A NEW SPECIES OF *CALMA* ALDER & HANCOCK, 1855 (GASTROPODA: NUDIBRANCHIA) WITH A REVIEW OF THE GENUS

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ABSTRACT

This paper presents the description of a new species of the genus *Calma* (Alder & Hancock, 1855). To date only one valid species, *Calma glaucoides* (Alder & Hancock, 1854), has been assigned to this genus, which feeds exclusively upon eggs of littoral teleost fishes. New morphological and ecological data, and review of the literature on the species attributed to this genus, lead us to conclude that there are two distinct species previously put together under the same specific name. *Calma gobioophaga* new species is described based upon consistent morphological differences, such as the diameter and position of the eyes, the size of the propodial tentacles, and the size of the metanefridium. Whereas *Calma gobioophaga* feeds on spawn of *Gobius niger*, *Calma glaucoides* feeds on eggs of *Lepadogaster lepadogaster*, *Lepadogaster purpurea*, *Lepadogaster candollei*, *Parablennius gattorugine*, and *Parablennius pilicornis*.

INTRODUCTION

Calma glaucoides (Alder & Hancock, 1854) is the only valid species attributed to the genus *Calma* Alder & Hancock, 1855. This species was originally described as *Eolis glaucoides*, but it was later considered to belong to its own distinct genus (Alder & Hancock, 1855). Friele & Hansen (1875) described *Eolis albicans* from Norway from based on a single specimen, pointing out its resemblance to the genus *Calma*. In that paper, the authors presented only one figure showing a lateral view of the radula, which is very similar to the one illustrated by Alder & Hancock (1855). Trinchese (1881) described *Forestia mirabilis* from Italy. Later, Trinchese (1889) redescribed the species, documenting its anatomy with numerous figures, although a view of the entire animal was lacking. Eliot (1910) included both *Eolis albicans* and *Forestia mirabilis* in the genus *Calma*. According to this author, *C. mirabilis* was the only Mediterranean representative of the genus, whereas *C. glaucoides* and *C. albicans* were the Atlantic members. He also proposed that *Eolis calvolini* Vérany, 1846, previously included in the genus *Calma*, should be placed in a new genus, *Calmella*, where it still remains. Presently, both *Eolis albicans* and *Forestia mirabilis* are considered synonyms of *Calma glaucoides* (see Evans, 1922). *Eolis glaucoides* is the type species of the genus *Calma*, validated by the International Commission on Zoological Nomenclature (I.C.Z.N., 1966), after Lemche's (1964) proposal to conserve the generic name. *Calma glaucoides* is an aeolid nudibranch inhabiting the Atlantic and Mediterranean coasts of Europe (Thompson & Brown, 1984; Picton & Morrow, 1994). Adults (7–16 mm) are normally found on spawn of teleost fishes, such as clingfishes (Gobiesocidae) and blennies (Blenniidae). The fishes deposit their eggs on the underside of boulders or on empty bivalve shells and the nudibranchs feed on them. *Calma* has a very atypical 'uniseriate' radula, previously described as a row of very small teeth with a group of a few larger teeth at the distal end (Evans, 1922). Calado & Urgorri (2001) found that although these bigger teeth could be absent from some adults, such a peculiar morphology is related to the animal's feeding habits. As already noted by other authors (Eliot, 1910; Evans, 1922), there is no anus or intestine. While searching for *Calma glaucoides* on fish spawn, we found some individuals in a spawn of the gobid fish *Gobius niger* L., 1758, which differ consistently in some external characters from previously collected *Calma glaucoides*. The purpose of this paper is to reassess the status of the valid species belonging to the genus *Calma* and to describe a new species. We also survey the literature concerning species attributed to this genus.

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MATERIAL AND METHODS

Collection

Most of the specimens studied were collected in several localities of the Arrábida Coast, Portugal (38°30′24″ N; 08°55′09″ W – 38°24′54″ N; 09°13′24″ W) or nearby, between 1998 and 2000. We have also analysed some specimens collected by one of us (V. U.) in Galicia, NW Spain in 1978 and 1979. Most specimens were collected by SCUBA diving, from 2 to 15 m depth. Two anatomically different groups of nudibranchs were defined: Group 1 (G1)—nudibranchs found on spawn of the following fishes: *Lepadogaster lepadogaster* (Bonaterre, 1788), *Lepadogaster purpurea* (Bonaterre, 1788), *Lepadogaster candollei* Risso, 1810, *Parablennius gattorugine* (Brünnich, 1768) and *Parablennius pilicornis* (Cuvier, 1829); Group 2 (G2)—nudibranchs found on spawn of *Gobius niger* L. 1758.

Anatomy

The animals were observed *in vivo*, photographed or drawn schematically. Whenever they were not needed alive for experimentation, they were anaesthetized (with magnesium chloride or by gentle freezing) and preserved in 70% ethanol. To study the radula morphology, the buccal masses of some animals were extracted and dissolved in a 5% NaOH solution for 24 h at 40°C. Isolated radulae were abundantly rinsed in water. Three radulae from each group were dried and coated with gold, prior to SEM examination. The reproductive system was recon-

structed based upon serial transverse 10-μm sections using traditional histological methods.

Egg capsule diameter

The maximum diameter of 30 egg-capsules belonging to seven different specimens of each group was measured. We used an average of 30 eggs from each animal and compared the 14 individuals using a Mann–Whitney test, since the heteroscedasticity necessary to perform an analysis of variance was not verified.

Copula tests

Recently-fed animals from both groups were kept in two 200-ml beakers of six individuals each (3G1 + 3G2) for 24 h, at a temperature the same as that of the sea (16–18°C). Animals were observed for several hours, searching for copulation between two individuals.

SYSTEMATIC DESCRIPTIONS

Calma Alder & Hancock, 1855

This genus was defined by Alder & Hancock (1855) as follows:

> Body depressed, rather broad; tentacles [including rhinophores] small simple, linear: branchiae [cerata] linear-fusiform, clustered on cylindrical footstalks; foot broad, anterior angles acute. Tongue [radula] very small and narrow, bearing a single spine.

Type species: Calma glaucoides (Alder & Hancock, 1854).

Calma glaucoides (Alder & Hancock, 1854)

(Specimens from group 1)

Eolis glaucoides Alder & Hancock, 1854: 102–105.
Eolis albicans Friele & Hansen, 1875: 69–80.
Forestia mirabilis Trinchese, 1881: 121–122.

Types: *Eolis glaucoides* Alder & Hancock, 1854: Holotype probably lost, it could not be located at BMNH (A. Campbell, personal communication) nor at the Hancock Museum, Newcastle-upon-Tyne (A. Valdés, personal communication). These are the two institutions where most of Alder and Hancock's type material is deposited. Type locality: Herm Island, Guernsey (United Kingdom).

Eolis albicans Friele & Hansen, 1875: Holotype probably lost, it could not be located at Bergen Museum (Norway), where Friele & Hansen's specimens are deposited (J. Evertsen, personal communication). Type locality: Florø, Norway.

Forestia mirabilis Trinchese, 1881: Holotype probably lost; it could not be located at Stazione Zoologica di Napoli (Italy). Trinchese worked for many years in this institution. Its type list was personally checked by one of us (G.C.). Type locality: Naples, Italy.

Neotype of *Calma glaucoides* (herein designated): animal 10.5 mm long, collected on 11 June, 2000, in Cozinhadouro, Arrábida, Portugal (38°26′48″ N; 09°02′24″ W) at 4 m depth, on a spawn of *Lepadogaster lepadogaster* (other features as in the species description). It is deposited at the Museo Nacional de Ciencias Naturales (MNCN) Madrid, Spain, with the registration number MNCN 15.05/43740, together with a photograph of the living animal.

Material examined: Several specimens collected at Arrábida Coast, Portugal between May 1998 and August 2000: Alpertuche (38°27′36″ N; 08°59′18″ W), Anicha (38°28′36″ N; 08°58′18″ W), Arflor (38°30′24″ N; 08°55′09″ W), Cozinhadouro, (38º26′48″ N; 09°02′24″ W), Ninho da Águia (38°27′18″ N; 09°00′30″ W), Três Irmãs (38°27′48″ N; 08°59′24″ W), on spawn of *Lepadogaster lepadogaster*, *Lepadogaster purpurea*, *Lepadogaster candollei*, *Parablennius gattorugine*, and *Parablennius pilicornis*. Eight specimens collected in Burela, Galicia, Spain (43°38′50″ N; 07°20′35″ W), in May 18th, 1999, one on a spawn of *Lepadogaster lepadogaster* and seven on a spawn of *Lepadogaster candollei*.

Anatomy (Figs 1A, 2A): Adults reach 16 mm in length, although lengths between 8 and 12 mm are more common, in which case the body is 4–5 mm wide. The body is depressed, generally of a white-yellowish colour. The stomach is easily seen through the transparent integument, and its colour depends on the nutritional state of the animal, the type of eggs ingested, and their development state when eaten. We found individuals whose body colour was dark yellow when they had fed on little-developed *Lepadogaster* spp eggs, purple when they had fed on little-developed *Parablennius* spp eggs, and brown when they had ingested further developed eggs or when digestion was more advanced. Cerata divided into 7–10 pairs of groups (generally 9) with 2–4 cerata in each group (generally 3). First two groups are pre-cardiac. Cerata are cylindrical with a pointed apex. A small, forward-pointing protruberance is located near the insertion point, though this is not visible in some individuals. The colour of the cerata derives mostly from the digestive gland, although some white spots are present in the integument and are more densely arranged in the sub-apical zone. Some of the larger individuals are completely covered by white opaque dots and some light-blue dots. This gives the animal a light blue-whitish general appearance. In these cases, it is not possible to see the colour of the digestive gland through transparency. The foot is broad, ending in a small narrow tail, and is usually covered by the last cerata. Anteriorly, the foot forms two small, acute propodial tentacles, smaller than the anterior cerata. Rhinophores and oral tentacles are smooth, broader at their bases, with a white spotted band in the distal third, which does not reach the apex. The eyes are small, about 80 μm in diameter, and situated behind the rhinophores, in the space between them and the first group of cerata. In some animals, the oesophagus has a reddish coloration. The metanephridium is easily recognizable through the transparent body. It lies dorsally between the second and the sixth (rarely fifth or seventh) groups of cerata. In the smallest (about 2 mm long) specimens collected, seven ceratal groups are already present, with one single ceras in each. White pigmentation on the rhinophores, oral tentacles, and cerata is still not very visible.

The gonad is divided into paired lateral groups, which match the insertion zones of the ceras groups. When fully developed, just before oviposition, the female and male acini may adopt a reniform (kidney-like) structure occupying the space between the insertions of two consecutive groups of cerata. The radula is uniseriate and formed by a row of very small denticles (about 1 μm long) and a group of a few larger teeth at the distal end. This latter group could be absent in some animals. Jaws are smooth, without denticles in the masticatory border. The reproductive system (Fig. 3A) matches the description by Evans (1922). A divided gonad leads into a hermaphroditic duct, which swells in a coiled ampulla, before the bifurcation into male and female ducts. The male and female openings are separate.

Remarks: A neotype is here designated to clarify the taxonomic status of *Calma glaucoides* and to fix the synonymy between *Eolis glaucoides, Eolis albicans* and *Forestia mirabilis*. The neotype locality (Arrábida, in the Portuguese west coast) is a compromise between Norway, U.K. and Italy, the former three type localities. The designated specimen mainly matches the characteristics contained in the three original descriptions, as in the short

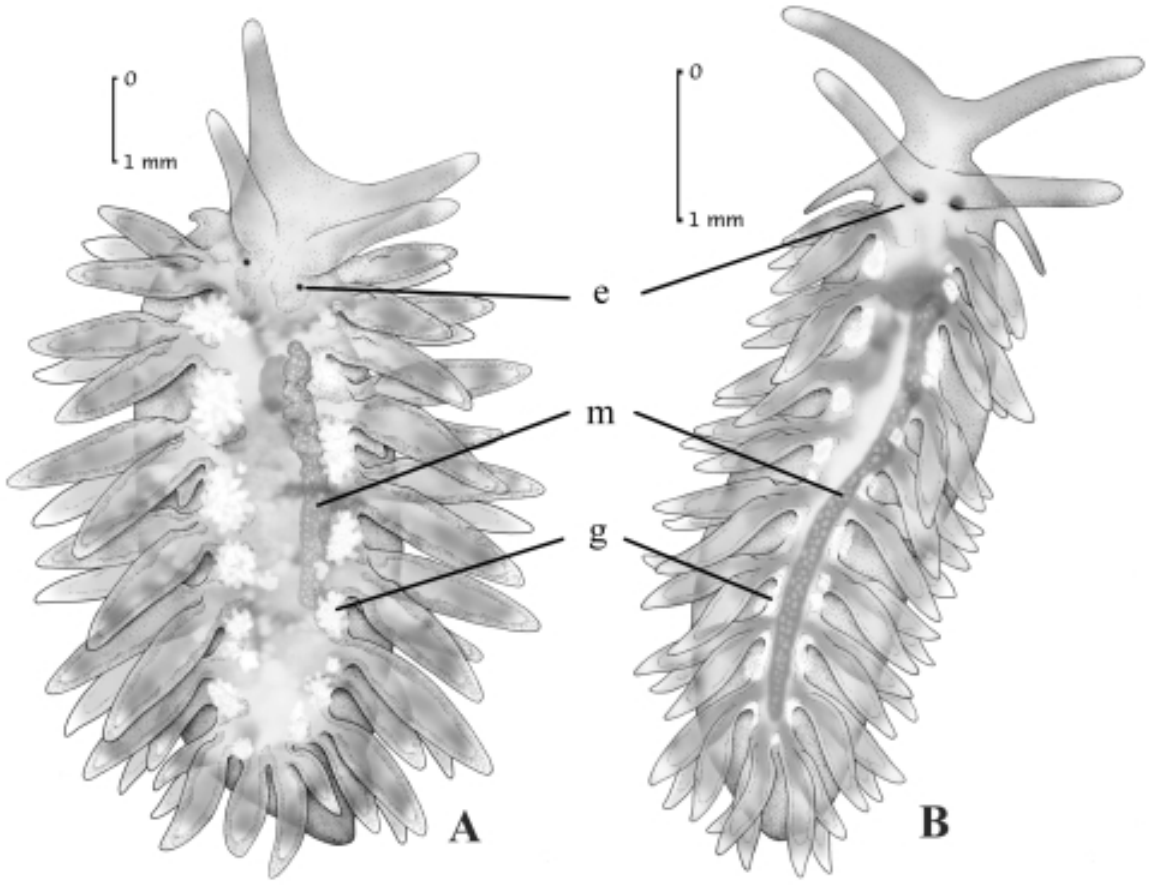

Figure 1. Dorsal views of both species. **A**. *Calma glaucoides*. **B**. *Calma gobioophaga*. Abbreviations: e, eye; g, gonadal unit; m, metanephridium.

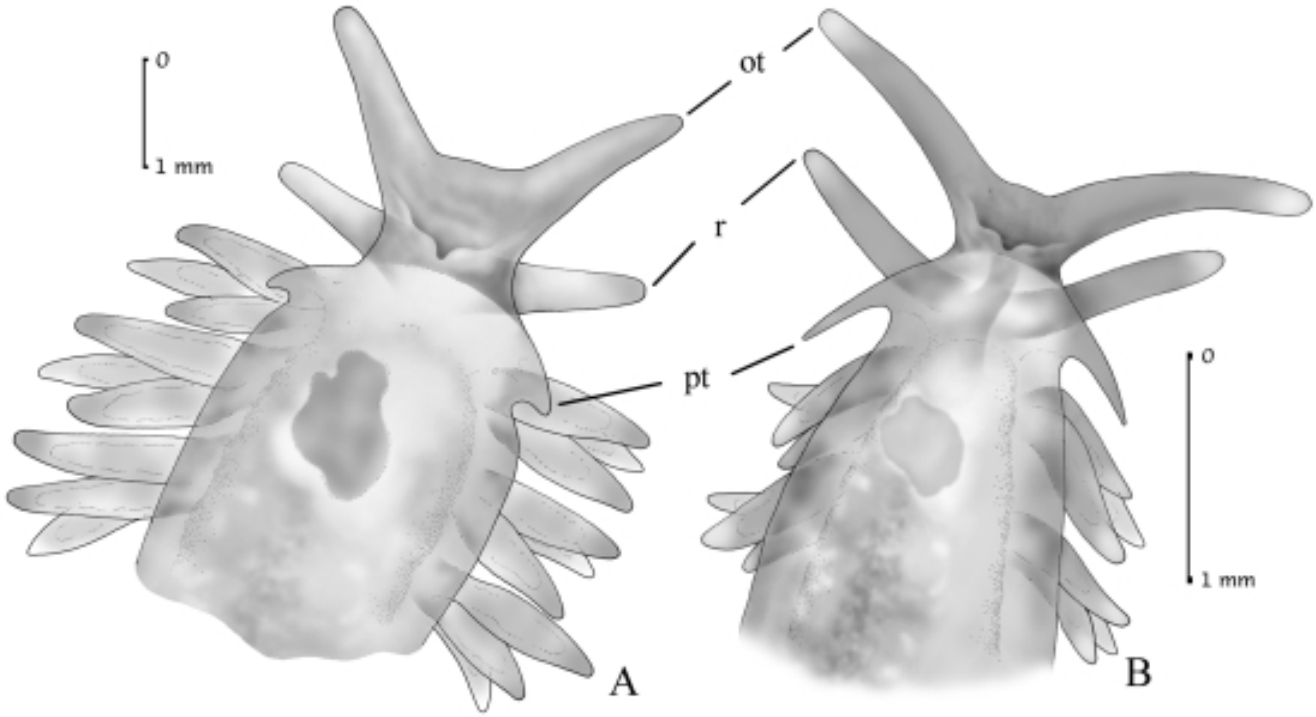

Figure 2. Ventral views of both species (detail). **A**. *Calma glaucoides*. **B**. *Calma gobioophaga*. Abbreviations: ot, oral tentacles; pt, propodial tentacles; r, rhinophores.

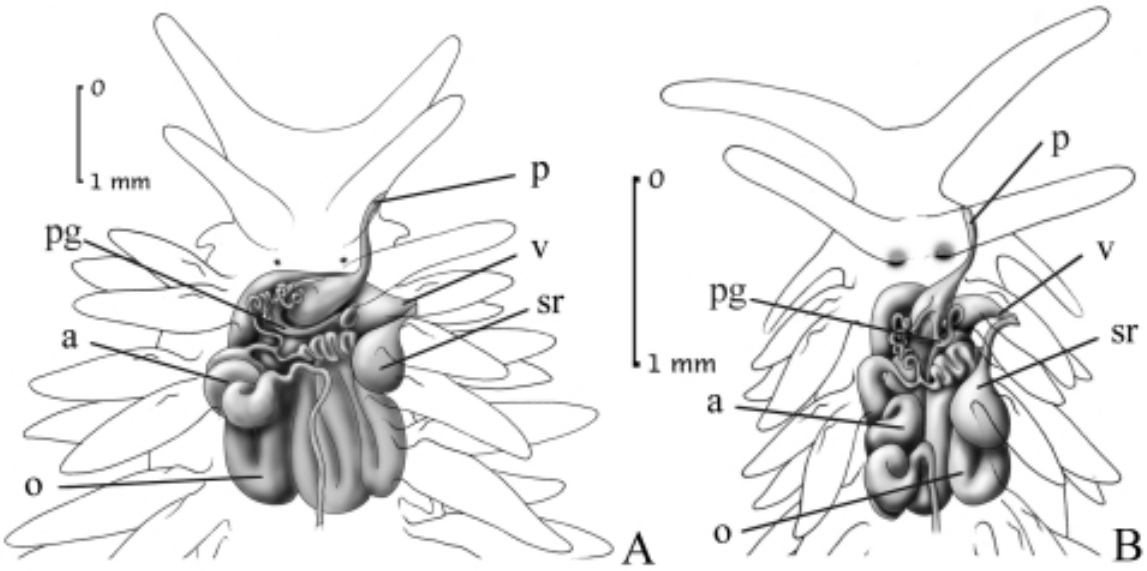

Figure 3. Reproductive systems of both species. **A**. *Calma glaucoides* **B**. *Calma gobioophaga*. Abbreviations: a, ampulla; o, oviduct; p, penis; pg, penial gland; sr, seminal receptacle; v, vagina.

size of the propodial tentacles (Alder & Hancock 1854; Friele & Hansen, 1875; Trinchese, 1881), and the red colour of the oesophagus (Friele & Hensen, 1875), which is visible through transparency between the eyes, although it was not present in all the animals we observed. The eye diameter, 80 μm, has the same value as that measure by Trinchese (1889) in a subsequent description of *Forestia mirabilis* (see species description and discussion below).

Calma gobioophaga new species
(Specimens from group 2)

Calma glaucoides (Alder & Hancock, 1854)—Hecht, 1896: 539–711.

Types: Holotype: animal 10 mm long, collected on 29 May, 2000, in Arflor, Arrábida, Portugal (type locality) (38°30′24″ N; 08°55′09″ W) at 10 m depth, on spawn of *Gobius niger*. It is deposited at the Museo Nacional de Ciencias Naturales (MNCN) Madrid, Spain, with the registration number MNCN 15.05/43741, together with a photograph of the living animal. Paratype 1: animal 10 mm long, collected on 29 May, 2000, in Arflor, Arrábida, Portugal (38°30′24″ N; 08°55′09″ W) at 10 m depth on spawn of *Gobius niger*. It is deposited at the Museu Oceanográfico do Parque Natural da Arrábida (MO/PNA), Setúbal, Portugal, with the registration number 558MOPNA, together with a photograph of the living animal. Paratype 2: animal 4 mm long, collected on 5 August, 1978, in A Cabana (Ría de Ferrol), Galicia, Spain (43°29′10″ N; 08°15′29″ W) at 2 m depth, on unidentified fish spawn. It is deposited at the Museo de Historia Natural 'Luis Iglesias' (MCNS), Santiago de Compostela, Spain, with the registration number MCNS-5MO. The remaining type series is deposited at the Instituto Português de Malacologia (Portugal, material from Portugal) and in Victoriano Urgorri's collection at the Departamento de Zooloxía, Universidade de Santiago de Compostela (Spain, material from Galicia, Spain).

Derivato nominis: The specific name *gobioophaga* derives from the fish *Gobius niger* (Pisces: Gobiidae), on whose eggs the nudibranch feeds, and among which it lives during non-larval life.

Material examined: Several specimens collected on Arrábida Coast, Portugal between May 1999 and August 2000: Alpertuche (38°27′36″ N; 08°59′18″ W) and Arflor (38°30′24″ N; 08°55′09″ W), on spawn of *Gobius niger*. 61 specimens collected in Galicia, Spain: A Cabana (Ría de Ferrol; one specimen, August 5th, 1978; 43°29′10″ N; 08°15′29″ W); Espigón de Cambados (Ría de Arousa; 58 specimens, 27 July, 1979; 43°31′17″ N; 08°49′18″ W); Enseada de Leuseda (Ría de Ferrol; two specimens, 19 August, 1979; 43°28′03″ N; 08°16′38″ W). All on unidentified fish spawn.

Anatomy (Figs 1B, 2B): Adults reach 10 mm in length, 3 mm in width. The body is depressed, generally of a brown-yellowish colour, darker in the area covering the digestive gland when developed fish eggs are ingested. The colour depends on the nutritional state of the animal, the type of eggs ingested, and how far the digestion has advanced. The cerata are divided into 7–10 groups of pairs (generally nine) with two pre-cardiac groups and generally three cerata per group. They are inflated with a pointed apex and a small forward-pointing protruberance, located near the insertion point. The colour of the cerata derives primarily from the digestive gland, although some white spots are present in the integument, more concentrated in the sub-apical zone. The foot is broad, ending in a small and narrow tail, being usually covered by the last cerata. Anteriorly, the foot forms two large, digitiform, notched propodial tentacles, about as large as the anterior cerata. Rhinophores and oral tentacles are smooth, broader at their base, with a white spotted band on the distal third, which does not reach the apex. Although not very visible through the notum, the gonad is also divided in paired lateral groups, which match the insertion zones of the post-cardiac cerata groups. The eyes are large, about 110 μm in diameter, and they are situated just behind the rhinophores or at their rear border. The metanephridium is easily visible through the transparent notum, lying dorsally between the second and the last group of cerata. In the smallest (about 2 mm long) collected specimens, six ceratal groups are already present, each one consisting of a single ceras. The eyes are already well developed. White pigmentation on the rhinophores, oral tentacles, and cerata is still not very visible.

Propodial tentacles are already distinguishable. The radula is uniseriate and formed by a row of very small denticles (about 1 μm long) and a group of a few larger teeth at the distal end (Fig. 4). This latter group, however, is absent in some animals. Jaws are smooth, without denticles in the masticatory border. The reproductive system (Fig. 3B) matches the description by Evans (1922) of *Calma glaucoides*. The gonad is divided and the gonadal subunits, composed of a central male acinus surrounded by a large number of female acini, are serially distributed in all the inter-ceratal spaces except the first. Paired efferent ducts lead into the hermaphroditic duct, which swells into a coiled ampulla, before the bifurcation into the male and female ducts. The male opening is situated in front of and below the level of the right rhinophore, whereas the female opening occupies a more usual position below the first ceratal group on the right. A long, tubular, penial gland connects with the deferent duct close to the male opening. The greatly enlarged oviduct is formed from folds of a glandular, dorsally coiled structure, which remains open ventrally in the first three lobes and closed in the fourth. The seminal receptacle is spherical. It lies close to the female opening and it is connected to the vagina by a short duct.

Egg mass: The spawn is generally spirally coiled, with the egg string secondarily twisted, corresponding to Type B of Hurst's (1967) classification. The egg capsules are elliptical in the larger section, having only one egg (rarely two) and they are randomly distributed in the jelly matrix in a single layer.

Comparative analysis of both species

Egg capsule diameter: The values of maximum diameter of 30 egg-capsules belonging to seven different nudibranchs of each species are illustrated in Fig. 5. Although there is some overlap of values, it is evident that individuals belonging to *C. gobioophaga* usually have smaller eggs. The Mann–Whitney test revealed significant differences between average values by individual ($Z = -2{,}36$; $P < 0.05$; $N_{C.\ glaucoides} = 7$; $N_{C.\ gobioophaga} = 7$).

Copula tests: In the trials performed, only copulation between individuals of the same group was observed, two cases in *Calma glaucoides* and one case in *Calma gobioophaga*. They occurred at night when animals were more active.

DISCUSSION

The two species studied herein differ consistently in some morphological characters, such as body length and width, the size of the metanephridium, the size and position of the eyes, and form and size of the propodial tentacles, which apparently are not related to each other in function. According to Mayr & Ashlock (1991) this lack of coevolution is a good indicator that they are separate species. It is also evident that at least during non-larval life, both species occupy different ecological niches. The fact that only intraspecific copulation was observed under artificial conditions, where both species were present, could indicate a pre-copulatory isolation mechanism. The only obvious

Figure 4. *Calma gobioophaga*: SEM micrograph of a radula. Scale bar = 25 μm.

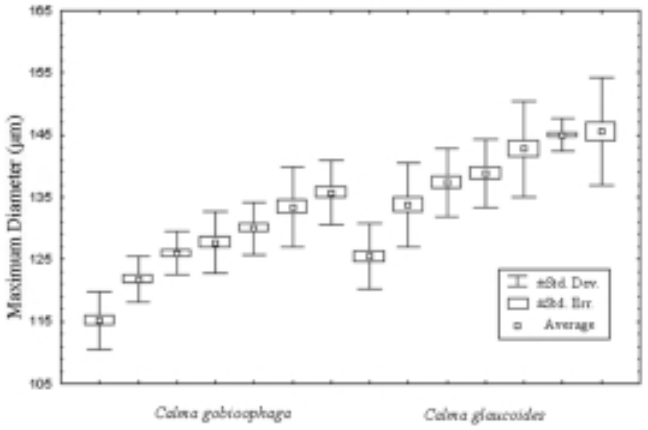

Figure 5. Main statistical parameters (mean, SE, SD) of maximum diameters of egg capsules measured in seven animals of both species (30 eggs each).

difference between the reproductive systems of both species is the size of the ampulla, which is generally bigger in *C. gobioophaga* than in *C. glaucoides* (Fig. 3). In the first case, the ampulla extends backwards beyond the oviduct, which was never observed in *C. glaucoides*. Nevertheless, this difference is less evident if the ampulla is not completely full of autosperms, as it was observed in one specimen of *C. gobioophaga*. These small anatomical differences should not constitute *per se* an isolation mechanism. Tardy (1969) tried to cross three different species of the genus *Aeolidiella* with no positive results, despite the great similarity in their reproductive systems.

Re-assessment of early descriptions and references

Although every effort was done to locate the holotypes of described species presumably belonging to the genus *Calma*, these were untraceable and presumably lost. Thus, re-evaluation of early studies was only based upon descriptions and original figures. The first illustrations attributed to *Calma glaucoides* are those of Alder & Hancock, (1855: family 3, plate 22). Some characteristics of the external morphology (short and acute propodial tentacles, and the reduced size of the eyes) lead us to conclude that it is not *C. gobioophaga*. The colour of illustrations 2 and 4 (plate 22) matches that observed in older living animals of *C. glaucoides* and was never observed in *C. gobioophaga*. The description of *Eolis albicans* by Friele & Hansen (1875) matches that of Alder & Hancock (1854, 1855) for *C. glaucoides*. The character they used to distinguish their new species is that the cerata are non-pedunculated while, according to them, in *C. glaucoides* they are pedunculated. Considering the animals that we have studied, this criterion is not applicable, since more or less pedunculated ceratal groups were observed, according to the nutritional condition of the animals. In 'empty' individuals, ceratal groups tend to appear more pedunculate than in 'full' ones. Furthermore, the only figure presented by Friele & Hansen (1875) is a lateral view of the radula, identical to that of Alder & Hancock (1845–55). Friele & Hansen (1875) also refer to the red colour of the oesophagus, which is visible through transparency between the eyes, which is probably food dependent and was never observed in *C. gobioophaga*. Even without a full image of the animal, the descriptions of Trinchese (1881, 1889), of *Forestia mirabilis*, are very detailed and generally match previous descriptions of *C. glaucoides*. As already pointed out by Evans (1922), the identification of the anal opening was mistaken with the nephropore. The diameter of the eyes (80 µm), as measured by Trinchese, leaves no doubt about the identity of this species. The individuals of *C. gobioophaga* with the same length as those observed by Trinchese (*C. glaucoides*) already have an eye diameter of 110 µm. Among the literature containing explicit references to *C. glaucoides*, only in two cases was it possible to determine that the authors were referring to specimens of *C. gobioophaga*, which could have been mixed with individuals of *C. glaucoides*, under the same specific name. The first one is that of Hecht (1896). The author showed in his figure 2, plate 1, one animal inside a typical gobiid spawn and in his figure 47, plate 4, the metanephridium extends backwards to the end of the body, which never occurs in *C. glaucoides*. Interestingly, Evans (1922) spotted this difference: 'Hecht (1896) gives a faithful description of the kidney [metanephridium], but represents the former as extending to the end of the body, whereas in all the numerous specimens examined for this paper the kidney [metanephridium] entirely in front of the seventh ceratal group'. Evans was obviously dealing with *C. glaucoides* and Hecht with *C. gobioophaga*. The second reference is that of Thompson & Brown (1984), who illustrated two 'forms', a and b, of *C. glaucoides* in their plate 36. Whereas figure a represents a typical adult of *C. glaucoides*, figure brepresents *C. gobioophaga*. The difference in body width should be noted, as well as the difference in the size of the propodial tentacles. The relative size and position of the eyes is not correctly represented. The references to *C. glaucoides* from NW Spain (Urgorri & Besteiro, 1983) can now be attributed to *C. gobioophaga*, since we have re-examined the specimens used in that paper. A similar situation probably occurs with many other faunistic contributions where species are not sufficiently described and no additional biological data have provided. References to the fish spawn in which nudibranchs were collected may provide an important clue, as in Templado, Talavera & Murillo (1987), where gobiid eggs are indicated as the collection substrate. If this is the case, the nudibranchs collected belong to the species *C. gobioophaga*. Table 1 summarizes the main differences between the two species of the genus *Calma*.

Table 1. Main differences between *Calma glaucoides* and *Calma gobioophaga*.

	Calma glaucoides	*Calma gobioophaga*
Maximum length	16 mm	10 mm
Maximum width	5 mm	3 mm
Propodial tentacles	Small and acute	Large and finger-like
Position of the eyes	Behind the rhinophores, in the space between these and the first group of cerata	Immediately behind the rhinophores or in its rear border
Diameter of the eyes	80 µm	110 µm
Position of the metanephridium	Between the 2nd and the 6th (rarely 5th or 7th) ceratal group	Between the 2nd and the last ceratal group
Size of the ampulla	Small, never extending to the back of the oviduct	Large, usually extending to the back of the oviduct
Average egg-capsule maximum diameter	138.37 µm (n = 210)	127.09 µm (n = 210)
Species of fish whose eggs were observed to be predated	*L. lepadogaster*, *L. purpurea*; *L. candollei*, *P. pilicornis*; *P. gattorugine*	*G. niger*

New generic diagnosis

The genus *Calma* was described by Alder & Hancock (1855) on page 21 of the Appendix. Considering the characteristics

common to both species, the character 'anterior angles acute' should be suppressed, since it only exists in *Calma glaucoides*, and the shape of the radula should also be redefined. The presence of a large, non-branched metanephridium is also a character present in the genus *Calma*. With the new evidence presented here a new diagnosis is proposed: body depressed, rather broad; oral tentacles and rhinophores small, simple and linear; cerata linear-fusiform, clustered on cylindrical footstalks, without cnidosacs; foot broad; radula very small and narrow, uniseriate, formed by a saw-like band of small fused denticles, occasionally with a few larger, hook-like, separate teeth in the distal end; metanephridium not branched, dorsally visible; male and female reproductive openings widely separated, with the penis in anterior position; animals prey exclusively upon eggs of littoral teleost fishes.

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