



<http://dx.doi.org/10.11646/zootaxa.3619.3.6>

<http://zoobank.org/urn:lsid:zoobank.org:pub:0C9F1EF2-B56A-4407-8697-0084054033B5>

Phylogenetic placement of the European sand gobies in Gobionellidae and characterization of gobionellid lineages (Gobiiformes: Gobioidei)

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Abstract

The Mediterranean, northeastern Atlantic, and inland freshwaters of Europe and the Ponto-Caspian region host a distinct fauna of gobiiform fishes, including the sand gobies (*Pomatoschistus* Gill and related genera), all of which have been classified in the most diverse goby group, the family Gobiidae. Recent molecular phylogenetic analyses have suggested that the sand gobies are not gobiids, and are instead part of their sister clade Gobionellidae (Thacker and Roje 2011). Phylogenetic analysis of *Pomatoschistus* in the context of both gobiid and gobionellid taxa indicates that *Pomatoschistus* is part of Gobionellidae, specifically the *Mugilogobius* lineage. Gobionellidae includes 93 genera, which are arrayed into four lineages (*Stenogobius*, *Mugilogobius*, *Periophthalmus* and Northern Pacific). These lineages exhibit variation in characters of the jaw and suspensorium, including the shapes and relative positions of the palatine, quadrate, and ectopterygoid. The observations of the palatopterygoid complex in Gobionellidae of Harrison (1989) and Larson (2001) are supported and augmented. Gobionellidae generally exhibit suspensoria that are overall more elongated and gracile than those of gobiids: the palatine/ectopterygoid pair features a very short (*Periophthalmus* lineage) or elongate, pointed palatine (*Mugilogobius*, Northern Pacific, and *Stenogobius* lineages), with a relatively slender ectopterygoid and a short quadrate articulation. In Gobiidae, the palatine extends about halfway along the length of the ectopterygoid, and the ectopterygoid generally features a large, flat articulation with the quadrate. Suspensoria of *Pomatoschistus* and relatives are similar to those of other taxa in the *Mugilogobius* lineage. Placement of *Pomatoschistus* and relatives in Gobionellidae rather than Gobiidae is significant in that it indicates that sand gobies are not closely related to other European gobies, and has implications for any comparative evolutionary or biogeographic studies.

Key words: Gobiidae, Gobionellidae, phylogenetics, *Pomatoschistus*, *Economidichthys*, *Knipowitschia*, *Gobiusculus*

Introduction

Pomatoschistus Gill is a genus of twelve species that inhabits the coastal waters and estuaries of the Eastern Atlantic and Mediterranean Sea (Miller 1986, 2004). *Pomatoschistus* and four additional genera, *Gobiusculus* Duncker (monotypic, distributed in the Eastern North Atlantic), *Knipowitschia* Iljin (17 species from the Ponto-Caspian region), *Economidichthys* Bianco, Bullock, Miller & Roubal (two species restricted to freshwater springs and streams in western Greece), and *Hyrnanogobius* Iljin (monotypic and restricted to the Caspian Sea), are collectively denoted the sand gobies, due to their frequent (but not exclusive) preference for sand substrates (Economidis and Miller 1990; McKay and Miller 1997; Huyse *et al.* 2004). The systematics of these genera has been thoroughly studied, and phylogenetic analyses have placed representatives of sand gobies as a distinct clade, sister to various Indo-Pacific (McKay and Miller 1997) or Mediterranean (Penzo *et al.* 1998; Huyse *et al.* 2004; Larmuseau *et al.* 2010; Vanhove *et al.* 2012) gobiids. One molecular phylogenetic analysis, focusing on Ponto-Caspian gobies but including *Pomatoschistus*, placed *Pomatoschistus* variably in a gobiid clade or a clade containing a mix of gobiid and gobionellid taxa, but those analyses were based on limited datasets and most nodes outside the focal ingroup were poorly supported (Neilson and Stepien 2009). McKay and Miller's (1997) discussion of sand goby relationships identified a diagnostic character for the group (loss of the postmaxillary process of the premaxilla) and advanced the possibility that they might be closely related to gobionellids based on pore and papillae patterns and vertebral counts. Their cluster analysis of allozyme variation as well as parsimony