# New Miocene Sulid Birds from Peru and Considerations on their Neogene Fossil Record in the Eastern Pacific Ocean

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Source: Acta Palaeontologica Polonica, 61(2) : 417-427

Published By: Institute of Paleobiology, Polish Academy of Sciences

URL: https://doi.org/10.4202/app.00170.2015

# New Miocene sulid birds from Peru and considerations on their Neogene fossil record in the Eastern Pacific Ocean

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Stucchi, M., Varas-Malca, R.M., and Urbina-Schmitt, M. 2016. New Miocene sulid birds from Peru and considerations on their Neogene fossil record in the Eastern Pacific Ocean. *Acta Palaeontologica Polonica* 61 (2): 417–427.

Boobies and gannets (family Sulidae) are the most specialized plunge divers among seabirds. Their fossil record along the Pacific coast of South America extends to the early Middle Miocene. Here we describe three new species of sulids: *Sula brandi* sp. nov., *Sula figueroae* sp. nov., and *Ramphastosula aguirrei* sp. nov., from the early Late Miocene of the Pisco Formation (Peru). Two of them are relatives of the living genus *Sula*, which represents medium and large-sized boobies. A new species of the extinct genus *Ramphastosula* is also described, adding to the discussion of possible alternative feeding strategies among sulids. The fossil record suggests that sympatric sulids exhibit different body sizes at least since the Oligocene epoch, a strategy related with resource partitioning. Furthermore, we find current analysis and knowledge of the fossil record unsuitable to evaluate properly seabird diversity changes through time.

Key words: Aves, Pelecaniformes, Sulidae, *Sula*, *Ramphastosula*, seabird evolution, Miocene, Peru.

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Received 24 April 2015, accepted 16 September 2015, available online 12 October 2015.

## Introduction

The family Sulidae currently includes three genera of medium-sized, strictly marine birds of pantropical distribution: *Papasula* (the Abbott's booby), *Sula* (other boobies) and *Morus* (gannets). They are highly specialized for plunge diving to catch fish, usually dropping from high altitudes (40–100 m) and reaching depths up to 8 meters below the water surface (Nelson 1979; Stucchi 2013). In South America, *Sula* is the dominant genus on the Pacific coast being particularly diverse though the west side, whereas *Morus* is restricted to southwestern South America and is completely absent in the East.

The Pacific coast of South America has yielded the most abundant and extensive fossil record of sulids in the Southern Hemisphere, from the Middle Miocene (Stucchi and DeVries 2003) to the Recent, recovered almost exclusively from the Late Miocene beds of the Bahía Inglesa Formation (northern Chile; Walsh and Hume 2001; Chávez-Hoffmeister 2007, 2008) and the Pisco Formation (Southwestern Peru; Stucchi 2003, Stucchi and Urbina 2004). In contrast to the relatively scarce Chilean fossil record, sulids are the most abundant birds in the Pisco Formation, and also the most diverse with at least three described boobies, one gannet (Stucchi 2003) and the extinct genus *Ramphastosula* (Stucchi and Urbina 2004). Furthermore, a high diversity of Miocene species has also been observed in marine outcrops off the northern Pacific Ocean, in which up to six species are recognized from California, USA (Stucchi 2003; Warheit 1992; see Table 1).

Here, we describe two new species of *Sula* along with a new species of the extinct genus *Ramphastosula*, all from Late Miocene localities of the Pisco Formation, Peru (Fig. 1). Additionally, we analyze the diversity of sulids from the Eastern Pacific Ocean over the course of the Neogene. *Sula* is diagnosed osteologically following the works of Tets et al. (1988), and Stucchi (2003; 2013), which describe the differences among *Sula*, *Morus*, and *Papasula*, and within the genus *Sula* (Stucchi 2013).

For comparative purposes we assigned species to categories as follows: "small-sized boobies" for *S. sula*; "medium-sized boobies" for *S. variegata*, *S. leucogaster*, and *S. nebouxii*; and "large-sized boobies" for *S. dactylatra*, *S. granti*, and *S. tasmani* (sensu Tets et al. 1988). Anatomical terminology follows Howard (1980). All materials were collected by one of the authors (MU-S) and are permanently

*Acta Palaeontol. Pol.* 61 (2): 417–427, 2016 http://dx.doi.org/10.4202/app.00170.2015

Table 1. List of the described species of the family Sulidae showing their geological age and geographical distribution. * Stucchi (2003) proposed nomina nuda for these species on the basis of classical morphometrical analysis; bold, species described in this study.

| Species | Miocene | | | Pliocene | | Pleistocene | Recent-extinct | Geographical region | Locality |
|---|---|---|---|---|---|---|---|---|---|
| | Early | Middle | Late | Early | Late | | | | |
| *Sula universitatis* Brodkorb, 1963* | × | | | | | | | Western Atlantic Ocean | Florida, USA |
| *Morus loxostylus* (Cope, 1871) | × | × | | | | | | Western Atlantic Ocean | Maryland, USA |
| *Morus vagabundus* Wetmore, 1930 | | × | | | | | | Northeastern Pacific Ocean | California, USA |
| *Morus avitus* (Wetmore, 1938) | | × | | | | | | Western Atlantic Ocean | Maryland, USA |
| *Morus pygmaea* (Milne-Edwards, 1874) | | × | | | | | | Western Atlantic Ocean | France |
| *Sarmatosula dobrogensis* (Grigorescu and Kessler, 1977) | | × | | | | | | Paratethys | Romania |
| *Morus olsoni* (Grigorescu and Kessler, 1988) | | × | | | | | | Paratethys | Romania |
| ***Sula brandi* sp. nov.** | | | × | | | | | Southeastern Pacific Ocean | Peru |
| ***Sula figueroae* sp. nov.** | | | × | | | | | Southeastern Pacific Ocean | Peru |
| *Morus willetti* (Miller, 1925) | | × | × | | | | | Northeastern Pacific Ocean | California, USA |
| *Sula pohli* Howard, 1958 | | × | × | | | | | Northeastern Pacific Ocean | California, USA |
| *Morus lompocanus* (Miller, 1925) | | | × | | | | | Northeastern Pacific Ocean | California, USA |
| *Morus media* (Miller, 1925) | | | × | | | | | Northeastern Pacific Ocean | California, USA |
| *Morus stocktoni* (Miller, 1935) | | | × | | | | | Northeastern Pacific Ocean | California, USA |
| *Morus magnus* Howard, 1978 | | | × | | | | | Northeastern Pacific Ocean | California, USA |
| *Sula sulita* Stucchi, 2003 | | | × | | | | | Southeastern Pacific Ocean | Peru |
| *Sula* aff. *variegata* (sensu Stucchi 2003) | | | × | | | | | Southeastern Pacific Ocean | Peru |
| *Morus peruvianus* Stucchi, 2003 | | | × | | | | | Southeastern Pacific Ocean | Peru |
| *Sula magna* Stucchi, 2003 | | | × | × | | | | Southeastern Pacific Ocean | Peru |
| *Sula guano* Brodkorb, 1955* | | | × | × | | | | Western Atlantic Ocean | Florida, USA |
| *Sula phosphata* Brodkorb, 1955* | | | × | × | | | | Western Atlantic Ocean | Florida, USA |
| *Ramphastosula ramirezi* Stucchi and Urbina, 2004 | | | | × | | | | Southeastern Pacific Ocean | Peru |
| ***Ramphastosula aguirrei* sp. nov.** | | | | × | | | | Southeastern Pacific Ocean | Peru |
| *Morus peninsularis* Brodkorb, 1955 | | | | × | | | | Western Atlantic Ocean | Florida, USA |
| *Bimbisula melanodactylus* Benson and Erickson, 2013 | | | | × | × | | | Western Atlantic Ocean | South Carolina, USA |
| *Morus humeralis* (Miller and Bowman, 1958) | | | | | × | | | Northeastern Pacific Ocean | California, USA |
| *Morus recentior* Howard, 1949 | | | | | × | | | Northeastern Pacific Ocean | California, USA |
| *Sula clarki* Chandler, 1990* | | | | | × | | | Northeastern Pacific Ocean | California, USA |
| *Morus reyanus* Howard, 1936 | | | | | | × | | Northeastern Pacific Ocean | California, USA |
| *Sula tasmani* Tets, Meredith, Fullagar, and Davidson, 1988 | | | | | | | × | Southwestern Pacific Ocean | Australia |

stored at the Museo de Historia Natural "Javier Prado" of the Universidad Nacional Mayor de San Marcos (Lima, Peru). The age of the Pisco Formation localities follows Ehret et al. (2012).

*Institutional abbreviations*.—MUSM, Museo de Historia Natural "Javier Prado", Universidad Nacional Mayor de San Marcos, Lima, Peru; USNM, National Museum of Natural History, Smithsonian Institution, Washington DC, USA.

*Nomenclatural acts*.—The electronic edition of this article conforms to the requirements of the amended International Code of Zoological Nomenclature, and hence the new names contained herein are available under that Code from the electronic edition of this article. This published work and the nomenclatural acts it contains have been registered in ZooBank. The ZooBank LSID (Life Science Identifier) for this publication is: urn: lsid: zoobank.org: pub: 12E70E13-D7F9-43BB-A388-6A93FF0E4A52.

The electronic edition of this work was published in a journal with an eISSN 1732-2421, and has been archived and is available from the following digital repository: http://www.app.pan.pl/article/item/app001702015.html

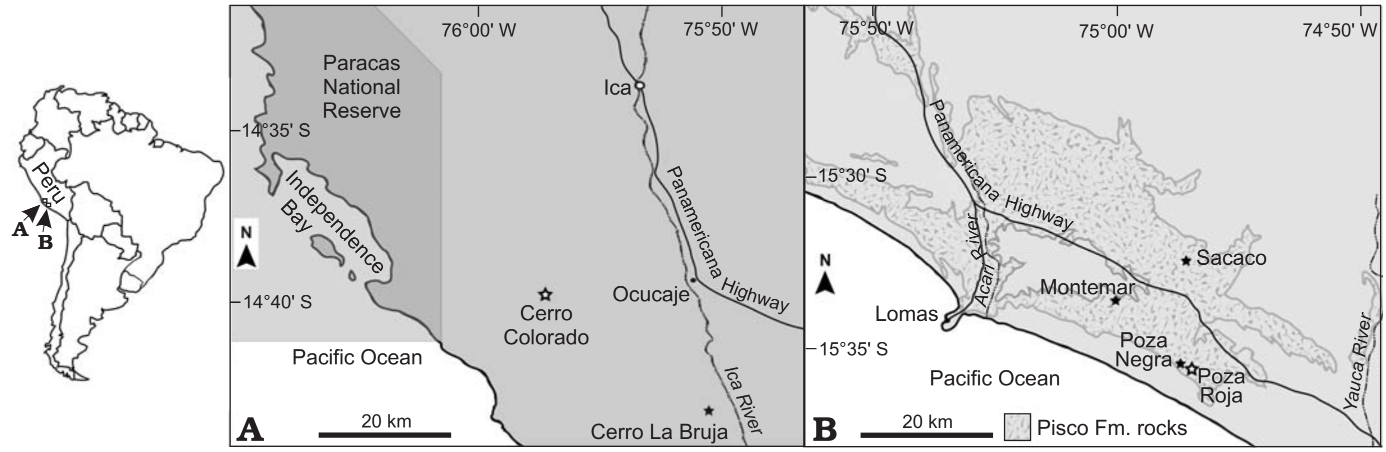

Fig. 1. Maps of the Ocucaje (**A**) and Sacaco (**B**, modified from Brand 2001) areas, southestern Peru, indicating the type localities of fossil sulids described in this paper.

# Systematic palaeontology

## Aves Linnaeus, 1758

## Sulidae Reichenbach, 1849

## Genus *Sula* Brisson, 1760

*Type species*: *Sula sula* (Linnaeus, 1766) or *Sula leucogaster* (Boddaert 1783), both Recent, no subsequent designation.

*Remarks*.—Generic definition follows Tets et al. (1988) and Stucchi (2003, 2013).

### *Sula brandi* sp. nov.

Fig. 2.

*ZooBank LSID*: urn:lsid:zoobank.org:act:B338FEDC-FDB1-4C17-88DB-628776BCA613

*Etymology*: In honor to Leonard Brand (Loma Linda University, USA) for his important contributions to Peruvian vertebrate paleontology, and to the understanding of the geology, stratigraphy, and taphonomic processes of the Pisco Formation.

*Holotype*: MUSM 2497; neurocranium lacking interorbital septum, lacrimals, palatines, pterygoids, jugals, quadrates, and right quadratojugal. Proximal portion of the beak, including most of the right dentary and angular.

*Type locality*: MUSM 2497 was collected from the Cerro Colorado locality (CCO), Pisco Formation, ~23 km west of Ocucaje District, Ica, Peru (Fig. 1A). Coordinates: 14°21’37.90” S, 75°53’17.90” W. The specimen (field number A3 of Bianucci et al. 2015) was found 1–2 km southwest of Cerro Colorado (Colorado hill), between the Wari and Paracas marker beds of its lower allomember (sensu Di Celma et al. 2015). The level from which the sulids were recovered (about 60 m of the stratigraphic column) is the second most fossiliferous in terms of quantity and species diversity, having produced more than 50 specimens, among them osteichthyans, elasmobranchs (myliobatids, *Carcharocles*, *Cosmopolitodus*), long-snouted crocodylians, delphinidans (the pontoporiid *Brachydelphis*, indeterminate delphinidans), ziphiids (*Messapicetus*), balaenopteroideans, cetotheriids, and physeteroideans (cf. *Acrophyseter*) (see Bianucci et al. 2015).

*Type horizon*: The age of this locality has been estimated according to the presence of the arcid bivalve *Anadara sechurana* in late Middle Miocene (ca. 12–13 Ma; Lambert et al. 2010). However, due to the occurrence of early Late Miocene diatoms *Denticulopsis hudstedtii* and *Lythodesmium reynoldsii* (9.9–8.9 Ma, Tortonian; Barron 2003) in the referred level, the age is younger than previously thought (see Di Celma et al. 2015). Thus, it is correlated with El Jahuay level (9.95 Ma; Muizon and Bellon 1986) and Montemar Norte (about 10 Ma; Stucchi 2007) in the Sacaco area, and possibly with Laguna Seca locality in the Ocucaje area (Stucchi et al. 2015).

*Diagnosis*.—*Sula* with braincase length similar to those of medium-sized boobies *S. variegata* and *S. leucogaster* but flattened, being the flattest among sulids; wide naso-frontal hinge, greater laterofacial angle, smaller cerebellar dome, and narrow sagittal crest. Shallow salt gland fossae and shallow postorbital fossae, as occurs in *Morus* and *Papasula*, but in contrast to the deep condition found in all other *Sula* species.

*Measurements*.—See SOM 1 (Supplementary Online Material available at http://app.pan.pl/SOM/app61-Stucchi_etal_SOM.pdf).

*Description*.—In lateral view (Fig. 2A) the length of the braincase fits well within the range of medium-sized boobies (SOM 1). The anterior region of MUSM 2497 has slightly pronounced supraorbital ridges above the fused frontals, as well as a straight dorsal profile, as it occurs in most species of *Sula* (note that *S. variegata* has a slightly domed profile, see Stucchi 2003, 2013). The middle region (parietal, squamosal and laterosphenoid) of MUSM 2497 has the same shape and disposition of *Sula*, but with a noticeable dorso-ventral flattening (SOM 1: measurement 3). Indeed, MUSM 2497 shows the most dorsoventrally compressed skull among sulids (SOM 1: proportion 6). In the posterior region, there is a large sagittal crest and a shorter and compressed prominentia cerebelaris (supraoccipital) under the posterior projection of the sagittal crest. However, it makes a more acute angle with respect to the horizontal plane.

In caudal (occipital) view (Fig. 2B), the flattening of the braincase is better appreciated. The whole region is proportionally wider than higher (SOM 1: proportion 6), differing from other sulids. The height at the vertical axis of the supraoccipital (between the superior border of the foramen magnum and the sagittal crest) represents 60% that of *S. variegata*. Additionally, the medial parasphenoid processes are more laterally placed than those of recent species.

In dorsal view (Fig. 2C), the face width of MUSM 2497 is wider than those of medium-sized boobies. This is seen in both the breadth at the preorbital skull roof and the width of the naso-frontal hinge. The width is greater than those of *S. variegata*, *S. leucogaster* and *S. sula*, but lies within the range of *S. nebouxii* (SOM 1: measurement 5). The breadth is greater and reaches the range of large-sized boobies (SOM 1: measurement 6). Therefore, the angle formed by the sagittal axis and the lateral margin of the frontal (latero-facial angle) is 10° in MUSM 2497, which contrasts with the angle reached by medium-sized boobies and *S. granti* (20° and 18°; Fig. 2C). The middle region exhibits a narrower and longer sagittal crest in comparison to modern species of *Sula*, except for *S. leucogaster.* In the posterior region, MUSM 2497 has a rounded supraoccipital, which projects posteriorly to the paroccipital processes of the exoccipitals. In other species of *Sula*, the supraoccipital is triangular and projects more posteriorly or is at the same level of the paroccipital processes. Both latter characters are also distinguished in other specimens from the Pisco Formation, for instance MUSM 249 (Aguada de Lomas locality, 8.0–8.8 Ma), MUSM 309 and 202 (Montemar locality, 8.70–6.45 Ma) and MUSM 361 (Sacaco Sur locality, 6.59–5.93 Ma), as well as in *Ramphastosula* (Stucchi and Urbina 2004).

In ventral view (Fig. 2D), the otic region, the articular with the quadrate, the basioccipital and medial parasphenoidal processes resemble those of living *Sula*. Likewise, the salt gland fossae and postorbital fossae are slightly shallower. The mandible is the same size and shape as those of medium-sized boobies (Fig. 2E).

*Remarks*.—MUSM 2497 has the typical cone-shaped skull of extant boobies, although it is more flattened and has a wider nasofrontal hinge. Thus, we infer a similar feeding ecology for this species. The sole character considered primitive is the shallow depth of the salt gland fossae and postorbital fossae which are both found in *Morus* (e.g., USNM 612654) and *Papasula* (e.g., USNM 560682), as well as inmature individuals of *Sula* (Stucchi 2013). Indeed, the derived condition is seen in adult *Sula*, which is more in line with their early divergence (23 Ma) from other sulids (according to Friesen and Anderson 1997).

*Stratigraphic and geographic range*.—Tortonian, Pisco depositional sequence, Pisco Formation, South-Central Peru.

### *Sula figueroae* sp. nov.

Fig. 3.

*ZooBank LSID*: urn:lsid:zoobank.org:act:F968A99A-AAF4-4066-B653-B68E1B3E8319

*Etymology:* In honor to Judith Figueroa (Asociación para la Investigación y Conservación de la Biodiversidad, Peru), for her valuable contributions to the knowledge of the natural history of Peruvian seabirds.

*Type material*: Holotype: MUSM 2501; nearly complete, well-preserved cranium and mandible lacking pterygoids and right lacrimal; one partial thoracic vertebra (? 19–21), three free cervical vertebrae (? 3–7), left scapula, right and partial left humeri, partial right and left ulnae, partial left radius, left carpometacarpus, pelvis without pubis, and partial tarsometatarsi. Paratype: MUSM 2502; associated furcula and sternum, coracoids, scapulae, humeri, distal fragments of ulnae, radius shaft, proximal fragment of left carpometacarpus, partial right carpometacarpus, right and distal fragment of left femora, right tibiotarsus, and right tarsometatarsus.

*Type locality*: MUSM 2501 and MUSM 2502 (A1 and A2 field numbers, respectively, of Bianucci et al. 2015) were both collected in Cerro Colorado locality, close to *Sula brandi* (Fig. 1A). MUSM 2501 coordinates: 14°21'47.30" S, 75°53'0.40" W, 596 masl. MUSM 2502 coordinates: 14°21'32.70" S, 75°53'21.90" W, 632 masl.

*Type horizon*: The same stratigraphic level as *Sula brandi*; early Late Miocene (Tortonian).

*Diagnosis*.—*Sula* having similar dimensions to the large-sized boobies *S. dactylatra* and *S. tasmani,* but with a more robust and much shorter humerus.

*Measurements*.—See SOM 1–3.

*Description*.—*Skull and mandible*: In lateral view (Fig. $3A_1$), the rostrum is approximately 50% larger than the braincase, which corresponds to the range of all known *Sula*, although *S. sula* shows a shorter rostrum (SOM 1: measurement 1). The length of MUSM 2501 is similar to that of *S. tasmani*, *S. nebouxii*, the largest specimens of *S. dactylatra* (sensu Tets et al. 1988), and possibly *S. granti*. The mandible has the same shape and proportions as those of extant species. The braincase length lies in the same range of large-sized boobies, but is shorter than that of *S. tasmani* (SOM 1: measurement 2). The anterior region of MUSM 2501 has slightly pronounced supraorbital edges above the fused frontals, a slightly domed skull roof, rather smaller than that of *S. variegata* (see Stucchi 2003, 2013). Posterior and middle regions of the braincase are slightly flattened compared with other species of *Sula* (SOM 1: proportion 3). Paroccipital processes of exoccipitals are lower with respect to the horizontal plane as in MUSM 220 (see Stucchi 2003). The width of the skull at the postorbital processes in dorsal view (Fig. $3A_4$) is proportionally similar to those of the more robust specimens of large-sized boobies, but with a larger postorbital process (SOM 1: measurement 8). A laterally narrow skull is observed in caudal view (Fig. $3A_2$), which is more evident in its constricted foramen magnum (SOM 1: proportion 4). Shallow salt gland fossae and postorbital fossae, as observed in *Morus* and *Papasula*, differing from the deep condition seen in *Sula*.

*Postcranium*: The humerus (Fig. $3B_5$–$B_7$) is similar to that of extant species of *Sula* (see Tets et al. 1988; Stucchi 2003) and *S. magna*, but more robust (SOM 2). The humerus length of both MUSM 2501 and 2502 falls within the range for *S. nebouxii*, their proximal width approaches those of *S. dactylatra* and *S. tasmani*, and their distal and mid-shaft maximum width are greater than that of *S. tasmani*. In lateral view (Fig. $3B_6$), a deformity (healed injury) is observed in the right humerus of MUSM 2502. The proximal width of the ulna is also wider in relation to the distal width of the humerus. The

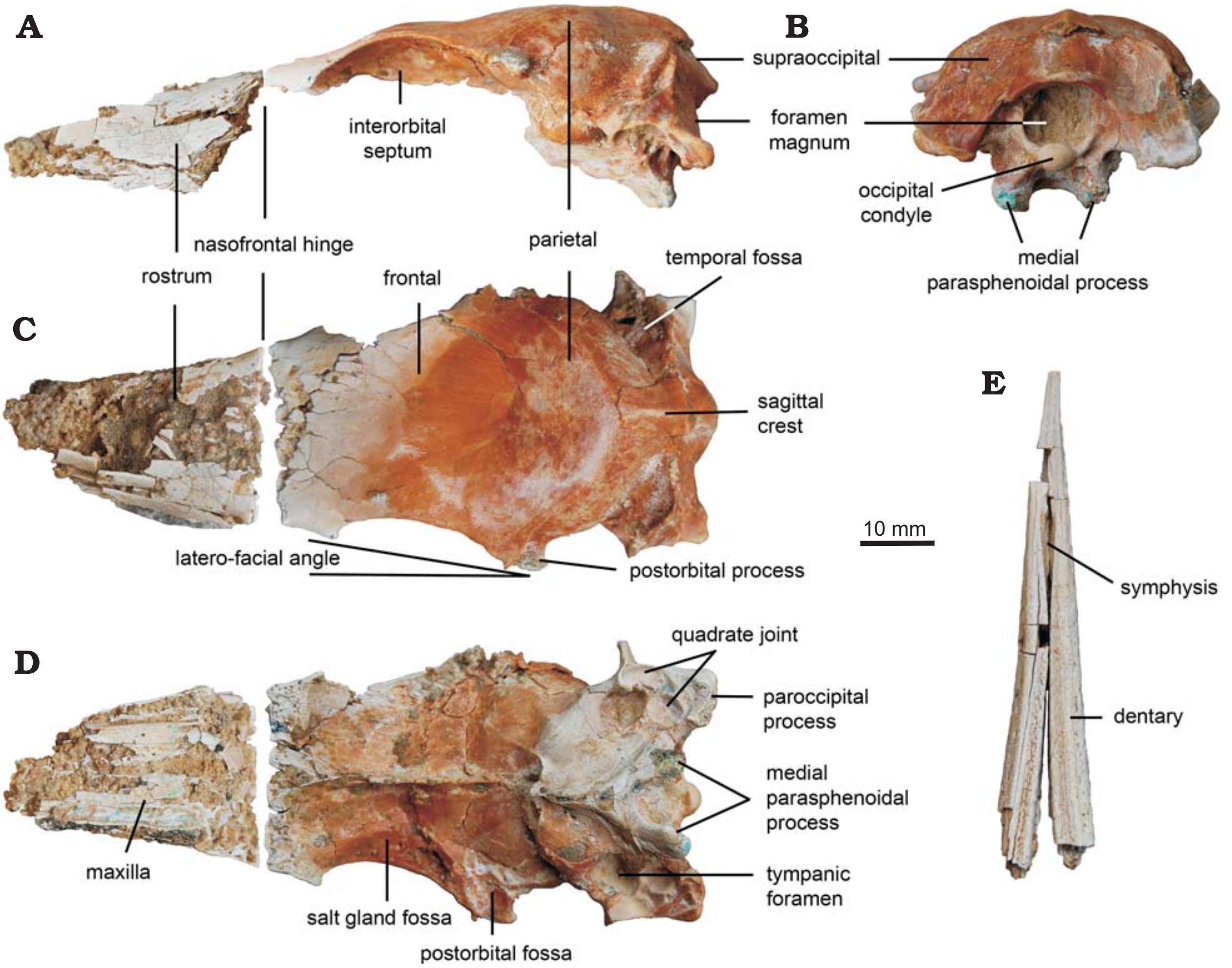

Fig. 2. Sulid bird *Sula brandi* sp. nov., holotype MUSM 2497 from Cerro Colorado locality, Peru, Pisco Formation, early Late Miocene. Skull in lateral (**A**), posterior (**B**), dorsal (**C**), and ventral (**D**) views; mandible in dorsal view (**E**).

remaining postcranial elements share a similar morphology with the other species of *Sula* as Warheit (1992) and Stucchi (2003) have pointed out. Some details could be observed when comparing *S. figueroae* with *S. variegata* in Stucchi (2011). Moreover, their proportions notably correspond to different species. Thus, carpometacarpus and tibiotarsus are similar in length to that of *S. tasmani*, whereas the tarsometatarsus is proportionally closer to *S. dactylatra*. The femur matches the range of those of indeterminate *Sula* individuals (see Stucchi 2003), which is larger than those of both *S. dactylatra* and *S. tasmani* (SOM 3). In addition, the sternum, pelvis and synsacrum reach the dimensions and proportions of large-sized boobies (including the *Sula* spp. group), wider than those of medium-sized boobies and considerably larger than that of *S. sula* (SOM 3), but are smaller than those of *S. magna*. Based on a small sample, we could tentatively say that the pelvis shows a conspicuous lateral crest on the spina dorsolateralis ilii, which is also found in *S. leucogaster* but shallow, and completely absent in *S. variegata*.

*Remarks*.—Although *S. figueroae* has a notably robust skull roof, it is narrow at the occipital region. This, however, does not affect the overall conical shape of the skull. Among the postcranial elements, the humerus is remarkable because of its proportions, being quite short relative to the proximal and distal widths. Thus, the humerus length is the same of *S. nebouxii*, even though its distal and proximal widths equal those of *S. tasmani* and *S. dactylatra*, which in turn are quite longer. The proportions concerning the length of the other postcranial bones of *S. figueroae* in comparison with other *Sula* species should be carefully addressed because of the limited sampling of the fossil (only two incomplete specimens). Warheit (1992) and Stucchi (2010) have already noted the importance of the quantity of specimens when evaluating the trends in dimensions and proportions (i.e. intraspecific variation) in a species. Despite that, the morphology and morphometric data of this extinct booby are more in line with the feeding and hunting strategies of its extant relatives, having the same basic body plan of the genus.

## Genus *Ramphastosula* Stucchi and Urbina, 2004

*Type species*: *Ramphastosula ramirezi* Stucchi and Urbina, 2004, Sacaco Sur locality (Poza Roja), Pisco Formation (Peru), Messinian (Late Miocene).

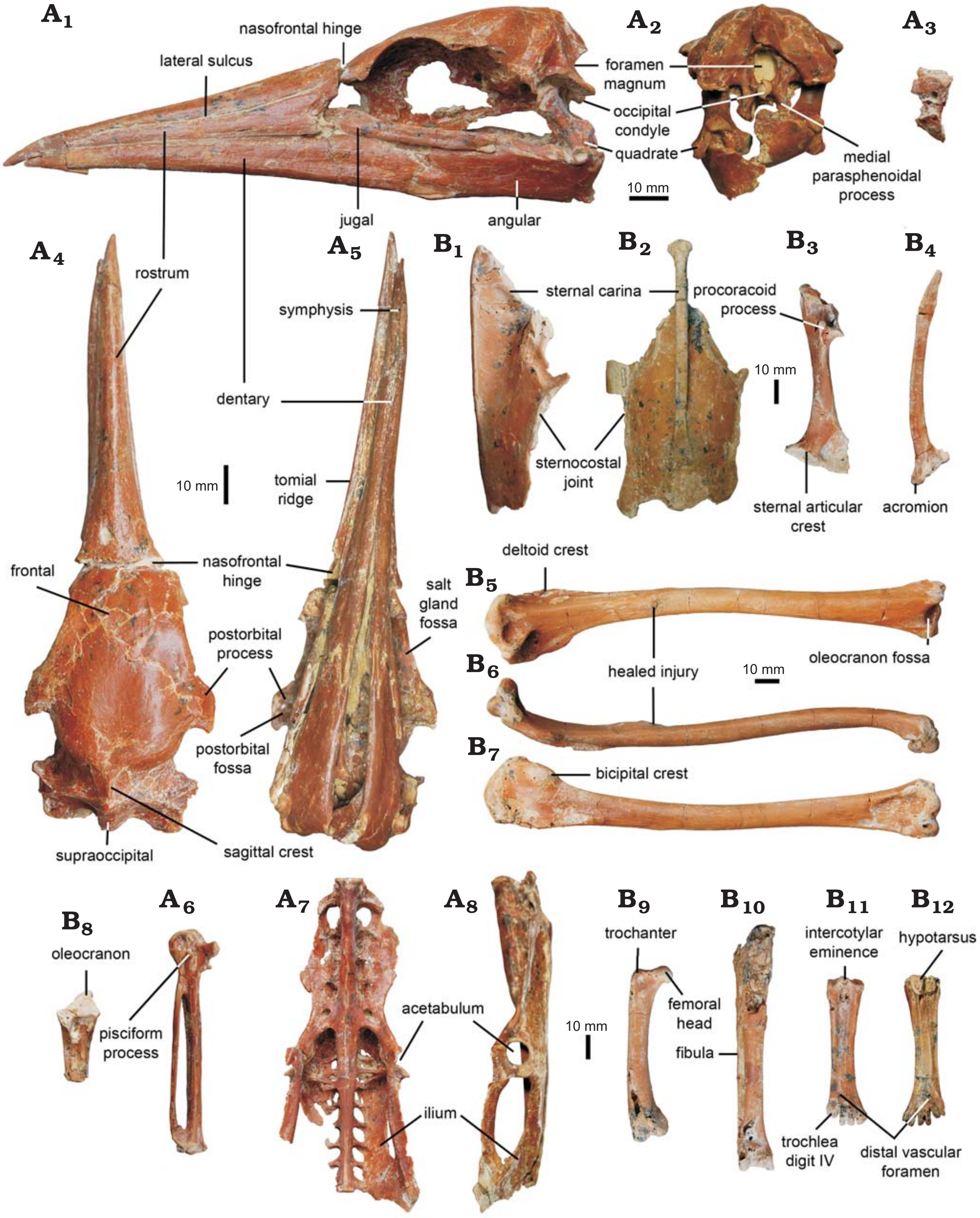

Fig. 3. Sulid bird *Sula figueroae* sp. nov. from Cerro Colorado locality, Peru, Pisco Formation, early Late Miocene. **A**. Holotype MUSM 2501. Skull in lateral ($A_1$), posterior ($A_2$), dorsal ($A_4$), and ventral ($A_5$) views. Isolated lacrimal in lateral view ($A_3$). Left carpometacarpus in ventral view ($A_6$). Synsacrum and pelvis in ventral ($A_7$) and lateral ($A_8$) views. **B**. Paratype MUSM 2502. Sternum in lateral ($B_1$) and ventral ($B_2$) views. Coracoid in ($B_3$) dorsal view. Left scapula in ($B_4$) lateral view. Right humerus in anterior ($B_5$), lateral ($B_6$), and posterior ($B_7$) views. Proximal portion of ulna in ventral view ($B_8$). Right femur in anterior view ($B_9$). Right tibiotarsus in anterior view ($B_{10}$). Right tarsometatarsus in anterior ($B_{11}$) and plantar ($B_{12}$) views.

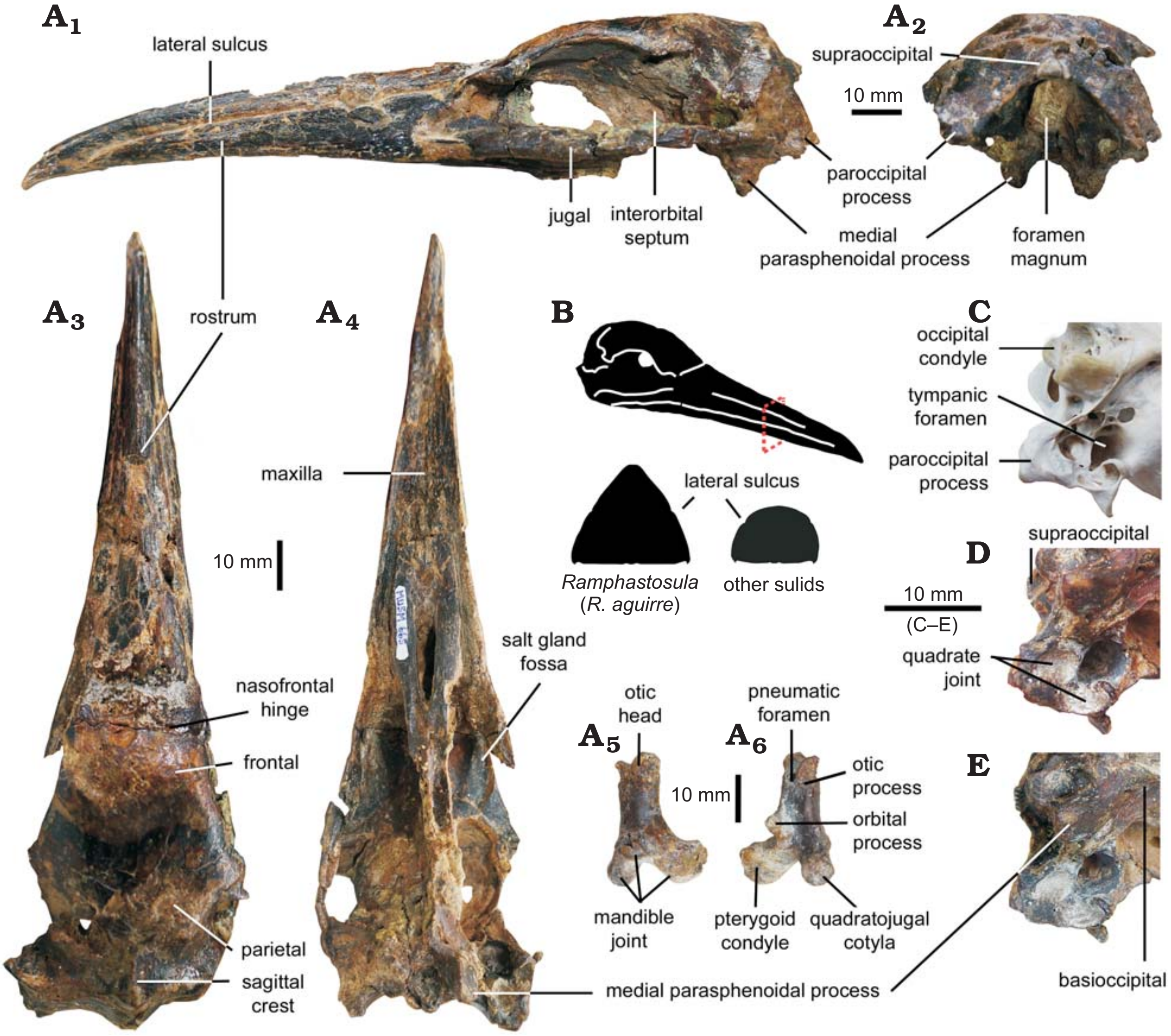

Fig. 4. Sulid bird *Ramphastosula aguirrei* sp. nov. from Poza Negra, Sacaco Sur (Peru), Pisco Formation, Late Miocene. **A** Holotype MUSM 665. Skull in lateral ($A_1$), posterior ($A_2$), dorsal ($A_3$), and ventral ($A_4$) views. Left quadrate in ($A_5$) anterior and ($A_6$) posterior views. **B**. Section of rostrum at its mid-length showing differences in the outline of *Ramphastosula* and other sulids. **C**–**E**. Comparison of the ear region in ventral view in the Peruvian booby *Sula variegata* DPV AM P8 (**C**) from Isla Lobos de Afuera, Lambayaque (Peru), Recent; *R. ramirezi* MUSM 264 (**D**) from Poza Roja , Sacaco Sur (Peru), Messinian (Late Miocene); and *R. aguirrei* MUSM 665 (**E**) from Poza Negra, Sacaco Sur (Peru), Messinian (Late Miocene).

*Emended diagnosis*.—*Ramphastosula* can be diagnosed from other sulids by the following combination of characters: (i) height of the rostrum at its mid-length is more than half the height at the nasofrontal hinge; (ii) slightly to strongly convex rostrum in all its dorsal edge; (iii) leromedially compressed rostrum forming a triangle in anterior view, in which the dorsal surface shows a strong ridge; (iv) well-developed occipital and temporal regions; (v) broad paroccipital procceses of the exoccipitals projecting laterally to the level of the postorbital processes; (vi) broad temporal fossae; (vii) robust frontal region.

## *Ramphastosula ramirezi* Stucchi and Urbina, 2004

*Emended diagnosis*.—Height of the rostrum at its mid-length is higher than the height at the nasofrontal hinge, and all its dorsal edge is strongly convex.

## *Ramphastosula aguirrei* sp. nov.

Fig. 4.

*ZooBank LSID*: urn:lsid:zoobank.org:act:51F31FFF-4D44-45B6-A221-07A128E4A5F3

*Etymology:* In honor to Walter Aguirre (MUSM, Peru), for his substantial work as a fossil preparator of the vertebrate paleontological collection of the MUSM.

*Holotype*: MUSM 665; almost complete, well-preserved skull with partial jugal bars, and lacking lacrimals and the right quadrate.

*Type locality*: MUSM 665 was collected from the Sacaco Sur (Sud-Sacaco or SAS) locality (Pisco Formation, Peru) which is dated to 6.59–5.93 Ma (Ehret et al. 2012) (Fig. 1B). There are two areas (sublocalities) recognized there: Poza Roja (red hole) and Poza Negra (black hole). The first refers to the type locality described in Muizon and DeVries (1985), where *R. ramirezi* was recovered. The second corresponds to underlying beds (18 m lower in the stratigraphic column of

Leonard Brand, unpublished material) being older than the former one and where *R. aguirrei* was recovered.

*Type horizon*: Sacaco Sur was formally dated as Pliocene age (Muizon and DeVries 1985), but new radiometric data suggests a Late Miocene age, (Messinian; see Ehret et al. 2012).

*Diagnosis*.—Height of the rostrum at its mid-length is 2/3 the height of the nasofrontal hinge, and its entire dorsal edge is slightly convex.

*Measurements*.—See SOM 1.

*Description*.—*Rostrum*: *R. aguirrei* has a robust and large rostrum, slightly larger than that of *R. ramirezi*. In lateral view, the lateral sulci (Fig. 4$A_1$, $A_3$) are oriented parallel to the culmen due to the ossification of primary nasal apertures. These sulci divide the rostrum rather equally into dorsal and ventral parts as in *R. ramirezi*, but in *Sula*, *Morus*, and *Papasula* the dorsal part comprises 1/3 of the rostrum (see Fig. 4$A_1$). Interestingly, we note that in *S. figueroae* this division is closer to the condition in *Ramphastosula* although this could be the product of lateromedial deformation. Furthermore, the height of the rostrum at its mid-length equals 2/3 the maximum height (at the level of the nasofrontal hinge). In *S. variegata* and generally among living sulids, this height equals 1/2 the maximum height, and in *R. ramirezi* the height at the mid-length of its rostrum is higher than the level of the nasofrontal hinge. Some individuals of the living species *S. leucogaster* and *S. dactylatra* show a slender protuberance in the posterior part of the rostrum (see Stucchi 2013: fig. 4). The rostrum is projected downward with respect to the horizontal plane since the nasofrontal hinge towards the tip in *R. aguirrei* and *Sula* spp., whereas *R. ramirezi* shows an upward angle until the mid-length of the rostrum where it begins to descend. In *R. aguirrei* the tip of the rostrum is ventrally curved in almost 40% of its maximum height from approximately its mid-length.

In dorsal view (Fig. 4$A_3$), *R. aguirrei* as well as *Sula* and *Papasula* exhibit a rough surface across its length. Ventrally (Fig. 4$A_4$), the rostrum has the typical schizognathous condition of the family. Palatines are separated in their cranial extremes and fused in the caudal extreme as in other sulids.

*Neurocranium*: The only noticeable difference between *R. aguirrei* and *R. ramirezi* in the braincase is located at its dorsal surface. From the nasofrontal hinge to the mid-length of the orbitals the frontals of *R. aguirrei* are lower than those of *R. ramirezi* with respect of the horizontal plane. Posterior to the mid-length of orbitals, the braincase is slightly inclined upward in *R. aguirrei* whereas that of *R. ramirezi* remains flat.

*Remarks*.—The morphology of *Ramphastosula* suggests closer affinities to *Sula* than to *Morus* or *Papasula*. Both *Sula* and *Ramphastosula* have a roughened maxilla surface in its posterior-most part, and both have reduced and bifurcated postorbital processes. Conversely, *Morus* has a smooth maxilla surface, but shows the same condition of the postorbital processes. *Papasula* shows long, sharp and ventrally-inclined postorbital processes but retains the roughened maxilla surface (Stucchi 2003; Stucchi and Urbina 2004). In this respect, the primitive condition of both characters is present in *Papasula* (according to Smith 2010).

The skull of *R. aguirrei* has an intermediate morphology between other sulids and *R. ramirezi*. Interestingly, the rostrum of *R. aguirrei* is more similar to that of *Sula* rather than *R. ramirezi*. Taking all this into account, along with the previously observed morphological stability in the cranium of sulids (Stucchi 2003), allows us to suggest that the specimens from Poza Negra and Poza Roja represent different species.

*Stratigraphic and geographic range*.—Messinian, Pisco depositional sequence, Pisco Formation, Southwestern Peru.

# Concluding remarks

**Ecomorphology**.—The acute morphology of the rostrum in some seabirds is suitable for hunting by plunge-diving. Among these, boobies typify this technique, although others such as the tropicbirds (Phaethontidae) and some species of terns (Sterninae, Laridae) and pelicans (Pelecanidae) also use this strategy (Nelson 1979; Field et al. 2011).

Sulids can perform plunge diving from high altitudes because they have (i) developed a cone-shaped rostrum filled with trabecular bone material and a modified mandibular symphysis, which allow them to withstand the plunge impact without damage (e.g., bending); and (ii) completed obliteration of the beak's nasal fossae, which displaces the respiratory function to a space located below the preorbital fenestra and jugal protected by the ramphotheca (MacDonald 1960; Stucchi 2013). However, the fossil record found in the Pisco Formation has revealed some species with different morphologies, as is the case of the toucan-booby *Ramphastosula*, which probably did not exhibit the same plunge-diving technique, not from high altitudes at least (Stucchi and Urbina 2004).

The upper jaw in tropicbirds and terns curves toward the tip as in *R. aguirrei*. These birds also swoop but from lower altitudes than sulids (slightly less than 10 m; Nelson 1979). Because of morphological superficial resemblance, *R. aguirrei* likely could have plunged in a similar way. Despite the limitations imposed by its larger size and weight to achieving a considerable altitude, it is possible that having more developed frontals and a flat cranial roof would give them greater resistance and aerodynamics, and thus attaining greater altitudes.

Interestingly, the occurrence in northern Peru of a female adult extant individual of *S. nebouxii* (see Stucchi 2013: fig. 5) with a rostrum morphology similar to that of *R. ramirezi* suggests this particular beak shape do not hinder them from feeding similarly to their extant relatives. Even though boobies can dive from altitudes up to 100 m, they generally dive from lower heights (a few meters), and reach less than a meter above the sea surface when they dive diagonally (MS, personal observation). In contrast, pelicans have their own plunge strategy as described Forbes (1914) for *Pelecanus thagus*, as well as Field et al. (2011) and Schreiber et al. (1975) for *P. occidentalis*, which are not morphologically comparable with *R. aguirrei*.

**Body size**.—In the Eastern Pacific Ocean, *Morus* was the predominant genus in the Northern Hemisphere (reported in Mexico and California, USA), whereas *Sula* was in the Southern Hemisphere (southern Peru and northern Chile) in past communities. Stucchi (2003) has noticed the sympatric occurrence of these species with disparate body sizes at least during the Late Miocene. In California, there are three big-sized gannets (*M. magnus*, *M. stocktoni*, and *M. lompocanus*) coexisting with the medium-sized *M. media*, and the small-sized *M. willetti*. Likewise, we found in the Messinian age the big-sized *S. magna*, the medium-sized *M. peruvianus* and *S.* aff. *variegata*, and the small-sized *S. sulita* co-occurring in southern Peru. This study also provides evidence that during the Tortonian age the medium-sized *S. brandi* and the large-sized *S. figueroae* cohabited in this southern area. In modern sulid communities, body size plays an important role in segregating sympatric seabirds with similar feeding strategies offering different solutions to foraging challenges and thus facilitating coexistence (i.e., allowing them feeding on different prey size items and in different areas), as exemplified by Duffy (1987), Jahncke et al. (1997), Jahncke and Goya (2000) and Young et al. (2010) in the case of congeneric species which live together but with different body sizes. This also occurs even in sexually dimorphic species, in which bigger individuals (females) feeds on bigger and heavier prey (García-R. and López-Victoria 2008). Of course, these differences do not prevent them from terrestrial habitat competition (see Duffy 1984 and Figueroa 2004). Body size could thus be tentatively used as ecomorphological proxy to indicate resource partitioning in either northern or southern extinct assemblages. Interestingly, differences in body size could be trace as far back as the late Oligocene in the sulid community of the Chandler Bridge Formation (South Carolina, USA) (Ksepka 2014), the oldest reliable sulids reported to date.

**Sulid paleodiversity**.—The fossil record of the genus *Sula* ranges from the Early to Middle Miocene Chilcatay formation (Stucchi and DeVries 2003) to the present, representing the largest timespan in this region. Since the Late Miocene age, several species have evolved including the largest sulid (*S. magna*), some large forms (*Sula* spp.), and even some related to modern species (*S.* aff. *variegata*) (Stucchi 2003). The set assigned to *Sula* spp. is undoubtedly the most abundant, occurring in all horizons. It is also one of the most complex in terms of its systematics due to size, overlapping among species such as *S. tasmani* or *S. dactylatra* and a paucity of morphological characters (Stucchi 2003). We cannot rule out the possibility that some material corresponds to more than one species, to an undescribed species, to some inmature material of *S. magna*, or even to *Ramphastosula* (only cranial material has been recovered). Considering the morphological affinities, the progressive change through time seen in the skull of *Sula* and *Ramphatosula*, and the relative abundance of *Sula* in layers under and overlying the Sacaco Sur level, and the late and restricted appearance of *Ramphastosula*, anagenetic evolution between these two genera is possible (contra Benson and Erickson 2013). Additional material is therefore necessary to clarify their affinities.

Biological drivers of seabirds diversity are difficult to test, at least with the available data. Although the diversity though time of marine primary producers such a diatoms have been used to explain the rise of top consumers (see Marx and Uhen 2010 for cetaceans), such correlations have several concerns, as diatom species richness is not necessarily related with their abundance (Pyenson et al. 2010), because diversity or richness are not related to biomass in temperate coastal upwelling ecosystems. In fact, their trophic dynamics is controlled not from bottom-up (i.e., diatoms) or top-down (i.e., seabirds, marine mammals) but rather from the intermediate trophic level (i.e., pelagic, planktivore fish) toward both sides (Cury et al. 2001; Bakun 2006). The Peruvian anchovy *Engraulis ringens* and the sardine *Sardinops sagax* currently dominate the productivity in the Peru–Chile Current ecosystem, although they are not ecological analogues as the anchovy prefer colder, coastal waters than the more oceanic sardine (Bakun 2006; Gutiérrez et al. 2007). Thus, it must be expected that similar fish (see Lambert et al. 2015 for the Miocene occurrence of the genus *Sardinops* in Peru) have driven the ecology in the region at least since the onset of the Antarctic Circumpolar Current (about 30 Ma; Scher et al. 2015), which mainly generated the conditions of upwelling (Marx and Uhen 2010). Unfortunately, the fossil record of fish is largely unknown in terms of both diversity and quantity in the southeastern Pacific Ocean preventing any assessment. Even assuming a dense fish fossil record, high species richness is commonly found not in temperate but in tropical latitudes, which coincides with the current sulid high species richness.

In similar manner, Stucchi (2003) has already pointed out that the sulid diversity peak occurred during the Late Miocene, but this observation could be misinterpreted. The relative abundance of sulids in some Peruvian localities rather than others could be explained by preservation bias due to different paleo-environments (see Marocco and Muizon 1988; Stucchi and Figueroa 2011), but it could also be affected by local conditions (e.g., volcanism). In short, analyzing global-scale diversity patterns require taking into account regional considerations of biotic and physical factors in an ecological context (Pyenson et al. 2014) to properly address biological questions.

# Acknowledgments

We thank Walter Aguirre (MUSM) for materials preparation. Giovanni Bianucci (Università di Pisa, Italy) funded the fieldtrip and preparation of *Sula brandi* with partial support of a National Geographic Society

Committee on Research Exploration grant (9410-13). Leonard Brand (Loma Linda University, Loma Linda, CA, USA) kindly shared his unpublished stratigraphic work on the Sacaco basin. We also thank editor Stephen Brusatte (University of Edinburgh, UK), and reviewers Daniel Ksepka (Bruce Museum, USA) and Daniel Field (Yale University, New Haven, CT, USA) for their constructive comments on the manuscript. Rodolfo Salas-Gismondi (MUSM) and Storrs Olson (USNM) allowed access to specimens in their care. Luciano Stucchi (Universidad del Pacífico, Lima, Peru), Manuel Plenge and Mauricio Bustamante (both Lima, Peru) provided inaccesible references.

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