Copeia, 2005(3), pp. 665–672

Grouped Tooth Replacement in the Oral Jaws of the Tripletail, *Lobotes surinamensis* (Perciformes: Lobotidae), with a Discussion of Its Proposed Relationship to *Datnioides*

ERIC J. HILTON AND WILLIAM E. BEMIS

***Lobotes surinamensis* is a widely distributed marine perciform and is the sole member of the family Lobotidae, which has unclear phylogenetic affinities. In this paper we describe and illustrate a mode of tooth replacement in *Lobotes* that we name "grouped" tooth replacement. Lateral oral teeth are replaced intraosseously, i.e., developing replacement teeth can clearly be seen beneath them within both the dentary and premaxillary bones. In contrast to the more typically seen pattern of alternate replacement, the replacement teeth of *Lobotes* develop as a group within the bone, lying directly beneath the group of teeth that they will replace. Within each tooth replacement group, the teeth show an anteroposterior gradient in age. Within the category of fully functional teeth there is a clear anterior to posterior gradient of eruption within a tooth group. Grouped tooth replacement may be a synapomorphy of *Lobotes* and *Datnioides*. As in *Lobotes*, the lateral oral teeth of *Datnioides* also are replaced intraosseously and in groups, although they are smaller and the groups are neither as distinct nor as regular. The significance and polarity of this character, as well as other osteological similarities of *Lobotes* and *Datnioides*, are difficult to evaluate given the lack of understanding of higher level relationships among perciforms and the paucity of information about modes of their tooth replacement.**

LOBOTES surinamensis, commonly known as the tripletail or blackfish, is a widely distributed marine perciform found in the Atlantic, eastern Pacific, and Indo-West Pacific. It occurs primarily in tropical and sub-tropical waters but at least occasionally enters temperate waters, and has been described as a "slothful, sluggish animal, much preferring to drift with the currents to take it where they will than to set a course and go to it" (Shipp, 1994:147). *Lobotes surinamensis* is the sole valid species of the nine nominal species in the genus (Eschmeyer, 1998: 2356). As have many authors (e.g., Weber and de Beaufort, 1936; Springer, 1982; Carpenter, 2001), Nelson (1994:359) included the genera *Lobotes* and *Datnioides* (= *Coius* of some authors; see Roberts and Kottelat, 1994; Kottelat, 2000) in the family Lobotidae, although he acknowledged that there is "no firm evidence that *Lobotes* and *Datnioides* form a monophyletic group." In contrast, Eschmeyer (1998) placed them in different families (i.e., Lobotidae and Datnioididae, as Coiidae; see Kottelat [2000] for discussion of the family name of Datnioididae). The phylogenetic affinities of these genera, both to each other and to other members of Perciformes, remain unclear. Also the anatomy of *Lobotes* is poorly known. Johnson (1984) described aspects of cranial ornamentation in the larvae and Ditty and Shaw (1994) described the morphology of larvae and small juveniles (≤23 mm SL) in their study of development in this species.

In this paper we describe an unusual mode of tooth replacement in the oral jaws of *Lobotes.* Tooth replacement of fishes has received intermittent but focused study, both as a general phenomenon (e.g., Tomes, 1876; Edmund, 1960; Osborn, 1977) and in specific groups of fishes (e.g., Moy-Thomas, 1934; Miller and Radnor, 1973; Johnson, 1986). Fink (1981) defined tooth attachment types in actinopterygians, and most recently, Trapani (2001) detailed various patterns of tooth replacement in teleostean fishes. He recognized two distinct patterns: extraosseus replacement, in which the replacement tooth develops outside of the bone and solely within soft tissue before attaching to a tooth-bearing bone; and intraosseus replacement, in which the replacement tooth develops within the bone to which it will eventually attach. Within each of these broad categories of tooth replacement, there are variations on a theme, both within a taxon (i.e., tooth replacement on different dentigerous bones) and between taxa. Here, we first describe the structure of the oral jaws of *L. surinamensis.* We then describe and illustrate the mode of tooth replacement in *Lobotes* that we name "grouped" tooth replacement. We conclude by reviewing some patterns

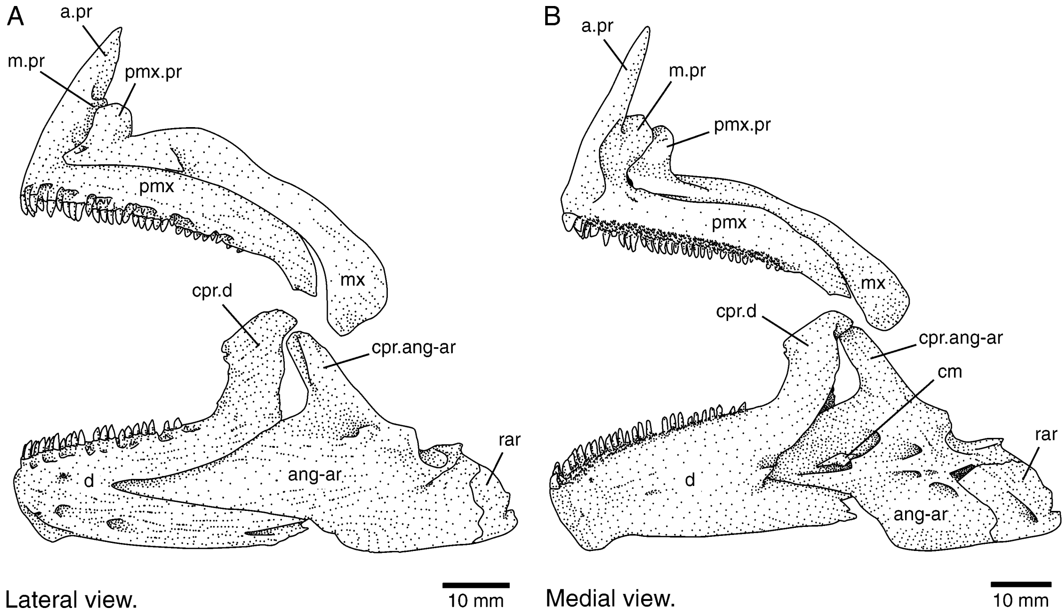

Fig. 1. Left oral jaws of *Lobotes surinamensis* (UMA F10891; 459 mm SL). (A) Lateral view. (B) Medial view. Anterior facing left (images in B reversed). Abbreviations: ang-ar = anguloarticular, a.pr = ascending process, cm = coronomeckelian, cpr.ang-ar = coronoid process of the anguloarticular, cpr.d = coronoid process of the dentary, d = dentary, m.pr = maxillary process of the premaxilla, mx = maxilla, pmx = premaxilla, pmx.pr = premaxillary process of the maxilla, rar = retroarticular.

of tooth replacement in perciforms and noting the similarity in the pattern of tooth replacement in *Lobotes* and *Datnioides*, which may represent a putative synapomorphy for these genera.

Materials and Methods

All but one specimen of *L. surinamensis* used in this study were prepared as dry skeletons (FMNH 20643 is a cleared-and-stained specimen prepared following a protocol modified from Dingerkus and Uhler, 1977). All newly collected specimens (i.e., the UMA specimens) were prepared following the method outlined by Bemis et al. (2004). The oral jaws of some specimens were removed from the rest of the skeleton and soaked in a weak solution of household ammonia and any remaining tissue was removed by hand.

Institutional abbreviations follow Leviton et al. (1985) with the addition of UMA for the University of Massachusetts Amherst Zoological Collections. The following specimens of *Lobotes* were examined: ANSP 77947 (est. 200 mm SL); FMNH 20643 (est. 50 mm SL); UMA F10698 (450 mm SL); UMA F10704 (440 mm SL); UMA F10891 (459 mm SL); UMA F10892 (425 mm SL); UMA F10924 (566 mm SL); UMA F10925 (505 mm SL); UMA F10926 (425mm SL); UMA F10927 (508 mm SL); UMA F11141 (398 mm SL). Skeletons of several additional percomorph taxa were also studied and include: *Canthidermis* sp. (UMA F10413, 275 mm SL); *Caranx hippos* (UMA F10954, 233 mm SL); *Cynoscion* sp. (UMA F10555, 276 mm SL); *Datnioides quadrifasciatus* (AMNH 94466SD, est. 250 mm SL; AMNH 37993SD, SL unknown but >300 mm); *Lutjanus campechanus* (UMA F10962, 665 mm SL); *Morone saxatils* (UMA F10192, SL unknown); *Mycteroperca bonaci* (UMA F10944, est. 460 mm SL); *Orthopristis chrysoptera* (UMA F10216, est. 165 mm SL); *Paralichthys lethostigmata* (UMA F11065, 410 mm SL); *Pomatomus saltatrix* (UMA uncat., SL unknown); *Scomberomorus maculatus* (UMA F10228, est. 600 mm SL); *Sphyraena barracuda* (UMA F11026, 1050 mm SL); *Stizostedion vitreum* (UMA F10204, est. 470 mm SL).

Results

Description of the oral jaws.—The oral jaws of *Lobotes* are illustrated in Figure 1. The upper jaws consist of the premaxillae and maxillae and, as usual for acanthomorph fishes, only the premaxillae bear teeth. The relatively slender maxilla terminates posteroventrally in a laterally flattened hook. The maxilla is tightly associated with the dorsolateral surface of the premaxilla, and the premaxillary process of the maxilla partially wraps around the maxillary process of the premaxilla. The lateral surface of the maxilla bears a distinct triangular process for the insertion of the maxillo-mandibular ligament or the ligamentum primordium. The well-developed ascending process of the premaxilla is continuous with the maxillary process.

The lower jaw of *Lobotes* consists of the dentary, anguloarticular, retroarticular, and coronomeckelian. The dentary and the anguloarticular are the largest elements of the lower jaw, forming much of the anterior and posterior halves, respectively. Both the dentary and anguloarticular bear well-developed coronoid processes that are offset from their dorsal margins. The relatively small retroarticular forms the posteroventral corner of the lower jaw, and is completely removed from the quadrate articulatory surface. The small coronomeckelian sits immediately anterior to the junction between Meckel's cartilage and the anterior portion of the angular.

Tooth replacement.—Both the dentary and premaxilla of *Lobotes* bear medial and lateral series of teeth. The medial series consist of small conical teeth that form a shagreen on the bone of attachment (Fig. 1B). Nothing is noteworthy about tooth replacement patterns for the medial series, for the teeth are replaced individually as is typical for other teleosts. The lateral series consist of large, antero-posteriorly flattened teeth that, when fully functional, are firmly ankylosed to their bone of attachment (although no determination of the degree of mineralization of the ankylosis was made; e.g., Fink, 1981). These teeth are replaced intraosseously, i.e., developing replacement teeth can clearly be seen beneath them in both the dentary and premaxilla. Remarkably, however, their replacement does not happen either alternately or with a ''one for one'' pattern as is typical of teleosts that exhibit intraosseus tooth replacement. Nor does it happen ''all at once'' as has been reported for some teleosts (e.g., Roberts, 1967; Berkovitz, 1975). Instead, several teeth develop as a group within the bone, lying deep to the group of teeth that they will replace. Within each tooth replacement group, the teeth show an anteroposterior gradient in age and no evidence of the more typically seen alternate tooth replacement.

Figure 2 shows the arrangement of nine replacement groups in the dentary and ten replacement groups in the premaxilla of a typical specimen of *L. surinamensis.* Each replacement group consists of one to five teeth visible

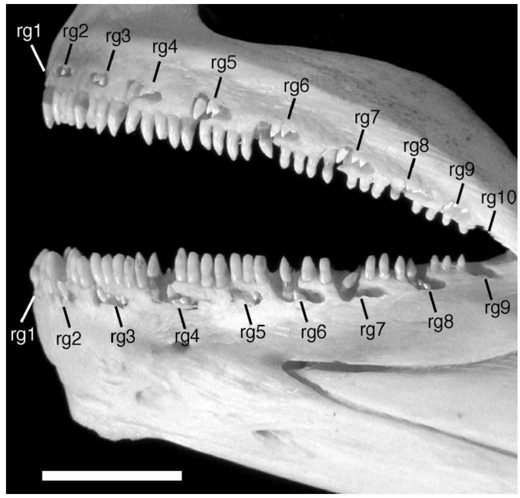

Fig. 2. Left oral jaws of *Lobotes surinamensis* in lateral view to show general arrangement of groups of replacement teeth (UMA F10698; 450 mm SL); anterior facing left. The premaxilla has ten replacement groups, denoted by rg1 to rg10. The dentary has nine replacement groups. Each replacement group consists of between one and five teeth associated with a replacement pore (for a single incoming tooth) or slit (for multiple incoming teeth). Within each replacement slit, there is a maximum of four teeth. Anterior to left; scale bar equals 10 mm.

through either a pore (for a replacement group that consists of only one tooth) or a slit (for a replacement group that consists of more than one tooth). The pores and slits represent the physical space through which the dental lamina passed from the jaw epithelium to the enamel organ that is needed for cap development in each replacement tooth. The pores and slits also serve as part of the eruption path for teeth as they grow out of the bone and become incorporated into the tooth row. Pores and slits are located on the lateral surfaces of both the dentary and premaxilla. Each of the slits is widest and most open at its anterior end, and the anteriormost replacement tooth is always the largest and most fully formed in any given replacement group.

Additional aspects of the replacement pattern are shown in Figure 3, which presents a detailed study of a single premaxilla. An occlusal view (i.e., ventral view; Fig. 3A) shows the medial and lateral series of teeth. Note that the teeth of the lateral series are much larger, they are compressed from anterior to posterior, and that they may be firmly attached to the surrounding bone. The tooth loci for the lateral series are numbered in Fig. 3B–D; note that not all tooth loci have ankylosed teeth. Slight texture and

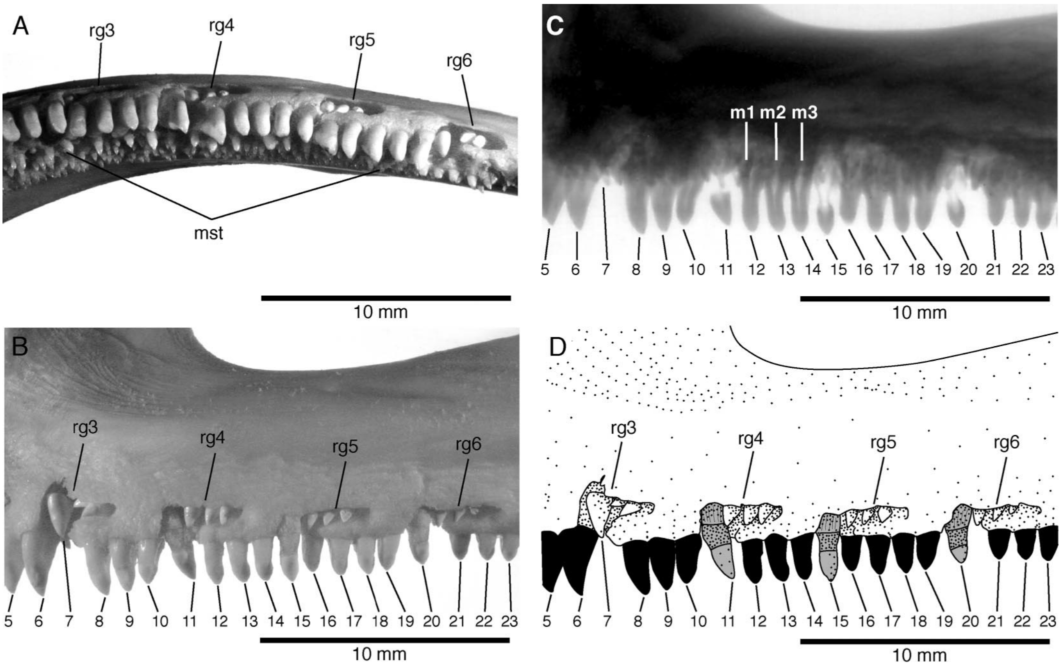

Fig. 3. Details of oral tooth attachment and replacement in *Lobotes surinamensis* (UMA F10698; 450 mm SL). All images are of the right premaxillae, reversed so that anterior faces left. (A) Occlusal view showing four tooth-replacement groups (rg3 to rg6) and the medial shagreen series of teeth (mst). (B) Photograph in lateral view. Replacement groups rg3 to rg6 are indicated and tooth loci are numbered 5 to 23. (C) X-ray in lateral view. Teeth at loci 11, 15, and 20 represent incoming teeth in which collar mineralization has not yet developed; such teeth are described as "incoming 2" (see text for explanation). Functional teeth in replacement group 4 are marked to show their relative ages. The oldest attached tooth in replacement group 4 is indicated by m1; note that its pulp cavity has largely been filled with mineralized dentine. The youngest extant tooth in replacement group 4 is indicated by m3; note that its pulp cavity is more open than is the pulp cavity of m1. (D) Line drawing matching images in B and C. Fully functional (i.e., firmly ankylosed) teeth are shaded black. Incoming 1 teeth, which are deeply set within replacement slits, lack any connection to the bone and are left white. Incoming 2 teeth are shaded gray.

color differences in the teeth and their ankyloses can be used to estimate the relative age of the tooth and its ankylosis. For example, teeth 12, 13, and 14 are relatively newly attached teeth as revealed both by their lighter color and the relative smoothness of the bone of attachment at their bases. Beneath the row of fully functional teeth, four replacement groups for the lateral series of teeth can be seen in Figure 3.

By rotating the premaxilla 90° (i.e., to lateral view; Fig. 3B), additional details of the four replacement groups can be seen. Replacement group 3 follows a fully functional tooth (tooth locus 6) and consists of three replacement teeth (tooth loci 7–9) in a large pore, with one that is just beginning to erupt into locus 7. Replacement group 4 (comprising tooth loci 11–13) consists of a large, newly-erupted tooth (tooth locus 11), and three additional replacement teeth in the slit and still below the gumline. A similar pattern is seen for replacement groups 5 and 6. An x-ray view of the same specimen (Fig. 3C) reveals details of mineralization needed to clarify the developmental stages of the replacement teeth. This information is synthesized in the schematic drawing shown in Figure 3D, in which fully functional teeth are shown with black shading and newly erupted teeth are shown in grey.

Within the category of fully functional teeth there is a clear anterior to posterior gradient of eruption within a tooth group. For example, teeth 12, 13, and 14 in Figure 3 are well ankylosed but the x-ray reveals that each of these teeth retains a relatively open pulp cavity. This indicates that these are relatively young teeth, for their pulp cavities have not yet been filled in by mineralization. Within this series of three teeth, the tooth at locus 12 has a more constricted pulp cavity than does the tooth at locus 14; this indicates that tooth 14 more recently erupted than did tooth 12. Replacement teeth that are developing but that are still in the slit and below the gumline can be described as "incoming 1" teeth; they have a mineralized tooth cap but no collar region and are still within the slit and below the gumline (these are unlabeled in Fig. 3). Teeth at loci 11, 15, and 20 can be seen in the x-ray to have well developed tooth caps and collar regions, but only very limited mineralization of their collars; these we describe as "incoming 2" teeth. Incoming 2 teeth have erupted above the gumline and the tooth that they will replace has already been lost from the jaw.

In Figure 3C, teeth at loci 10 and 14, which are in comparable positions within their respective groups, show different levels of constriction in their pulp cavities (i.e., the pulp cavity of the tooth at locus 10 is more constricted than is that of the tooth at locus 14). This suggests that the replacement of teeth in different groups is independent of their position within a group (i.e., that the replacement groups operate independently of each other). This interpretation is further supported by the fact that there are different numbers of teeth in different groups (if teeth of a certain position within a group were replaced at the same time–for instance, every 6th tooth along the dental arcade–then one would expect that all groups would have similar numbers of teeth). A more thorough examination of the actual replacement mechanism might help to clarify this.

It is also unclear if the groups remain "static" in their position along the jaw or if they "migrate" posteriorly during ontogeny. The smallest specimen examined here (50 mm SL) does not shed any light on this as the adult condition already has been reached in this specimen. This aspect of tooth development in *Lobotes* theoretically could be determined by making observations of a single specimen at different times and directly comparing the position of a single group during ontogeny.

Discussion

Tooth replacement of Lobotes in the context of Percomorpha.—Although percomorphs exhibit a wide array of tooth attachment modes and replacement patterns (e.g., see review by Trapani, 2001), the mode of tooth replacement described here for *Lobotes* is unusual among percomorph fishes. To our knowledge, no other fishes have such an arrangement except for a similar condition found in *Datnioides* (see below), although our survey included relatively few taxa. Table 1 presents an overview of tooth morphology, attachment, and replacement pat-

Table 1. Comparative Data for Some Characteristics of Tooth Morphology and Replacement Patterns among Percomorph Fishes.

Family	Species	Tooth shape	Deeply socketed teeth	Pattern of tooth replacement	Mode of tooth replacement	Replacement tooth position relative to old tooth
Moronidae	*Morone saxatilis*	conical	no	alternate	extraosseus	flanking
Serranidae	*Mycteroperca bonaci*	conical	yes	alternate	intraosseus	beneath
Percidae	*Stizostedion vitreum*	conical	yes	alternate	intraosseus	beneath
Pomatomidae	*Pomatomus saltatrix*	laterally compressed	yes	alternate	intraosseus	beneath
Carangidae	*Caranx hippos*	conical	firmly attached; not deeply socketed	alternate	intraosseus	beneath
Lutjanidae	*Lutjanus campechanus*	conical	yes	alternate	intraosseus	beneath
Lobotidae	*Lobotes surinamensis*	ant.-post. flattened	yes	grouped	intraosseus	beneath
Datnioididae	*Datnioides quadrifaciatus*	conical	no	grouped	intraosseus	beneath
Haemulidae	*Orthopristis chrysoptera*	conical	yes	alternate	extraosseus	beneath
Sciaenidae	*Cynoscion* sp.	conical	no	alternate	intraosseus	flanking
Sphyraenidae	*Sphyraena barracuda*	laterally compressed	yes	alternate	intraosseus	beneath
Scombridae	*Scomberomorus maculatus*	laterally compressed	yes	alternate	intraosseus	beneath
Pleuronectidae	*Paralichthys lethostigmata*	conical	firmly attached; not deeply socketed	alternate	extraosseus	flanking
Balistidae	*Canthidermus* sp.	incisor like	firmly attached; not deeply socketed	alternate	intraosseus	beneath

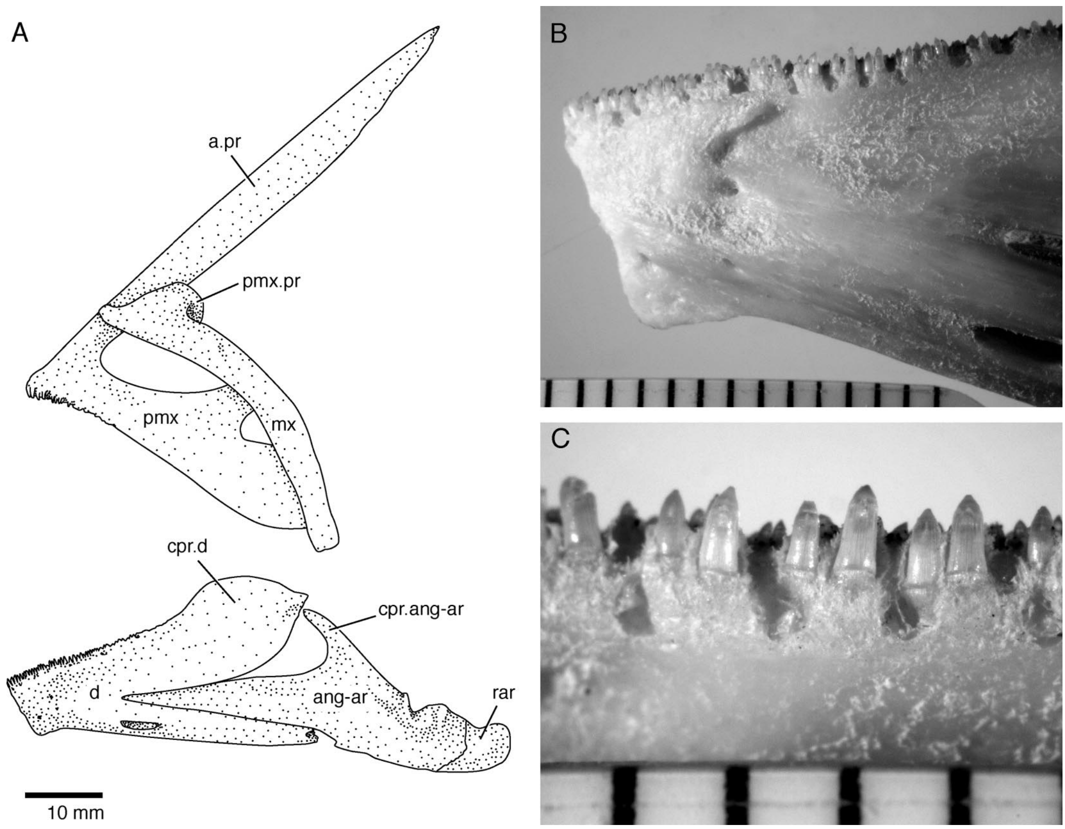

Fig. 4. Left oral jaws of *Datnioides quadrifasciatus* (AMNH 94466SD; est. 300 mm TL). (A) Jaws in lateral view. (B) Anterior portion of the dentary. (C) Close-up of some teeth also presented in B showing detail of a similar mode of tooth replacement as described for *Lobotes.* Scale in B and C in millimeters; anterior facing left in all. Abbreviations: ang-ar = anguloarticular, a.pr = ascending process, cm = coronomeckelian, cpr.ang-ar = coronoid process of the anguloarticular, cpr.d = coronoid process of the dentary, d = dentary, mx = maxilla, pmx = premaxilla, pmx.pr = premaxillary process of the maxilla, rar = retroarticular.

tern in several species of percomorphs. Even from this limited sample, however, variation in shape and mode of tooth attachment and replacement is evident. Most taxa showed a widespread replacement pattern in which teeth at alternate loci are replaced. Additionally, most taxa were found to have intraosseous tooth replacement. Those with extraosseous replacement have either a dense array of similarly sized villiform teeth along the margin of the jaw bones (e.g., *Morone, Orthopristis*) or a single row of large teeth that are loosely ankylosed to the jaws (e.g., *Paralichthys*). Most of the taxa with intraosseus tooth replacement, including *Lobotes,* have a dense array of teeth medially that are replaced extraosseously and a row of large teeth along the lateral margin of the jaw that are replaced intraosseously. However, of the taxa we surveyed, only Datnioididae and Lobotidae have grouped tooth replacement.

Relationship between Lobotes and Datnioides.—Although it is impossible in the context of this study to determine if a close relationship exists between *Lobotes* and *Datnioides*, the occurrence of grouped tooth replacement in these genera is interesting given the historic connection drawn between these two genera. Phylogenetic relationships of both genera have been in a continual state of flux. For instance, *Datnioides* was included in the family Teraponidae by Fowler (1931), although Vari (1978) found no evidence to justify this placement and favored a relationship between Lobotidae and Datnioididae. Johnson (1984:Table 119) included both *Datnioides* and Lobotidae (including only *Lobotes*) in his classification as Percoidei *incertae sedis.* Roberts (1989:164) did not see a phylogenetic connection between *Datnioides* and *Lobotes,* and was ''convinced that *Datnioides* does not belong . . . in any other percoid family.''

In contrast, we note several morphological similarities between *Datnioides* and *Lobotes*, both in overall morphology and specific points of anatomy (e.g., aspects of the caudal skeleton such as the number and pattern of hypurals, uroneurals, and epurals, and the exaggerated development of the hypurapophysis; pers. obs.). The significance and polarity of these similarities are difficult to evaluate given the lack of understanding of higher level perciform systematics (e.g., see discussion by Johnson, 1993) and their distribution among taxa.

The oral jaws and teeth of *Datnioides* are illustrated in Figure 4. As in *Lobotes*, there is a row of larger teeth laterally positioned on the jaw, with a dense array of smaller teeth arranged as a shagreen on the anteromedial surface of the dentary. All teeth (i.e., marginal and shagreen) are conical in shape, differing from the anteroposteriorly flattened marginal teeth of *Lobotes*. As described above for *Lobotes*, the lateral teeth of *Datnioides* are replaced intraosseously, laterally, and in groups, although the groupings are not as distinct or regular (e.g., in terms of their consistency along the length of the jaw; Fig. 4B, C) as found in *Lobotes*. Although we are not prepared to offer this as conclusive evidence, the apparent uniqueness of this mode of tooth replacement among percomorph fishes suggests the possibility of a relationship between *Lobotes* and *Datnioides*. It will be important for future studies to evaluate the phylogenetic significance of this similarity.

Acknowledgments

Most new specimens of *Lobotes* and other percomorphs examined in this study were collected at the Alabama Deep Sea Fishing Rodeo, and we thank the Mobile Area Jaycees, R. Shipp, and G. Crozier for their help and support during collection. For access to specimens in their care, we thank S. Schaefer, B. Brown, R. Arrindell, J. Lundberg, M. Sabaj, M. Westneat, and M. A. Rogers. We thank G. D. Johnson for comments on a draft of the manuscript. This research was conducted in part while EJH was supported by a Smithsonian Institution Postdoctoral Fellowship, and also benefited from funds from NSF (DEB 0128929, to Hilton, Grande, and Bemis; DEB 0414552, to Hilton and Grande). Travel to collect and prepare materials was provided by the Jane H. Bemis Fund for Research in Natural History at UMass Amherst.

Literature Cited

Bemis, W. E., E. J. Hilton, B. Brown, R. Arrindell, A. M. Richmond, C. Little, L. Grande, P. L. Forey, and G. J. Nelson. 2004. Methods for preparing dry, partially articulated skeletons of osteichthyans, with notes on making Ridewood dissections. Copeia 2004:603–609.

Berkovitz, B. K. B. 1975. Observations on tooth replacement in piranhas (Characidae). Arch. Oral Biol. 20:53–57.

Carpenter, K. E. 2001. Lobotidae, Tripletails, p. 2942–2945. *In*: The Living Resources of the Western Central Pacific. Volume 5 Bony Fishes Part 3 (Menidae to Pomacentridae). K. E. Carpenter and V. H. Niem (eds.). FAO, Rome, Italy.

Dingerkus, G., and L. D. Uhler. 1977. Enzyme clearing of alcian blue stained whole small vertebrates for demonstration of cartilage. J. Stain Technol. 52: 229–232.

Ditty, J. G., and R. F. Shaw. 1994. Larval development of tripletail, *Lobotes surinamensis* (Pisces: Lobotidae), and their spatial and temporal distribution in the northern Gulf of Mexico. Fish. Bull. 92: 33–45.

Edmund, A. G. 1960. Tooth replacement phenomena in the lower vertebrates. R. Ont. Mus. Life Sci. Div. 52:1–190.

Eschmeyer, W. N. (ed.). 1998. Catalog of Fishes, Volumes 1–3. California Academy of Science, San Francisco, California.

Fink, W. L. 1981. Ontogeny and phylogeny of tooth attachment modes in actinopterygian fishes. J. Morphol. 167:167–184.

Fowler, H. W. 1931. The fishes of the families Pseudochromidae, Lobotidae, Pempheridae, Priacanthidae, Lutjanidae, Pomadasyidae and Teraponidae, collected by the United States Bureau of Fisheries Steamer ''Albatross,'' chiefly in Philippine seas and adjacent waters. Bull. U.S. Natl. Mus. 100:1–388.

Johnson, G. D. 1984. Percoidei: Development and relationships, p. 464–498. *In*: Ontogeny and Systematics of Fishes. H. G. Moser, W. J. Richards, D. M. Cohen, M.P. Fahay, A. W. Kendall, Jr., and S. L. Richardson (eds.). Spec. Publ. 1, Amer. Soc. Ichthyol. Herpetol., Lawrence, Kansas.

———. 1986. Scombroid phylogeny: an alternative hypothesis. Bull. Mar. Sci. 39:1–41.

———. 1993. Percomorph phylogeny: progress and problems. *Ibid* 52:3–28.

Kottelat, M. 2000. The type species of the genus-group names *Coius* Hamilton, 1822 and *Datnia* Cuvier, 1829 and the type-genus of the family-group name Datnioididae Bleeker, 1858. J. South Asian Nat. Hist. 5:91–94.

Leviton, A. E., R. H. Gibbs, Jr., E. Heal, and C. E. Dawson. 1985. Standards in herpetology and ichthyology: part I. Standard symbolic codes for institutional resource collections in herpetology and ichthyology. Copeia 1985:802–832.

Miller, W. A. and C. J. P. Radnor. 1973. Tooth replacement in the bowfin (*Amia calva*–Holostei). J. Morphol. 140:381–396.

Moy-Thomas, J. A. 1934. On the teeth of the larval *Belone vulgaris*, and the attachment of teeth in fishes. Q. J. Microscop. Sci. 72:481–498.

Nelson, J. S. 1994. Fishes of the World, Third Edition. John Wiley and Sons, New York.

Osborn, J. W. . The interpretation of patterns in dentitions. Biol. J. Linn. Soc. 9:217–229.

Roberts, T. R. 1967. Tooth formation and replacement in characoid fishes. Stanford Ichthyol. Bull. 8:231–247.

———. 1989. The Freshwater Fishes of Western Borneo (Kalimantan Barat, Indonesia). California Academy of Sciences and Institute for Biological Exploration, San Francisco, California.

———, and M. Kottelat. 1994. The Indo-Pacific tigerperches, with a new species from the Mekong basin (Pisces: Coiidae). Ichthyol. Explor. Freshwaters 5:257–266.

Shipp, R. L. 1994. Dr. Bob Shipp's Guide to Fishes of the Gulf of Mexico. Fourth Printing, with corrections. KME Seabooks, Mobile, Alabama.

Springer, V. G. 1982. Pacific plate biogeography, with special reference to shorefishes. Smithson. Contrib. Zool. 367:1–182.

Tomes, C. A. 1876. On the development of the teeth of fishes (Elasmobranchii and Teleostei). Phil. Trans. Roy. Soc. London B 166:257–267.

Trapani, J. 2001. Position of developing replacement teeth in teleosts. Copeia 2001:35–51.

Vari, R. P. 1978. The terapon perches (Percoidei, Teraponidae). A cladistic analysis and taxonomic revision. Bull. Amer. Mus. Nat. Hist. 159:175–340.

Weber, M., and L. F. de Beaufort. 1931. The Fishes of the Indo-Australian Archipelago. Volume 6. Leiden, Netherlands.

(EJH) Division of Fishes, Smithsonian Institution, P.O. Box 37012, NMNH Rm. WG-12, MRC 0159, Washington, D.C. 20013–7012; and (WEB) Department of Ecology and Evolutionary Biology, Corson Hall, Cornell University, Ithaca, New York 14853. E-mail: (EJH) Hilton.Eric@nmnh.si.edu; (WEB) web24@cornell.edu. Send reprint requests to EJH. Submitted: 3 Dec. 2004. Accepted: 7 April 2005. Section editor: D. Buth.