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NOTES ON THE EMBRYOLOGY AND EVOLUTION OF THE MEGAPODES (AVES: GALLIFORMES)

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Members of the family Megapodiidae of Australia and the Pacific Islands incubate their eggs artificially using such heat sources as fermentation, volcanic activity, or the sun. The available data suggest that young megapodes receive almost no parental care. Young birds are exceedingly precocious, being able to fly on the day of hatching and feeding actively only a few days after hatching.

Portmann (1938, 1951, 1955) has listed as reptile-like the following characters of megapodes: no egg tooth at hatching, lack of down feathers in embryos or nestlings, lack of parental care, primitive method of incubation (by solar heat), long incubation period (8 weeks for *Leipoa*; Frith, 1956), large number of eggs laid, slow growth to adult size (especially for *Alectura*), primitive structure of the brain. These features have been interpreted as showing that the megapode method of reproduction has evolved directly from that of reptilian ancestors.

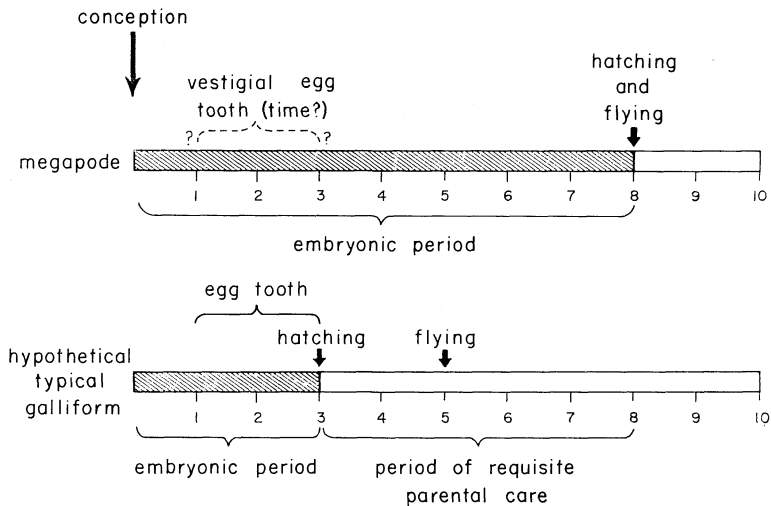
Contrary to this idea, Pycraft (1900, 1907, 1910) thought that the megapode reproductive adaptation had evolved from a more typical galliform reproductive pattern (see Fig. 1).

THE EGG TOOTH

In several embryos of *Talegalla jobiensis* a white spot on the anterior end of the upper jaw is in the same relative position as the egg tooth in a chick embryo (*Gallus domesticus*) shortly before hatching (see Fig. 2). The egg tooth is not so conspicuous in older *Talegalla* embryos. In *Megapodius pritchardii* an egg tooth is not apparent shortly before hatching (Friedmann, 1931). Megapodes hatch by kicking their way out of the shell (Campbell, 1903). The vestigial egg tooth indicates that the megapodes have evolved from birds which hatched relatively earlier in ontogeny. An analogous example of a vestigial character of phylogenetic significance is the egg tooth found in embryos of certain marsupials (Hill and de Beer, 1950).

THE LABIAL GROOVE

The labial groove of the upper jaw is conspicuous in the *Talegalla* embryo with the most prominent egg tooth (see Fig. 2). This groove was not found in somewhat older *Talegalla*



TIME IN WEEKS

Figure 1. Diagram of the hypothesized morphological and behavioral development of the megapode compared with that of more typical gallinaceous birds.

embryos. According to Hamilton (1952: 375), the remnants of the labial groove are shed on the nineteenth day of incubation in the chicken.

EARLY PLUMAGE SEQUENCES

The newly hatched megapode bears primarily pennaceous feathers in contrast to the "downy plumage" of more typical gallinaceous birds at hatching. Studer (1877, 1878, 1889) reported finding down feathers at the tips of the pennaceous feathers in *Megapodius* embryos. Both pennaceous feathers and down were ensheathed. Studer believed that the down feathers were lost before hatching. Blaszyk (1935) thought that what Studer had termed a down feather was merely the result of making a section through the distal end of an ensheathed pennaceous feather. Blaszyk (1935) and Becker (1959) found no traces of embryonic down feathers in *Megapodius*. Neither Blaszyk (1935) nor Becker (1959) commented on a study by

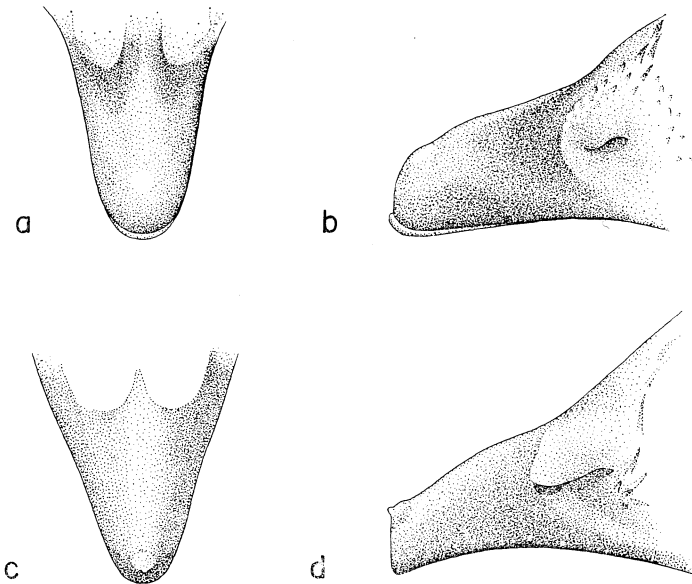


Figure 2. a. Dorsal view of the upper jaw of a *Talegalla* embryo; note the vestigial egg tooth. b. Lateral view of the upper jaw of the same *Talegalla* embryo; note the labial groove. c. and d. Dorsal and lateral aspects of the upper jaw of a chicken at the time of hatching.

Pycraft (1900), who had reported finding down-like rudiments on the tips of the first pennaceous feathers in *Megapodius* embryos. I have made a preliminary examination of embryonic *Talegalla* feathers and have found evidence that Pycraft's account is fundamentally correct.

Both the five week old pheasant (*Phasianus colchicus*; Westerskov, 1957: 20) and the newly hatched megapode bear predominantly juvenal plumage. Thus at roughly 8 weeks postconception the megapode and typical gallinaceous birds appear to reach similar levels of plumage development. Wallace (1860) commented that the newly hatched megapode behaves about as maturely as a chicken at one month posthatching.

SPECIAL EMBRYONIC ADAPTATIONS

Correlated with the prolongation of the prehatching period, certain embryonic adaptations are present in the megapodes. Meyer (1930: 5) reported that in *Megapodius* yolk weight was about 60% of total egg weight in boiled eggs; this was compared with a figure from the literature of 30% for *Gallus domesticus*.

Megapode eggs are usually incubated with the small end pointed downward. Bellechambers (1921) thought that this aided the escape of the newly hatched bird from the mound. Umanski (1926) reported on the effects of placing incubating chicken eggs on end. The proportion of teratological effects was greater in eggs placed with the blunt end down than in ones with the pointed end beneath. Normally when the chicken egg lies horizontally, the early embryo lies in a horizontal plane. Umanski suggested that the teratological forms found in eggs placed upright might result from the failure of the blastoderm and early embryo to reach a horizontal plane.

Experiments (Marshall, 1939) have shown a failure in hatching success in chicken eggs unturned during incubation. Megapode eggs usually are not turned and yet hatch relatively successfully. Marshall (1939) concluded that there must be anatomical and/or physiological differences between megapodes and the domestic fowl with respect to turning.

One of the presumed embryonic adaptations related to the long embryonic period of the megapodes is a general lack of

coordinated movement of the embryo until shortly before hatching. It is obvious that a megapode at six weeks post-conception (about two weeks prehatching) would not be so active as a chicken six weeks postconception (three weeks posthatching). I suggest that a physiological barrier prevents extensive coordinated behavioral activity of the megapode embryo during the latter part of the prehatching period. It would be profitable, perhaps, to examine the cholinergic system in the megapode embryo (Boell, 1955: 547).

In species using fermentation as a heat source for incubation the presence of aerobic bacteria should presumably greatly deplete the available oxygen supply. It has been suggested that one of the functions of mound regulation in such species is to provide oxygen for the embryos which would otherwise be under anaerobic conditions (Meyer and Stresemann, 1928: 68; Mayr, 1930: 105-106). *Megapodius* apparently does not open the mound during temperature regulation (Frith, 1959: 57). It would be of considerable interest for studies of developmental metabolism if megapodes were found to have an extended period of embryonic anaerobic respiration (Boell, 1955: 522-523).

Further studies on the egg tooth, plumage development, and other aspects of megapode embryology and anatomy are currently in progress at this laboratory.

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SUMMARY

A vestigial egg tooth in embryos of *Talegalla* is strong evidence that megapodes have evolved from gallinaceous birds which hatched relatively earlier in ontogeny. It is hypothesized that much of the maturation which occurs during the post-hatching development of typical gallinaceous birds occurs before hatching in megapodes. The vestigial egg tooth, the labial groove of the upper jaw, and vestiges of down feathers plus the state of plumage development and behavior in newly hatched megapodes support this hypothesis. Some speculations on possible unusual embryonic adaptations are presented.

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