

# Current studies on megapode phylogeny

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Key words: Megapodiidae; interfamilial relationships; intrafamilial relationships.

Hypotheses regarding the phylogenetic relationships between megapodes and other birds are reviewed, and it is concluded that the available evidence supports a sistergroup relationship between megapodes and all other galliforms. Current studies in this direction are discussed. The resolution of intrafamilial relationships has gained less attention so far and the most probable hypothesis based on traditional characters is presented.

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## Introduction

Some 19 species of megapodes are recognized, divided into six or seven genera (Stresemann, 1927-34; Peters, 1934; White & Bruce, 1986). Together they form a taxonomically closely knit group, and, although no avian systematist has taken the trouble to formulate their autapomorphies, megapodes are undoubtedly monophyletic. Traditionally they have been given family rank in classifications, and for convenience this is accepted in this paper.

For several reasons, both the intra- and interfamilial relationships of the Megapodiidae remain unresolved. The purpose of this paper is (1) to compare recent hypotheses on the interfamilial relationships, (2) to present the preliminary results of current studies on megapode phylogeny, (3) to evaluate the phylogenetic significance of characters that have been used in megapode classification in the past, and (4) to construct the best corroborated phylogenetic tree from these data.

## The interfamilial relationships of megapodes

Most authors are convinced that the megapodes constitute a monophyletic group within the Galliformes. Their opinions are based on anatomy, karyology, egg white proteins, and DNA-DNA hybridization (Shufeldt, 1919-20; Cracraft, 1972, 1973, 1981; Sibley, 1976; Olson, 1980; Sasaki et al., 1982; Belterman & de Boer, 1984; Sibley et al., 1988; Laskowski & Fitch, 1989). According to the most recent phylogenetic hypothesis, galliforms are the sistergroup of the anseriforms (Prager & Wilson, 1980; Cracraft & Mindell, 1989). On the phylogenetic position of the megapodes within the galliforms several theories exist.

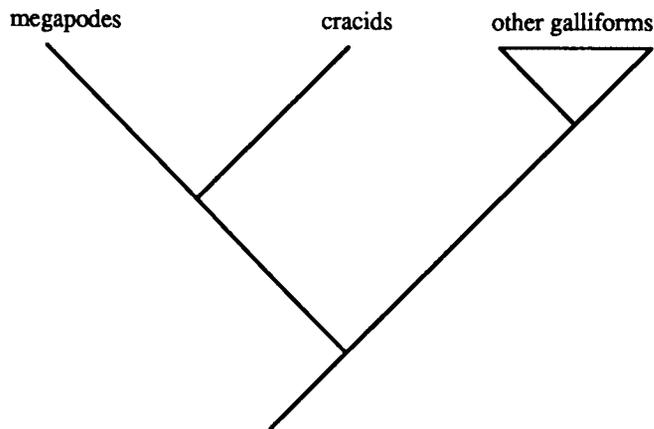


Figure 1. Phylogenetic position of megapodes as suggested by the myology of the wing (Hudson & Lanzillotti, 1964), DNA-DNA hybridization (Sibley & Ahlquist, 1985; Sibley et al., 1988), and amino acid sequence of ovomucoids (Laskowski & Fitch, 1989).

#### **A. Megapodes + cracids are the sistergroup of all other galliforms**

Peters (1934) and Wetmore (1960) classified the Megapodiidae with the Cracidae in the Cracoidea besides the other galliforms, the Phasianoidea. Stresemann (1927-34) and Verheyen (1956) recognized three families within the galliforms, the Megapodiidae, Cracidae, and Phasianidae, and the latter author noticed that megapodes and cracids are more similar to one another than to the Phasianidae. The study of the gross anatomy of wing muscles, led Hudson & Lanzillotti (1964) to the conclusion that Megapodiidae and Cracidae are more closely related to each other than either is to the Phasianidae (Fig. 1). DNA-DNA hybridization data seem to indicate that megapodes + cracids are the sistergroup of all remaining galliforms (Sibley & Ahlquist, 1985; Sibley et al., 1988), whereas the monophyly of Megapodiidae + Cracidae was further suggested by the biochemical analysis of ovomucoids (Laskowski & Fitch, 1989).

#### **B. Megapodes + cracids + guineafowl are the sistergroup of all other galliforms**

A second hypothesis, based on the lack of an intercarpal process, considered megapodes, cracids and guineafowl to form a monophyletic group (Rich & Van Tets, 1985), but the proposed phylogeny (Fig. 2) is in conflict with all other data currently available. The lack of an intercarpal process may be apomorphic within galliforms, but since we know of many other characters (such as gall bladder, uropygial gland, musculus ambiens, afterfeather) that have been lost independently in different lineages of birds, it is far from certain that this absence is synapomorphic for megapodes, cracids and guineafowl. Therefore, we regard the hypothesis by Rich & Van Tets (1985) that this character suggests a common Gondwanic origin for these taxa as mere speculation.

#### **C. Megapodes are the sistergroup of all other galliforms**

Fürbringer (1888: 1266) considered the Numidinae, Meleagrinae, Phasianinae, and Tetraoninae more closely related to one another than either is to Megapodiinae or Cracinae, but did not find evidence for a close relationship between the latter two

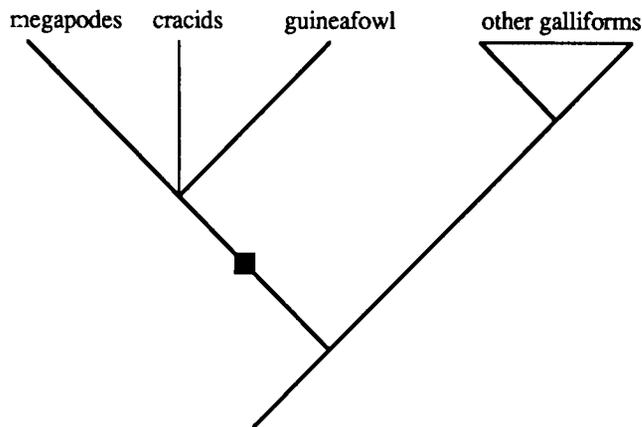


Figure 2. Phylogenetic hypothesis based on lack of intercarpal process (Rich & Van Tets, 1985).

groups. Osteological characters led Cracraft (1973; see also 1980) to the conclusion that Megapodiidae are the sistergroup of all remaining galliforms (Fig. 3). Moreover, the distribution of the mallophagan genus *Reticulipeurus* (von Kéler, 1958), the chemical composition of uropygial gland secretions (Edkins & Hansen, 1971), the biochemical analysis of egg white proteins (Sibley & Ahlquist, 1972; Sibley, 1976), and the structure of the eggshell (Board et al., 1982) pointed in the same direction. Based on immunological data, Prager & Wilson (1980) concluded that the relationships of the cracids to other gallinaceous birds are as remote as that between galliforms and anseriforms, but they did not include megapodes in their study. Furthermore, karyotype morphology has been interpreted as supportive of this hypothesis (Sasaki et al., 1982; Belterman & de Boer, 1984). However, this conclusion may be weakened by the facts that the phylogenetic interpretation of karyotypes is difficult to assess and megapodes resemble ratites, tinamous and ducks in many respects (Christidis, 1990).

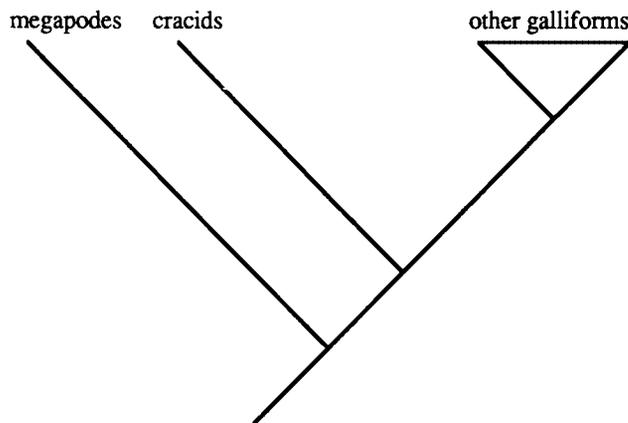


Figure 3. Phylogeny suggested by egg white proteins (Sibley & Ahlquist, 1972), osteological characters (Cracraft, 1973), structure of eggshell (Board et al., 1982), and karyology (Sasaki et al., 1982; Belterman & de Boer, 1984).

Since the data presented by Sibley & Ahlquist (1985) and Laskowski & Fitch (1989) did not yield character-states that can be interpreted cladistically, we consider hypothesis A insufficiently supported and conclude that a sistergroup relationship between megapodes and all other galliforms is the most likely hypothesis at the present time.

### Current studies on the interfamilial relationships of megapodes

#### A. Microstructure of feathers

Downy barbules at the base of contour feathers vary considerably in structure and show features by which many taxa of birds can be distinguished. In several groups of birds the nodes at the basalmost barbules attain a ringlike shape. In galliforms, tinamous, and turacos these rings sometimes break loose and slide along the pennulum. Usually a single detached node or dual nodes are observed, but occasionally up to ten of these rings slide together to form so called 'multiple nodes'. Detached and multiple nodes have been found in tinamous, cracids, tetraonids, phasianids, guineafowl, meleagrids, and turacos (Fig. 4). Many feathers of species from all megapode genera have been screened, showing that detached or multiple nodes are absent (Brom, 1991).

This observation supports the hypothesis that megapodes are the sistergroup of all other galliforms (Cracraft, 1973) rather than the sistergroup of the cracids (Sibley & Ahlquist, 1985), but at the same time it casts suspicion on the monophyly of both Palaeognathae and Galliformes.

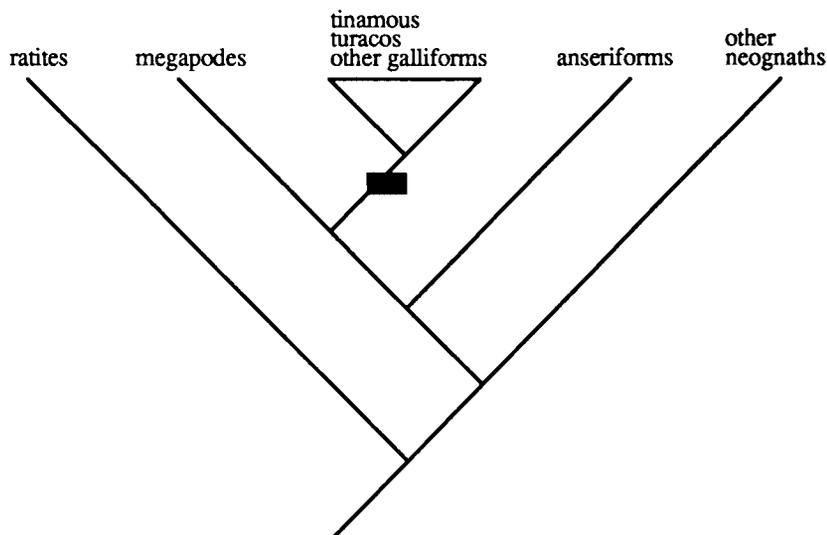


Figure 4. Cladogram showing detachable/multiple nodes as synapomorphy for Tinamidae, Cracidae, Tetraonidae, Phasianidae, Numididae, Meleagridae, and Musophagidae; black box indicates detachable/multiple nodes as synapomorphy.

### B. Growth and moult of flight-feathers

In chicks of Cracidae, Phasianidae, Meleagridae, Megapodiidae, and hoatzin, retardation in growth of the distal primaries is found (Pycraft, 1895; Heilmann, 1926). When the inner primaries are well developed, the two to four outermost ones are still absent or appear as downy tufts only. The differences in development between proximal and distal primaries are, however, much more pronounced in galliforms than in the hoatzin. Heilmann (1926: 107) further observed retardation of the innermost secondaries. It is evident that he considered this character primitive in birds. In tinamous (Stresemann & Stresemann, 1966; pers. obs.) and turacos (Pycraft, 1904) a similar retardation in growth is found. Stresemann & Stresemann (1966) considered this retardation a convergent similarity shared by galliforms and tinamous. Although this character is exclusively found in tinamous, galliforms, turacos, and hoatzin, apparently no one has interpreted it as indicative for a common ancestry of these taxa. Since this character is largely congruent with the occurrence of detachable/multiple nodes in the downy barbules of tinamous, turacos, and galliforms (see above), it cannot be excluded that this retardation in growth of juvenile remiges represents a synapomorphy for these taxa.

From the study of the moult patterns in flight-feathers of megapodes (pers. obs.), the following preliminary conclusions can be drawn. The primaries are moulted in a serially descendant sequence ("Staffelmauser"), which is found in many other birds. As in other galliforms, the outermost primaries (p9-p10), which develop much later than the inner ones, are retained in the post-juvenile moult and are probably replaced for the first time only after p8 has been renewed for the second time (see also Sutter, 1966, for *Alectura*). The onset of the post-juvenile moult in megapodes is strikingly similar to that in tinamous.

In most galliforms, moult of the secondaries starts at s3 (Raitt, 1961; Watson, 1962; Stresemann & Stresemann, 1966; Sutter, 1971), only the cracids start at s5 (Stresemann & Stresemann, 1966; Haffer, 1968), whereas moult of the secondaries in tinamous starts at s8 or s9 (pers. obs.). Therefore it would be very interesting to know at what position megapodes start to shed their secondaries, but since our studies on moult in megapodes have been confined to museum specimens in which secondaries are difficult to examine, no information is available as yet.

Patterns of tail-moult have played an important role in galliform taxonomy (e.g., Beebe, 1918-1922; Delacour, 1951; Stresemann, 1965). The following modes have been described: a) centrifugally (in regular sequence from central pair t1 outwards), b) centripetally (from outer pair inwards), c) from foci at t3 inwards and outwards (sequence: t3-4-2-5-1-6), d) from t5 inwards (sequence: t5-4-3-2-6-1). Since growth and post-juvenile moult in cracids follows the c-pattern, a comparison with megapodes would be the first thing to do. However, no studies have been published on this subject. Therefore the tail-moult in megapodes was examined in museum specimens of *Megapodius* spp., augmented with observations on *Aepyodius*, *Alectura*, *Leipoa*, *Macrocephalon*, and *Talegalla*. The moult-scores are difficult to interpret as yet, but preliminary analysis of the material definitely excludes the possibility of a centripetal moult pattern in megapodes (pers. obs.).

### C. Amino acid sequence of alpha A crystallin

In case the similarities between galliforms and tinamous should represent

synapomorphies rather than parallelisms, the monophyly of the Galliformes and the Palaeognathae will have been falsified and, hence, the phylogenetic position of megapodes may change. In order to clarify the relationships of both tinamous and megapodes, the analysis of the amino acid sequence of the eye lens protein alpha A crystallin (Stapel et al., 1984; Wattel et al., 1988), is currently being extended to representatives of both groups. The study of this protein in the elegant crested tinamou *Eudromia elegans* may show whether Cracraft & Mindell (1989) were correct in regarding the earlier reported synapomorphies for ratites as synapomorphic for palaeognaths, whereas the analysis of the malleefowl *Leipoa ocellata* may clarify the phylogenetic position of megapodes.

#### D. Amino acid sequence of osteocalcin

Biochemical analysis of the amino acid sequence of osteocalcin of swordfish, alligator, 11 mammalian species and two birds (P. Sandberg & G. Muyzer, unpubl.) revealed that this protein might be phylogenetically informative. Although only the emu *Dromaius novaehollandiae* and the domestic hen *Gallus spec.* have been included in this study, the observed substitutions in the amino acid sequences of these taxa may shed light on the early diversification of birds. Both species share four substitutions not found in any of the outgroups, which may turn out to be autapomorphic for birds. More importantly, however, each has several unique substitutions (emu three and domestic hen six) which might be synapomorphic for palaeognaths and galliforms, respectively. The inclusion in this osteocalcin analysis of *Eudromia elegans*, *Aepyodius arfakianus*, and some representatives of the other neognaths may yield information on the phylogenetic relationships of tinamous and megapodes.

### Intrafamilial relationships

The relationships between galliform birds have gained considerable interest in recent years. Different methods have been applied: karyology (Stock & Bunch, 1982), starch gel electrophoresis (Gutiérrez et al., 1983), DNA-DNA hybridization (Sibley & Ahlquist, 1985) and restriction mapping (Helm-Bychowski & Wilson, 1988), but the intrafamilial relationships of the megapodes have received no attention.

These ingroup relationships can only be assessed when the interfamilial affinities of the megapodes have been resolved. However, since these relationships have not been clarified unambiguously, and since the aforementioned biochemical data sets are not informative at intrafamilial level, we still have to depend on traditional (morphological) characters. These include structure of the wing, shape of nostril, presence of wattles, scutellation of tarsus, occurrence of tufted uropygial gland, presence of penis, and surface of eggshell.

#### A. Structure of wing

Initially, the galliforms have been described as eutaxic (Wray, 1887; Mitchell, 1899), but at the same time it was discovered that the wing of megapodes was diastataxic (fifth secondary absent) (Sclater, 1890; Pycraft, 1899, 1902). However, unlike other gallinaceous families, megapodes show variation in the presence of the fifth secondary. *Aepyodius*, *Alectura*, *Leipoa* and *Talegalla* are eutaxic, while *Macrocephalon*

and *Megapodius* are diastataxic (Steiner, 1918, 1956; Stresemann, 1927-34; Verheyen, 1958; Stephan, 1970; Table 1; Fig. 5). All other galliforms are eutaxic, whereas anseriforms are diastataxic (Stephan, 1970).

### B. Shape of nostril

In his determination key, Ogilvie-Grant (1893) used the shape of the nostril as a diagnostic character. Since oval nostrils are found in both megapodes and other galliforms, the rounded shape in *Aepyodius* and *Alectura* might be synapomorphic for these taxa (Fig. 5).

### C. Wattles

Among galliforms, wattles are commonly found. They are also encountered in related outgroups such as anseriforms and cassowaries. The absence of these structures in several megapodes might be considered a secondary loss. Although the same argument holds true as for the loss of an intercarpal process (see above), for the time being we postulate the lack of wattles as synapomorphic for *Leipoa*, *Talegalla*, *Macrocephalon* and *Megapodius* (Fig. 5).

### D. Scutellation of tarsus

Ogilvie-Grant (1893) described the scutellation of the tarsus in megapodes as follows: *Megapodius* and *Talegalla* bear a single row of large scutes. *Aepyodius* has a similar pattern, only the last two or three scutes are split down the middle. *Alectura* and *Leipoa* have a complete double row of large hexagonal plates down the front of the tarsus. *Macrocephalon* has the tarsus reticulated with small hexagonal scales. Since the different configurations are difficult to translate into character-states, they have not been incorporated in Fig. 5.

### E. Uropygial gland

According to Miller (1924) and Clark (1964), the uropygial gland is tufted in *Megapodius* and *Macrocephalon*, but naked in *Aepyodius*, *Alectura*, *Leipoa* and *Talegalla* (Table 1). However, Jacob & Ziswiler (1982) reported a tufted uropygial gland in *Leipoa*. Other galliforms and anseriforms have tufted uropygial glands, and therefore naked glands probably represent the apomorphic condition within megapodes. However, since the smallest number of tuft feathers among land birds have been found in tinamous and galliforms (Jacob & Ziswiler, 1982: 220), the distinction between the character states "small number of feathers" and "naked gland" becomes unclear and hence we refrain from using the feathering of the gland as a taxonomic character.

### F. Penis

The presence of a penis-like organ is undoubtedly symplesiomorphic in birds. This structure is found in ratites, galliforms (except phasianids), tinamous and anseriforms (Stresemann, 1927-34). Among megapodes, *Alectura* and *Leipoa* are reported to have a penis (D. Priddel, pers. comm.; D. Jones, pers. comm.), whereas it seems to be absent in *Megapodius* (D. Jones, pers. comm.). The absence represents the apomorphic condition, but information on other megapodes is needed to assess whether this character has any phylogenetic significance within the family.

### G. Surface of eggshell

Differences in the outer layer of eggshells have been noticed by Mayr (1930), Rand (1942) and Rappart & Karstel (1960). The eggs of *Leipoa*, *Macrocephalon*, *Megapodius*, *Talegalla* and are covered by a pinkish-brown powder (pers. obs. & D. Priddel, pers. comm.), which colour is apparently not found in the other species of megapodes nor in other galliforms (Fig. 5).

### H. Yolk content of eggs

The amount of yolk as a proportion of the egg contents weight is extremely high in megapodes compared with other birds (Sotherland & Rahn, 1987). It is apparent that, based on yolk percentage, the megapodes can be divided into two groups, which are separated by a distinct gap (Dekker & Brom, 1990). Although the use of ratios and indices in phylogenetic reconstruction is suspect (Pimentel & Riggins, 1987), the extremely high values found in eggs of *Megapodius* (J. Verheyen, pers. comm.) and *Macrocephalon* might indicate a sistergroup relationship between both genera (Fig. 5).

### I. Mallophaga

Of the ischnoceran featherlice of the megapodes, only the goniodid lice and those belonging to the genus *Oxylipeurus* have been reported from most host genera. These two are usually considered distinct species-groups. Tendeiro (1980, 1981-82) considered the goniodid species-group to consist mainly of two genera, *Aurinirmus* (known from *Aepyodius*, *Alectura* and *Talegalla*), and *Homocerus* (known from *Megapodius*). *Aurinirmus* is thought to be related to lice known from grounddoves and *Homocerus* to other *Goniodes* species groups. Mey (1982) regarded *Goniocotes macrocephalus* and *G. crassipes* (previously described as belonging to Tendeiro's *Aurinirmus*) to be true *Homocerus* and considered all other species known from *Megapodius* generically distinct. Although the phylogeny of these mallophaga has not been resolved unambiguously, they seem to indicate a split within the megapodes, but the position of *Macrocephalon maleo* and *Leipoa ocellata* is still uncertain due to lack of described lice from these species. Mallophaga collected from museum specimens of *Macrocephalon* resemble those found on *Megapodius* and probably belong to the same goniodid group (Henk Visser, pers. comm.).

Table 1. Variable characters in megapodes: structure of wing, shape of nostril, presence of wattles, scutellation of tarsus, uropygial gland, presence of penis, surface of eggshell, and yolk content of eggs.

taxa	wing	nostril	wattles	tarsus scales	uropygial gland	penis	egg	yolk content
<i>Aepyodius</i>	eutaxic	round	present	single row	naked	?	white	± 55%
<i>Alectura</i>	eutaxic	round	present	double row	naked	yes	white	48-52%
<i>Leipoa</i>	eutaxic	oval	absent	double row	naked?	yes	red	51-54%
<i>Talegalla</i>	eutaxic	oval	absent	single row	naked	?	red	?
<i>Megapodius</i>	diastataxic	oval	absent	single row	tufted	no	red	63-69%
<i>Macrocephalon</i>	diastataxic	oval	absent	many rows	tufted	?	red	61-64%

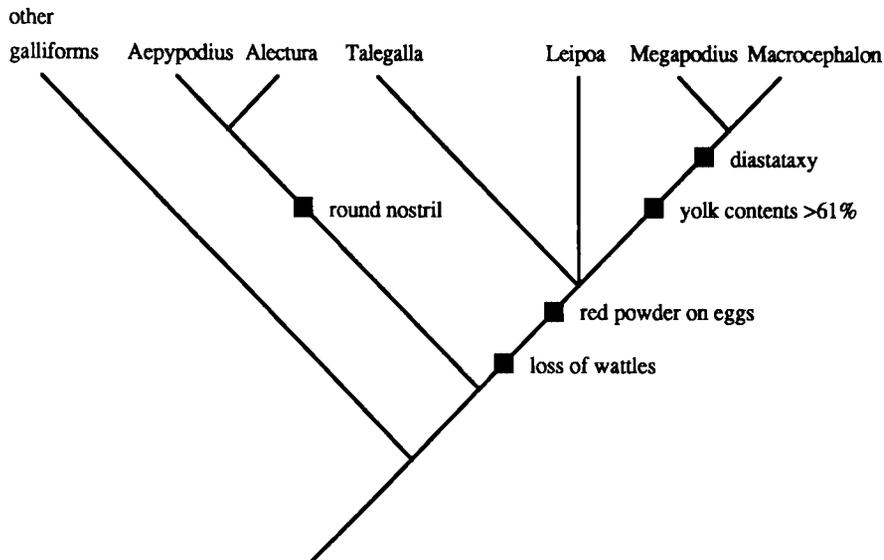


Figure 5. Most probable hypothesis on the ingroup relationships of megapodes, perforce based on traditional characters only (see Table 1).

Although the characters summarized in Table 1 are known to be highly variable in non-galliforms, congruence among putative synapomorphies may shed light on the ingroup relationships of megapodes, and hence, may help us understand the evolution of their different breeding strategies (Dekker & Brom, 1992).

### Acknowledgements

Thanks are due to Darryl Jones, David Priddel, J. Verheyen, and Henk Visser for providing additional information, and to Roger de Bats and Jan Wattel for commenting on the manuscript. The investigations were in part supported by the Foundation for Fundamental Biological Research (BION), which is subsidized by the Netherlands Organization for Scientific Research (NWO).

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