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Holocene vertebrate assemblages provide the first evidence for the presence of the barn owl (Tytonidae, *Tyto alba*) on Socotra Island (Yemen) ☆

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ABSTRACT

We describe the vertebrate remains found in a Holocene deposit inside the Taiti Cave, Socotra Island (Yemen). The fossils were found in a sand dune occupying almost entirely the main cavity of the Cave, with some bones collected on the surface and the majority of them found under its surface, in particular below a tiny level of hardened sand, the latter probably related to a guano deposit. They were mostly isolated bones, but under the guano layer, some of them were aggregated and recognizable as belonging to owl pellets. The analysis of the vertebrate remains reveals a great prey diversity and, together with the location of the pellet accumulation and the almost perfect preservation of the remains, indicates that the deposit derived from a pellet accumulation made by *Tyto alba*. This hypothesis is corroborated by a *Tyto alba* beak fragment found in the Hoq cave, in a deposit of uncertain stratigraphic context. The data presented herein represent the first documented evidence of the presence of *Tyto alba* on Socotra Island and indicate the probable existence of a now extinct population of *Tyto alba* on the island during the Holocene, already extinct at the time of the first ornithological surveys during the XIX Century.

1. Introduction

Socotra is the largest island of the Socotra Archipelago which includes four islands (Socotra, Abd al-Kuri, Samha and Darsa), belonging to the Yemen Republic. Socotra island is a fragment of Gondwana, formerly connected with Dhofar, South Oman (Samuel et al., 1997), which has been separated by the breakup of the eastern Gondwana during the Mesozoic (Braithwaite, 1987; Van Damme, 2009). The main island is located in the northern part of the Indian Ocean, between the Horn of Africa (230 km WSW) and the Arabian coast (350 km N) (Fig. 1).

Socotra holds an extremely varied terrestrial and marine biodiversity, with a high level of endemism, according to insular "disharmony" (Whittacker and Fernandez-Palacios, 2007). The long separation and the bioclimatic features led to the evolution of tropical and arid ecosystems with forest biotopes holding relict plants such as *Dracaena cinnabari* and the various species of *Boswellia* (Habrová and Buček, 2013), shrubby habitats and rocky landscapes flooded by transient watercourses, sometimes with high energy. Longstanding studies on Socotra have permitted to improve the conservation of their ecological peculiarity ending up with the designation of "World Heritage Site – UNESCO 2010" in 2008.

The terrestrial vertebrates of Socotra Islands include 30 species of reptiles, 27 of which endemic to Socotra archipelago (Razzetti et al., 2011), more than 220 species of birds, eleven of which endemic (Porter and Suleiman, 2013, 2014; Porter and Suleiman, 2020), and a few species of mammals, mostly domesticated, semi-domesticated or commensal species, with the exception of *Suncus madagascariensis* (Coquerel, 1848) and *Viverricula indica* Geoffroy, 1803, probably accidentally introduced by human activities, and four bat species, only one of them endemic to Socotra (Wranik,

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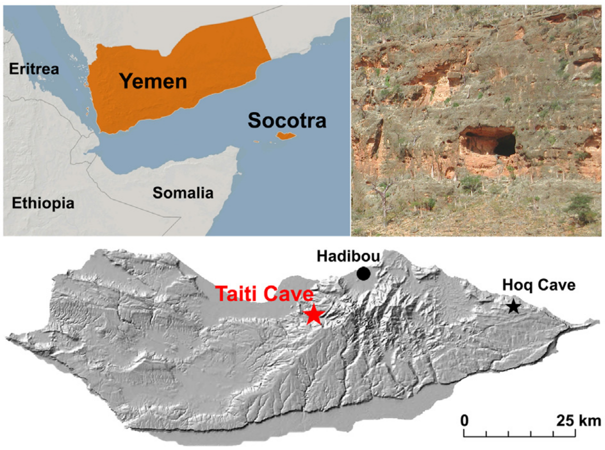

Fig. 1. Location map of the Socotra Island (Yemen), with the position of the two caves mentioned in the text and a view of the entrance of Taiti Cave (top right).

1998; Benda et al., 2017). A fossil skeleton of *Rousettus aegyptiacus*, a fifth bat species, was found embedded in a flowstone dated 6669 ± 70 yr. BP, representing the first fossil vertebrate known from Socotra Island (Van Damme et al., 2018).

Here we present the analysis of a Holocene fossil vertebrate accumulation collected in the Taiti Cave, central Socotra Island (Fig. 1), embedded in a 5 m high sand dune which occupies almost entirely the floor and the entrance of the cave. This study represents the second analysis of fossil terrestrial vertebrates from Socotra, following the one published by Van Damme et al. (2018).

2. Material and methods

The vertebrate remains were collected during two field surveys of Socotra Islands organized by the Dipartimento di Scienze della Terra of the Torino University in 2003 and 2004 (Gaetani et al., 2018). The fossil remains were found in the entrance of Taiti's cave, a cavity located in the Northern part of Socotra (12°34′30″ N, 53°55′28″ E) (Fig. 1), ca. 10 km from the coast. The cave is rather small with a circular entrance of ca. 6 m of diameter and 4–5 m deep. The cave has a main room and a small cavity opened on the bottom of its back wall. The main cavity is almost entirely occupied by a small sand dune (4–5 m high) in which the fossil remains have been found.

The bones were found in the dune. Some were collected on the surface but the majority of them was found under its surface, especially under a tiny level of hardened sand probably related to the presence of guano. The remains consist of both isolated bones and, especially under the guano layer, associated bony elements still recognizable as owl pellets. The sediment was sieved with a minimum mesh of 0.87 mm and all the vertebrate remains were analyzed. The scarce invertebrate remains are not considered in this analysis.

Other vertebrate remains of uncertain stratigraphic context and age were collected in two points of the entrance room of Hoq Cave, a huge cavity opened in the cliff of the northern coast of Socotra Island (15°35′12″ N, 54°21′15″ E) (Fig. 1). A few information regarding skeletal material from Hoq Cave are provided in the "Remarks" sections where appropriate.

The fossil remains are parts of the collections of the Museo di Geologia e Paleontologia, Dipartimento di Scienze della Terra of the Torino University (MGPT-PU). Reptiles and birds were compared with the recent skeleton collections housed in the Dipartimento di Scienze della Terra, Università degli Studi di Torino (Massimo Delfino Herpetological Collection, MGPT-MDHC; Marco Pavia Osteological Collection, MGPT-MPOC). For the Passeriformes, we analyzed only the cranial remains and the humeri, as they represent the most diagnostic bones within this Order. Taxonomy follows Razzetti et al. (2011) for reptiles, Gill et al. (2022) for birds, and the IUCN red list dataset for mammals (https://www.iucnredlist.org). Anatomical nomenclature follows Hoffstetter and Gasc (1969) and Villa and Delfino (2019) for reptiles, and Baumel and Witmer (1993) for birds.

3. Systematic paleontology

Diapsida Osborn, 1903
Squamata Oppel, 1811
Iguania Cuvier, 1817
Family Chamaeleonidae Rafinesque, 1825
Genus ***Chamaeleo*** Laurenti, 1768
Chamaeleo monachus Gray, 1865
Fig. 2(A-C)

Material: Two left maxillae (MGPT-PU 102206, 142384), one left dentary (MGPT-PU 142396), one trunk vertebra (MGPT-PU 142375).

Description: The tooth-bearing bones are characterized by acrodont teeth that are triangular in shape and provided of a central main cusp and two minor cusps (one anterior and one posterior to the main one). Both the well-preserved maxilla (MGPT-PU 142384; Fig. 2(A, B)) and the dentary (MGPT-PU 142396) have no anterior subpleurodont teeth. The small maxilla MGPT-PU 142384, preserving the first 11 tooth positions, clearly indicates that the nine anteriormost teeth are tightly-spaced (so that they form a continuous cutting edge), but the posterior ones are widely spaced and not in contact to each other. The anterior teeth are smaller than the posterior ones. The large, but fragmentary maxilla MGPT-PU 102206 (Fig. 2(C)) preserves only the posteriormost, well-spaced teeth. The tooth arrangement of the small left dentary MGPT-PU 142396 is congruent with the one shown by the maxilla MGPT-PU 142384, but only the first nine tightly-spaced teeth are preserved. The trunk vertebra MGPT-PU 142375 is distinctly anteroposteriorly elongated and hosts an anteroposteriorly broad and probably tall (it is not complete but has a robust base) neural crest located in the posterior half of the neural arch.

Remarks: The remains, referred to the only acrodont lizard present on the island of Socotra (Razzetti et al., 2011), have a morphology broadly congruent with that of *Chamaeleo chamaeleon* (Linnaeus, 1758) as described by Villa and Delfino (2019). The comparative skeletal morphology of *C. monachus* is currently unknown. Two further chameleon trunk vertebrae, MGPT-PU 102203, are also present in the Hoq collection.

Gekkota Camp, 1923
Family Phyllodactylidae Gamble et al., 2008
Genus ***Haemodracon*** Bauer, Good and Branch, 1997
Haemodracon riebeckii (Peters, 1882)
Fig. 2(D)

Material: One right maxilla (MGPT-PU 142385), one left quadrate (MGPT-PU 142386), one left dentary (MGPT-PU 142379), one trunk vertebra (MGPT-PU 142374).

Description: The perfectly preserved right maxilla MGPT-PU 142385 (Fig. 2(D)) is 13.5 mm long and shows 29 teeth positions, 22 of which host elongated, tightly-spaced pleurodont teeth. The facial process is tall and externally smooth: a marked concavity is present in its anteroventral area. The left quadrate MGPT-PU 142386 is very large, being 8.1 mm tall, and nearly complete (just a small portion of the conch is missing in the area around the squamosal notch). The conch is broadly developed but not as much as in, for example, *Tarentola mauritanica* (Villa et al., 2018: fig. 15J).

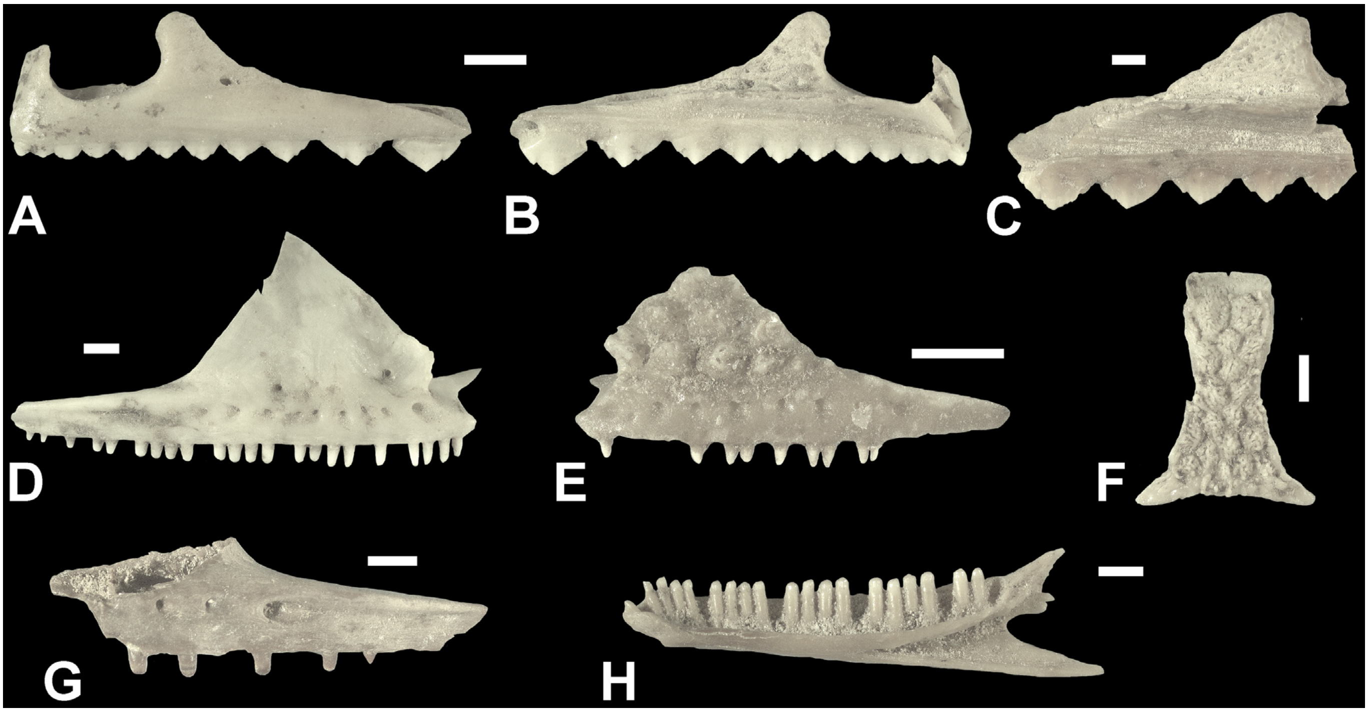

Fig. 2. Lizards from the Holocene of Taiti Cave, Socotra Island. **A-C.** *Chamaeleo monachus*. Left maxilla MGPT-PU 142384 in lateral (A) and medial (B) views; left maxilla MGPT-PU 102206 in medial view (C). **D.** *Haemodracon riebeckii.* Right maxilla MGPT-PU 142385 in lateral view. **E, F.** *Haemodracon trachyrhinus*. Left maxilla MGPT-PU 142388 in lateral view (E); fused frontals MGPT-PU 142387 in dorsal view (F). **G, H.** *Trachylepis socotrana*. Left maxilla MGPT-PU 142378 in lateral view (G); right dentary MGPT-PU 142427 in medial view (H). Scale bars: 1 mm.

The mandibular condyle is divided into two massive portions by a marked concavity. The left dentary MGPT-PU 142379 is complete and 16.9 mm long. The dental shelf, 14.2 mm long, has 30 tooth positions hosting 20 teeth positions. The teeth are morphologically congruent with those of the maxilla, but the tips are somewhat more truncated. The Meckelian canal is closed up to the level of the 25th tooth position. Both the superior and inferior processes are preserved (note that in Villa et al., 2018, they are inverted in fig. 21H). The trunk vertebra MGPT-PU 142374 is the largest amphicoelous vertebra of the whole Taiti Cave sample: its centrum is 4 mm long approximately (the anterior cotyle is slightly eroded). The deeply anteroposteriorly concave ventral surface of the centrum bears a marked sagittal keel with one relatively large foramen on each side.

Remarks: The large size of the skeletal elements here described grants their referral to the largest gekkotan taxon present in Scocotra, *Haemodracon riebeckii*. Even if the whole skull and lower jaw of *H. riebeckii* have been figured by Daza et al. (2017), the detailed morphology of the single skeletal elements is still undescribed. However, the evident concavity at the anteroventral corner of the maxillary facial process of MGPT-PU 142385 seems to be present also in Daza et al. (2017: fig. 4G).

Haemodracon trachyrhinus (Boulenger, 1899)
Fig. 2(E, F)

Material: One left maxilla (MGPT-PU 142388), three fused pairs of frontals (MGPT-PU 142387, 142389, 142404).

Description: The left maxilla MGPT-PU 142388 (Fig. 2(E)) is 4.8 mm long and preserves 24 pleurodont tooth positions, of which nine host a conical tooth provided (at least judging with an optical binocular) by a single cusp. The outer surface of the facial process hosts seven major and three minor tubercles with a bulging, irregular surface. Three fused paired frontals show the same ornamentation of the external surface. MGPT-PU 142387 (Fig. 2(F)) is 5.0 mm long, slightly broader posteriorly (3.9 mm) than anteriorly (1.9 mm), and moderately constricted in the middle (1.4 mm).

Remarks: The specific identification of the material relies on the external sculpturing that, despite being not uncommon in geckos (Glynne et al., 2020), is limited to *H. trachyrhinus* among the Socotran gekkotans (Razzetti et al., 2011). The size and morphology of the available skeletal remains from Taiti Cave is fully congruent with that of the comparative disarticulated skeleton of *H. trachyrhinus* MGPT-MDHC 369.

Gekkota indet.

Material: Two maxillae (MGPT-PU 142391, 142420), ten dentaries (MGPT-PU 142380, 142397, 142421), seven trunk vertebrae (MGPT-PU 142395, 142406, 142415, 142430).

Description and remarks: All the skeletal elements listed above have a general morphology similar to the one reported for *H. riebeckii*, but due their small size they could well belong to other taxa. Noteworthy is that eighteen species of geckos, grouped in three genera, are currently present in Socotra (Razzetti et al., 2011) and their skeletal morphology is largely unexplored. Therefore, all the skeletal element not having a very large size (congruent with *H. riebeckii*) or not showing a peculiar ornamentation (congruent with *H. trachyrhinus*) are referred to Gekkota indet.

Scincomorpha Camp, 1923
Family Scincidae Oppel, 1811
Genus ***Trachylepis*** Fitzinger, 1843
Trachylepis socotrana (Peters, 1882)
Fig. 2(G, H)

Material: One left maxilla (MGPT-PU 142378), three dentaries (MGPT-PU 142377, 142398, 142427).

Description: Few tooth-bearing bones are characterized by pleurodont, cylindrical teeth that are slender and provided with a small labial and a small lingual cusp. If the apex of the tooth is not worn, a light striation can be present on the lingual surface (seen in particular in MGPT-PU 142398 and 142427). The partially preserved left maxilla MGPT-PU 142378 (Fig. 2(G)) preserves the last 15 tooth positions and shows a medially broad palatal shelf. The lateral wall of the posterior process is longitudinally concave. The best-preserved dentary, MGPT-PU 142427 (Fig. 2(H)), is 10.7 mm long, has 25 tooth positions, and is characterized by a Meckelian canal closed up to the 16th tooth position. A central, bifid, posterior processus is present.

Remarks: The general morphology of the teeth and teeth bearing bones is congruent with that of scincid lizards and, more in particular, with that of *Trachylepis aurata* (Linnaeus, 1758) as described and figured by Villa and Delfino (2019). The dentary differs from that of *T. aurata* only for the degree of closure of the Meckelian canal and for the presence of a central posterior process.

The maxilla and the dentaries are here referred to the Socotran endemic species *Trachylepis socotrana* (Peters, 1882) on the basis of their size, significantly larger than that of the only other skink present in Socotra, the small *Hakaria simonyi* (Steindachner, 1899) (Schätti and Desvoignes, 1999). The osteology of both taxa is currently not known.

Non-snake Squamata

Material: One quadrate (MGPT-PU 142407), ten vertebrae (MGPT-PU 102202, 142381, 142382, 142399, 142411, 142412, 142417, 142418), one sacrum (MGPT-PU 102336), five humeri (MGPT-PU 142409–142414), one scapulocoracoid (MGPT-PU 142410), one coxal element (MGPT-PU 142416), nine femora (MGPT-PU 142383, 142403–142408, 142413), one tibia (MGPT-PU 142419).

Description and remarks: The remains here listed likely belong to the above mentioned lizards but they cannot be identified with precision because of their preservation status or because of the absence of comparative information on the skeleton of Socotran taxa. A right dentary with bicuspid teeth (MGPT-PU 102207) from Hoq Cave could belong to a further taxon, the lacertid *Mesalina balfouri* (Blanford, 1881) that represents the only lacertid lizard on the main island of Socotra (Razzetti et al., 2011). No evidence for lacertid lizards has been detected at Taiti Cave.

Serpentes Linnaeus, 1758

Scolecophidia Duméril and Bibron, 1844

Genus ***Xerotyphlops*** Hedges, Marion, Lipp, Marin and Vidal, 2014

Xerotyphlops socotranus (Boulenger, 1889)

Fig. 3(A, B)

Material: Eight trunk vertebrae (MGPT-PU 142392–142394, 142400, 142405).

Description: The largest and best-preserved trunk vertebra, MGPT-PU 142405 (Fig. 3(A, B)), is 3 mm long and wide (distance among the tip of the prezygapophyseal processes) in dorsal view. The broad prezygapophyseal facets have a main axis nearly anteriorly directed (only very little laterally directed) and massive, relatively robust and long processes that are nearly laterally directed (only very little anteriorly directed). The cotyle and the condyle are very small (much smaller than the neural canal) and dorsoventrally compressed. The neural arch is smooth, devoid of neural spine, and posteriorly very much depressed. The centrum is ventrally flat and broad, devoid of hypapophysis. A deep and well-defined groove separates the centrum and the paradiapophyses. The parapophysis and diapophysis are not well defined (they are nearly not separated). There are no parapophyseal processes.

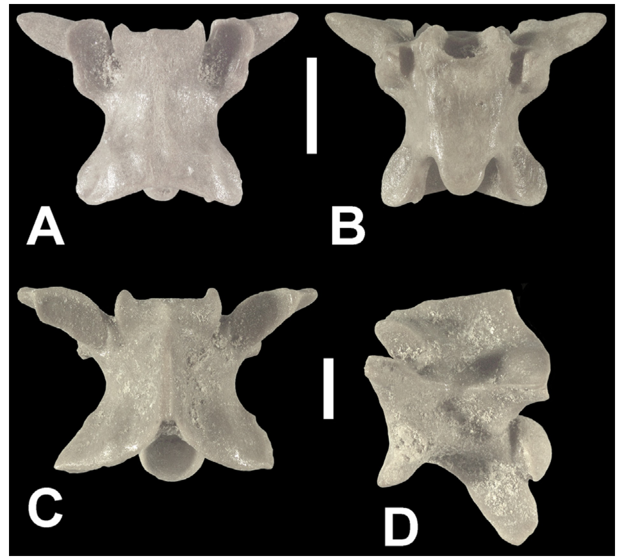

Fig. 3. Snakes from the Holocene of Taiti Cave, Socotra Island. **A, B.** *Xerotyphlops socotranus*. Trunk vertebra MGPT-PU 142405 in dorsal (A) and ventral (B) views. **C-D.** *Ditypophis vivax*. Trunk vertebra MGPT-PU 142390 in dorsal (C) and left lateral (D) views. Scale bars: 1 mm.

Remarks: The dorsoventrally compressed vertebrae with the neural arch devoid of neural spine and the centrum of hypapophyis, but provided with prezygapophyseal processes and zygosphene and zyganthrum, can be referred to scolecophidian snakes (Mead, 2013). Four species of scolecophidians inhabit Socotra, three leptotyphlopids and one typhlopid (Razzetti et al., 2011). The latter is significantly larger in size than the others (Schätti and Desvoignes, 1999). Direct comparison of the Socotran vertebrae with those of a 222 mm long (total length) extant *Xerotyphlops vermicularis* (Merrem, 1820) (MGPT-MDHC 294) from Europe indicate that they are larger than the largest leptotyphlopid from Socotra. Therefore, all the scolecophidian vertebrae can be referred to *Xerotyphlops socotranus* (Boulenger, 1889) on the basis of their relatively large size. A single scolecophidian vertebra (MGPT-PU 142426) comes from Hoq Cave.

Alethinophidia Nopcsa, 1923

Family Pseudoxyrhophiidae Dowling, 1975

Genus ***Ditypophis*** Günther, 1881

Ditypophis vivax Günther, 1881

Fig. 3(C, D)

Material: Four trunk vertebrae (MGPT-PU 142372, 142373, 142376, 142390).

Description: The best preserved trunk vertebra, MGPT-PU 142390 (Fig. 3(C, D)), shares with the other vertebrae the fact of being rather wide (4.9 mm from tip to tip of the prezygapophyseal processes) and anteroposteriorly short (3.0 mm in dorsal view). The neural spine is broken off at its base whereas the anteroposteriorly broad hypapophysis as a damaged tip. The anterolaterally directed prezygapophyseal facets are very long and narrow. The prezygapophyseal processes are comparatively short, apically rounded and laterally directed. The left parapophyseal process (the right one is not preserved) is well developed, apically rounded and anteroventrally directed. The zygosphenal roof is straight in dorsal view (with a distinct convexity on both the lateral edges). The posterior edge of the modestly depressed neural arch is rather straight in posterior view. The fragmentary vertebra MGPT-PU 142373 (mostly represented by the vertebral centrum) fully preserves an hypapophysis characterized by being anteroposteriorly broad (laminar) and distally truncated, with a pointed, slightly bifid, posterior tip.

Remarks: Four procoelous, trunk vertebrae provided with zygosphene and zyganthrum are referred to *D. vivax* on the basis of their strong anteroposterior compression and because of the presence of hypapophysis. In general, their whole morphology is broadly congruent with that of the posterior trunk vertebra of this species figured by Zaher et al. (2019: fig. D). The vertebral morphology of the only other alethinophidian snake from Socotra (Razzetti et al., 2011), *Hemerophis socotrae* (Günther, 1881), is unknown but it is expected that, being a colubrid formerly included in the genera *Zamenis*, *Hemorrois* and *Coluber*, it is characterized by the absence of hypapophysis in trunk vertebrae. Noteworthy is that abundant subrecent vertebral material of *D. vivax* (MGPT-PU 142422; 58 vertebrae) has been collected at Hoq Cave.

Serpentes indet.

Material: One fragmentary vertebra (MGPT-PU 142401), one fragmentary rib (MGPT-PU 142402).

Description and remarks: Few fragmentary elements, likely belonging to *D. vivax*, do not show diagnostic morphological features and are therefore referred to Order rank.

Aves Linnaeus, 1758
Columbiformes Latham, 1790
Family Columbidae Illiger, 1811
Genus ***Spilopelia*** Sundevall, 1873
Spilopelia senegalensis (Linnaeus, 1758)
Fig. 4(B, D, F, I)

Material: Four crania (MGPT-PU 135977, 135978, 135980, 135984), four mandibulae (MGPT-PU 135979, 146143, 146655, 135656); three sterni (MGPT-PU 135974, 135981, 135982), eleven coracoids (MGPT-PU 135860–135863, 135867, 145697, 145859–145862, 146202), ten scapulae (MGPT-PU 135964–135973), 25 humeri (MGPT-PU 135786–135811); 17 ulnae (MGPT-PU 135812–135821, 135823–135826, 135830–135833), nine radii (MGPT-PU 135954–135959, 135961–135963), 14 carpometacarpi (MGPT-PU 135924–135932, 135941–135943, 135949–135951), five phalanges digitis majoris (MGPT-PU 135934, 135935, 135948, 135952, 135953), 26 femora (MGPT-PU 135834–135858, 145626), 28 tibiotarsi (MGPT-PU 135896–135899, 135900–135923), 25 tarsometatarsi (MGPT-PU 135869–135887, 135890–135894, 146654).

Description: All the bones show the characteristics of the Columbidae (Cassoli, 1980; Louchart, 2011) with a rounded cranium with proportionately large orbitae and the rostrum maxillae slightly bent ventrally; the rami of the mandible relatively short and fragile with os dentale bent ventrally in correspondence of the angulus mandibulae which is well pronounced. The sternum shows a carina sterni well developed with pila carinae and apex carinae oriented cranially and spina interna and spina externa both well developed. The coracoid (Fig. 4(B)) shows a wide and deep sulcus m. supracoracoidei and a well-defined impression m. sternocoracoidei. The humerus (Fig. 4(D)) shows the peculiar shape of the Columbidae (Cassoli, 1980) with the prominent and pointed tuberculum dorsale on the crista deltopectoralis. The ulna shows the peculiarly curved diaphysis with the prominent papillae remigales caudales, the cotyla dorsalis flat with the processus cotylaris dorsalis well developed distally, and the incisura tendinosa forming a small crest toward the diaphysis. The radius shows a cotyla humeralis with a square section and a distal end with a flat section with two parallel crests on the dorsal side. The carpometacarpus (Fig. 4(F)) is short with a deep fossa infratrochlearis, pointed processus pisiformis; os metacarpale minus flattened and curved. The femur is straight with the caput femoris not well developed medially and the crista trochanteris well developed. The tibiotarsus is slightly short and curved with the incisura tibialis deeper than the facies articularis medialis and the two condyles of relatively small size and non-tilted medially as in other taxa with a very narrow incisura intercondylaris. The tarsometatarsus (Fig. 4(I)) is short with the typical proximal end with sharp and protruding crista medialis flexoris digitorum longus (Mayr, 2016), deep sulcus flexorius and deep fossa parahypotarsalis. The distal end is characterized by three separate and wide trochleae.

Remarks: *Spilopelia senegalensis* is resident and breeding on Socotra island (Porter and Suleiman, 2013). Any other Western Palaearctic dove of the genus *Streptopelia* has been reported on Socotra, but the direct comparison with the reference material allows to exclude *S. turtur* (Linnaeus, 1758) and *S. orientalis* (Latham, 1790) for their bigger size and to refer the fossil material to *Spilopelia senegalensis*. This taxon is widespread on the island in any kind of habitat and has the widest distribution of any bird species, but it is particularly common in the semi-evergreen woodland of limestone escarpments and sheltered ravines (Porter and Suleiman, 2013), which is one of the habitats in the vicinity of Taiti Cave.

Genus ***Oena*** Swainson, 1837
Oena capensis (Linnaeus, 1766)
Fig. 4(G, J)

Material: One carpometacarpus (MGPT-PU 135929), one tarsometatarsus (MGPT-PU 135895).

Description: The carpometacarpus (Fig. 4(G)) is short with deep fossa infratrochlearis, protruded processus pisiformis, less pointed than in *S. senegalensis*, and pointed processus alularis; the os metacarpale minus highly curved and flattened and the os metacarpale majus stout and curved at the end close to the epiphysis. The tarsometatarsus (Fig. 4(J)) is short with a sulcus flexorius pronounced and sharp along the diaphysis.

Remarks: The very small size of these two remains allow us to refer them to *Oena capensis*, the smallest of the African and Western Palearctic Columbidae. This species is now considered as accidental on Socotra Island (Porter and Suleiman, 2020), but these findings could indicate its more common presence in the past, as the preservation of vagrant individual is only exceptionally documented (Pavia and Bedetti, 2013).

Genus ***Treron*** Vieillot, 1816
Treron waalia (F.A.A. Meyer, 1793)

Material: One femur (MGPT-PU 146649).

Description: The preserved proximal femur shows the crista trochanteris very low and the fossa trochanteris virtually absent.

Remarks: The femur shows the typical morphology of middle-sized Columbidae and the morphology recalls that of *Treron* rather than *Columba*, also following Pavia (2020). *Treron waalia* is a breeding species on Socotra, widespread in the central and oriental part of the island (Porter and Suleiman, 2013).

Caprimulgiformes Ridgway, 1881
Family Apodidae Hartert, 1897
Genus ***Apus*** Scopoli, 1777
Apus sp.
Fig. 4(L, N)

Material: One cranium (MGPT-PU 135975), two sterni (MGPT-PU 135983, 146648), four coracoids (MGPT-PU 135864–135866, 135868), one humerus (MGPT-PU 135807), six ulnae (MGPT-PU 135817, 135822, 135827–135829, 146203), one radius (MGPT-PU 135960), six carpometacarpi (MGPT-PU 102319; 135933;

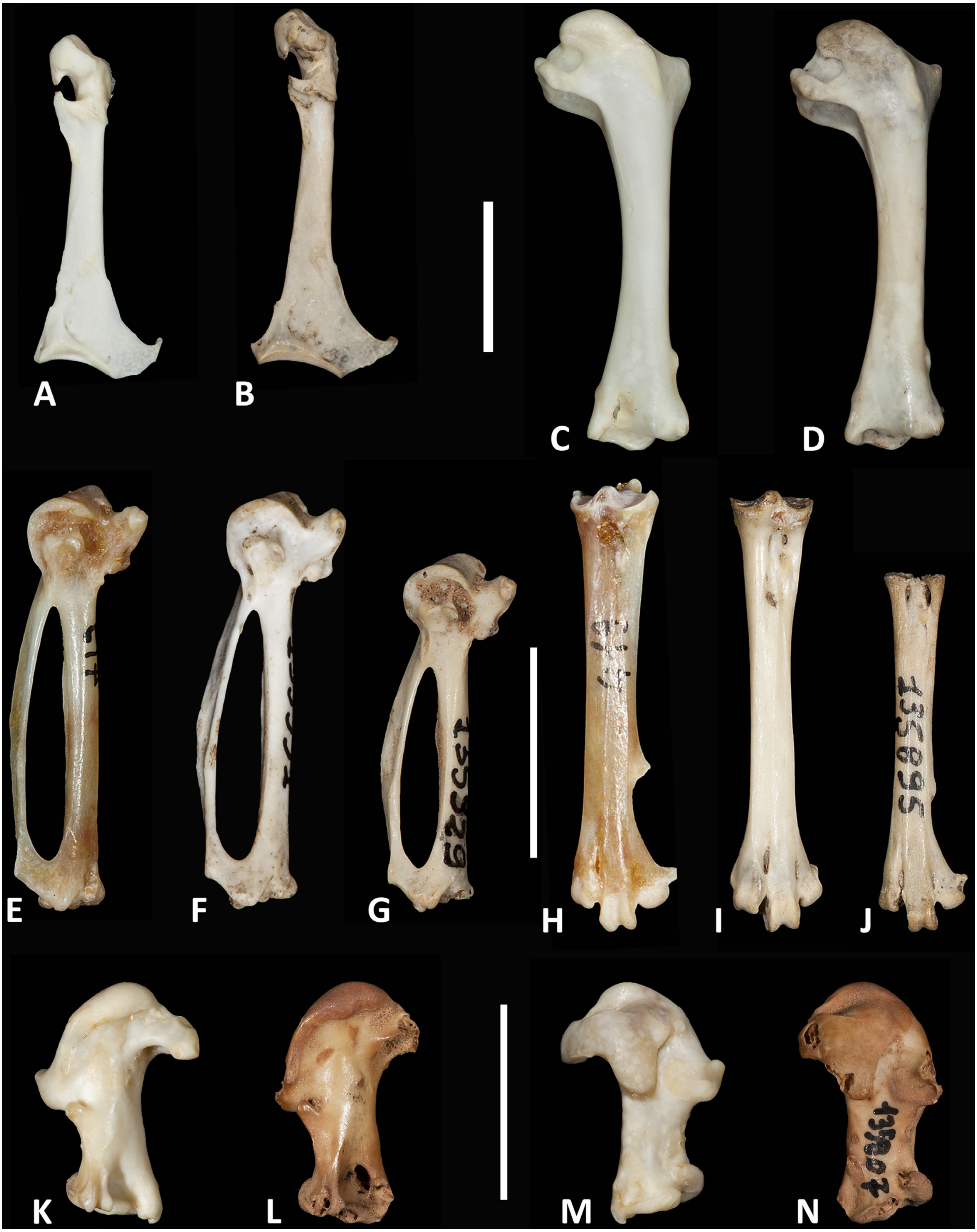

Fig. 4. Birds from the Holocene of Taiti Cave, Socotra Island, compared with recent skeletal elements. **A, C, E, H**. *Spilopelia senegalensis* recent (MGPT-MPOC 419). A: right coracoid in dorsal view; C: right humerus in caudal view; E: reversed right carpometacarpus in ventral view; H: right tarsometatarsus in dorsal view. **B, D, F, I**. *Spilopelia senegalensis* from Taiti Cave. B: right coracoid MGPT-PU 135867 in dorsal view; D: right humerus MGPT-PU 135788 in caudal view; F: left carpometacarpus MGPT-PU 135931 in ventral view; I: right tarsometatarsus MGPT-PU 135869 in dorsal view. **G, J.** *Oena capensis* from Taiti Cave. Left carpometacarpus MGPT-PU 135929 in ventral view (G); right tarsometatarsus MGPT-PU 135895 (J). **K, M**. *Apus pallidus* recent (MGPT-MPOC 1881), left humerus in caudal (K) and ventral (M) views. **L, N**. *Apus* sp. from Taiti Cave, left humerus MGPT-PU 135807 in caudal (L) and ventral (N) views. Scale bars: 10 mm.

135944–135947), 4 phalanges digitis majoris (MGPT-PU 135936–135939), two tarsometatarsi (MGPT-PU 135888, 135889).

Description: The rostrum maxillare is very short followed by a very thin os nasale typical of Apodidae; the sternum shows a pronounced carina sterni; the two spinae interna and externa are indistinguishable and with a weakly developed sulcus carinae; the coracoid is typically sturdy and characterized by a proximal epiphysis with a pointed tuberculum brachiale and a small processus supracoracoidei; the humerus (Fig. 4(L, N)) is very short, with a sulcus ligamenti transversus and impressio coracobrachialis deep and a fossa tricipitalis round and partially pneumatized; the ulna is a strong bone with very pointed olecranon, evident crista intercotylaris which separates cotylae dorsalis and ventralis; the radius is as short as the ulna with a round section; the carpometacarpus is stout with the os metacarpale minus very thin and slightly larger towards the distal part and the processus extensorius pointed and well developed; the tarsometatarsus shows the cotylae medialis and lateralis almost fused to each other, with the crista medialis hypotarsi more pronounced than crista lateralis hypotarsi, a relatively deep sulcus flexorius and the three distal trochleae very close to each other.

Remarks: The bones belong to a small-sized swift of the genus *Apus*, similar in size to both *Apus apus* Linnaeus, 1758 and A. *pallidus* Shelley, 1780 (Fig. 4(K, M)) and bigger than *Apus affinis* (J.E. Gray, 1830) and *A. caffer* (Lichtenstein, 1823). *Apus pallidus* is the closest relative to the Socotran endemic *Apus berliozi* Ripley, 1965, which is slightly bigger than the former on the basis of plumage measurements (Grieve and Kirwan, 2012). The osteology of *A. berliozi* is unknown, and we were unable to examine any skeleton of this species, but the size of the bones seems to exclude their attribution to the Socotran taxon and we prefer to leave them as *Apus* sp.

Order Passeriformes Linnaeus, 1758
Family Laniidae Rafinesque, 1815
Genus ***Lanius*** Linnaeus, 1758
Lanius excubitor Linnaeus, 1758
Fig. 5(B, D)

Material: One mandibula (MGPT-PU 146061), four humeri (MGPT-PU 145113, 145192, 145193, 145275).

Description: The mandible (Fig. 5(B)) shows a ramus straight until the pointed rostrum mandibulae with the os dentale slightly curved ventrally; the humerus (Fig. 5(D)) is characterized by a shallow fossa pneumoanconaea blended with the crus ventrale fossae and a fossa tricipitalis more pronounced and pneumatized.

Remarks: The remains found at Taiti Cave are comparable in morphology with a large species of *Lanius* (Janossy, 1983; Moreno, 1986) and their direct comparison with a skeleton of the endemic *Lanius excubitor uncinatus* Sclater and Hartlaub, 1881 from Socotra (MGPT-MPOC 422; Fig. 5(A, C)) showed no morphological differences, allowing us to refer them to *Lanius excubitor*. On the other hand, we prefer to not consider the subspecific level, given the taxonomic uncertainty of the Great-grey Shrike complex (Kirwan, 2007). Other two *Lanius* species are regularly reported on Socotra Island, *Lanius collurio* Linnaeus, 1758 and *L. isabellinus* Hemprich and Ehrenberg, 1833, both smaller than *L. excubitor*. *Lanius excubitor uncinatus* is a common breeding species on Socotra, with the highest densities in the semi-evergreen woodland of limestone escarpments and sheltered ravines (Porter and Suleiman, 2013).

Family Zosteropidae Bonaparte, 1853
Genus ***Zosterops*** Vigors and Horsfield, 1827
Zosterops abyssinicus (Neumann, 1908)

Material: One cranium (rostrum maxillare MGPT-PU 146171), one mandibula (MGPT-PU 135976), one humerus (MGPT-PU 102315).

Description: The cranium shows a rostrum maxillare very long and pointed, os nasale thin with nostrils of ovoidal shape; the mandible shows a narrow os dentale, pointed and slightly curved ventrally; the humerus shows a proximal epiphysis with a fossa pneumoanconaea less developed and a very deep fossa tricipitalis with a very thin crus dorsale fossae and a sharp crista deltopectoralis.

Remarks: The fossils are indistinguishable in size and morphology from the recent *Zosterops abyssinicus* from Socotra (MGPT-MPOC 731). The species is a fairly widespread breeding bird on Socotra Island, with the higher densities in the semi-evergreen woodland of limestone escarpments and sheltered ravines (Porter and Suleiman, 2013).

Family Muscicapidae Fleming, 1822
Genus ***Oenanthe*** Vieillot, 1816
Oenanthe sp.

Material: Seven humeri (MGPT-PU 102301, 145068, 145087, 145140, 145182, 145183, 145217).

Description: The humerus shows the fossa pneumotricipitalis ventralis deeper than the fossa pneumotricipitalis dorsalis with a well-developed crus dorsale fossae and a crista deltopectoralis short and sharp.

Remarks: The morphology of the humeri is perfectly comparable with the genus *Oenanthe*, also following Janossy (1983), and as confirmed with the direct comparison with recent comparative skeletons. No species of *Oenanthe* breeds in the Socotra archipelago (Porter and Suleiman, 2013), but as many as four species are regular during migration on Socotra Island. For this reason, giving the homogeneous osteological morphology of the various species of *Oenanthe*, we prefer to refer the fossil to generic level only.

Family Sylviidae Vigors, 1825
Sylviidae indet.

Material: Three humeri (MGPT-PU 145096, 145097, 145191).

Description: The humerus shows a fossa pneumotricipitalis dorsalis very shallow and a fossa pneumotricipitalis ventralis very deep, with a short crista deltopectoralis.

Remarks: The morphology of the bones indicates similarity with the Sylviidae s.l. (Janossy, 1983). Given that Socotra hosts two breeding species of this family (*Cisticola haesitatus* Sclater and Hartlaub, 1881, and *C. incanus* Sclater and Hartlaub, 1881) and is a stop-over site for different Palaearctic Sylviidae species during their migration, and taking into account the homogeneous osteological morphology of the groups, we prefer to leave the attribution of these remains to the family level.

Family Nectariniidae Vigors, 1825
Genus ***Chalcomitra*** Reichenbach, 1853
Chalcomitra balfouri (Sclater and Hartlaub, 1881)
Fig. 5(F)

Material: One humerus (MGPT-PU 145318).

Description: The humerus is very small and slender and characterized by the two distinct fossae in the proximal end, separated by the crus dorsale fossae (Fig. 5(F)). The fossa pneumotricipitalis dorsalis is shallow and the fossa pneumotricipitalis ventralis is very deep. The crista deltopectoralis is short and the fossa olecrani deep.

Remarks: The morphology of the fossil remain is indistinguishable from that of the recent *Chalcomitra balfouri* skeleton used for comparison (MGPT-MPOC 423; Fig. 5(E)), so we can refer this spec-

Fig. 5. Birds from the Holocene of Taiti Cave, Socotra Island, compared with recent skeletal elements. **A, C**. *Lanius excubitor uncinatus* recent (MGPT-MPOC 422). Mandibula in dorsal view (A); left humerus in caudal view (C). **B, D**. *Lanius excubitor* from Taiti Cave. Mandibula MGPT-PU 146061 in dorsal view (B); left humerus MGPT-PU 145113 in caudal view (D). **E.** *Chalcomitra balfouri* recent (MGPT-MPOC 423), right humerus in caudal view. **F.** *Chalcomitra balfouri* from Taiti Cave, right humerus MGPT-PU 145318 in caudal view. **G, I, K**. *Passer insularis* recent (MGPT-MPOC 421). Cranium in dorsal view (G); mandibula in dorsal view (I); right humerus in caudal view (K). **H, J, L**. *Passer insularis* from Taiti Cave. Cranium MGPT-PU 146009 in dorsal view (H); mandibula MGPT-PU 146114 in dorsal view (J); right humerus MGPT-PU 145141 in caudal view (L). **M-O.** *Rhynchostruthus socotranus* from Taiti Cave. Cranium MGPT-PU 146147 in dorsal view (M); mandibula MGPT-PU 146092 in dorsal view (N); left humerus MGPT-PU 145114 in caudal view (O). **P, Q.** *Emberiza* sp. from Taiti Cave. Mandibula MGPT-PU 146062 in dorsal view (P); right humerus MGPT-PU 145130 in caudal view (Q). Scale bars: 10 mm.

imen to the Socotran endemic sunbird. This species is widespread on Socotra Island, with higher densities recorded in the semi-evergreen woodland of limestone escarpments and sheltered ravines (Porter and Suleiman, 2013).

Family Passeridae Rafinesque, 1815
Genus ***Passer*** Brisson, 1760

Passer insularis (Sclater and Hartlaub, 1881)
Fig. 5(H, J, L)

Material: 96 crania (MGPT-PU 102277, 102278, 145650–145670, 145673–145679, 145681–145692, 146001–146046, 146144–146146, 146148, 146173–146176, 146198, 146642); 164 mandibulae (MGPT-PU 102274, 102276, 102280–102284, 146050, 146051, 146063–146091, 146093–146102, 146104–

146142, 146149–146170, 146172, 146177–197, 146643–646); 290 humeri (MGPT-PU 102298, 102300, 102302–123312, 135987–135991, 135994–135996, 145001–145009, 145012–145027, 145029–145031; 145033, 145034, 145036–145054, 145056–145067, 145069–145076, 145078–145080, 145082, 145084–145086, 145088, 145090, 145091, 145093–145095, 145101, 145103, 145104, 145106, 145116–145119, 145121–145129, 145131, 145133–145135, 145137, 145138, 145141, 145143, 145144, 145146, 145148–145160, 145162, 145163, 145165, 145166, 145168–145171, 145173, 145175–145180, 145184–145190, 145195–145199, 145201, 145202, 145204–145207, 145214–145216, 145218–145221, 145223, 145230, 145232, 145236–145239, 145247, 145250–145254, 145256–145260, 145262, 145264, 145266, 145267, 145269, 145270, 145276, 145282–145287, 145290–145294, 145296–145313, 145315–145317, 145319, 145321, 145323).

Description: The cranium (Fig. 5(H)) shows the general shape of granivorous species, with a conical bill, the rostrum maxillare is turned ventrally, the os nasare is short and wide, while the processus postorbitalis is pointed and thin, the mandible (Fig. 5(J)) shows a deep rostrum mandibulae turned ventrally as the rostrum maxillare and a processus mandibulae pointed and long; the humerus (Fig. 5(L)) shows two distinct fossae of almost the same size and depth, even if the fossa pneumotricipitalis dorsalis is narrower than the fossa pneumotricipitalis ventralis with a thin crus ventrale fossae to separate the two fossae and a crista deltopectoralis sharp with a pointed tip at the end.

Remarks: The fossils are morphologically very similar to the various *Passer* species examined and almost indistinguishable from the recent skeleton of *Passer insularis* examined (MGPT-MPOC 421; Fig. 5(G, I, K)). *P. insularis* is an endemic and very common breeding species on Socotra Island where it occupies a great variety of habitats, from anthropic settlements to semi-arid shrubs, with the highest densities in the open and woody-based herb communities on the limestone plateau (Porter and Suleiman, 2013).

Family Fringillidae Leach, 1820
Genus ***Rhynchostruthus*** Sclater and Hartlaub, 1881
Rhynchostruthus socotranus Sclater and Hartlaub, 1881

Material: Two crania (MGPT-PU 146147, 146641) three mandibulae (MGPT-PU 146092, 146103, 146640), nine humeri (MGPT-PU 135985, 145114, 145115, 145145, 145167, 145194, 145248, 145277, 145279).

Description: The cranium (Fig. 5(M)) shows a wide rostrum maxillare and a stout os nasale, the mandible (Fig. 5(N)) has a wide rostrum mandibulae, a flat cotyla lateralis, a pointed processus mandibulae medialis, and only the fenestra rostrum mandibulae is present; the humerus (Fig. 5(O)) is larger than in *Passer insularis* even if they are overall similar, also because they belong to the same morphological class (Janossy, 1983).

Remarks: The morphology of the cranium and particularly of the bill clearly recalls the granivorous birds and it is overall similar to European Greenfinch *Chloris chloris* (Linnaeus, 1758), but the fossils are bigger and stouter. The size of the humerus is comparable with that of *Coccothraustes coccothraustes* (Linnaeus, 1758), which is very close in size to *R. socotranus*. The species is endemic and fairly common on Socotra, where lives over almost all the island, but related to trees, with higher densities in the submontane shrubland on the slopes and cliffs of the granite mountains.

Family Emberizidae Vigors, 1831
Genus ***Emberiza*** Linnaeus, 1758
Emberiza sp.
Fig. 5(P, Q)

Material: Two mandibulae (MGPT-PU 102285, 146062), 18 humeri (MGPT-PU 102313, 135992, 145032, 145055, 145081, 145083, 145130, 145142, 145147, 145164, 145174, 145181, 145231, 145240, 145242, 145261, 145265, 145280).

Description: In the mandible (Fig. 5(P)) the os dentale is typically very curved ventrally and the rostrum mandibulae moderately wide but weak; the humerus (Fig. 5(Q)) is small with a broad proximal epiphysis in which the two fossae pneumotricipitales are not separated by the crus dorsale fossae.

Remarks: The morphology is consistent with the genus *Emberiza*, compared with the reference specimens of Western Palearctic species. Socotra hosts resident (*E. tahapisi* Smith, 1836 and *E. socotrana* (Ogilvie-Grant and Forbes, 1899)) and migrant Emberizidae thus, giving the unavailability of skeletal specimens of the resident species and the osteological homogeneity of the mid-sized Emberizidae, we prefer to leave them as *Emberiza* sp.

Mammalia Linnaeus, 1758
Rodentia Bodwich, 1821
Family Muridae Illiger, 1811
Genus ***Rattus*** Fischer, 1803
Rattus norvegicus Berkenhout, 1769

Material: Three crania (MGPT-PU 147047-049), 33 hemimandibulae (MGPT-PU 147056-089).

Description: The skull (Fig. 6(A, B)) is large (condylobasal length > 40 mm), and the first upper molar has 5 roots. The skull is elongated, with a species-specific forward narrowing of the parietal ridges, and has a rectangular profile. In the similar black rat *Rattus rattus*, the skull is rounded and has an oval profile (Amori et al., 2008; Paolucci and Bon, 2022).

Remarks: Both *Rattus rattus* (Linnaeus, 1758) and *Rattus norvegicus* are known to occur in Socotra (Suleiman and Taleb, 2010), but the former has not been detected in any owl pellet analyzed in this work.

Genus ***Mus*** Clerck, 1757
Mus domesticus Shwarz and Shwarz, 1943
Fig. 6(D, E)

Material: Two crania (MGPT-PU 147050, 147051), eleven hemimandibulae (MGPT-PU 147090-100).

Description: The skull is small (condylobasal length < 25 mm), and the first upper molar has 3 roots. The upper incisors have a characteristic notch on their back portion (Amori et al., 2008; Paolucci and Bon, 2022).

Remarks: Genetic analyses from samples from Socotra confirmed that the species occurring on this archipelago is *M. domesticus* rather than *M. musculus* Linnaeus, 1758 (Macholàn et al., 2012).

Eulipotyphla Waddell, Okada and Hasegawa, 1999
Family Soricidae Fischer, 1814
Genus ***Suncus*** Ehrenberg, 1832
Suncus madagascariensis (Coquerel, 1848)
Fig. 7(G, H)

Material: Two hemimandibulae (MGPT-PU 147101, 147102).

Description: The two hemimandibulae (Fig. 7(G, H)) show the typical Soricidae features, and their very small size (<8 mm) allows to refer them to *Suncus madagascariensis,* the only Soricidae found on Socotra (Benda et al., 2017).

Remarks: Previously identified as *Suncus etruscus* (Savi, 1822), the Socotran pigmy shrew belongs to *Suncus madagascariensis* species, which is an alien taxon in this archipelago, spread by human activities across the Indian Ocean (Benda et al., 2017).

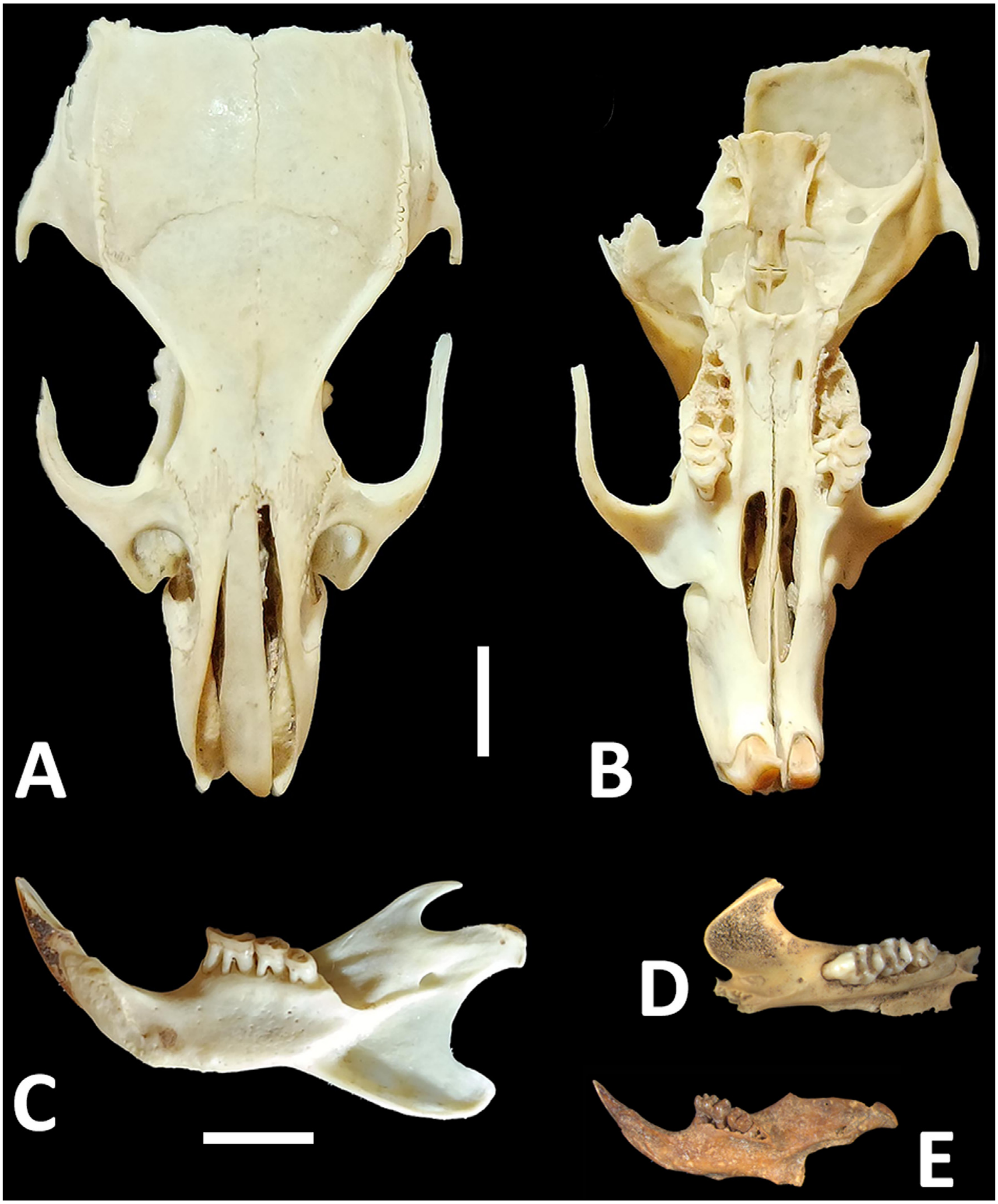

Fig. 6. Mammals from the Holocene of Taiti Cave, Socotra Island. **A-C.** *Rattus norvegicus*. Cranium MGPT-PU 147047 in dorsal view (A); cranium MGPT-PU 147049 in ventral view (B); right hemimandibula MGPT-PU 147057 in mesial view (C). **D, E.** *Mus domesticus*. Right hemimandibula MGPT-PU 147092 in mesial view (D); right maxilla MGPT-PU 147050 in ventral view (E). Scale bars: 5 mm.

Chiroptera Blumenbach, 1779
Family Rhinopomatidae Nowak, 1991
Genus ***Rhinopoma*** Geoffroy, 1818
Rhinopoma cystops Thomas, 1903
Fig. 7(E, F)

Material: Two crania (MGPT-PU 147052, 147053), twelve hemimandibulae (MGPT-PU 147103-114).

Description: Condylar length of mandibles > 10 mm. The palatal incision is broad and U-shaped, whereas dentition is robust, with all tooth elements in tight contact. Coronoid process of the mandible remarkably higher than tooth cusps.

Remarks: This species is the most widespread bat species of Socotra Island, including deserts and dry steppes, mostly roosting in underground caves (Benda et al., 2017).

Family Vespertilionidae Gray 1821
Genus ***Hypsugo*** Kolenati, 1856
Hypsugo lanzai Benda, Al-Jumaily, Reiter and Nasher, 2011.
Fig. 7(A, B)

Material: Six hemimandibulae (MGPT-PU 147115-120).

Description: Mandibles (Fig. 7(A, B)) are very small, <9 mm. Small unicuspid teeth. Coronoid process of the mandible slightly

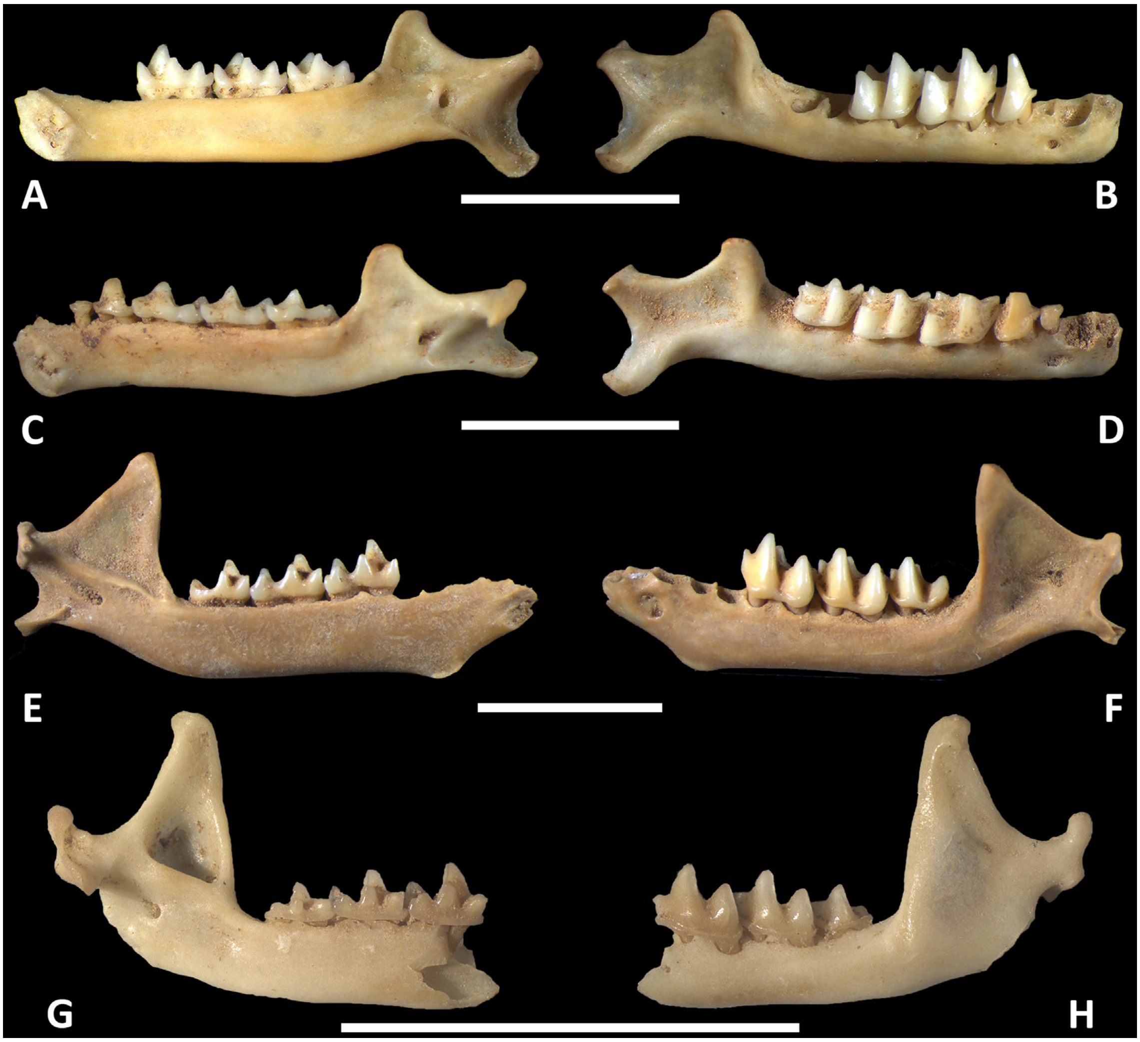

Fig. 7. Mammals from the Holocene of Taiti Cave, Socotra Island. **A, B.** *Hypsugo lanzai*, right hemimandibula MGPT-PU 147115 in mesial (A) and labial (B) views. **C, D.** *Rhinolophus clivosus*, right hemimandibula MGPT-PU 147121 in mesial (C) and labial (D) views. **E, F.** *Rhinopoma cystops*, left hemimandibula MGPT-PU 147104 in mesial (E) and labial (F) views. **G, H.** *Suncus madagascariensis*, left hemimandibula MGPT-PU 147101 in mesial (G) and labial (H) views. Scale bars: 5 mm.

higher than the highest tooth cusp, low relatively to condylar length of mandibles.

Remarks: This species is endemic to Socotra Island, where it replaces *H. ariel* Thomas, 1904, which occurs on the mainland (Benda et al., 2011, 2017).

Family Rhinolophidae Gray, 1825
Genus ***Rhinolophus*** Gray, 1825
Rhinolophus clivosus Cretzschmar, 1828.
Fig. 7(C, D)

Material: Two crania (MGPT-PU 147054, 147055), four hemimandibulae (MGPT-PU 147121-124).

Description: Skulls show an evident prefrontal bulge, premaxillary bones with incisors are well-separated from maxillary bones, as in other species of the same genus (Lanza, 2012; Paolucci and Bon, 2022). Condylar length of mandibles > 10 mm. Coronoid process of the mandible slightly higher than the highest tooth cusp.

Remarks: This species is widely distributed in the Maghreb and in the Middle East, also including several insular populations roosting in caves and buildings (Benda et al., 2017). The genetic divergence of the Socotran populations from the mainland ones suggests an old colonization (Benda et al., 2017).

4. Discussion

The majority of the vertebrate remains collected at the Taiti Cave were found in an accumulation of owl pellets embedded in a sandy dune in the main cavity of the cave. The assemblage includes *Rattus* and *Mus*, thus it was generated after the early colonization of Socotra Island linked to the early spread of anatomically modern humans out of Africa (Černý et al., 2009). The sand dune in which the fossils were embedded is not active as the large sand dunes on the northern coast of the island, suggesting a long lasting of this deposit inside Taiti cave. We thus hypothesize a non-recent Holocene age for the deposit, even if no absolute dating is available for the moment.

Most of the vertebrate remains were already isolated in the sandy matrix, while some pellets were still recognizable as dense sets of bones. It was not possible to estimate the number of sampled pellets, even roughly, but we collected and analyzed around five cubic decimeters, which represent only a part of the available fossiliferous deposit. The bones are well preserved, with scarce evidence of digestion, if any, and the faunal composition is notably diverse, with birds the commonest taxon.

Pellets are the indigestible prey remains ejected by larger predators and accumulated in favored eating places, in regular roosts and nest sites. Pellet accumulators can be identified through the detection of some diagnostic aspects such as the species composition of the assemblage, the size distribution of preys, and the peculiar modifications of their bones and teeth (Andrews, 1990). Predators always modify the bones and teeth by feeding activities and digestive process. Diurnal raptors dismember their preys before eating them and have got a more efficient digestion; consequently, they produce compact pellets with highly digested and often broken bones. In contrast, owls usually swallow their prey entire, this entails a pellet more reach in bones and teeth but less interested by digestion processes. Owls can produce a different number of pellets in a day. *Tyto alba* is among the most efficient accumulators of pellets, as this opportunistic predator captures preys in proportion to the prey's availability and vulnerability, so that its pellet assemblages provide a precise picture of the small vertebrate diversity of the area both in terms of species number and relative abundance of the various taxa (Andrews, 1990; Roulin, 2020). For this reason, the studies of the pellets are useful because they provide information about small vertebrate species occurrences in the studied area, as well as the extent of bone modifications after the regurgitation process (Rey-Rodríguez et al., 2019).

The type and location of pellet accumulation and the conservation status of the vertebrate remains indicate that the Taiti Cave deposit derived from a pellet accumulation of a mid-sized owl, as the abundance of bird remains exclude the small *Otus socotranus* (Ogilvie-Grant and Forbes, 1899) as accumulator agent. *Otus socotranus* is an endemic species (Pons et al., 2013) and the only breeding owl on Socotra Island (Porter and Suleiman, 2013); no other large owl species are present today on the island (Kirwan, 1998), with the exception of vagrant *Asio flammeus* (Pontoppidan, 1763). This latter species makes temporary roost, even during migration, but they are normally used for few days and never located in caves. The prey diversity observed from the fossils reported here and their almost perfect preservation agree with the hypothesis of an accumulation made by the barn owl (*Tyto alba*) (Andrews, 1990; Rey-Rodríguez et al., 2019), which was never recorded on Socotra Islands despite their bird fauna is well known.

Field studies on small vertebrate species, particularly on small mammals, in the Socotran Archipelago are still lacking. Nevertheless, our work provides support to the definition of the barn owl as a non-selective predator, particularly in island ecosystems (cf. Janžekovič and Klenovšek, 2020; Viganò et al., 2020). Great plasticity in the diet of the barn owl has been reported by several studies (Janžekovič and Klenovšek, 2020; Romano et al., 2020). Repeated studies in the same locality may provide useful information on prey population trends and their local environmental status (Romano et al., 2020; Saufi et al., 2020). This would be particularly important for a rare bat species endemic to Socotra, i.e., *Hypsugo lanzai* (Benda et al., 2011, 2017). Thus, also a study on potential prey densities in Socotra Island should be conducted to determine prey selection.

Most of the recognized vertebrate species found at Taiti Cave currently live around the cave and have the highest densities in the habitats surrounding the cave (Porter and Suleiman, 2013; Razzetti et al., 2011). This pattern is fully consistent with the accumulation made by *Tyto alba*, which normally has a limited hunting range and represents an opportunistic feeder rather than a specialized hunter, such as *Asio flammeus*, which is only recorded as a vagrant on Socotra Island (Porter and Suleiman, 2020).

The hypothesis that the Taiti Cave vertebrate accumulation was generated after the hunting activity of *Tyto alba* and, more generally, the presence of a now extinct population of barn owls on Socotra Island is also corroborated by a beak fragment found in Hoq cave, which belongs to *Tyto* (Fig. 8(A, C)), and here referred to *Tyto alba* because it is almost indistinguishable from the recent *Tyto alba* used for comparison (Fig. 8(B, D)), except for minor differences attributed to individual variation. This fragment has been found together with other vertebrate remains (including all the taxa described for Taiti Cave with the addition of *Mesalina balfouri*, *Anas* sp., *Puffinus persicus*, an indeterminate Scolopacidae, and *Coracias garrulus*) in the main entrance of the Hoq cave, a perfectly suitable location for a barn owl. Barn owls, even if they are mostly sedentary species, are very commonly found on islands, even on remote ones (Louchart, 2005), where they can rapidly become endemic taxa, sometimes of very big size (Ballmann, 1973; Pavia, 2004). In the case of Socotra, the number of *Tyto alba* was probably never big enough to establish a stable population or they probably became extinct in a short time after the colonization of the island.

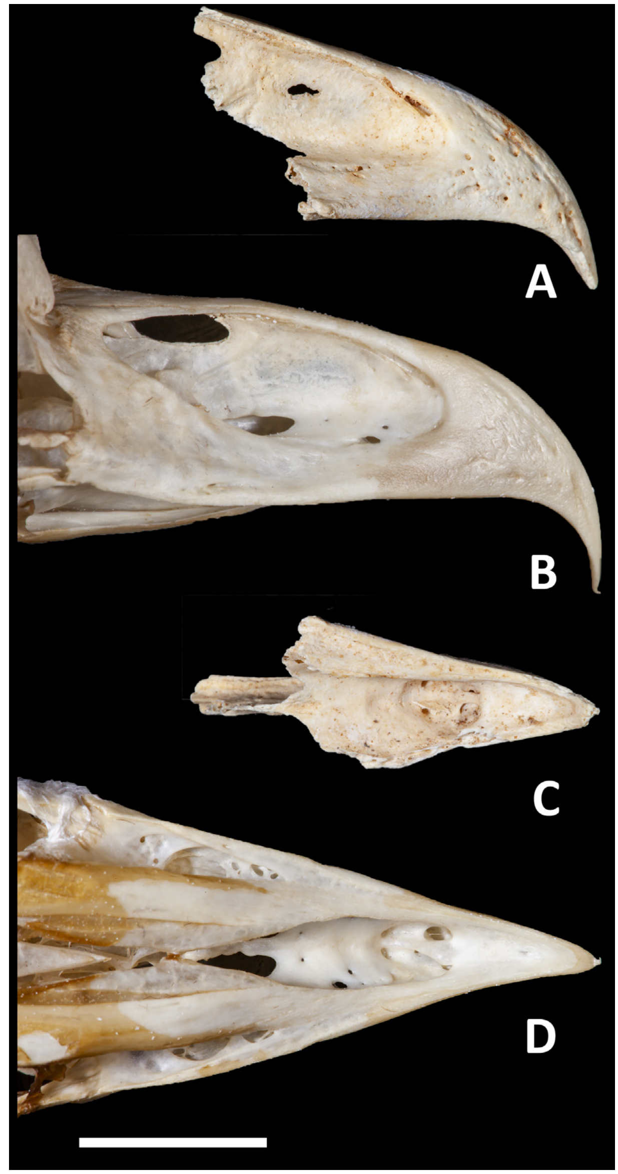

Fig. 8. Fragmentary maxilla of *Tyto alba* from Hoq Cave, Socotra Island (MGPT-PU 102118; **A, C**) compared with a skull of a recent *Tyto alba* (MGPT-MPOC 1842; **B, D**). Scale bar: 10 mm.

5. Conclusions

The fossil vertebrates from Taiti Cave described herein, together with the beak fragment found at Hoq Cave, provide evidence of the occurrence of *Tyto alba* on Socotra Island during the Holocene and represent the first evidence of this species on the island (Porter and

Suleiman, 2013; Porter and Suleiman, 2020). In fact, despite the numerous bird surveys and birding activities on Socotra Island in the last two centuries, no data on the occurrence of this species have been recorded. As the possibility of preservation of fossil remains is quite low even in suitable places such as caves, the presence of skeletal remains and pellets accumulation probably attest to the presence in early historical time of a now extinct population of this species. During our surveys, we visited a small number of caves and cavities, and we did not find any other direct or indirect evidence of the presence of *Tyto alba* or any fossil vertebrate accumulation, but more specific researches in the numerous caves and other suitable locations remain necessary in order to find additional evidence of the presence of *Tyto alba* on Socotra Island and to better understand the history of this peopling and the time of its extinction.

Data availability

Data will be made available on request.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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