A New Species of Extinct Parrot (Psittacidae: *Eclectus*) from Tonga and Vanuatu, South Pacific[1]

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Abstract: A new extinct species of parrot, *Eclectus infectus* Steadman, is described from 21 bones from archaeological (late Holocene) and paleontological (late Pleistocene) sites on three islands in the Kingdom of Tonga, with limited referred material (ulna, tibiotarsus) from a late Holocene archaeological site on Malakula, Vanuatu. Probably, therefore, the range of *E. infectus* also included at least the intervening island group of Fiji. The extinction of *E. infectus* occurred since the arrival of people in this region ca. 3,000 yr ago and presumably was due to human impact. A single, very fragmentary parrot tibiotarsus from Rota (Mariana Islands) may pertain to an indeterminate species of *Eclectus*. The only extant species of *Eclectus* is *E. roratus*, which occurs from the Solomon Islands westward to the Moluccas. *Eclectus infectus* provides the first evidence of the genus east of the Solomon Islands, although its biogeographic implications are not unique. Within Oceania (outside New Zealand and the Hawaiian Islands), human activities have eliminated the easternmost species in at least 17 other genera of land birds.

Parrots (order Psittaciformes, family Psittacidae sensu lato) have a substantial late Quaternary fossil record on tropical islands that includes many extinct species and populations. In the West Indies, for example, such losses have involved all three indigenous genera (*Ara*, *Aratinga*, and *Amazona* [Williams and Steadman 2001]). Fossils also have documented considerable late Quaternary losses of parrots on Pacific islands, especially in three genera, *Vini*, *Cacatua*, and *Eclectus* (Steadman in press). Here I describe a new species of *Eclectus* and discuss its biogeographic implications.

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materials and methods

The prehistoric parrot bones from sites in the Kindom of Tonga were obtained from vertically controlled excavations by sieving sediment through screens of 3.2- or 1.6-mm mesh. The stratigraphic, chronologic, and cultural details of the Tongan sites are explained in Steadman (1993), Burley (1999), Dickinson et al. (1999), and Steadman et al. (2002*a*,*b*). The Malua Bay archaeological site on Malakula, Vanuatu, is described in Bedford et al. (1998). Steadman (1992, 1999) described the bone deposit at Payapai Cave on Rota, Mariana Islands.

The prehistoric specimens of *Eclectus* are cataloged in the Division of Ornithology, Florida Museum of Natural History, University of Florida (uf). Multiple five-digit catalog numbers for a single specimen, such as uf 52069/52076 for the holotypical femur, are for bone fragments originally cataloged separately but found to fit together with further research. Modern comparative skeletons are from the American Museum of Natural History (amnh), uf, the National Museum of Natural History, Smithsonian Institution

(USNM), and the University of Washington Burke Museum (UWBM). Osteological nomenclature generally follows Baumel et al. (1993).

The following modern skeletons were examined: *Cacatua ducorpsi* UF 39463, 39446, 39513; *C. galerita galerita* UF 25728; *C. ophthalmica* AMNH 332597; *C.* (*Eolophus*) *roseicapilla* UF 25735; *Callocephalon fimbriatum* UF 25737; *Calyptorhynchus funereus* UF 25729; *Probosciger aterrimus* UF 25679; *Vini australis* UF 25591; *V. kuhlii* USNM 498417; *V. solitarius* USNM 277040, 277322; *Charmosyna papou* UF 39659, UWBM 43041; *C. pulchella* UF 40403; *Trichoglossus haematodus* UF 39561; *Lorius chlorocercus* UF 39487; *Chalcopsitta cardinalis* UF 39410, 39464; *Eos bornea* UF 18437; *Pseudeos fuscata* UF 25577; *Eclectus r. roratus* (female, male) USNM 557136, 557137; *Eclectus r. solomonensis* (2 males) UF 39525, 40175; *Eclectus roratus* [captive] (3 females, 5 males, 2?) UF 25936–25941, USNM 346723, 430501, 490124, 557942; *Geoffroyus geoffroyi* USNM 560810; *Prosopeia tabuensis* UF 26179, 26180, 40741, 40743; *Cyanoramphus auriceps* UF 25961; *C. n. novaehollaniae* UF 25958; *Eunymphicus cornutus* UF 42707; and *Micropsitta finschii* UF 39450, 39459.

COMPARATIVE OSTEOLOGY AND SYSTEMATICS

I compared the fossils from Tonga and Vanuatu with modern skeletal specimens representing most genera of cockatoos, lories, and parrots from Australia, New Guinea, and Indonesia and all genera from Oceania (see Materials and Methods), including especially the four genera that still occur in Polynesia (*Vini*, *Charmosyna*, *Prosopeia*, and *Cyanoramphus*). The fossil specimens are referred to *Eclectus* because of the following unique combination of characters.

Quadrate: base of processus orbitus concave; dorsal surface of condylus caudalis bulbous and medially oriented; concavity of lateral surface of condylus caudalis extends posteriad to processus zygomaticus.

Mandible: symphysis relatively flat, shallow, and wide, with rugose (not smooth) ventral surface texture; smooth medial outline of symphysis and ramus in ventral aspect.

Sternum: distal tip of spina externa blunt and not strongly bifurcated; lateral surfaces of spina externa partitioned by a muscle scar; in lateral aspect, overall anterior margin of spina externa convex rather than concave; dorsal surface of spina externa with proximomedial foramen; sulcus medianus sterni very pneumatic.

Coracoid: medial half of facies articularis sternalis gradually widens in a gentle arc.

Humerus: crista deltopectoralis originates nearly even with crista bicipitalis; fossa musculo brachialis shallow; attachment of anterior articular ligament elongate; tuberculum supracondylare ventrale large; sulcus humerotricipitalis deep.

Ulna: minimal curvature of proximal half of shaft in medial or lateral aspect; cross section of midshaft more angular (less circular); olecranon relatively large and distinctly offset by a deep sulcus tendineus; papillae remigiales caudales relatively indistinct; in ventral aspect, caudal margin of impressio brachialis relatively gently curved.

Radius: minimal curvature of proximal one-quarter of shaft; margo interosseus very distinct; sulcus tendineus consistently concave; sulcus ligamentum not deeply excavated.

Carpometacarpus: proximal intermetacarpal symphysis wide; fovea carpalis caudalis shallow.

Femur: in proximal aspect, facies articularis antitrochanterica relatively deep, resulting in little constriction at attachment of facies articularis acetabularis; linea intermuscularis cranialis avoids lateral margin of shaft but originates on medial margin of crista trochanteris; condylus medialis reaches its most proximal point near bone's midline rather than near epicondylus medialis; axis of condylus medialis oriented diagonally rather than parallel to axis of shaft; tuberculum musculo gastrocnemialis lateralis located relatively distal.

Tibiotarsus: extending from the distal extent of crista cnemialis cranialis, the anterior surface of the shaft is rather steeply raised diagonally, rather than gently rounded, to at least the midpoint of crista fibularis; in lateral aspect, crista fibularis thickens toward the distal end; in cranial aspect, shaft only slightly constricted above crista fibularis.

Tarsometatarsus: shaft stout; sulcus extensorius long; fossa metatarsi I located at base of trochlea metatarsi II (rather than more proximal); trochlea metatarsi II medially expanded.

Eclectus infectus Steadman, n. sp.
Figures 1–3

HOLOTYPE: UF 52069/52076, complete femur, Unit S6W2, Layer II, Level 15, 'Anatu, 'Eua, Tonga. Collected by D. W. Steadman, T. W. Stafford Jr., and J. G. Stull on 25 November 1989 (Figure 1).

PARATYPES: 'Anatu, 'Eua, Tonga: UF 50652/50653 sternum, UF 52117 radius (Layer I); UF 52003/52075 ulna, UF 52060/52062/52073 radius, UF 50608 tibiotarsus (Layer II); UF 52784 sternum, UF 52057, 52549, 52900 three radii (Layer III). Tongoleleka Site, Lifuka, Tonga (various strata): UF 58284 quadrate, UF 57920 mandible, UF 58294 coracoid, UF 58063, 58300 two humeri, UF 58548/58549 carpometacarpus, UF 58512 tarsometatarsus, UF 58518, 58519 pedal phalanges. Vaipuna Site, 'Uiha, Tonga: UF 58850 pedal phalanx (Unit 7, Level 9). Malua Bay archaeological site, Malakula, Vanuatu: UF 61449 ulna, UF 61450 tibiotarsus.

DIAGNOSIS: A species of *Eclectus* that differs from the only known congeneric species,

FIGURE 1. *Eclectus*. *a*, *b*, Femur in ventral (*above*) and dorsal (*below*) aspects. *c*, *d*, Tibiotarsus in dorsal (*above*) and ventral (*below*) aspects. *e*, *f*, Tarsometatarsus in plantar (*above*) and acrotarsial (*below*) aspects. *a*, *c*, *e*, *E. roratus roratus*, USNM 557136. *b*, *d*, *f*, *E. infectus*, n. sp., UF 52069/52076, 50608, 58512. Scale bars = 30 mm.

TABLE 1

Measurements (in mm) of Skeletal Elements in *Eclectus*, with Range and Sample Size (if >1)

Skeletal Element Parameter	*E. infectus*, n. sp., Tonga: 'Eua, Lifuka	*E.* cf. *infectus*, n. sp., Vanuatu: Malakula	*E. roratus solomonensis*, Solomons: Isabel	*E. roratus roratus*, Moluccas: Ternate, Tobelo	*E. roratus* subsp.? Captive
Quadrate					
Total height	15.9	—	14.0–14.2 2	15.6	13.7–14.2 2
Minimum width of processus oticus	2.3	—	1.9–2.2 2	1.8	1.8–1.9 2
Minimum depth of processus oticus	2.2	—	1.8–1.9 2	1.7	1.5–1.8 2
Combined width of capitulum oticum and capitulum squamosum	5.1	—	3.9–4.2 2	4.5	4.1 2
Mandible					
Depth at symphysis	2.9	—	2.5–2.8 2	2.8	2.7 2
Shortest oblique length of dentary	13.1	—	10.2–10.3 2	11.2	11.1–11.4 2
Sternum					
Width of pila carinae	3.2	—	3.0–3.1 2	2.9–3.2 2	2.9–3.4 8
Length of spina externae	7.6+	—	6.9–7.5 2	7.4–8.5 2	7.0–8.0 8
Humerus					
Midshaft width	5.1–5.2 2	—	5.7–5.8 2	6.1	5.8–5.9 2
Midshaft depth	4.4–4.5 2	—	4.8–4.9 2	5.2	4.5–5.1 3
Distal width	11.8	—	11.9–12.0 2	12.7	11.3–12.8 3
Ulna					
Proximal depth	7.7	—	6.6–6.9 2	6.7–7.7 2	6.8–7.7 6
Proximal width	9.1	—	8.3 2	9.0–10.5 2	9.0–9.5 6
Least width of shaft	3.9	4.0	3.3–3.4 2	4.0–4.4 2	3.6–4.4 6
Least depth of shaft	4.8	4.7	3.9–4.1 2	4.4–5.0 2	4.0–4.7 6
Radius					
Total length	73.4	—	66.5–68.4 2	68.5–75.4 2	67.8–74.4 6
Proximal width	4.0–4.2 3	—	3.2 2	3.8–3.9 2	3.1–3.8 6
Proximal depth	4.6–5.2 3	—	3.9–4.0 2	4.6–5.2 2	4.3–4.9 6
Least width of shaft	2.4	—	1.9–2.0 2	2.2–2.4 2	1.9–2.6 6
Least depth of shaft	2.2	—	1.6–1.8 2	2.0–2.3 2	1.7–2.1 6
Distal width	6.8	—	6.0–6.4 2	6.6–7.2 2	6.0–6.7 6

TABLE 1 (continued)

Skeletal Element Parameter	*E. infectus*, n. sp., Tonga: 'Eua, Lifuka	*E.* cf. *infectus*, n. sp., Vanuatu: Malakula	*E. roratus solomonensis*, Solomons: Isabel	*E. roratus roratus*, Moluccas: Ternate, Tobelo	*E. roratus* subsp.? Captive
Femur					
Total length	51.3	—	43.8–45.5 2	46.3–49.8 2	44.2–49.2 5
Midshaft width	4.7	—	3.2–3.4 2	3.6–3.9 2	3.4–4.4 5
Midshaft depth	5.4	—	3.4–3.6 2	4.1–4.2 2	3.8–4.4 5
Depth of head	5.4	—	4.4–4.5 2	4.5–5.2 2	4.5–5.3 5
Depth of medialis condylus	7.6	—	5.6–5.7 2	6.6–6.8 2	6.0–6.5 5
Tibiotarsus					
Width at midpoint of crista fibularis	5.9	5.7	4.0–4.1 2	4.4–4.8 2	4.3–5.0 5
Depth at midpoint of crista fibularis	3.6	4.1	3.1–3.2 2	3.5–3.6 2	3.2–3.5 5
Tarsometatarsus					
Least width of shaft	3.9	—	3.9–4.1 2	4.0	3.8

E. roratus, in its generally larger, more robust cranial and leg elements (Table 1) and in the following characters: quadrate (Figure 2) with capitulum oticus and capitulum squamosus fused; mandible (Figure 2) with ventral surfaces of symphysis less rounded in both posterior and lateral aspects; humerus (Figure 3) with deeper ventral portion of fossa musculo brachialis; ulna (Figure 3) with less protrudent tuberculum ligamentum collateralis ventralis and processus cotylaris dorsalis; radius (Figure 3) with sulcus tendinosus extending to make a concave outline of facies articularis radiocarpalis, and cotyla humeralis more circular (less ovoid) in proximal aspect; femur (Figure 1) with stouter shaft, and with condylus medialis on same plane as shaft in medial aspect; tibiotarsus (Figure 1) with more prominent intermuscular line on medial margin of shaft, opposite crista fibularis; tarsometatarsus (Figure 1) with more prominent fossa metatarsi I.

ETYMOLOGY: From the Latin *infectus* meaning "dyed, stained, tainted" (Brown 1956:438) in reference to the presumedly brightly colored plumage of this extinct parrot. The living *Eclectus roratus* is very brightly colored and unique among all birds in having the male plumage mainly green and the female plumage mainly red.

REMARKS: *Eclectus infectus* had proportionately slightly smaller wings than in *E. roratus*. This conforms to a general (though poorly documented) trend that volant land birds from remote Pacific islands have proportionately smaller wings than congeneric relatives from New Guinea, the Bismarcks, or the Solomons (J. Sailer, D.W.S., pers. obs.). I note that one tarsometatarsus of *E. infectus* from Lifuka (UF 58512 [Figure 3]) is nearly identical in size to that of modern *E. roratus*, unlike other leg elements that are larger in the extinct species.

The evidence that *Eclectus infectus* inhabited Vanuatu is limited to two specimens from Malakula that are similar in size to the Tongan specimens. The ulna (UF 61449) is a 3.5-cm-long portion of the shaft that agrees with *Eclectus* in having a cross section of the midshaft that is more angular (less circular)

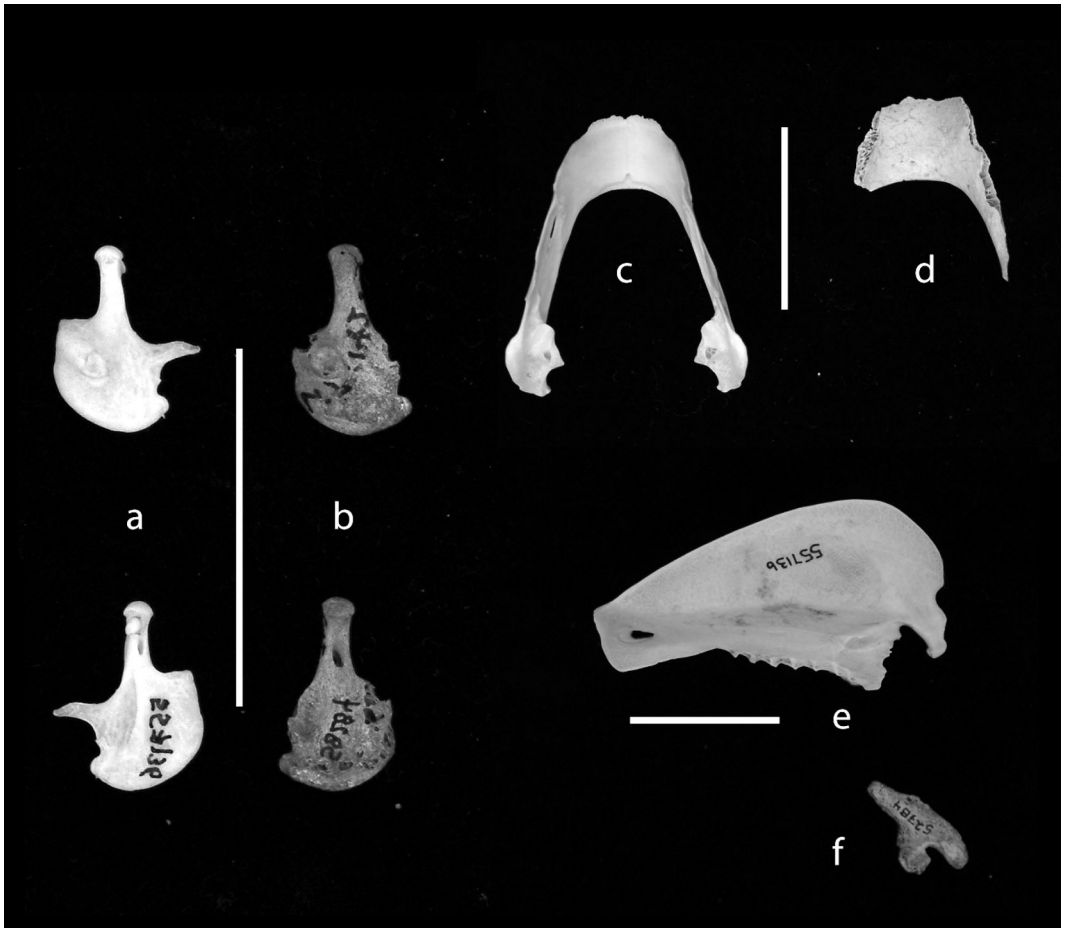

FIGURE 2. *Eclectus*. *a*, *b*, Quadrate in lateral (*above*) and medial (*below*) aspects. *c*, *d*, Mandible in dorsal aspect. *e*, *f*, Sternum in lateral aspect. *a*, *c*, *e*, *E. roratus roratus*, USNM 557136. *b*, *d*, *f*, *E. infectus*, n. sp., UF 58284, 57920. Scale bars = 30 mm.

than in other Oceanic genera. The tibiotarsus (UF 61450) is a 2.5-cm-long section of shaft (including crista fibularis) that agrees with *Eclectus* in having the anterior surface of the shaft steeply raised diagonally (rather than gently rounded) to the midpoint of crista fibularis. Pending discovery of more material, my referral of the Vanuatu specimens to *E. infectus* is tentative.

A single tibiotarsal fragment (USNM 436602) from Payapai Cave, Rota, Mariana Islands, is very tentatively referred to *Eclectus* species indeterminate. This specimen, from a bone deposit ca. 1,000 yr old (Steadman 1992, 1999, in press), is too fragmentary for positive identification to genus but does indicate the former presence of a large parrot in the Marianas, an island group devoid of parrots in modern times.

DISCUSSION

I regard all living parrots as best classified in a single family (Psittacidae) defined by a number of unique morphological and other traits (Smith 1975), but many recent authors recognize the cockatoos (Cacatuinae) and lories (Loriinae) as separate families (Cacatuidae,

FIGURE 3. *Eclectus*. *a*, *b*, Humerus in caudal (*above*) and cranial (*below*) aspects. *c*, *d*, Ulna in ventral (*above*) and radial (*below*) aspects. *e*, *f*, Radius in dorsal (*above*) and ulnar (*below*) aspects. *g*, *h*, Carpometacarpus in ventral (*above*) and dorsal (*below*) aspects. *a*, *c*, *e*, *h*, *E. roratus roratus*, USNM 557136. *b*, *d*, *f*, *g*, *E. infectus*, n. sp., UF 58063, 52003/52075, 52060/52062/52073. Scale bars = 30 mm.

Loriidae) from psittacine parrots (Sibley and Ahlquist 1990, Christidis et al. 1991, Boles 1993, Brown and Toft 1999). Whether these three groups are classified at the familial or subfamilial level, the order Psittaciformes as a whole is widely recognized as monophyletic. Among living genera of parrots, *Eclectus* may be most closely related to *Geoffroyus* as part of a poorly defined, possibly polyphyletic assemblage of psittacine parrots (Christidis et al. 1991) that may also include *Psittacula*, *Psittinus*, and *Tanygnathus* (Mayr and Göhlich 2004).

Although the Australian-Papuan-Oceanic region is the modern center of taxonomic diversity for parrots, the only Tertiary psittacid fossils there are of *Cacatua* sp. from the early to middle Miocene Riversleigh site, northwestern Queensland (Boles 1993). Late Quaternary parrot fossils, on the other hand, are phylogenetically and biogeographically important in providing evidence of many anthropogenically exterminated species and populations, especially in the genus *Vini* (Steadman and Zarriello 1987, Steadman in press). Of the 13 genera of parrots in tropical Oceania, seven are confined today to the Bismarcks and the Solomons. Two of these genera, *Cacatua* and *Eclectus*, occurred farther east in Oceania prehistorically (New Caledonia for *Cacatua*, Vanuatu and Tonga for *Eclectus* [Steadman in press, herein]).

Within Tonga, bones of *Eclectus infectus* have been found on three islands thus far. Es-

pecially considering that two of these, Lifuka and ʻEua, have the most extensive fossil records of any Tongan island, it seems likely that *E. infectus* was widespread if not found throughout Tonga at first human contact. *Eclectus roratus* occurs from the Moluccas eastward through New Guinea, northernmost Australia, and the Bismarcks to the Solomon Islands (Mayr and Diamond 2001). As the late Quaternary fossil record of Oceania improves, I believe that a form of *Eclectus* will be discovered as well in the Santa Cruz Group, Rennell and Bellona, New Caledonia, and Fiji.

Two species of parrots are found in Tonga today. The first, *Vini australis* (Blue-crowned Lorikeet), is widespread in the Haʻapai Group but has been extirpated in historic times on most other Tongan islands (Steadman 1998, Steadman and Freifeld 1998). The second, *Prosopeia tabuensis* (Red Shining Parrot), is not native to Tonga, but was introduced from Fiji in late prehistoric times (Rinke 1989). Bones from prehistoric sites (both cultural and precultural) in Haʻapai and on ʻEua represent *Vini australis*, *V.* (*Phigys*) *solitarius* (Collared Lorikeet [confined today to Fiji]), and *Eclectus infectus*, raising the Tongan native parrot fauna from one to three species.

In Vanuatu today, *Trichoglossus haematodus* (Rainbow Lorikeet) is widespread and *Charmosyna palmarum* (Green Palm Lorikeet) occurs more locally (Bregulla 1992:189–192). Bones of both species have been found in archaeological contexts (Steadman in press). As in Tonga, *Eclectus infectus* increases the native parrot fauna of Vanuatu to three species.

Finally, *Eclectus infectus* provides another instance of prehistoric bones from a species of land bird, usually extinct, being discovered farther east in Oceania than the current range of any living congeneric species. Other examples are found in night-herons (*Nycticorax*), ospreys (*Pandion*), hawks (*Accipiter*), megapodes (*Megapodius*), rails (*Gallirallus*, *Porzana*, *Porphyrio*), columbids (*Ducula*, *Macropygia*, *Caloenas*, *Gallicolumba*), cockatoos (*Cacatua*), cuckoos (*Cacomantis*), owls (*Ninox*), hornbills (*Aceros*), swallows (*Hirundo*), and starlings (*Aplonis*) (Steadman 1988, 1993, 1995, 1997, in press, Balouet and Olson 1989). A similar situation has been found in certain skinks and geckos (Pregill 1993) and bats (Koopman and Steadman 1995), once again revealing how deceptive modern distributions of Oceanic vertebrates can be.

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