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THE CYPRINID DERMOSPHENOTIC AND
THE SUBFAMILY RASBORINAE

BY WILLIAM A. GOSLINE

The Cyprinidae, the largest family of fishes, do not lend themselves readily to subfamily classification (Sagemehl, 1891; Regan, 1911; Ramaswami, 1955b). Nevertheless, it is desirable to divide the family in some way, if only to facilitate investigation. Since Günther's (1868) basic review of the cyprinids the emphasis in classification has shifted from divisions that are readily differentiable to groupings intended to be more nearly phylogenetic. In the course of this change a subfamily classification has gradually been evolved. Among the most notable contributions to the development of present subfamily concepts are those of Berg (1912), Nikolsky (1954), and Banarescu (e.g. 1968a). The present paper is an attempt to clarify the nature and relationships of one cyprinid subfamily—the Rasborinae. (The group was termed Danioinae by Banarescu, 1968a. Nomenclaturally, Rasborina and Danionina were first used as "family group" names by Günther; to my knowledge the first authors to include both *Rasbora* and *Danio* in a single subfamily with a name based on one of these genera were Weber and de Beaufort, 1916, who used Rasborinae.)

In many cyprinids, as in most characins, the infraorbital bones form an interconnected series of laminar plates around the lower border of the eye, from the lacrimal in front to the dermosphenotic posterodorsally. This series bears the infraorbital sensory canal, which is usually continued into the cranium above the dermosphenotic. The infraorbital chain of laminar plates is generally anchored in position relative to the skull anteriorly and

posteriorly. The anterior membranous attachment between the lacrimal and the lateral ethmoid is not considered here.

Posteriorly, the infraorbital series is normally anchored in position relative to the skull by the dermosphenotic. In the Cyprinidae this bone varies greatly, giving rise to certain problems of identification. Sometimes it is represented by a large, laminar ossification, as in the characin *Brycon* (Pl. I, Fig. 1A) or in the cyprinid *Salmostoma* (Pl. I, Fig. 2A), and is easily recognized. However, time and again in cyprinids (see below) the laminar component of the dermosphenotic becomes reduced or disappears completely from around the tube bearing the sensory canal between the infraorbital bone below and the skull (Pl. I, Fig. 3). In *Rhinichthys*, at least, cleared and stained material indicates some ossification in the walls of this tube, which is therefore considered a dermosphenotic even though it has no lamellar component (see Lekander, 1949, for a discussion of lamellar and tubular ossification in sensory canal bones of cyprinids). A different question regarding dermosphenotic identification arises in *Aspius* (Pl. I, Fig. 3). Here, it is possible that a ventral lamellar dermosphenotic component has become fused with the infraorbital bone below. However, in the absence of good evidence for such a fusion in *Aspius* or elsewhere the dermosphenotic is here considered as restricted to the small tubular unit above the laminar infraorbitals.

The dermosphenotic may be held in position relative to the skull in a variety of ways all of which can apparently be traced back to a condition similar to that in the characin *Brycon*. Dorsally the large, laminar dermosphenotic of *Brycon* (Pl. I, Fig. 1A) is contiguous with the skull, to which it is movably attached by a strong membrane, and anterodorsally the dermosphenotic is in contact with the supraorbital bone, which also has a strong membranous attachment to the skull. In addition, the sphenotic "spine" of *Brycon* extends down around the posterior border of the orbit (Pl. I, Fig. 1B) with its external rim forming a firm prop against the lower surface of the two uppermost infraorbital bones. Since there is no membranous attachment between the sphenotic "spine" and the overlying infraorbital bones, it appears that these bones can swing outward away from the sphenotic "spine", which merely sets a limit to their medial movement.

In a few cyprinids, e.g., *Salmostoma bacaila* (Pl. I, Fig. 2), there is a multiple system of support for the large, laminar

dermosphenotic essentially similar to that of *Brycon*. However, in at least some, and generally most, members of all cyprinid lineages the laminar part of the dermosphenotic is reduced. The reduction follows two patterns. In the one, followed by all cyprinid groups except the rasborines, the tubular portion of the dermosphenotic carries the infraorbital canal to the lateral rim of the skull either between the frontal and the pterotic or farther posteriorly, but the laminar part of the dermosphenotic on either side of the tube undergoes reduction (Pl. I, Fig. 3). As a result, an unroofed area of musculature occurs anterodorsal to the tube, and the dermosphenotic usually loses its contact with the supraorbital bone. In all but a few of the rasborines examined, by contrast, a close association between the dermosphenotic and the supraorbital bone is maintained. This association, which depends on the retention of a large supraorbital bone that extends well back over the orbit, has several secondary results. First, any reduction in the laminar component of the dermosphenotic takes place from back to front (Pl. I, Fig. 4). Second, the association between the dermosphenotic and the supraorbital bone tends to "pull" the infraorbital canal forward, so that it often enters the skull ahead of the frontal-pterotic junction. Finally, there is no unroofed musculature anterodorsal to the dermosphenotic in rasborines. (For an exception to these statements, see below.)

Certain aspects of variation in the dermosphenotic and associated structures in non-rasborine cyprinids are discussed first. When, among these, contact between the dermosphenotic and supraorbital bone is lost the supraorbital bone itself is frequently displaced anteriorly, reduced, or absent. Among the Cyprininae the only genera that I have seen in which such a contact is retained are *Squaliobarbus* and *Barbus*, and the usual non-rasborine sequence of dermosphenotic reduction seems to be well represented within the latter genus. In *B. bampurensis* the large, laminar dermosphenotic has a slight anterodorsal contact with the supraorbital. In *B. orphoides* there is also a large, laminar dermosphenotic, but all contact between it and the supraorbital has been lost. In this stage, frequent among cyprinines, the supraorbital may be reduced to a small plate over the anterior part of the orbit, as in *Carassius*. In *Barbus gonionotus* the laminar component of the dermosphenotic is present but reduced. Finally, in *B. schwanefeldi* the only dermosphenotic lamina is a small basal element attached by

membrane to the outer rim of the frontal anterodorsal to it. The infraorbital canal passes through this basal element, thence upward and backward across musculature in a tube to a point of entry into the lateral rim of the skull between the frontal and pterotic. In both *B. gonionotus* and *B. schwanefeldi* reduction of the dermosphenotic leaves an unroofed area of musculature anterodorsal to it.

A series of dermosphenotic reductions essentially similar to those of *Barbus* can be traced in other non-rasborine cyprinid groups. Also of widespread occurrence is a further stage in which there is no laminar dermosphenotic at all but merely a tube bearing the infraorbital canal between the lower parts of the infraorbital series of bones and the skull. In many cyprinids, e.g., in *Aspius* (Pl. I, Fig. 3), the infraorbital bone below the dermosphenotic remains laminar and has a ligamentous attachment between its anterior border and the outer rim of the frontal or supraorbital bone anterodorsal to it. But in some cyprinids, represented by such varied forms as *Macrochirichthys* and *Rhinichthys*, the whole infraorbital series behind the lacrimal is represented primarily or entirely by tubular units without particular attachment to the skull.

The relationship between the dermosphenotic and the skull is also affected by the configuration of two muscles, the *M. dilatator operculi* and the *M. levator arcus palatini* (muscle names follow Winterbottom, 1974).

Contraction of the *M. dilatator operculi*, as its name suggests, moves the posterior part of the operculum outward, expanding the gill cavity. In cyprinids, as in *Brycon* (Pl. I, Fig. 1B), this muscle inserts on the anterior rim of the upper end of the opercle and passes anterodorsally to an origin on the lateral wall of the cranium (Takahasi, 1925). The increased importance of this muscle in cyprinids, as compared to characins, is suggested by the development in the Cyprinidae of an anterodorsal process of the opercle for the insertion of the *M. dilatator operculi* that extends forward across, and generally includes, the preopercular lateralis canal (Pl. I, Figs. 2-4; see also Ramaswami, 1955a, b; Gosline, 1974).

In the relatively few cyprinids in which the dermosphenotic forms a large plate in broad contact with the cranium above, e.g., *Salmostoma* (Pl. I, Fig. 2A), *Cyprinus* (Tretiakov, 1946), the *M. dilatator operculi* is completely roofed. Under such circumstances the area of origin of the muscle may be expanded in

various ways, as was noted by Sagemehl (1891). Generally, however, in non-rasborine cyprinids the *M. dilatator operculi* extends anterodorsally between the dermosphenotic and the cranium to an unroofed origin on the dorsal surface of the skull.

The *M. levator arcus palatini* in *Brycon* has its origin on the lower border of the posterior surface of the sphenotic "spine" (Pl. I, Fig. 1B). A few cyprinids with small, high-set eyes, e.g., *Osteochilus*, *Hemibarbus*, *Gobio*, show this same arrangement. However, in most cyprinids the sphenotic extends more posteriorly than in *Brycon*. In some, for example *Salmostoma* (Pl. I, Fig. 2B), the sphenotic slants posteroventrally, and the *M. levator arcus palatini* originates in part on its anteroventral surface, thus separating the sphenotic from the orbital cavity. More commonly the sphenotic extends horizontally back from the posteroventral end of the frontal, with the origin of the *M. levator arcus palatini* on its ventral surface, often in a cavity as in many leuciscine cyprinids. In the forms discussed above the sphenotic usually forms a prop under the dermosphenotic base. In various large-mouthed cyprinids the area of origin of the *M. levator arcus palatini* may be expanded in either of two ways. In *Zacco* and more notably in *Opsariichthys* part of the *M. levator arcus palatini* extends up anterior to the sphenotic to an origin on the orbital roof. More commonly, for example in such varied cyprinids as *Aspius* (Pl. I, Fig. 3), *Macrochirichthys*, and a number of rasborines (see below), the *M. levator arcus palatini* extends up over the lateral rim of the sphenotic, separating that bone from the dermosphenotic.

The rasborine genera upon one or more members of which the following comments are based are *Aspidoparia*, *Barilius*, *Brachydanio*, *Chela*, *Chelaethiops*, *Danio*, *Engraulicypris*, *Esomus*, *Leptobarbus*, *Luciosoma*, *Nematabramis*, and *Rasbora*. Brittan (1954) revised the species of *Rasbora*, Silas (1958) and Banarescu (1968b) the species of *Chela*, and Banarescu (1971) those of *Nematabramis*. Sagemehl (1891) commented on the systematic position of *Leptobarbus*, and Ramaswami (1955b) has illustrated the head skeletons of *Rasbora caverii* and *Esomus barbatus*.

A number of rasborine genera resemble the cultrine genus *Salmostoma* (see below) in having large plate-like dermosphenotics closely bordered by the cranium above and the supra-orbital bone anteriorly. However, all of them differ from *Salmostoma* in one or both of two ways. In *Aspidoparia*, *Danio*,

Esomus (Ramaswami, 1955b, Fig. 3), and some species of *Rasbora* (Pl. I, Fig. 4) the infraorbital canal passes into the frontal bone, rather than to its usual entry point into the skull between the frontal and the pterotic. In *Aspidoparia*, *Barilius*, *Brachydanio*, *Chela*, *Chelaethiops*, *Engraulicypris*, *Leptobarbus*, and *Luciosoma* the M. levator arcus palatini extends upward over the outer rim of the sphenotic separating that bone from the dermosphenotic.

Particularly in the genus *Rasbora* the dermosphenotic undergoes considerable reduction. In the relatively large species *R. dusonensis* (Pl. I, Fig. 4), *R. lateristriata*, and *R. myersi* a small laminar component of the dermosphenotic is retained which is in contact with the supraorbital bone as usual in rasborines. In *R. lateristriata* the infraorbital canal passes upward into the skull between the frontal and pterotic in normal cyprinid fashion, but in *R. myersi* (as in *R. caverii*, see Ramaswami, 1955b, Fig. 2) it enters the frontal. In the small species *R. trilineata* the "dermosphenotic" is reduced to a simple membranous tube without particular attachment that carries the infraorbital canal across musculature to the skull between the frontal and the pterotic. Thus, the "dermosphenotic" of *R. trilineata* appears to have lost its rasborine characteristics and is no longer distinguishable from the reduced condition that occurs in many other cyprinid lineages.

In summary, the dermosphenotic appears to be a very useful diagnostic character for separating most rasborines from all but a few other cyprinid fishes. It breaks down, however, in two areas. First, there are some non-rasborine cyprinids, e.g., *Salmostoma*, that have a large laminar dermosphenotic in contact with the supraorbital bone that is typical of rasborines. Second, there is at least one small rasborine, *Rasbora trilineata*, with a dermosphenotic so reduced as to have apparently lost its rasborine traits.

It may be that a dermosphenotic-supraorbital contiguity is an ancient character inherited from the ancestral stock that gave rise to both characins and cyprinids. If so, most other cyprinids have lost it, but its retention in the various members of the group here called Rasborinae is no guarantee of their close interrelationship.

There is, however, another and well-known feature held in common by most rasborines that is quite clearly a specialization. As in so many cyprinids the lateral line dips low along the anterior part of the body, but in rasborines, unlike other groups, it

continues along the lower half of the caudal peduncle to the base of the tail. As a diagnostic feature separating the Rasborinae from other cyprinids, this character again breaks down at a few points. First, there are some small rasborines, notably in the genus *Rasbora*, in which the lateral line is incomplete, ending in front of the caudal peduncle. Second, Day (1876-1878, p. 588) stated that in some species of the rasborine genus *Barilius* the lateral line is on the middle of the caudal peduncle. Finally, there are some non-rasborine genera, e.g., *Salmostoma*, in which the lateral line may fail to swing back up to the midline of the caudal peduncle, even posteriorly.

Because of the dermosphenotic and lateral-line features discussed above, the Rasborinae as treated here appear to be a relatively well-marked and, in my opinion, monophyletic group. It is also, however, a very diverse and presumably old group. Its diversity results in a resemblance between certain rasborines and members of other cyprinid subfamilies. The most difficult problems of rasborine overlap lie in the Cultrinae and Cyprinae.

That both the Rasborinae and Cultrinae are basically midwater groups (the term midwater is broadly interpreted here to include the pelagic and/or surface-feeding forms of Brittan, 1961), contrasting in this respect with the more benthic Cyprinae and Gobioninae, is indicated by a number of morphological features, e.g., the low lateral line on the body and the relatively posterior dorsal position. As with other basically midwater groups, e.g., the Leuciscinae, some members of both the Rasborinae and Cultrinae have developed cultrate abdomens, some are long-jawed and probably predaceous, and some have up-turned mouths and other features presumably associated with feeding at or very near the surface of the water.

Most members of the Rasborinae and Cultrinae are readily separable, but considerable confusion between the two subfamilies occurs in the area of the old composite genus "*Chela*". Among its components the forms now assigned to *Salmostoma* (type species *S. bacaila*, see Banareescu, 1968c), *Pseudoxygaster* (monotypic, Banareescu, 1967) and *Oxygaster* (type species, *O. anomalus*, see Smith, 1945) seem to belong to the Cultrinae, whereas *Chela* sensu stricto (type species, *C. cachias*, see Smith, 1945) appears to be a rasborine genus. The following discussion concentrates on distinguishing between the rasborine and cultrine members of this complex. The main differences I can find have to do with either head shape or squamation.

The rasborines have a barrel-shaped head that is flattened

above, as is the dorsal surface of the nape region, however compressed the body may be. In the Cultrinae the head is more compressed and narrowly vaulted above, as is the nape. Though I can find no way of expressing these differences directly, they seem to be associated with a number of specializations that occur in one group but not the other.

In the Cultrinae, but not the Rasborinae, the high muscular vaulting of the nape region frequently works forward over the skull to between the eyes, as in *Pseudoxygaster*, *Oxygaster*, and *Macrochirichthys*. In contrast, the flattened head and nape region of the rasborines appears to be associated with a type of specialization that does not occur in the Cultrinae and seems to have to do with feeding very close to the water surface. In addition to the straight dorsal profile, two peculiarities may be involved. In *Chela laubuca* and *Danio devario* the small upwardly-directed mouth has premaxillaries with ascending processes that become laterally expanded above their bases (Pl. I, Fig. 5). (I have not seen ascending premaxillary processes of this shape elsewhere among the Cyprinidae.) Second, in *Chela laubuca* the anterior part of the supraorbital sensory canal and its first four pores are greatly expanded, and in *Brachydanio albolineatus* and *Nematabramis alestes* the whole supraorbital canal is enlarged and cavernous. In the Cultrinae, as in most rasborines, the supraorbital canal is normally developed.

The relatively compressed head of the Cultrinae appears to be associated with an osteological feature that occurs in some members of that group but is very rare elsewhere among cyprinids. In *Salmostoma bacaila*, *Paralaubuca harmandi* and *P. riveroi* (but not in *P. typus* or *P. barroni*), and in *Macrochirichthys macrochirus* there is an opening in the suspensorium bordered above by the metapterygoid and below by the symplectic (personal observations). This type of opening, reported by Regan (1911) for "*Chela*" and *Opsariichthys*, is also recorded from *Zacco* (Greenwood, et al., 1966) but is not known elsewhere among cyprinids, though it occurs in certain clupeids (Gosline, 1973), cobitids (Ramaswami, 1953), and most characins (see, for example, Weitzman, 1963). Gosline (1973) suggested that in characins and cyprinids this suspensorial opening provides additional space for contraction of the M. adductor mandibulae in strong-jawed forms, but its occurrence in only certain long-jawed cyprinids indicates that some additional feature is involved.

In *Opsariichthys*, which has by far the largest opening of this sort among cyprinids and which, like *Salmostoma*, *Paralaubuca*, and *Macrochirichthys*, has a high, compressed head and large jaws, the M. adductor mandibulae passes directly over this opening in the suspensorium (Takahasi, 1925). If this muscle is removed, an expanded part of the hyoid bar immediately internal to this opening becomes visible (Pl. I, Fig. 6). Presumably, the suspensorial opening provides additional space for vertical movement of the hyoid bar internally as well as for contraction of the M. adductor mandibulae externally. Such space requirements are probably more acute in strong-jawed fishes with compressed heads like the Cultrinae than in long-jawed barrel-headed forms like the rasborine *Luciosoma* where no such opening occurs.

Two final differences between the Rasborinae and the Cultrinae that are very striking, at least in the species available to me, have to do with squamation. The scales of the Cultrinae are moderate to small with the apical radii (Chu, 1935) moderately developed or absent. In the Rasborinae the scales are moderate or large with the apical radii well-developed. In the Rasborinae there is a definite middorsal line of scales behind the head; in the Cultrinae the scales along the middorsal line of the back are in more or less indefinite series.

To conclude concerning the resemblances between the Rasborinae and Cultrinae in the *Chela-Salmostoma* area, I am of the opinion that they are the result of convergence, perhaps combined with the retention of an ancestral type of dermosphenotic.

On the other hand there are similarities between the Rasborinae and Cyprininae that suggest to me a real phylogenetic relationship. Barrel-shaped heads and large scales are typical of both rasborines and cyprinines. A shared character that is unique to some members of both of these subfamilies is the presence of two well-separated barbels on each maxillary; the so-called rostral barbel does not occur elsewhere in the Cyprinidae. Finally, one rasborine genus, *Leptobarbus*, shows a mosaic of rasborine and cyprinine characters and has, indeed, usually been placed in the Cyprininae, e.g., by Smith (1945).

The Rasborinae, as here understood, appear to be a midwater ecological counterpart to the related, more benthic Cyprininae. Their morphological diversity suggests that the rasborines are an old group. Geographically, the rasborines are represented along the whole southern border of the Old World cyprinid distributional area from the Philippines to southern Africa, though two

cyprinine genera extend slightly farther south than the rasborines in Africa (Jubb, 1967). Rasborines and cyprinines occur together along this southern border; in the Philippines at one end of the range and in central and southern Africa at the other they are the only cyprinids present. Both subfamilies have their present center of diversification in Southeast Asia. Unlike the Cyprininae, however, the Rasborinae do not seem to occur in China or Europe.

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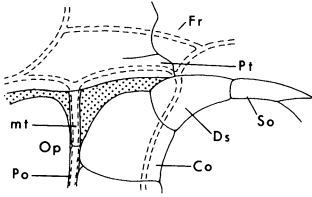
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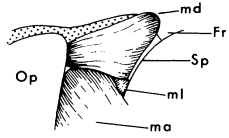
FIG. 1. A, Semidiagrammatic representation of the dermosphenotic area of *Brycon guatemalensis* to show bones and lateral-line canals (indicated by dashes where they pass within ossifications). Only the border between the frontal and the pterotic is shown among the cranial bones. B, Same view as A with the dermosphenotic and infraorbital bones removed to show the underlying musculature and the sphenotic "spine". FIG. 2. A, Structures of *Salmostoma bacaila* as in Figure 1A. B, Structures as in Figure 1B. FIG. 3. The dermosphenotic and associated structures in *Aspius aspius*. The flesh has been removed from the non-bony areas to show the underlying musculature. FIG. 4. The dermosphenotic and associated structures in *Rasbora dusonensis*. The flesh has been removed as in Figure 3. FIG. 5. The premaxillaries of *Danio devario*, from above. FIG. 6. The opening in the suspensorium of *Opsariichthys uncirostris* in relation to the underlying hyoid bar, lateral view of right side. Abbreviations used in the Figures: ap, ascending process of the premaxillary; Co, fifth infraorbital bone; Ds, dermosphenotic; Fr, frontal; hb, hyoid bar; Hm, hyomandibular; ic, infraorbital canal; ma, M. adductor mandibulae; md, M. dilatator operculi; Me, metapterygoid; ml, M. levator arcus palatini; mt, membranous tube; Op, opercle; os, opening in the suspensorium; pc, preopercular canal in the opercle; Po, preopercle; Pt, pterotic; Qu, quadrate; sc, supraorbital canal; So, supraorbital bone; Sp, sphenotic "spine"; and Sy, symplectic.

PLATE I

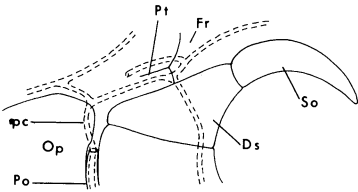
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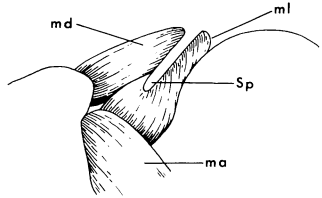
1B



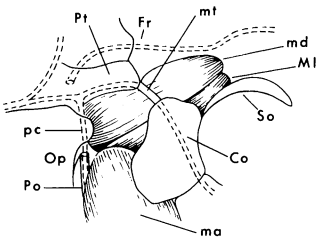
2A



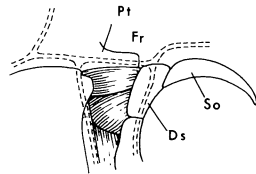
2B



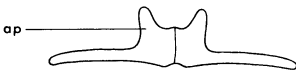
3



4



5



6

