The Spotted Green Pigeon *Caloenas maculata*: as dead as a Dodo, but what else do we know about it?

by Hein van Grouw

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Summary.—Described in 1783 and since then re-examined by many notable ornithologists, the single specimen known as the 'Spotted Green Pigeon' *Caloenas maculata* in the collections of the World Museum, Liverpool, has always been a mystery. No-one has ever doubted that it is a pigeon, and many researchers were convinced it was a distinct species. Although its taxonomic status remained unclear, it was officially declared extinct by BirdLife International in early 2008. Recent DNA analysis has now revealed that Spotted Green Pigeon can indeed be considered a distinct species within the extended Dodo *Raphus cucullatus* clade of morphologically very diverse pigeon species. Most members of this clade exhibit terrestrial or semi-terrestrial habits. Further morphological research into this unique specimen, initiated by the World Museum, demonstrates that Spotted Green Pigeon, in contrast to its fellow clade members, may have possessed strongly arboreal habits.

The Spotted Green Pigeon *Caloenas maculata*, represented by a single specimen held in the scientific collections of the World Museum, Liverpool, has always baffled ornithologists. Although its provenance is unknown, the confusion has mainly centred on whether it is a valid species; that the specimen is a pigeon has never been questioned. Because of its green-glossed plumage and slightly elongated hackles, it is usually assumed to be allied to Nicobar Pigeon *C. nicobarica*, although they share few other morphological features.

The possibility it being an aberrant individual of a known species or even a hybrid was often suggested in the past. Although Nicobar Pigeon seemed to be a good candidate as one of the parent species, no other known pigeon species could have been responsible for the remarkable spotting. Recent DNA analysis has now revealed a new and unknown DNA lineage for Spotted Green Pigeon with close affinities to Nicobar Pigeon, suggesting that it was correctly placed in *Caloenas* (Heupink *et al*. 2014). Its lineage cannot be explained by hybridisation, as the specimen's DNA is maternally inherited and does not mix with paternal DNA (T. H. Heupink *in litt*. 2013), so even if the specimen was a hybrid, this would mean that the mother (and her mother) was a new species close to *Caloenas*.

The DNA results have revealed that Spotted Green Pigeon is indeed a valid taxon, bringing the number of described species of *Caloenas* to three. The third species, described from sub-fossil remains, is Kanaka Pigeon *C. canacorum*, which is estimated to have been *c*.25% larger than Nicobar Pigeon, and occurred on New Caledonia and Tonga (Balouet & Olson 1989). The remains suggest that this species had no reduction in its ability to fly. As nothing is known about the feet, no tarsus or toe remains having being found, we know nothing concerning its behaviour (arboreal or terrestrial). Also, of course, external characters such as colour, markings and biometrics remain unknown.

Given, therefore, that of the genus *Caloenas* we have only the Nicobar Pigeon for direct comparison, the external morphology of Spotted Green Pigeon more closely resembles that of imperial pigeons *Ducula*. It may therefore have had a comparable behaviour and ecology

to these strongly arboreal species, which differ from those of the more terrestrial Nicobar Pigeon.

History of the specimen(s)

The first description of the species was in 1783 by John Latham (1740–1837) in *A general synopsis of birds*. Latham named it the Spotted Green Pigeon: 'Length twelve inches. Bill black, tipped with pale yellow: general colour of the plumage dark green, and glossy: the head and neck are darker than the rest, and of one plain colour: the feathers of the neck long and narrow, like the hackles of a Cock; every feather of the wings and scapulars tipped with a spot of very pale cinereous white, with a point running upwards, somewhat triangular: quills and tail black; the feathers of the first tipped with cinereous white, those of the last with ferruginous white, and even at the end: belly, thighs, and vent, dusky black: the legs are brown, and the shins covered half way with downy feathers: claws black.'

At the end of the description Latham (1783) added: 'In the collection of Major Davies. I likewise met with a specimen in that of Sir Joseph Banks. Native place uncertain.' This strongly suggests that Latham must have seen two Spotted Green Pigeon specimens; one belonging to Davies, the other to Joseph Banks.

Little is known about the collection of Major Thomas Davies (*c*.1737–1812), an army officer and topographical painter. Topographical drawing/panting was the only contemporary means of making a rapid and accurate visual record of military value and, as such, required the utmost attention to detail and fidelity to nature (Hubbard 1983). This may explain Davies' interest in birds. Between 1757 and 1790, he accompanied several expeditions as an army artist, mainly to Canada and North America (Hubbard 1983), during which he cultivated an interest in birds and taught himself to collect and prepare specimens (Davies 1770). Although he never visited the South Pacific, he nevertheless had contacts in New South Wales: Governor Philip, Colonel Nepean and Governor King all sent him specimens for his collection (Davies 1798, 1802), so his Spotted Green Pigeon may have originated from that region of the world.

After Davies' death his collection was auctioned in London (6 and 8 June 1812) and the Spotted Green Pigeon was bought by Lord Edward Smith Stanley (1775–1851), the 13th Earl of Derby, who held a substantial menagerie and private collection at his family seat, Knowsley Hall, just outside Liverpool. In Lord Stanley's personal copy of *A general synopsis of birds* (held in the World Museum, Liverpool), against Latham's statement, 'In the collection of Major Davies' there is an annotation, in Stanley's handwriting, 'now in mine'! It seems obvious from Latham's 1783 account that his description was entirely based on Davies' specimen, this therefore being recognised as the holotype of the species. In his collection's manuscript catalogue (also at the World Museum), Lord Stanley registered the specimen as, '324, Spotted Green Pigeon, *Columba maculata*' with the country of origin being given as 'uncertain'. His collection, originally known as the Knowsley Museum, came to the city of Liverpool by bequest in 1851. After its transfer it was known as the Derby Museum, the core of which later became the Liverpool Museum, now the World Museum, National Museums Liverpool.

The collection of Joseph Banks (1743–1820) was famous during his lifetime and included many specimens collected during Captain James Cook's three voyages around the world (1768–80). In 1792 Banks donated part of his collection to John Hunter (1728–93) and the rest to the British Museum. Following Hunter's death, his collection was purchased for the Company of Surgeons (which became the Royal College of Surgeons after 1800). These were later re-joined by some of the British Museum specimens, which had meanwhile been stored in a basement in a state of neglect and were purchased by the Royal College

of Surgeons in 1809. The specimens in Hunter's collection were numbered and, in 1806, catalogued under these numbers (Burton 1969).

The catalogue, Copy of Dr Shaw's catalogue of Natural History in the Hunterian Museum, is still present in the archives of the Royal College of Surgeons (ref. no. MS0471/2) and lists mainly spirit specimens. Only 87 'stuffed animals' are listed, both birds and mammals, but no *Columba maculata* is among them! The additional specimens acquired in 1809, however, were neither numbered nor catalogued, so their identification remains mysterious. Banks was, without doubt, the principal recipient of bird specimens collected on Cook's three voyages (Medway 2009) but, unfortunately, he appears to have placed little value in them, freely giving them away well before his more substantial donations to Hunter and the British Museum in 1792. Neither did he make a serious attempt to catalogue his material. The only extant catalogues appear to have been completed between *c*.1776 and 1782, and these only mention specimens acquired during the Cook voyages (Medway 1979, 2009). From the existing literature, there is no indication that a bird resembling a Spotted Green Pigeon was ever collected during one of the voyages (Whitehead 1969, Medway 1979, 2009). If Banks did indeed possess a Spotted Green Pigeon specimen, he may have received it from someone else, perhaps from the same source as Major Davies? In sum, Latham's statement is the only clue that Banks may ever have owned a specimen of Spotted Green Pigeon, or that a second specimen ever existed.

Latham made it clear that he did not know where the Spotted Green Pigeon specimens came from, and never speculated as to their provenance. Later authors, however, based on the relationship between Davies, Banks and Cook, made the assumption that the birds came from the South Pacific, although there is no evidence in the literature that a bird even faintly resembling a Spotted Green Pigeon was received by Banks after Cook's third voyage (Medway 1979, Stresemann 1949, 1950, 1953). However, Davies *did* have contacts in that region and, moreover, contacts that provided him with bird specimens.

Besides the two specimens he had seen earlier, Latham, in his *A general history of birds* (1823), also mentioned a drawing: 'We have only seen two specimens; one in the collection of Gen. [*sic*] Davies, the other in possession of Sir Joseph Banks. In a drawing of one at Sir Ashton Lever's, the end of the tail is deep ferruginous.'

The celebrated collection of Sir Ashton Lever (1729–1788) was housed in a museum named the Holophusicon and was opened to the public in February 1775. However, due to financial pressures, in March 1786 Lever was forced to sell his entire museum by public lottery. Only 8,000 tickets were sold. The winning ticket belonged to James Parkinson and on 1 September 1787 the museum was closed and Parkinson moved the collection to a new building, changing its name from the Holophusicon to the Leverian Museum (Kaeppler 2011).

Among the many artists who used the Leverian collection to produce illustrations for scientific works, the most prolific was Sarah Stone, whose artistic career centred on the Holophusicon. She continued her association with the collection during Parkinson's ownership (Kaeppler 2011). Whoever executed the drawing referred to by Latham, it was probably based on a specimen. Latham himself also made many bird drawings from Lever's collection, reproduced as engravings in *A general synopsis of birds*.

Whether the pigeon drawing in Lever's collection was made from a specimen in his own possession, or another, is unknown. However, in *A general history of birds*, 40 years after his original description, Latham depicted a Spotted Green Pigeon (Fig. 1). Exactly when and where this illustration was produced is unknown, but it is unlikely to have been based on Davies' specimen as will be shown below. More likely is that he copied it from the drawing in Lever's possession, as the bird in Latham's picture also has a 'deep ferruginous' tail-band.

Although Latham's bird barely resembles a pigeon in shape, most of the morphological details are correct: the yellow bill tip, the pointed neck feathers, the greenish and spotted upperparts and the long tail. The long and spotted primaries and the rather pale-coloured underparts do not, however, match Davies' specimen in Liverpool, but this may not have been an error after all, as will be presently explained.

History of the species

Gmelin (1788) used Latham's (1783) description to give the species a scientific name *Columba maculata* (meaning 'spotted pigeon'). Latham obviously accepted that name as he used it in his *Index ornithologicus* (1790), providing a much shorter description (originally in Latin): '*C. maculata*: Dark-green pigeon, with the body above spotted with whitish, the abdomen dusky, and the tail black, with a ferruginous tip.'

Temminck (1813) mentioned *Columba maculata* but, in addition to copying Latham's (1790) description, he questioned its status as a species. Stephens (1819) also mentioned the Spotted Green Pigeon, copying both of Latham's descriptions. Erroneously he called it *Columba Picazuro,* but this must have been a slip of the pen as in the text he refers to *Columba maculata* in Latham (1790), Gmelin (1788) and Temminck (1813). Latham again mentioned the Spotted Green Pigeon in *A general history of birds* (1823), this time also providing an illustration (Fig. 1). The English description is almost identical to the 1783 text, except for the addition of a note that the skin around the eyes is almost naked.

Wagler (1827) did not see the specimen, but he did mention *Columba maculata* based on Latham's and Gmelin's works, adding that, according to those descriptions, it might well be a juvenile *Columba gallus* (a synonym of *Caloenas nicobarica*). In Wagler's time the genus *Caloenas* had not been described (*Caloenas* G. R. Gray, 1840). A year earlier, Stephens (1826) placed *maculata* in *Ptilinopus*, suggesting India as its country of origin.

Salvadori (1893) included *Columba maculata* in the appendix among 'the doubtful species of Pigeons, which have not yet been identified', and repeated Latham's (1783) description. However, according to Forbes (1898), Spotted Green Pigeon was without doubt a *Caloenas* and a species: 'from the fact that there were two specimens in existence … we are inclined to the belief that the *Columba maculata* of Gmelin, should be recognised as a good species *Caloenas maculata*.'

Rothschild & Hartert (1901) briefly mentioned the species in a footnote related to Nicobar Pigeon, dismissing Wagler's species identification: 'The most peculiar *Caloenas maculata*—correctly identified as a *Caloenas* by Wagler—is certainly not the young of *C. nicobarica*, as the young are almost quite like the adults, and not spotted. It is extraordinary that the home of this bird is not yet discovered, and we suggest the possibility—although there were two specimens—that it is an abnormity.'

Also in a footnote, Peters (1937) stated that 'the Spotted Green Pigeon of Latham has never been satisfactorily identified with any known species', and that Rothschild & Hartert believed it to belong to the genus *Caloenas*.

In 1953 Reginald Wagstaffe, Keeper of Vertebrate Zoology at the Liverpool Museum, asked Captain C. H. B. Grant for his opinion of the presumed type specimen of *Caloenas maculata*. Grant, an Honorary Associate of the British Museum (Natural History) replied, after seeing the specimen: 'I would not hesitate to say that it … is adult, and has nothing to do with *C. nicobarica* … I do not think it is anything but a good and distinct species. It may have come from some remote island and maybe is now extinct' (letter in Liverpool Museum archive).

Figure 1. Drawing (engraving) by Latham of Spotted Green Pigeon *Caloenas maculata* in *A general history of birds* (1823), presumably based on a picture in Lever's possession; Lever's picture may have been based on a third specimen.

Figure 2. Depiction of Spotted Green Pigeon *Caloenas maculata* in Forbes (1898), made by Joseph Smit and based on how Forbes assumed the species looked like.

Figure 3. Depiction of Spotted Green Pigeon *Caloenas maculata* in Fuller (2002) by Brian Small and based on how Fuller assumed the species looked like (courtesy of Lynx Edicions, Barcelona)

Figure 4. Depiction of Spotted Green Pigeon *Caloenas maculata* in Gibbs *et al*. (2001), made by John Cox and based on how Gibbs assumed the species looked like; perching on a branch is probably more accurate than walking on the ground (courtesy of Pica Press / Bloomsbury, London)

Whether it was because of Grant's opinion or not, Wagstaffe (1978) considered it a valid species in the type catalogue of the Liverpool museum as he stated '…there is no doubt that it represents a perfectly recognisable form, presumably now extinct.'

Nevertheless, Spotted Green Pigeon is not mentioned in the first edition of *Extinct birds* (Fuller 1987) but it does appear in the second (2001), before *Caloenas maculata* was officially declared extinct by BirdLife International. Ignoring the fact that Latham (1783) named it Spotted Green Pigeon, and that it has been known by that name ever since, Fuller referred to it as 'Liverpool Pigeon' and, in his own words stated that '… there is no reason to suppose it other than a valid—and now extinct—species from an undetermined South Pacific island.'

Gibbs *in* Gibbs *et al*. (2001) examined the specimen and was also convinced of its specific status. However, he questioned whether it should be considered a *Caloenas* as, aside from the glossy green plumage and elongated neck feathers, the long tail, slender bill and delicate legs bear no resemblance to Nicobar Pigeon.

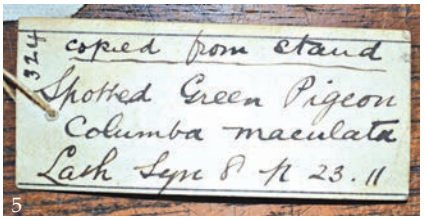
Still rejecting the name given by Latham, Fuller (2002) again called it Liverpool Pigeon. Obviously based on Fuller's misnomer, BirdLife International declared the 'Liverpool Pigeon' officially extinct in 2008. On the species factsheet on their website (October 2014), they further erred by stating that the extant specimen was collected between 1783 and 1823. Finally, Hume & Walters (2012) mentioned the species with its correct English name, but did not contribute any new information. They referred to the Spotted Green Pigeon as an enigma, which indeed is precisely what it remains.

The Spotted Green Pigeon re-examined

So, although much has been written about Spotted Green Pigeon, very little has *actually been said*. Latham described the species with access to just two specimens, and most subsequent publications are almost entirely based on Latham's descriptions. Even those authors who examined the specimen had nothing new to add to earlier descriptions. However, since Forbes (1898), some discrepancy as to the species' presumed appearance has arisen. In Latham's descriptions, the presence of a knob at the base of the bill, similar to that on the bill of a Nicobar Pigeon, is not mentioned; neither is one shown in the accompanying plate. Forbes on the other hand, convinced that the bird should be classified as a *Caloenas*, argued '…it has the frontal knob apparently fully developed.' He must have specifically instructed Joseph Smit, who produced the illustration of the bird, reproduced as a hand-coloured lithograph for Forbes' publication, to add a knob, despite that the lack of evidence that the specimen ever had one (Fig. 2). Although Fuller (2001) apparently saw the specimen, and must have noticed the absence of any sort of protuberance, he also stated that the species has a knob at the base of the bill. B. J. Small, who drew the species for Fuller (2002), also added a knob (Fig. 3). Only J. Cox, who drew the bird for Gibbs (2001), and had also seen the specimen, correctly depicted the bird without a knob (Fig. 4).

Gibbs gives a thoroughly detailed description of the specimen, although he too, as will be demonstrated below, appears to have missed certain details when he wrote: '….short and rounded wings in combination with a long tail' (Gibbs *et al*. 2001).

The specimen was originally mounted, and the taxidermy was probably carried out by Davies himself. Shortly after it was received from Lord Stanley by the Liverpool Museum it was re-prepared into a study skin, and the data from the stand were copied to a label (Fig. 5). Besides this label, the specimen also bears a (presumably more recent) red type label, a paper label and a textile label. The type label and the paper label are almost certainly from the same period, as the handwriting is the same on both. The textile label is probably the oldest of the three, based on the fact it has 'E. Mus. Derby' for the number pre-printed on it, and no 'Presented by'. This may indicate that these labels were produced during the



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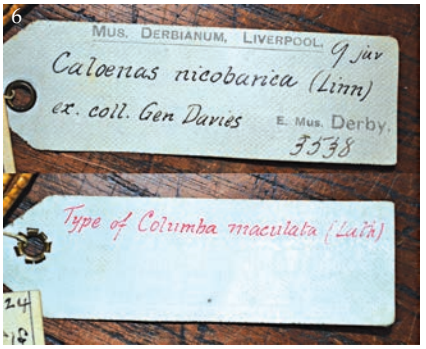

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Figure 5. First museum label after the Spotted Green Pigeon *Caloenas maculata* specimen was re-prepared into a skin (Hein van Grouw)

Figure 6. Textile label revealing that a former curator did not believe in the Spotted Green Pigeon *Caloenas maculata* as a species (Hein van Grouw)

Figure 7. Remains of red paint around the right eye socket suggests that the taxidermist thought (knew?) that Spotted Green Pigeon *Caloenas maculata* had red eyes (Hein van Grouw)

Figure 8. The feathers with the buff-coloured spots are clearly more worn than those with white spots (Hein van Grouw)

Figure 9. Rump feathers, from left to right, of Spotted Green Pigeon *Caloenas maculata* (54 mm), Polynesian Imperial Pigeon *Ducula aurorae* (49 mm) and Nicobar Pigeon *Caloenas nicobarica* (38 mm) (Hein van Grouw)

Figure 10. Polynesian Imperial Pigeon *Ducula aurorae*, immature plumage (dark specimen) BMNH 1935.5.27.2 and adult plumage BMNH 1928.10.27.24 (Harry Taylor / © Natural History Museum, London)

period when the museum contained only specimens from Lord Stanley, while in later years, when more new material was being acquired, labels were needed to mention other donors and new registration numbers. The curator who wrote the textile label apparently did not believe that Spotted Green Pigeon was a genuine species as he identified it as a juvenile Nicobar Pigeon. The name *Columba maculata* he added on the back of the label, suggesting it was a synonym of the latter (Fig. 6).

External features

When the specimen was re-prepared as a skin, the artificial eyes were removed. Given the age of the specimen, glass eyes were not yet available. The fake eyes may have been made of wax as, according to Davies' (1770) own account, this method was used in those days: '….The eyes will be best made by dropping drops of black sealing wax on a card of the size of the natural ones; the card must be cut something larger than the wax to prevent their falling out of the head...'.

After the fake eyes were fixed in the specimen, whether they were wax or not, they must have been painted in the required colour. As some red paint still remains around the right eye socket (visible after carefully removing the kapok used to fill the ocular orbits) it can be assumed that the taxidermist wanted it to have red eyes (Fig. 7). Whether or not this was based on knowledge, the true colour having been recorded while the specimen was alive, or purely an exercise of artistic licence, is unknown. Remarkably, however, the bird pictured by Latham in 1823, which was not apparently based on Davies' specimen, has red eyes too.

When I examined the specimen in November 2012 it was evident that its feet had been attached the wrong way round—the left leg where the right should be and vice versa. Clearly they were detached in the past, probably when it was re-prepared as a skin. However, the feet themselves appeared to be original ones belonging to the specimen. The long toes, large claws and relatively short tarsus are typical of arboreal species, such as imperial pigeons *Ducula*, in contrast to the shorter claws and longer tarsus of the largely ground-dwelling Nicobar Pigeon. In Spotted Green Pigeon (at least, in the way the legs *should* be attached), the base of the tarsus is slightly feathered, especially on the inside. That the illustration in Forbes shows the feathering on the *outside* of the tarsus is evidence that the feet must have been attached wrongly before 1898.

The conspicuous triangular spotting is remarkable, but not unique, in the Columbidae. The nominate races of Spot-winged Pigeon *Columba maculosa* and Speckled Pigeon *C. guinea* possess similar spotting, the result of a natural lack of melanin deposition during early feather development.

The yellow-buff colour of the spots in Spotted Green Pigeon is possibly the result of staining during life, or perhaps represents a different plumage, as these feathers are all very worn, while less worn feathers have clear white tips (Fig. 8), suggesting fresher plumage. In general, the plumage exhibits substantial wear and the overall coloration of the underparts is rather dull. The green iridescence is not as strong and glossy as that of an adult of any other species with similar plumage—e.g. Nicobar Pigeon and the many imperial pigeons—and more closely resembles the colour of juveniles of these species. Although the plumage is not suggestive of a juvenile, it is does not appear to be adult either as will be demonstrated in the Discussion.

Although not scientifically underpinned, the feel of the plumage is remarkably soft, and in that respect rather unpigeon-like. Also, the body feathers are rather long in relation to the size of the bird, which is probably, at least partially, the reason for their softness (Fig. 9). Unlike Nicobar Pigeon, the hackles are not extra-long in proportion to the rest of the body

plumage; it is the pointed shape that gives the elongated impression. In microstructure, the feathers do not differ from those of other pigeon species.

Another remarkable feature is the pigmentation. The body feathers of Spotted Green Pigeon are heavily pigmented all over (except, of course, the tips; Fig. 9). Normally, birds with dark body plumage have paler down feathers, but in this case the down is also heavily pigmented. This is usually only seen in aberrant, melanistic, dark plumage (pers. obs.).

Perhaps the most unexpected finding is that the wings were not as short and rounded as they at first appear. Close examination of the specimen reveals that in both wings the five outer primaries are missing. They have not been clipped or broken off as there are no quill remains present; the primaries must have been removed (pulled out) just before or after death. Based on the length and space between the remaining primaries one can estimate that the wing may have been *c*.50 mm longer (Table 1).

Discussion

That Spotted Green Pigeon did not have short, rounded wings makes it reasonable to believe it was not a ground-dwelling species after all. Although the total body length of a live bird cannot be reliably interpreted from a study skin—which may be stretched or compressed depending on the personal style of the taxidermist—overall, Spotted Green Pigeon appears to have been slightly smaller than the average Nicobar Pigeon (*cf*. Table 1). The body proportions, however, are totally different. The longer tail and shorter legs, in combination with the longest primaries reaching at least to the middle of the tail, suggest that in proportions and shape Spotted Green Pigeon was probably more comparable with the imperial pigeons *Ducula* spp. The feet, which are typical of fruit pigeon species foraging in trees, strengthen this argument. The coloured bill and presumably coloured eyes are also features of many fruit pigeon species, while the Nicobar Pigeon has a black bill and rather dark eyes. Dark eyes are a common feature in ground-dwelling species that feed mainly on the forest floor.

The green, metallic plumage of Spotted Green Pigeon does resemble that of Nicobar Pigeon, but is commonly found among imperial pigeons. Neither are the tapering hackles exclusive to Nicobar Pigeon. Different feather structure in the neck area is a rather common feature of the pigeon family and in *Ducula* it is clearly present in New Caledonian Imperial Pigeon *D. goliath*.

Different from all other *Ducula* species, the plumage of Polynesian Imperial Pigeon *D. aurorae* has the same softness as Spotted Green Pigeon, probably also due to its relatively long contour feathers. Interestingly, this species is unique among pigeons in having a distinct intermediate plumage between juvenile and adult (Gibbs *et al*. 2001): dull, sooty black-grey on the head, neck and underparts instead of a paler, ash-grey (Fig. 10). Although

TABLE 1
Measurements (mm) of Spotted Green Pigeon *Caloenas maculata* (taken by the author) compared to Nicobar Pigeon *C. nicobarica* and Pacific Imperial Pigeon *Ducula pacifica* (from Gibbs 2001). *Estimated wing length based on a full set of primaries (see main text).

Species	**Wing**	**Tail**	**bill**	**tarsus**
Nicobar Pigeon	243–264	71–85	21–25	30–44
Spotted Green Pigeon	225*	126	20	33
Pacific Imperial Pigeon	217–256	113–139	20–26	30–34

less extreme, Pacific Imperial Pigeon *D. pacifica* from the Cook Islands also has an indistinct post-juvenile immature plumage, before moulting to adult coloration. Given the overall appearance of the Spotted Green Pigeon specimen, especially the dull, brownish-black underparts (see above), it is possible that this species also had an immature plumage, and that this is an example of it. Adult Spotted Green Pigeon may have been brighter with paler underparts and whiter feather tips. So Latham's illustration (Fig. 1) may have been an accurate representation of an adult Spotted Green Pigeon. We now know that his depiction of longer wings was perfectly correct!

Conclusion

DNA demonstrates that Spotted Green Pigeon is sufficiently closely related to the Nicobar Pigeon to be placed in *Caloenas* (Heupink *et al*. 2014). Therefore the taxon lies in the extended Dodo *Raphus cucullatus* clade of morphologically very diverse pigeon species. This clade includes, in order of closeness to the Dodo and Rodrigues Solitaire *Pezophaps solitaria*, the genera *Caloenas*, *Goura* and *Didunculus* (Shapiro *et al*. 2002). Most of this clade show a characteristic mixture of terrestrial and arboreal traits, and exhibit a degree of affinity to islands. The same traits have been suggested for Spotted Green Pigeon. DNA prove the taxonomic relationships, but provide no information concerning the species' possible behaviour and ecology. Based on a morphological examination, however, it is probable that in both its appearance and ecology Spotted Green Pigeon was very much like imperial pigeons *Ducula* spp. Therefore it may have been almost entirely arboreal. That its provenance has never been discovered suggests a limited distribution typical of a small and remote oceanic island. Although presumably a strong flier, it may have been rather sedentary, avoiding prolonged flights over open water, like many *Ducula* species (Holyoak & Thibault 1984).

To date, it has been assumed that the ancestor of *Caloenas*, which was closely related to the ancestor of the Raphinae, had, aside from the ability to fly and an affinity for islands, semi-terrestrial habits. There is little we can learn from the incomplete sub-fossil remains of Kanaka Pigeon. Nicobar Pigeon is strongly terrestrial, spending most time foraging on the forest floor (Gibbs *et al*. 2001). Spotted Green Pigeon, however, shows all the characters of a strongly arboreal species and may even, like many other fruit pigeons, have kept exclusively to the dense canopy.

Whether Spotted Green Pigeon was indeed a *Caloenas* with appearance and habits suggestive of *Ducula* we shall probably never know. That the species does belong within the extended Dodo clade, a group of morphologically very diverse pigeon species, is certain.

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Address: Bird Group, Dept. of Life Sciences, The Natural History Museum, Akeman Street, Tring, Herts. HP23 6AP, UK, e-mail: h.van-grouw@nhm.ac.uk