17, 2.18

1926 *Columbellina americana* Wade, p. 153, pl. 53, figs. 14, 15.

1960 *Colombellina*? *americana* Wade; Sohl, p. 111, pl. 14, figs. 1–3, 6, 7.

2012 *Neocolombellina americana* (Wade); Bandel & Dockery, p. 102.

2016 *Colombellina americana* Wade; Bandel & Dockery, p. 51.

Holotype. USNM PAL 32933.

Material. Two specimens (ZPAL Ga.21/3, 4) from the upper Campanian of Coon Creek, McNairy County, Tennessee, USA.

Description. Shell thick, oval, with low spire; protoconch obtusely conical with 1.2 preserved whorls, the demarcation between the protoconch and the teleoconch is clearly visible; teleoconch consists of 2.5 convex whorls increasing rapidly in size and separated by incised suture; spire whorls ornamented with two thick nodose spiral cords and much thinner axial ribs; one thin nodose spiral cord located close to adapical suture; last whorl large and inflated, height of about five-sixths of shell height; last whorl ornamented with six strong nodose spiral cords with interspaces slightly wider than their thickness, and thinner axial ribs; the interspaces between the massive elements of ornamentation are covered with spiral and axial threads, which are clearly visible on the less eroded specimen ZPAL Ga.21/4 (Fig. 2.18); peristome siphonostomatous and thickened; columella with three folds; aperture oval with deep, curved short anterior canal and short posterior canal, which does not notch the peristome; columellar lip thickened by a callus spreading out onto the last whorl, with thickened edge which does not fit tightly to last whorl; columellar lip featuring approximately nine additional folds; surface of columellar lip with micro-ornamentation of distinct tubercles; outer lip with five denticles, two of which close to posterior canal are larger, with thickened edge and bent outward.

Measurements (mm):

Specimen number	H	W	WPr	SA
ZPAL Ga.21/3	6.4	4.7	0.85	85°
ZPAL Ga.21/4	6.2	3.4	0.74	84°

Remarks. Originally this species was included in the family Columbellariidae (Wade, 1926) and then in Colombellinidae (Sohl, 1960; Bandel & Dockery, 2012, 2016). Wade (1926: p. 153) noted that “there is no known American species of this genus with which it may be compared”,

so he compared it with *Colombellina* from the Neocomian (Lower Cretaceous) of France, although the Campanian specimens are twice times smaller and have a less acute spires.

In the description of *W. americana*, Wade (1926) noted that the protoconch is submerged. Sohl (1960: p. 111), examined his own material comprising ten specimens, listed in a table with measurements, and Wade's (1926) type material. He observed that "many of the specimens show

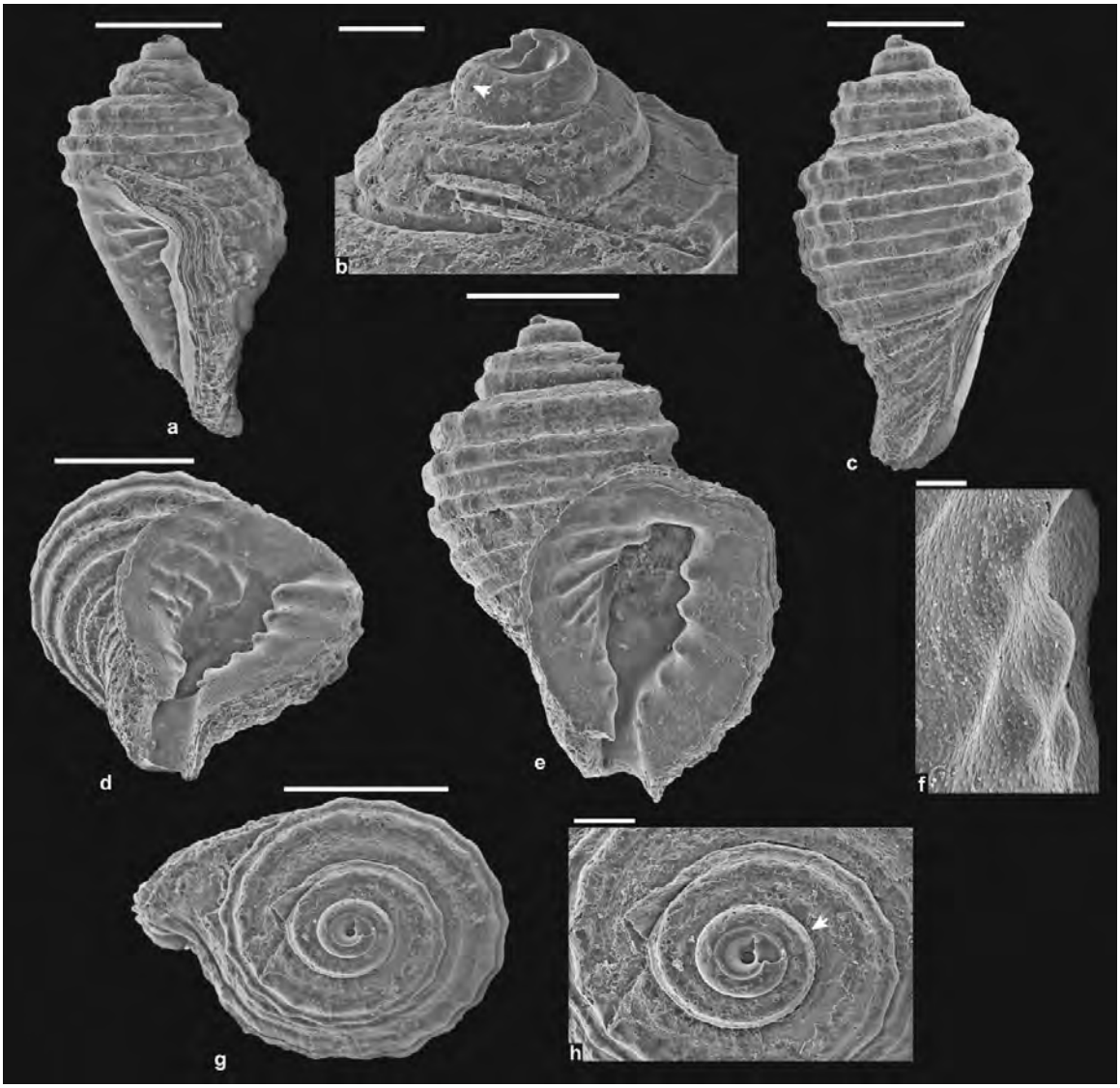

Fig. 2.17. — *Wadeina americana* (Wade, 1926) from the upper Campanian, Coon Creek Formation; Coon Creek, Tennessee, USA. A–H, ZPAL Ga.21/3. A, lateral view of thickened edge of outer lip, C, abapertural view, B, lateral view, detail of early whorls, D, oblique basal view, E, apertural view, F, apertural view, detail of columellar lip morphology, G, apical view, H, apical view, detail view of early whorls. White arrows indicate protoconch margin. Scale bars represent: 2 mm (A, C-E, G); 0.5 mm (B, H); 0.1 mm (F).

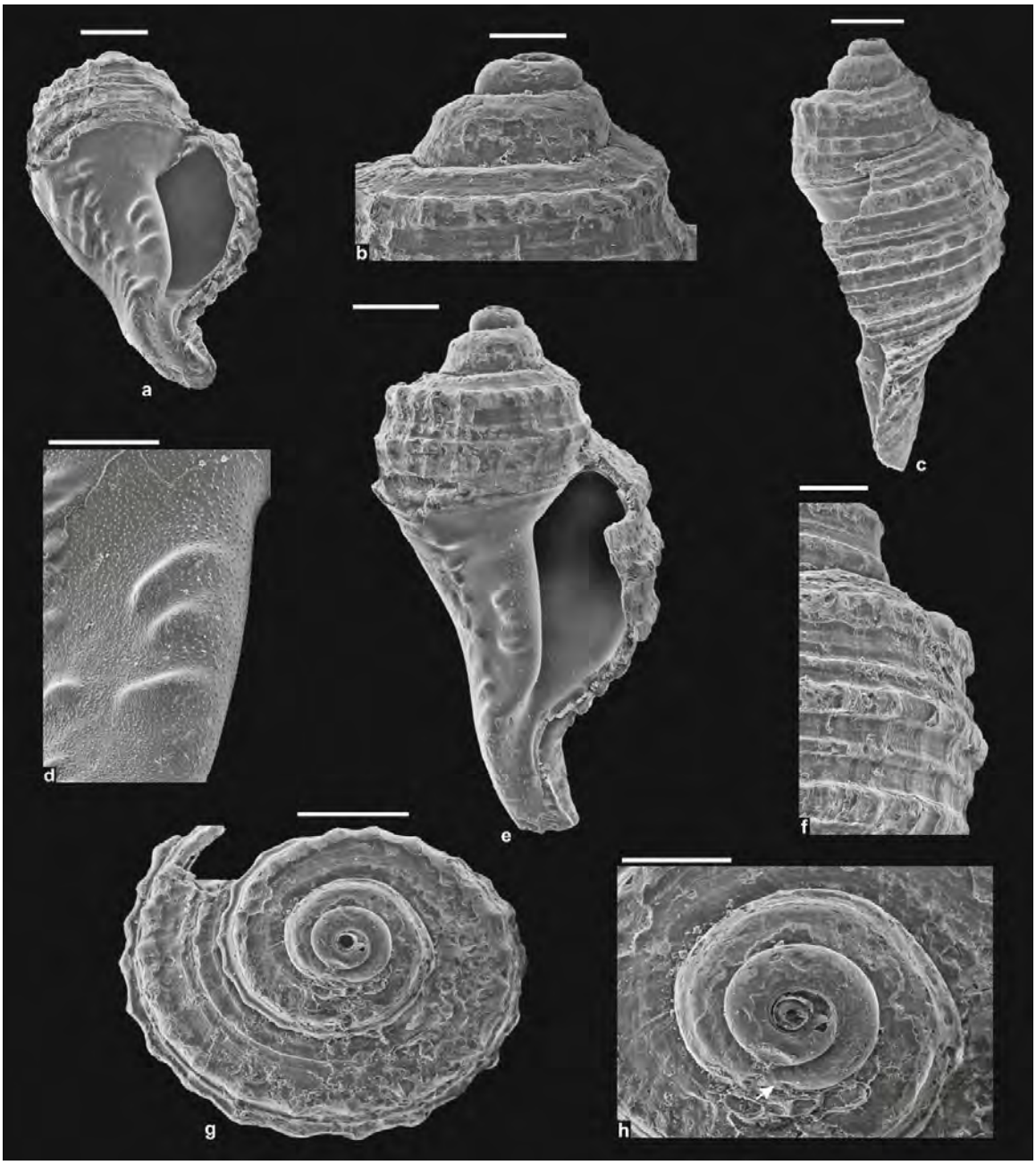

Fig. 2.18. — *Wadeina americana* (Wade, 1926) from the upper Campanian, Coon Creek Formation; Coon Creek, Tennessee, USA. A–H, ZPAL Ga.21/4. A, oblique basal view, B, lateral view, detail of early whorls, C, lateral view, D, apertural view, detail of columella folds, E, apertural view, F, lateral view, detail of last whorl ornamentation, G, apical view, H, apical view, detail view of early whorls. White arrow indicates protoconch margin. Scale bars represent: 1 mm (A, C, E); 0.5 mm (B, D, F-H).

the protoconch to be broken and the teleoconch to be sealed by a septum, which is adapically hemispherical and continuous with the inner shell layer". In our specimens, the protoconch is only partially preserved, missing the initial whorls, so we cannot definitively assert whether it is submerged. However, from the preserved part, it is evident that the protoconch is obtusely conical.

Bandel & Dockery (2012) described a new genus *Neocolombellina*, with a type species *N. cancellata* (Dockery, 1993) and assumed that it could be conspecific with *C. americana*. Later, Bandel & Dockery (2016) reverted to the earlier definition and placed *C. cancellata* and *C. americana* in *Colombellina*, but the reasons for this change were not disclosed.

Wadeina americana differs from *Neocolombellina cancellata* (allegedly tonnoid, see below) by its wider shell outline and the aperture morphology with a thickened and dentate outer lip, which Bandel & Dockery (2012) interpreted as probable maturity differences, though no evidence was provided to support this assumption. Additionally, *W. americana* differs from *N. cancellata* in its non-reticulate ornamentation and in a thickened peristome, at nearly having the same size and number of whorls (hence, approximately at the same growth stage). We therefore do not consider the thickened peristome of *W. americana* as result of a different maturity stage when compared to *N. cancellata*. In our opinion, the different aperture morphology of these species indicate that they belong to different genera.

Stratigraphic and geographic occurrence. Upper Campanian (Coon Creek Formation) of Tennessee and Mississippi, USA.

DISCUSSION

Family taxonomy and comparison with related taxa

Our revision has revealed that Colombellinidae should be restricted to two genera only—*Colombellina* d'Orbigny, 1842, and *Zittelia* Gemmellaro, 1869. All the other genera previously assigned to the family (Table 2.2) should be moved to other high rank taxa. After comparing the type species of *Colombellina* and *Columbellaria*, we did not find any significant differences to justify separating these two genera. Therefore, we consider *Columbellaria* as a junior subjective synonym of *Colombellina*. The genus *Zittelia* is fully justified by the presence of a unique diagnostic character i.e., a sinuosity that is present in the abapical part of the aperture (Bakayeva *et al.* 2025), which may, however, also be present in *Coffeacypraea* (see below).

The oldest record of cypraeids is known from two species—*Coffeacypraea gemmellaroi* (Di Stefano, 1882), and *Coffeacypraea tithonica* (Di Stefano, 1882)—documented from the *Tithonian* of Italy (Sicily) by Di-Stefano (1882) and recently reviewed by Nützel *et al.* (2025). This is followed by the Barremian–Aptian *Cypraea antiqua* Sayn, 1932 and *Coffeacypraea drumensis* (Sayn, 1932) from Barcelonne, France, where they are accompanied by a single species of *Colombellina* (Sayn, 1932).

Sayn (1932: p. 32, text-fig. 10, pl. 3, figs. 8, 9) originally assigned *Coffeacypraea drumensis* to the genus *Zittelia* (Bakayeva *et al.* 2025). Although the species, according to Sayn (1932), seem to display the characteristic anterior sinuosity typical of *Zittelia*, it also bears

approximately twenty fine columellar teeth—a feature not observed in other species of *Zittelia*. Since the shell outline and gross aperture morphology more closely resemble the recently described genus *Coffeacypraea* Nützel & Schneider, 2025, and the presence of an anterior sinuosity in the latter is uncertain (Nützel *et al.* 2025), Bakayeva *et al.* (2025) placed this species to *Coffeacypraea* with some hesitation. This might be an intermediate species (with a mix of characters) between *Zittelia* and *Coffeacypraea.*

Cypraea antiqua, which was compared by Sayn (1932) to some species of *Palaeocypraea* Schilder, 1928, from the Danian, Paleocene (Schilder, 1928), lacks denticles in the aperture, although this absence could also be due to preservation. On the other hand, this could represent a variation in family characters, as is observed in the Recent cypraeids. *Coffeacypraea* from the *Tithonian* exhibits characteristics (shell outline, aperture morphology) similar to modern and Late Cretaceous (Roman & Mazeran, 1920; Groves, 1990, 2004; Groves *et al.* 2011), as well as to the Paleocene species (Schilder, 1928; Groves & Squires, 2023). However, none of these authors noted the presence of anything resembling the anterior sinuosity that is diagnostic for *Zittelia* (Bakayeva *et al.* 2025) and, perhaps, also present in *Coffeacypraea*.

Nonetheless, some relationship between *Zittelia* and Cypraeidae, previously considered also by Sayn (1932) and Groves (1994), is still indicated by the presence of a prominent infracolumellar groove (which might be a homologue of the anterior sinuosity in *Zittelia*) at the abapical end of the aperture in the Oligocene species *Cypraeorbis* Conrad, 1865 (Cypraeidae), as demonstrated by Darragh (2011: fig. 1). Comparison between colombellinids and cypraeids, showing the morphological gradient between both groups, was recently discussed by Nützel *et al.* (2025).

The protoconchs of Colombellinidae (as revised herein) remain unknown to date. Some protoconchs were described from species of *Neocolombellina* from the Campanian (Upper Cretaceous) of Tennessee and Mississippi, USA (Dockery, 1993; Bandel & Dockery, 2012, 2016), which were previously included in Colombellinidae (Wade, 1926; Sohl, 1960) but are excluded from this family in the present study. During this research we noticed that another species, previously classified as *Columbellina americana* by Wade (1926), *Colombellina*? *americana* by Sohl (1960) and Bandel & Dockery (2016) and *Neocolombellina americana* by Bandel & Dockery (2012), differs from both colombellinids and *Neocolombellina* in the morphology of the peristome, characters of ornamentation, and *the absence of* varices. We, therefore, decided to describe the new genus, *Wadeina*, to accommodate this species. We assigned this new genus *to* the family *Personidae* (Tonnoidea) due to its peristome morphology and the obtusely conical protoconch. *Neocolombellina also resembles tonnoids in protochonch morphology and the presence of* varices, but most likely it belongs to yet another family within

Tonnoidea—mostly due to the significant differences in the peristome morphology. Despite the evident diagnostic differences, primarily expressed in the morphology of the aperture and posterior canal, there is some similarity between *Wadeina* and colombellinids in shell outline and siphonostomatous peristome gross morphology, with thickened plicato-dentate lips (Fig. 2.19). Interestingly, the obtusely conical protoconch of *Wadeina* with a clear demarcation with the teleoconch, also resembles purpurinid protoconchs which may indicate potential relationship of purpurinids with tonnoids and by extension also with colombellinids (Fig. 2.20).

Spatial and temporal distribution of Colombellinidae

A total of eighteen colombellinid species was so far recorded from the Jurassic (Fig. 2.1, Table 2.2), with eleven of them hypothetically crossing the Jurassic/Cretaceous boundary. However, this is not entirely clear, as stratigraphical ranges of some species are poorly constrained in the original descriptions, e. g., Tithonian–Valanginian of Sicily, Italy and Tithonian–Berriasian of Štramberk, Czechia, and may prove to be much narrower. The earliest species—*Colombellina bathonica*—comes from the Bathonian (Middle Jurassic) of France (Cossmann, 1899, 1913). Other species have been found in the Upper Jurassic of Germany, France, Switzerland, Italy, Czechia, Poland, and complemented herein by new materials from Bulgaria (a new species) and Czechia (Table 2.1).

Twenty-two species have been recorded from the Lower Cretaceous. In Europe, the family distribution includes France, Belgium, Switzerland, Austria, Czechia, Poland, and recently discovered from Bulgaria. Also, some species were identified in Asia, where they were documented in the Aptian–Albian (Lower Cretaceous) of Japan. It is noteworthy that while *Colombellina* extended beyond Europe, *Zittelia* is more geographically restricted and occurs in Europe only.

In the Cenomanian (lower Upper Cretaceous), the latest occurrence of the family Colombellinidae was recorded with two documented species: *Colombellina ornata* from France (d'Orbigny, 1842; Kollmann, 2005) and Germany (Kiel & Bandel, 2004), and possibly *Colombellina* sp. 1 from southern India (Stoliczka, 1867 and herein).

The majority of colombellinid species were described based on single specimen, with only a few species being recorded in larger numbers. For instance, Joukowsky and Favre (1913) recorded 25 specimens of *Zittelia picteti* from the Tithonian of Salève, France, whereas the original description by Gemmellaro (1869) was based on two specimens (Bakayeva *et al.* 2025).

Another species represented by a relatively large number of specimens is *Zittelia oppeli* from the Kimmeridgian of Valfin, France. It was noted by Guirand and Ogérien (1865) and Ogérien (1867) as being abundant enough to characterize a zone, although the authors did not

specify the number of studied specimens. We were able to examine the original material described by Guirand and Ogérien (1865), which is housed at the Museum of Confluences in Lyon, France. The collection comprises a total of 13 shells (Bakayeva *et al.* 2025). Apart from Valfin, *Zittelia oppeli* was also recorded in Rixouse and Salève, France (Étallon, 1859; de Loriol, 1886–1888; Joukowsky & Favre, 1913; Cossmann, 1904, 1913).

Two more species—*Zittelia laeviuscula* and *Z. crassissima*—are also relatively common judging from Zittel (1873) who listed 12 and ten specimens, respectively, from the Tithonian–Berriasian of Štramberk and Koňákov (both Czechia), and Wilamowice (Poland).

The genus *Colombellina* is represented by relatively few specimens. Only *C. corallina* has been recorded in greater numbers—Brösamlen (1909) documented 19 specimens from the Upper Jurassic of Nattheim and Württemberg, Germany, where the species had also been previously reported by Quenstedt (1852, 1858, 1884) and Cossmann (1913). Additionally, this species has been recorded from the Tithonian–Berriasian deposits of Štramberk, Czechia (Rolle, 1861; this study).

Palaeoecological insights

Colombellina is confined to shallow-water sediments with significant carbonate content in most of the cases where it was documented. The siliciclastic materials (sand, silt or clay) is mostly either absent or one of the subordinate components of the sediment. Thus, we assume that *Colombellina* was environmentally restricted to relatively shallow waters where carbonate was a main component of the sediment. *Colombellina* and the other colombellinid *Zittelia* are absent in the silty and clayey facies from the Jurassic and Cretaceous shelf areas extensively studied by Kaim (2001, 2004, 2008, 2011, 2012), Gründel (2003, 2007, 2010, 2012), and Tracey (2010). This clearly shows that the type of substrate (carbonate) and the water depth (shallow shelf, in or close to the photic zone) had a strong influence on the distribution of the group. An association with peri-reefal carbonates is likely (Bakayeva *et al.* 2025). A small number of findings might, to some extent, result from the family members being carnivores, and therefore their populations being relatively small. Because *Zittelia* and *Colombellina* preferred different types of bottom substrate and also displayed different distribution and especially abundance, it is possible, that *Zittelia* could be a scavenger or scavenger/predator, which commonly display gregarious behaviour (e.g., Morton, 1990; Morton & Jones, 2003) and *Colombellina* could be an apex predator. The differences in their feeding strategies may have also been expressed in size difference (*Colombellina* is larger in size than *Zittelia*, Fig. 2.13). Another reason for their scarcity could be taphonomic, as carbonate sediments frequently undergo recrystallization during diagenesis, with dissolution and recrystallization being a common processes among

aragonitic fossils. The diagenesis would be most detrimental to the preservation of juvenile and larval shells, which up to date have not been recorded. Notably, both colombellinid genera are absent from the very shallow water, lagoonal and peritidal carbonates in the study interval which are instead dominated by nerineid and acteonellid gastropods (Kollmann, 2014).

The Middle–Late Jurassic occurrences of *Colombellina* come from the north-western part of the Tethys where tropical carbonates were deposited. This was a time when western Tethys was tectonically fragmented to horst-and-graben structures, characterized by high horizontal and vertical facies variability, from peritidal to relatively deep marine (e.g., Basilone & Sulli, 2016; Granado *et al.* 2019). Therefore, insights into palaeoecology of *Colombellina* based on facies alone might be equivocal. In case of some materials with well established origins, like those from Tithonian–Berriasian of Štramberk area, it is clear that the materials come from peri-reefal facies associated with coral reefs (Vaňková *et al.* 2019). The same is true for Late Jurassic materials from Jura Platform in France and Switzerland which contains coral reefs (e.g., Enay, 1965; Bernier, 1984).

Early Cretaceous, especially Barremian–Aptian, was a time of wide-spread formation of the so-called Urgonian reefs formed chiefly of rudist bivalves and corals, with contribution of other biota like chaetitids, stromatoporoids and algae (e.g., Masse & Ferenci-Masse, 2013; Bonvallet *et al.* 2019). It is noteworthy that at least some French materials (*Colombellina hebertina* and *Colombellina* cf. *subaloysia*), could come from Urgonian reef-associated facies. This is also true for the Bulgarian specimens from Veliko Tarnovo, where the presence of Urgonian facies is well recognized (e.g., Kołodziej *et al.* 2012).

Colombellina was apparently restricted to the Western Tethys for most of its stratigraphic range (Bathonian–Aptian). It is only by the Aptian when first record from outside this area is know, that being *Colombellina oginoi* from Iwate Mts, northern Honshu, Japan (Kase, 1984). It is difficult to explain why *Colombellina* spread from the Western Tethys to Panthalassa only by the Aptian, ca. 47 Ma after it emerged. Its occurrence in the Aptian of Japan coincides with extension of rudist-bearing shallow-water facies as far north-east as Hokkaido (Sano, 1995), which could have been a contributing factor. Indeed, some small Aptian coral-rudist bioconstructions have been reported from Miyako Group in Iwate Mountains where *C. oginoi* comes from (Sano, 1991), an argument for the hypothesis that *Colombellina* dispersed via shallow-water peri-reefal environments where it lived. The timing of this dispersal is, however, unclear. Two possibilities are that (i) it was a gradual processes taking place during prior to the Aptian, but it has no reflection in the fossil record and hence the apparent isolated record in the Aptian of Japan, or (ii) it was more rapid process taking place shorty before and during the

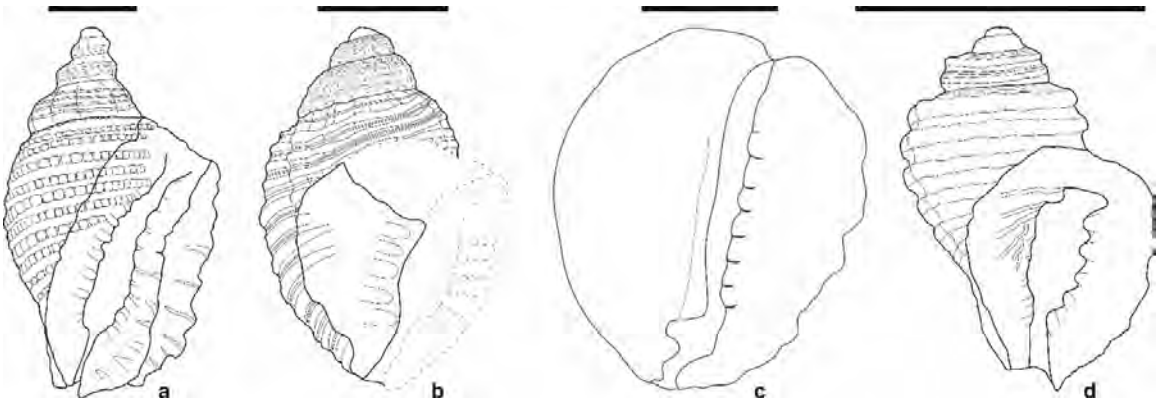

Fig. 2.19. — Comparison of colombellinid genera *Colombellina* d'Orbigny, 1842 (**A, B**) and *Zittelia* Gemmellaro, 1869 (**C**) with tonnoid genus *Wadeina* gen. n. (**D**). A – *Colombellina corallina* (von Quenstedt, 1852) – the type species of *Columbellaria* Rolle, 1961, that is synonymized with *Colombellina* herein. B – *Colombellina monodactylus* (Deshayes *in* Leymerie, 1842) – the type species of *Colombellina*. C – *Zittelia cipraeaeformis* Gemmellaro, 1869 – the type species of *Zittelia*. D – *Wadeina americana* (Wade, 1926) – the type species of *Wadeina*. Drawings are based on the specimens figured herein (Figs 2.5, 2.3, and 2.8 respectively). Type species of *Zittelia* from G.G. Gemmellaro collection (1869) is re-described by Bakayeva *et al.* 2025. Scale bars represent 5 mm.

Aptian, and the occurrence of *Colombellina* in present-day Japan reflects this. An arguments second possibility is a wide-spread distribution of Urgonian facies in Central Asia in the Barremian–Aptian, e.g., Iran and Turkmenistan (e.g., Prosorovsky, 1990; Cerević *et al.* 2013), indicating that the route of dispersal east via shallow-water carbonate facies was available at that time.

Although the protoconch of colombellinids remains unknown, the spatial restriction and even endemism of most species indicates a limited dispersal potential and probably a non-planktotrophic development. It is striking that their range was limited to the European shallow carbonate shelf seas extended further eastwards (Japan) only when wide-spread reef belt was established around the Barremian–Aptian enhancing their dispersal. Further studies of the Central Asian Early Cretaceous gastropod faunas are needed before this hypothesis can be discussed further.

With the onset of Cenomanian transgression, and progressive drowning of shallow-water carbonates, *Colombellina* progressively disappears from the fossil record. Two unusual records of *Colombellina* from Cenomanian break the pattern of association between this genus and shallow-water peri-reefal facies. First record comes from Kassenberg quarry near Mühlheim am den Ruhr (Northern Germany), where Cenomanian carbonate fillings in Carboniferous sandstone containing *Colombellina* represent deposit of the Cenomanian rocky shore (Kiel & Bandel, 2004). The second occurrence is *Colombellina* sp. coming from Cauvery Basin in southern India, and is remote in comparison with other occurrences of *Colombellina*. The precise geological context is unknown; its alleged occurrence is near Odium (Odiyam) in Tamil Nadu, where the

outcrops of Karai Shale occur (Watkinson *et al.* 2007). If this is to be taken literally, than this would be the only record of *Colombellina* coming from fine grained shale deposits. However, we are uncertain as to how precisely this locality is indicated, and are aware of shallow-water carbonates with corals occurring in the vicinity of Odium (Odiyam) (Watkinson *et al.* 2007). Likewise, Karai Shale does contain some shallow water sandstone beds (Watkinson *et al.* 2007) and beds of carbonates redeposited from shallow water situations (Chakraborty *et al.* 2018), therefore the Indian specimen may just as well originally come from shallow water siliciclastic or carbonate environments.

The available data thus indicate that, similarly to *Zittelia* (Bakayeva *et al.* 2025), *Colombellina* occurred mostly in shallow-water, peri-reefal environments of the tropical Tethys and adjacent areas, and reach peak of its palaeogeographic distribution when such environments become available in the Early Cretaceous. The Cenomanian transgression, while extended the geographic range of the genus even further beyond the tropical Tethys, contributed to its extinction as it eventually flooded the shallow-water environments where *Colombellina* lived.

Phylogenetic considerations

Wadeina is similar to *Colombellina* in peristome morphology and was previously considered congeneric (Wade, 1926; Sohl, 1960; Dockery, 1993; Bandel & Dockery, 2012, 2016). The obtusely conical protoconch with a clear demarcation between the teleoconch in *Wadeina* resembles the protoconch of both purpurinids and tonnoids. As discussed earlier (Bakayeva *et al.* 2024), tonnoids possibly evolved from purpurinids in the Early Jurassic, indicating that *Colombellina* may have similar ancestry. Temporal succession indicates that the common ancestor of colombellinids and tonnoids could be purpurinids, from which they separated probably in the Early Jurassic (Fig. 2.20). During the Middle Jurassic, these lineages further diverged, with one branch giving rise to tonnoids and the other to colombellinids.

Cypraea seems to be related to *Zittelia* due to the diagnostic characteristics mentioned above and discussed in detail by Nützel *et al.* (2025). The oldest record of cypraeids comes from the Tithonian (Di-Stefano, 1882; Groves, 1994; Nützel *et al.* 2025), while forms similar to recent *Cypraea* were documented from the Barremian–Albian alongside *Colombellina* from the same strata (Sayn, 1932). This may indicate that the branching of Cypraeidae from Colombellinidae occurred earlier than the Tithonian, perhaps around the Middle–Late Jurassic, when the radiation of colombellinids is observed.

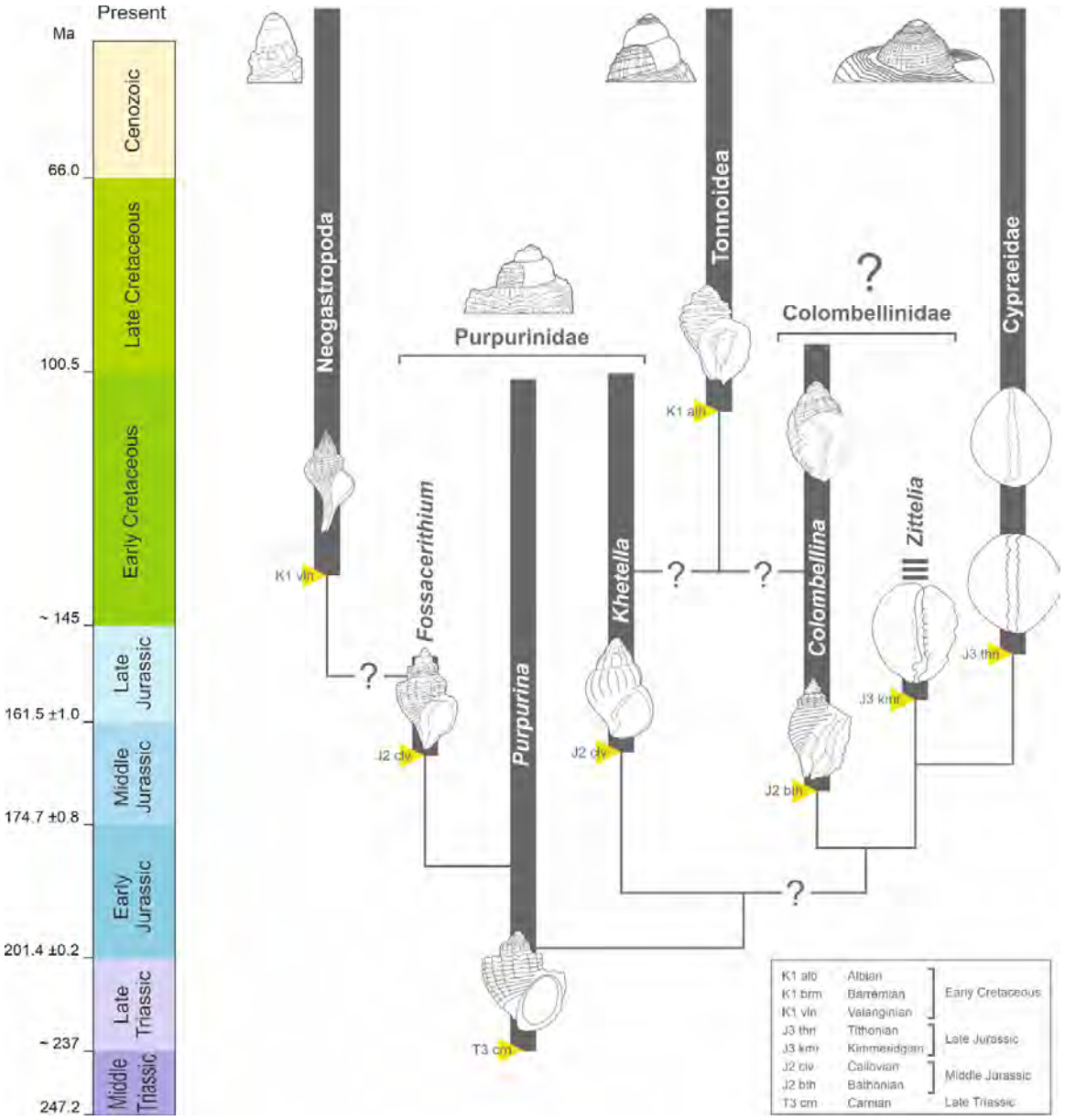

Fig. 2.20. — Hypothesised relationship of Colombellinidae with other clades. The earliest documented records of genera are indicated by yellow triangles.

CONCLUSIONS

The study of all available published data and recently collected materials has allowed a revision of the diagnosis and taxonomic composition of the family Colombellinidae. We include two genera—*Colombellina* d'Orbigny, 1842, and *Zittelia* Gemmellaro, 1869—within the family, while all other previously assigned genera should be excluded. *Columbellaria* Rolle, 1861, was synonymized with *Colombellina* as a junior subjective synonym. *Colombellina* comprises 19 species, and *Zittelia includes nine species. One genus of Tonnoidea, Wadeina, gen. n. from the*

Campanian of Tennessee (USA) and one species of Colombellinidae, Colombellina crassigranulata sp. nov. *from the Upper Jurassic of Bulgaria, are described.*

The similarities in shell morphology of *Wadeina gen. n.*, in particular the aperture, indicate possible phylogenetic connection between colombellinids and tonnoids, leading to a refined understanding of their relationship.

Colombellina monodactylus (Deshayes, 1842) has been recorded from the Barremian (Lower Cretaceous) of Veliko Tarnovo (Bulgaria) for the first time. In addition, a new species *C. crassigranulata* sp. nov. is described from the Upper Jurassic of Leskovets/Kopanitsa, also in Bulgaria. These records have expanded the known range of the genus, as *C. monodactylus* was previously known exclusively from France.

The occurrence of the group representatives exclusively in carbonate deposits indicates that they inhabited carbonate depositional environments, preferring shallow shelf seas, most likely the peri-reefal areas. Their low abundance and high endemism indicate that they could have been carnivorous.

The presence of an infracolumellar groove in some cypraeids, which might be a homologue of the anterior sinuosity, a diagnostic character of *Zittelia*, highlights their phylogenetic relations and supports the hypothesis that *Zittelia* is a stem group of the Cypraeidae. The separation of *Cypraea* from other colombellinids could have occurred around the Middle–Late Jurassic.

CHAPTER III

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

*Bakayeva, S., D'Arpa, C., Berthet, D., Hryniewicz, K., Nützel, A. & Kaim, A., 2025. Stem cypraeid gastropods – a revision of the genus *Zittelia* Gemmellaro, 1869. *Annales Societatis Geologorum Poloniae*, 95: 93–118. https://doi.org/10.14241/asgp.2025.09

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 cypraeaeformis* 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.

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. 3.1) and possibly lowermost Cretaceous (Berriasian–Valanginian) carbonate sediments from several localities within Europe (Fig. 3.2; Tab. 3.1; Étallon, 1859; Guirand and Ogérien, 1865; Gemmellaro, 1869; Zittel, 1873; Futterer, 1892; Brösamlen, 1909; Joukowsky and Favre, 1913; Gründel *et al.*, 2019, 2022).

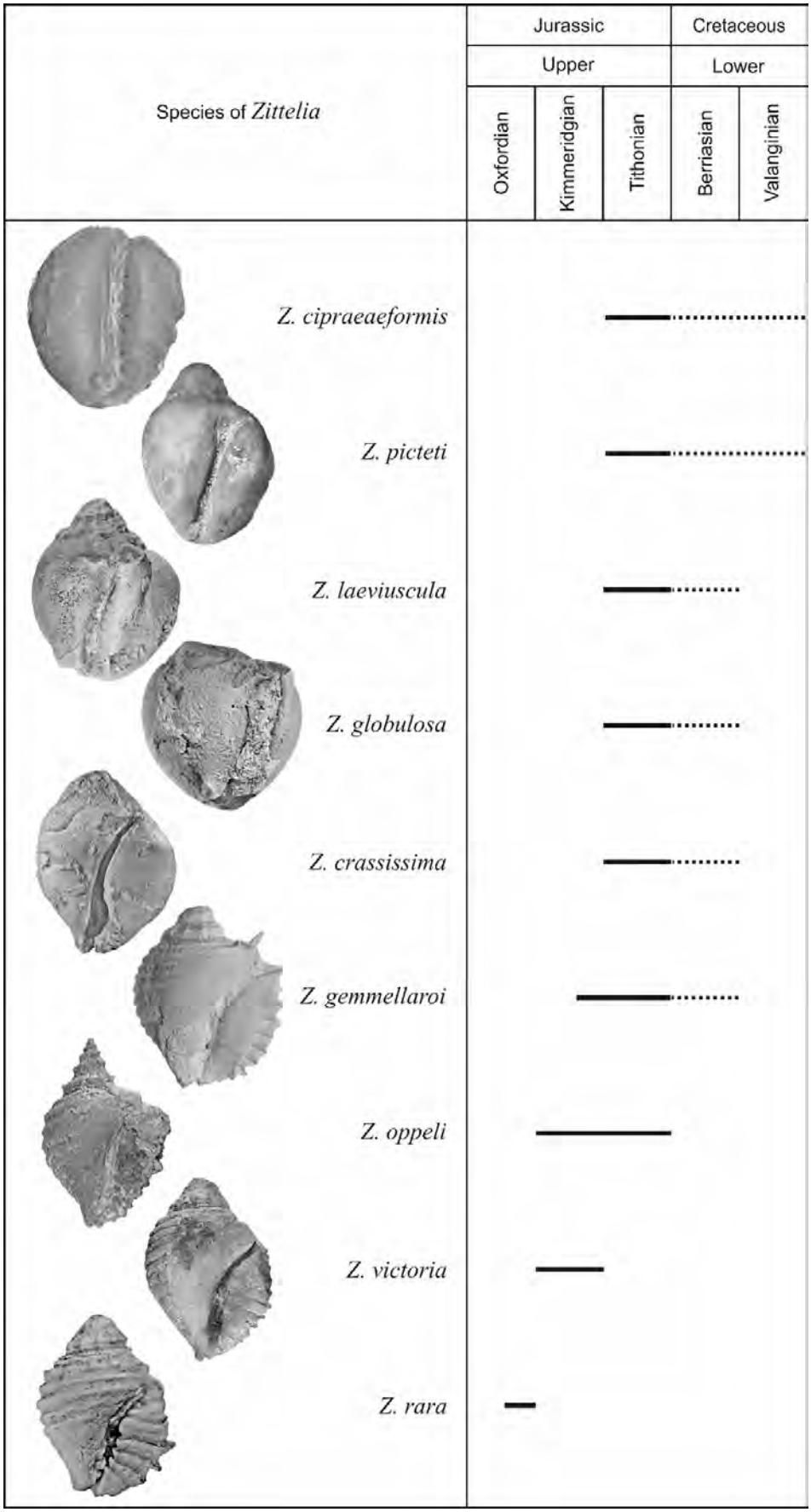

Fig. 3.1. — Stratigraphic distribution of *Zittelia* in the Upper Jurassic and Lower Cretaceous.

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*

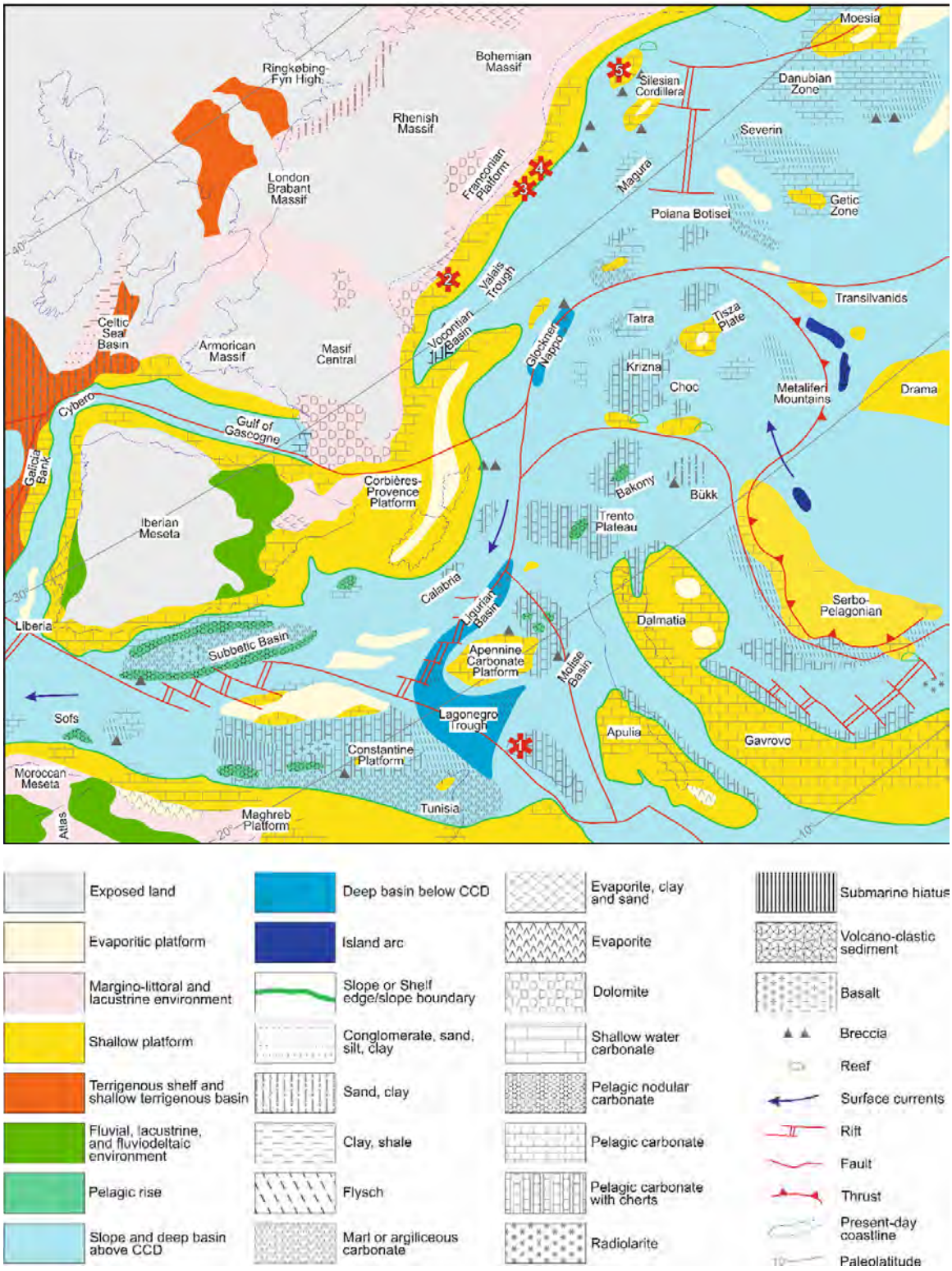

Fig. 3.2. — Late Tithonian palaeoenvironments (redrawn and simplified from Fourcade *et al.*, 1993) with records of *Zittelia*: 1 – Sicily, Italy, 2 – Rhône-Alpes, France, 3 – St-Ursanne, Switzerland, 4 – Swabia, Germany, 5 – Moravian-Silesian region, Czechia and Poland.

Table 3.1. — 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 and 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

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 and 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 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. 3.2 for the list of localities). The MGUP specimens were photographed by CDA, and the MDC specimens were photographed by DB. 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. 3.3), 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. 3.4J).

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.

The specimens housed at the Museum of Confluences in Lyon, France (Fig. 3.5) were originally described by Guirand and Ogérien (1865) and subsequently investigated again by de

Table 3.2. — 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 (lectotype), 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

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

Fig. 3.3. — *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.

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

Fig. 3.4. — 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. 3.5. — 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.

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 and Menkveld-Gfeller, 2022), and *Z. victoria* (Guirand and 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 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 3.3A, 3.4

*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.

Table 3.3. — 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°

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. 3.3) 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.

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 3.6, 3.7

*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

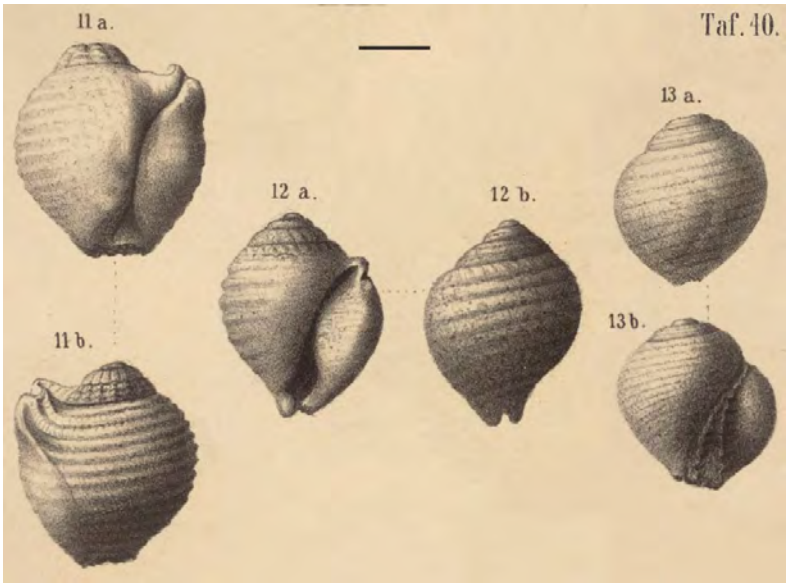

Fig. 3.6. — Reproduction of Zittel's (1873, pl. 40, figs 11–13) drawings of three specimens of *Zittelia crassissima* Zittel, 1873 from Štramberk (11, 12) and Koňákov (13), Czechia, illustrating differences in sizes and in shell shape: more elongated (12a, b) and almost globose (13a, b). An approximate scale bar represents 5 mm.

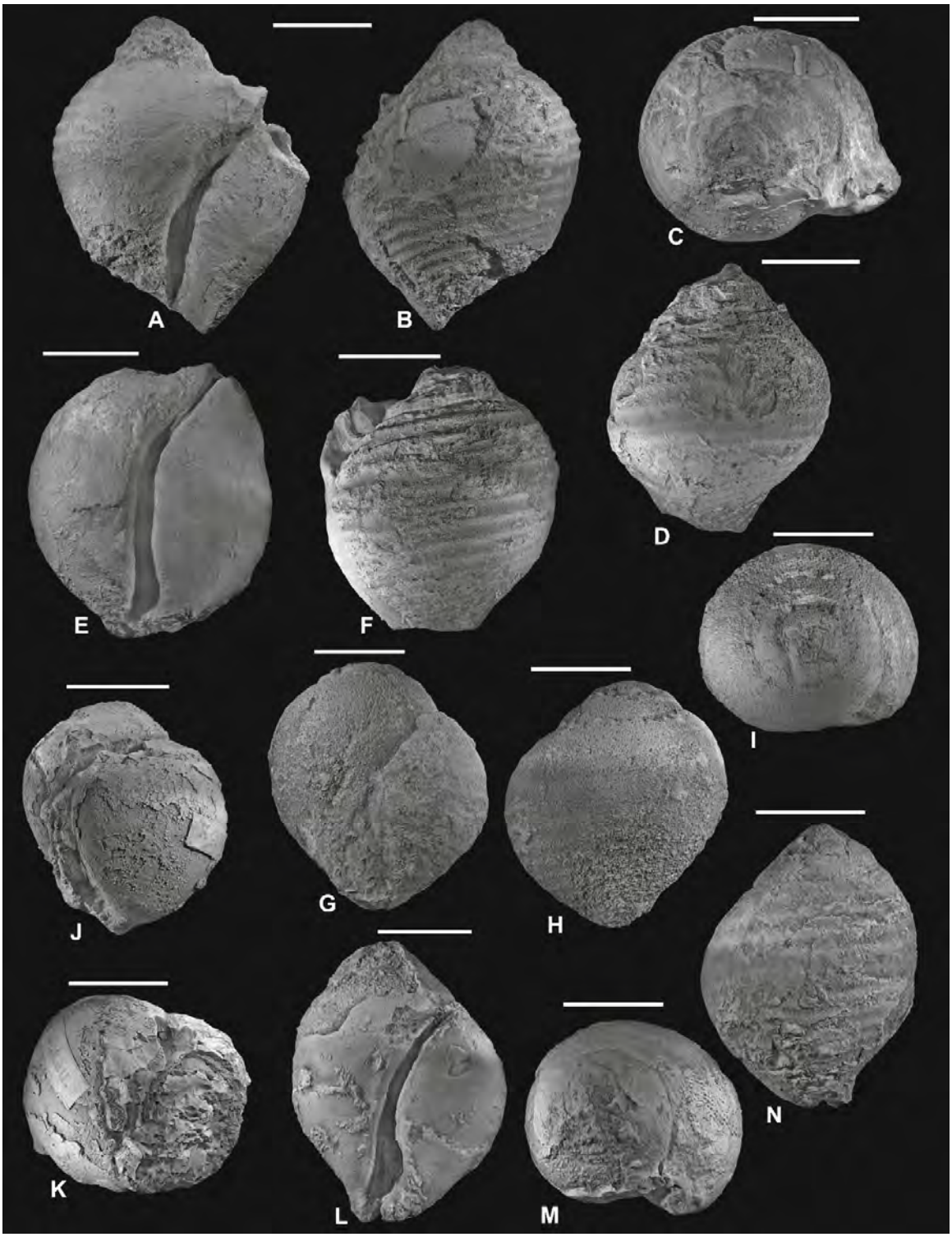

Fig. 3.7. — *Zittelia crassissima* Zittel, 1873 from the Tithonian–Berriasian of Czechia. **A–C**. SNSB-BSPG AS III 909, Štramberk; A – apertural view; B – abapertural view; C – apical view. **D**. SNSB-BSPG AS III 910, Štramberk, abapertural view. **E–F**. SNSB-BSPG AS III 897, Štramberk; E – apertural 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.

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.

Table 3.4. — 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°

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. 3.6A) 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. 3.4, Fig. 3.8).

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. 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 3.7A, B and 3.7E, F), probably were used to compose the illustration published by Zittel (1873, pl. 40, figs 11a, b) and reproduced in Figure 3.6 herein.

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

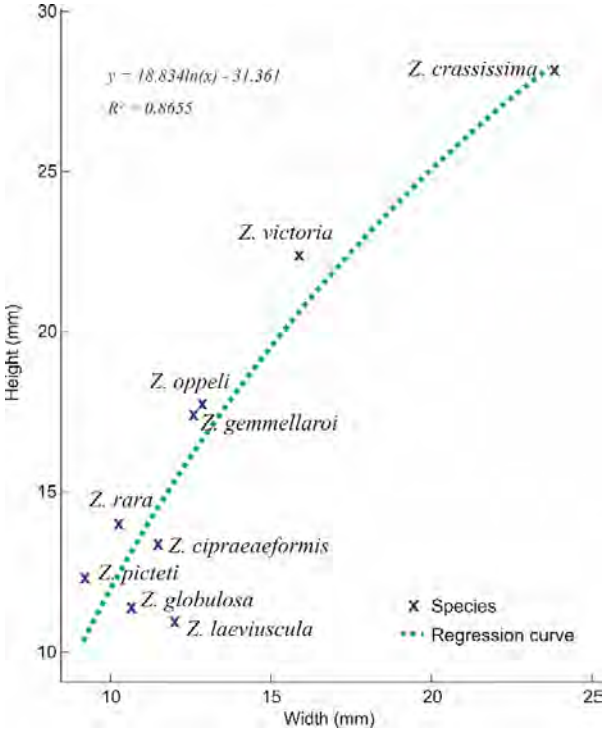

Fig. 3.8. — Height/width ratio in species of *Zittelia*. Each point represents the mean of all specimens of a separate species.

Zittelia gemmellaroi Zittel, 1873

Fig. 3.9

*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

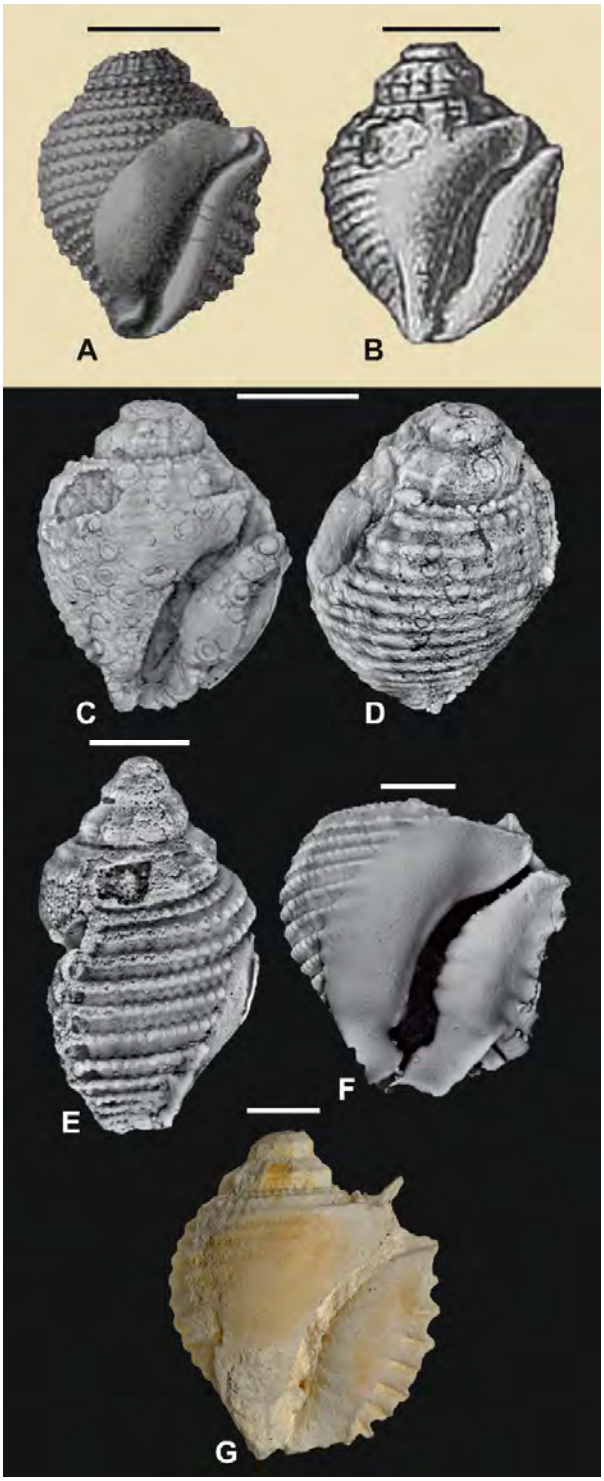

Fig. 3.9. — *Zittelia gemmellaroi* Zittel, 1873. **A**. Reproduction of Zittel's drawing (1873, pl. 40, fig. 10c), height 11 mm; Tithonian–Berriasian, Štramberk, Czechia. **B**. Reproduction from Brösamlen (1909, pl. 22, fig. 39), height 13 mm; Tithonian, Nattheim, Germany. **C–D**. Reproduction from 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; late Kimmeridgian, Saal, Germany. **G.** SNSB-BSPG 2016 XXI 1, height 25 mm; late Kimmeridgian; Saal, Germany. This specimen was also figured by Werner *et al.* (2017, figs 3A–C). Approximate (A–F) scale bars represent 5 mm.

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 the specimens from Sall exceed Zittel's (1873) and Brösamlen's (1909) specimens in size (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 (Germany); Tithonian–Berriasian of Štramberk (Czechia), Wilamowice (as Willamowitz in Zittel, 1873) and Iskrzyczyn (as Iskritschin in Zittel, 1873) (Poland), and Nattheim (Germany).

Zittelia globulosa Zittel, 1873

Figs 3.10, 3.11

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

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.

Table 3.5. — Measurements (mm) of *Zittelia globulosa* Zittel, 1873

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

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. 3.5) and different shell outline. He also stated that both the columellar and outer lip lack denticles. However, the aperture of the available specimens (Fig. 3.10) is covered with sediment, so its morphology remains unknown.

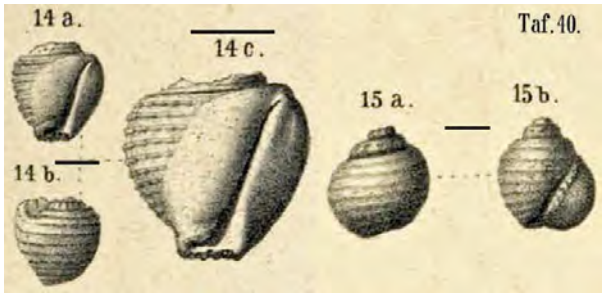

Fig. 3.10. — Reproduction of Zittel's (1873) drawings of two specimens of *Zittelia globulosa* Zittel, 1873 from Štramberk, Czechia (14) and Wilamowice (15), Poland. The repository of the specimen from Wilamowice (15) is unknown. An approximate scale bars represent 5 mm.

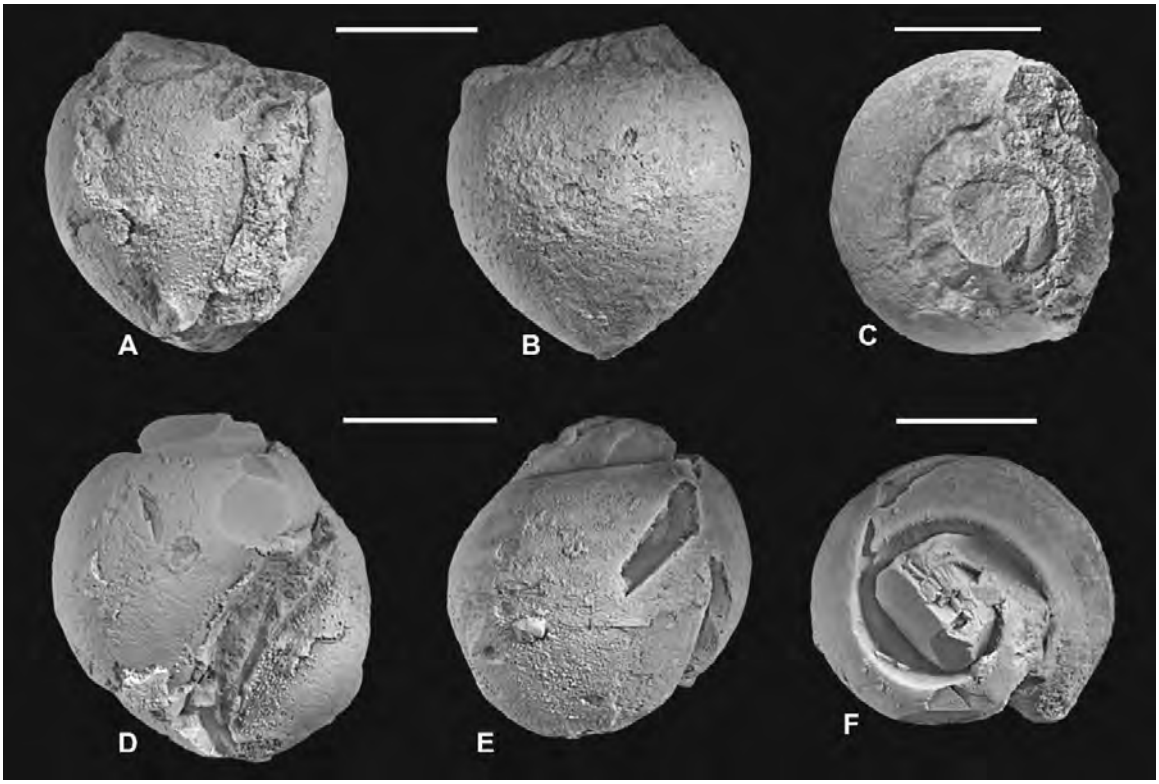

Fig. 3.11. — *Zittelia globulosa* Zittel, 1873 from the Tithonian–Berriasian of Štramberk, Czechia. **A–C**. SNSB-BSPG AS III 900; A – apertural view, B – abapertural view, C – apical view. **D–F**. SNSB-BSPG AS III 901; D – apertural view, E – abapertural view, F – apical view. Scale bars represent 5

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. 3.11) probably were used to compose the illustration published by Zittel (1873, pl. 40, fig. 14a–c), which is reproduced herein (Fig. 3.10). 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 3.12, 3.13

*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).

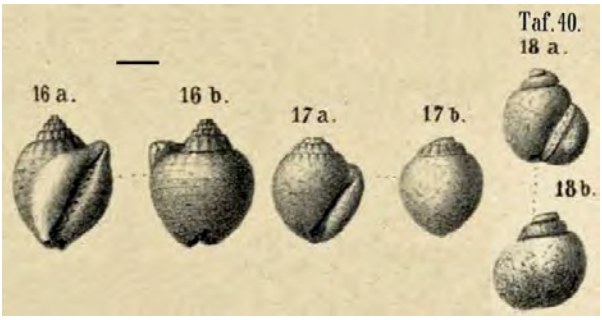

Fig. 3.12. — Reproductions of Zittel's (1873) drawings of *Zittelia laeviuscula* Zittel, 1873 from Štramberk (16) and Koňákov (17), Czechia, and Wilamowice (18), Poland, illustrating different types of preservation. The place of storage of the specimen from Koňákov (17) is unknown. An approximate scale 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.

Table 3.6. — 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°

Remarks: Two specimens (SNSB-BSPG AS III 906 and 907) are distinguished from others by a wider last whorl, a larger pleural angle (Tab. 3.6), 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.

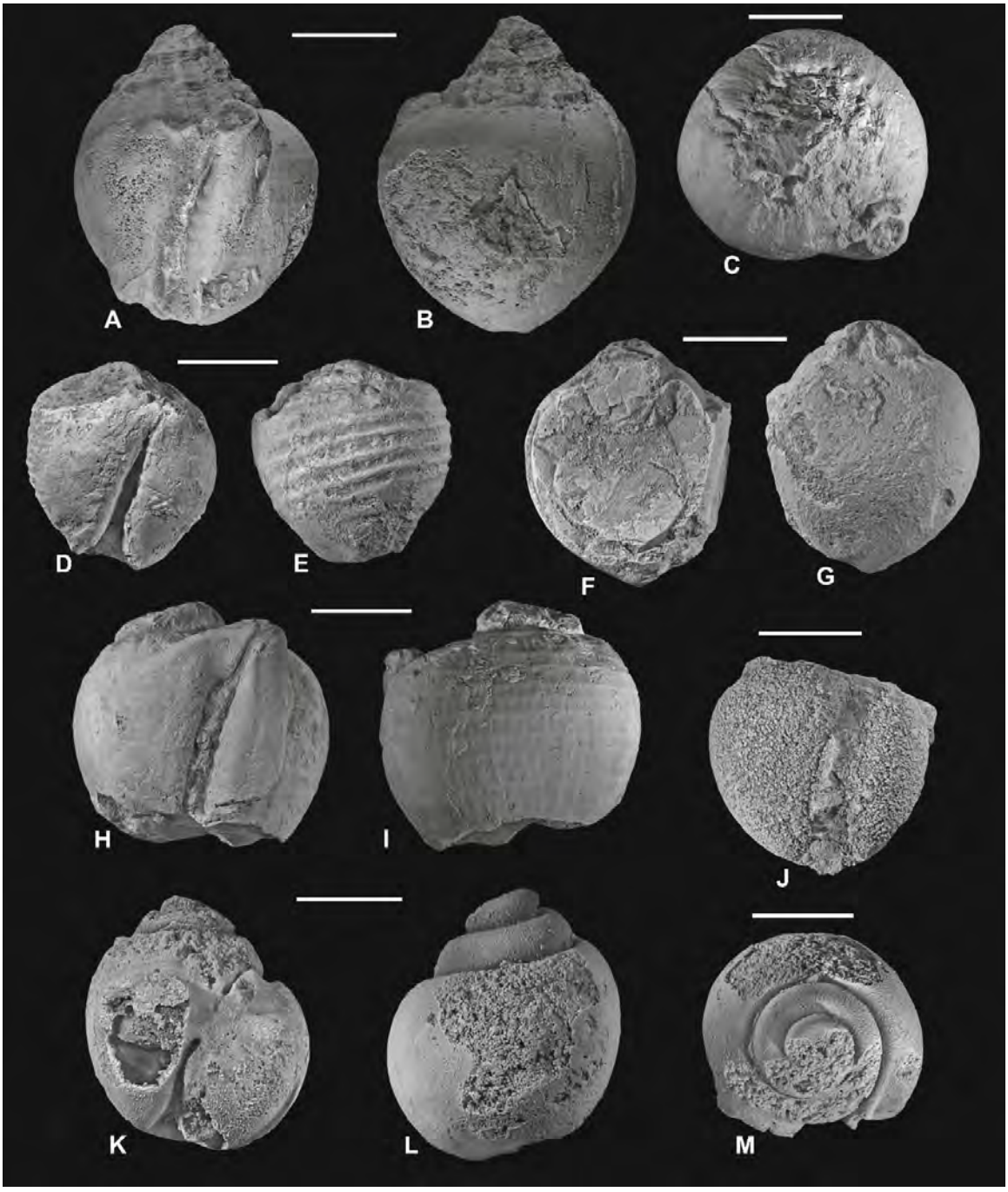

Fig. 3.13. — *Zittelia laeviuscula* Zittel, 1873 from the Tithonian–Valanginian of Štramberk, Czechia (A–J) and Wilamowice (Willamowitz), Poland (K–M). **A–C**. Lectotype SNSB-BSPG AS III 902 (designated herein); A – apertural view, B – abapertural view, C – apical view. **D–E.** SNSB-BSPG AS III 907; 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.

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 3.13A, 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 3.13H, I).

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

Zittelia oppeli (Étallon, 1859)

Figs 3.14, 3.15

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.

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

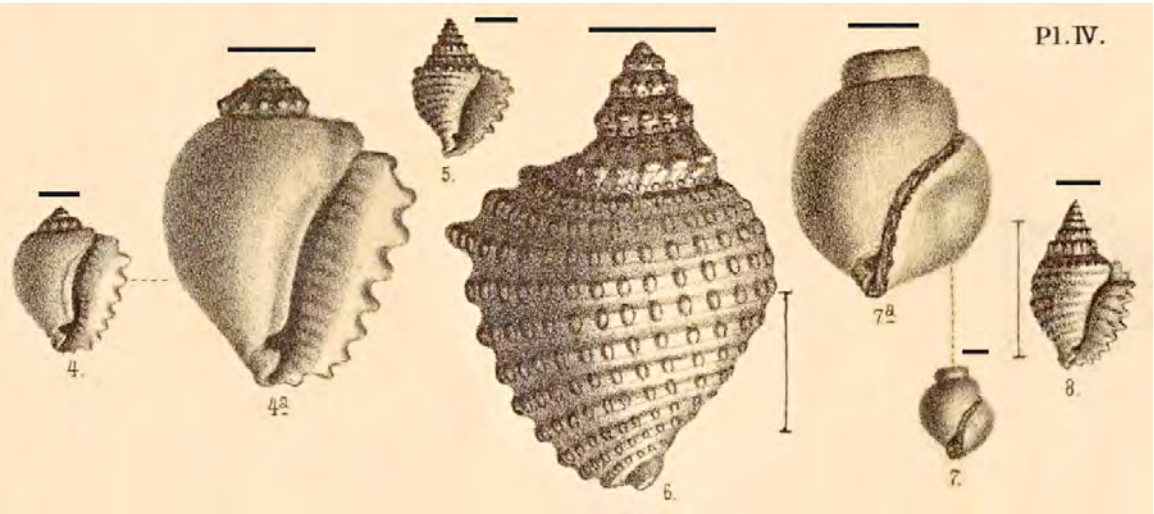

Fig. 3.14. — Reproductions of Loriol's (1886) drawings of *Zittelia oppeli* (Étallon, 1859) from the Kimmeridgian of Valfin, France. The specimen number 5 is MDC 20014062.1 and is figured herein (Fig. 3.15A–C). An approximate scale bars represent 5 mm.

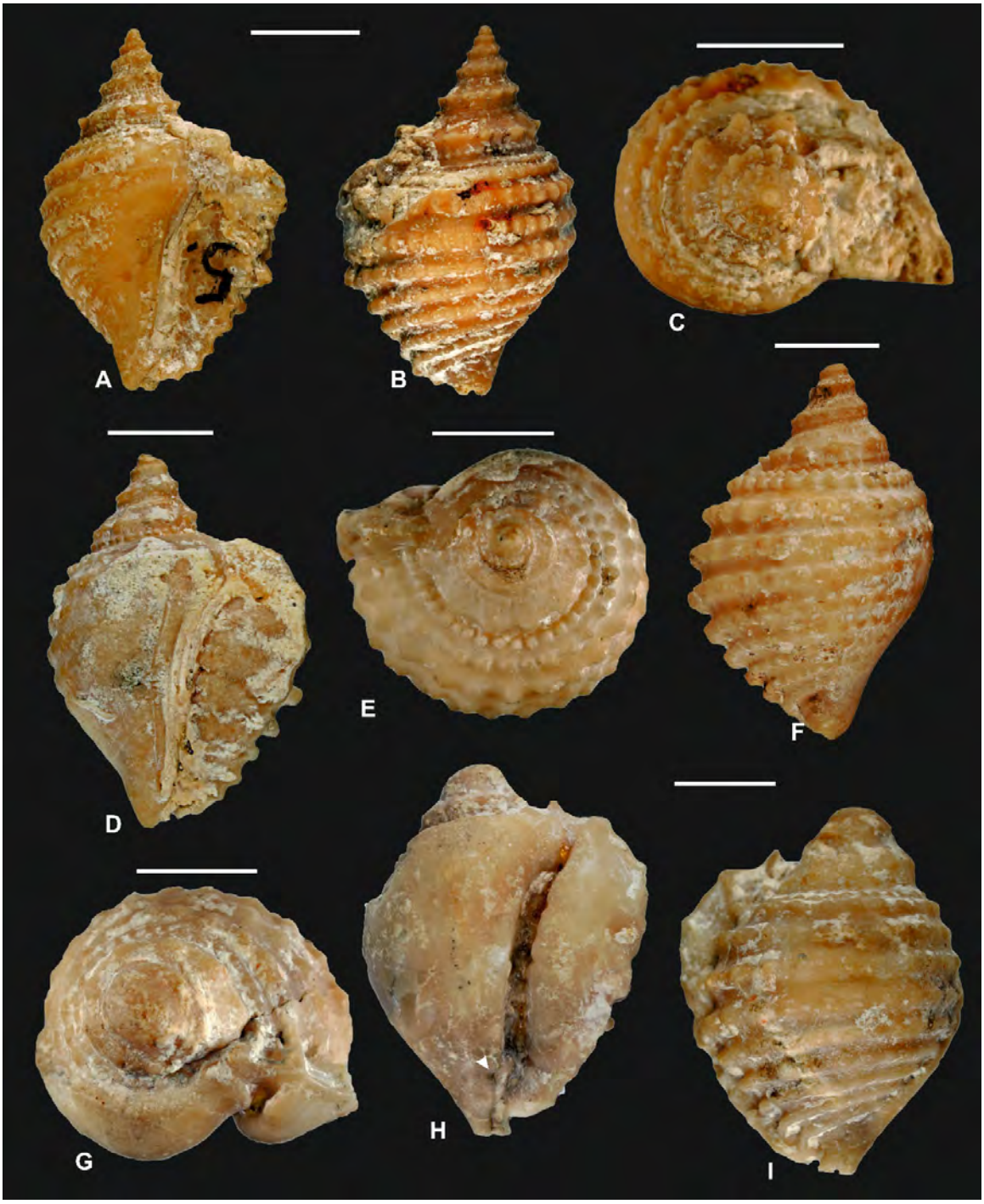

Fig. 3.15. — *Zittelia oppeli* (Étallon, 1859) from the Kimmeridgian of Valfin, France. **A–C.** MDC 20014062.1, this specimen corresponds the figure illustrated by de Loriol (1886, pl. 4, fig. 5), as evidenced by the inscribed number 5 on the shell; A – apertural view, B – abapertural view; C – apical 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.

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.

Table 3.7. — 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°

Remarks: *Z. oppeli* has a higher spire (Tab. 3.7) than other species of *Zittelia* (Fig. 3.4B) 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. 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 3.3B, 3.16

*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.

? 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

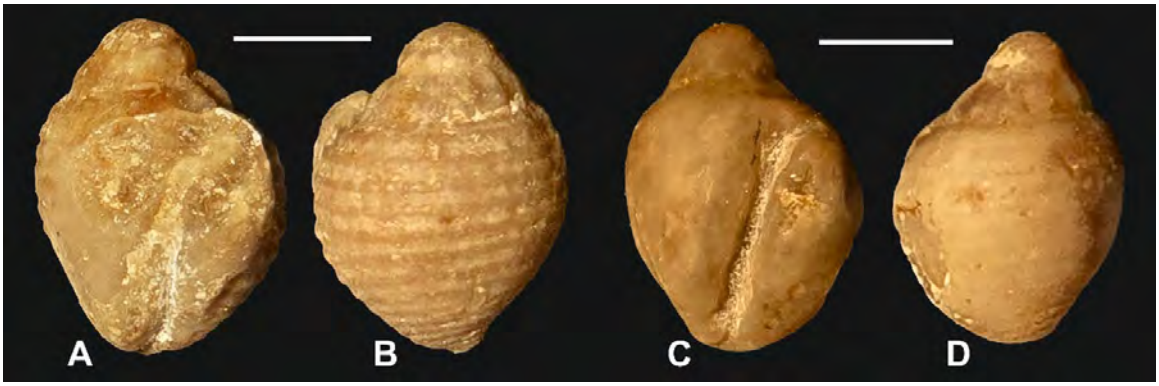

Fig. 3.16. — *Zittelia picteti* Gemmellaro, 1869, Tithonian–Valanginian, Carini near Palermo, Sicily, Italy. **A–B**. Lectotype MGUP-20-362.1 (designated herein); A – apertural view, B – abapertural view. **C–D**. MGUP-20-362.2; C – apertural view, D – abapertural view. Scale bars represent 5 mm.

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.

Table 3.8. — 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°

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. 3.8), and a straighter aperture. It can be distinguished from *Z. gemmellaroi* by its less convex last whorl and a straighter, less curved aperture.

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. 3.17

*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.

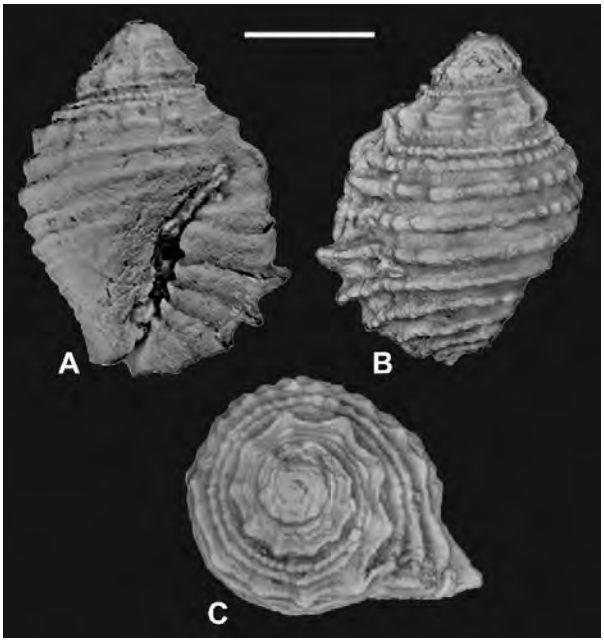

Fig. 3.17. — Reproduction of *Zittelia rara* (Gründel, Hostettler & Menkveld-Gfeller, 2022) (Gründel *et al.*, 2022, pl. 10, figs 12, 13, pl. 11, fig. 1 as *Columbellaria rara*) from the middle Oxfordian (coral facies of the St-Ursanne Formation) of St-Ursanne, Switzerland. **A.** Apertural view. **B.** Abapertural view. **C.** Apical view. An approximate scale bar represents 5 mm.

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

Zittelia victoria (Guirand and Ogérien, 1865)

Figs 3.18, 3.19

*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 and 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

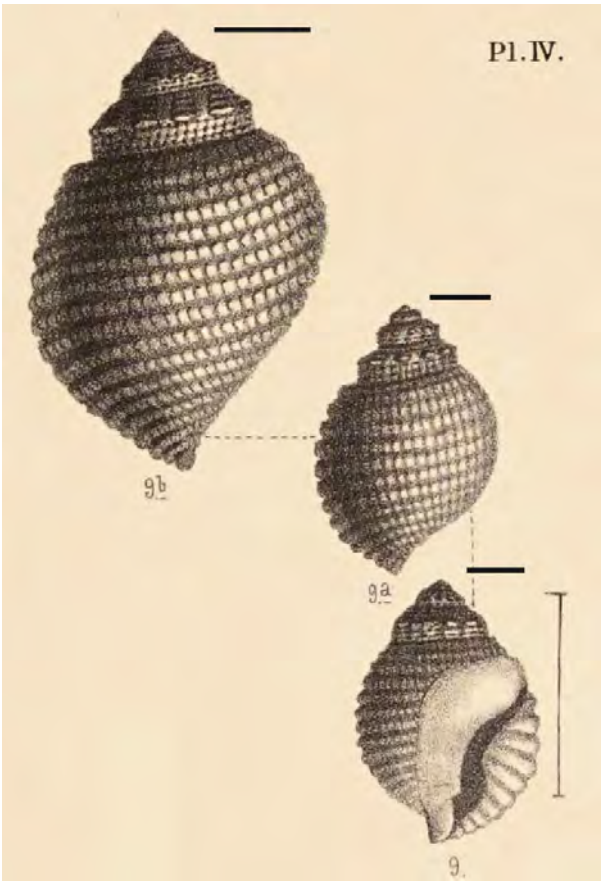

Fig. 3.18. — Reproduction of Loriol's (1886) drawings of *Zittelia victoria* (Guirand & Ogérien, 1865) from the Kimmeridgian of Valfin, France. This is the same specimen as MDC 20014042.1 and is designated herein as the lectotype (Fig. 3.19A–C). An approximate scale bars represent 5 mm.

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 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.

Table 3.9. — Measurements (mm) of *Zittelia victoria* (Guirand and 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	–

Remarks: This species is clearly distinguishable from *Z. oppeli* in the greater number of spiral cords and wider shape (Tab. 3.9). It differs from *Z. picteti* in its curved aperture and cords with smaller nodes.

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

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

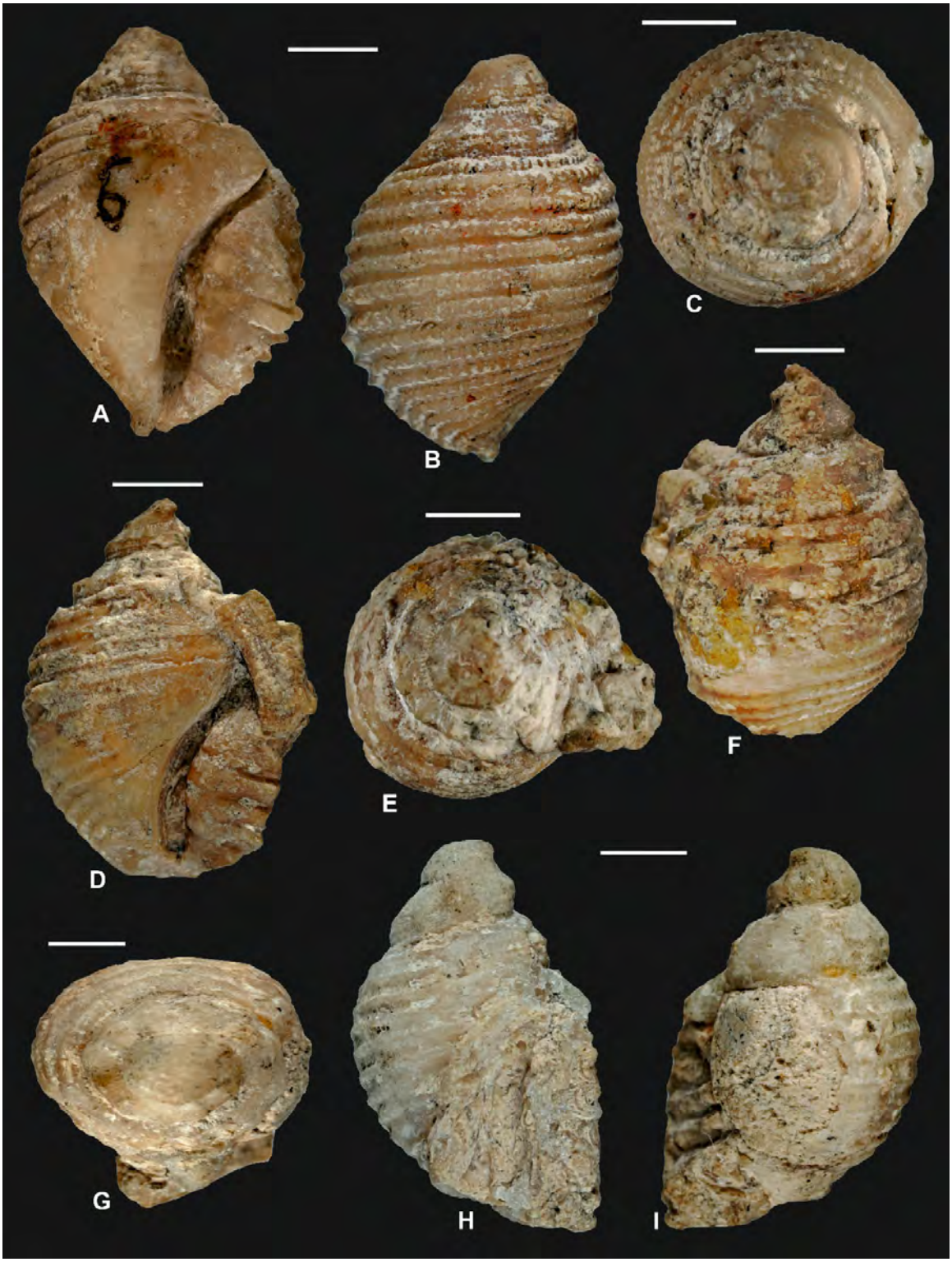

Fig. 3.19. — *Zittelia victoria* (Guirand and Ogérien, 1865) from the Kimmeridgian of Valfin, France. **A–C.** Lectotype MDC 20014042.1 (designated herein); A – apertural view, B – abapertural view, C – apical view. **D–F**. MDC 20014062.2; D – apertural view, E – apical view, F – abapertural view. **G–I**. MDC 20014062.3; G – apical view, H – apertural view, I – abapertural view. Scale bars represent 5 mm.

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 Early 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 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,

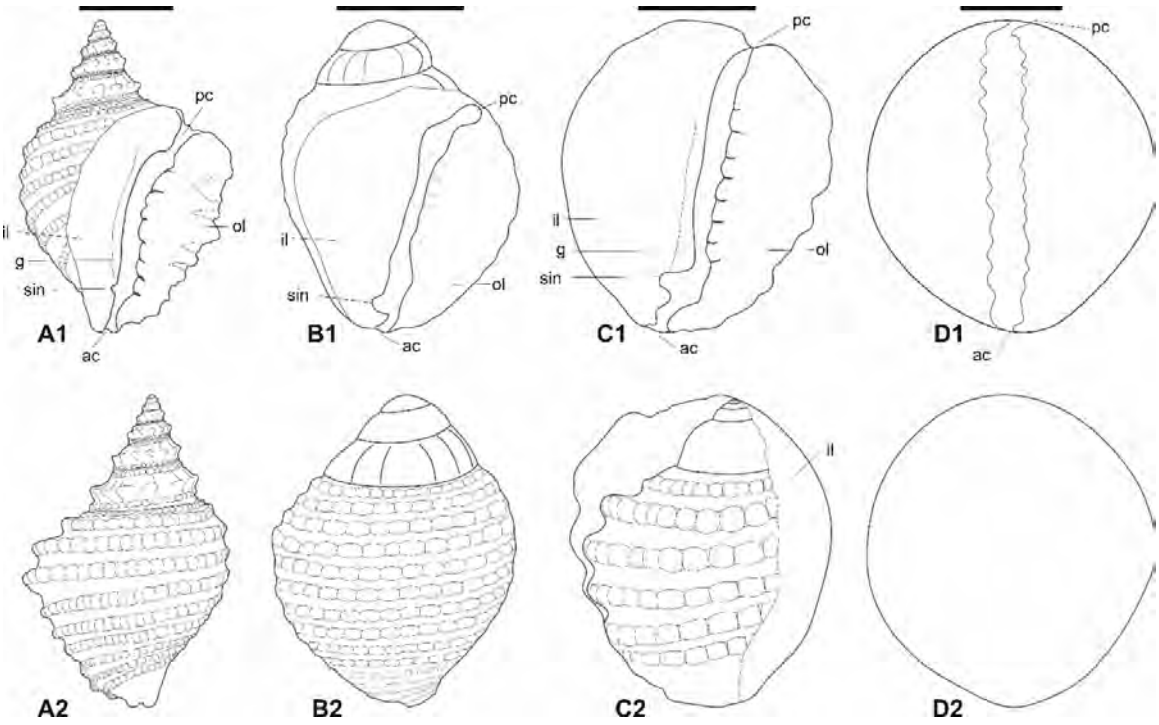

Fig. 3.20. — Morphological changes in *Zittelia* (A, B, C) from the Kimmeridgian (A) to the Tithonian (B, C) and comparison with *Coffeacypraea* (D). **A**. *Zittelia oppeli* (Étallon, 1859), Kimmeridgian of France (Valfin). **B**. *Zittelia picteti* Gemmellaro, 1869, Tithonian of Italy (Carini near 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.

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 these genera.

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–Berriasian(?). 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.

CHAPTER IV

The earliest cowries: the origin of cypraeoid gastropods*

Alexander Nützel, Simon Schneider, Sofia Bakayeva, and Andrzej Kaim

ABSTRACT

Cowries, the family Cypraeidae, form a diverse and conspicuous group of gastropods living in tropical to subtropical seas. Their shell is convolute (last whorl covers all previous ones) with a narrow, slit-like siphonate aperture bearing denticles ("teeth"). When extended, a large part of their shell surface is covered by a soft fleshy mantle. The earliest cowries were reported from the Upper Jurassic of Sicily: *Cypraea tithonica* and *C. gemmellaroi*. Subsequently, these species had been assigned to various cypraeid genera. Examination of the type material of *Cypraea tithonica* reveals that this species represents a new genus: *Coffeacypraea* Nützel & Schneider gen. nov. *Cypraea gemmellaroi* also belongs to this new genus and is potentially synonymous with *Coffeacypraea tithonica*. The Upper Jurassic caenogastropod genera *Colombellina* and *Zittelia* (family Colombellinidae) also have narrowly elongated siphonate apertures and are closely related to Cypraeidae but their shells are not convolute. The origination of Cypraeidae and Colombellinidae contributed considerably to the Mesozoic–Cenozoic caenogastropod radiation.

Key words: Cypraeoidea, Jurassic, taxonomy, systematics, evolutionary relationships.

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INTRODUCTION

Cowries, the family Cypraeidae Rafinesque, 1815, comprise approximately 400 living species and subspecies, and have a rich Cenozoic and sparse Cretaceous fossil record (e. g., Schilder and Schilder 1971; Lorenz 2017, 2018; MolluscaBase 2025). Two species of latest Jurassic (Tithonian) age, *Cypraea tithonica* and *C. gemmellaroi*, were first described from Sicily (Italy) by Di Stefano (1882) and later also reported from coeval strata on Capri (Italy) (Parona 1919); they represent the earliest cowries known to date. The present contribution revises the taxonomy and systematic placement of these early cypraeids, based on re-study of the type series of *Cypraea tithonica* Di Stefano, 1882.

Cowries are conspicuous in having a convolute shell, with the last whorl enclosing all previous whorls and forming a narrowly elongate, slit-like aperture with anterior and posterior canals. Cypraeids can cover their entire shell with a fleshy mantle, which enables them to produce a spotlessly smooth, glossy outer shell surface. While most of the modern diversity of Cypraeidae is located in the tropical Indo-Pacific, the family as a whole has a pantropical distribution between 35° N and S (Riedel 2000; Passamonti 2015; Lorenz 2017, 2018).

Juveniles of the type genus of the family, *Cypraea*, are herbivorous grazers, and are carnivorous or omnivorous grazers as adults, feeding on sponges and other sessile invertebrates (Tay et al. 2023 and references therein). All species of which early ontogeny and protoconchs are recorded have planktotrophic larval development. They have relatively large larval shells – generally approximately 1 mm high, but some reaching up to 1.5 mm – with a reticulate ornament (Bandel et al. 1997; Riedel 2000; Tay et al. 2023) (Fig. 4.1).

Cypraeidae have a taenioglossate radula and were placed in the traditional Mesogastropoda (e. g., Wenz 1938–1944). They are now assigned to the 'higher' Caenogastropoda within Latrogastropoda (e. g., Bouchet et al. 2017; Ponder et al. 2020; Li et al. 2024), which are characterized by an inhalant flow, commonly associated with the development of an anterior siphonal canal. While family-level phylogeny and systematics of the Cypraeidae within Gastropoda is relatively well resolved and stable (Meyer 2003, 2004), subdivision at the genus level is still under debate. So far, cypraeid genus-level systematics is largely based on shell morphology, which is rather conservative in this family, and modern anatomical and molecular studies are lacking (e. g., Passamonti 2015). More than 150 genus-level names have been proposed for extant and fossil Cypraeidae, and approximately 80 of these are currently considered valid (Schilder and Schilder 1971; Riedel 2000; MolluscaBase 2025).

The aim of this study is to revise the available cypraeid materials from the Late Jurassic of Italy and attempt to relate them to other caenogastropods which have narrowly elongated siphonate apertures.

Institutional abbreviations.— MGUP, Museo Geologico G. G. Gemmellaro, Università di Palermo, Sicily, Italy; MSTC, Museo di Paleontologia, Dipartimento di Scienze Biologiche, Geologiche e Ambientali, Università di Catania, Sicily, Italy; SNB-BSPG, Bayerische Staatssammlung für Paläontologie und Geologie, Richard-Wagner-Str. 10, 80333 München, Germany.

HISTORICAL BACKGROUND

As highlighted above, the earliest Cypraeidae have been described from the latest Jurassic of Sicily (Di Stefano 1882; Tracey et al. 1993; Groves and Landau 2021; Capasso 2024). However, the type material of *Cypraea tithonica* Di Stefano, 1882 and *C. gemmellaroi* Di Stefano, 1882 has never been restudied, and Zamberlan and Checchi (2014) and Capasso (2024) considered these specimens as lost. Thus, it came as a surprise that during a visit to the Museo di Geologia 'G. G. Gemmellaro' in Palermo, two of the authors (AN and SS) re-discovered the type series of *Cypraea tithonica*, which forms the base for the present contribution. The original material of *Cypraea gemmellaroi* was not found.

Besides their type locality, Termini Imerese near Palermo, both species were reported to occur in Tithonian strata on the island of Capri south of Naples, Italy by Parona (1919); as far as we are aware, his specimens were never illustrated. However, Zamberlan and Checchi (2014) figured a specimen from the Tithonian of Capri, which is part of the Viglino Collection (MSTC no. 186vi0950) curated at the Museo di Paleontologia, Dipartimento di Scienze Biologiche,

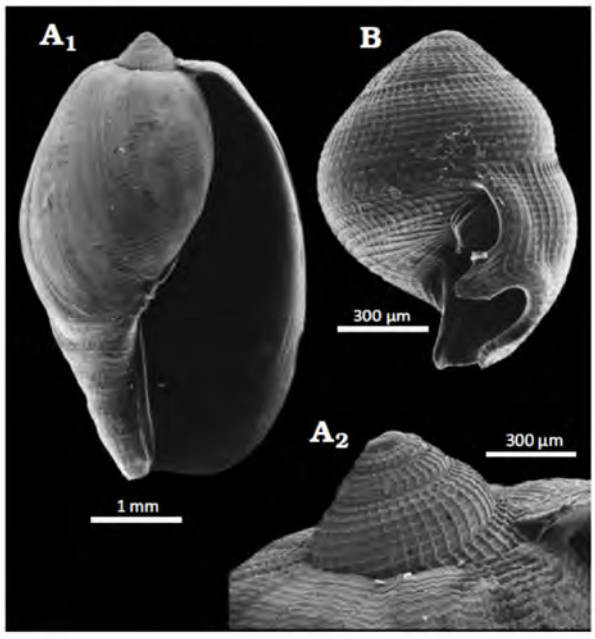

Fig. 4.1. — Early ontogenetic shells of Cypraeidae (from seagrass meadow at Bira, Sulawesi, Indonesia), SNSB-BSPG 2025 I 1. A, B. Juvenile cypraeid with protoconch. The last whorl, overgrowing all previous ones, is not yet developed; the aperture, while already elongated, is not yet slit-like. C. Isolated larval shell of a Recent cypraeid with sinusigera notches and cancellate ornament. This larval shell of the planktotrophic type is typical of modern cypraeids, but is not visible in full-grown specimens, due to overgrowth by the last whorl and diagenetic alteration.

Geologiche e Ambientali, Università di Catania, and was assigned to *Cypraea gemmellaroi*; they further stated that the same collection also contained specimens of *Cypraea tithonica* (MSTC no. 186vi0949). Recently, Capasso (2024) figured both specimens from Capri.

Cypraea tithonica was assigned to *Cyproglobina* De Gregorio, 1880 by Schilder (1927), a genus now placed in the Ovulidae (Fehse 2013). Later, Schilder and Schilder (1971) transferred the species to *Palaeocypraea* Schilder, 1928, where it was retained by Groves (1990, 1992, 1994), Tracey et al. (1993) and most recently Capasso (2024). Based on re-study of the type material of *C. tithonica*, this assignment is erroneous, as will be outlined below.

The second, larger species introduced by Di Stefano (1882), *Cypraea gemmellaroi*, was assigned by Schilder (1927) to his new subgenus *Bernaya* (*Protocypraea*), but later transferred to *Bernaya* Jousseaume, 1884 s. str. (Schilder and Schilder 1971). Again, Groves (1990, 1992, 1994), Zamberlan and Checchi (2014) and Capasso (2024) retained this combination. This assignment is equally untenable, and *C. gemmellaroi* is congeneric with *C. tithonica*.

MATERIAL AND METHODS

The material studied herein is housed at the Museo Geologico G. G. Gemmellaro in Palermo, Sicily, Italy. Only the type series of *Cypraea tithonica* Di Stefano, 1882, consisting of seven syntypes, which are archived under accession numbers MGUP-20-368a–g, was found during a visit in March 2017. The type series of *Cypraea gemmellaroi* Di Stefano, 1882 could not be traced.

The specimens come from an isolated limestone outcrop on the castle mountain of Termini Imerese (Palermo region, Sicily; coordinates: 37.9886, 13.6979, WGS1984). The castle mountain is part of a series of originally African structural domains (Sicilian–Maghrebide units; Fig. 4.2) that were obducted onto the European part of Sicily during Neogene times (Catalano et al. 2010, 2011). The strata that yielded the cypraeids are assigned to the informal *Ellipsactinia*

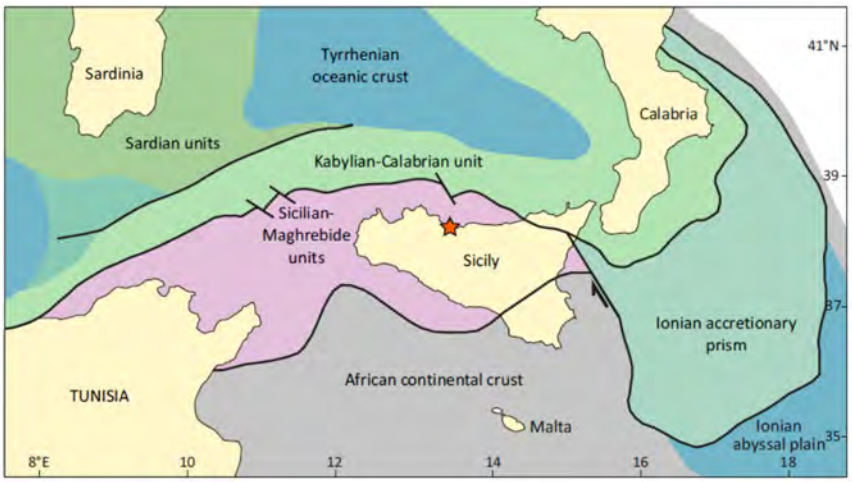

Fig. 4.2. — Overview of structural domains in the central Mediterranean (modified from Catalano et al. 2010). The location of Termini Imerese is indicated by a red star.

breccias member of the Crisanti Formation (Catalano et al. 2010; Basilone 2018), which comprises thick-bedded limestone breccias and conglomerates. The components of these rocks are characterised by shallow-water carbonate platform facies containing abundant corals and molluscs; the latter were monographed by Gemmellaro (1869a–d, 1871a–d, 1875) and Gemmellaro and Di Blasi (1874). The rocks are classically attributed to the Tithonian, but may partly be Berriasian (earliest Cretaceous) in age, based on calpionellid biostratigraphy (Catalano et al. 2010; Basilone 2018).

All seven specimens were coated with ammonium chloride, and photographs from those views deemed taxonomically informative were taken. The higher classification of the Gastropoda is adopted from Bouchet et al. (2017), Ponder et al. (2020) and MolluscaBase (2025). The descriptive terminology follows Groves and Squires (2023).

In 2024, SB and AK analysed the type material of the colombellinid *Zittelia cipraeaeformis* Gemmellaro, 1869 from the Gemmellaro collection stored at the same museum, which comprises nine syntypes (Bakayeva & Kaim unpublished data). All of them are stored under the inventory number MGUP-20-361.

SYSTEMATIC PALAEONTOLOGY

Class Gastropoda Cuvier, 1795
Infraclass Caenogastropoda Cox, 1960

Cohort Sorbeoconcha Ponder & Lindberg, 1997
Megaorder Hypsogastropoda Ponder & Lindberg, 1997
Superorder Latrogastropoda Riedel, 2000
Order Cypraeida Rafinesque, 1815
Superfamily Cypraeoidea Rafinesque, 1815
Family Cypraeidae Rafinesque, 1815

Genus *Coffeacypraea* Nützel & Schneider nov.

Zoobank LSID: urn:lsid:zoobank.org:act:C0956AF7-1075-4294-8F6F-14EC45D48245.

Type species.— *Cypraea tithonica* Di Stefano, 1882, by original designation herein.

Etymology.— A combination of the Latin genus names *Coffea*, which includes the coffee plant, and *Cypraea*, which is the type genus of the Cypraeidae, referring to the rather simple shell shape of the new genus, which resembles an oversized coffee bean.

Diagnosis.— Relatively small (up to 25 mm long), smooth-shelled Cypraeidae; short-ovate to almost circular in outline in dorsal view; basal side of shell widely flattened; dorsal side more or

less evenly arched and inflated. Aperture slit-like, narrow, in almost central position, straight, without widened anterior and posterior notches; columellar and labral denticles evenly sized and spaced (barely visible due to limited preservation). Anterior (siphonal) and posterior canals indistinct or very short.

Species included.— *Coffeacypraea tithonica* (Di Stefano, 1882) and *Coffeacypraea gemmellaroi* (Di Stefano, 1882).

Stratigraphic and geographic range.—Tithonian, Upper Jurassic of Italy and potentially Czechia.

Coffeacypraea tithonica (Di Stefano, 1882)

(Figs 4.3A–D, 4.4A–G, 4.5)

*1882 *Cypraea tithonica*, Di Stef.; Di Stefano: 76, pl. 4: 4, 5.

? 1911 *Cypraea tithonica* di Stef.; Blaschke: 162.

? 1919 *Cypr*. *tithonica* Di Stef.; Parona: 475.

1927 [*Cyproglobina*] *tithonica* di Stef.; Schilder: 71.

1971 *Palaeocypraea* (*Palaeocypraea*) *tithonica*; Schilder and Schilder: 24.

1990 *Palaeocypraea* (*P.*) *tithonica* (Stefano, 1882); Groves: 273.

1992 *Palaeocypraea* (*Palaeocypraea*) *tithonica* (Stefano, 1882); Groves: 101.

1993 *Palaeocypraea tithonica* – Tracey et al.: 148.

1994 *Palaeocypraea* (*Palaeocypraea*) *tithonica* (Steffano 1882) [sic!]; Groves: 26, figs 5, 6 [reproduced from Di Stefano 1882].

2014 *Bernaya gemmellaroi* (Di Stefano, 1882); Zamberlan and Checchi: 21, fig. 8 [not fig. 7].

2021 *Palaeocypraea tithonica* (Stefano, 1882); Groves and Landau: 8.

2024 *Palaeocypraea tithonica* (Di Stefano, 1882); Capasso: 165, figs 1, 2.

2024 *Bernaya gemmellaroi* (Di Stefano, 1882); Capasso: 166, fig. 4 [not fig. 3].

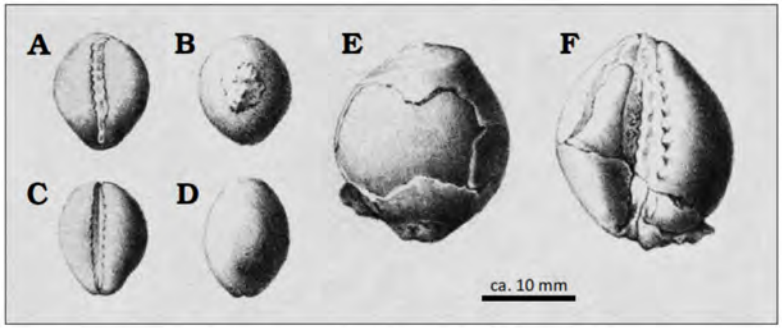

Fig. 4.3. — Reproduction of Di Stefano's (1882) drawings of "*Cypraea tithonica* Di Stefano, 1882" (A–D) and *Cypraea gemmellaroi* Di Stefano, 1882 (E, F), illustrating the significant difference in size. An approximate scale bar is added.

Emended diagnosis.— Small (up to 13 mm long), smooth-shelled Cypraeidae; short-ovate to almost circular in outline in dorsal view; basal side of shell widely flattened; dorsal side more or less evenly arched and inflated. Aperture slit-like, in almost central position, straight, without widened anterior and posterior notches; columellar and labral denticles evenly sized and spaced (barely visible due to limited preservation). Anterior (siphonal) and posterior canals very short.

Type locality.— Castle mountain of Termini Imerese, Palermo Region, Sicily;

Type horizon.— *Ellipsactinia* breccias member, Crisanti Formation, Tithonian, Upper Jurassic.

Material.— Seven syntypes, curated under catalogue numbers MGUP-20-368a–g; relatively well preserved shells. The specimen in Figure 4.4D (Di Stefano 1882: pl. 4: 4a, b; MGUP-20-368a) is designated as the lectotype herein, whereby the remaining six specimens become paralectotypes (MGUP-20-368b–g). Two additional specimens not examined by the authors come from Tithonian strata on the island of Capri (MSTC no. 186vi0949 and MSTC no. 186vi0950); see Zamberlan and Checchi (2014) and Capasso (2024).

Description.— Shell up to 13 mm long, 12.5 mm wide and 8 mm high; convolute, cypraeid in shape, with last whorl overgrowing all previous whorls; very short ovate to almost circular in outline in dorsal view; moderately and evenly inflated in lateral view, with basal (apertural) side flattened. Outer shell surface smooth. Aperture narrow, slit-like, in almost central position, straight without widened anterior and posterior notches. Columellar and labral sides of aperture with numerous teeth, in most specimens barely visible due to limited preservation.

Remarks.— The studied specimens of *Coffeacypraea tithonica* generally are similar to modern cypraeids with regard to shell morphology, but differ sufficiently from younger taxa to be placed in their own genus. The specimens illustrated in Figure 4.4A and B show that the last whorl overgrows the low-spired previous whorls and produces the typical cypraeid convolute shape. However, as noted by Capasso (2024), the shells are much shorter and more circular than in any other genera, with length/width ratios of 1.04 to 1.18 for *C. tithonica* and approximately 1.12 to 1.15 for *C. gemmellaroi* (measured from Fig. 4.3E, F). *Coffeacypraea* also differs from the other genera of the Cypraeidae by having a straight, rather narrow aperture in central position, which lacks the widened anterior and posterior notches seen in their Cretaceous and younger descendants. Moreover, the anterior and posterior canals are barely developed. Although the preservation of the specimens is not ideal, this is not a result of erosion, but a genuine feature. By far most other Cypraeidae have more or less curved apertures, which are opisthocyrt inclined and the siphonal (anterior) and posterior canals are usually much more pronounced.

Two specimens from the island of Capri, figured by Zamberlan and Checchi (2014) and Capasso (2024) under the names *Bernaya gemmellaroi* (Di Stefano, 1882) and *Palaeocypraea*

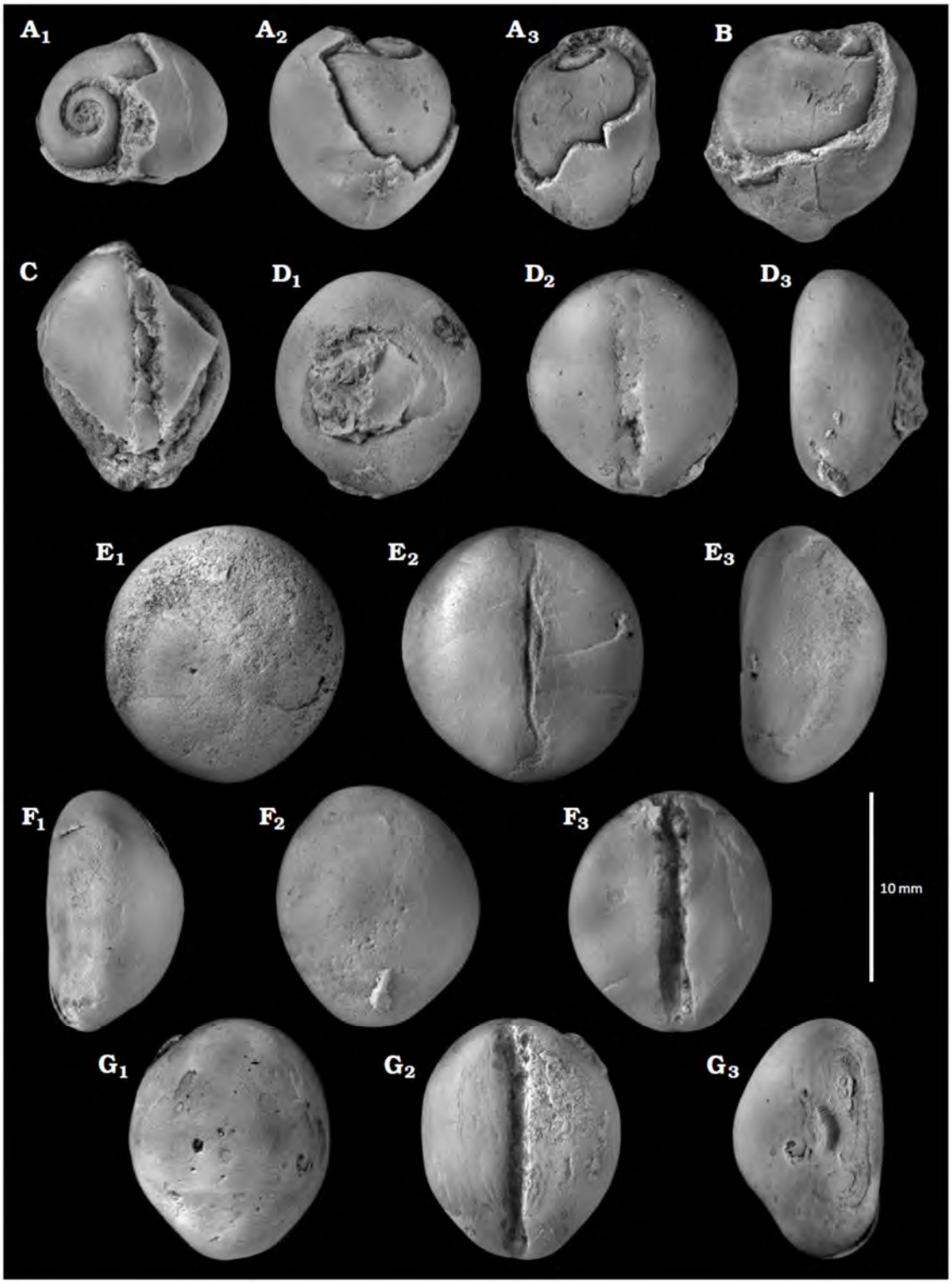

Fig. 4.4. — Cypraeid gastropod *Coffeacypraea tithonica* (Di Stefano, 1882) from the Tithonian, Upper Jurassic, of the castle mountain of Termini Imerese, Sicily, Italy. Type series of *Cypraea tithonica* Di Stefano, 1882. A, B. Specimens with broken last whorl, exposing the earlier whorls; paralectotypes, MGUP-20-368b, c. C. Fragmentary specimen, showing part of the aperture, with some of the denticles visible; paralectotype, MGUP-20-368d. D. Lectotype, with denticulate aperture; MGUP-20-368a. E. Largest and roundest specimen of the type series, with poorly preserved aperture; paralectotype, MGUP-20-368e. F. Faintly asymmetric specimen; paralectotype, MGUP-20-368f. G. Slightly irregularly shaped specimen, with a faint dent on the dorsal side, seen best in lateral view (G3); paralectotype, MGUP-20-368.

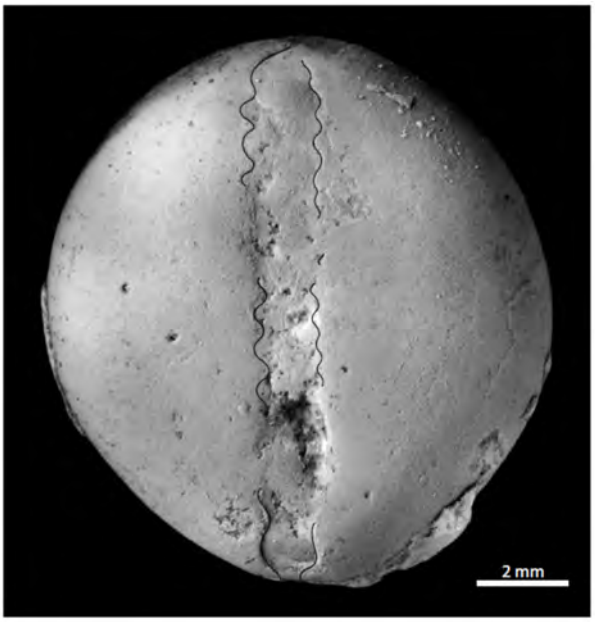

Fig. 4.5. — Cypraeid gastropod *Coffeacypraea tithonica* (Di Stefano, 1882) from the Tithonian, Upper Jurassic of the castle mountain of Termini Imerese, Sicily, Italy. The designated lectotype of *Cypraea tithonica*, with apertural denticles traced as far as visible; MGUP-20-368a.

tithonica (Di Stefano, 1882), fall into the size range and morphological variability of the type series of *C. tithonica*. Specimen MSTC no. 186vi0950 is slightly tapered posteriorly and has a shallow dent in its anterior part. However, similar features occur in the paralectotypes (Fig. 4.4B, C, G3) and should be attributed to intraspecific variability.

Whether the single specimen from the Tithonian–Berriasian of Štramberk (Czech Republic) reported by Blaschke (1911) should be assigned to *Coffeacypraea tithonica* is unconfirmed. The specimen was not illustrated and could not be traced among Blaschke's (1911) material, which only comprises the figured specimens (pers. comm. Thomas Nichterl, Natural History Museum, Vienna, January 2025).

In his first major revision of the Cypraeoidea, Schilder (1927) assigned *Cypraea tithonica*, the type species of *Coffeacypraea*, to *Cyproglobina* De Gregorio, 1880, a genus that is based on an Eocene type species from southeastern France and is presently placed in the family Ovulidae (see Fehse 2013 for subsequent type designation and taxonomy). Subsequently, *Cypraea tithonica* was assigned to the genus *Palaeocypraea* Schilder, 1928 by several authors (see synonymy above), which is based on a type species from the Paleogene (Danian) of Denmark, *Cypraeacites spiratus* Schlotheim, 1820. While comparable in size, *Palaeocypraea spirata* is significantly more elongated and has a distinctly curved aperture in a less central position. It also differs by having widened posterior and anterior canals. Owing to the curvature of the aperture, the apertural denticles vary in strength and inclination in *Palaeocypraea*, while they are apparently equal in size and orientation in *Coffeacypraea*. *Coffeacypraea tithonica* was not originally included when Schilder (1928) introduced *Palaeocypraea*, but was later transferred to that genus (Schilder and Schilder 1971).

Stratigraphic and geographic range.—Tithonian, Upper Jurassic of Italy and potentially Czechia.

Coffeacypraea gemmellaroi (Di Stefano, 1882)

(Fig. 4.3E, F)

*1882 *Cypraea Gemmellaroi*, Di-Stef.; Di Stefano: 75, pl. 4: 3.

? 1919 *Cypraea Gemmellaroi* Di Stef.; Parona: 475.

1927 [*Bernaya* (*Protocypraea*)] *gemmellaroi* di Stef.; Schilder: 88.

1928 [*Protocypraea*] *gemmellaroi* di Stef.; Schilder: 23.

1971 [*Bernaya* (*Bernaya*)] *gemmellaroi* Stefano 1882; Schilder and Schilder: 27.

1990 *Bernaya* (*B.*) *gemmellaroi* (Stefano, 1882); Groves: 273.

1993. *Bernaya gemmellaroi* Stefano, 1882; Tracey et al. 1993: 148.

1994. *Bernaya* (*Protocypraea*) *gemmellaroi* (Steffano 1882) [sic!]; Groves: 26, figs 3, 4 [reproduced from Di Stefano 1882].

non 2014 *Bernaya gemmellaroi* (Di Stefano, 1882); Zamberlan and Checchi: 21, fig. 8.

2021 *Palaeocypraea gemmellaroi* (Stefano, 1882); Groves and Landau: 8.

non 2024 *Bernaya gemmellaroi* (Di Stefano, 1882); Capasso: 166, fig. 4.

Emended diagnosis.— Relatively small (approximately 25 mm long), smooth-shelled Cypraeidae; rounded short-ovate in outline in dorsal view, with slightly tapering anterior and posterior portions; basal side of shell widely flattened, slightly subsiding towards the apertural slit; dorsal side evenly arched and inflated. Aperture slit-like, in almost central position, straight, slightly widened (?) in central part, without widened anterior and posterior notches; apertural denticles seen on columellar lip only, presumably due to limited preservation, evenly sized and spaced. Anterior (siphonal) and posterior canals very short.

Type locality.— Castle mountain of Termini Imerese, Palermo Region, Sicily, Italy.

Type horizon.—*Ellipsactinia* breccias member, Crisanti Formation, Tithonian, Upper Jurassic.

Material.— The type material of *Cypraea gemmellaroi* was not found during our visit to Palermo in 2017. From Di Stefano's (1882) description, it is unclear whether there were more specimens than the figured one. However, the expression 'height of the figured specimen' may be read as a hint that there were several syntypes.

Description.— Shell up to 25 mm long; convolute, cypraeid in shape, with last whorl overgrowing all previous whorls; rounded short-ovate in outline in dorsal view; anterior and posterior ends slightly tapering, the posterior one more so than the anterior one (note that the posterior end is facing upward in Figure 4.3E, F). Shell considerably and evenly inflated in lateral

view, with basal (apertural) side widely flattened, probably slightly subsiding towards the apertural slit. Outer shell surface smooth. Aperture relatively narrow, slit-like, in almost central position, slightly widened (?) in central part, straight without widened anterior and posterior notches. Apertural denticles evenly sized and spaced, clearly visible on columellar lip only, presumably due to limited preservation. Anterior (siphonal) and posterior canals very short; posterior canal more clearly marked than siphonal canal.

Remarks.— *Cypraea gemmellaroi* is also included in *Coffeacypraea*, which has a more bulbous shell than *Coffeacypraea tithonica* and is also significantly larger, almost twice the size. According to the original illustration by Di Stefano (1882), its slit-like aperture is also straight; the anterior and posterior canals are more distinct than in *Coffeacypraea tithonica* but still not very pronounced. In modern cypraeids, shell size is highly variable, and in some species, the largest individuals are three times the size of the smallest ones (e. g., Poppe and Goto 1991). This means that *Coffeacypraea tithonica* and *C. gemmellaroi* may represent a single species, based on their sizes alone. However, in view of the slight differences noted above, while relying only on Di Stefano's (1882) figures and description, both species are considered valid.

As mentioned above, *Coffeacypraea gemmellaroi* was assigned to *Bernaya* (*Protocypraea*) Schilder, 1927 with the original description of the subgenus (Schilder 1927; type species: *Cypraea orbignyana* Vredenburg, 1920; Upper Cretaceous, southern India; Groves (1994) reverted to this assignment without discussion, but subsequently transferred the species to *Bernaya* Jousseaume, 1884 sensu stricto (Schilder and Schilder 1971), which is based on a type species from the Eocene of France, *Cypraea media* Deshayes, 1835. *Bernaya* differs from *Coffeacypraea gemmellaroi* by having a curved aperture that is widened posteriorly, while that of *C. gemmellaroi* is straight and lacks a widened posterior part. Moreover, *Bernaya* is broadly pyriform in dorso-ventral view. In contrast, *Coffeacypraea gemmellaroi* is rounded short-ovate in outline. Besides the morphological differences, Eocene species of *Bernaya* are also significantly larger than *Coffeacypraea*, ranging between 37 and 62 mm in length (e.g., Pacaud 2018).

Stratigraphic and geographic range.—Tithonian, Upper Jurassic of Italy.

Discussion

Evolutionary relationships

The new genus *Coffeacypraea* in the Cypraeidae and the genera *Zittelia* and *Colombellina* in the Colombellinidae, all from the Late Jurassic of southern and central Europe, are among the oldest caenogastropods that share an elongated, slit-like aperture, although some Palaeozoic subulitoids also have narrow apertures. Furthermore, elongated apertures occur in

several Triassic, Jurassic and younger heterobranchs (e.g., Gründel and Nützel 2013; Hausmann and Nützel 2015). This feature has been interpreted as a convergent anti-predatory adaptation, which evolved repeatedly in the course of the Mesozoic Marine Revolution (Vermeij 1977, 1987).

With the exception of certain bellerophontoids, which are, however, isostrophically coiled, convolute gastropod shells (last whorl covering all previous ones) are unknown from the Palaeozoic and the Triassic. Convolute shells with elongate aperture are also known from the Late Jurassic onward in Heterobranchia (genus *Volvocylindrites* Cossmann, 1895, see Gründel and Nützel 2013). So far known, *Coffeacypraea* represents the earliest record of this type of convolute shell in Caenogastropoda and clearly is the earliest member of the Cypraeidae and the Cypraeoidea, as was assumed previously.

The relationship between the Jurassic colombellinid *Zittelia* and the Recent *Cypraea* was initially discussed by Sayn (1932), and later, Colombellinidae were considered the stem group of Cypraeoidea by Taylor and Morris (1988). This hypothesis, however, has never been critically assessed and Gemmellaro's (1869) type material had not been revised since the original description. Moreover, the characteristics of *Zittelia* and *Colombellina* have not been clearly demarcated. As a result, species have commonly been misplaced in either of these genera and taxa with entirely different characteristics were included in the family Colombellinidae (Bakayeva & Kaim unpublished data).

Colombellina is similar to *Zittelia* both with regard to its aperture morphology and its coarse nodular ornamentation (Fig. 4.6A, B). However, in *Colombellina*, the outer and inner lips are rather narrow, and the majority of the spire is not covered by them, whereas in *Zittelia* the lips are expanded over the spire and cover more than half of it (Fig. 4.6B2). This indicates that the mantle of *Zittelia* could envelop a significant portion of the shell. The spire, therefore, is not visible on the ventral side of the shell, as it is covered by the expansion of the lips.

According to Gemmellaro (1869d), one of the diagnostic characteristics of *Zittelia*, which distinguishes it from *Colombellina*, is its very narrow and slightly curved aperture, terminating both anteriorly and posteriorly in a notch or canal (Fig. 4.5B1). The similarity of *Zittelia* and *Cypraea* was highlighted by Gemmellaro (1869d) through the naming of one of the new species, *Zittelia cypraeaeformis*, which was subsequently designated as the type species of *Zittelia* by Cossmann (1904). Other Jurassic species of *Zittelia*, i.e., those described by Zittel (1873) and Brösamlen (1909) are still awaiting revision. In Cretaceous Cypraeidae, the notches seen in *Zittelia* have not been mentioned nor depicted (Sayn 1932; Roman and Mazeran 1920; Groves 1990, 2004; Groves et al. 2011). In the Eocene cypraeid *Cypraeorbis*, Darragh (2011: fig. 1)

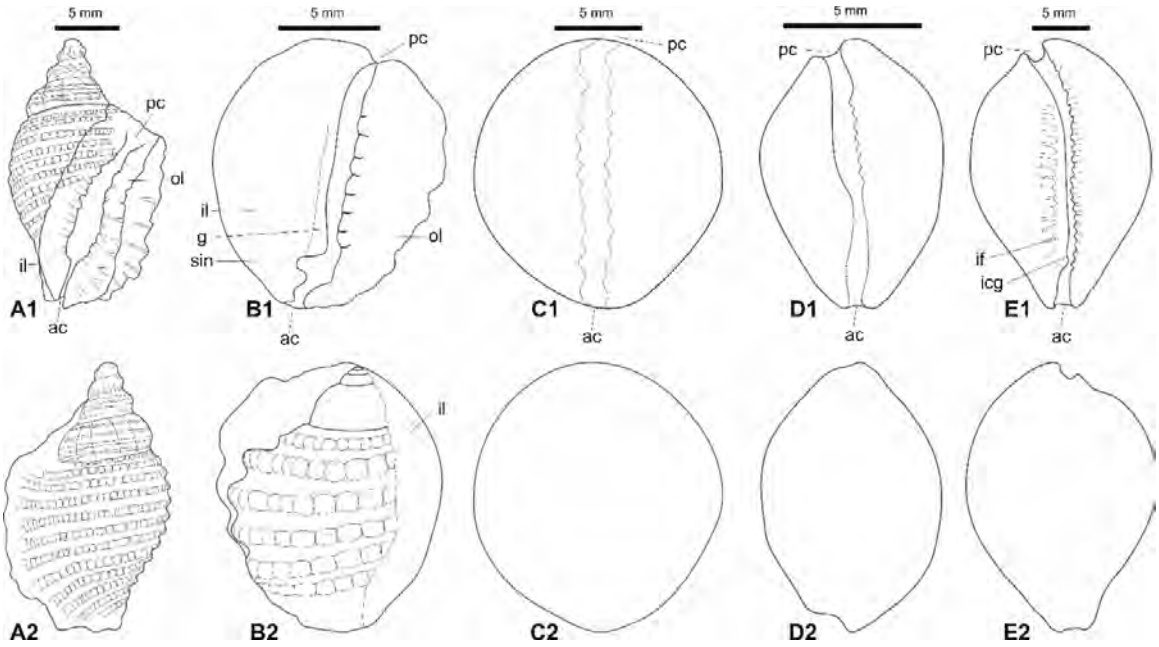

Fig. 4.6. — Comparison between colombellinids and cypraeids showing the morphological gradient from *Colombellina* through *Zittelia* and *Coffeacypraea* to *Cypraeorbis* (modern Cypraeidae). **A**. *Colombellina corallina* (Quenstedt, 1852), Tithonian, Upper Jurassic of Štramberk, Czechia. **B**. *Zittelia cipraeaeformis* Gemmellaro, 1869, Tithonian, Upper Jurassic of Carini near Palermo, Sicily, Italy. **C**. *Coffeacypraea tithonica* (Di Stefano, 1882), Tithonian, Upper Jurassic of the castle mountain of Termini Imerese near Palermo, Sicily, Italy. **D**. *Cypraea antiqua* Sayn, 1932, Barremian, Lower Cretaceous of Barcelonne, Drôme, France. **E**. *Cypraeorbis ventripotens* (Cossmann, 1903), Moodys Branch Formation, Upper Eocene of Town Creek, Jackson, Mississippi, USA. Abbreviations: ac – anterior canal, g – groove, icg – infracolumellar groove, if – incipient flange, il – inner lip, ol – outer lip, pc – posterior canal, sin – sinuosity.

noted a similar structure, termed infracolumellar groove, located at the anterior end of the aperture (Fig. 4.6E1), which might be a homologue of the anterior sinuosity.

In the Late Jurassic forms of *Colombellina*, *Zittelia*, and *Coffeacypraea*, the position of the posterior canal is on the right (labral) side of the shell axis (Fig. 4.6A, B, C, Tab. 4.1). In Early Cretaceous cypraeids, the posterior canal has already shifted to the left (Fig. 4.6D), where it also occurs in Recent representatives of the Cypraeidae. It might be, therefore, hypothesized that a gradual shift of the posterior canal from the right side of the shell axis to its left side occurred between the Tithonian (Late Jurassic) and Barremian (Early Cretaceous).

Furthermore, the infracolumellar groove at the anterior end of the aperture observed in some Cenozoic and Recent Cypraeidae may have evolved from the sinuosity or notches in *Zittelia* and may thus represent a derived trait. However, this characteristic does not consistently appear within all cypraeids. Nevertheless, its repetitive occurrence, along with the strongly expanded lips in *Zittelia*, may be considered as a strong support of the relationship between these genera. Their co-occurrence in the latest Jurassic of Sicily, Italy, and potentially also Czechia, may indicate that the Late Jurassic reefs and associated lagoons of the Tethys were a centre of

Table 4.1. — Comparison of morphological characteristics of some species of Colombellinidae and Cypraeidae.

Species	*Colombellina corallina*	*Zittelia cipraeaeformis*	*Coffeacypraea tithonica*	*Cypraea antiqua*	*Cypraeorbis ventripotens*
Age	Tithonian	Tithonian	Tithonian	Barremian	Eocene
Aperture	expanded in the central part and prosocyrt oblique	narrow and prosocyrt oblique	narrow and straight	narrow and opisthocyrt oblique	narrow and opisthocyrt oblique
Anterior canal (ac)	short	absent, only notch present	absent, notch also absent	weakly developed notch	prominent notch
Groove (g)	absent	present	absent	?	absent
Infracolumellar groove (icg)	absent	absent	absent	?	present
Incipient flange (if)	absent	absent	absent	?	present
Inner lip	present only on the last whorl, usually denticulated	covers more than half of the spire	covers the entire spire, denticulated	covers the entire spire	covers the entire spire, denticulated
Outer lip	narrow and separated from inner lip, usually denticulated	wide but separated from inner lip, denticulated	merged with inner lip, denticulated	merged with inner lip, denticulated	merged with inner lip, denticulated
Position of the posterior canal relative to the shell axis	right	right	right	left	left
Angle between shell axis and posterior canal	30°	20°	7°	10°	25°
Sinuosity	absent	present	?	?	absent

diversification of the Colombellinidae. In the same environments, decapod crustaceans underwent a remarkable diversification during Late Jurassic times (e.g. Klompmaker et al. 2013) and, as potential predators of the gastropods, may have indirectly contributed to the evolution of convolute shells with restricted apertures.

The origination of Cypraeidae with the new genus *Coffeacypraea* and the diversification of Colombellinidae in the Middle to Late Jurassic contributed considerably to the Mesozoic–Cenozoic caenogastropod radiation. Both taxa represent "higher" caenogastropods (Neomesogastropoda sensu Bandel (1991) and Latrogastropoda sensu Riedel (2000)). At approximately the same time, the family Purpurinidae likely gave rise to Neogastropoda (Bakayeva et al. 2024). Therefore, Middle to Late Jurassic was a pivotal time for the evolution of Caenogastropoda, one of the most diverse animal clades.

CONCLUSIONS

Based on the restudy of the type material of *Cypraea tithonica* from the Tithonian of Sicily, this species is placed in the new genus *Coffeacypraea* gen. nov. *Coffeacypraea tithonica* and *Coffeacypraea gemmellaroi* from the same formation represent the oldest undoubted members of Cypraeoidae. As was previously suggested, cypraeoids are closely related (possibly sister-group) to coeval Colombellinidae which also have narrow, elongate apertures but are not convolute. The origination of Cypraeidae and the diversification of Colombellinidae in the Middle to Late Jurassic contributed considerably to the Mesozoic–Cenozoic caenogastropod radiation.

CHAPTER V

The earliest (Early Cretaceous) record of a vasid gastropod and its importance for understanding the diversification of Neogastropoda*

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ABSTRACT

The emergence of Neogastropoda in the Early Cretaceous and its rapid radiation in the mid-Cretaceous remain poorly understood due to the extremely limited number of their early fossils. This is why each record from that critically important interval is essential for documenting the early history of the order, as well as for studies utilizing molecular clocks to test hypotheses about evolutionary rates and timing. Here, we describe a new vasid species, *Fimbrivasum bulgaricum* **sp. nov.**, with a preserved protoconch and a shell morphology with prominent ornamentation and characteristic columellar folds. The specimen also exhibits the earliest occurrences of some functional traits, such as varices and a labral tooth, in Neogastropoda. This finding suggests a much earlier origin of the family Vasidae than previously believed, dating it as the Barremian. It also indicates that neogastropod diversification was well underway in the earliest Cretaceous. We also review the earliest records of living neogastropod superfamilies and their diversification in the Cretaceous showing that the fossil record does not fit well with the molecular phylogeny in the current state of knowledge highlighting the poor fossil record of the group outside of Europe and the United States and challenges in identification of early members of particular clades.

Key words: Vasidae; *Fimbrivasum*; first appearance; phylogeny; varices; labral tooth; Barremian.

INTRODUCTION

[*] Bakayeva S., Herbert G. S., Hryniewicz K., and Kaim A. The earliest (Early Cretaceous) record of a turbinelloid gastropod and its importance for understanding the diversification of Neogastropoda (in review, submitted on December 22nd, 2025).

Neogastropoda is a group of carnivorous snails that are highly diverse today, making up around a quarter of all described living gastropods (Cunha et al., 2009, Ponder et al., 2019). They primarily inhabit marine environments, with their greatest abundance in the tropics. Nearly all high rank taxa of Neogastropoda attained worldwide distribution already by the latest Cretaceous, mostly due to the aftermath of the rapid mid-Cretaceous radiation (Vermeij, 1977; Tracey et al., 1993), whereas in the Early Cretaceous they were exceedingly rare. The oldest records of crown neogastropods are reported from the Valanginian (~140–133 Ma). One specimen, represented by a juvenile shell with a protoconch and identified only to the superfamily level (now Buccinoidea, see below), was recorded from the Valanginian of Poland (Kaim, 2004). Three other potential species from the Valanginian were described from Switzerland in the old monograph by Pictet & Campiche (1861–1864), but their systematic placement has never been revisited since their original description. A few other species are known from much younger, Aptian–Albian sediments (Pictet & Campiche, 1861–1864, Frebold, 1935, Wollemann, 1903, 1906, Allison, 1955), whereas the record of Neogastropoda from the rest of the early Early Cretaceous remains virtually unknown.

Geographically, the Barremian gastropod faunas are documented only within Eurasia: i.e., France (Sayn, 1932, Gründel & Kollmann, 2013), Albania (Kollmann & Peza, 1997a, b), central part of the East European Platform (Blagovetshenskiy & Shumilkin, 2006a, 2006b, 2012), the North Caucasus (Pchelintsev, 1927), and Japan (Kase & Maeda, 1980, Kase 1984, Isaji et al., 2022). These assemblages only occasionally yield well-preserved specimens.

The previous accounts on Barremian gastropods from Bulgaria by Athanassova-Deltcheva (1966) and Dimitrova (1974) were based on large specimens occasionally found in a number of localities. In contrast, the material from Veliko Tarnovo at our disposal consists primarily of small-sized specimens (< 1 cm), with only a few larger shells. Among all currently known Barremian gastropod faunas, this collection stands out both in terms of diversity and the exceptionally well-preserved shells.

After examining the entire gastropod collection from the Lower Cretaceous of Bulgaria, we found out that only one specimen belongs to Neogastropoda. This specimen was found at the locality listed in the collection catalogue as Veliko Tarnovo (Fig. 5.1). Following its careful preparation, we observed several characteristics important for familial and generic identification of this specimen, as well as earliest appearances in Neogastropoda of functional traits such as varices and a labral tooth. Since only a few examples of Neogastropoda members from the Early Cretaceous have been documented to date (Tab. 5.1), identifying this specimen to the genus level

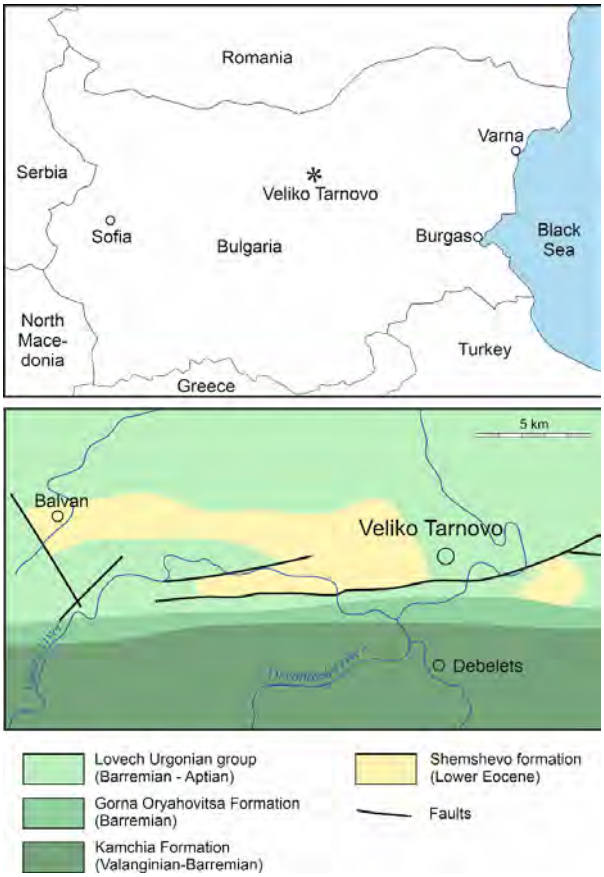

Fig. 5.1. — General location of Veliko Tarnovo within Bulgaria and geological map of sampling locality (after Cheshitev et al., 1989).

could be of particular interest for studies utilizing molecular clocks and for understanding of the emergence and diversification of Neogastropoda.

GEOLOGICAL SETTING

The collection of Early Cretaceous gastropods at our disposal comes from Veliko Tarnovo (and its vicinities) located in the north-central part of Bulgaria. In this region, the Lower Cretaceous (Barremian–Aptian) sediments are part of the Lovech Urgonian Group (Cheshitev et al., 1989), which consists of four terrigenous and four carbonate formations, represented by sandstones, limestones, marls and sandy marls. The stratigraphical position of the deposits within the Lower Cretaceous sequence was determined based on ammonites (Nikolov & Minkovska, 2012 and references therein). Small shells of gastropods were collected from marls of Gorna Oryahovitsa Formation.

MATERIAL AND METHODS

The research is based on the gastropod collection from the National Museum of Natural History of Bulgarian Academy of Sciences (Sofia, Bulgaria) collected mostly by R. Popov in the 1980s. This collection consists of nearly 600 specimens, all of which were examined, measured, and identified. Just one specimen was recognised as belonging to Neogastropoda. The specimen was

covered by a crust of clayey marl, so it was photographed before and after very careful mechanical preparation. The study employed traditional conchological analysis. Shell morphology was investigated using a scanning electron microscope Philips XL20 at the Institute of Paleobiology, Polish Academy of Sciences. The material is housed at the National Museum of Natural History in Sofia, Bulgaria, abbreviated NMNHS.

DESCRIPTIONS OF SPECIES AND SYSTEMATICS

Order Neogastropoda Wenz, 1938

Superfamily uncertain

Family Vasidae H. Adams & A. Adams, 1853

Genus *Fimbrivasum* Squires & Saul, 2001

Type species: *Fimbrivasum elegans* Squires & Saul, 2001,

Late Cretaceous (Campanian–?Maastrichtian), California, USA

Diagnosis. Fusiform turbinellid with two to three inner lip folds and sub-cancellate fimbriate sculpture (after Squires & Saul, 2001).

Species included. *Fimbrivasum elegans* Squires & Saul, 2001, *F. robustum* Squires & Saul, 2001, *F. medium* Squires & Saul, 2001, and *F. bulgaricum* sp. nov.

Remarks. All species of *Fimbrivasum* described to date were known exclusively from the upper Santonian to upper Campanian (or possibly Maastrichtian), i.e. the Upper Cretaceous, of the Pacific slope of North America (Squires & Saul, 2001). The genus was originally included in the family Turbinellidae. However, in light of a recent molecular study that found that species of the genus *Vasum* comprise a basal clade of Buccinoidea, separate from Turbinellidae (Fedosov et al., 2024), we feel that it should be placed in the Vasidae.

Vermeij (2024a, b) excluded *Fimbrivasum* from Vasidae due to the presence of true varices and a twisted siphonal canal in the former. Webster & Vermeij (2017) noted that some species of Vasidae, such as *Vasum turbinellus* (Linnaeus, 1758), form a shell lip that resembles a varix in being reinforced with knobby or spiny ribs but lack an essential second feature – a smaller type of axial element (intervarical ribs) separating the varices. However, Vokes (2019) argued that this is a distinction rather than a meaningful difference, and we agree for several reasons. The varices of *Fimbrivasum* and the shell lips of some vasids are similar developmentally in being thickened with additional shell on the apertural side. Thickening also implies periodic growth resting stages to reinforce the lip and, thus, functional similarity with varices as a passive defence against predators. The presence or absence of intervarical elements in some vasids is also ambiguous. In *Aristovasum cassiforme* (Kiener, 1840), for example, there are one to three axial elements that are morphologically distinct from the varices, and, thus,

potentially homologous with true intervarical axial elements. Like the varices, these intervarical elements are defined by small, recurved, and internally thickened spines rising from the primary spiral cords along the body whorl. They differ from the varices in the absence of the major spine arising from the shoulder cord as well as absence of spines arising from spiral cords on the siphonal canal. Developmentally, then, the condition of the axial ornamentation in *A. cassiforme* and species of *Fimbrivasum* – consisting of varices with intervarical axials – is comparable. Varices have evolved and been lost many times independently across and within neogastropod families, and variation in varix type, number, and developmental mode (periodic vs. continuous growth) can vary within families and even within species (Webster & Vermeij, 2017). Thus, the presence and expression of varices in Vasidae is not a strong argument for inclusion or exclusion of *Fimbrivasum* from Vasidae.

Like in modern vasids, the type species of the genus *Fimbrivasum*, *F. elegans*, possesses a siphonal fasciole. Additionally, both the Barremian specimen and the Late Cretaceous specimens (Squires & Saul, 2001) exhibit several features linking them to Vasidae, i.e., presence of spines on the last whorl, cancellate ornamentation, crenulated lip, and three columellar folds. Other evidence supporting the assignment of our species to the family Vasidae is the striking similarity of the protoconch preserved in our specimen (Fig. 5.2) to the protoconchs of recent representatives of the family (Morrison et al., 2021).

Vermeij (2024a, b) noted a very long time gap (~38 Ma) between the Late Cretaceous species of *Fimbrivasum* and the oldest (late Eocene) taxa, which he considered to belong to Vasidae. However, an even larger interval (~50 Ma) separates the Barremian species from its Late Cretaceous congeners, which suggests that these temporal gaps are sampling or preservational artifacts. We feel, therefore, that Vermeij's (2024a, b) exclusion of *Fimbrivasum* from Vasidae was premature. Despite doubts cast by Vermeij (2024b) about the familial position of *Fimbrivasum*, we still consider the new species from Bulgaria to be the oldest record not only of this genus but also of the entire family Vasidae worldwide.

Range. Cretaceous (Barremian–Campanian or possibly Maastrichtian)

Fimbrivasum bulgaricum sp. nov.

Figures 5.2, 5.3, 5.4, 5.5A, E, F,

Derivation of the name. After the Latinization of Bulgaria.

Material. One specimen (NMNHS-10911) from the Barremian of Veliko Tarnovo, Bulgaria.

Holotype. NMNHS-10911.

Stratigraphical range. Barremian, Lower Cretaceous.

Type locality. Veliko Tarnovo, Bulgaria.

Description. Small fusiform shell (spire angle 53°); height 7.2 mm, width 3.7 mm; protoconch paucispiral, with embryonal shell eroded and 1.3 convex smooth whorls preserved; demarcation between protoconch and teleconch thickened; teleconch consists of 3.5 angulated whorls separated by impressed suture; large last whorl height about three quarters of shell height; shell surface sculptured with strong, round prosocline axial ribs, which are most prominent in the middle part of whorls, and somewhat do not reach the sutures; number of axial ribs reduces with shell growth (from 14 on the first whorl to 9 on the last), while their width increases; at intersection of shoulder keel with axial ribs, nodes occur that turn into blunt, adapically oriented spines at older whorls; five varices occur on the shell, with the earliest one appearing almost at the end of the second whorl; three varices occur on the third whorl, with the angles between the first three approximately 100°, increasing to 135° between the third and fourth varices and to 160° between the fourth and fifth; varices differ from axial ribs only in their greater thickness; on the first teleoconch whorl, four primary spiral cords occur with the second adapical cord being stronger and becoming a peripheral keel before the end of the first whorl; total number of spiral cords increases rapidly due to appearance of infrasutural primary cords and new secondary cords in the interspaces; on the penultimate whorl a tertiary cord occurs below keel; both primary and secondary cords extend beyond the lip to form crenulations; subsutural primary cord, more prominent than the rest on the last whorl, forms an anterior keel and the center point of a triangulate labral tooth that spans the lip as a whole; labral tooth formed continuously at varices, axial ribs, and at smaller growth increments in between; shell surface slightly concave above the shoulder keel and flat below it; aperture broken; anterior canal partially preserved, elongated and slightly twisted; columella with 3 folds.

Remarks. Squires & Saul (2001) assigned to *Fimbrivasum* species that have a shell with a high spire, a tabulate shoulder, cancellate sculpture with strong spiral cords, a columella with or without a callus, and two or three columellar folds. Additionally, the siphonal canal is slightly twisted. All of these characteristics are also present in our specimen warranting confident assignment of our species to this genus. *Fimbravasion bulgaricum* **sp. nov.** differs, however, from the type species in having an enlarged primary cord that forms a labral tooth at the lip, its shell size, which, at around 7 mm in length, is relatively small both for the genus and for the family as a whole, as well as in the weaker elements of ornamentation and the aperture morphology with three (instead of two in the type species) columellar folds that are also less pronounced in our specimen. Squires & Saul (2001) also noted the presence of weak varices on

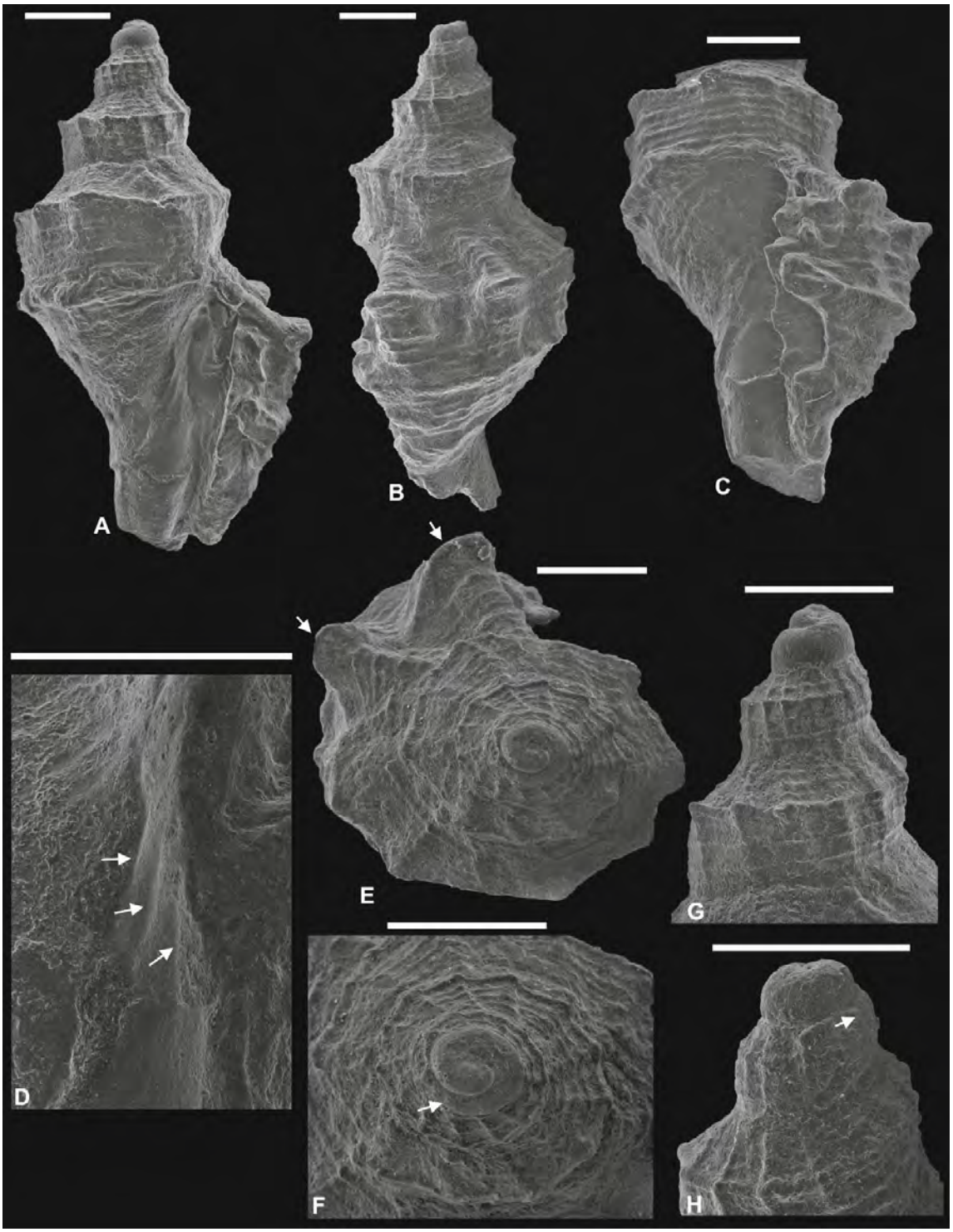

Fig. 5.2. — Turbinelloid neogastropod *Fimbrivasum bulgaricum* sp. nov. from the Barremian of Veliko Tarnovo, Bulgaria. A–H, holotype NMNHS-10911. A, aperture view, B, lateral view, note the ontogenetic change of the sculpture, C, oblique basal view, D, lateral view, detail of columella, arrows indicate columellar plaits, E, apical view, arrows indicate strongest spines on the last whorl, F, apical view, detail view of early whorls, arrow indicates the end of protoconch, G, lateral view, detail of early whorls, H, oblique lateral view, detail of early whorls with arrow indicating the end of protoconch. Scale bars represent 1 mm.

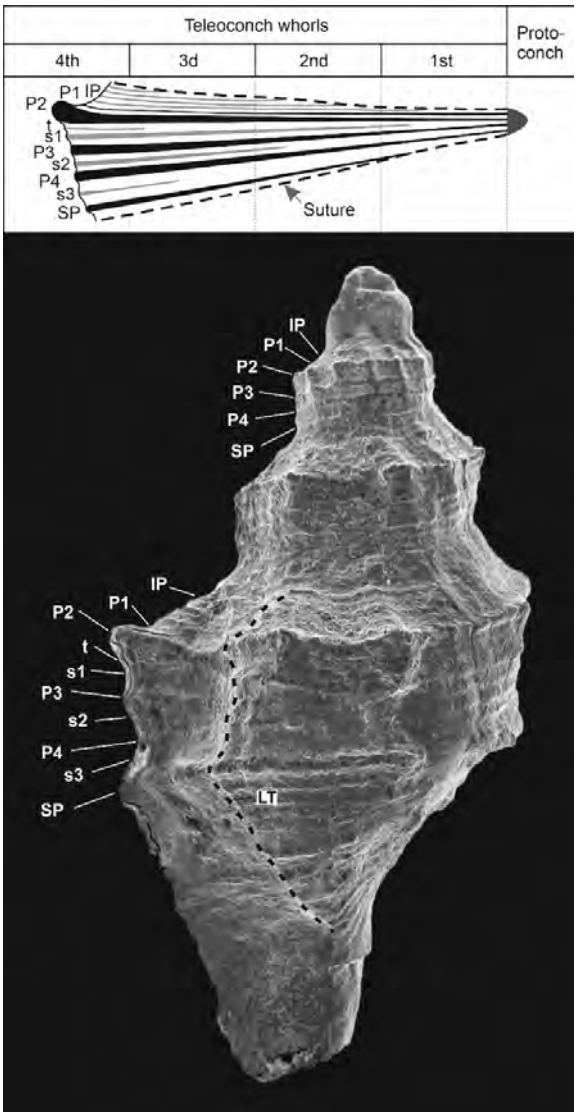

Fig. 5.3. — Primary and secondary sequences of appearance of the cords in *Fimbrivasum bulgaricum* sp. nov. Abbreviations: P1-P4 – primary cords; SP – subsutural primary cord; IP – infrasutural primary cords; s1, s2, s3 – secondary cords; t – tertiary cord; LT – outline of a labral tooth. Spiral cord terminology follows Merle (2001, 2005).

each of the whorls in *F. elegans*, which are weaker in our specimen due to its more delicate ornamentation (Figs 5.2E, 5.4).

The new species shows some similarity to some representatives of Fasciolariidae, both fossil (e. g., *Levifusus acutocarinata* Garvie, 2013 or *Fulgurofusus grande* Garvie, 2013 from Paleogene of Texas, USA (Garvie, 2013)) and recent (e.g., *Hemipolygona* Rovereto, 1899 (Vermeij & Snyder, 2006) or *Leucozonia* Gray, 1847 (Vermeij & Snyder, 2002)) in shell outline, fine spiral ornamentation, axial ribs and spines, in the possible long siphonal canal and the presence of columellar folds (features that may also occur in some fasciolariid taxa, e.g., *Leucozonia* (Vermeij & Snyder, 2002)). However, the protoconch morphology, considered the most plesiomorphic character, most closely resembles that of extant representatives of Vasidae (see the protoconch of *Tudivasum* in Morrison et al., 2021). Protoconchs of specimens from

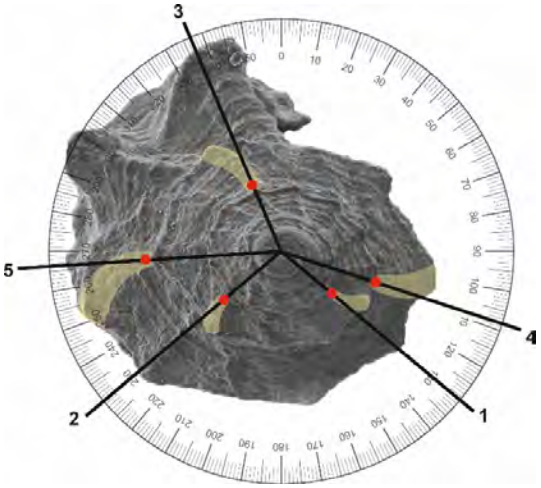

Fig. 5.4. — Apical view of *Fimbrivasum bulgaricum* sp. nov., illustrating the placement of varices and the method used to measure their spacing. Numbers indicate the order of varix appearance on the shell.

Paleogene are unknown, while usually, in fasciolariids, the protoconch is conical and multispiral, consisting of 3–3.5 whorls. The transition between protoconch and teleoconch terminates with several opisthocyrt axial ribs and teleoconch ornamentation begins with a few primary spiral cords, with axial ribs being more thicker. In contrast, the protoconch of our specimen is paucispiral, comprising up to two whorls, with a clearly visible demarcation between protoconch and teleoconch. Teleoconch ornamentation starts with four primary spiral cords and axial ribs of approximately equal thickness.

Other shared characters with fasciolariids include the presence of varices and a labral tooth in the new species, which may be related to close affinities with Buccinoidea (Fedosov et al., 2024) and thus reflect the presence of mixed characters at this stage of vasid evolutionary history.

Occurrences. Barremian, Lower Cretaceous, of Bulgaria.

DISCUSSION

Comparison with younger and extant vasids

There are several possible interpretations of the fact that the shell size of our specimen is relatively small for the family: (i) this shell represents a juvenile specimen, (ii) the majority of taxa in the collection from Veliko Tarnovo are of small size, suggesting environmental control against large size at this location, resulting in dwarfism, similar to common dwarfism in strombids (Landau et al., 2010), or (iii) vasids may have been smaller during the Barremian than they are today. The teleoconch of our specimen comprises 3.5 whorls, whereas adult American species typically consist of 4 to 5 teleoconch whorls (Squires & Saul, 2001), so we cannot confidently state that our specimen was a juvenile. However, small adult size in the new species is consistent with the presence of a labral tooth, since this feature is rarely formed in juvenile neogastropods (Vermeij, 2001). The smallest living neogastropod with a labral tooth is the

marginellid *Dentimargo idiochila*, which reach only 6 mm in length (Geerat Vermeij, personal communication 2025). Sizes of individuals of the new species could vary, but they probably did not reach the sizes of their Late Cretaceous congeners, which exceed our specimen by approximately 8–10 times. The closest extant species to *Fimbrivasum*—*Vasum ceramicum* Linnaeus, 1758—is also about 10 times larger than our shell, while maintaining overall similarity in shell outline and main characteristics such as aperture morphology and ornamentation. More material is required to address this discrepancy.

According to Abbott (1959), the family Vasidae, with the type species and genus *Vasum ceramicum*, comprises approximately 20 extant species, most of which are documented in the Indo-Pacific region. Following his revision, Vermeij (2024a) assigned to the family more than three times as many species. The species from this family typically inhabit the intertidal

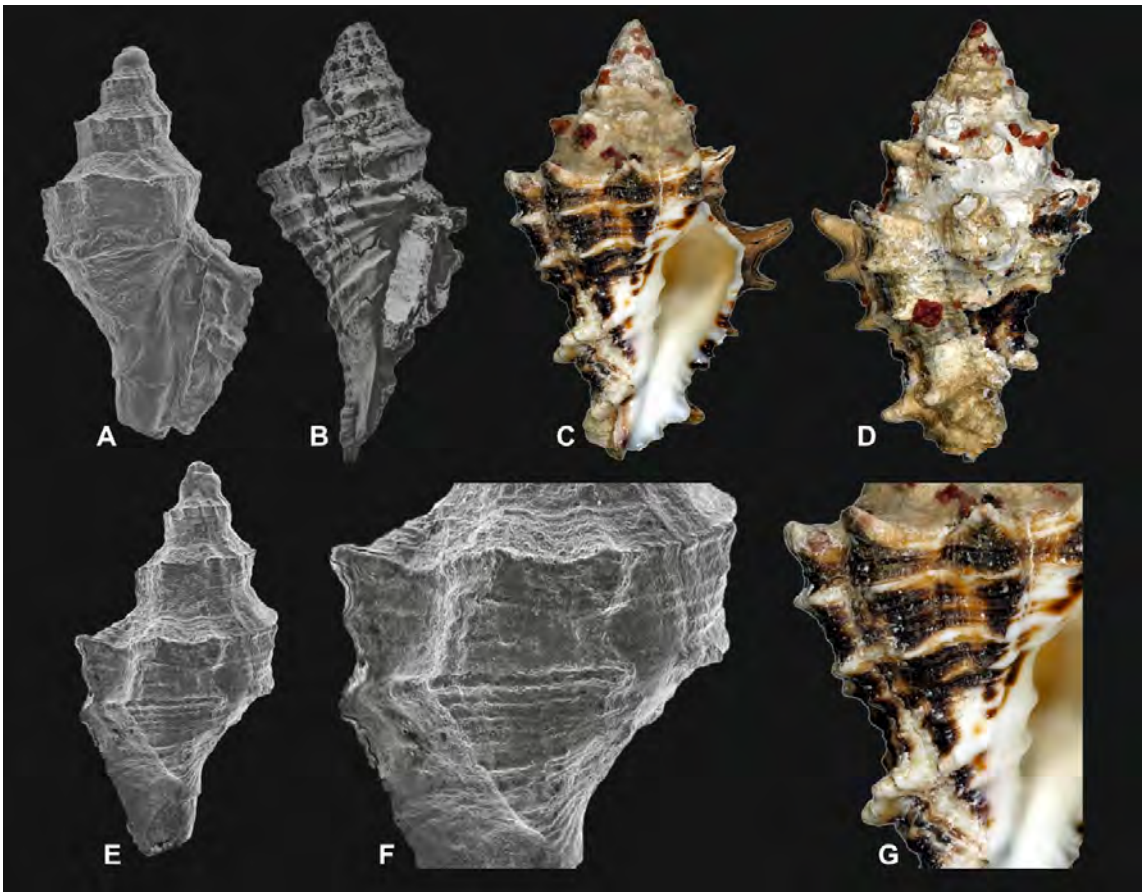

Fig. 5.5. — Comparison of fossil and recent species of the family Vasidae. A, E, F, *Fimbrivasum bulgaricum* sp. nov. from the Barremian of Bulgaria, holotype NMNHS-10911, height 7.2 mm. A, aperture view, E, lateral view, F, lateral view, detail view of the ornamentation of the last whorl. B, Reproduction of *Fimbrivasum elegans* Squires & Saul, 2001 (Squires & Saul, 2001: pl. 5, fig. 10) from the Campanian – ?Maastrichtian of California, USA, holotype SDSNH 67158, height 57 mm, aperture view. C, D, G, *Vasum ceramicum* Linnaeus, 1758, Amami-Oshima, Japan, University Museum, the University of Tokyo, UMUT RM34558, height 78.4 mm. C, aperture view, D, abapertural view, G, aperture view, detail view of the ornamentation of the last whorl.

zone or very shallow waters, although some are found at depths just below 200 meters. Certain species prefer reef flat habitats, while others are known from sandy and/or grassy bottoms (Abbott,1959). Generally, vasids are shallow water dwellers, what is reflected both in their shell thickness and in the robust ornamentation with spines. The biology of several modern vasids was also studied by Taylor (1984), who indicated that their primary diet consists of polychaetes. However, the presence of a labral tooth in the new species suggests that hard-skeleton prey formed at least a part of the new species' diet (e.g., bivalves, barnacles) (Vermeij, 2001).

It is rather difficult to speculate about other aspects of the autecology of the Barremian species. However, its relatively thin shell with fine ornamentation and small size suggests that it inhabited a low-energy environment. This is supported by the silty marls in which its shell was found, which are consistent with a low-energy, possibly neritic setting. The good shell preservation indicates that it was unlikely redeposited or transported over long distances. Surprisingly, all findings of Early Cretaceous crown (or modern-type) neogastropods are known from open marine settings on a soft, muddy bottom with a carbonate-terrigenous type of sedimentation. This includes the present vasid species as well as the records of buccinoids from the Valanginian (Pictet & Campiche, 1861–1864, Kaim, 2004).

Significance of new record and its place in the evolution of Neogastropoda

Including the specimen studied herein, 42 Early Cretaceous neogastropod species have been documented so far (Tab. 5.2, Fig. 5.6). Four species were reported from the Valanginian, with only one having a protoconch preserved (Kaim, 2004). No records of Neogastropoda were documented from the Hauterivian worldwide. Four species are known from well dated Aptian deposits, while another two were reported from undivided Aptian–Albian sediments. All other species were described from the Albian. Thus, the discovery of the Barremian species partly fills a gap between the earliest findings in the Valanginian (between ~140–133 Ma) and the Aptian (between ~121–113 Ma).

The good preservation of our specimen allowed precise identification and proved that the second group of Neogastropoda following the appearance of Buccinoidea in the Valanginian (Pictet & Campiche, 1861–1864, Kaim, 2004; see below) was the Vasidae. Additionally, since Vasidae is the basal sister group to what Fedosov et al. (2024) calls "major Buccinoidea," then is it also plausible to state that the split of Vasidae from "major Buccinoidea" must have predated the first appearance of Buccinoidea in the Valanginian. Nevertheless, the phylogenetic positions of both groups relative to one another and other Neogastropoda is pending additional fossil materials as well as more refined molecular studies based on Recent taxa.

Fig. 5.6. — Distribution of gastropod faunas in the Early Cretaceous worldwide (A) and within Europe (B). Paleogeographic reconstructions of continental configurations for the Early Cretaceous (Barremian) from Kocsis and Scotese (2021). Rectangles indicate Berriasian–Barremian, and circles represent Aptian–Albian gastropod faunas. Filled rectangles and circles denote neogastropod records of the respective ages.

The labral tooth in the new species is the first and only known example of this adaptation in the Vasidae and the earliest fossil occurrence of a labral tooth in the Neogastropoda, with all subsequent records documented from the Campanian onward (Vermeij, 2001, 2006). The presence of varices in the new species is also the first occurrence of this trait in the Neogastropoda. Other occurrences of varices are known in the Late Cretaceous Cancellariidae, which may be a stem group to the rest of the Neogastropoda or to Ficoidea-Tonnoidea (Fedosov et al., 2024), and Buccinoidea (Webster and Vermeij, 2017).

Molecular phylogeny vs. fossil record

We strived to trace all accounts on Cretaceous neogastropods available in the literature and critically evaluated the earliest occurrences of the neogastropod superfamilies (Tab. 5.1). The major problem tracing back neogastropod evolution and diversification from the fossil record is the credibility of identifications of the early records. Highlighting this problem is the superfamilial identification of the earliest crown neogastropods. The earliest reports of alleged crown Neogastropoda were reported from the Valanginian, represented by four taxa previously classified in Muricoidea. However, the specimen identified by Kaim (2004) as Muricoidea gen. et sp. indet. is a juvenile shell most similar to *Latirus rugosissimus* (Locard, 1897), which belongs to Fasciolariidae, and therefore should be classified as Buccinoidea gen et sp. indet. The other three species identified by Pictet & Campiche (1861–1864) as *Fusus valangiensis* Pictet &

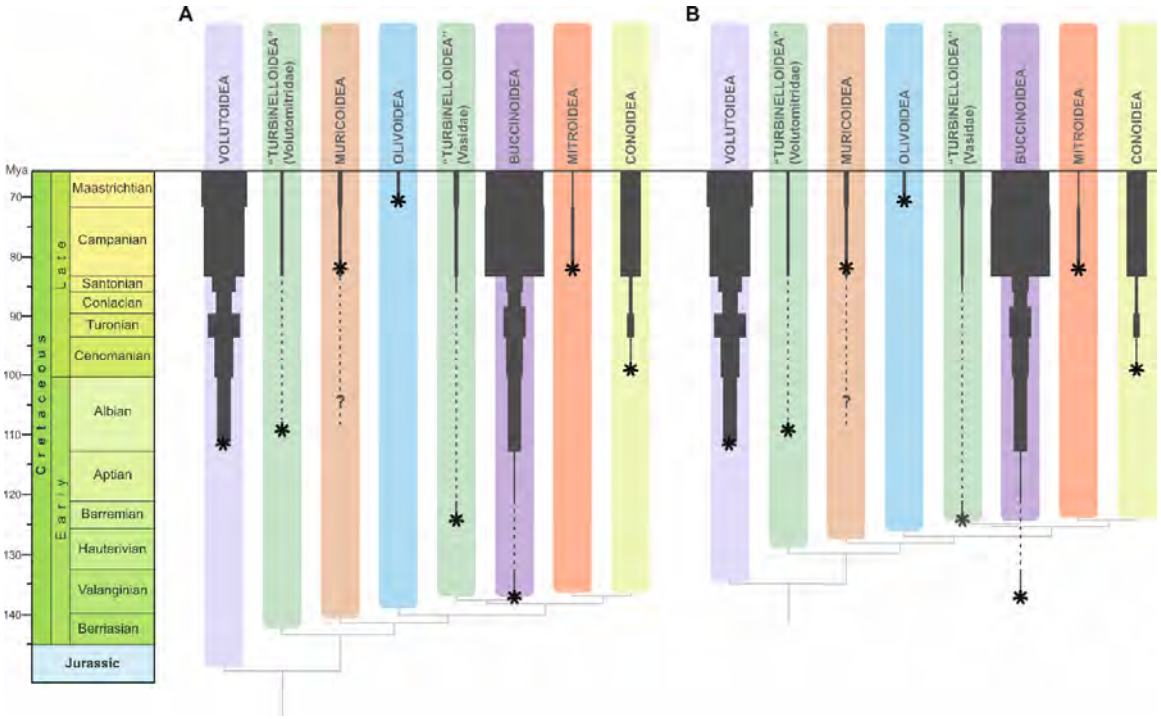

Fig. 5.7. — Reconciliation of the Neogastropoda fossil record with its phylogenetic tree (Lemarcis et al., 2022), rooted in the earliest record of Buccinoidea (A) and alternatively in the earliest record of Turbinelloidea (B). The first appearance of each superfamily is marked with an asterisk. The dashed lines indicate an interval without a fossil record. The thickness of the dark lines corresponds to the number of genera recorded for each time interval.

Campiche, 1864, *Fusus villersensis* Pictet & Campiche, 1864, and *Fusus*? sp. and classified as "Famille des Muricides" are more similar to species from families Busyconidae, Melongenidae or Fasciolariidae, all of which are included in Buccinoidea. Moreover, the genus *Fusus* Bruguière, 1789 (cited in Pictet & Campiche, 1861–1864) is currently a junior homonym of *Fusus* Helbling, 1779, which in turn is an unavailable name (ICZN Opinion 1765), and its type species is included in Colubrariidae Dall, 1904 (also Buccinoidea). Therefore, we consider the earliest-known crown Neogastropoda to be Buccinoidea rather than Muricoidea (compare also Taylor et al., 1980; Tracey et al., 1993; Kantor, 2002), though the revision of the material reported by Pictet & Campiche (1861–1864) is necessary to substantiate this identification.

Taking the above into account, and after critical re-evaluation of each superfamily's earliest record, we find that all neogastropod superfamilies appeared already in the Cretaceous, starting with Buccinoidea in the Valanginian (between ~140–133 Ma; Pictet & Campiche, 1861–1864; Kaim, 2004) and ending with Olivoidea in the Maastrichtian (~72–66 Ma) (Stephenson, 1941; Sohl, 1964). We note, however, that Cretaceous generic diversity in neogastropod superfamilies is very uneven (Fig. 5.7). Two superfamilies are rich in genera (Buccinoidea includes 49 genera, and Volutoidea – 43), two show moderate diversity (Conoidea – 19 and Pholidotomoidea – 18), while the remaining superfamilies do not exceed five genera each within

the Cretaceous. Furthermore, we also noted that neogastropods are very rare in the Early Cretaceous until its final stage, the Albian (~113–100 Ma).

We superimposed our fossil data over the molecular phylogeny of Lemarcis et al. (2022) and Fedosov et al. (2024). The first of the two scenarios (Fig. 5.7) claims the correct identification of Valanginian neogastropods as Buccinoidea, while the other highlights the uncertainty of these identifications and correlates the molecular phylogeny to the earliest turbinelloid reported in this paper, which is undoubtedly the earliest-known fossil record of this superfamily (though most likely polyphyletic, see below). The sequence of appearing the neogastropod superfamilies according to the current knowledge of the fossil record is as follows: Buccinoidea > "Turbinelloidea" (Vasidae) > Volutoidea > Muricoidea(?) > Conoidea > Mitroidea > Olivoidea. According to the molecular phylogeny (Lemarcis et al., 2022) the sequence should be as follows: Volutoidea > "Turbinelloidea" (Volutomitridae) > Muricoidea > Olivoidea > "Turbinelloidea" (Vasidae) > Buccinoidea > "Turbinelloidea" (Turbinellidae) > Mitroidea > Conoidea. Due to possible paraphyly of some neogastropod superfamilies (see e.g. Fedosov et al., 2024), we conservatively used the more ancient clade as the earlier-diverging one. This simple comparison clearly shows that the fossil record is at odds with recent molecular phylogenies.

Buccinoidea.—Judging from the shell characters, Buccinoidea is the first superfamily of crown neogastropods to appear in the fossil record (identified as muricoids in Pictet & Campiche, 1861–1864 and Kaim, 2004). As already pointed out by Kantor (2002), Buccinoidea are a rather derived group of neogastropods judging from typical anatomical features, i.e. possessing a long proboscis with a terminal buccal mass and lacking the accessory salivary and rectal glands (considered to be secondary loss). The derived status of Buccinoidea is also supported by most recent molecular phylogenies (Lemarcis et al., 2022; Fedosov et al., 2024). On the other hand, the shells of buccinoids have rather generic shapes that are not much different from stem neogastropods (i.e., Purpurinidae; compare Bakayeva et al., 2024). It might, therefore, be possible that, despite soft body modifications, buccinoids retained a plesiomorphic shell shape morphology while other groups of crown neogastropods did not. Thus, the taxon Buccinoidea, which comprises modern and early fossil "Buccinoidea", is most likely polyphyletic.

Volutoidea.—The Volutoidea is the superfamily considered to be the most basal in molecular phylogenies (Lemarcis et al., 2022), although it might be paraphyletic with Cancellariidae being more basal than the rest of Volutoidea (i.e. Volutidae). Lemarcis et al. (2022) and Fedosov et al. (2024) suggest that Cancellaridae might be more basal than Tonnoidea + Ficoidea. Either way, Volutoidea s.l. remain as the most basal group of crown neogastropods in the most recent molecular phylogenies. The oldest records of Volutoidea are known from the

Albian (~113–100 Ma). Four species of Volutidae and one species of Marginellidae, all belonging to the more derived clade of Volutoidea, are reported from the Albian of Madagascar (Collignon, 1949a, b) and should be treated as the oldest record of Volutoidea s.s. The oldest records of Cancellaridae come from the Losensteiner Schichten in Austria (Kollmann, 1976), which are dated as Albian–Cenomanian (~113–94 Ma) and Albian Kiowa Shales in Kansas, USA (Stanton, 1947). These records show that both clades already branched out by the Albian. Volutoidea s.s. have quite characteristic shells, which are relatively easy to identify. Cancellaridae, in turn, have a more generalized shell shape, which makes their fossil record much more difficult to interpret. Both adult shells and protoconchs of Cancellariidae (e.g., Harzhauser & Landau, 2012) are reminiscent of some stem neogastropods of the family Purpurinidae (Bakayeva et al., 2024). This similarity may potentially cause difficulty in the demarcation of stem Purpurinidae and crown Cancellaridae. It is also worth mentioning that Volutoidea s.s. first appear in abundance in the Southern Hemisphere (Madagascar), even though, in general, the southern fossil record of Cretaceous gastropods is excessively poor (Fig. 5.6) and requires more collection efforts.

Another interesting problem is the close molecular affinity of Volutoidea and Tonnoidea (Cunha et al., 2009; Osca et al., 2015; Lemarcis et al., 2022; Fedosov et al., 2024; Harasewych et al., 2024). The earliest crown tonnoideans—similar to Volutoidea—are also known from the Albian (Schröder, 1995; Tracey, 2010; Strong et al., 2019), strongly suggesting that both groups diverged earlier in the Early Cretaceous. According to Bakayeva et al. (2024, 2025), both groups originated from Purpurinidae or Colombellinidae in the Late Jurassic/Early Cretaceous. It remains uncertain what the ancestors of Tonnoidea/Volutoidea looked like, but it is plausible to argue that they were different from crown Volutoidea and possessed a more generic shell shape.

Turbinelloidea.—The second most basal superfamily of crown neogastropods after Volutoidea is Turbinelloidea. However, this superfamily poses a serious problem in interpreting the fossil record of Neogastropoda since molecular investigations (Fedosov et al., 2024) indicate that it is paraphyletic, being composed of at least five unrelated highly supported clades (Volutomitridae, Costellaridae, Columbariidae, Vasidae and Turbinellidae). Another family, i.e., Ptychatractidae, is also suggested to be paraphyletic, with one part being sister to Volutomitridae (*Exilioidea*) and another to Costellaridae (*Exilia*). However, the type genus of the family has not yet been sequenced. Out of all these families, Volutomitridae and Costellariidae (and thus Ptychatractidae) are placed between Marginellidae and Muricidae, and Columbariidae are sister to Muricidae. Vasidae are sister to “major” Buccinoidea (Fedosov et al., 2024), while Turbinellidae s.s. (with its type genus *Turbinella*) are sister to Mitroidea + Conoidea. The molecular data suggest, therefore, that the most basal families are Volutomitridae, Costellaridae,

Columbariidae, and Ptychatractidae. However, only Ptychatractidae and Costellaridae have their fossils recorded from the Cretaceous. The ptychatractid *Exilia* is reported from the Santonian–Maastrichtian of Europe and United States (Kaunhowen, 1897; Cossmann, 1901; Gardner, 1916; Wade, 1926) and *Breviexilia* from the Campanian of Palestine (Chavan, 1947), thus both from the upper Upper Cretaceous, while the costellarid *Mitridomus* is reported from the Campanian of the USA (Sohl, 1963, 1964). It should be stated, however, that all of these taxa require thorough review. For example, Sohl (1964) considers *Exilia ripleyana* Wade, 1926, to be a synonym of the conoidean *Amuletum macnairyensis* (Wade, 1926). Prior to this study, the earliest fossil Vasidae were known only from the Santonian–Campanian of the US West Coast (Squires & Saul, 2001); here, the record is extended to the Barremian of Bulgaria. Interestingly, Vasidae are placed as a sister group of "major" Buccinoidea in the molecular phylogeny by Fedosov et al. (2024), which is, as shown above, the first neogastropod group identified from the fossil record. The family Turbinellidae recovered as sister to Mitroidea + Conoidea by Fesodosov et al. (2024) is so far unknown from the Cretaceous.

Muricoidea.—The Muricoidea together with family Columbariidae form the first node of the "core Neogastropoda" sensu Fedosov et al. (2024). However, its Cretaceous fossil record is far from clear. In the past, some taxa from the Valanginian of Switzerland (Pictet & Campiche, 1861–1864) and Poland (Kaim, 2004) were classified as muricoids, but after cursory revision, we think that all of them might actually be buccinoids (see above). Two other genera that were previously classified in the superfamily were transferred to other groups. *Cretaceomurex* Mongin, 1985, from the Albian of France (Mongin in Mongin & Peybernes, 1985) has been recently suggested to belong to Spinilomatidae (a family of Stromboidea) (see www.stromboidea.de). However, it remains to be investigated. *Blackdownia* Kollmann, 1976, from the Albian of Great Britain (Sowerby, 1825) and Albian–Cenomanian of Austria (Kollmann, 1976) has been classified as capulid by Kiel and Bandel (2003), though this claim needs more evidence, as, in our opinion, it more likely belongs to the family Sarganidae, which may indeed belong to Muricoidea, as stated by Saul (1996), or to Tonnoidea, as suggested by Bandel and Dockery (2016). Bouchet et al. (2017) classified Sarganidae within the extinct Pholidotomoidea.

Kiel and Bandel (2003) tentatively placed *Trophon*? *umzambiensis* Kiel & Bandel, 2003 in Muricoidea, arguing that the familial assignment was uncertain because the protoconch of the specimen was unknown. However, in our opinion, the shell outline and overall morphology are closer to turrids (compare with *Unedogemmula* MacNeil, 1961) than to muricids, despite the absence of the protoconch.

The earliest member of Muricoidea might, therefore, be the Campanian *Paramorea* Wade, 1917, although even this genus is uncertain since Bandel & Dockery (2016) suggested it may belong to Tonnoidea.

An undoubted Cretaceous muricid is *Poirieria (Paziella) cretacea* Garvie, 1991 from the upper Maastrichtian of Texas (Garvie, 1991) assigned to *Flexopteron* Shuto, 1969 by Merle (2012). All pre-Maastrichtian occurrences of presumed Muricoidea require thorough review.

Olivoidea.—This superfamily branches out next after Muricoidea. The oldest undisputed records of Olividae come from the Maastrichtian of Texas (Stephenson, 1941) and Japan (Kase, 1990, 1992). Both *Eoancilla acutula* Stephenson, 1941 and *Tanimasanoria japonica* Kase, 1990 possess the characteristic ancillid band. Another possible species is Pseudolividae gen. et sp. indet. from the Maastrichtian of Western Siberia (Kaim & Beisel, 2005).

Mitroidea.—Mitroidea and Conoidea form the final bifurcation on the negastropod molecular tree (Lemarcis et al., 2022, Fedosov et al., 2024). The reports of Cretaceous Mitroidea are very sparse. The oldest record from the Turonian of France is represented by *Mitra conoidea* Matheron, 1842. Although both Matheron (1842) and Cernohorski (1970) originally placed it in Mitroidea, most likely it is a species of Acteonellidae, a group of extinct heterobranchs. Two other genera, *Mitridomus* Sohl, 1963 and *Paleofusimitra* Sohl, 1963 from the Campanian of USA, were included into Mitridae by Sohl (1963, 1964). However *Mitridomus* is included in the subfamily Vexillinae, which is currently included into Costellariidae (a family sister to the core-Neogastropoda clade according to Fedosov et al., 2024). This leaves *Paleofusimitra* as the only confirmed Cretaceous mitroid, since all the other taxa require revision.

Conoidea.—Conoidea is the most derived clade on the neogastropod molecular tree by Fedosov et al. (2024), but it has a surprisingly good fossil record in the Cretaceous (third most diverse clade). The oldest species is the turrid *Graphidula walcotti* (Stanton, 1893), known from the Cenomanian of Arizona (Kirkland, 1996). Until the end of the Cretaceous, the Turridae alone reach nearly 20 genera in total.

CONCLUSIONS

The discovery of *Fimbrivasum bulgaricum* **sp. nov.** indicates a much earlier origin of the family Vasidae than previously thought and dates it back to the Barremian. This record also extends the geographic distribution of the genus and indicates its emergence in the north-western part of the Tethys Ocean, although the poor fossil record of Early Cretaceous gastropods from the global south suggests this claim should be viewed as tentative.

The new representative of Vasidae shows that the major groups of Neogastropoda diverged well before the alleged radiation of the group in the mid-Cretaceous and started already

in the earliest Cretaceous but with very low density of taxa. This result is at odds with the hypothesis of Jablonski (1979) claiming that Neogastropoda reached present diversity by rapid origination at low taxonomic levels (i.e., species) but gradual accumulation of new families. Either way, the rarity of neogastropods in the Early Cretaceous poses serious problems in tracing the evolutionary history of the entire group. As shown above, the fossil record hardly matches the molecular tree of neogastropods with the presumed oldest record of buccinoids, which are core-neogastropods according to the molecular studies (Lemarcis et al., 2022; Fedosov et al., 2024). Additionally, our study shows that more comprehensive revision of Cretaceous neogastropods (family by family) is necessary to properly assess their evolutionary history. Even the survey of earliest records of particular clades shows high levels of misidentification superimposed on uncertainty of clades' monophyly highlighted by recent molecular studies. The most striking example of this is the superfamily Turbinelloidea with as many as five unrelated highly supported clades.

Table 5.1. — Representation of crown Neogastropoda within Early Cretaceous gastropod faunas

Age	**Region**	**Neogastropoda** (G – number of genera, S – number of species)	**References**
Neocomian undivided	France (Yonne)	none	Péron, 1899
	Germany (Teutoburg Forest)	none	Weerth, 1884
	Netherlands, Germany	none	Wollemann, 1900
Berriasian, Valanginian	North of Middle Siberia	none	Basel, 1983
Berriasian – Albian	Azerbaijan	none	Aliyev, 1988
Valanginian	Germany, Poland	none	Schröder, 1995
	Poland	Buccinoidea (G1/S1)	Kaim, 2001, 2004
	Caucasus	none	Pchelintsev, 1927
Valanginian – Hauterivian	Argentina	none	Cataldo, 2013, 2014; Cataldo and Lazo, 2012, 2016
Valanginian – Albian	Switzerland	Buccinoidea (G4/S7) Muricoidea? (G2?/S3?) Volutidae (G1/S1) Colombellinidae (G1/S3)	Pictet & Campiche, 1861–1864
	Austria (Vorarlberg)	none	Kollmann, 2002
	Bulgaria	none	Dimitrova, 1974
	Crimea	none	Pchelintsev, 1963, 1965
	West Siberian Plain	none	Kaim et al., 2004; Kaim and Beisel, 2005
	North America (California)	none	Kaim et al., 2014
Hauterivian	Crimea (Burulcha)	none	Pchelintsev, 1927
	Central part of East European Plain (Volga Region)	none	Glasunova, 1973
Hauterivian – Barremian	Central part of East European Plain (Volga Region)	none	Blagovetshenskiy, 2015, 2017; Blagovetshenskiy and Shumilkin, 2006a, 2006b, 2012; Blagovetshenskiy et al., 2010
Hauterivian, Aptian	Central part of East European Plain (Volga Region)	none	Golovinova and Guzhov, 2009
	Antarctic (SE Alexander Island)	none	Thompson, 1971
Houterivian – Albian	Caucasus	none	Pchelintsev, 1927
Barremian	France (Drôme)	none	Sayn, 1932
	SE France	none	Gründel and Kollmann, 2013
	Japan (East Honshu)	none	Isaji et al., 2022
	Japan	none	Kase, 1984
	Northern Caucasus	none	Pchelintsev, 1927

Barremian – Aptian	Japan (Choshi peninsula)	none	Kase and Maeda, 1980
	Albania	none	Kollmann and Peza, 1997a, b
	Bulgaria	Vasidae (G1/S1)	this paper
Early Aptian	Spain (Castellon)	none	Calzada, 1988, 2010
	Eastern Iran	none	Raisossadat and Noori, 2016
Aptian	NE Greenland (Koldewey Island)	Fasciolariidae? (G1/S1)	Frebold, 1935
Aptian – Albian	Mexico (Jalisco)	none	Mendoza et al., 2021
	Netherlands, Germany	none	Wollemann, 1903, 1906, 1908
	Southern part of West Siberian Plain	none	Sinzow, 1909
	Mexico	Fasciolariidae (G1/S1)	Allison, 1955
	NE Brazil (states of Pernambuco, Piauí and Ceará)	none	Pereira et al., 2022
Late Aptian – Early Albian	Mexico (Cerro de Tuxpan)	none	Buitron, 1986
Albian	England	none	Abbass, 1962, 1973
	SE France	none	Delpey, 1940
	Morroco	Buccinidae (G1/S1)	Collignon, 1972
	Madagascar	Buccinidae (G1/S1) Ptychatractidae (G1/S1) Fasciolariidae (G2/S2) Muricidae (G1/S1) Turbinellidae (G3/S4) Marginellidae (G1/S1) Volutidae (G4/S5)	Collignon, 1949a, b
	NW Madagascar	none	Kiel, 2006
	South England	Fasciolariidae (G1/S1) Buccinidae (G1/S1)	Tracey, 2010
	Eastern Indian Ocean (Batavia Knoll, Perth Abyssal Plain)	none	Wild and Stilwell, 2016
	USA (Texas)	none	Garvie and Symonds, 2022
	Crimea (Balaklava)	Fasciolariidae (G1/S1)	Pchelintsev, 1927
	France	Fasciolariidae (G1/S2)	Kollmann, 2005
Middle Albian – Early Cenomanian	Upper Austria	Buccinidae (G1/S1) Muricidae (G1/S1) Fasciolariidae (G1/S1)) Cancellariidae (G1/S1)	Kollmann, 1976, 1978, 1979, 1982

Table 5.2. — Described from Early Cretaceous neogastropod species (species names and their family attribution are given according to the original works)

Age	Region	Family	Species (number of specimens)	Reference
Valanginian	Poland	Muricoidea	Muricoidea gen. et sp. indet. (1)	Kaim, 2004
Valanginian	Switzerland	Muricidae	*Fusus valangiensis* Pictet et Campiche, 1864 (?) *Fusus villersensis* Pictet et Campiche, 1864 (?) *Fusus*? sp. (?)	Pictet & Campiche, 1861–1864
Barremian	Bulgaria	Vasidae	*Fimbrivasum bulgaricum* sp. nov. (1)	this paper
Aptian	Switzerland	Muricidae	*Fusus valdensis* Pictet et Renevier, 1854 (1) *Murex prestensis* Pictet et Campiche, 1864 (?)	Pictet & Campiche, 1861–1864
Aptian	Greenland	Fusidae	*Fusus*? sp. indet. (?)	Frebold, 1935
Aptian	Mexico	Fasciolariidae	*Euthriofusus wenzi* Allison, 1955 (6)	Allison, 1955
Aptian – Albian	Germany	—	*Buccinum gaultinum* d'Orbigny, 1842 (<5) *Rapana gracillima* Wollemann, 1903 (?)	Wollemann, 1903, 1906
Albian	Great Britain	Fasciolariidae	*Iscafusus rigidus* (J. de C. Sowerby, 1836) (?)	Tracey, 2010
		Buccinidae	*Cosnia gaultina* (d'Orbigny, 1842) (?)	
Albian	Switzerland	Muricidae?	*Fusus Dupinianus* d'Orbigny, 1842 (?) *Fusus Clementinus* d'Orbigny, 1842 (?) *Fusus vraconensis*, Pictet et Campiche, 1864 (?) *Murex carinella* Pictet et Roux,1849 (?) *Murex sabaudianus* Pictet et Roux, 1849 (?) *Murex bilineatus* Pictet and Roux, 1849 (?)	Pictet & Campiche, 1861–1864
Albian	Morroco	Buccinidae	*Cantharulus pondicherriensis* (Forbes, 1846) (?)	Collignon, 1972
Albian	Madagascar	Buccinidae	*Pseudoliva madagascariensis* Collignon, 1949 (2)	Collignon, 1949a
		Fusidae	*Exilia besairiei* Collignon, 1949 (3) *Cryptorhytis chavani* Collignon, 1949 (1) *Cryptorhytis (Piestochilus) falloti* Collignon, 1949 (1) *Fusus (Drilluta) ciryi* Collignon, 1949 (1) *Semifusus (Mayeria) milleri* Collignon, 1949 (1)	
		Turbinellidae	*Tudicula gracilis* Wilckens, 1905 (2) *Tudicula houreqi* Collignon, 1949 (1) *Fusus (Serrifusus)* cf. *dakotensis* Meek, 1876 (2) *Streptosiphon (Hercorhynchus)* cf. *monheimi* Müller, 1888 (1)	

		Marginellidae	*Marginella (Faba) houreqi* Collignon, 1949 (1)	
		Volutidae	*Volutilithes abadiei* Collignon, 1949 (?) *Athleta (Volutocorbis) debeyi* Binkhorst, 1861 (1) *Volutilithes (Neoathleta) plicatella* Deshayes, 1904 (?) *Voluta (Palaeopsephaea)* cf. *roemeri* Holzapfel, 1888 (1)	
Albian	Crimea	Columbellinidae	*Columbellina Dupini* d'Orbigny, 1843	Pchelintsev, 1927
Albian	France	Fasciolariidae	*Iscafusus dupinianus* d'Orbigny, 1843 *Iscafusus rigidus* (Sowerby *in* Fitton, 1836)	Kollmann, 2005
Albian – Cenomanian	Austria	Buccinidae	*Cantharulus* sp. (1)	Kollmann, 1976
		Muricidae	*Blackdownia quadrata* (Sowerby, 1823) (1)	
		Fasciolariidae	*Fusinus* cf. *rugosus* (Briart & Cornet, 1865) (1)	
		Cancellariidae	*Palaeocancellaria hoelleitenensis* Kollmann, 1976 (2)	

CHAPTER VI

A global review of the Cretaceous fossil record of Neogastropoda

All published records were synthesised into a comprehensive database of Cretaceous neogastropod genera and subgenera to examine temporal trends in diversification. For the Lower Cretaceous, all described species were included in Bakayeva et al. (submitted), whereas for the Upper Cretaceous only genera were considered, as species diversity increased considerably and these taxa require further extensive taxonomic revision.

The stratigraphic ranges of some genera remain uncertain, as they were assigned to broad intervals (e.g. the entire Cretaceous, Upper Cretaceous, or Senonian respectively). For the Upper Cretaceous, such genera are *Closteroides* Tomlin, 1929, *Sohlia* Cernohorsky, 1970, *Diptygmendon* Chavan, 1947, *Drillutopsis* Chavan, 1947, and *Terebritoma* Cossmann, 1894, whereas for the Senonian this applies to *Procancellaria* Wilckens, 1922. These taxa together constitute less than 5% of the total number of genera and, therefore, were excluded from the analysis.

For each time interval, the actual number of recognised genera is indicated. In cases where given genus exhibits a stratigraphic gap spanning several stages and subsequently reappears in a geographically distant region, these records may in fact represent distinct genera. Resolving this issue would require a comprehensive taxonomic revision of the generic composition, which is beyond the scope of the present large-scale study.

Overview of neogastropod taxonomic structure during the Cretaceous

By the end of the Cretaceous, all superfamilies of Neogastropoda are already present in fossil record. Among them, superfamilies Buccinoidea Rafinesque, 1815, and Volutoidea Rafinesque, 1815, stand out, encompassing the largest number of genera and accounting for approximately 31% and 27% of Neogastropoda, respectively (Fig. 6.1). Conoidea Fleming, 1822, represents about 12%, Pholidotomoidea Cossmann, 1896 – 11%, while a group of taxa not assigned to any superfamily constitutes a slightly smaller portion, accounting for about 8%. Muricoidea Rafinesque, 1815, and Turbinelloidea Swainson, 1835, each comprise approximately 4%, while Mitroidea Swainson, 1831, and Olivoidea Latreille, 1825, represent about 1% each. Despite a significant increase in overall diversity of Neogastropoda from the Early to the Late Cretaceous, the relative proportions of superfamilies show little change through the entire time interval (Fig. 6.2).

Fig. 6.1. — Ratio of neogastropod superfamilies (inner pie chart: number of genera – percentage) and families (outer doughnut chart) in the Cretaceous. The systematic order of superfamilies follows Bouchet et al. (2017). Families within each superfamily are arranged according to quantity (numbers indicate the number of genera).

At the family level, the most diverse are Volutidae Rafinesque, 1815, and Fasciolariidae Gray, 1853, represented by the largest numbers of genera (35 and 25, respectively). Turridae Adams & Adams, 1853 (1838) includes 18 genera, followed by Buccinidae Rafinesque, 1815 with 15 genera. Contributions from the remaining families are more modest: Perissityidae Popenoe & Saul, 1987 comprises 12 genera, Sarganidae Stephenson, 1923 – nine, Cancellariidae Forbes & Hanley, 1851 – seven, and Muricidae Rafinesque, 1815 – six. Moreidae Stephenson, 1941 and Melongenidae Gill, 1871 each include five genera, whereas Pholidotomidae Cossmann, 1896 is represented by four genera. The remaining nine families together account for

approximately 11% of the entire neogastropod diversity, with each family represented by one to three genera (Fig. 6.3). Family Purpurinidae, classified within the order Neogastropoda according to Bouchet et al. (2017), comprises two genera from the Early Cretaceous—*Khetella* Beisel, 1977 and *Cretadmete* Blagovetshenskiy & Shumilkin, 2006—which were not taken into account in this analysis. Their relationship with Neogastropoda and possible stem-group position was discussed by Bakayeva et al. (2024).

Although some genera have been revised, including *Deussenia* Stephenson, 1941 (Squires and Saul 2000), *Pyropsis* Conrad, 1860 (Squires 2011), *Sargana* Stephenson, 1923 (Bandel and Dockery 2001), and *Volutoderma* Gabb, 1877 (Saul and Squires 2008), and several families have been re-evaluated, such as Perissityidae (Saul 1988a), Pseudolividae (Vemieij 1998), and as well as Tudiclidae Cossmann, 1901, with Melongenidae (Saul 1988b), most taxa still require detailed revision of their taxonomic composition and a reassessment of morphological characters relevant to their family-level assignment. It should be also noted that

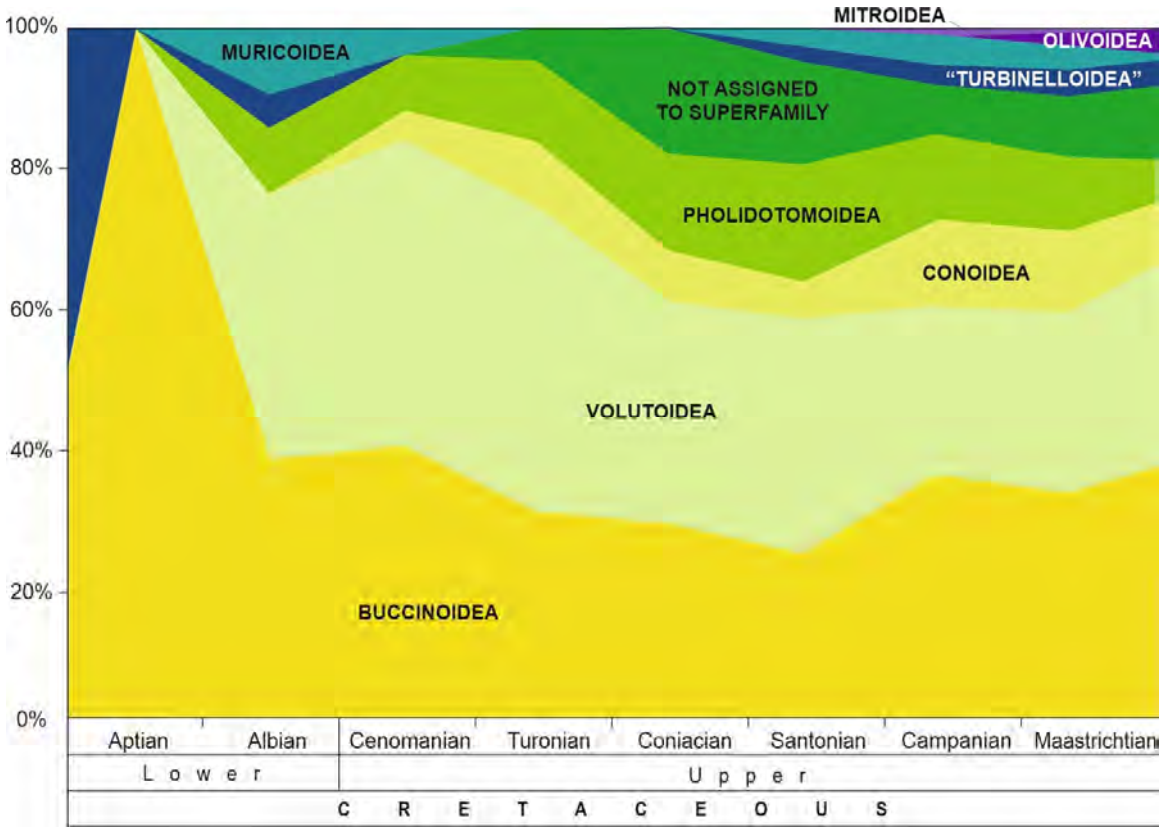

Fig. 6.2. — Changes in the proportions of neogastropod superfamilies during the Cretaceous.

a major problem tracing back the evolution and diversification of Neogastropoda lies in the uncertain reliability of the identifications, especially in older works, when access to comparative material and the exchange of scientific information were restricted both geographically and

temporally. This limitation also affects the superfamily-level assignment of the earliest crown groups (see Bakayeva et al. submitted).

Early Cretaceous Neogastropoda—10 families and 21 genera have been recorded from this epoch (see Apendix). The generic diversity remained low before the Albian, but increased significantly during that stage and continued to grow until the end of the period with two distinct radiation pulses: one in the Albian–Cenomanian and another in the Campanian–Maastrichtian

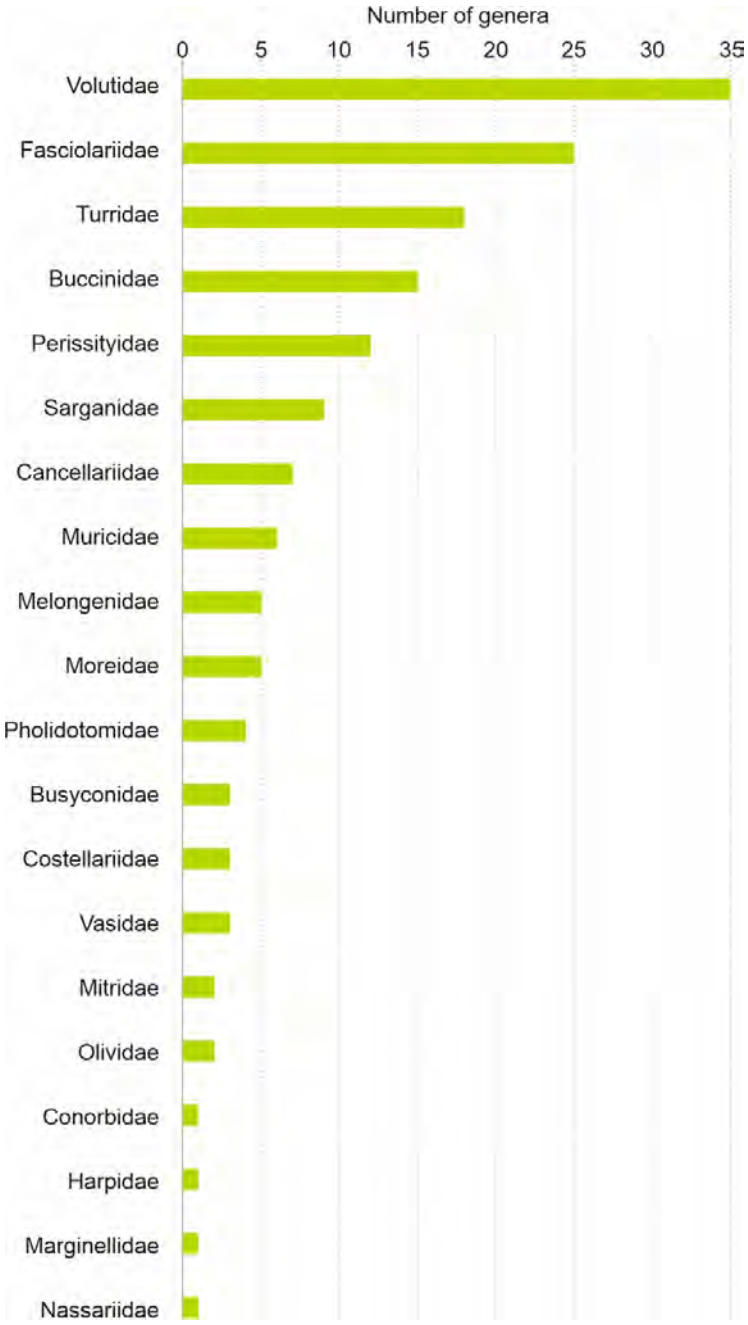

Fig. 6.3. — Representation of neogastropod families in the Cretaceous.

(Fig. 6.4).

The earliest record of the crown neogastropod known so far comes from the Valanginian of Poland (Tab. 6.2) and is represented by a juvenile shell with a preserved protoconch, identified only to the superfamily level (Kaim 2004) and now assigned to Buccinoidea (Bakayeva et al. submitted). Three other potential species from the Valanginian were described from Switzerland in the old monograph by Pictet and Campiche (1861–1864). However, their systematic placement has not been revisited since their original description, and, as these specimens were collected from carbonate deposits and are preserved as internal moulds, a more precise assignment to the higher taxonomic level is unlikely to be possible because of lack of preserved protoconchs. Thus, based on the current state of knowledge, Buccinoidea appears to represent the earliest documented record of Neogastropoda (Fig. 6.5). Another specimen with an almost complete shell, including a preserved protoconch and showing some evidence of functional traits in neogastropods, such as varices and a labral tooth, was recently described from the Barremian of Bulgaria (Bakayeva et al. (submitted)) and identified as the earliest representative of the family Vasidae Adams & Adams, 1853. These findings suggest that neogastropods had already begun to diversify by the early Early Cretaceous, although their overall diversity and abundance remained low.

A major radiation event appears to have initiated in the Aptian and became clearly documented in the Albian, as indicated by a significant increase in both taxonomic richness and geographic distribution. From the Aptian, several neogastropod species have been reported: one each from Mexico (Allison 1955) and Greenland (Frebold 1935), and two from Switzerland (Pictet and Campiche 1861–1864). The species from Mexico was assigned to Buccinoidea, whereas familial assignment of specimens from Greenland remains uncertain. Swiss specimens originally were identified as Muricoidea, however, the preservation of these specimens does not allow for confident taxonomic identification. These records are followed by two Albian species each from England (Taylor et al. 1983, Tracey 2010), France (Kollmann 2005), and Texas, USA (Stanton 1947), as well as one species each from Morocco (Collignon 1972) and Crimea (Pchelintsev 1927). All of these species were assigned to the superfamily Buccinoidea. In contrast, six species from Albian of Switzerland (Pictet and Campiche 1861–1864) originally were identified as Muricoidea (see above). Of particular significance is the Albian assemblage from Madagascar, which comprises 15 species from 10 genera, three superfamilies and at least six families (Collignon 1949), representing the most diverse Early Cretaceous neogastropod fauna known to date. From transitional Albian–Cenomanian deposits of Austria, a further four

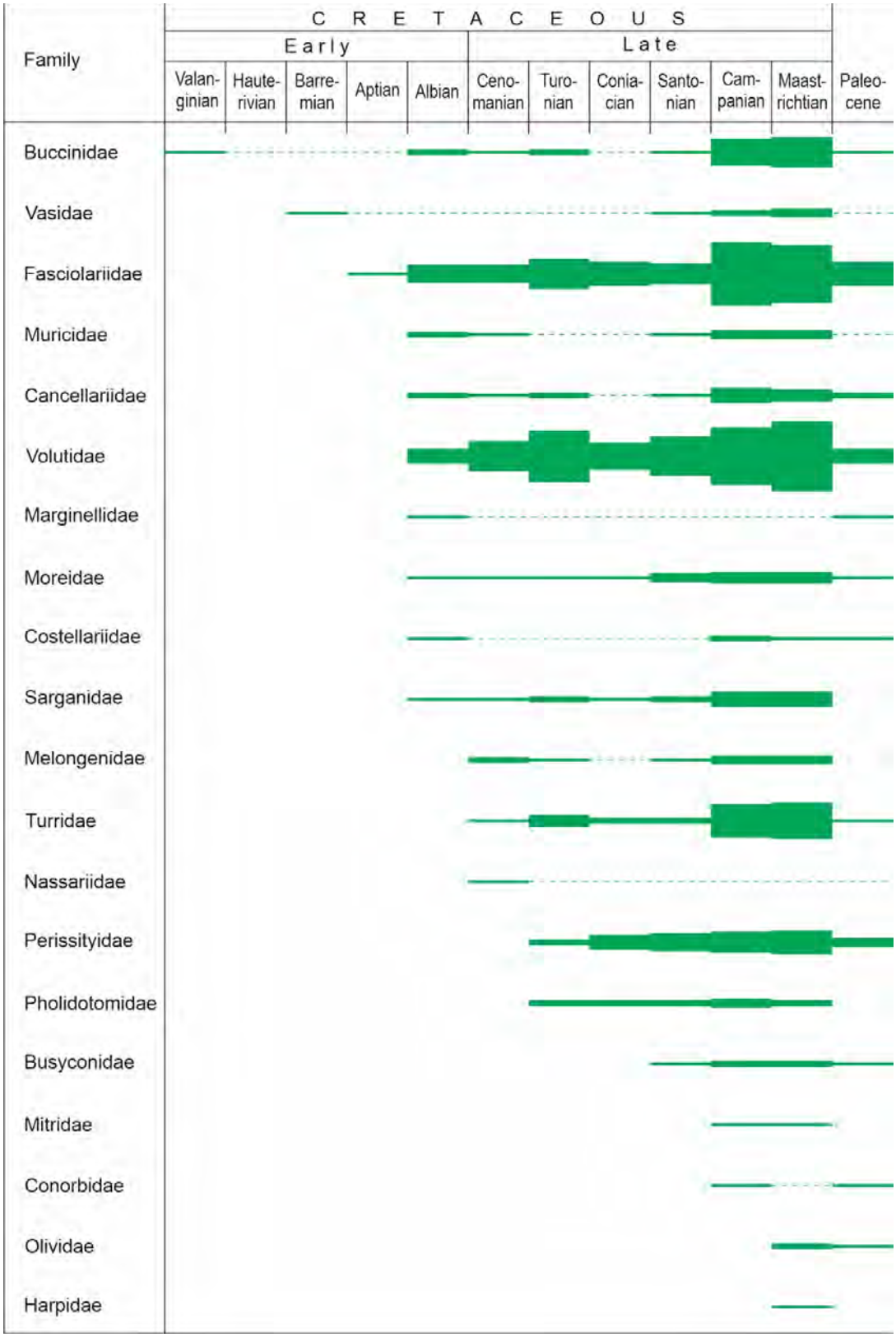

Fig. 6.4. — Family-level diversity dynamics of Neogastropoda throughout the Cretaceous, with evidence for genus-level survivorship across the K/Pg boundary. A dashed line indicates the absence of family fossil record, while the line thickness reflects the number of genera.

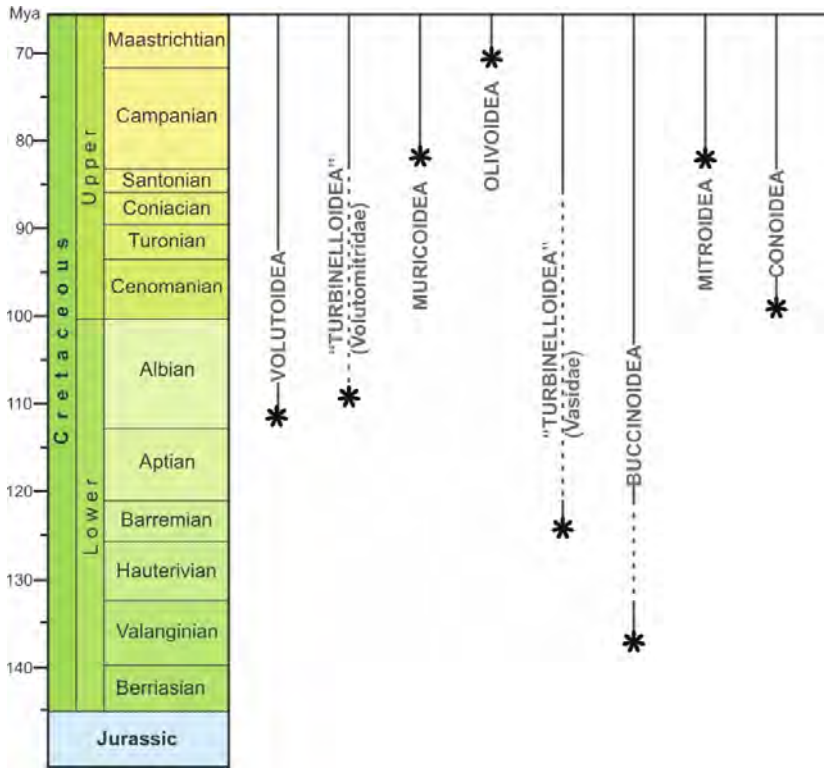

Fig. 6.5. — Stratigraphic ranges of neogastropod superfamilies throughout the Cretaceous, with asterisks marking the oldest occurrences and dashed lines indicating intervals lacking fossil evidence. Superfamilies are arranged from left to right to reflect their phylogenetic relationships, from basal to more derived lineages, as shown by Fedosov et al. (2024).

species from four families have been reported (Kollmann 1976). In total, nine neogastropod families and 21 genera have been documented from the Albian (Fig. 6.6), of which at least 20 genera make their first appearance during this stage (Tab. 6.3).

Thus, the Albian and the late Early Cretaceous can be interpreted as a pivotal time in the early evolutionary history of Neogastropoda. The emergence of multiple genera across several families suggests that neogastropods had already begun to occupy a variety of benthic predatory niches, indicating the early establishment of key ecological roles. Furthermore, a broad geographic distribution of Aptian–Albian neogastropods implies that environmental conditions during this interval may have promoted both faunal dispersal and ecological innovations, facilitating the early diversification of the group.

Late Cretaceous Neogastropoda—Beginning with the Cenomanian, the abundance of neogastropods in regional benthic faunas increased markedly, as reflected both by a rise in taxonomic diversity and an increase in the number of specimens documented at some localities. This is particularly true for the Campanian–Maastrichtian deposits of south-east North America (Gabb 1860, Gardner 1916, Wade 1916, 1917, 1926, Harbison 1945, Stephenson 1941, Weller

1962, Sohl 1964a, b, Dockery 1993, Akers and Akers 1997), Western Interior Seaway (Sohl 1967, Erickson 1974), Pacific Coast of North America (Squires 2011), and Alaska (Popenoe and Saul 1987) and in Europe (Abdel-Gawad 1986, Bakayeva 2011, Hansen 2019).

From the Cenomanian, 10 families and 25 neogastropod genera have been documented from France (Kollmann 2005), Ukraine (Plamadeala 1999, Bakayeva 2011), Central Asia (Pchelintsev 1953, Korobkov et al. 1974, Djalilov 1977, Poyarkova and Djalilov 1985), Egypt (Mekawy 2007, Ayoub-Hannaa and Fürsich 2011), Arizona and Texas, USA (Stephenson 1952, Kirkland 1996), and Brazil (Lexen 2013). In all these faunas, superfamilies Volutoidea and Buccinoidea stand out, accounting for 11 and seven genera, respectively.

The same number of families (10) was recorded from the Turonian. However, the number of genera increased to 43 compared with the Cenomanian. Turonian Neogastropoda have been reported from France (Cossmann 1896, Roman and Mazeran 1920, Kollmann 2005), Central Asia (Pchelintsev 1953, Korobkov et al. 1974, Djalilov 1977, Poyarkova and Djalilov 1985), India (Stoliczka 1867–1868, Bandel 2000), Egypt (Mekawy 2007, Ayoub-Hannaa and Fürsich 2011), Arizona and New Jersey, USA (Whitfield 1892, Kirkland 1996), Pacific Coast of North America (Saul and Popenoe 1993, Saul 1996, Squires 2011), and Brazil (Lexen 2013). The

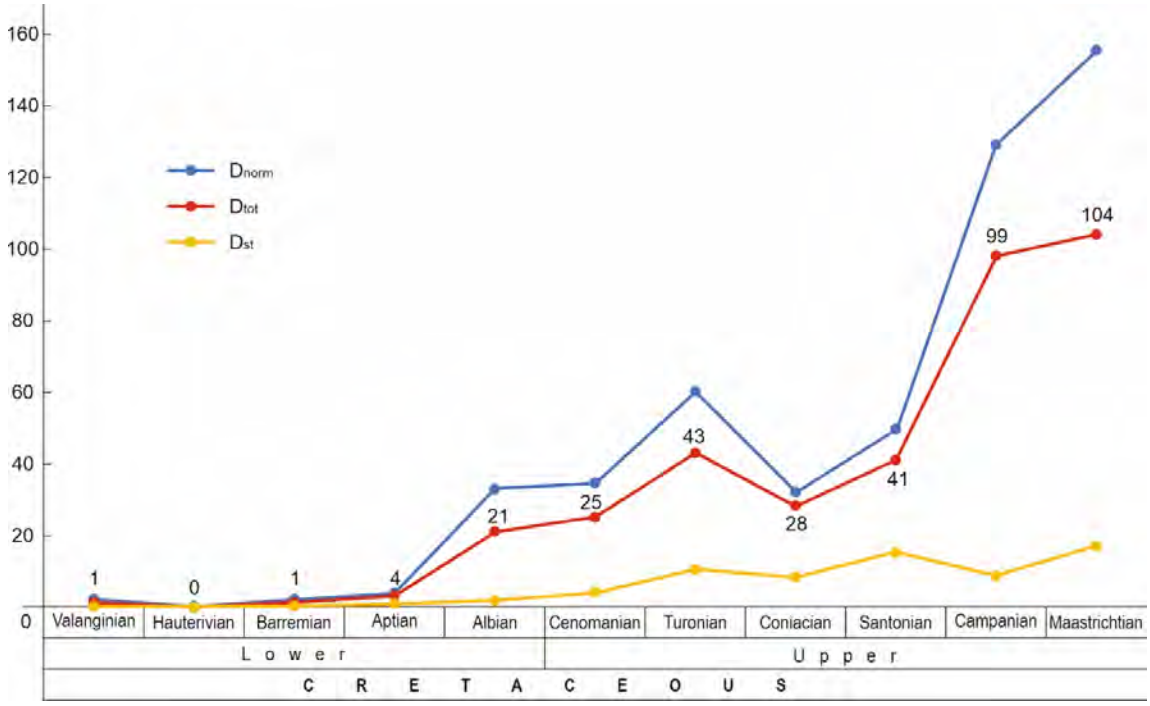

Fig. 6.6. — Changes in the generic diversity of Neogastropoda during the Cretaceous: D_{tot} – total diversity is defined as the total number of genera recorded from the time interval (stage); D_{norm} – normalized diversity is defined as the total diversity plus half the number of genera confined to the age interval or ranging beyond the time interval, but originating or ending within it; D_{st} – standardized diversity is defined as the total diversity divided by duration of time interval (stage); numbers indicate number of genera recorded for each stage.

dominance of Volutoidea and Buccinoidea persisted, with these superfamilies represented by 19 and 13 genera, respectively.

In the Coniacian neogastropod diversity decreased to seven families and 28 genera, documented from Central Asia (Pchelintsev 1953, Korobkov et al. 1974, Djalilov 1977, Poyarkova and Djalilov 1985), India (Stoliczka 1867–1868, Bandel 2000), Pacific coast of North America (Squires and Saul 2003a, Saul and Squires 2008, Squires 2011) and Egypt (Mekawy 2007). Volutoidea and Buccinoidea continued to dominate these assemblages, although they were represented by fewer genera than in the Turonian, with nine and eight genera, respectively.

In the Santonian, neogastropod diversity increased to 13 families and 41 genera, accompanied by a marked expansion of their geographic distribution. Neogastropods from Santonian strata have been documented from Germany (Müller 1851, Böhm 1885, Holzapfel 1888, Deninger 1905), Austria (Zekeli 1852, Stoliczka 1865), Czechia (Weinzettl 1910), Ukraine (Bakayeva 2011), Central Asia (Pchelintsev 1953, Djalilov 1977), Sakhalin and Kamchatka (Poyarkova and Djalilov 1985), India (Forbes 1846, Stoliczka 1867–1868, Bandel 2000), Egypt (Mekawy 2007), Algeria and Tunisia (Coquand 1862, Thomas and Peron 1889–1890), South Africa (Bandel and Dockery 2001, Kiel and Bandel 2003), Pacific Coast of North America (Squires and Saul 2003a, Squires 2011), and Alaska (Popenoe and Saul 1987). Volutoidea and Buccinoidea remained dominant, represented by 14 and 10 genera, respectively.

From the Campanian, 16 neogastropod families comprising 99 genera have been recorded across a wide geographic range, including Northern Ireland (Cleevely and Morris 2002), Spain (Kiel 2001), France (Kollmann 2005), the Netherlands (Binkhorst 1861, Kaunhowen, 1897), Germany (Müller 1851, Böhm 1885, Holzapfel 1888, Deninger 1905, Pietzonka et al. 2023), Austria (Zekeli 1852, Stoliczka 1865), Czechia (Weinzettl 1910), Poland (Abdel-Gawad 1986, 1990), Ukraine (Blank 1974, Bakayeva 2011), Palestine (Chavan 1947), Central Asia (Pchelintsev 1953, Djalilov 1977), Sakhalin and Kamchatka (Poyarkova and Djalilov 1985), India (Forbes 1846, Stoliczka 1867–1868, Bandel 2000), Japan (Kase 1990), South Africa (Bandel and Dockery 2001, Kiel and Bandel 2003), Mexico (Imlay 1937, Furque and Camacho 1949), Brazil (Squires and Saul 2003b), North America: East Coast (Gabb 1860, Gardner 1916, Weller 1962), Gulf Coastal Plain (Conrad 1858, 1860, Gabb 1860, Meek 1876, Wade 1916, 1917, 1926, Stephenson 1941, Harbison 1945, Sohl 1964a, b, Dockery 1993, Akers and Akers 1997), Western Interior Seaway (Hall and Meek 1854, Meek and Hayden 1856, Sohl 1967, Erickson 1974), Pacific coast (Squires 2011), and Alaska (Popenoe and Saul 1987). In terms of generic diversity, Buccinoidea dominate the Campanian assemblages with 35 genera, whereas Volutoidea are represented by 24 genera.

The highest generic diversity of neogastropods is recorded from the Maastrichtian, with 17 families comprising 104 genera documented worldwide, including the Netherlands (Binkhorst 1861, Kaunhowen, 1897), Poland (Abdel-Gawad 1986, 1990), Ukraine (Blank 1974, Bakayeva 2011), Western Siberia (Kaim and Beisel 2005), Sakhalin and Kamchatka (Poyarkova and Djalilov 1985), Central Asia (Pchelintsev 1953, Djalilov 1977), Japan (Kase 1990), Egypt and Libia (Quaas 1902, Rossi Ronchetti 1959, Bandel, 2003), Arabia (Lees 1928), Mexico (Kiel 2001, Kiel and Perrilliat 2004), Chile and Northern Peru (Olsson 1944, Bandel and Stinnesbeck 2000), Argentina (Griffin and Hunicken 1994), North America: East Coast (Gabb 1860, Gardner 1916, Weller 1962), Gulf Coastal Plain (Conrad 1858, 1860, Gabb 1860, Meek 1876, Wade 1916, 1917, 1926, Stephenson 1941, Harbison 1945, Sohl 1964a, b, Dockery 1993, Akers and Akers 1997), Western Interior Seaway (Hall and Meek 1854, Meek and Hayden 1856, Sohl 1967, Erickson 1974)), Australia (Darragh and Kendrick 1994), New Zealand (Wilckens 1922), and Antarctica (Oleinik and Zinsmeister 1996, Stilwell and Zinsmeister 2003). The proportional representation of superfamilies closely resembles that of the Campanian, with Buccinoidea represented by 34 genera and Volutoidea by 27 genera.

Overall, in the Cretaceous a consistent and rapid increase in neogastropod diversity is observed – from ten families and at least 21 genera documented in the Early Cretaceous to 20 families and at least 159 genera recorded from the Late Cretaceous.

Despite the profound impact of the end-Cretaceous mass extinction event on neogastropod diversity, 26 genera representing 12 families survived into the Paleogene (Tab. 6.3). The persistence of these taxa suggests that neogastropods had already attained a degree of ecological resilience and evolutionary flexibility that enabled them to recover and radiate again in the early Cenozoic.

Emergence and diversification of neogastropod taxa

As the comparison between the fossil record and molecular data has been discussed elsewhere (Bakayeva et al. (submitted)), this section focuses exclusively on fossil data.

SUPERFAMILY BUCCINOIDEA—As highlighted above (see Chapter V), Buccinoidea appears to represent the earliest documented fossil record of Neogastropoda (Fig. 6.5) and is the second most diverse superfamily in the Cretaceous in terms of generic richness, dominating neogastropod assemblages from the Campanian. In the Cretaceous, representatives of five families of Buccinoidea were documented (Figs. 6.1, 6.3).

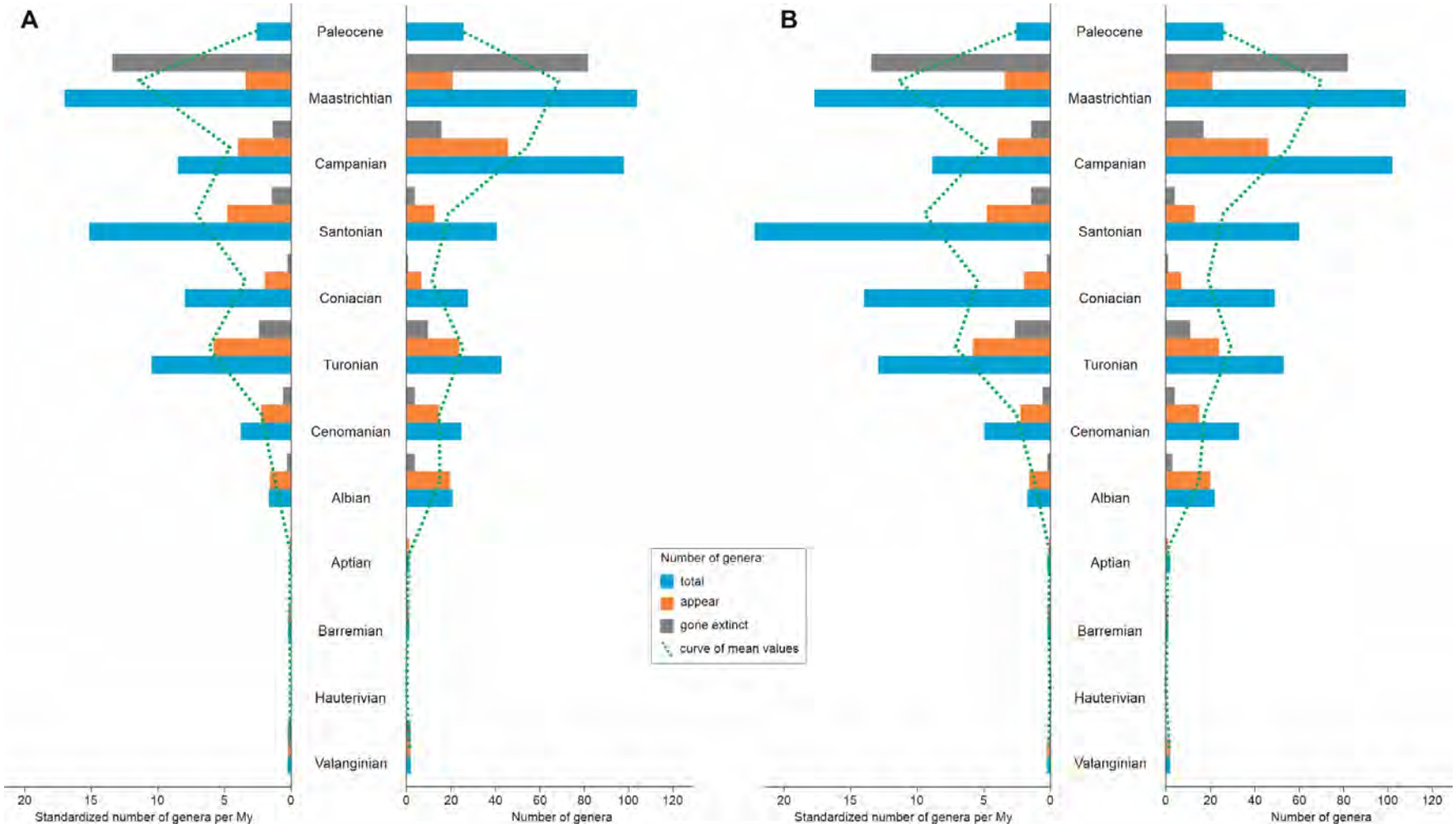

Fig. 6.7. — Changes in the generic composition of Neogastropoda during the Cretaceous: only factually documented records (**A**), assuming continuity of genera (**B**). For the Paleocene, only genera that survived from the Cretaceous are shown.

Fasciolariidae is the most diverse family within Buccinoidea and appears to be the oldest documented so far, with the earliest record being *Euthriofusus wenzi* Alisson, 1955, from the Aptian of Mexico (Alisson 1955). Bandel (2000) erected a new genus, *Profusinus* Bandel, 2000, which he assigned to the family Trichotropidae Gray, 1850 (now Capulidae Fleming, 1822), and included Cretaceous species of *Euthriofusus* Cossmann, 1901, within it. However, he noted that "a closer comparison with any of these will only be possible when the protoconch is known and compared" (Bandel 2000: p. 86). Subsequently, Bandel and Dockery (2012) suggested that the genus may belong to Paladmetidae Sohl, 1964 (Tonnoidea). Thus, the assignment of *Profusinus* to Fasciolariidae remains uncertain. Nevertheless, the oldest buccinoid occurrence was compared by Kaim (2004) with a recent representative of Fasciolariidae, supporting the interpretation that this family may indeed represent the earliest recorded buccinoid lineage. Six more genera were reported from the Albian (see Apendix), indicating that taxonomic diversification of the family was already well underway. Overall, 25 genera of Fasciolariidae have been identified in the Cretaceous.

The second most diverse family within Buccinoidea is Buccinidae, which includes 15 genera. The oldest species, *Cosnia gaultina* (d'Orbigny, 1843), was recorded from the Albian of Anglo-Paris Basin (d'Orbigny 1843, Kollmann 2005, Tracey 2010). Although some doubts regarding its systematic position have been raised by Tracey (2010), its shell shape, ornamentation, and aperture characteristics are most consistent with those of buccinids (Kollmann 2005). The next single buccinid, *Aliofusus balaniformis* Stephenson, 1952, was reported from the Cenomanian of Texas, USA (Stephenson 1952).

Family Melongenidae comprises five genera, with the oldest species, *Palaeatractus figarii* (Greco, 1916), from the Cenomanian of Egypt (Greco 1916–1918, Mekawy 2007). Two younger species, *Rhombopsis*? *huerfanensis* (Stanton, 1893) and *Saturnus dubius* (Packard, 1922), have been reported from the Turonian of Colorado (Stanton 1893, Kirkland 1996) and California (Saul and Popenoe 1993).

Family Busyconidae Wade, 1917, includes three genera. Its oldest representative, *Boltenella*? *africana* Kiel and Bandel, 2003, was recorded from the Santonian of South Africa (Kiel and Bandel 2003), while the type species of *Boltenella*, *B. excellans* Wade, 1917, was described from the Upper Campanian of Tennessee, USA (Wade, 1917, 1926, Sohl 1964).

In the Cretaceous, family Nassariidae Iredale, 1916, is represented by a single species, *Admetopsis subfusiformis* (Meek, 1873), reported from the Cenomanian of Arizona (Kirkland 1996) and Utah, USA (Meek 1873, Stanton 1893).

SUPERFAMILY "TURBINELLOIDEA"—This superfamily is the second oldest after Buccinoidea, with its earliest record dating to the Barremian. Recent molecular studies of this group (Fedosov et al. 2024) indicate that it is paraphyletic, being composed of at least five unrelated, strongly supported clades (see Bakayeva et al. (submitted), for discussion). In the Cretaceous, two clades have been recognised (Fig. 6.5).

One clade is represented by the family Vasidae, which comprises three genera, with the oldest occurrence recorded from the Barremian of Bulgaria and discussed in detail by Bakayeva et al. (submitted). The second clade is represented by the families Costellariidae MacDonald, 1860 and Ptychatractidae Stimpson, 1865, together comprising three genera. The oldest species within this clade is *Exilia besairiei* Collignon, 1949, from the Albian of Madagascar (Collignon 1949). Younger species of *Exilia* Conrad, 1860, have been reported from the Santonian–Maastrichtian of Europe and United States (Kaunhowen 1897, Cossmann 1901, Gardner 1916, Wade 1926). Another genus, *Breviexilia* Chavan, 1947, was described from the Campanian of Palestine (Chavan 1947), whereas *Mitridomus* Sohl, 1963 (Costellariidae) has been reported from the Campanian of the USA (Sohl, 1963, 1964). It should be noted, however, that all these taxa require thorough revision with respect to their both generic and familial identity (see Bakayeva et al. (submitted)). For this study, Costellariidae and Ptychatractidae are treated as a single clade without formal familial division.

SUPERFAMILY VOLUTOIDEA—Although Volutoidea is considered the most basal clade in molecular phylogenies (Lemarcis et al. 2022, Fedosov et al. 2024) and is the most diverse superfamily in terms of generic richness in the Cretaceous, its oldest fossil records date only from the Albian onwards, i.e. approximately 26 million years later than the earliest documented buccinoid occurrence in the Valanginian. In the Cretaceous, this superfamily comprises three families with different taxonomic diversity.

Volutidae is the most diverse family within Volutoidea and includes 35 genera (Fig. 6.3). Five genera (see Appendix) have been documented from the Albian of Madagascar. It is likely that the species identified by Collignon (1949) as *Palaeopsephaea roemeri* (Holzapfel, 1888) and *Volutocorbis debeyi* (Binkhorst, 1861) are not the same species as those from the original descriptions from the Senonian of Germany and the Netherlands (Holzapfel 1888, Binkhorst 1861); however, their assignment to the respective genera remains plausible. The species identified by Collignon (1949) as *Volutilithes* (*Neoathleta*) *plicatella* (Deshayes, 1835) illustrated in Cossmann and Pissarro (1910–1913) most probably belongs to the genus *Volutomorpha* Gabb, 1877, but the available material does not allow assignment to species, and it may therefore retained

in open nomenclature as *Volutomorpha* sp. *Eovolutilithes abadiei* (Collignon, 1949) is the type species of the genus *Eovolutilithes* Hacobjan, 1976, which has been recorded from the Albian to the Maastrichtian in various regions worldwide (Hacobjan 1976). *Drilluta ciryi* Collignon, 1949, appears to be similar to other species of *Drilluta* Wade, 1916, from the Campanian–Maastrichtian of the USA (Wade 1917, 1926, Stephenson 1941, Sohl 1964a, b, Bandel and Dockery 2016). All these genera are also present in other stages of the Upper Cretaceous. The high generic diversity of volutids in the Albian may indicate an earlier origin and diversification of the group that is either not documented or has not yet been discovered in the fossil record.

Family Cancellariidae comprises seven genera, with the oldest species, *Cancellaria*? *medicinensis* (Cragin, 1894), from the Albian of the USA (Stanton 1947), following by *Palaeocancellaria hoelleitenensis* Kollmann, 1976, from the Albian–Cenomanian of Austria (Kollmann 1976).

Family Marginellidae Fleming, 1828, is represented by a single species, *Marginella hourcqi* Collignon, 1949, from the Albian of Madagascar (Collignon 1949).

SUPERFAMILY PHOLIDOTOMOIDEA—This superfamily comprises three families and 18 genera, all of which are extinct.

Sarganidae is the most diverse family within Pholidotomoidea and includes nine genera, with the oldest species *Eomorea vibrayeana* (d'Orbigny, 1843), described from the Albian of France (d'Orbigny 1843; Kollmann 2005). Tracey (2010) reassigned *Eomorea* Kollmann, 2005, to the family Ranellidae Gray, 1854 (Tonnoidea). The protoconchs illustrated by Tracey (2010) indeed resemble those typical of tonnoideans; however, there is no certainty that the specimens described from the Albian of Folkestone, Great Britain, are conspecific with the material originally described from France (d'Orbigny 1843, Kollmann 2005), as they were treated under open nomenclature by Tracey (2010). The next two sarganid species—*Hillites multilirae* Stephenson, 1952, and *Hillites septarianus* Stephenson, 1952—were described by Stephenson (1952) from the Cenomanian of Texas, USA.

Moreidae comprises five genera, with *Pyropsis* Conrad, 1860, representing the earliest and most diverse genus. Its earliest record is documented from the Cenomanian of Madagascar, followed by several species from the Turonian to the Maastrichtian exhibiting an amphitropical distribution (Squires 2011).

Family Pholidotomidae includes five genera, three of which were recorded from the Turonian. Several species of *Pyrifusus* Conrad, 1858, were described by Whitfield (1892) from the Raritan clays of New Jersey, USA. *Trichifusus reussianus* (Stoliczka, 1868) has been reported from Tamil Nadu, India (Stoliczka 1868, Bandel 2000). *Pholidotoma subheptagonus* (d'Orbigny,

1850), recorded from France (d'Orbigny 1850, Cossmann 1896) and originally assigned to Turridae (Cossmann 1896), was subsequently reassigned to Pholidotomidae (Powell 1966).

SUPERFAMILY CONOIDEA—According to the molecular phylogeny of Fedosov et al. (2024), Conoidea is the most derived neogastropod clade, yet it has an unexpectedly good fossil record in the Cretaceous, where it ranks as the third most diverse superfamily, with two families and 18 genera recorded.

Family Turridae, comprising 17 genera, is the third most diverse neogastropod family in the Cretaceous (Fig. 6.3). The oldest species, *Graphidula walcotti* (Stanton, 1893), was reported from the Cenomanian of Arizona, USA (Kirkland 1996). It is followed by the Turonian *Beisselia oldhamiana* (Stoliczka, 1868) from Tamil Nadu, India (Stoliczka 1867–1868, Bandel 2000), and *Lutema hitzi* (Meek, 1876) from Arizona, USA (Kirkland 1996).

Cryptoconus mcnairyensis (Wade, 1917) from the Campanian of Tennessee, USA (Wade 1917, Sohl 1964), is the earliest and the only Cretaceous representative of the family Conorbidae de Gregorio, 1880, recorded so far.

SUPERFAMILY MURICOIDEA—Although this superfamily represents the earliest branching node within the "core Neogastropoda" (sensu Fedosov et al. 2024), it is represented in the Cretaceous by only a single family comprising six genera. One Valanginian and two Albian records previously attributed to Muricoidea have been transferred to other groups (see Bakayeva et al. (submitted)), suggesting that the earliest occurrence of the superfamily may be represented by *Paramorea* Wade, 1917, from the Campanian of Tennessee, USA (Wade 1917, 1926, Sohl 1964). However, Bandel and Dockery (2016) suggested that this taxon may instead belong to Tonnoidea. An undoubted Cretaceous muricid is *Poirieria (Paziella) cretacea* Garvie, 1991, from the upper Maastrichtian of Texas (Garvie 1991) assigned to *Flexopteron* Shuto, 1969, by Merle (2012). All pre-Maastrichtian occurrences of presumed Muricoidea require thorough review.

SUPERFAMILY MITROIDEA—This superfamily is represented by a single family, Mitridae Swainson, 1831, which may include two genera that require revision. The oldest species, *Paleofusimitra elongata* Sohl, 1963, is recorded from the Campanian of the USA (Sohl 1963, 1964).

SUPERFAMILY OLIVOIDEA—This superfamily is represented by a single family, Olividae Latreille, 1825, and is documented latest within the Cretaceous. Two genera can be confidently assigned to this family. Collignon (1949) suggested that *Pseudoliva madagascariensis*

Collignon, 1949, from the Albian of Madagascar, possesses a characteristic abapical band; however, the shell shape and ornamentation appear to differ from those of the type species of *Pseudoliva* Swainson, 1840, and this record therefore requires further study.

The oldest undisputed records of Olividae are from the Maastrichtian of Texas (Stephenson 1941) and Japan (Kase 1990, 1992). Both *Eoancilla acutula* Stephenson, 1941, and *Tanimasanoria japonica* Kase, 1990, exhibit the characteristic ancillid band. Another possible record is Pseudolividae gen. et sp. indet. from the Maastrichtian of Western Siberia (Kaim and Beisel 2005).

NOT ASSIGNED TO SUPERFAMILY—According to the latest nomenclator (Bouchet et al. 2017), two families occurring in the Cretaceous are included within Neogastropoda but are not assigned to any superfamily.

The family Perissityidae includes 12 genera, with the oldest species being *Cydas crossi* (Anderson, 1958) and *Pseudocymia aurora* Popenoe & Saul, 1987, from the Turonian of the Pacific Coast of North America (Anderson 1958, Popenoe and Saul 1987, Saul and Popenoe 1993).

Stephenson (1955) assigned *Eoharpa sinuosa* Stephenson, 1955, from the upper Maastrichtian of Mississippi and Missouri, USA, to Harpidae Bronn, 1849. Although Merle and Pacaud (2003) expressed doubts regarding the familial assignment of this species, it is here retained as representing a separate family, as its shell morphology clearly distinguishes it from other Cretaceous Neogastropoda.

New insights into the early evolution of Neogastropoda

During the Cretaceous, the diversity of neogastropods changes from a few species represented by single specimens in the Early Cretaceous to more than 100 genera recorded by the end of the Late Cretaceous (Fig. 6.6). This pattern provides compelling evidence for the evolutionary success and progressive ecological expansion of the group throughout this interval.

A clear increase in total diversity (D_{tot}, defined as the total number of genera recorded for each stratigraphic stage) is observed from Early to the Late Cretaceous. The increasing trend commences in the Aptian and continues to the Turonian, followed by a slight decline in the Coniacian. From the Coniacian to the Campanian, neogastropod diversity rises sharply, increasing almost fourfold.

To reduce edge effects associated with stratigraphic boundaries and to account for first and last appearances of taxa within individual stages the normalised diversity (D_{norm}) was calculated.

As a result, D_{norm} provides a more balanced estimate of diversity dynamics and better reflects underlying evolutionary trends in the fossil record. D_{norm} was calculated according to the formula:

$$D_{norm} = D_{tot} + 0.5 \times G_{term},$$

where G_{term} represents the number of genera confined to a single age interval (stage) or extending beyond it but originating or becoming extinct within that interval.

The curve of normalised diversity (D_{norm}) closely parallels the curve of D_{tot} and shows only minor deviations, with somewhat more pronounced peaks in the Turonian and Maastrichtian (Fig. 6.6). In the Turonian, this peak is driven by an increased number of newly recorded taxa, whereas in the Maastrichtian it reflects the high number of taxa that became extinct at the K/Pg boundary. Overall, this form of standardisation does not substantially alter the general diversity signal under relatively stable conditions, nor does it generate inverted trends. Instead, it accentuates intervals of extinction or rapid taxonomic turnover, expressed as more pronounced peaks.

In contrast, the standardised diversity (D_{st}, calculated as D_{tot} divided by the duration of each stratigraphic stage) displays a somewhat different pattern. While an overall increase in diversity is evident from the Aptian onwards, D_{st} shows a slight decline in the Coniacian and a reduction by almost half in the Campanian. At first glance, the Campanian decline appears paradoxical, given the exceptionally rich and diverse Campanian gastropod faunas described worldwide (see above). However, this pattern is readily explained by the unusually long duration of the Campanian (~ 14 Ma) relative to other Late Cretaceous ages. When diversity is normalised to time, the apparent slowdown reflects temporal averaging rather than a true taxonomical decline. Thus, the Campanian represents a period of sustained high diversity maintained over an extended interval, rather than a short-lived diversification pulse.

Two models of changes in neogastropod taxonomic diversity throughout the Cretaceous were compared (Fig. 6.7). The first model is based on factually documented records, whereas the second assumes continuity of genera. Although the D_{tot} values differ between the two models, the curves of mean values are almost identical, indicating that the assumption of continuity of genera does not affect the overall evolutionary trend.

Changes in standardised diversity have also been compared to climatic events documented during the Cretaceous (Fig. 6.8). The decline in D_{st}, first in the Coniacian and subsequently in the Campanian, coincided with major global climatic events. The Coniacian decline appears to be associated with the warm conditions that persisted throughout the Albian and culminated in the extreme warmth from the early-mid-Turonian to the late Santonian, associated with the Cretaceous Thermal Maximum (Huber et al. 2018). This pattern suggests that neogastropods underwent adaptation to these exceptionally warm conditions during the Coniacian, resulting in a temporary

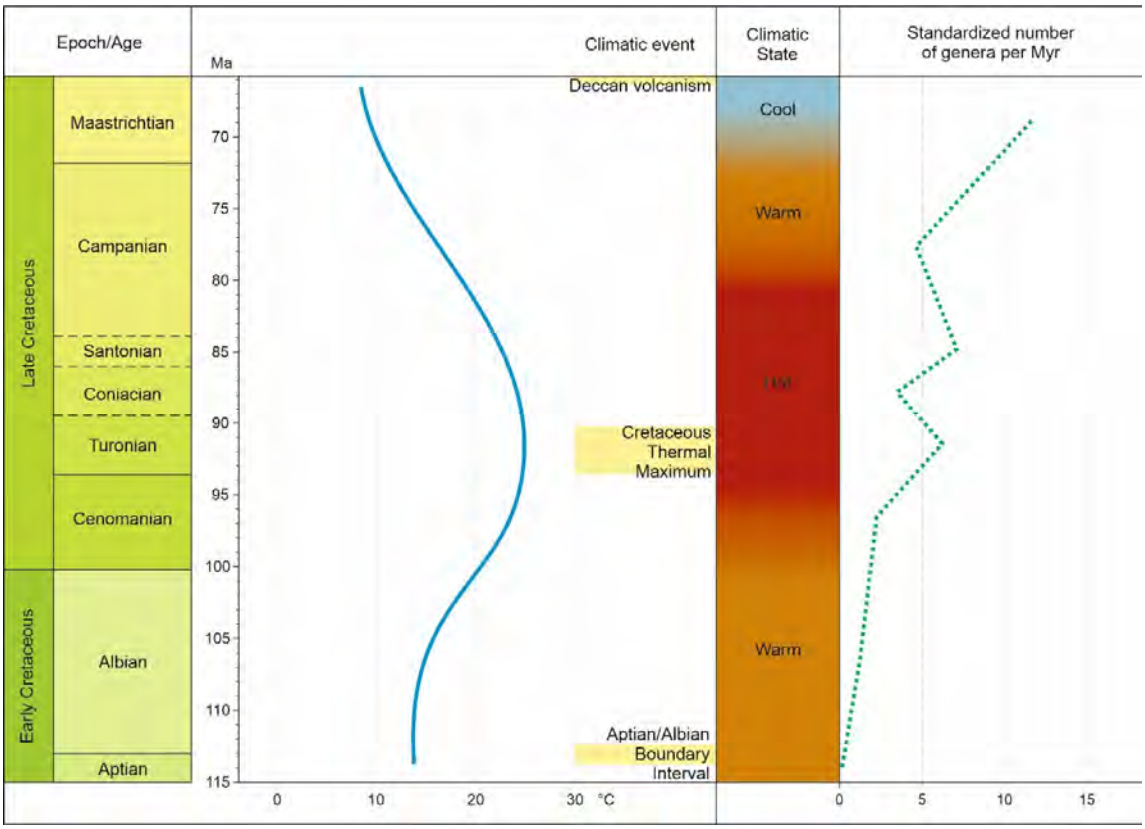

Fig. 6.8. — Comparison of changes in neogastropod standardized diversity with climatic events documented during the Cretaceous according to Huber et al. (2018).

slowdown in diversification compared with the Turonian, as indicated by the subsequent increase of D_{st} in the Santonian despite continued high temperatures. The Campanian marks the onset of prolonged cooling, reflected in a reduction of D_{st}. Nevertheless, by this age neogastropods had already attained a degree of ecological plasticity, allowing the group to adapt to changing temperatures, and diversity subsequently increased again, despite the culmination of Cretaceous thermal minima during the Maastrichtian.

The paleogeographic distribution of neogastropods across different ages was investigated to identify centres of diversification. The results showed that the earliest neogastropods were recorded in the temperate and subtropical zones of the Northern Hemisphere (corresponding to the present-day Poland and Switzerland, respectively), and later in the tropical-subtropical zone of the Southern Hemisphere, i.e. Madagascar (Zakharov et al. 2016) (Fig. 6.8). This bimodal distribution persisted into the Late Cretaceous (Fig. 6.9). However, it remains unclear whether this distribution is an artifact of limited knowledge about the gastropod fauna from tropical and equatorial regions, or represents a true phenomenon. Records from the late Early Cretaceous (Albian) and particularly the Late Cretaceous indicate a widespread distribution across multiple paleobiogeographic

provinces. This may suggests both a high dispersal capacity and ecological adaptability of the group to a range of environmental settings.

Two palaeogeographic centres of diversification of Neogastropoda were recognized to be:

i) the north-western part of the Tethys Ocean, where the earliest representatives of the group have been documented. Abundant and diverse neogastropod faunas were also recorded from the Late Cretaceous in the Western Tethys, suggesting that it played an important role during the Cretaceous phases of neogastropod diversification;

ii) the North Atlantic and the adjacent Western Interior Seaway. Neogastropoda are documented there from the Albian onwards, with a pronounced increase in both abundance and taxonomic diversity during the Turonian. During the Campanian–Maastrichtian, the molluscan fauna of the North American Gulf and Atlantic Coastal Plain displayed a distinctly modern aspect, with neogastropods comprising 60–70% of benthic assemblages (Jablonski 1979). This is documented by the most species-rich neogastropod fauna of this age (see above), suggesting that this region may have served as a major centre of neogastropod radiation during the Late Cretaceous.

As shown above, the Cretaceous witnessed an explosive radiation of Neogastropoda, leading to a substantial increase in their abundance and to a major restructuring of benthic communities driven by the group expansion. By the end of the Cretaceous, all superfamilies of Neogastropoda were already present in the fossil record, represented by 20 families and 159 genera. The large number of described species may indirectly suggests that evolution of Neogastropoda proceeded primarily at the species level, with a gradual accumulation of higher taxa. This evolutionary pattern likely underpinned the high diversity and considerable ecological plasticity of the group, enabling recovery after episodes of environmental stress.

A key period for the diversification of Neogastropoda was the mid-Cretaceous (Albian–Cenomanian), coinciding with rising seawater temperatures, whereas the Cretaceous Thermal Maximum and the subsequent cooling during the Campanian were associated with declines in diversity. Correspondingly, peaks and declines in diversity, as reflected in standardised metrics, closely coincide with major climatic extremes. Although temperature appears to be the most clearly expressed factor, it would be imprudent to assume that the evolution of the group was controlled by temperature alone. Rather, the evolutionary success of Neogastropoda was most likely the result of the interaction of multiple biological and ecological factors.

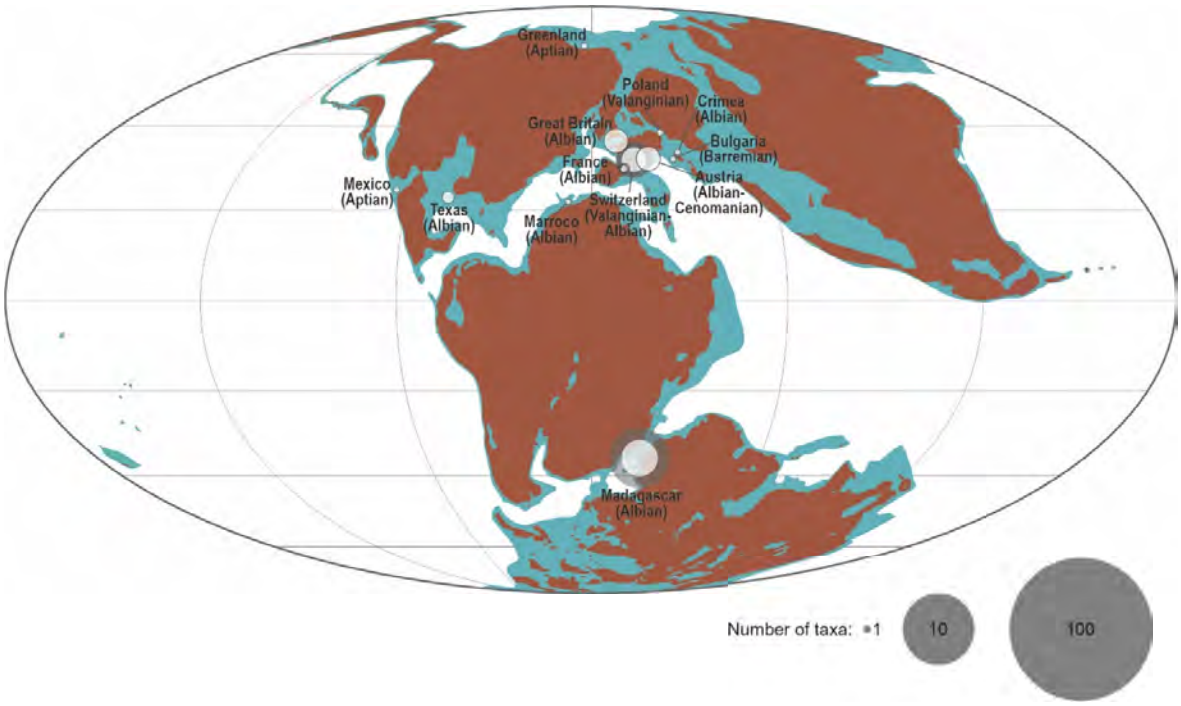

Fig. 6.9. — Distribution of neogastropod families (white) and genera (grey) in the Early Cretaceous. Source of paleomap of Kocsis and Scotese (2021).

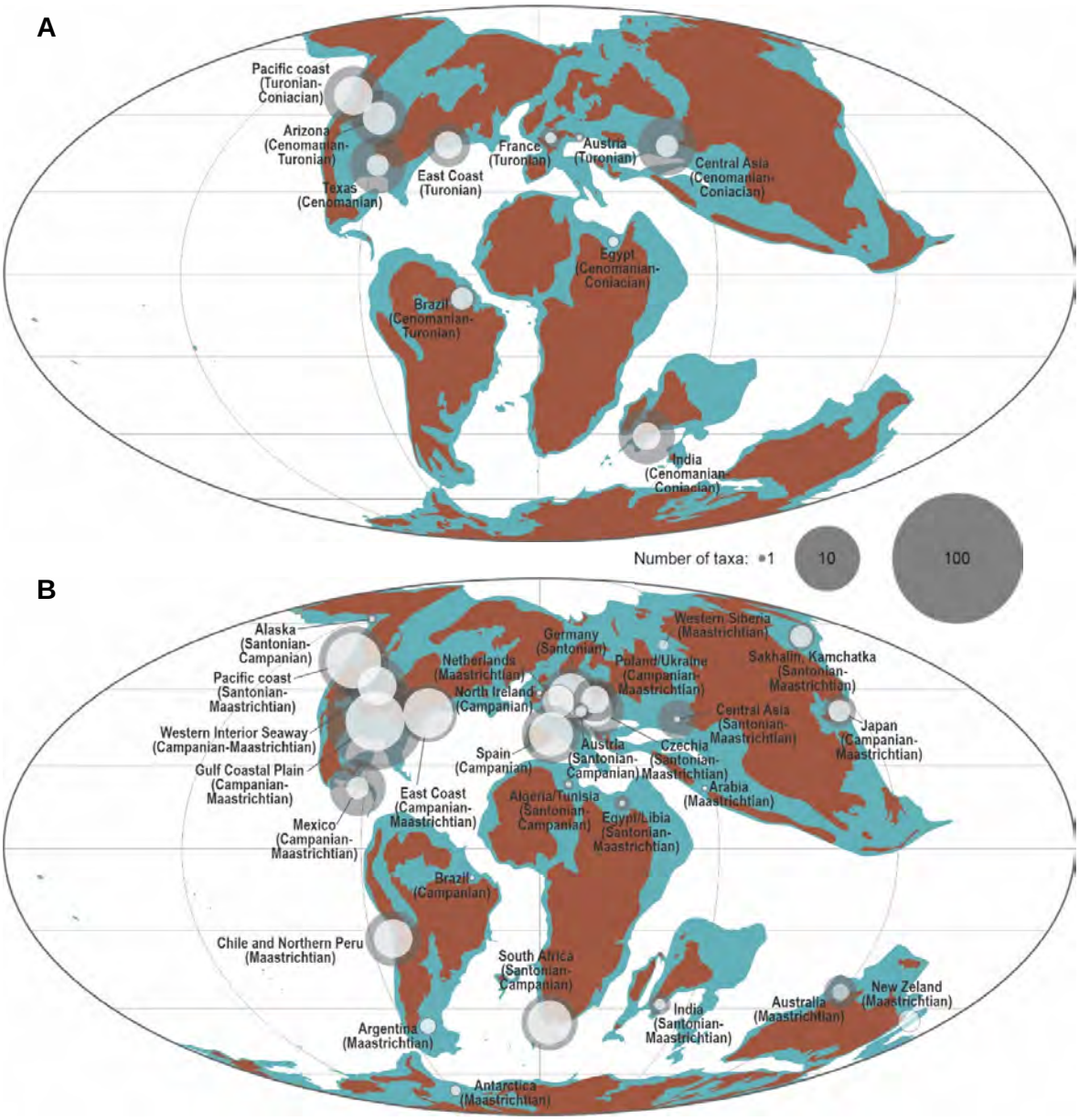

Fig. 6.10. — Distribution of neogastropod families (white) and genera (grey) in the early Late Cretaceous (A) and late Late Cretaceous (B). Source of paleomap of Kocsis and Scotese (2021).

Table 6.1. — Taxonomical composition of the order Neogastropoda according to different authors. Formulas retained in original form, i.e., † (denoting extinct taxa) and parentheses.

Wenz (1938)	Ponder (1973)	Bouchet and Rocroi (2005)	Bouchet et al. (2017)
BUCCINACEA	**CANCELLARIACEA**	Unassigned to superfamily	Unassigned to superfamily
Buccinidae	Cancellariidae	†Johnwyattiidae	Babyloniidae
Pyrenidae (Columbellidae)	Paladmetidae	†Perissityidae	Cystiscidae
Galeodidae (Melongenidae; Busyconidae; Fulguridae)	**CONACEA**	†Sarganidae	Harpidae
	Conidae	†Speightiidae	†Johnwyattiidae
	Speightiidae	†Taiomidae	Marginellidae
	Terebridae	†Weeksiidae	†Perissityidae
	Turridae	**BUCCINOIDEA**	†Pseudotritoniidae
Nassariidae (Nassidae, Alectryonidae)	**MURICACEA**	Buccinidae	†Purpurinidae
	Muricidae (=Thaididae, etc.)	Colubrariidae	†Speightiidae
Fasciolariidae		Columbellidae	Strepsiduridae
CONACEA	Buccinidae	Fasciolariidae	†Taiomidae
Conidae	Columbariidae	Melongenidae	**BUCCINOIDEA**
Terebridae	Colubrariidae (=Fusidae)	Nassariidae	Buccinidae
Turridae	Fasciolariidae	**CANCELLARIOIDEA**	Belomitridae
MURICACEA	Harpidae	Cancellariidae	Busyconidae
Muricidae	Galeodidae (=Melongenidae, Volemidae)	**CONOIDEA**	Colubrariidae
Magilidae (Coralliophilidae)		Conidae	Columbellidae
VOLUTACEA	Magilidae (=Coralliophilidae, Rapidae)	Clavatulidae	†Echinofulguridae
Olividae		Drilliidae(=Clavidae)	Fasciolariidae
Mitridae		Pseudomelatomidae	Melongenidae
Vasidae (Xancidae, Turbinellidae)	Marginellidae	Strictispiridae	Nassariidae
	Mitridae	Terebridae	Pisaniidae
Harpidae	Nassariidae	Turridae	**CONOIDEA**
Volutidae	Olividae	**MURICOIDEA**	Conidae
Marginellidae	Pyrenidae (=Columbellidae)	Muricidae	Borsoniidae
Cancellariidae		Babyloniidae	Bouchetispiridae
	Turbinellidae (=Vasidae, Xancidae)	Costellariidae	Clathurellidae
		Cysticidae	Clavatulidae
		Harpidae	Cochlespiridae
	Vexillidae	Mitridae	Conorbidae
	Volutidae	Marginellidae	†Cryptoconidae
	Volutomitridae	Pleioptygmatidae	Drilliidae
		†Pholidotomidae	Horaiclavidae
		Strepsiduridae	Mangeliidae
		Turbinellidae	Mitromorphidae
		Volutidae	Pseudomelatomidae
		Volutomitridae	Raphitomidae
		OLIVOIDEA	Strictispiridae
		Olividae	Terebridae
		Olivellidae	Turridae

		PSEUDLIVOIDEA Pseudolividae Ptychatractidae	**MURICOIDEA** Muricidae **MITROIDEA** Mitridae Charitodoronidae Pyramimitridae **TURBINELLOIDEA** Turbinellidae Columbariidae Costellariidae Ptychatractidae Volutomitridae **VOLUTOIDEA** Volutidae Cancellariidae †**PHOLIDOTOMOIDEA** †Pholidotomidae †Sarganidae †Moreidae †Weeksiidae **OLIVOIDEA** Olividae Ancillariidae Bellolividae Benthobiidae Pseudolividae

Table 6.2. — Distribution of Neogastropoda in the Cretaceous

Age	Region	Number of families	Number of genera
Valanginian	Poland (Kaim 2004)	1	1
	Switzerland (Pictet and Campiche, 1861–1864)	1?	2?
Barremian	Bulgaria (Bakayeva et al. (submitted))	1	1
Aptian	Switzerland (Pictet and Campiche 1861–1864)	1?	2?
	Greenland (Frebold 1935)	1?	1?
	Mexico (Allison 1955)	1	1
Albian	Great Britain (Taylor et al. 1983, Tracey 2010)	4	4
	Switzerland (Pictet and Campiche 1861–1864)	2?	2?
	France (Kollmann 2005)	1	2
	Crimea (Pchelintsev 1927)	1	1
	Morocco (Collignon 1972)	1	1
	Madagascar (Collignon 1949)	6	10
	USA, Texas (Stanton 1947)	2	2
Albian–Cenomanian	Austria (Kollmann 1976)	4	4
Cenomanian	USA, Texas (Stephenson 1952)	4	13
	Ukraine (Plamadeala 1999, Bakayeva 2011)	2	2
Cenomanian–Turonian	Brazil (Lexen 2013)	4	5
	USA, Arizona (Kirkland 1996)	6	12
	Egypt (Mekawy 2007, Ayoub-Hannaa and Fürsich 2011)	2	2
Cenomanian–Coniacian	Central Asia (Pchelintsev 1953, Korobkov et al. 1974, Djalilov 1977, Poyarkova and Djalilov 1985)	4	17
Turonian	France (Cossmann 1896, Roman and Mazeran 1920)	2	4
	East Coast of North America (Whitfield 1892)	5	8
Turonian–Santonian	India (Stoliczka 1867, Bandel 2000)	7	16
Turonian–Campanian	Pacific coast of North America (Gabb 1864, White 1889, Packard 1922, Stewart 1926, Saul and Popenoe 1993, Saul 1996, Squires and Saul 2003b, Saul and Squires 2008, Squires 2011)	7	18
Turonian–Campanian	Austria (Zekeli 1852, Stoliczka 1865)	2	5
Coniacian–Santonian	Egypt (Mekawy 2007)	1	1
Santonian–Campanian	Alaska (Popenoe and Saul 1987)	1	2
	South Africa (Bandel and Dockery 2001, Kiel and Bandel 2003)	8	12
	Germany (Müller 1851, Böhm 1885, Holzapfel 1888, Deninger 1905)	8	14
	Algeria and Tunisia (Coquand 1862, Thomas and Peron 1889–1890)	1	2
Santonian–Maastrichtian	Pacific coast of North America (Gaab 1864, Stewart 1926, Anderson 1958, Popenoe and Saul 1987, Saul 1988a, b, Squires and Saul 2000, 2001, 2003a, b, 2006, Saul and Squires 2008, Squires 2011, 2012, 2018)	10	27
	Sakhalin, Kamchatka (Poyarkova and Djalilov 1985)	4	5
	Czechia (Weinzettl 1910)	6	11

	Central Asia (Pchelintsev 1953, Djalilov 1977)	1	7
	India (Forbes 1846, Stoliczka 1867, Bandel 2000)	2	4
Campanian	Spain (Kiel 2001)	8	16
	Germany (Pietzonka et al. 2023)	7	11
	Mexico (Imlay 1937, Furque and Camacho 1949)	1	1
	Brazil (Squires and Saul 2003a)	1	1
	North Ireland (Cleevely and Morris 2002)	1	1
	Palestine (Chavan 1947)	2	3
Campanian–Maastrichtian	Western Interior Seaway (Hall and Meek 1854, Meek and Hayden 1856, Sohl 1967, Erickson 1974)	7	17
	Gulf Coastal Plain (Conrad 1858, 1860, Gabb 1860, Meek 1876, Wade 1916, 1917, 1926, Stephenson 1941, Harbison 1945, Sohl 1964a, b, Dockery 1993, Akers and Akers 1997)	17	76
	East Coast of North America (Gabb 1860, Gardner 1916, Weller 1962)	9	15
	Netherlands (Binkhorst 1861, Kaunhowen, 1897)	6	6
	Poland (Abdel-Gawad 1986, 1990)	5	8
	Ukraine (Blank 1974, Bakayeva 2011)	5	8
	Japan (Kase 1990)	4	6
Maastrichtian	Egypt and Libia (Quaas 1902, Rossi Ronchetti 1959, Bandel 2003)	1	3
	Arabia (Lees 1928)	1	1
	Western Siberia (Kaim and Beisel 2005)	2	2
	Mexico (Kiel 2001, Kiel and Perrilliat 2004)	4	12
	Chile and N Peru (Olsson 1944, Bandel and Stinnesbeck 2000,)	7	11
	Argentina (Griffin and Hunicken 1994)	3	3
	Australia (Darragh and Kendrick 1994)	3	6
	New Zealand (Wilckens 1922)	4	4
	Antarctica (Oleinik and Zinsmeister 1996, Stilwell and Zinsmeister 2003)	2	2

Table 6.3. — Changes of Neogastropoda generic composition during the Cretaceous including subgenera

Age	Genera	
	First record	Last record
Valanginian	Buccinoidea	
Barremian	*Fimbrivasum*	
Aptian	*Profusinus*	
Albian	*Blackdownia, Cancellaria, Cantharulus, Cosnia, Cretaceomurex, Cryptorhytis, Drilluta, Eomorea, Eovolutilithes, Exilia, Fusinus, Iscafusus, Marginella, Palaeocancellaria, Paleopsephaea, "Pseudoliva", Pyropsis, Serrifusus, Volutilithes, Volutocorbis*	
Cenomanian	*Aliofusus, Bellifusus, Cantharulus, Dolicholatirus, Latirus, Palaeatractus, Rhombopsis, Admetopsis, Hillites, Graphidula, Ascensovoluta, Carota, Tectaplica, Tovula, Volutoderma, Volutomorpha*	*Palaeocancellaria, Admetopsis, Hillites, Tovula*
Turonian	*Beisselia, Boncavailia, Cydas, Eripachya, Ficulopsis, Konistra, Lutema, Lyria, Mataxa, Mylecoma, Odontofusus, Pholidotoma, Praesargana, Pseudocymia, Ptychoris, Pyrifusus, Rostellana, Rostellinda, Rostellites, Sargana, Saturnus, Skyles, Trichifusus, Varens*	*Boncavailia, Cydas, Ficulopsis, Konistra, Mylecoma, Pholidotoma, Ptychoris, Saturnus, Skyles, Varens*
Coniacian	*Christitys, Micasarcina, Murphitys, Perissitys, Plectocion, Ripleyella, Zinsitys*	*Micasarcina*
Santonian	*Anomalofusus, Boltenella, Deussenia, Ficulomorpha, Forsia, Fusivoluta, Liopeplum, Longoconcha, Muteluma, Napulus, Rostellaca, Schizofusus, Xsosaites*	*Fusivoluta, Rostellinda, Trichifusus, Xsosaites*
Campanian	*Amuletum, Astandes, Beretra, Bonellitia, Breviexilia, Buccinopsis, Calkota, Caveola, Cryptoconus, Eopleurotoma, Fulgerca, Fusimilis, Haplovoluta, Hercorhyncus, Hippocampoides, Hydrotribulus, Lissapiopsis, Lomirosa, Lupira, Mesorhytis, Misricymbiola, Mitridomus, Morea, Myobarbum, Nipponitys, Odontobasis, Ornopsis, Paladmete, Paleofusimitra, Parafusus, Paramorea, Parvivoluta, Pentzia, Piestochilus, Pornosis, Protobusycon, Pseudecphora, Pseudobuccinum, Pseudorapa, Ptychosyca, Remera,*	*Blackdownia, Boltenella, Breviexilia, Christitys, Eripachya, Ficulomorpha, Forsia, Iscafusus, Lissapiopsis, Mitridomus, Muteluma, Plectocion, Praesargana, Rostellaca, Schizofusus, Tectaplica, Zinsitys*

	Remnita, Schizobasis, Sohliina, Stantonella, Woodsella, Zaglenum	
Maastrichtian	*Ancilla, Antarctissitys, Austrosphaera, Chilenopsis, Eoharpa, Heteroterma, Holzapfelia, Mexfusus, Misrimelo, Misriplicoliva, Nekewis, Pinella, Protogemmula, Pseudoperissitys, Rapopsis, Retipirula, Struthiolariopsis, Tanimasanoria, "Trigonostoma", Tryonella, Volutospina*	*Aliofusus, Amuletum, Anomalofusus, Antarctissitys, Astandes, Beisselia, Bellifusus, Beretra, Buccinopsis, Calkota, Caveola, Chilenopsis, Cryptorhytis, Deussenia, Drilluta, Eoharpa, Eovolutilithes, Fimbrivasum, Fulgerca, Fusimilis, Graphidula, Haplovoluta, Hercorhyncus, Hippocampoides, Holzapfelia, Hydrotribulus, Liomelon, Liopeplum, Lomirosa, Longoconcha, Lupira, Lutema, Lyria, Mataxa, Mexfusus, Misricymbiola, Misrimelo, Misriplicoliva, Morea, Murphitys, Myobarbum, Napulus, Nipponitys, Odontobasis, Ornopsis, Paladmete, Palaeatractus, Paleofusimitra, Paleopsephaea, Parafusus, Paramorea, Parvivoluta, Pentzia, Piestochilus, Pinella, Pornosis, Protogemmula, Pseudecphora, Pseudobuccinum, Pseudocymia, Pseudoperissitys, Ptychosyca, Pyrifusus, Rapopsis, Remera, Remnita, Rhombopsis, Ripleyella, Rostellana, Rostellites, Sargana, Schizobasis, Sohliina, Stantonella, Struthiolariopsis, Tanimasanoria, "Trigonostoma", Tryonella, Volutoderma, Volutomorpha, Woodsella, Zaglenum*
After the K/P boundary, the following Cretaceous genera *Ancilla, Ascensovoluta, Austrosphaera, Bonellitia, Cancellaria, Cantharulus, Cryptoconus, Dolicholatirus, Eopleurotoma, Exilia, Fusinus, Heteroterma, Latirus, Marginella, Mesorhytis, Nekewis, Odontofusus, Perissitys, Profusinus, Protobusycon, Pyropsis, Retipirula, Serrifusus, Volutilithes, Volutocorbis, Volutospina* continued to exist in the Paleocene, and some of them even longer.		

APPENDIX

List of genera recorded in each stage

Early Cretaceous

Valanginian (1? family and 2? genera): Buccinoidea (fam, gen, et sp. indet., genus "*Fusus*" (Pictet & Campiche, 1861–1864))

Barremian (1 family and 1 genus): Vasidae (genus *Fimbrivasum* Squires &Saul, 2001).

Aptian (1? family and 4 genera): Fasciolariidae (genus *Profusinus* Bandel, 2000), fam. indet. ("*Fusus*"(Pictet &Campiche, 1861–1864)).

Albian (9 families and 21 genera): Buccinidae (genus *Cosnia* Kollmann, 2005, "*Pseudoliva*" Swainson, 1840), Cancellariidae (*Cancellaria* Lamarck, 1799, *Palaeocancellaria* Kollmann, 1976), Costellariidae (*Exilia* Conrad, 1860), Fasciolariidae (*Cantharulus* Meek, 1876, *Cryptorhytis* Meek, 1876, *Fusinus* Rafinesque, 1815, *Iscafusus* Kollmann, 2005, *Profusinus* Bandel, 2000, *Serrifusus* Meek, 1876), Marginellidae (*Marginella* Lamarck, 1799), Moreidae (*Pyropsis* Conrad,1860), Muricidae (*Blackdownia* Kollmann, 1976, *Cretaceomurex* Mongin, 1985), Sarganidae (*Eomorea* Kollmann, 2005), Volutidae (*Drilluta* Wade, 1916, *Eovolutilithes* Hacobjan, 1976, *Paleopsephaea* Wade, 1926, *Volutilithes* Swainson, 1831, *Volutocorbis* Dall, 1890).

Late Cretaceous

Cenomanian (10 families and 25 genera): Buccinidae (genus *Aliofusus* Stephenson, 1941), Cancellariidae (*Palaeocancellaria* Kollmann, 1976), Fasciolariidae (*Bellifusus* Stephenson, 1941, *Cantharulus* Meek, 1876, *Dolicholatirus* Bellardi, 1884, *Fusinus* Rafinesque, 1815, *Latirus* Montfort, 1810, *Profusinus* Bandel, 2000), Melongenidae (*Palaeatractus* Gabb, 1869, *Rhombopsis* Gardner, 1916), Moreidae (*Pyropsis* Conrad, 1860), Muricidae (*Blackdownia* Kollmann, 1976), Nassariidae (*Admetopsis* Meek, 1873), Sarganidae (*Hillites* Stephenson, 1952), Turridae (*Graphidula* Stephenson, 1941), Volutidae (*Ascensovoluta* Pchelintsev, 1953, *Carota* Stephenson, 1952, *Drilluta* Wade, 1916, *Eovolutilithes* Hacobjan, 1976, *Paleopsephaea* Wade, 1926, *Tectaplica* Wade, 1916, *Tovula* Stephenson, 1952, *Volutilithes* Swainson, 1831, *Volutoderma* Gabb, 1877, *Volutomorpha* Gabb, 1877).

Turonian (10 families and 43 genera): Buccinidae (*Aliofusus* Stephenson, 1941, *Eripachya* Gabb, 1869), Cancellariidae (*Cancellaria* Lamarck, 1799, *Mataxa* Wade, 1916), Fasciolariidae (*Bellifusus* Stephenson, 1941, *Cantharulus* Meek, 1876, *Cryptorhytis* Meek, 1876, *Fusinus* Rafinesque, 1815, *Latirus* Montfort, 1810, *Mylecoma* Squires & Saul, 2003, *Odontofusus* Whitfield, 1892, *Profusinus* Bandel, 2000, *Serrifusus* Meek, 1876, *Skyles* Saul &Popenoe, 1993), Melongenidae (*Saturnus* Saul &Popenoe, 1993), Moreidae (*Pyropsis* Conrad, 1860), Perissityidae

(*Cydas* Saul & Popenoe, 1993, *Pseudocymia* Popenoe & Saul, 1987), Pholidotomidae (*Pholidotoma* Cossmann, 1896, *Pyrifusus* Conrad, 1858, *Trichifusus* Bandel, 2000), Sarganidae (*Praesargana* Saul & Popenoe, 1993, *Sargana* Stephenson, 1923), Turridae (*Beisselia* Holzapfel, 1889, *Graphidula* Stephenson, 1941, *Lutema* Stephenson, 1941), Volutidae (*Ascensovoluta* Pchelintsev, 1953, *Boncavailia* Roman & Mazeran, 1920, *Carota* Stephenson, 1952, *Eovolutilithes* Hacobjan, 1976, *Ficulopsis* Stoliczka, 1867, *Konistra* Saul & Popenoe, 1993, *Lyria* Gray, 1847, *Paleopsephaea* Wade, 1926, *Ptychoris* Gabb, 1877, *Rostellana* Dall, 1907, *Rostellinda* Dall, 1907, *Rostellites* Conrad, 1855, *Tectaplica* Wade, 1916, *Varens* Saul & Popenoe, 1993, *Volutilithes* Swainson, 1831, *Volutoderma* Gabb, 1877, *Volutomorpha* Gabb, 1877).

Coniacian (7 families and 28 genera): Fasciolariidae (*Bellifusus* Stephenson, 1941, *Cantharulus* Meek, 1876, *Cryptorhytis* Meek, 1876, *Latirus* Montfort, 1810, *Micasarcina* Squires & Saul, 2003, *Plectocion* Stewart, 1927, *Profusinus* Bandel, 2000, *Ripleyella* Harbison, 1945), Moreidae (*Pyropsis* Conrad, 1860), Perissityidae (*Christitys* Popenoe & Saul, 1987, *Murphitys* Popenoe & Saul,1987, *Perissitys* Stewart 1927, *Pseudocymia* Popenoe & Saul, 1987, *Zinsitys* Saul, 1988), Pholidotomidae (*Pyrifusus* Conrad, 1858, *Trichifusus* Bandel, 2000), Sarganidae (*Sargana* Stephenson, 1923), Turridae (*Beisselia* Holzapfel, 1889, *Lutema* Stephenson, 1941), Volutidae (*Ascensovoluta* Pchelintsev, 1953, *Eovolutilithes* Hacobjan, 1976, *Lyria* Gray, 1847, *Paleopsephaea* Wade, 1926, *Rostellana* Dall, 1907, *Rostellinda* Dall, 1907, *Volutilithes* Swainson, 1831, *Volutoderma* Gabb, 1877, *Volutomorpha* Gabb, 1877).

Santonian (13 families and 41 genera): Buccinidae (*Deussenia* Stephenson, 1941), Busyconidae (*Boltenella* Wade, 1917), Cancellariidae (*Cancellaria* Lamarck, 1799), Fasciolariidae (*Anomalofusus* Wade, 1916, *Bellifusus* Stephenson, 1941, *Cantharulus* Meek, 1876, *Cryptorhytis* Meek, 1876, *Plectocion* Stewart, 1927, *Profusinus* Bandel, 2000, *Serrifusus* Meek, 1876), Melongenidae (*Palaeatractus* Gabb, 1869), Moreidae (*Napulus* Stephenson,1941, *Pyropsis* Conrad,1860, *Schizofusus* Kiel & Bandel, 2003), Muricidae (*Blackdownia* Kollmann, 1976), Perissityidae (*Christitys* Popenoe & Saul, 1987, *Forsia* Saul, 1988, *Murphitys* Popenoe & Saul,1987, *Perissitys* Stewart 1927, *Pseudocymia* Popenoe & Saul, 1987, *Zinsitys* Saul, 1988), Pholidotomidae (*Pyrifusus* Conrad, 1858, *Trichifusus* Bandel, 2000), Sarganidae (*Sargana* Stephenson, 1923, *Xsosaites* Bandel & Dockery, 2001), Vasidae (*Fimbrivasum* Squires & Saul, 2001), Turridae (*Beisselia* Holzapfel, 1889, *Muteluma* Kiel & Bandel, 2003), Volutidae (*Eovolutilithes* Hacobjan, 1976, *Ficulomorpha* Holzapfel, 1888, *Fusivoluta* Martens, 1902, *Liopeplum* Dall, 1890, *Longoconcha* Stephenson, 1941, *Lyria* Gray, 1847, *Paleopsephaea* Wade, 1926, *Rostellaca* Dall, 1907, *Rostellana* Dall, 1907, *Rostellinda* Dall, 1907, *Volutilithes* Swainson, 1831, *Volutoderma* Gabb, 1877, *Volutomorpha* Gabb, 1877).

Campanian (16 families and 99 genera): Buccinidae (*Aliofusus* Stephenson, 1941, *Buccinopsis* Conrad, 1857, *Deussenia* Stephenson, 1941, *Eripachya* Gabb, 1869, *Hydrotribulus* Wade, 1916, *Odontobasis* Meek, 1876, *Pseudobuccinum* Meek & Hayden, 1857, *Stantonella* Wade, 1926, *Zaglenum* Squires & Saul, 2001), Busyconidae (*Boltenella* Wade, 1917, *Protobusycon* Wade, 1917), Cancellariidae (*Bonellitia* Jousseaume, 1887, *Cancellaria* Lamarck, 1799, *Caveola* Stephenson, 1941, *Mataxa* Wade, 1916, *Paladmete* Gardner, 1916), Conorbidae (*Cryptoconus* Koenen, 1867), Costellariidae (*Breviexilia* Chavan, 1947, *Exilia* Conrad, 1860, *Mitridomus* Sohl, 1963), Fasciolariidae (*Anomalofusus* Wade, 1916, *Bellifusus* Stephenson, 1941, *Calkota* Squires & Saul, 2003, *Cantharulus* Meek, 1876, *Cryptorhytis* Meek, 1876, *Dolicholatirus* Bellardi, 1884, *Fusinus* Rafinesque, 1815, *Haplovoluta* Wade, 1918, *Hercorhyncus* Conrad, 1869, *Iscafusus* Kollmann, 2005, *Mesorhytis* Meek, 1876, *Odontofusus* Whitfield, 1892, *Ornopsis* Wade, 1916, *Piestochilus* Meek, 1864, *Plectocion* Stewart, 1927, *Pornosis* Sohl, 1964, *Profusinus* Bandel, 2000, *Remera* Stephenson, 1941, *Ripleyella* Harbison, 1945, *Serrifusus* Meek, 1876, *Woodsella* Wade, 1926), Melongenidae (*Lissapiopsis* Imlay, 1937, *Pentzia* Squires & Saul, 2003, *Rhombopsis* Gardner, 1916), Mitridae (*Paleofusimitra* Sohl, 1963), Moreidae (*Morea* Conrad, 1860, *Napulus* Stephenson,1941, *Pyropsis* Conrad,1860, *Schizofusus* Kiel & Bandel, 2003), Muricidae (*Blackdownia* Kollmann, 1976, *Paramorea* Wade,1917, *Sohliina* Özdikmen, 2013), Perissityidae (*Christitys* Popenoe & Saul, 1987, *Forsia* Saul, 1988, *Murphitys* Popenoe & Saul,1987, *Nipponitys* Kase,1990, *Perissitys* Stewart 1927, *Pseudocymia* Popenoe & Saul, 1987, *Zinsitys* Saul, 1988), Pholidotomidae (*Astandes* Wade, 1917, *Pseudorapa* Holzapfel, 1888, *Pyrifusus* Conrad, 1858), Sarganidae (*Hippocampoides* Wade, 1916, *Praesargana* Saul & Popenoe, 1993, *Pseudecphora* Bandel & Dockery, 2001, *Sargana* Stephenson, 1923, *Schizobasis* Wade,1916), Vasidae (*Fimbrivasum* Squires & Saul, 2001, *Lupira* Stephenson, 1941), Turridae (*Amuletum* Stephenson, 1941, *Beisselia* Holzapfel, 1889, *Beretra* Stephenson, 1941, *Eopleurotoma* Cossmann, 1889, *Fulgerca* Stephenson, 1941, *Fusimilis* Stephenson, 1941, *Graphidula* Stephenson, 1941, *Lomirosa* Stephenson, 1941, *Lutema* Stephenson, 1941, *Muteluma* Kiel & Bandel, 2003, *Remnita* Stephenson, 1941), Volutidae (*Drilluta* Wade, 1916, *Eovolutilithes* Hacobjan, 1976, *Ficulomorpha* Holzapfel, 1888, *Liopeplum* Dall, 1890, *Longoconcha* Stephenson, 1941, *Lyria* Gray, 1847, *Misricymbiola* Bandel, 2003, *Myobarbum* Sohl, 1963, *Paleopsephaea* Wade, 1926, *Parafusus* Wade, 1918, *Parvivoluta* Wade, 1926, *Ptychosyca* Gabb, 1877, *Rostellaca* Dall, 1907, *Rostellana* Dall, 1907, *Rostellites* Conrad, 1855, *Tectaplica* Wade, 1916, *Volutilithes* Swainson, 1831, *Volutoderma* Gabb, 1877, *Volutomorpha* Gabb, 1877).

Maastrichtian (17 families and 104 genera): Buccinidae (*Aliofusus* Stephenson, 1941, *Austrosphaera* Furque & Camacho, 1949, *Buccinopsis* Conrad, 1857, *Deussenia* Stephenson, 1941, *Hydrotribulus* Wade, 1916, *Odontobasis* Meek, 1876, *Pseudobuccinum* Meek & Hayden,

1857, *Stantonella* Wade, 1926, *Tryonella* Stephenson, 1951, *Zaglenum* Squires & Saul, 2001), Busyconidae (*Pinella* Stephenson, 1941, *Protobusycon* Wade, 1917), Cancellariidae (*Cancellaria* Lamarck, 1799, *Caveola* Stephenson, 1941, *Mataxa* Wade, 1916, *Paladmete* Gardner, 1916), Costellariidae (*Exilia* Conrad, 1860), Fasciolariidae (*Anomalofusus* Wade, 1916, *Bellifusus* Stephenson, 1941, *Calkota* Squires & Saul, 2003, *Cryptorhytis* Meek, 1876, *Dolicholatirus* Bellardi, 1884, *Fusinus* Rafinesque, 1815, *Haplovoluta* Wade, 1918, *Hercorhyncus* Conrad, 1869, *Latirus* Montfort, 1810, *Mesorhytis* Meek, 1876, *Odontofusus* Whitfield, 1892, *Ornopsis* Wade, 1916, *Piestochilus* Meek, 1864, *Pornosis* Sohl, 1964, *Profusinus* Bandel, 2000, *Remera* Stephenson, 1941, *Ripleyella* Harbison, 1945, *Serrifusus* Meek, 1876, *Woodsella* Wade, 1926), Harpidae (*Eoharpa* Stephenson, 1955), Melongenidae (*Palaeatractus* Gabb, 1869, *Pentzia* Squires & Saul, 2003, *Rhombopsis* Gardner, 1916), Mitridae (*Paleofusimitra* Sohl, 1963), Moreidae (*Chilenopsis* Bandel & Stinnesbeck, 2000, *Morea* Conrad, 1860, *Napulus* Stephenson,1941, *Pyropsis* Conrad,1860), Muricidae (*Paramorea* Wade,1917, *Sohliina* Özdikmen, 2013, *"Trigonostoma"* Blainville, 1827), Olividae (*Ancilla* Lamarck, 1799, *Tanimasanoria* Kase, 1992), Perissityidae (*Antarctissitys* Stilwell & Zinsmeister, 2003, *Heteroterma* Gabb,1869, *Murphitys* Popenoe & Saul,1987, *Nekewis* Stewart, 1927, *Nipponitys* Kase, 1990, *Perissitys* Stewart 1927, *Pseudocymia* Popenoe & Saul, 1987, *Pseudoperissitys* Nagao & Otatume, 1938), Pholidotomidae (*Astandes* Wade, 1917, *Pyrifusus* Conrad, 1858), Sarganidae (*Hippocampoides* Wade, 1916, *Pseudecphora* Bandel & Dockery, 2001, *Rapopsis* Saul, 1988, *Sargana* Stephenson, 1923, *Schizobasis* Wade,1916), Vasidae (*Fimbrivasum* Squires & Saul, 2001, *Holzapfelia* Cossmann, 1901, *Lupira* Stephenson, 1941), Turridae (*Amuletum* Stephenson, 1941, *Beisselia* Holzapfel, 1889, *Beretra* Stephenson, 1941, *Eopleurotoma* Cossmann, 1889, *Fulgerca* Stephenson, 1941, *Fusimilis* Stephenson, 1941, *Graphidula* Stephenson, 1941, *Lomirosa* Stephenson, 1941, *Lutema* Stephenson, 1941, *Protogemmula* Oyama, 1966, *Remnita* Stephenson, 1941, *Struthiolariopsis* Wilckens, 1904), Volutidae (*Ascensovoluta* Pchelintsev, 1953, *Drilluta* Wade, 1916, *Eovolutilithes* Hacobjan, 1976, *Liomelon* Dall, 1907, *Liopeplum* Dall, 1890, *Longoconcha* Stephenson, 1941, *Lyria* Gray, 1847, *Misricymbiola* Bandel, 2003, *Misrimelo* Bandel, 2003, *Misriplicoliva* Bandel, 2003, *Myobarbum* Sohl, 1963, *Paleopsephaea* Wade, 1926, *Parafusus* Wade, 1918, *Parvivoluta* Wade, 1926, *Ptychosyca* Gabb, 1877, *Retipirula* Dall, 1907, *Rostellana* Dall, 1907, *Rostellites* Conrad, 1855, *Volutilithes* Swainson, 1831, *Volutocorbis* Dall, 1890, *Volutoderma* Gabb, 1877, *Volutomorpha* Gabb, 1877, *Volutospina* Newton, 1906), family indet. (*Mexfusus* Vermeij, Herbert, Vega & Perilliat, 2004).

CONCLUSIONS

The evolutionary history of Neogastropoda was poorly understood so far, particularly with regard to their origin and initial diversification during the Mesozoic, as relevant records are scattered across numerous taxonomic studies describing Cretaceous gastropod faunas from different regions worldwide. This dissertation addresses these gaps by presenting the first comprehensive synthesis of worldwide data on Cretaceous Neogastropoda, aimed at clarifying their origin and rapid radiation. As a result, a revised phylogenetic scheme is proposed for the relationships among stem and sister groups of higher caenogastropods, including representatives of the extinct families Maturifusidae, Pseudotritoniidae, Purpurinidae, and Colombellinidae, as well as Cretaceous representatives of Neogastropoda, Tonnoidea, and Cypraeidae that persist to the present day. Furthermore, an evaluation of the taxonomic diversity and spatio-temporal distribution of neogastropods throughout the Cretaceous, with particular emphasis on the Early Cretaceous, provides new insights into their earliest occurrences and enables the identification and reconstruction of patterns underlying their initial radiation and subsequent diversification.

The main results can be summarized as follows:

i) The generic composition of three extinct families—Maturifusidae, Pseudotritoniidae, and Purpurinidae—has been revised. It has been demonstrated that they differ from one another in morphological characteristics, especially in the protoconch morphology, which is crucial for the identification of familial-level taxa. Consequently, all three families should be kept as separate clades rather than synonymised in various combinations as previously proposed (Bouchet and Rocroi 2005, Bouchet et al. 2017).

ii) The oldest fossil record of *Purpurina* has been extended from the Early Jurassic to the Late Triassic, following the reinterpretation of *Paleotriton macrostoma* Kittl, 1894 (from the Carnian of the St Cassian Formation) based on protoconch morphology. It is also assumed that in the Jurassic, purpurinids were already divided into two clades. One of them, represented by *Khetella*, lead to Tonnoidea, while the other branch represented by *Fossacerithium*, could lead to Neogastropoda—a hypothesis, to be tested in future studies.

iii) The taxonomic composition of the family Colombellinidae has been revised, and the diagnostic characters of the family and genera included have been emended. The generic composition of the family is restricted to two genera, *Colombellina* d'Orbigny, 1842, and *Zittelia* Gemmellaro, 1869, whereas all other previously assigned genera are excluded. *Colombellina* comprises 19 species, and *Zittelia* includes nine species.

iv) A transition from *Zittelia* (Colombellinidae) to Cypraeoidea is demonstrated by gradual changes in shell morphology in the subsequent species of *Zittelia* ranging from the Oxfordian to the Tithonian–Valanginian. The presence of an infracolumellar groove in some cowries, which

might be a homologue of the abapical sinuosity—a diagnostic character of *Zittelia*—highlights their phylogenetic relations and supports the hypothesis that *Zittelia* is a stem group of the Cypraeoidea. The divergence of cypraeoids from colombellinids may have occurred around the Middle–Late Jurassic.

v) The occurrence of representatives of Colombellinidae exclusively in carbonate deposits indicates that they inhabited carbonate depositional environments, preferring neritic shelf seas, most likely the peri-reefal areas. Their low abundance and high endemism may indicate a carnivorous mode of life. The co-occurrence of *Zittelia* and the earliest cypraeoids 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.

vi) *Wadeina* gen. nov. from the Campanian of Tennessee (USA), with type species previously assigned to Colombellinidae, is re-assigned to Tonnoidea. Shell morphology of *Wadeina* gen. nov., particularly the morphology of aperture, suggests a possible phylogenetic connection between colombellinids and tonnoids, providing new insights into the evolutionary relationships between these groups.

vii) The discovery of the early vasid *Fimbrivasum bulgaricum* sp. nov. demonstrates that major lineages of Neogastropoda diverged earlier than previously thought, already in the early Early Cretaceous. This finding challenges the hypothesis of an initial mid-Cretaceous radiation and highlights a prolonged cryptic phase with low density.

viii) During the Cretaceous neogastropods underwent a significant radiation, culminating in the establishment of all main clades by the end of the period, represented by 20 families and 159 genera. This expansion led to a major restructuring of benthic communities and reflects high ecological plasticity, likely facilitated by diversification primarily at the species level with gradual accumulation of higher taxa.

ix) Fluctuations in generic diversity correlate with major climatic events, with mid-Cretaceous (Albian–Cenomanian) warming favouring diversification, and the Late Cretaceous (Turonian–Santonian) Cretaceous Thermal Maximum and subsequent cooling (Campanian) associated with diversity declines. Although temperature is the most clearly expressed factor, it alone cannot explain neogastropod evolutionary success, which likely resulted from the interaction of multiple biological and ecological factors.

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OŚWIADCZENIE / DECLARATION

Rozprawa pod tytułem “Pochodzenie i wczesna dywersyfikacja wyższych caenogastropodów (neogastropodów, tonnoidów i cypreidów)” składa się z sześciu rozdziałów. Wszystkie rozdziały, oprócz rozdziału VI, są pracami współautorskimi. Kolejne strony niniejszego oświadczenia zawierają szczegółowy opis mojego udziału w poszczególnych rozdziałach.

The dissertation entitled “Origin and early diversification of higher Caenogastropoda (Neogastropoda, Tonnoidea, and Cypraeidae)” consists of six chapters. All chapters, except Chapter VI, are co-authored. The following pages of this statement detail my contribution to each chapter.

Sofia Bakayeva

Rozdział I / Chapter I
An elusive ancestry of Neogastropoda: a potential of Maturifusidae, Pseudotritoniidae, and Purpurinidae as the stem groups

Ten rozdział powstał we współpracy z Alexandrem Nützelem (Ludwig-Maximilians-Universität München, Munich, Germany) i Andrzejem Kaimem (Instytut Paleobiologii Polskiej Akademii Nauk, Warszawa, Polska).

Alexander Nützel udostępnił okazy ze swojej kolekcji oraz fotografie, a także brał udział w redagowaniu tekstu manuskryptu. Andrzej Kaim pozyskał finansowanie oraz zorganizował prace terenowe w Dolomitach (Włochy) i w Tennessee (USA), z których uzyskane materiały stanowiły podstawę niniejszej publikacji, a także brał udział w redagowaniu tekstu manuskryptu. Mój udział polegał na opracowaniu koncepcji pracy i postawieniu hipotezy badawczej, doborze metod badawczych oraz przeprowadzeniu badań, wyselekcjonowaniu wszystkich okazów z grup badanych i ich identyfikacji, wykonaniu i obróbce fotografii, interpretacji wyników oraz sformułowaniu wniosków, a także przygotowaniu manuskryptu wraz z opracowaniem materiału graficznego.

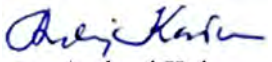
Oświadczam, że mój wkład w przygotowaniu rozdziału wynosi około 75 %.

This chapter was prepared in collaboration with Alexander Nützel (Ludwig-Maximilians-Universität München, Munich, Germany) and Andrzej Kaim (Institute of Paleobiology, Polish Academy of Sciences, Warsaw, Poland).

Alexander Nützel provided specimens from his collection and photographs, and participated in editing the manuscript. Andrzej Kaim secured funding and organized fieldwork in the Dolomites (Italy) and Tennessee (USA), the materials obtained from which formed the basis of this publication, and also participated in editing the manuscript. My contribution included developing the concept of the study and formulating the research hypothesis, selecting research methods and conducting the study, selecting all specimens from the investigated groups and identifying them, taking and processing photographs, interpreting the results and formulating the conclusions, as well as preparing the manuscript and graphic material.

I declare that my contribution to the preparation of this chapter amounts to approximately 75%.

Alexander Nützel



Andrzej Kaim

Rozdział II / Chapter II
At the dawn of higher caenogastropods—the importance of colombellinid gastropods in deciphering the origin of Tonnoidea and Cypraeidae

Ten rozdział powstał we współpracy z Krzysztofem Hryniewiczem (Instytut Paleobiologii Polskiej Akademii Nauk, Warszawa, Polska), Alexandrem Nützelem (Uniwersytet Ludwika i Maksymiliana w Monachium, Monachium, Niemcy), Petrem Skupienem (Politechnika Ostrawska, Ostrawa, Czechy) i Andrzejem Kaimem (Instytut Paleobiologii Polskiej Akademii Nauk, Warszawa, Polska).

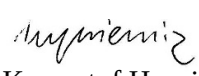
Krzysztof Hryniewicz rozszerzył część paleoekologiczną i brał udział w redagowaniu tekstu manuskryptu. Alexander Nützel udostępnił okazy ze swojej kolekcji oraz fotografie, a także brał udział w redagowaniu tekstu manuskryptu. Petr Skupien udostępnił okazy ze swojej kolekcji wraz ze szczegółową przyporządkowaną stratygrafią i brał udział w redagowaniu tekstu manuskryptu. Andrzej Kaim pozyskał finansowanie wizyty (w której uczestniczył) do kolekcji Petra Skupiena; ponadto udzielał konsultacji i brał udział w redagowaniu tekstu manuskryptu. Mój wkład obejmował opracowanie koncepcji pracy i sformułowanie hipotezy badawczej, dobór metod badawczych oraz przeprowadzenie badań, przegląd całej literatury dotychczasowej i identyfikację taksonów, wykonanie i obróbkę zdjęć, interpretację wyników oraz sformułowanie wniosków, przygotowanie manuskryptu i materiału graficznego, a także pozyskanie finansowania.

Oświadczam, że mój wkład w przygotowaniu rozdziału wynosi około 70 %.

This chapter was prepared in collaboration with Krzysztof Hryniewicz (Institute of Paleobiology, Polish Academy of Sciences, Warsaw, Poland), Alexander Nützel (Ludwig-Maximilians-Universität München, Munich, Germany), Petr Skupien (Technical University of Ostrava, Ostrava, Czechia), and Andrzej Kaim (Institute of Paleobiology, Polish Academy of Sciences, Warsaw, Poland).

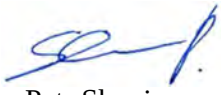
Krzysztof Hryniewicz expanded the paleoecological subsection and participated in editing the manuscript. Alexander Nützel provided specimens from his collection and photographs, and also participated in editing the manuscript. Petr Skupien provided specimens from his collection with detailed stratigraphic assignment and participated in editing the manuscript. Andrzej Kaim obtained funding (and participated in) for a visit to the collection of Petr Skupien; he also provided consultation and participated in editing the manuscript. My contribution included developing the concept of the study and formulating the research hypothesis, selecting research methods and conducting the study, reviewing all relevant literature and identifying the taxa, taking and processing photographs, interpreting the results and formulating conclusions, preparing the manuscript and graphic material, as well as securing funding.

I declare that my contribution to the preparation of this chapter amounts to approximately 70%.

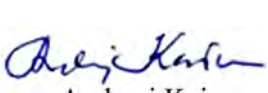


Krzysztof Hryniewicz

Alexander Nützel



Petr Skupien



Andrzej Kaim

Rozdział III / Chapter III
Stem cypraeid gastropods – a revision of the genus *Zittelia* Gemmellaro, 1869

Ten rozdział powstał we współpracy z Caroliną D'Arpa (Uniwersytet w Palermo, Palermo, Włochy), Didierem Berthetem (Muséum des Confluences, Lyon, Francja), Krzysztofem Hryniewiczem (Instytut Paleobiologii Polskiej Akademii Nauk, Warszawa, Polska), Alexandrem Nützelem (Ludwig-Maximilians-Universität München, Monachium, Niemcy) oraz Andrzejem Kaimem (Instytut Paleobiologii Polskiej Akademii Nauk, Warszawa, Polska).

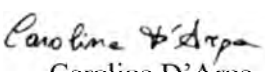
Krzysztof Hryniewicz rozszerzył część paleoekologiczną i brał udział w redagowaniu tekstu manuskryptu. Carolina D'Arpa, Didier Berthet oraz Alexander Nützel udostępnili okazy ze starych kolekcji oraz fotografie i uczestniczyli w redagowaniu tekstu manuskryptu. Andrzej Kaim pozyskał finansowanie wizyty (w której uczestniczył) do kolekcji Petra Skupiena; ponadto udzielał konsultacji i brał udział w redagowaniu tekstu manuskryptu. Mój wkład obejmował opracowanie koncepcji pracy i postawienie hipotezy badawczej, dobór metod badawczych oraz przeprowadzenie badań, identyfikację taksonów, wykonanie i obróbkę zdjęć, interpretację wyników oraz sformułowanie wniosków, przygotowanie manuskryptu i materiału graficznego, a także pozyskanie finansowania.

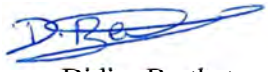
Oświadczam, że mój wkład w przygotowanie tego rozdziału wynosi około 70%.

This chapter was prepared in collaboration with Carolina D'Arpa (University of Palermo, Palermo, Italy), Didier Berthet (Museum of Confluences, Lyon, France), Krzysztof Hryniewicz (Institute of Paleobiology, Polish Academy of Sciences, Warsaw, Poland), Alexander Nützel (Ludwig-Maximilians-Universität München, Munich, Germany), and Andrzej Kaim (Institute of Paleobiology, Polish Academy of Sciences, Warsaw, Poland).

Krzysztof Hryniewicz expanded the paleoecological subsection and participated in editing the manuscript. Carolina D'Arpa, Didier Berthet, and Alexander Nützel provided specimens from old collections and photographs, and participated in editing the manuscript. Andrzej Kaim obtained funding (and participated in) for a visit to the collection of Petr Skupien; he also provided consultation and participated in editing the manuscript. My contribution included developing the concept of the study and formulating the research hypothesis, selecting research methods and conducting the study, identifying the taxa, taking and processing photographs, interpreting the results and formulating conclusions, preparing the manuscript and graphic material, as well as securing funding.

I declare that my contribution to the preparation of this chapter amounts to approximately 70%.


Carolina D'Arpa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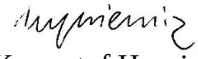
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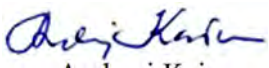
Alexander Nützel


Andrzej Kaim

Rozdział IV / Chapter IV
The earliest cowries: the origin of cypraeoid gastropods

Ten rozdział powstał we współpracy z Alexandrem Nützelem (Ludwig-Maximilians-Universität München, Monachium, Niemcy) we współpracy z Simonem Schneiderem (CASP, Cambridge, Wielka Brytania) i Andrzejem Kaimem (Instytut Paleobiologii Polskiej Akademii Nauk, Warszawa, Polska).

Mój wkład obejmował napisanie rozdziału 'Evolutionary Relationships', wyróżnienie cech diagnostycznych oraz przygotowanie rysunku graficznego i tabeli porównawczej taksonów.

Oświadczam, że mój wkład w przygotowanie tego rozdziału wynosi około 20%.

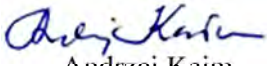
This chapter was prepared in collaboration with Alexander Nützel (Ludwig-Maximilians-Universität München, Munich, Germany) in collaboration with Simon Schneider (CASP, Cambridge, UK), and Andrzej Kaim (Institute of Paleobiology, Polish Academy of Sciences, Warsaw, Poland).

My contribution included writing the 'Evolutionary Relationships' section, identifying diagnostic characters, and preparing the graphic figure and comparison table of the taxa.

I declare that my contribution to the preparation of this chapter amounts to approximately 20%.

Alexander Nützel

Simon Schneider



Andrzej Kaim

Rozdział V / Chapter V
The earliest (Early Cretaceous) record of a turbinelloid gastropod and its importance for understanding the diversification of Neogastropoda

Ten rozdział powstał we współpracy z Gregorym S. Herbertem (University of South Florida, Tampa, USA), Krzysztofem Hryniewiczem oraz Andrzejem Kaimem (obaj z Instytutu Paleobiologii Polskiej Akademii Nauk, Warszawa, Polska).

Gregory S. Herbert podejmował decyzje taksonomiczne oraz przedstawił merytoryczne uwagi, które przyczyniły się do podniesienia wartości naukowej manuskryptu. Krzysztof Hryniewicz wniósł specjalistyczne uwagi, które zwiększyły klarowność i jakość interpretacji wyników. Andrzej Kaim uczestniczył w opracowaniu planu badawczego i koncepcji pracy, zapewnił dostęp do materiału, sprawował nadzór nad realizacją projektu oraz pozyskał finansowanie. Wszyscy współautorzy zapoznali się z ostateczną wersją manuskryptu i zaakceptowali ją. Mój wkład obejmował zaprojektowanie badań i sformułowanie hipotezy badawczej, dobór oraz zastosowanie metodologii, identyfikację taksonów, wykonanie i obróbkę fotografii, analizę i interpretację danych, sformułowanie wniosków, przygotowanie tekstu manuskryptu oraz ilustracji graficznych, a także pozyskanie finansowania.

Oświadczam, że mój wkład w przygotowanie tego rozdziału wynosi około 70%.

This chapter was prepared in collaboration with Gregory S. Herbert (University of South Florida, Tampa, USA), Krzysztof Hryniewicz and Andrzej Kaim (both from Institute of Paleobiology, Polish Academy of Sciences, Warsaw, Poland).

Gregory S. Herbert made taxonomic decisions and offered substantive comments that improved the scientific content of the manuscript. Krzysztof Hryniewicz contributed expert remarks that enhanced the clarity and interpretation of the results. Kaim participated in establishing the research plan and concept, provided access to the material, and supervised the project and secured financial support. All co-authors reviewed the manuscript and accepted its final version. My contribution comprised designing the study and formulating the research hypothesis, selecting and applying the methodological approach, identifying the taxa, taking and processing photographs, analysing and interpreting the data, drawing conclusions, preparing the manuscript text and graphical illustrations, as well as securing funding.

I declare that my contribution to the preparation of this chapter amounts to approximately 70%.

Gregory S. Herbert | Krzysztof Hryniewicz | Andrzej Kaim