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EARLY RADIATION OF 'PHOLIDOPHORIFORM' FISHES, WITH SPECIAL REFERENCE TO THE ITALIAN FORMS

The actinopterygians represent the largest group of modern vertebrates with an estimated 23.681 species arrayed in 431 families and 4.075 genera. Among them, the Teleostei is the largest group with about 23.600 species. The Triassic and Jurassic periods are of particular interest in the history of Actinopterygii because it is during this interval that the largest group of living fishes, the teleosts, first appeared and diversified.

The recognition of the first appearance of Teleostei depends on our definition of the group:

- 1) the first appearance is in the Late Triassic for those who accept certain 'pholidophoriforms' as basal teleosts;
- 2) the first appearance is in the Early Jurassic for those who consider the "true" teleosts (proleptolepids and more advanced forms) as basal teleosts;
- 3) the first appearance of the Teleocephala is in the Late Jurassic for those who are interested only in the crown-group teleosts.

Consequently, Late Triassic fishes are of particular interest, especially those from Austria and Italy, for those who favor the first alternative.

The 'Pholidophoriformes' are represented by numerous species from different parts of the world, and range from Triassic to Cretaceous in age. They have been assigned to the group based on characters that are now known to be plesiomorphic, e.g., head and vertebral patterns, squamation, and body shape. Several families have been included in the order based only on primitive resemblances. For instance, the Pholidophoridae, Ichthyokentemidae, Archaeomaenidae, Pleuropholidae, Oligopleuridae, Majokiidae, Ligullelidae, and Galkiniidae. Recent studies by the senior author have confirmed that the order 'Pholidophoriformes' and the family Pholidophoridae are not monophyletic taxa. According to available information, the only taxa unquestionably assignable to the family Pholidophoridae are a few Triassic (type-species: *Pholidophorus latiusculus*) and Liassic European species.

The goal of this contribution is to analyze the early radiation of the 'Pholidophoriformes', especially those from Italy.

LATE TRIASSIC 'PHOLIDOPHORIFORMS'

Late Triassic 'pholidophoriforms' are known from two continents, Asia and Europe. European 'pholidophoriforms' have been known since 1832, with the first description of a Late Triassic *Pholidophorus* from Austria. Later, new species were described

from the Upper Triassic of Italy. Recently, possible ‘pholidophoriforms’ from Switzerland have been mentioned, but the description of these specimens has not yet been published.

So far, five ‘pholidophoriform’ genera (*Eopholidophorus*, *Parapholidophorus*, *Pholidoctenus*, *Pholidophorus*, *Pholidorhynchodon*) have been reported from marine sediments of the Upper Triassic (Norian) of Lombardy and Friuli. Most taxa are represented by numerous specimens, and were studied mainly by Rocco Zambelli at the Museo Civico di Scienze Naturali “E. Caffi” (Bergamo) during the second part of the 20th century. The material is currently under systematic review by the authors. The study of new material and re-study of previous finds reveals the presence of new species (e.g., from Cene, Endenna) and new genera (e.g., from Ponte Giurino). At the moment, we consider them under the name pholidophoriforms, to avoid confusion, despite the fact that we are aware that the order is not monophyletic. Furthermore, it is unclear whether the Italian ‘pholidophoriform’ genera are teleosts, stem-group teleosts or halecomorphs.

EARLY RADIATION OF ‘PHOLIDOPHORIFORMS’

The earliest record of ‘pholidophoriforms’ is from the Late Triassic. It is interesting to remark that at least six genera are known from this interval, five of them from Italy, but there is the suggestion that the number will increase with the description of new genera and species. Probably, the presence of ‘pholidophoriforms’ in only two continents is a biased result due to the scarce knowledge of Upper Triassic localities world wide.

Among these six Late Triassic genera, only one seems to be present in the Early Jurassic of Europe (*Pholidophorus*). The Late Triassic forms were replaced by one new Asiatic and three new European genera in the Early Jurassic. By the Middle Jurassic the group had expanded (15 genera) to other continents (Asia, Africa, Australia); however, so far, ‘pholidophoriforms’ have not been recovered from European Middle Jurassic localities. The diversification continued and numerous new genera appeared in the Late Jurassic, most of them in European localities.

It is remarkable that all genera persisted for only a short period of time, and apparently had a very restricted geographical distribution. This opens interesting questions. The Asiatic Late Triassic (*Jianglichthys*) and Early Jurassic (*Hengnamia*) ‘pholidophoriforms’ are considered freshwater forms, whereas most of ‘pholidophoriforms’ are marine. How can we explain the colonization of freshwaters environments during these periods? Why have ‘pholidophoriforms’ not been found in Upper Triassic/Lower Jurassic of North American lakes that were the closest freshwater environment to the Western end of the Tethys, and where the richest ‘pholidophoriform’ assemblages dwelled in the Zorzino Limestone basins.

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