A NEW SUBSPECIES AND NEW RECORDS OF
PAPASULA ABBOTTI (AVES: SULIDAE) FROM
ARCHEOLOGICAL SITES IN THE
TROPICAL PACIFIC

David W. Steadman, Susan E. Schubel, and Dominique Pahlavan

Abstract.—An extinct new subspecies of Papasula abbotti, P. a. costelloi, is
described from seven bones found in archeological sites on Tahuata and Hiva
Oa islands, Marquesas. Papasula a. costelloi differs from the extant P. a. abbotti
in size and qualitative features. From an archeological site on Tikopia in
the Solomon Islands we report two bones of P. a. abbotti, known previously only
from Christmas and Assumption islands in the Indian Ocean. The former
presence of P. a. costelloi in the Marquesas and P. a. abbotti in the Solomons
suggests that this species was widespread in the Pacific until the human dis-
ruptions of the past several thousand years.

The late Holocene record of birds from
Polynesian archeological sites has revealed
many extinct species and new island records
of land birds (Steadman, in press). Herein
we report the first undescribed, extinct form
of seabird from these sites.

Materials and methods.—Comparative
skeletons are from the Division of Birds,
National Museum of Natural History
(USNM). Skeletons examined include Sula
sula (USNM 491921, 498134, 498275,
498364), S. leucogaster (USNM 289139,
298137, 488048, 499909), S. dactylatra
(USNM 498028, 498133, 498270, 498271),
Morus serrator (USNM 18770), M. capensis
(USNM 558367), and Papasula a. abbotti
(USNM 560682, 560683). The fossils are
from the Vertebrate Zoology Collection,
Bernice P. Bishop Museum (BPBM). Os-
teological terminology usually follows
Baumel et al. (1979). Measurements were
taken with dial calipers with 0.05 mm increments,
rounded to the nearest 0.1 mm.

Systematic Paleontology
Order Pelecaniformes
Family Sulidae
Genus Papasula Olson and Warheit

The specimens to be described are re-
ferred to Papasula (monotypic; contains only
P. abbotti) rather than to the other two gen-
era of Sulidae, Sula and Morus, because of
the following characters.

Axis vertebra—processus ventralis short,
wide, and blunt in lateral aspect (long, nar-
row, and blunt in Morus, long, narrow, and
pointed in Sula); dorso-medial process large
and stout (small in Morus, large but not
flattened dorsally in Sula); facies articularis
dorsalis wider in dorsal half than in ventral
half in Papasula and Morus (ventral half is
wider than dorsal half in Sula); lateral por-
tions of facies articularis caudalis more ex-
panded dorsally; lateral portions of facies
articularis caudalis expanded ventrally less
in Papasula and Morus than in Sula; for-
amen vertebrae nearly circular in cross-
section, with a small process interrupting
the dorso-medial surface of the circle (more
perfectly circular in Morus, dorso-ventrally
elongated in Sula).

Fourth cervical vertebra—in dorsal or
ventral aspect, the entire vertebra is nearly
square, with straight lines on all margins
(narrower, more elongated cranio-caudally,
and more laterally constricted in the mid-
section in Morus and Sula); facies articu-
laris larger and more dorsally oriented (small
and dorso-medially oriented in Sula, inter-
mediate in Morus); processus dorsalis stout,
dorsally extended, and rounded (narrow, short, and sharp in *Morus* and *Sula*); dorso-caudal margin straight (with medial indentation in *Morus* and *Sula*); medial facet of dorso-caudal surface larger than in *Sula*, and comparable in size with *Morus* but less expanded laterally; medial facet of dorso-caudal surface oriented more cranially (less ventrally); foramen transversarium smaller in *Papapula* and *Sula* than in *Morus*; facies articularis cranialis more ventrally flared.

Coracoid—sterno-lateral corner of facies articularis humeralis more squared and pointed in *Papapula* and *Morus* than in *Sula*; facies articularis humeralis narrower and less concave in *Papapula* and *Sula* than in *Morus*; shaft more concave on the immediate sternal side of facies articularis humeralis; sterno-medial portion of facies articularis humeralis extends less far sternally (relative to processus procoracoideus); processus procoracoideus stouter, straighter, and more pitted than in *Sula*.

Tarsometatarsus—cotyla lateralis shallow; sulcus extensorius much more deeply excavated, extending down the shaft to the foramen vasculare distale; foramina vascularia proximalia smaller in *Papapula* and *Morus* than in *Sula*; foramina vascularia proximalia penetrate straight through to plantar side in *Papapula* and *Sula*, but not in *Morus*; crista lateralis hypotarsi large with a sharp plantar surface; crista medialis hypotarsi narrower in *Papapula* and *Morus* than in *Sula*; crista lateralis hypotarsi and crista intermedialis hypotarsi incompletely fused, resulting in only one hypotarsal canal (two hypotarsal canals in *Morus* and *Sula*).
plantar surface of the shaft more sculptured with crista plantaris mediana especially distinct, long, and located more laterally on the shaft (plantar surface especially smooth in Morus); fossa parahypotarsalis medialis deep, angular, and non-pneumatic (very shallow, less angular, and non-pneumatic in Morus, shallow, less angular, and pneumatic in Sula); in lateral aspect, proximal margin of lateral trochlea metatarsi joins the shaft nearly perpendicularly (more obtusely in Morus and Sula); in dorsal aspect, medial groove of middle trochlea metatarsi shallower; in medial and lateral aspects, the middle trochlea metatarsi protrudes less dorsally from the plane of the shaft; in distal aspect, the medial margin of inner trochlea metatarsi is nearly straight (deeply incised in Morus and Sula); inner trochlea extends farther distally relative to middle trochlea in Papasula and Sula than in Morus; ridge from inner trochlea metatarsi to fossa metatarsi I more prominent and continuous; distal foramen smaller than in Sula; dorsal surface of shaft more excavated, especially on lateral side; dorso-lateral margin of shaft thin and sharp.

Among the characters used by Olson & Warheit (1988) in recognizing Papasula as distinct from Sula and Morus were certain of those used here for the coracoid, tibiotarsus, and tarsometatarsus. We agree with the generic distinction of Papasula, finding this genus to be no more similar osteologically to Sula than to Morus, at least in the five elements we have as fossils. Especially profound are the differences between the vertebrae of Papasula and those of Sula and Morus.
Papasula abbotti costelloi, new subspecies

Figs. 1–3

Holotype.—Complete tibiotalarsus, BPBM 167105, Hanamiai Site, Tahuata, Marquesas, square L12, Layer H35, depth 255-260 cm; B. Rolett, 1985.

Paratypes.—Hanamiai Site, Tahuata, Marquesas, collected in 1985 by B. Rolett: axis vertebra, BPBM 166874, fourth cervical vertebra, BPBM 166873, and tibiotalarsus, BPBM 166872, square N13, Layer H30, depth 245-250 cm; tarsometatarsus, BPBM 166923, square L13, Layer H27, depth 240-245 cm. Hanatekua Beach Site (MH-3-13, formerly known as MH-12), Hiva Oa, Marquesas, P. Bellwood, 1967: coracoid, BPBM 167758, test pit 2; tarsometatarsus, BPBM 167573, test pit 23, depth 30+ cm.

Diagnosis.—Diffsers from Papasula a. abbotti in being larger in all known elements (Tables 1–5) and as follows. Axis—in cranial aspect, ventral surface of facies articularis atlantica convex rather than concave. Tibiotarsus—crista fibularis shorter; lateral portion of pons supratendineus more constricted than in adult of P. a. abbotti but similar to that of immature individual of P. a. abbotti. Tarsometatarsus—dorso-lateral margin of shaft thicker in dorsal aspect; dorsal surface of shaft more deeply excavated just distal to foramina vascularia proxim-
malia; middle trochlea with more deeply excavated groove on dorsal and ventral surfaces; inner trochlea extends farther distally relative to middle trochlea; distal foramen relatively smaller.

Etymology.—Named for Lou Costello (1906–1959) of the popular comedy team “Abbott and Costello” of the 1940’s and 1950’s. The name costelloi complements the name P. abotti, which honors, however, ornithologist W. L. Abbott rather than Lou Costello’s partner, Bud Abbott. Tropical islands figured in two of Abbott and Costello’s movies, “Pardon My Sarong” and “Abbott and Costello Meet Captain Kidd” (C. Costello 1981).

Remarks.—Our classification of costelloi as a distinct subspecies rather than a full species is based in part on the level of quantitative difference between costelloi and ab-

botti (Tables 1–5), which corresponds with that found between different subspecies of modern species of Sula (K. I. Warheit, pers. comm.). The difference in size between costelloi and abotti exceeds that attributable to sexual dimorphism in species of Sula. While some of the non-quantitative differences between abotti and costelloi (see Diagnosis) would seem to indicate a species-level distinction, we prefer a more conservative approach for now, pending an increase in the sample sizes of fossil and modern specimens of Papasula.

Papasula abotti abotti (Ridgway 1893)


<table>
<thead>
<tr>
<th>Total length</th>
<th>Dorsal length at midline</th>
<th>Cranial width</th>
<th>Maximum width FV (CE)</th>
<th>Maximum depth FV (CE)</th>
<th>Maximum width of FAC</th>
<th>Maximum width of FACR</th>
<th>Width at midpoint</th>
</tr>
</thead>
<tbody>
<tr>
<td>P. a. abotti</td>
<td>USNM 560683, adult, Christmas Island</td>
<td>19.9</td>
<td>12.1</td>
<td>16.1</td>
<td>5.4</td>
<td>5.8</td>
<td>7.3</td>
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<tr>
<td>P. a. abotti</td>
<td>USNM 560682, immature, Christmas Island</td>
<td>20.5</td>
<td>13.0</td>
<td>18.4</td>
<td>5.9</td>
<td>7.4</td>
<td>8.0</td>
</tr>
<tr>
<td>P. a. costelloi</td>
<td>BPBM 166873, adult, Tahuata</td>
<td>21.8</td>
<td>13.1</td>
<td>20.3</td>
<td>6.1</td>
<td>6.4</td>
<td>9.3</td>
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</tbody>
</table>

Table 3.—Measurements (in mm) of the coracoid in Papasula. All specimens are unsexed. CS = cotyla scapularis. FAH = facies articularis humeralis. SE = sternal end.

<table>
<thead>
<tr>
<th>Width of FAH at midsection</th>
<th>Length of FAH</th>
<th>Width of SE of FAH</th>
<th>Width of CS</th>
</tr>
</thead>
<tbody>
<tr>
<td>P. a. abotti</td>
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<td></td>
<td></td>
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<tr>
<td>USNM 560683, adult, Christmas Island</td>
<td>7.8</td>
<td>11.0</td>
<td>9.4</td>
</tr>
<tr>
<td>P. a. abotti</td>
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<td></td>
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<tr>
<td>USNM 560682, immature, Christmas Island</td>
<td>6.9</td>
<td>10.3</td>
<td>9.1</td>
</tr>
<tr>
<td>P. a. abotti</td>
<td></td>
<td></td>
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<tr>
<td>BPBM 166283, adult, Tikopia</td>
<td>—</td>
<td>10.5</td>
<td>—</td>
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<tr>
<td>P. a. costelloi</td>
<td></td>
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<tr>
<td>BPBM 167758, adult, Hiva Oa</td>
<td>7.9+</td>
<td>—</td>
<td>10.7</td>
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</tbody>
</table>
Remarks.—These two specimens are referred to *P. a. abbotti* rather than to *P. a. costelloi* because of these characters: small size (Tables 3, 5); BPBM 166234 (Fig. 3) has a thin dorso-lateral margin of the shaft and a more shallowly excavated dorsal surface of the shaft just distal to the foramina vascularia proximalia.

### Discussion

Based mainly upon osteological characters, Olson & Warheit (1988) described the new genus *Papasula* to accommodate *abbotti*, noting that this species is as distinct from *Sula* Brisson (the "boobies") as it is from *Morus* Leach (the "gannets"). We agree, and find each of the five elements we have studied to be very different from those of both *Sula* and *Morus*. Nelson (1971) found the behavior of *P. abbotti* also to be aberrant within the Sulidae.

*Papasula a. abbotti* occurs today only on Christmas Island, south of Java in the Indian Ocean, although it was described (Ridgway 1893) from a specimen taken on Assumption Island in the western Indian Ocean, 6300 km west of Christmas Island. Subsequently, *P. a. abbotti* has been extirpated on Assumption Island (Nelson 1974, Bourne 1976, Stoddart 1981). The record of *P. a. abbotti* from Tikopia, a Polynesian outlier in the Solomon Islands, is an eastward range extension of 6400 km from Christmas Island. Considering the innumerable islands between Assumption and Tikopia, it is likely that *P. a. abbotti* has suffered a population decline much more severe than previously recognized. The true distribution of *P. a. abbotti* can be approximated only by the discovery of additional Holocene fossils.

*Papasula a. costelloi* is known thus far only from Hiva Oa and Tahuata, Marquesas Islands. This is a 4800 km eastward range

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**Table 4.** Measurements (in mm) of the tibiotarsus in *Papasula*. All specimens are unsexed. For the modern skeletons from Christmas Island, measurements are given for both the right and left tibiotarsi. *CC* = cristae enomialis cranialis et lateralis.

<table>
<thead>
<tr>
<th>Specimen</th>
<th>Proximal width</th>
<th>Total length without CC</th>
<th>Length of cristae phalangeales</th>
<th>Width at base of phalanges</th>
<th>Depth of foramen through excavales</th>
<th>Depth of lateral at base of shaft</th>
<th>Width at base of shaft</th>
</tr>
</thead>
<tbody>
<tr>
<td>USNM 560683, adult, Christmas Island</td>
<td>10.5</td>
<td>79.0</td>
<td>4.0, 4.1</td>
<td>5.8, 5.9</td>
<td>11.2, 11.3</td>
<td>8.1, 8.1</td>
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<tr>
<td>P. a. abbotti, USNM 560682, immature, Christmas Island</td>
<td>10.4, 10.6</td>
<td>81.6, 82.2</td>
<td>7.3</td>
<td>5.7, 5.7</td>
<td>11.9, 12.0</td>
<td>8.2, 8.4</td>
<td>1</td>
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<tr>
<td>P. a. costelloi, BPFM 167105, adult, Tahuata</td>
<td>12.5</td>
<td>87.0</td>
<td>13.7</td>
<td>7.3</td>
<td>13.7</td>
<td>12.0</td>
<td>1</td>
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<tr>
<td>P. a. costelloi, BPFM 166872, adult, Tahuata</td>
<td>13.3</td>
<td>13.3</td>
<td>13.7</td>
<td>7.3</td>
<td>13.7</td>
<td>12.0</td>
<td>1</td>
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**Table 4.** Measurements (in mm) of the tibiotarsus in *Papasula*. All specimens are unsexed. For the modern skeletons from Christmas Island, measurements are given for both the right and left tibiotarsi. *CC* = cristae enomialis cranialis et lateralis.
Table 5.—Measurements (in mm) of the tarsometatarsus in *Papasula*. All specimens are unsexed. For the modern skeletons from Christmas Island, measurements are given for both the right and left tarsometatarsus. DF = distal foramen. IT = inner trochlea. MT = middle trochlea. OT = outer trochlea.

<table>
<thead>
<tr>
<th>Specimen</th>
<th>Total length to DF</th>
<th>Proximal width</th>
<th>Proximal depth</th>
<th>Minimum width of shaft</th>
<th>Distal width</th>
<th>Depth of OT</th>
<th>Depth of MT</th>
<th>Depth of IT</th>
<th>Width of MT</th>
<th>Length from DF through MT</th>
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<tr>
<td><em>P. a. abbotti</em></td>
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<tr>
<td>USNM 560683, adult,</td>
<td>34.4, 34.7</td>
<td>12.5, 12.6</td>
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<td>7.7, 7.8</td>
<td>13.4, 13.5</td>
<td>7.2, 7.7</td>
<td>6.0, 6.2</td>
<td>4.8, 4.9</td>
<td>4.6, 4.8</td>
<td>9.8, 10.1</td>
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<tr>
<td>Christmas Island</td>
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<tr>
<td><em>P. a. abbotti</em></td>
<td>33.6, 34.1</td>
<td>12.7, 12.8</td>
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<td><em>P. a. costelloi</em></td>
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<td>BPBM 166923, adult,</td>
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<td>Tahuata</td>
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<td><em>P. a. costelloi</em></td>
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<tr>
<td>BPBM 167573, adult,</td>
<td>39.9</td>
<td>14.6+</td>
<td>10.9</td>
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extension for *P. abotti*. We believe that *P. a. costelloi* nested in the Marquesas, for the holotype tibiotsarsus (BPBM 166872) is filled with medullary bone, indicating a female either laying eggs or preparing to do so. Whether *P. a. costelloi* occurred outside of the Marquesas is unknown but seems likely. We also do not know where or if the ranges of *P. a. costelloi* and *P. a. abotti* once met in the Pacific. We have examined bones of sulids from archeological sites on Lifuka (Tonga), Huahine (Society Islands), Henderson (Pitcairn Group), and Nuku Hiva and Ua Huka (Marquesas), finding all to be referable to modern species of *Sula*.

Slud (1967) repeatedly sighted several individuals of an unusual sulid on Cocos Island, between Costa Rica and Galapagos. These birds, which did not agree in plumage with any living species of booby, were reminiscent of Abbott’s Booby in several aspects, such as the white wing patches, bluish skin behind the eye, tree-perching habits, and deep, croaking voice. The discovery of Abbott’s Booby in the Marquesas raises the possibility that the unknown species of sulid on Cocos Island might be *P. abotti*.

Many extinct species of land birds have been discovered in the archeological sites on Tahuata and Hiva Oa (Steadman 1988, in press; Steadman & Zarriello 1987). *Papasula a. costelloi* is the first extinct seabird to be reported from these sites, although study of the seabird bones is in preliminary stages and the faunas do include locally extirpated procellariids.

The initial human settlement of the Marquesas occurred at least 2000 years ago (Kirch 1986). Evidence from the Hanamiai Site on Tahuata suggests that *P. a. costelloi* survived into the second millennium of human occupation. The bones of *P. a. costelloi* from Hanamiai were recovered only from the lowest stratigraphic levels. Radiocarbon dates for these levels indicate a maximum age of around 920 ± 80 B.P. (Rolett 1988). The stratigraphic contexts of the two bones of *P. a. costelloi* from the Hanatekua Beach Site on Hiva Oa have not been correlated with artifactual assemblages. There are no radiocarbon dates for this site. The archeology of Hiva Oa has been described by Bellwood (1972), Sinoto (1979), and Kirch (1986).

On Tikopia, *Papasula a. abotti* may not have survived long after the first humans arrived. The Kiki Site, from which both bones of *P. a. abotti* were found, contains the richest sample of archeological materials from the initial occupation of Tikopia (Kirch & Yen 1982:111). Both of these bones are from Layer II, which is the lowest cultural layer at the site and is radiocarbon dated (on charcoal) at 2680 ± 90 years B.P. (Kirch & Yen 1982:313).

The apparent vulnerability of Abbott’s Booby to human activities is probably related to two factors. First, boobies provided a readily accessible food source for Polynesians, as shown by the occurrence of booby bones in archeological kitchen middens. Second, the clearing of forests removed nesting habitat. Unlike other species of sulids, Abbott’s Booby is known to nest only in tall trees.

The distribution of *Papasula*, as presently understood, is extremely scattered (Assumption and Christmas islands in the Indian Ocean; Tikopia, Hiva Oa, Tahuata, and perhaps Cocos islands in the Pacific). We presume that some combination of hunting and habitat destruction has removed these sulids from a significant number of the thousands of intervening islands.

Acknowledgments

Specimens from archeological sites were kindly made available by T. Han, P. V. Kirch, B. Rolett, and Y. H. Sinoto. Modern specimens were provided by B. Farmer, S. L. Olson, and K. I. Warheit. S. L. Olson and K. I. Warheit shared their knowledge of the osteology of the Sulidae. For constructive criticism of the manuscript, we thank P. V. Kirch, N. G. Miller, B. Rolett, and K. I.
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Literature Cited


