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The laterophysic connection in chaetodontid butterflyfish: morphological variation and speculations on sensory function

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The laterophysic connection is a novel specialization in chaetodontid butterflyfish, in which paired diverticula of the swim-bladder ('horns') extend anteriorly and approach or directly contact a medial fossa in the lateral line canal contained within the supracleithrum. This study examined the morphology of the laterophysic connection in eight ecologically diverse species belonging to five subgenera within *Chaetodon*. Two types of laterophysic connections, indirect and direct, were found among *Chaetodon* species. Intra-specific variation (including sexual dimorphism) in the morphology of the laterophysic connection was not found. The type of laterophysic connection is not correlated with ecological characteristics among *Chaetodon* species, but appears to be correlated with subgeneric affinities of *Chaetodon* species. The presence of swim-bladder horns probably increases pressure sensitivity to the inner ear. It is suggested that the presence of a direct laterophysic connection, and possibly an indirect laterophysic connection, imparts pressure sensitivity to the lateral line canal system as well.

Keywords: Chaetodontidae; swim-bladder; lateral line; pressure reception; laterophysic connection; hearing

1. INTRODUCTION

The swim-bladder of teleost fishes generally functions in a hydrostatic capacity to regulate buoyancy, but the presence of a swim-bladder has also been shown to increase the sensitivity of the inner ear to pressure stimuli (sound) (Schellart & Popper 1992). Many teleost fishes have anterodorsal diverticula, or 'horns', of the swim-bladder that approach or come in direct contact with the region of the skull containing the inner ear, and form an 'otophysic connection'. Otophysic connections are found among all four major lineages of teleost fishes, including a wide diversity of euteleost families (Schellart & Popper 1992). The functional significance of the variation in the length of the swim-bladder horns and the degree of contact with the otic capsule found among the two sub-families of holocentrid fishes (Nelson 1955) is correlated with sensitivity of the inner ear to pressure stimuli (Coombs & Popper 1979; reviewed in Schellart & Popper 1992).

The mechanosensory lateral line system is sensitive to local incompressible flow (unidirectional or oscillatory water flow, 'near field stimuli') and is not generally sensitive to pressure ('sound', 'far field stimuli') (Kalmijn 1989). In order for the lateral line system to be made

sensitive to pressure stimuli, such stimuli must be brought very close to the lateral line canals by the swim-bladder or swim-bladder horns, so that the near field component of the stimulus can cause water movement within the canals. Such morphological specializations have only been described in clupeomorphs (the recessus lateralis) and in one species of catfish (a specialization in addition to Weberian ossicles) (summarized by Webb 1998).

In a systematic revision of the family Chaetodontidae, the monophyly of *Chaetodon* is based on the presence of 'bilaterally, paired, bulbous, anterolateral diverticula' (Blum 1988, p.121), that are attached to the medial surface of the supracleithra forming a pseudo-otophysic connection, which probably enhances hearing sensitivity. Blum (1988, p.217) stated that this connection appears to be unique among fishes and that it represents 'the most substantial modification of internal anatomy known to occur in the family'. A recent histological study (Webb & Blum 1990; Webb 1998) showed that a 'medial fossa' in the lateral line canal of the supracleithrum is the site of a 'laterophysic connection', named for its similarity to the otophysic connection found in other fishes. Two types of laterophysic connections were described—one in which anterior diverticula (horns) of the swim-bladder are in direct contact with the tissue that fills the medial fossa (a direct connection), and another in which the anterior extensions of the swim-bladder approach, but do not come in direct contact with the medial fossa (an indirect connection).

We examined the morphology of the laterophysic connection in eight species of *Chaetodon* and asked two questions. Is there variation in the morphology of the

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Table 1. *Species examined for this study (genus Chaetodon), indicating sex (determined by histological examination of gonadal morphology), size and feeding ecology (using data from Hourigan 1989)*

(A total of 27 specimens were prepared histologically for this analysis.)

species	N	sex	standard length (mm)	feeding ecology
subgenus <i>Chaetodon</i>				
<i>C. capistratus</i>	1	female	49	omnivore
	2	not examined	25, 52	
subgenus <i>Lepidochaetodon</i>				
<i>C. kleinii</i>	1	male	85	planktivore
	2	female	74, 81	
	1	gonad not visible	70	
subgenus <i>Exornator</i>				
<i>C. miliaris</i>	4	gonad not visible	45–100	planktivore
<i>C. sedentarius</i>	1	not examined	50	omnivore
<i>C. multicinctus</i>	2	male	87, 90	corallivore
	2	female	83, 90	
subgenus <i>Discochaetodon</i>				
<i>C. octofasciatus</i>	3	male	64–77	corallivore
	4	female	58–73	
	1	not examined	50	
<i>C. rainfordi</i>	1	female	72	corallivore
subgenus <i>Citharoedus</i>				
<i>C. ornatissimus</i>	1	female	68	corallivore
	1	gonad not visible	61	

laterophysic connection within *Chaetodon* species? What are the patterns of morphological variation among *Chaetodon* species that are ecologically and phylogenetically diverse?

2. MATERIAL AND METHODS

The morphology of the laterophysic connection and associated connective tissues, including the swim-bladder, was examined in eight species of *Chaetodon* belonging to several subgenera (*sensu* Blum 1988) that have different ecological characteristics. Fishes used for this study were collected on the north shore of Oahu, Hawaii (*C. multicinctus*, under University of Hawaii permit) or obtained from commercial sources. A total of 27 specimens, belonging to five of the 12 *Chaetodon* subgenera were prepared histologically, including both males and females in some species (identified via separate histological examination of gonads (J. F. Webb and W. L. Smith, unpublished data) (table 1). Live fishes were anaesthetized in MS 222 until unresponsive (following the Institutional Animal Care and Use Committee approved protocol), fixed with cold 10% formalin in seawater, and radiographed within a few days after fixation in order to document gross morphology of the swim-bladder *in situ*. Each fish was bisected at the level of the pectoral fin base and then heads were trimmed and decalcified in CalEx (Fisher Scientific, Pittsburgh, PA, USA), or in 0.1 M di-sodium EDTA in 10% formalin in seawater, until decalcification could be confirmed radiographically. Tissue was trimmed and rinsed, dehydrated in ethanol, and infiltrated with and embedded in Histo-resin (Leica, Bannockburn, USA) or JB-4 (Polysciences, Warrington, PA, USA). Tissue was sectioned transversely at 5 µm, mounted on glass slides and stained with 0.5% cresyl violet. The length (rostrocaudal axis) and width (dorsoventral axis) of the neuromasts in the vicinity of the laterophysic connection (the canal neuromast in the supracleithral canal and the canal neuromasts in the first and second lateral line scales)

were measured by counting the number of sections in which a structure was present (rostrocaudal axis) or by using Scion Image (dorsoventral and mediolateral axes) (Scion Corporation, Frederick, MD, USA).

Cleared and stained material (*C. octofasciatus*, AMNH 43117) was used to examine the morphology of the cranial skeletal elements in the posterior region of the skull that contain the lateral line canals and include, or are in the vicinity of, the laterophysic connection.

3. RESULTS

A medial fossa in the supracleithrum (Webb 1998) was present in all individuals examined. The medial fossa measured about 500 µm in both rostrocaudal and dorsoventral axes in a species with a direct connection (*C. octofasciatus*) and in three species with an indirect connection (*C. miliaris*, *C. kleinii* and *C. multicinctus*). In these species, a single oval neuromast, which had a length of 200–700 µm, was found in the supracleithral canal, just rostral to the laterophysic connection. An oval neuromast was present in each of the first two lateral line scales, with a length of 200–500 µm (figure 1).

Analysis of multiple specimens in seven species and analysis of both males and females in three species (*C. kleinii*, *C. octofasciatus* and *C. multicinctus*) revealed that intraspecific variation, including sexual dimorphism, in the gross morphology of the laterophysic connection was not present. However, interspecific variation in the gross morphology of the laterophysic connection was present. *C. capistratus*, *C. kleinii*, *C. miliaris*, *C. multicinctus* and *C. sedentarius* have an indirect connection. The swim-bladder horns extend beyond the body of the swim-bladder, but do not make direct contact with the fossa in the supracleithrum. The horns extend to the level of the medial fossa in the supracleithrum, but muscle, nerve

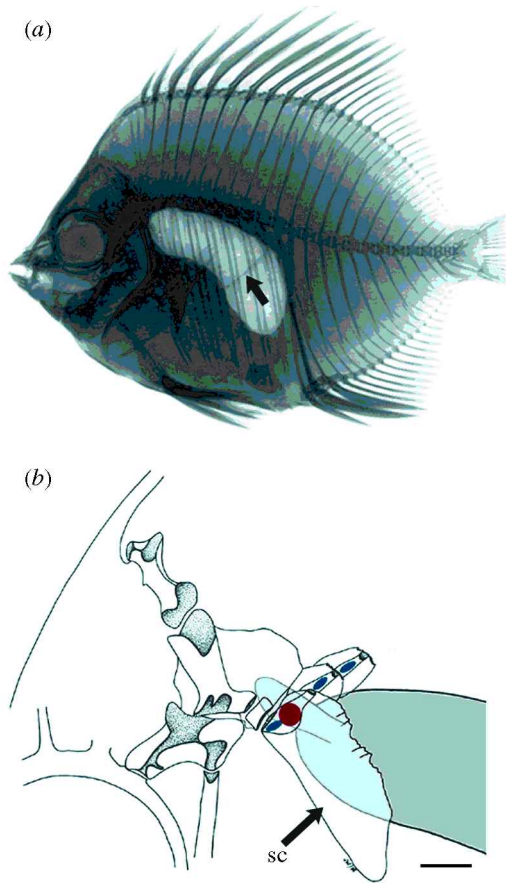


Figure 1. The swim-bladder and laterophysic connection in *C. octofasciatus*. (a) Radiograph in lateral view shows the robust swim-bladder, which approaches the posterior margin of the skull. A sphincter (arrow) formed by the infolding of the tunica interna divides the swim-bladder into two internal chambers. (b) Camera lucida drawing of the bony elements just behind the orbit at the posterior margin of the skull. The anterior horns of the swim-bladder (shaded) sit deep to the supracleithrum (sc). The laterophysic connection is denoted by the large red dot, the supracleithral neuromast (blue oval) is just rostral to it, and the neuromasts in the first two lateral line scales (blue ovals) are just caudal to it. Scale bar, ca. 1 mm.

and/or kidney tissue lie deep to the fossa preventing direct contact of the swim-bladder horns with it (figure 2a). The swim-bladder horns overlap the posterior-most extent of the caudal-most otolithic organs (which are medial, ventral to the brain and encased in the ossified otic capsule) by ca. 500–1000 μm in the rostro-caudal axis (in *C. kleinii*, *C. miliaris* and *C. multicinctus*). Of the species with an indirect connection (and long horns), only *C. kleinii* has a cushion of mucoid connective tissue in the medial fossa (figure 2b). In contrast, *C. octofasciatus* and *C. rainfordi* have a direct laterophysic connection where anterior horns of the swim-bladder make direct contact with the medial fossa of the lateral line canal in the supracleithrum (figure 2c). In these species, the fossa is filled by multiple layers of tissue that form a tympanum-like barrier between the lumen of the fluid-filled lateral line canal and the air-filled lumen of the swim-bladder horns. These layers are (from lateral to medial): the epithelial lining of the lateral line canal,

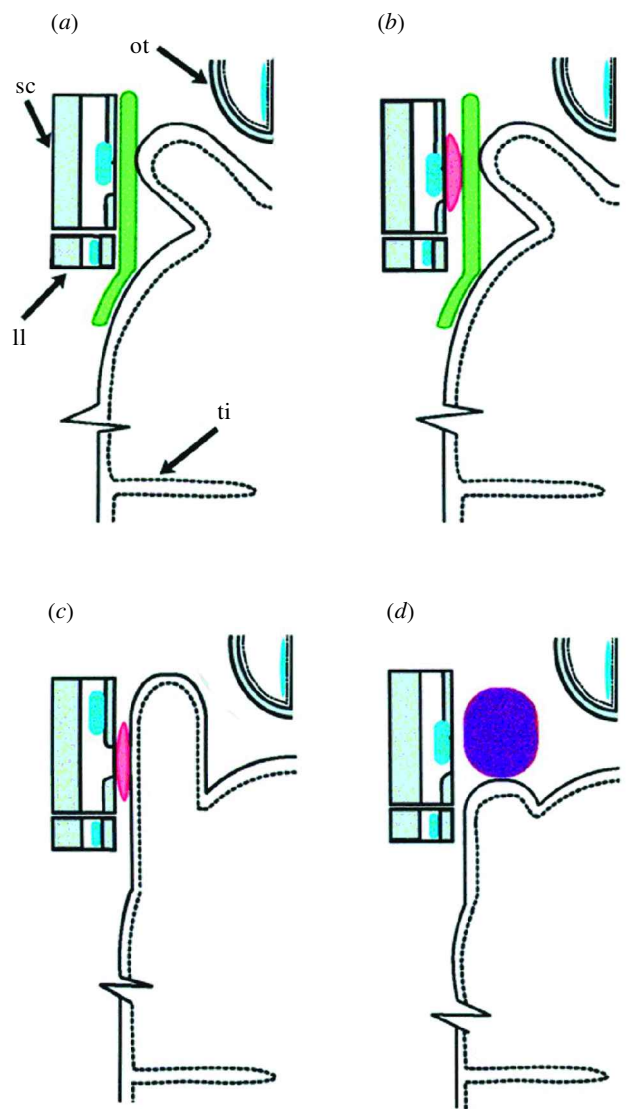


Figure 2. Schematic representation of the variation in the morphology of the laterophysic connection (in dorsal view) in eight species of *Chaetodon*, illustrating: skeletal elements (sc, supracleithrum; ll, first lateral line scale; ot, otic capsule), swim-bladder and swim-bladder horns (solid black line, tunica externa; dashed lines, tunica interna (ti)), other soft tissues (pink, mucoid connective tissue; green, muscle; purple, kidney), sensory organs (blue) of the lateral line system (neuromasts in the supracleithrum and first lateral line scale) and lagenar macula of the inner ear. (a) An 'indirect connection' (e.g. *C. capistratus*, *C. miliaris*, *C. sedentarius* and *C. multicinctus*); (b) an 'indirect connection' with mucoid connective tissue (*C. kleinii*); (c) a 'direct connection' (*C. octofasciatus* and *C. rainfordi*); (d) an 'indirect connection' with short ('stubby') horns (*C. ornatissimus*). See §3 for additional descriptions.

mucoid connective tissue (which stains pink with cresyl violet in contrast to the collagenous stratum compactum, which stains blue), the tunica externa of the swim-bladder horns (thinned in the vicinity of the fossa) and the thin, epithelial tunica interna. In contrast to the other seven species examined, *C. ornatissimus* has short ('stubby') swim-bladder horns that barely extend beyond the anterior end of the body of the swim-bladder. Kidney tissue fills the space rostral to the swim-bladder in which the

long swim-bladder horns are located in other species (figure 2*d*).

In all eight *Chaetodon* species examined, the swim-bladder is divided into two chambers by the infolding of the thin tunica interna, which forms a perforated diaphragm (or sphincter) that sits between one-half and two-thirds down the length of the swim-bladder and is clearly visible in freshly fixed material. This structure is not visible when examining the external surface of the swim-bladder, but is clearly evident in radiographs taken within a day of fixation (see figure 1*a*). Interestingly, the gross morphology of the swim-bladder varies among species with direct and indirect laterophysic connections. The swim-bladder of species with a direct connection is firm and characterized by a uniformly thick tunica externa and a kinked longitudinal contour (figure 1*a*). A thin peritoneum covers the swim-bladder, the posterior end of which is rounded and sits free from the posterior wall of the peritoneal cavity. In contrast, species with an indirect connection have a swim-bladder with a smooth longitudinal contour and a tunica externa that is thin dorsally and thick ventrally. The swim-bladder does not project into the peritoneal cavity. It is tightly adhered to the dorsal peritoneum (composed of dense fibrous connective tissue), so that the ventral surface of the swim-bladder appears to form the dorsocaudal wall of the peritoneal cavity.

4. DISCUSSION

The presence of a medial fossa in the supraclithrum, was confirmed histologically in all eight study species. Two different types of laterophysic connections were found among the eight species examined—a direct connection in which swim-bladder horns make contact with the supraclithral fossa, and an indirect connection (with long or short horns) where horns do not come in direct contact with the fossa. The absence of intraspecific variation, including sexual dimorphism, suggests that the gross morphology of the laterophysic connection is a good species characteristic in the genus *Chaetodon*. Interspecific variation in the morphology of the laterophysic connection is the result of variation in soft tissue morphology, which could only be detected through histological analysis. These data clarify, extend, and in some cases contradict Blum (1988) who stated that swim-bladder horns are present in all species of *Chaetodon* and that the swim-bladder horns are attached to the supraclithrum.

By examining the morphology of the laterophysic connection among species that are ecologically diverse we can look for correlations that may lead to hypotheses concerning the functional or behavioural role of this novel morphological feature. The eight species of *Chaetodon* examined are either corallivores, planktivores or omnivores (Hourigan 1989). The planktivorous and omnivorous species examined have an 'indirect' connection, but the corallivorous species, have either a 'direct' or 'indirect' connection (short or long horns). We conclude that the type of laterophysic connection present cannot be explained by feeding ecology.

The subgeneric affinities of the eight *Chaetodon* species reveal an interesting phylogenetic pattern. An indirect

connection with long horns is found in three subgenera (*Chaetodon*, *Lepidochaetodon* and *Exornator*), an indirect connection with short horns is found in one subgenus (*Citharoedus*), and a direct connection is found only in the subgenus *Discochaetodon*. The occurrence of an indirect connection in three species in the subgenus *Exornator*, and the occurrence of the direct connection in two species in the subgenus *Discochaetodon*, suggests that the morphology of the laterophysic connection is consistent within subgenera and may be useful as a character (or set of characters) for further clarification of subgeneric relationships within *Chaetodon*. A more comprehensive survey is being carried out in order to determine the phylogenetic significance of this morphological variation among subgenera (Smith 2000).

In holocentrid fishes, the functional significance of the otophysic connection is a function of whether swim-bladder horns approach or directly contact the otic capsule (Nelson 1955; Coombs & Popper 1979). This variation is similar to that which defines the indirect and direct laterophysic connections in *Chaetodon*. If the laterophysic connection in *Chaetodon* is functionally analogous to an otophysic connection in other teleost fishes, then variation in its morphology should be functionally significant. The presence of a swim-bladder in *Chaetodon* suggests that the inner ears of *Chaetodon* are pressure sensitive (following Myrberg & Spires 1980). The presence of swim-bladder horns should further increase pressure sensitivity of the ears due to the proximity of the compressible fluid in the swim-bladder horns to the otic capsule (except in *C. ornatissimus*, where the horns are short and do not extend much beyond the anterior end of the swim-bladder). We suggest that an indirect connection imparts pressure sensitivity to the lateral line system, if the near-field component of the pressure stimulus is transmitted through the soft tissues that sit between the horns and the medial fossa in the supraclithrum. Further, we suggest that a direct connection imparts pressure sensitivity to the lateral line system if the tissue filling the medial fossa functions like a tympanum and transmits the near-field stimulus into the lateral line canal causing stimulation of one or more neuromasts (Webb 1998). Finally, we suggest that the variation in the gross morphology of the swim-bladder (e.g. thickness of tunica externa, attachment to peritoneum—features that might affect swim-bladder resonance characteristics) that are correlated with variation in the morphology of the laterophysic connection, indicates that the swim-bladder plays an important role in the transmission of pressure stimuli, and thus in the functioning of the laterophysic connection in *Chaetodon*.

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