Megapode phylogeny and the interpretation of incubation strategies

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Among megapodes, several incubation stategies can be recognized. Eggs are incubated by heat generated from microbial decomposition, volcanism, or the sun. For a long time, controversy has existed whether these strategies represent primitive traits, inherited from reptilian ancestors, or have evolved from the 'regular' way of incubation in birds. In this paper these strategies are interpreted by superimposing them on the most recent phylogenetic hypotheses regarding the inter- and intrafamilial relationships of megapodes. We conclude that similarities shared with reptiles and kiwis are due to convergence. Arguments are put forward that mound-building represents the plesiomorphic condition in megapodes and that burrow-nesting has been derived from it. Furthermore, we infer that burrow-nesting at sun-exposed beaches has evolved from burrow-nesting in volcanically heated soils.

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Introduction

Superficially, the incubation strategies of megapodes show more resemblance to those of reptiles than to those of birds. Both megapodes and reptiles bury their eggs either in mounds of rotting leaves or in burrows and this has made some authors conclude that megapodes must have inherited their breeding behaviour directly from their reptilian ancestors (e.g. Portmann, 1955). Others believed that ancestral megapodes incubated their eggs like other galliform birds do (e.g., Guillemard, 1886; Pycraft, 1900; Heilmann, 1926; and Baltin, 1969). No one, however, based his argumentation on phylogenetic grounds.

The most detailed study regarding the question of megapode relationships and evolution of their incubation stategy has been published by Clark (1960, 1964a, 1964b), who became convinced that the megapode incubation strategy was not a reptilian trait, but evolved from the 'regular' way of incubating eggs with body heat. According to Clark (1964b), mound-building must have been developed first, to become modified later to burrow-nesting in the maleo *Macrocephalon maleo* and some *Megapodius* species.

Clark (1960) could falsify Portmann's (1938) assumption that certain characters of megapodes, such as the lack of an egg-tooth at hatching and lack of natal downs, were reptile-like. Clark (1964b) explained the large number of eggs, long incubation period, precocity of young at hatching, and lack of parental care to be one or two complexes of adaptations to their particular incubation strategy. Later, Seymour &

Ackerman (1980) supported Clark's (1964b) conclusion and also classified these reptile-like features as convergent adaptations to the aberrant nesting habits.

Not everyone who agreed that the megapode incubation strategy has been derived from the 'regular' avian way of incubation, also supported his view that burrow-nesting is supposedly derived from mound-building. Meyer & Wiglesworth (1898), Frith (1962), and Immelmann & Sossinka (1986) assumed that the most simple method, viz. burrow-nesting, might have been the phylogenetic precursor to mound-building.

In this paper an evolutionary scenario of megapode incubation strategy, based on the best phylogenetic hypotheses currently available (Brom & Dekker, 1992), will be presented. Similarities in breeding biology shared with reptiles and kiwis will be evaluated.

Incubation strategies

Among megapodes, four different incubation-strategies may be distinguished: 1) mound-building, 2) burrow-nesting between decaying roots of trees, 3) burrow-nesting at volcanically heated soils, and 4) burrow-nesting at sun-exposed beaches.

1) Mound-building: For the incubation of their eggs, mound-building megapodes construct piles of leaves, twigs, branches, and other organic and anorganic forest floor materials, such as humus and sand, which they rake together with their strong feet. The process of microbial decomposition (rotting) of the vegetative material, stimulated by the humid and warm climate of the (sub)tropical forests, generates the heat necessary for incubation. After a period of construction (see e.g. Crome & Brown, 1979; Jones, 1988), when the core of the mound reaches a suitable incubation temperature of approximately 32-34° C, egg laying begins. When an egg is about to be laid, the hen digs a hole in the top of the mound until she meets optimal incubation temperatures in the core. Here, in the egg chamber, she will lay her egg, which will be covered with leaves afterwards. During the maintenance phase, the period of egg-laying and incubation, mound-building megapodes spend day after day at the mound regulating the temperature. In some species, mounds are used year after year, often by more than one pair of birds. Such mounds may become several meters high and may contain tons of leaves.

Depending upon locality, the amount of leaves and sand varies considerably. The malleefowl *Leipoa ocellata*, an inhabitant of the open and dry *Eucalyptus* forests of southern Australia, builds mounds which consist largely of sand. Microbial decomposition, initiated by seasonal showers, generates the heat during the beginning of the egg-laying season. Once the warm, dry summer has begun, when the leaves have dried out and rotting has stopped, insolation becomes the main heat source for the eggs. Construction and maintenance of their mounds occupies malleefowl for approximately ten months per year.

2) Burrow-nesting between decaying roots of trees: This is the least studied megapode incubation strategy. It is only applied by several *Megapodius* spp. and easily overlooked because of the absence of a mound. Megapodes which apply this strategy dig a burrow (varying in shape between a hole, a pit, or a tunnel) at the base of trees which are still alive. The egg is deposited against or partially imbedded in the

decaying roots (Stresemann, 1941; pers. obs.). Depending upon location and the amount of leaves at the base of the tree, leaves may be added in the burrow when the hen fills it in upon egg-laying, thus contributing to the generation of heat. A burrow of this type, made by the Phillipine megapode *Megapodius cumingii* on a tiny islet off the coast of North-Sulawesi, did not contain any leaves. However, a nest of similar type made by the same species inside the tropical rainforest of the Dumoga-Bone National Park on North Sulawesi did (both pers. obs.). Microbial decomposition of the wood is responsible for the generation of the incubation heat.

3) Burrow-nesting at volcanically heated soils: Megapodes which apply this strategy dig burrows (which can have the shape of a simple hole or pit, or even tunnel in which the birds disappear entirely) at places where the ground is heated by geothermal activity. These nesting grounds, which can be several hectares in size, are often widely separated and thus not commonly available. They are therefore used communally by many pairs of birds. Nesting grounds are covered with permanent nesting-holes which look like small 'craters'. These craters originate as burrows which are used over and over again, and from which more sand has been removed during egg-laying than is added afterwards. The size of these permanent nesting holes depends on their 'age', frequency of use by the birds, and distance from the heat source. Inside these permanent holes the megapodes dig secondary burrows in which they lay their egg. One permanent nesting-hole can have one or more secondary burrows and can thus contain more than one egg. Secondary burrows are filled in with sand after the egg has been laid. Although, depending upon location in more or less dense forests, leaves may be added to the burrow or the sunshine may reach the ground, volcanism is the main source for the incubation heat. In contrast with mound-building megapodes, burrow-nesting species with this strategy only visit the site when an egg has to be laid and do not invest any time or energy in regulating the soil temperature. Therefore, periods of construction and maintenance as described by Jones (1988) do not apply for burrow-nesters.

4) Burrow-nesting at sun-exposed beaches: Megapodes which apply this strategy bury their eggs in holes or pits at communal nesting beaches. Because of the loose and sandy soil structure of most beaches the burrows collapse easily, and hence permanent nesting holes are less obvious or entirely absent. The main difference from volcanic heat incubation is the heat source: insolation rather than geothermal activity provides the heat for incubation. Megapodes which apply this strategy, like burrow-nesters which bury their eggs at volcanically heated soils, only visit the site when an egg is to be laid.

Mound-building is the most commonly used strategy. It is applied by 14 to 16 species representing all genera except *Macrocephalon*. The genera *Aepypodius*, *Alectura*, *Leipoa* and *Talegalla* consist of mound-builders which have never been observed laying their eggs in burrows on beaches or volcanic soils. *Macrocephalon maleo* is invariably a burrow-nester at volcanically heated sites and sun-exposed beaches. *Megapodius* is the only genus that encompasses both mound-building and burrow-nesting species. Four *Megapodius* species are strict mound-builders, while the Polynesian megapode *M. pritchardii* and the Moluccan megapode *M. wallacei* are obligate burrow-nesters. Both mound-building and burrow-nesting have been observed in different populations of the Philippine megapode *M. cumingii*, the

Melanesian megapode *M. eremita*, and the Micronesian megapode *M. laperouse*. The first two species even make use of different heat sources.

Egg-laying between decaying roots of trees has thus far only been recorded for *M. cumingii*, *M. eremita*, and the Vanuatu megapode *M. layardi*. The megapode on the small island of Niuafo'ou, *M. pritchardii*, lays its eggs at volcanically heated sites. It is possible that this species makes use of radiation heat as well.

Phylogeny and incubation

Ethological features have been used in various phylogenetic studies (e.g., Tembrock, 1989; Prum, 1990). There seems to be no reason not to use the breeding strategies, which can be regarded as behavioural adaptations, as character-states in this study.

Most recent hypotheses on the early diversification of birds consider the palaeognathous birds (ratites and tinamous) the sistergroup of all other extant birds (Cracraft & Mindell, 1989; and references therein). The anseriforms and galliforms (including the megapodes) branched off later during avian evolution. Taking into consideration the systematic position of the megapodes as the sistergroup of the remaining galliforms (Brom & Dekker, 1992), and the fact that ratites, tinamous, other neognathous birds, anseriforms and non-megapode galliforms incubate their eggs by means of body-heat (Fig. 6), the latter strategy may represent the plesiomorphic condition in the Galliformes. The megapode incubation strategy is apomorphic for the Megapodiidae. Thus follows that megapodes did not inherit their incubation strategy directly from the reptilian ancestors of birds. Similarities between the reproductive behaviour of reptiles and megapodes should therefore be regarded as convergent adaptations. Clark (1964a) and Seymour & Ackerman (1980) also came to this conclusion.

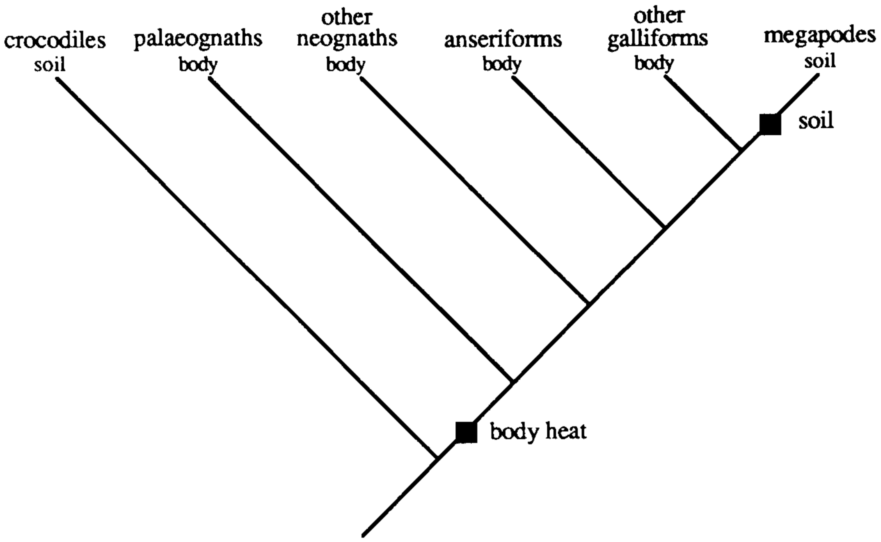

Figure 6. Incubation strategies plotted over the phylogenetic tree hypothesized by Cracraft (1973) and Cracraft & Mindell (1989).

Incubation strategy of the megapode ancestor

Theoretically, the question whether mound-building or burrow-nesting arose first in the course of evolution cannot be answered, since these strategies are confined to megapodes. Mound-building as well as burrow-nesting may be apomorphic within megapodes. Therefore, the various incubation strategies applied by megapodes will be superimposed on the best phylogenetic tree available at present (Brom & Dekker, 1992) in order to assess the ancestral character-state at the ingroup node (Maddison et al., 1984).

Fig. 7 shows that the ancestral state of incubation at the ingroup node is decisive: mound-building represents the plesiomorphic condition in megapodes.

In case Clark's (1964a) more conservative phylogenetic hypothesis is adopted, in which *Aepypodius, Alectura, Leipoa,* and *Talegalla* are presumed to form a monophyletic group, the ancestral state at the ingroup node would be equivocal: mound-building as well as burrow-nesting may represent the plesiomorpic condition. This implies that the megapode incubation strategy might have originated from burrow-nesting ancestors (Fig. 8a), from ancestors which were polymorphic with regard to incubation strategy (Fig. 8b), or from mound-building ancestors (Fig. 8c).

If the evolution of megapode incubation strategies would have followed the scenario illustrated in Fig. 8a, mound-building would have developed independently in two lineages, once in the group consisting of *Aepypodius, Alectura, Leipoa,* and *Talegalla* and once in *Megapodius,* and burrow-nesting would have been lost in *Aepypodius, Alectura, Leipoa,* and *Talegalla.*

Scenario 8b suggests a polymorphy as synapomorphy, mound-building and burrow-nesting have developed simultaneously in ancestral megapodes, which does not seem likely.

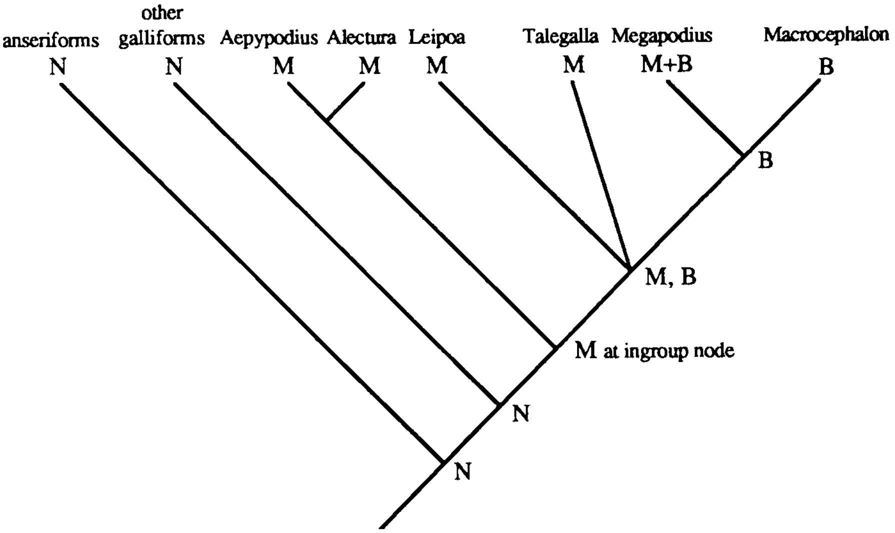

Figure 7. Character-state tree, with presumed ancestral states indicated at the nodes. (For topology of this tree, see Brom & Dekker, 1992). M = mound-building, B = burrow-nesting, N = 'normal' nesting by means of body heat. Since the intrageneric relationships are not known as yet, the breeding strategies within *Megapodius* are considered a polymorphy.

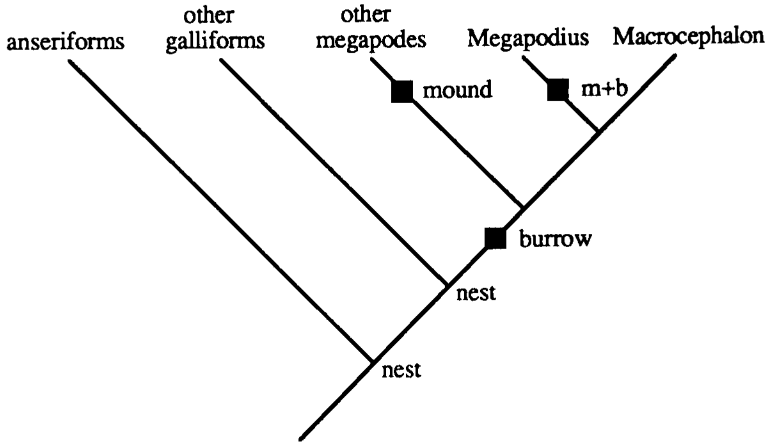

Figure 8a. Scenario for the evolution of megapode incubation strategies under the premise that *Aepypodius, Alectura, Leipoa,* and *Talegalla* should be monophyletic (Clark, 1964a). Burrow-nesting is hypothesized to be the ancestral condition.

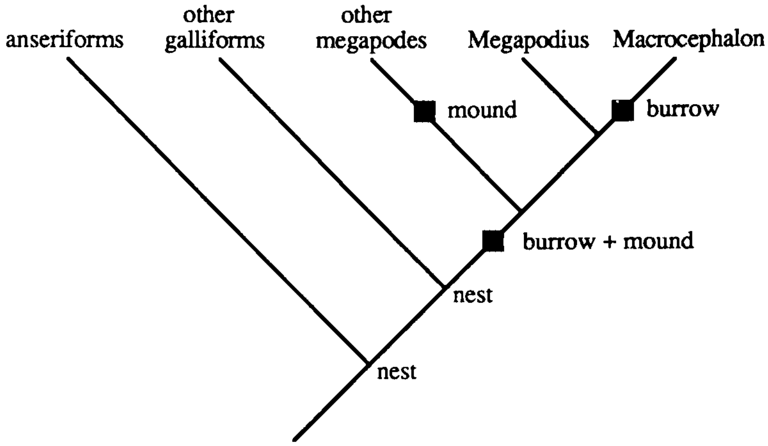

Figure 8b. Scenario for the evolution of megapode incubation strategies under the premise that *Aepypodius, Alectura, Leipoa,* and *Talegalla* should be monophyletic (Clark, 1964a). The presence of both strategies - burrow-nesting and mound-building - is hypothesized to be the ancestral condition.

If mound-building is plotted as the ancestral state in the same phylogenetic hypothesis (Fig. 8c), burrow-nesting must have developed after *Megapodius* and *Macrocephalon* had branched off. Mound-building was lost in *Macrocephalon*. After burrow-nesting developed in the *Megapodius - Macrocephalon* - group and resulted in a polymorphic character-state for this lineage, some individuals were mound-builders and others burrow-nesters. Burrow-nesting became fixated in *M. maleo* in which species mound-building behaviour was lost altogether. In the genus *Megapodius* the

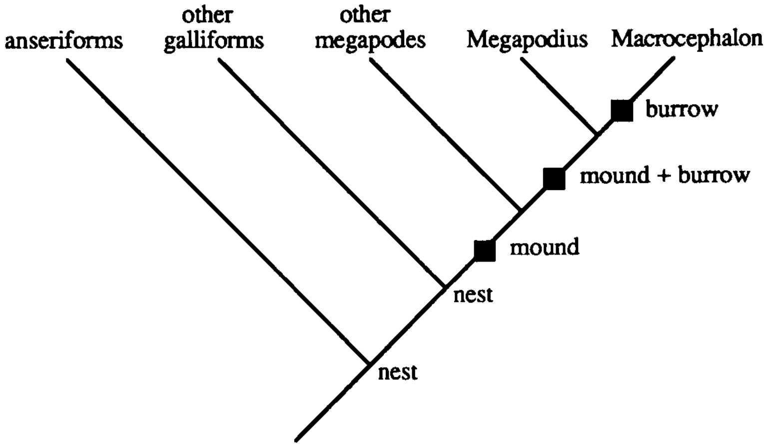

Figure 8c. Scenario for the evolution of megapode incubation strategies under the premise that *Aepypodius, Alectura, Leipoa,* and *Talegalla* should be monophyletic (Clark, 1964a). Mound-building is hypothesized to be the ancestral condition.

situation is more complicated. Some species are still polymorphic in their breeding behaviour (e.g. *M. cumingii* and *M. laperouse*), in others either mound-building (e.g. *M. pritchardii*) or burrow-nesting (such as the Nicobar megapode *M. nicobariensis* and the orange-footed megapode *M. reinwardt*) was lost.

In conclusion, even in Clark's (1964a) hypothesis, mound-building most likely represents the plesiomorphic condition in megapodes. Supportive evidence for this conclusion is given by the amount of yolk in eggs of mound-builders versus burrow-nesters (see below).

Yolk as indicator

Based on comparison with reptiles, Kramer (1953) and Portmann (1955) suggested that the earliest birds were super-precocious. Recently, this view has gained support by the discovery of embryonic avian skeletons in the Upper Cretaceous of the Gobi desert (Elzanowski, 1985). Precociousness is correlated with the amount of yolk in the eggs. The greater the proportion of yolk, the more developed the hatchlings are (Sotherland & Rahn, 1987). The eggs of the earliest birds are therefore supposed to have been rich in yolk, just like the eggs of their reptilian ancestors.

Kramer (1953) and Portmann (1955) were convinced that the megapode incubation strategy is a primitive trait. Above, we argued that this is not the case. Thus, megapodes must have evolved from birds that were not super-precocious. The strong development of the megapode chick at hatching should therefore be considered an apomorphic character for the group. Similarly, the high yolk content of their eggs (Fig. 9) should be regarded as an apomorphic rather than a plesiomorphic condition.

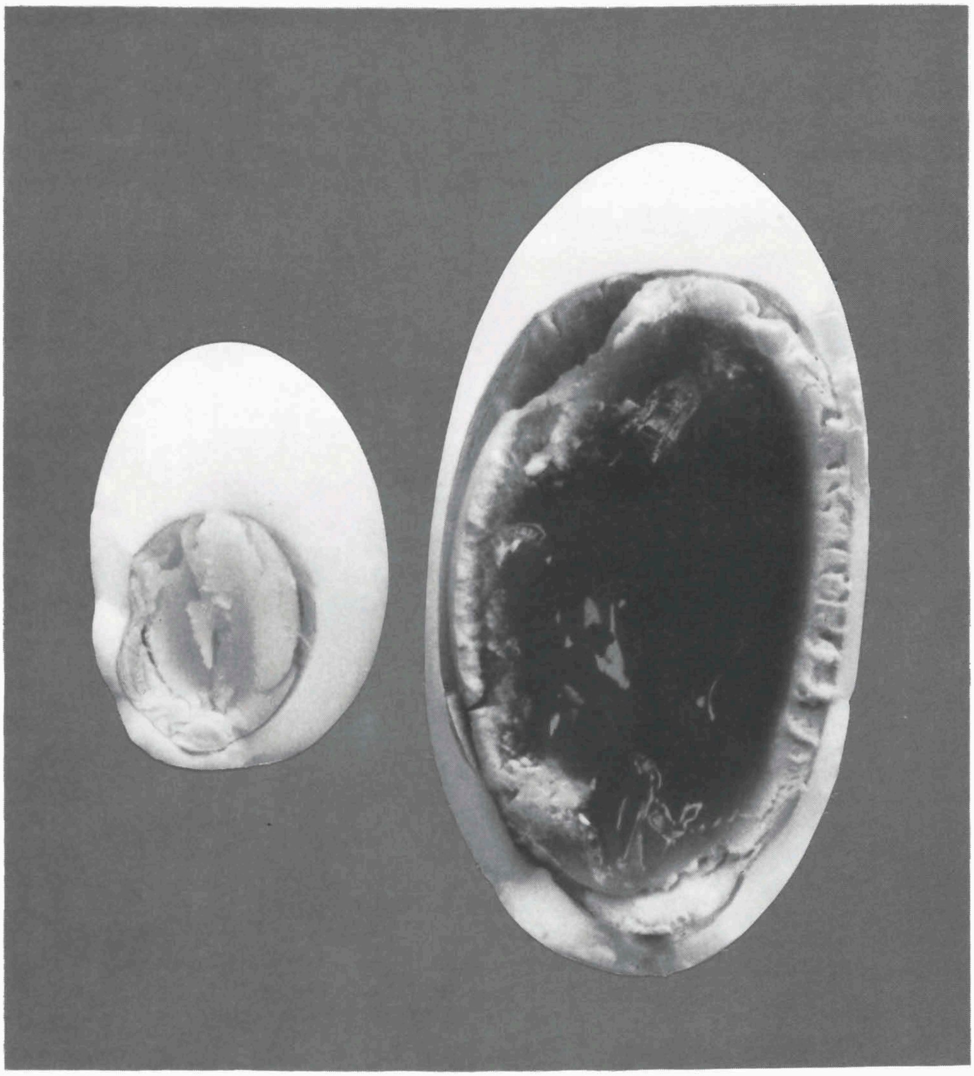

Figure 9. Cross sections of boiled fresh eggs of domestic hen *Gallus gallus* (left) and *Macrocephalon maleo* (right), showing differences in yolk content.

The eggs of small birds and birds with precocial chicks contain a higher proportion of yolk relative to the eggs of large birds or birds with altricial chicks. In eggs of palaeognathous birds (ratites and tinamous) the yolk ranges from at least 32-38% of the egg contents weight in *Struthio*, 40-42% in *Casuarius*, to 61-68% in *Apteryx* (Reid, 1971b; Calder et al., 1978; Sotherland & Rahn, 1987). The yolk content was as low as 28-30% in eggs of the elegant crested tinamou *Eudromia elegans* (pers. obs.). For anseriforms, yolk content ranges from 35 to 54%, and in galliforms (to the exclusion of megapodes) from 32 to 49% (Fig. 10). The amount of yolk in eggs of megapodes ranges from 48 to 55% for the mound-building *Aepypodius*, *Alectura*, and *Leipoa*, and it is especially high in the eggs of the burrow-nesting *Macrocephalon* (61-64%) and

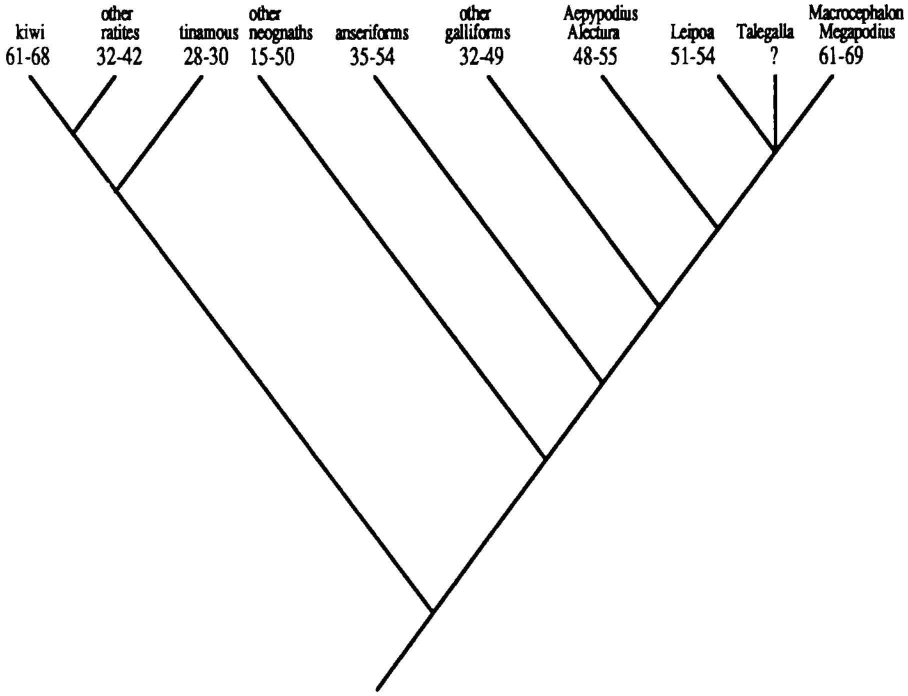

Figure 10. Cladogram showing the distribution of the amount of yolk as a percentage of the egg contents weight, superimposed on Cracraft & Mindell (1989) and Brom & Dekker (1992).

Megapodius spp. (63-69%) (Dekker & Brom, 1990; Brom & Dekker, 1992). Unfortunately no data are available for the Cracidae. In the remaining neognathous birds the relative yolk contents reaches a minimum of 15%, giving rise to altricial rather than precocial chicks (Romanoff & Romanoff, 1949; Carey et al., 1980; Sotherland & Rahn, 1987).

From comparison with the remaining galliforms, it is concluded that the high yolk content in *Megapodius* and *Macrocephalon* is apomorphic within the family Megapodiidae. This might be interpreted as additional support for the presumed sistergroup relationship between *Megapodius* and *Macrocephalon* (Clark, 1964a; Brom & Dekker, 1992).

Although the earliest birds appear to have raised super-precocious chicks, ancestral megapodes must have given birth to posterity which was less precocious than in extant megapodes. The same conclusion was reached by Clark (1964a). The relative yolk content in eggs of ancestral megapodes is supposed to have been less than in eggs of extant megapodes, resembling the condition in other galliforms. The large amount of yolk in megapode eggs could be regarded as an adaptation to their aberrant breeding strategy. The fact that eggs of *Macrocephalon* and *Megapodius* spp. contain more yolk than eggs of other megapodes may be interpreted as an indication of the direction in which the megapode breeding strategy developed: from precocious to super-precocious, or, from a large amount of yolk to an even larger amount, and from mound-building to burrow-nesting.

Similarities between megapodes and kiwis

Kiwis are the only birds with an equally high yolk percentage as found in some megapodes (Fig. 10). Apterygidae and Megapodiidae, which constitute Sotherland & Rahn's (1987) category 'Precocial I', share several other peculiarities in breeding biology (Table 2). Kiwis and some megapodes incubate their eggs in burrows; the main difference is, however, that kiwis incubate their eggs by means of body heat. The similarities ask for a more detailed discussion from an ethological and phylogenetic point of view.

As shown in Fig. 11, the high proportion of yolk is the key factor, which leads to large and elongated eggs (Dekker & Brom, 1990), to a high relative egg-weight (Dekker & Brom, 1990), to relatively dry eggs (Seymour, 1984; Sotherland & Rahn, 1987), to thin-shelled eggs (Stresemann, 1927-34: 258), and to a long incubation period (Lack, 1968: 205). Whether the high yolk content (and/or elongation of the egg, and hence absence of weight asymmetry) is also responsible for the absence of egg turning in both groups, remains unknown.

In kiwis, water loss is minimized by a much less porous structure of the shell than the avian average (Peat, 1990), but it remains unknown whether this also leads to the reduction or absence of an air-chamber. Megapode eggs are incubated in an environment with high humidity - which reduces water loss - leading to reduction of the air-chamber (Seymour, 1984). In megapodes, absence of an air-chamber requires quick hatching, allowing the lungs to take up oxygen and to expand instantaneously (Seymour, 1984). As a consequence an egg-tooth is absent shortly prehatching, although it is formed earlier during embryonic development (Clark, 1961). It remains unknown whether an egg-tooth is formed in the kiwi-embryo, but it is absent at hatching (Peat, 1990). Both megapode and kiwi chicks 'kick their way out of the egg' (Clark, 1960; Peat, 1990). Might the formation of an egg-tooth be demonstrated in the kiwi embryo, this would indicate that in kiwis the extremely high yolk content and the long incubation period are also apomorphic rather than primitive (cf. Stresemann, 1927-1934: 294).

Table 2. Similarities between burrow-nesting megapodes and kiwis.

	burrow-nesting megapodes	kiwis	reference
egg length/egg width	1.63 - 1.73	1.57 - 1.62	1, 4, 12, 14
shell weight/ egg weight	7 - 8%	5 - 6%	6, 9, 12, 13
egg weight/ body weight	13.8 - 18.0%	15.8 - 27.4%	6, 10, 12, 13
yolk percentage	61 - 69%	61 - 68%	6, 7, 12
air-chamber in egg	absent	?	8
incubation period	62 - 85 days*	70 - 92 days	4, 6, 10, 11, 13
turning of egg during incubation	no	no	11, 13
egg-tooth at hatching	absent	absent	2, 3, 13
parental care	no	no	11, 13

* Data from *Macrocephalon maleo* only.

References: 1 = Oates, 1901; 2 = Clark, 1960; 3 = Clark, 1961; 4 = Falla, 1964; 5 = Reid, 1971a; 6 = Reid, 1971b; 7 = Calder et al., 1978; 8 = Seymour, 1984; 9 = Schönwetter, 1985; 10 = Williams, 1985; 11 = Dekker, 1990; 12 = Dekker & Brom, 1990; 13 = Peat, 1990; 14 = pers. obs.

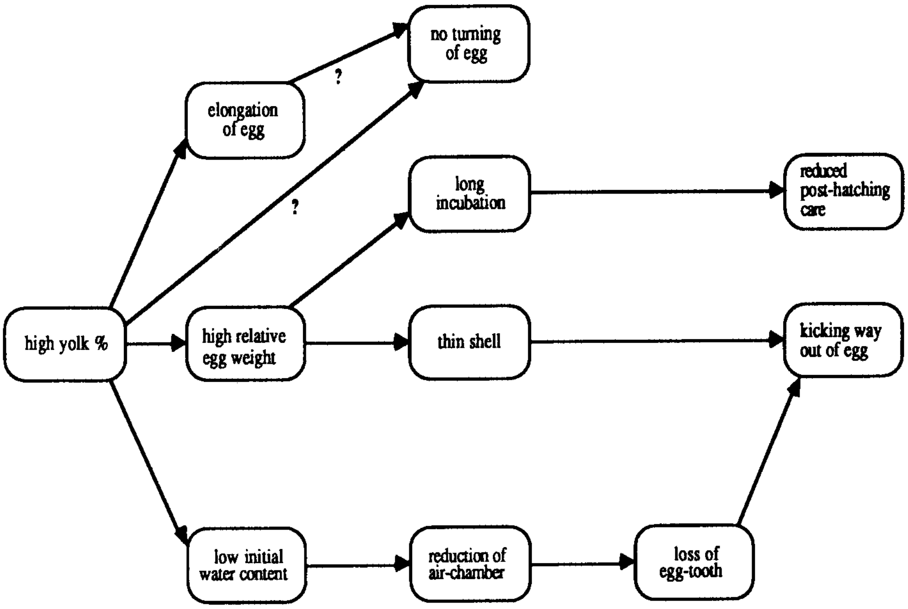

Figure 11. Similarities in breeding biology shared by burrow-nesting megapodes and kiwis, explained as convergent results of independently acquired high amounts of yolk.

In addition, similarities such as "burrow-nesting" and "no parental care" are of a linguistic rather than of a behavioural nature. Burrow-nesting in kiwis can be regarded as 'normal' avian nesting-behaviour in which the birds actively incubate in the safety of a hole, comparable to the nesting habits of many procellariiforms, whereas the passive burrow-incubation of megapodes is something completely different. Parental care in birds consists of several components, such as incubation, brooding, and feeding. In burrow-nesting megapodes none of these components is present. Although parental care in kiwis differs greatly from that in other birds, apparently a shift in investment took place from care of the young to care of the eggs. The fact that kiwis do not feed their chicks has often resulted in the opinion that parental care is absent, ignoring that kiwis brood their chicks for at least one week after hatching (Jolly & Colbourne, 1990).

We conclude that the high amount of yolk in eggs of burrow-nesting megapodes and kiwis, and thus superprecociousness, has evolved independently. Although it would be tempting from a biogeographic point of view to consider kiwis the megapodes of New Zealand, we regard the similarities as convergences. Only if new phylogenetic studies should indicate a close relationship between megapodes and kiwis, similar aspects in breeding biology between these groups should be reassessed.

From the forest to the beach or the other way around?

We have argued that in megapodes mound-building developed prior to burrow-nesting. Now we can address the question where burrow-nesting developed, at volcanic soils or at sun-exposed beaches? This question cannot be answered from a phylogenetic point of view, since we should look at species rather than generic level and the relationships within the genus *Megapodius* have not yet been unravelled. Therefore, the two burrow-nesting strategies using heat-sources other than microbial decomposition can not be evaluated by superimposing them on a phylogenetic tree. However, we think that the problem can be assessed from another direction.

Burrow-nesters at sun-exposed beaches may also apply other strategies, but, in turn, mound-builders can only make burrows on beaches provided that they also apply burrow-nesting between decaying roots and at volcanic soils. For example, in New Guinea, where numerous tropical beaches are available for potential burrow-nesters, all six species (belonging to three different genera) incubate their eggs in mounds, and none dig burrows on the beach. The maleo of Sulawesi, on the other hand, does use Sulawesi's beaches to incubate the eggs. In contrast to the megapodes of New Guinea, the forest-dwelling maleo is not a mound-builder but a burrow-nester which lays its eggs in volcanically heated soils. This may suggest that burrow-nesting at beaches can only be applied by species which are (or formerly were) burrow-nesters at volcanic soils. Burrow-nesting at beaches therefore seems to be derived from burrow-nesting at volcanic soils and not directly from mound-building. Study of the breeding strategy of the Polynesian and Moluccan megapodes *M. pritchardii* and *M. wallacei* may lend further support to this hypothesis.

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