17. A brief history of the Megapodes (*Megapodiidae*)

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**Abstract**

The fossil history of megapodes is long but rather sparse. It includes the giant Australian megapode *Progura gallinacea*, which may be the megafaunal form of the living Malleefowl.

Megapodes comprise a family of galliform birds that are notable for their breeding biology, including mode of incubation, absence of parental care and hyperprecociality of hatchlings. They occur mainly in Australo-Papua, where they have their greatest diversity, and the southeastern Pacific. This distribution is possibly constrained by competition with pheasants or predation by certain mammalian groups or both. Megapodes are regarded as the earliest diverging lineage of living galliforms. Their early fossil record is sparse but extends to the Late Oligocene (26-24 million years ago) of central Australia. Most fossil records come from the Pleistocene. Most island species were exterminated soon after the arrival of humans and their mammalian commensals. Species of scrubfowl were the most frequent victims, but there were also very large megapodes strikingly different from modern forms on Fiji and possibly New Caledonia. In Australia at this time, there was a giant megapode *Progura gallinacea*. It was closely related to the living Malleefowl and it has been suggested that Progura was the megafaunal form of that species.

**Introduction**

The megapodes (*Megapodiidae*) are a distinctive family in the avian order Galliformes. The common name 'megapode' and the name of the type genus *Megapodius*, from which the family name is also derived, draw attention to the size of the feet (*mega*, large + *podius*, foot). An examination of one of these birds will quickly reveal why this name is appropriate (Figure 1). It is not the feet, however, that have attracted the attention of scientists since the 1800s. Also known collectively as mound-builders or incubator birds, the megapodes are remarkable for their unusual breeding biology. Incubation is through the use of external heat sources (decaying vegetation, sun, geothermal). Other than for temperature regulation of the substrate in which the eggs are laid, there is no parental care of the young. The chicks hatch in a state of hyperprecociality, capable (and obligated) to look after themselves immediately and able to fly within a few hours of emerging from the nest.

While these unusual habits were known for many years, much of the pioneering work was conducted in Australia by Harry J. Frith (CSIRO Division of Wildlife Research) working on the Malleefowl (*Leipoa ocellata*). Like the majority of megapode species, Malleefowl place their eggs in a mound of soil or vegetable matter to be incubated by heat from the sun or decomposing plant matter. Some megapodes, however, lay the eggs in volcanically-warmed soils and others place them in accumulated vegetation among the roots at the bases of trees. A few species nest colonialy. Some species exhibit several of these strategies. Recent work has supported mound building as the ancestral incubation behaviour in megapodes, with burrow nesting having arisen independently on at least three occasions (Harris *et al.* 2014). The breeding habits of megapodes, and particularly the Malleefowl, and other aspects of their biology have been well described elsewhere and so will not be repeated here (see Frith 1959, 1962, Elliot 1994, Jones & Göth 2008, and particularly Jones *et al.* 1995, and references therein). This essay presents a brief introduction to the prehistory and history of the Megapodiidae.
Classification of the megapodes

The Megapodiidae family belongs to the Order Galliformes (Figure 2a), the fowl-like birds, which also includes the Cracidae (guans, chachalacas, curassows; Central and South America), Odontophoridae (New World quail; North and South America), Numididae (guineafowl; Africa) and the large and diverse Phasianidae (grouse, pheasants, turkeys, Old World quail, partridges, chooks, peafowl; cosmopolitan). Megapodes were once considered the sister-group to the Cracidae but are now thought to be the sister-group to all other living galliforms and the earliest diverging lineage among extant members in the Order.

Within the megapode family there are seven genera (Figure 2b) and 22 living species (Jones et al. 1995). These are given in Appendix 1, together with dates of description and distributions. Megapodes fall into two major clusters of taxa: the scrubfowls (Megapodius, Eulipoa, Macrocephalon) and brush-turkeys (Alectura, Aepypodius, Leipoa, Talegalla) (Figures 2b and 3) (Harris et al. 2014). Three species occur in Australia, the Malleefowl, the Australian Brush-turkey (Alectura lathami) and the Orange-footed Scrubfowl (Megapodius reinwardt). The family reaches its greatest diversity in the Australian-New Guinea region, but its distribution extends to the Philippine Islands and eastern Indonesia (Sulawesi, Lombok), east through the southwest Pacific islands currently as far as Tonga and north to Micronesia (Palau, Mariana Islands), with an outlier in the Nicobar Islands in the eastern Indian Ocean (Figure 4).
Figure 2a. Classification and relationships of the Families of the Order Galliformes.

Figure 2b. Classification and relationships of the genera of megapodes following the molecular phylogeny of Harris et al. 2014.
Figure 3. Representatives of the seven living genera of Megapodiidae. Images from references cited. Top row, left, *Alectura lathami* (Gould 1840), right, *Aepypodius bruijni* (Oustalet 1881).
European discovery of the Megapodiidae

The first western writer to mention megapodes was Antonio Pigafetta (1491-1534), an Italian explorer and scholar who was a member of Ferdinand Magellan's voyage to circumnavigate the world. Magellan was killed in the Philippines in 1521 and Pigafetta was injured in the same incident. Of the approximately 240 men who had accompanied Magellan when he departed in 1519, only 18 men returned to Spain in 1522, of whom Pigafetta was one. In a detailed journal he compiled during the trip, he described scrubfowls observed in the Philippine Islands before the incident and commented on their apparent habit of burying their eggs (Figure 5).

The first megapodes described to science were named in 1823 by the French naval surgeon and naturalist Joseph Paul Gaimard (Gaimard 1823). He collected specimens of two species on the voyage of the Uranie commanded by Louis Claude Desaulses de Freycinet (1817-1820). From Tinian, in the Marianas Island, Micronesia, he named Megapodius laperouse (Micronesian Megapode), commemorating an earlier French explorer, Jean-François de Galaup, comte de Lapérouse. From Waigeo, off the northwest coast of New Guinea, he acquired and named the original specimens of M. freycinet (Dusky Megapode). Gaimard also coined the names megapode and Megapodius.

In the same year Charles Henri Frédéric Dumont de Sainte-Croix named Megapodius reinwardt after Caspar Georg Carl Reinwardt, a Dutch naturalist and collector who worked in the region (Dumont 1823). The specimen on which the name was based came from Lombok on the extreme western edge of the species' distribution. The range of M. reinwardt is the greatest of any species of megapode. It occurs through eastern Indonesia and southern New Guinea and is one of the three species found in Australia, occurring northern Western Australia and Northern Territory and north-eastern and central eastern Queensland.
Figure 5. Historical localities in early western discovery of megapodes: site in Philippine Islands from which Antonio Pigafetta observed and described likely megapodes in 1521; islands from which first specimens of *Megapodius laperouse* and *M. freycinet* were collected (Gaimard 1823); and type locality of *M. reinwardt* (Dumont 1823).

Another Australian megapode, the Australian Brush-turkey, was known before these descriptions and had been illustrated earlier by the surgeon-scientist John Latham (Latham 1821). He was working with a dried specimen without the benefit of any knowledge of the live animal and so, impressed by the naked neck and somewhat curved bill, bestowed the name New Holland Vulture (Figure 6). Unfortunately for Latham, the rules of scientific zoological nomenclature dictated that a common name alone was not sufficient to officially describe a new species—a properly formulated scientific name was mandatory. Latham subsequently supplied a new generic name – *Alectura* – but never got around to providing a specific one (Latham 1824). Thus he missed out on being the author of this species’ name, beaten by the British zoologist John Edward Gray, who officially named this species in 1831 (Gray 1831). Gray graciously acknowledged Latham’s previous work by naming the bird after him: *Alectura lathami*.

The third Australian megapode, the Malleefowl, was described in 1840 by the famous ornithologist, John Gould, in his massive work, *The Birds of Australia* (Gould 1840). The specimen on which the name was based had been obtained by Gould’s collector, John Gilbert, in Western Australia the previous year. Gilbert had been informed by locals that these birds left their eggs in large mounds of soil to incubate. Based on this information, Gould gave the Malleefowl the generic name *Leipoa*, meaning ‘the bird that leaves its eggs’.
**Distribution**

Other than the Nicobar Island population, megapodes have a distribution with the revised Wallace’s Line as the western limit (Figure 7a). Factors contributing to this pattern have been debated. One suggestion is that the presence of megapodes is constrained through competition with pheasants. The latter group extends from the west from Southeast Asia to Wallace’s Line. There is only marginal overlap between megapodes and pheasants in a few islands: Palawan, Lesser Sunda Islands and northern edge of Borneo (Figure 7b) (Dekker 1989). The other idea is that megapodes cannot survive in the presence of predatory mammals, such as cats (Felidae) or civets (Viverridae) (Olson 1980). Both groups have distributions that are largely complementary to that of megapodes, again reaching Wallace’s Line but rarely crossing it. It is only in a few localities do the mammalian predators show overlap with megapodes. Whether one or both theories (or neither) explain the present day distribution of megapodes is not certain.

The somewhat anomalous occurrence of a scrubfowl on the Nicobar Islands has been attributed at times to human action. It is easy to transport eggs during oceanic travel and this practice may have contributed to the presence of megapodes on various locations throughout the range of the family. Scrubfowl are particularly vagile, however, and chicks have shown a great ability to disperse, sometimes for considerable distances over water.
Figure 7a. Wallace’s Line, the boundary between the Asian and Australasian faunas. The solid grey line is that originally delimited by Alfred Russel Wallace (Wallace 1860); the dashed line is the modification of the northern section by Thomas H. Huxley (1868). The latter is a better fit for the western boundary of the megapodes.

Figure 7b. Comparative distributions of Phasianidae (pheasants, excluding quail) in black and Megapodiidae in grey (adapted from Figure 1 of Olson 1980). Areas of overlap between pheasants and megapodes are shown with arrows (Palawan, northern Borneo, Lesser Sunda Islands).
**Hypothetical megapodes**

One curious report originates from the second voyage of Captain James Cook (1772-1775). The naturalist on that expedition, William Anderson, briefly made reference during his time on New Caledonia to a bird that he called *Tetrao australis* (‘southern grouse’), with the very short description ‘*Fusca nigraque; pedibus nudit*’ (‘brown and black; legs bare’). Many years later Robert Gray (1861) erected the name *Megapodius andersoni* on the basis of the original account in Anderson’s unpublished papers (Figure 8). Gray supposed it could not be attributed to any bird then known from New Caledonia. While the description could possibly have referred to a large rail, Anderson should have been able to distinguish such from a fowl-like bird. No megapodes occur in New Caledonia today, although Holocene-aged fossils have been recovered (see below).

A former resident on Sunday Island (now known as Raoul Island and uninhabited) in the Kermadec Islands (1100 km north-northeast of New Zealand and 900 km south-southwest of Tonga) recounted the presence of birds and their mounds in the mid-1870s (Figure 8a). These lived on the floor of one of the volcanic craters that dominate the island (Lister 1911). His observations imply the presence of a megapode on the island, although some workers suggested other possibilities. In any case, a volcanic eruption in 1876 razed the crater floor and with it, any obvious evidence of the bird’s existence.


Two species were each named on the basis of only a single egg donated to the British Museum by explorers in the 1800s (Gray 1861) (Figure 8a). These were from Western Samoa (*Megapodius stairi*) and the Ha’apai Group, Tonga (*M. burnabyi*), where megapodes do not occur today. Given the absence of other evidence, together with the practice of humans to transport eggs between islands, it was long considered that these eggs were those of *M. pritchardii* (Polynesian Megapode), today found elsewhere in Tonga (surviving only on Niuafo’ou). In addition, the size of the eggs overlapped those of *M. pritchardii* and several other species in the Pacific. The eggs were studied by David Steadman, an expert on megapodes of the Pacific islands.
He concluded that neither egg could indisputably be attributed to *M. pritchardii*, another living species or a recently extinct one (Steadman 1991). Given their unsettled attributions to any megapode living or dead, Steadman regarded them as *nomina dubia*.

**Fossil and archaeological record**

Some galliform fossils from late Eocene and early Miocene deposits in France were initially thought to be primitive representatives of the megapodes, hence the name Quercymegapodiidae after Quercy, one of the sites at which they were found (Mourer-Chauviré 1992). Subsequently, additional species were described from specimens elsewhere in Europe and from Brazil. Further studies since then have concluded that the quercymegapodes are early galliforms that share primitive characters with true megapodes, but were not particularly closely related within the Order (Mayr 2009). With the removal of this group, most of the megapode fossil record is confined to the last 1.6 million years (Quaternary).

The oldest known megapode is *Ngawupodius minya* from the Late Oligocene (26-24 million years ago) of north-eastern South Australia (Boles & Ivison 1999). It was described from a tarsometatarsus (foot bone), although other bones are now known but not yet described. This was a very small bird, about the size of a large quail. The proportions of the tarsometatarsus most closely resemble those of the living Malleefowl and it is conceivable that *Ngawupodius* was in the lineage leading to the Malleefowl.

Other than *Ngawupodius*, all other extinct forms come from Quaternary fossil deposits and archaeological sites (primarily Holocene; 10,000 years ago to the present), mostly on Pacific islands (Steadman 1999). With the exception of a few large and remarkable species, fossil megapodes of this age belong to the genus *Megapodius*. These demonstrate that the distribution of this genus (and hence family) was once more extensive than at present and that the number of species of *Megapodius* was previously considerably greater. David Steadman (1999) and others have documented the presence of both extant and extinct taxa from deposits throughout the Pacific, including from islands that do not currently support any megapodes (New Caledonia, Fiji, several island groups of Tonga, Samoa, Niue, and Pohnpei). The Samoan records extend the distribution of megapodes further east. The prehistoric presence of *Megapodius* on New Caledonia could conceivably be related to the hypothetical megapode *M. andersoni* of Captain Cook’s expedition. The fossils also show that on even some small islands three species of *Megapodius* co-existed. Steadman attributes the loss of these populations to the arrival of humans. No doubt any commensal animals (pigs, dogs, rats, etc.) would have also had major impacts. The naïve birds, plus the eggs supplied by the obvious mounds, would have been easily exploited food sources. This pattern of anthropogenic extinctions of not only megapodes but many bird groups has been documented across many Pacific islands. Steadman (1999) estimated that had people not exterminated so many populations, the number of megapode species would have probably been closer to 45-55.

Three large, now extinct, non-scrubfowl species warrant further comment. The largest galliform bird known to have existed, *Sylviornis neocaledoniae*, occurred in New Caledonia and the Île des Pins up until the Holocene. This was originally described as a ratite (Poplin 1980) and subsequently a megapode (Poplin et al. 1983) but further work has concluded that, while related to megapodes, it warrants placement in its own family (Mourer-Chauviré & Balouet 2005). This remarkable bird averaged 1.7 m in length and about 30 kg in mass. *Sylviornis* was flightless, its wings being greatly reduced. The bill was laterally compressed, dorsoventrally high and sported a large knob. Like megapodes, this bird apparently also incubated its eggs in mounds. Mounds 5 metres high and 50 metres wide found on the Île des Pins have been suggested as remnants of *Sylviornis* mounds. Humans wiped *Sylviornis* out soon after arrival on New Caledonia in 1,500 B.C.

Another large island form, this one a true megapode, was *Megavitiornis altirostris* from Late Pleistocene-Holocene deposits in Fiji (Worthy 2000). Like *Sylviornis*, it was flightless and had a markedly enlarged, laterally compressed bill. Trevor Worthy, who found and described this species, considered that the massive bill may have been used for cracking large, hard seeds. Fiji has several trees that produce seeds, but there are not animals now living on the islands that can open them. *Megavitiornis* was also a victim of humans soon after they colonized the islands.
Progura gallinacea was a turkey-sized megapode from south-eastern Australia. It was described in 1888 by C. W. de Vis, the head of the Queensland Museum from among fossilized bones from the Darling Downs region (c. 5-1 million years ago) (de Vis 1888). He is now known to have frequently assigned his fossils to the wrong groups and regarded Progura as a relative of the crowned pigeons (Goura) of New Guinea.

Nothing more was done with Progura until new bones were found at Naracoorte Caves, South Australia, leading G. F. van Tets of CSIRO Division of Wildlife Research to restudy the de Vis specimens together with the new ones (van Tets 1974). Progura has been well represented in this area because of the many caves and the birds’ apparent inadvertent practice of falling into them at regular frequency. Van Tets discerned that four of de Vis’ fossil birds (Progura, a purported stork, a purported bustard and a genuine megapode) actually represented a single species, which was in fact a very large megapode. The name Progura, having been published first, had priority for this bird. On the basis of the new specimens, van Tets also named a second, smaller species P. naracoortensis, which he distinguished on relative leg length and overall size. A few years later, however, he suggested that the two species of Progura might represent different sexes of the one species.

The discovery of additional and more complete specimens at Naracoorte and the surrounding area allowed a new study that revisited the conclusions of van Tets (Boles 2000). It addressed whether one or two species of Progura should be recognised and attempted to identify the closest living relative among living megapodes.

Modern megapodes exhibit minor differences in size related to gender, but show considerable variation between individual birds. The greater assemblage of Progura specimens provided no evidence of obvious sexual dimorphism. Instead, the variation seen appears individual in nature. This also led to the proportionally different leg lengths noticed by van Tets because the comparisons where made between bones from different individuals. This, together with the absence of an obvious break in the size range of specimens, implied that one species of Progura should be accepted. Thus, Progura naracoortensis van Tets, 1974, was synonymised with Progura gallinacea De Vis, 1888 (Boles 2008).

Of all living megapodes, that closest to Progura in morphology is the Malleefowl. In fact, the differences between the two are mainly quantitative (size), with essentially no other differences of significance (Figure 9). So close are Progura and Leipoa that recognition of two genera is not justified. Thus, Progura De Vis, 1888, becomes a synonym of Leipoa Gould, 1840 and the species name becomes Leipoa gallinacea (De Vis) (Boles 2008).

During the Late Pleistocene (more or less the last 100,000 years until 10,000 years ago), many groups of Australian animals began to show increases in body size. It was at this time that Diprotodon optatus, the largest marsupial ever to have lived, appeared. Collectively called the megafauna, these animals also included giant kangaroos, wombats and other mammals. Suddenly, about 30-40,000 years ago, these large animals went down one of two paths. Along one, the lineage died out. Along the other, the animals started getting smaller, a process called dwarfing. Much of the megafauna, such as Diprotodon, went down the former path. Others like the koalas and Tasmanian Devils went along the latter, as did the Eastern Grey Kangaroo (Macropus giganteus), reaching its modern proportions. The decrease in size ranged from only 4% in the Devils to more than 25% in the Kangaroo.

Progura gallinacea was a megafaunal member of Leipoa, which gives rise to the question, did it turn into modern Leipoa ocellata by dwarfing (analogous to Eastern Grey Kangaroo)? This would have required a reduction in size of 25-30%. While almost all of the fossil material from the Naracoorte region represents gallinacea, there is some evidence that ocellata was also present, which conflicts with the suggestion of dwarfing. Until further information become available, the two are retained as separate species.
As yet unpublished information from recently discovered fossil deposits in caves in the Nullarbor Plain points to an undescribed species present at the same time as *Progura*. Another intriguing aspect is the presence of large mound-like piles of stones known through parts of western New South Wales and elsewhere (Noble 1999). These do not appear to be geological formations, often differing strikingly from the underlying strata. The suggestion that these represent the remnants of old *Progura* mounds is a fascinating one, awaiting further study.

**The future for megapodes**

Work on archaeological sites through the Pacific has demonstrated the negative influence that human contact has had on megapodes in numerous locations, with many populations now extinct. This trend is continuing. A number of megapodes species are included on the IUCN Red List of Threatened Species as Endangered or Vulnerable, based on the evaluation of a range of criteria (Figure 10). An Endangered species is regarded as facing a very high risk of extinction in the wild in the near future. Four species of megapodes are listed as Endangered. A Vulnerable species, while not Endangered, is facing a high risk of extinction in the wild in the medium-term future. Six megapodes species are included in the Vulnerable category. One species has been evaluated and, while it does not satisfy the criteria for Endangered or Vulnerable, it is close to qualifying for the latter and so is listed as Near Threatened (NT). Those species that are considered Endangered, Vulnerable and Near Threatened are noted in Table 1 and their localities in Figure 10. It is worth noting that even most of the species regarded as Least Concern (those that do not qualify for any of the other categories) are nonetheless noted as decreasing.

Most megapode species face a similar suite of detrimental factors, with a scattering of other threats that may vary among species. Predation by humans on birds or, more often, overexploitation of eggs is common for the majority of populations outside Australia. Unsustainable harvesting of eggs, frequently illegal, can exceed the rate at which new individuals enter the population. Human-introduced animals often take a heavy toll on chicks and eggs. Competition with non-native grazing animals, such as goats and cattle, is a hurdle in some locations. As populations are reduced in size and area they can become increasingly susceptible to native predators that are not a problem in less disturbed situations. Loss of habitat and destruction of nesting areas from logging or agriculture are threatening processes for many species, while mining, road development and even tourism are implicated for some. Other risks come from fire, invasive vegetation and, for some populations on small islands, severe weather events. Of these causes, unregulated overexploitation by humans, predation by feral animals and habitat loss are probably the most severe.

The Malleefowl is somewhat unusual among the threatened species because it is the only one that has a continental distribution, rather than an insular one. Hunting of birds and eggs is not an important contributing factor to its decrease, but habitat loss, predation by feral animals, competition for habitat and fire are still significant dangers.

There are organisations in Australia and elsewhere working to conserve megapodes. This is not an easy task: there are many obstacles in their way. But many megapodes depend on it if they are to have a future.
Appendix 1. Genera and species of living Megapodiidae (following Jones et al. 1995), giving the scientific name, describer and date; IUCN category for threatened species; English name; and distribution. The IUCN categories are (V) Vulnerable, (E) Endangered, (NT) Near Threatened.

<table>
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<th>Scientific Name; Author; Date; (IUCN Category)</th>
<th>English Name</th>
<th>Distribution</th>
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<td>lathami J.E. Gray, 1831</td>
<td>Australian Brush-turkey</td>
<td>E Australia: N Queensland to EC NSW</td>
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<td>Wattled Brush-turkey</td>
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<td>Brujin’s Brush-turkey</td>
<td>Waigeo, West Papuan Islands</td>
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<td><strong>LEIPOA</strong> Gould, 1840</td>
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<td>Malleefowl</td>
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<td>Maleo</td>
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<td>Dusky Megapode</td>
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<td>Species</td>
<td>Subspecies</td>
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<td>Vanuatu Megapode</td>
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<td>Sula Is; Banggai Is.</td>
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<td>Melanesian Megapode</td>
<td>Bismarck Archipelago; Solomon Islands, peripheral islets</td>
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<td>Biak Megapode</td>
<td>Islands of Geelvink Bay, including Biak Is, Numfoor Is, Mios Num Is</td>
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<td><em>decollatus</em> Oustalet, 1878</td>
<td>New Guinea Megapode</td>
<td>N New Guinea; Yapen Is; offshore islands</td>
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<td>Tanimbar Megapode</td>
<td>Tanimbar Islands</td>
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References


