THE SYSTEMATIC RELATIONSHIPS OF *AECHMORHYNCHUS, PROSOBONIA,* AND *PHEGORNIS* (CHARADRIIFORMES; CHARADRII)

RICHARD L. ZUSI AND JOSEPH R. JEHL, JR.

SHOREBIRDS of the monotypic genera *Aechmorhynchus*, *Prosobonia*, and *Phegornis* live, or once lived, in remote or isolated regions. They are poorly represented in museum collections and have been little studied. All are small, slender-billed, and short-winged, with some barring on the tail feathers and a white or light-colored streak above the eye (Figure 1). These and other similarities led Seebohm (1888: 448) to merge them into a single genus, *Phegornis*, which he allied with *Tringa* and certain other sandpipers. Lowe (1931b: 722, 725) divided Seebohm's genus, placing *Phegornis mitchellii* in the Charadriidae and *Aechmorhynchus cancellatus* in the Scolopacidae. He made no mention of *Prosobonia leucoptera*. Our recent independent studies of plumage and structure, here combined, confirm Lowe's placement of the two genera in different families. In this paper we present the evidence for our views and attempt to clarify the relationships of the three shorebirds within their respective families. Although we recommend merging *Aechmorhynchus* with *Prosobonia*, we use the name *Aechmorhynchus* throughout the paper to prevent confusion. Otherwise our terminology corresponds to that Jehl (1968) used in his classification of the Charadrii, part of which is given below:

Family Charadriidae
  Subfamily Vanellinae
    Genus: *Vanellus*
  Subfamily Charadriinae
    Genera: *Charadrius, Anarhynchus, Phegornis, Pluvialis, Eudromias, Oreopholus, Pluvianellus*

Family Scolopacidae (in part)
  Subfamily Tringinae
    Tribe Numenini
    Genera: *Limosa, Numenius, Bartramia*
    Tribe Tringini
    Genera: *Tringa, Catoptrophorus, Xenus, Actitis, Heteroscelus*
    Tribe Prosoboniini
    Genus: *Prosobonia* [includes *Aechmorhynchus*]

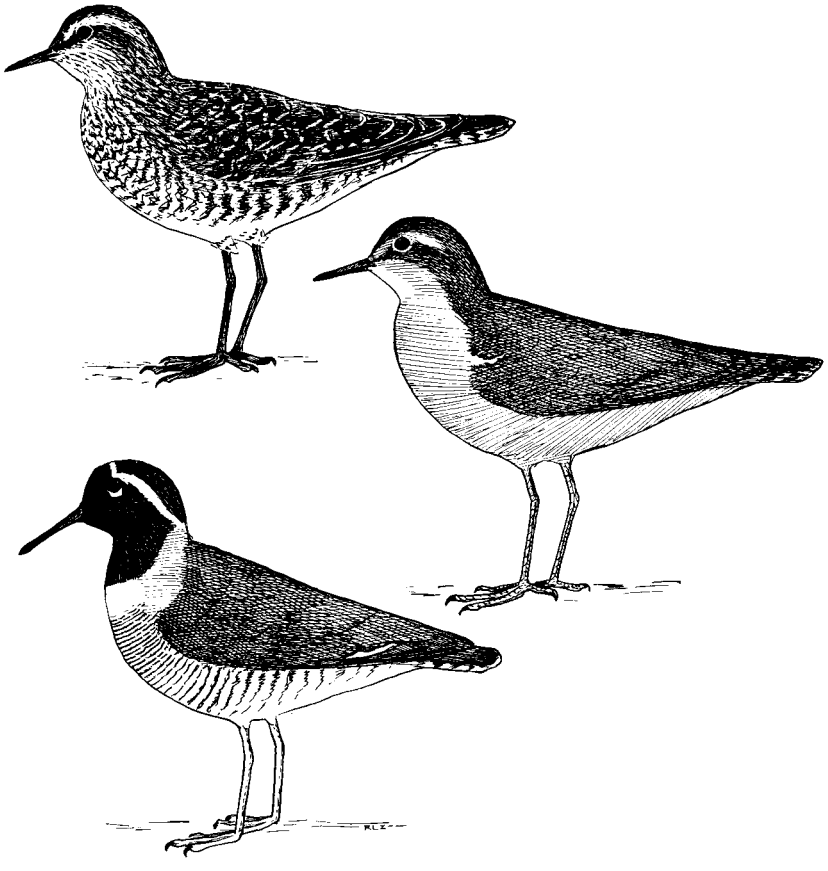

Figure 1. *Aechmorhynchus cancellatus* (above), *Prosobonia leucoptera* (middle), *Phegornis mitchellii* (below), drawn to same scale.

Materials and Acknowledgments

Prosobonia leucoptera once occurred on Tahiti and Eimeo in the Society Islands, but it is now extinct and represented by a unique mounted specimen in the Rijksmuseum von Natuurlijke Historie in Leiden, Netherlands. Zusi studied this specimen at Leiden in 1966 through the courtesy of G. F. Mees and obtained an X ray of the skull through the cooperation of P. Dullemeijer and his staff at the University of Leiden.

Aechmorhynchus cancellatus apparently once occurred widely throughout the Tuamotu (Paumotu or Low) Archipelago of the south-central Pacific Ocean; there is one record from Christmas Island, nearly 2,000 miles distant. It is now a very rare bird in the Tuamotus, although it is still plentiful on at least two small atolls (C. Jouanin in a letter to Frank B. Gill, 7 February 1967). Jehl examined the large series of specimens in the American Museum of Natural History, as well as the much smaller series in The University of Michigan Museum of Zoology and in the Smith-

sonian Institution (USNM). Through the courtesy of Dean Amadon, Zusi was able to study two spirit specimens of *Aechmorhynchus*, and both authors studied a skeleton that was made from another spirit specimen, all from the collections of the American Museum of Natural History.

Phegornis mitchellii is found in high valleys of the Andes from central Peru southward to Chubut, Argentina (Johnson, 1964). Our study is based upon skins, a skeleton (lacking skull), and a spirit specimen loaned to us by Robert W. Storer from the collections of The University of Michigan Museum of Zoology. Also studied were museum skins from the American Museum of Natural History and the Smithsonian Institution, and a downy chick from the British Museum (Natural History) loaned through J. D. Macdonald.

To those who made available specimens of these rare birds and facilitated our studies we extend our sincere appreciation. Zusi's studies in Leiden were supported by the Smithsonian Research Foundation, Grant Number Sq 0663049. Jehl's research was supported, in part, by the Frank M. Chapman Fund of the American Museum of Natural History and by a National Science Foundation Assistantship in Systematic and Evolutionary Biology administered by The University of Michigan Museum of Zoology (Grant GB-3366).

We are indebted to George E. Watson, Walter Bock, and Pierce Brodkorb for their helpful comments on the manuscript.

GENERIC HISTORY

Prosobonia and *Aechmorhynchus*.—Two species have been described in each of the genera *Prosobonia* and *Aechmorhynchus*. For reasons stated later we recognize only *Prosobonia leucoptera*, regarding *P. ellisi* as a synonym, and *Aechmorhynchus cancellatus*, regarding *A. parvirostris* as a synonym.

Prosobonia leucoptera and *Aechmorhynchus cancellatus* were originally placed in the genus *Tringa* (approximately equivalent to the family Scolopacidae) by Gmelin (1789). Bonaparte (1850), without stated reason, erected the subfamily Prosoboniinae and the genus *Prosobonia* for *Tringa leucoptera* of New Zealand (the locality is an error). As Bonaparte (1850, 1856) considered this species to be a member of the Rallidae, his reasons for erecting the subfamily and genus must have beeen based on comparisons with rails rather than with shorebirds.

In 1848 Peale named a third species, *Tringa parvirostris*, similar to *T. cancellatus*. Bonaparte (1856) considered Peale's *Tringa parvirostris* to be a variety of *Tryngites subruficollis*. Coues (1874: 506) later stated that the nearest relative of *parvirostris* among the North American species was *Bartramia longicauda*, and he proposed the generic name *Aechmorhynchus* for *parvirostris* "should it be deemed worthy of subgeneric separ[a]tion," without, however, specifying characters for the subgenus. Sharpe (1896) placed *Aechmorhynchus* and *Prosobonia* in the Scolopacinae next to *Tryngites*. Perhaps influenced by Coues' view, Lowe (1927, 1931a) believed that *Aechmorhynchus* was most closely related to the curlews

(*Numenius*) and cited similarities in plumage, the skull, and muscles of the thigh as evidence. Peters (1934) placed *Aechmorhynchus* next to *Prosobonia*, followed by *Bartramia* and *Numenius*.

Phegornis.—Gray (1849) proposed the name *Phegornis* to replace the preoccupied name *Leptopus*, and the alternate name *Leptodactylas*, also preoccupied, proposed by Fraser in describing the species *mitchellii* (Fraser, 1844). Des Murs' (1849) name, *Leptoscelis*, proposed to replace Fraser's names, was itself preoccupied. Gray placed *Phegornis* in the Charadriidae, but his generic "diagnosis" did not specify how *Phegornis* differed from other plover genera.

Seebohm (1888: 448) stated that *Prosobonia*, *Aechmorhynchus*, and *Phegornis* had many characters in common—short broad wings, more or less defined bars across the tail feathers, toes cleft to the base (*Phegornis* lacks a hind toe), slender bills very slightly expanded towards the tip, nostrils placed very near the frontal feathers, and a conspicuous white streak behind the eye. He therefore combined all three genera in *Phegornis*. Sharpe (1896) maintained the three genera and placed *Phegornis mitchellii* in the Scolopacinae between *Philohela* and *Rostratula*.

Phegornis is at present usually maintained as a monotypic genus for the species *mitchellii*. In his review of the plovers, Bock (1958) retained *Phegornis* in the Charadriidae in accordance with usage established by Lowe (1931b) and Peters (1934), but commented that *Phegornis* may be a sandpiper, "perhaps allied to *Aechmorhynchus* and *Prosobonia*" (p. 83). Jehl (1968) found similarities between the downy chicks of *Phegornis* and various plovers, and partly on this basis included *Phegornis* in the Charadriidae.

Phegornis

The external characters that usually distinguish plovers from sandpipers are bill shape and plumage pattern. In most plovers the bill is relatively short and straight, and the tip of the premaxilla is noticeably inflated or swollen. *Phegornis* has a long and slender bill, only slightly swollen at the tip; though atypical of the Charadriidae, its slender bill is similar to that of *Oreopholus ruficollis*.

Lowe (1931b: 738) characterized the plumage pattern of adult plovers by one or more of the following: "(a) Either a conspicuous white postnuchal band or an adumbrated pattern of one. (b) A thoracic band or area of darker coloration than the rest of the abdomen. (c) A dark terminal or subterminal band on the tail." Of these characteristics *Phegornis* has a white postnuchal band and a poorly marked subterminal band on the tail. Its white superciliary lines connected across the forehead resemble the patterns of certain plovers and differ from all sandpipers.

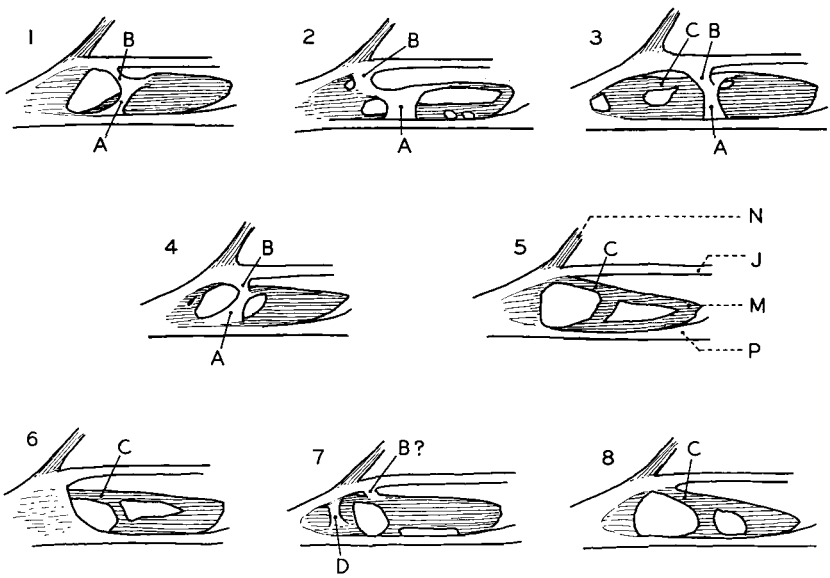

Figure 2. Morphology of maxillopalatine from ventrolateral view of left side. Charadriidae: 1, *Charadrius vociferus*; 2, *Charadrius alexandrinus*; 3, *Vanellus chilensis*; 4, *Phegornis mitchellii*; Tringinae: 5, *Aechmorhynchus cancellatus*; 6, *Bartramia longicauda*; 7, *Tringa melanoleuca*; 8, *Actitis macularia*. A, B, C, D; struts of the maxillopalatine. N, nasal bar; J, jugal bar; M, maxillopalatine; P, palatine. See text.

Downy plumage.—The color pattern of most plover chicks is distinctive and consists of a mottled crown separated from a similarly mottled back by a prominent white or light-colored band on the nape, but in *Charadrius bicinctus* and *C. novaeseelandiae* the nape is mottled. In some species bands of darker down of varying prominence occur on the occiput, midcrown, wings, midback, or rump; in several species the crown patch is encircled, or nearly encircled, by black down. All are white or whitish ventrally, but at least three species of *Vanellus* and three of *Charadrius* have a black pectoral band (Jehl, 1968: 32). The downy plumage of *Phegornis*, according to Johnson (1964), is uniform gray on the head and back with dove-gray throat, breast, and ventral surface. In three specimens Jehl examined the dorsal down was brownish-gray mottled with black, and the patterning of individual feathers was almost identical to that of *Charadrius semipalmatus*; there was no sign of a whitish nape band or other pattern above, and the underparts were grayish-white. Jehl (1968: 33) states that pattern loss in shorebird chicks is a derived condition that occurs most commonly in species nesting on uniformly colored substrates or on

sand and gravel flats along mountain streams. The latter habitat is characteristic of *Phegornis*, to judge from Johnson's (1964; 1965: 327–331) description of a nest among pebbles and stones on riverine sand and shingle flats in a high Andean valley. Except for the lack of a whitish nape band, the downy plumage of *Phegornis* is charadriine (see Figure 9, p. 779).

Palate.—Lowe distinguished plovers from sandpipers by the configuration of the maxillopalatine strut, a small bar of bone that, in plovers, runs transversely from the maxillopalatine to the jugal bar posterior to the junction of the jugal and nasal bars (Figure 2). He did not discuss such a maxillopalatine strut in the Scolopacidae but he illustrated and so labeled a strut running forward from the maxillopalatine to the confluence of the jugal and nasal bars. Lowe (1931b: 734) stated that the maxillopalatine strut was of the charadriine type in *Phegornis*, but as Lowe's drawing (1931b: 769) showed the strut of *Phegornis* lying anterior to the nasal bar, Bock (1958: 81–82), having only Lowe's drawing to work with, questioned whether it corresponded to the maxillopalatine strut of plovers or to another strut of the Tringinae illustrated but not named by Lowe (D in Figure 2).

Dissection of a spirit specimen of *Phegornis* revealed that the strut Lowe figured actually lies posterior to the nasal bar and corresponds to the maxillopalatine strut of plovers. We believe however that Lowe used the term "maxillo-palatine strut" for different struts in plovers and sandpipers, and that he overlooked another strut of greater importance for distinguishing the two groups.

Plovers appear to be best characterized by a bony strut (A) that joins the dorsal and ventral edges of the concave maxillopalatine, as a footbridge might cross a ditch (Figure 2); in some species or individuals the single strut is replaced by a network of struts. In addition either the dorsal edge of the maxillopalatine or strut A is connected by a strut (B), or bony sheet, to the jugal bar posterior to (but sometimes very near) that bar's connection with the nasal bar. This is the maxillopalatine strut that Lowe described for plovers. The two struts (A and B) may run into each other, appearing to be one, or they may be quite distinct as when B lies anterior to A. In addition to these struts, a third (C) runs forward from the anterodorsal edge of the maxillopalatine to bony lamina lying in the region where the jugal, nasal, palatine, and maxillary bars converge. In some species or individuals B and C appear to have merged, forming a bony sheet; in others C is apparently lacking.

In the Scolopacidae no strut A exists, but in various tringine species, as Bock noted, a strut resembling B runs from the dorsal edge of the maxillopalatine to the jugal bar. Curiously, Lowe did not mention this strut. Typically the only strut is one resembling C, which may attach as in

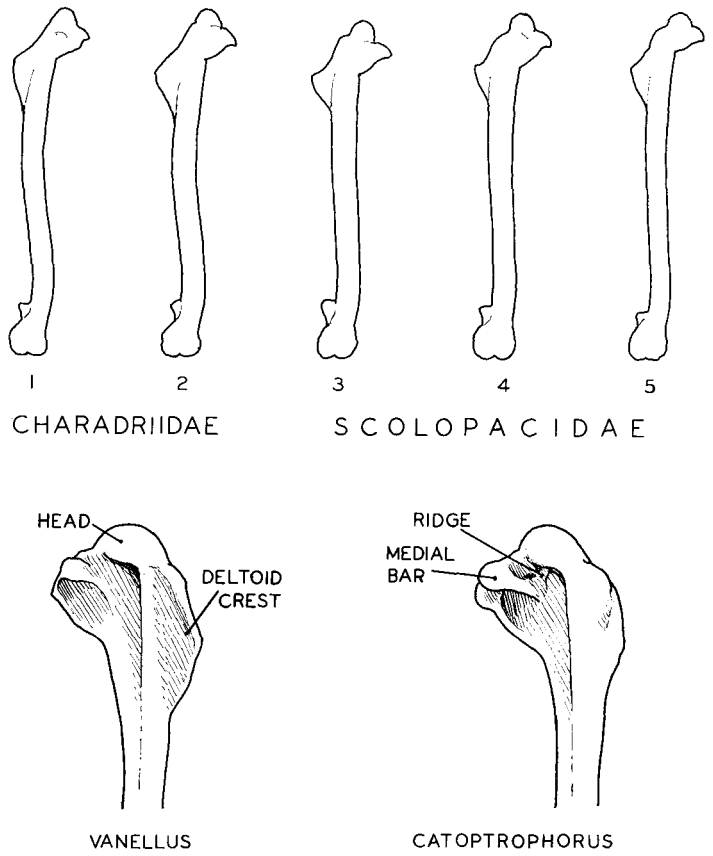

Figure 3. Characteristics of humerus in Charadriidae and Scolopacidae. Above, anterior view of: 1, *Phegornis mitchellii*; 2, *Charadrius melodus*; 3, *Calidris alba*; 4, *Actitis macularia*; 5, *Aechmorhynchus cancellatus*, showing S-curve of shaft in Charadriidae. Below; anconal view of *Catoptrophorus semipalmatus* and *Vanellus chilensis* showing ridge and convex deltoid crest in Scolopacidae.

plovers or may run anterolaterally to attach on the jugal bar (Figure 2). Sometimes another strut (D) runs transversely between the maxillary and the anterior end of the palatine—the "unnamed strut" of Bock (1958: Figure 6b). Lowe's maxillopalatine strut corresponds to our strut C in sandpipers, and to our strut B (and A?) in plovers. Because some tringine sandpipers have a strut that resembles B, the most diagnostic feature of plovers is the presence of strut A.

In *Phegornis* strut A is present and it angles forward and broadens as it joins the floor of the maxillopalatine (Figure 2). Strut A differs from that of other plovers in running straight ventrally to meet the floor of

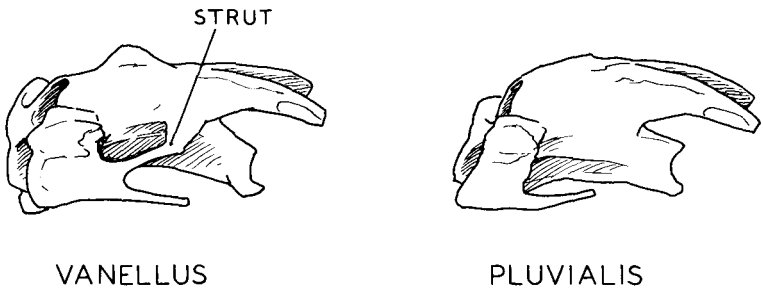

Figure 4. Cervical vertebrae of *Vanellus coronatus* and *Pluvialis squatarola*, showing strut characteristic of Vanellinae.

the maxillopalatine medial to that bone's juncture with the palatine. In other species A curves ventromedially to meet the free edge of the maxillopalatine. Strut C is either lacking or fused with B. The configuration of strut B and the presence of A as found in *Phegornis* are strong evidence that *Phegornis* is a plover.

Postcranial skeleton.—Features of the humerus and coracoid distinguish plovers from sandpipers. In plovers the shaft of the humerus is curved in an S-shape when viewed from its edge (Figure 3) and has a C-shaped curve in anconal view; the shaft in sandpipers is straighter, with only the barest suggestion of curvature. The anconal surface of the deltoid crest is concave in plovers whereas it is flat or slightly convex (sometimes becoming concave proximally) in sandpipers. In plovers the trough between the head of the humerus and the medial bar (terminology of Ashley, 1941) is uninterrupted; in sandpipers it is usually crossed by a low ridge (Figure 3). With the exception of *Charadrius melanops*, the coracoid in plovers has a prominent coracoidal foramen that is lacking in sandpipers. *Phegornis* has a coracoidal foramen, and its humerus has the curved shape, the concave deltoid crest, and the uninterrupted trough characteristic of plovers. Because of these characters and its maxillopalatine structure and downy plumage pattern, we place it in the Charadriidae.

Systematic position.—The position of *Phegornis* within the Charadriidae remains uncertain. A character distinguishing the vanelline plovers (except *Vanellus cayanus*) is a bony strut running from the transverse process to the neural arch on some of the cervical vertebrae (Figure 4); this strut is absent in charadriine plovers and in *Phegornis*. The interrelationships of charadriine species are not well known. Although the combination of external characters that distinguishes *Phegornis* is unique, most of its individual features can be found, at least in modified form, within the genus *Charadrius* (*sensu* Bock, 1958). *Phegornis* is quite similar to the

New Zealand species *Charadrius novaeseelandiae* in adult plumage pattern, except for the barred underparts. It also shows some resemblance to the southern South American *Charadrius modestus* in head and wing patterns of the adult and to the barred breast of the juvenal plumage of *modestus*. Until stronger evidence for its affinities is at hand we prefer to maintain *Phegornis* as a monotypic genus in the Charadriinae of the Charadriidae. *Phegornis* differs from other genera of the Charadriinae by its long, slender bill, by the configuration of strut A of the maxillopalatine, and by its barred underparts.

PROSOBONIA AND *AECHMORHYNCHUS*

Species status.—Prosobonia leucoptera was discovered during Captain James Cook's epic voyages to the Pacific Ocean. The type in the Leiden Museum, which is the only extant specimen, was collected at Tahiti in 1773 during Cook's second voyage. Another bird (two?) was collected at Eimeo (= Moorea) Island, 10 miles west of Tahiti, in 1777 during the third Cook expedition. Sharpe (1906) described the Eimeo bird as a new species, *ellisi*, on the basis of a drawing by William Ellis, a surgeon on the expedition. Sharpe noted that the bird had a double patch of white on the wing coverts, the median and greater wing coverts pale ferruginous, and a circlet of rufous around the eye. These are insufficient grounds for the recognition of a new species, in view of the variability in pattern of white and rufous in the wing coverts Latham (1785: 172) recorded for three specimens of *leucoptera*. Furthermore the Leiden specimen also has a rufous eye circlet (see Appendix). We follow Peters (1934) in treating *ellisi* as a synonym of *leucoptera*.

Two species of *Aechmorhynchus* have also been described. *Aechmorhynchus cancellatus*, known only from the type which is no longer extant, was collected at Christmas Island in late 1777 or the first days of 1778 (Stresemann, 1950: 77; Peters, 1934) during Cook's third voyage and was described by Gmelin (1789), based on Latham's (1785) "Barred Phalarope." *Aechmorhynchus parvirostris* was named by Titian Peale (1848: 235) from five specimens collected in August 1839 in the Tuamotu Archipelago, approximately 2,000 miles to the southeast of Christmas Island. The Whitney South Sea Expedition of the American Museum of Natural History took many specimens on the Tuamotus in 1922 and 1923.

Seebohm (1888: 451) merged *parvirostris* with *cancellatus* but Townsend and Wetmore (1919: 182) again recognized *cancellatus* and *parvirostris* as distinct species on the following grounds: Latham's (1785: 274) description of the type of *cancellatus* states that the bill was one inch long and that the underparts were white barred with dusky; by contrast, of four specimens of *parvirostris* available to Townsend and Wetmore in the U. S.

TABLE 1

MEASUREMENTS OF *PROSOBONIA* AND *AECHMORYNCHUS*[1]

	Prosobonia leucoptera	*Aechmorhynchus*	*cancellatus*
		USNM 329899 ♂	USNM 212181 ♀
Wing (left, chord)	113	107	105
(right, chord)	111	108	106
(left, arc)	118	107	106
(right, arc)	—	109	108
Tail (central feather)	54	57	—
(outer feather)	46	50	—
Tail beyond wing	9–10	10 (approx.)	—
Bill (culmen from feathers)	20.0	—	18.0
(to post. border nostril)	19.3	—	16.6
Nasal fossa	14.3	—	11.1
Mandible (from feathers)	15.5	—	12.7
(symphysis)	7.9	—	7.6
Tarsometarsus[2]	29	26	28
Unfeathered tibiotarsus[2]	13	11	12
Toe plus claw[2]			
1 (hallux)	10	11	12
2	21	22	24
3	26	26	29
4	22	23	26
Elevation of hallux	3	4	3–4
Number of acrotarsal scutes			
(left)	—	21	22–23
(right)	22–23	21	22

	AMNH 20 ♂ ♂	AMNH 20 ♀ ♀
Wing, chord	97–109 (102.5)	97–112 (105.2)
Tail	(2 ♂) 57, 62	(2 ♀) 59, 62
Culmen	15.5–17.8 (16.5)	15.3–18.0 (16.6)
Tarsometatarsus	22–27 (24.9)	23–27 (25.0)

[1] Measurements in mm. *Prosobonia* and USNM specimens measured by Zusi; AMNH specimens measured by Jehl.

[2] Average of right and left members.

National Museum, in the largest the bill was only 18 mm long. In all specimens the throat and abdomen were unmarked. They noted that the underparts of a fresh specimen taken by Dr. Townsend had a distinct buffy tinge. (Peale's specimens were too stained and discolored for comparison.)

The longest bill (culmen length) in the large series of *parvirostris* in the American Museum of Natural History is also 18.0 mm or nearly ¾ inch. In our opinion the "one inch" Latham gave for the Christmas Island bird is imprecise and does not necessarily indicate a longer-billed bird. For example, Latham gave the length of the bill in the Green Sandpiper, *Tringa ocrophus*, as 1½ inches when in fact it lies between 1¼ and 1⅜ inches; similarly he gave *Tringa* (= *Prosobonia*) *leucoptera* as 1 inch,

but Zusi measured it at slightly over ¾ inch. Barring on the underparts, supposedly a characteristic of *cancellatus*, is variable in specimens of *parvirostris* and thus cannot be used as a point of specific difference. Some birds are whitish and lightly barred ventrally whereas others are brownish and heavily barred; intermediate plumages are common. Jehl noted that females have a tendency to be larger, whiter-bellied, and less barred ventrally than males. Thus the color differences alleged for the Christmas Island bird (the sex of which is unknown) appear to be within the range of variation of the extant population. On the basis of present evidence, we conclude that only one species of *Aechmorhynchus*, i.e. *cancellatus*, should be maintained.

Measurements and plumage.—In Table 1 measurements of the *Prosobonia* specimen are compared with those of two skins of *Aechmorhynchus* measured by Zusi and with additional measurements of *Aechmorhynchus* taken by Jehl. The statement of Rothschild (1907: 119) that *Aechmorhynchus* has a much longer hind toe than *Prosobonia* is clearly in error. *Prosobonia* has slightly longer wings, bill, and tarsometatarsus, and slightly shorter tail and toes than *Aechmorhynchus*. Both species have scutellate-reticulate tarsi, but *Aechmorhynchus* differs in having the planta tarsi scutellate (with occasional reticulate irregularities) on its upper portion. The shape of the folded wing is rounded in both species, with primary 9 the longest, 8 the second longest, and 10 (outer) and 7 shorter and about equal in length in *Prosobonia*; in *Aechmorhynchus* 10 and 8 are about equal in length. The tail pattern is also similar in both species. Barring, which first appears as pale intrusions along the outer edge or edges of the central or second pair of retrices becomes increasingly pronounced on the lateral tail feathers forming well-defined bars in *Prosobonia* and in some specimens of *Aechmorhynchus*. Barring in the tail of other tringine species also resembles that of *Aechmorhynchus* and of *Prosobonia*, but the importance of barring in *Prosobonia* lies in the implication that its plain-colored body and wings may have been derived from a patterned ancestor. This is also suggested by the presence of russet edges on the sooty underwing coverts (see Appendix).

Although Seebohm (1888) and Rothschild (1907) illustrate *Prosobonia* with a white patch behind the eye, the white feathers in fact represent the posterior part of a broken superciliary line that is pale rust anteriorly. The position and extent of the eye line is similar to that of *Aechmorhynchus* (Figure 1).

Skull.—As revealed by X rays, the skull of the mounted specimen of *Prosobonia* is almost complete, with only a portion of the posterior wall of the cranium damaged or lacking. To obtain a meaningful comparison

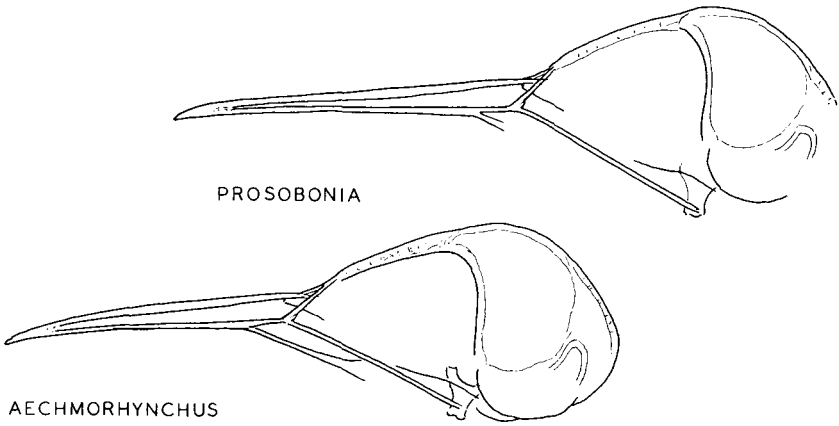

Figure 5. Drawing of X rays of skulls of *Aechmorhynchus cancellatus* and *Prosobonia leucoptera.*

with *Aechmorhynchus*, Zusi X-rayed a spirit specimen of *Aechmorhynchus* that was skeletonized later. The cleaned skull was not useful for this comparison because the slender upper jaw warped and dried at an unnatural angle. Enlarged outline drawings made from the lateral X rays of the two species show the shapes of the crania to be very similar, as are the contours of the braincase, the orbital region, the angle of the nasal strut to the upper jaw and jugal bar, and the angle of the upper jaw to any given baseline representing the braincase or orbital region (see Figure 5). The upper jaws differ in length, and in *Aechmorhynchus* the tip is slightly decurved.

The laterally compressed lacrymals of *Aechmorhynchus*, which configuration Lowe (1927: 127) considered unusual in the Scolopacidae, are like those of *Prosobonia* as revealed by a ventral X ray of the skull. In both species the lacrymals are mere projections from dorsal view and the greatest interlacrymal width expressed as a percentage of cranial length is similar (Table 2).

Generic status.—*Aechmorhynchus* and *Prosobonia* are similar in proportions, skull morphology (based on limited comparison), and in certain aspects of plumage pattern. The main difference lies in general plumage pattern, which is barred and mottled in *Aechmorhynchus* and plain in *Prosobonia*. Their differences are no greater than those found within other genera of shorebirds (for example *Limosa*, *Tringa*, and *Calidris*) or between breeding and nonbreeding plumages of some species. The overall morphological similarity between these species, in addition to their geographical distributions, indicate that they are very closely related—closer to each other than either is to any other known scolopacid. We therefore recom-

TABLE 2
CRANIAL MEASUREMENTS OF *AECHMORHYNCHUS* AND *PROSOBONIA*

	Aechmorhynchus	*Prosobonia*
Cranial length[1]	17.7	19.7
Inter-lacrymal width[2]	5.0	5.9
Inter-lacrymal/cranial length × 100	29.9	28.2

[1] Frontonasal hinge to posterior border of vertical semicircular canal, measured from X rays.
[2] *Aechmorhynchus* measured from skull; *Prosobonia* from X ray made with dorsal surface of skull against film.

mend that *Aechmorhynchus* be merged with *Prosobonia*, though to avoid confusion we use both *Prosobonia* and *Aechmorhynchus* throughout the remainder of this paper.

THE SYSTEMATIC POSITION OF *AECHMORHYNCHUS*

According to Lowe (1927: 116), *Aechmorhynchus cancellatus* is a "somewhat generalized Scolopacine type" representing an intermediate stage in the evolution of the curlews from an unknown generalized stock. He based his opinion on plumage characters, pterylography, skull morphology, and thigh muscle formula. In the sections that follow we present a reappraisal of some of his evidence and conclusions.

Plumage.—Lowe (1927: 118) considered the coloration and pattern of *Aechmorhynchus* to be "like that of some diminutive Curlew," noting that the scapulars, upper wing coverts, and mantle were barred and notched as in *Numenius*. In our opinion the plumage pattern of *Aechmorhynchus* also closely resembles that of several species of *Tringa*, particularly *glareola*.

Pterylography.—Lowe's study of pterylosis is neither detailed nor extensive enough to serve as a basis for sound taxonomic conclusions. He stated that the feather tracts in *Aechmorhynchus*, unlike those of other Charadrii, lacked an obvious separation between the anterior and posterior portions of the spinal tract. Nevertheless Kozlova's (1961: 19) illustrations show that the dorsal tract in *Tringa nebularia* and *Limosa lapponica* closely resembles that of *Aechmorhynchus* (cf. Lowe, 1927: 120, text-figure 6).

Skull.—Lowe (1915) enumerated characters of the skull by which the Eroliinae (= Calidridinae) and the Tringinae (= Tringini) could be distinguished. In a later study (Lowe, 1927: 126), he stated that "the skull of *Aechmorhynchus* does not closely resemble the Tringine or Eroliine type, although it has a certain superficial similarity to the former group." He concluded that it more closely resembled the Limosinae (= Numenini). Our discussion is built on Lowe's work, but we have added several characters and omitted others that do not appear to be significant. We examined

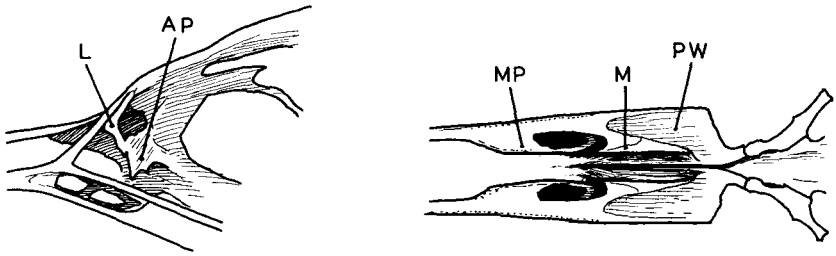

Figure 6. Features of the skull of *Aechmorhynchus cancellatus*. Left, lateral view of left side. Right, ventral view of palate (vomer missing). AP, antorbital plate; L, lacrymal; M, mediopalatine; MP, maxillopalatine; PW, palatine wing.

one skeleton of *Aechmorhynchus* and one or more of a wide range of tringine and calidridine species.

Aechmorhynchus resembles the Tringini and differs from the Calidridinae in having 1) a tapered, narrow symphysis of the upper jaw with sparse, linear sensory pits; 2) the premaxillary bar of the upper jaw flattened and flexible at its base; 3) the nasal bar broader and probably inflexible ventrally; 4) a relatively small angle between the nasal and jugal bars, and a relatively large angle between the jugal and maxillary bars; 5) palatines with essentially parallel outer edges; 6) maxillopalatines free from the palatines for their posterior half; 7) mediopalatine portion of palatine wing as long as or longer than maxillopalatine portion; and 8) braincase protruding posteriorly—not rounded. *Aechmorhynchus* resembles the Calidridinae in that the outer and posterior edges of the palatine wing approximate a right angle rather than forming an obtuse angle (Figure 6). In addition the posteroventral corners of the palatine wing lie considerably ventral to the edges of the mediopalatine processes rather than roughly on the same plane as in the Tringini.

The following characters cited by Lowe (1927) to show a special relationship between *Aechmorhynchus* and the Numenini we found to be equally applicable to some species or individuals of the Tringini: 1) backward protrusion of the occipital region, 2) occipital fontanelles facing more directly backwards, 3) interorbital roof narrow, 4) edges of interorbital roof beveled, 5) lacrymals almost invisible from above, 6) conformation of antorbital plate, and 7) nasal septum tapering to a point anteriorly. In two important characters we found *Aechmorhynchus* to resemble the Tringini and to differ from the Numenini. First, its lacrymal is a flattened, curved bar that lies anterior to the antorbital plate (Figure 6); in *Numenius* and *Bartramia* it is straighter and forms a dorsal extension of the lateral edge of the antorbital plate. Second, the dorsal edge (strut C) of

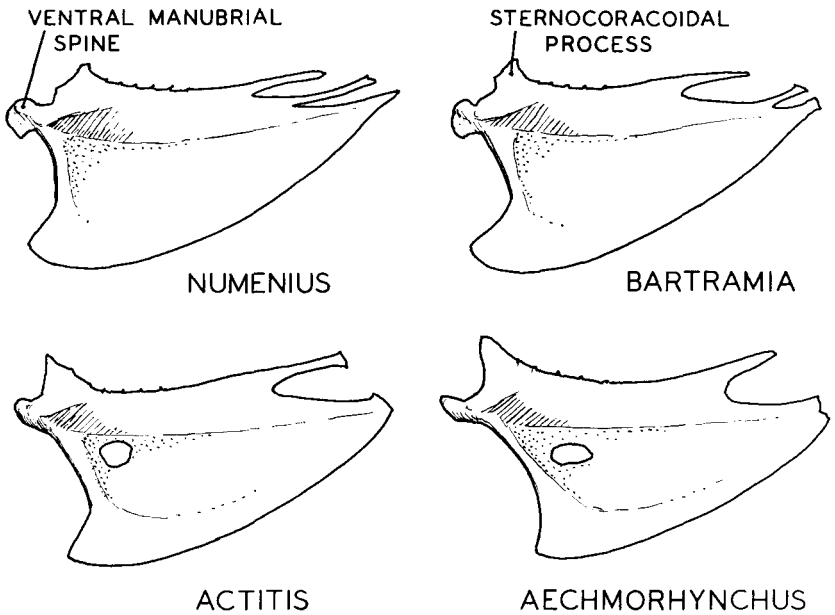

Figure 7. Lateral view of sternum in *Numenius tahitiensis*, *Bartramia longicauda*, *Actitis macularia*, and *Aechmorhynchus cancellatus*.

the maxillopalatine attaches at or just posterior to the base of the nasal bar in *Aechmorhynchus* and the Tringini; in the Numenini it usually attaches medial to the nasal bar and the attachment flares out to form a shelf that is partly or wholly hidden in ventral view by another bony shelf between the palatine and maxillary bones (Figure 2).

In summary, the skull of *Aechmorhynchus* shows no special relationship with the Numenini. Its characters, except for the shape of the palatine wing, can be matched within the Tringini.

Sternum.—Lowe (1927: 126) stated that postcranial osteology of *Aechmorhynchus* had "no features of any special interest," but we note that several sternal characters differ within the Scolopacidae (Figure 7): 1) in some species the ventral manubrial spine is a rounded, upturned projection, whereas in others it is flanged and resembles an axe blade; 2) the anterior edge of the sternocoracoidal process may slope backward, or it may be perpendicular or sloped slightly forward; 3) some species have a carinal foramen; and 4) the posterior border of the sternum may be two- or four-notched (described earlier by Shufeldt (1903: 68)). Individually these features may vary within a genus or species, but taken in combination they shed some light on the relationships of *Aechmorhynchus*.

TABLE 3

CHARACTERS OF THE STERNUM IN THE SCOLOPACIDAE[1]

	Ventral manubrial spine knob-like (+) or blade-like (—)	Sternocoracoidal process slopes forward (+) or backward (—)	Carinal foramen present (+) or absent (—)	Sternum two-notched (+) or four-notched (—)
Limosa[2]	—	—	—	—
Numenius[3]	—	—	—	—
Bartramia (10)	—	—	—	—
Tringa[4]	—	—	—	—
T. solitaria (7)	—	—	—	+
Catoptrophorus (9)	—	—	—	—
Aechmorhynchus (1)	+	+	+	+
Actitis macularia (4)	+	+	2 +, 2 —	+
A. hypoleucos (4)	+	+	3 +, 1 —	3 +, 1 —
Heteroscelus brevipes (1)	+	—	—	—
H. incanus (8)	4 +, 4 —	—	+	—
Calidris pusilla (5)	+	+	3 +, 2 —	—
Tryngites (4)	+	+	—	2 +, 2 —
Philomachus (3)	—	—	—	2 +, 1 —

[1] Numbers represent number of specimens examined.

[2] *L. haemastica* (8), *jedoa* (7), *lapponica* (2), *limosa* (3).

[3] *N. americana* (4), *arquatus* (1), *phaeopus* (11), *tahitiensis* (2).

[4] *T. melanoleuca* (6), *flavipes* (8).

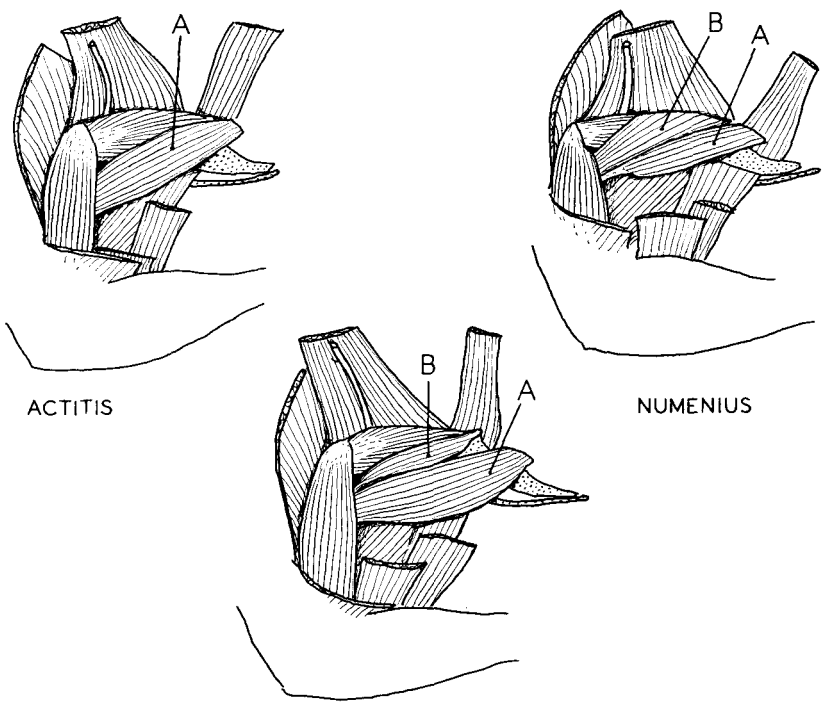

Figure 8. Lateral view of thigh muscles of *Actitis hypoleucos*, *Numenius tahitiensis*, and *Aechmorhynchus cancellatus*, dissected to reveal the piriformis muscle—pars caudofemoralis (A), and pars iliofemoralis (B). See text.

In a single skeleton of *Aechmorhynchus* the manubrial spine is knoblike, the sternocoracoidal process slopes forward, a carinal foramen is present, and the sternum is two-notched. Elsewhere in the Scolopacidae these characters occur together only in *Actitis* (Table 3); by contrast *Aechmorhynchus* differs from *Numenius* in all four characters.

Thigh muscles (Figure 8).—Lowe (1931a) noted that a specimen of *Numenius arquatus* and one of *Aechmorhynchus* had similar thigh muscles—both ABXY in terms of Garrod's (1874) formula. M. piriformis, pars iliofemoralis (or accessory femorocaudal muscle), represented by B in the formula, is usually lacking in the Scolopacidae whereas M. piriformis, pars caudofemoralis (muscle A), is always present. Lowe (1931a) interpreted the presence of B as further evidence that *Aechmorhynchus* is a "generalized or early form of Curlew." Examination of spirit specimens of each of the following species by Zusi revealed the following pattern of

occurrence of muscle B (number of specimens in parentheses): present in *Numenius tahitiensis* (2) and *Bartramia longicauda* (2); absent in *Tringa totanus* (1), *Catoptrophorus semipalmatus* (1), *Actitis hypoleucos* (2), *Actitis macularia* (2), *Phalaropus fulicarius* (1), and *Limosa lapponica* (1). According to Fleming (1966) muscle B is absent in *Tryngites subruficollis*, *Limnodromus griseus*, and *Gallinago gallinago*. Lowe (1927: 123) reported B absent for *Aechmorhynchus*, but later (1931a: 242) stated that it was present, lying "very close and parallel to the femoro-caudal [A], so that the two at first sight look like one large triangular femoro-caudal." In both legs of one specimen and in one leg of another of *Aechmorhynchus* Zusi found pars caudofemoralis (A) to be broad and flat on the thigh, narrowing as it crossed the posterior border of the ilium. There was no separation into two muscles and no attachment on the pelvis. In the other leg of the second specimen the piriformis muscle had a smaller dorsal slip attaching on the posterior end of the iliac ridge (Figure 8). This slip differed from muscle B in *Numenius* and *Bartramia* in having a much more restricted attachment on the ilium and a smaller attachment on the femur than that of muscle A. The dorsal slip in *Aechmorhynchus* may represent muscle B, but its complete absence in one individual and its absence from one leg of another suggest that the muscle is vestigial and of little taxonomic value.

Breeding biology.—Practically nothing is known of the nesting biology of *Aechmorhynchus*. Greenway (1958: 262) wrote of a pair nesting on Kauehi Island, and of a nest at Tunake Island at which the parents were seen. This suggests that both parents are solicitous of the nesting territory and perhaps that both share in incubation and in rearing of the young—the usual condition in the Scolopacidae, although notable exceptions occur (*Scolopax*, *Phalaropus*, and within the Calidridinae). According to Greenway (1958: 262) the two known eggs of *Aechmorhynchus* are most like those of *Bartramia*, which in turn differ from those of the Tringini and of *Numenius*. The significance of these similarities and differences will not be known until more eggs of *Aechmorhynchus* are available and until the adaptive and taxonomic value of egg color patterns in the Scolopacidae are better understood.

Conclusion.—*Aechmorhynchus* is more closely related to the Tringini than to the Numenini. It is distinguished from the former by the shape of the palatine wing, and by the presence in some individuals of M. piriformis, pars iliofemoralis. The rounded wings and relatively long, stout hind toe also set *Aechmorhynchus* and *Prosobonia* apart from other Tringini. Pending further evidence on the relationships of these birds we recommend that *Prosobonia leucoptera* and *Aechmorhynchus cancellatus* be considered congeneric and placed in a tribe, Prosoboniini, of the Tringinae.

SUMMARY

The systematic positions of three little-known shorebirds—*Phegornis mitchellii*, *Prosobonia leucoptera*, and *Aechmorhynchus cancellatus*—are evaluated from comparative studies of osteology, myology, and plumage patterns of adults and chicks. *Phegornis* belongs in the Charadriinae of the Charadriidae. We regard *Aechmorhynchus* as congeneric with *Prosobonia*, constituting a tribe, Prosoboniini, in the subfamily Tringinae of the Scolopacidae. The reconstituted genus *Prosobonia* thus contains the species *cancellatus* and *leucoptera*. The Prosoboniini are most closely related to the Tringini.

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APPENDIX

A redescription of the type specimen of *Prosobonia leucoptera* is presented here from notes taken by Zusi in 1966. (See also illustrations of *Prosbonia* in Seebohm (1888), Rothschild (1907), and Fisher and Peterson (1964: 56). *Aechmorhynchus* is illustrated in Seebohm (1888), Rothschild (1907), Lowe (1927), and Greenway (1958).)

DESCRIPTION OF *PROSOBONIA LEUCOPTERA*.—Plain-colored, except for barring on the tail and pale edges on underwing coverts. Wings and back sooty brown; top and sides of head and neck paler sooty brown, shading into the darker back. Rump russet (close to "ferruginous" of Ridgway (1912). Chin and gular region whitish, with some buff. Malar region and entire remaining underparts russet; narrow eye ringlet of paler russet. Broken superciliary line, of which anterior part is pale russet, running from bill to anterodorsal corner of eye; stripe reappears above eye, where it is pale russet, and abruptly changes to white above auricular region. Feathers at color boundary along side of neck and at bend of wing have sooty bases and russet tips. Crescent-shaped patch of white on lesser wing coverts near bend of wing continuous across leading edge of wing with similar but smaller white patch on under side. Wing lining dusky brown; some feathers with russet edges, especially prominent on coverts bordering flight feathers. Inner surfaces of flight feathers dusky, but paler than wing lining. Axillars sooty brown. Ten primaries.

Tail rounded, twelve rectrices. Central tail feathers sooty brown with russet tips;

other feathers have prominent russet tips and become progressively more heavily barred with russet toward lateral pair. (Four lateralmost right tail feathers and left central one missing; left lateral feather detached but accompanies specimen.)

Bill dark above, lower mandible slightly paler. Legs straw-colored and slightly greenish, boundaries of scutes dark and clear. Legs scutellate-reticulate. Scutes extend about half way around either side of tarsometatarsus and toes. Tibiotarsus with 22–23 scutes. (One scute of left leg appears only laterally, being crowded out medially by scutes above and below.) No webbing between toes 2 and 3, slight membrane between 3 and 4. Nails laterally compressed, sharp, and curved.

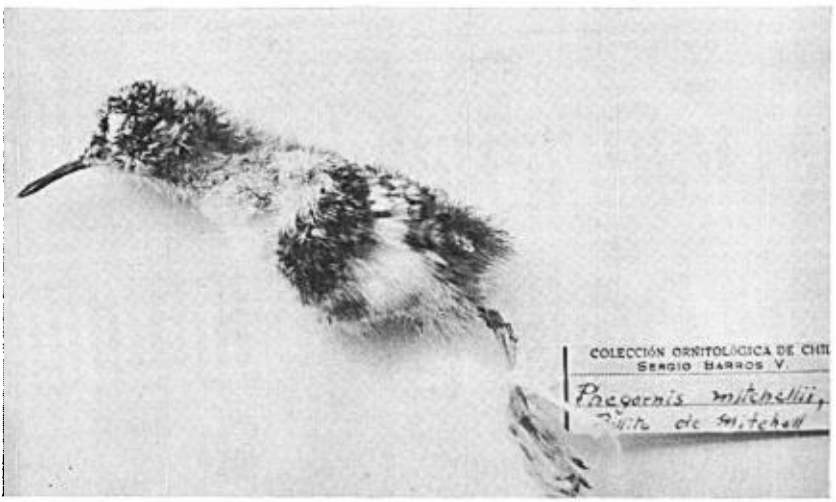

Figure 9. Downy chick of *Phegornis mitchellii* photographed by Jehl at Universidad de Concepción, Chile. Specimen taken in Andes near Santiago, Chile. (Photograph received after article was in page proof.—Ed.)

National Museum of Natural History, Smithsonian Institution, Washington, D. C. 20560, and *Natural History Museum, San Diego, California 92112.*