JURIJ ALEXANDROVICH ORLOV MEMORIAL NUMBER
JOURNAL OF THE PALAEONTOLOGICAL SOCIETY OF INDIA
VOL. 20, 1977 pp. 16—20 (*For* 1975).

EVOLUTIONARY MODIFICATIONS OF THE TEETH STRUCTURE IN THE PALÆOZOIC CROSSOPTERYGII

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ABSTRACT

Two types of folded teeth of osteolepiform Rhipidistia (polyplocodont and eusthenodont, Schultze, 1969) demonstrate their variability and are connected through the transitional modifications both with each other and with dendrodont type, peculiar to Porolepiformes. All three types represent different stages of the evolutionary changes of the teeth structure in Crossopterygii and could be achieved independently (parallel) within different lines of Rhipidistia and in some early tetrapods. In this connection teeth microstructure can be considered as a diagnostic feature but by no means it may always be used as an indicator of the close phylogenetic relations. The solution of controversial problems concerning the origin of land vertebrates surely can not be based only on the pattern of teeth structure.

The teeth of Crossopterygii are found in Palaeozoic deposits very often and attract our attention with a view of their use both in the stratigraphy and systematic. But isolated from bones and resorbed these teeth are usually not sufficient for their definition. They are very similar in shape in many Crossopterygii except of those of certain peculiar genera (*Homodus*, *Onychodus*, *Thysanolepis*). The mode of striation on the outer wall of the tooth (fine, coarse, double; striae pattern) is often considered to be the diagnostic feature but it makes us possible to define them only up to the level of the order or, at the best, to that of the family. Histological structure of teeth seems to be the most informative feature because among Crossopterygii there are forms both with the simple (not plicated) and complexly plicated teeth. The latter attract our attention due to their diverse structures: specific plication pattern on the orthodentin round the pulp cavity and the structure of the cavity itself. Some of these complexly plicated teeth demonstrate far reaching histological resemblance to the teeth of the lower tetrapods, in particular to that of Stegocephalia; Phylogenetic constructions and a solution of the problem concerning ancestors of the tetrapods were sometimes based on this resemblance.

HISTORY

The diversity of the plicated teeth structure in Rhipidistia was known already in Ch. Pander's time (Pander, 1860); and consequently two types of the plication, "dendrodont" and "rhizodont", have been distinguished. It was noted the resemblance of rhizodont teeth to the complexly plicated teeth of some Triassic Labyrinthodontia. As a result of this the term "labyrinthodont" plication becomes widely used in relation both to Crossopterygii and the ancient amphibias. The extent of the similarity of this type of plication served at times to estimate a rate of phylogenetic relation of these groups of vertebrates (Bystrow, 1939; Vorobyeva, 1962; Vorobyeva & Obruchev, 1964).

A. P. Bystrow (1939) was the first who accomplished the most detailed comparative study of the teeth structure of Rhipidistia and Labyrinthodontia. He described simple (non-plicated or weakly plicated) teeth with a hollow pulp cavity characteristic of one of the most ancient groups, Osteolepidinae (order *Osteolepiformes*). He also distinguished three types of complexly plicated teeth of Rhipidistia. One of them, "dendrodont" is peculiar to Porolepiformes, the other two, "polyplocodont" and "eusthenopteront", to Osteolepiformes. Later on H. P. Schultze (1969, 1970) modified these three types of plication into dendrodont, polyplocodont and eusthenodont ones and made some corrections in their characteristics. The first type is characterized by the complex and uniformly plicated ("plumose") branching of the orthodentine[1] and a pulp cavity filled with osteodentine (Schultze, 1970). The second type is distinguished by its hollow pulp cavity, rather simple and uneven plication of the orthodentine with plicae of the

[1]Plicidentin.

first and second order and bone of attachment extended between folds.

The third type differs from the second one in the pulp cavity filled in with the osteodentine and usually somewhat more complex plication of the orthodentine.

Close similarity of polyplocodont teeth structure in *Panderichthys* (Osteolepiformes) and in *Ichthyostega* (Amphibias) allowed for a long time to consider the former as an ancestral form of tetrapods (Bystrow, 1939; Vorobyeva, 1962; Schmalhausen, 1964; Schultze, 1970). But at present *Panderichthys* and *Ichthyostega* are practically proved to belong to the divergent evolutionary lines due to the structure of the pectoral finds of *Panderichthys* (Vorobyeva, 1975). And they seem to achieve similar teeth structures quite independently as a result of parallel development from the non-plicated teeth to the ancient Osteolepiformes. I. I. Schmalhausen (1940) regarded such parallelismes quite possible in the evolution.

EVOLUTIONARY MODIFICATIONS OF THE TEETH STRUCTURE IN CROSSOPTERYGII

Simple non-plicated teeth are peculiar to two orders of Crossopterygii, i.e. Coelacaanthiformes and Onychodontformes known from the Devonian. At the same time they are traced within the most primitive and conservative Osteolepiform group——Osteolepidinae—lasting from the middle Devonian to the early Carboniferous, that is almost from the very beginning of the adaptive radiation of Crossopterygii. And since the type of teeth plication of the subsequent forms of certain phyla obviously becomes more complicate, it is surely to believe that the simple non-plicated teeth of Crossopterygii evolutionally precede the complexly plicated ones. The degree of complexity of the plication could indicate then the evolutionary level of the teeth structure in Crossopterygii.

Polyplocodont type of orthodentine plication should be recognized as the most primitive one, which is peculiar to many forms and among them to geologically rather young Osteolepiformes and probably to the oldest tetrapods (Tab. I.).

Eusthenodont type of plication is undoubtedly more progressive in comparison with the polyplocodont one. Previously it was known only in three genera of Osteolepiformes (*Litoptychius*, *Eusthenodon*, *Platycephalicthys*—Schultze, 1970), and now, in eight genera (Tab. 1) including one porolepiform, *Powichthys*, from the lower Devonian of the Eastern Canada.[1]

Comparison of teeth microstructure in forms of different geological age and belonging to different lines reveals that this type of plication could be evolved parallel from the polyplocodont or non-plicated teeth of the ancestors (Tab. 1). Early appearance of eusthenodont teeth in the evolution of Crossopterygii (*Powichthys*) indicates rather uneven and at times accelerated evolution of their teeth structure.

Dendrodont type of plication seems to be the most specialized one. The fact that this type is peculiar only to a narrow group of porolepiforms can serve as an indirect evidence of their relationship, but by no means it should be considered as the most convincing argument for the latter. Theoretically (by analogy with polyplocodont and eusthenodont teeth) dendrodont teeth could be evolved also parallel from the simple non-plicated teeth of the ancestors.

PECULIARITIES OF THE MODIFICATION OF TEETH STRUCTURE IN OSTEOLEPIFORMES

By the number of known forms, Osteolepiformes are now the most extensively investigated group of Crossopterygii with respect to their teeth microstructure. Schultze based his work (1969, 1970) on the analysis of 15 genera of these fishes. After personal study of the teeth structure of 19 species (Tab. 1) the author increased this list to 23 genera.

All data available show a considerable variability of teeth structure of Osteolepiformes and somewhat conditional mode of their division into phyla by the plication type. There are some transitional grades between simple non-plicated teeth of the ancient Osteolepidinae and complexly plicated teeth of more late Osteolepiformes, as well as between different types of plication including dendrodont one.

Series transitional between various types of teeth structures are found both by the comparison of different stages of teeth growth, from fine to very large (Bystrow, 1939; Vorobyeva, 1962) and in phylogeny, in particular among eusthenopterids and rhizodontids (Tab. 1). In the course of evolution teeth structure of Osteolepiformes was becoming more complicate and apparently more consolidate due to : (1) the deepening of primary orthodentine plicae and appearance in them of branches of the second and third order; (2) the development of peripherial bone-septae between plicate at the base of the teeth; (3) filling in the pulp cavity with osteodentine septae connecting the central plicae of orthodentine. The modifications proceeded sometimes quite independently. They resulted in a variety of polyplocodont and eusthenodont types of teeth structure (Plate 1). Thus depending on the depth of bone invasion between orthodentine plicae two subtypes are distinguished within the polyplocodont pattern. The first and more common one is characterized by the deep (up to the end of plical)

[1]The author had an opportunity to study the microstructure of the teeth of this fish together with Prof. H. P. Schultze on the specimen provided by Dr. G. Jessen in Tubingen.

Table 1

List of forms	Geological age	Non-plicated teeth	Plicidentin: Polyplocodontian s	Polyplocodontian ns	Eusthenodontian s	Eusthenodontian ns	Dendrodontian
Onychodontiformes	D_2—D_3	+					
Coelacanthiformes	D_2	+					
Porolepiformes							
Powichthys	D_1				+		
Porolepis	D_1—D_2						+
Holoptychiidae	D_2—D_2						+
Osteolepiformes							
I. Osteolepididae							
Osteolepidinae	D_2—C_1	+					
Gyroptychiinae	D_2	+	+				
Glyptopominae	D_3	?					
Megistolepididinae	D_3						
Megistolepis	D_3		+				
Cryptolepis	D^2_3		+				
Megalichthyinae	C—P_1						
Megalichthys	C—P_1		+				
?Viluichthys	C_1						
Thysanolepidinae							
Thysanolepis	C_1		+				
II. Lamprotolepididae							
Lamprotolepis	C_1		+				
III. Eusthenopteridae							
Eustenopterinae							
Tristichopterus	D^2_1		+				
Eusthenopteron	D_3		+				
Jarvikina	D^1_3				+		
Eusthenodon	D^2_3				+		
Platycephalichthyinae							
Platycephalichthys	D_3				+		
IV. Panderichthyidae							
Panderichthys	D_3			+			
?Obruchevichthys	D_3						+
V. Rhizodopsidae							
Rhizodopsis	C		+				
VI. Rhizodontidae							
Rhizodus	C_1		+				
Strepsodus	C		+				
Pyenoctenion	C				+		
Inc. sed.							
Litoptychius	D_3				+		
Sauripterus	D^2_3				+		

s—plical separated by bones
ns—plical not separated by bones.

invasion of peripheral bone into orthodentine (Tab. 1, Plate IB, ID). The second type peculiar to Panderichthyidae (Plate IC, II) is distinguished by the comparatively moderate insertion of the bone between plicae. As a result of this, central plicae are in contact with each other and imitate local "fire-like" branching distinctive of the dendrodont type of teeth structure of Porolepiformes. Analogous central—contacting orthodentine plicae are also observed in the representatives with the eusthenodont type of teeth structure, in particular in the Late Devonian *Obruchevichthys* (Plate IA)[1] which has a teeth structure very similar to that of the early Devonian porolepiform, *Powichthys*.

As a rule, deepening and branching of plicae seems to be accompanied in Crossopterygii by the invasion of the connecting bone between plicae. In this respect teeth structure of the Carboniferous *Thysanolepis micans* (endemic subfamily *Osteolepididae* from Yakutia) (Plate IIID) is very representative. Lingual side of its tooth is non-plicated while the labial side bears prominent primary plicae showing a bony tissue gradually invading between them. In Panderichthyidae and Porolepiformes the invasion was most probably delayed because of some deviations occurring in the early stages of the tooth growth. This assumption is confirmed by ontogenetic series of the teeth structure in *Panderichthys rhombolepis* (Plate A—C) in which the late stages reveal not only more complex plication system but also more deep invasion of bony tissue into orthodentine (Plate IIB, C). At the same time splitting of plicae and corresponding invasion of bone between them becomes more pronounced in the phylogeny of this genus (Plate IID) although the plication does not become much more complicate. In consequence, in the Famenian *Panderichthys bystrovi* some plicae turn out to be almost completely separated by bone.

In the geologically late format of one and the same genetic row complication of the teeth structure accelerates with the increase of the teeth size. It could be well demonstrated by eusthenopterids when compared different-sized teeth of *Tristichopterus* and *Eusthenopteron*, from one side (Plate ID), and those of *Jarvikina* (Plate IVA), *Eusthenodon* and *Platycephalichthys* (Plate IIIA, IVD), from the other. Analogous picture is displayed by Megistolepidinae distinctive by their polyplocodont type of teeth structure. In Frasnian *Megistolepis doroshkoi* the difference between the small jaw teeth (Plate VA) and fangs (Plate VB) is hardly traceable while in the late (Famenian) representative of this genus (*Megistolepis klementzi*) the complication of plicidentine proceeds together with the teeth growth (Plate VC).

[1]Based on this feature we provisionally refer *Obruchevichthys* to Panderichthyidae.

Comparison of the histological teeth structure with the account to geological age of the forms can confirm (or refute) their affiliation to one or another phylogenetic branch. In some cases it helps to imagine their evolutionary course. Thus, based on their different teeth structures *Panderichthys* (Plate IIC), *Eusthenopteron* (Plate ID), *Thysanolepis* (Plate IID) and *Pycnoctenion* (Plate IB) can be claimed to belong to different lines. And on the other hand, considering progressive evolution of the teeth structure in the phylogeny of eusthenopterids it is hardly to doubt that *Eusthenopteron* (having polyplocodont teeth) represents the original form, from which *Jarvikina* and *Eusthenodon* (with their complicate eusthenodont teeth) were derived.

However, it is obvious, that the question whether the similar teeth structures were gained by the compared forms due to their genetic relationship or to their parallel development may be solved only when other proofs of their relationship will be obtained. Thus, rhombic pattern of scales in Platycephalichthys permits to assert very early derivation of this genus from the common eusthenopterid stem and its divergence from the line *Eusthenopteron—Jarvikina—Eusthenodon*. Consequently, it can be assumed that complexly plicated teeth of eusthenodont type were evolved in *Platycephalichthys* parallel to that in *Jarvikina* and *Eusthenodon*.

It succeeds well to observe the cases of the profound parallelismes on different stages of teeth morphogenesis and of their phylogenetic modifications. Thus, the structure of small jaw teeth in *Platycephalichthys skuenicus* and *Pycnoctenion jakuticus* which are of the same size (Plate IIIA, C) as well as that of a fang in *Pycnoctenion sibiriacus* (Plate IVC) and of a small jaw tooth in *Platycephalichthys bischoffi* (Plate IVD) reveal their obvious parallel development; the same is true for the structure of a fang of *Cryptolepis* (Plate IIIB) and a small jaw tooth of *Thysanolepis* (Plate IIID) and finally, for that of the fangs of *Jarvikina* (Plate IVA), *Viluichthys* (Plate IVB) and *Pycnoctenion* (Plate IVC).

When comparing teeth structures of Osteolepifirmes we distinguish one more feature, which previously was not taken into consideration, namely, relative width of bone septae between orthodentine plicae. This feature can be used as a diagnosic one in certain forms. Extensive bone invasion between plicae could probably compensate for the relatively weakly developed plication of the tooth, as it is the case with the Carboniferous *Pycnoctenion jacuticus* (Plate IB); Here again we find one more way of teeth strengthening. Similar arrangement of wide bone septae between weak plicated tooth walls can be observed in some tetrapods, for example in

Ichtyosauria, i.e. in the Triassic *Stenopterygius* (Schultze, 1969, Tab. XXIII, Fig. 18).[1]

The analysis of teeth structure of lower tetrapods (Schultze, 1970) shows that to a certain degree structural types of Crossopterygii could be developed here due to parallel evolution. In a number of the most probable cases of this parallelism such common features in *Ichthyostega* and *Panderichthys* may be interpreted as a weak development of bone of attachment extended between folds and the meandering pattern of the latters.

CONCLUSION

1. There is no doubt that all three types of complexly folded teeth structure of Rhipidistia vary in details and are connected through the transitional modifications.

2. These types could be evolved in parallel within different lines.

3. Complicated dendrodont teeth structure was acquired as early as in the Lower Devonian (*Porolepis*). It could be connected with the development of a complex "firelike" branching of orthodentine on relatively early stages of ontogenesis that probably favoured the reduction of bone septae between folds.

4. Occurrence of eusthenodont type of plication in Porolepiformes (Lower Devonian *Powichthys*) gives evidence in favour of the genetic unity of the Rhipidistia. As a rule, late representatives of different lines of Osteolepiformes had the most complicate eusthenodont type of teeth. This similarity could be achieved independently.

5. Because of wide occurrence of the parallelism teeth structure of Crossopterygii may be used only as an accessory evidence in the definition of their relationships.

6. Allowing for the profound parallelismes in the development of teeth structure in Rhipidistia and tetrapods this characteristic is hardly to be considered as a decisive one in solution of the question about the origin of land vertebrates.

[1]Peripherial bone in *Stenopttrygius* is connected, unlike that in *Pycnoctenion*, with osteodentine of the pulp cavity and appears to show more progressive stage of the development of bone septae.

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EXPLANATION OF PLATES

PLATE I

Variety of the eusthenodont (A, B) and polyplocodont (C, D) types of plication in Osteolepiformes. Transverse section across the base of teeth. d=diameter of teeth base.

A—*Obruchevichthys gracilis*, Upper Devonian (Frasn.), Latvia, d=4 mm; B—*Pycnoctenion jacuticus*, Lower Carbonian, Jakutia, d=8 mm.; C—*Panderichthys stolbovi*, Upper Devonian (Frasn.), Leningrad region, d=2, 5 mm.; D—*Eusthenopteron sävesöderberghi*, Upper Devonian (Frasn.), Leningrad region, d=5 mm.

PLATE II

Conversion of teeth structure of *Panderichthys*. Transverse section across the bases (B, C, D) and the upper half of the teeth.

A—*Panderichthys rhombolepis*, Upper Devonian (Frasn.), Leningrad region, river Oredezh, d=2. 8 mm.; B—*P. rhombolepis*, Upper Devonian (Frasn.), Latvia, river Brasla, d=2, 5 mm.; C—*P. rhombolepis*, Upper Devonian (Frasn.), Latvia, river Gauya, d=4 mm.; D—*P. bystrowi* Upper Devonian (Fam.) Latvia, d=5 mm.

PLATE III

Parallel modifications of teeth structure in *Panderichthys*. Transverse section across the teeth bases:

A—*Platycephalichthys skuenicus*, Upper Devonian (Fam.), Latvia, d=1, 5 mm.; B—*Cryptolepis grossi*, Upper Devonian (Fam.), Latvia, d=10 mm. (fang); C—*Pycnoctenoin jacuticus*, Lower Carbonif., Jakutia, d=1, 5 mm.; D—*Thysanolepis micans*, Lower Carbonif. Jakutia, d=1,7 mm.

PLATE IV

Parallelismes in the teeth structure among Osteolepiformes. Transverse section across the teeth base:

A—*Jarvikina wenjukowi*, Upper Devonian (Frasn.), Leningrad district, fang; B— *Viluichthys fradkini*, Lower Carbonifer., Jakutia, fang; C—*Pycnoctenion* sp., Lower Carbonif., Siberia, Iltekovka, d=11 mm; D—*Platycephalichthys bischoffi*, Upper Devonian (Frasn.), Staraya Russa area, River Lovat, d=4 mm.

PLATE V

Plicidentine in the Devonian *Megistolepis*. Transverse section across the teeth base:

A, B—*Megistolepis doroschkoi*, Upper Devonian (Frasn.), Krasnoyarsk region; d=4 mm, d=8 mm., (fang); C—*M. klementzi*, Upper Devonian (Fam.), Tuva, d=6, 5 mm.