Historical Biology
An International Journal of Paleobiology

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ISSN: (Print) (Online) Journal homepage: www.tandfonline.com/journals/ghbi20

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To cite this article: Pablo J. Gaudioso, Joaquín Arroyo-Cabrales, M. Julieta Pérez, Iván Alarcón-D & J. Alberto Cruz (01 May 2025): Fossil bats of the Late Pleistocene from Huautla System Caves (Oaxaca, Mexico) and the importance of carpus bones to fossil identification, Historical Biology, DOI: 10.1080/08912963.2025.2490068

To link to this article: https://doi.org/10.1080/08912963.2025.2490068

HISTORICAL BIOLOGY
https://doi.org/10.1080/08912963.2025.2490068

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RESEARCH ARTICLE

Fossil bats of the Late Pleistocene from Huautla System Caves (Oaxaca, Mexico) and the importance of carpus bones to fossil identification

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ABSTRACT

The carpal bones, which show a notorious specialisation towards flight are poorly studied. These bones have only been the subject of study in 0.2% of all extant bat species. The use of bones from the carpal region has not been extensively investigated in palaeontology, mainly due to the scarcity of osteological studies and the fact that they are rarely collected during excavations. Therefore, we document the identification of a Pleistocene bat using the: scaphocentralunates. The material was collected from sediments associated with the extinct sloth *Meizonyx salvadorensis*, found in the caves of Sistema Huautla, Oaxaca, Mexico. A combination of qualitative and quantitative morphological characteristics made it possible to identify the scaphocentralunar bones at the generic level, which were subsequently determined to belong to the bat species *Sturnira* sp. This finding demonstrates that the carpal bones in bats exhibit distinctive diagnostic characteristics for the identification of fossil material. The discovery represents the second record for the genus for the Pleistocene of Mexico and the seventh in the Americas continent. In addition, the significance of collecting sediments associated with megafauna to obtain a more comprehensive understanding of past diversity is underscored.

ARTICLE HISTORY
Received 1 October 2024
Accepted 2 April 2025

KEYWORDS
Scaphocentralunate; Phyllostomidae; southern Mexico; postcranial skeleton; *Sturnira*

HANDLING EDITOR
Dr Mark Thomas Young, University of Edinburgh, UK

Introduction

The fossil record of bats is scarce worldwide, since either many palaeontologists mostly focus on large mammal bones or bat bones that have not been collected during the excavations (Jiménez Hidalgo et al., 2024). However, findings for the Quaternary sediments are more abundant because the skeletons were mostly preserved in karstic deposits or caves where fossilisation conditions are optimal (e.g. Czaplewski et al., 2007; Eiting & Gunnell, 2009; Morgan & Czaplewski, 2012). Most identifications on fossil bat remains are made using regions with numerous diagnostic characteristics, such as cranial bones, mandibles, and teeth (e.g. Brizuela & Tassara, 2021; Czaplewski et al., 2003, 2014; Fracasso & Salles, 2005; Galán, Cuenca-Bescós, et al., 2016; Gaudin et al., 2011; Hadler et al., 2018; López-García et al., 2009; Merino et al., 2007; Sevilla & Chaline, 2002, 2011; Topál, 1979; Van Den Hoek Ostende et al., 2018). Nonetheless, other elements of the postcranial skeleton (e.g. scapulae, humerus, radii, femurs and coxal bones) present valuable taxonomic information that can be used to make identifications for bat fossil remains (e.g. Arroyo-Cabrales & Álvarez, 1990; Czaplewski & Rincón, 2021; Czaplewski et al., 2007, 2014; Horáček et al., 2013; Moretto et al., 2017; Pelletier et al., 2017; Salles et al., 2014; Ubilla et al., 2019). Similarly, the anterior and posterior autopodial elements, particularly carpal and tarsal bones, present anatomical features with great taxonomic potential in bats (Gaudioso, 2019; Gaudioso et al., 2022), as demonstrated in other groups of mammals (e.g. Dunn et al., 2019; Salton & Sargis, 2008; Salton & Szalay, 2004; Stafford & Thorington, 1998). Despite that, carpal and tarsal bones have been largely overlooked in the identification of fossil bat material (e.g. Czaplewski & Peachey, 2003; Samonds, 2007), and have been underexplored for their potential in describing and utilising the most optimal fossil specimens of bats in evolutionary studies (e.g. Gunnell & Simmons, 2005; Jepsen, 1966; Rietbergen et al., 2023; Storch et al., 2002).

The little use of carpal bones in the identification of bat fossil material is due to scarce comparative material with the presence of disarticulated carpal bones (Samonds, 2007), but comprehensive osteological studies of carpals were recently developed (Gaudioso, 2019; Gaudioso et al., 2022). The scarcity of these remains in palaeontological sites can be attributed to several factors such as the lack of sieving of sediments associated with larger fossil material (Trusler, 2014); the type of mesh used in the sieves (Jiménez Hidalgo et al., 2024; Lyman, 2012; Stahl, 1996) or the misidentification of these remains during the separation of the material. The presence of scaphocentralunars in the Pleistocene bat record was reported first by Czaplewski and Peachey (2003), assigning one to *Myotis thysanodes* from a deposit in Arkestone Cave, Arizona. Posteriorly, Samonds (2007) assigned a specimen to *Eidolon dupreanum* in Anjohibe Cave, Madagascar. In this context, we describe qualitatively and quantitatively two Late Pleistocene scaphocentralunars from Basura Cave, Sistema Huautla, Oaxaca, Mexico, and compare them with 101 species from seven Neotropical bat families.

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Supplemental data for this article can be accessed online at https://doi.org/10.1080/08912963.2025.2490068.

Published online 01 May 2025

Geological setting of the study area

The Huautla System, in the Sierra Mazateca, Oaxaca, is the deepest cave in the Americas at 1560 m, and the fifth longest in Mexico with 8.9 kilometres, elevation between 2500 and 3500 m above sea level (Francke et al., 2021). The Huautla System is a karstic aquifer of mainly Cretaceous limestones but also includes dolomites and siltstones (Smith, 2002). One of the caves that make up this complex system is Cueva Basura (Figure 1), which has two entrances with two 35–40-m-deep shafts. It has a main hall approximately 35 m high and conical in shape, with an ellipsoidal floor (Alarcón-Durán & Arroyo-Cabrales, 2016). The current climate of the area is temperate sub-humid, with a marked dry period between March and May. The average annual rainfall is approximately 2500 mm, and the average annual temperature is 23.6°C (Francke et al., 2021).

Studies conducted in the Huautla System include the detailed geology and hydrology of the site (Smith, 2002); the presence of the giant sloth *Meizonyx salvadorensis* (Xenarthra, Megalonychidae; McDonald et al., 2020), which is interesting for being the second record for this species and the biogeographic implications of the findings. The collection of fossils from the Huautla System belong to Late Pleistocene (McDonald et al., 2020), includes horse (*Equus*

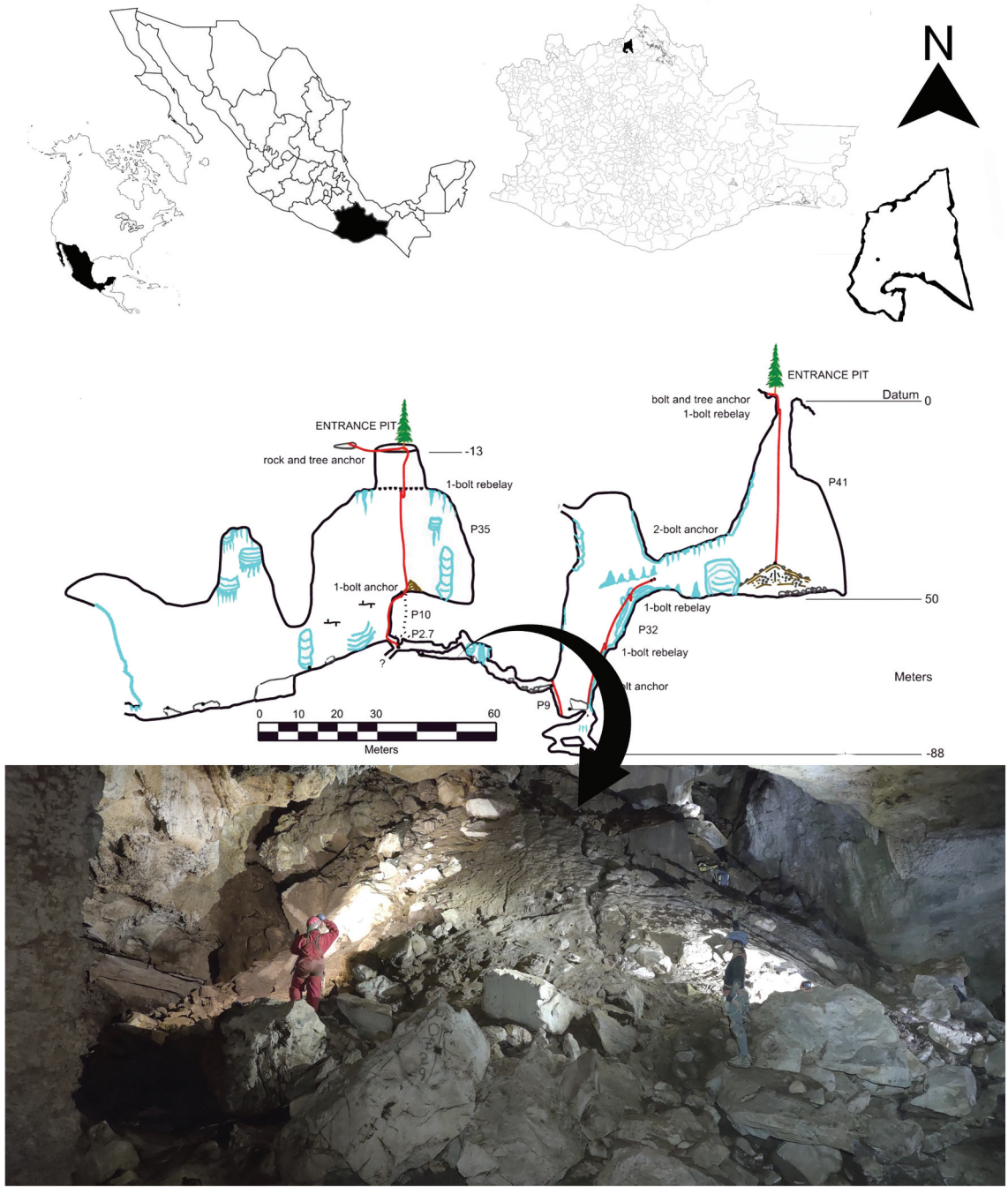

Figure 1. Map showing the geographical location of Basura Cave in Mexico. In the centre of the figure, a schematic of the Huautla System is presented, highlighting the area within Basura Cave where fossil bat remains associated with the giant sloth *Meizonyx salvadorensis* (Xenarthra, Megalonychidae) were discovered (McDonald et al., 2020). Furthermore, at the bottom of the figure, an image of the section of Basura Cave where the fossil find took place is included.

sp.), porcupine (*Coendu* sp.), extinct deer (*Navahoceros fricki*), rodent (*Neotoma mexicana*), bat (*Pteronotus* sp., and *Mormoops megallophyla*), roadrunner (*Geococyx* cf. *G. velox*) and swallow material (*Hirundo* cf. *H. fulva*) (Alarcón-Durán & Arroyo-Cabrales, 2015, 2016; Alarcón-Durán et al., 2017).

Materials and methods

The specimens were collected from the sediments associated with the skull of the extinct sloth *M. salvadorensis* found in the Basura Cave, Huautla System (Figure 1). The age of the palaeontological site was dated at 10,608 ± 66 ^{14}C BP (14,512 ± 130 Cal BP) in bones of the giant sloth *M. salvadorensis* (McDonald et al., 2020). The Pleistocene sediments, recovered from the Basura Cave, correspond to eroded siltstones that form orange-coloured clays ranging from a few cm to 10 m thick (Smith, 2002). Sediment samples were sieved in a tower with different mesh sizes (0.7, 0.5, 0.3, 0.2, 0.1 mm), recovering small vertebrate remains including amphibians, reptiles, and mammals.

We used the Comparative Osteologial Collection, Arqueozoology Lab (acronynm, DP), National Institute of Anthropology and History (INAH, Instituto Nacional de Antropología e Historia), México City, to identify the fossil material. Osteological comparison and morphometric measurements were conducted on 285 specimens, representing 100 species, 51 genera, and seven families of extant bats including: Emballonuridae (8 species, 5 genera, and 19 specimens), Natalidae (1 species, 1 genus, and 4 specimens), Noctilionidae (2 species, 1 genus, and 6 specimens), Molossidae (7 species, 4 genera, and 17 specimens), Mormoopidae (5 species, 2 genera and 21 specimens), Phyllostomidae (45 species, 27 genera, 9 subfamilies and 141 specimens), and Vespertilionidae (32 species, 11 genera and 77 specimens) (Appendix 1). We follow to Gaudioso (2019) and Gaudioso et al. (2022) for the terminology of the scaphocentralunar (Figure 2).

The measurements taken of the scaphocentralunate were as follows: medio-lateral width (MLW), proximal-distal length (PDL), and dorsal-palmar height (DPH) (Figure 3, Table 1). These measurements were taken with a Fowler vernier with an accuracy of 0.01 mm. Images were obtained using an OLYMPUS stereoscopic microscope (model SZX7) and a JEOL scanning electron microscope (model JSM 6460, Japan Electron Optics Laboratory).

The multivariate morphometric analysis was performed initially on species of the family Phyllostomidae (138 specimens), given that the fossil materials present exhibited unique morphological characteristics observed exclusively within this family. Subsequent analyses were then conducted, comparing species from the subfamilies Glossophagine (37 specimens) and Stenodermatine (48 specimens), as both groups shared common morphological traits. Furthermore, we exclusively examined species of the Stenodermatine subfamily, as we hypothesise that the fossil materials belong to a species of this group (see results: comparative description). To do this, principal component analysis (PCA) was employed to examine and illustrate

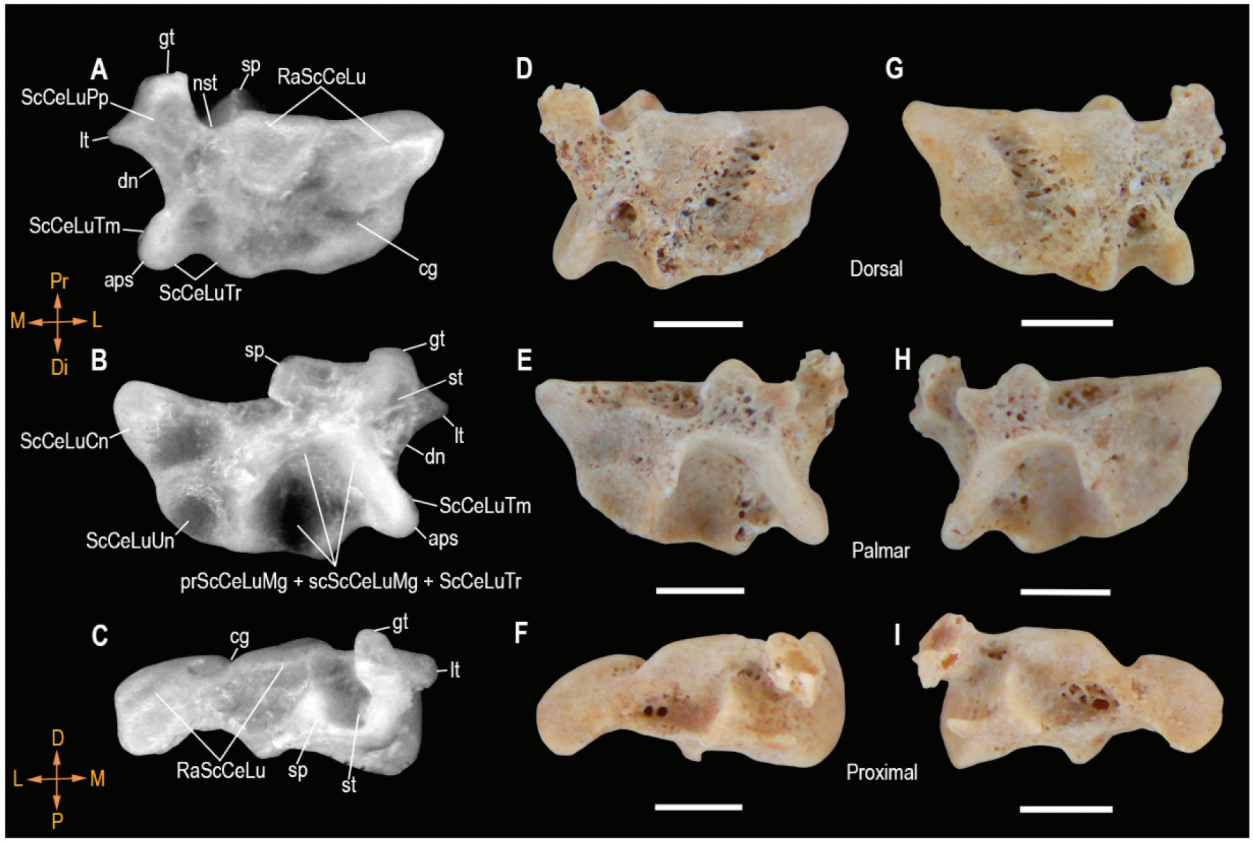

Figure 2. Anatomical terminology of the scaphocentralunar (ScCelu) in dorsal (A, D, G), palmar (B, E, H), and proximal (C, F, I) of *Sturnira parvidens* (DP 7213, Phyllostomidae, A–C) and fossil (*Sturnira* sp., DP 5899) left (D-F) and right (G-I) ScCeLu. Abbreviations: *join facets*: prSccelumg: principal scaphocentralunatemagnum; RaScCeLu: radiusscaphocentralunate; ScCeLuCn: scaphocentralunatecuneiform; ScCeLuPp: scaphocentralunateprepollex; ScCeLuTm: scaphocentralunatetrapezium; ScCeLuTr: scaphocentralunatetrapezoid; ScCeLuUn: scaphocentralunateunciform; scSccelumg: secondary scaphocentralunatemagnum. *Topographical (nonarticular) bony details*: aps: articular process of the scaphocentralunates; cg: central groove; dn: distal notch; gt: greater tubercle; lt: lateral tubercle; nst: notch of the scaphocentralunate tunnel; sp: scaphocentralunate process; st: scaphocentralunate tunnel. The arrows indicate the orientation for the dorsal and palmar view of left bones only (A–C; D–F): D: dorsal, Di: distal, L: lateral; M: medial; P: palmar, Pr: proximal. Scale bar = 1 mm.

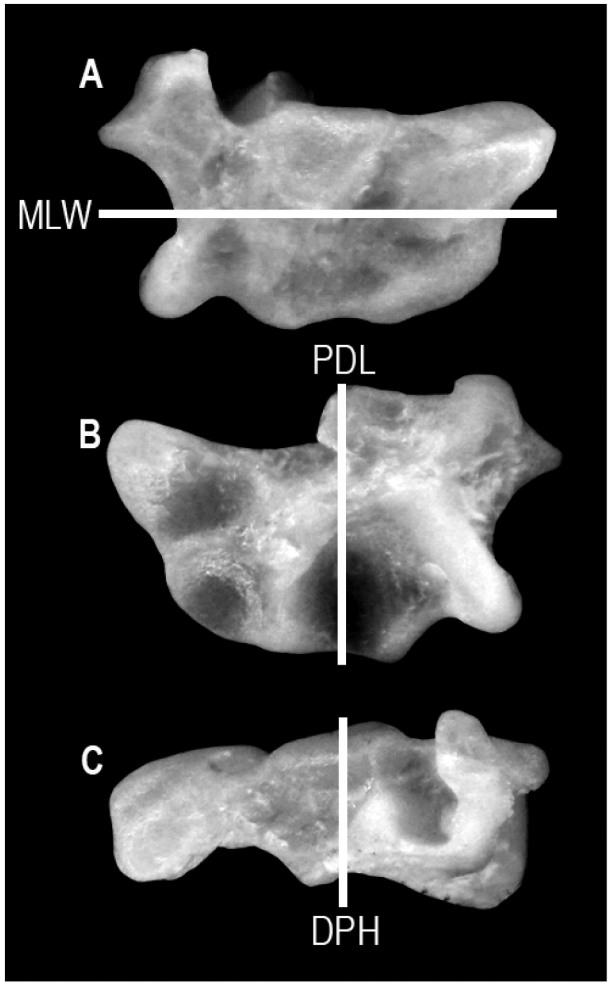

Figure 3. Osteological measurements taken from the left scaphocentralunates of the *Sturnira parvidens* (DP 7213, Phyllostomidae). MLW: medial-lateral width (A, dorsal view); PDL: proximal-distal length (B, palmar view); DPH: dorsal-palmar height (C, proximal view). Unscaled.

the morphometric similarity of the fossil remains concerning the phyllostomids bat species studied here. Three separate principal component analyses (PCAs) were performed on raw measurements using the scales package version 1.2.1 (Wickham & Seidel, 2022) in R suite (R Core Team, 2022). Meaningful PCs were assessed using the broken stick method as implemented in the vegan 2.5–3 R package (Oksanen et al., 2018).

Results

Systematic paleontology

Order Chiroptera Blumenbach, 1779
Family Phyllostomidae Gray, 1825
Subfamily Stenodermatinae Gervais, 1856
Genus *Sturnira* Gray, 1842

Geographic and stratigraphic occurrence. Cueva Basura, Sistema Huautla, Oaxaca, Mexico; Late Pleistocene (McDonald et al., 2020).

Referred material. Right and left (DP 5899) scaphocentralunars, which are well preserved (Figure 2(D–I)).

Table 1. Osteological measurements (arithmetic averages) taken from the scaphocentralunar of 45 species of the family Phyllostomidae. MLW: medio-lateral width; PDL: proximal-distal length; DPH: dorsal-palmar height. *Sturnira* sp. (DP 5899) these are the fossil specimens of Basura Cave of the Huautla System.

Species	MLW	PDL	DPH
Micronycteris microtis	2.31	1.55	1.11
Lampronycteris brachyotis	2.64	2.04	1.26
Glyphonycteris sylvestris	2.93	1.95	1.33
Macrotus californicus	2.77	1.71	1.22
Macrotus waterhousii	2.95	1.92	1.28
Lonchorina aurita	3.12	2.09	1.29
Lophostoma nicaraguae	2.46	1.67	1.15
Mimon cozumelae	4.29	2.42	1.62
Gardnerycteris crenulatum	3.44	1.94	1.42
Phyllostomus discolour	4.12	2.56	1.82
Phyllostomus hastatus	5.58	4.08	2.73
Trachops cirrhosus	4.06	2.65	1.68
Dermanura phaeotis	2.95	1.99	1.35
Dermanura tolteca	3.08	1.91	1.35
Dermanura azteca	3.41	2.23	1.49
Dermanura watsoni	2.87	1.91	1.26
Artibeus hirsutus	3.97	2.54	1.81
Artibeus intermedius	4.82	3.02	2.32
Artibeus jamaicensis	4.18	2.67	1.88
Artibeus lituratus	4.79	2.95	2.11
Sturnira hondurensis	3.34	2.15	1.48
Sturnira parvidens	3.09	2.01	1.41
Sturnira sp.	3.36	2.13	1.48
Uroderma davisi	3.07	2.11	1.52
Uroderma convexum	3.34	1.96	1.54
Chiroderma villosum	3.65	2.65	1.76
Platirrinus helleri	3.01	1.93	1.37
Vampyressa thyone	2.51	1.60	1.11
Enchisthenes hartii	2.88	1.86	1.27
Centurio senex	3.58	2.19	1.62
Carollia sowelli	3.06	2.07	1.41
Carollia castanea	2.78	2.01	1.28
Carollia perspicillata	3.15	2.19	1.51
Carollia subrufa	2.95	2.04	1.46
Desmodus rotundus	3.48	2.30	1.42
Diphylla ecaudata	3.73	2.21	1.49
Anoura peruana	2.85	2.02	1.34
Glossophaga mutica	2.61	1.74	1.18
Glossophaga commissarisi	2.34	1.69	1.22
Glossophaga leachii	2.49	1.79	1.28
Glossophaga morenoi	2.31	1.77	1.22
Choeronycteris mexicana	2.89	2.08	1.46
Musonycteris harrisoni	2.44	1.85	1.32
Leptonycteris yerbabuenae	3.26	2.30	1.63
Leptonycteris nivalis	3.44	2.53	1.68
Hylonycteris underwoodi	2.17	1.60	1.07

Remarks. Both scaphocentralunars are considered to belong to the same individual since only those bones and few others (an axis, two clavicles, a fragment of the articular region of the scapula, and two proximal epiphyses of the ulna) were recorded in the same levels, probably pertaining to the same individual (Figure 2(D–I)).

Description. Both bones exhibit signs of diagenesis, revealing their internal trabecular structure. It is important to note that although the scaphocentralunar (**ScCeLu**) may have foramens in the dorsal, proximal, and palmar regions in the seven families of species analysed, we cannot be sure which ones are real in the fossil elements. Therefore, we will not include this trait in the description.

The right **ScCeLu** has a medio-lateral width (MLW) = 3.41 mm, proximal-distal length (PDL) = 2.14 mm, and dorso-palmar height (DPH) = 1.51, while the left **ScCeLu** has an MLW = 3.31, PDL = 2.11, and DPH = 1.45 mm. The morphology of the **ScCeLu** is complex, although simplified it is fish-shaped and flattened (Figure 2(D–I)). The radiusscaphocentralunate facet (**RaScCeLu**) is the most complex, it extends almost over the entire proximal region of the

bone; the proximal edge of the **RaScCeLu** facet straight relative to the latero-medial axis of the bone and is divided into two articular sub-facets by a deep and notable central groove (Figure 2(A,C)); the lateral sub-facet of the **RaScCeLu** is elongated and elliptical with a very evident projection oriented laterally (Figure 4(A,D)); and the medial sub-facet of the **RaScCeLu** is sub-triangular (Figure 4(A)). In proximal view, the lateral sub-facet of the **RaScCeLu** presents an obvious, robust, palmar projection; the cavity of the **RaScCeLu** facet is deep (Figure 4(C)).

The medial region where the prepollex articulates does not have good preservation in both bones, preserving only the greater tubercle, which may extend beyond the scaphocentralunate process, although it can be noted that it is oriented in a proximal direction forming an angle of approximately 120º concerning the lateromedial axis of the bone (Figure 4(D,E)). The notch of the scaphocentralunate tunnel is narrow and excavated, unlike the distal notch, which is wide, and shallower (Figure 4(D)). The articular process of the scaphocentralunates is prominent, semicircular, compressed, and oriented medially forming an angle of approximately 120º about the latero-medial axis of the bone (Figure 4(A,B)). The scaphocentralunatetrapezoid facet (**ScCeLuTr**) encompasses the lateral region of the articular process of the scaphocentralunates and expands to an obvious projection of the distal edge of the bone (Figure 4(A)); the scaphocentralunatetrapezium facet (**ScCeLuTm**) occupies a large part of the disto-medial articular area of the articular process of the scaphocentralunates.

In palmar view, there are articular facets arranged in a curved manner in the disto-lateral region (Figure 2(E,H)); in the lateral región, the scaphocentralunatecuneiform facet is observed (**ScCeLuCn**), small and triangular; in the central region is located the scaphocentralunateunciform facet (**ScCeLuUn**) with a kidney-shaped or semicircular shape; between this last facet and the articular process of the scaphocentralunates there is a large, concave and deep facet, composed of the fusion of the principal scaphocentralunatemagnum facet (**prScCeLuMg**) + secondary scaphocentralunatemagnum facet (**scScCeLuMg**) + scaphocentralunatetrapezoid facet (**ScCeLuTr**) (Figure 2(B,E)); the scaphocentralunate process is triangular and projects slightly beyond the margin of the bone. The scaphocentralunar tunnel is observed; we cannot infer whether the tunnel is semi-closed or closed due to taphonomic processes.

Comparative description. The **ScCeLu** exhibits notable distinctions when compared at the family taxonomic level (Figure 5). The fossil materials (DP 5899) show two diagnostic characters, which combined, are observed in Phyllostomidae: presence of the scaphocentralunate tunnel and fusion of the facets **prScCeLuMg** + **scScCeLuMg** + **ScCeLuTr** (Figure 5(B)). Although the scaphocentralunate tunnel is a variable character within phyllostomids (absent or present; when present it can be open, semi-closed, or closed) it is also present in *Noctilio* (Noctilionidae) (Figure 5(G)). Morphological differences in **ScCeLu** separate *Noctilio* from phyllostomid species, mainly in the general shape of the bone, very evident in dorsal view, and in specific features such as the fusion of the articular facets **prScCeLuMg** + **scScCeLuMg** + **ScCeLuTr** (Figure 5(A–B,F–G); see Gaudioso, 2019 fig. 64–67). The fusion of these facets is a character shared with *Natalus mexicanus* (Natalidae), although it evidences anatomical disparities with Phyllostomidae (e.g. general shape of the bone and shape of the articular process of the scaphocentralunates) (Figure 5(A–B,J–K)). The taxonomic assignment to Emballonuridae, Molossidae, Mormoopidae, and Vespertilionidae is ruled out, as they do not exhibit the combination of aforementioned characters observed in the two fossil bones (Figure 5). The family Phyllostomidae displays significant morphological disparity in the scaphocentralunate

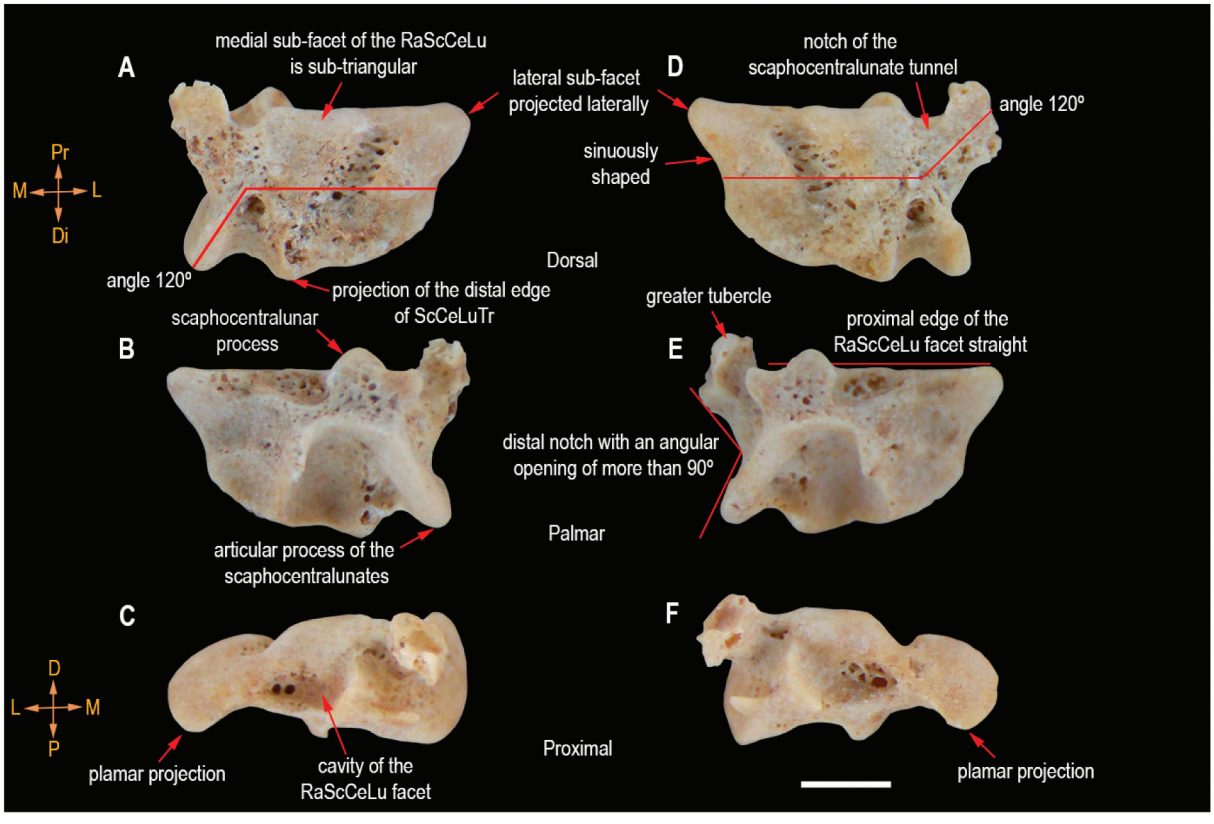

Figure 4. Characteristics of the escofocentrolunar of the fossil from Basura Cave, Huautla System. Left (DP 5899) (A–C), and right (DP 5899) (D–F). Scale bar = 1 mm.

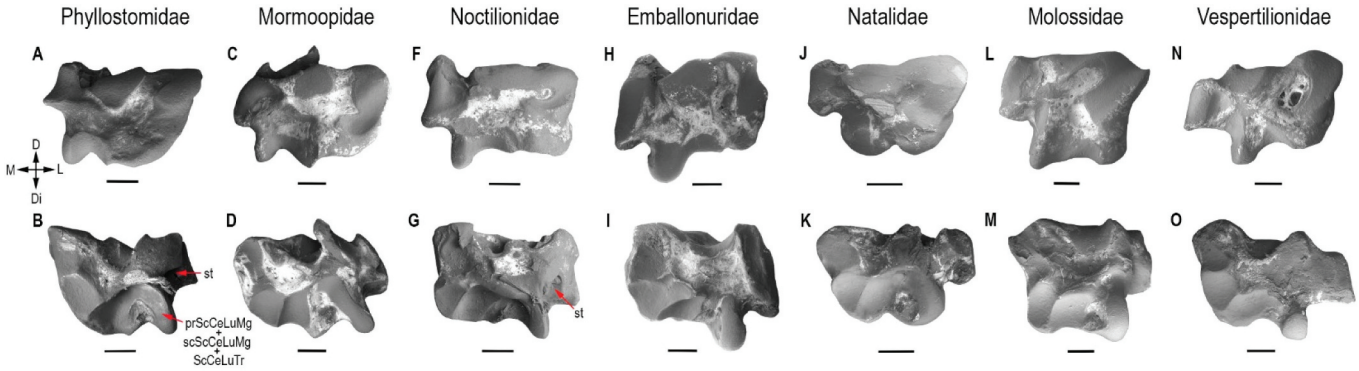

Figure 5. Comparison of the scaphocentralunte in different species of Neotropical bats (top dorsal view, and bottom palmar view of left bone). *Hylonycteris underwoodi* (DP 5965, Phyllostomidae) (A, B); *Mormoops megalophylla* (DP 8718, Mormoopidae) (C, D); *Noctilio leporinus* (DP 8115, Noctilionidae) (E, F); *Diclidurus virgo* (DP 6413, Emballonuridae) (H, I); *Natalus mexicanus* (DP457, Natalidae) (J, K); *Molossus sinaloae* (DP 9015, Molossidae) (L, M); *Antrozous pallidus* (DP7358, Vespertilionidae) (N, O). Note the presence (red arrow) of the scaphocentralunate tunnel (st) and the fusion of the three facet joints (**prScCeLuMg**: principal scaphocentralunatemagnum; **ScCeLuTr**: scaphocentralunatetrapezoid; **scScCeLuMg**: secondary scaphocentralunatemagnum) in *H. underwoodi* a phylostomid bat. The arrows indicate the orientation of the bone for the dorsal view of left bones only: D: dorsal, Di: distal, L: lateral; M: medial; P: palmar, Pr: proximal. Scale bar = 0, 5 mm.

among its species of the nine subfamilies analysed (Figure 6; see Gaudioso, 2019). Glossophaginae and Stenodermatinae show a character observed in fossil materials: the **RaScCeLu** facet divided by an evident central groove, originating two articular sub-facets (Figure 6 see *Musonycteris harrisoni* and *Uroderma davisi*). Fossil **ScCeLu** shows a set of characters that combined are observed in *Sturnira* (Stenodermatinae): articular process of the scaphocentralunate oriented medially forming an angle of approximately 120º about the latero-medial axis of the bone (in dorsal view, Figure 4 (A)); lateral sub-facet of the **RaScCeLu** facet markedly projected laterally (in dorsal view, Figure 4(A,D)); robust and square scaphocentralunar process (in palmar view, Figure 4(B)); lateral edge of the **RaScCeLu** facet with robust and obvious palmar projection (in proximal view, Figure 4(C,F)); lateral margin sinuously shaped (in dorsal view, Figure 4(D)); medial region (includes the **ScCeLuPp** and scaphocentralunate tunnel plus other structures) oriented in a proximal direction forming an angle of approximately 120º about the latero-medial axis of the bone (in dorsal view, Figure 4(D)); proximal edge of the **RaScCeLu** facet straight relative to the latero-medial axis of the bone (in dorsal and palmar view, Figure 4(D,E)); wide distal notch with an angular opening of more than 90º (in palmar view, Figure 4(E)). The fossil bones display a semi-closed scaphocentralunar tunnel, which differs from the revised species of *Sturnira*, which has a closed tunnel (including *S. erythromos*, see Gaudioso, 2019). However, this trait varies within the Phyllostomidae bats at the intraspecific and intrageneric levels, so it requires careful and thorough evaluation. Based on the mentioned characteristics, we conclude that the fossil materials belong to the genus *Sturnira*.

Multivariate analysis

Morphospace within phyllostomidae

In the PCA, the first two PCs accounted for more than 99% of the total variation (see Table 2 and Figure 7). The variable loadings of PC1 (96%) were predominantly influenced by MLW and to a lesser extent by PDL and DPH, respectively. As indicated by PC1, species exhibiting higher values of these measures and greater body mass are situated in the positive sector of PC1 (e.g. *Phyllostomus hastatus*, *Artibeus lituratus*), while species with lower values and lower body mass occupied the negative sector (e.g. *Hylonycteris underwoodi*, *Micronycteris microtis*). On PC2, this pattern is evident in the negative sector (e.g. *Phyllostomus hastatus*, *Anoura peruana*), while it is more evenly distributed in the positive sector (e.g. *Diphylla ecaudata*, *Mimon cozumelae*). The fossil materials are positioned on the scatter plot within the stenodermatine bat cluster, near species of *Sturnira* and *Dermanura*.

Morphospace within glossophaginae and stenodermatinae

In the PCA, the first two PCs accounted for more than 99% of the total variation (see Table 2 and Figure 8), and the scatter plot pattern is similar to that observed in the Phyllostomidae family. The positive sector of PC1 (97%); is primarily occupied by stenodermatines (e.g. *Artibeus lituratus*, *A. intermedius*), while the negative sector is occupied by glossophagines and stenodermatines with reduced body mass (e.g. *Hylonycteris underwoodi*, *Vampyresa thyone*). The fossil materials are situated on the scatter plot near the *Sturnira* and *Dermanura* species.

Morphospace within stenodermatinae

In the PCA, the first two PCs accounted for more than 99% of the total variation (see Table 2 and Figure 9). The scatter plot pattern is similar to that observed in the Phyllostomidae family, and Glossophaginae – Stenodermatinae subfamilies. PC1 accounts for 98% of the variance, exhibiting a comparable associaton with the first two PCAs. Therefore, the species are associated in a similar way to the previous analyses (e.g. *Artibeus lituratus*, *A. intermedius* in the positive sector; *Vampyresa thyone, Enchisthenes hartii* in the nagetive sector); as well as on PC2 (1%) (*Chiroderma villosum*, *Artibeus jamaicensis* in the nagetive sector; *Artibeus lituratus*, *Uroderma convexum* in the positive sector). Once more, fossil materials are situated within a sector that is closely associated with species of *Sturnira* and *Dermanura*.

Discussion

The present study provides qualitative and quantitative anatomical evidence to support the identification of the two fossil carpal bones from Pleistocene sediments of the Basura Cave of Sistema Huautla as belonging to the yellow-shouldered bat *Sturnira* (Stenodermatinae subfamily, family Phyllostomidae). This finding represents the second record of the genus for the Pleistocene of

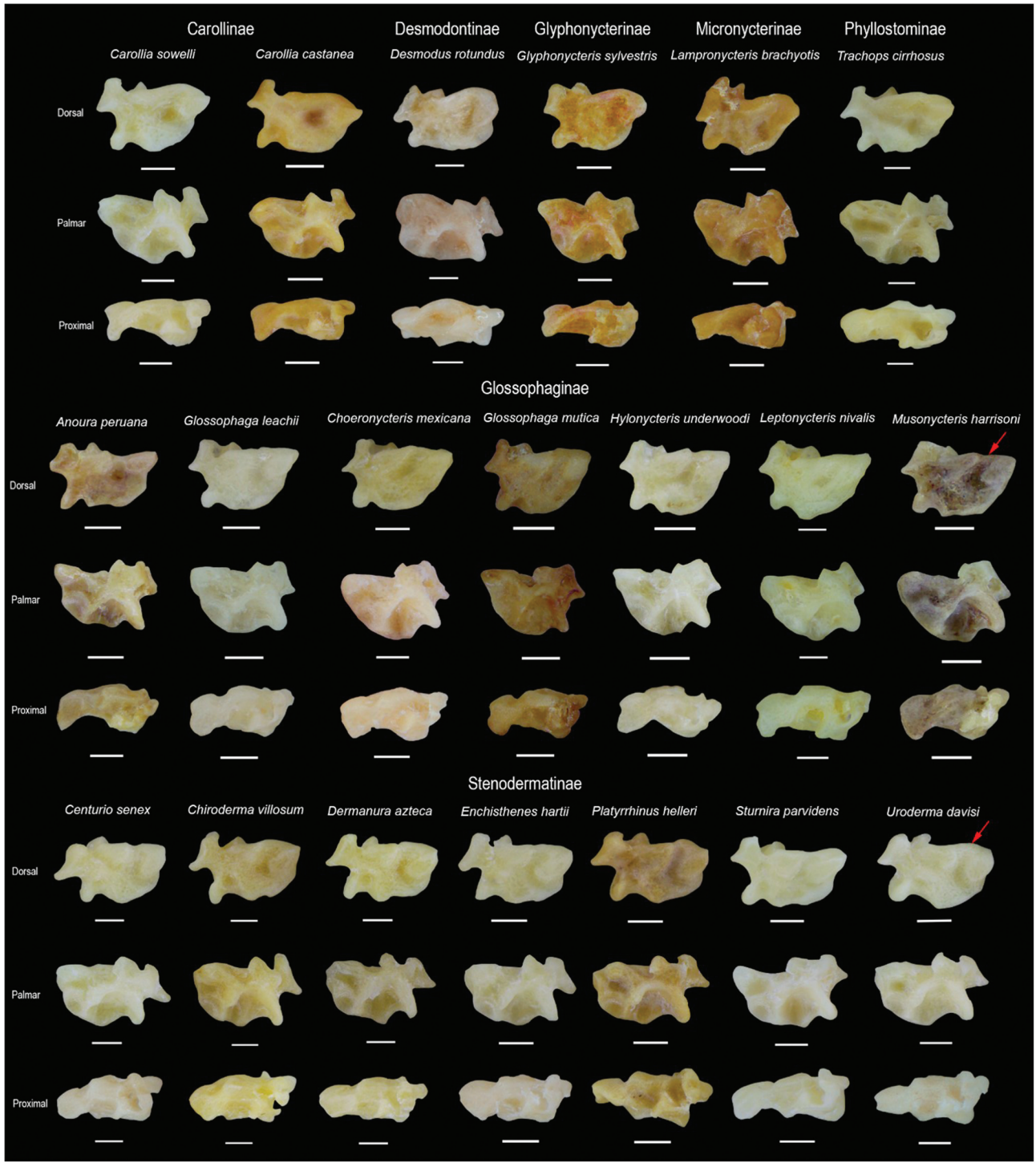

Figure 6. Comparison of the scaphocentralunte (left bone) in different species and subfamilies of the Phyllostomide family. Note the **RaSccelu** facet divided by the evident central groove, originating two articular sub-facets presence (red arrow) in Glossophaginae and Stenodermatinae. See Figure 2 for the orientation of the bones. Scale bar = 1 mm.

Table 2. Loadings of each variable for the two first axes in PCA.

	Phyllostomidae		Stenodermatinae – Glossophaginae		Stenodermatinae	
Variables	PC1	PC2	PC1	PC2	PC1	PC2
MLW	**0,81**	**0,58**	**0,82**	**0,55**	**0,79**	**0,55**
PDL	**0,48**	**-0,72**	**0,45**	**-0,75**	**0,47**	**-0,81**
DPH	0,34	–0,36	0,34	–0,34	0,37	–0,13
% Explained variance	96%	3%	97%	2%	98%	1%

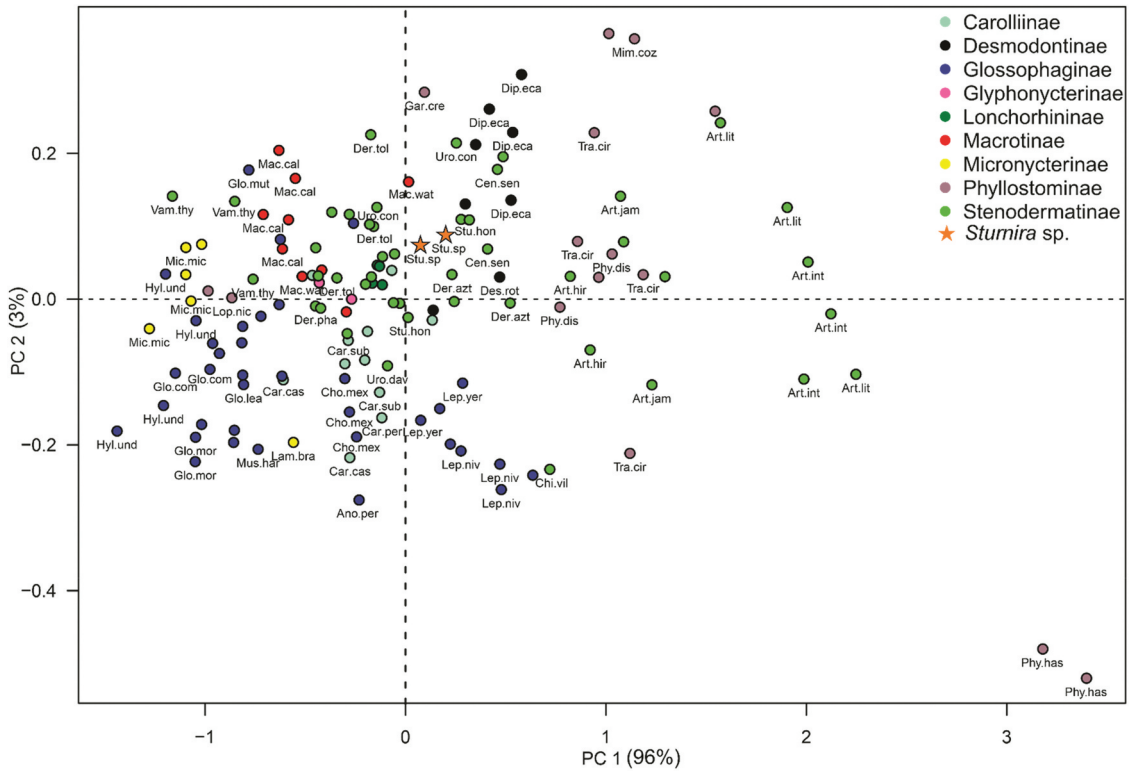

Figure 7. Morphospaces depicted by the first two principal components of the nine subfamilies into the Phyllostomidae. Circles represent the species from the different subfamilies, while the orange star denotes the two fossil materials.

Mexico. The first record was *Sturnira lilium* in the Pleistocene and Holocene of the Gruta de Loltún in Yucatán (Álvarez, 1982; Arroyo-Cabrales & Álvarez, 1990). Findings in the American continent were also made in Quaternary sediment-bearing caves (Pleistocene-Holocene): *Sturnira* sp. was recorded in Cebada Cave, Chiquibul System, Belize (Czaplewski et al. 2003); *Sturnira lilium* was recorded in Lapa da Escrivania Cave (Winge, 1893, Igrejinha Cave (Salles et al., 1999), Nossa Senhora Aparecida Cave (Salles et al., 1999), and Serra da Mesa (Fracasso & Salles, 2005), in Brazil. In this context, the new fossil record of the genus *Sturnira* in the Huautla System represents the seventh in the Americas and the northernmost for the Pleistocene, although it is currently distributed further north in Mexico (Velazco & Patterson, 2013).

Sturnira fossils have been identified using skulls or cranial fragments (e.g. maxillae, mandibles, teeth) as well as postcranial skeletal elements (humeri, radii and femurs) (Álvarez, 1982; Arroyo-Cabrales & Álvarez, 1990; Fracasso & Salles, 2005; Salles et al., 1999; Winge, 1893), as it is generally done with the identification of fossil remains of bats (e.g. Argenti et al., 2008; Czaplewski et al., 2005; Galán et al., 2019; Galán, Cuenca-Bescos, et al., 2016; González-Dionis et al., 2022; Gunnell et al., 2015; Lindenau, 2005; Salari & Kotsakis, 2011; Sevilla, 1990). The use of carpal bones in the identification of bat skeletal remains has only been used by Czaplewski et al. (2003), who assign the scaphocentralunar bones to *Myotis thysanodes* only by association with the rest of the fossil material, without mentioning characters that would allow taxonomic assignment. Samonds (2007) assigns the fossil scaphocentralunar to *Eidolon dupreanum*, providing a short description of the scaphocentralunar, but the taxonomic assignment was made only by bone size. The scarce use of carpal elements in the identification of bat remains is mainly due to the scarce osteological study (Gaudioso, 2019; Gaudioso et al., 2022). However, in other groups of mammals such as ungulates, carpal bones are among the most used for the identification of fossil material (e.g. Alberdi et al., 2014; Marín-Leyva et al., 2019; Schellhorn, 2021; Schellhorn & Pfretzschner, 2014; Thomason, 1985). The significance of the carpal bones in mammals has been demonstrate to have phylogenetic and locomotor implications in a range of species, including ungulates, cetaceans, rodents, tenrecids, carnivores, dermoptera and scadentia (e.g. Dunn et al., 2019; Gavazzi et al., 2020; Salton & Sargis, 2008; Schellhorn & Pfretzschner, 2014; Stafford & Thorington, 1998; Thorington & Stafford, 2001; Yalden, 1971), and in the case of bats, the taxonomic use for the process of identification of fossil material, as is the case in the present work. Additionally, they provide information that can be used to make functional and biomechanical inferences about the flight (Gaudioso, 2019; Gaudioso et al., 2022; Stafford & Thorington, 1998; Vaughan, 1959, 1970). It should be noted that defining characters of the carpal region in bats and extending this to therian mammals in general, is a challenging and indeed experimental task (Gaudioso, 2019). This complexity can result in errors or inaccuracies, as evidenced in the work of O'Leary et al. (2013), which is discussed by Gaudioso (2019, pp. 154–155).

On the other hand, we consider that the absence in the study of carpal bones in fossil bats is due to the type of mesh used in the sieving process (Lyman, 2012; Stahl, 1996). This is because, meshes exceeding 2 mm in diameter may have precluded the recovery of the fossil scaphocentralunar bones under investigation. However,

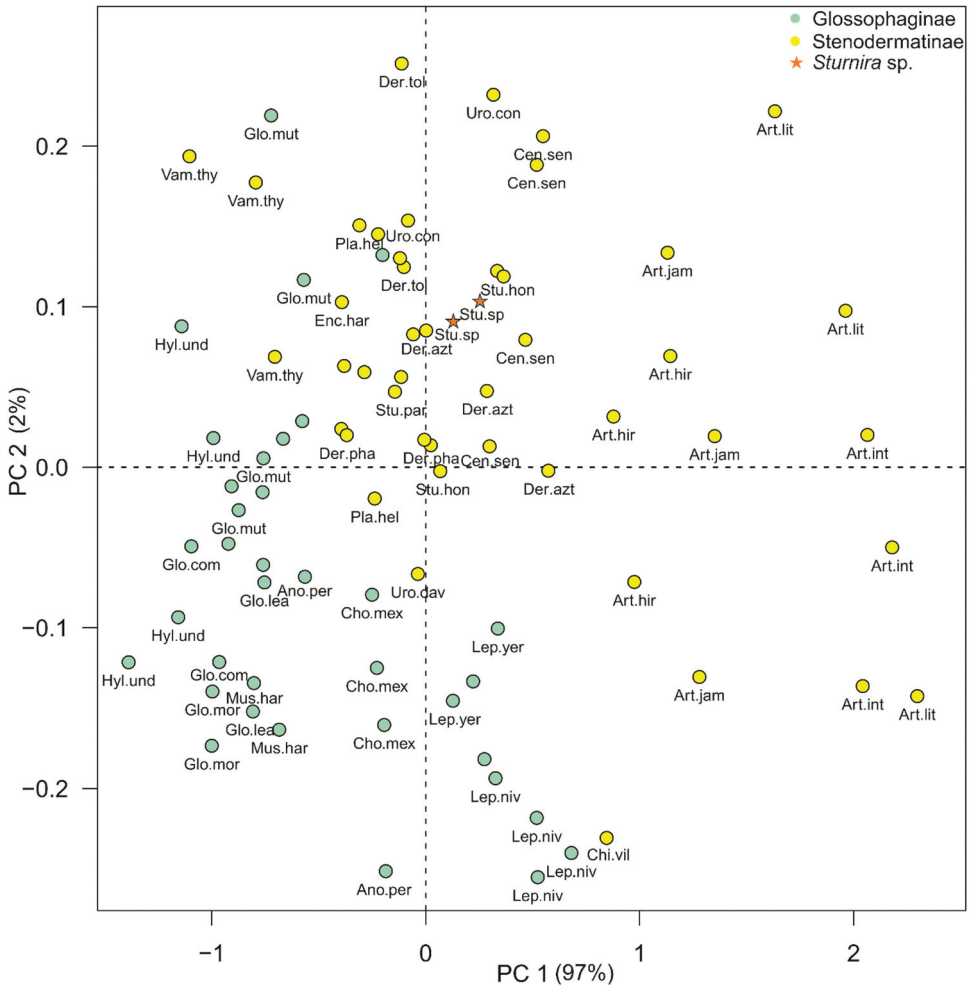

Figure 8. Morphospaces depicted by the first two principal components of the Stenodermatinae and Glossophaginae subfamilies (depicted in yellow and green circles, respectively), while the star (in orange) denotes the two fossil materials.

there are other bats such as *Balantiopteryx io* in which the carpal elements are even smaller, less than 2 mm, which could be lost even in sieves with a mesh size of one millimetre. Therefore, more rigorous and sustained effort be undertaken to collect and preserve small vertebrate specimens (Jiménez Hidalgo et al., 2024; Lyman, 2012).

The genus *Sturnira* is present in the Huautla System area with the species *S. parvidens* (Velazco & Patterson, 2013). *Sturnira parvidens* is a medium sized frugivorous bat and it can be found at elevations between 0 and 2000 m. This species is commonly founded in bodies of water, fruit crops, margins of the forest, and canyons (Hernández-Canchola & León-Paniagua, 2020). The origin of *Sturnira* was probably 15.9–12.6 Ma and the most recent diversification durtin the Pliocene-Pleistocene (3.7–2.2 Ma) (Hernández-Canchola et al., 2020). The presence of this bat in the palaeontological site indicates paleoenvironmental conditions similar to the Present one, with a mid-elevation and probably with a mesic environment with an open forest with oak-dominant or a tropical environment, because *S. parvidens* is considered as an indicator of forest disturbance and is more abundant in the early stages of secondary forest (Hernández-Canchola & León-Paniagua, 2020), which allowed the presence of *Meizonyx salvadorensis* (McDonald, 2023) and are conditions where we can currently find to *Sturnira parvidens* (Hernández-Canchola & León-Paniagua, 2020). This is consistent with the corridor hypothesis where a tropical corridor (Ceballos et al., 2010)

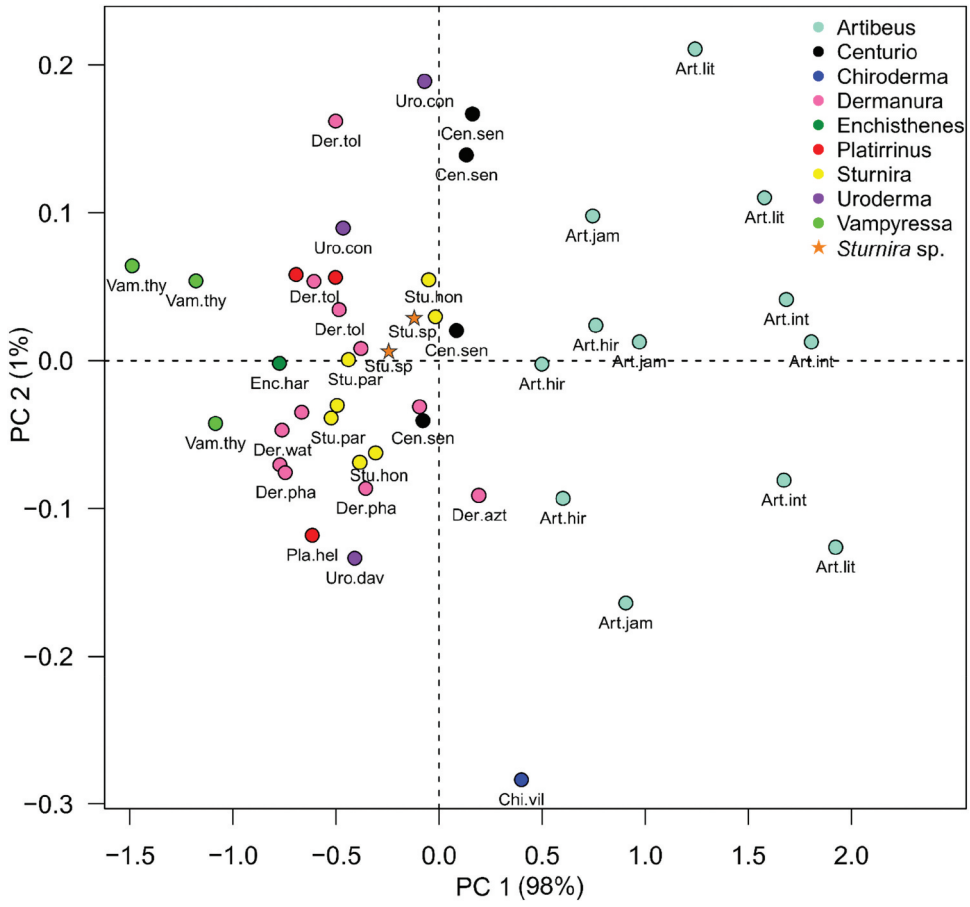

Figure 9. Morphospaces depicted by the first two principal components of the Stenodermatinae subfamily, with species represented in different colours, while the star (in orange) denotes the two fossil materials.

allow the presence of *M. salvadorensis* since El Salvador to Oaxaca, México (McDonald, 2023).

Conclusion

The morphological analysis of **ScCeLu** enabled us to conduct taxonomic identification at the generic level within one of the most diverse groups of mammals. Consequently, we can confidently affirm that this carpal element demonstrates significant taxonomic utility for identifying fossil remains. Hence, we confirm the presence of the yellow-shouldered bat, *Sturnira*, in Pleistocene sediments from Cueva Basura, Sistema Huautla, Oaxaca, México. Moreover, we underscore the significance of gathering sediments linked with megafauna and employing small sieve meshes of 1 mm or less to retrieve material crucial for understanding the diversity of past microvertebrates.

Acknowledgments

The authors are grateful to Rubén Barquez, curator of the Colección Mamíferos Lillo–Universidad Nacional de Tucumán. The author PJG thanks Guillermina Krieger for her help in drafting the manuscript, as well as in revising and improving the English.

The authors thank the two anonymous reviewers for their comments and recommendations for the publication of this manuscript.

Disclosure statement

No potential conflict of interest was reported by the author(s).

Funding

This work has been supported by a CONICET (Consejo Nacional de Investigaciones Científicas y Técnicas) postdoctoral fellowship and Partial Funding for Short Stays Abroad grant awarded to PJG. This work has been funded by [Agencia Nacional de Promoción de la Investigación, el Desarrollo Tecnológico y la Innovación, PICT-2020-SERIEA-00987, FONCyT]. This JAC work was supported by [CONAHCYT Investigadoras e Investigadores por México program, grant number 74243], Mexico.

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CRediT authorship contribution statement

Pablo J. Gaudioso, J. Alberto Cruz, and J. Arroyo-Cabrales: Writing – review & editing, Writing – original draft, Methodology, Investigation, Conceptualization. Pablo J. Gaudioso and M. Julieta Pérez: Formal analysis, Data curation. Joaquín Arroyo-Cabrales, Iván Alarcón-D.: Excavation. Pablo J. Gaudioso, J. Alberto Cruz, M. Julieta Pérez, Joaquín Arroyo-Cabrales, Iván Alarcón-D.: Writing and revising the final manuscript.

Data availability statement

Calculations and analyses are published in this article, raw data may be made available upon request to the authors.

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