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The Paradox of “Clam Shrimp” Paleoecology

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Abstract

Clam shrimp are small (~1 – 10 mm) bivalved crustaceans traditionally placed in the paraphyletic Conchostraca [1], now divided into the diverse Spinocaudata, the much less diverse Laevicaudata, and the low diversity and small but widespread Cyclestherida [2]. The have a hinged carapace composed of a multi-laminar chitin composite variously hardened with calcium phosphate [3] and/or calcite. Today, all but the Cyclestherida are apparently restricted to temporary bodies of fresh to low salinity water - basically playas, pans, and puddles - lacking predatory fish [1,4], with the latter generally assumed to be what excludes them from permanent waters. With considerable taxonomic diversity, clam shrimp are by far the most abundant larger fresh water crustaceans found in Late Paleozoic, Mesozoic, and Early Cenozoic lacustrine deposits [5], and nearly all palaeontologists and geologists have used their present adaptive zone as the key to their past sedimentary environments. However, fossil clam shrimp commonly co-occur with fossil fish and often in lithologies, such as microlaminated, articulated-fish-bearing mudstones, that otherwise would be interpreted as not just perennial lakes, but giant perennial lakes, such as the Middle Devonian Caithness Flagstones of Scotland [6], the Late Triassic Lockatong Formation of eastern North America [7], the Jehol Group of China [8], and the Eocene Green River Formation [9], to cite several iconic exemplars. In fact, clam shrimp are frequently found in fish coprolites [10], and therefore they persisted despite predation. Based on the fossil record, clam shrimp were the dominant zooplankton in pre-Neogene lakes, and this glaring conflict with their present adaptive zone presents the paradox of their paleoecology. Very few (e.g., Hethke [11]) have accepted the overwhelming evidence from ancient environments and concluded that some clam shrimp lived in permanent waters. This “paradox of clam shrimp paleoecology” presents the difficult biological question, “why did their adaptive zone change if the clam shrimp did not?”. Plausibly, the vast narrowing of the clam shrimp adaptive zone is related to the late Paleogene-Neogene revolutionary rise of diatom dominance [12,13] among lacustrine phytoplankton. There is a tight temporal linkage of the two trends, both of which are independent of the timing of the establishment of clades of modern predators such as diverse teleost fishes, which become common in lakes much earlier. A potentially testable hypothesis is that the filter-feeding clam shrimp might consistently lose under predator-mediated competition with filter-feeding Cladocera (their smaller sister group), given the late Paleogene replacement of previously dominant less refractory phytoplankton by diatoms. Regardless, of the proximal cause of their present exclusion from permanent waters, clam shrimp were major perennial lake zooplankters for two-thirds of the Phanerozoic (at least ~360 M.y.). Their present is not the key to their past.

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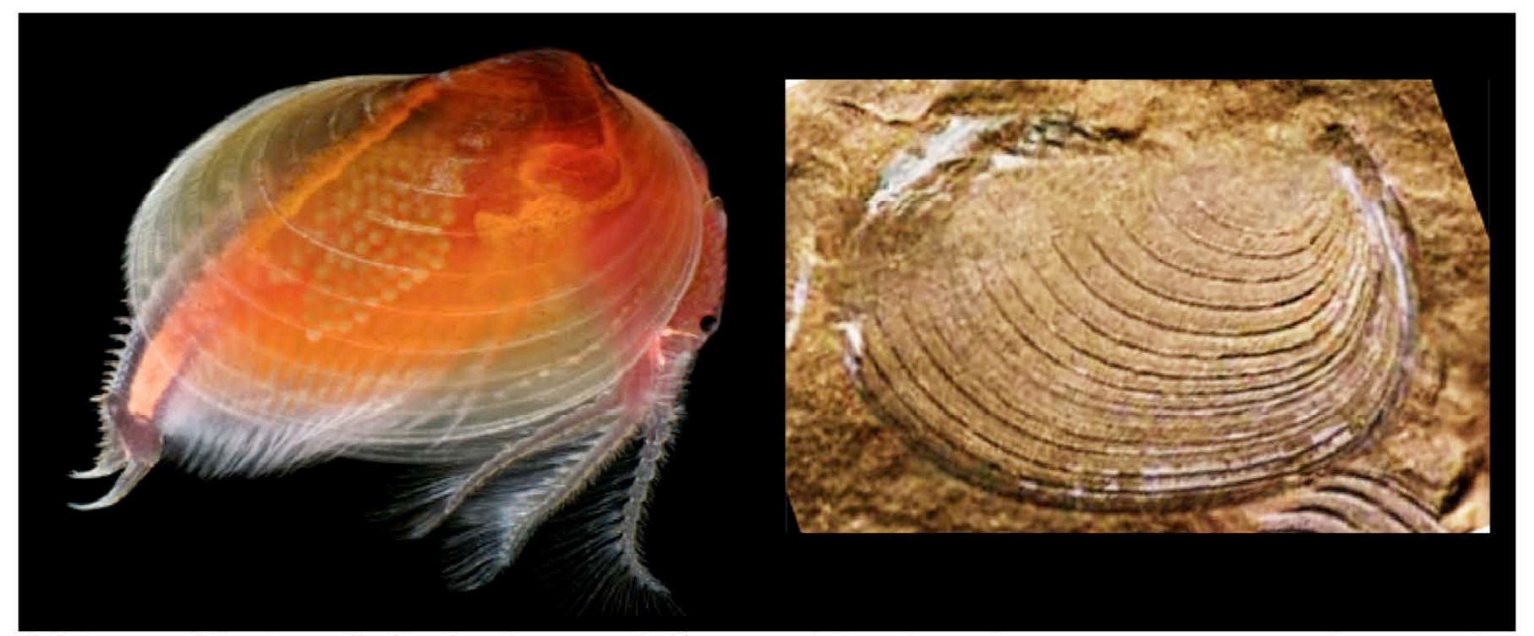
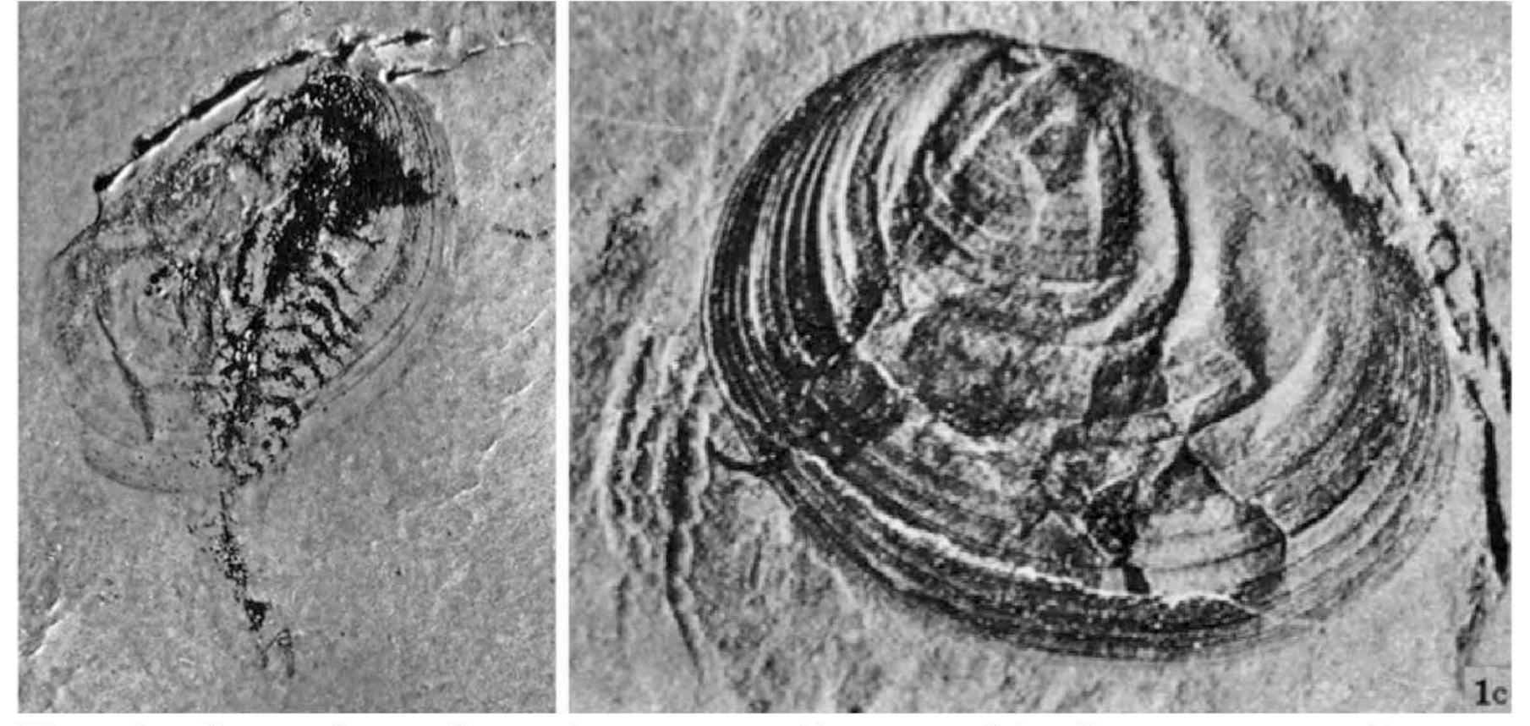


“Clam Shrimp” (left, from 14) are bivalved crustaceans formerly called conchostracans, but now separated into several separate groups. They are common fossils in Devonian to Paleogene lacustrine strata and are still common today mostly in ephemeral pools. Spinocaudatans are of interest hereå.

Soft part Preservation



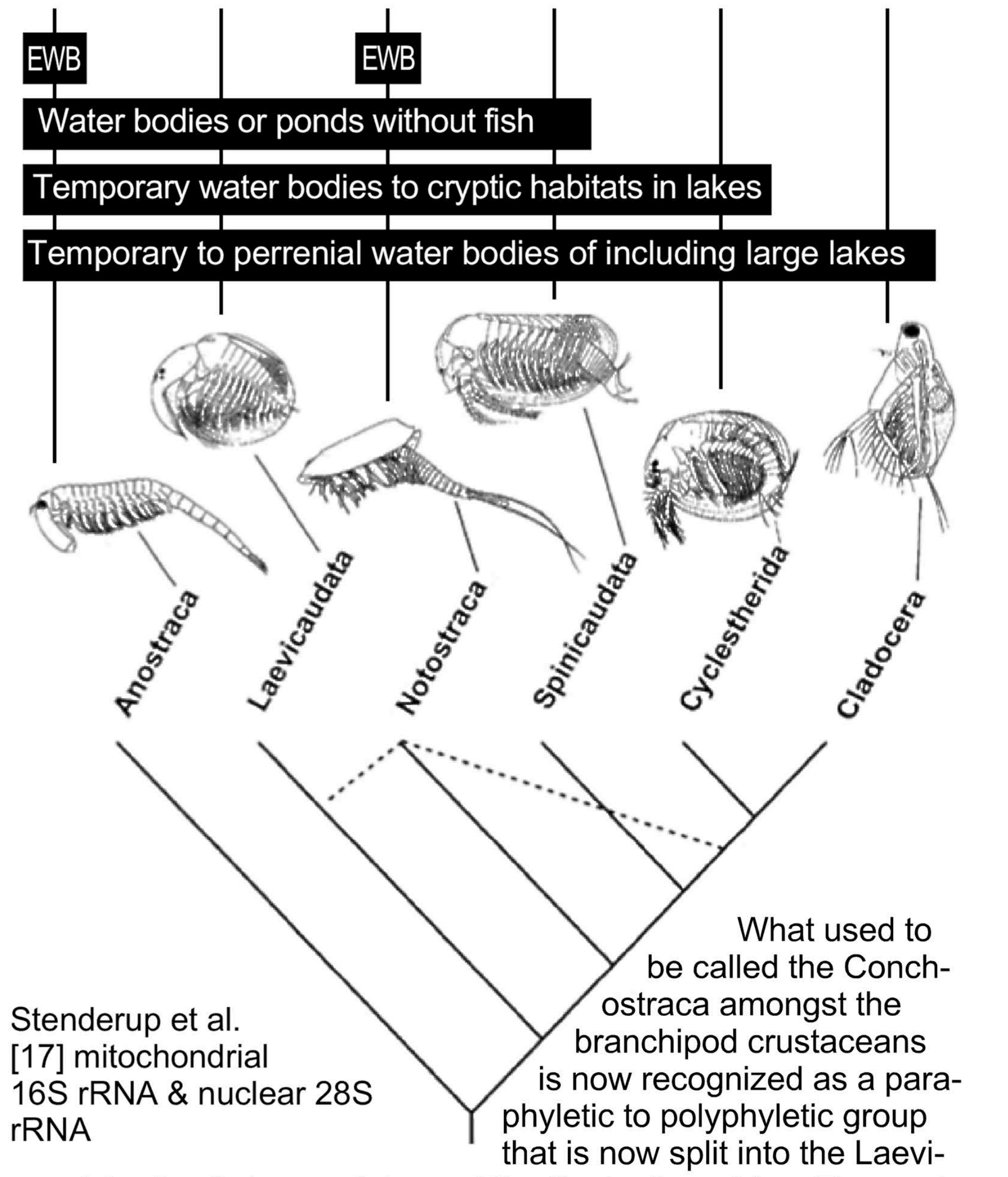
Rarely, there is soft part preservation, and in those cases there are no obvious differenences with extant forms. Above left [15] is a Middle Triassic *Palaeolimnadia alsatica* and above right is *Euestheria luanpingensis* [16].

What is the paradox?

The fundamental issue is that the present spinocaudatan adaptive zone of is dramaticaly limited compared to what is seen in the Devonian to Paleogene fossil record, with a the major change to the modern pattern occuring at the beginnng of the Neogene.

Modern Spincaudatan Environments

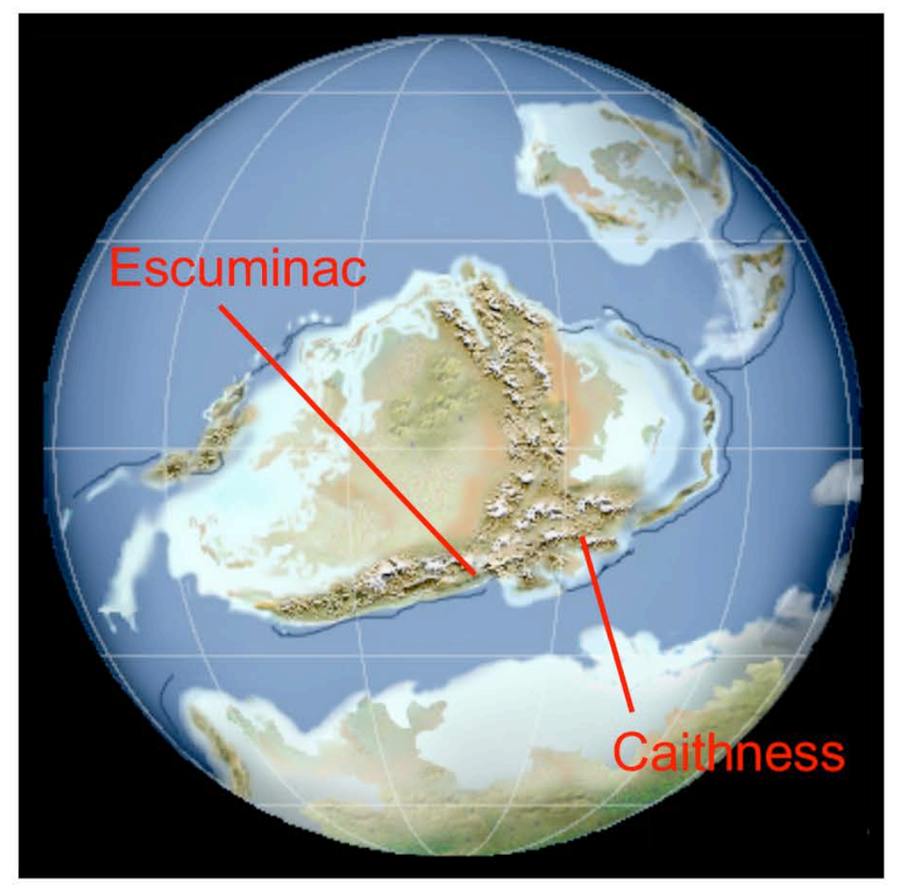
Today, spinocaudatans are restricted to temporary bodies of water such as the West Texas playa.



Stenderup et al. [17] mitochondrial 16S rRNA & nuclear 28S rRNA

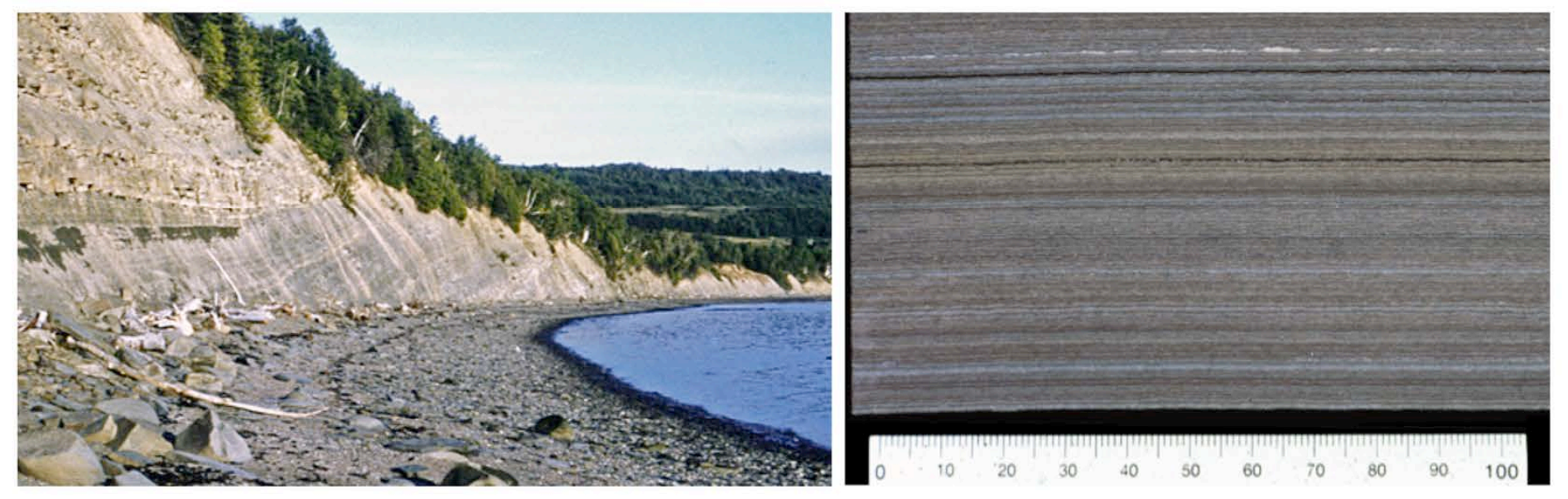
What used to be called the Conchostraca amongst the branchipod crustaceans is now recognized as a paraphyletic to polyphyletic group that is now split into the Laevicaudata, the Spinocaudata, and the Cyclesthereridae. The modern haibiats are mapped here upon the cladogram, with the more basal groups presently restricted to more ephemeral or saline habitats. EWB = ephemeral water bodies.

Devonian

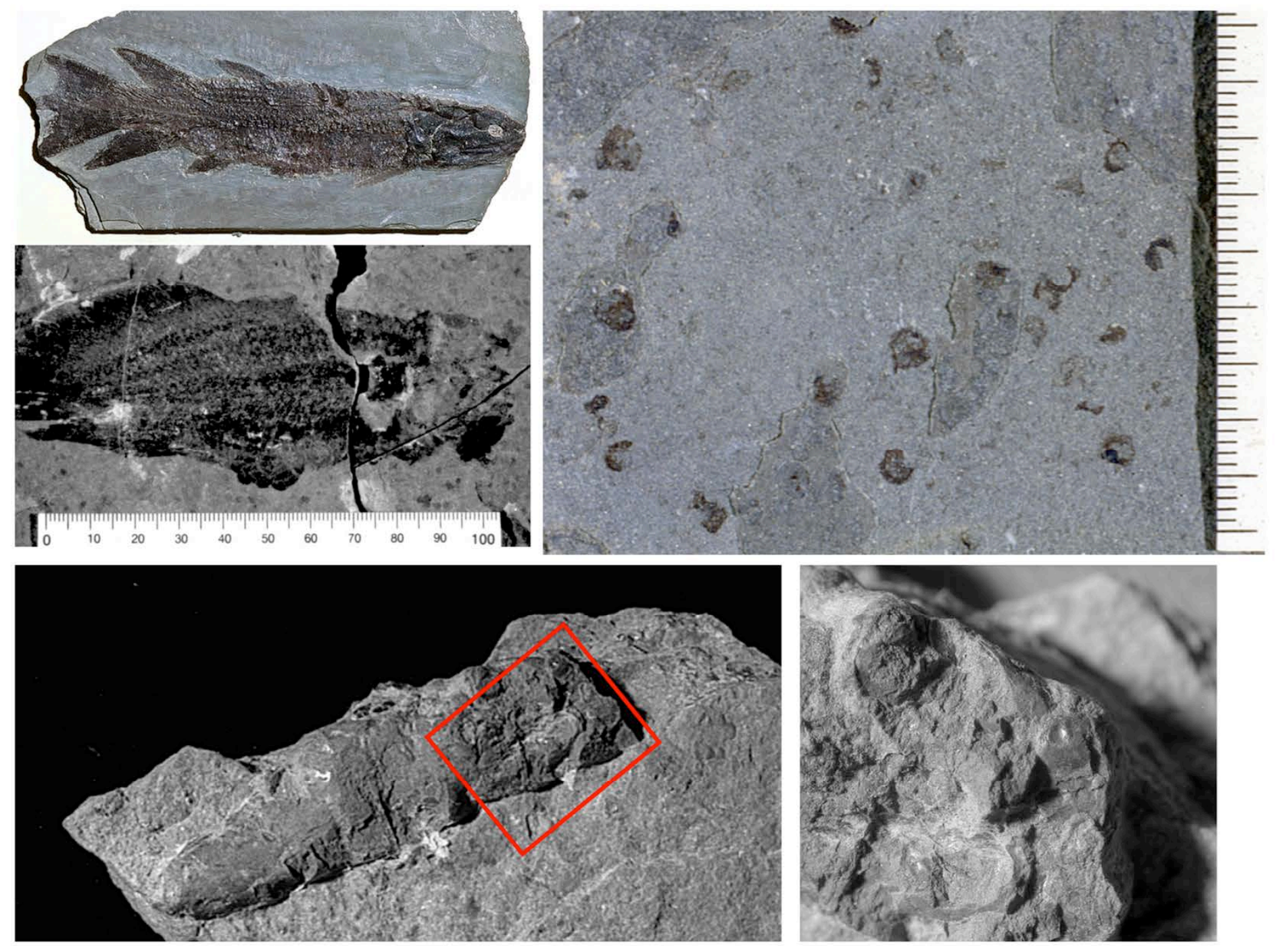


Spinocaudatans first appear in abundance in Devonian lacustrine deposits, particularly the Middle Devonian Caithness Flagstone Group of Scotland and the Late Devonian Escuminac Formation of Quebec. Both have spinocaudatans, particularly Asmussia, in laminated perennial lake strata with abundant whole fossil fish.

Devonian Escuminac Fm.



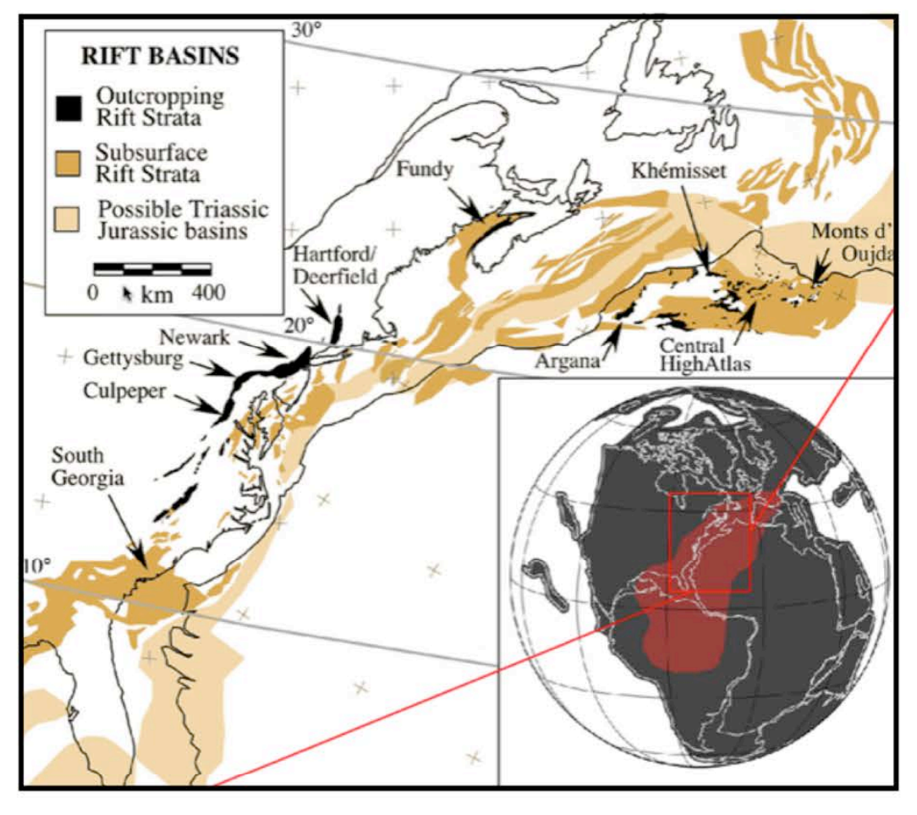
Outcrops of the Escuminac Fm., Quebec CAN (left) and a cut slab of the microlaminated, spinocaudatan- and fish-bearing facies (right).



Fish & spinocaudatans from the Escuminac Fm. The iconic *Eusthenopteron* (top left) and the lungfish *Scaumenacia curta* surrounded by *Asmussia* (mid-left). *Asmussia* on bedding plane. Below, coprolite with *Asmussia* with detail (red box) on right.

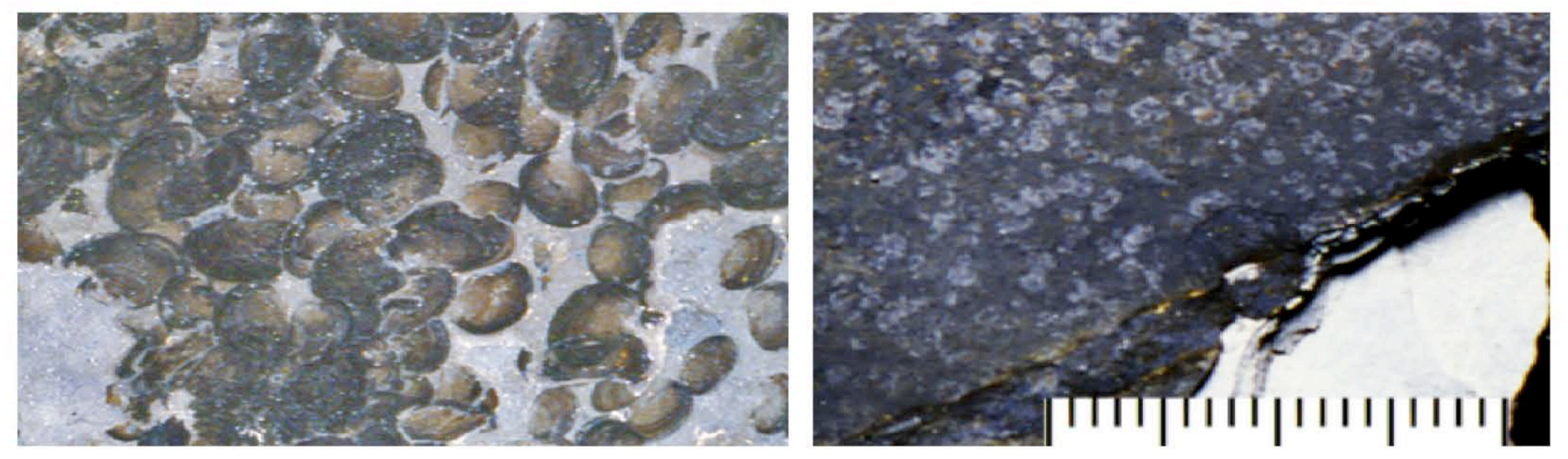
Triassic-Early Jurassic

Rift basins of the central Atlantic margin have abundant spinocaudatans in many facies. These deposits may show the disparity between the modern and ancient environmental preferences of spincaudatans because of the certainty of correlation over large distances indicative of the size of the lakes. Newark and Hartford basins are highlighted here.



Late Triassic

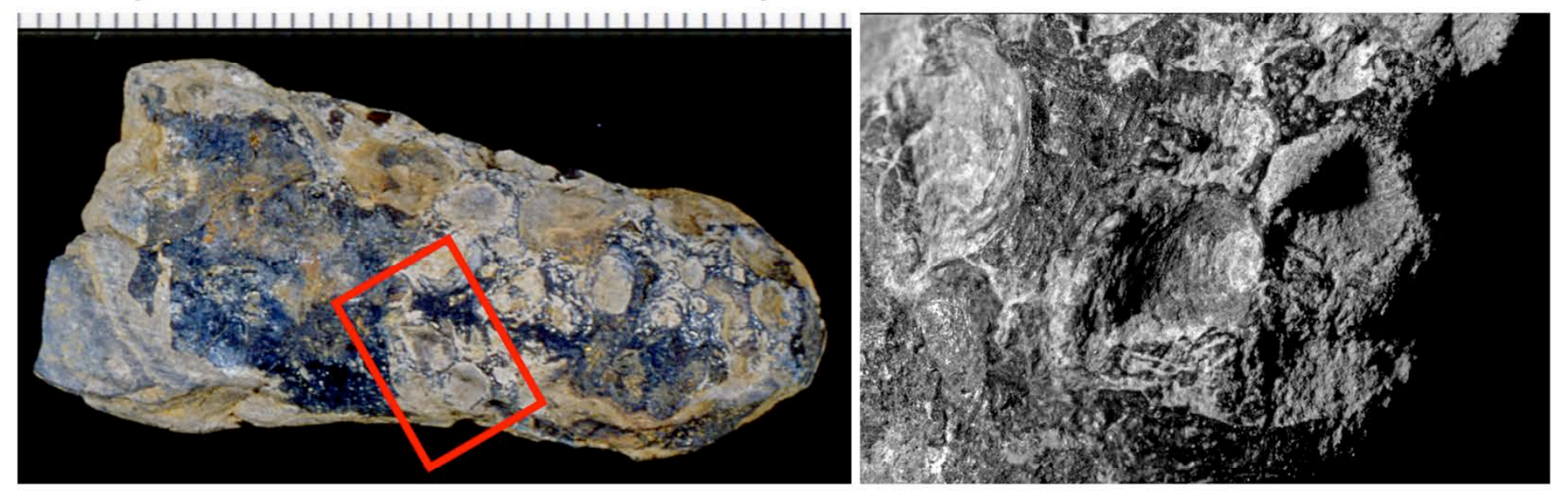
Spinocaudatans are amongst the most common fossils in these perennial lacustrine deposits. Their presence is a good guide to the presence of fossil fish, completely at odds with their current distribution. Above, are lake-level cycles paced by climatic precession. Each dark layer was deposited in a deep-water, very large, perrenial lake with abundant spinocaudatas.



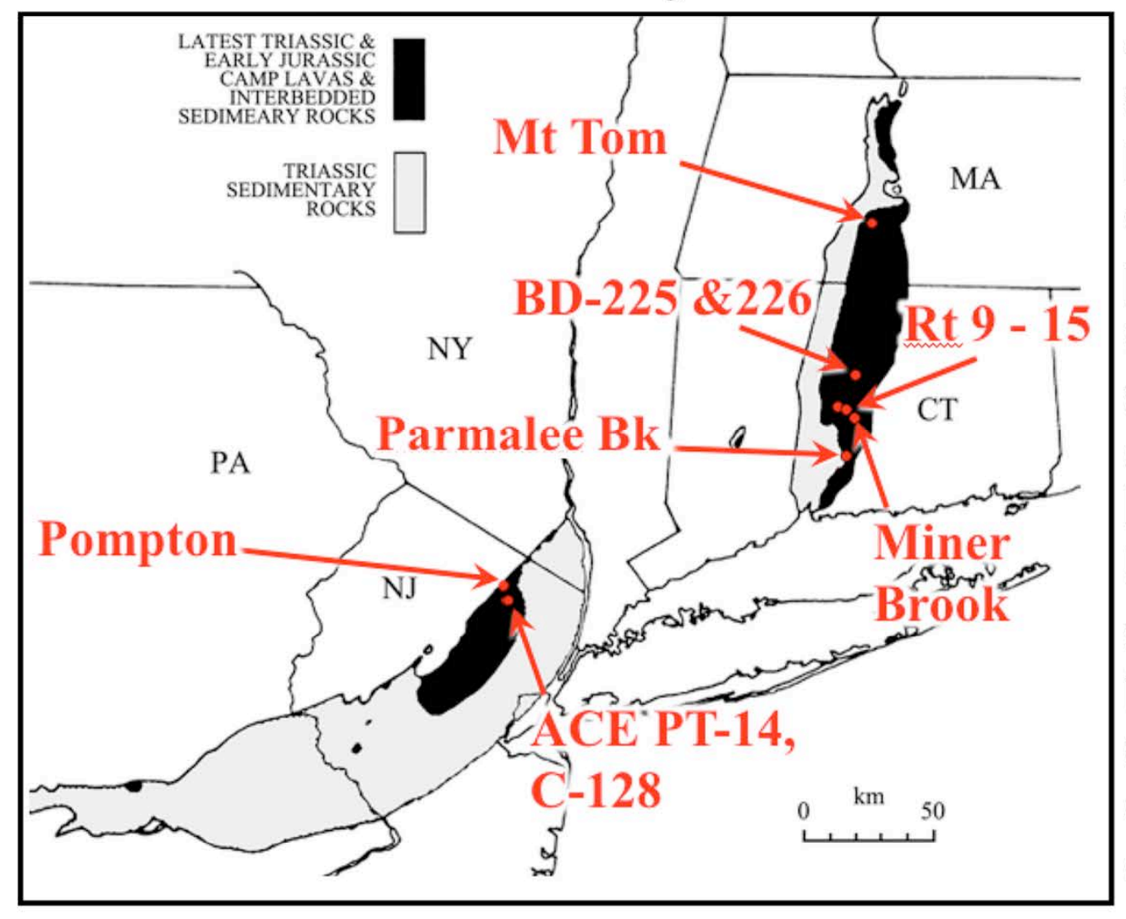
Above left, Euestheria sp. and above right, Palaeolimnadia sp,

Below is Semionotus braunii surronded by Palaelimnadia sp.

Below: Lockatong fish coprolite with abundant spincaudatans (*Euestheria* sp.) This style of coprolite is found in association with coelacanths. On right is detail of red box on left. Clearly, fish ate the spinocaudatans without extirpation.



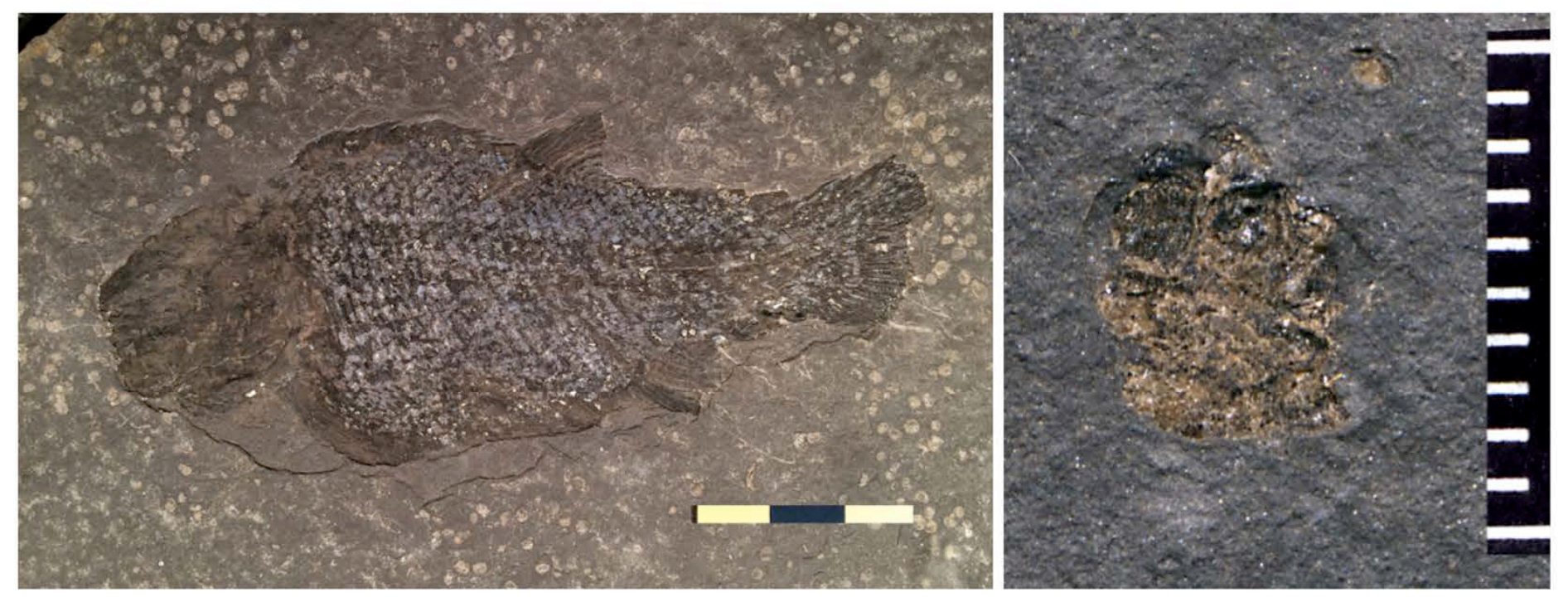
Early Jurassic



An andesitic to basaltic airfall ash is present at the same climatic precession-paced lake level cycle in the Towaco and East Berlin fms. of the Newark and Hartford basins, USA. Seen this far at 5 outcrops and four cores, spinocaudatians are common in these correlative strata.

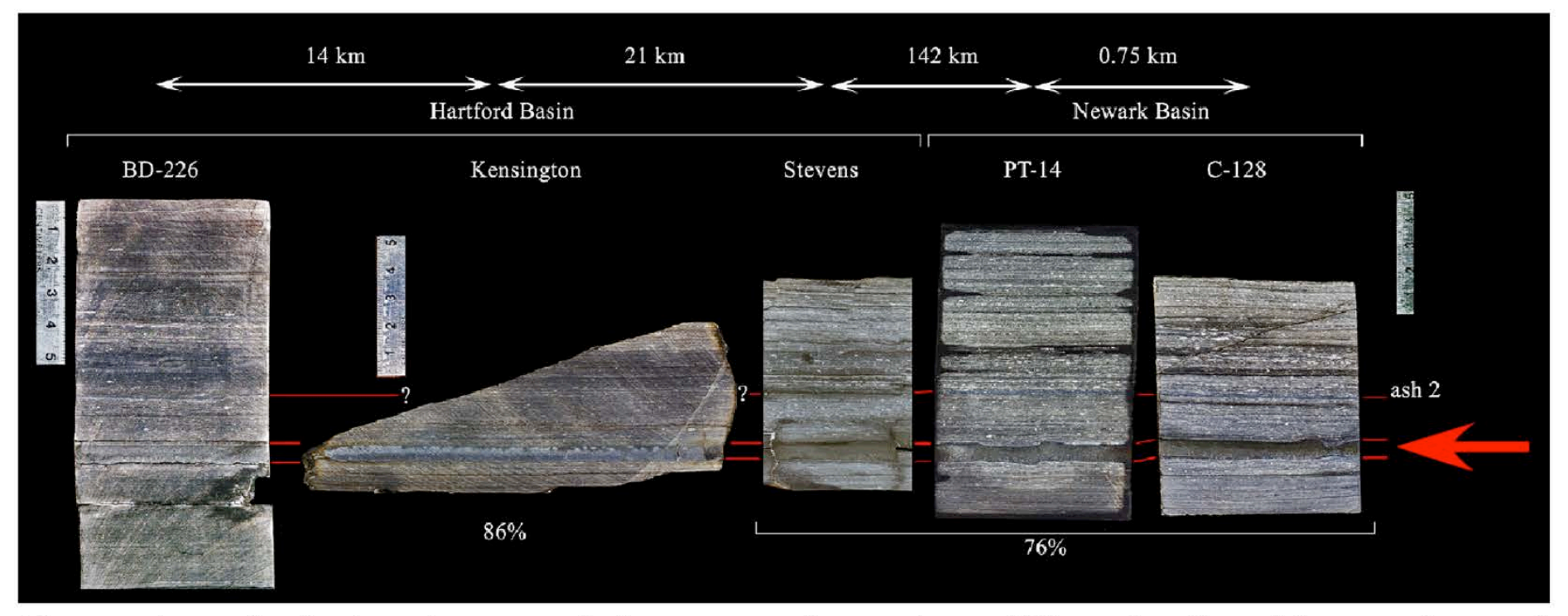
The sedimentary, climate-precession-paced cycle, the Westfield Bed (left) in the Hartford Basin and the Colfax Road Bed in the Newark Basin, contain the Pompton Ash (right from Hartford basin). Abundant spinocaudatans and fish are presant above the ash in the Newark and Hartford basins.

Above are examples of the small spinocaudatan *Bulblimnadia* sp. from above the Pompton Ash.Two panels, above left, are from the Hartford Basin, and on the right from the Newark Basin.



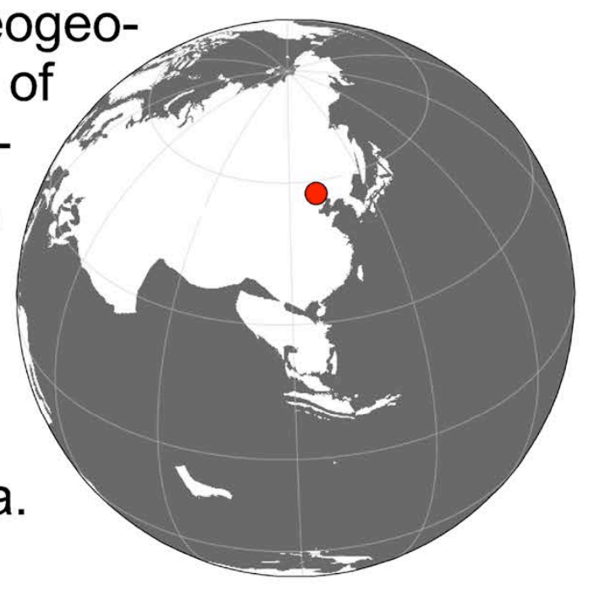
The fish, *Semiontous*, and *Bulblimnadia*, left and a gastric ejection of comminuted *Bulblimnadia*. Both from the Hartford Basin.

Thin sections of Pompton Ash: left, showing abundant plagioclase laths (crossed nicols) and right, low magnification, showing grading.

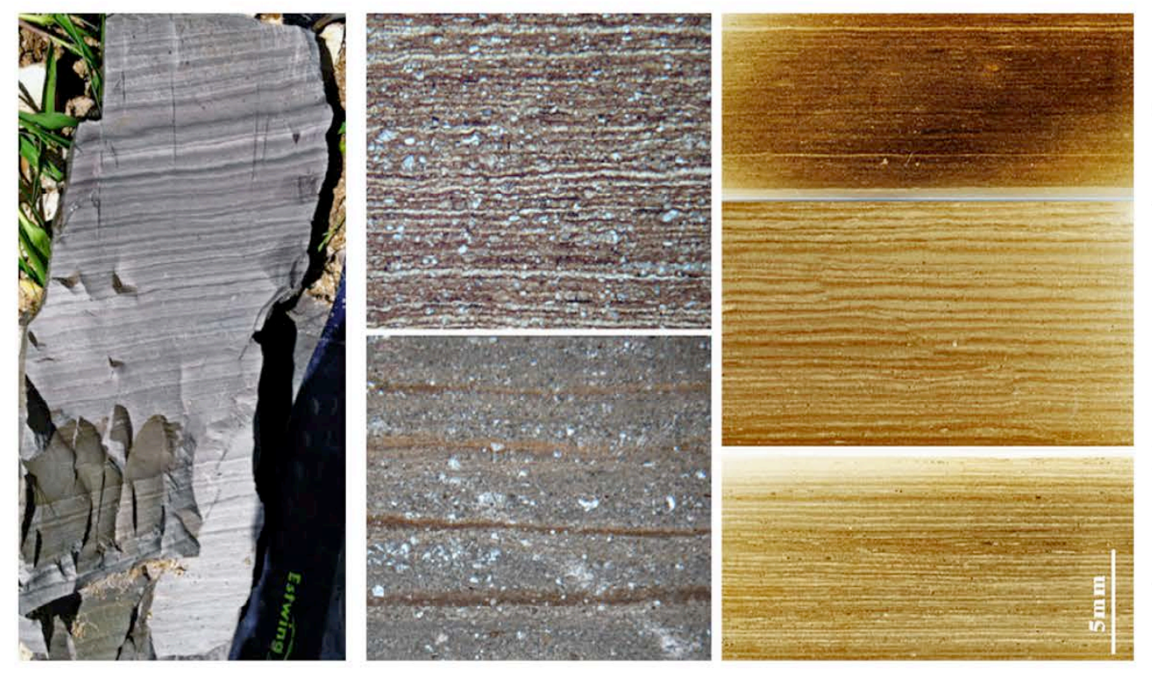


Pompton Ash (red arrow) from various localities in the Newark and Hartford Basins showing match of varves over nearly 200 km. The lake that deposited these sediments was a huge perennially stratified lake with abundant fish that ate the indigenous *Bulblimadia*.

Late Jurassic & Early Cretaceous

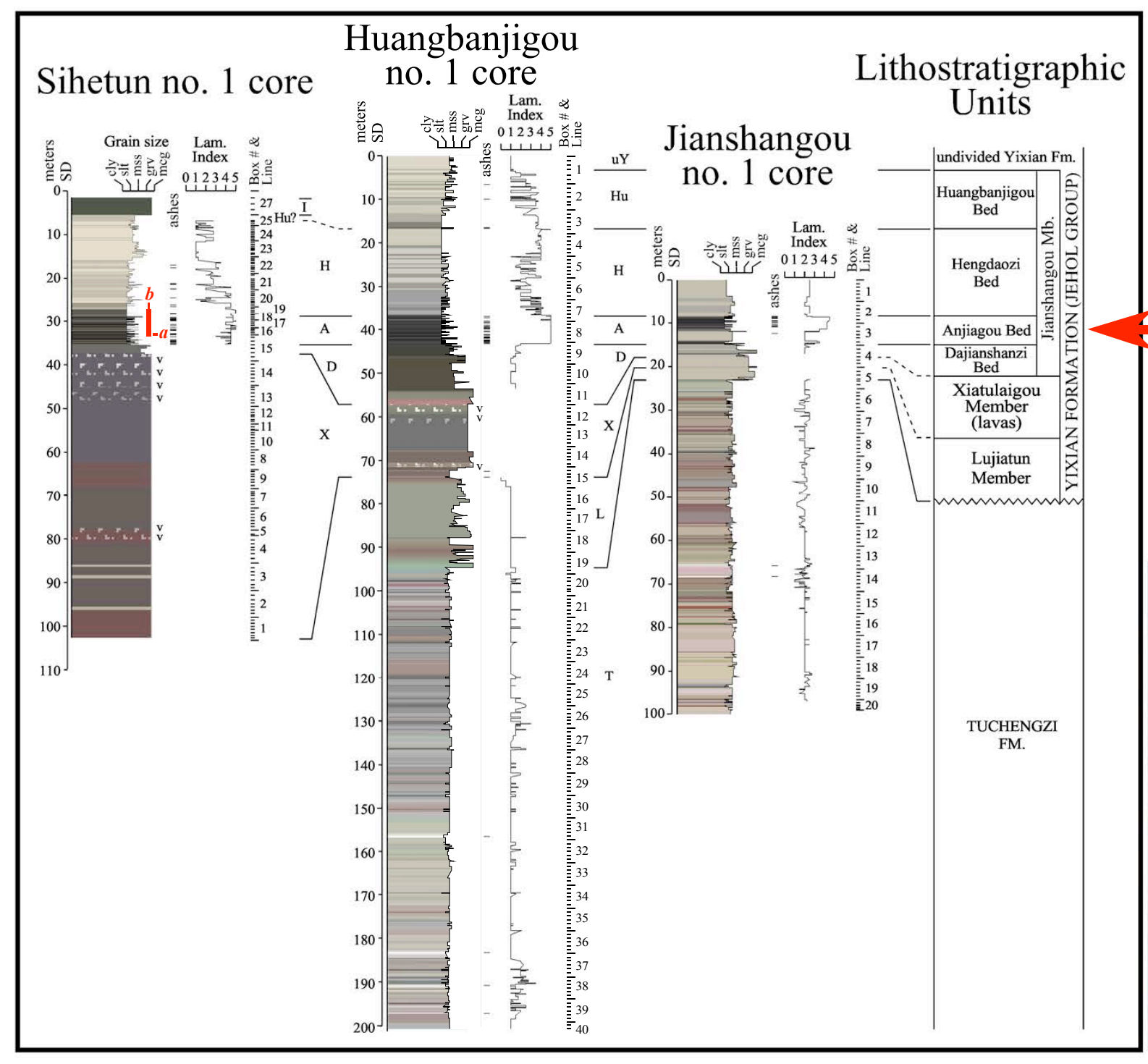


Left, Late Jurassic paleogeography and position of deposits with Daohugou biota. Right, Early Cretaceous paleogeography with location of strata with Jehol Biota. Both in China.



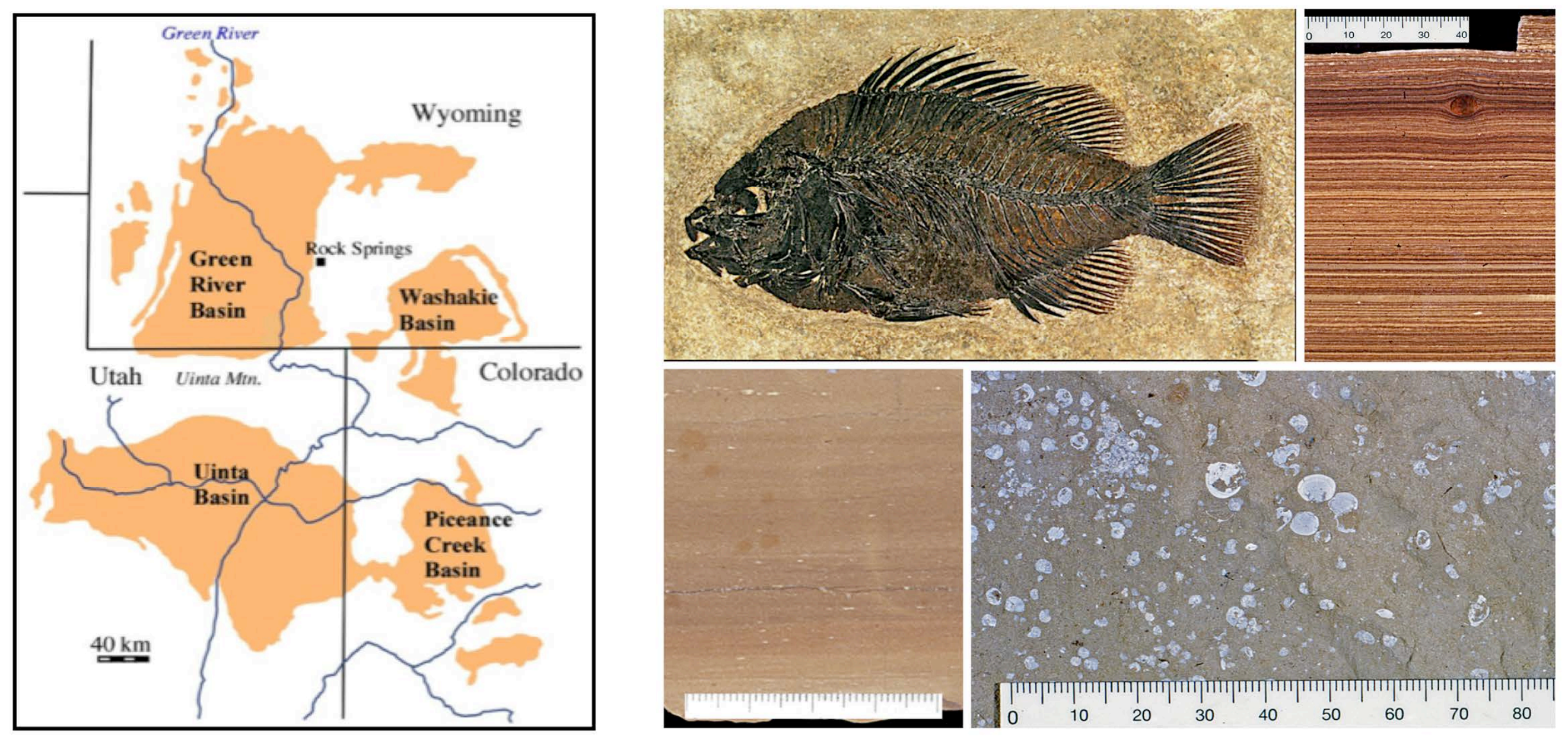
Left, microlaminated, Tiaojishan Fm. mudstone with Daohugou Biota. Right, two panels, microlaminated mudstone of Yixian Fm. mud-stone with Jehol Biota (from 18).

Left examples of salamander *Jeholotriton paradoxus* with spinodaudatans as stomach contents (from 19). All lake strata with definitive Daohugou Biota lack fish and salamaders evidently took their ecological role. Right panel, teleost fish *Lycoptera* with many large spinocaudatans from Sihetun locality in Jianshangou Mb. of Yixian Fm. famous for its exceptional Jehol Biota.



Cores (left and below) from the Sihetun subbasin show the lateral correlation of the Anjiagou Bed (Jianshangou Mb, Yixian Fm.) (red arrow) containing iconic exemplars of the Jehol Biota with no indications of subaerial exposure minimally over 10s of km. Spinocaudatans lived in this large perennially stratified lake. From ref. 20.

Eocene Green River



The Green River Fm. of western USA (orange, left) was deposited in giant lakes. Fish are preserved in microlaminated deep-water strata (above right) without spinocaudatans. But spinocaudatans (*Prolynceus* & *Cyclestherioides*) are abundant in marginal thin-bedded shallow-water strata deposited above the chemocline in the same lakes (above, lower right).

Miocene Lacustrine Diatomites

Neogene and modern strata deposited in stratified lakes differ from all older examples by being dominated by diatomites. While the biostratomy is identical to pre-Neogene examples, spinocaudatans are entirely absent. From refs. 21 (left) and 22 (right).

Conclusions

1. Pre-Neogene examples of spinocaudatans in deposits of large perennial lakes are common.
2. Biostratonomy of spinocaudatans is inconsistent with them being “washed in”.
3. Fish or other aquatic predators are common in these same lake deposits.
4. Coprolites and gastric ejections show that the predators commonly ate spinocaudatans.
5. Neogene lake perennial deposits completely lack spinocaudatans.
7. Abundant diatoms in lake deposits correlates with absence of spinocaudatans.
8. Most parsimonious conclusion is that spinocaudatans are excuded from modern perennial lakes by predator-mediated competition with other zooplankton now that diatoms are the dominant phytoplankton.
9. *The present is NOT the key to spinocaudatans past; their PAST is key to their present.*

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