

Tongue Bite Apparatus of Osteoglossomorph Fishes: Variation of a Character Complex

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Osteoglossomorpha were first defined on the basis of two characters: (1) the parasphenoid-tongue bite apparatus (TBA); and (2) the presence of processes associated with the second hypobranchial and/or basibranchial element of the ventral gill arches. These two characters have continued to be cited as unambiguous support of the monophyly of this group of basal teleostean fishes. The TBA has been vaguely defined as a “bite” of gill arch dentition against that of the parasphenoid and palatoquadrate bones. Historical definitions include both plesiomorphic (e.g., enlarged teeth on palatoquadrate bones and gill arches) and apomorphic (e.g., enlarged teeth on the parasphenoid and a direct connection between the sternohyoideus muscle and the ventral gill arch skeleton) character states. Also, the processes associated with the second gill arches are likely components of the osteoglossomorph TBA by providing an additional attachment surface for the sternohyoideus (i.e., in addition to the sternohyoideus-urohyal connection). There is variation both of presence and form of these processes within osteoglossomorphs. To use both the presence or absence of a TBA as well as its component characters in systematic analyses artificially weights the value of this character complex. This character complex should not be used in place of, and especially not in addition to, its component characters.

O STEOGLOSSOMORPHA are morphologically diverse and considered to be the sister group of all other living teleosts (Patterson and Rosen, 1977; Lauder and Liem, 1983; Patterson, 1994), although their position within teleosts has been challenged recently by both morphological (e.g., Arratia, 1996, 1997, 1999) and molecular (e.g., Lê et al., 1993) evidence. Greenwood et al. (1966) first defined Osteoglossomorpha on the basis of two characters: (1) the parasphenoid-tongue bite apparatus (TBA); and (2) the presence of paired processes associated with the second hypobranchial and/or basibranchial elements of the ventral gill arches. Both of these characters continue to be regarded as unambiguous synapomorphies of Osteoglossomorpha (e.g., Li and Wilson, 1996, 1999; Arratia, 1999). However, the TBA has never been precisely defined, and the homology within Osteoglossomorpha of the second gill arch processes, which are likely components of the TBA, is questionable.

Garstang (1931:256) was among the first to define the osteoglossomorph TBA simply as “Opposing teeth on hyoid and parasphenoid.” Greenwood et al. (1966:361) elaborated this definition by defining the TBA as “the primary bite between the parasphenoid and the tongue (basihyals and glossohyal), the bones involved being well toothed.” Lauder and Liem (1983:121) described the osteoglossomorph TBA as: “The palatal bones (mesopterygoid and ectopterygoid) are toothed . . . and as the basihyal teeth

move dorsally to ‘bite’ against the parasphenoid as a result of hyoid protraction, shearing of the prey occurs between the basihyal teeth and the lateral mesopterygoid and/or ectopterygoid teeth.” This served as the basis of the definition used by Sanford and Lauder (1989:379): “the presence of an impressive bite between teeth on the hyoid apparatus (the ‘tongue’) and teeth on the palate and base of the skull . . . anatomically intercalated between the mandibular jaw apparatus (MJA) anteriorly and the pharyngeal jaw apparatus (PJA) posteriorly. . . .” Most recently, Taverne (1998:104) offered a synthesis of previous definitions: “The considerable development of intrabuccal dentition associated with a hyoid protraction mechanism that permits prey to be torn not only by the teeth of the parasphenoid, basihyal toothplate and the basibranchial toothplate, but also by those of the pterygoid bones.” Many of these definitions include a functional component. For example, Lauder and Liem (1983) shift the emphasis of the TBA away from simple occlusion between parasphenoid and branchial dentition, and toward a “shearing” of prey between branchial and palatal dentition. Little direct study has been made of the function of the osteoglossomorph TBA, and what has been done concerns very few taxa (e.g., Kershaw, 1976; Sanford and Lauder, 1989, 1990). An important finding of these studies is that functional variation of the osteoglossomorph TBA exists, both within a species (Sanford and Lauder, 1989; Frost and Sanford,

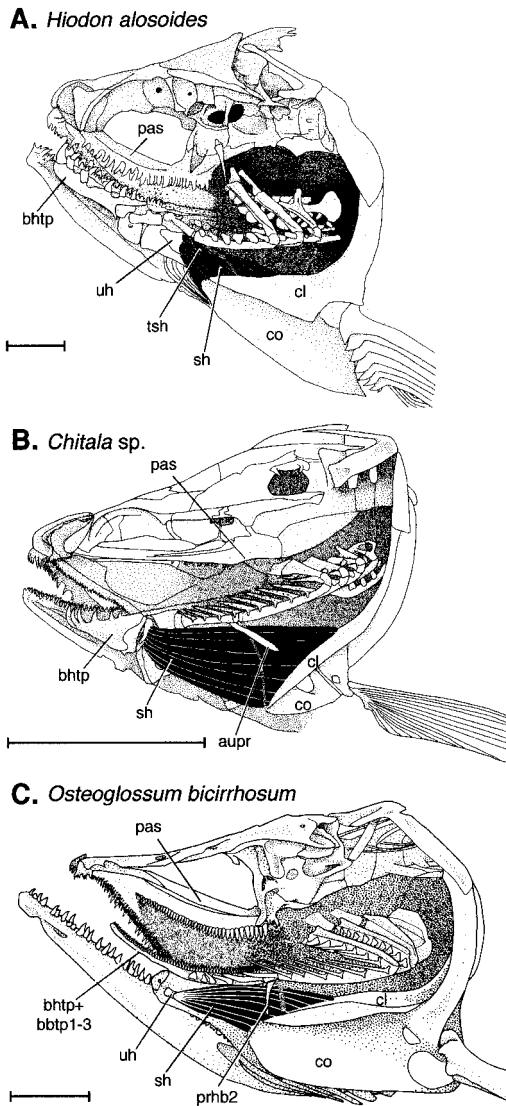


Fig. 1. The three osteoglossomorphs examined in this study showing the overall variation in the structure of the TBA. These specimens are seen in left lateral view with the left "cheek" skeleton removed; anterior is facing left. In addition to variation in the distribution and form of intraoral dentition, these taxa differ in orientation of the pectoral girdle. In Notopteroidei (represented by *Chitala* sp.), the pectoral girdle is more vertical, which brings it more posterior than in Hiodontiformes and Osteoglossoides (represented by *Hiodon alosoides* and *Osteoglossum bicirrhosum*, respectively), in which the pectoral girdle has a distinct anterior horizontal arm. Osteoglossiformes (Notopteroidei + Osteoglossoides) share the presence of autogenous bones (notopteroids) or processes (osteoglossoids) associated with the second gill arch, although the homology of these elements is questionable. The sternohyoideus muscle is shown in black and the orientation of the CBL is shown by a heavy gray line (the CBL actually lies between the left

and right halves of the sternohyoideus). (A) *Hiodon alosoides* (UMA F10150; SL = 293 mm); (B) *Chitala* sp. (UMA F10341; SL = 75 mm); (C) *Osteoglossum bicirrhosum* (UMA F10335; SL = 236 mm). Abbreviations: auapr, autogenous processes associated with basibranchial 2; bbtp, basibranchial toothplates; bhtp, basihyal toothplate; cl, cleithrum; co, coracoid; pas, parasphenoid; prhb2, bony process of basibranchial 2; sh, sternohyoideus; tsh, tendinous connection of the sternohyoideus to the skeleton of the second gill arch; uh, urohyal. Scale bars = 10 mm.

1999) and between species (Sanford and Laurer, 1990). Such functional variation of the TBA suggests unappreciated complexity of the morphology of the TBA.

In this study, I examined the morphological variation in a character complex, the so-called tongue-bite apparatus (TBA), in three genera (*Hiodon*, *Osteoglossum*, and *Chitala*), which represent three living clades of Osteoglossomorpha (Fig. 1). The monophyly of Osteoglossomorpha, even without the TBA (Patterson and Rosen, 1977; Shen, 1996), is well supported (Greenwood, 1973; Li and Wilson, 1996; Taverner, 1998), although Shen (1996) questioned inclusion of some Asian Mesozoic genera. In addition to the TBA and processes on the second hypobranchials and/or basibranchials (Greenwood et al., 1966), Li and Wilson (1996) listed six characters indicating monophyly of Osteoglossomorpha, including (1) 18 or fewer principle caudal fin rays (Patterson and Rosen, 1977), (2) intestine passing to the left of the stomach (Nelson, 1972), (3) one or zero epurals, (4) supramaxilla absent, (5) supraorbital absent, and (6) fused infraorbital 4 and 5. Therefore, monophyly of the group is not under question here. Rather, this paper is concerned with describing the variation within a character complex and emphasizing the importance of clearly defining and illustrating component characters. Often, variation is poorly known even in frequently used phylogenetic characters. Morphological variation may influence the way that researchers make statements of homology (Grande and Bemis, 1991, 1998; Hilton and Bemis, 1999), which in turn may influence phylogenetic analyses. Character complexes also may add difficulty to the study of character evolution. It often is an unsubstantiated assumption that all components of a character complex evolved simultaneously (Fink and Fink, 1996). Additionally, the component characters of a complex may be multistate, and to lump them

all into a dichotomous "present or absent" character ignores this variation.

MATERIALS AND METHODS

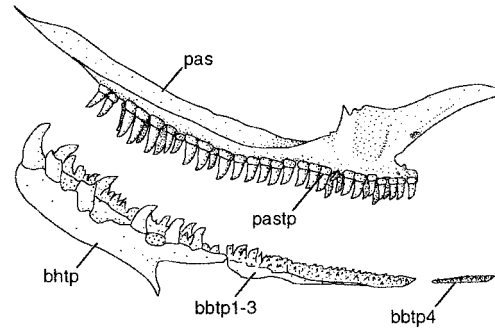
Specimens studied are from the collections of the University of Massachusetts Museum of Natural History, Amherst (UMA) and Harvard University's Museum of Comparative Zoology (MCZ). Skeletal material examined consists of both dry and cleared-and-double-stained (Dingerkus and Uhler, 1977) specimens: *Hiodon alosoides*: UMA F10150 (SL = 293 mm), UMA F10337 (SL = 99 mm), and UMA F10338 (SL = 255 mm); *Chitala* sp.: UMA F10341 (SL = 75 mm), UMA F10342 (SL = 71 mm), and UMA F10349 (SL = 437 mm); *Osteoglossum bicirrhosum*: UMA F10335 (SL = 236 mm), UMA F10336 (SL approximately = 55 mm), and UMA F10160 (SL = 365 mm), *Osteoglossum* sp.: UMA F10334 (SL = 185 mm).

Fresh, frozen, cleared-and-double-stained, and formalin-fixed specimens stored in 70% ethanol were dissected to examine musculature and ligaments: *Hiodon alosoides*: UMA F10149 (2 specimens; SL = 170 and 300 mm), UMA F10159 (SL = 300 mm), UMA F10340 (2 specimens; SL = 120 and 180 mm) and UMA F10380 (SL = 280 mm); *Chitala* sp.: UMA F10339 (SL = 70 mm) and MCZ 156815 (5 specimens, 2 dissected; SL = 320 mm); *Osteoglossum* sp.: MCZ 99472 (SL = 260 mm), MCZ 128261 (head only; SL approximately = 300 mm), and MCZ 156813 (2 specimens, 1 dissected; SL approximately = 80 mm). Dissections were made using a Wild M5A dissecting microscope equipped with fiber optic lights. Lugol solution (Weigert variation; Humason, 1979) was used during muscle dissection to help distinguish fiber direction and extent. Muscle names follow Winterbottom (1974). Specimens were photographed using 35 mm slide film or 9 × 12 cm sheet film, and line drawings were created from these photographs using Adobe Illustrator software. Character analysis was performed using the heuristic search option of PAUP (vers. 3.1.1, D. L. Swofford, PAUP: phylogenetic analysis using parsimony, Smithsonian Institution, Washington, DC, 1993, unpubl.) and MacClade (vers. 3.06, W. P. Maddison and D. R. Maddison, 1996, unpubl.).

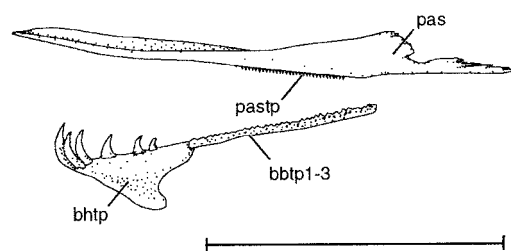
RESULTS

Osteological variation.—As shown in Figure 1, the overall arrangement of skeletal components of the TBA differ dramatically in *Hiodon*, *Chitala*, and *Osteoglossum*. *Hiodon* bears enlarged teeth

A. *Hiodon alosoides*



B. *Chitala* sp.



C. *Osteoglossum bicirrhosum*

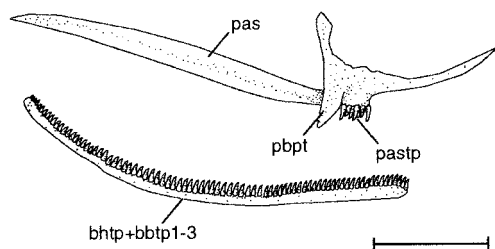


Fig. 2. Isolated parasphenoid bones, basihyal toothplates and basibranchial toothplates from (A) *Hiodon alosoides* (UMA F10150; SL = 293 mm), (B) *Chitala* sp. (UMA F10341; SL = 75 mm), and (C) *Osteoglossum bicirrhosum* (UMA F10335; SL = 236 mm), showing the variation of tooth form and distribution of tooth bearing elements. Anterior facing left. Abbreviations: bbtp, basibranchial toothplates; bhtp, basihyal toothplate; pas, parasphenoid; pastp, parasphenoid tooth patch; pbpt, basipterygoid process. Scale bars = 10 mm.

along almost the entire ventral surface of the parasphenoid (Fig. 2A). In contrast, *Chitala* bears small, anteriorly directed teeth on the middle portion of the parasphenoid (Fig. 2B). *Osteoglossum* has a small patch of teeth far posterior on the parasphenoid, positioned between the basipterygoid processes (= ventrolateral

processes of Arratia and Schultze, 1991; Fig. 2C).

The basihyal toothplate of *Hiodon* possesses paired posteroventral processes and greatly enlarged teeth along its lateral borders with smaller teeth distributed randomly between them (Fig. 2A). The basihyal toothplate of *Chitala* (Fig. 2B) is similar in overall form to that of *Hiodon* but is much shorter. *Hiodon* and *Chitala* both have an anterior basibranchial toothplate lying over basibranchials 1–3 (Fig. 2A–B). A small, separate toothplate lies dorsal to basibranchial 4 in *Hiodon* (Fig. 2A). The anterior margin of the basibranchial toothplate in *Hiodon* tightly contacts the basihyal toothplate, although the two elements remain separate. The basihyal and basibranchial toothplates of *Chitala* are not as closely united as in *Hiodon* but contact each other along their lateral edges. The basibranchial toothplates of *Hiodon* and *Chitala* bear small, randomly distributed conical teeth. In *Osteoglossum*, the basihyal and basibranchial toothplates are fused to form a single, elongate, dorsally curved toothplate (Fig. 2C) that bears small conical teeth, with those along the margin being slightly enlarged. The basibranchial portion of this toothplate lies dorsal to basibranchials 1–3; the toothplate for basibranchial 4 has presumably been lost.

The endopterygoid in *Hiodon* bears a small patch of teeth along its lateral edge (Fig. 3A). *Chitala* has a few small teeth organized in one or two rows along the medial edge of the endopterygoid, which, as in *Hiodon*, is a fairly thin bone (Fig. 3B). *Chitala* also has a small patch of small teeth in the posterior region of the endopterygoid. The endopterygoid is much more robust in *Osteoglossum* than in either *Hiodon* or *Chitala*, and bears mostly short and rounded teeth, with the exception of a single medial row of enlarged and slightly laterally curved teeth (Fig. 3C).

The ectopterygoid and dermopalatine bones form the lateral margin of the suspensorium. In *Chitala* and *Osteoglossum*, these two elements are fused, although the tooth patches remain distinct. In *Hiodon* (Fig. 3A), the dermopalatine teeth are organized in two rows, with those of the lateral row slightly smaller than those of the medial row, although similar in number. The lateral-most row of teeth on the ectopterygoid are of similar form and size as those of the dermopalatine. Medially, however, the much smaller teeth are scattered in several rows anteriorly and a single row posteriorly. The distribution of ectopterygoid and dermopalatine teeth in *Chitala* is nearly identical to the condition found in *Hiodon*, with the exception that the medial der-

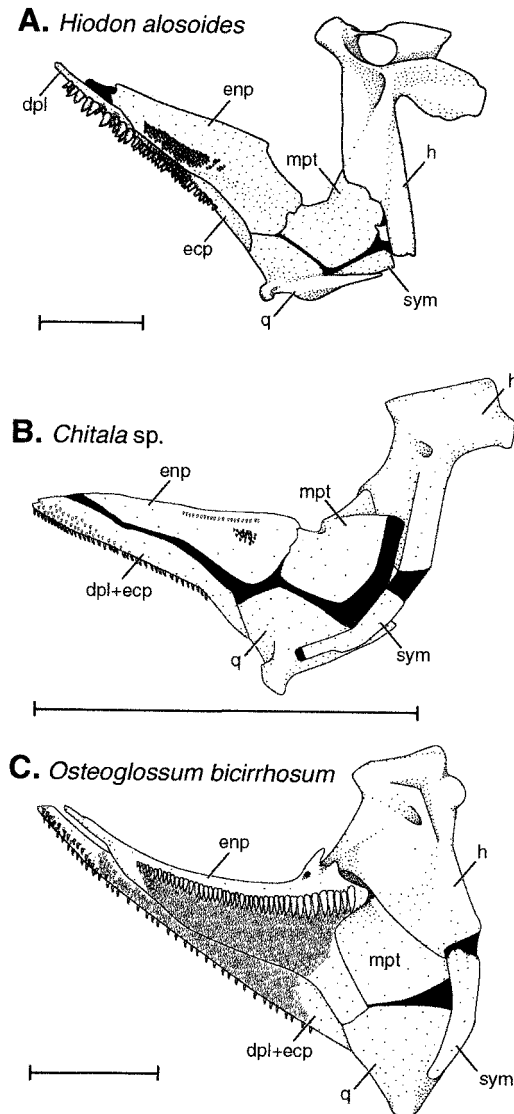


Fig. 3. Suspensoria from (A) *Hiodon alosoides* (UMA F10150; SL = 293 mm), (B) *Chitala* sp. (UMA F10342; SL = 71 mm), and (C) *Osteoglossum bicirrhosum* (UMA F10160; SL = 365 mm), showing the variation of tooth form and distribution on these elements. Anterior facing left. Abbreviations: dpl, dermopalatine; ecp, ectopterygoid; enp, endopterygoid; h, hyomandibula; mpt, metapterygoid; q, quadrate; sym, symplectic. Scale bars = 10 mm.

mopalatine teeth in *Chitala* are scattered in more than two rows (Fig. 3B). The ectopterygoid of *Osteoglossum* (Fig. 3C) bears a patch of small rounded teeth. Along the lateral edge of this patch, the teeth become sharply pointed. This lateral row of teeth is continuous with the outer row of teeth on the dermopalatine, which

are small, sharply pointed, medially recurved and scattered in three or four rows.

Hiodon lacks processes associated with the second hypobranchial and basibranchial elements, although a tendon from the sternohyoideus muscle inserts on the second hypobranchial and basibranchial (Fig. 4A). In *Chitala*, a pair of autogenous processes (Sanford and Lauder, 1989) lie lateral to the sternohyoideus muscle. The proximal ends of these elements are associated with, but not fused to, both hypobranchial 2 and basibranchial 2 (Fig. 4B). In *Osteoglossum*, there is an elongate process extending ventrally from the proximal end of the second hypobranchial (Fig. 4C) and was found to be already well developed in a small specimen (UMA F10336; SL = approximately 55 mm).

Myological variation.—A protractor hyoideus muscle (= fused posterior intermandibularis and interhyoideus muscles) is present in *Hiodon* and *Osteoglossum*; in *Chitala* the posterior intermandibularis is elongate, separate from the interhyoideus and serves as the hyoid protracting muscle (Table 1). These muscles run from the anterior elements of the gill arches (e.g., ceratohyal) and attach to the lower jaw near the symphysis of the dentaries. The “protractor hyoideus complex” of *Hiodon* (Greenwood, 1971: 9) is best described as a protractor hyoideus muscle because the division between the posterior intermandibularis and interhyoideus muscles described by Greenwood (1971) was not observed in large specimens dissected here (e.g., 300 mm SL; UMA F10159). Greenwood (1971) stated that the two muscles do share some fibers; thus, it is possible these muscles become increasingly fused during ontogeny, because his largest specimen was only 185 mm SL. Dissection of smaller individuals (e.g., 120–180 mm SL; UMA F10340) showed that the fusion of the posterior intermandibularis and interhyoideus muscles was of varied extent, with some individuals resembling the specimen figured by Greenwood (1971:fig. 3).

In *Hiodon*, thick connective tissue joins both the hypaxial musculature and the sternohyoideus to the ventral “keel” formed by the paired coracoid bones, indirectly connecting the hypaxial musculature of the trunk to the ventral portion of the sternohyoideus. In contrast, the hypaxial and sternohyoideus muscles of *Chitala* and *Osteoglossum* are separate.

In *Hiodon*, a portion of the sternohyoideus muscle originates from the dorsal surface of the horizontal arm of the pectoral girdle; it runs forward and inserts onto the urohyal. A tendon, arising from superficial dorsal sternohyoideus

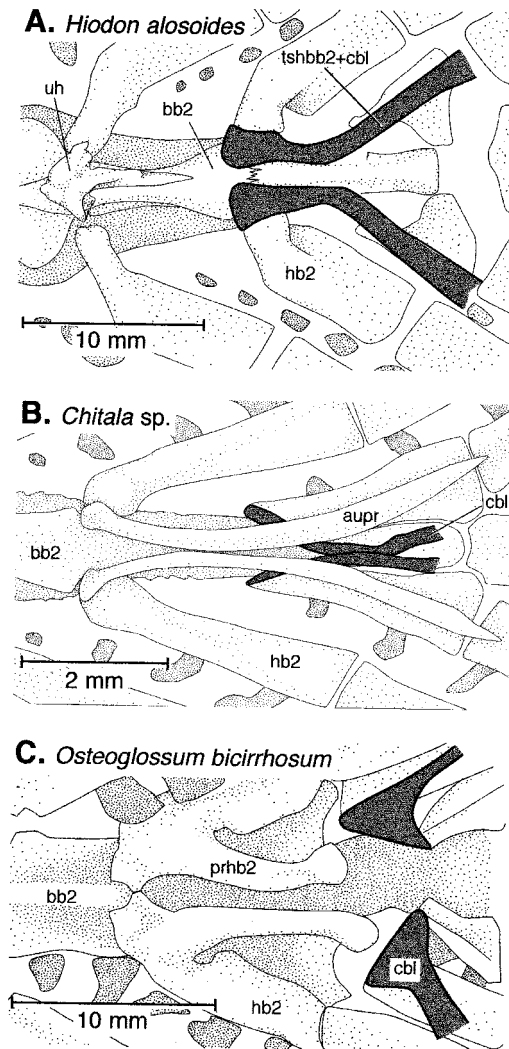


Fig. 4. Ventral surface of the gill arches in three osteoglossomorph fishes showing the variation of the “second hypobranchial process.” (A) *Hiodon alosoides* (UMA F10338; SL = 255 mm), (B) *Chitala* sp. (UMA F10342; SL = 71 mm), and (C) *Osteoglossum bicirrhosum* (UMA F10160; SL = 365 mm). The sternohyoideus has been omitted from this figure to show the more dorsal skeletal and soft tissue structures. Ligaments and tendons are shown in gray and illustrate their proximal attachments (i.e., drawn as if they have been cut distally). Interarcual ligaments (ligaments between gill arches) have been omitted. Anterior facing left. Abbreviations: aupr, autogenous processes associated with basibranchial 2; bb2, basibranchial 2; cbl, cleithrobranchial ligament; hb2, hypobranchial 2; prhb2, bony process of basibranchial 2; tsh, tendinous connection of the sternohyoideus to the skeleton of the second gill arch; uh, urohyal.

TABLE 1. SUMMARY OF SOME CHARACTERS OF THE TBA MENTIONED IN TEXT. Abbreviations: aupr, autogenous processes associated with basibranchial 2; CBL, cleithrobranchial ligament; bb2, basibranchial 2; cha, anterior ceratohyal; hbpr2, bony process of hypobranchial 2; hh, hypohyal; PH, protractor hyoideus; PIM, posterior intermandibularis; tshhb2, tendon from the sternohyoideus to hypobranchial 2.

Taxa	2nd Gill arch process	Sternohyoideus origin	Sternohyoideus insertion	Hyooid protractor	CBL
<i>Hiodon</i>	none	cleithrum and hypaxial muscles	uh and bb 2	PH	present (+tshhb2)
<i>Chitala</i>	autogenous processes	cleithrum	uh, hh, cha and aupr	PIM	present
<i>Osteoglossum</i>	bony process	cleithrum	uh and hbpr2	PH	present

fibers and a fan of superficial ligamentous tissue attached to the cleithra, joins the cleithrobranchial ligament (see below) and inserts on hypobranchial 2 and basibranchial 2 (Fig. 4A; Greenwood, 1971:fig. 4). In *Chitala*, the sternohyoideus originates entirely from the dorsal surface of the pectoral girdle, which is positioned more vertically than in either *Hiodon* or *Osteoglossum* (Fig. 1), resulting in a more horizontal path of the sternohyoideus muscle (Fig. 1). In *Osteoglossum*, the greater portion of the sternohyoideus originates from the dorsal surface of the pectoral girdle, although the ventral portion originates from the anterior edge of the coracoid (Fig. 1).

The autogenous processes of *Chitala* are closely associated with the sternohyoideus, with a few fibers attaching directly on their medial surface (Greenwood, 1971; pers. obsv.). The sternohyoideus is completely medial and partially ventral to these bones. In *Osteoglossum*, the second hypobranchial processes are also closely associated with the sternohyoideus muscle, with fibers attaching to the length of this process (Greenwood, 1971; pers. obsv.).

A cleithrobranchial ligament (CBL) provides a direct link between the pectoral girdle and the gill arch skeleton. The paired CBL in *Hiodon* run from the dorsal surface of the horizontal arm of the cleithra, between the left and right portions of the sternohyoideus, to the second basibranchial, and are joined by the tendons arising from the sternohyoideus muscle. The CBL of *Chitala* and *Osteoglossum* is Y-shaped. It originates on the pectoral girdle as a single ligament, splits and attaches at two points on the ventral surface of the gill arch skeleton. In *Chitala*, the CBL runs dorsally from the ventral apex of the cleithra (Fig. 1) and attaches to the proximal end of hypobranchial 3 (Fig. 4B). In *Osteoglossum*, the CBL originates from the dorsal surface of the horizontal arm of the cleithra and runs nearly vertical before fanning out and

attaching to the proximal ends of hypobranchial 3 and possibly hypobranchial 4 (Fig. 4C).

DISCUSSION

Occurrence and variation of the parasphenoid-tongue bite.—Small dentition on a single basihyal tooth plate and a tooth plate associated with the first three basibranchials is primitive for teleostean fishes, and many groups have independently enlarged the teeth of these plates (Nelson, 1969). Arratia and Schultze (1991) found the presence of teeth on elements of the suspensorium to be plesiomorphic for actinopterygians. These teeth are often greatly enlarged in osteoglossomorphs, as well as in other lineages of teleosts (e.g., albuloids, Forey, 1973; Osmeriformes, Williams, 1997). Parasphenoid teeth are present in many groups of basal teleosts (Patterson, 1975; Arratia, 1997, 1999). Arratia (1999, character 12) distinguished a plesiomorphic and two apomorphic states for the presence of parasphenoid teeth, and found that presence of small, denticle-like teeth is primitive for teleosts, enlarged parasphenoid teeth is a synapomorphy of Osteoglossomorpha and loss of parasphenoid teeth is a synapomorphy of clupeocephalans. However, as noted by Arratia (1999:fig. 19), neither of the apomorphic states are uniquely derived and there are many exceptions for each of these groups. For example, small parasphenoid teeth are found in the fossil ostariophysans †*Gordichthys* and †*Tischlingerichthys*, and the fossil euteleost †*Leptolepides* (Arratia, 1997, 1999) and the fossil clupeomorph †*Diplomystus* possesses a tooth patch “which looks very much like the parasphenoid tooth patch in *Osteoglossum*” (Grande, 1982:8). Among living teleosts, parasphenoid tooth patches are found only in osteoglossomorphs, elopiformes, and some percoids (Gosline, 1971). When present, these patches typically consist of small, denticle-like teeth (e.g., *Elops*; Forey, 1973), although some taxa,

such as *Albula*, have greatly enlarged, molariform teeth. As demonstrated by the small sample of osteoglossomorph diversity described here, great variation in the distribution and form of parasphenoid teeth exists among osteoglossomorphs, and this variation only increases with a survey of more taxa. For example, the parasphenoid in *Gymnarchus* (a mormyroid) and *Heterotis* (an osteoglossoid) are edentulous (Taverne, 1972, 1977). Taverne (1969, 1971, 1972) showed that mormyroids have substantial tooth patches on the parasphenoid (with the exception of *Gymnarchus*), but the teeth range from relatively small and conical (e.g., *Hippopotamyrus*) to large and molariform (e.g., *Hyperopisus*).

Both the presence and condition of the bony processes associated with the second hypobranchial elements are variable within Osteoglossomorpha, and the condition of these processes is unknown for many fossil taxa. Additionally, such processes are likely involved in the TBA of osteoglossomorph fishes by providing a direct link between the sternohyoideus muscle and the ventral branchial skeleton. Greenwood (1971) remarked on the tendinous attachment of the sternohyoideus muscle to the second hypobranchials in *Hiodon* and suggested that it was significant in the evolution of the hypobranchial processes of other osteoglossomorphs. However, it is likely that these tendons represent a derived state of the cleithrobranchial ligament (i.e., they have a tendinous component rather than being pure ligaments, as in other neopterygians that possess CBLs). The development of the hypobranchial processes is insufficiently understood to validate the statement of homology between the autogenous processes of notopteroids and the bony processes of mormyroids and osteoglossoids. Nelson (1968) questioned the homology between the autogenous processes of the notopterids and the second hypobranchial processes of osteoglossoids and mormyroids. Greenwood (1973) described a "line of fusion" between the process and its hypobranchial in small specimens of *Heterotis*, *Osteoglossum*, and *Scleropages*, but not in *Pantodon*, *Arapaima*, *Petrocephalus*, and *Marcusenius*, suggesting that the hypobranchial processes of osteoglossoids and mormyroids develop as independent ossifications, thus supporting the homology with the autogenous processes of notopterids. The presence of well-developed hypobranchial processes in a small specimen of *Osteoglossum* studied here shows that this statement of homology is still in question. Even within mormyroids and osteoglossoids, there is considerable variation in the form of these processes. For example, the pro-

cesses in the mormyroid *Gnathonemus* are thin, elongate elements that lie lateral to the sternohyoideus, whereas in the osteoglossoid *Arapaima*, these processes are very short and are just barely imbedded in the sternohyoideus (pers. obsv., Greenwood, 1971). A detailed study comparing the development of the second hypobranchial processes within Osteoglossomorpha might help to clarify this homology.

A CBL occurs in many actinopterygians (Sanford and Lauder, 1989), and within osteoglossomorphs this ligament has a variable orientation, which may have consequences in the function of the TBA. The condition of having a tendon attached to the branchial skeleton is unique to *Hiodon* (Fig. 5). Fibers of the sternohyoideus directly attach to the autogenous processes of notopteroids and the bony processes of osteoglossoids and mormyroids (Fig. 5). What appears unique to Osteoglossomorpha is the more general character of having a direct connection of the sternohyoideus muscle to the posterior portion of the ventral gill arch skeleton (i.e., posterior of the hyoid arch), although this character is dependent on the presence of either a tendon, as in *Hiodon*, or a process on the gill arch skeleton, as in other osteoglossomorphs, and is thus of questionable nature as a discrete systematic character (Fig. 5). The presence of such a musculo-skeletal link is unlikely to be directly observed in fossil osteoglossomorphs, although it may be confidently inferred by the presence of the paired processes associated with the second gill arch skeleton (autogenous or attached). However, this still does not allow for the recognition of this component character of the TBA in fossil *Hiodontiformes* or stem-group osteoglossomorphs, because the connection in at least *Hiodon* is comprised of soft-tissue (i.e., is tendinous) and the presence of this tendon cannot be inferred through osteological correlates (e.g., scarring on the bone due to the insertion of the tendon); for these fossil taxa, this character would need to be coded as "unknown." Inclusion of such a character may add to the cladistic information (e.g., Fig. 5) but cannot be used in addition to the osteological character of the paired bony processes.

A tongue bite apparatus has been reported in several teleost groups, both with morphological definitions (e.g., albulids, Forey, 1973; osmeroids, galaxiids, and salmonids, Fink and Weitzman, 1982; Williams 1997) and functional definitions (e.g., salmonids, C. P. Sanford, pers. comm.). Some of these (e.g., osmeroids, galaxiids, and salmonids) are fundamentally different from the TBA of osteoglossomorph fishes

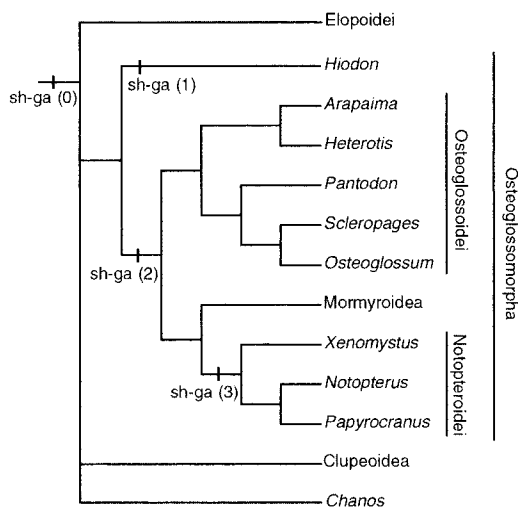


Fig. 5. A hypothesis of relationships among living osteoglossomorph fishes derived from analysis of the data matrix of Li and Wilson (1996) after deletion of their character 6 ("primary bite between parasphenoid and basihyal") and character 8 ("paired tendon bones on 2nd hypobranchial"). This tree is the consensus of two equally parsimonious trees (56 steps for 48 characters) and relationships within Osteoglossomorpha are consistent in topology to the tree presented by Li and Wilson (1996). Plotted on this tree is the distribution of various character states of the connection of the sternohyoideus to the skeleton of the ventral gill arches (sh-ga). No direct connection is the primitive state for teleosts (0). A tendinous connection of the sternohyoideus to the second branchial arch is found only in *Hiodon* (1). A direct connection via a bony process of the hypobranchial 2 is found in osteoglossoids and mormyroids (2). A direct connection via autogenous bony elements associated with the second branchial arches is found in the notopteroids (3).

because the dentition is excluded from the parasphenoid. However, there are a number of examples in which the parasphenoid is involved in the "bite," most notably Elopiformes (including albulids). Forey (1973:193) described occlusion of palatal/parasphenoid and branchial dentition in a number of elopiforms and stated, "The similarity [of elopiforms and osteoglossomorphs] in buccal occlusion may be explained as the retention of a primitive feature, such as is found in pholidophorids, and is therefore of little use in indicating relationship [between elopiforms and osteoglossomorphs]." If occlusion of teeth on the dorsal and ventral elements of the oral cavity (a "parasphenoid-tongue bite") is the plesiomorphic condition at this level of Teleostei (see also Ridewood, 1904:213), then it is necessarily plesiomorphic to Osteoglossomorpha. Furthermore, with teeth appro-

priately distributed, any movement of the gill arches in either the dorso-ventral or antero-posterior plane would produce a bite between the teeth of the gill arches and those of the palate and cranium.

Lauder (1995) suggested that function of the TBA in osteoglossomorphs could not be inferred from morphology alone, citing the kinematic variation discovered by Sanford and Lauder (1990). If the osteoglossomorph TBA is defined in functional terms and, as according to Lauder (1995), function cannot be inferred from form and the osteoglossomorph TBA can only be identified by a preconceived idea of relationships, then the use of the tongue bite as a synapomorphy of Osteoglossomorpha is logically circular. However, if a strictly morphological definition is followed, the TBA can be divided into component characters and may be identifiable in fossils and in living organisms in which function is not studied directly. Lauder's (1995) statement followed a model of a single "tongue bite morphology." To reduce the TBA to a single character misrepresents the morphological diversity of Osteoglossomorpha.

The parasphenoid-tongue bite as a character complex.—If this character is coded as "parasphenoid TBA: present or absent," with the TBA defined simply as occlusion of palatoquadrate and parasphenoid dentition with basihyal and basi-branchial dentition (as is currently understood from the literature), then parsimony dictates that the TBA is plesiomorphic for teleosts. However, the morphology, and the TBA itself, is not that simple. The TBA of Osteoglossomorpha is best regarded as a complex of both the plesiomorphic condition of tooth bearing elements of the cranium, palatoquadrate and gill arches and the apomorphic condition of possessing enlarged teeth on the parasphenoid and a direct musculo-skeletal connection between the pectoral girdle and the posterior ventral gill arch skeleton. The mode of this connection is variable, dependent on the morphology of the ventral gill arch skeleton (e.g., presence and type of processes) and each of the derived states of the musculo-skeletal connection is diagnostic of certain subgroups of Osteoglossomorpha and not of the group as a whole (Fig. 5). The processes are a component of the TBA which may be identified in both fossil (given adequate preservation) and living taxa.

Oversimplification of complex characters may lead to spurious conclusions in the analysis of relationships and the evolution of morphology within groups of fishes. Fink and Fink (1996), in discussion of the Weberian apparatus of os-

tariophysan fishes, emphasize the distinction between the components of a complex character evolving at a single time and the components of a complex character evolving *all* at a single time. In their character list, Fink and Fink (1996) suggest that the Weberian apparatus is a culmination of various characters and character states, which only when present together diagnose Otophysi, a subgroup of Ostariophysini. Information regarding the acquisition of characters and character states related to the Weberian apparatus would be lost if this character were reduced to a dichotomous, present or absent character. This example is analogous to the TBA of Osteoglossomorpha. If the component characters of the TBA, such as the connection of the sternohyoideus to the gill arch skeleton, are analyzed as independent characters, greater resolution of the acquisition of character states related to the TBA is discovered. Additionally, to use both the presence or absence of the TBA as well as its component characters would increase the weight of this character complex in systematic analyses. In certain instances, simplification of complex characters to a single character may be possible. However, the TBA should not be used in place of, and especially not in addition to, its component characters as support of Osteoglossomorpha.

ACKNOWLEDGMENTS

I thank C. P. Sanford, who enthusiastically shared many of his ideas about the tongue-bite apparatus, including unpublished results of functional studies. Comments and suggestions of W. E. Bemis, E. L. Brainerd, L. Grande, N. J. Kley, C. P. Sanford, P. L. Forey, B. Gardiner, G. D. Johnson, M. V. H. Wilson, H.-P. Schultze, and an anonymous reviewer greatly improved the clarity and content of both this project and the resulting paper. I thank W. E. Bemis, M. Mandica, P. Cieslewicz, and J. Hendrickson for donation of some specimens, and K. Hartel for loan and permission to dissect specimens borrowed from the MCZ. This research was in part supported by a National Science Foundation Doctoral Dissertation Improvement Grant (DEB-0073066), the Margaret E. and Howard E. Bigelow Gift to O. E. B. (UMass Amherst), Sigma-Xi Grants-in-Aid of Research, Woods Hole Scholarship Fund (UMass Amherst), and a research assistantship from the Graduate Program in Organismic and Evolutionary Biology (UMass Amherst).

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