

## THE FOSSIL FLAMINGOS OF AUSTRALIA

By ALDEN H. MILLER

When the abundant bird fossils collected in recent years in the Lake Eyre basin of Australia were first tentatively assorted, the most surprising discovery was that of flamingos (Stirton, Tedford, and Miller, 1961:35). This type of bird is absent from the continent of Australia today and flamingos do not occur at points nearer than north-west India; there are records in historic times from Ceylon, and their bones occur along with remains of the Dodo in Mauritius. The further study of our collections, especially those obtained in 1961, shows that flamingos were present not only in mid-Tertiary time as previously noted but also in the Pleistocene, although strangely they did not appear among the Pleistocene collections DeVis (1906) reported on from Cooper Creek in the Lake Eyre area. In all, there are four species represented, three of which are here described as new. In two of the faunas two kinds of flamingo occur together. This is not an unusual situation in this order of birds. Three species live today in the highland playa lakes of the arid sections of Chile, and the presence of several species together in the Oligocene of France was well documented by Milne-Edwards (1867-1871).

Flamingos in general are well represented in the fossil record, both the typical group, the family *Phoenicopteridae*, and the extinct *Palaeolodidae*, a group of birds that is straight-billed and also less slim and elongate than the true flamingos. The environment in which such birds live, namely relatively shallow, muddy lakes of wide expanse, has been particularly favorable to the preservation of their bones. Thus the record of the order extends back to the Cretaceous and geographically to many parts of Europe and North America. Fossils and modern occurrences are not known from Southeast Asia or the East Indies. The lack of fossil records for South America and Africa probably reflects in part the relatively slight attention given to the fossil birds of those continents.

The support of the National Science Foundation in 1961 and 1962 made possible further field work in Australia and the processing of collections, both of the essential Recent bird skeletons and of fossils. The study of fossil vertebrates in South Australia has continued to receive the generous support of the South Australian Museum and its staff. We were especially aided in 1961 by Norman B. Tindale, Paul F. Lawson, and Harry J. Bowshall. R. A. Stirton, Richard H. Tedford, and Virginia D. Miller of our field party provided critical assistance during the 1961 expedition. Stirton particularly has given constant support and encouragement to the investigation of the Australian fossil birds and has supplied details concerning the collecting localities. I am indebted also to Philip S. Humphrey of the United States National Museum for the loan of skeletons of *Phoenicopterus ruber*.

## DESCRIPTION OF MATERIAL

*Phoenicopterus novaehollandiae*, new species

*Type*.—Right tarsometatarsus, the distal end essentially complete, although with many fractures proximal to the articular surfaces; about 95 per cent of shaft represented; no. P13648, South Australian Mus.; locality no. V6150, Univ. Calif. Mus. Paleo., Lake Pitikanta; Ngapakaldi Fauna, middle Tertiary, probably late Oligocene or early Miocene; figures 1*a*, *c*, 2*a*.

*Type locality*.—Etadunna Formation in escarpment on west side Lake Pitikanta about 600 yards from south end; Lake Eyre region, South Australia; green to greenish-brown mudstone below upper gray calcareous mudstone and near contact with lower gray calcareous mudstone.

*Diagnosis.*—Similar in foot structure to *Phoenicopterus ruber* (includes *Phoenicopterus ruber roseus*) but scar for articulation of metatarsal I present; distal tarsal foramen apparently not perforating plantar surface and on anterior surface situated more proximally; trochlea IV closer to trochlea III; posterior extension of trochlea II narrower mediolaterally and proximodistally. Size within limits of variation of *ruber* but near maximum of range.

*Analysis and comparison.*—The species *novaehollandiae* has the same general configuration, slender construction and articular system of the foot as that of the modern greater flamingo, *P. ruber*, of Africa, southern Europe, and the West Indies. The most interesting departure is in the presence of the articulation for a first toe which can only mean that this digit was of a size and functional importance much greater than in modern flamingos. In the present-day *Phoenicopterus* it is reduced to a length of about 18 mm. and seems to have little use. In the genus *Phoeniconaias* it is further reduced and in *Phoenicoparrus* it is lacking. Even in the first two, there is no flattened scar for articulation at the point of attachment on the medial ridge of the plantar surface, the toe being held at that point rather loosely by weak ligaments.

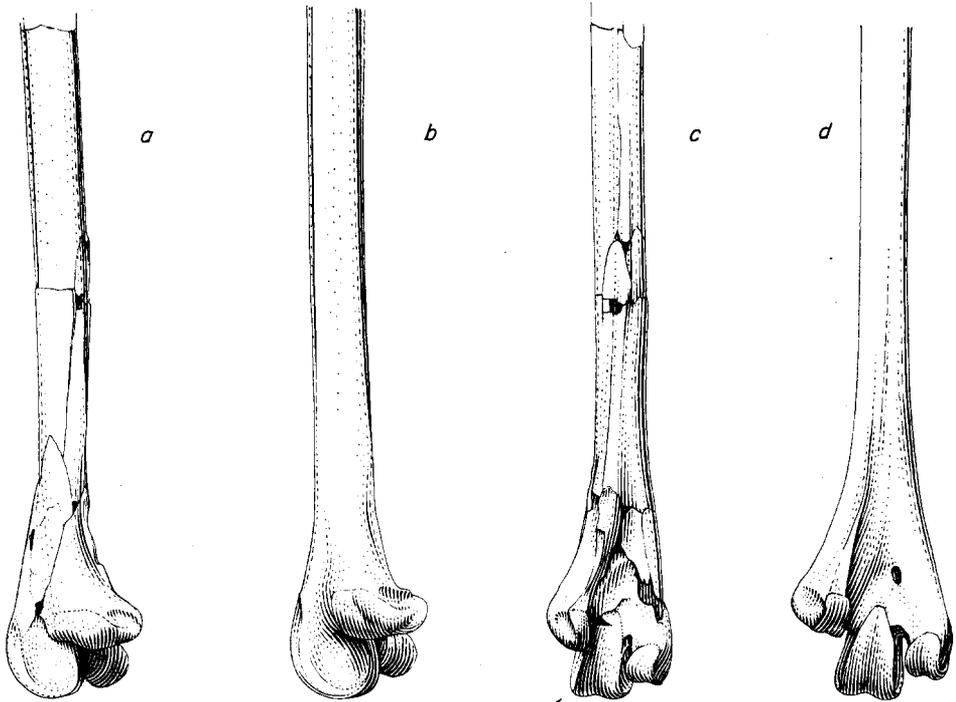


Fig. 1. Distal ends of right tarsometatarsi of flamingos, natural size. *a*, type of *Phoenicopterus novaehollandiae*, medial view; *b*, modern *Phoenicopterus ruber roseus*, no. 289737, U. S. Nat. Mus., medial view; *c*, type of *P. novaehollandiae*, plantar view; *d*, *P. r. roseus*, plantar view. Drawings in figures 1 to 6 by Augusta Lucas.

The other features of *Phoenicopterus novaehollandiae* in respect to the trochleae reflect a lesser spread of the toes and perhaps weaker support for the medial bracing ligaments of the inner toe. These differences are of small magnitude and probably limited functional significance but are consistent departures from the configuration in the

modern *ruber* in that none of the considerable sample of *ruber* shows them. They are therefore useful species characters.

*Phoenicopterus novaehollandiae* had an overall length and slenderness equivalent to specimen no. 289737, U. S. Nat. Mus., a large male *P. ruber* (figs. 1*b*, *d*, 2*b*). This length is judged from the distance from the distal end to the beginning of the expansion of the proximal end, which expansion is present in the fossil even though the proximal articular surfaces and the hypotarsus are entirely lacking. The shaft, which was lying in place, but in a much fragmented condition, has been fitted together, all junctions but one being natural contacts. Because of the one gap in mid-shaft, which is believed to be small, the estimate of length is minimal, but it is not likely to be more than 5 per cent below the true value.

Five extinct species of flamingos of the genus *Phoenicopterus* have already been described from other parts of the world. Two of these are very small species, neither of which is represented by the distal end of the tarsometatarsus. By reason of small size at least, they are not confusable with *novaehollandiae*. These two are *Phoenicopterus minutus* Howard (1955) from the late Pleistocene of California and *Phoenicopterus stocki* L. Miller (1944) from the Pliocene of Chihuahua.

*Phoenicopterus copei* Shufeldt (1892) of the Pleistocene of Oregon, consisting of several unassociated parts, does include a distal segment of a tarsometatarsus as designated type material. Howard (1946: 157-158) did not find characteristics in this part of the tarsus either in size or shape which separated *copei* from *ruber*, in the inclusive sense, although there were features of the tibiotarsus that did so distinguish it. The figure of the tarsometatarsus prepared by Shufeldt himself shows this bone in anterior aspect to have none of the compression of the trochleae of *novaehollandiae*, and a completely perforate distal foramen is present and situated as in *ruber*.

*Phoenicopterus floridanus* Brodkorb (1953) from the Pliocene of Florida is based on a tibiotarsus but there are referred specimens of the tarsometatarsus. Brodkorb's figure of this element shows none of the characteristic shape of trochlea II of *novaehollandiae*. Moreover the shaft is much deeper in *floridanus* and the distal foramen is perforated and situated more as in *ruber*.

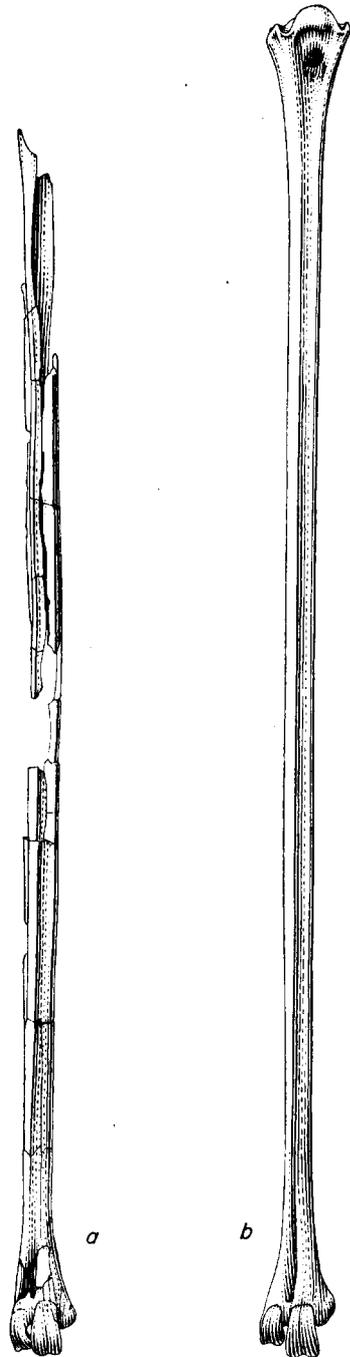


Fig. 2. Anterior views of tarsometatarsi,  $\times \frac{1}{2}$ . *a*, type of *Phoenicopterus novaehollandiae*; *b*, modern *Phoenicopterus ruber roseus*, no. 289737, U. S. Nat. Mus.

The only old world fossil of the genus *Phoenicopterus* which has been given a specific name is *Phoenicopterus croizeti* Gervais of the Aquitanian (Oligocene) of France. This was founded on a tibiotarsus. Much additional material has been referred to it, including several tarsometatarsi. Milne-Edwards (1867-1871:pl. 81) in figuring these tarsi shows none of the features that would suggest *novae-hollandiae*. For example trochlea II is not compressed or tapered posteriorly and the lateral rim of trochlea IV is not produced and therefore does not reflect compression; in both these respects it is like *ruber*. The distal foramen clearly is placed rather far distally, not proximally as in *novae-hollandiae*. Unfortunately the plantar surface is not figured or commented on so that evidence for the development of digit I cannot be assessed. It would be most interesting to know if *croizeti* as a species of similar age to *novae-hollandiae* gave indication of having a similar large hind toe unlike the later flamingos.

TABLE 1

MEASUREMENTS IN MILLIMETERS OF TARSOMETATARSII OF SPECIES OF *Phoenicopterus*

	Total length	Least width of shaft	Least depth of shaft	Width across trochleae
<i>P. novae-hollandiae</i>	354 <sup>2</sup>	6.9	7.0	17.6 <sup>3</sup>
<i>P. ruber roseus</i> , no. 289737 (♂) U.S.N.M. <sup>1</sup>	356	6.2	6.9	21.6
<i>P. ruber roseus</i> , no. 224858 U.S.N.M. <sup>1</sup>	364	5.6	6.7	20.6
<i>P. ruber roseus</i> , no. 79026 M.V.Z.	275	5.8	6.4	18.5
<i>P. ruber ruber</i> , no. 140923 M.V.Z. (Galápagos Islands)	253	5.7	6.2	18.0
<i>P. chilensis</i> , no. 125159 (♂) M.V.Z.	276	5.6	5.3	19.3
<i>P. chilensis</i> , no. 125158 (♀) M.V.Z.	236	5.3	4.8	16.7

<sup>1</sup> Largest two skeletons of 16 of this form in U. S. Nat. Mus.<sup>2</sup> Estimate extrapolated from comparison with no. 289737 U. S. Nat. Mus.<sup>3</sup> Dimension may be somewhat reduced (less than 10 per cent) by distortion in preservation.***Phoeniconotius eyrensis*, new genus and species**

*Type*.—Distal end of left tarsometatarsus, consisting of trochleae II and III and adjoining foot area and fragmented trochlea IV, the shaft lacking; proximal phalanx of left digit III and proximal phalanx of right digit IV; no. P13649, South Australian Mus.; locality no. V5763, Univ. Calif. Mus. Paleo., Lake Palankarina, Ngapakaldi Fauna, middle Tertiary, probably late Oligocene or early Miocene; figure 3.

*Type locality*.—Base of escarpment on west shore of Lake Palankarina between turtle quarry (V5762) and Perikoala locality (V5375); Lake Eyre region, South Australia; float from Etadunna Formation with other bird, reptile and fish remains derived from green mudstone and fine-grained sandstone units, about 10 feet in thickness, above lower limestone member.

*Diagnosis*.—Resembles *Phoenicopterus* but articular surface of trochlea III on plantar surface truncated proximally, not long and tapered; trochlea II with smooth, broad and conspicuous concavity bordering articular surface proximally, the medial ridge delimiting it sharp and displaced far toward medial surface; prominent scar present for articulation of metatarsal I; trochlea III more robust and wider; basal phalanx of middle toe more robust but relatively shorter, the plantar fossa at its base deeper. Size somewhat larger than largest males of *Phoenicopterus ruber*, at least in breadth and depth of foot.

*Association*.—The material representing *Phoeniconotius* was picked up at one spot on the surface of the formation but was not in articulated position. The base of the middle toe fits the articular surface of trochlea III and belongs to the same side of the body. The basal part of toe IV appears from its shape to pertain to the opposite foot and because of this and since trochlea IV is incomplete, its relation to the other parts

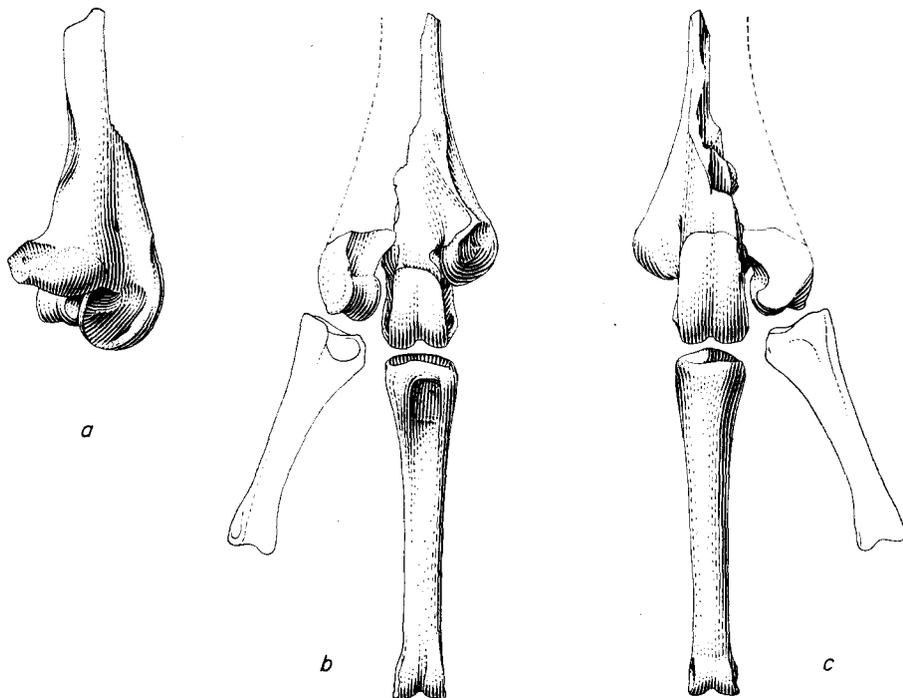


Fig. 3. Distal end of left tarsometatarsus and base of toes of *Phoeniconotius eyrensis*, type, natural size. *a*, medial view; *b*, plantar view; *c*, anterior view. The outline of the basal phalanx of digit IV is derived by reversing the drawing of the example of the right phalanx.

cannot be clearly demonstrated. All three units are of the same gray color and are highly mineralized.

*Analysis and comparison.*—*Phoeniconotius* like other phoenicopterids has the characteristically elevated trochlea II which is deflected strongly toward the plantar surface. *Grus* has some of these features, but trochlea II of this genus is much more elevated and the posterior spur of trochlea II is narrow and set off sharply from the articular surface.

In the family Paloelodidae trochlea II is of very different shape in medial profile, being broad and rounded and having no true posterior spur as in *Phoenicopterus* and cranes. *Phoeniconotius* in none of these respects approaches *Paloelodus* and *Megapaloelodus* and is instead a typical flamingo of the Family Phoenicopteridae. However, in general massiveness, as judged from the middle trochlea, it is the equivalent of *Megapaloelodus connectens* from the Miocene of South Dakota (A. H. Miller, 1944:86, fig. 1).

The structural features of *Phoeniconotius* suggest that it was less equipped to swim than *Phoenicopterus* and its small modern relatives. This is shown by the articular surface of the plantar aspect which is less extended to accommodate extreme flexion of the toes. In swimming groups generally this surface is well extended whereas in more terrestrial waders or walkers, such as cranes, it is not. *Phoeniconotius* may then have been a flamingo less adapted than the other genera for deep water wading or swimming. Its relatively short, stout basal phalanx of digit III further suggests this.

As in *Phoenicopterus novaehollandiae*, the first toe in *Phoeniconotius* was evidently better developed than in modern flamingos, for the articulation for metatarsal I is con-

TABLE 2

MEASUREMENTS IN MILLIMETERS OF PARTS OF FEET OF GENERA OF FLAMINGOS			
	<i>Phoeniconotius</i>	<i>Phoenicopterus ruber</i> (no. 224858 U.S.N.M.)	<i>Megapalaelodus</i>
Tarsometatarsus:			
Greatest anteroposterior dimension of trochlea II	15.0	13.9	16.0
Greatest anteroposterior dimension of trochlea III	12.5	11.1	13.7
Greatest width of trochlea III	10.5	8.3	9.0
Distance from tip of trochlea III to plantar end of articular surface	11.1	12.3	12.8
First phalanx digit III:			
Length	45.5	48.8	
Proximal width	9.9	9.1	
Proximal depth	11.5	10.8	
Distal width	6.3	6.2	
Distal depth	6.4	6.2	
First phalanx digit IV:			
Length	31.9	30.8	
Proximal width	8.5	7.3	
Proximal depth	11.0	9.9	
Distal width	4.7	5.3	
Distal depth	6.7	7.0	

spicuous and broad. Milne-Edwards' figures (*op. cit.*: pl. 82; pl. 87, 2) suggest this toe was well developed in *Paloelodus*, but the evidence for this is not available for the Oligocene *Phoenicopterus croizeti*, as already noted. A fairly large hind toe and articulation are present also in the cranes and of course in the storks and ibises.

In summary, then, *Phoeniconotius* was a large, massive, true flamingo, less specialized for swimming than other flamingos and possibly more adapted than others for shallow-water and terrestrial locomotion. Without knowledge of its linear dimensions, we cannot judge whether its legs were elongate in such great degree as in other members of the Phoenicopteridae. The details of its foot and toe articulation suggest no significant approach to or link phyletically with the massive, relatively shorter-legged flamingos of the family Paloelodidae.

#### *Phoeniconaias gracilis*, new species

*Type*.—Distal end of left tarsometatarsus, complete except for some abrasion of anterior surfaces of trochleae II and III; plantar surfaces and most of articular surfaces well preserved; no. 13650, South Australian Mus.; locality no. V5772, Univ. Calif. Mus. Paleo., Lake Kanunka, Kanunka Fauna, early Pleistocene; figures 4a, c.

*Type locality*.—Katipiri Sands at northwest corner of Lake Kanunka; Lake Eyre region, South Australia; coarse to medium white and ferruginous stained quartz, stream-channel sands with clay balls, pebbles, coprolites and abraded bones; channel sands have cut through Tirari Formation and rest on green mudstones of Etadunna Formation (Stirton, Tedford, and Miller, 1961).

*Diagnosis*.—Smaller and more slender than *Phoeniconaias minor*; posterior extension of trochlea II much less rounded and of lesser proximodistal dimension; articular surface of trochlea IV less extensive proximally on plantar surface.

*Analysis and comparison*.—Among living flamingos, the small species are separated generically from *Phoenicopterus* as *Phoenicoparrus* and *Phoeniconaias* on the basis of substantial differences in the rostrum and skull. Generic differentiation in the tarsometatarsus is slight, but the small species have a more tapered and relatively longer articular surface at the plantar base of trochlea III. This is particularly evident in *Phoeniconaias minor* although I have been able to compare only one of the two species

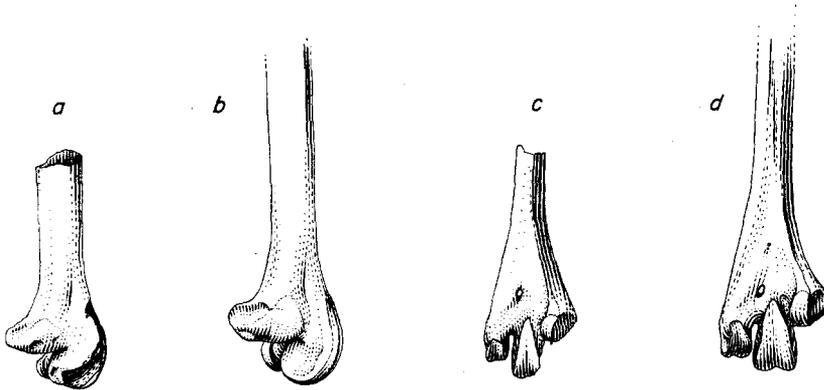


Fig. 4. Distal ends of left tarsometatarsi of flamingos of the genus *Phoeniconaias*, natural size. *a*, type of *Phoeniconaias gracilis*, medial view; *b*, modern *Phoeniconaias minor*, no. 133411, Mus. Vert. Zool., medial view; *c*, type of *P. gracilis*, plantar view; *d*, *P. minor*, plantar view.

of *Phoenicoparrus*, namely *andinus*. Furthermore, in *Phoeniconaias* trochlea II is relatively shallow and less rounded in the four specimens examined than in *Phoenicoparrus andinus*, *Phoenicopterus ruber*, and *Phoenicopterus chilensis*. In these respects the fossil *gracilis* accords with *Phoeniconaias minor* or exceeds it in differentiation from the other genera. These circumstances and the greater geographic proximity of *Phoeniconaias* of Africa and northern India favor placing *gracilis* in this genus even though

TABLE 3

MEASUREMENTS IN MILLIMETERS OF THE TARSOMETATARSII OF SPECIES OF *Phoeniconaias*

	<i>P. gracilis</i> type	<i>P. minor</i>			
		♀, no. 133408 MVZ	♀, no. 133409 MVZ	♀, no. 133410 MVZ	♂, no. 133411 MVZ
Greatest width across trochleae	13.0	14.7	15.3	15.8	14.8
Width of trochlea IV	3.3	3.9	4.0	4.4	4.1
Greatest anteroposterior dimension of trochlea III	8.8	8.4	8.7	8.7	8.5
Greatest anteroposterior dimension of trochlea II	8.5	9.1	9.2	9.6	9.2
Minimum width of shaft	4.7	5.6	5.5	6.0	5.5
Maximum depth of shaft	5.6	5.7	5.3	5.8	5.6
Total length	....	205	214	219	230

one would prefer, were it possible, to make the allocation on the basis of the substantial skull differences known in the modern types.

Other small fossil flamingos already mentioned (p. 291) are not known in respect to the foot area of the tarsometatarsus and occurred in western North America. Both appear to have been significantly smaller than females of *Phoeniconaias minor* but not quite as small as *gracilis* which is about 10 per cent smaller than the known minimum of *minor*. It is safe to say that *gracilis* was as small as any flamingo thus far recorded and it has features of configuration in the foot distinct from those of other flamingos in which that part is represented.

*Additional material.*—A fragmentary right tarsometatarsus consisting chiefly of trochleae II and III, no. 60561, Univ. Calif. Mus. Paleo., was found at the same local-

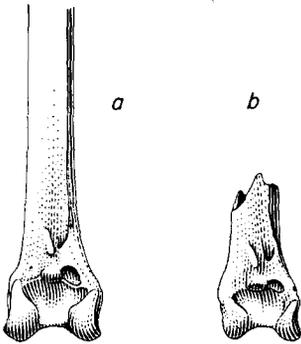


Fig. 5. Distal ends of tibiotarsi of flamingos of the genus *Phoeniconaias*, anterior view, natural size. *a*, *Phoeniconaias minor*, no. 133411, Mus. Vert. Zool.; *b*, fossil no. 56887, Univ. Calif. Mus. Paleo. referred to *Phoeniconaias gracilis*.

ity as the type in a subsequent year. It shows the same features of trochlea II, the slight departures from the type apparently being due to some abrasion. It was of the same small size and slender build.

*Referred material.*—The distal end of a right tibiotarsus (fig. 5*b*), no. 56887, Univ. Calif. Mus. Paleo., from the same locality, differs from *Phoeniconaias minor* in smaller size in the same degree as does the type tarsometatarsus. It matches *minor* well in configuration of the anterior surface, which area, including the tendinal canal, is well preserved. The condyles are abraded extensively on the posterior surface. Because of correspondence in size to *gracilis*, it is referred to that species.

The distal end of a left humerus, no. 56882, Univ. Calif. Mus. Paleo., from the same locality is also abraded, especially on the posterior surface, but shows enough of its configuration to place it as a flamingo. Its size is the same as that of specimen no. 133411, Mus. Vert. Zool., of *Phoeniconaias minor*. It is therefore not as extremely small as *gracilis* as known from the leg bones. However, it possibly falls within the limits of variation in size of that species which of course might not have shown in the wing the very slim build and small size that it did in the leg. It seems best, therefore, to refer the fragmentary humerus to *gracilis*.

#### *Phoenicopterus ruber* Linnaeus

*Material.*—Fragmentary distal end of a right tarsometatarsus lacking part of trochlea IV and the posterior spur of trochlea II; no. 60583, Univ. Calif. Mus. Paleo.; locality no. V5772, Univ. Calif. Mus. Paleo.; *in situ* in Katipiri Sands, Lake Kanunka, Kanunka Fauna, early Pleistocene; figure 6*a*.

Distal end of left humerus, well preserved but part of entepicondyle abraded; no. 56360, Univ. Calif. Mus. Paleo.; locality no. V5866, Univ. Calif. Mus. Paleo.; Cooper Creek, Malkuni Fauna, late Pleistocene; figures 6*b*, *c*.

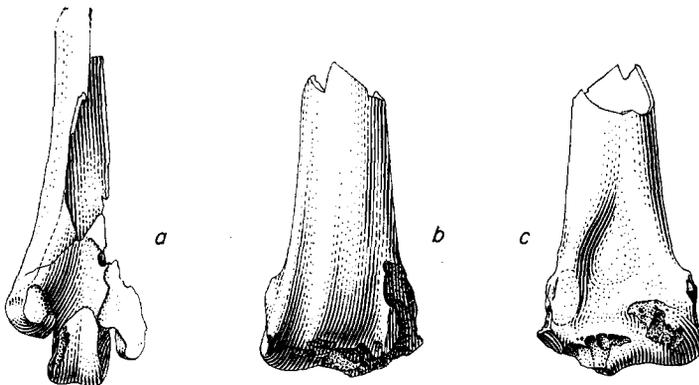


Fig. 6. Pleistocene fossils of *Phoenicopterus ruber*, natural size. *a*, distal end of right tarsometatarsus, no. 60583, Univ. Calif. Mus. Paleo., Kanunka Fauna, plantar view; *b*, distal end of left humerus, no. 56360, Univ. Calif. Mus. Paleo., Malkuni Fauna, anconeal view; *c*, same as *b*, palmar view.

*Localities.*—For locality V5772, see p. 294. Locality V5866: site 14, Katipiri Formation on north bank Cooper Creek across bend of creek west of Malkuni waterhole and Emu Camp (Stirton, Tedford, and Miller, 1961); highly ferruginous red and yellow cross-bedded sands with interbedded gray, yellow-brown, dark-red, and green clay bases; overlain by 20 feet of dune deposits; base of formation not observable.

*Characters.*—The tarsometatarsus shows the diagnostic shape of trochlea II of *Phoenicopterus* in respect to the articular surface and ligamental scars, and the length of this trochlea and its plantar deflection in all respects match *Phoenicopterus ruber*; only the tip of the posterior spur is lacking to prevent a verification of this part. Trochlea III likewise matches *ruber* in all details of shape including the plantar extension of the articular surface. The distal tarsal foramen is fully perforated and of size and position normal for *ruber*. In size the fossil is a close match for *P. ruber* no. 224858, U.S. Nat. Mus. (see table 2, p. 294). The parallel measurements of no. 60583 are: greatest anteroposterior dimension of trochlea III, 10.9 mm.; greatest width of trochlea III, 8.2 mm.

The humerus, no. 56360, shows configurations and ligamental scars of the lateral surface of the ectepicondyle identical with those of *Phoenicopterus ruber*. On the anconeal surface, the external tripetal groove is broad, deep and extended far proximally as normal in flamingos. The palmar surface shows the characteristic deep brachial depression with an elevated and elongate scar for the anterior articular ligament. The size of this fragment accords well with 140923, Mus. Vert. Zool., a male *Phoenicopterus ruber ruber*, smaller than the large males of the old world race, but well within the range of variation of that race. The fossil is much too large for *Phoeniconaias*.

Thus both the early Pleistocene and late Pleistocene representatives of a large flamingo show nothing to suggest any departure in osteologic detail or size from the modern *Phoenicopterus ruber*, and they may properly be assigned to that species.

#### DISCUSSION

A question at once posed by the record of fossil flamingos in Australia is why these species became extinct. Explanations of extinction are never more than speculative for any group of animals, but some possibilities may be suggested for these flamingos. The Tertiary species, *Phoeniconotus eyrensis* and *Phoenicopterus novaehollandiae*, were both very specialized wading types that must have functioned much like modern flamingos. Indeed the latter especially was so similar in structural design as to suggest that it had very similar methods of foraging. If anything it was more of a stilt-like wading type than the modern species even though it had a larger hind toe. In the early Pleistocene, the two species present were in one instance identical with a modern form and in the other a very slender, miniature counterpart of the living small flamingos. They, even more surely than the Tertiary flamingos, must have had the same ecologic requirements as the modern species. It should be noted further that the number of remains in the early Pleistocene of South Australia is considerably greater than in the much larger general collection of bird bones from the late Pleistocene in which we have found but a single flamingo bone.

These several circumstances point to the presence of good shallow water lakes in interior Australia up through early Pleistocene in which flamingos could wade, forage, and presumably nest. Probably in order to sustain colonies, permanence of such lakes was important, if not a particular lake or shore line, a series of lakes in the desert center or its bordering semi-arid regions among which these presumably social, colonial nesters could move and always find favorable conditions. There appear to be shallow

lakes today, such as Goyder's Lagoon and the lake at Menindee, that might support flamingo colonies, but these may dry out too much in some years and alternate sites may be too few to sustain a colony of these large birds. Thus with the increasing aridity in the late Pleistocene the lake habitat may have become reduced in amount and dependability to a point below the requirement levels of these large, colonial water birds and extinction ensued.

The fossil deposits from which the flamingos are derived are claystones and mudstones along the borders of old lakes. In the early Pleistocene the matrix was a stream channel sand but this may have well been in a flat stream-mouth area bordering a lake and it was certainly not far from the former shoreline of Lake Eyre. At the time the Ngapakaldi Fauna flourished in this region, the shoreline of a much larger Lake Eyre was near the several fossil-bearing localities and some 30 miles east of the shore of the present and usually dry Lake Eyre.

The evolution of flamingos to their present stage of specialization had largely taken place by Oligocene time; the record in Europe shows some subsequent increase in bill flexure and specialization but no significant change in the feet and legs. The Australian Tertiary fossils reaffirm this attainment in the Tertiary of the modern foot structure. In the retention of a fairly large hind toe in the genus *Phoenicopterus* at that time we may have persistence of an earlier ancestral condition; subsequent reduction of this toe, which is of little structural significance, has taken place. Complete loss of it has been accomplished only in the modern *Phoenicoparrus*.

*Phoeniconotius eyrensis* was a more massively built phoenicopterid than other members of the family, paralleling in this respect the Paloelodidae, but not in any way connecting with that group. *Phoeniconotius* was possibly less of a deep-water or deep-mud wader than the other phoenicopterids, with concomitant reduction of swimming ability. As such it could represent a separate phyletic branch in that group.

#### SUMMARY

Fossil flamingos have been found in the Lake Eyre basin of central Australia in middle Tertiary, early Pleistocene, and late Pleistocene time. The Tertiary representatives consist of two species, here described as new, one of which belongs to a new genus, *Phoeniconotius*. In the Pleistocene the modern *Phoenicopterus ruber* occurred in both early and late faunas and a very small, slender-footed species of the modern genus *Phoeniconaias* is described as new from the earlier fauna.

The Tertiary species showed a level of evolution of the flamingo foot equivalent to that of the modern bird but with the persistence of a larger hind toe than in the living representatives. The genus *Phoeniconotius* of the Tertiary was a more massive, somewhat less aquatically adapted member of the Phoenicopteridae probably representing a separate phyletic branch in that family.

The extinction of flamingos in Australia at the end of the Pleistocene could have been caused by increasing aridity which reduced the number and stability of large, shallow lakes.

#### LITERATURE CITED

- Brodkorb, P.  
1953. A Pliocene flamingo from Florida. Nat. Hist. Misc., Chicago Acad. Sci., no. 124:1-4.
- De Vis, C. W.  
1906. A contribution to the knowledge of the extinct avifauna of Australia. Ann. Queensland Mus. no. 6:1-25, pls. 1-9.

## Howard, H.

1946. A review of the Pleistocene birds of Fossil Lake, Oregon. Carnegie Inst. Washington, publ. 551:141-195.  
1955. Fossil birds from Manix Lake, California. Geol. Surv. Prof. Paper 264-J:199-206, pl. 50.

## Miller, A. H.

1944. An avifauna from the Lower Miocene of South Dakota. Univ. Calif. Publ. Bull. Dept. Geol. Sci., 27:85-100.

## Miller, L.

1944. A Pliocene flamingo from Mexico. Wilson Bull., 56:77-82.

## Milne-Edwards, A.

- 1867-1871. Recherches anatomiques et paléontologiques pour servir a l'histoire des oiseaux fossiles de la France (G. Masson, Paris), vol. 2; atlas, vol. 1.

## Shufeldt, R. W.

1892. A study of the fossil avifauna of the *Equus* beds of the Oregon desert. Jour. Acad. Nat. Sci., Phila., 9:389-425.

## Stirton, R. A., Tedford, R. H., and Miller, A. H.

1961. Cenozoic stratigraphy and vertebrate paleontology of the Tirari Desert, South Australia. Rec. South Australian Mus., 14:19-61.

*Museum of Paleontology, University of California, Berkeley, California. December 24, 1962.*