



Postcranial evolution of the insular lineage of *Nesiotites* Bate, 1944 (Lipotyphla: Nectogalini) from *Asoriculus* to extinction

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Abstract

The Balearic shrew *Nesiotites* represents one of the most remarkable examples of insular evolution among Mediterranean mammals. While most previous studies have focused on its cranial anatomy, little attention has been paid to the postcranial skeleton and its evolutionary transformations through time. In this study, we analyze and compare postcranial elements—including humeri, ulnae, femora, tibiae, and pelves—across the entire temporal range of the *Nesiotites* lineage in Mallorca, from its earliest representative (*Asoriculus* sp., earliest Pliocene, ~5.3 Ma) to the terminal species of the Holocene *Nesiotites hidalgo*, which survived until after 3,000 cal BC. Drawing on the most complete osteological series available for this lineage, we quantify changes in skeletal proportions and functional morphology to explore patterns of morphological differentiation and life history evolution in an insular context. Comparisons with extant Soricinae and Crocidurinae species provide additional insights into body size trends, limb allometry, and potential locomotor adaptations. We discuss these results in the framework of the “island syndrome”, evaluating the extent to which *Nesiotites* evolved under relaxed predation, resource limitation, and extended longevity. Our findings highlight the value of postcranial anatomy in reconstructing insular evolutionary trajectories and contribute new data to the paleobiology of extinct shrews.

Keywords Balearic Islands · Functional morphology · Island rule · Neogene · Quaternary · Soricinae

Introduction

The insular lineage of *Nesiotites* Bate, 1944 (Lipotyphla: Nectogalini) is the least known of the classical triad of mammalian lineages that evolved on the island of Mallorca (Balearic Islands, western Mediterranean), from their arrival during the Messinian (5.6–5.33 Ma) until their extinction, which most likely occurred after the arrival of humans (Bover et al. 2016). The terminal genus was later expanded to include *Nesiotites similis* (Hensel, 1855) from Sardinia (originally described as *Sorex similis* Hensel, 1855) and *Nesiotites corsicanus* Bate, 1944 from Corsica.

Currently, the *Nesiotites* lineage in Mallorca includes three formally described species: *Nesiotites hidalgo* Bate, 1944, from the Late Pleistocene-Holocene; *Nesiotites ponsi* Reumer, 1979, from the Late Pliocene; and *Nesiotites rafelinensis* Rofes et al., 2012, from the late Early Pliocene. Additional fossil material from Early Pleistocene and Late Pliocene deposits has been attributed to *N. aff. ponsi* (Alcover et al. 1981). *Nesiotites meloussae* Pons-Moyà and Moyà-Solà, 1980 was described from the Early Pleistocene

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of Menorca; however, to date, no indisputable Late Pleistocene remains attributable to *N. hidalgo* have been documented on the island. (e.g., Furió, 2007; Rofes et al. 2012).

Previous research studies of the genus *Nesiotites* have focused predominantly on cranial and dental remains, whereas the postcranial skeleton has remained comparatively overlooked. Apart from a popular science monograph illustrating several long bones of *N. hidalgo* (Alcover et al. 1981), a conference abstract describing the pelvis morphology in *N. hidalgo* (Pons-Monjo et al. 2010), and the use of postcranial measurements of *Nesiotites* species for body mass estimation (Moncunill-Solé et al. 2016), little has been published on limb morphology or locomotor adaptations in this extinct lineage. Consequently, it remains unclear whether *Nesiotites* evolved functional specializations in response to insular conditions beyond the well-documented increase in overall body size—a question directly relevant to assessing the extent to which this lineage conforms to the expectations of the “island syndrome” described for other insular mammals (Lomolino 2005; Lomolino et al. 2013; van der Geer et al. 2013).

Bate's (1944) original description placed *Nesiotites* within the Soricinae (red-toothed shrews) and suggested affinities with species now assigned to the tribe Nectogalini. Its inclusion in this tribe is supported both by diagnostic morphological features and by genetic evidence. Morphologically, *Nesiotites* shares the following characters with other Nectogalini (Bate 1944; Bühler 1964; Spitzenberger 1990): (1) a strongly domed cranial vault elevated above the rostrum; (2) a postglenoid process forming a disc with a central opening; (3) a slightly concave or straight anterior margin of the nasal bones; (4) in lateral view, a kinked rostrum above U1, elevated compared to *Sorex*; (5) a straight (non-indented) lower margin of the articular process in buccal view; (6) a narrow bony bridge connecting the articular surfaces of the condyle in caudal view; (7) a strongly curved anterior cusp of the upper incisor, directed anteriorly and inferiorly; (8) no more than four upper unicuspid, the last of which (when present) is minute and single-rooted; (9) elongated posterior margins of the remaining unicuspid in lateral view, with tips pointing posteriorly and supported by two roots; (10) a single, weakly defined cusp on the cutting edge of the lower incisor; and (11) teeth with slightly pigmented or unpigmented tips.

In addition to morphological evidence, the inclusion of *Nesiotites* in the Nectogalini is supported by ancient DNA analyses. Bover et al. (2018) identified *Soriculus nigrescens* Gray, 1842 as its closest living relative. According to this study, the lineages of *Soriculus* and *Nesiotites* diverged between 8.36 and 4.68 Ma. This estimated divergence time aligns well with the assumed colonization of Mallorca during the Messinian (5.6–5.3 Ma), and with the proposed

derivation of *Nesiotites* from a species of the extinct genus *Asoriculus* Kretzoi, 1959. *Asoriculus* is known in mainland Europe from the Late Miocene through the Pleistocene and is widely regarded as the ancestral form of several insular Plio-Pleistocene shrew lineages in the western Mediterranean.

In this context, here we investigate the postcranial skeleton of *Nesiotites* to address this longstanding gap. By conducting a comprehensive morphofunctional analysis of limb and pelvic elements spanning from the earliest representative (*Asoriculus* sp., early Zanclean), through the late Piacenzian *N. ponsi*, to the Holocene *N. hidalgo*, we aim to: (1) provide a detailed morphological characterization of postcranial proportions and structural robusticity; (2) compare these traits with those of a broad range of extant soricids from both the Soricinae and the Crocidurinae, to place *Nesiotites* within a wider functional and ecological framework; (3) identify evolutionary trends in skeletal robusticity, limb proportion, and potential insular adaptations; and (iv) examine pelvic morphology (particularly the pubic symphysis and sacro-pelvic integration) to evaluate their functional significance. This approach integrates comparative anatomy with functional indices to interpret how insular evolution influenced the locomotor capabilities and life history of *Nesiotites*.

Materials and methods

Paleontological material and comparative sample

We analyzed paleontological postcranial material from the principal evolutionary stages of the Mallorcan *Nesiotites* lineage (Fig. 1). The earliest *Asoriculus* sp. fossils come from the karstic sites of Na Burguesa-1 and 2, biochronologically dated to the Early Pliocene (latest Messinian–earliest Zanclean; ~5.3–5.0 Ma), and represent the ancestral form of the lineage (Bover et al. 2014; Torres-Roig et al. 2024). The sample of *N. ponsi* is derived from the Late Pliocene deposits of Pedrera de s'Ònix (Reumer 1979). *Nesiotites hidalgo* is represented by assemblages from three Holocene cave sites spanning the final existence of the lineage: Cova Estreta (latest Pleistocene–Early Holocene transition; Encinas and Alcover 1997), Cova de Canet (Middle Holocene; Pons-Moyà et al. 1979; Pons-Moyà and Coll 1986), and Cova des Garrover (latest Holocene, immediately pre-extinction; Bover and Alcover 2008). Together, these samples provide a temporal series from initial colonization to just before extinction. In addition, we assembled a comparative dataset of extant shrews to contextualize the measurements of the extinct shrews. A complete list of all paleontological and comparative specimens examined,



Fig. 1 Geographic location of the sites discussed in the study. Left: Iberian Peninsula and western Mediterranean showing the location of the Balearic Islands. Right: Mallorca with the fossil localities indicated

including catalogue numbers and provenience, is provided in Online Resource 1.

Published morphometric data were taken from Woodman and Wilken (2019) and Woodman (2023) for a broad range of sorcid species. To this, we added new measurements of five extant species not in the published sources (*Crocidura pachyura*, *Crocidura gueldenstaedtii*, *Crocidura zimmermanni*, *Suncus etruscus*, *Sorex coronatus*, and *Sorex minutus*) using osteological specimens housed at the Mediterranean Institute for Advanced Studies (IMEDEA). In total, the extant comparative sample includes over 20 species encompassing a diversity of locomotor ecologies (mostly generalist terrestrial shrews, with a few semi-fossorial or semi-aquatic species for reference). All skeletal specimens, paleontological and modern, are curated in the collections of IMEDEA or collaborating institutions (see Online Resource 2 for raw measurements and Online Resource 1 for more details of the specimens).

Measurements and body mass estimation

For each paleontological and extant specimen, a total of 13 linear measurements were recorded, including 12 postcranial dimensions comprising bone lengths, midshaft diameters, distal widths, and selected muscle attachment lengths of the humerus, ulna, femur and tibia, and one mandibular measurement (TRLM1), following established protocols (Fig. 2). Postcranial measurements were used for functional and locomotor analyses, whereas TRLM1 was recorded exclusively for body mass estimation. Whenever possible, we measured maximum bone lengths (e.g., humerus length, functional ulna length, tibia length) as well as midshaft or

by black dots and lowercase letters: **a.** Cova Estreta; **b.** Cova des Garrover; **c.** Pedrera de s'Ònix; **d.** Na Burguesa; **e.** Cova de Canet. Scale bar equals 30 km

distal breadths (e.g., least diameter of humeral shaft, distal width of femur), which serve as indicators of bone robusticity. Given the minute size of many shrew bones, measurements were obtained from high-resolution digital images using a calibrated digital microscope (Dino-Lite Edge, AM7915MZZ model). Variables were measured from the resulting images using the program ImageJ (Schneider et al. 2012; <https://imagej.nih.gov/>), calibrated with the scale included in each image. All measurements are reported to the nearest 0.01 mm and are provided in the Online Resource 2.

As a proxy for body size, we estimated body mass from selected craniodental and postcranial dimensions. We applied the allometric regression equations developed by Moncunill-Solé et al. (2016) specifically for sorcids. These equations relate body mass to skeletal measurements based on a calibration set of extant shrews. For each fossil species and site, body mass was computed from multiple variables (i.e., long-bone length and widths, and one mandibular length). Mean body mass and 95% confidence intervals were calculated for each taxon at each site (one sample for *Asoriculus* and *N. ponsi*, and three samples for *N. hidalgo*) to track size evolution through time.

To assess whether body mass estimates differed systematically depending on the type of predictor used, we compared cranial- and postcranial-derived estimates, as well as length-versus width-derived postcranial estimates, within selected fossil samples using two-tailed Mann–Whitney U tests, as recommended for non-normal biometric data (Davis 1996). These comparisons were used as an exploratory assessment of predictors differences in estimation outcomes (see Online Resource 3: Fig. S1).

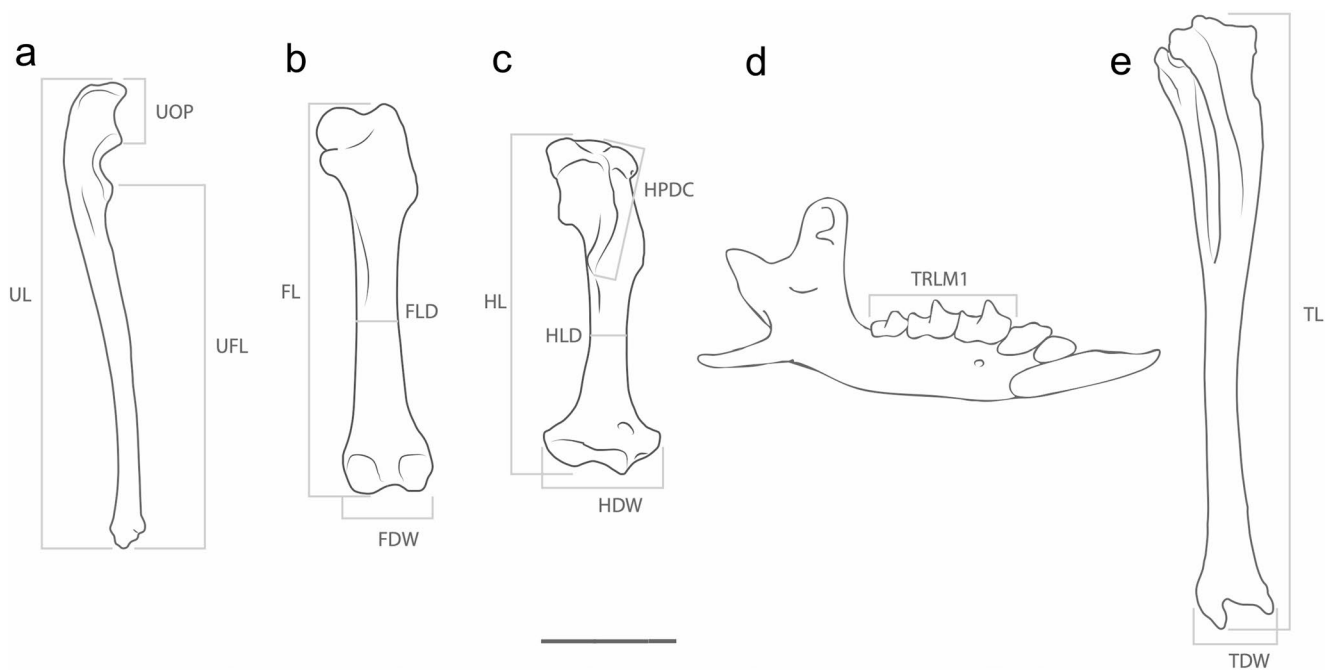


Fig. 2 Osteological measurements. **a.** ulna; **b.** femur; **c.** humerus; **d.** mandible; **e.** tibia. **Abbreviations:** FDW, distal femoral width; FL, femur length; FLD, femoral least diameter; HDW, distal humeral width; HL, humerus length; HLD, humeral least diameter; HPDC,

humeral deltopectoral crest length; TDW, distal tibial width; TL, tibia length; TRLM1, lower molar tooth row length; UL, ulna length; UFL, ulna functional length; UOP, olecranon process length. Scale bar equals 5 mm

Locomotor indices and functional analysis

To evaluate locomotor function and limb morphology, we calculated a suite of osteological indices from the postcranial measurements of each taxon. In total, ten indices were considered (Table 1), based on metrics previously used to characterize locomotor mode and substrate-related adaptations among soricids (Woodman and Wilken 2019; Woodman 2023), rodents (Samuels and Van Valkenburgh 2008; Elissamburu and De Santis 2011), and other mammals

(Hopkins and Davis 2009). To partly overcome the problem of missing data, indices were calculated from species mean values of the underlying measurements. Each index is a dimensionless ratio capturing a specific aspect of limb form or mechanical advantage.

Although a total of 12 postcranial measurements were recorded, only a subset of these variables was combined into dimensionless ratios to calculate locomotor indices. As a result, the number of indices derived was lower than the number of original measurements. Two index datasets were therefore assembled to maximize taxonomic coverage: Set A comprised seven indices that could be calculated for all taxa, including *Asoriculus*, whereas Set B included the full set of eleven indices but excluded *Asoriculus*, which lacked some of the required measurements (see Online Resource 4). For every species (extant and extinct), each index value was converted into a percentile relative to the distribution of that index across the entire sample. This transformation allowed us to compare disparate indices on a common scale of 0 to 100, where a higher percentile generally indicates a more extreme morphology associated with specialized locomotion (e.g., more fossorial), and lower percentiles indicate more generalized ambulatory traits (see Woodman and Wilken 2019). We then calculated the mean percentile rank (MPR) for each taxon as the arithmetic mean of its index percentiles, providing a single composite score of locomotor morphology. An MPR near 0 indicates an overall morphology

Table 1 Locomotor and limb proportion indices used in this study, expressed as dimensionless ratios and reported as percentages. Index formulas are provided for reference; the anatomical measurements used to compute each index are illustrated in Fig. 2 and defined in the abbreviations section. Additional discussion on the functional relevance of these indices is provided in Online Resource 4. See Bover et al. (2010) and Woodman and Wilken (2019) for further background

Index	Abbreviation	Formula
Brachial	BI	UFL/HL
Crural	CI	TL/FL
Femoral epicondylar	FEB	FDW/FL
Femoral robustness	FRI	FLD/FL
Humeral epicondylar	HEB	HDW/HL
Humeral robustness	HRI	HLD/HL
Intermembral	IM	(HL+UL) / (FL+TL)
Olecranon length	OLI	UOP/UFL
Shoulder moment	SMI	HPDC/HL
Tibial robustness	TRI	TDW/TL

firmly within the range of typical ground-dwelling shrews, whereas higher MPR values would suggest a trend toward the morphospace of semi-fossorial or semi-aquatic species.

In parallel, we performed linear discriminant analysis (LDA) to statistically classify locomotor modes based on the index data. Extant shrew species were assigned to one of several locomotor categories defined in prior work (Woodman and Wilken 2019; Woodman 2023): primarily ambulatory (terrestrial generalist), semifossorial, or semiaquatic, with a small number of truly fossorial forms as well. Following Woodman and Wilken (2019), “ambulatory” denotes shrews that move on the ground surface and lack clear skeletal specializations for digging, climbing, or swimming. The LDA was trained on the extant species with known ecology and then used to predict the class of each fossil population by projecting their index values into the discriminant space. This approach tests whether the fossils cluster with modern ground-dwelling shrews or if they exhibit deviations toward the multidimensional profiles of digging or swimming specialists (see Bover et al. 2010 for a similar approach applied to *Hypnomys morpheus*). All statistical analyses were conducted in R version 4.4.1 (R Core Team 2024) using RStudio version 2024.12.1 + 563. Analyses and plotting relied on the R packages MASS (Venables and Ripley 2002), dplyr (Wickham et al. 2025), ggplot2 (Wickham 2016), and ggrepel (Slowikowski 2024); data import and string handling used readr and stringr. Classification posterior probabilities were used to assess the confidence of locomotor assignments. Linear discriminant analyses were performed on both index datasets: results based on Set A, which includes *Asoriculus*, are presented in the main text, whereas the complementary analysis based on Set B, without *Asoriculus*, is provided in the Online Resource 5. By combining the MPR metric and LDA classification, we obtain both a continuous measure of locomotor morphology and a categorical prediction of locomotor mode for the extinct taxa.

In addition to the quantitative morphometric analyses of limb proportions and robusticity, we examined the pelvis to explore qualitative aspects of postcranial anatomy in *Nesiotites*. Although not included in the statistical datasets due to the scarcity of complete specimens, pelvic morphology provides complementary information relevant to locomotor function and life-history inference. This element preserves traits that, while subtle, can reveal aspects of sexual dimorphism, age-related skeletal changes, and potential insular adaptations not captured by linear measurements alone.

Abbreviations: **BI**, brachial index; **CI**, crural index; **FEB**, femoral epicondylar breadth; **FL**, femur length; **FLD**, femoral mediolateral diameter; **FRI**, femoral robusticity index; **FTW**, distal femoral transverse width; **HEB**, humeral epicondylar breadth; **HL**, humerus length; **HPDC**, humeral deltopectoral crest length; **HRI**, humeral robusticity index;

IM, intermembral index; **LDA**, linear discriminant analysis; **LD**, linear discriminant axis; **MPR**, mean percentile rank; **OLI**, olecranon length index; **SMI**, shoulder moment index; **TDW**, distal tibial transverse width; **TL**, tibia length; **TRLMI**, lower molar tooth row length; **UL**, ulna length; **UFL**, ulna functional length; **UOP**, olecranon process length.

Results

Body mass estimates through time

Based on the regressions published by Moncunill-Solé et al. (2016) for fossil shrews, estimated body mass in the Mallorcan *Asoriculus*–*Nesiotites* lineage shows a clear, progressive increase through time (Table 2). The lowest estimates correspond to *Asoriculus* sp. from Na Burguesa 1–2, with those derived from FL, HL, and TDW clustering around 16–19 g. In *N. ponsi* from the Middle Pliocene site of Pedrera de S’Ònix, mean values rise substantially to c. 25–29 g, representing roughly a 50% increase relative to the Messinian ancestor. Late Pleistocene and Holocene *N. hidalgo* shows the largest body mass, with mean estimates ranging from c. 28–33 g in Cova Estreta to 29–39 g in Cova de Canet and reaching 29–41 g in Cova des Garrover.

Although the overall pattern is one of progressive size increase, some inconsistencies emerge when comparing body mass estimates derived from cranial versus postcranial dimensions and from different anatomical axes (length vs. width). Following the recommendations of Davis (1996) for biometric studies of mammals, we tested for such discrepancies within our dataset. As an exploratory example, in the case of the sample of *N. hidalgo* from the Cova Estreta, significant differences we detected between length and width-based estimates (Mann–Whitney test; $U=30$; $p=0.02$), indicating that anatomical axes can influence the outcome (see Online Resource 3).

Limb morphometrics and locomotor classification

Robusticity and limb proportions

Accompanying the increase in body mass, the long bones of *Nesiotites* become more robust in cross-section relative to their length. Both *N. ponsi* and *N. hidalgo* consistently exhibit high values for the robusticity indices of the humerus and femur (Table 3). The HRI in *Nesiotites* falls around the 70th–90th percentile of the modern-shrew distribution, and the FRI is similarly in the 75th–90th percentile range. By contrast, the ancestral *Asoriculus* displays lower values, with HRI and FRI corresponding to approximately the 50th and 40th percentiles, respectively.

Table 2 Mean body mass estimates (in g) for Mallorcan extinct soricids based on cranial and postcranial predictors. Values are given as mean $\pm$ standard deviation (SD), with 95% confidence intervals derived from the underlying allometric regressions shown in parentheses. Sample size (n) is indicated for each estimate. **Abbreviations:** FL, femur length; FTW, distal femoral transverse width; HL, humerus length; HTW, distal tibial transverse width; TDW, distal tibial transverse width; TL, tibia length; **TRLM1**, lower molar tooth row length. See Moncunill-Solé et al. (2016: fig. 3) for methodological details

Variable	<i>Asoriculus</i> sp. (Na Burguesa 1–2)	<i>Nesiotites ponsi</i> (Pedrera de S'Ònix)	<i>Nesiotites hidalgo</i> (Cova Estreta)	<i>Nesiotites hidalgo</i> (Cova de Canet)	<i>Nesiotites hidalgo</i> (Cova des Garrover)
FL	167.15 ($n=1$)	26.95 $\pm$ 0.71 (25.13–28.77; $n=6$)	34.26 $\pm$ 1.93 (28.12–40.40; $n=4$)	36.39 $\pm$ 1.31 (32.76–40.12; $n=5$)	37.32 $\pm$ 1.97 (32.24–42.40; $n=6$)
FTW	15.74 ($n=1$)	23.13 $\pm$ 0.36 (22.20–24.06; $n=6$)	26.71 $\pm$ 0.75 (23.44–29.97; $n=3$)	30.24 $\pm$ 0.82 (27.97–32.50; $n=5$)	29.10 $\pm$ 0.60 (27.54–30.66; $n=6$)
HL	17.14 ($n=1$)	27.12 $\pm$ 0.67 (25.27–28.97; $n=5$)	30.88 $\pm$ 0.49 (29.60–32.17; $n=6$)	31.63 $\pm$ 0.95 (28.98–34.28; $n=5$)	30.21 $\pm$ 0.613 (28.64–31.79; $n=6$)
HTW	13.24 ($n=1$)	23.53 $\pm$ 0.76 (21.41–25.65; $n=5$)	29.14 $\pm$ 0.58 (27.64–30.64; $n=6$)	29.45 $\pm$ 1.04 (26.56–32.35; $n=5$)	29.32 $\pm$ 1.11 (26.45–32.19; $n=6$)
TDW	19.29 $\pm$ 1.95 (17.33–21.24; $n=2$)	29.99 $\pm$ 1.17 (26.72–33.24; $n=5$)	35.30 ($n=1$)	39.96 $\pm$ 2.19 (34.60–45.31; $n=7$)	42.16 $\pm$ 2.51 (35.19–49.14; $n=5$)
TL	-	24.30 $\pm$ 0.48 (22.22–26.36; $n=3$)	30.39 $\pm$ 0.29 (26.58–34.20; $n=2$)	32.14 $\pm$ 1.97 (26.65–37.63; $n=5$)	31.01 $\pm$ 0.65 (29.18–32.81; $n=5$)
TRLM1	13.93 $\pm$ 0.71 (13.22–14.64; $n=2$)	20.79 $\pm$ 0.72 (17.68–23.90; $n=3$)	30.43 $\pm$ 0.73 (28.57–32.30; $n=6$)	28.07 ($n=1$)	27.88 ($n=1$)
Length (all)	16.92 $\pm$ 0.21 (16.71–17.14; $n=2$)	26.44 $\pm$ 0.49 (25.39–27.49; $n=14$)	31.93 $\pm$ 0.80 (30.16–33.70; $n=12$)	33.39 $\pm$ 0.97 (31.30–35.47; $n=15$)	32.96 $\pm$ 1.08 (30.67–35.24; $n=17$)
Width (all)	16.89 $\pm$ 1.67 (13.24–21.24; $n=4$)	25.40 $\pm$ 0.90 (23.47–27.32; $n=16$)	29.60 $\pm$ 0.99 (27.39–31.80; $n=11$)	34.01 $\pm$ 1.56 (30.71–37.31; $n=17$)	33.02 $\pm$ 1.68 (29.46–36.58; $n=17$)

Table 3 Percentile ranks calculated for 11 postcranial functional indices across a comparative sample of extant and fossil soricine shrews. Mean percentile ranks (MPRs) summarize the relative locomotor adaptation of each taxon on a scale from 0 to 100, with lower values indicating more generalized ambulatory morphologies and higher values reflecting increased specialization towards fossorial or semi-fossorial behaviors. Percentile values are calculated relative to the extant comparative dataset. Abbreviations and formulas for the functional indices are provided in Table 1. Detailed percentile values and extended comparative results are provided in Online Resource 3

Taxon	BI	CI	FRI	FEB	HEB	HRI	IM	OLI	SMI	TRI	MPR
<i>Asoriculus</i> sp. (Na Burguesa 1–2)	48	—	41	31	10	52	—	3	17	—	29.1
<i>Nesiotites ponsi</i> (Pedrera de S'Ònix)	7	48	76	28	24	76	28	3	72	59	40.9
<i>Nesiotites hidalgo</i> (Cova Estreta)	3	52	86	17	38	69	45	3	28	72	39.4
<i>Nesiotites hidalgo</i> (Cova de Canet)	0	52	90	24	41	86	59	3	24	66	37.9
<i>Nesiotites hidalgo</i> (Cova des Garrover)	3	59	76	21	41	86	59	3	24	34	36.4

OLI values are uniformly low in all extinct taxa. Both *Asoriculus* and *Nesiotites* fall near the lower extreme of the extant distribution (approximately the 3rd percentile; see Online Resource 3). BI values are likewise low in *N. hidalgo* (near the minimum of the comparative sample) and in *N. ponsi*. SMI values differ between species, being moderate to high in *N. ponsi* (around the 72nd percentile) and lower in *N. hidalgo* (around the 25th percentile). Hind limb proportion indices, including CI and IM, fall within the low to mid percentiles (generally 40th–60th) for all extinct taxa. Overall, index values for *Nesiotites* fall within the range of variation documented for extant ambulatory shrews.

Discriminant analysis and locomotor mode

The multivariate classification of locomotor modes reinforces the patterns observed in the univariate analyses. Fossil specimens of *Asoriculus* and *Nesiotites* were analyzed

using LDA trained on extant shrews of known ecology (Set A: seven indices; includes *Asoriculus*). In this dataset, LD1 accounted for 77.96% of the among-group variance, LD2 for 16.35%, and LD3 for 5.69%. Cross-validation on extant taxa yielded 83% correct classification, with a single extant specimen misclassified (a fossorial taxon assigned to the ambulatory category; see Online Resource 5).

Group centroids along LD1 separate fossorial taxa (mean centroid = 11.31) from semi-fossorial forms (2.29), whereas ambulatory and semiaquatic taxa cluster at negative values (−1.38 and −1.48, respectively). Along LD2, semiaquatic species show positive centroid (2.33), while ambulatory taxa cluster at negative values (−0.87). Loadings indicate that LD1 is primarily influenced by OLI (−0.72), HEB (−0.63), and SMI (0.57), whereas LD2 is most strongly associated with FEB (0.62), BI (0.58), and FRI (0.54).

All extinct taxa were classified as ambulatory with high posterior probabilities (≈ 1.00). Projected scores place

Asoriculus (−2.35, −1.68), *N. ponsi* (0.52, −1.63), and *N. hidalgo* from Cova Estreta (−1.20, −1.46), Cova de Canet (−1.09, −1.58), and Cova des Garrover (−0.85, −2.15) within the region occupied by extant ambulatory shrews. In LDA plots (Fig. 3), all extinct specimens cluster well within the ambulatory morphospace and are clearly separated from the centroids of semifossorial and semiaquatic taxa.

A complementary summary is provided by the MPR values (see Online Resource 4). *Asoriculus* shows an MPR of approximately 29, *N. ponsi* samples values ranging between c. 30–40. These values fall within the range observed for extant ambulatory shrews and are markedly lower than those characteristic of fossorial or semiaquatic specialists. Across all indices and multivariate analyses, extinct taxa remain within the distribution of extant terrestrial shrews.

Pelvic morphology

Although sexual dimorphism is generally considered negligible in shrews, it can be detected through subtle differences in pelvic morphology (Becker 1955; Clevedon Brown and Twigg 1970; Carraway 2009); a skeletal element that is seldom examined in detail. In soricids, the two halves of the pelvis (ossa coxae) remain unfused at the pubic symphysis throughout life, a condition confirmed in all examined *N. hidalgo* and *N. ponsi* specimens. As in other shrews (e.g., *Sorex*), adult males exhibit a pronounced caudal expansion of the ischium (sometimes referred to as a postatrial or interlocking process), which is absent from females and juvenile individuals of both sexes (Leche 1883; Becker 1955; Dolgov 1961; Carraway 2009). This feature provides reliable

osteological criterion for identifying adult males in *Nesiotites* (Fig. 4).

In addition, a small number of *N. hidalgo* specimens show sacro-pelvic fusion, in which the iliac portion of the pelvis is co-ossified with the sacrum, forming a single skeletal unit (Fig. 5). This condition was previously reported by Pons-Monjo et al. (2010) and is confirmed here as a rare occurrence within the species.

Discussion

Insular body size increase and skeletal robusticity

The evolutionary trajectory of *Nesiotites* exemplifies the island rule tendency for small mammals to become larger in insular environments (Lomolino et al. 2013; van der Geer et al. 2013). Starting from an estimated ~17 g ancestor (*Asoriculus* sp.), the Balearic shrews nearly doubled in mass, reaching ~30–40 g in *N. hidalgo*. This substantial size enlargement occurred in the absence of mammalian predators on Mallorca prior to human arrival (Bover and Alcover 2008) and likely under conditions of reduced interspecific competition, a combination of factors that generally favor “gigantism” in insular small mammals (Lomolino 2005; Lomolino et al. 2013). By growing larger, *Nesiotites* could exploit a broader range of food resources, perhaps preying on larger invertebrates or even small vertebrates (Churchfield 1990) and may have experienced improved fasting endurance in an island setting with fluctuating resource availability (McNab 2010). In addition, increased body

Fig. 3 Scatterplot of the first two axes of the linear discriminant analysis (LD1 and LD2) based on seven locomotor indices. Extant taxa are grouped according to locomotor habit (ambulatory, fossorial, semi-aquatic, and semi-fossorial), as indicated by colors. Circles represent individual extant taxa, and diamonds indicate group centroids calculated from the extant taxa used to train the discriminant model. Ellipses represent 95% confidence intervals around group centroids. Fossil specimens of *Nesiotites* are labeled by locality. Percentages indicate the proportion of variance explained by each discriminant axis

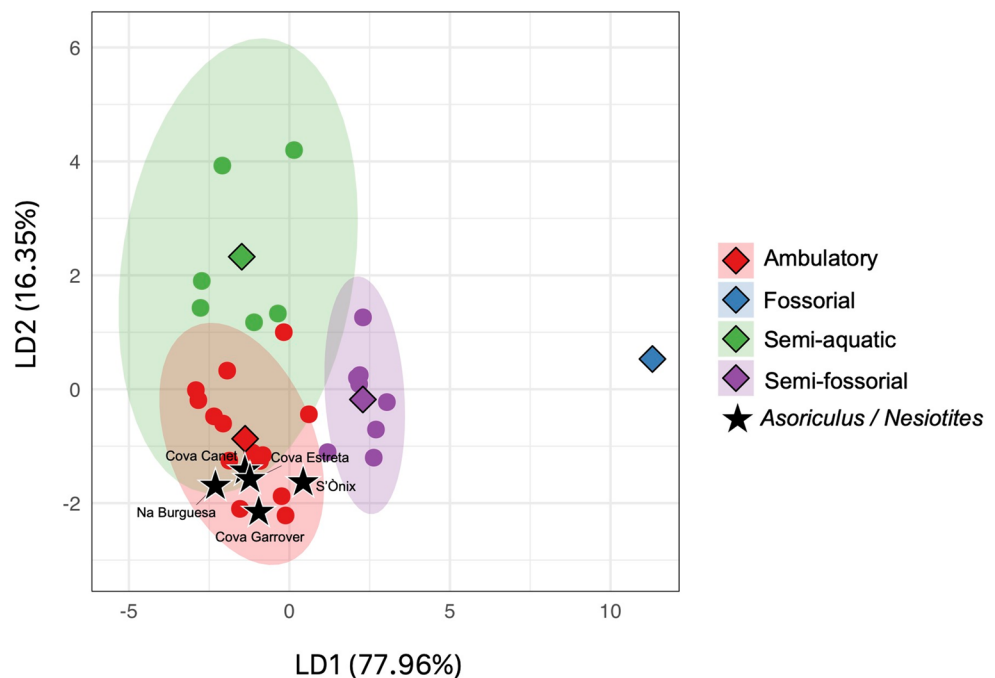


Fig. 4 Left innominates in lateral (left) and medial (right) views. **a.** *Crocidura gueldenstaedtii* (IMEDEA 13458); **b.** *Neomys fodiens* (IMEDEA 95595); **c.** *Sorex coronatus* (IMEDEA 95598); **d.** *Suncus etruscus* (IMEDEA 98337); **e.** *Nesiotites hidalgo* (IMEDEA 64573). Scale bar equals 5 mm

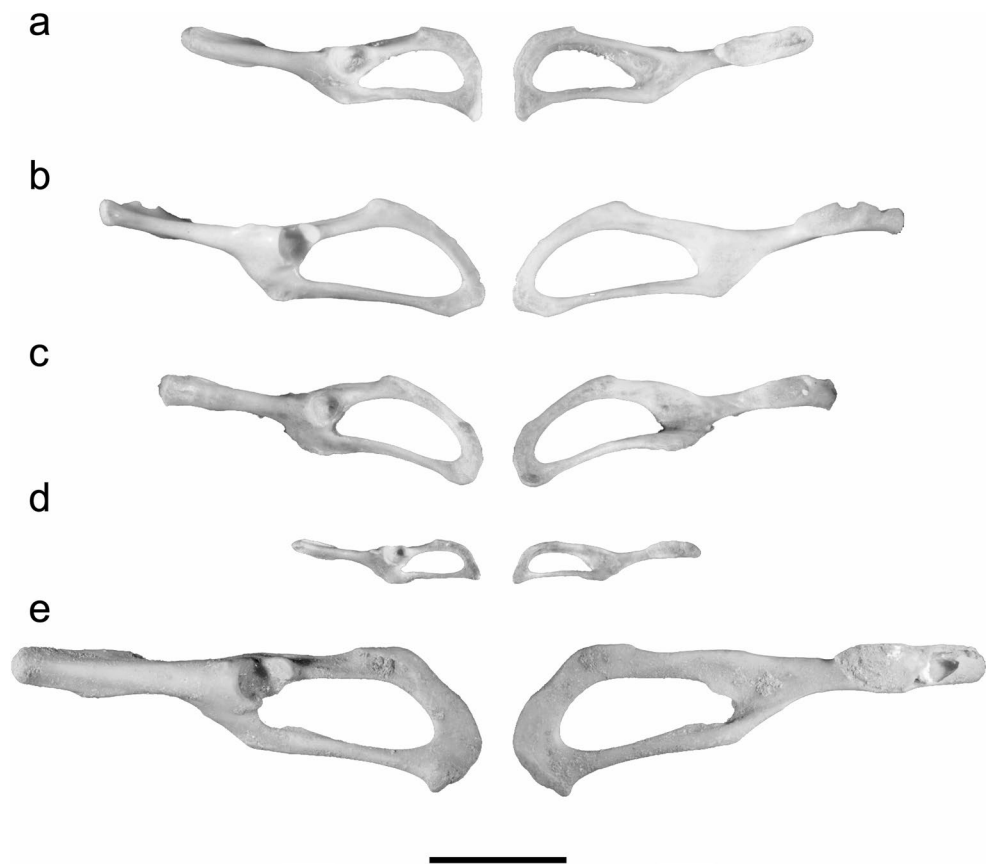


Fig. 5 Fused pelves and sacral vertebrae of *Nesiotites hidalgo*. **a-b** IMEDEA 111575 in ventral (**a**) and lateral (**b**) views; **c-d** IMEDEA 64581 in ventral (**c**) and lateral (**d**) views. Scale bar equals 10 mm



size in mammals is often associated with a shift toward the slow end of the life-history continuum, including extended longevity and reduced turnover rates, a pattern well documented in insular systems (e.g., Köhler and Moyà-Solà 2009; Kuperinen et al. 2023).

This nearly two-fold increase in body mass across the insular lineage is consistent with the general trend toward body size enlargement documented for Mediterranean island shrews (Bover et al. 2010; Moncunill-Solé et al. 2016). Notably, the largest estimates obtained for *N. hidalgo* fall at

the upper extreme of body masses recorded for insular sori-cids, underscoring the pronounced gigantism attained by the Balearic lineage prior to its extinction.

The increase in body size was accompanied by a commensurate strengthening of the postcranial skeleton: limb bones became more robust, presumably to maintain structural integrity and locomotor ability under the higher body mass. The high robusticity indices in *N. ponsi* and *N. hidalgo* indicate a thickening of cortical bone and enlargement of muscle attachment areas, features also observed in

other insular mammals that undergo size increase as a bio-mechanical necessity to support greater weight (Köhler and Moyà-Solà 2004; van der Geer et al. 2013). Unlike some island rodents that evolve low-slung, stocky builds for digging (van der Geer et al. 2013), *Nesiotites* maintained a generally gracile overall form despite its larger size; its limbs, though robust in cross-section, were not shortened or modified in proportions beyond the typical range of mainland shrews (see Online Resource 6). This suggests that selection on Mallorca did not drive *Nesiotites* into a radically new adaptive zone, but rather it remained a scaled-up version of a generalized shrew.

At the same time, our results highlight that body mass estimates in extinct soricids are sensitive to the choice of skeletal element and anatomical axis used for inference. Differences between dental- and postcranial-based estimates, as well as between length- and width-derived values, echo the cautionary observations of Moncunill-Solé et al. (2016) and underscore the need for careful interpretation of absolute mass values. Rather than uncritically pooling estimates derived from disparate measurements, it is more informative to consider the overall trajectory and relative differences through time, which consistently indicate a marked trend toward size increase in the *Asoriculus*–*Nesiotites* lineage.

Crucially, the locomotor apparatus of *Nesiotites* shows no evidence of specialization toward a novel locomotor niche. Although limb bones became more robust as body mass increased, limb proportions remained conservative and within the range of variation documented for extant terrestrial shrews. All morphological indicators point to *N. hidalgo* and its predecessors being predominantly ambulatory, ground-active insectivores. This is perhaps not surprising, given that the vast majority (~77%) of the more than 300 extant shrew species worldwide are classified as terrestrial foragers lacking extreme locomotor specializations (Hutterer 1985; Churchfield 1990).

In particular, the uniformly low olecranon length index values observed in both *Asoriculus* and *Nesiotites* indicate that the relative length of the elbow lever arm remained extremely short throughout the lineage. Such values are characteristic of generalized terrestrial shrews and contrast sharply with the elongated olecranon processes seen in fossorial or semi-fossorial mammals, where increased triceps leverage enhances digging performance (Hopkins and Davis 2009). The persistence of very low OLI values therefore indicates that *Nesiotites* did not evolve forelimb adaptations associated with scratch-digging or other fossorial behaviors.

Similarly, brachial index values in *Nesiotites* are consistently low, reflecting relatively elongated proximal forelimb segments compared to distal segments. While such proportions may approach the cursorial end of the spectrum within

Soricinae, they remain well within the normal range of variation for terrestrial shrews and do not indicate a true specialization for rapid running. Differences in shoulder moment index values between *N. ponsi* and *N. hidalgo* suggest some variability in relative shoulder muscle attachment development through time, but again without exceeding the range observed among extant ambulatory species. Hind limb proportions, as reflected by the crural and intermembral indices, likewise remain within low to intermediate percentiles, further supporting the absence of specialized locomotor modes.

Taken together, these results indicate that the Balearic shrews underwent a marked increase in skeletal robusticity without accompanying changes in limb segment configuration or joint leverage that would signal functional specialization. Rather than exploiting a new adaptive zone, *Nesiotites* appears to have retained the generalized locomotor strategy of its ancestors, effectively becoming a scaled-up version of a mainland shrew. This interpretation is reinforced by the results of the linear discriminant analyses, which consistently classify all extinct populations as ambulatory, placing them firmly within the morphospace of modern ground-dwelling shrews. Together, these multivariate and univariate approaches yield a fully congruent functional signal.

The retention of a generalist locomotor mode despite pronounced changes in body size and bone robusticity likely reflects the ecological context of insular Mallorca, where the absence of strong selective pressures favoring fossorial, arboreal, or aquatic specializations reduced the impetus for locomotor divergence. In this setting, increased body size and skeletal reinforcement appear to have been accommodated primarily through changes in bone thickness rather than through reorganization of limb proportions or locomotor biomechanics.

Life history implications and the island syndrome

One of the most intriguing aspects of the postcranial anatomy of *Nesiotites* is the occasional occurrence of sacro-pelvic fusion in *N. hidalgo*. While Pons-Monjo et al. (2010) suggested a potential parallel with the extreme postcranial modifications of the African hero shrew (*Scutisorex some- reni*), the condition observed in *N. hidalgo* is more parsimoniously interpreted as progressive ankylosis associated with advanced age, rather than as a functional or taxonomically distinctive trait.

The occurrence of such age-related skeletal changes has life-history implications. In living mainland shrews, which follow a “fast” life-history strategy, individuals rarely survive long enough to develop pronounced degenerative fusions. The presence of sacro-pelvic ankylosis in *N. hidalgo* is consistent with the increased longevity relative

to body size, consistent with a shift toward the ‘slow’ end of the slow–fast life-history continuum (Köhler and Moyà-Solà 2009; Köhler 2010; Orlandi-Oliveras et al. 2016; Köhler et al. 2023). This pattern parallels observations in other large insular mammals from the Balearics, such as *Myotragus* (Köhler and Moyà-Solà 2004; Jordana and Köhler 2011; Jordana et al. 2012), *Hypnomys* (Bover et al. 2010), and *Nuralagus* (Quintana et al. 2011), which evolved extended lifespans and delayed somatic development under conditions of reduced predation pressure. Functionally, aside from this rare fusion, the overall pelvic morphology of *Nesiotites* (including acetabular orientation and pelvic canal dimensions) remains within the range of typical terrestrial soricids and shows no evidence of locomotor specialization beyond that expected for an ambulatory ground-dweller.

It is important to note that while we infer increased longevity and a shift toward the ‘slow’ end of the life history continuum, *Nesiotites* was still a small mammal and probably did not attain extreme lifespans beyond a few years. However, even a moderate extension (e.g., living 3–4 years instead of 1–2; see Hutterer 1985; Churchfield 1990) would have significant ecological and evolutionary implications. A longer-lived shrew could reproduce over multiple seasons and might adopt a more energy-conserving lifestyle, consistent with the lower population turnover often observed in island species (McNab 2010). The pelvic fusion finding is a qualitative evidence supporting this, and future analyses of bone histology or incremental growth markers could further test the longevity hypothesis.

In sum, the patterns we document in *Nesiotites* align well with classic island syndrome predictions (Lomolino et al. 2013; van der Geer et al. 2013). The lineage underwent body size enlargement yet remained ecologically and functionally similar to its ancestor (no novel locomotor modes), and it exhibited signs of a shift toward slower life history (extended lifespan and possibly delayed aging). This combination of traits (i.e., gigantism without gross morphological novelty, and enhanced survival) likely reflects an altered predation regime, particularly the absence of mammalian predators, together with a stable but resource-limited insular environment during the Pleistocene–Holocene of Mallorca. Importantly, this does not imply a complete release from predation pressure, as avian predators such as owls were certainly present and likely continued to prey upon small mammals. In this context, increased body size may have functioned not only as a life-history correlate but also as a partial defense against predation, without driving the evolution of new locomotor specializations. While *Nesiotites* grew larger and sturdier, it did not need to out-run or out-dig predators, nor diversify into new niches, which may help explain the retention of an ambulatory locomotor form. Ultimately, the extinction of *N. hidalgo* in the Holocene

was probably driven by external factors with human arrival, including habitat fragmentation and the introduction of new ecological pressures, rather than by any inherent inability to persist within its ecological niche (Bover and Alcover 2008; Bover et al. 2018).

Conclusions

The present morphofunctional analysis of the *Nesiotites* postcranial skeleton offers new insights into its adaptive evolution on Mallorca. By integrating quantitative limb measurements, body mass estimates, and functional indices, we have traced how this insular shrew lineage became larger and more robust yet remained a terrestrial generalist in locomotion. The findings highlight the value of postcranial anatomy in reconstructing the biology of extinct species. *Nesiotites* exemplifies how insular mammals can undergo marked size and life-history shifts while largely retaining ancestral locomotor behaviors. These results contribute new data to the understanding of island evolution in mammals, illustrating that even within a single small lineage, different trait complexes (size, shape, and life history) may evolve along distinct trajectories under insular conditions. Our study underscores the importance of careful functional interpretation of the postcranium for evaluating evolutionary responses to island environments, complementing evidence from craniodental remains and paleoecological context.

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Data availability The datasets generated during and/or analyzed during the current study are included in this published article and its Online Resource files.

Declarations

Competing interests The authors declare no competing interests.

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