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Morphology and paleoecology of the Late Pleistocene extinct dung beetle *Onthophagus pilauco* (Coleoptera, Scarabaeidae, Onthophagini)

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MORPHOLOGY AND PALEOECOLOGY OF THE LATE PLEISTOCENE EXTINCT DUNG BEETLE *ONTHOPHAGUS PILAUCO* (COLEOPTERA, SCARABAEIDAE, ONTHOPHAGINI)

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Abstract. The extinct dung beetle *Onthophagus pilauco* Tello, Verdú, Rossini & Zunino represents the southernmost paleorecord of the onthophagine dung beetle fauna in the New World. Here, we report new fore-, mid-, and posterior leg fossil remains of this extinct beetle and present a morphological comparison of the leg phenotypes observed in the fossil record. Moreover, we illustrate and describe the fossil legs and provide paleoecological inferences based on morphological analysis. We hypothesized that the differences in size and morphology of the remains are related to sexual dimorphism. To test this hypothesis, we applied parametric and non-parametric statistical approaches to the measurement of leg traits. Based on the leg traits identified in *O. pilauco*, we also discuss the phylogenetic affinities with modern species. Significant differences in foretibial morphology (*i.e.*, length, width, tooth shape, curvedness) support the sexual dimorphism hypothesis. We found that *O. pilauco*'s forelegs shared a lack of secondary denticles with the *O. hippopotamus* species complex, although our diagnostic suggests that this trait evolved independently in these species groups. Finally, we discuss the paleoecology of the species based on the morphology of males and females and propose that this extinct species had paracoprid and hypophagic nesting behavior.

Key words. Fossil records. Morphology. Extinct species. Quaternary. Insects. Dung beetles.

Resumen. MORFOLOGÍA Y PALEOECOLOGÍA DEL ESCARABAJO ESTERCOLERO *ONTHOPHAGUS PILAUCO* (COLEOPTERA, SCARABAEIDAE, ONTHOPHAGINI) EXTINTO DEL PLEISTOCENO SUPERIOR. El escarabajo estercolero extinto *Onthophagus pilauco* Tello, Verdú, Rossini & Zunino, representa el registro fósil más austral de la fauna de escarabajos del género *Onthophagus* en el Nuevo Mundo. En este trabajo, reportamos nuevos restos fósiles de patas anteriores, medias y posteriores de esta especie. Además, comparamos morfológicamente las diferencias entre los fenotipos de patas observados en los registros fósiles. Así, este estudio pretende ilustrar y describir estos restos fósiles y proporcionar inferencias paleoecológicas basadas en el análisis morfológico. Nuestra hipótesis es que las diferencias en el tamaño y la morfología de los restos fósiles estudiados están relacionadas con el dimorfismo sexual de la especie. Para poner a prueba esta hipótesis, aplicamos enfoques estadísticos paramétricos y no paramétricos sobre la medición de los rasgos de las patas. Basándonos en los rasgos encontrados en las patas de *O. pilauco*, discutimos las afinidades filogenéticas con especies modernas. Se observaron diferencias significativas en la morfología de la tibia anterior (*i.e.*, longitud, anchura, forma de los dientes, así como en su curvatura) entre los morfotipos evaluados, lo que apoya la hipótesis del dimorfismo sexual. Encontramos que las patas delanteras de *O. pilauco* comparten la falta de dentículos secundarios con el complejo de especies modernas, *O. hippopotamus*. Nuestro diagnóstico sugiere que este rasgo evolucionó de forma independiente en ambas especies. Por último, discutimos la paleoecología de la especie basándonos en la morfología de machos y hembras. Por lo tanto, proponemos que esta especie extinta tenía comportamiento de nidificación de los tipos paracóprido e hipofágico.

Palabras clave. Registros fósiles. Morfología. Especies extintas. Cuaternario. Insectos. Escarabajo estercolero.

RECENT taxonomical and biogeographical approaches have increased our knowledge about the onthophagine dung beetle fauna of the New World (Coleoptera, Scarabaeidae, Onthophagini, *Onthophagus* Latreille, 1802) (Rossini *et al.*, 2018; Halffter *et al.*, 2019; Moctezuma, 2021; Moctezuma *et al.*, 2021). However, the fossil record of *Onthophagus* has remained largely unexplored and poorly known, resulting in a lack of information about its evolutionary history (Tarasov *et al.*, 2016). The recently discovered extinct species *Onthophagus pilauco* Tello *et al.*, 2021 from the

Chilean Pleistocene–Holocene boundary (*ca.* 16.5 to 12.7 kyr BP) provides the first evidence of the presence of this genus in southern South America (Tello *et al.*, 2021a). Thus, the discovery of this species undoubtedly demonstrates that *Onthophagus* was present at more southern latitudes (43°S, 71°W) than its current distribution and that it inhabited the southern temperate *Nothofagus* forests and Patagonian environments.

The previous morphological analysis of the head of *O. pilauco* provided information on the affinities of this extinct species with modern taxa, showing similarities with Asian and American *Onthophagus* (Tello *et al.*, 2021b). In addition, the previous authors observed that female-type specimens lack a clypeal carina, which is a trait commonly used to distinguish sexes within extant American *Onthophagus*. Thus, three fossil morphotypes were related to the extinct dung beetle *O. pilauco*: a female form with two small and conical horns in frons, lacking clypeal and frontal carina; a male minor form, with two flattened and slender horns forming a V-shaped structure in the frons, with a reduced horn situated in the center of the clypeal disc; and a male major form, distinguishable from the minor form by its strongly developed clypeal horn (Tello *et al.*, 2021b).

Based on this evidence (*i.e.*, the lack of clypeal and frontal carina in the three forms and polymorphism in males), the identity of the female form remained unclear (as females of the majority of extant *Onthophagus* species from the New World have a distinct clypeal carina), and the affinities with other modern species still needed to be evaluated.

Here, we report new fossil remains of the fore-, mid-, and posterior legs of *O. pilauco* recorded from a Late Pleistocene sequence of the Pilauco site in southern Chile. We compared the morphology of the leg phenotypes observed in the fossil records, with the goal of illustrating and describing the remains and providing a paleoecological inference based on the morphological analysis. We hypothesized that the differences in the size and morphology of the remains are due to the differences between males and females of this species, *i.e.*, sexual dimorphism. This hypothesis is based on the extant ecology and traits of the American *Onthophagus*, which presents a clear sexual dimorphism. In addition, we used this morphological information to infer aspects of the paleoecology of *O. pilauco*, *e.g.*, nesting behavior.

MATERIAL AND METHODS

We studied material from the Pilauco paleo-archeological site of Chile. This site contains a Late Pleistocene–Holocene layer dated between 14,300 ± 40 to 3,944 ± 30 ^{14}C yrs BP, equivalent to 17,340 and 4,340 yrs BP, respectively. The chronostratigraphic and paleo-archeological context of the site has been extensively treated in several studies due to its faunistic/floristic and early human occupation importance (see Labarca *et al.*, 2014; Moreno *et al.*, 2019; Pino *et al.*, 2019; Abarzúa *et al.*, 2020; Tello *et al.*, 2021a, 2023; Pérez-Balarezo *et al.*, 2024). Additionally, the insect excavation process and the methodology applied for the storage of insect fossil materials were described in detail by Tello *et al.* (2021a, 2023).

Images of the specimens' legs were obtained using scanning electron microscopy (SEM-EVO with variable pressure), while the remaining captures were obtained using a Leica FLEXACAM C1 camera attached to a Leica S6D stereomicroscope. All figures were edited with Photoshop CC 2024 software.

Morphological measurements

To compare the morphological traits, we measured the maximum width (hereinafter referred to as width) and maximum length (hereinafter referred to as length) of each piece. In the case of fore tibia, we used the measurement of tooth length, which is a vector extending from the base of the tibiae to the beginning of the first teeth. This trait was previously used by Nervo *et al.* (2022) and proved useful for differentiating polymorphism in the fore tibia of *O. verticicornis* (Laicharting, 1781) (A. Roggero, pers. comm.). All measurements were performed using a Leica S6D stereomicroscope with LAS X software v 5.1.0.

Data analysis

To test for differences in the observed phenotypes of the fossil legs (morphological hypothesis), we performed both parametric and non-parametric analyses. First, to evaluate the differences between male and female sizes of the measured traits, we conducted a t-test ($\alpha = 0.05$) using the “t.test” function of the “stats” R package. The normality of data was previously checked by the Shapiro–Wilk test, using the “shapiro.test” function in the “stats” R package. Secondly, to supplement the univariate analysis, we performed a permutational multivariate analysis of variance (PERMANOVA; Anderson, 2017) to determine the differences between male and female size and morphology. Comparisons were carried out using the “adonis2” function in the “vegan” R package, based on Bray–Curtis dissimilarity matrices and 999 random permutations. To visualize these differences, we conducted a redundancy analysis (RDA) through the “rda” function in the “vegan” R package, which summarizes linear relationships between components of response variables (Legendre & Legendre, 2012). To avoid the inclusion of missing values in the PERMANOVA and RDA analyses (originating from broken pieces of some fossils), we replaced the missing data with the mean of the true values in each measured trait. All analyses and graphs were made in R software v4.0.1 using the RStudio interface (R Core Team, 2024).

RESULTS

Sexual dimorphism in *O. pilauco*

We recorded seven male and 13 female fore tibia, three middle femora, one fore femur, three hind femora, and one hind femur (Tab. 1). Based on morphological comparisons, we found two highly distinguishable foretibial morphotypes. The Shapiro–Wilk tests showed that our analyzed variables were not significantly different from the Gaussian distribution (length: W = 0.960, $p = 0.606$; tooth length: W = 0.930, $p = 0.195$; width: W = 0.923, $p = 0.149$); therefore, we assumed normality in the data. The t-test results showed that the length (df = 12.7, $t = -2.916$, $p < 0.012$), tooth length (df = 12.0, $t = -6.969$, $p < 0.001$), and width (df = 15.5, $t = 3.398$, $p = 0.003$) were statistically different when comparing both phenotypes (*i.e.*, male and female phenotypes; Figs. 1.1 to 1.3). Additionally, the PERMANOVA result (df = 19, pseudo-$R^2 = 0.333$, $p = 0.002$) also supported this assumption. Moreover, the RDA ordination showed a clear differentiation between male and female phenotypes (Fig. 1.4).

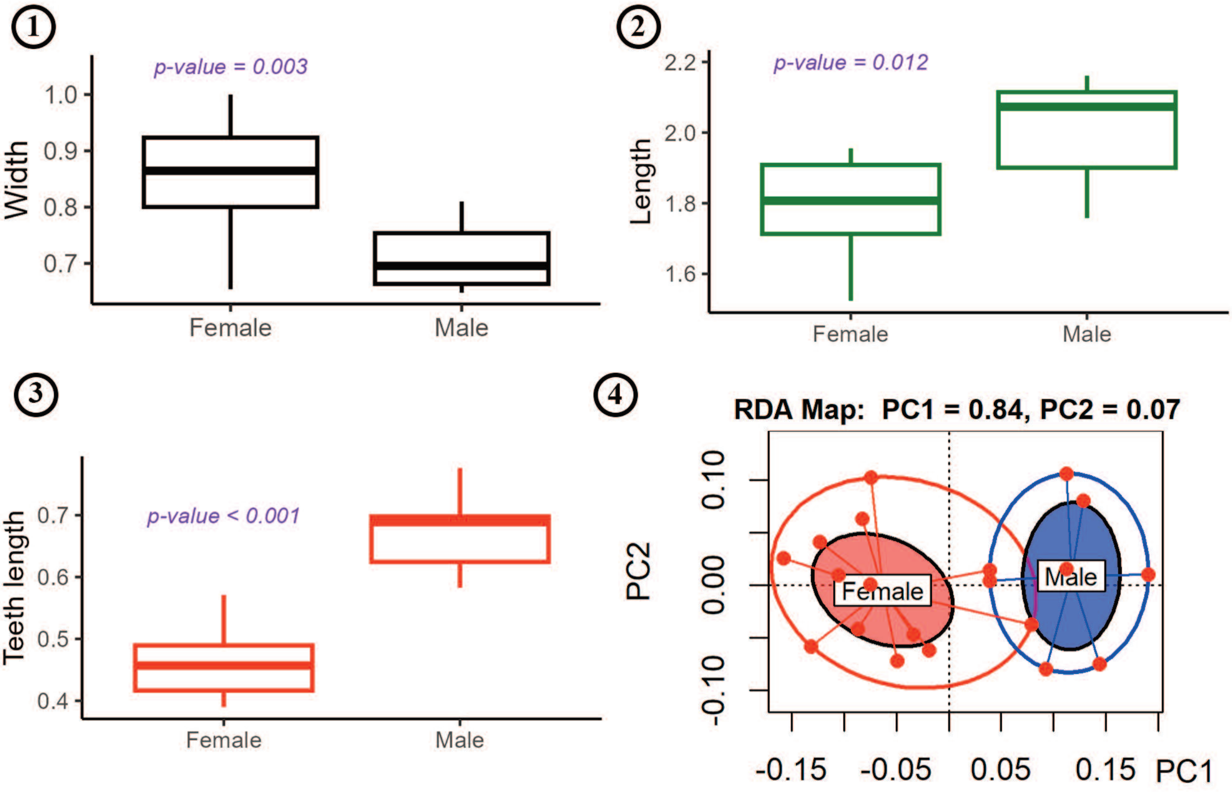

Figure 1. Results of t-test and RDA analysis. **1,** Comparisons between male and female maximum width of fore tibia; **2,** comparisons between male and female maximum length of fore tibia; **3,** comparisons between male and female distance of the base of the fore tibia to the beginning of the last secondary denticle; **4,** redundancy analysis (**RDA**) ordination plot illustrating male and female sexual clustering. Each point represents a fossil.

TABLE 1 – List of the trait measurements in each fossil.

Fossil code	Sex	l_max	w_max	t_L	t_I	t_II	t_III	t_IV	Piece
ZLMYZO	Female	1.561	0.705	0.398	0.458	0.570	0.686	0.604	Foretibia
Q0JSSO	Female	1.761	0.898	0.446	0.524	0.702	0.898	0.847	Foretibia
J3CSFI	Female	1.955	1.000	0.502	0.660	0.894	1.044	0.924	Foretibia
YQGNTC	Female	+	1.000	+	+	0.757	1.029	+	Foretibia
ZGGJFZ	Female	1.921	0.891	0.458	0.552	0.757	0.891	0.858	Foretibia
5KJJNG	Female	1.931	0.814	0.477	0.507	0.684	0.814	0.791	Foretibia
FVY9RO	Female	1.882	1.000	0.391	0.572	0.746	1.000	0.976	Foretibia
P5T4XA	Female	1.896	0.883	0.457	0.503	0.720	0.883	0.838	Foretibia
94YESS3	Female	1.524	0.820	0.390	0.449	0.638	0.820	0.762	Foretibia
HWFXBP	Female	1.665	0.846	0.435	0.441	0.630	0.846	+	Foretibia
FADA95	Female	+	+	+	0.524	0.710	+	+	Foretibia
GF223J	Female	1.789	0.654	0.537	0.409	0.529	0.654	0.658	Foretibia
66235N	Female	1.807	0.759	0.571	0.427	0.598	0.759	0.694	Foretibia
WVKUPX	Male	2.161	0.810	0.776	0.419	0.584	0.810	0.888	Foretibia
FSEDPV	Male	1.895	0.702	0.632	0.381	0.570	0.700	0.654	Foretibia
GE4EZL	Male	1.758	0.648	0.617	+	0.529	0.648	0.706	Foretibia
NNN7Q2	Male	2.078	+	0.689	0.387	0.545	+	0.771	Foretibia
FFVLND	Male	2.151	0.655	0.696	0.354	0.545	0.668	0.681	Foretibia
JBWVEY	Male	1.906	0.771	0.583	0.449	0.617	0.771	0.785	Foretibia
FA247V	Male	2.073	0.689	0.700	0.454	0.601	0.689	0.671	Foretibia
VQAE4F	Unknown	2.254	0.909	-	-	-	-	-	Middle femur
YL5L65	Unknown	2.161	0.819	-	-	-	-	-	Forefemur
XRKRYB	Unknown	2.147	0.850	-	-	-	-	-	Middle femur
JWHKU8	Unknown	2.175	0.834	-	-	-	-	-	Middle femur
5L86YX	Unknown	2.043	0.939	0.408	0.241	0.397	0.493	0.866	Hind tibia
SDZSSW	Unknown	2.682	0.871	-	-	-	-	-	Hind femur
KFK83K	Unknown	2.007	0.640	-	-	-	-	-	Hind femur
U5MXWM	Unknown	1.837	0.749	-	-	-	-	-	Hind femur

Abbreviations: l_max and **w_max** are the measurements of the maximum length and width of each fossil. **t_L** are the measurements of distance at the base of foretibia to the beginning of the last secondary denticle. **t_I**, **t_II**, **t_III**, and **t_IV** are the measurement of each major denticle, respectively. The symbol + refers the missing or broken section of the fossil pieces, while the - symbol refers to the traits absent in the fossil piece.

SYSTEMATIC PALEONTOLOGY

Order COLEOPTERA Linnaeus, 1758
Suborder POLYPHAGA Emery, 1886
Family SCARABAEIDAE Latreille, 1802

Genus ***Onthophagus*** Latreille, 1802

Type species. *Scarabaeus taurus* Schreber, 1759. Holocene; North America, Europe, and Australia.

Onthophagus pilauco Tello *et al.*, 2021
Figures 2.1–2.6, 3

Referred material. The final repository of the examined material is the Museo Pleistocénico de Osorno, Osorno, Chile. Details of the examined materials are accessible in the Supplementary Online Information (SOI1).

Geographical occurrence. Osorno, Región de Los Lagos, Chile.

Stratigraphic occurrence. PB-7 and PB-8 layers in the Pilauco site, dated between 14,300 ± 40 to 3,944 ± 30 ^{14}C yrs BP, equivalent to 17,340 and 4,340 yrs BP, respectively

Description of male fore tibia. Elongated, slightly curved at the apex. Maximum length mean: 2.00 mm; maximum width mean: 0.712 mm. Green metallic sheen, dorsal surface smooth. Four blunt teeth in the external margin, the base of the fore tibia lacking the secondary denticles. Ventral carina extended longitudinally from the apical margin to the base. A ventral row of setal insertions is situated parallel to the carina in the internal margin. Two setal insertion rows dorsally, both extended from the apex to the base, following the shape of the teeth. Spur and tarsal insertions ventrally visible, without obvious modifications (Fig. 2.1).

Description of female fore tibia. Wider *tibiae*. Maximum length mean: 1.79 mm; maximum width mean: 1.00 mm. Teeth notably curved ventrally. Dark green metallic sheen, no obvious microsculpture, smooth. A ventral carina extends longitudinally from the base and decreases at the apex to the margin of the tarsal insertion. Spur and tarsal insertions ventrally visible, without obvious modifications (Figs. 2.2–2.3).

Description of the unsexed fore femora. Maximum length mean: 2.161 mm; maximum width mean: 0.819 mm. Usually recorded in fossil deposits as connected to a piece of the trochanter. Dark green sheen, no obvious microsculpture. Insertion of *setae* in a semi-circular shape close to the base of the femur, visible ventrally; if there is preservation of the *setae* (SSI), they are light brown (Fig. 2.4).

Description of unsexed hind tibiae. Maximum length: 2.04 mm; maximum width: 0.94 mm. Dark green sheen, no obvious microsculpture. Transversal carina ventrally visible. Tarsal and spur insertions are visible from the anterior face (Fig. 2.5).

Description of unsexed hind femora. Maximum length mean: 2.17 mm; maximum width mean: 0.819 mm. General shape oblong. Dark green sheen, no obvious microsculpture. Dorsally flat (Fig. 2.6).

Description of fore tibia variation. Fore tibiae are wider in female than male specimens. The female teeth are notably curved ventrally and the distance between teeth is greater in males than females. The internal margin curve is more pronounced in males than in females. Some females have a narrower base (Fig. 2.3).

Remarks. Based on these new findings, three fossil morphotypes are related to the extinct dung beetle *O. pilauco*: a female form with two small and conical horns in frons, lacking clypeal and frontal carina, with forelegs without secondary denticles; a male minor form, with two flattened and slender horns forming a V-shaped structure in the frons, with a reduced horn situated in the center of the clypeal disc, with forelegs lacking the secondary denticles; and a male major form, distinguishable from the minor form by its strongly developed clypeal and frons horns (Tello *et al.*, 2021a, 2021b). This species can be clearly distinguished from other South American groups by the lack of a clypeal carina in females.

DISCUSSION

Morphological traits and intra-species variation of *O. pilauco*'s legs

The genus *Onthophagus* is currently one of the most speciose genera of beetles in the world, comprising more than 2,200 species (Howden & Cartwright, 1963; Breeschoten *et al.*, 2016; Schoolmeesters, 2023). Therefore, it is reasonable to postulate that the morphological differences observed in the Pilauco fossil records can be attributed to more than one

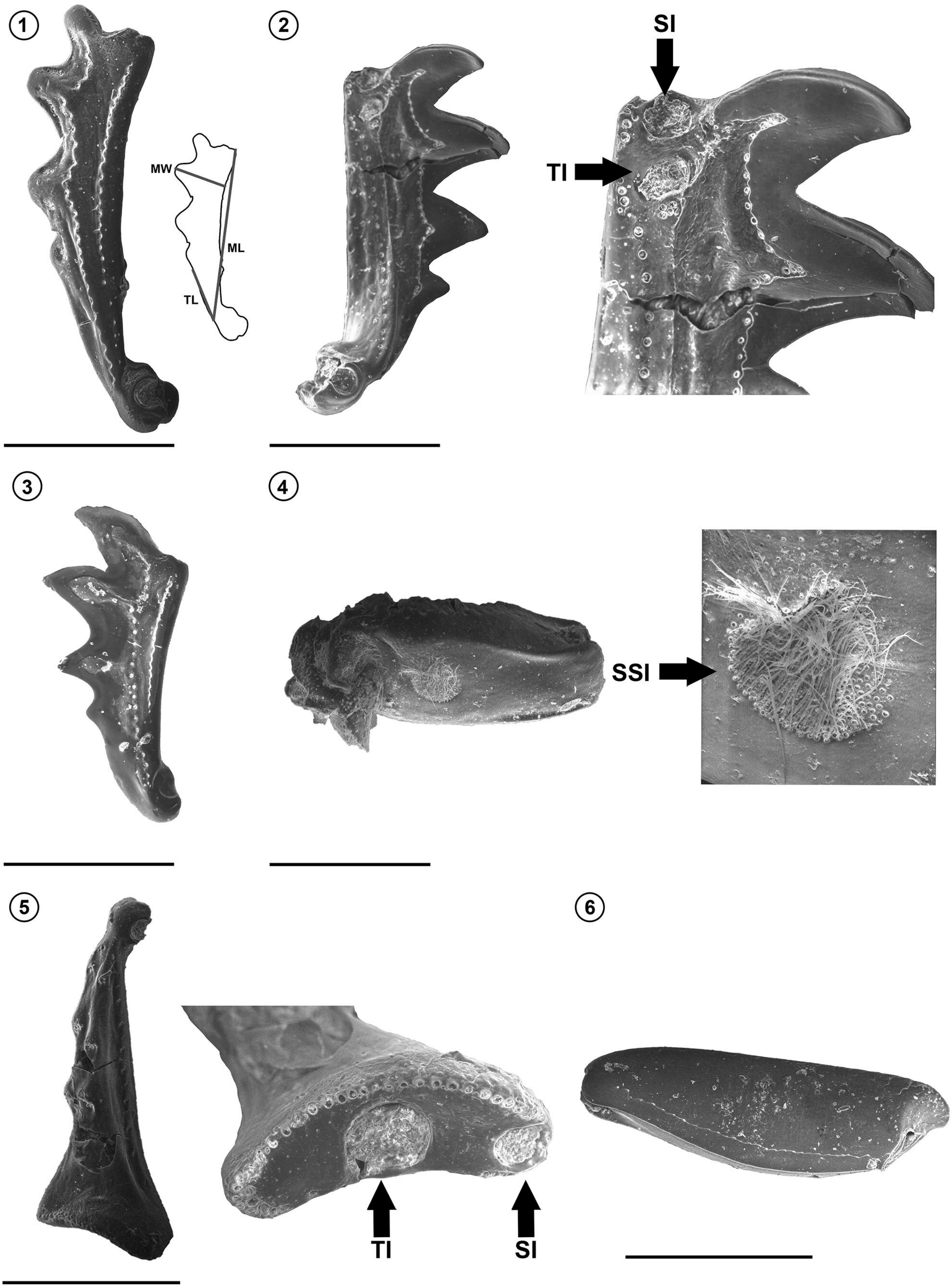

Figure 2. SEM images of ***Onthophagus pilauco*** legs. **1,** Male fore tibia in dorsal view, showing a scheme of the traits measured; **2,** female fore tibia in ventral view showing the tarsal and spur insertions (**TI** and **SI**, respectively); **3,** female fore tibia in dorsal view; **4,** unsexed fore femur in dorsal view showing the semi-circular setal insertion (**SSI**); **5,** unsexed hind tibia showing the tarsal and spur insertions (**TI** and **SI**, respectively); **6,** unsexed mid-, hind-, or fore femora in ventral view. Scale bars= 1 mm.

species, rather than to different morphotypes of a single taxon. However, we assume that our findings represent a single taxon, based on the following criteria: (1) the allometric ratio between the head and forelegs is remarkably symmetric (Tello *et al.*, 2021b); (2) the colors of the tegument are consistently observed in all remains, including the colors observed in the fossil heads—indeed, most of the literature on Quaternary beetles shows that the color and integument sculpture of their fossils remains stable in deposits (*e.g.*, Hoganson & Ashworth, 1992; Kuzmina *et al.*, 2023); (3) no evidence of distinctive traits was detected in any forelegs here studied, including different numbers of minor denticles or notable differences in the shape of setal, tarsal, and spur insertions (see Tab. 1); (4) the taphonomic process in the Pilauco deposit was described as slow and occurring *in situ* (Pino *et al.*, 2017), which would have maintained the stability of the chitin of the beetles (Tello *et al.*, 2023). Therefore, we assume that the coloration, integument sculptures, and the shape of body parts correspond to the original traits of the beetle, with the exception of the disarticulated and broken pieces; (5) finally, the assemblage composition of this deposit is stable in the layers, where no significant differences in species composition have been identified thus far within the age range under consideration (Tello *et al.*, 2017).

Thus, we found significant morphological differences in the shape and size of the legs in the extinct dung beetle *O. pilauco*. We consider these differences to be sexual dimorphism, such as those observed in several extant *Onthophagus* species (*e.g.*, *O. taurus* Schreber, 1759; *O. istmenus* Moctezuma *et al.*, 2020). Thus, these results are supported by the previous work that showed a polymorphic condition of the heads in this fossil species (Tello *et al.*, 2021b).

The first morphotype, assigned to a female form, is characterized by ventrally curved and serrated teeth, which are smaller in size (length) than the male morphotypes. The second morphotype, assigned to the male form, is characterized by: straight teeth; the internal margin being moderately curved in dorsal view; the tibiae being straight in lateral view, not curved as in females; and a larger size than the female morphotype. In males, we suggest that the dimorphism observed could be related to inter and/or intraspecific competition, efficiency in the use of resources, and sex-based roles in nest construction and defense, such as in extant species (Emlen & Philips, 2006; Simmons & Ridsdill-Smith, 2011).

Additionally, we noted that the distance between the base of the fore tibia and the basal margin of the last teeth (teeth_L) is useful for differentiating these two morphotypes. Namely, a shorter distance between these traits suggests a female form, while a larger distance suggests a male form. Therefore, this trait could be useful for recognizing polymorphism or polyphenism, including in other extant Onthophagini species.

Our analysis did not detect the male polyphenism—*i.e.*, major and minor forms' leg differences—that has been described based on the head of this species. We suggest two hypotheses for this result: (1) both leg morphotypes here detected correspond to minor and major male forms, respectively, and a third morphotype (female) has not yet been recovered in the fossil record; therefore, the female form remains unknown; or (2) these differences are due to sexual differentiation and the forelegs of both the major and minor males are indistinguishable. Based on the comparisons with modern species, we consider the second hypothesis more plausible.

Phylogenetic affinities based on leg morphology traits

A particularly interesting trait that *O. pilauco* shows is the lack of secondary denticles in the external margin of its forelegs. This character is shared with the *O. hippopotamus* species group, which is a taxonomic grouping of extant North American dung beetles (Zunino & Halffter, 1988; Halffter *et al.*, 2019). Species within the *O. hippopotamus* species group are characterized by their fairly well-known fossorial habits: most of them are inquilines of burrows of the family Geomyidae in temperate montane environments and they seem to be specialized in feeding on the fecal pellets produced by gophers (Zunino & Halffter, 1988, 2007; Delgado, 1999; Sánchez-Huerta *et al.*, 2015, 2018). In the case of the *O. hippopotamus* species complex, the lack of secondary denticles in the external margin of the forelegs (along with the internal margin being moderately curved in the middle and near the apex, and the apical spur being strongly curved inwards with an acute and sickle-shaped apex) is considered as an adaptation that allows adequate management of the gopher excrement to make brood masses (Zunino & Halffter, 1988; Sánchez-Huerta *et al.*, 2015, 2018).

The knowledge of the relationship between the *O. hippopotamus* species complex and *O. pilauco* is still incipient. Nevertheless, we can hypothesize that the lack of secondary denticles in both might be a consequence of convergent evolution. The monophyly of the *O. hippopotamus* species complex has not been proven by phylogenetic analyses to date, but the cephalic characters of all the species that currently make up this species complex differ from those of *O. pilauco* (Zunino & Halffter, 1988; Delgado, 1999; Sánchez-Huerta *et al.*, 2015, 2018): females of the *O. hippopotamus* species complex show a distinct clypeal carina, while this is absent in *O. pilauco*. Furthermore, males of the *O. hippopotamus* species complex never show a clypeal protrusion, as in the case of *O. pilauco*. We cannot reject the lack of secondary denticles in *O. pilauco* being an adaptation to exploit the excrement of fossorial rodents, or this species having exploited the dung produced by mammalian megafauna. To confirm this, it would be necessary to find the apical spur of the forelegs; however, none of the fossils known to date have this structure preserved.

Paleoecological inferences based on leg morphology traits

Based on the serrated and elongated tooth shape of *O. pilauco* females, we suggest paracoprid and hypophagic behaviors. For instance, Linz *et al.* (2019) showed that tibial tooth length and serration shape contribute to increasing the efficiency of burying brood balls. Additionally, the set of setal insertions in the fore femur (SOI; Fig. 2.4) of *O. pilauco* might function as a sort of brush for cleaning the surfaces of the joints and ventral side during burrowing activities, as was hypothesized by Houston (1986) for other subterranean Scarabaeoidea. It is also worth noting that previous works on *O. pilauco* show a major male morphotype with a large horn; the presence of horns in dung beetles was proven by phylogenetic evidence to be linked to tunneling behavior (Emlen & Philips, 2006).

Furthermore, the observed blunt teeth in males may have resulted from wear and tear throughout the life cycle of this species, particularly due to their nesting behavior. The combination of traits, including straight and blunt teeth, a straight ventral view shape, and the strongest clypeal horn, indicates that males may have had a limited role in nest construction compared to females. The robust female fore tibia demonstrates a clear affinity for digging processes, whereas the slightly longer male fore tibia indicates a proclivity for other types of nesting and reproductive activities, such as nest protection and male–male disputes (Simmons & Ridsdill-Smith, 2011). Consequently, the presence of blunt male teeth in this species should be attributed to a genetic predisposition rather than the result of wear from nest-building activities.

Finally, our work provides new evidence on the morphology and behavior of this enigmatic species. In addition to the already-known traits of the head, we describe the unusual traits of the forelegs, resulting in an accumulative number of traits unique to this species. Consequently, further morphological and other technical studies are still needed to establish the affinity of *O. pilauco* with its congeners.

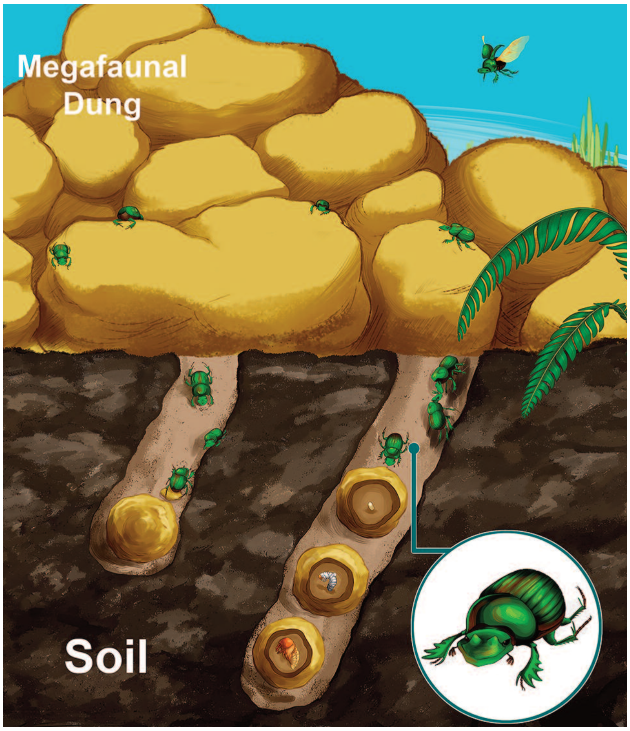

Figure 3. Artistic reconstruction of the habitat, morphology, and behavior of ***Onthophagus pilauco*** in their paleoenvironment. Created by Claudia León.

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