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PATTERNS OF RECOVERY OF AMPHIBIAN DIVERSITY IN THE TRIASSIC

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Late Permian faunal extinction, albeit affecting the land tetrapod communities in a more or less uniform way, resulted in different starting conditions for the subsequent recovery of amphibian and reptilian components. Distinct from reptiles, the diversity of temnospondyl amphibians notably increased by the early Scythian, as compared with the terminal Permian. This was manifested in a rise of 4-5 new widespread temnospondyl families instead of only the two that existed immediately before the extinction event. Like this event *per se*, such a situation was ultimately underlain by overall uplifting of Pangea, which led to increase in aridity on land and dismembering of former lowland biotopes. These factors in turn forced the surviving tetrapod life to concentrate within, and around, local water basins, which initially gave an advantage to aquatic and subaquatic forms, primarily the amphibians.

As a whole, the dynamics of recovery of the Triassic temnospondyl amphibian fauna suffered a distinctive change with time. Basically, two principal consecutive patterns are discernible in the evolution of this fauna, referred to as the epoch of archaic diversity (Induan-earliest Olenekian) and the epoch of conservative development (mostly from late Olenekian to the end of the Triassic). These are linked by some intermediate types.

The archaic diversity pattern indicated the condition of a much disintegrated and impoverished terrestrial biota, whose existence immediately followed the Permian extinction and fell on the peak of aridification. Under this condition, the ecosystem's control over stability of tetrapod body plans was much weakened. Accordingly, the temnospondyl families of that time are mostly characterized by the following: (a) marked morphological diversity, sometimes producing chimeric structural types, and not necessarily combined with high taxonomic diversity; (b) short-term existence; and (c) quick spatial expansion resulting in worldwide, although much uneven, dispersal over the land.

The most ephemeral cosmopolitan groups demonstrating to various degrees this radiation mode are the Induan families Lydekkerinidae and Tupilakosauridae. The former, which originated and much diversified in southern Gondwana, succeeded in penetrating the north of Western Laurasia via nearshore marginal biotopes. Conversely, the tupilakosaurids that arose in Laurasia are known to rapidly have spread southwards into India, South Africa and Antarctica. Their morphology shows a combination of characters that otherwise seem incompatible in terms of standard temnospondyl structural patterns. A somewhat more long-lasting group of this type is the Gondwanan family Rhytidosteidae (latest Permian-late Olenekian), documented in the northern hemisphere by only two Early Olenekian genera from the coastal biotopes of the Eurasian Arctic margin. It demonstrates an especially wide range of both structural and taxonomic diversification, such that some genera combine advanced cranial features with those shared only by the most archaic Permocarboniferous forms.

Some further groups may be regarded (in terms of their diversification mode) as intermediate between the above-surveyed ones and those typifying the conservative development. One of them is the typical (non-lonchorhynchine) Trematosauridae, which originated in Laurasia in the latest Induan-early Olenekian, underwent a wide radiation in lacustrine and brakish-water basins during the Olenekian and rapidly came to decline in the Ladinian-Carnian. A short-term epibole and wide dispersal displayed by these amphibians are combined with a much limited scope of structural diversity, a character typical of the later advanced temnospondyls. Another example of similar kind is provided by the smaller family Brachyopidae, which shows a rather short, continuously documented history (Olenekian-Early Anisian) in combination with structural uniformity and restricted (Gondwanan) population area. The two Triassic taxa from outside this area currently assigned to brachyopids (from the Olenekian of Russia and Anisian of North America) are most likely the offshoots of Laurasian tupilakosaurids and dvinosaurids, respectively. The unquestionable brachyopid expansion to the northern hemisphere has been recorded only for Jurassic relicts.

The "conservative epoch" in the history of recovery and decline of temnospondyl amphibians may be first exemplified by the evolution of the Capitosauroidea, the largest and most diversified temnospondyl group that had spread over all the continents. Known since the very onset of the Triassic, the capitosauroids s.str. become rather common in

the late Olenekian and attain their peak of abundance in the Anisian-Ladinan. At first sight, their worldwide expansion and vast taxonomic diversity do not allow for clear-cut discrimination of the mode of their evolution from the "archaic diversity" pattern as outlined above. But this impression actually seems to result from very poor knowledge of capitosauroid taxonomic structure. The conservatism and homogeneity of their morphology, coupled with homoplasy and the scarcity of material available for most taxa, make it extremely difficult to distinguish the principal higher rank subdivisions within the group. As a consequence, the bulk of it looks like the product of a single, much diversified and cosmopolitan Triassic radiation. However, in those cases that enable discernment of the particular capitosauroid families (Stenotosauridae, Cyclotosauridae, Mastodonsauridae), one can see that in fact each of these included only a few members and inhabited strictly limited geographic realms. It seems most likely that, with a more accurate assessment of capitosauroid interrelationships, the same picture will be revealed for the rest of their contained taxa.

A total switch towards conservative patterns in amphibian evolution by the second half of the Triassic is further demonstrated by the other principal temnospondyl groups of this age. Like the capitosauroids, each of these exhibits very restricted scope of modifications in skeletal morphology. The longest persistence is documented for the Plagiosauroidea, which originated in the Scythian and flourished in the Middle-Late Triassic, producing three stable morphological types. Evaluation of its fossil record, which is limited to Europe, the European Arctic shelf and Thailand, leads to the conclusion that the group (along with accompanying cyclotosaurid capitosaurs) inhabited the Laurasian landmasses bordering the Tethys from the north. A basically similar pattern is demonstrated by the Metoposauridae, a family recorded with confidence only in the Late Triassic. Its population area included the southern Tethyan margin (North Africa and India), a part of the northern margin (Europe) and projected far westwards into the North America. Lastly, the Chigutisauridae, known mainly from the Late Triassic (except one Scythian genus, and putting aside late Mesozoic relicts), never expanded outside of Gondwana.

The above generalizations show that evolutionary changes observed among Triassic temnospondyls tended to slow up with time, while the ranges exhibited by particular lineages underwent reduction. It seems obvious that these trends reflected the gradual recovery and integration of the terrestrial biota, which was primarily expressed in diversification of its reptilian component. The growth of ecosystem stability left ever less room for structural variations attainable for large aquatic amphibians, thus returning them to a position they occupied in tetrapod communities right before the Permian extinction.