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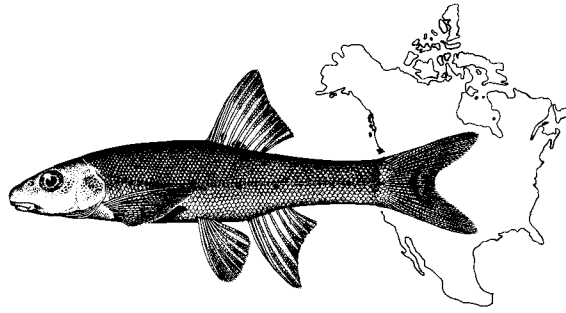
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Systematic Relationships within the Cyprinid Genus *Rhinichthys*

David A. Woodman

As presently understood the genus *Rhinichthys* consists of seven species: *R. atratulus*, *R. bowersi*, *R. cataractae*, *R. deaconi*, *R. evermanni*, *R. falcatus*, and *R. osculus* (Lee et al., 1980; Matthews et al., 1982; Miller, 1984; Goodfellow et al., 1984). The genus is mostly western in distribution but *R. atratulus* is restricted to the eastern portion of North America. *Rhinichthys cataractae* is the only other species found in eastern North America, but substantial populations also exist west of the Continental Divide. *Rhinichthys falcatus* is restricted to the Fraser and Columbia river system and *R. osculus* is native to all major western drainages from the Columbia and Colorado rivers south to Sonora, México (Lee et al., 1980) with disjunct populations showing high degrees of endemism. *Rhinichthys evermanni* is restricted to the Umpqua River system in Oregon.

The monotypic western genera *Agosia* and *Tiaroga* have also been viewed by some writers (Lee et al., 1980) as derivatives of *Rhinichthys* or a *Rhinichthys*-like stock. *Agosia* has long been associated with a subset of what we now recognize as *Rhinichthys*, specifically the subgenus *Apocope* (Jordan and Evermann, 1896; Jordan et al., 1930). *Agosia* is common in the Bill Williams and the Gila rivers but its southern limits are not well defined (Lee et al., 1980). *Tiaroga* is restricted to the upper Gila River basin in Arizona and New Mexico. As a result of a phylogenetic analysis inferring genealogical relationship, I present arguments in support of including the nominal genera *Agosia* and *Tiaroga* within *Rhinichthys*. Consequently, I will refer to these species as *Rhinichthys chrysogaster* and *Rhinichthys cobitis*, respectively.

Taxonomic History

Prior to 1937, most systematic and taxonomic works on *Rhinichthys* were restricted to alpha-level decisions examining the diversity of this widespread genus. Jordan and Evermann (1896) listed the genus *Rhinichthys* as containing three species,

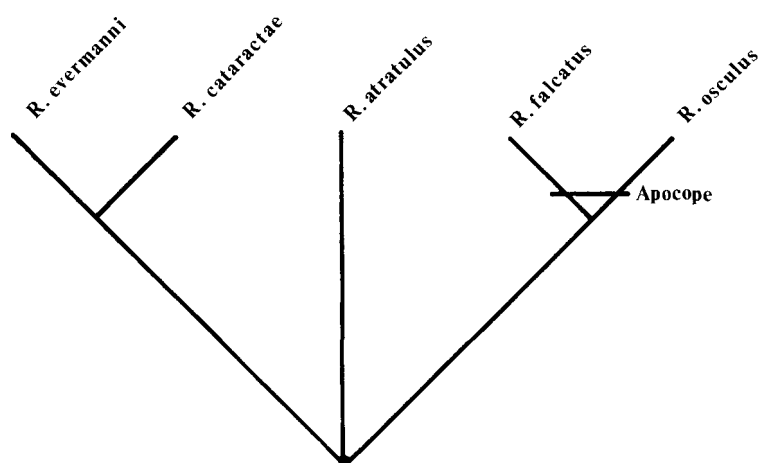


Figure 1.
Relationships within the
genus *Rhinichthys* as implied
by Hubbs et al. (1974).

R. cataractae (with 2 subspecies), *R. atronassus* (= *atratulus*; Hubbs, 1936), (with three subspecies), and *R. simus*. Ten species (in two subgenera, *Apocope* and *Agosia*) were included in the western genus *Agosia*. Jordan et al. (1930) redefined the genus and elevated all subspecies to specific status, increasing the species diversity in *Rhinichthys* to eight. In that analysis the two subgenera of *Apocope* were elevated to generic status. *Apocope* consisted of 12 species; *Agosia* consisted of a single species, *A. chrysogaster*.

Hubbs and Kuhne (1937) accepted the recognition of *Apocope* from *Agosia* and referred the numerous local forms of *Apocope* to the wide ranging species *Apocope oscula*. The genus *Apocope* was first synonymized with *Rhinichthys* by Murphy (1941), a position followed by Hubbs and Miller (1948). Justification for combining both genera was not provided in either case.

Two additional relict cyprinid genera from Nevada, *Eremichthys* and *Moapa*, were described by Hubbs and Miller (1948). Based on gross morphological similarities they concluded that the genera *Agosia* and *Moapa* were sister taxa. Important characteristics included (1) a small, inferior, and nearly horizontal mouth with the lower jaw included; (2) pharyngeal arches of similar shape; (3) a hidden frenum; (4) a rather small eye; (5) small scales with radii on all fields; (6) a broad, blackish mid-dorsal stripe; and (7) a conspicuous black spot at the base of the caudal fin. These authors also described many similarities between these genera and the genus *Rhinichthys*, but still related *Agosia* to *Moapa*. An unstated weighting of characteristics, based on unstated criteria, probably led to the acceptance of one group of shared similarities over the other. Unfortunately, as in much of the work then done, no uniquely derived characters were used to define the relationships between the genera. Characters 1–5 are also shared with various populations of *R. osculus* and characters 6 and 7 are found in most western and in some eastern North American minnow genera.

Phylogenetic relationships for members of the genus *Rhinichthys*, as described by Hubbs et al. (1974), are represented in Figure 1. The subgenus *Apocope* was recognized as consisting of *R. osculus* and *R. falcatus*. In spite of the proposed sister group relationship between *R. osculus* and *R. falcatus*, these authors felt that since *R. falcatus* was "trenchantly different" from other *Rhinichthys* it could have been assigned to another (monotypic) genus. This change was not made. While no subgenus was

recognized for other members of the genus *Rhinichthys*, Hubbs et al. (1974) defined another group consisting of *R. cataractae*, *R. evermanni*, and *R. atratulus*. *Rhinichthys atratulus* was separated from the *cataractae* group of Hubbs et al. (1974) by Matthews et al. (1982). This separation was justified on the basis of the development of breeding pads in the *R. atratulus* group. These pads were found on "most of the distal half of rays 2–4, 5 or 6 of pectoral fins of nuptial male" (Matthews et al., 1982). Miller (1984) concurred with this evaluation and defined three species groups in the genus *Rhinichthys*, the *R. cataractae* group (including *R. evermanni*), the *R. atratulus* group, and the *R. osculus* group (synonymous with the subgenus *Apocope* and including *R. falcatus*). The *R. osculus* group was diagnosed by (typically) lacking nuptial tubercles on the first pectoral-fin ray and on all other fins, and by a weaker (often absent) frenum.

METHODS

Specimens used for osteological studies were cleared and double stained using the methods described in Dingerkus and Uhler (1977), Kelly and Bryden (1983), and Wassersug (1976). Preparations were dissected and examined under a microscope and sketches were made using a *camera lucida* attachment. In all drawings articular surfaces are represented by a stippled pattern. The *adductor mandibulae* muscles were exposed by removing the infraorbital bones and surrounding skin; underlying muscles were stained following Bock and Shear (1972). Photographs of the muscles were made using a Nikon camera with a 55 mm Micro Lens and bellows.

Analytical Methods

Species relationships were determined using uniquely derived characters (synapomorphies). Synapomorphies were determined by outgroup comparison, a method considered appropriate for determining character polarity (Watrous and Wheeler, 1981; Wiley, 1981). If used with realistic outgroup comparison, as described below, this method provides unambiguous character polarizations.

Watrous and Wheeler (1981:5) outlined an operational rule and a series of observations relating to the use of the outgroup method of determining character polarity. Their operational rule is: "*for a given character with 2 or more states within a group, the state occurring in related groups is assumed to be the plesiomorphic state. If the character contains only 2 states, the alternative state is assumed to be apomorphic, thereby forming a more restricted character.*"

There are some important differences in the analytical methods herein and those proposed in Watrous and Wheeler (1981).

1. In the event that a character could not be polarized using the operational rule of Watrous and Wheeler (1981) (i.e., when an outgroup shows the presumed apomorphic state) the character was considered uninformative and was excluded from the analysis. Effectively, characters that could not be polarized, given the differences stated above, were assigned a weight of 0, while those that could be polarized were assigned a weight of 1. Watrous and Wheeler (1981) advocated reducing the number of the outgroups to remove the incongruous

taxon and hence render the character polarizable. Incongruous polarized character distributions were resolved using a most parsimonious solution to propose a hypothesis of relationships between the species.

2. Determination of polarity for a single character did not influence polarity determination of another character; i.e., congruence in character polarity was not an assumption required in this method (even though advocated by Watrous and Wheeler, 1981; Wiley, 1981). This concept was originally presented by Maslin (1952) when discussing character polarity and "paradromic" characters. Arnold (1981) advocated restricted paradromy, (i.e., polarities of a substantial number of characters had to be established before paradromy could be employed), but argued against the general use of this method.

In addition, my analytical method utilized multiple outgroup species, all of which did not form a monophyletic group and were objectively paraphyletic with respect to the ingroup. The use of a single species, or a group of species that together form a monophyletic group, as an outgroup will, in some instances, force the assumption that all character states found within the outgroup are primitive and the alternate character states found within the ingroup, derived. This is in contrast to the outgroup rooting methods such as the Lundberg option of Swofford (1984) where no such assumptions are made since the method is essentially an ingroup, minimum step analysis. The method advocated by Maddison et al. (1984), where a parsimony analysis within the outgroup is used to arrive at plesiomorphic character states, results in a conclusion similar to that obtained when a single outgroup species is used. It becomes apparent that, at the level of the determination of the monophyly of the ingroup, an ambiguity exists as far as the polarization of a character is concerned. This ambiguity I call the sister-group fallacy, fully described in Woodman (1987). The use of multiple species as an objectively paraphyletic outgroup helps ensure that the character states supporting ingroup monophyly are not plesiomorphic.

When a single outgroup is used, the choice and arrangement of the outgroup taxa (with respect to the ingroup) changes the cladistic arrangement of taxa within the ingroup (Colless, 1985). Because character polarity in my analysis was not dependent upon the structure/hierarchy of a higher level phylogeny, the otherwise legitimate observations of Colless (1985) were not significant to this method.

It may be noted that the method advocated herein is generally in keeping with the method proposed by Neff (1986) in that it accepts the primacy of character polarization and the notion that all characters are not equal. Character polarity, however, is determined by outgroup comparison, but not by the methods described in Neff (1986), such as geological precedence and ontogeny. In essence, while my method utilized cladistic methodology, it stressed character analysis, in the form of rigorous outgroup comparison, as the basis for polarity determinations rather than *a posteriori* determinations based on most-parsimonious cladograms. As noted by Bryant (1989), the role of pure parsimony methods in cladistic analysis is not consistent with that of the hypothetico-deductive method proposed for phylogenetic systematics by Wiley (1981:19).

The species considered in this study were *R. atratulus*, *R. cataractae*, *R. chrysogaster*, *R. cobitis*, *R. evermanni*, *R. falcatus*, and *R. osculus*. Not studied were *R. bowersi* and *R. deaconi*. Specimens of *R. bowersi* could not be obtained for study. The status of the

Table 1. The distribution of character states described in the Appendix.

Species	Characters																										
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27
<i>R. atratulus</i>	2	2	1	2	1	1	1	1	2	1	2	1	1	2	1	3	1	2	2	1	2	1	1	2	2	1	1
<i>R. cataractae</i>	1	2	2	2	1	1	1	2	2	1	1	2	1	1	2	1	1	2	2	1	1	1	2	1	2	1	1
<i>R. chrysogaster</i>	2	2	1	1	1	2	1	1	1	1	1	1	2	2	2	3	2	1	2	1	2	1	2	2	2	1	2
<i>R. evermanni</i>	1	2	2	2	2	1	1	1	1	2	1	1	1	1	1	1	2	2	1	2	1	1	2	2	2	1	1
<i>R. falcatus</i>	2	2	2	2	2	1	1	1	2	1	1	2	1	2	2	3	2	2	2	1	2	1	1	1	2	1	1
<i>R. cobitis</i>	2	2	2	1	2	1	2	1	2	1	1	2	1	2	2	3	2	2	1	2	2	1	2	2	2	1	1
<i>R. osculus</i>	2	2	1	1	1	1	1	2	2	1	2	2	1	2	2	3	1	2	1	1	2	1	1	1	1	1	1
<i>C. anomalum</i>	2	2	1	1	2	1	1	2	2	2	2	2	1	3	2	1	2	1	2	3	2	2	2	2	1	2	1
<i>E. acros</i>	2	2	1	1	1	1	1	1	1	1	1	1	1	1	2	2	1	1	1	1	1	2	1	3	2	2	2
<i>M. aestivalis</i>	2	1	2	1	2	1	1	2	1	1	2	2	1	1	2	1	1	1	2	1	2	1	1	2	2	1	1
<i>N. ludibundus</i>	2	2	1	1	2	1	1	2	1	1	2	2	1	2	1	2	1	1	2	1	2	1	2	2	2	1	1
<i>S. atromaculatus</i>	2	2	2	1	1	2	2	2	1	1	1	1	1	2	1	2	2	1	1	1	1	1	2	2	2	1	1
<i>I. phlegethontis</i>	2	2	2	1	2	2	2	2	2	1	2	2	1	1	1	2	2	2	2	1	2	1	1	2	2	1	1
<i>G. robusta</i>	2	2	2	1	1	2	2	2	1	1	2	1	1	2	1	2	2	2	1	2	2	1	2	1	2	1	1
<i>P. neogaeus</i>	2	2	2	1	2	2	2	2	1	1	2	2	1	1	1	2	1	1	2	1	2	1	2	2	2	1	1

various constituents of the *R. osculus* complex, including *R. deaconi*, was considered to be a separate problem. *Campostoma anomalum*, *Eremichthys acros*, *Gila robusta*, *lotichthys phlegethontis*, *Macrhybopsis aestivalis*, *Notropis ludibundus*, *Phoxinus neogaeus*, and *Semotilus atromaculatus* were considered the outgroup. Of these, *E. acros*, *G. robusta*, *P. neogaeus*, *S. atromaculatus*, and *I. phlegethontis* were not members of the eastern clade of North American minnows (Mayden, 1989:figs. 1–6) and so the outgroups used did not themselves form a monophyletic group. Fifty-four characters were examined. All character states, and their distribution among the species examined, are listed in the Appendix and Table 1, respectively. The characters examined and described below are those that could be polarized using the outgroup comparison method described above; other characters could not be polarized and were not used. The polarized characters were then subjected to additional outgroup comparisons to further establish their uniqueness. They were evaluated for occurrence in the species *Hybognathus hankinsoni*, *Macrhybopsis storeriana*, *Platygobio gracilis*, *Moapa coriacea*, *Phoxinus eos*, and *Catostomus catostomus*. In addition to this, a literature search (Takahasi, 1925; Ramaswami, 1955a, b; Liem, 1970; Shukla and Verma, 1972; Patterson, 1975; Howes, 1980, 1984a, b, 1985; Fink and Fink, 1981; Coburn, 1982; Mayden, 1989) was conducted to evaluate the occurrence of these character states in other taxa.

RESULTS

The genus *Rhinichthys*, as comprised by Hubbs et al. (1974), and as presently formed, was found not to represent a monophyletic group. An examination of "closely related" species indicated that *Tiaroga cobitis* and *Agosia chrysogaster* also should be members of *Rhinichthys* (Fig. 4). This conclusion was based on variations of the *m. adductor mandibulae*.

Table 1. Continued

	Characters																																		
	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53	54								
<i>R. atratulus</i>	1	1	2	1	1	2	1	1	1	1	1	2	2	1	2	1	1	2	1	1	1	2	1	2	2	2	2	2							
<i>R. cataractae</i>	1	1	1	1	1	1	1	1	1	1	1	2	1	1	2	1	1	1	1	2	1	2	2	2	1	2	2								
<i>R. chrysogaster</i>	1	1	1	1	1	2	1	1	2	1	1	1	1	3	1	1	1	1	2	1	2	1	1	2	2	1	2								
<i>R. evermanni</i>	1	1	2	1	1	1	1	1	1	1	1	1	1	1	2	1	1	2	1	2	1	2	1	1	1	2	2								
<i>R. falcatus</i>	1	1	2	1	1	1	1	1	1	1	1	2	2	1	2	2	1	2	1	2	2	2	1	2	2	2	2								
<i>R. cobitis</i>	1	1	1	1	2	2	2	1	1	3	1	2	2	1	2	1	1	1	1	2	2	1	1	1	2	2	2								
<i>R. osculus</i>	1	1	1	1	1	2	1	1	1	2	1	1	2	2	1	1	2	1	2	1	1	2	2	1	2	1	2								
<i>C. anomalum</i>	2	2	2	2	2	2	1	2	2	3	1	2	2	3	1	2	2	2	2	2	1	1	1	1	2	1	1								
<i>E. acros</i>	2	1	2	1	1	2	1	1	2	2	1	1	2	3	2	2	2	2	1	2	1	2	?	1	2	2	1	1							
<i>M. aestivalis</i>	1	1	2	2	2	2	1	2	2	1	1	1	1	3	2	2	1	1	2	2	1	2	1	2	2	1	1								
<i>N. ludibundus</i>	1	1	2	2	2	2	1	2	2	2	2	2	1	3	2	2	1	2	1	2	2	2	1	2	2	1	1								
<i>S. atromaculatus</i>	1	1	1	2	2	2	1	1	2	1	1	2	1	1	1	2	1	2	1	2	2	2	2	2	2	1	1								
<i>I. phlegethontis</i>	1	2	2	2	2	2	1	2	2	1	1	2	2	2	2	2	1	2	1	2	1	2	1	1	2	1	1								
<i>G. robusta</i>	2	1	1	2	2	2	1	1	2	2	2	2	2	1	1	2	1	2	1	2	2	2	2	2	2	2	1	1							
<i>P. neogaeus</i>	1	1	1	1	2	2	1	2	2	2	1	2	1	3	1	2	2	1	2	2	2	2	1	2	2	1	1								

The *m. adductor mandibulae* lies on the cheek region directly on the outer surface of the pterygoid, preopercle, and interopercle. It can be divided into four layers (Harder, 1975). These include the *m. maxillaris*, the superficial layer, the *m. mandibularis*, which constitutes the middle and the profound layer, and the *m. mentalis*, which constitutes the symphyseal layer. This study deals exclusively with the *m. maxillaris*.

The *maxillaris* branch of the *m. adductor mandibulae* originates on the preoperculum and quadrate bones (Takahasi, 1925) and inserts on the outer surface of the maxillary. The *mandibularis* branch of the *adductor mandibulae* lies just medial to the *maxillaris*. Howes (1984a) stated that the primitive condition of the *maxillaris* is an undivided element with a simple insertion on the maxilla. In the derived state the *maxillaris* is divided into two portions, the A_1 anterior, which is the anterior portion of the *maxillaris* originating on the horizontal arm of the preoperculum and the quadrate; and the A_1 posterior, originating on both the horizontal and the vertical arm of the preoperculum. A detailed examination of this muscle reveals that it is simplistic to define only the divided state as derived because considerable variations exist with regard to the insertions and positions of the tendons for these two subdivisions and in the direction of their fibers. Takahasi (1925) listed *Cyprinus carpio* as having the *maxillaris* divided into two portions. In this species, the two muscles are united for a short distance toward the origin. The A_1 anterior is ventral to the A_1 posterior at their origins, but lies superficial to the posterior muscle at the insertion on the maxilla. Howes (1984a) stated that the derived divided *maxillaris* is found in only the neobolines and certain bariliines. His representation of the muscle in *Engraulicypris*, *Leptocypris*, *Raiamas*, *Osparidium* (Howes, 1980), and *Rastrineobola* (Howes, 1984a) is similar to that described for *Cyprinus carpio* by Takahasi (1925). All species show the dorsal placement of the insertion of the A_1 anterior with respect to the insertion of the A_1 posterior. My studies on the *maxillaris* in *Catostomus catostomus* (Fig. 2a) of the family Catostomidae, considered the sister-group of the

Cyprinidae by Eaton (1935) and Ramaswami (1955a, b), show similarity in placements of the insertions of both these muscles to the insertions of the two *maxillaris* muscles in *Cyprinus carpio* and the Bariliine.

In the genus *Rhinichthys*, two characteristics of the muscle are evident (Fig. 2) and concern the tendinous insertion and direction of the fibers of the A_1 anterior portion. In all members of the genus, the A_1 anterior tendon slips beneath the A_1 posterior muscle and inserts into the fascia of the A_1 posterior. This is derived with respect to the condition seen in the outgroups where the tendons of the A_1 anterior and the A_1 posterior insert on the dorsal crest of the maxilla adjacent to each other. The direction of the A_1 anterior fibers is also important as in *R. atratulus*, *R. cataractae*, *R. cobitis*, *R. evermanni*, and *R. falcatus* (Fig. 2a), where the fibers insert at an angle to the fibers of the A_1 posterior muscle (Woodman, 1987: pl. 1f, a, b, d, and e). In *R. chrysogaster* (Fig. 2c) and *R. osculus* (Woodman, 1987: pl. 1g), the two bundles are not as clearly distinguishable and the fiber direction is nearly parallel. In this latter condition the muscle is divided and has insertions similar to those observed in the other species of *Rhinichthys*. Insertion of the anterior muscle into the fascia below the posterior muscle is considered a synapomorphy of *Rhinichthys*. The angle of the A_1 anterior fibers relative to the angle of the A_1 posterior fibers is derived compared to the primitive parallel condition. This synapomorphy defines a group consisting of all members of *Rhinichthys*, except *R. chrysogaster* and *R. osculus*.

An examination of species more closely related to *Rhinichthys* than to *Cyprinus carpio* and *Catostomus catostomus* shows that in *Eremichthys acros* (Fig. 2d), *Hybognathus hankinsoni*, *Gila robusta*, and *Moapa coriacea* (Woodman 1987:pl. 1h-k), *Iotichthys phlegethontis*, *Phoxinus eos*, *P. neogaeus*, *Semotilus atromaculatus*, and *S. margarita* (Woodman, 1987) the *maxillaris* is undivided and the tendinous separation seen in *Rhinichthys* is not observed. Therefore, the suggestion of Hubbs and Miller (1948) that *Moapa* is closely related to *Agosia* (and hence *Rhinichthys*) is rejected.

Additional characters used to elucidate species relationships within the genus are the following (character numbers in brackets refer to character numbers in the Appendix and Table 1).

Infraorbital bones [Character 1]

The infraorbitals form the ventral margin of the orbit. Each infraorbital bone is a flat plate upon which run the bony tubes of the infraorbital lateralis.

The two character states of the infraorbitals included reduced elements with no bony extensions beyond sensory canals (Fig. 3a), and with bony extensions beyond sensory canals (Fig. 3b).

In all the species except for *R. evermanni* (Woodman, 1987:fig. 6.01c) and *R. cataractae*, the infraorbital bones extended beyond the bony tubes of the infraorbital canal (Fig. 3a). In *R. cataractae* and *R. evermanni* the bony plates were absent and only the bony tubes were observed (Fig. 3b). The reduced condition was considered derived relative to ossification beyond the margins of the sensory tubes. In all aspinine cyprinids (Howes, 1984b) and in the genus *Cyprinella* (Mayden, 1985), the infraorbitals showed bony expansion beyond the margins of the sensory canals.

Palatine [Character 4]

The palatine bone lies lateral and posterior to the preethmoid bone of the

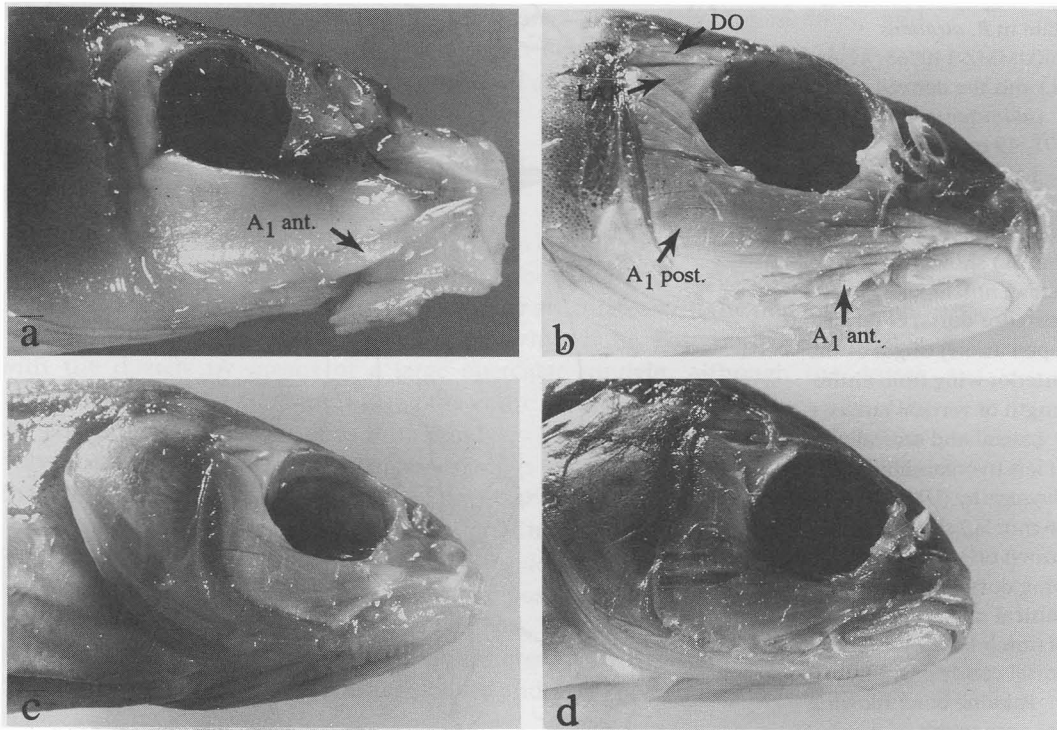


Figure 2.

Cheek muscles in Cyprinidae. a. *Rhinichthys falcatus* (UMMZ 188951, 70 mm SL); b. *Catostomus catostomus*, (DAW 83-102, 102 mm SL); c. *R. chrysogaster* (UMMZ 162668, 40 mm SL); d. *Eremichthys acros* (UMMZ 141590, 40 mm SL). A₁ ant. = Anterior portion of the *maxillaris* of the *adductor mandibulae*; A₁ post. = Posterior portion of the *maxillaris* of the *adductor mandibulae*; DO = dilator operculi; LAP = Levator arcus palatini.

cranium, articulates anteriorly with the maxilla and the premaxilla, and posteriorly with the mesopterygoid. Of the variation observed, only one character was polarizable.

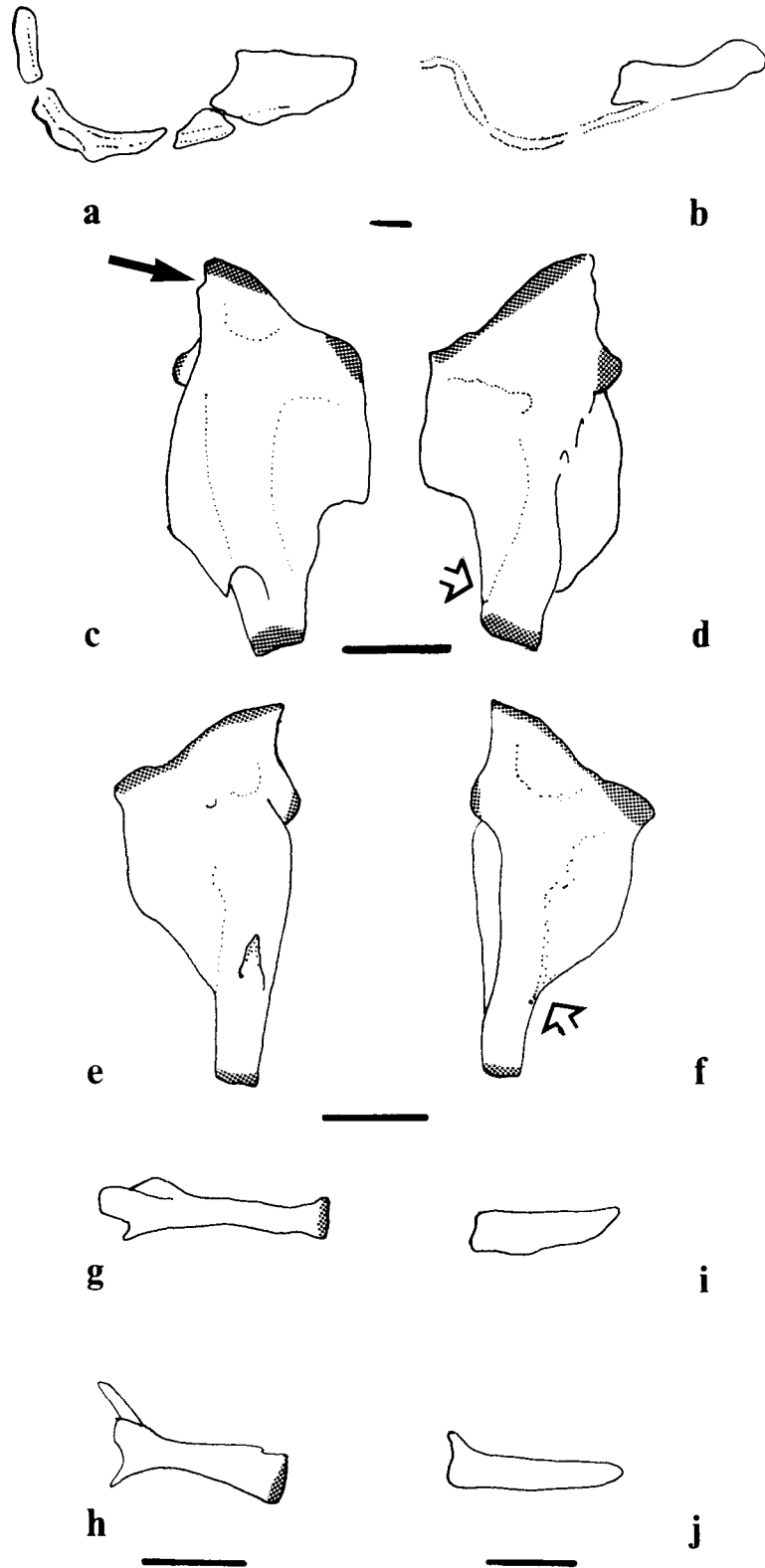
The palatine of *R. falcatus*, *R. evermanni* (Fig. 3g), *R. cobitis*, and *R. cataractae* (Woodman, 1987:fig 6.02) had a shaft of uniform width and without a constriction. All other species examined had a palatine with a constricted shaft (Fig. 3h). The uniform width of the palatine was held to be a derived morphology. An examination of Mayden (1989) showed that palatine bones in the species examined were not of uniform width thereby indicating the uniqueness of the characteristic.

Subopercle [Character 13]

This flat bone is ventral to the opercle and usually has a slightly concave dorsal edge and slightly convex ventral margin. Anteriorly, the subopercle may have a thin knob (Fig. 3j) arising from the anterodorsal angle. The knob was present in all outgroup and ingroup members, except for *R. chrysogaster* (Fig. 3i), where it was

Figure 3.

a, b: Suborbital bones showing in the primitive state in *R. atratulus* (a)(UMMZ 140963, 47 mm SL) and the derived state in *R. cataractae* (b)(DAW 83-101, 49 mm SL); c, d: Lateral and medial views of right hyomandibular of *R. falcatus* (UMMZ 188951, 54 mm SL) showing (solid arrow) notch below posterior dorsal condyle and (open arrow) origin of the anterior wing from entire length of vertical ramus; e, f: Lateral and medial views of left hyomandibular of *R. chrysogaster* (UMMZ 162668, 46 mm SL) showing (open arrow) origin of anterior wing dorsal to ventral end of vertical ramus and absence of notch below posterior dorsal condyle; g, h: Palatine bone showing the even width of the shaft in *R. evermanni* (g)(UMMZ 94149 50 mm SL) and constriction along the length of the shaft in *G. robusta* (h)(UMMZ 125001, 50 mm SL); i, j: The subopercle showing derived state present in *R. chrysogaster* (i)(UMMZ 162668, 46 mm SL) and primitive state in *R. osculus* (j)(UMMZ 141621, 36 mm SL). Bars = 1mm.



absent. This knob also occurred in the genera *Tribolodon*, *Pogonichthys*, and *Ptychocheilus* (Howes, 1984b), and several other North American species (Mayden, 1989). The absence of the knob was considered derived.

Hyomandibular [Characters 33, 34, and 36; Fig. 3c–f; Woodman, 1987:fig. 6.19]

The hyomandibular fits dorsally into a socket on the ventral surface of the cranium formed by the prootic, pterotic, sphenotic, and pterosphenoid bones (Mayden, 1989). Anteriorly, the hyomandibular articulates with the metapterygoid, and ventrally with the symplectic and the interhyal bone. Posteriorly, it articulates with the opercle by means of a large opercular condyle. Although the dorsal articulation with the cranium is along the entire dorsal edge of the hyomandibular, the anterior and posterior ends form condyles (Fig. 3c–f). The bone consists of a heavy central strut with thin flanges or wings extending on either side. Of the characters observed the following were polarizable.

Posterodorsal condyle of hyomandibular [Character 33]: **notched, or smooth.** *Rhinichthys cataractae*, *R. evermanni*, and *R. falcatus* (Fig. 3c and d) each had a hyomandibular with a notch just below the posterodorsal condyle. There was no such notch in other members of *Rhinichthys* (Fig. 3e and f), nor in any member of the outgroup. Mayden (1989) found no notch present in the genus *Cyprinella*. The presence of the notch was considered derived and a synapomorphy for *R. falcatus*, *R. cataractae*, and *R. evermanni*.

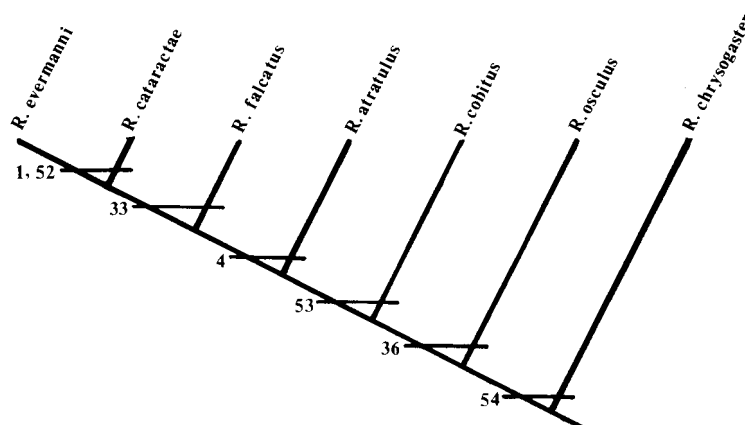
Position of the anterodorsal condyle of the hyomandibular [Character 34]: **dorsal or ventral to the level of the opercular condyle.** The position of the anterodorsal condyle with respect to the opercular condyle varied within the ingroup. In *R. cobitis* (Woodman, 1987:fig. 6.19m and n) the anterior hyomandibular condyle was at a level below that of the opercular condyle. This character state was considered an autapomorphy for *R. cobitis*. In other ingroup members and all outgroups, the condyle was at a level equal to or higher than that of the opercular condyle (Fig. 3c–f).

Anterior wing of the hyomandibular [Character 36]: **arises along the entire length of the ventral ramus, or does not arise along the entire length of the ventral ramus.** The anterior hyomandibular wing originates along the entire length of the ventral ramus in all ingroup members (Fig. 3c and d) except *R. chrysogaster* (Fig. 3e and f). In all the outgroups, the anterior wing did not extend along the entire length of the ventral ramus, but began dorsal to the ventral edge of the ramus. The condition found in ingroup members, except *R. chrysogaster*, was considered derived and a synapomorphy for the group.

Frenum [Character 43]

The frenum is the non-protractile fleshy portion of the upper lip lying between the premaxilla and the maxilla (Hubbs et al., 1974). In *Rhinichthys*, this structure was either present or absent. The frenum was present in *R. cataractae*, *R. evermanni*, *R. cobitis*, and *R. atratulus*. *Rhinichthys chrysogaster* has “a hidden frenum” (Hubbs and Miller, 1948). The frenum was absent in *R. falcatus* and in some populations of *R. osculus*. It was absent in all members of the designated outgroup. The presence of the frenum was considered to be derived.

Figure 4.
The most parsimonious
cladogram based upon
polarized character distribu-
tions. Numbers on cla-
dogram nodes follow the
appendix.



Postcleithrum [Character 52]

This bone typically articulates on the medial surface of the dorsal half of the cleithrum. Two character states of the postcleithrum occurred in *Rhinichthys*.

The post-cleithrum was absent in *R. cataractae* and *R. evermanni*. In all other species the post-cleithrum was present. The presence of this bone was also noted in the species *Barilius bola*, an Asian cyprinid (Shukla and Verma, 1972), and in many North American cyprinids (Mayden, 1989). The absence of the postcleithrum was a derived character and a synapomorphy for *R. cataractae* and *R. evermanni*.

DISCUSSION

The distributions and polarities of the observed character variations among the ingroup and the outgroup taxa support the monophyly of *Rhinichthys* and a dichotomous pattern of species relationships within the genus (Fig. 4). Contrasting these relationships with those described by Hubbs et al. (1974) (Fig. 1), it is evident that some incongruencies exist.

The traditionally recognized subgenus *Apocope* is a paraphyletic grouping because *R. falcatus* and *R. osculus* are not sister species. *Rhinichthys cobitis* is a member of the genus based on the derived status of the *maxillaris* branch of the *adductor mandibulae* [Character 53]. Similarly, *R. chrysogaster* is considered a member of *Rhinichthys* based upon the possession of a dorsal tendinous insertion of the A_1 anterior portion of the *maxillaris* branch of the *adductor mandibulae* into the fascia of the A_1 posterior muscle [Character 54]. *Rhinichthys chrysogaster* is considered a member of the genus *Rhinichthys* in spite of being the phylogenetic sister-group for the following reasons. Smith and Patterson (1988:130) state that "the rank allocated to a monotypic taxon is intended to express an opinion rather than to group species. That opinion may express either ignorance (of the relationship of the species to others) or a judgment about the phenetic distance that separates this species from its closest relatives." Because I support the relationships of *R. chrysogaster*, and because this analysis is not intended to be phenetic, I include this species in the genus *Rhinichthys*.

Apparent falsifiers for the inclusion of *R. chrysogaster* in *Rhinichthys* are the characters supporting the inclusion of the species in the large eastern clade of Mayden

(1989). The monophyly of this clade is supported by the presence of an "open" posterior myodome. It is necessary to evaluate this character and other characters relating this species to taxa within that clade.

The posterior myodome is the location of the origin of the rectii muscles of the eye. The floor of the myodome is formed by the parasphenoid, the prootic, and the basioccipital, and its roof is the exoccipital. An open posterior myodome is present when this structure is "unfloored" i.e., the parasphenoid and the basioccipital do not lie ventral to it. The closed myodome is present when these structures are present ventral to the myodome. In my examination of the species *R. chrysogaster* I have not been able to find an open myodome. Further, Howes (1980) used this character [although see Mayden (1989) for apparent differences in the interpretation of the homology of this character] as one of the synapomorphies defining the bariliine cyprinid group from Africa and Asia, and this character has been found in the cyprinid genus *Leptocypris* and the species *Engraulicypris sardella* (Howes, 1980). Patterson (1975) noted the presence of the open posterior myodome in the leptolepid fishes, a group of extinct actinopterygians. Fink and Fink (1981) questioned the use of the open posterior myodome by Howes (1980) in the determination of the monophyly of the bariliine assemblage. They considered this character to be primitive given the information contained in Patterson (1975).

In addition to the posterior open myodome, placement of *R. chrysogaster* in the chub clade (Mayden, 1989) was based upon three additional characters, two in the palatine and one found in the urohyal. I have found it difficult to objectively evaluate the palatine characters; however, the derived state of the urohyal character (a horizontal plate with a smooth and oval posterior margin) is also seen in all species of the genus *Rhinichthys* (Woodman, 1987). From such observations it becomes difficult to recognise *Agosia* and to accept Mayden's (1989) inclusion of *chrysogaster* as a member of the eastern North American clade of cyprinids within the chub clade.

The distribution of the frenum, a derived character state, is a falsifier of the relationships shown in Figure 4. However, the frenum occurs in the genus *Exoglossum* and is variably present in *R. osculus* (Hubbs et al., 1974), being present in some populations and absent in others. An examination of collections in my possession shows that even when there is a superficial indication of the absence of the frenum, the rostral groove is much reduced compared to genera such as *Notropis* and *Gila* where the groove is deep and separates the premaxilla and the maxilla completely. Based on a parsimony analysis of uniquely derived character states I conclude that the frenum was independently lost in *R. falcatus*.

Characters postulated as synapomorphies for group definition are themselves hypotheses (Neff, 1986). While parsimony methods have postulated that it is the system of relationships that need, to be tested, it is quite evident that untested assumptions of synapomorphy postulated on the basis of parsimony increase the "noise" in any analysis and thereby render the system of relationships suspect. The preceding character analysis reveals that one can ascertain with relative confidence the polarity of characters used in cladistic analyses. Every character initially polarized utilizing a relatively large number of outgroups was further examined for occurrence in still other taxa. While questions may be raised as to how many outgroup taxa are sufficient to realistically determine character polarities it is sufficient to state that single outgroup comparisons fall short of the extensive outgroup comparisons required to establish the uniquely derived characters demanded by this method.

SUMMARY

The membership of and the relationships within the cyprinid genus *Rhinichthys* have been redefined using cladistic methodology with strict outgroup comparisons. Character states present in the ingroup and the outgroup were considered plesiomorphic and inappropriate for the analysis. Eight species of cyprinids were used as the paraphyletic outgroup. Fifty-four osteological and myological characters were examined initially. Of these, 11 characters survived the strict outgroup comparison, two were uninformative (autapomorphic), two falsify my cladogram and seven support a completely resolved cladogram. The remaining characters were deleted from the analysis since objective decisions regarding their homology and polarity could not be made. This method differed from a compatibility analysis in that all character states polarized utilizing the stated method were used in the determination of the phylogeny. The analysis revealed that *Tiaroga cobitis* is embedded deep within *Rhinichthys* and *Agosia chrysogaster* is the sister to *Rhinichthys* (+ *Tiaroga*). Both *Agosia* and *Tiaroga* are placed in *Rhinichthys* so that the classification is consistent with the phylogeny of the species.

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SPECIMENS EXAMINED

Museum acronyms below follow Leviton et al. (1985) except as follows: CAS-SU, Stanford University collections now at CAS; DAW, Personal collections of the author; ISNM, Idaho State University, Museum of Natural History. *Campostoma anomalum* DAW 83-201 (2 cs). *Catostomus catostomus* DAW 83-102 (2). *Eremichthys acros* UMMZ 141590 (10, 10 cs). *Gila robusta* UMMZ 125001 (5, 5 cs). *Hybognathus hankinsoni* DAW 82-101 (1 cs). *Iotichthys phlegethontis* UMMZ 141435 (5, 5 cs). *Macrhybopsis aestivalis* DAW 83-401 (3 cs). *Macrhybopsis storeriana* DAW 83-402 (5 cs). *Moapa coriacea* UMMZ 177086 (20, 5 cs). *Notropis ludibundus* DAW 83-301 (2 cs). *Phenacobius mirabilis* DAW 83-401 (2 cs). *Phoxinus eos* DAW 82-202 (2 cs). *Phoxinus neogaeus* DAW 82-201 (4 cs). *Platygobio gracilis* DAW 83-403 (7 cs). *Rhinichthys atratulus* UMMZ 140963 (46, 4), 180523 (16, 4 cs); UNO 79-006 (10). *Rhinichthys cataractae* UMMZ 134090 (15), 180012 (191, 3cs); DAW 83-101 (5 cs). *Rhinichthys chrysogaster* UMMZ 162668 (10, 10

cs); KU 8084 (5 cs). *Rhinichthys cobitis* UMMZ 162690 (35, 5 cs), 162783 (19, 4 cs). *Rhinichthys evermanni* OS 0813 (4 cs), 9578 (23); UMMZ 94149 (8, 1 cs). *Rhinichthys falcatus* UMMZ 188951 (30, 10 cs). *Rhinichthys osculus* CAS 23858 (8); CAS-SU 34918 (52), 37804 (51), 40694 (22), 40700 (10), 40701 (4), 41696 (26); ISNM 30035 (6), 30039 (4), 30049 (20), 30402 (10); OS 1918, (1)2812 (1), (1)3994 (1), (2)2405 (42), (2)5389 (30), (2)5391 (95), (5)4433 (14), (6)4382 (1), (6)5415 (16), (6)5418 (5), (6)10626 (13), (6)10984 (2); SIO 054-103 (1); UIM 518 (47), 626 (11), 922 (22), 979 (29), 1562 (14); UMMZ 98772 (56), 105709 (12), 112932 (25), 124986 (484, 4 cs), 130633 (25), 140425 (10), 141621 (183, 13 cs), 141642 (393, 4 cs), 141678 (49), 141693 (30), 162949 (30), 180436 (25, 5 cs), 180443 (30). *Semotilus atromaculatus* DAW 84-201 (1 cs).

APPENDIX—CHARACTERS EXAMINED

1. Infraorbitals. 1: reduced, no bony extensions beyond the sensory canals; 2: with bony extensions beyond sensory canals.
2. Palatine. 1: anterior processes long and anteriorly directed; 2: anterior processes short and not directed anteriorly.
3. Palatine. 1: with medial protruberance; 2: without medial protruberance.
4. Palatine. 1: with constricted shaft; 2: shaft of unvarying width.
5. Mesopterygoid. 1: long anterior process; 2: short anterior process.
6. Articular surfaces of the metapterygoid. 1: one posteroventral surface; 2: one posteroventral and one posterodorsal surface present.
7. Metapterygoid. 1: metapterygoid process present; 2: metapterygoid process absent.
8. Metapterygoid. 1: with a ventral notch; 2: without a ventral notch.
9. Quadrate. 1: anterior edge of body is upright; 2: anterior edge of body slanted posteriorly.
10. Quadrate. 1: large articular condyle; 2: small articular condyle.
11. Symplectic. 1: with a dorsal protruberance; 2: without a dorsal protruberance.
12. Interopercle. 1: with a notch on the posterior edge; 2: without a notch on the posterior edge.
13. Subopercle. 1: with an anterior knob; 2: without an anterior knob.
14. Ascending ramus of the premaxilla. 1: slender ascending process; 2: broad ascending process; 3: ascending process absent.
15. Horizontal ramus of the premaxilla. 1: gradual attenuation; 2: sudden attenuation toward distal end.
16. Shape of the dorsal crest of the maxilla. 1: triangular; 2: square with a knob on the dorsal surface; 3: square.
17. Anterior lateral plate of maxilla. 1: wide; 2: narrow.
18. Posterior lateral plate of maxilla. 1: narrow; 2: wide.
19. Rostral process of maxilla. 1: long and slender; 2: short and robust.
20. Position of anterolateral foramen on dentary. 1: medial along the length of the dentary; 2: within the anterior 1/3 of the dentary; 3: within the posterior 1/3 of the dentary.
21. Size of anterolateral foramen on dentary. 1: small; 2: large.
22. Length of dentary. 1: long; 2: short.

23. Coronoid process. 1: upright; 2: sloping posteriorly.
24. Shape of apex of coronoid process. 1: flat; 2: rounded; 3: notched.
25. Shape of the coronoid process. 1: medially constricted; 2: of uniform width.
26. Angular. 1: long and slender; 2: short and broad.
27. Posterior socket of angular. 1: well developed; 2: weak.
28. Articular. 1: long; 2: short.
29. Sensory canals on dentary. 1: clearly visible on ventral edge; 2: not visible.
30. Posterior flange of hyomandibular. 1: extends beyond posterior edge of opercular condyle; 2: does not extend beyond posterior edge of opercular condyle.
31. Ventral ramus of hyomandibular. 1: curves anteriorly; 2: erect.
32. Lateral hyomandibular foramen. 1: within ventral 1/3 of ventral ramus; 2: within middle 1/3 of ventral ramus.
33. Posterodorsal condyle of hyomandibular. 1: notched; 2: without notch.
34. Position of anterodorsal condyle of hyomandibular. 1: dorsal to level of opercular condyle; 2: ventral to level of opercular condyle.
35. Anterior wing of hyomandibular. 1: broad; 2: narrow.
36. Anterior wing of hyomandibular. 1: arises along entire length of ventral ramus; 2: does not arise along entire length of ventral ramus.
37. Urohyal. 1: ventral plate pointed posteriorly; 2: ventral plate not pointed posteriorly; 3: ventral plate small.
38. Urohyal. 1: dorsal plate extends beyond posterior edge of ventral plate; 2: dorsal plate does not extend beyond posterior edge of ventral plate.
39. Urohyal. 1: foramen basal to anterior arms; 2: no foramen present.
40. Urohyal. 1: anterior arms separated by deep notch; 2: anterior arms not separated by deep notch.
41. Pharyngeal teeth. 1: 2-4-4-2; 2: 1-4-4-1; 3: 0-4-4-0.
42. Dentigerous plate of pharyngeal arch. 1: wide; 2: narrow.
43. Frenum. 1: present; 2: absent.
44. Pelvic girdle. 1: basipterygium large and robust; 2: basipterygium small.
45. Pelvic girdle. 1: medial ischiadic processes small; 2: medial ischiadic processes prominent.
46. Pelvic girdle. 1: anterior processes of basipterygium broad; 2: anterior processes of basipterygium narrow.
47. Pectoral girdle. 1: lateral plate on vertical ramus of cleithrum small; 2: lateral plate on vertical ramus of cleithrum large.
48. Pectoral girdle. 1: foramen scapulae large; 2: foramen scapulae small.
49. Pectoral girdle. 1: coracocleithral foramen absent; 2: coracocleithral foramen present.
50. Pectoral girdle. 1: mesocoracoid with broad articular surface with scapula; 2: mesocoracoid with narrow articular surface with scapula.
51. Pectoral girdle. 1: mesocoracoid broad; 2: mesocoracoid slender.
52. Post-cleithrum. 1: present; 2: absent.
53. Adductor mandibulae muscle. 1: muscle fibres of A_1 anterior and A_1 posterior parallel and virtually indistinguishable from each other; 2: muscle fibres of A_1 anterior and A_1 posterior clearly distinguishable and fibres of A_1

- anterior slip under fibres of A_1 posterior; 3: muscle bundle of A_1 anterior runs over the A_1 posterior.
54. Tendons of Adductor mandibulae. 1: tendons of A_1 anterior and A_1 posterior insert on dorsal crest of maxilla adjacent to each other; 2: tendon of A_1 anterior inserts into musculature of A_1 posterior dorsally; 3: tendon of A_1 anterior runs over A_1 posterior and inserts on dorsal crest of maxilla.

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