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Insights from the skull and postcranial osteometry of the Sardinian pine marten (*Martes martes latinorum*). Does it obey the island rule?

Marco Zedda | ORCID: 0000-0003-2347-9264
Department of Veterinary Medicine, University of Sassari, Italy
Corresponding author: *mzedda@uniss.it*

Ramona Babosová | ORCID: 0000-0002-0951-1902
Department of Zoology and Anthropology, Constantine the Philosopher University, Nitra, Slovak Republic

Massimo Canargiu
Independent researcher in Zoology, Sardinia, Italy

Ľubomír Bútora
Department of Applied Zoology and Wildlife Management, Technical University, Zvolen, Slovak Republic

Maria Rita Palombo | ORCID: 0000-0002-2104-2176
CNR-IGAG, Research Unit Roma 1, 00015 Monterotondo (Rome), Italy

Pierangela Cabras
Istituto Zooprofilattico Sperimentale della Sardegna, Tortolì, Italy

Giovanni Giuseppe Leoni | ORCID: 0000-0002-9726-1463
Department of Biomedical Sciences, University of Sassari, Italy

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Abstract

This study investigates the osteometric differences between the Sardinian pine marten (*Martes martes latinorum*) and its continental counterpart (*Martes martes martes*), focusing on both

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cranial and postcranial skeletal elements. According to the island rule, small mammals on islands tend to increase in size. The Sardinian pine marten exhibits an increase in skull size (+12% in both sexes) compared to European subspecies, while its overall body mass shows a smaller increase (+9%). Analysis of the masticatory apparatus suggests hypertrophy of the temporalis and masseter muscles, reflected in a more robust zygomatic arch and a narrower postorbital constriction (–3.5% in males, –2.9% in females), suggesting a dietary shift toward increased meat consumption. The cranial capacity of Sardinian pine martens (22.85 cm^3 in males, 21.48 cm^3 in females) remains relatively large, possibly due to the cognitive demands associated with predation. Limb bones are longer in Sardinian females (+5.8%) but show negligible difference in males (< 1%) compared to the European subspecies. This study provides the first comprehensive osteological analysis of *M. m. latinorum*, demonstrating that the Sardinian marten population forms a distinct insular cluster, as also confirmed by genetic data. Historical and archeological evidence suggests that the Sardinian pine marten was introduced during the Neolithic (approximately 8,000 years ago). Therefore, the observed skeletal modifications, including the increased size of the skull, occurred in a relatively short evolutionary timescale.

Keywords

skull morphology – island syndrome – insular mammals – biodiversity – size variation

Introduction

The European pine marten (*Martes martes* Linnaeus, 1758) is a small carnivorous mammal that inhabits forests, where it acts as an opportunistic predator, feeding on small mammals, birds, fruits, and insects. Its distribution range extends from Western Europe, including the Mediterranean islands, to Siberia and the Middle East (De Marinis & Masseti, 1995; Herrero et al., 2016). The species has distinctive facial features, including an elongated snout and triangular ears with a yellowish sheen along their edges. Unlike the stone marten (*Martes foina* Erxleben, 1777), it has a dark brown to black nose. The coat color varies seasonally, ranging from bright yellowish-cream in summer to dark brown black in winter (Genovesi & De Marinis, 2003; Monakhov, 2022). A characteristic yellow or slightly orange patch, resembling a bib, is often present on its throat and between the forelimbs. The paws are brown to black and densely furred in winter. The bushy tail, which measures from one-half to two-thirds of the body length, is similar in color to the back and ends in a pointed tip (Monakhov, 2022).

Over time, about ten subspecies of *M. martes* have been proposed, often with conflicting classifications, leading to the widely accepted view that the taxonomy of the European pine marten requires revision. Without delving deeper into this issue, as it is beyond the scope of this study, several subspecies have been described in regions bordering the Mediterranean Basin. These include the continental European subspecies (*M. m.*

martes), which inhabits the Iberian Peninsula and Majorca, the southern Italian and Sicilian subspecies (*M. m. notialis* Cavazza, 1912), the Minorcan subspecies (*M. m. minoricensis* Alcover, Delibes, Gosálbez & Nadal, 1986), and the Sardinian subspecies (*M. m. latinorum* Barret-Hamilton, 1904) (Vecchioni et al., 2022).

Island-dwelling mammals have long attracted the interest of researchers in zoology and evolutionary biology, as they frequently exhibit morphological and morphometric differences from their mainland counterparts. More specifically, the 'island rule', first proposed over 50 years ago (Foster, 1964; van Valen, 1973) and later refined for much larger datasets of mammal species by others (e.g. Lomolino, 2005; Raia & Meiri, 2006; Lomolino et al., 2012, 2013; Palombo, 2018; Benítez-López et al., 2021), predicts that large mammals tend to evolve toward smaller body size (insular dwarfism), while small mammals tend to become larger (insular gigantism). Although insular non-carnivorous mammals follow the island rule with few exceptions, the extent to which insular carnivores conform to it remains a matter of debate. Some researchers consider this rule valid for this group, at least for a number of species or populations (Lomolino, 2005; Lomolino et al., 2012, 2013), while others reject it (Meiri et al., 2005, 2006, 2007; Lokatis & Jeschke, 2018). Describing morphological and behavioral characteristics typical of endemic island mammals has often raised interpretative challenges for their taxonomic classification. In addition to genetic studies aimed at highlighting the relationship with continental forms, which are crucial for understanding the origin of insular populations (Lokatis & Jeschke, 2018; Hunt et al., 2022; Portanier et al., 2023), researchers have particularly focused on possible differences in body size among insular mammals (Mura et al., 2013).

The Sardinian pine marten was first described and confirmed as a subspecies of the European marten in the early twentieth century (Barret-Hamilton, 1904; Cavazza, 1912), based on distinctive morphological characteristics. These include a darker brown coat, an intense yellow gular patch with an orange hue, and a slightly larger body size than that of continental European pine martens (Fig. 1A). Morphometric studies of pine martens have primarily relied on biometric measurements of the entire body (Alcover et al., 1986; Murgia et al., 1995; Barja, 2014; Bartolommei et al., 2014). However, whole-body measurements can sometimes be misleading, leading to erroneous interpretations. Such errors may arise from variations in hair length (especially at the end of the tail) or from differences in the posture in which the animal is positioned during measurement. For instance, the natural curvature of the spinal column may be flattened when the animal is stretched out, altering the total body length by several centimeters. Similarly, the degree of extension at limb joints can introduce further discrepancies. Moreover, many authors fail to account for the age of the individuals, increasing the risk of misclassifying subadults as adults, which can lead to significant measurement inaccuracies. For these reasons, comparative studies based on skeletal osteometry provide a more accurate approach to assessing body size and proportions. Osteometric analyses not only allow for the determination

FIGURE 1 Taxidermy specimen of Sardinian pine marten (A) and areas of Sardinia (B, C) from which the animals studied originated: 1, Monte Linas territory; 2, forests of Sarrabus; 3, territory of Ogliastra; 4, forests of Monte Limbara

of skeletal maturity, confirming whether an individual has reached full adulthood, but also offer a reliable means of sex determination. In cases of uncertainty, the presence of the baculum (*os penis*) serves as definitive proof for identifying male specimens.

There are only a few studies on bone measurements of pine martens, and the published ones focus almost exclusively on the skull (Reig & Ruprecht, 1989; Lòpez-Martin et al., 2006; Monakhov & Monakhova, 2014; Wereszczuk et al., 2023). Among osteometric analyses, craniometry is widely used to determine species affiliation in vertebrates. However, this approach can be particularly challenging in the case of the pine marten (Anderson, 1970; Reig, 1992). To our knowledge, only the study by Baumann and Gornetzki (2017) provides osteometric data on postcranial bones. Their study aimed to distinguish the skeleton of the pine marten (*M. martes*) from that of the beech marten (*M. foina*).

The individuals examined in their research most likely belonged to the continental subspecies and can therefore be classified as the European pine marten (*M. m. martes*), as they originated from several German zoological museums, collections, and university institutes. Hutterer & Geraets (1978) and Murgia et al. (1995) reported some osteometric data on the skull of the Sardinian pine marten (*M. m. latinorum*), whereas no studies have yet examined postcranial bones. Recently, microsatellite variability analyses confirmed the taxonomic status of the subspecies *M. m. latinorum* (Colli et al., 2011).

Our study analyzes the osteometric characteristics of the Sardinian pine marten, focusing on both the skull and, for the first time, the postcranial skeleton. The aim is to determine whether the skeletal dimensions of this insular subspecies support the island rule, according to which small mammal species on islands tend to evolve larger body size compared to their continental ancestors. The exact period of the pine marten's introduction to Sardinia remains unclear and is still a matter of debate, but it is believed that humans introduced the species during prehistoric times (Zeder, 2008). For this reason, the present study is particularly interesting, as it helps to shed light on the timeframe during which morphological changes may have occurred.

Additionally, comparative anatomy and skeletal osteometry are particularly interesting fields of research because they allow archeozoologists and paleontologists to put subfossil and fossil remains into a broader context, helping to uncover the roots of the island's anatomical and

dimensional diversity. Osteometry also enables us to reconstruct body size, allowing us to recognize cases of insular gigantism or dwarfism (Palombo & Zedda, 2016, 2022; Palombo et al., 2024). The study of bone surfaces makes it possible to identify a greater functional involvement of some muscles compared to others, suggesting possible behavioral patterns and types of locomotion (Giua et al., 2014; Zoboli et al., 2018; Zedda et al., 2020; Zedda & Babosova, 2021). Lastly, this contribution provides a collection of skeletal elements that could serve as a valuable resource for future archeological and paleontological comparative research.

Material and methods

A total of 23 Sardinian pine martens (*M. m. latinorum*) were analyzed in this study, comprising 14 males and 9 females, all of which were confirmed as adults. Adulthood was determined based on the fusion of the long bone epiphyses and the complete closure of the nasal suture, which are reliable indicators of sexual maturity and adulthood (Alcover et al., 1986). Sex was identified not only through external physical characteristics but also by the presence of the penile bone (baculum).

The pine martens, which consisted of roadkills, were collected and delivered to the Laboratory of Anatomy of the Department of Veterinary Medicine at the University of Sassari (Italy), where skeleton preparation and measurements were carried out and where the specimens are currently stored. These individuals inhabited wooded areas and Mediterranean scrub clearings in four regions of Sardinia (Fig. 1B, C).

The skeleton of each individual was isolated and cleaned, first by manual tissue removal, followed by maceration in a solution of water and detergents containing proteolytic enzymes with frequent washing, and finally by boiling.

To assess potential craniometric differences between Sardinian and European martens (*M. m. martes*), 36 skulls from forests in Slovakia were examined. The sample consisted of 19 males and 17 females, belonging to the collection of the Department of Applied Zoology and Wildlife Management, Technical University in Zvolen (Slovakia), and were measured at the Department of Zoology and Anthropology, Constantine the Philosopher University in Nitra (Slovakia).

All measurements were taken using a digital sliding caliper with an accuracy of 0.01 mm. For postcranial osteometric comparisons, the following bones were analyzed: atlas, axis, sacrum, scapula, humerus, radius, ulna, pelvis, femur, tibia, and fibula. All measurements were based on those proposed by von den Driesch (1976) for *Canis*, arranged and adapted for pine martens. Two additional species-specific measurements for the axis were included, as proposed by Baumann & Gornetzki (2013). The original numbering and acronyms used by these authors were retained, with explanations provided in Figures 2–5 using lines and arrows. The cranial capacity was measured by quantifying the volume occupied by millet seeds.

For each measurement, the mean value, standard deviation, and variation were calculated, along with percentage differences

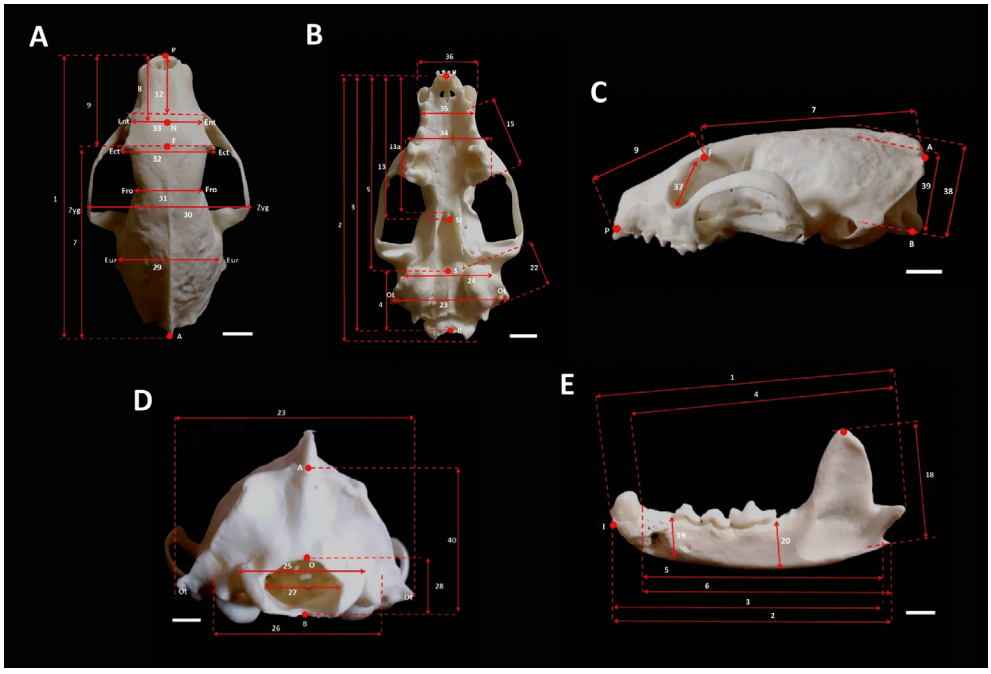

FIGURE 2 Measurements of the cranium (A, B, C and D, in dorsal, ventral, lateral, and aboral view respectively) and mandible (E, in medial view) of Sardinian pine marten (*M. m. latinorum*). For the cranium: 1, total length: *akrokranion* (A) – *prosthion* (P); 2, condylobasal length: line corresponding to the aboral border of the occipital condyles – *prosthion* (P); 3, basal length: *basion* (B) – *prosthion* (P); 4, basicranial axis: *basion* (B) – *synsphenion* (S); 5, basifacial axis: *synsphenion* (S) – *prosthion* (P); 7, upper neurocranium length: *akrokranion* (A) – frontal midpoint (F); 8, upper viscerocranium length: *nasion* (N) – *prosthion* (P); 9, facial length: frontal midpoint (F) – *prosthion* (P); 12, snout length: line corresponding to oral border of the orbits – *prosthion* (P); 13, median palatal length: *staphylion* (St) – *prosthion* (P); 13a, least palatal length: line corresponding to the deepest indentations of the choanae – *prosthion* (P); 15, length of the cheektooth row; 22, greatest diameter of the auditory bulla; 23, greatest mastoid breadth: *otion* (Ot) – *otion* (Ot); 24, breadth of the external auditory meatus; 25, greatest breadth of the occipital condyles; 26, greatest breadth of the bases of the paraoccipital processes; 27, greatest diameter of the foramen magnum; 28, height of the foramen magnum: *basion* (B) – *opisthion* (O); 29, greatest neurocranium breadth: *euryon* (Eur) – *euryon* (Eur); 30, zygomatic breadth: *zygion* (Zyg) – *zygion* (Zyg); 31, least breadth of skull: *frontostenion* (Fro) – *frontostenion* (Fro); 32, frontal breadth: *ectorbitale* (Ect) – *ectorbitale* (Ect); 33, least breadth between the orbits: *entorbitale* (Ent) – *entorbitale* (Ent); 34, greatest palatal breadth; 35, least palatal breadth; 36, length between the lateral border of the canine alveoli; 37, greatest diameter of the orbit; 38, skull height: *basion* (B) – highest elevation of the sagittal crest; 39, skull height without the sagittal crest; 40, height of the occipital triangle: *akrokranion* (A) – *basion* (B). For the mandible: 1, total length: condyle process – *infradentale* (I); 2, length: angular process – *infradentale* (I); 3, length from indentation between the condyle process and the angular process – *infradentale* (I); 4, length between the condyle process and the aboral border of the canine alveolus; 5, length from the indentation between the condylar and angular processes – aboral border of the canine alveolus; 6, length between the angular process and the aboral border of the canine alveolus; 18, height of the vertical ramus: angular process – *coronion* (C); 19, height of the mandible at M1; 20, height of the mandible between P2 and P3. Scale bar = 1 cm

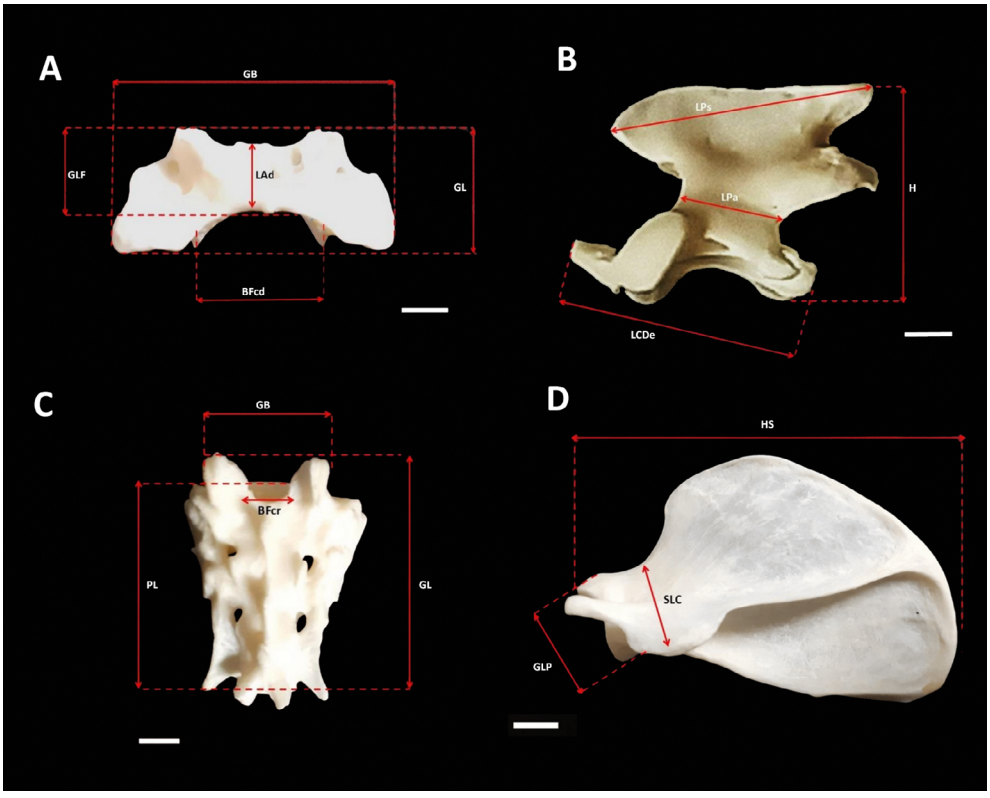

FIGURE 3 Measurements of the atlas (A, dorsal view), axis (B, lateral view), sacrum (C, dorsal view) and the left scapula (D, lateral view) of Sardinian pine marten (*Martes martes latinorum*). For the atlas: GB, greatest breadth; GL, greatest length; GLF, greatest length from the cranial articular surface to the caudal articular surface; BFcd, greatest breadth of the caudal articular surface; LAd, median length of the dorsal arch. In the axis: LCDe, greatest length of the corpus including the dens; H, greatest height; LPa, smallest length of the pediculus vertebralis; LPS, length of the processus spinosus. In the sacrum: GL, greatest length; PL, physiological length (measured between the center of the body of the most cranial and the most caudal vertebra); GB, greatest breadth; BFcr, breadth of the cranial articular surface. For the scapula: HS, height; SLC, smallest length of the neck; GLP, greatest length of the glenoid cavity including borders and processus. Scale bar = 5 mm

in aggregated values by sex between the Sardinian and European pine martens. Additionally, postcranial measurements conducted by Baumann & Gornetzki (2017) on 27 pine martens from German forests were included for comparison, representing the European subspecies (*M. m. martes*) as well. This sample consisted of 19 males and 8 females.

Values were compared between *M. m. latinorum* and *M. m. martes*, separated by sex, using a Kruskal–Wallis test, considering results significant at $P \leq 0.5$. The body mass of *M. m. latinorum* was determined from weight measurements of the studied individuals and from data reported in the literature. This made it possible to calculate the size index (Si), defined as the ratio

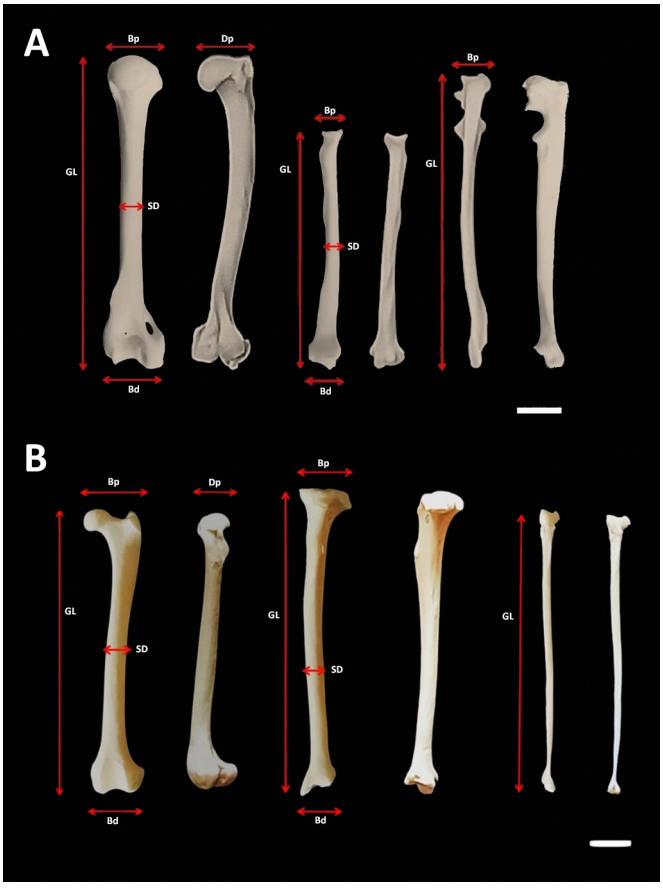

FIGURE 4 Measurements of the main long bones of the thoracic limb (A, from left to right humerus, radius and ulna) and pelvic limb (B, femur, tibia and fibula) of Sardinian pine marten (*M. m. latinorum*). GL, greatest length; Bp, breadth of the proximal epiphysis; Bd, breadth of the distal epiphysis; SD, smallest diameter of the diaphysis; Dp, depth of the proximal epiphysis. Scale bar = 1 cm

of the mean body mass of insular individuals to that of their nearest mainland or ancestral population, based on the data of Lomolino et al. (2012).

Results

Morphological observations of skulls from different views reveal subtle but consistent differences between the Sardinian pine marten (*M. m. latinorum*) and its continental European counterpart (*M. m. martes*). In continental subspecies, the neurocranial vault exhibits an almost hemispherical convexity. Conversely, in the Sardinian subspecies, it more closely resembles a sixth arch, a feature accentuated by a well-developed external sagittal crest (Figs. 2 and 6).

It is noteworthy that the entire surface of the flat bones of the neurocranium

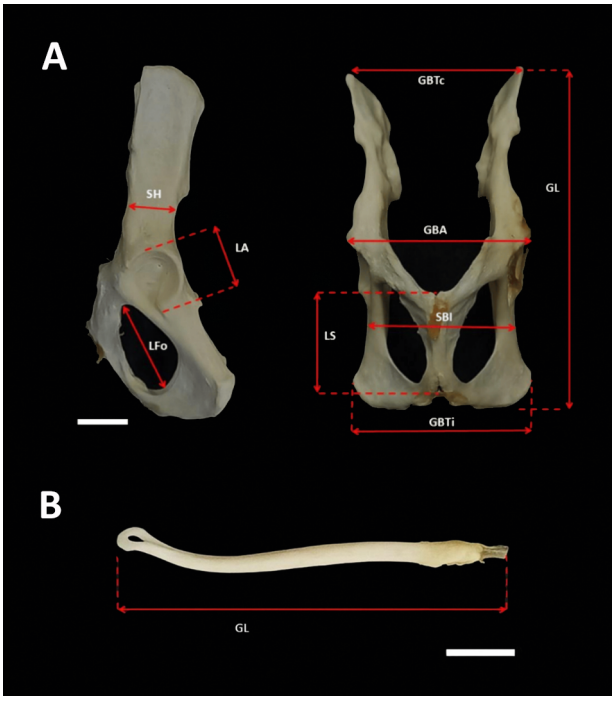

FIGURE 5 Measurements of the pelvis (A, lateral and ventral view) and the baculum (*os penis*) (B) of Sardinian pine marten (*M. m.s latinorum*). GL, greatest length; LA, length of the acetabulum including the lip; LS, length of the symphysis; SH, smallest length of the ilium; LFo, greatest length of the *foramen obturatum*; GBTc, greatest length across the *tubera coxarum*; GBTi, greatest length across the *tubera ischiadica*; GBA, greatest length across the lips of the acetabula; SBI, smallest breadth across the ischia. Scale bar = 1 cm

appears visibly more wrinkled in the Sardinian specimens than in the Slovakian ones, suggesting more extensive and pronounced muscle attachments. Other notable differences concern the robustness of the nuchal crest, the temporal line, the zygomatic process of the frontal bone, and the overall structure of the zygomatic arch. In Sardinian pine martens, the zygomatic arch is more curved, robust, and positioned farther from the lateral skull wall compared to that of their continental relatives. From a morphological point of view, no differences were detected between males and females. It should be noted, however, that differences in the strength of muscle insertions may be partly attributed to age variation among the adult specimens examined, representing a limitation of this study.

Osteometric data from the examined skulls corroborate these morphological observations. Measurements taken from 40 cranial parameters are reported in Tables 1 and 2 (showing data from the dorsal, lateral, ventral, and caudal views

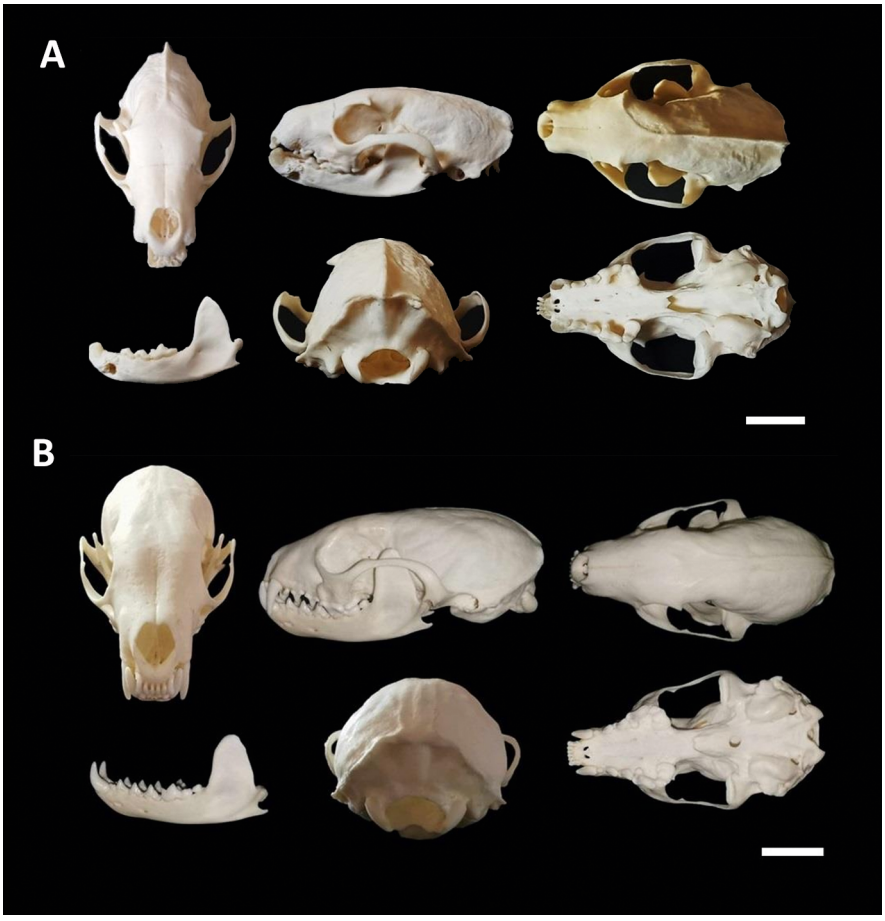

FIGURE 6 Skulls of Sardinian pine marten (*M. m. latinorum*, A) and continental European pine marten (*M. m. martes*, B) by different views. Scale bar = 2 cm

for the cranium and for the mandible, respectively). Data concerning the axial postcranial skeleton and limb bones are presented in Table 3. In these tables, two columns indicate the percentage differences between the two subspecies, separated by sex.

Transverse skull measurements are also larger in the Sardinian subspecies, including those related to the neurocranium (measurements 23, 24 and 29; Table 1) and the splanchnocranium (measurements 32, 33, 34 and 35; Table 1). Overall, the Sardinian pine marten is slightly larger than the European pine marten. This size increase is observed throughout the skeleton but is particularly pronounced in certain cranial measurements. For example, the total skull length of the Sardinian pine marten, measured from the most caudal point of the skull (*akrokranion*) to the most cranial (*prosthion*), is approximately +12.0% longer in both females and males than in the European subspecies (P = 0.24). The mandible follows the same trend, showing an average size increase of approximately

TABLE 1 Skull measurements of pine martens in dorsal, lateral, ventral and caudal views. For measurement numbers, see Fig. 2. Values are in mm. Asterisks indicate no significance ($P > 0.5$)

	Sardinian pine marten (*Martes martes latinorum*)						European pine marten (*Martes martes martes*)						Differences in % between *M. m. latinorum* and *M. m. martes*	
	Males (# 14)			Females (# 9)			Males (# 19)			Females (# 17)				
	Mean value	SD	Var	Mean value	SD	Var	Mean value	SD	Var	Mean value	SD	Var	Males	Females
1	94.03	4.02	9.86	90.85	3.44	9.61	83.78	3.11	9.67	81.22	3.16	10.02	+12.2	+11.9
2	88.60	3.44	9.17	85.55	3.47	10.71	81.93	3.20	10.24	79.24	3.22	10.34	+8.1	+7.9
3	84.51	2.76	8.34	82.32	3.25	11.34	72.41	2.86	8.18	70.39	3.50	12.22	+16.7	+16.9
4	19.26	1.98	2.23	18.03	1.12	1.56	17.51	1.48	2.19	16.38	1.03	1.06	+9.9	+10.0
5	65.25	3.34	9.40	64.28	4.26	8.48	54.90	3.19	10.17	54.00	3.28	10.73	+18.8	+19.1
7	57.34	2.86	7.13	55.28	2.17	6.99	52.66	2.56	6.57	50.81	1.99	3.97	+8.8	+8.8
8	22.92	1.93	2.89	22.48	1.84	2.86	21.72	1.64	2.70	21.19	1.65	2.74	+5.5	+6.1
9	36.69	2.44	4.64	35.47	2.28	4.61	31.13	2.07	4.30	30.41	2.22	4.92	+17.8	+16.6
12	22.81	2.13	3.51	20.96	1.81	3.57	20.65	1.79	3.19	19.87	1.44	2.07	+10.5	+5.5
13	49.96	2.72	3.79	48.52	2.74	4.90	39.57	2.01	4.03	37.99	2.05	4.21	+26.2	+27.7
13a	47.67	1.85	3.08	47.07	2.36	4.73	36.75	1.72	2.97	35.67	2.14	4.58	+29.7	+31.9
15	26.84	1.21	1.24	25.31	1.43	1.13	25.17	1.04	1.09	24.73	0.90	0.80	+6.6	+2.3*
22	18.03	1.28	1.35	17.99	1.28	1.82	18.01	1.17	1.36	17.95	1.11	1.23	+0.1*	+0.1*
23	41.29	5.46	16.73	40.61	2.06	3.64	38.78	5.04	25.09	36.56	1.61	2.58	+6.5	+11.7
24	36.39	2.04	3.76	35.00	1.95	2.78	27.66	1.78	3.16	27.27	1.14	1.29	+31.5	+28.3
25	18.71	2.11	1.34	18.08	0.84	2.61	18.13	0.87	0.75	18.01	0.77	0.59	+3.2*	+0.4*
26	26.63	3.47	4.12	25.47	1.23	1.23	26.16	1.74	3.04	24.83	1.49	2.21	+1.8*	+2.6*
27	11.40	2.48	1.95	10.96	2.37	3.59	11.36	0.60	0.36	10.82	0.54	0.29	+0.4*	+1.3*
28	10.84	1.29	0.94	10.10	1.48	2.07	10.33	0.76	0.58	10.02	0.56	0.38	+4.9	+0.8*
29	39.87	1.89	3.12	38.43	1.77	2.82	36.61	1.64	2.70	36.34	1.66	2.76	+8.09	+5.8
30	53.51	3.37	5.47	52.04	1.93	1.44	46.79	2.26	5.09	45.06	1.72	2.95	+14.4	+15.5
31	19.06	1.65	1.82	19.12	2.20	2.17	19.68	1.28	1.64	19.70	1.20	1.44	−3.5*	−2.9*
32	28.42	1.73	1.59	28.51	1.38	1.15	24.01	1.21	1.46	22.69	1.15	1.32	+18.3	+25.6
33	22.88	0.94	0.70	20.85	1.66	1.43	21.30	0.78	0.61	20.24	1.24	1.53	+7.4	+3.1*
34	20.47	1.12	0.82	20.14	1.17	1.08	19.53	0.88	0.78	19.32	0.85	0.73	+4.9	+4.3*
35	16.00	0.91	0.89	15.43	0.92	0.65	13.85	0.82	0.67	13.67	0.60	0.37	+15.52	+12.9
36	19.62	0.67	0.44	18.54	0.64	0.91	15.89	0.59	0.35	15.44	0.74	0.55	+23.5	+20.0
37	15.51	1.12	1.24	14.86	1.17	2.38	13.70	0.82	0.68	13.71	1.03	1.05	+13.2	+8.6*
38	33.42	1.55	2.13	32.46	1.64	2.76	33.37	1.41	1.99	32.40	1.42	2.01	+0.2*	+0.2*
39	29.12	1.73	2.44	28.45	1.87	3.16	29.04	1.54	2.38	28.29	1.72	2.95	+0.3*	+0.3*
40	23.95	1.83	1.54	21.87	2.15	2.65	19.84	1.01	1.01	19.43	1.32	1.74	+20.7	+12.6

15%, and these measurements show significant differences ($P < 0.3$).

The only cranial measurement in which the Sardinian pine marten is smaller than the European subspecies is the least breadth of the skull, which corresponds to the distance between the two *frontostenion* points (measure 31 in Fig. 1 and Table 1). This measurement is –3.5% in males and –2.9% in females, with no

TABLE 2 Mandible measurements of pine martens. For measurement numbers, see Fig. 2. Values are in mm. All the values of two last columns in the right show significance ($P \leq 0.5$)

	Sardinian pine marten (*Martes martes latinorum*)						European pine marten (*Martes martes martes*)						Differences in % between *M. m. latinorum* and *M. m. martes*	
	Males (# 14)			Females (# 9)			Males (# 19)			Females (# 17)				
	Mean value	SD	Var	Mean value	SD	Var	Mean value	SD	Var	Mean value	SD	Var	Males	Females
1	61.81	3.47	4.11	58.45	3.15	2.75	52.94	2.33	5.44	50,77	2,92	8,53	+16.75	+15.1
2	60.32	2.40	2.56	57.94	2.48	3.60	52.02	2.36	5.56	49,71	2,68	7,17	+15.9	+16.6
3	58.78	2.84	3.12	56.38	2.63	4.22	50.43	2.19	4.78	48,49	2,51	6,30	+16.5	+16.2
4	53.91	2.51	3.24	52.55	2.74	3.81	46.87	1.91	3.63	45,58	2,41	5,82	+15.0	+15.3
5	51.30	2.65	2.75	50.19	2.45	3.98	45.11	1.99	3.97	44,11	2,55	6,49	+13.7	+13.8
6	52.86	4.78	3.17	50.96	5.77	6.04	44.17	2.00	3.99	42.84	2.31	5.33	+19.6	+18.9
18	26.35	2.93	4.72	25.27	4.32	3.75	23.98	1.12	1.26	23,10	1,33	1.77	+9.9	+9.4
19	9.05	3.10	3.68	8.74	2.41	2.86	8.10	0.50	0.25	7,53	0,62	0.38	+11.7	+16.0
20	11.23	1.23	2.67	9.04	2.09	2.68	9.23	0.56	0.31	8,96	0,48	0.23	+21.6	+5.1

significant difference ($P = 0.73$ and $P = 0.58$, respectively).

Regarding sexual dimorphism, osteometric data from the skulls show an average difference of approximately 7.8% across all measurements, indicating that males are larger than females. The mean cranial capacity of Sardinian pine martens is 22.85 cm^3 in males and 21.48 cm^3 in females, whereas in European pine martens from Slovakia it is 21.18 cm^3 in males and 20.35 cm^3 in females. This represents a sex-related difference of +6.37% in Sardinian pine martens and +3.41% in the European ones. The difference between the two subspecies is +7.88% in males and +5.56% in females.

Measurements of the postcranial axial skeleton of Sardinian pine martens show a moderate increase in the length and breadth of the atlas and axis compared to European pine martens. This difference is slightly more evident in females (mean value of the three compared measurements: +2.4%) than in males (+1.1%).

It is noteworthy that there are no significant differences in limb bones between Sardinian and European males (the mean percentage difference is less than 1%). However, the long bones of Sardinian females are, on average, 5.8% longer than those of European ones. Overall, the differences between the two subspecies are not significant ($P > 0.5$), except for the greatest length of the radius, ulna, femur, and tibia in females ($P < 0.3$).

The greatest length of the baculum (*os penis*) also deserves attention. It has a mean value of 48.4 mm in Sardinian males, representing an increase of about +19% compared to European males ($P = 0.13$). This bone, which provides structural

TABLE 3 Postcranial axial skeleton measurements of pine martens. For measurement numbers and acronyms, see Figs. 3–5. Data for continental European pine martens are from Baumann & Gornetzki (2017). Values are in mm. Asterisks indicate no significance ($P > 0.5$)

		Sardinian pine marten (*Martes martes latinorum*)						European pine marten (*Martes martes martes*)		Differences in % between *M. m. latinorum* and *M. m. martes*	
		Males (# 14)			Females (# 9)			Males (# 15)	Females (# 8)		
		Mean value	SD	Var	Mean value	SD	Var	Mean value	Mean value	Males	Females
Atlas	GL	16.24	1.13	2.20	14.75	1.34	2.56	16.17	14.69	−0.19*	+0.41*
	GLF	12.98	1.24	2.64	11.32	1.08	2.41				
	Lad	6.53	0.47	1.35	5.84	0.67	1.58				
	GB	32.69	2.86	5.13	29.66	2.61	5.03	31.79	28.51	+2.83*	+4.03*
	BFcd	15.05	1.40	2.97	14.02	1.27	2.89				
Axis	LCDe	17.46	1.31	2.73	15.87	1.03	2.99				
	H	17.99	2.07	4.94	16.20	1.48	3.47				
	1	11.26	0.74	1.83	9.92	1.07	2.34				
	2	21.03	1.41	2.07	19.36	1.63	2.21	20.91	18.81	+0.57*	+2.92*
	4	5.97	0.37	1.11	4.83	0.51	1.04				
Sacrum	GL	25.02	1.27	2.75	23.89	2.41	4.12				
	PL	24.10	1.86	3.96	22.72	2.86	5.37				
	GB	20.07	1.47	3.81	17.87	2.19	4.28				
	BFcr	9.72	1.03	2.44	9.94	1.34	3.52				
Scapula	HS	48.52	3.12	6.84	46.23	3.90	8.43				
	GLP	12.37	1.35	2.75	11.84	1.64	3.45				
	SLC	10.41	1.63	4.12	10.36	1.85	3.58				
Humerus	GL	73.07	2.94	3.72	68.41	3.17	7.14	73.59	66.26	−0.77*	+3.32*
	Bp	12.83	0.78	2.18	10.96	0.85	1.44				
	Dp	14.27	0.91	2.13	13.03	0.74	2.01				
	SD	5.25	0.37	1.07	5.00	0.36	1.23				
	Bd	14.95	0.89	24	13.16	0.92	2.27				
Radius	GL	58.08	3.65	4.18	55.68	4.08	8.93	58.12	52.64	−0.07*	+5.77
	Bp	7.01	0.37	1.26	6.28	1.10	2.80				
	SD	3.52	0.18	2.75	3.32	0.19	0.85				
	Bd	9.08	0.67	1.84	8.61	0.74	2.04				
Ulna	GL	69.38	2.86	5.81	67.55	3.25	7.99	69.82	63.56	−0.64*	+6.27
	Bp	0.93	0.06	0.38	0.85	0.17	0.58				
Pelvis	GL	60.21	3.24	6.44	57.52	3.88	8.22				
	LA	12.74	0.82	1.95	11.48	1.12	3.07				
	LS	20.3	1.17	2.78	18.47	1.63	4.21				
	LFo	17.24	1.04	3.06	15.89	1.48	3.87				
	GBtc	31.63	1.89	4.27	28.63	2.77	5.73				
	GBA	28.10	2.01	4.11	26.40	2.84	6.09				
	GBti	30.73	2.18	3.79	27.36	2.56	6.41				
	SH	8.56	0.70	1.56	7.24	1.18	3.18				
	SBI	25.64	1.13	3.42	23.71	3.81	7.58				
Femur	GL	81.88	3.77	6.83	78.93	6.49	11.73	81.81	74.82	+0.09*	+5.49
	Bp	16.14	0.95	2.15	15.08	1.28	3.85				
	Dp	7.79	0.48	1.24	6.11	0.76	2.24				
	SD	5.76	0.36	1.05	4.92	0.94	2.74				
	Bd	15.15	1.14	2.86	14.27	1.76	2.69				
Tibia	GL	89.50	3.89	7.85	86.47	4.35	8.55	89.51	80.03	−0.02*	+8.05
	Bp	15.93	0.82	2.27	15.08	1.62	4.10				
	SD	5.12	0.45	1.94	4.37	1.16	3.81				
	Bd	10.58	0.71	2.47	9.65	1.84	4.26				
Fibula	GL	83.81	3.72	6.88	79.07	4.11	9.17				
Baculum	Gl	48.41	0.71	1.68	Absent			40.63	Absent	+19.15	

support and stability during mating, has a distinctive shape typical of the species. It exhibits a sinusoidal curvature and ends with a rounded ring-shaped appendage (Fig. 5).

In summary, Sardinian pine martens are generally larger than European ones. This size difference is most pronounced in the skulls of both sexes, while it is barely detectable in the postcranial axial skeleton and absent in the limb bones of males. Conversely, it is significant in the radius (P = 0.36), ulna (P = 0.40), femur (P = 0.27) and tibia (P = 0.33) of females.

Discussion

Our results show that the Sardinian pine marten (*M. m. latinorum*) exhibits notable osteomorphometric differences compared to continental European pine martens, including a greater development of the masticatory apparatus and a slight overall increase in size. The skeletal parts showing the largest dimensions relative to the continental pine martens are the skull (+12% in both sexes) and the long bones of the limbs in females (+5.8%). The increase in skull proportions is mainly caused by the increase in the size and strength of the zygomatic arch, which serves as an anchor for the masseter muscle. Together with the temporalis muscle, this is the most powerful component of the masticatory system in carnivores. The hypertrophy of this muscle is probably best explained as an adaptation of the Sardinian pine marten to a diet differing from that of the other European subspecies.

A recent study analyzing 158 pine martens collected over the past century from various Polish regions, showed how some osteological features, such as the condylobasal and palatal length and postorbital constriction, are strongly correlated with climate change and shifts in feeding habits (Wereszczuk et al., 2021, 2023). These authors draw attention to the connection between the rise in temperature during the last 60 years and the corresponding increase in pine marten size. A similar study conducted on 434 American pine martens from Alaska reported an increase in body size associated with global warming over the last 50 years, which led to greater food availability (Yom-Tov et al., 2008). These findings suggest that the pine marten may be among the species that contradict Bergmann's rule (Reig, 1992; Riemer et al., 2018; Monakhov & Hamilton, 2020), which predicts that small-bodied animals tend to increase in size in colder climates and decrease in warmer ones (Bergmann, 1847). However, explaining the size increase observed in the Sardinian pine marten remains challenging, as it likely results from the synergistic effects of biotic and abiotic selective pressures. These include the geographic, climatic, and ecological characteristics of the islands, levels of productivity, remoteness and duration of isolation, the structure of insular communities, species interaction, ecological displacement, relaxed predation, interspecific competition, and biological traits of the species, such as the ancestral body size of the endemic form. The resulting balance may shift in response to new selective pressures characteristic of island environments (Millien, 2006; Lomolino et al., 2012, 2013).

Some authors have questioned the applicability of the island rule to certain

mammalian groups, particularly carnivores (e.g. Lokatis & Jeschke, 2018). Among insular carnivores, significant size changes compared to mainland ancestors are mostly observed in extinct species. For example, different degrees of size reduction have been documented in two fossil canid species, the Sardinian dog (*Cynotherium sardous*) (Lyras et al., 2010) and the Trinil (Java) smaller form (*Xenocyon trinilensis*) (van der Geer et al., 2018a), as well as in the Sardinian hunting hyena (*Chasmaporthetes melei*). In contrast, the Javanese canid *Xenocyon merriami* appears to have been larger than its continental ancestor, *Xenocyon lycaonoides* (van der Geer et al., 2018a). Significant or moderate size increases have also been observed in some extinct otters (Lyras et al., 2010), such as the Sardinian *Megalenhydris barbaricina* and *Algarolutra majori*, the Corsican *Cyrnolutra castiglionis*, and the endemic Sicilian species ascribed by some to the genus *Lutra* (Willemsen, 2006) and by others to *Lutraeximia* (Cherin et al., 2016; Lyras et al., 2021; Marciszal & Bower, 2025). The only mustelid known to have increased in size is the Sardinian galictine *Enhydrictis* sp. (Lyras et al., 2010; van der Geer et al., 2018). Furthermore, Theodorou et al. (2007) reported that the Cypriot viverrid *Genetta plesictoides* showed a moderate size increase compared to the extant *Genetta genetta*. In extant mammals, body size change is less frequent and more variable among carnivores than in most other mammals, due to the influence of factors such as the number and nature of competitors and prey availability. A few extant species have undergone extreme size reduction, more than 60% (e.g. the gray fox *Urocyon cinereoargenteus* from the Californian Channel Islands, the white-nosed coati (*Nasua narica*) from Cozumel Island, Mexico, and the wolf (*Canis lupus*) from Baffin Island, Mexico). Others, conversely, have increased in size, such as the American mink (*Mustela vison*) from Vancouver Island (Canada) and the Admiralty Islands (introduced; Papua New Guinea) (Lomolino et al., 2012). In their comprehensive study of 376 extant insular mammal species, these authors calculated the size index (Si), which corresponds to the ratio of the mean body mass of insular individuals to that of their nearest mainland or ancestral population. According to their results (Lomolino et al., 2012; van der Geer et al., 2018b), several insular species of the genus *Martes* experienced only a slight decrease in body mass, such as *M. americana* from Guilford (Si = 0.96), Mitkof Island (Si = 0.68), and Revillagigedo Island (Si = 0.89), *M. flavigula* from Borneo (Si = 0.80) and Taiwan (Si = 0.82), *M. foina* from Crete (Si = 0.82) and Zealand (Si = 0.95) (both introduced), *M. martes* from Majorca (Si = 0.94) and Zealand (Si = 0.99) (both introduced), and *M. melampus* from Kyushu (Si = 0.88). A few species showed negligible increases in body mass compared to their continental ancestors (Si > 1), such as *M. americana* from Chichagof Island (Si = 1.07), Graham Island (Si = 1.02), and Prince of Wales Island (Si = 1.07), *M. foina* from Fyn (Si = 1.01), Ibiza (Si = 1.02; introduced) and Lolland (Si = 1.02), and *M. martes* from Minorca (Si = 1.05; introduced), while others evolved a more substantial increase in body mass, such as *M. americana* from Admiralty Island (Si = 1.27) Moresby Island (Si = 1.22), and Vancouver (Si = 1.14). The value for *M. m. latinorum* from Sardinia

(Si = 1.09, introduced) agrees with those pine martes from the former group of islands, albeit at the upper range.

Although changes in body size are among the best-known adaptations to insular conditions, they are not the most typical phenomenon. Endemic insular mammals often exhibit morphofunctional modifications, particularly in their craniodental anatomy, in response to shifts in diet.

One of the most interesting findings of our study is the remarkable robustness of the masticatory apparatus in the Sardinian pine marten, both in terms of size and muscle attachment areas. The strength of the zygomatic arch, which serves as the attachment site for the masseter muscle, the roughness of the bony surface of the temporal fossa, where the temporalis muscle inserts, and the overall sturdiness of the mandible all indicate that this animal is a highly efficient chewer. Another interesting parameter is the postorbital constriction, which corresponds to the narrowest part of the skull and is measured as the distance between the two *frontostenion* points (measurement 31 in Fig. 2 and Table 1). In contrast to the majority of other skull dimensions that show an increase in size, this measurement is reduced compared to that of the European pine marten (–3.5% in males and –2.9% in females). This parameter is particularly useful for inferring dietary adaptations over the course of a species' evolutionary history. A narrowed postorbital constriction (accompanied by a widening of the zygomatic arch) creates additional space for the temporalis and masseter muscles, the two most powerful masticatory muscles in carnivores. This morphology suggests an adaptation toward hypercarnivory (Wiig, 1982, 1986; Van Valkenburgh, 1999; Loy et al., 2004), whereas an expanded postorbital constriction is associated with feeding on insects and fruits (Haba et al., 2008). Based on these observations, the Sardinian pine marten appears to be specialized for stronger chewing. The fact that Sardinia has a low diversity of mammalian carnivores ecologically supports this interpretation. Besides the pine marten, the only other native carnivorous species on the island are the red fox (*Vulpes vulpes ichnusae*), the wildcat (*Felis silvestris lybica*), and the weasel (*Mustela nivalis boccamela*), all endemic subspecies of Sardinia. Notably, the beech marten (*Martes foina*), an ecologically similar species to the pine marten, is absent from Sardinia. On islands, changes in prey availability and reduced competition from larger predators can lead to shifts in diet and feeding adaptations. For example, the extinct Sardinian canid *Cynotherium sardous* reduced its masticatory strength and adapted to feed on small prey, mainly the endemic ochotonid *Prolagus sardus* (Zedda et al., 2022). In contrast, some small carnivores, such as the Cypriot *G. plesictoides*, had a more carnivorous diet compared to extant genets (Theodorou et al., 2007).

Compared to continental habitats such as Slovakia, Sardinia harbors a markedly lower diversity of small mammals, a typical feature of insular ecosystems (Barreto et al., 2021). This limited species pool, shaped by island size and isolation, reduces the availability of mammalian prey and increases the reliance of the pine marten on alternative resources such as birds, reptiles, or insects (Masseti, 2019). These groups also display a distinct and partly

TABLE 4 Comparison of the condylobasal length of pine martens from insular and continental regions. Values are in mm. The numbers in brackets indicate the number of measured individuals

Subspecies	Geographic area	Males	Females	Source
European pine marten (*M. m. martes*)	Spain (Cantabrian and Pyrenean mountains)	85.9 (N = 67)	78.9 (N = 27)	Lòpez-Martin et al., 2006
	Spain (Pyrenean mountains)	86.6 (N = 9)		Reig, 1992
	Spain (Cantabrian mountains)	86.5 (N = 113)		Reig, 1992
	Spain (Cantabrian mountains)	85.8 (N = 20)		Alcover et al., 1986
	Majorca	83.1 (N = 16)		Alcover et al., 1986
	Poland	85.6 (N = 57)	78.8 (N = 25)	Reig, 1992
		77.12 (N = 158)		Wereszczuk et al., 2022
	Slovakia	81.93 (N = 19)	79.24 (N = 17)	This study
Minorcan pine marten (*M. m. minoricensis*)	Minorca	87.8 (N = 21)	79.9 (N = 17)	Lòpez-Martin et al., 2006
		88.3 (N = 12)		Alcover et al., 1986
Sardinian pine marten (*M. m. latinorum*)	Sardinia	83.15 (N = 2)	77.4 (N = 2)	Hutterer & Geraets, 1978
		84.72 (N = 7)	77.92 (N = 2)	Murgia et al., 1995
		88.60 (N = 14)	85.55 (N = 9)	This study

endemic composition on Sardinia (Corti et al., 2022). Moreover, the scarcity of large predators allows medium-sized carnivores such as *M. martes* to exploit more specialized trophic niches (Barreto et al., 2021; Ferri et al., 2023). In contrast, the richer and more diverse Slovak fauna provides predators with greater dietary flexibility and reduces the need for specialization (Obuch, 1995). Altogether, these ecological differences are consistent with the cranial adaptations observed in Sardinian martens, supporting the hypothesis of a dietary shift toward hypercarnivory. Indeed, insular isolation and reduced competition are known to promote trophic specialization.

We selected the skull condylobasal length as a representative parameter for

detecting the osteometric differences between the skull dimensions of insular and continental populations (measurement 2 in Table 1 and Fig. 2; data synthesis in Table 4). Our results show considerable variation among different geographical regions, and even within the same region, discrepancies emerge depending on data sources. Our measurements differ slightly from previously published values. However, it is important to note that earlier studies were based on small, age-unknown samples without distinguishing between sexes (Alcover, 1986), which may have introduced sampling bias. The Sardinian pine marten appears to be slightly larger, and its skeletal dimensions closely resemble those of the insular subspecies from Minorca (*M. m. minoricensis*), known from subfossil remains. Interestingly, martens and foxes are no longer present on Minorca today. Unfortunately, craniometric data from other Mediterranean island martens and additional continental regions are lacking, limiting the potential for broader comparisons at this time.

Regarding cranial capacity, our results for the Sardinian pine marten show a mean value of 22.85 cm^3 in males and 21.48 cm^3 in females, consistent with the findings of Deiana et al. (1998), who reported 23.8 cm^3 in males and 19.7 cm^3 in females for this subspecies. These data fall within the species' known range of variability across various populations, which ranges from 22.6 to 26.0 cm^3 in males and from 18.4 to 23.0 cm^3 in females (Reig, 1992; Murgia et al., 1995). Only a few studies have been published on brain size in insular mammals, and their results are often contradictory. For instance, a reduction in brain size has been documented in the Balearic small bovid *Myotragus*, which lived in a predator-free environment and likely experienced decreased exposure to external neuronal stimuli (Köhler & Moyà-Solà, 2004; Palombo et al., 2008). Similar reductions have been reported for *Hippopotamus lemerlei* and *H. madagascariensis* (Weston & Lister, 2009; Lyras, 2019). By contrast, the brain of the Sicilian dwarf elephant *Palaeoloxodon falconeri* showed a relative increase in size (Palombo & Giovinazzo, 2005; Lyras, 2019). Among insular otters, Willemsen (1980) described modification in brain morphology in *Lutrogale cretensis*.

Except for insular dwarf elephants, whose brains remained relatively large (Larramendi & Palombo, 2015), the reduction in brain size is commonly observed in insular herbivores but not in carnivores (Lyras, 2009, 2019; Castiglione et al., 2021; Köhler et al., 2023). The brain of the Sardinian pine marten does not appear to have undergone any significant reduction in size. This fact may be due to the species' hypercarnivorous diet, which likely demanded sustained cognitive engagement for prey acquisition, as well as to the relatively short evolutionary time since its introduction.

Indeed, no Pleistocene remains of fossil martens have been found in Sardinia, suggesting that the species was introduced by humans in prehistoric times, probably during the Neolithic period (7th–6th millennium BC) (Zeder, 2008). Since then, considering that pine martens reach sexual maturity at approximately 24 months of age (Jonkel & Weckwerth, 1963), Sardinian pine martens have evolved in isolation under ecological conditions distinct

from those of the mainland, leading over roughly 8,000 years (about 4,000 generations) to the emergence of the subspecies *M. m. latinorum*. The evolutionary changes reported here are less pronounced than those documented over comparable evolutionary timescales in non-carnivorous mammals, such as the Pleistocene Jersey red deer (Lister, 1989, 1995) or the introduced feral cattle of Amsterdam Island (Rozzi & Lomolino, 2017).

Conclusion

This study presents the first comprehensive osteological analysis of the Sardinian pine marten, offering an evolutionary perspective on its morphological adaptations. The most evident non-uniform osteometric size increase was observed in the skull of both sexes and in the limb bones of females, amplifying sexual dimorphism compared to the continental pine marten.

The observed enlargement moderately supports the island rule, according to which small mammals tend to increase in size in insular environments. Overall, the Sardinian pine marten represents an interesting example of an introduced island species that has undergone modest but clear morphofunctional adaptations. These changes are less pronounced than those documented over comparable evolutionary timescales in non-carnivorous mammals, such as the Pleistocene Jersey red deer or the introduced feral cattle of Amsterdam Island. Our findings demonstrate that osteological and osteometric analyzes are effective tools for detecting and quantifying morphological change in extant insular species.

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