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Functional and Phylogenetic Implications of the Vesicular Swimbladder of *Hemiramphus* and *Oxyporhamphus convexus* (Beloniformes: Teleostei)

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Dissection and histological analyses revealed the swimbladder of *Hemiramphus far* and *H. robustus* to comprise a matrix of discrete, gas-filled vesicles of 1–6 mm in diameter. The vesicles are not richly vascular and no discrete capillary bed organs were found. The anterior and posterior ends of the swimbladder have asymmetric projections that extend rostrad and caudad, respectively. These projections and some surrounding fatty tissue contain what we term protovesicles, which have thick walls that we infer expand to become the thin-walled vesicles of the main vesicular swimbladder. Dissection of museum specimens of other species of *Hemiramphus* and *Oxyporhamphus convexus* confirmed the presence of a vesicular swimbladder. However, examination of museum specimens of other hemiramphids, including *O. micropterus*, and flyingfishes revealed only a simple sac-like swimbladder. Presence of this unusual swimbladder in two genera within the same family is indicative of a strong synapomorphy that, in conjunction with recent molecular data, suggests that *Hemiramphus* and *Oxyporhamphus convexus* are closely related.

THE swimbladder is typically a gas-filled, sac-like evagination of the gut that primarily regulates buoyancy in bony fishes (Maina, 2000). However, the beloniform genus *Hemiramphus* is characterized by the presence of a vesicular swimbladder (Parin et al., 1980). Interestingly, the adults of one species of the genus *Oxyporhamphus*, *O. convexus*, which has been assigned variously to either of the two families of the superfamily Exocoetoidea, the Hemiramphidae (Collette, 2004) or the Exocoetidae (Dasilao et al., 1997), also possess a vesicular swimbladder. Parin (1961a) referred to this structure as a ''meristocystis'' swimbladder, naming *O. meristocystis*, now a junior synonym of *O. convexus* (Collette, 2004). This elaboration of the swimbladder as a series of vesicles is rare among teleosts. From our survey of the literature, only billfishes (Istiophoridae) also appear to have a swimbladder that is vesicular (La Monte, 1955), being composed of many separate compartments (La Monte, 1958; Nakamura, 1985). The related swordfish has a large, thick-walled, single-chambered swimbladder.

Compartmentalization of the organ seemingly contradicts our present understanding of the development (Goodsell et al., 1996; Zwerger et al., 2002), morphology (Harder, 1975), vascularization, and function (Zheng and Liu, 1988; Pelster, 2001, 2004) of the teleost swimbladder. Considerations of the functional morphology of the unusual swimbladder found in some halfbeaks must reflect on both the mode of inflation and maintenance of gas pressure and also the potential functions of the swimbladder. Accordingly, we investigated the structure of the vesicular swimbladder of *Hemiramphus*, *Oxyporhamphus,* and their close relatives to provide a detailed description of its morphology and to assess the potential value of the character in resolving a contentious area of beloniform phylogeny.

MATERIALS AND METHODS

To assess previous reports on the distribution of the vesicular swimbladder we investigated museum specimens of the following genera: *Arrhamphus*, *Chriodorus*, *Hemiramphus*, *Hyporhamphus*, *Melapedalion*, *Oxyporhamphus*, *Rhynchorhamphus,* and *Zenarchopterus* from the Hemiramphidae, and three genera of Exocoetidae. Note, however, that Collette (2004) and Aschliman et al. (2005) place *Zenarchopterus* in a separate family, Zenarchopteridae. *Arrhamphus sclerolepis krefftii* were captured by angling from the Brisbane River, southeast Queensland. *Hyporhamphus regularis ardelio* were captured by seine net from One Mile Beach, Moreton Bay. *Zenarchopterus buffonis* were captured by rotenone poisoning from Musgrave Creek, Cape York, north Queensland. Preserved material from the collection of the National Museum of Natural History was also dissected (Table 1).

Fish were measured for standard length using a ruler (± 1 mm), and viscera were removed through a cut along the ventral midline. A blunt probe was used to detach the peritoneum from the swimbladder, after which digital images were taken using a Nikon Coolpix 990.

Examination of unfixed material was performed on *Hemiramphus far* purchased frozen

TABLE 1. SPECIES, SOURCE, LENGTH, AND NOTES ON SWIMBLADDER STRUCTURE FOR SELECTED HEMIRAMPHIDS AND EXOCOETIDS*.

Species	Source	Standard length (mm)	Swimbladder
Arrhamphus sclerolepis krefftii	Brisbane River, Queensland	60–200	Simple single chamber, non-vesicular
**Cheilopogon heterurus*	USNM 158181, Alabama	134–170	Simple single chamber, non-vesicular
**Cheilopogon melanurus*	USNM 360730, Navassa I.	152–205	Simple single chamber, non-vesicular
**Cheilopogon pinnatibarbatus melanocercus*	Hervey Bay, Queensland	60	Simple single chamber, non-vesicular
Chriodorus atherinoides	USNM 292746, Florida	145	Simple single chamber, non-vesicular
Euleptorhamphus viridis	USNM 200593, Line Islands	270–290	Simple single chamber, non-vesicular
**Exocoetus volitans*	USNM 380581, South Atlantic	154–174	Simple single chamber, non-vesicular
Hemiramphus archipelagicus	USNM 348270-2, Philippine Islands	155–220	Vesicular
H. balao	San Salvador, Bahamas	193	Vesicular
H. bermudensis	USNM 292592, Bermuda	105	Vesicular, smaller vesicles posteriorly
H. brasiliensis	USNM 344910, Cuba	215–260	Vesicular
H. depauperatus	USNM 52723, Hawaii	235	Vesicular
H. far	North Queensland	189–210	Vesicular
H. lutkei	USNM 348266, Philippine Islands	190	Vesicular, large and clearly defined vesicles
H. marginatus	USNM 148022, Red Sea	133	Vesicular
H. robustus	Moreton Bay, Queensland	150–330	Vesicular, greater proportion of anterior and posterior small vesicle regions in smaller specimens
H. saltator	USNM 188885, Gulf of California	310	Vesicular
**Hirundichthys rondeletti*	USNM 211515, W.N. Atlantic	129–153	Simple single chamber, non-vesicular
Hyporhamphus regularis ardelio	Moreton Bay, Queensland	150	Simple single chamber, non-vesicular
Melapedalion breve	USNM 137604, Philippine Islands	190	Simple single chamber, non-vesicular
Oxyporhamphus micropterus	USNM 294296, Atlantic tropical	142	Simple single chamber, non-vesicular
O. convexus convexus	USNM 216279, New Guinea	97	Vesicular
O. convexus bruuni	USNM 321000, Somalia	150	Vesicular
Rhynchorhamphus georgii	USNM 214093, Gulf of Thailand	116, 200	Simple single chamber, non-vesicular
R. malabaricus	USNM 320998, India	173	Simple single chamber, non-vesicular
Zenarchopterus buffonis	Musgrave Creek, Queensland	75	Simple single chamber, non-vesicular

from a bait and tackle shop; *H. balao* supplied frozen by the Gerace Research Station in San Salvador, Bahamas; and *H. robustus* (150–330 mm SL) captured by seine netting from Myora, Moreton Bay, southeast Queensland. One fresh *H. robustus* (285 mm SL) and *Hyporhamphus regularis* (170 mm SL), also captured from Myora, were examined using X-ray imaging to assess whether the vesicular structure might be apparent by that method. We used a Toshiba Model KXO-60G X-ray Generator with a Toshiba Model DXB-0324CS=A X-ray tube taking images

on Fuji Medical X-ray film UM-MA HC at 45 kVp 100 mA for 80 msec.

Six *Hemiramphus robustus* from Myora (300–330 mm SL) were euthanized in ice slurry and the visceral cavity opened to allow penetration of the neutral buffered formalin fixative (10% NBF/seawater). A 300 mm SL specimen for histological analysis was trimmed of axial musculature to reduce the diameter of resultant cross sections, decalcified in Gooding and Stewart's solution (Gray, 1954), dehydrated in an ascending alcohol series, infused with xylene (two changes), embedded in paraffin wax at 57 C, the second being in vacuum, before the entire specimen was blocked in paraffin. The block when cooled was cut into four smaller blocks of equal length, serial transverse sections (8–10 μm) taken with a Spencer rotary microtome and mounted on gelatinized glass slides. Transverse sections were stained with Mayer's haematoxylin and 1% eosin in 70% ethanol and viewed under an Olympus BX41 compound light microscope. Images were captured using either an Olympus DP11 digital microscope camera or a Nikon Coolpix 990 through the triocular.

The resonant frequencies of vesicles in the swimbladder were estimated using the program Convert (Mandrake Linux). Vesicles were assumed to be perfect spheres, so volume was estimated as $4/3\Pi r^3$.

Results

Gross morphology.—The swimbladders of all ten species of *Hemiramphus* and both subspecies of *Oxyporhamphus convexus* are physoclistous and vesicular, whereas all other species examined are similar to the typical teleost physoclistous condition, having elongate, sac-like, single chambered swimbladders (Table 1). The non-vesicular hemiramphid and exocoetid swimbladders are thin walled, transparent (following removal of the guanine and pigment-rich peritoneum), poorly vascularized, have a pair of simple anterior projections, lack obvious communication with major blood vessels, and appear to lack both the rete mirabile and the oval body. All specimens lacked sonic muscles and the hypertrophied vascular structures usually associated with swimbladders: gas gland/rete mirabile and oval body.

Dissection revealed the swimbladder of *H. robustus* to consist of a matrix of small vesicles 3–5 mm in diameter and 2–4 vesicles deep, lying between the body cavity and the rib cage (Fig. 1A). While vesicles are variable in shape, they are broadly polygonal with hexagonal facets. Three anterior projections, which we refer to as horns, are bilaterally asymmetric and overlain with fatty tissue (Fig. 1B). They have a length of about 10 mm and contain many minute vesicles ranging between 0.1–0.5 mm in diameter. A flat, spade-shaped section of the swimbladder lies at the posterior end of the swimbladder (Fig. 1C). Like the anterior end, it is composed of minute vesicles and has a frothy appearance. This posterior section is approximately 15 mm long and 8 mm wide at the larger end, forming a tapering triangle that is 1–2 vesicle layers thick. Limited vascularization of the swimbladder tissue is apparent. Capillaries are infrequent within the matrix of vesicles and are more evident toward either end of the swimbladder. Puncturing individual vesicles in the swimbladder did not deflate adjacent vesicles, indicating that they are not interconnected in the fashion of alveoli, and the entire structure may be removed inflated from the gut cavity (Fig. 1D). An X-ray image of a 236 mm SL specimen of *H. robustus* indicated that the organ extends from vertebra 5 to vertebra 31/32 (Fig. 2A). The precise length and extent of the swimbladder is difficult to determine in dissections as the spatial relationships change during its separation from the peritoneum, rendering such images useful. Neither the anterior nor posterior horns were visible in oblique X-ray images indicating that they might not be gas filled. Apart from slight differences in position there were few differences apparent between the X-ray images of the swimbladder of *H. robustus* and that of *Hyporhamphus regularis* (Fig. 2B).

The swimbladder of *Hemiramphus far* is similar to that of *H. robustus*. It is composed of a matrix of thin-walled, translucent, gas-filled vesicles that are 1–6 mm in diameter. The swimbladder lies ventral to the kidneys and dorsal to the digestive tract, running from a point just posterior to the esophagus to just above the anus, and is 2–4 vesicles in diameter. Like *H. robustus* the organ is surrounded by the peritoneum, which is silver externally and black internally, and no muscles are associated with the wall of the swimbladder. Both the anterior and posterior extremities of the swimbladder terminate with lateral projections, horns (Fig. 3). The anterior medial horn is smaller than the lateral horns and appears to lack their structural complexity. The anterior and posterior horns are replete with minute (<1 mm dia.) vesicles, which have a frothy appearance. No well developed gas gland/rete mirabile vascular system was observed on that part of the swimbladder that comprised large vesicles, although small capillaries could be observed ramifying over the surface of vesicle walls. Puncturing vesicles did not cause adjacent vesicles to deflate,

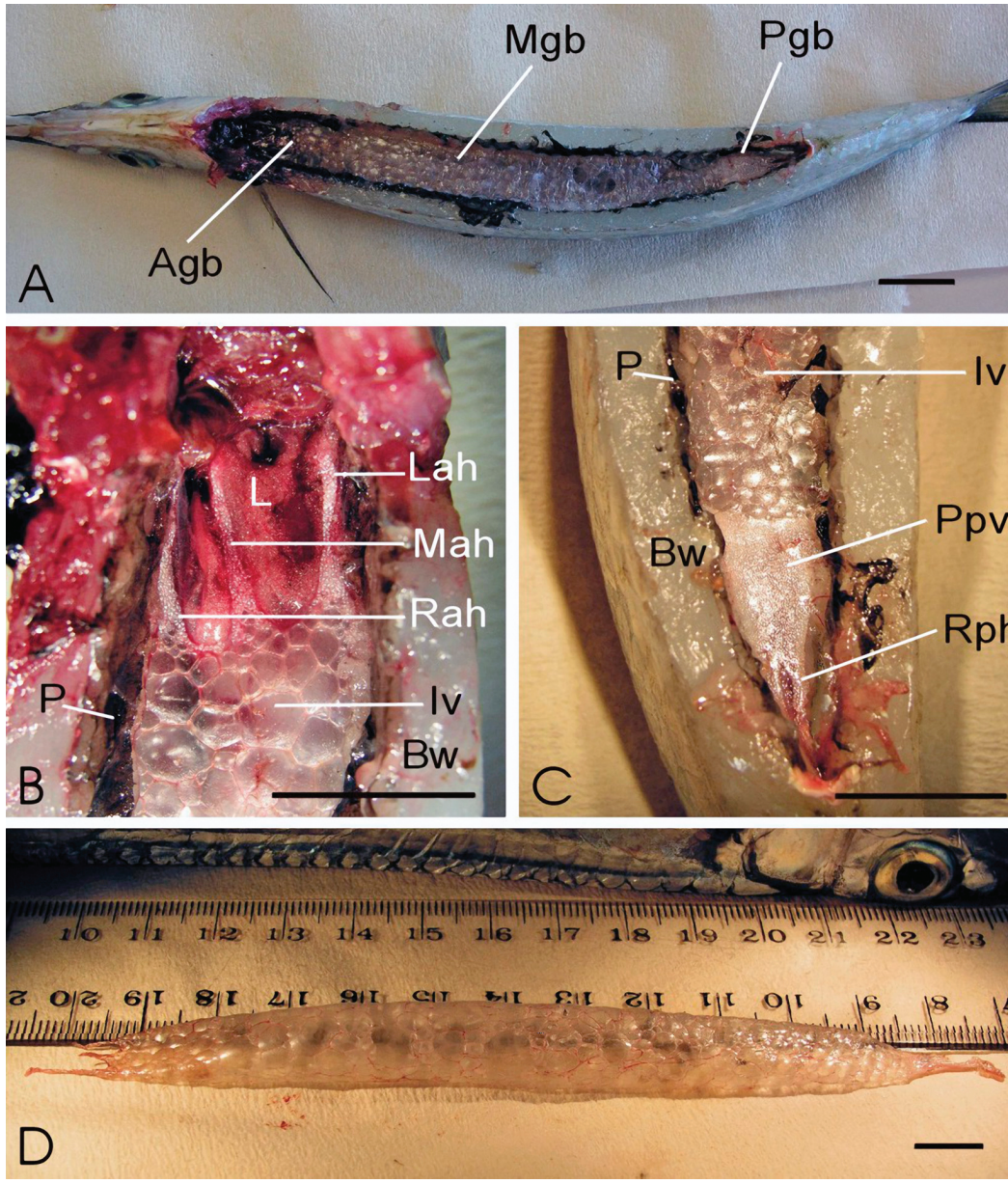

Fig. 1. Vesicular swimbladder of *Hemiramphus robustus* (200 mm SL). (A) Swimbladder of *H. robustus* 300 mm SL *in situ*, peritoneum and tunica externa removed, extending the entire length of the visceral cavity. Anterior to the left. (B) Ventral view of the three asymmetrical anterior horns. Note the frothy appearance of protovesicles and posteriorly fully expanded vesicles. Anterior to the top. (C) Ventral view of the spatulate posterior section of the swimbladder. Note the extensive field of frothy protovesicles lying posterior to fully expanded vesicles. Anterior is to the top. (D) Intact excised swimbladder showing retention of shape following excision. Anterior is to the left. Agp, anterior swimbladder; Bw, body wall; Iv, inflated vesicle; L, lipid tissue; Lah, left anterior horn containing protovesicles; Lph, left posterior horn; Mah, medial anterior horn; Mgb, mid swimbladder; P, peritoneum; Ppv, posterior protovesicles; Pgb, posterior swimbladder; Rah, right anterior horn. Scale bar = 1 cm.

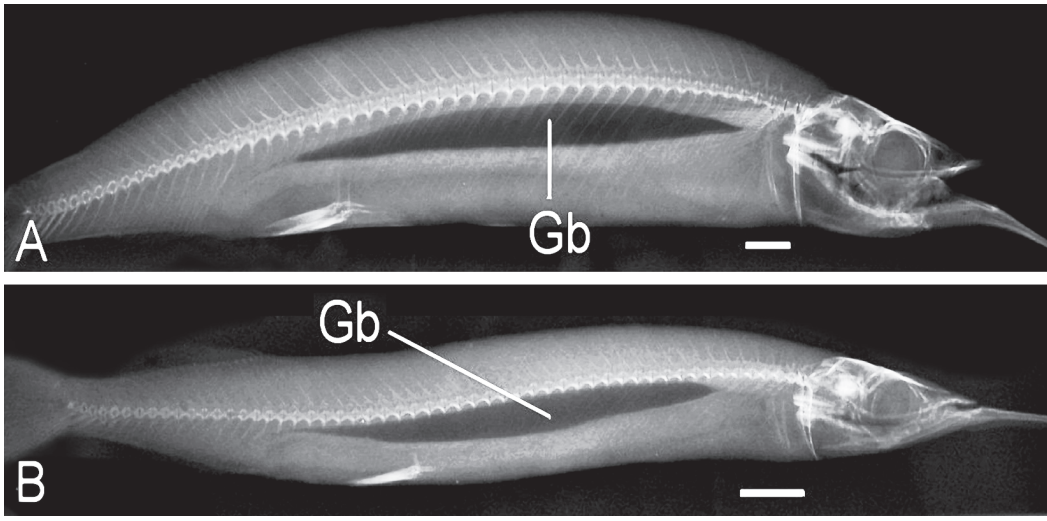

Fig. 2. X-ray images of the swimbladder (GB). (A) *Hemiramphus robustus* (285 mm SL) lateral. (B) *Hyporhamphus regularis* (170 mm SL) lateral. Scale bar = 1 cm.

indicating that the lumens of adjacent vesicles are not interconnected. Deflating about one-third of vesicles had little effect on the overall shape of the swimbladder.

Hemiramphus balao (193 mm SL) possesses a swimbladder that is characterized by a matrix of translucent, gas-filled vesicles 1–7 mm in diameter. The swimbladder is 3–5 vesicle layers in depth and terminates cranially with two bilaterally asymmetric horns. Vesicles within the horns diminish in size nearer the tips of the organ, which are located dorsal to the esophagus. Posteriorly, the swimbladder tapers to a spade-shaped structure that is saturated with minute vesicles. No hypertrophied vascular system appears to accompany the swimbladder.

Despite being quite delicate due to age and fixation, the swimbladders of *Oxyporhamphus convexus bruuni* and *O. convexus convexus* appear to consist of translucent, gas-filled vesicles of varying sizes. No vascular system was apparent, and no anterior or posterior horns could be discerned in the material we examined.

Microstructure.—Histological analysis of transverse sections of the anterior swimbladder of *Hemiramphus robustus* revealed small, relatively thick-walled vesicles with small lumens within the adipose tissue surrounding the anterior end of the swimbladder (Fig. 4A). These small vesicles occur both in clumps and independently (Fig. 4B, 4C) and seem to lack any connection with the main body of the swimbladder. Serial sections passing in sequence caudally revealed progressively more of these vesicles to be inflated, their walls becoming thin and their lumens very large relative to the thickness of the wall. This increase in size was not uniform among vesicles in any one section, as some remained uninflated when adjacent vesicles are of considerable size. The walls of the vesicles appear to be rich in elastin (Fig. 4B), although this was not confirmed by histochemistry.

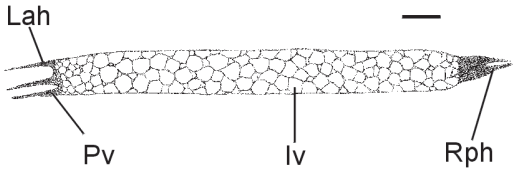

Fig. 3. Drawing of a swimbladder removed from the visceral cavity of *Hemiramphus robustus* (200 mm SL) in ventral view. Iv, inflated vesicle; Lah, left anterior horn; Pv, protovesicle; Rph, right posterior horn. Scale bar = 1 cm.

Discussion

The swimbladder of *Hemiramphus* and both subspecies of *Oxyporhamphus convexus* are characterized by a matrix of gas-filled vesicles ranging from 0.1–6 mm in diameter with the mid swimbladder having a width varying from 2–5 vesicle layers. The structure was termed by Parin (1961a) the ''meristocystis'' swimbladder in his description of *O. meristocystis*. No prominent rete and oval vascular system is apparent, and the organ terminates, anteriorly and posteriorly in

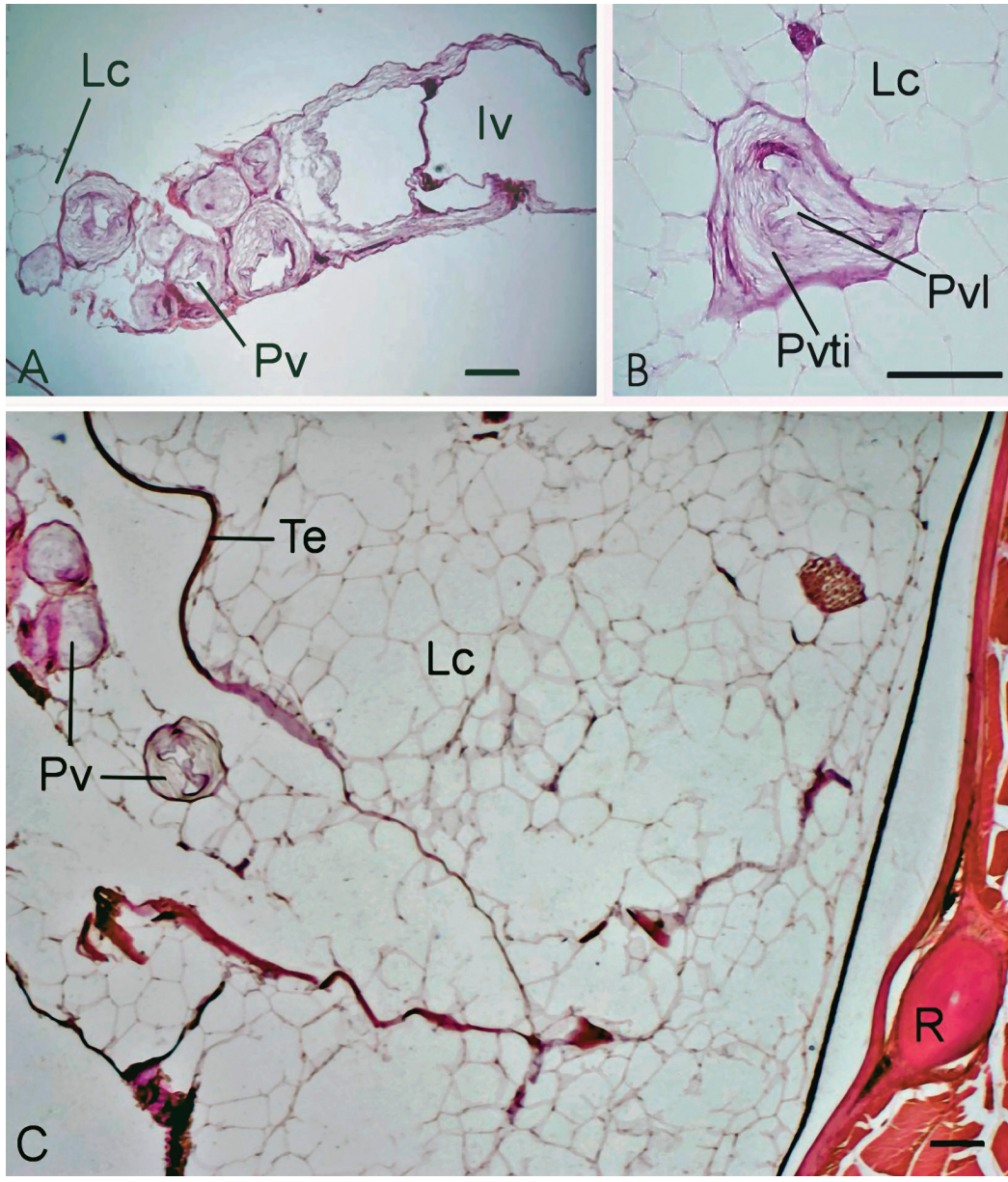

Fig. 4. Histology of the vesicular swimbladder of *Hemiramphus robustus* (300 mm SL). (A) Light micrograph of TS anterior vesicular swimbladder H&E. (B) Individual protovesicle among lipid cells (TS). (C) Relationship between the body wall, connective tissues, and the swimbladder (TS). Iv, inflated vesicle; Lc, lipid cell; P, peritoneum; Pv, protovesicles (wall, tunica interna); R, rib; Te, tunica externa; Pvl, protovesicle lumen. Scale bar = 100 μm.

a series of projections. These horns are replete with a multitude of minute vesicles, similar in structure to those in the mid portion of the swimbladder. In contrast, other physoclistous exocoetoids (*Arrhamphus, Cheilopogon, Chriodorus, Euleptorhamphus, Exocoetus, Hirundichthys, Hyporhamphus, Melapedalion, Rhynchorhamphus,* and the second species of *Oxyporhamphus*), with the exception of a discernible hypertrophied vascular system (viz., rete mirabile and oval body), have a single-chambered swimbladder. This confirms conclusions by Parin et al. (1980), who also refer to the swimbladder of these genera as single-chambered. Consequently, the morphology of the vesicular swimbladder has developmental, functional, and phylogenetic

implications for *Hemiramphus* and *Oxyporhamphus*.

Developmental implications.—Ontogenetic development of the vesicular swimbladder requires elucidation. Although the period of swimbladder development from juvenile to mature stages exhibits a great amount of structural diversity in fishes (Harder, 1975; Zheng and Liu, 1988; Zwerger et al., 2002; Yamada et al., 2004), detailed analysis of developmental stages will be required to understand both the function and phylogeny of the vesicular swimbladder. However, the presence of minute vesicles (which we term protovesicles due to the apparent developmental sequence observed by histological analysis) at the anterior and posterior ends of the swimbladder and among the adipose tissue of the anterior portion of the organ may indicate a possible mode of swimbladder development. These vesicles may differentiate within the terminal lateral horns of the swimbladder before being inflated and becoming incorporated in the mid, fully inflated, portion of the swimbladder. This is in contrast to the swimbladder of typical teleost fishes, which typically consists of a single undivided compartment that is thought to be inflated during a single event during development (Zheng and Liu, 1988; Goodsell et al., 1996; Zwerger et al., 2002; McCune and Carlson, 2004).

Understanding the development of the vesicular swimbladder in *Hemiramphus* will be of importance in determining the extent to which the swimbladder of *Hemiramphus* is homologous to that of *Oxyporhamphus*, and in addition will provide a useful perspective on its origin. Parin et al. (1980) reported of *Oxyporhamphus convexus* that the swimbladder is single-chambered in juveniles less than 100 mm SL and vesicular in fishes greater than 120 mm SL. In fishes of intermediate length, the anterior part of the swimbladder is vesicular and the posterior part is simple. This suggests that vesicularization is derived as an elaboration subsequent to the formation of a basic swimbladder, possibly by infolding of the tunica interna. However, histologically *Hemiramphus* appeared to have some protovesicles in lipid tissue surrounding the anterior swimbladder. Thus, at least in one small group of teleosts, elaboration of the swimbladder might be possible by a mechanism other than the simple inflation of an evagination of the endoderm. The derivation of the organ from both mesodermal and endodermal tissue might explain this. Such a mechanism has been proposed (Hoar, 1937; Pelster, 2004). The arrangement and histology of the tissues, with respect to the relative positions of the peritoneum and associated pigment and crystal layers, certainly indicate that the structure is homologous with the general teleost swimbladder. However, this potentially idiosyncratic mode of deriving new units for inflation in the formation of this swimbladder might promote closer examination of the tissues involved in organogenesis in other teleosts.

Functional implications.—The mode of operation of the vesicular swimbladder as an organ for buoyancy control is also of considerable interest and uncertainty. The vesicles have no connection, making the utility of the organ for gas exchange (Liu, 1993) untenable. Also, gases in a single-chambered swimbladder are typically regulated by a hypertrophied vascular system including the rete mirable and the oval body (Prem and Pelster, 2000; Yamada et al., 2004), neither of which was found in the vesicular swimbladder. Inflation of vesicles likely occurs throughout the animal's development. Whether any senescence among vesicles occurs, requiring their replacement by neighboring uninflated vesicles is uncertain. Certainly there seems to be a pool of potential replacements, even in the region of greatest swimbladder diameter. Conversely, these interstitial, uninflated vesicles (protovesicles) may be either held available to accommodate increase in overall swimbladder volume with growth, particularly if the vesicles are fairly constant in maximum diameter, or merely packing to maintain the organ's shape. Beloniformes, including halfbeaks and flyingfishes, are epipelagic (Parin, 1961b). They likely have a very limited requirement for movement at depths exceeding a few meters. A swimbladder in which the vesicles once inflated remain so with little exchange of gases might have energetic advantages over the usual gas exchange system.

Functionally, the vesicular swimbladder may impart hydrostatic benefits on its possessor, largely a consequence of the added integrity of the swimbladder due to the numerous internal partitions. When removed, the bladder retains its shape and its structure is largely unaffected by puncturing even a third of the vesicles. The possible adaptive advantage of this increased swimbladder integrity is hard to determine, particularly given that so many of their relatives occupy an identical habitat yet lack this structure.

While hydrostatic advantages are conceivable, the flimsy walls of the vesicular swimbladder are unlikely to confer auditory benefits for its possessor. Auditory functions such as communication (Connaughton, 2004) and enhanced hearing (Laming and Morrow, 1981), including prey detection by sound amplification (Ramcharitar et al., 2004) have been suggested for teleost swimbladders. The calculated resonant frequency

of the inflated vesicles (15–19 kHz) falls well above the frequency of the cricket-like sounds (4 kHz; IT, pers. obs.) produced by operation of the hemiramphid pharyngeal jaw (Burkenroad, 1931; Tibbetts, 1991; Tibbetts and Carseldine, 2003), making a role in intraspecific communication through the amplification of stridulatory sounds (Rome et al., 1996) unlikely. However, compartmentalizing the swimbladder might reduce the amplification of sounds that might be detectable by predators, such as those generated by food processing activities in the pharynx, by a resonant organ. The use of audition in prey detection is unlikely, as these fishes consume plankton in the case of *Oxyporhamphus* and both plankton and floating plants in the case of *Hemiramphus*. The calculated resonant frequency of protovesicles (80 kHz) falls within the range used by dolphins in echolocation (40–140 kHz), so it is possible that if these small vesicles resonate then they might amplify the echolocatory sounds of a predator (Shane, 1990).

Future discussion about the function of vesicular swimbladders must include reference to the Istiophoridae (La Monte, 1955, 1958), which share this trait and are also epipelagic. However, istiophorids descend to much greater depths than beloniforms. Interestingly *Oxyporhamphus* is a prey item of certain istiophorids (Vaske et al., 2004). The independent derivation of a vesicular swimbladder in this habitat, yet apparently nowhere else in the diversity of fishes, moreover between predator and prey, is remarkable.

Phylogenetic implications.—The vesicular swimbladder found in *Hemiramphus* and one species of *Oxyporhamphus* may also have phylogenetic implications. Conflicting viewpoints exist as *Oxyporhamphus* has been included in the Hemiramphinae by Collette (2004) yet assigned to the Exocoetidae by Dasilao et al. (1997). The swimbladder of *Oxyporhamphus convexus* is morphologically similar to those of *Hemiramphus* in that those of adults contain a matrix of gas-filled vesicles of various sizes and are multiple vesicle layers in thickness with no apparent hypertrophied vascular system. While the character is both present and absent in two *Oxyporhamphus* species, indicating a degree of evolutionary lability, it is unlikely that such an elaborate character was derived independently in two closely related genera. This suggests that the vesicular swimbladder may be a very useful synapomorphy between the two genera. Whether this is useful evidence that the genus *Oxyporhamphus* is more closely related to *Hemiramphus* than it is either to other halfbeaks or flyingfishes depends on whether or not it was derived in a common ancestor or derived independently from a similar genome (Fig. 5). This can only be resolved by a comparative developmental study of representatives of the two genera and an evaluation of this character in the context of other characters. Juvenile *Oxyporhamphus* resemble juvenile *Hemiramphus* in body banding and pigmented dorsal fins (Collette et al., 1984). The vesicular swimbladder seemingly provides evidence of a close link between an animal that looks like a flyingfish but is widely considered a halfbeak, and a halfbeak. However, and intriguingly, recent genetic evidence suggests that the genus *Hemiramphus* is sister genus to *Oxyporhamphus*, which together may be more closely related to flying fishes than to other halfbeaks (Lovejoy et al., 2004). Thus *Hemiramphus* becomes the oddity, looking like a halfbeak while having closer evolutionary affinities with the flyingfishes.

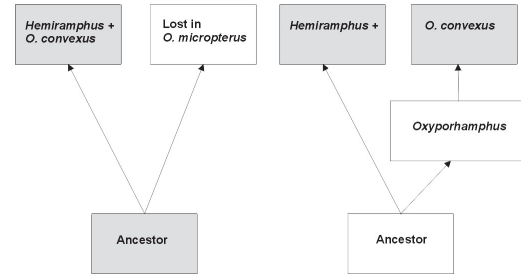

Fig. 5. Competing evolutionary hypotheses concerning the genera *Oxyporhamphus* and *Hemiramphus* and their swimbladder morphology. Stippled boxes = vesicular swimbladder.

The collection of a developmental series of members of the two genera will be required to assess the similarity of the developmental sequence. If it is similar, then the character would provide a good putative synapomorphy to be tested by comprehensive phylogenetic analysis. However, while the vesicular swimbladder is likely to be of import to those few who strive to resolve conundrums in beloniform phylogeny, the structure has far wider implications for our understanding of the development and function of swimbladders. Generally, the investigation of swimbladder functional morphology could well benefit from greater attention being given to anomalies of swimbladder morphology and development.

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