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Better Alone Than in Bad Company: New Species of Caudofoveate Limifossorid (Mollusca, Aplacophora) Unravels Patterns of Distribution Hidden in the Deep Atlantic

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Aplacophorans are common inhabitants of the deep-sea, where many places remain unexplored regarding their biodiversity. Filling a gap in knowledge about these animals from the South Atlantic, *Scutopus variabilis* sp. nov. (Caudofoveata, Limifossoridae) is described; further, species distribution modelling (SDM) was performed to elucidate the distribution patterns of Atlantic species of *Scutopus*. The type materials of *S. megaradulatus* Salvini-Plawen (1972) and *S. chilensis* Salvini-Plawen (1972), were examined and a search was performed for specimens of *Scutopus* held in museum collections. *Scutopus variabilis* sp. nov. has a slender and highly variable body form and a very distinct suture line is present midventrally. Two dominant types of trunk sclerites were observed by Scanning Electron Microscopy (SEM): one elongated with lateral margins slightly concave in medial portion, and another longer, with narrower base; its radula bears up to eight rows of heavily sclerotized teeth bearing 12–16 small denticles. The species occurs in a wide bathymetric range (40–1300 m), being more abundant at the edge between the continental shelf and upper slope. Outside the areas from where these samples were obtained, suitable areas for *S. variabilis* sp. nov. were found in the Southern Caribbean Sea (from where *S. megaradulatus* is recorded) and in the Brazilian Northern coast; the Gulf of Mexico and the Brazilian Northeastern coasts were found as unsuitable. Species of *Scutopus* appear to exhibit different patterns of geographical distribution: the European *S. ventrolineatus* Salvini-Plawen (1968) and *S. robustus* Salvini-Plawen (1970) are known as widely distributed, while non-European representants, the American *S. megaradulatus*, *S. chilensis* and *S. variabilis* sp. nov., and the Japanese *S. schanderi* Saito and Salvini-Plawen (2014) and *S. hamatamii* Saito and Salvini-Plawen (2014) have more restricted distributions. However, clear and definite patterns of distribution of some of these species are probably blurred by sampling bias, for the European area is better studied. In the Atlantic, the SDM showed that species of *Scutopus* occur in a way that overlapping is minimized. Great sampling efforts combined with detailed descriptions based on SEM have revealed an interesting, abundant and up to now undescribed Brazilian deep-sea malacofauna.

Keywords: taxonomy, biogeography, species distribution modeling, Caudofoveata, Limifossoridae

INTRODUCTION

Ubiquitous among the deep-sea organisms, aplacophorans form a molluscan group of particular phylogenetic interest (e.g., Kocot et al., 2011; Smith et al., 2011; Vinther et al., 2012, 2017; Mikkelsen et al., 2018, 2019), ecological importance (Scheltema, 1987, 1997; Scheltema and Ivanov, 2009), and biogeographical relevance (Scheltema, 1985; Ivanov and Scheltema, 2008; Corrêa et al., 2014, 2018; Bergmeier et al., 2017, 2019; Cobo and Kocot, 2020). They are generally characterized by their worm-like bodies covered by sclerites, and formed by two clades: Solenogastres, which are epifaunal and bear a ventral pedal furrow, and Caudofoveata, whose species are infaunal, without a ventral locomotory organ, and have an oral shield (that is absent in solenogasters). A total of 420 species of aplacophorans have been described so far, most of them occurring on the continental slope (Todt, 2013).

In the deep Atlantic Ocean, most reports on caudofoveates are for species from both European or North American waters, and fewer are based on specimens collected in the Southern Hemisphere. For the Brazilian coast (Southwestern Atlantic), in particular, eight species are known: *Chevroderma turnerae* Scheltema, 1985 recorded by Scheltema (1985) and Ivanov and Scheltema (2008), and *Spathoderma bulbosum* Ivanov and Scheltema, 2008 by Ivanov and Scheltema (2008); *Falcidens targatus* Salvini-Plawen, 1992 and *F. acutargatus* Salvini-Plawen, 1992 studied by Corrêa et al. (2014); *Claviderma amplum* Ivanov and Scheltema, 2008, *C. crassum* Ivanov and Scheltema, 2008 and *C. virium* Corrêa, Miranda and Passos, 2018 investigated by Corrêa et al. (2018); and *F. australocaudatus* Passos, Corrêa and Todt, 2016 described by Passos et al. (2018). Passos et al. (2019) have summarized all the records of aplacophorans from Brazilian waters up to that time, pointing out that most of them are from restricted oil-rich areas, there remaining large parts of its coast in which these molluscs were never reported (as its southernmost and northernmost portions), and that there are many other species to be investigated.

In the present contribution, a new species of the genus *Scutopus* Salvini-Plawen, 1968 is described, through the analysis of many specimens collected along the southeastern and southern coasts of Brazil, with some records for regions never explored before. This genus of Caudofoveata was created by Salvini-Plawen (1968), based on the description of *S. ventrolineatus* Salvini-Plawen, 1968, originally discovered near Bergen, Norway, Scandinavia. Afterward, a second European species was described by Salvini-Plawen (1970), *S. robustus* Salvini-Plawen, 1970, and two others by Salvini-Plawen (1972), *S. megaradulatus* Salvini-Plawen, 1972 and *S. chilensis* Salvini-Plawen, 1972, from the Caribbean Sea and Chile, respectively. More recently, Saito and Salvini-Plawen (2014) recorded *S. schanderi* Saito and Salvini-Plawen, 2014 and *S. hamatanii* Saito and Salvini-Plawen, 2014 from the Sea of Japan. The Brazilian new species is here described based on the general body morphology and on the details of its oral shield, sclerites, and radula, in comparison with those congeneric six species; further, their bathymetric and geographical distributions are modeled and discussed regarding how these can advance delineation and identification of deep-sea

caudofoveate species. It is here emphasized that this new species has a highly variable body form, and only through the observation of the many available specimens it was possible to describe it in detail, complementing ongoing recent discoveries that have been performed on the malacofauna of the Brazilian deep-sea waters.

MATERIALS AND METHODS

Most specimens were collected off the coasts of the Espírito Santo (ES) and Rio de Janeiro (RJ) States, southeast Brazil, obtained from bottom sediment samples collected by box-corers and Van Veen grabs, through the activities of the Projects “Habitats” and “Ambes” [for details about these projects, see Passos and Machado (2014) and Machado and Passos (2016)]. These samples were initially fixed in 4% formaldehyde and after sieving the animals were sorted and transferred to a solution of 70% ethanol. Apart from the material of these projects, other samples were collected off the States of São Paulo (SP) (also in the southeast), and in the southern States of Paraná (PR) and Rio Grande do Sul (RS). These latter samples were obtained by three research projects: “Projeto Integrado,” which occurred from 1985 to 1986 and collected in the shelf of Ubatuba (São Paulo) (Pires-Vanin and Matsuura, 1993), and by the Projects “MBT” and “Revizee,” in which more scattered bottom samplings were performed along all this area, the former in 1970/1, the latter in 1998/9. These materials are deposited in the molluscan collections of the following institutions: Museum of Zoology of the State University of Campinas (ZUEC APL), Campinas (SP), Museum of Zoology of University of São Paulo (MZSP), SP, National Museum of Rio de Janeiro (MNRJ), RJ, and Museum of Zoology of Federal University of Sergipe (CZUFS APL), São Cristóvão (SE), all in Brazil.

The animals were initially observed under stereomicroscopes, and then some were sorted for more detailed analysis using Scanning Electron Microscopy (SEM). The methods employed were the same as the ones of Corrêa et al. (2014, 2018) and Passos et al. (2018). Because individuals (and specially the smaller ones) are hard to identify through only the general morphology, some of their sclerites were extracted from the trunk by using fine needles, and then placed on slides, air-dried and covered with Entellan and a cover slip for permanent preparations; these slides are also deposited in the respective collections.

Apart from the Brazilian specimens, samples of *S. megaradulatus* analyzed by Scheltema (1981) from North Carolina, United states, deposited in the Museum of Comparative Zoology (MCZ), Harvard University, Cambridge, MA, United states, as well as the samples of this species and of *S. chilensis* deposited in the American Museum of Natural History (AMNH), New York, United states, were observed. Further, while an analysis was performed in the MCZ and in the National Museum of Natural History, Smithsonian Institution (USNM) (Miranda et al., 2020), specimens identified as species of *Scutopus* were also searched in these molluscan collections.

To further investigate the potential distribution of the *Scutopus* species in the Atlantic, a species distribution model (SDM) was performed using MaxEnt 3.4.4.k (Phillips et al.,

2006), for the new species described herein, *S. robustus* and *S. ventrolineatus*. *Scutopus megaradulatus* was not included due to the few records available in literature (<10). For the new species, a total of 33 records were used, based on the samples observed in this study. For *S. robustus* (24 records) and *S. ventrolineatus* (15 records), datasets of records were produced based on the literature (see **Table 3**); those of *S. robustus* from Salvini-Plawen (1977) were not included as they are considered doubtful (Ivanov and Scheltema, 2001).

Environmental data were obtained from the Global Marine Environment Datasets (GMED) (Basher et al., 2018) with a resolution of 5' (approx. 9.2 km near equator). As caudofoveates are benthic organisms, variables reflecting environment near the seabed were used, namely depth, slope, bottom temperature, primary productivity and bottom silicate. These variables had a weak to medium correlations ($r < 0.7$), calculated by the Pearson correlation in ENMTools 1.4.3 (Warren et al., 2010). To generate the model, 100,000 random background points were used, with a regularization multiplier of 1. 75% of presence records were randomly chosen and used in the model training while the remaining 25% were used in the model testing. Also, the “fade by clamping” option was set to reduce prediction into areas with environmental conditions that were not found during model training, and 10 replicates using Bootstrap as “Replicated run type” (Basher and Costello, 2016). All other parameters were used as default. To test model goodness of fitting, the area under the curve operating characteristics was used (AUC). The potential distribution was computed as Cloglog. Later, with this the output, to define the Minimum Presence Threshold (MPT), “10 percentile training presence” threshold was used (Morueta-Holme et al., 2010). The final output rasters were classified in not suitable (below the MPT) and suitable (above MPT) areas.

RESULTS

Family Limifossoridae Salvini-Plawen, 1969

Genus *Scutopus* Salvini-Plawen, 1968

Type species: *Scutopus ventrolineatus* Salvini-Plawen, 1968 by original designation.

Remarks: Salvini-Plawen (1968) characterized *S. ventrolineatus* by its long, undivided, cylindrical body which coils up spirally when it is disturbed, its radula composed by multiple rows of paired teeth, each tooth bearing median denticles, an undivided or homogeneous, post-oral shield, and the presence of a long midgut sac or digestive gland, and by its sclerites that ventrally are positioned in a divergent way forming a clear external ventral sutural line. Later, Salvini-Plawen (1975) and Ivanov (1981) highlighted that the characters of the oral shield and the radula are typical of *Scutopus* species. The new species described herein has these main characteristics, as shown below.

Scutopus variabilis sp. nov. Passos, Corrêa and Miranda (**Figures 1–6, 8**)

LSID: urn:lsid:zoobank.org:act:A734DD68-A074-42FB-A9C4-A1DFAD68D4B9

Type Material

Holotype: ZUEC APL 277, sta HAB6-C7-R2(2-5) (22°59'52.609"S, 40° 47' 45.008"W) (Brazil – off Rio de Janeiro State), “Habitats” Project coll., 30/vi/2008, 689.4 m; entire individual (**Figure 1A**) plus one slide with its sclerites. Total length: 11 mm; anterium plus neck: 2 mm; trunk: 8 mm; posterium: 1 mm.

Paratypes: All collected in the southeastern and southern Brazilian coasts, from off States of ES, RJ, SP, PR, and RS; 188 specimens in 71 samples (**Table 1**).

Type locality. Off Rio de Janeiro, 40°47'45.008"W, 22°59'52.609"S, 689.4 m.

Non-type material. All collected in the southeastern Brazilian coasts, from off States of ES and RJ; 153 specimens in 61 samples (**Supplementary Table 1**).

Diagnosis. Body long, slender, up to 14 mm in length, often contorted, almost uniform in diameter; in most specimens divided in three parts: an anterior part separated by a main collar from a median part, and a slightly tapered posterior part. Oral shield post-oral, ventral to the mouth. Midventral suture line present. Two main types of sclerites: one elongated, with lateral margins slightly concave in medial portion, with base wider and about a half of the blade length, and another shorter, triangular, base and blade with continuous straight lateral margins; in both, blade ornamented with a central keel and weak adjacent longitudinal grooves. Radula distichous, with up to eight transversal rows of heavily sclerotized teeth (except for the two most proximal pairs); each tooth inwardly curved, with 12–16 small median bent denticles present in all the extension of the concave, inner margin.

Etymology. The name *variabilis* refers to the variable form and color exhibited by the specimens of this species.

Description

External Appearance

Body whitish to brownish in color, opaque in most adult specimens; cylindrical in form, long, slender, up to 14 mm in length, often contorted; almost uniform in diameter, up to 0.9 mm in width (**Figures 1, 2A–D,G**). Body almost homogeneous throughout its length, but in most specimens with three externally distinguishable parts: an anterior, separated by a main collar from a median part (**Figures 1B,F,I,K,M,O, 2A–C,G**), and a slightly tapered posterior part (**Figures 1A,C,K**). Anterior part whitish to transparent, composed by a sometimes protruded peribuccal region (or anterium) (**Figures 1C,I, 2A,B**) and a short foregut region (neck or prothorax) (**Figures 1A,H, 2A,B**). Median part (trunk or metathorax) dark brown, reflecting the presence of the midgut internally; a secondary collar sometimes present separating this median part in two regions: an anterior short midgut region, and a long posterior midgut sac region (**Figure 1H**). Posterior part short, composed by a narrower, transparent prepallial region and a pallial region which is often slightly inflated; secretions of the animal occur over the sclerites, giving a reddish color to the entire posterior part, or more often around the pallial region or in the center of the posterior end (**Figures 1A,B,D–F,I,K**). When the peribuccal

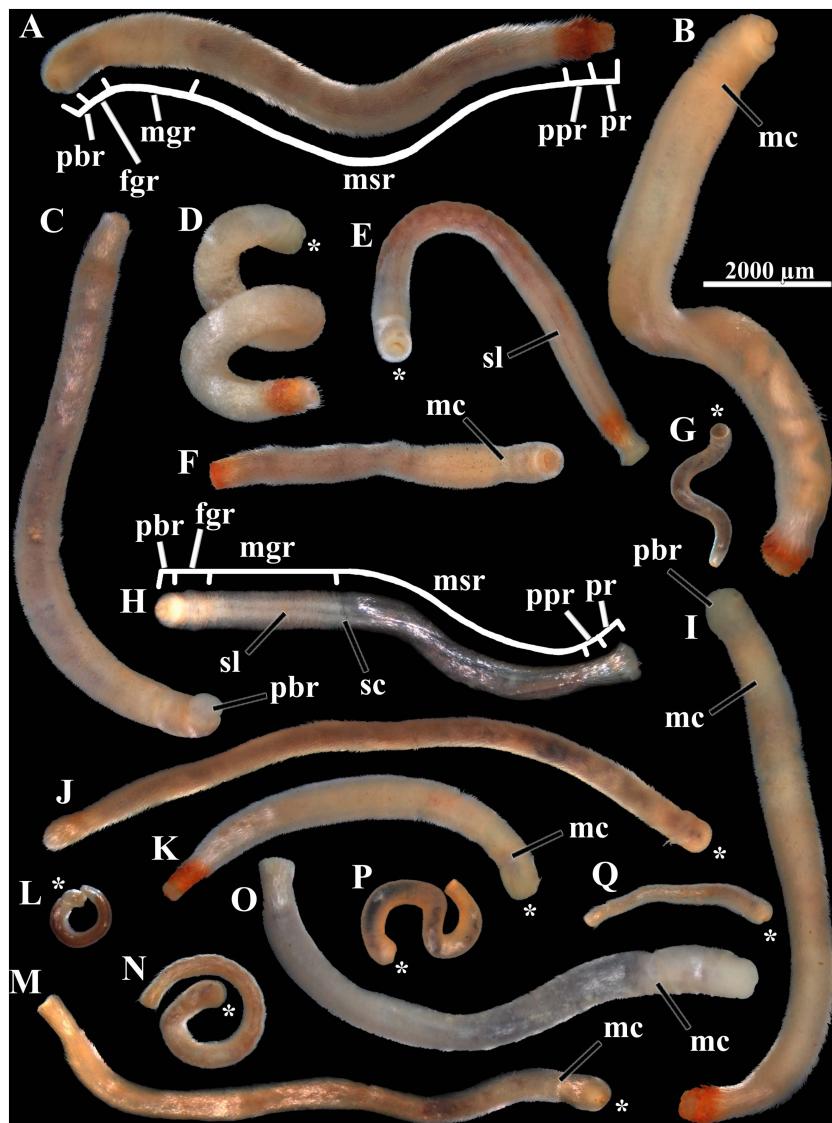


FIGURE 1 | *Scutopus variabilis* sp. nov. Photomicrographs under stereomicroscope of specimens of different sizes showing their variable body form and color (all in same scale). The body regions are shown in (A) (holotype) and (H), (B) and (D) had their soft parts dissolved for the extraction of their radulas [which are shown in Figures 4A,E, respectively and of their sclerites from the different body regions. The peribuccal region is protruded in (C) and (I)). The midventral suture line is visible in (E) and (H); the main collar in (B), (F), (I), (K), (M), and (O); and the secondary collar in (H). The asterisks in (D), (E), (G), (J–N), (P), and (Q) show the anterior end. fgr - foregut region; mc - main collar; mgr - midgut region; msr - midgut sac region; pbr - peribuccal region; ppr - prepalial region; pr - pallial region; sc - secondary collar; sl - midventral suture line. Voucher numbers: (A) – ZUEC APL 277, (B) – ZUEC APL 285, (C) – ZUEC APL 287, (D) – ZUEC APL 284, (E) – ZUEC APL 279, (F) – ZUEC APL 282, (G) – ZUEC APL 306, (H) – ZUEC APL 298, (I) – ZUEC APL 286, (J) – MZSP 154099, (K) – ZUEC APL 286, (L) – ZUEC APL 326, (M) – MN RJ 23638, (N) – ZUEC APL 331, (O) – ZUEC APL 291, (P) – ZUEC APL 311, (Q) – ZUEC APL 283.

region is swollen, the ventral oral shield is visible (Figure 2E); when contracted, the oral shield contracts in its midline, appearing divided in two lateral parts (bipartite) (Figures 2F,H). Sclerites uniformly cover all the surface of the body, except ventrally, where they are positioned in a divergent way, forming a midventral suture line along the foregut region and all the midgut and midgut sac regions (Figures 1E, 2A–C,G). Variations in color and form occur among specimens of the same size, and among juveniles and adults; the main collar is not visible in many individuals and so they appear to have

an undivided body (Figure 1J); smaller individuals tend to be slender, transparent, with the main collar and the ventral suture line quite indistinguishable (Figures 1G,L,N,P,Q).

Sclerites

Adpressed to the mantle, positioned parallel to the longitudinal body axis, except in the midgut region, where they are bristling in some specimens (Figures 2C,G). In the peribuccal region flat, small, 50 μm long \times 25 μm wide, drop-shaped, without waist, pointed at the tip, smooth (Figure 3A); or triangular,

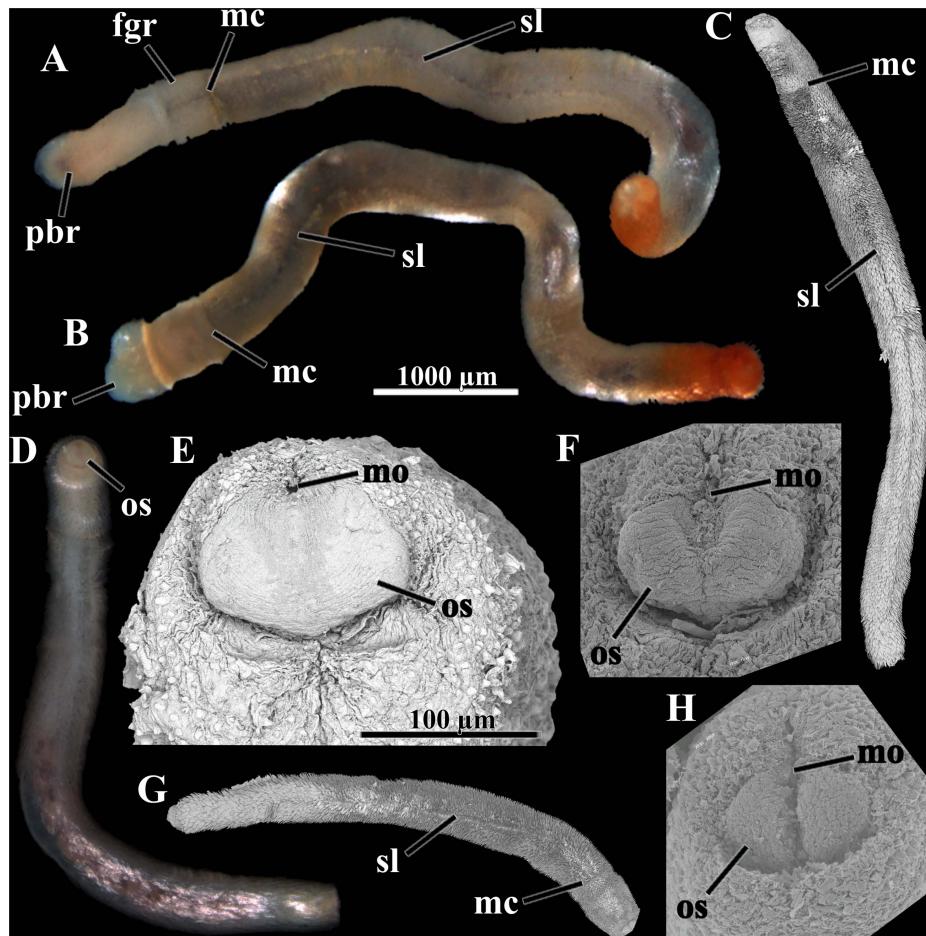


FIGURE 2 | *Scutopus variabilis* sp. nov. Photomicrographs under stereomicroscope [(A), (B), and (D)] and SEM (C,E–H); (A–D) and (G) are in same scale, as are (E), (F) and (H). (E), (F), and (H) are a detail of the anterior end, showing the oral shield in different degrees of contraction; (E) is the oral shield of (D), which is in the most relaxed state; in (F) it is in an intermediary state and in (H) it is strongly contracted appearing bipartite. The peribuccal region is protruded in (A) and (B). The midventral suture line and the main collar are visible in (A–C) and G. fgr – foregut region, mc – main collar, mo – mouth, os – oral shield, pbr – peribuccal region, sl – midventral suture line. Voucher numbers: (A,B) – MNRJ 23639, (C) – ZUEC APL 306, (D) – ZUEC APL 280, (E) – ZUEC APL 280, (F) – ZUEC APL 314, (G) – ZUEC APL 312, (H) – ZUEC APL 299.

longer, 86 μm long \times 36 μm wide, with a distinct waist, base longer and wider than blade, blade ornamented with a central keel and pointed at the tip, basal margin almost straight (Figure 3B). In the foregut region 118 μm long \times 28 μm wide, with a weak waist, base shorter but wider than blade, blade ornamented by a median keel sided by weak longitudinal grooves, basal margin almost straight (Figure 3C). In the midgut region, triangular, 95 μm long \times 39 μm wide, without waist, base and blade with continuous straight lateral margins, blade ornamented by a central keel (Figure 3D); or elongated, 131 μm long \times 56 μm wide, lateral margins slightly concave in medial portion, base wider and about a half of the blade length, blade ornamented with a keel and weak adjacent longitudinal grooves, basal margin slightly notched (Figure 3E). In midgut sac region, two dominants: one with the same shape as the latter, up to 162 μm long \times 56 μm wide (Figure 3F), and another, longer, with narrower base, up to 194 μm long \times 45 μm wide

(Figure 3G); a third type, drop-shaped, less abundant, shorter, 86 μm long \times 45 μm wide (Figure 3H). Midventral suture line with two types: one elongated, base wider, one third of the total length, blade with parallel lateral margins (Figure 3I), and other tapered in medial portion, with base weakly wider than blade (Figure 3J), both up to 193 μm long \times 37 μm wide, with a keel and longitudinal grooves in blade, and a rounded basal margin. Prepallial region with two very elongated types: one lanceolate, with continuous base and blade lateral margins, 262 μm long \times 62 μm wide (Figure 3K), and another narrower, with short base and long blade, parallel margins in most of its length, 287 μm long \times 37 μm wide (Figure 3L); both with several grooves on blade and rounded basal margin. In pallial region: spatulate, narrow, short, 73 μm long \times 11 μm wide, with a pointed smooth blade and wider base, present in the posterior margin of pallial region (Figure 3M); and large, 390 μm long \times 48 μm wide, needle shaped or wider at base, with a

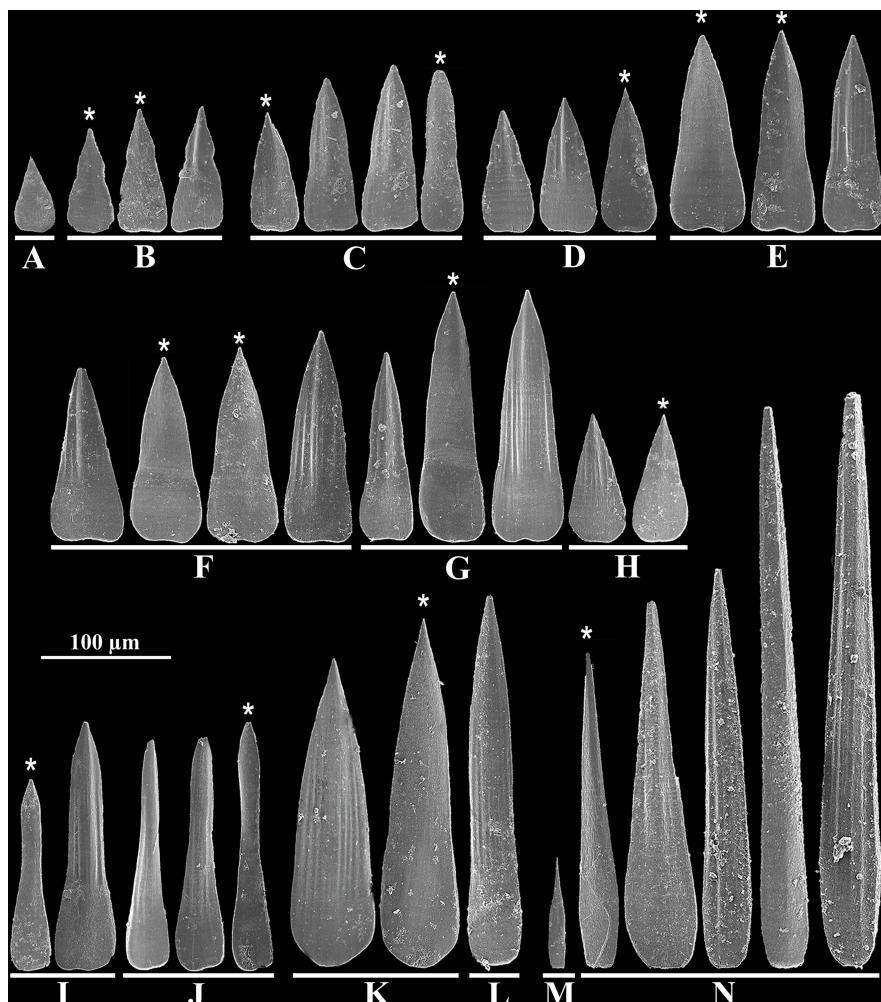


FIGURE 3 | *Scutopus variabilis* sp. nov. SEM photomicrographs of isolated sclerites from the different body regions: **(A), (B)**, peribuccal region; **(C)**, foregut region; **(D), (E)**, midgut region; **(F–H)**, midgut sac region; **(I), (J)**, midventral suture line; **(K), (L)**, prepallial region; **(M), (N)**, pallial region. The asterisks point out the sclerites shown from the side facing the body. All in same scale.

keel and longitudinal grooves on all along the base and blade (**Figure 3N**). All the sclerites have a smooth surface facing the body (**Figure 3**, asterisks).

Radula

Large and elongated, up to 1.2 mm long, distichous, with up to eight transversal rows of paired teeth, which are heavily sclerotized, except the two most proximal pairs (**Figure 4A**). Each tooth is inwardly curved, up to 790 µm long × 385 µm wide, with 12–16 small median bent denticles that are present along the whole extension of the concave, inner margin of the tooth (**Figures 4B–E**).

Bathymetric and geographical distribution: A total of 342 specimens distributed in 133 samples were examined, most of them (123 samples) obtained from the States of Espírito Santo and Rio de Janeiro by the “Habitats” and “Ambes” Projects (**Figure 5**). In this area, samplings were more intensive and occurred in a wide bathymetric range, and so the specimens of

S. variabilis sp. nov. were collected from 40 to 1300 m, with 62 samples coming from the shelf waters (less than 200 m). Ten samples were obtained from scattered points outside this area, proving that this species occurs all along the Brazilian southeastern and southern coasts; these samples were collected from only the continental shelf (less than 130 m depth) (**Figure 6**). The number of specimens per sample varies from 1 to 12, but in most (98 samples) there are up to 3 three individuals. This species can be characterized as occurring in a wide bathymetric range, with a great abundance at the edge (140–200 m) between the continental shelf and upper slope (**Figure 5**).

Species Distribution Modeling

For all the three analyzed species, the distribution model has a mean AUC > 0.996 for the training and test data, with a standard deviation of 0.001. The 10 percentile training presence threshold was 0.1167, 0.3075, and 0.4359, for *S. variabilis* sp. nov., *S. robustus*, and *S. ventrolineatus*, respectively. The

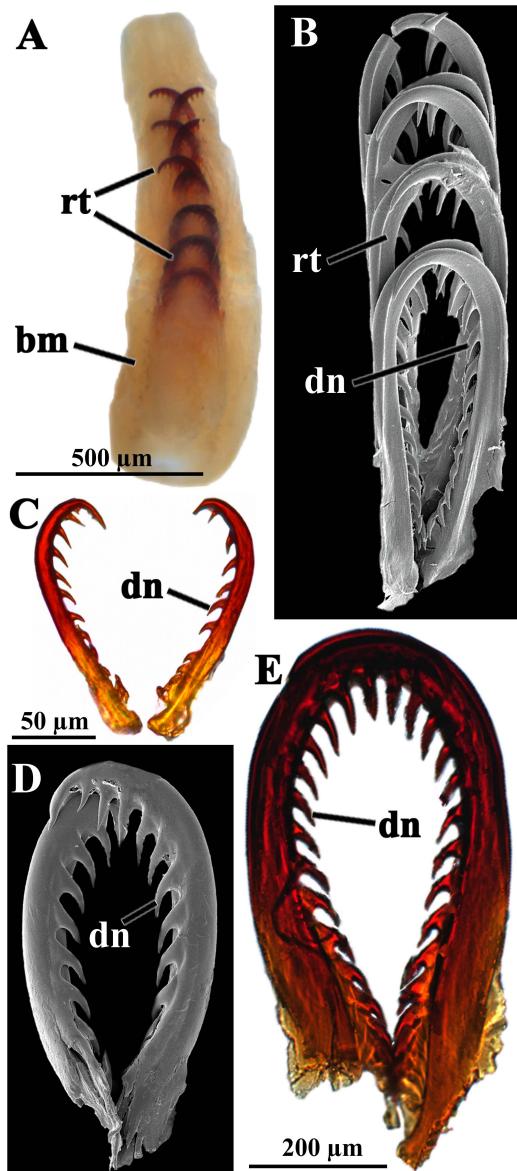


FIGURE 4 | *Scutopus variabilis* sp. nov. Photomicrographs under stereomicroscope (**A**), SEM [**(B)** and **(D)**] and light microscopy [**(C)** and **(E)**] of the radula. In **(A)** (ZUEC APL 284) the entire radula of the individual shown in **Figure 1D** is viewed immersed in the buccal mass. In **(B)** (ZUEC APL 319) four pairs of radular teeth are viewed in detail, and isolated pairs in **(C-E)**; in **(C)** (ZUEC APL 321) and **(D)** (ZUEC APL 319) the teeth were obtained from two small specimens (up to 4 mm in length), and in **(E)** (ZUEC APL 285) from the larger animal (about 11 mm) shown in **Figure 1B**. **(B-D)** are in same scale. bm – buccal mass, dn – median denticles, rt – radular tooth.

environmental layer that most explained the potential habitat suitability of *S. variabilis* sp. nov. is depth, followed by bottom temperature (**Table 2**). Each of the other variables explained less than 10% of the habitat suitability. Depth and temperature had similar influences on the distribution of *S. robustus* (**Table 2**). Although depth had similar values of importance, for *S. ventrolineatus* silicates and primary productivity had

relatively great importance in the final habitat suitability, with slope and temperature explaining less than 10% of habitat suitability (**Table 2**).

The generated maps show that main suitable areas of occurrence of *S. variabilis* sp. nov. are the Brazilian Southeastern and Southern coasts (Figure 7); the limits of distribution are the North of Espírito Santo in the north edge of this area, and the Chuí in the south. There were also some hotspots of suitability in Southern Caribbean Sea and a very narrow hotspot in the Brazilian Northern coast, east to the Amazon River mouth (States of Pará and Maranhão, Brazil). No suitability was found for *S. variabilis* sp. nov. in the Gulf of Mexico and in the Brazilian Northeastern coasts. In the Eastern Atlantic, points of suitability were found in Cape Verde and Angola Basins, in the Adriatic Sea (Albania) and in the area of the Suez Isthmus (Egypt).

Scutopus ventrolineatus was the species with the wider estimated distribution. The main suitable areas were between Southern Scandinavia and Britain, English Channel, Southwestern Ireland, Bay of Biscay, Iberian Peninsula, Strait of Gibraltar and Mediterranean of France (Figure 7). Wide suitable areas were found in Cape Verde, Guinea and Angola Basins in Africa. Outside the Eastern Atlantic, a continuous suitable area was found from Newfoundland to the North of Florida. Other areas were the Northern Gulf of Mexico, Tierra del Fuego, and Argentine Basin.

For *S. robustus*, the map shows that the main suitable areas are the Northwestern of Norway, Scotland, North of Ireland, South of Iceland, and Northern Lusitania, occurring in the outer part of West European Basin (Figure 7). In the Western Atlantic, suitable areas were found in Northeastern Falklands.

Through modeling, small areas of overlapping distribution of these species were detected (Figure 7). *Scutopus ventrolineatus* and *S. robustus* had the largest overlap in Southern Norway, and a small area occurred in the Iberian Basin. *Scutopus variabilis* sp. nov. had many islands of overlapping areas with *S. ventrolineatus* in Angola and Cape Verde Basins. No overlaps were found between *S. robustus* and *S. variabilis* sp. nov. or shared by all the three species.

Comments on Other Examined Species of *Scutopus*

Two lots of *S. megaradulatus* deposited in the AMNH collection were examined. One of them (AMNH 265347) was from the single sample listed by Salvini-Plawen (1972), which had two specimens when he originally described this species. Currently, this lot AMNH 265347 contains two small tubes: one bears the anteriormost body part of a specimen (the oral shield is visible) that lost some of its sclerites (Figures 8A,B); and the other has an incomplete animal (with its anterior body part missing, see detail in Figure 8C) which is the same illustrated in the original description of this species (compare Figure 8C with fig. 21 of Salvini-Plawen, 1972). The radula described by Salvini-Plawen (1972) was surely extracted from the latter individual, which was in turn designated as the lectotype by Boyko and Sage (1996). The other lot (AMNH 265348) contains a fragment of the trunk, presumably from the midgut region (the bristling

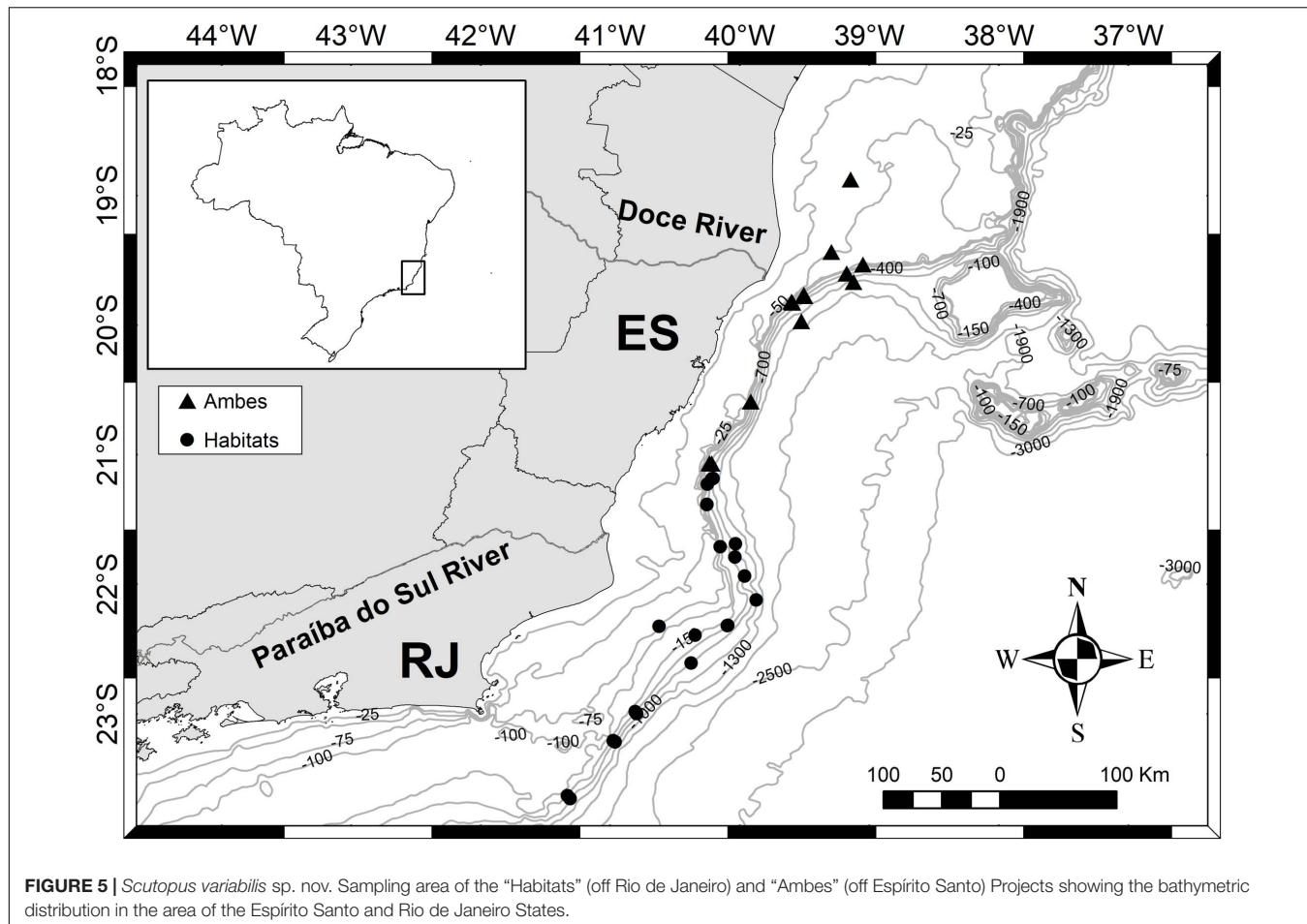


FIGURE 5 | *Scutopus variabilis* sp. nov. Sampling area of the “Habitats” (off Rio de Janeiro) and “Ambes” (off Espírito Santo) Projects showing the bathymetric distribution in the area of the Espírito Santo and Rio de Janeiro States.

sclerites are visible; **Figure 8D**) of one individual cited by Salvini-Plawen (1992) as a second examined sample collected in the same area of the Gulf of Darien, Caribbean Sea, at about 900 m depth, off Panama. Salvini-Plawen (1992) also referred to a third sample of *S. megaradulatus* which was obtained at 1861 meters depth off the western Cape coast, South Africa, but the place where it is deposited could not be tracked, and thus this single record of this species from the eastern Atlantic was not confirmed. Scheltema (1981) examined specimens of *S. megaradulatus* collected at 650 m depth off Cape Hatteras, and these compose the lot MCZ 396015.

Regarding *S. chilensis*, two lots deposited in the AMNH collection were examined, both with labels indicating that they were from the same sample collected in the Strait of Magellan, southern Chile, which was one of the three samples used by Salvini-Plawen (1972) for the description of this species; at that time, this sample contained two specimens and a type was not designated. Currently, the lot (AMNH 265349) has an individual which had its anterior and posterior parts dissected (**Figure 8E**), and it is not possible to affirm this is the same of the figure 26 of Salvini-Plawen (1972); the other (AMNH 265350) is a slide containing a hardly visible radula. They were designated by Boyko and Sage (1996) as the lectotype and paralectotype, respectively.

In the collection of the USNM, all the lots identified as *Scutopus* were analyzed, including the samples examined by Teece (1979) from the Gulf of Mexico, but they revealed to belong to species from other genera (*Psilodens*, for example). In South America, records of *Scutopus* spp. from Brazil were made by Rios (1994, as “*Scutopus cf. megaradulatus*”; and 2009, as “*Scutopus* sp.”), and from Uruguay by Forcelli and Narosky (2015, as “*Scutopus* sp.”). However, the samples on which they were based could not be found, and so these records are doubtful.

DISCUSSION

Scutopus has been traditionally classified in the family Limifossoridae, along with other two genera, *Limifossor* Heath, 1904 and *Psilodens* Salvini-Plawen (1977), whose species have a characteristic multiseriate distichous radula; the inclusion of a fourth genus, *Metachaetoderma* Thiele, 1913, is debated and unsolved (Salvini-Plawen, 1969; Ivanov, 1981). In *Psilodens* and *Scutopus* the body is slender, sometimes bearing an annular constriction separating an anterior (formed by peribuccal plus foregut regions) from the median body part, while species of *Limifossor* have stouter bodies without externally visible divisions. Apart from this, the radula of *Psilodens* and *Scutopus*

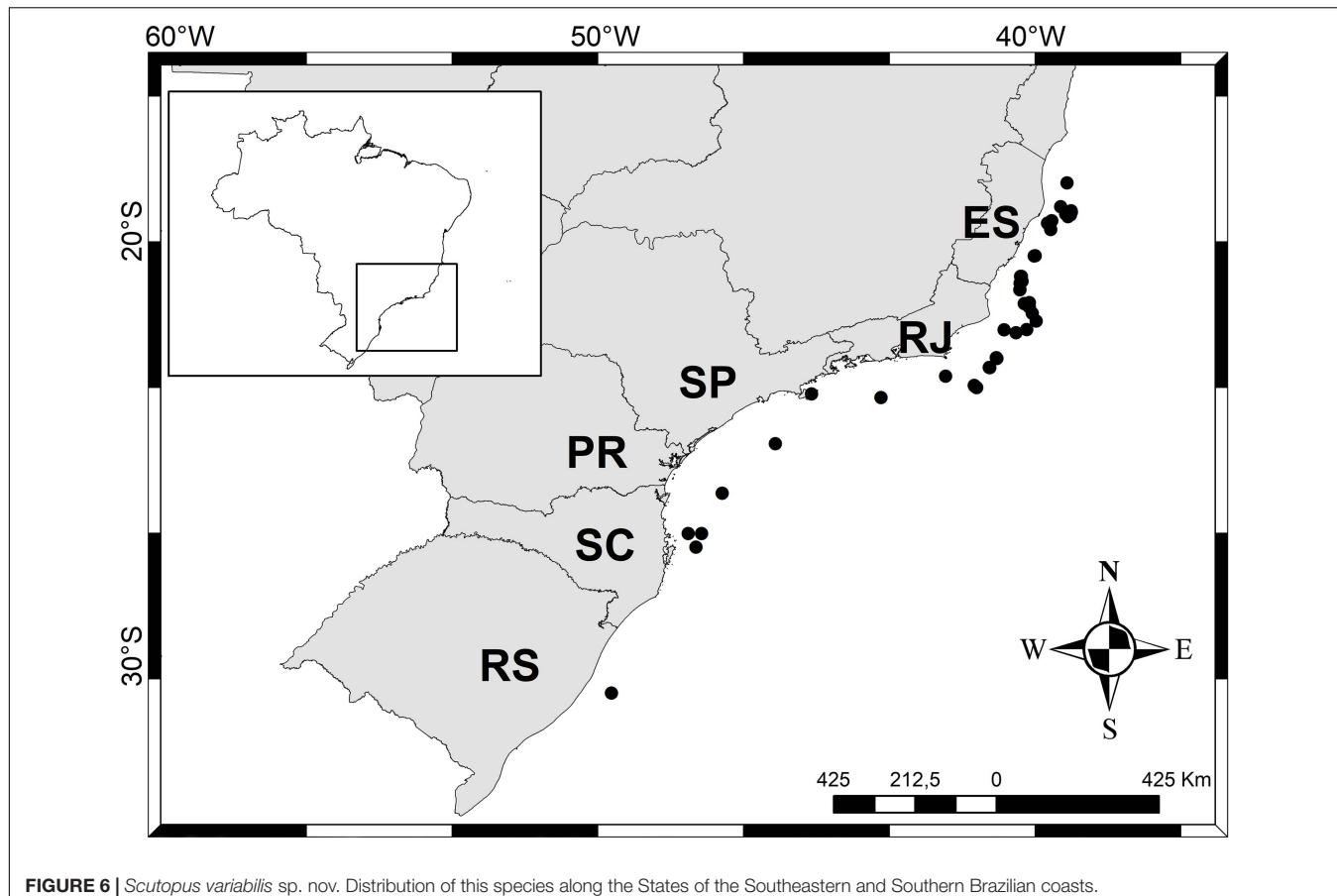


FIGURE 6 | *Scutopus variabilis* sp. nov. Distribution of this species along the States of the Southeastern and Southern Brazilian coasts.

is quite distinct from the one of *Limifossor*: in the former genera, each tooth is inwardly curved, like a sickle, the ones of *Scutopus* having a variable number of denticles distributed all along or in a part of the concave inner side of each tooth, while in *Psilodens* there are no denticles; in *Limifossor* each tooth consists of broad plates that bear a main lateral projection like a long hook-shaped stylet, and one or two small additional projections which form a jagged cutting inner edge (Salvini-Plawen, 1968, 1977, 1992; Ivanov, 1981; Scheltema, 1981). Differences among these genera also occur in the shape of the oral shield, that is undivided in species of *Scutopus* and bipartite in *Limifossor* and *Psilodens* (Salvini-Plawen, 1968, 1977, 1992; Ivanov, 1981; Scheltema, 1981). To date there are five species of *Limifossor* and three of *Psilodens*, and together with the seven species of *Scutopus* they characterize the Limifossoridae as the less diverse family among the caudofoveate aplacophorans; its other valid families, Chaetodermatidae Théel, 1875 and Prochaetodermatidae Salvini-Plawen (1972), have 85 and 39 described species, respectively.

As in other genera of Caudofoveata, the species of *Scutopus* are distinguished by external characters of the body morphology in conjunction with more detailed characteristics of the sclerites and radula (Table 3). Therefore, the presence of the midventral suture line, the size, shape, and sculpture of the sclerites from the different body regions, as well as the number and position

of denticles in each radula tooth, have been the main characters for description of its species (Table 3). All of them have a long body shape, most presenting an anterior collar separating the anterior from the median body part. With many specimens available for the present study, it was possible to observe that the fixed specimens of *S. variabilis* sp. nov. exhibit a great variation in the form of the body caused by contractions of the musculature, being often contorted in different ways, narrowed and modified in its length:width proportions and in the relative sizes of the different body regions (specially the peribuccal, the foregut and the midgut regions). The anterior main collar is not visible in many specimens, this being particularly frequent in young individuals. For this reason, many animals can easily be confounded with other co-occurring caudofoveates, such as two undescribed species of *Psilodens* and *Falcidens*; in these cases, extraction of the sclerites is desirable for a more definite identification.

The midventral line is present in most species of *Scutopus* (Salvini-Plawen, 1968, 1972, 1975; Osorio, 1981; Saito and Salvini-Plawen, 2014), but was characterized as inconspicuous in *S. megaradulatus* (Salvini-Plawen, 1972), being absent only in *S. robustus* (Salvini-Plawen, 1970, 1972). Apart from this genus, the midventral line has been also recorded in *Falcidens sagittiferus* Salvini-Plawen (1968) (Ivanov et al., 2009) and in *Psilodens balduri* Mikkelsen and Todt (2014) (Mikkelsen and Todt, 2014),

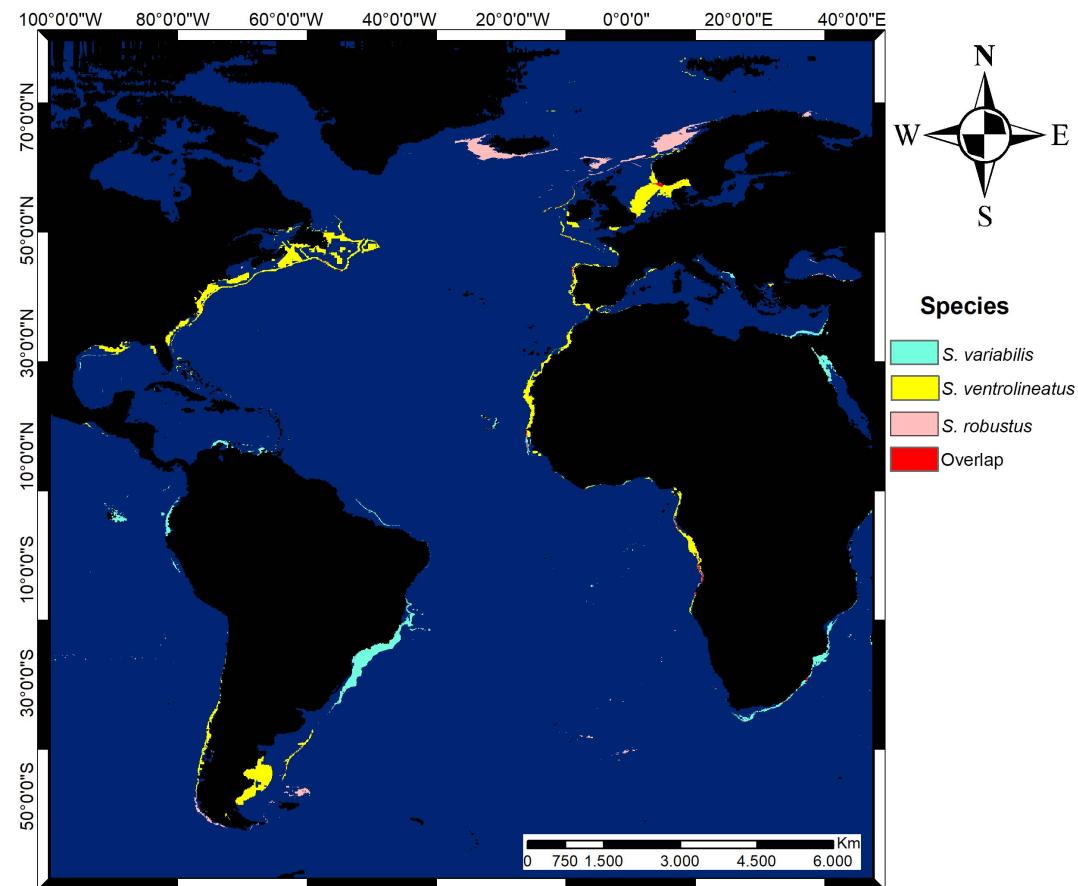


FIGURE 7 | Potential distribution map of suitable areas of *Scutopus* species in the Atlantic Ocean in thresholded format (10 percentile training presence). Overlapping areas of estimated species distribution are in red.

both on the anterior trunk, exhibiting characteristic adjacent sclerites, distinct in shape and size from the ones of the other body parts. In the Brazilian new species, the suture line is well visible in most specimens, especially by SEM, and has two types of adjacent sclerites, one with a wider base and longer blade that has almost parallel sides, and another which is narrower in the medial portion. This latter type was also observed in other species of *Scutopus*, such as *S. ventrolineatus*, *S. chilensis*, *S. schanderi*, and *S. hamatanii* (Salvini-Plawen, 1968, 1972; Saito and Salvini-Plawen, 2014), but not in *S. megaradulatus* (Salvini-Plawen, 1972).

In past times, SEM was a tool only for a general characterization in Caudofoveata (Scheltema, 1985, 1997; Scheltema et al., 1994), but more recently it has been used to furnish more complete descriptions (Schander et al., 2006; Ivanov et al., 2009; Mikkelsen and Todt, 2014; Saito, 2020), becoming a routine technique for the studies of the Brazilian species (Corrêa et al., 2014, 2018; Passos et al., 2018). In such way, apart from the general morphology of the animals, important characteristics of the oral shield, radula and sclerites can be observed. Regarding species of *Scutopus*, the sclerites are variable in form and size in the different body parts, there being dominant trunk sclerites

which are important for the distinction of its species (Figure 9). Among them, *S. variabilis* sp. nov. is the first to have its sclerites described by SEM, with two dominant types observed in the median part: one elongated with lateral margins slightly concave in medial portion, and another longer, with narrower base. These are distinct from the ones of *S. megaradulatus*, in which they are slender and have parallel margins in the blade (Salvini-Plawen, 1972), and from the ones of *S. schanderi*, where they have an oar-blade shape (Saito and Salvini-Plawen, 2014). Some of the sclerites of *S. ventrolineatus*, *S. robustus*, *S. chilensis*, and *S. hamatanii* are like the ones of *S. variabilis* sp. nov., but in those species, there are dominant drop-shaped or lanceolate sclerites (Salvini-Plawen, 1968, 1972, 1975; Saito and Salvini-Plawen, 2014). The longitudinal sculpture of the sclerites appears to be also an important distinctive character: in *S. variabilis* sp. nov. the trunk sclerites have a main ridge and weak adjacent grooves in the blade, like in *S. megaradulatus* and *S. schanderi*, while in all other species there is only a main ridge, which appears to be more restricted to the distal end of the blade in *S. ventrolineatus*, *S. robustus*, and *S. chilensis*.

The present work also furnishes SEM images of the radula of a *Scutopus* species, a caudofoveate genus in which each species

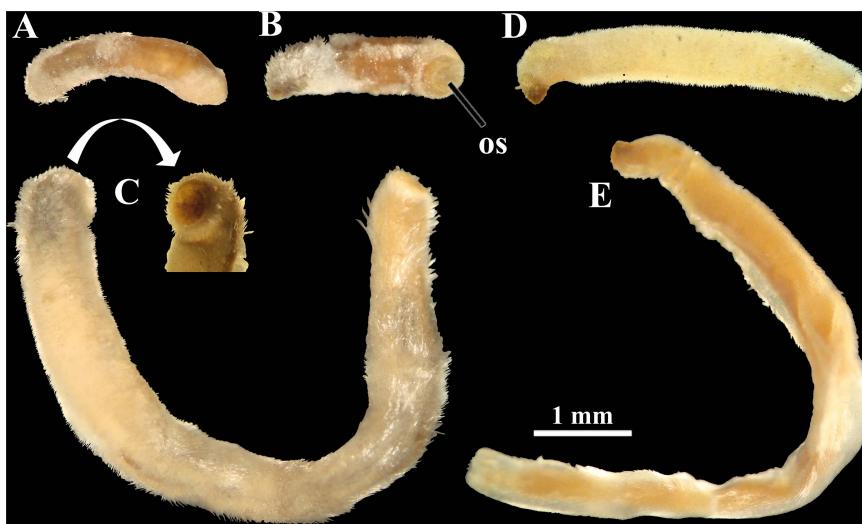


FIGURE 8 | Photomicrographs under stereomicroscope of examined lots of *Scutopus megaradulatus* (A–D) and *S. chilensis* (E). (A–C), AMNH 265347: this lot contains two tubes, one with the anteriormost body part [(A), (B)], in right lateral and ventral views, respectively; the oral shield is visible in (B)], and another with a dissected specimen (C) which has its anterior end missing (viewed in detail); note that this latter specimen is the same as the one illustrated by Salvini-Plawen (1972: fig. 21) (although he photographed it from the opposite left side). (D), AMNH 265348, a fragment of the trunk (probably from the midgut region), shown from the left side. (E), AMNH 265349, viewed from the left side. All in same scale. os - oral shield.

has a characteristic number of rows of radular teeth, which in turn are strengthened by different degrees of sclerotization and bear a number of median denticles (Table 3, Figure 9). In *S. variabilis* sp. nov., the radula is heavily sclerotized and has eight pairs of teeth, characters that are similar to *S. robustus*, *S. megaradulatus*, and *S. schanderi* (up to ten rows), and different from *S. ventrolineatus*, *S. chilensis*, and *S. hamatianii*, in which teeth are more numerous (more than 10 rows) and weakly sclerotized. The median denticles are more variable, but in those heavily sclerotized radulas they tend to occur in a higher number (12–22 denticles) and all along the inner margin of the teeth, while in the radulas with weak sclerotization the teeth bear a lower number of denticles (less than 11; except *S. chilensis*). In these latter cases, the denticles are proximally positioned, leaving a distal hook. Interestingly, these radular differences reflected in ecological characteristics found in species distribution modeling, as, excluding depth, *S. robustus* and *S. variabilis* sp. nov. were influenced by bottom temperature, while *S. ventrolineatus* were more influenced by silicate and primary productivity. These may reflect unknown interactions between the characteristics of the radula and the environment, like the advantage of one type of radula in one environment over another due to food availability, or perhaps one type of radula may be easier to produce in environments with higher concentration of silicate. Further studies are necessary to clarify if this radular and ecological variability may represent different genera.

Regarding the geographical and bathymetric distribution, patterns exhibited by the different species of *Scutopus* appear to be distinct among European and non-European representants, although clear and definite figures are probably blurred by sampling bias. *S. ventrolineatus* and *S. robustus* are well known

from Scandinavia, Western Europe and the Mediterranean Sea (Salvini-Plawen, 1968, 1970, 1972, 1975, 1977; Ivanov and Scheltema, 2001, 2014; Mikkelsen and Todt, 2014; Señaris et al., 2017), and were also investigated in more detail in relation to aspects of their natural history (Salvini-Plawen, 1968), anatomy (Scheltema, 1981; Scheltema et al., 1994), larval morphology (Salvini-Plawen, 1990, 2003), and molecular biology (Osca et al., 2014; Mikkelsen et al., 2019). *Scutopus ventrolineatus* was recorded as abundant species in some places of the Nowergian Sea (Salvini-Plawen, 1975; Todt, 2013) and apart from European waters, it occurs in the Southwestern Indic Ocean (off Durban) (Salvini-Plawen, 1972), but its supposed distribution all along the eastern African coast has not been noticed. So, at least one of these European species (*S. ventrolineatus*) seems to be generally characterized as having wide geographical and bathymetric distributions.

The wide recorded distribution of *S. ventrolineatus* was reinforced by the species distribution modeling, through which suitable areas were found in the Western African coast, in Cape Verde, Guinea and Angola Basins. Although Prochaetodermatidae is well known from West Africa (Scheltema and Ivanov, 2000), records of limifossorids are still lacking for these areas and thus more surveys and studies are necessary to understand the real diversity of caudofoveates in this region. The suitability in North American coast and Gulf of Mexico for *S. ventrolineatus* deserves future investigations. These areas were extensively explored, *S. megaradulatus* was already recorded from North Carolina (Scheltema, 1981), but this species is morphologically related with other *Scutopus*, like *S. robustus* and *S. variabilis* sp. nov. In the Gulf of Mexico, the recorded limifossorids do not belong to *Scutopus*. The suitability found in Tierra del Fuego and Falklands for *S. ventrolineatus* and

TABLE 1 | *Scutopus variabilis* sp. nov. Paratype samples.

Catalog No.	State	Station	Collector	Coordinates	Depth (m)	Date	Content
ZUEC APL 278	RJ	HAB4-CANG7-R3(5-10)	Habitats	21°56'11.264"S, 39°57'43.702"W	712.6	28/v/08	1 spm
ZUEC APL 279	RJ	HAB6-A7-R1(2-5)	Habitats	23°39'20.061"S, 41°18'30.264"W	693.7	23/vi/08	4 spms + 1 slide with sclerites + 1 stub with 1 spm
ZUEC APL 280	RJ	HAB6-A7-R3(2-5)	Habitats	23°39'19.981"S, 41°18'30.534"W	732.9	25/vi/08	1 stub with 1 spm
ZUEC APL 281	RJ	HAB6-B7-R3(2-5)	Habitats	23°13'2.006"S, 40°57'36.765"W	724.6	28/vi/08	2 spms + 2 slides with sclerites
ZUEC APL 282	RJ	HAB6-B7-R3(5-10)	Habitats	23°13'2.006"S, 40°57'36.765"W	724.6	28/vi/08	1 spm + 1 slide with sclerites
ZUEC APL 283	RJ	HAB6-C7-R1(2-5)	Habitats	22°59'51.839"S, 40°47'42.838"W	710.1	29/vi/08	1 spm + 1 slide with sclerites
ZUEC APL 284	RJ	HAB6-C7-R1(5-10)	Habitats	2°59'51.839"S, 40°47'42.838"W	710.1	29/vi/08	1 stub with 6 radular teeth + 6 stubs with sclerites
ZUEC APL 285	RJ	HAB6-C7-R2(2-5)	Habitats	22°59'52.609"S, 40°47'45.008"W	689.4	30/vi/08	2 spms + 1 slide with sclerites + 1 slide with radula + 6 stubs with sclerites
ZUEC APL 286	RJ	HAB6-C7-R3(2-5)	Habitats	22°59'52.279"S, 40°47'45.398"W	686.1	01/vii/08	4 spms + 3 slides with sclerites
ZUEC APL 287	RJ	HAB6-CANAC7-R2(2-5)	Habitats	21°47'26.614"S, 40°2'13.765"W	752.5	06/vii/08	1 spm + 1 slide with sclerites
ZUEC APL 288	RJ	HAB6-D7-R2(2-5)	Habitats	22°36'27.325"S, 40°22'29.335"W	700	15/vii/08	1 spm
ZUEC APL 289	ES	HAB6-I7-R1(2-5)	Habitats	21°11'12.183"S, 40°12'52.020"W	693.9	17/vii/08	2 spms + 2 slides with sclerites
ZUEC APL 290	RJ	HAB7-C6-R1(5-10)	Habitats	22°59'1.179"S, 40°48'24.830"W	399.7	04/vii/08	1 spm
ZUEC APL 291	ES	HAB7-I7-R3(2-5)	Habitats	21°11'2.632"S, 40°12'18.218"W	792.4	05/vii/08	1 spm + 1 stub 1 pair and 8 radular teeth + 5 stubs with sclerites
ZUEC APL 292	RJ	HAB8-A7-R1(0-2)	Habitats	23°39'19.742"S, 41°18'28.369"W	699	28/i/09	2 spms
ZUEC APL 293	RJ	HAB8-A7-R2(2-5)	Habitats	23°39'20.559"S, 41°18'28.196"W	701	28/i/09	1 spm + 1 slide with sclerites
ZUEC APL 294	RJ	HAB8-B7-R2(2-5)	Habitats	23°13'2.799"S, 40°57'37.798"W	741.6	28/i/09	1 spm + 1 slide with sclerites
ZUEC APL 295	RJ	HAB8-C7-R2(0-2)	Habitats	22°59'53.839"S, 40°47'45.022"W	393.6	29/i/09	1 spm + 1 slide with sclerites
ZUEC APL 296	RJ	HAB9-CANG7-R3(2-5)	Habitats	21°56'12.105"S, 39°57'45.173"W	720	07/ii/09	1 spm + 1 slide with sclerites
ZUEC APL 297	RJ	HAB9-H7-R3(2-5)	Habitats	21°41'12.521"S, 40°1'56.515"W	702	06/ii/09	1 spm
ZUEC APL 298	ES	HAB9-I7-R3(0-2)	Habitats	21°11'12.228"S, 40°12'51.745"W	683	04/ii/09	1 stub with 1 spm
ZUEC APL 299	RJ	HAB13-I5-R3	Habitats	21°23'2.093"S, 40°15'9.173"W	145	06/iii/09	1 stub with 1 spm
ZUEC APL 300	RJ	HAB16-E5-R3	Habitats	22°23'39.088"S, 40°20'41.226"W	150	04/vii/09	1 spm + 1 slide with sclerites
ZUEC APL 301	RJ	HAB17-I5-R1	Habitats	21°23'3.544"S, 40°15'9.352"W	140	21/vii/09	1 stub with radula
ZUEC APL 302	ES	AMB3-CAND4-R3(0-10)	Ambes	19°31'51.66"S, 39°3'4.04"W	171	09/xii/11	1 spm + 1 slide with sclerites
ZUEC APL 303	ES	AMB5-A5-R1(2-5)	Ambes	21°4'9.61"S, 40°13'7.38"W	410	30/xii/11	4 spms + 4 slides with sclerites
ZUEC APL 304	ES	AMB6-CANWN4-R3(0-10)	Ambes	19°49'7.27"S, 39°36'8.52"W	158	14/i/12	3 spm + 3 slides with sclerites
ZUEC APL 305	ES	AMB6-CANWN5-R3(0-10/5-10)	Ambes	19°49'37.21"S, 39°35'41.25"W	410	14/i/12	1 spm + 1 slide with sclerites
ZUEC APL 306	ES	AMB6-D4-R1(0-10)	Ambes	19°45'55.39"S, 39°30'25.74"W	149	15/i/12	7 spms + 7 slides with sclerites + 1 stub with 1 spm
ZUEC APL 307	ES	AMB6-D4-R3(0-2)	Ambes	19°45'55.39"S, 39°30'25.74"W	149	15/i/12	12 spms + 12 slides with sclerites
ZUEC APL 308	ES	AMB6-D4-R3(2-5)	Ambes	19°45'55.39"S, 39°30'25.74"W	149	15/i/12	5 spms + 5 slides with sclerites
ZUEC APL 309	ES	AMB6-E4-R3(0-2)	Ambes	19°36'5.17"S, 39°10'32.93"W	153	24/i/12	1 spm
ZUEC APL 310	ES	AMB7-B4-R2	Ambes	20°35'25.16"S, 39°54'58.31"W	157	21/i/12	1 spm
ZUEC APL 311	ES	AMB7-D4-R2	Ambes	19°45'54.56"S, 39°30'25.23"W	144	15/i/12	5 spms + 5 slides with sclerites

(Continued)

TABLE 1 | Continued

Catalog No.	State	Station	Collector	Coordinates	Depth (m)	Date	Content
ZUEC APL 312	ES	AMB7-E4-R1	Ambes	19°36'4.32"S, 39°10'34.07"W	147	15/i/12	1 spm + 2 slides with sclerites + 1 stub with 1 spm
ZUEC APL 313	ES	AMB7-E4-R2	Ambes	19°36'4.32"S, 39°10'34.07"W	147	15/i/12	1 spm + 2 slides with sclerites + 1 stub with 1 spm
ZUEC APL 314	ES	AMB7-E4-R3	Ambes	19°36'4.32"S, 39°10'34.07"W	147	15/i/12	1 stub with 1 spm
ZUEC APL 315	ES	AMB7-F2-R3	Ambes	18°52'32.61"S, 39°8'42.82"W	40	18/i/12	1 spm
ZUEC APL 316	ES	AMB11-A5-R1(0-2/2-5)	Ambes	21°4'4.67"S, 40°13'6.06"W	415	08/vi/13	3 spms + 3 slides with sclerites + 1 stub with 1 spm
ZUEC APL 317	ES	AMB12-CAND4-R2(0-10)	Ambes	19°31'51.68"S, 39°3'4.79"W	171	29/vi/13	4 spms + 5 slides with sclerites
ZUEC APL 318	ES	AMB12-CANWN4-R2(0-2)	Ambes	19°49'6.26"S, 39°36'9.34"W	181	29/vi/13	11 spms + 11 slides with sclerites
ZUEC APL 319	ES	AMB12-D4-R1(5-10)	Ambes	19°45'53.43"S, 39°30'25.97"W	143	27/vi/13	1 spm + 2 slides with sclerites + 1 stub with radula
ZUEC APL 320	ES	AMB12-D4-R3(2-5)	Ambes	19°45'53.43"S, 39°30'25.97"W	143	27/vi/13	1 spm + 2 slides with sclerites
ZUEC APL 321	ES	AMB12-E4-R2	Ambes	19°36'3.57"S, 39°10'33.64"W	143	29/vi/13	1 slide with sclerites + 1 stub with 1 spm
ZUEC APL 322	ES	AMB14-A4-R3	Ambes	21°4'4.56"S, 40°14'14.08"W	141	11/vii/13	1 spm + 1 slide with sclerites + 1 slide with radula
MZSP 38414	SP	Sta. 6665	Revizee	25°26.88"S, 46°38.85'W	80	16/xii/97	1 spm + 1 slide with sclerites
MZSP 38416	SP	Sta. 6657	Revizee	25°17.30'S, 46°55.60'W	60	09/ii/98	3 spm
MZSP 38447	RJ	MBT 219	MBT	23°25'00"S, 42°00'00'W	100	06/vi/71	2 spms + 1 slide with sclerites
MZSP 38451	RJ	MBT 204	MBT	23°55'00"S, 43°31'00'W	125	03/vi/71	4 spms + 1 slide with sclerites
MZSP 84438	SP	Sta. 344	Projeto Integrado	23°34'S, 44°43'W	No depth	No date	1 spm + 1 slide with sclerites
MZSP 137395	SP	Sta. 13 – PI	Projeto Integrado	23°50'00"S, 45°09'00'W	38	21/i/86	1 spm + 1 slide with sclerites
MZSP 137411	PR	Sta. 6789	Revizee	27°45'12.5"S, 48°3'00'W	95	15/iii/98	1 spm + 1 slide with sclerites
MZSP 137414	PR	Sta. 6780	Revizee	27°7'00"S, 47°44'12.5'W	102	13/iii/98	1 spm + 1 slide with sclerites
MZSP 137416	PR	Sta. 6788	Revizee	27°26'00"S, 47°52'00'W	110	15/iii/98	3 spms + 1 slide with sclerites
MZSP 143012	RS	MBT 139	MBT	30°52'00"S, 49°51'00'W	126	27/vi/70	1 spm + 1 slide with sclerites
MZSP 154097	RJ	HAB8-A8-R1(2-5)	Habitats	23°41'7.814"S, 41°16'4.710'W	1017.9	12/i/09	1 spm + 1 slide with sclerites
MZSP 154098	ES	HAB9-I7-R2(2-5)	Habitats	21°11'12.073"S, 40°12'52,126'W	680	04/ii/09	2 spms + 2 slides with sclerites
MZSP 154099	ES	HAB9 I7 R3 2-5	Habitats	21°11'12.228"S, 40°12'51.745'W	683	04/ii/09	4 spms + 4 slides with sclerites
MZSP 154100	ES	AMB7-A4-R1	Ambes	21°4'4.76"S, 40°14'14.14'W	153	23/i/12	7 spms + 7 slides with sclerites
MZSP 154101	ES	AMB7-A4-R2	Ambes	21°4'4.76"S, 40°14'14.14'W	153	23/i/12	8 spms + 8 slides with sclerites
MZSP 154102	ES	AMB7-D4-R3	Ambes	19°45'54.56"S, 39°30'25.23'W	144	15/i/12	3 spms + 3 slides with sclerites
MZSP 154103	ES	AMB11-B5-R1(0-10)	Ambes	20°35'15.33"S, 39°53'45.22'W	415	18/vi/13	3 spms + 3 slides with sclerites
MNRJ 23636	RJ	HAB4-CANG7-R2(0-2)	Habitats	21°56'10.244"S, 39°57'43.438'W	709.7	28/v/08	2 spms + 2 slides with sclerites
MNRJ 23637	RJ	HAB8-C6-R3(2-5)	Habitats	22°59'0.677"S, 40°48'28.837'W	376.6	31/i/09	2 spms + 2 slides with sclerites
MNRJ 23638	ES	HAB9-I7-R1(2-5)	Habitats	21°11'12.170"S, 40°12'51.838'W	682	04/ii/09	5 spms + 5 slides with sclerites
MNRJ 23639	RJ	HAB16-H4-R1	Habitats	21°42'53.895"S, 40°10'14.920'W	97	07/vii/09	3 spms + 3 slides with sclerites
MNRJ 23640	ES	AMB7-D4-R1	Ambes	19°45'54.56"S, 39°30'25.23'W	144	15/i/12	6 spms + 6 slides with sclerites
MNRJ 23641	ES	AMB12-CAND6-R2(0-10)	Ambes	19°37'45.14"S, 39°3'58.75'W	1050	25/vi/13	4 spms + 4 slides with sclerites
CZUFS APL 11	ES	AMB3-CAND4-R2(0-10)	Ambes	19°31'51.66"S, 39°3'4.04'W	171	09/xii/11	5 spms + 5 slides with sclerites
CZUFS APL 12	ES	AMB6-E4-R3(2-5)	Ambes	19°36'5.17"S, 39°10'32.93'W	153	24/i/12	2 spms + 2 slides with sclerites
CZUFS APL 13	ES	AMB12-E4-R1(2-5)	Ambes	19°36'3.57"S, 39°10'33.64'W	143	29/vi/13	2 spms + 2 slides with sclerites

TABLE 2 | Percentage of contribution of environmental layers in the species distribution modeling for each species.

Variable	<i>S. robustus</i>	<i>S. ventrolineatus</i>	<i>S. variabilis</i> sp. nov.
Depth	47.3	48.3	42.2
Bottom temperature	30.8	1.7	38.7
Silicates	11.1	23.9	8.6
Slope	4.1	6.4	6.8
Primary productivity	6.8	19.6	3.7

S. robustus sounds to be unlikely for both species, as it is a region very far from European waters, where these species are recorded. Besides this, these areas of the Southern Hemisphere are still unknown regarding their diversity of caudofoveates, and future exploration may clarify if a sister species is found there.

Outside European waters, all other species of *Scutopus* have been reported upon by only a few studies. In the Americas, *S. megaradulatus* is known from the Caribbean, where it was originally described (Salvini-Plawen, 1972), and from samples from North Carolina identified by Scheltema (1981). Its occurrence from off Cape coast, South Africa (Salvini-Plawen, 1992) is presumably doubtful, and the fact that this species has an amphiatlantic distribution must be confirmed. The record of *S. megaradulatus* from Brazil (Rios, 1994) should definitely be discharged. In the Pacific Ocean, *S. chilensis* appears to be restricted to Chile (Salvini-Plawen, 1972; Osorio, 1981), and *S. hamatianii* and *S. schanderi* were only recorded from the Sea of Japan (Saito and Salvini-Plawen, 2014). Accordingly, *S. variabilis* sp. nov. is probably a species of restricted distribution, occurring in the shelf and the upper continental slope of the Brazilian southeastern and southern coasts; the great effort of collection was, however, restricted to this area and so its occurrence further to the north, in the northeast and north of Brazil, and in the south (Uruguay and Argentina) deserves future investigations.

The potential distribution modeling showed that the main suitable areas of *S. variabilis* sp. nov. are the Brazilian Southeastern and Southern coasts, followed by some hotspots of suitability in the Southern Caribbean Sea and Brazilian Northern coast in the Western Atlantic, mainly explained by depth and temperature. Regarding the diversity of caudofoveates, the Caribbean Sea is only known by the few and punctual records of two species (Salvini-Plawen, 1972, 1992). Although it has a tropical climate and usually very narrow continental shelves, the Caribbean Sea has hundreds of islands that create suitable areas for species with the characteristics of *S. variabilis* sp. nov. Considering that *S. megaradulatus* is already recorded from this region, the hotspots in the Caribbean Sea for *S. variabilis* sp. nov. are expected and should indicate that these are sister species which live in similar environmental conditions. The suitable areas found in the Brazilian Northern coast can be explained by the enlargement of the shelf close to the Amazon River mouth, creating suitable conditions for establishing a viable population of a species of *Scutopus*. This area is still almost unknown regarding to its deep-sea benthic

fauna. Thus, more investigations are necessary to verify if there is an isolated population of *S. variabilis* sp. nov. or a new species in the area. Outside the Western Atlantic, the suitability found in the Mediterranean sounds an unlikely occurrence area, but more investigations are required to prospect possible occurrences of *S. variabilis* sp. nov. in the islands of Angola and Cape Verde basins, where no limifossorids were described so far.

The Gulf of Mexico and the Brazilian Northeastern coast were found as unsuitable areas for *S. variabilis* sp. nov. In the Gulf of Mexico, the unsuitability reinforced our results of not finding a *Scutopus* species in museum collections from this area. Although the Gulf has shelf areas similar to those of the Brazilian Southeastern and Southern coasts, the existence of warmer waters in the Gulf can prevent the occurrence of suitable areas for *S. variabilis* sp. nov. Ivanov and Scheltema (2008) characterized as similar the patterns of diversity of Prochaetodermatidae from the Gulf of Mexico (7 species, 2 endemic) and the Mediterranean Sea (4 species, 1 endemic). This similarity in Prochaetodermatidae contrasts with the different pattern of *Scutopus* for both regions. For the Brazilian Northeastern coast, through previous analysis of material from this region any *Scutopus* species were found (Miranda and Passos, pers. obs.), observation that was reinforced by modeling. This non-occurrence can be explained by the tropical climate and narrow shelf characteristic of this region, which acts like a barrier that creates unsuitable areas for the occurrence of *S. variabilis* sp. nov.

By modeling, very few and small potential overlapping areas were found, even among the European species, which in some cases were already recorded from the same geographical areas (Salvini-Plawen, 1975). In the European Atlantic, *S. robustus* tends to occur in the Northern areas like Iceland, Scotland and Northern Norway, whereas *S. ventrolineatus* mainly occurs in southern areas, between southern Norway, south of England and Bay of Biscay, with few and small overlaps in Northern Iberian Peninsula and South of Norway, as an effect of differential influences of environmental variables in both species. In relation with *S. ventrolineatus* and *S. variabilis* sp. nov., exceedingly small potential overlaps were found in islands of Cape Verde and Angola Basins. This suggests that competition for space and resources are reduced by occurrences of different species of *Scutopus* in distinct regions.

Deep-sea organisms are hard to access, as their collections are less common, the environment is less accessible, the logistics is expensive, and in many cases, species are encountered in low specimen numbers. Moreover, many cruise collections protocols still use formalin to preserve specimens, making the use of molecular techniques problematic. However, these problems have been minimized, as the number of samples of deep-sea organisms are growing in museum collections due to increasing studies required for exploitation of fisheries, oil, gas and mining, although specialists for these groups are still scarce. This is the case of Brazil, in which a great amount of useful data for taxonomy and biogeography have been available through the analysis of extensive collections, as those

TABLE 3 | Summary data of main diagnostics characters, geographical and bathymetric distribution data of all *Scutopus* species described.

Species	Radula Sclerotization	Number of radular teeth rows	Number of median denticles of the radular teeth	Suture line	Bathymetry (m)	Distribution	References
<i>S. chilensis</i>	Weakly sclerotized	11 – 18	18 – 20	Present	263 – 642	Southeastern Pacific Ocean: Chile (from Valparaiso to Strait of Magellan)	Salvini-Plawen (1972, 1992); Osorio (1981); Linse (1999)
<i>S. hamatani</i>	Sclerotized (except the 2 posteriomost pairs)	12	8 – 9	Present	51 – 105	Northwestern Pacific Ocean: Sea of Japan	Saito and Salvini-Plawen (2014)
<i>S. megaradulatus</i>	Heavily Sclerotized (except for the last posteriomost pair)	7	16 – 18	Inconspicuous	40 – 1300 (1861?) [*]	Northwestern Atlantic Ocean: North America, United States (North Carolina); Central America, Panama, Gulf of Darien	Salvini-Plawen (1972; 1992*); Scheltema (1981); Rios (1994**, 2009**); Forcelli and Narosky (2015***)
<i>S. robustus</i>	Heavily sclerotized (except the 1-3 posteriomost pairs)	6 – 10	20 – 22	Absent	50 – 800 (3542?) [*]	Northeastern Atlantic Ocean: Norway, England, Iceland, and Mediterranean	Salvini-Plawen (1970, 1972, 1975, 1977*, 1997); Salvini-Plawen and Warén (1972); Scheltema (1981); Ivanov and Scheltema (2001****); Ivanov and Scheltema (2014); Mikkelsen and Todt (2014); Señaris et al. (2017)
<i>S. schanderi</i>	Heavily sclerotized (except the 2 posteriomost pairs)	8	16 – 18	Present	69 – 102	Northwestern Pacific Ocean: Sea of Japan	Saito and Salvini-Plawen (2014)
<i>S. ventrolineatus</i>	Weakly sclerotized (limited to the 2-4 anterior pairs)	10 – 16	9 – 11	Present	40 – 1248	Atlantic Ocean: Scandinavia (Western Sweden, Norway), Western Scotland, Irish Sea, Bay of Biscay and Mediterranean. Southwestern Indian Ocean: off Durban, South Africa,	Salvini-Plawen (1968, 1970, 1972, 1975, 1997), Osca et al. (2014)
<i>Scutopus variabilis</i> sp. nov.	Heavily sclerotized (except the 2 posteriomost pairs)	8	12 – 16	Present	40 – 1300	Southwestern Atlantic Ocean, Brazil, South and Southeastern coast	This study

* Salvini-Plawen (1992, tab. 1) cites the occurrence of *S. megaradulatus* in a coordinate of western Cape of Africa at 1861 m depth with 2 individuals of *Falcidens non-tartarus*, but did not illustrate the material and said that its geographical distribution is complemented in his paper. This material was not deposited in any museum, thus we did not consider this record as valid.

** Rios (1994, 2009) cites the occurrence of *Scutopus cf. megaradulatus* and *Scutopus* sp. for Rios de Janeiro Coast in his Seashells catalogs, but did not furnish any bibliographical reference or material deposited in any museum, thus we did not consider this record as valid.

*** Forcelli and Narosky (2015) cite the occurrence of *Scutopus* sp. deposited in the “Museo Argentino de Ciencias Naturales ‘Bernardino Rivadavia’” (Buenos Aires, Argentina), but this record was not confirmed in that institution (Alejandro Tablado, pers. commun.).

**** Salvini-Plawen (1977) recorded *S. robustus* from the Mediterranean Sea at 2415, 2917, and 3540 m depth, but these were considered doubtful by Ivanov and Scheltema (2001).

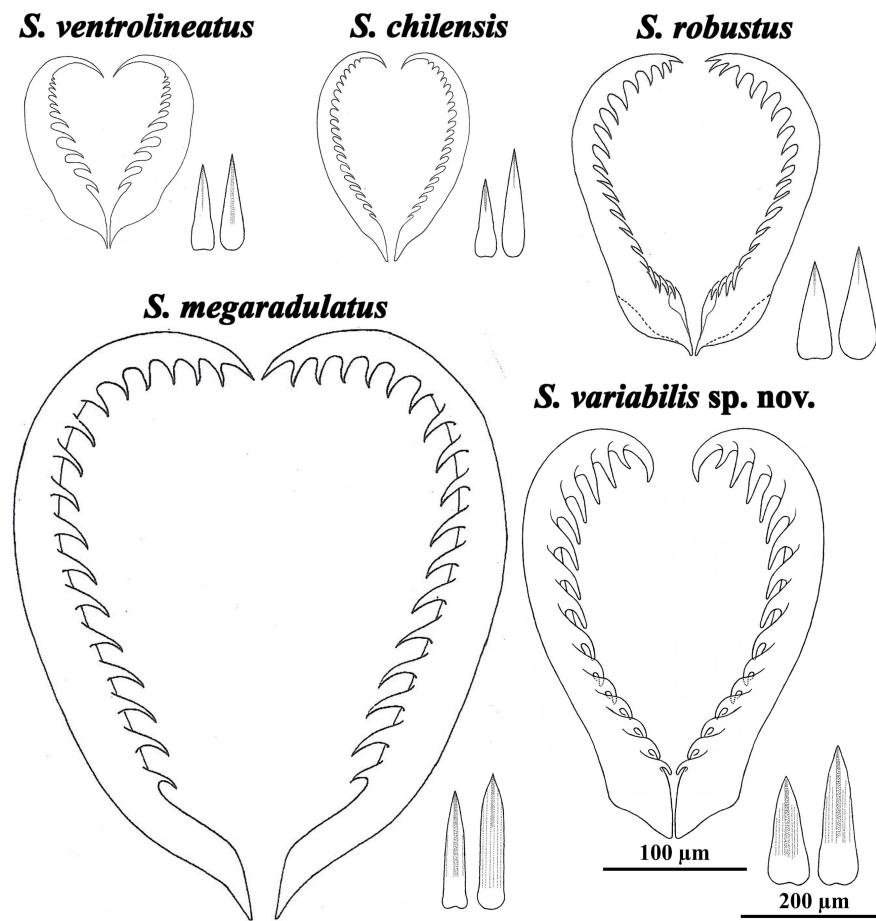


FIGURE 9 | Radula (in same scale) and trunk sclerites (idem) of *Scutopus* species, obtained from different sources: Salvini-Plawen (1970): figs. 1 (radula) and 3(i, l) (sclerites) of *S. ventrolineatus*, figs. 2 (radula) and 4(e, g) (sclerites) of *S. robustus*; Salvini-Plawen (1972): figs. 22 (radula) and 24(g, h) of *S. megaradulatus*, figs. 27 (radula) and 23(m, p) (sclerites) of *S. chilensis*. The radula of *S. variabilis* sp. nov. was drawn based on the **Figure 4**; its sclerites were based on the first illustrated in row (E) and the last of row (G) of **Figure 3**. The radula and sclerites of the Pacific *S. schanderi* and *S. hamatanii* were illustrated by Saito and Salvini-Plawen (2014).

made by the “Habitats” and “Ambes” projects. With these and in association with examination of other museums samples, a species distribution modeling was performed, this being a quantitative technique that started to be used only recently for deep-sea organisms (e.g., Basher and Costello, 2016; Schnurr et al., 2018; Bowden et al., 2021); it is used here for the first time for aplacophoran molluscs.

As it occurs with other deep-water animals, Aplacophora is a clear example of lesser-known group. However, especially in the last decade, this scenario is rapidly changing (Todt, 2013; Passos et al., 2019). Some techniques, like SEM and birefringence microscopy, particularly important for the study of these animals, are becoming more accessible (e.g., Corrêa et al., 2014, 2018; Mikkelsen and Todt, 2014; Passos et al., 2018; Saito, 2020), making the descriptions more detailed; moreover, previous molecular obstacles have been surpassed (e.g., Kocot et al., 2011; Mikkelsen et al., 2018, 2019; Bergmeier et al., 2021). Museum collections are increasingly with materials coming from new unexplored areas like the South Atlantic, allowing studies by recent biogeographical and

ecological techniques, like species distribution modeling. In the specific literature on aplacophorans, there are some citations of undescribed species of *Scutopus*, for example, from off California and Oregon, United States (Barwick and Cadien, 2005; Mikkelsen et al., 2019), and Chile (Linse, 1999), and in fact there are large areas of the Pacific and Indian Oceans which are still very poorly sampled. As a part of a larger project that has been performed on the molluscan diversity of the Brazilian coast, in comparison with other Atlantic species (Corrêa et al., 2014, 2018; Passos et al., 2018, 2019; Miranda et al., 2020), this study gives a little step toward a better knowledge of these animals from the deep-sea of the Southern Hemisphere.

DATA AVAILABILITY STATEMENT

The original contributions presented in the study are included in the article/**Supplementary Material**, further inquiries can be directed to the corresponding author.

AUTHOR CONTRIBUTIONS

FP designed the study and prepared the text. PC conducted the morphological analysis, species distribution modeling, and made a critical review of the final version of the manuscript. MM designed the study, conducted the morphological analysis, species distribution modeling, and prepared the text. All authors contributed to the article and approved the submitted version.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/fmars.2021.669478/full#supplementary-material>

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