

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

Jacqueline F. Webb and W. Leo Smith

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and apoculations on concery function** Iaterophysic connection in chaetodontid<br>butterflyfish: morphological variation<br>and speculations on sensory function

### **Jacqueline F. Webb**\* **and W. Leo Smith**{ *Department of Biology,Villanova University,Villanova, PA 19085, USA*

Department of Biology, Villanova University, Villanova, PA 19085, USA<br>The laterophysic connection is a novel specialization in chaetodontid butterflyfish, in which paired diver-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 latera 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 latera ticula 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 c laterophysic connection in eight ecologically diverse species belonging to five subgenera within *Chaetodon*.<br>Two types of laterophysic connections, indirect and direct, were found among *Chaetodon* species. Intra-<br>specifi Two types of laterophysic connections, indirect and direct, were found among *Chaetodon* species. Intra-<br>specific variation (including sexual dimorphism) in the morphology of the laterophysic connection was<br>not found. The specific variation (including sexual dimorphism) in the morphology of the laterophysic connection was<br>not found. The type of laterophysic connection is not correlated with ecological characteristics among<br>*Chaetodon* speci 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 sw 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 presenc 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 sens

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

### **1. INTRODUCTION**

**1. INTRODUCTION**<br>The swim-bladder of teleost fishes generally functions in<br>a hydrostatic canacity to regulate huoyancy but the **EXECTS 12**<br>The swim-bladder of teleost fishes generally functions in<br>a hydrostatic capacity to regulate buoyancy, but the<br>presence of a swim-bladder has also been shown to The swim-bladder of teleost fishes generally functions in<br>a hydrostatic capacity to regulate buoyancy, but the<br>presence of a swim-bladder has also been shown to<br>increase the sensitivity of the inner ear to pressure stimuli 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-(sound) (Schellart & Popper 1992). Many teleost fishes<br>have anterodorsal diverticula, or 'horns', of the swim-<br>bladder that approach or come in direct contact with the<br>region of the skull containing the inner ear and form have anterodorsal diverticula, or 'horns', of the swimbladder 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 fou bladder that approach or come in direct contact with the<br>region of the skull containing the inner ear, and form an<br>'otophysic connection'. Otophysic connections are found<br>among all four major lineages of teleost fishes inc region of the skull containing the inner ear, and form an<br>'otophysic connection'. Otophysic connections are found<br>among all four major lineages of teleost fishes, including<br>a wide diversity of euteleost families (Schellart 'otophysic connection'. Otophysic connections are found<br>among all four major lineages of teleost fishes, including<br>a wide diversity of euteleost families (Schellart & Popper<br>1992) The functional significance of the variati among all four major lineages of teleost fishes, including<br>a wide diversity of euteleost families (Schellart & Popper<br>1992). The functional significance of the variation in the a wide diversity of euteleost families (Schellart & Popper<br>1992). The functional significance of the variation in the<br>length of the swim-bladder horns and the degree of<br>contact with the otic capsule found among the two sub 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-<br>families of bolocentrid fishes (Nelson 1955) is correlat length of the swim-bladder horns and the degree of contact with the otic capsule found among the two subfamilies of holocentrid fishes (Nelson 1955) is correlated with sensitivity of the inner ear to pressure stimuli contact with the otic capsule found among the two sub-<br>families of holocentrid fishes (Nelson 1955) is correlated<br>with sensitivity of the inner ear to pressure stimuli<br>(Coombs & Popper 1979; reviewed in Schellart & Popper families of holocentrid fishes (Nelson 1955) is correlated<br>with sensitivity of the inner ear to pressure stimuli<br>(Coombs & Popper 1979; reviewed in Schellart & Popper<br>1992) 1992). (Coombs & Popper 1979; reviewed in Schellart & Popper 1992).<br>The mechanosensory lateral line system is sensitive to

1992).<br>The mechanosensory lateral line system is sensitive to<br>local incompressible flow (unidirectional or oscillatory<br>water flow 'near field stimuli') and is not generally sensi-The mechanosensory lateral line system is sensitive to<br>local incompressible flow (unidirectional or oscillatory<br>water flow, 'near field stimuli') and is not generally sensi-<br>tive to pressure ('sound', 'far, field stimuli') local incompressible flow (unidirectional or oscillatory<br>water flow, 'near field stimuli') and is not generally sensi-<br>tive to pressure ('sound', 'far field stimuli') (Kalmijn<br>1989) In order for the lateral line system to 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 sensitive to pressure stimuli, such stimuli must be brought<br>very close to the lateral line canals by the swim-bladder<br>or swim-bladder borns, so that the near field component sensitive to pressure stimuli, such stimuli must be brought<br>very close to the lateral line canals by the swim-bladder<br>or swim-bladder horns, so that the near field component<br>of the stimulus can cause water movement within very close to the lateral line canals by the swim-bladder<br>or swim-bladder horns, so that the near field component<br>of the stimulus can cause water movement within the<br>canals. Such morphological specializations have only or swim-bladder horns, so that the near field component<br>of the stimulus can cause water movement within the<br>canals. Such morphological specializations have only<br>been described in cluneomorphs (the recessus lateralis) of the stimulus can cause water movement within the<br>canals. Such morphological specializations have only<br>been described in clupeomorphs (the recessus lateralis)<br>and in one species of catfish (a specialization in addition canals. Such morphological specializations have only<br>been described in clupeomorphs (the recessus lateralis)<br>and in one species of catfish (a specialization in addition<br>to Weberian ossicles) (summarized by Webb 1998) been described in clupeomorphs (the recessus lateralis)<br>and in one species of catfish (a specialization in addition<br>to Weberian ossicles) (summarized by Webb 1998).<br>In a systematic revision of the family Chaetodontidae, d in one species of catfish (a specialization in addition<br>Weberian ossicles) (summarized by Webb 1998).<br>In a systematic revision of the family Chaetodontidae,<br>e-monophyly of *Chaetodon* is based on the presence of

the monophyly of *Chaetodon* is based on the presence of In a systematic revision of the family Chaetodontidae,<br>the monophyly of *Chaetodon* is based on the presence of<br>'bilaterally, paired, bulbous, anterolateral diverticula'<br>(Blum 1988, p.121), that are attached to the medial 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 Surface of the surface of the supercolateral diverticular (Blum 1988, p.121), that are attached to the medial surface of the supracleithra forming a pseudo-otophysic connection which probably enhances bearing sensitivity (Blum 1988, p.121), that are attached to the medial surface of the supracleithra forming a pseudo-otophysic connection, which probably enhances hearing sensitivity. surface of the supracleithra forming a pseudo-otophysic<br>connection, which probably enhances hearing sensitivity.<br>Blum (1988, p. 217) stated that this connection appears to<br>be unique among fishes and that it represents 'the connection, which probably enhances hearing sensitivity.<br>Blum (1988, p. 217) stated that this connection appears to<br>be unique among fishes and that it represents 'the most<br>substantial modification of internal anatomy known Blum (1988, p. 217) stated that this connection appears to<br>be unique among fishes and that it represents 'the most<br>substantial modification of internal anatomy known to<br>occur in the family'. A recent histological study (W 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 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 similar 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 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 w 'laterophysic connection', named for its similarity to the<br>otophysic connection found in other fishes. Two types of<br>laterophysic connections were described—one in which<br>anterior diverticula (horns) of the swim-bladder are otophysic connection found in other fishes. Two types of<br>laterophysic connections were described—one in which<br>anterior diverticula (horns) of the swim-bladder are in<br>direct contact with the tissue that fills the medial fos 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 anterior diverticula (horns) of the swim-bladder are in<br>direct connection), and another in which the anterior<br>extensions of the swim-bladder annroach but do not 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 indir direct connection), and another in which the anterior<br>extensions of the swim-bladder approach, but do not<br>come in direct contact with the medial fossa (an indirect<br>connection) connection). me in direct contact with the medial fossa (an indirect<br>nnection).<br>We examined the morphology of the laterophysic<br>nnection in eight species of *Chaetedon* and asked two

connection).<br>We examined the morphology of the laterophysic<br>connection in eight species of *Chaetodon* and asked two<br>questions. Is there variation in the morphology of the 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. *Sp ecies examined for this study* (*genus* Chaetodon)*, indicating sex* (*determined by histological examination of gonadal morphology*)*, size and feeding ecology* (*using data from Hourigan 1989*) morphology), size and feeding ecology (using data from Hourigan 1989)<br>(A total of 27 specimens were prepared histologically for this analysis.)



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

### **2. MATERIAL AND METHODS**

The morphology of the laterophysic connection and associated connective tissues, including the swim-bladder, was exam-The morphology of the laterophysic connection and asso-<br>ciated connective tissues, including the swim-bladder, was exam-<br>ined in eight species of *Chaetodon* belonging to several subgenera<br>(cance Plum 1099) that have diffe ciated connective tissues, including the swim-bladder, was examined in eight species of *Chaetodon* belonging to several subgenera<br>(*sensu* Blum 1988) that have different ecological characteristics.<br>Fisher used for this st Find in eight species of *Chaetodon* belonging to several subgenera<br>
(*sensu* Blum 1988) that have different ecological characteristics.<br>
Fishes used for this study were collected on the north shore of<br>
Only Havaii (Comult (*sensu* Blum 1988) that have different ecological characteristics.<br>Fishes used for this study were collected on the north shore of<br>Oahu, Hawaii (*C. multicinctus*, under University of Hawaii<br>parmit) ar obtained from comme Fishes used for this study were collected on the north shore of<br>Oahu, Hawaii (*C. multicinetus*, under University of Hawaii<br>permit) or obtained from commercial sources. A total of 27<br>generimans belonging to five of the 12 Oahu, Hawan (*C. multicunctus*, under University of Hawan<br>permit) or obtained from commercial sources. A total of 27<br>specimens, belonging to five of the 12 *Chaetodon* subgenera were permit) or obtained from commercial sources. A total of 27<br>specimens, belonging to five of the 12 *Chaetodon* subgenera were<br>prepared histologically, including both males and females in<br>seme enories (identified via separat specimens, belonging to five of the 12 *Chaetodon* subgenera were<br>prepared histologically, including both males and females in<br>some species (identified via separate histological examination of<br>grands (J. E. Webb. and W. J. 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 unregonads (J. F. Webb and W. L. Smith, unpublished data) gonads (J. F. Webb and W. L. Smith, unpublished data)<br>(table l). Live fishes were anaesthetized in MS 222 until unre-<br>sponsive (following the Institutional Animal Care and Use<br>Committee annound protecol) fixed with sold 10 (table I). Live fishes were anaesthetized in MS 222 until unresponsive (following the Institutional Animal Care and Use<br>Committee approved protocol), fixed with cold 10% formalin in<br>converter and protocologies within a few 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 Each fish was bisected at the level of the pectoral fin base and<br>then heads were trimmed and decalcified in CalEx (Fisher<br>Scientific, Pittsburgh, PA, USA), or in 0.1M di-sodium EDTA in<br>10% formaling in acquisition with dec then heads were trimmed and decalcified in CalEx (Fisher<br>Scientific, Pittsburgh, PA, USA), or in 0.1 M di-sodium EDTA in<br>10% formalin in seawater, until decalcification could be<br>confirmed policyrephically Tierre was trimme 10% formalin in seawater, until decalcification could be confirmed radiographically. Tissue was trimmed and rinsed, dehydrated in ethanol, and in¢ltrated with and embedded in confirmed radiographically. Tissue was trimmed and rinsed,<br>dehydrated in ethanol, and infiltrated with and embedded in<br>Historesin (Leica, Bannockburn, USA) or JB-4 (Polysciences,<br>Warrington, PA, USA) Tissue was sectioned t dehydrated in ethanol, and infiltrated with and embedded in<br>Historesin (Leica, Bannockburn, USA) or JB-4 (Polysciences,<br>Warrington, PA, USA). Tissue was sectioned transversely at<br>5.um, mounted an glass elides and stained w Warrington, PA, USA). Tissue was sectioned transversely at<br>5 µm, mounted on glass slides and stained with 0.5% cresyl violet. The length (rostrocaudal axis) and width (dorsoventral 5  $\mu$ m, mounted on glass slides and stained with 0.5% cresyl<br>violet. The length (rostrocaudal axis) and width (dorsoventral<br>axis) of the neuromasts in the vicinity of the laterophysic<br>connection (the same large neuromast violet. The length (rostrocaudal axis) and width (dorsoventral<br>axis) of the neuromasts in the vicinity of the laterophysic<br>connection (the canal neuromast in the supracleithral canal and<br>the samel neuromasts in the first a connection (the canal neuromast in the supracleithral canal and<br>the canal neuromasts in the first and second lateral line scales)

were measured by counting the number of sections in which a were measured by counting the number of sections in which a<br>structure was present (rostrocaudal axis) or by using Scion<br>Image (demountine) and medialateral axea) (Scion Corporation were measured by counting the number of sections in which a<br>structure was present (rostrocaudal axis) or by using Scion<br>Image (dorsoventral and mediolateral axes) (Scion Corporation,<br>Fredericks MD USA) Image (dorsoventral and mediolateral axes) (Scion Corporation,<br>Fredericks, MD, USA).

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

#### **3. RESULTS**

A medial fossa in the supracleithrum (Webb 1998) was **present in all individuals examined.** The medial fossa<br>present in all individuals examined. The medial fossa<br>measured about 500 um in both rostrocaudal and A medial fossa in the supracleithrum (Webb 1998) was<br>present in all individuals examined. The medial fossa<br>measured about 500 µm in both rostrocaudal and<br>dorsoventral axes in a species with a direct connection present in all individuals examined. The medial fossa<br>measured about  $500 \mu m$  in both rostrocaudal and<br>dorsoventral axes in a species with a direct connection<br> $(C.\operatorname{octofa}(\text{sciative})$  and in three species with an indirect measured about 500  $\mu$ m in both rostrocaudal and<br>dorsoventral axes in a species with a direct connection<br>(*C. octofasciatus*) and in three species with an indirect<br>connection (*C. miliaris*, *C. kleimi*, and *C. multicin* dorsoventral axes in a species with a direct connection (*C. otofasciatus*) and in three species with an indirect connection (*C. miliaris*, *C. kleinii* and *C. multicinctus*). In these species a single oval neuromast whi  $(C. octof a scalar)$  and in three species with an indirect connection  $(C. mili airis, C. kleinii$  and  $C. muli cintus$ ). In these species, a single oval neuromast, which had a connection *(C. miliaris, C. kleinii* and *C. multicinatus)*. In these species, a single oval neuromast, which had a length of 200–700  $\mu$ m, was found in the supracleithral cannot in the supracleithral these species, a single oval neuromast, which had a<br>length of 200–700  $\mu$ m, was found in the supracleithral<br>canal, just rostral to the laterophysic connection. An oval<br>neuromast was present in each of the first two latera length of 200–700  $\mu$ m, was found in the supracleithral<br>canal, just rostral to the laterophysic connection. An oval<br>neuromast was present in each of the first two lateral line<br>scales with a length of  $200-500 \text{ µm}$  (fou 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  $200-500 \,\mu m$  (figure 1). uromast was present in each of the first two lateral line<br>ales, with a length of  $200-500 \mu m$  (figure 1).<br>Analysis of multiple specimens in seven species and<br>alvsis of both males, and females in three species

scales, with a length of 200–500  $\mu$ m (figure 1).<br>Analysis of multiple specimens in seven species and<br>analysis of both males and females in three species<br>(*C* kleinii, *C* extensions and *C* multicinative) revealed that Analysis of multiple specimens in seven species and<br>analysis of both males and females in three species<br>(*C. kleinii*, *C. octofasciatus* and *C. multicinctus*) revealed that<br>intraspecific variation including sexual dimers analysis of both males and females in three species  $(C. kleinii, C. octofasciatus)$  and  $C. multicinctus)$  revealed that intraspecific variation, including sexual dimorphism, in (*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 va intraspecific variation, including sexual dimorphism, in<br>the gross morphology of the laterophysic connection was<br>not present. However, interspecific variation in the gross<br>morphology of the laterophysic connection was pres the gross morphology of the laterophysic connection was<br>not present. However, interspecific variation in the gross<br>morphology of the laterophysic connection was present.<br>C constratus C kleinii C miliaris C multicinatus and mot present. However, interspecific variation in the gross<br>morphology of the laterophysic connection was present.<br>*C. capistratus*, *C. kleinii*, *C. miliaris*, *C. multicinctus* and<br>*C. sedentarius* have an indirect conne morphology of the laterophysic connection was present.<br> *C. capistratus*, *C. kleinii*, *C. miliaris*, *C. multicinctus* and<br> *C. sedentarius* have an indirect connection. The swim-C. capistratus, C. kleinii, C. miliaris, C. multicinctus and<br>C. sedentarius have an indirect connection. The swim-<br>bladder horns extend beyond the body of the swim-<br>bladder but do not make direct contact with the fossa in *C. sedentarius* have an indirect connection. The swim-<br>bladder horns extend beyond the body of the swim-<br>bladder, but do not make direct contact with the fossa in<br>the supracleithrum. The horns extend to the level of the bladder horns extend beyond the body of the swim-<br>bladder, but do not make direct contact with the fossa in<br>the supracleithrum. The horns extend to the level of the<br>medial fossa in the supracleithrum, but muscle, nerve bladder, but do not make direct contact with the fossa in<br>the supracleithrum. The horns extend to the level of the<br>medial fossa in the supracleithrum, but muscle, nerve

PHILOSOPHICAL<br>TRANSACTIONS



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

 $ca.$  1 mm.<br>and/or kidney tissue lie deep to the fossa preventing and/or kidney tissue lie deep to the fossa preventing<br>direct contact of the swim-bladder horns with it<br>(figure  $2a$ ). The swim-bladder horns overlap the  $\text{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 posteriormost extent of the caudal-most- $\text{to the total mass of the total mass.}$$ direct contact of the swim-bladder horns with it (figure 2*a*). 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 (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  $ca. 500-1000 \mu m$  in the rostro-(which are medial, ventral to the brain and encased in the ossified otic capsule) by  $ca$ . 500–1000  $\mu$ m in the rostrocaudal axis (in *C. kleinii*, *C. miliaris* and *C. multicinctus*). Of the species with an indirect con ossified otic capsule) by *ca*. 500–1000  $\mu$ m in the rostro-<br>caudal axis (in *C. kleinii*, *C. miliaris* and *C. multicinctus*). Of<br>the species with an indirect connection (and long horns),<br>only *C. kleinii* has a cushio caudal axis (in *C. kleinii*, *C. miliaris* and *C. multicinetus*). Of<br>the species with an indirect connection (and long horns),<br>only *C. kleinii* has a cushion of mucoid connective tissue in<br>the medial fossa (figure 2b). the species with an indirect connection (and long horns),<br>only *C. kleinii* has a cushion of mucoid connective tissue in<br>the medial fossa (figure 2*b*). In contrast, *C. octofasciatus*<br>and *C. rainfordi* have a direct late only *C. kleinii* has a cushion of mucoid connective tissue in<br>the medial fossa (figure 2*b*). In contrast, *C. octofasciatus*<br>and *C. rainfordi* have a direct laterophysic connection<br>where anterior horns of the swim-bladd 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 and *C. rainfordi* have a direct laterophysic connection<br>where anterior horns of the swim-bladder make direct<br>contact with the medial fossa of the lateral line canal in<br>the supracleithrum (forme  $2c$ ). In these species, t where anterior horns of the swim-bladder make direct<br>contact with the medial fossa of the lateral line canal in<br>the supracleithrum (figure  $2c$ ). In these species, the fossa<br>is filled by multiple layers of tissue that for contact with the medial fossa of the lateral line canal in<br>the supracleithrum (figure  $2c$ ). In these species, the fossa<br>is filled by multiple layers of tissue that form a<br>tympapum-like barrier between the lumen of the fl the supracleithrum (figure  $2c$ ). In these species, the fossa<br>is filled by multiple layers of tissue that form a<br>tympanum-like barrier between the lumen of the fluid-<br>filled lateral line canal and the air-filled lumen of is filled by multiple layers of tissue that form a<br>tympanum-like barrier between the lumen of the fluid-<br>filled lateral line canal and the air-filled lumen of the<br>swim-bladder horns. These layers are (from lateral to tympanum-like barrier between the lumen of the fluid-<br>filled lateral line canal and the air-filled lumen of the<br>swim-bladder horns. These layers are (from lateral to<br>medial): the enithelial lining of the lateral line canal 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, *Phil. Trans. R. Soc. Lond.* B (2000)



Figure 2. Schematic representation of the variation in the<br>morphology of the laterophysic connection (in dorsal view) Figure 2. Schematic representation of the variation in the<br>morphology of the laterophysic connection (in dorsal view)<br>in eight species of *Chaetodon*, illustrating: skeletal elements (sc Figure 2. Schematic representation of the variation in the<br>morphology of the laterophysic connection (in dorsal view)<br>in eight species of *Chaetodon*, illustrating: skeletal elements (sc,<br>supracleithrum: Il, first lateral morphology of the laterophysic connection (in dorsal view)<br>in eight species of *Chaetodon*, illustrating: skeletal elements (s<br>supracleithrum; ll, first lateral line scale; ot, otic capsule),<br>swim-bladder and swim-bladder 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 swim-bladder and swim-bladder horns (solid black line,<br>tunica externa; dashed lines, tunica interna (ti)), other soft<br>tissues (pink, mucoid connective tissue; green, muscle; purple,<br>kidney), sensory organs (blue) of the la tunica externa; dashed lines, tunica interna (ti)), other soft<br>tissues (pink, mucoid connective tissue; green, muscle; purple<br>kidney), sensory organs (blue) of the lateral line system<br>(neuromasts in the sunracleithrum and tissues (pink, mucoid connective tissue; green, muscle; purple,<br>kidney), sensory organs (blue) of the lateral line system<br>(neuromasts in the supracleithrum and first lateral line scale)<br>and lagenar macula of the inner ear kidney), sensory organs (blue) of the lateral line system<br>(neuromasts in the supracleithrum and first lateral line scale)<br>and lagenar macula of the inner ear. (*a*) An 'indirect connection' (e.g. *C. capistratus*, *C. miliaris*, *C. sedentarius* and 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 connection' (e.g. C. capistratus, C. miliaris, C. sedentarius is C. multicinctus); (b) an 'indirect connection' with mucoi<br>connective tissue (*C. kleinii*); (c) a 'direct connection'<br>(*C. ectofasciatus* and *C. rainfordi* (*C. octofasciatus* and *C. rainfordi*); (*<sup>d</sup>* ) an `indirect connection' connective tissue  $(C. \text{ kleinii})$ ;  $(c)$  a 'direct connection'<br> $(C. \text{octof} \text{ascitus} \text{ and } C. \text{rain} \text{fordi})$ ;  $(d)$  an 'indirect connection'<br>with short ('stubby') horns  $(C. \text{orn} \text{atisfying})$ . See § 3 for (*C. octofasciatus* and *C. rain*<br>with short ('stubby') horr<br>additional descriptions.

mucoid connective tissue (which stains pink with cresyl<br>violet in contrast to the collagenous stratum compactum mucoid connective tissue (which stains pink with cresyl<br>violet in contrast to the collagenous stratum compactum,<br>which stains blue), the tunica externa of the swim-bladder mucoid connective tissue (which stains pink with cresyl<br>violet in contrast to the collagenous stratum compactum,<br>which stains blue), the tunica externa of the swim-bladder<br>horns (thinned in the vicinity of the fossa) and t violet in contrast to the collagenous stratum compactum,<br>which stains blue), the tunica externa of the swim-bladder<br>horns (thinned in the vicinity of the fossa) and the thin,<br>epithelial tunica interna. In contrast to the o which stains blue), the tunica externa of the swim-bladder<br>horns (thinned in the vicinity of the fossa) and the thin,<br>epithelial tunica interna. In contrast to the other seven<br>species examined Cornatissimus has short ('stu horns (thinned in the vicinity of the fossa) and the thin,<br>epithelial tunica interna. In contrast to the other seven<br>species examined, *C. ornatissimus* has short ('stubby')<br>swim-bladder horns that barely extend beyond the epithelial tunica interna. In contrast to the other seven<br>species examined, *C. ornatissimus* has short ('stubby')<br>swim-bladder horns that barely extend beyond the ante-<br>rior end of the body of the swim-bladder Kidney tiss species examined, *C. ornatissimus* has short ('stubby') swim-bladder horns that barely extend beyond the ante-<br>rior end of the body of the swim-bladder. Kidney tissue<br>fills the space rostral to the swim-bladder in which t wim-bladder horns that barely extend beyond the ante-<br>rior end of the body of the swim-bladder. Kidney tissue<br>fills the space rostral to the swim-bladder in which the

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**PHILOSOPHICAL**<br>TRANSACTIONS  $\overline{0}$  long swim-bladder horns are located in other species  $\begin{array}{c} \text{long sum-b} \\ \text{(figure 2d)}. \\ \text{In all eiv} \end{array}$ 

(figure  $2d$ ).<br>In all eight *Chaetodon* species examined, the swimbladder is divided into two chambers by the infolding of In all eight *Chaetodon* species examined, the swim-<br>bladder is divided into two chambers by the infolding of<br>the thin tunica interna, which forms a perforated<br>dianhragm (or sphincter) that sits between one-half and bladder is divided into two chambers by the infolding of<br>the thin tunica interna, which forms a perforated<br>diaphragm (or sphincter) that sits between one-half and<br>two-thirds down the length of the swim-bladder and is the thin tunica interna, which forms a perforated<br>diaphragm (or sphincter) that sits between one-half and<br>two-thirds down the length of the swim-bladder and is<br>clearly visible in freshly fixed material. This structure is diaphragm (or sphincter) that sits between one-half and<br>two-thirds down the length of the swim-bladder and is<br>clearly visible in freshly fixed material. This structure is two-thirds down the length of the swim-bladder and is<br>clearly visible in freshly fixed material. This structure is<br>not visible when examining the external surface of the<br>swim-bladder, but is clearly evident in radiographs clearly visible in freshly fixed material. This structure is<br>not visible when examining the external surface of the<br>swim-bladder, but is clearly evident in radiographs taken<br>within a day of fixation (see figure la). Intere swim-bladder, but is clearly evident in radiographs taken<br>within a day of fixation (see figure 1*a*). Interestingly, the gross morphology of the swim-bladder varies among 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.<br>The swim-bladder of species with a direct connecti gross morphology of the swim-bladder varies among<br>species with direct and indirect laterophysic connections.<br>The swim-bladder of species with a direct connection is<br>firm and characterized by a uniformly thick tunica The swim-bladder of species with a direct connection is<br>firm and characterized by a uniformly thick tunica The swim-bladder of species with a direct connection is characterized by a uniformly thick tunica (*†*<br>externa and a kinked longitudinal contour (figure 1*a*). A<br>thin peritoneum covers the swim-bladder, the posterior firm and characterized by a uniformly thick tunica<br>externa and a kinked longitudinal contour (figure la). A<br>thin peritoneum covers the swim-bladder, the posterior<br>end of which is rounded and sits free from the posterior externa and a kinked longitudinal contour (figure la). A<br>thin peritoneum covers the swim-bladder, the posterior<br>end of which is rounded and sits free from the posterior<br>wall of the peritoneal cavity. In contrast, species w thin peritoneum covers the swim-bladder, the posterior<br>end of which is rounded and sits free from the posterior<br>wall of the peritoneal cavity. In contrast, species with an<br>indirect connection have a swim-bladder with a smo end of which is rounded and sits free from the posterior<br>wall of the peritoneal cavity. In contrast, species with an<br>indirect connection have a swim-bladder with a smooth<br>longitudinal contour and a tunica externa that is t wall of the peritoneal cavity. In contrast, species with an<br>indirect connection have a swim-bladder with a smooth<br>longitudinal contour and a tunica externa that is thin<br>dorsally and thick ventrally. The swim-bladder does n indirect connection have a swim-bladder with a smooth<br>longitudinal contour and a tunica externa that is thin<br>dorsally and thick ventrally. The swim-bladder does not<br>project into the peritoneal cavity. It is tightly adhered longitudinal contour and a tunica externa that is thin<br>dorsally and thick ventrally. The swim-bladder does not<br>project into the peritoneal cavity. It is tightly adhered to<br>the dorsal peritoneum (composed of dense fibrous dorsally and thick ventrally. The swim-bladder does not<br>project into the peritoneal cavity. It is tightly adhered to<br>the dorsal peritoneum (composed of dense fibrous<br>connective tissue) so that the ventral surface of the sw project into the peritoneal cavity. It is tightly adhered to<br>the dorsal peritoneum (composed of dense fibrous<br>connective tissue), so that the ventral surface of the swim-<br>bladder annears to form the dorsocaudal wall of the the dorsal peritoneum (composed of dense fibrous connective tissue), so that the ventral surface of the swimbladder appears to form the dorsocaudal wall of the peritoneal cavity. connective tissue), so that the ventral surface of the swim-

### **4. DISCUSSION**

The presence of a medial fossa in the supracleithrum, 4. DISCUSSION<br>The presence of a medial fossa in the supracleithrum,<br>was confirmed histologically in all eight study species.<br>Two different types of laterophysic connections were The presence of a medial fossa in the supracleithrum,<br>was confirmed histologically in all eight study species.<br>Two different types of laterophysic connections were<br>found among the eight species examined—a direct was confirmed histologically in all eight study species.<br>Two different types of laterophysic connections were<br>found among the eight species examined—a direct<br>connection in which swim-bladder horns make contact Two different types of laterophysic connections were<br>found among the eight species examined—a direct<br>connection in which swim-bladder horns make contact<br>with the supracleithral fossa and an indirect connection found among the eight species examined—a direct<br>connection in which swim-bladder horns make contact<br>with the supracleithral fossa, and an indirect connection<br>(with long or short horns) where horns do not come in connection in which swim-bladder horns make contact system, if the near-field component of the pressure<br>with the supracleithral fossa, and an indirect connection stimulus is transmitted through the soft tissues that sit<br>(w direct contact with the fossa. The absence of intraspecific (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 direct contact with the fossa. The absence of intraspecific<br>variation, including sexual dimorphism, suggests that the<br>gross morphology of the laterophysic connection is a<br>good species characteristic in the genus *Chaetodan* gross morphology of the laterophysic connection is a good species characteristic in the genus *Chaetodon*. Intergross morphology of the laterophysic connection is a<br>good species characteristic in the genus *Chaetodon*. Inter-<br>specific variation in the morphology of the laterophysic<br>connection is the result of variation in soft tissu good species characteristic in the genus *Chaetodon*. Inter-<br>specific variation in the morphology of the laterophysic<br>connection is the result of variation in soft tissue<br>morphology which could only be detected through his specific variation in the morphology of the laterophysic<br>connection is the result of variation in soft tissue<br>morphology, which could only be detected through histo-<br>logical analysis. These data clarify, extend, and in som connection is the result of variation in soft tissue<br>morphology, which could only be detected through histo-<br>logical analysis. These data clarify, extend, and in some morphology, which could only be detected through histo-<br>logical analysis. These data clarify, extend, and in some<br>cases contradict Blum (1988) who stated that swim-<br>bladder horns are present in all species of *Chaetodon* a logical analysis. These data clarify, extend, and in some cases contradict Blum (1988) who stated that swimbladder horns are present in all species of *Chaetodon* and that the swim-bladder horns are attached to the supracases contradict Blum (1988) who stated that swim-<br>bladder horns are present in all species of *Chaetodon* and<br>that the swim-bladder horns are attached to the supra-<br>cleithrum cleithrum. that the swim-bladder horns are attached to the supracleithrum.<br>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 can look for correlations that may lead to hypotheses<br>concerning the functional or behavioural role of this<br>novel morphological feature. The eight species of<br>*Chaetodon* examined are either corallivores planktivores or concerning the functional or behavioural role of this<br>novel morphological feature. The eight species of<br>*Chaetodon* examined are either corallivores, planktivores or<br>omnivores (Hourigan 1989) The planktivorous and omninovel morphological feature. The eight species of<br>Chaetodon examined are either corallivores, planktivores or<br>omnivores (Hourigan 1989). The planktivorous and omni-<br>vorous species examined have an 'indirect' connection Chaetodon examined are either corallivores, planktivores or<br>omnivores (Hourigan 1989). The planktivorous and omni-<br>vorous species examined have an 'indirect' connection,<br>but the corallivorous species, have either a 'direct omnivores (Hourigan 1989). The planktivorous and omnivorous species examined have an 'indirect' connection,<br>but the corallivorous species, have either a 'direct' or<br>'indirect' connection (short or long borns). We conclude vorous species examined have an 'indirect' connection,<br>but the corallivorous species, have either a 'direct' or<br>'indirect' connection (short or long horns). We conclude<br>that the two of laterophysic connection present canno 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 armords of the subgeneric affinities of the eight *Chaetodon* species<br>The subgeneric affinities of the eight *Chaetodon* species<br>veal an interesting phylogenetic pattern. An indirect

explained by feeding ecology.<br>The subgeneric affinities of the eight *Chaetodon* species<br>reveal an interesting phylogenetic pattern. An indirect *Phil. Trans. R. Soc. Lond.* B (2000)

connection with long horns is found in three subgenera (*Chaetodon*, *Lepidochaetodon* and *Exornator*), 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 (*Citharoedus*), and a direct connection is found only in the 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 *Exama* (*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 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 th connection in three species in the subgenus *Exornator*, and<br>the occurrence of the direct connection in two species in<br>the subgenus *Discochaetodon*, suggests that the morphology<br>of the laterophysic connection is consisten the occurrence of the direct connection in two species in<br>the subgenus *Discochaetodon*, suggests that the morphology<br>of the laterophysic connection is consistent within sub-<br>genera and may be useful as a character (or set the subgenus *Discochaetodon*, suggests that the morphology<br>of the laterophysic connection is consistent within sub-<br>genera and may be useful as a character (or set of charac-<br>ters) for further clarification of subgeneric 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 ters) for further clarification of subgeneric relationships<br>within *Chaetodon*. A more comprehensive survey is being<br>carried out in order to determine the phylogenetic signifi-<br>cance of this morphological variation among s within *Chaetodon*. A more comprehensive survey is being<br>carried out in order to determine the phylogenetic signifi-<br>cance of this morphological variation among subgenera<br>(Smith 2000) carried out in o.<br>cance of this m<br>(Smith 2000).<br>In holocentri nce of this morphological variation among subgenera<br>
In holocentrid fishes, the functional significance of the<br>
polysic connection is a function of whether swim-

(Smith 2000).<br>In holocentrid fishes, the functional significance of the<br>otophysic connection is a function of whether swim-<br>bladder horns approach or directly contact the otic In holocentrid fishes, the functional significance of the otophysic connection is a function of whether swimbladder horns approach or directly contact the otic cansule (Nelson 1955; Coombs  $\&$  Popper 1979) This otophysic connection is a function of whether swim-<br>bladder horns approach or directly contact the otic<br>capsule (Nelson 1955; Coombs & Popper 1979). This<br>variation is similar to that which defines the indirect and bladder horns approach or directly contact the otic<br>capsule (Nelson 1955; Coombs & Popper 1979). This<br>variation is similar to that which defines the indirect and<br>direct laterophysic connections in *Chaetodan* If the latero capsule (Nelson 1955; Coombs & Popper 1979). This<br>variation is similar to that which defines the indirect and<br>direct laterophysic connections in *Chaetodon*. If the latero-<br>physic connection in *Chaetodon* is functionally 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 physic connection in *Chaetodon* is functionally analogous<br>to an otophysic connection in other teleost fishes, then<br>variation in its morphology should be functionally signifi-<br>cant. The presence of a swim-bladder in *Chaet* to an otophysic connection in other teleost fishes, then<br>variation in its morphology should be functionally signifi-<br>cant. The presence of a swim-bladder in *Chaetodon*<br>suggests that the inner ears of *Chaetodon* are press 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 presen cant. 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 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 tive (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 swim-bladder horns should further increase pressure<br>sensitivity of the ears due to the proximity of the<br>compressible fluid in the swim-bladder horns to the otic<br>cansule (except in *C* aradissimus, where the horns are 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 compressible fluid in the swim-bladder horns to the otic<br>capsule (except in *C. ornatissimus*, where the horns are<br>short and do not extend much beyond the anterior end<br>of the swim-bladder). We suggest that an indirect capsule (except in *C. ornatissimus*, where the horns are<br>short and do not extend much beyond the anterior end<br>of the swim-bladder). We suggest that an indirect<br>connection imparts pressure sensitivity to the lateral line short and do not extend much beyond the anterior end<br>of the swim-bladder). We suggest that an indirect<br>connection imparts pressure sensitivity to the lateral line<br>system if the near-field component of the pressure of the swim-bladder). We suggest that an indirect<br>connection imparts pressure sensitivity to the lateral line<br>system, if the near-field component of the pressure<br>stimulus is transmitted through the soft tissues that sit connection imparts pressure sensitivity to the lateral line<br>system, if the near-field component of the pressure<br>stimulus is transmitted through the soft tissues that sit<br>between the horns and the medial fossa in the sunrabetween the horns and the medial fossa in the suprastimulus is transmitted through the soft tissues that sit<br>between the horns and the medial fossa in the supra-<br>cleithrum. Further, we suggest that a direct connection<br>imparts pressure sensitivity to the lateral line system between the horns and the medial fossa in the supra-<br>cleithrum. Further, we suggest that a direct connection<br>imparts pressure sensitivity to the lateral line system if the<br>tissue filling the medial fossa functions like a t cleithrum. Further, we suggest that a direct connection<br>imparts pressure sensitivity to the lateral line system if the<br>tissue filling the medial fossa functions like a tympanum<br>and transmits the near-field stimulus into th 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 tissue filling the medial fossa functions like a tympanum<br>and transmits the near-field stimulus into the lateral line<br>canal causing stimulation of one or more neuromasts<br>(Webb 1998) Finally we suggest that the variation in and transmits the near-field stimulus into the lateral line<br>canal causing stimulation of one or more neuromasts<br>(Webb 1998). Finally, we suggest that the variation in the<br>gross morphology of the swim-bladder (e.g. thickne canal causing stimulation of one or more neuromasts<br>(Webb 1998). Finally, we suggest that the variation in the<br>gross morphology of the swim-bladder (e.g. thickness of<br>tunica externa attachment to peritoneum—features that (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 gross morphology of the swim-bladder (e.g. thickness of<br>tunica externa, attachment to peritoneum—features that<br>might affect swim-bladder resonance characteristics) that<br>are correlated with variation in the morphology of th tunica externa, attachment to peritoneum—features that<br>might affect swim-bladder resonance characteristics) that<br>are correlated with variation in the morphology of the<br>laterophysic connection, indicates that the swim-bladd might affect swim-bladder resonance characteristics) that<br>are correlated with variation in the morphology of the<br>laterophysic connection, indicates that the swim-bladder<br>plays an important role in the transmission of press are correlated with variation in the morphology of the<br>laterophysic connection, indicates that the swim-bladder<br>plays an important role in the transmission of pressure<br>stimuli and thus in the functioning of the laterophysi laterophysic connection, indicates that the swim-bladder<br>plays an important role in the transmission of pressure<br>stimuli, and thus in the functioning of the laterophysic<br>connection in *Chaetodon* plays an important role in the transmission of pressure<br>stimuli, and thus in the functioning of the laterophysic<br>connection in *Chaetodon*.<br>We thank Natasha Kelly, Nicole Cicchino and George Seavy<br>who assisted with the pre

We thank Natasha Kelly, Nicole Cicchino and George Seavy<br>who assisted with the preparation of histological material,<br>Melissa Tarby who prepared the drawn figures and Carl Meyer We thank Natasha Kelly, Nicole Cicchino and George Seavy<br>who assisted with the preparation of histological material,<br>Melissa Tarby who prepared the drawn figures and Carl Meyer<br>(University of Hawaii) who collected fishes f who assisted with the preparation of histological material,<br>Melissa Tarby who prepared the drawn figures and Carl Meyer<br>(University of Hawaii) who collected fishes for us. The Ameri-<br>can Museum of Natural History provided Melissa Tarby who prepared the drawn figures and Carl Meyer<br>(University of Hawaii) who collected fishes for us. The Ameri-<br>can Museum of Natural History provided a loan of skeletal and<br>cleared and stained material. This wo (University of Hawaii) who collected fishes for us. The American Museum of Natural History provided a loan of skeletal and cleared and stained material. This work was supported by National Science Foundation grant IBN 9603 can Museum of Natural History provided a loan of skeletal<br>cleared and stained material. This work was supported<br>National Science Foundation grant IBN 9603896 to J.F.W.

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