



OPEN The deeper the rounder: body shape variation in lice parasitizing diving hosts

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Seal lice, unique among insects, show remarkable adaptability to the extreme conditions of the deep sea. Evolving with their seal and sea lion hosts, they have managed to tolerate hypoxia, high salinity, low temperature, and elevated hydrostatic pressure. Given the diving capabilities of their mammalian hosts, which can reach depths of hundreds to thousands of meters, our study examines the morphological variation among closely related seal lice species infesting hosts with different maximum diving depths. In particular, our research reveals a significant morphological difference between lice associated with regular and deep-diving hosts, where lice from deep-diving hosts tend to be rounder. This could be an adaptation to withstand the high hydrostatic pressures found in the deep ocean. The rounded shape optimizes the louse's ability to withstand external pressure by redistributing it over a larger ventral/dorsal plane. This in turn minimizes the internal energy required to support body deformations, thereby increasing the louse's resilience in the deep sea environment.

Keywords Diving adaptations, Marine insects, Morphometrics, Seal lice, Pinnipeds

The colonization of the oceans by marine mammals has had a significant impact on the parasitic fauna associated with them. Several authors^{1–4} have hypothesized that the ocean acted as an ecological barrier for parasites during the transition from land. However, in the case of pinnipeds, they have preserved some taxa of originally terrestrial parasites. Remarkably, sucking lice are among those parasites that have successfully co-evolved and diversified in close association with their mammalian hosts.

Sucking lice are obligate haematophagous insects that live as permanent ectoparasites in the fur or hair of their mammalian hosts, attached to the skin. The family Echinophthiriidae (Phthiraptera: Anoplura) comprises a remarkable group of species that infest amphibious hosts, such as pinnipeds (walruses, seals and sea lions) and river otters^{5,6}. Pinnipeds are diving mammals, and some of them, such as sea lions and fur seals typically dive to ~ 100 m, while true seals can reach depths exceeding 1000 m^{7,8}. The most exceptional diving seal is the southern elephant seal *Mirounga leonina*, which may dive beyond 2000 m depth⁸.

During the evolutionary transition of pinnipeds from land to sea, echinophthiriid lice have had to cope with the gradual transition to an amphibian lifestyle together with their hosts, some of which manage to spend more than 80% of their time submerged and perform frequent extreme dives^{7,8}. These obligate and permanent ectoparasites have adapted to tolerate hypoxia, high salinity, low temperature and even very high hydrostatic pressure⁹. Many questions remain as to how do lice manage survive the challenges of the marine environment, and what morphological, physiological and behavioral adaptations are responsible for their success as the only insects capable of surviving in the depths of the ocean.

Concerning lice's morphological adaptations, only the presence of scales over the body has been the object of attention, resulting in different hypotheses advanced by Murray¹⁰ and by Hinton¹¹ relative to their function.

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According to the literature, the main features of seal lice are (1) a large development of legs, strongly adapted to grasp hair fibers; (2) spiracles with an elaborate closing device that could preserve atmospheric air in the tracheal system and prevent the entry of seawater during immersion; (3) a membranous and thick abdomen, the significance of which is not clear⁹. However, it is clear that seal lice have faced strong developmental constraints and selective pressures during their evolution.

The adaptation of the body form to specific bio-mechanical constraints can be analyzed by evaluating using an approach of geometric morphometrics, since allometric growth in different species can be associated with shifts in environmental conditions across their evolutive history, favoring traits that optimize individual survival (see Gould¹² among others). In this study, we investigated the morphological variability of closely related seal lice species infesting hosts with different diving habits, in order to quantify the phenotype-environment co-variation of these unique marine insects. On the other hand, we propose a physical hypothesis regarding the hydrodynamic and hydrostatic lice body shape adaptation.

Material and methods

Sampling

A total of 130 adult lice were collected from five host seals species (Table 1).

Capturing the body shape and size

Lice 2D images were photographed using a Carl Zeiss binocular magnifying glass equipped with AxioVision Rel.4.5 software (©Carl Zeiss Imaging Solutions) in order to obtain the body ventral view (Fig. 1).

Lice were placed with their dorsal side facing down to avoid pitching or rolling effects. We capture the lice ventral body shape using the following landmark and semi-landmark configuration illustrated in Fig. 1. One observer (FM) made the digitization process using TPSDig2 software¹⁸. Due to the lice body shape presents object symmetry¹⁹, a perpendicular axis of bilateral symmetry (left-right axis) that was defined between landmarks 1, 41, and 21. To standardize, translation, rotation, and scale in a symmetry object, we made a Procrustes fit with reflection²⁰. Then, the variation around the mean shape was decomposed into the symmetric and asymmetric components^{20,21}. Due to our interest is in symmetry, the asymmetric variation components were dismissed. Previously, to homologate semi-landmarks, we used a mathematical algorithm that slid each semi-landmark in an iterative process, minimizing the TPS function's bending energy. To do this we used TpsRelw software²². The centroid size, the square root of the sum of the squared distances from the landmarks to the centroid which they define, was used as a proxy for size²³.

Statistical analyses

The statistical analyses for geometric morphometrics analyses were performed in the MorphoJ, version 1.07a²⁴. To evaluate and control the allometry effect (change in the lice shape related to size increment), a pooled-seal lice species multivariate regression between aligned Procrustes coordinates (dependent variables) and centroid sizes (independent variable) was calculated, running a permutation test (10,000 rounds).

The principal component analysis of the variance-covariance matrix was done to explore and display the major features of the seal lice body shape²³. Then, to display axes of maximum discrimination among seal lice species shapes, we performed a canonical variate analysis (CVA). Finally, to test statistical differences among seal lice species, we used a cluster analysis UPGMA-MDGC^{25,26}. This method successfully determines the number of groups based on inferential statistics in hierarchical cluster analysis. The graphical output of the MDGC test is a useful tool since it shows a clear distinction between statistically different groups as well as their relationships²⁷.

Results

Seal louse body size (centroid size) differed significantly among species ($H = 60.49$, $p < 0.0001$). Lice from elephant seals were bigger than the others (Fig. 2).

Seal lice growth was allometric. The relationship between body shape and size pooled within seal lice species was statistically significant (permutation test with 10,000 random permutations, $p < 0.0001$) and accounted for 11.72% of the shape variation (Fig. S.1, Supplementary Material section A). Therefore, the regression residuals were used as free-allometric shape variables in subsequent statistical analyses.

Principal component (PC) analysis of body shape variation showed that 82.62% of the total shape variation was concentrated in the first three PC scores. Interpretation of shape variation using wire-frame plots showed that PC1 (which explained 50.25% of the total variance) was related to body slenderness, which was associated

| Louse species | Code | n | Host | Max/average diving depth (m) | Average host body mass (kg) | |
|------------------------------------|------|----|-------------------------|-----------------------------------|-----------------------------|--------|
| | | | | | Male | Female |
| <i>Lepidophthirus macrorhini</i> | Lm | 45 | Elephant seals | 2388/549.8 ± 84.1 ^{8,13} | 2998 | 688 |
| <i>Antarctophthirus carlinii</i> | Ac | 26 | Weddell seal | 700/458 ± 113 ¹⁴ | 425 | 450 |
| <i>Antarctophthirus ogmorhini</i> | Ao | 2 | Leopard seal | 424/44 ± 48 ¹⁵ | 300 | 325 |
| <i>Antarctophthirus lobodontis</i> | Al | 29 | Crabeater seal | 776/248 ± 141 ¹⁶ | 232 | 249 |
| <i>Antarctophthirus microchir</i> | Am | 28 | South American sea lion | 256/158 ± 32 ¹⁷ | 325 | 145 |

Table 1. Lice species and their host analyzed in this study.

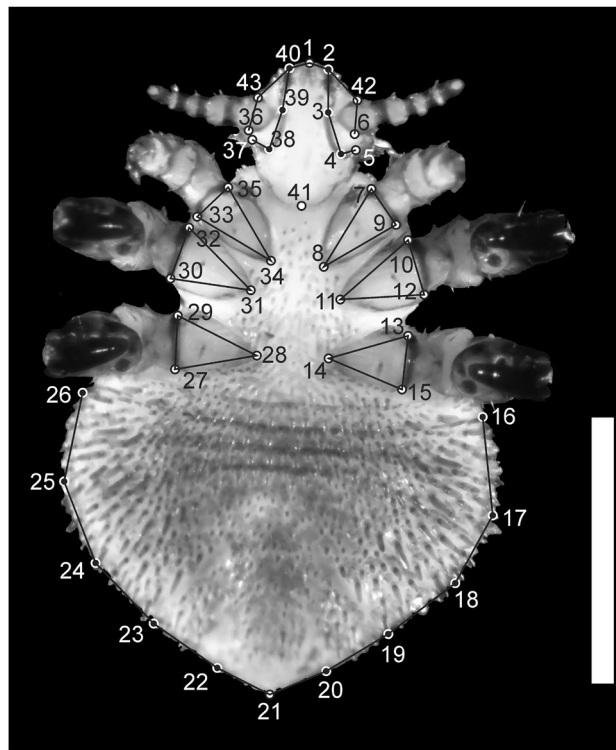


Fig. 1. Ventral aspect and wire-frame of the louse *Antarctophthirus lobodontis* showing the position of the 27 landmarks and 16 semi-landmarks used to perform geometric morphometric analysis. These landmarks are: (1) the anterior edge of the head, (2–4) semi-landmarks placed between landmark 1 and 5, (5) end of postantennal angle, (6) posterior base of the first segment of the antenna, (7) anterior extreme of the first coxal condyle, (8) base of the first coxal condyle, (9) posterior extreme of the first coxal condyle, (10) anterior extreme of the second coxal condyle, (11) base of the second coxal condyle, (12) posterior extreme of the second coxal condyle, (13) anterior extreme of the third coxal condyle, (14) base of the third coxal condyle, (15) posterior extreme of the third coxal condyle, (16–26) semi-landmarks around the abdomen outline, (21) apex of the abdomen, (27) posterior extreme of the left third coxal condyle, (28) base of the left third coxal condyle, (29) anterior extreme of the left third coxal condyle, (30) posterior extreme of the left second coxal condyle, (31) base of the left second coxal condyle, (32) anterior extreme of the left second coxal condyle, (33) posterior extreme of the left first coxal condyle, (34) base of the left first coxal condyle, (35) anterior extreme of the left first coxal condyle, (36) posterior base of the left first segment of the antenna, (37) end of left post antennal angle, (38–40) semi-landmarks placed between landmark 1 and 37, (41) maximum curvature of the neck, (42) anterior base of the first segment of the antenna, and (43) anterior base of the left first segment of the antenna. Scale bar = 1 mm.

with posterior expansion and rostral development. Individuals at the positive extreme were associated with a rounded body shape, exhibited lateral rostral and lateral expansion, posterior constriction, and posteriorly directed expansion of the coxae. In contrast, individuals at the negative extreme showed speculative variations in body shape (slender). Individuals at the positive extreme of PC2 (25.25%) showed right-left lateral constrictions and less rostral development. On the contrary, individuals from the negative extreme showed the opposite shape variations (Fig. 3).

CVA showed that lice body shape can be successfully used to discriminate between species. Pairwise comparisons of Mahalanobis distances between the five lice species revealed significant differences in mean body shape (Table 1). Values of CV1 (89.77%) separated *Lepidophthirus macrorhini* (positive values) from the others, with a more rounded posterior part, a posterior projection of the coxae and an expanded rostrum. While CV2 (8.41%) separated *Antarctophthirus microchir* (negative values) from the other lice species of the genus *Antarctophthirus* (positive values), *L. macrorhini* was found in between, close to the consensus shape. CV2 variation was associated with robust (positive values) to slender body shapes (Fig. 4). Hierarchical clustering using the cutting criteria from the MDGC test indicated three groups ($p < 0.05$), one of host Antarctic seal lice, one of South American sea lions and one of elephant seals (Fig. 5). The Antarctic seal host group showed no significant differences in lice body shape ($p > 0.05$). This large group was linked to the group formed by the three species of the *Antarctophthirus* genera. The most divergent group is *Lepidophthirus macrorhini*, the louse that parasitises the deeper-diving species.

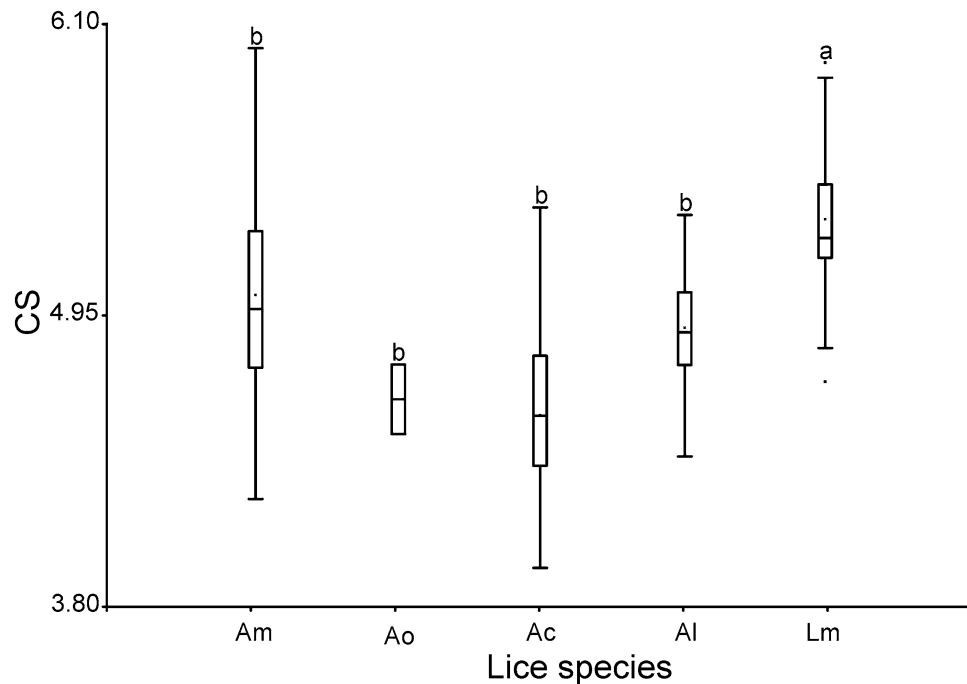


Fig. 2. Body size (CS) variations between seals lice species. The central dot represents the mean; the median is represented as a central line; the limits of the box, the first and third quartiles, and the whiskers the 95% confidence interval; the dots out the whiskers are outliers. Different letters indicate significant differences ($p < 0.05$) in pairwise comparisons test. Am: *Antarctophthirus microchir*, Al: *Antarctophthirus lobodontis*, Lm: *Lepidophthirus macrorhini*, Ac: *Antarctophthirus carlinii*, and Ao: *Antarctophthirus ogmorhini*.

Discussion

This study used geometric morphometrics to compare the variation in the shape of different species of seal lice. We also provide compelling graphical and analytical evidence that these species differ in allometric growth forms. We hypothesize that shape reflects environmental constraints and adaptation to marine conditions. Indeed, our results showed a tendency for those species with deeper diving behavior to be more rounded.

A general rule for parasites, known as Harrison's rule, states that large-bodied host species have large-bodied parasite species^{28,29}. This relationship has been demonstrated in a wide variety of parasitic taxa, including worms, crustaceans, fleas, flies, lice, ticks, aphids, beetles, flies, thrips, flower mites and moths^{30–36}. Harrison described this pattern by analyzing avian lice, and it is in this group that it is most well documented³⁷. In fact, the rule has been demonstrated in 581 species of bird lice belonging to dozens of genera³⁸. For sucking lice, Cannon³⁹ found that they conform to Harrison's rule, at least in the three families analyzed. Our results are partially consistent with this general rule. We found that lice from elephant seals were bigger but also rounder than the others.

On the other hand, parasites allocate much more resources to attachment structures or organs⁴⁰. For example, in intestinal parasites, attachment organs increase disproportionately with body size because the greater the size, the greater the risk of detachment⁴⁰. In feather lice, the ability to attach is not a determinant of host specificity, even though lice have a long co-evolutionary history with their hosts^{41,42}. The same appears to be true for seal lice. Our results do not show a higher development of legs or claws. In *Lepidophthirus macrorhini* we found a posteriorly directed extension of the coxae. In contrast to most *echinophthiriids*, the first pair of legs in this species are robust and the tarsal claw is modified into a well-developed nail. This difference in the function of the first pair may explain the position and development of the coxae.

Although four of the five species analyzed belong to the same genus, it is important to note the differences between the hosts. Three groups can be distinguished. *Antarctophthirus microchir*, which infects sea lions; the Antarctic seal lice, including *A. lobodontis*, *A. weddelli*, and *A. ogmorhini*; and *L. macrorhini* from the southern elephant seal. These groups were successfully distinguished by the body shape of the lice. *Lepidophthirus macrorhini* has a more rounded posterior part, a posterior projection of the coxae and an expanded rostrum. While *A. microchir* could be separated from the other *Antarctophthiruses* by CV2. CV2 variation was associated with robust to slender body shapes. Different allometric relationships may reflect selective pressures and elucidate past evolutionary trends, especially in related species⁴⁰. In particular, parasites may allocate more resources to the growth of structures whose importance scales allometrically with size⁴⁰. As we mentioned above, an example of this is the size of attachment organs. In general, parasites display a wide range of body shapes and sizes as well as differences in anatomical structures⁴⁰. However, how these shapes are modeled by selective pressure remains unclear.

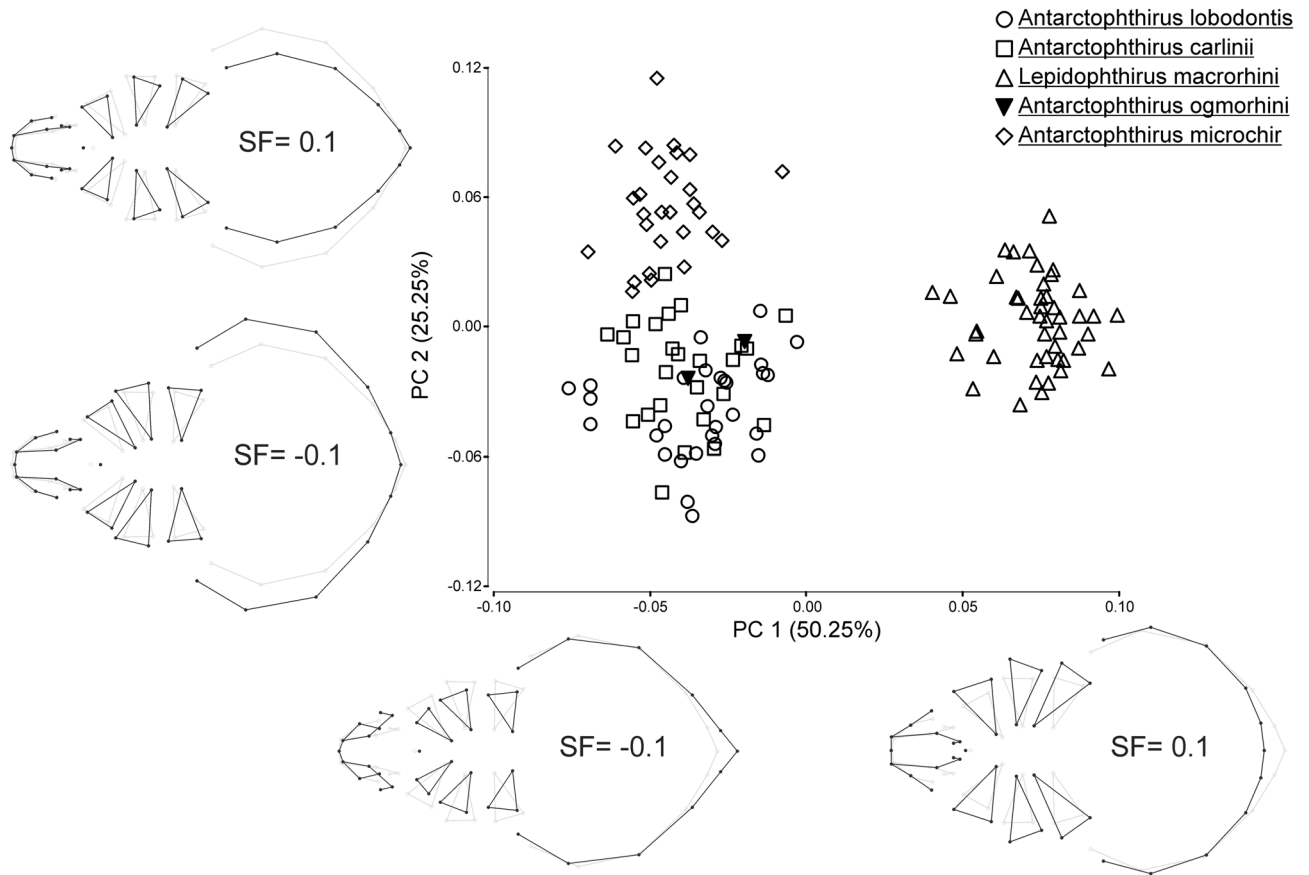


Fig. 3. Plot of the first two principal components (PC1 versus PC2) for different species of lice, based on Procrustes distances. The figures represent the displacement vectors from the overall mean shape (gray wire-frame) to the positive and negative extreme shape (black wire-frame) for each PC. Shape changes have been exaggerated (scale factor: $SF \pm 0.1$) in the graphic for better visualization. Percentages of explained variance for each axis are in parentheses.

Although other organisms living permanently in high hydrostatic pressure environments in the deep sea and abyssopelagic zone have not all evolved round shapes, sea lice have been subject to different selective pressures that have affected their body allometry compared to them. In particular, the forces acting on their bodies change rapidly over a wide range. Close to the surface they experience atmospheric pressure, but at maximum diving depths they can be exposed to hydrostatic pressures of 200–250 atm.

From a physical point of view, the rounded shape of an insect can help it to adapt better to high hydrostatic pressures due to structural advantages. An increased area on its ventral/dorsal plane (Fig. S.2 Supplementary Material section B) allows the external pressure to be better redistributed along the entire body volume, reducing the internal energy expended to support the body deformations undergone, making a louse with a larger wet area better able to withstand the external pressure. As an increase in external pressure is proportional to surface area (and not volume), an oblate individual will experience less energy expenditure due to pressure compression than an elongated (prolate) shape. This characteristic of deep-diving lice may be related to hydrostatic pressure at great depths.

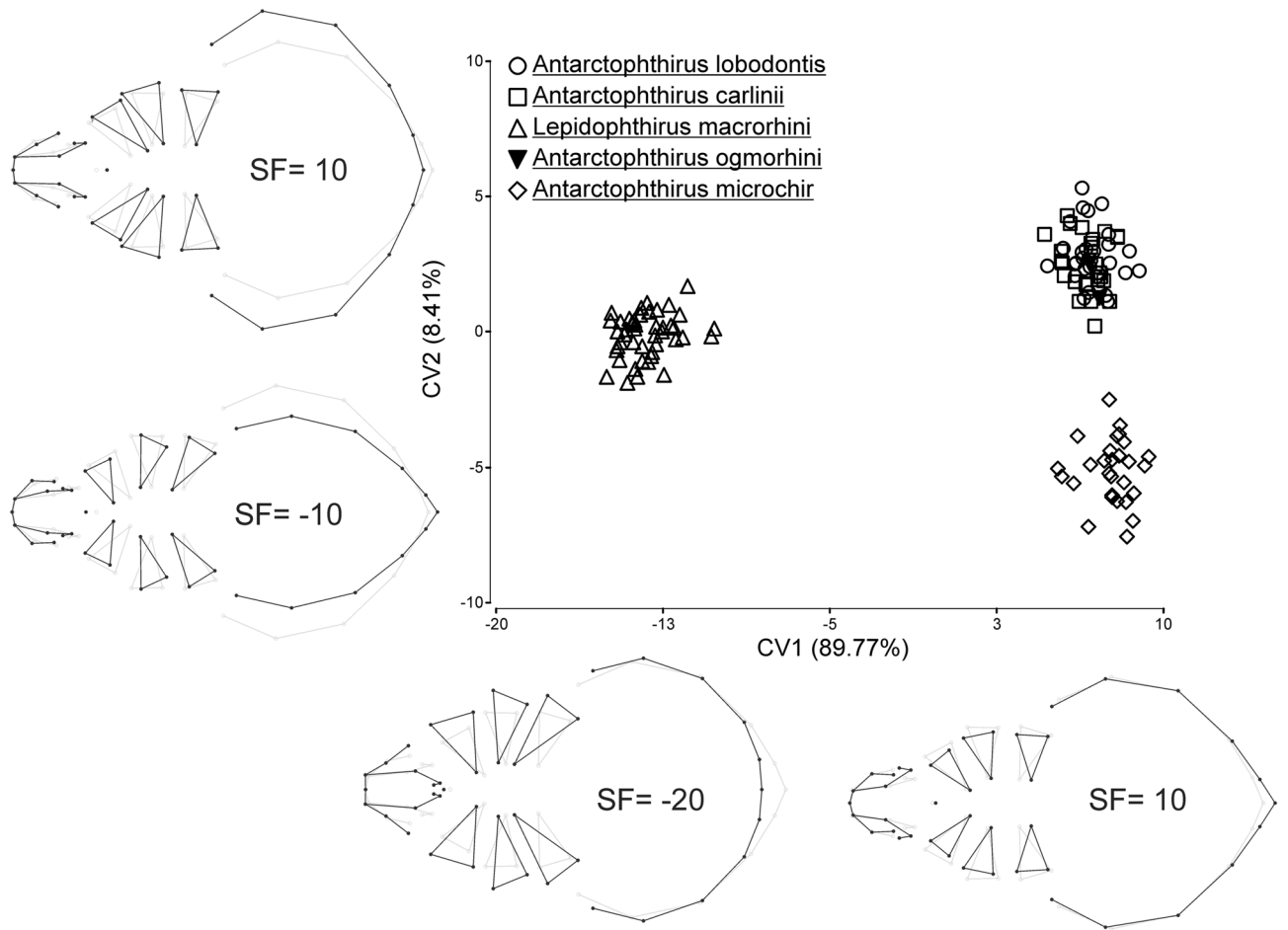


Fig. 4. Canonical variate analysis showing the maximum separation of ventral shape differences among lice species. Wire-frame show shape changes from mean shape (gray vectors) to the positive and negative extreme (black vectors) in both axis.

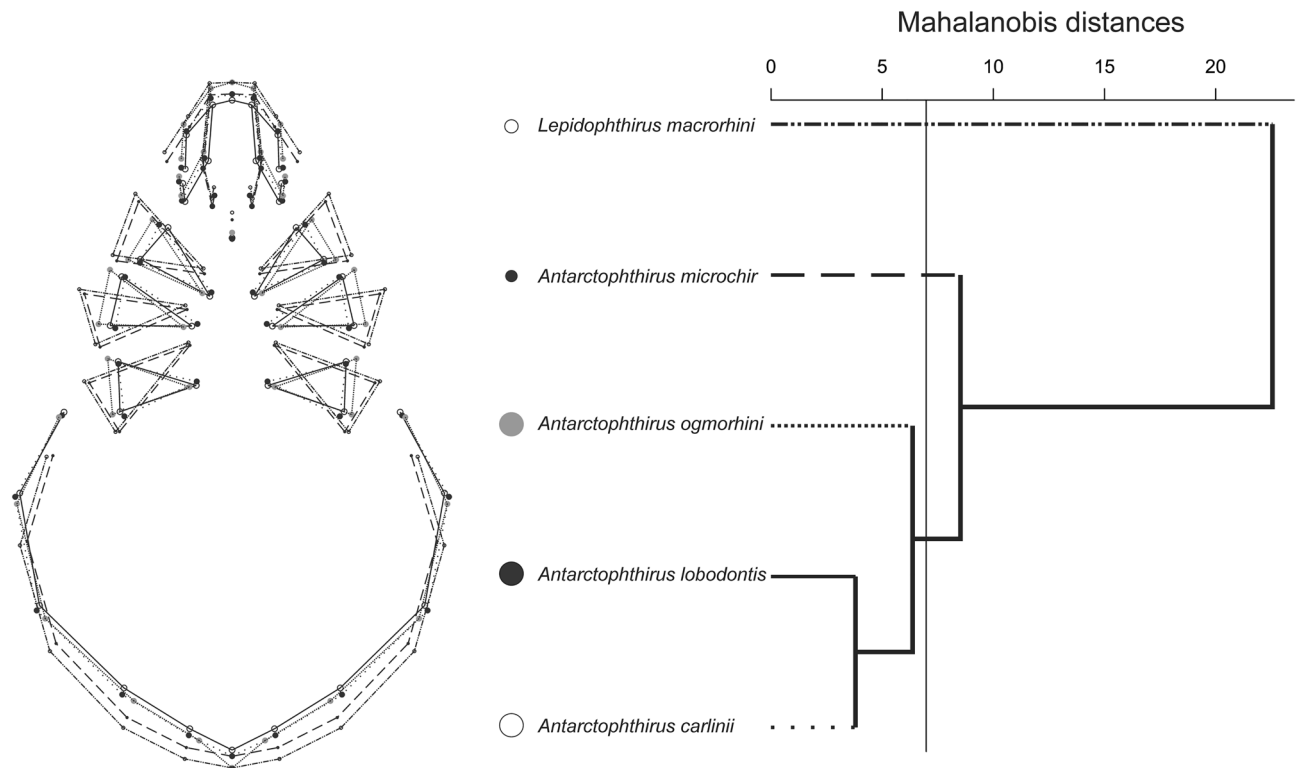


Fig. 5. Cluster diagram showing the ventral shape relationships among lice species and the overlapped wire-frames of the reconstructed consensus configurations to each ones. The cut-off criterion ($p = 0.05$) obtained with the MDGC test is indicated with a horizontal line. Three statistically different groups of ventral shapes were identified by this method.

Data availability

The data described in this article can be freely and openly accessed as Supplementary material.

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Author contributions

MSL: Conceptualization, Data Curation, Methodology, Investigation, Validation, Visualization, Writing – Original Draft, Writing – Review & Editing. RRP: Conceptualization, Data Curation, Formal Analysis, Physics Solver, Validation, Visualization, Writing Original Draft, Writing – Review & Editing. HLO: Formal Analysis, Physics Solver, Validation, Visualization, Writing Original Draft, Writing – Review & Editing. CL: Conceptualization, Investigation, Writing – Original Draft, Writing – Review & Editing. JN: Data Curation, Investigation, Writing Original Draft, Writing – Review & Editing. FM: Conceptualization, Data Curation, Formal Analysis, Methodology, Software, Validation, Visualization, Writing – Original Draft, Writing – Review & Editing. All authors contributed critically to the drafts and gave final approval for publication.

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Competing interests

The authors declare no competing interests.

Additional information

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