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The Median-Fin Skeleton of the Eastern Atlantic and Mediterranean Clingfishes *Lepadogaster lepadogaster* (Bonnaterre) and *Gouania wildenowi* (Risso) (Teleostei: Gobiesocidae)

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ABSTRACT Previous research on the osteology of the Gobiesocidae focused mostly on the neurocranium and the thoracic sucking disc (formed by the paired-fin girdles). Little attention has been paid to the skeleton of the median fins. The dorsal- and anal-fin skeleton of *Lepadogaster lepadogaster* and other gobiesocids (excluding *Alabes*, which lacks these fins) are characterized by the absence of spines, branched fin-rays, and middle radials. In gobiesocids, the distal radials never ossify and consist of elastic hyaline-cell cartilage. *Gouania wildenowi* is unique among gobiesocids in having further reductions of the dorsal- and anal-fin skeleton, including a notable decrease in the size of the proximal-middle radials in an anterior–posterior direction. Unlike *L. lepadogaster*, which exhibits a one-to-one relationship between the dorsal- and anal-fin rays and proximal-middle radials, *G. wildenowi* has a higher number of proximal-middle radials than distal radial cartilages and fin rays in the dorsal and anal fins. In *G. wildenowi*, the dorsal- and anal-fin rays do not articulate with the distal tip of the proximal-middle radials but are instead positioned between proximal-middle radials, which is unusual for teleosts. Previously unrecognized dorsal and ventral pads of elastic hyaline-cell cartilage are also present in the caudal skeleton of *L. lepadogaster*, *G. wildenowi*, and all other gobiesocids examined. J. Morphol. 271:215–224, 2010. © 2009 Wiley-Liss, Inc.

KEY WORDS: Gobiesocidae; *Lepadogaster lepadogaster*; *Gouania wildenowi*; osteology; dorsal fin; anal fin; caudal fin

INTRODUCTION

Members of the family Gobiesocidae (46 genera, ~140 species) inhabit the intertidal zones of the Atlantic (including the Mediterranean), Indian, and Pacific Oceans, and the freshwaters of Central and northern South America (Briggs, 1955). Commonly referred to as clingfishes, they range in size from a few centimeters to over 30 cm in standard length. They possess an adhesive disc, formed either by elements of the pelvic fins only (Parenti and Song, 1996) or by a combination of pectoral and pelvic-fin elements (Briggs, 1955), which they use to adhere to the substrate. In addition to this thoracic sucking disc, the skeleton of the Gobiesocidae is characterized by numerous losses (loss of the basisphenoid, orbitosphenoid, pterosphenoid, ectopterygoid, endopterygoid, scales, and dorsal- and anal-fin spines) and reductions (including a reduction in the number of infraorbital bones, sensory canals, and hemibranchs), which provide strong support for gobiesocid monophyly (Springer and Fraser, 1976).

Several studies have focused on the external morphology of the gobiesocids (Briggs, 1955; Fishelson, 1972; Shiogaki and Dotsu, 1983), but few have investigated their osteology in detail. These studies, however, are either limited taxonomically (Guitel, 1888; Hayashi et al., 1986) or anatomically (Guitel, 1904; Leray, 1961; Gosline, 1970; Springer and Fraser, 1976; Rosen and Patterson, 1990), with most emphasis being placed on the neurocranium and the structure of the paired-fin girdles. To date, very little attention has been paid to the median fin skeleton of gobiesocid fishes (Monod, 1968; Hayashi et al., 1986; Fujita, 1990), and to the best of our knowledge, only one study has described and illustrated the dorsal and anal fin skeleton of a member of this group (Hayashi et al., 1986).

During our investigations of the osteology of gobiesocids, we noticed several previously unrecognized peculiarities in the median-fin skeleton of the Eastern Atlantic and Mediterranean clingfishes *Lepadogaster lepadogaster* and *Gouania wildenowi*. *L. lepadogaster* is a “typical” clingfish, with a broad head and a spatulate snout (Fig. 1A),

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Fig. 1. (**A**) *Lepadogaster lepadogaster*, (BMNH 2009.3.16.10). (**B**) *G. wildenowi*, (BMNH 2009.3.16.1).

occurring along the shoreline of the Eastern Atlantic, the Mediterranean, and the Black Sea (Hofrichter and Patzner, 2000). *G. wildenowi*, endemic to the Mediterranean, is an elongate species (Fig. 1B) that inhabits the narrow interstices between course gravel along sheltered and exposed shorelines (Hofrichter and Patzner, 2000). Here, we describe the median-fin skeleton of *L. lepadogaster* and *G. wildenowi* and make comparisons with other gobiesocids and more generalized percomorphs.

MATERIALS AND METHODS

Selected specimens were cleared and double stained following the protocol of Taylor and Van Dyke (1985). A 36 mm specimen of *G. wildenowi* was embedded in paraplast for serial sectioning and stained with AZAN after Domagk (Romeis, 1986). Specimens of *L. lepadogaster* were not available for serial sectioning. A 22 mm specimen of *Acyrtops beryllinus* (a small western Atlantic clingfish) was instead embedded in paraffin for serial sectioning and stained with hematoxylin and eosin (following standard protocols) to make general comparisons with *G. wildenowi*. Dissections were carried out under a Zeiss stereomicroscope. All photographs of cleared and stained specimens were taken from the left side. The photographs were taken using a Jenoptik ProgRes 12 C digital fitted to a Zeiss Tessovar, a Zeiss digital camera fitted to a Zeiss Discovery V20 dissecting scope or a Nikon Coolpix E4500 attached to a Nikon Microscope Eclipse E600. Line drawings were prepared from photographs. Different cartilage types where identified in *Gouania* and *Acyrtops*, using histological sections, based on the type of cellular matrix present (Benjamin, 1990; Benjamin et al., 1992). As the caudal-fin skeleton of the gobiesocids is composed entirely of unbranched fin-rays, criteria for identifying principal caudal-fin rays based on the position of branched and unbranched rays (Arratia, 2008) are not easily applied. Herein, principal caudal-fin rays are defined as those rays articulating with the hypurals (following Smith-Vaniz, 1971) and procurrent rays are defined as those caudal fin-rays anterior to the uppermost and lowermost principal caudal-fin rays (refer Fig. 2).

We refer to the proximal cartilaginous element of the pterygiophores of the dorsal and anal fins as proximal-middle radials and to the proximal ossifications within that precursors as the proximal radials and if present to the distal ossifications as the middle radials.

We compare *Lepadogaster* and *Gouania* with *Dicentrarchus labrax* as a typical member of the Percomorpha. Materials examined are housed in the collections of the Natural History Museum, London (BMNH).

Materials Examined

Gobiesocidae. *A. beryllinus* (Hildebrand and Ginsburg), BMNH 2009.3.16.14, 1 specimen, cleared and stained (c&s), 16 mm standard length (SL).

A. beryllinus (Hildebrand and Ginsburg), 1 specimen, serial sectioned, 22 mm SL, property of Saint Louis University.

Apletodon sp. (Briggs), BMNH 2009.3.16.15, 1 specimen (c&s), 24 mm SL.

Diademichthys lineatus (Sauvage 1883), BMNH 1983.3.25.1174, 1 specimen (c&s), 28.9 mm SL.

G. wildenowi (Risso); BMNH 2009.3.16.2-8, 8 specimens (c&s), 14–45 mm SL; BMNH 2009.3.16.1, 1 alcohol specimen, 33 mm SL.

G. wildenowi (Risso), 1 specimen, serial sectioned, 36 mm SL, property of the University of Tuebingen.

L. lepadogaster (Bonnaterre), BMNH 2009.3.16.11-13, 3 specimens (c&s), 20–41 mm SL; BMNH 2009.3.16.10, 1 alcohol specimen, 42 mm SL.

Moronidae. *D. labrax* (Linnaeus), BMNH 2009.3.16.16-24, 1 specimen (c&s), 28 mm SL.

RESULTS

Median-Fin Skeleton of *L. lepadogaster*

Dorsal-fin skeleton (Figs. 1A, 2A, and 3A). There are 16-18 dorsal-fin rays associated with 16-18 pterygiophores, the first of which inserts in the

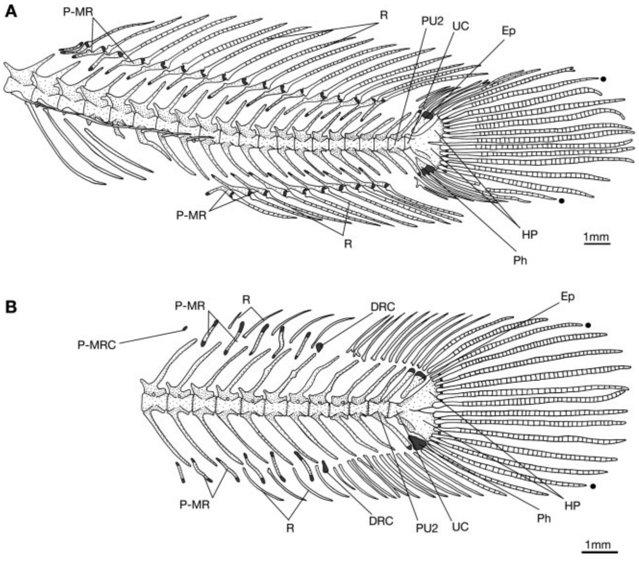

Fig. 2. Illustration of the median-fin skeleton and associated axial skeleton. (**A**) *Lepadogaster lepadogaster* (BMNH 2009.3.16.16-24). (**B**) *G. wildenowi* (BMNH 2009.3.16.2-9). Black circles indicate the uppermost and lowermost principal caudal-fin ray. Distal radial cartilages, elastic hyaline-cell cartilage pads, and inter-pterygiophore ligaments are not illustrated.

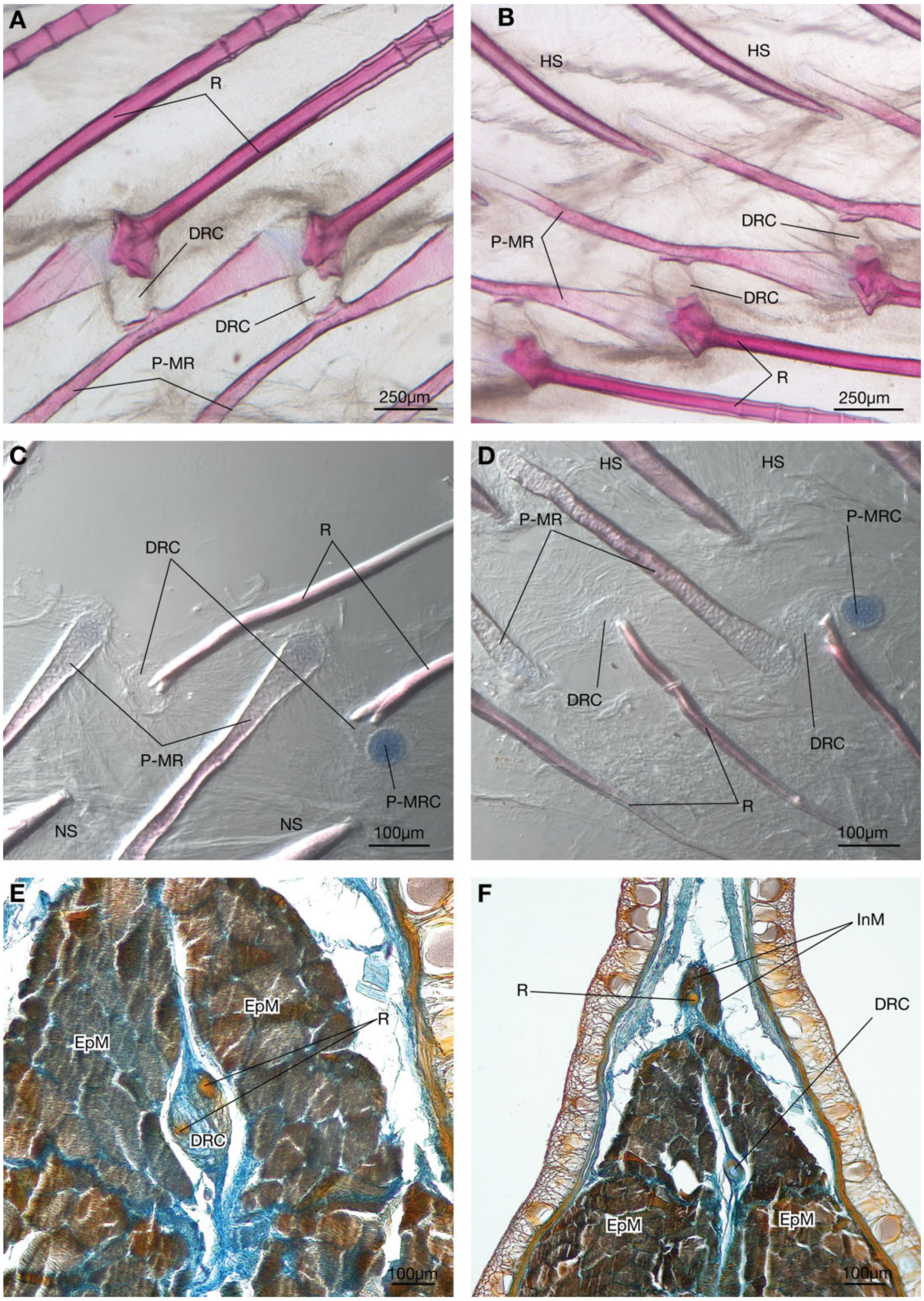

Fig. 3. Selected elements of the dorsal- and anal-fin of *Lepadogaster lepadogaster* and *G. wildenowi*. (**A**) *Lepadogaster lepadogaster* (BMNH 2009.3.16.16-24); dorsal-fin pterygiophores, inserting in the interneural space between the neural spines of vertebrae 20 and 24. (**B**) *Lepadogaster lepadogaster* (same specimen as in A); anal-fin pterygiophores, inserting in the interhemal space between the neural spines of vertebrae 20 and 24. (**C**) *G. wildenowi* (BMNH 2009.3.16.2-8); dorsal-fin pterygiophores, inserting in the interneural space between the neural spines of vertebrae 31 and 33. (**D**) *G. wildenowi* (same specimen as in C); anal-fin pterygiophores, inserting in the interhemal space between the neural spines of vertebrae 31 and 33. (**E**) Histological section through the anterior region of the dorsal fin of *G. wildenowi*. (**F**) Histological section through the dorsal fin of *G. wildenowi* more posterior to that shown in E.

interneural space between the neural spines of vertebrae 11-12. One out of the three cleared and stained specimens has one pterygiophore anteriorly that comprises a small proximal-middle radial (P-MR) only. These reduced pterygiophores lack an associated fin ray. All remaining pterygiophores are in serial association with a fin ray and consist of a P-MR and a cartilaginous distal radial (DRC), which consists of elastic hyaline cell cartilage (see results *G. wildenowi* and discussion). Middle radials are absent. All P-MRs are endochondrally ossified, rod shaped elements (membrane bone outgrowths are absent) capped with small cartilaginous tips. All P-MRs, except for the most anterior one, exhibit a small nodular process on their anterior face at the point closest to the distal tip of the preceding P-MR.

The DRCs of *L. lepadogaster* (Fig. 3A), which did not stain with alcian blue in cleared and stained specimens, insert anterodorsally on to the posteroventral tip of serially associated P-MRs. All DRCs, except for the posteriormost, attach posteroventrally on to the nodular process on the anterior face of succeeding P-MRs. The posteriormost DRC caps only the cartilaginous distal end of the P-MR and articulates with the serial associated fin ray dorsally. Each fin ray articulates with its associated pterygiophore via the distalmost tip of the P-MR and the anterodorsalmost point of the DRC. All fin rays are segmented and unbranched.

Anal-fin skeleton (Figs. 1A, 2A, and 3B). There are nine to ten anal-fin rays associated with 10 pterygiophores, the first of which inserts in the interhemal space between the hemal spines of vertebrae 17-18. As in the dorsal fin, all pterygiophores consist of P-MR and DRC only (middle radials are absent). All P-MRs, except for the anteriormost, are roughly rod-shaped, endochondrally ossified elements with anterodorsally directed proximal tips. The anteriormost P-MR, which is smaller than succeeding P-MRs, is roughly boomerang-shaped with its proximal tip directed anteroventrally. Distal radial cartilages are identical in general appearance to those described for the dorsal fin and insert on to their serially associated P-MR and fin ray in an identical manner. All pterygiophores articulate with an unbranched fin ray in the same way as in the dorsal fin.

Caudal-fin skeleton (Fig. 4A,D). There are 12-13 (7-6 + 6) principal caudal-fin rays and five to six dorsal and five ventral procurrent rays, supported by a large hypural plate, the parhypural, dorsal and ventral pads of elastic hyaline-cell cartilage (see discussion) and the neural and hemal spines of preural centrum 2 (PU2). Preural centrum 2 bears a large neural spine, which is inclined posterodorsally and contacts the distal tip of the epural. The hemal arch of PU2 is fused to the centrum and the hemal spine reaches the distal tip of the parhypural. Of the three cleared and stained specimens examined; one bears two neural and two hemal spines on PU2, and a second bears two neural spines and a single hemal spine. The lower and upper hypurals are fused to each other and to the ural centrum (UC). The broad distal tip of the epural remains cartilaginous and the proximal tip is inclined anteriorly.

The parhypural is broadest distally and tapers proximally to a narrow point. Its distal tip remains cartilaginous. It does not contact the UC nor does it enclose the caudal artery proximally. The dorsal and ventral procurrent rays are supported by pads of hyaline-cell cartilage, which do not stain with alcian blue in cleared and stained specimens. The dorsal pad extends along the dorsal surface of the hypural plate anteriorly, terminating ventral to the first dorsal procurrent ray. It encloses the cartilaginous distal tips of the epural, the long neural spine of PU2 and a single dorsal caudal radial cartilage (DCRC), lying at the bases of the anteriormost procurrent fin ray.

The ventral pad is similar in size and shape to the dorsal pad and encloses the distal tips of the parhypural and the hemal spine of PU2 as well as two ventral caudal radial cartilages (VCRC), lying at the bases of the two anteriormost procurrent fin rays.

Median-Fin Skeleton of *G. wildenowi*

Dorsal-fin skeleton (Figs. 1B, 2B, and 3C,E,F). There are five to six dorsal-fin rays and seven to ten poorly developed pterygiophores, the first of which inserts in the interneural space between the neural spines of vertebral centra 25-26. The anteriormost and posteriormost pterygiophores consist of a small circular or elliptical knob-shaped proximal-middle radial cartilage (P-MRC) only. The remaining pterygiophores are composed of weakly ossified proximal-middle radials (P-MR) and distal radial cartilages (DRC) only (middle radials are absent). All P-MRs are elongate, roughly rod-shaped endochondral ossifications that are oriented dorsoventrally. The proximal and distal tips of all P-MRs are cartilaginous. The DRCs are dissociated from the distal ends of their serial P-MRs but articulate dorsally with the fin-ray bases. In cleared and stained specimens, the DRCs are transparent and only detectable in transmitted light. In the sectioned specimens, the DRCs stained blue with an AZAN-Domagk stain and appear to consist of a dense matrix of large elastic hyaline-cell cartilage (see discussion).

The dorsal-fin rays are unbranched and unsegmented, and are similar in shape to the anteriormost unsegmented dorsal procurrent rays of the caudal fin. The distal tips of the dorsal-fin rays are located in a fleshy, ridge-like structure, which is confluent with the caudal fin (Fig. 1B). The forked bases of the rays are located within the epaxial

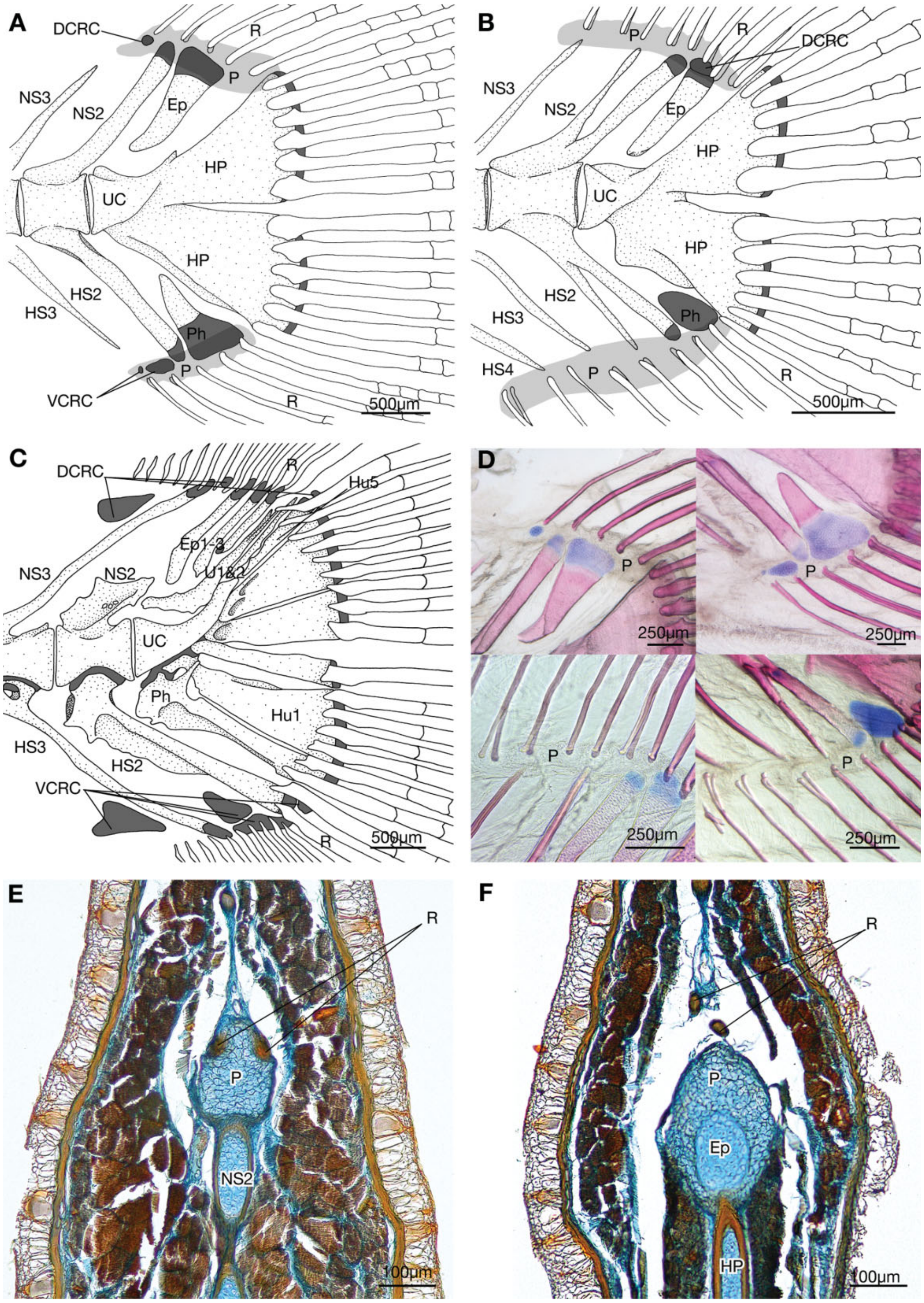

Fig. 4. Caudal-fin skeletons of cleared and stained specimens. (**A**) *Lepadogaster lepadogaster* (BMNH 2009.3.16.16-24). (**B**) *G. wildenowi* (BMNH 2009.3.16.2-9). (**C**) *D. labrax* (BMNH 2009.3.16.16). (**D**) Dorsal and ventral pads of elastic hyaline-cell cartilage in the caudal-fin skeleton of *Lepadogaster lepadogaster* (above) and in *G. wildenowi* (below), both same specimens are illustrated in A and B. (**E**) Histological section through the anterior region of the dorsal pad of elastic hyaline-cell cartilage in *G. wildenowi*. (**F**) Histological section through the dorsal pad of elastic hyaline-cell cartilage in *G. wildenowi* more posterior to that shown in E.

musculature (see below) and are associated only with the reduced DRCs of their serially associated pterygiophore. A pair of dorsal inclinator muscles attach to each fin ray laterally, dorsal to their point of insertion within the epaxial body musculature (Fig. 3F).

Anal-fin skeleton (Figs. 1B, 2B, and 3D). There are four to eight anal-fin rays and six to nine poorly developed pterygiophores, the first of which inserts in the interhemal space between the hemal spines of vertebral centra 25-26. In the majority of specimens, the anteriormost and posteriormost pterygiophores consist of a small circular or elliptical knob-shaped P-MRC only. The remaining pterygiophores are composed of weakly ossified P-MRs and reduced DRCs only (middle radials are absent). All P-MRs and DRCs are identical in general appearance to those of the dorsal-fin skeleton. The DRCs are associated with the anal-fin rays, which, like the dorsal-fin rays, are also unbranched and unsegmented.

Caudal fin (Fig. 4B,D–F). There are 12 (6 + 6) principal caudal-fin rays, 9 to 12 dorsal, and 9 to 14 ventral procurrent rays. The procurrent rays are supported by dorsal and ventral pads of elastic hyaline-cell cartilages and by the neural and hemal spines of the second preural centrum (PU2). In a small number of specimens (two out of eight), PU2 bears two neural spines. In these specimens, the anterior neural spine of PU2 is completely ossified and more similar in general appearance to those neural spines of more anterior centra than to the posterior neural spine of PU2, which is much thicker and exhibits a cartilaginous distal tip. Only one out of the eight cleared and stained specimens examined exhibited a second hemal spine on PU2. The hemal arch of PU2 is fused to the centrum. The lower and the upper hypurals are fused to each other and to the ural centrum. The lower hypural plate is extended by a lamina of membrane bone anteroventrally. The parhypural cartilage is located between the distal ends of the hemal spine of preural centrum 2 and the hypural plate and is roughly triangular in shape. The parhypural cartilage is even more foreshortened than the parhypural in *L. lepadogaster*, and there is no canal for the passage of the caudal artery at its base. The epural is ossified perichondrally, except at its distal tip, which remains cartilaginous.

As in *L. lepadogaster*, the ventral and the dorsal procurrent rays are supported by large pads of elastic hyaline-cell cartilage, which did not stain with Alcian Blue in our cleared and stained specimens but did stain blue with AZAN-staining in the histological sections (Fig. 4F). The dorsal pad surrounds the cartilaginous distal tip of the epural and the neural arches of PU2 and PU3 and (if present) a DCRC. The ventral pad surrounds the distal end of the parhypural and the hemal spines of PU2, PU3, and PU4.

Median-Fin Skeleton of *D. labrax*

Dorsal- and anal-fin skeleton (Fig. 5A,B). The dorsal fin bears spines anteriorly (Fig. 5A) and segmented fin rays posteriorly (Fig. 5B). The spines become gradually shorter towards the posterior, except for the last spine, which is much longer than the preceding spine and is associated with the branched fin rays of the second dorsal fin. The anteriormost P-MR bears two supernumerary spines. The anal fin has three spines followed by 10-12 soft rays. The majority of dorsal and anal-fin pterygiophores comprise P-MRs and DRCs only, the latter represented by distal radials (DRs) in larger specimens (Fig. 5A,B). A small number of the pterygiophores associated with the spinous dorsal fin (the 5th–10th) are composed of proximal and middle radials, and DRCs. The distal tips of the P-MRs are thickened and inclined posteriorly (Fig. 5A,B). The P-MRs supporting the spines of both dorsal and anal fins are laterally expanded by laminae of membrane bone. The DRCs articulate with their serially associated P-MR anteroventrally and caudoventrally with a small bony platform on the anterodorsal tip of the succeeding P-MR (Fig. 5A,B). Additionally a posteriorly oriented process of the DRC is linked with the succeeding P-MR via a ligament that passes through a foramen on the proximal end of the serially associated spine (referred to as chain link association; Bridge, 1896; Johnson and Patterson, 1993). Proximal-middle radials in serial association with soft rays exhibit weakly developed outgrowths of membrane bone and the DRCs exhibit a thin perichondrally ossified laminae of bone (the distal radial) along their dorsal surface at the point of articulation with the serially associated fin ray (Fig. 5B).

Caudal fin (Fig. 4C). The PU 2 bears a short neural spine that is fused to the centrum and an autogenous hemal spine. Ventral to the UC the caudal skeleton comprises five separate hypurals, of which hypural 5 is the smallest. A parhypural, with a canal for the caudal artery and a well-developed parhypurapophysis lies anterior to hypural 1. Three epurals are present dorsally to the UC, which decrease in size posteriorly. Two pairs of uroneurals are located between the epurals and hypural 5. The anterior pair is larger than the posterior and is inclined anteroventrally. The fin rays are supported by seven distal caudal radial cartilages of varying sizes (Fig. 4C).

DISCUSSION

The systematic position of the Gobiesocidae remains uncertain (Gill, 1996). We follow Nelson (2006) who placed the family within the Percomorpha, and therefore, we make general comparisons between the median-fin skeleton of the gobiesocids

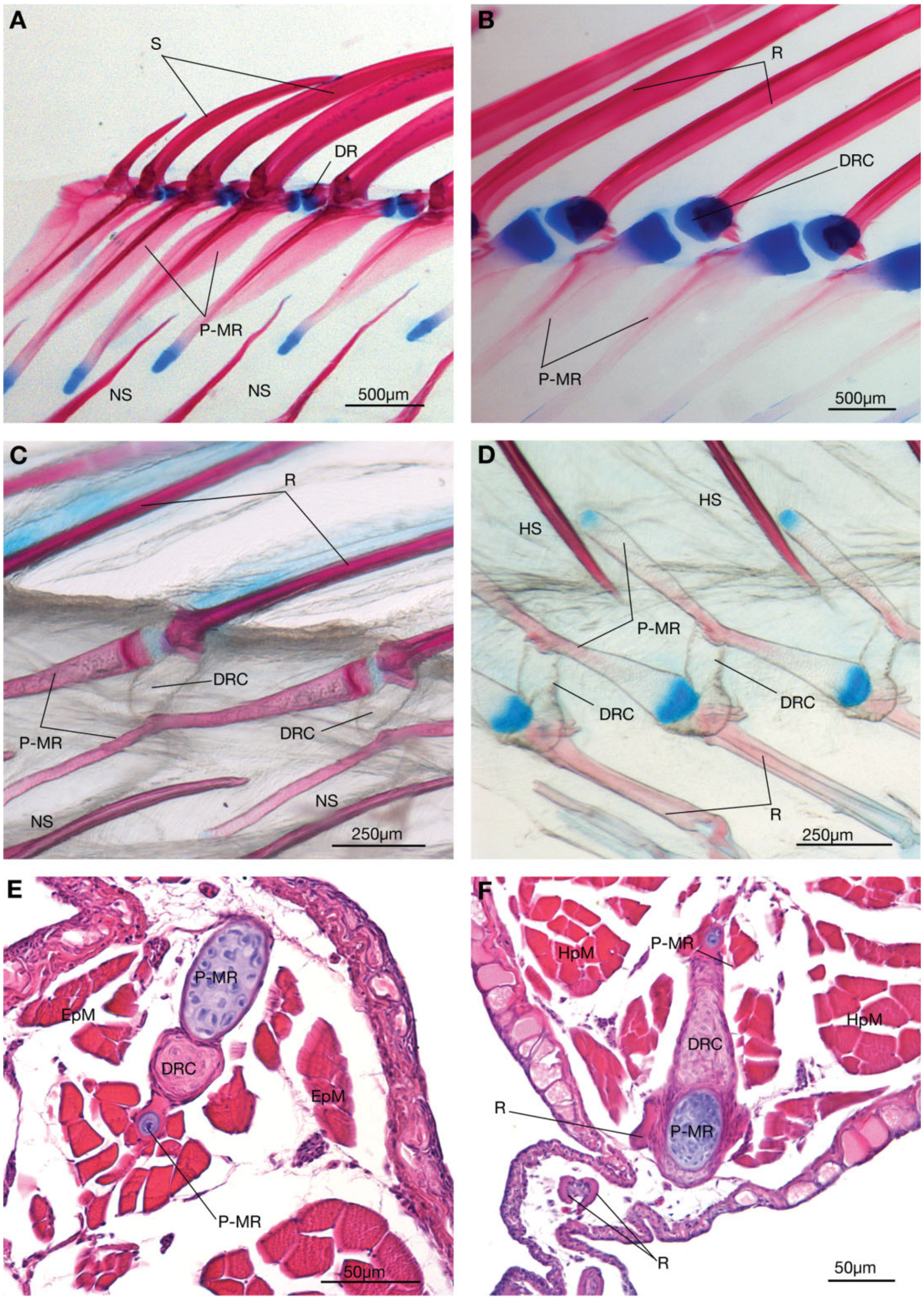

Fig. 5. Selected elements of the dorsal- and anal-fin of skeleton of cleared and stained specimens. (**A**) *D. labrax* (BMNH 2009.3.16.16); spinous-dorsal fin pterygiophores inserting in the interneural space between the neural spines of vertebrae 1 and 6. (**B**) *D. labrax* (same specimen as in A); soft-dorsal fin, pterygiophores inserting in the interhemal space between the neural spines of vertebrae 14 and 18. (**C**) *Apletodon* sp. (BMNH 2009.3.16.15); dorsal-fin pterygiophores inserting in the interneural space between the neural spines of vertebrae 17 and 20. (**D**) *A. beryllinus* (BMNH 2009.3.16.14); anal-fin pterygiophores, inserting in the interhemal space between the neural spines of vertebrae 15 and 19. (**E**) Histological section through the dorsal fin of *A. beryllinus*, 22 mm SL. (**F**) Histological section through the anal fin of *A. beryllinus* (same specimen as in E).

and the situation in a general percomorph (described earlier for *D. labrax*).

All gobiesocids lack the anterior spinous part of the dorsal and anal fins and also lack the chain link association of the pterygiophores exhibited by generalized percomorphs (Bridge, 1896; Johnson and Patterson, 1993). The most peculiar feature of the pterygiophores of the gobiesocids is the distal radial cartilage (DRC), which differ from other percomorphs. In all gobiesocids examined, the DRCs do not ossify and do not stain with alcian in cleared and stained specimens. The histological sections through the DRCs of *G. wildenowi* and *A. beryllinus* show cartilage cells embedded in a large amount of fibrous material. According to Benjamin (1990) and Benjamin et al. (1992), this type of cartilage, elastic hyaline-cell cartilage, is a subtype of hyaline-cell cartilage that is characterized by having more elastic fibers in the matrix and fewer cartilage cells. Benjamin et al. (1992) found elastic hyaline-cell cartilage in the caudal skeleton of the cypriniform *Botia horae* and in the oral sucker of another cypriniform, *Gyrinocheilus aymonieri*. Although the position of the DRCs in relation to the serial associated and succeeding P-MRs in gobiesocids (excluding *Gouania*) closely resembles that of other percomorphs, the connection between the DRCs and the P-MRs differs markedly. In gobiesocids (excluding *Gouania*), the DRCs are connected to the P-MRs via a dense matrix of connective tissue, and as such the arrangement and connection between the DRC and the P-MR is more reminiscent of the connection between a ligament and a skeletal element. In other percomorphs, the DRC (or DR) is distinct and easily distinguished from the thin layer of connective tissue that connects these structures to their serial associated PM-R. The DRC (or DR) is also distinct from its succeeding P-MR, to which it is connected, at least in the spinous (anterior) part of the dorsal and anal fins, via a ligament (Bridge, 1896; Johnson and Patterson, 1993). Little attention has been paid to the articulation between DRCs (or DRs) and P-MRs in those pterygiophores associated with the soft fin rays of the dorsal and anal fins and comparative data are lacking.

Although consisting of elastic hyaline cell cartilage, as in other gobiesocids, the DRCs of *G. wildenowi* differ in general appearance from those of other gobiesocids. *In G. wildenowi*, the DRCs are small nodules, dissociated from both the serial and the succeeding P-MR, articulating only with their serially associated fin ray (refer below). A possible explanation for the dissociation of the DRCs from the serial and succeeding P-MRs in *G. wildenowi* is that the distal tips of the P-MRs (which are usually bent caudally in other percomorphs) are also reduced and only the shafts remain. If this is the case, the dorsal- and anal-fin skeleton of *G. wildenowi* would exhibit even further reductions compared to the condition exhibited by other gobiesocids.

The fin rays of the dorsal and anal fin in the majority of percomorphs are associated with the DR (or DRC) of the serially associated pterygiophore anteroventrally (dorsal fin) or anterodorsally (anal fin) and also posteroventrally (dorsal fin) or posterodorsally (anal fin) with the P-MR of the succeeding pterygiophore. Unlike the aforementioned situation in percomorphs in *L. lepadogaster* and other gobiesocids (excluding *G. wildenowi* and also *Alabes*, which lacks the dorsal- and anal-fin skeleton entirely; Springer and Fraser, 1976) the fin rays articulate only with their serially associated pterygiophore, without contact to the succeeding pterygiophore. In *L. lepadogaster* and other gobiesocids (except *Alabes*), the enlarged distal ends of the P-MRs, which are inclined posteriorly, are not closely associated with the anterodorsal face of the succeeding pterygiophore, as is the case in *D. labrax*.

G. wildenowi has unbranched and unsegmented dorsal- and anal-fin rays that resemble the dorsal- and anal-fin spines of other percomorphs. These reduced fin rays also bear some resemblance to the small, anteriormost unsegmented procurrent rays of the caudal skeleton, with which they are serially confluent in several of the larger specimens examined. The rays of both the dorsal and anal fins are also completely separate from their serially associated P-MR or P-MRC. We find three reasons to reject the hypothesis that the unsegmented dorsal- and anal-fin rays of *G. wildenowi* are homologous to the fin-spines of percomorphs: (1) all other gobiesocids lack spines; (2) *G. wildenowi* would be the only member of the Gobiesocidae (except *Alabes*) in which the soft fin rays of the dorsal and anal fins are absent; (3) *G. wildenowi* would represent a rare case among percomorphs in which the anal fin is composed entirely of spines (occurring elsewhere to the best of our knowledge in the Stichaeidae and Scytalinidae only; Nelson, 2006; Hilton, 2009). We find two reasons to reject the hypothesis that the fin-rays of the dorsal and anal fin of *Gouania* are homologous with the procurrent rays of the caudal fin, rather than the segmented dorsal- and anal-fin rays of other gobiesocids: (1) the base of the unsegmented rays in the dorsal and anal fin are associated with inclinator muscles (Fig. 3F), muscles that are associated only with the rays of the dorsal and anal fins in other teleosts (procurrent rays are rarely associated with the supra- and infracarinales posterior mucles; Winterbottom, 1974); and (2) the association between the base of these fin rays and DRCs, a distinguishing characteristic of dorsal- and anal-fin rays (Johnson and Britz, 2005). On the basis of these points, we suggest that the rays in the dorsal and anal fins of *G. wildenowi*, although unsegmented, are homologous with the segmented dorsal- and anal-fin rays of other gobiesocid fishes. As far as we are aware, unsegmented fin-rays occur elsewhere only in the enigmatic zoarcoid *Ptilichthys goodei* (Hilton and Kley, 2005). Unlike the unsegmented fin-rays of *G. wildenowi*, however, the unsegmented fin-rays of *P. goodei* are composed of two separate hemitrichs (Hilton, unpublished data). Spines in Acanthomorpha as defined by Johnson and Patterson (1993) are unsegmented, bilaterally fused fin rays. We do not have ontogenetic material to confirm this but we suspect that this is also true for *G. wildenowi*, and therefore, these elements are similar to the spines of acanthomorphs. But on the basis of the arguments provided above and the uncertainty of the phylogenetic position of the gobiesocids we doubt that the spine-like rays of the dorsal and anal fins of *G. wildenowi* are homologous in a phylogenetic sense to the dorsal- and anal-fin spines of acanthomorphs.

The caudal-fin skeleton of the gobiesocid taxa described here is similar to those described previously (Monod, 1968; Springer and Fraser, 1976; Hayashi et al., 1986). The most variable element of the caudal-fin skeleton appears to be the parhypural, which may be ossified as in *L. lepadogaster* (Fig. 4A) or cartilaginous as in *G. wildenowi* (Fig. 4B) and *Aspasma minima* (Hayashi et al., 1986; Fujita, 1990). When present, the parhypural element is always dissociated from the preural centrum and lacks the canal for the passage of the caudal artery. The principal caudal fin rays are reduced from the usual 17 (9 + 8) in percomorphs (Johnson, 1984) to 12-13 (6-7 + 6) in *L. lepadogaster* or 12 (6 + 6) in *G. wildenowi* and *A. minima* (Hayashi et al., 1986; Fujita, 1990). Briggs (1951) does not distinguish between procurrent and principal caudal fin rays in his monograph and so his caudal fin ray counts are much higher and not comparable with the counts provided here.

Our investigation also uncovered a previously undescribed feature of the caudal skeleton of the gobiesocids, elastic hyaline-cell cartilage pads in association with the base of the dorsal and ventral procurrent fin rays. We observed identical pads in *Apletodon* sp., *D. lineatus*, and *A. beryllinus* (although difficult to identify in the latter). Monod (1968) did not describe these structures for the species of *Lepadogaster* available to him and neither Hayashi et al. (1986) nor Fujita (1990) reported these structures in *A. minima*. Although we were unable to examine these taxa we suspect that these pads were also present in theses species. Similar structures have been described in gobioids and blennioids, although these structures are reported to consist of cartilage cells instead of elastic hyaline-cell cartilage (Monod, 1968; Fujita, 1990). Fujita (1990) interpreted the large cartilaginous pads in the caudal skeleton of gobioids and blennioids as the product of the fusion of the smaller cartilages present in the caudal skeleton of other percomorphs. Interestingly, in *G. wildenowi* both dorsal and ventral pads of hyaline cell cartilage and dorsal and/or ventral caudal radial cartilages (alcian stained) are present in the caudal skeleton and as such we can neither reject nor confirm Fujita's (1990) hypothesis.

The majority of previous studies on the osteology of gobiesocid fishes have paid little attention to, or have completely excluded, the skeleton of the median fins (Guitel, 1888; Briggs, 1951; Leray, 1961; Springer and Fraser, 1976). The results of our study indicate that *G. wildenowi* exhibits a large number of previously unrecognized derived features, including: loss of dorsal- and anal-fin ray segmentation, a higher number of pterygiophores than fin rays and a disassociation between serially associated P-MRs and DRCs. Such derived features appear to be unique among gobiesocids, if not among teleosts, and are interpreted herein as autapomorphies of *Gouania*. The DRCs of gobiesocids are also highly derived, composed of elastic hyaline cell cartilage. Unlike the condition in *Gouania*, however, the DRCs of other gobiesocids are in contact with both the serial and succeeding P-MRs to which they are attached via a dense connective tissue matrix that gives the DRCs a ligament-like appearance.

Several authors noted the numerous losses and reductions that characterize the skeleton of the Gobiesocidae (Briggs, 1955; Gosline, 1970; Springer and Fraser, 1976; Gill, 1996). Our study indicates that the dorsal- and anal-fin skeleton of the gobiesocids also exhibits a high degree of reduction. Interestingly, gobiesocids also exhibit a high degree of variation in the number of dorsal- and anal-fin rays, with counts, ranging from 2 (in *Posidonichthys*) to 21 (in *L. lepadogaster*) for the dorsal, and 2 (in *Posidonichthys*) to 15 (in *Lepadichthys frenatus*) for the anal fin (Briggs, 1955, 1993). Members of one genus, *Alabes*, are even characterized by the complete absence of the dorsal and anal fin skeleton (Springer and Fraser, 1976). This variation in the dorsal- and anal-fin skeleton among members of a single family and our present investigation of the median-fin skeleton of the Gobiesocidae is the foundation for a broader comparative study that may uncover additional characters with the potential to help resolve the interrelationship of this understudied group of percomorphs.

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