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Notes on the Anatomy and Relationships of the Bedotiid Fishes of Madagascar, with a Taxonomic Revision of the Genus *Rheocles* (Atherinomorpha: Bedotiidae)

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ABSTRACT

In a wide-ranging comparative study the anatomy and relationships of the bedotiid fishes of Madagascar are investigated. Evidence supporting the following hypotheses is presented and discussed: (1) the mugiloids (sensu Nelson, 1984) are the sister group of the Atherinomorpha (sensu Rosen, 1964), (2) the Atherinomorpha are monophyletic, (3) the Bedotiidae are monophyletic, (4) *Bedotia* is monophyletic, (5) *Rheocles* is monophyletic. Counterevidence to claim (1), supporting

an alternative scheme for a monophyletic Percomorpha (including the mugiloids) is also presented.

There follows a taxonomic revision of the genus *Rheocles* Jordan and Hubbs, 1919. Four species of *Rheocles* are recognized in the present study, one of which, *Rheocles wrightae*, is newly described. The intrarelationships of *Rheocles* are resolved and a species-level cladogram is presented.

INTRODUCTION

In their analysis of atherinomorph monophyly and relationships, Rosen and Parenti (1981) challenged earlier notions of a monophyletic Atherinoidei, preferring instead to recognize a division I atherinoid group consisting of six families (Atherinidae, Bedotiidae, Isonidae, Melanotaeniidae, Phallo-

stethidae, and Telmatherinidae) of unresolved relationships. Their scheme has been amended recently by Parenti (1984b) with the formal recognition of a monophyletic Phallostethoidea (Phallostethidae + Dentatherinidae), but as yet there exists no consensus regarding the interrelationships of this diverse

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atherinomorph division (see Patten, 1978; Allen, 1980; Parenti, 1984b; White et al., 1984; Ivantsoff et al., 1987).

Members of the Madagascan bedotiid radiation are generally considered to represent the most generalized or "primitive" of living atherinoids (e.g., Jordan and Hubbs, 1919b; Rosen, 1964). Three bedotiid genera have been described to date; *Bedotia* Regan, 1903, *Rheocles* Jordan and Hubbs, 1919, and *Rheocloides* Nichols and LaMonte, 1931, but despite their suspected key phylogenetic position in relation to the remaining Atherinomorphs (Rosen and Parenti, 1981; Parenti, 1984b), very little is known of the structure or interrelationships of this assemblage.

Much of the reason for the dearth of information on bedotiid anatomy results from their poor representation in museum collections. Fortunately, a recent ichthyological survey of the fresh waters of the eastern highlands of Madagascar (Reinthal and Stiassny, in rev.) has made available a good size collection enabling a detailed anatomical and taxonomic study to be undertaken. The results of that study form the nucleus of the present paper, and the impetus for the higher level systematic investigations reported herein.

OUTGROUP SELECTION AND ASSOCIATED PROBLEMS

In seeking to resolve the status and relationships of the basal atherinomorph clades of Madagascan bedotiids, a number of problems have been encountered. The first concerns the selection of appropriate outgroups for analysis.

In broad outline, figure 1 represents the current state of our knowledge of acanthomorph interrelationships. In view of the dubious status of the Paracanthopterygii (Rosen, 1973, 1985; Stiassny, 1986), selection of "appropriate" outgroups from this heterogeneous assemblage is problematical. Where possible I have examined a range of paracanthopterygian taxa with an emphasis on members of the percopsiform "clade" (Rosen, 1962; Patterson and Rosen, 1989). The position of *Polymixia* seems more firmly established as the sister group to the remaining acanthomorphs (Rosen, 1985; Stiassny, 1986), and this taxon has been included for

study. Historically one acanthomorph group, the Mugiliformes, has been closely allied with various of the atherinomorph lineages (Jordan and Hubbs, 1919b; Myers, 1928; Berg, 1940; Gosline, 1968, 1971). Following Rosen (1964) and Nelson (1984) I adopt the vernacular names "mugiloid," "sphyraenoid," and "polynemoid" for the mugiliform components of interest here, and have emphasized the inclusion of representatives of each of these lineages in comparative study. Selection from among the numerous other percomorph lineages has necessarily been somewhat arbitrary although I tended to concentrate on the more morphologically generalized taxa (Rosen, 1973; Johnson, 1980, 1984; Stiassny, 1981). Among other more derived atherinomorphs a range of atherinoids have been incorporated for study, as have representative cyprinodontiforms and beloniforms.

A list of the acanthomorph species included in this study follows:

Polymixia lowei (AMNH 49674), *Percopsis omiscomaycus* (AMNH 41145, 42032), *Aphredoderus sayanus* (AMNH 33540, 55089), *Pollachius virens* (AMNH 40584), *Gadus morhua* (AMNH 2972), *Molva molva* (AMNH uncat.), *Merluccius bilinearis* (AMNH 55086), *Opsanus tau* (AMNH 73813), *Hoplostethus mediterraneus* (AMNH 49718), *Anomalops katopferon* (AMNH 37949), *Gibberichthys pumilus* (AMNH 49679), *Scopelogobius* sp. (AMNH 49710), *Zeus faber* (AMNH 29458), *Polynemus approximans* (AMNH 73388), *Polynemus opercularis* (AMNH 16003), *Polydactylus virginicus* (AMNH 74250), *Sphyraena borealis* (AMNH 4339), *Sphyraena barracuda* (AMNH 20609), *Agonostomus monticola* (AMNH 31538), *Mugil curema* (AMNH 39162), *Mugil cephalus* (AMNH 15481), *Liza macrolepidotis* (AMNH 88044), *Centropomus ensiferus* (AMNH 35244), *Morone americana* (AMNH 44691), *Ambassis urotaenia* (AMNH 88082), *Kurtus gulliveri* (AMNH 43396), *Micropterus dolomieu* (AMNH 68385), *Lutjanus fulviflamma* (AMNH 88161), *Serranus tigrinus* (AMNH 43172), *Gerres rappa* (AMNH 88058), *Ptychochromis oligacanthus* (AMNH 88117, 88102), *Monodactylus argenteus* (AMNH 58794), *Hypseleotris tohizonae* (AMNH 85099, 88048), *Deltentosteus* sp. (AMNH uncat.), *Melanotaenia maccullochi* (AMNH 44401), *Melanotaenia nigrans* (AMNH 55067, 20574), *Melanotaenia goldiei* (AMNH 13900), *Chilatherina lorentzi* (AMNH 15028), *Telmatherina ladigesii* (AMNH 35378), *Atherina pinguis* (AMNH 9434),

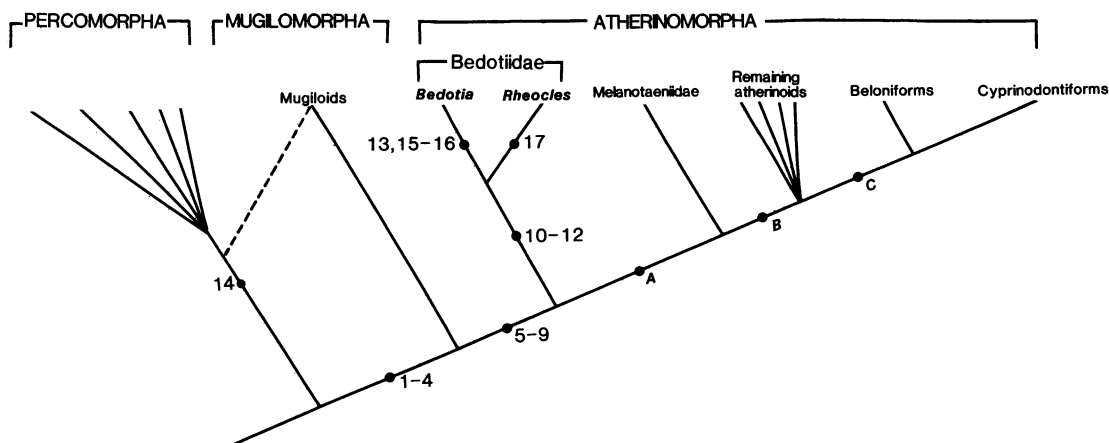


Fig. 2. Cladogram of acanthomorph relationships, summarizing the results of the present study. Characters are: 1. Subdivision of the pharyngocleithralis muscle. 2. Pharyngohyoideus reduced to a small fan-shaped muscle with an elongate tendon. 3. Levator externus 1 separated from levatores externi 2-4 by the levatores interni 1-2. 4. Anterior neural arches expanded. 5. The A_1 section of the adductor mandibulae with a tendon to the medial face of the lachrymal bone (tA_{lac}). 6. The fifth ceratobranchials with well-developed ventral process. 7. The lateral horns of the fifth ceratobranchials with well-developed muscular processes. 8. Supraneural bones absent. 9. Both PU3ds and PU3vt radial cartilages in the caudal fin skeleton absent. 10. Posterior six or seven caudal vertebrae are markedly thickened. 11. A single elongate infraorbital element behind the lachrymal. 12. Medial processes of the pelvic girdle asymmetrical. 13. Absence of anteromedial spines, and reduction of posteromedial spines on the medial processes of the pelvic girdle. 14. Pelvic girdle united medially, anteromedial processes ventrally displaced. 15. Third basibranchial toothplates paired. 16. Premaxilla with a deep notch on dentigerous face. 17. Parhypural fused with urostyle and hypurals 1+2.

For a discussion of characters supporting levels A, B and C see Rosen and Parenti, 1981 and Parenti, 1984b.

of the anatomy of outgroups when compared with the conditions found in the basal atherinomorpha. The monophyly of the Atherinomorpha is attested to by a remarkable array of morphological, reproductive, and developmental features unique to the clade (see Rosen and Parenti, 1981, for a summary). The resultant group is, in many respects, highly autapomorphic with many character systems and functional components markedly transformed. It is frequently the case, when dealing with such highly autapomorphic groups, that characters found in the basal clades (and often further transformed at higher levels within the group) have no readily comparable equivalent outside the group. In such a situation it is not always possible to designate a polarity to the condition or conditions within the study group by analysis of adult specimens. Study of ontogenetic character transformation and the application of the Outgroup Method (Wattous and Wheeler, 1981; Maddison et al.,

1984) to ontogenetic data may be of particular value in these situations.

In the course of this rather wide-ranging comparative study a number of anatomical features bearing upon the resolution of systematic problems at a variety of levels have been investigated. In the following sections evidence is presented supporting six hypotheses:

1. The Percomorpha are monophyletic. See figure 2, character 14.
2. The mugiloids are the sister group of the Atherinomorpha (sensu Rosen, 1964). See figure 2, characters 1-4.
3. The Atherinomorpha are monophyletic. See figure 2, characters 5-9 (see also characters listed by Rosen and Parenti, 1981).
4. The Bedotiidae are monophyletic. See figure 2, characters 10-12.
5. *Bedotia* is monophyletic. See figure 2, characters 13, 15, 16.

6. *Rheocles* is monophyletic. See figure 2, character 17.

There follows a taxonomic revision of the genus *Rheocles* (understood here to include *Rheocloides*). The intrarelationships of *Rheocles* are resolved and a species-level cladogram is presented.

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Finally, I would like to acknowledge the contribution of Peter Reinthal, without whom this revision would not have been possible. I thank him for his help and companionship during our expedition to Madagascar, and in memory of our shared delight at catching our first Madagascan endemic: *Rheocles alaotrensis* in the beautiful forest of Perinet.

ABBREVIATIONS

Institutional

AMNH	American Museum of Natural History, New York
BMNH	The Natural History Museum, London
MNHN	Muséum National d'Histoire Naturelle, Paris

Anatomical

A ₁	adductor mandibulae division 1
A _{2,3}	adductor mandibulae division 2,3

acc	accessory cartilage
add5	fifth adductor muscle
ams	anteriomedial spine (pelvic)
ant.ram	anterior ramus (urohyal)
bb3	third basibranchial
bb3-tp	toothplates of third basibranchial
cb 3-5	ceratobranchials 3-5
ep4	fourth epibranchial
epl	epipleural ribs
fr	frontal
hyo	hyomandibulum
inf.orb	infraorbital
iop	interoperculum
lac	lachrymal
lat.eth	lateral ethmoid
LAP	levator arcus palatini muscle
le 1-4	levatores externi muscles
li 1-2	levatores interni muscles
lp	levator posterior muscle
l.eth-mx	ethmomaxillary ligament
l.mx-md	maxillo-mandibular ligament
mes	mesethmoid
ms.pr	muscular process of the fifth ceratobranchial
mpr	medial process (pelvic)
mx	maxilla
nas	nasal
ns1	first neural spine
od.p	obliquus dorsalis posterior muscle
operc	operculum
opisth.cart	opisthural cartilage
phc.e	pharyngocleithralis externus muscle
phc.i	pharyngocleithralis internus muscle
phyp	parhypural
phy	pharyngohyoideus muscle
pl	pleural ribs
pms	posteriomedial spine (pelvic)
pmx	premaxilla
preop	preoperculum
PU2,3 ds	preural dorsal radials
PU2,3 vt	preural ventral radials
sop	suboperculum
spn	supraneural
stern	sternohyoideus muscle
tA _{1mx}	tendon of adductor mandibulae A ₁ to maxilla
tA _{1lac}	tendon of adductor mandibulae A ₁ to lachrymal
t.phy	tendon of the pharyngohyoideus muscle
un	uroneural
uroh	urohyal
vt.pr	ventral process of fifth ceratobranchial

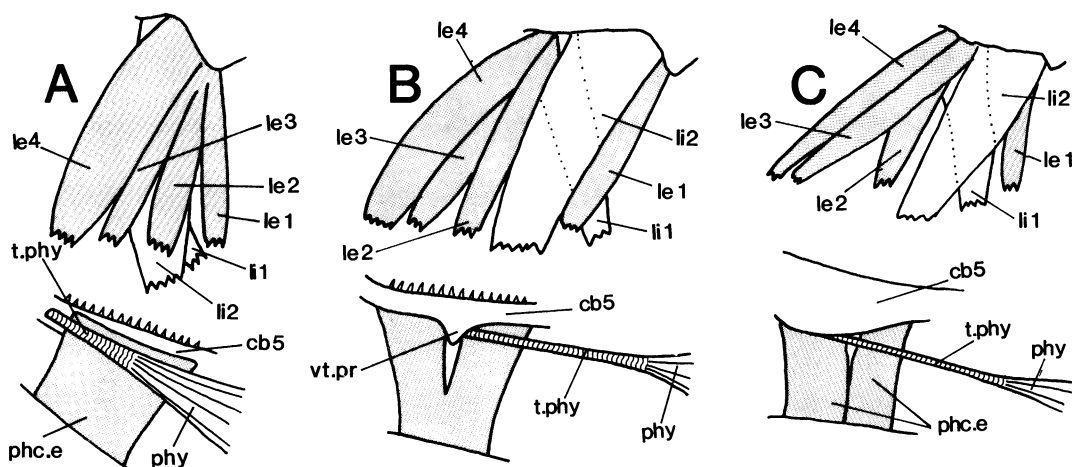


Fig. 3. Schematic diagram of the dorsal and ventral branchial arch musculature in lateral view representing the standard configuration in a: A. percomorph, B. atherinomorph, C. mugiloid.

ANATOMICAL REVIEW

VENTRAL BRANCHIAL MUSCULATURE

PHARYNGOCLEITHRALIS MUSCLE

(= pharyngoclavicularis of Winterbottom, 1974)

CHARACTER 1 (figs. 3, 4): This muscle, which functions as a major antagonist of the

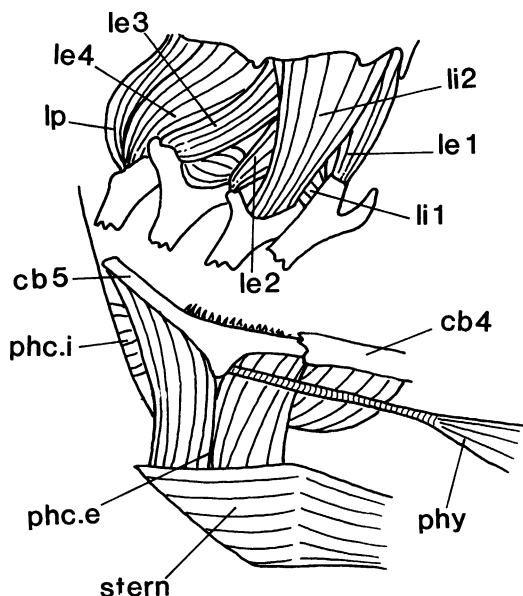


Fig. 4. *Rheocles alaotrensis* (AMNH 88171) dorsal and ventral branchial arch musculature in lateral view.

pharyngohyoideus (Lauder, 1983), is subdivided into an internus and externus component in most teleostean groups (Winterbottom, 1974). Primitively in acanthomorphs the externus division is a simple muscle sheet originating from the lower limb of the cleithrum and inserting onto the lateral aspect of the fifth ceratobranchial. The muscle has undergone various processes of subdivision in a number of derived percomorph taxa (e.g., tetradontiforms: Winterbottom, 1974; Periplophthalms: Sponder and Lauder, 1981; labroids: Stiassny, 1982).

Lauder (1983) noted a distinctive division of the pharyngocleithralis externus in the cyprinodont, *Fundulus*, and the poeciliid, *Belonesox*. A similar, although less marked, subdivision is present in bedotiids (e.g., fig. 4) and in all other division I atherinoids and cyprinodontiform taxa examined. In hemiramphid and exocoetid beloniforms the anterior division of the pharyngocleithralis externus has been lost and a single posterior component remains (personal obs.). This modification is interpreted here as a secondary development associated with a complex remodeling of the exocoetoid pharynx possibly associated with the type of pharyngognathia exhibited by this clade (Stiassny and Jensen, 1987).

The plesiomorphic configuration of the atherinomorph pharyngocleithralis externus, with a division into distinct anterior (phc.e

ant) and posterior (phc.e post) sections, is not mirrored in any nonatherinomorph group other than mugiloids (e.g., fig. 3C). Among mugiloids the least modified state of the pharyngocleithralis externus is found in the genus *Agonostomus* in which a subdivision very similar to that of bedotiids is developed. In more derived mugiloids the separation of the two subdivisions is more marked, as is the case in most nonbedotiid atherinomorphs. Within each clade there has been an interesting (parallel) development of increased anatomical division and ultimate separation of the two muscle components.

The pharyngocleithralis externus in sphyraenoids and polynemoids, as well as that of all other percomorph taxa examined, is a simple, single muscle slip.

PHARYNGOHYOIDEUS MUSCLE

(= rectus communis of nonctenosquamate taxa, Lauder, 1983)

CHARACTER 2 (figs. 3 and 4): In acanthomorphs this muscle originates tendinously on the fifth ceratobranchial, passes lateral to the pharyngocleithralis externus, and inserts on the urohyal. Primitively the tendinous component of the muscle is short and broad (e.g., fig. 3A). Such is not the case in atherinomorph fishes where the tendon of the pharyngohyoideus is extremely thin and elongate and the reduced muscularous component of the pharyngohyoideus is small and fan-shaped (e.g., figs. 3B, 4). Among other acanthomorphs a similar arrangement of the pharyngohyoideus muscle and its tendon is found only in mugiloid fishes (e.g., fig. 3C).

DORSAL BRANCHIAL MUSCULATURE

THE LEVATORES EXTERNI AND INTERNI MUSCLE SERIES

CHARACTER 3 (figs. 3, 4): Euteleostean dorsal branchial musculature has undergone considerable modification and functional reorientation (Lauder, 1983). However, by the level of the Ctenosquamata the site of origin and inclination of the levator externus and internus series has more or less stabilized.

The plesiomorphic ctenosquamate configuration is represented in figure 3A. The levator externus series (le_{1-4}) originate together

on the postorbital neurocranium and insert on their respective epibranchial elements. The levatores interni (li_{1-2}) arise *medial* to the externus series, levator internus 1 originates medial to levator internus 2, and passes rostrad to insert on pharyngobranchial 2.

Atherinomorphs have a rather different configuration of the levatores. In these fishes the origin of the first levator externus (le_1) is separated from that of levatores externi 2–4 by the levatores interni (e.g., figs. 3B, 4). The levatores interni retain their relations with one another and levator internus 1 originates medial to levator internus 2. A markedly similar, although somewhat modified, configuration is apparent in mugiloid fishes (fig. 3C). As in atherinomorphs, the first levator externus is separated from levatores externi 2–4 by the levatores interni, however, levatores externi 1 and 2 originate medial to the remaining muscle mass. Once again, it is the plesiomorphic mugiloid *Agonostomus* which exhibits the least modified pharyngeal muscle configuration. In the highly modified pharyngeal apparatuses of the other mugiloid lineages, these derived levatores relations are nonetheless still apparent.

Because the development of a complex pharyngobranchial organ has resulted in a major pharyngeal reorganization in mugiloid fishes, it is difficult to interpret the differences and similarities between the mugiloid and atherinomorph levatores configurations. The two are not morphologically identical, although they are extremely similar in major plan and both deviate markedly from the plesiomorphic ctenosquamate condition (see Discussion).

ANTERIOR NEURAL ARCH MORPHOLOGY

CHARACTER 4 (fig. 5): Atherinomorph fishes characteristically exhibit a pattern of expansion of the anterior neural arches. Typically, the first vertebral centrum bears an unexpanded neural arch followed by four or five centra bearing expanded arches (e.g., fig. 5C). An essentially similar pattern is present in most cyprinodontiforms, although in many clades the first neural arch is also frequently modified (see Parenti, 1981). Similarly, beloniform fishes usually have an expanded first

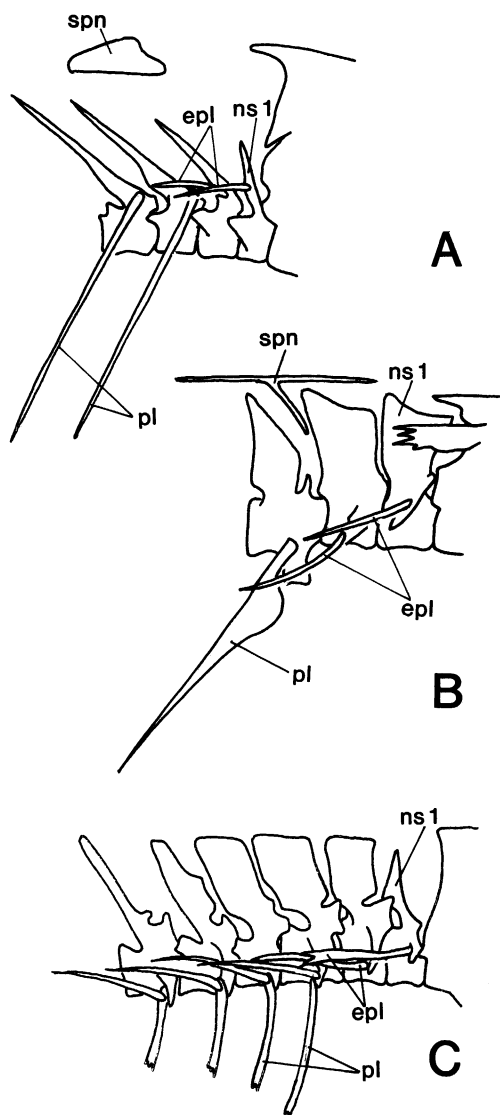


Fig. 5. Anterior vertebrae and associated structures in A. *Percopsis* (AMNH 41145), B. *Agnostomus* (AMNH 31538), C. *Rheocles* (AMNH 28127).

neural arch in addition to the following five or six (see Parin, 1961). Among the other acanthomorphs examined, a similar pattern of neural arch expansion is found only in the mugiloids (fig. 5B); the remaining taxa exhibit a neural arch configuration as represented in figure 5A. In mugiloids the first neural arch is invariably expanded, as are the following three or four arches.

CHEEK MUSCULATURE

CHARACTER 5 (fig. 6): Alexander (1967) outlined in some detail the anatomy of the atherinomorph jaw apparatus (see also Rosen, 1964; Parenti, 1981). In the course of the current investigation a novel connection between the A_1 section of the adductor mandibulae and the lachrymal of atherinomorph fishes has been identified. Unlike the standard percomorph arrangement in which an A_1 or an $A_{1,2}$ adductor division is connected with the maxilla via a tA_1 tendon and the maxillo-mandibular ligament (Stiasny, 1981), in division I atherinoids the A_1 section of the adductor mandibulae has lost all association with the maxillo-mandibular ligament and has two tendons; a tA_{1mx} passes rostrad to insert onto the median face of the maxillary shaft (fig. 6C), the second, tA_{1lac} , arises lateral to tA_{1mx} and passes rostrodorsad to insert on the median face of the lachrymal bone (fig. 6B). A tA_{1lac} has been found in all representative division I atherinoids, but is lacking in cyprinodontiform taxa (see figures in Rosen, 1964, and Alexander, 1967). However, in all of the beloniform taxa included in this study a tA_{1lac} ligament is present (see also *Arrhamphus* Rosen, 1964: plate 4, unlabeled). A tA_{1lac} has not been found in any of the other acanthomorphs examined.

In view of this distribution within the Atherinomorpha, I think it reasonable to interpret the presence of a tA_{1lac} as a synapomorphy of atherinomorph fishes which has subsequently been lost in the cyprinodontiform clades.

FIFTH CERATOBANCHIAL ELEMENT

CHARACTER 6 (fig. 7): Atherinomorphs share two features of the fifth ceratobranchial elements of the branchial apparatus not found outside the clade. Mention has already been made of the peculiar division of the atherinomorph pharyngocleithralis externus muscle (pp. 6–7). In atherinomorphs, division of the pharyngocleithralis is on either side of a well-developed process on the ventral face of the fifth ceratobranchial elements (vt.pr in fig. 7). This ventral process usually also serves as the site of tendinous origin of the pharyngohyoideus muscle (e.g., fig. 3B). This feature differs in exocoetoid beloniforms, where the

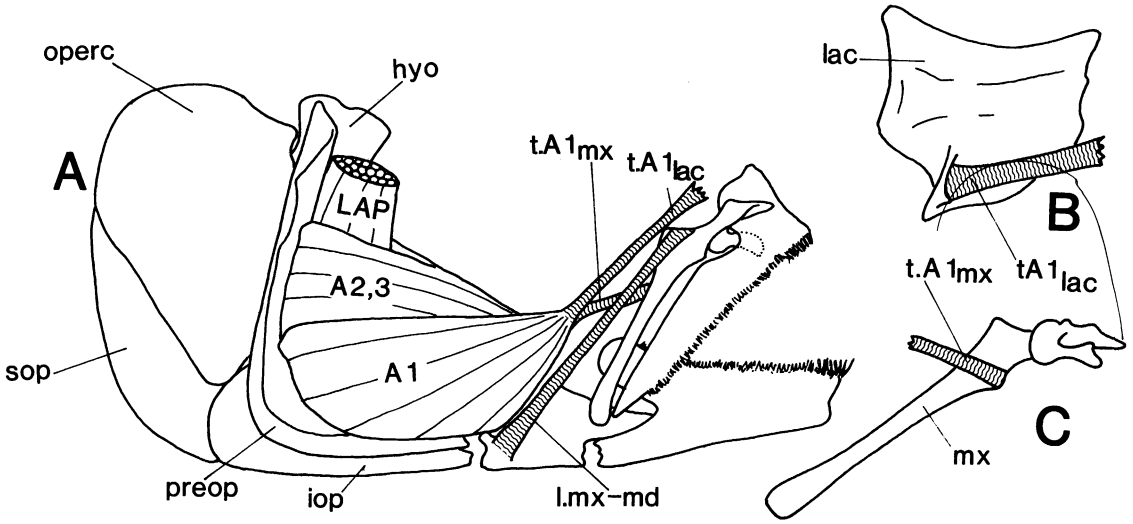


Fig. 6. *Rheocles alaotrensis* (AMNH 88001). A. Lateral view of superficial cheek musculature and associated structures. B. medial view of isolated lachrymal bone with insertion of $t.A1_{lac}$. C. medial view of isolated maxilla with insertion of $t.A1_{mx}$.

fifth ceratobranchials are robust heavily ossified elements fully united in the midline (see Parin, 1961; Collette, 1974, 1977; Stiassny and Jensen, 1987). As with the modification of the pharyngocleithralis externus of exocoetoids, the modification of the exocoetoid lower pharyngeal jaw is interpreted as a secondary feature of pharyngognath in the clade.

A ventral process is not present on the highly modified fifth ceratobranchials of mu-

giloids, nor in any other acanthomorph taxon examined.

CHARACTER 7 (figs. 7, 8): The second derived feature of the atherinomorph fifth ceratobranchial is the presence of an extremely well-developed muscular process on each lateral horn (fig. 7, ms.pr). This expansive process serves as the insertion site for the fifth adductor and a particularly well-developed obliquus dorsalis posterior muscle (fig. 8). These processes, which are present in all atherinoids and cyprinodontiform lineages sampled, are lacking in exocoetoids but are present in a somewhat modified form in other belontiiform lineages (see Stiassny and Jensen, 1987: fig. 2B). Similarly developed muscular processes are not present in other acanthomorph taxa.

SUPRANEURAL BONES

CHARACTER 8 (fig. 5): Supraneural bones (= predorsals of most authors, see Mabey, 1988; Patterson and Rosen, 1989) are entirely lacking in atherinomorphs (e.g., fig. 5C). The absence of supraneurals is not a simple correlate of the presence of expanded anterior neural arches as mugiloids, which also have expanded arches, typically possess an elongate supraneural situated above and between the second and third neural arches (fig. 5B).

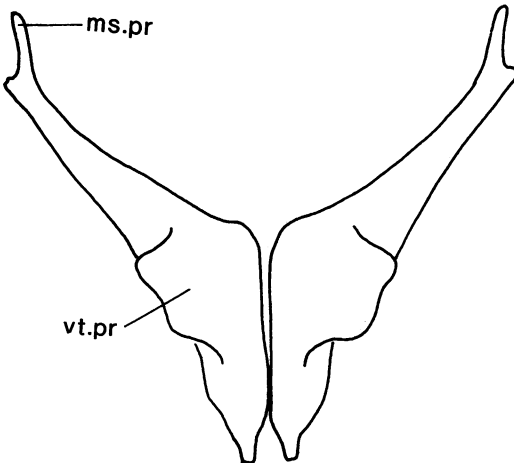


Fig. 7. *Rheocles alaotrensis* (AMNH 88001), isolated fifth ceratobranchial elements in ventral view.

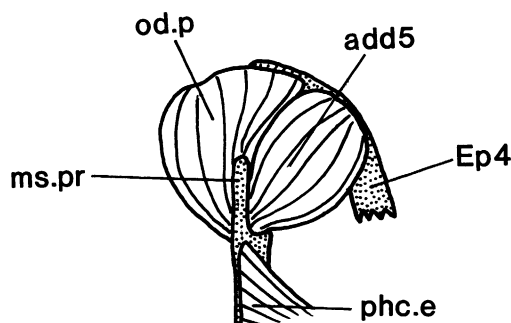


Fig. 8. *Rheocles alaotrensis* (AMNH 88171) muscular process of fifth ceratobranchial element and associated musculature.

The presence of three supraneurals situated close in front of the first dorsal pterygiophore appears to represent the modal acanthomorph condition, and three are retained in *Polymixia* (Patterson and Rosen 1989; personal obs.). Supraneural reduction to absence occurs in a number of paracanthopterygian lineages (Patterson and Rosen, 1989), as well as in certain percomorph families (Smith and Bailey, 1961). Despite the somewhat mosaic pattern of supraneural loss in related groups, I interpret the absence of supraneural bones in atherinomorphs as further evidence of their monophyly.

CAUDAL FIN SKELETON

CHARACTER 9 (figs. 9, 10, 11): Rosen (1973) illustrated so-called accessory cartilages in the caudal skeleton of the stomatoid genus, *Maurollicus*, and in certain cetomimoid acanthomorphs. Most of these accessory (or radial) cartilages serve to support procurent fin rays and they are variously developed in stomiiform (Weitzman, 1974; Fink and Weitzman, 1982), salmonoid (Rosen, 1985: fig. 44), and acanthomorph lineages. I have been unable to find a citation of the presence of accessory cartilages in noneurypterygian acanthomorphs but an exhaustive study has not been undertaken and the cartilages are often omitted in published drawings. There is much scope for a thorough analysis of the distribution of these structures among euteleosts.

Johnson (1983) noted that a third preural radial cartilage is found in many actinopterygian families, and I can extend this observation to include most acanthomorph taxa.

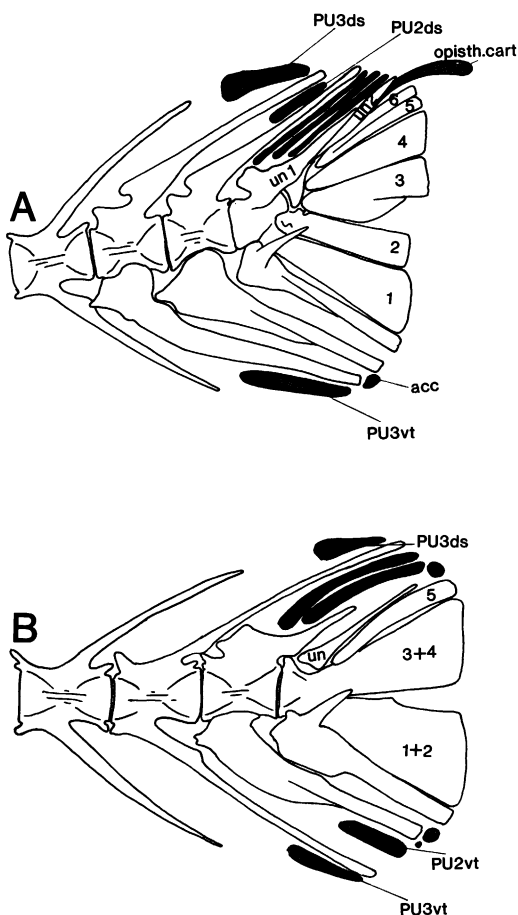


Fig. 9. Caudal fin skeleton of (A) *Polymixia* (AMNH 49674), (B) *Agonostomus* (AMNH 31538).

The configuration in *Polymixia* is indicated in figure 9A and as can be seen from that figure, a well-developed third preural radial is present in both dorsal (PU_{3ds}) and ventral (PU_{3vt}) positions. A PU_{2ds} is also present, but a true PU_{2vt} element is lacking. A small spherical accessory cartilage is present in the ventral PU_{3-2} position. Such small, spherical accessory cartilages are variously developed both inter- and intraspecifically in numerous acanthomorph taxa (figs. 9B, 10A, 11B), and seem to lack the taxonomic stability of the larger radial cartilage blocks.

The radial cartilage pattern in atherinomorphs, with respect to the PU_{3ds} and PU_{3vt} elements, is more or less uniform; that is to say they are usually completely absent (figs.

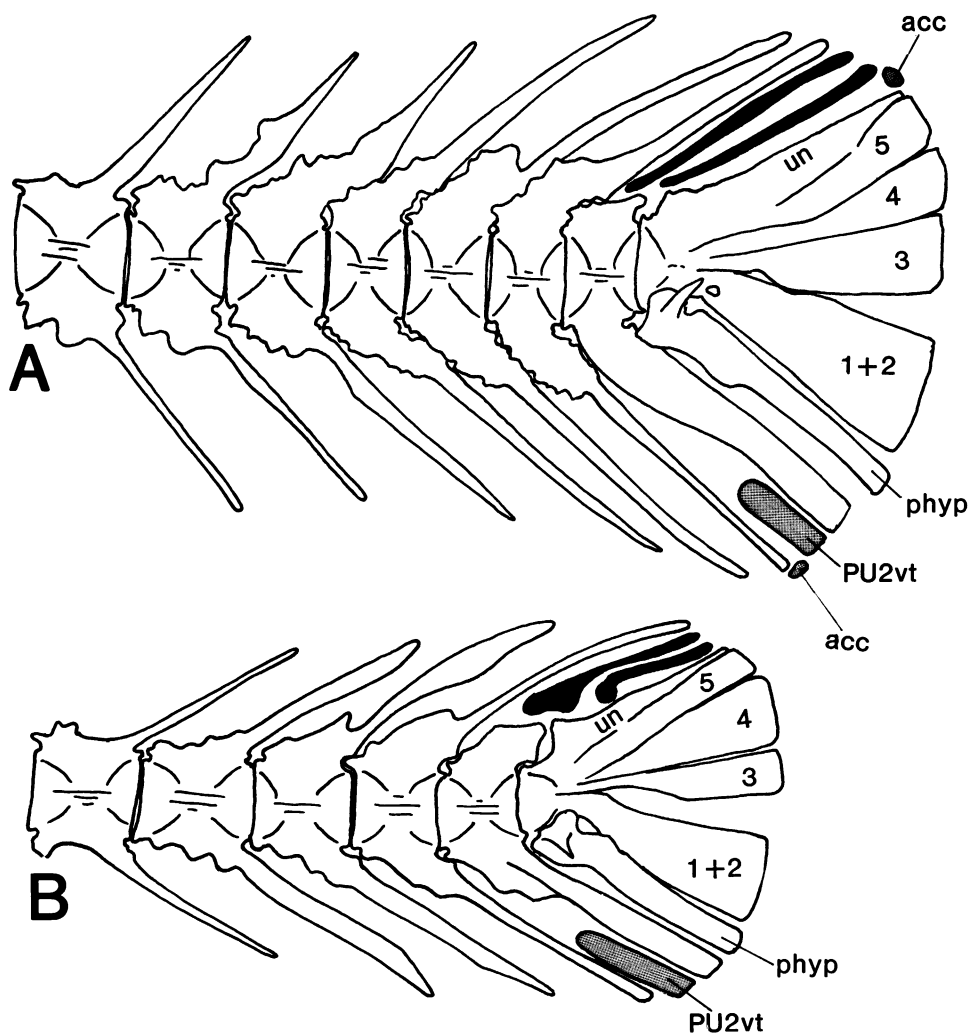


Fig. 10. Caudal fin skeleton and associated vertebrae of (A) *Bedotia* (AMNH 88074), (B) *Teramulus* (AMNH 88141).

10, 11). In a few taxa PU_3 elements are present but greatly reduced, and interestingly in these taxa supernumerary elements are frequently also present (*Orestias elegans* Parenti, 1984a: fig. 18B; *Cyprinodon meeki* personal obs.). Both dorsal and ventral PU_3 radial cartilages are present in mugiloids (e.g., fig. 9B), and in the great majority of actinopterygians examined. Radial cartilages are generally lacking in paracanthopterygians (but see Markle, 1989: fig. 17) and this is probably associated with the extensive caudal fin modifications of this assemblage (Rosen and Patterson, 1969; Patterson and Rosen, 1989).

Johnson (1983) cautioned that it is probable that the loss of PU_3 cartilages occurred independently several times within the Percoidei, and the same is probably true among paracanthopterygians. Despite the apparent "ease" of loss of these structures, I think it reasonable to interpret their absence in atherinomorphs as homologous, and as such they are further evidence of a shared common ancestry of this clade.

There is considerable variation in the presence and position of accessory radial cartilages among acanthomorph taxa and a study of the various configurations may prove to

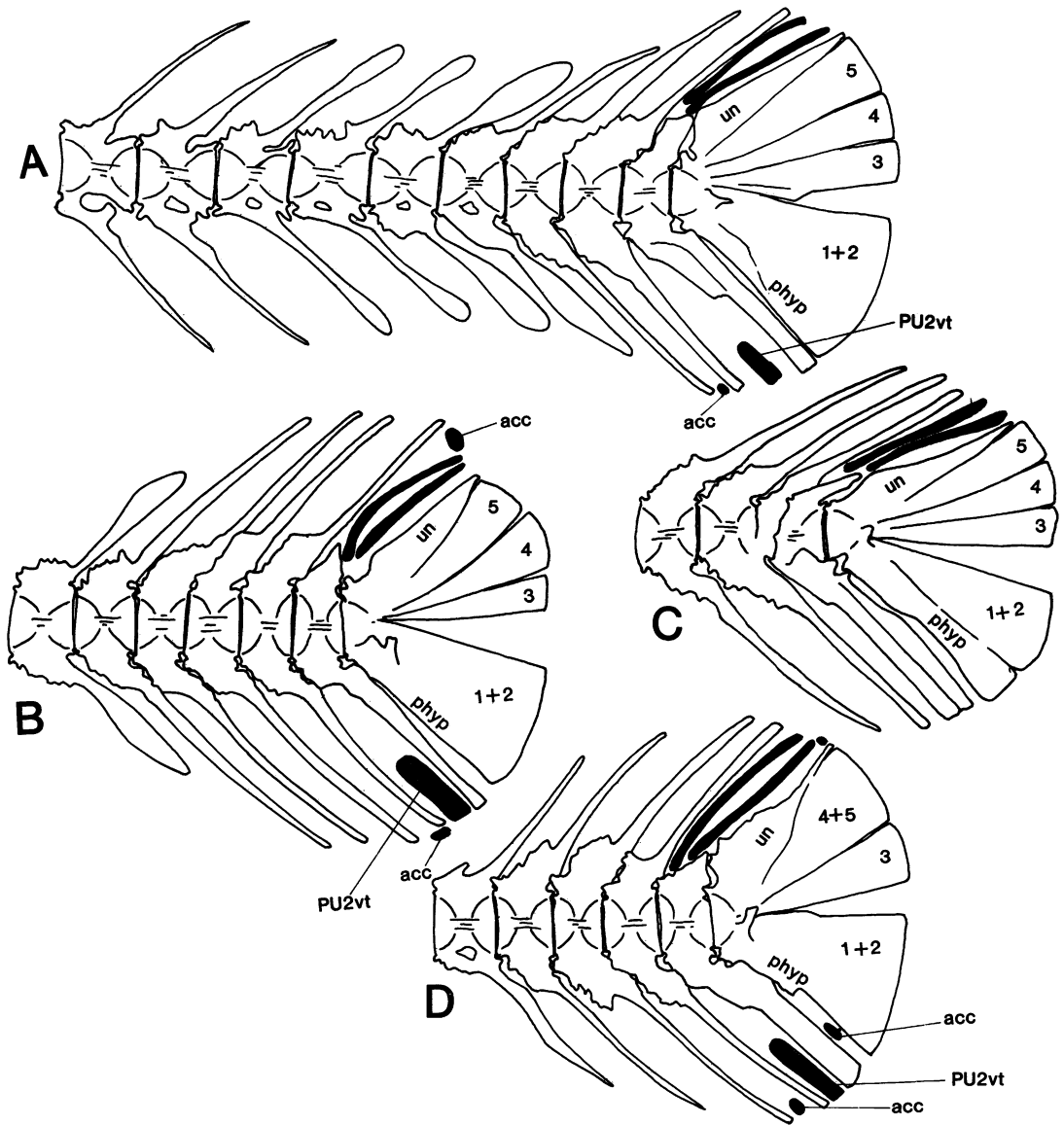


Fig. 11. Caudal fin skeleton and associated vertebrae of (A) *Rheocles sikorae* (AMNH 28127) (B) *R. wrightae* sp. nov. (MNHN 1989-1614), (C) *R. pellegrini* (AMNH 9696), (D) *R. alaotrensis* (AMNH 88001).

be of some considerable value in interfamilial and intergeneric phylogenetic analysis.

VERTEBRAL COLUMN

CHARACTER 10 (figs. 10A, 11): In all bedotiid taxa the posterior six or seven caudal vertebrae bear elaborate crenulations and thickening of the prezygapophyses, par-

apophyses, centra, and neural and hemal spine bases (figs. 10A, 11). This elaboration and posterior thickening of the bedotiid vertebral column is very marked and in some individuals appears almost as a pathological condition.

Some caudal thickening is evident in many division I atherinoid and beloniform taxa (see *Teramulus*, fig. 10B; Chernoff, 1986b), but in

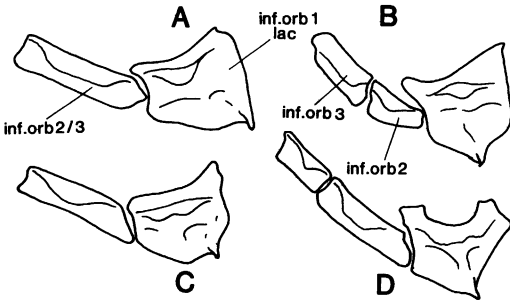


Fig. 12. Infraorbital elements of (A) *Rheocles* (AMNH 88001), (B) *Melanotaenia* (AMNH 55067), (C) *Bedotia* (AMNH 88074), and (D) *Teramulus* (AMNH 88141).

no other taxon does the degree and extent of posterior caudal thickening match that exhibited by the bedotiid clade.

INFRAORBITAL SERIES

CHARACTER 11 (fig. 12): Primitively, division I atherinoids have a lachrymal and two additional bones in the infraorbital series (e.g., figs. 12B, D; see also Chernoff, 1986b). Bedotiid taxa exhibit a derived configuration in having a single elongate element behind the

lachrymal (e.g., figs. 12A, C) rather than two separate, although frequently closely apposed, infraorbitals. Chernoff (1986b) noted a parallel reduction in infraorbital number in most New World atherinoids, as well as in the Australian genus, *Craterocephalus*.

PELVIC GIRDLE

CHARACTER 12 (figs. 13, 14): The pelvic girdle of *Polymixia* (fig. 13A) represents the plesiomorphic acanthomorph configuration in which simple medial processes of bilateral pelvic elements overlap in the midline. An essentially similar girdle is found in percopisiform paracanthopterygians (see Rosen and Patterson, 1969: fig. 27) and, with some modification, in the remaining paracanthopterygian lineages (see Fahay, 1989: fig. 11).

Among atherinoids an essentially similar girdle is generally present, although there is some elaboration of the medial processes with the development of a series of medial and accessory spines (Chernoff, 1986b). The bedotiid pelvic girdle is rather simple (fig. 14), but is noteworthy in the expression of a marked asymmetry of the medial processes. In other atherinoid taxa (Allen, 1980; Ivant-

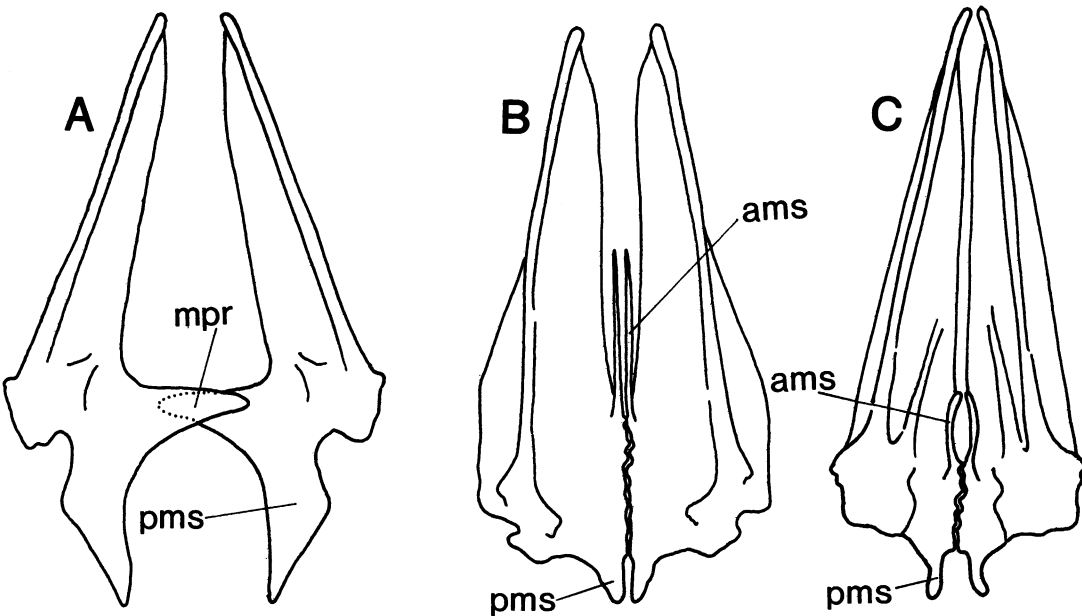


Fig. 13. Pelvic girdles, in ventral view, of (A) *Polymixia* (AMNH 49674), (B) *Agonostomus* (AMNH 31538) (C) *Ptychochromis* (AMNH 88102).

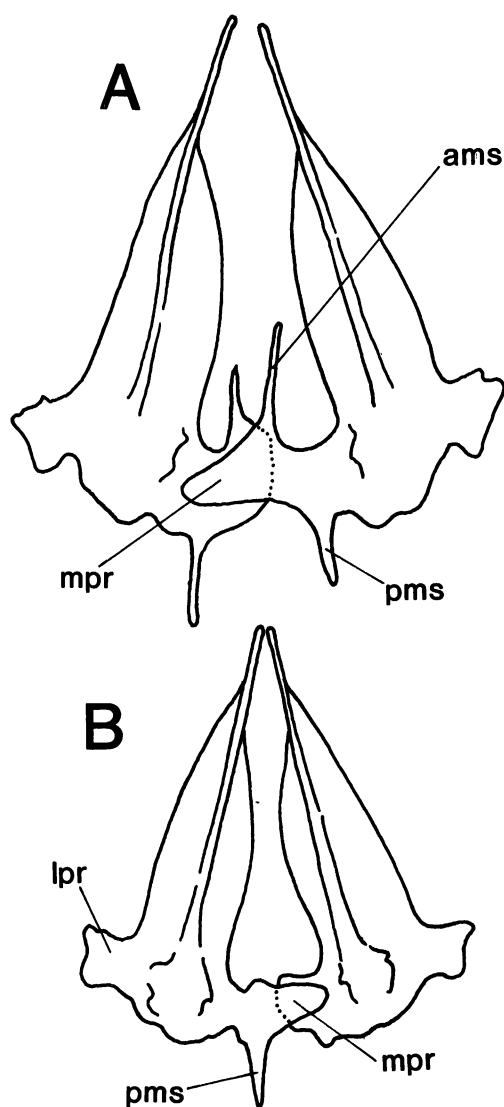


Fig. 14. Pelvic girdles, in ventral view, of (A) *Rheocles* (AMNH 88001) and (B) *Bedotia* (AMNH 88074).

soff et al., 1987: personal obs.) the medial processes are overlapping and more or less symmetrical.

CHARACTER 13: *Bedotia* (fig. 14B) differs from *Rheocles* (fig. 14A) in lacking anteromedial spines (ams) and reduction of posteromedial spines (pms). Among actinopterygians the presence of both posteromedial and anteromedial spines is the widespread condition, and I concur with Chernoff (1986b)

in his view that reductions or loss represent derivations from the plesiomorphic state. The loss of anteromedial pelvic spines and the reduction of posteromedial spines are thus interpreted as evidence of group monophyly.

CHARACTER 14: The pelvic girdle of percomorph fishes differs markedly from the plesiomorphic condition described here for non-percomorph acanthomorphs. Typically in percomorphs the girdle is united along the midline forming a single unit (e.g., fig. 13C). Union is usually by a central suture in the posterior field of the girdle or by close apposition of both halves: in either case overlapping medial processes are entirely lacking. Anteromedial processes are usually present in the form of two small, ventrally displaced bony prongs. The medial plates are much expanded and frequently meet in the midline. In essential features this pelvic morphology is common to all percomorph taxa examined and is interpreted here as a synapomorphy indicative of a shared common ancestry for the Percomorpha. Lauder and Liem (1983: 163) noted that the series Percomorpha is "... ill-defined and their internal classification is very tentative, confusing, and problematic." The positive indication of percomorph monophyly, provided here by the recognition of a derived pelvic morphology, is therefore of particular interest.

Needless to say, nothing connected with percomorph systematics is straightforward. The pelvic configuration in mugiloids (fig. 13B) is in conflict with my placement of this taxon as the sister group to the remaining Atherinomorpha. Mugiloids have an unmistakably percomorphlike pelvic girdle, complete with the loss of overlapping medial processes, and the development of a central sutural union of the two pelvic components. Furthermore, in typical percomorph fashion, the anteromedial processes are represented as two elongate, ventrally displaced bony prongs. In all of these unambiguously derived features, the mugiloid girdle is indistinguishable from that of percomorph fishes. Such character conflict is frustratingly familiar to systematists working at the resolution of problems of actinopterygian interrelationships (see Discussion).

A study of the complex associated pelvic myology provides an interesting corollary to

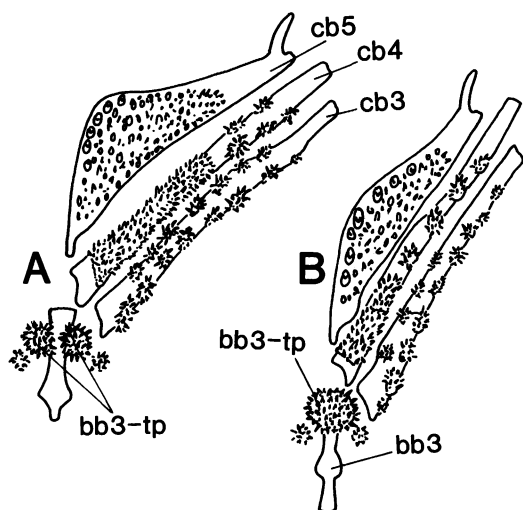


Fig. 15. Ventral branchial arches (l.h.s.) of: (A) *Bedotia* (AMNH 88074) and (B) *Rheocles* (AMNH 88171).

the current investigation, and will be the subject of a forthcoming paper.

BASIBRANCHIAL TOOTHPLATES

CHARACTER 15 (fig. 15): The arrangement of ventral pharyngeal toothplates and gill rakers in *Rheocles* (fig. 15B) and *Bedotia* (fig. 15A) differ in a number of minor details most noteworthy among which is the arrangement of the third basibranchial toothplates (bb₃-tp). In *Rheocles* the toothplate is a single, medially situated element, whereas in *Bedotia* the element is represented by paired, laterally displaced toothplates.

In the great majority of acanthomorph taxa in which a third basibranchial toothplate is present, that toothplate is consolidated into a single central element. The paired configuration exhibited by *Bedotia* is unique within the Atherinomorpha, and is highly unusual among acanthomorphs generally. The paired condition is therefore considered to be derived and as such is interpreted as further evidence of the monophyly of *Bedotia*.

PREMAXILLARY NOTCH

CHARACTER 16 (fig. 16): The presence of both ascending and articular premaxillary processes, the loose association of the rostral cartilage, and the resulting jaw mechanism of bedotiid and melanotaeniid (minus *Pseudo-*

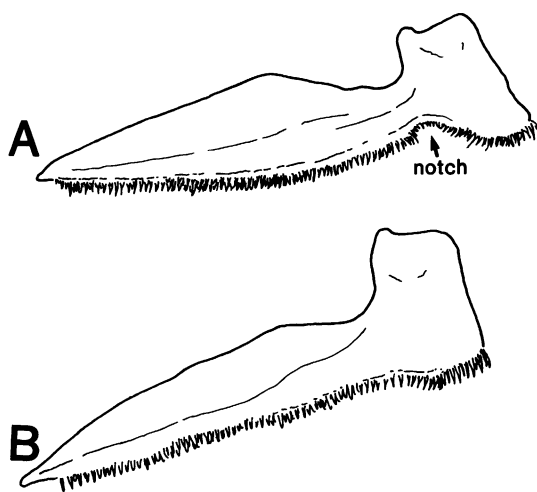


Fig. 16. Right premaxillae of: (A) *Bedotia* (AMNH 28132) and (B) *Rheocles* (AMNH 28127).

mugil) atherinoids is considered by Parenti (1984b) to represent the plesiomorphic atherinomorph configuration. The findings of the current investigation fully support Parenti's (1984b) conclusions regarding the plesiomorphic nature of the bedotiid jaw apparatus, however *Bedotia* does exhibit a peculiar feature of the premaxilla which presumably represents an autapomorphy of the genus.

The premaxilla of *Bedotia* (fig. 16A) bears a deep excavation of its dentigerous border forming the so-called *Bedotia* notch. This excavation is lacking in *Rheocles* (fig. 16B), and although Allen (1980) illustrated a somewhat similar premaxillary morphology in certain melanotaeniids, I have been unable to find such a marked premaxillary notch as that exhibited in *Bedotia*.

Rheocles: Evidence supporting the monophyly of *Rheocles* has been surprisingly hard to locate. Despite a rather coherent and characteristic "facies" for all species, in virtually every aspect of anatomy *Rheocles* seems to exemplify the most generalized atherinomorph condition. However, in the caudal fin skeleton there appears to be one feature of potential value in the cladistic diagnosis of the genus.

CHARACTER 17 (fig. 11): In *Rheocles* (fig. 11) the lower hypural fan is a single unit composed of the parhypural element fully fused with the urostylar PU₁ + U₁ centra and hypurals 1 + 2. A similar parhypural fusion has

been described in melanotaenniids by Allen (1980). *Bedotia* and other atherinoids exhibit the plesiomorphic caudal configuration with a fully autogenous parhypural (e.g., fig. 10A).

DISCUSSION

One of the more controversial findings arising from the foregoing analysis is the suggested placement of the mugiloid fishes as the sister group of the atherinomorph assemblage. To my knowledge this alignment has not previously been proposed and it seems appropriate here to add a few comments.

The mugiloids have traditionally posed problems for systematists, and as a result they have had a somewhat checkered taxonomic history (e.g., Berg, 1940; Gosline, 1968; McAllister, 1968). Perhaps the real problem associated with any definitive placement of the mugiloids is the lack of a satisfactory cladistic definition for the Percomorpha (see Lauder and Liem, 1983). It is somewhat ironic that in the course of the current study a character supporting percomorph monophyly (character 14, fig. 2) has been located, only to be thrown into question by my placement of the mugiloids.

The four derived characters located in this study as evidence of a mugiloid/atherinomorph relationship have been described in the previous sections (characters 1–4, fig. 2). It should be noted, however, that three of these are features of pharyngobranchial myology. The functional (and phylogenetic) independence of these features is open to doubt, particularly in view of the extreme remodeling of the mugiloid pharynx as a result of the development of a complex pharyngobranchial organ in these fishes. It is, of course, possible that the mugiloid configuration (fig. 3C) simply mirrors that of atherinomorphs (fig. 3B) and has been derived independently from the plesiomorphic acanthomorph arrangement (fig. 3A) as a result of a quite different process. The fourth character (character 4, fig. 2), neural arch expansion, is less obviously functionally correlated, yet a similar argument for parallel acquisition can always be made.

In my view the strongest argument against the alignment of mugiloids and atherinomorphs, is not one of possible “functional

correlation of characters” and “parallel evolution,” but the fact that mugiloids share with other percomorphs (and no atherinomorphs) a peculiar, and clearly derived, pelvic girdle anatomy (character 14, fig. 2).

Parsimony dictates that the scheme outlined in figure 2 be adopted, and that the mugiloid pelvic modifications are to be interpreted as having been independently derived from those of percomorphs. Needless to say, I am fully cognizant that future analyses may reveal additional characters that may conflict with my assessment of relationships. But this is always true, and it is to be hoped that this study, and the conflicts it highlights, will act as an impetus for additional studies at these particularly perplexing levels of the acanthomorph hierarchy.

My analysis poses a nomenclatural problem which needs to be addressed. Given the scheme presented in figure 2, a number of alternatives are presented. For example, Rosen's (1965) concept of an Atherinomorpha could be expanded to include the mugiloid fishes. I do not favor this alternative, as a non-mugiloid Atherinomorpha is very well established in the literature. Following Nelson's sequencing convention, the mugiloids could be elevated to the rank of Series, i.e., the Mugilomorpha. The Percomorpha is then the sister group of a monophyletic Mugilomorpha plus a monophyletic Atherinomorpha.

This seems to be the least disruptive or obtrusive alternative, and I therefore suggest that in the future the members of the suborder Mugiloidei (see Nelson, 1984, for a summary of included taxa) be referred to as mugilomorphs, or more formally as members of the series Mugilomorpha. The type, and single family of the Mugilomorpha, is the Mugilidae.

TAXONOMIC REVISION OF THE GENUS *RHEOCLES*

Jordan and Hubbs, 1919

Rheocles Jordan and Hubbs, in Jordan, 1919a: 343 (type species: *Eleotris sikorae* Sauvage, 1891, by original designation).

Rheocloides Nichols and LaMonte, 1931: 1–2 (type species: *Rheocloides pellegrini* Nichols and LaMonte, 1931, by original designation).

DIAGNOSIS: robust Madagascan bedotiids with little lateral body compression, distinguished from other genera by the presence of a lower hypural fan that is a single unit composed of the parhypural element fully fused with the urostylar $PU_1 + U_1$ centra and hypurals 1 + 2.

DESCRIPTION: Head shape somewhat variable, with predorsal profile either interrupted by short premaxillary pedicels or smoothly rounded in outline. Mouth large with an impressive gape. In overall facies *Rheocles* bears a striking resemblance to the cyprinid genus *Barilius*.

Both buccal jaws bear numerous rows of fine, caniniform teeth. Premaxillae complete, without a *Bedotia* notch. Tooth patches variously developed on the vomer, palatine, endopterygoid, and ectopterygoid bones of the suspensorium. The third basibranchial tooth plate is a single, medial element. Gill raker number is relatively low, ranging from 7 to 11 stout rakers along the lower limb of the first branchial arch. Scales, where present, are large, cycloid, and regularly imbricate. Longitudinal scale counts range between 34 and 40. Dorsal, anal, and caudal scale sheaths and axillary pelvic scales are lacking. The first dorsal fin bears a weak spine and 3 to 6 rays, the second dorsal fin also bears a weak spine and 10 to 16 rays. The two fins are separated by 2 to 3 scales, and internally, by two short, rayless pterygiophores. The anal fin bears a weak spine and 13 to 16 rays. The pelvic fins bear a weak spine and five rays. Total vertebral counts range from 34 to 41, invariably with higher abdominal than caudal counts.

Rheocles is an exclusively freshwater genus of Madagascan bedotiid ecologically restricted to heavily forested streams. Despite their large gape and predatory facies, the genus appears to feed almost exclusively on allochthonous material, primarily insects falling onto the water surface. Geographical distribution records for the genus indicate a restricted generic range (fig. 17), limited to small regions of the central and eastern highlands.

KEY TO SPECIES OF RHEOCLES

- 1. Mouth large, upper jaw extending to well beyond vertical line through anterior margin of orbit (fig. 18A, B). Genital papilla darkly pigmented 2

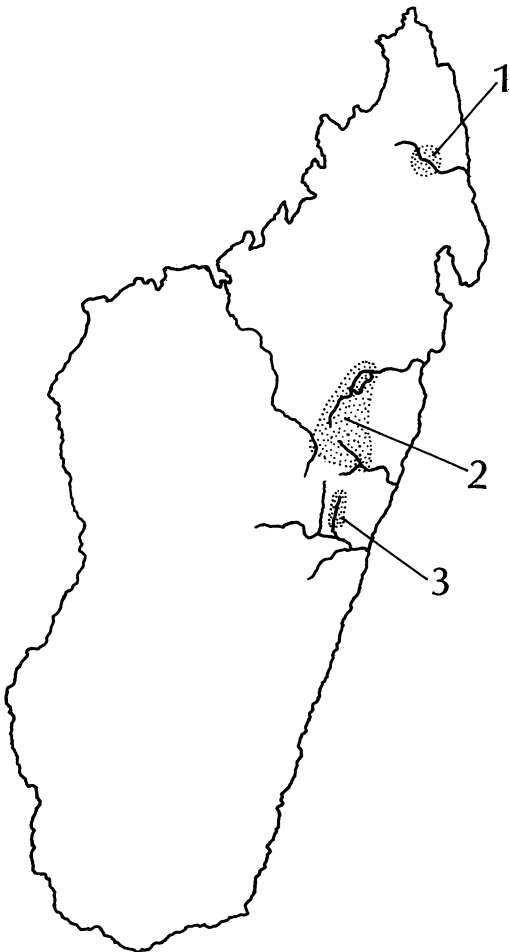


Fig. 17. Madagascar, stippling represents distributional ranges of: (1) *Rheocles pellegrini*, (2) *Rheocles alaotrensis*, and (3) *Rheocles sikorae* and *Rheocles wrightae*, sp. nov.

- Upper jaw reaching only to vertical line through anterior margin of orbit. Genital papilla lacking dark pigmentation 3
- 2. Premaxillary pedicels interrupt predorsal head profile (fig. 18C). Rostral cartilage more or less contained by premaxillary pedicels. 36–39 vertebrae *R. sikorae*
- Dorsal head profile smoothly rounded (fig. 18A). Rostral cartilage extruded beyond level of premaxillary pedicels. 40 vertebrae *R. wrightae*, sp. nov.
- 3. Cheek, chest, and anterior dorsum to origin of first dorsal fin naked. 6 or 7 gill rakers along lower limb of first branchial arch *R. pellegrini*
- Cheek, chest, and anterior dorsum fully scaled.

TABLE 1
Rheocles sikorae (Sauvage, 1891)

	N	min	max	m	SD		
Standard length	15	38.5	90.6				
PreD ₁ (%SL)	15	46.9	51.0	49.1	0.13		
PreD ₂ (%SL)	15	59.9	66.9	62.5	0.12		
Preanal (%SL)	15	58.8	61.9	60.4	0.10		
Prepelv. (%SL)	15	40.4	43.6	41.7	0.10		
A base (%SL)	15	19.7	23.2	21.4	0.10		
D ₂ base (%SL)	15	18.2	22.6	19.9	0.10		
Body depth (%SL)	15	23.1	28.3	24.6	0.13		
Head length (%SL)	15	25.8	29.4	27.4	0.01		
Snout length (%HL)	15	25.0	33.1	30.1	0.21		
Eye depth (%HL)	15	25.8	32.5	28.6	0.26		
Lower jaw length (%HL)	15	60.0	66.1	60.8	0.34		
Upper jaw length (%HL)	15	46.2	57.7	51.5	0.38		
Caud. peduncle lgth (%HL)	15	65.4	83.3	74.0	0.58		
Caud. peduncle wdth (%HL)	15	33.3	39.2	35.6	0.19		
P ₁ –P ₂ (%SL)	15	18.2	24.8	21.2	0.17		
P ₂ –D ₂ (%SL)	15	29.7	35.7	32.8	0.16		
D ₁ –A (%SL)	15	25.6	29.0	27.3	0.12		
D ₂ –A (%SL)	15	21.0	26.6	23.4	0.15		
Distribution							
Longitudinal scales	15	36	39	36 (2)	37 (5)	38 (3)	39 (5)
Gill rakers (lower arch)	15	9	11	9 (1)	10 (10)	11 (4)	15 (3)
D ₂ rays	15	12	15	12 (1)	13 (4)	14 (6)	15 (4)
Anal rays	15	15	16	15 (10)	16 (5)		
Vertebrae	15	38	39	20 + 19 (7)	20 + 18 (5)	19 + 19 (3)	

9–11 gill rakers along lower limb of first branchial arch *R. alaotrensis*

RHEOCLES SIKORAE
(SAUVAGE, 1891)

Synonymy: *Eleotris sikorae* Sauvage, 1891, Hist. Madag. Poiss. 16: 521, pl. XLIVc, fig. 2.
Atherina sikorae, Boulenger, 1892, Zool. Rec. 28: 20.
Rheocles sikorae, Jordan and Hubbs, 1919a, Proc. Acad. Nat. Sci. Philadelphia 70: 343.
Citations: *Atherina sikorae*, Pellegrin, 1907: 206; 1914a: 48; 1914b: 433. — Boulenger, 1916: 76.
Rheocles sikorae, Jordan and Hubbs, 1919b: 20. — Pellegrin, 1929: 46; 1933: 160, pl. 3, fig. 1; 1934: 429; 1937: 129. — Arnoult, 1959: 53. — Kiener, 1961: 117; 1963: 74, pl. 40. — Smith, 1965: 631, pl. 102, fig. 1. — Maugé, 1986: 278.

HOLOTYPE: MNHN 1891-727 “rivières du versant Est du grand massif central de Madagascar.” Male 90.6 mm SL.
VERNACULAR NAME: Sardine d’eau douce, Zona.

DIAGNOSIS: *Rheocles sikorae* is readily distinguished from *R. alaotrensis* and *R. pellegrini* in bearing a strongly pigmented genital papilla. It differs from *R. wrightae* in dorsal head profile; the premaxillary pedicel interrupts the profile in *R. sikorae* while the profile is uninterrupted and smoothly rounded in *R. wrightae*. In *R. sikorae* the rostral cartilage is more or less contained by the premaxillary pedicel while in *R. wrightae* the cartilage is extruded well beyond the pedicel.
DESCRIPTION: Based on the holotype and 14 additional specimens. Morphometric measurements and meristic counts are given in table 1. See also figure 19.
Rheocles sikorae, which attains a standard length of 90.6 mm, is a relatively robust species which exhibits little belly curvature anteriorly but is distinctly rounded dorsally. The greatest body depth is situated at the vertical through the origin of the pelvic fins. The relatively broad-based second dorsal fin

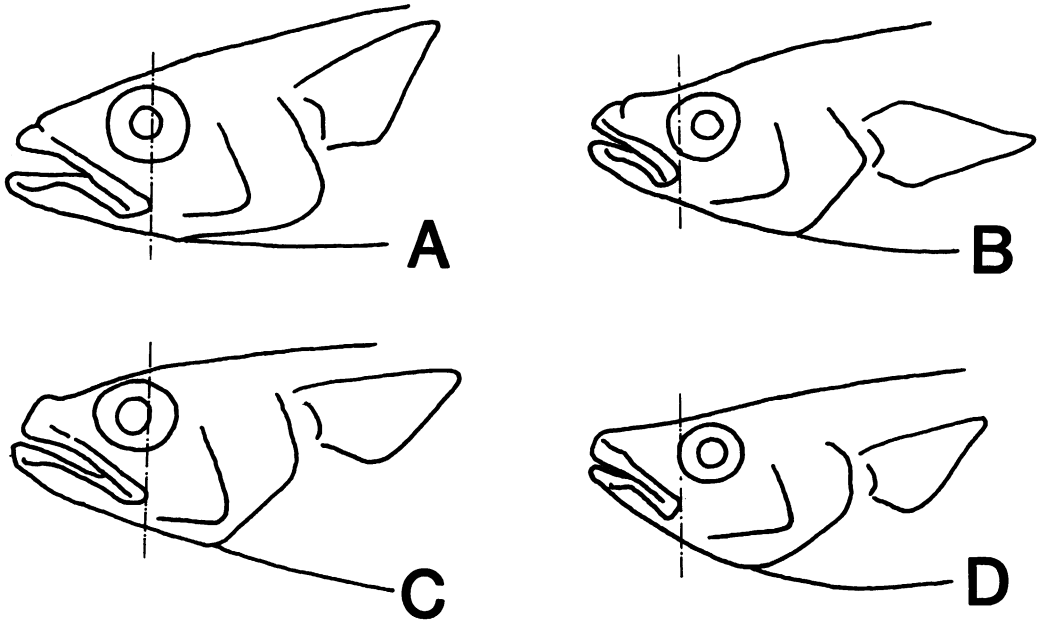


Fig. 18. Head outlines of: (A) *Rheocles wrightae* sp. nov., (B) *Rheocles pellegrini*, (C) *Rheocles sikorae*, and (D) *Rheocles alaotrensis*.

originates a little behind the vertical through the origin of the anal fin.

The head is of moderate length with a relatively acutely pointed and narrow snout. The dorsal head profile is interrupted by the premaxillary pedicel. The species is prognathous and the gape inclination is approximately 15–20° to the horizontal when the mouth is closed. The mouth is large and the premaxilla and maxilla of the upper jaw reach well beyond the level of the anterior margin of the orbit (see fig. 18C).

Teeth: Both upper and lower jaws bear 4–6 rows of numerous irregularly implanted small recurved unicuspid teeth. There is little differentiation between inner and outer row teeth. Relatively large tooth patches are present on the vomer, palatine, endopterygoid, and ectopterygoid bones of the suspensorium.

Gill Rakers: 2 or 3 stout hypobranchial and 7 or 8 elongate ceratobranchial rakers are present along the lower limb of the first branchial arch.

Scales: The body is covered with large, regularly imbricate, cycloid scales. The predorsal scales range from 15 to 18 along the midline. Longitudinal scales range from 36 to 39,

and there are three scales separating first and second dorsal fins. Dorsal, anal, and caudal scale sheaths and an axillary scale are lacking. The region from the rounded interpelvic scale to the genital papilla is fully scaled (fig. 20B).

Fins: The first dorsal fin bears a weak spine and 4–6 soft rays. The relatively long-based second dorsal bears a weak spine and 12–16 soft rays. The anal fin bears a weak spine and 15–16 soft rays. The first and second dorsal fins are somewhat truncate in outline with no sexual dimorphism evident. The anal fin is markedly more falcate than illustrated in figure 19, and is, in fact, as illustrated for *R. wrightae* in figure 23. The pectoral fins are high set and short with a rounded, fan-shaped outline when expanded. The caudal fin is strongly emarginate with forked lobes.

Osteology and Other Anatomical Features: Vertebral counts range from 38 to 39. The fourth and fifth hypurals of the caudal skeleton are separate.

The dorsal ramus of the urohyal bone is broad and dorsally expanded (fig. 21A). I find no concomitant modification of the basi-branchial and hypobranchial elements associated with the ramus.

All trace of an ethmomaxillary ligament is

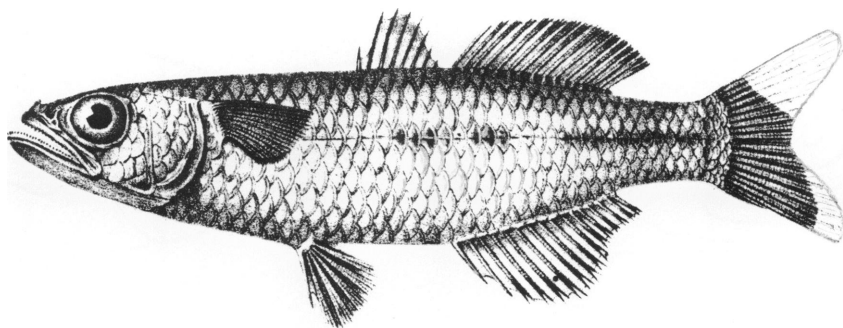


Fig. 19. Lateral view of the holotype of *Rheocles sikorae* (MNHN 1891-727). After Sauvage, 1891.

lost from the upper jaw apparatus. The rostral cartilage is more or less contained by the premaxillary pedicel and is not extruded.

The genital papilla is prominent in both sexes and is darkly pigmented along its whole length (e.g., fig. 20B) even in juvenile specimens.

COLORATION: Sauvage (1891: 521) described the coloration of *sikorae* as follows: "Jaunâtre, avec le bord des écailles rembruni au-dessus de la ligne latérale; une bande noirâtre mal définie le long de cette ligne; une large tache noire à l'opercule; une band de même couleur à la base de la pectorale; première dorsale en partie noirâtre; un mince liséré noir à l'extrémité de l'anale et de la dorsale molle." Pellegrin (1933: 160) noted that "La

pectorale et la 1^{re} dorsale sont gris foncé, la 2^e dorsale et l'anale jaunes avec un liséré noir. La pectorale est jaunâtre." Kiener (1963) added only that there are "... taches noires irrégulièrement reparties" along the lateral band.

ADDITIONAL MATERIAL: MNHN 1962-188 (4) Anosibe: MNHN 1966-914 (51) Point km 44 sur route de Moramanga-Anosibe, District d'Anosibe, Province de Tamatave.: AMNH 28127 (2) Manambola River, Anosibe-Moramanga.

DISTRIBUTION (fig. 17, area 3): Sauvage (1891: 521) gave no type locality for *R. sikorae*, saying only that this new species "... habite les rivières du versant est du grand massif centrale" and this claim has been re-

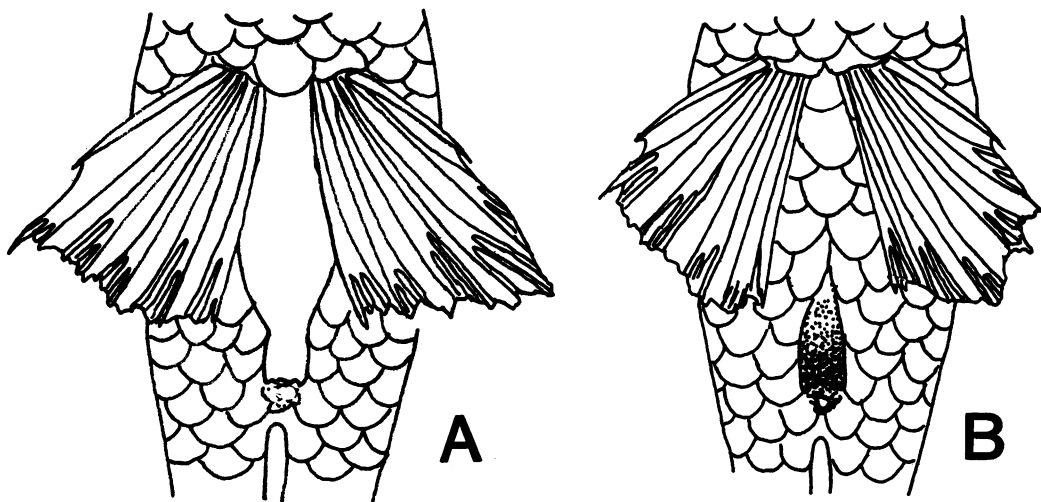


Fig. 20. Abdominal squamation patterns and genital pigmentation in: (A) *Rheocles alaotrensis* and (B) *Rheocles sikorae*.

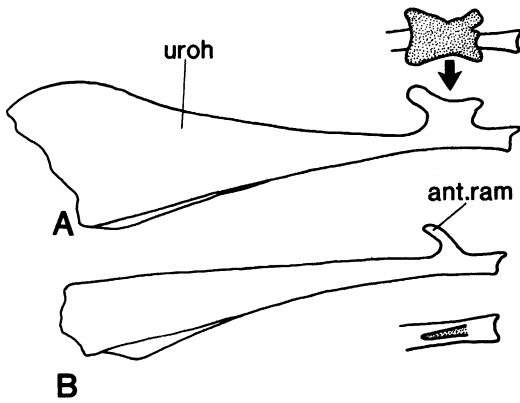


Fig. 21. Urohyal bone of: (A) *Rheocles sikorae* (AMNH 28127) and (B) *Rheocles alaotrensis* (AMNH 88171).

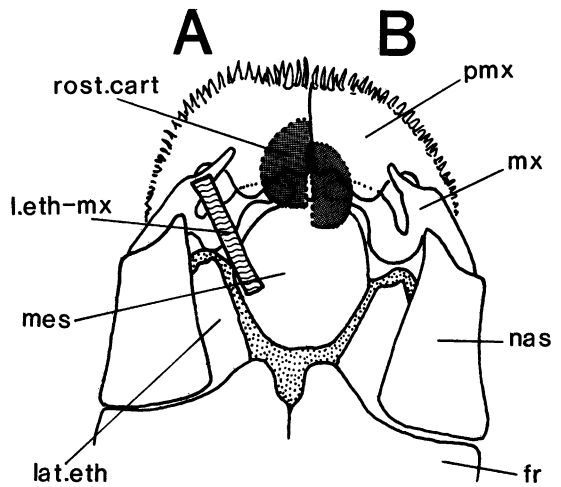


Fig. 22. Schematic representation of the ethmovomerine region and associated structures, in dorsal view, (A) *Rheocles alaotrensis* and (B) *Rheocles wrightae*.

peated by subsequent authors (e.g., Pellegrin, 1933; Maugé, 1986). *Rheocles sikorae* is poorly represented in museums and of the nontypical specimens deposited in collections all appear to be from a relatively short stretch of the Manambola River. The Manambola is a major tributary of the Mangoro River, a large eastern coastal drainage.

In view of the foregoing it seems probable that Sauvage's (1891) claim is erroneous and that *R. sikorae* in fact has (had?) an extremely circumscribed distribution in the Manambola River, possibly occurring only in the region of the small settlement of Anosibe (19°24'S, 48°11'E). Today this region is almost entirely deforested with intensive rice agriculture and concomitant aquatic habitat degradation (Reinthal and Stiassny, in rev.), it seems sadly probable that *R. sikorae* is no longer extant.

ETYMOLOGY: Named by Sauvage for M. Sikora who collected the holotype.

RELATIONSHIPS (fig. 27): *Rheocles sikorae* is the sister species of *R. wrightae* with which it appears to occur in sympatry (see p. 24). Evidence for this phylogenetic alignment is to be found in a range of different attributes of the two species.

Both share certain derived features of pigmentation patterning that are unique to the two species clade. The presence of a series of irregular black spots along the lateral aspect of the body is common in individuals of both species. When present, these black spots are

situated along the lateral body stripe (e.g., figs. 19, 23), and spotted individuals may bear along the flank from one (typically in *wrightae*), to four or five spots (in *sikorae*). Interestingly the disposition of spots is completely asymmetrical with spots on one side being no predictor of their presence on the other.

A lateral body stripe is common to all bedotiid taxa as well as to most other atherinoid species (see Jordan, 1905; Jordan and Hubbs, 1919b; Smith, 1965; Allen, 1980; Chernoff, 1986a) and its presence is probably plesiomorphic for atherinomorphs. However, among atherinoids, lateral spotting appears to be restricted to these two *Rheocles* species and as such is interpreted as evidence of their close relationship.

The first dorsal fin is darkly pigmented, as is the distal margin of the caudal fin. Among bedotiids both of these features are restricted in distribution to this species pair and their presence is reasonably interpreted as further evidence of their close phylogenetic relationship.

The large genital papilla of *R. sikorae* is prominent and darkly pigmented, while in *R. wrightae* the prominent papilla is darkly pigmented on its distal portion. Such is not the case in other bedotiids or in the great majority of other atherinoids where genital pig-

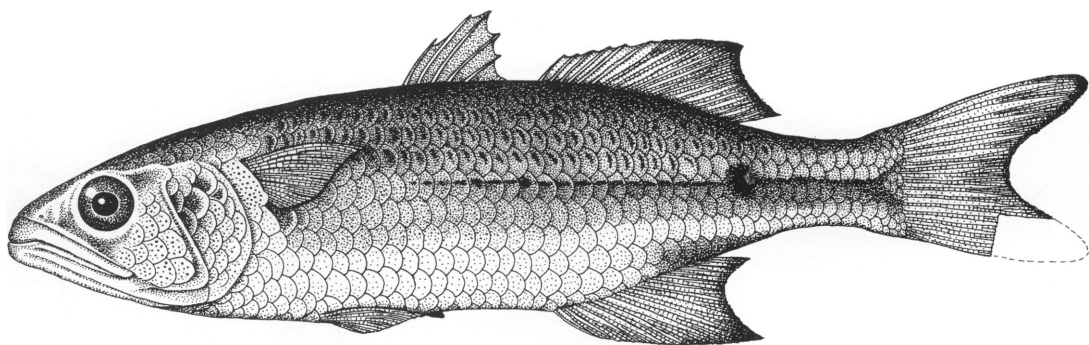


Fig. 23. Lateral view of the holotype of *Rheocles wrightae* sp. nov. (MNHN 1942-77). Drawn by Patricia Wynn.

mentation is lacking. Once again, this feature is considered derived and indication of a sister-group relationship between the species.

The urohyal is similarly modified in *R. sikorae* and *R. wrightae*, where in both taxa the anterior ramus is broad and dorsally expanded (see fig. 21A). This is not the case in other bedotiids where the anterior ramus is rather thin and somewhat pointed on its dorsal surface (e.g., fig. 21B). The latter condition is widespread among Old and New World atherinoids as it is among atherinomorphs and percomorphs generally. Interestingly a similar dorsal expansion of the anterior ramus is encountered in the menidiine assemblage (Chernoff, 1986b). In view of this rather anomalous distribution (i.e., in two *Rheocles* species and in the distantly related New World menidiines) it seems reasonable to interpret the presence of a dorsally expanded anterior ramus of the urohyal as further evidence of a sister-group relationship between *R. sikorae* and *R. wrightae*, and as having been independently derived in the distantly related New World menidiines.

An ethmomaxillary ligament is primitively present in acanthomorph fishes (Stiassny, 1986). Within the Atherinomorpha the ligament has undergone some modification; for example, Chernoff (1986b) noted that in most New World atherinids the ligament is divided in a characteristic manner. Although, as noted by Parenti (1981), the ligament is lacking in certain cyprinodont lineages, it is clear that the presence of a ligament is primitive for atherinoids and its complete absence in *R. sikorae* and *R. wrightae* is unique to these two taxa within the bedotiid clade.

Other features shared by *R. sikorae* and *R. wrightae* are less readily interpreted in a phylogenetic context. For example, both species have an elevated vertebral count (see p. 28) and a relatively long based second dorsal fin with an elevated soft ray count (see p. 28). They also both have extremely large mouths capable of impressive gapes.

In total there seems to be an impressive array of anatomical evidence supporting the proposed sister-group relationship of these two species.

Rheocles wrightae, new species

HOLOTYPE: MNHN 1942-77 Rivière Sandrangato, au sud de Moramanga. Male 92.0 mm SL.

PARATYPES: MNHN 1989-1614 Rivière Sandrangato, au sud de Moramanga. 100.2–62.0 mm SL. AMNH 58908 Rivière Sandrangato, au sud de Moramanga. 95.6 mm SL.

DIAGNOSIS: *Rheocles wrightae* is readily distinguishable from both *R. alaotrensis* and *R. pellegrini* in bearing a strongly pigmented genital papilla. It differs from *R. sikorae* in dorsal head profile, which is uninterrupted and smoothly rounded in *R. wrightae* and interrupted in *R. sikorae*. *Rheocles wrightae* is further distinguished from *R. sikorae* by a consistently higher longitudinal scale count (40 versus 36–39).

DESCRIPTION: Based on the holotype and 11 paratypes. Morphometric measurements and meristic counts are given in table 2. See also figure 23.

Rheocles wrightae, which attains a stan-

TABLE 2
Rheocles wrightae, new species

	N	min	max	m	SD
Standard length	12	62.0	100.2		
PreD ₁ (%SL)	12	48.8	52.6	50.9	0.13
PreD ₂ (%SL)	12	60.8	65.7	63.2	0.15
Prealanal (%SL)	12	60.3	64.1	61.8	0.13
Prepelv. (%SL)	12	41.4	44.3	43.1	0.09
A base (%SL)	12	20.1	22.9	21.5	0.10
D ₂ base (%SL)	12	20.0	22.4	21.1	0.07
Body depth (%SL)	12	23.7	26.4	24.9	0.08
Head length (%SL)	12	26.8	29.7	28.9	0.08
Snout length (%HL)	12	30.5	34.4	32.9	0.11
Eye depth (%HL)	12	25.0	28.4	26.5	0.13
Lower jaw length (%HL)	12	59.1	66.0	61.8	0.22
Upper jaw length (%HL)	12	51.1	59.0	55.0	0.25
Caud. peduncle lgth (%HL)	12	60.3	70.1	65.2	0.33
Caud. peduncle wth (%HL)	12	31.0	35.5	33.6	0.12
P ₁ -P ₂ (%SL)	12	21.0	23.6	23.1	0.07
P ₂ -D ₂ (%SL)	12	30.8	35.3	32.9	0.12
D ₁ -A (%SL)	12	26.3	29.0	27.4	0.08
D ₂ -A (% SL)	12	23.6	25.5	24.2	0.07
Distribution					
Longitudinal scales	12	40	40		
Gill rakers (lower arch)	12	9	11	9 (1)	10 (6)
D ₂ rays	11	14	16	14 (1)	15 (8)
Anal rays	12	15	16	15 (3)	16 (9)
Vertebrae	12	39	41	22 + 18 (1)	21 ± 19 (7)
				21 + 18 (1)	20 + 19 (3)

dard length of 100 mm SL, is similar to *R. sikorae* in overall body shape, being rather robust with little belly curvature anteriorly and exhibiting a distinctly rounded dorsum. Greatest body depth tends to lie somewhat posterior to the vertical through the origin of the small pelvic fins. The broad-based second dorsal fin originates a little behind the vertical through the origin of the anal fin. The head is of moderate length with a relatively acute and narrow snout. The dorsal head profile is smoothly rounded and is not interrupted by the premaxillary pedicels as in *R. sikorae*. The lower jaw is somewhat prognathous and angled at about 15–20° to the horizontal when the mouth is closed. The mouth is large and the premaxilla and maxilla reach well beyond the vertical through the anterior margin of the orbit (fig. 18A).

Teeth: Upper and lower jaws bear 3–4 rows of small rather blunt-cusped conical teeth. There is no apparent differentiation between

inner and outer row teeth, which are not separated by a gap. Small tooth patches are present on the vomer, palatine, endopterygoid, and ectopterygoid bones of the suspensorium. Generally the teeth of *R. wrightae* are smaller and blunter than those of other *Rheocles* species.

Gill Rakers: 2 or 3 stout hypobranchial rakers and 7 or 8 elongate ceratobranchial rakers are arrayed along the lower limb of the first branchial arch.

Scales: The body is covered with large regularly imbricate cycloid scales. Predorsal scale counts range from 16 to 20 along the midline. All specimens examined have 40 longitudinal scales, and two scale rows separate the first and second dorsal fins. Dorsal, anal, and caudal fins lack scaly sheaths, and there is no axillary pelvic scale. As in *R. sikorae* the region from the rounded interpelvic scale to the prominent genital papilla is fully scaled.

Fins: The first dorsal bears a weak spine

and 4 or 5 soft rays. The long-based second dorsal bears a weak spine and 14 or 15 soft rays. The anal fin bears a weak spine and 15 or 16 soft rays. The second dorsal fin is somewhat falcate and the anal fin is markedly so. The pectoral fins are short and high set with a rounded outline when expanded. The caudal fin is strongly emarginate with forked lobes.

Osteology and Other Anatomical Features: Vertebral counts range from 39 to 41. The fourth and fifth hypurals of the caudal skeleton are separate.

The dorsal ramus of the urohyal bone is broad and dorsally expanded. There is no trace of an ethmomaxillary ligament in the upper jaw. The rostral cartilage is expansive and somewhat extruded beyond the premaxillary pedicel (fig. 22B).

The genital papilla is prominent and darkly pigmented on the free end in all specimens examined.

COLORATION: Unfortunately no data are available on the live coloration of this species. The following description is based on pigmentation patterns of preserved individuals.

The background color is pale yellow-brown with all scales on the dorsum being ringed in brown around the free edge. A dark wedge-shaped blotch is present on the operculum and the snout and dorsum are a dusky brown. A broad midline stripe is present along the posterior half to two-thirds of the body. One or occasionally two black spots overlie the lateral body stripe in some individuals. The first dorsal fin is dusky brown-black and the pale second dorsal is fringed with black as are the caudal and soft anal fins.

DISTRIBUTION (fig. 17, area 3): *Rheocles wrightae* is known from a single collection made in the Sandrangato River by M. Decary and donated to the Paris Museum in 1945. The Manambola and Sandrangato rivers are the same body of water: Sandrangato is applied to the river north of the town of Anosibe, and Manambola to the river south of that town. It would seem likely that *R. wrightae* and *R. sikorae* occurred in sympatry in this region. Unfortunately, however, it is highly probable that both *R. sikorae* and *R. wrightae* have succumbed to the pressures of regional deforestation and habitat degradation (see p. 21).

ETYMOLOGY: Named for Dr. Patricia Wright who has been so generous with her knowledge of the Madagascan rainforests and their fauna. It seems particularly appropriate that this species, so obviously threatened by habitat degradation, should be named for Pat, who has been unstinting in her efforts in the field of Madagascan rainforest management and conservation.

RELATIONSHIPS (fig. 27): The immediate relationships of *R. wrightae* lie with *R. sikorae* (see discussion on pp. 21–22), a species with which it appears to occur in sympatry.

Rheocles alaotrensis (Pellegrin, 1914)

Synonymy: *Atherina alaotrensis* Pellegrin, 1914a, Bull. Soc. Zool. Fr. 39: 46.

Rheocles alaotrensis, Jordan and Hubbs, 1919b, Stanf. Univ. Publ. 40: 20.

Citations: *Atherina alaotrensis*, Pellegrin, 1914b: 433. — Boulenger, 1916: 76. — Regan, 1920: 421. — Pellegrin, 1929: 46.

Rheocles alaotrensis, Pellegrin, 1929: 46; 1932: 293; 1933: 161, pl. 3, fig. 2; 1934: 429; 1937: 129. — Arnoult, 1959: 52, pl. 8, fig. 2. — Kiener, 1961: 41; 1963: 74, pl. 40. — Smith 1965: 631, pl. 102, fig. 2. — Moreau, 1979: 41. — Maugé, 1986: 278.

LECTOTYPE: MNHN 1913-333 Lac Alaotra, District d'Ambatondrazaka. Male 96 mm SL.

PARALECTOTYPES: MNHN 1913-327, 328, 329, 330, 331, 332 Lac Alaotra, District d'Ambatondrazaka. 102.1–44.5 mm SL. MNHN 1913-334 (six specimens) Lac Alaotra, District d'Ambatondrazaka.

VERNACULAR NAMES: Zono (riverine), Katrana (adult, Lake Alaotra), Antsiriva (juvenile, Lake Alaotra).

DIAGNOSIS: *Rheocles alaotrensis* is readily distinguishable from both *R. sikorae* and *R. wrightae* in lacking pigmentation of the genital papilla. *R. alaotrensis* differs from *R. pellegrini* in being fully scaled on the cheek and chest (scales lacking in *R. pellegrini*), and bearing 10–11 gill rakers on the lower limb of the first arch (7 in *pellegrini*). *Rheocles alaotrensis* is unique among *Rheocles* species in displaying a complete fusion of the fourth and fifth hypural elements of the caudal fin.

DESCRIPTION: Based on the lectotype, 4 paralectotypes, and 25 additional specimens. Morphometric measurements and meristic

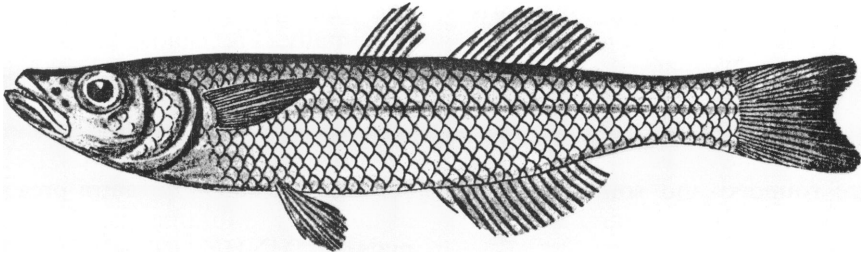


Fig. 24. Lateral view of a specimen of *Rheocles alaotrensis*. After Pellegrin, 1933.

counts are given in table 1. See also figures 24 and 25.

This species attains a standard length of up to 102 mm and is moderately deep-bodied, with strong belly curvature that is particularly marked in large lacustrine specimens (SL > 60 mm). The head and dorsum are more or less straight and the relatively short-based second dorsal fin originates a little behind the vertical through the origin of the anal fin.

The head is of moderate length and the relatively short snout is blunt and somewhat rounded anteriorly. The jaws are isognathous and the gape inclination is approximately 40° to the horizontal when the mouth is closed. The premaxilla and maxilla of the upper jaw are relatively short and only just reach the vertical through the anterior margin of the orbit (see fig. 18D).

Teeth: Both upper and lower jaws bear four to five rows of numerous small strongly recurved unicuspid teeth. In the lower jaw the anterior 8 to 10 outer row teeth are often slightly enlarged and procumbent. Small tooth patches are present on the vomer, palatine,

endopterygoid, and ectopterygoid bones of the suspensorium.

Gill Rakers: 2 or 3 stout hypobranchial rakers and 7 or 8 somewhat elongate ceratobranchial rakers are present on the lower limb of the first branchial arch.

Scales: The body is covered with large regularly imbricate cycloid scales. The predorsal scale count is somewhat variable and ranges from 14 to 18 scales along the dorsal midline. Longitudinal scale counts range from 34 to 36 scales. There are three scales separating the first and second dorsal fins. Dorsal, anal, and caudal scale sheaths, and an axillary pelvic scale are lacking. The region from the rounded interpelvic scale to the genital papilla and anus is scaleless (see fig. 20A). In large lacustrine specimens this naked region is more extensive than is the case in the smaller individuals from fluviatile biotopes.

Fins: The first dorsal fin bears a weak spine and three to five soft rays. The relatively short-based second dorsal fin also bears a weak spine followed by 10–12 soft rays. The anal fin bears a weak spine and 13–16 soft rays.

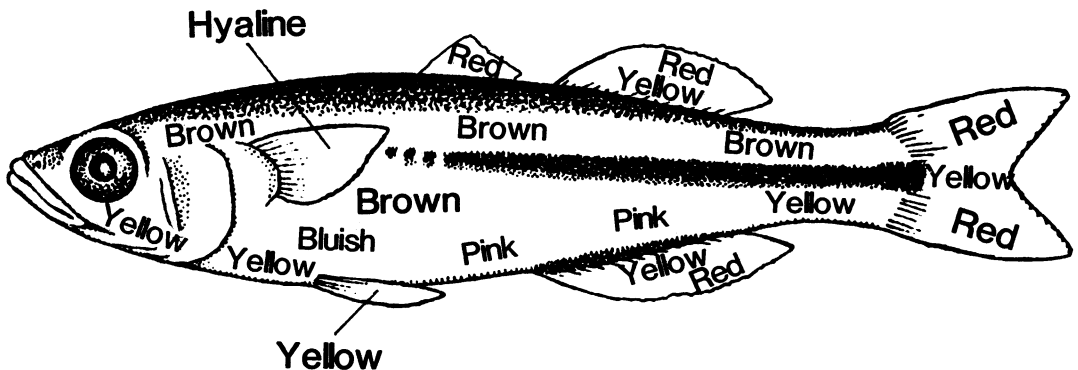


Fig. 25. Lateral view of a specimen of *Rheocles alaotrensis* with life colors indicated. Drawn by Patricia Wynn, from a photograph by Peter Reinthal.

The soft second dorsal and anal fins are distinctly rounded in outline with no sexual dimorphism evident. The pectoral fins are high set and short, the longest upper rays rarely reaching beyond the vertical from the origin of the pelvic fin. The distal margin of the pectorals are rounded and somewhat fan-shaped. The caudal fin is emarginate with rounded lobes.

Osteology and Other Anatomical Features: Vertebral counts are somewhat variable and range from 34 to 37. There is some differentiation between riverine and lacustrine populations with the former having modal vertebral counts of 34 and the latter with an elevated modal count of 36.

Rheocles alaotrensis is unique among betotiids in displaying a complete fusion of the fourth and fifth hypural elements of the caudal fin (fig. 11D); these elements are separate in other members of the clade (see fig. 11A, B, C). Interestingly, a similar fusion of hypural elements is common among melano-taeniids (Allen, 1980), and the New World menidiines (Chernoff, 1986b).

The dorsal ramus of the urohyal bone is simple and unexpanded (fig. 21B).

Rheocles alaotrensis retains a well-developed ethmomaxillary ligament (fig. 22A).

COLORATION: In his original description of the species Pellegrin (1914a: 47) made the following observations "La coloration est verdâtre sur le dos, jaune sur les côtés et le ventre. La ligne argentée latérale des Athérines est surtout visible dans la moitié postérieure du corps et n'occupe guère qu'une rangée longitudinale d'écailles. Les nageoires sont gris noirâtre, sauf les ventrales qui sont jaunes." This description differs little from that of Kiener (1961: 21) who added only that the fins are "rose-rouges." My own observations of live coloration in *R. alaotrensis* accord well with these descriptions, however some additional details may be added (see also fig. 25). The narrow black (rather than silvery) lateral band which is restricted to the posterior half of the body is thickened on the caudal peduncle, terminating in a broad wedge at the base of the caudal fin. The base of the anal fin bears a thin border of black pigmentation. Each body scale is ringed around its exposed posterior border with a fine black line. The eye, cheek, operculum, and anterior ventrum are flecked with silver. The dorsal

and anal fins are red distally and yellow proximally. The caudal fin is red along the distal portion of each lobe and bright yellow centrally. The pectoral and pelvic fins are hyaline.

ADDITIONAL MATERIAL: MNHN 1966-1074 (15) Rivière Analamazaotra pres station forestiere. S/P Moramanga, Province de Tamatave.: MNHN 1966-1075 (15) Rivière Ranomena, km 160 (Route Tananarive-Tamatave). S/P Moramanga, Province de Tamatave.: MNHN 1962-187 (6) Analamazaotra pres station Pisciculture.: MNHN 1934-275 (7) Ballia de la rivière Sahabe (sud du lac Alaotra) environ 800 m: MNHN 1934-276 (7) Ballia de la rivière Sahabe (sud du lac Alaotra) environ 800 m: MNHN 1932-28,29 (2) Lac Alaotra: MNHN 1919-10 (1) Lac Alaotra: MNHN 1913-334 (6) Lac Alaotra, District d'Ambatondrazaka: BMNH 1920.3.2:33-36 Lake Alaotra: AMNH 28135 (9) River Analamazaotra (Perinet region), District of Moramanga.: AMNH 88171 Small outflow stream from Lac Vert at Perinet (48°25'E, 18°56'S), altitude c. 950 m.: AMNH 88001 (38) Small stream 100 m east of Lac Vert, Perinet.

DISTRIBUTION (fig. 17, area 2): *Rheocles alaotrensis* is the most widespread of *Rheocles* species. Kiener (1961) and Maugé (1986) recorded the species as occurring in the fresh waters of central eastern Madagascar including Lake Alaotra, the upper Maningory River system, and Anjozorobe, in tributaries of the Betsiboka, on the west slope of Madagascar. The Betsiboka River catchment includes the eastern central plateau and the town of Anjozorobe (18°22'S, 47°52'E) is a central eastern locality, rather than western slope as stated by Maugé (1986).

Additional riverine populations are present in the forest reserve of Perinet (21°03'S, 51°20'E) in the Sahatandra and Analamazaotra tributaries of the Rianila River system.

The demise to extinction of the Alaotra populations has been well documented by Moreau (1979), and Reinthal and Stiassny (in rev.) discuss the further attrition of riverine populations due to the combined onslaught of deforestation and the introduction of exotic species. It seems probable that today *R. alaotrensis* is restricted to the protected waters of forest reserves, principally the small reserve of Perinet in the district of Moramanga.

TABLE 3
Rheocles alaotrensis (Pellegrin, 1914)

	N	min	max	m		SD	
Standard length	30	44.5	102.1				
PreD ₁ (%SL)	30	46.2	51.6	49.2		0.16	
PreD ₂ (%SL)	30	63.0	67.1	65.0		0.14	
Prealanal (%SL)	30	59.5	67.4	62.4		0.14	
Prepelv. (%SL)	30	41.4	48.3	43.5		0.18	
Abase (%SL)	30	18.6	23.2	21.2		0.12	
D ₂ base (%SL)	30	14.3	19.1	16.5		0.14	
Body depth (%SL)	30	22.2	27.4	24.7		0.16	
Head length (%SL)	30	26.4	30.8	28.6		0.12	
Snout length (%HL)	30	27.9	33.9	30.1		0.18	
Eye depth (%HL)	30	22.3	32.0	26.5		0.28	
Lower jaw length (%HL)	30	46.3	56.7	52.3		0.27	
Upper jaw length (%HL)	30	39.0	45.3	42.5		0.19	
Caud. peduncle lgth (%HL)	30	58.2	58.2	67.4		0.46	
Caud. peduncle wth (%HL)	30	32.6	40.9	36.4		0.28	
P ₁ -P ₂ (%SL)	30	18.0	22.0	20.6		0.12	
P ₂ -D ₂ (%SL)	30	31.5	39.5	34.4		0.20	
D ₁ -A (%SL)	30	23.2	27.5	25.7		0.14	
D ₂ -A (%SL)	30	19.6	25.9	22.8		0.17	
Distribution							
Longitudinal scales	30	30	36	30 (1) 35 (14)	31 (1) 36 (1)	33 (5)	34 (8)
Gill rakers (lower arch)	30	10	11	10 (10)	11 (20)		
D ₂ rays	30	10	12	10 (11)	11 (14)	12 (5)	
Anal rays	30	13	16	13 (3)	14 (18)	15 (8)	
Vertebrae	30	34	37	20 + 16 (1) 18 + 17 (14)	19 + 18 (3) 18 + 16 (2) 17 + 18 (1)	19 + 17 (3)	17 + 17 (6)

ETYMOLOGY: Named by Pellegrin presumably in reference to the locality in which specimens were first collected.

RELATIONSHIPS (fig. 27): The immediate relationships of *R. alaotrensis* lie with the little known northern species, *R. pellegrini*. Evidence supporting this alignment is found principally in the squamation characteristics of the two species. As has been noted above, *R. alaotrensis* is scaleless from the rounded interpelvic scale to the genital papilla and anus. This is also the case in *R. pellegrini*, where the cheek, chest, and dorsum anterior to the first dorsal fin origin are also naked (see p. 29). Both *R. sikorae* (fig. 20B) and *R. wrightae* are fully scaled, as are the related bedotiids and atherinids (see also Allen, 1980).

Allen (1980) illustrated the interpelvic region in *Melanotaenia* where a naked V-shaped enclosure is formed by a membranous at-

tachment between the innermost pelvic ray and the abdomen. In view of the number of derived features attesting to the monophyly of the bedotiid assemblage (p. 4), the loss of squamation associated with the interpelvic modification in melanotaeniids is best interpreted as an independent development to that exhibited in the *R. alaotrensis*-*R. pellegrini* pair.

Rheocles alaotrensis and *R. pellegrini* share further similarities in meristic features. Unfortunately, determining the polarity of meristic characters, particularly in the absence of clear disjuncts, is extremely problematical. However, a review of the distribution of meristic patterns among atherinoids and relevant outgroups does provide some indication as to the probable plesiomorphic configuration in basal atherinomorphs (see also White et al., 1984).

Both *R. alaotrensis* and *R. pellegrini* have

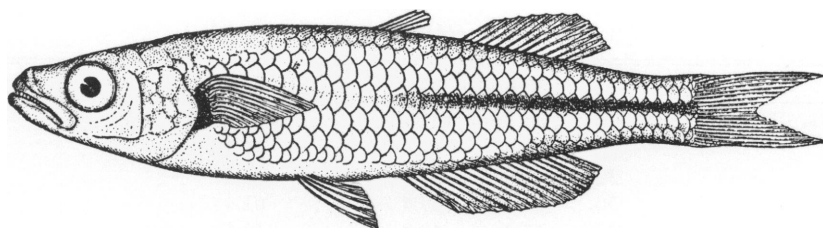


Fig. 26. Lateral view of the holotype of *Rheocles pellegrini* (AMNH 9696). After Nichols and LaMonte, 1931.

low fin ray numbers in the second dorsal fin (10–11), and as a result the fin base length is also relatively short. In *R. sikorae* and *R. wrightae* the second dorsal fins are longer and usually comprise 14–16 rays. Other bedotiids also have low second dorsal counts (10–13), as do the majority of melanotaeniids (Allen, 1980) and atherinid genera. Low second dorsal counts seem also to characterize mugiloids and the basal paracanthopterygian clades (Rosen and Patterson, 1969) whereas polymixoids have a single dorsal with numerous soft rays.

Although far from overwhelming, the evidence seems to favor an interpretation of a low second dorsal count as being primitive for atherinomorphs. As such, the occurrence of low counts in *R. alaotrensis* and *R. pellegrini* cannot reasonably be interpreted as further evidence of their sister-group relationship within *Rheocles*.

When compared with *R. sikorae* and *R. wrightae* (38–41) both *R. alaotrensis* and *R. pellegrini* are seen too have relatively low vertebral counts (34–37). Other bedotiids also have low vertebral numbers, with total counts falling within the *R. alaotrensis/pellegrini* range (Stiassny, unpubl.). Melanotaeniids tend also to have low vertebral counts with most in the 27–35 range, although the range for the family extends to 38 in the phylogenetically derived clades (Allen, 1980). Ranges for atherinids fall between 31 and 60 (e.g., Rosen, 1964) with counts of more than 38 commonly encountered (Allen, 1980). In potential atherinomorph outgroups, wide ranges are encountered. For example, among the various paracanthopterygian lineages total vertebral counts of 28–80+ are not uncommon, although the polymixoids and mugiloids tend, like the majority of percomorphs,

to have lower total counts of around 24–28. In the face of such variation I am loath to attempt to polarize the minor vertebral differences between the *R. alaotrensis/pellegrini* and *R. sikorae/wrightae* clades.

Rheocles pellegrini
(Nichols and LaMonte, 1931)

Synonymy: *Rheocloides pellegrini* Nichols and LaMonte, 1931, Am. Mus. Novitates 508: 1–2, fig. 1.

Citations: *Rheocloides pellegrini*, Pellegrin, 1933: 162, pl. 3; 1934: 429; 1937: 130. — Arnould, 1959: 51, pl. 8, fig. 3. — Kiener, 1963: 74, pl. 40. — Smith, 1965: 631, pl. 102, fig. 3. — Maugé, 1986: 278.

HOLOTYPE: AMNH 9696 “one day west” of Andapa, Madagascar. (Andapa = 14°39'S, 49°40'E). Male 68.0 mm SL.

PARATYPES: The original description is based on the holotype with comparative measurements of three syntopic specimens. Of those three paratypes, one is at the American Museum (AMNH 11699, SL 45.0 mm) and a second in the Paris Museum (MNHN 1932-24, SL 69.0 mm). I am unable to locate the third paratype.

DIAGNOSIS: *Rheocles pellegrini* is readily distinguished from its congeners by its reduced head and anterior body squamation. The cheek, head, and anterior dorsum to the origin of the first dorsal fin are naked, as is the chest and ventrum. The species also has the lowest gill raker count of the genus (6–7 rakers along the lower limb of the first branchial arch).

DESCRIPTION: Based on the holotype and a single paratype. Data on the two other paratypes is taken from Nichols and LaMonte (1931) and Pellegrin (1933). Morphometric

TABLE 4
Rheocles pellegrini (Nichols and LaMonte, 1931)

	N	min	max			
Standard length	2	44.0	67.8			
PreD ₁ (%SL)	2	44.1	52.8			
PreD ₂ (%SL)	2	65.3	66.4			
Prealanal (%SL)	2	58.3	64.8			
Prepelv. (%SL)	2	41.1	42.6			
A base (%SL)	2	17.7	26.1			
D ₂ base (%SL)	2	17.5	19.3			
Body depth (%SL)	2	22.3	23.0			
Head length (%SL)	2	27.7	30.5			
Snout length (%HL)	2	29.1	34.0			
Eye depth (%HL)	2	23.9	27.6			
Lower jaw length (%HL)	2	47.3	48.5			
Upper jaw length (%HL)	2	38.8	40.3			
Caud. peduncle lgth (%HL)	2	59.0	67.9			
Caud. peduncle wdth (%HL)	2	31.4	32.1			
P ₁ –P ₂ (%SL)	2	18.9	20.7			
P ₂ –D ₂ (%SL)	2	32.7	34.5			
D ₁ –A (%SL)	2	21.1	25.9			
D ₂ –A (%SL)	2	21.6	22.4			
				Distribution		
Longitudinal scales	4	33	36	33 (1)	35 (2)	36 (1)
Gill rakers (lower arch)	2	6	7			
D ₂ rays	4	12	12			
Anal rays	4	16	17	16 (1)	17 (3)	
Vertebrae	2	36	37	19 + 18 (1)	18 + 18 (1)	

measurements and meristic counts are given in table 4. See also figure 26.

The largest known specimen of *R. pellegrini* is 69 mm standard length. All individuals are relatively elongate, fusiform fishes not becoming very deep-bodied anteriorly and with little belly curvature. There is some dorsal body curvature and the relatively short-based second dorsal fin originates well behind the vertical through the origin of the anal fin.

The head is of moderate length, and the blunt rounded snout is short and broad. The dorsal head profile is interrupted by the premaxillary pedicel lending a rather pugnacious aspect to the fish. The jaws are isognathous and the gape inclination is about 20–30° to the horizontal when the mouth is closed. The premaxilla and maxilla of the upper jaw are relatively short and only reach the vertical through the anterior margin of the orbit (see fig. 18B).

Teeth: Both upper and lower jaws bear two

to three rows of robust strongly recurved unicuspid teeth. In both jaws the outer row teeth are larger than those of the inner one or two rows from which they are separated by a small gap. A clear differentiation between inner and outer row teeth is evident.

Pellegrin (1933) recorded the presence of teeth on the vomer and palatine; however, I am unable to confirm this observation with the material available to me.

Gill Rakers: 1 or 2 stout hypobranchial rakers and 5 elongate ceratobranchial rakers are widely spaced along the lower limb of the first branchial arch.

Scales: The posterior body is covered with moderately large, regularly imbricate cycloid scales. Longitudinal scale counts range between 36 (holotype) and 35–33 (paratypes). There are two scales separating the first and second dorsal fins. The cheek and head are naked, although a few scales are present on the operculum. The chest and ventrum are

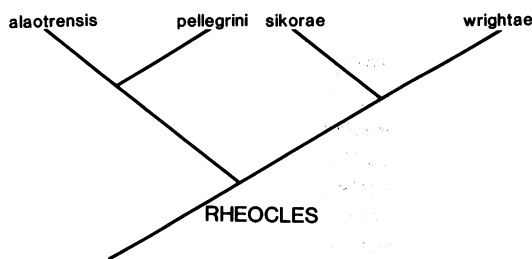


Fig. 27. Cladogram depicting the intrarelationships of *Rheocles*. Characters supporting the scheme are given in the text.

naked, as is the anterior dorsum to the region of the origin of the first dorsal fin.

Fins: The first dorsal fin bears a weak spine and four rays. The relatively short-based second dorsal also bears a weak spine followed by 12 soft rays (13 according to Nichols and LaMonte who apparently mistook the first spine for a ray). The anal fin bears a weak spine and 15–16 soft rays. The second soft dorsal and anal fins are rounded in outline and the pectorals are high set and short. The longest upper rays of the pectorals do not reach beyond the vertical through the origin of the small pelvic fins. The distal margin of the pectorals are rounded and the fin is fan-shaped when expanded. The caudal fin is strongly emarginate with forked lobes.

Osteology and Other Anatomical Features: Vertebral counts for the holotype and AMNH paratype are 19 + 18 (37) and 18 + 18 (36), respectively.

As judged from X-rays, the fourth and fifth hypurals of the caudal fin skeleton are separate.

The dorsal ramus of the urohyal is simple and unexpanded. *Rheocles pellegrini* retains a well-developed ethmomaxillary ligament.

COLORATION: In their original description Nichols and LaMonte (1931) had little to say about the coloration of *R. pellegrini*. They noted only “Color pale, a dark streak in the center of the side posteriorly. A dark blotch across the base of the pectoral; pectorals and ventrals pale, other fins more or less dusky.”

DISTRIBUTION (fig. 17, area 1): the single known locality for *R. pellegrini* is given by Nichols and LaMonte (1931) as being “one day west of Andapa.” The fish were collected by A. L. Rand and P. A. DuMont who were

participants in the “Archibold Expedition” to the island. Andapa is a small town in northeast Madagascar (14°39’S, 49°40’E) and a day’s trek west would, in all likelihood, have put Rand and DuMont in the region of the Ankavia River, a large eastern coastal drainage (Kiener, 1963).

ETYMOLOGY: Named by Nichols and LaMonte for Dr. Jacques Pellegrin of the Paris Museum.

RELATIONSHIPS (fig. 27): While noting the similarity with *Rheocles*, Nichols and LaMonte (1931) erected the genus *Rheocloides* for their new species. Although implicit, their rationale for this action was presumably the perceived “morphological gap” distancing *R. pellegrini* from other *Rheocles*; *R. pellegrini* is unique in its rather striking pattern of reduced squamation.

As discussed on page 27, *R. pellegrini* and *R. alaotrensis* are judged to be each other’s closest relatives. In view of this, the continued exclusion of *R. pellegrini* from *Rheocles* seems to serve little purpose and simply adds to the overabundance of monotypic Malagasy genera. For this reason I have opted to sink *Rheocloides* into synonymy with *Rheocles* rather than adopt the alternative option of trying to extend the definition of *Rheocloides* to include the less morphologically aberrant *R. alaotrensis*.

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