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The Revolution of Small Snails and the Early Modern Evolutionary Fauna

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Abstract: The species richness of major clades and functional groups among gastropods, a key element of Modern Evolutionary Fauna (MEF), underlines the dominant role of carnivorous Caenogastropoda and Heterobranchia, including small ectoparasites and micrograzers, at modern tropical latitudes. Neogastropoda are active predators that radiated in the Cretaceous, but their early Mesozoic MEF roots are poorly understood. The escalation hypothesis emphasises prey–predator interactions as gastropods' macroevolutionary drivers during the Mesozoic Marine Revolution but overlooks the significance of highly diversified smaller forms. The tropical fossil record of the Permian–Triassic mass extinction (PTME) and the Triassic rise of MEF suggests that non-carnivorous species dominated gastropod fauna immediately before and after the PTME: Permian micrograzers mainly fed on sponges and waned during the rise of MEF, while ectoparasites and micrograzing carnivores diversified starting from the Ladinian period. Patterns of gastropod species richness, size, and form, the fossil record of reef builders and other benthic invertebrates, and an analysis of stem neogastropods jointly suggest a Middle Triassic revolution of small-sized gastropods, triggered by the emergence of scleractinian corals and the diversification of echinoderms. Habitat heterogeneity and new food sources offered niches for the early radiation of modern gastropod clades.

Keywords: Gastropoda; tropical ecosystems; microcarnivory; Permian–Triassic mass extinction; evolutionary radiation

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1. Introduction

Times of crisis are times of opportunity, as eminently expressed by the modern marine fauna originating in the aftermath of the heaviest biotic crisis in animal history, the Permian–Triassic mass extinction (PTME) [1,2]. About 251 million years ago, when 81% of marine genera were wiped out [3], taxa were selected that would newly fill the ecospace, and a functional shift from the Palaeozoic to Modern Evolutionary Fauna (MEF) took place [4–7]. The class Gastropoda features among the clades that were hit by the PTME, survived the crisis, and spread to become one of the most taxonomically diverse clades of MEF [8–10]. At a salient interval of the Mesozoic, mainly after the Jurassic, the macroevolutionary trajectory of gastropods was driven by predator–prey interactions. The hypothesis of escalation emphasises the role of skeleton-destroying predators, such as fishes and crustaceans, in promoting shell sturdiness and size. This global arms-race, peaking in the Late Cretaceous and Cenozoic, defines the Mesozoic Marine Revolution [11]. What exactly happened in the interval between the PTME and the advent of modern sturdy and large marine gastropods? What key modern innovations can be found in the Triassic record?

Experts estimate that gastropods account for 15–17% of the global marine species diversity [12–14], but see Refs. [15–17], an expression of their extraordinary diversity in morphology, ecology, and developmental modes [18]. Among the two most speciose marine groups of MEF, the number of newly described gastropod species in the 2018–2022 period exceeds that of crustaceans (28% against 21%) [19], a measure of the rising interest in their study. Similarly to what happens with insects in continental settings [17], gastropods are good indicators of marine biodiversity in general [20,21] and surrogates of key tropical ecosystems such as reefs [22–24] and mangroves [25,26]. Similarly to insects, the total number of gastropod species living in tropical regions is hard to compute, given that many are of a small size and go undetected without a special sampling design [27–32].

Unlike insects [33], gastropods have the most taxonomically diverse fossil record among all classes of Phanerozoic animals (generic level, together with articulate brachiopods) [34], providing researchers with the opportunity to explore what innovations structured the geologic history of MEF [8,11,35]. The adaptations of extinct taxa can be inferred with difficulty [36], but analogical thinking based on the study of shell morphology and size allows researchers to make hypotheses. Within the framework of the Mesozoic Marine Revolution, gastropod shells of medium and large sizes have been preferentially tackled, considering their exoskeletons to have been selected either to subdue prey or as a defence against predators [11,37–40]. However, a large number of modern species are <5 mm [28–32], a character which qualifies also Permian and Triassic assemblages [41]. The challenge to functionally interpret Triassic small-sized gastropods dates back to the nineteenth century, when the idea that tiny shells represent dwarf forms was rejected for the first time (Carnian, San Cassiano Fm. [42]; Ladinian, Sciliar Fm. [43], p. 99), continuing in modern times [44,45], when a relationship with the Mesozoic Marine Revolution was first considered [41].

In this paper, I first look at the taxonomic diversity of modern gastropod clades across a latitudinal and longitudinal gradient, seeking for major patterns of taxonomic and ecological distribution, and then at their fossil record, in search for a connection between the aftermath of the PTME and the Jurassic–Cretaceous rise of modern gastropods, taking shell size and form as a key to past adaptations. Considering that the tropics yield several-fold more species than surrounding areas [46], I explore the Permian and Triassic to see what part of the adaptive landscape was occupied by gastropods at low latitudes before and after the PTME. I finally make hypotheses on the macroevolutionary drivers behind the first radiation of MEF. Following a recent lead in tackling hypothetical adaptations of small-sized snails [41], I propose functional roles within the full size range of Permian and Triassic forms and look at other invertebrates of MEF in search for potential macroecological interactions.

2. Materials and Methods

2.1. Systematics

The data used for this study were taken from the literature and arranged according to the current consensus classification, recognizing six subclasses of gastropods: Patellogastropoda, Vetigastropoda, Neomphaliones, Neritimorpha, Caenogastropoda, and Heterobranchia [47,48] (the last comprising both marine and terrestrial forms). Here, I adopted the proposal to group Vetigastropoda *s.s.* and Neomphaliones within Vetigastropoda *s.l.* [18] (hereafter, Vetigastropoda). Patellogastropoda are the sister lineage to all others, divided into two main clades: (1) Vetigastropoda and (2) Neritimorpha + (Caenogastropoda + Heterobranchia) (together forming Apogastropoda) [18,48]. For the largely extinct Pleurotomariida, I followed a recent subdivision based on a fossilised birth–death model [10].

I used available checklists to count the number of species (S, or species richness) and thereby measure the relative importance of major groups within a given area. Subdivisions included subclasses Patellogastropoda, Vetigastropoda, and Neritimorpha, and eight subgroups of the remaining two subclasses. Four of them included Littorinimorpha, Triphoroidea, Epitonioidea, and Neogastropoda, consistently taken from current consensus classification of Caenogastropoda [47,49,50]. Triphoroidea includes families Triphoridae and Cerithiopsidae and is monophyletic [51,52]. Epitonioidea is also monophyletic and, like the former, is of uncertain position within the subclass [51–53]. Neogastropoda are considered monophyletic and the most derived lineage among Caenogastropoda, whereas the monophyly of Littorinimorpha is uncertain [54], which was, however, irrelevant to the present analysis. I considered an informal group of "Lower Caenogastropoda", which included all families not belonging to the previously mentioned clades. The Heterobranchia were hereby divided in three subgroups: "Lower Heterobranchia" (including Mesopleura), Shelled Heterobranchia (Euthyneura), and Nudipleura (Nudibranchia and Pleurobranchidia, or sea slugs) [55,56].

Permian (Upper Cisuralian–Lopingian) and Triassic subgroups include extinct and extant clades. Extinct clades were grouped in the category "basal gastropods" (Bellerophontida, Euomphaloidea, Raphistomatidae, Trochonematoidea, and Loxonematoidea) [47]. Among modern Heterobranchia, Nudipleura lack a fossil record (and, in any case, probably originated after the Triassic) [55,57].

2.2. Species Distribution Across Latitudinal and Longitudinal Gradients

The relative importance of each taxonomic group was measured by counting the number of species in nine marine areas using updated checklists (Supplementary Materials, Table S1). Recent checklists were preferred to online global distribution datasets like OBIS [58] because the checklists reported a larger number of species, particularly small gastropods. Checklist (1) includes all verified species from Atlantic coastal and deep-sea waters under European jurisdiction and the Mediterranean and Black Seas [59]. The checklists for smaller European regions include (2) Scandinavian waters [60], seas under Spanish jurisdiction [61] (small corrections were applied following [62]), split into (3) Atlantic (including the Canaries) and (4) Mediterranean waters, and (5) the seas surrounding Italy, also within the Mediterranean [63]. European subregions form a latitudinal gradient, from the polar–cold temperate Atlantic to the warm temperate Mediterranean setting and the subtropical waters surrounding the Canary Islands. Four checklists allowed us to measure gastropod species richness in tropical settings, aligned to form a longitudinal, E-W gradient: (6) Thailand, including waters of the narrow Andaman coast and its rapidly deepening seafloor, and the shallow waters of the Gulf of Thailand [24]; (7) waters of Kimberley, in Western Australia [32,64]; (8) a relatively small area facing Koumac, in New Caledonia [28]; and (9) French Polynesia [65] (Figure 1A).

Checklist (1) pools data on species recorded over a very vast area (10^7 km^2 of sea bottom); Checklists 2–6 and 9 are from areas of intermediate extent (10^5 km^2 of seafloor); Checklists 7–8 are from comparably very small areas (10^2 km^2 of seafloor). The sampling effort behind the nine checklists varies too: the European, Thai, and Polynesian checklists are the outcome of a long history of taxonomic research; the diversity present in Kimberly waters was measured from both historical sources and a recent massive fieldwork study; and Koumac molluscs were listed following a single campaign, with an effort amounting to 400 day-persons [28] (gastropods from New Caledonia have, however, been studied since the 19th century, e.g., [66]).

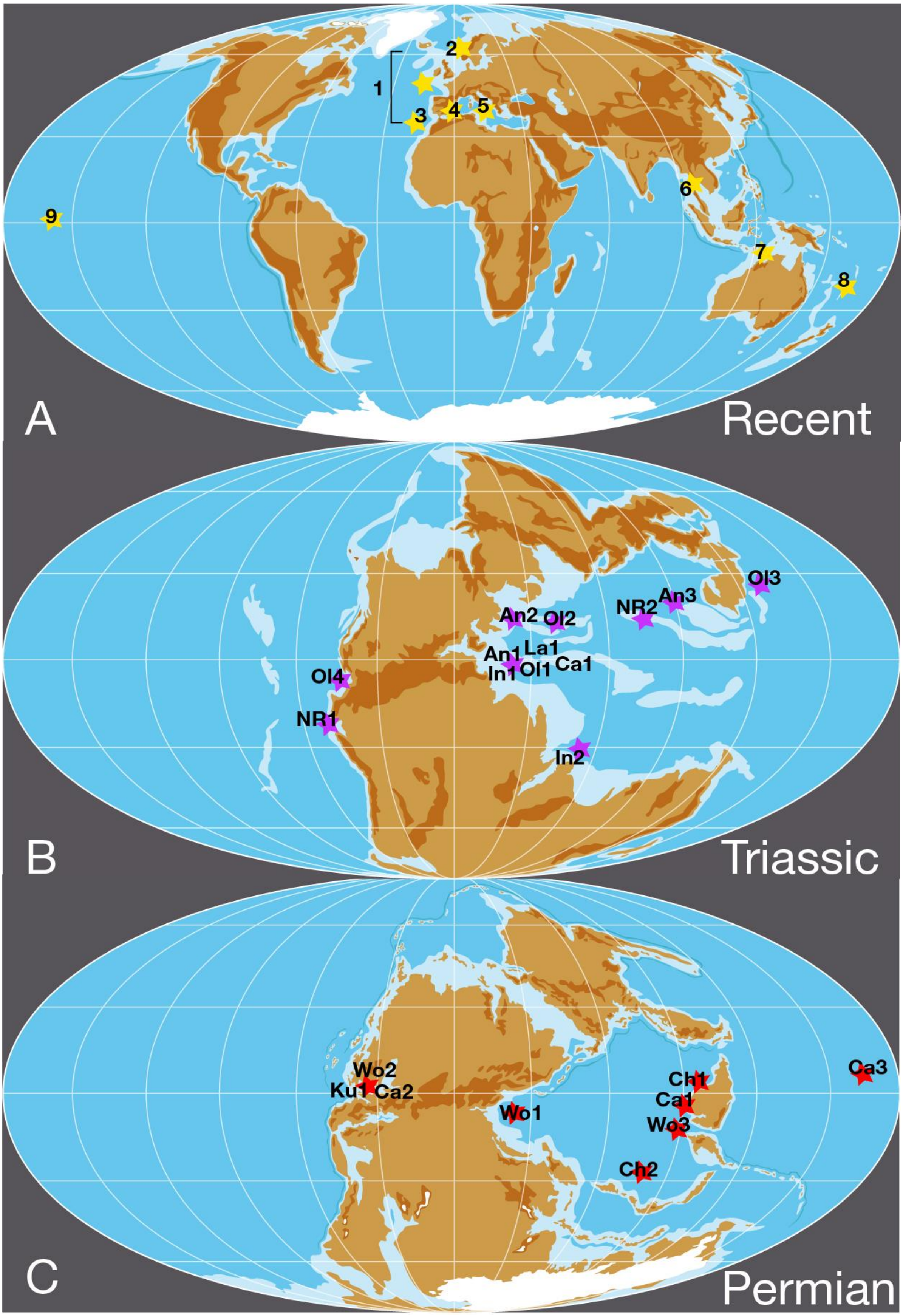

Figure 1. Regions sampled for marine gastropod diversity. (**A**) Geographical relationships between representative modern faunas. 1: Europe; 2: Scandinavia; 3: Atlantic (Spanish waters); 4: Mediterranean (Spanish waters); 5: Mediterranean (Italian waters); 6: Thailand; 7: Kimberley; 8: Koumac;

9: Polynesia. (**B**) Palaeogeographical relationships between representative Triassic tropical faunas. In, Induan, with (1) S Europe and (2) Iran; Ol, Olenekian, with (1) S Europe, (2) W Europe, (3) Russia, and (4) the USA; An, Anisian, with (1) S Europe, (2) E Europe, and (3) China; Ladinian, with (1) S Europe; Carnian, with (1) S Europe; and NR, Norian/Rhaetian, with (1) Peru and (2) NE Iran. (**C**) Palaeogeographical relationships between representative Permian tropical faunas. Ku, Kungurian, with (1) the USA; Wo, Wordian, with (1) Italy, (2) the USA, and (3) Thailand; Ca, Capitanian, with (1) Cambodia, (2) the USA, and (3) Japan; and Ch, Changhsingian, with (1) China and (2) Pakistan.

All checklists were updated following modern taxonomies [50], and the results were confronted considering the latitudinal and longitudinal gradients, the latter connecting Thai, Western Australian, and Polynesian waters neighbouring the Coral Triangle (or Indo-Australian Archipelago), to which belongs Koumac, in New Caledonia. The Coral Triangle is characterised by the highest known marine species richness and endemicity for molluscs [46]; see Ref. [67] for further information.

2.3. Past Diversity

To measure the relative importance of Permian–Triassic clades, I downloaded from the Paleobiology Database [68] data relative to some of the richest fossil assemblages from palaeotropical settings of Paleotethys and Panthalassa (Figure 1B,C) and checked them against modern systematics [50] (Supplementary Materials, Table S2). These were subdivided into the following time bins: Kungurian (Cisuralian); Wordian; Capitanian (Guadalupian): Changhsingian (Lopingian); Induan; Olenekian (Early Triassic); Anisian; Ladinian (Middle Triassic); Carnian; and Norian–Rhaetian (Late Triassic). To correct for sampling intensity relative to each group of collections, values of S were interpreted in light of the number of formations and localities involved [45].

2.4. Limitations

The use of checklists to compute modern marine diversity may pose general problems of taxonomic inflation attributed by synonymies, emendations, and alternative representations [69] (see [62] for a pertinent example on gastropods). This influence was hereby mitigated by the recent revision of expert European taxonomists, a community comprising the largest number of WoRMS editors [19] and including researchers responsible for seven out of the nine checklists. The remaining two are the work of Australian taxonomists, also particularly active in documenting gastropod marine biodiversity and ensuring good quality and an even taxonomic expertise.

The measure of Permian and Triassic species richness poses limitations due to taphonomy, with small-sized species preferentially lost [41,70]. For the stratigraphic distribution of many Triassic assemblages, I followed Ref. [45] and assigned species of the Sinbad Fm to the Induan period, although some authors have attributed them to the Olenekian period [70].

Groups of fossil collections are generally only linked to time bins to obtain a time series and, since stages have different durations, some groups may represent longer intervals than others. The focus on the relative frequency of subgroups within each group overcomes this limitation in the current work.

2.5. Functional Groups

Each modern family was assigned to one of seven ecological categories: (1) macroherbivory; (2) suspension feeding; (3) detritivory; (4) suctorial parasitism; (5) grazing carnivory; (6) predation on preys of limited mobility; and (7) active predation or scavenging on larger preys (Supplementary Materials, Table S1). Organisms belonging to the first three categories mainly eat plants and microorganisms, whereas the remaining four directly or indirectly depend on other metazoans for food. Categories 5–7 involve the ability to move from prey to prey, while 6–7 involve the death of the prey. All suctorial ectoparasites (Category 4) are of small size (<5 mm), lack a radula, and have long modified proboscides used for piercing and sucking host tissue [41,71]. Hosts are their habitat and often show a degree of specificity to the parasite [72]. The assignment of a family to a given ecological category is often arbitrary, as feeding is seldom observed directly [41] and species of the same clade may evolve new feeding modes [73]. The relative representation of functional groups was weighted in terms of S.

Adaptations of Permian and Triassic gastropods were hypothesised through the following: (1) family-level, taxonomic uniformitarian principles, considering the timing of divergence of major lineages and the fossil record of extant clades (whereby the ecospace occupied by extinct families could be reasonably hypothesised from the phylogenetically closest clade among extant ones); (2) innovations recognised in the record of body fossils, including reinforced external sculpture to resist predators [11,37,74], a small size to hide, and expanded apertures to graze; and (3) the ichnological record of biotic interactions to recognise drilling predation [75,76]. Each of the above criteria posed limitations [41,77,78] but jointly helped me assign fossil species to a functional group (Supplementary Materials, Table S2).

Finally, a large dataset was assembled to include the maximum dimension ever recorded for a significant number of Triassic and modern species representing all major gastropod family- and supra-family-level taxa. The type species of type genera were particularly targeted for a meaningful and more even representation. To make consistent hypotheses on the major adaptive peaks conquered by gastropods during their Triassic radiation, size distributions were quantitatively assessed across five intervals representing the Triassic. Triassic and modern gastropod sizes were compared across both major taxa and functional groups (Supplementary Materials, Table S3).

3. Results

3.1. Adaptation and Stratigraphic Record of Modern Clades

3.1.1. Non-Carnivore Gastropods

Large parts of vetigastropods, neritimorphs, lower caenogastropods, and part of littorinimorphs eat filamentous algae, protists, and other microorganisms by scraping such “detritus” from the substratum surface, and it is assumed that the primitive molluscan diet was microphagous, with food particles small enough for intracellular digestion [79,80]. Among the caenogastropods, the few suspension feeders similarly acquire mainly unicellular organisms and detrital particles from the water column, and the few deposit feeders take in particulate food, including organic detritus, bacteria, fungi, and protists. Most non-carnivore snails can thus be grouped under the same trophic category of “unselective microphagous feeding”, which was probably also the plesiomorphic mode of feeding of the phylum Mollusca as a whole (Figure 2).

Similarly to the range of occupied habitats (from intertidal to deep-sea chemosynthesis-based ecosystems), living microphagous snails have a wide range of sizes and forms [81–85]. Microphagous species with shells <5 mm are found among vetigastropods (Lepetellida, Fissurellida, and Trochida), nerithimorphs (Cycloneritida), “Lower Caenogastropoda” (Cerithioidea), and Littorinimorpha (Truncatelloidea and Rissooidea). To the latter clade belongs Rissoidae, one of the most species-rich gastropod families, living from shallow to deep-sea environments [86,87].

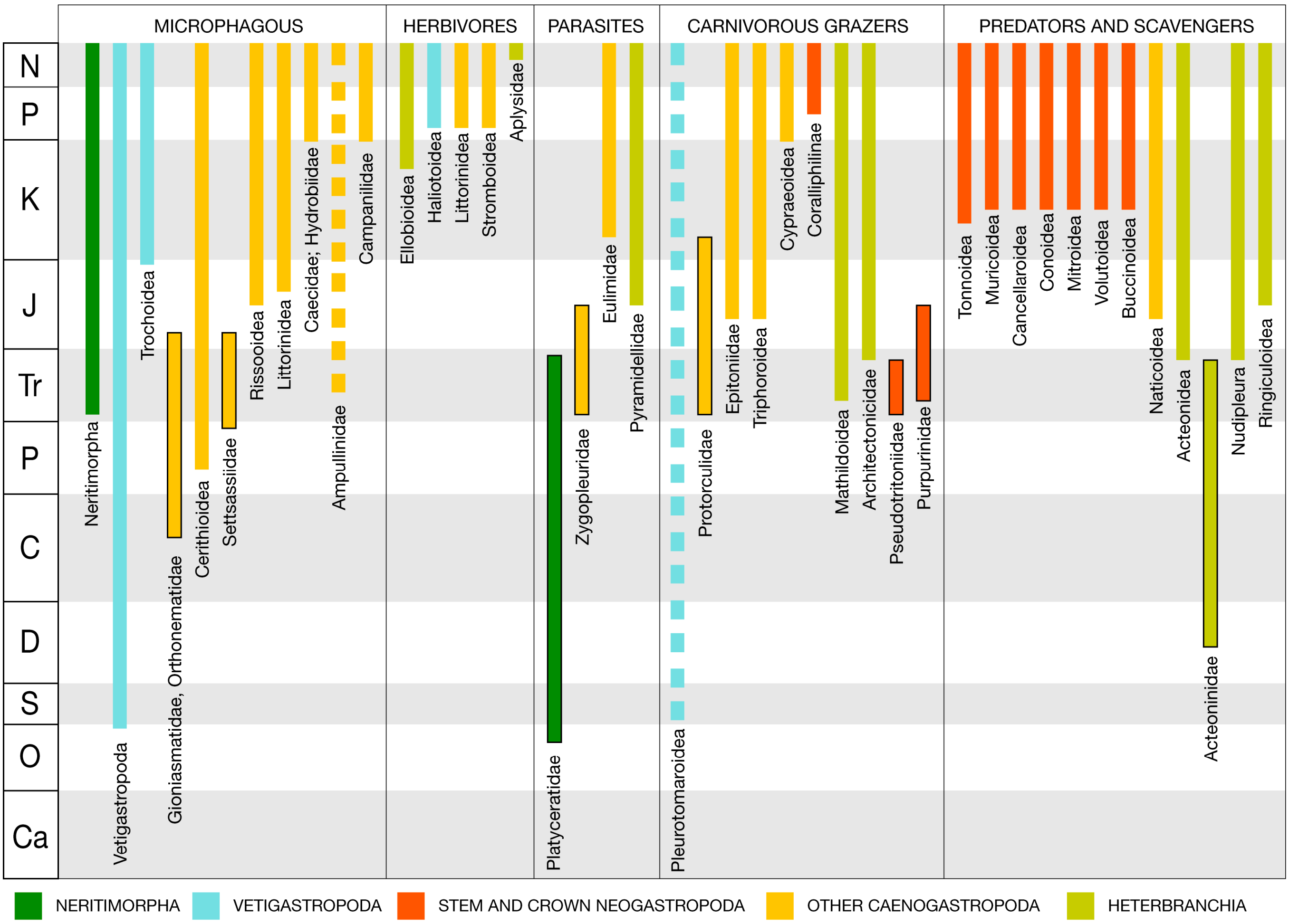

Figure 2. Stratigraphic distribution of the most important gastropod clades, divided by functional group. Thick lines are used for extinct clades (putative feeding type based on analogy).

True herbivores, feeding through extracellular digestion and enzymatic activity, very effective in breaking down the tissue of larger algae and other plants, are found in all major clades: vetigastropods (Haliotidae and Trochidae), patellogastropods (Lottiidae and Patellidae), lower caenogastropods (Ampullinidae), littorinimorphs (Littorinidae and Strombidae), and heterobranchs (Aplysiidae). Similarly to carnivorous snails and differently from most microphagous species, they feed discontinuously [80] and are often large.

Neritimorpha date back to the Late Triassic [88–90], but extinct families are more numerous than extant ones [50], and the clade may be as old as the Devonian period [91] (Figure 2). Shells of Triassic Naticopsoidea are up to 105 mm in size [92–94], while those of Neritopsoidea are up to 40 mm [91]. Modern Neritimorpha spread during the Cretaceous, but large marine forms are now confined to inhospitable habitats such as intertidal splash zones or otherwise occupy small crevices in the deep sea [88–90,95].

The fossil record of true limpets (=Patellogastropoda) reached back to the Late Triassic [36,81]. The most diverse vetigastropod clade, the Trochoidea, diverged during the Cretaceous [96].

The Campaniloidea, a clade presently represented only by *Campanile* (Campanilidae), *Cernina* (Ampullinidae), and *Plesiotrochus* (Plesiotrochidae) [97,98], was species-rich during the Palaeogene and Early Neogene, with some of the largest shells among the various fossils (Campanilidae, >900 mm [99]; Ampullinidae, >300 mm [100]), but has been rapidly declining in diversity ever since [101].

Among modern successful caenogastropods, the oldest fossil cerithioideans (“Lower Caenogastropoda”) are Permian, high-spired, and rather small, ranging 2–16 mm in size (e.g., *Protostylus* [102,103]). All modern cerithioidean groups, in any case, spread after the Jurassic [102–106].

The oldest fossil record of microphagous littorinimorphs dates back to the Middle Jurassic (Rissoidae [107,108]) or is even more recent (e.g., Caecidae, in the Eocene [109]; Hydrobiidae, in the Palaeocene [110]).

The fossil record of almost all modern macroherbivorous gastropod clades indicates their late appearance during the Cenozoic and radiation during the Miocene (Haliotidae [111]; Littorinidae [112]; and Strombidae [113]). The Ampullinidae are a possible exception and, if all fossil ampullinids had the same trophic strategy of the only living survivor (*Cernina*, grazer on macroalgae [114]), something which is far from proven [115,116], the oldest accepted records would date back to the Late Triassic–Early Jurassic [117,118].

3.1.2. Suctorial Ectoparasites

Parasitic snails have existed since the Palaeozoic among the Neritimorpha [119], but today, they are encountered only among higher gastropods, in the form of high-spired specimens < 5 mm in size, with some even as small as <1 mm [32,41]. They live on the host, usually a freely moving animal (echinoderms, crustaceans, or other molluscs), cause harm to it without causing its death [120], and show grades of specialisation to host associations, and their niche cannot be quantified in the same manner as free-living snails [121]. High-spired ectoparasites include the two most speciose families—Eulimidae (Littorinimorpha) and Pyramidellidae (Heterobranchia) [71,72]—but other shell shapes are possible (e.g., Caledoniellidae [73]).

Of the two extant families containing only ectoparasites, the Pyramidellidae (Heterobranchia) were first recorded in the Middle Jurassic [108] (see [41] for a possibly more recent origin), while the Eulimidae (Littorinimorpha) were first found in the Late Cretaceous [122,123]. Convergence in size and form has been noted with Triassic Zygopleuridae, Permian Pseudozygopleuridae, and Devonian Donalidinidae [41] (Figure 2).

3.1.3. Grazing Carnivores

Grazing carnivores thrive on corals and other encrusting sessile metazoans and can be kept distinct from ectoparasites [41] (see [124,125]). Better-studied corallivorous snails belong to Epitoniidae, Ovulidae (Littorinimorpha), Coralliophilinae (Muricidae, Neogastropoda), Mathilididae, and Architectonicidae (Lower Heterobranchia). Corals provide snails with food, protection against predators, and shelter from turbulence, with some species appearing to be highly host-specific [125–130].

The environmental distribution of coralliophilinae neogastropods broadly coincides with that of stony corals, ranging from shallow water tropical reef [128,131] to deep-sea coral banks [132–134]. Littorinimorpha (Epitoniidae and Ovulidae) and Lower Heterobranchia (Mathilididae and Architectonicidae) are also associated with scleractinian corals and other anthozoans within a variety of shallow- and deep-sea environments [126,135–138].

Grazing carnivores that feed on sponges are found in shallow- to deep-sea settings (Pleurotomariida and some Seguenzoidea among vetigastropods [138,139]; Cypraeidae and Triphoroidea among caenogastropods [41]). Cowries associated with sponges in coral reefs are smaller than their deep-sea counterparts [140]. Pleurotomariodeans may also feed on soft cnidarians [141]. The shell size of grazing carnivores is larger than that of ectoparasites but is usually <25 mm in derived clades (Epitoniidae [142]; Coralliophilinae [143,144]; and Mathildidae and Architectonicidae [145]), except for species adapted to deep-water habitats [140,141].

The oldest fossils of a clade tentatively associated with spongivorous species are Late Cambrian Pleurotomariida [10,139], but most of the oldest records of grazing carnivores among extant families date back to the Mesozoic (Figure 2). The oldest Epitoniidae were recorded in the Late Cretaceous but could have been as old as the Middle Jurassic [41]. Consistently, in phylogenetic analyses, Epitonioidea are found among the earliest diverging branches within Caenogastropoda [54]; see [146].

Triphoroidea, currently reported to be sponge feeders, were already diversified in the early Palaeocene in association with cold-water coral ecosystems [147]. The fossil record suggests that this clade may have origins dating back as far as the Middle Jurassic [41].

Cypraeoidea (Littorinimorpha), including corallivorous Ovulidae and spongivorous or macroherbivore Cypraeidae, are a sister taxon to the clade Tonnoidea + Neogastropoda (morphological analysis [98,148]; see [54,97]), and the oldest fossil cowries are Eocene [140,149].

Coralliophilinae belong to the diverse carnivorous family Muricidae (Neogastropoda), and both their time-calibrated phylogeny and the fossil record indicate a Middle Eocene origin. From shallow-water ancestors associated with zooxanthellate corals, they spread offshore, down to abyssal, cryptic habitats associated with other cnidarians [132,150–152] (Figure 2).

3.1.4. Active Predators and Scavengers

Modern active predators and scavengers belong to different clades, ranging from moon snails and cowries (Naticidae and Cypraidae, Littorinimorpha) to purple die and auger snails (Muricidae and Terebridae, Neogastropoda) and Scaphandridae (Heterobranchia) [76]. Many share relatively large and heavy adult shells [11,153], most >10 mm in size [154–156], although exceptions occur, with slugs that lack a shell altogether (Nudipleura) or snails with shells smaller than <5 mm (e.g., among neogastropods, some members of Conoidea [32]; bubble snails, or Ringiculoidea among euthyneuran heterobranchia [157]). Many have planktotrophic veliger larvae and hatchling occurs at a size larger than in non-predators [158].

Neogastropoda are the most noteworthy and best-studied clade [159] and the only group with embryonic shells >1 mm [150]. Neogastropods display a vast array of feeding strategies connected to specialised glands and other anatomical features used to subdue their prey [160], corresponding to a vast array of shell features and ethologies [161,162]. Predators among snails often share hard morphologies with non-predators, and, as such, these were probably selected to avoid being preyed upon [11]. These include backward-pointing tubercles or spines [81], smooth shells enveloped by soft tissue [163], terminal varices [164], the remodelling of previously formed parts of the shell [165], and stabilising structures [52]. Other shell features, however, like apertures specialised for drilling hard-shelled prey, were selected to facilitate predation [166].

Caenogastropods and heterobranchs share a common ancestor that possibly lived during the Permian [57], but the medium-to-large size presently associated with most members of this guild specifically evolved after the Triassic [35]. The Mesozoic record also indicates an increase in predator–prey size ratios, reflecting increases in prey abundance, prey nutrient content, and predation among predators [40].

Among caenogastropods, carnivorous Littorinimorpha and Neogastropoda explosively diversified during the Cretaceous, largely in relation to new feeding strategies [11,80,159,160,167,168]. The oldest undisputed fossil tonnoidean dates back to the (Late) Early Cretaceous [148], and the stem from which modern Tonnoidea + Neogastropoda diverged was very likely the extinct family Purpurinidae, ranging from the Middle Triassic (Ladinian) to the Late Cretaceous [169] (Figure 2).

3.2. Diversity Trends

3.2.1. Modern Geographic Gradients

Species richness in the studied checklists (S) ranges 2494–1074. Considering only areas of a similar extent (Figure 3A), the comparison indicates that the diversity almost doubles going from the Spanish Atlantic (S = 1361) to the tropical waters of Thailand (S = 2302), a trend expected from previous gastropod studies [22]. This trend continues into the Indo-Australian Archipelago, with the small area explored during the Koumac survey yielding about the same richness (S = 2226) as the entirety of Thailand. The species richness of French Polynesia, in the tropics, is comparable to that found in Thai waters (Figure 3A,B), whereas the one recorded in Kimberley is less than a half that of Koumac, despite being almost the same area, suggesting the existence of a longitudinal trend moving in and out of the Coral Triangle.

Looking at the distribution of species richness among subgroups, basal subclasses Patellogastropoda and Neritimorpha contribute little to total gastropod diversity and are inversely related, with the former restricted to temperate latitudes and the latter to the tropics (Figure 3C). Vetigastropoda score around 10% in all areas. The "Lower Caenogastropoda" score 3.5–7.5% in tropical regions but recorded less than 2% diversity in temperate and polar waters. Epitonioidea's score is 1.5–4%, whereas Littorinimorpha record high diversities in all regions (18–25%), although neither shows clear latitudinal trends. This is not the case for Neogastropoda, scoring always less than 20% at high latitudes but reaching 32–47% in the tropics. The relative S measured for Triphoroidea is 1.5–3.5% in temperate regions, increasing to 6–12% at low latitudes, with the exception of Thailand (2.7%). Heterobranchia show a trend opposite to that of Neogastropoda and Triphoroidea, being more diversified in temperate and polar waters (38–46%) than in tropical ones (13–28%). Among Heterobranchia, nudipleuran sea slugs are particularly species-rich in Scandinavia (about 20%) compared to regions within, or close to, the Coral Triangle (3–7%, Figure 3C).

3.2.2. Distribution of Functional Groups

The higher richness of Neogatropoda and Triphoroidea, accompanied by a small representation of Heterobranchia and Epitonioidea, indicates a larger influence of carnivore species in the tropics, amounting to 63–78% of the total richness of the present analysis (Figure 3D). Active and relatively larger predators are particularly diversified (36–50%, as opposed to 18–24% in temperate and polar waters). Ectoparasites and grazing carnivores account for 21–40% of the total diversity in all studied checklists.

Ectoparasites and grazing carnivores show lower richness in Kimberley with respect to the other three tropical regions (21% against 26–39%), possibly due to a relatively lower sampling effort [60].

In summary, animal–animal relationships account for 74–78% of tropical trophic interactions and 55–68% in temperate areas, whereas the joint richness of detritivores, suspension feeders, and macroherbivores (all gastropods feeding at low trophic levels) is higher in temperate and polar regions and Kimberley (32–36%) than in Thailand, Koumac, and Polynesia (22–26%).

3.2.3. Size of Modern Gastropods

The size range of modern species is 1–772 mm (S = 572), the largest gastropods belonging to Neogastropoda, a clade with most shells 10–40 mm in size, whereas other caenogastropods usually range 4–30 mm in size (Figure 4A). The clade with, on average, the smallest size is Heterobranchia (mostly 3–6 mm). Vetigastropoda are generally smaller than 20 mm, but Pleurotomariida are much larger (average 100 mm, reaching up to 300 mm). Patellogastropoda present a wide range of maximum sizes. While taxonomic clades largely overlap, most functional clades can be distinctly separated based on shell size, except for microphagous and carnivores, which can be of all sizes (Figure 4B). Spongivores form two groups, divided on taxonomic grounds: Triiphoroidea are small, while Pleurotomariida are large (Supplementary Materials, Table S3).

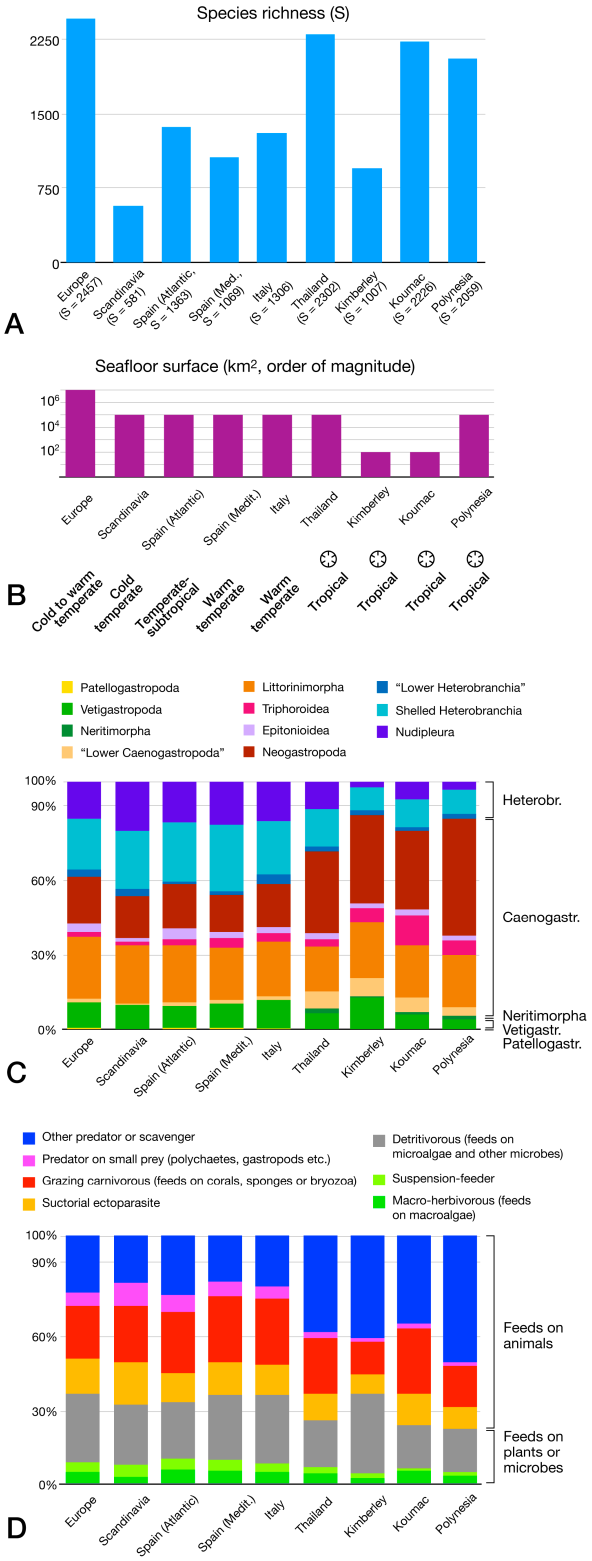

Figure 3. Modern diversity and ecology of major gastropod groups represented as the number of species: (**A**) total species richness for each region (S); (**B**) seafloor surface (km^2, measured by order of magnitude) and climatic zone (coral symbol for gastropod faunas associated with zooxanthellate coral reefs); (**C**) percent species richness by taxonomic group; and (**D**) percent species richness by functional group.

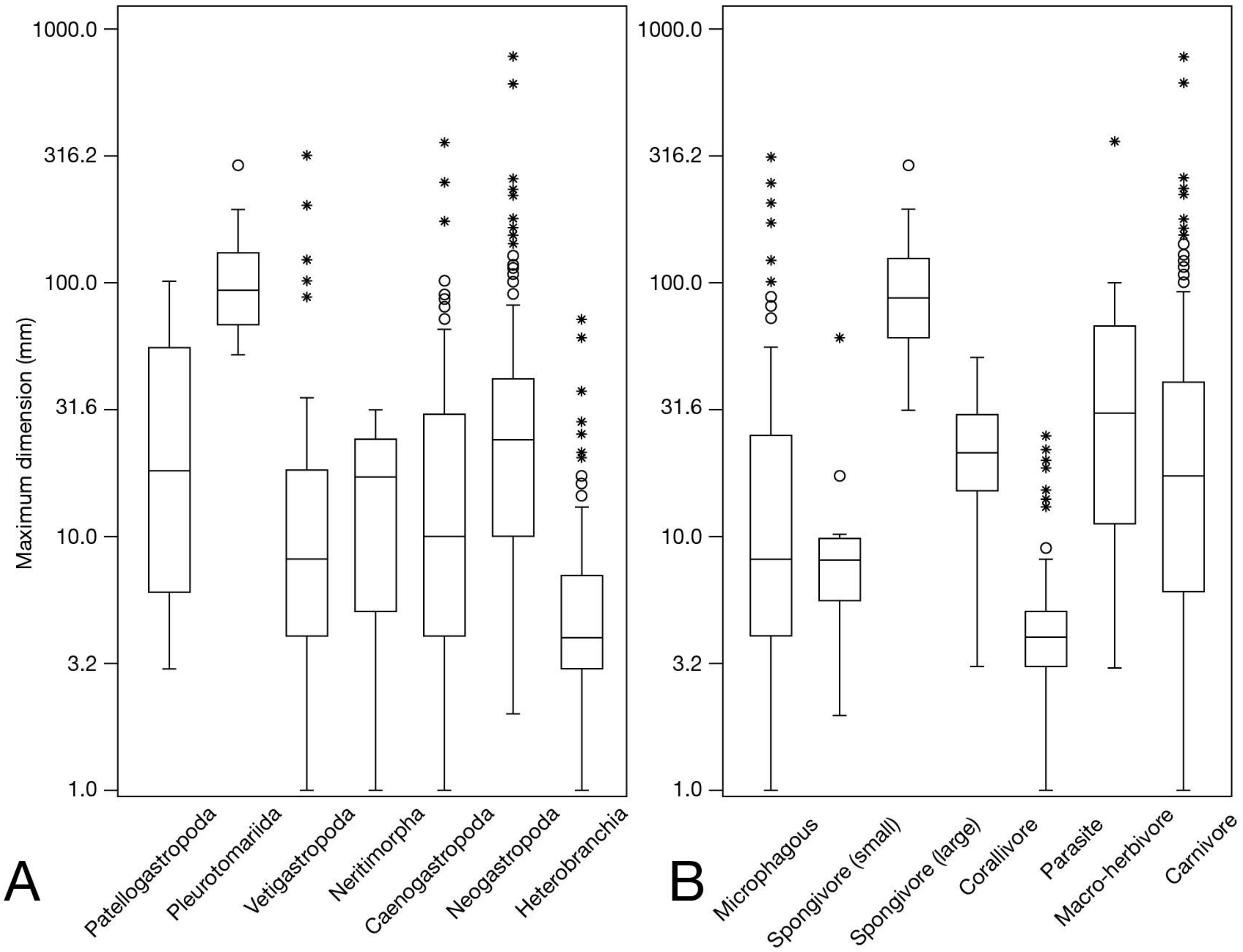

Figure 4. Distribution of maximum dimensions of living species (S = 573; log scale): (**A**) grouped by clade and (**B**) trophism. Mild outliers are marked with a circle (O), extreme outliers with an asterisk (*).

3.3. Permian and Triassic Tropical Gastropods

3.3.1. Diversity Across the PTME

The studied Late Palaeozoic–Early Mesozoic tropical record ranges S = 403–1761, being skewed towards the Triassic in terms of representativity. However, within each period, the number of localities representing each time bin can be confronted to a degree. The overall trend is characterised by a bimodal pattern in gastropod species richness, with a Permian peak during the Capitanian (260–265 Ma) and a Triassic peak in the Late Ladinian–Early Carnian (236–239 Ma [170]). The Anisian record indicates a richness higher than that found during the Ladinian, however this is from a higher number of formations. Between the two peaks, the Olenekian record shows the lowermost richness in the study interval (but from fewer formations and localities than the Induan period, shown in Figure 5; good preservation is rare in Early Triassic materials, adding a taphonomic bias [70]).

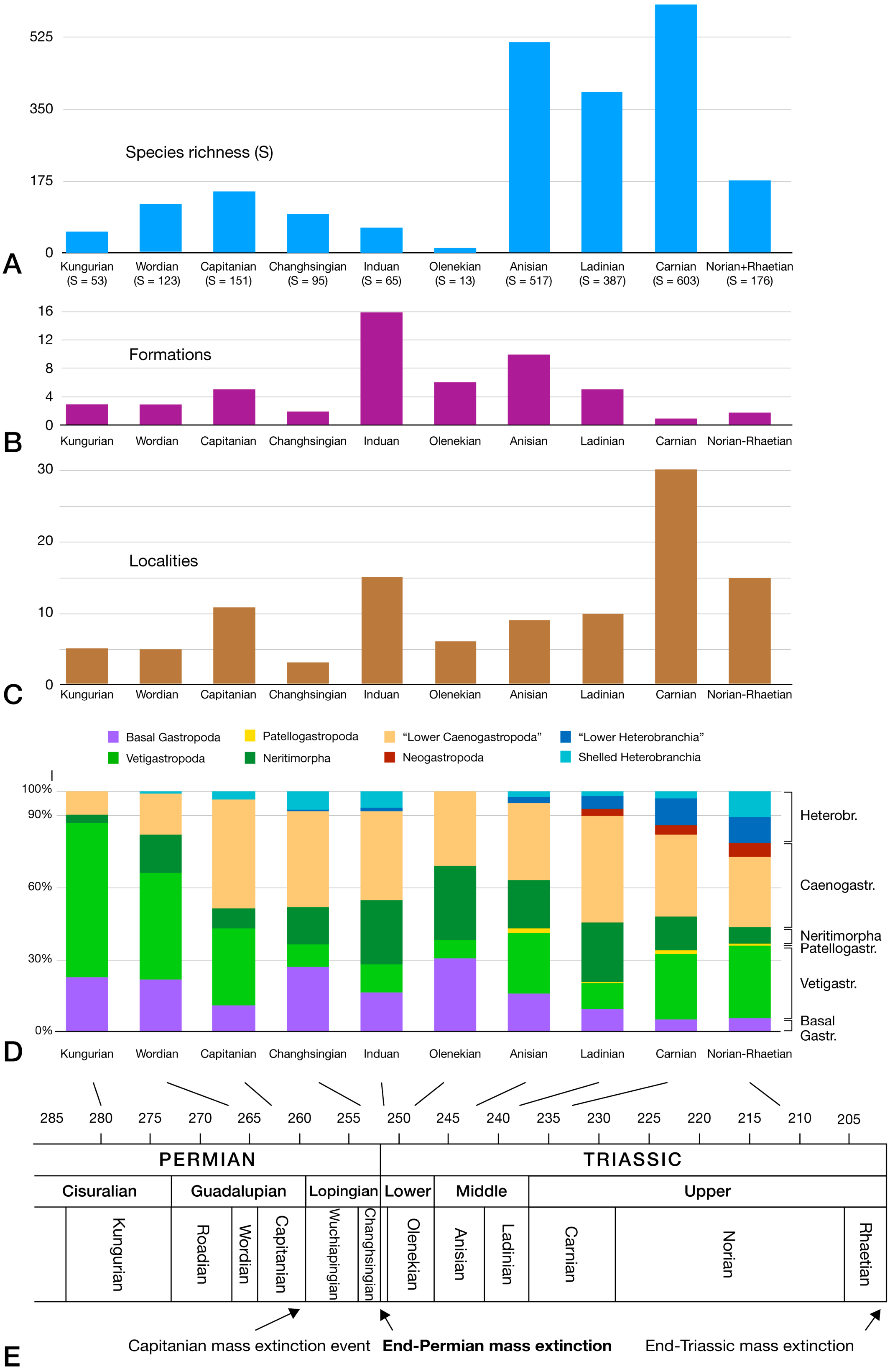

Figure 5. Permian (S = 403) and Triassic species richness (S = 1729) of major gastropod clades grouped by representative stages: (**A**) species richness (S); (**B**) number of formations considered; (**C**) number of localities considered; (**D**) percent species richness by taxonomic group; and (**E**) geological timescale for the study interval.

Regarding the Permian, gastropod richness increased during the interval Cisuralian–Guadalupian, then decreased in the Lopingian. The Capitanian peak (S = 151, Figure 5A) was influenced by the larger number of formations and localities analysed. However, richness was also high in the Wordian (Guadalupian, S = 123), nearly double that recorded in the Kungurian (Cisuralian, S = 53), notwithstanding a comparable sample size (Figure 5B,C). During the Changhsingian, in the latest Lopingian, richness decreased (S = 93) and further dropped in the Earliest Triassic (Induan, S = 60), notwithstanding the larger number of formations and localities analysed, and reached the lowest values in the Olenekian (S = 13). The fossil record points to a hyperbolic Middle Triassic increase, spanning the Anisian (S = 517) and Ladinian stages (S = 387), with the same number of localities (Figure 5B,C). The Carnian yielded the highest richness in the present report (S = 603), an impressive number considering that this was from just one formation. However, this record was achieved by exploiting, for centuries, 30 different localities and a wide range of settings [44], representing the largest sampling effort for a single formation of the whole dataset, double that analysed to describe the Induan fauna and three times that for the Ladinian period in terms of localities (Supplementary Materials, Table S3). The gastropod richness recorded in the Norian and Rhaetian localities considered here (Figure 5B,C) was much lower than the Carnian one (S = 176), probably indicating a global phenomenon.

The relative distribution of the subsets of gastropod richness, from the Cisuralian to the Guadalupian, shows a decrease in importance of Vetigastropoda to the advantage of Neritimorpha, Lower Caenogastropoda, and Heterobranchia, a trend continuing in the Uppermost Lopingian. Overall, basal gastropods contributed an important part of the total Permian richness and did not show a consistent trend (23–27%, but only 11% of Capitanian assemblages, as shown in Figure 5D). The overall trend did not change across the Permian–Triassic boundary, as Induan assemblages were also prevalently represented by Neritimorph and Lower Caenogastropod species, with 9% richness belonging to Heterobranchia. The latter were not recorded in the Olenekian assemblages analysed here, an interval during which basal gastropods reached 31%. The Permian–Lower Triassic's overall trend in composition was interrupted in the Anisian assemblages, at which point basal gastropods dropped to 16%, Vetigastropoda increased in richness, Patellogastropoda appeared for the first time, and Heterobranchia reappeared in the sampled faunas, diversifying within themselves. In the Ladinian, Caenogastropoda also diversified, with the appearance of Neogastropoda, first recorded in numbers which were already high (12 species, shown in Supplementary Materials, Table S2). This trend continued in the Late Triassic, with new clades further diversifying, to the disadvantage of basal and neritimorph gastropods (Figure 5D).

3.3.2. Size of Triassic Gastropods

Triassic species (S = 638) range in size from 1 to 133 mm, reaching the maximum size in high-spired caenogastropods and globular neritimorphs. Most heterobranchs have a size range of 3–10 mm, but all clades show large overlaps, with maximum sizes lower than 30 mm on average (Figure 6A). A tentative attribution of single measured species to a given functional group (Supplementary Materials, Table S3), based on taxonomic affinity (Figure 2) and analogy in size and form with modern species (Figure 4B), shows slightly more distinct intervals (Figure 6B). Like modern forms, these groups are microphagous gastropods (some vetigastropods, all neritimorphs, and many caenogastropods, including coelostylinid caenogastropods), two functional groups of spongivores identified on taxonomic grounds (small-sized Worthenelliini, diversifying in the Ladinian and the Carnian, and larger Pleurotomariini, leading to modern and even larger deep-sea forms [10]), a group of candidate corallivore gastropods mostly ranging <20 mm in size (stem neogastropods), even smaller parasites <10 mm in size (some zygopleurid caenogastropods, all heterobranchs), and some large macroherbivores (patellogastropods, Figure 6B; Supplementary Materials, Table S3)

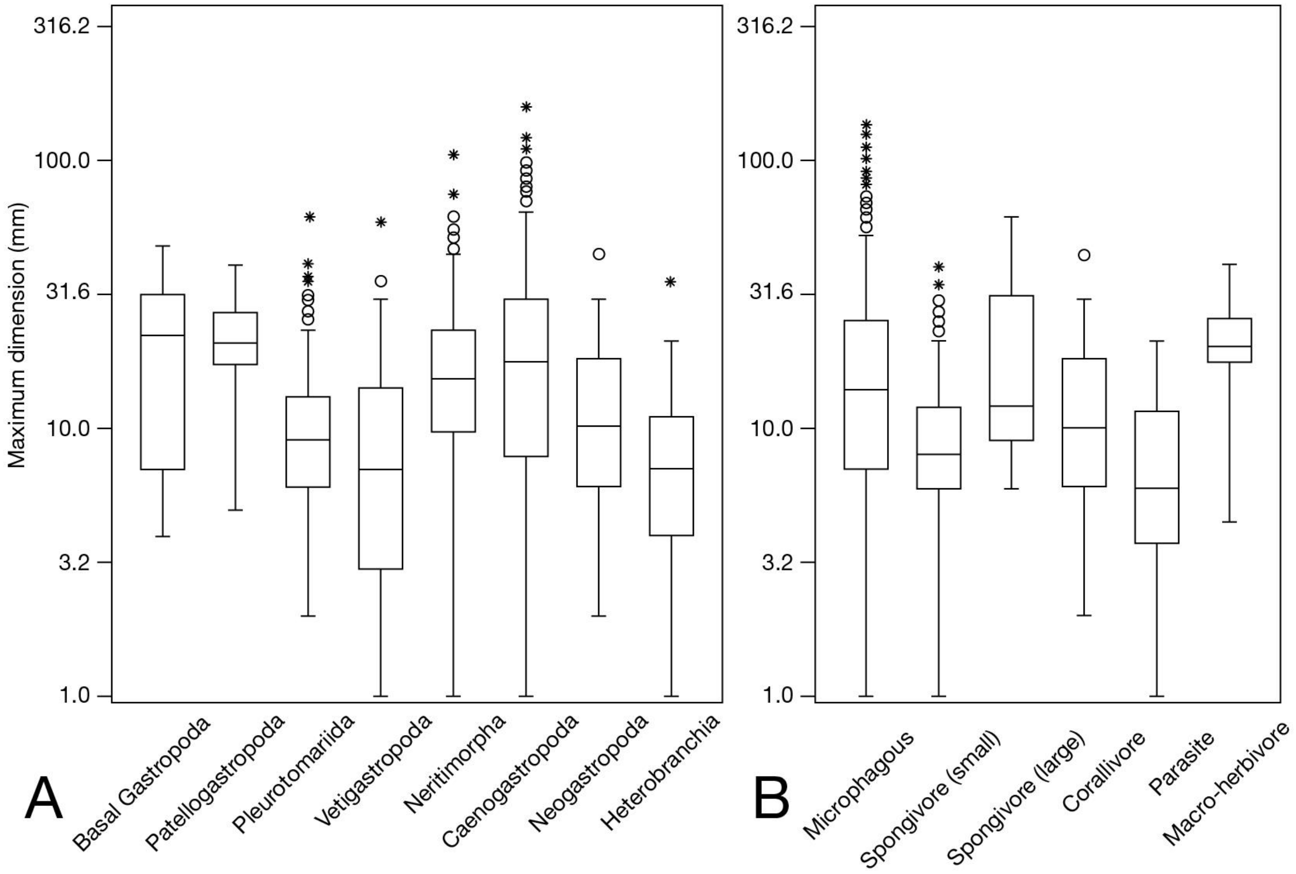

Figure 6. Distribution of maximum dimensions of Triassic species (S = 638; log scale), (**A**) grouped by clade and (**B**) trophism. Mild outliers are marked with a circle (O), extreme outliers with an asterisk (*).

When placed in stratigraphic context, all clades show a size increase from the Early Triassic to the Anisian, followed by an average decrease from the Anisian to the Ladinian (no available data for Anisian Neogastropoda), coupled with an increase in the maximum size of neritimorphs and caenogastropods and with Ladinian coelostylinids reaching more than 160 mm in size (Figure 7; Supplementary Materials, Table S3). The Carnian fauna presented here accounts for the smallest sizes, followed by a second genereal increase in maximum size during the Norian + Rhaetian. These data suggest that the Ladinian–Carnian high species richness (Figure 3) is largely accounted for by small species, with large outliers occurring among lower caenogastropods (Figure 7).

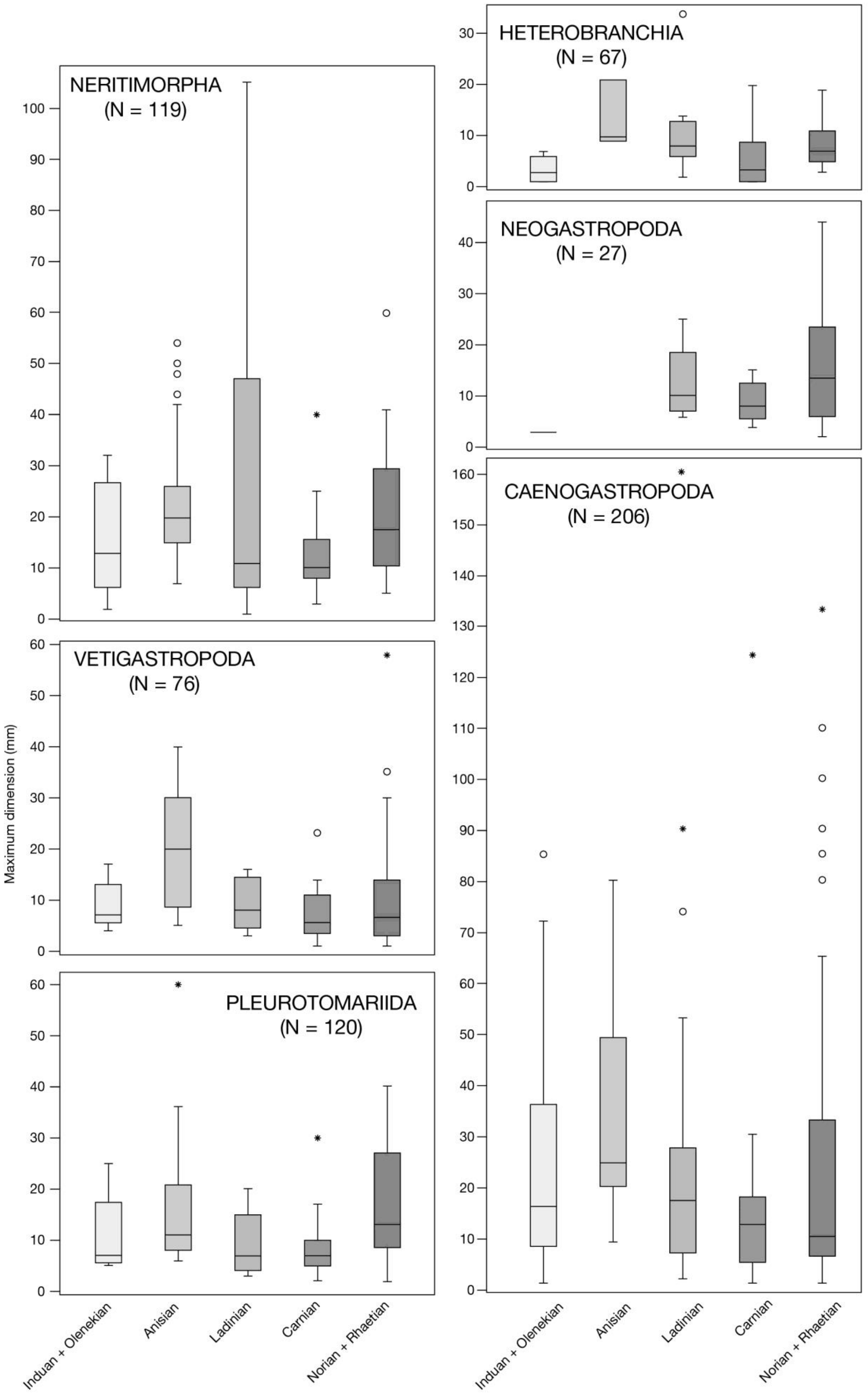

Figure 7. Stage-level distribution of maximum shell dimensions of major Triassic clades (S = 627). Mild outliers are marked with a circle (O), extreme outliers with an asterisk (*).

4. Discussion

Modern hotspots of gastropod diversity coincide with coral reef ecosystems of the Indo-Australian Archipelago [22,46] and with the highest species richness of the subclass Caenogastropoda (Figure 3). It is generally assumed that the success of the gastropods as a major component of the Modern Evolutionary Fauna is related to the Jurassic–Cenozoic coevolution of predator–prey marine ecosystems and the adaptation of gastropods to their enemies, in episodes coherently framed within an escalation hypothesis [11,37]. However, species <5 mm in size are a currently undervalued component of tropical marine diversity (Figure 2), and known gastropod diversity is bound to greatly expand as soon as micro-gastropods become targeted by the adoption of special collecting, sorting, and handling techniques [27–32,171]. Adult gastropods of small and medium size of subclasses Caenogastropoda and Heterobranchia largely belong to ectoparasite and microcarnivore functional groups [41], a guild which largely escapes the current tenets of the escalation hypothesis. These gastropods have particularly coevolved with sponges, corals, and echinoderms—larger animals offering food, habitat, and protection from predators—and the roots of such tropical benthic ecosystems date back to the aftermath of the PTME.

4.1. Permian vs. Triassic Gastropods

Marine diversity hotspots are known to travel in deep time, and corals and gastropods have likely moved in parallel [46]. At palaeotropical latitudes, the Guadalupian is marked by the adaptive radiation of a diverse gastropod fauna [8,172] (Figure 3). New high-spired caenogastropods can be included in microphagous guilds like the modern Cerithioidea, to which they are related [96]. Other snails that rely on microphagy are the neritimorphs and the basal gastropods, while candidate carnivores are either of a small size, and possibly parasitic (heterobranchs), or medium-sized (plurotomariids) grazers, like their modern descendants. If the latter is the case, larger Permian vetigastropods would have preyed upon sponges, possibly also on bryozoans and tabulate or rugose corals. The nature of an End Guadalupian mass extinction continues to be controversial [2,3,173–176], but the diversity loss, whether prolonged or abrupt, apparently affected different phyla of marine benthic invertebrates, including corals and bryozoans among reef builders (Figure 8) [177–179]. Molluscs as a whole were less heavily hit [173,180,181], but the parallelism between the diversity trends of tropical reef builders and gastropods fits with a hypothesis of a causal link. Pleutoromariids were severely affected [8–10], consistently with the Early Lopingian [182] and Early Triassic [183] crises of calcareous sponges (Figure 8). Microphagous snails would have likely also been negatively affected by the decreased habitat complexity of the tropical reef biota.

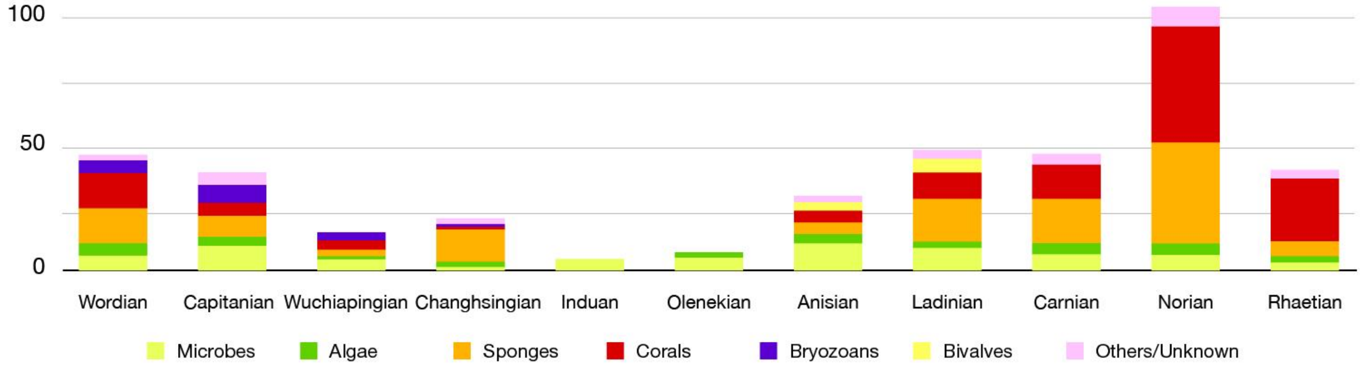

Figure 8. Stage-level distribution of Permian and Triassic reef builders (number of reef sites per reef builder) data from [178].

The Middle Triassic was marked by a hyperbolic diversity increase largely generated by gastropods. This took place in two steps, the first in the Anisian [45,179] and the second in the Ladinian [35,170,172]. The present analysis indicates that the Anisian rebound was largely connected to microphagous feeders such as neritimorphs and lower caenogastropods and the rebound of spongivorous pleurotomariids [9,10], whereas the Ladinian increase was related to an increased species richness of carnivores, including heterobranchs, possibly some lower caenogastropods, and stem neogastropods (Figure 3) [170], a trend confirmed by the Late Triassic record [169]. Pleurotomariid vetigastropods gradually decreased in importance after the Carnian [9,10], giving way to the trochids (microphagous) among vetigastropods.

Middle and Late Triassic purported carnivores were either small-sized (<5 mm, e.g., many zygopleurid caenogastropods and heterobranchs of the Acteonimorpha group) or medium-sized (6–20 mm, e.g., pleurotomariids, lower Heterobranchs, and stem neogastropods) [9,184–186], split between two groups potentially relying on suctorial ectoparasitism and grazing carnivory, respectively.

Considering analogies with modern ecosystems [41], the Middle Triassic radiation of small-sized ectoparasites may have been connected with the contemporaneous increase in the diversity of crinoids, ophiuroids, echinoids, and asteroids, well documented during the Carnian but already taking place in the Ladinian [187–189]. The range of potential hosts was further increased by Palaeozoic clades surviving the PTME bottleneck [190–193].

4.2. Coevolution

In parallel, the diversity increase in grazers could be causally linked to the Middle and Late Triassic return of Permian-type reef communities after a protracted Early Triassic non-reef interval [45,194]. This return, however, also coincided with the advent of scleractinian corals, first radiating with the sponges [195], then gradually taking their place among tropical reef builders (Figure 8) [177–179,196] (thence the decline of pleurotomariids [175]). Sponges and encrusting algae dominated the Anisian reef-building community [195], when all gastropod clades peaked in average size at tropical latitudes (Figure 6A, in parallel with epifaunal bivalves [197]). During the Ladinian, scleractinian corals increased in diversity and frequency and dominated fore-reef buildups with sponges and solenoporaceans, while dasycladacean and blue-green algae still thrived in back-reef, high-energy settings [198,199]. Consistently, Ladinian gastropods showed a bimodal pattern: clades adopting a small size and microcarnivory as a form of adaptation, such as pleurotomariids (particularly the Worthenelliini), stem neogastropods, and heterobranchs (Figures 6 and 7), were associated with coral-dominated buildups (Figure 9), while neritimorphs and coelostylind caenogastropods of the microphagous guild, on the opposite side, attained very large dimensions for the epoch (outliers in Figure 6A) in low-diversity, back-reef environments (Figure 10) [199]. The generalised size decrease recorded in the Carnian was associated with a hyperbolic diversity increase in both zooxanthellate and non-zooxanthellate corals [200].

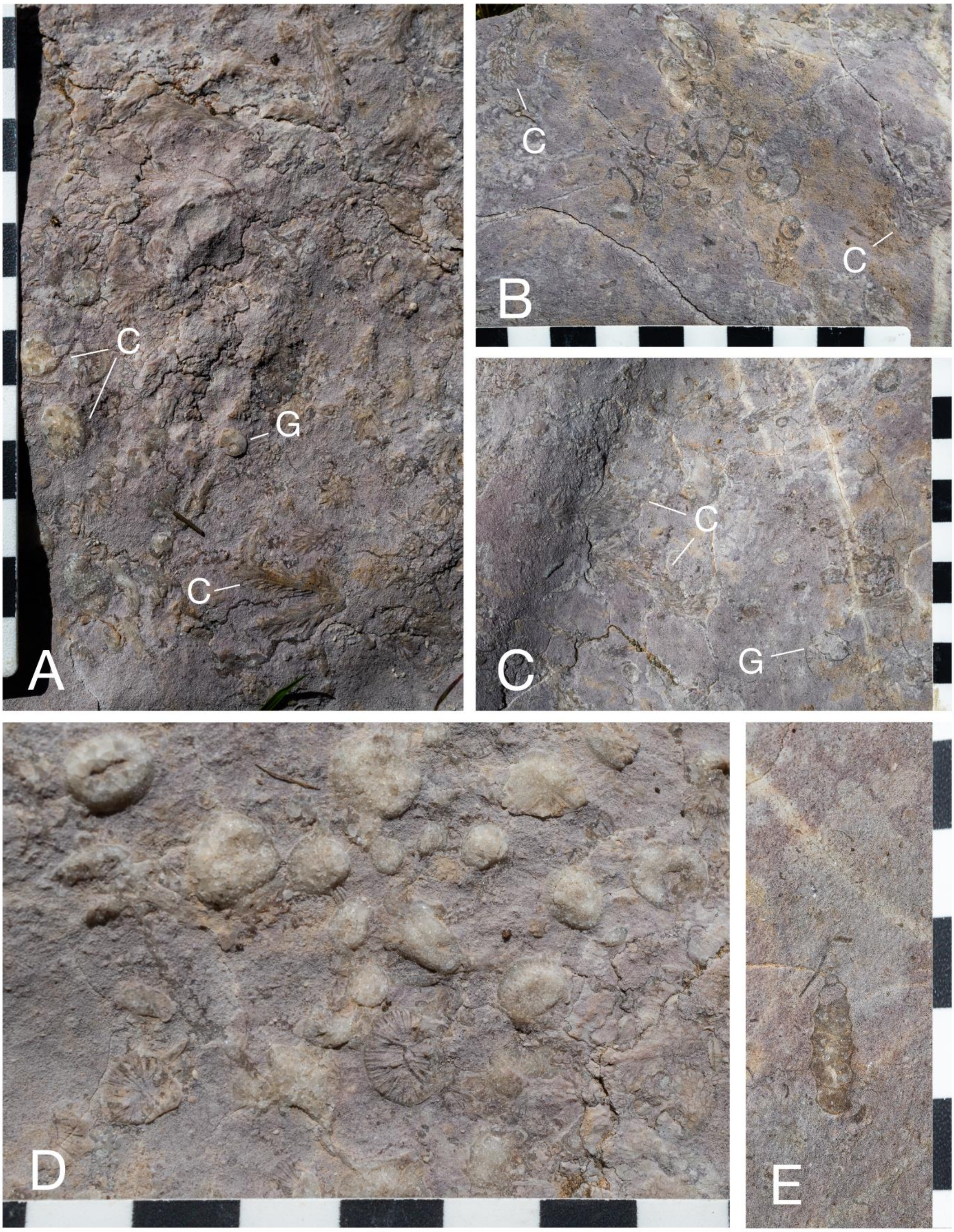

Figure 9. Upper Ladinian coral reef assemblages from Col delle Capre (Sciliar Fm., W Dolomites, Italy; see [170] for the location). Field pictures showing the relative position and size of gastropods and phaceloid scleractinian corals (*Retiophyllia*-type). C: corals; and G: gastropods. (**A**,**C**) Life assemblages, with a low-spired plaurotomariid in (**C**); (**B**) sedimentological assemblage; (**D**) detail of *Retiophyllia*-type corals; and (**E**) high-spired medium-sized gastropod (possibly a mathildid). Scale bars in cm.

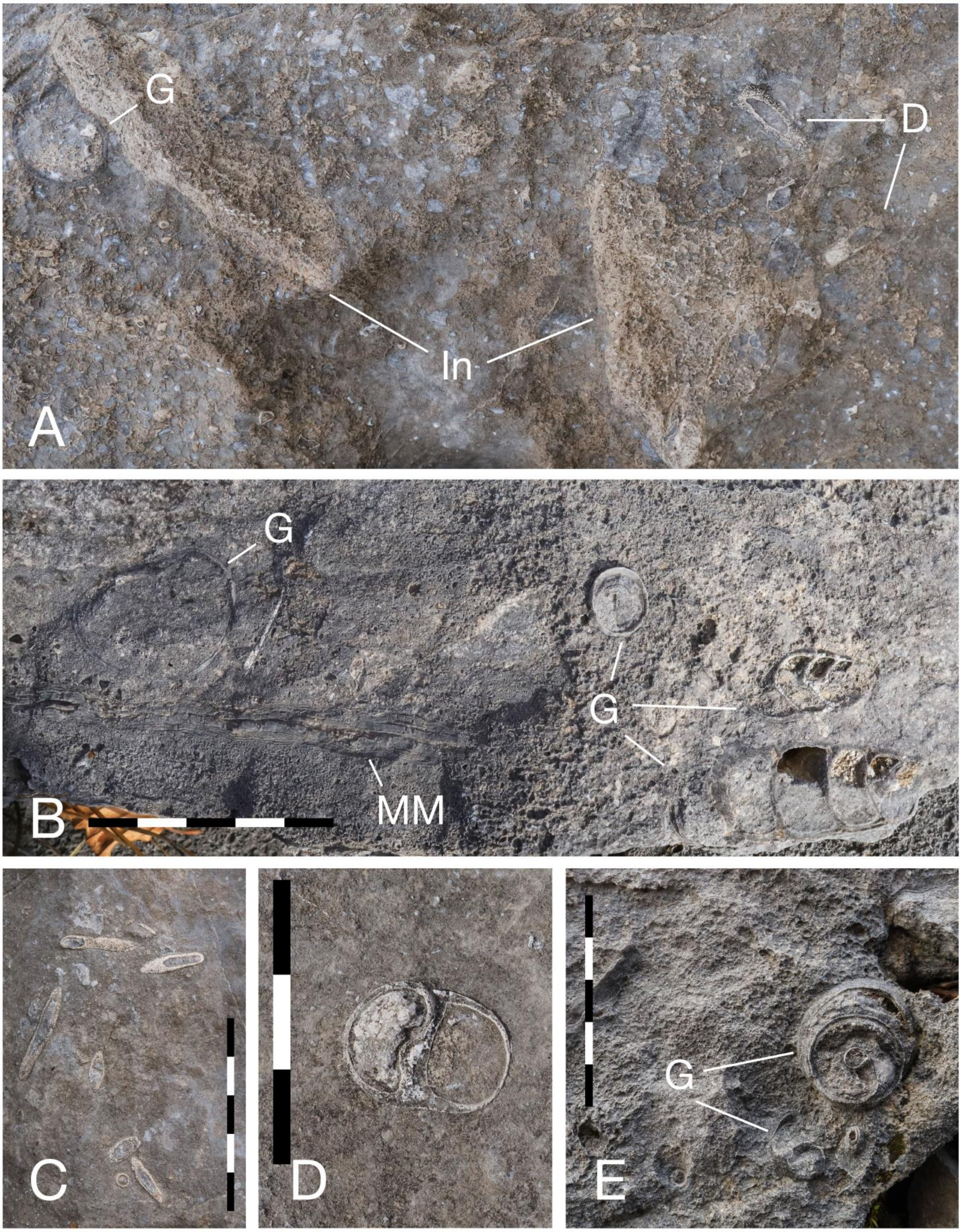

Figure 10. Upper Ladinian back-reef assemblage from Pizzo del Cich (Esino Fm., Grigne Group, Lombardy, Italy; [see 199] for the location). (**A**,**B**) Field pictures showing the relative position and size of gastropods and algal fragments (*Diplopora* and blue-green algae). G: gastropods; D: *Diplopora*;

MM: microbial mat; and In: intraclasts. (**A**) Transported assemblage in peloidal/intraclast packstone, including a gastropod (left), large intraclasts, and fragments of dasycladacean algae (*Diplopora*, right); (**B**) transported assemblage with four large gastropods (a naticopsid on the left and three high-spired coelostylinids on the right, including *Omphaloptycha* spp.) and a platy fragment of blue-green algae (MM) in peloidal/intraclast packstone; (**C**) fragments of *Diplopora*; (**D**) Naticopsid; and (**E**) an undetermined gastropod and a large high-spired coelostylinid on the right. Scale bars in cm.

Additional evidence supports a causal connection between the radiation of microcarnivore gastropods and Middle and Late Triassic reef builders and dwellers. Corals, sponges, and echinoderms have been associated with small- and medium-sized gastropod assemblages since the Anisian (reef facies [195]), assemblages which became highly diverse in the Ladinian [170] and Carnian [44,201]. Gastropod-associated Middle Triassic scleractinian corals mostly belonged to the phaceloid *Retiophyllia* type, showing low integration among individual corallites (Anisian [195]; Ladinian, Sciliar Fm., Figure 9). Carnian reef builders were instead characterised by larger corallites [202] and a broad spectrum of morphologies, including highly integrated thamnasteriod colonies which exhibited analogous ecological adaptations to modern symbiotic corals [203,204]. Within a wide depth range, these corals built reef ecosystems that hosted molluscan communities of low dominance and high alpha and beta diversities, with values comparable to those of modern tropical reefs [205].

Morphological adaptations of the gastropod shell imputable to coral grazing are shared by Triassic and modern coral grazers, including a fusiform shell and a large aperture with expanded inner and outer lips, ensuring better adherence to a hard substrate and facilitating grazing. These features were encountered in Late Ladinian *Pseudoscalites karapunari* and Early Carnian *Pseudotritonium venustum* and *Pseudotritonium laubei* (Figure 11A,B,F), three species belonging to two genera and two families of stem neogastropods: Purpurinidae and Pseudotritoniidae, respectively [169]. The same characteristics are today seen in corallivorous snails of the highly derived neogastropod subfamily of Coralliophilinae (Figure 11G,H) [149,150]. In the same functional group are the highly diverse Epitoniidae, sharing their small size and general shell form with Triassic stem neogastropods, but with a holostomous aperture (Figure 9C,E). These features strongly point to the iterative evolution of the gastropod shell in the medium-size shell range, driven by the interaction with corals of both the dendroid and thamnasterioid type. The same size range characterises other caenogastropod clades diversifying in reef ecosystems, such as cypraeids in the Tethys during the Oligocene and in the modern Coral Triangle [140].

Briefly, newly evolved tropical onshore communities of Paleotethys offered spatial heterogeneity to a host of new carnivores among gastropods, all of small or medium size, among which was the stem group from which diversity was later selected during the Mesozoic Marine Revolution. Adaptations of stem Neogastropoda are thus distinct from those of most modern Neogastropoda.

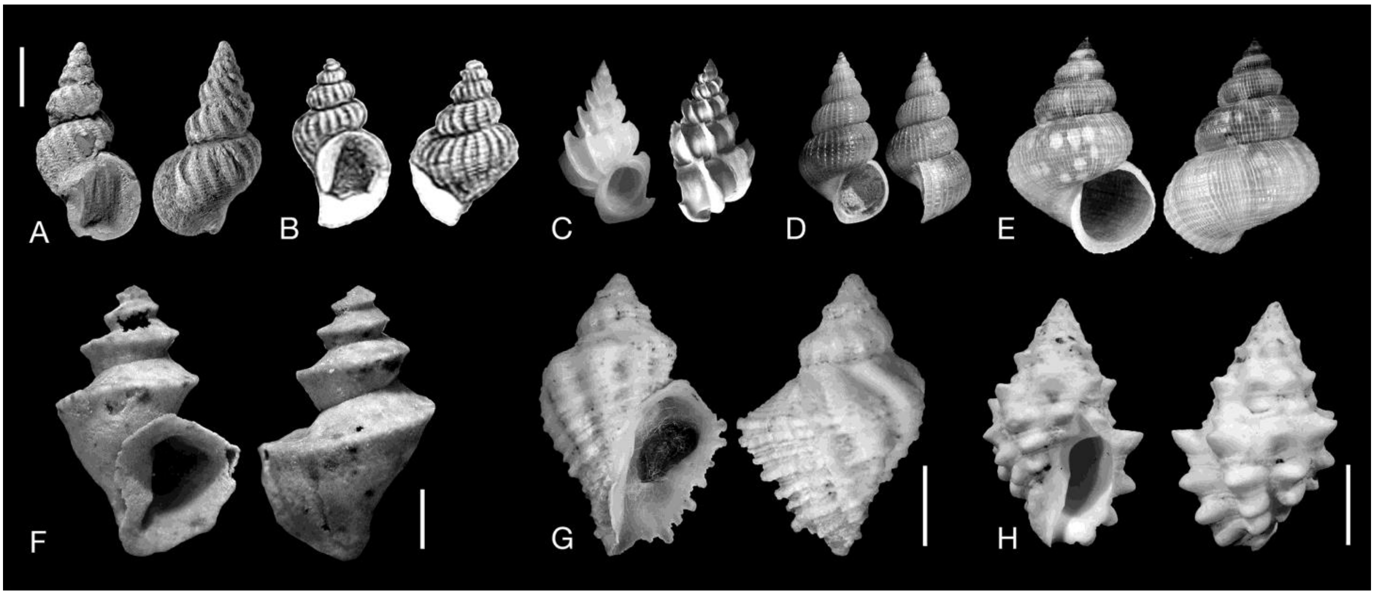

Figure 11. Shell morphology and size of Middle–Late Triassic putative microcarnivores compared to modern analogues (anterior and poster view to show spire and aperture). (**A**) Holotype of *Pseudotritonium venustum* from the Early Carnian, Cassian Fm., Dolomites (Italy) [206] (Figure 4). (**B**) Holotype of *Pseudotritonium laubei* from the Early Carnian, Cassian Fm., Dolomites (Italy) [207] (Plate 11, Figure 10). (**C**) Holotype of *Epitonium graviarmatum*, recent specimen from the Maldives [127] (Figures 46–47). (**D**) *Epidendrium dendrophylliae* [50], recent specimen from Morocco. (**E**) *Epidendrium aureum*, recent specimen from Japan [208] (Figure 1). (**F**) Holotype of *Pseudoscalites karapunari* from the Upper Ladinian, Sciliar Fm., Dolomites (Italy) [170] (Figure 20, AK-AR). (**G**) *Coralliophila caribaea*, recent specimen from Tobago [50]. (H) *Drupella cornus* recent specimen from Indonesia [50]. Scale bars equal 2 mm in (**A**–**F**) and 10 mm in (G,H).

4.3. Paradise Lost

In a phylogenetic analysis of modern corallivorous Muricidae of the subfamily Coralliophilinae and their hosts, scleractinian corals were found to be the ancestral host for most clades, supporting the hypothesis that the subfamily originated in shallow waters in the Middle Eocene and then shifted to deep-water habitats over at least three major instances [152]. An analogous path has been suggested for Mathildoidea, from the genus *Promathildia*, radiating in the Middle and Late Triassic reef ecosystems [70,170,209], to species surviving the Triassic–Jurassic mass extinction, to the modern Mathildidae [41,210], small-sized micrograzers associated with corals found at a wide range of depths, from shallow-water reef ecosystems to cold-water, bathyal settings [135,138]. As for Guadalupian shallow-water reef dwellers, Pleurotomarioidea gradually disappeared during the Triassic [9,10], surviving today in the deep sea with a very low number of species, capable of fighting back predators [139] but, evidently, on the verge of losing the overall arms-race.

Other examples could be found among tropical gastropods [155,211] and scleractinian corals [200], but the above three cases suffice to speak of a repeated pattern of onshore innovation to offshore refuge, long recognised in the fossil records [212–214]. The youngest clade (Eocene Coralliophilinae, Neogastropoda) maintains a rather important richness in onshore tropical settings (tens of species globally [152]); the intermediate (Triassic Mathildoidea, Lower Heterobranchia) is presently a very minor constituent of nearshore tropical communities (three species in Koumac [28]); the oldest (Palaeozoic Pleurotomarioidea, Vetigastropoda) has completely vanished onshore [139]. Early in their geologic history, these clades underwent an increase in their diversification rate, as they widened environmental occupancy, but were then displaced from nearshore settings.

5. Conclusions

The integrated study of the modern global diversity distribution of gastropod clades and functional groups and their Permian and Triassic record in tropical regions helps to uncover which factors controlled species richness at times of diversifications following times of crisis. Guadalupian gastropod diversity peaked in parallel with the diversification of reef-building sponges, bryozoans, and corals. Snails in tropical marine ecosystems were characterised by basal gastropods, pleurotmariid vetigastropods, and caenogastropods, both microphagous and microcarnivores. After the End Guadalupian mass extinction event and the PTME, through the Early Triassic recovery phase, the diversity of tropical gastropods remained low. The Anisian rapid increase in diversity was characterised by microphagous gastropods, some of which were of a large size, in reef ecosystems dominated by sponges and the very first scleractinian corals. Diversity and the number of microcarnivores and ectoparasites rapidly increased in an interval of about 3 million years, including the Late Ladinian and Early Carnian, around the Middle–Late Triassic turn. This event was associated with the first records of a broad spectrum of coral morphologies, including zooxanthellate corals of modern type and a higher variety of echinoderms.

Adaptations of modern gastropod clades to analogous habitats and food sources suggest that Triassic gastropod diversity responded to the opportunities offered by an increased number of preys and spatial niches. The radiating guild of microcarnivores was characterised by shells of small and medium sizes. Stem Neogastropoda diversified, marking the emergence of MEF with morphologies similar to modern corallivorous snails, ahead of the Cretaceous spread of modern Neogastropoda. Analogies between Palaeozoic, Triassic, and Cenozoic macroecological and macroevolutionary dynamics indicate increases in the diversification rate and widening of habitat occupancy early in the geologic history of tropical snails, followed, in the long run, by their displacement from nearshore, high-competition habitats.

Supplementary Materials: The following supporting information can be downloaded at: https://www.mdpi.com/article/10.3390/d17020120/s1, Gastropod species lists for modern (Table S1) and fossil clades (Table S2) and a quantitative database on shell size, for both fossil and modern species (Table S3), including functional groups and references for ecological data.

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