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Folded Teeth and the Monophyletic Origin of Tetrapods

BY HANS-PETER SCHULTZE[1]

Because many groups of mammals have teeth that are characteristic in form, tooth form has become an important indicator of phyletic relationships within the Mammalia. In contrast, the simple conical teeth of most reptiles, amphibians, and fishes are barely differentiated in external form, and generally the tooth form is of little phyletic significance. However, among crossopterygians and lower tetrapods there are groups that have teeth of peculiar internal structure, involving an infolding of the orthodentine of the pulp cavity wall. Such orthodentine is called "folded dentine" (plicidentine), and teeth possessing it are "folded teeth."

Folded teeth have been studied by Bystrow (1938, 1939) and Schultze (in press), among others. Bystrow worked mainly with isolated teeth, and Schultze with articulated material. Schultze's results have some bearing on the current controversy of "monophyletic" versus "diphyletic" origin of tetrapods. These results are briefly summarized in the present paper for the purpose of discussing the phyletic significance of folded teeth and internal tooth structure in crossopterygians and lower tetrapods.

TEETH OF CROSSOPTERYGIANS

Within Coelacanthiformes and Struniiformes, folded teeth are unknown, but within Rhipidistia there are folded teeth of three types (fig. 1).

[1] Assistant Professor, Geological and Palaeontological Department, University of Göttingen, Göttingen, Germany.

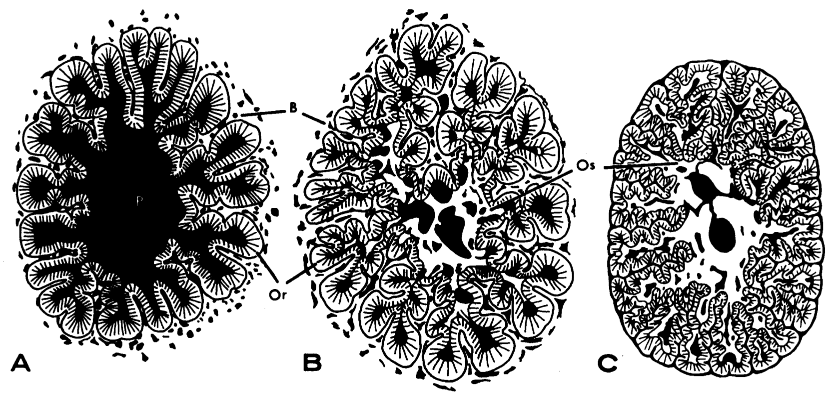

FIG. 1. Types of folded teeth in parabasal section. A. Polyplocodont (*Eusthenopteron*). B. Eusthenodont (*Eusthenodon*). C. Dendrodont (*Hamodus,* after Bystrow, 1939, fig. 8C).

Abbreviations: B, bone; Or, orthodentine; Os, osteodentine; P, pulp cavity.

These may be described as follows:

A. Polyplocodont: free pulp cavity; orthodentine folded simply and irregularly with branches of first or second degree; bone of attachment extended between folds.

B. Eusthenodont: pulp cavity filled with osteodentine; folding of orthodentine often more complicated; bone of attachment extended between folds.

C. Dendrodont: pulp cavity filled with osteodentine; orthodentine with complicated and regular folding ("firelike" branching); bone of attachment restricted to base of tooth and not extended between folds.

OSTEOLEPIFORMES: Within Osteolepiformes occur simple conical teeth with little or no folding of the orthodentine (*Gyroptychius, Latvius, Osteolepis, Thursius*); polyplocodont teeth (*Eusthenopteron, Megalichthys, Panderichthys, Rhizodopsis, Rhizodus, Sauripteris, Strepsodus, Tristichopterus*); and eusthenodont teeth (*Eusthenodon, Litoptychus, Platycephalichthys*). Except for *Tristichopterus* and *Panderichthys,* the genera from the Middle Devonian possess simple conical teeth. The folding in the teeth of *Tristichopterus* is very simple relative to that of the Upper Devonian genera. Small differences in the polyplocodont tooth structure separate Osteolepiformes into two groups: one group, represented by *Eusthenopteron* (fig. 2, E) and *Strepsodus* (fig. 2, S), has dentine with very irregular branching, and bone of attachment reaching to the ends of the folds and branches; the other group, represented by *Panderichthys* (fig. 2, Pa), has dentine with folds,

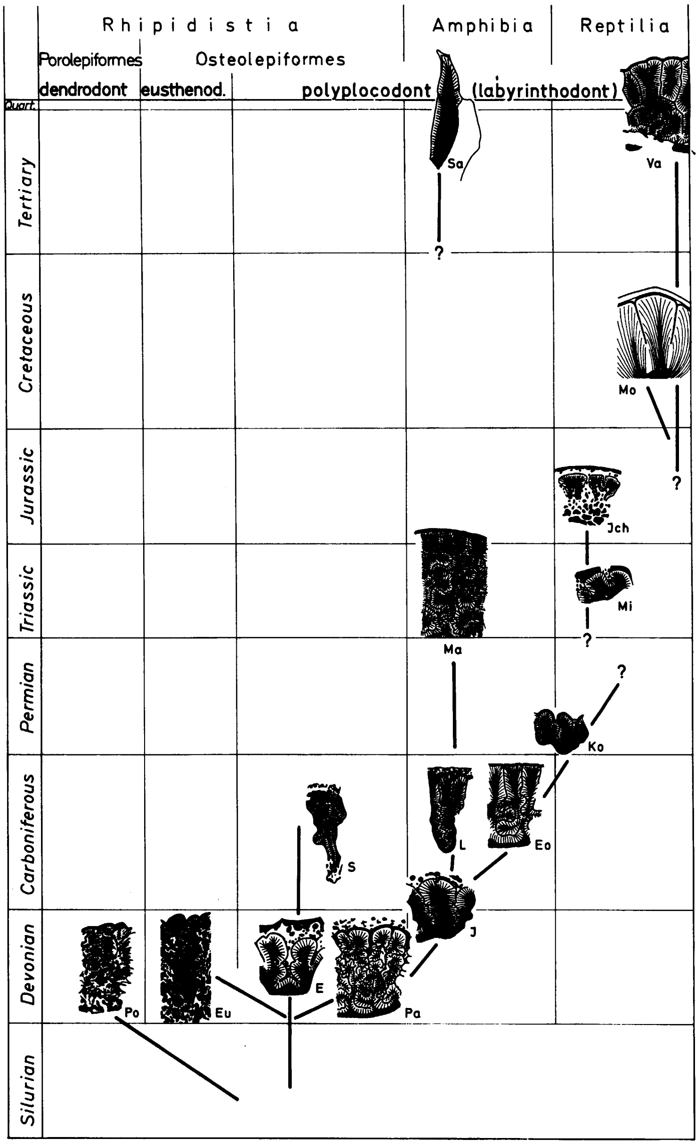

FIG. 2. Distribution of tooth types within geological time with the probable phyletic trends, in parabasal section, except where indicated.

Abbreviations: E, *Eusthenopteron;* Eo, *Eogyrinus;* Eu, *Eusthenodon;* I, *Ichthyostega;* Ich, *Eurypterygius;* Ko, *Kotlassia;* L, *Loxomma;* Ma, *Mastodonsaurus;* Mi, *Mixosaurus;* Mo, *Mosasaurus;* Pa, *Panderichthys;* Po, *Porolepis;* S *Strepsodus;* Sa, *Salamandra* (vertical section representative also of Anura); Va, *Varanus.*

meandering branches, and bone of attachment extending only a short distance between the folds. The folding in the teeth of *Panderichthys* is very similar to that of *Ichthyostega* (fig. 2, I) and other Labyrinthodontia.

POROLEPIFORMES: All known Porolepiformes have dendrodont teeth, and dendrodont teeth, so far as is known, are restricted to this group. In the teeth of the Lower Devonian genus *Porolepis,* there is a boundary between the growth of the orthodentine and the osteodentine in the top of the pulp cavity (Schultze, in press). However, both orthodentine and osteodentine grow closely connected in all later genera of Porolepiformes, and no sharp boundary is developed between these two hard tissues. Unfolded teeth are unknown within Porolepiformes. Even the smallest teeth are folded, and their pulp cavities are filled with osteodentine.

TEETH OF FOSSIL AMPHIBIANS

The Labyrinthodontia are a group of fossil amphibians named after their tooth structure. The labyrinthodont tooth (fig. 2, Ma, Eo, Ko) is a variant of the polyplocodont tooth: the branches of the folds are apparently lost, and the folds meander only. Usually the bone of attachment does not penetrate into the folds. The teeth of the earliest Labyrinthodontia, the Ichthyostegalia (fig. 2, I) and the Loxommatoidea (fig. 2, L), have a plicidentine with folds branching like those of the osteolepiform *Panderichthys.* With the loss of the branches the intensity of folding sometimes increases by meandering. For example, the pulp cavity in the Triassic *Mastodonsaurus* (fig. 2, Ma) is filled with plicidentine (i.e. folded orthodentine, not osteodentine, which fills the pulp cavity of eusthenodont and dendrodont teeth). There is pronounced folding, also, in the teeth of Carboniferous Anthracosauria but less in the teeth of Seymouriomorpha (fig. 2, Ko). All other fossil and Recent Amphibia (see below) apparently lack folded teeth.

TEETH OF REPTILES

Within Reptilia, plicidentine occurs only in a few forms: Ichthyosauria, Varanoidea, and possibly *Limnoscelis* and *Champsosaurus* (the Seymouriomorpha and the Anthracosauria are listed with the Amphibia because of their identical tooth structure; the extent of folding in the teeth of the Anthracosauria is similar to that in the teeth of the amphibian Capitosauroidea). True labyrinthodont folding, however, apparently does not occur within Reptilia (for comments on the condition in *Limnoscelis* [Captorhinomorpha] and *Champsosaurus* [Choristodera], see Schultze, in press).

The plicidentine of Ichthyosauria (fig. 2, Mi, Ich) and Varanoidea (fig. 2, Mo, Va) has possibly developed independently. At least the folding in the teeth of the oldest known Ichthyosauria (fig. 2, Mi) and Varanoidea (fig. 2, Mo) is so simple that comparisons with the folding in the teeth of Seymouriomorpha, Anthracosauria, Labyrinthodontia, or Rhipidistia have little meaning. Later Ichthyosauria (fig. 2, Ich) and Varanoidea (fig. 2, Va) have a peculiar development of the plicidentine for which an ancestral type of folded tooth has not been found among Reptilia, or even among Rhipidistia.

In the evolution from the reptilian to the mammalian grade, folding in the teeth was apparently lost. Tooth structure of the mammals *Orycteropus* and *Galeopithecus* cannot be compared with the plicidentine of Rhipidistia and Labyrinthodontia.

TEETH OF RECENT AMPHIBIANS

The teeth of nearly all Recent Amphibia are divided into a basal pedicel and a distal crown, which are interconnected by fibers (Parsons and Williams, 1962). The division occurs within the orthodentine, either of the upper part or near the base of the tooth, and never between the orthodentine and bone as in some Actinopterygii (Kerr, 1960). For urodele teeth with the division near the base, the division develops before the orthodentine of the pedicel grows together with the jaw bone (Kerr, 1960, fig. 2B: orthodentine densely stippled, bone lightly stippled).

Few species of Recent Amphibia have teeth without a division. The discussion of the exceptions by Parsons and Williams (1962, pp. 373–378) demonstrated that traces of the division are not entirely absent even in these forms. In contrast to Parsons and Williams (1962, pp. 376–377), but in agreement with Hoffmann (1873–1878, p. 390, pl. 30, fig. 4), I can demonstrate teeth without a division in *Necturus* (fig. 3A). But in this instance, too, some indication of a division can be seen: the pulp cavity is narrow where the outside is constricted (the constriction is apparently caused by an insufficient calcification of the outer part of the tooth, as indicated by the globular structure of the orthodentine). One may tentatively conclude, therefore, that a division (or traces of it) is a character common to the teeth of all Recent Amphibia, and that where a division is absent it is absent secondarily.

In teeth without a division, the pulp cavity is often filled with hard tissue. On the basis of this observation Oltmanns (1952) defined three types of amphibian teeth: (1) teeth with a division and a free pulp cavity; (2) teeth with a reduced or absent division and a pulp cavity penetrated by trabecles of bone (*Proteus:* Gö 50/378 [slide in the collection of the Geological and Palaeontological Department of the University of Göt-

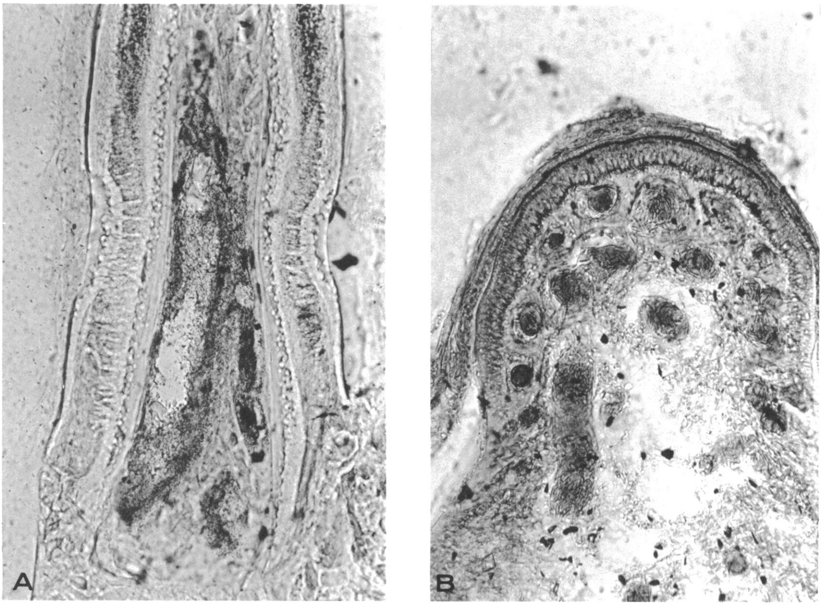

FIG. 3. A. *Necturus maculosus* Rafinesque, vertical section of upper-jaw teeth, showing indication of division (Gö 50/371, × 100). B. *Ceratophrys cornuta* Linné, parabasal section of developing upper-jaw tooth before calcification (Gö 50 /392, alizarin stained, × 100).

tingen]; Oltmanns, 1952, fig. 22a,b; *Discoglossus:* Oltmanns, 1952, fig. 23; *Necturus:* Oltmanns, 1952 p. 385); (3) teeth with no division and a pulp cavity filled with hard tissue (*Ceratophrys:* figs. 3B, 4A, B; Gö 50/385-6; 50/390-5; Oltmanns, 1952, figs. 26, 27). The hard tissue filling the pulp cavity of *Ceratophrys* is a special kind of dentine, but apparently not plicidentine as Oltmanns (1952) termed it. The peripheral dentine develops as orthodentine until the tissue within the pulp cavity begins to achieve a definitive form (fig. 3B). During calcification of the peripheral dentine, cells become included within it (fig. 4). In this respect it resembles pallial-semidentine (Ørvig, 1967, p. 101), but unlike pallial-semidentine it lacks cells that are elongated in radial directions. The hard tissue in the pulp cavity is composed of denteons within interstitial cellular bone tissue. In some denteons, odontoblasts are included, as in the dentine surrounding the pulp cavity. The bone cells in the interstitial tissue and the odontoblasts included in the denteons suggest a classification, osteo-semidentine. Semidentine in the sense of Ørvig (1967, p. 101) is a hard tissue peculiar

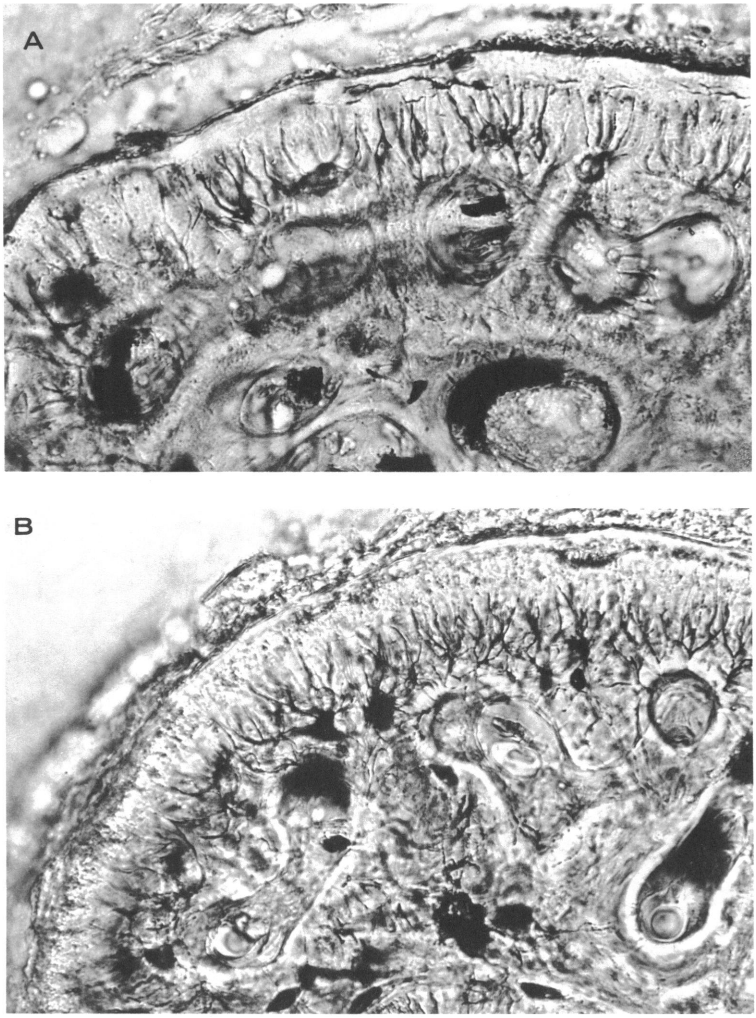

FIG. 4. *Ceratophrys cornuta* Linné, parabasal section of parts of developing upper-jaw teeth (Gö 50/395, alizarin stained, × 300). A. Pallial dentine calcified and hard tissue within pulp cavity partly calcified. B. Pallial dentine and hard tissue within pulp cavity fully calcified.

to the Arthrodira.

The peculiar nature of the hard tissue in the teeth of *Ceratophrys* suggests that the tissue is a secondary development. This kind of hard tissue has not been observed in other fossil Amphibia or Rhipidistia. Indeed, in the teeth of Rhipidistia, the pulp cavity is filled with hard tissue only with the development of plicidentine. In addition, the teeth of *Ceratophrys* are monocuspidate (most of them without a division) in adults, but develop from bicuspidate teeth with a division (Lehman, 1968, p. 311). The ontogenetic development from bicuspidate to monocuspidate teeth, is further evidence suggesting that teeth without a division occur only secondarily among Recent Amphibia (see also Oltmanns, 1952; Lehman, 1968; cf. Parsons and Williams, 1962).

A bibliography on folded teeth has been given by Schultze (in press); and Parsons and Williams (1962) have provided a bibliography on divided teeth.

CONCLUSIONS

1. The dendrodont tooth is a highly advanced type of folded tooth peculiar to Porolepiformes. Apparently no more advanced type of tooth has ever evolved from it, and no tooth type closely comparable with it is known, either among fishes or among tetrapods. These facts, therefore, support the hypothesis of common ancestry for Porolepiformes, but lend no support to the theory that the Urodela, or any other group of tetrapods, have evolved from Porolepiformes.

2. The eusthenodont tooth is a moderately advanced type of folded tooth known to occur only in *Eusthenodon, Litoptychus,* and *Platycephalichthys*. It is not certain that this tooth type indicates common ancestry for these three genera.

3. The polyplocodont tooth is a primitive type of folded tooth occurring in many Osteolepiformes and some early tetrapods. Tooth structure of *Panderichthys* is nearly identical to that of *Ichthyostega* and Loxommatoidea. Among Rhipidistia, a type of folded tooth primitive enough to have given rise to the folded teeth of Amphibia consequently occurs only in Osteolepiformes. Among Rhipidistia, in addition, unfolded teeth, which could have given rise to the unfolded teeth of fossil and Recent Amphibia, are known only among Osteolepiformes (the adults of early Osteolepiformes and the juveniles of late Osteolepiformes). It therefore may be concluded that tooth structure supports the derivation of tetrapods from Osteolepiformes, but not from Porolepiformes (another advanced feature involving porolepiform teeth, without a parallel among Osteolepiformes and tetrapods, is the arched, parasymphysial dental plates. The comparison of these plates with the rows of teeth of urodele larvae [Jarvik, 1963, p. 69] seems to involve a similarity in position only; in any case, teeth occur in this position in Osteolepiformes also [Jessen, 1967]. A more substantial comparison, perhaps, would be one of the

fangs of Osteolepiformes, particularly those at the anterior end of the dentary of *Panderichthys* with those of Labyrinthodontia).

4. For the specialized tooth structure of Ichthyosauria and Varanoidea, a suitable ancestral type of folded tooth could not be found. The folding in the teeth of these groups appears to be of a type peculiar to them.

5. Divided teeth, a specialization within the tetrapods, occur in nearly all Recent Amphibia, and are lost, apparently secondarily, only in a few forms. Divided teeth could not be found in Rhipidistia or early tetrapods.[1] These facts suggest that the Urodela, Anura, and Apoda have had a common ancestry even after their derivation from osteolepiformlike, or labyrinthodontlike ancestors.

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[1] Bolt (1969) has recently found divided teeth within Labyrinthodontia, in the new genus *Doleserpeton*. Evidently related to rhachitomous amphibians, *Doleserpeton* is the only genus of that group known to have divided teeth. Thus, divided teeth probably appeared among Labyrinthodontia first. This conclusion supports the argument against the diphyletic theory involving the derivation of Urodela from Porrolepiformes and Anura from Osteolepiformes.

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