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Diversity of Platyhelminthes Proseriata in Western Mediterranean sandy beaches: a database of species occurrences and traits

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Keywords: beach, checklist, Mediterranean Sea, meiofauna, Platyhelminthes, Proseriata.

SUMMARY

We present here a first comprehensive database on the diversity of proseriate flatworms (Platyhelminthes: Rhabditophora: Proseriata) on Western Mediterranean microtidal, wave dominated beaches. We sampled 116 stations in two years, through Spain (22 beaches, including Balearic Islands), France (25 beaches, including Corsica), Italy (63 beaches, including Sardinia, Sicily, and Lampedusa), and Tunisia (6 beaches). In each beach, we sampled at three depths, corresponding to the swash, shoal, and subtidal zones. For each sample, we obtained environmental data. The research yielded a total of 152 species, of which 93 were new to science. For each of the species found, we coded and described 16 functional traits. We discuss the functional meaning of the selected traits, as well as on diversity patterns and emerging biogeographic signals across the investigated regions. We particularly focused on the most widespread and dominant species in our dataset, concentrating on their putative adaptations to high energy environments; as well as the high number (58) of the species only found once. Finally, we discussed the coverage of our sampling by estimating the diversity at each investigated region and comparing it to the actual diversity. All information provided is available through the Global Biodiversity Information Facility (GBIF) and the Open Science Framework (OSF) following the Darwin Core Standard.

INTRODUCTION

The impact of anthropogenic-driven disturbance on natural environments is growing at an unprecedented rate, thereby affecting both local and global biodiversity patterns (Ripple et al., 2017). Species are getting extirpated from large parts of their distribution ranges, or even extinct globally, whereas others are shifting their distribution areas in order to compensate for climate changes (Pecl et al., 2017; Lenoir et al., 2020; Cancellario et al., 2022). Dataset on distribution of species in space and time in formats that are both understandable by humans and computers are crucial to assess the extent of these changes and, ideally, to develop strategies that may ameliorate their consequences.

Unfortunately, whereas current biodiversity databases accumulate a large amount of information for certain taxa and habitats (e.g., Martinez et al., 2018; Froese and Pauli, 2019; Horton et al., 2020; García-Herrero et al., 2021; Pekár et al., 2021, Rubio-López et al., 2022), there is a critical knowledge gap on the distribution of meiofaunal species (Vanreusel et al., 2023). The inadequacy of information in global databases is especially conspicuous for soft-bodied meiofauna, whose diagnostic features need to be observed on living individuals, requiring examinations of samples in the field, as these organisms cannot be properly retrieved from fixed material (Higgins and Thiel, 1988; Curini-Galletti et al., 2012). In most taxa of free-living Platyhelminthes, problematics linked with the study in vivo are coupled with the difficulty in handling particularly sticky, microscopic organisms, and the need to reconstruct the fine details of the morphology of their complex, hermaphroditic reproductive system by serial sectioning. For all these reasons, Platyhelminthes merit their repute as a difficult taxon, "unsuitable for beginners to study" (cited from Hyman, 1951).

Unsurprisingly, Platyhelminthes are among the most affected groups by the taxonomy crisis (Curini-Galletti et al., 2020a).

The lack of biodiversity data on Platyhelminthes might be problematic in the long run, because at least some of them (Rhabdocoela and Proseriata above all) are among the main components of the interstitial communities around the world, and may dominate the interstitial fauna of certain habitats, particularly sandy beaches (Fonseca et al., 2010). Indeed, the wave breaking zone of sandy beaches has been traditionally referred to as "Otoplanen-zonen" due to the abundance of this peculiar genus of proseriate platyhelminth, *Otoplana* (Gerlach, 1953). If we considered that sandy beaches are expected to be dramatically affected by global sea rise and the human population growth (Fanini et al., 2020), by lacking information on proseriates, we might be missing a useful tool to understand human- or climate-driven changes in biodiversity at both local and regional scales. Furthermore, proseriate flatworms exhibit very restricted distribution ranges (Curini-Galletti et al., 2020a) and present a wide range of functional traits, potentially providing an interesting model system to understand theoretical questions on biogeography and functional community ecology.

We here provide a first comprehensive database on the diversity of proseriate flatworms (Platyhelminthes: Rhabditophora: Proseriata) on Western Mediterranean sandy beaches, not only including distribution records but also novel information on their functional traits. All the data here included has been collected over two years across 116 microtidal, wave-dominated beaches across Spain, France, Italy, and Tunisia, including also the Balearic Islands, Corsica, Sardinia, Sicily, and Lampedusa. Our dataset includes 152 species, for which 16 functional traits have been characterized. Along with this information, we here discuss the functional meaning of the selected traits, as well as the diversity patterns and biases through the investigated regions.

MATERIALS AND METHODS

Sampling design

From May 2020 to June 2022, we sampled 116 microtidal, wave-dominated, reflective beaches in the Western Mediterranean marine province distributed as follows: 1 beach in the Alborán Sea, 11 in Spanish Levante, 6 in the Balearic Islands, 22 in the Northern Western Mediterranean, 35 in the Sardinian-Corsican complex, 22 in the Western Peninsular Italy, 9 in Sicily, 3 in the Ionian Sea, 6 in Tunisia, and 1 in Lampedusa.

In each beach, we collected semiquantitative samples of sediment at three levels, corresponding to the wave-breaking zone, the shoaling, and the subtidal level. The wave-breaking zone in reflective beaches corresponds to the swash + surging breaking zone (thereafter referred to as swash level, for simplicity) (McLachlan and Defeo, 2017). We defined swash level as the beach front that directly receives the waves, typically between 0.1-1 m depth (McLachlan and Turner, 1994). We considered the shoaling level as the wave formation area, characterized by the presence of ripple marks and extending between 1-2 m depth depending on the beach exposure. Finally, we identified the subtidal level as the following area, ranging between 2-5 m deep and lacking ripple marks. In each level, we sampled 6 liters of sediments using jars from the 5 cm upper sand, where most of the fauna occurs (Curini-Galletti et al., 2020a).

Proseriate data

Each sample was studied within 24-48 hours after collection. Firstly, we placed the sediment from each sample in an isotonic dilution of magnesium chloride for 15 minutes in order to anesthetise the bulk meiofauna, and then, we filtered the supernatant containing the meiofauna five times through a stack of sieves of decreasing mesh size (1 mm, 0.5 mm, 0.25 mm, 0.125 mm, 0.063 mm). We placed each sieve in a different petri dish with clean seawater,

allowing the animals to recover and crawl through the sieve. Finally, we picked up the proseriates from the dishes using glycerine-coated pipettes, sorted them into different genera under the stereomicroscope, whole mounted alive and identified to species using a compound microscope. Functional traits were observed for all whole mounted individuals (see below for specific details).

Individuals requiring further studies were fixed and preserved in Bouin or in 95% ethanol and stored in collection of Marco Curini-Galletti. Animals belonging to undescribed species were assigned to unofficial but consistent codes for all the studied beaches.

Granulometric data

Granulometric data were obtained by sieving 100 g of sediment for 30 min through a stack of sieves of decreasing meshes size (8 mm; 4 mm; 2 mm; 1 mm; 500 μm; 250 μm; 125 μm; 63 μm) and then weighing the fraction retained in each of the sieves and passing through the last sieve.

Sample statistics (x: mean; σ: sorting; SK: skewness; K: kurtosis) were calculated with the software Gradistat 8.0, method: Folk and Ward (Blott and Pye, 2001).

Descriptive analyses

We calculated the species richness for each of the Western Mediterranean regions (Alboran, Balearic Islands, Western Continental Italy, Ionian Sea, Lampedusa, Levante, Northern Mediterranean, Sardinian-Corsican area, Sicily, Tunisia) using occurrence data. We calculated the Chao2 estimator for the total species richness in each region using the functions 'specpool', and then, we used the function 'specaccum' to calculate the rarefaction curve with 1000 permutations. Both functions are included in the R software version 4.1.2 (R Core Team, 2023), package vegan version 2.6-2 (Oksanen et al., 2022). We considered individual samples collected in each beach (i.e., three levels: swash,

shoaling, and subtidal) as the standard unit of sampling effort in each Western Mediterranean region (Güler et al., 2016; Montes et al., 2021).

THE DATASET

The dataset consists of three tables (as .xlsx files): a table with records, a table with granulometric data, and a table of species traits. In the table of records, each row represents the single record of a proseriate species in one beach and at a beach level (Supplementary Table 1). The data of occurrence records are also available as a GBIF dataset (https://doi.org/10.15468/64xtt9).

In the granulometric table, each row represents a beach level (swash, shoal, deep) for each station, along with granulometric variables (Supplementary Table 2).

The table of species traits includes information for 16 morphological functional traits collected at the species level, as well as information on the taxonomic status of the species (described or undescribed) (Supplementary Table 3).

Dataset name: Proseriata from marine beaches in the Western Mediterranean.

Format name: xlsx/csv.

Character encoding: UTF-8.

Distribution: the full datasets are available as supplementary tables to this paper. The occurrence records are also available under GBIF (https://doi.org/10.15468/64xtt9) and Styogofauna Mundi (https://www.lifewatchitaly.eu/iniziative/stygofauna-mundi). The traits database is also available in Open Science Framework (osf.io/6ut2s).

Date of publication: 07.08.2023.

Date of last review: 28.03.2023.

Update policy: none.

Language: English.

Resource citation: Curini-Galletti, M., Fontaneto, D., Martínez A., 2023. A dataset of

marine beach Proseriata from the Western Mediterranean (Platyhelminthes). Biogeographia 38(2): a029.

Management details

Database manager: Marco Curini-Galletti.

Temporal coverage: from May 2020 to June 2022.

Record basis: Field collections.

Funding grants: Fondazione Sardegna – 2016 (grant: "The contribute of interstitial flatworms in monitoring the effects of the climate change") and "National Biodiversity Future Center – NBFC" funded by the Italian Ministry of University and Research, PNRR, Project CN00000033.

Geographic coverage

Study area: Western Mediterranean marine province, covering the Mediterranean coasts of Peninsular Spain, France, Italy, and Tunisia, as well as the islands of Sicily, Sardinia, Tavolara, Asinara, and Lampedusa (Italy), Corsica (France), and Mallorca (Spain).

Bounding box: 33° to 46° N, 18° W to 6° E; WGS84 reference system.

Countries: Spain, France, Italy, Tunisia.

Sampling design: We sampled 116 microtidal, wave dominated, reflective beaches in the Western Mediterranean marine province, across Spain (22 beaches, including Mallorca), France (25 beaches, including Corsica), Italy (63 beaches, including Sardinia, Sicily, and Lampedusa), and Tunisia (6 beaches).

Biogeographic region: Temperate Northern Atlantic realm.

Quality control for geographic data: Quality control was performed by displaying coordinates within the Marine Ecoregions Of the World (MEOW) boundaries using the R package mapview v. 2.10.0 (Appelhans et al., 2016).

Ecological data

Habitat type: We considered three habitats corresponding to three beach levels: (1) wave-breaking level, the area of high hydrodynamic turbulence between 0.1-1 m depth; (2) shoaling level or area of wave formation, characterized by the presence of ripple marks in the sediments extending between 1-2 m depth; and (3) subtidal level, ranging between 2-5 m deep and lacking ripple marks.

Depths: 0-5 m.

Quality control for ecological data: All samples were collected by Marco Curini-Galletti, who verified the assignment of the habitat in the field.

Taxonomy

Taxonomic ranks: Species level.

Species names: Described species were assigned to the current accepted name (according to WoRMS). APHIA ID numbers are included for each of the described species to facilitate the retrieval of the information. Animals belonging to undescribed species were consistently assigned to the same taxonomic unit using unofficial but consistent codes for all the studied beaches, so they can also be included in further analyses.

Taxonomic methods: All specimens of Proseriata from the samples were identified alive by Marco Curini-Galletti, taxonomic expert of the group. Individuals requiring further study were subsequently fixed in Bouin or in 95% ethanol, preserved as vouchers and stored in Marco Curini-Galletti's collection.

Taxonomic specialist: Marco Curini-Galletti.

Quality control for taxonomic data: All included taxonomic ranks were verified by using WoRMS resources.

Taxonomic and ecological remarks: In the taxonomic remarks column of the dataset there is information on whether the species

corresponds to a new species for science or not. Species identification exclusively relies on morphology. Therefore, there may be cryptic species complexes within each of the reported species names, warranting further research.

Functional traits

Resolution of the trait collection: Species level.

Number of traits: 16, with 2 continuous, 10 discrete multistate, and 4 discrete binary.

Trait resolution: coarse, including the average of each species and without accounting for intraspecific variability.

Trait sources: original measurements and observations.

Trait selection: we selected all traits related to adaptation to hydrodynamics, as well as few additional traits linked to the presence of sensory organs and reproductive structure.

Description of the traits and discussion of their functional meaning:

- Body size (continuous, range = 0.61-5.87 mm).

- Body width (continuous, range = 0.07-0.4 mm).

Proseriata are comparatively large for a meiofaunal taxon (Smith et al., 2020). They range from minute, slender, delicate forms, less than 1 mm long, to larger, stouter species, more than 10 mm long (Ax, 1995) (Figs. 1 A-H, M). Morphology determines their lifestyle: smaller species are strictly interstitial, while larger, thicker species dislodge and burrow among sand grains (Curini-Galletti, 2001). Measuring the average length and width of a proseriate species may be challenging. Proseriates lack external cuticle and the contraction of their thick circular and longitudinal musculature allow appreciable changes in size (Marco Curini-Galletti, pers. obs.). In this study, we measured 2-5 anesthetised, mature individuals per species, lightly pressed under a coverslip. Observed size ranges from 0.6 mm in length (*Postbursoplana*

fibulata) to 5.9 mm (*Monostichoplana* n. sp.). Monocelidids measured less than 0.1 mm wide; a few taxa (species of the genera *Monocelis*, *Otoplana*, *Invenusta*) reached 0.4 mm in width.

- Body shape (multistate, 0: flattened; 1: cylindrical; 2: globular).

Most proseriates are immediately recognizable among meiofaunal organisms for their slender, elongate, and nearly cylindrical shape (Figs. 2 A, C). This is by far the most widespread morphology for representatives of most of the families of Proseriata (Smith et al., 2020), and appears suited for both burrowing and interstitial lifestyles. A major exception is represented by members of the Otoplanidae, most of which are characterized by a flattened, ribbon-shaped habitus, or ovoid to leaf-like shape (see, e. g., Ax, 1956) (Figs. 1 H, M; Fig. 3 A). Broad and flat species, such as *Pseudorthoplana foliacea* (Fig. 1 C), occur in coarse to gravelly substrates in high energy environments (Ax et al., 1978), where their shape may facilitate adhesion to the substrate. Exceptionally, members of the genus *Monotoplana* are short and globular (Fig. 1 D); they are often seen swimming agilely in the petri dish (Marco Curini-Galletti, pers. obs.), and may swim above the substrate, rather than be strictly interstitial.

- Adhesiveness (multistate, 0: tail obtuse, poorly adhesive; 1: tail pointed, poorly adhesive; 2 pointed, adhesive; 3: adhesive patch).

Proseriates are often highly adhesive, and whoever tried to handle them may have noticed how tenaciously they may stick to the pipette, sometimes irretrievably so. Their adhesiveness results from a combination of mucous and adhesive glands (Pjeta et al., 2019), and its coding into character states may be challenging. We here consider the position and numerosity of adhesive glands as indicative of a species' adhesiveness. We collected this information at the level that may be observed with an optical microscope, given that the majority of the species of Proseriata lack scanning electron microscopic studies.

Most of the adhesive glands in Proseriata concentrate on their tail (Pjeta et al., 2019). In extreme cases, the tail may be produced into three 'digits', richly endowed with adhesive glands – a trait only evolved in a neotropical lineage of Monocelididae (Curini-Galletti et al., 2020b).

Most proseriates have a simple, pointed tail: to this category belong most of Monocelididae and many Otoplanidae. Number and position of glands differ throughout species. Species with relatively few adhesive glands around the periphery of the tail have been coded as 'poorly adhesive' (Fig. 2 F), whereas species with very elongate tails bearing numerous adhesive glands, have been coded as 'adhesive' (Fig. 2 E). Large species, such as those of Archimonocelididae, Coelogynoporidae, and Unguiphora, have obtuse, unspecialised tails, with very few adhesive glands (Fig. 2 A). Members of Parotoplaninae uniquely possess an adhesive caudal patch with numerous glands, fan-shaped in living specimens, and an additional row of adhesive glands along both sides of the body (Ax, 1956) (Fig. 2 D).

- Body ciliation (binary, 0: body entirely ciliated; 1: cilia on a ventral sole only).

Representatives of most of the families of Proseriata are entirely ciliated or almost so. In Monocelididae and Archimonocelididae, ciliary coverage may thin out dorsally toward tail leaving, a small patch almost devoid of cilia on the extreme posterior end of body; apart from that, the dorsal surface is completely ciliated (Martens and Curini-Galletti, 1993) (Figs. 2 A, C). On the contrary, representatives of Otoplanidae (with the notable exception of *Archotoplana holothricha*) have ciliation restricted to a ventral creeping sole, and the entire dorsal surface is entirely unciliated. In *Otoplana bosporana*, the creeping sole is split into separate patches with areas bereft of cilia around ventral pores (pharynx, common genital pore) (Ax, 1956) (Fig. 2 B).

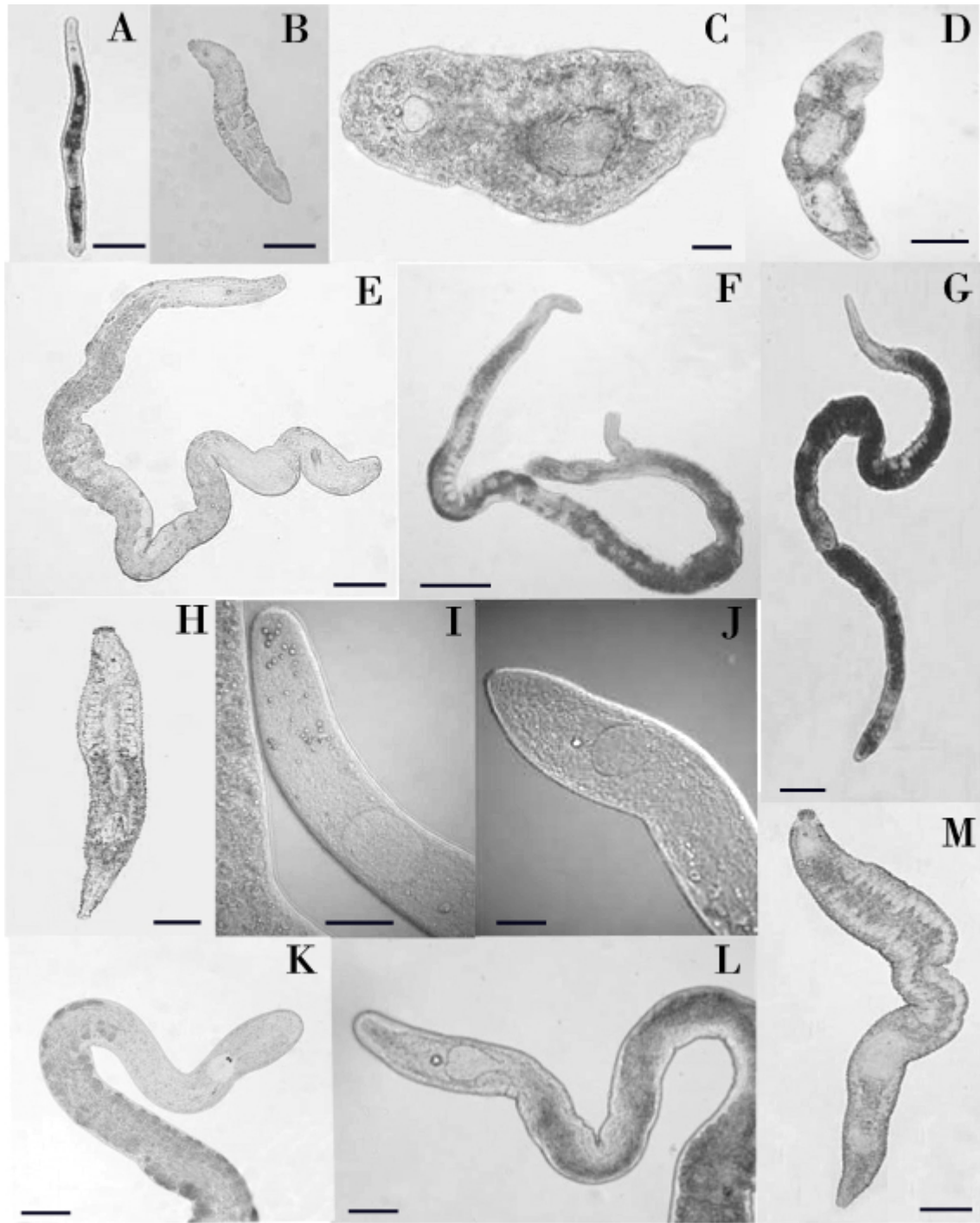- Body pigmentation (binary, 0: absent, 1: present).

Figure 1. A: *Archilina* 'brachycirrus complex sp. I' (Cervione, Corsica). B: *Postbursoplana fibulata* (Alcudia, Balearic Is.). C: *Pseudorthoplana foliacea* (Sao Miguel, Açores). D: *Monotoplana diorchis* (Porto Cesareo, Apulia). E: *Coelogynopora* 'gallica complex sp. I' (Gaeta, Latium). F: *Monostichoplana neapolitana* (Baia Cea, Sardinia). G: *Archimonocelis crucifera* (Porto Palo, Sardinia). H: *Parotoplana procerostyla* (Castelldefels, Catalunya). I: *Nematoplana* cf. *corsicana* (Sciacca, Sicily). J: *Coelogynopora* n. sp. 'Eloro' (Eloro, Sicily). K: *Nematoplana riegeri* (Golfo Aranci, Sardinia). L: *Coelogynopora* cf. *gynocotyla* (Santa Severa, Latium). M: *Otoplana bosporana* (Ansedonia, Tuscany). Scale bar: A-H, M: 100 μm; I, J: 25 μm; K, L: 50 μm.
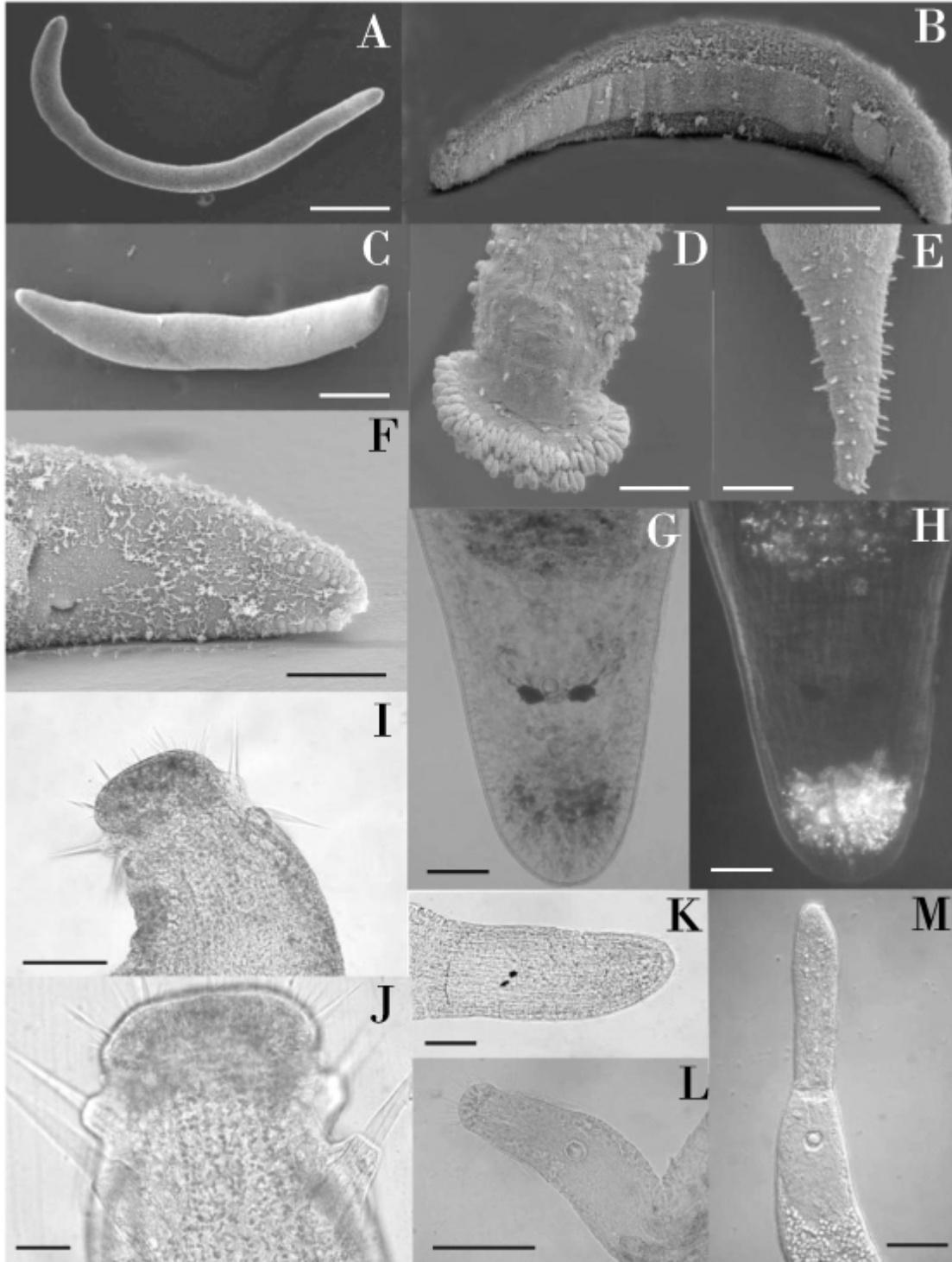
Figure 2. A: *Coelogynopora* cf. *gynocotyla* (La Maddalena, Sardinia). B: *Otoplana bosporana* (Lu Bagnu, Sardinia). C: *Monocelis lineata* (Porto Torres, Sardinia). D: *Parotoplana renatae* complex (Calvi, Corsica). E: *Boreocelis urodasyoides* (Castiglione della Pescaia, Tuscany). F: *Otoplana bosporana* (Lu Bagnu, Sardinia). G, H: *Monocelis* n. sp. '*longiceps* sp. I' (Porto Cesareo, Apulia) (at incident (G) and reflected (H) light). I, J: *Otoplana bosporana* (I: Geremeas, Sardinia; J: Diamante, Calabria). K: *Nematoplana riegeri* (Porto Palo, Sicily). L: *Postbursoplana fibulata* (Hospitalet de l'Infant, Catalunya). M: *Duplominona paucispina* (Empuria brava, Catalunya). Scale bar: A, B: 500 μm; C: 200 μm; D-F, L: 50 μm; G, H, J: 10 μm; I: 25 μm; J, K, M: 20 μm.

Most Proseriata are unpigmented, with few species showing some colour (Curini-Galletti, 2001). Pigment may be widespread in the parenchyma of the whole body or limited to the cephalic area. Most often, pigments give the animal a sober brownish colour (e.g., *Monocelis fusca*), but a few species possess white, red, yellowish, or even pink pigments (Ax et al., 1978). Cephalic pigment is often arranged as a dark band over brain and light receptors, accompanied or not by a similarly or contrasted pigmented band on the extreme anterior tip of the body (Curini-Galletti et al., 2011) (Figs. 2 G, H). Body pigmentation in interstitial proseriates appears related to a lifestyle that includes exposure to light, either as camouflage when outside the sediment (Armonies, 1989) or as a protection from ultraviolet damages (Sopott-Ehlers, 1995).

- Photoreceptors (multistate, 0: unpigmented; 1: pigmented; 2: pigment shield).

Most proseriates lack pigment granules in the mantle cells surrounding the two cephalic photoreceptors, whose presence and position are thus invisible in living specimens and can only be appreciated at using electron microscopy. They are located either inside the brain, or between the brain and the statocyst (Bedini and Lanfranchi, 1974). Pigment-cup ocelli are limited to a few members of Unguiphora (Figs. 1 K, 2 K), most of which are likewise unpigmented (Fig. 1 J). A unique type of pigmented photoreceptors is found in some species of Monocelididae (notably in the genera *Monocelis* and *Pseudomonocelis*). Similarly to the rest of Proseriata Lithophora, they lack pigment granules in the mantle cells, but a shading device is built up by an additional multicellular pigment shield, overlaying the photoreceptors (Sopott-Ehlers, 1995) (Fig. 2 G).

- Cephalic specialized sensory area (binary, 0: absent, 1: present).

The anterior tip of Proseriata is provided with nervous fibres originating from the brain that supply the sensory bristles (Rieger et al., 1991). In most species, this sensorial cephalic area bears only a few, short bristles, interpreted as mechanoreceptors (Ehlers and Ehlers, 1977) (Figs. 1 I, J; Figs. 2 K, M) On the contrary, members of the Otoplanidae have a specialized cephalic sensory area, consisting of a series of large, thick sensory bristles arising from both sides of head, and a subapical, ciliated sensorial furrow (Figs. 2 I, J, L). This specialized cephalic sensory area is particularly well developed in members of the genus *Otoplana* and has been interpreted as a tactile sensorial area (Hofsten, 1918; Ax, 1956). Given the density and length of cilia, and the habit of *Otoplana bosporana* to slightly raise its head when resting (MCG, pers. obs.), a rheoreceptive function may also be envisaged.

- Statocysts (binary, 0: absent, 1: present).

Statocysts are static sense organs located in front of the cerebral ganglion in proseriates (Rieger et al., 1991). The presence of statocyst is one of the most obvious characters of Proseriata Lithophora, allowing immediate recognition of the taxon (Sopott-Ehlers, 1985) (Figs. 1 J, L; Figs. 2 L, M). The statocyst is absent in Proseriata Unguiphora (Figs. 1 I, K; Fig. 2 K).

- Brain capsule (multistate, 0: absent; 1: poorly developed; 2: present).

As a rule, the brain of Proseriata is lined by a thick extracellular matrix capsule (Rieger et al., 1991) (Figs. 1 I, J, L; Fig. 2 K). The capsule is particularly conspicuous in large, burrowing species, and is interpreted as a protection for the brain when dislodging sand grain (Curini-Galletti, 2001). A few, tiny, interstitial Otoplanidae, such as members of Postbursoplana, have a poorly developed brain capsule (Fig. 2 L). A brain capsule is absent in members of the Monocelididae (Fig. 2 M), most of which are small interstitial forms, and may not need a specialized brain protection (Curini-Galletti, 2001).

- Pharynx type (multistate, 0: collar shaped; 1: tubular; 2: glandular).

All proseriates possess a *plicatus tubiformis* pharynx type (Ax, 1995). The

pharynx may be held anterior-posteriorly, aligned with the main body axis (Fig. 3 B), or dorso-ventrally oriented, appearing collar-shaped in living specimens (Fig. 3 A). Horizontal pharynges range from bell-shaped in Otoplanidae to long and tubular, as in Monocelididae and most Archimonocelididae. This type of pharynx is mobile, often seen protruding outside the mouth in order to enter the body of prey and suck its fluids and tissues (MCG, pers. obs.; Watzin, 1985). Vertical pharynges are instead short and poorly mobile. They may be applied directly on wounds of prey or carrion, or swallow small prey whole (Marco Curini-Galletti, pers. obs.). The cnidarian-preying Archimonocelididae possess very long, horizontal pharynges with a strongly glandular proximal region (Martens and Curini-Galletti, 1993) (Fig. 3 B), whose secretion might allow the ingestion of intact nematocysts from preys (interstitial Hydrozoa). Cnidae are later stored in special structures (cnidosacs), often aligned in dorsal, longitudinal row(s), where they retain their viability and confer protection to the worm (Karling, 1966).

- Sclerotised structures of the copulatory organ (multistate, 0: unarmed copulatory organ; 1: stylet only; 2: atrial spines only; 3: stylet + girdle with spines all alike; 4: stylet with girdle with differentiated spines; 5: copulatory spines and differentiated girdle; 6: spiny cirrus).

Sclerotised structures of the copulatory organ are among the most important taxonomic characters in Proseriata, allowing discrimination at the species-level (e.g., Curini-Galletti et al., 2019). The wide range of morphologies of the copulatory structures found in the group made necessary its coding into numerous states.

- Species with an eversible cirrus usually have scale-like spines, often arranged in girdles that may vary in size and morphology along the length of the cirrus. The number of spines may range from very few (less than 10) to hundreds (Fig. 3 E; Figs. 4 A-F).

- Species with a penis papilla may present a stylet surrounded by or contiguous to a girdle of needle-like spines. These spines may be all alike (Fig. 3 H) or different, usually with the most proximal spines to the stylet markedly differing from the rest of the girdle (Fig. 3 K). Rarely, only the stylet is present (Fig. 3 G).

- In most Otoplanidae, a stylet is absent and the distalmost part of the ejaculatory duct is surrounded by two copulatory spines. Those are often gutter-shaped and act as functional stylets. These large spines are accompanied by one or more girdles of needle-like spines of different shapes (Fig. 3 J).

- Rarely, the penis papilla might be unarmed, but surrounded by spines formed by the tissue lining the male atrium. In our sample, this state is only shown by members of Calviiridae, unmistakable for their spectacular atrial spines complex (Fig. 3 I).

- Type of copulatory organ (multistate, 0: papilla inermis; 1: copulatory stylet; 2: cirrus).

An eversible cirrus is rare in Proseriata, restricted to the Monocelididae (except for the subfamily Monocelidinae) (Fig. 3 E), a few genera of Coelogynoporidae, and one east-Australian species attributed to Otoplanidae (Sopott, 1972; Miller and Faubel, 2003). A penis papilla is found in all the families of Proseriata. In most instances, it is provided with spines and/or stylet (Figs 3 H, J, K). Only rarely, hard structures are completely lacking, and the penis is unarmed (papilla inermis), as in most Monocelidinae, and in few Coelogynoporidae and Calviriidae (Sopott, 1972; Litvaitis et al., 1996; Schockaert et al., 2011) (Fig. 3 D).

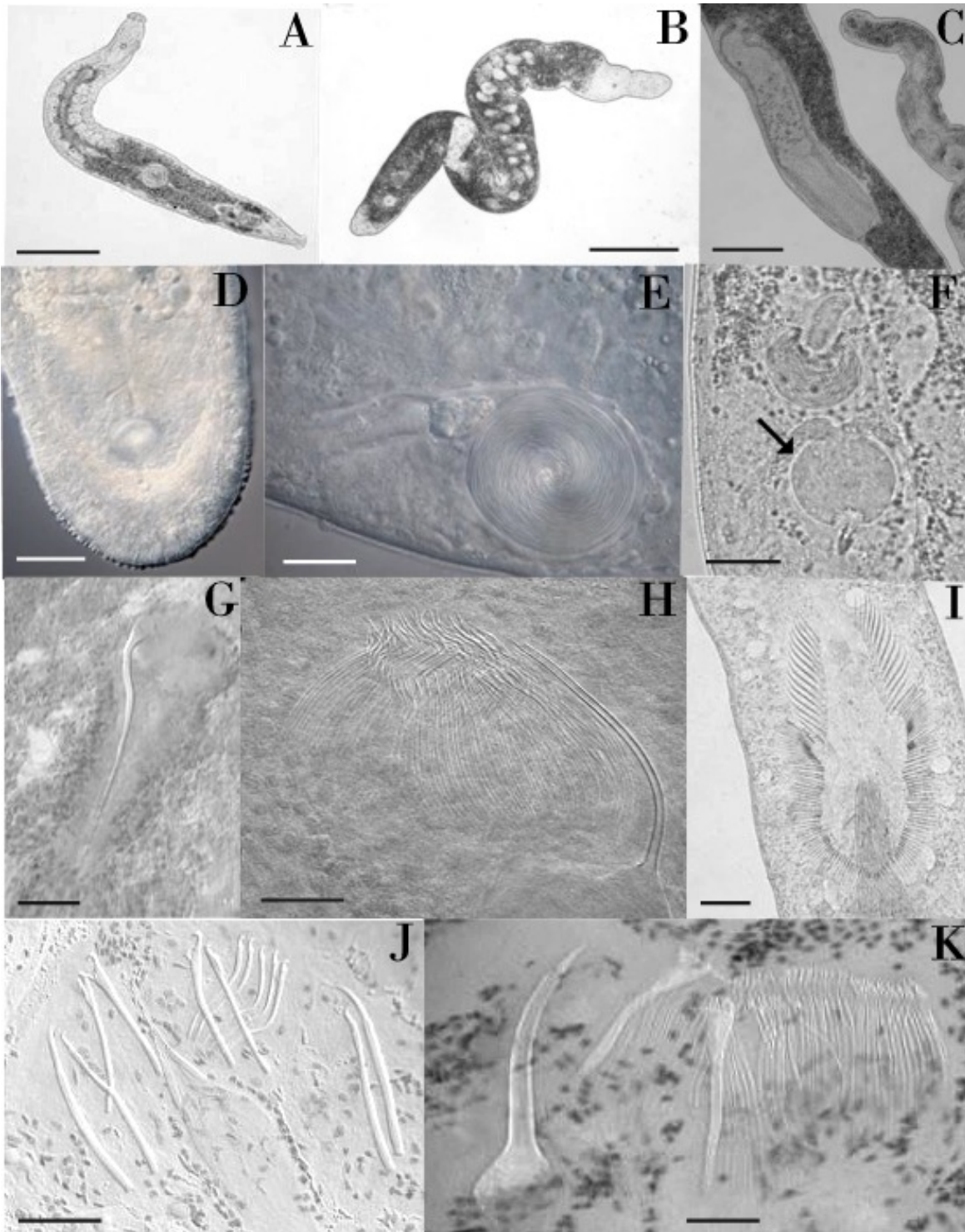- Accessory spiny organs (binary, 0: absent, 1: present).

Figure 3. A: *Parotoplana crassispina* (Castiglione della Pescaia, Tuscany). B: *Monocelis* cf. *mediterranea* (Molara, Sardinia). C: *Archimonocelis carmelitana* (Lu Bagnu, Sardinia). *Pseudomonocelis ophiocephala* (Torre degli Ulivi, Sardinia). E: *Archilina* n. sp. 'Hospitalet' (Hospitalet de L'infant, Catalunya). F: *Duplominona* 'istanbulensis complex Pirulì' (Pirulì, Catalunya) (arrow points to the accessory spiny organ). G: *Monocelis longistyla* (Les Grottes, Tunisia). H: *Archimonocelis carmelitana* (Lu Bagnu, Sardinia). I: *Calviria solaris* (Ses Covetes west, Balearic Is.). J: *Parotoplana procerostyla* (Baia Cea, Sardinia). K: *Archimonocelis staresoi* (Point Revellata, Corsica). Scale bar: A, B: 200 µm; C, D, F, I, J: 50 µm; E: 15 µm; G, H, K: 25 µm.
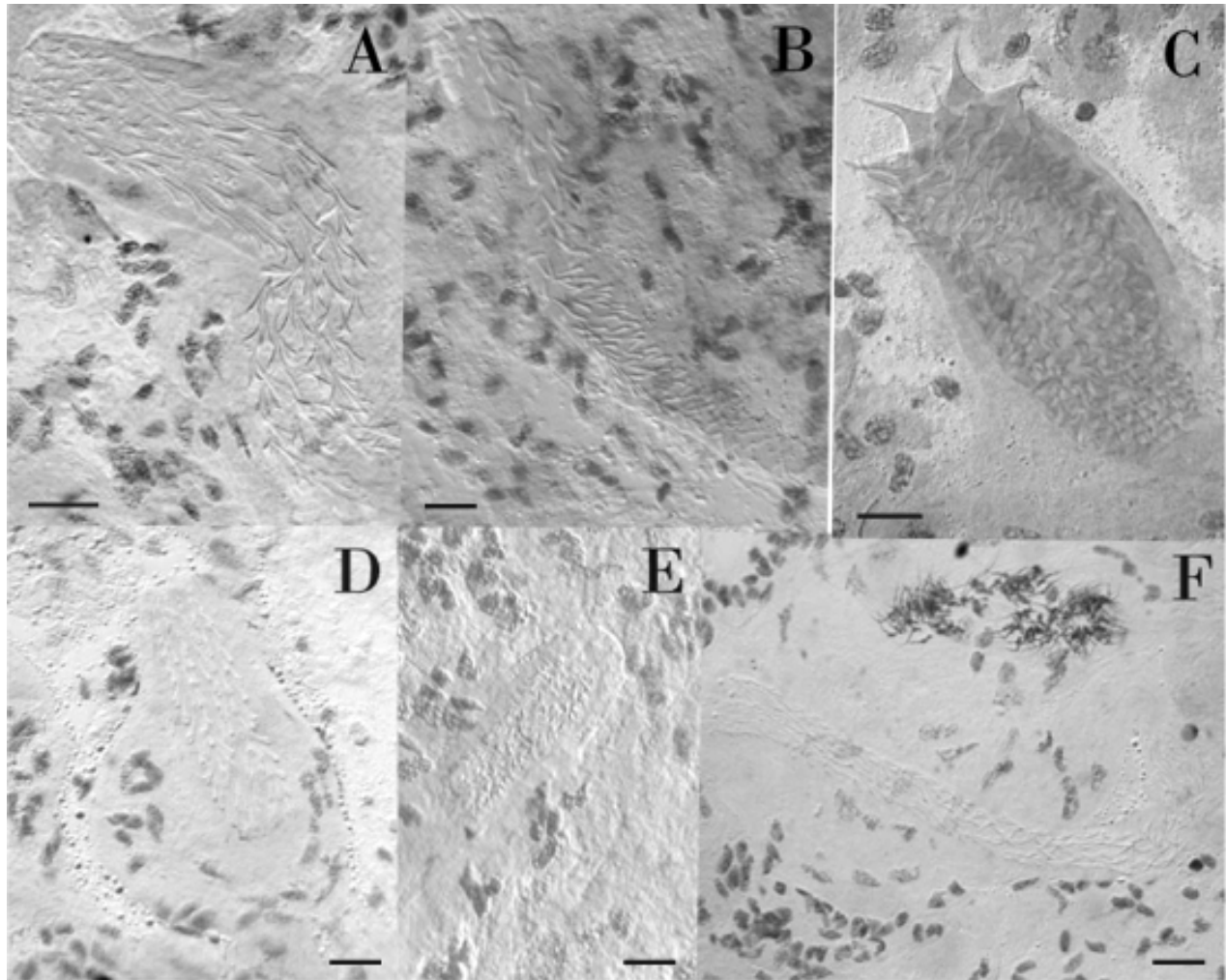
Figure 4. A: *Archilina etrusca* (Calvi, Corsica). B: *Archilina* n. sp. 'etruscoides' (Castellammare, Sicily). C: *Archilina* n. sp. 'etrusca-complex sp. III' (Lampedusa, Sicily). D: *Archilina* n. sp. 'etrusca-complex sp. IV' (Torrenostra, Catalunya). E: *Archilina* n. sp. 'short cyrrus, Balearic' (Port Alcudia, Baleari Is.) F: *Archilina* n. sp. 'long cyrrus, Balearic' (Port Alcudia, Baleari Is.). Scale bar: 10 μm.

In addition to the copulatory organ, a variety of accessory spiny organs may be present in proseriates. They consist of a claw-shaped stylet connected to a glandular organ, and they are provided with their own external pore (Litvaitis et al., 1996). Often termed 'prostatoid organs' (Karling, 1978), their exact function is not clearly known. Spectacular and often reported in textbooks (e.g., Brusca and Brusca, 1990), is the row of numerous accessory organs in members of Polystyliphora, ranging to several dozen (Curini-Galletti, 1998). In several members of Monocedidae, a single organ is present, usually posterior to the copulatory organ (Fig. 3 F). Presence of an accessory spiny organ has been hypothesized as the plesiomorphic condition for the Monocelididae, with multiple, independent losses within the family (Litvaitis et al., 1996). In our sample, an accessory spiny organ is also present in members of Calviriidae (Martens and Curini-Galletti, 1993).

RESULTS AND DISCUSSION

Species diversity

Our survey of the proseriates of the Western Mediterranean yielded a total of 152 species (Supplementary Table 1). This substantially

increases the knowledge of the diversity and composition of proseriates in the Mediterranean, given that before this study only 93 species were known from the whole Mediterranean basin (Curini-Galletti et al., 2020a). During the research, we found most of the species already known in the Mediterranean, with the major exception of species whose *locus typicus* resides outside the Western Mediterranean (notably Alboran Sea, Adriatic Sea, and eastern Mediterranean) (Curini-Galletti and Martens, 1992; 1995; Curini-Galletti et al., 2007; Delogu and Curini-Galletti, 2007; Delogu et al., 2008; Delogu and Curini-Galletti, 2009), and whose distribution range may not extend to the sampled area.

Even more remarkable is the number of the undescribed species found, totalling 95 and surpassing 60% of the total number of recorded species. The finding of new species of proseriates is not surprising and indeed any sampling campaign conducted so far revealed new species of the taxon (Willems et al., 2009; Curini-Galletti et al., 2012; Martínez et al., 2019; Curini-Galletti, 2021; Jörger et al., 2021). However, the Western Mediterranean Sea is one of the world's most intensely studied areas for Proseriata (Curini-Galletti et al., 2020a); thus, the sheer number of new species is noticeable, stressing once again how little we know about the diversity of interstitial platyhelminths (Appeltans et al., 2012; Armonies, 2018, 2023). The number of new species found call for a justification regarding our taxonomic approach. Since molecular studies in Proseriata are lagging behind (see Scarpa et al., 2017 for an inclusive report on the species molecularly studied), there are no, at present, available clues that may integrate morphology for most populations found in the course of our study. Morphology-based taxonomy in proseriates involves a two-step process: generic assessment mostly involves the shape, position and connections of the reproductive organs, and most often needs sectioning of paraffin-included specimens (e.g., Curini-Galletti, 2014). Once genus allocation is achieved, species hypotheses are most often

exclusively based on the sclerotised structures of copulatory organ (e.g., Jouk et al., 2019), which are involved in mate recognition, preventing interspecific crossbreeding, and are particularly differentiated in sympatric congeneric species of proseriates (Scarpa et al., 2019 b). In our study, exemplary in this regard is the pair of *Archilina* species exclusively found in the Balearic Islands, in the same samples, and differing dramatically for size and shape of the cirrus (Figs. 4E, F). Different, and more problematic, is the case of allopatric, congeneric populations showing small differences in their hard structures that may be interpreted either as intra- or inter-specific variability, making, in the absence of other clues, taxonomic decisions somewhat arbitrary. In fact, Proseriata, as most interstitial flatworms, lack any dispersal stage during their life cycle (Curini-Galletti, 2001), and allopatric, congeneric species may not necessitate sharply differentiated copulatory structure in order to prevent crossbreeding. In this research, we adopted a conservative approach and attributed the rank of species only to allopatric populations showing unique markers in their hard structures. Here we report, as an example, the case of *Archilina* with elongate cirrus and acutely triangular spines (the *Archilina etrusca* complex). Although the basic morphology is the same, we distinguished species on the basis of differences in size and morphology of the spines: *Archilina etrusca* from central Mediterranean, with an asymmetrical cirrus, provided with long spines for most of its length, and with tiny spines, about 1 μm long, on one side, (Fig. 4 A); *A. 'etruscoides'* (from Sicily), with a symmetrical cirrus lacking any tiny spines (Fig. 4 B); *A. 'etrusca* III species' (Lampedusa) with a densely spiny cirrus and with broadly triangular distal spines (Fig. 4 C); *A. 'etrusca* IV species' (Catalunya), with a short cirrus and slender spines, not varying in morphology and size along the length of the cirrus (Fig. 4 D); and *A. 'long cirrus, Balearic'* (Balearic Islands), with needle-like spines distally, triangular sub-proximally, and again needle-like proximally (Fig. 4 F). It is worth noting that our approach significantly

differs from that of Norena et al. (2007), who attributed to *Archilina papillosa* (Ax and Ax, 1977), a species described from Galapagos, specimens found in the European Atlantic coast, based on the shared presence of a spiny cirrus, regardless of fine details of its morphology.

Species distribution

Our samples yielded a heterogeneous assemblage of Proseriata, sharply differing across most stations. Only three of the 152 found species were widespread and found in about half of the 116 beaches sampled:

Coelogynopora cf. *gynocotyla* (64 stations; Figs. 1 L; Fig. 2 A). The genus *Coelogynopora* shows its maximum diversity in cold, boreal waters, where most of the species occur (Ax, 2008), with one, isolated species recently described from subantarctic areas (Volonterio et al., 2021). Besides *C. gynocotyla*, only *C. gallica* and *C. schockaerti* are known from the Mediterranean, both limited to the North-Western sector (Gulf of Lyon) and considered as cold-water relics (Sopott-Ehlers, 1976; Jouk et al., 2019). However, this may not apply to the genus as a whole in the Mediterranean, as our research revealed five additional, undescribed species, even in stations as south as Sicily and Tunisia. *Coelogynopora gynocotyla* is the only member of the genus that is widely distributed along the Atlantic coasts (from Spitsbergen south to the Belgian North Sea Coast) and the Mediterranean Sea (Sopott, 1972; Schockaert et al., 1989; Ax, 2008; Marco Curini-Galletti, unpubl. data). However, *C. gynocotyla* is also one of the very few *Coelogynopora* species lacking sclerotised structures in its copulatory organ, the key factor for species assessment in the genus (Jouk et al., 2019), and the conspecificity of populations across such a wide range should be more thoroughly investigated. As a precautionary step, the disjunct distribution of Atlantic and Mediterranean populations suggested its provisional determination as *Coelogynopora* cf. *gynocotyla*. In our sample, *Coelogynopora* cf.

gynocotyla was ubiquitous, and appeared indifferent to depth and sediment texture, also occurring, though rarely, in the swash zone. As most members of the genus, *C.* cf. *gynocotyla*, is large, stout, slow-moving, with an almost perfectly cylindrical body, obtuse head and tail, thick brain capsule, without specialized sensorial cephalic area and with few adhesive glands. This morphology strongly suggests that *C.* cf. *gynocotyla* is a member of burrowing meiofauna, and this may explain its apparent indifference for a specific granulometry.

Otoplana bosporana (62 stations; Fig. 1 M; Figs. 2 B, F, I, J). Members of the genus *Otoplana* are so common and characteristic of the swash zone in the Mediterranean to have become the namesake of the level of the beach where it abounds, i. e. the 'Otoplana-zone', worldwide (Gerlach, 1953). The genus *Otoplana*, however, has a very characteristic morphology (Ax, 1956) and is endemic to the Atlantic-Mediterranean region. It occurs from southern Portugal to the Canary Islands towards the south and the Mediterranean levantine coast towards the East (Scarpa et al., 2017). Elsewhere, members of other genera (e.g., *Kata*, *Kataplana*, *Bothriomolus*) play the same ecological role as the members of *Otoplana* in the Mediterranean (Ax, 1956; Luther, 1960; Curini-Galletti, 2014). Specific attribution of the specimens found in our samplings has been problematic. In fact, seven species of the genus *Otoplana* have been described so far for the Mediterranean alone (Tyler et al., 2006-2023). Species descriptions have been mainly based on very few specimens, and based on a single, type-population, with limited or no report on the extent of morphological variability (Du Plessis, 1889; Ax, 1959, Lanfranchi, 1969, Lanfranchi and Melai, 2007, 2010; Meini, 2013). In our sample, we observed such a marked variability, not only at intra and inter-populational levels, but also linked to different developmental stages, which may encompass the morphologies of most of the species described (Marco Curini-Galletti, pers. obs.). Indeed, the first molecular survey on the genus did not reveal significant

differences in the Mediterranean specimens analysed and attributed to *Otoplana bosporana* (Scarpa et al., 2019a). Therefore, we here adopted the oldest name available for an *Otoplana* with a central aculeus, surrounded by a girdle of spines (i.e., *Otoplana bosporana*) (Ax, 1959). *Otoplana bosporana* strongly prefers high energy, coarse sediment habitats, where it crawls very quickly on its ventral ciliated sole. Furthermore, it is flat and broad, with well-developed cephalic sensorial area (Figs. 2 I, J), and with adhesive glands located ventrally around the periphery of the body, allowing firm adherence to sediment particles (Fig. 2 F).

Postbursoplana fibulata (56 stations; Figs. 1 B, 2 L). A Mediterranean endemic species found extensively in our sampling, especially in higher energy habitats. It may represent the epitome of an interstitial proseriate: tiny (the smallest species found in our sample), slender, extremely agile and fast-moving among sand grains– to an extent that this behaviour makes its isolation particularly difficult (Marco Curini-Galletti, pers. obs.). Furthermore, it also presents a long, adhesive tail, and a particularly developed cephalic sensorial area.

Also worthy of consideration are the three next-ranking species in terms of the number of occurrences in our stations. Remarkably, all three are aberrant members for their genera/families:

Monostichoplana neapolitana (47 stations; Fig. 1 F). A most unusual otoplanid, unique within the family, in having a very long, filiform, almost cylindrical body with few adhesive glands caudally and lacking a specialized cephalic sensorial area (Ax et al., 1978). Its morphology suggests a burrowing lifestyle, unusual for an otoplanid. Indeed, living individuals observed at small magnification in petri dishes appear almost indistinguishable from members of *Archimonocelis* (Marco Curini-Galletti, pers. obs.). *Monostichoplana neapolitana* is common and widespread in subtidal areas, but also found in the shoal and,

rarely, in the swash zone. Originally described as a subspecies of the Atlantic *M. filum*, the marked differences in sclerotised structures and size (Ax et al., 1978) suggests the erection of the Mediterranean populations to full species-rank.

Archimonocelis crucifera (35 stations; Fig. 1 G). Most members of the genus *Archimonocelis* occur in subtidal sediments, rich in organic detritus, where the specific preys (Hydrozoa) occur (Karling, 1966). *Archimonocelis* species are usually large, stout, cylindrical, poorly adhesive, with an evident brain capsule, and with or without a chorda intestinalis, i.e., a thick, solid cephalic diverticulum of the gut, reaching the anterior tip of the body, and further protecting the brain when the worm burrows (Ax and Ax, 1969; Martens and Curini-Galletti, 1993). Archimonocelid species occurred only occasionally in our samples, where Hydrozoa were but very rarely observed. *Archimonocelis crucifera* was the only exception, as it has been found extensively in the shoal, and, on occasions, in the swash zone. It is a Mediterranean endemic species, with a wide distribution from the Western Mediterranean to the coast of the Levant Sea (Martens and Curini-Galletti, 1993). As all members of the genus, it preys on Hydrozoa; however, stored cnidae ("cleptocnids") are few in number and poorly organized (Marco Curini-Galletti, pers. obs.): it may thus also subsist on preys other than Hydrozoa. *Archimonocelis crucifera* is also considerably smaller, slenderer and more agile than congeneric species (Martens and Curini-Galletti, 1993).

Parotoplana procerostyla (34 stations; Fig. 3 A). The genus *Parotoplana* is particularly well represented in our dataset. Most of the species have been found in the subtidal, and most are limited to a few stations, if not to a single one. *Parotoplana procerostyla* differs in this regard, as it is the only species of the genus with a wide distribution range across the Mediterranean, and, exceptionally for the genus, also occurs in the swash zone. *Parotoplana procerostyla* also differs morphologically from

most congeneric species, as it is comparatively very small, agile, and leaf-shaped, resembling, in general appearance and behaviour, more an *Otoplana* than a *Parotoplana*, suggesting that the species is adapted to high energy habitats.

Furthermore, it is worth considering the potential biogeographical signal of the fraction of species only found in sectors of the Mediterranean:

The "western species": species limited to the westernmost fringe of our sampled area, both on the northern (Spain and France) and southern (Tunisia) shores. A few of them extend from the west coast of Atlantic Europe to Sicily and Sardinia, but all are lacking from the continental coast of Italy (e.g., *Necia* sp. complex.; Monocelidinae n. gen. 1 n. sp. 1; *Parotoplana primitiva*; *Parotoplana bicupa*).

Species limited to single sectors:

Sicily: *Archilina* n. sp. '*etruscoides*'; *Archilina* n. sp. '*siculo-ctenophora*'; *Archilina* n. sp. '*dubia*-Sicily', *Phylosirtis* sp. 1.

Balearic Islands: *Archilina* 'short cirrus', *Archilina* 'long cirrus'; *Parotoplana* n. sp. '*angelica*'; *Parotoplana* n. sp. '*minigaeta*-baleari'.

Sardinian-Corsican complex: *Archilina* n. sp. '*ctenophora*'; *Pseudomonocelis occidentalis*; *Parotoplana* n. sp. '*multispinosa*-complex sp. III'; *Parotoplana ichnusae*; *Parotoplana pulchrispina*.

Gulf of Lyon: *Archilina* n. sp. '*brachycirrus* complex sp. IV'; Monocelidinae n. gen. 2 n. sp. 1; *Orthoplana mediterranea*; *Parotoplana multispinosa*; *Parotoplanella progermaria*.

Eastern Tyrrhenian sea: *Parotoplana* n. sp. '*minigaeta*'; *Archilina* n. sp. '*principina*'; *Duplominona* n. sp. 'Castiglione'; *Parotoplana* n. sp. '*falsiprimitiva*'; *Archilina* n. sp. '*nova-paestum*'; *Parotoplana* n. sp. *multispinosa*-complex sp. V'.

Tunisia: *Parotoplana chartagoensis*; *Parotoplana* n. sp. '*microchartagoensis*'; *Parotoplana* n. sp. 1.

Regarding the overall faunistic similarities among areas of Western Mediterranean, two main blocks can be evidenced, one encompassing northern and eastern shores (Spain north of Barcelona, West Peninsular Italy, Sardinian-Corsican complex), and another covering the southern and eastern shores (Balearic Islands, Spanish Levante, Tunisia, Sicily) (Fig. 5 A). It is suggestive to link the existence of these two blocks to the poor dispersal potential of Proseriata (Curini-Galletti, 2001), leading to strongly regionalised community compositions. It is thus not surprising that both the main insular complexes of Western Mediterranean (Balearic Islands, Sardinian-Corsican complex) cluster with the neighbouring continental coasts, also considering the lowered glacial sea levels, which narrowed the geographic gap among these areas (Thiede, 1978). Conversely, the grouping of Lampedusa Islands, with Ionian and Alborán sea (Fig. 5 A), which includes all the stations with the lowest numbers of species, is likely an artifact due to the severely limited sampling in these areas.

Remarkably, a large fraction of the species (58) has been only found in a single beach. In some instances, this might be attributed to the occasional presence of species occurring in deeper or different types of sediments, such as those of the neighbouring rocky coasts, but the presence of such a large number of singletons questions the adequacy of our samplings to yield the full richness of sandy beach proseriate communities. Indeed, in none of the sectors a complete coverage of the expected species has been attained (Table 1, Fig. 5 B). Although this result could have been foreseen for poorly sampled areas, such as Lampedusa, with a single station, and 11 species, representing a 23% estimation of the number of species expected, this is however the case also for the most intensely sampled areas, such as the Sardinian-Corsican complex, with 35 stations

and the highest number of species found per area (58), where, nonetheless, the rarefaction curve does not reach a plateau, and we found 80% of expected species for the sector.

Species composition

All the marine families of Proseriata are represented in our dataset. Although comparisons with the diversity of proseriates outside the Mediterranean is hampered by the general, poor state of knowledge of composition and distribution of free-living Platyhelminthes (Appeltans et al., 2012), some parallels are evident, as the two most species-rich families in Mediterranean (Monocelididae, with 66 species and Otoplanidae, with 60 species) are also the most diverse globally (187 and 139 species described, respectively) (Tyler et al., 2006-2023). The other families are noticeably less diverse globally, and Archimonocelididae and Unguiphora, with eight and six species respectively in our dataset, appear comparatively well represented. This is not the case for Coelogynoporidae and Calviriidae, with nine and one species in our sample: these are predominantly cold-water taxa, poorly represented in the Mediterranean (Ax, 2008; Schockaert et al., 2011). Only few species of Yorkniidae are known globally, with one to three species at maximum in each biogeographical region (Scarpa et al., 2017); the single species we found is thus not an exception to this rule.

Our sample of Western Mediterranean proseriate fauna showed a marked taxonomic unbalance in terms of number of species per genera, given that three genera alone made up more than half of the species found: *Parotoplana* (with 40 species; 23 of which are new); *Archilina* (29 species; 22 new); and *Duplominona* (16 species; 14 new). As remarkable as the large fraction of new species of *Archilina* and *Duplominona* may seem, it may not come as a particular surprise, as most of them are tiny, fragile, interstitial forms occurring in subtidal areas, difficult to characterize at the species level for their exceedingly small and poorly sclerified copulatory structure; thus, so far, they have attracted limited attention in the Western Mediterranean (Martens, 1984; Martens and Curini-Galletti, 1993). This scenario, however, does not apply to *Parotoplana*, whose large sclerotised structures, often consisting of few pieces with very different morphologies, are easy to study and to utilize for taxonomic resolution at the species level; the genus, indeed, has been comparatively well studied at least in parts of the Western Mediterranean (Ax, 1956; Lanfranchi, 1978; Delogu and Curini-Galletti, 2007: Delogu et al., 2008; Delogu and Curini-Galletti, 2009; Casu et al., 2014). Notwithstanding this potential good knowledge on the genus, numerous new species have been found in our research, especially in areas where sampling have been so far little or none, suggesting that the census of the genus in the Mediterranean Sea is far from complete.

Table 1. Number of species in our database, stations sampled per sector, and estimated coverage based on Chao2 estimator.

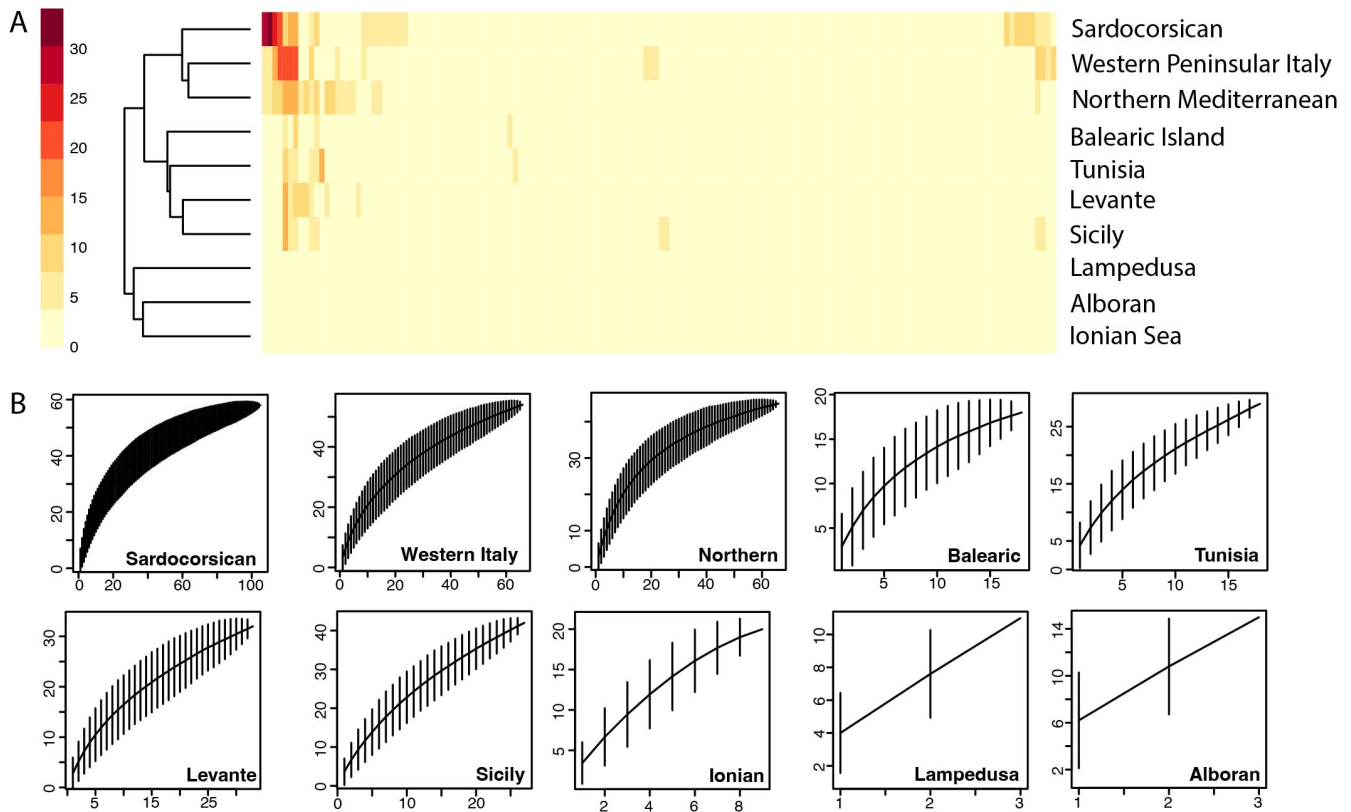|	Number of species	Number of stations	Chao	Estimation
Alboran	15	1	43.2	35%
Balearic	18	6	25.7	70%
Western Continental Italy	54	22	77.8	69%
Ionian Sea	20	3	23. 3	86%
Lampedusa	11	1	47. 7	23%
Levante	32	11	60.0	53%
Northern Mediterranean	45	22	53.9	84%
Sardinian-Corsican	58	35	72.1	80%
Sicily	42	9	72.8	58%
Tunisia	29	6	69. 3	42%

Figure 5. A: Heatmap representing the number of records of each species across different Mediterranean provinces. Dendrogram on the left is based on Bray-Curtis distances. B: Rarefaction curves showing the sampling effort in each region based on Chao estimator.

The three dominant genera in the Western Mediterranean Sea appear noticeably less diverse in the neighbouring Atlantic. It is indeed remarkable that only one species each of the genera *Archilina* and *Duplominona*, so species-rich in our dataset, have been so far reported from the entire coast of western Europe (Martens, 1983; Noreña et al., 2007), suggesting a high degree of endemism of the Mediterranean proseriate fauna, as well as intra-basin speciation patterns. However, further studies in this regard must necessarily include assessment of phylogenetic relationships based on clues other than morphology, as well as a more detailed knowledge of composition and distribution of Proseriata outside the Mediterranean than what is available at present.

CONCLUSIONS

Reconstructions of biodiversity patterns of meiofauna pointed out that exposed, coarse sand beaches are among the habitats with the lowest meiofauna diversity (Vanreusel et al., 2023). A taxonomic bias is however apparent; these studies were mostly based on few selected taxa, like Nematoda and Copepoda, easily retrievable from fixed samples, to the exclusion of most soft-bodied taxa. Our result, on the contrary, showed that exposed, reflective beaches harbour a rich and highly diverse fauna of Proseriata. Indeed, in our samples, Proseriata were dominant in terms of number of individuals and species in the swash zone, and in most of the sampled shoaling zones, while, at the same levels, we found few, if any, nematodes and copepods, but rather other members of soft-bodied fauna, like Annelida and Nemertea (own

unpublished data). We wonder how a complete picture of beach ecology can be obtained excluding a dominant category: problems inherent to the study of flatworms have undoubtedly led to an undervaluation of the taxon in ecological study.

Noticeable exceptions to the widespread neglect of Platyhelminthes are the studies utilizing metagenetic approaches, which have re-evaluated the rank abundance of the group in sandy beaches (Fonseca et al., 2010, Leasi et al., 2018; Martínez et al., 2020). However, in most instances, the lack of GenBank match of the sequences retrieved has so far limited the use of the technique, and attribution of sequences only to higher-rank taxa allowed a partial description of biodiversity and limited or null inferences on the biological properties of the species found. Indeed, the sheer number of undescribed species found during our research indicates that α-taxonomy level species descriptions of marine flatworms are severely lagging behind and will require a more focused commitment.

Reconstruction of biogeographical patterns of meiofauna suffer from the same taxonomic bias: the recent study by Garraffoni et al. (2021) on the biogeography of meiofauna does not include Platyhelminthes. Furthermore, our results, showing signals of biogeographical structuring within a comparatively small area as the shores of the Western Mediterranean Sea, may question whether the large geographical areas of coastal and shelf areas of the world presented by Spalding et al. (2007), based on distribution data of macrofauna, and used as biogeographical units by Garraffoni et al. (2021), may be extended to groups like Proseriata, sticking to sand grain and lacking any ways for dispersal, and that may thus perceive barriers in a different ways than either macrofauna and other meiofaunal groups.

However, the lack of datasets on distribution in time and space of Platyhelminthes has so far drastically hampered their consideration: they simply do not exist. The present work should thus be considered the first step in the direction to fill such a knowledge gap on marine flatworms.

SUPPLEMENTARY MATERIAL

Supplementary Table 1. Dataset of the distribution of Proseriata in Western Mediterranean. Columns: station levels (swash, shoal, deep); row: species.

Supplementary Table 2. Granulometric data.

Supplementary Table 3. Morphological functional traits of the species found in the survey.

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