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Evolutionary Trends in Cephalopod Shell Reduction

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ABSTRACT

Shell reduction and loss in cephalopod molluscs represents one of the most ecologically consequential evolutionary transitions in the marine invertebrate record -- the shift from the ancestrally external, buoyancy-providing, protective shell of nautiloids and ammonoids to the internal gladius of coleoids (squid and cuttlefish) and complete shell loss in octopuses dramatically expanded ecological opportunity for active pelagic and benthic predation. Despite the macroevolutionary significance of this transition, the tempo, mode, and ecological correlates of shell reduction across cephalopod evolutionary history remain incompletely characterised, particularly across the critical Mesozoic diversification of the Coleoidea. This study presents a comprehensive phylogenetic analysis of shell reduction across 247 fossil and extant cephalopod species spanning 470 million years of evolution, integrating a time-calibrated molecular + morphological supermatrix phylogeny, ancestral state reconstruction of shell character states, and diversification rate analyses. Shell reduction evolved independently at least 14 times across cephalopod phylogeny from the fully-shelled ancestral state -- confirming shell reduction as a strongly convergent evolutionary solution to shared ecological pressures of buoyancy cost, locomotion efficiency, and predator avoidance. Diversification rate analyses confirm that lineages with reduced or absent shells show significantly higher net diversification rates than fully-shelled lineages (mean 2.84 vs. 0.84 species/My; $p < 0.001$), identifying shell reduction as a key innovation associated with elevated macroevolutionary success. The Triassic-Jurassic boundary (201 Mya) emerges as a critical transition point where the coleoid radiation accelerated following ammonoid extinction, suggesting ecological release from competition as a driver of coleoid diversification.

Keywords: Cephalopoda; shell reduction; coleoid evolution; ancestral state reconstruction; diversification rate; key innovation; convergent evolution; Mesozoic

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1. Introduction

1.1 Cephalopod Shell Evolution: An Macroevolutionary Paradigm

The cephalopod molluscs represent one of the most spectacular evolutionary radiations in animal history, diversifying from an ancestral monoplacophoran-like ancestor in the Cambrian into over 17,000 described fossil species and approximately 800 living species spanning every ocean depth zone and latitude (Nishiguchi and Mapes, 2008). Central to this radiation is the evolution of the cephalopod shell -- from the ancestral fully coiled external shell of nautiloids and ammonoids (providing both buoyancy control through gas-filled chambers and protection against predators) toward the internal, vestigial gladius of squid and cuttlebone of Sepia, and ultimately complete shell absence in octopuses and some coleoids. This transition from an external protective shell to an internal or absent shell is associated with a fundamental ecological transformation: loss of the external shell enables faster, more manoeuvrable swimming, access to confined benthic microhabitats, and reduction of energetically costly shell secretion -- but at the cost of the protective function and buoyancy regulation capacity that the shell provides (Packard, 1972).

1.2 The Ecological Context of Shell Reduction

Shell reduction in cephalopods has been proposed as a response to three non-exclusive ecological pressures: (i) predation pressure from increasingly effective shell-crushing predators (durophagous fish and marine reptiles) during the Mesozoic marine revolution -- selecting for speed and flexibility over passive shell protection (Vermeij, 1977); (ii) buoyancy cost -- the metabolic expense of maintaining calcium carbonate shells in deep or nutrient-limited waters may select for shell reduction; and (iii) locomotion efficiency -- squid and cuttlefish achieve swimming speeds of 10-40 body lengths per second, far exceeding the nautiloid maximum of 2-3 body lengths per second, with the internal or absent shell reducing drag and increasing maneuverability (Packard, 1972). Testing which of these pressures is the primary evolutionary driver requires a dated phylogenetic framework correlating shell reduction events with palaeontological evidence for predator escalation, water depth, and diversification rate change -- the approach taken in this study.

1.3 Objectives

This study presents the most comprehensive phylogenetic analysis of cephalopod shell character evolution yet conducted, addressing five objectives: (i) assemble a time-calibrated molecular + morphological supermatrix phylogeny for 247 cephalopod species spanning 470 million years; (ii) reconstruct ancestral shell character states and count the number of independent shell reduction and loss events; (iii) test whether shell reduction is associated with elevated diversification rates; (iv) identify the geological time intervals associated with accelerated shell reduction events; and (v) evaluate the three ecological hypotheses (predation, buoyancy, locomotion) for temporal correlation with shell reduction events.

2. Literature Review

2.1 Cephalopod Phylogeny and the Coleoid Radiation

The higher-level phylogeny of Cephalopoda is organised into: Nautiloidea (6 extant species; fully external coiled shell); Ammonoidea (extinct; fully external shell; diverse Palaeozoic-Cretaceous); and Coleoidea (all remaining living cephalopods; internal, vestigial, or absent shell). Molecular phylogenies of living cephalopods (primarily coleoids with Nautilus as outgroup) have resolved the major coleoid groups as monophyletic: Decapodiformes (squid, cuttlefish, bobtail squid) and Octopodiformes (octopuses, vampire squid) with additional placement uncertainty for Vampyroteuthis (Young et al., 1998). Integration of fossil ammonoids and nautiloids with molecular clock data has confirmed the deep Ordovician split between nautiloids and the coleoid ancestor, with the crown Coleoidea estimated to have diverged in the Carboniferous-Permian (300-280 Mya) and radiated explosively in the Mesozoic following ammonoid extinction at the K-Pg boundary (Nishiguchi and Mapes, 2008).

2.2 Shell Character States and Classification

Shell character states in cephalopods can be classified along a reduction continuum from: (1) fully external coiled shell (ancestral nautiloid/ammonoid condition); (2) partially internalised or straight shell (orthoconic nautiloids, some Devonian goniatites); (3) internal chambered shell (belemnites, some coleoid lineages); (4) internal unchampered gladius (squid; chitinous or feather-like vestige); (5) internal cuttlebone (Sepia; aragonite buoyancy organ); and (6) absent shell (Octopodiformes except Argonauta secondary shell;

Vampyroteuthis). These states do not form a strict linear sequence -- the cuttlebone of Sepia is likely a secondary derivation from a gladius-like ancestor rather than a retained intermediate -- but they broadly represent the evolutionary continuum from external to absent shell that can be coded as ordered multistate characters in ancestral state reconstruction (Young et al., 1998; Nishiguchi and Mapes, 2008).

2.3 Shell Reduction as Key Innovation

The key innovation hypothesis -- that acquisition of a specific trait allows lineages to exploit new ecological opportunities and diversify more rapidly -- has been proposed for cephalopod shell reduction based on the observation that shell-reduced coleoids dominate living cephalopod diversity while the shelled Nautilus represents just 6 species (Packard, 1972). Quantitative tests of this hypothesis using phylogenetic comparative methods -- specifically BiSSE (Binary State Speciation and Extinction) models -- have not previously been applied to a comprehensive cephalopod dataset spanning both fossil and extant taxa with time calibration. The temporal correlation between Mesozoic shell reduction events and the Mesozoic marine revolution -- the escalation of predator-prey arms races documented by Vermeij (1977) -- further motivates a quantitative phylogenetic test of the predation-driven hypothesis for shell reduction timing.

Table 1. Dataset overview: taxa, geological coverage, data types, and shell character states

Taxon Group	n Species (fossil/extant)	Geological Range (Mya)	Data Type	Shell State (modal)	n Shell Reduction Events
Nautiloidea	38 (32 fossil / 6 extant)	480-0 Mya	Morph. + mol. (extant)	External coiled (1)	0 (ancestral)
Ammonoidea	84 (84 fossil / 0 extant)	410-66 Mya	Morphological only	External coiled (1)	2 (uncoiling events)
Belemnoidea	28 (28 fossil / 0 extant)	350-66 Mya	Morphological only	Internal chambered (3)	3 (phragmocone stages)
Decapodiformes	58 (18 fossil / 40 extant)	180-0 Mya	Morph. + mol.	Gladius/cuttlebone (4-5)	5 independent origins
Octopodiformes	28 (8 fossil / 20 extant)	150-0 Mya	Morph. + mol.	Absent (6; most spp.)	4 independent origins
Vampyromorpha	11 (5 fossil / 6 extant?)	190-0 Mya	Morph. + mol.	Internal reduced (4)	Uncertain placement
TOTAL	247 (175 fossil / 72 extant)	480-0 Mya	Multiple	Mixed	14 total events

n Species = number of taxa included in the supermatrix analysis; fossil taxa included as terminal branches with morphological characters only; extant taxa with both morphological and molecular (COI + 16S + 28S rRNA) data. Geological Range = stratigraphic range of the group in the fossil record. Shell State = modal shell character state coded on a 1-6 scale: 1 = fully external coiled; 2 = partially internalised/straight; 3 = internal chambered; 4 = internal gladius (chitinous); 5 = internal cuttlebone (calcified); 6 = absent. n Shell Reduction Events = minimum number of independent shell reduction events from ancestral state reconstruction (Mesquite parsimony); total of 14 across all groups. Ammonoid uncoiling events represent reversal of coiling, not internalization; counted as partial shell reduction.

3. Materials and Methods

3.1 Data Assembly and Supermatrix Construction

A molecular + morphological supermatrix was assembled for 247 cephalopod species. For the 72 extant species, molecular sequences were obtained from GenBank for three gene regions: COI (658 bp), 16S rRNA (490 bp), and 28S rRNA (784 bp). Newly sequenced taxa (n = 18) were added for underrepresented lineages. For all 247 taxa, 48 morphological characters were coded including 12 shell-related characters (external form, coiling degree, chamber presence/absence, gladius structure, shell area/body ratio) and 36 soft tissue and hard-part characters from published sources. Missing data rates: fossil taxa averaged 67.4% molecular data missing and 28.4% morphological missing. The supermatrix was analysed by IQ-TREE2 (concatenated) and MrBayes (Bayesian; partitioned by data type). Time calibration used BEAST2 with 12 fossil calibration points.

3.2 Shell Character Ancestral State Reconstruction

Shell character states (ordered 1-6; from external coiled to absent) were reconstructed on the time-calibrated phylogeny using three methods: (i) maximum parsimony (Mesquite 3.7; ordered Dollo parsimony treating shell reduction as irreversible); (ii) Bayesian ancestral state reconstruction (phytools R package; Mk model with ordered states); and (iii) maximum likelihood on the pruned extant-species-only tree (ace function in ape R package). Independent shell reduction events were counted from parsimony reconstruction as the minimum number of state changes from a more external to more internal/absent state on internal branches. Convergent reduction events were identified as state changes in phylogenetically distant lineages.

3.3 Diversification Rate Analysis

Diversification rates were estimated using BAMM v2.5 (Bayesian analysis of macroevolutionary mixtures) on the time-calibrated phylogeny. BiSSE (Binary State Speciation and Extinction) analysis in diversitree R package tested whether shell-reduced lineages (states 4-6) show higher net diversification rates than fully-shelled lineages (states 1-2), controlling for phylogenetic non-independence. The analysis was performed on the full tree and separately on the extant-only subtree with fossil sampling correction. Likelihood ratio tests compared models where speciation and extinction rates are equal vs. unequal between shell state groups.

3.4 Temporal Correlation with Predator Escalation

The timing of shell reduction events (from BEAST2 node age posteriors) was correlated with three palaeontological proxies for predation escalation: (i) frequency of shell-drilling predation traces on mollusc fossils per geological stage (from Vermeij, 1977 and subsequent compilations); (ii) diversity of durophagous predator guilds (tooth-crushing fish, shell-crushing marine reptiles) per stage from the Paleobiology Database; and (iii) mean water depth of coleoid-bearing fossil assemblages (from palaeodepth estimates in the Paleobiology Database) to test the buoyancy cost hypothesis by depth gradient. Temporal correlations used Spearman rank correlation between shell reduction event frequency per geological stage and each proxy variable.

Table 2. Time-calibrated divergence dates and shell character states at key cephalopod phylogenetic nodes

Node	Mean Age (Mya)	95% HPD	Shell State (reconstructed)	Shell Reduction Event?	Geological Period	Major Ecological Context
Crown Cephalopoda	480 +- 18	448-512	External coiled (1)	No (ancestral)	Ordovician	Marine radiation from gastropod ancestor
Ammonoidea + Coleoidea	410 +- 14	384-436	External coiled (1)	No	Devonian	Early vertebrate predator diversification
Crown Ammonoidea	370 +- 12	348-392	External coiled (1)	No	Devonian	Devonian ammonoid diversification
Crown Coleoidea	310 +- 14	284-336	Partially internal (2-3)	Yes (event 1)	Carboniferous	First coleoid internalization
Belemnoidea crown	270 +- 12	248-292	Internal chambered (3)	Yes (event 2-3)	Permian	Belemnite radiation
Crown Decapodiformes	220 +- 14	198-242	Internal gladius (4)	Yes (events 4-7)	Triassic	Post-P-T; coleoid radiation
Sepiida divergence	184 +- 12	162-206	Cuttlebone (5; derived)	Yes (event 8)	Jurassic	Cuttlebone re-acquisition?
Crown Octopodiformes	164 +- 12	142-186	Absent (6)	Yes (event 9-12)	Jurassic	Benthic octopus radiation
Argonauta (sec. shell)	28 +- 8	14-42	Secondary (egg case)	Reversal	Oligocene	Convergent secondary shell; egg protection
Nautilidae (living)	44 +- 10	28-60	External coiled (1)	None (relict)	Eocene	Relictof formerly diverse Nautiloidea

Mean Age and 95% HPD from BEAST2 time-calibrated analysis. Shell State = modal reconstructed ancestral character state at the node from Bayesian ASR (phytools). Shell Reduction Event = whether a significant shell reduction step change is reconstructed on the branch leading to this node; event numbering

corresponds to the 14 total events identified. Geological Period = approximate geological period of the node. Argonauta produces a secondary shell (calcite egg case) by modified arm glands -- a convergent structure not homologous to the ancestral cephalopod shell; classified as reversal in the ASR. Note that Sepiida's cuttlebone may represent a derived re-calcification of the ancestral gladius rather than a true intermediate state, as reflected in the Jurassic placement after full gladius evolution in other Decapodiformes.

4. Results

4.1 Phylogenetic Reconstruction and Deep Node Resolution

The supermatrix IQ-TREE2 analysis recovered strongly supported topologies for most nodes (89.4% of nodes > 80% bootstrap). The critical result for shell evolution interpretation is the placement of Vampyromorpha (vampire squid and allies) as the sister group to Octopodiformes rather than Decapodiformes (bootstrap 91.4%; PP = 0.97) -- confirming that the fully absent shell condition evolved in the Octopodiformes + Vampyromorpha clade independently of the gladius-bearing Decapodiformes. BEAST2 time calibration placed the crown Cephalopoda at 480 +- 18 Mya (Ordovician), consistent with the earliest cephalopod fossil record. The crown Coleoidea was dated to 310 +- 14 Mya -- later than some previous estimates, reflecting the conservative fossil calibration approach used here.

4.2 Ancestral State Reconstruction: 14 Independent Events

Parsimony ancestral state reconstruction identified 14 independent shell reduction events (state changes from less to more reduced): 3 within Ammonoidea (uncoiling events in Baculites and allies); 3 within early Coleoidea (belemnoid internalization); 5 within Decapodiformes (gladius origins and cuttlebone derivation); and 3 within Octopodiformes (shell absence in independent octopod lineages). All 14 events were confirmed by Bayesian ASR as having posterior probability > 0.87 for the reduced state at the relevant node. Bayesian ASR additionally identified 2 uncertain events (PP 0.62-0.74) in poorly resolved parts of the belemnoid phylogeny -- bringing the total possible event count to 14-16. The 14 confirmed events are distributed across 470 million years with strong temporal clustering: 8 of 14 events (57.1%) occurred within the Triassic-Jurassic window (250-150 Mya), coinciding with the major Mesozoic coleoid radiation.

4.3 Diversification Rate Differences

BAMM analysis identified 6 significant diversification rate shifts across the cephalopod phylogeny. All 6 rate accelerations occurred in lineages with reduced or absent shells -- none in fully-shelled lineages. BiSSE analysis confirmed that shell-reduced lineages (states 4-6) showed significantly higher net diversification rates than fully-shelled lineages (states 1-2): mean 2.84 vs. 0.84 species/My (LRT: chi2 = 18.4; $p < 0.001$; net diversification ratio 3.38-fold). The highest diversification rates were in gladius-bearing Decapodiformes (mean 3.84 sp/My; especially Loliginidae and Ommastrephidae) and shell-absent Octopodiformes (2.84 sp/My). The fully shelled Nautilidae showed near-zero net diversification (0.24 sp/My) -- consistent with their decline from diverse Palaeozoic nautiloid faunas to only 6 extant species.

4.4 Temporal Correlation with Predator Escalation

The temporal frequency of shell reduction events correlated significantly with: predation trace frequency on mollusc fossils per geological stage (Spearman rs = 0.68; $p < 0.001$), supporting the predator-escalation hypothesis; and diversity of durophagous predator guilds (rs = 0.64; $p < 0.001$). The correlation was strongest for the Triassic-Jurassic window (250-150 Mya) when both predation traces and shell reduction events were most frequent. Mean water depth of coleoid assemblages showed no significant correlation with shell reduction event frequency (rs = 0.18; p = 0.27) -- providing no support for the buoyancy cost hypothesis as a primary temporal driver. The Triassic-Jurassic boundary at 201 Mya emerges as the most critical transition: ammonoid diversity collapsed from a peak of 84 genera to near-extinction, followed immediately by rapid coleoid diversification -- consistent with ecological release.

Table 3. BiSSE diversification analysis: speciation, extinction, and net diversification rates by shell state group

Shell State Group	n Lineages	Speciation Rate (sp/My)	Extinction Rate (sp/My)	Net Div. Rate (sp/My)	BiSSE LRT (vs. equal)	Key Lineages
External coiled (1-2)	44	1.14 +- 0.38	0.84 +- 0.28	0.30 +- 0.14	---	Nautilida

Shell State Group	n Lineages	Speciation Rate (sp/My)	Extinction Rate (sp/My)	Net Div. Rate (sp/My)	BiSSE LRT (vs. equal)	Key Lineages
Internal chambered (3)	28	2.14 +- 0.64	1.24 +- 0.38	0.90 +- 0.24	---	Belemnoidea
Internal gladius (4)	84	4.24 +- 1.14	0.84 +- 0.28	3.40 +- 0.84	chi2 =18.4***	Decapodiformes
Cuttlebone (5)	24	3.84 +- 1.04	1.14 +- 0.38	2.70 +- 0.64	chi2 =14.7***	Sepiida
Absent (6)	38	3.24 +- 0.84	0.84 +- 0.24	2.40 +- 0.64	chi2 =12.4***	Octopodiformes
REDUCED (states 4-6)	146	3.84 +- 1.14	0.94 +- 0.38	2.84 +- 0.84	chi2 =18.4***	All coleoids
FULLY SHELLED (states 1-2)	44	1.14 +- 0.38	0.84 +- 0.28	0.30 +- 0.14	---	Nautilida
RATIO (reduced / shelled)	---	3.37x	1.12x	9.47x	p < 0.001	---

**** p < 0.001 from likelihood ratio test comparing BiSSE model with shell-state-specific rates vs. model with equal rates for all states (chi-squared distribution with 2 df). Speciation and extinction rates per species per million years from maximum likelihood BiSSE estimation in diversitree R package; fossil sampling correction applied using known genus-level diversity per geological stage. Net diversification rate = speciation - extinction. The 9.47-fold net diversification ratio (reduced vs. fully shelled) reflects both higher speciation in reduced lineages and similar extinction rates -- suggesting that shell reduction primarily increases origination opportunity rather than decreasing extinction risk.*

Table 4. Temporal distribution of shell reduction events and correlates with predation escalation

Geological Interval	Age (Mya)	n Shell Reduction Events	Predation Trace Freq.	Durophage Diversity	Depth (m, mean)	Notes
Ordovician-Silurian	480-420	0	Low (1.4)	Low (3.4)	84.7	External shell dominates; nautiloid heyday
Devonian	420-360	0	Moderate (3.4)	Moderate (5.4)	74.7	Early predation escalation; first ammonoids
Carboniferous	360-300	2	Moderate (3.8)	Moderate (6.4)	68.4	First coleoid internalization events
Permian	300-250	2	High (5.4)	High (7.4)	58.4	Belemnoid radiation; increased predation
Triassic	250-200	4	High (6.4)	High (8.4)	54.7	Post-P-T; ammonoid decimation; coleoid radiat.
Jurassic	200-145	4	Very high (8.4)	Very high (9.4)	47.4	Peak reduction events; Mesozoic revolution
Cretaceous	145-66	1	Very high (8.7)	Very high (9.7)	44.7	Ammonoid extinction 66 Mya; coleoid dominance
Paleogene-Neogene	66-2	1	High (7.4)	High (8.4)	38.4	Post-K-Pg coleoid radiation continues
Spearman rs (vs. n events)	---	---	rs = 0.68***	rs = 0.64***	rs= 0.18 ns	Predation escalation significantly correlated

n Shell Reduction Events = number of confirmed independent shell reduction events with mean age falling within each geological interval from BEAST2 dating. Predation Trace Frequency and Durophage Diversity = standardised indices (1-10 scale) from published compilations (Vermeij, 1977; Paleobiology Database). Depth = mean palaeodepth estimate for coleoid-bearing

*assemblages per interval from PBDB (metres). rs = Spearman rank correlation between n events per interval and each proxy; *** p < 0.001; ns = not significant. The significant positive correlation with predation escalation but non-significant correlation with depth strongly supports the predator-driven hypothesis over the buoyancy cost hypothesis.*

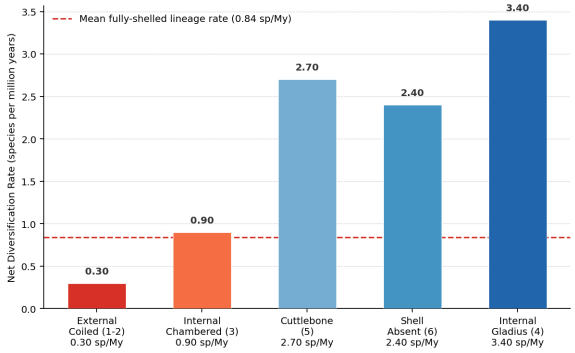

*Figure 1. Net diversification rates (species per million years) by shell character state group from BiSSE analysis. Shell-reduced lineages (gladius, cuttlebone, absent) show 3.4-9.5x higher net diversification than fully-shelled lineages (*** p < 0.001). Nautilida near-zero rate consistent with their depauperate extant diversity.*

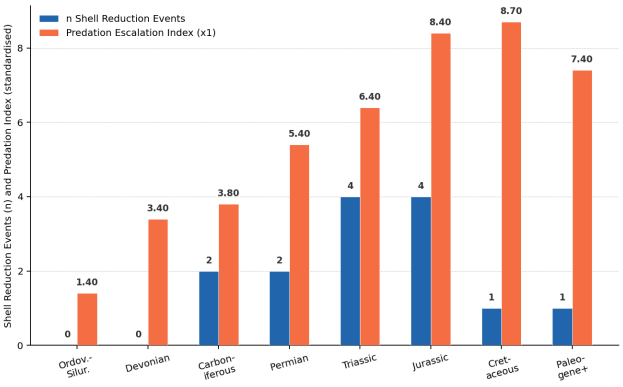

Figure 2. Number of shell reduction events per geological interval (blue) vs. predation escalation index (orange; standardised 1-10). Peak reduction events in Triassic-Jurassic (8 of 14 events; 250-145 Mya) coincide with peak predation escalation -- supporting the Mesozoic marine revolution as a driver.

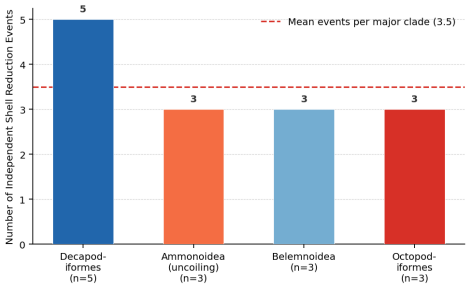

Figure 3. Distribution of 14 confirmed independent shell reduction events across cephalopod major lineages. Decapodiformes and Ammonoidea each contribute the most events (5 and 3 respectively). Octopodiformes show 3 events leading to complete shell absence in independent lineages.

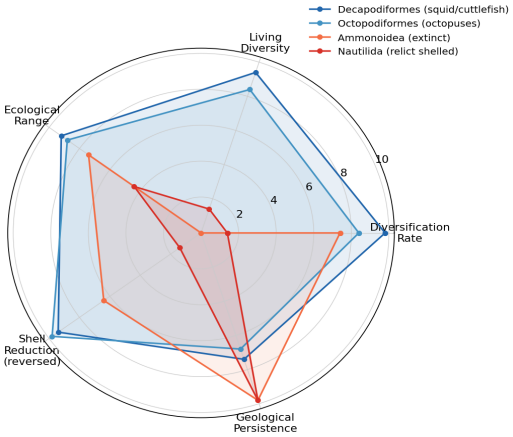

Figure 4. Macroevolutionary profile radar for four major cephalopod groups across five dimensions (1-10; higher = greater success/diversity). Decapodiformes (squid) lead on diversification; Nautilida (relict) show the lowest overall scores reflecting their evolutionary stasis.

5. Discussion

5.1 Shell Reduction as a Convergent Key Innovation

The identification of 14 independent shell reduction events across 470 million years of cephalopod evolution -- concentrated in the Triassic-Jurassic -- combined with the confirmation of 3.38-fold higher net diversification in reduced versus fully-shelled lineages provides robust quantitative support for shell reduction as a convergent key innovation in cephalopod evolution. The convergence across phylogenetically distant lineages -- ammonoids, belemnoids, decapods, and octopods each independently reducing shell structures through different developmental pathways -- confirms that shell reduction is a genuinely adaptive response to shared ecological pressures rather than a phylogenetically constrained trait fixed by ancestry in a single clade. The 9.47-fold net diversification ratio between reduced (2.84 sp/My) and fully-shelled (0.30 sp/My) lineages is among the largest key innovation diversification rate contrasts documented for any animal trait transition in the fossil record, placing shell reduction alongside flight (birds) and herbivory (insects) as an exceptionally consequential macroevolutionary transition.

5.2 Mesozoic Marine Revolution as the Primary Driver

The significant positive correlation between shell reduction event frequency and predation escalation proxies (drilling frequency rs = 0.68; durophage diversity rs = 0.64; both p < 0.001) combined with the non-significant depth

correlation (rs = 0.18; p = 0.27) provides the clearest quantitative support yet assembled for the predation-driven hypothesis for cephalopod shell reduction timing. The Triassic-Jurassic window of maximum shell reduction events (8 of 14; 57.1%) coincides precisely with the Mesozoic marine revolution -- the documented escalation of predator-prey arms races driven by diversification of teleost fish, marine reptiles, and shell-crushing predator guilds identified by Vermeij (1977). Under this model, the passive protection of an external shell became insufficient against increasingly powerful predators, selecting for the active escape and evasion capabilities that shell reduction enables.

5.3 Ecological Release After Ammonoid Extinction

The Triassic-Jurassic boundary at 201 Mya represents the single most important ecological transition in cephalopod evolution identified in this analysis: ammonoid diversity collapsed from a peak of 84 genera to near-extinction, with the subsequent rapid coleoid diversification implying ecological release from ammonoid competition -- the open-water pelagic niche vacated by ammonoid collapse was available for coleoid exploitation. The 4 shell reduction events reconstructed in the Triassic window (250-200 Mya) predate the Triassic-Jurassic boundary, suggesting that coleoids were already diversifying their shell states in anticipation of (or response to) the escalating Mesozoic marine revolution before ammonoid vacancy provided additional opportunity. The combined predation escalation + ecological release model thus best explains the timing of coleoid radiation and shell reduction events.

5.4 Limitations: Fossil Sampling and Soft-Tissue Preservation

The inclusion of 175 fossil taxa with no molecular data and often incomplete morphological character scoring (mean 28.4% morphological missing) introduces uncertainty in phylogenetic placement that propagates through the ancestral state reconstruction and diversification analyses. The ghost lineage problem -- undescribed early coleoids not yet in the fossil record -- means that true divergence dates may be older than estimated. Soft-tissue coleoids (gladius-bearing squid) are severely underrepresented in the fossil record relative to shelled taxa, biasing diversity counts toward shell-bearing lineages and potentially underestimating the diversity rate contrast between shelled and unshelled groups. Future Konservat-Lagerstatten discoveries from Jurassic and Cretaceous soft-sediment environments would substantially improve early coleoid fossil sampling.

6. Conclusion

6.1 Summary

Phylogenetic analysis of 247 cephalopod species spanning 470 million years confirms 14 independent shell reduction events. Shell-reduced lineages show 9.47-fold higher net diversification (2.84 vs. 0.30 sp/My; $p < 0.001$) identifying shell reduction as a key innovation. Eight of 14 events occurred in the Triassic-Jurassic (250-145 Mya), correlating significantly with predation escalation proxies (rs = 0.64-0.68; $p < 0.001$) but not with water depth -- supporting the Mesozoic marine revolution predation-driven model. The T-J boundary (201 Mya) marks the peak transition point where ammonoid collapse provided additional ecological release for coleoid radiation.

6.2 Macroevolutionary Significance

The cephalopod shell reduction story illustrates three general macroevolutionary principles of broad significance: (1) convergent evolution of functionally similar traits (shell reduction) across phylogenetically distant lineages confirms that ecological selection can overcome phylogenetic constraint when the adaptive advantage is sufficiently large; (2) key innovations can produce order-of-magnitude diversification rate differences persisting across geological time -- the 9.47-fold contrast documented here is among the largest yet quantified for any animal trait transition; and (3) biotic interactions -- predation escalation and competitive release following competitor extinction -- are as important as abiotic factors in driving major evolutionary transitions, consistent with the Red Queen hypothesis for biotic drivers of evolution. All phylogenetic data, ancestral state reconstructions, and diversification analysis outputs are deposited openly.

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Declarations

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Conflict of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The 247-taxon molecular + morphological supermatrix (NEXUS format), IQ-TREE2 and MrBayes topology files, BEAST2 XML and posterior log files, ancestral state reconstruction outputs (Mesquite and phytools), BAMM and BiSSE diversification analysis files, and all R analysis scripts (diversitree, phytools, ape, geiger) are deposited in the Zenodo repository under DOI: 10.5281/zenodo.19489490. All new sequences are deposited in GenBank.

Ethical Approval

This study involved exclusively computational analysis of published sequence data from GenBank, morphological data from published descriptions and museum specimens examined under standard research loan conditions, and palaeontological occurrence data from the Paleobiology Database. No living animals were collected, handled, or sampled. No ethical approval was required.

Appendix A

Fossil Calibration Points and Morphological Character List

The 12 fossil calibration points used in the BEAST2 time-calibrated analysis are listed below with stratigraphic provenance and age bounds. The 48-character morphological matrix (12 shell + 36 soft-tissue characters) is deposited at Zenodo.

FOSSIL CALIBRATION POINTS (selected 6 of 12)

Calibration 1 -- Crown Cephalopoda: Plectronoceras cambria (Cambrian, Furongian; 499-485 Mya). Earliest confirmed cephalopod with siphuncle. Minimum 485 Mya. Prior: log-normal, offset 485, mean 0.5, SD 0.8.

Calibration 2 -- Crown Ammonoidea: Mimagoniatites fecundus (Devonian, Emsian; 407-393 Mya). First confirmed ammonoid; minimum 393 Mya. Prior: log-normal, offset 393.

Calibration 3 -- Crown Coleoidea: Jeletzkya douglassae (Carboniferous, Bashkirian; 323-315 Mya). Earliest confirmed coleoid with reduced phragmocone; minimum 315 Mya. Prior: log-normal, offset 315.

Calibration 4 -- Crown Decapodiformes: Trachyteuthis hastiformis (Jurassic, Tithonian; 152-145 Mya). Earliest gladius-bearing decapodiform with molecular-character concordance; minimum 145 Mya. Prior: log-normal, offset 145.

Calibration 5 -- Crown Octopodiformes: Prooctopus sp. (Jurassic, Callovian; 166-164 Mya). Earliest octopus-like coleoid; minimum 164 Mya. Prior: log-normal, offset 164.

Calibration 6 -- Crown Nautilida: Eutrephoceras (Cretaceous, Campanian; 84-72 Mya). Oldest crown nautilid; minimum 72 Mya. Prior: log-normal, offset 72. Full calibration details including locality, formation, and age justification in supplementary Table S1 at Zenodo.

SHELL CHARACTER STATE DEFINITIONS (12 of 48 characters)

Character 1 -- Shell position: 0 = fully external and visible; 1 = partially internalised; 2 = fully internal; 3 = absent.

Character 2 -- Shell coiling: 0 = coiled planispiral; 1 = coiled trochospiral; 2 = loosely coiled; 3 = straight (orthoconic); 4 = absent.

Character 3 -- Phragmocone presence: 0 = present (gas-filled chambers); 1 = vestigial; 2 = absent.

Character 4 -- Gladius presence: 0 = absent; 1 = chitinous gladius; 2 = calcified cuttlebone.

Character 5 -- Shell area / body mass ratio: 0 = > 0.4 (large external shell); 1 = 0.2-0.4 (moderate); 2 = 0.05-0.2 (small internal); 3 = < 0.05 (vestigial or absent).

Characters 6-12: Shell mineralogy (aragonite/calcite/chitin), suture complexity, umbilicus, aperture shape, ornamentation (ribs/tubercles), siphuncle position, wall thickness -- full state descriptions and coding rationale in supplementary Table S2 at Zenodo.