

# Phylogenetic relationships of the Megapodiidae as indicated by their ischnoceran, in particular goniodid, chewing lice (Insecta: Phthiraptera)\*

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Inter- and intrafamilial relationships among the Megapodiidae are presented and discussed based on their host-specific chewing louse fauna, in particular the Goniodidae (Ischnocera). Use is made of both empirical evidence and statistical methods. So far, 53 species of chewing lice have been described which are found only on megapodes, a number which is still growing. The relationships among the Goniodidae genera on megapodes have been analysed using Wagner parsimony analysis rooted by character polarity (51 morphological features). Based on their chewing lice, the Megapodiidae seem to be more closely related to the Phasianidae than to the Cracidae. Megapodes share no Ischnocera with the cracids, while they share a single genus *Goniocotes* Burmeister, 1838 (one species only, on *Macrocephalon maleo* S. Müller, 1846) with the Phasianidae. The distribution of 18 Ischnocera genera support the following intrafamilial division: *Alectura* Latham, 1824, and *Aepyodius* Oustalet, 1880, on the one hand and *Megapodius* Gaimard, 1823, and *Eulipoa* Ogilvie-Grant, 1893, on the other form respective sister groups. The relationships between *Leipoa* Gould, 1840, *Talegalla* Lesson, 1828, and *Macrocephalon* S. Müller, 1846, remain unclear.

## Introduction

Phylogenetic relationships of plant or animal groups can be revealed by looking at their permanent obligate parasites. It depends on the assumption that hosts and their parasites co-evolve; in other words that they share millions of years of evolutionary history. The speciations undergone during this time by the hosts have been paralleled by the parasites, though mostly involving much less radical changes than affected their hosts. The initial foundations for the idea of co-speciation were laid by Christian Ludwig Nitzsch (1782-1837), who first formulated the idea during intensive study of insect and mite parasites on animals around 1815. Nitzsch is mostly overlooked in historical outlines in the English-language literature.

Since then the idea of co-speciation has been taken up many times, e.g. by the avian systematist Jean Cabanis in 1853. However, it was not until the turn of the century that its formulation and application as a working hypothesis were undertaken, independently of each other, by the American Vernon Lyman Kellogg (1867-1937) and the short-lived Launcelote Harrison (1880-1928) from Sydney. Wolfdietrich Eichler (1912-1994) further developed their ideas on parallel phylogeny of host and parasites, in particular animals and their lice, finally formulating them in correlation rules. Fahrenholz's Rule (which, to be historically accurate, should really be called Nitzsch-Kellogg-Harrison's Rule) states (simplified): parasite phylogeny mirrors host phy-

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logeny, while Szidat's Rule states: the more primitive the host, the more primitive the parasites which it harbours. Critics of these hypotheses often overlooked the fact that they do not claim to be absolute and universal; they cannot be applied automatically in every case. The argument is often used that secondary infestation (stragglers, host-switching), as well as secondary absence as a result of extinction, are not adequately considered, and thus cast doubt on the methods of comparative parasitology (Mauersberger & Mey, 1994).

The current picture of differential chewing lice distribution, built up by several generations of taxonomists, clearly comes down in favour of the existence of the evolutionary process of co-speciation (which includes co-adaptation) in birds and their permanent obligatory ectoparasites, such as chewing lice. Each avian order is characterized by its own particular ensemble of chewing lice genera. No genera of chewing lice typically found on ducks (Anseriformes), pigeons (Columbiformes) or songbirds (Passeriformes) have permanently settled on birds of prey (Falconiformes) or owls (Strigiformes). As a rule, there has been no exchange of closely-related chewing lice species even among these predatory birds. The Common Cuckoo *Cuculus canorus* Linnaeus, 1758, harbours exclusively cuckoo chewing lice, not those of its foster parents. Order, not chaos, is what nature shows us in the distribution of these tiny creatures. That this order is occasionally upset by events such as host-switching, or what we take to be host-switching, is no reason to question the entire concept, which would be to ignore the biological evidence. Each concrete case must be tested against the apparently possible and probable evolutionary events. A strict mathematical application of Fahrenholz's Rule is therefore out of the question. No one would seriously entertain the idea of placing the Musk Duck *Biziura lobata* (Shaw, 1796) close to the penguins simply because it is infested by *Austrogoniodes metoecus* Clay, 1971, a typical penguin chewing louse, or of calling the Figbird *Sphecotheses viridis* Vieillot, 1816, a relative of the pigeons because it harbours *Columbicola paradoxus* Tendeiro, 1965. The heuristic value of the parasitological method is not lessened by these examples. When weighed against the number of primary host-parasite relationships they are simply exceptions, albeit extremely interesting ones.

Within the last 20 years there has been a considerable revival of interest in this area of research as a result of the emergence of Hennigian cladistics (Hoberg et al., 1997; Paterson et al., 1995). Parsimony analysis and/or component analysis now appears in place of the earlier pure empiricism. However, to talk of a paradigm shift in comparative parasitology on this basis is an exaggeration (Hoberg et al., 1997). Taxonomic experience and empirical evidence cannot be replaced by a computer program. In addition, no fundamental correction to the hypothesis of parallel phylogeny of a host and its permanent obligate ectoparasites, in particular Phthiraptera, has been necessary. This paper is based on taxonomic expertise in my particular field and computer-based analysis. A three-step procedure on the path to illuminating the host-parasite co-speciation in megapodes and their chewing lice seems advisable (Paterson & Gray, 1997):

1. Independent reconstruction of the phylogenetic tree of the family of the host on the one hand, and of the chewing lice on the other;
2. Comparison of both trees using a quantitative analysis, e.g. parsimony analysis;
3. Testing of the congruences and incongruences of both phylogenetic trees.

### How much do we know about megapode chewing lice?

The chewing lice from megapodes that we have at our disposal is incomplete and insufficiently studied. Application of the ideal procedure is at best only partly possible. Table 1 shows a summary of the distribution of all known chewing lice taxa (up to September 1998), among the seven host genera.

Table 1. Number of described and undescribed species of genera of chewing lice parasitic on megapodes (Megapodiidae) (after Mey 1997 and unpublished data). Le = *Leipoa*; Ae = *Aepyodius*; Al = *Alectura*; Ta = *Talegalla*; Me = *Megapodius*; Eu = *Eulipoa*; Ma = *Macrocephalon*.

Phthiraptera Chewing lice	Megapodiidae						
	Le	Ae	Al	Ta	Me	Eu	Ma
<b>Amblycera</b>							
<b>Menoponidae</b>							
<i>Amyrsidea</i> ( <i>Argimenopon</i> )	-	-	-	-	2	-	1
<i>Kelerimenopon</i>	-	1	1	4	3	1	-
<b>Colpocephalidae</b>							
" <i>Colpocephalum</i> " incl. <i>Talegalligogus</i>	1	2	2	3	2	-	1
<b>Ischnocera</b>							
<b>Gonioididae</b>							
<i>Leipoielli</i>	1	-	-	-	-	-	-
<i>Megatheliella</i>	1	-	-	-	-	-	-
<i>Maleophilus</i>	-	-	-	-	3	-	-
<i>Maleoicus</i>	-	-	-	-	6	-	-
<i>Homocerus</i>	-	2	1	3	-	-	1
<i>Euligoniodes</i>	-	-	-	-	-	1	-
<i>Weelahia</i>	-	1	1	-	-	-	-
<i>Lobicrotaphus</i>	-	-	-	-	1	-	-
<i>Goniocotes</i>	-	-	-	-	-	-	1
<b>Lipeuridae</b>							
<i>Oxylipeurus</i>	-	1	1	1	4	1	-
undesc. genus	-	-	-	1	-	-	-
<i>Talegallipeurus</i>	-	-	-	1	-	-	-
<i>Megathellipeurus</i>	1	1	1	1	-	-	1
<i>Malaulipeurus</i>	-	-	-	-	5	1	-
<i>Lipeuroides</i>	-	-	-	2	-	-	-
<b>Degeeriellidae</b>							
<i>Megapodiella</i>	1	1	-	1	-	-	-
total	5	9	7	17	26	4	5

A total of 53 described chewing lice taxa, perhaps less than half of all existing forms, are known from megapodes. More than 15 undescribed chewing louse species are still waiting to be described. Altogether we know of the existence of around 73 species (see table 1). Almost all descriptions of megapode chewing lice are based on specimens taken from museum skins. I have been successful in obtaining an example of all these chewing lice taxa from skins of megapodes held in several German museums as well as in the National Museum of Natural History in Leiden, The Netherlands. Figure 1 shows that skins of the seven megapode genera exist in sufficient numbers in the collections to make statistical analyses possible. It was surprising that almost every adult megapode skin still harboured mummified chewing lice.

Megapodes are infested by chewing lice found on no other host group. Among the Ischnocera (Goniodidae), only the genus *Goniocotes* Burmeister, 1838, is an exception to this as it contains one species, *G. pallidiflavus* Piaget, 1890, which infests the maleo *Macrocephalon maleo* S. Müller, 1846, while all other representatives of this genus are found only on the Phasianidae and Numididae (Guineafowl).

The picture is less clear when we look at the Amblycera: *Colpocephalum* Nitzsch, 1818 sensu lato, infests the Ciconiiformes, Columbiformes and Passeriformes; *Kelerimenopon* Conci, 1942, is also known from pittas (Pittidae) and parrots (Psittacidae) of the Australasian and Oriental Region; *Amyrsidea* Ewing, 1927, is found only on *Megapodius forstenii* ssp. and *M. cumingii* ssp. and in an undescribed form on

*Macrocephalon maleo* as well as on all other galliform families. Because of their heterogeneous distribution among several bird families, and until they are taxonomically revised, these chewing lice groups are not very suitable for inclusion in comparative studies. This does not mean, however, that they should be completely excluded. The following treatment on parasite phylogeny will focus mainly on the Goniodidae. Figure 2 shows a representative of each of the nine genera distinguished here. The fact that all these genera, except *Goniocotes*, are found only on megapodes is a clear indication, though not proof, of megapode monophyly. This proof, while shown for the megapodes, remains to be demonstrated for their chewing lice.

### Interfamilial relationships

From the mallophagological point of view, there is no doubt that megapodes belong to the Galliformes (Kettle, 1981; Ward, 1958). At least five of the chewing lice genus-complexes unique to the Galliformes (also recently Craciformes, sensu Sibley &

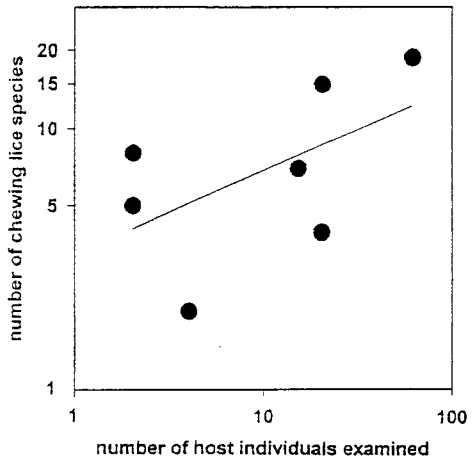


Fig. 1. Correlation between the number of megapode (museum) skins examined (seven genera) and the number of chewing lice species collected (after Mey, 1997).

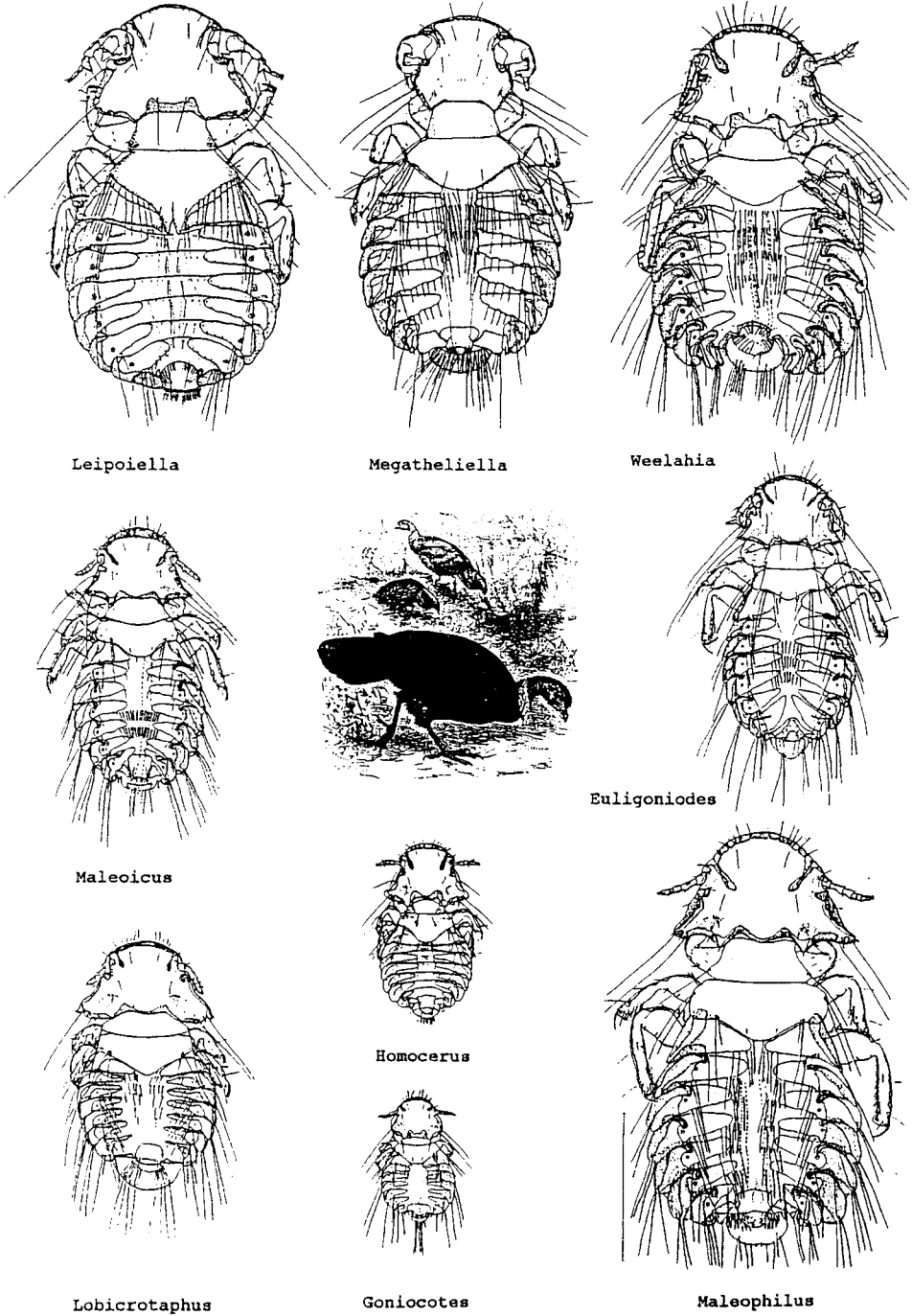


Fig. 2. The genera of goniodid chewing lice (Insecta: Phthiraptera: Ischnocera) parasitic on megapodes. Only males are illustrated in their relative natural body sizes. Drawing E. Mey.

Ahlquist, 1990) support this: these are *Goniodes* Nitzsch, 1818, *Lipeurus* Nitzsch, 1818, *Oxylipeurus* Mjöberg, 1910, *Cuclotogaster* Carriker, 1936 and *Menacanthus* Neumann, 1912, complexes. Only the *Goniodes* complex has perhaps a convergent parallel in the Columbiformes, whose Gonioididae have developed a diversity of forms similar to those on the Galliformes. The even more diverse Heptapsogasteridae associated with the Tinamiformes are very far removed from these complexes.

There are two opinions in the discussion about the sister group relation of the megapodes. On the one hand the Cracidae are regarded as their nearest relatives (Sibley & Ahlquist, 1990; Mourer-Chauviré, 1992), and on the other the ensemble of all the other galliform groups (see Jones et al., 1995). To make a clear decision in favour of one of these hypotheses on the basis of the mallophagological findings is at present not possible, although the data do appear to exclude the former proposal while lending some support to the latter. Bearing in mind that the Cracidae have been little studied with regard to their ectoparasites, although not less than other Galliformes, it is very striking just how impoverished their chewing lice fauna is. Two genera of Amblycera (*Cracimenopon* Carriker, 1954, and *Eomenacanthus* Uchida, 1926) and three genera of Ischnocera (*Trichodomea* Carriker, 1945, *Labicotes* von Kéler, 1939, *Reticulipeurus* von Kéler, 1958, sensu lato) are unique to the cracids. No close affinity to any other genus of megapode-infesting chewing lice can be recognized. By contrast, the cracids do appear to be close to the Odontophoridae and the New World Phasianidae, particularly via *Chelopistes* von Kéler, 1939 (aff. *Trichodomea* Carriker, 1945) and *Reticulipeurus* sensu stricto. On the other hand, megapodes harbour *Goniocotes* (although only in *Macrocephalon* S. Müller, 1846) and *Amyrsidea* (only on *Megapodius* Gaimard, 1823, and *Macrocephalon*), which seems to point to their genealogical roots being with the Old World Phasianidae and the Numididae. This assumption still rests on a rather weak foundation because it has to be borne in mind that *Goniocotes* has been shown to have infested *Macrocephalon* secondarily, and that too little is known about the actual distribution of *Amyrsidea* on megapodes.

Summarizing, the chewing lice infesting the Cracidae and the Megapodiidae, the former more than the latter, both show a phylogenetic connection to those of the Phasianidae but not directly to each other. This contradicts the view of Sibley & Ahlquist (1990) who have united the Cracidae and the Megapodiidae in the order Craciformes, setting against that the order Galliformes, containing the Phasianidae, Numididae and Odontophoridae.

### Intrafamilial relationships

Our understanding of the co-speciation of megapodes and their chewing lice is still in its very early stages. Despite this the results of two parsimony analyses are presented here.

In total 51 morphological characters from all nine megapode-infesting Gonioididae genera were evaluated according to their apomorphic and plesiomorphic states and entered in a matrix (table 2). This resulted, using Wagner parsimony analysis, in a single most parsimonious phylogenetic tree (figure 3).

The genera *Leipoielli* Mey, 1986, *Megatheliella* Mey, 1986, and *Euligoniodes* Mey, 1997, which are distinguished by several autapomorphies, each constitute basally diverging

branches in the phylogenetic tree of the megapode-infesting goniodids. This fact, particularly in the case of *Leipoiella* and *Megatheliella*, serves to emphasize the apparently unusual systematic position of the *Leipoa ocellata* Gould, 1840. The limited distribution of *Euligoniodes*, occurring only on *Eulipoa wallacei* (G.R. Gray, 1860), can also be explained in this light. *Euligoniodes* is the sister group of all six of the other Goniodidae genera that parasitize megapodes. The multidimensional scaling of the character-matrix (see table 2 and Appendix) underlines the separate position of *Leipoiella*, *Megatheliella*, and *Euligoniodes* (figure 4). *Euligoniodes* stands in a sister-group relationship to the grouping that includes *Maleophilus* Mey, 1997, as well as *Maleoicus* Mey, 1997, at its root. This constella-

Table 2. Goniodid chewing louse morphology data. Polarity from 0 to 3 (see Appendix).

Chewing louse genera	characters
	0000000001111111112222222222333333333344444444455 123456789012345678901234567890123456789012345678901
<i>Leipoiella</i>	121000022201011001110101000001000000200011001110011
<i>Megatheliella</i>	011100021211110120100001000010000111010111000000010
<i>Maleophilus</i>	020101000100100120101211011110100211020110000000102
<i>Maleoicus</i>	010111000100110120101211001110100111031100010000002
<i>Euligoniodes</i>	010111021211111120111211000010101211131011000001112
<i>Homocerus</i>	100101110010110120101211100010000211030000010000002
<i>Weelahia</i>	120101200100110120001211100010000211010000010100012
<i>Lobicrotaphus</i>	110101300000100120112200201110100221020010100000002
<i>Goniocotes</i>	100110200000000010110001101110110211030200110000002

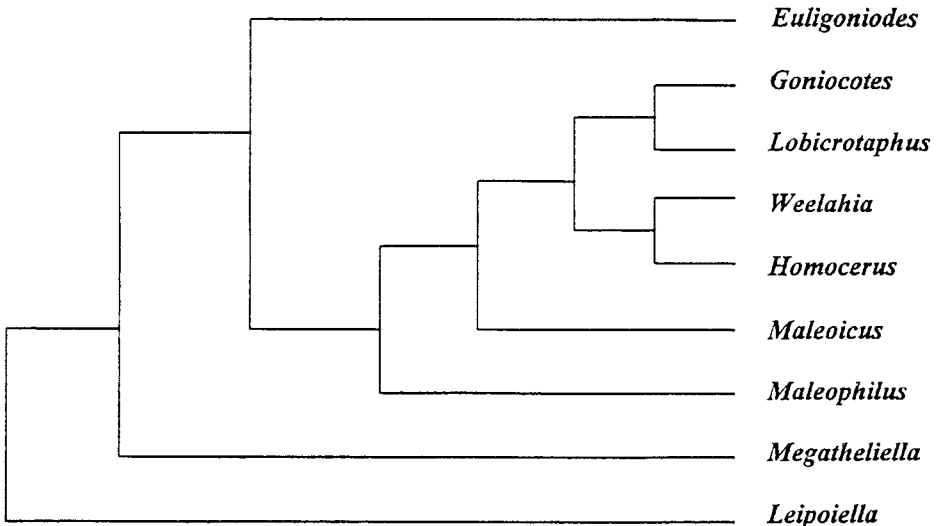


Fig. 3. Hypothetical relationships among the genera of Goniodidae on megapodes. Single most parsimonious tree using Wagner parsimony analysis rooted by character polarity (51 morphological features, see table 2) (Felsenstein, 1993).

tion (see figure 3) points to the close relationship between *Eulipoa* Ogilvie-Grant, 1893, and *Megapodius* that is undisputed from an ornithological viewpoint (Brom & Dekker, 1992).

While it can be assumed that almost all the gonioid genera dealt with here originated on megapodes or their ancestors, this cannot be said of *Goniocotes*. In this case two assumptions are possible: the occurrence of *Goniocotes* on *Macrocephalon* is the result of a secondary colonization deep in the past, or the genus has become extinct on all Megapodiidae with this one exception. The grouping postulated here of *Goniocotes* with *Lobicrotaphus* Mey, 1997, will most probably not survive a further phylogenetic analysis, especially if this interpretation were to be extended to include other galliform host families, or even include the Columbiformes.

Based on the occurrence of 15 different Ischnocera genera (see table 3) which, except for *Goniocotes*, are found only on megapodes, the consensus tree suggests a division of the Megapodiidae as in figure 5.

The Megapodiidae can be split into two lines of descent, at the ends of which stand *Megapodius*/*Eulipoa* on one the hand and *Aepyodius* Oustalet, 1880/*Alectura* Latham,

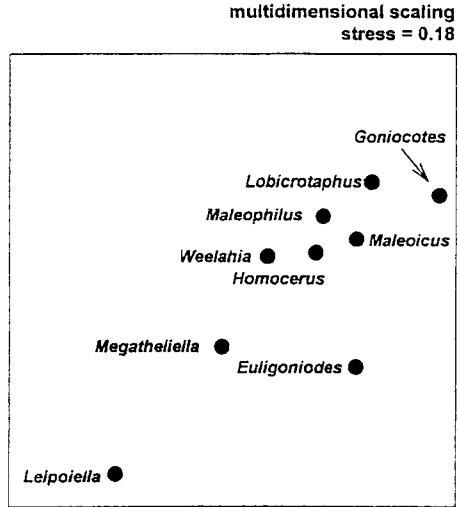


Fig. 4. Representation of similarity among the genera of gonioid chewing lice parasitic on megapodes. Multi-dimensional scaling (Euclytic distance) using the data-matrix (see table 2).

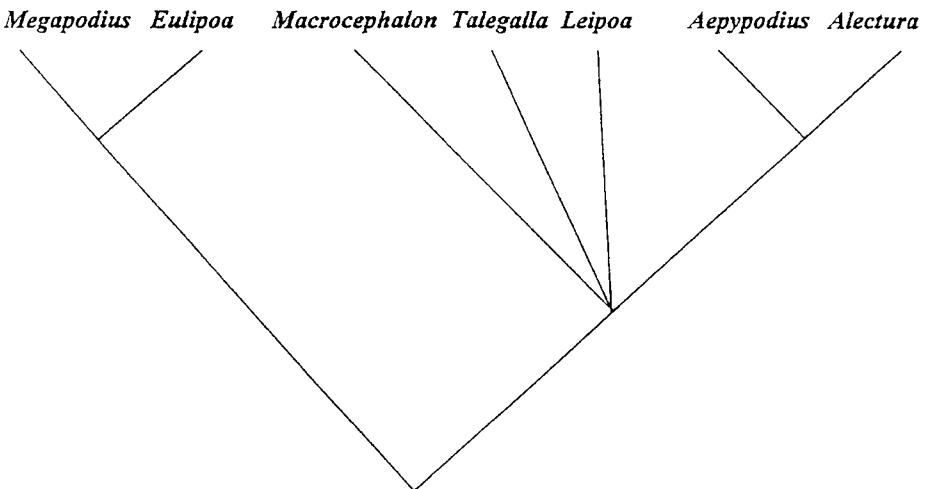


Fig. 5. Megapode cladogram generated from presence/absence of their ischnoceran chewing lice (see table 3). Wagner parsimony analysis (Felsenstein, 1993).



Table 3. Ischnoceran chewing louse presence/absence data for megapode species.  
0 = absent; 1 = present (derived state).

Host species	characters (absent/present)	chewing louse genera
	000000000111111111	
	123456789012345678	
<i>Alectura lathamii</i>	000001100101000100	01 = <i>Leipoiella</i>
<i>Aepyodius arfakianus</i>	000001100101000100	02 = <i>Megatheliella</i>
<i>A. bruijnii</i>	000001100000000100	03 = <i>Maleophilus</i>
<i>Talegalla cuvieri</i>	000001000000000000	04 = <i>Maleoicus</i>
<i>T. fuscirostris</i>	000001000101100011	05 = <i>Euligoniodes</i>
<i>T. jobiensis</i>	000001000001100001	06 = <i>Homocerus</i>
<i>Leipoa ocellata</i>	110000000101000000	07 = <i>Weelahia</i>
<i>Macrocephalon maleo</i>	000001001001000000	08 = <i>Lobicrotaphus</i>
<i>Eulipoa wallacei</i>	000010000010001000	09 = <i>Goniocotes</i>
<i>Megapodius pritchardii</i>	001100000010000000	10 = <i>Megapodiella</i>
<i>M. laperouse</i>	001100000010000000	11 = <i>Malaulipeurus</i>
<i>M. nicobariensis</i>	001100000000001000	12 = <i>Megathelliipeurus</i>
<i>M. cumingii</i>	001100000010011000	13 = <i>Lipeuroides</i>
<i>M. bernsteini</i>	0001000000000001000	14 = <i>Oxylipeurus inaequalis</i> -group
<i>M. tenimberensis</i>	001100000010000000	15 = <i>O. appendiculatus</i> -group
<i>M. freycinet</i>	001100010010001000	16 = <i>O. ischnocephalus</i> -group
<i>M. geelvinkianus</i>	001000000000000000	17 = undesc. gen. aff. <i>Oxylipeurus</i>
<i>M. forstenii</i>	001100000010011000	18 = <i>Talegalliipeurus</i>
<i>M. eremita</i>	001100000010001000	
<i>M. layardi</i>	000000000010000000	
<i>M. decollatus</i>	001100000010001000	
<i>M. reinwardt</i>	001100000010011000	

1824, on the other. The position of *Macrocephalon*, *Talegalla* Lesson, 1828, and *Leipoa* remains unclear. All that can be said of these three genera is that they show much stronger affinities with *Aepyodius* / *Alectura* than with *Megapodius* / *Eulipoa*. The distribution of certain groups of feather mites (Pterolichidae) points in this direction to some extent, indicating that *Talegalla* might be very close to *Aepyodius* / *Alectura* (Atyeo, 1992). What is remarkable is that there is agreement in two details between the phylogenetic tree of Brom & Dekker (1992) and the one presented here: both identify *Aepyodius* / *Alectura* and *Megapodius* / *Eulipoa* as sister group pairs. Otherwise there do exist differences between the megapode phylogenetic tree based on mallophagological evidence on the one hand and on ornithological evidence on the other (see Jones et al., 1995), leaving the impression that the incongruences result from imbalances in the parasitological and/or ornithological data and their interpretation. However, any further interpretation is premature given the present state of knowledge.

Finally, I would like to discuss an interesting phenomenon regarding the distribution of the genus *Maleoicus*. This genus comprises of several forms, four described and at least two undescribed. Using differential diagnostics these can be easily separated into two species groups: the *Maleoicus biordinatus* Clay, 1940, -group and the *M. minor* Piaget, 1880, -group (Mey, 1997). Representatives of both groups are found only on the genus *Megapodius*, although never together on the same species or subspecies. It only

remains to be discovered which *Maleoicus* taxon infests *Megapodius geelvinkianus* A.B. Meyer, 1874, and *M. layardi* Tristram, 1879. We expect to find that *M. biordinatus* sensu lato occurs on both species. As shown in table 4 and figure 6, *Megapodius* can be divided into two groups, which include the isolated relict species *Megapodius nicobariensis* Blyth, 1846, *M. laperouse* Gaimard, 1823, and *M. pritchardii* G.R. Gray, 1864.

*Maleoicus* is the commonest Gonioididae on *Megapodius*, and is often found together with *Maleophilus*. Work has yet to be done on whether *Maleophilus* shares the same

Table 4. The genus *Megapodius* can be divided into two species groups according to the occurrence of *Maleoicus* spp. (see figure 6). The *Megapodius reinwardt* group is parasitized only by *Maleoicus minor* sensu lato, the *Megapodius freycinet* group only by *Maleoicus biordinatus* sensu lato (both species of *Maleoicus* presumably involve some subspecies). \* occurrence of *Maleoicus* unknown.

<i>Megapodius reinwardt</i> group	<i>Megapodius freycinet</i> group
<i>M. reinwardt</i>	<i>M. freycinet</i>
<i>M. cumingii</i>	<i>M. decollatus</i>
<i>M. nicobariensis</i>	<i>M. forstenii</i>
<i>M. bernsteinii</i>	<i>M. eremita</i>
<i>M. tenimberensis</i>	<i>M. pritchardii</i>
	<i>M. laperouse</i>
	<i>M. layardi</i> *
	<i>M. geelvinkianus</i> *

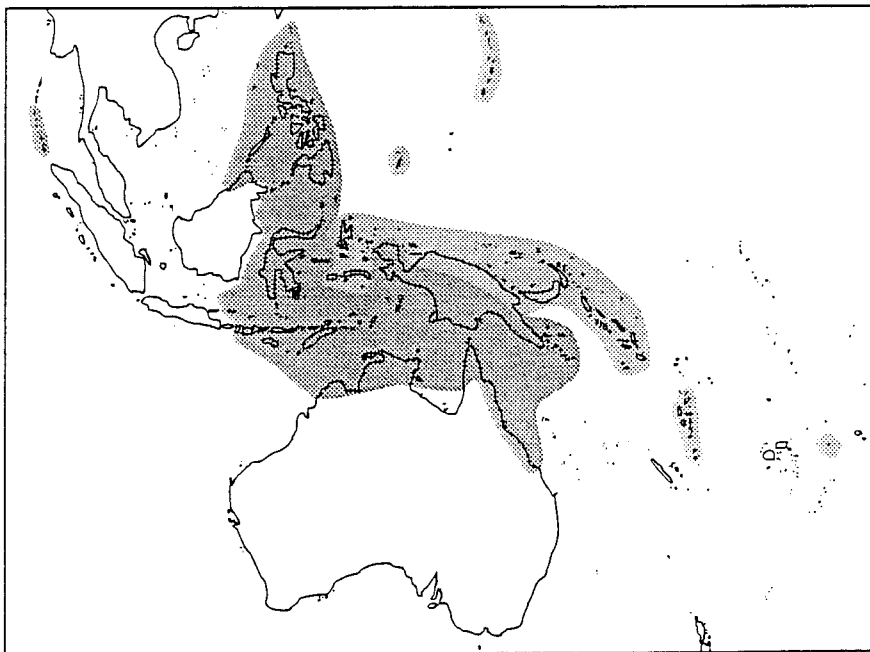


Fig. 6. Distribution of the *Megapodius reinwardt* group (dark shading) and *Megapodius freycinet* group (light shading) indicated by the occurrence of the gonioidids *Maleoicus minor* s. l. (dark shading) and *M. biordinatus* (light shading).

host-dependent distribution as *Maleoicus*. However, we can assume that both *Maleoicus* and *Maleophilus* together parasitized the ancestor of *Megapodius* prior to its evolutionary radiation. This radiation probably originated not in one but in two closely related forms. In other words, it is very likely that this is a case of co-speciation involving *Megapodius* and its own specific Goniodidae ectoparasites. This could be a hint to taxonomists to investigate whether this process can be traced by looking at the characters of *Megapodius* forms themselves.

I am convinced that a more intensive study of the systematic problems dealt with here will reveal, by the principle of mutual illumination, even more interesting correlations in the phylogeny of megapodes and their ectoparasites.

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## Appendix

List of goniodid chewing louse morphological characters. 0 = plesiomorph; 1, 2, 3 = apomorph.

### Body

- (1) body length: male as large as female (variation ranges overlap, on average male smaller than female) 0; male clearly smaller than female (ranges not overlapping) 1.
- (2) body length: small species (1-1,6 mm) 0; medium-sized species (1,7-2,2 mm) 1; large species (> 2,3 mm) 2.

### Head

- (3) head form not sexually dimorphic 0; sexually dimorphic 1.
- (4) clypeal carina narrow 0; broad 1.
- (5) clypeal carina uniform in breadth 0; medially broader than laterally 1.
- (6) nodus limbatus short, not reaching mouth-parts 0; long, reaching mouth-parts 1.
- (7) clavus always conical 0; conical or truncated cone-shaped 1; always truncated cone-shaped 2; almost club-shaped 3.
- (8) antennae not sexually dimorphic 0; slightly sexually dimorphic 1; greatly sexually dimorphic 2.
- (9) male scape (slightly longer than clavus) not enlarged 0; greatly enlarged without projection 1; greatly enlarged with projection 2.
- (10) male scape basiposterior without cone-like sclerotisation 0; with slight cone-like sclerotisation 1; with increased cone-like sclerotisation (in male much greater than in female) 2.
- (11) male pedicellus as long as in female 0; longer than in female 1.
- (12) male flagellum I without apical projection 0; with apical projection 1.
- (13) ommatidium present 0; absent 1.
- (14) ocular seta not sexually dimorphic 0; sexually dimorphic (in male long, in female short) 1.
- (15) male, preantennal seta as microchaete 0; as macrochaete (much longer than scape) 1.
- (16) male, preocular seta: before temple angle 0; on temple angle 1.
- (17) male, preocular seta fine 0; spine-like not on temple angle 1; spine-like on temple angle 2.
- (18) preocular seta not sexually dimorphic 0; sexually dimorphic 1.
- (19) temple setae: mts 1-3 as macrochaetae 0; mts 1+3 as macrochaetae and mts 2 as microchaeta 1.
- (20) male, posttemporal setae as microchaetae 0; as macrochaetae reaching over margin of occiput 1.
- (21) male, temple angle without prolongation 0; with wart-like prolongation 1; with greatly increased prolongation 2.
- (22) prolongation on temple angle absent 0; present and not sexually dimorphic 1; present in female, absent in male 2.
- (23) temple angle rounded 0; pointed 1.
- (24) occipital angle absent 0; present 1.

### Thorax

- (25) form of pronotum trapeze-like 0; flattened trapeze-like 1; discus-like 2.
- (26) pronotum lateral before posterior angle: straight 0; curved 1.
- (27) posterior angle of pronotum not pointed 0; pointed 1.
- (28) pronotal seta not apical on angle of prothorax 0; apical on angle of prothorax 1.
- (29) posterior margin of mesometanotum with regular row of macrochaetae on each side 0; two distal pairs of macrochaetae 1.
- (30) mesometanotum posterior-median rounded 0; double-pointed 1.
- (31) mesometanotum laterally straight (with two "angles") 0; arched (with three "angles") 1.
- (32) setae of mesometasternum absent 0; present (four setae) 1.

### Abdomen

- (33) proximal part of tergopleurits (male, seventh to eighth; female, eighth) apical mediad 0; apical caudad 1.
- (34) third to eighth segments with a pair of sternit plates each side 0; only one sternit plate 1.
- (35) male ninth segment as wide as tenth and without point 0; much smaller than ninth and with bristled point 1; tenth segment joined with ninth and without bristled point 2.
- (36) male, genitoanalconus slightly enlarged 0; distinctly enlarged 1.
- (37) female, end of abdomen broadly and median not or slightly arched 0, broadly and median deeply arched (two-lobed) 1; conically extended and median slightly arched 2.
- (38) number of postspiracular macrochaetae on second and third segment each sides: second three, third two 0; second and third two 1; second one, third two 2; second and third one 3.
- (39) female, paragenital swelling (tylus) absent 0; present 1.
- (40) female, margin of vulva (lobus portae) with setae complete and almost regular 0; with setae regular in groups 1; laterally with spine-like setae 2.
- (41) male, genitale solenoid 0; modified 1.
- (42) male, genitalia softly and weakly sclerotised 0; strongly sclerotised 1.
- (43) male, genitalia almost as long as abdomen 0; clearly shorter than abdomen 1.
- (44) male, genitalia apically symmetric 0; asymmetric 1.
- (45) male, genitalia anterior end of basal apodeme convex 0; turned back 1.
- (46) paramere fusion: fused totally with basal apodeme 0; not totally fused with basal apodeme 1.
- (47) male, apical-posterior part of genitalia (paramere) laterally smooth 0; laterally porous (appearing serrated) 1.
- (48) paramere without barb inwards 0; with barb inwards 1.
- (49) male, endomeron absent 0; present 1.
- (50) male, endophallus spiraculation absent 0; present 1.
- (51) male, second to eighth segments (between postspiracular setae) with row of tergal setae, bristles of same length regulary ordered 0; bristles of different lengths regulary ordered 1; reduced to groups of setae 2.