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Oryzias madagascariensis Arnoult Redescribed and Assigned to the East African Fish Genus *Pantanodon* (Atheriniformes, Cyprinodontoidei)

By Donn Eric Rosen[1]

INTRODUCTION

The species of the genus *Oryzias* have been known only from Asia and the Indo-Australian archipelago. Arnoult's (1963) report of a new member of this group from eastern Madagascar was, therefore, of considerable interest zoogeographically. At the present writer's request Professor Arnoult generously sent two male and two female paratypes of *Oryzias madagascariensis* for study, and these unexpectedly proved to be a new representative of the hitherto monotypic genus *Pantanodon.* Equally unexpected was the discovery that *Pantanodon madagascariensis* has well-toothed jaws, for the only formerly known species, *P. podoxys* Myers from east Africa, lacks jaw teeth and was thus considered by Myers (1955) and Whitehead (1962) as the type of distinct subfamily, the Pantanodontinae, based largely on that edentulous characteristic. Numerous anatomical features not concerned with dentition leave no doubt, however, that Arnoult's species is indeed a form of *Pantanodon* and at the same time seem clearly to call for subfamilial, and possibly even familial, separation of these killifishes.

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Abbreviations of Institutions

A.M.N.H., the American Museum of Natural History, New York
B.M.(N.H.), British Museum (Natural History), London
M.N.H.N., Muséum National d'Histoire Naturelle, Paris

Abbreviations Used in Illustrations

ACT, actinost or radial
ART, articular
BB, basibranchial
CB, ceratobranchial
CH, ceratohyal
CL, cleithrum
CO, coronoid process of dentary
COR, coracoid
DN, dentary
EB, epibranchial
ECT, ectopterygoid
EH, epihyal
ENT, entopterygoid
EOC, exoccipital
EP, epiotic
FR, frontal
GH, glossohyal
HH, hypohyal
IF, inferior pharyngobranchial
LAT, lateral ethmoid
MX, maxilla
NA, nasal
PAL, autopalatine
PAS, parasphenoid
PB, superior pharyngobranchial
PFR, prefrontal
PMX, premaxilla
PT, pterotic
PTT, posttemporal
QU, quadrate
SC, scapula
SCL, supracleithrum
SOC, supraoccipital
SPH, sphenotic

MATERIALS

Dissections and alizarin-stained skeletons of the following species were prepared:

Aphyosemion australe (Rachow); A.M.N.H. Nos. 14746, 14758, 14781
Aphyosemion bivittatum (Lönnberg); A.M.N.H. No. 14767
Aplocheilichthys antinorii (Vinciguerra); A.M.N.H. No. 8276

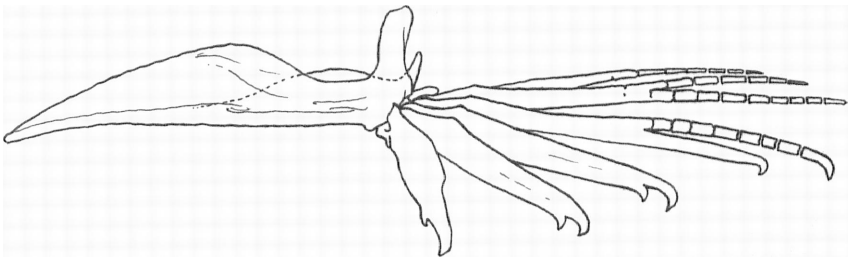

FIG. 1. Left pelvic girdle and fin of adult male *Pantanodon madagascariensis* (Arnoult).

Aplocheilichthys baudoni (Myers); A.M.N.H. No. 8151
Aplocheilichthys pumilus (Boulenger); A.M.N.H. No. 8274
Aplocheilichthys schoelleri (Boulenger); A.M.N.H. No. 8275
Aplocheilichthys spilauchena (Duméril); A.M.N.H. Nos. 6307, 8272
Aplocheilus panchax (Hamilton-Buchanan); A.M.N.H. No. 5159
Epiplatys macrostigma (Boulenger); A.M.N.H. No. 18209
Hypsopanchax platysternus (Nichols and Griscom); A.M.N.H. No. 6078
Lamprichthys tanganicanus (Boulenger); A.M.N.H. Nos. 11728, 11731
Nothobranchius guentheri (Pfeffer); A.M.N.H. No. 8280
Pachypanchax playfairi (Günther); A.M.N.H. No. 20476
Pantanodon madagascariensis (Arnoult); A.M.N.H. No. 20526; M.N.H.N.
Pantanodon podoxys Myers; B.M.(N.H.)
Procatopus gracilis Clausen; A.M.N.H. No. 20613

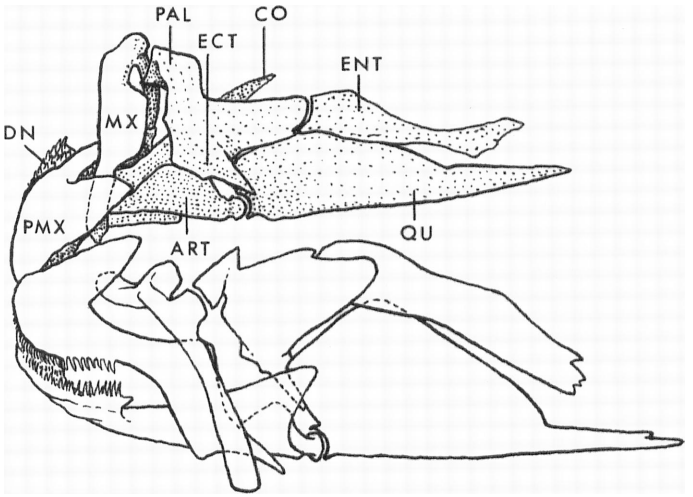

FIG. 2. Jaws and anterior upper and lower jaw suspension of adult male *Pantanodon madagascariensis* (Arnoult).

TABLE 1

COMPARISON OF THE SPECIES OF *Pantanodon*

Character	*podoxys*	*madagascariensis*
Dorsal fin rays	7 or 8	8 or 9
Anal fin rays	20 or 21	19 or 20
Caudal fin rays		
Branched	16 to 18	15
Unbranched	10 to 12	12
Pectoral fin rays, left side	12	9
Pelvic fin rays, left side	6	6
Scales in lateral series on body	26 or 27	30
Vertebrae		
Precaudal	10	13
Caudal	19	19
Branchiostegal rays	5	4 or 5

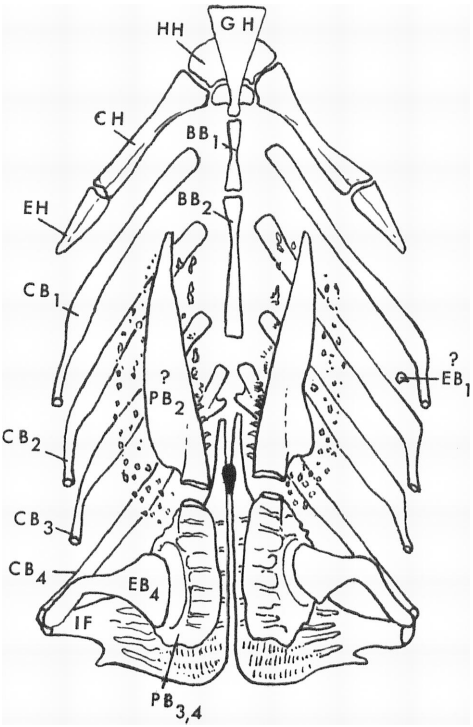

FIG. 3. Pharyngobranchial apparatus of adult male *Pantanodon madagascariensis* (Arnoult). Median ossicle between superior pharyngeal bones in solid black.

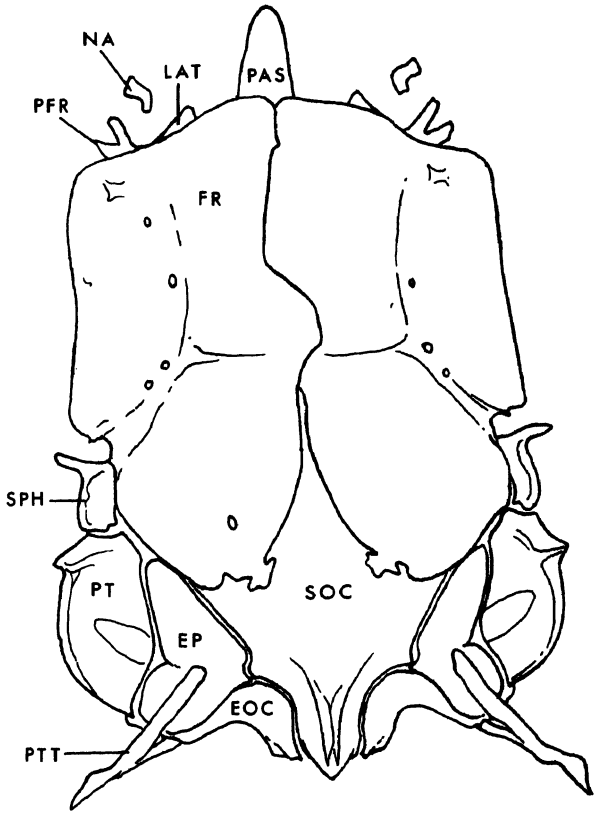

FIG. 4. Dorsicranium of adult male *Pantanodon madagascariensis* (Arnoult).

DISCUSSION

The distinctive features that unite *Pantanodon podoxys* and *P. madagascariensis* and at the same time separate both from all other known killifishes follow: first three or four pelvic rays in male thickened, spinous, with clawlike hooks at their tips (fig. 1); pelvic fins in male united; gill rakers in form of minute, triangular fans; coronoid process on dentary enormous, extending upward and backward to cover smaller coronoid process of articular and to overlap anterior border of quadrate (fig. 2); hypobranchial ossifications wanting (fig. 3); only last epibranchial normally developed (all others absent or obsolescent); with a very long lanceolate bone (fig. 3) embedded in an oval pad of tooth-bearing connective tissue joined to the forward edge of each ankylosed os pharyn-

geum superioris 3 and 4 (the lanceolate bone is perhaps a modified second pharyngobranchial, but without epibranchials present to show its original association its genesis is uncertain).

Additional features are shared by *podoxys* and *madagascariensis* that occur also in other groups of killifishes. For example, both species lack parietal, mesethmoidal, and prevomerine ossifications (fig. 4; see also Rosen and Bailey, 1963, and Rosen, 1964); in both, the posttemporal is bifid, that is, has a distinct lower arm; the hemal arch in each of the first few hemal spines is greatly expanded (the first and in some cases the second arch of *podoxys* and the first five arches of *madagascariensis*), a feature common also to various Old-World rivulins.

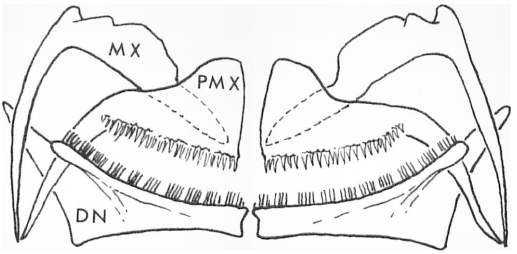

FIG. 5. Upper and lower jaws of adult male *Pantanodon madagascariensis* (Arnoult), frontal view.

The species differ in a number of ways (see also table 1). *Pantanodon madagascariensis* has jaw teeth (figs. 5 and 6), as already noted, whereas *podoxys* does not. In a single specimen of *madagascariensis* there is a tiny ossicle medial to the upper end of the first ceratobranchial on the right side that perhaps is a relict of a first epibranchial. In *madagascariensis* but not in *podoxys* there is slightly above and between the pharyngobranchials a tiny, teardrop-shaped, medial element within the ligamentous suspension of the gill basket from the basicranium, and in *madagascariensis* the hypural plates in the caudal skeleton are united, not separated (fig. 7).

In the basicranium of *madagascariensis* the parasphenoid is without a ventral arm to make prootic contact at a lateral commissure as in killifishes generally. Instead, the dorsal arm of the parasphenoid, which distally is sutured to the trigeminofascialis process of the prootic, has a proximal posterior extension that meets a corresponding elevation on the forward edge of the prootic, thus dividing the posterior myodome in two.

There are several points in Whitehead's account of *podoxys* that call for

special comment. The first concerns his statement that an ectopterygoid is not present. On his page 128 (fig. 15), however, a small ectopterygoid is clearly illustrated as joined dorsally with the autopalatine. Such an arrangement is typical of cyprinodontoid killifishes, as was discussed and figured by Rosen (1964).

The second point relates to Whitehead's discussion of the feeding mechanism of *podoxys* in which he wrote: "Divergence of the Pantano-

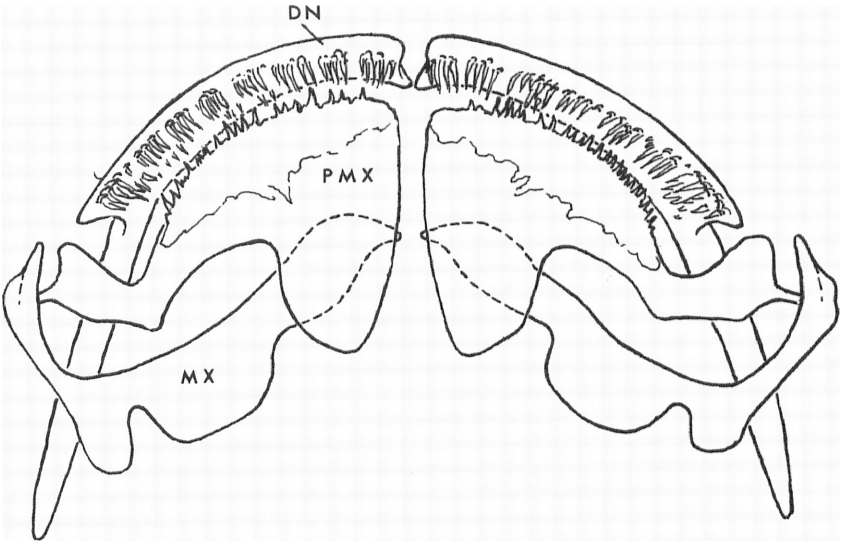

FIG. 6. Upper and lower jaws of adult male *Pantanodon madagascariensis* (Arnoult), dorsal view.

dontinae has been almost entirely concerned with trophic adaptation to a filter-feeding habit. Specialisation towards a microphagous diet has apparently involved both the loss and modification of certain structures. Thus jaw teeth have been entirely lost which may preclude the seizure of prey in the normal cyprinodont manner. Secondly, the mouth gape is directed upwards while the premaxillae are more or less fixed. This precludes bottom-feeding and implies that *Pantanodon* must obtain its food from the surface. The third specialisation is in the form of the gillrakers." Whitehead's statement is obviously inconsistent with the occurrence of jaw teeth in *madagascariensis,* especially in view of the extensive similarities in other aspects of the feeding mechanism (e.g., the gillrakers) in the two species. Moreover, B. Turner (personal communication) has suc-

cessfully maintained *podoxys* under aquarium conditions, using tubificid worms, daphnia, and brine shrimp as the primary food sources.

Lastly, the present writer has examined Whitehead's specimens of *podoxys* in the British Museum (Natural History) and finds that, as in *madagascariensis,* there are present the lanceolate bony forward extension of the superior pharyngeal elements, a definite articular bone with a coronoid expansion, a disclike supracleithrum (although this is narrowly joined anteriorly to the base of the posttemporal bone), and a scapular

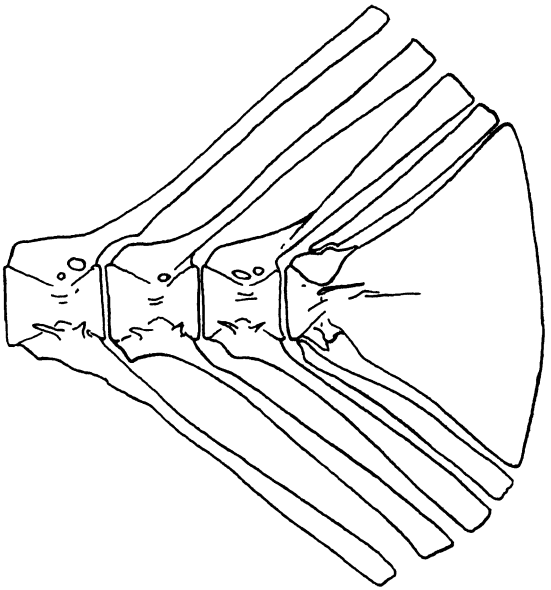

FIG. 7. Caudal skeleton of adult male *Pantanodon madagascariensis* (Arnoult).

foramen (as shown here in the illustration of *madagascariensis,* fig. 8), none of which were figured or discussed by Whitehead in his account.

The relationships of the species of *Pantanodon* to other killifishes pose a special problem. Rosen (1964) pointed out that *Oryzias* and its relatives in the Adrianichthyoidea differ from other killifishes (the Cyprinodontoidea) in many fundamental characteristics, and on the basis of that separation *Pantanodon* clearly enters the Cyprinodontoidea. The species of *Pantanodon* resemble adrianichthyid and oryziatid fishes in lacking a prevomerine ossification and in having a greatly enlarged coronoid expansion of the dentary. Prevomerine ossifications are absent also in some

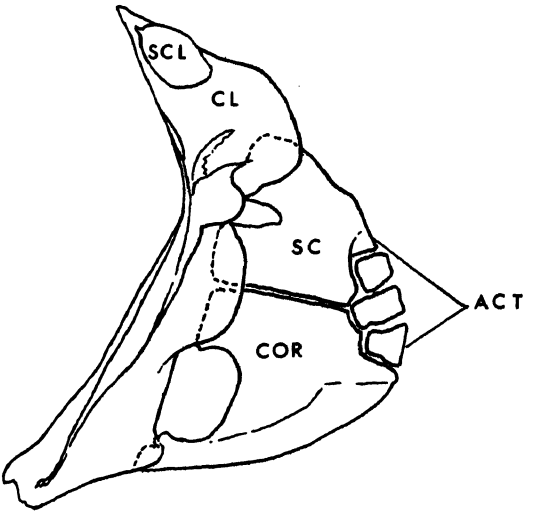

FIG. 8. Left pectoral girdle of adult male *Pantanodon madagascariensis* (Arnoult), outer view. Note upper actinost (radial), partly ankylosed with scapula.

cyprinodontoids (e.g., in various Poeciliidae and in *Procatopus*), and in *Pantanodon* (unlike adrianichthyoids) there is present a coronoid expansion of the articular bone that is obscured by the enlargement of the dentary. On the other hand the species of *Pantanodon* differ greatly from all other cyprinodontoids in the coronoid enlargement of the dentary, in the structure of the pharyngobranchial apparatus, and in the pelvic structure of the male. No species of the Old World tropical genera *Nothobranchius, Epiplatys, Aplocheilus, Hypsopanchax, Lamprichthys, Procatopus, Aplocheilichthys, Aphyosemion, Micropanchax,* or *Pachypanchax* examined has been seen to resemble *Pantanodon* in these ways. *Pantanodon* is similar to some Old-World rivulins in the expansion of the anterior hemal arches, as mentioned above; to *Aplocheilichthys* in the structure of the gillrakers; and to *Procatopus* in having only three free pectoral radials (see, for example, fig. 8) and no prevomerine ossification. These several characters, however, appear scarcely to form a sufficient basis for determining relationships in view of the other profound differences. The writer rejects Whitehead's assessment of the relationships of *Pantanodon* on the grounds of his failure to discover and hence to consider some of the major anatomical peculiarities of this genus. For the time being, and until a thorough osteological analysis of the genera of Cyprinodontoidea is undertaken, the taxonomic position of *Pantanodon* cannot be decided,

but it seems possible that the Pantanodontinae ultimately may be accorded family rank.

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