



Convergent and Parallel Evolutionary Traits in Early Cretaceous Rudist Bivalves (Hippuritidina)

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Abstract

Early Cretaceous Hippuritida clades, requieniide (family Requiieniidae) and hippuritide (families Radiolitidae, Polyconitidae, Caprinidae, "Caprinulidae" and Caprinuloideidae), show distinctive myophoral arrangements and shell structures. Nevertheless they share some characters, such as the transverse shell thickening of the myophores of the attached valve which are convergent traits in *Lovetchenia* (Requiieniidae) and *Homopleura* (Monopleuridae). The bent posterior myophore of the right valve of *Pseudotoucasia* (Requiieniidae) closely resemble the posterior myophore of the left valve of *Horiopleura* and *Polyconites* (Polyconitidae). The shell cellular structure is one of the key attributes of the family Radiolitidae (e.g. *Eoradiolites*) but this structure is also present in some advanced Requiieniidae ("*Toucasia-Apricardia*" group). Canaliculate shell structures are convergent evolutionary traits which are common in the Caprinidae and Caprinuloideidae and also exist in the Polyconitidae and "Caprinulidae". In most of the foregoing canaliculated groups, two trends are well expressed, reflecting parallel evolution: expansion of canals into the entire shell and increasing complexity of canal architecture. Convergent taxa took some advantages by using former innovations. An Albian peak of convergence coincided with the emergence of new clades, which suggests a reset following the mid-Aptian extinction event.

Keywords: Monopleuridae; Eoradiolites; Caprinulidae; Hippuritidine Clade; Myophoral; Polyconitidae; Caprinidae

Introduction

Evolutionary convergence is implicated when two or more lineages with distinct ancestors independently evolve a similar morphological trait, a concept close to evolutionary parallelism which postulates that similarity may appear in lineages having a common origin and/or changed together in roughly similar fashion [1,2]. In bivalves, evolutionary convergence was established for post-Paleozoic Crassatellidae and Astartidae [3]. It was also documented for the acquisition of an opisthogyrate rostrate shell habit observed in infaunal taxa belonging to unrelated lineages, as an adaptation to shallow burrowing and allowing the animal to reach the water-sediment interface while the main body remained below the sediment surface [4,5]. In rudist bivalves

canaliculated shell structures have also been regarded as convergent traits [6,7].

The objectives of the present paper are to compile examples of convergent versus parallel evolution in Lower Cretaceous rudist bivalves (order Hippuritida) belonging to distinctive suborders or families from the Mediterranean, Caribbean and Asiatic paleobiogeographic entities. We first address two clades, the requieniide clade and the hippuritidine clade [8,9] (Figure 1) in which the arrangement of myophores and the shell structure show some similar patterns. We will also reappraise the similarity in distribution of canaliculated shell structures in distinctive families of the hippuritidine clade, and subclades, including their evolution through time. We discuss the relevance of the

concept of convergence and/or parallelism applied to the foregoing pattern of characters and analysed their relative timing. In the following we use the family names and authors proposed by Skelton [8,9].

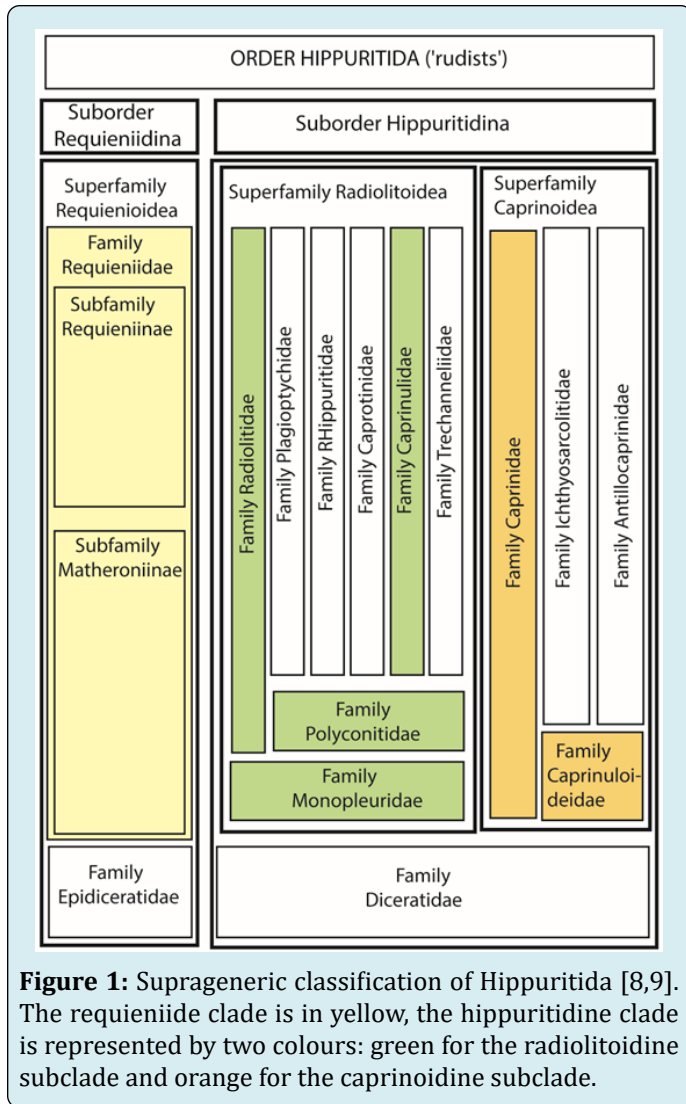


Figure 1: Suprageneric classification of Hippuritida [8,9]. The requieniide clade is in yellow, the hippuritidine clade is represented by two colours: green for the radiolitoidine subclade and orange for the caprinoidine subclade.

Abbreviations and codes used for the paleontological descriptions: BC, body cavity; A, anterior side; P, posterior side; m, anterior and posterior muscles; am, anterior myophore; pmp, posterior myophoral plate; pmc, posterior myophoral cavity pt, posterior tooth; at, anterior tooth; as, anterior socket; ps, posterior socket. Muscles are figured in pale blue.

Myophoral Arrangement in Rudist Bivalves

Myophores are fundamental in rudist systematics and their diversity and phylogenetic conservatism are remarkable and possess a high taxonomic value [6,7]. Similar

myophoral organisations recorded in distinctive clades may suggest phylogenetic affinities or may afford the opportunity to evaluate other patterns.

The Requiieniide Clade

In the requieniide clade the shell is attached by the left valve (LV). Myophoral evolutionary patterns are well illustrated in the family Requieniidae Kutassy, which includes five genera having contrasting myophoral arrangements [10,11]. In *Matheronia* right valve (RV) myophores are located on low, salient bulges, whereas the LV myophores are on shell wall. In *Requienia* the RV is flattened and bears a posterior myophoral plate, the anterior is a low bulge; LV myophores being inconspicuous. *Toucasia* is characterized by posterior myophoral plates on both valves and the posterior side of the RV is raised above the commissure. The myophores of *Lovetchenia* are represented by shell transverse thickenings on both valves, and the RV is salient (Figure 2A) As *Toucasia*, *Pseudotoucasia* has posterior myophoral plates on both valves but the myophore of the RV is bent with an elbow shape (Figure 3A).

The Hippuritidine Clade

In the hippuritidine clade the shell is attached by the RV. Myophoral evolutionary patterns are well illustrated in two families, Monopleuridae Munier -Chalmas and Polyconitidae MacGillavry. As stated by Masse and Fenerci-Masse [12], the family Monopleuridae includes two groups of genera. To the first group belong *Monopleura* Matheron emend. and *Homopleura* Masse and Fenerci-Masse [12] with RV myophores located on flat transverse shell thickenings present either only on the posterior side, as in *Monopleura* or on both the anterior and posterior sides, as in *Homopleura* (Figure 2B). In the family Polyconitidae the LV posterior myophore is a bent lamina which consists of a plate subparallel to the commissure, attached basically to the shell by a pedicle, (Figure 3B), the anterior myophore is a vertical plate, in *Horiopleura* the RV posterior myophore is on a transverse shell thickening, the anterior on shell wall [13]. In *Polyconites* the myophoral organisation of the LV is nearly the same, the RV myophores being on shell wall. Pediculate myophores also exist in some Caprinuloideidae Damestoy, this is the case for the LV posterior myophore of *Amphistricoelus warringi* Harris and Hodson, represented by a vertical, slightly convex, plate supported by a pedicle attached to the posterior tooth [14] (Figure 3C).

Convergent Patterns in Myophoral Arrangement

The foregoing shows convergent patterns between the two clades, requieniide (family Requieniidae) and hippuritidine (families Monopleuridae, Polyconitidae and Caprinuloideidae), whereas the convergent traits are

recorded on the RV of the first group, they are located in the LV of the second group.

In *Monopleura* (Monopleuridae), *Matheronia* and *Requienia* (Requieniidae), the myophoral arrangement of the attached valve is similar. This similarity is recorded in primitive taxa of the two families. The transverse shell thickening of the myophores of the attached valve are convergent traits in *Lovetchenia*, i.e. *L. lovetchensis* (Zklatarski) (Requieniidae) (Figure 2A) and *Homopleura*, i.e. *H. balkanica* Masse and Fenerci-Masse (Monopleuridae) (Figure 2B); this morphology characterises relatively advanced taxa. In that case morphological identity corresponds with functional similarity. Inflated transverse myophores appear first in the requieniide clade in the Hauterivian then in the hippuritidine clade in the Barremian, it may reflect the resurgence of a primitive trend (atavism) recorded in diceratids [15].

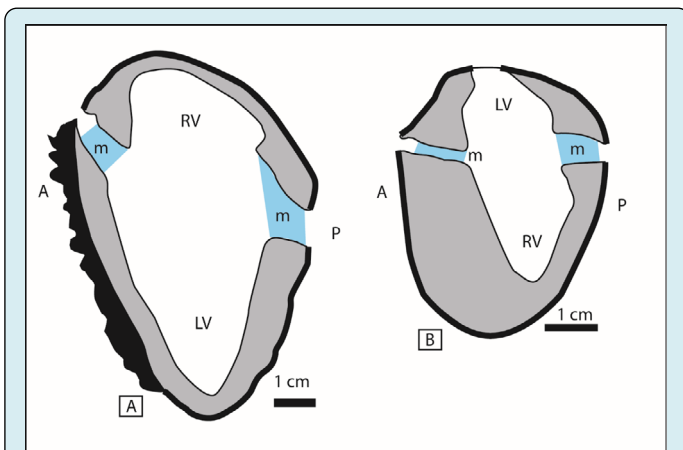


Figure 2: Convergent myophoral arrangement: transverse shell thickening, figures based on longitudinal sections of bivalve specimens. A, *Lovetchenia lovetchensis* (Zlatarski), from Lovetch, Bulgaria (Requieniidae) [15]. B, *Homopleura balkanica* Masse and Fenerci-Masse, from Emen, Bulgaria (Monopleuridae) [12]. Inner aragonitic shell layer is in grey, the calcitic outer shell layer in black.

The bent posterior myophore of the RV of *Pseudotoucasia* (Requieniidae) closely resembles the posterior myophore of the LV of *Horiopleura* and *Polyconites* (Polyconitidae). In *Pseudotoucasia santanderensis* (Douvillé) the myophore is elbow shaped (Figure 3A) and its tip points posteriorly, which mimics that of *Horiopleura* (Figure 3B). A similar myophoral organisation was described by Ayoub-Hannaa and Fürsich [16] in the Cenomanian requieniid “*Apricardia*” *noncarinata* from Egypt. The morphological similarity does not imply a functional identity in *Pseudotoucasia* for instance the muscle is inserted at the inflated apex of the myophore whereas in the Polyconitidae the muscle insertion is on the plate itself which parallels the commissural plan. This myophoral geometry typifies an advanced taxon of

the Requieniidae and primitive forms of the Polyconitidae, it has a generic significance in *Pseudotoucasia* whereas in the Polyconitidae it is a marker of the family. The posterior myophore of the LV of *Amphitriscoelus* (Caprinuloideidae) is also pediculate (Figure 3C), the pedicle supports a vertical plate facing the posterior shell side [14].

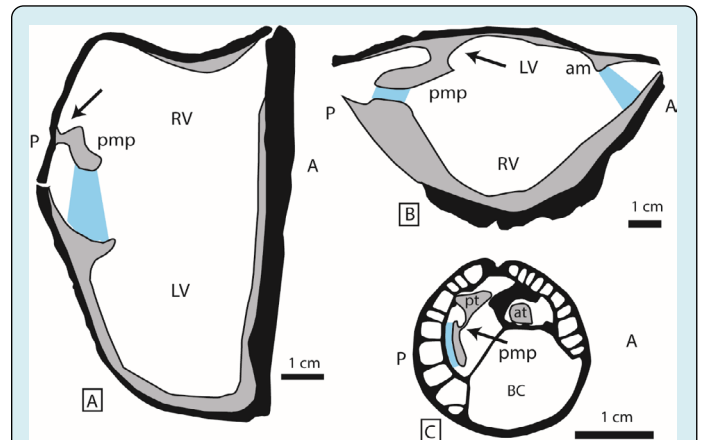


Figure 3: Convergent myophoral arrangement: bent (elbow shape) or pediculate myophores. A, B, longitudinal sections of bivalve specimens. A, *Pseudotoucasia santanderensis* (Douvillé), from Santander (Spain) [17]. B, *Horiopleura gemmellaroi* (di Stefano), from Northern Tunisia [13]. C, transverse section of a RV of *Amphitriscoelus warringi* Harris and Hodson, from Trinidad [14]. Arrow indicates the pediculate portion of the myophore. For Figure A and B, the shell layers are represented as in Figure 2.

Shell Structures

The basic shell structure of rudist bivalves is two layers, i.e. an inner shell layer, originally made of aragonite, from which myocardial features are built, and an outer shell layer made of prismatic calcite [18]. In most taxa, but one, belonging to the requieniide clade, the double layer has a compact microstructure. In the Lower Cretaceous the hippuritine clade is also dominated by taxa having a compact double layering, but two additional arrangements have their FO during this time interval: cellular structures present in the calcitic outer shell layer, and canaliculated structures restricted to the inner formerly aragonitic shell layer. During the early Cretaceous the two basic structures didn't coexist whereas they were coeval in some late Cretaceous forms, e.g. the Campanian *Pseudosabinia klinghardti* (Boehm) [19,20].

Cellular Versus Compact Structures

The so-called cellular structure has been attributed to the association of funnel plates and radial plates [21], forming a network which is one of the key attributes of the family Radiolitidae d'Orbigny [22]. Early Cretaceous

representatives of the family are represented by *Eoradiolites* with a quadrangular outer shell layer structure and *Archaeoradiolites* with radially arranged branching walls.

It is worth noting that the primitive, Barremian member of the family, i.e. *Agriopleura*, has a compact outer shell [23,24]. A similar acellular structure, is recorded in the late Aptian-Albian radiolitid genus *Auroradiolites*, assumed to be a marker of the Asian-Pacific province [25,26]. The acellular *Auroradiolites* was considered as a direct descendant of *Agriopleura* [26], in that case the compact shell structure might be just inherited. Given the distinctive paleogeography (Asiatic versus Mediterranean) and the time gap (Barremian-early Aptian versus late Aptian-Albian) between the two genera, an alternative interpretation is proposed. *Auroradiolites* might derive through convergence from a former cellular form, e.g. *Eoradiolites*. Actually the development of cellular structures in advanced radiolitids shows that this pattern follows a juvenile compact stage through ontogeny [27], heterochrony is thus a more likely interpretation of the compact structure of *Auroradiolites*. Another case of convergence is illustrated by the genus *Gorjanovicia* which documents the re-inception of acellular Radiolitidae in the late Cretaceous [28].

Cellular structures tend to characterize the hippuritidine clade, nevertheless they have been also recorded in “*Toucasia* like” requieniids (unpublished data from the authors). Quadrangular cellular structures are present on the ventral side of the LV of specimens of Albian age from Laguna Colorada-El Madrono (Queretaro, Mexico) [29] and southern Italy. Similar structures were described by Palmer [30] in the requienid “*Apricardia*” *asymmetrica* Palmer from Paso del Rio, Colima (Mexico) in beds of Albian age (formerly assigned to the Cenomanian).

Canaliculate Structures

Canals tend to develop between vertical blades, when aligned along the outer shell margin one refers to pallial canals. They originate from the partitioning of cavities or gutters and have a significant record in several families with Lower Cretaceous representatives, e.g. Caprinidae d’Orbigny and Caprinuloideidae. Canals have their FO in *Pachytraga tubiconcha* Astre (Caprinidae) of Hauterivian age [31,32]. They play a major role in Caprinidae, e.g. *Praeacprina varians* Paquier (Figure 4A), *Offneria* (Figure 4B) and the Caprinuloideidae, e.g. *Amphistroelus warringi* (see Figure 3C). Pallial canals are present in the unrelated clade of “Caprinulidae” Yanin, 1990 (a family not recognized by Rineau, 2017, but independent from the Caprinidae), including *Sellaea* and *Neocaprina* [33,34]. Assuming a phylogenetic relationship between *Himeraelites* and *Sellaea* it is worth noting that canals, absent in *Himeraelites*, settled

in *Sellaea* on the RV anterior shell margin, but not in the LV perimyophoral cavity, usually canaliculated in the Caprinidae. The existence of anterior and posterior canals is recorded in *Neocaprina raghawiensis*, (Figure 4C) a putative descendant of *Sellaea* [35]. Canals are not uncommon in Polyconitidae. The RV of *Polyconites operculatus* (Roulland) (pro *Radiolites polyconilites* d’Orbigny, 1842) has dorsal, vertical canals (see d’Orbigny, 1842, pl. 574, Figure 3). The LV posterior perimyophoral cavity of *Magallanesia canaliculata* Sano, et al. [36] (Figure 4D) and *M. rutogensis* Rao, et al. [25], bear a row of radial canals. In the LV posterior perimyophoral cavity of *Praeacprina yegashii* (Yehara) canals are present in some specimens [37]. The foregoing data are a perfect illustration that canals evolved independently in several different clades [18,7]. So they are typical convergent evolutionary traits.

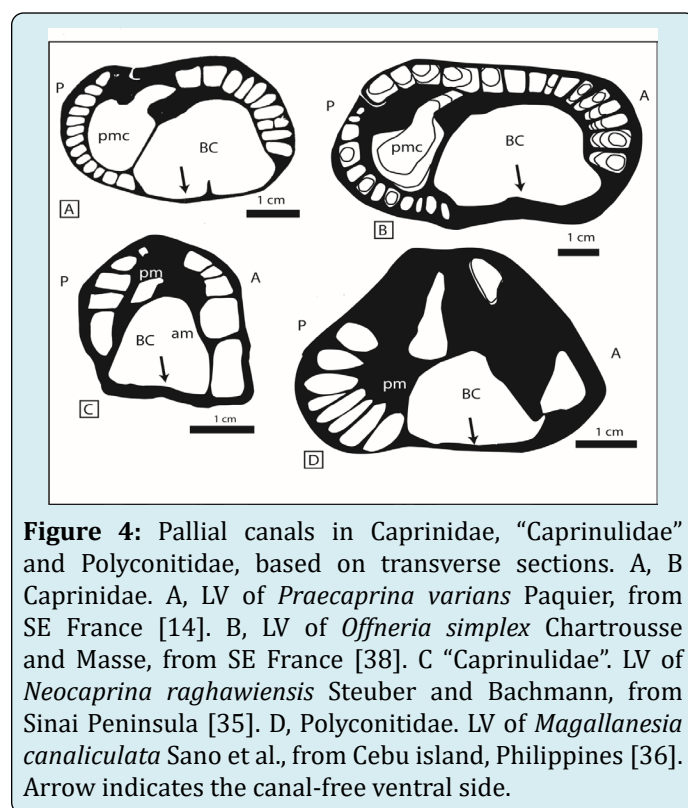


Figure 4: Pallial canals in Caprinidae, “Caprinulidae” and Polyconitidae, based on transverse sections. A, B Caprinidae. A, LV of *Praeacprina varians* Paquier, from SE France [14]. B, LV of *Offneria simplex* Chartrousse and Masse, from SE France [38]. C “Caprinulidae”. LV of *Neocaprina raghawiensis* Steuber and Bachmann, from Sinai Peninsula [35]. D, Polyconitidae. LV of *Magallanesia canaliculata* Sano et al., from Cebu island, Philippines [36]. Arrow indicates the canal-free ventral side.

Evolutionary Parallelism

In the families Caprinidae, Caprinuloideidae and “Caprinulidae” the geometry, mode of development and expansion of canals in the shell are nearly identical and evolved similarly. As shown by Coogan [39] and Coogan in Dechaseaux, et al. and Mitchell [40,41], canals of primitive forms are characterized by few simple radial walls, as in *Praeacprina* (Caprinidae) (Figure 4A), *Amphistroelus* (Caprinuloideidae) (Figure 3C) and *Neocaprina* (Caprinulidae) (Figure 4C). In these families the ventral side of primitive forms lack pallial canals, this is the case for *Praeacprina* (Figure 3A), *Amphistroelus* (Figure 3C),

Pediculate posterior myophores are recorded in the Mediterranean hippuritide clade, in the Barremian -early Aptian genus *Horiopleura*, their Caribbean counterparts are nearly contemporaneous, e.g. the early Aptian *Amphitriscoelus warringi*. The convergent requieniide *Pseudotoucasia*, is younger, late Aptian- Albian. Cellular structures have their FO in the late Aptian radiolitid genera *Archaeoradiolites* and *Eoradiolites*, but the convergent requieniide representative "*Toucasia-Apricardia* group", is younger, Albian. Acellular species of Radiolitidae, i.e. *Auroradiolites*, are late Aptian-Albian. Canal system developed in late Hauterivian- Barremian and early Aptian, in Caprinidae and Caprinuloideidae, and evolved parallel patterns. By contrast canaliculate Polyconitidae and "Caprinulidae" started to expand in the Albian and Cenomanian.

The foregoing shows that a peak in convergent traits is in the late Aptian- Albian, mostly in the context of the "Albian radiation" of Rineau [7]. This radiation is marked by emergence of new clades and, in the Caribbean, by a diversity peak in the caprinuloids [47] with a strong turnover of the Youngicaprininae [41]. The late Aptian-Albian events suggest a reset following the mid-Aptian extinction event [33,48].

Discussion

The strategy of pediculation implies that by contrast with a myophore on shell wall, muscles were not supported by a double (calcite+aragonite) shell layer, but a single nacre-made layer. Actually nacre consists of aragonitic nanobricks and a complex organic phase, having a high tensile strength, high elasticity and high resistance to breaking [49,50]. Given the orthogonal geometry of the pedicle -myophore device we tentatively assign to elasticity a major functional role. As discussed earlier [22] the development of a cellular shell structure had several advantages: minimizing the cost of metabolic energy used for skeletal production, acquisition of thick shells, facilitating quick growth and increasing resistance to shell breakage and sponge boring. The restatement of compact shell structures has a clear paleobiogeographic component and so most probably a link with environmental conditions prevailing in the Asian-Pacific faunal province [33]. Convergent traits were essentially taken by taxa from Caribbean, Asiatic and Apulian regions, the rarity of European representatives is probably the result of a contemporaneous lowering in diversity due to an Albian environmental deterioration [51-58]. Convergent taxa took some advantages by using former innovations assumed to be driven by both biological processes or by environmental constraints.

Conclusion

Two clades of the Lower Cretaceous Hippuritida,

requieniide (family Requiieniidae) and hippuritide (families Radiolitidae, Polyconitidae, Caprinidae, "Caprinulidae" and Caprinuloideidae), possess distinctive myophoral arrangements and shell structures. But they share some similar characters located in the RV of the first group and in the LV of the second group. The transverse shell thickening of the myophores of the attached valve are convergent traits in *Lovetchenia* (Requiieniidae) and *Homopleura* (Monopleuridae). The bent posterior myophore of the RV of *Pseudotoucasia* (Requiieniidae) closely resembles the posterior myophore of the LV of *Horiopleura* and *Polyconites* (Polyconitidae). The shell cellular structure is one of the key attributes of the family Radiolitidae (e.g. *Eoradiolites*) but this structure is also present in some advanced Requiieniidae ("*Toucasia-Apricardia*" group). The restatement of acellular Radiolitidae is a late Aptian -Albian event connected with the Asian -Pacific faunal province. Canaliculate shell structures which are common in the Caprinidae and Caprinuloideidae are also present in Polyconitidae and "Caprinulidae", and have long been considered as convergent evolutionary traits. In the foregoing canaliculated groups, with the exception of the Polyconitidae two trends are well expressed, 1- the expansion of canals into the entire shell, i.e. the invasion into the ventral margin, 2- the increasing complexity of canal architecture through time, these two phenomena reflect parallel evolution. Convergent taxa took some advantages by using former innovations. The late Aptian-Albian peak of convergence coincides with the emergence of new clades, mostly in the Caribbean and South Tethyan Mediterranean margins, it suggests a reset following the mid-Aptian extinction event.

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