The history and morphology of Lord Howe Gallinule or Swamphen *Porphyrio albus* (Rallidae)

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Summary.—The extinct Lord Howe Gallinule or Swamphen *Porphyrio albus* (White, 1790) is known from a number of written accounts, from at least ten contemporary paintings and from two skins, but the provenance of the specimens is confused and the taxonomic literature riddled with error. We present a review of the evidence and its reliability, demonstrate that the two extant specimens were collected on Lord Howe Island, provide details about when they were taken and by whom, and how they subsequently arrived in England. We further present evidence to demonstrate that Lord Howe Gallinule possessed several unique morphological characters.

'Although generally believed to be absolutely extinct, I should not be surprised to hear of a specimen being taken in the recesses of the mountains, many parts of which have not yet been explored' (Bassett-Hull 1909).

Lord Howe Gallinule or Swamphen *Porphyrio albus* (White, 1790) was endemic to remote Lord Howe Island, a small island *c*.10 km long and 0.3–2.0 km wide, located *c*.600 km east of Australia. It was considered common when initially discovered in 1788, but quickly succumbed to over-hunting, and had disappeared by 1834 (Hindwood 1940, Hume & Walters 2012, Hume & van Grouw 2014). The population contained all-blue and all-white birds, as well as individuals with a variable mix of blue and white feathers. Just two specimens are extant: the type (NMW 50.761), in the Naturhistorisches Museum, Vienna, has reliable documentation linking it to Lord Howe Island. There is no doubt that this specimen is the type, as White (1790) stated that the bird on which his Lord Howe Gallinule drawing was based was deposited in the Leverian Museum (Pelzeln 1860, 1873). The specimen was purchased during the sale of the Leverian collection in 1806 by the Vienna Museum (Pelzeln 1860, 1873, Forbes 1901), being catalogued as 'Lot 2782: White fulica, *Fulica alba*, New Holland'. However, the provenance of the second specimen held in the World Museum, Liverpool (WML D3213), is uncertain. The discovery and subsequent descriptions of Lord Howe Gallinule have resulted in a wealth of confusing literature, exacerbated by uncertainty over provenance. We provide evidence to suggest that some of the accounts were based on hearsay, and provide historical and morphometric evidence to ascertain that the Liverpool skin was indeed collected on Lord Howe. We further show that *P. albus*, although exhibiting several unique characters, was most similar morphometrically to Purple Swamphen *P. porphyrio melanotus* of Australia and New Zealand. Finally, we show that *P. albus* was uniquely coloured in its natural purple-blue plumage-variant, of which no specimen exists.

The early literature

To clarify a complicated situation, we compiled all of the contemporary literature describing or illustrating the species and have listed it chronologically, providing information concerning the reliability of each account and illustration. The accounts describing live birds on Lord Howe Island and collection of specimens occurred in March–

May 1788 by crew members on visiting ships, and the paintings were executed between 1788 and 1790. Five ships arrived on Lord Howe in 1788, the outgoing *Supply*, as well as the *Sirius*, which was supplying a newly founded penal colony on Norfolk Island from Sydney in 1788–90, and the returning transports of the First Fleet, the *Scarborough*, *Charlotte* and *Lady Penrhyn* (Hindwood 1940). After the first landing on 19 March 1788 by the *Supply* en route from Norfolk Island, the *Supply* returned to Lord Howe again together with the *Sirius* and the three transports on 16–18 May 1788, during which period the crews from each ship plundered the avifauna. There are no more reports detailing landings on Lord Howe or ornithological observations until 1853 (see below).

The accounts

Lieutenant Henry Lidgbird Ball, commander on the ship *Supply*, who first observed Lord Howe Island on 17 February 1788, en route to Norfolk Island to establish the penal colony, and named and claimed Lord Howe for Britain on his return trip (Nichols 2006). Ball went ashore on 19 March, and according to Arthur Bowes Smythe, who also wrote about Ball's discovery (see below), members of the crew captured Lord Howe Gallinules for the first time, as Ball did not provide any details himself.

First-hand accounts

1. David Blackburn (landed 19 March 1788 and 16 May 1788) was Master on the *Supply* and apparently part of the first landing party on Lord Howe on 19 March, as well as the second on 16 May, on both occasions when the *Supply* was returning from Norfolk (Hindwood 1940). His account was written in a letter to a friend in England (Blackburn 1934). He was the only person to mention the diet of Lord Howe Gallinule: '…on the shore we caught several sorts of birds, … and a white fowl – something like a Guinea hen, with a very strong thick & sharp pointed bill of a red colour – stout legs and claws – I believe they are carnivorous they hold their food between the thumb or hind claw & the bottom of the foot & lift it to the mouth without stopping so much as a parrot'.

2. Arthur Bowes Smythe (landed 16 May 1788) was surgeon on the *Lady Penrhyn* and mentioned Lieutenant Ball's discovery in his journal (Bowes Smythe MS 22 March 1787–August 1789). He stated: 'The *Supply* in her return [from Norfolk] landed at the island [Lord Howe] she made in going out & were very agreeably surpris'd to find great numbers of fine Turtle on the beach, & on the Land amongst the trees great Nos. of fowls like a Guinea hen [Lord Howe Gallinule], & another species of fowl [Lord Howe Woodhen *Gallirallus sylvestris*] not unlike the landrail in England, & all so perfectly tame that you cd. frequently take hold of them with your hands but cd. at all times knock down as many as you thought proper wt. a short stick'.

Bowes Smythe finally experienced the naivety of the Lord Howe avifauna himself on the morning of 16 May 1788 (Bowes Smythe 1787–89) and stayed overnight (Hindwood 1940). After going ashore, he remarked: 'When I was in the Woods amongst the Birds I cd. not help picturing to myself the Golden Age as described by Ovid to see the Fowls (or Coots) some white, some blue & white, others all blue wt. large red bills & a patch of red on the top of their heads, …'. Bowes Smythe also executed the first illustration of Lord Howe Gallinule at this time (*in* Hindwood 1932), when he depicted three individuals, one completely white and the others tinged with blue (Fig. 1).

3. Thomas Gilbert (landed 16 May 1788) was commander on the *Charlotte* and wrote a detailed account of the avifauna on Lord Howe, including Lord Howe Gallinule (Gilbert

1

Figure 1. Watercolour of three Lord Howe Gallinules *Porphyrio albus* by Arthur Bowes Smythe, *c.*1788, based on live birds that Bowes Smith observed during his visit to Lord Howe Island in May 1788. The handwritten note reads 'Representation of a Bird of the Coot kind, found at Lord Howe Island, in the South Sea' (National Library of Australia, Canberra)

2

Figure 2. White Gallinule, pl. 44 in Phillip (1789), probably based on a live specimen (Hein van Grouw, Natural History Museum, Tring)

1789): 'Among the different kinds of birds we met with, there was one about the size of a large barn-door fowl, quite white, with long yellow legs, and a remarkably strong beak. I caught six of them by running them down among the low bushes. The cocks were very beautiful, their white feathers being tipped with azure blue'.

4. Arthur Phillip (account written in 1789) was the first Governor of New South Wales and sailed with the first fleet in 1787 (Phillip 1789). Governor Phillip received Lord Howe bird specimens in Sydney, including live individuals, possibly collected by Lieutenant Ball or his crew. Some were sent to Lady Mary Elisabeth Chatham in England aboard the *Alexander* in 1788, whereupon they were probably purchased by Sir Joseph Banks (Barton 1889, Bladen 1901, Hindwood 1940). Lady Chatham was married to John Pitt, Second Earl of Chatham, and sister-in-law to the Prime Minister, William Pitt the Younger (Stanhope 1861). Phillip never visited Lord Howe Island, so he almost certainly based the first part of his account on those of Blackburn, Lieutenant Ball and / or Bowes Smythe, in which they compare Lord Howe Gallinule with a guineafowl. Phillip stated (p. 182): 'There are also many very large pigeons, and the white birds resembling the Guinea fowl, which were found at Norfolk Island, were seen here also in great numbers. The bill of this bird is red, and very strong, thick, and sharp pointed'.

Phillip (1789) illustrated the bird and also provided a detailed description, which strongly suggests that they were based on a live gallinule he received in Sydney (Fig. 2): 'WHITE GALLINULE. This beautiful bird greatly resembles the purple Gallinule in shape and make, but is much superior in size, being as large as a dunghill fowl. The length from the end of the bill to that of the claws is two feet three inches; the bill is very stout, and the colour of it, the whole top of the head, and the irides red; the sides of the head around the eyes are reddish, very thinly sprinkled with white feathers; the whole of the plumage without exception is white. The legs the colour of the bill. This species is pretty common on Lord Howe's Island, Norfolk Island, and other places, and is a very tame species. The other sex, supposed to be the male, is said to have some blue on the wings.'

Phillip (1789) referred to the gallinule occurring on 'Norfolk Island and other places', but does not indicate where the 'other places' are. His provenance of Norfolk Island is also in error (see below).

5. John Hunter (present early 1790?) was Captain on the *Sirius* and later replaced Phillip as Governor of New South Wales (Percival 1949). Captain Hunter did not mention visiting Lord Howe, but presumably landed there while supplying the penal colony on Norfolk. The *Sirius* was wrecked on Norfolk on 19 March 1790, and Captain Hunter and George Raper (see below), along with the rest of the crew, were marooned there for 11 months until a rescue ship arrived from Sydney (Percival 1949, Hindwood 1964, 1965). Hunter was a keen naturalist and artist, and illustrated a Lord Howe Gallinule (Hunter MS; Fig. 3). The painting forms part of Hunter's *Birds & flowers of New South Wales drawn on the spot in 1788, '89 & '90*, so the Lord Howe Gallinule illustration must have been executed sometime between 1788 and 1790 (Wheeler & Smith 1988). It is not known if his illustration is based on a live bird when on Lord Howe, or from memory when marooned on Norfolk.

6. George Raper (present early 1790?) was Midshipman on the *Sirius* (Hindwood 1964) and, like Captain Hunter (Hindwood 1965), illustrated Lord Howe Gallinules presumably while on Lord Howe or while marooned on Norfolk. Raper's depiction of a single bird is dated 1790 (Fig. 4). G. P. Whitley (*in* Hindwood 1940) examined a volume of drawings in the Alexander Turnbull Library, Wellington, and discovered an unsigned painting of two Lord Howe Gallinules (Fig. 5), which has been assigned to George Raper and is also dated 1790. This painting is particularly important as it details two plumage variations of the gallinule.

Figure 3. Ground Bird of Lord Howe Island; a Lord Howe Gallinule *Porphyrio albus* depicted by John Hunter (1788–90) (National Library of Australia, Canberra)

Second-hand accounts

1. John White (account written in 1790) was a ship's surgeon and in his book (White 1790: 135), which was more or less a journal of his time in New South Wales, he also presented descriptions of the animals on Lord Howe based on either Lieutenant Ball's or Bowes Smythe's accounts, or on those of other sailors, as he apparently never visited Lord Howe Island himself. White may have questioned the sailors in Sydney, as they had first been to Norfolk Island on the *Supply*, and had stopped at Lord Howe Island on their return: 'They

Figure 4. Ground Bird of Lord Howe Island; a Lord Howe Gallinule *Porphyrio albus* depicted by George Raper (1790), presumably after a live bird; drawing No. 71, George Raper Drawings Collection, Library and Archives, NHMUK London (Natural History Museum, London)

[sailors] also found on it, in great plenty, a kind of fowl, resembling much of the Guinea fowl in shape and size, but widely different in colour; they being in general all white, with a red fleshy substance rising, like a cock's comb, from the head, and not unlike a piece of sealing-wax. These not being birds of flight, nor in the least wild, the sailors availing themselves of their gentleness and inability to take wing from their pursuits, easily struck them down with sticks'.

In his book's appendix, White described the Lord Howe Gallinule, giving it the name *Fulica alba* and the provenance as Lord Howe Island, and illustrated it with a painting by Sarah Stone from a specimen in the Leverian Museum (Fig. 6). It is not known with certainty if White had seen the specimen, but his account categorically states that he was describing a skin. The editor of White's book approached Stone to illustrate the gallinule once the specimen became available at the Leverian Museum (White 1790: A2): 'THE WHITE FULICA. Fulica alba. White Fulica, with the bill and front red, shoulders spined, legs and feet yellow? The body is about the size of a domestic fowl. The shoulders [wrists]

Figure 5. Illustration of two Lord Howe Gallinules *Porphyrio albus*, one all white and one still variegated, by George Raper (1790); this painting is particularly important as it clearly shows two stages of the colour aberration progressive greying (Alexander Turnbull Library, Wellington)

are furnished with a small crooked spine. In the dried specimen the legs and feet are yellow; but, perhaps, in the living bird might have been of the same colour with the beak.'

2. Anon. artist (Thomas Watling collection) (illustration dated *c*.1792, almost certainly incorrectly). Two Lord Howe Gallinule illustrations, executed by an anonymous artist, referred to as the 'Port Jackson artist' (Macinnis 2012), formed part of the Thomas Watling collection, and are now at the Natural History Museum, London (NHMUK-L-Watling-329-M-1 and NHMUK-L-Watling-330-M-1). Watling was a convict and artist who assisted John White by copying natural history illustrations (Pearce 1989). It is not certain if Watling was the artist of these Lord Howe Gallinule paintings, and the date of *c*.1792 that accompanies the paintings is a later addition that is almost certainly incorrect. The mystery is that White (1790) used engravings in his book that possess matching paintings in Watling's collection, yet Watling did not arrive in Sydney until 1792 (Macinnis 2012), hence the *c*.1792 attribution. It is probable therefore that Watling obtained illustrations by other artists after his arrival, and subsequently copied them; this is almost certainly the case with the Lord Howe Gallinules. However, the handwritten notes on the paintings suggest that the artist had either seen a live bird himself, or obtained information from someone else. The note on no. 329 reads: 'This bird is of Lord Howe and when young is intirely [*sic*] black, from that to a bluish grey and from that to an intire [*sic*] white. The bird feeds itself with its feet like a parrot' (Fig. 7). The second painting no. 330 states: 'Three stages of this Bird, taken at Lord Howes Island, before it arrives at maturity' (Fig. 8).

Figure 6. The White Fulica, pl. 27 in White (1790), as depicted by Sarah Stone based on the mounted specimen in the Leverian Museum (Hein van Grouw, Natural History Museum, Tring)

Extinction

The period between the discovery of Lord Howe and the date of the last mention of living Lord Howe Gallinules spanned only 1788–90. Lord Howe Island was first settled in 1834, but whalers and sealers regularly used the island for supplies prior to this (Hume & Walters 2012). Foulis (1853) was on the island from 1844 until 1847 with 16 other residents.

Figure 7. Illustration by an anonymous artist of a Lord Howe Gallinule *Porphyrio albus* from Thomas Watling's collection, NHMUK-L-Watling-329-M-1; the handwritten notes read 'This bird is of Lord Howe and when young is intirely [*sic*] black, from that to a bluish grey and from that to an intire [*sic*] white. The bird feeds itself with its feet like a parrot' (Natural History Museum, London)

He made an ornithological report, the first survey of the avifauna of Lord Howe Island for 63 years, but did not mention the gallinule (Foulis 1853, Hindwood 1940). No doubt a poorly volant, chicken-sized gallinule quickly fell prey to whalers and sealers, and disappeared extremely rapidly, possibly even by the end of the 18th century. And, although Bassett-Hull (1909) hoped for its rediscovery, the confirmed existence of the Lord Howe Gallinule spanned just two years.

Confusion over provenance

There is no doubt that there was once a population of predominantly white gallinules on Lord Howe Island, with the discovery of subfossil remains confirming this (Hume & Walters 2012). However, there is no substantiating evidence to suggest that a white gallinule historically occurred on Norfolk Island (*contra* Pelzeln 1860, 1873, Gray 1862, Sharpe 1894, Rothschild 1907, Mathews 1928), but subfossil *Porphyrio* remains pre-dating European discovery of the island have been recovered (Holdaway & Anderson 2001). Norfolk Island lies *c*.900 km north-east of Lord Howe and was visited by the capable naturalists the Forsters in 1774 during Cook's discovery of the island; they did not mention a white

Figure 8. Illustration by an anonymous artist of three Lord Howe Gallinules *Porphyrio albus* from Thomas Watling's collection, NHMUK-L-Watling-330-M-1; the handwritten note reads 'Three stages of this Bird, taken at Lord Howes Island, before it arrives at maturity (Natural History Museum, London)

gallinule (*cf*. Iredale 1910, Hindwood 1932). Despite this lack of first-hand evidence, several commentators confused the provenance, even leading to the description of supposed Norfolk Island birds as a second species of white gallinule.

Confusion was initiated when Arthur Phillip mentioned white gallinules on Lord Howe, Norfolk 'and other places' (Phillip 1789), which was followed by Latham (1790, 1801), who gave only Norfolk Island as their provenance. Latham based his locality on the accounts of Phillip (1789) and White (1790) alone, but White gave Lord Howe as the provenance (p. 135). There is some doubt as to the accuracy of the accounts of both Phillip and White, as they were published in popular books (Phillip 1789, White 1790), in which much information was gleaned from official and semi-official documents (Hindwood 1940). White and Phillip also never landed on Lord Howe or Norfolk themselves, so both authors discussed the observations of others in describing the islands, although Phillip did see live Lord Howe Gallinules in Sydney. White (1790: 238) confirmed his lack of field observation when he stated: 'in the dried specimen the legs and feet are yellow; but, perhaps, in the living bird might have been of the same colour with the beak'.

Pelzeln (1860, 1873) repeated Latham's (1790, 1801) statement that the Vienna specimen was obtained on Norfolk Island, and in the Leverian sale it was catalogued as originating in New Holland (= Australia), presumably in reference to it having been sent from Sydney, rather than any suggestion that it had been collected there. These errors almost certainly arose from misinterpretation of the collectors' voyages. Supply ships regularly sailed between Sydney and Norfolk, often stopping at Lord Howe, making confusion over provenance extremely likely.

Figure 9. Illustration of *Porphyrio stanleyi*, based on the Liverpool specimen, by J. G. Keulemans *in* Rowley (1875), as Rowley thought the Liverpool bird was a different species; it is probable that the present pose of the Liverpool specimen (see Fig. 11) is modelled on this picture (Hein van Grouw, Natural History Museum, Tring)

White (1790) sent his manuscript to England prior to 1790, as he did not return to England until after 1794 (Nelson 1998). As Sarah Stone was able to illustrate the Lord Howe Gallinule pre-1790 for White's volume based on a specimen in the Leverian Museum (White 1790, Pelzeln 1860), it is plausible that White had sent a Lord Howe Gallinule along with the manuscript from Sydney. This was the specimen obtained by Sir John Lever for the Leverian Museum and now in Vienna. Alternatively, this skin might have arrived earlier, possibly also sent by Governor Phillip with the Liverpool bird (see below). Unfortunately, there is no surviving correspondence, as far as is known, from White or Phillip to clarify this conundrum.

The Liverpool skin was probably obtained, without date or provenance, on its arrival in England by Sir Joseph Banks, one of the naturalists on Cook's first voyage, but it was supposed to have come from New Zealand (Rowley 1875, Forbes 1901). It is extremely likely that a Lord Howe Gallinule was included with the 1788 consignment sent by Governor Phillip to Lady Chatham in England, after which it was presumably purchased by Banks and eventually reached Liverpool. Nothing is known as to the whereabouts of the specimen until it eventually came into the possession of William Bullock, whose collection, including the gallinule, was auctioned in 1819 (Forbes 1901), when it was catalogued as 'Lot 60, White

Figure 10. Illustration of a Takahe-like Lord Howe Gallinule *Notornis alba* in Salvin (1873) by J. G. Keulemans, based on a sketch provided by Pelzeln of the Vienna specimen (Hein van Grouw, Natural History Museum, Tring)

Gallinule (F)ulica) alba); New Zealand, rare; brought by Sir J. Banks'. The specimen was purchased by Lord Stanley and, along with his Knowsley collection, bequeathed to the people of Liverpool and finally donated to the free public museums of Liverpool by the 13th Lord Derby around 1850 (Rowley 1875, Forbes 1901).

Taxonomic muddle

Confusion over provenance resulted in Rowley (1875: 37, pl. 9; Fig. 9) providing a new name for the Liverpool bird, *Porphyrio stanleyi*, in honour of Lord Stanley, and giving the type locality as Lord Howe Island or New Zealand. He also considered the specimen to be a probable juvenile. Based on the Vienna specimen, Pelzeln (1860: 331) was first to assign Lord Howe Gallinule to the genus *Notornis*, but thought Norfolk was the provenance, as did Latham (1790), Rowley (1875) and Rothschild (1907); all failed to note the Lord Howe provenance of the Vienna specimen recorded by White (1790). Salvin (1873) agreed

Figure 11. Liverpool specimen of *Porphyrio albus* (WML D3213), probably collected March or May 1788 on Lord Howe Island, and the type of *Porphyrio stanleyi* Rowley, 1875, which was probably re-prepared (modelled) after Keuleman's illustration (see Fig. 9) (Hein van Grouw)

with Pelzeln (1860) that Lord Howe Gallinule was more similar to New Zealand Takahe *Notornis mantelli* and therefore should be placed in *Notornis*, as shown in the accompanying illustration by J. G. Keulemans (Fig. 10). However, Salvin apparently never saw the Vienna specimen and based his attribution purely on a drawing of it provided to him by Pelzeln, stating: 'I therefore (depending, of course, upon the accuracy of the drawing sent me, which has been placed on stone by Mr. Keulemans on a slightly larger scale than the original sketch) have little hesitation in adding this species to the genus *Notornis*, thereby confirming the position pointed out for it by Herr von Pelzeln…'. Salvin's caution seems justified as, in our opinion, Pelzeln must have been biased towards Takahe when he provided the sketch.

Rowley (1875) described a number of superficial differences between the two specimens to support his assignation, stating that *P. stanleyi* of Lord Howe was morphologically similar to Purple Gallinule *P. porphyrio*, whereas *Notornis alba* of Norfolk was more akin to Takahe. Rowley probably also never saw the Vienna specimen himself and based his conclusions on the descriptions by Phillip (1789), White (1790), Pelzeln (1860, 1873) and the illustration in Salvin (1873). Here again, it seems that Pelzeln's inaccurate reproduction of the bird confused matters. Furthermore, Forbes (1901) noted that the Liverpool specimen had probably been 'remade' since the time of Bullock, and that its pose had been modelled on the plate in White (1790; Fig. 6). However, the present pose of the Liverpool bird (Fig. 11) is nothing like the illustration in White, but Rowley's plate (Fig. 9), which was also prepared

Figure 12. Lateral (top) and dorsal views of the specimen at the Naturhistorisches Museum Wien (NMW 50761), probably collected March 1788 on Lord Howe Island, the type specimen of *Porphyrio alba* (White, 1790) (A. Schumacher, © Naturhistorisches Museum Wien)

by Keulemans, is identical in pose to the Liverpool mount. So either Forbes was in error, or the specimen has been remade (again) since Forbes, based on the plate in Rowley. Sarah Stone's illustration of the Vienna bird was probably derived from the original pose of the mounted specimen, rather than the specimen being modelled on her painting; the skin is now demounted with legs outstretched (Fig. 12).

Rowley (1875) also noted that the wings were longer in the Liverpool specimen and considered that this individual, his *P. stanleyi*, was clearly volant. Remarkably, Rothschild (1907) recorded that the wings of both specimens were of the same length (nine inches), but also remarked that the wing-coverts of the two specimens differed in length, and then muddled the situation even further by stating that *stanleyi* and *alba* were both flightless. Following Forbes (1901), Rothschild (1907) assigned them to *Notornis*, but disagreed with Forbes that both specimens represented *alba*. Rothschild (1907) was of the opinion that the bird described and pictured in Phillip (1789) was *N. stanleyi* of Lord Howe Island (= Liverpool specimen), while White's bird (1790) was *N. alba* from Norfolk Island (= Vienna specimen). He distinguished them only by the difference in length of the wing-coverts, based solely on the inadequate details in the figures of Phillip (1789) and White (1790). Although Rothschild (1907) had seen the Vienna specimen personally, the reproduction of *N. alba* (Fig. 13), a third depiction by Keulemans, also seems slightly biased towards Takahe, rather than a gallinule. Furthermore, dark-coloured primaries were added to the figure and, as this was supposed to represent the Vienna bird (all white), their inclusion was borne wholly out of Rothschild's muddled imagination. Therefore, both the figures provided by Pelzeln (*in* Salvin 1873) and Rothschild (1907) were probably reconstructed to justify a relationship with *Notornis*.

If this was not already sufficiently confusing, Mathews (1928) decided that the above-mentioned painting of Lord Howe Gallinule by George Raper (Fig. 4) was sufficiently distinct from *Porphyrio albus* that another name should be applied to it, describing *Porphyrio*

Figure 13. Illustration of a Takahe-like Lord Howe Gallinule *Notornis alba* in Rothschild (1907) by J. G. Keulemans, based on how Rothschild thought the species would have appeared in life; although it is based on the Vienna specimen, artistic license permitted Rothschild / Keulemans to erroneously picture the bird with coloured primaries (Hein van Grouw, Natural History Museum, Tring)

raperi in recognition of the artist. His grounds were extremely dubious to say the least and, subsequently, when Mathews (1936) had reproduced the Raper painting (Fig. 14) and compared it to the Vienna skin, he admitted his error and synonymised *P. raperi* under *P. albus*.

Some authors questioned the validity of the white gallinule skins altogether. Temminck (1820), Gray (1844) and Mayr (1941) considered *N. alba* to be an albino of New Zealand Purple Swamphen *P. melanotus*, as did Rowley (1875) with respect to his *P. stanleyi*, despite describing it as a new species in the same publication! Buller (1888), Sharpe (1894) and Hindwood (1932) all synonymised *P. stanleyi* under *P. melanotus* and also considered it to be an albino. The Norfolk Island provenance was finally and correctly refuted by Iredale (1910), who provided plausible evidence to suggest that a white gallinule had not occurred on any island in recent times, other than on Lord Howe. It is almost certain therefore that *P. albus* was endemic to Lord Howe and historical records of its occurrence on Norfolk Island are in error.

Records of Purple Gallinule on Norfolk and Lord Howe

The eastern subspecies of Purple Gallinule *P. p. melanotus* has been noted as a straggler to Lord Howe Island for at least 130 years, but has become established as a breeder only

Figure 14. Reconstruction of Raper's painting 1790 in Mathews (1936) (Hein van Grouw, Natural History Museum, Tring)

since 1987 (Ripley 1977, Hutton 1990). Also on Norfolk Island, the species is probably self-introduced and has been recorded since the earliest European occupation (Christian 2005). In early 1900 it was not uncommon and recorded as breeding (Bassett-Hull 1909), but since the 1990s the number of breeding birds has increased dramatically (Christian 2005).

As *P. p. melanotus* was prone to white feathering, Mayr (1941) considered Lord Howe Gallinule nothing more than a 'partially-albinistic' population of the widespread Purple Gallinule; the survival of blue individuals was due to them being less conspicuous, following the disappearance of the original population of white birds. That Mayr was incorrect is demonstrated by our reconstruction of normal-coloured Lord Howe Gallinule, which was nothing like *P. p. melanotus* or any other *Porphyrio* subspecies. Hindwood (1940) considered that the island population was white but that occasional blue birds arrived from Australia and interbred with *P. albus*, but this was due to a misunderstanding of the cause of blue and white coloration in the resident *P. albus* population (see below). Furthermore, the distinct mtDNA, morphology and behaviour of *P. albus* strongly suggests that Lord

Howe birds no longer hybridised with *P. p. melanotus*. Taylor & van Perlo (1998), following Hindwood (1940) and Hutton (1991), also considered the blue-and-white birds to be hybrids of Lord Howe Gallinule with Purple Gallinule, rather than pure Purple Gallinules with aberrant white feathers, which was also not true (see below). Whether the odd white-feathered *P. p. melanotus* visited Lord Howe Island in the past is unknown, but it appears that, since establishing as a breeder, only normal-coloured *P. p. melanotus* has occurred on Lord Howe (Hutton 1991).

Inadequate knowledge of colour aberrations

As Lord Howe Gallinule exhibited white plumage, at least in adults, it was considered by several authorities to represent an aberration of an existing species. Aberrant white feathering is a rather common phenomenon in wild birds, but knowledge of colour aberrations and inheritance was poorly known until recently. For example, the term 'albino' was, and still is, widely used for many different colour aberrations. The aberration albino is far less common than previously thought, and aberrant white plumage is rarely caused by albinism. In general, it is a result of either a form of inheritable leucism or a phenomenon termed progressive greying (see van Grouw 2012, 2013). In both leucism and progressive greying, white feathers are produced by the absence of melanin pigment-producing cells (van Grouw 2014). In leucism the absence of melanin cells is congenital and inheritable, therefore the white pattern is already present in juvenile plumage and the amount of white feathering does not change with age. In progressive greying, however, loss of pigment-producing cells results in age-related white feathering, so juvenile plumage is always normal-coloured (van Grouw 2013, 2014). Furthermore, the loss of pigment cells appears to be progressive; the bird will gain an increasing number of white feathers following every moult, and in many birds the entire plumage eventually becomes white.

Different forms of progressive greying appear to exist, but the causes of most of these are unknown. Some are clearly inheritable and based on a single mutation. Other forms, however, do not seem to be directly related to inheritance and may be entirely age-related, while in others the progressive loss of pigment cells can be a result of (heritable) disorders such as vitiligo (pigment disease) or related to environment (van Grouw 2012, 2013).

The handwritten notes on the painting in Thomas Watling's collection (Fig. 7) that state 'young were all black, turning bluish grey, then pure white with maturity', are probably based on observations of live birds by the artist or first-hand information. This observation demonstrates that the adult white plumage in Lord Howe Gallinule is caused by a form of progressive greying. Furthermore, as all adult Lord Howe Gallinules exhibited white feathers to a certain degree, we can safely assume that in this case the progressive greying was a heritable form.

Progressive greying is the most common cause of white feathers in birds. It has been recorded in many different species including several Rallidae, e.g. Common Coot *Fulica atra*, Common Moorhen *Gallinula chloropus*, Weka *Gallirallus australis* and Corn Crake *Crex crex* (Figs. 15–18). In some of these taxa it occurs frequently, especially Common Coot, and in Australian / New Zealand *P. p. melanotus* it is, or at least was, also fairly common (Buller 1888, 1905, Mayr 1941, Austin 1955). Buller (1888) mentioned several *melanotus* specimens in his own collection (Fig. 19) and others in the Colonial Museum (now Te Papa Museum, Wellington). More recent examples are also available at Te Papa and in other collections in both New Zealand and Australia. Although Buller incorrectly described them as 'albino' and 'partial albino', the aberrant white feathers of these all-white and variegated birds were all the result of different stages of progressive greying. Buller (1905) subsequently mentioned a few more (partly) white specimens, and also specifically quoted Mr Robert Wilson, who

Figure 15. Two specimens of Weka *Gallirallus australis* showing different stages of progressive greying; top: NHMUK 2004.15.419 (in the final stage of progressive greying), below: NHMUK 1939.12.9.3710 (Harry Taylor, © Natural History Museum, London)

wrote to him from Rangtikei: 'I obtained two specimens of Pukeko [Swamphen] which are partial albinos, but the pure white one I had seen I was not able to get, though he was seen again'.

Morphological comparison of *P. albus* with subspecies of *P. porphyrio*

Our data show that wing chord and tail lengths of the Vienna *Porphyrio albus* are the shortest, whereas the Liverpool *P. albus* has a similar wing and tarsus length to Philippine *P. p. pulverulentus* and African *P. p. madagascariensis*, which have the shortest wings and tarsi of all subspecies examined (Table 1). However, the Philippine and African subspecies are also the smallest subspecies, so proportionately their wings and tarsi are longer than in *P. albus*,

16

17

Figure 16. Two specimens of Common Moorhen *Gallinula chloropus* showing different stages of progressive greying; left: NHMUK 1996.41.2095, right: NHMUK 1996.41.2359 (Harry Taylor, © Natural History Museum, London)

Figure 17. Two specimens of Corn Crake *Crex crex* showing different stages of progressive greying; top: NHMUK 1939.12.9.3702, below: NHMUK 2004.15.413 (in final stage of progressive greying (Harry Taylor, © Natural History Museum, London)

Figure 18. Two Common Coots *Fulica atra* showing different stages of progressive greying; top: Tolkamer, the Netherlands, 29 June 2006 (© Harvey van Diek), below (in final stage of progressive Greying): Capelle aan den IJssel, the Netherlands, 28 March 2004 (© Chris van Rijswijk)

Figure 19. Pl. 31 in Buller (1888); full image (left) and inset (right) of New Zealand Swamphen *P. p. melanotus* with progressive greying based on a specimen in Buller's collection (Hein van Grouw, Natural History Museum, Tring)

TABLE 1

Measurements of *Porphyrio* specimens used in our analysis. Unless stated, all specimens are held at the Natural History Museum, Tring. All measurements were made using dial callipers (to the nearest 0.1 mm) and a 300-mm rule (to the nearest 1.0 mm). Measurements of wing chord (bend of 'wrist' to primary tip) were obtained from the flattened wing. Tarsus was measured from the top of the tarsi at the junction with the tibia (heel joint) to the joint of tarsi with the first phalanx of the middle toe. Tail was measured from the skin at the base of the tail to the tip of the two central rectrices.

***Porphyrio p. porphyrio* (Europe)**

Specimen	Wing	Tarsus	Tail	Middle toe
♂ 1891.8.1.40	260	99.9	88	99.9
Ad. 1905.6.28.1010	263	104.8	95	104.8
Ad. 1934.1.1.2049	259	102.8	94	102.9
Ad. 1851.4.29.2	256	100	94	100.9
Mean	**259.5**	**101.9**	**92.8**	**102.1**

***Porphyrio p. madagascariensis* (Africa)**

Specimen	Wing	Tarsus	Tail	Middle toe
♀ 1904.10.23.76	234	88.8	79	88.8
♀ 1935.10.16.107	234	87.9	86	88.2
♂ 1940.4.7.96	241	87.8	93	88.8
♂ 1955.6.N.1736	242	89	89	91
Mean	**237.8**	**88.4**	**86.8**	**89.2**

***Porphyrio p. poliocephalus* (India)**

Specimen	Wing	Tarsus	Tail	Middle toe
♀ 1889.11.3.187	252	87.2	93	89
♀ 1938.7.15.1396	237	92.3	81.3	92.6
♂ 1889.11.1.256	237	90	92	89.5
♂ 1881.12.29.31	258	94	102	96.8
Mean	**246**	**90.9**	**92.1**	**92**

***Porphyrio p. melanotus* (Australia)**

Specimen	Wing	Tarsus	Tail	Middle toe
Ad. 1887.5.2.66	263	95.6	97	89
♀ 1969.4.48	243	87.1	98	80
♂ 1969.4.49	275	97.2	96	93.3
♂ 1898.5.17.179	274	105.5	99	97.6
Mean	**263.8**	**96.4**	**97.5**	**90**

***Porphyrio p. melanotus* (New Zealand)**

Specimen	Wing	Tarsus	Tail	Middle toe
♀ 1889.11.1.285	266	93	95	84.5
♀ 1926.10.10.8	272	91.2	100	85.2
♂ 1849.12.12.7	258	88.2	85	84
♂ 1889.11.1.287	285	100.1	96	95
Mean	**270.3**	**93.1**	**94**	**87.2**

***Porphyrio p. melanotus* (Norfolk Island)**

Specimen	Wing	Tarsus	Tail	Middle toe
Ad. WML 11950	254	91.4	91	80.5
Ad. WML 16090	270	99.9	95	93.7
Mean	**262**	**95.7**	**93**	**87.1**

***Porphyrio p. pulverulentus* (Philippines)**

Specimen	Wing	Tarsus	Tail	Middle toe
Ad. RMNH 99515	235	85	80	88
Ad. 1896.6.6.1255	234	88	80	82.6
Ad. 1842.2.15.140	241	87	-	88.9
Ad. 1881.5.1.5677	233	85	-	86.3
Mean	**235.8**	**86.3**	**80**	**86.5**

***Porphyrio albus* (Lord Howe Gallinule)**

Specimen	Wing	Tarsus	Tail	Middle toe
NMW 50.761	218	86	73.3	77.7
WML D3213	235	88.4	-	66.5
Mean	**226.5**	**87.2**	**73.3**	**72.1**

and their wing load (relation between wing area and body mass, in g / cm^2) is lower. Lord Howe Gallinule was comparable in size to *P. p. melanotus* (Phillip 1789; pers. obs. based on specimens), up to 50 cm in total length, which, together with nominate *P. p. porphyrio*, is one of the largest subspecies (Taylor & van Perlo 1998). Therefore, the wings of *P. p. melanotus* are proportionately longest (Table 1), as they are large and heavy birds, whereas the longest tarsus is exhibited in *P. p. porphyrio*. Although we do not know its body weight, as *P. albus* was such a large bird, its wing load was probably the highest of all. To support relationships between populations, morphological ratios, e.g. wing-tail index, tarsus-toe index and/or wing-tarsus index can be compared between taxa (see Table 2). However, as there was such a significant difference in body mass between *P. albus* and many *P. porphyrio* subspecies, this tool appears unreliable for our dataset. For example, both the wing-tail index and tarsus-toe index are smallest in *P. albus*, suggesting that Lord Howe Gallinule was not only absolutely but also relatively the smallest representative of all populations, but this is incorrect.

TABLE 2
WTI: wing-tail index (ratio wing / tail lengths); TarsI: tarsus-toe index (ratio tarsus / toe lengths); WTarsI: wing-tarsus index (ratio wing / tarsus lengths). For specimen details, see Table 1.

Subspecies	**WTI**
P. albus	32.4
P. p. pulverulentus	33.9
P. p. melanotus NZ	34.8
P. p. melanotus Norfolk	35.5
P. p. porphyrio	35.8
P. p. madagascariensis	36.5
P. p. melanotus AUS	37.0
P. p. poliocephalus	37.4
Subspecies	**TarsI**
P. albus	84.1
P. p. pulverulentus	92.7
P. p. melanotus AUS	93.4
P. p. melanotus Norfolk	97.2
P. p. porphyrio	100.2
P. p. madagascariensis	100.9
P. p. melanotus NZ	101.0
P. p. poliocephalus	101.2
Subspecies	**WTarsI**
P. p. melanotus NZ	34.4
P. p. melanotus Norfolk	36.5
P. p. melanotus AUS	36.5
P. p. pulverulentus	36.6
P. p. poliocephalus	37.0
P. p. madagascariensis	37.2
P. albus	38.5
P. p. porphyrio	39.3

The ratio wing/tarsus length of *P. albus*, however, is second largest, indicating a substantial proportional change towards a terrestrial lifestyle. This is also supported by the high wing load.

The most striking difference between *P. albus* and other *Porphyrio*, except *P. p. melanotus*, is the short middle toe, which is especially reduced in the Liverpool specimen. In all other *P. porphyrio* subspecies, the middle toe is the same length or even slightly longer than the tarsus, but in *P. p. melanotus*, however, the middle toe is shorter than the tarsus, just as in *P. albus*. The tail of the Vienna

Figure 20. 'Shoulders' (left and right side) of Liverpool specimen of Lord Howe Gallinule *Porphyrio albus* (WML D3213) showing a few remnant purple-blue feathers, a colour not found in the shoulder/upperparts plumage of any subspecies of Purple Swamphen *P. porphyrio* (Hein van Grouw)

Figure 21. Reconstruction of a blue-coloured (i.e. younger) Lord Howe Gallinule *Porphyrio albus*, before it becomes white (Julian P. Hume)

Figure 22. Coloration of different subspecies of Purple Swamphen *Porphyrio porphyrio*, dorsal (above), ventral (below), from left to right: *P. p. porphyrio* (NHMUK 1905.6.28.1010), *P. p. madagascariensis* (NHMUK 1955.6.N.17.38), *P. p. poliocephalus* (NHMUK 1881.12.29.31), *P. p. pulverulentus* (NHMUK 1842.2.15.140) and *P. p. melanotus* (NHMUK 1887.5.2.66) (Harry Taylor, © Natural History Museum, London)

specimen (tail lacking in Liverpool skin) is also the shortest of all specimens examined. Further confusion has arisen from measurements of the Liverpool bill (exposed culmen) compared to the Vienna bird; e.g. Ripley (1977) and Taylor & van Perlo (1998) reported a culmen length of 63 mm and 79 mm, respectively. Rowley (1875) described the bill as badly broken, but our study has shown that the rhamphotheca has entirely disappeared in the Liverpool skin, a fact that has not been previously reported, and that the underlying bony core of the bill has been painted red, simulating an undamaged bill. This explains

23

24

Figure 23. White Swamphen *Porphyrio albus* in Mathews (1928); for Mathews the spur was motive to remove the species to a new genus, *Kentrophorina*, as, according to him, no wing claw was present in the type of the genus *Porphyrio* (Hein van Grouw, Natural History Museum, Tring)

Figure 24. Detail of the right wing of the Vienna specimen of Lord Howe Gallinule *Porphyrio albus* showing the spur (Hans-Martin Berg, © Naturhistorisches Museum Wien)

the 16 mm difference in culmen length between the specimens; consequently, only the bill measurement of the Vienna bird is reliable.

In coloration, the Vienna skin is pure white, whereas the Liverpool skin has individual blackish-blue feathers on the head and neck, blue feathers on the breast and a few purple-blue feathers on the back and shoulders (Fig. 20). From the distribution of the coloured feathers, we were able to reconstruct the natural purple-blue coloration of this extinct species (Fig. 21). It differed primarily from other *Porphyrio* (Fig. 22) in having the lores, forehead, crown, nape and hindneck blackish blue, the mantle, back and wings purple-blue, rump and uppertail-coverts darker, and underparts all dark greyish blue.

A wing claw or spur was used as a discernible taxonomic character in *P. albus* by White (1790), Rowley (1875), Forbes (1901) and Mathews (1928). It is remarkable, however, that of all of the depictions of *P. albus* based on the Vienna specimen, only those in White and Mathews (Figs. 6, 23) show the spur. Mathews (1928) considered the spur sufficiently diagnostic to place *alba* in a new genus, *Kentrophorina*, as no wing claw is evident in the type of the genus *Porphyrio*. We compared the wing claw of *P. albus* with *P. porphyrio* subspecies, and noted that the claw is longest and most distinct in the Vienna *P. albus* specimen (Fig. 24), but extremely variable in all material examined. In some it is small and pointed, in others longer and less sharp, and in a few completely absent. In the Liverpool *P. albus*, it is sharp but buried below the wing feathers (Rowley 1875). Therefore, the variability of the claw is such that it cannot be used as a reliable taxonomic character.

We conclude that both extant specimens of Lord Howe Gallinule exhibited reduced wing length with correspondingly more robust legs and short toes, all characteristics of an increasingly terrestrial mode of life, and in the process of becoming flightless. Although wing and tarsus length differ slightly between the specimens, and the Vienna bird possesses larger wing spurs, both are *Porphyrio albus*. The Liverpool specimen is also a younger bird than that of Vienna, of which the latter had become entirely white, having completely passed through the progressive loss of pigment cells to final moult.

Discussion

Recent DNA work suggests that the Vienna specimen of *P. albus* is a distinct taxon (Garcia-R. & Trewick 2015). Morphometrics further demonstrate that Lord Howe Gallinule had evolved into a terrestrial species and support the hypothesis that it was distinct from *P. porphyrio*. According to Garcia-R. & Trewick (2015), however, Lord Howe Gallinule may have been most closely related to the Philippine subspecies (*P. p. pulverulentus*) but as many clades in their phylogeny, including those containing *P. albus*, show weak statistical support, this result may change significantly should a more complete dataset become available. Furthermore, this relationship is not supported by morphometrics or by coloration (this paper). The short middle toe of the Australian / New Zealand bird and tendency to white feathering are shared with *P. albus*, although the former was clearly volant. Garcia-R. & Trewick (2015) suggested that *P. albus* arose from a small number of migrants of *P. p. pulverulentus* during the late Pleistocene (*c*.500 MYA), but expressed some caution in drawing this conclusion, as dispersal from the Philippines required dispersal beyond other islands en route.

Wing length of Lord Howe Gallinule suggests it was probably capable of flight, but may have become behaviourally flightless; a characteristic observed in some other island endemics, notably parrots (Hume 2007, Hume & Winters 2015). Tarsus length in *P. albus* is much more reduced and this characteristic, along with the short toes, is also indicative of a terrestrial lifestyle or flightlessness (Livezey 2003). In coloration, Lord Howe Gallinule was a variable population comprising all-white and variable white-and-blue individuals, all indicative of birds exhibiting progressive greying (Hume & van Grouw 2014). The large number of white individuals was presumably due to an inheritable form of the condition (Hume & van Grouw 2014), probably linked to a small founding population. Based on a middle toe that is shorter than the tarsus, close proximity geographically, the fact that progressive greying is not uncommon in *P. p. melanotus*, and that Lord Howe and Norfolk have both been naturally re-colonised by this subspecies, we suggest it is more likely that *P. albus* derived from Australian / New Zealand *P. p. melanotus*, rather than Philippine *P. p. pulverulentus*.

Garcia-R. & Trewick (2015) were unable to retrieve amplifiable DNA from the Liverpool specimen, but our data suggest that it also originated on Lord Howe Island. The distribution of blackish-blue feathers on the head and neck and purple-blue feathers on the upperparts of the Liverpool specimen enabled us to reconstruct the purple-blue plumage variant of *P. albus*, which demonstrates that this coloration was unique in *Porphyrio* (Fig. 21). The Liverpool specimen was also a younger bird than that of Vienna (see above).

It appears that the wealth of illustrative and documentary evidence made available to 18th- and 19th-century scientists, some of it riddled with errors, clearly muddled the provenance of Lord Howe Gallinule. However, our data show that the Liverpool specimen was collected on Lord Howe along with the Vienna bird between March and May 1788, and that the former differs from the Vienna specimen in being younger in age and preserving some of the original purple-blue coloration.

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References:

Austin, H. W. 1955. Classified summarised notes. *Notornis* 6: 85–108.

Barton, C. B. 1889. *History of New South Wales from the records*, vol. 1. Sydney.

Bassett-Hull, A. F. 1909. The birds of Lord Howe and Norfolk Islands. *Proc. Linn. Soc. NSW* 34: 636–693.

Blackburn, D. 1934. Letters of David Blackburn. *J. Roy. Austral. Hist. Soc*. 20: 318–334.

Bladen, F. M. 1901. Notes on the Life of John Hunter, Admiral, Governor of New South Wales. *J. Proc. Austral. Hist. Soc*. 1(3): 21–27.

Bowes Smyth, A. [1787–89]. Journal of Arthur Bowes Smyth, March 22, 1787–August 1789. MS. Mitchell Library, Sydney.

Buller, W. L. 1888. *A history of the birds of New Zealand*, vol. 2. Second edn. London.

Buller, W. L. 1905. *Supplement to the birds of New Zealand*, vol. 1. London.

Cheke, A. S. & Hume, J. P. 2008. *Lost land of the Dodo*. A. & C. Black, London.

Christian, M. L. 2005. *Norfolk Island … the birds.* Green Eyes, Norfolk Island.

Forbes, H. O. 1901. Note on Lord Stanley's Water Hen. *Bull. Liverpool Mus*. 3(2): 62–68.

Foulis, J. 1853 [1851]. Statement of circumstances in reference to Lord Howe's Island, situated off the coast of New South Wales, between the heads of Port Jackson and Norfolk Island. *Votes and Proceedings of the Legislative Council, Sydney*, 268A 1853.

Garcia-R., J. C. & Trewick, S. A. 2015. Dispersal and speciation in purple swamphens (Rallidae: *Porphyrio*). *Auk* 132: 140–155.

Gilbert, T. 1789. *Voyage from New South Wales to Canton in the year 1788, with views of the islands discovered*. J. Debrett, London.

Gray, G. R. 1844. Birds of New Zealand. Pp. 1–39 *in* Richardson, J. & Gray, J. E. (eds.) *Voyage of the Erebus & Terror*, vol. 1. E. W. Janson, London.

Gray, G. R. 1862. A list of birds of New Zealand and the adjacent islands. *Ibis* 4: 214–254.

Greenway, J. C. 1958. *Extinct and vanishing birds of the world*. American Committee for International Wild Life Protection, New York.

Greenway, J. C. 1967. *Extinct and vanishing birds of the world*. Second edn. Dover, New York.

van Grouw, H. 2012, What colour is that sparrow? A case study: colour aberrations in the House Sparrow *Passer domesticus*. *Intern. Stud. Sparrows* 36: 30–55.

van Grouw, H. 2013. What colour is that bird? The causes and recognition of common colour aberrations in birds. *Brit. Birds* 106: 17–29.

van Grouw, H. 2014. Some black-and-white facts about the Faeroese white-speckled Common Raven *Corvus corax varius*. *Bull. Brit. Orn. Cl.* 134: 4–13.
Hindwood, K. A. 1932. An historic diary: the journal of the voyage of the Lady Penrhyn 1787-89. *Emu* 32: 17–29.
Hindwood, K. A. 1940. The birds of Lord Howe Island. *Emu* 40: 1–86.
Hindwood, K. A. 1964. George Raper: an artist of the First Fleet. *J. Proc. Roy. Austral. Hist. Soc.* 50: 32–57.
Hindwood, K. A. 1965. John Hunter: a naturalist and artist of the First Fleet. *Emu* 65: 83–95.
Holdaway, R. N. & Anderson, A. 2001. Avifauna from the Emily Bay settlement site, Norfolk Island: a preliminary account. *Rec. Austral. Mus.* (*Suppl.*) 27: 85–100.
Hume, J. P. 2007. Reappraisal of the parrots (Aves: Psittacidae) from the Mascarene Islands, with comments on their ecology, morphology and affinities. *Zootaxa* 1513: 1–76.
Hume, J. P. & van Grouw, H. 2014. Colour aberrations in extinct and endangered birds. *Bull. Brit. Orn. Cl.* 134: 168–193.
Hume, J. P. & Walters, M. 2012. *Extinct birds*. T. & A. D. Poyser, London.
Hume, J. P. & Winters, R. 2015. Captive birds on Dutch Mauritius: bad-tempered parrots, warty pigeons and notes on other native animals. *Hist. Biol.* 8: 812–822.
Hunter, J. 1788–90. Birds & flowers of New South Wales drawn on the spot in 1788, '89 & '90. MS. Rex Nan Kivell Collection NK2039. National Library of Australia, Canberra.
Hutton, I. 1991. *Birds of Lord Howe Island, past and present*. Lithocraft Graphics, South Melbourne.
Iredale, T. 1910. An additional note on the birds of Lord Howe and Norfolk Islands. *Proc. Linn. Soc. NSW* 35: 773–782.
Latham, J. 1790. *Index ornithologicus, sive systema ornithologiae*. Leigh & Sotheby, London.
Latham, J. 1801. *General synopsis of birds*, suppl. II. Leigh, Sotheby & Son, London.
Livezey, B. C. 2003. *Evolution of flightlessness in rails (Gruiformes: Rallidae): phylogenetic, ecomorphological, and ontogenetic perspectives*. *Orn. Monogr.* 53.
Macinnis, P. 2012. *Curious minds: the discoveries of Australian naturalists*. National Library of Australia, Canberra.
Mathews, G. M. 1910. *Birds of Australia*, vol. 1. H. F. & G. Witherby, London.
Mathews, G. M. 1928. *The birds of Norfolk and Lord Howe Islands and the Australian South Polar quadrant*. H. F. & G. Witherby, London.
Mathews, G. M. 1936. *A supplement to the birds of Norfolk and Lord Howe Islands*. H. F. & G. Witherby, London.
Mayr, E. 1941. Taxonomic notes on the birds of Lord Howe Island. *Emu* 40: 321–322.
Nelson, E. C. 1998. John White's journal of a voyage to New South Wales (London, 1790): bibliographic notes. *Arch. Nat. Hist.* 25: 109–130.
Nichols, D. 2006. *Lord Howe Island rising*. Tower Books, Frenchs Forest.
Pearce, B. 1989. *Australian artists, Australian birds*. Angus & Robertson, Sydney.
Pelzeln, A. 1860. Zur ornithologie der Insel Norfolk. *Sitz.- Ber. Akad. Wissen. Wein* 41: 319–332.
Pelzeln, A. 1873. On the birds in the Imperial Collection at Vienna obtained from the Leverian Museum. *Ibis* 15: 14–54.
Percival, S. 1949. Phillip, Arthur (1738–1814), admiral, and first governor of New South Wales. *Dictionary of Australian biography*. Project Gutenberg, Australia.
Phillip, A. 1789. *The voyage of Governor Phillip to Botany Bay; with an account of the establishment of the colonies of Port Jackson & Norfolk Island; compiled from authentic papers, which have been obtained from the several departments, to which are added the journals of Lieuts. Shortland, Watts, & Capt. Marshall, with an account of their new discoveries*. John Stockdale, London.
Rabone, H. R. 1972. *Lord Howe Island: its discovery and early associations 1788 to 1888*. Australis, Sydney.
Ripley, S. D. 1977. *Rails of the world*. D. R. Godine, Boston.
Rothschild, W. L. 1907. *Extinct birds*. Hutchinson, London.
Rowley, G. D. 1875. *Ornithological miscellany*. Trubner and Co., Bernard Quaritch & R. H. Porter, London.
Salvin, O. 1873. Note on the *Fulica alba* of White. *Ibis* 15: 295.
Serle, P. 1949. "Hunter, John". *Dictionary of Australian biography*. Angus & Robertson, Sydney.
Sharpe, R. B. 1894. *Catalogue of the birds in the British Museum*, vol. 23. Trustees of Brit. Mus., London.
Stanhope, P. H. 1861. *Life of the Right Honourable William Pitt*, vol. 1. J. Murray, London.
Taylor, B. & van Perlo, B. 1998. *Rails: a guide to the rails, crakes, gallinules and coots of the world*. Pica Press, Robertsbridge.
Temminck, C. J. 1820. *Manuel d'ornithologie, ou tableau systématique des oiseaux qui se trouvent en Europe*. Second edn. H. Cousin & E. d'Ocagne, Paris.
Wheeler, A. & Smith, B. (eds.) 1988. *The art of the First Fleet and other early Australian drawings*. Yale Univ. Press, New Haven, CT & London.
White, J. 1790. *Journal of a voyage to New South Wales*. J. Debrett, London.

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