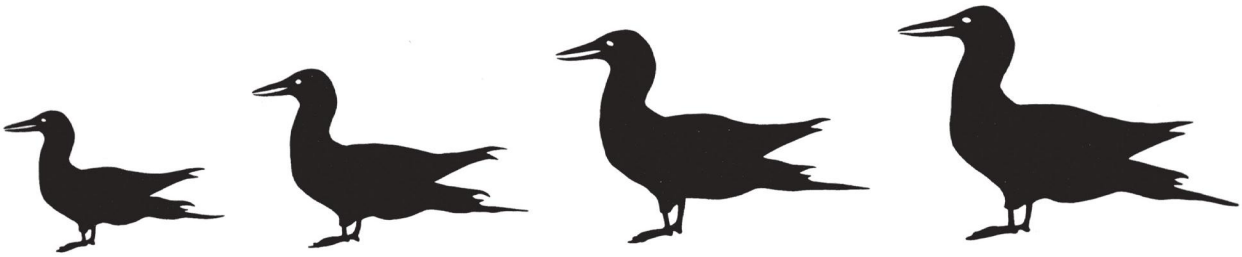
A NEW GENUS AND SPECIES OF BOOBY (SULIDAE: AVES) FROM THE PLIOCENE OF SOUTH CAROLINA, WITH A NEW COROLLARY TO THE NATURE OF SISTER TAXA

RICHARD D. BENSON and BRUCE R. ERICKSON



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Frontispiece. Silhouettes, from right to left, of typical *Morus* (gannets), *Bimbisula* (new genus), *Papasula* (Abbott's Booby and Costello's Booby), and *Sula* (boobies). Subtle differences in the silhouettes mask the greater osteological differences. By outgroup comparison, *Morus* (although derived in its own way) shares more character states with anhingas and cormorants than does *Sula*. *Papasula* is an older radiation of boobies and shares almost as many *Morus*-like character states as *Sula*-like character states. The fossil genus *Bimbisula* is intermediate, character-wise, between *Morus* and *Papasula*.

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MONOGRAPH

VOLUME 7: PALEONTOLOGY

The Science Museum of Minnesota

120 West Kellogg Blvd.

Saint Paul, Minnesota 55102

USA.

May 20, 2013

MONOGRAPH

VOLUME 7: PALEONTOLOGY

International Standard Book Number **911338-87-X**

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Abstract

A new genus and species of booby is described from the Goose Creek Limestone (middle Blancan) of South Carolina. Based on a partial skeleton of one individual and the referred cranium of another, the new taxon, a gannet-booby mosaic, resembles gannets (*Morus*: Morini) as much as boobies (*Sula* and *Papasula*: Sulini) by count of characters. Although devoid of unambiguous autapomorphies of its own, the new taxon is an unlikely ancestor to modern boobies, as it is more primitive than *Sula guano* Brodkorb, a somewhat earlier (early Pliocene) species. The known antiquity of the sulid family (early Oligocene) is probably of greater age than that of the most recent common ancestor of gannets and boobies (subfamily Sulinae), on the evidence of both molecular distance and the morphology of the earliest (and certain Miocene) sulids. Therefore some fossil sulids should be placed in at least one extinct subfamily rather than in modern genera. Although sulid fossils throughout the Miocene have been assigned to *Sula*, we find little evidence that *Sula* is that ancient. The new genus here described indicates a greater sulin generic diversity, in which *Sula* is a relatively young genus most closely related to other sulin (but gannet-like) taxa. Several paleogenera have been placed in the gannet clade. Whether the extant genus *Morus* is a relatively young or a persistent old genus among these paleogenera, a ghost lineage connects the seemingly younger Sulini with its sister group, the Morini. If it is true that sister taxa are of equal age, then the unknown members of the ghost lineage of the apparently younger sister taxon are expected to closely resemble, and be confusable with, the members of the other sister taxon, as the earliest sulins are expected to be confusable with morins. Similar examples from other groups in the fossil record are given.

Key Words: Aves, Sulidae, Blancan, Pliocene, cladistic theory, ghost lineage, Goose Creek Limestone, South Carolina.

Introduction

Inhabiting tropical, subtropical, and temperate oceans, the 10 extant sulid species of 3 gannets and 7 boobies seem to be a family undergoing faunal turnover. Although as a whole the sulid family remains in decline from its diversity peaks during the Miocene, the gannets have suffered the greater loss. As the once speciose and wide-spread gannet clade has declined, the (apparently) geologically younger booby clade has maintained a more steady diversity, which includes the newly recognized species *Sula granti* (Nazca Booby), formerly considered a subspecies of *S. dactylatra* (Masked Booby) (Friesen et al. 2002). Boobies have reclaimed at least some of the former geographic range of the gannets; e.g., the range of *Sula leucogaster* (Brown Booby) now includes a small, Asiatic, portion of the north Pacific, from which the gannets seem to have been excluded by Neogene pinnipeds and gulls (Warheit and Lindberg 1988, Warheit 1992a). Restriction of oceanic area by tectonic change, however, would seem to be the cause of the absence of any modern sulid in the Black Sea region, where the Miocene Tethyan Sea gannets *Sarmatosula dobrogensis* and *Morus olsoni* were collected (Grigorescu and Kessler 1988).

No Pacific gannets are known from Asia or from North America north of California after the middle Miocene, although numerous species of gannets persisted throughout the late Miocene in California (Warheit 1992a,b). Two species of gannets and two species of boobies are known from the Pliocene San Diego Formation (Chandler 1990), but the extinct *Morus reyanus* is the only sulid known from the

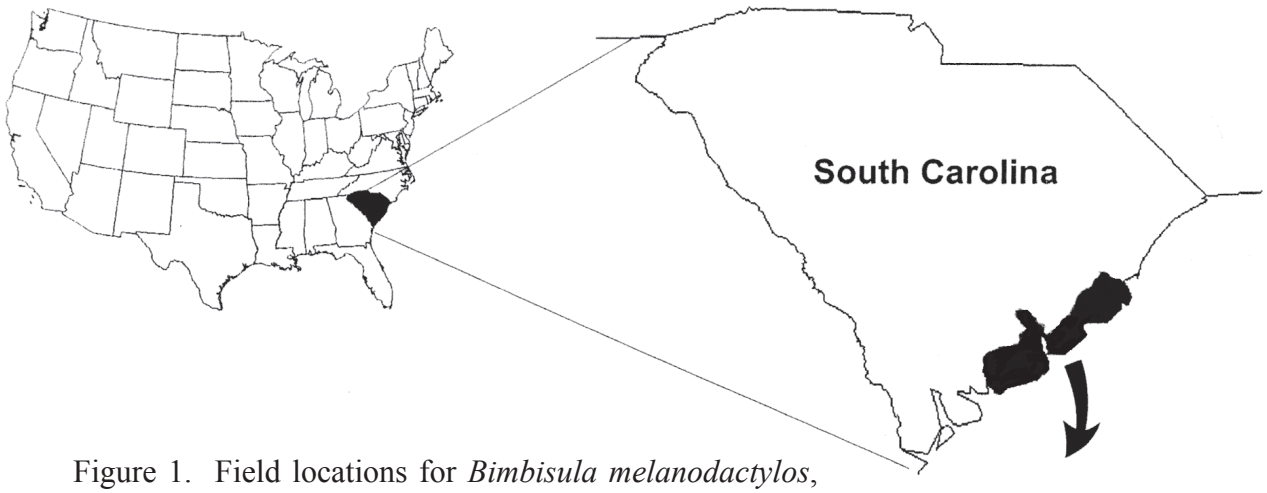
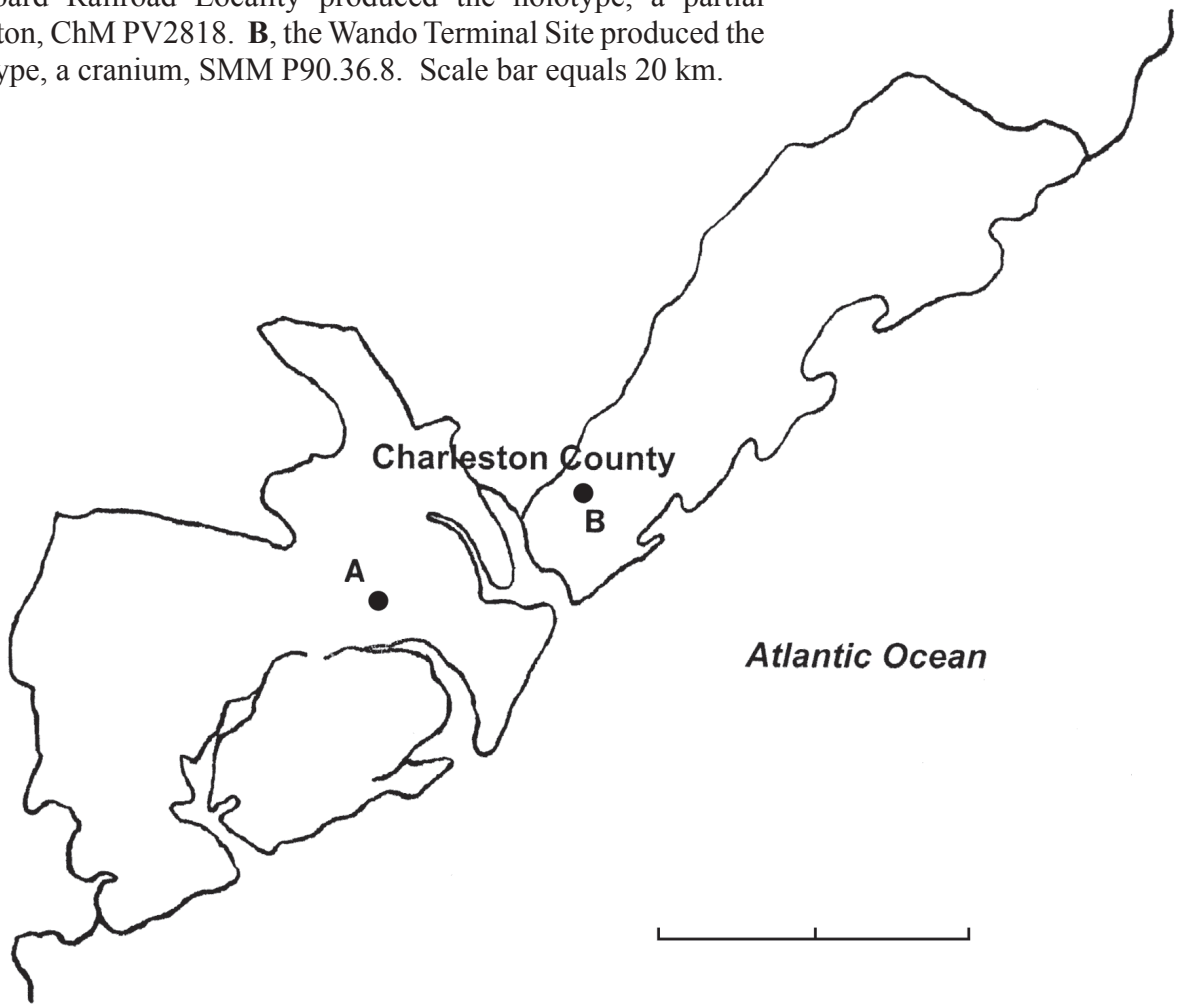


Figure 1. Field locations for *Bimbisula melanodactylos*, gen. et sp. nov., in Charleston County, South Carolina. **A**, the Seaboard Railroad Locality produced the holotype, a partial skeleton, ChM PV2818. **B**, the Wando Terminal Site produced the paratype, a cranium, SMM P90.36.8. Scale bar equals 20 km.



Pleistocene of California (Howard 1983, Jefferson 1991), where no living sulids occur.

In the Atlantic, however, an apparent decline in the diversity of boobies has also occurred. In this paper a new genus and species of primitive booby is described from the Pliocene of South Carolina, an area outside the present range of any sulid except for *Morus bassanus* (Northern Gannet).

Taxonomic Background

One, two, or three genera are recognized for the 10 extant sulid species, according to the various authorities. The monumental *Handbook of the Birds of the World* (del Hoyo et al. 1992), for example, includes all extant sulids in the single genus *Sula*. Even some specialists in the Sulidae have preferred to classify all of the extant family members in one genus (e.g., Nelson 1978). In the *Check-list* of the American Ornithologists' Union (1983) *Morus* was recognized only as a subgenus of *Sula*, despite the acceptance by Bent (1922) and by Peters (1931) of *Morus* as a valid genus. In their revision of Peters (1931), Mayr and Cottrell (1979:183) preferred to synonymize *Morus* with *Sula*, but provided a footnote that *Morus* is "a subgenus . . . or possibly a distinct genus." Because there are numerous osteological differences between gannets and boobies (reviewed by Van Tets et al. 1988 and Warheit 1990), paleontologists have long been among those who readily recognized a separate genus (*Morus*) for the gannets (e.g., Wetmore 1926, Compton 1936, Howard 1936, Miller and DeMay 1942); even Romer (1966), a self-described "'lumper' by nature" (Romer 1968:191), recognized the genus *Morus*. Eventually, the American Ornithologists' Union (1989, 1998) reversed the judgment of Mayr and Cottrell (who out-lumped Romer) and again restored *Morus* to genus rank. Meanwhile, the aberrant, but rarely collected, Abbott's Booby ("*Sula*" *abbotti*) of the Indian Ocean was recognized as belonging to a third genus, *Papasula* Olson & Warheit 1988. We recognize all three of these genera as valid, as do Steadman et al. (1988), Sibley and Monroe (1990), and Dickenson (2003). Steadman et al. (1988) have published the only known fossils of *Papasula*, which now includes not only Abbott's Booby but also Costello's Booby (*Papasula abbotti costelloi*).

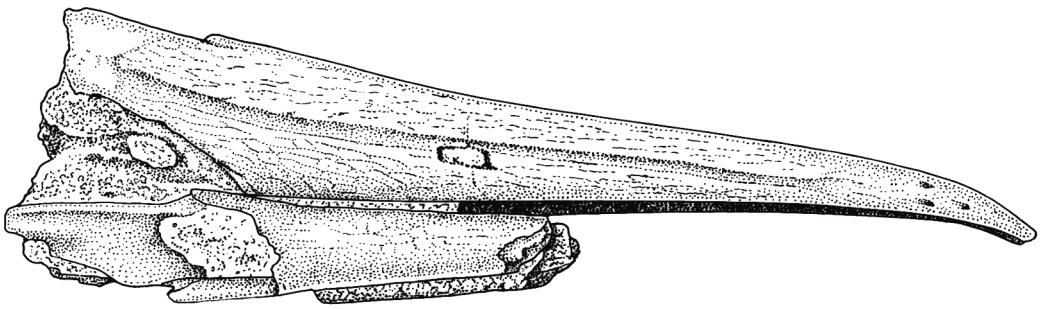


Figure 2. Rostrum and fragmentary mandible of *Bimbisula melanodactylos*, gen. et sp. nov., ChM PV2818, in right lateral view. Scale bar equals 5 cm.

By a simple count of character states, the boobies (*Sula* and *Papasula*) seem to be more derived than the gannets (*Morus*) by outgroup comparison with cormorants (Phalacrocoracidae) and anhingas (Anhingidae) and also by our interpetation of the sulid fossil record. On the other hand, the genus *Morus* is

derived in its own way; properly speaking, certain character states, not taxa, are primitive. Any unqualified statement (e.g., devoid of reference to outgroup comparison) that *Morus* is more primitive than *Sula* (or that *Sula* is more primitive than *Morus*) would be meaningless. Perhaps no fossil sulid of greater than latest Miocene (Hemphillian equivalent) age is properly assigned to the genus *Sula* (original observation), but species identifiable as gannets (*Morus*, *sensu lato*) are known throughout the Miocene. Regarding the Miocene and Oligocene sulids–especially those that were still classified as *Sula* in Brodkorb's (1963a) *Catalogue of Fossil Birds*, or by other authors after that date–the following should be stated.

In his *Catalogue* Brodkorb (1963a) presented the family Sulidae undivided by any tribes or subfamilies, but consisting of five genera, three of them extinct. Anomalously, none of the extinct genera appear to be older than Miocene, while the modern genus *Sula* was made to include two Oligocene species which probably existed before the time of *Sula-Morus* divergence. (Nothing in this paragraph is intended as criticism of Brodkorb, whose *Catalogue* was, after all, a catalogue and not necessarily a revision.) Brodkorb (1963a) listed 18 sulid paleospecies, and noted one more, *Morus atlanticus* (Shufeldt) 1915, which, following Wetmore (1926), he synonomized with *Morus loxostylus* (Cope) 1870. (Subsequently, Olson and Rasmussen (2001) determined on the basis of additional material that *M. atlanticus* and *M. loxostylus* are separate species.) Of these 19 species, 8 are included in *Sula*, 5 of them incorrectly, although by original designation. These are the two Oligocene species (of Milne-Edwards (1867) which are now reassigned to *Prophalacrocorax* Harrison 1975a and *Empheresula* Harrison 1975b), the early Miocene "*Sula*" *universitatis* Brodkorb 1963b, and "*S*ula" *willetti* Miller 1925 and "*Sula*" *pohlorum* Howard 1958, both from the late Miocene of California. As for the remaining three paleospecies which Brodkorb (1963a) assigned, correctly, to *Sula*, they are all of Pliocene age.

The *universitatis* taxon, "known from only an incomplete, waterworn carpometacarpus" (Becker 1987:31), resembles *Sula* rather than *Morus* only by character states which are primitive for the order Pelecaniformes except for one (compressed fossa for the ulnare) which is homoplasious with the more derived species within *Sula* (Warheit 1990); Warheit (2002) regards this species as Sulidae, *Incertae Sedis*.

The *willetti* taxon is regarded as a species of *Morus* by Warheit (1990, 1992a, 2002) and subsequent authors. Although in 1925 Miller was not yet using the genus *Morus*, he well knew the difference between gannets and boobies and noted the resemblance of both "*S.*" *willetti* and "*S.*" *atlantica* to the Northern Gannet.

The *pohlorum* taxon is based on bones of an individual's wings and pectoral girdle (in a difficult diatomaceous shale matrix) so degraded that Howard (1958) was able to discuss few of its characters; in assigning the fossil to *Sula* rather than to *Morus* she used only three characters, all of them primitive for the suborder Sulae (unenlarged coracoidal head, humerus with distinct central ridge, humerus longer than ulna). Howard (1958) did point out that this species differs from *Sula* in having its epicondyles nearly equal to the condyles in distal extent, thus giving the distal contour of the humerus a straight, square appearance. This condition (which as Howard correctly states, is unlike *Sula*) is typical of anhingas and cormorants. In our opinion, a sulid with such an apparently primitive humerus might represent a late survival of a now-extinct subfamily; in any case, it shares no derived character states with *Sula*. Regarding the spelling of *pohlorum* (not *pohli*), Article 32.5.1 of the International Code of Zoological Nomenclature provides for correction of *lapsus calami* such as an incorrect singular when the original author's plural intention is explicitly stated. Howard (1958: 4, 5) stated that the species was named for the two Pohl "boys", Michael

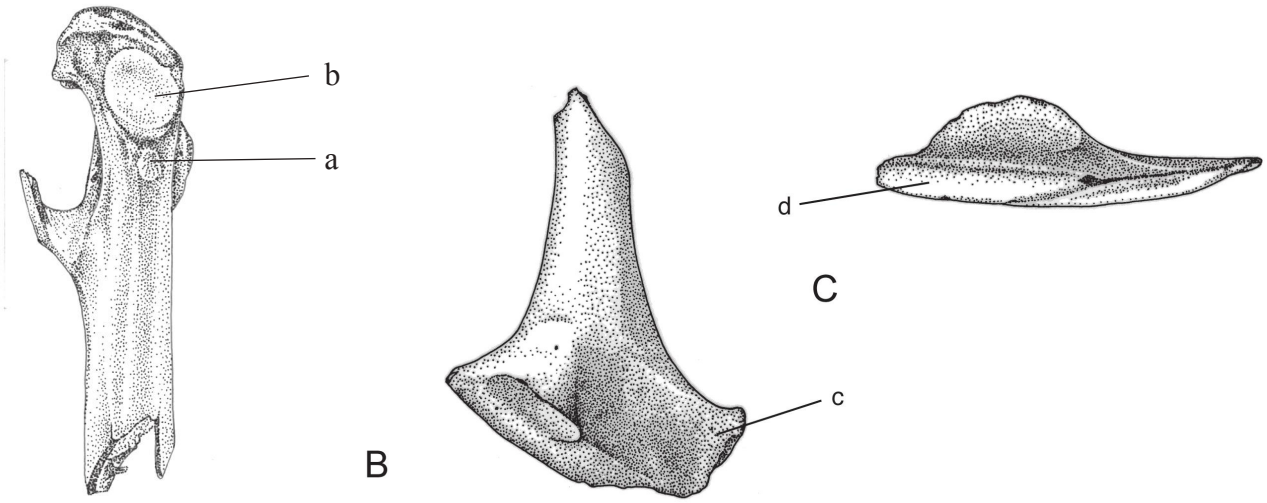


Figure 3. Pair of coracoids of *Bimbisula melanodactylos* gen. et sp. nov., CM PV2818. **A**, furcular end of left coracoid in anterior view; (a) bicipital attachment, (b) furcular facet. **B**, sternal end of right coracoid in posterior view; (c) sternocoracoidal process. **C**, right coracoid in sternal view; (d) anterior sternal facet. Scale bars equal 3 cm.

and Terry, who collected the specimen. Olson (1986, 1987) has correctly emended analogous dedicatory nomina.

Brodkorb (1963a) listed six paleospecies of *Morus*, three of them *Morus* (or *Moris*, a once-prevalent incorrect spelling) by original designation, the others being *M. loxostylus* (and *M. atlanticus*), already mentioned, and *M. lompocanus* (Miller) 1925. Miller himself (Miller and DeMay 1942) had already reassigned this species as "*Moris lompocana*". The geologically oldest of these six are *M. atlanticus* and *M. loxostylus*, both middle Miocene. Subsequently, early Miocene (late Hemingfordian) gannet bones from Delaware were assigned by Rasmussen (1998) as *Morus* cf. *M. loxostylus*.

The remaining five sulid paleospecies in Brodkorb (1963a) are distributed among the genera *Microsula* Wetmore 1938, *Miosula* Miller 1925, and *Palaeosula* Howard 1958. Warheit (1990, 1992a, 2002) synonomized all of these genera, along with *Sarmatosula* Grigorescu & Kessler 1977, with *Morus* on the grounds that they are all gannets, despite apparent genus-level differences. For example, Miller (1925) and Chandler (1990) note the different forelimb/hindlimb proportions in *Miosula* and *Morus*, and Howard (1958) notes that in humerus/ulna proportions *Miosula* is intermediate between *Morus* and *Palaeosula*. None of the named species of *Miosula* or *Palaeosula* are older than late Miocene, but *Microsula* dates to the early Miocene. The age of *Microsula pygmaea* (Milne-Edwards) has often been listed as middle Miocene, beginning with Brodkorb (1955, 1963a) and followed by most other authors, although Wetmore (1926, 1956) gave its age as early Miocene. Milne-Edwards (1874: 1, 11) called this French fossil "Aquitanian" (*aquitanienne*), but only in a geographic sense (not in a geologic-time sense) and specified its age only as Miocene; in any case, *M. pygmaea* dates to the Burdigalian rather than to the Aquitanian portion of the early Miocene. Darga et al. (1999) and Göhlich (2003) specify the early Miocene age of *M. pygmaea* as MN 2-3. The European Mammal Neogene zones 2 and 3 are shown by Daxner-Höch et al. (2004) to

span ~22-18 Ma, an interval about equivalent to the North American Hemingfordian. Göhlich (2003) and Daxner-Höch et al. (2004), however, have assigned to *M. pygmaea* a newly discovered middle Miocene (MN 5: 15.1 Ma: Barstovian equivalent) humerus and femur from Austria. Because of the 3-My minimal age difference in these sulids, the Austrian material might be better listed as *Microsula* cf. *M. pygmaea*.

Since the time of Brodkorb's *Catalogue*, additional Miocene material has been assigned to "*Sula*" by Ono in Japan and by Stucchi in Peru. Ono (1983) described a "gannet" from the middle Miocene of Japan as "*Sula* sp." With the discovery of additional material, however, Ono and Sakamoto (1991) reassigned this gannet to *Microsula* sp.

Stucchi and DeVries (2003) reported a middle Miocene *Sula* sp., based on a sternal fragment, from the Chilcatay Formation in Peru. We agree that this sternal specimen bears derived characters shared with *Sula* and represents the booby clade (if not the genus *Sula*) in the middle Miocene. Stucchi and Urbina (2004) subsequently described the new genus and species *Ramphastosula ramirezi*, a large Pliocene sulid with a remarkably derived toucan-like bill, from the Pisco Formation in Peru. We agree with Stucchi and Urbina (2004) that the closest affinity of *Ramphastosula*, known solely from cranial and rostral remains of several individuals, is with *Sula*. Stucchi and Urbina (2004:977) go on to state that *R. ramirezi* may have evolved from "one of the larger forms of *Sula* present in the older levels of the Pisco Formation . . ." This is a reference to the late Miocene *Sula magna* Stucchi 2003, based on wing and shoulder-girdle bones from the lower levels of the Pisco Formation. Of course, if *Sula magna* were such an ancestor it would be cladistically a member of the genus *Ramphastosula*. Similarly, the older "*Sula* sp." from the Chilcatay Formation may also be a member of the genus *Ramphastosula*. These three Peruvian taxa (middle Miocene *Sula* sp. Stucchi & DeVries 2003, late Miocene *Sula magna* Stucchi 2003, and Pliocene *Ramphastosula ramirezi* Stucchi & Urbina 2004) are all larger-bodied than any extant sulid. This unusual character, together with their common provenience, is suggestive of a mutual affinity for these three taxa. Two other sulids from the Pisco Formation, *Sula sulita* Stucchi 2003 and *Morus peruvianus* Stucchi 2003, both of the late Miocene (Hemphillian equivalent), seem to be correctly assigned to genus.

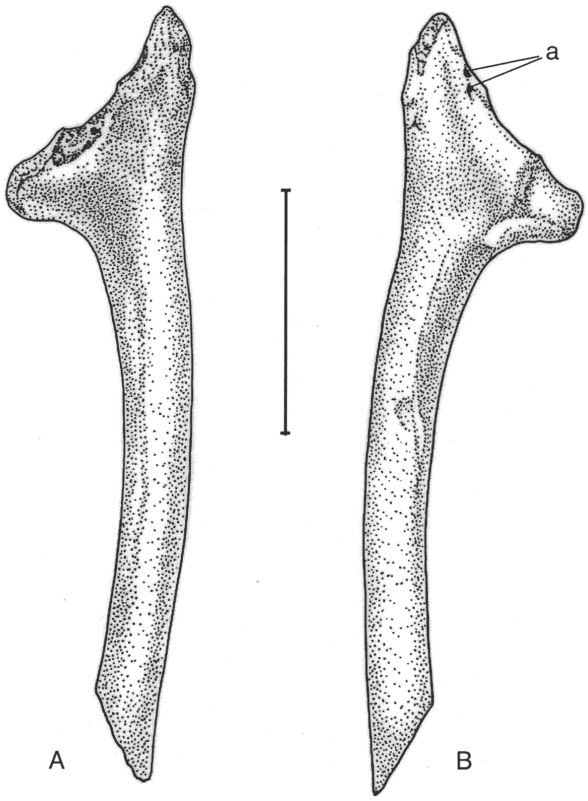


Figure 4. Left scapula of *Bimbisula melanodactylos* gen. et sp. nov., ChM PV2818. **A**, ventral view. **B**, dorsal view; (a) pneumatic foramina. Scale bar equals 2 cm.

Sulin Antiquity

Olson and Warheit (1988:10) stated that "the fossil record shows that the divergence between gannets (*Morus*) and boobies (*Sula, sensu stricto*) had already taken place by the middle Miocene, some 16 million years ago . . ." The burden of the passage from which this quotation is taken was primarily to emphasize the differences between *Morus* and *Sula*, and Olson and Warheit (1988) did not specify what 16 Ma (Barstovian age) *Sula* (if any) they had in mind. Apparently, they only meant that, since identifiable gannets already existed by 16 Ma, then their sister group (boobies) are also required to have diverged by that time, notwithstanding the nonappearance of identifiable booby fossils of such an age. Of course, had they recognized the early Miocene age of the morin *Microsula pygmaea*, they would have placed the divergence earlier, at least 20 Ma. And yet sulins have long appeared to be absent for much of this time. For example, regarding the Barstovian sulids of the Calvert Formation, Olson (1984:220) noted: "all the Calvert sulids are more similar to *Morus* [than to *Sula*]"; more decisively, Olson and Rasmussen (2001:261) observed: "All fossil Sulidae from Lee Creek Mine and the Calvert Formation are referrable to the genus *Morus* . . ." Warheit (2002: 42, 53), however, lists an undescribed small-bodied *Sula* sp. from the middle Miocene of Maryland, according to "Warheit & Olson, unpub. data". Although Olson and Warheit (1988) are correct in noting that the two clades of gannets and boobies must have diverged at some time deep in the Miocene, pre-Hemphillian sulins have been slow to be found. Fortunately, this situation has begun to change with the documentation of Stucci and DeVries' (2003) middle Miocene *Sula* sp. (? *Ramphastosula* sp.)

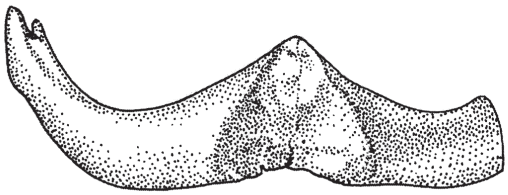


Figure 5. Furcula of *Bimbisula melanodactylos* gen. et sp. nov., ChM PV2818, in posterior view. Scale bar equals 1 cm.

Olson and Warheit (1988) regarded *Papasula* as more primitive than both *Morus* and *Sula*, and Sibley and Monroe (1990) consequently arranged the three genera in the following order: *Papasula*, *Morus*, *Sula*. Warheit (1990), however, determined by cladistic analysis that *Papasula* is more closely related to *Sula* than to *Morus*. Even though *Sula* and *Papasula* are thus shown to form a clade, the separate genus *Papasula* remains valid, in our opinion, as a taxon representing an earlier radiation of boobies which possesses almost as many *Morus*-like character states as it does *Sula*-like character states. In our opinion, *Papasula* is probably outside the clade of *Sula* + *Ramphastosula*. Like *Papasula*, the Atlantic Pliocene sulid described in this paper is also morphologically intermediate between *Morus* and *Sula*, but has considerably more *Morus*-like features than does Abbott's Booby. Although the new taxon shares one character state (of the coracoid) exclusively with *Papasula*, cladistc analysis places it as the sister group to *Papasula* plus *Sula*.

Geological and Paleoecological Setting

The Goose Creek Limestone, occurring throughout the area now occupied by the Cooper River meander in the vicinity of Charleston, South Carolina, is recognized as middle Pliocene and is also known by strata in Georgia and North Carolina (Weems et al. 1982, Campbell and Campbell 1995). Lithologically the Goose Creek Limestone in South Carolina is a medium-to-coarse-grained, buff-light gray quartzose and phosphate calcarenite containing abundant invertebrate fossils as well as some vertebrate remains. The latter have been relatively poorly known as the Goose Creek Limestone has been sampled for the most part by auger hole testing. The invertebrates, described by Tuomey and Holmes (1857), are represented largely by molluscs, usually as remnants of leached shells in the form of molds and casts (Weems et al. 1982).

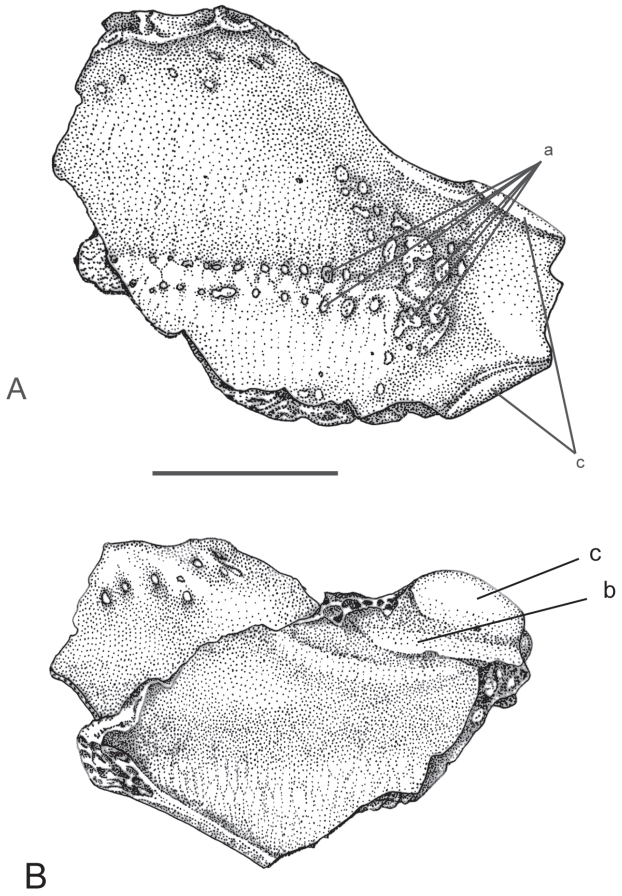


Figure 6. Sternum of *Bimbisula melanodactylos* gen. et sp. nov., ChM PV2818. **A**, dorsal view; (a) pneumatic foramina. **B**, right lateral view; (b) ventral lip of coracoidal sulcus, (c) dorsal lip. Scale bar equals 2 cm.

The closely related Raysor Marl of Cook (1936), renamed the Raysor Formation by Blackwelder and Ward (1979), has traditionally been placed stratigraphically beneath the Goose Creek Limestone. Weems et al. (1982) state that the term Raysor Formation should be restricted to early Pliocene biocalcarenites with quartzose matrix, and that the term Goose Creek Limestone should be restricted to early-to-middle Pliocene biocalcarenites with calcareous matrix; Weems et al. (1982) allow, however, that the stratigraphic relation between these two units is unclear and may represent onshore and offshore facies of a single depositional cycle. Campbell and Campbell (1995) divide the Goose Creek Limestone into (lithologically indistinct) lower and upper units on the basis of molluscan biostratigraphy, and place the unconformity with the Raysor Formation locally above rather than below the Goose Creek. They suggest that the Raysor is a laterally equivalent, coeval lithofacies of the upper Goose Creek, *contra* Blackwelder and Ward (1979). At the locations in which the remains of the two sulid individuals were collected, the Goose Creek Limestone overlies the late Oligocene Ashley Formation.

Aside from well logs and auger holes, the Goose Creek Limestone in South Carolina is found in a few exposures associated with stream banks and excavation sites such as marl pits and rock quarries with their attendant spoil piles. Distribution of the Goose Creek outcrops and records of subcrops are plotted by Weems et al. (1982). As with many other Goose Creek fossils, the two described herein were exposed

in terrain disturbed by excavation activities, thus precluding a precise knowledge of their stratigraphic positions.

The holotype, a partial skeleton (cavities of which contain the gray calcareous matrix typical of the Goose Creek Limestone), was found in excavation-disturbed sediments immediately above a lag deposit of phosphate nodules in a ditch along a railroad right-of-way, at the Seaboard Railroad Locality. Campbell and Campbell (1995) assign the Seaboard Railroad Locality to the upper unit of the Goose Creek Limestone.

A referred cranium was collected at the water's edge along the Cooper River at Wando Terminal in a dredge spoil of mixed sediments of the late Oligocene Ashley Formation, the Goose Creek Limestone, and the Pleistocene Wando Formation. The original stratigraphic level of this specimen is indicated by a matrix sample removed from the foramen magnum. The sample consists of Goose Creek gray calcareous matrix, unlike that of either the Ashley or Wando formations. Whether the cranium came from the upper or the lower unit of the Goose Creek Limestone cannot be determined.

Age. The age of the Goose Creek Limestone is dated at 3.9 to 3.2 Ma by Bybell (1990) on the basis of nannoplankton index fossils. Campbell and Campbell (1995) date the units of the Goose Creek Limestone more narrowly by a combination of molluscan zones and the best fit of the two units to the Krantz sea-level curve. They conclude that the lower unit of the Goose Creek corresponds to the Krantz curve's transgression 3, with a deposition date of 3.9 to 3.8 Ma, and that the upper unit dates to transgression 5, for an age of 3.6 to 3.5 Ma. This 3.9-3.5 Ma interval falls within the middle third of the Blancan North American Land Mammal Age.

Paleoecology. The environment in which the Goose Creek sediments were laid down was a broad coastal plain with valleys and streams. The climate was subtropical, although the hotter Mid-Pliocene Warm Period of 3.3-3.0 Ma was yet to come (Williams et al. 2009). The shallow marine deposits of the Goose Creek Limestone fill depressions to a thickness ranging 3-18 m in the Charleston area (Weems et al. 1982). This system is characterized by oysters (*Ostrea* sp.) dominating the epifauna and by an infauna evidenced by abundant calcareous annelid tubes, together with a host of other warm-water forms, many of which remain only as molds due to leaching (Campbell and Campbell 1995).

The vertebrate taxa associated with these warm-water deposits include unpublished specimens of the fossil walrus *Prorosmarus alleni* and of unnamed mysticete and odontocete whales; none of these perhaps far-migrating faunal members are good warm-temperature indicators (A. E. Sanders, personal communication). The modern *Odobenus rosmarus* (walrus), a cold-water species, is known to migrate as far south as North Carolina (Nowak and Paradiso 1983). In any case, the fossil record of the walrus family reveals a greater diversity of temperature preferences, including temperate and subtropical, than would be indicated by that of its one surviving species (Deméré 2006). The extinct walrus *Odobenus huxleyi*, a contemporary of *Prorosmarus alleni*, has been found in Florida (Morgan 1994, Deméré et al. 2003). Several shark taxa also occur in the Goose Creek sediments (Campbell and Campbell 1995).

Taphonomy. Some taphonomic alterations to the holotype of the new taxon by scattering and breakage are apparent. The disarticulation and scattering over a distance of a few feet (A. E. Sanders, personal communication) suggest that the skeleton was not buried intact but that some transporting agent, probably moving water, dissociated most of the skeleton. Of the 15 bones recovered all are unweathered and show sharp, unabraded edges where surfaces were broken. The general condition of the holotype indicates that little or no reworking occurred. No evidence of predation, scavenging, or hydrodynamic

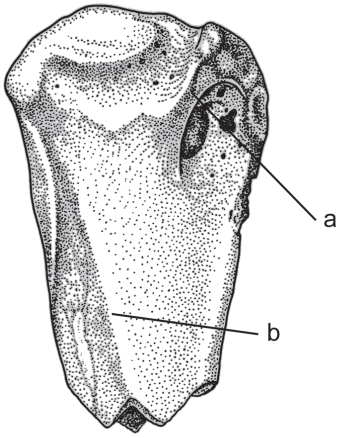


Figure 7. Proximal end of left humerus of *Bimbisula melanodactylos* gen. et sp. nov., ChM PV2818, in anconal view; (a) median crest, (b) central ridge. Scale bar equals 3 cm.

sorting was apparent. Breakage occurs as simple step-fractures rather than fractures in spiral patterns. The lack of spiral fractures indicates that the remains were not subjected to carnivore scavenging; "fresh" or "green" bone tends to fracture in a spiral pattern (Behrensmeyer et al. 1989). The simple fractures indicate either prolonged exposure and weathering (Conybeare and Haynes 1984), or, more likely in this case, crushing. The fractures were probably postdepositional and caused by sediment compaction. The paratypic cranium shows some distortion, which long burial typically imparts to fossil skulls, plus minor bone damage, probably from minimal transport.

Systematic Paleontology

Class Aves
Order Pelecaniformes
Suborder Sulae
Family Sulidae
Bimbisula melanodactylos gen. et sp. nov.

Etymology. Genus name: "Dawn Booby", from Bimbi, Gullah personal name, from Fula (Nigerian and West African lingua franca) *bimbi* ("dawn"). The Gullah name has reference to the South Carolinian locality of the type specimens, and avoids the overly-used element *Eo-* (from Greek *Eos*, "Dawn"). Traditionally, sulid generic names have reference to the "foolish" lack of fear in these birds to human predation (Icelandic *sula* = Greek *moros* = English *booby* = "fool"). Not part of this tradition, *Bimbisula* does not intentionally resemble the word "bimbo" or the word "imbecile". The gender of *Bimbisula*, like that of *Sula*, is feminine. Species epithet: Greek for "black-fingered", by analogy with the Homeric expression *rhododactylos Eos* ("rosy-fingered Dawn", *Odyssey* 5.121, 23.241). The Black-fingered Dawn Booby's name has reference to the black color of the iron-darkened type specimens, which do include a finger bone, and also pays homage to another sulid species, *Sula dactylatra*, whose name also seems to signify "black-fingered". *Bimbisula melanodactylos*, like other sulids, may have had black primaries. Like *rhododactylos*, *melanodactylos* is a common-gender adjective (masculine and feminine).

Diagnosis. Sulid larger than any extant species of boobies (genera *Sula* and *Papasula*), of similar body size to the smaller modern gannets (*Morus serrator*, *M. capensis*); without observable autapomorphies of its own in the holotype, a mosaic of gannet-like and booby-like character states, including the following features possessed by *Morus* but not by *Sula*: rostrum covered by rough rhamphotheca except just anterior to nasofrontal hinge; coracoid with anterior sternal facet long and narrow; scapula with pneumatic foramen at acromion on the dorsal side; sternum with ventral lip of coracoidal sulcus having greater posterior extent than does dorsal lip; humerus with median crest approximately parallel to shaft; synsacrum with anterior articular facet of centrum deeper than wide; femur slender, shaft width <10% of femur length; tibiotarsus with inner cnemial crest trending medially and making contact with the ligamental attachment; tarsometatarsus with intercotylar prominence short and gently rounded; and the following features possessed by *Sula* but not by *Morus*: coracoid with long axis of furcular facet rotated about 35° from axis of the shaft so that it is parallel with head of coracoid; furcula with sternal facet as wide as it is deep; sternum with anterior pneumatic foramina mostly paired left and right, not occurring on midline; humerus with angular central ridge; femur with fibular groove deeply right-angled and posterolaterally oriented; tarsometatarsus with tubercle for M. tibialis anticus as high on the shaft as the distal rims of the proximal foramina.

Holotype. Charleston Museum PV2818, partial skeleton of a single individual including the rostrum, left and right mandibular fragments, furcular end of left coracoid, sternal end of right coracoid, symphyseal fragment of furcula, anterior ends of both scapulae, fragmentary sternum, proximal end of left humerus, mostly complete right manual phalanx II:1, fragmentary right vertebral rib, fragmentary synsacrum, complete right femur, proximal end of right tibiotarsus, and complete right tarsometatarsus; collected by James Malcom, 1980.

Referred specimen. Science Museum of Minnesota P90.38.8, cranium collected by B. R. Erickson, 27 October 1990.

Horizon. Middle Pliocene, middle Blancan. Holotype: Goose Creek Limestone, upper unit; absolute age: 3.6-3.5 Ma. Referred cranium: Goose Creek Limestone, unit unknown; absolute age: 3.9-3.8 or 3.6-3.5 Ma.

Locality (Fig. 1). South Carolina, Charleston County. Holotype: Seaboard Railroad Locality: north ditch along Seaboard Coast Line Railway, 1.0 mi (1.6 km) W of Dorchester Road overpass. Referred cranium: Wando Terminal Site.

Description and Comparison

For description of the skeleton of *Bimbisula melanodactylos* and comparison with that of other sulids, see Appendix: List of Character States. The variety of elements in the partial skeleton of this taxon enables perception of its *Morus-Sula* mosaic nature, which would have been less obvious had it been represented by a single-bone holotype (as is all too common in paleornithology). Although this mosaicism can be seen in most of the known bones of *Bimbisula*, five elements–coracoid, sternum, femur, tarsometatarsus, and referred cranium–will be especially noted as most striking in this respect.

In the coracoid of *Bimbisula* (Fig.3) the anterior sternal facet is primitively long and narrow as in *Morus* and the outgroups, rather than triangular as in *Sula* and *Papasula*; and yet the sternocoracoidal process is tabular and unelevated as in *Sula* and *Papasula* rather than slightly elevated as in *Morus* and *Anhinga*.

Also, the long axis of the furcular facet is tilted medially from the axis of the shaft as in *Sula* and *Papasula* rather than being parallel with the shaft as in *Morus* and *Phalacrocorax*. The derived state of enlargement of the head of the coracoid, which is uniquely shared by all gannets, is apparently lacking in *Bimbisula*. Unfortuately, Howard's (1936) quantification of this (using ratios of several measurements of the coracoidal head to coracoidal length) cannot be directly applied to *Bimbisula*. Furcular and sternal ends of the left and right coracoids, respectively, are its only coracoidal specimens. Although these two specimens would seem to overlap in a composite (complete) coracoid, there are no characters of the shaft that would indicate the amount of overlap and thus the length of the coracoid. If, however, the length were to be extrapolated from the head measurments, an un-*Morus*-like result is given: *Bimbisula* must lack coracoidal head enlargement, unless its coracoid were to be anomalously stubby for a sulid.

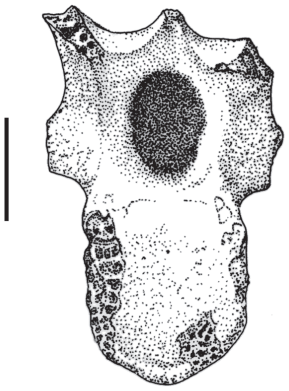


Figure 8. First sacral vertebra of *Bimbisula melanodactylos* gen. et sp. nov., ChM PV2818, in anterior view. Scale bar equals 0.5 cm.

In the sternum of *Bimbisula* (Fig. 6) the ventral lip of the coracoidal sulcus has greater posterior extent than does the dorsal lip, as in *Morus* and the outgroups, although this primitive state is also shared with *Papasula*; in *Sula* the dorsal lip has the greater posterior extent. *Bimbisula* shares with *Sula* and *Papasula* the derived state of arrangement of the anterior pneumatic foramina: numerous, more or less paired left and right and not occurring on the midline. In the differently derived condition in *Morus* the foramina are also numerous but not paired left and right, with some on the midline.

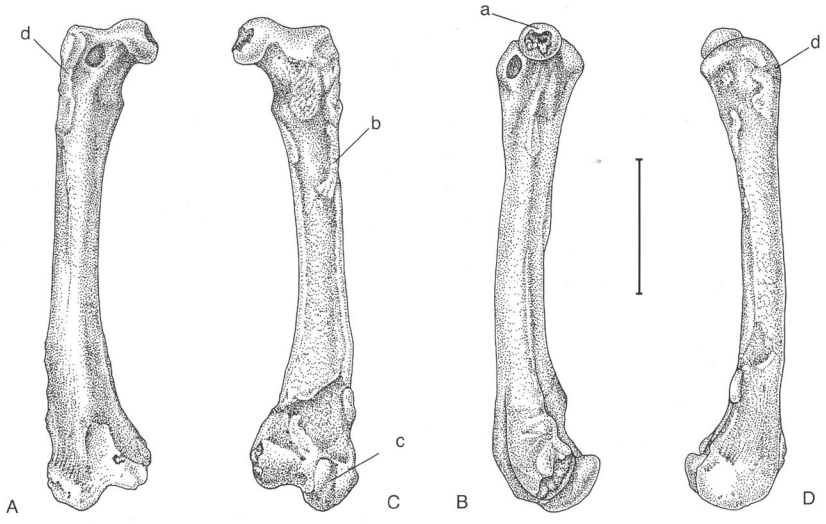


Figure 9. Right femur of *Bimbisula melanodactylos* gen. et sp. nov., ChM PV2818. **A**, anterior view. **B**, medial view, showing (a) smooth surface of head where attachment of round ligament (broken away in this specimen) would have occurred if it had been in the more proximal position as in *Sula*. **C**, posterior view; (b) impression of insertion of M. flexor ischiofemoralis, (c) fibular groove. **D**, lateral view; (d) trochanteric ridge. Scale bar equals 2 cm.

The femur of *Bimbisula* (Fig. 9) is a *Morus-Sula* mosaic entirely by the retention of primitive character states. For example, its *Morus*-like posterior position of the impression of M. flexor ischiofemoralis is shared with the outgroups, and its deep, right-angled fibular groove is shared not only with *Sula* and *Papasula*, but also with the outgroups. The lack of a shallow fibular groove (derived in gannets) is at least suggestive of non-gannet status.

The tarsometatarsus of *Bimbisula* (Fig. 11) shares with that of *Morus* a short, gently-rounded intercotylar prominence. The middle calcaneal ridge in *Bimbisula*, like that of *Morus* and the outgroups, is undeveloped, although this condition is also shared with *Papasula* and *Sula sula*; the other species of *Sula* have the derived state of a large middle calcaneal ridge. Most remarkably, *Bimbisula* shares with *Sula* and *Papasula* the derived location of the tubercle for M. tibialis anticus at the height of the distal rims of the proximal foramina, rather than more distally as in *Morus* and the outgroups.

In the referred cranium of *Bimbisula* (Fig. 12), as in that of *Morus*, the supraoccipital overhangs the foramen magnum without obscuring its upper rim in posterior view (obscured in *Sula* and *Papasula*); the shape of the foramen magnum in *Bimbisula*, however, is like that of *Sula* and *Papasula*, somewhat squarish, rather than higher than wide as in *Morus*. The two foramina for cranial nerves IX and X-XI are close together so that the cranial surface between them appears strut-like as in *Papasula* and the more down-clade species of *Sula*, rather than being further apart as in *Morus*. The foramina for cranial nerve XII are positioned as in *Papasula* and most species of *Sula* rather than more ventrally as in *Sula nebouxii* and *S. variegata*, or more dorsally as in *Morus* and the outgroups. The basitemporal plate of *Bimbisula* displays large subcondylar foramina as in *Morus* and *Papasula* (small or absent in *Sula*); *Bimbisula* shares, however, with *Sula* and *Papasula* the transverse ridge on the basitemporal plate rather than the transverse fossa of *Morus*.

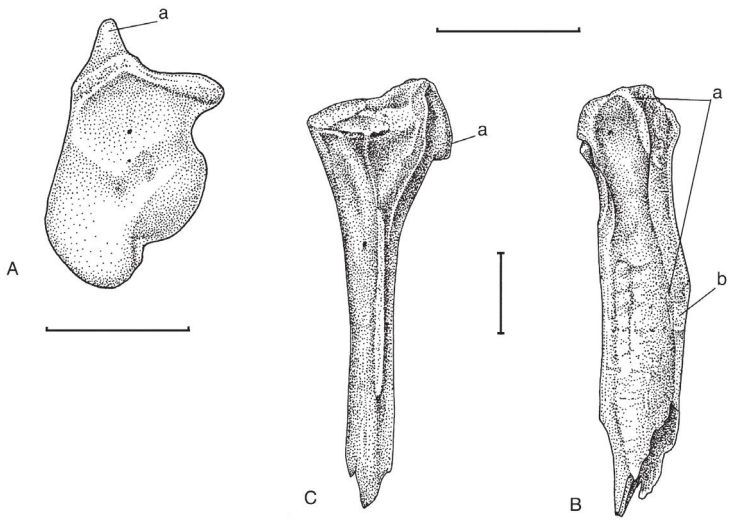


Figure 10. Proximal end of right tibiotarsus of *Bimbisula melanodactylos* gen. et sp. nov., ChM PV2818. **A**, proximal view. **B**, anterior view; (a) inner cnemial crest, (b) ligamental attachment. **C,** lateral view. Scale bars equal 1 cm.

Discussion

This study supports the finding of Warheit (1990) that *Papasula* is a booby genus rather than the sister taxon to gannets plus boobies. *Sula* and *Papasula* are shown in the present study to be booby genera more derived than *Bimbisula*. In Warheit (1990) *Papasula* is found to resemble *Morus* more than *Sula* in 48% of characters in which *Morus* and *Sula* differ and in which *Papasula* is scored the same as one or the other (N = 75; 36:39). We can confirm this finding for *Papasula* by noting that in 30 additional characters used in this study which were not used in Warheit (1990), *Papasula* resembles *Morus* more than *Sula* in 40% (12:18). Combining the data of Warheit (1990) and of this study, *Papasula* resembles *Morus* more than *Sula* in 46% of characters. In contrast, the (noncranial) characters in which the holotype of *Bimbisula melanodactylos* resembles *Morus* more than *Sula* amount to 70% (N = 40; 28:12). The resemblance of *Bimbisula* to *Morus* drops to 50%, however, when *Papasula* is included as an allied booby. That is, the holotype of *Bimbisula melanodactylos* resembles gannets rather than boobies in only 50% of all characters in which *Morus* and *Sula* + *Papasula* differ (12:12). In cranial characters in which *Morus* and *Sula* differ, the referred cranium resembles that of *Morus* rather than *Sula* in 60% (6:4). Again, with *Papasula* included, the cranial specimen resembles gannets rather than boobies in only one-third of the characters in which *Morus* and *Sula* + *Papasula* differ (2:4). Thus, in the phyletic series (outgroup, *Morus, Bimbisula, Papasula, Sula*), between *Bimbisula* and more derived boobies there is a morphological distance of a magnitude similar to that between *Papasula* and *Sula*. (Note: Sometimes in the literature the words "cranial" and "cranium" are used as if they were synonymous with "skull", even though expressions such as "craniofacial" should remind one that "cranium" is less inclusive than "skull". In this paper such elements of the head skeleton as the rostrum and schleral ossicles are considered noncranial.)

Without unambiguous autapomorphies of its own, *Bimbisula* might have appeared to be a possible ancestor of later boobies. The cranial specimen referred to *Bimbisula melanodactylos* bears this taxon's only autapomorphy, the low angle of temporal-nuchal ridge divergence, a state homoplasious with that of *Sula nebouxii* and *S. variegata* (Blue-footed and Peruvian Boobies). However such an autapomorphy might preclude *Bimbisula melanodactylos* from a position ancestral to modern boobies, *B. melanodactylos* is in any case too primitive too late to be such an ancestor. The coracoid of this species is still a *Morus*-*Sula* mosaic in the mid-Blancan, whereas *Sula guano* Brodkorb 1955 already possesses a coracoid of modern *Sula* aspect in the earliest Blancan. One of us (RDB) has examined copies of the coracoids of *Sula guano* and the sympatric *Morus peninsularis* Brodkorb 1955 in the paleontological collections of the University of Kansas. *Sula guano* shares all of the derived character states of the coracoid of *Sula* recognized in this study (Appendix: 7-12).

Despite its closeness in age to *Bimbisula melanodactylos*, *Sula guano* from the early Pliocene of Florida, in light of its more derived character states, cannot be an earlier member of an Atlantic genus *Bimbisula*. *S. guano* is validly assigned to *Sula*. Nor do we think that *Morus peninsularis*, from the same paleofauna as *S. guano*, is assignable to *Bimbisula*; *M. peninsularis* lacks derived character states of the coracoid shared by *Bimbisula* and *Sula*, and is a good species of *Morus*, with which it shares at least one derived character state (enlarged coracoidal head). *M. peninsularis*, formerly known only by two coracoids and a cervical vertebra, is now better known by discoveries of additional coracoids and limb bones from the Yorktown Formation in North Carolina (Olson and Rasmussen 2001), and of numerous specimens from the late Pliocene of Morocco (Mourer-Chauviré and Geraads 2010).

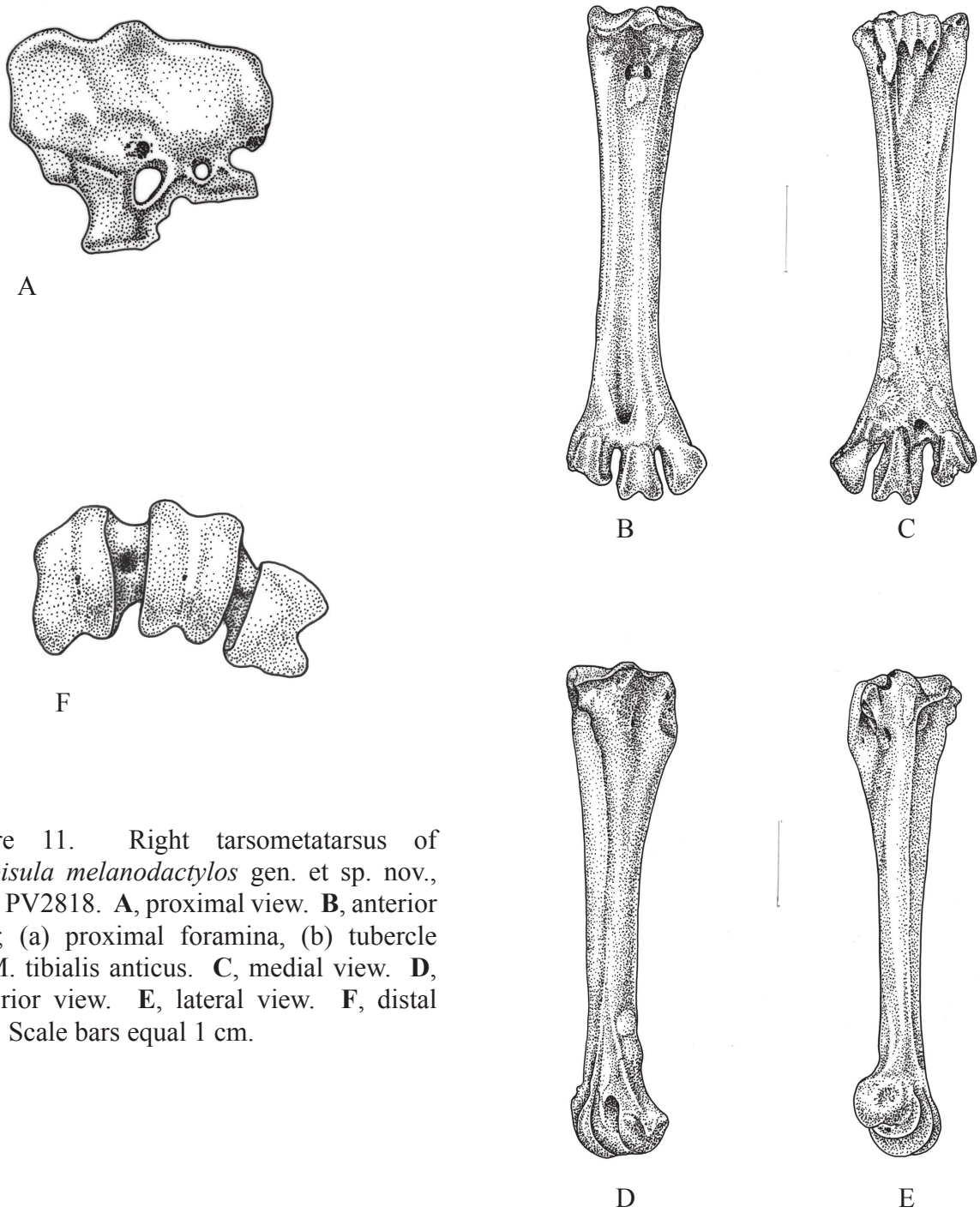


Figure 11. Right tarsometatarsus of *Bimbisula melanodactylos* gen. et sp. nov., ChM PV2818. **A**, proximal view. **B**, anterior view; (a) proximal foramina, (b) tubercle for M. tibialis anticus. **C**, medial view. **D**, posterior view. **E**, lateral view. **F**, distal view. Scale bars equal 1 cm.

A Corollary for Sister Taxa with Ghost Lineages

Bimbisula melanodactylos is apparently a "persistent ancestral form"–a late member of its genus (which is otherwise unknown)–in view of the fact that the Pliocene date of its type specimens is certainly later than the time of the divergence of the two clades *Bimbisula* and *Papasula* + *Sula*. Such a lack of fossil evidence for the true temporal range of a taxon is by no means unusual in avian paleontology, and in this case necessitates a ghost lineage extending from the middle Pliocene to the oldest known sulin, the middle Miocene *Sula* sp. Stucchi & DeVries 2003 (possibly *Ramphastosula* sp.). New discoveries can have the effect of either lowering or increasing the mean ghost lineage duration (GLD) for its group (Weishampel 1996), and the ghost lineage required by the new *Bimbisula* clade is slightly longer than average for the Sulidae. Using Weishampel's (1996) method of calculating mean GLD in a three-taxa tree with Morini (including *Microsula*) known from the early Miocene, *Sula* + *Ramphastosula* from the middle Miocene, and *Papasula* with Recent subfossils only (Steadman et al. 1988), we have a mean GLD of about 11 My. With *Bimbisula* (known from the Blancan only) added to make a four-taxa tree, the mean GLD becomes about 12 My.

It might be objected that it seems unlikely that the relatively primitive *Bimbisula* would be known only from a late relict species in the middle Pliocene and yet never recognized among the thousands of sulid fossils known from the middle Miocene through early Pliocene of the western North Atlantic. However, these thousands of (Lee Creek Mine, or PCS Phosphate Mine) fossils, most recently reviewed by Olson and Rasmussen (2001) and assigned to various paleospecies of *Morus*, are disarticulated bones (rarely partial skeletons) which "may be the result of shark regurgita" (Olson and Rasmussen 2001:238), or are in any case of similar taphonomic sorting. *Bimbisula* would best be recognized from partial skeletons, and many of its bones, or fragments thereof, in isolation would appear to be of *Morus*.

This situation should not be surprising. If it is true that sister taxa are of equal age, it should then be an expected corollary, for sister taxa with apparently different times of origin, that the earliest, apparently missing, members of the apparently younger sister group probably resemble the other sister group so closely as to make the earliest members of the two groups mutually confusable. Numerous analogous examples of this can be cited from the fossil record, but two cases can suffice here:

(1) Among saurischian dinosaurs, a late-Triassic-spanning ghost lineage formerly connected the (derived) Sauropoda to its apparently older sister group, the Prosauropoda (e.g., Wilson and Sereno 1998), but now "the stratigraphic gap between the first appearances of Sauropoda and Prosauropoda no longer exists" (Yates and Kitching 2003). The gap was filled in not only by discoveries of several late Triassic sauropods but also by the realization that the late Triassic melanorosaurids are sauropods and not prosauropods, which they resemble; despite general resemblance of melanorosaurs to prosauropods, melanorosaurs display some sauropod synapomorphies, e.g., suprapostzygapophyseal laminae on the dorsal vertebrae, elongated pedal unguis I, and shortened metatarsal, among other characters (Yates and Kitching 2003, Wilson 2005).

(2) Among the early tetrapods, the Seymouriamorpha (previously thought to be included in some way among the reptiliomorphs) were shown by the cladistic analysis of Vallin and Laurin (2004) to be the sister group to Amphibia + Reptiliomorpha. Vallin and Laurin (2004) did not mention the problem that Seymouriamorpha, known as being probably restricted to the Permian Period, is apparently too young to be such a sister group. The oldest known seymouriamorph, *Utegenia shpinari*, shown by Klembara (2005)

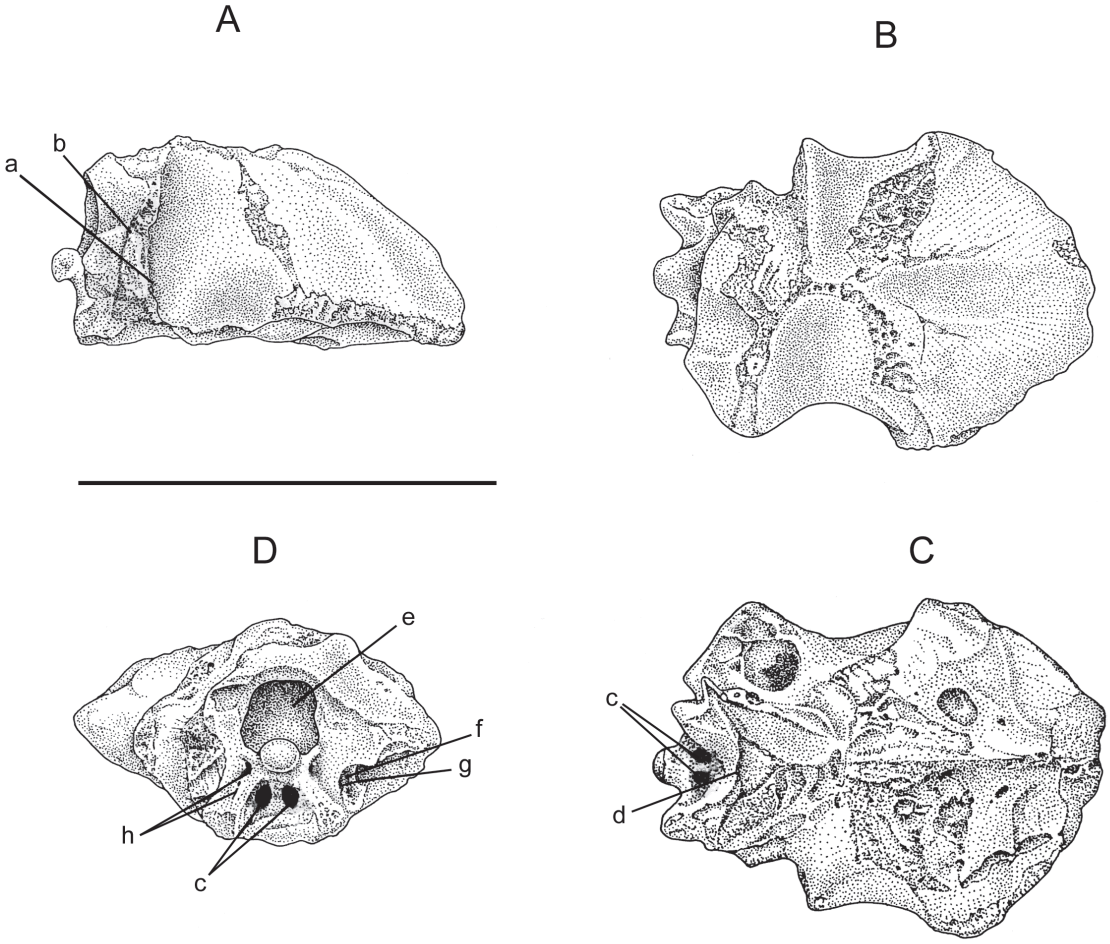


Figure 12. Cranium, SMM P90.38.8, referred to *Bimbisula melanodactylos*, gen. et sp. nov., as paratype. **A**, right lateral view; (a) temporal ridge, (b) nuchal ridge. **B**, dorsal view. **C**, ventral view; (c) subcondylar foramina, (d) transverse ridge. **D**, ventrally oblique posterior view; (e) foramen magnum, (f) foramen for cranial nerve IX, (g) foramen for cranial nerves X-XI, (h) foramina for cranial nerve XII. Scale bar equals 5 cm.

to be the most basal seymouriamorph, is from the Kurgalian Formation in Kazakhstan of early Permian, or questionably late Pennsylvanian, age (Laurin 1996). In light of the above, it might be fruitful to ask if the Carboniferous-spanning ghost lineage of seymouriamorphs older than *Utegenia* could possibly be populated from misidentified fragmentary "reptiliomorphs" of the Carboniferous. The method would be to look among Carboniferous tetrapods for otic tubes, reduced posttemporal fossae, postorbital with elongate ramus for the prefrontal, or some other derived seymouriamorph characters.

It is reasonable to expect that there may have been sulin analogues of sauropod (non-prosauropod) malanorosaurs, or seymouriamorph "reptiliomorphs", i.e., old sulins that resembled morins. These morin-like sulins might be detectable by the possession of some of the derived states noted above: e.g., a medial tilt of the coracoid's furcular facet, a sulin arrangement of the anterior pneumatic foramina in the sternum, a sulin transverse ridge on the basitemporal plate, etc.

Phylogenetic Analysis

The holotype (a partial skeleton without cranium) and a cranium referred to *Bimbisula melanodactylos* represent two individuals of presumably the same species, sulids of the same body size, but without overlapping skeletal elements. Both indivuals occupy identical cladistic positions with other Sulidae when cranial and noncranial characters are analyzed separately, a result consistent with their belonging to the same species. The cladogram shown in Figure 13 is generated by PAUP Version 4.0b10 on the basis of 77 unordered and equally weighted characters: 65 noncranial and 12 cranial characters, relating to the holotype (lacking a cranium) and the paratype (cranium only), respectively. Characters which should logically have been ordered came out ordered in the resulting tree despite being entered as unordered. *Pelecanus* was designated as the outgroup, with suborder Sulae (including *Anhinga* and *Phalacrocorax*) treated as the ingroup. A branch and bound search yielded a single most parsimonious tree of 142 steps (Consistency Index = 0.7958, Retention Index = 0.9052). When *Bimbisula* was represented separately by the holotype and by the referred cranium, trees identical to those of Figure 13 were obtained (except that *Anhinga* appears as sister taxon to *Phalacrocorax* in the cranial-character tree). The cladogram for the holotype (using 65 noncranial characters) has a length of 113 steps (Consistency Index = 0.7788, Retention Index = 0.9020); the cladogram for the cranium (using 12 cranial characters) has a length of 28 steps (Consistency Index = 0.8929, Retention Index = 0.9412).

Temporal calibration. Friesen and Anderson (1997) published a molecular distance study of the Sulidae, by which one might estimate the time of divergence of the two clades *Morus* and *Bimbisula* + *Papasula* + *Sula* independently of the fossil record. Friesen and Anderson's (1997) cladogram of the Sulidae is congruent with that of Warheit (1990) and of the present paper except in two respects: they resolve the relationships of the three extant species of *Morus*; and their cladogram is differently rooted, so as to make *Papasula* a member of the gannet clade (discussed below).

Temporal equivalence of molecular distance is fraught with uncertainty since rates of base substitution vary greatly between taxa (Welch and Bromham 2005). We do not dispute, however, that the rate of 0.2%/My for transversions in sulid cytochrome *b* used by Friesen and Anderson (1997) is a reasonable approximation. The cytochrome *b* transversions reported by Friesen and Anderson (1997), moreover, seem to be unsaturated and useful for estimating genus- and family-level divergences. Divergence dates derived from their distance data and suggested base-substitution rate can be taken only as approximations,

but do have the merit of congruency with the fossil record as we understand it. Their average transversion distance of 8.55% between their cormorant outgroup and the sulid ingroup would give a cormorant-sulid divergence date in the middle Eocene (43 Ma: late Uintan); this is consistent with the fossil record, in which the oldest known cormorant is of at least early Oligocene age (Phosporites du Quercy: Unwin 1993). The average transversion distance between *Papasula* and *Sula*, 3.94%, suggests an early Miocene date (20 Ma: mid-Hemingfordian) for their divergence, which would approximate the minimal age of the common ancestor of *Bimbisula*, *Papasula*, and *Sula*. This is not in conflict with a presumed date of ~17 Ma for the middle Miocene *Sula* sp. (? *Ramphastosula* sp.) of Peru "en la base del Mioceno medio" (Stucchi and DeVries 2003:97-98). The average transversion distance between *Morus* and *Papasula* + *Sula*, 4.51%, would provide a date somewhat earlier in the early Miocene (23 Ma: late Arikareean) for the approximate age of their latest common ancestor (not in conflict with the oldest possible date for *Microsula pygmaea*, ~22 Ma). As noted above, a gannet-booby divergence so dated would preclude the aberrant Oligocene sulids *Empheresula arvernensis* and *Prophalacrocorax ronzoni* from membership in either of the two fundamental clades of extant sulids. *Masillastega rectirostris* Mayr 2002 from the middle Eocene Messel Formation (49 Ma) in Germany was tentatively assigned to "?Sulidae"; although there seem to be good anatomical reasons for this assignment, the fresh-water, non-plunge-diving (long-beaked) *Masillastega* probably antedates the cormorant-sulid divergence.

By a difference in rooting, Friesen and Anderson (1997) show *Papasula* forming a clade with *Morus* rather than with *Sula*. This was apparently caused by their outgroup, *Phalacrocorax pelagicus* (Pelagic Cormorant), becoming attached to the midpoint of their ingroup tree (on the long line segment between *Papasula* and *Sula*) by long-branch attraction, as uninformative outgrops can do. Smith (1994:281) has noted that rooting by outgroups is more reliable in morphological than in molecular analyses: "Outgroup rooting in morphological data works best by including the two most successive sister-groups, but for sequence data this may not be sufficient by itself to reduce overprinting at variant sites to a level that will ensure the success of tree-building algorithms." Klicka et al. (2003:170) observe "Using a more distant outgroup results in a root placement on the longest internal branch" in molecular analyses.

Retrieving Friesen and Anderson's (1997) molecular data from Genbank, we explored their data using MacClade. With transitions and transversions equally weighted, we find the cladogram with *Sula* and *Papasula* constrained to be sister taxa only 4 steps longer than Friesen and Anderson's cladogram with *Morus* and *Papasula* as sister taxa (402 steps vs. 398 steps). According to standard statistical tests (provided by PAUP Version 4.0.0d64), the lengths of these two trees lack significant dfference (Templeton test: P = 0.3898; Winning-sites test: P = 0.4990; Kishino-Hasegawa test: P = 0.3374). Using transversions only, we find the tree with *Sula* and *Papasula* constrained to be sister taxa only 3 steps longer than Friesen and Anderson's tree (122 steps vs. 119 steps). Again, these lengths lack significant difference (Templeton test: P = 0.4236; Winning-sites test: P = 0.5488).

Acknowledgments and Institutional Abbreviations

We thank the following for their helpful assistance: A. E. Sanders of the Charleston Museum (ChM) for the loan of the holotype of *Bimbisula melanodactylos*, and for sharing his knowledge of the Goose Creek Limestone; R. M. Zink of the Bell Museum of Natural History, University of Minnesota (MMNH), for loan of skeletal specimens and for providing laboratory access to PAUP and MacClade; G. F. Barrowclough of the American Museum of Natural History (AMNH), S. L. Olson of the U.S. National Museum (USNM), and R. O. Prum of the Museum of Natural History, University of Kansas (KU), for loans of skeletal specimens; L. D. Martin, also of KU, for access to the paleontological collection; Julie Martinez and Jeffery Birch, both of the Science Museum of Minnesota, for drawing the figures and the cover illustration, respectively; Timothy Erickson for redacting the figures; and Jim Weil and Emily Purcell, both of the Science Museum of Minnesota, for translation of German, Spanish, and French literature. This paper was improved by the comments of two anonymous reviewers.

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Appendix: List of Character States

Characters which are taken from, or are similar to, those described in Warheit (1990) and/or Van Tets et al. (1988) are noted at the end of each character listed below. "W" followed by a character designation refers to the character-state list and matrix in Warheit (1990), and "V" followed by a number refers to page number in Van Tets et al. (1988). Characters not so noted were determined independently of those two sources.

1. Schlerotic ring: (0) 15 plates; (1) 13 plates; (2) 12 plates; (3) 10 plates. (0: *Pelecanus*; 1: *Phalacrocorax*; 2: *Anhinga*, *Morus*, *Papasula*; 3: *Sula*; ?: *Bimbisula*) [W OSS 1]

2. Rostrum: posterior dorsal area, directly in front of nasofrontal hinge: (0) smooth (as elsewhere on surface of rostrum); (1) smooth (unlike the rest of surface of rostrum); (2) covered by rough rhamphotheca (as elsewhere on surface of rostrum). (0: *Pelecanus*, *Phalacrocorax*, *Anhinga*; 1: *Morus*, *Bimbisula*; 2: *Papasula*, *Sula*) [W SKL 9; V 36-37]

3. Rostrum: elevation of nasal groove: (0) at mid-height; (1) above mid-height. (0: *Pelecanus*, *Phalacrocorax*, *Anhinga*, *Morus*, *Bimbisula*, *Papasula*; 1: *Sula*).

4. Rostrum: cross-sectional shape at posterior end: (0) ventral margin broader laterally than the dorsal margin, measured at level of nasal grooves, producing a trapezoidal cross-section; (1) ventral and dorsal margins equal or subequal in lateral bredth, producing a rectangular cross-section. (0: *Phalacrocorax*, *Anhinga*, *Morus*, *Bimbisula*, *Papasula*; 1: *Pelecanus*, *Sula*) [W SKL 12]

5. Mandible: lateral cotyle: (0) anterior end terminates with a dorsally extending articular surface; (1) anterior end terminates with a smooth and anteriorly extending articular surface. (0: *Pelecanus*, *Phalacrocorax*, *Anhinga*, *Morus*, *Papasula*, *Sula sula*; 1: other *Sula*; ?: *Bimbisula*) [W MAN 1]

6. Mandible: caudal fossa, dorsal rim: (0) concave; (1) convex. (0: *Pelecanus*, *Phalacrocorax*, *Anhinga*, *Morus*, *Papasula*; 1: *Sula*; ?: *Bimbisula*).

7. Coracoid: furcular facet: (0) long axis parallel to shaft; (1) long axis tilted medially and parallel with head; (2) long axis almost perpendicular to shaft. (0: *Pelecanus*, *Phalacrocorax*, *Morus*; 1: *Bimbisula*, *Papasula*, *Sula*; 2: *Anhinga*)

8. Coracoid: bicipital attachment: (0) shallow; (1) well-defined; (2) deeply defined. (0: *Pelecanus*, *Phalacrocorax*, *Anhinga*, *Morus*; 1: *Bimbisula*, *Papasula*; 2: *Sula*; [W COR 6]

9. Coracoid: furrow between bicipital attachment and glenoid facet: (0) asymmetrical; glenoid side steep, bicipital side more reclined; (1) narrow and symmetrical by steepening of both sides; (2) broad and symmetrical by relative reclension of both sides. (0: *Phalacrocorax*, *Morus*, *Bimbisula*, *Papasula*; 1: *Pelecanus*, *Sula*; 2: *Anhinga*) [W COR 9; V 40]

10. Coracoid: anterior sternal facet: (0) long and narrow; (1) triangular. (0: *Pelecanus*, *Phalacrocorax*, *Anhinga*, *Morus*, *Bimbisula*; 1: *Papasula*, *Sula*) [W COR 1; V 39-40]

11. Coracoid: sternocoracoidal process: (0) elevated above sternal facets; dorsal margin steeply upswept; (1) slightly elevated above sternal facets; dorsal margin gently upswept; (2) not elevated; process tabular. (0: *Pelecanus*, *Phalacrocorax*; 1: *Anhinga*, *Morus*; 2: *Bimbisula*, *Papasula*, *Sula*) [W COR 3; V 40]

12. Coracoid: path of anterior intermuscular line: (0) ventralmost extent is lateral to widest part of anterior sternal facet; (1) swerves medially to connect with widest part of anterior sternal facet. (0: *Pelecanus*, *Phalacrocorax*; 1: *Anhinga*, *Morus*, *Bimbisula*, *Papasula*, *Sula*)

13. Scapula: pneumatic foramen at acromion: (0) absent; (1) in dorsal side; (2) in ventral side. (0: *Pelecanus*, *Phalacrocorax*, *Anhinga*; 1: *Morus*, *Bimbisula*, *Papasula*; 2: *Sula*) [W SCP 2; V 39]

14. Scapula: blade: (0) essentially straight; (1) distal end bent. (0: *Pelecanus*, *Phalacrocorax*, *Anhinga*, *Morus*; 1: *Papasula*, *Sula*; ?: *Bimbisula*)

15. Furcula: pneumatic foramen between coracoidal facet and scapular tuberosity: (0) absent; (1) present. (0: *Pelecanus*, *Phalacrocorax*, *Anhinga*, *Papasula*, *Sula*; 1: *Morus*; ?: *Bimbisula*) [W FUR 1; V 39]

16. Furcula: coracoidal facet: (0) apneumatic, or with tiny foramina, in region ventral and posterior to facet; (1) pneumatic, but without extensive excavation; (2) pneumatic and excavated. (0: *Phalacrocorax*, *Anhinga*, *Papasula*; 1: *Pelecanus*, *Morus*; 2: *Sula*; ?: *Bimbisula*) [W FUR 3]

17. Furcula: clavicle in lateral view: (0) much thinner near symphysis than near coracoidal facet; (1) about same thickness near symphysis and near coracoidal facet. (0: *Pelecanus*, *Phalacrocorax*, *Anhinga*, *Papasula*, *Sula*; 1: *Morus*; ?: *Bimbisula*) [V 39]

18. Furcula: ridge extending from sternal facet across dorsal surface of clavicle: (0) absent; (1) present. (0: *Pelecanus*, *Phalacrocorax*, *Morus*, *Bimbisula*, *Papasula*; 1: *Anhinga*, *Sula*)

19. Furcula: sternal facet: (0) left-right axis greater than dorsal-ventral axis; (1) deeper than wide. (0: *Pelecanus*, *Phalacrocorax*, *Anhinga*, *Bimbisula*, *Papasula*, *Sula*; 1: *Morus*) [V 39]

20. Sternum: anterior pneumatic foramina: (0) few in number, usually paired left and right, sometimes with one at midline; (1) numerous, scattered, and unpaired, with some on midline; (2) numerous, tend to be paired left and right, do not occur on midline. (0: *Pelecanus*, *Phalacrocorax*, *Anhinga*; 1: *Morus*; 2: *Bimbisula*, *Papasula*, *Sula*)

21. Sternum: shape of anterior end: (0) blunt; (1) lateral ends of coracoidal sulci more medially placed than those in state (0), giving the anterior end of the sternum an anteriorly extended appearance; (2) as in (1), except the anterior edges of the sternum just posterior to the sulci are laterally pinched. (0: *Pelecanus*, *Phalacrocorax*, *Anhinga*; 1: *Bimbisula*, *Papasula*, *Sula*; 2: *Morus*) [W STN 3]

22. Sternum: coracoidal sulci: (0) gap between medial ends of sulci relatively broad; (1) sulci touch, or nearly touch; (2) sulci overlap. (0: *Pelecanus*, *Anhinga*, *Bimbisula*, *Papasula*, *Sula*; 1: *Morus*; 2: *Phalacrocorax*) [W STN 4]

23. Sternum: dorsal and ventral lips of coracoidal sulcus: (0) ventral lip has greater posterior extent;

(1) dorsal lip has greater posterior extent. (0: *Pelecanus*, *Phalacrocorax*, *Anhinga*, *Morus*, *Bimbisula*, *Papasula*; 1: *Sula*)

24. Sternum: ventral manubrial spine: (0) prominent; (1) absent. (0: *Pelecanus*, *Phalacrocorax*, *Anhinga*, *Morus*; 1: *Papasula*, *Sula*; ?: *Bimbisula*) [W STN 1; V 38]

25. Sternum: furcular facet on carinal apex in lateral view: (0) straight or slightly convex; (1) concave. (0: *Phalacrocorax*, *Anhinga*, *Papasula*, *Sula*; 1: *Morus*; ?: *Pelecanus*, *Bimbisula*) (sternum, furcula fused in *Pelecanus*) [W STN 5; V 38]

26. Sternum: sternal processes: (0) 4 or 5; (1) 6. (0: *Pelecanus*, *Phalacrocorax*, *Anhinga*, *Morus*, *Papasula*, *Sula sula*; 1: other *Sula*; ?: *Bimbisula*) [W STN 6]

27. Sternum: posterior lateral process: (0) broad anteriorly, abruptly narrow posteriorly; (1) broad, ends rounded or blunt; (2) narrow, ends rounded or pointed. (0: *Phalacrocorax*; 1: *Pelecanus*, *Anhinga*, *Morus*, *Sula dactylatra*; 2: other *Sula*, *Papasula*; ?: *Bimbisula*)

28. Humerus: (0) shorter than ulna; (1) longer than ulna. (0: *Pelecanus*, *Phalacrocorax*, *Papasula*, *Sula*; 1: *Anhinga*, *Morus*; ?: *Bimbisula*) [W HUM 19; V 40]

29. Humerus: median crest: (0) relatively long; distal extent about equal to midpoint of bicipital crest; trends approximately parallel to shaft; (1) short, with considerably less distal extent; trends externally; (2) short, trends almost perpendicular to shaft. (0: *Pelecanus*, *Anhinga*, *Morus*, *Bimbisula*; 1: *Papasula*, *Sula*; 2: *Phalacrocorax*) [W HUM 15; V 40]

30. Humerus: central ridge: (0) prominent, angular; (1) indistinct, rounded. (0: *Phalacrocorax*, *Anhinga*, *Bimbisula*, *Papasula*, *Sula*; 1: *Pelecanus*, *Morus*) [W HUM 9; V 40]

31. Humerus: central ridge: (0) extends proximally to a point distal to the median crest; (1) extends proximally to a point between the head and the distal end of the median crest. (0: *Pelecanus*, *Phalacrocorax*, *Anhinga*, *Morus*, *Bimbisula*, *Papasula*, *Sula sula*; 1: other *Sula*) [W HUM 10]

32. Humerus: attachment of M. latissimus dorsi posterior: (0) much closer to central ridge than to edge of deltoid crest; (1) about midway between central ridge and edge of deltoid crest. (0: *Pelecanus*, *Phalacrocorax*, *Anhinga*, *Papasula*, *Sula sula*; 1: other *Sula*, *Morus*, *Bimbisula*) [W HUM 4]

33. Humerus: ligamental furrow: (0) relatively deep and U-shaped, undercutting bicipital crest; (1) shallow and relatively open on distal surface, not undercutting bicipital crest. (0: *Phalacrocorax*, *Anhinga*, *Papasula*, *Sula*; 1: *Pelecanus*, *Morus*, *Bimbisula*) [W HUM 8]

34. Humerus: furrow at distal margin of bicipital surface: (0) absent; (1) present. (0: *Pelecanus*, *Phalacrocorax*, *Anhinga*, *Morus*; 1: *Bimbisula*, *Papasula*, *Sula*)

35. Humerus: impression of M. brachialis anticus: (0) shallow; (1) deeply excavated, pit-like, but abruptly shallowing externally; (2) uniformly deep. (0: *Pelecanus*, *Phalacrocorax*, *Anhinga*, *Morus*; 1: *Sula*; 2: *Papasula*; ?: *Bimbisula*) [W HUM 16; V 40]

36. Humerus: ventral supracondylar tubercle: (0) relatively flat or planar; (1) with convexity at cranial surface. (0: *Pelecanus*, *Phalacrocorax*, *Anhinga*, *Morus*, *Papasula*; 1: *Sula*; ?: *Bimbisula*) [W HUM 17]

37. Humerus: olecranal fossa: (0) apneumatic, or pneumatic with small, scattered foramina; (1) pneumatic with one or more relatively large foramina on dorsal wall of fossa, undercutting the ventral surface of the ventral edge of the sulcus M. scapulotricipitis. (0: *Pelecanus*, *Phalacrocorax*, *Anhinga*, *Morus*, *Papasula*; 1: *Sula*; ?: *Bimbisula*) [W HUM 3]

38. Manual phalanx 2:1: length/width ratio: (0) relatively slender (facet-to-facet length about 4x

proximal width); (1) relatively wide (length considerably less than 4x proximal width). (0: *Pelecanus* 4.09, *Phalacrocorax* 3.95, *Morus* 3.94 4.12 4.15, *Bimbisula* 4.14, *Papasula* 4.07; 1: *Anhinga* 3.47, *Sula* 3.22 3.27 3.30 3.41 3.58)

39. Synsacrum: anterior articular facet of centrum: (0) deeper than wide; (1) wider than deep. (0: *Phalacrocorax*, *Anhinga*, *Morus*, *Bimbisula*; 1: *Pelecanus*, *Papasula*, *Sula*) [V 42]

40. Ilium: caudal region above and behind ilioischiatic fenestra, in dorsal view: (0) does not taper posteriorly; (1) tapers posteriorly, causing posterior elongation of ilioischiatic fenestra. (0: *Pelecanus*, *Phalacrocorax*, *Anhinga*, *Papasula*, *Sula*; 1: *Morus*; ?: *Bimbisula*) [V 42]

41. Ilium: posterior process: (0) tabular; (1) tapering to a point; (2) spearhead-shaped. (0: *Anhinga*, *Morus*, *Papasula*; 1: *Pelecanus*, *Sula*; 2: *Phalacrocorax*; ?: *Bimbisula*) [V 42]

42. Femur: shape: (0) relatively thin; shaft width about 10%, or less, of femur length; (1) relatively thick; shaft width greater than 10% of femur length; (2) as in (1), but shaft greatly bent anteroposteriorly. (0: *Anhinga*, *Morus*, *Bimbisula*; 1: *Pelecanus*, *Papasula*, *Sula*; 2: *Phalacrocorax*) [V 43]

43. Femur: attachment of round ligament: (0) oriented proximomedially; (1) oriented proximally. (0: *Pelecanus*, *Phalacrocorax*, *Anhinga*, *Morus*, *Bimbisula*, *Papasula*; 1: *Sula*) [W FEM 5]

44. Femur: trochanteric ridge: (0) rounded; anterior foramen absent; (1) rounded; anteriormost point distal to center of foramen; (2) slightly angular; anteriormost point proximal to center of foramen. (0: *Pelecanus*, *Phalacrocorax*, *Anhinga*; 1: *Morus*, *Bimbisula*, *Papasula*, *Sula sula*, *S. leucogaster*, *S. dactylatra*; 2: *S. nebouxii*, *S. variegata*)

45. Femur: trochanter, in proximal view: (0) posterior end of lateral margin depressed medially by impression of the insertion of M. obturator internus; (1) lateral margin smoothly curved, without deep impression. (0: *Phalacrocorax*, *Anhinga*, *Bimbisula*, *Papasula*, *Sula*; 1: *Pelecanus*, *Morus*) [W FEM 2]

46. Femur: impression of the insertion of M. flexor ischiofemoralis: (0) located at the extreme posterior edge of the lateral surface of the femur and clearly visible on the posterior surface of the femur; (1) faces laterally on lateral surface of femur. (0: *Pelecanus*, *Phalacrocorax*, *Anhinga*, *Morus*, *Bimbisula*; 1: *Papasula*, *Sula*) [W FEM 3]

47. Femur: fibular groove: (0) deep, right-angled and posterolaterally oriented; (1) shallow and oriented mostly posteriorly. (0: *Pelecanus*, *Phalacrocorax*, *Anhinga*, *Bimbisula*, *Papasula*, *Sula*; 1: *Morus*) [W FEM 1]

48. Femur: femur/tarsometatarsus ratio: (0) femur more than 15% longer than tarsometatarsus; (1) femur longer than tarsometatarsus, but by less than 15%; (2) femur shorter than tarsometatarsus. (0: *Anhinga* 1.26, *Morus* 1.23 1.21 1.16, *Bimbisula* 1.20, *Papasula* 1.26, *Sula sula* 1.30; 1: other *Sula* 1.12 1.10 1.09 1.03; 2: *Pelecanus* 0.84, *Phalacrocorax* 0.94)

49. Tibiotarsus: shape in proximal view: (0) anteroposteriorly elongated (depth > 1 1/3 the width); (1) more squarish (depth not > 1 1/3 the width) (0: *Pelecanus* 1.4, *Phalacrocorax* 1.4, *Anhinga* 1.36, *Morus* 1.57 1.41 1.36, *Bimbisula* 1.52, *Papasula* 1.45, *Sula sula* 1.36; 1: other *Sula* 1.29 1.25 1.21 1.21)

50. Tibiotarsus: external articular surface: (0) extends distally along the lateral surface of the shaft where the fibula articulates with the tibiotarsus; this gives the lateral edge of the articular surface a rounded or convex appearance, especially anteriorly; a sharp lateral edge is present posteriorly; (1) does not extend greatly along lateral edge of shaft, producing a relatively straight or sharp lateral edge to the articular surface anteriorly. (0: *Pelecanus*, *Phalacrocorax*, *Anhinga*, *Morus*, *Bimbisula*; 1: *Papasula*, *Sula*) [W TTR 2]

51. Tibiotarsus: inner cnemial crest: (0) hooked; (1) not hooked; somewhat angular; (2) not hooked; rounded and upswept. (0: *Morus*, *Bimbisula*, *Papasula*, *Sula sula*; 1: other *Sula*; 2: *Pelecanus*, *Phalacrocorax*, *Anhinga*) [W TTR 10; V 43-44]

52. Tibiotarsus: inner cnemial crest, distal end: (0) trends medially, so that it makes contact with ligamental attachment, and continues distally, parallel to shaft, below the ligamental attachment; (1) as in (0), but does not extend distal to ligamental attachment; (2) extends a short distance, trending straight distally so that it does not make contact with ligamental attachment. (0: *Phalacrocorax*; 1: *Anhinga*, *Morus*, *Bimbisula*; 2: *Pelecanus*, *Papasula*, *Sula*) [W TTR 1]

53. Tibiotarsus: shaft width: (0) relatively slender (least width less than one fifteenth of length, and least depth less than one twentieth of length); (1) relatively thick (least width more than one fifteenth of length, and least depth more than one twentieth of length). (0: *Phalacrocorax*, *Anhinga*, *Morus*; 1: *Pelecanus*, *Papasula*, *Sula*; ?: *Bimbisula*) [V 43]

54. Tibiotarsus: supratendinal bridge: (0) almost horizontal, or inclined less than 45°; (1) inclined more than 45°. (0: *Pelecanus*, *Phalacrocorax*, *Anhinga*, *Morus*, *Papasula*, *Sula sula*; 1: other *Sula*; ?: *Bimbisula*) [W TTR 8]

55. Tibiotarsus: internal condyle, proximal extent on posterior side: (0) does not protrude prominently from shaft; (1) protrudes prominently from shaft. (0: *Pelecanus*, *Phalacrocorax*, *Anhinga*, *Morus*; 1: *Papasula*, *Sula*; ?: *Bimbisula*) [W TTR 7]

56. Tibiotarsus: anterior intercondylar fossa: (0) relatively narrow; (1) relatively broad. (0: *Phalacrocorax*, *Anhinga*, *Morus*; 1: *Pelecanus*, *Papasula*, *Sula*; ?: *Bimbisula*) [W TTR 6]

57. Tibiotarsus: external condyle, posterior extent in distal view: (0) equal or subequal to that of internal condyle; (1) considerably less than that of internal condyle. (0: *Pelecanus*, *Phalacrocorax*, *Anhinga*, *Morus*, *Papasula*; 1: *Sula*; ?: *Bimbisula*) [W TTR 5]

58. Tarsometatarsus: shape: (0) slender (length at least 7x greater than least width); (1) wide (length less than 7x greater than least width). (0: *Pelecanus* 11, *Phalacrocorax* 11, *Morus* 7.0 7.2 7.4, *Bimbisula* 7.9, *Sula nebouxii* 7.3; 1: other *Sula* 5.3 5.7 6.0 6.4, *Papasula* 5.8, *Anhinga* 6.4) [V 44]

59. Tarsometatarsus: intercotylar prominence: (0) relatively long with a distinct proximal projection; (1) relatively short, but with a slight proximal projection; (2) short and rounded, without proximal projection. (0: *Pelecanus*, *Phalacrocorax*, *Anhinga*; 1: *Papasula*, *Sula*; 2: *Morus*, *Bimbisula*) [W TMT 2]

60. Tarsometatarsus: tubercle for M. tibialis anticus: (0) located distal to the proximal foramina so that there is a gap between the two structures; (1) located on the distal edge of a foramen, or between the foramina, so that there is no gap. (0: *Pelecanus*, *Phalacrocorax*, *Anhinga*, *Morus*; 1: *Bimbisula*, *Papasula*, *Sula*) [W TMT 10]

61. Tarsometatarsus: middle calcaneal ridge of hypotarsus: (0) has less ventral projection than does medial calcaneal ridge; (1) equal to medial ridge in ventral projection. (0: *Pelecanus*, *Phalacrocorax*, *Anhinga*, *Morus*, *Bimbisula*, *Papasula*, *Sula sula*; 1: other *Sula*) [W TMT 1]

62. Tarsometatarsus: middle trochlea, proximal end of dorsal surface: (0) lacks depression; (1) with well-defined depression. (0: *Pelecanus*, *Phalacrocorax*, *Morus*, *Bimbisula*, *Sula sula*; 1: other *Sula*, *Papasula*, *Anhinga*) [W TMT 7]

63. Tarsometatarsus: trochleae, distal extent: (0) middle greatest; (1) medial about equal to, or greater than, middle; (0: *Pelecanus*, *Phalacrocorax*, *Morus*; 1: *Anhinga*, *Bimbisula*, *Papasula*, *Sula*) [W

TMT 9]

64. Tarsometatarsus: trochleae in distal view: line of curvature passing through the midpoint of each: (0) only slightly arched; (1) relatively highly arched; midpoint of middle trochlea about equal to anteriormost extent of medial trochlea. (0: *Phalacrocorax*, *Anhinga*, *Morus*, *Bimbisula*, *Papasula*, *Sula sula*, *S. leucogaster*; 1: other *Sula*, *Pelecanus*)

65. Tarsometatarsus: tarsometatarsus/manual phalanx II:1 ratio. (0) tarsometatarsus considerably less than 50% longer than manual phalanx II:1; (1) tarsometatarsus about 50% longer than the phalanx; (2) tarsometatarsus considerably more than 50% longer than the phalanx. (0: *Morus* 1.27 1.31 1.34, *Bimbisula* 1.37, *Papasula* 1.30, *Sula sula* 1.09, *S. leucogaster* 1.31; 1: other *Sula* 1.45 1.48 1.58; 2: *Anhinga* 1.77, *Phalacrocorax* 2.17, *Pelecanus* 2.23)

66. Frontal: ventral surface: (0) without excavation immediately anterior to cranial cavity; (1) with deep excavation. (0: *Pelecanus*, *Phalacrocorax*, *Anhinga*, *Morus*, *Bimbisula*, *Papasula*, *Sula sula*; 1: other *Sula*)

67. Postorbital process: (0) process short and unnotched; (1) somewhat elongated process with deep notch; (2) elongated process without notch due to loss of its anterior branch; (3) as in (2), but with a shallow notch creating a secondary, smaller anterior branch. (0: *Pelecanus*, *Phalacrocorax*, *Anhinga*; 1: *Morus*; 2: *Papasula*; 3: *Sula*; ?: *Bimbisula*) [W SKL 7]

68. Postorbital process: ventral surface: (0) smooth, with no distinct depression or pit; (1) with distinct depression. (0: *Pelecanus*, *Phalacrocorax*, *Anhinga*, *Morus*, *Bimbisula*, *Papasula*, *Sula sula*; 1: other *Sula*) [W SKL 8]

69. Transverse temporal ridge in dorsal view: (0) chevron-like, pointing posteriorly; (1) essentially a straight transverse line, but deviates posteriorly at midline; (2) as in (1), but without deviation at midline; (3) as in (2), but deviates anteriorly at midline. (0: *Pelecanus*, *Phalacrocorax*, *Anhinga*; 1: *Sula sula*, *S. leucogaster*; 2: other *Sula*; 3: *Morus*, *Bimbisula*, *Papasula*)

70. Temporal fossa, dorsal angle (angle of divergence of transverse temporal ridge and transverse nuchal ridge): (0) no angle (both transverse ridges bordering the fossa are separate and parallel for the entire transverse distance across the skull); (1) >30°; (2) <20°. (0: *Pelecanus*, *Phalacrocorax*; 1: *Anhinga*, *Morus* 37° 36° 33°, *Papasula* 32°, *Sula sula* 40°, *S. leucogaster* 38°, *S. dactylatra* 33°; 2: *S. nebouxii* 18°, *S. variegata* 17°, *Bimbisula* 15°)

71. Supraoccipital: (0) does not posteriorly overhang foramen magnum; (1) overhangs foramen magnum, but the dorsal rim of the foramen appears in posterior view; (2) overhangs foramen magnum so that dorsal rim of foramen appears only in ventral or ventroposterior views. (0: *Phalacrocorax*, *Anhinga*; 1: *Pelecanus*, *Morus*, *Bimbisula*; 2: *Papasula*, *Sula*)

72. Foramen magnum: (0) wider than high; (1) width and height about equal; (2) higher than wide. (0: *Phalacrocorax*, *Anhinga*; 1: *Pelecanus*, *Bimbisula*, *Papasula*, *Sula*; 2: *Morus*)

73. Basitemporal plate: (0) relatively flat; subcondylar foramina small or absent; (1) concave; foramina small or absent; (2) concave; foramina large. (0: *Pelecanus*, *Phalacrocorax*, *Anhinga*; 1: *Sula*; 2: *Morus*, *Bimbisula*, *Papasula*) [W SKL 1]

74. Glossopharyngeal foramen (cranial nerve IX): (0) foramina IX and X-XI occur as small and large (respectively) foramina on a flat cranial surface; (1) as in (0), but foramina IX and X-XI occur in a recessed area; foramen IX about as large as foramen X-XI, with a ridge between the two foramina; (2) as in (1), but the two foramina are closer together so that the intervening cranial surface appears strut-like.

(0: *Pelecanus*, *Phalacrocorax*, *Anhinga*; 1: *Morus*, *Sula dactylatra*, *S. nebouxii*, *S. variegata*; 2: *S. sula*, *S. leucogaster*, *Bimbisula*, *Papasula*)

75. Vagus and accessory foramen (cranial nerves X-XI): (0) visible in posterior view; level with top of occipital condyle; dorsal to dorsalmost hypoglossal foramen; (1) foramen is slitlike in posterior view; ventral to top of occipital condyle; level with or dorsal to dorsalmost hypoglossal foramen; (2) as in (1), but foramen recessed out of sight under the vault between the opisthotic and the exoccipital; (3) as in (1), but dorsal to occipital condyle. (0: *Pelecanus*, *Phalacrocorax*, *Anhinga*; 1: *Morus*, *Bimbisula*, *Sula sula*; 2: other *Sula*; 3: *Papasula*) (Note: Figure 12D is more ventrally oblique than the posterior orientation of the above description.)

76. Hypoglossal foramina (cranial nerve XII): (0) dorsalmost pair of foramina level with top half of occipital condyle, ventralmost foramina level with bottom half of condyle; (1) dorsalmost foramina level with occipital condyle, and ventralmost foramina ventral to occipital condyle; (2) as in (1), but dorsalmost foramina level with bottom half of occipital condyle. (0: *Pelecanus*, *Phalacrocorax*, *Anhinga*, *Morus*; 1: *Bimbisula*, *Papasula*, *Sula sula*, *S. leucogaster*, *S. dactylatra*; 2: *S. nebouxii*, *S. variegata*) (Note: Figure 12D is more ventrally oblique than the posterior orientation of the above description.)

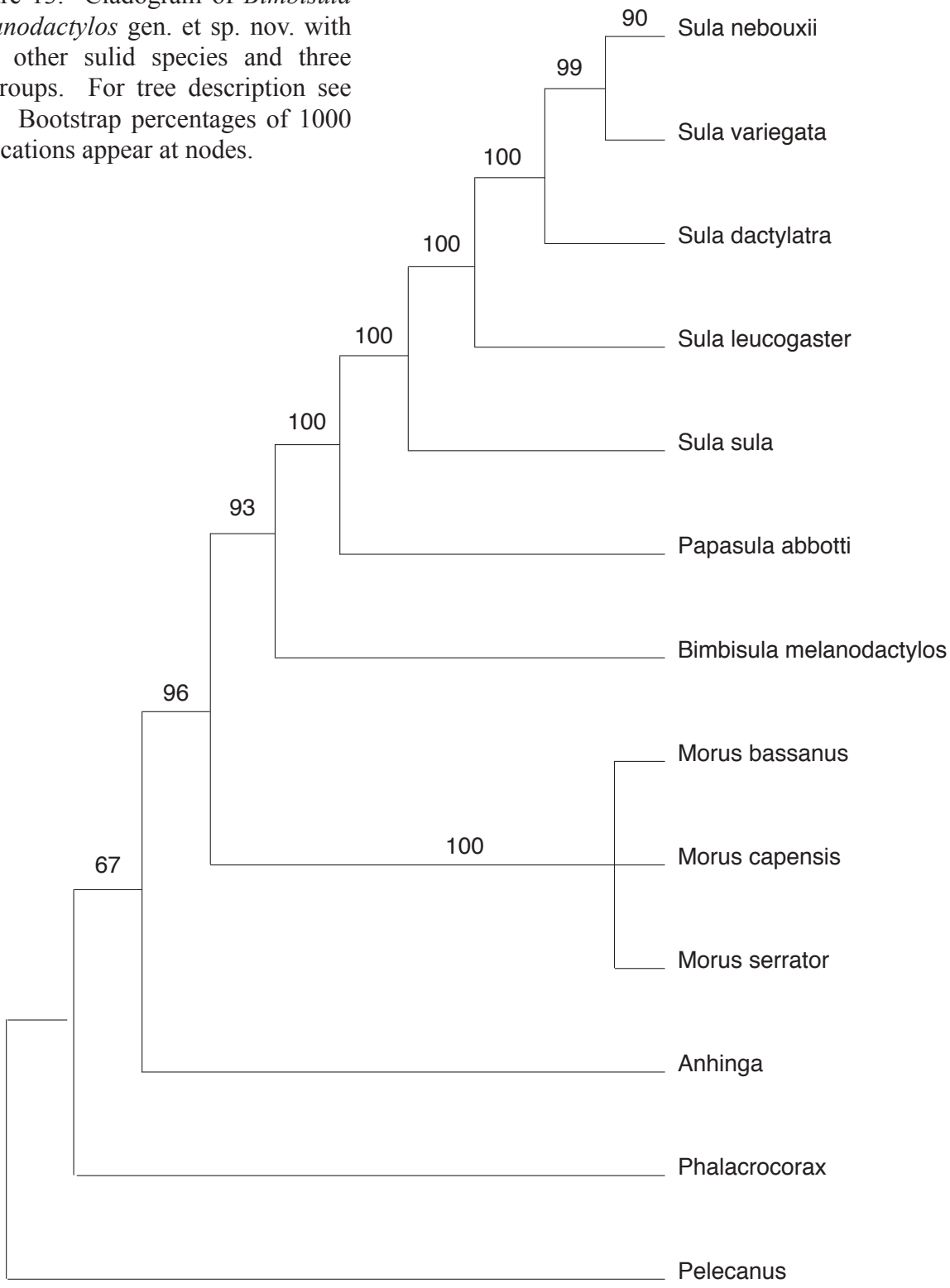
77. Basitemporal plate, ventral view: (0) shield-shaped, with point at anterior end; (1) Y-shaped, with transverse fossa; (2) Y-shaped, with transverse ridge. (0: *Pelecanus*, *Phalacrocorax*, *Anhinga*; 1: *Morus*; 2: *Bimbisula*, *Papasula*, *Sula*)

Table of measurements (mm)

	Bimbisula melano-dactylos	*Morus bassanus*	*Papasula abbotti*	*Sula dactylatra*	*Sula nebouxii*
CRANIUM					
max. width (1)	31.7	52.5	45.9	40.3	32.0
ROSTRUM					
length	~94	104.1	90.4	96.0	92.0
width (2)	~21	26.0	29.4	24.6	19.5
CORACOID					
(3)	__	60.0	50.2	58.2	55.2
(4)	13.1	14.9	13.5	13.8	12.5
(5)	15.0	19.0	15.5	15.6	14.8
(6)	28.2	28.8	18.1	25.0	23.5
MANUAL PHALANX 2:1					
length (7)	44.3	47.8	35.0	38.0	34.7
proximal width	10.7	11.6	8.6	10.6	10.6
FEMUR					
length	73.0	73.4	57.5	61.7	55.9
TIBIOTARSUS					
(8)	17.5	18.0	15.2	14.2	12.9
(9)	11.5	12.8	10.5	11.7	9.7
TARSOMETATARSUS					
length	60.9	60.7	45.6	60.0	51.3
proximal width	13.7	14.3	12.9	15.5	12.0
shaft least width	7.7	8.7	7.9	10.6	7.0

(1) posterior to postorbital process.
(2) at nasofrontal hinge.
(3) length from head to internal point of sternal edge.
(4) width of head.
(5) width at level of scapular facet.
(6) distance from tip of head to beneath scapular facet.
(7) facet-to-facet.
(8) depth of proximal end.
(9) width of proximal end.

Figure 13. Cladogram of *Bimbisula melanodactylos* gen. et sp. nov. with nine other sulid species and three outgroups. For tree description see text. Bootstrap percentages of 1000 replications appear at nodes.



MONOGRAPH IN PALEONTOLOGY

The Lepidosaurian Reptile *Champsosaurus* in North America, by Bruce R. Erickson 1972, Vol. 1: Paleontology, pages 1-91, 65 figures, 2 tables.

Osteology of the Early Eusuchian Crocodile *Leidyosuchus formidabilis*, sp.nov., by Bruce R. Erickson,1976, Vol. 2; Paleontology, pages 1-61, 36 figures, 2 tables.

The Estuarine Crocodile *Gavialosuchus carolinesis* n. sp. (Crocodylia: Eusuchia) From the late Oligocene of South Carolina, North America, by Bruce R. Erickson and Glen T. Sawyer, 1996, Vol. 3: Paleontology, pages 1-47, 30 figures, 3 tables.

Paleopathology of the Paleocene Crocdodile *Leidyosuchus(=Borealosuchus) fomidabilis,* by Glen G. Sawyer and Bruce R. Erickson, 1998, Vol. 4: Paleontology, pages 1-38, 17 figures, 6 tables.

Lower Permian Tracks and Traces in the Science Museum of Minnesota: Ichnofossils, III, by Bruce R. Erickson, Hal E. Halvorson, and Jon M. Kramer, 2011, Vol. 5, Paleontology, pages 1-126, 119 figures.

History of the Wannagan Creek Expeditions 1970-1996 by Bruce R. Erickson 2012, Vol. 6: Paleontology, pages 1-40, 30 figures, 3 appendices.

A New Genus and Species of Booby (Sulidae: Aves) From The Pliocene of South Carolina, with a New Corollary to the Nature of Sister Taxa, By Richard D. Benson and Bruce R. Erickson, 2013, Vol. 7: Paleontology, pages 1-35, 13 figures, 1 appendix, 1 table.