SENSORY HEAD PORES AND CANALS IN GOODEID FISHES

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Goodeids comprise a family of about 35 species of livebearing cyprinodont fishes largely autochthonous to the central highlands of México. The last family revision (Hubbs and Turner, 1939) was based mostly on reproductive features of females and embryos. These features emphasize the monophyletic origin of the family but are sometimes too variable to be reliable as a single source of information in characterizing species and developing a natural or phylogenetic family classification (Mendoza, 1965; Miller and Fitzsimons, 1971; Fitzsimons, 1972, 1979). More recently, taxonomic and evolutionary studies in the family have drawn information from several sources; in addition to "conventional" morphology, these sources include behavior (Fitzsimons, 1972, 1976; Kingston, 1979), biochemistry (Turner et al., 1980; Turner and Grosse, 1980), karyology (Miller and Fitzsimons, 1971; Uyeno and Miller, 1972; Fitzsimons, 1972, 1974; Smith and Miller, 1980), and fossils (Alvarez and Arreola, 1972; Smith et al., 1975; Smith, 1980, 1981). Although several papers have used features of the cephalic sensory canal system of goodeids as taxonomic characters, only the report by Gosline (1949) compared several genera and assessed the use of canal-system characters in the classification of the family. As part of a broad analysis of sensory canals in cyprinodont fishes, Gosline examined supraorbital canal patterns in 17 species representing 14 genera of goodeids. My report augments Gosline's study by including information on dorsal head pores for each of the family's currently recognized 35 species and 17 genera. In addition, counts are included for the preorbital (lachrymal), preopercular, and mandibular series. Taxonomic and evolutionary implications of cephalic sensory canal data are considered.

MATERIALS AND METHODS

Preserved specimens were examined from 74 collections at the University of Michigan Museum of Zoology and the Louisiana State University Museum of Zoology. The numbers of head pores and patterns of canals connecting them were studied by dipping the fish's head in liquid and directing a jet of air to the set of pores being observed through a microscope. Young adults were best for study. In small fishes, the canals were often partially or entirely open, making it impossible to determine the number of pores that would be present in the adult. In large fishes, the pores were sometimes very small or completely closed, and canal patterns were not always visible under the thicker tissue and heavier pigmentation. The numbering of dorsal head pores and classification of canal types (Fig. 1) follows Gosline's scheme (1949).

RESULTS AND DISCUSSION

The supraorbital canal system of most goodeids has nine or 10 pores with one or more discontinuities in the canal connecting them (Fig. 1, Table 1). Large portions of the canal are missing in three genera (all three species in *Neoophorus* Hubbs and Turner, both species of *Allotoca* H & T, and, occasionally, in one species of *Allodontichthys* H & T), while dorsal head pores and canals are entirely lacking in another three genera (*Girardinichthys* Bleeker, *Hubbsina* de Buen, and *Skiffia* Meek). However, with a single exception (*Ilyodon* Eigenmann), the supraorbital canal patterns of each goodeid genus are assignable to only one of the three canal system groups described by Gosline. In Group I (seen only in *Ilyodon*), the supraorbital canal is continuous between the second and third pores (Fig. 1). In Group II (14 genera), the canal is interrupted between the second and third pores (2a and 2b), and, in Group III (three genera), the canals are replaced by pit organs. Second and third breaks in the dorsal canal are frequent among Group II genera. The additional disruptions persist in adults of a few species but are gradually lost in others. A second break in the canal is common between the fifth and sixth pores (4a and 4b) of 10 genera and, occasionally, between the sixth and seventh (5a and 5b) of one genus (*Alloophorus* H & T). A third break between the eighth and ninth pores (6a and 6b) occurs in young adults of *Ameca* Miller and Fitzsimons and *Xenotoca* H & T but usually disappears with growth. No similar ontogenetic change occurs in Group III genera in which the supraorbital canal is replaced entirely by pit organs; no dorsal canals develop in even the oldest animals. Members of the same species from different localities

TYPE I   TYPE II
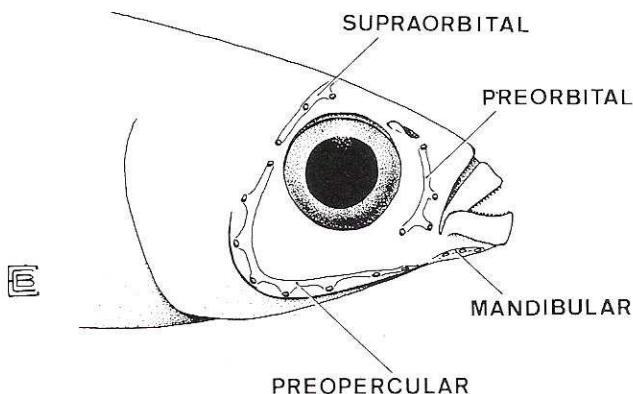
SUPRAORBITAL

PREORBITAL

MANDIBULAR

PREOPERCULAR
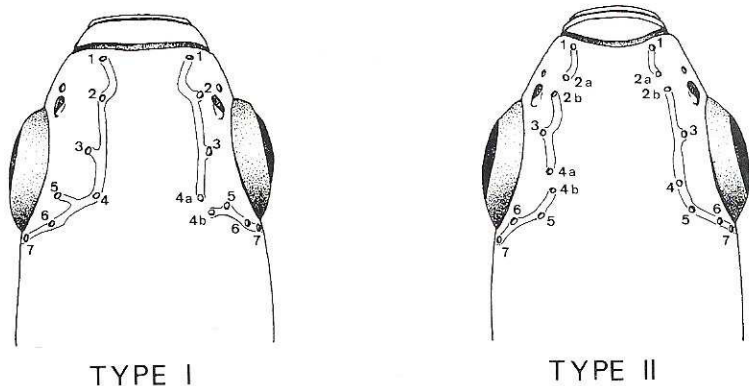
FIGURE 1. Diagrammatic Representation of Sensory Head Pores and Canals in Goodeid Fishes

and habitats showed the same number and arrangement of pores and canals.

With a single exception (re mandibular pores in *Allotoca maculata* Smith and Miller), adults of the species with Group I and II supraorbital canal patterns have well-developed canals with pores in the mandibular, preorbital, and preopercular series. Again with one exception, i.e., preorbital and preopercular pores in *Skiffia bilineata* (Bean), fishes in Group III lack the lateral and ventral cephalic canal series as well as those on top of the head.

Representing both Group I and II, members of the genus *Ilyodon* are uniquely variable among goodeid fishes in having two types of dorsal canal patterns; the species are also distinctive in having identical complements of mandibular, preorbital, and preopercular pores. Although Gosline recorded only the Group I supraorbital pattern for *Balsadichthys xantusi* H & T (*Balsadichthys = Ilyodon* according to Miller and Fitzsimons, 1971) and *Ilyodon furcidens* (Jordan and Gilbert), Kingston's extensive data (1979) on this genus and my fewer observations indicate characteristics of both Group I and II canal system types for the three described species of *Ilyodon* and an undescribed form from Jalisco.

Goodeids assignable to Group II may be segregated artificially into 10 subdivisions based on supraorbital canal patterns and predominant numbers of mandibular, preorbital, and preopercular pores without regard to whether similarities are primitive or derived (Table 1).

Goodea Jordan, *Alloophorus, Neoophorus,* and *Allotoca* are easily separable from other Group II genera. The three species of *Goodea* are practically identical in the configuration of the cephalic sensory canals and pores with the low number of mandibular pores being diagnostic for the genus. Each species in *Goodea* is less variable in head-pore characters than is any other species in Group II. The monotypic *Alloophorus* appears intermediate between *Xenotoca variata* (Bean) and *X. melanosoma* Fitzsimons, but the combination of high numbers of mandibular and preopercular pores and the usual single break in the supraorbital system of adults distinguishes these fish from other goodeids. In adults of *Neoophorus* and *Allotoca* a section of the supraorbital canal is lacking (site of pores 3b-6 and 2b-6 respectively). The nature of the dorsal canal and numbers of lateral and ventral head pores collectively distinguish *Neoophorus* and *Allotoca* from other goodeid genera. Species-specific differences, not apparent in *Neoophorus,* are marked in *Allotoca. Allotoca maculata* differs from *A. dugesi* (Bean) in having lower numbers of preorbital and preopercular pores and in lacking mandibular pores (Smith and Miller, 1980); the predominant sensory-pore complement for either species is diagnostic among family members. Gosline listed *Allotoca vivipara* de Buen, now referable to *A. dugesi* according to Smith and Miller (1980), in Group II but did not indicate that a portion of the dorsal canal was degenerate.

Ameca, Chapalichthys Meek, *Xenoophorus* H & T, and *Zoogoneticus* Meek are arbitrarily separated from *Allodontichthys, Characodon* Günther, *Xenotaenia* Turner, and *Ilyodon* by having an additional pore in the preopercular series. *Chapalichthys encaustus* (Jordan and Snyder) and *C. pardalis* Alvarez are indistinguishable in head-pore characters. Data for

Xenoophorus captivus (Hubbs) include information for populations formerly recognized as *X. erro* H & T and *X. exsul* H & T (Fitzsimons, 1979). Gosline's decision to retain *Allodontichthys zonistius* (Hubbs) in Group II in spite of partial degeneration of the supraorbital canal is supported by additional data for this species and its congeners. In *A. zonistius,* an absence of the canal between the third and fifth pores (2b-4a) is usually restricted to smaller fish (less than about 40 mm SL); the lack of a portion of the canal was not observed in *A. hubbsi* Miller and Uyeno or *A. tamazulae* Turner. *A. hubbsi* is dissimilar to its close relatives in having three, rather than four, sensory pores on each side of the lower jaw (Miller and Uyeno, 1980).

In head-pore features *Xenotoca eiseni* Rutter more closely resembles *Ataeniobius toweri* (Meek) than its congeners, *X. variata* (Bean) and *X. melanosoma*. In these characters, the difference between *X. eiseni* and *X. melanosoma* is greater than that seen between other congeners in Group II, yet these species are sufficiently genetically similar that they can produce viable hybrids in forced or no-choice laboratory crosses where only a heterospecific mate is available (Fitzsimons, 1972); *eiseni-melanosoma* hybrids are intermediate between parental types in numbers of preopercular and mandibular pores (Fitzsimons, 1974).

Comprising Group III, *Girardinichthys, Hubbsina,* and *Skiffia* differ from other goodeids as they lack canals and pores in the supraorbital series. *Skiffia bilineata* has from 0 to 2 preorbital, 0 to 8 preopercular, and 0 mandibular pores, but the predominant condition in this species, as in other species of Group III, is the complete loss of canals and sensory head pores.

EVOLUTIONARY AND TAXONOMIC IMPLICATIONS

The presence of well-developed sensory canals on the head of goodeids is assumed to represent the primitive condition. This condition is the predominant one in the Goodeidae (about 80 percent of 35 species) and in four other families of cyprinodont fishes (also about 80 percent of 31 species representing 30 genera; Gosline, 1949). Again on the basis of relative frequency, the Group II supraorbital canal system (canal discontinuous between the second and third pores), occurring in over two-thirds of the family, is regarded as ancestral to Group I (one genus, canal continuous between the second and third pores) and Group III (three genera, supraorbital canal and pores replaced by pit organs). The predominant condition in goodeids in which two breaks (2a-2b and 4a-4b) occur

Table 1. SENSORY HEAD PORES AND CANALS IN GOODEID FISHES. Brackets [ ] indicate missing pores and canals; parentheses ( ) indicate means. Species are listed according to supraorbital canal group (Gosline, 1949) and similarities in pore numbers.

Species	Number of specimens	Standard length, mm	Supraorbital Canal System group	predominant patterns	Predominant and Mean Number of Pores mandib.	preorb.	preop.	Source
Ilyodon furcidens	50	24-68	I II	1-4a 4b-7 1-2a 2b-4a 4b-7	3(3.0)	4(4.0)	7(7.0)	1, 2, 3
I. whitei	178	13-83	II II I	1-2a 2b-4a 4b-7 1-2a 2b-7 1-4a 4b-7	3(3.0)	4(4.0)	7(7.1)	1, 3
I. xantusi	170	25-88	II I II	1-2a 2b-7 1-7 1-2a 2b-4a 4b-7	3(3.0)	4(4.0)	7(7.0)	1, 2, 3
I. sp.	40	12-67	I I II	1-7 1-4a 4b-7 1-2a 2b-4a 4b-7	3(3.0)	4(3.8)	7(7.0)	1, 3
Ameca splendens	32	17-69	II II	1-2a 2b-4a 4b-7 1-2a 2b-4a 4b-6a 6b-7	4(3.7)	4(4.0)	8(8.0)	1, 4
Chapalichthys encaustus	40	23-55	II II	1-2a 2b-4a 4b-7 1-2a 2b-7	4(4.0)	4(4.0)	8(8.2)	1, 2
C. pardalis	35	45-60	II	1-2a 2b-4a 4b-7	4(4.0)	4(4.0)	8(8.4)	1
Xenoophorus captivus	191	15-49	II II	1-2a 2b-4a 4b-7 1-2a 2b-7	4(4.0)	4(3.6)	8(8.4)	2, 5
Zoogoneticus quitzeoensis	40	16-52	II	1-2a 2b-4a 4b-7	3-4(3.0)	4(3.8)	8-9(8.5)	1, 2
Allodontichthys hubbsi	30		II	1-2a 2b-7	3(3.0)	4(4.0)	7(7.0)	6
A. tamazulae	8	22-49	II	1-2a 2b-7	4(4.0)	4(3.9)	7(6.9)	1
A. zonistius	12	29-48	II II	1-2a 2b-7 1-2a [2b-4a] 4b-7	4(4.0)	4(4.0)	7(7.0)	1, 2
A. sp.	18	24-50	II	1-2a 2b-7	4(4.0)	4(4.0)	7(6.9)	1
Characodon lateralis	127	23-38	II II	1-2a 2b-7 1-2a 2b-4a 4b-7	4(4.0)	4(4.0)	7(7.0)	1, 2, 7
Xenotaenia resolanae	6	50-73	II	1-2a 2b-4a 4b-7	4(4.0)	4(4.0)	7(6.8)	1, 2

	Species	N	Range		Formula				Ref.
✓	*Goodea atripinnis*	20	13-92	II	1-2a 2b-4a 4b-7	2(2.2)	4(4.0)	8(8.1)	1
✓	*G. gracilis*	5	13-47	II	1-2a 2b-4a 4b-7	2(2.0)	4(4.0)	8(8.0)	1
✓	*G. luitpoldi*	18	18-96	II II	1-2a 2b-4a 4b-7 1-2a 2b-7	2(2.0)	4(4.0)	8(8.0)	1, 2
✓	*Ataeniobius toweri*	27	43-75	II	1-2a 2b-4a 4b-7	3(2.9)	4(4.0)	8(7.8)	1
✓	*Xenotoca eiseni*	229	16-75	II II	1-2a 2b-4a 4b-7 1-2a 2b-4a 4b-6a 6b-7	3(3.4)	4(4.0)	8(8.2)	7
✓	*X. variata*	338	12-73	II II	1-2a 2b-7 1-2a 2b-4a 4b-7	4(3.9)	4(4.0)	9(8.7)	2, 7
✓	*Alloophorus robustus*	16	29-36	II II	1-2a 2b-8 1-2a 2b-5a 5b-8	5(5.0)	4(4.2)	9(8.9)	1, 2
✓	*Xenotoca melanosoma*	178	14-79	II II	1-2a 2b-4a 4b-7 1-2a 2b-4a 4b-6a 6b-7	5(5.0)	4(4.0)	9-10(9.8)	7
✓	*Neoophorus catarinae*	44	30-55	II	1-2a 2b-3a [3b-6] 7-8	4(3.8)	5(4.7)	10(10.2)	1
✓	*N. diazi*	14	34-67	II II	1-2a 2b-3a [3b-6] 7-8 1-2a 2b-4a [4b-6] 7-8	4(3.7)	5(4.6)	10(9.6)	1, 2
✓	*N. meeki*	16	28-46	II II	1-2a 2b-3a [3b-6] 7-8 1-2a 2b-4a [4b-6] 7-8	4(3.6)	5(4.5)	10(9.6)	1
✓	*Allotoca dugesi*	30	18-36	II	1-2a [2b-6a] 6b-7	3(2.6)	5(4.8)	10(9.4)	1, 2
✓	*A. maculata*	20	10-35	II	1-2a [2b-6a] 6b-7	0(0)	3(2.7)	7-8(7.3)	8
✓	*Girardinichthys multiradiatus*			III	pit organs only	0(0)	0(0)	0(0)	2, 4
✓	*G. viviparus*			III	pit organs only	0(0)	0(0)	0(0)	4
✓	*Hubbsina turneri*	10		III	pit organs only	0(0)	0(0)	0(0)	1, 4
	Skiffia francesae	30		III	pit organs only	0(0)	0(0)	0(0)	9
	S. lermae	59		III	pit organs only	0(0)	0(0)	0(0)	1, 2, 10
	S. multipunctata	74		III	pit organs only	0(0)	0(0)	0(0)	1, 2, 10
	S. bilineata	44		III	pit organs only	0(0)	0(0.9)	0(3.8)	1, 10

1—present study; 2—Gosline, 1949; 3—Kingston, 1979; 4—Miller & Fitzsimons, 1971; 5—Fitzsimons, 1979; 6—Miller & Uyeno, 1980; 7—Fitzsimons, 1972; 8—Smith & Miller, 1980; 9—Kingston, 1978; 10—Kingston, pers. comm.

in the supraorbital canal system has been reported for *Profundulus* and *Fundulus,* cyprinodont genera regarded as primitive by Parenti (1981).

The variable supraorbital canal pattern of *Ilyodon* (both Group I and II canal types represented) is tentatively regarded as derived from the condition seen in all Group II genera. The interrelationships of the recognized species of *Ilyodon* are not well understood, and there are probably additional populations which will eventually gain species status. The two supraorbital canal patterns were seen occasionally in individual fish but is an open question whether the presence of two canal types in these animals can be attributed to polymorphism within a species as has been hypothesized to explain differences in mouth widths and allozyme loci for *Ilyodon* in the Río Terrero, Jalisco, and the Río de Comala, Colima (Turner and Grosse, 1980). Neither Kingston's study (1979) nor mine (Table 1) shows a correlation of pore systems with mouth width in *Ilyodon*.

Within Group II, the predominant supraorbital canal pattern of 1-2a 2b-7 and its derivatives with one or two additional breaks plus 4 mandibular, 4 preorbital, and 7 or 8 preopercular pores, seen in seven genera, is regarded as primitive. A reduction in the number of pores (e.g., mandibular pores in *Goodea*), the partial loss (dorsal series in *Neoophorus* or *Allotoca*), or complete loss of a set of pores (mandibular series in *Allotoca maculata*) is considered derived. Similarly, an increased number of pores (such as in the mandibular series in *Alloophorus* and in the preopercular series in *Allotoca*) is an advanced condition. The close similarity in head pore data for many Group II genera, notably *Ameca, Chapalichthys, Xenoophorus,* and *Zoogoneticus,* as one group, and *Allodontichthys, Characodon,* and *Xenotaenia,* as another, is paralleled by resemblances in other morphometric features, such as fin-ray numbers in the first group, vertebral numbers and certain fin-ray counts in the second group, and proportional measurements in both. Generic consolidations among these fishes are likely. Cephalic sensory data support the integrity of the genus *Goodea* and may indicate an affinity with *Ataeniobius,* the monotypic genus formerly regarded as the most primitive member of the family because developing embryos lack trophotaeniae (Hubbs and Turner, 1939). *Xenotoca* exhibits marked interspecific variability in head-pore characters; however, the relationship of these fishes and the single species of *Alloophorus* probably lies with the group including *Ameca, Chapalichthys, Xenoophorus,* and *Zoogoneticus. Neoophorus* and *Allotoca* are allied in lacking a middle portion of the supraorbital canal, but, since different amounts of the canal are missing in the two genera, comparison with other characters is needed to judge whether the condition is homologous.

Genera in Group III have the most derived condition of the cephalic lateralis system, but it is questionable whether the sharing of this derived character state is attributable to parallelism rather than convergence. In certain meristic and proportional characters, *Girardinichthys* and *Hubbsina* are strikingly different from *Skiffia;* more information is needed to evaluate the possibility that in the evolution of goodeid fishes the development of the condition in Group III has occurred independently in two or more phyletic lines.

Information on the cephalic sensory pore system of goodeids shows promise for taxonomy. With the exception of *Xenotoca melanosoma*, congeners occur together or at least contiguously in the essentially one-character classificatory scheme presented in Table 1. Head-pore data alone identify five genera *(Ilyodon, Goodea, Alloophorus, Neoophorus,* and *Allotoca)* and six species *(Xenotoca variata, X. melanosoma, Alloophorus robustus, Allotoca dugesi, A. maculata,* and *Skiffia bilineata),* but the use of these data to indicate boundaries and interrelationships of natural groups of species or genera will depend on whether they are corroborated by other characters from diverse sources.

ACKNOWLEDGMENTS

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