

Jaws and Teeth of American Cichlids (Pisces: Labroidei)

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ABSTRACT The morphology of the upper, lower, and pharyngeal jaws is very similar among American cichlids. Common conditions are: (1) the presence of a premaxillary dentigerous arm shorter than the ascending arm (exceptions are *Astronotus*, *Cichla*, and *Crenicichla semifasciata*), (2) a narrow couler area; in contrast, a broad couler area is found in the Crenicichline Group, in certain chaetobranchines, and in *Apistogramma*, (3) the mandibular sensory canal exists to the skin through five or six simple pores; in contrast, it exits through numerous small pores that increase in number during ontogeny in the Chaetobranchine Group, certain crenicichlines, such as *Cichla*, *Crenicichla lepidota*, *Crenicichla proteus*, and *Crenicichla vittata*, and certain genera of the Cichlasomine Group A, such as *Caquetaia*, *Petenia*, *Neetroplus*, and "*Cichlasoma*," and (4) the premaxilla and dentary of American cichlids commonly bear unicuspid, conical teeth with a few exceptions such as *Neetroplus* (with scraping blade teeth) and "*Cichlasoma*" *facetum*, "*C.*" *cyanoguttatum*, "*C.*" *guttulatum*, and "*C.*" *spilurum* (with bicuspid [hooked] teeth). In contrast to the near uniformity of the upper and lower jaws, the upper and lower pharyngeal jaws present a great diversity of tooth shapes. At least seven types are found in American cichlids; usually, several types exist on a single tooth plate, but the combination of tooth types differs among some genera.

The pharyngobranchial 4 tooth plate has significant evolutionary transformations in labroids. The caudal margin of the pharyngobranchial 4 tooth plate bears the frayed zone in cichlids and embiotocids. The presence of a broad frayed zone bearing one to seven concavities represents a synapomorphy for the family Cichlidae, whereas a deep, narrow frayed zone is a synapomorphy of Embiotocidae. The absence of the frayed zone is a synapomorphy of Pomacentridae, whereas the loss of the pharyngobranchial 4 is a synapomorphy of Labridae. © 1993 Wiley-Liss, Inc.

The family Cichlidae with more than 1,000 species is among the most speciose of perciform families. Together with the Embiotocidae, Labridae, and Pomacentridae, the Cichlidae comprise the Suborder Labroidei, a taxon that includes ~5–10% of all living fishes (Stiassny and Jensen, '87).

Cichlids have a widespread distribution, which includes Africa, Madagascar, southern India, the Middle East, Sri Lanka, South and Central America, parts of North America, and the Antilles. On the American continents, cichlids are less speciose than their African relatives and are represented by ~300–350 species (Kullander, '83, '86; Kullander and Nijssen, '89) included in 35 genera.

The monophyly of the Cichlidae is currently recognized. However, authors who have worked with cichlids disagree as to their sistergroup relationships. Cichlidae is the sister taxon of Embiotocidae plus Labridae (Kaufman and Liem, '82; Lauder and Liem, '83), or the sister taxon of the remaining labroids (Stiassny and Jensen, '87). The phylogenetic interrelationships of most genera within the Cichlidae remain obscure; among them, those of American cichlids are mainly unresolved (Stiassny, '91).

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Tooth shape and tooth and jaw structure have provided ichthyologists with important features for characterizing certain fish groups (Fink, '81; Lauder and Liem, '83; Liem, '91). For example, among teleosts, the number of premaxillary tooth rows diagnoses characid subfamilies (Eigenmann, '15, '17) and distinguishes genera in combination with other characters of the premaxilla (Weitzman and Fink, '83). In cichlid fishes, tooth shapes and structures also provide important taxonomic and evolutionary characters (Greenwood, '81; Trewavas, '83). According to Liem ('74), the cichlids' feeding apparatus, especially the pharyngeal jaws, gave them a distinct selective advantage during the invasion and subsequent colonization of new lacustrine environments in Africa. Briefly, the cichlid feeding apparatus consists of two parts, the "true" jaws (upper and lower jaws) and the pharyngeal jaws. The latter consist of the sutured ceratobranchials 5 and their tooth plates, the unsutured pharyngobranchials 2-3 with their toothplates, and the toothplate of the pharyngobranchial 4. The advantage of the complex cichlid jaw mechanism is that the pharyngeal jaws are able to prepare food as well as transport it (Liem, '74; Liem and Osse, '75), a condition derived among perciforms but not unique to cichlids, because it is also present in other labroids (Kaufman and Liem, '82; Lauder and Liem, '83).

Although in the Neotropics, cichlids are not as species-rich as their African relatives, endemism and trophic specialization are common (McKaye, '77). However, these specializations do not seem to be accompanied by much change in tooth shape (Travassos and Ypiranga Pinto, '57: Figs. 3, 4, 7-9; Kullander, '83: Figs. 50, 55, 59, 112; Kullander, '86: Figs. 19, 24, 33, 40, 42, 83, 92, 113, 161, 164).

The objectives of this study are to: (1) describe and analyse the morphology of the upper, lower, and pharyngeal jaws, (2) describe the external morphology, arrangement, and number of jaw teeth; and (3) discuss their systematic importance in 21 American cichlid genera.

MATERIALS AND METHODS

Jaws and dentition of 40 American species of cichlids were studied. The taxonomic arrangement of the material follows Stiassny ('91).

The specimens (specs.) are deposited in the institutions listed below (institutional abbreviations follow Leviton et al., '85). SL repre-

sents standard length, TL, total length, and C&S, cleared and stained specimens.

New World cichlids examined Chaetobranchine Group

Astronotus ocellatus (Agassiz): MCZ 46098, 1 spec. of 78.8 mm SL (C&S); KU 10574, 2 specs. of 122.2, 146.6 mm SL. *Chaetobranchopsis orbicularis* (Steindachner): MCZ 15843, 1 spec. of 61.7 mm SL (C&S). *Chaetobranchius flavescens* Heckel: MCZ 15717, 1 spec. of 76.9 mm SL (C&S); KU 10573, 2 specs. of 130.8 and 135.2 mm SL.

Cichlasomine Group A

Acaronia nassa (Heckel): MCZ 15444, 6 specs. of 26.6-51.2 mm SL (C&S); MCZ 52608, 1 disarticulated spec. (C&S). *Caquetaia myersi* (Schultz): KU 13838, 2 specs. of 25.5 and 27.7 mm SL (C&S); KU 13837, 1 spec. of 40.8 mm SL (C&S) and 1 spec. of 74.3 mm SL; KU 13836, 1 spec. of 80.5 mm SL. "*Cichlasoma*" *beani* (Jordan): KU 5428, 1 disarticulated spec. (C&S). "*Cichlasoma*" *citrinellum* (Günther): KU 21915, 1 disarticulated spec. (C&S); KU 21917, 7 specs. of 28.7-73.9 mm SL (C&S). "*Cichlasoma*" *facetum* (Jenyns): MLP 8924, 20 specs. of 30.0-180.0 mm SL (C&S); MLP 8941, 7 specs. of 5.6-13.3 mm SL (C&S). "*Cichlasoma*" *cyano-guttatum* (Baird and Girard): KU 3032, 1 spec. of 116.0 mm SL (C&S); KU 4400, 4 specs. of 77.5-153.2 mm SL (C&S). "*Cichlasoma*" *guttulatum* (Günther): KU 1571, 1 spec. of 16.2 mm SL; KU 1576, 1 spec. of 123.5 mm SL. "*Cichlasoma*" *spilurum* (Günther): KU 10375, 2 specs. of 53.9-57.5 mm SL; KU 11112, 5 specs. of 36.2-66.9 mm SL. *Neetroplus nematopus* Günther: KU 18706, 3 specs. of 45.4-65.7 mm SL (C&S) and 7 specs. of 62.2-80.3 mm SL. *Petenia splendida* Günther: KU 22716, 2 specs. of 45.7 and 114.7 mm SL (C&S) and 3 specs. of 86.4-98.9 mm SL; KU 4432, 1 spec. of 152.5 mm SL.

Cichlasomine Group B

"*Aequidens*" *rivulatus* (Günther): KU 20006, 3 specs. of 50.1-70.4 mm SL (C&S); KU 20016, 2 specs. of 65.3, 81.5 mm SL. *Aequidens tetramerus* (Heckel): KU 13841, 4 specs. of 35.2-62.5 mm SL (C&S) and 4 specs. of 101.5-139.9 mm SL. *Bujurquina moriorum* Kullander: KU 13875, 3 specs. of 53.9-61.0 mm SL (C&S); KU 13879, 3 specs. of 70.5-85.2 mm SL. *Bujurquina vittata* (Heckel): MLP 8920, 15 specs. of 53.0-65.0 mm SL.

(C&S); MLP 8921, 7 specs. of 5.2–11.4 mm SL (C&S). *Cichlasoma dimerus* (Hensel): MLP 8922, 18 specs. of 46.0–140.0 mm SL (C&S); MLP 8923, 7 specs. of 6.2–16.4 mm SL (C&S). *Cichlasoma orinocense* Kullander: KU 20094, 1 spec. of 29.4 mm SL (C&S). *Laetacara dorsigera* (Heckel): MLP 8940, 15 specs. of 34.5–51.9 mm SL (C&S).

Crenicichline group

Cichla monoculus Spix: KU 20117, 1 spec. of 117.2 mm SL. *Cichla* cf. *ocellaris* Schneider: KU 10575, 1 spec. of 174.1 mm SL. *Cichla temensis* Humboldt: MCZ 15312, 5 specs. of 25.4–58.5 mm SL (C&S). *Crenicichla* cf. *iguassuensis* (Haseman): MLP 8925, 4 specs. of 148.0–206.0 mm SL (C&S). *Crenicichla lepidota* Heckel: MLP 8926, 10 specs. of 94.2–204.0 mm SL (C&S); MLP 8927, 9 specs. of 23.4–25.4 mm SL (C&S). *Crenicichla proteus* Kullander: KU 13806, 8 specs. of 120.9–135.4 mm SL. *Crenicichla scottii* (Eigenmann): MLP 8928, 7 specs. of 91.2–116.8 mm SL (C&S). *Crenicichla semifasciata* (Heckel): MLP 8919, 4 specs. of 81.0–114.6 mm SL (C&S). [*C. semifasciata* was previously described in the genus *Batrachops*.] *Crenicichla vittata* Heckel: MLP 8930, 7 specs. of 106.0–304.0 mm SL (C&S) and 1 disarticulated spec. 340 mm TL (C&S); MLP 8931, 5 specs. of 41.5–48.2 mm SL (C&S).

Geophagine group

Acarichthys heckelii (Heckel): MCZ 52606, 1 spec. of 76.2 mm SL (C&S) and 2 specs. of 72.4 and 88.7 mm SL. *Apistogramma borellii* (Regan): MLP 8917, 10 specs. of 27.0–28.7 mm SL (C&S). *Apistogramma commbrae* (Regan): MLP 8918, 10 specs. of 25.2–28.3 mm SL (C&S). “*Geophagus*” *brasiliensis* (Quoy and Gaimard): MLP 8939, 2 specs. of 59.6–69.4 mm SL (C&S). [According to Kullander ('83) “*Geophagus*” *brasiliensis* and “*Geophagus*” *crassilabris* are not *Geophagus*, they belong to different genera.] “*Geophagus*” *crassilabris* Steindachner: KU 17722, 1 spec. of 31.0 mm SL (C&S). *Gymnogeophagus australis* (Eigenmann): MLP 8932, 5 specs. of 72.0–100.0 mm SL (C&S). *Gymnogeophagus balzanii* (Perugia): MLP 8933, 6 specs. of 110.0–114.0 mm SL (C&S). *Gymnogeophagus gymnogenys* (Hensel): MLP 8935, 1 spec. of 71.9 mm SL (C&S). *Gymnogeophagus meridionalis* Reis and Malabarba: MLP 8936, 20 specs. of 47.3–94.0 mm SL (C&S) and 12 specs. of 4.8–13.5 mm SL (C&S). *Gymno-*

geophagus rhabdotus (Hensel): MLP 8938, 2 specs. of 63.9 and 72.6 mm SL (C&S). *Papiliochromis ramirezi* (Myers and Harris): KU 20109, 2 specs. of 35.1 and 36.1 mm SL (C&S).

Specimens in comparative studies

Old World cichlids

Ptychochromine group. *Ptychochromis oligacanthus* (Bleeker): AMNH uncat., 2 specs. of 33.5–43.5 mm SL (C&S).

Tilapiine group. *Oreochromis niloticus* (Linnaeus): MCZ 46387, 1 spec. of 60.8 mm SL (C&S); UMMZ 166639, 1 spec. of 89.5 mm SL (C&S). *Oreochromis mossambicus* (Peters): UMMZ 190401, 1 spec. of 66.1 mm SL (C&S). *Tilapia sparrmanii* Smith: MCZ 52466, 1 spec. of 61.0 mm SL (C&S). *Tilapia tholloni congica* (Sauvage): MCZ 64796, 2 specs. of 59.6 and 62.8 mm SL (C&S). *Tilapia zilli* Gervais: MCZ 48606, 1 spec. of 61.9 mm SL (C&S).

Hemichromine group. *Hemichromis bimaculatus* Gill: MCZ 48602, 2 specs. of 62.2 and 63.2 mm SL (C&S). *Hemichromis fasciatus* Peters: MCZ 48603, 1 spec. of 58.9 mm SL (C&S); UMMZ 199391, 2 specs. of 50.2 and 52.2 mm SL (C&S).

Chromidotilapiine group. *Nanochromis parilus* Roberts and Stewart: MCZ 50475, 1 spec. of 32.7 mm SL (C&S).

Lamprologine group. *Julidochromis regani*: UMMZ 196161, 1 spec. of 70.5 mm SL (C&S). *Lamprologus elongatus* Boulenger: UMMZ 199768, 1 spec. disarticulated (C&S). *Lamprologus furcifer* Boulenger: MCZ 50831, 7 specs. of 18.5–44.5 mm SL (C&S). *Lamprologus werneri* Poll: MCZ 50473, 1 spec. of 39.9 mm SL (C&S).

Etropline group. *Etroplus maculatus* (Bloch): UMMZ 199385, 2 specs. of 37.2 and 39.0 mm SL (C&S). *Paretroplus polyactis* (Bleeker): AMNH 98171, 1 spec. of 66.2 mm SL (C&S).

The Rest, nonmonophyletic group (according to Stiasny, '91). *Ectodus descampsi* Boulenger: UMMZ 196158, 1 spec. of 86.4 mm SL (C&S). *Hemibates stenosoma* (Boulenger): UMMZ 199808, 1 spec. of 108.8 mm SL (C&S); MCZ 50829, 1 spec. of 111.3 mm SL (C&S). *Hemihaplochromis strigigena* (Pfeffer): UMMZ 169019, 1 spec. of 62.6 mm SL (C&S). *Ophthalmochromis ventralis* (Boulenger): UMMZ 199879, 1 spec. of 73.1 mm

SL (C&S). *Telmatochromis* sp.: MCZ 50693, 5 specs. of 16.4–32.5 mm SL (C&S). *Thoraco-chromis wingatii* (Boulenger): UMMZ 199389, 2 specs. of 20.0 and 21.5 mm SL (C&S).

Cichlids not included in any group. *Paratilapia polleni* Bleeker: UMMZ 199408, 1 spec. of 50.8 mm SL (C&S). AMNH uncat., 1 spec. of 79.8 mm SL (C&S). *Tylochromis leonensis* Stiassny: AMNH uncat., 2 specs. of 36.8 and 45.4 mm SL (C&S).

Noncichlids labroids

Embiotocidae. *Cymatogaster aggregata* Gibbons: KU 9988, 3 specs. of 75.3–90.0 mm SL (C&S). *Embiotoca lateralis* Agassiz: KU 18114, 2 specs. of 56.9 and 60.0 mm SL (C&S). *Hysterochrysurus traski* Gibbons: KU 12147, 1 spec. of 68.5 mm SL (C&S). *Rhacochilus vacca* Girard: KU 6824, 1 spec. of 68.5 mm SL (C&S).

Labridae. *Halichoeres dispilus* (Günther): CAS 38024, 1 spec. of 68.9 mm SL (C&S); CAS 38024, 1 spec. of 69.1 mm SL (C&S). *Halichoeres* sp.: KU 21642, 4 specs. of 26.7–56.4 mm SL (C&S). *Thalassoma bifasciatum* (Bloch): KU 21688, 1 spec. of 15.7 mm SL (C&S). *Thalassoma duperry* (Quoy and Gaimard): KU 18256, 1 spec. of 116.4 mm SL (C&S). *Xyrichtys rosipes* Jordan and Gilbert: CAS(SU) 45904, 2 specs. of 37.0 and 43.5 mm SL (C&S).

Pomacentridae. *Abudefduf glaucus* (Cuvier and Valenciennes): KU 21625, 2 specs. of 46.7 and 53.5 mm SL (C&S). *Abudefduf saxatilis* (Linnaeus): KU 11154, 2 specs. of 21.0 and 22.8 mm SL (C&S). *Abudefduf* sp.: CAS(SU), 2 specs. of 13.5 and 16.2 mm SL (C&S). *Chromis hanui* Randall and Swardloff: KU 18265, 1 spec. of 52.1 mm SL (C&S). *Chromis punctipinnis* (Cooper): KU 9990, 1 disarticulated spec. (C&S). *Microsphaodon niveatus* (Poey): CAS(SU) 45870, 1 spec. of 48.0 mm SL (C&S). *Pomacentrus albofasciatus* Schegel and Müller: KU 21648, 1 spec. of 69.1 mm SL (C&S). *Stegastes leucostictus* (Müller and Troschel): CAS(SU) 45871, 1 spec. of 45.0 mm SL (C&S).

General methodology

Specimens of each species were cleared and stained variously by the methods of Hollister ('34), Taylor ('67), Dingerkus and Uhler ('77), and Arratia and Schultze ('92). Representatives of each species were prepared for scanning electron microscopy (SEM) examination

(Phillips 501). These specimens were cleaned in borax and trypsin using ingredients in the proportions recommended by Taylor ('67), dehydrated in an ethanol series, and air dried.

All the following measurements were taken on the premaxilla and lower jaw.

The *premaxillary dentigerous arm length* (DL; Fig. 1) extends from the caudal end of the dentigerous arm to the rostral-ventral point of the premaxilla.

The *premaxillary ascending arm length* (AL; Fig. 1) extends from the dorsal tip of the ascending spine to the rostral-ventral point of the premaxilla.

The *ascending arm width* (AAW; Fig. 1) is the widest part of the premaxillary ascending arm.

The *anguloarticular length* (AAL; Fig. 2B) extends from the caudal tip of the postarticular process of the angular portion of the anguloarticular to the rostral tip of the bone.

Abbreviations

| | |
|------------|---|
| a | unicuspid recurved teeth |
| AAD | anguloarticular depth |
| AAL | anguloarticular length |
| AAW | ascending arm width |
| AL | premaxillary ascending arm length |
| ang-ar | anguloarticular |
| ANT | anterior |
| a.q | articular facet for quadrate |
| asc.arm | ascending arm |
| asc.spi | ascending spine |
| b | bicuspid crenulate teeth |
| c | caudal symphyseal ridge |
| CAD | coulter area depth |
| CAW | coulter area width |
| co | coronomeckelian |
| d | bevelled teeth |
| DD | dorsal dorsad |
| den | dentary |
| dentig.arm | dentigerous arm |
| dent.s | toothed surface |
| DL | premaxillary dentigerous arm length |
| f.1–7 | lateral line foramina 1–7 |
| fo.lam. | fossa lamellar |
| i | interfacet depression |
| l | ligament |
| m | maxillad articular facet |
| m.s.c. | mandibular sensory canal |
| n.pr | nipple process |
| "n."pr | "nipple" process |
| phb2–3 | pharyngobranchial 2–3 |
| pr.pr | primordial process (or coronoid process of anguloarticular) |
| pr.q | process of anguloarticular that articulates in a cavity of quadrate |
| rar | retroarticular |
| r | dentigerous arm ridge |
| s | symphyseal articular facet |
| tp-phb2–4 | toothplate of pharyngobranchial 2–4 |
| \bar{x} | average |
| α | alpha angle |
| β | beta angle |
| ϵ | epsilon angle |
| γ | gamma angle |

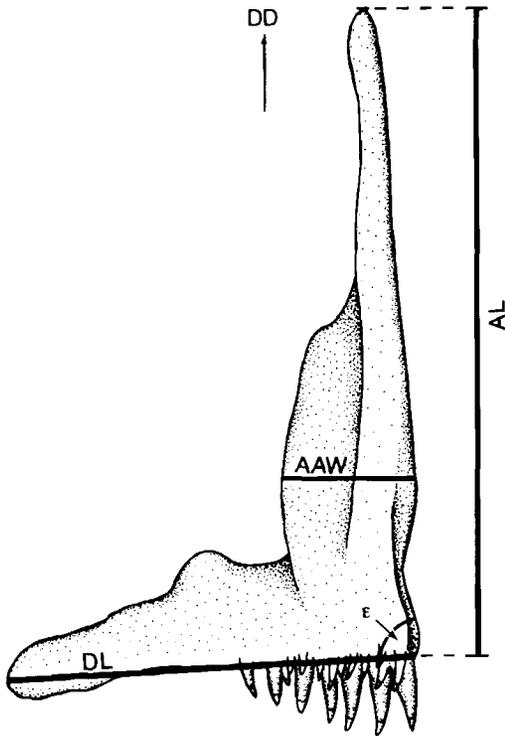


Fig. 1. Diagrammatic premaxilla (medial view) illustrating measurements and angles taken in different cichlid species.

Anguloarticular depth (AAD; Fig. 2A) extends from the tip of the primordial or coronoid process of the angular portion of the anguloarticular to the ventral edge of the couler area.

Couler area depth (CAD; Fig. 2B) runs along the caudal edge from the tip of the postarticular process to the caudad-ventrad tip of the retroarticular bone.

Couler area width (CAW; Fig. 2B) extends in a parallel line to the ventral edge of the anterior arm of the anguloarticular bone passing by the rostral-ventral tip of the second mandibular lateral line foramen. *Apistogramma borelli* lacks the mandibular canal; therefore, the couler area width was measured in a parallel line to the ventral edge of the anterior arm of the anguloarticular passing by the uppermost point of the suture between the retroarticular and the anguloarticular.

The *alpha angle* (Fig. 2A) is formed where the rostral margin of the couler area and the ventral edge of the articular anterior arm of the anguloarticular meet.

The *beta angle* (Fig. 2A) is formed by the prolongation of the ventral edge of the articular anterior arm of the anguloarticular and the ventral edge of the mandibular canal running on the anguloarticular.

The *gamma angle* (Fig. 2A) is formed by caudal margin of the couler area and the prolongation of the ventral edge of the articular anterior arm of the anguloarticular bone.

The *epsilon angle* (Fig. 1) is formed by the confluence of the ascending and the dentigerous arms of the premaxilla.

Other measures are the depth of the anguloarticular, expressed in percentage of its length, and the depth and width of the couler area, expressed in percentage of the anguloarticular length.

The nomenclature of the bone structures follows Barel et al. ('76, '77).

COMPARATIVE MORPHOLOGY OF JAWS

The jaws of cichlids include the upper jaws formed by a well-developed pair of dentate premaxillae and maxillae that lack teeth, the lower jaws with a pair of dentaries that bear teeth, and the pharyngeal jaws.

Premaxilla

A description of the premaxilla—based on the African cichlid *Astatotilapia elegans*—is found in Barel et al. ('76). However, the taxa considered below vary from that description.

Acarichthys. The dentigerous arm is shorter than the ascending one in *Acarichthys heckelii*. The ascending arm is slender, its width ~14% of the ascending arm length. The angle formed by the confluence of the ascending and the dentigerous arms is ~86°. The maxillad articular facet is interrupted before reaching the ascending spine. Dorsally, the caudal symphyseal ridge is sharp and it runs near the maxillad articular facet. Ventrally, the ridge is blunt and it runs near the rostral symphyseal ridge. The dentigerous arm is high where the external margin of the maxillad articular facet and the dentigerous arm ridge meet. Its height decreases toward the caudal tip. The ventral margin of the dentigerous arm is excurved near the symphyseal zone and incurved in the remaining section of the margin. There are unicuspid teeth almost the full length of the dentigerous arm. There are one to four inner tooth rows. The teeth of the outer series are much longer than the inner ones.

Acaronia (Fig. 3A). The slender ascending arm is longer than the dentigerous one.

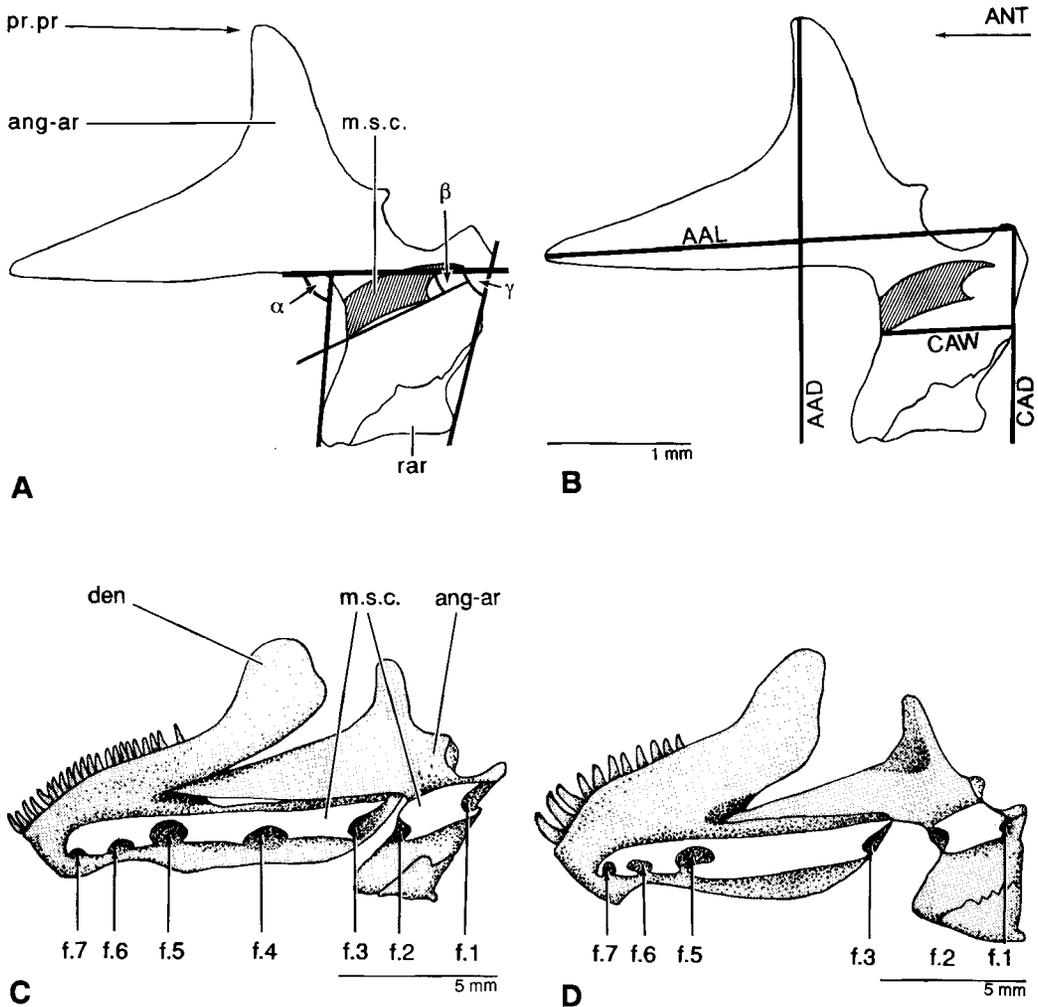


Fig. 2. Diagrammatic lower jaw (lateral view) in cichlids. Posterior part illustrating angles (A) and measurements (B) in different species. Lateral views illustrating the lateral line foramina in *Gymnogeophagus gymnogenys* (C) and in "*Cichlasoma*" *facetum* (D).

The ascending arm width is 9–11% ($\bar{x} = 10\%$) of the ascending arm length. The angle formed by the confluence of the ascending and the dentigerous arms is 77–81° ($\bar{x} = 79^\circ$). The caudal symphyseal ridge runs over the ascending arm along the middle of it. The ridge is well developed and sharp in the lower half of the ascending arm length; beyond this point the caudal symphyseal ridge becomes low and blunt. The maxillad articulatory facet is long, reaching almost to the ascending spine. The dentigerous arm ridge sometimes bears a low process at the middle of its length. The ventral margin of the dentigerous arm is

slightly curved, bearing small unicuspid teeth. There are one to three inner tooth rows.

Aequidens. The premaxilla of "*A.*" *rivulatus* is very similar to that of *Bujurquina* (see below). The dentigerous arm is shorter than the ascending one; the ascending arm width is 11–13% of ascending arm length. The angle formed by the confluence of the ascending and the dentigerous arms is 75–78°. There are one to four rows of inner unicuspid teeth.

Apistogramma (Fig. 4B). The dentigerous arm is shorter than the ascending one.

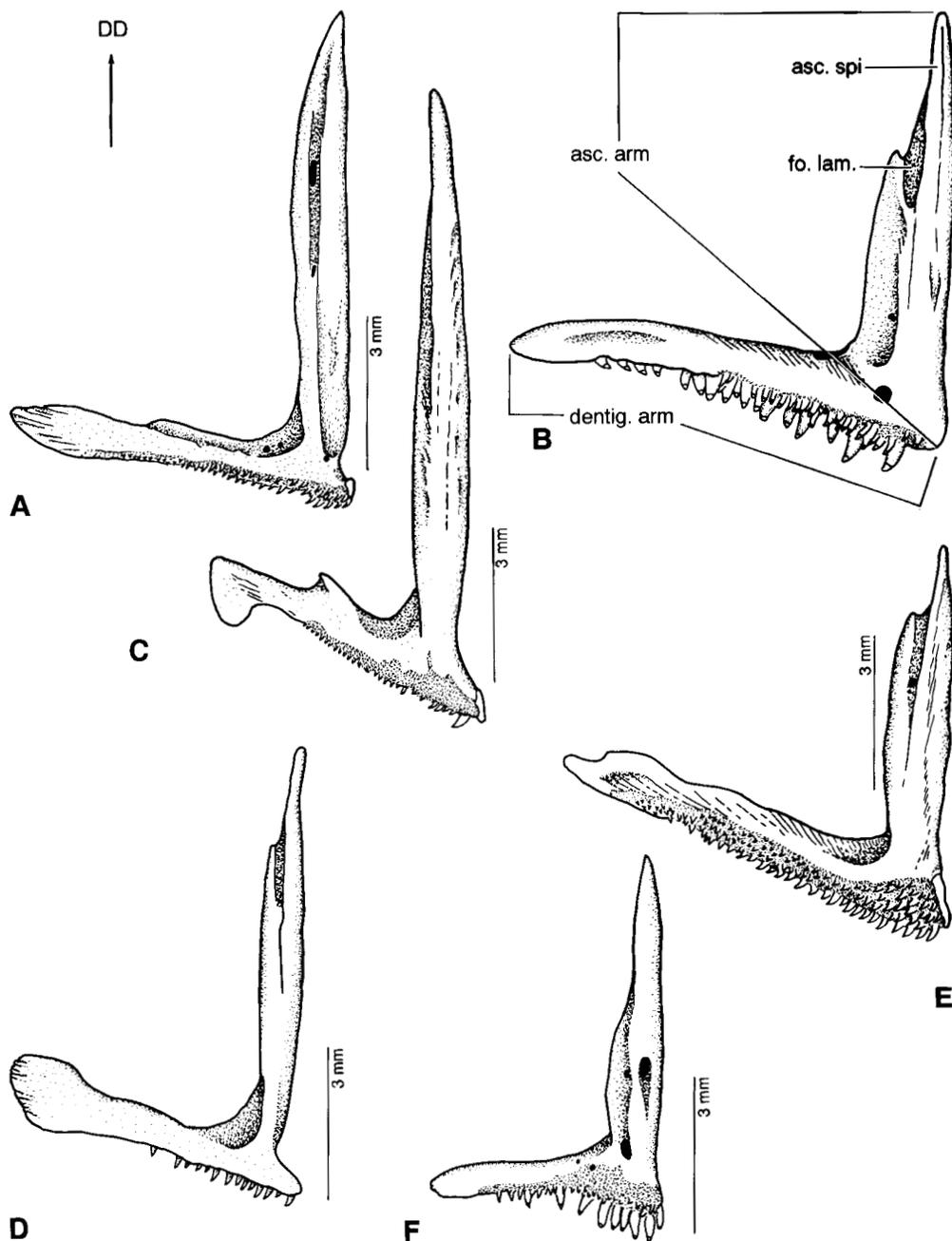


Fig. 3. Premaxillae (in medial view) of *Acaronia nassa* (A), *Astronotus ocellatus* (B), *Petenia splendida* (C), *Chaetobranchus flavescens* (D), *Cichla temensis* (E), and *Aequidens tetramerus* (F). A, B, same scale.

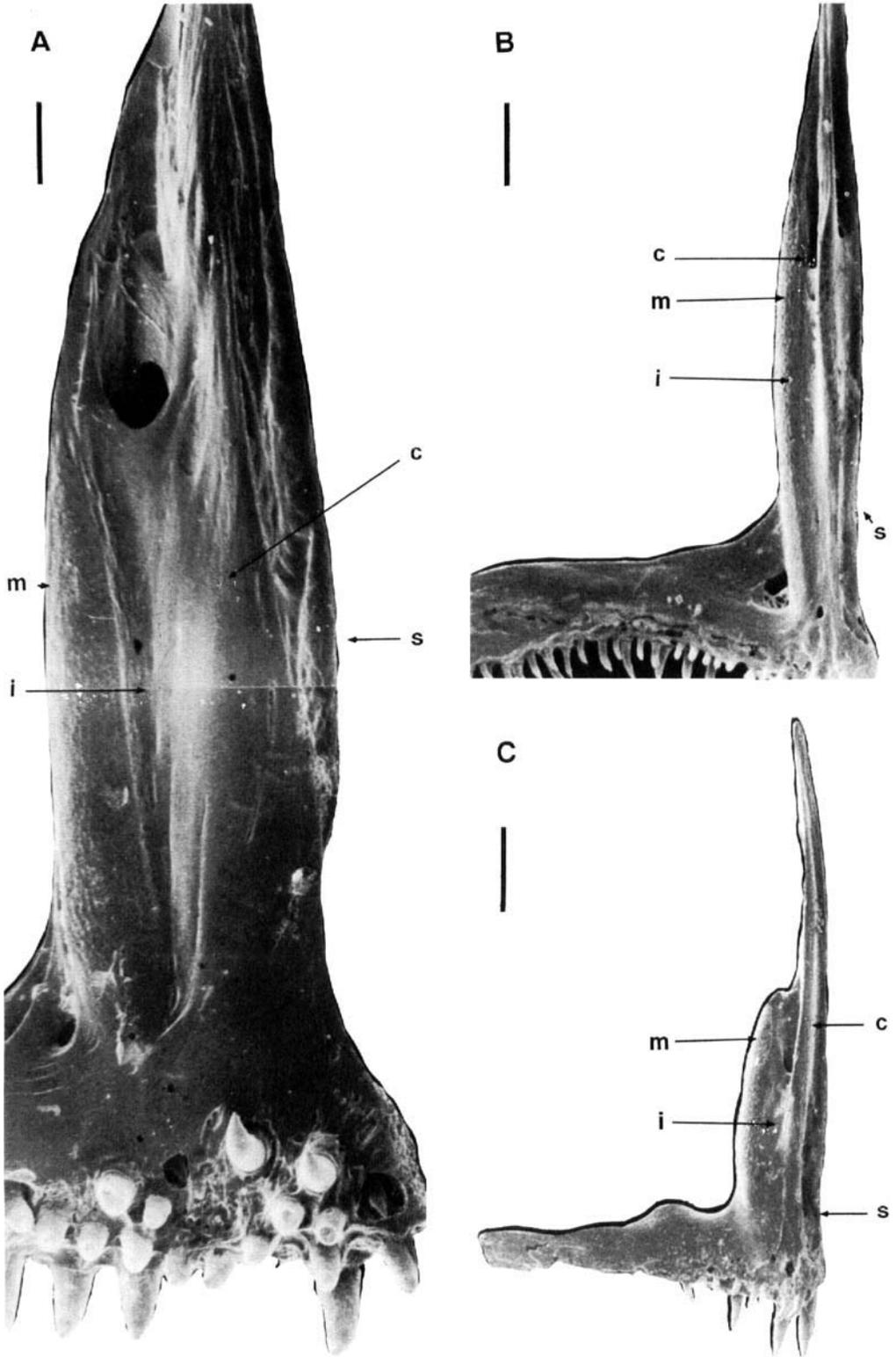


Fig. 4. SEM of premaxillae (in medial view) of *Crenicichla semifasciata* (A), *Apistogramma borellii* (B), and *Laetacara dorsigera* (C). Bars = 500 μ .

The ascending arm is slender; its width is 11–14% ($\bar{x} = 13\%$) of the ascending arm length. The angle formed by the confluence of the ascending and dentigerous arms is 75–84° ($\bar{x} = 80^\circ$). The caudal symphyseal ridge runs near the middle of the ascending arm; its ventral tip extends beyond the dentigerous arm ridge level. Only the dorsal half of the caudal symphyseal ridge is sharp; the basal half is rather blunt. The maxillad articulatory facet is not expanded in the middle of the ascending arm length, but it extends practically over the entire ascending arm length, ending at the ascending spine tip. The ventral margin of the dentigerous arm is slightly incurved. There are one to three inner unicuspid tooth rows. There are no differences in the shapes of the premaxillae of *A. borelli* and *A. commbrae*.

Astronotus (Fig. 3B). The ascending arm is shorter than the dentigerous and is wide. Its width is ~18% of the ascending arm length. The angle formed by the confluence of the ascending and the dentigerous arms is ~78°. The caudal symphyseal ridge runs along the middle of the ascending arm. It is well developed only in the upper two-thirds of the ascending arm length. The ventral margin of the dentigerous arm is excurved near the symphyseal zone and incurved in the remaining ventral margin. There are one to three inner tooth rows. The ventral dentigerous margin bears strong unicuspid teeth in the outer series.

Bujurquina (Fig. 5C). The ascending arm of *B. vittata* is longer than the dentigerous arm. The ascending arm is slender; its width is 11–14% ($\bar{x} = 12\%$) of the ascending arm length. The angle formed by the confluence of the ascending and the dentigerous arms is 80–89° ($\bar{x} = 83^\circ$). The caudal symphyseal ridge runs nearer the external margin of the maxillad articulatory facet than the one corresponding to the rostral ridge. Ventrally, the caudal symphyseal ridge extends up to the dentigerous arm ridge level and is well developed along its entire length. The ventral margin of the dentigerous arm is slightly incurved. There are one to four inner unicuspid tooth rows.

Caquetaia and Petenia (Fig. 3C). The ascending arm in these genera is longer than the dentigerous one. The ascending arm is slender; its width is 9–11% ($\bar{x} = 10\%$) of the ascending arm length. The angle formed by the confluence of the ascending and the den-

tigerous arms is 64–68° ($\bar{x} = 66^\circ$). The caudal symphyseal ridge runs over the ascending arm along its middle. The caudal symphyseal ridge is well developed only in the upper two-thirds of the ascending arm length. The dorsal margin of the dentigerous arm produces a small, broad process about the middle of its length. The ventral margin is nearly straight but curved near the distal tip. There are one to four inner tooth rows.

Chaetobranchopsis. The ascending arm is longer than the dentigerous one, and slender. The ascending arm width is ~11% of the ascending arm length. Where the ascending and the dentigerous arms meet they form an angle of ~86°. The caudal symphyseal ridge runs over the ascending arm along its middle. This ridge is well developed and sharp along its full length. The maxillad articulatory facet is long, reaching almost to the ascending spine. The ascending arm is narrow, and the maxillad articulatory facet is not expanded laterad-caudad. The dentigerous arm ridge bears a process with its tip directed caudad. The distal two-thirds of the dentigerous arm is taller than the remaining part of the dentigerous arm. Its ventral margin is slightly curved. There are two unicuspid inner tooth rows.

Chaetobranchus (Fig. 3D). The premaxilla of the *Chaetobranchus flavescens* is similar to that of *Chaetobranchopsis orbicularis*, but the ascending arm is a bit curved laterad-caudad. The angle formed by the confluence of the ascending and the dentigerous arms is ~72°. The caudal symphyseal ridge runs along the middle of the dentigerous arm. The dentigerous arm at the zone close to the symphysis is projected rostrad. The ventral margin of the dentigerous arm bears small unicuspid teeth situated only in the proximal half of the dentigerous arm length. There is one inner unicuspid tooth row.

Cichla (Fig. 3E). The ascending arm is shorter than the dentigerous. The width of the ascending arm is 14–17% ($\bar{x} = 16\%$) of the ascending arm length. The angle formed by the meeting of the two arms is 64–74° ($\bar{x} = 70^\circ$). The caudal symphyseal ridge runs along the middle of the ascending arm; it is blunt and poorly developed. The maxillad articulatory facet is long but does not reach the ascending spine. The ventral margin of the dentigerous arm is slightly excurved near the symphyseal zone and slightly incurved in the remaining part of it. This margin bears

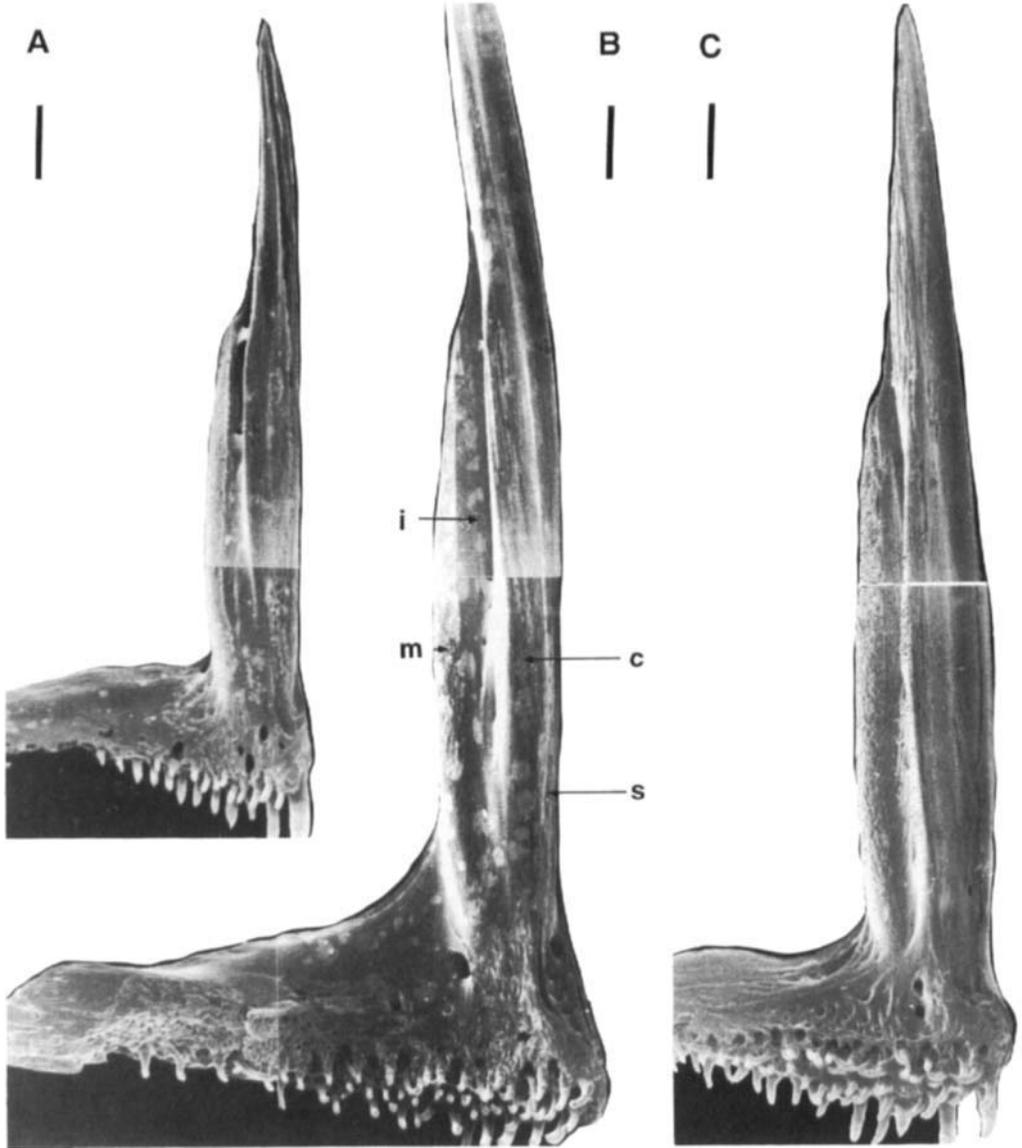


Fig. 5. SEM of premaxillae (in medial view) of "*Cichlasoma*" *facetum* (A), *Gymnogeophagus australis* (B), and *Bujurquina vittata* (C). Bars = 500 μ .

small unicuspid teeth almost all over its length. There are one to six inner unicuspid tooth rows.

Cichlasoma and *Aequidens tetramerus* (Fig. 3F). The dentigerous arm is shorter than the ascending arm. The latter is widened at its basal half because the maxillad articular facet is expanded laterad-caudad. The width of the ascending arm is 13–

17% (\bar{x} = 15%). The angle formed by the confluence of the ascending and the dentigerous arms is 81–85° (\bar{x} = 82°). The caudal symphyseal ridge runs over the ascending arm along its middle. Ventrally, it does not reach the dentigerous arm ridge. The caudal symphyseal ridge is sharp all along its length. The ventral margin of the dentigerous arm is slightly incurved. There are one to three in-

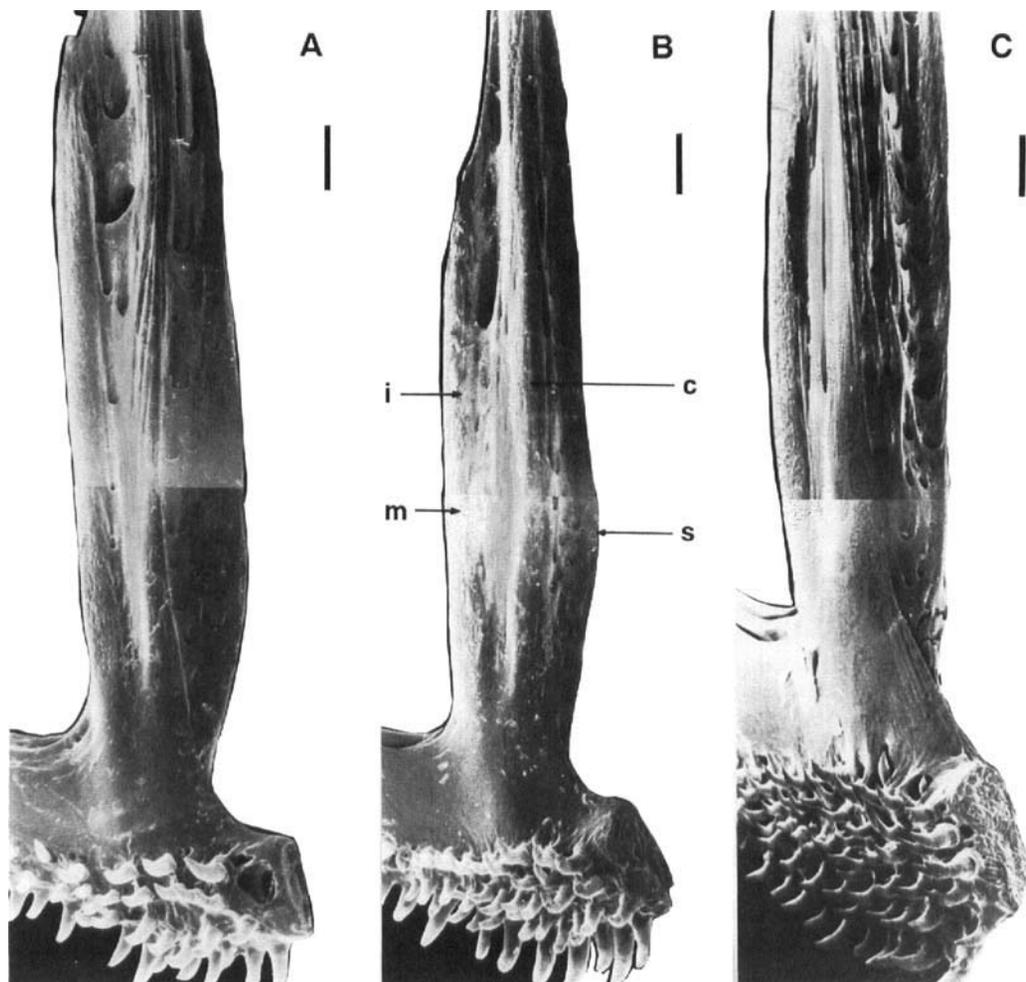


Fig. 6. SEM of premaxillae (in medial view) of *Crenicichla lepidota* (A), *Crenicichla scottii* (B), and *Crenicichla vittata* (C). Bars = 500 μ .

ner unicuspid tooth rows. There are no differences in the premaxillae of *Cichlasoma* and *Aequidens tetramerus*.

"*Cichlasoma*" (Fig. 5A). The dentigerous arm is shorter than the ascending one. The ascending arm is slender; its width is 11–15% (\bar{x} = 14%) of the ascending arm length. The angle formed by the confluence of the ascending and the dentigerous arm is 75–85° (\bar{x} = 81°). The caudal symphyseal ridge runs over the ascending arm along its middle, or nearer to the external margin of the maxillad articular facet. This ridge reaches ventrally only halfway along the maxillad articular facet. The facet does not

expand laterad-caudad. The ventral margin of the dentigerous arm is almost straight in the symphyseal zone but incurved in the caudal zone. There are one to five unicuspid inner tooth rows. There are no differences in the premaxillae of "*C.*" *facetum* and "*C.*" *cyanoguttatum*.

Crenicichla (Figs. 4A, 6A–C). The ascending arm is longer than the dentigerous one. The ascending arm width is 13–16% (\bar{x} = 14%), except in *C. semifasciata*. The angle formed by the juncture of the ascending and the dentigerous arms is 58–66° (\bar{x} = 62°). *C. vittata* and *C. scottii* have a caudal symphyseal ridge that is somewhat

blunt in its basal third. In *C. vittata* this ridge runs over the ascending arm along the middle of it, whereas in *C. scottii* it runs a bit nearer the external margin of the rostral symphyseal ridge. *C. scottii* and *C. cf. iguazuensis* have similar premaxillae. The ascending arm of *C. lepidota* (Fig. 6A) is expanded as a result of the widening of the interfacet depression and of the symphyseal articulatory facet. This widening is more evident in the zone where the dentigerous and ascending arms meet. At their juncture the internal margin has a different curvature (Fig. 6A). The caudal symphyseal ridge is sharp. The *Crenicichla* species examined have the ventral margin of the dentigerous arm convex in the symphyseal zone and straight or slightly incurved in the caudal half. There are one to seven unicuspid inner tooth rows, except in *C. semifasciata* who has one to four unicuspid inner tooth rows. The premaxilla of *C. semifasciata* differs from those found in the other species. The dentigerous arm of the premaxilla is shorter than the ascending (Fig. 4A). The ascending arm is wide, 22–24% ($\bar{x} = 23\%$) of the ascending arm length. The angle formed by the confluence of the ascending and the dentigerous arms is 60–65° ($\bar{x} = 62^\circ$). The caudal symphyseal ridge is wide; it runs over the ascending arm in a more or less oblique direction. The ventral margin of the dentigerous arm is slightly convex.

Gymnogeophagus, “*Geophagus*” *brasiliensis*, and “*Geophagus*” *crassilabris* (Fig. 5B). The ascending arm is longer than the dentigerous. The ascending arm is slender; its width is 9–12% ($\bar{x} = 11\%$). The angle formed by the confluence of the ascending and the dentigerous arms is 74–79° ($\bar{x} = 76^\circ$). The maxillad articulatory facet is interrupted before reaching the ascending spine. Dorsally, the caudal symphyseal ridge is sharp and runs along the middle of the ascending arm. Ventrally, the ridge is blunt and runs nearer to the symphyseal border. The dentigerous arm is high in the symphyseal zone. Its height decreases toward the caudal tip. The ventral margin of the dentigerous arm is excurved near the symphyseal zone and incurved in the distal one. Occasionally there are teeth all along the dentigerous arm. There are one to four unicuspid inner rows of teeth. The premaxillae of *Gymnogeophagus australis*, *G. balzanii*, *G. meridionalis*, *G. gymnogenys*, *G. rhabdotus*, and “*Geophagus*” *crassilabris* are similar.

The premaxilla of “*Geophagus*” *brasiliensis* has the same shape as that in *Gymnogeophagus*, but in “*G.*” *brasiliensis* two-thirds of the length of the dentigerous arm bear teeth. There are only one to two unicuspid inner rows of teeth, and these teeth are much smaller than those of the outer series.

Laetacara (Fig. 4C). The dentigerous arm of *L. dorsigera* is shorter than the ascending one. The ascending arm has its basal half widened because the maxillad articulatory facet is expanded laterad-caudad; the width of the dentigerous arm is 18–19% ($\bar{x} = 18\%$) of the ascending arm length. The angle formed by the confluence of the ascending and the dentigerous arms is 86–90° ($\bar{x} = 88^\circ$). The caudal symphyseal ridge runs over the ascending arm along the middle of it, this ridge is sharp at the adjacent zone to the maxillad articulatory facet and its ventral tip can surpass the dentigerous arm ridge level. The dentigerous arm ridge occasionally bear a process approximately in the middle of the dentigerous arm ridge. The ventral margin of the dentigerous arm is slightly incurved. There are one to two unicuspid inner tooth rows.

Neetroplus (Fig. 7A). The ascending arm is longer than the dentigerous one. In *N. nematopus* the ascending arm width decreases gradually from its basal point to the distal one; its width is 15–17% ($\bar{x} = 16\%$) of the ascending arm length. The angle formed by the ascending and the dentigerous arms is 85–91° ($\bar{x} = 87^\circ$). The caudal symphyseal ridge runs much nearer the external margin of the maxillad articulatory facet than the one corresponding to the rostral edge. The maxillad articulatory facet is narrow, whereas the symphyseal articulatory facet is broad. Ventrally, the symphyseal articulatory ridge extends up to the dentigerous arm ridge level and is well developed in its basal two-thirds. The dentigerous arm is high where it joins with the ascending arm. Its height is ~50% of the dentigerous arm length, decreasing suddenly from this point to the distal tip of the dentigerous arm. The outer teeth resemble a scraping blade and are implanted at a higher level than the inner tooth rows. The outer teeth are much larger than the inner ones. There are two or three inner rows of scraping blade teeth, but the innermost rows may also have unicuspid teeth.

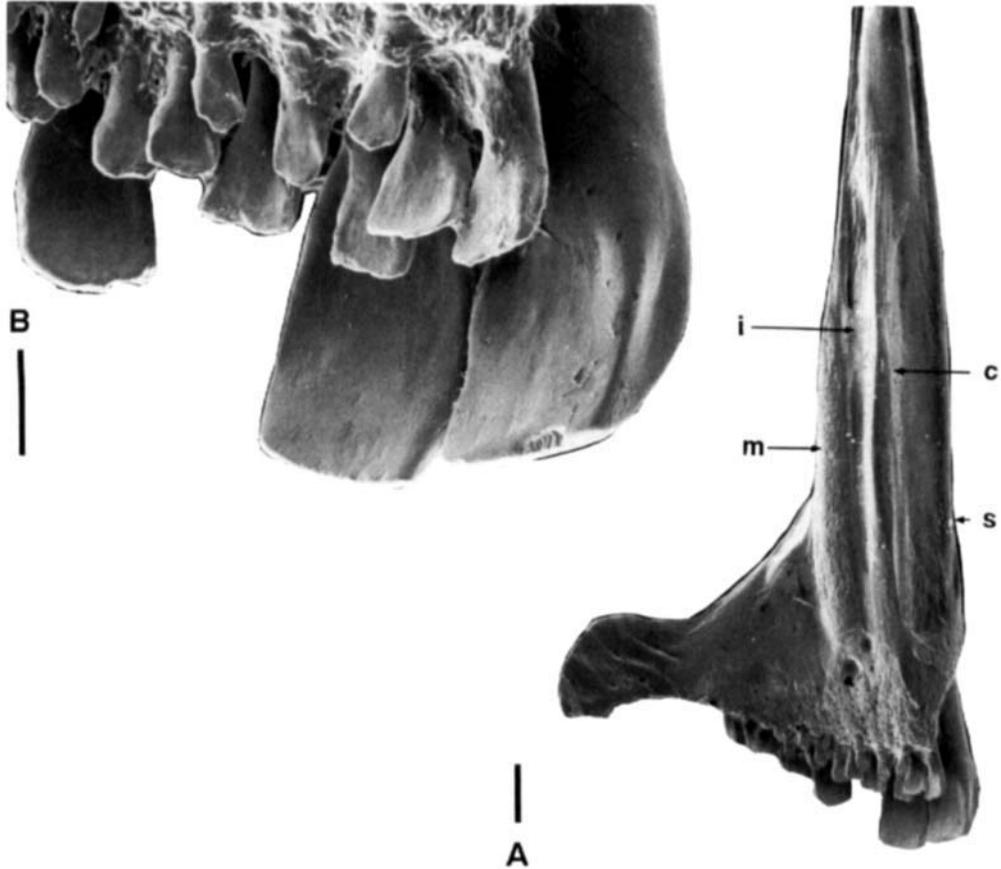


Fig. 7. SEM of premaxilla in medial view of *Neotroplus nematopus* (A) and enlargement of the scraping blade teeth (B). Bars = 200 μ .

Papiliochromis. The premaxilla of *P. ramirezi* resembles that of other geophagines such as *Gymnogeophagus* (Fig. 5B), "*Geophagus*" *brasiliensis*, and "*Geophagus*" *crassilabris*. Nevertheless, the ascending arm is a bit wider at the maxillad articular facet level in *P. ramirezi*; its width is 14–15% of the ascending arm length. The ascending arm is longer than the dentigerous. The angle formed by the ascending and the dentigerous arms is 82–83°. The caudal symphyseal ridge is sharp and runs along the middle of the ascending arm. Similarly to *Gymnogeophagus*, the dentigerous arm is high in the proximal half, its length decreases toward the distal tip. The proximal half of the ventral margin of the dentigerous arm is excurved; however the distal portion is incurved. There are one to two inner unicuspid tooth rows.

Lower jaw

A detailed description of the lower jaw—based on the African cichlid *Astatotilapia elegans*—is found in Barel et al. ('76). However, the taxa considered below vary from that description. The common condition of the American cichlids examined below is the presence of unicuspid, conical teeth; only the exceptions are noted below. In all specimens studied there are always two lateral line foramina (foramina 1 and 2) on the sensory bony tubelike canal running in the anguloarticular (Fig. 2C, D), with the exception of *Apistogramma borellii*, which lacks the mandibular canal. Four or five foramina are found in the dentary (Fig. 2C, D); five corresponds to the higher number of foramina found in the cichlid dentary. In most species studied

pores 2 and 3 of the bony tubelike canal are separated from each other but both open to the skin through a common pore; the exceptions are noted below.

Acaronia (Fig. 8A). The lower jaw is long and low. The anguloarticular depth is 55–58% (\bar{x} = 56%) of its length. The primordial process of the anguloarticular is long and directed rostradorsad with respect to the ventral margin of the anguloarticular. The coulter area is wider than deep; depth 20–25% (\bar{x} = 22%); width 46–52% (\bar{x} = 49%). The alpha angle is 57–58° (\bar{x} = 57°). The caudal edge of the coulter area is curved, with the retroarticular bone projecting caudad; the gamma angle is 123–129° (\bar{x} = 126°). The section of the mandibular canal in the anguloarticular runs obliquely along the coulter area; the beta angle is 12–15° (\bar{x} = 13°). There are four foramina on the bony mandibular canal in the dentary. There are one to three inner unicuspid tooth rows.

"*Aequidens*" (Fig. 8B). The lower jaw of "*A.*" *rivulatus* is short and high. The anguloarticular depth is 64–65% of its length. The primordial process is high and its tip is directed rostradorsad. The coulter area is deeper than wide; depth 36–38%; width 28–29%. The alpha angle is 89–90°. The caudal edge of the coulter area is almost straight and oblique, except at the ventral-caudal tip of the retroarticular. The gamma angle is 68–70°. The mandibular canal in the anguloarticular runs obliquely along the coulter area; the beta angle is 19–20°. There are four foramina on the bony mandibular canal in the dentary. There are one to three unicuspid inner rows of teeth.

Aequidens tetramerus and *Cichlasoma* (Fig. 8C). The lower jaw is short and high. The anguloarticular depth is 67–82% (\bar{x} = 74%) of its length. The primordial process is high; its tip is directed rostradorsad. The coulter area is deeper than wide; depth 29–43% (\bar{x} = 37%), width 23–26% (\bar{x} = 24%). The alpha angle is 93–107° (\bar{x} = 100°). The caudal edge of the coulter area is almost straight, except at the small posteroventral process of the retroarticular; the gamma angle is 74–89° (\bar{x} = 83°). The caudal edge is almost parallel to the rostral one. The mandibular canal runs obliquely on the anguloarticular; the beta angle is 30–35° (\bar{x} = 33°). There are four exit foramina on the bony mandibular canal in the dentary (Fig. 2C).

There are one to three inner unicuspid tooth rows.

Apistogramma (Fig. 8D). The lower jaw is short and high. The anguloarticular depth is 63–68% (\bar{x} = 64%) of its length. The primordial process is high, its tip is directed rostradorsad. The coulter area is wider than deep; width 37–39% (\bar{x} = 37%), depth 26–32% (\bar{x} = 28%). The alpha angle is 31–58° (\bar{x} = 52°). The caudal edge of the coulter area is curved; the caudal-ventral corner of the retroarticular bears a small posteroventral process; the gamma angle is 78–82° (\bar{x} = 80°). There is no bony mandibular canal in the coulter area in any of the specimens of *A. borellii* that were examined, but there is a bony canal in the dentary. In *A. commbrae* the mandibular canal runs obliquely by the coulter area; the beta angle is 16–22° (\bar{x} = 19°). Both species bear five exit foramina on the bony mandibular canal in the dentary. There are one to two inner unicuspid teeth rows.

Astronotus (Fig. 8E). The lower jaw is short and high; the anguloarticular depth is ~68% of its length. The primordial process of the anguloarticular is long and directed rostradorsad with respect to the ventral margin of the anguloarticular anterior arm. The coulter area is deeper than wide; depth ~33%, width 27%. The alpha angle is ~95°. The caudal margin of the coulter area is straight except where the retroarticular process is situated; the gamma angle is ~91°. The mandibular canal on the anguloarticular runs obliquely over the coulter area; the beta angle is ~20°. There are five foramina on the bony mandibular canal in the dentary as in *Apistogramma*, but they open differently to the skin. In *Apistogramma*, as well as most cichlids studied here, the mandibular canal opens to the skin through simple pores, one per foramen in the bony canal. In *Astronotus*, numerous small foramina pierce the skin covering each foramen in the bony canal. There are one to two inner unicuspid tooth rows.

Bujurquina (Fig. 8F). The lower jaw of *B. vittata* is short and high. The anguloarticular depth is 70–74% (\bar{x} = 71%) of its length. The primordial process of the anguloarticular is high; its tip is directed rostradorsad. The coulter area is a bit deeper than wide; depth 38–43% (\bar{x} = 40%), width 31–36% (\bar{x} = 34%). The alpha angle is 85–92° (\bar{x} = 89°). The caudal edge of the coulter area

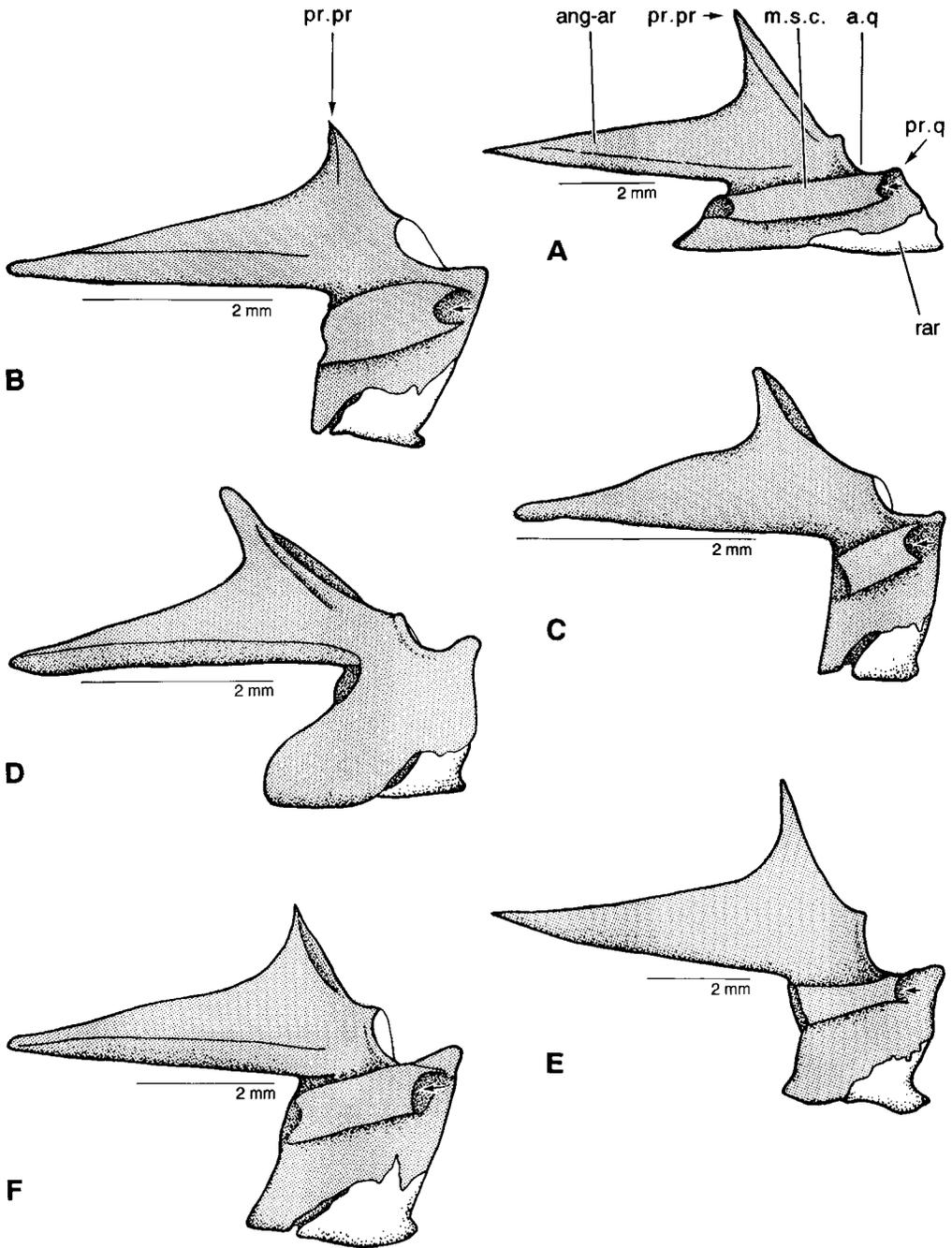


Fig. 8. Posterior part of lower jaws (in lateral view) of certain American cichlids. **A:** *Acaronia nassa*. **B:** "*Aequidens*" *rivulatus*. **C:** *Cichlasoma dimerus*. **D:** *Apistogramma borellii*. Note the absence of a bony enclosed mandibular sensory canal. **E:** *Astronotus ocellatus*. **F:** *Bujurquina vittata*. Arrows indicate the posterior opening of the mandibular sensory canal.

is straight (except at the ventral-caudal tip of the retroarticular), oblique and parallel to the rostral edge; the gamma angle is 73–81° (\bar{x} = 77°). The mandibular canal on the anguloarticular runs obliquely over the coultter area; the beta angle is 16–20° (\bar{x} = 17°). There are four foramina on the bony mandibular canal in the dentary. There are one to four inner unicuspid tooth rows.

Caquetaia and Petenia (Fig. 9A). The lower jaws of *C. myersi* and *P. splendida* are long and low. The anguloarticular depth is 24–30% (\bar{x} = 27%) of its length. The primordial process is low, its tip is directed dorso-rostrad. The coultter area is wider than deep; depth 12–15% (\bar{x} = 14%), width 30–41% (\bar{x} = 36%). The alpha angle 83–125° (\bar{x} = 105°). The caudal edge of the coultter area is deeply excurved, and the retroarticular bears a conspicuous process; the gamma angle is 129–135° (\bar{x} = 131°). The mandibular canal runs obliquely over the coultter area; the beta angle is 6–13° (\bar{x} = 10°). There are four exit foramina on the bony mandibular canal in the dentary that open to the skin through numerous small pores. There are one to two inner tooth rows.

Chaetobranchopsis. The lower jaw is long. The anguloarticular depth is ~57% of its length. The primordial process of the anguloarticular is long and directed rostradorsad with respect to the ventral margin of the anterior arm of the anguloarticular. The coultter area is wider than deep; depth ~21%, width ~29%. The alpha angle is ~60°. The caudal margin of the coultter area is almost straight; the gamma angle is ~98°. The mandibular canal of the anguloarticular runs obliquely over the coultter area; the beta angle is ~20°. In medial view, the rostral-dorsal zone of the coultter area bears a blunt process directed dorsad that it is identified herein as "nipple" process. There are five foramina on the bony mandibular canal in the dentary that open to the skin through several small pores. There are one to two inner series of small unicuspid teeth.

Chaetobranchus (Fig. 9D). The lower jaw is long. The anguloarticular depth is ~55% of its length. The primordial process of the anguloarticular is long and directed dorso-rostrad with respect to the ventral margin of the anterior arm of the anguloarticular. The coultter area is a bit wider than deep at the level of the ventral portion of the second mandibular lateral line foramen; its depth is

~26%, its width ~27% of the anguloarticular anterior arm length. The caudal margin of the coultter area is almost straight, except for a small process of the retroarticular; the gamma angle is ~95°. The mandibular canal of the anguloarticular runs obliquely over the coultter area; the beta angle is ~23°. There are five foramina on the bony mandibular canal in the dentary that open to the skin through numerous small pores. There are one to two inner unicuspid tooth rows.

Cichla (Fig. 9B). The lower jaw is elongate. The anguloarticular depth is 50–55% (\bar{x} = 53%) of its length. The primordial process of the anguloarticular is long and directed dorso-rostrad. The coultter area is wider than deep at the level of the ventral portion of the second mandibular lateral line foramen; depth 14–18% (\bar{x} = 16%), width 31–35% (\bar{x} = 34%). The alpha angle is 35–40° (\bar{x} = 36°). The caudal margin of the coultter area is almost straight, the retroarticular process is small; the gamma angle is 74–75° (\bar{x} = 74°). The mandibular canal on the anguloarticular runs obliquely over the coultter area; the beta angle is 15–20° (\bar{x} = 17°). There are five foramina on the bony mandibular canal in the dentary; the canal opens to the skin by a series of small openings. There are up to three inner rows of unicuspid small teeth.

"Cichlasoma" (Figs. 2D, 9C). "*C.*" *facetum* has a short and high lower jaw. The anguloarticular depth is 62–78% (\bar{x} = 74%) of its length. The primordial process is high and its tip is directed rostradorsad. The coultter area is deeper than wide; depth 24–44% (\bar{x} = 36%), width 27–33% (\bar{x} = 28%). The alpha angle is 79–133° (\bar{x} = 117°). The caudal edge of the coultter area is curved, the gamma angle is 85–90° (\bar{x} = 87°). The mandibular canal on the anguloarticular runs obliquely over the coultter area; the beta angle is 11–22° (\bar{x} = 17°). There are four foramina on the bony mandibular canal in the dentary that open by one pore on the skin in "*C.*" *facetum*, "*C.*" *beani*, and "*C.*" *cyanoguttatum*, and by numerous pores in "*C.*" *citrinellum*. There are one to four inner unicuspid tooth rows. The lower jaws of "*C.*" *citrinellum*, "*C.*" *beani*, and "*C.*" *cyanoguttatum* are similar to those of "*C.*" *facetum*.

Crenicichla (Fig. 9E). The members of this genus have an elongate and low lower jaw. The anguloarticular depth ranges between 53–57% (\bar{x} = 55%) of its length. The

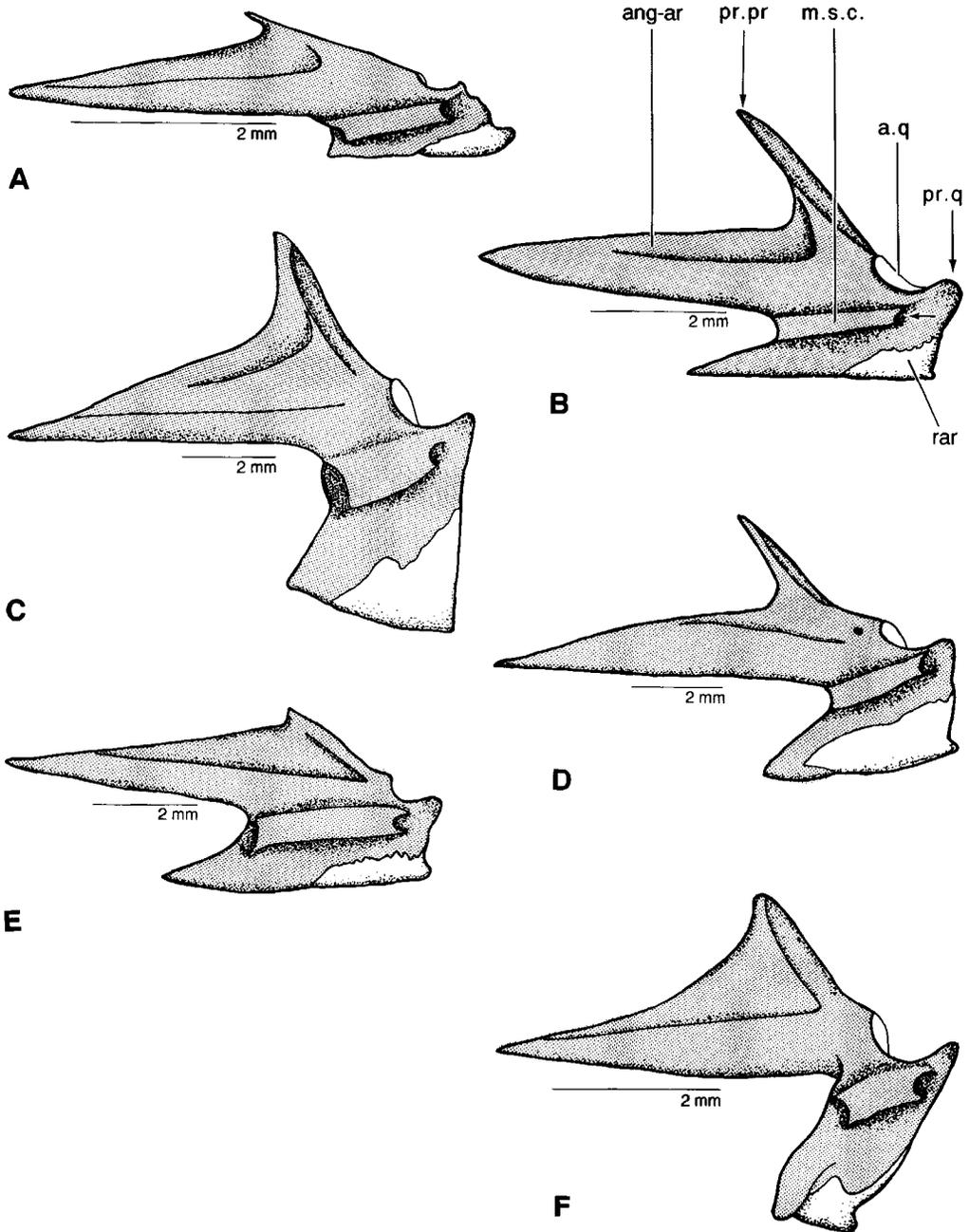


Fig. 9. Posterior part of lower jaws (in lateral view) of certain American cichlids. A: *Caquetaia myersi*. B: *Cichla temensis*. C: "*Cichlasoma*" *facetum*. D: *Chaetobranchius flavescens*. E: *Crenicichla lepidota*. F: *Gymnogeophagus australis*.

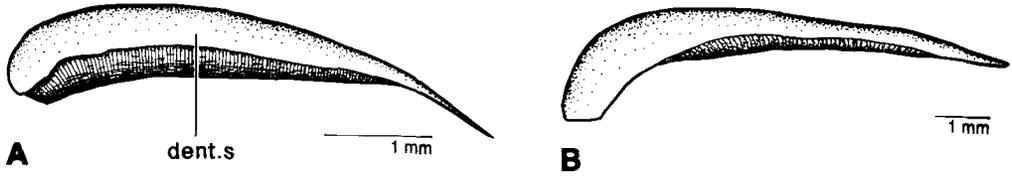


Fig. 10. Diagrammatic view of the oral margin of the dentary of "*Cichlasoma*" *facetum* (A), and of *Crenicichla vittata* (B).

primordial process of the anguloarticular is short and directed dorsorostrad, but in one individual of *C. scottii* (320 mm TL) and in one specimen of *C. vittata* (340 mm TL) this process is directed dorsad. The couler area is wider than deep; its depth 14–27% (\bar{x} = 18%), its width 43–52% (\bar{x} = 48%). The alpha angle is 28–55° (\bar{x} = 40°). The caudal edge of the couler area is straight, except at the caudal-ventral corner where the retroarticular bears a small process; the gamma angle is 79–87° (\bar{x} = 82°). The mandibular canal on the anguloarticular runs obliquely by the couler area; the beta angle is 13–25° (\bar{x} = 18°). In dorsal view, the rostral third of the dentary is more curved than in the remaining genera (compare A and B, Fig. 10). There are five foramina on the bony mandibular canal in the dentary; each opens to the skin through a simple pore in *C. cf. iguassuensis*, *Crenicichla scottii*, and *C. semifasciata*, but through several small pores in *C. proteus*, *C. lepidota*, and *C. vittata*. There are one to three inner unicuspid rows of teeth in *C. semifasciata* and one to seven in the remaining *Crenicichla*.

Acarichthys, *Gymnogeophagus*, "*Geophagus*" *brasiliensis*, and "*G.*" *crassilabris* (Figs. 2C, 9F). These genera present a short and high lower jaw. The anguloarticular depth is 70–75% (\bar{x} = 72%) of its length. The primordial process of the anguloarticular is high, and its blunt tip is directed rostrad. The couler area is deep and narrow; depth is 32–45% (\bar{x} = 41%) and width is 20–22% (\bar{x} = 21%). The alpha angle is 55–84° (\bar{x} = 70°). The caudal edge of the couler area is oblique and parallel to the rostral edge, the gamma angle is 65–70° (\bar{x} = 68°). The mandibular canal on the anguloarticular runs oblique over the couler area; the beta angle is 24–27° (\bar{x} = 26°). There are five foramina on the bony mandibular canal in the dentary (Fig. 2D). *Acarichthys* bears three or four small pores perforating the skin in front of each

foramen in the bony canal; *Gymnogeophagus* has only one. There are one to three inner teeth rows.

Laetacara (Fig. 11A). The lower jaw is short and high. The anguloarticular depth is 74–87% (\bar{x} = 80%) of its length. The primordial process is high, its tip directed rostrad. The couler area is deeper than wide; its depth is 41–44% (\bar{x} = 43%) and width is 24–27% (\bar{x} = 25%). The alpha angle is 86–92° (\bar{x} = 90°). The caudal edge of the couler area is curved; the gamma angle is 80–87° (\bar{x} = 83°). The mandibular canal on the anguloarticular runs obliquely by the couler area; the beta angle is 20–25° (\bar{x} = 23°). There are four foramina on the bony mandibular canal in the dentary. There are one to three inner unicuspid teeth rows.

Neetroplus (Fig. 11C, D). The lower jaw is short and high. The anguloarticular depth is 90–93% (\bar{x} = 92%) of its length. The primordial process is high, its tip directed rostrad. The couler area is deeper than wide; its depth 40–44% (\bar{x} = 43%), width 20–29% (\bar{x} = 25%). The alpha angle is 86–88° (\bar{x} = 87°). The caudal edge of the couler area is curved; the gamma angle is 72–76° (\bar{x} = 74°). The mandibular canal on the anguloarticular runs obliquely over the couler area; the beta angle is 25–30° (\bar{x} = 27°). In medial view, the rostral-dorsal zone of the couler area bears a blunt process directed dorsad, the "nipple" process (Fig. 11D). A similar process is also found in *Chaetobranchopsis*, although absent in all Cichlasomine Group A studied herein. In the same view, the zone where the coronoid and ventral arms of the dentary meet is expanded mediad. There are four foramina on the bony mandibular canal in the dentary that open to the skin through several small foramina. Similar to the premaxilla (Fig. 7A), the dentary outer teeth are implanted in a steplike pattern

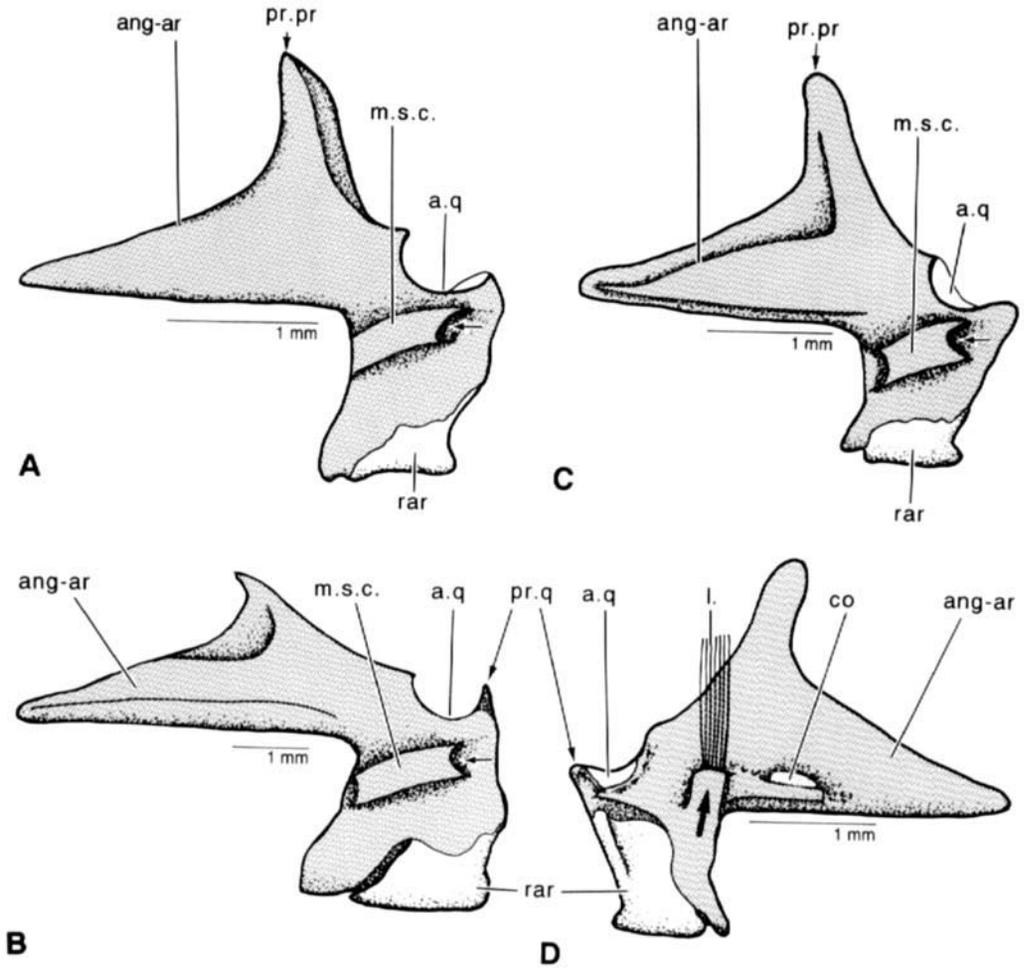


Fig. 11. Posterior part of lower jaws in lateral (A–C) and medial (D) views. **A:** *Laetacara dorsigera*. **B:** *Papiliochromis ramirezi*. **C, D:** *Neetroplus nematopus*. Arrows indicate the posterior opening of the mandibular sensory canal; large arrow points to the “nipple” process.

dorsal to the inner ones. There are one to three inner unicuspid tooth rows.

Papiliochromis (Fig. 11B). The lower jaw is short and high. The anguloarticular depth is 70–78% of its length. The primordial process is high and its tip is directed rostrodor-sad. The coulter area is deeper than wide; depth 43–62%, width 34–43%. The alpha angle is 66–73°. The caudal edge of the coulter area is curved, with a blunt process at one-half of its length; the gamma angle is 89–91°. The postarticular process is acute. The mandibular canal on the anguloarticular runs obliquely over the coulter area; the beta angle is 15–20° (\bar{x} = 17°). There are five foram-

ina on the bony mandibular canal of the dentary, and one or two inner unicuspid tooth rows.

Pharyngeal jaws

The upper pharyngeal jaws include pharyngobranchials 2, 3, and the fourth represented by cartilage, and their dentigerous plates (Fig. 12A). Pharyngobranchial 2 is the anterior-most element; it bears a slightly elongate dentigerous plate with <10 teeth. Pharyngobranchial 3 is the largest bone of the series and bears the largest dentigerous plate in all the genera examined except *Chaetobranchop-sis* and *Chaetobranchus*, which have larger

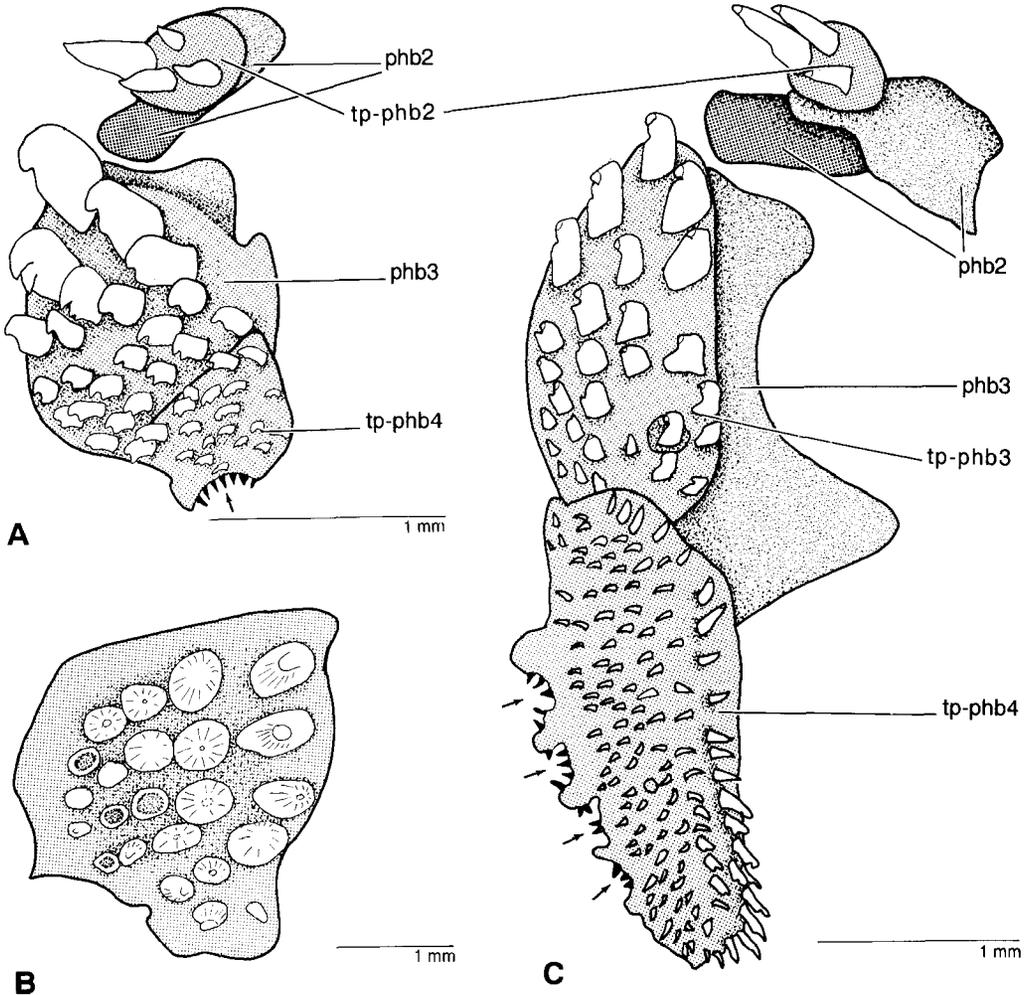


Fig. 12. Upper pharyngeal jaws of certain American cichlids. **A:** *Laetacara dorsigera* (frayed zone indicated by arrow). **B:** Pharyngobranchial 3 of *Crenicichla semifasciata* illustrating the molariform dentition. **C:** *Chaetobranchius flavescens* (arrows point to frayed zone).

tooth plates on the cartilaginous pharyngobranchial 4 than on pharyngobranchial 3 (Fig. 12C). The caudal edge of pharyngobranchial 3 articulates with the anterior edge of pharyngobranchial 4 tooth plate.

The dentigerous plates of pharyngobranchials 3 and 4 bear unicuspid, bicuspid (hooked), and/or molariform teeth. The largest teeth are in the rostral region of the pharyngobranchial plates.

Most species have unicuspid and bicuspid (hooked) teeth. Exceptions to this rule are found in *Cichla*, which bear exclusively unicuspid teeth, and in *Crenicichla semifasci-*

ata, "*Cichlasoma*" *citrinellum* (Meyer, '90a; herein), and "*Cichlasoma*" *cyanoguttatum* with molariform teeth (Fig. 12B).

The caudal margin of the pharyngobranchial 4 tooth plate bears the frayed zone (sensu Barel et al., '76). The frayed zone is present in all New and Old World cichlids and consists of one or several (two to seven) shallow concavities bearing numerous, small unicuspid teeth attached on their wall[s] (Figs. 12A, C, 13A–D). In the remaining labroids, the frayed zone is absent in Pomacentridae and in Labridae. However, the condition is different between the two families,

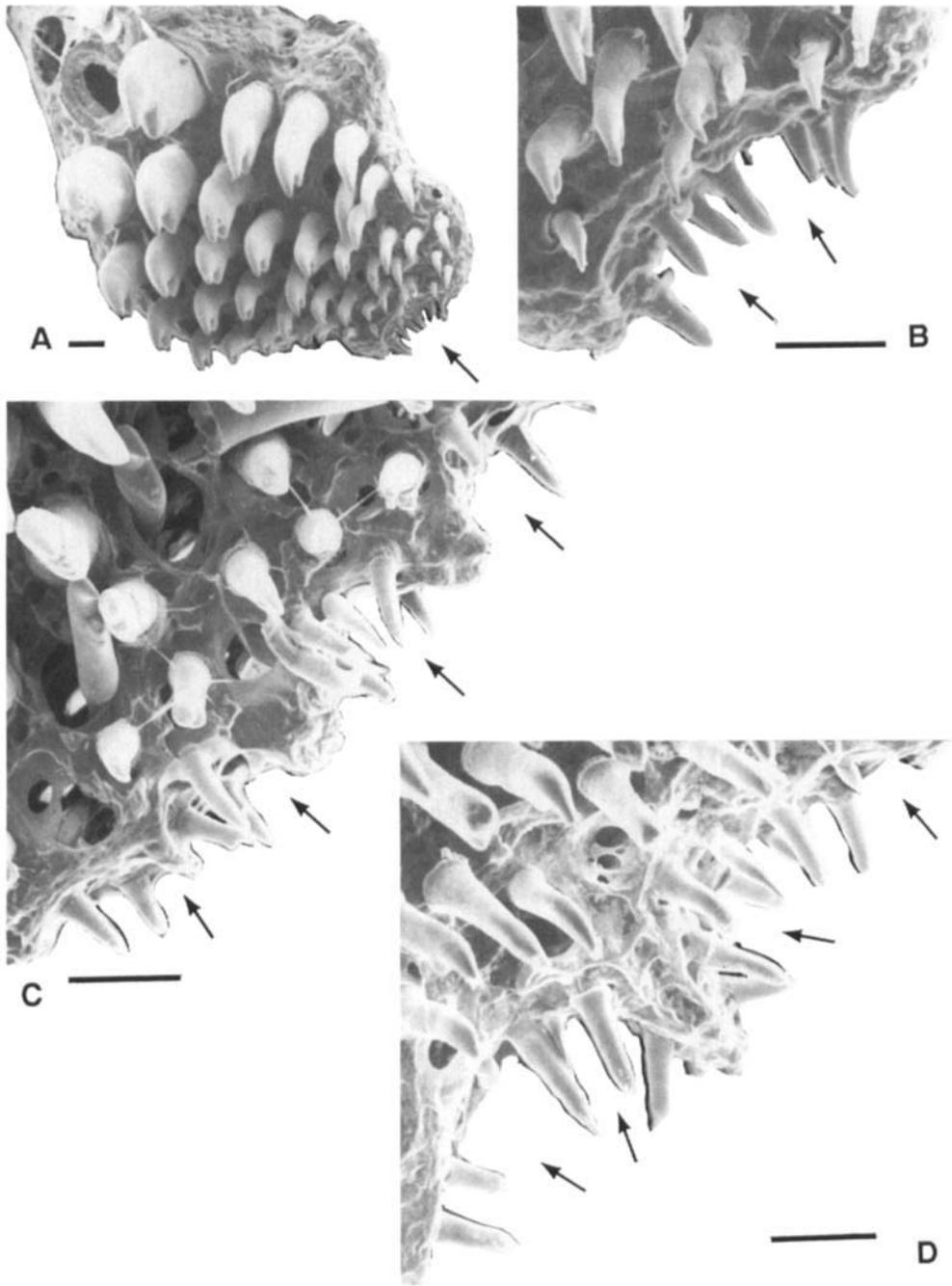


Fig. 13. SEM of upper pharyngeal jaw illustrating the frayed zone (indicated by arrows) in certain American cichlids. **A.** Upper pharyngeal jaw of *Laetacara dorsigera* (arrow indicates frayed zone with only one concavity) and enlargement of frayed zone (**B**). **C.** Frayed zone with several concavities (indicated by arrows) of "*Cichlasoma*" *facetum*. **D.** Frayed zone with two concavities (indicated by arrows) of *Cichlasoma dimerus*. Bars = 100 μ .

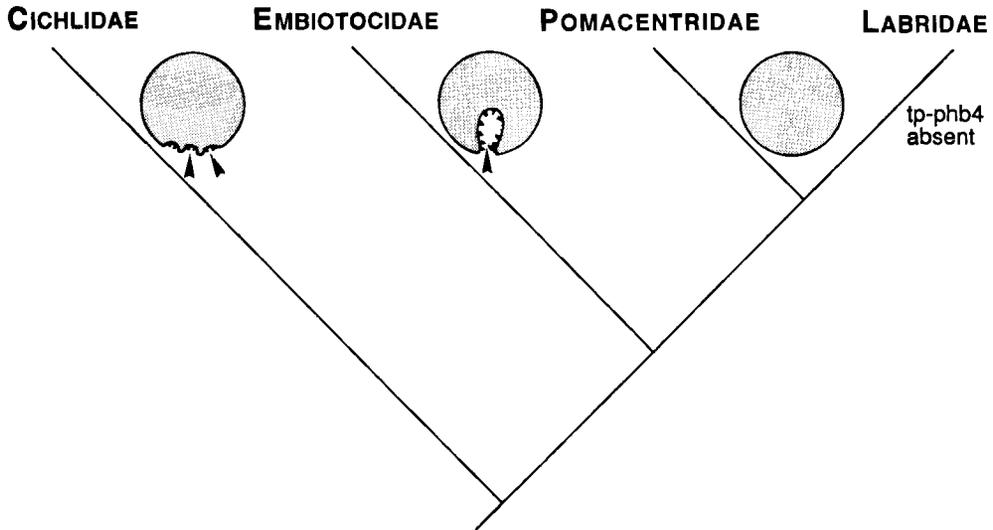


Fig. 14. Distribution of the frayed zone (indicated by arrowheads) and pharyngobranchial 4 tooth plate in labroids. Hypothesis of phylogenetic relationships according to Stiassny and Jensen ('87).

because Labridae lacks the fourth pharyngobranchial tooth plate. Embiotocidae is the other labroid, besides the cichlids, that bears a frayed zone. However, the frayed zone in Embiotocidae is always formed by only one cavity and it is much narrower and deeper than those present in cichlids (Fig. 14). Outside the labroids, a frayed zone is absent in basal percoids.

We have examined larval and juveniles of *Bujurquina vittata*, *Cichlasoma dimerus*, "*Cichlasoma*" *facetum*, and *Geophagus meridionalis* and in these species the frayed zone is well developed from early in ontogeny (individuals of ~ 10 mm SL).

A frayed zone with only one concavity is present in *Acaronia*, "*Aequidens*" *rivulatus*, *Crenicichla*, *Bujurquina*, *Caquetaia*, *Laetacara*, and in the Geophagine Group (Figs. 12A, 13A).

Two concavities (Fig. 13D; Kullander, '83; Fig. 21B, C) are present in *Aequidens tetramerus*, *Cichlasoma orinocense*, *Cichlasoma dimerus*, and *Cichlasoma amazonarum*. In *C. dimerus* the frayed zone is formed by only one concavity in individuals up to 14.6 mm SL, then the sole concavity separates into two by development of a bony ridge. Two concavities were also found in some specimens of *Neetroplus nematopus*. Three to seven concavities were found in *Astronotus*, *Chaetobranchopsis*, *Chaetobran-*

chus, *Cichla*, "*Cichlasoma*," *Neetroplus*, and *Petenia* (Fig. 13C).

The overall morphology of the lower pharyngeal jaws as illustrated by "*Cichlasoma*" (Fig. 15A) is similar in most of the taxa examined; however there is variation in some of them. For example, *Crenicichla semifasciata* and "*Cichlasoma*" *cyanoguttatum* have hypertrophied lower pharyngeal jaws (sensu Hoogerhoud and Barel, '78) with stout bases, short horns, and molariform teeth (Fig. 15B). In *Chaetobranchopsis* and *Chaetobranchus*, the lower pharyngeal jaws are slender, with elongate rostral arms that bear numerous small teeth, whereas a single tooth is present in the rostral region (Fig. 15C; Kullander, '86; Fig. 21).

The lower pharyngeal jaws may be sutured all along the sagittal axis or not. In *Cichla* the lower pharyngeal jaws are not sutured all along the sagittal axis (Fig. 15D; Stiassny, '82) contrary to all other cichlids. American cichlids with sutured lower pharyngeal jaws may present both jaws joined by a harmonic suture (e.g., "*Aequidens*" *rivulatus*, *Apistogramma*, *Astronotus*, *Caquetaia*, *Chaetobranchus*, *Chaetobranchopsis*, *Laetacara*, *Papiliochromis*, and *Petenia*) or by a dentate suture (e.g., *Acarichthys*, *Acaronia*, *Aequidens*, *Bujurquina*, *Cichlasoma*, "*Cichlasoma*," "*Geophagus*" *brasiliensis*, and *Neetroplus*), observed in the ventral aspect of jaws. A harmonic

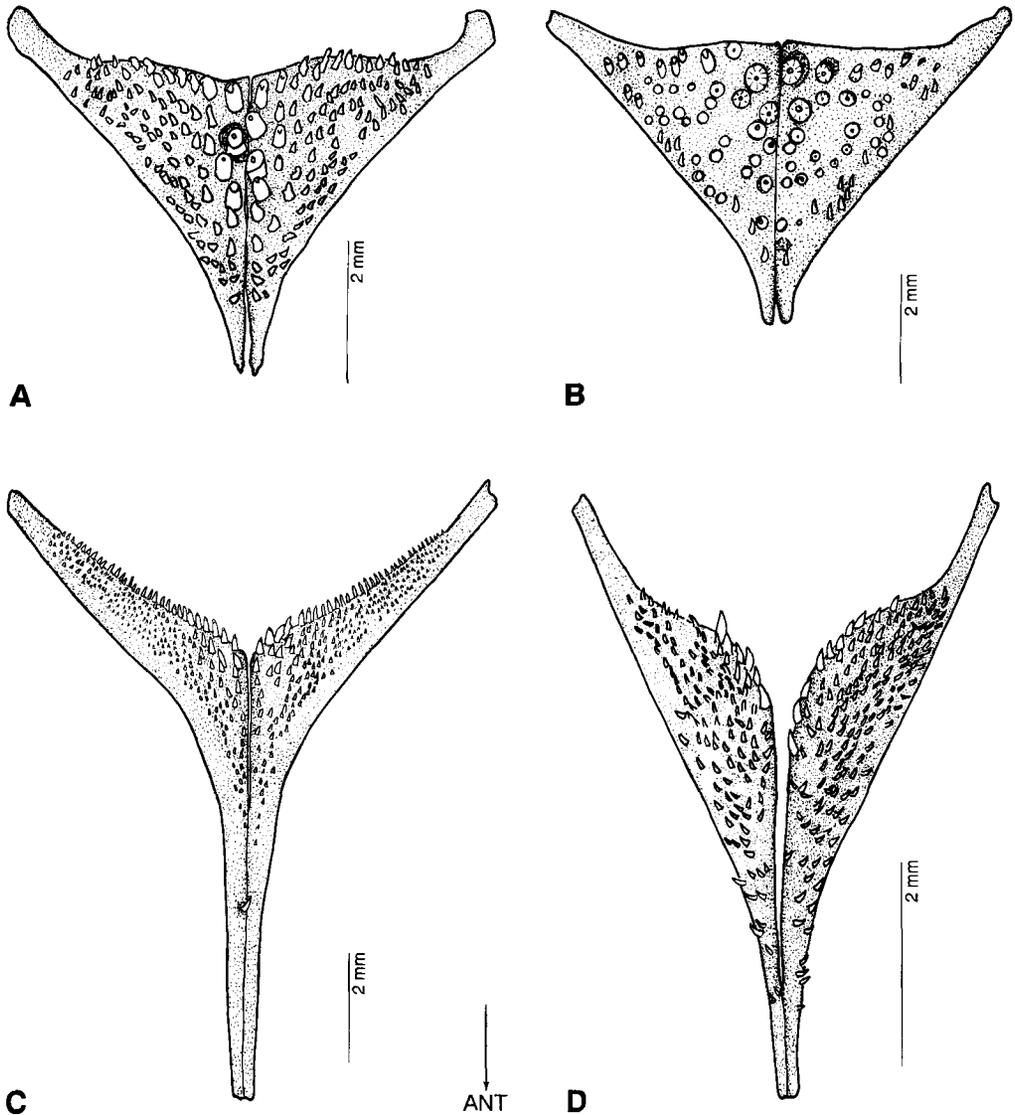


Fig. 15. Lower pharyngeal jaws (occlusal view) of "*Cichlasoma*" *facetum* (A); *Crenicichla semifasciata* (B); *Chaetobranchus flavescens* (C); and *Cichla temensis* (D).

suture is present in *Gymnogeophagus*, with the exception of *G. gymnogenys*, which has only one indentation joining both part of the jaw; a similar condition is observed in "*Geophagus*" *crassilabris*.

Among American cichlids with a dentate suture between the lower pharyngeal jaws, there is ontogenetic variation in the development of the suture. First, both articular surfaces are smooth (harmonic suture), and during growth, indentations begin to appear in

the articular surface producing a dentate suture. The number of indentations increases during ontogeny.

Some species bear gill rakers on the lateral sides of the lower pharyngeal jaws. These structures can be situated all along the lateral margins or restricted to some portion of the lower pharyngeal jaws. Well-developed gill rakers bearing teeth are present in *Crenicichla* (Fig. 16A, B), with the exception of *Crenicichla semifasciata*. Reduced gill rak-

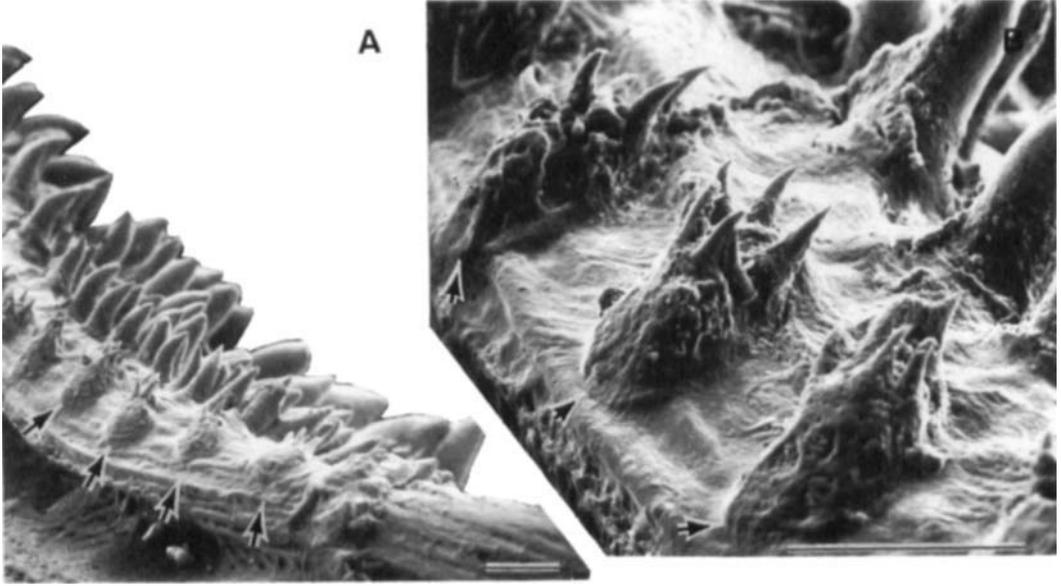


Fig. 16. SEM of dentated gill rakers (A, B), indicated by arrows, on the lower pharyngeal jaw of *Crenicichla scottii*. Bars = 500 μ .

ers without teeth occur in *Cichla* and most geophagines such as *Apistogramma*, *Acarichthys*, "*Geophagus*" *brasiliensis*, and "*Geophagus*" *crassilabris*.

COMPARATIVE MORPHOLOGY OF TEETH

Most of the species examined have both premaxilla and dentary that bear unicuspid, acutely conical teeth (Figs. 2C, D; 17A). Different shapes in teeth were found only in *Neotroplus nematopus* and in "*Cichlasoma*" *facetum*, "*C.*" *cyanoguttatum*, "*C.*" *guttulatum*, and "*C.*" *spilurum*. In *Neotroplus nematopus* the teeth of both upper and lower jaws have crownlike, scraping blades, with their bases broadened and compressed laterad, and their crowns compressed rostrocaudad (Fig. 7B). These teeth are directed forward and almost parallel to the horizontal plane.

Bicuspid teeth with a second cusp (minor cusp of Barel et al., '76) similar to a tubercle in the inner face of the neck zone are present in individuals of great size (~150 mm SL) of "*Cichlasoma*" *facetum* (Fig. 17B; Kullander, '83; Fig. 102), in "*C.*" *cyanoguttatum*, and "*C.*" *guttulatum* (~116 mm SL), and in individuals of small or great size of "*C.*" *spilurum*.

Teeth with strongly compressed crowns (Fig. 7B) are found in *Neotroplus nematopus*,

and moderately compressed occur in "*C.*" *cyanoguttatum*.

The degree of curvature of the teeth is variable, ranging from vertical to strongly recurved within one individual. The strongly recurved type is frequent in the inner series of teeth in *Crenicichla*.

During ontogeny the first teeth arising on the jaws are those of the outer series and those situated near the symphyseal zone. The teeth of the inner series are not well developed in individuals <10.5 mm SL of *Bujurquina vittata*, *Cichlasoma dimerus*, "*Cichlasoma*" *facetum*, and *Gymnogeophagus meridionalis*.

The teeth of the upper and lower jaws are ordered in an outer row plus several inner rows. Most genera have up to four inner rows of teeth close to the symphyseal zone, *Crenicichla* has up to seven, with the exception of *Crenicichla semifasciata*, and *Cichla* has up to six. The largest teeth are found in the outer row and close to the symphyseal zone.

The number of teeth on the jaws increases rapidly in early ontogeny. For instance, we observed eight teeth in the outer hemiseries in one individual of *Cichlasoma dimerus* of 4.6 mm SL, but the number increases to 12 at 14.6 mm SL, to 14 at 16.4 mm SL, and 15

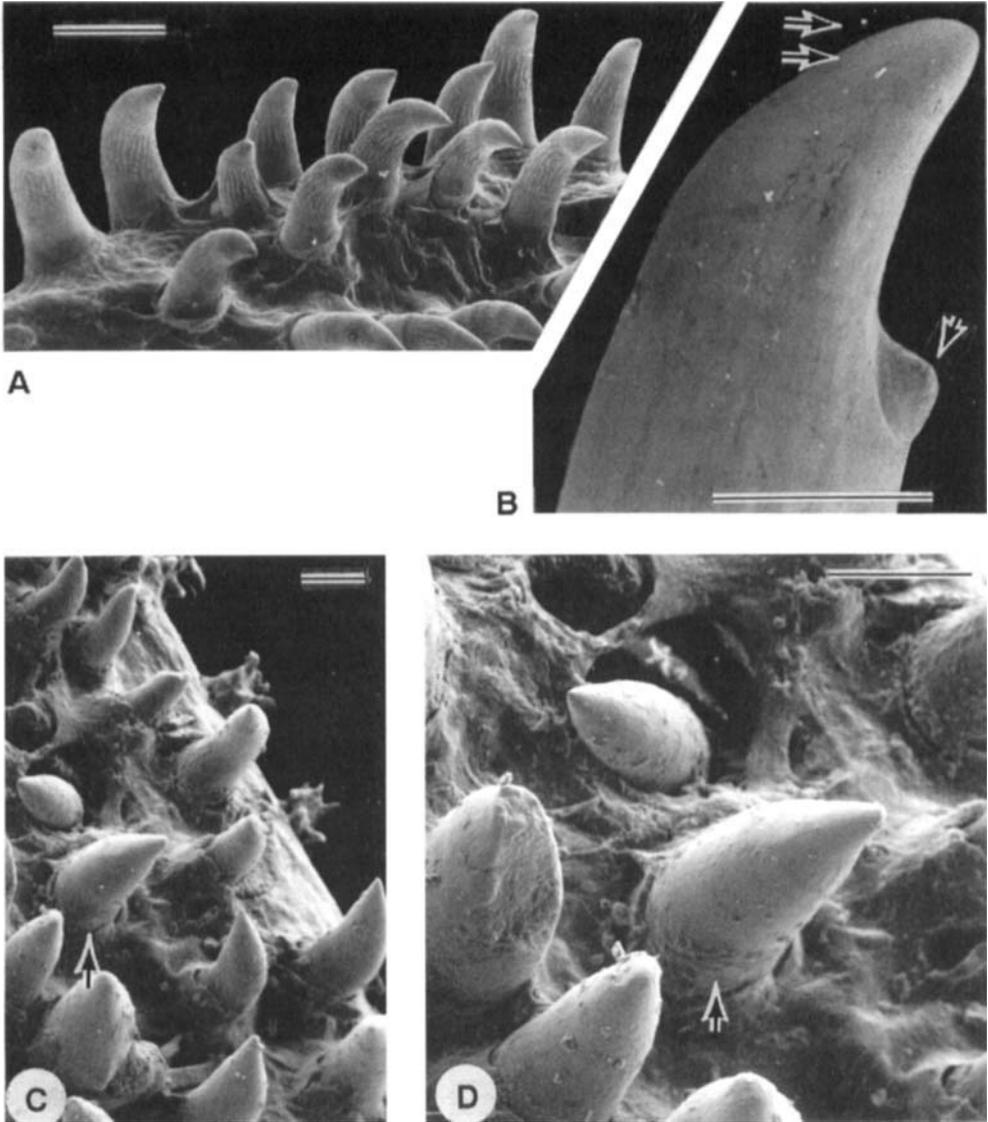


Fig. 17. SEM of teeth of certain American cichlids. Premaxillary teeth of *Crenicichla vittata* (A) and "*Cichlasoma*" *facetum* (B). Two arrows point to the major cusp and one arrow points to the minor cusp. Bars = 250 μ . C, D: Lower pharyngeal jaw unicuspid tooth curved anteriorly in *Crenicichla scottii*. Bars = 200 μ .

at 17.5 mm SL. Fifteen teeth are found in individuals of 46.0–140.0 mm SL.

The number of teeth in the outer row varies intraspecifically in the species examined (Table 1). Differences occur intraspecifically among premaxillary and/or dentary teeth, and also between left and right premaxillae and/or dentaries.

Replacement teeth are commonly observed on premaxillae and dentaries.

Pharyngeal jaw teeth

The greatest diversity of tooth shapes is found on the pharyngeal jaws. Seven morphological types (A–G) are observed in the following specimens examined.

TABLE 1. Number of premaxillary and dentary teeth of the outer row in American cichlids

| Species | n ¹ | Premaxillary teeth range | \bar{x} ² | Dentary teeth range | \bar{x} ² |
|--|----------------|--------------------------------|------------------------|---------------------------|------------------------|
| <i>Acarichthys heckelii</i> | 1 | 19 | — | 23 | — |
| <i>Acaronia nassa</i> | 5 | 27-33 | 30 | 25-34 | 29 |
| " <i>Aequidens</i> " <i>rivulatus</i> | 2 | 8-9 | — | 15-16 | — |
| <i>Aequidens tetramerus</i> | 4 | 13-15 | 14 | 20-25 | 23 |
| <i>Bujurquina vittata</i> | 15 | 14-21 | 16 | 19-20 | 18 |
| <i>Bujurquina moriorum</i> | 3 | 14-19 | 16 | 19-20 | 18 |
| <i>Apistogramma borellii</i> | 10 | 16-19 | 18 | 17-21 | 19 |
| <i>Apistogramma commbrae</i> | 10 | 15-23 | 18 | 18-25 | 20 |
| <i>Astronotus ocellatus</i> | 1 | 18 | — | 20 | — |
| <i>Caquetaia myersi</i> | 3 | 12-15 | 13 | 20-22 | 17 |
| <i>Cichla temensis</i> | 3 | 30-35 | 33 | 33-36 | 34 |
| <i>Chaetobranchopsis orbicularis</i> | 1 | 25 | — | 11? | — |
| <i>Chaetobranchus flavescens</i> | 1 | 15 | — | — | — |
| <i>Cichlasoma dimerus</i> | 18 | 8-21 | 13 | 14-21 | 17 |
| <i>Cichlasoma orinocense</i> | 1 | 16 | — | 22 | — |
| " <i>Cichlasoma</i> " <i>beani</i> | 1 | 14 | — | 13 | — |
| " <i>Cichlasoma</i> " <i>citrinellum</i> | 8 | 12-15 | 13 | 17-24 | 21 |
| " <i>Cichlasoma</i> " <i>cyanoguttatum</i> | 4 | 14-20 | 17 | 16-24 | 9 |
| " <i>Cichlasoma</i> " <i>facetum</i> | 20 | 8-19 | 12 | 8-17 | 13 |
| <i>Crenicichla</i> cf. <i>iguassuensis</i> | 4 | 20-26 | 24 | 20-30 | 27 |
| <i>Crenicichla lepidota</i> | 10 | 35-42 | 38 | 35-41 | 38 |
| <i>Crenicichla scottii</i> | 4 | 27-30 | 27 | 22-33 | 28 |
| <i>Crenicichla semifasciata</i> | 4 | 18-26 | 20 | 17-25 | 20 |
| <i>Crenicichla vittata</i> | 7 | 35-42 | 38 | 27-40 | 34 |
| <i>Gymnogeophagus australis</i> | 5 | 19-25 | 22 | 18-27 | 26 |
| <i>Gymnogeophagus balzanii</i> | 6 | 10-24 | 16 | 13-22 | 16 |
| <i>Gymnogeophagus gymnogenys</i> | 1 | 24 | — | 19 | — |
| <i>Gymnogeophagus rhabdotus</i> | 2 | 9-12 | — | 12-18 | — |
| <i>Gymnogeophagus meridionalis</i> | 20 | 10-17 | 14 | 17-22 | 19 |
| " <i>Geophagus</i> " <i>brasiliensis</i> | 2 | 11-16 | — | 16-20 | — |
| " <i>Geophagus</i> " <i>crassilabris</i> | 1 | 12 | — | 16 | — |
| <i>Lactacara dorsigera</i> | 15 | 5-9 | 7 | 5-20 | 14 |
| <i>Neetroplus nematopus</i> | 3 | 7-9 | 8 | 7-11 | 9 |
| <i>Papiliochromis ramirezi</i> | 2 | 10-12 | — | 17-23 | — |
| <i>Petenia splendida</i> | 1 | 27 | — | 31 | — |

¹Number of specimens examined.²Average.

Type A: *Unicuspid curved anteriorly* (Figs. 12C, 15A-D, 16A, 17C, D) is found in the marginal areas of the lower pharyngeal jaws in most species.

Type B: *Unicuspid recurved* (Fig. 18B,a) is present in the upper pharyngeal jaws of all species examined and in the lower pharyngeal jaws of *Acaronia*, *Caquetaia*, *Cichla*, *Crenicichla*, *Petenia*, and juveniles of *Crenicichla semifasciata*. In *Acaronia*, teeth of type B are restricted to the medial-rostral part of the lower pharyngeal jaw (Fig. 19B), whereas in crenicichlines, with the exception of *Crenicichla semifasciata*, *Caquetaia*, and *Petenia* they can occupy > 50% of the dentigerous area of the lower pharyngeal jaw (Figs. 15D, 19A). In subadult specimens of *Crenicichla semifasciata*, teeth of type B are restricted to the rostral part of the lower pharyngeal jaws, whereas in adults they are absent and replaced by molariform teeth. A

similar type B was observed in species of the African cichlid *Ramphochromis* by Stiassny ('81). The presence of type B may be related to the mode of ingestion and carrying of food.

Type C: *Bicuspid curved anteriorly [hooked]* (Fig. 18A) is most common in the lower pharyngeal jaws of the examined species. Teeth of this type are laterally compressed elements, with a major acute cusp and a minor one, somewhat blunted.

Type D: *Bicuspid curved posteriorly [hooked]* (Figs. 12A, C, 13A) is present in the upper pharyngeal jaws of all species, except for *Cichla*.

Type E: *Bicuspid crenulate, curved anteriorly* (Fig. 18B,b) is a variation of the hooked one described by Barel et al. ('77) as type C. Type E teeth are present in the lower and upper pharyngeal jaws of *Acaronia*, *Caquetaia*, and *Crenicichla*, with the exception of *C. semifasciata*. They are laterally com-

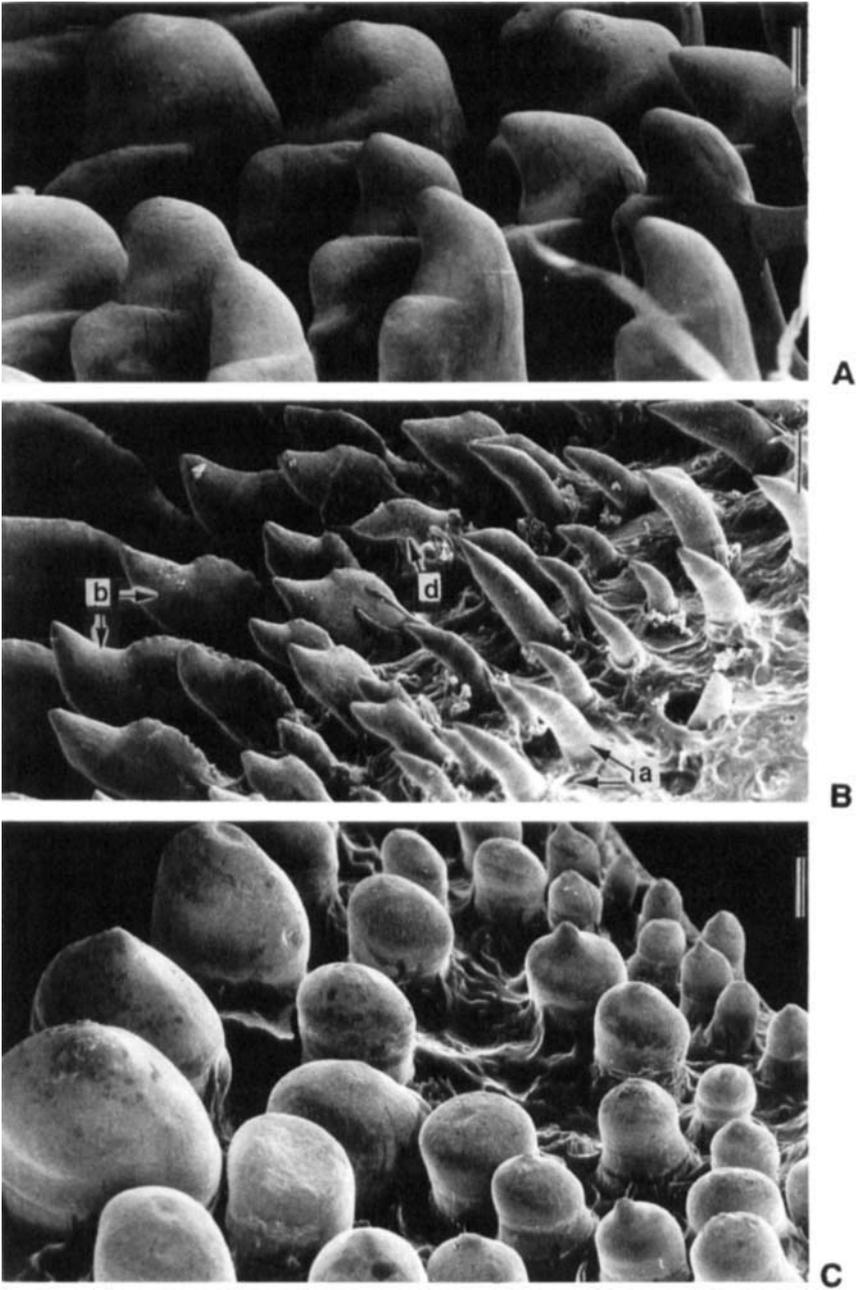


Fig. 18. SEM of lower pharyngeal jaw teeth of certain American cichlids. **A:** *Gymnogeophagus balzanii*, illustrating bicuspid dentition. **B:** *Crenichla lepidota*: (a) unicuspid recurved teeth; (b) bicuspid crenulate teeth; and (d) bevelled teeth. **C:** Molariform teeth of *Crenichla semifasciata*. Bars = 250 μ .

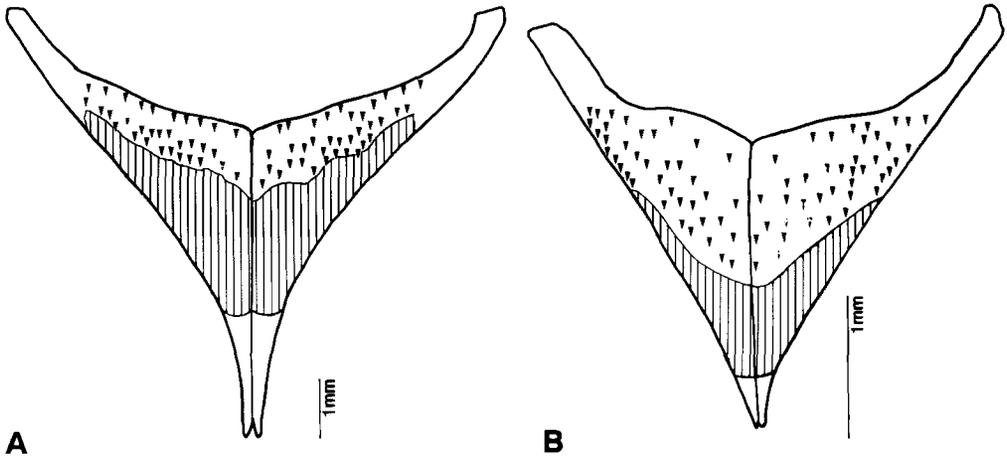


Fig. 19. Diagrammatic lower pharyngeal jaws illustrating the distribution of unicuspid recurved teeth (with vertical bars) and other tooth shapes (triangles) in *Crenicichla lepidota* (A) and *Acaronia nassa* (B).

pressed, with the major cusp acute and the minor provided with numerous crenulations. The hooked type of Barel et al. ('77) lacks crenulations and according to Witte and Barel ('76) would crush the prey between the pharyngeal plates before swallowing them.

The bevelled teeth of *Type F: Bevelled* (Fig. 18B,d) have a well-developed major cusp dorsal (Fig. 18B,c); an inconspicuous minor cusp is often present. This type was observed in the lower pharyngeal jaws of species of *Crenicichla*. In this genus, the bevelled teeth are more abundant between the unicuspid recurved and bicuspid crenulate elements. According to Witte and Barel ('76), these teeth serve to pinpoint a fish prey on the lower pharyngeal element.

Type G: Molariform (Figs. 12B, 18C) teeth present a wide and flat crown that occasionally bears a small central cusp. They are uncurved and sometimes less high than the other types. Molariform teeth, which are largest, occupy the central and posterior parts of the dentigerous area on the pharyngeal jaws. Among the cichlids studied, molariform teeth occur in *Cichlasoma dimerus*, "*Cichlasoma*" *facetum*, "*Cichlasoma*" *citrinellum*, "*Cichlasoma*" *cyanoguttatum*, *Crenicichla semifasciata*, *Gymnogeophagus balzanii*, "*Geophagus*" *brasiliensis*, and *Acarichthys heckelii*. The molariform teeth of the lower pharyngeal jaws of *Gymnogeophagus balzanii*, "*Geophagus*" *brasiliensis*, *Acarichthys heckelii*, and those of the upper pharyngeal jaw of "*Cichlasoma*" *citrinellum* are higher ele-

ments than the ones present in the remaining species. In "*C.*" *citrinellum*, the molariform teeth of the lower pharyngeal jaw are situated in two series in the posterior half of the bone, close to the sagittal suture. According to Meyer ('90a), "*C.*" *citrinellum* exhibits a distinct trophic polymorphism in the structure of its pharyngeal jaws. Fish have either strong molariform pharyngeal jaws or weak papilliform jaws.

Fourth ceratobranchial teeth

Other bones that may bear teeth are the fourth pair of ceratobranchials. Teeth on the fourth ceratobranchial have been observed by several authors (e.g., Pellegrin, '03; Kullander, '83). The teeth are unicuspid; they may be straight or curved posteriorly and are arranged in small patches in a variable number on ceratobranchial 4. The tooth patches are present in "*Aequidens*," *Acarichthys*, *Caquetaia*, *Cichlasoma*, *Cichla*, "*Cichlasoma*," *Crenicichla*, *Gymnogeophagus*, "*Geophagus*" *brasiliensis*, "*Geophagus*" *crassilabris*, *Papiliochromis*, *Caquetaia*, *Petenia*, and *Neetroplus*. Ceratobranchial teeth are present in *Gymnogeophagus meridionalis* that are > 11.5 mm SL. Specimens of *Cichlasoma dimerus* and "*Cichlasoma*" *facetum* between 4.6 mm and 17.5 mm SL do not have ceratobranchial teeth. In *Gymnogeophagus balzanii* (16.9 mm SL), we found four teeth on each bone, and in *Crenicichla lepidota* and *C. vittata* (41.5 mm SL), the teeth are arranged

in small patches with no more than three teeth per patch.

DISCUSSION

In general, the jaws of New World cichlids are very similar to those of Old World cichlids, and they provide one character (discussed below) that can be considered a synapomorphy for the family. However, the jaws supply several characters that are autapomorphies at the generic or specific level [e.g., the maxillad articulatory facet reaching the ascending spine (Fig. 4B) in *Apistogramma*, and the premaxillary dentigerous arm projecting rostrad at the symphysis (Fig. 3D) in *Chaetobranchius*]. In this respect, we are cautious in proposing a conclusion because in certain cases a few species or specimens of broadly diversified genera were examined.

The common condition among American cichlids is the presence of a premaxilla with the dentigerous arm shorter than the ascending arm (Figs. 3A, C, D, F, 4C, 5A, B). In contrast, *Astronotus*, *Cichla*, and *Crenicichla semifasciata* have the dentigerous arm longer than the ascending one (Fig. 3B, E). Following the scheme of phylogenetic relationships of Stiassny ('91), we interpret that the ascending arm shorter than the dentigerous one is an apomorphic state. It is an homoplastic character that has evolved independently in *Astronotus* and *Cichla* and *Crenicichla semifasciata*.

Most American cichlids do not have a process on the dorsolateral aspect of the premaxillary dentigerous ridge; this process (Fig. 3C) is present in a few genera such as *Petenia* and *Caquetaia* (members of Cichlasomine Group A), and in part of the Chaetobranchine Group (e.g., *Chaetobranchopsis*). Again, based on the scheme of relationships by Stiassny ('91), we consider that the process is an homoplastic character that has evolved independently in part of the Cichlasomine Group A and in the Chaetobranchine Group.

The relation between the width of the couler area versus its depth deserves a few comments. A wide couler area, wider than its depth, is found in *Cichla* (Fig. 9B), in the Chaetobranchine Group (Fig. 9D; with the exception of *Astronotus*) and in the Crenicichline Group (Fig. 9E). A narrow couler area, or one almost as wide as deep, is present in part of the Cichlasomine Group A (Figs. 9C, 11C, D) and Group B (Fig. 8B, C). Both conditions (wide and narrow) are present in the Cichlasomine Group A (e.g., *Neetroplus* has a narrow couler area in comparison to

Acaronia and *Caquetaia* with a wide couler area) and in the Geophagine Group (e.g., *Apistogramma* has a wide couler area, but other geophagines studied herein have a narrow one).

Barel et al. ('76; Fig. 205) described a small, blunt process in the medial aspect of the couler area near the lateral line foramen 2 in *Astatotilapia*; they named this protuberance a nipple process. A similar process was described for another African cichlid, *Rhamphochromis*, by Stiassny ('81) and was found herein in *Ectodus*. Among the American cichlids, a process in similar position to that in *Astatotilapia* is present in the Chaetobranchine Group (genus *Chaetobranchopsis*) and in the Cichlasomine Group A (genus *Neetroplus*; Fig. 11D). According to the distribution of this character (Fig. 20), we consider that the process present in the American cichlids is not homologous with that in the African *Astatotilapia* and *Rhamphochromis* and we identify it a "nipple" process. Considering that the phylogenetic relationships among the American cichlids are unresolved, we can not address properly the question of homology of these processes in *Chaetobranchopsis* and *Neetroplus*. However, based on the scheme of relationships by Stiassny ('91), these processes seem to be nonhomologous (Fig. 20).

Most cichlids have a complete mandibular canal enclosed by bone (primitive condition), whereas there is no canal (advanced condition) in the anguloarticular in *A. borellii* (Fig. 8D). A similar apomorphic condition is present in *Biotocus dicentrarchus* (Kullander, '89). The maximum known number of lateral line foramina of the bony sensory tubelike canal of the cichlid lower jaw is seven (Fig. 2C). Seven or six foramina are commonly found among the American cichlids (Fig. 2C, D). Seven lateral line foramina are present in the Crenicichline, the Chaetobranchine, and the Geophagine Groups studied herein. However, the condition varies in the Geophagine Group because seven foramina are present in *Apistogramma commbrae*, but only five in *A. commbrae*. Six lateral line foramina—two in the anguloarticular and four in the dentary—are observed in the Cichlasomine Groups A and B studied herein, corroborating Kullander ('83), who considered that the cichlasomines can be defined primarily by having four dentary lateralis foramina. The reduction in number of the foramina in the dentary is due to the loss of lateral line foramina

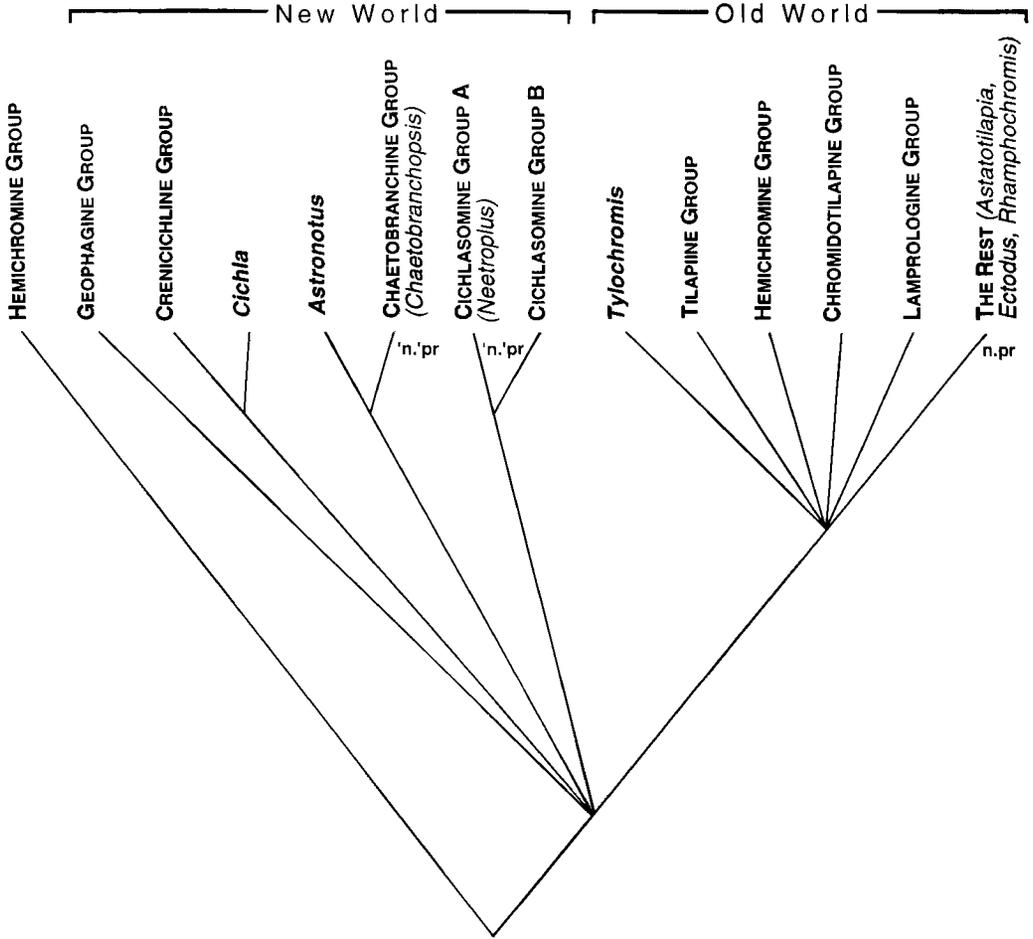


Fig. 20. Distribution of the nipple and "nipple" processes in certain cichlids indicated in parentheses. Abbreviated hypothesis of phylogenetic relationships of Old and New World cichlids according to Stiassny ('91). The Rest includes all the remainder African genera not included in the groups outlined in the figure.

4 or 5, but with the available information we can not prove one or another condition.

The lateral line foramina found in the lateral wall of the bony tubelike canal enclosing the mandibular sensory canal permit the exit of the mandibular canal to the skin that is effected through five or six single pores or by many small pores that perforate the skin covering the lateral line foramina piercing the bone. The determination of the presence of one pore or of numerous small pores on the skin can only be done in large individuals; we have observed that the latter condition develops during ontogeny and the number of pores in the skin increases during growth

and it is interpreted here as the apomorphic condition by comparison with the African and American cichlids examined. The presence of single pores associated to the lateralis foramina is the common condition observed in the cichlids examined (e.g., "*Cichlasoma*" and *Gymnogeophagus*); however, both conditions, single or numerous pores, are found in species included in the Crenicichline and Cichlasomine Group A. For instance, among the crenicichlines, single pores occur in *Crenichla iguassuensis*, *S. scottii*, and *C. semifasciata*, and numerous pores occur in *C. proteus*, *C. lepidota*, *C. vittata*, and *Cichla*. The presence of numerous pores

is an homoplastic character occurring in parallel in cichlasomines, chaetobranchines, crenicichlines, and geophagines.

The presence of the frayed zone in the caudal margin of the fourth pharyngobranchial tooth plate (Figs. 12A, C, 13A-D, 14) may be considered as a symplesiomorphy of Labroidei (Cichlidae and Embiotocidae) that is lost in advanced labroids (Labridae and Pomacentridae). However, the frayed zone has unique characteristics in both clades. One to seven shallow concavities are found in Cichlidae, whereas in Embiotocidae, the frayed zone is composed of only one cavity much deeper and narrower than those present in cichlids. The condition present in Embiotocidae is interpreted herein as a different character state from that present in the Cichlidae. According to the distribution of the frayed zone in labroids (Fig. 14) and its absence in their possible ancestors, the frayed zone in cichlids and embiotocids is interpreted herein as independently acquired in both families.

The frayed zone of cichlids may have one or more (up to seven) concavities (Figs. 12A, C, 13A-D). Only one concavity is found in the Geophagine Group. More than one concavity is found in the Chaetobranchine Group. Presence of one, or more than one, concavity is the condition found among members of the Cichlasomine Group A (e.g., *Acaronia* and *Caquetaia* have one concavity and the remaining genera more than one). Both conditions are also present in the Cichlasomine Group B (e.g., "*Aequidens*" *rivulatus*, *Bujurquina*, and *Laetacara* have only one concavity, whereas *Cichlasoma* and *Aequidens* have more than one). All Old World cichlids examined herein have two to seven concavities in the frayed zone; thus this condition, which is also present in some New World cichlids, is considered herein as the plesiomorphic one.

Hypertrophied lower pharyngeal jaws (Fig. 15B) are present in *Crenicichla semifasciata*. In contrast, lower pharyngeal jaws of "modal" shape, as illustrated in Figure 15A, are found in *Crenicichla* as well as in most American cichlids. Among the chaetobranchines, *Chaetobranchius* and *Chaetobranchopsis* share a unique derived character that is the presence of elongate lower pharyngeal jaws; in contrast, *Astronotus* shows the "modal" condition.

The lower pharyngeal jaw of cichlids may be fully sutured along the sagittal axis or not (Fig. 15A-D). The absence of a complete su-

ture along the sagittal axis was considered plesiomorphic by Liem ('74) because this feature is present in numerous perciform taxa. In contrast, Cichocki ('76) considered it an apomorphic state. Cichocki ('76) noted that the absence of a complete suture is a secondary specialization for swallowing large fishes. We consider the incomplete suture exhibited by *Cichla* as the apomorphic state because it does not occur in any other labroids, even though it may be a reversal in light of the similar condition in basal perciforms. Stiassny ('82: 450) noted that the shape and dentition of the lower pharyngeal jaw is autapomorphic for *Cichla*; we prefer to consider the incomplete suture as the apomorphic state and not the shape of the lower pharyngeal jaw, because jaws of similar shape may be found in other cichlids, but the difference is in the extension of the suture between both jaws. In addition, we think that the extension of the dentition is independent of the shape of the lower pharyngeal jaw; therefore, it should be considered as a separate character.

The lower pharyngeal jaws may bear gill rakers on their lateral sides (Fig. 16A,B), or not. The gill rakers are absent in most American cichlids such as the Cichlasomine Groups A and B and the Chaetobranchine Group. Small gill rakers are present in *Cichla*, *Crenicichla semifasciata*, and among Geophagines, in *Acarichthys*, *Apistogramma*, "*Geophagus*" *brasiliensis* and "*Geophagus*" *crassilabris*. Well-developed gill rakers are characteristic of most examined *Crenicichla* (Fig. 17B). We consider the presence of gill rakers on the lateral sides of the lower pharyngeal jaw as the apomorphic condition because gill rakers are absent in all Old World cichlids examined herein.

The presence of unicuspid teeth on the premaxilla and dentary is the generalized condition among American cichlids. However, there is some variation from this common pattern. Scraping blade teeth (Fig. 7A, B) are characteristic of *Neetroplus*. Bicuspid teeth [hooked] are present in the South American "*Cichlasoma*" *facetum* (Fig. 17B) and some species of Central and North American "*Cichlasoma*" such as "*C.*" *cyanoguttatum*, "*C.*" *guttulatum*, and "*C.*" *spilurum*, and probably this is a unique character of "*Cichlasoma*." Bicuspid [hooked] teeth constitute an interesting character linking "*Cichlasoma*" *facetum*, a species distributed in the southernmost subtropical or temperate areas of the family range, with some

"*Cichlasoma*" species distributed in Central and/or North America. A close relationship between "*C.*" *facetum* and some Central and North American "*Cichlasoma*" was first proposed by Kullander ('83), who based part of his argument on the similarity of the color pattern and the presence of bicuspid teeth (hooked) in the anterior part of the upper and lower jaws in some individuals of great size.

The second (minor) cusp in bicuspid teeth [hooked] clearly appears late during ontogeny, at least in "*C.*" *facetum*. Changes in tooth shape in late ontogeny were reported in *Astatotilapia elegans*, *Heterochromis nigripinnis*, and *Gaurochromis angustifrons* by Barel et al. ('76). In these species, the adult individuals have bicuspid teeth (not hooked), whereas adults of great size present slightly curved, unicuspid teeth.

In contrast to the similarity between the upper and lower jaw dentitions, there is variation in tooth shape of the upper and lower pharyngeal jaws. This variation includes the presence of only unicuspid teeth in *Cichla*, unicuspid and bicuspid teeth (most American cichlids), molariform teeth (e.g., *Crenicichla semifasciata*; Figs. 12B, 18C, and "*Cichlasoma*" *citrinellum*; Meyer, '90), bicuspid crenulate teeth (Fig. 18B,b) and bevelled teeth (Fig. 18B,d) in the remaining *Crenicichla* spp. According to the distribution of this character, we consider the presence of unicuspid and bicuspid teeth as the plesiomorphic character state in American cichlids. The presence of molariform teeth is an advanced condition that occurs in a variety of species such as *Cichlasoma dimerus*, "*Cichlasoma*" *facetum*, "*C.*" *citrinellum*, *Crenicichla semifasciata*, *Gymnogeophagus balzanii*, "*Geophagus*" *brasiliensis*, and *Acarichthys heckelii*. Therefore, this character state is interpreted as homoplastic.

Kullander ('83) argued that great variability in the number of lower pharyngeal teeth in *Cichlasoma* results from both individual variation and an increase in the number of teeth during ontogeny. Similar results were obtained by Meyer ('90) in "*Cichlasoma*" *citrinellum*. These observations can be extended to all the species examined here and to the teeth present on premaxillae, dentaries, and pharyngeal jaws. Therefore, the number of teeth is not a significant character in the differentiation of the species. However, there is a considerable increase in the number of teeth in elongate forms such as species

of the genera *Crenicichla* and *Cichla*, with the exception of *Crenicichla semifasciata*.

The molarization process is occasionally produced by the erosion out of bicuspid teeth (e.g., *Cichlasoma dimerus* and *Gymnogeophagus balzanii*). The transition of the bicuspid type of teeth to molariform is readily observable; even in the most extreme cases of molarization, a remnant of the secondary cusp remains. In "*Cichlasoma*" *facetum* the molariform teeth are not the result of wearing out of preexisting teeth, at least not in specimens of great size, because replacement teeth are already molariform when they erupt. The greater molarization depends on growth of the individual. However, dietary changes influence trophic morphology during ontogeny in certain species such as *Cichlasoma managuense* (Meyer, '87).

Phylogenetic hypotheses concerning American cichlids were built by Regan ('06), de Miranda Ribeiro ('15), and more recently by Newsome ('71), Cichocki ('76), Oliver ('84), and Stiassny ('91). Regan ('06) considered *Cichla* as the most primitive American cichlid, a view supported by most workers. The interrelationships proposed by de Miranda Ribeiro ('15) show *Crenicichla* followed by *Batrachops* (= *Crenicichla semifasciata* herein) to be the most primitive American cichlids; he based this assumption on similarities of these forms with marine fishes. Newsome ('71) placed *Chaetobranchus* at the base of the tree and *Cichla* in a position more advanced than *Chaetobranchus*. The primitiveness of *Chaetobranchus* was supported by the presence of an apparently ossified, medially toothed basibranchial 4 and/or "median" teeth fused to basibranchial 3. The single specimen that we examined does not have such teeth. This character was discussed extensively by Cichocki ('76: 172, 173), who gave solid arguments against the primitiveness of the presence of teeth on both basibranchials 3 and 4 as the primitive state. Cichocki ('76), although he did not use the cladistic methodology as did most recent authors noted above, proposed the most complete hypothesis of interrelationships among American cichlids up to now. This author placed *Cichla* at the base of the American cichlids, but he was uncertain whether *Cichla* was part of the American or the African clade. Stiassny ('91) was the first author to recognize the monophyly of the American cichlids based on one synapomorphy (strongly interdigitating suture between the vomerine posterior pro-

cess and the parasphenoid). Stiassny ('91: Fig. 1.20) proposed an hypothesis of relationships for the whole family (Fig. 20); the New World representatives are the sistergroup of the clade including most African cichlids, whereas the Asian and Madagascan and some African genera are placed below the African + American clade. The following American cichlid groups were considered in that analysis: Crenicichline, Chaetobranchine, Geophagine, Cichlasomine Group A, and Cichlasomine Group B. In Figure 20, the Geophagine, Crenicichline, Chaetobranchine, and [Cichlasomine Group A + Cichlasomine Group B] form an unresolved polytomy. This analysis does not confirm or reject *Cichla* as the sister group of the remainder of the American genera. According to Stiassny ('91), the Geophagine, Crenicichline, Chaetobranchine, Cichlasomine Group A, and Cichlasomine Group B are putative monophyletic groups. However, this author did not present characters supporting the monophyly of both the Geophagine Group and the Cichlasomine Group A. The jaws and tooth morphology presented herein do not show any derived features supporting these putative clades.

The genus *Batrachops* Heckel, represented herein by *Crenicichla semifasciata*, was considered a synonym of *Crenicichla* by Günther (1862), Pellegrin ('03), Kullander ('83, '86), Ploeg ('87), and Stiassny ('91). Because the status of *Batrachops* depends on the inclusiveness of *Crenicichla* and the later has >60 species from which we only examined five, we are not able to discuss this taxonomic subject. However, although in this work *Batrachops* is synonymized with *Crenicichla*, we found some differences in jaw and tooth morphology between *Crenicichla semifasciata* and the remaining species of *Crenicichla*. The features that characterize *Crenicichla semifasciata* are: (1) the presence of a broad premaxillary ascending arm width (20% or more of its length), a feature that separates *C. semifasciata* from the remaining *Crenicichla* spp. with a narrow premaxillary ascending arm, (2) one to four upper and lower jaw inner tooth rows in *C. semifasciata*, whereas one to seven premaxillary inner tooth rows occur in the remaining *Crenicichla* spp., (3) presence of a hypertrophied lower pharyngeal jaw (Fig. 15B), whereas *Crenicichla* spp. have a "modal" shape, (4) presence of molariform teeth on the lower pharyngeal jaws (Figs. 15B, 18C); in contrast, *Crenicichla* spp. have unicuspid teeth

curved posteriorly that cover more >50% of the surface of the lower pharyngeal jaw, and (5) *Crenicichla semifasciata* has small gill rakers on the lateral sides of the lower pharyngeal jaw, whereas the remaining *Crenicichla* spp. have well-developed gill rakers bearing strong teeth.

If we compare the dentition among the species examined with those that inhabit the great lakes of Africa (see Barel et al., '77; Greenwood, '74; Liem, '74; Liem and Stewart, '76), it becomes apparent that the species examined here have less variety of tooth shape in the upper and lower jaws than their African relatives. As far as we know, all American species, except those with bicuspid (hooked) teeth and *Neotroplus nematopus* with scraping blade teeth, have recurved unicuspid teeth. On the contrary, in African cichlids bicuspid (not hooked) teeth have been considered as generalized structures; they are also found in young stages of those species whose adults have teeth of varied forms. It is possible to find great diversity in tooth shape (Greenwood, '74).

The lower pharyngeal jaw is the only bony element on which several morphotypes of teeth occur (Fig. 18B). It can bear unicuspid recurved, bevelled, and bicuspid crenulate teeth that are adapted to an ichthyophagous regime (see Witte and Barel, '76) and molariform teeth that are commonly associated with a malacophagous diet (Greenwood, '74; Barel, '83; Barel et al., '77; Meyer, '89, '90b). Despite these specializations, there is not always a strong correlation between the biting morphology and a particular feeding mode (Gottfried, '86). For example, in some species of *Crenicichla*, whose dental morphology predicts ichthyophagy, fishes are not the principal item in the diet (see Oliveros, '80; MacConnell-Lowe, '69; Knopel, '70). There are also taxa with molariform teeth (e.g., "*Cichlasoma*" *facetum*) in which snails do not represent the fundamental food either (Escalante, '84; Gutierrez et al., '86). Actually, all the species examined are more or less omnivorous, varying their diet in response to circumstances offered by the environment.

CONCLUSIONS

1. Endemism and trophic specialization of American cichlids do not seem to be accompanied by much modification in jaw structure and tooth shape. Upper and lower jaws are very much alike among American cichlids, with a premaxillary dentigerous arm shorter

than the ascending arm and a narrow coultter area. Several exceptions are noted below.

1. A premaxillary dentigerous arm longer than the ascending arm is an homoplastic character present in *Astronotus*, *Cichla*, and *Crenicichla semifasciata*. This character state is an autapomorphy of *Astronotus* among the chaetobranchines. A broad coultter area is an homoplastic character present in *Cichla* and in the chaetobranchines, with the exception of *Astronotus*. A broad coultter area is an autapomorphy of *Cichla* among the crenicichlines, whereas its absence is a reversal characterizing *Astronotus* among chaetobranchines.

2. Unicuspid conic teeth are commonly found on the premaxilla and dentary of American cichlids. Advanced conditions are the presence of scraping blade teeth (an autapomorphy of *Neotroplus*) and bicuspid [hooked] teeth (an autapomorphy of "*Cichlasoma*").

3. The mandibular sensory canal runs enclosed by bone in the dentary and anguloarticular in most American cichlids. However, it is not enclosed by the anguloarticular in *Apistogramma borellii* and *Biotococcus dicentrarchus*; this advanced condition is interpreted as an autapomorphy, that evolved independently in each species. Four lateralis foramina in the bony tube enclosing the mandibular canal is the common condition in the American cichlid dentary, with the exception of the chaetobranchines.

4. Although the overall morphology of the upper and lower pharyngeal jaws is very similar among American cichlids, they present a significant diversification of tooth shapes. For instance: unicuspid curved anteriorly; unicuspid recurved; bicuspid curved anteriorly [hooked]; bicuspid curved posteriorly [hooked]; bicuspid crenulate, curved anteriorly; bevelled; and molariform teeth.

Unicuspid and bicuspid teeth curved anteriorly and posteriorly are present in the pharyngeal jaws of most American cichlids examined. Bevelled teeth occur in the lower pharyngeal jaws of species of *Crenicichla*. Molariform teeth occur in a variety of cichlids such as *Cichlasoma dimerus*, "*Cichlasoma*," *Crenicichla semifasciata*, and *Gymnogeophagus balzanii*. Bicuspid crenulate and molariform teeth represent advanced conditions. Because they occur in various clades, they are homoplastic characters whose value as autapomorphies of certain taxa need more investigation.

5. The frayed zone of American cichlids can have one wide concavity or two to seven small concavities. More than one concavity is the condition present in chaetobranchines, *Cichla*, *Cichlasoma*, "*Cichlasoma*," *Petenia*, *Neotroplus*, and *Aequidens* among American cichlids, and in the outgroups proposed by Stiassny ('91). The presence of only one concavity in the frayed zone corresponds to the advanced condition present in cichlids such as *Crenicichla*, *Acaronia*, *Caquetaia*, *Bujurquina*, and *Laetacara*. Because of its distribution among American cichlids, this is an homoplastic character. A broad frayed zone bearing one to seven concavities is a synapomorphy of Cichlidae.

6. Most of the morphological characters of jaws and dentition are homoplasies at different levels among American cichlids. At least two unique characters can be mentioned: the presence of bicuspid [hooked] teeth in the upper and lower jaws of "*Cichlasoma*," and lower pharyngeal jaws not fully sutured along the sagittal axis in *Cichla*.

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