# A new genus of frogmouth (Podargidae) from the Solomon Islands – results from a taxonomic review of *Podargus ocellatus inexpectatus* Hartert 1901

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The frogmouth taxon occurring on the Solomon Islands has been known as *Podargus ocellatus inexpectatus*, a subspecies endemic to four islands in the Solomon Islands of a species that also inhabits New Guinea and Australia. Our morphological, osteological and molecular studies support recognition of *inexpectatus* at the species level, and further reveal that it merits placement in its own genus, which we describe here. Compared with the two other extant podargid genera, *inexpectatus* does not seem to be more closely related either to *Batrachostomus* (confined to the Indo-Malayan faunal region) or to *Podargus* of the Papuan–Australian faunal region. We also review the specimen history of the Solomon Islands Frogmouth, and discuss what little is known about its ecology, natural history and distribution.

The archipelagos in northern Melanesia (the Solomon Islands and Bismarck Archipelago) harbour the most diverse avifaunas in the tropical Pacific (Mayr & Diamond 2001). Despite expansive radiations of birds at the species level, these islands, which have never been connected to the continental terrains of New Guinea and Australia, have relatively few endemic genera compared with either the more remote Hawaiian Islands or with the very old Gondwanan islands of New Zealand and New Caledonia. The endemic non-passerine genera in northern Melanesia are the monotypic owl *Nesasio solomonensis*, the extinct columbid *Microgoura meeki* and two undescribed, extinct genera of Columbidae (Steadman 2006). Each of these genera is found in a group of islands in the Solomons that was formerly joined as the large Pleistocene island called Greater Bougainville (Spriggs 1997) or Greater Bukida (Mayr & Diamond 2001).

With rising sea-levels during the Holocene, Greater Bukida became divided into the modern islands of Buka, Bougainville, Choiseul, Isabel, San Jorge and some smaller satellite islands (Fig. 1).

The avifauna of the Solomon Islands is derived largely from the nearby 'mainlands' of Australia and New Guinea (Mayr & Diamond 2001). One taxon in the Solomon Islands that has, up to now, been unquestionably associated with the Papuan and Australian avifauna is the Marbled Frogmouth (*Podargus ocellatus*). According to standard references, *P. ocellatus* occurs in eastern and northern Australia, New Guinea, and land-bridge islands off New Guinea, but then skips the large islands of the Bismarcks (which lie between New Guinea and the Solomons) only to be found again on the islands that once comprised Greater Bukida in the Solomons, as the endemic subspecies *P. o. inexpectatus*. Here we re-examine the taxonomic position of *P. o. inexpectatus*, using multiple character sets, including plumage and morphometrics, osteology, and molecular genetics. We demonstrate that *inexpectatus* differs markedly from *P. ocellatus* and from all other frogmouths, whether in the genus *Podargus* or *Batrachostomus*.

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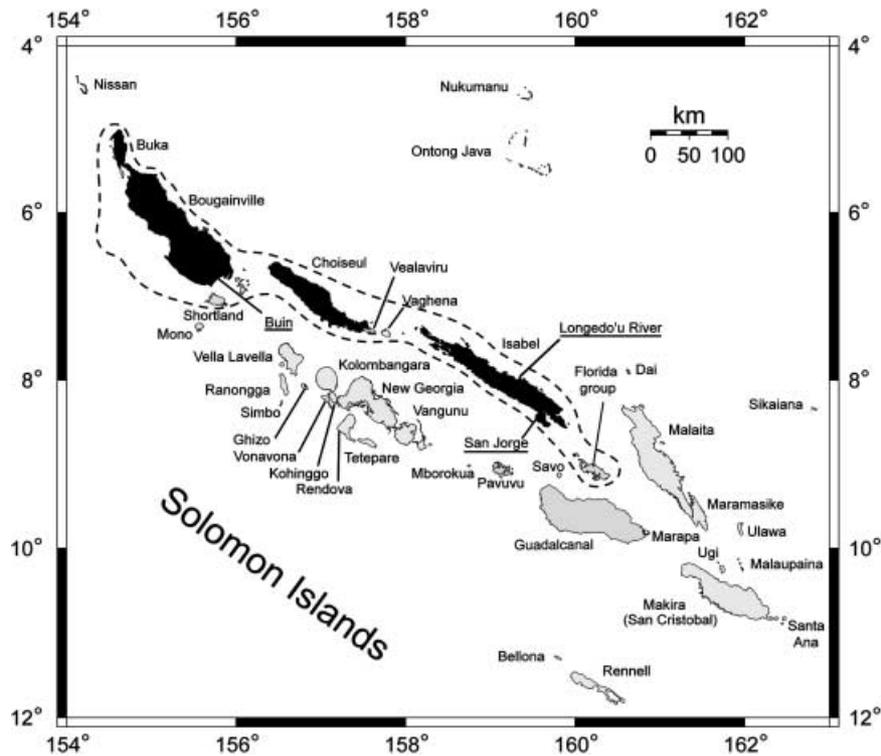
**Figure 1.** The Solomon Islands and adjacent areas, showing the distribution (darkened islands) and known collecting localities (underlined sites) of the frogmouth *Rigidipenna inexpectata*. Dashed line shows extent of the late Pleistocene (*c.* 18 000 years BP) island Greater Bukida (Mayr & Diamond 2001).

## SYSTEMATICS

Order *incertae sedis* (typically placed in Caprimulgiformes)
Family Podargidae
*Rigidipenna* gen. nov.

## TYPE SPECIES

*Podargus inexpectatus* Hartert, 1901.

## DIAGNOSIS

A large podargid with eight rectrices, not ten as found in all species of *Podargus* and *Batrachostomus* (Fig. 2). Outer rectrices generally very coarse, with 9 barbs/ cm compared with approximately 15 barbs/cm in other genera (Fig. 3). The central rectrices are broad, coarse and stiff with rounded tips, further separating it from *Podargus*, which generally has narrower, softer and more pointed central rectrices. As in *Podargus*, sexes differ slightly in plumage coloration, with the male having darker dorsal plumage than the female (such dimorphism more extreme in *Batrachostomus*).

Unique osteological characters are as follows. Coracoid: processus procoracoideus deep. Sternum: processus craniolateralis wide and irregularly tapering in lateral aspect; carini sterni dramatically expanded over dorsal half in anterior aspect. Humerus: proximal part of fossa musculo brachialis gradual and shallow. Ulna: tuberculum ligamentum collateralis ventralis protrudes gradually. Carpometacarpus: proximal tubercle on os metacarpale minus large, distad. Femur: proximo-ventral surface of corpus femoris convex; condylus lateralis and trochlea fibularis shallow and blunt in lateral aspect (Fig. 4). Tarso-metatarsus: cotyla medialis barely flared from shaft in acrotarsial aspect (Fig. 4); trochlea metatarsi IV shallow with relatively flat plantar surface in lateral aspect.

## ETYMOLOGY

*Rigidipenna* is formed from the Latin words *rigidus* (stiff, hard, inflexible) and *penna* (feather). The name refers to the distinctively stiff rectrices. *Rigidipenna* is feminine and the scientific name therefore becomes

**Figure 2.** *Rigidipenna inexpectata* (UF 40210; B,E), *Batrachostomus hodgsoni* (UMMZ 142642; A,D) and *Podargus ocellatus ocellatus* (UMMZ 215554; C,F). Top three, ventral view; bottom three, dorsal view.



**Figure 3.** Tails of *Rigidipenna inexpectata* (UF 40210; middle), *Batrachostomus hodgsoni* (UMMZ 142642; top) and *Podargus ocellatus ocellatus* (UF 41456; bottom). Bird's right side of tail in this view spread to show all rectrices.

*Rigidipenna inexpectata*. We propose the English name Solomon Islands Frogmouth.

## GEOGRAPHICAL RANGE

*Rigidipenna inexpectata* occurs only in the Solomon Islands (Fig. 1), where it has been recorded in primary and secondary forest to 500 m elevation on the islands of Bougainville, Choiseul, Isabel and San Jorge (Hadden 1981: 66, our specimen data). Hadden (2004: 157) noted without details that it had been 'recently reported for the first time on Buka.'

## TAXONOMY AND SPECIMEN HISTORY

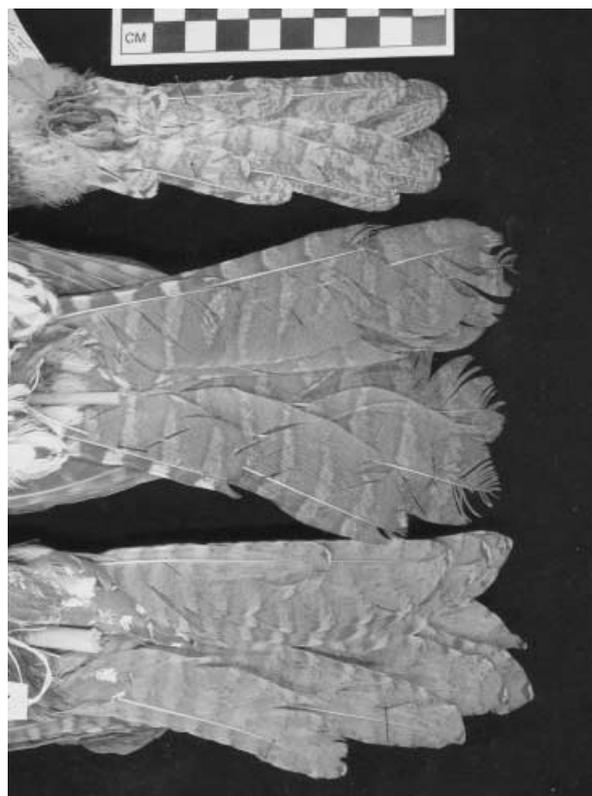The family Podargidae was established by Bonaparte (1838) to accommodate the genus *Podargus* Vieillot, 1818 (three Papuan–Australian species) and the genus *Batrachostomus* Gould, 1838 (about nine species from tropical mainland Asia and the Greater Sundas). This treatment of two genera within the Podargidae has generally continued to the present day (e.g. Cleere 1998, Holyoak 2001), although the two genera have also been separated at the subfamilial (Holyoak 1999) or familial level (Sibley *et al.* 1988).

The three species of *Podargus* currently recognized are the Papuan Frogmouth *P. papuensis*, Tawny Frogmouth *P. strigoides* and Marbled Frogmouth *P. ocellatus*. The last is a polytypic species that exhibits far more geographical variation than the other two. The six taxa that have been treated as subspecies of Marbled Frogmouth are *P. o. ocellatus* (New Guinea and offshore islands), *P. o. marmoratus* (northeastern Australia), *P. o. plumiferus* (coastal eastern Australia), *P. o. meeki* (Sudest Island in the Louisiade Archipelago), *P. o. intermedius* (Trobriand Islands and the D'Entrecasteaux Archipelago) and *P. o. inexpectatus* (Solomon Islands).
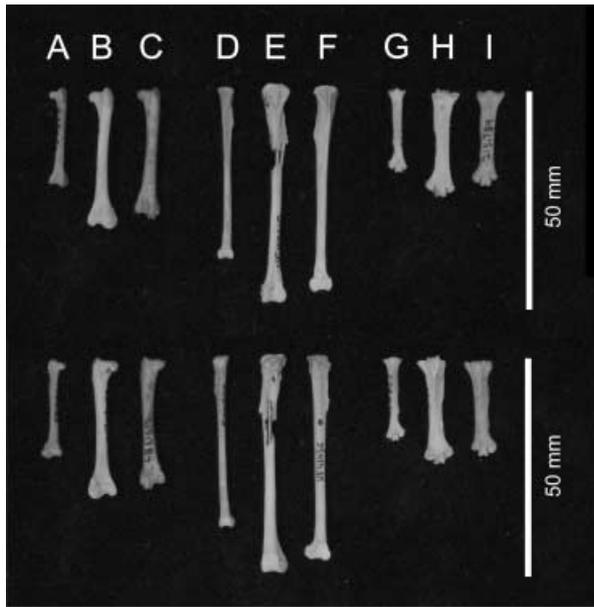
**Figure 4.** Hindlimb skeletal elements of podargids (A–C, femur; D–F, tibiotarsus; G–I, tarsometatarsus). A,D,G, *Batrachostomus septimus* UMMZ 233065; B,E,H, *Rigidipenna* UF 40210; C,F,I, *Podargus ocellatus ocellatus* UMMZ 215784. F is from the right side. All others are from the left side.

As was common in the 19th century, subspecies of *Podargus ocellatus* were originally described as full species, with *P. inexpectatus* the last to be named (Hartert 1901). A few years later, Mathews (1913) placed *P. marmoratus* in a poorly defined new genus (*Micropodargus*) that was said to differ from *Podargus* only in its much smaller size and stronger bill. Without explanation, Mathews (1927) subsequently treated six taxa, including *marmoratus* and *inexpectatus*, as races of *ocellatus* within *Micropodargus*. Peters (1940) treated *Micropodargus* as a synonym of *Podargus*, which has remained the sole genus for all Papuan–Australian–Oceanic frogmouths to the present day.

In addition to *Micropodargus*, three other generic names have been used but synonymized for species in *Podargus*, none of which was intended or previously used for *inexpectatus*. These are *Celuro* Jarocki, 1821 (for *Podargus strigoides*), *Cyphorhina* Lesson, 1843 (for *P. papuensis*) and *Megapodargus* Mathews, 1913 (for *P. papuensis*).

The Solomon Islands Frogmouth is poorly represented in museum collections; only 19 study skins have been located and examined (Table 1). The first specimen, a male taken on Bugotu (= San Jorge, a

**Table 1.** Summary of all known specimens of *Rigidipenna inexpectata*.

| Museum | Age | Date | Locality | Collector | Field no. | Notes |
|---|---|---|---|---|---|---|
| AMNH 632360 | adult | 23 June 1901 | Isabel | A.S. Meek | 3372 | Paralectotype |
| AMNH 632361 | adult | 11 June 1901 | Isabel | A.S. Meek | 3239 | Paralectotype |
| AMNH 632362 | adult | 22 June 1901 | Isabel | A.S. Meek | 3368 | Lectotype |
| LivCM T16738 | adult | 1890 | Bugotu (= San Jorge) | Dr Welchman | | Tristram collection |
| UF 40210 | adult | 3 July 1998 | Isabel; Longedo'u River | M. Hafe | AWK 1437 | skin + partial skeleton + tissues |
| AMNH 632357 | adult | 12 December 1903 | Choiseul | A.S. Meek | A929 | |
| AMNH 632358 | adult | 10 January 1904 | Choiseul | A.S. Meek | A1127 | |
| AMNH 632359 | adult | 12 January 1904 | Choiseul | A.S. Meek | A1141 | |
| AMNH 632356 | adult | 28 April 1904 | Bougainville | A.S. Meek | A1676 | |
| BMNH 1937.4.14.4 | adult | 22 August 1936 | Bougainville; Buin | W.F.H. Rosenberg | 15 | |
| BMNH 1937.4.14.5 | adult | 4 October 1936 | Bougainville; Buin | W.F.H. Rosenberg | 16 | |
| BMNH 1969.41.1073 | adult | 16 January 1938 | Bougainville; Buin | | H3.380 | Hewitt collection |
| OUM B/2837 | immature? | 15 February 1936 | Bougainville; Buin | J.B. Poncelet | | C.M.N. White collection |
| OUM B/2838 | immature? | 3 May 1936 | Bougainville; Buin | J.B. Poncelet | | C.M.N. White collection |
| MNHN CG1938.64 | immature? | 15 February 1937 | Bougainville; Buin | J.B. Poncelet | | |
| MNHN CG1938.65 | adult | 4 March 1937 | Bougainville; Buin | J.B. Poncelet | | |
| MCZ 194928 | adult | 27 September 1937 | Bougainville | W.F.H. Rosenberg | | |
| MCZ 194929 | adult | 10 September 1937 | Bougainville | W.F.H. Rosenberg | | leg. J.B. Poncelet? |
| CSIRO 3102 | adult | 24 August 1964 | Bougainville; Barilo | R. Schodde | | |

Key to museum abbreviations: AMNH – American Museum of Natural History, New York, USA; BMNH – The Natural History Museum (Bird Group), Tring, UK; CSIRO – Commonwealth Science & Industrial Research Organization, Canberra, Australia; MCZ – Museum of Comparative Zoology, Harvard University, Cambridge, MA, USA; MNHN – Muséum National d'Histoire Naturelle, Paris, France; LivCM – National Museums and Galleries on Merseyside, Liverpool, UK; OUM – Oxford University Museum, Oxford, UK; UF – Florida Museum of Natural History, University of Florida, Gainesville, FL, USA.

small island just off Isabel) by Dr Welchman in 1890, was noted as the first record of *Podargus ocellatus* for the Solomon Islands (Tristram 1892) rather than being recognized as a new taxon. The next records were of two males and a female taken by A.S. Meek on Isabel between 11 and 23 June 1901. After being sent to the Rothschild collection in Tring, they were described as *Podargus inexpectatus* by Hartert (1901). This description was repeated almost verbatim the following year by Rothschild and Hartert (1902). Meek went on to collect four more specimens for Walter Rothschild, three females on Choiseul between 12 December 1903 and 12 January 1904, and a female on Bougainville on 28 April 1904. These specimens were also sent to Tring and were documented in Rothschild and Hartert (1905). Hartert (1925) selected a male from the original three specimens as the type of *Podargus inexpectatus*. This specimen, collected on Isabel on 22 June 1901, therefore became the lectotype of *P. inexpectatus*, with the remaining two becoming paralectotypes. When Rothschild sold his collection to the American Museum of Natural History in New York in 1931, all seven specimens were transferred there. In a catalogue of the types deposited in the American Museum of Natural History, Greenway (1978) listed the specimen selected by Hartert (1925), but did not indicate its status as a lectotype.

The Whitney South Sea Expedition in the 1920s failed to record any frogmouths (Hartert 1929). Then, from 15 February 1936 to 16 January 1938, nine specimens were collected, all on Bougainville and mostly from the Buin region in the southern part of the island. At least four of these specimens, collected by or for the dealer W.F.H. Rosenberg, found their way to the British Museum of Natural History (now in Tring) and the Museum of Comparative Zoology at Harvard University. The remaining five birds appear to have been taken by Father J.B. Poncelet, a French missionary on Bougainville. Two of these were initially in the collection of C.M.N. White (White 1937) but are now in the Oxford University Museum in Oxford, UK. Two others, documented by Danis (1938), now reside in the Muséum National d'Histoire Naturelle in Paris. The fifth specimen, collected before 1938, was described as a possible immature female in poor condition with all of its tail feathers missing (Danis 1937). The only specimen that we examined with no rectrices is MCZ 194929, but this bird was apparently obtained from W.F.H. Rosenberg; its measurements differ slightly from those in Danis (1937). Nevertheless,

because Rosenberg was a dealer as well as a collector, this specimen may well have originated from J.B. Poncelet.

It was approximately 30 years before the next specimen became available, a male collected at Barilo on Bougainville on 24 August 1964 (Schodde 1977). This specimen is now in the CSIRO collection in Canberra, Australia. The only other specimen known to us is the most recent, a female taken by Mark Hafe along the Longedo'u River on Isabel on 3 July 1998 (Kratter *et al.* 2001a, 2001b). This bird was calling in mid-elevation forest (*c.* 500 m) from a thicket of introduced bamboo (*Bambusa* sp.) in pre-dawn hours. In addition to a museum study skin, this specimen also provided the first skeletal and tissue specimens.

## SPECIES DESCRIPTION

*Adult (either sex)*: Crown brown, usually lightly mottled with pale buffish spots. Nape, back and rump brown (sometimes tinged rufous), faintly barred or speckled blackish-brown. Lores and ear coverts brown with blackish-brown mottling. Supercilium generally pale buff, paler and more distinct in front of eye. Scapulars whitish-grey to pale brown, faintly barred darker. Upper wing-coverts with a number of large, very conspicuous white spots. Wing coverts brown to rufous brown, speckled or barred blackish-brown, median and greater coverts with bold white or buff spots on tips of outer webs. Underwing-coverts buff, barred dark brown. Primaries dark brown boldly spotted tawny or buff along outer webs and indistinctly barred tawny or buff along inner webs. Secondaries and tertials brown barred pale tawny and speckled blackish-brown. Chin and throat brown speckled blackish-brown and often boldly spotted whitish. Breast and flanks slightly paler brown than upperparts, speckled blackish-brown and boldly spotted white or very pale buff. Undertail coverts buff, feathers tipped or edged pale tawny or brownish. Tail brown, broadly barred pale buff, bars speckled and edged blackish-brown.

Earlier authors noted that the male had brown upperparts with fine vermiculations and obvious vermiculations on the tail, but was darker than the female on the rump and head and less rufous overall. They further distinguished it from *Podargus ocellatus* by its broader bill, lack of distinct blackish-brown crescent-shaped markings on the sides of throat and chest, more uniform upperparts, rounder white apical spots on the wing-coverts, uniformly coloured and more sharply spotted under wing-coverts, and

more distinctly barred tail, especially compared with *P. o. intermedius* (Hartert 1901, Rothschild & Hartert 1902).

## BARE PART COLORATION

The few data available are from specimen labels. Iris yellow, pale orange-yellow, yellowish-brown or brown. Bill brown, smoky-horn, turkey-umber or mid reddish-brown. Mouth/gape pale lemon. Feet (or tarsus and toes) horn, pale yellow or cream. Claws pale yellow-grey.

## BIOMETRICS

The condition of many of the specimens prevents certain measurements (Table 2) from being taken without causing damage. One specimen (MCZ 194929) is missing its entire tail. Seven other specimens are missing one or two rectrices, and another is missing five; in each of these cases, however, an accurate tail measurement was possible. Only the two most recent specimens (CSIRO 3102 and UF 40210) were weighed at the time of collection (Table 2). With so few museum specimens available, little consideration has been given to intraspecific variation within *Rigidipenna inexpectata*. Three females from Choiseul and one from Bougainville were noted as being shorter winged than a female from Isabel (Rothschild & Hartert 1905, Hartert 1925), although this was not supported by White (1937) or by Danis (1938). Our data reveal no dramatic inter-island variation in size (Table 3) or plumage. For now, we consider *R. inexpectata* to be monotypic. In wing and tail length,

**Table 2.** Linear measurements (in mm) and body mass (in grams) of specimens of *Rigidipenna inexpectata*.

| Museum | Island | Sex | Wing | Tail | Bill (L) | Bill (D) | Gape | Body mass | R5 width |
|---|---|---|---|---|---|---|---|---|---|
| AMNH 632360 | Isabel | F | 216 | 179 | 33.6 | n/m | 48.3 | n/m | 32 |
| UF 40210 | Isabel | F | 202 | 170 | 35 | 16.6 | 48.1 | 175 | 34 |
| AMNH 632361 | Isabel | M | 234 | 188 | 37 | n/m | 56 | n/m | 37 |
| AMNH 632362 | Isabel | M | 216 | 185 | n/m | n/m | n/m | n/m | n/m |
| NMGM T16738 | San Jorge | M | 200 | 163 | 29 | 18.2 | 45.6 | n/m | 27 |
| AMNH 632357 | Choiseul | F | 200 | 164 | 34.1 | 18.7 | 50 | n/m | 35 |
| AMNH 632358 | Choiseul | F | 206 | 165 | n/m | n/m | 49 | n/m | n/m |
| AMNH 632359 | Choiseul | F | 195 | 167 | 33.6 | n/m | 50.7 | n/m | 30 |
| AMNH 632356 | Bougainville | F | 203 | 173 | 35.7 | 18.7 | 49.8 | n/m | 33 |
| BMNH 1937.4.14.4 | Bougainville | F | 205 | 180 | 29.3 | 19.1 | 51.5 | n/m | 35 |
| BMNH 1969.41.1073 | Bougainville | F | 200 | 164 | 31.8 | 20.2 | 48 | n/m | 35 |
| MNHN CG1938.65 | Bougainville | F | 201 | 178 | 33.1 | 20.3 | 55.2 | n/m | 35 |
| OUM B/2838 | Bougainville | F | 210 | 167 | 29.4 | n/m | 55.2 | n/m | 30 |
| BMNH 1937.4.14.5 | Bougainville | M | 206 | 175 | 30.2 | 18 | 47.7 | n/m | 36 |
| OUM B/2837 | Bougainville | M | 218 | 179 | 32.7 | n/m | 56.3 | n/m | 30 |
| MNHN CG1938.64 | Bougainville | M | 207 | 160 | 32.7 | 25.1 | 56.3 | n/m | n/m |
| MCZ 194928 | Bougainville | M | 209 | 183 | 31.5 | 20.9 | 52.1 | n/m | n/m |
| MCZ 194929 | Bougainville | M | 207 | n/m | 35.5 | 21.9 | 53.7 | n/m | n/m |
| CSIRO 3102 | Bougainville | M | 223 | 190 | n/m | n/m | 55.2 | 205 | 31 |

Wing = flattened (maximum) wing length; tail = insertion of central rectrices to tip; bill (L) = bill length from tip to forehead; bill (D) = depth of bill at feathering; gape = width of bill at commissure; R5 width = breadth of central tail feather (rectrix) at mid length. n/m = not measured.

**Table 3.** Summary of wing and tail measurements of *Rigidipenna inexpectata*, with mean (sample size) and range.

| | Isabel | Choiseul | Bougainville |
|---|---|---|---|
| **Wing** | | | |
| Male | 225 (2), 216–234 | no data | 212 (6), 206–223 |
| Female | 206 (2), 197–216 | 200 (3), 195–206 | 204 (5), 200–210 |
| **Tail** | | | |
| Male | 186 (2), 185–188 | no data | 177 (5), 160–190 |
| Female | 174 (2), 169–179 | 165 (3), 164–167 | 172 (5), 164–180 |

males average larger than females, although there is considerable overlap.

## OSTEOLOGY AND PALAEONTOLOGY

Of 38 osteological characters (Table 4), *Rigidipenna* is unique in 13, agrees with *Batrachostomus* but not *Podargus* in ten, is more similar (but not identical) to *Batrachostomus* than *Podargus* in six, and is not clearly more similar to one genus or the other in nine. In no osteological character does *Rigidipenna* agree with *Podargus* to the exclusion of *Batrachostomus*. In all four characters of the cranium and mandible, *Rigidipenna* consistently agrees with *Batrachostomus* but not *Podargus*. The 13 unique characters of *Rigidipenna* (see Diagnosis) are found on the pectoral girdle (coracoid, scapula, sternum), wing (humerus, ulna, radius, carpometacarpus) and leg (femur, tarsometatarsus), i.e. throughout the postcranial skeleton. We note that these characters are pronounced, easily discernible features that would typically be characteristic of differences among genera. Within a genus, species-level osteological characters tend to be fewer and more subtle.

We assigned possible polarities to the osteological characters using three outgroups: Caprimulgidae (*Caprimulgus* + *Chordeiles*), Nyctibiidae (*Nyctibius*) and Steatornithidae (*Steatornis*). We note, however, that there is considerable uncertainty about which taxa might be appropriate outgroups for the Podargidae. Mayr (2002) used osteological evidence to question whether the Podargidae (and Steatornithidae) belong in the Caprimulgiformes, an order to which he assigned only the Caprimulgidae, Nyctibiidae and Aegothelidae, with Apodiformes (Apodidae, Trochilidae) as sister. Similarly, molecular studies have not resolved the ordinal affinities of Podargidae (Mariaux & Braun 1996, Mindell *et al.* 1997, Johansson *et al.* 2001), nor have combined morphological and molecular analyses (Mayr *et al.* 2003).

We agree that the ordinal placement of podargids remains unresolved. Among 38 osteological characters (Table 4), the character states were so different that no assignment of polarity (primitive vs. derived) for *Rigidipenna* was possible for 16 characters, regardless of the putative outgroup taxon. Looking at the distribution of possibly primitive or derived characters among the three outgroups, no clear picture emerges about the relationship of *Rigidipenna* that could not be discerned through non-polarized comparative osteology.

The fossil record of the Podargidae is restricted to three extinct genera from the Early Tertiary (Palaeogene) of Europe, namely *Palaeopsittacus* from the Early Eocene of England, *Masillapodargus* from the Middle Eocene of Germany and *Quercypodargus* from the Late Eocene of France (Mourer-Chauviré 1989, Mayr 1999, 2001, 2003, 2005). These extinct genera differ substantially from any of the three living genera of Podargidae in such characters as: coracoid short and stout with a foramen for the supracoracoideus nerve; sternum with smaller incisions on the posterior margin; humerus short and stout; and distal tibiotarsus with a wide intercondylar incision.

Although the Palaeogene fossils from Europe might seem to be biogeographically anomalous considering the modern distribution of the Podargidae, the oldest fossils assigned to the Nyctibiidae, Steatornithidae and many other currently tropical families of birds also are from early Tertiary deposits in the temperate Northern Hemisphere (Olson 1987, Mourer-Chauviré 1989).

## MOLECULAR ANALYSIS

### Methods

Tissue or DNA samples were obtained for seven podargids and five caprimulgiform outgroup taxa (Table 5), although we note again that we are uncertain about which if any of these taxa are truly appropriate as an outgroup for the Podargidae. DNA was extracted from tissue samples by a standard proteinase K-phenol/chloroform procedure (Mariaux & Braun 1996) with Phase Lock Gel (Eppendorf) as an aid to phase separation. The cytochrome *b* gene was amplified via polymerase chain reaction (PCR) in 25-µL reactions using Ready-To-Go PCR Beads (Amersham Biosciences). The final reaction conditions were: 200 µM each dNTP, 50 mM KCl, 1.5 mM MgCl$_2$, 10 mM Tris-HCl (pH 9), 0.06 U/µL *Taq* DNA polymerase, 0.6 µM each amplification primer and 25 ng of template DNA. For most taxa, full-length PCR products were obtained with primers L14764 and H16060 (Robbins *et al.* 2005). PCR was performed in a DNA Engine Tetrad thermal cycler (Bio-Rad) with the following cycling profile: 3 min at 95 °C, followed by 25 cycles of 15 s at 95 °C, 15 s at 55 °C and 30 s at 72 °C, and a final extension phase of 10 min at 72 °C. The PCR products were purified by PEG precipitation and cycle sequenced with BigDye 3.1 chemistry (Applied Biosystems) according to the manufacturer's instructions using the full-length amplification primers and internal primers mentioned below. BigDye Terminator v1.1/3.1 sequencing buffer was used to

**Table 4.** Osteological characters in extant species of Podargidae.

| ELEMENT Character | *Podargus strigoides* (UMMZ 214237, UF 32479) | *P. ocellatus* (UF 41456, UMMZ 215784) | *Batrachostomus septimus* (UMMZ 233065) | *Rigidipenna* (UF 40210) | Character agreement for *Rigidipenna* | C | N | S |
|---|---|---|---|---|---|---|---|---|
| **CRANIUM** | | | | | | | | |
| Processus postorbitalis & crista nuchalis temporalis | fused | fused | unfused | unfused | B | P | P | P |
| Foramen magnum | wider than high | wider than high | as high as wide | as high as wide | B | P | P | P |
| **MANDIBLE** | | | | | | | | |
| Posterior margin of processus mandibulae medialis in dorsal aspect, relative to ramus | nearly parallel | nearly parallel | more perpendicular | more perpendicular | B | -- | -- | P |
| **CORACOID** | | | | | | | | |
| Medial ventral margin of humeral 1/3 of shaft | intermediate | sharp | sharp | more rounded | U | -- | -- | D |
| Processus procoracoideus in dorsal aspect | shallow | shallow | shallow | deep | U | -- | -- | -- |
| Facies articularis clavicularis in medial aspect | diagonally more triangular | diagonally more triangular | diagonally oblong | diagonally oblong | U | P | P | P |
| Facies articularis sternalis | deep | deep | shallow | shallow | B | -- | -- | D |
| Sterno-medial margin of shaft | more rounded | more rounded | sharp | sharp | B | D | D | D |
| **SCAPULA** | | | | | | | | |
| Area between facies articularis clavicularis & facies articularis humeralis in proximal aspect | thin | thin | intermediate | thick | U | D | P | D |
| Facies articularis humeralis | wider proximally than distally | wider proximally than distally | wider distally than proximally | wider distally than proximally | B | -- | -- | -- |
| **STERNUM** | | | | | | | | |
| Length & width relative to length of forelimb bones (trabeculae lateralis excluded) | intermediate in length, narrow | short, narrow | long, wide | long, wide | B | P | P | P |
| Processus craniolateralis in lateral aspect | narrow; steadily tapers anteriorally | narrow; steadily tapers anteriorally | narrow; steadily tapers anteriorally | wide; tapers irregularly | U | D | D | D |
| Apex carina in ventral aspect | distinctly expanded | distinctly expanded | thickens just barely & very gradually | thickens barely & gradually | ±B | P | -- | -- |
| Trabecula lateralis | long, narrow | long, narrow | short, narrow | short, wide | B | -- | -- | -- |
| Carina sterni in anterior aspect | remains thin; nearly perpendicular to sternal plate | remains thin; nearly perpendicular to sternal plate | remains thin; nearly perpendicular to sternal plate | expands dramatically over dorsal half; angle with sternal plate more obtuse | U | P | P | P |

**Table 4.** *Continued.*

| ELEMENT Character | *Podargus strigoides* (UMMZ 214237, UF 32479) | *P. ocellatus* (UF 41456, UMMZ 215784) | *Batrachostomus septimus* (UMMZ 233065) | *Rigidipenna* (UF 40210) | Character agreement for *Rigidipenna* | Character polarity of *Rigidipenna* C | N | S |
|---|---|---|---|---|---|---|---|---|
| **HUMERUS** | | | | | | | | |
| Proximal part of fossa musculo brachialis | distinct & deep | distinct & deep | distinct & deep | gradual & shallow | U | -- | D | D |
| Epicondylus ventralis in palmar aspect | expanded ventrally | expanded ventrally | expanded both distally and ventrally | expanded distally | ±B | -- | P | D |
| **ULNA** | | | | | | | | |
| Junction of cotyla dorsalis with shaft | abrupt | abrupt | intermediate | gradual | ±B | P | P | P |
| Protrusion of tuberculum ligamentum collateralis ventralis | abrupt | abrupt | abrupt | gradual | U | P | P | P |
| Tuberculum carpale | long, pointed | long, pointed | short, rounded | short, rounded | B | D | -- | -- |
| **RADIUS** | | | | | | | | |
| Lateral compression of shaft | moderate | moderate | great | great | B | -- | D | P |
| Position of disto-ventral tubercle | medial | intermediate | lateral, intermediate | lateral | ±B | D | D | -- |
| Overall stoutness of distal end | broad, shallow | narrow, shallow | narrow, intermediate depth | broad, deep | ±B | P | P | -- |
| **CARPOMETACARPUS** | | | | | | | | |
| Proximal tubercle on os metacarpale minus | small | small | small | large | U | D | D | D |
| **FEMUR** | | | | | | | | |
| Facies articularis antitrochanterica in proximal aspect | wide, shallow, curved | narrow, deep, straight | narrow, deep, straight | narrow, deep, curved | – | -- | -- | D |
| Proximo-ventral surface of corpus femoris | concave | concave | concave | convex | U | P | D | D |
| Fossa poplitea | deeply concave | intermediate | intermediate | barely concave | – | P | D | D |
| Condylus medialis in medial aspect | deep, rounded | intermediate | shallow, oblong | shallow, oblong | ±B | D | D | -- |
| Condylus lateralis and trochlea fibularis in lateral aspect | deep, more pointed | specimens damaged | deep, more pointed | shallow, blunt | U | P | -- | -- |
| **TIBIOTARSUS** | | | | | | | | |
| Condylus medialis in medial aspect | shallow, rounded | deep more pointed | shallow, rounded | shallow, rounded | – | P | P | D |
| Condylus medialis in distal aspect | intermediate | extends straight dorsad | intermediate | splayed mediad | – | -- | -- | D |
| Condylus lateralis in lateral aspect | deep, rounded | deep, rounded | deep, rounded | shallow, flatter | – | D | P | -- |

**Table 4.** *Continued.*

| ELEMENT Character | *Podargus strigoides* (UMMZ 214237, UF 32479) | *P. ocellatus* (UF 41456, UMMZ 215784) | *Batrachostomus septimus* (UMMZ 233065) | *Rigidipenna* (UF 40210) | Character agreement for *Rigidipenna* | Character polarity of *Rigidipenna* | | |
|---|---|---|---|---|---|---|---|---|
| | | | | | | C | N | S |
| **TARSOMETATARSUS** | | | | | | | | |
| Hypotarsus | wide | intermediate in width | intermediate in width | narrow | ±B | P | D | -- |
| Dorso-lateral margin of cotyla lateralis in proximal aspect | squared | more rounded | more rounded | more rounded | – | -- | -- | D |
| Cotyla medialis in acrotarsial aspect | well flared from shaft | well flared from shaft | well flared from shaft | barely flared from shaft | U | P | D | P |
| Cotyla lateralis in acrotarsial aspect | pointed more proximally | pointed more laterally | pointed more laterally | pointed more laterally | – | -- | -- | -- |
| Trochlea metatarsi IV in lateral aspect | deep, with rounded plantar margin | deep, with rounded plantar margin | deep, with more pointed plantar surface | shallow, with relatively flat plantar surface | U | D | P | D |
| Trochlea metatarsi IV in acrotarsial aspect | extends less distally | extends less distally | extends more distally | intermediate | I | -- | -- | -- |
| Total 'derived' characters | -- | -- | -- | -- | – | 9 | 11 | 15 |
| Total 'primitive' characters | -- | -- | -- | -- | – | 13 | 11 | 7 |
| Total characters without assigned polarity | -- | -- | -- | -- | – | 16 | 16 | 16 |

Character agreement for *Rigidipenna*: B, agrees with *Batrachostomus* but not *Podargus*; I, intermediate between *Podargus* and *Batrachostomus*; U, unique to *Rigidipenna*; –, differs from at least one species of *Podargus* but character state unclear. In no character does *Rigidipenna* agree with *Podargus* but not *Batrachostomus*. For character polarity of *Rigidipenna*, P = primitive, D = derived, and -- = condition so different that polarity cannot be evaluated. The outgroups are Caprimulgidae (C; *Caprimulgus carolinensis* UF 43286, *Chordeiles minor* UF 43320), Nyctibiidae (N; *Nyctibius griseus* UF 38711, *Nyctibius grandis* UF 32480), and Steatornithidae (S; *Steatornis caripensis* UF 43350). Osteological nomenclature generally follows that of Baumel *et al.* (1993).

**Table 5.** Specimens sequenced for cytochrome *b*.

| Species | Institution | Catalogue no. | Locality or source | Collector |
|---|---|---|---|---|
| **PODARGIDAE** | | | | |
| *Rigidipenna inexpectata* | UWBM | AWK1437 | Solomon Islands: Isabel; Longedo'u River, 8°10.5'S, 159°35'E, 500 m | Mark Hafe |
| *Podargus strigoides* | LSUMNS | B8654 | Audubon Zoo, New Orleans, LA | A. P. Capparella |
| *Podargus papuensis* | MV | C876 | Australia: Queensland; Silver Plains, 13°59'S, 143°33'E | J. Wombey |
| *Podargus ocellatus* | MV | C332 | Australia: Queensland, Conondale Range | L. Christidis |
| *Batrachostomus septimus* | CMC | CMNH B499 | Phillipines: Panay; Antique Prov. Mt. Madja-as, 11°23'N, 122°09'E, *c.* 1265 m | |
| *Batrachostomus cornutus* | MVZ | CS2350 | Malaysia: Sabah | D. Foote and J. Schmidt |
| *Batrachostomus auritus* | ZMUC | 115604 | Indonesia: Sumatra | |
| **OUTGROUPS** | | | | |
| *Chordeiles rupestris* | ANSP | T2755 | Ecuador: *c.* 10 river km below junction of Rio Lagarto and Rio Aguarico | F. Sornoza M. |
| *Eurostopodus papuensis* | MV | E660 | Papua New Guinea: Veimauri River | R. Schodde |
| *Nyctibius griseus* | USNM | B493 | Panama: Bocas del Toro; Cuan Creek | 1989 Bocas del Toro Expedition |
| *Steatornis caripensis* | LSUMNS | B7474 | Venezuela: Amazonas; Cerro de la Neblina, 1800 m | D. E. Willard |
| *Aegotheles cristatus* | MV | W0191 | Australia: SA, 15 km from Lagoon Witt, Mabel Creek | P. Baverstock |

UWBM = Burke Museum, University of Washington, Seattle; ZMUC = Zoological Museum, University of Copenhagen; MV = Museum Victoria, Melbourne, Australia; MVZ = Museum of Vertebrate Zoology, University of California, Berkeley; CMC = Cincinnati Museum Center, Cincinnati, Ohio; LSUMNS = LSU Museum of Natural Science Collection of Genetic Resources; ANSP = Academy of Natural Sciences, Philadelphia; USNM = US National Museum of Natural History.

reduce by 75% the amount of Ready Reaction Premix needed. Reaction products were purified with Sephadex G-50, and sequences were determined on an ABI 3100 capillary DNA sequencer (Applied Biosystems). Consensus sequences were assembled for each individual using Sequencher 4.1.2 (GeneCodes). All sequences were determined completely on both strands.

Three samples would not support PCR amplification of full-length cytochrome *b* due to degradation of the tissue (*Rigidipenna*, *Batrachostomus auritus*) or intentional shearing of the DNA for molecular hybridization experiments (*Batrachostomus cornutus*). These samples were amplified and sequenced in overlapping fragments using external primers L14764 and H16060 in combination with a number of internal primers, many of which were designed to be frogmouth-specific using sequence data obtained from full-length amplicons of other taxa in the study. Internal primer sequences are available from C.J.H. Overlapping sequences from the same taxon matched perfectly, suggesting they were authentic and of mtDNA origin. Full-length cytochrome *b* sequences of 1143 bp were reconstructed from all taxa except *B. auritus*, for which only the first 129 bp at the 5'

end was obtained. Several samples were previously sequenced for a 656-bp fragment of cytochrome *b* by Mariaux and Braun (1996), and the present data allow us to correct six ambiguities or *Taq* polymerase errors in that dataset (three each in *Eurostopodus papuensis* and *Podargus papuensis*). All sequences have been submitted to GenBank with accession numbers X95767, X95771, X95772, X95775, X95776, X95778, X95780, and EF100671–EF100675.

All sequences had open reading frames throughout and sequence characteristics (e.g. base composition, substitution patterns) consistent with an mtDNA origin. Base composition was not significantly heterogeneous when all sites and all taxa were considered ($P = 0.99$, $\chi^2$ test), but heterogeneity was exposed when only variable sites among ingroup taxa were considered ($P = 0.02$). Most of the heterogeneity was due to the *B. septimus* sequence ($P = 0.55$ without *B. septimus*). However, the base compositional bias of the *B. septimus* sequence was still strongly in the direction of other mtDNA sequences (high in C, low in G), so it seems unlikely to represent a laboratory artefact or a significant problem for phylogeny reconstruction.

Sequences were aligned using Clustal W (Thompson *et al.* 1994) and no internal gaps were required. Phylogenetic analyses were performed with PAUP* 4.0b10 (Swofford 2003). Maximum parsimony tree searches were conducted with all characters equally weighted, ten random addition heuristic searches with TBR branch-swapping per dataset and 1000 bootstrap pseudoreplicate datasets. For maximum-likelihood (ML) analysis, models of sequence evolution and rate heterogeneity parameters were evaluated using methodologies described in Model-Test version 3.5 package (Posada & Crandall 1998). First, a neighbour-joining (NJ) tree was produced via PAUP* using Jukes–Cantor distances. Parameters were then calculated for 56 nested models of sequence evolution on the NJ tree and the models evaluated with ModelTest using the Akaike Information Criterion (AIC) and the successive approximations approach suggested by Swofford *et al.* (1996). In this case, general time-reversible model with invariant sites and $\Gamma$-distributed rates (GTR+I+$\Gamma$) was selected, allowing for unequal base frequencies (A = 0.3047, C = 0.3754, G = 0.1144, T = 0.2055), unequal mutation rates (A–C = 3.3171, A–G = 12.6038, A–T = 5.0499, C–G = 0.8542, C–T = 27.3928, G–T = 1.0000), and among-site rate variation ($\Gamma$-shape parameter $\alpha$ = 1.3731; proportion invariant sites = 0.4614). This model was then applied to heuristic ML tree searches performed with PAUP*. The original data were analysed with TBR branch-swapping and ten random addition searches. One thousand bootstrap pseudoreplicate datasets were analysed, with TBR branch-swapping and one random addition search per dataset. Bayesian phylogenetic analysis was performed using MrBayes 3.1 (Huelsenbeck & Ronquist 2001) and a GTR+I+$\Gamma$ model. Six Markov chains were run for 10 million generations each. Topology and model parameters were sampled every 500th generation and used to determine the posterior probabilities of clades and estimates of model parameters. The first 500 samples were discarded to allow for burn-in to the target distributions; default settings were used for all other options.

## Results and discussion

Sequence divergence between taxa was estimated by the method of Kimura (1980) for comparison to a large compilation of cytochrome *b* genetic distances in vertebrates (Johns & Avise 1998). The genetic distance between *Podargus ocellatus plumiferus* and *Rigidipenna* is 0.183 (Table 6). This is much higher

**Table 6.** Estimated sequence divergence (Kimura 1980) of avian cytochrome *b* genes.

| Comparison | n | K2P distance | |
| --- | --- | --- | --- |
| | | Mean | Range |
| *P. ocellatus – Rigidipenna* | 1 | 0.183 | – |
| Intrageneric | | | |
|   Within *Podargus* | 3 | 0.089 | 0.06–0.11 |
|   Within *Batrachostomus*\* | 1 | 0.162 | – |
|   Within other bird genera† | 88 | ~0.07 | 0.02–0.15 |
| Intergeneric | | | |
|   *Podargus – Rigidipenna* | 3 | 0.195 | 0.18–0.20 |
|   *Batrachostomus*\* *– Rigidipenna* | 2 | 0.199 | 0.20–0.20 |
|   *Batrachostomus*\* *– Podargus* | 6 | 0.215 | 0.20–0.22 |
|   Confamilial bird genera† | 37 | ~0.12 | 0.07–0.22 |

\**B. auritus* excluded owing to partial data; its mean distance to other *Batrachostomus* was 0.232 over 129 bp.
†Estimated from Johns and Avise (1998).

than any value reported for a legitimate avian intraspecific divergence. Typical distances are of the order of 0.01 within bird species, and distances of 0.03–0.04 often evoke discussion of taxonomic splitting of species. Intrageneric divergence between the two full-length *Batrachostomus* sequences is 0.162, and averages 0.089 among three species of *Podargus*. Divergence of *Rigidipenna* from either genus is higher, averaging 0.199 from *Batrachostomus* and 0.195 from *Podargus*. The distances to *Rigidipenna* are higher than those found within any other nightbird genera that have been examined (Mariaux & Braun 1996), and are more in line with intergeneric distances for most birds (Table 6). On the whole, the genetic distance data (Table 6) suggest that most frogmouth lineages may be quite old compared with other bird lineages of the same taxonomic rank. This point has been previously noted for frogmouths and other nightbirds (Sibley & Ahlquist 1990, Mariaux & Braun 1996, Brumfield *et al.* 1997).

The phylogenetic analyses (Fig. 5) showed strong support for monophyly of frogmouths and for monophyly of the genus *Podargus* (minus *inexpectata*). These clades were found in more than 95% of bootstrap replicates and had posterior probabilities of 1.0. The optimal position of *inexpectata* was basal to the three *Podargus* species in all analyses, but the topology was imperfectly resolved as indicated by the relatively low support values on that node. This phylogenetic position, when considered together with the large sequence divergence from either existing frogmouth
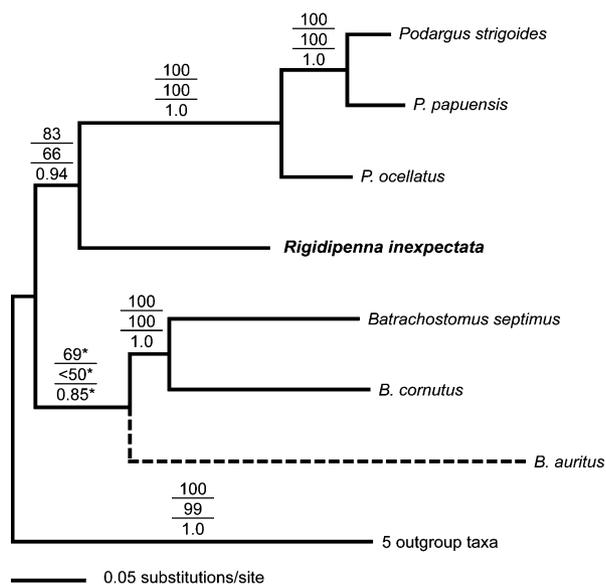
**Figure 5.** Phylogenetic relationships of cytochrome *b* sequences in the Podargidae. Branch lengths are from the optimal maximum likelihood tree. Nodal support values are maximum likelihood bootstrap (top), maximum parsimony bootstrap (middle) and Bayesian posterior probability (bottom). Primary analyses did not include the short *Batrachostomus auritus* sequence. Asterisks on support values for the *Batrachostomus* clade indicate that those values are derived from a second set of analyses that included *B. auritus*.

genus (Table 6), is best recognized by placing *inexpectata* in its own genus, the newly named *Rigidipenna*.

The three *Batrachostomus* sequences formed a clade in all analyses. The low support values grouping *B. auritus* with the other two species of *Batrachostomus* probably are due to the short sequence recovered for it (129 bp). Nevertheless, cytochrome *b* distances were large among these three taxa (Table 6). Coupled with the complicated geographical variation and our generally poor knowledge of the group (Cleere 1998, Holyoak 2001), these distances suggest that more cryptic diversity may await discovery. Collecting new skin, anatomical and tissue samples should remain a priority, as comparatively few are available.

## ECOLOGY

Very little is known about *Rigidipenna inexpectata* in life, other than it is nocturnal, arboreal and probably prefers forests. Hadden (2004: 156) described its habitat as 'Forest, second growth, occasionally close to gardens. Coastal to the foothills but probably well up into the mountains.' Information from the 19

specimens includes locality data more specific than an island for only three sites (Table 1). On Bougainville, Buin is a village on the southern coast (Fig. 1), and presumably the seven specimens were collected in lowland forests nearby. The specimen taken in 1998 (Longedo'u River, Isabel, Fig. 1) was collected in dense hill forest at 500 m altitude.

At Tirotonga on Isabel, G.D. and Mark Hafe (who collected the UF specimen) noted two vocalizations given by *R. inexpectata*. The first is a series of short whistles that rise in pitch and are repeated at irregular intervals (Fig. 6). The second is a series of descending whistles that are repeated in quick succession. Hadden (1981: 66) and Doughty *et al.* (1999: 128) described the call on Bougainville as 'soft repeated koo-loo', although both appear only to have repeated voice descriptions (e.g. Pizzey & Doyle 1980: 207, Coates 1985: 382) that refer to the rather different calls of Australian or New Guinean races of *Podargus ocellatus* (Fig. 7).

One specimen (CSIRO 3102, Bougainville, 24 August 1964) was on a shallow nest containing an almost fledged nestling. The nest was built of sticks and situated on the horizontal fork of a branch *c.* 25 m above ground, in the canopy of a tall secondary forest tree (Schodde 1977). Platform stick nests are known in species of *Podargus*; species of *Batrachostomus* build smaller nests composed mostly of feathers and lichens (Holyoak 1999).

Native names recorded for the Solomon Islands Frogmouth are 'bauroo' on San Jorge (Tristram 1892), probably 'nauroga' on Isabel (Webb 1992), and 'mokogo' and 'mookogo' on Bougainville (Danis 1938, Schodde 1977).

## DISCUSSION

Discovering that the podargid taxon *inexpectata* is generically separable from *Podargus* (and *Batrachostomus*) changes our understanding of the biogeography and evolution of frogmouths. With its previous treatment as a subspecies of *Podargus ocellatus*, the Solomon Island podargid taxon would seem clearly to have been derived from the Australian/Papuan region, as has been proposed for most of the avifauna in the Solomon Islands (Mayr & Diamond 2001; but see Filardi & Moyle 2005). Now, with generic-level status, *Rigidipenna* joins the extinct columbid *Microgoura meeki* and the large extant owl *Nesasio solomonensis* as genera that are endemic, as far as we know, to the islands that once formed the large Pleistocene island of Greater Bukida (Mayr & Diamond 2001). Along
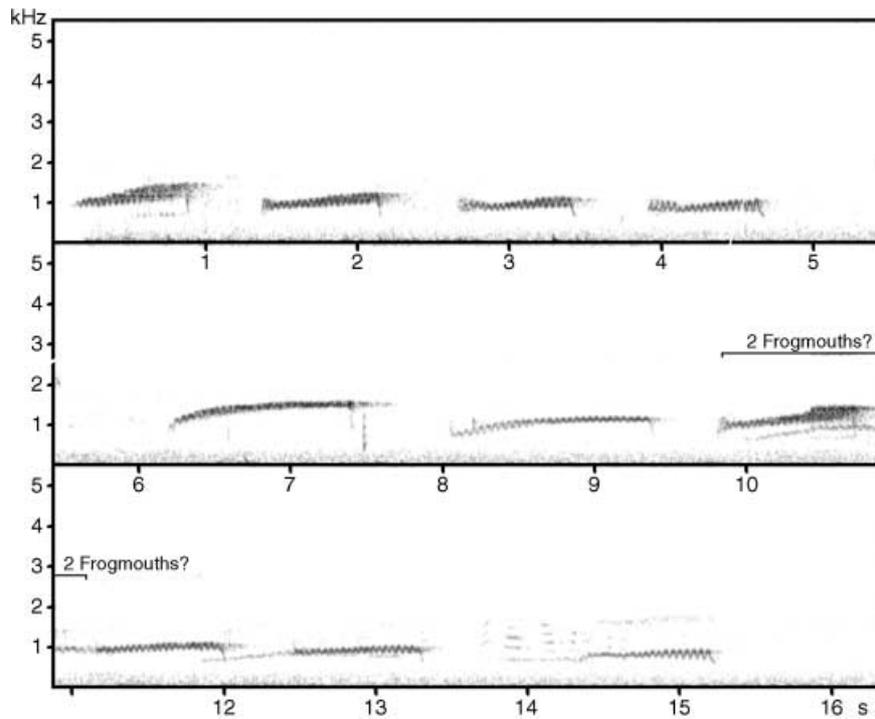
**Figure 6.** Sonagram depicting calls of *Rigidipenna inexpectata*, recorded at Tirotonga village, near Buala, Isabel, Solomon Islands, by G. Dutson in September 2004. Prepared with Avisoft-SASlab program at The British Library Sound Archive, London. Analysis parameters: Window Hamming, FFT (Hz) 512, Frame (%) 75, Overlap (%) 88.
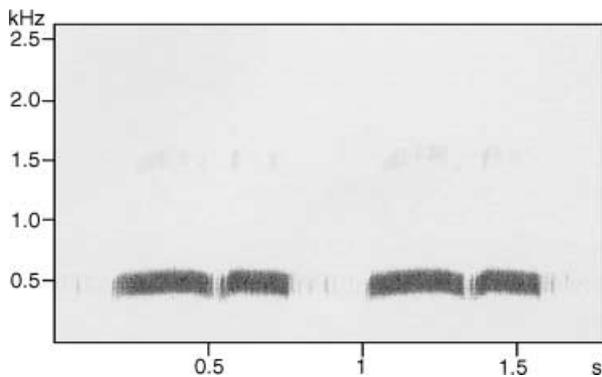


**Figure 7.** Sonagram depicting calls of *Podargus ocellatus marmoratus*, recorded in the Iron Range, Cape York Peninsula, Australia, by David Stewart on 24 September 1984 (Stewart 2002). Prepared with Kay Digital Sona-Graph 7800 at the Florida Museum of Natural History. Analysis filter, 150 Hz.

with two undescribed extinct genera of Columbidae from a late Pleistocene cultural site on Buka (Steadman 2006), *Microgoura*, *Nesasio* and *Rigidipenna* are the only generally recognized non-passerine genera endemic to northern Melanesia.

Having two of the three extant genera of the Podargidae confined to the Papuan–Australian–Oceanic region, and with the possibility that *Rigidipenna* is basal in the family, might suggest a Southern Hemisphere origin of the Podargidae, with *Batrachostomus* subsequently dispersing into the Indo-Malayan region. Given the Early Tertiary podargid fossils from Europe, however, the geographical origins of the Podargidae remain unclear, especially considering the uncertainty of the interfamilial relationships of frogmouths. Having made progress in documenting the modern diversity of podargids, we now await development of a middle and late Tertiary fossil record to bridge the morphological, temporal and geographical gaps between the high-latitude, Early Tertiary fossils and the low-latitude living taxa.

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