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Living specimen of *Anamenia gorgonophila* (Kowalevsky, 1880).

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New data on the biodiversity of Solenogastres (Mollusca, Aplacophora) in the Mediterranean Sea: findings from the program "Our Planet Reviewed" Corsica 2019-2022

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ABSTRACT
The discovery and description of new species of Solenogastres (Mollusca, Aplacophora) is still routine, even from relatively well-known regions, but less effort is focused on the redescription of known species. Phylogenetic studies have shown that significant revisionary systematic work is needed in this group and enhanced morphological descriptions and molecular data will be valuable in these pursuits. Additionally, advancing knowledge on the real distribution and diversity of these molluscs adds to an increased understanding of marine biodiversity in general. Here, we present the study of 47 solenogasters collected during the "Our Planet Reviewed" expedition to Corsica (Mediterranean Sea). Following an integrative taxonomic approach (considering observations of live animals, habitat, morphology, and DNA barcoding), we identified ten species across seven different families: Dondersiidae Simroth, 1893; Lepidomeniidae Pruvot, 1902; Pruvotinidae Heath, 1911; Rhopalomeniidae Salvini-Plawen, 1978; Simrothiellidae Pilsbry, 1898; Proneomeniidae Simroth, 1893 and Strophomeniidae Salvini-Plawen, 1978. Notably, these findings constitute the first documented records of solenogasters off Corsica. In light of the studied material, the synonymy of three Pruvotinidae species (*Eleutheromenia sierra* (Pruvot, 1890), *E. carinata* Salvini-Plawen & Öztürk, 2006, and *Gephyroherpia impar* Zamarro, García-Álvarez & Urgorri, 2013) is proposed. This taxonomic clarification highlights the need for more study of Pruvotinidae. Further, the value of live observations (very rare in solenogasters) for better description of species and their importance for species identification is emphasized in this work. Taken together, the outcomes of our investigation demonstrate the value of species redescriptions, underscore the necessity for revisionary systematics and taxonomy of Solenogastres, and address a gap in our understanding of their diversity in the Mediterranean Sea with the first documentation of the group in Corsican waters.

KEY WORDS
Solenogastres, biodiversity, Mediterranean Sea, Corsica, redescription, new records, new synonymies.

RÉSUMÉ
Nouvelles données sur la biodiversité des Solenogastres (Mollusca, Aplacophora) de la Méditerranée : résultats du programme « La Planète Revisitée » Corse 2019-2022.
La découverte et la description de nouvelles espèces de Solenogastres (Mollusca, Aplacophora) sont encore monnaie courante, même dans des régions relativement bien connues, mais les efforts déployés pour redécrire les espèces connues sont moindres. Les études phylogénétiques ont montré qu'un important travail de révision systématique est nécessaire dans ce groupe et des descriptions morphologiques et des données moléculaires améliorées seront précieuses dans ces efforts. En outre, l'avancement des connaissances sur la distribution réelle et la diversité de ces mollusques contribue à une meilleure compréhension de la biodiversité marine en général. Nous présentons ici l'étude de 47 solénogastres collectés lors de l'expédition « La Planète Revisitée » en Corse (mer Méditerranée). En suivant une approche taxonomique intégrative (prenant en compte l'observation d'animaux vivants, l'habitat, la morphologie et le Barcode ADN), nous avons identifié dix espèces dans sept familles différentes : Dondersiidae Simroth, 1893 ; Lepidomeniidae Pruvot, 1902 ; Pruvotinidae Heath, 1911 ; Rhopalomeniidae Salvini-Plawen, 1978 ; Simrothiellidae Pilsbry, 1898 ; Proneomeniidae Simroth, 1893 et Strophomeniidae Salvini-Plawen, 1978. Ces résultats constituent notamment les premiers signalements documentés de solénogastres au large de la Corse. À la lumière du matériel étudié, la synonymie de trois espèces de Pruvotinidae (*Eleutheromenia sierra* (Pruvot, 1890), *E. carinata* Salvini-Plawen & Öztürk, 2006, et *Gephyroherpia impar* Zamarro, García-Álvarez & Urgorri, 2013) est proposée. Cette clarification taxonomique met en évidence la nécessité d'étudier davantage les Pruvotinidae. En outre, ce travail souligne la valeur des observations de spécimens vivants (très rares chez les solénogastres) pour une meilleure description des espèces et leur importance pour l'identification des espèces. Dans l'ensemble, les résultats de nos recherches démontrent la valeur des redescriptions d'espèces, soulignent la nécessité de réviser la systématique et la taxonomie des solénogastres, et comblent une lacune dans notre compréhension de leur diversité en mer Méditerranée avec la première mention du groupe dans les eaux corses.

MOTS CLÉS
Solenogastres,
biodiversité,
Corse,
mer Méditerranée,
redescription,
signalisations nouvelles,
synonymies nouvelles.

INTRODUCTION

Much of the recent research on Solenogastres (Mollusca, Aplacophora von Ihering, 1876) diversity and taxonomy has been focused on remote, deep-sea communities (e.g., Gil-Mansilla *et al.* 2012; Bergmeier *et al.* 2017, 2019, 2021; Ostermair *et al.* 2018; Cobo & Kocot 2021). Less effort is dedicated to the study of solenogasters from relatively well-known areas or to more detailed studies of already described species. However, recollection of described species can be valuable for understanding species distributions and ecology, and redescriptions can provide new anatomical information (e.g., García-Álvarez *et al.* 2009; Scheltema *et al.* 2012; Pedrouzo *et al.* 2019) and fresh material suitable for molecular work, which are important to ongoing revisionary systematics work on this group. Notably, around 80% of the 311 described solenogaster species were named based on the study of one or very few specimens and are only known from the type locality. Therefore, new collection records and redescriptions are critical for a better understanding of this interesting but neglected group of molluscs.

To date, 31 species of Solenogastres have been formally described from the Mediterranean Sea; 18 have only been recorded from the type locality, while 13 have a broader distribution with ten of them also collected from localities in the European North Atlantic (Table 1). The Mediterranean Sea is relatively easily accessible and was extensively studied in the early years of aplacology (e.g., Kowalevsky 1881; Marion & Kowalevsky 1886; Pruvot 1890; Simroth 1893), but few recent works have been focused on the solenogaster fauna of this region. The first "modern" compilation of the aplacophoran molluscs of the Mediterranean Sea was published in 1986 by Salvini-Plawen, followed by an updated one by the same author four years later (Salvini-Plawen 1990). Five additional species have been described from the region since then (see Salvini-Plawen 2003; Salvini-Plawen & Öztürk 2006; Pedrouzo *et al.* 2014). In addition, a work by Scheltema *et al.* (2012) contains valuable redescriptions, but it does not include newly sampled material. Other recent works dealing with Mediterranean Solenogastres include collection reports of known species or checklists, some of them in more general works comprising several taxa or broader regions (e.g., Salvini-Plawen 2008; Mifsud *et al.* 2008; García-Álvarez *et al.* 2014; Pedrouzo *et al.* 2014; Gofas *et al.* 2017; Curini-Galletti *et al.* 2020). Besides, the most recent study focused on symbiotic bacteria in the cuticle of an unidentified solenogaster (Vortsepneva *et al.* 2021).

The program "Our Planet Reviewed" led by the Muséum national d'Histoire naturelle (Paris, France) organized, in partnership with the "Collectivité de Corse" and the "Office français de la Biodiversité" (OFB), three expeditions (CORSICABENTHOS 1: 2019; CORSICABENTHOS 2: 2020 and CORSICABENTHOS 3: 2021) off Corsica (Mediterranean Sea) (Le Gall *et al.* 2014). A total of 47 specimens of

TABLE 1. — Mediterranean species of Solenogastres. Species found off Corsica are indicated in **bold**. Species with a Mediterranean-Atlantic distribution are underlined. Symbol: *, type material missing.

Species	Type locality	Other localities	Depth range (m)	References
Dondersiidae				
Dondersia festiva	Gulf of Naples (Italy); 60 m	Mediterranean Sea (Western Italy, Corsica)	60-100	Hubrecht 1888; Simroth 1893; Nierstrasz & Stork (1940); Heath 1911; Salvini-Plawen 1978; García-Álvarez & Salvini-Plawen 2007; Scheltema *et al.* 2012
Nematomenia flavens	Banyuls-sur Mer (France); 45-90 m*	NW Atlantic (Shetland Islands)	45-167	Pruvot 1890; Simroth 1893; García-Álvarez & Salvini-Plawen 2007; García-Álvarez *et al.* 2014
Nematomenia banyulensis	Roussillon, Côte Vermeille (France); 45 m *	Mediterranean Sea (Dalmatia; Adriatic Sea, Naples, Corsica). NW Atlantic (Norway fjords, English Channel, Shetland Islands, Roscoff, Giiteborg)	31-300	Pruvot 1890; Thiele 1894, 1913; Seaward 1982, 1990; Salvini-Plawen 1986, 1997 Handl & Salvini-Plawen 2001; Salvini-Plawen 2003; García-Álvarez & Salvini-Plawen 2007; García-Álvarez *et al.* 2014
Nematomenia corallophila	La Calle (Algeria): 73 m*	–	75 -183	Kowalevsky 1881; García-Álvarez & Salvini-Plawen 2007
Ichthyomenia ichthyodes	Roussillon (France); 80 m *	–	80	Pruvot 1890; García-Álvarez & Salvini-Plawen 2007
Stylomenia salvatori	Banyuls-sur-Mer (France); Littoral *	–	Littoral	Pruvot 1899; García-Álvarez & Salvini-Plawen 2007
Micromenia subrubra	Malta; 140 m	–	140	Salvini-Plawen 2003 García-Álvarez & Salvini-Plawen 2007
Lepidomeniidae	–	–	–	–
Lepidomenia hystrix	Marseille (France); 30 m *	–	30	Marion & Kowalevsky 1886; García-Álvarez & Salvini-Plawen 2007
Lepidomenia swedmarki	Marseille (France); Interstitial *	–	Littoral	Salvini-Plawen 1986; García-Álvarez & Salvini-Plawen 2007
Tegulaherpia stimulosa	Dalmatia (Croatia); 75-80 m	–	75-80	Salvini-Plawen 1983; García-Álvarez & Salvini-Plawen 2007
Tegulaherpia myodoryata	Banyuls-sur-Mer (France); 75 m	Mediterranean Sea (Livorno and Malta) NW Atlantic (Norway, Celtic Sea Cantabric Sea)	75-1150	Salvini-Plawen 1988; Salvini-Plawen 1997; Handl & Salvini-Plawen 2001; Salvini-Plawen 2003; García-Álvarez & Salvini-Plawen 2007; García-Álvarez *et al.* 2014
Gymnomeniidae				
Wirenia argentea	Sunde, Hardangerfjord (Norway); 150 m	Mediterranean Sea (Adriatic and Aegean seas. NW Atlantic (NW Spain)	95-700	Odhner 1920; García-Álvarez & Salvini-Plawen 2007
Macellomeniidae				
Macellomenia palifera	Port Vendres (France); 80 m *	–	80	Pruvot 1890; García-Álvarez & Salvini-Plawen 2007
Macellomenia adenota	Strait of Gibraltar (Spain); 25-40 m	–	25-40	Salvini-Plawen 2008
Neomeniidae				
Neomenia carinata	Bohuslän (Sweden); 90 m *	Mediterranean Sea. NW Atlantic (Roscoff; Norway, British Islands, Iceland)	10-565	Tullberg 1875; García-Álvarez & Salvini-Plawen 2007
Pruvotiniidae				
Pararrhopalia pruvoti	Banyuls-sur Mer (France); 80 m *	NW Atlantic (NW Iberian Peninsula)	80 -600	Simroth 1893; García-Álvarez & Salvini-Plawen 2007
Pruvotina impexa	Banyuls-sur Mer (France); 60-80 m *	–	60-80	Pruvot 1890; García-Álvarez & Salvini-Plawen 2007
Eleutheromenia sierra	Portaló Island (Spain), 75 m *	NW Atlantic (Roscoff; Irish Sea; Norway)	40-128	Pruvot 1890; Salvini-Plawen & Öztürk 2006; Salvini-Plawen 2003; García-Álvarez & Salvini-Plawen 2007; García-Álvarez *et al.* 2014
"Eleutheromenia carinata"	Bay of Izmir (Turkey); 75 m	–	?	Salvini-Plawen & Öztürk 2006; García-Álvarez & Salvini-Plawen 2007
Hypomenia Nierstrasz	Gulf of Naples (Italy) Depth unknown	Mediterranean Sea (Monaco)	150-200	Van Lummel 1930; García-Álvarez & Salvini-Plawen 2007
Uncimenia neapolitana	Gulf of Naples (Italy); 45-70 m	–	70	Nierstrasz 1903; García-Álvarez & Salvini-Plawen 2007

Table 1. — Continuation.

Species	Type locality	Other localities	Depth range (m)	References
Unciherpia hirsuta	Banco de Galicia (NW Iberian Peninsula); 760 m	Mediterranean Sea (Alboran Sea)	349-760	García-Álvarez *et al.* 2001; García-Álvarez & Salvini-Plawen 2007
Rhopalomeniidae				
Rhopalomenia aglaopheniae	Banyuls-sur-Mer (France); 60-80 m *	Mediterranean Sea (S Peloponnese). NW Atlantic (Schottland)	50-137	Marion & Kowalevsky 1886; García-Álvarez & Salvini-Plawen 2007
Pruvotia sopita	Banyuls-sur-Mer (France); 45-70 m *	–	45-80	Pruvot 1891; García-Álvarez & Salvini-Plawen 2007
Urgorria monoplicata	Costa Brava (Spain); 35 m	–	35	Salvini-Plawen 2003; García-Álvarez & Salvini-Plawen 2007
Amphimeniidae				
Amphimenia neapolitana	Gulf of Naples (Italy); 30-35 m	–	30-35	Thiele 1889; García-Álvarez & Salvini-Plawen 2007
Paragymnomenia richardi	Cap Martin (Monaco); 46-60 m	–	46-60	Leloup 1947; García-Álvarez & Salvini-Plawen 2007
Simrothiellidae				
Simrothiella margaritacea	Boknfjord (Norway); 75-115 m	NW Atlantic (NW Iberian Peninsula). Corsica, first record in the Mediterranean Sea	75-800	Koren & Danielssen 1877; Nierstrasz 1908; Odhner 1920; Scheltema & Schander 2000; Salvini-Plawen 2004; García-Álvarez & Salvini-Plawen 2007; García-Álvarez *et al.* 2014; Pedrouzo *et al.* 2014
Kruppomenia minima	Gulf of Naples (Italy); 950-1100 m	–	950-1100	Nierstrasz 1903; García-Álvarez & Salvini-Plawen 2007
Strophomeniidae				
Strophomenia lacazei	La Calle (Algeria); Litoral *	–	?	Pruvot 1899; García-Álvarez & Salvini-Plawen 2007
Anamenia gorgonophila	East Algeria; depth ¿? *	Neotype: NW Atlantic (Gorringe Bank) Mediterranean Sea (multiple locations) NW Atlantic (Azores, NW Iberian Peninsula)	65-845	Kowalevski 1880; Pruvot 1891; Nierstrasz & Stork 1940; Leloup 1947; Salvini-Plawen 1972; García-Álvarez *et al.* 1998; García-Álvarez & Salvini-Plawen 2007; Mifsud *et al.* 2008; Pedrouzo *et al.* 2014; García-Álvarez *et al.* 2014
Proneomeniidae				
Proneomenia desiderata	Marseille (France); 20-30 m *	–	20 -30	Kowalevsky & Marion 1887; García-Álvarez & Salvini-Plawen 2007
Dorymenia vagans	Marseille (France); 20 m	Mediterranean Sea (Naples, Livorno)	20-60	Kowalevsky & Marion 1887; Nierstrasz & Stork 1940; García-Álvarez & Salvini-Plawen 2007; García-Álvarez *et al.* 2014

solenogasters were collected during these events. The general small size (≤ 5 mm) and scarce knowledge about their habitat, compromise the finding of solenogaster during sampling or sorting material. Therefore, their presence in scientific collections is rare and valuable. Here we present the study of these 47 specimens representing ten different species based on external aspect, sclerites, DNA barcodes, and the study of internal anatomy. The main goal of the present work was to improve understanding of the diversity of solenogasters off Corsica and in the Mediterranean Sea. By combining updated morphological information and DNA barcodes for all species investigated here, the study of these samples contributes not only to better defining the biodiversity of the region but also to the general knowledge of this group of molluscs. In addition, the need for taxonomical revision of some groups of solenogasters is highlighted here.

The traditional taxonomy of Solenogastres (García-Álvarez & Salvini-Plawen 2007) requires the study of certain internal organs and of the calcareous spines and scales that cover their body (sclerites) (García-Álvarez & Salvini-Plawen 2007; Todt 2013). The key diagnostic internal characters are the radula (García-Álvarez & Salvini-Plawen 2007: fig. 12), the digestive glands associated with the foregut (or pharynx) (García-Álvarez & Salvini-Plawen 2007: fig. 10; reviewed in Handl & Todt 2005), and several characters of the reproductive system as for example, the presence/absence of copulatory stylets (García-Álvarez & Salvini-Plawen 2007; Scheltema *et al.* 2012). Because of the small size of most Solenogastres, histology is generally necessary to characterize the internal organs. This is a time-consuming and challenging technique that involves the risk of losing samples or obtaining sections with inadequate quality. Moreover, the whole specimen is

often used for this purpose and the histological sections are usually the only lasting type material. A recent publication using micro-computed tomography confirmed that this non-destructive method is promising for solenogaster studies (Martínez-Sanjuán *et al.* 2022). Still, this methodology is costly, and advances are needed to improve the resolution to characterize some important organs. Although there is a general uniformity in external appearance among most members of major solenogaster groups, exceptionally, certain species have bright colorations (e.g., Hubrecht 1888; Scheltema & Jebb 1994; Salvini-Plawen 1997) or cuticular keels that are useful for their identification. The sclerites allow to classify solenogasters within one of the traditional orders, and, in rare cases, sclerites alone are useful to classify solenogasters into a family (e.g., Pruvotinidae Heath, 1911 with hollow, hook-shaped sclerites and Macellomeniidae Salvini-Plawen, 1978 with nail-shaped sclerites) or genus (e.g., *Wirenia* Odhner, 1920; leaf-shaped scales with a central keel as an exclusive character). The combined study of sclerites, external appearance, and DNA barcodes has been a common practice in solenogaster taxonomy since the publication of Bergmeier *et al.* (2017). This workflow has been demonstrated to speed the identification process, with most animals classified to the family level, and to provide an estimation of number of species (Bergmeier *et al.* 2017, 2019). However, greatly expanding the available DNA barcode library will be necessary to make meaningful identifications based on sequence data possible, meaning histology and taxonomic expertise are still mandatory for confident identifications and the description of new species.

MATERIAL AND METHODS

Material examined

The 47 specimens studied here belong to the malacological collection of the Muséum national d'Histoire naturelle (Paris) and were collected during the three expeditions of the program "Our Planet Reviewed" Corsica (2019-2022) (France) (Table 2; Fig. 1). The collection methods included the direct visual recollection of specimens by divers, the use of vacuum device by divers, and the use of dredges for deeper localities from boat. When possible, specimens were photographed alive in the field before preservation (95% ethanol). Preserved specimens were later imaged in the laboratory using an Olympus SZX16 stereomicroscope with an Olympus SC50 digital camera.

Initial classification into morphospecies, SEM, DNA extractions and sclerites

Specimens were classified into morphospecies based on the study of habitus (coloration, sclerite appearance, presence or absence of body protrusions, etc.) and mantle sclerites. The length of each specimen in lateral view was measured along the axial midline; the dorso-ventral height was also measured in lateral view. Sclerites of all the animals were dislodged with a thin needle onto a slide with distilled water and observed under a Nikon Eclipse E200 light microscope.

SEM, DNA barcoding and sclerites for light microscopy

At least one specimen of each morphospecies was selected for further studies. These specimens were cut into three parts. The medial body region was air-dried and imaged (uncoated) using a Phenom Pro scanning electron microscope (SEM) under low vacuum with a low accelerating voltage (5-10 kV) to study the sclerites. Subsequently, dried tissue samples were put directly into Omega Bio-tek E.Z.N.A. MicroElute kit tissue lysis (TL) buffer and frozen at -80°C for later DNA extraction. The anterior and posterior regions were retained in 95% ethanol or used for histology (Table 3).

DNA was extracted from 17 specimens (at least one specimen of each morphospecies) using the Omega Bio-tek E.Z.N.A. MicroElute kit following the manufacturer's protocol. PCR amplification of a fragment of the mitochondrial 16S rDNA (SSU) and cytochrome c oxidase subunit I (COI) were performed using Hot Start Taq 2X Master Mix (VWR) following the manufacturer's instructions. For 16S, the solenogaster-specific primers 16Soleno-r and -f (Bergmeier *et al.* 2017) were used with the following cycling parameters: 2 min at 95°C, (5 s at 98°C, 5 s at 50°C, 20 s at 72°C) × 40 cycles, 1 min 72°C and finally cooling at 10°C. For COI, the primers LCO_Apl (TTTCTACTAAYCATAARGATATTGG) and HCO 2198 (Folmer *et al.* 1994) were used with the following cycling parameters: 2 min at 95°C, (20 s at 95°C, 15 s at 52°C, 30 s at 72°C) × 40 cycles, 7 min 72°C and finally cooling at 10°C. PCR success was determined with gel electrophoresis using 1X SB buffer at 120 volts for 20 minutes. Products were directly purified using the Omega Bio-tek EZNA Cycle Pure Quick kit and eluted in 25 µL of elution buffer. The concentration of the purified PCR products was measured using a Nanodrop Lite (Thermo). Purified PCR products were sent to GeneWiz for bidirectional Sanger sequencing. Sequencing was performed using the premix option with 10 µL of PCR product and 5 µL of 5 mM primer for each reaction. Successful DNA sequences were assembled into contigs, inspected, and manually edited for quality if needed using Sequencher version 5.4.6. Finally, a BLAST search against the NCBI Nucleotide database was performed to check for any contaminated sequences. All newly generated sequences have been made publicly available via NCBI (https://www.ncbi.nlm.nih.gov/) (Table 4).Intact sclerites from the mid body region were isolated after lysis and preserved in buffered ethanol for later slide mounting with DEPEX mounting medium (Electron Microscopy Science) for light microscopy analysis. Preparations were observed under a Nikon Eclipse 50i light microscope.

Phylogenetic analysis and species delimitation

To confirm our morphology-based species concepts, a phylogenetic analysis and a species delimitation analysis were performed based COI sequences (Fig. 2). In addition to the sequences generated in this study from the Corsica specimens (Table 3), available sequences for species from Norwegian waters were obtained from BOLD and included in the analysis, as many solenogaster species found in the Mediterranean have distributions that extend into Norwegian waters (Table 1). Additional sequences from the NCBI Nucleotide database

TABLE 2. — Collection data sorted by expedition and station code. Letter codes preceding the station number correspond with the sampling method: **CD**, dredge used from boat; **CR**, visual recollection of specimens by divers; **CS**, vacuum device used by divers to collect sediment.

Expedition/MUSEUM #	ID	Station Code	Depth (m)	Latitude	Longitude
CORSICABENTHOS1					
MNHN-IM-2019-16174	*Dondersia festiva* Hubrecht, 1888	CD06	60	42.8956	9.533
MNHN-IM-2019-16181	*Dondersia festiva*	CD11	90	42.8505	9.517
MNHN-IM-2019-16184	*Dondersia festiva*	CD18	60	42.7408	9.479
MNHN-IM-2019-13920	*Dondersia festiva*	CD35	100	42.811	9.5305
MNHN-IM-2019-16169	*Dondersia festiva*	CD35	100	42.811	9.5305
MNHN-IM-2019-16172	*Dondersia festiva*	CD35	100	42.811	9.5305
MNHN-IM-2019-16178	*Nematomenia banyulensis* (Pruvot, 1890)	CD41	95	42.997	9.3106
MNHN-IM-2019-16185	*Dondersia festiva*	CD41	95	42.997	9.3106
MNHN-IM-2019-16177	*Nematomenia banyulensis*	CD50	60	42.7195	9.4658
MNHN-IM-2019-16180	*Nematomenia banyulensis*	CD50	60	42.7195	9.4658
MNHN-IM-2019-16179	*Pruvotina impexa* (Pruvot, 1890)	CD50	60	42.7195	9.4658
MNHN-IM-2019-16170	*Dondersia festiva*	CS06	32	42.7278	9.46545
MNHN-IM-2019-16183	*Dondersia festiva*	CS06	32	42.7278	9.46545
MNHN-IM-2019-16173	*Dondersia festiva*	CS09	29	42.7360	9.46668
MNHN-IM-2019-16176	*Tegulaherpia* cf. *myodoryata*	CS11	41	42.7858	9.32984
MNHN-IM-2019-16175	*Dondersia festiva*	CS19	15	42.8308	9.30673
MNHN-IM-2019-13916	*Dondersia festiva*	CS24	33	42.7278	9.4657
MNHN-IM-2019-13917	*Dondersia festiva*	CS24	33	42.7278	9.4657
MNHN-IM-2019-13918	*Dondersia festiva*	CS24	33	42.7278	9.4657
MNHN-IM-2019-13919	*Dondersia festiva*	CS24	33	42.7278	9.4657
MNHN-IM-2019-16171	*Dondersia festiva*	CS24	33	42.7278	9.4657
MNHN-IM-2019-16182	*Dondersia festiva*	CS24	33	42.7278	9.4657
MNHN-IM-2019-16186	*Dondersia festiva*	CS24	33	42.7278	9.4657
CORSICABENTHOS2					
MNHN-IM-2019-1744	*Pruvotia* cf. *sopita*	CC02	80	41.4142	9.0226
MNHN-IM-2019-1746	*Pruvotina impexa*	CD87	73	41.3495	9.1763
MNHN-IM-2019-1748	*Pruvotina impexa*	CD91	60	41.3925	9.0690
MNHN-IM-2019-1747	*Nematomenia banyulensis*	CD102	68	41.329	9.2924
MNHN-IM-2019-1749	*Eleutheromenia sierra* (Pruvot, 1890)	CD117	40	41.36161	9.2065
MNHN-IM-2019-1745	*Pruvotina impexa*	CD118	60	41.38465	9.2796
CORSICABENTHOS3					
MNHN-IM-2019-18286	*Simrothiella margaritacea* (Koren & Danielssen, 1877)	CD159	122	42.5975	8.7079
MNHN-IM-2019-18285	*Pruvotina impexa*	CP07	122	42.40118	8.5559
MNHN-IM-2019-18281	*Pruvotina impexa*	CP07	122	42.40118	8.5559
MNHN-IM-2019-18279	*Unciherpia hirsuta* García-Alvarez, Urgorri & Salvini-Plawen, 2001	CP07	122	42.40118	8.5559
MNHN-IM-2019-18282	*Unciherpia hirsuta*	CP07	122	42.40118	8.5559
MNHN-IM-2019-18283	*Unciherpia hirsuta*	CP07	122	42.40118	8.5559
MNHN-IM-2019-18284	*Unciherpia hirsuta*	CP07	122	42.40118	8.5559
MNHN-IM-2019-18280	*Simrothiella margaritacea* (Koren & Danielssen, 1877)	CP07	122	42.40118	8.5559
MNHN-IM-2019-18287	*Simrothiella margaritacea*	CP07	122	42.40118	8.5559
MNHN-IM-2019-18270	*Anamenia gorgonophila* (Kowalevsky, 1880)	CR150	50	42.23641	8.5316
MNHN-IM-2019-18271	*Dorymenia vagans* (Kowalevsky & Marion, 1887)	CS83	50	42.35306	8.53551
MNHN-IM-2019-18272	*Dorymenia vagans*	CS83	50	42.35306	8.53551
MNHN-IM-2019-18274	*Dorymenia vagans*	CS83	50	42.35306	8.53551
MNHN-IM-2019-18275	*Dorymenia vagans*	CS83	50	42.35306	8.53551
MNHN-IM-2019-18273	*Pruvotina impexa*	CS83	50	42.35306	8.53551
MNHN-IM-2019-18276	*Dorymenia vagans*	CS83	50	42.35306	8.53551
MNHN-IM-2019-18277	*Dondersia festiva*	CS87	56	42.23641	8.53168
MNHN-IM-2019-18278	*Dorymenia vagans*	CS87	56	42.23641	8.53168

were also included. These sequences were selected to broadly span the diversity of Solenogastres based on the results of Kocot *et al.* (2019) with dense sampling of close relatives of the Corsica species in order to improve the sensitivity of species delimitation. The caudofoveates *Chaetoderma nitidulum* Lovén, 1844 and *Scutopus ventrolineatus* Salvini-Plawen, 1968 were used as the outgroup. BOLD accession numbers (ALPNB- numbers) and NCBI accession numbers (all others) for all sequences are indicated in Figure 2.

Sequences were aligned using the MAFFT web server (https://www.ebi.ac.uk/Tools/msa/mafft/; accessed on 20 June 2023; Katoh & Standley 2013) and the resulting alignment was manually refined to ensure all sequences were in the correct open reading frame. A phylogenetic analysis was conducted on the resulting alignment using maximum likelihood in IQ-TREE 2 using the best-fitting model of nucleotide substitution and 1000 rapid bootstraps (Minh *et al.* 2020). Species delimitation was performed using Assemble Species by Automatic Partitioning (ASAP) with simple distance and default parameters on the ASAP web server (https://bioinfo.mnhn.fr/abi/public/asap/asapweb.html; accessed on 26 June 2023; Puillandre *et al.* 2021).

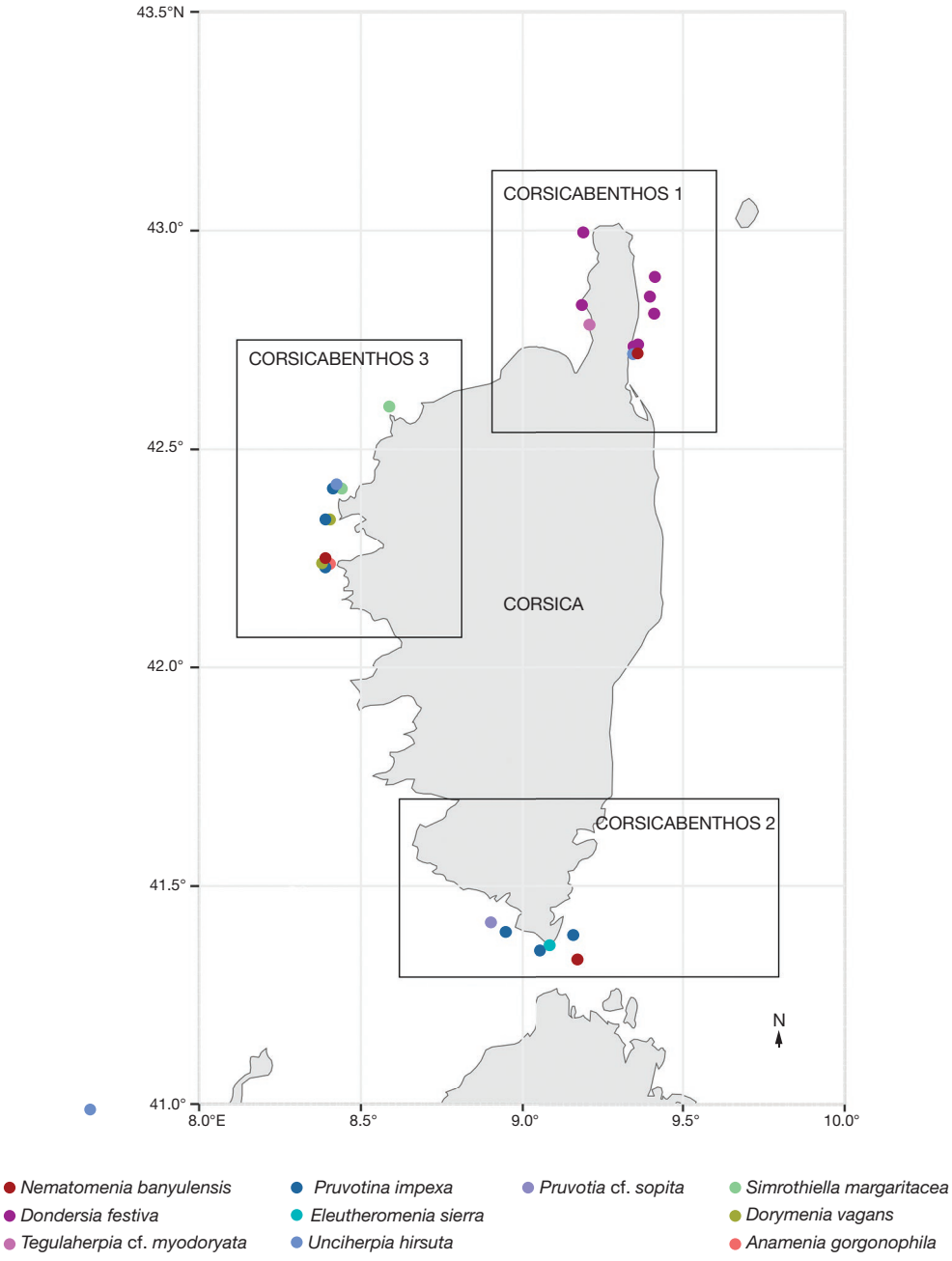

Fig. 1. — Map of Corsica indicating the areas sampled during CORSICABENTHOS 1, 2 and 3 and the Solenogastres species collected in each area.

Histology and internal reconstructions

To analyze internal anatomy, the anterior and posterior body regions of 12 specimens (Table 3) representing seven species were decalcified with EDTA solution (2 ml of distiller water; 1 ml of 10% formalin; and 2 ml of 0.5M EDTA) overnight, dehydrated with a graded ethanol series (20 min for each soak: 70%-90%-90%-95%-95%-100%-100% ethanol) followed by a xylene soak (10-15 min; until the tissue was translucent), embedded in paraffin (Leica Paraplast Regular) following three soaks in fresh paraffin for 1 h each, cut in 5 µm serial transverse sections using a Leica RM2235 rotary microtome, and stained with Mallory's trichrome stain. The staining protocol followed Gil-Mansilla *et al.* (2008) except the xylene step was reduced to one soak, the embedding in paraffin step to two hours instead of three, and the second stain was performed for 20 minutes. Histological sections were imaged using an Olympus BX53 compound microscope with an SC50 digital camera. Figures containing images of histological sections were prepared in Corel Draw such that all histological section images, aside from enlargements (indicated by a dotted line), are presented at the same scale.

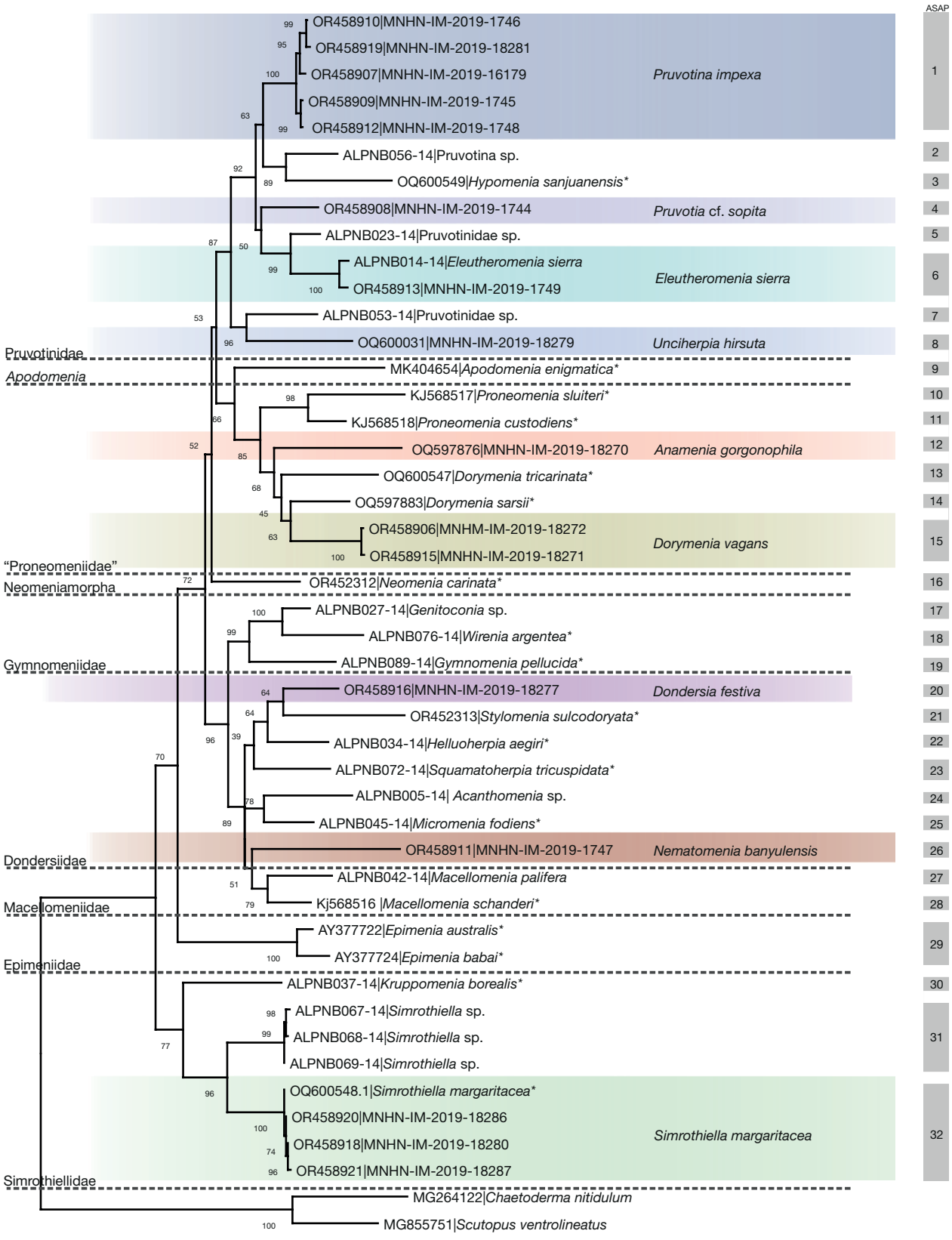

FIG. 2. — Maximum likelihood phylogenetic reconstruction based on COI. MNHN CORSICABENTHOS specimens are shaded with colors corresponding to those used in Fig 1. BOLD (ALPNB #s) and NCBI accession numbers precede species names for publicly available sequences and both NCBI accession numbers and museum catalog numbers precede the species names for the Corsica specimens. Symbols: * , the taxa considered as reference sequences based on Kocot *et al.* (2019); **gray blocks**, species delimitation results according to Assemble Species by Automatic Partitioning (ASAP, Puillandre *et al.* 2021).

TABLE 3. — Studied specimens classified by family and genera. (x) indicates the data that was obtained for the present study.

Taxon	MUSEUM #	Expedition	Station	Picture code	SEM	Histology	NCBI Accession # 16S	COI
Dondersiidae								
Dondersia festiva	MNHN-IM-2019-16174	CORSICABENTHOS1	CD06	PL-CD-06-174	–	–	–	–
	MNHN-IM-2019-16181	CORSICABENTHOS1	CD11	–	–	–	–	–
	MNHN-IM-2019-16184	CORSICABENTHOS1	CD18	–	–	–	–	–
	MNHN-IM-2019-16169	CORSICABENTHOS1	CD35	GD-CD35-642	×	×	–	–
	MNHN-IM-2019-16172	CORSICABENTHOS1	CD35	PM-CS09-222	–	–	–	–
	MNHN-IM-2019-13920	CORSICABENTHOS1	CD35	PM-CS09-222	–	–	–	–
	MNHN-IM-2019-16185	CORSICABENTHOS1	CD41	–	–	–	–	–
	MNHN-IM-2019-16170	CORSICABENTHOS1	CS06	PL-CS06-96	×	–	–	–
	MNHN-IM-2019-16183	CORSICABENTHOS1	CS06	–	–	–	–	–
	MNHN-IM-2019-16173	CORSICABENTHOS1	CS09	GD-CD35-643	–	–	–	–
	MNHN-IM-2019-16175	CORSICABENTHOS1	CS19	GD-CS19-652	–	–	–	–
	MNHN-IM-2019-13916	CORSICABENTHOS1	CS24	–	–	–	–	–
	MNHN-IM-2019-13917	CORSICABENTHOS1	CS24	–	–	–	–	–
	MNHN-IM-2019-13918	CORSICABENTHOS1	CS24	–	–	–	–	–
	MNHN-IM-2019-13919	CORSICABENTHOS1	CS24	–	–	–	–	–
	MNHN-IM-2019-16171	CORSICABENTHOS1	CS24	GD-CS241-627	–	–	–	–
	MNHN-IM-2019-16182	CORSICABENTHOS1	CS24	–	–	–	–	–
	MNHN-IM-2019-16186	CORSICABENTHOS1	CS24	–	–	–	–	–
	MNHN-IM-2019-18277	CORSICABENTHOS3	CS87	GD-CS87-686	×	×	OR456222	OR458916
Nematomenia banyulensis	MNHN-IM-2019-16178	CORSICABENTHOS1	CD41	GD-CD41-716	–	–	–	–
	MNHN-IM-2019-16177	CORSICABENTHOS1	CD50	PM-CD50-830	–	–	–	–
	MNHN-IM-2019-16180	CORSICABENTHOS1	CD50	GD-CD50-831	–	–	–	–
	MNHN-IM-2019-1747	CORSICABENTHOS2	CD102	GD-CD102-676	×	×	OR456215	OR458911
Lepidomeniidae								
Tegulaherpia cf. *myodoryata*	MNHN-IM-2019-16176	CORSICABENTHOS1	CS11	GD-CS11-320	×	–	OR456213	–
Pruvotinidae								
Pruvotina impexa	MNHN-IM-2019-16179	CORSICABENTHOS1	CD50	PM-CD50-827	×	×	–	OR458907
	MNHN-IM-2019-1746	CORSICABENTHOS2	CD87	GD-CD87-395	×	×	–	OR458910
	MNHN-IM-2019-1748	CORSICABENTHOS2	CD91	GD-CD91-514	×	×	–	OR458910
	MNHN-IM-2019-1745	CORSICABENTHOS2	CD118	GD-CD118-855	×	–	–	OR458909
	MNHN-IM-2019-18281	CORSICABENTHOS3	CP07	GD-CP07-734	×	×	–	OR458919
	MNHN-IM-2019-18285	CORSICABENTHOS3	CP07	–	–	–	–	–
	MNHN-IM-2019-18273	CORSICABENTHOS3	CS83	GD-CS83-592	–	–	–	–
Eleutheromenia sierra	MNHN-IM-2019-1749	CORSICABENTHOS2	CD117	GD-CD117-817	×	×	OR456216	OR458913
Unciherpia hirsuta	MNHN-IM-2019-18279	CORSICABENTHOS3	CP07	GD-CP07-726	×	×	OQ600031	OQ597875
	MNHN-IM-2019-18282	CORSICABENTHOS3	CP07	–	–	–	–	–
	MNHN-IM-2019-18283	CORSICABENTHOS3	CP07	–	–	–	–	–
	MNHN-IM-2019-18284	CORSICABENTHOS3	CP07	–	–	–	–	–
Pruvotia cf. *sopita*	MNHN-IM-2019-1744	CORSICABENTHOS2	CC02	GD-CC02-655	×	–	OR456214	OR458908
Simrothiella margaritacea	MNHN-IM-2019-18280	CORSICABENTHOS3	CP07	GD-CP07-725	×	–	OR456220	OR458918
	MNHN-IM-2019-18287	CORSICABENTHOS3	CP07	–	×	–	OR456221	OR458921
	MNHN-IM-2019-18286	CORSICABENTHOS3	CD159	–	×	–	–	OR458920
Dorymenia vagans	MNHN-IM-2019-18272	CORSICABENTHOS3	CS83	GD-CS83-579	×	×	–	OR458906
	MNHN-IM-2019-18274	CORSICABENTHOS3	CS83	–	–	–	–	–
	MNHN-IM-2019-18275	CORSICABENTHOS3	CS83	–	–	–	–	–
	MNHN-IM-2019-18276	CORSICABENTHOS3	CS83	–	–	–	–	–
	MNHN-IM-2019-18271	CORSICABENTHOS3	CS83	GD-CS83-586	×	×	OR456218	OR458915
	MNHN-IM-2019-18278	CORSICABENTHOS3	CS87	–	–	–	–	–
Anamenia gorgonophila	MNHN-IM-2019-18270	CORSICABENTHOS3	CR150	GD-CR150-681	×	×	OQ600030	OQ597876

ABBREVIATIONS

Institution

MNHN Muséum national d'Histoire naturelle, Paris.

Morphology

as abdomnial spicules;
at atrium;
cfg circumpharyngeal glands;
cg cerebral ganglion;
cu cuticle;
dg dorso-pharyngeal gland;
dts dorsoterminal sensory organ;
fo foregut;
h heart;
mc pallial cavity;
mi midgut;
mic midgut caecum;
mo mouth;
pc pericardium;
pcd pericardioduct;
pgl pedal glands;
ra radula;
re rectum;
rs radular sac;
spd spawning duct;
so pre atrial sensory organ;
st copulatory stylets;
sv seminal vesicles;
vfg ventrolateral foregut glands.

TABLE 4. — Main diagnostic characters of subfamilies and genera in the family Pruvotinidae (Table based on Pedrouzo *et al.* 2022). Symbols: +/-, presence/absence of a character.

	Hook-shaped sclerites	Ventrolateral foregut glands	Cyrcumpharyngeal glands	Doso-pharyngeal gland	Radula	Atrio-buccal cavity	Copulatory stylets	Respiratory folds	Dorsoterminal sensory organ(s)
Pruvotininae Heath, 1911									
Pruvotina Cockrell, 1903	+	A	–	+	Distichous	In part separated	–	+	+
Pararrhopalia Simroth, 1893	+	A	–	+	Distichous	–	+	–	+
Labidoherpia Salvini-Plawen, 1978	+	A	–	+	Distichous	+	+	+	+
Eleutheromeniinae Salvini-Plawen, 1978									
Eleutheromenia Salvini-Plawen, 1967	+	A	–	–	Distichous	+	–	+	+
Gephyroherpia Salvini-Plawen, 1978	+	A	–	–	Distichous	In part separated	–	+	+
Luitfredia García-Álvarez & Urgorri, 2001	+	A	–	–	–	+	–	+	+
Lophomeniinae Salvini-Plawen, 1978									
Lophomenia Heath, 1911	–	A	–	+	Distichous	+	–	?	+
Metamenia Thiele, 1913	–	A	–	+	Distichous	–	–	–	+
Hypomenia Van Lummel, 1930	–	A	–	+	Distichous	–	–	–	?
Halomeniinae Salvini-Plawen, 1978									
Halomenia Heath, 1911	–	A	–	–	Distichous	–	–	+	+
Forcepimenia Salvini-Plawen, 1969	–	A	–	–	Distichous	–	?	?	–
Uncimenia Nierstrasz, 1903	+	–	+	–	–	+	–	+	+
Sialoherpia Salvini-Plawen, 1978	–	–	+	–	–	In part separated	?	?	+?
Unciherpia García-Álvarez, Salvini-Plawen & Urgorri 2001	+	–	+	–	–	+	–	+	+
Scheltemaiinae Pedrouzo, García-Álvarez & Urgorri, 2022									
Scheltemaia Salvini-Plawen, 2003	+	C	–	–	Distichous	+	+	+	+

RESULTS

SPECIES IDENTIFICATION

To determine the number of species in the collection, we performed molecular work and SEM to image the sclerites for at least one specimen of each morphospecies. In some cases, more than one specimen was used to confirm our species hypothesis and/or examine intraspecific variation within a species (Table 3). In addition, we conducted serial histological sectioning on 12 specimens to collect internal anatomical data. Based on our morphological studies analyses (Fig. 2), the 47 specimens were identified as belonging to ten species representing seven families (Table 3). The characteristic external appearance of some species made it relatively easy to identify them. These include *Dondersia festiva* Hubrecht, 1888 (19 specimens) (Fig. 3A, A'), *Nematomenia banyulensis* (Pruvot, 1890) (four specimens) (Fig. 3C), and *Anamenia gorgonophila* (Kowalesky, 1888) (one specimen) (Fig. 3B, B'). Both *D. festiva* and *N. banyulensis* have a distinct external aspect, characterized by their bright colors. *A. gorgonophila* is a well-known solenogaster species that is commonly found on gorgonians in the Atlantic and Mediterranean Sea (compiled in García-Álvarez *et al.* 2014). These identifications based on habitus were confirmed by the study of sclerites and internal anatomy and were reinforced by the relative proximity of Corsica to the type localities. The external aspect of four species was likewise helpful for preliminary identification, but histology or DNA barcoding were necessary to confirm these initial identifications. These were *Dorymenia vagans* (Kowalevsky & Marion, 1887) (six specimens) (Fig. 3D), *Simrothiella margaritacea* (Koren & Danielssen, 1877) (three specimens) (Fig. 4E), *Unciherpia hirsuta* García-Alvarez, Urgorri & Salvini-Plawen; 2001 (four specimens) (Fig. 4D), and *Eleutheromenia sierra* (Pruvot, 1890) (one specimen) (Fig. 4B). One specimen was tentatively identified as *Tegulaherpia myodoryata* Salvini-Plawen, 1988 based on the habitus and sclerites (Fig. 4A, A'), but this specimen was too small for routine histology with paraffin. Further studies, including the analysis of the internal anatomy of this and related species would be desirable for a confident identification. One specimen, found on the hydrozoan *Sertularella* sp., was identified as *Pruvotia* cf. *sopita* (Pruvot, 1891) (Fig. 4C) based on this association and its characteristic habitus. However, the specimen was damaged, which precluded the histological sectioning needed to confirm this tentative identification. The remaining seven specimens were classified in the family Pruvotinidae Heath, 1911 based on the sclerites and DNA barcoding. The study of internal anatomy and application of species delimitation methods were necessary for the confident identification of them as *Pruvotina impexa* (Pruvot, 1890) (Fig. 5).

PHYLOGENETIC ANALYSIS AND SPECIES DELIMITATION

DNA barcoding was performed to provide reference sequences for two commonly used molecular markers (COI and 16S) and to evaluate our morphology-based species concepts using

Fig. 3. — Habitus of **A**, *Dondersia festiva* Hubrecht, 1888 (photo of the living animal – MNHN-IM-2019-18277); **A'**, *Dondersia festiva* (photo of the living animal – MNHN-IM-2019-16169); **A"**, detail of the dorsoterminal sensory organs (MNHN-IM-2019-16169); **B**, *Anamenia gorgonophila* (Kowalevsky, 1880) (photo of the living animal on *Paramuricea* sp.): **B'**, *Anamenia gorgonophila* (photo of the preserved specimen – MNHN-IM-2019-18270); **C**, *Nematomenia banyulensis* (Pruvot, 1890) (photo of the preserved specimen – MNHN-IM-2019-16178); **D**, *Dorymenia vagans* (Kowalevsky & Marion, 1887) (photo of the preserved specimen – MNHN-IM-2019-18274). Scale bars: 1 mm. Symbols: **arrows**, dorsoterminal sensory organs; **stars**, anterior end of the animals.

molecular data. PCR amplification success was high, but not perfect, for both genes. For COI, we obtained 16 sequences with at least one successful sequence for nine of the 10 species (all but *Tegulaherpia* cf. *myodoryata*) resulting in 16 sequences from nine species. For 16S, we likewise obtained at least one successful sequence for nine of the 10 species. Despite multiple attempting to amplify this gene from five different individuals, none of our attempts to obtain this gene from *Pruvotina impexa* were successful resulting in 10 sequences from nine species (Table 3). Our phylogenetic analysis (Fig. 2) recovered each species from Corsica sampled for more than one individual monophyletic with maximal bootstrap support (bs = 100). Except for *Pruvotina*, which was recovered paraphyletic with respect to *Hypomenia* Van Lumen, 1930, all genera were recovered monophyletic. The results of the species delimitation analysis (Fig. 2) are consistent with our morphology-based species hypotheses. The number of species inferred by ASAP according to the partition with the best asap-score (3.00) was 32. The only disagreement between ASAP and available species identifications was that *Epimenia australis* and *Epimenia babai* were recovered as the same species (consistent with the results of Cobo *et al.* 2023), but this has no bearing on the Corsica species.

Order PHOLIDOSKEPIA Salvini-Plawen, 1978
Family DONDERSIIDAE Simroth, 1893

Genus *Dondersia* Hubrecth, 1888

TYPE SPECIES. — *Dondersia festiva* Hubrecht, 1888. Mediterranean Sea (Northern Gulf of Naples); 60 m.

Dondersia festiva Hubrecht, 1888

Dondersia festiva Hubrecht, 1888: 324.

MATERIAL EXAMINED. — **Corsica** (France) [19 specimens] • 2 specimens (used for sclerite preparation, DNA extraction and histology); CORSICABENTHOS 1, 3 (Table 2); 15-200 m depth; MNHN-IM-2019-16169 (1 microscope slide with sclerites, 24 slides with 5 µm serial sections); MNHN-IM-2019-18277; GenBank: OR456222: OR458916 (1 microscope slide with sclerites, 1 SEM stub; 9 slides with 5 µm serial sections) • 16 specimens (preserved in 95%); CORSICABENTHOS 1, 3 (Table 2); 15-200 m depth ethanol; MNHN-IM-2019-13916, MNHN-IM-2019-13917, MNHN-IM-2019-13918, MNHN-IM-2019-13919, MNHN-IM-2019-13920, MNHN-IM-2019-16171, MNHN-IM-2019-16172, MNHN-IM-2019-16173, MNHN-IM-2019-16174, MNHN-IM-2019-16175, MNHN-IM-2019-16181, MNHN-IM-2019-16182, MNHN-IM-2019-16183, MNHN-IM-2019-16184, MNHN-IM-2019-16185, MNHN-IM-2019-16186 • 1 specimen (mounted for SEM and preserved on the SEM stub); CORSICABENTHOS 1, 3 (Table 2); 15-200 m depth; MNHN-IM-2019-16170.

DESCRIPTION

Elongate animal (10-15 × 1-2 mm) with a posterior digitiform projection preceded by a bulbous lobe and a beak-like anterior end. Of bright purple color (Fig. 3A). Color fading after preservation in 95% ethanol but remaining light pink. Dorso-terminal sensory organs (two to four) externally visible as small, rounded holes in the cuticle (Fig. 3A'). Of the 19 specimens, clearly observed four dorso-terminal sensory organs in 12, in one specimen three and in three specimens observed two. In remaining three specimens, difficult to count, but at least one dorso-terminal sensory organ observed in each before preserving in ethanol. Pedal groove and opening of the pallial cavity marked externally (Fig. 3A). With characteristic scale-like sclerites of different types (Fig. 6): entire body covered by a basal layer of small, oval-shaped scales (10-18 × 5-10 µm) with a proximal rim and a pointed distal end (Fig. 6B), pallet-shaped (trowel-like) scales of four types and solid acicular sclerites are arranged between them (Fig. 6A, B, F, I, J). Pallet-shaped scales vary in their total length and the length of the stem: 1) shorter pallet-shaped scales with long stem (58-60 × 10-14 µm, where the stem is around 20 µm) (Fig. 6A, C); 2) shorter pallet-shaped scales with a short stem (38-50 × 12-18 µm, where the stem is around 8 µm) (Fig. 6D, E), less abundant; 3) longer pallet-shaped scales with long stem (80-120 × 8-10 µm, where the stem is around 20 µm) (Fig. 6E, F, G, H); and 4) longer pallet-shaped scales with short stem (75-100 × 10 µm, where the stem is around 5 µm) (Fig. 6E, I). In addition, one type of pallet-shaped scale (40-50 × 10-14 µm) located just around the atrio-buccal cavity (Fig. 6L). Acicular sclerites (100-160 × 15-18 µm) are curved, striated and with rounded ends (Fig. 6J, K), mostly located at the mid-ventral areas of the body (Fig. 6J). Radula monoserial with eight to nine rows of small teeth (30-40 × 12 -14 µm) formed by a pair of middle denticles fused for most of their length and terminating in a thin distal tip (Fig. 10A, A') and with smaller, distally pointed, downwardly curved, lateral denticles. Ventrolateral foregut gland of type A (García-Álvarez & Salvini-Plawen 2007) / *Acanthomenia* type (Handl & Todt 2005) (Fig. 10A). With folded mantle cavity but without real respiratory folds (Fig. 10D, E). With copulatory stylets (Fig. 10B-D).

REMARKS

Dondersia festiva Hubrecht, 1888 has a characteristic coloration and body shape with a posterior projection that facilitated the identification of the Corsica specimens. Besides, the other diagnostic morphological characters (monoserial radula, copulatory stylets, dorso-terminal sensory organ(s) and absence of respiratory folds) were found in the examined animals. Particularly important for the identification of Dondersiidae species is the types of sclerites (Scheltema *et al.* 2012; Cobo & Kocot 2021). The sclerites of the Corsica specimens (Fig. 6) can be compared to those described previously for the species (Hubrecht 1888: fig. 2a; Scheltema *et al.* 2012: figs 1-3). Nevertheless, the use of SEM allowed us to observe details not described before: 1) it was possible to determinate that the acicular sclerites are striated; 2) the exact shape and position of the oval-shaped scales, that are embedded in the cuticle by their rounded, rimmed proximal end (Fig. 6A, B); and 3) we confirmed that the pallet-shaped scales have pointed ends and not flat ends as described before (Hubrecht 1888; Scheltema *et al.* 2012: figs 1-3a); the previously described

FIG. 4. — Habitus of **A**, *Tegulaherpia* cf. *myodoryata* (photo of the living animal – MNHN-IM-2019-16176); **A'**, *Tegulaherpia* cf. *myodoryata* (photo of the preserved specimen – MNHN-IM-2019-16176); **B**, *Eleutheromenia sierra* (Pruvot, 1890) (photo of the preserved specimen – MNHN-IM-2019-1749); **C**, *Pruvotia* cf. *sopita* (photo of the preserved specimen – MNHN-IM-2019-1744 – on *Sertularella* sp.); **D**, *Unciherpia hirsuta* García-Alvarez, Urgorri & Salvini-Plawen, 2001 (photo of the living animal – MNHN-IM-2019-18279); **E**, *Simrothiella margaritacea* (Koren & Danielssen, 1877) (photo of the preserved specimen – MNHN-IM-2019-18280). Scale bars 1 mm. Symbols: **arrow**, copulatory stylets; **stars**, anterior end of the animals.

flat-ended pallet-shaped sclerites correspond with broken sclerites (Fig. 6G). Previous works (Nierstrasz 1902, 1908; van Lummel 1930; Nierstrasz & Stork 1940) stated the existence of two dorso-terminal sensory organs, not distinguished by Hubrecht (1888) or Scheltema *et al.* (2012). Observations of living animals revealed that *D. festiva* can have between two and four of these organs. We did not find any relationship between the size of the specimen and the number of dorso-terminal sensory organs, although we found that after fixation it was more difficult, or not possible, to find this organ externally and it was also challenging to distinguish it in the serial sections (Fig. 10E). The original description of *D. festiva* and subsequent descriptions (material and literature reviewed in Scheltema *et al.* 2012) state the absence of respiratory folds. The obtained sections of the Corsica specimens (Fig. 10D, E) show a strongly ciliated mantle cavity. In addition to the morphological data, we obtained DNA barcodes for this species for the first time. The characteristics of the copulatory stylets (the bag they are included in Figure 10B, and the accessory spicules, Figure 10C), coincide with what was described and shown by Scheltema *et al.* (2012).

D. festiva was described from the Mediterranean Sea (Western Italy) from depths between 60 and 65 m. The specimens from Corsica were collected between 15 and 100 m extending not only the geographical but also the bathymetric distribution of the species. Of the type series, one specimen was collected on the hydrozoan *Aglaophenia* sp. and another specimen on the hydrozoan *Lytocarpia myriophyllum* (Linnaeus, 1758), although the identification of this last specimen is doubtful (Hubrecht 1888; Scheltema *et al.* 2012). Specimens from Corsica were not observed on cnidarians, likely due to the sampling methods used (dredge and manual suction pump sampler; Table 2).

Genus *Nematomenia* Simroth, 1893

TYPE SPECIES. — *Nematomenia flavens* (Pruvot, 1890). Mediterranean Sea (Banyuls-sur Mer); 45-90 m.

Nematomenia banyulensis (Pruvot, 1890)

Dondersia banyulensis Purvot, 1890: XXII.

Nematomenia banyulensis – Handl & Salvini-Plawen 2001: 371.

MATERIAL EXAMINED. — **Corsica** (France) [4 specimens] • 1 specimen (used for sclerite preparation, DNA extraction and histology); CORSICABENTHOS 2 (Table 2); 60-100 m depth; MNHN-IM-2019-1747; GenBank: OR456215; OR458911; (1 microscope slide with sclerites, 1 SEM stub; 12 slides with 5 µm serial sections) • 3 specimens (preserved in ethanol); CORSICABENTHOS 1, 2 (Table 2); 60-100 m depth; MNHN-IM-2019-16177, MNHN-IM-2019-16178, MNHN-IM-2019-16180.

DESCRIPTION

Elongate-bodied animal (15-30 × 1 mm) of bright red color (Fig. 3C). Color fading after fixation and turning orange to yellowish. Without a cuticular keel but with a prominent dorsal line formed by the sclerites that is translucent and shiny. Usually coiled, even while alive. Thin cuticle, with imbricate, rounded leaf-like scales (Fig. 7A) with a bifid proximal end (65-78 × 40-45 µm) (Fig. 7D), with less abundant oar-shaped scales (60-70 × 20 µm) (Fig. 7B) between them. With differentiated knife-shaped scales along the pedal groove (40 × 10-14 µm) (Fig. 7C). Without radula. Ventrolateral foregut gland of type A / *Acanthomenia* type. Without copulatory stylets. With a dorso-terminal sensory organ visible externally in live animals.

REMARKS

As for the previous species, the external aspect was important for species identification. *N. banyulensis* is, however, similar to *N. flavens*, a species described from the same locality and in the same work (Pruvot1890). An important difference between both species is the external aspect when they are alive, as *N. banyulensis* is bright red and *N. flavens* is yellow (Pruvot 1890, 1891: figs1, 2; Odhner1920; Salvini-Plawen 2003; Handl & Salvini-Plawen 2001). Color can be lost after fixation; thus, it has been suggested that some later records of the species may be a misidentification (Salvini-Plawen 2003). Nevertheless, they can be distinguished based on the sclerites, as the short scales with a bifid proximal end (founded in the Corsica specimens, Figure 7D) are exclusive to *N. banyulensis* (Pruvot 1890; compilation of sclerite drawings in Handl & Salvini-Plawen 2001: figs 7-9). A third species of *Nematomenia* has also been described from the Mediterranean Sea, *N. corallophila* (Kowalevsky, 1881). While *N. corallophila* shares coloration with *N. banyulensis*, it is important to note that the former's description lacks detailed anatomical information and it just highlights that it is epizootic on *Corallium rubrum* (Linnaeus, 1758) (Kowalevsky 1881; Salvini-Plawen 2003). The absence of type material impedes a comprehensive comparison of the two species and as a result, we agree with Salvini-Plawen (2003), and the identification of specimens as *N. corallophila* can be only considered when observed on this specific coral. For the first time we include here DNA barcodes for *N. banyulensis.* The quality of the obtained serial sections does not allow to a perfect reconstruction of all the internal organs but was good enough to confirm the absence of radula and copulatory stylets.

N. banyulensis was first described off Banyuls-sur-Mer (France) at a depth of between 60 and 80 m (Pruvot 1890, 1891) which corresponds with the depths of the localities from Corsica. Other records of this species include localities in the Adriatic Sea, off Naples and in the North Atlantic Ocean (English Channel, Shetland Islands, Roscoff, Giiteborg and Norwegian fjords) at depths between 45 and 300 m (Thiele 1894; Pruvot 1899; Seaward 1990; Handl & Salvini-Plawen 2001), and it has been found epizoically on hydrozoans, including *Lafoea dumosa* (Fleming, 1820), *Lytocarpia myriophyllum* (Linnaeus, 1758) and *Grammaria abietina* (Sars, 1851) in muddy bottoms (García-Álvarez *et al.* 2014). With the specimens included in this work, we add new locations in the Mediterranean Sea. Specimens from Corsica were not observed on cnidarians, but this can be explained as they were collected using dredges and found while sorting sieved material.

Fig. 5. — Habitus of *Pruvotina impexa* (Pruvot, 1890): **A**, MNHN-IM-2019-18281 (photo of the preserved specimen); **A'**, MNHN-IM-2019-18281 (photo of the living animal); **A"**, detail of the atrio-buccal region of MNHN-IM-2019-18281, **arrow** indicates the muscular ridge separating the atrium and pedal pit; **B**, MNHN-IM-2019-1746 (photo of the living animal); **C**, MNHN-IM-2019-1748 (photo of the living animal); **D**, MNHN-IM-2019-1745 (photo of the preserved specimen); **E**, MNHN-IM-2019-18285 (photo of the preserved specimen); **F**, MNHN-IM-2019-18273 (photo of the living animal and expelled gut contents); **G**, MNHN-IM-2019-16179 (photo of the preserved specimen). Scale bar: 1 mm. Symbols: **stars**, the anterior end of the animals.

Family Lepidomeniidae Pruvot, 1902

Genus *Tegulaherpia* Salvini-Plawen, 1983

Type species. — *Tegulaherpia stimulosa* Salvini-Plawen, 1983. Dalmatia (Mediterranean Sea); 75-80 m.

Tegulaherpia cf. ***myodoryata*** Salvini-Plawen, 1988

Tegulaherpia myodoryata Salvini-Plawen, 1988: 377.

Material examined. — **Corsica** (France) • 1 specimen (preserved in 95% ethanol in two pieces, middle region used for sclerite preparations and DNA extraction); CORSICABENTHOS 1 (Table 2); 41 m depth; MNHN-IM-2019-16176; GenBank: OR456213 (1 microscope slide with sclerites, and tissue in ethanol).

Description

Small (3.8 × 0.4-1 mm) bright white animal, anterior end wider than the posterior (Fig. 4A, A'). Light brown color in the midgut region when alive (Fig. 4A'). With imbricate oval scales (30-40 × 20-25 µm) (Fig. 7E). Knife-like scales around the pedal groove (40 × 28 µm). With a small pallial cavity opening visible externally in the live specimen in which a protruding copulatory stylet was also observed.

Remarks

The family Lepidomeniidae includes three genera that differ essentially, following the existent classification, in the shape of the sclerites (Kowalevsky 1883; Kowalevsky & Marion 1887; Heath 1918; Salvini-Plawen 1983; García-Álvarez *et al.* 2000; Salvini-Plawen2003): *Lepidomenia* Kowalesky, 1883 with triangular scales; *Nierstrazia* Heath, 1918 with leaf-shaped scales and *Tegulaherpia* Salvini-Plawen, 1983 with oval scales (Kowalevsky 1883; Heath 1918; Salvini-Plawen 1983). In addition, *Lepidomenia hystrix* Marion & Kowalevsky, 1885 lacks copulatory stylets (Kowalevsky & Marion 1887), thus the lack of this structure is included in the diagnosis of the genus (García-Álvarez & Salvini-Plawen 2007), as they exist in the other two genera. The Corsica specimen has oval scales and copulatory stylets. Based on this, it was placed in the genus *Tegulaherpia*. The identification of the specimen from Corsica as *Tegulaherpia* cf. *myodoryata* is justified by the external similarities (color, size and sclerites) of the examined specimen to published data on this species (Salvini-Plawen 1988; Handl & Salvini-Plawen 2001: fig. 13) and the sclerites. The scales of the Corsica specimen correspond, in shape and size, with those described for *Tegulaherpia myodoryata* (Handl & Salvini-Plawen 2001: 17; Salvini-Plawen 2003: fig. 7). *Tegulaherpia* includes another Mediterranean species, *T. stimulosa* Salvini-Plawen, 1983 that can be differentiated from *T. myodoryata* based on the sclerites: more oval in *T. myodoryata* (Salvini-Plawen 1988; Salvini-Plawen 2003). Nevertheless, a study of the internal anatomy, especially the posterior organs, is important for confident identification. Due to the small size of the available specimen, we discarded histology, as a genus-level identification was adequate for the aims of this study. Moreover, the distinction between the genera in Lepidomeniidae is most likely in need of revision (*personal observations*) for which the analysis of the diagnostic characters, including a thorough and updated description of the sclerites of all the species is necessary.

T. myodoryata has been recorded from the Mediterranean (Banyuls-sur-Mer and Livorno) and the North Atlantic Ocean (Norway and Irish Sea). If the identification of the specimen from Corsica is confirmed, the distribution of this species would be extended to the Mediterranean Sea and the minimum depth at which it can be found would be decreased from 70 to 40 m. As with previous findings of *T. myodoryata* (García-Álvarez *et al.* 2014), the specimen from Corsica was collected from a sandy bottom.

Order "CAVIBELONIA" Salvini-Plawen, 1978
Family Pruvotinidae Heath, 1911
Subfamily Pruvotininae Heath, 1911

Genus *Pruvotina* Cockerell, 1903

Type species. — *Pruvotina impexa* (Pruvot, 1890). Banyuls-sur mer (Mediterranean Sea); 80 m.

Pruvotina impexa (Pruvot, 1890)

Paramenia impexa Pruvot, 1890: XXIII.

Pruvotina impexa – Cockerell 1903: 118.

Material examined. — **Corsica** (France) [7 specimens] • 4 specimens (used for sclerite preparations, DNA extractions and histology); CORSICABENTHOS 1, 2 and 3 (Table 2); 50-122 m depth; MNHN-IM-2019-18281; GenBank: OR458919 (1 microscope slide with sclerites, 1 SEM stub; 11 slides with 5 µm serial sections); MNHN-IM-2019-1748; GenBank: OR458910 (1 microscope slide with sclerites, 1 SEM stub; 24 slides with 5 µm serial sections); MNHN-IM-2019-1746; GenBank: OR458910 (1 microscope slide with sclerites, 1 SEM stub; 26 slides with 5 µm serial sections); MNHN-IM-2019-16179; GenBank: OR458907 (1 microscope slide with sclerites, 1 SEM stub; 15 slides with 5 µm serial sections) • 1 specimen (used for sclerite preparations and DNA extraction); CORSICABENTHOS 2 (Table 2); 50-122 m depth; MNHN-IM-2019-1745; GenBank: OR458909 (1 microscope slide with sclerites) • 2 specimens (preserved in 95% ethanol); CORSICABENTHOS 3 (Table 2); 50-122 m depth; MNHN-IM-2019-18285; MNHN-IM-2019-18273.

Description

Elongate body when alive, rounded in cross-section (4-12 × 0.5-0.8 mm), rounded ends. Length and shape, especially anterior body, notably changes animal movement and preservation (Fig. 5). Four specimens reddish to orange color in the midbody region (Fig. 5B, C, F), when collected. Living animal observations showing coloration due to midgut content; some specimens expelled material from anterior end (Fig. 5F). While cutting the animals, colored material visible inside body, not the cuticle or epidermis. Color fading with time when preserved in ethanol (Fig. 5D). Two specimens when alive (MNHN-IM-2019-18281, MNHN-IM-2019-18285) (Fig. 5A, E). Sclerites protrude slightly from the cuticle, es-

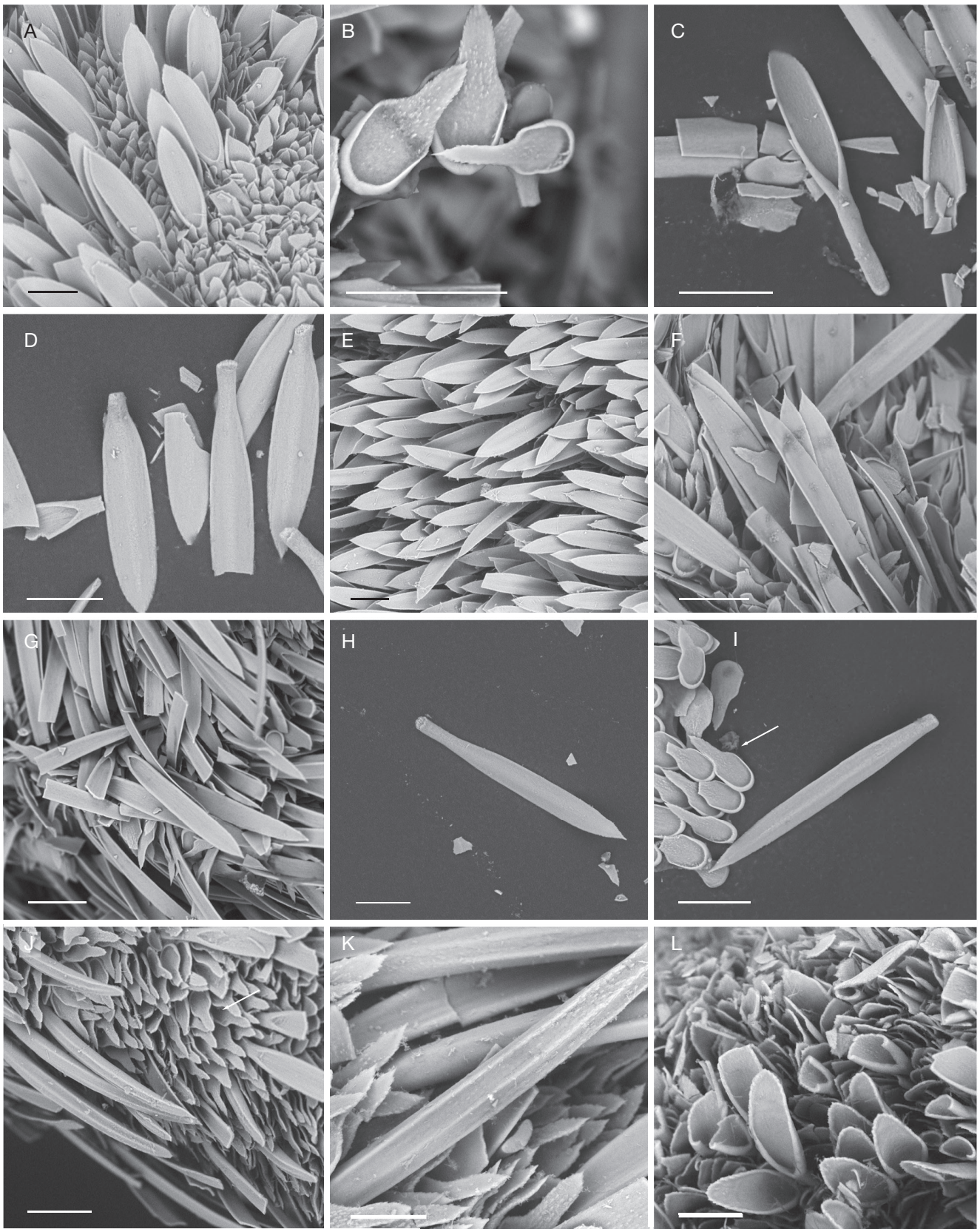

FIG. 6. — SEM images of the sclerites of *Dondersia festiva* (Pruvot, 1890) (MNHN-IM-2019-16170): **A**, layer of oval-shaped scales (many are broken) with pallet-shaped scales among them; **B**, oval-shaped scales; **C**, short pallet-shaped scales with a long stem; **D**, short pallet-shaped scales with a short stem; **E**-**G**, distal end of long pallet-shaped scales. **H**, long pallet-shaped scales with a long stem; **I**, long pallet-shaped scales with a short stem.; **J**, striated acicular sclerites; **K**, detail of the striated acicular sclerites; **L**, pallet-shaped scales of the anterior region. Scale bars: 20 µm. Symbols: **arrows**, oval-shaped scales from the basal layer.

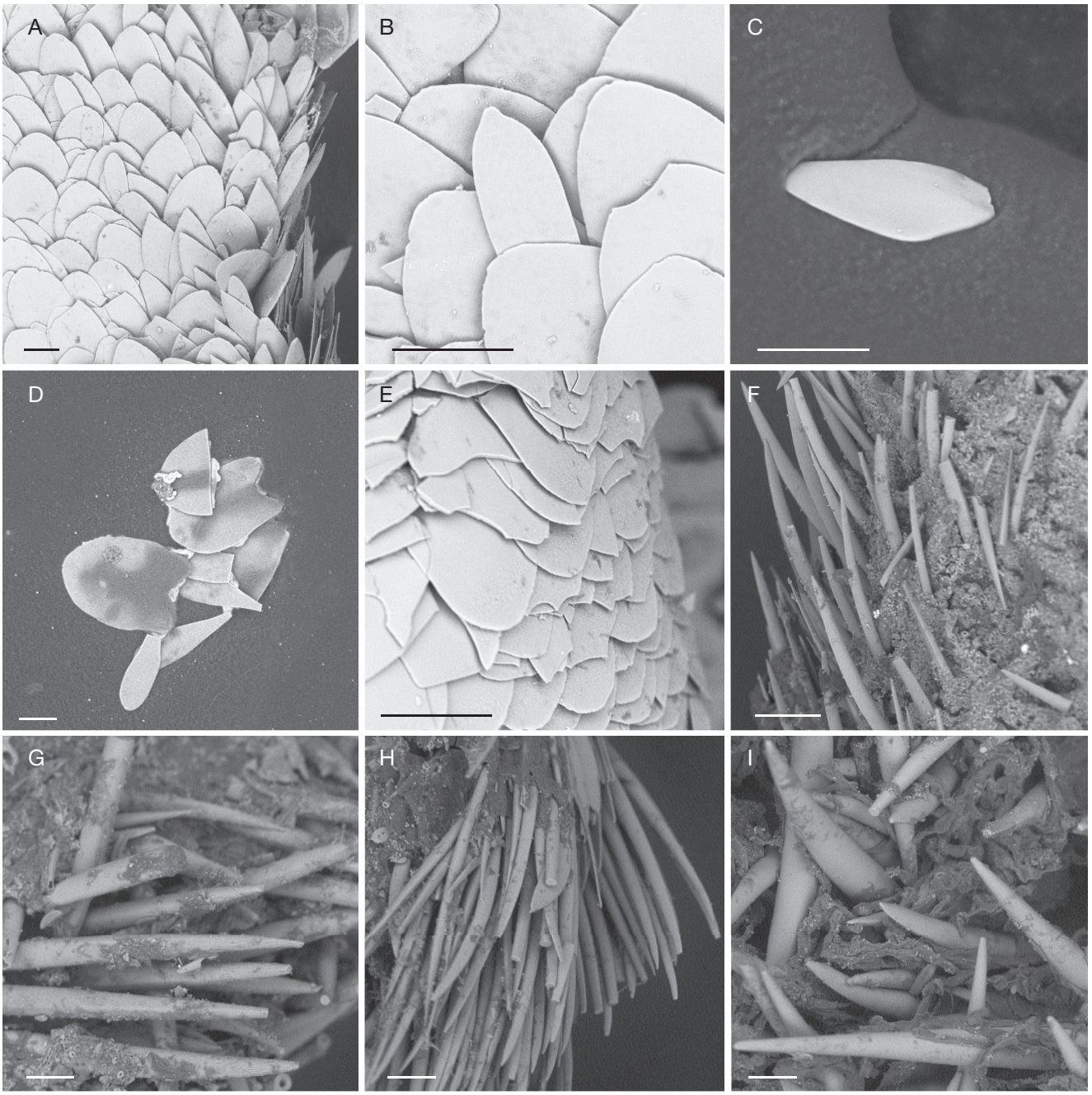

FIG. 7. — SEM images of the sclerites of **A**-**D**, *Nematomenia banyulensis* (Pruvot, 1890) (MNHN-IM-2019-1747); **E**, *Tegulaherpia* cf. *myodoryata* (MNHN-IM-2019-16176); **F**, *Simrothiella margaritacea* (Koren & Danielssen, 1877) (MNHN-IM-2019-18280); **G**, **H**, *Dorymenia vagans* (Kowalevsky & Marion, 1887) (MNHN-IM-2019-18274); **I**, *Anamenia gorgonophila* (Kowalevsky, 1880) (MNHN-IM-2019-18270). Scale bars: 20 µm.

pecially in the posterior region (Fig. 5A'), giving a slightly hirsute appearance. With hollow sclerites of three main types (Fig. 8A, B): hollow acicular sclerites with hook-shaped distal end, hollow acicular sclerites with pointed ends, and hollow acicular sclerites that are serrated distally. Hook-shaped sclerites of two types. Both with a spine located at the apex of the sclerite where it reflexes to form a hook with the same size (90-150 µm × 4-8 µm), differences between them in the length and shape of the distal region of the hook (Fig. 8D): in one type, longer (55-60 µm length), narrower and curved distally (Fig. 8D, E, G) whereas in the second type shorter and uniform in width (45 × 8 µm) (Fig. 8D, E, F). Most of the hollow acicular sclerites with pointed end (Fig. 8B) slightly curved (80 -210 × 4-8 µm) but some also straight and narrower (50-150 × 2-3 µm). Acicular sclerites creating a dense layer in the ventral region of the body, around the pedal groove, the (Fig. 8B). Hollow acicular sclerites that are slightly curved and with a serrated distal end (100 × 3-5 µm), less abundant type (Fig. 8E). With knife-shape scales of the pedal groove (45 × 8 µm), located between the acicular sclerites (Fig. 8B).

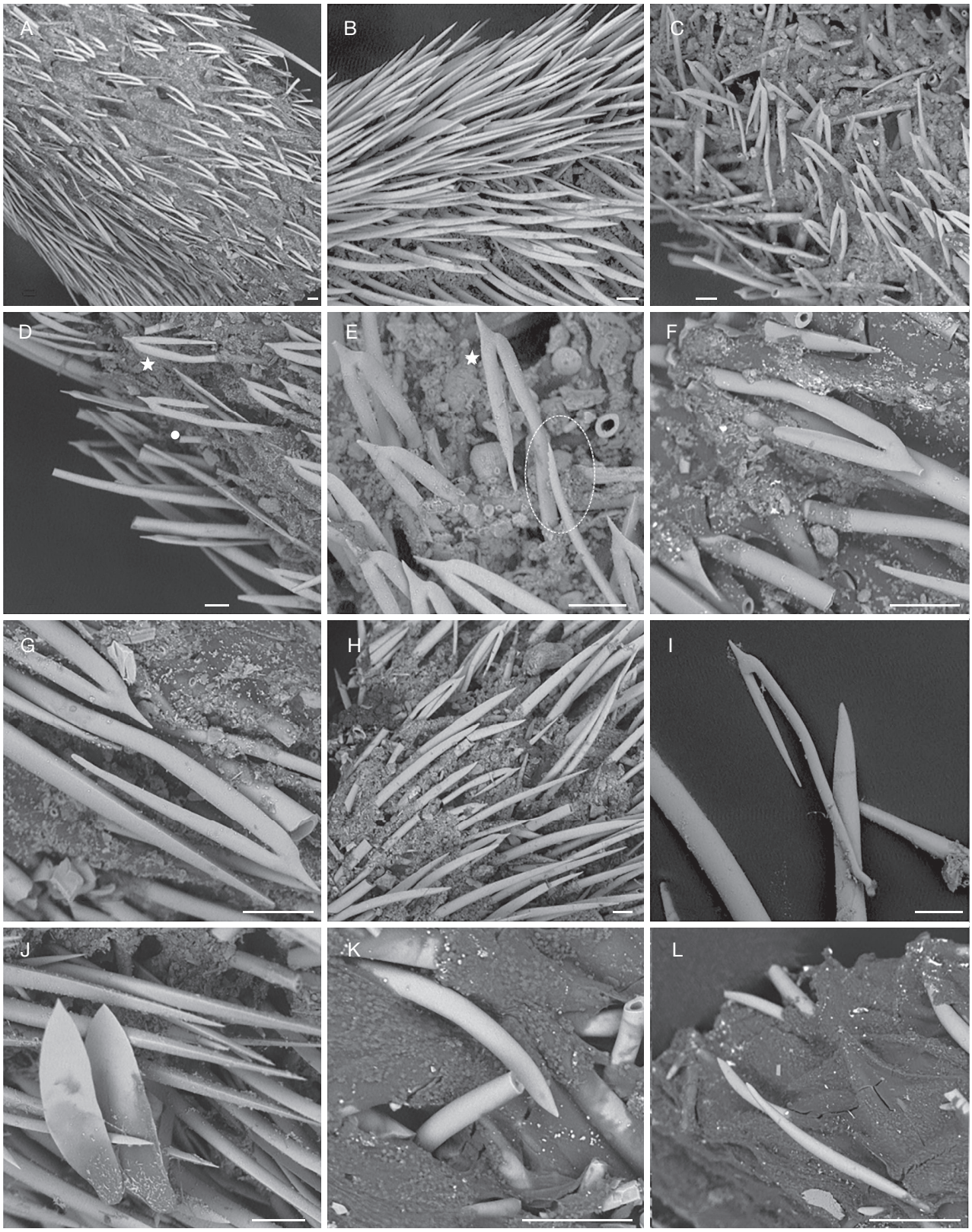

FIG. 8. — SEM images of the sclerites of **A**-**G**, *Pruvotina impexa* (Pruvot, 1890): **A**, general view of the sclerites in the dorsal body region (MNHN-IM-2019-18281); **B**, acicular sclerites and scales of the pedal groove (**arrow**) in the ventral region of the body (MNHN-IM-2019-18281); **C**, general view of the sclerites in the dorsal body region (MNHN-IM-2019-1746); **D**, two types of hook-shaped sclerites (**star**, long distal region of the hook; **dot**, short distal region of the hook) (MNHN-IM-2019-1746); **E**, hook-shaped sclerites with long distal region of the hook (**star**) and the serrated sclerites (**encircled**) (MNHN-IM-2019-18281); **F**, hook-shaped sclerites with short distal region of the hook (MNHN-IM-2019-18281); **G**, hook-shaped sclerites with long distal region of the hook (MNHN-IM-2019-18281); **H**-**J**, *Pruvotina impexa* (MNHN-IM-2019-16179): **H**, general view of the sclerites in the dorsal region of the body; **I**, hook-shaped sclerite; **J**, scales of the pedal groove; **K**, **L**, acicular sclerites of *Pruvotia* cf. *sopita* (MNHN-IM-2019-1744). Scale bars: 20 µm.

With a pre-atrial dorsal sensory organ (Fig. 11B) and a bilobed atrium (Fig. 11A-C). Mouth (Fig. 12A-C) partially separated from the atrium by a wall with musculature but without a cuticular layer separating the two openings (Fig. 11H, I). The atrium with single and bilobed papillae (Fig. 11A-C). With a dorso-pharyngeal papilla gland (Fig. 12A-C) and ventrolateral foregut glands of type A / *Pararrhopalia* type (Handl & Todt 2005) (Fig. 12E). Radula distichous with three to four median denticles (Fig. 12D, D'). With a pedal fold that enters the mantle cavity. With seminal vesicles and a tripartite spawning duct in its middle region (Fig. 12F). With between 12 and 18 respiratory folds (Fig. 12H). With a pair of bundles of 12 to 16 abdominal spicules (Fig. 12G, G'). Dorso-terminal sensory organ located in a terminal position (Fig. 12I). The posterior region (especially the respiratory folds and dorso-terminal sensory organ) difficult to study in the obtained serial sections of one of the specimens (MNHN-IM-2019-1748), but these structures perfectly observed in the other sectioned specimens (MNHN-IM-2019-1746 and MNHN-IM-2019-18281). Serial sections of MNHN-IM-2019-16179 not of adequate quality to characterize all the main diagnostic characters, but the existence of a dorso-pharyngeal papilla gland and remains of a radula determinate. Besides this, no noteworthy differences in the internal organs between the three examined specimens.

Remarks

Externally, and when analyzing the preserved material, the seven specimens were at first glance assumed to be four different morphospecies: 1) MNHN-IM-2019-1748, MNHN-IM-2019-1746, MNHN-IM-2019-18273, with orange coloration; 2) MNHN-IM-2019-1745, with shorter body, more rounded anterior end and pinkish to orange coloration; 3) MNHN-IM-2019-18285, MNHN-IM-2019-18281, white and elongated body; and 4) MNHN-IM-2019-16179, white-yellowish and shorter body. The results of the phylogenetic analysis and the species delimitation methods (Fig. 2), along with the study of morphology (Figs 5; 8; 11; 12) and our observations in the field, led to the identification of all of them as the same species: *Pruvotina impexa* (Pruvot, 1890).

Pruvotinidae is a diverse family and the only one in Solenogastres divided into subfamilies. The main differences between the subfamilies are the presence/absence of hook-shaped sclerites and the glands associated with the foregut (García-Álvarez & Salvini-Plawen 2007). Species of the subfamily Pruvotininae Heath, 1911 have dorso-pharyngeal papilla gland and ventrolateral foregut glands of type A/ *Pararrhopalia* type, a distichous radula and hook-shaped sclerites (García-Álvarez & Salvini-Plawen 2007; Pedrouzo *et al.* 2022). These characteristics place these specimens in the subfamily Pruvotininae Heath, 1911, which includes three genera (Table 4) and two described Mediterranean species *Pruvotina impexa* (Pruvot, 1890) and *Pararrhopalia pruvoti* (Pruvot, 1891).

Traditionally, the three genera within Pruvotininae (*Pruvotina* Cockerell, 1903; *Pararrhopalia* Simroth, 1893; *Labidoherpia* Salvini-Plawen, 1978) are distinguished by a combination of characters related to the atrio-buccal cavity, respiratory folds, and copulatory stylets (Table 4) (García-Álvarez & Salvini-Plawen 2007; Zamarro *et al.* 2013: Table 1; Pedrouzo *et al.* 2022). A solenogaster is said to have a common atrio-buccal cavity when the mouth opens at the posterior region of the atrium cavity. On the contrary, a clear separation between the atrium and mouth occurs when there are two separated cavities with a ridge or septum (with musculature and cuticular covering) between them (Zamarro *et al.* 2013). In certain species, a musculature-supported ridge lacking cuticle partially separates the mouth and atrium (Zamarro *et al.* 2013). *Labidoherpia* (monospecific genus constituted by the species *L. spinosa* (Thiele, 1913)) has a common atrio-buccal cavity, in *Pararrhopalia* the mouth and atrium are separated, and in *Pruvotina* the mouth and atrium are partially separated (García-Álvarez & Salvini-Plawen 2007; Pedrouzo *et al.* 2022). Nevertheless, a review of the available descriptions casts doubts on the reliability of this character. Salvini-Plawen (1978) mentions a ridge between the mouth and atrium without sclerites in *Labidoherpia spinosa*, which corresponds with a partial separation as the one described for *Pruvotina* species (e.g., Salvini-Plawen 1978, Zamarro *et al.* 2013). In the description of the type species of *Pararrhopali*a (*Pararrhopali*a *pruvoti*; misidentified as "*Proneomenia vagans*" Kowalevsky & Marion, 1887 *in* Pruvot 1891), it is pointed out that atrium seemed to be separate from the mouth in the sections, something not observed in the living animals, and it is suggested that "this seems to be due only to the retraction of the cephalic extremity at the time of death" (Pruvot 1891). In addition, Pedrouzo *et al.* (2022) did not observe a cuticular layer in the septum between the mouth and atrium in the specimens they identified as *Pararrhopalia pruvoti*. Similarly, in the description of *Pararrhopalia oscari* Pedrouzo & Urgorri, 2022 it is stated that "atrium and mouth are separated by a small muscular groove (ridge) without cuticle" (Pedrouzo *et al.* 2022). In view of all this, we consider that the atrio-buccal cavity is not a valid character to differentiate between genera in the subfamily Pruvotininae, and that its taxonomic value should be revaluated. Respiratory folds are diagnostic of *Pruvotina* and *Labidoherpia*, while they are absent in *Pararrhopalia* (García-Álvarez & Salvini-Plawen 2007; Pedrouzo *et al.* 2022). *Pruvotina* is the only genus of the subfamily without copulatory stylets. Taking all this together, the specimens from Corsica were classified within *Pruvotina*: mouth and atrium partially separated, respiratory folds present and without copulatory stylets.

The comparison of our specimens and the literature led to the identification of our specimens as *Pruvotina impexa* (Pruvot 1890, 1891; Cockerell 1903; Simroth 1893; Todt 2006; García-Álvarez & Salvini-Plawen 2007; Salvini-Plawen 2008; Pedrouzo *et al.* 2022). Nevertheless, we also found some juxtaposition of characters with *Pararrhopalia pruvoti* and thus a discussion considering both Mediterranean species is necessary. Remarkably, the only available descriptions of *Pruvotina impexa* are based on the type material (Pruvot 1890, 1891). On the contrary, for *Pararrhopalia pruvoti* there are updated redescriptions and new records (Todt 2006; Salvini-Plawen 2008; Pedrouzo *et al.* 2022). In the original comparison of the two species, Pruvot (1891)

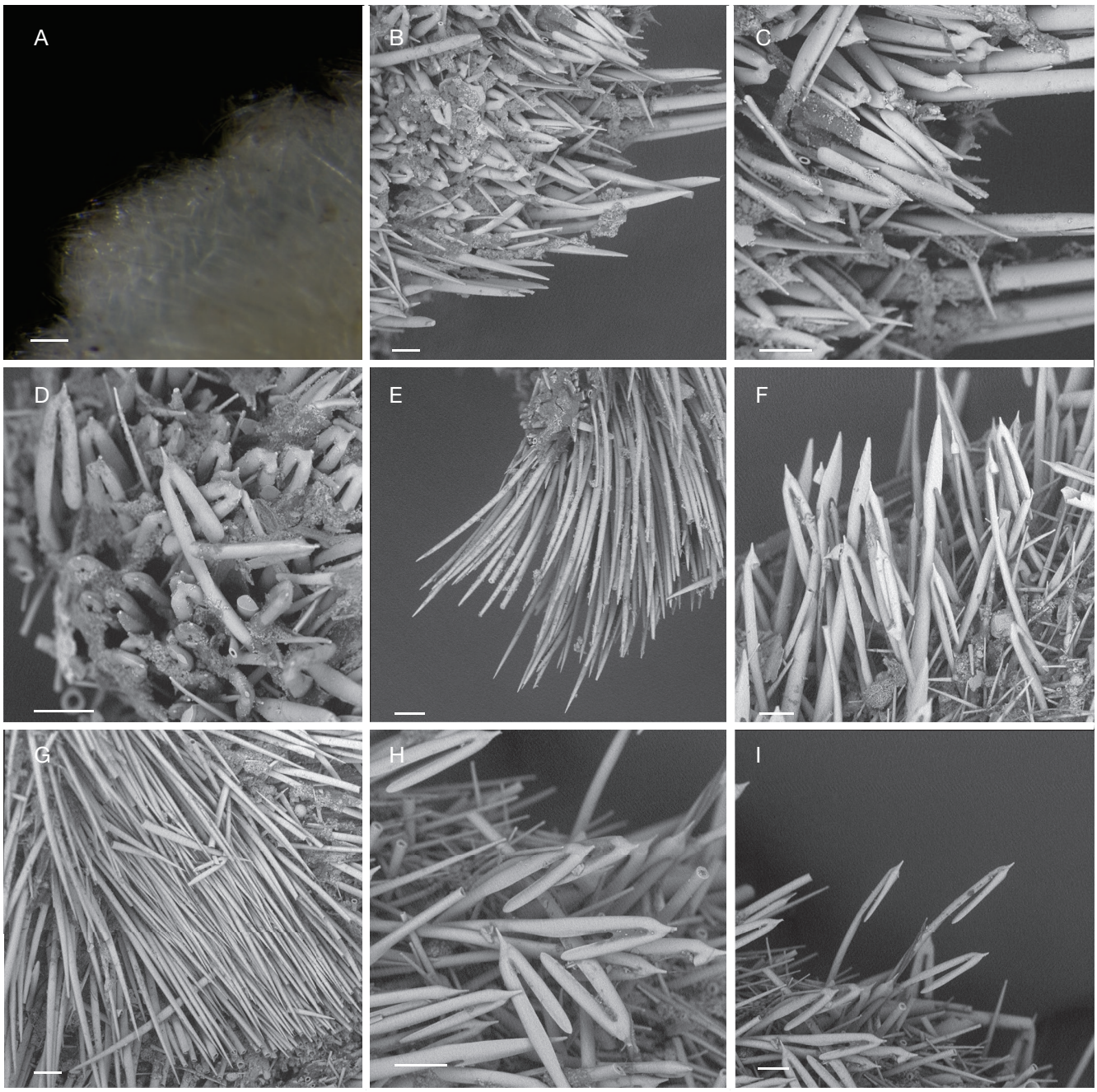

Fig. 9. — Sclerites of **A**-**E**, *Eleutheromenia sierra* (Pruvot, 1890) (MNHN-IM-2019-1749): **A**, light microscopy image of the cuticle (the dorsal keel); **B**, general view of the sclerites in the dorsal region of the body; **C**, closer view of the hook-shaped sclerites and acicular sclerites in the dorsal region of the body (**arrow**, thin sclerites; star: longer and thicker sclerites); **D**, detail of the hook-shaped sclerites; **E**, acicular sclerites in the ventral region of the body; **F**-**I**, *Uncicherpia hirsuta* (MNHN-IM-2019-18279): **F**, hook-shaped and harpoon-shaped sclerites (**star**, harpoon-shaped sclerites); **G**, acicular sclerites in the ventral region of the body; **H**, **I**, hook-shaped sclerites. Scale bars: A, 200 µm, B-I, 20 µm.

pointed out that they are very similar with the only difference in the anterior region being the atrio-buccal cavity, with the aforementioned nuances (Pruvot 1891: fig. 55). In the Corsica specimens, the mouth and atrium are partially separated (Figs 11; 12A-D) as the ridge or septum between both openings lacks a cuticular layer (Fig. 11H vs Fig. 12D). In the live animals, like Pruvot (1891), we did not observe two independent cavities, but there is a muscular septum arising from each wall of the opening in its central region (Fig. 5A', A").

The main difference between the two species is the existence of respiratory folds in *Pruvotina impexa*, whose presence was used as justification for the definition of the genus (Simroth 1893). Although the absence of respiratory folds in *Pararrhopalia pruvoti* was corroborated by a redescription of the species based on newer material (Salvini-Plawen 2008), another recent work (Pedrouzo *et al.* 2022) described folds in the mantle cavity of a specimen identified as *Pararrhopalia pruvoti* (around 10 folds; Pedrouzo *pers. comm.*). The interpre-

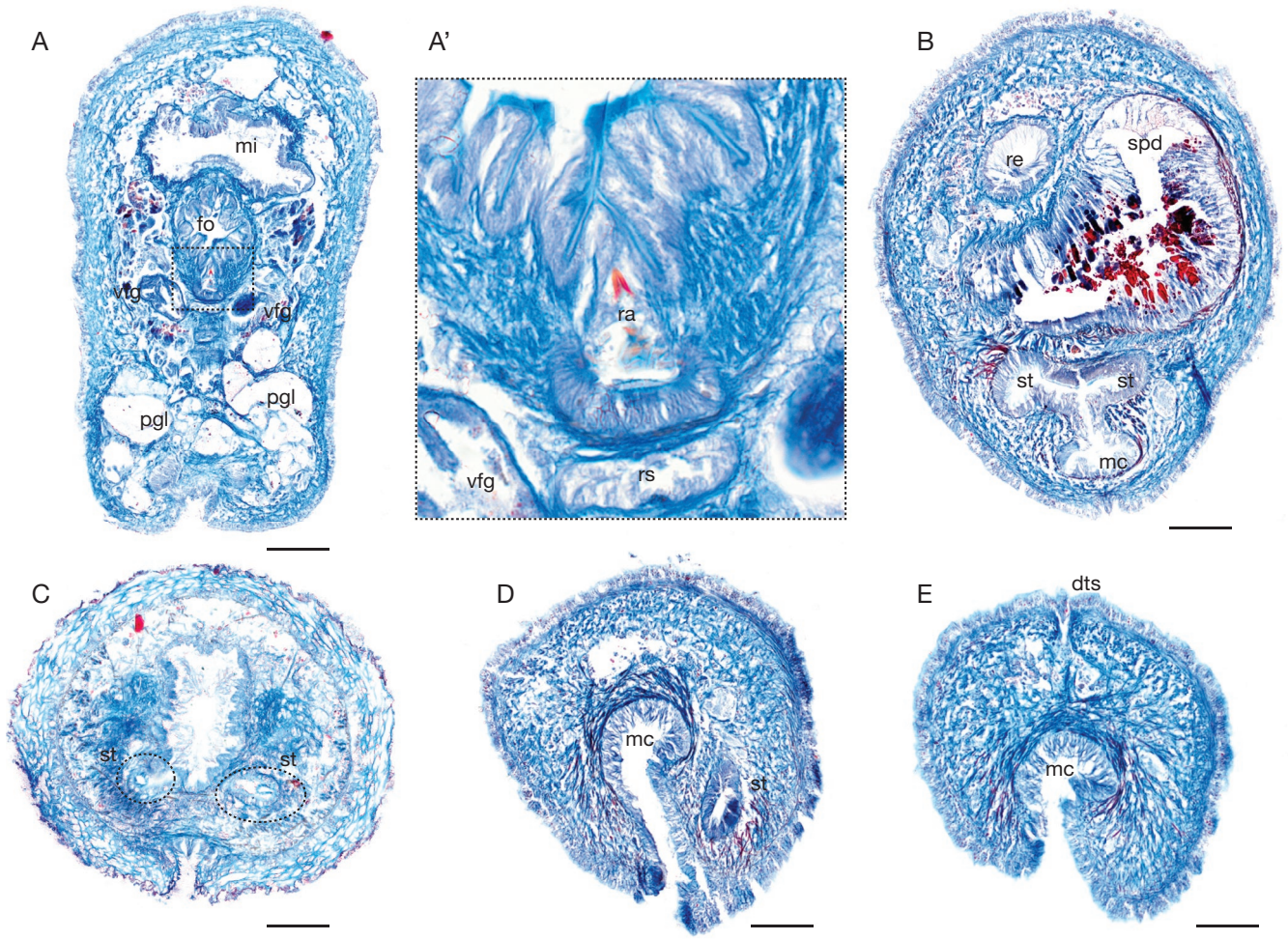

FIG. 10. — Histological sections of *Dondersia festiva* (MNHN-IM-2019-18272): **A**, radular region; **A'**, detail of the radula and radular sac; **B**, posterior region, spawning duct, and bag of the copulatory stylets; **C**, posterior section with copulatory stylets (**circled**) (MNHN-IM-2019-16169); **D**, posterior region, mantle cavity; **E**, mantle cavity and dorsoterminal sensory organ. Abbreviations: see Material and methods. Scale bars: 100 µm.

tation of these folds as respiratory organs cannot be discarded. Moreover, Pedrouzo *et al.* (2022) described a folded wall in the pallial cavity of another *Pararrhopalia* species, *P. oscari*, "without forming real respiratory folds." In addition, in the description of *Pararrhopalia fasciata*, the absence of respiratory folds is followed by a question mark (Salvini-Plawen 1978). In two of the Corsica specimens (MNHN-IM-2019-1746 and MNHN-IM-2019-18281) the respiratory folds correspond with what was described for *Pruvotina impexa* (Pruvot 1891: Plate XXV, fig. 5a). In a third specimen (MNHN-IM-2019-1748), however, the respiratory folds are not so evident. In view of this, we consider that the apparent absence of respiratory folds should be assessed with caution.

Another purported distinction between these two species involves the presumed presence of copulatory stylets in *Pararrhopalia pruvoti*, absent in *Pruvotina impexa*. Pruvot (1891) identified four specimens as "*Proneomenia vagans*" Kowalesky & Marion, 1887 (now accepted as *Dorymenia vagans*) based on the presence of copulatory stylets that Simroth (1893) later named as a new species: *Pararrhopalia pruvoti*. The putative copulatory stylets of these specimens were described as bundles of 16 spicules (Pruvot 1891; Plate XXX, fig. 60a), that differs from the rounded single and long copulatory stylets of *Dorymenia vagans* (Kowalesvky & Marion 1887: Plate V, fig. 27; fig. 14B in the present work). There is no reference to copulatory stylets or abdominal spicules in Pruvot's work concerning *Pruvotina impexa*, and thus the lack of these structures has been inferred, although his description of the animal's posterior region is incomplete (Pruvot 1891). Notably, the specimens from Corsica identified as *P. impexa* exhibit paired bundles of hard copulatory structures numbering between 12 and 16 (Fig. 12H, H'). These bundles correspond in size and position to what was called as abdominal spicules in other *Pruvotina* species, such as *P. glandulosa* (Pedrouzo *et al.* 2022) and their appearance in the serial sections and number of spicules in the bundles is comparable with the structures referred to as copulatory stylets in *P. pruvoti* (Pruvot, 1891: fig. 60a; Pedrouzo *et al.* 2022: fig. 5D) (Fig. 12H, H'). Therefore, both species have hard copulatory structures. The nomenclature for these struc-

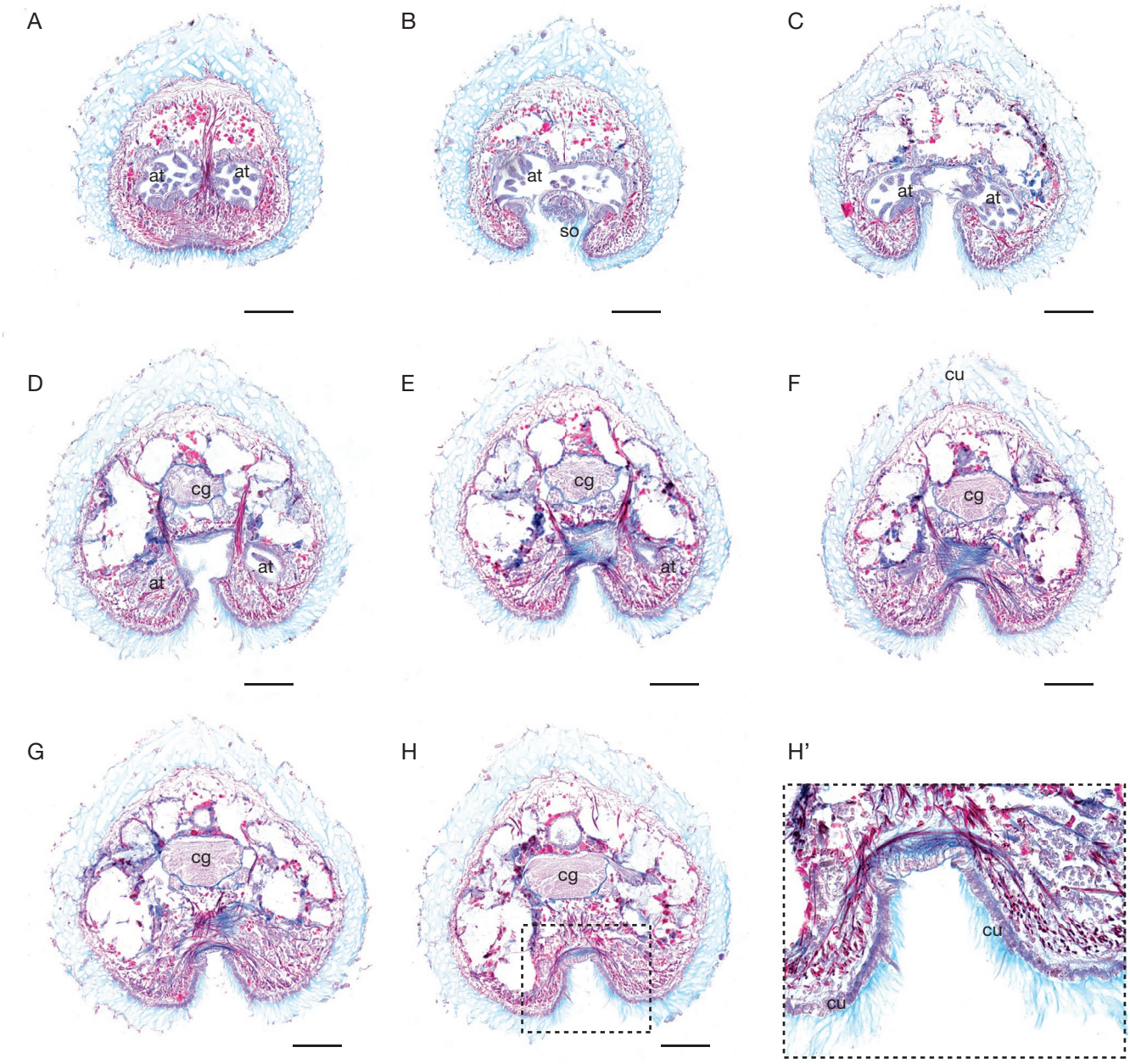

Fig. 11. — Histological sections of the anterior region of *Pruvotina impexa* (Pruvot, 1890) (MNHN-IM-2019-1746): **A-D**, atrial cavity; **E-H'**, region between the atrial opening and the mouth; **H´**, detail of the ventral region between the opening of the atrium and the mouth, without cuticular layer. Abbreviations: see Material and methods. Scale bars: 100 µm.

tures can be ambiguous. In general, abdominal spicules are short and numerous, located at both sides of the opening of the pallial cavity. Copulatory stylets, on the other hand, are longer structures, that emerge from the pallial cavity in a more central position. They are typically single or double structures but may have accessory spicules and have muscular reinforcement. For some families as for example Proneomeniidae, the distinction between these structures is clear (e.g., Scheltema *et al.* 2012). The nomenclature used in Pruvotinidae requires revision for consistency.

Besides, the external aspect of the examined specimens corresponds with the description of *Pruvotina impexa* by Pruvot (1891), particularly in the way the sclerites protrude from the cuticle in the posterior region (Pruvot 1891). This was especially evident in observations of living specimens (Fig. 5A'). There is not a previous mention of the orange color that we found in some of the animals, but this is likely because it fades after preservation. *Pruvotina impexa* is described as a white animal (Pruvot 1890), which correspond with some of our specimens (MNHN-IM-2019-18281, MNHN-IM-2019-18285). The

mantle sclerites are also comparable with Pruvot's descriptions who did not find differences between the sclerites of *Pruvotina impexa* and *Pararrhopalia pruvoti* (Pruvot 1891: fig. 5a). Nevertheless, in one of the specimens from Corsica (MNHN-IM-2019-18281), we found serrated sclerites, as Pedrouzo *et al.* (2022) did for the specimen they identified as *Pararrhopalia pruvoti*. The hook-shaped sclerites with the longer, narrower, and distally curved distal region of the hook, which were very abundant in the Corsica specimens, were not described before. We attribute this to the fact that the thinner region is easily broken when scraping sclerites onto microscope slides (as we have seen in our own optical microscope slides produced for this species).

Taken together, and especially considering the respiratory folds and habitus, the identification of the specimens from Corsica as *Pruvotina impexa* is certain. However, our redescription adds important details for the species (hard copulatory structures and observations of the habitus), highlighting overlap in the diagnostic characters of *Pruvotina impexa* and *Pararrhopalia pruvoti.* Therefore, more studies comparing the two species are needed, including molecular analysis. Especially significant, because of their importance to pruvotinid taxonomy, is the need of a better understanding of the respiratory folds and copulatory stylets / abdominal spicules.

Pruvotina impexa was described from Banyuls-sur-Mer (South of France, Mediterranean Sea) and collected at 80 m depth (Pruvot 1890, 1891). With the specimens included in this work we add a new location and depths (60-70 m) for the species in the Mediterranean Sea.

Subfamily Eleutheromeniinae Salvini-Plawen, 1978

Genus *Eleutheromenia* Salvini-Plawen, 1967

Type species. — *Eleutheromenia sierra* (Pruvot, 1890). Costa Brava (Spain, Mediterranean Sea); 80 m. Type material missing.

Eleutheromenia sierra (Pruvot, 1890)

Paramenia sierra Pruvot, 1890: XIII.

Eleutheromenia sierra – Salvini-Plawen 1967: 398.

Eleutheromenia carinata Salvini-Plawen & Öztürk, 2006: 220, **n. syn.**

Gephyroherpia impar Zamarro, García-Álvarez & Urgorri, 2013: 435, **n. syn.**

Material examined. — **Corsica** (France) • 1 specimen (used for sclerite preparations, histology, and DNA extraction); CORSICA-BENTHOS 2 (Table 2); 40 m depth; MNHN-IM-2019-1749; GenBank: OR456216; OR458913 (1 microscope slide with sclerites, 1 SEM stub; 15 slides with 5 µm serial sections).

Description

White animal, elongate body (12 × 1.5-2.5 mm) with a median discontinuous serrated keel, with at least 17 lobes (Fig. 4B; 9A). Hollow sclerites somewhat protruding from the cuticle. With one type of hook-shaped sclerite (80-120 × 8 µm; the inner part of the hook is 30 µm long) (Fig. 9B, C, D) and acicular sclerites of different sizes: big and slightly curved sclerites (160-180 × 8 µm) (Fig. 9B); curved and thin sclerites (80-100 × 3-4 µm); straight and long acicular sclerites (190-210 × 6-7 µm), the latter mostly located in the ventral region of the body (Fig. 9E). Hook-shaped sclerites in the ventral region of the body. Hook-shaped sclerites occupying the sides of the dorsal lobes, with some thin acicular sclerites among them. Bigger curved acicular sclerites at the apical regions of the lobes (Fig. 9A). With knife-shaped scales of the pedal groove (80 × 25 µm). Atrium with single and paired atrial papillae (Fig. 13A), divided into three parts in its posterior region. Mouth and atrium separated by a muscular wall without cuticle (Fig. 13B). With a single pedal fold. Ventrolateral foregut glands of type A / *Pararrhopalia* type (Fig. 13D). With a distichous radula formed by hook-shaped teeth without medial denticles (Fig. 13D, D'). Very glandular esophagus. Midgut with an antero-dorsal caecum (Fig. 13D) and lateral constrictions. With respiratory folds (Fig. 13G). With seminal vesicles (Fig. 13E, E'). With abdominal spicules in a pair of ventral pouches of the mantle cavity (Fig. 13F).

Remarks

The specimen was placed in the subfamily Eleutheromeniinae Salvini-Plawen, 1978 based on its resemblance to three known species of the subfamily that also have a discontinuous serrated keel: both species of *Eleutheromenia* (*E. sierra* (Pruvot, 1890) and *E. carinata* Salvini-Plawen & Öztürk, 2006) and *Gephyroherpia impar* Zamarro, García-Álvarez & Urgorri, 2013. The classification within this subfamily is also justified by the presence of hook-shaped sclerites, ventrolateral foregut glands of type A and the absence of a dorso-pharyngeal papilla gland (García-Álvarez & Salvini-Plawen 2007) (Table 4).

The specimen from Corsica has a keel with clearly differentiated lobes, at least 17, mostly in the anterior region of the body, that were more easily distinguishable when the animal was alive. The serial sections reveal a separation between the lobes as described by Salvini-Plawen (2003) for *E. sierra*. The keel of *E. sierra* has been reported to consist of between 15 and 16 lobes (Pruvot 1890; Salvini-Plawen 2003: fig. 11). In *E. carinata* the keel is continuous but the lobes "vary somewhat in height" (Salvini-Plawen & Öztürk 2006: fig. 2). The keel in *G. impar* was described as "continuous that varies somewhat in its height along its course and shows, in the medial body region, 10 lobulations," although in the image of the holotype at least 15 lobes can be distinguished (Zamarro *et al.* 2013: fig. 8). We observed that the lobes in the Corsica specimen are less evident after fixation and thus the external aspect can be compared with all three species mentioned here. The observed differences in the keel among the three species may be due to the preservation of the specimens.

In the specimen from Corsica, we did not observe serrated sclerites, described for the *Eleutheromenia* species but not in *G. impar* (Zamarro *et al.* 2013: fig. 8). We did find harpoon-shaped sclerites (Fig. 9F), described for *E. carinata* (Salvini-Plawen 2003; fig. 8b) but not *E. sierra* (Salvini-Plawen & Öztürk 2006: fig. 3) or *G. impar* (Zamarro *et al.* 2013: fig. 8).

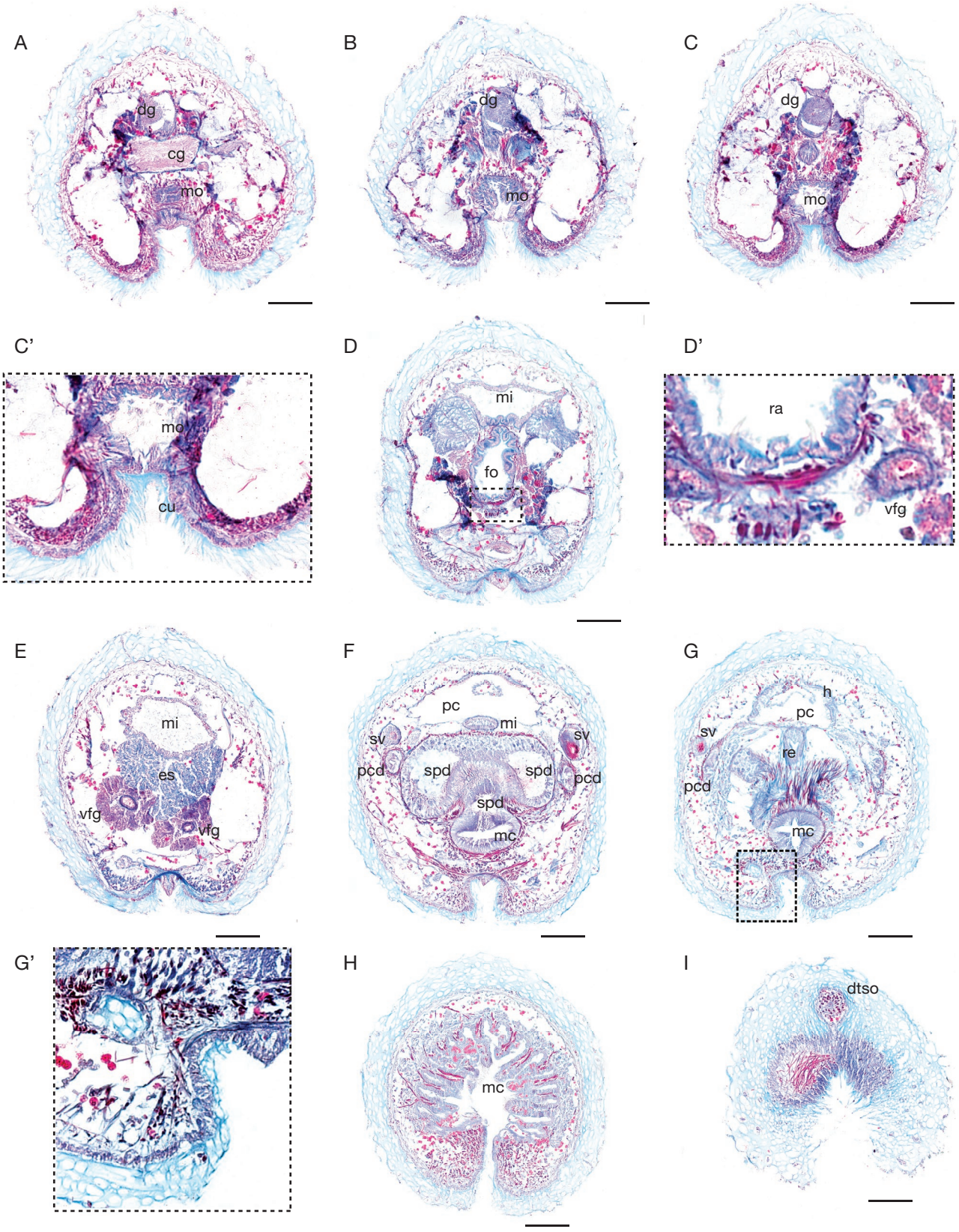

FIG. 12. — Histological sections of *Pruvotina impexa* (Pruvot, 1890) (MNHN-IM-2019-1746) **A**-**E**, anterior region (continuation of Fig. 11): **A**-**C**, mouth and dorsal gland; **C'**, detail of the ventral cuticle between the opening of the mouth and the pedal pit; **D**, radular region of the foregut; **D'**, detail of the radula; **E**, section of the glandular esophagus; **F**, **G**, posterior region: **F**, mid region of the spawning duct; **G**, section of the abdominal spicules; **G'**, detail of the abdominal spicules; **H**, respiratory folds; **I**, posterior region of the body with the dorsoterminal sensory organ. Abbreviations: see Material and methods. Scale bars: 100 µm.

The lack of observation of a specific type of sclerites, such as the serrated acicular sclerites, may be because SEM images or sclerite preparations were obtained from a region of the body where that type does not occur. Our SEM images were taken only from a small piece of the mid-body region, for example. In addition to the study of the mid body region sclerites under SEM, we prepared sclerites from other body regions by dislodging them with a thin needle in an attempt to observe any body region-specific sclerite types, but it is of course possible that particularly rare or fragile sclerite types were missed. Therefore, a thorough study of additional specimens would be desirable. Given the impossibility of differentiating these three Eleutheromeniidae species based on the sclerites and keel, it is necessary to study the internal anatomy.

Regarding the anterior internal anatomy, *Gephyrohepia* and *Eleutheromenia* (García-Álvarez & Salvini-Plawen 2007) are distinct as the atrium and mouth are separate in *Gephyrohepia* while *Eleutheromenia* species have an atrio-buccal cavity (Pedrouzo *et al.* 2022). In the Corsica specimens mouth and atrium are partially separated. As discussed above for the subfamily Pruvotininae, the atrio-buccal cavity is also an ambiguous character in Eleutheromeniidae. The reconstructions included in the original descriptions of *E. carinata* (Pruvot 1891: fig. 16) and *E. sierra* (Salvini-Plawen & Öztürk 2006: fig. 4) show the mouth opening into the posterior part of the atrium, but Salvini-Plawen (2003), in the description of a specimen identified as *E. sierra*, states that "mouth opening in the dorso-posterior area of the common atrio-buccal cavity, connected with the sensory region by a groove (ridge)." According to the original descriptions of *G. antarctica* and *G. impar*, the mouth is separated from the atrium by a cuticularized ridge with musculature (Salvini-Plawen 1978; Zamarro *et al.* 2013). Nevertheless, Salvini-Plawen describes this ridge in *G. antarctica* Salvini-Plawen, 1978 as "a tegumental ridge without spicules". In the same way, a cuticle with sclerites is not evident in the section of *G. impar* presented by Zamarro *et al.* (2013: fig. 10a, b) and the separation between the two cavities is consistent with what we have observed in the sections of the Corsica specimen (Fig. 12B), which lacks cuticle and sclerites in this area. The specimen from Corsica shares other anterior internal characteristics with *G. impar* (Zamarro *et al.* 2013) that are all comparable with what was described also for both *E. sierra* and *E. carinata* (Salvini-Plawen & Öztürk 2006): atrium posteriorly trilobed; central region of the atrium forming a blind pouch with single or paired atrial papillae; one pedal fold; hooked radula teeth without medial denticles; glandular esophagus; unpaired antero-dorsal midgut caecum. The only distinctive posterior characteristic of *G. impar* compared with *E. sierra* and *E. carinata* is the lack of abdominal spicules (Pruvot 1890; Salvini-Plawen & Öztürk 2006; Zamarro *et al.* 2013). In the Corsica specimen there are abdominal spicules (Fig. 12F) and their shape and position correspond with those described in both *E. sierra* and *E. carinata* (Salvini-Plawen 2003; Salvini-Plawen & Öztürk 2006). However, although not described for *G. impar*, the internal reconstruction of the holotype of this species shows a ventro-anterior pouch of the pallial cavity (Zamarro *et al.* 2013: fig. 9b) that corresponds with the position of the abdominal spicules in both *Eleutheromenia* species (Salvini-Plawen 2003; Salvini-Plawen & Öztürk 2006) and in *G. antarctica* (Salvini-Plawen 1978). Finally, the presence of epidermal papillae is a diagnostic character for the genus *Gephyroherpia* (Salvini-Plawen 1978) whereas the diagnosis of *Eleutheromenia* indicates the absence of these structures. In studying the available images of sections of *G. impar*, we did not observe epidermal papillae (Zamarro *et al.* 2013; fig. 10). There are no epidermal papillae in the Corsica specimen.

Considering all the above, it is not possible to make a distinction between *G. impar* and *E. sierra* based on anatomy. Furthermore, the only clear difference between *E. sierra* and *E. carinata* is the length of the paired region of the spawning duct and the exact position of its opening in the mantle cavity (Salvini-Plawen & Öztürk 2006), but the description of *E. carinata* was based on a juvenile. Therefore, we propose the synonymy of *E. sierra*, *E. carinata* and *G. impar* Consequently, the specimen from Corsica is identified as *E. sierra*. In addition, the phylogenetic analysis of COI and the results of both species delimitation methods (Fig. 2) indicate that the Corsica specimen is the same species as a specimen from Norway identified as *E. sierra*. Therefore, and considering that the separation between atrium and mouth is not a good diagnostic character, we propose a new classification for the subfamily Eleutheromeniinae: *Eleutheromenia* Salvini-Plawen, 1978 including *E. sierra* and *E. antarctica* n. comb. for *G. antarctica* Salvini-Plawen, 1978 and the monospecific genus *Luitfriedia* García-Álvarez & Urgorri, 2001 (with *L. minuta* García-Álvarez & Urgorri, 2001) differing by the lack of radula.

Given the synonymy proposed here, the distribution of *E. sierra* is extended and includes Portaló Island, Cabo de Creus (Spain), Bay of Izmir (Turkey) and Corsica Island (France) in the Mediterranean Sea (40-75 m depth) and the NW of the Iberian Peninsula in the Atlantic Ocean (598 m depth) (Salvini-Plawen & Öztürk 2006; Zamarro *et al.* 2013; García-Álvarez *et al.* 2014). As previously collected specimens, the specimen from Corsica was collected from a sandy bottom.

Subfamily Unciherpiinae García-Álvarez, Urgorri & Salvini-Plawen, 2001

Genus *Unciherpia* García-Álvarez, Urgorri & Salvini-Plawen, 2001

Type species. — *Unciherpia hirsuta* García-Alvarez, Urgorri & Salvini-Plawen, 2001. NW Atlantic (Banco de Galicia, NW Iberian Peninsula); 760-769 m.

Unciherpia hirsuta García-Álvarez, Urgorri & Salvini-Plawen, 2001

Unciherpia hirsuta García-Álvarez, Urgorri & Salvini-Plawen, 2001: 114.

Material examined. — **Corsica** (France) [4 specimens] • 1 specimen (used for sclerite preparations, histology, and DNA extraction); CORSICABENTHOS 3 (Table 2); 122 m depth; MNHN-IM-2019-18279;

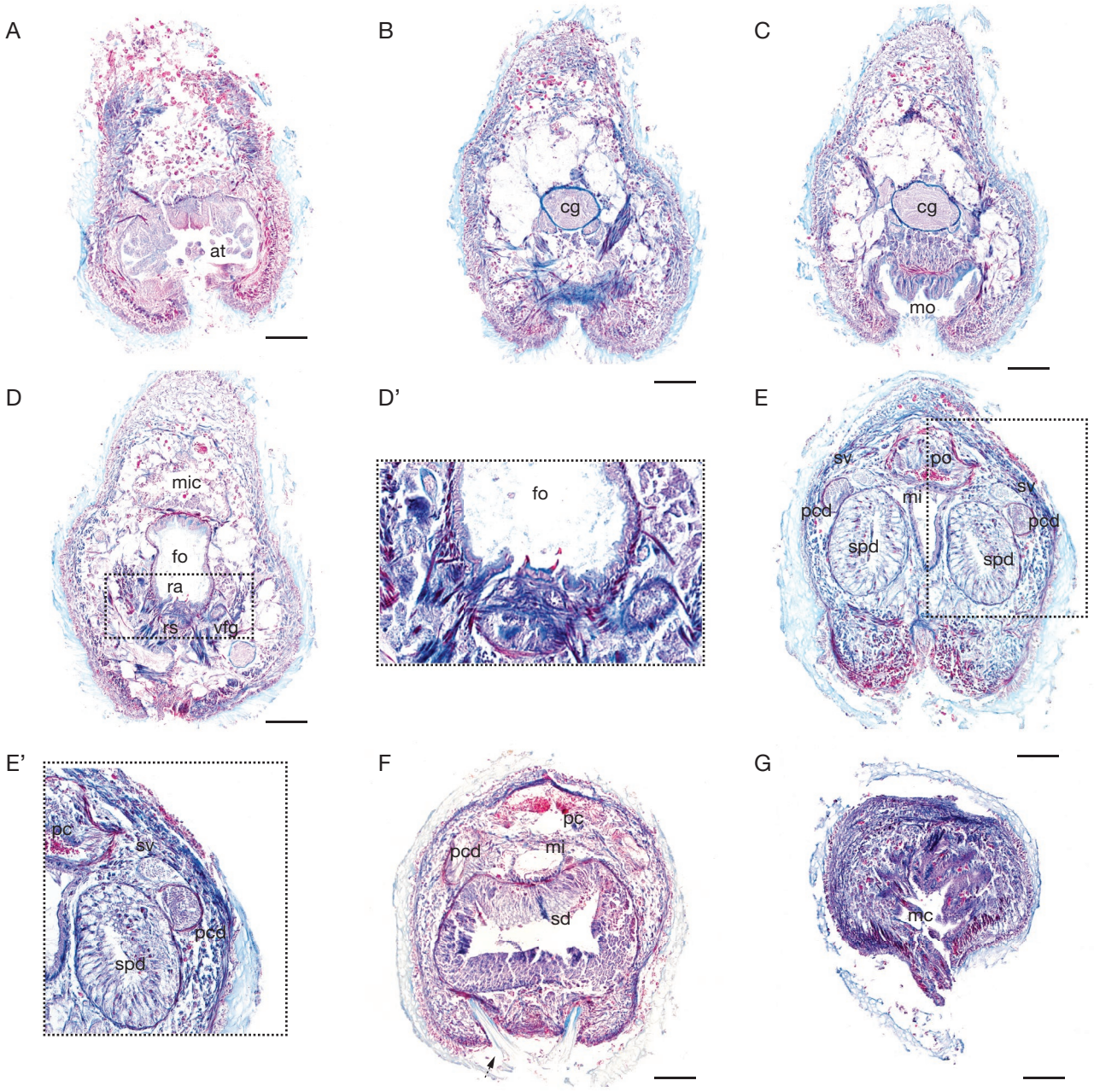

FIG. 13. — Histological sections of the anterior region of *Eleutheromenia sierra* (Pruvot, 1890) (MNHN-IM-2019-1749): **A**, atrial cavity; **B**, region between the atrial opening and the mouth, without ventral cuticle; **C**, opening of the mouth; **D**, radular region of the foregut; **D'**, detail of the radula; **E**, paired region of the spawning duct; **E'**, detail of the seminal vesicles; **F**, fused region of the spawning duct. ; **G**, opening of the mantle cavity with respiratory folds. Abbreviations: see Material and methods. Symbol: **Arrows** indicate the outlet of the abdominal spicules Scale bars: 100 µm.

GenBank: OQ600031; OQ597875 (1 microscope slide with sclerites, 1 SEM stub; 4 slides with 5 µm serial sections) • 3 specimens (preserved in 95% ethanol); CORSICABENTHOS 3 (Table 2); 122 m depth; MNHN-IM-2019-18282, MNHN-IM-2019-18283, MNHN-IM-2019-18284.

DESCRIPTION

Animals with elongate body (10-15 mm × 0.8-2 mm), without keels or protuberances and with the anterior region wider than the posterior. White to yellow with a strongly hirsute appearance (Fig. 4D). With hollow acicular sclerites: long straight acicular sclerites (200-300 × 5-6 µm) (Fig. 9G); acicular sigmoid sclerites (120-160 × 5-7 µm); straight and long sclerites with harpoon-shaped distal end (360-520 × 8-14 µm) (Fig. 9F); serrated acicular sclerites (230-300 × 8-10 µm) only in the anterior half of the body; and hook-shaped sclerites (150-180 × 7-9 µm) (Fig. 9H-I). With one type of knife-shaped scales of the pedal groove (75-85 × 12 -14 µm). Mouth opening at the posterior end of the atrial cavity. Without radula. With 16 circum-pharyngeal subepithelial follicular glands (Fig. 14A).

Remarks

Within Pruvotinidae, the subfamily Unciherpiinae García-Álvarez, Urgorri & Salvini-Plawen, 2001 is characterized by the absence of a radula and by having circum-pharyngeal follicular glands instead of ventrolateral foregut glands (García-Álvarez *et al.* 2001; García-Álvarez & Salvini-Plawen 2007; Pedrouzo *et al.* 2022) (Table 4). The three genera in this subfamily, all of which are represented by a single described species, can be differentiated based on the sclerites. *Uncimenia* Nierstrasz, 1903 and *Unciherpia* have harpoon-shaped and hook-shaped sclerites, but the hook-shaped sclerites lack an apical prominence in *Uncimenia*. *Sialoherpia* Salvini-Plawen, 1978 lacks hook-shaped sclerites and has solid, acicular sclerites (Salvini-Plawen 1978; García-Álvarez *et al.* 2001). The specimen from Corsica was identified as *Unciherpia hirsuta* based on the external aspect and sclerites (García-Álvarez *et al.* 2001: fig. 1; Pedrouzo *et al.* 2014: fig. 2). In addition, this identification was confirmed by the study of the internal anatomy: common atrio-buccal cavity, 16 follicular glands surrounding the pharynx (Fig. 14A), midgut with a short, paired rostral caecum, respiratory folds and one dorso-terminal sensory organ (García-Álvarez *et al.* 2001; Pedrouzo *et al.* 2014).

The known geographical distribution of *U. hirsuta* includes several localities near the type locality (NW Iberian Peninsula) (García-Álvarez *et al.* 2001; Pedrouzo *et al.* 2019) and the Alboran Sea (Mediterranean Sea) (Pedrouzo *et al.* 2014). The Atlantic specimens were found at depths between 760 and 1499 m (García-Álvarez *et al.* 2001; Pedrouzo *et al.* 2014) while the specimen collected in the Alboran Sea was found at a greater depth (349-365 m) (Pedrouzo *et al.* 2014). The specimens from Corsica were collected at 122 m in sandy bottoms, which corresponds in terms of habitat with previous localities in which the species was found (García-Álvarez *et al.* 2014).

Family Rhopalomeniidae Salvini-Plawen, 1978

Genus *Pruvotia* Thiele, 1894 (position uncertain)

Type species. — *Pruvotia sopita* (Pruvot, 1891). Banyuls-sur-Mer (France) ; 45-70 m.

Pruvotia cf. ***sopita*** (Pruvot, 1891)

Proneomenia sopita Pruvot, 1891: 721.

Pruvotia sopita – Thiele 1913: 273.

Material examined. — **Corsica** (France) • 1 specimen (used for sclerite preparations and DNA extraction); CORSICABENTHOS 2 (Table 2); 80 m depth; MNHN-IM-2019-1744; GenBank: OR456214; OR458908 (1 microscope slide with sclerites, anterior and posterior regions preserved in 95% ethanol).

Description

Small white animal (7 × 1-1.5mm) with the anterior region slightly wider than the posterior one, rounded ends (Fig. 4C). With hollow acicular sclerites (80-100 × 6-8 µm) (Fig. 8K, L). Sclerites barely protruding from cuticle. Found on *Sertularella* sp. (Hydrozoa).

Remarks

The tentative identification of the specimen as *Pruvotia sopita* is based on its external appearance and the way it is attached to the *Sertularella* sp. colony. The habitus of the Corsica specimen, characterized by a small, white body, and the absence of coiling around its host but rather attachment solely at the anterior region of the body to the hydrozoan branches, closely mirrors the description provided by Pruvot (1891) for *Pruvotia sopita*. This resemblance is further sustained by our own observations of this species (Castro-Claros *et al.* pers. comm.). Histology was not performed due to the specimen's small size and the fact that it was damaged. Consequently, our identification relies on these characteristic external features. Interestingly, our phylogenetic analysis recovers the Corsica specimen well within Pruvotinidae with strong support (bootstrap support: 92%; Fig. 2). Confirmation of the identification of this specimen as *Pruvotia sopita* would necessitate a reevaluation of not only *Pruvotia*'s classification within Rhopalomeniidae but also of the monophyly of Pruvotinidae with respect to Rhopalomeniidae.

Family Simrothiellidae Salvini-Plawen, 1978

Genus *Simrothiella* Pilsbry, 1898

Type species. — *Simrothiella margaritacea* (Koren & Danielssen, 1877). Boknfjord (Norway); 75-115 m.

Simrothiella margaritacea (Koren & Danielssen, 1877)

Solenopus margaritaceus Koren & Danielssen, 1877: 120.

Material examined. — **Corsica** (France) • 3 specimens (anterior and posterior regions of the specimens preserved in 95% ethanol. Middle regions used for sclerite preparations and DNA extractions); CORSICABENTHOS 3 (Table 2); 122 m depth; MNHN-IM-2019-18280; GenBank: OR456220; OR458918 (1 microscope slide with sclerites, 1 SEM stub); MNHN-IM-2019-18287; GenBank: OR456221; OR458921 (1 microscope slide with sclerites); MNHN-IM-2019-18286); GenBank: OR458920 (1 microscope slide with sclerites).

Description

Elongate animal (15 × 1.5-2 mm). With rounded ends, the anterior end being slightly wider than the posterior. White to cream color (Fig. 4E). Cuticle relatively thin with hollow acicular sclerites slightly curved (160 -200 × 3-4 µm) (Fig. 7F) intersecting in two or three layers giving a characteristic hirsute appearance.

Remarks

The external aspect and sclerites of these three Corsica specimens are distinctive from of Simrothiellidae species and correspond with *Simrothiella margaritacea* (Scheltema & Schander 2000;

fig. 11, 20; Zamarro *et al.* 2016: fig.1). For the identification of this species, the DNA barcodes were decisive as there were previously available sequences for this species (Fig. 2). Sequences from the Corsica *Simrothiella* specimens closely matched available ones for this species, and therefore supported our identification. This is important given the existence of at least one undescribed look-alike species for which sequence data are also publicly available. This demonstrates that further development of a DNA barcode library with sequences from confidently identified specimens is essential to improve the accuracy and speed of the identification process in solenogasters (Bergmeier *et al.* 2017), a group for which numerous "known unknowns" are waiting to be formally described (Todt 2013).

The type locality of *S. margaritacea* is Boknfjord (Norway) and it has been collected in Norwegian waters (75-115 m) and the NW of the Iberian Peninsula (800 m) (Zamarro *et al.* 2016) (Table 1). With these three specimens from Corsica, the geographical distribution of *S. margaritacea* is extended to the Mediterranean Sea (122 m).

Family Strophomeniidae Salvini-Plawen, 1978

Genus *Anamenia* Nerstrasz, 1908

Type species. — *Proneomenia amboinensis* Thiele, 1902. Ambon Island (NW Pacific); unknown depth.

Anamenia gorgonophila (Kowalesky, 1880)

Neomenia gorgonophila Kowalevsky, 1880: 190.

Anamenia gorgonophila – Nierstrasz 1908: 11.

Material examined. — **Corsica** (France) • 1 specimen (used for sclerite preparations, DNA extraction and histology); CORSICABENTHOS 3 (Table 2); 50 m depth; MNHN-IM-2019-18270; GenBank: OR456217; OR458914 (1 microscope slide with sclerites, 44 slides with 5 µm serial sections).

Description

Relatively large animal (30 × 2 mm), without keels or protrusions and with rounded body ends. Brown (Fig. 3B) to a lighter yellowish color after fixation (Fig. 3B'). Sclerites hollow, acicular, slightly curved and with a wide variety of sizes (125-325 × 18-20 µm). Knife-like scales of the pedal groove (80-90 × 30-40 µm). Foregut very glandular in its anterior region (Fig. 14C). Radula with two transverse rows (Fig. 14D, D') bearing around seven denticles each. Ventrolateral foregut glands of type B / *Imeroherpia* type (Fig. 14D, D'). With abdominal spicules (Fig. 14E) and one dorso-terminal sensory organ.

Remarks

This is a commonly encountered species that is easy to identify based on external aspect and habitus, as it is frequently found coiled on corals. The specimens studied here were found on a colony of *Paramuricea* sp. (Anthozoa, Octocorallia) (Fig. 3B) at a depth of 50 m, which corresponds to the information available for the species, that can be found epizootic on several species of octocorals in depths between 60 and 900 m (compiled in García-Álvarez *et al.* 2014). This together with the external appearance (animals up to 20 mm long, brownish, or yellow) and the sclerites (long acicular sclerites, and knife-shaped scales in the pedal groove region) facilitated the identification. The information obtained from the histological sections also corresponds with what was previously described (Thiele 1902; Pedrouzo *et al.* 2014; Martínez-Sanjuán *et al.* 2022). With the specimen included here, we expand its known distribution in the Mediterranean Sea.

Family Proneomeniidae Simroth, 1893

Genus *Dorymenia* Heath, 1911

Type species. — *Dorymenia acuta* Heath, 1911. Holotype: Santa Barbara Islands (California, USA) (Albatross St. 4415); 550-1150 m.

Dorymenia vagans (Kowalevsky & Marion, 1887)

Proneomenia vagans Kowalevsky & Marion, 1887: 29.

Dorymenia vagans – Nierstrasz & Strork 1940: 15.

Material examined. — **Corsica** (France) [6 specimens] • 2 specimens (used for sclerite preparations, DNA extractions and histology); CORSICABENTHOS 3 (Table 2); 50 m depth; MNHN-IM-2019-18271; GenBank: OR456218; OR458915 (1 microscope slide with sclerites, 23 slides with 5 µm serial sections); MNHN-IM-2019-18272; GenBank: OR458906 (1 microscope slide with sclerites, 9 slides with 5 µm serial sections) • 4 specimens (preserved in 95% ethanol); CORSICABENTHOS 3 (Table 2); 50 m depth; MNHN-IM-2019-18274, MNHN-IM-2019-18275, MNHN-IM-2019-18276, MNHN-IM-2019-18278.

Description

Robust animal (5-6 × 1.5-2 mm) (Fig. 3D), with a slightly pointed posterior end, but without a clear digitiform projection. Brownish to yellow. With a thick cover of hollow acicular sclerites (120-260 × 18-20 µm) (Fig. 7H). With longer and slightly distally flattened sclerites (125-200 × 20-22 µm) and knife-like scales next to the pedal groove (84 × 40 µm) (Fig. 7H). Polyserial radula with 14 teeth per row, the two central teeth being wider than the laterals. With a pair of large copulatory stylets (Fig. 14B) and two bundles of abdominal spicules. Opening of the mantle cavity narrow and elongate. With one dorso-terminal sensory organ (Fig. 14B), not visible externally.

Remarks

Based on their external aspect and the proximity of the collection locality to the type locality of *Dorymenia vagans* (Kowalevsky & Marion 1887), these six specimens were tentatively identified as belonging to this species. Nevertheless, there are two species of "Proneomeniidae" Simroth, 1911 (non-monophyletic according to Kocot *et al.* 2019 and Cobo *et al.* 2023) known from the Mediterranean Sea: *Dorymenia vagans*

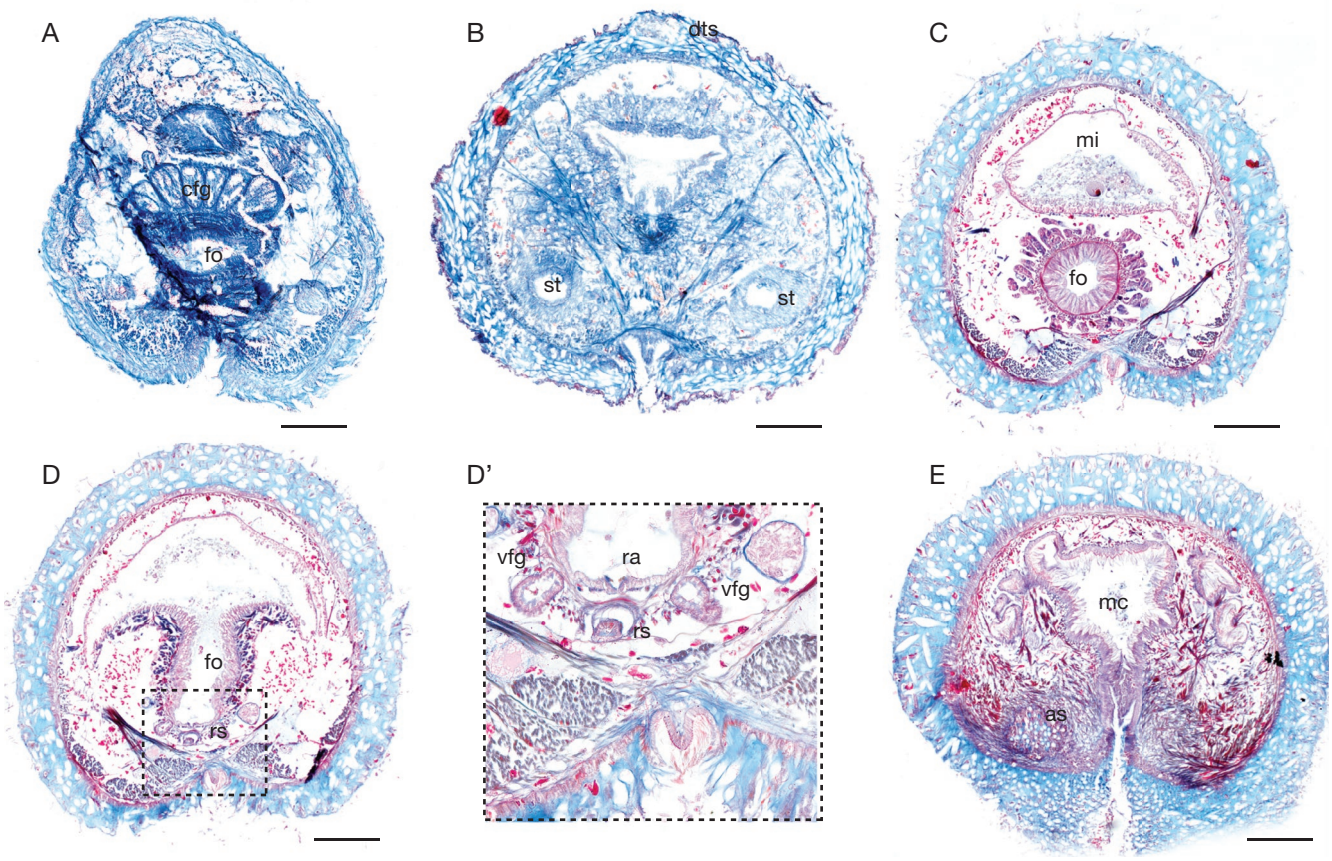

FIG. 14. — Histological sections of **A**, *Unciherpia hirsuta* (MNHN-IM-2019-18279): circumpharyngeal glands and **B**, *Dorymenia vagans* (MNHN-IM-2019-18271): copulatory stylets; **C**-**E**, *Anamenia gorgonophila* (MNHN-IM-2019-18270): **C**, anterior foregut region; **D**, radular region; **D'**, detail of the radula, radular sac and ventrolateral foregut glands; **E**, oblique section of posterior region with abdominal spicules visible on the animal's right side. Abbreviations: see Material and methods. Scale bars: 100 µm.

and *Proneomenia desiderata* Kowalevsky & Marion, 1887. These species have a similar distribution and almost identical external aspect. DNA barcoding was useful in this case to confirm the classification of the Corsica specimen in the genus *Dorymenia*. Moreover, the existence of copulatory stylets and the general configuration of the internal anatomy corresponds with what was described for *D. vagans* (Kowalevsky & Marion 1887; Nierstrasz & Stork 1940; García-Álvarez *et al.* 2009), confirming the initial identification based on the habitus.

The four specimens collected in Corsica (50-56 m) extend the distribution of *D. vagans* in the Mediterranean Sea. This species was first described from Marseille (France) from a depth of 20 m and a neotype was established from the Gulf of Naples (Italy) from a depth of 20-60 m (Nierstrasz & Stork 1940). As was the case for the Corsica specimens, the species was collected before from sandy bottoms with *Posidonia* (Nierstrasz & Stork 1940; García-Álvarez *et al.* 2009).

Solenogastres diversity and distribution off Corsica

This work includes the first records of solenogasters species in Corsica (Mediterranean Sea), extending the geographical and depth range of nine Mediterranean species and constitutes the first record of *Simrothiella margaritacea* in this area. With this and the proposed synonymy between *Eleutheromenia sierra* and *E. carinata*, the number of known Mediterranean species remains at 31.

Based on the study of the available collection (47 specimens) we identified ten different species occurring off Corsica. The samples came from three expeditions around Corsica sampling the North, South and West coast of the island (Fig. 1). Solenogasters were collected in 11 sampled stations during CORSICABENTHOS 1 (23 specimens belonging to four species), six stations during CORSICABENTHOS 2 (six specimens, four species) and five stations during CORSICABENTHOS 3 (18 specimens, six species) (Table 2). The number of specimens collected at each station was homogeneous, with only one specimen recovered at most stations, regardless of the sampling method. Although there are exceptions (Table 2) and stations CP07, with eight specimens collected, CS24 with seven and station CS83, with six specimens, stand out (Table 2). *Dondersia festiva* is the most abundant species off Corsica according to our data, with 19 specimens collected in two of the expeditions, followed by *Pruvotina impexa* with seven, *Dorymenia vagans* with six specimens and *Unciherpia hirsuta* with four (Fig. 1; Table 3). On the contrary, for four of the species only one specimen was collected (*Tegulaherpia* cf. *myodoryata*, *Pruvotia* cf. *sopita*, *Eleutheromenia sierra* and *Anamenia gorgonophila*).

DISCUSSION

This work improves our understanding of the diversity and distribution of Mediterranean solenogasters with the first record of solenogasters off Corsica. An in-depth study of available material from the "Our Planet Reviewed" Corsica expeditions leads to the recognition of ten distinct species (Table 3). Eight of the species were already known from other Mediterranean areas (Table 1) thus their geographical distribution is extended. In addition, *Simrothiella margaritacea* was found for the first time in the Mediterranean Sea. The extended distribution of *Simrothiella margaritacea*, which resembles that of several species with a Mediterranean – NW Atlantic distribution (Table 1), shows how new records of already described species can be highly valuable to understanding the distribution of these molluscs, which can be broader than initially expected. Nonetheless, it would be interesting to obtain further samples of some of these species to study potential differences between the different localities, both in terms of morphology and molecular data. This demonstrates that there is still diversity to be discovered, even in well-studied areas such as the Mediterranean Sea.

The external aspect (habitus) was a determining factor in the confident identification of seven of the species, all of which were confirmed by DNA barcoding or the study of the internal anatomy. For two of the species (*Tegulaherpia* cf. *myodoryata* and *Pruvotia* cf. *sopita*), further studies on the family with updated morphological descriptions and including molecular data are necessary. For seven of the specimens, combined analysis of the sclerites and DNA barcodes did not provide sufficient information to classify them more specifically than to the family level (Pruvotinidae Heath, 1911). Several genera within Pruvotinidae have characteristic hook-shaped sclerites. This was the case for all the Pruvotinidae (and one purported Rhopalomeniidae) specimens collected off Corsica, which made it easy to identify them to the family level. However, to be able to classify them into a subfamily or genus, it was necessary to also study the internal anatomy. This (along with DNA barcoding) proved particularly important in one case where we identified four distinct morphospecies based on externally visible characters, whereas the analysis of internal anatomy in combination with species delimitation methods based on COI revealed that all were in fact the same species (*Pruvotina impexa*). This result highlights the potential for researchers to be misled when establishing species hypotheses based on differences in coloration among live specimens, which may be affected by colored gut contents, and overall body shape in preserved specimens, which can vary dramatically depending on how relaxed or contracted the specimen was when preserved. The use of SEM to study sclerites revealed some characteristics not previously reported (e.g., hook-shaped sclerites with a long distal region of the hook described here for the first time for *P. impexa*, and the better characterization of the sclerites of *D. festiva*, including a type only found around the atrial cavity). These new details about these species scleritomes provide additional characters by which they can be distinguished from their relatives. These observations bolster arguments made about the usefulness of detailed studies of sclerites (Scheltema *et al.* 2012; Kocot & Todt 2014; Bergmeier *et al.* 2017; Cobo & Kocot 2021).

Our results also have important implications with respect to solenogaster systematics. The study of the serial sections along with the analysis of the diagnostic characters for the subfamily Pruvotininae raises doubts about the current classification. Nonetheless, our studies of this collection led us to question the validity of the separation between mouth and atrium as a diagnostic character, following Zamarro *et al.* (2013), for Pruvotininae and Eleutheromeniinae. A revision of the family Pruvotinidae is likely necessary in this regard because, despite its ambiguity, this character is still routinely considered (e.g., Pedrouzo *et al.* 2022). With the changes proposed here, the subfamily Eleutheromeniidae Salvini-Plawen, 1968 is defined by the existence of hook-shaped and serrated sclerites, ventral foregut glandular organs of type A/ *Pararrhopalia*-type and the absence of dorso-pharyngeal papilla gland. This subfamily comprises two genera: *Eleutheromenia* Salvini-Plawen, 1967, with *Eleutheromenia sierra* (Pruvot, 1890) and *Eleutheromenia antarctica* (Salvini-Plawen, 1978) n. comb., and the monotypic *Luitfriedia* García-Álvarez & Urgorri, 2001, with *Luitfriedia minuta* García-Álvarez & Urgorri, 2001. The differences between these two genera are 1) the absence of radula in *Luitfredia* while *Eleutheromenia* possess a ditischious radula; and 2) the configuration of the mouth: mouth opening within a common atrio-buccal cavity in *Luitfredia* and mouth opening within a common atrio-buccal opening or mouth and atrium partially separated in *Eleutheromenia*.

Moreover, a confident identification of *Pruvotia* cf. *sopita* would support the reclassification of this species within Pruvotiniidae as suggested by the presence of hollow, hook-shaped sclerites and our phylogenetic analysis of COI. Further, more molecular data from other species of Rhopalomeniidae would be valuable to evaluate the reciprocal monophyly of Pruvotinidae (possibly inclusive of *P. sopita*) and Rhopalomeniidae.

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