



Research article

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A new genus for the Lesser Moorhen *Gallinula angulata* Sundevall, 1850 (Aves, Rallidae)

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Abstract. Molecular phylogenetic analysis has demonstrated that the genus *Gallinula* is not monophyletic and comprises four major lineages. A review of the nomenclature of *Gallinula* shows that generic names are available for three lineages but that a fourth is as yet unnamed. A new monotypic genus, *Paragallinula* gen. nov., is described for Lesser Moorhen (*Gallinula angulata* Sundevall, 1850).

Key words. Gallinules, morphology, nomenclature, *Paragallinula* gen. nov., phylogenetics.

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Introduction

Recent molecular phylogenetic analysis has clarified the relationships among rails and has shown that several currently recognized genera are not monophyletic (García-R *et al.* 2014a). The study included nuclear and mitochondrial sequence data representing 70 species of rails in 22 of the 33 extant genera, including seven species traditionally placed in *Gallinula* Brisson, 1760. *Gallinula* as traditionally circumscribed (e.g., Sibley & Monroe 1990; Taylor & van Perlo 1998) was found to be paraphyletic with respect to *Fulica* Linnaeus, 1758 and *Porzana* Vieillot, 1816. Spot-flanked Gallinule *Gallinula melanops* (Vieillot, 1819) was sister to three (of eleven) species of *Porzana*, and two further species of *Gallinula* (*G. mortierii* (Du Bus, 1840) and *G. ventralis* Gould, 1837) were found to be their sister group. Surprisingly, the Lesser Moorhen *Gallinula angulata* Sundevall, 1850, which until now has always been placed in the genus *Gallinula*, was resolved as sister to a clade comprising *Fulica* Linnaeus, 1758 and all other species of *Gallinula*. These relationships are well-supported and suggest that taxonomic revision is warranted.

Current knowledge of the phylogenetic relationships among coots and gallinules leaves two major options for the generic assignment of *G. angulata*. *Fulica* and several species of *Gallinula* including *G. angulata* could be combined in a single genus for which *Fulica* has nomenclatural priority. Alternatively, *G. angulata* could be removed from *Gallinula* and placed in a separate genus. Merging *Gallinula* with *Fulica* would result in the change of at least six species names (*G. chloropus* (Linnaeus, 1758), *G. galeata* (M.H.C. Lichtenstein, 1818), *G. comeri* Allen, 1892, *G. nesiotis* P.L. Sclater, 1861, *G. tenebrosa* Gould, 1846 and *G. angulata*), and it would fail to recognise the widely accepted ecological, morphological and phylogenetic distinction between gallinules (*Gallinula* as defined below) and coots. Placement of *G. angulata* in a separate genus minimises taxonomic instability and maximises the information content of genus limits because it allows *Gallinula* and *Fulica* to be retained as separate genera. However, this strategy requires additional adjustments (some of which have already been adopted) to reconcile the systematic status of the gallinules, which are not a natural group. In this paper, we provide an updated molecular phylogeny of the “*Fulica*” clade (*sensu* García-R *et al.* 2014a), including a member of the putative genus “*Porphyriornis*” (*Gallinula nesiotis*) which was not previously sampled (García-R *et al.* 2014a), and a description of morphological characters to propose a new genus for the Lesser Moorhen.

Materials and methods

We conducted a phylogenetic analysis of the *Fulica*-clade using the same sequences and methods as García-R *et al.* (2014a), but also including an available cytochrome *b* sequence of *G. nesiotis* obtained from GenBank (EF681998) which is the only marker shared between the datasets of Groenenberg *et al.* (2008) and García-R *et al.* (2014a). Thus, we conducted Bayesian and Maximum Likelihood analyses of ~2900 bp of mitochondrial DNA (partial sequences of the mitochondrial genes cytochrome *b*, cytochrome oxidase subunit I and 16S ribosomal RNA) and ~1900 bp of nuclear DNA (fragments of beta-fibrinogen intron 7 and Recombination Activating Gene 1). We rooted the tree using an outgroup comprising species within the “*Aramides*” clade (García-R *et al.* 2014a).

We review the nomenclatural status of all generic names applied to *Gallinula* (*sensu* Sibley & Monroe 1990; Taylor & van Perlo 1998) to assess if any of these apply to *G. angulata*. The diagnosis of the new genus is based on the morphological dataset of Livezey (1998), which represents the most comprehensive and detailed comparison of morphological variation in rails. Livezey’s (1998) study included all extant species of *Fulica* and *Gallinula* plus a number of extinct species, including *Gallinula nesiotis* and *Gallinula (Pareudiastes) pacifica* (Hartlaub & Finsch, 1871).

Results

Phylogenetics

A phylogeny of the *Fulica*-clade is shown in Fig. 1. The topology is identical to that of García-R *et al.* (2014a), but with *G. nesiotis* added as the sister of *G. gallinula* and *G. galeata*. *Gallinula* (*sensu* Sibley & Monroe 1990; Taylor & van Perlo 1998) was resolved as paraphyletic and comprised four major lineages: (1) *G. chloropus*, *G. galeata*, *G. nesiotis* and *G. tenebrosa*; (2) *G. ventralis* and *G. mortierii*; (3) *G. melanops*; and (4) *G. angulata* (Fig. 1).

Nomenclature

The genus *Gallinula* Brisson, 1760 has *G. chloropus* as its type species (lineage 1 in Fig. 1). The synonymy of *Gallinula* (*sensu* Sibley & Monroe 1990; Taylor & van Perlo 1998) includes at least 10 names, although some of these have been reinstated as valid genera in recent classifications. However, none of these names can be applied to *G. angulata*.

Hydrogallina Lacépède, 1799 (type species *Fulica chloropus* Linnaeus, 1758, currently *Gallinula chloropus*) and *Stagnicola* Brehm, 1831 (type species *Fulica chloropus* Linnaeus, 1758, currently *Gallinula chloropus*) are junior synonyms of *Gallinula*.

Tribonyx Du Bus, 1840 (type species *Tribonyx mortierii* Du Bus, 1840) has been used for two Australian species, Tasmanian Native-hen *G. mortierii* and Black-tailed Native-hen *G. ventralis* by some authors (e.g., Christidis & Boles 2008; Dickinson & Remsen 2013). Recognition of *Tribonyx* as a separate genus from *Gallinula* is supported by phylogenetic studies of morphology (Livezey 1998) and DNA sequences (García-R *et al.* 2014a), which showed that *G. mortierii* and *G. ventralis* are not closely related to other species of *Gallinula* (lineage 2 in Fig. 1). Neither study indicated a close relationship between these species and Lesser Moorhen, and the name *Tribonyx* is thus not applicable to *G. angulata*.

Brachytrallus Lafresnaye, 1840 (type species *Brachytrallus ralloides* Lafresnaye, 1840, currently *Tribonyx mortierii* Du Bus, 1840) is a junior synonym of *Tribonyx* and not applicable to *G. angulata*.

Porphyriops Pucheran, 1845 (type species *Fulica crassirostris* J.E. Gray, 1829; now *Gallinula melanops crassirostris*) has been used for the Spot-flanked Gallinule (e.g., Wolters 1975; Blake 1977; Livezey 1998). Its recognition as a separate genus from *Gallinula* is now supported by phylogenetic studies of morphology (Livezey 1998) and DNA sequences (García-R *et al.* 2014a) (lineage 3 in Fig. 1). Again, neither study indicated a close relationship between Spot-flanked Gallinule and Lesser Moorhen. Therefore, *Porphyriops* is not applicable to *G. angulata*.

Pareudiastes Hartlaub & Finsch, 1871 (type species *Pareudiastes pacificus* Hartlaub & Finsch, 1871) and *Edithornis* Mayr, 1933 (type species *Edithornis silvestris* Mayr, 1933) have been proposed as the generic names of Samoan Moorhen and San Cristobal Moorhen, respectively. These two species have

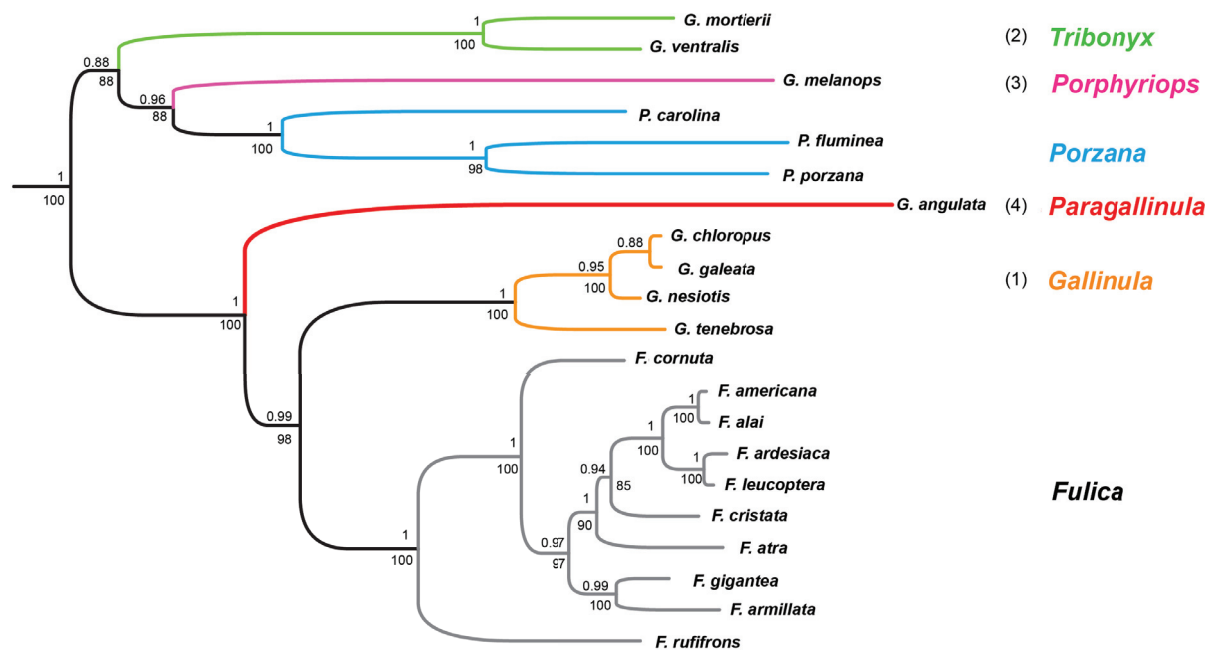


Fig. 1. Bayesian analysis of the *Fulica*-clade (*sensu* García-R *et al.* 2014a). Numbers above nodes indicate posterior probabilities from Bayesian analysis. Numbers below nodes are percent bootstrap values from Maximum Likelihood analysis. Colours indicate relevant clades with current nomenclature at branch tips. Coloured genus names are those adopted here to reconcile phylogeny and known morphological diversity.

both been placed in *Gallinula* in the past (e.g., Sibley & Monroe 1990; Taylor & van Perlo 1998) but they share a number of unique character states and are now typically combined in the genus *Pareudiastes* (Olson 1973, 1975a; Livezey 1998; Dickinson & Remsen 2013). A phylogenetic analysis of morphological characters indicates that *G. angulata* is not closely related to *Pareudiastes* (Livezey 1998). In addition, *G. angulata* does not share any unique apomorphies with *Pareudiastes* and differs from the latter by at least 14 integumentary characters (listed below). Thus, the name *Pareudiastes* is not applicable to *G. angulata*.

Porphyriornis Allen, 1892 (type species *Porphyriornis comeri* Allen, 1892) is sometimes used as the generic name of Gough Moorhen *G. comeri* and Tristan Moorhen *G. nesiotis* (e.g., Peters 1934; Livezey 1998). However, because both species are closely related to *G. chloropus*, these are typically placed in *Gallinula* (Wolters 1975; Sibley & Monroe 1990; Taylor & van Perlo 1998; Dickinson & Remsen 2013), an arrangement supported by a molecular phylogenetic study (Groenenberg *et al.* 2008; see also Fig. 1). *Porphyriornis* represents a synonym of *Gallinula*.

Microtribonyx Sharpe, 1893 (type species *Gallinula ventralis* Gould, 1837) is sometimes used for a monotypic genus comprising *T. ventralis* (Wolters 1975), but this name is now generally regarded as a synonym of *Tribonyx* or *Gallinula*, depending on whether the former is recognised as a separate genus (with two species), as we advocate here.

Pyramida Oliver, 1955 (type species *Rallus hodgeni* Scarlett, 1955, currently *Tribonyx hodgenorum*) was proposed for an extinct flightless species, now known from both North and South Island, New Zealand. Subsequently, Scarlett (1970) placed this species in the genus *Capellirallus* Falla, 1954, whereas Olson (1975b) transferred it to *Tribonyx*, which he considered a subgenus of *Gallinula*. In Livezey's (1998) phylogenetic analysis of morphological characters, this species was included within a polytomy comprising *Tribonyx*, *Pareudiastes*, *Edithornis*, *Porphyriornis*, *Gallinula* and *Fulica*. In any case, *Pyramida* is not applicable to *G. angulata*.

As no generic name appears to be available for *G. angulata*, we propose a new genus taxon.

Class Aves Linnaeus, 1758
Order Gruiformes (Bonaparte, 1854)
Family Rallidae (Rafinesque, 1815)

***Paragallinula* gen. nov.**

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Type species

Gallinula angulata Sundevall, 1850. Monotypic.

Differential diagnosis

Paragallinula gen. nov. differs from *Gallinula*, *Pareudiastes*, *Tribonyx* and *Porphyriops* in that (i) the orange suffusion on the frontal shield does not encompass the entire shield (in *Gallinula* encompassing entire frontal shield (Fig. 2); in *Pareudiastes*, *Tribonyx* and *Porphyriops* no suffusion of orange). In addition, *Paragallinula* gen. nov. differs from most species in the *Fulica*-clade (except *T. ventralis*) in (ii) showing marked sexual plumage dimorphism (Taylor 1996; Taylor & van Perlo 1998). *Paragallinula* gen. nov. further differs from *Gallinula* in (iii) the lack of a contrasting reddish band (“garter”) on the legs immediately proximal to the ankle joint (present in *Gallinula*) (Fig. 2).

Paragallinula gen. nov. differs from *Fulica* in (ii) gradual change in colouration on hindneck from dark grey head to paler lower neck and back (abrupt change in *Fulica*); (iii) absence of broad cutaneous lobes on digits II–IV of feet (present in *Fulica*); and (iv) presence of narrow cutaneous folds on lateral and medial sides of digits I–IV of feet (absent in *Fulica*). *Paragallinula* also differs from *Fulica* in at least 12 diagnostic osteological characters (characters 120, 124, 125, 127, 139, 216, 274, 298, 311, 312, 316, 343 in Livezey 1998, to which is referred for descriptions of characters and their states).

Paragallinula gen. nov. further differs from the two species of *Pareudiastes* in (iii) frontal shield with acuminate posterior margin (squared margin in *Pareudiastes*); (iv) ventroanterior position of nasal depression (ventromedial in *Pareudiastes*); (v) fully feathered lores (in *Pareudiastes*, lores with sparsely feathered, yellow-orange area from base of maxilla to orbit); (vi) gradual change in colouration on hindneck from dark grey head to paler lower neck and back (very dark without noticeable change in colour from head to back in *Pareudiastes*); (vii) flank feathers with large white streaks (no streaks in *Pareudiastes*); (viii) undertail-coverts white dorsolaterally, black ventromedially (entirely black or brownish-black in *Pareudiastes*); (ix) six pairs of rectrices (four in *Pareudiastes*); (x) rectrices forming normally-shaped tail (in *Pareudiastes*, rectrices very short barely protruding beyond uppertail- and undertail-coverts); (xi) leading edge of distalmost primary with narrow white margin (absent in *Pareudiastes*); (xii) underwing-coverts with white bars (not barred in *Pareudiastes*); (xiii) bend of wing whitish (no white colouration in *Pareudiastes*); and (xiv) presence of narrow cutaneous folds on lateral and medial sides of digits I–IV of feet (absent in *Pareudiastes*).

Paragallinula gen. nov. further differs from *Tribonyx* in (ii) broad naked area on crown in downy plumage (absent in *Tribonyx*); (iii) long, filamentous white filoplumes in downy plumage (absent in *Tribonyx*); (iv) frontal shield with acuminate posterior margin (rounded in *Tribonyx*); (v) undertail-coverts white dorsolaterally, black ventromedially (entirely blackish in *Tribonyx*); (vi) six pairs of rectrices (eight in *Tribonyx*); (vii) underwing-coverts dark grey, blackish or black (medium brown in *Tribonyx*); and (viii)



Fig. 2. Lesser Moorhen *Paragallinula angulata* Sundevall, 1850, Kgomo Kgomo, South Africa, Feb. 2011 (photo by Mark Tittley). This photograph illustrates two diagnostic character states differentiating *Paragallinula* from the genus *Gallinula*: the orange colouration on the frontal shield does not cover the entire shield, and the lack of a contrasting reddish band on the legs proximal to the ankle joint.

bend of wing whitish (no white colouration in *Tribonyx*). *Paragallinula* also differs from *Tribonyx* in a single osteological character: (ix) ossa digitorum pedis, digiti tertius, phalanx intermedialis (secundi) is equal to or longer than phalanx quartus (in *Tribonyx* modally shorter than phalanx distalis (tertius)).

Paragallinula gen. nov. further differs from *Porphyriops* (*P. melanops*) in (iii) broad naked area on crown in downy plumage (absent in *Porphyriops*); (iv) long, filamentous white filoplumes in downy plumage (absent in *Porphyriops*); (v) ventroanterior position of nasal depression (ventromedial in *Porphyriops*); (vi) feathers at base of bill, lores and crown not contrasting with rest of head (in *Porphyriops* contrastingly black); (vii) flank feathers mostly plain but with large white streaks at tips (flank feathers brown-grey, spotted white in *Porphyriops*); (viii) central belly dark slate-grey (whitish in *Porphyriops*); (xi) undertail-coverts white dorsolaterally, black ventromedially (white in *Porphyriops*); and (x) rectrices dark grey or black (brown in *Porphyriops*). In addition, there are two diagnostic osteological differences between *Paragallinula* and *Porphyriops*: (xi) os frontale, facies dorsalis moderately convex (flat or slightly concave in *Porphyriops*), and (xii) os squamosum, fossa temporalis distinct, separated medially from each other by significantly broad, elevated expanse of os frontale (in *Porphyriops*, indistinct, shallow, limited to region immediately ventral to processus postorbitalis).

Etymology

The generic name is derived from the Greek *para* (beside) and the Latin *gallinula* (a little hen or chicken). It denotes the resemblance of *P. angulata* to species of *Gallinula* but highlights that they are independent evolutionary lineages. The gender of the name is feminine.

Distribution

Paragallinula angulata is found in most of the African continent from Senegal and Gambia to Ethiopia, Namibia, Botswana and South Africa.

Discussion

In the past, the validity and systematic position of many monotypic genera of birds were problematic. This is because the genera were not based on phylogenetic studies but on subjectively inferred evolutionary distinctiveness which in turn was based on phenotypic distinctiveness and commonly their insular location. Indeed, some taxonomists have placed large numbers of species in monotypic genera for such reasons, but the introduction of molecular phylogenetic methods in avian taxonomy revealed that many of these were nested within other genera (e.g., Johnson *et al.* 2001; Gibson & Baker 2012; Alström *et al.* 2015). The resulting gradual elimination of monotypic genera in many bird groups has enhanced understanding of avian diversification. Conversely, several species have been shown to occupy a phylogenetic position inconsistent with their traditional generic assignment, resulting in the recognition of new monotypic genera (e.g., Chesser *et al.* 2009; Slager & Klicka 2014). It is for this latter reason that, to re-circumscribe *Gallinula* as a monophyletic group and so eliminate its current paraphyly, we erect a new monotypic genus *Paragallinula* gen. nov. for *G. angulata*. This reflects the well-supported phylogenetic position of *G. angulata* outside the *Gallinula-Fulica* clade and avoids the inclusion of five species of *Gallinula* in the distinctive genus *Fulica*, and accords with pleas for ‘economy of nomenclatural change’ (Vences *et al.* 2013).

The contents of the genus *Gallinula* have been gradually revised by the transfer of phylogenetically divergent species to other genera. Several species of rails which are still referred as “gallinules” have sometimes been placed in the genus *Gallinula*, including Allen’s (*Porphyrio alleni* Thomson, 1842), Purple (*P. martinicus* (Linnaeus, 1766)) and Azure (*P. flavirostris* (J.F. Gmelin, 1789)) gallinules (e.g., Ripley 1977; Howard & Moore 1991). Molecular phylogenetic evidence accords with plumage features showing a closer relationship to *Porphyrio* swamphens and far removed from *Gallinula* moorhens

(e.g., typical *G. chloropus*) (Trewick 1997; García-R *et al.* 2014a). Such discoveries demonstrate the effect of convergence in body-form and coloration of separate rail lineages on taxonomic inference. Reconciliation using molecular data helps us understand how phenotypic traits evolve in response to ecological conditions, and in this case shows that the informal composition of gallinules is not a natural grouping.

Analysis of the timing and pattern of diversification within Rallidae established on fossils and complete mitochondrial genomes is revealing (García-R *et al.* 2014a, 2014b). The node that separates *Fulica* from the most closely related group of *Gallinula* (including *G. chloropus*) dates to 18 Mya (95% highest posterior density interval of 10–26 Mya), whereas the mean age of the *Fulica* group is under 10 Mya. The position of *G. angulata* as the sister of *Fulica* and *Gallinula* indicates that the time of divergence between Lesser Moorhen, *Gallinula* and *Fulica* is similar to or exceeds that of several widely accepted genera of rails, including *Amaurolimnas* Sharpe, 1893 / *Aramides* Pucheran, 1845, *Neocrex* Sclater & Salvin, 1869 / *Pardirallus* Bonaparte, 1856, *Amauornis* Reichenbach, 1853 / *Gallicrex* Blyth, 1852 and *Aramidopsis* Sharpe, 1893 / *Lewinia* G.R. Gray, 1855 (García-R *et al.* 2014a, 2014b). This further supports that *Gallinula* and *Fulica* are best retained as separate genera but that Lesser Moorhen should be placed in a different genus. Our treatment reconciles paraphyly of *Gallinula* as follows: *Gallinula* comprising *G. chloropus*, *G. galeata*, *G. comeri*, *G. nesiotis* and *G. tenebrosa*; *Tribonyx* comprising *T. ventralis* and *T. mortierii*; *Porphyriceps melanops*; and *Paragallinula angulata*.

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