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Colonization of empty shells by cryptic fauna: a global event and important ecological innovation in Ordovician benthic ecosystems

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In all modern seas, empty mollusc shell interiors are often heavily encrusted by cryptic invertebrates, whereas globally in the Cambrian, all shell interiors of molluscs and other invertebrates remained free of encrustation, though cryptic organisms themselves occurred in other types of cavities. The colonization of cryptic surfaces within empty shells constitutes a global event and an important ecological innovation in Ordovician benthic marine ecosystems, marking the beginning of a new ecological niche. The earliest colonization in mollusc shells by cryptic invertebrates occurred in the Middle Ordovician, while heavily encrusted shell interiors are known since the Late Ordovician. The taxonomic composition of Ordovician cryptic communities in gastropod, bivalve, and nautiloid shells is generally similar, though substrate architecture influenced encruster abundance and body size rather than overall community structure. The major expansion of cryptic ecological niches occurred during the Ordovician biodiversification, driven by the increase in predation pressure, the diversification of encrusting organisms, and a general increase in the size of mollusc shells.

Keywords Global event, Colonization of empty shells, Cryptic fauna, Evolution of encrustation, Ordovician

In modern marine environments, the interiors of empty molluscan shells are frequently densely colonized by cryptic invertebrates¹. In contrast, during the Cambrian, shell interiors of molluscs and other invertebrates worldwide show no evidence of encrustation, even though cryptic organisms inhabited other types of cavities^{2,3}. This changed in the Ordovician when interiors of empty molluscan shells became encrusted for the first time. The Great Ordovician Biodiversification Event (GOBE) represents one of the most significant increases in biodiversity during the Phanerozoic^{4–9}, but its influence on the evolution of cryptic faunas remains poorly understood.

During the Early Palaeozoic, cryptic communities underwent a period of substantial diversification, both in species richness and in the range of higher taxa represented¹⁰. Within Ordovician hard-substrate ecosystems, bryozoans and echinoderms were dominant colonizers, with bryozoans forming the principal framework of many cryptic assemblages¹¹. The structure of these ancient cryptic communities shows striking parallels to modern analogues. At the phylum level, ancient and modern cryptic communities have prominent bryozoans and tube-dwelling organisms. There is also a distinct trend of species diversity and surface coverage decreasing from the more illuminated margins toward the darker, deeper portions of the cavity^{10,12}.

The taxonomic development and spatial distribution of Phanerozoic cryptic biotas have been examined in considerable detail from the Palaeozoic through to modern marine systems^{2,10–23}. Collectively, this body of work has established a broad understanding of the taxonomic composition, ecological strategies, and long-term persistence of cryptic communities in a variety of concealed or sheltered habitats. These studies also demonstrate that cryptic biotas are not a marginal phenomenon, but rather a recurring and ecologically significant component of marine ecosystems throughout the Phanerozoic^{2,10–23}.

Despite this progress, the interiors of empty shells, a distinct habitat within the broader category of cryptic habitats, is comparatively understudied. Unlike reef cavities, borings, or interstitial spaces, vacant shells are discrete, mobile substrates that undergo a clear transition from biogenic structure to available habitat following

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the death of the host organism. This transformation creates opportunities for colonization by cryptic organisms, yet the processes governing the initial establishment of such communities remain poorly understood. At present, there is no widely accepted general model that explains how, why, and when colonization of empty shells began in marine settings.

Several fundamental questions, therefore, remain unresolved. It is unclear at what point in geological history this ecological strategy first emerged, and whether its origin was a localized phenomenon confined to specific basins or environments, or instead a more widespread, potentially global development. Likewise, the tempo of its emergence is uncertain: colonization may have developed gradually over extended intervals, tracking broader ecological innovations, or it may have appeared more abruptly in response to specific environmental or evolutionary triggers.

In addition, the broader evolutionary and palaeoecological context of empty shell colonization has not been adequately integrated into current frameworks. Key aspects—such as its relationship to increases in skeletal production, changes in predation pressure, or shifts in benthic community structure—remain insufficiently explored. As a result, although the presence of cryptic biotas is well documented, the origins and drivers of the exploitation of empty shells as habitats in marine environments remain incompletely understood.

The aim of this review is to analyze early shell-related cryptic faunas in terms of evolutionary palaeoecology. We here deal with shell-related cryptic faunas in the context of stratigraphy, paleogeography, global events, and evolutionary biology.

Methods

Data on cryptic associations were mostly taken from published literature. The relevant literature was found using three literature databases: (1) Google Scholar, (2) Web of Science and (3) Scopus. We used keywords such as “cryptic+fauna+ordovician”; “cryptic+steinkerns+ordovician”, “encrustation+internal surface+ordovician”, and “cryptic+encrusters+ordovician”, “cryptic+sclerobionts+ordovician” and “encrustation+cambrian”, “sclerobionts+cambrian”. In addition to database searches, basic Google search was used with same keywords. The papers found during the initial search were studied for further literature references, especially for those in non-Latin alphabet languages. Additional data (i.e., personal observations) include numerous steinkerns of molluscs in the Ordovician of Baltica and North America collected in the past twenty years.

Results

Empty shells in the Cambrian seas

There was a massive appearance of diverse shelly fossils in the Early Cambrian²⁴, and since then, the empty shells have been common on the sea floor. They were represented by gastropods, bivalves, nautiloids, hyolithids, brachiopods, and numerous minor skeletal groups^{25–27}. Cambrian shells were generally smaller than their Ordovician counterparts. The shells in the Cambrian seas were encrusted only on the exterior¹¹, though episkeletobionts are uncommon in Cambrian deposits¹¹. There are no reports of Cambrian shells containing cryptic fauna. Only a limited number of inarticulate brachiopods and eocrinoids have been reported on arthropod remains²⁸. In addition, Daley²⁹ documented solute echinoderms attached to trilobite fragments, which may themselves have been fixed within the seafloor.

Cryptic faunas in empty shells in the Ordovician

Most reports of cryptic faunas are associated with mollusk shells, i.e., nautiloids, bivalves, gastropods, and monoplacophorans^{20,30–33}. Cryptic organisms also colonized the shells of hyolithids (O. Vinn, personal observations) and conulariids³⁴, though rarely. Most diverse cryptic faunas have been reported from nautiloid shells, followed by gastropods and bivalves^{18,20,30–33} (Figs. 1, 2, 3, 4 and 5, Appendix 1).

The nautiloid shells were inhabited by bryozoans (both runner and sheet form), cornulitids, craniid brachiopods, encrusting graptolites, hydroids, and sponges^{18,20,33}. Bivalves contained bryozoans, cornulitids, craniid brachiopods, and sponges^{20,32}. Gastropod shells were colonized by bryozoans, cornulitids, graptolites, and sponges^{20,35}. The conulariids were colonized by monoplacophorans³⁴, and hyolithids by craniid brachiopods (O. Vinn, personal observations).

Cryptic organisms rely on sufficient water movement to supply suspended food and remove metabolic byproducts. Therefore, hydrodynamic conditions inside shell cavities were likely a critical factor influencing colonization success. In cases where bivalve shells remained articulated after death, the wide opening between the valves would have promoted effective through-flow circulation within the cavity¹. This likely accounts for the relatively high proportion of encrusted bivalve specimens observed in Vinn et al.³². Likewise, nautiloid body chambers generally have large apertures, producing a more open internal environment than that of gastropods and thus supporting a higher occurrence of cryptic encrusting fauna³³. By contrast, most gastropods possess narrow openings and coiled shell morphologies, conditions that tend to limit colonization by cryptic invertebrates³⁵.

All encrusting organisms identified within molluscan interiors are suspension feeders^{32,33,35}. Similar taxa have previously been documented in nautiloid shells, particularly bryozoans, cornulitids, and graptolites, as well as in bivalves, where cornulitids and bryozoans are common. In gastropod shells, cryptic encrusters are typically very small, generally smaller than comparable species found in empty bivalve³² or nautiloid shells³³.

The taxonomic makeup of cryptic communities inhabiting gastropod, bivalve, and nautiloid shells is largely comparable^{32,33,35}. A notable exception is the absence of encrusting brachiopods in gastropod shells^{32,33,35}. In bivalves, such brachiopods are usually located near the commissural opening, where water circulation is stronger, and food supply is greater³². Their absence in gastropods likely reflects restricted water exchange and

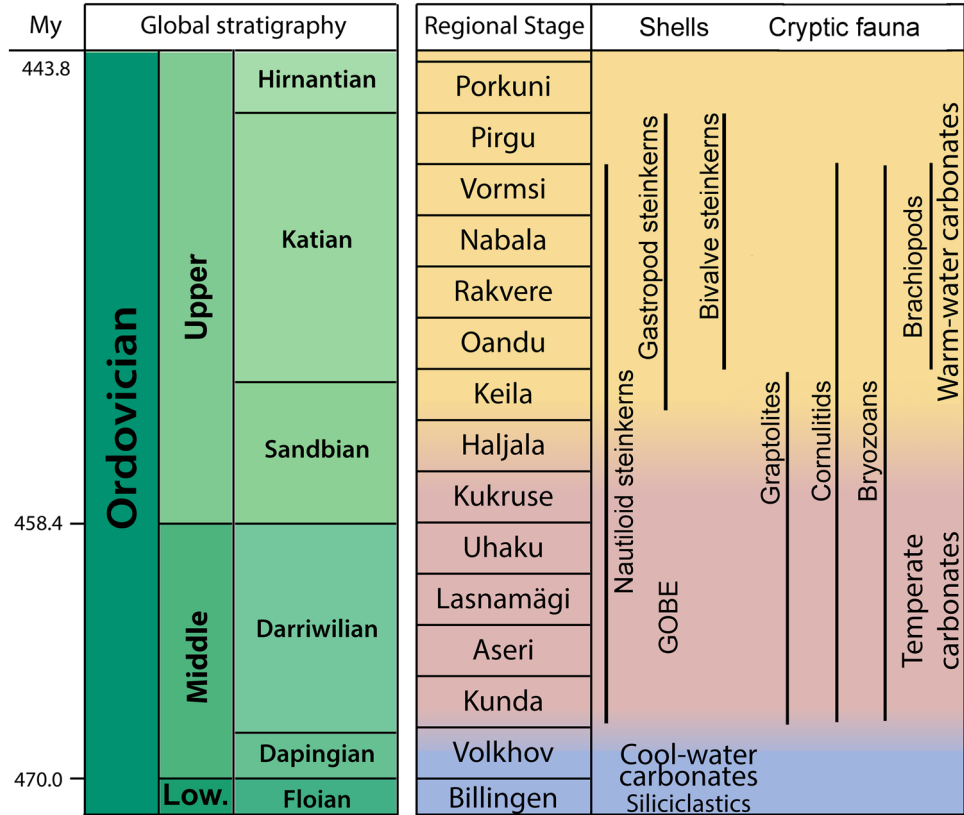


Fig. 1. Stratigraphy of colonization of empty shells by cryptic fauna in the Middle and Upper Ordovician of Baltica.

potentially low-oxygen conditions within the coiled shell interior, which would have hindered colonization by these more flow-dependent suspension feeders³⁵.

Temporal order of cryptic faunas in empty shells and paleobiogeography

Cryptic faunas first appeared in empty shells in the Darriwilian of Baltica^{30,31,33}. The temporal order of colonization by different encruster groups is only known for Baltica (Fig. 1). In the Darriwilian, the first cryptic cornulitids, bryozoans, and graptolites appeared^{30,31,33}. The cryptic craniid brachiopods appeared later in the Sandbian^{32,33}. By shell type, the first were colonized nautiloid shells at the beginning of the Darriwilian^{30,31,33}, then gastropod and hyolithid shells in the late Sandbian³⁵, and lastly bivalve shells at the beginning of the Katian³²(Fig. 1).

In Laurentia, the earliest cryptic faunas from empty shells are known since the Cincinnati¹⁸. The Late Ordovician (Cincinnati) strata on Laurentia (across Ohio, Indiana, and Kentucky) provide numerous instances of cryptic biotic assemblages inhabiting vacant molluscan shells^{18,36,37}. After the death of the original organism, the inner surfaces of gastropod, monoplacophoran, bivalve, and nautiloid shells were colonized by skeletobionts. These communities are predominantly composed of encrusting sheet- and runner-form bryozoans, along with cornulitids, and include occasional craniid brachiopods and microconchids^{18,37}. Epibiotic bryozoans growing on the cryptic side of hyolithid shells have been reported from Ordovician deposits of Laurentia^{38,39}.

Similarly, cryptic faunas are preserved in Late Ordovician empty molluscan shells (i.e., bivalves, gastropods, and nautiloids) in South China. The only cryptic organisms reported from the South China Plate are sponges²⁰. The only cryptic organisms reported from Gondwana (Czech Republic) are monoplacophoran *Barrandicella* found in conulariid thecae from the Middle Ordovician (Darriwilian) deposits³⁴.

The cryptic faunas were most diverse in Baltica and Laurentia, and these faunas are also most similar at higher taxonomic levels.

Discussion

Empty shells and cryptic faunas in the Cambrian world

Molluscan and other skeletal shells were already common elements of shallow-marine substrates in Early Cambrian ecosystems, forming part of the available hardground mosaic on the seafloor^{9,11}. In principle, such empty shells could have provided enclosed cavities suitable for colonization by cryptic organisms. Yet clear evidence for cryptic encrusting communities within these early shell substrates is absent¹¹, although cryptic communities flourished in thrombolite cavities in the Cambrian^{2,3}. One plausible explanation lies in the limited diversity and ecological prominence of encrusting metazoans at that time. Cambrian benthic communities contained relatively few taxa capable of persistent skeletal encrustation compared with later Palaeozoic faunas,

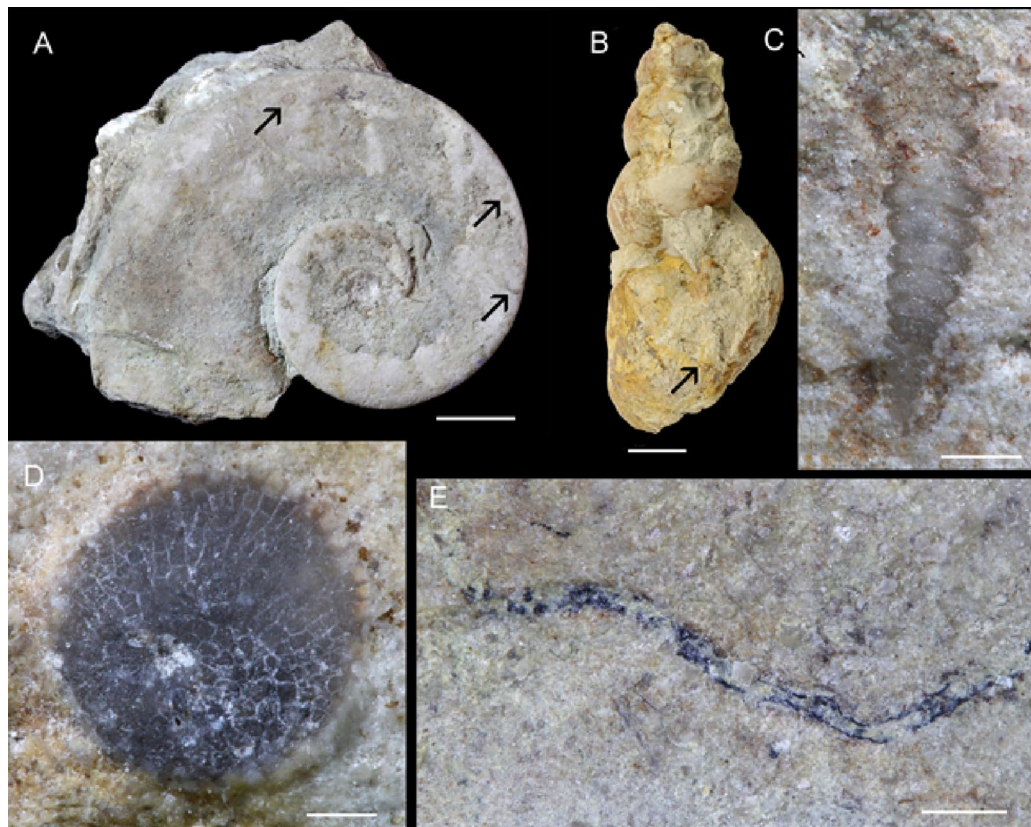


Fig. 2. Gastropod steinkerns with cryptic fauna. (A) Steinkern of *Maclurites neritoides* containing cryptic fauna cornulitids, bryozoans, and graptolites (arrows) from Haapsalu, Pirgu Regional Stage, Katian (GIT 897–112). Scale bar 10 mm. (B) Steinkern of *Hormotoma insignis* containing cryptic cornulitid (arrow) from Rakvere, Rakvere Regional Stage, Katian (TUG 665–251). Scale bar 10 mm. (C) Cryptic *Cornulites* sp. in steinkern of *Maclurites neritoides* (GIT 840–87) from Hosholm shore, Vormsi Island, Pirgu Regional Stage. Scale bar 0.5 mm. (D) Cryptic bryozoan in steinkern of *Maclurites neritoides* from Vohilaid, Pirgu Regional Stage (GIT 404–1000). Scale bar 0.5 mm. (E) Cryptic encrusting graptolite in steinkern of *Maclurites neritoides* (GIT 840–87) from Hosholm shore, Vormsi Island, Pirgu Regional Stage. Scale bar 1 mm.

and the ecological strategies associated with sessile suspension-feeding colonizers were still in an early stage of expansion, although Cambrian archaeocyathid and thrombolite “reefs” also contain some crowded crypts^{2,3}. As a result, even though potential substrates in the form of empty shells were present, the biological capacity to exploit them may not yet have been fully developed. Moreover, many shelly taxa were generally smaller in the Cambrian, and the Ordovician saw a clear expansion toward larger average shell volumes, especially in cephalopods and gastropods, though groups like hyolithids show weaker trends^{40–42}. Thus, a small shell volume may have also prevented colonization of empty shells by cryptic fauna in the Cambrian.

Global event of colonization of empty shells by cryptic fauna

In contrast to the Cambrian, the Ordovician witnessed a substantial increase in both taxonomic diversity and ecological importance of encrusting organisms^{9,11} associated with the broader restructuring of marine ecosystems during the Great Ordovician Biodiversification Event. Bryozoans, cornulitids, echinoderms, and other sessile encrusters became abundant components of hard-substrate communities¹¹, enhancing competition for space and expanding the range of exploited microhabitats. The colonization of empty molluscan shells by cryptic suspension feeders can therefore be viewed not only as a response to ecological pressures such as intensified predation on exposed surfaces, but also as a reflection of the evolutionary maturation of encrusting life modes themselves. As these organisms diversified and increased in abundance, previously underutilized microhabitats, including enclosed shell cavities, became viable ecological opportunities. Moreover, the evolutionary increase of shell volume in molluscs^{40–42} may have made the empty molluscan shell more suitable for cryptic fauna in the Ordovician as compared to generally small shells in the Cambrian.

By the Late Ordovician, shells on shallow marine seafloors were frequently subject to dense external encrustation¹¹, with skeletal surfaces supporting diverse epifaunal assemblages. Such intense occupation of exposed surfaces may have further promoted settlement within sheltered cavities, either through competitive exclusion or through selective advantages offered by protected environments. Consequently, the emergence of cryptic shell-dwelling communities represents a convergence of substrate availability, ecological competition, and evolutionary innovation. Rather than reflecting a simple change in environmental conditions alone, the



Fig. 3. Reconstruction of an empty gastropod shell (not to scale) on the Ordovician sea floor showing cryptic cornulitid tubeworms and bryozoans.

Ordovician global expansion of cryptic encrusters illustrates how the diversification of benthic organisms reshaped patterns of habitat exploitation, transforming empty shells into ecologically significant microhabitats within Palaeozoic marine ecosystems.

The colonization of cryptic surfaces within empty molluscan shells represents an important ecological innovation in Ordovician benthic ecosystems, occurring on Baltica, Laurentia, South China, and Gondwana^{18,20,30–34}. Ordovician cryptic assemblages in molluscan shells typically include bryozoans, cornulitids, craniid brachiopods, monoplacophorans, sponges, and graptolites^{20,30–34}. Evidence from the Ordovician record of Baltica and other palaeocontinents indicates that the earliest well-documented occurrences of such communities are associated with nautiloid body chambers during the Darriwilian, when vacant cephalopod conchs began to function as enclosed hard substrates on the seafloor^{30,31}. These cavities provided protected microenvironments distinct from exposed skeletal surfaces, enabling settlement by small suspension-feeding encrusters. Due to their high internal volume and surface area, nautiloid shells were best water-circulated (i.e., nutrient-rich) and well oxygenated, which may be why they were first colonized. By the Late Ordovician, the range of exploited substrates expanded to include the interiors of bivalve³² and gastropod shells, suggesting a broadening ecological utilization of cryptic habitats and perhaps the appearance of more specialized cryptobionts able to thrive in cavities with inferior conditions compared to those in nautiloid shells. By the Late Ordovician, cryptic faunas inhabiting empty shells had become widespread^{20,30–34}, indicating that colonization of enclosed shell cavities was an established component of benthic community structure.

Paleobiogeographic and paleoenvironmental dimensions

Cryptic faunas inhabiting empty shells are first recorded in the Darriwilian of Baltica^{30,31,33}, before their more widespread Late Ordovician occurrence elsewhere^{18,20,34}. This earlier appearance suggests that the ecological strategy of exploiting vacant shells as cryptic habitats may have originated in this region before becoming more broadly established. The Darriwilian record from Baltica argues in favor of an earlier origin there; however, this interpretation must be treated cautiously, as it may partly reflect sampling and research bias, given that a substantial proportion of documented occurrences derive from Baltic material^{30–33}.

Both Baltica and Laurentia host the most taxonomically diverse and compositionally rich cryptic assemblages^{18,30–33}. During the Ordovician, these palaeocontinents were situated relatively close to one another, facilitating faunal exchange and ecological similarity. At higher taxonomic levels, their cryptic faunas show strong overlap, indicating either shared evolutionary origins or ongoing biogeographic connectivity. Importantly, in both regions, these communities are closely associated with carbonate platforms^{18,30–33}, suggesting a strong environmental control on their development. This pattern supports the hypothesis that either Baltica or Laurentia served as the primary center for the initial colonization of empty shells by cryptic organisms.

Ordovician encrusting communities are widespread in peri-Gondwanan regions, such as the Czech Republic^{34,43,44} as well as in Iran⁴⁵ and in Gondwana, including South Africa⁴⁶. However, reports of cryptic

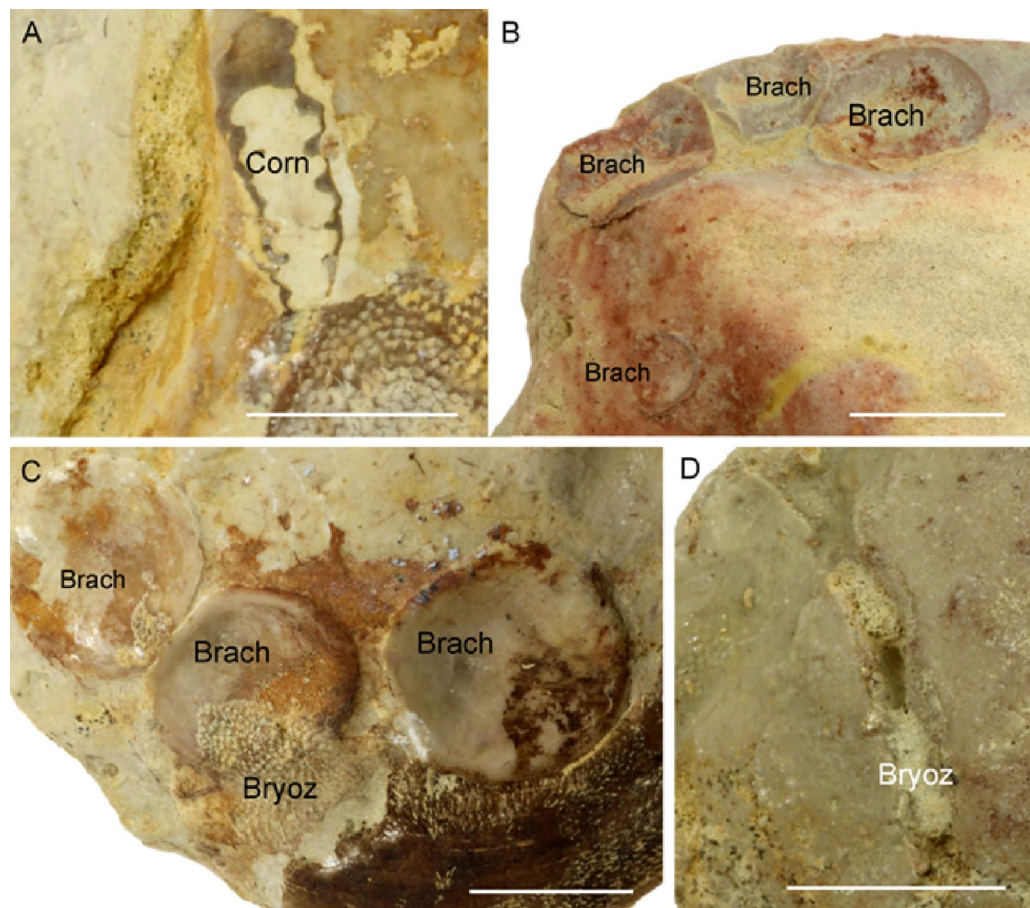


Fig. 4. Cryptic fauna in bivalve steinkerns from the Upper Ordovician of Estonia. (A) Cryptic *Cornulites* sp. (TUG 1779–455). (B) Cryptic *Petrocrania* sp. (TUG 76–160). (C) Cryptic *Petrocrania* sp. (TUG 1779–468). (D) Cryptic bryozoan (TUG 1779–444). Scale bars 5 mm.

epibionts remain relatively uncommon. For example, in the Darriwilian strata of the Prague Basin, most encrusting organisms—such as edrioasteroids, possible crinoid holdfasts, and bryozoans—are attached to exposed shell surfaces. A notable exception is the monoplacophoran *Barrandicella*, which colonized concealed surfaces inside empty conulariid thecae³⁴. Molluscs from the Late Ordovician of China commonly contain patches of “spicular” demosponge remains²⁰.

In conclusion, the colonization of empty shells by cryptic faunas appears to have been strongly linked to carbonate platform settings. Several factors likely explain this association. Carbonate platforms are characterized by high rates of skeletal production, generating an abundance of empty shells that can serve as substrates for encrusting fauna⁴⁷. These environments also typically exhibit clear, well-oxygenated waters with active hydrodynamic regimes⁴⁷, conditions that favor suspension-feeding organisms and promote effective water circulation within cavities. In addition, carbonate settings often support complex benthic ecosystems with diverse hard substrates⁴⁷, increasing opportunities for larval settlement and ecological specialization. Together, these factors would have made carbonate platforms particularly suitable for the early establishment and diversification of cryptic, shell-inhabiting communities.

Cryptic fauna in empty shells and the GOBE

The temporal pattern of colonization of empty shells by cryptic faunas parallels the ecological restructuring associated with the Great Ordovician Biodiversification Event (GOBE), which led to significant diversification of encrusting faunas⁷. At the same time, the diversification of benthic predators, including grazing, drilling, and durophagous taxa⁴⁸, increased biological disturbance on exposed surfaces of hard substrates. Under these circumstances, sheltered microhabitats such as shell interiors may have provided partial refugia from predation and mechanical disruption, thereby favoring their occupation by delicate suspension-feeding encrusters. Colonization of cryptic environments can therefore be interpreted not only as an opportunistic exploitation of available substrate, but also as an adaptive response to intensifying ecological pressures within increasingly complex trophic networks.

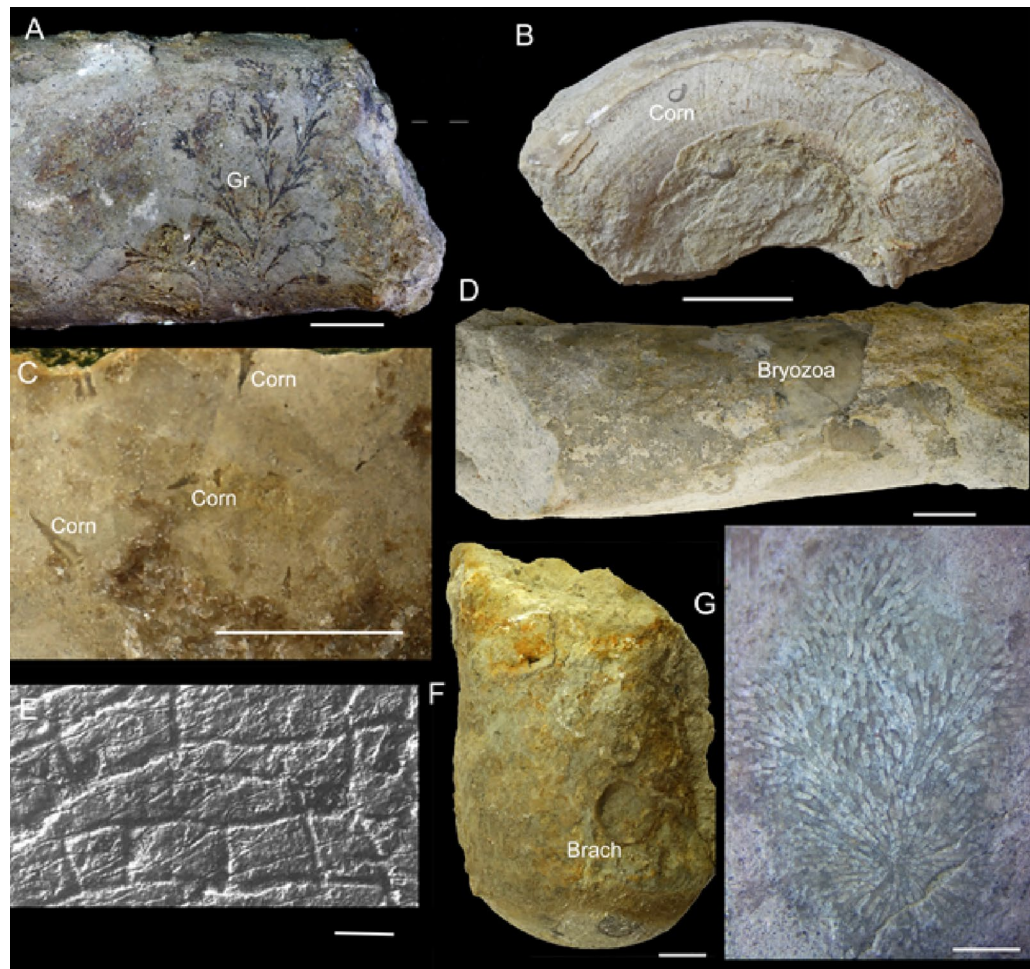


Fig. 5. (A) A mould of an orthoconic nautiloid body chamber (TUG 1317-3) contains a single large graptolite colony of *H. ramulus*, lower Katian, Keila Regional Stage, Lilli. (B) Body chamber of *Discoceras saemanni* (GIT 426–395) contains a single cryptic cornulitid. (C) Body chamber of nautiloid (Multiceratoidea) contains multiple small cryptic cornulitids (TUG 1743-37), Vormsi Regional Stage, Vormsi Island, Saxby Beach. (D) Body chamber of an unidentified nautiloid contains four large bryozoan colonies (TUG 663-8), Haljala Regional Stage, Sandbian, Männiku. (E) Bioimmured hydroid on the internal surface of nautiloid body chamber, Kentucky, USA, Upper Ordovician (after Wilson et al.¹⁸). (F) Body chamber of nautiloid *Kiaeroceras* contains cryptic brachiopods *Petrocrania* spp. (TUG 1745–201), Vormsi regional Stage, Katian, Kärda Quarry. (G) Cryptic bryozoan colony in nautiloid *Lituites lituus* body chamber from Ilumäe Quarry, Lasnamägi Regional Stage, Darriwilian (TUG 94–1). A–D, F, scale bars 10 mm. E, scale bar 0.2 mm. G, scale bar 2 mm.

Evolutionary paleoecology of early cryptic faunas in empty shells

Different encrusting groups appear to have adopted cryptic niches at different stages of their evolutionary histories. Bryozoans and cornulitids, both early and successful encrusters on open substrates, colonized cryptic shell interiors soon after their first appearance in the fossil record. Their modular or tube-dwelling growth forms and capacity to exploit low-light environments likely facilitated this ecological transition. The runner-type bryozoan *Corynotrypa* was prominent in cryptic habitats of the Ordovician⁴⁹, likely because it could quickly occupy narrow and restricted spaces³⁶. In contrast, brachiopods inhabiting cryptic niches appear later and are comparatively rare in early records of shell-cavity colonization, occurring only in well-ventilated cryptic spaces. Their delayed appearance in such settings may reflect stricter physiological or hydrodynamic requirements, including greater dependence on sustained water circulation for feeding, which would have limited their establishment in poorly ventilated microhabitats.

The progressive expansion of cryptic encrusters across different shell types also highlights the importance of substrate architecture in structuring early community evolution. Nautiloid body chambers offered relatively spacious and accessible cavities³⁰, whereas bivalve commissural openings³² and gastropod apertures imposed varying degrees of restriction on water flow and larval entry. Such differences likely governed the timing and intensity of colonization, influencing both community density and taxonomic composition.

In summary, the emergence and diversification of cryptic encrusting communities within empty shells during the Ordovician reflect a complex interplay of ecological opportunity, evolutionary innovation, and environmental pressure. The early adoption of these habitats by certain taxa and the later participation of others illustrate how

substrate availability and ecosystem restructuring during the GOBE shaped the trajectory of benthic community development. These cryptic assemblages thus provide valuable insight into the expanding ecological complexity of Palaeozoic marine ecosystems and the adaptive strategies of early suspension-feeding encrusters.

Other potential shell types and future research directions

Skeletons of echinoderms, especially cystoids and echinoids, constitute another class of potential cryptic habitats in the Ordovician seas. However, their calcitic walls usually fossilize, and their interiors are difficult to access. However, in siliciclastic settings where calcitic fossils have been dissolved, their internal molds could reveal traces of possible cryptic fauna. Similarly, calcitic brachiopods do not commonly occur in carbonate rocks as steinkerns, and their interiors are also difficult to access. It is almost entirely in siliciclastic settings where brachiopod walls have been dissolved that their internal molds can reveal traces of cryptic fauna. On the other hand, valves of dead brachiopods often remain closed, reducing the likelihood that brachiopod shells will be colonized by cryptic organisms. There are scattered reports of conchicoles (i.e., mobile animals) occupying empty gastropod and nautiloid shells^{50,51}, and one could ask what effects they might have on the encrusting fauna inside shells. It is likely that larger mobile animals, such as hermit crabs, could have prevented the settlement of encrusting fauna, as their activity would have been too disruptive to encrusting suspension feeders. However, smaller mobile animals may have coexisted with cryptic encrusting suspension feeders.

Conclusions

The occupation of sheltered internal surfaces within empty mollusc shells represents a notable ecological development in Ordovician benthic systems, a global event that marks the beginning of the utilization of a new ecological niche. During this interval, marine communities underwent a pronounced rise in both taxonomic richness and functional significance of encrusting organisms, reflecting the large-scale ecological reorganization associated with the Great Ordovician Biodiversification Event. Bryozoans, cornulitids, echinoderms, and other sessile forms became widespread colonizers of hard substrates, intensifying spatial competition and promoting exploitation of increasingly diverse microhabitats. The use of vacant shell cavities by suspension-feeding encrusters should therefore be interpreted not solely as a reaction to escalating predation pressures on exposed surfaces, but also as evidence of the progressive ecological expansion of encrusting strategies and an increase in average empty molluscan shell volume. As these taxa diversified and proliferated, environments that had previously seen limited utilization—including enclosed shell interiors—were incorporated into their ecological repertoire as accessible and exploitable habitats.

Data availability

All data are included in Appendix 1.

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Declarations

Competing interests

The authors declare no competing interests.

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