

Morphological Variation of the Palatal Organ and Chewing Pad of Catostomidae (Teleostei: Cypriniformes)

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ABSTRACT We studied the morphology and shape variation of the palatal organ and chewing pad of sucker fishes, family Catostomidae. The palatal organ is a muscularized structure that forms a large mass on the roof of the posterior part of the buccopharyngeal cavity in cypriniform fishes. It functions in coordination with the branchial arches to separate food items from inorganic debris during feeding. The palatal organ exhibits considerable variability in morphology among catostomids. It is shorter, narrower, and thinner in species of the subfamily Cycleptinae (e.g., *Cycleptus elongatus*) than in other catostomid subfamilies. The thickest and widest palatal organ is seen in species of the subfamily Ictiobiinae (e.g., *Ictiobus cyprinellus*). The shape and size of the palatal organ generally varies between these extremes in species of subfamily Catostominae (e.g., *Catostomus* and *Moxostoma* species). Principal components analysis and analysis of variance has differentiated means of various palatal organ measurements for each monophyletic subfamily and tribe of Catostomidae with statistical significance. These results corroborate previously established typological classification of catostomids based on pharyngeal tooth count, pharyngeal tooth morphology, and diet. A keratinized chewing pad forms on the posterior surface of the palatal organ in catostomids or on a skeletal process in cyprinids and serves as an occlusion surface for pharyngeal teeth. The chewing pad is lunate in catostomids and generally ovoid in cyprinids. It is absent from the species of loaches (e.g., botiids, cobitids, and nemacheilids) and gyriinocheilids examined. A synonymy of terms used in the past to describe the palatal organ and chewing pad of Cypriniformes is provided. *J. Morphol.* 272:1092–1108, 2011. © 2011 Wiley-Liss, Inc.

KEY WORDS: buccopharyngeal cavity; Cyprinidae; feeding structures; pharyngeal pad

INTRODUCTION

The Cypriniformes are a diverse group of freshwater fishes with 3,268 species classified in about 350 genera in nine families (Nelson, 2006; Mayden et al., 2009). The buccopharyngeal cavity is important for seizure, retention and transport of food items (Kapoor et al., 1975), and because cypriniforms lack oral and palatal teeth, all mastication of food items occurs in the pharyngeal region (Vandewalle et al., 2000). The palatal organ (PO) is a muscular pad that forms the roof of the anterior pharynx in cypriniform fishes. Generally, it is cordate or sub-rectangular in shape, usually wider anteriorly

and narrower posteriorly (Fig. 1). A histological study of the PO in the sucker, *Catostomus catostomus*, indicated that it is composed of striated muscle, adipose and connective tissues, and collagen fibers (Weisel, 1962). The surface is composed of stratified epithelium (Sibbing, 1986) and numerous taste buds in the carp, *Cyprinus carpio*. The osteological structure of the PO comprises four pairs of pharyngobranchials and four pairs of epibranchials anteriorly, and the pharyngeal process of the basioccipital bone posteriorly (Weisel, 1960; Eastman, 1977; Sibbing and Uribe, 1985). The PO extends below from the posterior portion of the parasphenoid bone to the pharyngeal process of the basioccipital (Willink, 2002). In the cyprinid *Carassius auratus*, the PO begins to form at 6 mm total length and is adult-like at 9 mm (Lamb and Kiyohara, 2005).

The PO functions in separating food items from inorganic debris during feeding (Sibbing, 1986; 1988; Willink, 2002). This is especially important in benthic suction feeding fishes such as catostomids (Willink, 2002) and some cyprinids (Osse et al., 1997; Sibbing, 1988) that intake substrate with prey, and the PO is generally larger in species of these groups. Contractions of striated muscles in the PO form localized bulges, which restrict the pharyngeal cavity except for spaces between the PO and the gill rakers (Sibbing and Uribe, 1985). The bulges of the PO pins food items against the gill rakers and then small waste particles, inorganic material, and water are flushed out of the cavity through the operculums. Food items are transported to the posterior pharynx for

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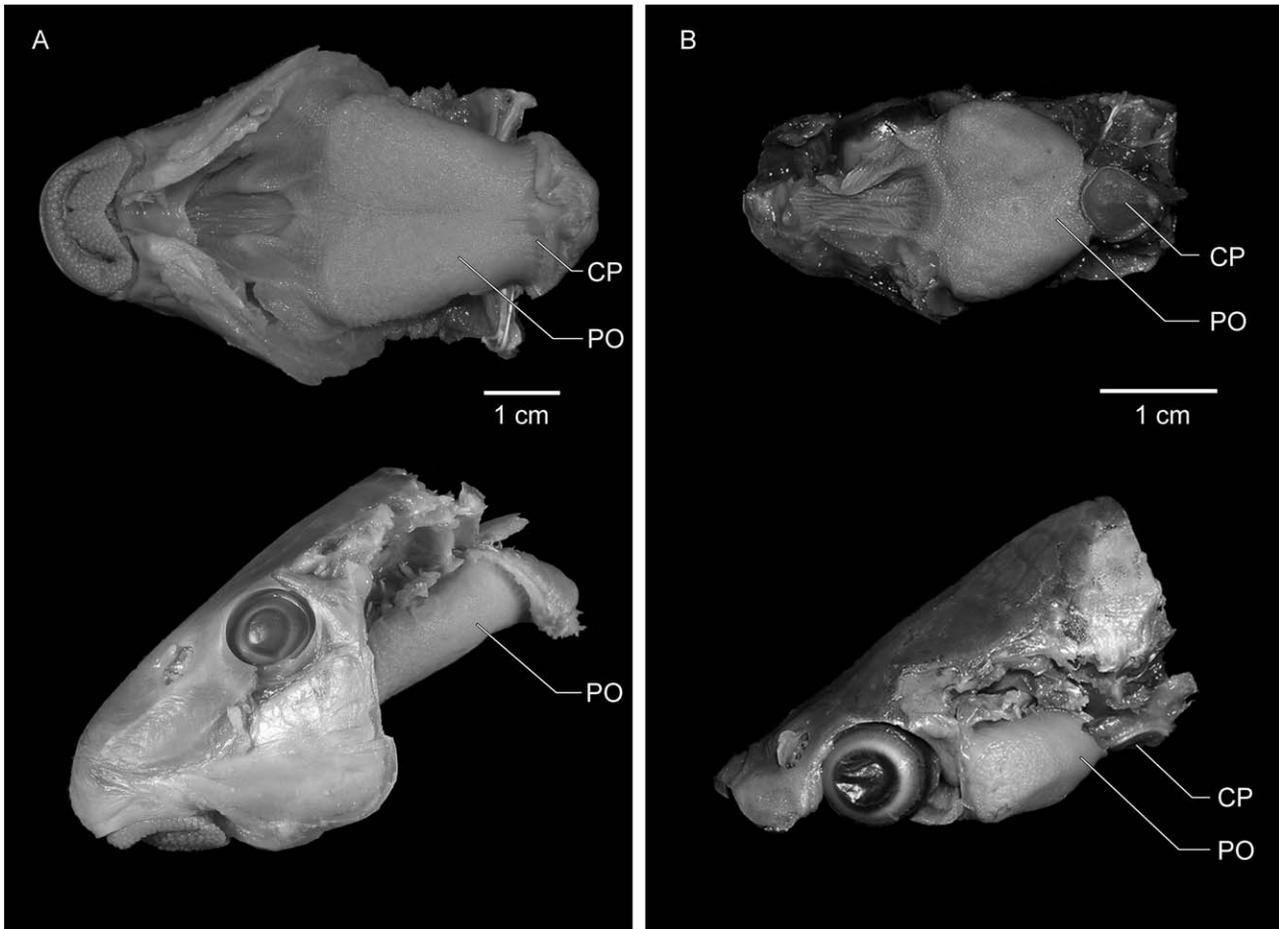


Fig. 1. Dorsal parts of heads illustrating the palatal organ (PO) and chewing pad (CP) in ventral view (top) and lateral view (bottom). Operculums and pharyngeal arches have been removed from both specimens and jaws have been removed from B. **A:** *Catostomus occidentalis* TU 47294. **B:** *Carassius auratus* TU 30624.

mastication by coordinated muscular contractions between the PO and the postlingual organ (Sibbing, 1988).

The chewing pad (CP) is a keratinized structure located at the posterior end of the PO. The pharyngeal teeth grind against the CP to masticate food items. In cyprinids, the CP attaches directly to the ventral surface of the pharyngeal process of the basioccipital bone (Howes, 1991). The shape of the CP varies, but is generally ovoid or lozenge-shaped in cyprinids (Fig. 1B). In Catostomidae, the CP is lunate (Fig. 2A) and the lateral margins extend dorsally around the PO (Eastman, 1977). The CP of Catostomidae and Cyprinidae are similar histologically (Willink, 2002).

Family Catostomidae (suckers) is a group of predominantly large-bodied, benthic cypriniforms native to lotic and lacustrine habitats of North America and Asia (Smith, 1992). Suckers are generally benthic feeders with inferior mouths and thick, fleshy, plicate or papillose lips. Most catostomids feed on benthic macroinvertebrates, plant

material, algae, or zooplankton, but a few species are midwater planktivores (Jenkins and Burkhead, 1994). Two extant suckers, *Moxostoma carinatum* and *M. hubbsi*, and the extinct species *M. lacerum* are specialized mollusk feeders (Jenkins and Burkhead, 1994; Fink and Humphries, 2010). Catostomidae has 72 described and several undescribed species grouped into four subfamilies and 13 genera: Myxocyprininae (*Myxocyprinus asiaticus*), Ictiobinae (*Carpiodes*, 3 species; *Ictiobus*, 5 spp.), Cycleptinae (*Cycleptus* 2 spp.), and Catostominae (*Catostomus*, 24 spp.; *Chasmistes*, 4 spp.; *Deltistes luxatus*; *Erimyzon*, 3 spp.; *Hypentelium*, 3 spp.; *Minytrema melanops*; *Moxostoma*, 21 spp.; *Thoburnia*, 3 spp.; *Xyrauchen texanus*) (Nelson, 2006). The monophyly of the family has been firmly established by phylogenetic analysis of diverse character sets (Doosey et al., 2010; Harris and Mayden, 2001; Smith, 1992). There are two major clades of catostomids, one is a monophyletic Catostominae, and the other contains the three remaining subfamilies with the following relation-

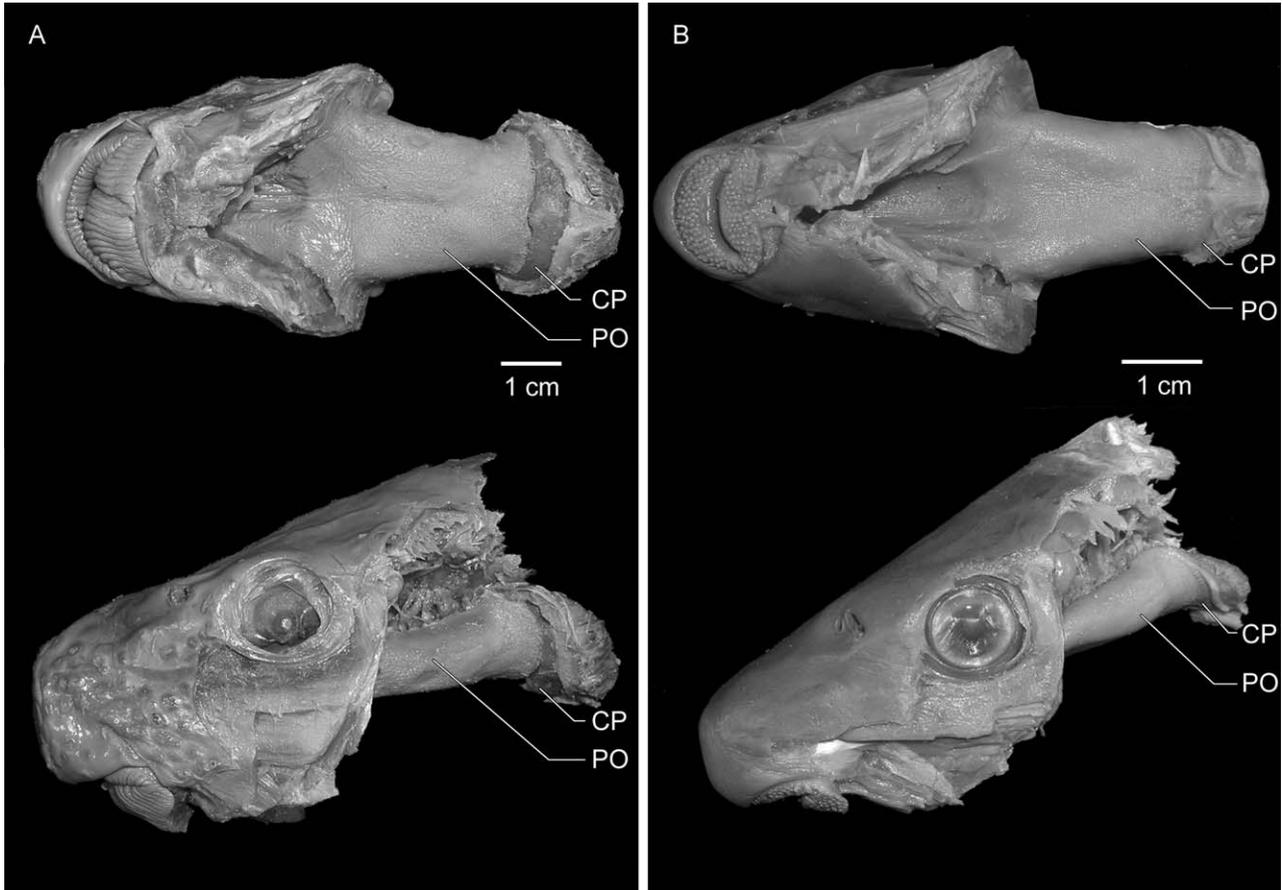


Fig. 2. Dorsal parts of heads illustrating the palatal organ (PO) and chewing pad (CP) in ventral view (top) and lateral view (bottom). Operculums and pharyngeal arches have been removed. **A:** *Moxostoma carinatum* TU 40354. **B:** *Cycleptus elongatus* TU 36949.

ships: (Cycleptinae, (Myxocyprininae, Ictiobinae)) (Doosey et al., 2010). Within the Catostominae the relationships of the tribes are as follows: (Erimyzonini, (Catostomini, (Thoburniini, Moxostomatini))) (Doosey et al., 2010).

The primary purpose of this study is to elucidate shape variation of the PO in species of family Catostomidae. We describe for the first time morphological variation of the PO and CP in catostomid fishes and make comparisons of these structures among the subfamilies and tribes of suckers. We also compare catostomid PO and CP morphology with members of other cypriniform families including Cyprinidae, Gyriinocheilidae, Botiidae, Cobitidae, and Nemacheilidae. We provide a synonymy to standardize terminology used to describe the PO and CP. Lastly, we compare our results with Eastman's (1977) typological classification of catostomids based on pharyngeal tooth count, pharyngeal tooth morphology, and feeding ecology.

MATERIAL AND METHODS

Palatal organ morphology was studied in all genera and 51 species of catostomids (Table 1). Members of the cypriniform

families Botiidae, Cyprinidae, Cobitidae, Gyriinocheilidae, and Nemacheilidae were studied to determine the morphological variation among cypriniform fishes and for comparison with catostomids. Members of the ostariophysan families Chanidae, Anostomidae, Characidae, Curimatidae, Ictaluridae, and Gymnotidae were studied for outgroup comparisons. Dissections were performed on formalin fixed and alcohol preserved specimens for study of the PO and CP and a list of material examined is in Appendix. Standard length (SL), head length (excluding the opercular membrane), head width, and body depth were measured following Hubbs and Lagler (1958). The PO and CP were studied with the aid of a Leica M205 C microscope. Digital photographs were made with a Nikon CoolPix digital camera.

Subdivisions of the buccopharyngeal cavity follow Sibbing et al. (1986), whereby the anterior pharynx is the region of the gill arches and PO and the posterior pharynx is the region occupied by the CP. Four measurements were made to the nearest 0.01 mm with digital calipers to represent the general shape (length, width, and depth) and size of the PO in catostomids (Fig. 3), and how shape and size varies among species. Descriptive statistics, analysis of variance (ANOVA), and principal components analysis (PCA) were computed with Minitab 15 (Minitab Incorporated, State College, Pennsylvania). Each of the measurements was regressed on SL, which was used as a size estimator. Residuals were retained and submitted to ANOVA to test for differences among subfamilies and tribes of Catostomidae. Tukey's method was used to test all pairwise differences among group means and the family error rate was set at 0.05. The confidence intervals computed for each pair indicate signifi-

TABLE 1. List of catostomid species used in the study of the palatal organ (PO) and means of various measurements expressed as thousandths of standard length

Species	n	L	GW	LW	D
<i>Carpionodes carpio</i>	7	0.123	0.120	0.059	0.064
<i>Carpionodes velifer</i>	9	0.117	0.125	0.060	0.072
<i>Catostomus ardens</i>	4	0.096	0.101	0.058	0.039
<i>Catostomus catostomus</i>	5	0.094	0.096	0.056	0.024
<i>Catostomus clarkii</i>	6	0.086	0.089	0.051	0.020
<i>Catostomus columbianus</i>	5	0.089	0.089	0.055	0.033
<i>Catostomus commersonii</i>	8	0.091	0.091	0.057	0.028
<i>Catostomus discobolus</i>	5	0.093	0.084	0.051	0.017
<i>Catostomus insignis</i>	9	0.098	0.102	0.062	0.031
<i>Catostomus latipinnis</i>	10	0.091	0.096	0.060	0.029
<i>Catostomus macrocheilus</i>	3	0.095	0.102	0.064	0.038
<i>Catostomus occidentalis</i>	3	0.090	0.091	0.056	0.031
<i>Catostomus plebeius</i>	10	0.091	0.090	0.049	0.021
<i>Catostomus tahoensis</i>	6	0.096	0.098	0.055	0.029
<i>Chasmistes liorus mictus</i>	6	0.104	0.108	0.051	0.040
<i>Cycleptus elongatus</i>	6	0.070	0.057	0.040	0.017
<i>Deltistes luxatus</i>	3	0.085	0.092	0.043	0.032
<i>Erimyzon oblongus</i>	5	0.086	0.098	0.057	0.043
<i>Erimyzon sucetta</i>	4	0.101	0.107	0.058	0.057
<i>Erimyzon tenuis</i>	10	0.097	0.088	0.051	0.042
<i>Hypentelium etowanum</i>	4	0.130	0.115	0.070	0.028
<i>Hypentelium nigricans</i>	13	0.114	0.109	0.063	0.030
<i>Ictiobus bubalus</i>	7	0.119	0.119	0.074	0.074
<i>Ictiobus cyprinellus</i>	2	0.127	0.128	0.068	0.073
<i>Ictiobus niger</i>	4	0.120	0.122	0.073	0.072
<i>Minytrema melanops</i>	8	0.107	0.101	0.058	0.040
<i>Moxostoma anisurum</i>	9	0.100	0.097	0.062	0.040
<i>Moxostoma ariommum</i>	1	0.083	0.082	0.058	0.022
<i>Moxostoma breviceps</i>	7	0.086	0.068	0.051	0.022
<i>Moxostoma carinatum</i>	7	0.090	0.083	0.065	0.030
<i>Moxostoma cervinum</i>	2	0.082	0.080	0.046	0.023
<i>Moxostoma collapsum</i>	1	0.106	0.091	0.052	0.033
<i>Moxostoma congestum</i>	8	0.093	0.093	0.064	0.035
<i>Moxostoma duquesnii</i>	8	0.084	0.090	0.059	0.037
<i>Moxostoma erythrurum</i>	7	0.093	0.097	0.061	0.042
<i>Moxostoma hubbsi</i>	2	0.093	0.083	0.058	0.026
<i>Moxostoma lachneri</i>	8	0.088	0.087	0.061	0.029
<i>Moxostoma macrolepidotum</i>	2	0.075	0.071	0.056	0.023
<i>Moxostoma pappillosum</i>	9	0.095	0.095	0.064	0.035
<i>Moxostoma poecilurum</i>	8	0.090	0.095	0.061	0.034
<i>Moxostoma robustum</i>	1	0.066	0.073	0.055	0.027
<i>Moxostoma rupiscartes</i>	1	0.067	0.072	0.051	0.023
<i>Moxostoma</i> sp. "Apalachicola redhorse"	3	0.079	0.091	0.060	0.033
<i>Moxostoma</i> sp. "brassy jumprock"	2	0.083	0.084	0.072	0.030
<i>Moxostoma</i> sp. "sickle fin redhorse"	4	0.078	0.074	0.046	0.028
<i>Moxostoma valenciennesi</i>	3	0.099	0.096	0.061	0.040
<i>Myxocyprinus asiaticus</i>	1	na	na	na	na
<i>Thoburnia atripinnis</i>	4	0.078	0.092	0.056	0.028
<i>Thoburnia hamiltoni</i>	4	0.072	0.073	0.048	0.016
<i>Thoburnia rhothoeca</i>	5	0.080	0.084	0.050	0.023
<i>Xyrauchen texanus</i>	1	0.096	0.088	0.048	0.025

n, sample size; L, length of PO lobe; GW, PO greatest width; LW, PO least width; D, PO depth.

cant differences in means if the interval does not include zero. Principal components analysis was performed on the residual variables to summarize and graphically represent variance in PO shape among catostomid subfamilies and tribes. Results of PCA were used to determine if the morphological variation of the PO was correlated with the evolutionary history of catostomids and if PO shape could be generalized for each subfamily and tribe. Principal component scores were calculated and group scatterplots for descriptive factors were produced. Structure (i.e., clusters of data points) was identified in the scatterplots and interpreted in terms of the variables contributing to separation of the clusters (i.e., exhibiting high positive or negative loadings on PC axes).

SYNONYMY OF THE PALATAL ORGAN AND CHEWING PAD

Morphological studies can be confused by the variety of names that are sometimes applied to particular structures. Thus, it is important to establish standard terminology for the structures, just as it is to develop synonymies of taxonomic names in revisionary studies. Standard terminology and synonymy for feeding structures in the dorsal pharyngeal region of Cypriniformes is herein pro-

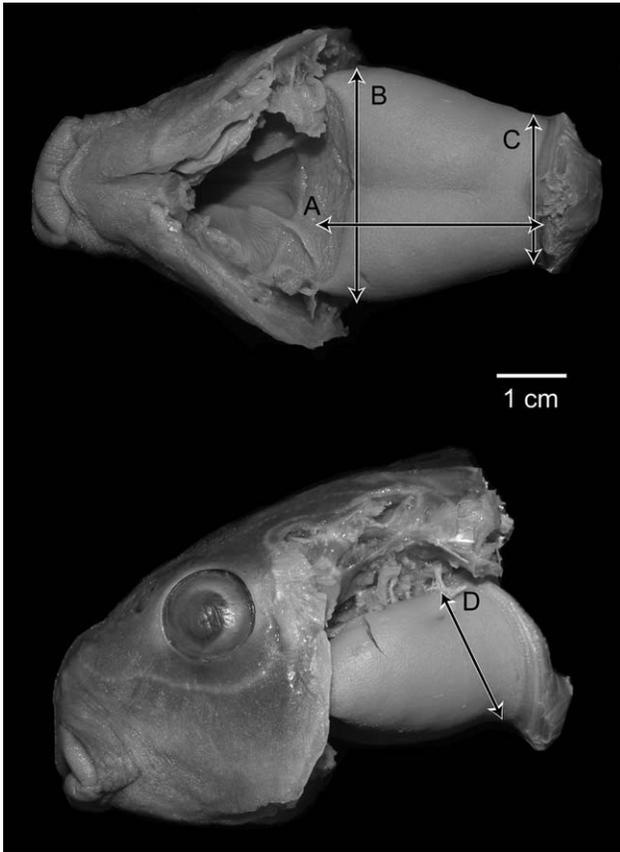


Fig. 3. Dorsal parts of the head of *Ictiobus bubalus* TU 163467 illustrating measurements of the palatal organ (PO) in ventral view (top) and lateral view (bottom). Operculums and pharyngeal arches have been removed. A, lobe length; B, greatest width; C, least width; D, depth.

posed. Because no rules exist for establishing priority of anatomical nomenclature, priority is given to names that are descriptive and have had consistent proper usage in the literature.

The term palatal organ should be used to describe the muscular pad on the dorsal surface of the pharynx that opposes the branchial basket in cypriniform fishes. The term palatal organ is chosen because it is among the earliest and most consistently applied names in the literature (Table 2). The name is appropriate because of its position on the dorsal pharynx anterior to esophagus. The name "palatal" was probably originally used because of the analogy of the area of the pharynx where the structure occurs with the tetrapod hard palate or because it lies dorsally.

Aristotle in his *Parts of Animals* (circa 350 BC) was the first to describe the PO, referring to a structure he observed in the common carp, *Cyprinus carpio* (Ogle, 1882). He wrote that the palate "is so very flesh-like and soft as to be taken by careless observers for a tongue" (Ogle, 1882). Aristotle did not give a name to the PO but speculated

on its gustatory function. In 1554, Rondelet noted that the structure was a substitute for a tongue in *C. carpio* (Cole, 1944). Weber (1827) described the gustatory function of the PO in *C. carpio* and named it *Geschmacksorgan*, which translates literally to "taste organ." Valatour (1861) was the first to use the term PO, or *organe palatin*, as he termed it, and also commented on the structure and function of the organ in *C. carpio*. Valatour (1861) noted that Cuvier considered the structure to be a gland. Owen (1866) wrote in his classic anatomy text: "In the cyprinoids (= Cyprinidae) the palate is cushioned with a thick soft vascular substance...remarkable for its irritable or contractile property." Girgis (1952a; b) made reference to the structure as the "palatal organ of Valatour." The use of PO for description of cypriniform pharyngeal anatomy became nearly uniform in the mid-1960s.

The term chewing pad should be applied to the keratinized or cornified pad that is either on the surface of the PO or attached directly to the basioccipital bone of cypriniform fishes. The studies of Eastman (1971) and Sibbing (1982) are followed in proposing this terminology. A synonymy for terms referring to the CP of cypriniform fishes is provided in Table 3. Owen (1866) was first to write about the CP of cypriniforms. His utilization of "pharyngeal grinding tooth" was inaccurate because the CP is not tooth-like, in that it is composed of keratinized epithelial cells (Curry, 1939). Regan (1911) was presumably the first author to use the term "horny pad" to describe pharyngeal structures he noted as occurring in members of the Cyprinidae. Eastman (1971) may have been the first to use chewing pad, and this is the terminology that is used most frequently in contemporary literature.

RESULTS

In general, the PO of catostomids is widest anteriorly (averaging 9.6% SL) and narrows towards the posterior (5.8% SL). The mean overall length of the PO averages roughly 12% SL, the length of the lobe averages 10% SL, and the mean depth averages 3.6% SL, but these values vary greatly among species. The ratio of the mean lobe length to the mean greatest width of the PO is nearly equal (1.004:1.000); however, the means of the measurements expressed as per cent of standard length overlap considerably among catostomid species (Table 1). Four discrete characters were identified to describe the PO of catostomids and cyprinids: 1) the occurrence of a median groove that fully or partially divides the PO into symmetrical lobes; 2) the occurrence of a U-shaped notch near the junction of the buccal and pharyngeal cavities; 3) the occurrence and condition of the pair of anterior projections (pointed or knobbed) on the U-

TABLE 2. Synonymy of terms and phrases used to describe the palatal organ of cypriniform fishes (¹Catostomidae, ²Cyprinidae, ³Cobitidae)

Name or description	Taxa	Source
<i>Geschmacksorgan</i>	<i>Cyprinus carpio</i> ²	Weber, 1827
<i>organe palatin</i>	<i>Cyprinus carpio</i> ²	Valatour, 1861
Palatal organ of Valatour	<i>Cyprinus carpio</i> ²	Curry, 1939
Palatal organ	<i>Cyprinus carpio</i> ²	Jara, 1957
	<i>Carpiodes velifer</i> ¹	Miller and Evans, 1965
	<i>Cobitis taenia</i> ³	
	<i>Cobitis elongata</i> ³	
	<i>Misgurnus fossilis</i> ³	
	<i>Sabanejewia romanica</i> ³	Mester, 1973
	Catostomidae	Eastman, 1977
	<i>Pseudorasbora parva</i> ²	Kiyohara et al., 1980
	<i>Orthodon microlepidotus</i> ²	Sanderson et al., 1991
	<i>Aristichthys nobilis</i> ²	Liu et al., 1992
	<i>Abramis brama</i> ²	Hoogenboezem, 2000
	<i>Cirrhinus mrigala</i> ²	Yashpal et al., 2009
Muscular cushion	<i>Cirrhinus mrigala</i> ²	Majumdar, 1951
Pharyngeal pad	<i>Labeo horie</i> ²	Girgis, 1952a,b
	<i>Catostomus macrocheilus</i> ¹	Weisel, 1960
	<i>Ptychocheilus oregonensis</i> ²	Weisel, 1962
	Cyprinidae	Matthes, 1963
	<i>Carassius carassius</i> ²	Nakao et al., 1984
Thick pad of connective tissue	<i>Cycleptus elongatus</i> ¹	Branson, 1962
Large, thick pad of connective tissue and epithelium		
	Catostomidae	Jenkins, 1970
Supra-pharyngeal pad	<i>Salmostoma bacaila</i> ²	Singh and Singh, 1973
Palatine organ	<i>Carassius auratus</i> ²	King, 1975
Pharyngeal cushion	Cyprinidae	Reid, 1982
Posterior papillose pad	<i>Cobitis taenia</i> ³	Robotham, 1982

shaped notch; 4) the occurrence of a transverse shelf at the anterior end of the PO.

Morphological Variation of the Palatal Organ in Catostomids

Subfamily Cycleptinae. The PO of Cycleptinae was studied in *Cycleptus elongatus*. The anterior portion of the PO is concave and the surface flattens posteriorly (Fig. 2B). The PO of *Cycleptus elongatus* lacks a median groove, U-shaped notch, and transverse shelf, and has an extremely shallow depth that is only 1.7% SL, which is significantly shallower than the PO in other groups of suckers. The roof of the buccal cavity has a deep furrow. *Cycleptus elongatus* has an extremely

small head relative to its elongated body. Mean head length and width is 18.3% and 12.0% of SL, respectively, which makes it the smallest head among the catostomids studied. Comparisons of means of four PO measurements among subfamilies reveal that Cycleptinae has a significantly smaller PO than any of the other groups of suckers (Fig. 4A). Cycleptinae is monophyletic and sister to Myxocyprinae and Ictiobinae (Dosey et al., 2010). The small size of the cycleptine PO is a specialization of the subfamily that seems to be correlated with its small head size.

Subfamily Myxocyprinae. Only a single juvenile (67 mm SL) *Myxocyprinus asiaticus* was available for study of the PO. The anterior portion

TABLE 3. Synonymy of terms used to describe the chewing pad of cypriniform fishes (Catostomidae,¹ Cyprinidae²)

Name or description	Taxa	Source
Pharyngeal grinding tooth	<i>Cyprinus carpio</i> ²	Owen, 1866
Horny pad	Cyprinidae	Regan, 1911
	<i>Mylopharyngodon piceus</i> ²	Liu et al., 1990
Callous pad	<i>Campostoma anomalum</i> ²	Rogick, 1931
	<i>Mylopharyngodon piceus</i> ²	Zhai et al., 1988
Cornified pad	<i>Cyprinus carpio</i> ²	Curry, 1939
	<i>Ptychocheilus oregonensis</i> ²	Weisel, 1962
A "firm" or "hard" pad embedded in soft tissue		
	<i>Moxostoma carinatum</i> ¹ , <i>Moxostoma hubbsi</i> ¹	Jenkins, 1970
Chewing pad	<i>Cyprinus carpio</i> ²	Eastman, 1971
	Catostomidae	Eastman, 1977
	<i>Cirrhinus mrigala</i> ²	Yashpal et al., 2009
Masticatory pad	<i>Schizothorax richardsonii</i> ²	Dixit and Bisht, 1972
Pharyngeal pad	<i>Carassius auratus</i> ²	King, 1975
Keratinized pad	Cyprinidae	Howes, 1991

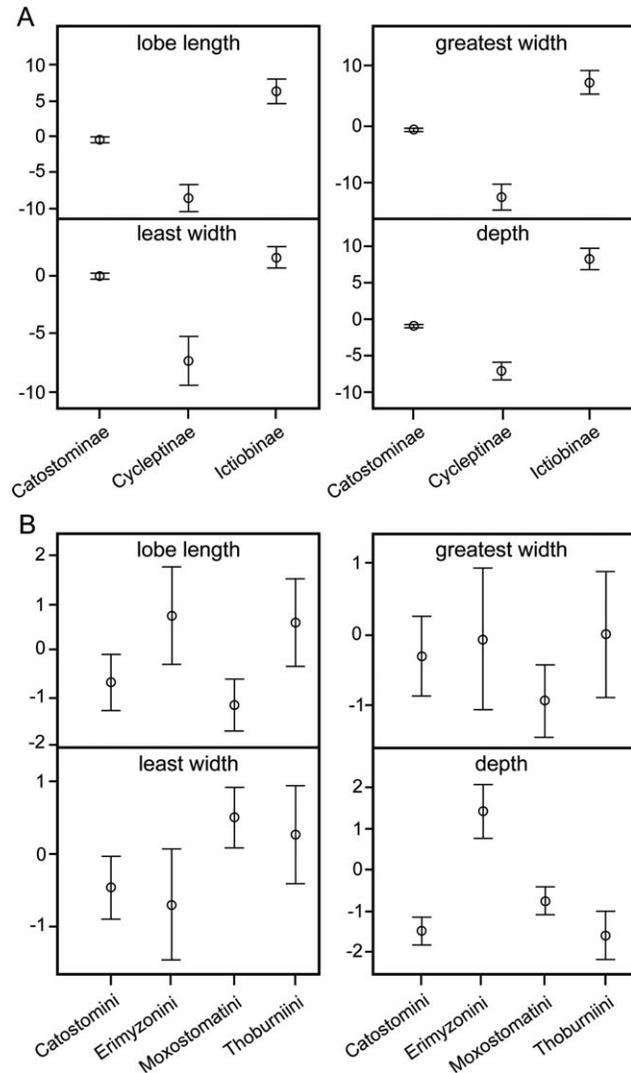


Fig. 4. Plots of means (circle) and 95% confidence limits (bar) of the residuals for four PO measurements illustrate shape variation among the taxonomic groups. **A:** Subfamilies of family Catostomidae. **B:** Tribes of subfamily Catostominae.

of the PO is concave. The median groove is not deeply incised, but instead forms a wide valley. Similar to *Cycleptus*, a U-shaped notch and transverse shelf are lacking.

Subfamily Ictiobinae. Palatal organ morphology was studied in five species of Ictiobinae. In general, ictiobines have the thickest (7.2% SL) and widest (12.3% SL) PO of all catostomid subfamilies. Comparisons of means of four PO measurements among subfamilies reveal that Ictiobinae has a significantly larger PO than any of the other groups of suckers (Fig. 4A). All of the species examined have a U-shaped cleft, a long median groove, and transverse shelf. All species lack projections on the U-shaped cleft. The PO is thicker in *Ictiobus* compared to *Carpiodes* when expressed as a ratio, 7.6% SL and 6.9% SL, respectively. The

depth is not significantly different between the two genera when the regression residuals are used as variables ($F = 0.49$, $df = 1$, $P = 0.492$). There is no difference in the means of the greatest width between *Carpiodes* and *Ictiobus* ($F = 1.32$, $df = 1$, $P = 0.260$); however, there is a difference in the means of the least width between the genera ($F = 12.97$, $df = 1$, $P = 0.001$) with *Carpiodes* having a narrower width of the posterior PO. The PO of the *Carpiodes* species examined (*C. carpio* and *C. velifer*) is bulbous and exceptionally deep (Fig. 5A). The median groove is deep and extends for nearly the entire length of the lobe of the PO. A single median papilla is present in the center of the buccal cavity. The PO is significantly deeper in *C. velifer* (7.2% SL) compared to *C. carpio* (6.4% SL; $F = 6.07$, $df = 1$, $P = 0.027$). Space in the pharyngeal lumen is extremely restricted because of the volume of the PO and its close association with the pharyngeal arches. There are no differences in means of the other PO measurements. As in *Carpiodes*, the PO is deep and bulbous in the species of *Ictiobus* studied (*I. bubalus* (Fig. 3), *I. cyprinellus*, and *I. niger*). The median groove is shallow, but it does extend for nearly the entire length of the PO. Comparisons of means of PO proportions among the three species indicate that the PO of *I. cyprinellus* is longer than that of *I. bubalus*, but not significantly longer than *I. niger* (data not shown). There is no significant difference among means of the depth of the PO in the three *Ictiobus* species. *Ictiobus cyprinellus* (14.9% SL) has a PO that is significantly wider than *I. bubalus* (11.9% SL). Ictiobinae is a monophyletic group and the genera *Carpiodes* and *Ictiobus* are also monophyletic (Smith, 1992; Doosey et al., 2010). The large and bulbous PO is a unique specialization shared by all ictiobine species studied. Some species of Erimyzonini have a thick PO, but their morphology is the result of convergence.

Subfamily Catostominae. Palatal organ morphology was studied in 44 species of catostomines. Comparisons of means of four PO measurements among subfamilies reveal that Catostominae has a PO that is of intermediate size compared to Cycleptinae or Ictiobinae (Fig. 4A). However, variation in PO morphology is so great among catostomines that it is difficult to make broad generalizations at the subfamily level, but generalizations can be made for each of the tribes (Fig. 4B). Species of Erimyzonini (9.8% SL) and Thoburniini (9.5% SL) have a significantly longer mean PO length than species of Moxostomatini (8.8% SL). Erimyzonini (4.5% SL) has the deepest PO. Thoburniini (2.5% SL) has the thinnest PO, but the mean is not significantly different than the mean of Catostomini (2.9% SL). No differences in means of width of the PO were detected among catostomine tribes. Variation in PO morphology is discussed separately for each tribe.

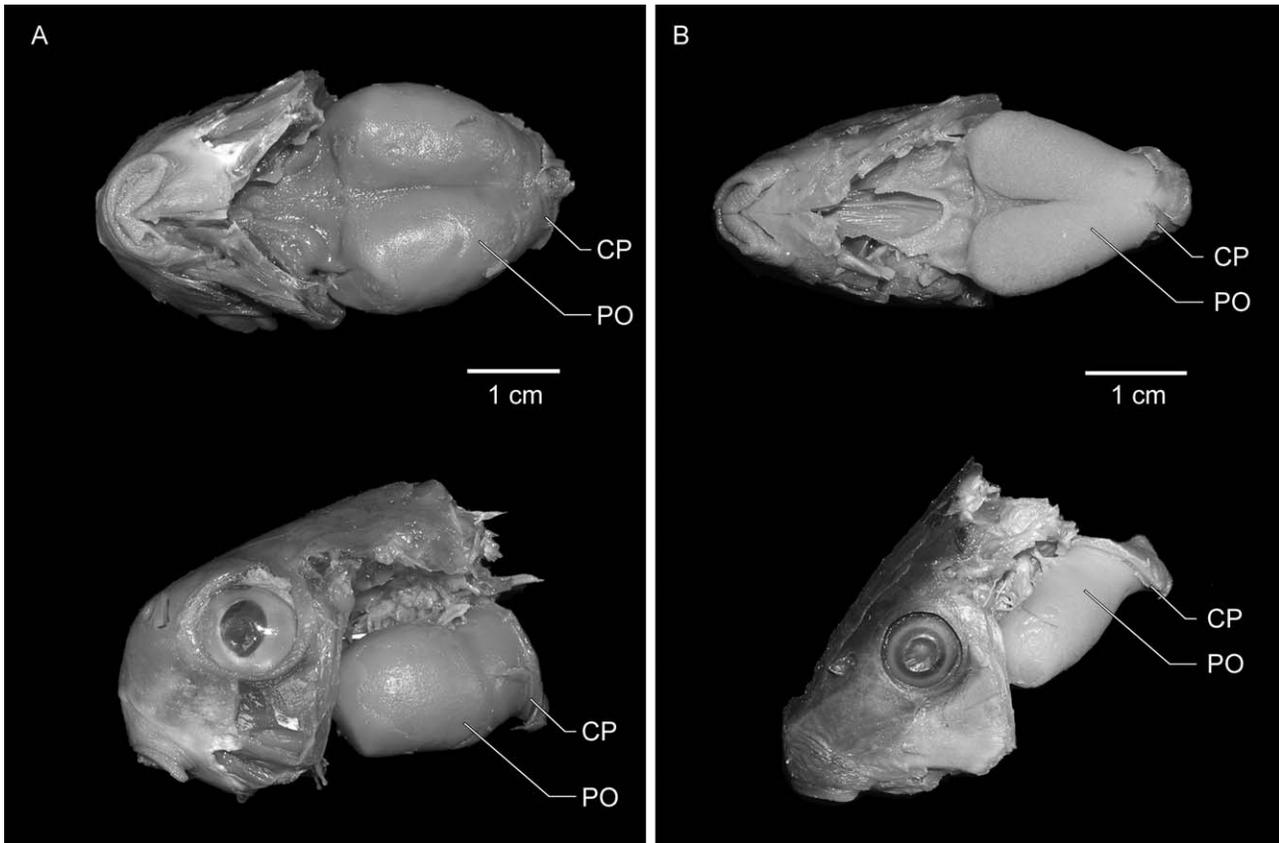


Fig. 5. Dorsal parts of heads illustrating the palatal organ (PO) and chewing pad (CP) in ventral view (top) and lateral view (bottom). Operculums and pharyngeal arches have been removed. **A:** *Carpiodes velifer* TU 15956. **B:** *Erimyzon sucetta* TU 20648.

Tribe Erimyzonini. Palatal organ morphology was studied in all four species of Erimyzonini. The PO is remarkably cordate in *Erimyzon*, especially *E. sucetta* (Fig. 5B), but less so in *Minytrema melanops*. A short median groove and transverse shelf occurs in all species. The U-shaped cleft is present in all species and the projections are pointed in *Erimyzon* and knobby in *Minytrema*. *Minytrema* has a significantly longer PO than *Erimyzon* ($F = 6.75$, $df = 1$, $P = 0.016$). *Minytrema* also has a significantly wider PO than *Erimyzon* ($F = 4.36$, $df = 1$, $P = 0.048$). Erimyzonini species have the deepest PO compared to other catostomine tribes (Fig. 4B). *Erimyzon sucetta* has a significantly deeper PO (5.7% SL) than the other two *Erimyzon* species and *Minytrema melanops*. The least width of the PO in *E. tenuis* (5.1% SL) is significantly less than that of *M. melanops* (5.8% SL).

Tribe Catostomini. Palatal organ morphology was studied in 15 species of Catostomini. In *Xyrauchen texanus*, the PO is slightly concave anteriorly and flat towards the posterior end with the median groove extending for nearly the entire length of the PO. A U-shaped notch and transverse shelf are lacking. The shape of the PO in

Deltistes luxatus is similar to *Xyrauchen*; however, the median groove is very shallow and extends about half the length of the PO. A U-shaped notch is present in *Deltistes* and the projections are pointed. The PO of *Chasmistes liorus mictus* has a similar shape to *Xyrauchen* and *Catostomus* species in general. The U-shaped notch is present with knobbed ventral projections. A median groove and transverse shelf are both absent. In general, the PO of the 12 *Catostomus* species examined is widest anteriorly (9.9% SL) and gradually narrows posteriorly (5.6% SL). Mean length of the PO lobe is 9.2% SL. *Catostomus occidentalis* is illustrated to represent the PO morphology of a typical species of *Catostomus* (Fig. 1A). There are significant differences in all PO measurements, except the least width, between *Catostomus* and *Chasmistes* (Fig. 6A). *Xyrauchen texanus* and *Deltistes luxatus* were excluded from the analysis because only one *Xyrauchen* specimen was studied and SL had to be estimated for the specimens of *Deltistes*. The PO of *Chasmistes liorus mictus* is significantly longer (10.4% SL vs. 9.2% SL), wider (10.8% SL vs. 9.4% SL), and has a greater depth (4.0% SL vs. 2.8% SL) than the means for *Catostomus* species. The

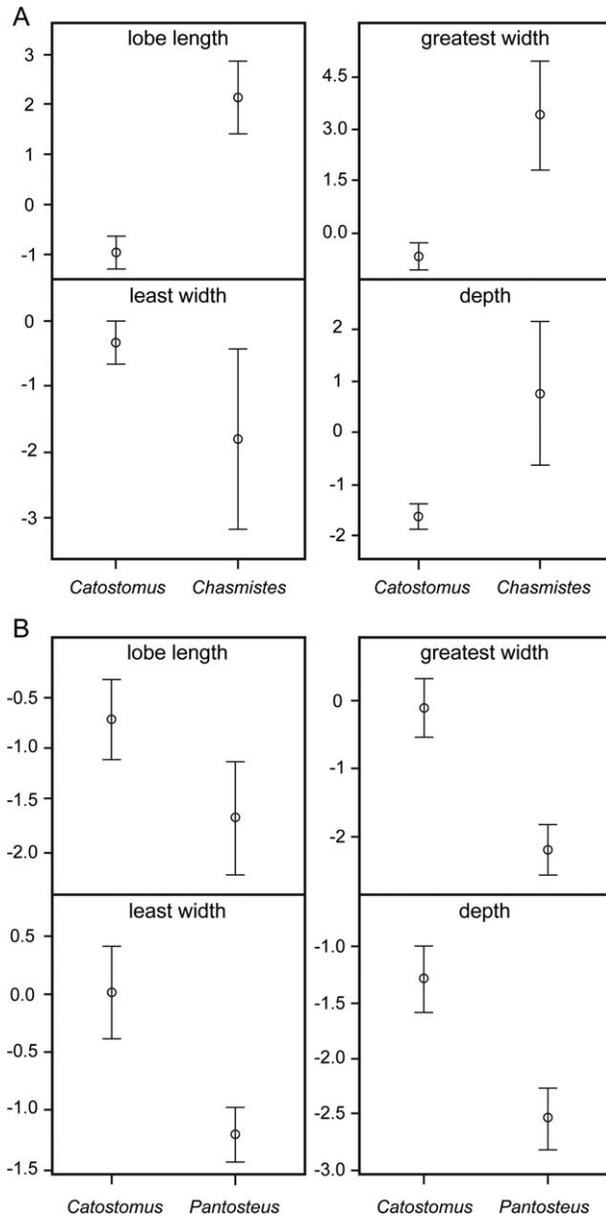


Fig. 6. Plots of means (circle) and 95% confidence limits (bar) of the residuals for four PO measurements illustrate shape variation among the taxonomic groups. **A:** Genera *Catostomus* and *Chasmistes*. **B:** Subgenera of *Catostomus*.

U-shaped notch is present with knobby projections in all *Catostomus* species examined. The median groove is present, except in species of subgenus *Pantosteus* (*C. clarkii*, *C. discobolus*, *C. plebius*), and *C. insignis*, *C. latipinnis*, *C. macrocheilus*, and *C. tahoensis*. The transverse shelf is present, except in species of subgenus *Pantosteus* and *C. occidentalis*. Within the genus *Catostomus*, there are significant differences in all PO measurements between subgenera *Catostomus* and *Pantosteus* (Fig. 6B). Species in subgenus *Catostomus* have a significantly longer (9.3% SL vs. 9.0% SL), wider

(9.6% SL vs. 8.8% SL), and deeper (3.1% SL vs. 1.9% SL) PO compared to species of subgenus *Pantosteus*. *Catostomini* is a monophyletic group; however, the genus *Catostomus* is paraphyletic because *Chasmistes*, *Deltistes*, and *Xyrauchen* are deeply nested within the *Catostomini* clade (Doosey et al., 2010). The general PO morphology of *Catostomini* genera is fairly conserved except for some size differences between genera *Catostomus/Chasmistes* and subgenera *Catostomus/Pantosteus*. It is interesting to note the significant PO size differences between subgenera *Catostomus* and *Pantosteus* because there is evidence for the monophyly of *Pantosteus* in both morphological (Smith, 1992) and molecular (Doosey et al., 2010) phylogenetic studies.

Tribe Thoburniini. Palatal organ morphology was studied in five of the six species of *Thoburniini*. The PO is very flat and the mean greatest width (11.2% SL) is nearly twice the mean of the least width (6.6% SL) in both species of *Hypentelium* examined. The length of the PO lobe in *H. etowanum* is 13.0% SL, the longest of all catostomids measured (Fig. 7B). The U-shaped notch and median groove are present. There are no projections on the U-shaped notch and the transverse shelf is lacking. In general, the PO of *Thoburnia* species is very small, even for small-bodied fishes. The PO is concave anteriorly and very thin (2.3% SL). *Thoburnia hamiltoni* has the thinnest PO of all catostomids (1.6% SL). Only *T. rhothoeca* has a U-shaped cleft and only *T. atripinnis* has a median groove. All species of *Thoburnia* lack a transverse shelf. The PO of *Hypentelium* is significantly longer (12.2% SL vs. 7.7% SL), wider (11.2% SL vs. 8.3% SL), and deeper (2.9% SL vs. 2.3% SL) than that of *Thoburnia* (Fig. 8).

Tribe Moxostomatini. Palatal organ morphology was studied in 18 species of *Moxostoma*. No other genus of suckers exhibits such a broad range of size and shape variation of the PO than *Moxostoma*. All of the species examined except for *M. ariommum* have a U-shaped notch. The presence of a notch could not be confirmed in *M. hubbsi*, *M. robustum*, *M. sp.* 'sickle fin redhorse,' or *M. sp.* 'Appalachicola redhorse' because the PO was dissected from the pharynx and slightly damaged in specimens examined of these species. All species of *Moxostoma* have a median groove in the PO except *M. ariommum* and *M. hubbsi*. The groove is usually deepest anteriorly and only extends about one-third the length of the PO lobe. The projections on the U-shaped notch are usually knobbed. These projections are absent in *M. cervinum*. The transverse shelf is present in all species except *M. ariommum*, *M. carinatum*, and *M. erythrurum*. *Moxostoma erythrurum* is illustrated to represent the PO morphology of a typical redhorse sucker (Fig. 7A). The PO morphology of a mollusk feeder is represented by *M. carinatum* (Fig. 2A). Its PO is

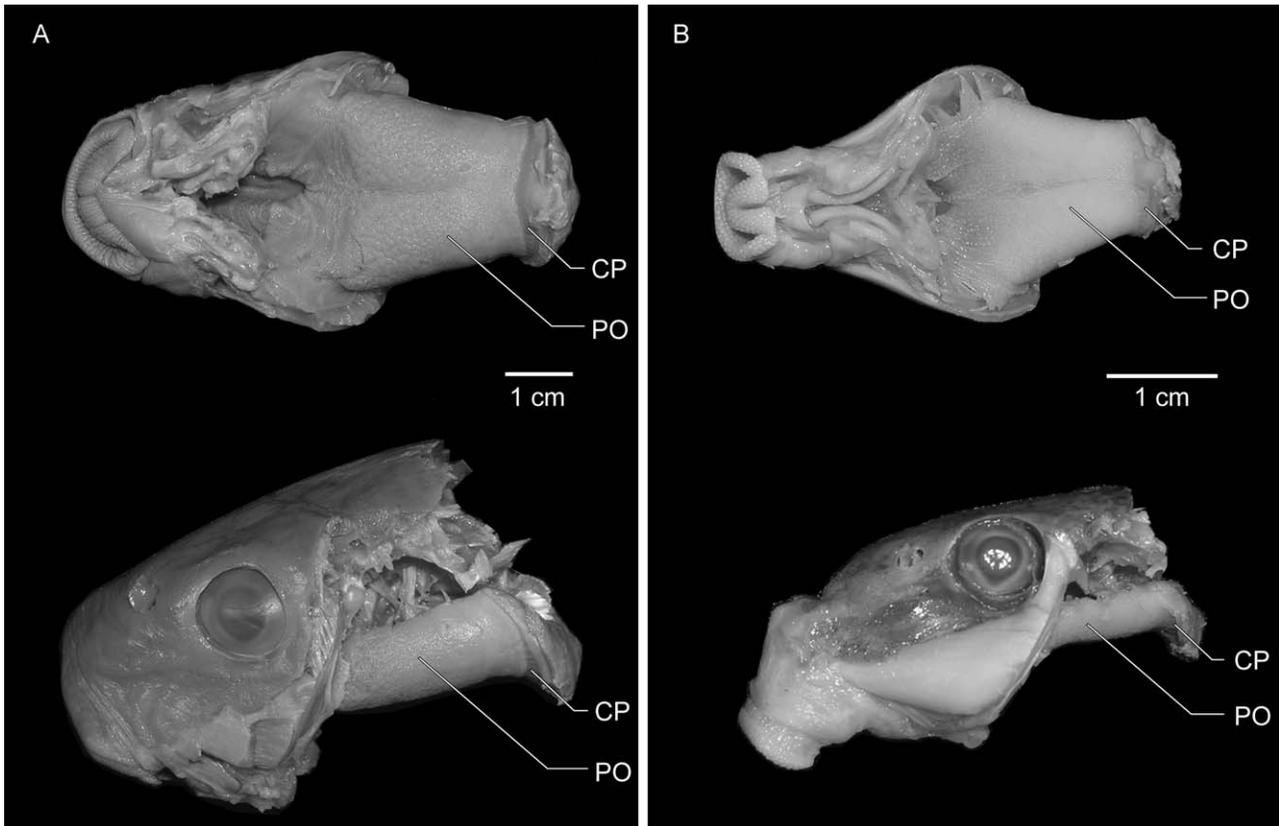


Fig. 7. Dorsal parts of heads illustrating the palatal organ (PO) and chewing pad (CP) in ventral view (top) and lateral view (bottom). Operculums and pharyngeal arches have been removed. **A:** *Moxostoma erythrurum* TU 78107. **B:** *Hypentelium etowanum* TU 176548.

very flat, and the longitudinal groove in the buccal cavity is wide, presumably to permit large and hard prey to enter the pharynx. There are significant differences in means of the PO depth and greatest width when species of *Moxostoma* are grouped by morphology of the pharyngeal teeth (molariform vs. comb-like). In the three species with molariform teeth (*Moxostoma carinatum*, *M. hubbsi*, and *M. robustum*), mean depth of the PO is 2.7% SL, whereas the PO is significantly deeper (3.2% SL) in species with flattened, comb-like pharyngeal teeth ($F = 14.77$, $df = 1$, $P < 0.001$). There was also a significant difference in the greatest PO width between these two groups. The mean greatest width is 8.8% SL and 8.0% SL for comb-like teeth and molariform teeth, respectively ($F = 8.37$, $df = 1$, $P = 0.005$).

Principal Components Analysis

In the PCA of residuals of PO shape variables for catostomid subfamilies, PC1, PC2, and PC3 accounted for 97.4% of the variation in the data (Supporting Information S-Table 1). Scatterplots of PC scores clearly delineate Cycleptinae from Ictiobinae along PC1 (Fig. 9A). Ictiobines have a much

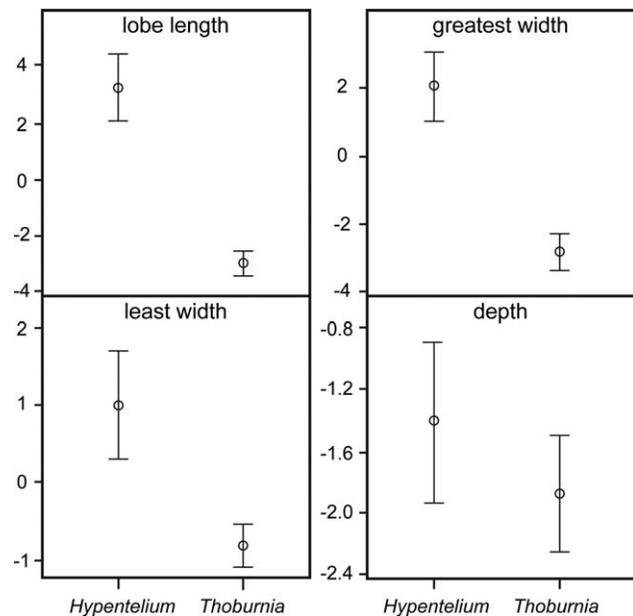


Fig. 8. Plots of means (circle) and 95% confidence limits (bar) of the residuals for four PO measurements for genera *Hypentelium* and *Thoburnia*.

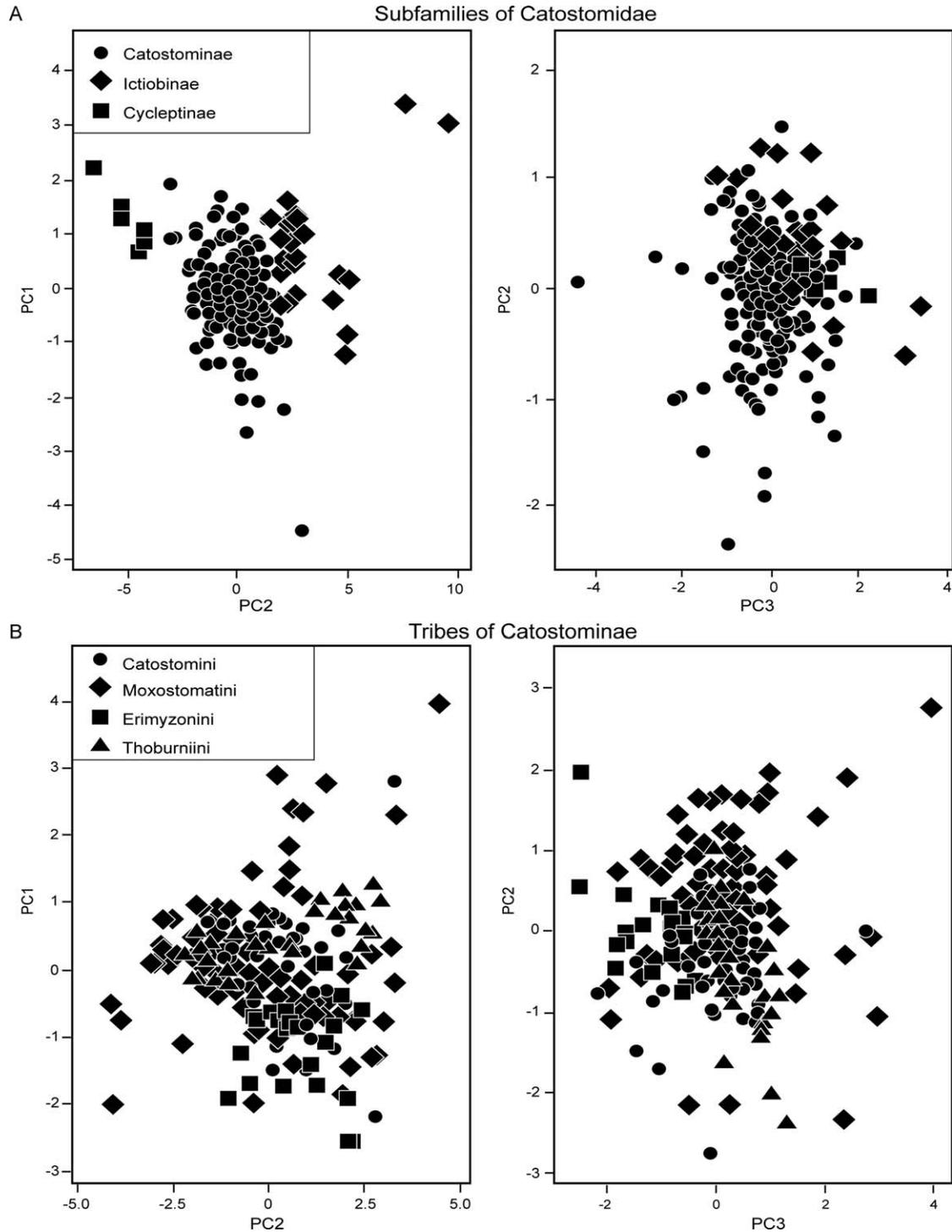


Fig. 9. PCA scatterplots illustrate change in shape of the palatal organ. **A:** Subfamilies of Catostomidae. **B:** Tribes of Catostominae.

deeper PO than *Cycleptus* and most catostomines. Also, the posterior end of the PO is much narrower in *Cycleptus* than in Ictiobinae. Catostominae is intermediate between Cycleptinae and Ictiobinae in the scatterplots of Figure 9A, reflecting its intermediate PO depth and least width. Principal com-

ponents analysis revealed no differences in PO shape among ictiobines (data not shown). In the PCA of residuals of PO shape variables for tribes of subfamily Catostominae, PC1, PC2, and PC3 accounted for 94.2% of the variation in the data (Supporting Information S-Table 2). Scatterplots of

PC scores illustrate near complete separation of Erimyzonini from Thoburniini (Fig. 9B). The distinction of the groups is primarily due to depth of the PO (PC2). The PO of erimyzonines is much deeper than thoburniines. Figure 9B also illustrates the great diversity in the shape of the PO in *Moxostoma* species as there is nearly complete overlap of the three other tribes by Moxostomatini.

Morphological Variation of the Palatal Organ of Other Cypriniforms

Cyprinidae. Twenty-eight species of the family Cyprinidae were examined for comparison with members of Catostomidae. The PO of members of subfamily Cyprininae is most similar in morphology to members of Catostomidae. The morphology and function PO of *Cyprinus carpio* has been studied in detail previously (Eastman, 1971; Sibbing and Uribe, 1985; Sibbing, 1988). In brief, the PO of *C. carpio* is triangular in shape, being widest anteriorly (13.0% SL) and distinctly narrower at the CP (4.6% SL). The median groove is present in smaller specimens, but the PO surface becomes uniformly smooth as body size increases. The PO lobe is quite long (11.8% SL), but it is not very deep (2.7% SL). The thickness of the PO in *C. carpio* is comparable to that seen in many catostomids. It lacks pharyngeal characters that occur in many catostomids (i.e., U-shaped notch, anterior knobs, and transverse shelf). The PO of *Carassius auratus* is cordate, being widest anteriorly and narrower at the CP (Fig. 1B). A distinct median groove is present in specimens less than 100 mm SL, but the groove is less pronounced in larger specimens. Oblique indentations are present in the PO from contact with the gill arches. *Bangana dero*, *Barbus trimaculatus*, *Garra annandalei*, and *Labeo cylindricus* (Fig. 10A) have a PO that has a similar shape as observed in catostomids, but it is thinner than the PO of catostomids, *Cyprinus*, and *Carassius*.

In species of the other cyprinid subfamilies studied, e.g., Leuciscinae, Gobioninae, Rasborinae, Cultrinae, and Acheilognathidae, the PO is generally much thinner and flatter than catostomids and species of Cyprininae. Usually the roof of the buccal cavity has longitudinal grooves, whereas the PO is covered with ridges of papillae, as exemplified in *Ptychocheilus grandis* (Fig. 10B). In *P. grandis*, the roof of the buccal cavity consists of longitudinal grooves that extend to the PO. The PO is very thin and composed of numerous papillae. The pharyngeal lumen is wide to accommodate large prey and the postlingual organ is wide and extends the entire length of the pharynx. An exception to the typical non-Cyprininae cyprinid morphology occurs in *Hypophthalmichthys molitrix*. The anatomy of the pharyngeal region *H. molitrix* was described and illustrated by Howes (1981).

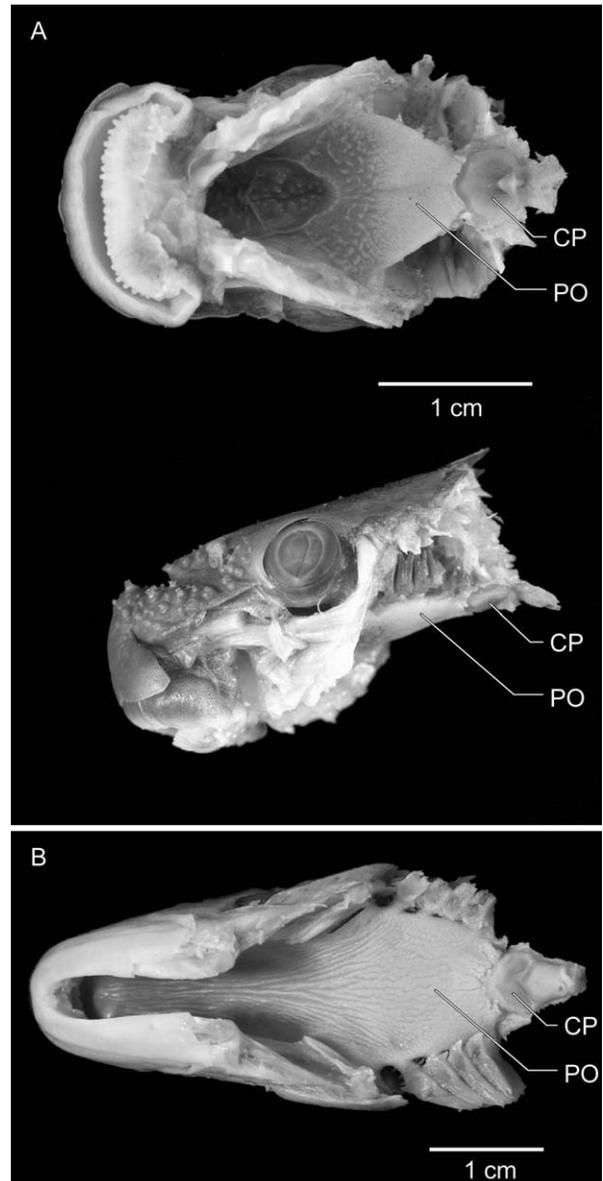


Fig. 10. Dorsal parts of heads illustrating the palatal organ (PO) and chewing pad (CP) in ventral view (top) and lateral view (bottom). Operculums and pharyngeal arches have been removed. A: *Labeo cylindricus* CU 93875. B: *Ptychocheilus grandis* TU 47277.

Briefly, each side of the moderately thick PO comprises four longitudinal folds that the gill arches fit into to form a remarkable sieving structure that can filter very small particles (as small as $7\mu\text{m}$) from the water column (Smith, 1989). *Hypophthalmichthys molitrix* also possess a pair of lateral epibranchial organs, which are formed from cartilaginous extensions of the fourth epibranchial bones (Howes, 1981). The morphology of the buccal cavity of *Cirrhinus mrigala* consists of an anterior lamellar organ (Yashpal et al., 2009). The lamellar organ is a specialized structure that consists of

two rows of 9–10 lamellae, which may function for selection, sorting, and retention of food items in the pharynx and the PO occupies the posterior region of the pharynx (Yashpal et al., 2009). The anterior portion of the PO has a shallow depression and the posterior region is covered with epithelial projections (Yashpal et al., 2009).

Loaches. The PO of the loach species examined from the families Botiidae, Cobitidae, and Nemacheilidae are similar in morphology. Generally, the PO is thin, flat, wide anteriorly, and covered with small papillae. In the cobitid loach, *Lepidocephalichthys guntea*, the buccal region has longitudinal grooves that extend to the anterior pharyngeal region. The PO is flat except for a slight ventral curve at its posterior end and there is no median groove. It is likely that mucus cells are present in the PO as was described for *Cobitis taenia* (Robotham, 1982). A CP is also lacking and the pharyngeal teeth do not protrude through the epithelium of the pharyngeal floor for the entire length of the pharyngeal bone. Only the ventral and medial teeth protrude through the epithelium of the pharyngeal floor. The pharyngeal anatomy of the nemacheilid loaches, *Acanthocobitis botia*, *Barbatula* sp., and *Schistura beavani*, are similar to *L. guntea*.

Gyrinocheilidae. The roof of the pharynx is pyramidal in the gyrinocheilids, *Gyrinocheilus aymonieri* and *G. pennocki*. The PO is much thinner than in species of other cypriniform families. The pyramid shape seems to be due to the morphology of the neurocranium and a ventral keel of the parasphenoid. Four oblique grooves are present on the surface of the PO, which the gill arches fit snugly in to. Pharyngeal teeth and CP are absent.

Chewing Pad Morphology of Cypriniformes

Chewing pad morphology was studied in 51 species of catostomids and 28 species of cyprinids. It is well known that all species of Cyprinidae possess a keratinized CP at the ventral part of the pharyngeal process (Howes, 1991). It was previously understood that only the mollusk feeding species of suckers, *Moxostoma carinatum* and *M. hubbsi*, have a CP (Weisel, 1960; Jenkins, 1970). The shape of the CP varies but it is generally ovoid or sub-rectangular in Cyprinidae (Fig. 1B). Several of the species examined (e.g., *Carassius auratus*, *Hypophthalmichthys molitrix*, and *Labeo cylindricus*) have indentations or depressions from contact with the pharyngeal teeth. In Catostomidae, the CP is lunate and the lateral margins extend dorsally around the PO for the entire length of the pharyngeal bone (Eastman, 1977). In all catostomids, the pharyngeal teeth occur in a single row of 20–180 teeth (Eastman, 1977) and protrude through the tissue surrounding the pha-

ryngeal bone for the entire length of the bone. The only variation in the catostomid CP is its thickness and width. The discussion of the morphological variation of the chewing pad of suckers will be arranged by subfamily and by tribe within subfamily Catostominae.

Subfamily Cycleptinae. In *Cycleptus elongatus*, the CP is of uniform width until it begins to curve dorsally on the sides of the PO. It becomes gradually thinner towards the dorsal end of the pharyngeal bone (Fig. 2B). The CP is firmer in *Cycleptus elongatus* than in species of *Carpiodes* or *Ictiobus*. The CP of *Myxocyprinus asiaticus* could not be adequately studied; however, one juvenile was examined to confirm the occurrence of the CP.

Subfamily Ictiobinae. Species of subfamily Ictiobinae have a fragile pharyngeal bone with many minute, comb-like teeth (Eastman, 1977). The pharyngeal teeth barely protrude through the epithelium of the postlingual organ and the CP is extremely thin and very narrow, even at its widest point at the ventral midline. Muscles attached to the pharyngeal bone are poorly developed, suggesting that the CP and pharyngeal teeth are not capable of masticating hard prey items (Eastman, 1977). The CP is exceptionally thin in *Carpiodes velifer* (Fig. 5A) and weakly developed even in adult specimens of *Ictiobus bubalus* (Fig. 3).

Tribe Erimyzonini. Species of Erimyzonini have similar CP morphologies. In *Minytrema melanops*, the CP has a uniform width ventrally and gradually narrows towards the dorsal end of the pharyngeal bone. On the ventral midline the CP is slightly interrupted by the opening of the esophagus. The CP of *Erimyzon* species (Fig. 5B) are nearly identical to each other and to the CP of *Minytrema*. *Erimyzon tenuis* has a CP that is firmer and slightly more robust than the other *Erimyzon* species.

Tribe Thoburniini. The CP of *Thoburnia* species are fragile and discontinuous at the ventral midline in *T. hamiltoni* and *T. rhothoeca* because of the opening for the esophagus. In *T. atripinnis* the CP is widest at the ventral midline and sharply narrows towards the dorsal end of the pharyngeal bone. It is very thin compared to the other species of *Thoburnia*. *Hypentelium etowanum* and *H. nigricans* have nearly identical CP morphologies. Their CP is widest at the ventral midline and sharply narrows towards the dorsal end of the pharyngeal bone. There is a slight curve to the anterior near the esophagus, but it is not as pronounced like the condition observed in *Catostomus* species.

Tribe Catostomini. The CP of the 15 catostomine species examined are very similar. Each is widest on the ventral midline and gradually narrows towards the dorsal end of the pharyngeal bone. However, the CP is not a smooth arcing cres-

cent. The CP of *Catostomus* species is slightly curved to the anterior near the opening for the esophagus. As a result of this curvature, the CP appears to be W-shaped. The CP of *Chasmistes liorus mictus* and of *Deltistes luxatus* is very similar to that seen in species of *Catostomus*. It differs in these species by being slightly thinner and sometimes discontinuous at the ventral midline because of a low ridge that is present at the opening of the esophagus. *Xyrauchen texanus* has a CP that is widest on the ventral midline and narrows towards the dorsal end of the pharyngeal bone; however, it does not have an anterior curve as in species of *Catostomus*.

Tribe Moxostomatini. The CP of *Moxostoma* species are nearly identical in shape. They only differ in width at the ventral midline and thickness. Twenty species of *Moxostoma* were examined and all have CP that are widest at the ventral midline and gradually become thinner towards the dorsal end of the pharyngeal bone. There are extremes in the general *Moxostoma* CP morphology. The widest and most robust CP belongs to *M. hubbsi*. In the two specimens examined (491-514 mm SL) the CP had a greatest width of 14.90 mm and 15.99 mm (about 3.1% SL) and thickness of 8.23 mm and 9.45 mm (about 1.8% SL), respectively. In the other mollusk feeding sucker, *M. carinatum*, the width of the CP is about 2.1% SL in five specimens examined. The CP is much less well developed in smaller-bodied *Moxostoma* species (e.g., *M. ariommum* and *M. cervinum*).

Morphology of the Dorsal Anterior Pharynx of the Outgroups

Representative species from non-cypriniform ostariophysan families were studied to determine the plesiomorphic conditions of the PO and CP. There is no PO or CP in *Chanos chanos*; however, there is an epibranchial organ present posterior to the gill arches comprising paired diverticula of the pharynx (Kapoor, 1954) that is adapted to aid the digestive system (Bertmar et al., 1969). The epibranchial organ is supported by the cartilaginous fifth epibranchial and ends of the fourth and fifth ceratobranchials (Johnson and Patterson, 1997). In the four species of order Characiformes studied (*Astyanax mexicanus*, *Bryconamericus ricao*, *Curimata peruana*, and *Ichthyoelephas humeralis*) there is no muscular PO on the roof of the anterior pharynx. The upper gill arch bones (pharyngobranchials and epibranchials) interact directly with the ventral gill arch bones. *Bryconamericus ricao* (Characidae) has a pad on the dorsal part of the buccopharyngeal cavity and *Curimata peruana* (Curimatidae) has lamellae in the buccal cavity that extend posteriorly to the first gill arch, but these structures are not supported by upper gill arches or the basioccipital bone. In the ictalurids,

Ameiurus melas and *Noturus flavus*, the roof of the buccopharyngeal cavity is not thickened and a PO is not present. Upper pharyngeal tooth plates are present and contact the floor of the anterior pharynx, which comprises the ventral gill arch bones. Similarly, in the gymnotid, *Gymnotus carapo*, the roof of the buccopharyngeal cavity is not muscularized and the upper gill arch bones interact directly with lower bones. None of the non-cypriniform ostariophysans examined have a CP attached to the basioccipital bone.

DISCUSSION

The morphology of the PO varies considerably among cypriniform fishes. Palatal organ morphology is most diversified in terms of size and shape in the family Catostomidae. Species of the other cypriniform families studied do not have a PO that is developed to the size observed in suckers. In the representatives that were studied from the other cypriniform families the PO is usually thinner and flatter. A CP occurs in all catostomids and cyprinids, but is lacking from the other groups. The CP occurs in a similar location in suckers and minnows, but its shape is very different between the families.

Catostomid pharyngeal morphology is most similar to family Cyprinidae. All catostomids possess a thickened and muscular PO that is strikingly different from the epithelium in the buccal cavity. On the other hand, only a few of the cyprinid groups examined have a thick and muscular PO. For example, the PO of *Cyprinus carpio*, *Carassius auratus*, and *Hypophthalmichthys molitrix* are the most similar morphologically to the PO of catostomids. In these species, the PO is thick and muscular and clearly differentiated from the dorsal buccal epithelium. In other cyprinid genera examined, e.g., *Gobio*, *Labeo*, *Ptychocheilus*, *Tor*, and *Zacco*, the PO is relatively thin. Of course, only a few of the several hundred genera of cyprinids were examined for comparison to suckers.

Within Catostomidae, there is significant variation in PO morphology. Subfamily Cycleptinae has the shortest, narrowest, and thinnest PO of all the subfamilies. This fact is supported by evidence from ANOVA on residuals of PO measurements (Fig. 4A) and confirmed by PCA (Fig. 9A). Means of these measurements are significantly different from means of Catostominae and Ictiobinae (Fig. 4A); however, there is overlap of ranges for some PC scores among the subfamilies (Fig. 9A). Subfamily Ictiobinae has the thickest and widest PO among the subfamilies (Fig. 4A). The PO of ictiobines is bulbous and exceptionally deep (Fig. 5A). In general, the shape and size of the PO in Catostominae is intermediate between the other subfamilies, but the range of measurements is wider. The PO of Erimyzonini and Thoburniini are signif-

icantly longer than Moxostomatini (Fig. 9B). Erimyzonini have the deepest PO and, Thoburniini has the thinnest PO among Catostomine tribes (Fig. 9B). All of the catostomid subfamilies and tribes are monophyletic (Doosey et al., 2010), and the differentiation of the means of the PO measurements has correlation with the phylogeny.

Only catostomids and cyprinids possess a CP. The loaches examined in this study do not have a CP, even though they have pharyngeal teeth. In cyprinids, the CP is usually ovoid or subtriangular and attached to the masticatory plate of the pharyngeal process. The distal ends of the pharyngeal teeth grind against the CP to masticate food items. In catostomids, the CP is lunate and located at the posterior end of the PO. It encircles the PO for the entire length of the pharyngeal bone. In this study it has been discovered that all suckers have a CP, not only *Moxostoma carinatum* and *M. hubbsi*, as previously thought (Jenkins, 1970; Eastman, 1977). In general, the shape of the catostomid CP is conserved, and only the width and thickness vary among the species.

Eastman (1977) proposed three categories for suckers based on the pharyngeal feeding structures and diet. Sucker diet data were summarized from Eastman (1977) and Jenkins and Burkhead (1994). His type I species include the mollusk feeders, *Moxostoma carinatum* and *M. hubbsi*, which have a thin PO, thick CP, and molariform pharyngeal teeth that are well suited for crushing hard prey items. *Moxostoma robustum* may also be included in the type I group. Eastman's (1977) type II species include members of subfamilies Cycleptinae and Catostominae (exclusive of *M. carinatum*, *M. hubbsi*, and *M. robustum*). These species have a PO that is intermediate in size, moderately developed CP, and 43-90 comb-like pharyngeal teeth (Eastman, 1977). The diet of adult type II suckers mainly comprises aquatic insect larvae, crustaceans, amphipods, diatoms, small or thin-shelled mollusks, and algae. Eastman's (1977) type III species include members of subfamily Ictiobinae. These species have a PO that is greatly enlarged, weakly developed CP, and 134-184 very small, comb-like pharyngeal teeth that are not suitable for crushing or grinding (Eastman, 1977). Ictiobines generally feed on small and soft prey, for example, chironomids, crustaceans, algae, and plant material. This study presented evidence from morphological variation of the PO (Figs. 4A and 9A) that supports the groupings proposed by Eastman (1977). However, among the groups proposed by Eastman (1977), only type III species, which include all ictiobines are a monophyletic group (Smith, 1992; Harris and Mayden, 2001; Doosey et al., 2010). Type I species with a thin PO and thick CP have evolved multiple times in the sucker tree of life because these taxa do not form a monophyletic group (Doosey et al., 2010). The type

II condition, which is applied to the majority of the sucker genera and species, may be the ancestral condition of the Catostomidae given the phylogenetic tree of Doosey et al. (2010). It is likely that the ancestor of the Catostominae had a PO, CP, and diet that fits the type II condition.

Consideration of diets of the various groups of catostomids and some of the cyprinids examined suggests that a large PO is correlated with suction feeding over soft bottom habitats and preference for small prey items. For example, convergence of PO morphology (Figs. 1 and 5) is evident in Ictiobinae, Erimyzonini, and some Cyprininae (i.e., *Carassius* and *Cyprinus*); groups that are not hypothesized to be closely related (Doosey et al., 2010). Species in these groups also have similar benthic suction feeding habits in which substrate and prey are indiscriminately sucked into the buccopharyngeal cavity. Conversely, the species with a thinner PO generally prey on larger and often harder food items. Even though there are convergent morphologies among catostomids and cyprinids, there are characteristics that distinguish the PO of these groups, specifically the U-shaped notch, anterior knobs, and transverse shelf. Also, the morphology of the basioccipital bone is significantly different between suckers and minnows and a research article detailing the morphological variation and evolution of the basioccipital bone is forthcoming.

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LITERATURE CITED

- Bertmar G, Kapoor BG, Miller RV. 1969. Epibranchial organs in lower teleostean fishes—an example of structural adaptation. *Int Rev Gen Exp Zoo* 4:1–48.
- Branson BA. 1962. Comparative cephalic and appendicular osteology of the fish family Catostomidae. Part I, *Cycleptus elongatus* (Lesueur). *Southwestern Naturalist* 7:81–153.
- Cole FJ. 1944. *A History of Comparative Anatomy from Aristotle to the Eighteenth Century*. London: MacMillan. 524 p.

- Curry E. 1939. The histology of the digestive tube of the carp (*Cyprinus carpio communis*). *J Morphol* 65:53–78.
- Dixit RK, Bisht JS. 1972. Histomorphology of the alimentary canal of hill-stream teleost, *Schizothorax richardsonii* (Gray and Hard). *Zoo Beiträge* 18:321–338.
- Doosey MH, Bart HL Jr., Saitoh K, Miya M. 2010. Phylogenetic relationships of catostomid fishes (Actinopterygii: Cypriniformes) based on mitochondrial ND4/ND5 gene sequences. *Mol Phylogenet Evol* 54:1028–1034.
- Eastman JT. 1971. The pharyngeal bone musculature of the carp, *Cyprinus carpio*. *J Morphol* 134:131–140.
- Eastman JT. 1977. The pharyngeal bones and teeth of catostomid fishes. *Am Midland Naturalist* 97:68–88.
- Fink WL, Humphries JM. 2010. Morphological description of the extinct North American sucker *Moxostoma lacerum* (Ostariophysi, Catostomidae), based on high-resolution x-ray computed tomography. *Copeia* 2010:5–13.
- Girgis S. 1952a. The bucco-pharyngeal feeding mechanism in an herbivorous bottom-feeding cyprinoid, *Labeo horie* (Cuvier). *J Morphol* 90:281–315.
- Girgis S. 1952b. On the anatomy and histology of the alimentary tract of an herbivorous bottom-feeding cyprinoid fish, *Labeo horie* (Cuvier). *J Morphol* 90:317–362.
- Harris PM, Mayden RL. 2001. Phylogenetic relationships of major clades of Catostomidae (Teleostei: Cypriniformes) as inferred from mitochondrial SSU and LSU rDNA sequences. *Mol Phylogenet Evol* 20:225–237.
- Hoogenboezem W. 2000. On the feeding biology of bream (*Abramis brama*). *Neth J Zoo* 50:225–232.
- Howes G. 1981. Anatomy and phylogeny of the Chinese major carps *Ctenopharyngodon* Steind., 1866 and *Hypophthalmichthys* Blkr., 1860. *Bull Brit Museum Nat Hist (Zoo Ser)* 41:1–52.
- Howes GJ. 1991. Systematics and biogeography: An overview. In: Winfield IJ, Nelson JS, editors. *Cyprinid Fishes: Systematics, Biology, and Exploitation*. London: Chapman and Hall. pp 1–33.
- Hubbs CL, Lagler KF. 1958. *Fishes of the Great Lakes Region*. Michigan: Cranbrook Institute of Science. 213 p.
- Jara Z. 1957. On the morphology and function of the so-called palatal organ of the carp (*Cyprinus carpio* L.). *Prezgrad Zoo* 1:176–178.
- Jenkins RE. 1970. *Systematic Studies of the Catostomid Fish Tribe Moxostomatini*. New York: Cornell University. 799 p.
- Jenkins RE, Burkhead NM. 1994. *Freshwater Fishes of Virginia*. Maryland: American Fisheries Society. 1079 p.
- Johnson GD, Patterson C. 1997. The gill-arches of gonorhynchiform fishes. *South African J Sci* 93:594–600.
- Kapoor BG. 1954. The pharyngeal organ and its associated structures in the Milk-fish, *Chanos chanos* (Forsk.). *J Zoo Soc India* 6:51–58.
- Kapoor BG, Smit H, Verighina IA. 1975. The alimentary canal and digestion in teleosts. *Adv Marine Biol* 13:109–239.
- King RE. 1975. The morphology of the buccal cavity of the goldfish, *Carassius auratus*. *South African J Sci* 71:179–183.
- Kiyohara S, Yamashita S, Kitoh J. 1980. Distribution of taste buds on the lips and inside the mouth in the minnow, *Pseudorasbora parva*. *Physiol Behav* 24:1143–1147.
- Lamb C, Kiyohara S. 2005. Development of the vagal taste system of goldfish. *Chem Senses* 30 (Suppl 1):i58–i59.
- Liu H, Chui H, Li L, Sun C, Zhu W. 1992. A study on the biology of post-larval development of the filtering apparatus in bighead carp (*Aristichthys nobilis*). *J Dalian Fish Col* 7:1–10.
- Liu H, Li H, Zhai B, Liu W. 1990. Post-larval development of the masticating apparatus of black carp *Mylopharyngodon piceus* (Richardson). *Acta Hydrobiol Sinica* 14:310–320.
- Majumdar NN. 1951. On the anatomy and histology of the palate of *Cirrhitina mrigala* (Hamilton), with special reference to the papillae present on it together with comments on their possible respiratory function. *J Zoo Soc India* 3:255–265.
- Matthes H. 1963. A comparative study of the feeding mechanisms of some African Cyprinidae (Pisces: Cypriniformes). *Bijdragen tot de Dierkunde* 33:3–35.
- Mayden RL, Chen W-J, Bart HL Jr., Doosey MH, Simons AM, Tang KL, Wood RM, Agnew MK, Yang L, Hirt MV, Clements MD, Saitoh K, Sado T, Miya M, Nishida M. 2009. Reconstructing the phylogenetic relationships of the Earth's most diverse clade of freshwater fishes—order Cypriniformes (Actinopterygii: Ostariophysi): A case study using multiple nuclear loci and the mitochondrial genome. *Mol Phylogenet Evol* 51:500–514.
- Mester L. 1973. Comparative study of the bucco-pharyngeal cavity in some species of fishes belonging to the Cobitidae family. *Rev Roum de Biol-Ser Zoo* 18:137–144.
- Miller RJ, Evans HE. 1965. External morphology of the brain and lips in catostomid fishes. *Copeia* 1965:467–487.
- Nakao T, Ishizawa A, Suzuki S, Saito M. 1984. An electron microscopic study of two types of muscle fibers in the pharyngeal pad of Prussian carp, *Carassius carassius*. *Anat Record* 209:433–443.
- Nelson JS. 2006. *Fishes of the World*. New York: Wiley. 601 p.
- Ogle W. 1882. *Aristotle on the Parts of Animals*. London: Kegan Paul, Trench and Co. 263 p.
- Osse JGM, Sibbing FA, van den Boogaart JGM. 1997. Intra-oral food manipulations of carp and other cyprinids: Adaptations and limitations. *Acta Physiol Scand* 161:47–57.
- Owen R. 1866. *On the Anatomy of Vertebrates*, vol. 1. Fishes and Reptiles. London: Longmans, Green and Co. 650 p.
- Regan CT. 1911. The classification of the teleostean fishes of the order Ostariophysi.—1. Cyprinoidea. *Ann Mag Nat Hist Ser* 8:13–39.
- Reid GM. 1982. The form, function and phylogenetic significance of the vomero-palatine organ in cyprinid fishes. *J Nat Hist* 16:497–510.
- Robotham PWJ. 1982. An analysis of a specialized feeding mechanism of the spined loach, *Cobitis taenia* (L.), and a description of the related structures. *J Fish Biol* 20:173–181.
- Rogick MD. 1931. Studies of the comparative histology of the digestive tube of certain teleost fishes, II. a minnow (*Camposotoma anomalum*). *J Morphol Physiol* 52:1–25.
- Sanderson SL, Cech JJ, Patterson MR. 1991. Fluid dynamics in suspension-feeding blackfish. *Science* 251:1346–1348.
- Sibbing FA. 1982. Pharyngeal mastication and food transport in the carp (*Cyprinus carpio* L.): A cineradiographic and electromyographic study. *J Morphol* 172:223–258.
- Sibbing FA. 1986. Structure of the palatal and postlingual organ and their function in food processing by the carp. *Acta Morphol Neerlandico-Scand* 24:56.
- Sibbing FA. 1988. Specializations and limitations in the utilization of food resources by the carp, *Cyprinus carpio*: A study of oral food processing. *Environ Biol Fish* 22:161–178.
- Sibbing FA, Osse JGM, Terlouw A. 1986. Food handling in the carp (*Cyprinus carpio*): Its movement patterns, mechanisms and limitations. *Proc Zoo Soc London (A)* 210:161–203.
- Sibbing FA, Uribe R. 1985. Regional specializations in the oropharyngeal wall and food processing in the carp (*Cyprinus carpio*). *Neth J Zoo* 35:377–422.
- Singh DP, Singh OP. 1973. The anatomical features of bucco-pharynx and brain in *Sisor rhabdophorus* (Ham.) and *Chela bacaila* (Ham.) in relation to their feeding habits. *Agra Univ J Res: Sci* 22:47–58.
- Smith DW. 1989. The feeding selectivity of silver carp, *Hypophthalmichthys molitrix* Val. *J Fish Biol* 34:819–828.
- Smith GR. 1992. Phylogeny and biogeography of the Catostomidae, freshwater fishes of North America and Asia. In: Mayden RL, editor. *Systematics, Historical Ecology, and North American Freshwater Fishes*. Stanford, CA: Stanford University Press. pp 778–826.
- Valatour MM. 1861. Recherches sur les glandes gastriques et les tuniques musculaires du tube digestif dans les poissons osseux et les batraciens. *Ann Sci Nat Zoo Biol Anim Ser* 4:219–285.
- Vandewalle P, Parmentier E, Chardon M. 2000. The branchial basket in teleost feeding. *Cybiurn* 24:319–342.
- Weber EH. 1827. Ueber das Geschmacksorgan der Karpfen und den Ursprung seiner Nerven. *Arch Anat Physiol* 2:309–315.

- Weisel GF. 1960. The osteocranium of the catostomid fish, *Catostomus macrocheilus*: A study in adaptation and natural relationship. *J Morphol* 106:109–129.
- Weisel GF. 1962. Comparative study of the digestive tract of a sucker, *Catostomus catostomus*, and a predaceous minnow, *Ptychocheilus oregonense*. *Am Midland Nat* 68:334–346.
- Willink PW. 2002. Function and variation of gill rakers in the fish family Catostomidae with comments on phylogenetic tests of natural selection. Ann Arbor, MI: University of Michigan. 318 p.
- Yashpal M, Kumari U, Mittal S, Mittal AK. 2009. Morphological specializations of the buccal cavity in relation to the food and feeding habit of a carp *Cirrhinus mrigala*: A scanning electron microscopic investigation. *J Morphol* 270:714–728.
- Zhai B, Liu W, Li H, Liu H. 1988. The histological study on the germination and development of the pharyngeal tooth and callous pad of the black carp (*Mylopharyngodon piceus*). *J Dalian Fish Col* 1:23–36.
- bus cyprinellus* TU 200699(3); *Ictiobus niger* TU 54571(4); *Minytrema melanops* TU 11814(1), TU 102758(2), TU 110243(5); *Moxostoma anisurum* RC-REJ(3), TU 81294(3), TU 173920(1), TU 176977(1), TU 179819(1); *Moxostoma ariommum* TU 72653(1); *Moxostoma breviceps* RC-REJ(1), TU 192329(1), TU 200598(5); *Moxostoma carinatum* RC-REJ(5), TU 40209(1), TU 40354(4), TU 50430(1); *Moxostoma cervinum* TU 72300(2); *Moxostoma collapsum* RC-REJ(1); *Moxostoma congestum* RC-REJ(2), TU 36952(3), TU 97445(3); *Moxostoma macrolepidotum* RC-REJ(3), TU 46936(2), TU 49611(3), TU 175160(1), TU 179211(1); *Moxostoma erythrurum* TU 73024(2), TU 78107(3); *Moxostoma hubbsi* RC-REJ (2); *Moxostoma lachneri* RC-REJ(1), TU 175428(4), TU 176010(3); *Moxostoma macrolepidotum* RC-REJ(2); *Moxostoma pappillosum* RC-REJ(4), TU uncataloged(5); *Moxostoma poecilurum* RC-REJ(2), TU 79956(6); *Moxostoma robustum* RC-REJ(1); *Moxostoma rupiscartes* RC-REJ(1); *Moxostoma valenciennesi* OSM 14356(3); *Moxostoma* sp. “Apalachicola redhorse” RC-REJ(3); *Moxostoma* sp. “brassy jumprock” RC-REJ(2); *Moxostoma* sp. “sickle fin redhorse” RC-REJ(4); *Myxocyprinus asiaticus* TU uncataloged(1); *Thoburnia atripinnis* AUM 10926(3), RC-REJ (1); *Thoburnia hamiltoni* TU 25654(4); *Thoburnia rathoeca* TU 200599(5); *Xyrauchen texanus* TU uncataloged(1).

APPENDIX

Specimens used in this study. Institutional abbreviations are as follows: AUM, Auburn University; BYU, Brigham Young University; CAS, California Academy of Sciences; CU, Cornell University; KU, University of Kansas; OS, Oregon State University; OSM, Ohio State University; RC-REJ, Roanoke College, uncataloged collection of R. E. Jenkins; TU, Tulane University; UAIC, University of Alabama; UW, University of Washington. Catalog numbers, when available, follow institutional abbreviation. Number of specimens studied is in parentheses.

BOTIIDAE: *Botia lohachata* KU 28800(1).

CATOSTOMIDAE: *Carpionodes carpio* TU 66172(8), TU 70223(2); *Carpionodes velifer* TU 15956(5), TU 94941(4); *Catostomus ardens* TU 104180(4); *Catostomus catostomus* TU 25285(1), UW 003289(1), UW 014469(2), UW 116350(1); *Catostomus clarkii* TU 89784(6); *Catostomus columbianus* UW 005140(1), UW 015419(3), UW 016544(1); *Catostomus commersonii* RC-REJ(2), TU 14565(1), TU 90711(6); *Catostomus discobolus* TU 95184(5); *Catostomus insignis* TU 90755(6), TU 94432(3); *Catostomus latipinnis* TU 79115(7), TU 95255(3); *Catostomus macrocheilus* TU 121819(3); *Catostomus occidentalis* TU 47297(3); *Catostomus plebeius* TU 33743(10); *Catostomus tahoensis* TU 83166(6); *Chasmistes liorus mictus* BYU 227122(1), BYU 227123(1), BYU 227124(1), BYU 227186(1), BYU 227187(1), BYU 227188(1); *Cycleptus elongatus* RC-REJ(1), TU 36979(2), TU 83166(3); *Delstistes luxatus* KU 40829(1), OS 5106(2); *Erimyzon oblongus* RC-REJ (1), TU 141301(4); *Erimyzon sucetta* TU 20648(3), TU 102543(2); *Erimyzon tenuis* TU 23003(4), TU 150907(6); *Hypentelium etowanum* TU 37668(2), TU 176548(4); *Hypentelium nigricans* RC-REJ(1), TU 55534(8), TU 169198(6); *Ictiobus bubalus* RC-REJ (1), TU 127586(1), TU 163467(4), TU 173199(3); *Ictio-*

COBITIDAE: *Cobitis taenia* KU 23518(1); *Lepidocephalichthys guntea* TU uncataloged(2).

CYPRINIDAE: *Acrocheilus alutaceus* KU 12411(1); *Agosia chrysogaster* KU 8108(1); *Aspidoparia morar* KU 29434(1); *Bangana dero* KU 29443(1); *Barbus trimaculatus* KU 33403(1); *Barilius bendelisis* KU 29598(1); *Campostoma oligolepis* TU 33152(2); *Carassius auratus* TU 30624(3), TU 60273(2); *Cyprinus carpio* TU 86280(1), TU 118906(3), TU 119030(3); *Exoglossum maxillingua* KU 18924(1); *Garra annandalei* KU 29604(1); *Gila robusta* TU 103356(1); *Gobio gobio* KU 23519(1); *Hypophthalmichthys molitrix* TU 193384(1), TU uncataloged(3); *Labeo cylindricus* CU 93875(3); *Mylopharodon conocephalus* TU 47278(1); *Neolissochilus hexagonolepis* KU 29516(1); *Nocomis biguttatus* KU 19134(1); *Notemigonus crysoleucas* KU 23281(1); *Paralaubuca* sp. KU 22793(1); *Platygobio gracilis* KU 5524(1); *Ptychocheilus grandis* TU 47277(2); *Puntius conchonus* KU 28729(1); *Rasbora lateristriata* KU 22809(1); *Schizothorax progastus* KU 27808(1); *Semotilus atromaculatus* TU 197841(1); *Tor putitora* KU 29537(1); *Zacco platypus* KU 12320(1).

GYRINOCHEILIDAE: *Gyrinocheilus aymonieri* CAS 79057(1); TU uncataloged(2); *Gyrinocheilus pennocki* CAS 93907(1), UAIC 14180.51(1).

NEMACHEILIDAE: *Acanthocobitis botia* TU uncataloged(2); *Barbatula* sp. KU 23516(1), *Schistura beavani* KU 29073(1).

OUTGROUPS: CHANIDAE: *Chanos chanos* TU 200811(1);

ANOSTOMIDAE: *Ichthyoelephas humeralis* KU 20021(1); CHARACIDAE: *Astyanax fasciatus* KU 21727(1), *Bryconamericus ricca* KU 1115(1); CURIMATIDAE: *Curimata peruana* KU 13488(1); ICTALURIDAE: *Ameiurus melas* KU 40073(1), *Noturus flavus* KU 26022(1); GYMNOTIDAE: *Gymnotus carapo* KU 13793(1).