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PENSOFT

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Revalidation of the genus *Ichthyocoris* Bonaparte, 1840 (Actinopterygii: Blenniiformes: Blenniidae)

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Abstract

Combtooth blennies belonging to the genus *Salaria* were known to have marine and freshwater species. However, recent molecular studies highlighted this genus as paraphyletic, clearly distinguishing both marine and freshwater species. In this paper, we revalidate the genus *Ichthyocoris*, which corresponds to the freshwater species: *Ichthyocoris atlantica* (Doadrio, Perea et Yahyaoui, 2011), new combination, *Ichthyocoris economidisi* (Kottelat, 2004), new combination, and *Ichthyocoris fluviatilis* (Asso y del Rio, 1801), new combination. It is distinguishable by the presence of brownish bars on the flanks not contrasted with black dots conferring a marble coat, a dorsal fin slightly notched between spined and soft rays (except for *I. atlantica*), 16–18 dorsal-fin soft rays, 16–20 anal-fin soft rays, 34–38 vertebrae, 8–9 circumorbital pores, 8–11 preopercular pores, and 3 supratemporal pores. The genus *Salaria* corresponds to the marine species *Salaria basilisca* (Valenciennes, 1836) and *Salaria pavo* (Risso, 1810).

Keywords

combtooth blennies, generic concept, integrative taxonomy, *Salaria*

Introduction

Combtooth blennies are small benthic fish belonging to the family Blenniidae with a worldwide distribution in the marine environment, but some taxa are also encountered in fresh or brackish waters. They inhabit coastal, intertidal, rocky areas, coral reefs, and mangroves. Blenniids are divided into five subfamilies, 57 genera, and almost 400 species (Hastings and Springer 2009). Blenniids' classification, based on morphological and anatomical data, was the subject of extensive discussions (Norman 1943; Springer 1968; Smith-Vaniz and Springer 1971; Springer and Smith-Vaniz 1972; Papaconstantinou 1977a, 1977b; Bath 1977, 1996, 2001; Zander 1978; Bock and Zander 1986; Williams 1990). However, the molecular advent has brought taxonomical changes (Stepien et al. 1997; Almada et al. 2005, 2009; Hundt et al. 2014; Vecchioni et al. 2019; Mehraban et al. 2021).

In this study, we focused on the genus *Salaria* Bath [ex Forsskål], 1977 (see Fricke 2008 for nomenclature changes in relation to *Salaria* Forsskål, 1775). This genus, belonging to the Salariinae subfamily and the Parableniini tribe (Hastings and Springer 2009), is characterized by a dorsal fin with XII to XIV spines and 15 to 25 rays, an anal fin with II spines and 18 to 26 rays, pectoral fins with 13 to 15 rays, absent or small supraorbital and nasal tentacles, a lateral line formed by anterious tubes more or less continuous, one row of teeth with one canine on each side of each jaw with 14 to 35 teeth on the upper jaw and 14 to 25 teeth on the lower jaw, a toothed vomer, a wide gill opening, a gill membrane not joined with isthmus and a sexual dimorphism, with the presence of a crest on the male's head (Norman 1943; Bath 1977, 2001; Krupp and Schneider 1989; Gharred and Ktari 2001; Orlando-Bonaca and Lipej 2010). It includes five species,

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two marine and three freshwater: *Salaria basilisca* (Valenciennes, 1836) occurring in the Mediterranean Sea, *Salaria pavo* (Risso, 1810) found in the eastern Atlantic (Bay of Biscay, Iberic coast) and the Mediterranean Sea (Almada et al. 2001), *Salaria fluviatilis* (Asso y del Rio, 1801) occurring in coastal catchments of the Mediterranean basin and the Atlantic Guadiana drainage in Spain (Perdices et al. 2000; Kottelat and Freyhof 2007), *Salaria economidisi* Kottelat, 2004 which is endemic to the lake Trichonis in Greece (Kottelat 2004), and *Salaria atlantica* Doadrio, Perea et Yahyaoui, 2011 which is endemic to the Sebou drainage in Morocco (Doadrio et al. 2011). All these species are distinguishable according to morphology, molecular and ecology data, as well as color patterning (Perdices et al. 2000; Kottelat 2004; Almada et al. 2009; Orlando-Bonaca and Lipej 2010; Doadrio et al. 2011; Geiger et al. 2014; Belaiba et al. 2019; Vecchioni et al. 2019; Tiralongo 2020; Wagner et al. 2021). Nuclear markers also highlighted that the two marine species *S. basilisca* and *S. pavo* can hybridize (Belaiba et al. 2019).

The genus *Salaria* has also a complex taxonomic history: these blennies species belonged first to the genus *Blennius* Linnaeus, 1758 (see Bath 1973) or as a *Salaria* subgenus (Norman 1943), which was later split into several genera by Bath (1977), thus revalidating *Salaria*. Using morphological data, Bock and Zander (1986) included *Salaria* within the genus *Lipophrys* Gill, 1896. Finally, molecular data strongly support the validity of the genus *Salaria* (see Almada et al. 2005, 2009; Wagner et al. 2021). However, both marine and freshwater species are well discriminated with a common ancestor estimated at the Miocene (around 35–5 Ma according to studies of Almada et al. 2009; Belaiba et al. 2019; Wagner et al. 2021). Moreover, this genus seems to be paraphyletic according to mitochondrial and nuclear markers (Hundt et al. 2014; Vecchioni et al. 2019, 2022).

The type species of the genus *Salaria* Bath [ex Forsskål], 1977, designated by Fricke (2008), is *Gadus salaria* Walbaum [ex Forsskål], 1792 and is a *nomen oblitum* synonym of *Salaria basilisca*. So, the genus *Salaria* corresponds to the marine clade. Bonaparte (1840) described the genus *Ichthyocoris* corresponding to freshwater blennies. Its type species, designated by Jordan (1919), is *Salarias varus* Risso, 1827 which is a junior synonym of *Salaria fluviatilis* (see Fricke et al. 2007). *Ichthyocoris* is currently considered as a *nomen oblitum* synonym of *Salaria* Bath [ex Forsskål], 1977 (see Fricke 2008).

The generic concept is widely discussed by Dubois (1982, 1988a, 1988b). According to him, a genus is considered as monophyletic, a genetic unit with the possibility of hybridization between species, and an ecological unit as genera occupy defined adaptative zones. Marine and freshwater *Salaria* fill these conditions, even if no hybridization between freshwater species was highlighted due to the absence of sympatry. According to Freyhof and Yoğurtçuoğlu (2020), a genus should be also diagnosable morphologically. In this paper, we bring a morphological diagnosis in order to validate the genus *Ichthyocoris* following an integrative taxonomy approach (e.g., Padial et al. 2010; Schlick-Steiner et al. 2010).

Material and methods

In order to distinguish genera, we did a bibliographical review of diagnoses published (Wirtz 1976; Bath 1977; Papaconstantinou 1977a, 1977b; Gharred and Ktari 2001; Kottelat 2004; Kottelat and Freyhof 2007; Doadrio et al. 2011; Kara and Quignard 2018; Keith et al. 2020) as well as the original descriptions of both genera *Salaria* and *Ichthyocoris* (see Bonaparte 1840; Bath 1977) and their type species respectively *Gadus salaria* and *Salarias varus* (see Walbaum 1792; Risso 1827). Color patterning characterization follows Orlando-Bonaca and Lipej (2010). We used available pictures on GBIF and Kottelat (2004) as well as our own pictures to characterize color patterning. X-ray pictures were also taken on specimens in collections. Notation for dorsal and anal-fin rays' counts follows Hubbs and Lagler (1947). The following characters were examined: color patterning, dorsal-fin rays, anal-fin soft rays, pectoral-fin rays, pelvic-fin rays, number of teeth on each jaw, number of vertebrae, the form of the supraopercular tentacle.

Abbreviations used. GBIF, Global Biodiversity Information Facility; **ICZN**, International Code of Zoological Nomenclature; **MHNG**, Muséum d'Histoire naturelle de Genève, Genève; **MNCN**, Museo Nacional de Ciencias Naturales, Madrid; **MNHN**, Muséum national d'Histoire naturelle, Paris; **SL**, standard length; **USNM**, Smithsonian Institution National Museum of Natural History, Washington DC.

Comparative material. *Salaria basilisca* (Valenciennes, 1836): Italy • 1; Syntype of *Blennius basiliscus*; Mediterranean Sea at Genoa; MNHN-IC-A-1779 • 1; Syntype of *B. basiliscus*; Mediterranean Sea in Sardinia; MNHN-IC-A-1829. FRANCE • 2; Syntypes of *B. basiliscus*; Mediterranean Sea at Toulon; MNHN-IC-A-1842. Greece • 4; Evoikos Gulf; MNHN-IC-1975-0497 •1; Adriatic Sea; USNM RAD 106716 • see Bath (1977).

Salaria pavo (Risso, 1810): France • 3; Mediterranean Sea at Nice; MNHN-IC-A-1851 • 1; Mediterranean Sea at Nice; MNHN-IC-A-1852 • 1; Mediterranean Sea at Nice; MNHN-IC-A-2137 • 1; Mediterranean Sea at Nice • 1; Mediterranean Sea at Nice; MNHN-IC-A-2138 • 1; Etang de Thau at Mèze; 43°25′09″N, 003°36′09″E; MNHN-IC-2012-0250 • 1; Atlantic Ocean at Trégunc, 47°51′24″N, 003°53′12″W; MNHN-IC-2012-0252. Spain • 1; Balearic Islands at Minorca; 39°48′53″N, 004°17′05″E; MNHN-IC-2012-0254 • see Bath (1977).

Systematic account

Family Blenniidae

Ichthyocoris Bonaparte, 1840

(Fig. 1, Table 1)

Feminine gender

Type species. *Salarias varus* Risso, 1827.

Synonyms. *Salariopsis* Vecchioni, Ching, Marrone, Arculeo, Hundt et Simons, 2022 (see remarks below).

Included species. Three species: *Ichthyocoris atlantica* (Doadrio, Perea et Yahyaoui, 2011), new combination; *Ichthyocoris economidisi* (Kottelat, 2004), new combination; *Ichthyocoris fluviatilis* (Asso y del Rio, 1801), new combination.

Material examined. *Ichthyocoris atlantica*: MOROCCO • 1; Ouerrha River at Ouazzane; MNCN 280135 (2, 48–61 mm SL) • see Doadrio et al. (2011).

Ichthyocoris economidisi: GREECE 10; Lake Trichonis; MNCN 120747–120756 • see Kottelat (2004) and Doadrio et al. (2011).

Ichthyocoris fluviatilis: FRANCE • 2; Têt River at Perpignan; 42°42′21″N, 002°54′04″E; Persat and Denys coll. leg.; MNHN-IC-2013-0674. SPAIN • 10; Ebro River at Zaragoza; MNCN 13657–13666 • see Kottelat (2004) and Doadrio et al. (2011).

Diagnosis. *Ichthyocoris* is distinguishable from *Salaria* by the presence of brownish bars on the flanks not contrasted with black dots conferring a marble coat (Fig. 1) (vs. brownish bars on the flanks very contrasted with blue stripes and dots conferring a marbled coat; Fig. 2); dorsal-fin slightly notched between spined and soft rays (Fig. 1) except for *I. atlantica* (vs. not notched; Fig. 2); 16–18 dorsal-fin soft rays (vs. 21–27); 16–20

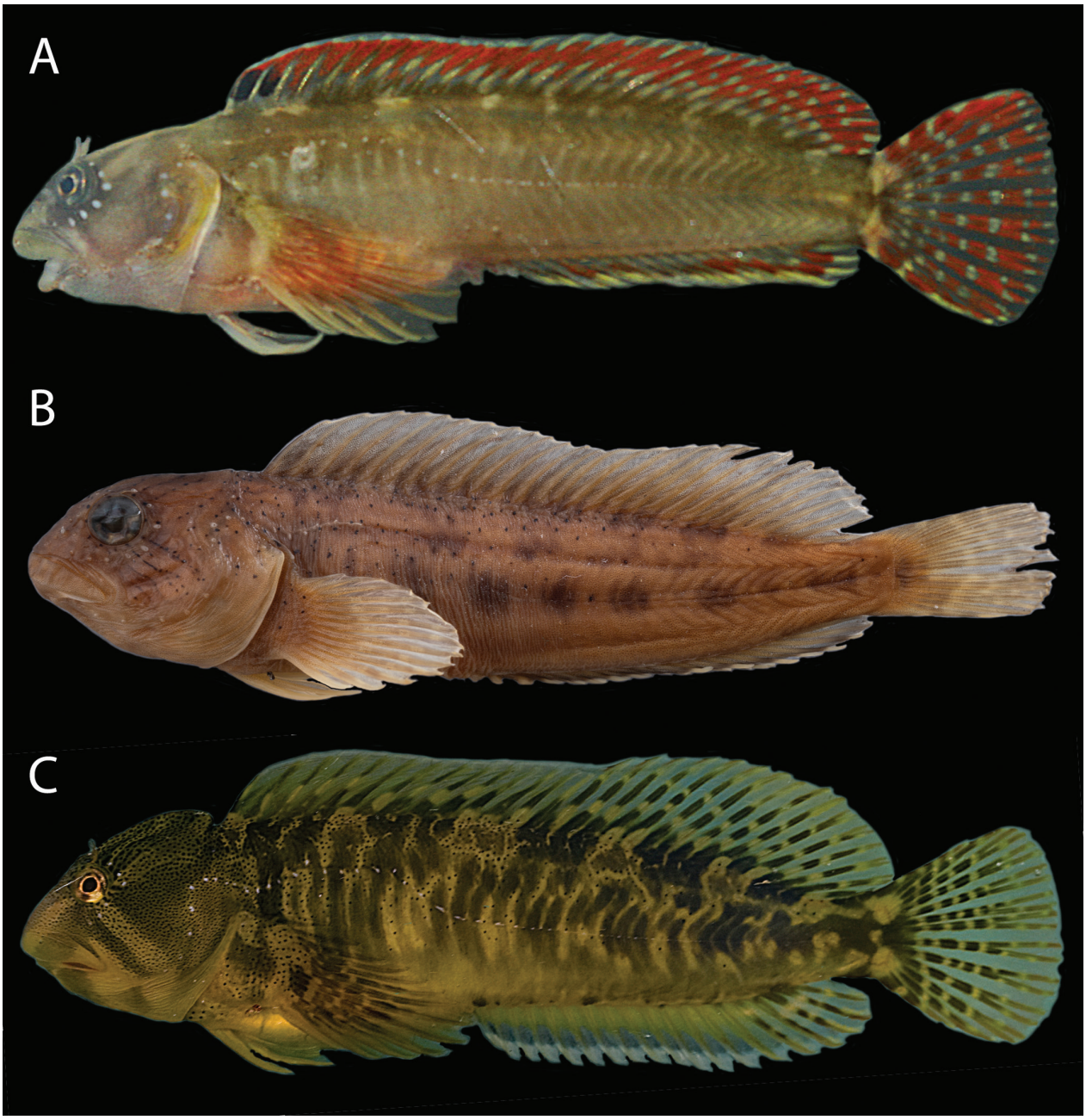


Figure 1. Lateral view of *Ichthyocoris* spp.: *I. atlantica*, MNCN 280135, 61 mm SL, Morocco, Ouerrha River (Sebou drainage) at Ouazzane (**A**; photo credits: I. Doadrio); *I. economidisi*, MHNG 2641.89, holotype, 60.8 mm SL, Greece, Lake Trichonis east of Panetolio (**B**; photo credits: R. Covain); *I. fluviatilis*, 89 mm SL, Spain, Jerea River (Ebro drainage) at Virués (**C**; photo credits: I. Doadrio).

Table 1. Meristic characters characterizing *Ichthyocoris* and *Salaria* species.

Character	*Ichthyocoris*			*Salaria*	
	I. atlantica	***I. economidisi***	***I. fluviatilis***	***S. basilisca***	***S. pavo***
Dorsal-fin rays	XII–XIII 16–17	XII–XIII 16–17	XII–XIII 16–18	XI–XIII 23–27	XI–XIII 21–24
Anal-fin rays	II 16–17	II 16–20	II 16–20	II 24–28	II 20–26
Vertebrae	34	36–37	34–38	40–44	38–42
Teeth upper jaw	13–15	25–30	16–24	25–33	19–28
Teeth lower jaw	14–16	20–27	16–20	22–28	16–23
Circumorbital pores	8–9	9	8	6–7	7
Preopercular pores	8–9	(9)10–11	9–10	6–8	6–8
Supratemporal pores	3	3	3	2	2



Figure 2. Lateral view of *Salaria* spp.: *S. basilisca*, MNHN-IC-A-1779, syntype, 138 mm SL, Italy: Mediterranean Sea at Genoa (**A**; photo credits: J. Pfliger); *S. pavo*, MNHN-IC-2012-0254, 74 mm SL, Balearic Islands at Menorca (**B**; photo credits: S. Iglesias).

anal-fin soft rays (vs. 20–28); 34–38 vertebrae (vs. 38–44); 8–9 circumorbital pores (vs. 6–7); 8–11 preopercular pores (vs. 6–8); 3 supratemporal pores (vs. 2) (Table 1).

Distribution. *Ichthyocoris* is present in drainages of the Mediterranean basin, in catchments of the Atlantic coast in Morocco and Spain as well as in the Black Sea.

Ecology. All *Ichthyocoris* species occur in freshwaters. However, due to their marine ancestry, *I. fluviatilis* has a one-month planktonic larval phase (Gil et al. 2010) and a high tolerance for salt water (Plaut 1998), allowing migration through marine waters (Perdices et al. 2000; Almada et al. 2009; Laporte et al. 2016; Méndez et al. 2019; Wagner et al. 2021).

Remarks. Comparing our diagnosis with the description of *Salarias varus* from Risso (1827), the three species do belong to the genus *Ichthyocoris*: the presence of dark dots on the body, 29 dorsal-fin spined and soft rays, and 19 anal-fin spined and soft rays. In the same fashion, comparing characters of *S. basilisca* and *S. pavo* with the diagnosis of *Gadus salaria* from Walbaum (1792), both species belong to the genus *Salaria*: the presence of 36 dorsal-fin spined and soft rays and 26 anal-fin spined and soft rays.

Other characters may discriminate between both genera: Papaconstantinou (1977a) distinguished *I. fluviatilis* from *S. basilisca* and *S. pavo* by the two lateral ethmoid bones between the median ethmoid and the vomer (vs. median ethmoid connected to the vomer). However, this character state is shared by other blenniids and needs to be checked within the two other *Ichthyocoris* species. Similarly, karyotype studies pointed out differences between *I. fluviatilis* and *S. pavo* (heterochromatin concentrated on the entire arm of two chromosome pairs like *Lipophrys* spp., vs. homogeneous distribution of heterochromatin like *Parablennius* spp. (Cataudella and Civitelli 1975; Unal et al. 2016). This character needs to be explored as well to characterize both *Ichthyocoris* and *Salaria* genera.

In a recent study, Vecchioni et al. (2022) also split the genus *Salaria*, distinguishing marine *Salaria* spp. from

freshwaters species. They described a new genus *Salariopsis* with *Blennius fluviatilis* Asso y del Rio, 1801 as type species (mentioning erroneously the new combination *Salariopsis fluviatilis*) and grouping as a new combination *Salariopsis fluviatilis*, *Salariopsis economidisi*, and *Salariopsis atlantica*. This new genus is distinguished from *Salaria* by 16–17 dorsal-fin soft rays (vs. 22–27) and 16–19 anal-fin soft rays (vs. 23–28) from only bibliographical references (Bath 1977; Kottelat 2004; Doadrio et al. 2011; Tiralongo 2020). Their diagnosis is similar to ours for *Ichthyocoris* for these two characters. Thus, *Salariopsis* and *Ichthyocoris* designate the same taxa. However, the nomen *Ichthyocoris* Bonaparte, 1840 is older than *Salariopsis* Vecchioni, Ching, Marrone, Arculeo, Hundt et Simons, 2022. Thus, the principle of priority must be applied (art. 23.1 ICZN): *Ichthyocoris* must be the valid nomen and *Salariopsis*, its junior synonym.

Kottelat (2004) suspects a population from Lake Kinneret (Israel) to belong to a distinct species. Molecular studies confirm that populations of the Eastern Mediterranean basin form a distinct evolutionary lineage (Doadrio et al. 2011; Geiger et al. 2014; Belaiba et al. 2019; Wagner et al. 2021). Another evolutionary lineage in the Guadiana catchment of the Atlantic basin from Spain was also highlighted with molecular data (Perdices et al. 2000; Almada et al. 2009; Doadrio et al. 2011; Belaiba et al. 2019; Méndez et al. 2019; Wagner et al. 2021). These two evolutionary lineages may correspond to two new *Ichthyocoris* species if morphological characters were to be found.

Identification key of blenniids genera belonging to the Parablenniini tribe (adapted from Bath (1977), Chirichigno and Vélez (1998), Orlando-Bonaca and Lipej (2010), and Tiralongo (2020)

1 Gill opening wide, branchiostegal membrane not fused with the body 2
– Gill opening restricted to the side of the head, branchiostegal membrane fused with the body 11
2 Absence of supraorbital tentacles 3
– Presence of supraorbital tentacles 5
3 Triangular, fleshy skin flap in the anterior neck area. Canines only in the lower jaw ..... *Coryphoblennius*
– No triangular, fleshy skin flap in the anterior neck area. Canines in both jaws 4
4 13 pectoral-fin rays. Body laterally compressed posteriorly. Relatively large mouth with a thick upper lip. General body color yellowish with dark brownish vertical bars. Dark brownish eyespot behind the eye. Mature males without bright coloration on cheeks ..... *Lipophrys*
– 12 pectoral-fin rays. Body well compressed laterally. Small mouth with thin lips. Absence of eyespot behind the eye. Mature males with bright yellow cheeks ..... *Microlipophrys*
5 Canines in both jaws 6
– Canines only in the lower jaw ..... *Scartella*
6 Presence of teeth on the vomer 7
– Absence of teeth on the vomer 9
7 Supraorbital tentacles well developed, 3 mm in height minimum. Orbital canal with 2–3 rows of pores. I 4 pelvic fin rays. Male without any neck crest ..... *Aidablennius*
– Supraorbital tentacles hardly visible, less than 3 mm in height. Orbital canal with only one row of pores. I 3 pelvic fin rays. Male with neck crest 8
8 Presence of brownish bars on the flanks not contrasted with black dots conferring a marble coat. Dorsal fin notched between spined and soft rays (except for *I. atlantica*). 16–18 dorsal fin soft rays. 16–19(20) anal fin soft rays. 34–38 vertebrae. 8–9 circumorbital pores. 8–11 preopercular pores. 3 supratemporal pores ..... *Ichthyocoris*
– Brownish bars on the flanks very contrasted with blue stripes and dots conferring a marble coat. Dorsal fin not notched between spined and soft rays. 21–27 dorsal fin soft rays. 20–28 anal fin soft rays. 38–44 vertebrae. 6–7 circumorbital pores. 6–8 preopercular pores. 2 supratemporal pores ..... *Salaria*
9 12 pectoral fin rays ..... *Bathyblennius*
– 13–14 pectoral fin rays 10
10 14 pectoral fin rays. Presence of tentacles on the anterior nostril ..... *Parablennius*
– 13 pectoral fin rays. Absence of tentacles on the anterior nostril ..... *Lupinoblennius*
11 Presence of canines in both jaws ..... *Hypleurochilus*
– Absence of canines in either jaw 12
12 Body skin loose and flaccid, encompassing dorsal and anal fins. XII–XIV dorsal fin pines ..... *Chalaroderma*
– Body skin not loose and flabby, not reaching over the fins. XI–XII dorsal fin pines 13
13 The skin of the dorsal fin extends over to the proximal quarter of the caudal ..... *Chasmodes*
– The skin of the dorsal fin does not extend to the caudal 14
14 IX–X 25 dorsal fin rays. 24 anal-fin soft rays. 15–16 pectoral fin rays ..... *Parahypsos*
– XI–XII 15–18 dorsal fin rays. 12–20 anal fin soft rays. 13–15 pectoral fin rays ..... *Hypsoblennius*

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