

THE GENUS *HAMINOEA* (GASTROPODA: CEPHALASPIDEA) IN PORTUGAL, WITH A REVIEW OF THE EUROPEAN SPECIES

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ABSTRACT

The study of specimens of *Haminoea* collected on the coast of Portugal, together with the re-evaluation of historical specimens used by Nobre (1938–40) in his main work on the Portuguese molluscs, recognized the presence of two species, *Haminoea navicula* (da Costa, 1778) and *H. orbignyana* (Férussac, 1822), and confirmed the misidentification of *H. orbignyana* as *H. elegans* (Gray, 1825). Anatomical analysis found intraspecific variability in the radula of *H. navicula* and *H. orbignyana* and in the seminal duct of the latter. The systematic value of taxonomic features including the shell, external morphology, animal coloration, radula, jaws, gizzard plates, prostate gland, seminal duct, penis and egg-masses is discussed. For all European species but *H. orbignyana*, identification is only possible when anatomical data are considered, and the most relevant character is the male reproductive system. SEM images of the penis and prostate of *H. navicula* and *H. orbignyana* are given for the first time. A synoptic table for the recognition of the European species is provided.

INTRODUCTION

The genus *Haminoea* Turton & Kingston, 1830, comprises herbivorous species living worldwide on temperate and tropical coasts in habitats of mud and seagrass, but also on rocky shores with algal assemblages (Rudman, 1971; Schaefer, 1992; Malaquias, Martínez & Abreu, 2002).

Most of the worldwide species were described based only on shells, which are very similar in shape, colour and proportion within the genus. This has made the taxonomy of this group very confused, with many species being of doubtful taxonomic status (Thompson, 1981; Talavera, Murillo & Templado, 1987; Gibson & Chia, 1989). According to Rudman (1971) the differences between species are found in the animal and not in the shells and, therefore, adequate description requires the study of anatomical structures.

At present, eight species of *Haminoea* are recognized as valid in Europe (Table 1), although in many geographical areas some of them have been identified based only on shells. This is the case for *Haminoea elegans* (Gray, 1825), *H. hydatis* (Linné, 1758) and *H. navicula* (Da Costa, 1778) in Portugal. In this work we give detailed descriptions of the two species in Portugal that we identified as *H. navicula* and *H. orbignyana* (Férussac, 1822), based on specimens collected along the coast of Portugal, and we re-evaluate part of the material used by Augusto Nobre (1938–40) in his classic work on the Portuguese molluscs. Moreover, we assess the variability and systematic value of various anatomical and morphological characters in *Haminoea*, and provide a synoptic table for the identification of the European species.

MATERIAL AND METHODS

Specimens were collected along the coast of Portugal between 2000 and 2002. Surveys were undertaken on intertidal and subtidal areas down to 20 m deep in habitats of seagrass, algae, sandy-mud, mud and on rocky shores, and specimens sampled by direct collection, airlifting, brushing rocks and dredging

using a van Veen grab. Egg masses found in the vicinity of specimens were also collected.

Historical specimens housed in the Museu Zoológico da Universidade de Coimbra (hereafter designated MZUC) used by the Portuguese malacologist Augusto Nobre (Nobre, 1938–40) were studied.

Specimens (shell length, H) and egg masses were measured, described under a dissection microscope, and photographed. Egg masses were preserved in 70% ethanol, and animals first relaxed in freezing salt-water before preservation in 70% ethanol. Shell microsculpture and anatomy were studied by scanning electron microscopy. Soft tissues were first critical-point dried.

The total number of eggs per egg mass was estimated by counting the number of eggs in five strings and multiplying this value by the total number of strings. The average egg and capsule dimensions were measured after preservation, considering 10 eggs and capsules from one egg mass.

SYSTEMATIC DESCRIPTION

Haminoea navicula (da Costa, 1778)

Material examined: Ria de Aveiro, 30 specimens (H ~ 24 mm) and several egg masses; Mondego estuary (40°08' N, 08°50' W), 20 specimens, H = 30–35 mm; Ria Formosa, Canal do Ramalhete (37°00'31" N, 07°88'43" W), 3 specimens, H = 13–42 mm; Ria Formosa, Ilha de Faro (37°14'37" N, 08°11'26" W), 1 specimen, H = 20 mm. Nine specimens dissected and mounted for SEM. Voucher specimens housed in Museu de Ciências Naturales de Madrid, Spain (MNCN 15.05/45.842; MNCN 15.05/45.843).

External morphology: Cephalic shield trapezoidal, posteriorly developed into two conspicuous lobes covering anterior part of shell. Hancock's organ with 12–16 leaves. Parapodial lobes overlapping dorsally, covering more than half of the shell, and in larger specimens almost all the shell. Pallial lobe rounded posteriorly and expanded anteriorly beyond spire (Fig. 2A–C).

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Table 1. Synoptic table for the recognition of the European species of the genus *Haminoea*.

	<i>H. callidegenita</i>	<i>H. exigua</i>	<i>H. fusari</i>	<i>H. hydatis</i>	<i>H. navicula</i>	<i>H. orbignyana</i>	<i>H. ortei</i>	<i>H. templadoi</i>
Shell spiral striae	Present, very fine	Absent	Absent	Absent	Present, conspicuous	Absent	Absent	Absent
Cephalic lobes	Large and overlapping each other	Small non-overlapping	Small non-overlapping	Small non-overlapping	Small non-overlapping	Small non-overlapping	Small non-overlapping	Small non-overlapping
Periocular area	Unpigmented	Unpigmented	Unpigmented	Unpigmented	Unpigmented	Unpigmented	Pigmented	Unpigmented
Hancock's organ	Tubular	Perfoliate	Perfoliate	Perfoliate	Perfoliate	Perfoliate	Perfoliate	Perfoliate
Number of prostate lobes	1	2	2	2	2	2	2	2
Prostate lobes	Granulose, distal part wider	Contiguous; distal larger than proximal	Separated by narrow zone	Separated by narrow zone	Contiguous; distal 2/3 of total prostate length	Contiguous; wider than distal	Contiguous; distal larger than proximal	Contiguous, distal larger than proximal
Penial tip	Smooth	Apical crest with 8 lamellae	Smooth with small sharpened tip	Smooth	Spiculose	Smooth	Apical crest with 10 lamellae and 2 lateral lobes	Apical crest with 10 lamellae and 1 lateral lobe
Jaws	Symmetrical	Asymmetrical	Symmetrical	Symmetrical	Symmetrical	Symmetrical	Asymmetrical	Symmetrical
Number of ridges on gizzard plates	12	15	17–18	13–17	8–15	15–18	30–32	20–22
Lateral radular teeth	Inner lateral with secondary inner cusp	Inner lateral denticulate	Inner lateral smooth	Inner lateral denticulate	Inner lateral and first outer lateral (in juveniles) either denticulate or smooth	Inner lateral smooth	Inner lateral denticulate	Inner lateral and first outer lateral denticulate

This table is an extended version of those presented by Schaefer (1992) and Álvarez *et al.* (1993a).

Animal coloration: General colour dark grey, in some cases almost black. Cephalic shield with abundant black pigmentation and few scattered orange and white spots. Striking dark patch present between eyes. White line present between this patch and cephalic lobes. Periocular area not pigmented. Buccal mass not visible through the epidermis. Edges and posterior area of parapodial lobes with conspicuous black patches. Remaining area pigmented by black and few white spots. Mantle visible through shell and pigmented by black and smaller orange dots and fewer white spots. Pallial lobe lighter than body, with black dots, accretions of white pigments and lower numbers of orange spots (Fig. 2A–C). Foot lighter than body, with abundant white pigmentation and scattered black and orange spots.

Shell: Globose shape, fragile, thin, hyaline, truncated posterior, formed by last whorl. Aperture wider in anterior region and slightly longer than spire, which is involute. Lip thin, sharp (Fig. 1A–D). Columellar callus with varying levels of thickness (Fig. 3C, D). Growth lines conspicuous. Spiral striae thin, present all over shell (Fig. 3A, B). Periostacum thin, orange-brown in colour.

Radula: Radular formula $28 \times 44-39.1.1.1.39-44$ ($H = 18$ mm) and $29 \times 58-51.1.1.1.51-58$ ($H = 24$ mm). Rachidian tooth broad with three cusps, the central more developed. Inner lateral teeth triangular-spatulate shape, outer edge either denticulate (faintly or conspicuously) or smooth; both forms can occur in the same specimen. Inner lateral teeth smooth in juveniles. Outer lateral teeth hook-shaped with smooth edges (Figs 4A–F, 5A, B).

Jaws: Symmetrical, crescentic or half-moon shaped. Formed of long, thin, overlapping rodlets, producing a scale-like sculpture with denticulate edges (Fig. 3E–G).

Gizzard plates: Three gizzard plates, with 12–15 ridges. Semispherical sculpture present on top of ridges and rachis (Fig. 5C–E).

Male genital system: Prostate 1.2 mm in a juvenile ($H = 10$ mm) and 3–4 mm in adults ($H = 18-24$ mm). Formed by two contiguous lobes with smooth surfaces. Distal lobe twice the size of proximal. Seminal duct short and thick, sometimes slightly coiled. Penial sheath 1.2 mm in a juvenile ($H = 10$ mm) and 4–5 mm in adults (Fig. 6A). Penis 1.3 mm, cylindrical, with broad, spherical apical tip; armed in adults with apical corneous spines (Fig. 6B–E); armature not developed in juveniles (Fig. 6F).

Egg masses: Ribbon-shaped, slightly coiled, formed by thick, gelatinous yellowish-hyaline matrix, 20–75 mm in length, 15–18 mm high ($H = 23-24$ mm). Eggs spherical, enclosed by a capsule. One egg per capsule. Eggs and capsules 0.147 ± 0.007 mm and 0.355 ± 0.016 mm in diameter, respectively. Eggs arranged in rows inside a hyaline 'tube', coiling along the smaller axis of the egg mass. Number of eggs between 7700 (egg mass, 55 mm length) and 15500 (egg mass, 75 mm length).

Ecology: Intertidal areas of coastal lagoons and estuaries with beds of green algae (*Ulva* spp. and *Enteromorpha* spp.) or seagrass

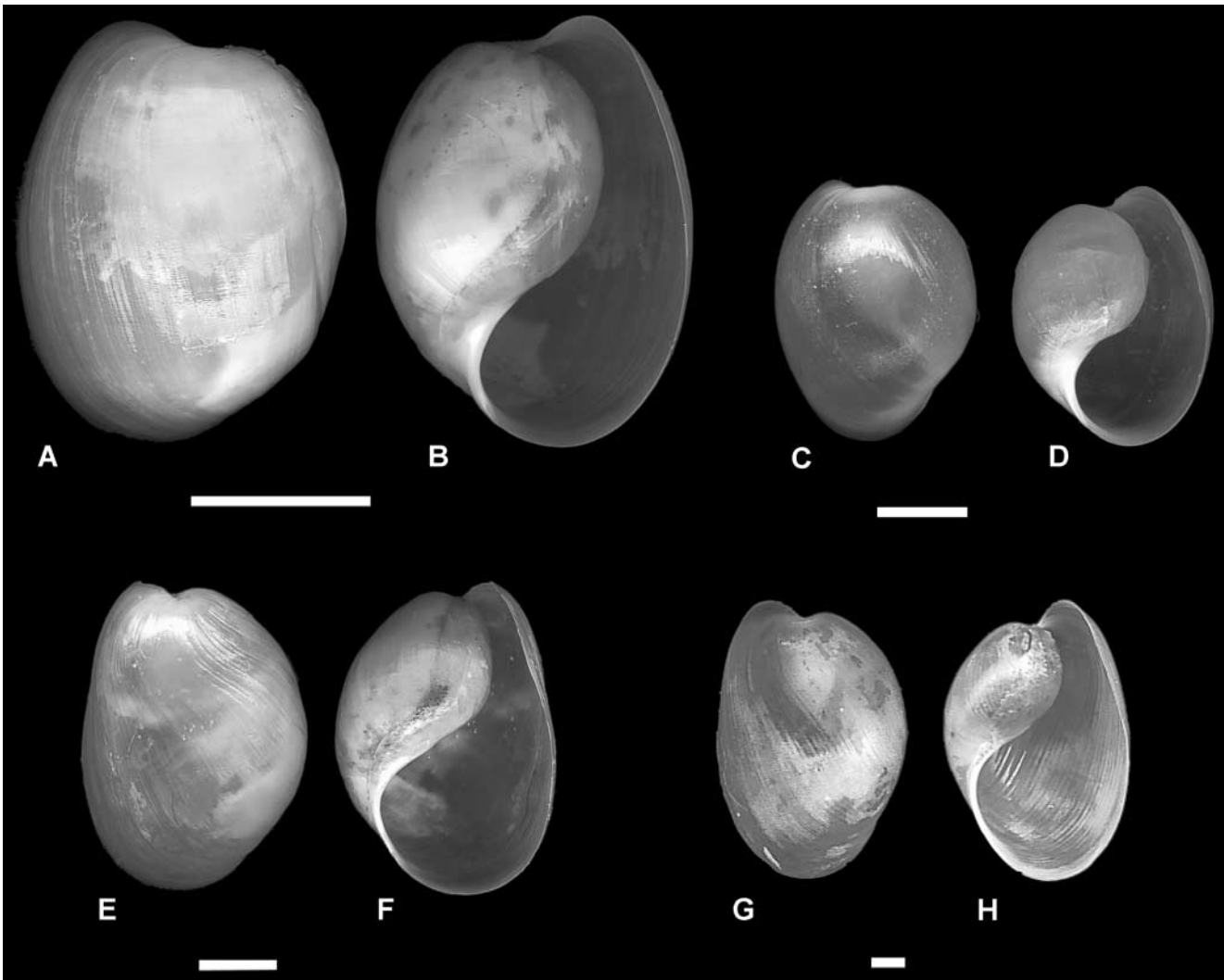


Figure 1. A–D. *Haminoea navicula*. A. Adult, adapertural view. B. Adult, apertural view. C. Juvenile, adapertural view. D. Juvenile, apertural view. E–H. *Haminoea orbignyana*. E. Adult, adapertural view. F. Adult, apertural view. G. Juvenile, adapertural view. H. Juvenile, apertural view. Scale bars: A, B = 10 mm, C–F = 5 mm, G–H = 1 mm.

(*Zostera noltii*), and in subtidal areas down to 4 m depth on sandy-mud bottoms.

Distribution: Eastern Atlantic, from southern England and Ireland, France (Thompson, 1976), Ibero-Atlantic coasts, Strait of Gibraltar, Mediterranean Sea to Malta (Talavera *et al.*, 1987; Cervera *et al.*, 1988; Sammut & Perrone, 1998).

Remarks: The type locality of *H. navicula* is Weymouth, Dorset in the south of England (da Costa, 1778). We were unable to trace the type specimens (empty shells) used by da Costa (1778: 28–29, table I, Fig. 10), and our identification follows the diagnosis outlined in Talavera *et al.* (1987) and Thompson (1988).

Haminoea orbignyana (Férussac, 1822)

Material examined: Ria de Aveiro, 60 specimens (H ~ 14–35 mm); Mondego estuary, 2 specimens (H = 14 mm); Mira estuary, 28 specimens (H ~ 13 mm); Ria Formosa, Esteiro das Charradas, 45 specimens (H = 8–17 mm); Ria Formosa, Ramalhete, 5 specimens (H = 13 mm); Ria Formosa, Cacela Velha, 15 specs; Sapal

de Castro Marim, 10 specimens (H ~ 4–6 mm); Guadiana estuary, 15 specimens (H ~ 11 mm). Seventeen specimens dissected and nine mounted for SEM. Voucher specimens housed in Museu de Ciências Naturales de Madrid, Spain (MNCN 15.05/45.839; MNCN 15.05/45.840; MNCN 15.05/45.841). Four specimens (MZUC), Mengo collection, Faro, Portugal, H = 11–12 mm; 4 specimens (MZUC), A. F. Müller collection, Cabo de Santa Maria (nearby Faro), Portugal, H = 11–13 mm; 6 specimens (MZUC as *Haminoea hydatis*; in Carvalho, 1945: Pleurocoela No7), Vila Real de Santo António.

External morphology: Cephalic shield trapezoidal, developed posteriorly into two small cephalic lobes, covering the anterior part of the shell. Hancock's organ with 12–13 leaves in adult specimens. Parapodial lobes extended dorsally, occasionally overlapping. Pallial lobe rounded posteriorly and developed anteriorly as far as the spire (Fig. 2C–E).

Animal coloration: Ground colour grey-brown to brownish both in juveniles and adults. Cephalic shield edges densely black-pigmented from eyes towards cephalic lobes. Periocular

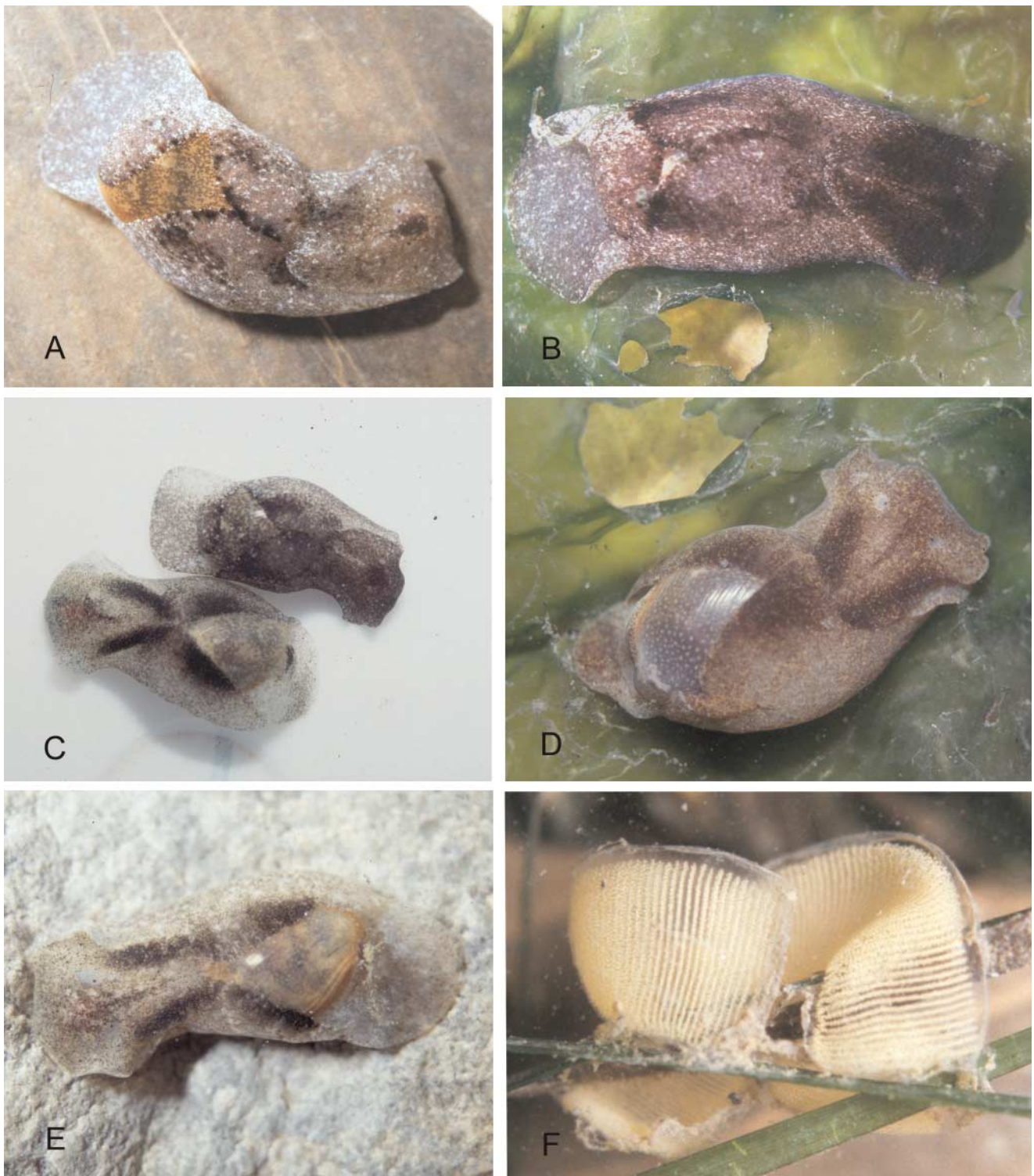


Figure 2. **A.** *Haminoea navicula* (Ria Formosa, H = 35 mm). **B.** *Haminoea navicula* (Ria de Aveiro, H = 55 mm). **C.** *Haminoea navicula* (above, Mondego River estuary, H = 33 mm) and *H. orbignyana* (below, Mondego River estuary, H = 35 mm). **D.** *Haminoea orbignyana* (Ria de Aveiro, H = 34 mm). **E.** *Haminoea orbignyana* (Rio Mira estuary, H = 35 mm). **F.** Egg mass of *H. orbignyana* attached to a leaf of *Zostera noltii* (Ria Formosa, 25 × 5 mm).

area unpigmented. Buccal mass visible through the epidermis, of pale rose colour. Conspicuous fine black line extending between the eyes and cephalic lobes. Edges of parapodial lobes black-pigmented, creating conspicuous dark area. Mantle visible through-out shell, with orange dots and aggregations of fine white pigmentation. Pallial lobe lighter than body, with black spots,

accretions of white pigments and fewer orange dots (Fig. 2C–E). Foot lighter than body, with fine black pigmentation over surface, and scattered white and orange pigmentation.

Shell: Pyriform, fragile, hyaline, formed by last whorl, aperture broad in the anterior part and narrow posteriorly. Lip thin,

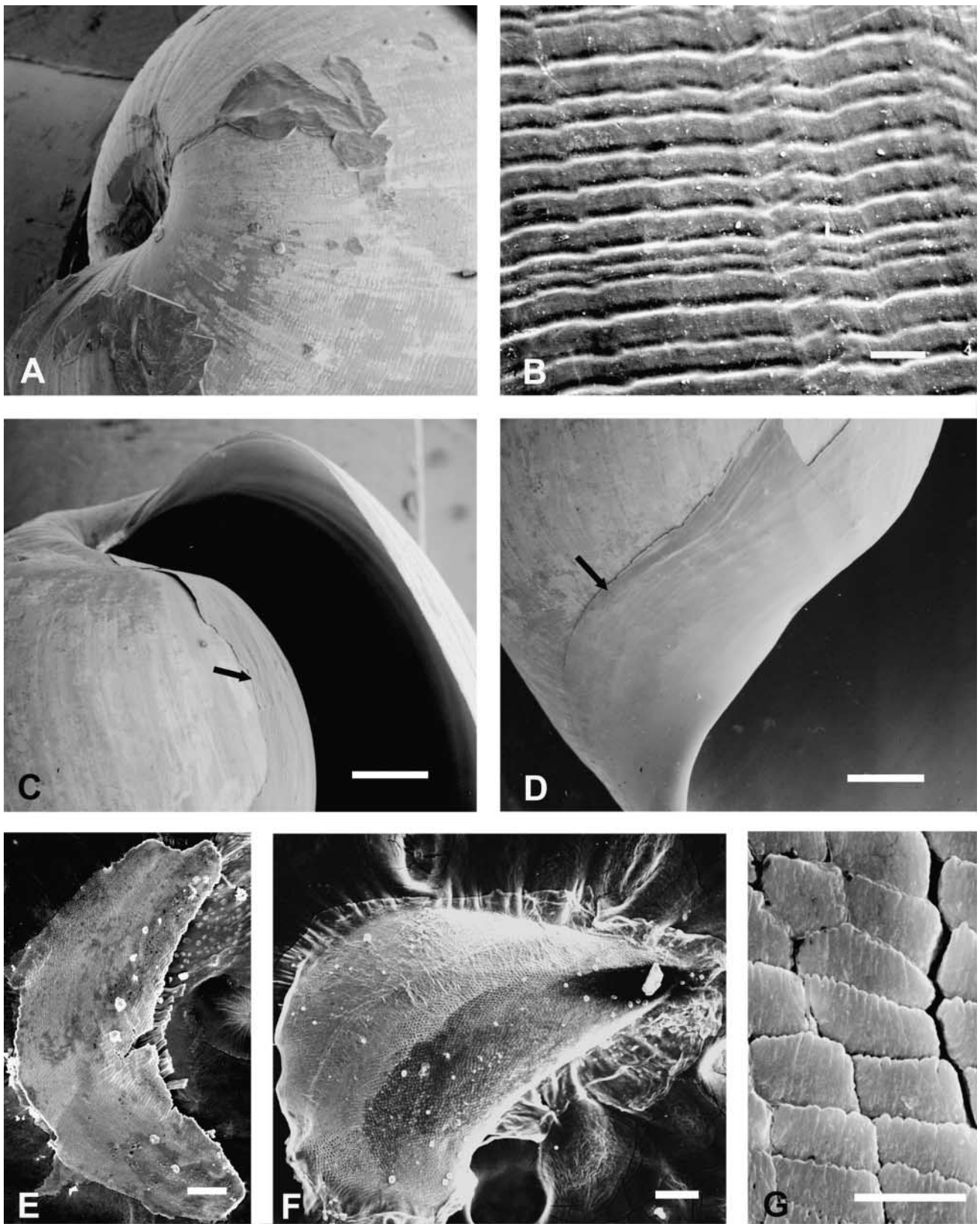


Figure 3. *Haminoea navicula*. **A.** Detail of the spire area. **B.** Spiral striae on the adapertural side of the shell. **C.** Columellar callus on the posterior part of the aperture. **D.** Columellar callus on the anterior part of the aperture. **E.** Jaw (adult specimen). **F.** Jaw (juvenile specimen). **G.** Jaw micro-sculpture. Scale bars **A, C, D** = 1 mm; **B, E–J** = 100 μ m.

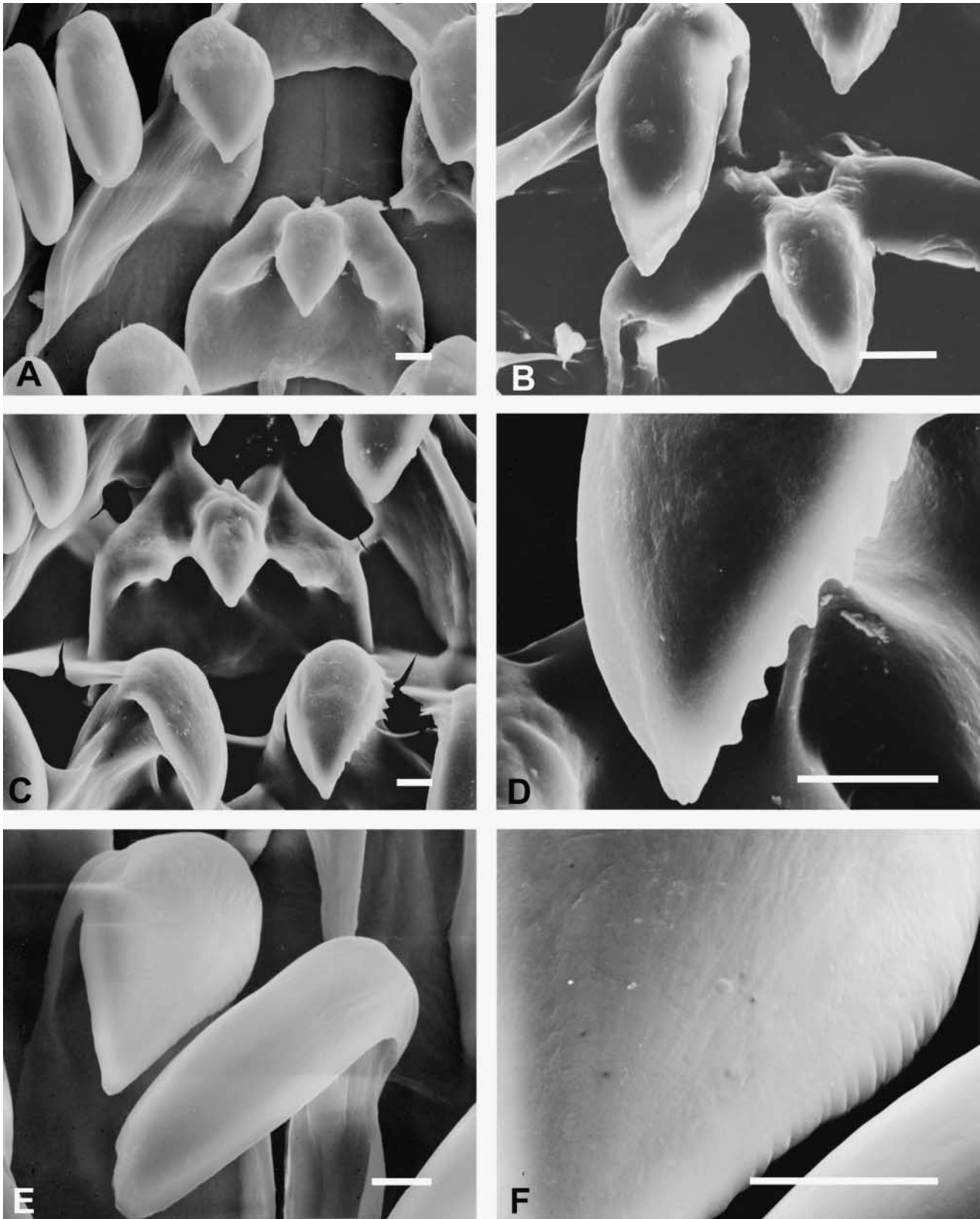


Figure 4. *Haminoea navicula*. **A.** Rachidean and lateral teeth. **B.** Rachidean and left inner lateral teeth from an immature specimen. **C.** Rachidean and inner lateral teeth (note: left tooth with smooth outer edge and right tooth with denticulate outer edge). **D.** Detail of the right inner lateral tooth figured in C. **E.** Inner lateral and first outer lateral teeth. **F.** Detail of the outer edge of the inner lateral tooth figured in E. Scale bars = 10 μm .

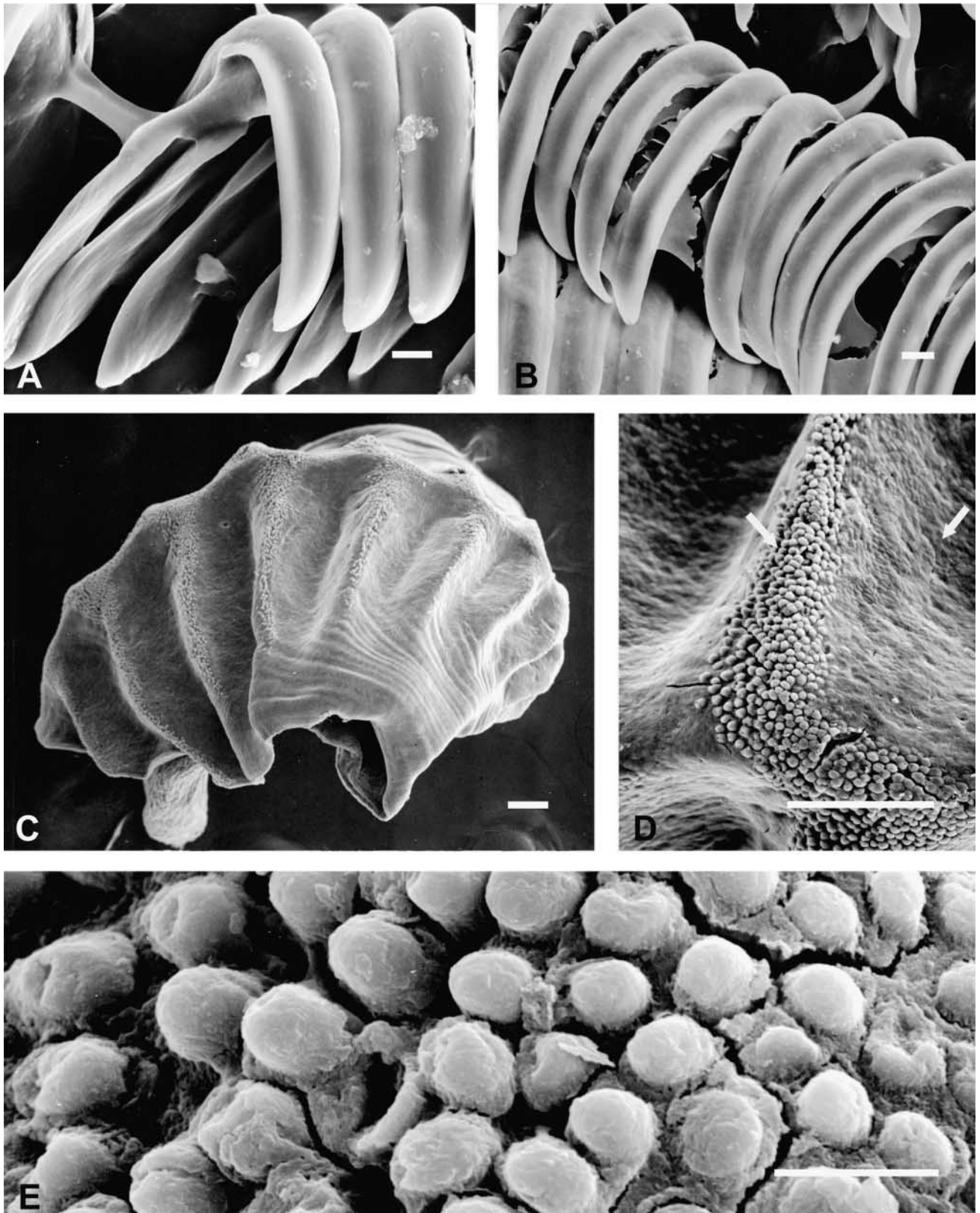


Figure 5. *Haminoea navicula*. **A.** Right side outer lateral teeth. **B.** Left side outer lateral teeth. **C.** Gizzard plate. **D.** Detail of the gizzard plate sculpture (left arrow pointing to top of ridge and right arrow pointing to area between ridges). **E.** Detail of the gizzard plate sculptural forms. Scale bars **A, B, E** = 10 μm ; **C, D** = 100 μm .

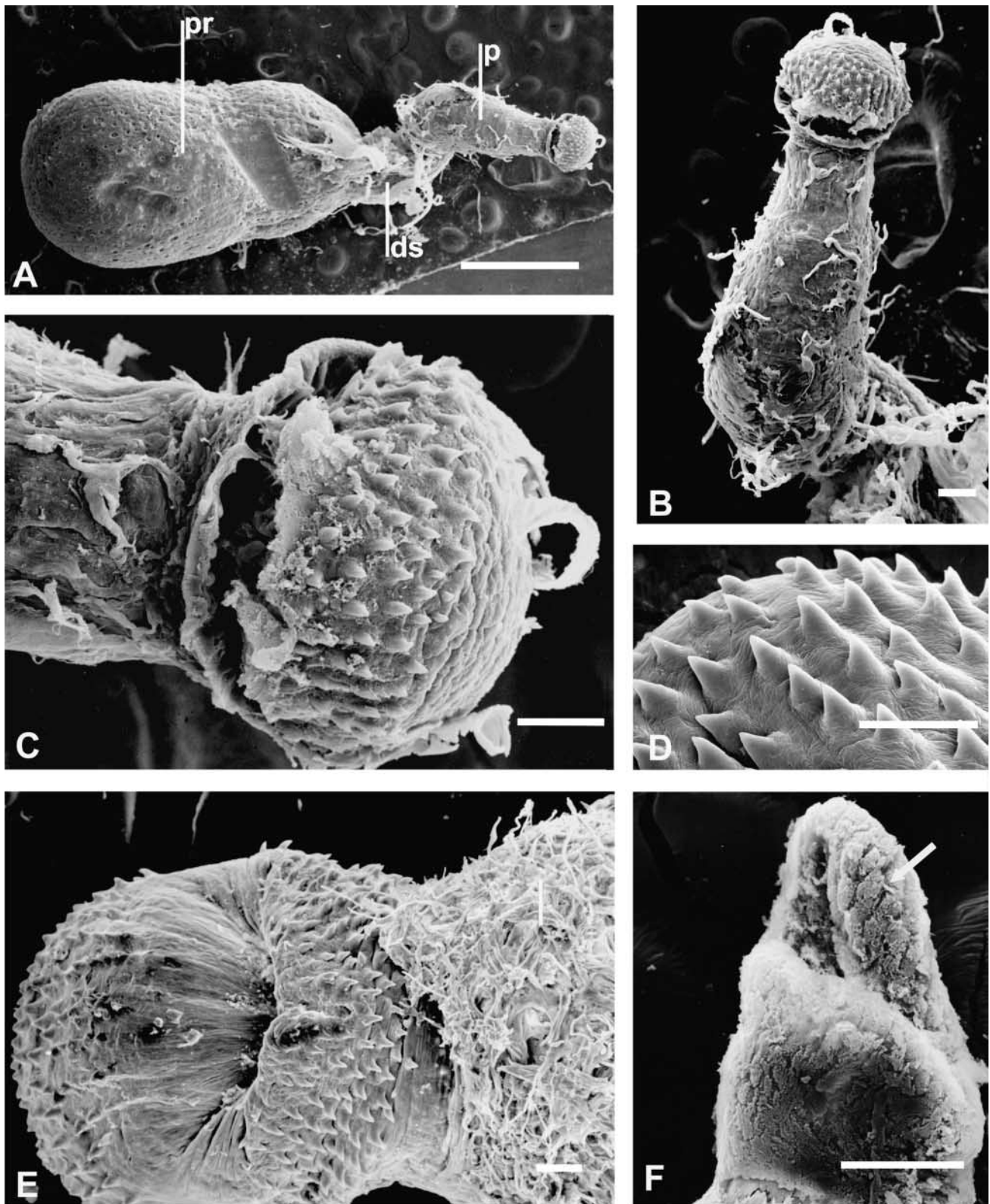


Figure 6. *Haminoea navicula*. **A.** Male copulatory apparatus: ds, seminal duct; p, penis; pr, prostate. **B.** Penis. **C, E.** Detail of the apical tip of the penis. **D.** Detail of the penial armature. **F.** Penial apical region from an immature specimen. Scale bars **A** = 1 mm; **B–F** = 100 μ m.

sharp, slightly larger than spire, which is involute (Fig. 1E–H). Columella covered by thin callus (Fig. 7D, E). Abundant, fine growth lines (Fig. 7A–C). Periostracum thin, orange-brown.

Radula: Radular formula $30 \times 51-43.1.1.1.43-51$ ($H = 15$ mm) and $29 \times 41-33.1.1.1.33-41$ ($H = 17$ mm). Rachidian tooth broad, three cusps, central larger with one small cusp on each side. The small cusps can vary both in relative size and sharpness among specimens. Inner lateral teeth spatulate, smooth edges, asymmetrical bilobed base. First outer lateral sharply hook-shaped (Fig. 9A–E).

Jaws: Symmetrical, crescentic, formed by long overlapping rodlets, with scale-like edges (Fig. 9F).

Gizzard plates: Three gizzard plates with 15–18 ridges, covered with sharp rods on tops of ridges and rachis, and less developed sculpture between ridges (Fig. 8D–F).

Male genital system: Prostate 2–3 mm in length ($H = 12-16$ mm), acorn-like shape, formed from two distinct, contiguous lobes with granulose surfaces. Distal lobe more slender than proximal and slightly longer, to two-thirds total prostate length. Seminal duct 3–4 mm (Fig. 7F). Penis 2–3 mm in length, smooth, with conspicuous warts along sides, tip spatulate (Fig. 8A–C).

Egg masses: Ribbon-shaped, slightly coiled, 9–25 mm in length and 5 mm high (Fig. 2F). Eggs contained in a yellowish-hyaline gelatinous matrix, placed inside a capsule. Egg and capsule diameter 0.071 ± 0.003 mm and 0.102 ± 0.006 mm, respectively. Number of eggs between 4662 (9 mm egg mass) to 10080 (25 mm egg mass).

Ecology: Estuaries and coastal lagoons on intertidal areas of mud or muddy-sand, with seagrass *Zostera noltii* or green algae. Egg masses were found attached to leaves of seagrass (Fig. 2F).

Distribution: East Atlantic, from France (Férussac, 1822), Galicia, Spain (Cervera *et al.*, 1988), Portugal (Hidalgo, 1917; Nobre, 1938–40; both authors as *H. elegans*), Témara, Morocco (Pruvot-Fol, 1953), Canary Islands southward to Cape Verde archipelago (Talavera *et al.*, 1987), Spanish Mediterranean coast (Murillo & Talavera, 1983), Malta and central Mediterranean (Sammot & Perrone, 1998).

Remarks: The type locality of this species is near La Rochelle, Bay of Biscay, France (Férussac, 1822). Type material is housed in the Muséum National d'Histoire Naturelle, Paris (4 syntype shells), and was previously studied by Valdés & Héros (1998: 704, Fig. 4B). The shell shape of our specimens match these types. In fact this is considered to be the only European species of *Haminoea* with a distinctive shell. Furthermore, the anatomical features of our specimens agree with those described by Talavera *et al.* (1987).

DISCUSSION

Shell

Shells in the genus *Haminoea* are very similar among species; they are globular, ovoid, fragile, thin, hyaline, covered with a thin periostracum and with the greatest diameter at mid-length. The aperture is the same size or slightly longer than the involute spire. Both intra-specific and inter-populational variation occur (Rudman, 1971; Talavera *et al.*, 1987; García, Perez-Hurtado & García-Gómez, 1991; Schaefer, 1992). According to Talavera *et al.* (1987), *Haminoea orbignyana* is the only European species that can be distinguished by its shell, which is pyriform with a

broad anterior part of the aperture. Different degrees of calcification of the shells of this species were observed during this study, which might be due either to older age of the thicker specimens or to different mineralogical properties of the environment. Ontogenetic variability was also found, with juveniles showing a thinner shell, oval in shape with the anterior part of the aperture broader when compared with adults (Fig. 1E–H). In contrast, the species *H. navicula* has a globose shell with conspicuous spiral striae. No ontogenetic variability was found (Fig. 1A–D). Although *H. navicula* has a shell very similar in shape to all the other European species (except for *H. orbignyana*), it is the only one other than the invasive *H. callidegenita* (Alvarez *et al.*, 1993b) to have spiral striae. However, the striae in *H. navicula* are conspicuous, whereas in *H. callidegenita* they are faint.

Coloration

Despite the fact that in some species the animal shows a specific and diagnostic coloration, such as *H. cymbalum* from Fiji (Rudman, 1971), most of the species have a ground pattern of drab colours with some degree of chromatic variation, as described for *H. zelandiae* from northern New Zealand (Rudman, 1971), *H. callidegenita* from Washington State (Gibson & Chia, 1989) and in the European species *H. hydatis*, *H. navicula*, *H. orbignyana* and *H. oratei* (Talavera *et al.*, 1987). The species *H. oratei* is the only species in Europe with pigmented pericocular areas (Talavera *et al.*, 1987). Although *H. navicula* and *H. orbignyana* show similar pigmentation, the distribution of the pigments is considerably different, especially on the cephalic shield and parapodial lobes (see Systematic Description and Fig. 2). In *H. orbignyana* intra-specific colour variation was observed, with specimens being either grey-brown or completely brown. In *H. navicula*, chromatic variations seem to occur as a response to different substrates or stress conditions. Edlinger (1982) reported that this species can adjust its coloration by migration and contraction/relaxation of melanophore cells.

External morphology

The use of external morphological features (shape of cephalic shield, parapodial lobes, pallial lobe) has been considered useful by some authors (e.g. Talavera *et al.*, 1987). However, these characters must be used with caution since their shape can easily change with stress caused by handling, leading to inaccurate descriptions. Nevertheless, some of these structures can be strikingly different, allowing an immediate recognition of certain species. For example, in Europe *H. callidegenita* has a unique cephalic shield, with very long and overlapping cephalic lobes (Gibson & Chia, 1989). Despite the few morphological differences between most European species, some can be found between *H. navicula* and *H. orbignyana*. According to Thompson (1976) *H. navicula* can reach 32 mm in shell length, whereas Talavera *et al.* (1987) reported a maximum of 20 mm for *H. orbignyana*. The maximum length found in the studied specimens was 24 mm in the former and 17 mm in the latter species. A conspicuous difference between these species relates to the area of the shell covered by the parapodial and pallial lobes. Whereas in *H. navicula* almost the entire shell is enclosed by these lobes (only a small area of the posterodorsal part remains visible), in *H. orbignyana* the majority of the shell is visible (only the anterior-lateral areas and the posterior part up to the spire are covered by these lobes; Fig. 2).

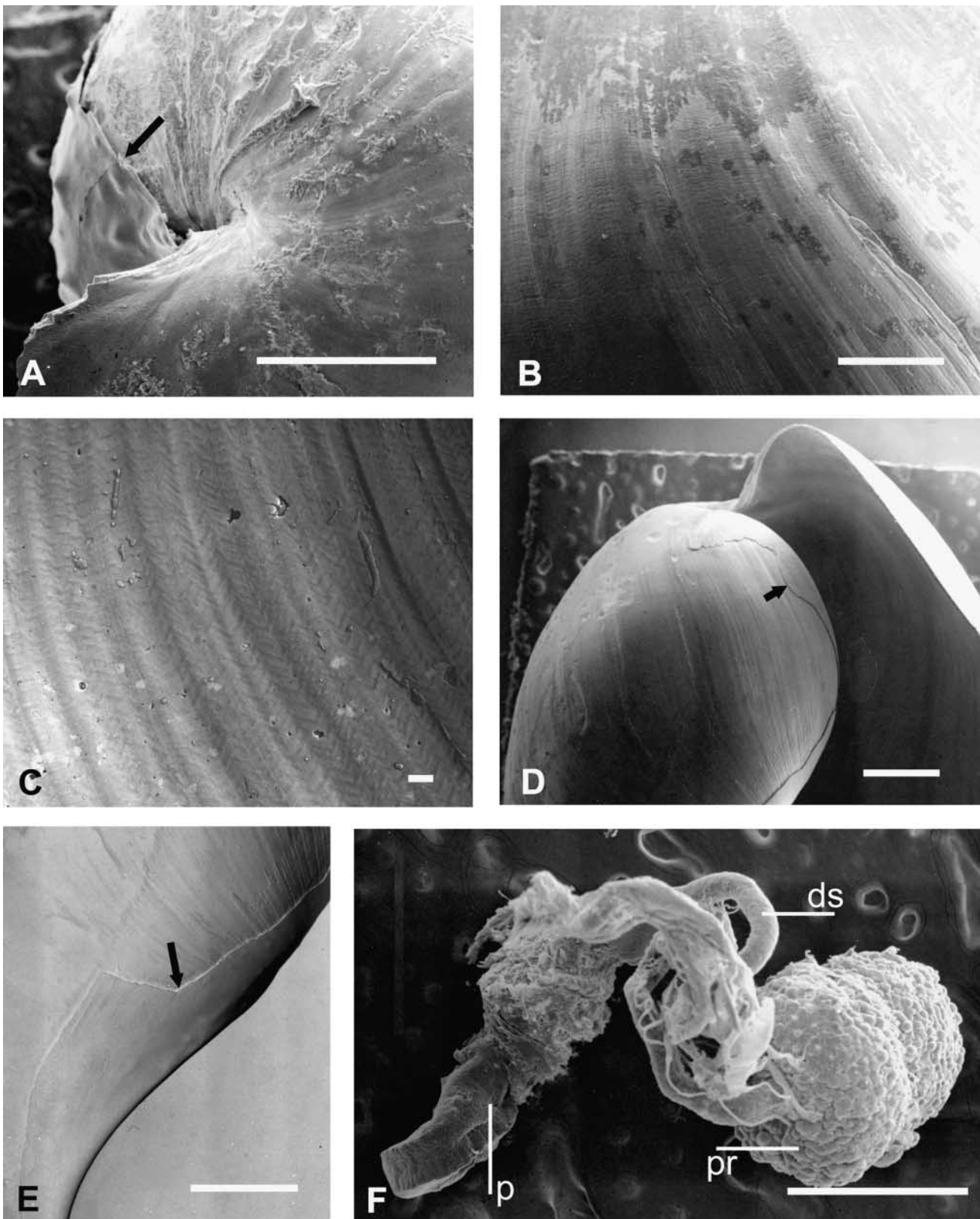


Figure 7. *Haminoea orbignyana*. **A.** Detail of the spire area. **B.** Detail of the posterior adapertural part of the shell. **C.** Detail of the anterior adapertural part of the shell. **D.** Detail of the columellar callus on the posterior area of the aperture. **E.** Detail of the columellar callus on the anterior area of the aperture. **F.** Male copulatory apparatus: ds, seminal duct; p, penis; pr, prostate. Scale bars **A, B, D–F** = 1 mm; **C** = 100 μ m.

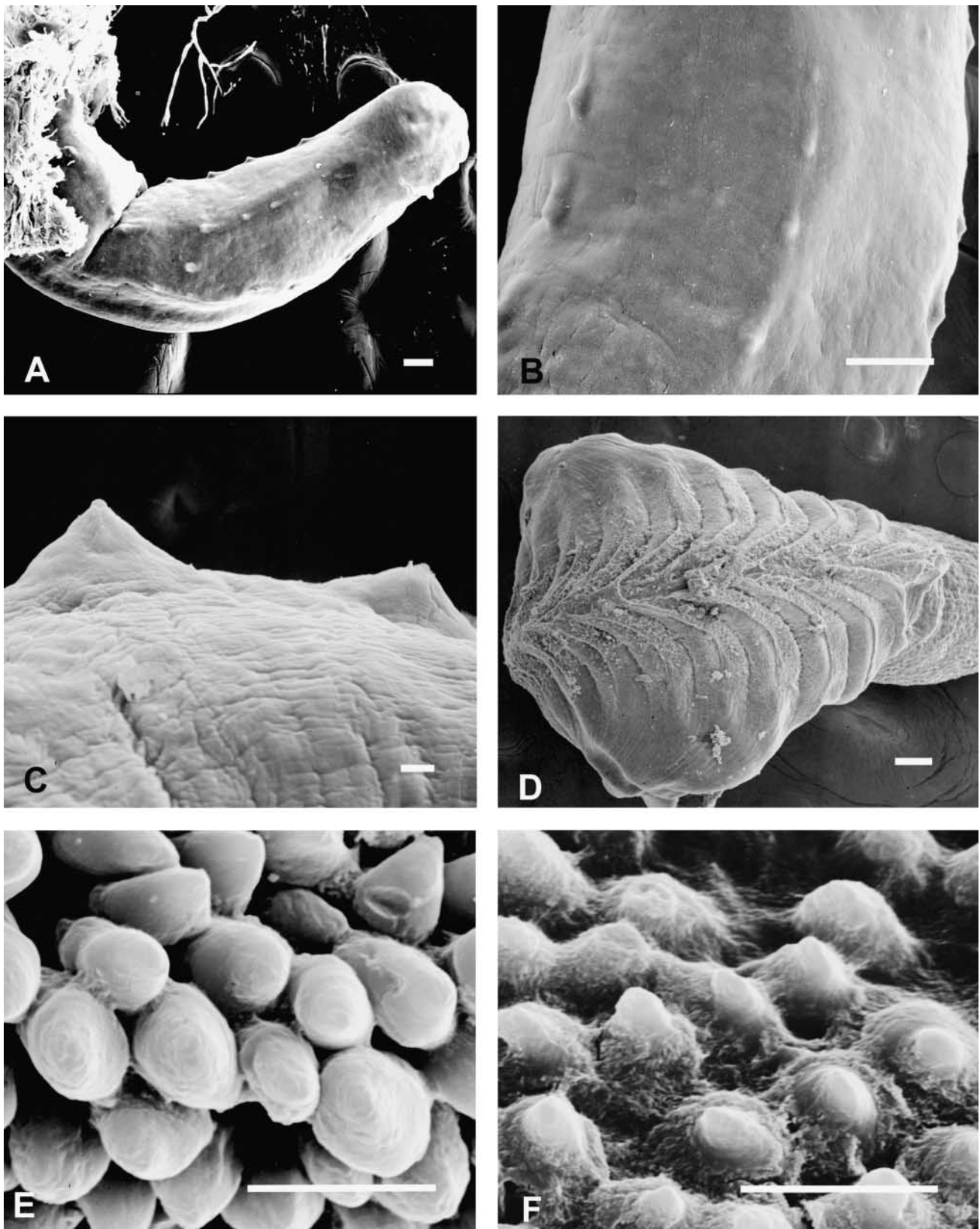


Figure 8. *Haminoea orbignyana*. **A.** Penis. **B.** Detail of the central region of the penis figured in A. **C.** Warts on side of the penis. **D.** Gizzard plate. **E.** Detail of the sculpture on the top of the ridges. **F.** Detail of the sculpture on the area between ridges. Scale bars **A, B, D** = 100 μm ; **C, E, F** = 10 μm .

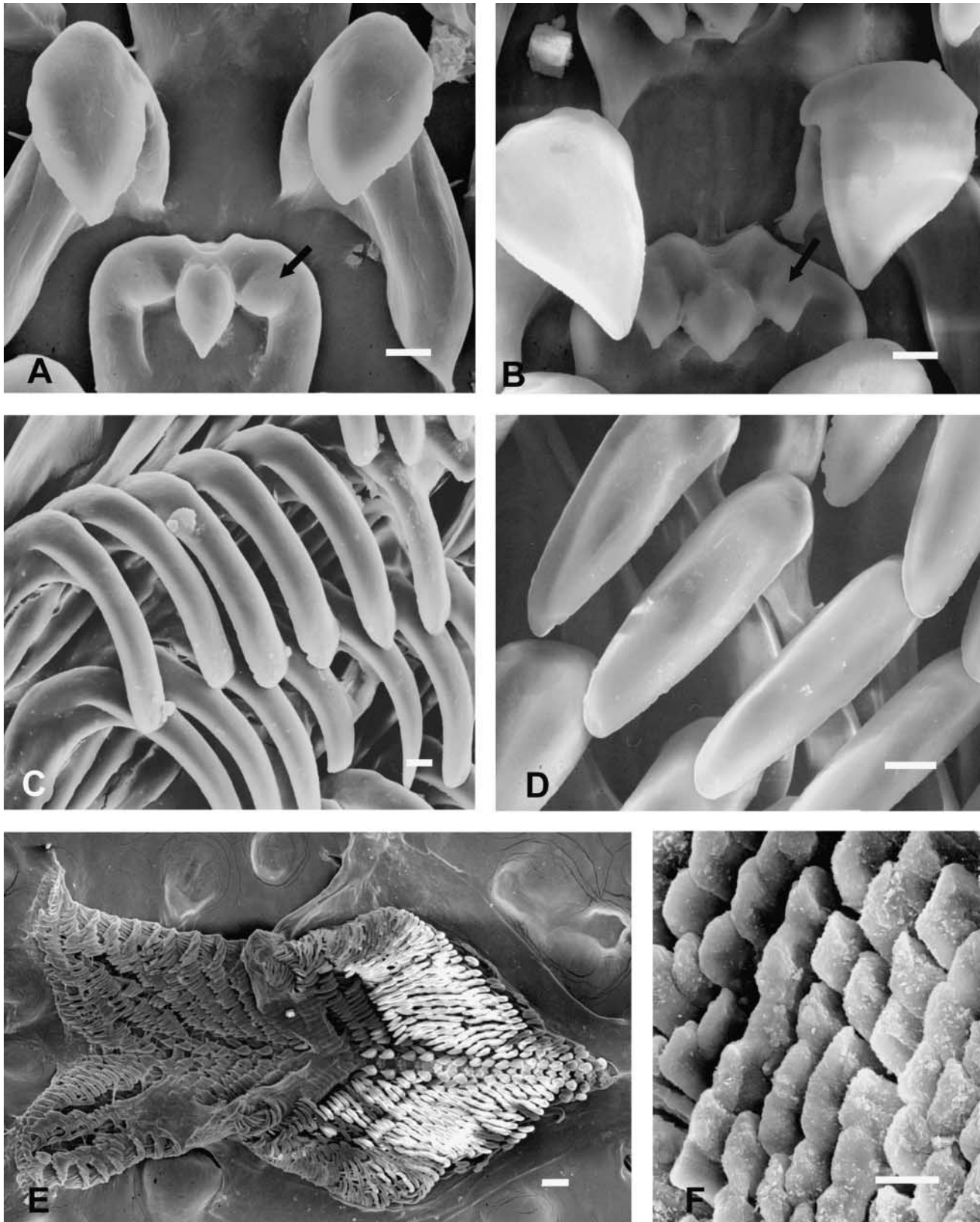


Figure 9. *Haminoea orbignyana*. **A, B.** Rachidian and inner lateral teeth. **C.** Right side outer lateral teeth. **D.** Detail of the left side outer lateral teeth. **E.** General view of the radula. **F.** Detail of jaw ornamentation. Scale bars **A–D, F** = 10 μm ; **E** = 100 μm .

Hancock's organ

Hancock's organ has two forms in the genus *Haminoea* (Marcus & Marcus, 1967). It can be either tubular (e.g. *H. zelandiae*, *H. callidegenita*, *H. cymbalum*; Gibson & Chia, 1989), or more commonly perfoliate with a variable number of lamellae (e.g. *H. hydatis*, *H. ortei*; Álvarez, García & Villani, 1993a). Both *H. navicula* and *H. orbignyana* have a perfoliate Hancock's organ, with an overlapping range of leaves, which makes this character useless for distinguishing them.

Radula

Several authors have found that the radula is not useful in the systematics of the genus *Haminoea* (Rudman, 1971; Thompson, 1981; Talavera *et al.*, 1987). According to Talavera *et al.* (1987), inter-specific variations are of the same magnitude as intra-specific ones. In addition, the numbers of tooth rows and of outer lateral teeth seem to change with age and length (Marcus, 1957; Thompson, 1988; Schaefer, 1992).

In Europe only *H. templadoi* and *H. callidegenita* are clearly distinguished by their radula. The former has a fine denticulation on the outer edge of the inner lateral and first pair of outer lateral teeth, and the latter has an inner cusp on the inner lateral teeth. The species *H. orbignyana* and *H. fusari* are easily distinguished from the remaining ones by the consistent absence of denticulation on the teeth, although differentiation between these two species is difficult (García *et al.*, 1991; Álvarez *et al.*, 1993a).

The species *H. navicula* is described in the literature as having inner lateral teeth with denticulate outer edges. Thompson (1976) claims that juveniles can also have denticulation in the first pair of outer laterals. The studied specimens revealed the existence of intra-specific variability, particularly in the inner lateral teeth, which show either denticulate or smooth outer edges. In one specimen both morphologies were even found in the same row (Fig. 4C). Regarding *H. orbignyana*, variability was found mainly in the rachidian teeth. The cusps can change between specimens of similar lengths both in size and sharpness (Fig. 9A, B). Also the number of outer lateral teeth can vary within each of these species. The occurrence of variability of the radula of *H. hydatis*, *H. ortei* and *H. navicula* has already been noted by Talavera *et al.* (1987), although no details were given by the authors.

Jaws

Although Talavera *et al.* (1987) pointed out that jaw micro-sculpture varies between species, differences are subtle and therefore hard to use (Schaefer, 1992). Among the European species only *H. ortei* and *H. exigua* are clearly distinguishable by their jaws, which are asymmetrical (Talavera *et al.*, 1987; Schaefer, 1992). Despite the micro-sculpture and shape similarities between *H. navicula* and *H. orbignyana*, ontogenetic variability was found in the former species, with juveniles showing a crescentic shape, whereas adults showed a semicircular shape (Fig. 3E, F).

Gizzard plates

Differences in the gizzard plates among European species have been described as almost imperceptible (Schaefer, 1992). Nevertheless they can in fact be conspicuous, as described by Gibson & Chia (1989) for north Pacific species. The two species studied here have shown several differences that enable their separation. *Haminoea navicula*, although the larger species, has fewer plate ridges (12–13), whereas *H. orbignyana* has 15–18 ridges. A striking difference occurs in the plate sculpture; *H. navicula* has sculpture only on the rachis and tops of the ridges

(Fig. 5C–E), whereas *H. orbignyana* has the entire plate covered with sculpture (Fig. 8D–F).

According to Marcus & Marcus (1967) and Schaefer (1992) the number of ridges on the gizzard plates increases with age. However, our observations in juveniles and adult specimens of both species do not confirm this view. The variations found between juveniles and adults are of the same magnitude as the variation found either in juveniles or adults.

Reproductive system

Based on four species of *Haminoea*, three from the Indo-Pacific (*H. cymbalum*, *H. zelandiae* and *H. crocata*) and one from the Western Atlantic (*H. solitaria*), Rudman (1971) stated that the reproductive system is very conservative and constant within the genus, with the exception of the male genitalia. At present, the male copulatory system (penis and prostate gland) is considered the most important systematic feature by which to differentiate species (Marcus & Marcus, 1967; Rudman, 1971; Talavera *et al.*, 1987; Gibson & Chia, 1989; Schaefer, 1992), which is strengthened by the results obtained in the present work.

However, there are several cases in which identification based only on the male genital system, either penis or shape of prostate gland, could be misleading. Schaefer (1992) pointed out the similarity between the reproductive systems of the European species *H. exigua* and *H. ortei*, and Thompson (1981) claimed the same for *H. antillarum* (Florida) and *H. alfredensis* (False Bay, South Africa). Despite the fact that the male genital system is regarded as conservative within a species, some variability was found in the seminal duct of *H. orbignyana*. This duct is narrow, but is not always elongated and twisted as quoted by Talavera *et al.* (1987) and Schaefer (1992). The duct can be short and untwisted, or elongated and twisted, and sometimes even doubly twisted (Fig. 10).

Egg masses

Data on egg masses are known for several species and differences have been reported. However, the extent of these differences is not known and their systematic value remains uncertain (Schaefer, 1996). Striking differences have been found between the egg masses of *H. navicula* and *H. orbignyana*. The shape and dimensions of the egg masses, capsules and eggs, varies between these species. Nevertheless, egg masses of *H. navicula* described by Schaefer (1996) in specimens collected in the Venice Lagoon, Italy, do not accurately match the features of those studied from Portugal in the present work. Schaefer (1996) described egg masses with smaller average length and fewer eggs. These differences could result either from different lengths of the studied specimens (15 mm by Schaefer and 23–24 mm in the present work), or might reflect the occurrence of inter-population variability, perhaps due to different environmental parameters. Regarding egg and capsule sizes, the values found by Schaefer (1996) are similar to ours.

Additional characters

According to Talavera *et al.* (1987) life cycles may differ between species of *Haminoea*. These authors claim to have found differences among the life cycles of *H. hydatis*, *H. navicula*, *H. ortei* and *H. orbignyana*. However, they did not describe these differences and nothing further has been published about the subject. Life histories are known for just three species, namely *H. vesicula* and *H. callidegenita* (see Gibson & Chia, 1991; Eastern Pacific) and *H. orbignyana* (see Malaquias & Sprung, 2005; Western Atlantic). Although these species exhibit different life-history patterns, it is not clear if these are species-specific features or related to geographical or ecological factors. Latitudinal

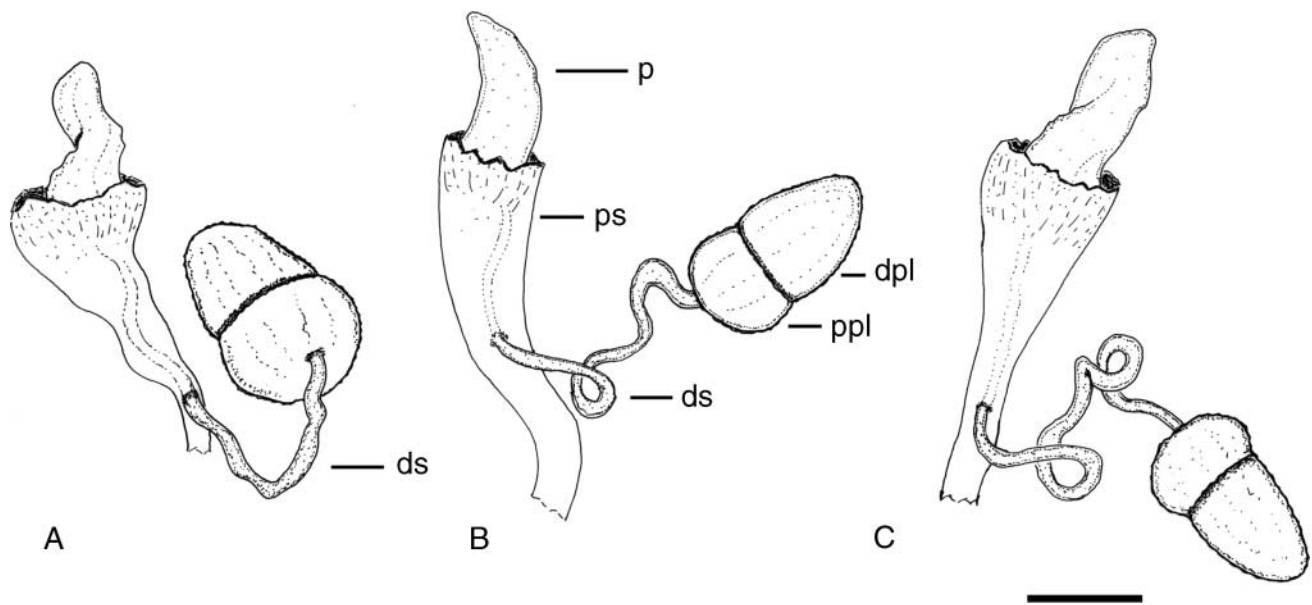


Figure 10. *Haminoea orbignyana*. Variability in the seminal duct. **A.** Untwisted. **B.** Twisted. **C.** Double twisted. Abbreviation: dpl, distal prostate lobe; ds, seminal duct; p, penis; ppl, proximal prostate lobe; ps, penial sheath. Scale bar = 1 mm.

changes are known to influence life-history patterns in some invertebrate species (Fish & Fish, 1974; Bachelet & Kassab, 1987; Plannas & Mora, 1987; Reid, 1996; Sola, 1996; Cardoso *et al.*, 2002; Ferreira *et al.*, 2004).

A recent work on secondary metabolites in the Mediterranean species of *Haminoea* (*H. callidegenita*, *H. fusari*, *H. hydatis*, *H. navicula*, *H. orbignyana* and *H. ortei*; Marín *et al.* 1999), revealed the existence of specific chemical patterns. Secondary metabolites were shown to be constant and not dependent on geography or diet, and are therefore good characters to distinguish between species.

The genus *Haminoea* in Europe

At present, eight species of *Haminoea* are recognized as valid in Europe (Table 1). Until the late 1980s only three species were known namely *Haminoea hydatis* (Linné, 1758), *H. navicula* (Da Costa, 1778) and *H. orbignyana* (Férussac, 1822). The species *H. ortei* Talavera, Murillo & Templado, 1987, *H. templadoi* García, Perez-Hurtado & García-Gómez, 1991, *H. exigua* Schaefer, 1992 and *H. fusari* Álvarez, García & Villani, 1993 have recently been added to the list, and Álvarez *et al.* (1993b) increased this inventory with an additional species, *H. callidegenita* Gibson & Chia, 1989, described from specimens collected on the Pacific American coast (Washington State), but recorded also in the Mediterranean Sea (Venice Lagoon, Italy) and in the Atlantic (Galicia and Asturias, Spain; Álvarez *et al.*, 1993b). According to these authors the occurrence of *H. callidegenita* in Europe is a result of the trade of oyster spat from the United States to Europe. More recently this species has also been found in the south of the Iberian Peninsula (Cadiz Bay, Spain) inside aquaculture tanks (J. L. Cervera, unpublished).

This work confirms for the first time the occurrence of *H. orbignyana* on the Atlantic coast of the Iberian Peninsula. We regard the records of *H. elegans* in Portugal as the result of misidentifications. The species *H. elegans* was quoted by Nobre (1938–40) on the basis of specimens housed in the collections of the MZUC. The re-examination of these specimens shows that they belong to *H. orbignyana*. In spite of several citations of *H. elegans* in the eastern Atlantic, from Gabon to Mauritania,

Canary Islands, Portugal, British Isles and Mediterranean (Leach, 1852; Hidalgo, 1917; de Carvalho, 1945; Nicklès, 1947, 1950; Marche-Marchad, 1958; Nordsieck & García-Talavera, 1979; Bernard, 1984; Sabelli, Gianuzzi-Savelli & Bedulli, 1990; Macedo, Macedo & Borges, 1999), all must be regarded as doubtful since they are shell-based identifications. Martínez & Ortea (1997), after studying living specimens of what they claimed to be *Haminoea elegans*, confirmed its occurrence in Congo and São Tomé and Príncipe, and stated that in the eastern Atlantic this species is restricted to the equatorial belt. However, the type locality of *H. elegans* is the 'Mare Britannicum et Mediterraneum' (Gray, 1825: 408). In our opinion this species is probably a junior synonym of *H. navicula*, since Gray (1825) mentioned 'dense spiraliter striata', a feature shown only by *H. navicula* among the northern European species. The specimens studied by Martínez & Ortea (1997) are likely to belong to a different species with tropical affinities.

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