New Data on *Pterygodermatites (Pterygodermatites) plagiostoma* Wedl, 1861 (Nematoda, Rictulariidae) Parasite of the Algerian Hedgehog *Atelerix algirus* Linnaeus, 1758 (Eulipotyphla: Erinaceidae) from the Canary Islands †

Jordi Miquel 1,2,*, Alexis Ribas 1,2, Román Pino-Vera 3, Elena Izquierdo-Rodríguez 4, Natalia Martín-Carrillo 4, Carlos Feliu 1 and Pilar Foronda 3,4,*

**Abstract:** A redescription of *Pterygodermatites (Pterygodermatites) plagiostoma* (Nematoda, Rictulariidae) is made by means of light and scanning electron microscopy, including the first data on male specimens. The morphologic study was based on specimens recovered from two Algerian hedgehogs from Tenerife and Gran Canaria islands (Canary Archipelago, Spain). The main differential characteristics of *P. (P.) plagiostoma* males are the number of cuticular projection pairs, the number of precloacal fans, and the size of spicules. The cloacal papillae are arranged according to the Ascaridida type, with two precloacal pairs, an unpaired precloacal papilla, one pair lateral to the cloaca, six postcloacal pairs, and a pair of phasmids. Females are mainly characterized and differentiated by the number of prevulvar pairs of cuticular projections, by the total number of cuticular projection pairs, by the level of differentiation from combs to spines and by the position of the vulva in relation to the esophagus–intestine junction. The comparison with species of the subgenus *P. (Pterygodermatites)* shows *P. (P.) plagiostoma* as a species clearly differentiated from the remaining species of this subgenus.

**Simple Summary:** A redescription of *Pterygodermatites (Pterygodermatites) plagiostoma* (Nematoda, Rictulariidae) is made by means of light and scanning electron microscopy, including the first data on male specimens. The morphologic study was based on specimens recovered from two Algerian hedgehogs from Tenerife and Gran Canaria islands (Canary Archipelago, Spain). The main differential characteristics of *P. (P.) plagiostoma* males are the number of cuticular projection pairs, the number of precloacal fans, and the size of spicules. The cloacal papillae are arranged according to the Ascaridida type, with two precloacal pairs, an unpaired precloacal papilla, one pair lateral to the cloaca, six postcloacal pairs, and a pair of phasmids. Females are mainly characterized and differentiated by the number of prevulvar pairs of cuticular projections, by the total number of cuticular projection pairs, by the level of differentiation from combs to spines and by the position of the vulva in relation to the esophagus–intestine junction. The comparison with species of the subgenus *P. (Pterygodermatites)* shows *P. (P.) plagiostoma* as a species clearly differentiated from the remaining species of this subgenus.

Citation: Miquel, J.; Ribas, A.; Pino-Vera, R.; Izquierdo-Rodríguez, E.; Martín-Carrillo, N.; Feliu, C.; Foronda, P. New Data on *Pterygodermatites (Pterygodermatites) plagiostoma* Wedl, 1861 (Nematoda, Rictulariidae) Parasite of the Algerian Hedgehog *Atelerix algirus* Linnaeus, 1758 (Eulipotyphla: Erinaceidae) from the Canary Islands. *Animals* 2022, 12, 1991. https://doi.org/10.3390/ani12151991

**Publisher’s Note:** MDPI stays neutral with regard to jurisdictional claims in published maps and institutional affiliations.

**Copyright:** © 2022 by the authors. License MDPI, Basel, Switzerland. This article is an open access article distributed under the terms and conditions of the Creative Commons Attribution (CC BY) license (https://creativecommons.org/licenses/by/4.0/).
Keywords: Pterygodermatites (Pterygodermatites) plagiostoma; Rictulariidae; Atelerix algirus; Erinaceidae; Canary Islands

1. Introduction

Pterygodermatites (Pterygodermatites) plagiostoma is a rictulariid nematode frequently found parasitizing hedgehogs. It has been recorded in Atelerix algirus, Erinaceus europaeus, Hemiechinus auritus, and Paraechinus aethiopicus [1–8]. It has also been cited parasitizing the bat Vespertilio mystacinus (=Myotis mystacinus) (Vespertilionidae), the rodent Scirius melanogaster (=Callosciurus melanogaster) (Sciuridae), and the carnivores Vulpes vulpes niloticus (Canidae) and Paguma larvata (Viverridae) [9–12]. However, the P. plagiostoma specimens of Parona [10] in C. melanogaster from Mentawei (Sumatra) were later studied by Jägerskiöld [3], who identified them as a new species Rictularia fallax, currently P. (Mesopectines) fallax after Quentin [13]. Moreover, the record of Sonsino [11] in the fox from Egypt was later considered Rictularia affinis (=Pterygodermatites (Multipectines) affinis) by Jägerskiöld [3]. The report of Willemoes-Suhm [12] in M. mystacinus from Germany, described as Ophiostomum spinosum and later identified as Rictularia plagiostoma [14,15], was finally considered as P. (P.) spinosa by Quentin [13]. Finally, the finding of Leiper [9] in the palm-civet P. larvata obtained from the London Zoo is probably a misidentification or an accidental parasitism [7] and, therefore, it must be considered with caution.

Pterygodermatites (P.) plagiostoma is the type species of both genus and nominal subgenus. The subgenus P. (Pterygodermatites) has only six species, namely P. (P.) plagiostoma, P. (P.) aethechini, P. (P.) atlanticaensis, P. (P.) mexicana, P. (P.) shaldibini, and P. (P.) spinosa [13,16–18]. In the original description of P. (P.) plagiostoma, Wedl [8] illustrates the caudal extremity of a male specimen showing two unequal spicules, but no other morphologic characteristic or measurements are presented. Despite the numerous posterior findings [1–7], to date, the detailed morphology of the male remains unknown [13,19].

The aim of the present study is to describe for the first time the male of P. (P.) plagiostoma and contribute with new data on females from a hedgehog A. algirus from the Canary Islands. In addition, the sequence of the mitochondrial cytochrome c oxidase subunit I gene (MT-CO1) of P. (P.) plagiostoma is provided.

2. Materials and Methods

2.1. Specimens

Two Atelerix algirus Linnaeus, 1758 (Eulipotyphla: Erinaceidae), were found dead on the road in El Rosario (Tenerife Island) on 3 June 2021 and in Jinámar (Gran Canaria Island) (Canary Archipelago, Spain) on 9 October 2019 and then they were scanned for intestinal helminths. A total of 149 rictulariid nematodes (38 males and 111 females) were found in the gastrointestinal tract of the two hedgehogs. They were identified as P. (P.) plagiostoma following the available literature [7,13].

2.2. Scanning Electron Microscopy Study

Six P. (P.) plagiostoma males and eight females were preserved for scanning electron microscopy (SEM) examination, fixed in 70% ethanol and posteriorly dehydrated in an ethanol series and critical point dried with carbon dioxide in an Emitech K850X (Quorum Technologies Ltd., Laughton, East Sussex, UK). Finally, specimens were mounted on stubs with conductive adhesive tape and colloidal silver, coated with carbon in an Emitech K950X (Quorum Technologies Ltd., Laughton, East Sussex, UK) evaporator, and examined using a Field Emission SEM JSM-7001F (Jeol) (Jeol Ltd., Tokyo, Japan) at 10 kV in the “Centres Científics i Tecnològics” of the University of Barcelona (CCiTUB).
2.3. Molecular Analyses

Genomic DNA samples were isolated from the mid-section fragment of *P. (P.) plagiostoma* following López et al. [20]. The DNA extraction procedure was checked using DeNovix DS-11+ Spectrophotometer (DeNovix Inc., Wilmington, DE, USA).

DNA amplification by PCR was conducted using the primer cocktail as described by Prosser et al. [21], for the barcode region of the mitochondrial cytochrome c oxidase subunit I gene (MT-CO1). The PCR amplification contained 1X Buffer (Bioline, London, UK), 0.2 mM of each dNTP (Bioline), 0.5 µL of each primer cocktail (10 µM of a three-forward-primers mix, and 10 µM of a three-reverse-primers mix), 1U of Taq DNA polymerase (Bioline), 1.5 mM MgCl₂ (Bioline), and 20–30 ng of total genomic DNA in a total volume of 50 µL. Amplification was conducted with XP Cycler (Bioer Technology) using the following parameters: 94 °C for 1 min; five cycles at 94 °C for 40 s, 45 °C for 40 s, 72 °C for 1 min; followed by 35 cycles at 94 °C for 40 s, 51 °C for 40 s, 72 °C for 1 min; and a final extension at 72 °C for 5 min [21]. The resulting amplifications were visualized on 1.2% agarose gel at 100 V for 45 min.

The product of PCR was sequenced in Macrogen (Madrid, Spain) with primers NemF1_t1 and NemR1_t1 [21]. The analysis of the sequences was carried out with software MEGA X [22], using the multiple alignment program ClustalW included in MEGA X, and minor corrections were made by hand.

A phylogenetic analysis based on the MT-CO1 gene sequences of *P. (P.) plagiostoma* and other *Pterygodermatites* species available in GenBank was performed using Neighbor-Joining distance method (NJ) with the p-distance model [23] and Maximum-Likelihood (ML) method with Tamura–Nei model [24], both with at least 1000 bootstrap replications in MEGA X [22]. The sequence *Plectus aquatilis* KX017524 was used as the outgroup.

3. Results

3.1. Taxonomic Summary

*Family Rictulariidae* Hall, 1913.

*Genus Pterygodermatites* Wedl, 1861.

*Subgenus Pterygodermatites* (Pterygodermatites) Quentin, 1969.

*Pterygodermatites* (Pterygodermatites) plagiostoma Wedl, 1861 (Figures 2A–C, 3A–E, 4A–E, 5A,B and 6A–E).

Type host: *Atelerix algirus* Linnaeus, 1758 (Eulipotyphla: Erinaceidae).

Type locality: El Rosario (Tenerife Island, Canary Archipelago, Spain) (28°25′57.15″ N, 16°22′6.328″ W).

Other localities: Jinámar (Gran Canaria Island, Canary Archipelago, Spain) (28°1′58.457″ N, 15°25′8.994″ W).

Site of infection: small intestine.

Prevalence and intensity: two *A. algirus* studied with an intensity of 49 worms (15 males and 34 females) in the hedgehog from El Rosario and 100 worms (23 males and 77 females) in the hedgehog from Jinámar.

Type specimens: deposited in Muséum National d’Histoire Naturelle (Paris, France), under accession nos. MNHN HEL 1822 (8 males) and MNHN HEL 1823 (7 females).

Mitochondrial cytochrome c oxidase subunit I gene (MT-CO1) sequence: a fragment of 700 bp was obtained for the MT-CO1 of *P. (P.) plagiostoma* isolated from *A. algirus* in El Rosario, Tenerife. A 551 bp fragment was successfully sequenced and submitted to the GenBank database under the accession number ON502379.

3.2. Phylogenetic Tree

The phylogenetic trees created using NJ and ML (Figure 1) methods based on the MT-CO1 gene showed similar results. *P. (P.) plagiostoma* is included in a clade together with *P. (Paucipectines) zygodontomis* and *P. (Pa.) jügerskiöldi* with a high bootstrap value (100%), and clearly separated from these two species. In the other clade *P. (Mesopectines) whartoni* and *P. (Me.) nycticebi* are included.
3.2. Phylogenetic Tree
The phylogenetic trees (Figure 1) were constructed based on the maximum likelihood method, with the p-distance and 1000 bootstrap replications. Two clades were obtained. One included Pa. zygodontomis (Ripidomyys maculosus - Brazil) and Pa. whartonii (Leopardomyys sp. - Vietnam) with 100% support. The other clade included Pa. aequivalvis (Atelea pygmaea - Canary Islands, Spain) with a high bootstrap value of 90% (Figure 1).

3.3. Description
General: medium-sized nematodes. Dorsal oral opening, surrounded by 6 internal labial papillae, 4 external pairs of cephalic papillae, and two lateral amphids (Figures 2A, 3A and 6A). Oral opening with irregularly distributed oral denticles of different sizes (Figure 4B); 3 internal esophageal teeth at the bottom of the buccal capsule, 1 dorsal and 2 lateroventral (Figures 2A, 3A,B and 5A). Well-developed buccal capsule. Two subventral rows of cuticular projections along the body, in the form of combs and spines both in males and females (Figures 3A,B, 4E, 5A and 6C–E).

Male (17 specimens measured, mean in parentheses): Well-developed buccal capsule, oriented dorsally (Figures 2A and 3B). Oral opening surrounded by irregular denticles. Presence of three dorsi-ventral teeth (Figures 2A and 3A,B). Total pairs of combs 49–53 (50). Body length 5.36–7.67 mm (6.23 mm); width at the level of the esophagus basis 413–619 µm (498 µm). Esophagus length 2.09–2.87 mm (2.45 mm); width at base 111–180 µm (148 µm). Nerve ring located at 206–375 µm (269 µm) from the cephalic extremity; at the level of 3–4 pairs of cuticular combs. Deirids located at 516–795 µm (654 µm) from the cephalic extremity; at the level of 6–8 pairs of cuticular combs. Posterior end of body strongly curved ventrally (Figures 2B, 3C,D, 4A, 4E). Distance between the last cuticular spine and the tail tip 702–1060 µm (870 µm). The pericloacal surface is ornamented with cuticular markings (Figure 4B–D). Total of 19 caudal papillae which are sessile; 2 pairs of precloacal papillae (pairs 1 and 2), 1 unpaired precloacal papilla, 1 pair of papillae lateral to cloaca (pair 4), and 6 pairs of postcloacal papillae (pairs 3 and 5–9) (Figures 2C and 4B,C). Pairs of papillae 1, 4, and 8 in a dorsolateral position, particularly the pair 8 that is located outside the ornamented area (Figures 2C and 4B–D). A pair of phasmids near the tip of tail (Figures 2C and 4D). One or two (generally one) precloacal midventral fans immediately before the first pair of precloacal papillae (Figures 2C, 3C,D and 4A,B). Spicules unequal in size; right spicule 98–123 µm (110 µm); left spicule 185–236 µm (217 µm) (Figures 2B and 3C–E). Gubernaculum 28–39 µm (34 µm) (Figure 3E).

**Figure 1.** Phylogenetic analysis using the Maximum Likelihood method with p-distance and 1000 bootstrap replications based on the MT-CO1 gene sequences exploring the relationships among *Pterygodermatites* species including the nucleotide sequences obtained in this study (shown in bold). *Plectus australis* was used as the outgroup.
outside the ornamented area (Figures 2C and 4B–D). A pair of phasmids near the tip of tail (Figures 2C and 4D). One or two (generally one) precloacal midventral fans immediately before the first pair of precloacal papillae (Figures 2C, 3C,D, and 4A,B). Spicules unequal in size; right spicule 98–123 µm (110 µm); left spicule 185–236 µm (217 µm) (Figures 2B and 3C–E). Gubernaculum 28–39 µm (34 µm) (Figure 3E).

Figure 2. Pterygodermatites (Pterygodermatites) plagiotoma male. (A) Cephalic extremity, dorsal view. (B) Caudal extremity, lateral view. (C) Cloacal papillae. (*) Unpaired precloacal papilla; (Ph) phasmids.
Figure 3. *Pterygodermatites* (*Pterygodermatites*) *plagiostoma* male, light microscopy. (A) Cephalic extremity, dorsal view showing the two lateroventral esophageal teeth (lvT) and four internal labial papillae (arrows). (B) Cephalic extremity, lateral view showing dorsal (dT) and lateroventral (lvT) esophageal teeth. (C) Caudal extremity of a male with one midventral fan (F). (D) Caudal extremity of a male with two midventral fans. (E) Detail of the right spicule (rSp), left spicule (lSp), and gubernaculum (G). (C) Cuticular combs; (O) esophagus; (Sp) spicules.
Figure 4. Pterygodermatites (Pterygodermatites) plagiostoma male’s caudal extremity, scanning electron microscopy. (A) Precloacal position of the midventral fan (F). (B) Lateral view showing the distribution cloacal papillae (pairs 1–9). (C) Cloacal region showing the unpaired precloacal papilla (*). (D) Position of phasmids (Ph) near the tail tip. (E) Lateral view illustrating the last cuticular spines (arrows). (Cl) Cloaca.
Female (17 gravid specimens measured, mean in parentheses): Well-developed buccal capsule, oriented dorsally (Figures 5A and 6A). Oral opening surrounded by irregular denticles (Figure 6B). Presence of three esophageal teeth. Body length 12.07–17.54 mm (14.52 mm); width at the level of the vulva 423–712 µm (539 µm). Esophagus length 3.11–4.13 mm (3.71 mm); width at base 129–180 µm (154 µm). Nerve ring located at 285–463 µm (349 µm) from the cephalic extremity; at the level of 2–4 pairs of cuticular combs. Deirids located at 578–753 µm (644 µm) from the cephalic extremity; at the level of 6–9 pairs of cuticular combs. Total pairs of combs and spines 71–77 (74); prevulvar pairs of combs 43–46 (44); prevulvar combs in close contact to one another (Figures 5A,B and 6C,D); at the level of vulva combs transform into two small pairs of combs and later into spines, and become more spaced from each other (Figures 5B and 6C–E); postvulvar pairs of spines 28–32 (30); comb transformation to spines at the vulva or immediately posterior to the vulva (Figure 6C,D). Vulva located at 3.20–4.67 mm (3.99 mm) from the cephalic extremity; posterior to the esophageal–intestine junction (Figure 3B). Tail 177–350 µm (236 µm); with a terminal spine. Eggs oval, with a thick eggshell; embryonated 51.4–56.6 × 38.6–41.7 µm (55.6 × 42.1 µm); unembryonated 46.3–48.9 × 30.9–36.0 µm (47.5 × 33.1 µm).

Figure 5. *Pterygodermatites (Pterygodermatites) plagiostoma* female, light microscopy. (A) Cephalic extremity, lateral view showing the dorsal esophageal tooth (dT). (B) Vulvar region. Note the posterior position of the vulva (V) in relation to the esophageal–intestinal junction (arrow). (C) Cuticular combs; (I) intestine; (O) esophagus.
Figure 6. *Pterygodermatites* (*Pterygodermatites*) plagiostoma female, scanning electron microscopy. (A) Apical view showing the internal circle of labial papillae (*). (B) Detail of oral opening showing the irregular peribuccal denticles (arrows). (C,D) Vulvar region of two females showing the transition from combs to spines at a vulvar level or slightly posterior to the vulva (V), respectively. Note the presence of two reduced combs (arrows) before the appearance of spines. (E) Morphology of the most terminal spines.

4. Discussion

Within the subgenus *P. (Pterygodermatites)* there are only six described species (see Table 1). Considering male specimens, there is data for only three species, namely *P. (P.) aethechini*, *P. (P.) mexicana*, and *P. (P.) shaldybini* [13,16,17]. In the original description of *P. (P.) plagiostoma* [8], there was no additional data on males other than a caudal extremity showing the presence of two unequal spicules. In the present study, for the first time, we extensively describe the male of *P. (P.) plagiostoma*. 
Table 1. Main morphological characteristics, host group, and geographical distribution of the species of the subgenus *Pterygodermatites* (*Pterygodermatites*) Quentin, 1969.

| Species                  | Males | Females | Host Group | Geographical Distribution | References |
|--------------------------|-------|---------|------------|---------------------------|------------|
|                          | CP    | Spicule length right/left (in µm) | Fans | CP diff. * | VP # | Prevulvar CP/ Total CP |                  |                        |
| *P. (P.) aethechini*     | 50    | Unequal 118–132/190–225 | 1    | Post | Post | 42/75 | Eulipotyphla | South Africa | [13,17] |
| *P. (P.) atlanticaensis* | –     | –       | –       | Post | Ant  | 44–47/56–72 | Chiroptera | Brazil | [18] |
| *P. (P.) mexicana*       | 40    | Unequal 30–50/83–111 | 3–4   | Post | Post | 40/66 | Chiroptera | Mexico | [16] |
| *P. (P.) plagiotoma*     | 49–53 | Unequal 98–123/185–236 | 1–2   | Vulva-Post 1 | Post | 43–46/71–77 1 | Eulipotyphla | Saudi Arabia, Mainland Spain, Egypt, Tunisia, Algeria, Eivissa Island (Spain), Canary Islands (Spain), London Zoo, [1,2,7,3,8,13,4,5,6,9,13] Present study | [1,2,7,3,8,13,4,5,6,9,13] Present study |
| *P. (P.) shaldybini*     | –     | Unequal 70/140 | –     | –     | –    | 42/84 | Chiroptera | Kazakhstan, Turkmenistan, Mongolia | [13,25,26] |
| *P. (P.) spinosa*        | –     | –       | –       | –     | –    | 43–44/77 | Chiroptera | Germany | [12,13] |

(*) Cuticular projections differentiation (combs to spines) in relation to the vulva; (#) position of vulva in relation to esophagus–intestine junction; (Ant) anterior; (CP) cuticular projections; (Post) posterior; (VP) position of the vulva; (–) unknown data; (?) doubtful data. 1 Present study in *Atelerix algirus* from Tenerife and Gran Canaria islands (Canary Archipelago, Spain); 2 according to Miquel et al. [7] in *Erinaceus europaeus* from mainland Spain; 3 according to Jägerskiöld [3] in *Erinaceus auritus lybicus* (=Hemiechinus auritus) from Egypt.
In the Rictulariidae, the number of cloacal papillae of males is constant (19 papillae arranged in nine pairs of papillae and an unpaired papilla [13]). Thus, there are two pre-cloacal pairs, an unpaired precloacal papilla, either another precloacal pair or a pair located laterally to the cloaca and six postcloacal pairs. Additionally, near the tail tip there is a pair of phasmids. Quentin [13] analyzed the disposition of male cloacal papillae in numerous rictulariids and described three types of arrangement of papillae: the type Ascaridida presenting some pairs of papillae not aligned and slightly dorsolateral, the type Spirurida with all pairs of papillae aligned, and a third type with pedunculated and grouped papillae. In males of P. (P.) plagiocestoma, the cloacal papillae arrangement corresponds to the type Ascaridida [13,27] having the pairs 1, 4, and 8 in a dorsolateral position, particularly the µP. (pairs 1, 2, 4, 8, and 9) and four subventral pairs (pairs 3, 5, 6, and 7) but no unpaired P. There is also a higher number of both prevulvar and total pairs of cuticular projections P. particularly those belonging to the subgenus P. (Pauicipetes), e.g., P. (Paucipetes) coloradensis, P. (Pa.) microti, P. (Pa.) ondatrae, P. (Pa.) zygodontomis, P. (Neopaucipetes) desportesi, R. citelli, R. diana, R. halli, R. lucifugus, R. macdonaldi, and R. pruni, among others. After the review of Quentin [13], the Ascaridida type of arrangement of cloacal papillae has been described in other species, particularly those belonging to the subgenus P. (Pauicipetes), e.g., P. (Pa.) andryaccola, P. (Pa.) argentinensis, P. (Pa.) baionymis, P. (Pa.) chaetophracti, and P. (Pa.) hispanica [28–31]. With respect to the subgenus P. (Pterygodermatites), Le Roux [17] reported only three pre-cloacal and five postcloacal pairs of cloacal papillae in P. (P.) aethechini. However, the original description of Le Roux was illustrated with a lateral view of the male caudal extremity showing probably the unpaired precloacal papilla. In a posterior study concerning P. (P.) mexicana, Caspeta-Mandujano et al. [16] described in five sublateral pairs of cloacal papillae (pairs 1, 2, 4, 8, and 9) and four subventral pairs (pairs 3, 5, 6, and 7) but no unpaired pre-cloacal papilla are mentioned.

Within the P. (Pterygodermatites) subgenus, males present three characters that are useful to discriminate between species: the number of cuticular projection pairs (combs and spines), the number of midventral fans, and the size of spicules [13,19,32]. Considering the species of the subgenus P. (Pterygodermatites) for which information on males is available, there are differences in the male of P. (P.) plagiocestoma in the characters spicules size, number of fans, and number of cuticular projection pairs (see Table 1). In fact, in comparison to P. (P.) aethechini [17], the spicule sizes, particularly the right spicule is 98–123 µm in P. (P.) plagiocestoma vs. 118–132 µm in P. (P.) aethechini. Additionally, in comparison to P. (P.) mexicana [16], P. (P.) plagiocestoma presents a higher number of cuticular projection pairs (49–53 vs. 40 in P. (P.) mexicana), larger spicules (98–123 µm (right) and 185–236 µm (left) vs. 30–50 µm (right) and 83–111 µm (left) in P. (P.) mexicana) and lower number of midventral fans (1–2 vs. 3–4 in P. (P.) mexicana). Finally, in comparison to P. (P.) shaldybini [13], P. (P.) plagiocestoma presents larger spicules (98–123 µm (right) and 185–236 µm (left) in vs. 70 µm (right) and 140 µm (left) in P. (P.) shaldybini).

Concerning females, the most discriminant characters between species are the prevulvar and total number of cuticular projection pairs, the body level where the transition from combs to spines occurs, and the position of the vulva in relation to the esophagus–intestine junction [13,19,32]. In fact, the differentiation of cuticular projections (from combs to spines) occurs at the level of the vulva in P. (P.) plagiocestoma whereas it occurs at a posterior level in P. (P.) aethechini [17]. On the other hand, the vulva position is posterior to the esophagus–intestine junction in P. (P.) plagiocestoma whereas it is anterior in P. (P.) atlanticaensis [18]. There is also a higher number of both prevulvar and total pairs of cuticular projections (combs and spines) (43–46 /71–77) in P. (P.) plagiocestoma in comparison to the number of these characters (40/66) in P. (P.) mexicana [16] although the number of cuticular projection pairs in P. (P.) plagiocestoma (71–77) is surpassed by the 84 pairs described in P. (P.) shaldybini [13]. However, none of these discriminant characters of females differ between P. (P.) plagiocestoma and P. (P.) spinosa [13].

Pterygodermatites (P.) plagiocestoma is present in several hedgehog species (A. algirus, E. europaeus, H. auritus, and P. aethiopicus), and has a wide geographical distribution, including
North Africa (Algeria, Tunisia and Egypt), Saudi Arabia, and Spain [1–8]. As for the remaining species of the subgenus, *P. (P.) atlanticaensis* and *P. (P.) mexicana* are parasites of bats in Brazil and Mexico [16,18], *P. (P.) spinosa* were detected in bats from Baviera (Germany) [12], *P. (P.) shaldybini* were found in bats and hedgehogs from Asia (Kazakhstan, Turkmenistan, and Mongolia) [13,25,26], and *P. (P.) aethechini* were recorded in the hedgehog *Atelerix frontalis* from South Africa [16]. The present study enlarges the distribution of *P. (P.) plagioistoma* to the Tenerife and Gran Canaria islands (Canary Archipelago, Spain).

5. Conclusions
The present work on the rictulariid nematode *P. (P.) plagioistoma* contributes with the first morphoanatomical study of male specimens since its original description and provides further information on females. Moreover, the current finding in Tenerife and Gran Canaria islands (Canary Archipelago, Spain) enlarges the geographical distribution of this rictularid.

The most useful characteristics to differentiate *P. (P.) plagioistoma* from the remaining species of the subgenus *P. (Pterygodermatites)* are the total number of pairs of cuticular projections, the size of spicules and the number of midventral fans for males, and the number of prevulvar and total cuticular projection pairs and the position of the vulva in relation to the esophagus–intestine junction for females. The parasitized hosts and the geographical distribution are also useful criteria. The arrangement of cloacal papillae in males of *P. (P.) plagioistoma* follows the type Ascaridida and this type seems to be a characteristic of the subgenera *P. (Pterygodermatites)*, *P. (Paucipectines)*, and *P. (Neopaucipectines)*.

The analysis of available data on the species of *P. (Pterygodermatites)* emphasizes the need for more research, particularly in respect to male specimens, for which data are scarce or unknown for several species.

Author Contributions: Conceptualization, J.M., A.R., C.F. and P.F.; methodology, J.M., R.P.-V; E.I.-R., N.M.-C. and P.F.; investigation, J.M., A.R., R.P.-V., E.I.-R., N.M.-C. and P.F.; resources, J.M., A.R., R.P.-V., E.I.-R., N.M.-C. and P.F.; writing—original draft preparation, J.M., N.M.-C. and P.F.; writing—review and editing, J.M., A.R., C.F. and P.F.; supervision, J.M., C.F. and P.F.; project administration, C.F. and P.F.; funding acquisition, P.F. All authors have read and agreed to the published version of the manuscript.

Funding: This study was funded by “Gobierno de Canarias” and FEDER Canarias 2014–2020 grant number ProID2021010013; and Gobierno de Canarias-ULL agreement (“Estudio de patógenos en aves migratorias y en especies exóticas en un escenario de cambio climático”).

Institutional Review Board Statement: Animal work was approved in accordance with the Spanish Government Laws 42/2007 and RD 630/2013, the Canary Government law 151/2001 (references FYF141/10, FYF205/09, EEI-007/2019, ADL/mjb, MRR/rsh, A/EST-030/2016, AFF115/16, and EEI-007/2019), and the Ethic Committees of Research and Animal Wellness of Universidad de La Laguna (CEIBA2018-0330).

Informed Consent Statement: Not applicable.

Data Availability Statement: The type specimens are available upon request from MNHN Paris. Additional specimens are available upon request from the corresponding author.

Acknowledgments: The authors wish to thank the staff of the “Centres Científics i Tecnologies” of the University of Barcelona (CCiTUB) for their assistance in the preparation of SEM samples. A.R. and J.M. are members of the 2017-SGR-1008 research group.

Conflicts of Interest: The authors declare no conflict of interest.

References
1. Amin, O.M.; Heckmann, R.A. Nematodes and cestodes from the desert hedgehog, *Paracrinus aethiopicus* (Ehrenberg) in Central Saudi Arabia, revealed by SEM and microscopy, with notes on histopathology. *Sci. Parasitol.* 2016, 17, 26–35.
2. Feliu, C.; Blasco, S.; Torres, J.; Miquel, J.; Casanova, J.C. On the helminthfauna of *Erinaceus europaeus* Linnaeus, 1758 (Insectivora, Erinaceidae) in the Iberian Peninsula. *Rev. Ibérr. Parasitol.* 2001, 61, 31–37.
3. Jägerskiöld, L.A. Nematodem aus Ägypten und dem Sudan (eingesammelt von der Schwedischen Zoologischen Expedition). I. Rictularia und Dichelyne. In Results of the Swedish Zoological Expedition to Egypt and the White Nile 1901 under the Direction of LA Jägerskiöld; Part I. K.W.; Appelberg: Upsala, Sweden, 1904; pp. 1–66.

4. Jirié, J.; Bordes, F.; Morand, S.; Neifar, L. A survey of nematode parasites of small mammals in Tunisia, North Africa: Diversity of species and zoonotic implications. Comp. Parasitol. 2015, 82, 204–210. [CrossRef]

5. Khaldi, M.; Torres, J.; Samsó, B.; Miquel, J.; Biche, M.; Beneytou, M.; Béarch, G.; Benelkadi, H.A.; Ribas, A. Endoparasites (helminths and coccidians) in the hedgehogs Atelerix algirus and Paraechinus aethiopicus from Algeria. Afr. Zool. 2012, 47, 48–54. [CrossRef]

6. Mas-Coma, S.; Esteban, J.G.; Fuertes, M.V.; Bargues, M.D.; Valero, M.A.; Galán-Puchades, M.T. Helminth parasites of small mammals (insectivores and rodents) on the Pituysic Island of Eivissa (Balearic Archipelago). Res. Rev. Parasitol. 2000, 60, 41–49.

7. Miquel, J.; Blasco, S.; Marchand, B.; Torres, J.; Feliu, C. Etude en microscopie électronique à balayage de la femelle de Pterygodermatites (Pterygodermatidae) plagiostoma (Nematoda: Rictulariidae) chez un nouvel hôte. Vie Milieu 1997, 47, 213–220.

8. Wedl, K. Zur Helminthenfauna Ägyptens. III Nematoda. Sitz. Akad. Wiss. Math-Naturwiss. Kl. 1861, 44, 463–482.

9. Leiper, R.T. Demonstration or Nematode Parasites obtained from animals in the Zoological gardens during the year ending November 1910. Proc. Zool. Soc. Lond. 1911, XLIV, 620–621.

10. Parona, C. Sopra alcuni elmi di Vertebrati Birmani raccolti da Leonardo Fea. Ann. Mus. Civ. Stor. Nat. Genova Ser. 2 1889, 7, 765–780.

11. Sonsino, P. Notices helminthologiques. II. Rictularia plagiostoma et espèces semblables. Arch. Ital. De Biol. 1888, 10, 192–196.

12. von Willemoes-Suhm, R. Helminthologische Notizen. Z. Wiss. Zool. 1869, XIX, 469–475.

13. Quentin, J.-C. Essai de classification des Nematodes Ricturales. Mém. Mus. Natn. Hist. Nat. Sér. A, Zool. 1969, 54, 55–115.

14. von Willemoes-Suhm, R. Helminthologische Notizen III. Z. Wiss. Zool. 1873, XXIII, 331–345.

15. Blanchard, R. Notices helminthologiques (Première série). Bull. Soc. Zool. Fr. 1886, XI, 294–304.

16. Caspeta-Mandujano, J.M.; Jiménez, F.A.; Feralta-Rodríguez, J.L.; Guerrero, J.A. Pterygodermatites (Pterygodermatidae) mexicana n. sp. (Nematoda: Rictulariidae), a parasite of Balantiopteryx plicata (Chiroptera) in Mexico. Parasite 2013, 20, 47. [CrossRef] [PubMed]

17. Le Roux, P.L. A New Nematode (Rictularia Aethechini sp. nov.) a Physaloptera and an Acanthocephala from the Hedgehog (Aethochinus Frontalis), with notes on hosts and geographical distribution. Syst. Parasitol. 2019, 29, 253–283. [CrossRef]

18. Lopes, C.; Clemente, S.; Almeida, C.; Brito, A.; Hernández, M. A genetic approach to the origin of Millepora sp. in the eastern Atlantic. Coral Reefs 2015, 34, 631–638. [CrossRef]

19. Prosser, S.W.J.; Velarde-Aguilar, M.G.; León-Réggagnon, V.; Hebert, P.D.N. Advancing nematode barcoding: A primer cocktail for the cytochrome c oxidase subunit I gene from vertebrate parasitic nematodes. Mol. Ecol. Resour. 2013, 13, 1108–1115. [CrossRef]

20. Kumar, S.; Stecher, G.; Li, M.; Knyaz, C.; Tamura, K. MEGA X: Molecular evolutionary genetics analysis across computing platforms. Mol. Biol. Evol. 2018, 35, 1547–1549. [CrossRef]

21. Saitou, N.; Nei, M. The neighbor-joining method: A new method for reconstructing phylogenetic trees. Mol. Biol. Evol. 1987, 4, 406–425. [PubMed]

22. Tamura, K.; Nei, M. Estimation of the number of nucleotide substitutions in the control region of mitochondrial DNA in humans and chimpanzees. Mol. Biol. Evol. 1993, 10, 512–526. [PubMed]

23. Babaev, Y.A.; Kolodenko, A.I. Studies on helminth fauna of insectivorous mammals from the Turkmen-SSR USSR. Izv. Akad. Nauk Turkm. SSR Ser. Biol. Nauk 1975, 4, 71–75.

24. Tinnin, D.S.; Ganzorig, S.; Gardner, S.L. Helminths of small mammals (Erinaceomorpha, Soricomorpha, Chiroptera, Rodentia, and Lagomorpha) of Mongolia. Fac. Publ. Harold W. Manter Lab. Parasitol. Special Publ. Mus. Texas Tech. Univ. 2011, 59, 1–50.

25. Chabaud, A.G.; Petter, A.J. Remarques sur l’évolution des papilles cloacales chez les Nématodes phasmiidiens parasites de Vertébrés. Parasitologia 1961, 3, 51–70.

26. Cardia, D.F.; Tebaldi, J.H.; Fornazari, F.; Menozzi, B.D.; Langoni, H.; Nascimento, A.A.; Bresciani, K.D.S.; Hoppe, E.G.L. Pterygodermatites (Pauciptecines) andyaciana n. sp. (Spirurida: Rictulariidae), an intestinal nematode of Neotropical Molossidae bats from Brazil. Comp. Parasitol. 2015, 82, 296–300. [CrossRef]

27. Ezquiaga, M.C.; Rios, T.A.; Abba, A.M.; Navone, G.T. A new Rictulariidi (Nematoda: Spirurida) in xenarthrans from Argentina and new morphological data of Pterygodermatites (Pauciptecines) chaetophrae. J. Parasitol. 2017, 103, 727–735. [CrossRef] [PubMed]

28. Lynggaard, C.; García-Prieto, L.; Guzmán-Cornejo, C.; Osorio-Sarabia, D. Pterygodermatites (Pauciptecines) bayonidis n. sp. (Nematoda: Rictulariidae), a parasite of Baiomys taylori (Cricetidae). Parasite 2014, 21, 58. [CrossRef] [PubMed]

29. Quentin, J.-C. Un nouveau nématode Rictulaire Pterygodermatites hispanica n. sp., parasite de rongeur en Espagne. Bull. Mus. Natn. Hist. Nat. 1973, 183, 1395–1401.

30. Dollfus, R.P.; Desportes, C. Sur le genre Rictularia Froelich 1802 (Nematodes Spiruroidea). Ann. Parasitol. Hum. Comp. 1945, 20, 6–34. [CrossRef]