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## Phylogeny of species formerly assigned to the genus *Archocentrus* (Perciformes: Cichlidae)

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### Abstract

A phylogeny for 28 cichlid species that have been included in or near the same clade as *Archocentrus centrarchus* (type species of the genus) in previous phylogenetic analyses is presented, based on 98 morphological characters (osteology, gut-coiling pattern, pigmentation, squamation, meristics, and others), plus one cytogenetic character. Monophyly is supported for *Archocentrus* sensu stricto, *Cryptoheros*, *Hypsophrys*, *Amatitlania*, and *Rocio*; the relationships among these genera are not resolved. The three subgenera of *Cryptoheros* are also supported; *Cr. panamensis* is the sister group of the rest of the species in the genus. Within *Cryptoheros* (*Cryptoheros*), *Cr. chetumalensis* is the sister group of the clade *Cr. spilurus* + *Cr. cutteri*. Within *Amatitlania* the pattern is: (*Am. coatepeque* (*Am. nigrofasciata* (*Am. siquia* + *Am. kanna*))).

**Key words:** phylogeny, cichlids, Middle America

### Resumen

Se presenta una filogenia para 28 especies de cíclidos que han aparecido dentro o cerca del mismo clado que *Archocentrus centrarchus* (especie tipo del género) en hipótesis filogenéticas previas, con base en 98 caracteres morfológicos (osteología, patrones de convolución intestinal, coloración, escamación, merística y otros), además de un carácter citogenético. Se demuestra monofilia para *Archocentrus* sensu stricto, *Cryptoheros*, *Hypsophrys*, *Amatitlania* y *Rocio*; las interrelaciones de estos géneros no quedan resueltas. Se apoya también la monofilia de los tres subgéneros de *Cryptoheros*; *Cr. panamensis* es la especie hermana de las demás en ese género. Dentro de *Cryptoheros* (*Cryptoheros*), *Cr. chetumalensis* es hermana del clado *Cr. spilurus* + *Cr. cutteri*. Dentro de *Amatitlania*, el patrón es: (*Am. coatepeque* (*Am. nigrofasciata* (*Am. siquia* + *Am. kanna*))).

## Introduction

The cichlid fish genus *Archocentrus* Gill has been redefined by Schmitter-Soto (2007) to include only *Ar. centrarchus* Gill in Gill & Bransford, 1877 (type species), *Ar. spinosissimus* (Vaillant & Pellegrin, 1902), and *Ar. multispinosus* [formerly *Herotilapia multispinosa* (Günther, 1867)]. Other species that have sometimes been assigned to *Archocentrus* were reassigned in that paper to the new genera *Amatitlania* [*Am. nigrofasciata* (Günther, 1867) and three new species] and *Rocio* [*R. octofasciata* (Regan, 1903) and two new species], as well as *Cryptoheros* Allgayer [*Cr. panamensis* (Meek & Hildebrand, 1913), *Cr. spilurus* (Günther, 1862), the resurrected *Cr. cutteri* (Fowler, 1932), *Cr. septemfasciatus* (Regan, 1908), *Cr. altoflavus* Allgayer, 2001, *Cr. nanoluteus* (Allgayer, 1994), *Cr. myrnae* (Loiselle, 1997), *Cr. sajica* (Bussing, 1974), and one new species] and *Hypsophrys* Agassiz [*H. nicaraguensis* Günther, 1864 and *H. nematopus* (Günther, 1867)]. The present article provides the cladistic support for these decisions.

Attempts to solve the ex-*Cichlasoma* problem have had a less-than-moderate success. Cichocki's (1976) dissertation supported the hypothesis that all species then assigned to *Cichlasoma* Swainson formed a monophyletic group, and proposed several lineages within it; however, he chose to work out the relationships by means of a clique analysis, thus rendering his results hard to compare with subsequent parsimony-based hypotheses (Kullander 1996).

Stiassny (1991) presented a review of cichlid relationships; she demonstrated monophyly for the New World cichlids and established two main clades, one of which, her "cichlasomine group A," included all Middle American cichlids along with a few taxa from South America (e.g. *Caquetaia* Fowler).

Kullander (1998) examined South American cichlids and established the tribe Heroini, which includes, among others, the species formerly in *Cichlasoma*; he did not offer resolved relationships within the Heroini (and he did not include species from Middle America), but nevertheless he concluded that "the morphological basis for phylogeny reconstruction is practically available."

Roe et al. (1997) performed the first molecular analysis of Middle American cichlids, using complete cytochrome *b* sequences of 19 species. These authors found that *Cr. spilurus* and *Nandopsis* (= *Parachromis*) *dovii* (Günther) were part of the same clade as the true *Amphilophus* Agassiz [restricted by these authors to *A. citrinellus* (Günther) and *A. labiatus* (Günther)]. They found this clade to be basal to the "cichlasomine group A" clade, i.e. the Heroini (Kullander 1998).

The same gene allowed Martin and Bermingham (1998) to produce a partial phylogeny of *Archocentrus*, in the context of an analysis of 21 Middle American (almost exclusively Costa Rican) cichlids. In the present work, some of Regan's (1905) "sections" were recognised, including a restricted version of *Archocentrus*. However, the authors felt that the "relationships among the genera remain elusive," except for the monophyly of *Hypsophrys* + *Neetroplus* Günther (a clade that apparently contradicted morphological phylogenetic analyses, although it is supported in the present paper).

Farias et al. (1999, 2000, 2001) essentially focused on South American taxa, but they did include additional taxa from Middle America, among them 'Cichlasoma' *octofasciatum*, *Archocentrus citrinellus* (sic), and *Ar. nigrofasciatum*, which showed up together in one clade with *Petenia splendida* Günther and *Caquetaia spectabilis* (Steindachner); hence the choice of additional material for the present study.

The phylogenetic reconstruction here presented establishes the monophyly and species composition of *Archocentrus*, along with a redefinition of *Cryptoheros* and *Hypsophrys*, and supports the diagnosis of two newly described genera (*Amatitlania* and *Rocio*—Schmitter-Soto, 2007). The cladistic analysis treats all nominal species ever assigned to the genus *Archocentrus* and six newly described species (Schmitter-Soto, 2007), as well as the species that have been included in the same clade as (or as sister group to) *Ar. centrarchus* in relevant published phylogenetic analyses (see above).

Diagnoses and descriptions are given in Schmitter-Soto (2007), where an identification key is also available.

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## Material and methods

The specimens examined include representatives from all nominal species that have at various times been assigned to the genus *Archocentrus* in scientific publications (Schmitter-Soto, 2007: table 1), as well as comparative material of species that appeared in the same clades as species assigned to *Archocentrus* in Roe et al. (1997), Martin and Bermingham (1998), and Farias et al. (2000) (Table 1). Material examined is the same listed by Schmitter-Soto (2007: appendix 1).

**TABLE 1.** List of species included in this phylogenetic analysis. Schmitter-Soto (2007) provides details on material examined; names in brackets refer to the name more frequently used in recent literature (e.g. Kullander 2003). *Petenia*, *Tomocichla*, and *Oreochromis* were found to lie outside the ingroup.

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<i>Amatitlania nigrofasciata</i> [= <i>Archocentrus nigrofasciatus</i> ]
<i>Am. coatepeque</i>
<i>Am. kanna</i>
<i>Am. siquia</i>
<i>Amphilophus citrinellus</i>
<i>Archocentrus centrarchus</i>
<i>Ar. multispinosus</i> [= <i>Herotilapia multispinosa</i> ]
<i>Ar. spinosissimus</i>
<i>Caquetaia spectabilis</i>
<i>Cryptoheros (Panamius) panamensis</i>
[= <i>Archocentrus panamensis</i> ]
<i>Cr. (Bussingius) altoflavus</i> [= <i>Ar. altoflavus</i> ]
<i>Cr. (B.) myrnae</i> [= <i>Ar. myrnae</i> ]
<i>Cr. (B.) nanoluteus</i> [= <i>Ar. nanoluteus</i> ]
<i>Cr. (B.) sajica</i> [= <i>Ar. sajica</i> ]
<i>Cr. (B.) septemfasciatus</i> [= <i>Ar. septemfasciatus</i> ]
<i>Cr. (Cryptoheros) spilurus</i> [= <i>Ar. spilurus</i> ]
<i>Cr. (Cr.) chetumalensis</i>
<i>Cr. (Cr.) cutteri</i>
<i>Hypsophrys nicaraguensis</i>
<i>H. nematopus</i> [= <i>Neetroplus nematopus</i> ]
<i>Parachromis dovii</i>
<i>P. loiselii</i>
<i>Rocio octofasciata</i> [= ‘ <i>Cichlasoma</i> ’ <i>octofasciatum</i> ]
<i>R. gemmata</i>
<i>R. ocotal</i>
<i>Petenia splendida</i>
<i>Tomocichla sieboldii</i> [= <i>Paraneetroplus sieboldii</i> ]
<i>Oreochromis mossambicus</i>

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Pigmentation patterns were assessed primarily from preserved specimens. Osteological methodology (i.e., clearing and staining) follows Taylor and van Dyke (1985, as modified by W.L. Fink, pers. comm.). Radiographs and skeletonised specimens were also used. Bone measurements were taken with an ocular micrometer.

Because the choice of a sister group was not evident, the comparative material was considered part of the ingroup, as a test of monophyly for *Archocentrus*. An African cichlid, *Oreochromis mossambicus* (Peters), was used as outgroup to root the tree (same choice of Roe et al. 1997). Cladistic analyses were based on

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maximum parsimony, and reconstructions were performed with PAUP\* 4.0 (Swofford 1998). I used heuristic search and strict consensus; character states were considered unordered, multistate, or binary; all received the same weight. Meristic characters were used only if satisfactorily amenable to statistical coding: their states were determined by means of an ANOVA followed by a Duncan a posteriori test (homogeneous subset coding, Simon 1983); where differences were significant at  $\alpha < 0.05$ , homogeneous groups with no overlap were chosen as different character states. Optimisation followed the ACCTRAN option in order not to lose any putative synapomorphy (Kitching et al. 1998).

Homoplasy level in the most parsimonious cladogram was evaluated with consistency (CI) and retention (RI) indices. Homoplasy (hi) and retention (ri) indices were also computed for every character, and synapomorphies were considered relevant only when strict, or when the concerned character had a hi  $> 0.50$ , or a hi  $< 0.50$  but compensated by a relatively high ri (Kitching et al. 1998). Robustness of internal nodes was evaluated with a 1000-replicate bootstrap analysis (Felsenstein 1985). Branches with bootstrap support below 50% were collapsed, unless they displayed at least one strict synapomorphy.

## Results

### Character description and analysis

The list treats 98 characters (see matrix: Table 2), selected mostly because they were amenable to reasonably objective coding. Many of them have been used before, but all relevant anatomical material was reevaluated; I compare my interpretations mainly against those of Cichocki (1976) and Kullander (1998). Many characters (43) are binary, but most are multistate, non-additive, unordered. I did not exclude terminal autapomorphies (12, which leaves 86 informative characters) because they provide special support for species diagnoses (Schmitter-Soto, 2007). I did not leave out highly homoplasious traits either: “Dismissing conflicting characters [...] might be defended for small sets of taxa and characters. For more complex situations, however, selection of characters not only introduces a bias but also leaves out potentially useful character sets” (Kullander 1998: 471). Homoplasy (hi: Archie 1989) and retention (ri: Farris 1989) indices are indicated where relevant. Characters for species outside *Archocentrus*, *Cryptoheros*, *Amatitlania*, *Rocio*, and *Hypsophrys* are usually not illustrated.

#### Gill arches, characters 1–11

1. Angle between arms of first epibranchial bone

[0] arms divergent (Fig. 1a); [1] arms parallel (Fig. 1b).

Homoplasious (hi=0.89, ri=0.20). Fixed for state 1 in *Rocio*, but occurring in several other taxa. Cichocki’s (1976) character 30, “relative direction of the posterior arm [uncinate process] of the first epibranchial bone,” distinguished three degrees of divergence: an angle of 35° or more, 15–30°, or less than 15°; however, the polarity is the same. He found *Am. nigrofasciata* to have my state 0, but in my view that species has parallel arms, although the rest of the genus *Amatitlania* has divergent arms.

This is also Kullander’s (1998) character 3, “angle of the uncinate process of epibranchial 1 relative to the main axis of the bone;” same polarity as here, although Kullander united Cichocki’s first two states and included a new state for those taxa where both limbs are parallel but angled relative to the bone axis.

2. Relative width of arms of first epibranchial

[0] arms subequal; [1] posterior arm distinctly wider.

Homoplasious (hi=0.88, ri=0.25); fixed for state 1 in *Archocentrus*, polymorphic in *Cr. chetumalensis*. Polarity as in Kullander’s (1998, character 4), who observed that the “derived condition may have been developed by increased relative width of the uncinate process or decreased width of the anterior arm.”

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**TABLE 2.** Character matrix used for parsimony analysis of character distribution in Cichlidae once or presently assigned to the genus *Archocentrus*. See cladogram in Fig. 26.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
<i>mossambicus</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>sieboldii</i>	0	0	1	4	1	0,1	0	0	2	0	1	0	2	2	0	0	1	0	1	0
<i>splendida</i>	0	1	4	1	0	0	1	0	1	1	0	1	0	1	1	0	1	1	1	1
<i>dovii</i>	0	0	1	3	0	1	1	0	2	0	1	2	1	0	0	0	1	0	1	1
<i>loisellei</i>	0	1	1	3	0	1	1	0	2	0	1	2	1	0	0	0	1	0	1	1
<i>spectabilis</i>	0	1	1	4	2	1	1	0	2	0	1	1	1	5	0	0	1	0	1	1
<i>citrinellus</i>	0	0	2	1	1,5	0	0	2	4	0	1	4	1	4	0	0	1	0	1	2
<i>nicaraguensis</i>	1	1	3	3	1	0	1	0	3	1	1	1	1	1	0	0	1	0	0	2
<i>nematopus</i>	0	0	1	3	1	0	1	0	2	0	1	3	3	3	0	1	1	0	1	0
<i>panamensis</i>	0	0	1	4	1	1	1	?	?	?	?	2	1	0	0	1	0	1	0	0
<i>chetumalensis</i>	1	0,1	1	4	1	0	1	1	2	0,1	1	5	2	1	2	0	1	0	1	0
<i>cutteri</i>	0	0	1	4	1	0	1	1	2	1	1	5	2	4	2	0	1	0	1	0
<i>spilurus</i>	1	0	1	4	1	0	1	1	2	0,1	1	5	2	1	2	0	1	0	1	0
<i>altotflavus</i>	1	0	1	4	1	1	1	1	2	1	1	5	2	4	2	0	1	0	1	0
<i>nanoluteus</i>	?	?	1	4	1	0	0	1	?	1	?	?	2	4	2	0	1	0	1	0
<i>septemfasciatus</i>	0	0	1	4	1	0	0	1	2	1	1	6	4	1	0,2	0	1	0	1	0
<i>myrnae</i>	0	0	1	4	0	0	1	1	2	1	1	6	4	4	0	0	1	0	1	0
<i>sajica</i>	1	0	1	4	1	0	0	1	2	1	1	5	4	4	2	0	1	0	1	2
<i>spinosisimus</i>	1	1	1	4	1	0	1	0	2	0	1	5	2	2	0	0	1	0	1	2
<i>centrarchus</i>	1	1	0	2	3	0	1	0	2	1	1	5	2	5	0	0	1	0	1	2
<i>multispinosus</i>	0	1	1	4	1	0	1	0	2	0	1	3	2	5	2	0	1	0	1	0
<i>gemma</i>	1	0	1	4	4	1	1	0	2	0	1	6	5	6	0	0	1	0	1	2
<i>octofasciata</i>	1	0	1	4	4	0	0,1	0	2	0	1	6	5	6	0	0	1	0	1	2
<i>ocotal</i>	1	?	1	4	4	1	0	0	2	0	?	6	5	6	0	0	1	0	1	2
<i>kanna</i>	0	1	1	4	1,5	1	0	0	2	0	1	3	2	1	0	0	1	0	1	2
<i>siquia</i>	0	0	1	4	1,5	1	0	0	2	0	1	3	4	1	0	0	1	0	1	2
<i>nigrofasciata</i>	1	1	1	4	1	1	0	0	2	0	1	6	2	1	0	0	1	0	1	2
<i>coatepeque</i>	0	0	1	4	1	1	1	0	2	1	1	6	2	1	0	0	1	0	1	2

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**TABLE 2** (cont.).

	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40
<i>mossambicus</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
<i>sieboldii</i>	0	0	1	0	0	2	0	2	0	1	0	1	2	0	0	0	1	0	0	
<i>splendida</i>	3	1	2	0	1	2	1	1	0	0	0	1	1	0	0	0	1	1	0	
<i>dovii</i>	2	0	1	0	1	2	0	1	2	0	0	0	2	0	0	1	0	1	0	
<i>loisellei</i>	2	0	1	1	1	2	0	1	2	0	0	0	2	0	0	1	0	1	0	
<i>spectabilis</i>	2	2	3	1	1	2	1	0	0	0	0	1	1	0	0	0	0	1	0	
<i>citrinellus</i>	1	0	1	1	1	2	0	0	1	0	0	1	2	0	0	0	1	0	1	
<i>nicaraguensis</i>	0	0	1	0	1	2	0	2	1	0	0	1	2	0	0	1	1	0	0	
<i>nematopus</i>	0	0	0	0	1	2	2	2	2	0	0	1	2	2	0	2	1	0	0	
<i>panamensis</i>	0	0	1	1	0	2	0	0	?	1	0	1	2	0	0	2	1	0	1	
<i>chetumalensis</i>	0	0	1	1	1	2	0	0	0	1	0	1	4	0	1	1	1	0	1	
<i>cutteri</i>	0	0	1	1	1	2	0	0	1	1	0	1	4	0	1	2	0	0	1	
<i>spilurus</i>	0	0	1	1	1	2	0	0	1	1	0	1	4	0	1	1	1	0	1	
<i>altoflavus</i>	0	0	1	0	1	2	0	2	1	1	0	1	4	0	1	2	0	0	1	
<i>nanoluteus</i>	0	0	1	0	1	2	0	2	1	1	0	1	?	0	1	2	0	0	1	
<i>septemfasciatus</i>	0	0	1	0	1	2	0	2	1	1	0	1	2	0	1	2	0	0	1	
<i>myrnae</i>	0	0	1	0	1	2	0	2	1	1	0	1	4	0	1	2	0	0	1	
<i>sajica</i>	0	0	1	0	1	2	0	2	1	1	0	1	2	0	1	1	1	0	0	
<i>spinossissimus</i>	0	0	1	0	1	2	0	0	0	0	1	1	2	0	0	1	1	0	0	
<i>centrarchus</i>	0	0	1	1	1	2	0	0	0	0	0	1	2	0	0	1	1	0	0	
<i>multispinosus</i>	0	0	1	1	0	2	0	0	0	0	1	1	2	1	0	1	1	0	0	
<i>gemma</i>	1	0	1	0	0	1	0	1	1	0	0	1	4	0	0	1	1	0	1	
<i>octofasciata</i>	1	0	1	0	0	2	0	0	0	0	0	1	4	0	0	0	1	0	1	
<i>ocotal</i>	1	0	1	0	0	2	0	0	0	0	0	1	4	0	0	1	1	0	1	
<i>kanna</i>	1	0	1	0	1	2	0	0	0	1	0	1	4	0	0	2	1	0	1	
<i>siquia</i>	1	0	1	1	1	2	0	0	1	1	0	1	4	0	0	2	1	0	0,1	
<i>nigrofasciata</i>	1	0	1	1	1	2	0	0	1	1	0	1	2	0	0	1	0	0	1	
<i>coatepeque</i>	1	0	1	0	1	2	0	0	1	1	0	1	3	0	0	1	1	0	1	

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**TABLE 2** (cont.).

	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60
<i>mossambicus</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
<i>sieboldii</i>	6	1	2	0	0	2	0	3	1	0	1	1	0	1	0	1	0	0	0	2
<i>splendida</i>	1	1	1	1	1	0	1	0	0	3	1	1	0	1	0	1	1	1	0	1
<i>dovii</i>	1	2	3	2	0	0	1	4	0	0	1	1	0	0	0	1	0	1	0	1
<i>loisellei</i>	1	2	3	2	0	0	1	1	0	1	1	1	0	0	0	0	0	1	0	1
<i>spectabilis</i>	1	2	3	2	0	0	1	2	1	2	1	1	0	1	0	0	0	1	0	1
<i>citrinellus</i>	1	1	1	0	0	0	1	1	0	0	1	1	1	0	0	0	0	1	1	2
<i>nicaraguensis</i>	1	1	3	0	0	2	0	1	0	0	1	1	1	0	0	0	0	1	1	2
<i>nematopus</i>	2	1	3	0	0	2	0	1	0	2	1	1	1	0	0	0	0	1	1	2
<i>panamensis</i>	5	1	3	1	0	1	0	1	0	0	1	1	0	0	0	0	0	1	0	3
<i>chetumalensis</i>	1	1	5	0	0	1	0	1	1	0	1	1	1	1	0	0	0	1	0	2
<i>cutteri</i>	1	1	5	0	0	1	0	1	0,1	0	1	1	0	0	0	0	0	1	0	2
<i>spilurus</i>	1	1	5	0	0	1	0	1	1	0	1	1	0	0	0	0	0	1	0	2
<i>altoflavus</i>	4	1	5	0	0	1	0	0	1	0	?	1	1	1	0	0	0	1	0	2
<i>nanoluteus</i>	4	1	3	0	0	1	0	1	0	0	?	1	1	1	0	0	0	1	0	2
<i>septemfasciatus</i>	1	1	5	0	0	1	0	1	0	0	1	1	1	1	0	0	0	1	0	2
<i>myrnae</i>	4	2	3	0	0	1	0	0	0	0	1	1	1	1	0	0	0	1	0	2
<i>sajica</i>	4	1	3	0	0	1	0	0	1	0	1	1	1	1	0	0	0	1	0	2
<i>spinosissimus</i>	1	1	3	0	0	0	0	1	1	0	1	1	1	1	0	0	0	2	0	2
<i>centrarchus</i>	1	1	3	0	0	0	1	1	0	1	1	1	0	0	0	0	0	2	0	2
<i>multispinosus</i>	3	1	4	0	0	1	0	1	1	1	1	1	0	1	0	0	0	2	0	2
<i>gemma</i>	1	2	5	1	0	0	0	1	0	0	1	1	0	1	0	0	0	1	0	1
<i>octofasciata</i>	1	2	5	1	0	0	0	1	0	0	1	1	1	0,1	0	0	0	1	0	2
<i>ocotal</i>	1	2	1	1	0	0	0	1	0	0	1	1	0	1	0	0	0	1	0	2
<i>kanna</i>	1	2	3	1	0	1	0	1	0,1	0	1	1	1	1	1	0	0	1	0	2
<i>siquia</i>	1	2	3	1	0	1	0	1	0	0	1	1	1	1	1	0	0	1	0	2
<i>nigrofasciata</i>	1	2	3	1	0	1	0	1	0,1	0	1	0,1	1	1	0	0	0	1	0	2
<i>coatepeque</i>	1	2	3	1	0	1	0	1	0	0	1	1	0,1	1	0	0	0	1	0	2

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**TABLE 2** (cont.).

	61	62	63	64	65	66	67	68	69	70	71	72	73	74	75	76	77	78	79	80
<i>mossambicus</i>	0	0	-	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	-
<i>sieboldii</i>	0	1	0	1	2	1	0	2	0	0	0	1	1	0	0	0,1	1	0	2	0
<i>splendida</i>	0	0	-	0	?	1	1	1	1	0	1	1	1	0	1	1	1	0	1	0
<i>dovii</i>	0	1	0	1	0	0	1	0	0	0	0	2	1	0	0	0	1	1	1	0
<i>loisellei</i>	0	1	0	1	0	2	1	0	0	1	1	2	1	1	0	0	1	1	1	1
<i>spectabilis</i>	0	2	0	2	2	2	0	1	2	0	1	2	1	1	0	0	3	0	1	1
<i>citrinellus</i>	0	1	2	1	0	2	0	1	0	0	1	2	1	1	0	0	1	0	1	1
<i>nicaraguensis</i>	0	1	0	1	0	2	0	2	0	1	2	2	1	1	0	0	0	0	1	1
<i>nematopus</i>	0	1	2	1	0	0	0	2	0	1	0	2	1	1	2	0	0	0	7	1
<i>panamensis</i>	0	1	0	1	0	2	0	0	0	1	1	2	1	1	2	1	1	0	5	?
<i>chetumalensis</i>	0	1	2	1	2	2	0	1	0	1	1	2	1	1	0	0,1	1	0	5	1
<i>cutteri</i>	0	1	2	1	2	2	0	2	0	1	1	2	1	1	0	2	1	0	5	1
<i>spilurus</i>	0	1	2	1	2	2	0	2	0	1	1	2	1	1	0	0,1	1	0	5	1
<i>altoflavus</i>	0	1	3	1	2	2	0	1	0	1	1	2	1	1	0	1	1	2	5	1
<i>nanoluteus</i>	0	1	3	1	2	2	0	1	0	1	1	2	1	1	0	1	1	2	5	?
<i>septemfasciatus</i>	0	1	0	1	0	2	0	0	0	1	1	2	1	1	0	1	1	2	5	1
<i>myrnae</i>	0	1	3	1	0	2	0	0	0	1	1	2	1	1	0	1	1	2	1	1
<i>sajica</i>	0	1	0	1	0	2	0	1	0	1	1	2	1	1	0	1	1	2	1	1
<i>spinosissimus</i>	1	1	2	1	3	2	1	0	0	1	1	3	1	1	0	2	1	3	1	0
<i>centrarchus</i>	0	1	0	1	2	2	0	2	0	1	1	3	1	1	0	2	2	3	1	1
<i>multispinosus</i>	0	1	1	1	1	2	1	0	0	1	1	3	1	1	0	2	2	3	4	-
<i>gemma</i>	1	1	0	1	0	2	1	0	0	1	0	2	1	0	0	2	1	0	1	0
<i>octofasciata</i>	1	1	2	1	0	2	1	0	0	1	0	2	1	1	0	2	1	0	1	1
<i>ocotal</i>	1	1	2	1	0	2	1	1	0	1	0	2	1	1	0	1,2	1	0	1	1
<i>kanna</i>	0	1	2	1	0	2	0	0	0	1	1	2	1	1	0	1	1	0	1	1
<i>siquia</i>	0	1	0	1	0	2	0	1	0	1	1	2	1	1	0	1	1	0	3	1
<i>nigrofasciata</i>	0	1	2	1	2	2	0	1	0	1	1	2	1	1	0	1	1	0	1	1
<i>coatepeque</i>	0	1	0	1	0	2	0	2	0	1	1	2	1	1	0	1	1	0	6	1

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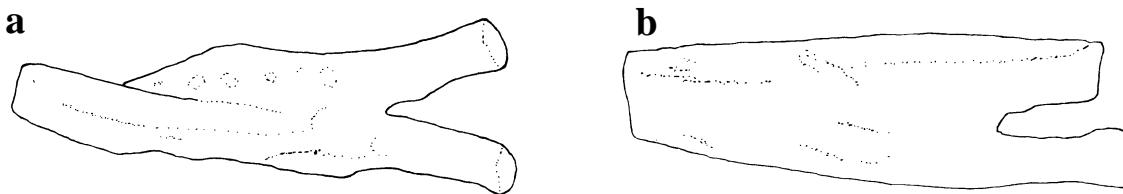
**TABLE 2** (cont.).

	81	82	83	84	85	86	87	88	89	90	91	92	93	94	95	96	97	98
<i>mossambicus</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	-	-
<i>sieboldii</i>	0	0	0	1	1	1	1	0	1	0	0	1	1	4	0	1	0	0
<i>splendida</i>	1	0	0	1	1	1	0	2	-	0	0	1	2	0	0	1	0	0
<i>dovii</i>	4	0	1	1	1	1	1	1	0	0	0	1	2	1	0	1	0	0
<i>loisellei</i>	3	0	0	1	0	5	1	1	0	0	0	1	3	1	0	1	0	0
<i>spectabilis</i>	2	2	0	0	0	2	1	0	0	0	0	1	0	1	0	1	1	0
<i>citrinellus</i>	4	2	1	0	0	3	0,1	1	0	0	0	1	0	0,1	0	1	1	1
<i>nicaraguensis</i>	4	0	0	0	0	1	1	2	-	0	0	1	0	1	0	1	1	0
<i>nematopus</i>	4	2	0	0	0	2	0	1	0	0	0	1	0	0	0	0	-	-
<i>panamensis</i>	?	0	1	0	0	1	1	1	0	0	1	1	0	2	0	3	0	0
<i>chetumalensis</i>	1	0	0	1	0	3	0	1	0	1	0	3	0	0	0	3	0	0
<i>cutteri</i>	1	0	0	1	0	3	0	1	0	1	1	3	0	3	0	3	0	0
<i>spilurus</i>	1	0	0	1	0	3	0	1	2	1	1	3	0	0,1	0	3	0	0
<i>altoflavus</i>	1	0	0	0	0	1	1	1	0	0	1	3	1	1	1	2	0	0
<i>nanoluteus</i>	1	0	0	0	0	4	1	1	4	1	1	3	1	1	1	1	0	0
<i>septemfasciatus</i>	1	0	0	0	0	3	1	1	1	0	1	3	0	2	1	3	0	0
<i>myrnae</i>	1	0	0	0	0	3	1	1	0	0	1	3	2	1	1	2	0	0
<i>sajica</i>	1	0	0	0	0	3	1	1	1	1	0	4	0	2	0	-	-	-
<i>spinosisimus</i>	1	1	1	0	1	1	1	1	1	0	0	3	3	2	0	1	0	0
<i>centrarchus</i>	1	2	1	0	0	6	1	1	0	1	1	4	0	4	0	1	0	1
<i>multispinosus</i>	1	2	1	0	0	1	1	1	0	0	0	1	0	1	0	1	0	0
<i>gemma</i>	4	2	1	2	1	1	2	0	1	0	0	1	3	2	0	1	1	1
<i>octofasciata</i>	4	2	1	0	1	1	1	0	1	0	0	1	3	0	0	1	1	1
<i>ocotal</i>	4	2	1	0	0	1	0	0	1	0	0	1	3	1	0	1	1	1
<i>kanna</i>	1	2	0	1	0	2	0	1	3	2	0	2	0	1	0	1	0	0
<i>siquia</i>	5	2	0	1	0	2	0	1	3	2	0	2	0	1	0	3	0	0
<i>nigrofasciata</i>	0	2	0	0	0	2	1	1	3	2	0	2	0	0	0	1	0	0
<i>coatepeque</i>	2	2	0	0	0	2	1	1	3	2	0	2	0	?	0	1	0	0

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**FIGURE 1.** Angle between arms of first epibranchial bone: (a) divergent (*Cryptoheros cutteri*, UMMZ 173195); (b) parallel (*Cr. chetumalensis*, UMMZ 197224). Scales: a, 40X; b, 66X.

### 3. Number of lower gill rakers on first arch

[0] mode 13 or more; [1] mode 8 or less; [2] mode 11; [3] mode 9; [4] mode 10.

High numbers of lower gill rakers (state 0) occurred only in the tilapia and in *Ar. centrarchus*, a reversal. Fewer lower gill rakers (state 1) are a putative synapomorphy of most Neotropical cichlids examined (except for the autapomorphic modes of *Petenia*, *Amphilophus*, and *H. nicaraguensis*). For this trait,  $hi=0.20$ ,  $ri=0.50$ .

No seriality was proposed for meristic characters because no genetic reason prevents a priori “jumping” from a low to a high number of elements or viceversa without “going through” intermediate numbers of elements. For coding procedure of meristic characters, see Materials and methods.

This is Kullander’s (1998) character 15 (in part, because he considered distribution as well as number of gill rakers). His states were: about 8–10, shape normal; 10–60; 4–10, short; 0–2. I agree with him that there is no definite tendency to increase or decrease the number of gill rakers.

### 4. Total number of gill rakers on first arch

[0] mode 16–17; [1] mode 13–14; [2] mode 19 or more; [3] mode 11; [4] mode 10 or fewer.

By “total number” I mean both those on the ceratobranchial and on the epi- and hypobranchials. (Using the number of epibranchial gill rakers instead of the total number of gill rakers on the entire first branchial arch would have resulted in just two states, one of them autapomorphic for *Ar. centrarchus*.)

This character is not quite linked to character 3, because it does not duplicate it: for character 4, state 4 occurs in all Neotropical cichlids examined except *Petenia* and *Amphilophus* (state 1), and *Parachromis Agassiz* and *Hypsophrys* (state 3, synapomorphically). State 2 is autapomorphic for *Ar. centrarchus*;  $hi=0.33$ ,  $ri=0.50$ .

### 5. Main gill-raker shape

[0] digitiform, blunt (Fig. 2a); [1] trapezoidal or bifid (Fig. 2b); [2] triangular (Fig. 2c); [3] elongated, slender (Fig. 2d); [4] with a mediad projection at base (Fig. 2e).

This character refers to the largest gill rakers on the first ceratobranchial, near the angle with the epibranchial. State 1, where the gill-raker tip has a rather distinct “trapezoidal” end (i.e. with one acute and one obtuse angle) is a synapomorphy of the Neotropical cichlids examined except *Petenia* and *Parachromis*, which retain the plesiomorphic digitiform, blunt, shape. There are reversals (*Cr. myrnae*) and autapomorphies (state 3, *Ar. centrarchus*), and further transformations: to state 2 in *Caquetaia*, and to the strictly synapomorphic state 4 in *Rocio*. *Am. kanna* and *Am. siquia* share a possible state 5, a polymorphism between state 1 and a bifid tip of the gill rakers, paralleled in *Amphilophus*;  $hi=0.50$ ,  $ri=0.50$ .

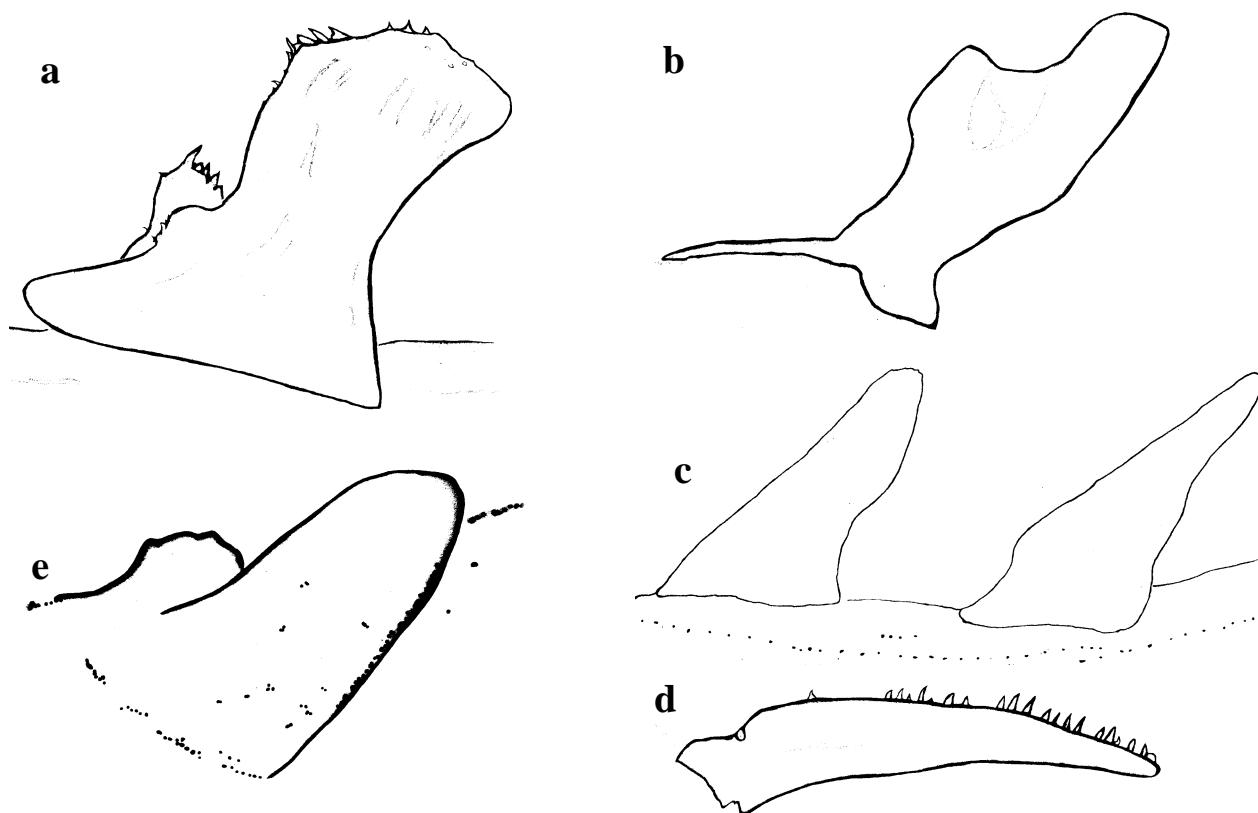
This is Kullander’s (1998) character 16. He found “slender, subtriangular” to be the plesiomorphic condition, with three other states: slender, short, triangular; “fingerlike;” and “enormously elongated.” However, in my data set, not only the tilapia, but also the two following basal clades display my state 0, which explains the polarity found here. Moreover, Kullander’s (1998: fig. 11) cladogram shows Old World cichlids predominantly “fingerlike,” including *Heterochromis* Regan, which he considered the sister group of a clade

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that includes the Middle American species. Thus, I do not agree with the polarity that Kullander (1998) found a posteriori for this character.



**FIGURE 2.** Main gill-rakers on first arch: (a) digitiform, blunt, denticulated, with a basal process (*Parachromis dovii*, UMMZ 188256); (b) trapezoidal or bifid, no basal process (*Amphilophus citrinellus*, UMMZ 188309); (c) triangular (*Amatitlania nigrofasciata*, UMMZ 197392); (d) elongated, slender, denticulated (*Archocentrus centrarchus*, UMMZ 224131); (e) with a mediad projection at base (*Rocio octofasciata*, ECOCH 5468). Scales: a, 40X; b, 32X; c, 40X; d, 66X; e, 50X.

#### 6. Basal process on main gill-rakers

[0] absent; [1] present (Fig. 2a).

The character refers to the largest gill rakers on the first ceratobranchial. State 1 is an homoplasious synapomorphy of *Amatitlania* and of *Parachromis*, with several parallelisms and a polymorphism in *Tomocichla* Regan;  $hi=0.88$ ,  $ri=0.40$ .

#### 7. Main gill-rakers denticulation

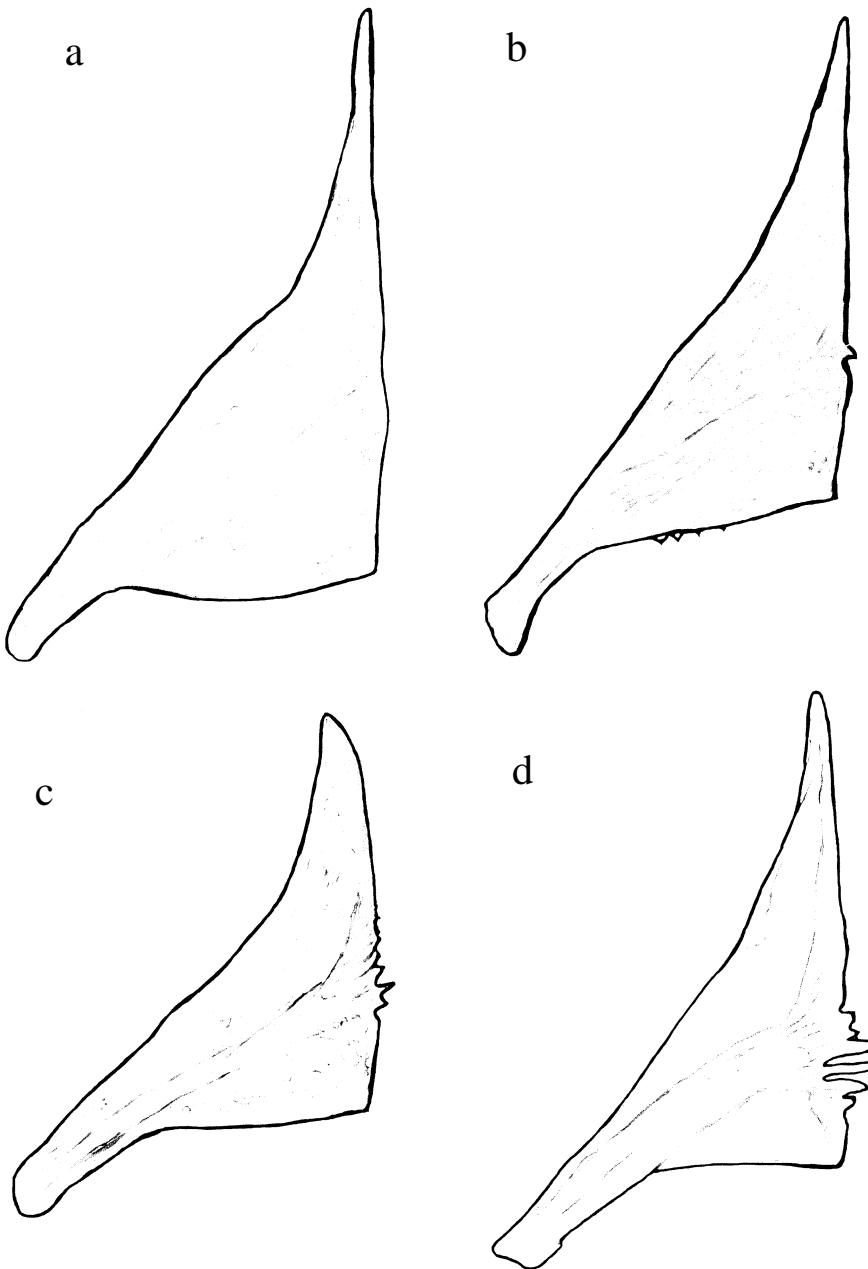
[0] no denticulation; [1] denticulation present (Figs. 2a,d).

Homoplasious ( $hi=0.89$ ,  $ri=0.22$ ), apparently fixed independently for state 1 in *Archocentrus*, the subgenus *Cryptoheros*, *Parachromis*, *Hypsophrys* and elsewhere.

Kullander (1998, character 17) found denticulate gill-rakers to be the plesiomorphic condition. However, according to his cladogram (his fig. 11), not only Old World species have toothless gill-rakers, but also a large South American clade sister to the clade that includes Middle American species does, which supports the polarity found here.

#### 8. Sutural connection between halves of lower pharyngeal jaw

[0] not sutured (Fig. 3a) or very slightly so (Fig. 3b); [1] 3–5 acute interdigitations (Fig. 3c); [2] strongly, digitiformly sutured (Fig. 3d).



**FIGURE 3.** Connection between halves of lower pharyngeal jaw: (a) not sutured (*Archocentrus multispinosus*, UMMZ 199539); (b) very slightly sutured (*Rocio octofasciata*, UMMZ 176671); (c) 3-5 acute interdigitations (*Cryptoheros sajica*, UMMZ 194239); (d) strongly, digitiformly sutured (*Amphilophus citrinellus*, UMMZ 188309). Scales: a, 32X; b, 16X; c, 40X; d, 8X.

State 1 is a synapomorphy of *Cryptoheros*. It corresponds to Kullander's (1998, character 20) "partly sutured." State 2 is autapomorphic for *A. citrinellus*;  $hi=0.00$ ,  $ri=1.00$ .

Kullander believed that a strong interdigitation between the two halves of the pharyngeal jaw was related to the presence of "hard items in the diet." I find the same polarity.

#### 9. Rows of teeth on lower pharyngeal jaw

[0] 25 rows wide (one half of lower pharyngeal jaw), 18 rows long; [1] 9 rows wide, 11 rows long; [2] 9-14 rows wide, 5-9 rows long; [3] 19 rows wide, 11 rows long; [4] 16 rows wide, 9 rows long.

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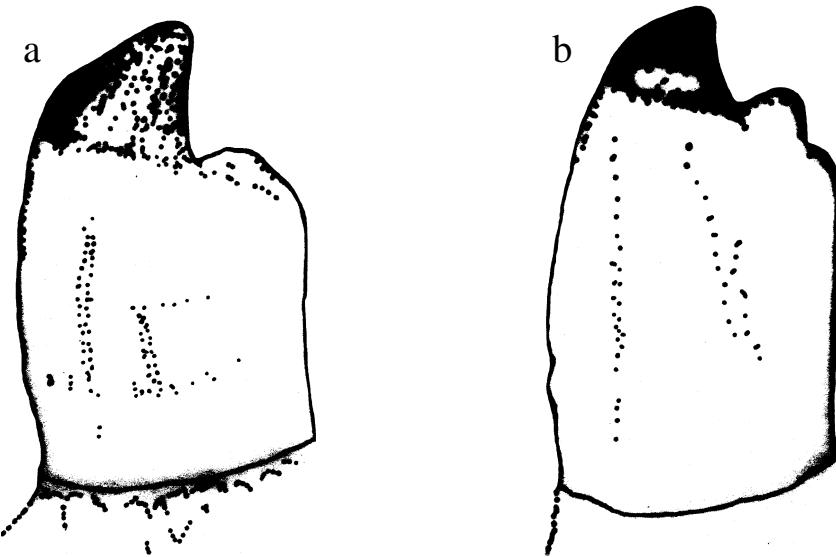
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State 1 is autapomorphic for *Petenia*. State 2 is common to the rest of the Neotropical cichlids examined, with autapomorphic changes to state 3 in *H. nicaraguensis* and state 4 in *Amphilophus*.

10. Main tooth type on upper pharyngeal jaw  
[0] bicuspidate (Fig. 4a); [1] tricuspidate (Fig. 4b).

State 1 appears in several places in the cladogram; it is fixed in *Cryptoheros* (although polymorphic in some species). The bicuspidate condition might appear to be due to grinding of the two proximal cusps, which are close together and not very pronounced; however, in polymorphic taxa the trait seems not to be associated with age. Large amount of homoplasy,  $hi=0.86$ , but informative to some degree,  $ri=0.56$ .



**FIGURE 4.** Main tooth-type on upper pharyngeal jaw: (a) bicuspidate (*Rocio gemmata*, ECOCH 1468); (b) tricuspidate (*Cryptoheros myrnae*, UMMZ 217739). Scale: 66X.

11. Width vs. length, upper pharyngeal jaw  
[0] narrower; [1] subequal or wider.

“Width” was measured from tip to tip across both halves of the jaw. State 1 is present in all Neotropical cichlids examined, except *Petenia*;  $hi=0.50$ , but character uninformative,  $ri=0.00$ .

**Hyoid series, character 12**

12. Posterior and dorsal edges of urohyal

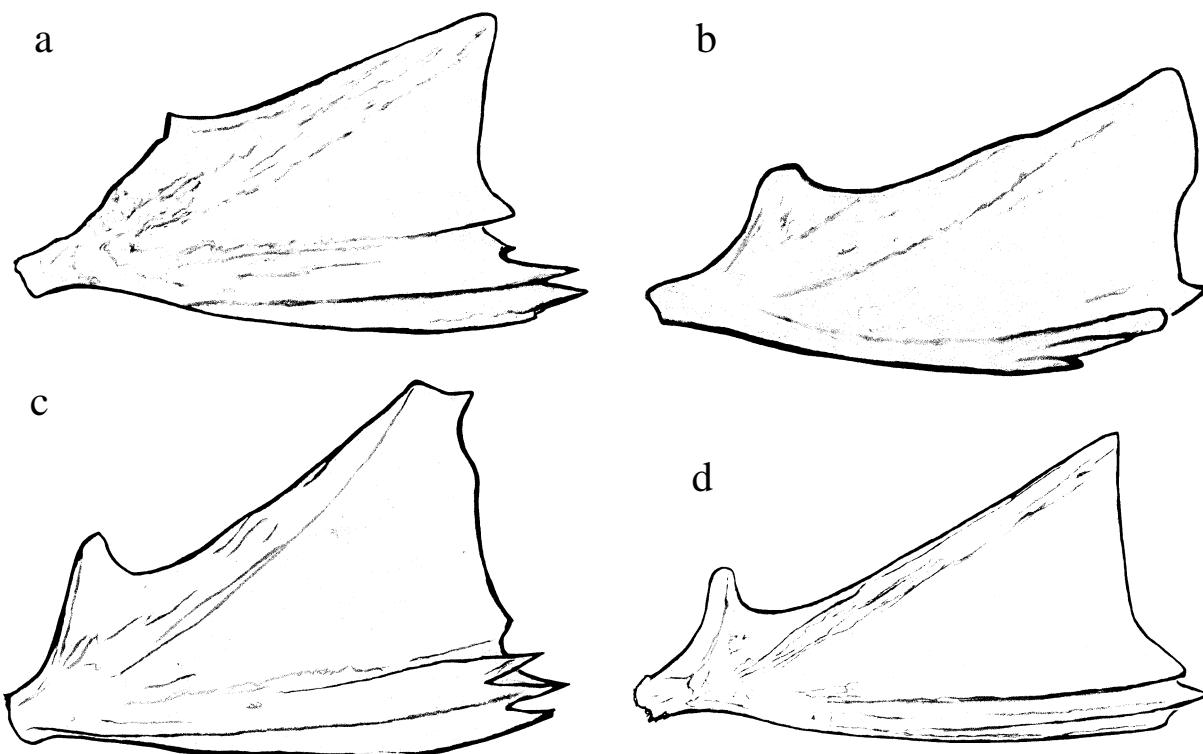
[0] posterior edge concave, dorsal edge with a spine (Fig. 5a); [1] concave, with a posterior spine, dorsally convex; [2] posteriorly sigmoid, with a slightly protruding dorsal convexity (Fig. 5b); [3] sigmoid; [4] dorsally sigmoid, posteriorly straight-slanted; [5] irregular (Fig. 5c); [6] concave, simple (no spines or convexities) (Fig. 5d).

State 1 might support Burgess’ (2000, based on Miller in litt., 1996) view of a relationship between *Caquetaia* and *Petenia*; the state appears in *H. nicaraguensis*, too. Although it is here interpreted as an homoplasy, for the sake of testing that hypothesis the character was not deleted. State 2 is a strict synapomorphy of *Parachromis*. State 3 occurs in several clades, synapomorphically in *Am. kanna + siquia*. State 4 is an autapomorphy of *A. citrinellus*. State 5 is most characteristic in *Cryptoheros* and *Archocentrus*; state 6 is a synapomorphy of *Rocio*, but occurs also in *Amatitlania* and *Cryptoheros*;  $hi=0.50$ ,  $ri=0.54$ .

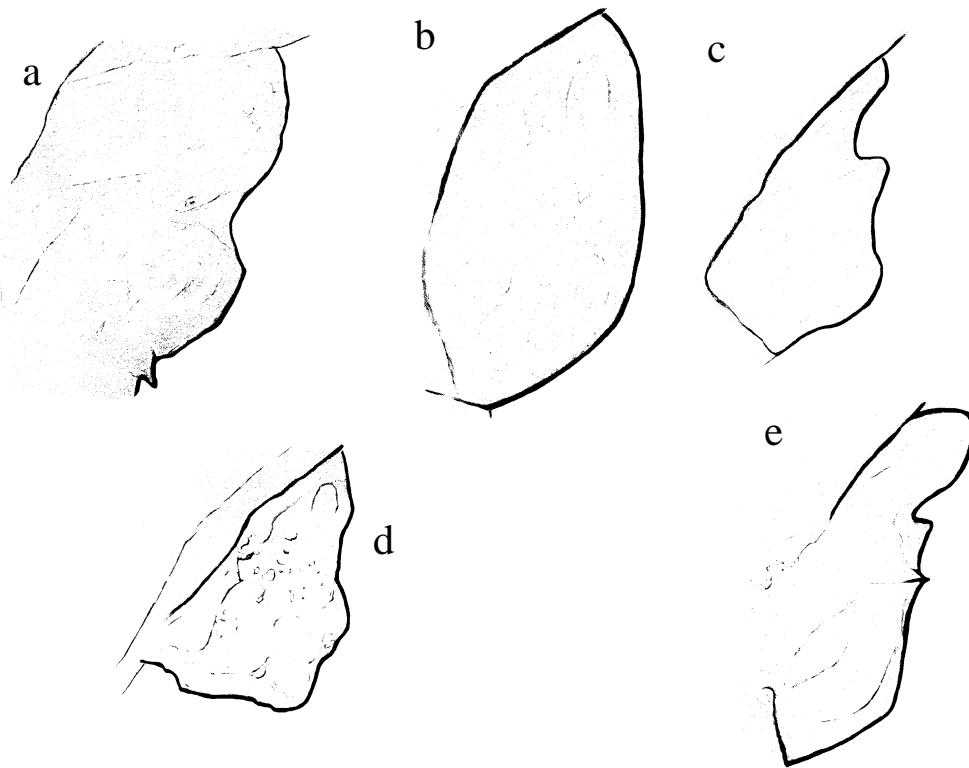
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**FIGURE 5.** Posterior and dorsal edges of urohyal: (a) posterior edge concave, dorsal edge with a spine (*Tomocichla sieboldii*, UMMZ 194240); (b) posteriorly sigmoid, with a slight protruding dorsal convexity (*Parachromis loisellei*, UMMZ 203897); (c) irregular (*Cryptoheros cutteri*, UMMZ 199678); (d) concave, simple, no spines or convexities (*Rocio gemmata*, ECOCH 1468). Scale: a, 32X; b, 8X; c, 25X; d, 20X.

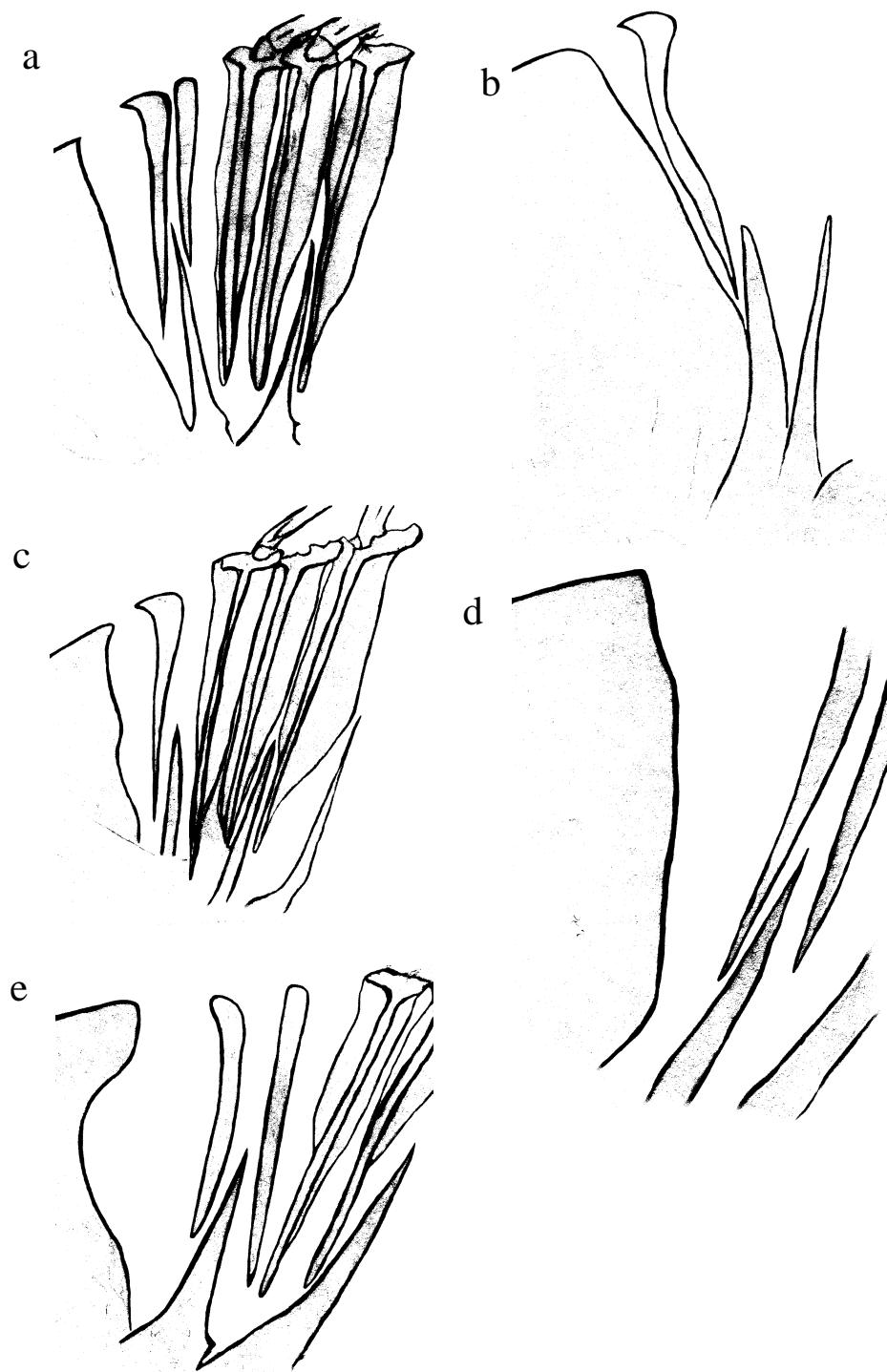


**FIGURE 6.** Posterior edge of mesethmoid: (a) with indentation (*Amphilophus citrinellus*, UMMZ 188309); (b) rounded (*Amatitlania kanna*, UMMZ 145716); (c) *nematopus*-type (*Hypsophrys nematopus*, UMMZ 197507); (d) straight-irregular (*Amatitlania siquia*, UMMZ 196948); (e) with an indentation and a posteriad spine (*Rocio gemmata*, ECOCH 1468). Scales: a, 12X; b,d, 50X; c,e, 32X.

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**FIGURE 7.** Occipital region: (a) caudal edge of supraoccipital crest straight, vertical, dorsal tip angled, predorsal with rostrad process, first neural spine antrorse, three dorsal elements between first two first neural spines; anterodorsal spine on first dorsal pterygiophore (*Amatitlania siquia*, UMMZ 196948); (b) caudal edge straight, inclined rostrad, dorsal tip rounded (*Hypsophrys nematopus*, UMMZ 197507); (c) caudal edge undulating, no deep concavity, first neural spine retrorse, two dorsal elements between first two first neural spines (*Cryptoheros cutteri*, UMMZ 173195); (d) caudal edge convex, first neural spine retrorse (*Archocentrus centrarchus*, UMMZ 224131); (e) undulating, with a deep concavity, first neural spine retrorse, three dorsal elements between first two first neural spines (*Rocio gemmata*, ECOCH 1468). Scales: a,d,e, 16X; b, 20X; c, 12X.

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**Neurocranium, characters 13–16**

## 13. Mesethmoid posterior edge

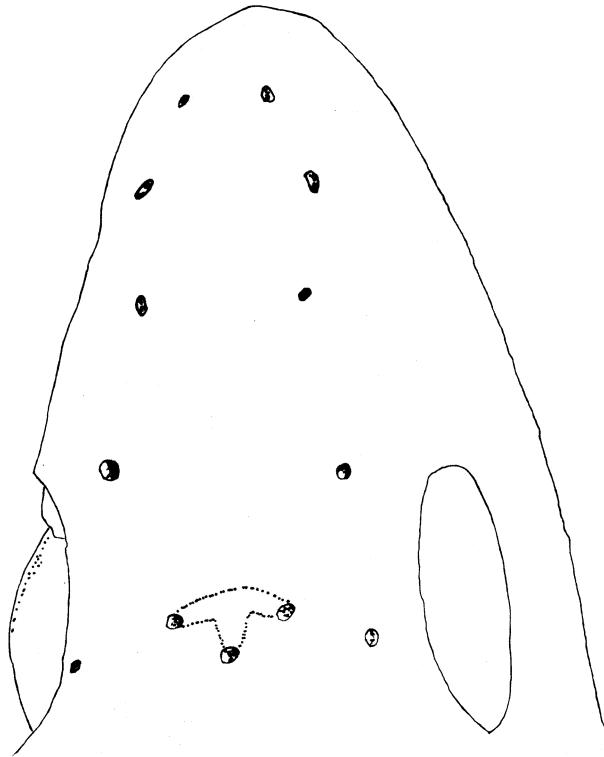
[0] straight-concave, covered by lateral ethmoid; [1] with a double indentation (Fig. 6a); [2] rounded (Fig. 6b); [3] *nematopus*-type (Fig. 6c); [4] straight-irregular (Fig. 6d); [5] with an indentation and a posteriad spine (Fig. 6e).

State 1 is an homoplasious synapomorphy for *Parachromis*; state 2 occurs in several clades, such as *Archocentrus* and most of *Amatitlania* and *Cryptoheros*. State 3 is autapomorphic for *H. nematopus*. State 4 is common in the subgenus *Bussingius*; state 5 is a strict synapomorphy for *Rocio*; hi=0.58, ri=0.30.

## 14. Supraoccipital crest, caudal edge

[0] irregularly undulating; [1] straight, vertical, dorsal tip angled (Fig. 7a); [2] concave; [3] straight, inclined rostral, dorsal tip rounded (Fig. 7b); [4] undulating, no deep concavity (Fig. 7c); [5] convex (Fig. 7d); [6] undulating, with a deep concavity (Fig. 7e).

States 1 and 2 are homoplasious, although state 1 is fixed in *Amatitlania*. State 3 is autapomorphic for *H. nematopus*. State 4 may be synapomorphic for *Cryptoheros*, but reversed several times. State 5 might be a synapomorphy of *Ar. centrarchus* + *multifasciatus*, with a parallelism in *Caquetaia*. State 6 is a strict synapomorphy of *Rocio*; hi=0.54, ri=0.42.



**FIGURE 8.** Coronal pore triple, tubes T-shaped (*Cryptoheros cutteri*, UMMZ 188136). Semidiagrammatic. Scale: 6X.

## 15. Coronal pore

[0] single; [1] none; [2] triple, tubes T-shaped (Fig. 8).

Cichocki (1976, character 3) defined this character in a more complex manner, as the “configuration of the coronal frontalis lateralis canals and associated frontal ridges” and established eleven character states. However, my coding coincides with Cichocki’s only in distinguishing *Petenia*, with a coronal pore “obliterated by development of a median trough running the full length of the skull roof” (my state 1: no

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coronal pore). He combined my states 0 and 2 as “united medially, raised on medial frontal ridge as common anterodorsally directed coronal tube with single coronal pore.” However, I find that state 2, a triple coronal pore, with the three pores joined by tubes shaped like a T, is synapomorphic for *Cryptoheros*, with a reversal in *Cr. myrnae*, a polymorphism in *Cr. septemfasciatus* (states 0 and 2), and a parallelism in *Ar. multispinosus* ( $hi=0.50$ ,  $ri=0.71$ ).

On the other hand, Cichocki (1976) coded a *Parachromis*, *P. friedrichsthalii* (Heckel), as having a different character state, “coronal canal directed straight dorsally and moderately elevated in the median frontal crest...,” with a figure (his fig. 1.6 D) depicting a single coronal pore. As I construct the character, I fail to see a difference in either *P. loisellei* (Bussing, 1989) or *P. dovii*, both of them being single-pored, state 0.

16. Supraoccipital crest height on postethmoid skull roof length

[0] 0.33 or more; [1] 0.27 or less.

State 1 is autapomorphic for *H. nematopus*.

Cichocki (1976, character 2) recognised five character states, with not quite the same polarity found here: 0.26–0.50, 0.18–0.20, 0.10 or less, 0.52–0.55, and 0.80 or more; within his state 1 (which he applies to *H. nematopus* and the other taxa which occur in both studies), I find two different states, separated by a well-defined gap.

### **Infraorbitals, characters 17–19**

17. Sensory canals on lachrymal

[0] five marginal-directed canals; [1] four marginal-directed canals.

State 1 is a synapomorphy of all Neotropical cichlids examined,  $hi=0.00$ .

This character and its states are in part Cichocki's (1976, character 45) “configuration of the infraorbital ossicles associated with the anterior four neuromasts,” with eight states, and Kullander's (1998, character 38) “configuration of the lateralis canal in the lachrymal,” which in addition to the number of openings (marginal-directed canals) considered the number of lachrymal bones, 1 or 2. All the species considered here have just one lachrymal. I find the same polarity as Kullander (1998).

I refrained from using the shape of the lachrymal (Kullander's [1998] character 40, Cichocki's [1976] character 46) because it is strongly affected by ontogeny (juveniles of all species tend to have wider lachrymals). It is also a very homoplasious character: a wide lachrymal (in adults) is parallel between *Caquetaia*, *Petenia*, *Amphilophus*, and *Ar. centrarchus*, and a deep one is convergent between *H. nematopus* and *Tomocichla*.

I would have coded this second part of the character (shape of the lachrymal) as Cichocki (1976) did. He recognised that there are two trends in its evolution: one towards wider, the other one towards deeper lachrymals. Kullander (1998), however, noted that heroines (that is, all my study taxa except the tilapia) and cichlasomines have all an “approximately square form.”

18. Overlap between lachrymal and second infraorbital

[0] some overlap; [1] no overlap.

An autapomorphy of *Petenia*. Cichocki's (1976) character 47 and its states are the same; however, Kullander's (1998, character 44) distinguished two degrees of overlap (distal connection vs. extensive overlap) and found the opposite polarity, although both the Malagasy-Indian *Etroplus* Cuvier +*Ptychochromis* Steindachner and *Heterochromis*, sister group of the clade that includes Middle American cichlids (Kullander 1998), show his state 2, which supports my view (and Cichocki's, 1976) that the overlap represents the plesiomorphic condition.

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## 19. Number of infraorbitals posterior to lachrymal

[0] five; [1] four.

State 1 is synapomorphic for all Neotropical cichlids examined, with the sole autapomorphic reversal of *H. nicaraguensis*; hi=0.50, but ri=0.00.

Same interpretation as Kullander's (1998) character 41, although he needed two more states, for species with three or two infraorbitals.

**Mouth and oral jaws, characters 20–47**

## 20. Anterior vs. posterior palatine arms

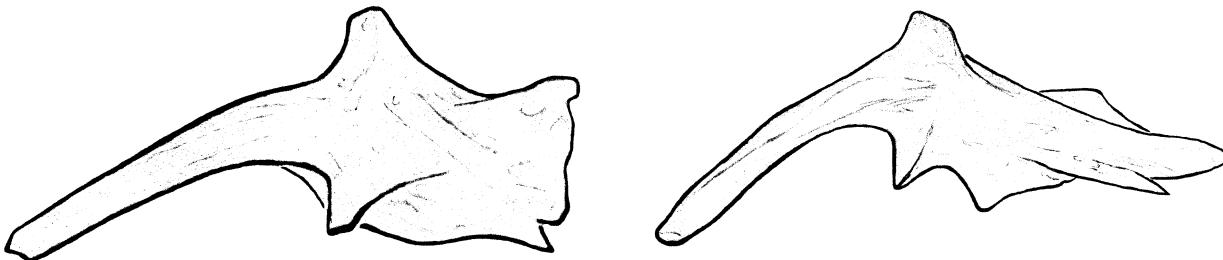
[0] anterior longer (Fig. 9a); [1] posterior longer; [2] subequal (Fig. 9b).

State 1 seems to be a convergent adaptation (hi=0.75) for the piscivore habit, occurring in *Parachromis*, *Caquetaia*, and *Petenia*. State 2 is synapomorphic (ri=0.57) for *Amatitlania*, *Rocio*, and *Archocentrus*, although reversed in *H. nematopus* and *Ar. multispinosus* and parallel in *Cr. sajica* and *Amphilophus*.

## 21. Ascending premaxillary process on orbit

[0] process not reaching eye rim; [1] process to anterior eye rim; [2] process to mid-eye; [3] process beyond posterior eye rim.

The elongation of the dorsal process (ascending arm) of the premaxillary bone is an adaptation to make the mouth protrusible. State 1 is synapomorphic for *Rocio* and *Amatitlania*; state 2 appears to have evolved separately in *Caquetaia* and *Parachromis*. State 3 is autapomorphic for *Petenia*. State 0, once used to diagnose *Archocentrus* (e.g. Allgayer 2001), is just a symplesiomorphy of these small-mouthed Heroini; hi=0.50, ri=0.67.



**FIGURE 9.** Anterior vs. posterior palatine arms: (a) anterior longer (*Cryptoheros chetumalensis*, UMMZ 197224); (b) subequal (*Archocentrus centrarchus*, UMMZ 224131). Scales: a, 32X; b, 40X.

## 22. Ascending premaxillary process on skull length

[0] ratio 0.20–0.66; [1] ca. 0.76; [2] 0.87 or more.

States 1 and 2 are autapomorphic for *Petenia* and *Caquetaia*, respectively. An obvious coding alternative would be to combine them into a putative synapomorphy, which would support the view of a close relationship between those taxa; however, the difference between them is as large as, or larger, than the one between *Petenia* and the rest of the examined species.

Cichocki (1976, character 12) recognised 10 character states for this trait, based on several combinations of the ascending premaxillary process relative to the prefrontal and standard skull lengths. He conferred *Caquetaia kraussi* Steindachner and *Petenia* the same state, "ascending process extremely long," both with respect to prefrontal skull and standard skull lengths. *H. nematopus* and *Amatitlania* also had one same state, "ascending process moderate with respect to prefrontal skull, long with respect to standard skull length," but *Amphilophus* had a different state, "ascending process long with respect to prefrontal skull, long with respect to standard skull length."

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## 23. Ascending vs. dentigerous arms of premaxilla

[0] ascending arm shorter; [1] ascending arm longer (ascending / dentigerous = 1.18–2.03); [2] ascending arm much longer (ca. 2.37); [3] ascending arm longer still (2.44–2.47).

State 1 is a synapomorphy for the Neotropical cichlids examined, apart of *Petenia* (and the autapomorphic reversal in *H. nematopus*);  $hi=0.25$ , but  $ri=0.00$ . A much longer dorsal process hints at a relationship between *Petenia* and *Caquetaia*, but the still longer ascending arm of *Caquetaia* is interpreted here as a different character state. Kullander (1998, character 64) followed Casciotta and Arratia (1993) in uniting my states 2 and 3, but the polarity that he found is the same as mine.

I was not able to code Cichocki's (1976) character 14, the length of the articulating process relative to the dorsal process. He distinguished two states, 0.40–0.69 and 0.70–0.90 (ratio articulating / ascending), but they overlap in my material, not allowing a statistical definition of states. Also Kullander (1998) did not consider the character to be "general" enough to be useful.

## 24. Dorsal convexity on dentigerous arm of premaxilla

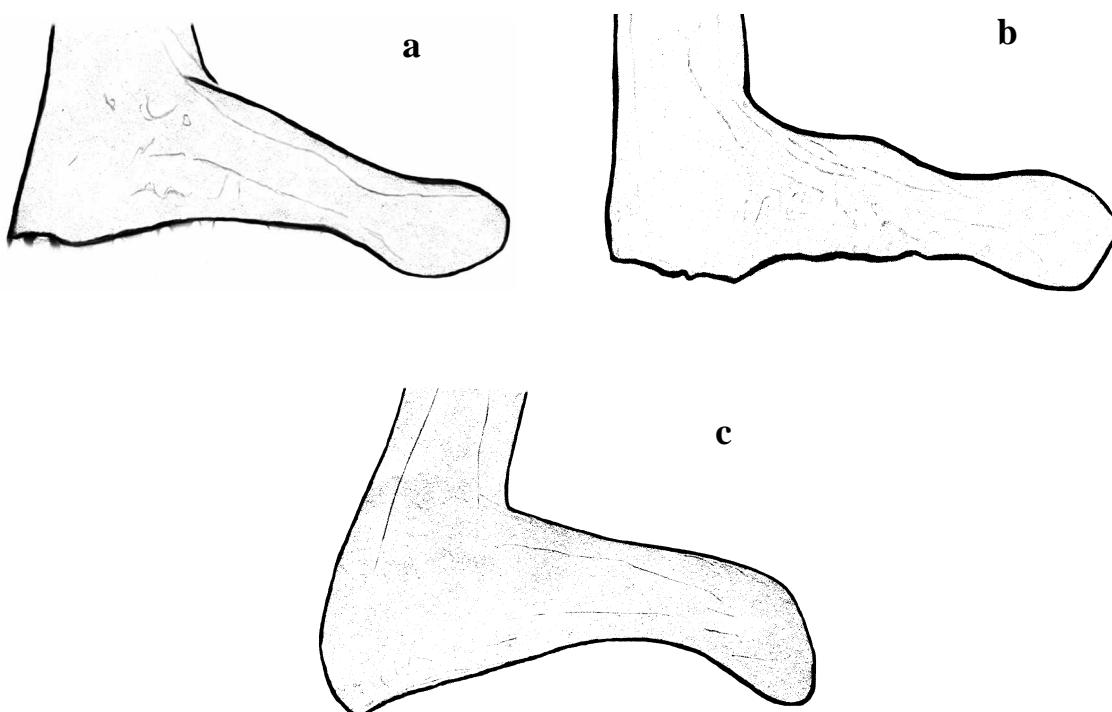
[0] not distinct (Fig. 10a); [1] distinct (Fig. 10b).

Quite homoplasious ( $hi=0.89$ ), but state 1 appears to be synapomorphic for *Cryptoheros* ( $ri=0.20$ ), with a reversal for the five species in the subgenus *Bussingius*, and also for *Ar. centrarchus + multispinosus* within *Archocentrus*, with parallelisms elsewhere over the tree.

## 25. Narrowest point of dentigerous arm of premaxilla

[0] at caudal tip (Fig. 10c); [1] before caudal tip (Figs. 10a,b).

State 1 is synapomorphic for the Neotropical cichlids examined, although with several reversals, most importantly in *Rocio*;  $hi=0.75$ ,  $ri=0.50$ .



**FIGURE 10.** Dentigerous arm of premaxilla: (a) dorsal convexity not distinct, arm narrowest before caudal tip (*Amatitlania coatepeque*, UMMZ 181823); (b) dorsal convexity distinct, arm narrowest before caudal tip (*Am. siquia*, UMMZ 196948); (c) arm narrowest at caudal tip (*Rocio octofasciata*, ECOCH 5468). Scales: a,b, 40X; c, 25X.

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## 26. Toothed length in premaxilla

[0] ca. 0.97 total length of dentigerous arm; [1] ca. 0.84; [2] 0.30–0.80.

State 2 is synapomorphic for the Neotropical cichlids examined; state 1 is autapomorphic for *R. gemmata*; hi=0.00.

Cichocki (1976, character 18) called this character “outer premaxillary tooth distribution,” with the same polarity as here, but states defined as 0.75–1.00, 0.50–0.67, and 0.25 or less, thus not only not quite the same as mine, but also somewhat conflicting (apparently he did not observe specimens with toothed length between 0.26 and 0.50). I defined states by looking for non-overlapping value distributions.

## 27. Width vs. length, posterior premaxillary expansion

[0] 0.21–0.40; [1] ca. 0.18; [2] 0.41 or more.

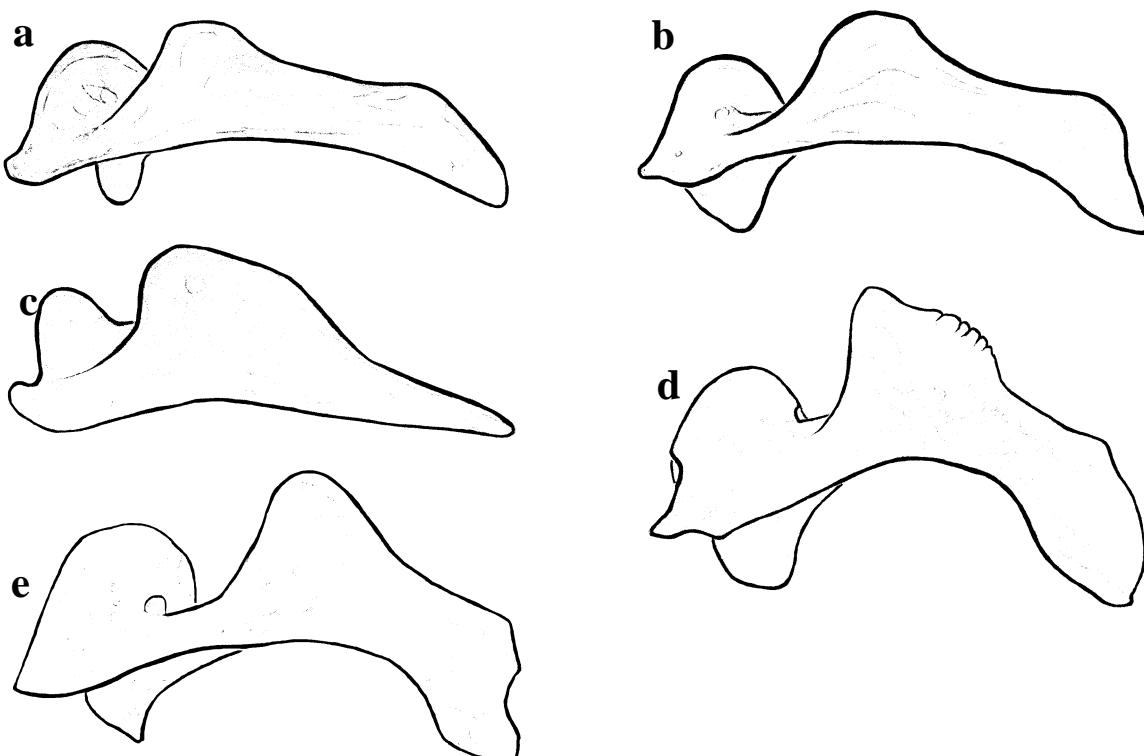
State 1 is another possible synapomorphy (here considered a convergence) for *Petenia* and *Caquetaia*; state 2 is autapomorphic for *H. nematopus*; hi=0.33, but ri=0.00.

Cichocki (1976, character 27) recognised four states: 0.20–0.33, 0.34–0.36, 0.38–0.43, and 0.14–0.17, delimited by breaks in the range of variation; his polarity is the same as mine. The species here examined show too extensive an overlap within the range 0.21–0.40 to warrant recognition of Cichocki’s first three states.

## 28. Maxillary on orbit

[0] maxillary reaches only to horizontal level of orbit; [1] maxillary reaches orbit both horizontally and vertically; [2] maxillary falls short of orbit.

Homoplasious (hi=0.71); fixed for state 1 in *Parachromis* and for state 2 in *Hypsophrys*, the subgenus *Bussingius* of *Cryptoheros*, etc. (ri=0.50).



**FIGURE 11.** Maxillary: (a) rostral end convex, no notch, caudal end entire (*Rocio octofasciata*, UMMZ 187779); (b) rostral end notched or at least concave, dorsal edge not serrated (*R. gemmata*, ECOCH 1468); (c) no notch at rostral end, but a dorsad protuberance (*Hypsophrys nematopus*, UMMZ 197507); (d) dorsal edge serrated (*Cryptoheros altoflavus*, UMMZ 145722); (e) caudal end with a concavity (*Archocentrus multispinosus*, UMMZ 199539). Scales: a, 16X; b, 25X; c, 32X; d,e, 40X.

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29. Rostral end of maxillary

[0] convex, no notch (Fig. 11a); [1] notched or at least concave (Fig. 11b); [2] no notch, but a dorsad spine (Fig. 11c).

Homoplasious ( $hi=0.78$ ) but somewhat informative ( $ri=0.42$ ). State 1 is fixed in *Cryptoheros* (reversal in *Cr. chetumalensis*); state 2 fixed in *Parachromis*.

30. Dorsal edge of maxillary

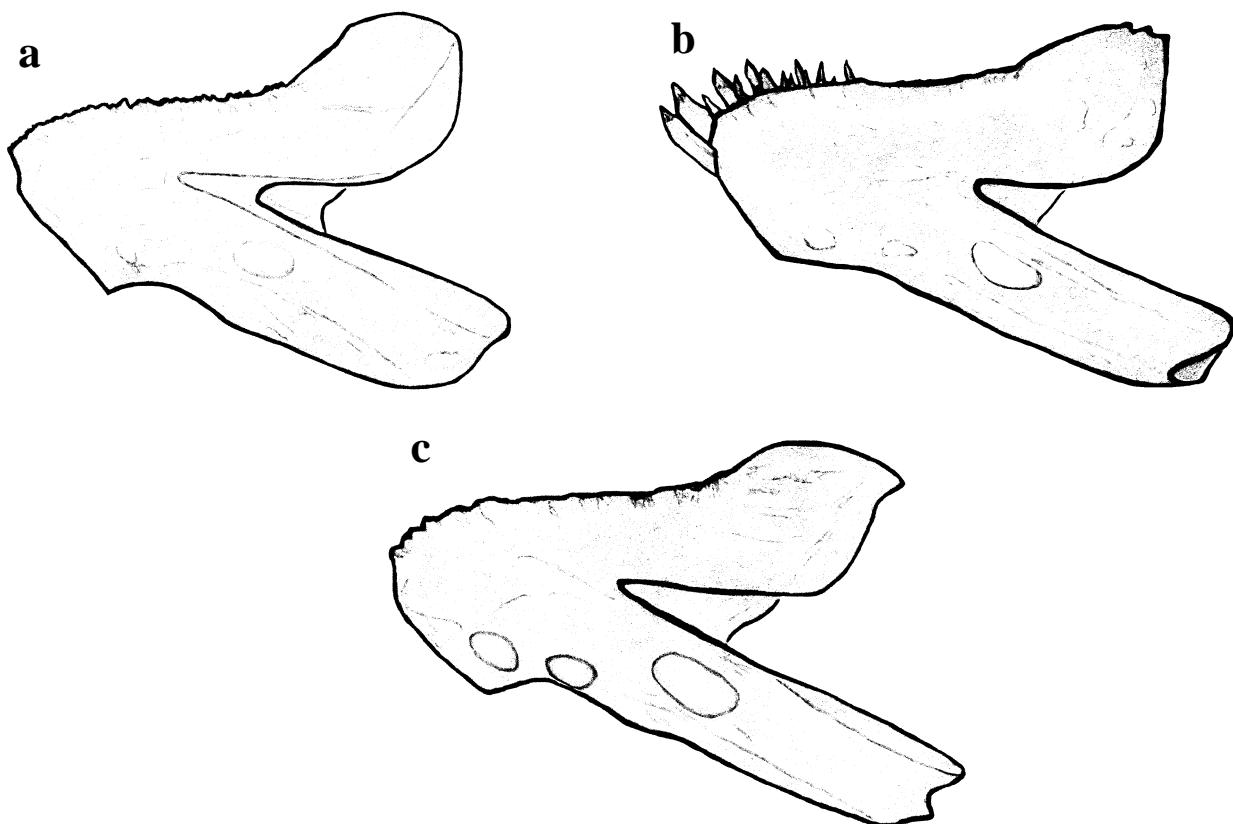
[0] not serrated (Fig. 11a,b); [1] serrated (Fig. 11d).

State 1 is fixed in *Amatitlania* and *Cryptoheros*, parallel in *Tomocichla*;  $hi=0.67$ , but a high retention index,  $ri=0.85$ .

31. Posterior end of maxillary

[0] entire (Figs. 11a–d); [1] with a concavity (Fig. 11e).

State 1 appears in *Ar. spinosissimus* and *Ar. multispinosus*, either as a parallelism or as a synapomorphy for *Archocentrus* with a reversal in *Ar. centrarchus*;  $hi=0.50$ , but  $ri=0.00$ .



**FIGURE 12.** Posterior end of dentigerous arm of dentary: (a) rounded or squarish (*Amatitlania nigrofasciata*, UMMZ 188245); (b) triple-spined (*Am. coatepeque*, UMMZ 181823); (c) bluntly pointed (*Am. siquia*, UMMZ 196948). Scales: a, 40X; b, 32X; c, 50X.

32. Arms of dentary

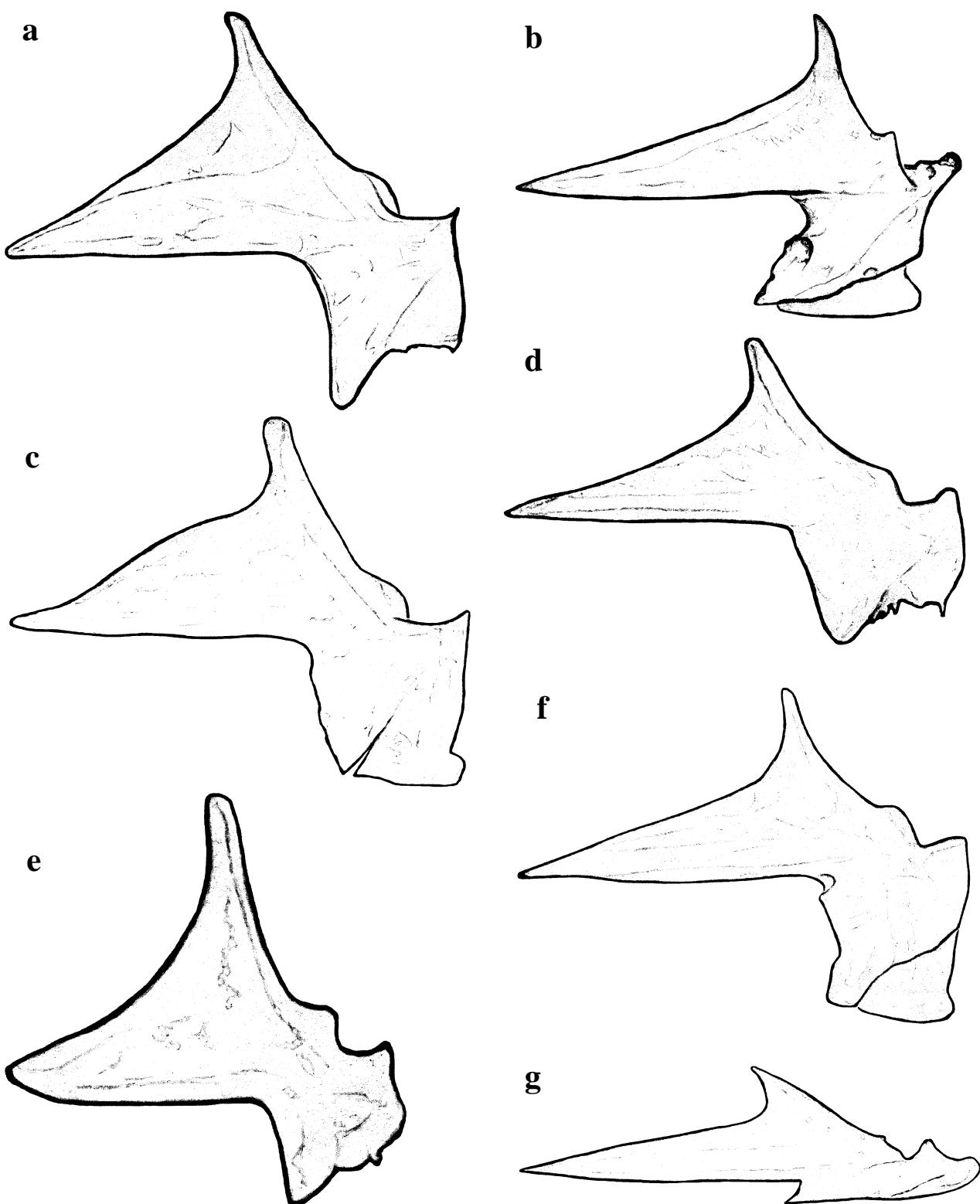
[0] subequal, or dentigerous longer than ventral (dentigerous / ventral = 0.93–1.62); [1] ventral longer than dentigerous (dentigerous / ventral, ca. 0.88) (Fig. 12).

State 1 is synapomorphic for the Neotropical cichlids examined, with a reversal in *Parachromis* ( $hi=0.50$ ,  $ri=0.50$ ). Among the rest, only *H. nematopus* and *Tomocichla* occasionally have a dentigerous / ventral length ratio slightly less than 1.

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**FIGURE 13.** Articular and retroarticular: (a) dorsal edge straight, ventral angle right, no rostrad pronounced convexity on ventral process (*Amatitlania nigrofasciata*, UMMZ 188245; retroarticular not shown); (b) ventral angle acute (*Rocio octofasciata*, UMMZ 187779); (c) dorsal edge convex, ventral angle obtuse (*Cryptoheros altoflavus*, UMMZ 145722); (d) dorsal edge straight, ventral angle obtuse (*Am. siquia*, UMMZ 190199; retroarticular not shown); (e) arms of articular equal, no posteriad projection on retroarticular (*Hypsophrys nematopus*, UMMZ 197507); (f) dorsal edge straight, ventral angle right, a rostrad pronounced convexity on ventral process (*R. gemmata*, ECOCH 1468); (g) retroarticular much elongated antero-caudally (*Petenia splendida*, UMMZ 196461). Scales: a,c. 40X; b,e, 20X; d, 50X; f, 32X; g, 10X.

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## 33. Posterior end of dentigerous arm of dentary

[0] tapering; [1] sharply pointed; [2] rounded or squarish (Fig. 12a); [3] triple-spined (Fig. 12b); [4] bluntly pointed (Fig. 12c).

State 1 is a convergence of *Caquetaia* and *Petenia* (see Cichocki 1976: fig. 1.9E). State 2 seems synapomorphic for the Neotropical cichlids examined, with an autapomorphic progression to state 3 in *Am. coatepeque* and to state 4 in *Am. kanna + siquia* and *Cryptoheros* (some reversals to state 2); hi=0.56, ri=0.50.

## 34. Arms of articular

[0] rostral clearly longer than dorsal (dorsal / rostral = 0.41–0.77) (Figs. 13a–d); [1] dorsal / rostral, ca. 0.87; [2] rostral and dorsal equal (Fig. 13e).

State 1 is autapomorphic for *Ar. multispinosus*. State 2 is autapomorphic for *H. nematopus*.

## 35. Dorsal edge of articular

[0] straight (Figs. 13a,d); [1] convex (Fig. 13c).

State 1 is a strict synapomorphy of *Cryptoheros* (without the basal *Cr. panamensis*); hi=0.00, ri=1.00.

## 36. Ventral angle of articular

[0] acute (Fig. 13b); [1] right (Fig. 13a); [2] obtuse (Fig. 13d).

State 1 occurs in most Neotropical cichlids examined; state 2 is most common within *Cryptoheros*, and is synapomorphic for the clade *Am. kanna + siquia*; hi=0.82, ri=0.31.

## 37. Anteriorly directed pronounced convexity on ventral process of articular

[0] absent (Figs. 13a,c,d); [1] present (Fig. 13f).

State 1 occurs in most Neotropical cichlids examined, with many reversals, notably in most *Cryptoheros* and *Parachromis*. Fixed for *Rocio*, *Archocentrus*, and *Hypsophrys*; hi=0.88, ri=0.22.

## 38. Shape of retroarticular

[0] slightly elongated (Figs. 13a–f); [1] much elongated anterocephally (Fig. 13g).

State 1 is probably a convergence of piscivores: *Petenia*, *Caquetaia*, and *Parachromis* (hi=0.67, ri=0.33). The same is the case for many of these mouth and oral jaw characters; this is the reason why Kullander (1998) shunned most of Casciotta and Arratia's (1993) characters, whose emphasis on trophic-related traits led to lumping in one clade all piscivores in their matrix. I feel, nevertheless, that the convergence hypothesis, however plausible, should be tested by inclusion of these characters in a larger matrix.

## 39. Posteriad projection on ventroposterior angle of retroarticular

[0] absent (Fig. 13g); [1] present (Figs. 13b–d,f).

State 1 is homoplastically synapomorphic for *Cryptoheros* (with reversal in *Cr. sajica*), *Rocio*, and *Amatitlania* (hi=0.86, but ri=0.64). *Cr. myrnae* and *Am. siquia* are polymorphic for the trait.

## 40. Quadrat

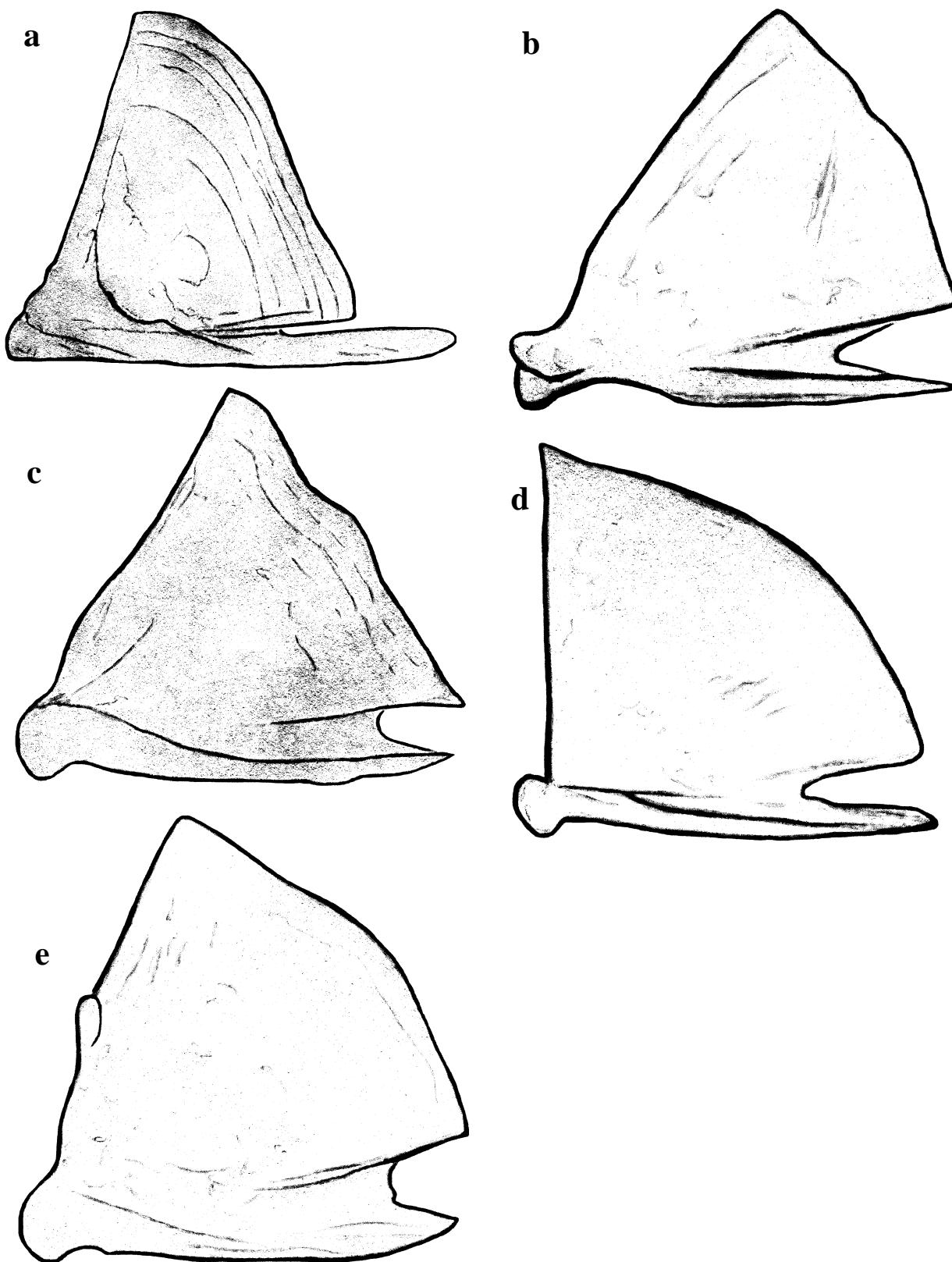
[0] no indentation on posterior edge, longer than wide (Fig. 14a); [1] no indentation on posterior edge, wider than long (Fig. 14b); [2] a dorsoposterior concavity (Fig. 14c); [3] shaped like a quarter-circle (Fig. 14d); [4] with a spine (Fig. 14e).

State 1 is a synapomorphy of *Cryptoheros*, although occurring homoplastically also in *Petenia*, *H. nematopus*, and *Am. kanna*. State 2 is a synapomorphy of *Archocentrus*, albeit it is present also in *Caquetaia* and *Amphilophus*. State 3 is common in *Amatitlania* and *Rocio*; state 4 is an autapomorphy of *R. gemmata*; hi=0.56, but ri=0.58.

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**FIGURE 14.** Quadrate: (a) no indentation on posterior edge, bone longer than wide (*Oreochromis mossambicus*, UMMZ 199401); (b) no indentation on posterior edge, bone wider than long (*Petenia splendida*, UMMZ 196461); (c) a dorsoposterior concavity (*Amphilophus citrinellus*, UMMZ 188309); (d) shaped like a quarter-circle (*Amatitlania nigrofasciata*, UMMZ 202707); (e) with a spine on rostral margin (*Rocio gemmata*, ECOCH 1468). Scales: a,b, 16X; c, 10X; d, 32X; e, 25X.

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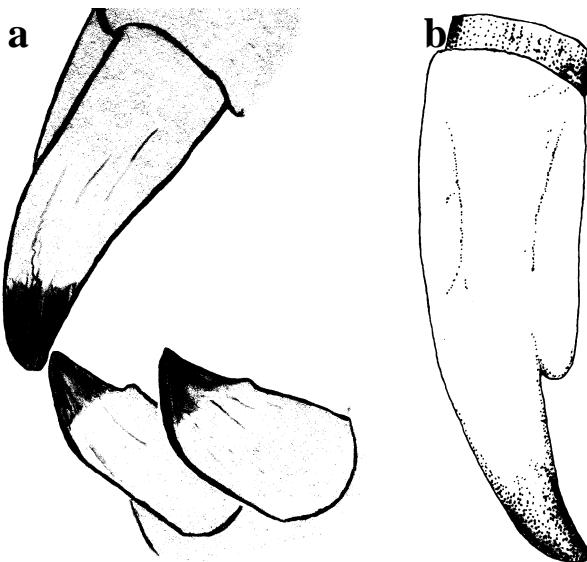
## 41. Upper symphysial teeth shape

[0] villiform, curved, a lateral cusp near tip; [1] canine or conical, unicuspid (Fig. 15a); [2] true incisors (edge straight); [3] tricuspid; [4] oval in section, compressed, medially widest, a strong lingual cusp (Fig. 15b); [5] "false incisors" (edge rounded); [6] triangular, pointed, much compressed, some incisor-like.

State 1 is a synapomorphy for the Neotropical cichlids analysed except *Tomocichla*, with many transitions to more derived character states: states 2, 3, 5, and 6 are autapomorphies; state 4, a synapomorphy of the subgenus *Bussingius* of *Cryptoheros*, with a reversal in *Cr. septemfasciatus*; hi=0.25, ri=0.33.

The incisors of *H. nematopus*, *Cr. panamensis*, and *Tomocichla* are only convergently similar. Solely *H. nematopus* has true incisors, with straight edges that form a continuous cutting line with the adjacent teeth, even in juveniles (Cichocki 1976: fig. 1.11F). The "incisors" of *Cr. panamensis* are rounded, not forming a continuous line, and they are pointed in juveniles; adjacent teeth (beyond the central 2 or 3 pairs) are conical. The teeth of *T. sieboldii* may approach an incisor-like form because they are compressed; however, their sides are not parallel, but convergent towards a pointed tip.

This character has no clear seriality, although the ontogeny of *Cr. panamensis* suggests that state 5 is derived directly from state 1.



**FIGURE 15.** Symphysial teeth: (a) canine, lingual cusp slight or non-existent in upper symphysial; lower symphysial bicuspidate, not much retrorse (*Rocio gemmata*, ECOCH 1468); (b) oval in section, compressed, a strong lingual cusp (*Cryptoheros chetumalensis*, UMMZ 197224; only upper symphysial shown). Scale: 66X.

Kullander's (1998) character 65 refers to all jaw teeth, not just the symphysial. He used five states: my states 0, 1, and 3, as well as "[only] inner teeth tricuspid" and "all teeth bicuspid." He found my state 1 to be the plesiomorphic condition, with the African type (my state 0) derived. However, the basal clade in his cladogram shows mostly my state 0. Cichocki (1976, character 17) also considered simple canines as the plesiomorphic condition, but not so much based on outgroup comparison as in "the frequency of occurrence among the major groups of cichlids" (although he added that this is also the condition for most percoids).

Within my state 1, some taxa, for example *Rocio*, show a small lingual cusp; however, this trait is polymorphic. Casciotta and Arratia (1993) and Kullander (1996) believed that the lingual cusp diagnosed either all species of Heroini or a subset of them; given the variability of this trait, I cannot fully agree.

## 42. Upper symphysial teeth relative to adjacent

[0] symphysial teeth lower; [1] symphysial teeth (sub)equal; [2] symphysial teeth abruptly larger.

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State 0 occurs only in the tilapia. State 2 is homoplastically synapomorphic for *Parachromis*, *Rocio*, and *Amatitlania*, with parallelisms in *Cr. myrnae* and *Caquetaia*; hi=0.67, but ri=0.60.

**43. Lower symphysial teeth shape**

[0] multicuspitate; [1] canine retrorse; [2] oval in section, medially widest; [3] conical, not much retrorse; [4] tricuspidate; [5] bicuspidate (Fig. 15a).

State 2 is autapomorphic for *Tomocichla*. State 3 is most common within the Neotropical cichlids examined, fixed in *Amatitlania*, *Hypsophrys*, and *Parachromis*. State 4 is an autapomorphy for *Ar. multispinosus*, once diagnostic for the monotypic genus *Herotilapia*. State 5 appears in *Rocio* (without *R. ocotal*) and *Cryptoheros*; hi=0.50, ri=0.38.

**44. Lower symphysial teeth relative to adjacent**

[0] symphysial teeth (sub)equal; [1] symphysial teeth lower; [2] symphysial teeth much lower, almost completely embedded.

State 1 is homoplastically synapomorphic for *Rocio* and *Amatitlania*, and occurs also in *Cr. panamensis* and *Petenia*. State 2 is synapomorphic for *Parachromis*, convergent with *Caquetaia*; hi=0.67, but ri=0.60.

**45. Number of lower mandibular external teeth**

[0] modally less than 20; [1] modally more than 24.

State 1 is autapomorphic for *Petenia*.

**46. Protruding lower jaw**

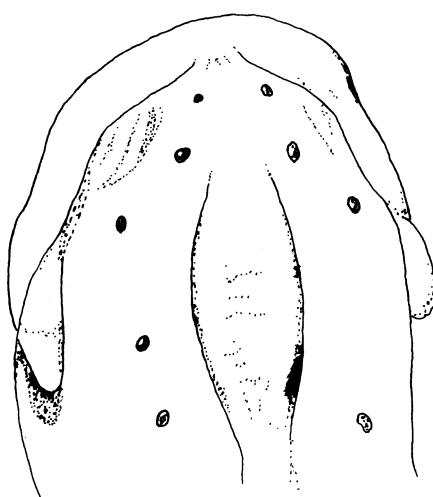
[0] yes (prognathous), at least slightly; [1] no (mouth terminal); [2] lower jaw receding (mouth inferior).

State 1 is homoplastically synapomorphic for *Amatitlania* and for *Cryptoheros*, and parallel also in *Ar. multispinosus*. State 2 is a synapomorphy of *Hypsophrys*, convergent in *Tomocichla*; hi=0.60, but a high ri, 0.75.

**47. Frenum**

[0] present (Fig. 16); [1] absent.

Once considered diagnostic of genera (*Heros* Heckel vs. *Cichlasoma*, according to Jordan & Evermann 1898), this character (a medial interruption of the lower lip fold) has long been considered very variable among species (e.g. Pellegrin 1904). Nevertheless, state 1 is fixed in *Parachromis*; hi=0.80, ri=0.20.



**FIGURE 16.** Frenum and dentary pores (*Rocio ocotal*, UMMZ 171140). Note fifth dentary pore on right dentary. Scale: 16X.

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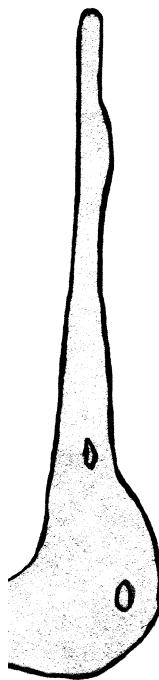
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**Preopercle, opercle, and pectoral girdle, characters 48–51**

## 48. Preopercular posterior edge

[0] convex to straight; [1] slightly, roundly concave (Fig. 17); [2] irregular, no lobes; [3] squarely concave (“bracket-shaped”); [4] irregular, with lobes.

State 1 occurs in all Neotropical cichlids examined outside *Tomocichla* and *Petenia*, with reversals within *Cryptoheros*. States 2–4 are autapomorphies; hi=0.50, but ri=0.00.



**FIGURE 17.** Posterior edge of preopercle: slightly, roundly concave (*Amatitlania coatepeque*, UMMZ 181823). Scale: 10X.

## 49. Spine on dorsal margin of opercle

[0] absent (Fig. 18a); [1] present (Fig. 18b).

Highly homoplasious (hi=0.90). Some species are polymorphic for this trait; however, it supports some structure (e.g., it is a synapomorphy of the subgenus *Cryptoheros*, with a polymorphism in *Cr. cutteri*); ri=0.14.

## 50. Shape of dorsal margin of opercle

[0] evenly convex, no protuberances (Fig. 18a); [1] evenly convex, with a dorsoanterior protuberance (Fig. 18c); [2] extremely convex, almost semicircular (Fig. 18d); [3] almost straight.

State 1 is a putative synapomorphy of *Ar. centrarchus* + *multispinosus* (but ri=0.00), with a parallelism in *P. loisellei*. State 2 occurs in *H. nematopus* and *Caquetaia*. State 3 is autapomorphic for *Petenia*; hi=0.50.

## 51. Foramen in scapula

[0] slanted (Fig. 19a); [1] parallel to anteroposterior axis of bone (Fig. 19b).

State 1 is a synapomorphy of all Neotropical cichlids examined; hi=0.00.

**Axial skeleton, characters 52–59**

## 52. Rostrad process on first predorsal element

[0] absent; [1] present (Fig. 7).

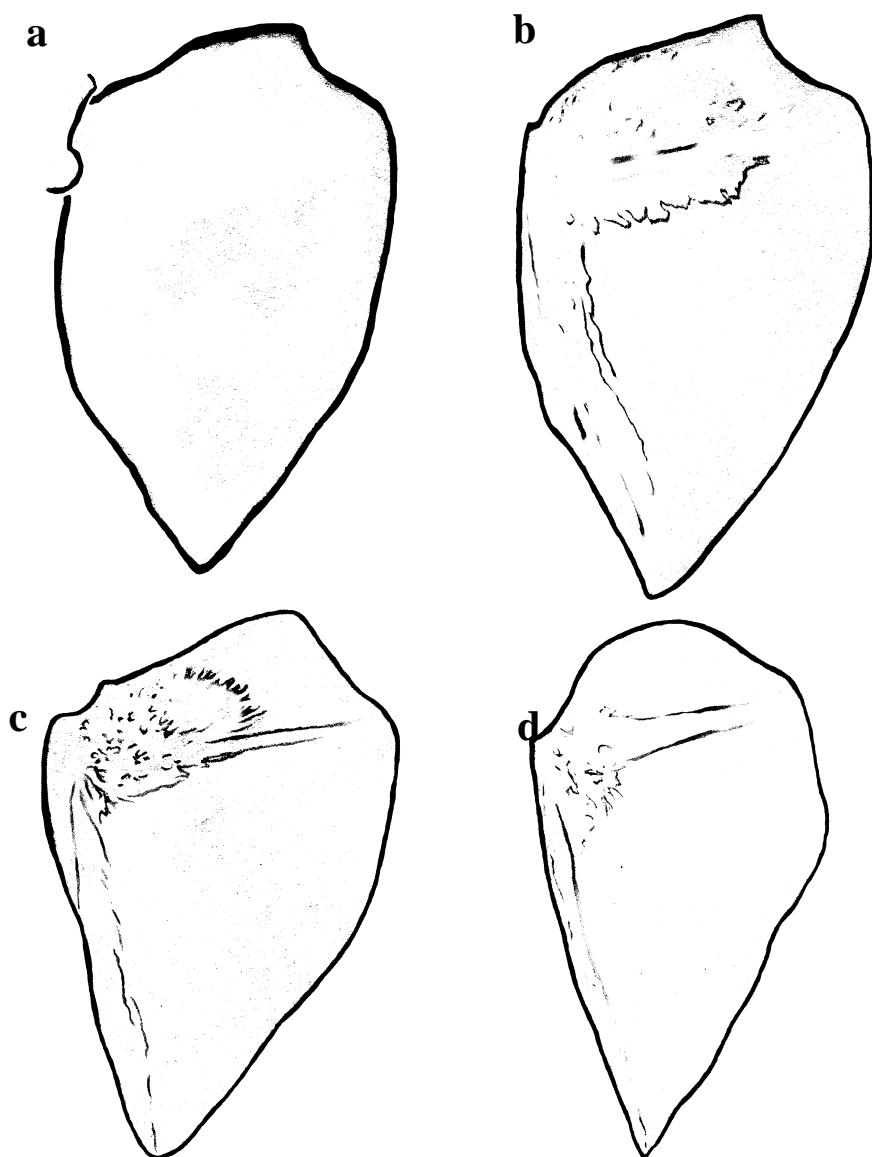
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A synapomorphy for the Neotropical cichlids examined; *Am. nigrofasciata* is polymorphic for this trait. The process may be pointed (Fig. 7a–c) or blunt (Fig. 7e), often varying in shape intraspecifically; hi=0.50.

I discarded the number of predorsal elements, Cichocki's (1976) character 50 and Kullander's (1998) character 66. Contrary to what I found, they discovered few polymorphisms among cichlids (e.g. *Thorichthys* Meek); in my dataset, at least *Cr. panamensis*, *Cr. chetumalensis*, and *Ar. centrarchus* are polymorphic for the trait. Moreover, my polarisation of the character would be opposite to theirs. A survey of predorsal element numbers in cichlids (Cichocki 1976: table 1.1) typically shows 1 for African taxa and 2 for (Middle American) Neotropical species. Kullander (1998) observed that “most of the smaller South American cichlids” and, in fact, “the majority of cichlids” also have 1 predorsal bone. However, Cichocki (1976) recalled that the “typical percoid” has three predorsals (and he did observe “reductional stages of the second predorsal” in *Thorichthys*), and so polarised the character according to a reductive trend. Stiassny's (1991) earlier view that Madagascar cichlids are basal to all the rest also supports this polarity. Although Sparks (2003) proved that Malagasy cichlids are not basal, in his Neotropical clade 1-predorsalled species show up nested within the others, too.

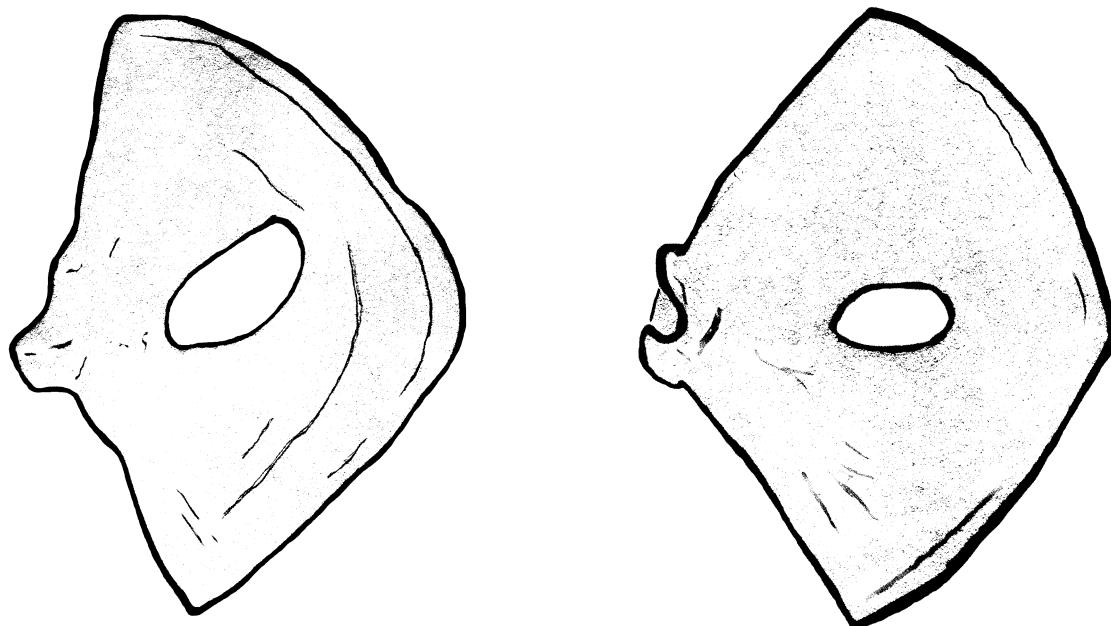


**FIGURE 18.** Opercle: (a) dorsal spine absent, margin evenly convex, no protuberances (*Cryptoheros cutteri*, UMMZ 188136); (b) dorsal spine present (*Cr. chetumalensis*, UMMZ 197224); (c) dorsal margin evenly convex, but with a small dorsoanterior protuberance (*Archocentrus centrarchus*, UMMZ 224131); (d) dorsal margin strongly convex, almost semicircular (*Hypsophrys nematopus*, UMMZ 197507). Scales: a, 10X; b,d, 16X; c, 12X.

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**FIGURE 19.** Foramen in scapula: (a) slanted (*Oreochromis mossambicus*, UMMZ 199401); (b) parallel to anteroposterior axis of bone (*Amphilophus citrinellus*, UMMZ 188309). Scales: a, 25X; b, 8X.

53. Orientation of first neural spine

[0] retrorse (Fig. 7c,d); [1] antrorse (Fig. 7a,b).

Very homoplasious ( $hi=0.88$ ), sometimes polymorphic, but nevertheless informative ( $ri=0.50$ ). State 1 is synapomorphic in *Hypsophrys* and in *Cryptoheros* (without the basal *Cr. panamensis*, and with a reversal in the clade *Cr. spilurus + cutteri*); it is also fixed in *Amatitlania* (polymorphic in *Am. coatepeque*).

54. Number of dorsal elements between first two epineural spines

[0] two (Fig. 7c); [1] three (Fig. 7a,e).

By “dorsal elements” I mean both the predorsal bones and the anteriormost pterygiophores of the dorsal fin. State 1 is fixed in *Amatitlania*, *Rocio*, and in *Cryptoheros* without the basal *Cr. panamensis*, and with a reversal in the clade *C. spilurus+ cutteri*, but it homoplastically occurs in many other species ( $hi=0.86$ ,  $ri=0.38$ ). It is polymorphic in *R. octofasciata*.

55. Spinous anterodorsal process on first dorsal pterygiophore

[0] absent; [1] present (Fig. 7a).

Cichocki (1976, character 51) found the derived state to be rare among Cichlidae. I find a minute anterodorsal spine to be an homoplasious synapomorphy of *Am. kanna + siquia*, parallel with *Cr. chetumalensis*;  $hi=0.50$ ,  $ri=0.50$ .

56. Number of total vertebrae

[0] modally fewer than 31; [1] modally 31 or more.

State 1 occurs convergently in *Petenia*, *Tomocichla*, and *P. dovii*;  $hi=0.67$ ,  $ri=0.00$ . Cichocki (1976, character 57) coded for more character states based on “breaks in the frequency distribution,” but he assumed the range 26–30 to be primitive based on his extensive outgroup survey, a polarity that I concur with. On the other hand, he coded *H. nematopus* as having 31–34 vertebrae, but all specimens I have seen show 30 vertebrae.

Kullander (1998, character 67) also coded for more states, considering not just the total number but also the number of abdominal vertebrae, absolute and relative to caudal vertebrae. He found “abdominal vertebrae

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14–15, the number of caudal vertebrae equal or higher” to be the plesiomorphic condition, acknowledging that “there is no obvious polarity in the outgroup criterion.” In my taxa, the number of caudal vertebrae is always equal or higher, except in *Cr. panamensis*.

**57. Number of caudal vertebrae**

[0] modally fewer than 18; [1] modally 18 or more.

State 1 is an autapomorphy of *Petenia*. See preceding character.

Caudal vertebrae are taken to be those that present haemal spines, either forming an arch or not.

**58. Anal pterygiophores in contact with first haemal spine**

[0] one or two; [1] three or four; [2] usually five.

State 1 is synapomorphic for the Neotropical cichlids examined, without *Tomocichla*; state 2 is a strict synapomorphy of *Archocentrus* ( $hi=0.00$ ,  $ri=1.00$ ). The character is associated with the number of anal spines (Kullander 1998).

This is Cichocki’s (1976, character 53) “number of anal-fin pterygiophores associated with and supported by the first haemal vertebral spine,” with the same polarity as here. He coded *Petenia* as having my state 0; that is not what I see in the material at hand. He needed a fourth state, seven pterygiophores, for *Sympoduson* Heckel.

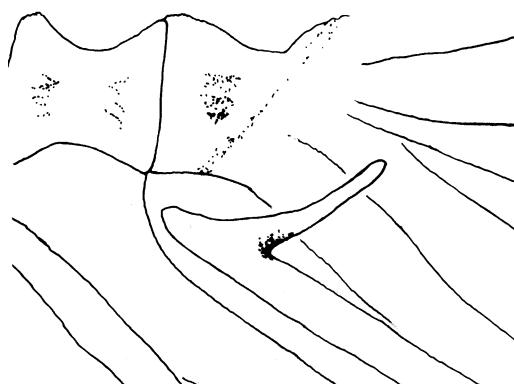
Kullander (1998, character 72) coded this character in the same way and found the same polarity, except that he did not use a fourth state, but defined it as 5–7 pterygiophores articulating with the first haemapophysis.

**59. Parhypurapophysis**

[0] present (Fig. 20); [1] absent.

State 1 is a synapomorphy of *Hypsophrys*, parallel with *Amphilophus*;  $hi=0.50$ ,  $ri=0.50$ .

Character and polarity as Cichocki’s (1976, character 60), who nevertheless distinguished two states within my state 0, based on the relative length of the parhypurapophysis, and considered it present in *H. nematopus*, contrary to what I observe.



**FIGURE 20.** Parhypurapophysis present in caudal skeleton (*Caquetaia spectabilis*, UMMZ 215564). Scale: 66X.

**Squamation, characters 60–68****60. Number of scale rows in cheek**

[0] modally 2 rows; [1] modally 7–8 rows; [2] modally 4–6 rows; [3] modally 3 rows.

No Neotropical cichlid examined had state 0. State 2 seems synapomorphic for all of them, except for the piscivores, whose large jaws may be responsible for an expansion of the cheek and hence more scale rows on

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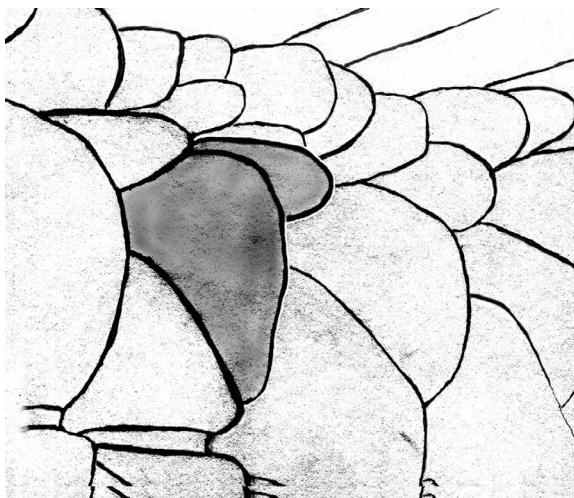
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it (state 1). An autapomorphic reduction (state 3) towards (but not reaching) the plesiomorphic state occurs in *Cr. panamensis*; hi=0.50, but ri=0.25.

**61. Number of scale rows between lateral line and base of first dorsal ray**

[0] modally 3 or fewer; [1] modally 3.5 or more.

A “half-scale,” as in “3.5 scales,” is a scale distinctly smaller than those in the adjacent row on the body side, but not forming part of the scaly sheath at the base of the dorsal fin (Fig. 21). State 1 is synapomorphic for *Rocio* (with a convergence in *Ar. spinosissimus*); hi=0.50, ri=0.67.



**FIGURE 21.** Scale rows between lateral line and base of first dorsal ray: 1.5 rows (*Amatitlania siquia*, UMMZ 196948). Scale: 32X.

**62. Longest interradial scale row on dorsal fin**

[0] no scale rows; [1] longest row modally 2–12 scales long (Fig. 22); [2] longest row up to 23 scales long.

State 1 is a synapomorphy of all Neotropical cichlids examined except *Petenia* (convergence in *Tomocichla*). An extremely long interradial scale row is autapomorphic for *Caquetaia*; hi=0.33, ri=0.00.

**63. Number of rows of interradial scales on dorsal fin**

[0] one row; [1] two rows at base; [2] distally two rows (Fig. 22); [3] one row with sporadic supplementary scales.

State 1 is autapomorphic for *Ar. multispinosus*. State 2 is a putative synapomorphy for the Neotropical cichlids examined, except *Tomocichla* and *Parachromis* (not applicable in *Petenia*), but with many reversals (hi=0.75, ri=0.18). State 3 occurs only in the subgenus *Bussingius* of *Cryptoheros*, although not in *Cr. sajica* and *Cr. septemfasciatus*. Most species show state 0 as juveniles, an ontogenetic criterion that reinforces the polarity found.

Kullander (1998: 483) believed that “fin squamation has considerable potential as a source of phylogenetic information, but requires more careful study,” a view I concur with.

**64. Longest interradial row of scales on anal fin**

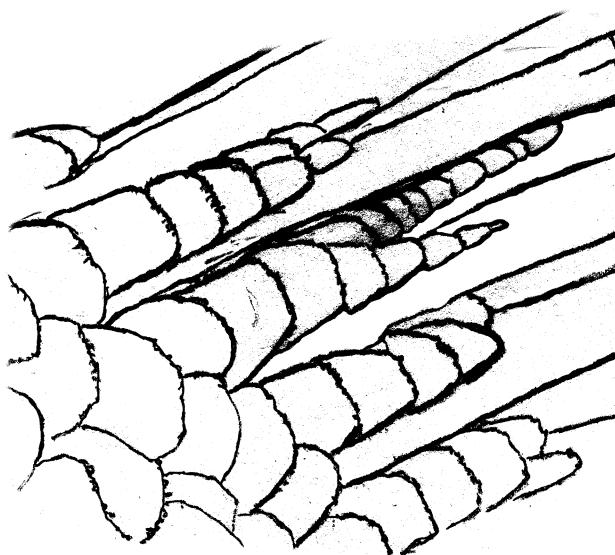
[0] 0–1 scales; [1] modally 3–10 scales; [2] up to 47 scales.

State 1 is synapomorphic for all Neotropical cichlids examined, except *Petenia*. State 2 is an autapomorphy of *Caquetaia*; hi=0.33, ri=0.00.

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**FIGURE 22.** Interradial scales on dorsal fin: longest row 12-scales long, distally two rows (*Amatitlania kanna*, FMNH 59243). Scale: 16X.

65. Number of rows of interradial scales on anal fin

[0] one row; [1] basally two rows; [2] distally two rows; [3] distally three rows.

States 1 and 3 are autapomorphies of *Ar. multispinosus* and *Ar. spinosissimus*, respectively. State 2 is fixed only in the subgenus *Cryptoheros*; hi=0.67, ri=0.25.

66. Number of scales between interpelvic scale and vent

[0] modally 16 scales; [1] modally 19 scales; [2] modally 13 scales or fewer.

The interpelvic scale is an enlarged scale (sometimes a group of scales) between the bases of the innermost pelvic-fin rays, overlapping the rays. States coded through the statistical procedure outlined above. State 1 homoplasically occurs in *Petenia* and *Tomocichla*, perhaps as a by-product of their relatively longer bodies. State 2 is synapomorphic for the rest of the Neotropical cichlids examined, with reversals in *P. loisellei* and *H. nematopus*; hi=0.60, ri=0.00.

67. Number of circumpeduncular scales

[0] modally 18 or fewer; [1] modally 19 or more.

Homoplastically synapomorphic for *Rocio*, *Parachromis*, and *Archocentrus* (reversal in *Ar. centrarchus*); hi=0.80, but ri=0.43, not very low.

68. Secondary caudal pores

[0] none or sporadic; [1] yes, isolated; [2] yes, forming rows

By “secondary” caudal pores I mean those pored scales that do not continue the lateral line, but appear between other caudal fin rays. The character is highly homoplasious (hi=0.86), but it is synapomorphically fixed for state 2 in *Cr. spilurus* + *cutteri* and in *Hypsophrys* (ri=0.20).

**Fins, characters 69–77**

69. Number of dorsal fin spines

[0] modally 16 or more; [1] modally 15; [2] modally 14 or fewer.

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States 1 and 2 are autapomorphic for *Caquetaia* and *Petenia*, respectively. A tendency within state 0 to increase the number of dorsal spines (a formerly diagnostic character for *Archocentrus* sensu lato, that is, for most of the Neotropical cichlids examined here) was not detected by the statistical coding procedure.

## 70. Number of dorsal fin rays

[0] modally 11 or more; [1] modally 10 or fewer.

State 1 occurs in most Neotropical cichlids examined, without *Petenia* and *Tomocichla*, with reversals in *Caquetaia*, *Amphilophus*, and *P. loisellei*; hi=0.80, ri=0.20.

## 71. First dorsal fin ray

[0] not divided; [1] divided; [2] spiniform.

State 1 is synapomorphic for the Neotropical cichlids examined without *Petenia* and *Tomocichla*, with reversals to State 0 in *Rocio*, *H. nematopus*, and *P. dovi*. State 2 is autapomorphic for *H. nicaraguensis*, and it is probably nested within state 0; considering this, the reversal for *H. nematopus* may actually be interpreted as an additional synapomorphy for *Hypsophrys*; hi=0.60, ri=0.50.

## 72. Number of anal fin spines

[0] modally 3; [1] modally 5; [2] modally 6–10; [3] modally 11–12.

The states may show seriality. State 1 is homoplasious between *Petenia* and *Tomocichla*. State 2 is a synapomorphy of the rest of the Neotropical cichlids examined. State 3 is a strict synapomorphy of *Archocentrus*; it was considered a diagnostic character since the description of the genus, which confirms Regan's (1906) intuitions (Kullander 1998: 464); hi=0.25, ri=0.67.

Cichocki (1976, character 52) “arbitrarily partitioned” the character into three states: 3, 4–6, and 7 or more anal spines. My statistical coding does not fully coincide with his decision, but the polarity is the same. All his non-cichlid outgroups had 2 or 3 spines.

Kullander (1998, character 82) determined only two states, 4 or fewer vs. 5 or more anal spines; he found the same polarity as here. He observed a correlation between number of anal fin elements and body depth.

## 73. Number of anal fin rays

[0] modally 10 or more; [1] modally 9 or fewer.

State 1 is synapomorphic for all Neotropical cichlids examined; hi=0.00. This character and my character 36 are part of Kullander's (1998) character 31, total anal fin count (spines + rays).

## 74. Dorsal and anal fins bearing filaments

[0] no; [1] yes.

Filaments trailing caudad from the last rays of the dorsal and anal fins are putatively synapomorphic for all Neotropical cichlids examined, without *Petenia* and *Tomocichla*, and with reversals in *R. gemmata* and *P. loisellei*; hi=0.75, ri=0.25.

## 75. Relative position of pelvic vs. dorsal fins

[0] pelvic behind dorsal; [1] pelvic below dorsal; [2] pelvic much behind dorsal.

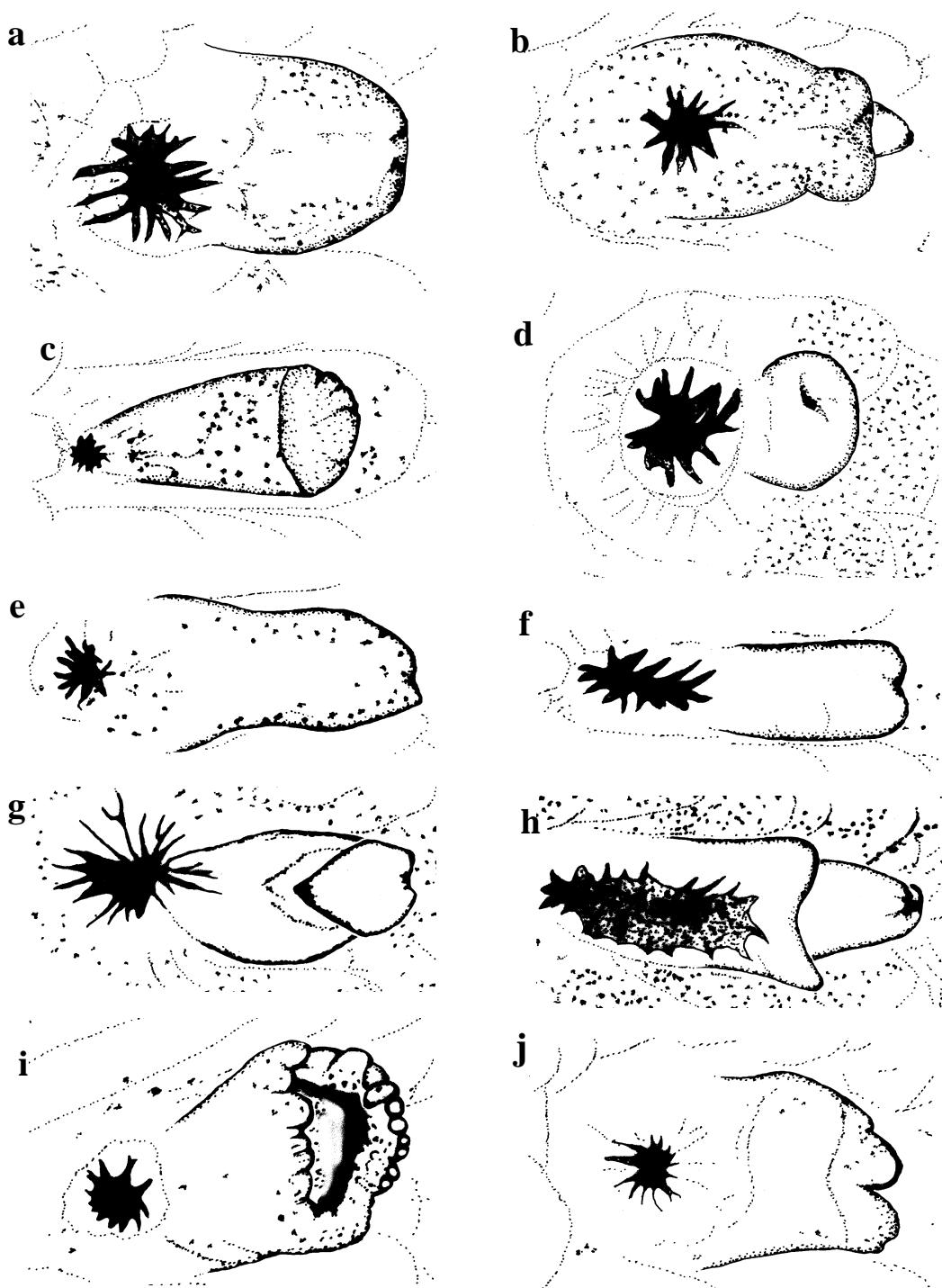
State 1 is present only in *Petenia*. State 2, which is easily distinguishable from state 1 (origin of pelvic much more than 1 or 2 scale rows behind dorsal origin), is one of the few characters supporting the hypothesis that *Cr. panamensis* and *H. nematopus* belong in a same genus, *Neetroplus*; here it is interpreted as an homoplasy: hi=0.33, relatively low, but ri=0.00.

I discussed above the supposed incisors of *Cr. panamensis* and the status of *Neetroplus*, synonymised by Schmitter-Soto (2007) with the formerly monotypic *Hypsophrys*.

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**FIGURE 23.** Shape of genital papilla and pore (fish head to the left): (a) papilla oval, feminine opening oval, not (much) crenulated (*Cryptoheros chetumalensis*, UMMZ 197224); (b) same state, medially-constricted variation (*Amatitlania siquia*, UMMZ 196948); (c) same state, vase-shaped variation (*Am. kanna*, UMMZ 145716); (d) same state, circular variation (*Hypsophrys nicaraguensis*, FMNH 5996); (e) same state, longer papilla (*Am. siquia*, UMMZ 213938); (f) papilla with mostly parallel contours, rounded terminal notch (*Parachromis dovii*, UMMZ 199651); (g) papilla oval, feminine opening proximally (rostrally) V-shaped (*Cr. altoflavus*, MNHN 2001-1164); (h) same state, V-shape less pronounced (*Cr. myrnae*, UMMZ 217739); (i) papilla oval, feminine opening very crenulated (*Archocentrus spinosissimus*, UMMZ 197249); (j) same state, opening deeply and not roundly notched (*Ar. centrarchus*, FMNH 5982). [Anal creases or folds were counted from the outside; for example, the count in (f) is 14.] Scales: a,b, 16X; c,h, 20X; d, 12X; e, 66X; f,g, 32X; i, 40X; j, 25X.

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**76. Number of procurent caudal rays, dorsal side**

[0] four or more; [1] three; [2] two.

Often polymorphic. State 1 is frequent in *Cryptoheros* and fixed in *Amatitlania*; state 2 is homoplastically synapomorphic for *Archocentrus* and *Rocio* ( $ri=0.64$ ). The reductive trend has been followed several times ( $hi=0.80$ ).

Kullander (1998, character 84) found the same polarity, but distinguished only two character states: more than three vs. three procurent rays.

**77. Caudal fin profile**

[0] emarginate; [1] rounded-truncate; [2] definitely truncate; [3] definitely rounded.

State 1 is common to all Neotropical cichlids examined. *Hypsophrys* has synapomorphically reverted to state 0. State 2 is a strict synapomorphy of *Ar. centrarchus* + *multispinosus*. State 3 is an autapomorphy of *Caquetaia*;  $hi=0.40$ ,  $ri=0.33$ .

Kullander (1998, character 83) found an emarginate caudal fin to be the plesiomorphic condition too, but distinguished only two other states, namely truncate-subtruncate (my states 1 and 2) and rounded.

**Genitals and internal organs, characters 78–81****78. Shape of genital papilla and pore**

[0] papilla oval, opening oval, not (much) crenulated (Figs. 23a–e); [1] papilla with mostly parallel contours, rounded terminal notch (Fig. 23f); [2] papilla oval, opening proximally (rostrally) V-shaped (Figs. 23g,h); [3] papilla oval, opening very crenulated (Figs. 23h,i).

Oval papillae with the pore and distal end not much crenulated (state 0) occur in *Oreochromis*, *Petenia*, and most species in the study group. There are minor variations, especially in the “oval” profile of the rostral side of the papilla, which may in some individuals be peanut-shaped (medially constricted) in *Am. siquia* (Fig. 23b), vase-shaped in *R. octofasciata* and *Am. kanna* (Fig. 23c), or approximately circular in *H. nicaraguensis* (Fig. 23d). Long papillae (twice as long as wide) may occur in *Am. siquia* (Fig. 23e), *Cr. chetumalensis* (Fig. 23a), or *Cr. altoflavus* (Fig. 23g), among others, but never with such parallel contours as in the two examined *Parachromis*, whose rounded terminal notch is also characteristic (state 1), a strict synapomorphy.

The opening, in its proximal-rostral end, is V-shaped (not always markedly, e.g. Fig. 23h) in the subgenus *Bussingius*, a strict synapomorphy (state 2).

The edge of the pore varies from very crenulated (Fig. 23i) to deeply and not roundly notched (Fig. 23j) in *Archocentrus*; a strict synapomorphy (state 3).

There is no obvious seriality in the four states;  $hi=0.25$ ,  $ri=0.88$ .

**79. Gut-coiling pattern**

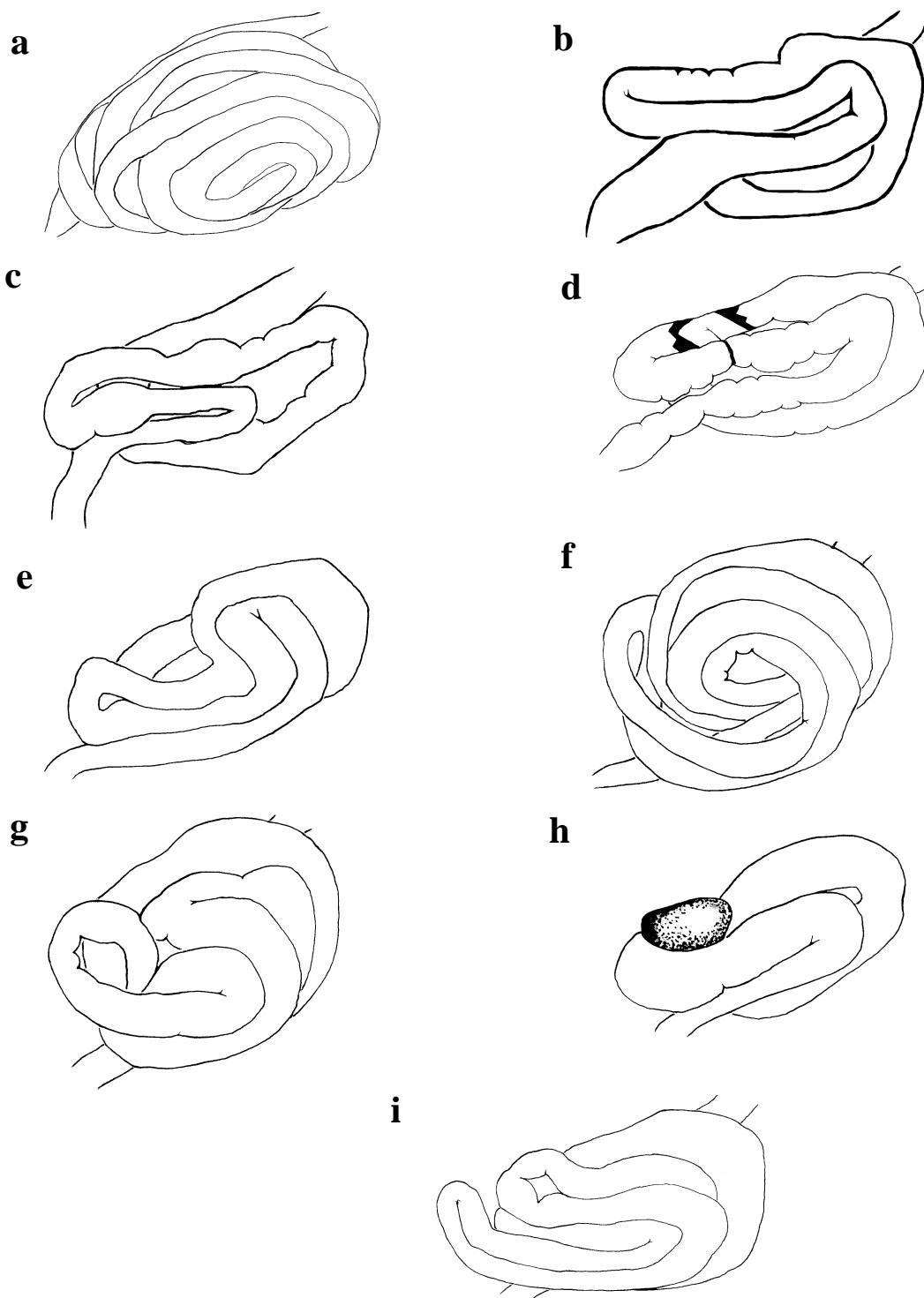
[0] IP=13 in adults (Fig. 24a); [1] simple, S-shaped in adults (Figs. 24b,c); [2] double medial loop in adults, *Tomocichla*-type (Fig. 24d); [3] “S” folded ventrorostrally in adults, anal loop and medial loop not touching (Fig. 24e); [4] IP=6 in adults (Fig. 24f); [5] median loop twisted in adults (Fig. 24g); [6] double medial loop in adults, *coatepeque*-type (Fig. 24h); [7] “S” folded ventrorostrally in adults, anal loop and medial loop nearly touching (Fig. 24i).

The Intersecting Point (IP) is a complexity index defined by Yamaoka (1982) as the number of intersections of the gut with an imaginary left-right line (here modified as a dorsoventral line). No Middle American cichlid approximates the IP of *Oreochromis* (state 0). In the study group, closest in complexity is *Ar. multispinosus* (state 4), although its autapomorphic spiral coiling pattern is quite different. IP is probably correlated with gut length, which is greater in herbivores.

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**FIGURE 24.** Gut type (view from right side of fish): (a) IP=13 in adults (*Oreochromis mossambicus*, UMMZ 213374); (b) simple, S-shaped in adults (young *Cryptoheros septemfasciatus*, UMMZ 190367); (c) same state, "S" shortened in adults (*Caquetaia spectabilis*, UMMZ 190822); (d) double medial loop in adults (secondary loop projecting away from observer, shown underneath gut), *Tomocichla*-type (*T. sieboldii*, UMMZ 194240); (e) "S" folded ventrostrally in adults, anal loop and medial loop not touching (*Amatitlania siquia*, UMMZ 190191); (f) IP=6 in adults (*Archocentrus multispinosus*, UMMZ 199539); (g) median loop twisted in adults (*Cr. cutteri*, UMMZ 199678); (h) double medial loop in adults (secondary loop projecting towards observer), *coatepeque*-type (*Am. coatepeque*, UMMZ 181823); (i) "S" folded ventrostrally in adults, anal loop and medial loop nearly touching (*Hypsophrys nematopus*, UMMZ 197507). Scales: a,c,d,e,f,g,h,i, 6X; b, 16X.

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Most widespread within the examined species is the pattern here termed “simple,” or “S-shaped” (state 1), which is retained from juveniles to adults in most cichlids: when viewed from the right side (in order to keep stomach and liver, which are on the left side, out of view), the gut depicts an S, forming first (from the vent to the mouth) an “anal loop” rostrally, then turning caudad to form a “medial loop,” then again rostral to a “rostral esophageal loop,” then once again caudad to a “caudal esophageal loop,” and finally to the esophagus, which it joins at approximately the same point as the stomach. The rostral esophageal loop and the caudal esophageal loop are less abruptly folded than the anal and median loops, which are rather evenly rounded.

The “simple” type has several variations. In *T. sieboldii*, the median loop is doubled, with a secondary loop projected to the left of the fish. The secondary loop occurs between the anal and median loops; this is an autapomorphy (state 2). In *Am. coatepeque* there is also a secondary medial loop, but this is not a parallelism with *Tomocichla*, but another autapomorphy (state 6), because the secondary loop occurs between the median and rostral esophageal loops, and it is projected to the right of the fish.

Another apparent parallelism here interpreted as separate autapomorphies occurs between *H. nematopus* and *Am. siquia*. In *H. nematopus* (state 7), the basic S-shape becomes ventrorostrally folded with growth, and the anal loop is displaced caudad until it almost touches the median loop. In *Am. siquia* (state 3), the fold is not so abrupt, and the anal loop is displaced more dorsad than caudad, so that it does not come in contact with the median loop; it may even come under the rostral esophageal loop.

In *Cryptoheros* there is a synapomorphic pattern similar to that of *H. nematopus*, but the median loop and sometimes also the anal loop are usually twisted clockwise (state 5). The presence of state 1 in *Cr. myrnae* and *Cr. sajica* is a reversal.

In some piscivores, the S-shape is retained throughout ontogeny, but the distance between the anal loop and the median loop becomes shorter (Fig. 24c), as gut length itself becomes shorter (relative to body length). This occurs in the carnivores *P. dovii* (although apparently not in *P. loisellei*), *Petenia*, and *Caquetaia*, and is probably an adaptive convergence. It is coded as state 1 (but see character 80, below).

The fact that most species show the “simple” pattern as juveniles supports considering this state plesiomorphic (following an ontogenetic criterion), but, aside from that, there seems to be no clear seriality in the states of this character; hi=0.22, ri=0.67.

#### 80. Contact of anal loop and rostral esophageal loop

[0] loops not adjacent (Fig. 24c); [1] loops adjacent (Figs. 24b,d,e,g–i).

In the “simple” gut-coiling pattern, the anal and rostral esophageal loops may or may not be adjacent (in touch). This seems not to depend on the size of the liver or the repletion of the stomach (for states 2,3,5–7 in character 79, the anal loop and the rostral esophageal loop are always adjacent).

This is a possible synapomorphy for all examined Neotropical cichlids except *Petenia* and *Tomocichla*, but it is highly homoplasious (hi=0.80), with reversals in at least three species in different clades.

#### 81. Peritoneum

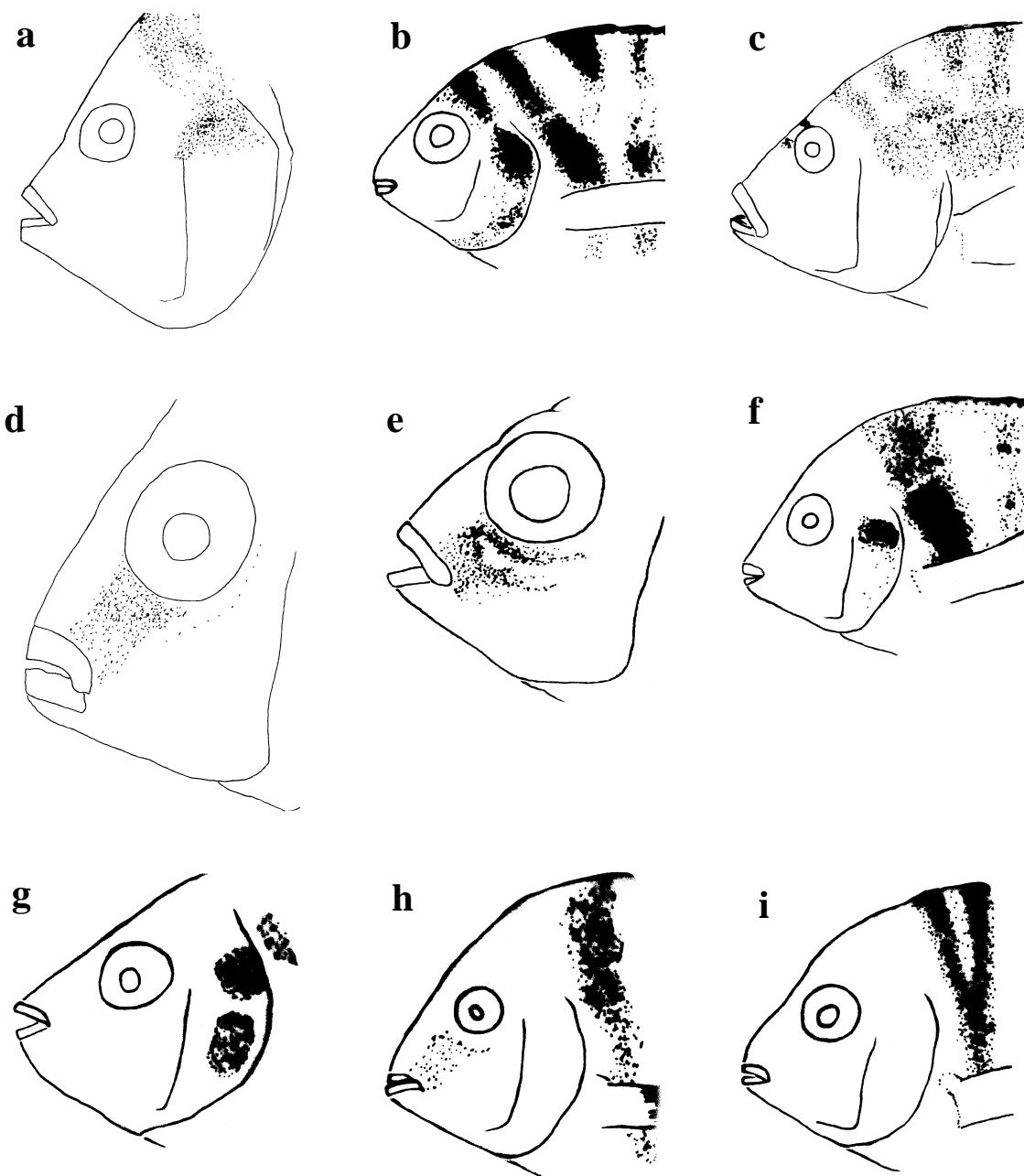
[0] uniformly dark; [1] moderate pigmentation dorsolaterally; [2] pigmentation uniformly sparse; [3] only roof of cavity pigmented; [4] only anterodorsally pigmented; [5] only rostrally pigmented.

State 0 differs from state 2 because the latter shows distinct melanophore concentrations, although sparse and uniformly distributed over the lining of the body cavity. State 1 is common in several clades, fixed in *Archocentrus* and *Cryptoheros*, and may be plesiomorphic to states 3, 4, and 5 (although here the trait is coded unordered). State 4 is an homoplasious synapomorphy of *Rocio* and *Hypsophrys*. States 3 and 5 are autapomorphies; hi=0.50, ri=0.44.

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**FIGURE 25.** Head and anterior-body coloration (semidiagrammatic): (a) a vertical bar just extending across nape, opercular spots part of bar (*Archocentrus spinosissimus*, MNHN A-0352); (b) a vertical bar fully across opercle; anteriormost bar on body sides Y-shaped, marked, its caudal arm discontinuous (*Amatitlania siquia*, UMMZ 245585); (c) interorbital bands present; spot on opercle part of longitudinal stripe on body sides; anteriormost bar on body sides approximately Y-shaped, diffuse (*Rocio octofasciata*, UMMZ 196387, spmn. 1); (d) full snout-eye stripe (*Cryptoheros chetumalensis*, ECOCH 5467); (e) interrupted snout-eye stripe (live *Rocio gemmata*); (f) one opercular spot, not located at angle of opercle; anteriormost bar on body sides Y-shaped (or V-shaped), marked, both arms continuous, rostral arm curved rostrad (*Cr. nanoluteus*, MNHN 1993-0260); (g) two opercular spots, aligned vertically (live *Ar. centrarchus*); (h) anteriormost bar on body sides I-shaped (*Cr. cutteri*, ANSP 53930); (i) anteriormost bar on body sides Y-shaped, marked, arms continuous, rostral arm not curved rostrad (*Cr. spilurus*, BMNH 1864.1.26.52).

### Pigmentation pattern, characters 82–98

#### 82. Vertical bar on head

[0] none or faint; [1] just extending across nape (Fig. 25a); [2] full bar across opercle (Fig. 25b).

State 1 is autapomorphic for *Ar. spinosissimus*. State 2 is homoplastically synapomorphic for *Archocentrus*, *Rocio*, and *Amatitlania* (albeit bar much stronger in the latter genus); hi=0.67, but ri=0.64.

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I concur with Kullander (1998: 483) that “there is more phylogenetic information in pigmentation pattern than currently recognized.” He used only four colour-pattern characters; as for Cichocki (1976), not one of his 64 characters was based on pigmentation. Colour-pattern characters are usually easily observable, even in old museum specimens, and quite constant (except in such polymorphic species as *A. citrinellus*).

**83. Interocular bands**

[0] absent; [1] present (Fig. 25c).

State 1 is fixed in *Rocio* and *Archocentrus*;  $hi=0.80$ ,  $ri=0.50$ . I do not consider the “mask” of *T. sieboldii* to be homologous, because its position is different.

**84. Snout-eye stripe**

[0] absent or diffuse; [1] present, full (Fig. 25d); [2] interrupted (Fig. 25e).

State 1, homoplasious ( $hi=0.67$ ), but synapomorphic ( $ri=0.50$ ) for the subgenus *Cryptoheros*, the clade *Am. kanna + siquia*, and *Parachromis*. State 2 is autapomorphic for *R. gemmata*; the “interruption” of the dark snout-eye stripe is a dorsorostral extension of the white-bluish subocular streak.

**85. Speckles on cheek**

[0] absent; [1] present.

State 1 hints at a synapomorphy for *R. octofasciata + gemmata*, with convergences in *Ar. spinosissimus* and *P. loisellei* (and *Petenia*). However,  $hi=0.83$  and  $ri=0.00$ .

**86. Spots on opercle**

[0] one, at angle; [1] as part of longitudinal stripe (Fig. 25c); [2] as part of bar on head (Fig. 25b); [3] none; [4] one, not at angle (Fig. 25f); [5] two, aligned diagonally from eye; [6] two, aligned vertically (Fig. 25g).

State 1 is homoplasious, plesiomorphically fixed in *Rocio*. State 2 is synapomorphic for *Amatitlania*, with parallelisms in *Caquetaia* and *H. nematopus*. State 3 is synapomorphic for *Cryptoheros* (without the basal *panamensis*), with a convergence in *Amphilophus* and a reversal in *Cr. altoflavus*. States 4–6 are autapomorphic;  $hi=0.40$ ,  $ri=0.64$ .

This is not Kullander’s (1998) character 90, a “strongly pigmented opercular spot,” which is “one of the stronger synapomorphies of African cichlids.” The also strong, usually ocellated opercular spot of *Thorichthys* would have been coded here as a different character state.

**87. Dots on scales**

[0] none; [1] smaller than scales; [2] larger than scales.

State 1 shows up independently in several clades; although homoplasious ( $hi=0.71$ ), it supports some structure ( $ri=0.38$ ). State 2 is an autapomorphy of *R. gemmata*. Some species, like *A. citrinellus*, are polymorphic for these pigmentation features.

**88. Number of bars on sides of body**

[0] 8 bars; [1] 7 bars; [2] 6 bars.

State 1 is probably a synapomorphy for all examined Neotropical cichlids, except *Petenia* and *Tomocichla*, although with several changes to states 0 or 2 ( $hi=0.60$ ,  $ri=0.50$ ). The reversal to state 0 in *Rocio* is a synapomorphy for the new genus (the bars can be hard to discern, but they are present, in *R. ocotal*, called “entirely black” by Miller 1957).

Although number of bars in itself is not an homologous feature, it seems that state 1 is accounted for by the same mechanism in all examined species, i.e. the loss of the peduncular bar (bar number 2, counting posterorostrally—Kullander & Silfvergrip 1991).

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**89. Shape of anteriormost bar on sides of body**

[0] I-shaped (Fig. 25h); [1] Y-shaped, diffuse (Fig. 25c); [2] Y-shaped, marked, arms continuous, rostral arm not curved rostrad (Fig. 25i); [3] Y-shaped, marked, caudal arm discontinuous (Fig. 25b); [4] Y-shaped (or V-shaped), marked, arms continuous, rostral arm curved rostrad (Fig. 25f).

This character was interpreted as not applicable in species with only 6 bars (state 2 in character 88). States 1–3 were defined separately because their differences are more conspicuous than their general Y-shape; perhaps more “Y-shaped” states might be identifiable, especially within state 1, the diffusely Y-shaped bar of *T. sieboldii*, *Rocio*, some *Archocentrus*, and some *Cryptoheros*. State 3, a Y-shaped bar with the caudal limb discontinuous (or at least not uniformly intense), is a strict synapomorphy of *Amatitlania*. States 2 and 4 are autapomorphies; hi=0.50, ri=0.56.

**90. Extension into dorsal and anal fins by bars on sides of body**

[0] no extension; [1] partial extension, only at fin bases; [2] full extension, to edge of fins.

State 1 is very common within *Cryptoheros*: a probable synapomorphy, although with some reversals and a parallelism in *Ar. centrarchus*. State 2 is a strict synapomorphy of *Amatitlania*; hi=0.60, ri=0.63.

**91. Ocellus on dorsal fin of mature females**

[0] absent; [1] present.

State 1 is synapomorphic for *Cryptoheros* (ri=0.57), although with reversals in *Cr. sajica* and *Cr. chetumalensis*, and a parallelism in *Ar. centrarchus* (hi=0.75). The extension to the dorsal fin of a bar in *Amatitlania* was not considered a true ocellus (except in *Am. nigrofasciata*, where an ocellated spot was observed in 2 specimens out of 559 examined), and it is apparently not sexually dimorphic in that genus.

This ocellus occurs between the spines; not to be confused with the “tilapia spot” (Kullander 1998, character 91), which appears on the base of the soft dorsal.

**92. Medial intensification of bars on sides of body**

[0] on bars 3, 6, 7; [1] on bar 5, sometimes also on 6; [2] on bars 6, 7, sometimes also on 8; [3] only on bar 6; [4] none.

Numbering of bars follows Kullander and Silfvergrip (1991). These medial intensifications of bars on sides of body can look like a series of blotches. State 0 does not occur in the Neotropical cichlids examined. State 1 is most widespread. State 2 is a strict synapomorphy of *Amatitlania*. State 3 is a synapomorphy of *Cryptoheros* without the basal *Cr. panamensis*; *Cr. sajica* and *Ar. centrarchus* convergently have state 4 (hi=0.33, ri=0.82).

**93. Longitudinal stripe on sides**

[0] none; [1] from opercle to pectoral origin; [2] full, to caudal origin; [3] from eye to lateral blotch.

State 1 occurs in *Cr. nanoluteus* and *Cr. altoflavus*, with a parallelism in *Tomocichla*. State 2 is a convergence of *P. dovii* and *Cr. myrnae*. State 3 is a synapomorphy for *Rocio*, with parallelisms in *Ar. spinosissimus* and *P. loisellei*; hi=0.67, ri=0.25.

**94. Predominant abdominal colour in life**

[0] whitish or greyish; [1] yellowish-reddish; [2] blue or green; [3] wine-coloured; [4] yellow green.

This is not properly a colour-pattern character, but a true colour trait. States were taken from Mayland (1995) and Werner and Stawikowski (1998), from personal observation in the field (for *Petenia*, *Cr. chetumalensis*, and *R. gemmata*), and from FishBase (Froese & Pauly 2004).

The character is quite homoplasious and uninformative (hi=0.75, ri=0.00). Allgayer's (2001) assertion that *Cryptoheros* may be divided into “yellow” and “grey” species is only partially sustained: *C. spilurus* may

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occasionally be yellowish, whereas *Cr. septemfasciatus* and *Cr. sajica* (but not *Cr. myrnae*) are greyish. A wine-coloured abdomen (and fins) is autapomorphic for *C. cutteri*, the so-called “weinrotflossiger Buntbarsch” of German aquarists (Velasco 2001).

**95. Abdominal black blotch in mature females**

[0] absent; [1] present.

State 1 occurs only in the subgenus *Bussingius* (not in *Cr. sajica*); hi=0.67, ri=0.33. It is only partly correlated with character 91, the other trait exclusive to mature females.

**96. Horizontal position of caudal spot**

[0] on fin; [1] on peduncle; [2] on both.

A majority of the Neotropical species examined have a caudal spot (actually most Heroini and Cichlasomini: Kullander 1998, his character 88), usually on the base of the caudal fin rays (state 1). State 2, a spot exclusively on the caudal peduncle, occurs only in *Cr. altoflavus* and *Cr. myrnae*; state 3, a spot about two-thirds on the peduncle and one-third on the fin, is synapomorphic for *Cryptoheros* (with reversals, and a parallelism with *Am. siquia*); hi=0.63, ri=0.38.

It can be questioned whether these states are homologous or not. However, it seems more parsimonious to postulate, for example, that the totally peduncular spot of most *Amatitlania* is homologous to the two-thirds-peduncular, one-third-pterygial, spot of *Am. siquia*, than to postulate for this latter species a second spot on the fin, complementing the oval shape of the first, peduncular spot. Another example of a caudal spot whose position varies between the peduncle and the fin can be found in the ‘Cichlasoma’ *urophthalmus* complex (Barrientos-Medina 2005).

**97. Vertical position of caudal spot**

[0] crossing lateral line; [1] completely above lateral line.

State 1 is homoplasically synapomorphic for *Rocio*; hi=0.75, ri=0.40.

**98. Margin of caudal spot**

[0] not ocellated; [1] ocellated.

A true caudal ocellus, with a whitish-bluish margin, is synapomorphic for *Rocio*, but homoplasious with *A. citrinellus* (where it is polymorphic), *Ar. centrarchus*, and many other taxa not examined here, e.g. “C.” *urophthalmus*, *Cichla* Bloch & Schneider, and *Astronotus* Swainson; hi=0.67, ri=0.50.

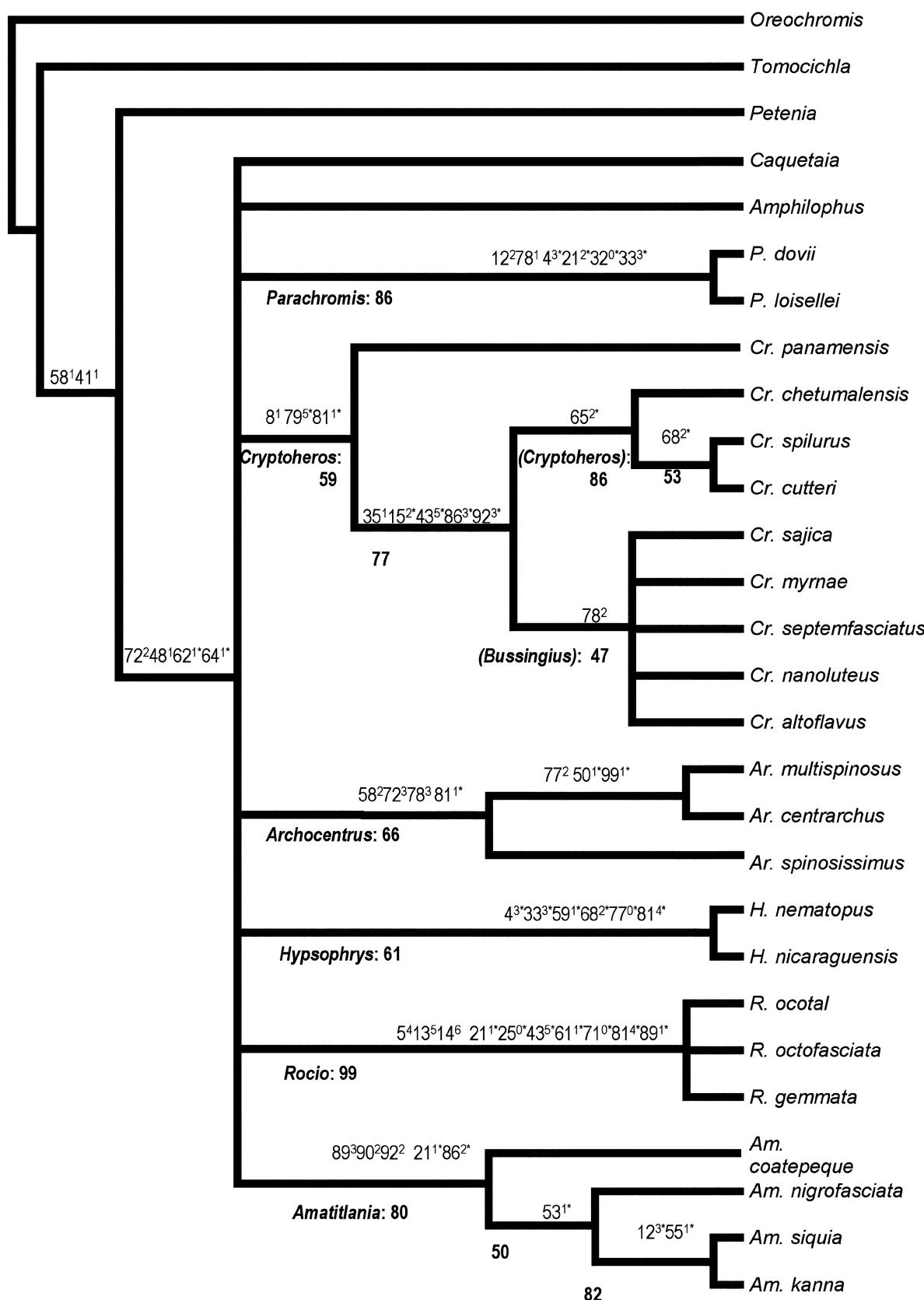
## Cytotaxonomy

Thompson's (1979) cytogenetic data (corroborated for some species by Salas & Boza 1991) were tried as a 99<sup>th</sup> character, with three states: [0] 48 chromosomes, 8 (sub)metacentric (sm) / 40 (sub)telocentric (st); [1] 48, 6 sm / 42 st; [2] 48, 4 sm / 44 st. For simplicity, *Oreochromis*, with a fundamental number different from 48, was considered not applicable. Polarity was argued by Thompson (1979) himself. Most of the species included here had to be coded as unknown. The character was not particularly homoplasious (hi=0.50): *A. citrinellus*, *H. nematopus* and *P. dovii* showed state 0; *Archocentrus* (*Ar. centrarchus* and *Ar. multispinosus*), *Cr. septemfasciatus* and *R. octofasciata* had state 1, thus homoplasically synapomorphic for *Archocentrus*; *Amatitlania* displayed state 2.

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**FIGURE 26.** Strict consensus of the three minimum-length trees under ACCTRAN optimization in PAUP (556 steps, CI=0.42, RI=0.45, HI=0.61). Clades with less than 50% bootstrap support are shown collapsed, except for those that have a strict synapomorphy with a character whose  $hi = 0.50$ , even when not recovered by the bootstrap procedure. Numbers above lines are synapomorphies, with the exponent indicating the character state and an asterisk marking homoplasious synapomorphies. Numbers below lines are bootstrap support. For character numbering, see Character description and analysis.

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## Phylogeny

An exhaustive search was not feasible; three most-parsimonious trees were found by a heuristic search. Figure 26 shows the strict consensus of those minimum-length trees (556 steps, CI=0.42, RI=0.45, HI=0.61). Excluding uninformative characters (12 autapomorphies), the hypothesis does not substantially weaken: CI=0.40, HI=0.60.

The consensus cladogram shows no evidence in support of *Archocentrus* as commonly used in the literature (e.g. Bussing 1998). *Archocentrus* as traditionally used actually consists of three clades (*Archocentrus*, *Cryptoheros*, and *Amatitlania*), one of which contains the former monotypic genus *Herotilapia* in a derived, not basal, position.

Other taxa at various times associated with *Archocentrus* are also probably distinct, contained in the clades *Rocio* and *Hypsophrys* (which includes the former monotypic genus *Neetroplus*). Beyond that level, the tree collapses (Fig. 26; synapomorphies discussed above). According to this hypothesis, *Tomocichla* is the sister taxon to the rest of the American cichlids examined; *Petenia* is basal to the rest, and then there is a polytomy, including *Amphilophus*, *Caquetaia*, and the following resolved groups:

- *Archocentrus* sensu stricto consists of *Ar. centrarchus*, *Ar. multispinosus*, and *Ar. spinosissimus*, the latter being basal to the others.
- *Amatitlania* consists of *Am. nigrofasciata*, *Am. coatepeque*, *Am. kanna*, and *Am. siquia*, the Salvadoran species being basal to the rest, and the southernmost species-pair being most derived.
- *Rocio* consists of *R. octofasciata*, *R. ocotal*, and *R. gemmata*. Internal structure of this clade was not resolved.
- *Cryptoheros* consists of *Cr. spilurus*, *Cr. chetumalensis*, *Cr. cutteri* (the three of them integrating the subgenus *Cryptoheros*, with *Cr. chetumalensis* in the basal position), and the five species in the new subgenus *Bussingius* (no internal structure resolved), as well as *Cr. panamensis*, which is the sister group of the other two subgenera.
- *Hypsophrys nicaraguensis* and *H. nematopus* show up together in one clade.
- The two examined species of *Parachromis* appear alone in their own clade.

Including the cytogenetic data did not alter the topology of the tree (now with 561 steps, CI=0.43, same RI and HI).

## Discussion

The present interpretation of *Archocentrus* (synonymizing *Herotilapia*—Schmitter-Soto 2007) hinges on three strict synapomorphies: five pterygiophores in contact with the first haemal spine, eleven or more anal-fin spines, and genital papilla oval, its opening very crenulated to deeply and not roundly notched. The first two characters are part of the traditional diagnosis of *Archocentrus*; in spite of their recurrent use in the literature, and in spite of their being probably correlated between themselves (Kullander 1998), I do not think that they have been overused, since they constitute a strict, robust, synapomorphy in the context of the present matrix.

Other many-spined cichlids, like *Sympodus*, have been considered to have a different character-state (Cichocki 1976): 7 or more, rather than 5 or more spines. The peritoneal pigmentation pattern, although apparently acquired independently by *Archocentrus*, *Cryptoheros*, and other cichlids, is another synapomorphy for the genus as here construed.

Martin and Bermingham's (1998: fig. 4) cladogram implied restricting *Archocentrus* to *Cr. septemfasciatus*, *Am. nigrofasciatus*, and *Ar. centrarchus*. These authors suggested that *Cr. myrnae* and *Cr. sajica*, which appeared in a different clade, might belong in their own distinct genera. *Cr. myrnae* and *Cr. sajica* clustered together in their cladogram with species of *Parachromis* and *Hypsophrys* (with *Neetroplus*), and this clade had a sister-group relationship to the purely-*Archocentrus* clade mentioned above; *Paraneetroplus* (= *Tomocichla*) *sieboldii* was the sister group of these clades. On the other hand, although

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*Archocentrus* resulted paraphyletic in Martin and Bermingham's (1998) work, cladograms constraining the genus to be monophyletic were not significantly different in terms of changes per site.

Previously (Roe et al. 1997: fig. 2A), *Cr. spilurus* showed up in the same clade as representatives of *Amphilophus* and *Parachromis*. Typically, *Cryptoheros* and *Parachromis* were sister groups in the cladograms of Roe et al. (1997); evidence for such a relationship is lacking in my study.

Kullander (1998) found a suite of characters which "express the deep body" (high number of anal-fin spines, presence of laminar expansions on anterior haemapophyses, lachrymal deeper than wide, etc.) in the clade that consists of the heroine genera *Sympoduson*, *Heros*, *Uaru* Heckel, *Mesonauta* Günther, and *Pterophyllum* Heckel. It seems that these characters are not associated together in the same way in *Archocentrus*; for example, the lachrymal is wider than deep in adult *Ar. centrarchus*.

Further characters that could a priori be considered part of a deep-body gestalt, such as a low number of vertebrae, do not unequivocally characterise either *Archocentrus* or the *Sympoduson* clade; still others, like a high number of circumpeduncular scales, are (rather paradoxically) convergent between the deep-bodied *Archocentrus*, the slender *Parachromis*, and *Rocio*, whose body depth tends to decrease ontogenetically.

Other deep-bodied American cichlids include *Heroina* Kullander, some *Theraps* Günther, and *Heros*, among others, but none of these has ever been considered close to *Archocentrus* by traditional standards or found near *Archocentrus* in phylogenetic analyses. On the contrary, most of them have appeared quite apart from *Archocentrus* in published cladograms. Hence, they were not included in the present analysis, and it seems unlikely that future work will change this, given that they lack the synapomorphic characters of the genus (see also Kullander 1998).

The placement of *Ar. multispinosus*, the former *Herotilapia*, constitutes a conflict between morphology and molecules. Several workers (e.g. Farias et al. 2001; P. Chakrabarty, in litt., 2003; Concheiro Pérez et al., 2007) have found *Herotilapia* to lie far outside the clade that includes the type species of *Archocentrus*. However, in addition to the synapomorphies for the genus, *Ar. multispinosus* shares characters with the type species, *Ar. centrarchus*: the caudal fin profile, definitely truncate, is a uniquely derived character within the species suite examined, whereas the evenly-convex dorsal margin of the opercle (with a dorsoanterior protuberance) is homoplastically synapomorphic, same as the combination of 6 (sub)metacentric and 42 (sub)telocentric chromosomes (Thompson 1979). Thus, *Ar. multispinosus* occurs well within the *Archocentrus* clade, on morphological grounds.

On the other hand, the conflicting cytochrome-*b* data may possibly suffer from the general problem with such information as applied to Middle American cichlids (Schmitter-Soto 2007; see below). In addition, the large number of autapomorphies of *Ar. multispinosus* might be a confounding factor (the "long-branch attraction" phenomenon—cf. Wiens & Hollingsworth 2000). Hulsey et al. (2004) were unable to place *Ar. multispinosus* unambiguously in their cladogram. Data based on genes other than cytochrome *b* should help clarify this problem.

Notwithstanding the large number of "trophic characters" in my study, piscivores (*Parachromis*, *Petenia*, and *Caquetaia*) did not cluster together. Considering this, their resemblance is most likely due to adaptive convergence, as Kullander (1998) believed, and contra Miller (1993, Miller et al. 2005), who suggested that *Caquetaia* should be classified as a subgenus of *Petenia*. Hulsey et al. (2004) coincided in differentiating *Caquetaia* from *Petenia*; Martin and Bermingham (1998) even suggested that *Caquetaia* was polyphyletic.

On the other hand, a nuclear-gene analysis by Farias et al. (2000) did find *Caquetaia* in the same clade as *Petenia* and *Rocio*, a "piscivore clade." Farias et al. (1999) found *Caquetaia* and *Petenia* lumped together with *A. citrinellus* and *Cr. nigrofasciatus*, and the clade persisted in a later hypothesis (Farias et al. 2001), where *Parachromis*, *Paraneetroplus*, and "Nandopsis" were added. My cladogram speaks against including either *Caquetaia*, *Parachromis*, or *Rocio* in a clade with *Petenia*, but it cannot rule out a clade consisting of the former three genera.

*Rocio* is the most strongly supported clade in my tree. According to Miller (1993, Miller et al. 2005), it is an *Archocentrus*. Regan (1908) put *R. octofasciata* in section *Archocentrus*, but he acknowledged that its

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relationships were “rather doubtful,” and shortly later (Regan 1909) he considered it a *Parapetenia*, mirroring the fact that *Rocio* species are deep-bodied (*Archocentrus*-like) when young and as they grow they become slender-bodied (*Parachromis*-like). Farias et al. (2000) located the species within a “piscivore clade” with *Petenia* and *Caquetaia*; Kullander (2003) listed *R. octofasciata* as incertae sedis. The present hypothesis cannot rule out a *Rocio+Archocentrus* clade, but it doesn’t forbid a possible *Rocio + Parachromis* clade either, or indeed any combination of *Rocio*, *Parachromis*, *Amphilophus*, *Cryptoheros*, *Archocentrus*, *Amatitlania*, and *Hypsophrys*.

The strict synapomorphies supporting *Rocio* have to do with gill rakers and neurocranium. A hint at a putative *Rocio-Parachromis* relationship like the one found by the molecular studies cited above might be, for example, the state 2 of character 42, symphysial teeth abruptly larger than adjacent teeth: another “piscivore trait,” which occurs in *Rocio*, *Parachromis*, and *Caquetaia* (also in *Amatitlania* and elsewhere, but not in *Petenia*). These characters tend to be highly homoplasious, as might be expected of adaptive structures; moreover, in the present hypothesis “piscivore characters” tend to be apomorphic and convergently evolved in different clades, which reinforces the idea that they constitute adaptations (Coddington 1988).

Schmitter-Soto’s (2007) decision to exclude *Amatitlania* from *Archocentrus* (or *Cryptoheros*) will not remain uncontroversial. Previously, Martin and Bermingham (1998) and Hulsey et al. (2004) found *Am. nigrofasciata* in a clade with *Cr. septemfasciatus*. However, *Amatitlania* is fairly well supported in the present cladogram, exhibiting three strict synapomorphies: the shape of the anteriomost bar on sides, the degree of extension of bars on sides onto dorsal and anal fins, and the type of medial intensification of these bars.

The synapomorphies of *Amatitlania* are all related to pigmentation. Available published information on colour (also live colour) and relation to behaviour could be used more deeply for phylogenetic analyses. Loiselle (pers. comm. 2005) suggested exploring as cladistic characters the presence/absence of sexual colour dimorphism and its polarity; presence/absence of yellow or red pigment in quiescent, courting and parental fish; enhancement or suppression of vertical elements in the melanophore pattern of parental individuals; presence/absence of reverse countershading in parental individuals; etc.

Although homologisation might remain a problem for many live colour and behavioral characters, it is interesting that *Archocentrus* is (almost) not sexually dimorphic, contrary to *Amatitlania* and *Cryptoheros*, whose sexual dimorphism is strong. Moreover, *Archocentrus* species are open-substrate breeders, whereas *Amatitlania* and *Cryptoheros* lay their eggs under stones (Stawikowski & Werner 1998). Predominant abdominal colour in life was used, but it was not a particularly informative character, as yellow or red pigment is present in many clades. A blue iris occurs in *Cr. myrnae* and *Cr. septemfasciatus*, but such a clade was not supported in this hypothesis. The reverse countershading of mature *H. nematopus* (Bussing 1998) seems to be another autapomorphy of that species.

*Cryptoheros* including *Cr. panamensis* is not a very robust clade: its bootstrap support is only 59%, compared to 77% for *Cryptoheros* without *Cr. panamensis*, or 86% for the subgenus *Cryptoheros*. The placement of *Cr. panamensis* is controversial: it was described as a *Neetroplus* (Meek & Hildebrand 1913), Bussing (1998) considered it a *Hypsophrys*, and Kullander (2003) felt that it belonged in *Archocentrus* (including *Cryptoheros*).

*Cr. panamensis* is clearly not related to *Hypsophrys* (including *Neetroplus*), the supposedly incisor-like teeth having a different ontogeny from the true incisors of *H. nematopus*; other similarities, for example the posterior-end shape of the dentigerous arm of the dentary bone, are symplesiomorphies. It is not an *Archocentrus*, either, the shared characters being primitive. It lacks important synapomorphies of the rest of the genus *Cryptoheros*, such as the convex dorsal edge of the articular bone; however, it shows the strict synapomorphy of having the very characteristic three to five acute interdigitations between the halves of the lower pharyngeal jaw.

There are similarities in breeding coloration between *Cr. panamensis* and species of *Tomocichla* (Loiselle, pers. comm., 2005). However, *T. sieboldii* lies quite far from the clade that includes *Cryptoheros*, both in the present cladogram and in previous hypotheses (e.g. Martin & Bermingham 1998). Hulsey et al. (2004) found *Tomocichla* to be polyphyletic, but *T. underwoodi* Regan was even farther away from *Cryptoheros* in their cladogram.

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The subgenera of *Cryptoheros* are biogeographically disjunct: *Cryptoheros* in the northwest, *Bussingius* in the southeast. The subgenus *Cryptoheros* shows no strict synapomorphy, but a bootstrap support of 86%; its homoplasious synapomorphies concern the number of scale rows on the anal fin and the presence of a spine on the dorsal margin of the opercle, among others. *Bussingius* has a very low bootstrap support (below 50%), but one strict synapomorphy, a characteristically V-shaped opening of the genital papilla.

The subtribe Archocentrina Allgayer (2001) is not recovered in my hypothesis: no character unequivocally unites *Archocentrus*, *Cryptoheros*, and *Amatitlania* but excluding *Cr. panamensis*. An irregular posterior edge of the urohyal bone characterises *Cryptoheros* and *Archocentrus*, but not *Amatitlania*; the limbs of the palatine bones are subequally long in *Amatitlania* and *Archocentrus*, but not in *Cryptoheros* (except *Cr. sajica*); the posterior end of the dentigerous arm of the dentary bone is bluntly pointed in *Amatitlania* and *Cryptoheros*, but not in *Archocentrus*; etc.

The monophyletic pair *Hypsophrys* + *Neetroplus* has been sustained by several workers on molecular grounds (Martin & Bermingham 1998, Hulsey et al. 2004, Concheiro Pérez et al., 2007). However, the very striking autapomorphies of both species seem to have discouraged any decision to synonymise their monotypic genera.

As represented in this study, *Parachromis* is monophyletic, a fact which supports recognition of this taxon, for which there has been no study including all species assignable to the genus.

The tilapia, a rather derived African cichlid, was not always applicable as an outgroup. However, replicating the analysis using *Tomocichla* and *Petenia* as outgroups yields the same result. I saw no need to include other South American or non-American cichlids, because the monophyly of Heroini is already well-established (Kullander 1998; Farias et al. 1999, 2000, 2001).

As discussed above, the results of the available phylogenies are partly at variance with mine, but they vary among themselves as well. Martin and Bermingham (1998) rather gloomily observed that the Heroini "...are unfortunately refractory to phylogenetic inference using cytochrome b gene sequences..." Meyer (1994) commented also that "...cytochrome b may not be ideally suited for inferring the evolutionary history of Central American cichlids," and Doyle (1992) pungently characterised many (most?) molecular studies, especially those based on the non-recombinant mtDNA, as "one-character phylogenies." Moore (1995) added: "...single-gene reconstructions may lead to inconclusive discrimination of species trees among gene trees." I think it is consilience, the congruence between independent analyses and datasets, either molecular or morphological, that gives strength to evolutionary hypotheses (cf. Farias et al. 2000).

On the other hand, consistency for the phylogenetic hypothesis presented here may seem low (0.42), but the figure is not atypical, compared to other works on cichlids: 0.57 for Roe et al. (1997) and 0.48 for Kullander (1998), but 0.37 for the total-evidence cladogram of Farias et al. (2000), 0.35 for Sparks (2003) and 0.22 for Farias et al. (2001). The large number of taxa and the inclusion of many homoplasious (although informative to greater or lesser extent) characters is the cause of this, and the phenomenon seems hard to avoid in (heroine) cichlid phylogenies, whether morphological or molecular.

The use of statistics for coding quantitative characters has been criticised (e.g. Pimentel & Riggins 1987) for using attributes of populations, not of individuals. It remains true, however, that overlapping variability may exist also in "qualitative" characters (Kitching et al. 1998), and a statistical coding approach allows for a more objective decision on what constitutes a "representative" individual (i.e., one displaying the most representative character states) for a taxon. "It is expected that taxa that inherit a particular character state for a metric attribute from a common ancestor will inherit both the central tendency *and distribution* of the state unchanged" (Rae 1998, his italics).

Kullander (1998) found that meristic scale characters were too variable to be useful for cladistic investigations of cichlids. In the present study, for example, the number of predorsal scales was statistically amenable to the distinction of two states, modally less than 16 vs. 16 or more, but the difference failed to be significant; moreover, the distribution of state 1 was highly homoplasious (although this was not in itself a

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reason for discarding the information). Other meristic characters, however, did provide useful data, with retention index values up to 0.67.

The use of gut-coiling data is not new in fish systematics (Yamaoka 1982). One synapomorphy of family Cichlidae lies in the position of the intestine relative to the stomach (Stiassny 1991). Takahashi (2003) provides a recent example with cichlids from Lake Tanganyika; although the gut of these African cichlids is much more complex than that of the Mesoamerican Heroini, the latter often also require some ontogenetic information to define character states. In any case, the consistence of the patterns must be considered, but this is true of almost any taxonomic character.

Two main evolutionary trends are apparent in gut-coiling patterns. One is associated with the relative reduction of intestine length in carnivores (as seen in *Parachromis*, *Petenia*, and *Caquetaia*). The other one is the elongation of the gut in herbivores, an adaptation for a better digestion of vegetal matter. The problem of accomodating an elongated gut within the limited space of the coelom provides more informative patterns; Shen and Wu (1995) were able to construct a phylogeny for Balistidae and Monacanthidae using only intestinal-coiling pattern data. Middle American Heroini show much simpler patterns than those found in these families, or than the patterns of tilapiines; the rather subtle differences found (minute variations on the S-shape theme) are mostly autapomorphic, except for the interesting intestinal synapomorphy of *Cryptoheros* (including *Cr. panamensis*).

The external morphological diversity of genital papillae in cichlids is probably not adaptive. Genital papillae provided strict synapomorphies for *Archocentrus*, *Bussingius*, and *Parachromis*, which show character states that are independent modifications of the basic oval-shaped papilla with a simple, not much crenulated opening: in *Parachromis* the papilla elongates, in *Bussingius* and *Archocentrus* the opening shows diverse degrees of divergence from the plesiomorphic evenly-rounded pore.

Functional differences of the genital apparatus, for example in the timing and intensity of spawning, are controlled by internal structures such as the presence and type of sphincter muscles (Rasotto & Shapiro 1998), and relative differences in size may be mediated by differences in androgen levels, which in cichlids can be socially modulated (Oliveira et al. 2002). The internal musculature of the genital apparatus in cichlids may hold promise to the discovery of further cladistic characters.

A formal biogeographic analysis of the present phylogenetic hypothesis remains to be performed, but examination of the distributional patterns within each clade suggests interesting generalities:

Basal species apparently tend to be inland isolated endemics: such is the case within *Amatitlania*, where the crater-lake species *Am. coatepeque* is the sister group of the other three species in the genus. Within *Rocio* there was no cladistic resolution, but one could speculate that the highland *R. ocotal* would be basal to the other two species; indeed, *R. octofasciata* and *R. gemmata* do exhibit putative synapomorphies (e.g. bicuspidate lower symphysial teeth, speckled cheeks), although a larger sample of characters will be needed to elucidate this issue.

Basal species apparently tend to be native to northern-western Central America: this is the pattern within *Cryptoheros* (*Cryptoheros*), with the Mexican-Belizean *Cr. chetumalensis* basal to the other two species, one dwelling in the Izabal drainage, the other in Honduran waters. The pattern appears also in *Amatitlania* (without *Am. coatepeque*), where *Am. nigrofasciata* of Guatemala-Honduras is basal to the other two species, which occur from Nicaragua to Panama. This is seen again in *Archocentrus*, with *Ar. spinosissimus* of Guatemala basal to the Honduran-Nicaraguan-Costa Rican species.

Northern Central America or “Nuclear Central America” (Kesler 1971) corresponds roughly to the highlands of Chiapas and Guatemala. It is a geologically complex area, which remained available to freshwater fishes while Lower Central America did not fully emerge to connect the region to South America. The biogeographic patterns outlined above seem consistent with a recolonisation of Lower Central America from Nuclear Central America by several cichlid lineages, after the initial northwards colonisation by their ancestors (the first colonisation of Nuclear Central America by cichlids most likely occurred before a fully

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freshwater connection from South America was established—Bussing 1976, Álvarez del Villar 1977). This scenario might hold for other fishes as well, for example *Rhamdia laticauda* Heckel (Perdices et al. 2002: 185).

Deeper in the cladogram, the pattern is coherent with the invasion of Middle America from South America, because the Panamanian *Cr. panamensis* is basal to Costa Rican-Nicaraguan and Guatemalan-Mexican clades. However, the South American *Caquetaia* lies within the ingroup; virtually all previous workers have also found *Caquetaia* nested within the Mesoamerican cichlids (Martin & Bermingham 1998; Farias et al. 1999, 2000, 2001; Chakrabarty in litt., 2003; Hulsey et al. 2004), which speaks against monophyly of the strictly Middle American cichlids and underscores the probably great complexity of their biogeographical history.

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