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An Extinct New Rail (*Gallirallus*, Aves: Rallidae) Species from Rapa Island, French Polynesia †

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Abstract: A new species of rail, *Gallirallus astolfoi* sp. nov., is described from Rapa Island (Rapa Iti), French Polynesia. The holotype (and single known specimen) is a left tarsometatarsus recovered from Tangarutu Cave. This rail species was apparently endemic to Rapa Iti and potentially flightless. It became extinct after human colonisation of the island.

Keywords: endemic species; flightlessness; *Gallirallus astolfoi* sp. nov.; Holocene; Rapa Iti

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1. Introduction

Rapa Island, also known as Rapa Iti, is a subtropical island in the South Pacific and the southernmost inhabitable island of French Polynesia. It has an area of circa 38 km^2 and its origin as a volcanic caldera resulted in a jagged topography that rises abruptly from the sea, with its highest point being Mont Perau at 650 m above sea level [1]. The first Polynesian settlers most likely arrived on Rapa Iti between 1100 and 1200 CE and the first Europeans in 1791 CE [2–4].

The island fauna was dominated by birds, with no native mammals or terrestrial reptiles [5]. Among other species, Rapa Iti is home to the critically endangered Rapa fruit-dove *Ptilonopus huttoni* Finsch, 1874, while the Rapa shearwater *Puffinus myrtae* Bourne, 1959, once present on the island, is now confined to offshore islets.

A number of bird bones from archaeological sites are also known from Rapa Iti, which were studied by Tennyson & Anderson [5]. Among the species those authors identified was a "*Gallirallus*-type rail", which they hypothesized could be an endemic form and commented that further analysis was necessary to determine its identity. The occurrence of island-endemic species, particularly when reduced flight capability (or flight loss) is in play, is a common occurrence in many genera of Rallidae worldwide [6–12]. This is a particularly widespread phenomenon on the islands of the Caribbean and the South Pacific, including several species known only from Quaternary fossil material [8,13–16].

In the present paper, we analyse the rail material of Tennyson & Anderson [5] from Rapa Iti, comparing it to other known living and extinct *Gallirallus* spp. and describing it as a new species.

2. Material & Methods

The material of the "*Gallirallus*-type rail" available from the study of Tennyson & Anderson [5] is a single left tarsometatarsus, housed in the Museum of New Zealand Te Papa Tongarewa (NMNZ, Wellington, New Zealand). It is part of a large series of animal remains (mostly fish) recovered from archaeological sites along the coast of Rapa Iti. The rail bone is very well preserved and was found in Tangarutu Cave (in Section S1, described in [17]). For more details on the site and depositional environment, see [17].

The new tarsometatarsus was compared to specimens of living and extinct rails described in the literature, with a focus in the South Pacific taxa of *Gallirallus* Lafresnaye, 1841, as well as specimens in the collection of the NMNZ (refer to Appendix A for a full list). A digital calliper (0.01 mm precision, rounded to the nearest 0.1 mm) was used to take the following measurements of the specimen of interest and comparative material (Table 1): total length, distal width, proximal width, mid-shaft width, and mid-shaft depth. Measurements of further species for comparison were taken from the literature (Table 1). The osteological nomenclature used here follows [18–20].

The species classification in *Gallirallus* used here follows [21]. A recent phylogenetic study [22] has split *Gallirallus* Lafresnaye, 1841 into four genera. For those authors, *Gallirallus* contains only two species: the weka *G. australis* and the New Caledonian rail *G. lafresnayanus*. They classified the invisible rail *G. wallacii* into the monospecific genus *Habroptila* G.R. Gray, 1861, and erected a further monospecific genus, *Aptenorallus* Kirchman, McInerney, Giarla, Olson, Slikas & Fleischer, 2021 (formally described in [23], a corrigendum to that publication), solely for the Calayan rail *G. calayanensis*. All remaining species were allocated to the genus *Hypotaenidia* Reichenbach, 1853 by those authors. While the taxonomy of this group remains in flux, we retain all species in *Gallirallus* (Table 1).

Table 1. *Gallirallus* spp., with their known distribution, status (extinct or living), flight capability, and tarsometatarsus measurements (given in mm). Sex: females (F) and males (M), when known; Fossil material (†). Number of measured specimens indicated inside parentheses. References for the measurements are given in the respective column (see Appendix A for a list of specimens measured for the present study).

***Gallirallus* spp.**	**Geographic Distribution**	**Flight**	**Status**	**Total Length**	**Distal Width**	**Proximal Width**	**Mid-Shaft Width**	**Mid-Shaft Depth**	**Reference**
G. astolfoi sp. nov.	Fench Polynesia (Rapa Iti)	flightless	extinct	†: 34.6 (1)	†: 5.8 (1)	†: 5.8 (1)	†: 2.7 (1)	†: 2.1 (1)	this paper
G. australis (Sparrman, 1786)	New Zealand	flightless	living	†: 60.8–70.7 (7)	†: 11.1–12.8 (7)	†: 9.7–11.9 (7)	†: 4.7–6.0 (7)	†: 4.1–5.0 (7)	this paper
G. calayanensis Allen et al., 2004	Philippines (Calayan Is.)	flightless	living	—	—	—	—	—	—
G. dieffenbachii (G.R. Gray, 1843)	New Zealand (Chatham Is.)	flightless	extinct	†: 42.0–48.0 (10)	†: 7.8–8.8 (10)	†: 7.3–8.3 (10)	†: 3.4–4.3 (10)	†: 3.2–4.0 (10)	this paper
G. epulare Kirchman & Steadman, 2007	French Polynesia (Nuku Hiva)	flightless	extinct	—	†: 6.5 (1)	—	†: 3.5 (1)	†: 2.4 (1)	[24]
G. ernstmayri Kirchman & Steadman, 2006	Papua New Guinea (New Ireland)	flightless	extinct	—	—	—	—	—	[8]
G. gracilitibia Kirchman & Steadman, 2007	French Polynesia (Ua Huka)	flightless	extinct	—	—	—	—	—	[8]
G. huiatua Steadman et al., 2000	Niue	flightless	extinct	†: 39.2 (1)	†: 6.5 (1)	†: 5.4 (1)	†: 2.7 (1)	†: 2.5 (1)	this paper
G. insignis (P.L. Sclater, 1880)	Papua New Guinea (New Britain)	flightless	living	—	—	—	—	—	—
G. lafresnayanus Verreaux & Des Murs, 1860	New Caledonia	flightless	extinct	—	—	—	—	—	—
G. modestus (Hutton, 1872)	New Zealand (Chatham Is.)	flightless	extinct	†: 26.4–32.1 (4)	†: 4.8–5.4 (4)	†: 4.4–5.0 (4)	†: 2.1–2.4 (4)	†: 1.7–2.1 (4)	this paper
G. okinawae (Yamashina & Mano, 1981)	Japan (Okinawa)	flightless	living	—	—	—	—	—	—
G. owstoni (Rothschild, 1895)	Guam, Mariana Islands	flightless	living	F: 49.6 (1) M: 49.6–53.7 (2)	—	F: 7.1 (1) M: 7.1–8.2 (2)	—	—	[13]
G. pacificus (Gmelin, 1789)	French Polynesia (Tahiti)	flightless?	extinct	—	—	—	—	—	[12]

Table 1. *Cont.*

Gallirallus spp.	Geographic Distribution	Flight	Status	Total Length	Distal Width	Proximal Width	Mid-Shaft Width	Mid-Shaft Depth	Reference
G. pendiculentus Kirchman & Steadman, 2006	Northern Mariana Is. (Tinian)	flightless	extinct	†: 38.4–46.5 (7)	†: 6.1–6.8 (14)	†: 5.6–7.3 (17)	†: 2.7–3.7 (17)	—	[8]
G. philippensis (Linnaeus, 1766)	Oceania	volant	living	F: 40.8–45.2 (6) M: 45.3–49.0 (6) †: 36.7–43.9 (4)	F: 6.0–6.9 (6) M: 6.7–7.5 (6) †: 6.2–7.5 (4)	F: 5.8–6.6 (6) M: 6.7–7.2 (6) †: 5.6–7.1 (4)	F: 2.8–3.3 (6) M: 3.1–3.6 (6) †: 3.1–3.9 (4)	†: 2.5–3.3 (4)	F/M: [8] †: this paper
G. pisonii Kirchman & Steadman, 2006	Northern Mariana Is. (Aguiguan)	flightless	extinct	—	†: 6.1 (1)	†: 5.6–5.7 (2)	†: 3.0–3.1 (2)	—	[8]
G. poecilopterus (Hartlaub, 1866)	Fiji	flightless	extinct	†: 66.6–70.0 (2)	†: 10.0 (1)	†: 9.5 (1)	†: 4.0 (1)	—	[25]
G. ripleyi Steadman, 1986	Cook Is. (Mangaia)	flightless	extinct	†: 33.1 (1)	†: 6.3–6.5 (3)	†: 5.7–5.9 (2)	†: 2.8–3.1 (2)	—	[8,13]
G. roletti Kirchman & Steadman, 2007	French Polynesia (Tahuata)	flightless	extinct	—	†: 8.7 (1)	†: 7.9 (1)	†: 3.5–3.9 (2)	†: 2.5–2.8 (2)	[24]
G. rovianae Diamond, 1991	Solomon Is.	flightless	living	—	—	—	—	—	—
G. sp. *sensu* Steadman & Bollt, 2010	Fench Polynesia (Rurutu)	flightless	extinct	—	—	—	—	—	[26]
G. steadmani Worthy & Bollt, 2011	Fench Polynesia (Tubuai)	flightless	extinct	†: 40.0 (1)	†: 6.2 (1)	†: 5.9–6.4 (3)	†: 2.9–3.1 (3)	—	[27]
G. storrsolsoni Kirchman & Steadman, 2006	Fench Polynesia (Huahine)	flightless	extinct	—	—	†: 7.4 (1)	†: 4.1 (1)	†: 2.8 (1)	[28]
G. sylvestris (P.L. Sclater, 1870)	Australia (Lord Howe Is.)	flightless	living	M: 49.6 (1)	M: 8.9 (1)	M: 8.7 (1)	M: 4.4 (1)	M: 3.4 (1)	this paper
G. temptatus Kirchman & Steadman, 2006	Northern Mariana Is. (Rota)	flightless	extinct	†: 47.4 (1)	†: 7.4 (1)	†: 6.4–6.8 (2)	†: 3.3–3.5 (2)	—	[8]
G. torquatus (Linnaeus, 1766)	Indonesia, Papua New Guinea, Philippines	volant	living	M: 54.2 (1)	—	M: 7.4 (1)	—	—	[13]

Table 1. *Cont.*

Gallirallus spp.	Geographic Distribution	Flight	Status	Total Length	Distal Width	Proximal Width	Mid-Shaft Width	Mid-Shaft Depth	Reference
G. vavauensis (Worthy & Burley, 2020)	Tonga (Vava'u)	flightless	extinct	†: 70.9–73.0 (2)	†: 12.2–13.1 (2)	†: 12.9–13.2 (3)	†: 5.9–6.7 (6)	†: 5.4–6.0 (6)	[25]
G. vekamatolu Kirchman & Steadman, 2005	Tonga ('Eua)	flightless	extinct	†: 45.1 (1)	—	†: 7.7–8.6 (2)	—	—	[13]
G. wakensis (Rothschild, 1903)	USA (Wake Is.)	flightless	extinct	F: 33.3 (1) M: 35.6 (1)	F: 5.9 (1) M: 6.2 (1)	F: 5.5 (1) M: 6.0 (1)	F: 2.5 (1) M: 2.9 (1)	—	[8]
G. wallacii (G.R. Gray, 1861)	Indonesia (Halmahera)	flightless	living	—	—	—	—	—	—
G. woodfordi (Ogilvie-Grant, 1889)	Solomon Is.	flightless	living	F: 67.7–72.0 (3) M: 69.8–72.3 (3)	F: 10.5–10.6 (3) M: 10.7–11.0 (3)	F: 9.9–10.1 (3) M: 10.2–10.7 (3)	F: 4.4–4.7 (3) M: 4.8–5.0 (3)	—	[8]

3. Systematics

The morphology of the Rapa Iti tarsometatarsus indicates that it could only belong to the Order Gruiformes and family Rallidae, given the presence of two open tendinal canals, one distal foramen, and the tendinal bridge [19]. More specifically, the Rapa Iti fossil can be allocated to the genus *Gallirallus* due to the following diagnostic features of the tarsometatarsus (as per [8]: p. 8): "corpus tarsometatarsi much wider than deep; medial sulcus hypotarsi not enclosed; fossa parahypotarsalis medialis shallow in proximal aspect; fossa metatarsi I short and shallow; crista plantaris mediana slopes gradually (not steeply) to hypotarsus; distal end of trochlea metatarsi tertii sloped toward medial trochlea; cotyla medialis is rectangular in proximal aspect with flat (not rounded) dorsal margin". According to our comparative analysis with tarsometatarsi of living and extinct species of *Gallirallus* (see below), we are confident in assigning the present fossil to a new species, apparently endemic to Rapa Iti.

Family Rallidae
Genus *Gallirallus* Lafresnaye, 1841
***Gallirallus astolfoi* sp. nov.**
(Figure 1)

rail (cf. *Gallirallus*): Tennyson & Anderson, 2012: 108.

ZooBank reg. nr.: urn:lsid:zoobank.org:act:F606759B-4C48-491E-93F0-0E8C018B3B97.
Holotype: NMNZ S.044399 (left tarsometatarsus; A. Anderson col. 21/vii/2002).
Type locality: French Polynesia, Rapa Island (Rapa Iti), Tangarutu Cave, Section S1 (30–40 cm).
Etymology: The specific epithet honours Astolfo, one of Charlemagne's fictional paladins. In the epic *Orlando Furioso*, Astolfo becomes trapped on a remote island because of the sorceress Alcina.
Diagnosis: Tarsometatarsus small (ca. 34.5 mm long), of delicate appearance, with narrow and shallow shaft, and narrow trochleae (particularly the trochlea metatarsi II).
Differential diagnosis: The tarsometatarsus of *Gallirallus astolfoi* sp. nov. (Figure 1) is considerably smaller than most other congeners (Table 1), with the exception of *G. ripleyi* from the Cook Islands and *G. wakensis* from the Wake Island, both flightless and extinct [8,24]. Its shaft, however, is proportionately much narrower and shallower, which gives the bone a more delicate appearance. The Chatham Island rail *G. modestus* (previously classified into its own genus, *Cabalus*) is much smaller and its tarsometatarsi have a more compact appearance.

The single known tarsometatarsus of *G. huiatua* from Niue is similar to that of *G. astolfoi* sp. nov. in its delicate appearance (i.e., shaft width and depth, and trochleae width), but it is more elongate. The tarsometatarsus of *G. pendiculentus* from the Northern Marianas and of *G. steadmani* from Tubuai, French Polynesia, are similar in shape to *G. astolfoi* sp. nov. but are much larger (Table 1). Furthermore, *G. steadmani* apparently has proportionately narrower trochlea (trochlea metatarsorum III and IV), though that could have been overemphasized by the sub-optimal preservation of the specimens ([27]: figure 4L).

In comparison with larger congeners, the tarsometatarsus of *G. astolfoi* sp. nov. is more delicate, with its proportionately narrower and shallower mid and distal shaft, as well as its narrower trochleae. Compared with *G. philippensis* and other species from French Polynesia, namely *G. epulare* from Nuku Hiva, *G. roletti* from Tahuata, and *G. storrsolsoni* from Huahine, the latter two, in particular, have much stouter tarsometatarsi, with a wider mid-shaft ([24]: figure 6A,B). Furthermore, the trochlea of digit 2 (trochlea metatarsi II) of *G. astolfoi* sp. nov. is less expanded than in *G. philippensis* and some island-endemic congeners such as *G. roletti* and *G. dieffenbachii*.

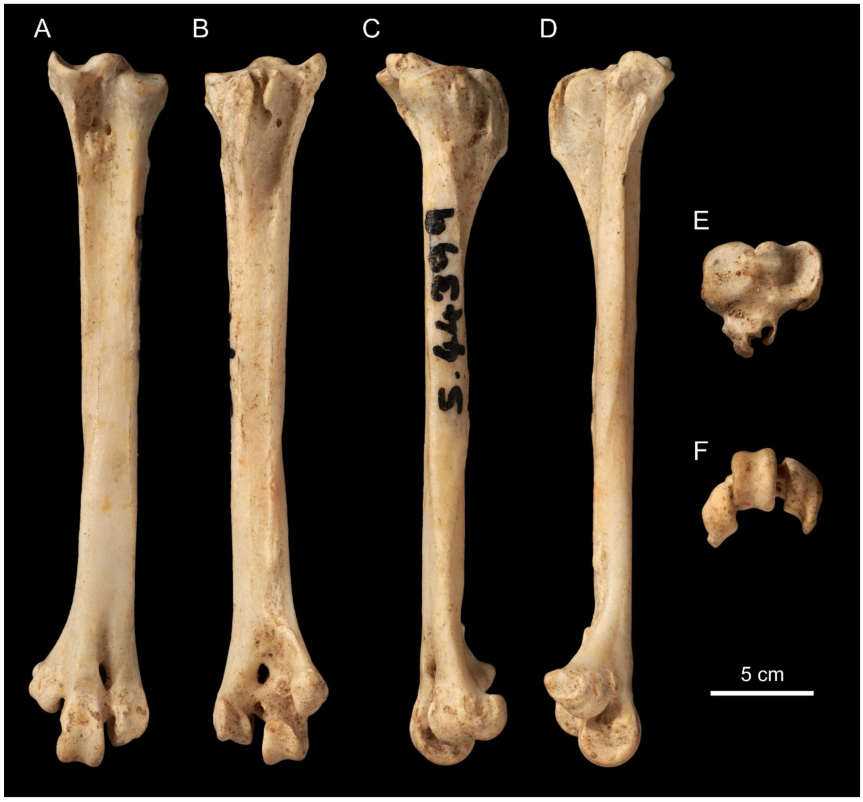

Figure 1. Left tarsometatarsus (holotype, NMNZ S.044399) of *Gallirallus astolfoi* sp. nov. in different views: (**A**) anterior, (**B**) caudal, (**C**) lateral, (**D**) medial, (**E**) proximal, (**F**) distal.

There are two further extinct endemic flightless species from French Polynesia: *G. gracilitibia* from Ua Huka and *G. pacificus* from Tahiti [12,24] (Table 1). No tarsometatarsi are known for these taxa, which precludes comparison with *G. astolfoi* sp. nov. Nevertheless, there is little chance that they could be conspecific as these islands are respectively 2100 km and 1200 km away from Rapa Iti. The only other Rallidae species on Rapa Iti is the widespread and much smaller spotless crake, *Zapornia tabuensis* (Gmelin, 1789) [5]. There is a further undescribed fossil species, *Gallirallus* sp. of [26], that is endemic to Rurutu (and extinct), though there is no published information or photographs available.

4. Discussion

Tennyson & Anderson [5] identified four extinct species on Rapa Iti, among which is *Gallirallus astolfoi* sp. nov. On the tropical Pacific islands, extinction of the avifauna is assigned to anthropogenic impact and the numbers of extinct land bird species are dominated by rails [29,30]. More specifically in French Polynesia (albeit similar to many other islands worldwide), the main causes of population crashes and extinctions are predation of adults, chicks and eggs by mammals (particularly humans, Pacific rats *Rattus exulans*, and feral cats), alongside land alteration and habitat destruction by humans and feral goats [3,31,32]. While Pacific rats were introduced by Polynesians, cats and goats (alongside cattle, pigs and dogs) were introduced by Europeans [5,32–34].

While we have little direct evidence to ascertain whether *Gallirallus astolfoi* sp. nov. was hunted for food by humans, this seems probable. While most of the animals eaten by the inhabitants of rock shelters like Tangarutu Cave, where the present rail bone was found, seem to have been fish [2], birds were potentially consumed too. Seven species of birds were reported from Section S1 of Tangarutu Cave alone (from a total of 15 bird taxa from all archaeological sites on Rapa Iti) [5]. While there was no clear evidence of the bones being deposited as part of a midden rather than by natural accumulation (i.e., no signs of butchery or charring), the cultural context of the sites is clear [5]. Occupation of Tangarutu

Cave likely dates back to between 1400 and 1600 CE [2]. Thus, the deposit happened after human settlement; furthermore, in the case of Tangarutu Cave, this age is also supported by the presence of rat bones in Section S1.

Given its smaller size in comparison to volant congeners and its presence on a remote island, we hypothesize that *Gallirallus astolfoi* sp. nov. had reduced flight capacity or, potentially, it was flightless. As mentioned above, flightlessness is a common feature in Rallidae, occurring independently in several genera and different species within the same genus. Earlier workers [11,35] hypothesized that flightlessness in rails was a neotenic condition involving little genetic modification and thus able to occur through rapid evolution. Later works offered support to the heterochrony hypothesis, arguing that a change in timing of development could lead to the observed allometric differences in rails (see [9] for a review). Likewise, molecular clock estimates have supported the hypothesis that evolution of flightless *Gallirallus* species in Oceania has been rapid after the appearance of the genus in the Late Miocene [22,36–38]. Furthermore, phylogenetic studies offered evidence that flightlessness can evolve prior to reproductive isolation [38].

Only two out of circa 30 species of *Gallirallus* are volant and widespread (Table 1); most species are flightless and endemic to single islands (or multiple islands, in cases where they were formerly connected due to the lower sea levels of the late Pleistocene [28]). Of the two volant species, *G. philippensis* is the most widespread and it is hypothesized that breakaway populations of it have colonized many islands throughout the Pacific, giving rise to the endemic forms [8]. As such, it is notable that most of these endemic species evolved the common pattern of flightlessness plus increased body size (e.g., *G. roletti* in French Polynesia; Table 1). It has been argued that loss of flight was typically related to increased body size, which could mean that such a combination has a greater selective advantage and/or is ontogenetically more parsimonious [9]. Nevertheless, *Gallirallus astolfoi* sp. nov. is one of the few species of the genus that apparently underwent a decrease in size (Table 1). Therefore, despite the relatively similar areas and environments of these islands, it seems that different selective pressures towards local optima were in play on each of them and that *Gallirallus* defies generalizations of insular gigantism/dwarfism (cf. [9]).

5. Conclusions

Gallirallus astolfoi sp. nov. from Rapa Iti is the seventh extinct species in the genus to be described from French Polynesia (Table 1), excluding the potential undescribed one mentioned above. Excluding the volant *G. philippensis*, the species geographically closest to *G. astolfoi* sp. nov. is *G. steadmani* from Tubuai, ca. 700 km NW from Rapa Iti. As new specimens continue to be discovered and described, the scenario of a multitude of endemic rail species across the Pacific Islands is becoming more evident, offering further evidence in support of the above-mentioned hypothesis [8,30]. Likewise, the list of species extinct after human contact during the past millennia is becoming more extensive, adding to the corpus of data on the demise of insular faunas.

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Conflicts of Interest: The authors declare no conflict of interest.

Appendix A

The following specimens of Rallidae from the NMNZ collection were used for comparison. The list is arranged alphabetically by species name, with acronym (NMNZ) omitted from registration numbers for brevity. Measured specimens (used in Table 1) are identified by an asterisk (*).

Capellirallus karamu Falla, 1954: S.023241. *Diaphorapteryx hawkinsi* (Forbes, 1892): OR.007997. *Fulica atra australis* Gould, 1845: OR.024566. *Fulica chathamensis* Forbes, 1892: S.026519. *Fulica prisca* Hamilton, 1893: S.033721. *Gallinula hodgenorum* (Scarlett, 1955): S.033724. *Gallinula tenebrosa* Gould, 1846: OR.024520. *Gallinula ventralis* Gould, 1837: OR.022100. *Gallirallus australis australis* (Sparrman, 1786): OR.014994. *Gallirallus australis greyi* (Buller, 1888): S.00573, S.023353*, S.023387*, S.027815*, S.034078*, S.042193*, S.045588*. *Gallirallus australis hectori* (Hutton, 1873): OR.0025361. *Gallirallus australis scotti* (Oglivie-Grant, 1905): OR.018327. *Gallirallus dieffenbachii* (G.R. Gray, 1843): S.026625*, S.026924*, S.026943*, S.027616*, S.027766*, S.030037, S.031762*, S.032013*, S.032092*, S.033198*, S.044038*. *Gallirallus huiatua* Steadman et al., 2000: S.037708* (holotype). *Gallirallus modestus* (Hutton, 1872): S.026258*, S.026967*, S.027607*, S.031303*, S.031755. *Gallirallus philippensis assimilis* (G.R. Gray, 1843): OR.023821. *Gallirallus philippensis goodsoni* (Mathews, 1911): S.035228*. *Gallirallus philippensis mellori* (Mathews, 1912): S.045796*. *Gallirallus philippensis sethsmithi* (Mathews, 1911): S.038224*, S.038383*. *Gallirallus sylvestris* (P.L. Sclater, 1870): S.027218a*. *Lewinia muelleri* (Rothschild, 1893): OR.025556. *Porphyrio mantelli* (Owen, 1848): S.028440. *Porphyrio hochstetteri* (A.B. Meyer, 1883): OR.024641. *Porphyrio melanotus melanotus* Temminck, 1820: OR.024252. *Zapornia pusilla affinis* (J.E. Gray, 1845): OR.024417. *Zapornia tabuensis tabuensis* (Gmelin, 1789): OR.020984, S.044596.

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