Evolution of Complexity in Paleozoic Ammonoid Sutures

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The septal sutures of 588 genera of Paleozoic ammonoids showed a 1600 percent increase in mean complexity over 140 million years. Within 475 ancestor/descendant pairs, descendants were more than twice as likely to be more complex than their ancestors. Twelve subclades (373 genera) averaged 34 percent increased complexity. These patterns are compatible with an active or driven system of long-term bias for increased complexity. Mass extinctions acted in opposition to this long-term trend, tending to eliminate more-complex forms and resetting the trend with each extinction event.

Two long-held evolutionary generalizations are that size and complexity have tended to increase through time (*1*, *2*). Two mechanisms have been proposed for producing large-scale trends such as this. One is a random or passive process of diffusion away from bounded minima (the "left-wall effect," where the only way to go is to the right), and the other is a nonrandom, active, or driven process of biased branching toward increased size or complexity (*2*–*6*). However, there have been few empirical studies of such trends, and those that exist present contrasting conclusions [for example (*3*, *7*)]. Some documented trends appear compatible with passive diffusion away from a minimum (*8*, *9*), whereas others seem to represent active or driven selection (*10*, *11*). However, this dual view may be found to be simplistic; it has been argued that passive (or random) trends so dominate evolutionary history that if driven trends do occur, they are rare, incidental by-products of contingency (*5*). An alternative view is that active trends are real, and may reflect evolution away from unstable equilibria and toward optima, or even attractors (*3*, *4*).

We report the results of tracking the evolution of complexity in the septal sutures of Paleozoic ammonoids (*12*) over 140 million years and spanning three mass extinctions. We have largely followed the lines of testing passive versus driven trends suggested by McShea (*4*), which involves tracking changes in minima through time; comparing the proportion of increases versus decreases in ancestor/descendant pairs; and examining the skewness of subclades drawn from a right-skewed parent clade (*4*).

Paleozoic ammonoids comprise 588 genera ranging over 140 million years, from their appearance in the Lower Devonian to their near-termination at the Permian/Triassic boundary (Fig. 1) (*13*). This large clade of extinct mollusks was among the fastest evolving groups known in the fossil record (*14*). The occurrence of three mass extinctions over this period (*15*, *16*) provides an opportunity to evaluate the effects of external processes on this long-term record. Because these extinctions violate stochastic constancy (*4*), Devonian ammonoids were segregated from Mississippian-Permian ammonoids, which comprise a taxonomically discrete clade bracketed by the Devonian/Mississippian (D/M) and Permian/Triassic (P/Tr) extinctions.

We identified 475 ancestor/descendant genus pairs (165 Devonian and 310 Mississippian-Permian) on the basis of well-established phylogenies (*13*), which rely partly on similarities in the configuration of the suture, but not on overall complexity. There was no presumption of increased complexity in selecting A/D pairs, or within subclades; indeed, many complexity decreases are known (*13*). Twelve subclades were segregated for closer examination (Table 1). To examine survivors of the P/Tr extinctions, we included basal Triassic ammonoids (10 genera) in some aspects of the analysis (*13*).

Considerable emphasis has been placed on the "behavior of the minimum" in evaluating long-term trends (*2*, *4*, *9*–*11*). In an active or driven system, minimum values will tend to increase through time, whereas in a passive system the minimum will tend to show only passive diffusion (with decreases, stasis, or even slight increases) through time. Minimum suture complexity is 1. For comparison, living *Nautilus* has a suture complexity index (SCI) of about 1.3. The sutures of the earliest ammonoids (Lower Devonian) were about as simple as they could be: 97% had SCI < 3 and 67% had SCI < 2 (four genera had sutures less complex than that of *Nautilus*). Ignoring the effects of extinction events, complexity minima increased slowly through the Paleozoic, from SCI 1.2 to 2.6, but jumped to SCI 7 after the P/Tr extinction (Fig. 2). Maximum complexity increased rapidly during the Pennsylvanian and Permian, when many new suture patterns emerged (*11*), reaching ammonitic levels (SCI >300) by the end of the Permian. Overall, mean complexity increased 1600% between the Lower Devonian–Upper Permian, and there is a strong correlation between absolute time and mean complexity ($r^2 = 0.70$, t ratio $=$ 6.3, $P > t < 0.0001$; F ratio $= 28.1$, $P > F$ 0.0002). This trend was a combined product of greatly increased variance and steady attrition (by extinction) in the proportion of simple sutured genera (SCI < 4), which declined from ∼80% in the Devonian to ∼10% by the Permian (Fig. 3).

In a passive system with no bias, less-complex descendants should be as frequent as more-complex ones (*4*). In 159 simple-sutured Devonian A/D pairs (mean SCI 3.7), complexity increased +20% on average, with 55% of descendants showing increases compared with 31% decreases (hypothetical

Table 1. Selected Paleozoic ammonoid subclades (1 to 4, Devonian; 5 to 12, Mississippian-Permian). N, number of genera in subclade; A/D, phylogenetic ancestor/descendant genus pairs; SCI, mean suture complexity index of subclade; SK, subclade skewness (− negative skew; 0, symmetric distribution; + positive skew); Net %, mean net change in suture complexity; I:D(S), ratio of increases to decreases (stasis = <5%).

Subclade	N	A/D	SCI	SK	Net %	I:D(S)
1. Agoniatitina	23	18	2.0	1.6	+19.3	11:5(2)
2. Anarcestina	66	55	5.8	2.6	+27.9	32:20(3)
3. Goniatitida	52	43	3.4	1.8	+16.4	23:10(10)
4. Clymeniida	64	43	2.5	1.6	+18.0	21:15(7)
Mean	51	40	3.4	1.9	+20.4	22:12(6)
5. Schistocerataceae	18	13	8.7	1.6	+25.7	6:3(4)
6. Neoicocerataceae	28	25	6.1	1	+ 9.9	13:8(4)
7. Adrianitaceae	18	15	15.5	0.2	+48.6	12:3(0)
8. Marathonitaceae	15	13	21.1	1.2	+41.8	8:4(1)
9. Prolecanitida	40	36	33.4	0.7	+38.6	28:5(3)
10. Cyclolobaceae	18	14	61.8	2.4	+63.0	13:0(1)
11. Ceratitida	21	7	9.3	1.4	+26.6	5:2(0)
12. Shumarditaceae	10	9	21.3	0.9	+75.4	9:0(0)
Mean	21	17	22.2	1.2	+41.2	12:3(2)

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mean = 0: *t* test = 5.847, degrees of freedom (df) = 164, $P < 0.0001$). Stasis (less than 5% change) occurred in 14% of descendants. However, because Devonian sutures were on average so simple (and hence close to left-wall minima), these early increases in complexity could reflect either passive or driven trends.

Among 310 moderately complex Mississippian-Permian A/D pairs (mean SCI 9.6) there was an average complexity gain of +22%, with more than twice as many descendants (58%) showing increases as decreases (24%); 18% exhibited stasis (*t* test = 8.369, df = 309, $P < 0.0001$) (Fig. 4). In a subset of 71 Mississippian-Permian A/D pairs segregated to minimize any left-wall influence (SCI >10), the trend was even stronger: Mean net change was +36%, with 71% showing increases, 23% decreases, and 6% stasis (*t* test = 5.393, df = 70, $P < 0.0001$). When net change is plotted through time, the strong bias for increased complexity is readily apparent (Fig. 5).

In a driven system, the subclade test assumes that the skew of subclade distributions drawn from the upper part of a positively skewed parent distribution will also be positive; the system is probably passive if average subclade skew is neutral (symmetric distribution) or negative (*4*). All four major Devonian subclades show positive skew (mean SK 1.9) (Table 1). However, because the majority of Devonian taxa are simple-sutured (SCI ~1 to 3) and might reflect the influence of minimal bounds, the Devonian subclade results are not regarded as conclusive.

By contrast, Mississippian-Permian ammonoids (389 genera) have an essentially unbroken (~100 million years) evolutionary history, they show much higher average suture complexity (mean SCI 12.5) than their Devonian counterparts, and their overall frequency distribution is strongly skewed (SK 7). Of eight subclades with mean SCI 6 to 62 segregated for closer analysis, distributions of seven are positively skewed, and one is neutral (no skew; Table 1). Inasmuch as these subclades had complexity values far from left-wall minimum values, each could theoretically have evolved reduced suture complexity. But each subclade showed increased complexity through time (averaging +41%), increases outnumbered decreases by 4:1, and the magnitude of the increases averaged +59% compared with −21% for decreases. The subclade data suggest there was pervasive bias for increased complexity.

In general, mass extinctions eliminated highly complex sutures, but each event exerted its own influences.

1) Upper Devonian Frasnian/Famennian [367 million years ago (Ma)]. Surprisingly high levels of suture complexity had evolved by the Upper Devonian; four Frasnian families reached SCI >20. But only five genera (all simple-sutured, SCI ~2.6) survived the Frasnian/Famennian (F/F) extinction, which reduced complexity by half (mean SCI ~6 to 3; minimum ~2 to 1), and maximum SCI declined by 75% (SCI ~35 to 9). If the F/F extinction had not occurred, ammonitic levels of complexity may have become commonplace by the Mississippian.

2) Devonian/Mississippian (354 Ma). After the F/F extinction was the most diverse ammonoid radiation in the Paleozoic: More than half of 116 Famennian genera are clymeniids, an enigmatic clade that first ap-

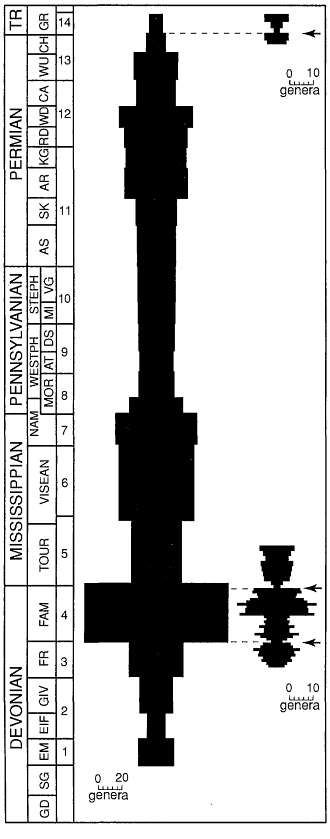


Fig. 1. Ammonoid genus diversity through the Paleozoic. Arrows and expanded spindles show Frasnian/Famennian (367 Ma), Devonian/Mississippian (354 Ma), and Permian/Triassic (250 Ma) mass extinctions (*13*, *19*). Intervals 1 to 14 correspond to chronostratigraphic divisions in Figs. 2 and 3; for abbreviations see (*20*).

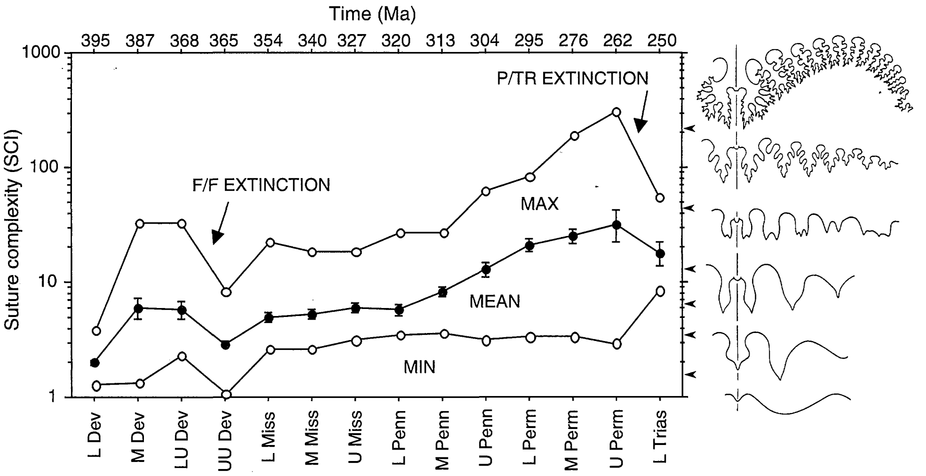


Fig. 2. Plots of minimum, mean (±SE), and maximum suture complexity through the Paleozoic (*13*). Representative sutures are *Gyroceratites* (SCI 1.7), *Irinoceras* (3.7), *Branneroceras* (6.1), *Tabantalites* (13.5), *Metaperrinites* (47.3), and *Timorites* (203).

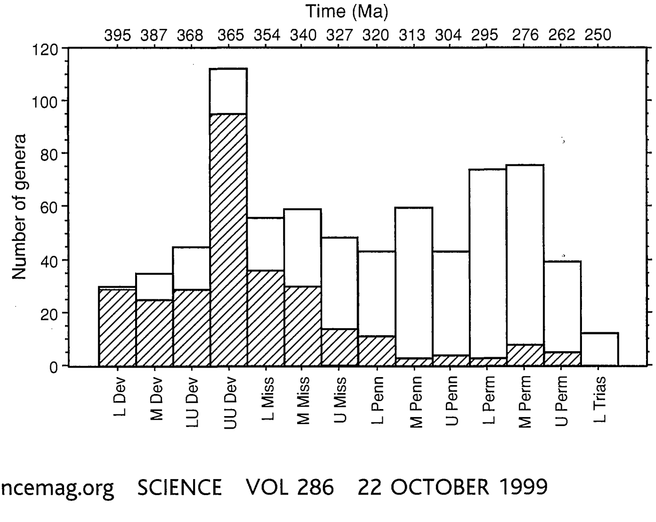
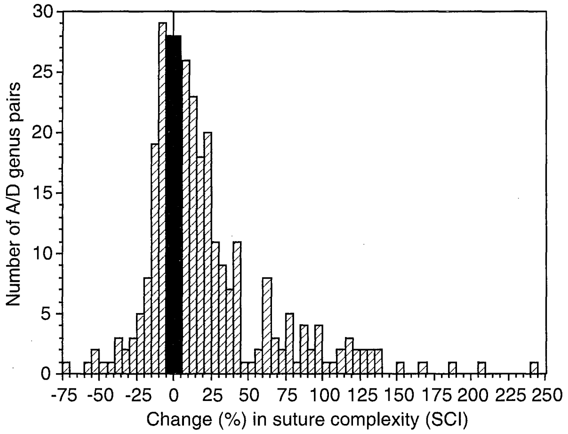


Fig. 3. Frequency distribution of Lower Devonian–basal Triassic ammonoids (598 genera), showing decline in proportion of simple sutures (SCI < 4, shaded).



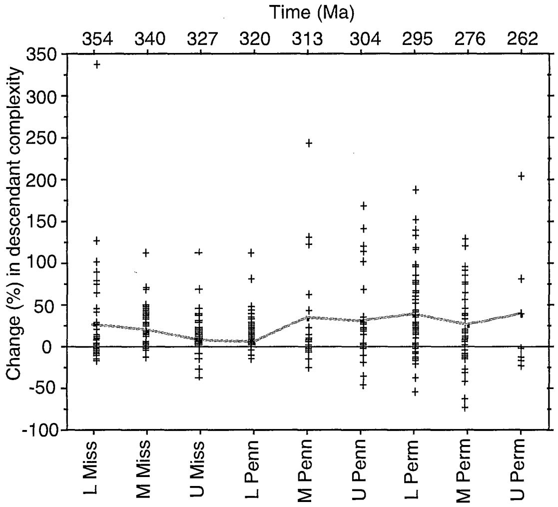


Fig. 4 (left). Change in suture complexity in 310 Mississippian-Permian ancestor/descendant genus pairs. More than twice as many descendants (58%) showed increases as decreases (24%), and 18% showed stasis (<5% change, in black). **Fig. 5 (right).** Change in complexity (percent) in 310 Mississippian-Permian ancestor/descendant genus pairs; gray line connects the mean for each interval (overall change was +22%).

peared in the mid-Famennian, but was extinct by the end of the stage. If the D/M extinction had not eliminated clymeniids, the late Paleozoic may have been dominated by these simple-sutured (SCI ~3) forms. This extinction nearly eliminated ammonoids altogether; only three simple-sutured goniatitids survived (SCI ~3.6), giving rise to a long interval of low complexity (Fig. 2).

3) Permian/Triassic (250 Ma). The organic effects of the P/Tr extinction are widely known (*16*), and ammonoids were affected as severely as any other group. Only two Upper Permian genera survived: highly complex *Episageceras* (SCI 57.8), which became extinct shortly thereafter, and *Xenodiscus* (SCI 7.7), which was ancestral to all Mesozoic clades. This extinction had several effects: Minimal complexity was ratcheted upward from SCI ~3 to 7; maximum complexity fell from SCI >300 to ~60; and mean complexity declined from SCI ~32 to 18, equivalent to being set back ~50 million years. The only long-term P/Tr survivor was a ceratitid with a simple, serrate suture; this might have eliminated old developmental constraints and introduced a new Mesozoic sutural template that was quite different from that of its Paleozoic predecessors.

Despite differential survival of simple-sutured genera during mass extinctions, the trend toward increased complexity started anew (or resumed) after each extinction event. It is remarkable that ammonoids survived these events at all, and that after each extinction they radiated once again. This rise-and-fall diversity persisted through the Mesozoic, although it appears that complexity stabilized after the P/Tr extinctions (*9*), possibly suggesting that optima were reached, sensu (*3*), by the time of their final extinction at the Cretaceous/Tertiary boundary.

Active or driven trends may reflect a number of influences, including selection, differential survival or extinction, phylogeny or development, and functional constraints (*6*). Our results indicate that most of these factors were involved: (i) There was selective extinction of low-complexity genera through time (Fig. 3); (ii) descendants favored increased complexity by at least 2:1 (Figs. 4 and 5); and (iii) increased complexity prevailed within individual subclades (Table 1). But evaluating the role of functionality remains elusive, as it confronts the "ammonoid suture problem": What was the function of the ammonoid suture and why were more-complex sutures selected for? Although this 160-year-old controversy resists unequivocal explanation, it has been widely accepted that more-complex septa provided greater buttressing effects against hydrostatic pressure (*17*). Recently, however, finite element stress analysis has shown that any departure from a hemispherical shape (a straight suture) yields higher, not lower, hydrostatic stresses on a septal surface, which is the weakest part of the chambered shell (*18*). Thus, the evolution of septal complexity involved a trade-off: Increasingly complex sutures meant lower septal strength and hence shallower depth limits. This might explain why complexly sutured forms were more susceptible to mass extinctions, which often coincided with eustatic events (*15*, *16*), and why simple-sutured nautilaceans seem to have been largely unaffected by extinction events and persist even today in deep-water habitats.

These results show that there were several nonrandom processes operating in apparent opposition during the course of Paleozoic ammonoid evolution. Overall, there was pervasive long-term bias for increased complexity, both within individual subclades and across the ammonoid clade as a whole. But during times of biotic crisis, there was an opposing tendency to selectively eliminate more-complex sutures. This had the effect of periodically setting back or even reversing, but not halting, the driven long-term trend toward increased complexity.

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A Triassic Fauna from Madagascar, Including Early Dinosaurs

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The discovery of a Middle to Late Triassic (~225 to 230 million years old) terrestrial vertebrate fauna from Madagascar is reported. This fauna documents a temporal interval not well represented by continental vertebrate assemblages elsewhere in the world. It contains two new prosauropod dinosaurs, representing some of the earliest dinosaur occurrences known globally. This assemblage provides information about the poorly understood transition to the dinosaur-dominated faunas of the latest Triassic.

A historical perspective of Madagascar's unique modern fauna and flora has long been obscured by the island's meager Mesozoic-Cenozoic fossil record (*1*). An outline of precisely how the Malagasy biota formed over time is only beginning to emerge from phylogenetic analyses of living groups and paleontological discoveries from the Cretaceous (*1*). Research (*2*) in older strata provides complementary evidence about this diversification and insights into the origin of dinosaurs (*3*).

Much of Madagascar's sedimentary sequence occurs within two large western basins (*4*). Fossils described below are from the southern of these (Morondava Basin) and are derived from the geographically widespread Isalo "Group" (*2*, *5*), a lithostratigraphic unit from which only three adequately represented tetrapod taxa have been described (*2*, *6*, *7*).

We recovered diverse terrestrial vertebrate remains near the base of the Isalo II in the region east of Sakaraha (about 22° to 23°S, 44° to 44.5°E). Silicified wood and fragments of the rhynchosaur *Isalorhynchus* (*7*) were the only fossils known previously from the region. The geochronology of this portion of the Isalo "Group" has long been poorly understood, reflecting limited biostratigraphic control and lack of interfingering marine units. The Isalo II is traditionally considered to be Early to Middle Jurassic in age (*5*, *8*), but Buffetaut (*7*) argued that it is considerably older (Middle Triassic). Our findings confirm Buffetaut's estimate of a Triassic (but not necessarily Middle Triassic) age for the base of the Isalo II in this region.

Our basal Isalo II sites have yielded abundant remains of a variety of diapsid reptiles, including two prosauropod dinosaurs, two rhynchosaurs [*Isalorhynchus*, originally described as a rhynchosaurine (*7*), all others of which are Ladinian or older, plus a second new taxon (*9*)], and a sphenodontian. Several synapsids also occur, including a kannemeyeriid dicynodont and at least four eucynodont species. These phylogenetically important occurrences greatly improve the basis for biostratigraphic correlation of the basal Isalo II beds (see below).

Of the two new prosauropods, one most resembles *Azendohsaurus* from the Carnian Argana Formation of Morocco (*10*). The Malagasy taxon is known from several maxillae and dentaries (Fig. 1A); it is referred to the Prosauropoda on the basis of the following synapomorphies (*10*): (i) a downward curvature of the anterior dentary, (ii) a robust dorsal process of maxilla, with its base located in the anterior third of the bone, and (iii) a series of small nutrient foramina on the medial face of the maxilla. Furthermore, it shares the following derived characters with *Azendohsaurus* (*10*): (i) prominent longitudinal keel on the medial face of the maxillary, (ii) fossa on the medial face of the maxilla posterior to the dorsal fossa, (iii) a neck between the crown and root of teeth consistently present, and (iv) anteroposterior expansion of crowns always beginning at their bases. There are differences between the jaws and teeth of the Isalo II and Moroccan material: (i) a maxillary tooth count of 11 to 13, as opposed to 15 or 16 in *Azendohsaurus*, (ii) the presence of prominent wear facets on the maxillary teeth (absent in *Azendohsaurus*), and (iii) the presence of an attenuate, caudoventrally projecting posterior process on the maxilla (absent in *Azendohsaurus*). We defer assigning the Malagasy form to *Azendohsaurus* or a new taxon, awaiting the anticipated recovery of more complete material.

The second basal Isalo II dinosaur (Fig. 1B) is also a prosauropod. Its tooth morphology (elongate crowns and tightly packed teeth lacking expanded crowns) is distinct from that of the other Isalo II prosauropod and *Azendohsaurus*. This kind of dentition typifies most other prosauropods, including anchisaurids such as *Sellosaurus* (*11*) and *Thecodontosaurus* (*12*).

The basal Isalo II dinosaurs are most remarkable for their great antiquity. The horizon's age is now better constrained biostratigraphically, permitting temporal correlation to other terrestrial faunas worldwide. Rhynchosaurs and dicynodonts are not known elsewhere after the Carnian [early Late Triassic (*13*)], whereas prosauropods and sphenodontians are not known elsewhere before the Carnian (*13*), suggesting an undifferentiated Carnian age at a minimum (Fig. 2) and an approximate temporal correlation to the Ischigualasto Formation of Argentina [generally considered to be middle or late Carnian in age, on the basis of faunal evidence (*3*, *13*)], which hosts the most complete early dinosaurs known.

Given that the basal Isalo II fauna is at least as old as Carnian, previously undocumented taxon co-occurrences provide evidence that it is either older than other dinosaur-bearing faunas worldwide or represents a unique Carnian fauna preserving the latest occurrences of several other taxa. The pres-

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