# A MORPHOLOGICAL PHYLOGENY WITH A TAXONOMIC REVISION OF AFRICAN SPECIES OF *GONIODES* (INSECTA: PHTHIRAPTERA: ISCHNOCERA) *SENSU LATO* FROM THE GALLIFORMES (AVES)

BY

MATHYS J. MEYER

DISSERTATION

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Doctoral Committee:

Adjunct Assistant Professor Kevin P. Johnson, Chair and Director of Research
Professor May R. Berenbaum
Adjunct Assistant Professor Christopher H. Dietrich
Associate Professor Bettina M. Francis
Professor James Whitfield

**ABSTRACT**

Parasites are the most diverse metazoan group on earth and are important in understanding ecological and evolutionary processes. Given their high host specificity, simple life cycle and distinctive molecular evolution, the approximately 5000 species of ectoparasitic lice in the order Phthiraptera are ideal models for such work. Unfortunately, study of this group is hindered by a history of poor taxonomy and a lack of a widely accepted higher-level phylogeny for the Phthiraptera. This study broadly contributes to our understanding of the suborder Ischnocera, and more specifically the family Goniodidae. Chapter 1 is a description of *Picicola donwebbi*, a new species of chewing louse from the Rufous-sided Broadbill (*Smithornis rufolateralis* Gray, 1864) from Ghana. It is the first species of Ischnocera recorded from broadbills (Passeriformes: Eurylaimidae) and, based on morphology, is placed in the *Picicola quadripustulosus* species group recorded from the Pittidae (Passeriformes). To evaluate its genetic distinctiveness and phylogenetic position in the *Degeeriella* complex sequences of nuclear (elongation factor-1) and mitochondrial (cytochrome oxidase I) genes for this species are compared to that of various other species. Although *P. donwebbi* is genetically distinct its phylogenetic position within the larger complex remains unclear. Chapter 2 consists of the first phylogenetic analysis of the basal ischnoceran genus *Goniodes* based on morphological data. The analysis includes 36 species of *Goniodes* representing all 13 recognized intrageneric groups, as well as 9 taxa representing 4 additional ischnoceran genera: *Goniocotes* (6 species), *Physconelloides* (1 species), *Campanulotes* (1 species), and *Heptapsogaster* (1 species) as outgroups. The parsimony analysis of 262 morphological characters found 5 most parsimonious trees with a length

of 2486 steps (CI: 0.276; RI: 0.561; RC: 0.150). A consensus is mostly resolved with the exception of disagreement between two weakly supported basal groups containing a single species of *Goniodes* and species of the genus *Goniocotes*. The overall tree topology, characterized by a continuous stepwise branching pattern, is largely a grade with the placement of taxa strongly correlated with general size. Clay's subgeneric classification, although not fully substantiated, is largely confirmed. However, it largely confirms broad relationships, showing that smaller, medium, and large-bodied species cluster together. Even so, monophyletic and strongly supported apical groups cannot from a gross taxonomic perspective be effectively "described/circumscribed" in light of morphology alone. It is thus apparent that the reality of the biological complexities associated with ubiquitous morphological convergence in the Ischnocera at large, and *Goniodes* specifically, cannot effectively be separated from the artificial intricacies imposed by classification. Chapter 3 reviews the African species of *Goniodes* placing 31 species in 8 intrageneric groups following Clay's revision. An additional 5 species from 3 intrageneric groups that are incidental or introduced to Africa are also briefly discussed. This chapter provides an extensive review of the taxonomic and nomenclatural histories, host associations of each species, and concludes with an discussion of the current status of each species. The intrageneric groups, including the component species with their type hosts are: Group F – *G. wilsoni* ex *Afropavo congensis*; Group G – *G. numidae* ex *Numida m. meleagris*, *G. hopkinsi* ex *Guttera edouardi seth-smithi*, *G. meyi* ex *Numida meleagris meleagris*, *G. klockenhoffi* ex *Numida meleagris reichenowi*, *G. reichenowii* ex *Numida meleagris reichenowi*, *G. plumiferae* ex *Guttera plumifera schubotzi*, *G. schoutedenii* ex *Guttera edouardi verreauxi*, *G. inaequalis* ex *Guttera edouardi barbata*;

Group H – *G. gigas* ex *Gallus gallus*, *G. agelastes* ex *Agelastes meleagrides*, *G. bifurcus* ex *Guttera pucherani pucherani*, *G. zairensis* ex *Guttera plumifera schubotzi*, *G. gutterae* ex *Guttera plumifera plumifera*, *G. phasidus* ex *Phasidus niger*; Group I – *G. emersoni* ex *Francolinus psilolaemus*; Group K – *G. assimilis* ex *Francolinus capensis*, *G. ammoperdix* ex *Ammoperdix griseogularis*, *G. antennatus* ex *Francolinus leucoscepus leucoscepus*, *G. oreophilus* ex *Francolinus psilolaemus elgonensis*, *G. scleroptilus* ex *Francolinus levaillantoides jugularis*, *G. isogenos* ex *Francolinus africanus africanus*, Group L – *G. soueefi* ex *Coturnix chinensis australis*, *G. astrocephalus* ex *Coturnix coturnix coturnix*, *G. moucheti* ex *Francolinus nobilis*, *G. lootensi* ex *Coturnix chinensis adansonii*. Species introduced or incidental to Sub-Saharan Africa includes: Group A – *G. pavonis* introduced via its type host *Pavo cristatus*; Group B – *G. meinertzhagenii* introduced via its type host *Pavo cristatus*; Group K – *G. dispar* introduced via its type host *Perdix perdix* (*Perdix cinerea*) to Robben Island, South Africa, and also known from single specimen collected from zoo specimen of *Francolinus afer cranchii* in Zimbabwe, *G. securiger* incidental in Sub-Saharan Africa via its type host *Alectoris barbara barbara*, *G. dissimilis* ex *Gallus gallus* incidental in Sub-Saharan Africa via domestic chickens. Chapter 4 in keeping with the recommendations of the International Code of Zoological Nomenclature is the first published listing of the Phthirapteran (Insecta) type material housed in the Royal Museum for Central Africa in Tervuren, Belgium. This annotated catalogue lists the primary and secondary types of 63 chewing lice taxa from the suborder Amblycera (families Menoponidae and Laemobothriidae) and Ischnocera (families Philopteridae and Trichodectidae), and includes data for 39 holotypes, 488 paratypes (including 23 allotypes), 7 metatypes, and 34 “type” specimens of unknown status. Relevant taxa are listed alphabetically by specific epithet, original generic assignment, and (in parentheses) the current family designation. Also included are the author, year of description, and original citation, followed by the type, original collection and host data, any relevant taxonomic remarks, and its current taxonomic status. Appendix A, is a collaborative study investigating a major host switches in the Goniodidae. Such host switches by parasites between highly divergent host lineages are important for understanding new opportunities for parasite diversification. One such major host switch is inferred for avian feather lice (Ischnocera) in the family Goniodidae, which parasitize two distantly related groups of birds: Galliformes (pheasants, quail, partridges, etc.) and Columbiformes (pigeons and doves). Although there have been several cophylogenetic studies of lice at the species level, few studies have focused on such broad evolutionary patterns and major host-switching events. Using a phylogeny based on DNA sequences for goniodid feather lice, we investigated the direction of this major host switch. Surprisingly, we found that goniodid feather lice have switched host orders, not just once, but twice. A primary host switch occurred from Galliformes to Columbiformes, leading to a large radiation of columbiform body lice. Subsequently, there was also a host switch from Columbiformes back to Galliformes, specifically to megapodes in the Papua-Australasian region. Our results further reveal that although morphologically diagnosable lineages are supported by molecular data, many of the existing genera are not monophyletic and a revision of generic limits is needed.

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*Numquam ponenda est pluralitas sine necessitate – Plurality ought never be posited without neccessity*

William of Ockham (1285-1349)

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# GENERAL INTRODUCTION

Parasites are the most diverse metazoan group on earth and their study has led to numerous insights into ecological and evolutionary processes (Page 2003; Poulin 2007). Given the intimate relationship between parasite and host, parasites can over time come to reflect their hosts' phylogenetic history. This correlation first noted by either Jardine (1841) according to Hopkins (1951); or Kellogg (1914)(see Klassen, 1992; and Choudry *et al*. 2002 for historical reviews); and articulated as Fahrenholz' rule by Eichler (1941, 1942, 1948). Fahrenholz' rule suggests that the phylogenetic history and cladogenesis of a parasite reflects that of its host. Studies of cospeciation have had broad utility in general ecological and evolutionary studies, being used in comparative studies of adaptation (Clayton *et al*. 2004; Johnson and Clayton 2003a; Lee and Clayton 1995; Rózsa *et al*. 1996; Vas *et al*. 2011a); behavior (Barbosa *et al*. 2002; Whiteman and Parker 2004; Kose and Möller 1999; Kose *et al*. 1999); transmission (Brooke 2010; Brooke and Nakamura 1998; Harbison *et al*. 2008; Harbison *et al*. 2009; Hilgarth 1996; Lindholm *et al*. 1998); health (Booth *et al*. 1993; Brown *et al*. 1995; Dik 2006; Humphreys 1975; Kuiken *et al*. 1999; Taylor 1981; Wobeser *et al*. 1974); relative rates of evolution (Barker *et al*. 2003; Hafner *et al*. 1994; Johnson and Whiting 2002; Johnson *et al*. 2003a; Moran *et al*. 1995; Murrell and Barker 2005; Page *et al*. 1998; Paterson *et al*. 2000; Smith *et al*. 2004; Smith *et al*. 2011; Vas *et al*. 2012; Yoshizawa and Johnson 2003, 2010); host population histories (Banks *et al*. 2006; Hughes *et al*. 2007; Johnson *et al*. 2002a; Johnson *et al*. 2011; Malenke *et al*. 2009; Toon and Hughes 2008; Whiteman *et al*. 2004); host and parasite conservation (Perez and Palma 2001; Whiteman and Parker 2005; Vas and Fuisz 2011); and even ecological restoration (Moore 2005). Historically the reciprocal nature of cospeciation has most frequently been used to elucidate and interpret the evolutionary history and biogeography of parasite and/or its host (Barker 1994; Brooks 1981; Clayton and Johnson 2003; Gómez-Díaz *et al*. 2007; Hafner *et al*. 1994; Hennig 1966; Hopkins 1942; Hugot 1999; Johnson *et al*. 2002; Weckstein 2004). Ectoparasitic lice have played an especially important role in these efforts.

The Phthiraptera (Insecta), contains approximately 5000 species in four suborders, Rhynchophthorina, Amblycera, Ischnocera and Anoplura, which parasitize 5000 bird and mammal species (Durden and Musser 1994; Price *et al*. 2003; Smith 2004; Triplehorn and Johnson 2005). They are unique among insect parasites in that they lack a free-living dispersal stage, and most are unable to survive off a host for long. As a result, lice are poor dispersers, dispersing primarily through vertical transmission from parents to offspring (Clayton and Tompkins, 1994; Brooke, 2010; Lee and Clayton, 1995), or through horizontal transmission during mating (Hillgarth, 1996). Dispersal opportunities other than these are probably infrequent, but do occur. The following situations and mechanisms have been used to explain transmission of lice; communal roosts (Kellogg, 1896; Rózsa *et al*. 1996; Whiteman and Parker, 2004); kleptoparasitic behavior (Hopkins, 1942); courtship feeding (Lindholm *et al*. 1998); host aggregations (Brooke and Nakamura, 1998); sequentially shared nest holes (Harrison, 1915; Johnson *et al*. 2002a; Weckstein, 2004); communal sand or dust baths (Hoyle, 1938; Hopkins, 1949b; Price *et al*., 2003a); shared nesting islands (Banks *et al*., 2006); straggling from prey to host (Whiteman *et al*., 2004); and phoresy, a phenomenon in which lice “hitch- hike” from one host to another by attaching themselves to hippoboscid flies or other flying insects (see Clay and Meinertzhagen, 1943; Harbison *et al*. 2009; Keirans, 1975 for reviews).

The relative importance of these mechanisms is still unclear. In particular, phoresy may play an important role in the dispersal of some groups of lice (Harbison and Clayton 2011).

In comparison to other ectoparasites, species of Phthiraptera are highly host specific and a number of lice have followed their hosts to extinction (Mey 1990, 2005; Stork and Lyal 1993). This high host specificity, in combination with their simple life cycle and distinctive molecular evolution, make lice ideal models for studying cospeciation (Clayton *et al*. 2004; Johnson and Clayton 2003a, 2003b, 2004; Page 2003). However, study of this group is hindered by a history of poor taxonomy (Clay and Hopkins 1950, 1955; Ledger 1980; Mey 2003, 1998; Price *et al*. 2003) and the lack of a widely accepted higher-level phylogeny for the Phthiraptera (Smith *et al*. 2004).

The relationships among the avian feather lice in the suborder Ischnocera are particularly problematic (Cruickshank *et al*. 2001; Johnson *et al*. 2001; Smith 2000, 2001; Smith *et al*. 2004). Lack of consensus results from a variety of factors including high levels of convergence, the variety of classification schemes historically employed, and the discordance between morphological and molecular data (Kéler 1939, Eichler 1963, Hopkins and Clay 1952, 1953, 1955; Price *et al*. 2003, Smith *et al*. 2004, Johnson *et al*. 2001, Johnson *et al*. 2011). As a result, the number of accepted families in Ischnocera ranges between two (Ward 1957; Palma and Barker 1996; Price *et al*. 2003), three (Hopkins and Clay 1952), four (Smith 2000), and a staggering 21 (Eichler 1963).

The family Goniodidae, first proposed by Mjöberg (1910) on the basis of the distinctive head shape and afforded family status by Kéler (1939), has received particular attention. Though not recognized in recent checklists (Palma and Barker 1996; Price *et* *al*. 2003), possibly because family status would render the Philopteridae paraphyletic (Smith *et al*. 2004), this group is nonetheless supported by morphological and molecular data in a number of recent studies (Cruickshank *et al*. 2001; Johnson *et al*. 2001a; Lyal 1985a; Mey 1994, 1997; Smith 2000, 2001; Smith *et al*. 2004). The precise generic content and taxonomy of the Goniodidae remains ambiguous with the exception of broad support for separate columbiform and galliform clades (Smith *et al*. 2004): The *Coloceras* complex *sensu* Clay (1976) parasitic on pigeons and doves, and the *Goniodes* complex *sensu* Clay (1940, 1976) parasitic on the galliforms (Johnson *et al*. 2001).

The subject of this study is *Goniodes* Nitzsch 1818, the largest genus in the *Goniodes* complex. I aim to decipher and stabilize the problematic nomenclature; describe and standardize the morphology, and establish a phylogeny of *Goniodes*, in order to gain a better understanding of; 1) the evolutionary relationships in *Goniodes* specifically with regards to existing classifications (Clay 1940; Kéler 1939; Eichler 1963); 2) the monophyly of *Goniodes* with respect to *Goniocotes* Burmeister 1838; and 3) the alpha-level taxonomy of the Sub-Saharan African species in the genus. I realize this goal in the following chapters:

**Chapter 1. A new species of *Picicola* Clay and Meinertzhagen, 1938 (Phthiraptera: Ischnocera) parasitic on the Rufous-sided Broadbill (Passeriformes: Eurylaimidae) in Ghana**. This description of a new species of louse in the genus *Picicola* was important in my overall understanding of comparative morphology in ischnoceran lice.

**Chapter 2. A morphological phylogeny of the ischnoceran louse genus *Goniodes* Nitzsch, 1818 (Insecta: Phthiraptera: Ischnocera) parasitic on the**

**Galliformes (Aves)**; provides a working hypothesis based on morphology for evolutionary relationships in *Goniodes*. I use this hypothesis to specifically explore the intrageneric classification proposed by Clay (1940), and more generally the alternatives proposed by Kéler (1939) and Eichler (1963).

**Chapter 3. A taxonomic revision of Sub-Saharan members of the ischnoceran louse genus *Goniodes* Nitzsch, 1818 (Insecta: Phthiraptera: Ischnocera)**; provides an important first step in stabilizing taxonomy and nomenclature, and provides a critical foundation for a comprehensive taxonomic revision of this large homogeneous taxon.

**Chapter 4. Type specimens of chewing lice (Insecta: Phthiraptera: Amblycera and Ischnocera) in the Royal Museum for Central Africa, Tervuren, Belgium**; serves to stabilize the problematic nomenclature of specifically African Ischnocera and Amblycera, and contributes to phthirapteran nomenclature in general.

These five chapters in combination form a solid foundation, a prodromus, to the genus *Goniodes*. It will facilitate a better understanding of the nomenclature, taxonomy, systematics, and evolutionary relationships in *Goniodes*, but has only scratched the surface of the complex morphology and relationships that exist between species in this genus. More importantly it supports the mission and goals of the organized international effort to better understand the often neglected, but important Phthiraptera. In addition to these chapters I also include two additional papers completed during this work as appendices.

**Appendix A: There and back again: switching between host orders by avian body lice (Ischnocera: Goniodidae)** is the results of a collaborative study investigating a major host switches in the Goniodidae. Such host switches by parasites between highly divergent host lineages are important for understanding new opportunities for parasite diversification. In this study one such major host switch is inferred for avian feather lice (Ischnocera) in the family Goniodidae, which parasitize two distantly related groups of birds: Galliformes (pheasants, quail, partridges, etc.) and Columbiformes (pigeons and doves). Although there have been several cophylogenetic studies of lice at the species level, few studies have focused on such broad evolutionary patterns and major host-switching events. Using a phylogeny based on DNA sequences for goniodid feather lice, we investigated the direction of this major host switch. Surprisingly, we found that goniodid feather lice have switched host orders, not just once, but twice. A primary host switch occurred from Galliformes to Columbiformes, leading to a large radiation of columbiform body lice. Subsequently, there was also a host switch from Columbiformes back to Galliformes, specifically to megapodes in the Papua-Australasian region. Our results further reveal that although morphologically diagnosable lineages are supported by molecular data, many of the existing genera are not monophyletic and a revision of generic limits is needed.

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## CHAPTER 1:

## A new species of *Picicola* Clay and Meinertzhagen, 1938 (Phthiraptera: Ischnocera) parasitic on the Rufous-sided Broadbill (Passeriformes: Eurylaimidae) in Ghana[1]


### ABSTRACT

*Picicola donwebbi*, a new species of chewing louse from the Rufous-sided Broadbill (*Smithornis rufolateralis* Gray, 1864) collected in Ghana, is herewith described and illustrated. This is the first species of Ischnocera recorded from the broadbills (Passeriformes: Eurylaimidae) and, based on morphology, is placed in the *Picicola quadripustulosus* species group recorded from the Pittidae (Passeriformes). To evaluate its genetic distinctiveness and phylogenetic position in the *Degeeriella* complex sequences of nuclear (elongation factor-1) and mitochondrial (cytochrome oxidase I) genes for *Picicola donwebbi* are compared to various other species. Although this new species is genetically distinct its phylogenetic position within the larger complex is unclear.



**Key words:** Africa, chewing lice, *Picicola donwebbi*, *Smithornis rufolateralis*, *Degeeriella* complex, elongation factor-1, cytochrome oxidase I, maximum-likelihood.


### INTRODUCTION

No species of chewing louse (Insecta: Phthiraptera) of the suborder Ischnocera has been described from the broadbills (Aves: Eurylaimidae). This family of birds is an Old World group of suboscine songbirds (Passeriformes). The other major family of

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[1] This chapter has been published. Meyer, M. J., R. D. Price, and K. P. Johnson. 2008. *Zootaxa* 1762: 63-68. Reproduced with permission.

suboscines that occurs in the Old World is the Pittidae, which has 10 valid species of *Picicola* (Ischnocera) recorded from 10 host species (Price *et al*. 2003; Somadder and Tandan 1977). Here we describe the first ischnoceran louse collected from the family Eurylaimidae and place it in the genus *Picicola* Clay and Meinertzhagen, 1938.

*Picicola* was originally erected for three species of Ischnocera found on the Picidae (Piciformes) by Clay and Meinertzhagen (1938). Price *et al*. (2003) considered 29 of the 39 named species in the genus valid. Subsequent to Price *et al*. (2003), an additional seven species have been described (Price and Weckstein 2006; Valim and Linardi 2006). Of these 36 species, 18 have been recorded from the avian order Piciformes (Picidae, Bucconidae, and Galbulidae) and 18 from the Passeriformes (Pittidae, Tyrannidae, Furnariidae, Mimidae, Parulidae, Cracticidae, Dicruridae, and Ptilonorhynchidae). Dalgleish (1969) revised species of *Picicola* from the Picidae, Somadder and Tandan (1977) those from the Pittidae, and Williams (1979) those of the Passeriformes excluding those from the Pittidae. Most recently, Price and Weckstein (2006) reviewed the species from the Bucconidae and Galbulidae.

*Picicola* falls within the larger *Degeeriella* complex and although the monophyly of this historically recognized taxonomic complex (Clay 1958, Eichler 1963) is strongly supported by morphological (Smith 2001) and molecular data (Cruickshank *et al*. 2001), the same cannot be said for the generic classification within the complex. Johnson *et al*. (2002) shows that current definitions of genera in the *Degeeriella* complex do not represent monophyletic groups; instead, most genera, including *Picicola*, are currently paraphyletic with respect to other genera. In order to evaluate the genetic distinctiveness and phylogenetic position of the species of *Picicola* from broadbills within the larger

*Degeeriella* complex we sequenced its nuclear (elongation factor-1) and mitochondrial (cytochrome oxidase I) genes and analyzed these sequences in relation to those published by Johnson *et al*. (2002).

## MATERIALS & METHODS

We collected lice, using ethyl acetate fumigation as described by Clayton and Drown (2001), from a specimen of Rufous-sided Broadbill (*Smithornis rufolateralis* Gray, 1864) collected during a expedition to Ghana. Lice specimens were mounted on slides in Canada balsam following the procedure given in Price *et al*. (2003) and the DNA voucher specimen was prepared following the procedure in Johnson *et al*. (2002).

Classification follows Howard and Moore (1991) for hosts and Price *et al*. (2003) for lice. Morphological terminology follows Dalgleish (1969), Somadder and Tandan (1977), Williams (1979), and Price and Weckstein (2006) in an attempt to simplify placement of the new species in existing keys.

All measurements (in millimeters) are given as a range followed by the mean in parentheses. Abbreviations for measured characters are: TW, temporal width; HL, head length; CI, cephalic index (HL/TW); PW, prothorax width; MW, metathorax width; AWV, abdomen width at segment V; GL, male genitalia length; PL, male penis length; and TL, total length. Specimens are deposited in the following collections (acronyms follow Evenhuis and Samuelson 2007): BMNH – The Natural History Museum, London, United Kingdom; FMNH – Field Museum of Natural History, Chicago, Illinois, USA; INHS – Illinois Natural History Survey, Champaign, Illinois, USA; OSEC – K. C. Emerson Museum, Oklahoma State University, Stillwater, Oklahoma, USA.

Extraction and sequencing of the nuclear (elongation factor-1) and the mitochondrial (cytochrome oxidase I) genes from lice specimens follow the laboratory protocols in Johnson *et al*. (2002). We evaluated the phylogenetic position of the broadbill *Picicola* by maximum likelihood analysis of the new sequences together with the previously published data of Johnson *et al*. (2002), using the same model parameters. DNA sequences analyzed for *P. donwebbi* are deposited in GenBank (Accession numbers pending).

### ***Picicola donwebbi*** **Meyer, Price, and Johnson, new species**

**(Figs. 1.1–1.3)**

**Type host.** *Smithornis rufolateralis* Gray, 1864, Rufous-sided Broadbill.

*Description*. Both sexes similar except for terminalia and dimensions. General aspects of body and chaetotaxy as in Fig. 1.1 for male and Fig. 1.3 for female. Head with marginal carina well developed, with both outer edge and inner border medially pointed; lateral notch present and interrupting but not breaking marginal carina at point of curvature around frons. Preantennal suture distinct. Frontal plate located anterior to preantennal suture, distinct and sculptured, but without thickened posterior edge. Tip of conus usually not reaching distal end of 1$^{st}$ antennal segment (scape). Abdominal tergites divided, II–VII with 2 central setae, VIII with 4. Abdominal segments with prominent pleural thickening and reentrant heads. Margin of male tergite IX with long seta posteriolateral to shorter one on either side. Female subgenital plate vulval margin with 16 short setae and row of 6 very short setae lateromedial to this marginal row, with 4 additional short setae displaced latero-anteriorly. Male genitalia (Fig. 1.2) with single sensillum on each endomeral arm. Dimensions (in millimeters): Male: TW, 0.32–0.33 (0.33); HL, 0.43–0.48 (0.45); CI, 1.33–1.49 (1.38); PW, 0.21–0.22 (0.21); MW, 0.27–0.28 (0.27); AWV, 0.38–0.46 (0.40); GL, 0.24–0.28 (0.27); PL, 0.03–0.04 (0.04); TL, 1.43–1.55 (1.48). Female: TW, 0.34–0.37 (0.35); HL, 0.45–0.48 (0.47); CI, 1.31–1.33 (1.32); PW, 0.22–0.25 (0.23); MW, 0.29–0.30 (0.30); AWV, 0.40–0.44 (0.42); TL, 1.61–1.78 (1.72).

*Type material*. Holotype male is labeled "ex *Smithornis rufolateralis*, GHANA: Goaso, K. P. Johnson, 28 Mar 2003, BDM 851" and is deposited in INHS. Paratypes: 4 males, 5 females with same data as holotype and deposited as follows: 1 male, 1 female (BMNH); 1 male, 1 female (FMNH); 1 male, 2 females and a DNA voucher specimen (INHS); 1 male, 1 female (OSEC).

*Diagnosis*. *Picicola donwebbi* differs from *Picicola* collected from the Picidae by the anterior shape of the head being medially pointed rather than smoothly rounded (*P. candidus* and *P. snodgrassi* species groups), or with an apical depression or truncate (*P. thripias* species group); by the marginal carina being well developed and complete rather than well developed but thinner where it curves around the frons; and by the lateral notch being present rather than absent. *Picicola donwebbi* differs from the *Picicola* found on the passeriform families Tyrannidae, Furnariidae, Mimidae, Parulidae, Cracticidae, Dicruridae, and Ptilonorhynchidae by having the preantennal suture distinct rather than indistinct; by the frontal plate lacking a thickened posterior edge; and by the marginal carina thin but not interrupted where it curves around the frons rather than nearly broken where it curves around the frons. *Picicola donwebbi* is morphologically most similar to the *Picicola* found on the Pittidae as defined by Somadder and Tandan (1977) and is, therefore, placed in their *P. quadripustulosus* species group. In this species group it is most closely allied with *P. angolensis* Somadder and Tandan, 1977 by the males having only two sensilla associated with the genitalia; by the number of setae on abdominal tergites III–VI equaling 2 central (< 11 total); and by the size of the conus which does not reach the base of the 1st antennal segment (scape). However, overall *P. donwebbi* is smaller than *P. angolensis* in TW, HL, PW, MW, AWV, and TL, but has a significantly higher CI in both sexes. Further differences involve the posterior margin of segment IX–XI not emarginate in females of *P. donwebbi* and the number of preantennal setae (7 vs. 6). In "Degeerielline Ischnocera (Insecta: Phthiraptera) of the Pittidae (Aves)" (Somadder and Tandan 1977), *P. donwebbi* keys out to couplet 6. The following is a modification of that couplet:

6. Ocular seta and marginal temporal seta 2 very long; pigmentation pattern of abdominal dorsum characteristic (Figs. 4, 15):

- with posterior margin of segment IX–XI in female emarginate; both male and female with CI < 1.0 ……………………………….…*angolensis* (Somadder and Tandan 1977)
- with posterior margin of segment IX–XI in female not emarginate; both male and female with CI > 1.0…………………..…………………………..…*donwebbi*, sp. nov.

*Etymology*. This species is named in honor of Dr. Donald Webb on occasion of his retirement after 40 years of service to the Illinois Natural History Survey and generations of entomology graduate students at the University of Illinois.

## DISCUSSION

Sequences of nuclear (elongation factor-1) and mitochondrial (cytochrome oxidase I) genes from *P. donwebbi* confirms the genetic distinctiveness of this new species. However, these data do not currently fully support the taxonomic placement of *P. donwebbi* within the genus *Picicola* (Fig. 1.4). Based on this analysis *P. donwebbi* is excluded from the large clade containing all species of *Austrophilopterus* and *Picicola* as well as *Degeeriella carruthi* recovered by Johnson *et al*. (2002). Instead it falls within a large group in which relationships are less clear. Here it is the sister taxa to a well-supported grouping of *Capraiella* sp. ex *Eurystomus* (an African roller) and *D. fulva* (from a North American Hawk). This well supported grouping (*Capraiella* sp. ex *Eurystomus* + *Degeeriella fulva*) is also recognized based on morphological similarities according to Johnson *et al*. (2002). Sister to this less well-supported grouping of ((*Capraiella* sp. ex *Eurystomus* + *D. fulva)* + (*P. donwebbi*)) is a consistently recovered grouping of two species of *Cotingacola* from a new world suboscine. *Smithornis rufolateralis* the host of *P. donwebbi* is in one of the old world suboscine families Eurylaimidae, no *Picicola* from the Pittidae, the second old world family of suboscines, were available for this analysis. However, the close placement of *P. donwebbi* to *Cotingacola* might indicate some influence of host relationship on phylogenetic relationships among the species of lice in this group.

In summary, the outcome of this analysis does support the genetic distinctiveness of *P. donwebbi*. However, a better understanding of the phylogenetic relationship between *P. donwebbi* and other species within the larger *Degeeriella* complex remains unclear. This confirms Johnson *et al*.'s (2002) assessment that many genera in the complex are not monophyletic and that a taxonomic revision is warranted. We, therefore, consider the placement of this species into the genus *Picicola* as tentative until a revision of the generic level definitions in the *Degeeriella* complex is performed.

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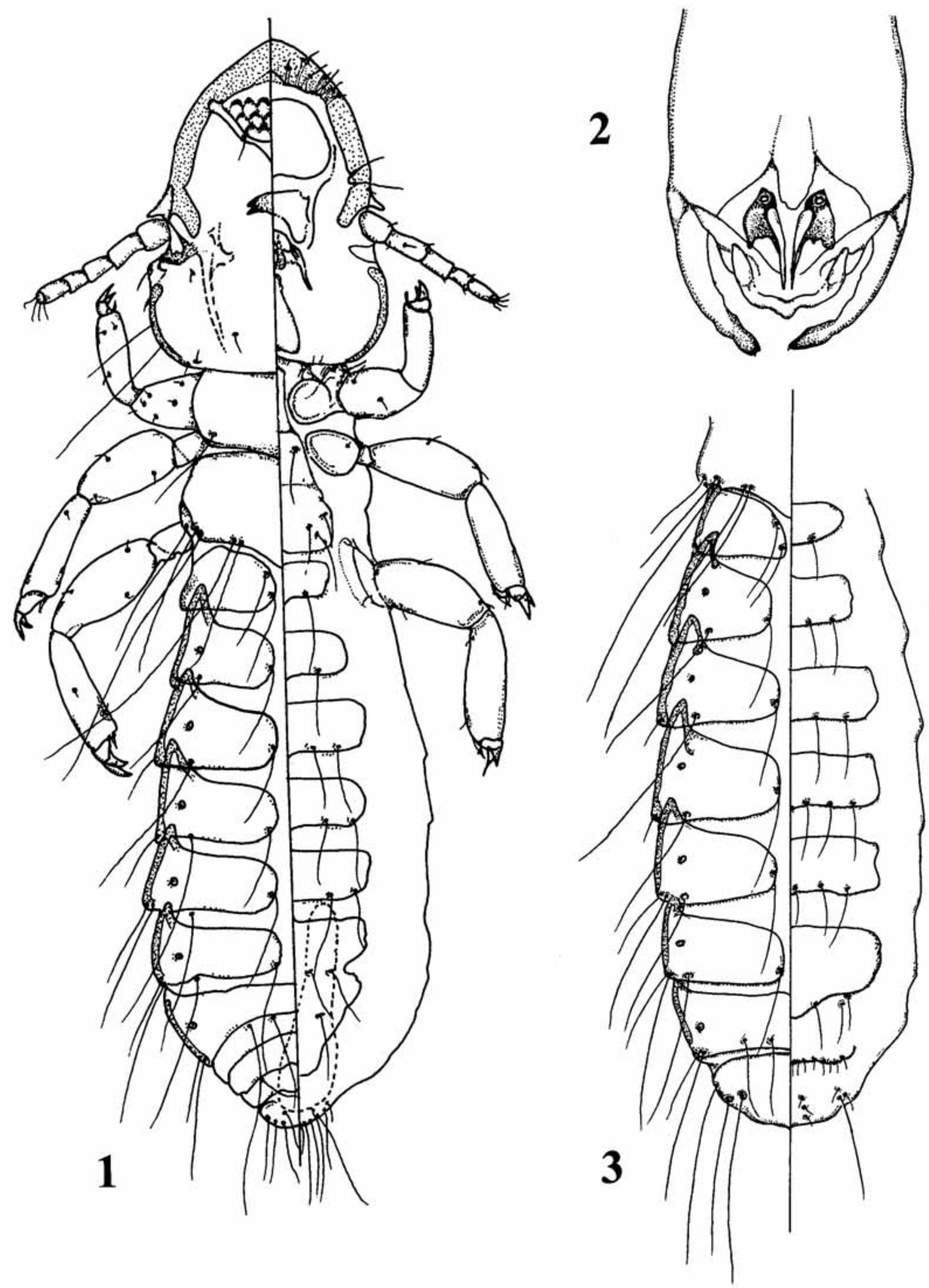
## FIGURES




**Figures 1.1–1.3.** *Picicola donwebbi*. 1.1. Entire dorsoventral male. 1.2. Male genitalia. 1.3. Female metanotum and dorsoventral abdomen.

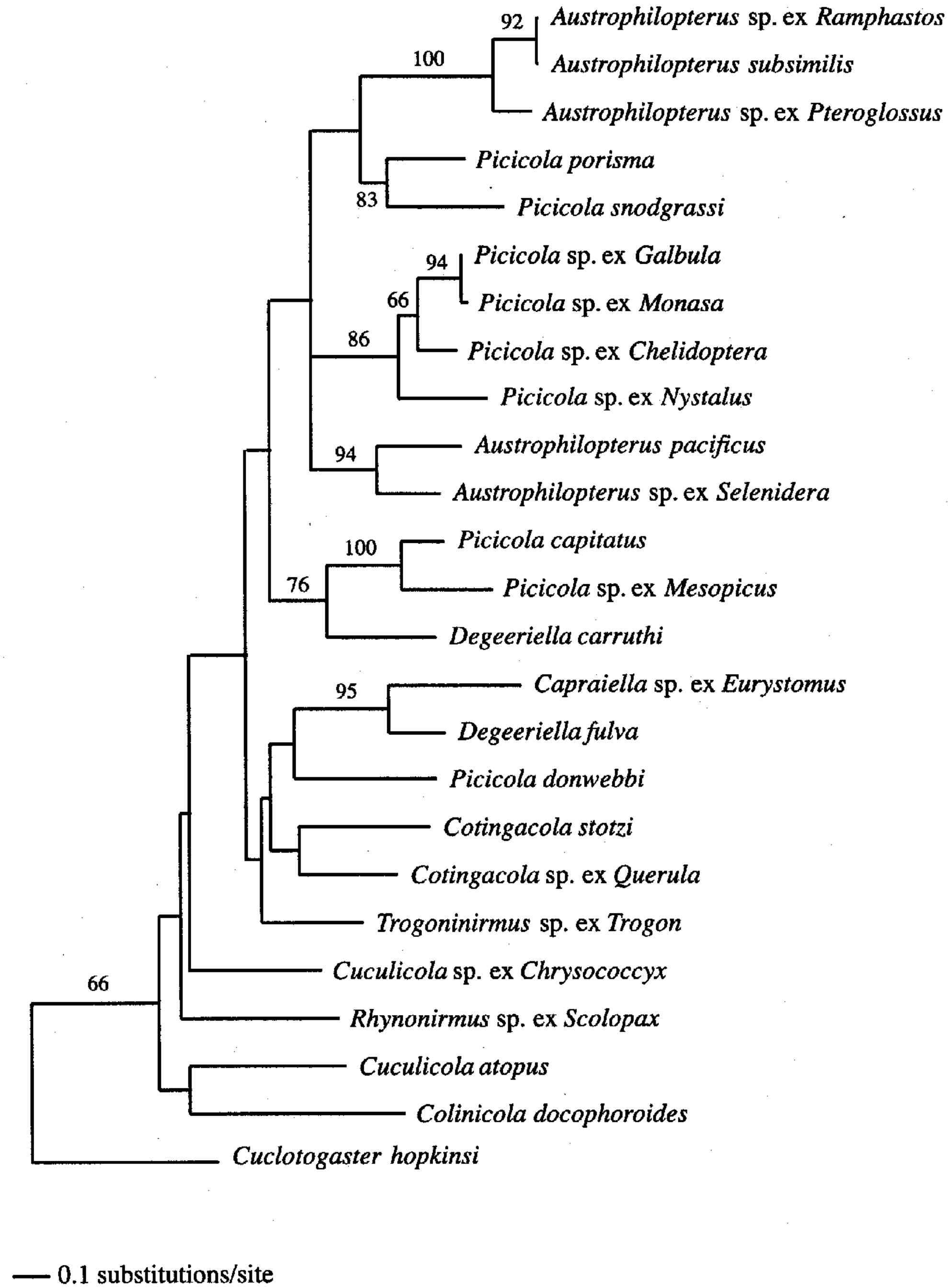



**Figure 1.4.** Phylogenetic tree derived from maximum-likelihood analysis of combined mitochondrial COI (379 bp) and nuclear EF-1 (348 bp) DNA sequences. Numbers above branches indicate support from 100 maximum-likelihood bootstrap replicates.

# CHAPTER 2:

## A morphological phylogeny of the ischnoceran louse genus *Goniodes* Nitzsch, 1818 (Insecta: Phthiraptera: Ischnocera) parasitic on the Galliformes (Aves)

### ABSTRACT

In this paper, I offer the first phylogenetic analysis of the basal ischnoceran genus *Goniodes* based on morphological data. The analysis includes 36 species representing all 13 recognized intrageneric groups in the genus, as well as 9 taxa representing 4 additional ischnoceran genera: *Goniocotes* (6 species), *Physconelloides* (1 species), *Campanulotes* (1 species), and *Heptapsogaster* (1 species) as outgroups. The final parsimony analysis of 262 morphological characters found 5 most parsimonious trees with a length of 2486 steps (CI: 0.276; RI: 0.561; RC: 0.150). A consensus of these are mostly resolved with the exception of the disagreement between two weakly supported basal groups containing a single species of *Goniodes* and species of the genus *Goniocotes*. The overall tree topology, characterized by a continuous stepwise branching pattern, is largely a grade with the placement of taxa strongly correlated with general size, in which Clay's subgeneric classification, although not fully substantiated, is largely confirmed. However, this is largely confined to giving us some idea of how these groups are broadly related. Although showing a general trend that smaller, medium, and large-bodied species cluster together, even the monophyletic and strongly supported apical groups cannot from a gross taxonomic perspective be effectively "described/circumscribed" in light of morphology. It is thus apparent that the reality of the biological complexities associated with ubiquitous morphological convergence in the Ischnocera at large, and

*Goniodes* specifically, cannot effectively be separated from the artificial intricacies imposed by classification.

## INTRODUCTION

Recent efforts to understand the suborder Ischnocera (Insecta: Phthiraptera) have been frustrated by the lack of resolution for relationships in the family Goniodidae. With the exception of broad support for a separate columbiform and galliform clade, the precise generic content of the Goniodidae has proved elusive (Smith *et al*. 2004). Unfortunately, this situation not only impedes our understanding of evolutionary patterns emerging from large-scale phylogenetic studies, but also renders the interpretation of any patterns capricious. Johnson *et al*. (2001: 867) concludes that any subfamilial classification of the Goniodidae is premature because of the need for additional sampling in the *Goniodes* complex.

In Goniodidae, the *Goniodes* complex *sensu* Clay (1976), parasitic on the galliforms, is sister to the *Coloceras* complex *sensu* Clay (1976) and together reflects Eichler's Goniodinae, Astrocotinae, Homocerinae, Goniocotinae, and Physconelloidinae (1941). The taxonomy and systematics of genera in the monophyletic *Coloceras* complex is at least partly understood (Clayton and Johnson 2003; Johnson and Clayton 2003a; Johnson *et al*. 2001, 2002; Smith *et al*. 2004). However, the generic and subgeneric classification of the *Goniodes* complex, composed of approximately 150 species in *Goniodes* Nitzsch 1818: 293 and *Goniocotes* Burmeister 1838: 431, remains largely ambiguous (Clay 1940, 1976; Ledger 1980; Price *et al*. 1999). Monophyly of the two genera with respect to one another has been questioned on morphological (Clay

1951b; Ledger 1980; Smith 2000, 2001) and molecular grounds (Johnson *et al*. 2001, 2011; Smith *et al*. 2004).

The largest genus, *Goniodes*, with highest diversity in the Old World (Clay 1976; Johnson *et al*. 2001), contains approximately 100 species parasitic on 132 galliform hosts (Price *et al*. 2003). There are, however, many unpublished host records and associations (Table 1). Although it has received broad taxonomic treatment (Clay 1940; Kéler 1939), the generic and subgeneric delimitations are poorly understood and in urgent need of revision (Ledger 1980).

Understanding *Goniodes* is complicated by two separate, but not mutually exclusive, factors: firstly, the reality of the biological complexities associated with ubiquitous morphological convergence (see Johnson *et al*. 2011, 2012; Smith 2000, 2001) and, secondly, the more artificial intricacies imposed by classification (see Ledger 1980; Mey 2003). *Goniodes*, like many genera of Ischnocera, has been victim of the historic conflict between complex classification schemes of authorities such as Kéler (1957); Eichler (1963); and Tendeiro (1960, 1965b, 1980b, 1988, 1989 among others, also see Literature Cited) on the one hand and the more conservative approaches of authorities such as Hopkins and Clay (1952, 1953, 1955) and Price *et al*. (2003) on the other (reviewed in Ledger 1980; Mey 2003; and summarized in Table 2). This situation is further complicated by the fact that some critical studies on *Goniodes*, mainly those of João da Silva Tendeiro (1916-1991), and to a lesser extend those of Stefan von Kéler (1897-1967) and Wolf Dietrich Eichler (1912-1994), were published almost exclusively in Portuguese, French, and German, making them inaccessible to many workers. As a result the literature is characterized by inconsistent classification and taxonomy, incompatible nomenclature, duplicate descriptions, and a host of generic and specific synonyms, making classification not only highly variable but also authority depended. Large scale concentrated efforts by Clay and Hopkins (1950, 1951, 1954, 1955, 1960), Hopkins (1938, 1940, 1941a, 1942, 1947a, 1948, 1949, 1950), as well as Hopkins and Clay (1952, 1953, 1955) during the first half of the 19$^{th}$ century; and more recently Price *et al*. (2003) has afforded some nomenclatural stability for the Phthiraptera. However, as of yet, no explicitly tested hypothesis of classification within a phylogenetic framework for *Goniodes* has been advanced.

An obvious, if not convenient, basis for addressing this situation is Clay's seminal revision of *Goniodes* (1940). Her strong opposition to the use of host associations in taxonomy (Clay 1951b) in contrast to Eichler's insistence on the same (Eichler 1941, 1966, 1967, 1973, 1980) and his stubborn opposition to *hennigsche Kladistische Systematik* (1978, 1982; also see Mey 1998, 2003) makes her work an ideal framework for phylogenetic analysis. In this taxonomically outdated, but still widely accepted (Ledger 1980; Price *et al*. 2003), study, Clay divides *Goniodes* into thirteen intrageneric species groups (A-M) based on morphology (Table 3). Although she maintains that these groups are of no generic value, she obviously employed some level of phylogenetic argumentation in her arrangement of species. This idea is supported both by her language and the fact that many of her groups, at least partially, reflect elements of host relationships being limited to either a single or a few closely related hosts. She (Clay 1940) ultimately concludes that, … *the only method to represent the actual phylogenetic relationships is either to split up the species groups from different host orders into genera… or include the whole complex in one genus*.

Here I present the first comparative analysis of the ischnoceran genus *Goniodes* based on morphological data, including the first quantitative hypothesis of evolutionary relationships that includes representatives from all 13 intrageneric groups recognized by Clay (1940). I document morphological variation throughout the genus, emphasizing characters important in differentiating subgeneric groupings. The possible role of these characters in a better understanding of the infra and intrageneric classification of *Goniodes* is considered and its implications for future work is discussed.

## MATERIAL & METHODS:

### TAXON CHOICE

Since Clay published her monograph (1940)(see Table 3), eleven of the 60 species included in her study have been synonomized, 47 additional species described, and one of her subgeneric groups modified (Emerson and Price 1984). To reflect our current understanding of both *Goniodes* Nitzsch 1818, and its component species, the generic, subgeneric, and specific nomenclature was updated to follow Price *et al*. (2003) as summarized in Table 4. New species have been incorporated into Clay's classification scheme based on the original descriptions, morphological similarity to other species, and/or subsequent taxonomic work. I agree with Hopkins and Clay (1952) that it is … *essential that the primary considerations should be morphological and that* (host) *distribution should only be used for purposes of confirmation*, and all such instances are noted in Table 4. Despite the obvious heuristic value of these designations, they remain conditional pending the necessary taxonomic work.

Practical limitations imposed by the sheer number of species and characters, in addition to the availability of material, constrain the number of taxa that could realistically be included in this study. Therefore a subset of 36 exemplars (Table 5), representing all thirteen subgeneric groups, is included in the analysis. Selection of these specific exemplars was driven by the desire to not only maximize the range of morphological variation observed in *Goniodes*, but also to include a diversity of species and hosts from each of Clay's groups. The limited sampling inherent to the use of exemplars obviously raises questions regarding the repeatability of characters between all intrageneric groups and species, but the approach is nevertheless endorsed on theoretical grounds (Yeates 1995; Bininda-Edmonds *et al*. 1998) and prior use in phthirapteran studies.

**OUTGROUP SELECTION**

The selection of outgroups closely follows the findings of recent work by Johnson *et al*. (2001), Smith (2000, 2001), and Smith *et al*. (2004). The putative sister group to *Goniodes* is obviously *Goniocotes*, but both historic and more recent data indicate that these genera are not monophyletic with respect to one another. In order to shed more light on the relationship between *Goniodes* and *Goniocotes*, seven species of latter are included in the ingroup. Given the established relationship between the *Goniodes* and *Coloceras*-complex, one species of each of the two genera parasitic on the columbiformes, *Physconelloides* and *Campanulotes*, are included in the outgroup. A single species of *Heptapsogaster* from the putative sister family Heptapsogasteridae, parasitic on tinamous (Tinamiformes), is also included (See Table 5).

**SPECIMENS**

For a majority of the taxa, ten male and female slide mounted specimens were examined using both phase contrast and transmitted light microscopy. In order to minimize complications due to ontogenetic variation, this study included only adult specimens (but see Mey 1994). Data were collected from a total of 887 specimens, which included 36 species of *Goniodes*, six species of *Goniocotes*, as well as three outgroup species from three different ischnoceran genera; *Physconelloides*, *Campanulotes*, and *Heptapsogaster* (Table 6).

Specimens utilized were obtained from the following collections (acronyms follow Evenhuis and Samuelson 2007): BMNH – The Natural History Museum, London, United Kingdom; FMNH – Field Museum of Natural History, Chicago, Illinois, USA; INHS – Illinois Natural History Survey, Champaign, Illinois, USA; OSEC – K. C. Emerson Museum, Oklahoma State University, Stillwater, Oklahoma, USA; SMPM – University of Minnesota Insect Collection, St. Paul; Minnesota, USA; USNM – United States National Museum of Natural History, Washington, D. C.; RMCA – Musee Royal de L´Afrique Central, Tervuren, Belgium.

**CHARACTER CODING**

Many coding methods have been suggested for dealing with complex characters (see Strong and Lipscomb 1999 and Wiens 2000 for reviews). Reductive coding entails an initial delimitation of a character followed by any number of dependent "sub characters" scored as inapplicable where appropriate; whereas composite coding combines the presence of a part and any variability in the condition in a single character. Although this study employs both reductive and composite character coding, there is bias towards the former. I favor reductive coding as it maximizes phylogenetic information and reduces overly complex characters and the inherent dependence and redundancy of such characters (see Jenner 2002). Composite coding was primarily employed in cases where a confident proposal of homology was not possible.

Morphometric characters were coded using Thiele's (1993) gap weighing method implemented in MorphoCode 1.1.0 (Schols *et al*. 2003) using a 10 bin option. Frequency methods, in this case gap weighting, have been shown to be as accurate as discrete methods for coding quantitative characters in simulations (Wiens and Servedio 1997, 1998), statistical analysis (Wiens 1995), and congruence testing (Wiens 1998b). The large number of taxa used in this study precludes the use of the more precise step-matrix approaches promoted by Wiens (1995, 2001) as well as Berlocher and Swofford (1997), as the implementation of such methods for a large number of taxa requires more than the 32 unique character states currently available in PAUP* (Stephens and Wiens 2003). Following Thiele (1993) and Schols *et al*. (2003), all morphometric characters were treated as ordered.

**CHARACTER CHOICE**

Until recently, comparative morphological studies of the ischnoceran lice were difficult due to a paucity of basic reliable characters and the variable and inconsistent morphological terminology historically employed. Fortunately, this study benefited greatly from both historic and recent efforts by Clay (1951), Mey (1994, 1997, 1999), and Smith (2000, 2001) to stabilize ischnoceran morphological terminology. In the case of the latter authors, their modern perspective greatly facilitated access to the rich, but often neglected, historical literature relating to phthirapteran morphology. This study benefitted greatly from the general works by Blagoveshtchensky and Bei-Bienko 1967; Lakshminarayana 1985; Lonc and Modrzejewska 1987; Cope 1940; Haub 1971, 1972; Kéler 1939; Lyal 1985; Matsuda 1970; Nelson 1972; Risler 1951; Snodgrass 1899; Snodgrass 1944; Symmons 1952. More specific work include those by Cummings 1913, 1916; Snodgrass 1905 on mouth part morphology; Clay 1946, 1951b; Harrison 1919; on preantennal head morphology; Baker and Chandrapatya 1992; Clay 1969; Harrison 1915; Slifer 1976, on antennal morphology; Matsuda 1965; Rudolph 1982, 1983; on postantennal morphology; Mey 1994; Smith 2000 on chaetotaxy; Snodgrass 1957 on reproductive organs.

Character definitions and descriptions are the most vital components of any phylogenetic analysis. However, this component is often trivialized, leading to subjectivity, vague homology statements, and un-repeatability (see Jenner 2001, 2002; as well as Riepell and Kearney 2002). This situation is exacerbated in the case of lice given their stereotypical morphology and problematic taxonomic history. More specifically, a lack of homology assessments in the Ischnocera and within the *Goniodes* complex means many of the character systems explored are complex. As a result character identity, delimitation, and the coding of states are in many cases difficult, speculative, and necessarily assumption laden. Although an initial comparative examination and survey of historical and recent taxonomic and review papers identified approximately 350 candidate characters, 63 were subsequently excluded because I was unable to accurately define, reliably interpret, and repeatedly score them. During preliminary analysis an additional 25 characters turned out to be constant or phylogenetically uninformative and were excluded from the final analysis.

**CHARACTERS AND OBSERVATIONS**

General morphology of *Goniodes* is illustrated in Figure 1. Terminology follows that of Smith (2000, 2001) Clay (1951) and Mey (1994, 1997, 1999), with exceptions noted in specific character descriptions. The same is true for general head morphology (Fig. 2) and setal arrangement (Fig. 3). Smith offers an excellent recent review of the morphology of the Ischnocera in general (2001) and the Goniodidae specifically (2000).

Where possible the original source of characters are included in specific character descriptions:

***Characters of the head:***

General and Preantennal Characters:

1. *Head shape:* (1) Not sexually dimorphic; (2) Slightly dimorphic; (3) Sexually dimorphic.
2. *General head shape: Male:* (1) Round - length approximately equal to width; (2) Squat - length less than width; (3) Elongate - length exceeds width.
3. *General head shape: Female:* (1) Round; (2) Squat; (3) Elongate.
4. *Frons shape: Male:* (1) Broadly convex and apically rounded; (2) Broadly convex and apically flattened; (3) Narrowly convex appearing elliptical.
5. *Frons shape: Female:* (1) Broadly convex and apically rounded; (2) Broadly convex and apically flattened; (3) Narrowly convex appearing elliptical.
6. *Medial dorsal groove in preantennal and/or mandibular region of head* (Smith 2000: 78): *Male:* (1) Absent or indistinct; (2) Present; (3) Present and distinct with structure.
7. *Medial dorsal groove in preantennal and/or mandibular region of head* (Smith 2000: 78)*: Female:* (1) Absent or indistinct; (2) Present; (3) Present and distinct with structure.
8. *Marginal carina (m.c.) width: Male:* (1) Thin; (2) Medium; (3) Thick.
9. *Marginal carina (m.c.) width: Female:* (1) Thin; (2) Medium; (3) Thick
10. *M.c. internal margin shape:* (1) Convex - follow external margin; (2) Slightly convex to flattened - does not follow margin; (3) Pointed posteriorly.

11. *M.c. width:* (1) Uniform; (2) Somewhat thicker medially and thinner laterally; (3) Significantly thicker medially and thinner laterally; (4) Somewhat thicker laterally and thinner medially.
12. *M.c. inner margin pattern:* (1) Smooth or with slight undulations; (2) Pronounced pattern with a ragged appearance; (3) Pronounced pattern with a blocked appearance.
13. *M.c. outer margin:* (1) Smooth or with only slight undulations; (2) With distinct setal pits.
14. *M.c. setal channels:* (1) Absent or poorly delimited; (2) Present and uniform in shape and size; (3) Present, but highly variable in shape and size.
15. *Nodus limbati (other than the preantennal)*: (1) Absent; (2) Present.
16. *M.c. striations across width:* (1) Absent or indistinct; (2) Distinct.
17. *M.c. striations parallel:* (1) Absent or only present as a thin sclerotized layer on posterior edge of m.c.; (2) Present as indistinct layers; (3) Present as distinct blocks.
18. *Dorsal aspect of m.c. (Edge):* (1) Absent or indistinct, largely under the ventral carina, or more noticeable laterally; (2) Present as a distinct apical area; (3) Present across the width of head and delimited to varying degrees; (4) Present apically as a posteriorly pointing medial extension.
19. *Dorsal aspect of m.c. (Sculpturing):* (1) Absent or indistinct; (2) Present and distinct.
20. *General size of the ventral carina (v.c.) and pulvinus:* (1) Small; (2) Medium; (3) Large.

21. *V.c. and pulvinus anterior margin:* (1) Widely separated from m.c.; (2) Narrowly separated from m.c.

22. *V.c. and anterior margin of the pulvinus:* (1) Anterior edge of pulvinus level with anterior origin of preantennal nodus; (2) Anterior edge of pulvinus posterior to the anterior origin of preantennal nodus.

23. *V.c. and anterior margin of the pulvinus:* (1) Continuous and merges with ventral aspect of preantennal nodus at the level of the mandibular structure; (2) Merges with ventral aspect at the preantennal nodus; (3) Does not merge with the preantennal nodus.

24. *V.c. general:* (1) Weakly sclerotized; (2) Sclerotized; (3) Heavily sclerotized at least basally.

25. *V.c. margin (the chitenized margin of pulvinus sensu* Symmons (1952 Fig. 36)*:* (1) Thin; (2) Thick.

26. *Pulvinus shape:* (1) Small and well separated laterally from preantennal nodus and anteriorly from dorsal aspect of m.c.; (2) Medium and touching either laterally, or anteriorly, but not both; (3) Large and greatly expanded filling the bulk of the preantennal region; (4) Small and well separated as in state 1, but compressed.

27. *Clavus: Male:* (1) Undeveloped, barely reaching scape; (2) Hardly developed, barely overhanging scape and expanded posteriorly; (3) Developed and overhanging the scape, expanded and extended posteriorly; (4) Greatly developed and overhanging more than a quarter of the scape.

28. *Clavus: Female:* 1) Undeveloped, barely reaching scape; (2) Hardly developed

barely overhanging scape and expanded posteriorly; (3) Developed and overhanging the scape, expanded and extended posteriorly; (4) Greatly developed and overhanging more than a quarter of the scape.

29. *Male clavus primarily:* (1) Membranous; (2) Variable; (3) Sclerotic.
30. *Female clavus primarily:* (1) Membranous; (2) Variable; (3) Sclerotic.
31. *Male clavus most distal tip:* (1) Rounded; (2) Pointed; (3) Squared or lobed.
32. *Female clavus most distal tip:* (1) Rounded; (2) Pointed; (3) Squared or lobed.
33. *Orientation of clavus most distal tip*: (1) More lateral than posterior; (2) More posterior than lateral.
34. *Male preantennal nodus shape:* (1) Straight; (2) Distinctly bulbous with basal constriction and the bulb round; (3) Distinctly bulbous with basal constriction and bulb elliptical; (4) Distinctly bulbous but interrupted and the bulb as a separate round sclerite (*G. gigas*); (5) Hook (*Physconelloides*).
35. *Female preantennal nodus shape:* (1) Straight; (2) Distinctly bulbous with basal constriction and the bulb round; (3) Distinctly bulbous with basal constriction and bulb elliptical; (4) Distinctly bulbous but interrupted and the bulb as a separate round sclerite (*G. gigas*); (5) Hook (*Physconelloides*).
36. *Male preantennal nodus orientation:* (1) Straight and oriented postero-medially; (2) Straight and oriented posteriorly; (3) Curved and oriented medially; (4) Curved and oriented posteriorly.
37. *Female preantennal nodus orientation:* (1) Straight and oriented postero-medially; (2) Straight and oriented posteriorly; (3) Curved and oriented medially; (4) Curved and oriented posteriorly.

38. *Preantennal nodus constriction:* (1) Constricted at the base; (2) Not constricted; (3) Very constricted and appearing stalk-like.

39. *Preantennal nodus:* (1) Flattened distally; (2) Flattened medially; (3) Not flattened; (4) Uniformly flattened.

40. *Preantennal nodus:* (1) Largely membranous; (2) Sclerotized.

41. *Clypeofrontal suture associated with preantennal nodus* (Symmons 1952 Fig. 36)*:* (1) Barely distinguishable; (2) Distinct.

Antennal Characters:

42. *Antennae:* (1) Not sexually dimorphic, monomorphic; (2) Sexually dimorphic, heteromorphic; (3) Slightly sexually dimorphic, heteromorphic.

43. *Antennae basal lengths – Monomorphic species:* (1) Scape equal to pedicel; (2) Scape somewhat shorter than pedicel; (3) Scape significantly shorter than pedicel.

44. *Antennae basal lengths – Heteromorphic species: Male:* (1) Scape equal to pedicel; (2) Scape longer than pedicel; (3) Scape shorter than pedicel; (4) Scape significantly shorter than pedicel; (5) Scape significantly longer than pedicel.

45. *Antennae basal lengths – Heteromorphic species: Female:* (1) Scape equal to pedicel; (2) Scape longer than pedicel; (3) Scape shorter than pedicel; (4) Scape significantly shorter than pedicel; (5) Scape significantly longer than pedicel.

46. *Antennae distal lengths – Monomorphic species:* (1) $1^{st}$ flagellomere equal to $2^{nd}$ equal to $3^{rd}$; (2) $1^{st} > 2^{nd} = 3^{rd}$; (3) $1^{st} = 2^{nd} > 3^{rd}$; (4) $1^{st} > 2^{nd} < 3^{rd}$; (5) $1^{st} = 2^{nd} < 3^{rd}$; (6) $1^{st}$ significantly $> 2^{nd} = 3^{rd}$; (7) $1^{st}$ significantly $> 2^{nd} < 3^{rd}$.

47. *Antennae distal lengths – Heteromorphic species: Male:* (1) $1^{st}$ flagellomere equal to

$2^{nd} = 3^{rd}$; (2) $1^{st} > 2^{nd} = 3^{rd}$; (3) $1^{st} = 2^{nd} > 3^{rd}$; (4) $1^{st} > 2^{nd} < 3^{rd}$; (5) $1^{st} = 2^{nd} < 3^{rd}$; (6) $1^{st}$ significantly $> 2^{nd} = 3^{rd}$; (7) $1^{st}$ significantly $> 2^{nd} < 3^{rd}$.

48. *Antennae distal lengths – Heteromorphic species: Female:* (1) $1^{st}$ flagellomere $= 2^{nd} = 3^{rd}$; (2) $1^{st} > 2^{nd} = 3^{rd}$; (3) $1^{st} = 2^{nd} > 3^{rd}$; (4) $1^{st} > 2^{nd} < 3^{rd}$; (5) $1^{st} = 2^{nd} < 3^{rd}$; (6) $1^{st}$ significantly $> 2^{nd} = 3^{rd}$; (7) $1^{st}$ significantly $> 2^{nd} < 3^{rd}$.

49. *Antennae $2^{nd}$ and $3^{rd}$ flagellomere length: Male:* (1) $2^{nd} = 3^{rd}$; (2) $2^{nd} < 3^{rd}$; (3) $2^{nd}$ significantly $< 3^{rd}$.

50. *Antennae $2^{nd}$ and $3^{rd}$ flagellomere length: Female:* (1) $2^{nd} = 3^{rd}$; (2) $2^{nd} < 3^{rd}$; (3) $2^{nd}$ significantly $< 3^{rd}$.

51. *Antennae comparative lengths (M = male; F = female):* (1) M pedicel = F pedicel; (2) M pedicel > F pedicel; (3) M pedicel < F pedicel; (4) M pedicel significantly < F pedicel; (5) M pedicel significantly > F pedicel.

52. *Antennae comparative lengths:* (1) M scape = F scape ; (2) M scape > F scape; (3) M scape < F scape; (4) M scape significantly < F scape; (5) M scape significantly > F scape.

53. *Male scape process:* (1) Absent; (2) Indistinct; (3) Distinct.

54. *Male scape process condition, if present:* (1) Broad raised area or tubercle; (2) Elongate process; (3) Large flattened triangular structure.

55. *Female scape process:* (1) Absent; (2) Broad raised area or tubercle; (3) Large flattened triangular structure.

56. *Scape process tip:* (1) Rounded; (2) Forked.

57. *Scape process tip:* (1) No ornamentation; (2) Sculptured.

58. *Male pedicel posterior margin:* (1) Unmodified; (2) Slight thickening; (3) Distinct

raised area; (4) Expanded.

59. *Female pedicel posterior margin:* (1) Unmodified; (2) Slight thickening; (3) Distinct raised area; (4) Expanded.

60. *Male pedicel posterior margin structure from character # 58 setal type:* (1) 2 small microsetae; (2) 2 small thorn-like setae; (3) 1 small microseta and 1 small thorn-like seta.

61. *Female pedicel posterior margin structure from character # 59 setal type:* (1) 2 small microsetae; (2) 2 small thorn-like setae; (3) 1 small microseta and 1 small thorn-like seta.

62. *Male antennae 1st flagellomere:* (1) Unmodified; (2) With a small wart-like tubercle; (3) With a gently curved elongate process; (4) With an expanded club-shaped process; (5) With a gently curved short tooth like process (see *Heptapsogaster*).

63. *Antennae 1st flagellomere process on the distal internal margin in males:* (1) Rounded; (2) Flat and smooth; (3) Flat and serrated.

64. *Heteromorphic antennae sub terminal attachment 2nd and 3rd flagellomeres*: (1) Absent; (2) Indistinct; (3) Distinct.

65. *Preocular nodus:* (1) Weakly developed with only a slight expansion of the marginal temporal carina; (2) Well developed and enlarged.

66. *Preocular nodus condition:* (1) Largely membranous; (2) Only weakly sclerotized; (3) Well sclerotized.

67. *Preocular nodus shape anteriorly – articulation surface with scape:* (1) Absent or indistinct; (2) Distinct but only weakly sclerotized; (3) Distinct and well sclerotized.

68. *Preocular nodus articulation mechanism with scape; convex/pointed structure (see* G. cervicornis *for this structure):* (1) On scape; (2) On both (see *G. eurygaster*); (3) Absent.

Postantennal Characters:

69. *Ocular (Eye):* (1) Barely distinguishable; (2) Distinct.

70. *Eye size:* (1) Small; (2) Large.

71. *Ocular condition:* (1) Indistinguishable and sclerotized; (2) Membranous.

72. *Ocular seta:* (1) Not sexually dimorphic; (2) Sexually dimorphic.

73. *Ocular seta location:* (1) Anterior portion of eye; (2) Central portion of eye; (3) Posterior portion of eye.

74. *Ocular seta location:* (1) Marginal; (2) Medial.

75. *Male ocular setal type:* (1) Micro seta; (2) Macro seta, medium; (3) Macro seta, long; (4) Thorn-like seta.

76. *Female ocular setal type:* (1) Micro seta; (2) Macro seta, medium; (3) Macro seta, long; (4) Thorn-like seta.

77. *Post ocular nodus size:* (1) Weakly developed with only a slight expansion of the marginal temporal carina; (2) Well developed and enlarged; (3) Undeveloped.

78. *Post ocular nodus condition:* (1) Largely membranous; (2) Weakly sclerotized; (3) Sclerotized.

79. *Temporal sculpturing:* (1) Absent; (2) Present.

80. *Temple margin:* (1) Not sexually dimorphic; (2) Only slightly sexually dimorphic; (3) Sexually dimorphic.

81. *Male temple margin:* (1) Barely expanded; (2) Expanded; (3) Greatly expanded.

82. *Female temple margin:* (1) Barely expanded; (2) Expanded; (3) Greatly expanded.

83. *Male temple margin:* (1) Angular; (2) Rounded; (3) Intermediate; (4) Elongate process.

84. *Female temple margin:* (1) Angular; (2) Rounded; (3) Intermediate; (4) Elongate process.

85. *Male margin anterior to temple angle* (Ledger 1980)*:* (1) Straight; (2) Convex; (3) Concave.

86. *Female margin anterior to temple angle* (Ledger 1980)*:* (1) Straight; (2) Convex; (3) Concave.

87. *Margin posterior to temple angle, is angled posteriomedially and…* (1) Straight; (2) Convex; (3) Concave; (4) Angular; (5) Flat.

88. *Male temple angle process:* (1) Absent or indistinct; (2) Present and distinct.

89. *Female temple angle process:* (1) Absent or indistinct; (2) Present and distinct.

90. *Male most distal point of temple:* (1) approximately half-way between posterior margin of eyes and posterior point of occipital extensions; (2) closer to posterior margin of the eyes; (3) closer to posterior margin of occipital extensions; (4) behind occipital extensions.

91. *Female most distal point of temple:* (1) approximately half-way between posterior margin of eyes and posterior point of occipital extensions; (2) closer to posterior margin of the eyes; (3) closer to posterior margin of occipital extensions; (4) behind occipital extensions.

92. *Male temporal carina:* (1) Indistinct; (2) Evident from posterior margin, but not

delimited; (3) Evident from posterior margin as a distinguishable lateral edge; (4) Evident from posterior margin forming a band.

93. *Female temporal carina:* (1) Indistinct; (2) Evident from posterior margin, but not delimited; (3) Evident from posterior margin as a distinguishable lateral edge; (4) Evident from posterior margin forming a band.

94. *Occipital sculpturing:* (1) Absent; (2) Present.

95. *Occipital margin:* (1) Not extended; (2) Barely extended posteriorly; (3) Extended posteriorly.

96. *Occipital extensions/margins:* (1) Absent; (2) Rounded; (3) Triangular.

97. *Occipital extension seta:* (1) Apical; (2) Not apical located laterally; (3) Not apical located medially.

98. *Occipital extension tip:* (1) Rounded; (2) Pointed.

99. *Occipital extension setal type:* (1) Thorn-like seta; (2) Microseta.

Setal Characters:

100. *Dorsal anterior setal type:* (1) Microsetae or a very short macrosetae; (2) Macro setae, medium; (3) Macro setae, long.

101. *Additional dorsal setae:* (1) Absent; (2) Microsetal pair posterolaterally to dorsal pair; (3) Many macro- and microsetae scattered over dorsal surface; (4) Microsetal pair nearly directly posterior to dorsal anterior pair; (5) Microsetal pair posteriomedially to dorsal anterior pair; (6) In addition to microsetal pair posterolaterally to dorsal pair, there is additional microsetae scattered over dorsal surface.

102. *Dorsal anterior setal position:* (1) Posterolaterally to dorsal sub marginal pair; (2)

Directly posterior to dorsal sub marginal pair; (3) Posteromedial to dorsal sub marginal pair.

103. *Male dorsal preantennal setal type:* (1) Macroseta = very small; (2) Macroseta = shorter than scape; (3) Macroseta = medium, approximately as long as scape; (4) Macroseta = long, approximately 0.5 length of antennae; (5) Macroseta = very long, approximately length, or longer, than antennae.

104. *Female dorsal preantennal setal type:* (1) Macroseta = very small; (2) Macroseta = shorter than scape; (3) Macroseta = medium, approximately as long as scape; (4) Macroseta = long, approximately 0.5 length of antennae; (5) Macroseta = very long, approximately length, or longer, than antennae.

105. *Male dorsal preantennal seta position:* (1) Medial = small and indistinct on pocket in preantennal nodus (see *G. pavonis*); (2) Lateral = edge of scape, not closely associated with preocular nodus or clavus; (3) Lateral = on anterior curve of clavus; (4) Lateral = on dorsal aspect of clavus; (5) Lateral = on edge of dorsal aspect of clavus; (6) Lateral = closely associated with lateral margin of dorsal aspect of clavus, on the edge; (7) Between scape and clavus extended area.

106. *Female dorsal preantennal setal position*(1) Medial = small and indistinct on pocket in preantennal nodus (see *G. pavonis*); (2) Lateral = edge of scape, not closely associated with preocular nodus or clavus; (3) Lateral = on anterior curve of clavus; (4) Lateral = on dorsal aspect of clavus; (5) Lateral = on edge of dorsal aspect of clavus; (6) Lateral = closely associated with lateral margin of dorsal aspect of clavus, on the edge; (7) Between scape and clavus extended area.

107. *Dorsal postnodal setal type:* (1) Microseta; (2) Macroseta = Short; (3) Macroseta =

Medium; (4) Macroseta = Long; (5) Thorn-like seta.

108. *Male dorsal postnodal setal position:* (1) Anterior to eye, level with anterior half of preocular nodus; (2) Level with anterior margin of eye, level with middle of preocular nodus; (3) Level with anterior portion of eye, level with posterior portion of preocular nodus; (4) Level with midpoint of eye, level with posterior edge of preocular nodus.

109. *Female dorsal postnodal setal position:* (1) Anterior to eye, level with anterior half of preocular nodus; (2) Level with anterior margin of eye, level with middle of preocular nodus; (3) Level with anterior portion of eye, level with posterior portion of preocular nodus; (4) Level with midpoint of eye, level with posterior edge of preocular nodus.

110. *Male dorsal anterior setal vs. preantennal setal vs. postnodal setal length:* (1) 1 = 3 > 2; (2) 3 > 1 > 2; (3) 1 > 3 > 2; (4) 1 = 3 < 2; (5) 1 = 2 = 3; (6) 2 = 3 > 1; (7) 1 > 2 > 3.

111. *Female dorsal anterior setal vs. preantennal setal vs. postnodal setal length:* (1) 1 = 3 > 2; (2) 3 > 1 > 2; (3) 1 > 3 > 2; (4) 1 = 3 < 2; (5) 1 = 2 = 3; (6) 2 = 3 > 1; (7) 1 > 2 > 3.

112. *Male dorsal submarginal setae:* (1) Microsetae; (2) Macrosetae = short; (3) Macrosetae = medium; (4) Macrosetae = long; (5) Thorn-like setae.

113. *Female dorsal submarginal seta:* (1) Microsetae; (2) Macrosetae = short; (3) Macrosetae = medium; (4) Macrosetae = long; (5) Thorn-like setae.

114. *Dorsal post temporal setal type:* (1) Macroseta = very short; (2) Macroseta = short; (3) Macroseta = medium; (4) Macroseta = long.

115. *Dorsal post temporal setal position:* (1) On occipital margin, slightly anterior to marginal temporal carina; (2) On marginal temporal carina, medially anterior; (3) On marginal temporal carina, laterally anterior; (4) On marginal temporal carina, laterally posterior; (5) On marginal temporal carina, medially posterior.

116. *Ventral submarginal setal type:* (1) Micro- or very short macrosetae; (2) Short to medium macrosetae; (3) Long macrosetae.

117. *Ventral anterior setal type:* (1) Micro- or very short macrosetae; (2) Macrosetae = short; (3) Macrosetae = medium; (4) Macrosetae = long.

118. *Ventral preconal setal position:* (1) Approximately half way between clypeofrontal suture and the base of clavus; (2) Base of clavus; (3) Not on base, but closer to base of clavus than clypeofrontal suture; (4) Not on base, but closer to clypeofrontal suture than base of clavus.

119. *Ventral mandibular setal type:* (1) Micro- or short macroseta; (2) Medium to long macroseta.

120. *Male ventral mandibular setal position:* (1) Medial third of preantennal nodus; distal side, marginal; (2) Medial third of preantennal nodus; distal side, medial; (3) Last third of preantennal nodus; distal side, marginal; (4) Last third of preantennal nodus; distal side, medial; (5) Posterior and medial to preantennal nodus, separated; (6) Posterior to end of preantennal nodus, separated.

121. *Female ventral mandibular setal position:* (1) Medial third of preantennal nodus; distal side, marginal; (2) Medial third of preantennal nodus; distal side, medial;

(3) Last third of preantennal nodus; distal side, marginal; (4) Last third of preantennal nodus; distal side, medial; (5) Posterior and medial to preantennal nodus, separated; (6) Posterior to end of preantennal nodus, separated.

122. *Marginal temporal setae (m.t.s) 1 position:* (1) On temple angle; (2) Anterior to temple angle; (3) Posterior to temple angle; (4) Medial to temple angle.

123. *M.t.s 2 setal type:* (1) Microseta; (2) Macroseta = short; (3) Macroseta = medium; (4) Macroseta = long; (5) Thorn-like seta.

124. *M.t.s 4 setal type:* (1) Microseta; (2) Macroseta = short; (3) Macroseta = medium; (4) Macroseta = long; (5) Thorn-like seta

125. *M.t.s 5 setal type:* (1) Microseta; (2) Macroseta = short; (3) Macroseta = medium; (4) Macroseta = long; (5) Thorn-like seta.

126. *Male m.t.s 5 position:* (1) Apical on occipital angle/extension; (2) Medial to occipital angle/extension; (3) Lateral to occipital angle/extension.

127. *Female m.t.s 5 position:* (1) Apical on occipital angle/extension; (2) Medial to occipital angle/extension; (3) Lateral to occipital angle/extension.

128. *Male m.t.s 5 orientation:* (1) Posteriorly; (2) Laterally; (3) Medial.

129. *Female m.t.s 5 orientation:* (1) Posteriorly; (2) Laterally; (3) Medial.

130. *Post ocular setae* (Clay's marginal temporal setae 1; Mey's (1994) "Praeocular-borste")*:* (1) Not sexually dimorphic; (2) Sexually dimorphic.

131. *Male post ocular setal type:* (1) Microseta; (2) Short macroseta; (3) Thorn-like seta; (4) Long macroseta.

132. *Female post ocular setal type:* (1) Microseta; (2) Short macroseta; (3) Thorn-like seta; (4) Long macroseta.

133. *Male post ocular setal location:* (1) On temple angle; (2) Anterior to temple angle.

134. *Female post ocular setal location:* (1) On temple angle; (2) Anterior to temple angle.

***Characters of the Thorax:***

Dorsal Prothorax:

135. *Prothorax shape:* (1) Rectangular; (2) Trapezoid; (3) Rounded; (4) Rhombic.

136. *Prothorax medial anterior border:* (1) Straight; (2) Convex; (3) Concave.

137. *Prothorax medial posterior border:* (1) Straight; (2) Concave.

138. *Prothorax lateral anterior border:* (1) Angled; (2) Rounded.

139. *Prothorax lateral posterior border:* (1) Angled; (2) Rounded; (3) Lobed; (4) Square.

140. *Prothorax most distal lateral point orientation:* (1) Anteriorly; (2) Medially; (3) Posteriorly.

141. *Prothorax angle:* (1) With process; (2) Without process.

142. *Prothorax process:* (1) Rounded lobe; (2) Small expansion/swelling; (3) Elongate lobe; (4) Triangular extension.

143. *Posterior angle of prothorax:* (1) Rounded; (2) Notched; (3) Curved.

144. *Prothorax cervical setae:* (1) Microsetae of similar size; (2) 2 macrosetae and 1 spear-like seta.

145. *Prothorax lateral and/or posterior setal arrangement:* (1) 1 + 1; (2) 3 + 3; (3) 4 + 4; (4) 8 + 8.

146. *Prothorax lateral and/or posterior seta* (see Smith 2001: 132 & Fig. 7b)*:* (1) Posterior; (2) Medial; (3) Scattered.

147. *Prothorax lateral and/or posterior seta:* (1) Anterior; not apical on angle of prothorax; (2) Posterior; not apical on angle of prothorax; (3) Apical on angle of prothorax; (4) Scattered.

148. *Prothorax spiracle – size:* (1) Small; (2) Medium; (3) Large.

149. *Prothorax spiracle aperture – shape:* (1) Round; (2) Elongated.

150. *Prothorax rhombic sclerite:* (1) Small, weakly developed, posteriorly delimited anteriorly shield-shaped; (2) Medium to large as an elongate bar; (3) Medium to large and shield-shaped; (4) Medium to large drop-shaped; (5) As in *G. tibetanus*; (6) As in *G. fissus*.

Dorsal Pterothorax:

151. *Pterothorax shape:* (1) Rectangular; (2) Trapezoid; (3) Shield; (4) Triangular.

152. *Pterothorax condition:* (1) Complete; (2) Complete with small medial split posteriorly; (3) Complete with medial furrow.

153. *Pterothorax medial anterior border:* (1) Straight; (2) Convex; (3) Concave.

154. *Pterothorax medial posterior border:* (1) Rounded and double pointed; (2) Laterally straight with 2 angles; (3) Arched with 3 angles.

155. *Pterothorax lateral anterior border:* (1) Angled; (2) Rounded; (3) Lobed.

156. *Pterothorax lateral posterior border:* (1) Angled; (2) Rounded.

157. *Pterothorax most distal lateral point:* (1) Anteriorly; (2) Medially; (3) Posteriorly.

158. *Pterothorax posterior angle:* (1) Narrowly rounded; (2) Pointed; (3) Flattened; (4) Triple pointed; (5) Double pointed.

159. *Additional medial setae on posterior third of pterothorax* (see Smith 2001: 132)*:* (1) Absent; (2) Present.

160. *Position of setal pairs from character #159:* (1) Both on the lateral margin of pterothorax; (2) 1 pair lateral and other pair on posterior margin of pterothorax.

161. *Setal numbers for pair from character # 159:* (1) Both pairs = 2 seta; (2) #1 = 3, #2 = 1/2; (3) #1 = 2, #2= 1/3; (4) #1 more than 3, #2= 2/3.

162. *Pterothorax, posterior margin:* (1) Lacking a regular row of macrosetae on each side; (2) With a regular row of macrosetae on each side.

Ventral Thorax:

163. *Proepimeron development:* (1) Short and not reaching the posterior medial base of the 2nd coxa; (2) Medium and reaching the posterior medial base of the 2nd coxa, but not rounding it; (3) Long reaching and rounding the posterior medial base of the 2nd coxa and connecting with the 3rd coxa (see *G. gigas*); (4) Long reaching and rounding the posterior medial base of the 2nd coxa and nearly continuous with the structure on 3rd coxa (see *G. retractus*); (5) Greatly developed, broad structure fused in middle (see *G. crassipes*).

164. *Proepimeron development, direction:* (1) Posteriorly; (2) Anteriorly; (3) Neither.

165. *Proepimeron medial gap between left and right legs:* (1) Smaller or equal to the width of profurcal pit; (2) Approximately twice as large as the width of the profurcal pit; (3) Not applicable (see *G. crassipes*).

166. *Mesofurcal pit:* (1) Small and poorly developed; (2) Large and well developed.

167. *Mesofurcal pit opening on proepimeron:* (1) Located in the middle of the “leg” on the inside edge - medially; (2) Located in the middle of the “leg” on the outside edge - laterally.

168. *Meso- and metasternal plate* (see Smith 2001: 132 & Figs. 8I & J)*:* (1) Absent; (2)

Present.

169. *Meso-metasternal plate condition:* (1) Small and round, sometimes with a pair of macrosetae; (2) Indistinct, poorly delimited and not very clear; (3) See *G. securiger*; (4) See *G. fissus*.

170. *1st Sternal plate (abdominal)* (see Smith 2001: 132 & Figs. 8I & J)*:* (1) Absent; (2) Present.

171. *Ventral pterothoracic setae* (see Smith 2001:132) *or meso- and metatarsal hairs sensu* Clay 1940*:* (1) Absent; (2) Present.

172. *Trichoid seta on pterothorax, location:* (1) Sublateral; (2) Lateral.

173. *Thorn-like seta associated with trichoid seta:* (1) Absent or indistinct; (2) Present located posterior medially to the trichoid; (3) Present located anterior medially to trichoid.

174. *Trichoid seta location relative to paired dorsal setae in an anterior/posterior aspect:* (1) Anterior; (2) Posterior; (3) Level.

175. *Trichoid seta location relative to paired dorsal setae in a medial/lateral aspect:* (1) Medial; (2) Lateral; (3) Level.

### ***Characters of the Abdomen:***

General Abdominal:

176. *Male general abdominal shape:* (1) Rounded; (2) Oval; (3) Elliptical elongated; (4) Oval/pear shaped.

177. *Female general abdominal shape:* (1) Rounded; (2) Oval; (3) Elliptical elongated; (4) Oval/pear shaped.

178. *Male widest lateral point of abdomen:* (1) Segment IV; (2) Segment V; (3)

Segment III.

179. *Female widest lateral point of abdomen:* (1) Segment IV; (2) Segment V; (3) Segment III.

180. *Polygonal marks over cuticular surface of the abdomen:* (1) Absent; (2) Present, but indistinct; (3) Present and distinct.

Segments II-VIII – General and Dorsal:

181. *Abdominal segment II vs. III size* (Clay "Key": 4; Ledger 1980: 9; & Smith 2000: 83, Fig. 71)*:* (1) II shorter than III; (2) II equal to III; (3) II longer and wider than III.

182. *Tergopleurite sclerotization segment IV-VII* (Smith 2001: 134)*:* (1) Weakly sclerotized; (2) Sclerotized.

183. *Tergites: Tergal Plates* (Clay 1940: 3)*:* (1) Narrowly separated; (2) Widely separated; (3) Intermediate; (4) Not separated.

184. *Male: Small sclerite present at the medial tips of tergite 2 (see G. spinincornis):* (1) Absent; (2) Present.

185. *Male tergopleurites (7$^{th}$–8$^{th}$):* (1) Apically mediad and pointing straight inwards; (2) Apically caudad and tilted slightly apically; (3) Apically caudad and tilted apically.

186. *Female tergopleurites (8$^{th}$):* (1) Apically mediad and pointing straight inwards; (2) Apically caudad and tilted slightly apically; (3) Apically caudad and tilted apically.

187. *Male dorsal medial division of abdominal segment II:* (1) Absent; (2) Present; (3) Bridged by extensions with pterothorax see *G. spinicornis*.

188. *Female dorsal medial division of abdominal segment II:* (1) Absent; (2) Present; (3) Bridged by extensions with pterothorax see *G. spinicornis*.

189. *Stigmatal scar on abdominal segment II:* (1) Absent or indistinct; (2) Present.

190. *Condition of all abdominal spiracle atria* (Smith 2001: 134 & Figs. 11O, P*):* (1) Small and round, uniform and in same relative position; (2) Small, but not all round, not uniform, or in same relative position, sometimes obscured.

191. *Cell shaped cuticular structure or sculpturing on dorsal abdominal* surface (Smith 2001: 101, 134, Figs. 11Q, 13D)*:* (1) Absent or indistinguishable; (2) Present, but indistinct; (3) Present and distinct.

192. *Cuticular structures* (Smith 2001: 101, 134, Figs. 11Q, 13D)*:* (1) Only on spiracle bearing segments (III-VIII); (2) On spiracle bearing segments (III-VIII) + IX; (3) On spiracle bearing segments (III-VIII) + II; (4) On all abdominal segments.

193. *Cuticular structures* (Smith 2001: 101, 134, Figs. 11Q, 13D)*:* (1) Only single main dorsal pit associated with spiracle; (2) Main dorsal pit with 2 smaller pits medially; (3) Absent; (4) Main dorsal pit with one smaller pit medially; (5) All over.

194. *Male tergal plate IX* (Clay 1940: 4)*:* (1) Continuous across segment; (2) Interrupted.

195. *Female tergal plate IX* (Clay 1940: 4)*:* (1) Continuous across segment; (2) Interrupted; (3) See *G. numidae*.

196. *Pleural ribs and knots on segments IV – VII* (Clay 1940:3) *usually broad with complicated re-entrant heads:* (1) Lateral where the anterior head is level or lateral relative to the spiracle; (2) Level where the anterior head is level or medial

relative to the to spiracle; (3) Medial where the anterior head is medial relative to the spiracle.

197. *Medial fusion between tergopleurite II and III (see G. gigas):* (1) Absent; (2) Present.

198. *Tergal thickenings (additional small, medial, tergal plates)*(Intertergital chitin Clay 1940: 26)*:* (1) Absent; (2) Present.

199. *Median dorsal setae on abdominal segment II: Rows & Types* (Smith 2001: 133 & Fig. 11C)*:* (1) Absent; (2) 1 pair or row; (3) 2 pairs or rows.

200. *Male dorsal abdominal setal rows* (Smith 2001: 134): (1) Single medial group (2); (2) Approximately 10, with 5 (4-8) setae each side; (3) Approximately 20 with 10 each side; (4) Approximately 40 with 20 each side.

201. *Female dorsal abdominal setal rows* (Smith 2001: 134): (1) Single medial group (2); (2) Approximately 10 with 5 (4-8) setae each side; (3) Approximately 20 with 10 each side; (4) Approximately 40 with 20 each side.

202. *Male number of postspiracular macrosetae on each side of II segment:* (1) Absent; (2) 1-2; (3) 3-4; (4) 5 or more.

203. *Male number of postspiracular macrosetae on each side of III segment:* (1) Absent (5); (2) 1-2; (3) 3-4; (4) 5 or more.

204. *Female number of postspiracular macrosetae on each side of II segment:* (1) Absent; (2) 1-2; (3) 3-4; (4) 5 or more.

205. *Female number of postspiracular macrosetae on each side of III segment:* (1) Absent; (2) 1-2; (3) 3-4; (4) 5 or more.

206. *Male setae on the posterolateral margin of abdominal segment II and III, excluding*

*rows of setae on the ventral posterior lateral border:* (1) II = 0 and III = 1; (2) II = 1 and III = 1; (3) II and III > 5 (clusters); (4) II and III = 0.

207. *Female setae on the posterolateral margin of abdominal segment II and III, excluding rows of setae on the ventral posterior lateral border:* (1) II = 0 and III = 1; (2) II = 1 and III = 1; (3) II and III > 5 (clusters); (4) II and III = 0.

Segments II-VIII – Ventral:

208. *Sternites III- VIII abdominal segments* (in part sternal thickenings sensu Clay 1940: 3)*:* (1) Single pair of sternites; (2) More than a single pair.

209. *Condition of additional pair/pairs in relation to 1st pair from character #208:* (1) single split pair close together medially; (2) Additional smaller pair lateral to first; (3) 2 pairs of similar size 1 lateral.

210. *Condition of additional lateral plates (if present):* (1) At least 1, sometimes 2 or 3 smaller sclerites similar in appearance to 1st pair; lateral to 1st pair and spiracles; (2) 1 sclerite lateral to 1st pair and spiracle, heavily sclerotized relative to the 1st pair.

Segments II-VIII – Lateral:

211. *Male abdominal segment II lateral margin/most distal point:* (Clay 1940: 3)*:* (1) Attached, rounded; (2) Attached, angular; (3) Extended, pointed; (4) Extended, rounded.

212. *Female abdominal segment II lateral margin/most distal point:* (Clay 1940: 3)*:* (1) Attached, rounded; (2) Attached, angular; (3) Extended, pointed; (4) Extended, rounded.

213. *Trichoid seta abdominal segment VIII* (Smith 2001: 135, Figs. 11R, S, T)*:* (1)

Absent; (2) Present with no or only an indistinct pit; (3) Present with a distinct pit.

214. *Pleurites:* (1) Not, or only slightly, broad and lateral to spiracles; (2) Broad and level with spiracles; (3) Broad and medial to spiracles.

215. *Pleurites:* (1) Not thickened; (2) Thickened.

Segments IX-XI – Male:

216. *End of male abdomen* (Clay 1940: 3; Blagoveshchenskii and Bei-Bienko 1967; "Key": 396; Smith 2000: 84 Fig 9a)*:* (1) Not, or only slightly, extended past natural margin of the abdomen; (2) Composed of a prominent lobe extending beyond the natural margin of the abdomen; (3) Not extending beyond natural margin of the abdomen, but with a lobe.

217. *Male abdomen* (Clay "Key":4 & Ledger 1980: 91*):* (1) Male abdomen Type D: Genital and anal openings close together on dorsal surface lying between, or only slightly posterior to tergal plates IX-X; (2) Male abdomen Type D: Genital and anal openings terminal, or nearly so; (3) Male abdomen Type D: VIII lying posterior to IX-X.

218. *Terminal end of male abdomen "lobe"* (Clay 1940; genitaloconus *sensu* Mey 1994)*:* (1) Slightly enlarged; (2) Distinctly enlarged; (3) Not enlarged.

219. *Terminal end of male abdomen "lobe"* (Clay 1940; genitaloconus *sensu* Mey 1994)*:* (1) Posteriorly flattened; (2) Pointed; (3) Rounded; (4) Indented.

220. *Terminal end of male abdomen "lobe"* (Clay 1940; genitaloconus *sensu* Mey 1994)*: Posterior margin:* (1) Broadly rounded; (2) Narrowly rounded, nearly pointed; (3) Bilobed and somewhat concave medially; (4) Bilobed.

221. *Terminal end of male abdomen "lobe"* (Clay 1940; genitaloconus *sensu* Mey 1994)

- *ventral chaetotaxy of posterior margin:* (1) Setose with various small, medium, and large macrosetae arranged both medially and laterally; (2) 1 pair macrosetae medially; (3) 3 pairs of macrosetae.

222. *Genitalconus* (*sensu* Mey 1994) – *anterior lateral and medial region (ventrally):* (1) Approximately 5 macrosetae slightly anterior and lateral to marginals with 10 larger ones scattered anteriomedially (See *G. pavonis*); (2) Only 10 larger macrosetae anteriomedially compressed (See *G. megaceros*); (3) Approximately 20 large macrosetae spread anteriorly (See *G. eurygaster*); (4) 2 pair with a large pair mediolaterally and a small pair lateral to these; (5) 8 macrosetae medially in anterior-posterior line; (6) Absent; (7) 3 pairs.

223. *Terminal end of male abdomen "lobe*" (*sensu* Clay 1940)*:* (1) Without sclerotized rim or plate; (2) With sclerotized plate rim/plate.

224. *Dorsal plate segment IX* (Smith 2000: 85 = Fig 9a #II)*:* (1) Absent or indistinct, flattened; (2) Distinct with the posterior margin bilobed, standard; (3) Distinct with posterior margin straight, pear; (4) Fused with sclerites from character #225 apparently a single unit.

225. *Sclerites medial to dorsal plate segment IX* (Smith 2000: 85 = Fig. 9a #III)*:* (1) Absent or indistinct; (2) Large, sclerites either side; (3) Small anterior extensions; (4) Flaps; (5) Pear-shaped, see *G. numidae*.

226. *Male genital opening* (Clay 1940)*:* (1) Not prolonged; (2) Prolonged.

227. *Male genital opening* (Clay 1940)*:* (1) Not bilobed; (2) Bilobed.

228. *Genitalia shape* (Mey 1999; Smith 2000: 85 Fig. 11)*:* (1) Solenoid/Simple; (2) Modified/Complex; (3) Solenoid with bulbous expansion medially.

229. *Genitalia shape* (Mey 1999)*:* (1) Symmetrical; (2) Asymmetrical.

230. *Genitalia shape* (Mey 1999) *Anterior end of basal apodeme:* (1) Convex; (2) Folded; (3) Diverging; (4) See illus character list.

231. *Genitalia shape* (Mey 1999; Smith 2000: 85) *posterior tip of parameres level with IX:* (1) As long as abdomen; (2) Shorter than abdomen.

232. *Genitalia overall structure:* (1) Weakly sclerotized; (2) Sclerotized; (3) Strongly sclerotized.

233. *Parameres* (Mey 1999): (1) Absent; (2) Not totally fused with basal apodeme; (3) Totally fused with basal apodeme.

234. *Parameres if present* (Mey 1999)*:* (1) Paramere without barb inwards; (2) With barb inwards; (3) Folded back medially.

235. *Parameres if present* (Mey 1999)*:* (1) Without endomeron; (2) With endomeron.

Segments IX-XI – Female:

236. *Terminal end of female abdomen* (Blagoveshchenskii and Bei-Bienko 1967"Key": 396)*:* (1) Not extending prominently past natural margin of the abdomen; (2) Extending beyond the natural margin of the abdomen.

237. *Terminal dorsal abdominal plates (IX-XI)*(Smith 2001: 135 & Figs. 11U, W, A', B'; Clay "Key": 4; Ledger 1980: 91)*:* (1) Segment IX-XI fused, appearing as a single unit; (2) Segment X-XI fused; segment IX indistinguishable.

238. *Female genital opening = vulva* (Clay 1940: 4)/Vulval margin (Smith 2000:86)*:* (1) Terminal; (2) At level of segment VIII; (3) Not terminal, but posterior to VIII.

239. *Female vulva form* (Clay 1940: 4)*:* (1) (see illustrations) Sheet 11/11/08; (2) (see illustration); (3) (see illustration); (4) (see illustration).

240. *Vulval marginal setae* (Clay 1940; Smith 2000:85)*:* (1) Setal fringe absent; (2) Fringed by one or more rows of setae.

241. *Vulval margin setal fringe number regardless of setal type* (Smith 2000:85 Fig 10)*:* (1) Single (Fig 10a); (2) Double (Fig. 10b); (3) Triple; (4) 4 rows.

242. *Vulval margin setal fringe types & numbers anterior row:* (1) Lateral corners only; (2) Regular row (3) Tooth-like setae (approximately 6 on each side)

243. *Round sclerite structure posterior and lateral to vulval corner:* (1) Absent; (2) Present.

244. *Lateral edge vulval margin setal #* (Smith 2000:85 fig 10 C and D)*:* (1) Absent; (2) Patch of setae (micro to normal macrosetae), very loosely scattered; (3) Row of setae (micro to normal macrosetae); (4) 2 or 3 distinct setae only; (5) Cluster of approximately 10 normal macrosetae; (6) 30 –50 seta of various sizes.

245. *Female genital bifid structure* (Clay 1940*):* (1) Absent; (2) Indistinct; (3) Distinct.

246. *Female spinous process genital region* Clay 1940 *(denticle shaped appendages sensu* Blagoveshchenskii and Bei-Bienko 1967"Key": 395*):* (1) Absent; (2) Present.

247. *Female spinous process genital region* Clay 1940 *(denticle shaped appendages sensu* Blagoveshchenskii and Bei-Bienko 1967"Key": 395*): size and orientation:* (1) Orientation ↓↘; (2) Orientation ↓→; (3) Orientation →↘.

***Morphometrics:***

Head:

248. *Temple width (TW) Male:* 9 states.

249. *TW Female:* 10 states.

250. *Head length (HL) Male:* 10 states.

251. *HL Female:* 9 states.

252. *Cephalic index (CI) Male:* 8 states.

253. *CI Female:* 9 states.

Thorax:

254. *Pronotum width (PW) Male:* 10 states.

255. *PW Female:* 10 states.

256. *Metanotum width (MW) Male:* 10 states.

257. *MW Female:* 9 states.

Abdomen:

258. *Abdomen width at segment IV (AWV) Male:* 10 states.

259. *AWV Female:* 9 states.

260. *Genitalia Length (GL) Male:* 9 states.

261. *Total Length (TL) Male:* 10 states.

262. *TL Female:* 10 states.

**PHYLOGENY RECONSTRUCTION AND CLADISTIC ANALYSIS**

Phylogenetic analysis and interpretation of the 262 morphological characters (Table 7) excluding 12 constant and 13 uninformative characters were performed in PAUP* version 4.0b10 (Swofford 2002) and MacClade version 4.08 (Maddison and Maddison, 1992). The analysis utilized parsimony (see Wiens and Hillis 1996) and the heuristic search option with stepwise addition and tree bisection reconstruction (TBR) branch swapping. Ten thousand (10, 000) random addition sequence replicates were used to increase the probability of finding all most parsimonious trees. All characters were considered of equal weight and treated as unordered with the exception of morphometric characters, which were ordered. Levels of branch support were investigated using two character resample techniques – bootstrap (Felsenstein 1985) and jackknife (Farris et al. 1996), as well as Bremmer support indices (Bremmer 1988, 1994) implemented in TreeRot version 3.0 (Sorenson 1999).

## RESULTS

The phylogenetic analysis favored 5 most parsimonious trees (MP) with a length of 2486 steps (CI: 0.276; RI: 0.561; RC: 0.150). The consensus tree (Figure 4) for the combined cladograms is mostly resolved with the exception of the disagreement between two weakly supported groups containing *G. curvicornis* and the genus *Goniocotes*. The low C.I. value 0.276 is not unexpected given morphological data and the size of the dataset and the retention index (RI = 0.562) might as a result be a more suitable indicator of overall support.

### *CLADISTIC ANALYSIS*

The overall tree topology, characterized by a continuous stepwise branching pattern, is largely a grade with the placement of taxa strongly correlated with general size. A strict consensus of these trees (not shown) shows some resolution and reveals several notable groups of species (see Fig. 4). Basally a group of small to very small taxa including three species (2 from the Australian megapodes) of *Goniodes* is embedded in *Goniocotes* to form the sister group to the rest of *Goniodes*, with reasonable support (Bootstrap 68; Jackknife 78; Bremmer 6).

This pectinate cluster contains two monophyletic clades. The first, a monophyletic grouping of *G. major* and *G. australis*, is weakly supported with a jackknife value of 61 and Bremmer support of 3); while the second, consisting of *G. dispar*, *G. securiger*, and

*G. assimilis*, has good support (Bootstrap 82, Jackknife 90, Bremmer 3), with additional support for a sister relationship between *G. dispar* and *G. securiger* (Bootstrap 74, Jackknife 84, Bremmer 5).

A grouping of medium sized species in the central part of the tree (Bootstrap 58; Jackknife 77; Bremer 6) contains two clades. Although overall support for the first, composed of *G. retractus*, *G. soueefi*, *G. coronatus*, *G. ortygis* and *G. ammoperdix*, is rather weak (Jackknife 54, Bremmer 3). There is reasonable support (Jackknife 61, Bremmer 6) for a sister relationship between *G. coronatus* and a strongly supported monophyletic group composed of *G. retractus* and *G. soueefi* (Bootstrap 100, Jackknife 100, Bremmer 19). The second clade in the central part of the tree (Bootstrap 52, Jackknife 65, Bremer 3) includes, in a stepwise arrangement, *G. columbianus*, *G. leucurus*, *G. corpulentus*, with better support for a monophyletic grouping of *G. ithaginis* and *G. chrysolophi* (Bootstrap 65; Jackknife 71; Bremmer 3).

A well resolved and supported (Bootstrap 62; Jackknife 73; Bremmer 2) apical clade contains very large robust species including *G. spinicoris*, *G. megaceros*, *G. eurygaster*, *G. pavonis*, *G. numidae*, *G. hopkinsi*, *G. wilsoni*, *G. gigas*, *G. processus*, and *G. cervicornis*. In this clade *G. spinicoris* and *G. megaceros* form a group (Bootstrap 99; Jackknife 100; Bremmer 10) sister to *G. eurygaster* (Bootstrap 78; Jackknife 88; Bremmer 7). In turn *G. pavonis* is the strongly supported sister to this assemblage with a bootstrap value of 96; jackknife of 99, and a Bremmer support value of 16. A clade containing *G. numidae*, *G. hopkinsi*, and *G. wilsoni* forms the well-supported (Bootstrap 87; Jackknife 95; Bremmer 11) monophyletic sister group (Bootstrap 98, Jackknife 100, Bremmer 11) to the aforementioned taxa. *G. numidae* as sister to *G. hopkinsi* is very strongly supported with both bootstrap and jackknife values of 100 and a Bremmer support value of 20. Sister relationships between these and the remaining taxa in a stepwise pattern from apical to basal are generally well supported and include *G. gigas* (Bootstrap 62; Jackknife 74; Bremmer 2), *G. processus* (Bootstrap 89, Jackknife 97, Bremmer 7), and *G. cervicornis* (Bootstrap 62, Jackknife 73, Bremmer 2).

## DISCUSSION

Within this arrangement, Clay's subgeneric classification, although not fully substantiated, is largely confirmed. Many smaller groups, as well as subsets of larger ones, are well supported (Figure 4). It is important to note that *Goniodes* exhibit considerable variation in size and morphology and that many characters not only grade into each other, but are also sexually dimorphic or polymorphic, while some appear to be artifacts of preservation. As a result very few characters unequivocally define any groupings. General trends do emerge, but limited sampling precludes a detailed discussion of synapomorphies that could reliably define any of the larger groups.

The paraphyletic grade at the base of the tree containing lice from both *Goniodes* and *Goniocotes* support historic and more recent data that these genera are not monophyletic with respect to one another. Clay's group M (1940) might form a "taxonomic intermediate" (Kettle 1981) between *Goniodes* and *Goniocotes*. This idea is also partly reflected in Johnson *et al*. 2011 (see Appendix A) based on molecular data. However, the relationships between these taxa might be much more complex, involving multiple host switches between lice from the Galliformes and Columbiformes (Johnson *et al*. 2011).

This analysis lends some credence to Clay's subgeneric groups. As such, it does confirm that her classification has phylogenetic content/utility. However, her classification does not define monophyletic groups but rather gives an idea of how some groups are broadly related. Obviously the general trends confirm that the smaller, medium, and large-bodied species cluster together. However, even the monophyletic and strongly supported apical groups cannot from a gross taxonomic perspective be effectively "described/circumscribed" in light of morphology. This morphological analysis largely confirms Clay's assessment that all groups (and to a certain extent species within groups) grade into each other, as is obvious from the phylogeny. There is phylogenetic structure, but given the limited sampling and the general inability to accurately define, reliable interpret, and repeatably score many of the characters, it is unclear how to interpret the results and define this sub-structure, without obscuring it in the minutiae it has historically been wrapped up in.

From a morphological perspective it is unlikely that additional characters for *Goniodes* will be found. However, re-evaluating some existing characters and improving homology assessments will be beneficial. In this regard, I believe that the chaetotaxy of the head, general traits of the abdomen, and the male and female terminalia will ultimately be most important in better defining groups in morphological terms. Pending the expansion of the current data set, and wider taxon sampling within *Goniodes* any such definitions are premature.

Equally important is a better understanding of character convergence in the Ischnocera. Many of the characters used in this study, especially related to sclerotization, sculpturing, prescence or absence of crop teeth or the genital sac are problematic. Not only are they highly sensitive to preservation and mounting technique, but also they are also convergent, being present in distantly related taxa. The sexual dimorphism of the antennae might also have skewed the current analysis given that highly specialized antennae in males might be influenced by size dimorphism and the actual mechanics of mating (Adams *et al*. 2005; Clay 1949; Oniki 1999). The same might hold true for tergal combs, and spinous genital process in females of some species.

However, recent work shows that the synergy between ischnoceran ecology and morphological convergence might be more complex than initially presumed. Johnson *et al*. (2012) reveal that chewing lice are likely subject to repeated adaptive radiations. This phenomenon involves morphological divergence within a host group, and morphological convergence between host groups, mediated by micro-habitat specialization.

It is apparent that the reality of the biological complexities associated with ubiquitous morphological convergence in the Ischnocera at large, and *Goniodes* specifically, cannot effectively be separated from the artificial intricacies imposed by classification. These factors are definitely not mutually exclusive, and morphology alone will not be able to resolve these issues. Molecular data might be able to curtail some of the issues associated with morphological convergence (see Appendix A: Johnson *et al*. 2011) and allow for the assessment and value of specific characters that might be useful in classification.

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# TABLES

**Table 2.1.** Current classification of galliforms host to *Goniodes*. Host nomenclature and number of species in each genus (Sp.) are from Madge *et al*. 2002. Number of *Goniodes* species (Gsp.) on each host genus follows Price *et al*. 2003 while new host records (Nhr) & occurrences (Nho) are based on new material. Generic African distribution follow Sinclair and Ryan 2003

| **GALLIFORMES** | | | | **Sp.** | **Gsp.** | **Nhr** | **Nho** | **Distribution** |
|---|---|---|---|---|---|---|---|---|
| MEGAPODIDAE | | *Alectura* | | 1 | 3 | - | - | |
| | | *Aepypodius* | | 2 | 3 | 1 | - | |
| | | *Talegalla* | | 3 | 4 | - | - | |
| | | *Leipoa* | | 1 | 2 | - | - | |
| | | *Megapodius* | | 13 | 7 | - | - | |
| PHASIANIDAE | | | | | | | | |
| | Perdicinae | *Tetraophasis* | | 2 | 1 | - | - | |
| | | *Tetraogallus* | | 5 | 2 | 1 | - | |
| | | *Ammoperdix* | | 2 | 1 | 1 | - | |
| | | *Alectoris* | | 7 | 3 | - | 1 | Africa |
| | | *Francolinus* | | 41 | 7 | 5 | 3 | Africa |
| | | | *Francolinus* | 5 | - | - | - | Africa |
| | | | *Peliperdix* | 5 | - | - | - | Africa |
| | | | *Scleroptila* | 7 | - | - | - | Africa |
| | | | *Acentrortyx* | 1 | - | - | - | Africa |
| | | | *Pternistis* | 23 | - | - | - | Africa |
| | | *Perdix* | | 3 | 1 | 1 | 1 | |
| | | *Margaroperdix* | | 1 | 1 | - | - | |
| | | *Coturnix* | | 9 | 6 | - | 3 | Africa |
| | | *Anurophasis* | | 1 | 0 | 1 | 1 | |
| | | *Arborophila* | | 21 | 3 | 0 | 5 | |
| | | | *Arborophila* | 18 | - | - | - | |
| | | | *Tropicoperdix* | 3 | - | - | - | |
| | | *Rollulus* | | 1 | 1 | - | - | |
| | | *Ptilopachus* | | 1 | 1 | - | - | Africa |
| | | *Bambusicola* | | 2 | 1 | - | 1 | |
| | Phasianinae | *Ithaginis* | | 1 | 1 | - | - | |
| | | *Tragopan* | | 5 | 2 | - | - | |
| | | *Pucrasia* | | 1 | 2 | - | - | |
| | | *Lophophorus* | | 3 | 3 | - | - | |
| | | *Gallus* | | 4 | 2 | - | - | |
| | | *Lophura* | | 12 | 5 | 0 | 0 | |
| | | | *Gennaeus* | 2 | - | - | - | |
| | | | *Hierophasis* | 4 | - | - | - | |
| | | | *Acomus* | 2 | - | - | - | |
| | | | *Euplocamus* | 3 | - | - | - | |
| | | | *Lobiophasis* | 1 | - | - | - | |
| | | *Crossoptilon* | | 4 | 2 | - | - | |
| | | *Catreus* | | 1 | 1 | - | - | |
| | | *Syrmaticus* | | 5 | 2 | - | - | |
| | | *Phasianus* | | 2 | 2 | 1 | - | |
| | | *Chrysolophus* | | 2 | 1 | - | - | |
| | | *Argusianus* | | 2 | 2 | - | - | |
| | | *Pavo* | | 2 | 3 | - | - | |
| | | *Afropavo* | | 1 | 1 | - | - | Africa |
| NUMIDAE | | *Agelastes* | | 2 | 1 | - | - | Africa |
| | | *Numida* | | 1 | 5 | - | - | Africa |
| | | *Guttera* | | 3 | 8 | 5 | - | Africa |
| | | *Acryllium* | | 1 | - | - | 1 | Africa |
| TETRAONIDAE | | *Falcipennis* | | 2 | 1 | - | - | |
| | | *Dendragapus* | | 1 | 1 | - | - | |
| | | *Lagopus* | | 4 | 2 | - | - | |
| | | *Tetrao* | | 2 | 3 | - | - | |
| | | *Bonasa* | | 1 | 1 | - | - | |
| | | *Centrocercus* | | 2 | 1 | - | - | |
| | | *Tympanuchus* | | 3 | 2 | - | - | |
| ODONTOPHORIDAE | | *Oreotyx* | | 1 | 1 | - | - | |
| | | *Callipepla* | | 4 | 1 | 1 | - | |
| | | *Philortyx* | | 1 | - | - | 1 | |
| | | *Colinus* | | 4 | 2 | 1 | 1 | |
| | | *Odontophorus* | | 15 | - | - | 1 | |
| | | *Rhynchortyx* | | 1 | 1 | - | - | |

**Table 2.2**. Eichler's (1963) classification of the Goniodidae, with emphasis on *Goniodes*. Genera containing species of *Goniodes* are bold.

**Ischnocera Kellogg**

- Goniodoidea (Eichler 1941)
  - Goniodiformia Eichler 1941
    - Goniodidae Mjöberg 1910
      - Archigoniodinae Eichler in Conci 1946 (also see Conci 1952)
        - ***Archigoniodes***
        - ***Clayarchigoniodes***
      - Goniodinae Kéler 1939
        - ***Goniodes***
        - ***Astrocotes***
        - ***Astrodes***
        - ***Claygoniodes***
        - *Goniodella*
        - ***Gonocephalus***
        - ***Gonotyles***
        - ***Kelergoniodes***
        - ***Oulocrepis***
        - *Passonomedea*
        - ***Solenodes***
        - *Pachyskelotes*
      - *(Bunocerinae Tendeiro 1954:90 = Archigoniodinae*)*
        - ***Keleria*** *Tendeiro 1954:94*
      - Goniocotinae Eichler 1937
        - *Goniocotes*
        - *Auricotes*
        - ***Dictyocotes***
      - Homocerinae Kéler 1939
        - ***Homocerus***
        - ***Margaritenes***
        - ***Stenocrotaphus***

* Synonomy by Tendeiro 1955a (*Adenda):* 162

**Table 2.3.** Clay's (1940) species group classification for *Goniodes*. Nomenclature, taxonomic status & host abbreviations follow Price *et al*. 2003. Generic host classification and distribution follows Madge *et al*. 2002. Species utilized in this study are in bold text.

| Clay's Groups | | **Status** | **Hosts** |
|---|---|---|---|
| **Group A** | ***G. pavonis*** | Valid | Phasian: Phasianinae: *Pavo* |
| **Group B** | *G. meinertzhageni* | Valid | Phasian: Phasianinae: *Pavo* |
| | ***G. spinicornis*** | Valid | Phasian: Phasianinae: *Tragopan* |
| | *G. tragopan* | Valid | Phasian: Phasianinae: *Tragopan* |
| | ***G. megaceros*** | Valid | Phasian: Phasianinae: *Lophophorus* |
| **Group C** | ***G. eurygaster*** | Valid | Phasian: Phasianinae: *Lophophorus* |
| **Group D** | ***G. coronatus*** | Valid | Phasian: Perdicinae: *Rollulus* |
| | *G. indicus* | Valid | Phasian: Perdicinae: *Arborophila* |
| **Group E** | ***G. processus*** | Valid | Phasian: Perdicinae: *Arborophila* |
| **Group F** | ***G. wilsoni*** | Valid | Phasian: Phasianinae: *Afropavo* |
| **Group G** | ***G. hopkinsi*** | Valid | Numi: *Guttera* |
| | ***G. numidae*** | Valid | Numi: *Numida* |
| | *G. fimbriatus* = Syn. | *G. numidae* | - |
| | *G. perlatus* = Syn. | *G. numidae* | - |
| **Group H** | ***G. gigas*** | Valid | Numi: *Numida,* & *Guttera** |
| | *G. agelastes* | Valid | Numi: *Agelastes* |
| **Group I** | ***G. bituberculatus*** | Valid | Tetraoni: *Tetrao* |
| | *G. tetraonis* | Valid | Tetraoni: *Tetrao* |
| | *G. centrocerci* | Valid | Tetraoni: *Centrocercus* |
| | *G. cupido* | Valid | Tetraoni: *Tympanuchus* |
| | ***G. lagopi*** | Valid | Tetraoni: *Lagopus* |
| | ***G. corpulentus*** | Valid | Tetraoni: *Dendragapus* |
| | ***G. merriamanus*** | Valid | Tetraoni: *Dendragapus* |
| | ***G. ithaginis*** | Valid | Phasian: Phasianinae: *Ithaginis* |
| | *G. colchici* | Valid | Phasian: Phasianinae: *Phasianus* |
| | ***G. chrysolophi*** | Valid | Phasian: Phasianinae: *Chrysolophus* |
| | *G. dentatus* = Syn. | *G.ocellatus* | - |
| | *G. sectus* | Valid | Phasian: Phasianinae: *Catreus* |
| | *G. crossoptilon* | Valid | Phasian: Phasianinae: *Crossoptilon* |
| | *G. dolani* | Valid | Phasian: Phasianinae: *Crossoptilon* |
| | *G. mamillatus* = Syn. | *G. stefani* | - |
| | ***G. dissimilis*** | Valid | Phasian: Phasianinae: *Gallus* |
| **Group J** | *G. intermedius* | Valid | Phasian: Phasianinae: *Pucrasia* |
| | *G. humlae* | Valid | Phasian: Phasianinae: *Syrmaticus* |
| | *G. longus* | Valid | Phasian: Phasianinae: *L. (Euplocamus)* |
| | *G. diardi* | Valid | Phasian: Phasianinae: *L. (Euplocamus)* |
| | ***G. cervinicornis*** | Valid | Phasian: Phasianinae: *L. (Gennaeus* |
| **Group K** | *G. teraogallae* = Syn. | *G. costatus* | - |
| | *G. oreophilus* | Valid | Phasian: Perdicinae: *Francolinus* |
| | *G. extraneus* = Syn. | *G. temporalis* | - |
| | ***G. assimilis*** | Valid | Phasian: Perdicinae: *Francolinus* & *Ptilopachus* |
| | ***G. antennatus*** | Valid | Phasian: Perdicinae: *F. (Pternistis)* |
| | *G. scleroptilus* | Valid | Phasian: Perdicinae: *F. (Scleroptila)* |
| | ***G. dispar*** | Valid | Phasian: Perdicinae: *Alectoris* & *Perdix* |
| | ***G. securiger*** | Valid | Phasian: Perdicinae: *Alectoris* |
| | *G. isogenos* | Valid | Phasian: Perdicinae: *F. (Scleroptila)* |
| | ***G. ortygis*** | Valid | Odontophori: *Colinus* |
| | ***G. ammoperdix*** | Valid | Phasian: Perdicinae: *Ammoperdix* |
| | *G. keleri* | Valid | Phasian: Perdicinae: *Margaroperdix* |
| **Group L** | ***G. retractus*** | Valid | Phasian: Perdicinae: *Coturnix* |
| | *G. astrocephalus* | Valid | Phasian: Perdicinae: *Coturnix* |
| | ***G. soueefi*** | Valid | Phasian: Perdicinae: *Coturnix* |
| **Group M** | *G. minor minor* = Syn. | *G. minor* | - |
| | *G. minor confusio* = Syn. | *G. confusio* | - |
| | ***G. biordinatus*** | Valid | Megapodii: *Megapodius* |
| | ***G. major*** | Valid | Megapodii: *Megapodius* & *Tallegalla* |
| | ***G. fissus*** | Valid | Megapodii: *Aepypodius* & *Alectura* |
| | *G. ocrea* | Valid | Megapodii: *Megapodius* |
| | *G. discogaster* | Valid | Megapodii: *Megapodius* |
| | ***G. crassipes*** | Valid | Megapodii: *Talegalla* |
| | *G. macrocephalus* | Valid | Megapodii: *Alectura* |

* *G. gigas* was originally described from *Gallus domesticus*, its true hosts are the Numidae (Clay 1940 p. 33).

**Table 2.4.** Currently valid species of *Goniodes* (Price *et al*. 2003) described since Clay (1940) placed in her classification. Placement based on primary literature by designation, or tentatively on similarity to other species of *Goniodes* (S), and/ or on host associations (A). Nomenclature, taxonomic status, and host abbreviations follow Price *et al*. 2003. See Price *et al*. 2003 for full records of citations in this table. Generic host classification follows Madge *et al*. 2002. Species utilized in this study are in bold text.

| **Clay's** | | **Placement** | **Hosts** |
|---|---|---|---|
| **Group A:** | *G. argus* | S (Eichler 1947) | Phasiani: Phasianinae:*Argusianus* |
| | ***G. curvicornis*** | A (Price et al 2003) | Phasiani: Phasianinae:*Argusianus* |
| **Group G:** | *G. plumiferae* | Tendeiro 1988 | Numi: *Guttera* |
| | *G. schoutedenii* | Tendeiro 1988 | Numi: *Guttera* |
| | *G. inaequalis* | Tendeiro 1988 | Numi: *Guttera* |
| | *G. meyi* | Tendeiro 1988 | Numi: *Numida* |
| | *G. klockenhoffi* | Tendeiro 1988 | Numi: *Numida* |
| | *G. reichenowii* | Tendeiro 1988 | Numi: *Numida* |
| **Group H:** | *G. zairensis* | Tendeiro 1988 | Numi: *Guttera* |
| | *G. gutterae* : | Tendeiro 1988 | Numi: *Guttera* |
| | *G. bifurcus* | Tendeiro 1988 | Numi: *Guttera* |
| | *G. phasidus* | Tendeiro 1988 | Numi: *Agelastes* |
| **Group I:** | *G. montschadskyi* | A (Price et al. 2003) | Tetraoni: *Tetrao* |
| | *G. nebraskensis* | S (Carriker 1945) | Tetraoni: *Tympanuchus* |
| | ***G. leucurus*** | S (Emerson 1952) | Tetraoni: *Lagopus* |
| | *G. bonasus* | Emerson 1948 | Tetraoni: *Bonasa* |
| | *G. capitatus* | A (Price et al. 2003) | Phasiani: Phasianinae: *Phasianus* |
| | *G. lophurus* | Liu 1989 | Phasiani: Phasianinae: *Lophura* |
| | *G. ocellatus* | S (Clay 1940) | Phasiani: Phasianinae: *Lophura* & *Pucrasia* |
| | *G. bambusicolus* | Liu 1989 | Phasiani: Perdicinae: *Bambusicola* |
| | *G. chloropus* | Emerson & Elbel 1957 | Phasiani: Perdicinae: *Arborophila* & *Tropicoperdix* |
| | *G. emersoni* | Tendeiro 1965 | Phasiani: Perdicinae: *F. (Scleroptila)* |
| | ***G. columbianus*** | S (Carriker 1945c) | Odontophori: *Colinus* |
| | *G. pictus* | A (Emerson 1950b) | Odontophori: *Oreortyx* |
| | *G. submamillatus* | A (Emerson 1950b) | Odontophori: *Calipepla* |
| | *G. squamatus* | A (Emerson 1950b) | Odontophori: *Callipepla* |
| | *G. stefani* | S (Clay 1940) | Odontophori: *Calipepla* |
| | *G. ovoidalis* | A (Price et al. 2003) | Odontophori: *Calipepla* |
| | *G. rhynchortyx* | A (Carriker 1956) | Odontophori: *Rhynchortyx* |
| **Group J:** | ***G. sinensis*** | Emerson & Stojanovich 1964 | Phasiani: Phasianinae: *Syrmaticus* |
| **Group K:** | *G. costatus* | S (Clay 1940) | Phasiani: Perdicinae: *Tetraogallus* |
| | ***G. tibetanus*** | A/S (Eichler 1950e) | Phasiani: Perdicinae: *Tetraogallus* |
| | *G. tetraophasis* | Chou & Liu 1986 | Phasiani: Perdicinae: *Tetraophasis* |
| | *G. temporalis* | S (Clay 1940) | Phasiani: Perdicinae: *F. (Francolinus)* |
| | *G. graecus* | A/S (Liu 1994) | Phasiani: Perdicinae: *Alectoris* |
| | *G. columbianus* | A/S (Price et al. 2003 | Odontophori: *Colinus* |
| | *G. picta = pictus* | A (Emerson 1950b) | Odontophori: *Oreortyx* |
| | *G. submamillatus* | A (Emerson 1950b) | Odontophori: *Calipepla* |
| | *G. squamatus* | A (Emerson 1950b) | Odontophori: *Callipepla* |
| **Group L:** | *G. moucheti* | Tendeiro 1959 | Phasiani:Perdicinae: *F. (Pternistis)* |
| | *G. lootensi* | Tendeiro 1959 | Phasiani:Perdicinae: *Coturnix* |
| **Group M:** | *G. arfakianus* | Tendeiro 1983 | Megapodii: *Aepypodius* |
| | *G. aepypodius* | Tendeiro 1983 | Megapodii: *Aepypodius* |
| | *G. neokeleri* | Tendeiro 1983 | Megapodii: *Alectura* |
| | ***G. australis*** | Emerson & Price 1986 | Megapodii: *Leipoa* |
| | *G. leipoae* | Emerson & Price 1984 | Megapodii: *Leipoa* |
| | *G. minimus* | Tendeiro 1980c | Megapodii: *Megapodius* |
| | *G. talegallae* | Tendeiro 1983 | Megapodii: *Talegalla* |
| | *G. curtiprothorax* | S (Mey 1982) | Megapodii: *Talegalla* |

**Table 2.5.** Taxa used in the cladisitc analysis, including outgroups and host distributions. Nomenclature, taxonomic status & host abbreviations follow Price *et al*. 2003.

| **Taxon** | **Authority** | **Material/Hosts** |
|---|---|---|
| *Goniodes* | | |
| *G. pavonis* | (L., 1758) | *Pavo* |
| *G. curvicornis* | Nitzsch, 1866 | *Argusianus* |
| *G. spinicornis* | Nitzsch, 1866 | *Tragopan* |
| *G. megaceros* | Kellogg & Paine, 1914 | *Lophophorus* |
| *G. eurygaster* | Piaget, 1885 | *Lophophorus* |
| *G. coronatus* | (Giebel, 1874) | *Rollulus* |
| *G. processus* | Kellogg & Paine, 1914 | *Arborophila* |
| *G. wilsoni* | Clay, 1938 | *Afropavo* |
| *G. hopkinsi* | Clay, 1940 | *Guttera* |
| *G. numidae* | Mjöberg, 1910 | *Numida* |
| *G. gigas* | (Taschenberg, 1879) | *Numida, & Guttera** |
| *G. bituberculatus* | Rudow, 1869 | *Tetrao* |
| *G. lagopi* | (L., 1758) | *Lagopus* |
| *G. columbianus* | Carriker 1945c | *Colinus* |
| *G. leucurus* | Emerson, 1952 | *Lagopus* |
| *G. corpulentus* | Kellogg & Mann, 1912 | *Dendragapus* |
| *G. merriamanus* | Packard, 1873 | *Dendragapus* |
| *G. ithaginis* | Clay, 1940 | *Ithaginis* |
| *G. chrysolophi* | Clay, 1940 | *Chrysolophus* |
| *G. dissimilis* | Denny, 1842 | *Gallus* |
| *G. cervinicornis* | Giebel, 1874 | *L. (Gennaeus* |
| *G. sinensis* | Emerson & Stojanovich, 1964 | *Syrmaticus* |
| *G. assimilis* | Piaget, 1880 | *Francolinus & Ptilopachus* |
| *G. antennatus* | Clay, 1940 | *F. (Pternistis)* |
| *G. dispar* | Burmeister, 1838 | *Alectoris & Perdix* |
| *G. securiger* | Nitzsch, 1866 | *Alectoris* |
| *G. ortygis* | Denny, 1842 | *Colinus* |
| *G. tibetanus* | (Eichler, 1950e) | *Tetraogallus* |
| *G. ammoperdix* | Clay, 1940 | *Ammoperdix* |
| *G. retractus* | Le Souëf, 1902 | *Coturnix* |
| *G. soueefi* | Clay, 1940 | *Coturnix* |
| *G. biordinatus* | Clay, 1940 | *Megapodius* |
| *G. major* | (Piaget, 1880) | *Megapodius & Tallegalla* |
| *G. fissus* | (Rudow, 1869) | *Aepypodius & Alectura* |
| *G. crassipes* | (Piaget, 1888) | *Talegalla* |
| *G. australis* | Emerson & Price 1986 | *Leipoa* |
| | | |
| *Goniocotes* | | |
| *G. diplogonus* | Nitzsch, 1866 | *Tragopan* |
| *G. gallinae* | (De Geer, 1778) | *Calloperdix, Gallus, Meleagris* |
| *G. haplogonus* | Nitzsch, 1866 | *Lophophorus* |
| *G. pallidomaculatus* | Piaget, 1890 | *Arborophila* |
| *G. parviceps* | (Piaget, 1880) | *Pavo* |
| *G. reticulates* | Kéler, 1939 | *Lophura, Phasianus* |
| | | |
| **Outgroups** | | |
| *Physconelloides* | | |
| *P. montana* | Carriker, 1961* | *Geotrygon, Leptotila* |
| *Campanulotes* | | |
| *C. bidentatus* | (Scopoli, 1763) | *Columba* |
| *Heptapsogaster* | | |
| *H. temporalis* | Carriker, 1936 | *Crypturellus* |

*= *P.ceratoceps* Ewing, 1927*

**Table 2.6.** The following genera and species of *Goniodes* and other Ischnocera were used for character formulations and coding of the matrix see Table?. The in-group utilized is composed of 36 species of *Goniodes* and 6 species of *Goniocotes*. The out-group consists of 1 species each from the genera *Physconelloides*, *Campanulotes*, and *Heptapsogaster*. Taxonomy follows the recent world check-list by Price *et al*. 2003. Collectionand museum acronyms follow Evenhuis and Samuelson 2007.

**INGROUP:**

***Goniodes*** Nitzsch, 1818

***G. pavonis*** (L., 1758).

**33 specimens (16 males, 17 females): OSEC:** 2 specimens ex "Pea Fowl": USA: 1 male, 1 female (Baton Rouge, LA, May 9-1957, Coll: E. Cancienne, Det. K. C. Emerson, Host: No. 32418 (Lot57-6363)). 6 specimens ex *Pavo cristatus*: UNITED KINGDOM: 3 males, 3 females (Bridgenorth, Shropshire, 11.viii.1934, Coll: Frances Pitt, Det. K. C. Emerson). 1 specimen ex *Pavo cristatus*: NEPAL: 1 female (Bhogbhawanpur Banke Dist., 3 April 1968, Host: NP-452). 1 specimen ex *Pavo cristatus*: NEPAL: 1 female (Bhogbhawanpur Banke Dist., 5 April 1968, Det. K. C. Emerson, Host: NP-460). 1 specimen ex *Pavo muticus imperator*: SIAM: 1 female (Nakhon Phanom, Nakae Kanluang, Kho Mt., Coll: Elbel, Det. K. C. Emerson, Host: B30924, RE 3912). 1 specimen ex *Pavo muticus*: THAILAND: 1 female (Nansa, Ban Phahang, 8 Dec. 1961, Coll: Mr. Kittithonglongya, Det. K. C. Emerson, Host. V139). **FMNH:** 2 specimens ex *Pavo cristatus*: NEPAL: 2 males (Bhogbhawanpur Banke Dist., 5 April 1968, Host: NP-460). 2 specimens ex "Peacock": USA: 1 male, 1 female (Michigan, 28 May 1929, Coll: A. F. Franzen, Det. R. A. Ward, Host: Fresh). 1 specimen ex *Pavo cristatus*: NEPAL: 1 female (Bhogbhawanpur Banke Dist., 3 April 1968, Host: NP-452). **NMNH:** 2 specimens ex. *Pavo cristatus*: NEPAL: 2 males (Bhogbhawanpur Banke Dist., 6 April 1968, Det. R. E. Lewis, Host: NP-482, Lewis Collection). 2 specimens ex *Pavo cristatus*: NEPAL: 1 male, 1 female (Bhogbhawanpur Banke Dist., 31 Mar. 1968, Host: NP-425). 2 specimens ex "Pea Fowl": USA: 1 male, 1 female (Baton Rouge. LA, May 9-1957, Coll: E. Cancienne, Host: No. 32418 (Lot57-6363)). 2 specimens ex *Pavo cristatus*: USA: 1 male, 1 female (Chicago Zool. Park, 18 Jan. 1967, Coll: Ursula Rowlatt, Host: 182-65). 4 specimens ex *Pavo muticus imperator*: THAILAND: 2 males, 2 females (Nakhon Phanom, Nakae Kanluang, Kho Mt., 16 July 1954, Coll: Elbel & Boonsong, Host: B30924, RE 3912). 4 specimens ex *Pavo muticus imperator*: THAILAND: 2 males, 2 females (Nakhon Phanom, Nakae Kanluang, Kho Mt., 25 July 1954, Coll: R. E. Elbel, Host: B30924, RE 3912).

***G. curvicornis*** Nitzsch, 1866

**12 specimens (6 males, 6 females): OSEC:** 2 specimens ex *Argusianus argus*: MALAYSIA: 1 male, 1 female (Malaya, Gombak, 16-Feb. 1963, Det. K. C. Emerson, OK 3854, Host: M-02409). 10 specimens ex *Argusianus argus*: MALAYSIA: 5 males, 5 females (Sarawak, Kapit Dist., Det. K. C. Emerson, OK 3857 (5), OK 3858, OK 3859 (2), OK 3861 (3), Host: FOG-23008).

***G. spinicornis*** Nitzsch, 1866

**19 specimens (9 males, 10 females): FMNH:** 2 specimens ex *Tragopan b. blythii*: BURMA: 1 male, 1 female (Mt. Victoria, Apr-May 1938, Coll: G. Heinrich, Det. R. A. Ward, Host: Male). **OSEC:** 2 specimens ex *Tragopan satyr*: NEPAL: 1 male, 1 female (Kasuwa Khola, 13 May 1973, Det. K. C. Emerson, OK 12460, Host: HE 0127). 2 specimens ex *Tragopan satyra*: NEPAL: 1 male, 1 female (Namsangsang, NE Melumchi, 8 Nov. 1969, Det. K. C. Emerson, OK 4015(2), Host: NP-3358). 1 specimen ex *Tragopan b. blythii*: BURMA: 1 male (Mt. Victoria, May 4, 1938, Det. K. C. Emerson, OK 4014(3)). 1 specimen ex Crimson-horned Pheasant: NEPAL: 1 female (Namsangsang, NE Melumchi, 8 Nov. 1969, Host: NP-3358). **SMPM:** 2 specimens ex Crimson-horned Pheasant: NEPAL: 1 male, 1 female (Kaldapeh Slope, nr. Melumchi, 23 Nov.1969, Host: NP-3397). **USNM:** 1 specimen ex *Tragopan temmincki*: CHINA: 1 female (Li Kiang Mts., Coll: J. F. Rock, Host: U.S.N.M. 296074). 2 specimens ex *Tragopan satyra*: USA: 1 male, 1 female (Concord, Calif., June 9-1937. Coll: J. Moffitt, (M#2063), Host: Bish.No. 27624; Lot 37-25266). 2 specimens ex *Tragopan satyr*: NEPAL: 1 male, 1 female (Sankhuwa Sabha Chainpur, 23 Jan. 1973, Host: HE-0074). 2 specimens ex *Tragopan satyr*: NEPAL: 1 male, 1 female (Kasuwa Khola, 13 May 1973, Host: HE 0127). 2 specimens ex *Tragopan b. blythii*: BURMA: 1 male, 1 female (Mt. Victoria, Apr-May, 1938, Coll: G. Heinrich, Det. R. A. Ward, Host: Male).

***G. megaceros*** Kellogg & Paine, 1914

**10 specimens (7 males, 3 females): FMNH:** 6 specimens ex *Lophophorus impejanus*: NEPAL: 5 males, 1 female (Dhukpu, Sindhu Palchok Dist., 9 August 1969, Host: NP-2956). **OSEC:** 2 specimens ex *Lophophorus impejanus*: NEPAL: 1 male, 1 female (Newakot District, Phulung Ghyang, 11-May-67, Coll: C. D. Maser, Det. K.C. Emerson, OK 3981, Host: MN-416). 2 specimens ex *Lophophorus impejanus*: NEPAL: 1 male, 1 female (Dhukpu, Sindhu Palchok Dist., 9 August 1969, Det. K. C. Emerson, OK 3989, Host: NP-2956).

***G. eurygaster*** Piaget, 1885

**25 specimens (13 males, 12 females): BMNH:** 2 specimens ex Monal Pheasant: NEPAL: 1 male, 1 female (Nuwakot Dist., Uring Ghang, 30-Aug-68, Host: NP-1090). **FMNH:** 3 specimens ex "Dafne": NEPAL: 3 males (Langtang Valley, 13 May 1969, Host: NP-2480). 1 specimen ex "Dafne": NEPAL: 1 male (Langtang Valley, 7 May 1969, Host: NP-2480). 1 specimen ex *Lophophorus impeyanus*: USA: 1 female (Brookfield Zoo, Chicago, ILL, 18 Jun. 1941, Coll: W. J. Gerhart, Det. R. A. Ward). **OSEC:** 2 specimens ex *Lophophorus impeyanus*: NEPAL: 2 males (Thodung, Jiri Ramechap Dist., 13 Oct. 1969, Host: NP-3302). 1 specimen ex "Dafne": NEPAL: 1 female (Langtang Valley, 12 May 1969, Host: NP-2540). 1 specimen ex *Lophophorus impeyanus*: NEPAL: 1 female (Samar Kharka, Melumchi, 24 April 1970, Det. K. C. Emerson, OK 3926, Host: NP-3831). 1 specimen ex *Lophophorus impeyanus*: NEPAL: 1 female (Langtang Valley, 13 May 1969, Det. K. C. Emerson, OK 3933, Host: NP-2556). 1 specimen ex *Lophophorus impeyanus*: NEPAL: 1 female (Langtang Valley, 7 May 1969, Det. K. C. Emerson, OK 3932, Host: NP-2480). **SMPM:** 2 specimens ex Monal Pheasant: NEPAL: 1 male, 1 female (Uring Ghang, Nuwakot Dist., 30 August 1968, Host: NP-1090). 2 specimens ex "Dafne": NEPAL: 1 male, 1 female (Langtang Valley, 13 May 1969, Host: NP-2556). **USNM:** 8 specimens ex *Lophophorus impeyanus*: NEPAL: 4 males, 4 females (Dhukphu, Sindhu Palchok Dist., 13 August 1969, Host: NP-3007).

***G. coronatus*** (Giebel, 1874)

**35 specimens (20 males, 15 females): BMNH:** 6 specimens ex *Rollulus roulroul*: BORNEO: 3 males, 3 females (Borneo, Jan. 1901, Coll: Meinertzhagen, Host: Male 3655). 5 specimens ex *Rollulus roulroul*: BORNEO: 3 males, 2 females (Borneo, Coll: Meinertzhagen, Host: 10891). 7 specimens ex *Caloperdix o. oculea*: SIAM: 5 males, 2 females (Siam, Nov. 1938, Coll: Meinertzhagen, Det. Elbel & Price, Host: 13517). **FMNH:** 2 specimens ex *Rollulus roulroul*: THAILAND: 1 male, 1 female (Nakhon Si Thammarat, Chawang Chang Klang, Ban Na, 9 March 1954, Coll: B. Lekagul, Det. K. C. Emerson, Host: Sc 503, RT B-22785). 1 specimen ex *Rollulus roulroul*: JAVA: 1 male (Abalecoa, Det. K. C. Emerson). **OSEC:** 2 specimens ex *Rollulus sp*. BL: THAILAND: 1 male, 1 female (Phataluug (Prova Dist) Ban Na, Phap Pha Mt., 5-Feb-55, Coll: B Lekagul, Det. K. C. Emerson, Host: Sc 2229). 2 specimens ex *Rollulus roulroul*: JAVA: 1 male, 1 female (Abalecoa, Det. K. C. Emerson, OK 3827). 4 specimens ex *Rollulus roulroul*: THAILAND: 2 males, 2 females (HGD, Nakhon Si Thammarat, Chawang Chang Klang, Ban Na, 9 March 1954, Coll: B. Lekagul, Det. K. C. Emerson, OK 3842 (4), Host: Sc 503, RT B-22785). **USNM:** 4 specimens ex *Rollulus sp*. BL: THAILAND: 3 males, 1 female (Phataluug (Prova Dist) Ban Na, Phap Pha Mt., 5 Feb 1955, Coll: B. Lekagul, Det. KCE, Host: Sc 2229 (JM 5 Apr 1951)). 2 specimens ex *Rollulus roulroul*: NORTH BORNEO: 2 females (Membakut, Br.N.B, 26 Sept. 1959, Det. KCE, Host: FOG-21033).

***G. processus*** Kellogg & Paine, 1914

**31 specimens (16 males, 15 females): BMNH:** 4 specimens ex *Arborophila brunneopectus erythrophrys*: NORTH BORNEO: 2 males, 2 females (Thus Madi Mt. Pamparyi Ulu Kainguran, 7-Aug-53, Coll: US Army-Brit. Col. Off. Med. Res. Unit, Det. K. C. Emerson, B 19735, Host: R40222, RT B-19735). 2 specimens ex *Arborophila rufogularis intermedia*: BURMA: 2 males (Burma, 1898, Coll: Meinertzhagen, Host: Male 3605 (BMNH 14555)). 1 specimen ex *Arborophila atrogularis*: BURMA: 1 male (Myitkyina, 35 miles West, 3.iv.1945, Coll: H. S. Fuller, Host: B.M.1947-321(98)). 1 specimen ex *Arborophila t. torqueola*: ASSAM: 1 male (Assam, Nov. 1896, Coll: Meinertzhagen, Host: Female 3608). **OSEC:** 2 specimens ex *Arborophila brunneopectus*: SIAM: 1 male, 1 female (Banmaed, Koksathon, Dansai, Loei, 1-Apr-54, Coll: Elbel, Det. K. C. Emerson, OK 3994, Host: RE 3576, RT B-22730). 2 specimens ex *Arborophila rufogularis*: THAILAND: 1 male, 1 female (Doi Inthanon, Chieng Mai, 13 Nov. 1964, Coll: H. E. MaClure, Det. K. C. Emerson, OK 4001 (1), Host: SE-1882). 2 specimens ex *Arborophila atrogularis*: BURMA: 1 male, 1 female (Myitkyina, 35 miles West, 3.iv.1945, Coll: H. S. Fuller, Det. K. C. Emerson, OK 3996 (3), OK 3997 (4), Host: B.M.1947-321(98)). **USNM:** 1 specimen ex *Arborophila brunneopectus erythrophrys*: NORTH BORNEO: 1 male (Thus Madi, Pampang Ulu Kaingaran, 4000ft., Aug. 1953, Coll: Elbel (Inst. Med. Res.), Det. KCE, Host: R40171-1, RT-B19709). 4 specimens ex *Arborophila atrogularis*: BURMA: 1 male, 3 females (Myitkyina, 35 miles West, 3.iv.1945, Coll: H. S. Fuller, Host: B.M.1947-321(98)). 1 specimen ex *Arborophila brunneopectus erythrophrys*: NORTH BORNEO: 1 female (Thus Madi Mt. Pamparyi Ulu Kainguran, 31 July 1953, Coll: US Army-Brit. Col. Off. Med. Res. Unit, Det. K & P, Host: R40140, RT B 19693). 3 specimens ex *Arborophila brunneopectus erythrophrys*: NORTH BORNEO: 1 male, 2 females (Thus Madi Mt. Pamparyi Ulu Kainguran, Aug. 1953, Coll: US Army-Brit. Col. Off. Med. Res. Unit, Host: R40199, RT-B19725). 8 specimens ex *Arborophila brunneopectus erythrophrys*: NORTH BORNEO: 4 males, 4 females

(Thus Madi Mt. Pamparyi Ulu Kainguran, 7 Aug. 1953, Coll: US Army-Brit. Col. Off. Med. Res. Unit, Host: R40222, RT B-19735).

***G. wilsoni*** Clay, 1938

**8 specimens (4 males, 4 females): OSEC:** 2 specimens ex *Afropavo congensis*: BELGIAN CONGO: 1 male, 1 female (Tshuapa, 1956, Coll: R.P. Lootens, Det. K. C. Emerson, OK 4026). **USNM:** 2 specimens (paratypes) ex *Afropavo congensis*: CONGO: 1 male, 1 female (Congo, Coll: Meinertzhagen, Host: 10606). **RMCA:** 2 specimens ex *Afropavo congensis*: BELGIAN CONGO: 1 male, 1 female (Tshuapa, Ikela, 26.x.1955, Coll: P. Lootens). 2 specimens ex *Afropavo congensis:* BELGIAN CONGO: 1 male, 1 female (Tshuapa, 1956, Coll: R.P. Lootens).

***G. hopkinsi*** Clay, 1940

**12 specimens (3 males, 9 females): BMNH:** 2 specimens ex *Guttera pucherani*: TANGANYIKA: 1 male, 1 female (Tanganyika Territory, Coll. R. E. Moran, Hopkins Collection; "on dry skin"). 1 specimen ex *Guttera edouardi*: SOUTH RHODESIA: 1 male (Chitsa, 13.vi.1950, Brit. Mus.1956-353). 1 specimen ex *Guttera plumifera schubotzi*: CONGO: 1 female (Congo, Coll: Meinertzhagen, Host: 12561). 4 specimens ex *Guttera edouardi sclateri*: CAMEROONS: 4 females (Cameroons, 1898, Coll: Meinertzhagen, Det. Tendeiro (1985), Host: Male 3635). **OSEC:** 2 specimens (paratypes) ex *Guttera edouardi seth-smithi*: UGANDA: 2 females (Budango, Det. K. Emerson (#54 K. C. Emerson)). **USNM:** 2 specimens ex *Guttera pallosi seth-smithi*: EAST AFRICA: 1 male, 1 female (Budango Forest, Unjoro, 1912, Coll. C. E. Akeley, Prep: R. C. Simpson, Det. E.W.S, Host: 388709).

***G. numidae*** Mjöberg, 1910

**48 specimens (21 males, 27 females): BMNH:** 4 specimens (paratypes *G. perlatus*) ex *Numida meleagris major*: UGANDA: 2 males, 2 females (Buganda, Coll: Meinertzhagen, Det. Clay, Host: 11687). 2 specimens ex *Numida meleagris major*: UGANDA: 1 male, 1 female (Uganda, Det. Clay (as *G. perlatus*), Host: III). 2 specimens ex *Numida meleagris major*: UGANDA: 1 male, 1 female (Uganda, Det. Clay (as *G. perlatus*), Host: XXXI). 2 specimens ex *Numida meleagris marunguensis*: RHODESIA: 2 females (N.W. Rhodesia, 1939, Meinertzhagen Collection, Host: 13333; BM 1951-171). 2 specimens ex *Numida meleagris coronate*: SOUTH AFRICA: 1 male, 1 female (Vryburg, Cape Province, 11-vii-1934, Hopkins Collection, Det. Tendeiro (1985)). 4 specimens ex *Numida meleagris*: BELGIAN CONGO: 2 males, 2 females (Vallée Akangaru, xi-1939, Coll: A. Lestrade, Det. Tendeiro (1985), Host: Brit.Mus. 1951-546).

4 specimens ex *Guttera edouardi chapini*: ANGOLA: 1 male, 3 females (Benguella, Oct. 1901, Coll: Meinertzhagen, Det. Tendeiro (1985), Host: 3140). 2 specimens ex *Numida meleagris galeata*: SIERRA LEONE: 1 male, 1 female (Sierra Leone, Oct. 1904, Coll: Meinertzhagen, Det. Clay (as *G. fimbriatus*), Host: 3128 Male). 3 specimens ex *Numida meleagris sabyi*: MAROCCO: 2 males, 1 female (Marocco, Coll: Meinertzhagen, Det. Clay (as *G. fimbriatus*), Host: 12550). **FMNH:** 1 specimen ex *Numida meleagris major*: UGANDA: 1 male (Buvuma Island, 1948, Det. K. C. Emerson (as *G. perlatus*)). **INHS:** 1 specimen ex *Numida meleagris major*: UGANDA: 1 female (Buvuma Island, 1948, as *G. perlatus*). **OSEC:** 2 specimens ex *Numida meleagris major*: UGANDA: 1 male, 1 female (Buvuma Island, 1948, Det. K. C. Emerson). 6 specimens (paratypes) ex *Numida meleagris major*: UGANDA: 1 male, 5 females (Busoga, 11-viii-37 Det. K. C. Emerson (as *G. perlatus*), Host: 4 (KCE #62)). **SMPM:** 3 specimens ex *Numida meleagris*: SOUTH AFRICA: 3 males (Bloemfontein Dist., 1 May 1994, Coll: G. Kopij, Host: 94.A.37). **USNM:** 4 specimens ex *Numida meleagris*: SOUTH AFRICA: 2 males, 2 females (Union of South Africa, Ndumu, Zululand, Dec.16. 1958, Coll: O. G. Babcock, Host: B.12, Det. *G. perlatus*). 1 specimen ex *Numida meleagris* major: UGANDA: 1 female (Buvuma Island, 1948, Det. K. C. Emerson, as *G. perlatus*). 1 specimen ex *Numida meleagris galeata*: SENEGAL: 1 male (Senegal, Coll., & Det. (*G.* perlatus) KCE "from skin"). 1 specimen ex *Numida meleagris mitrata*: MADAGASCAR: 1 female (Tanosy, Ft. Dauphin Dist., Nov. 12-1948, Coll: H. Hoogstraal, Host: Lot 52-1033). **RMCA:** 4 specimens ex *Numida meleagris*: BELGIAN CONGO: 2 males, 2 females (Vallée Akangaru, xi-1939, Coll: A. Lestrade, Det. Clay (1951)(as *G. perlatus*)).

***G. gigas*** (Taschenberg, 1879)

**40 specimens (19 males, 21 females): BMNH:** 2 specimens ex *Guttera edouardi seth-smithi*: UGANDA: 2 females (Bustimla, viii-1946, Coll: R.G.C. van Someren). 4 specimens ex *Guttera edouardi seth-smithi*: KENYA: 2 males, 2 females (Coll: Meinertzhagen, Host: 10854). 2 specimens ex *Numida meleagris*: SOUTH AFRICA: 1 male, 1 female (Pretoria, 24.iv.1966, Coll: M. S. Markus, Det. T. Clay, Host: Brit.Mus.1966-334.4). 6 specimens ex *Numida meleagris sabyi*: MAROCCO: 3 males, 3 females (Marocco, Dec. 1938, Coll: Meinertzhagen, Host: 12513 "Hatched under fowl"). **INHS:** 4 specimens ex Domestic hen: USA: 2 males, 2 females (Rushville, IL, July 9, 1905, Coll: Anna T. Walken, Det. Malcomson (1937)). **OSEC:** 2 specimens ex *Numida meleagris*: SOUTH AFRICA: 1 male, 1 female (RSA, Bloemfontein Dist., 1-May-94, Coll: G. Kopij, Host: 94.A.37 or 39). 1 specimen ex *Numida meleagris galeata*: SENEGAL: 1 male (Senegal, Det. K. C. Emerson). 1 specimen ex *Numida meleagris major*: UGANDA: 1 female (Buvuma Island, 1948, Det. K. C. Emerson). 1 specimen ex *Guttera pucherani:* SOMALILAND: 1 female (Somaliland, Det. K. C. Emerson, OK 3944 (4)). **SMPM:** 3 specimens ex *Gallus gallus*: CUBA: 2 males, 1 female (Habana, Coll: I. Perez Viqueras, Det. R. D. Price (1962)). 4 specimens ex *Numida meleagris*: SOUTH AFRICA: 2 males, 2 females (Kruger National Park). **USNM:** 3 specimens ex *Numida meleagris major*: UGANDA: 3 males (Busuli, Duyanda, 1940, Det. G. H. E. Hopkins). 2 specimens ex *Numida meleagris*: SOUTH AFRICA: 1 male, 1 female (Union of South Africa, Ndumu, Zululand, Dec.16.1958, Coll: O. G. Babcock, Host: B.12). 5 specimens ex Guinea Fowl: USA: 1 male, 4 females (Bexar Co. Texas, 2-xii-66).

***G. bituberculatus*** Rudow, 1869

**20 specimens (10 males, 10 females): OSEC:** 5 specimens ex *Tetrao u. urogallus*: GERMANY: 4 males, 1 female (Germany, 1952, Det. K. C. Emerson, OK 3807(3), OK 3808, OK 3810, OK 3817(1)). 5 specimens ex *Tetrao u. urogallus*: GERMANY: 1 male. 4 females (Germany, Nov 6 '98, skin, K. C. Emerson Collection, OK 3816(6), OK 3815(10), OK 3819(4). **SMPM:** 5 specimens ex *Tetrao urogallus* SWEDEN: 3 males, 2 females (Gillivare, 25.3.1934, Coll: S. Sjoberg, Host: 96). 3 specimens ex *Tetrao urogallus*: SWEDEN: 1 male, 2 females (S. K. Asljunga, 20.4.1939, Coll: A. Lundstrom, Host: 94). 2 specimens ex *Tetrao urogallus*: SWEDEN: 1 male, 1 female (Vrml. Himkebol, 16.9.1939, Coll: A. Lundstrom, Host: 70). 1 specimen ex *Tetrao urogallus*: SWEDEN: 1 male (Sweden, 11.7.1939, Coll: A. Lundstrom, Host: 92). 1 specimen ex *Tetrao urogallus*: SWEDEN: 1 female (Hastveda, 7.10.1954, Host: 66).

***G. lagopi*** (L., 1758)

**22 specimens (11 males, 11 females): FMNH:** 1 specimen ex Ptarmigan: CANADA: 1 male (Old Crow River, Yukon, April 5, 1957, Det. K. C. Emerson). **OSEC:** 4 specimens ex *Lagopus lagopus*: CANADA: 2 males, 2 females (N.W.T., Yellow Knife, 26 April 1968, Det. K. C. Emerson, OK 1816). 2 specimens ex *Lagopus lagopus*: USA: 1 male, 1 female (Cape Thompson, Alaska, 1961, Coll: Max Thompson, Det. K. C. Emerson, OK 1814 (1)). 2 specimens ex *Lagopus lagopus*: USA: 1 male, 1 female (Cape Thompson, Alaska, 1961, Coll: M C T, Host: 1580). 2 specimens ex *Lagopus mutus dixoni*: USA: 1 male, 1 female (3mi. E. of Juneau, Alaska, Nov. 20-1949, Coll: R. B. Williams, Det. K. C. Emerson, OK 1826 (6), Host: #217 (Lot 49-18692)). **SMPM:**

1 specimen ex *Lagopus lagopus*: SWEDEN: 1 male (Lule, Lappmark, July-Aug 1944, Coll: P. Brinck & K. G. Wingstrand - Virihaure-Expedition, Host: 172). 2 specimens ex *Lagopus lagopus* SWEDEN: 1 male, 1 female (Lule, Lappmark, July-Aug 1944, Coll: P. Brinck & K. G. Wingstrand - Virihaure-Expedition, Host: 170). 1 specimen ex *Lagopus lagopus*: SWEDEN: 1 female (Granbergi, 30.12.1957, Coll: O. Bergman, Host: 159). 4 specimens ex *Lagopus lagopus*: CANADA: 2 males, 2 females (N.W.T., Yellow Knife, 26 April 1968). **USNM:** 3 specimens (paratypes of *G. lagopi greenlandicus*) ex *Lagopus sp*: GREENLAND: 1 male, 2 females (Jensen Id., Melville Bay, July 23, 1934, Coll: H. Lance, Det. M. A. Carriker, Jr.).

***G. columbianus*** Carriker 1945

**20 specimens (10 males, 10 females): BMNH:** 2 specimens (paratypes) ex *Colinus leucopogon decorates*: COLOMBIA: 1 male, 1 female (Codazzi, Dept. Magdalena, Mar. 12 1942, Det. Carriker, Host: 2045; Meinertzhagen Coll. #17674). 2 specimens (paratypes) ex *Colinus cristatus leucotis*: COLOMBIA: 1 male, 1 female (Codazzi, Dept. Magdalena, Mar.12, 1942, Det. Carriker, Host: 2045, Hopkins Collection). **OSEC:** 2 specimens (paratypes) ex *Colinus leucopogon decorates*: COLOMBIA: 1 male, 1 female (Codazzi, Dept. Magdalena, Mar.12, 1942, Det. Carriker, K. C. Emerson Collection: Paratype slide: 334). 2 specimens ex *Colinus cristatus leucotis*: COLOMBIA: 1 male, 1 female (La Plata Huila, IV-10-52, Det. Carriker, K. C. Emerson Collection: OK 3826, Host: 22279). **USNM:** 1 specimen (paratype) ex *Colinus cristatus decorates:* COLOMBIA: 1 female (Codazzi, Dept. Magdalena, xii-22-1946, Coll: M. A. Carriker, Jr., Det. M. A. Carriker, Jr., Host: 9199). 1 specimen ex *Colinus cristatus*: COLOMBIA: 1 male (Atanquez, Magdalena, May 27/45, Coll: M. A. Carriker, Jr., Det. M. A. Carriker, Jr., Host: 6082). 7 specimens ex *Colinus cristatus littoralis*: COLOMBIA: 4 males, 3 females (Mamatoco, Magdelena, 12/18-45, Coll: M. A. Carriker, Jr., Det. M. A. Carriker, Jr., Host: 7234-5). 2 specimens ex *Colinus cristatus leucotis*: COLOMBIA: 1 male, 1 female (Santana Santanders, Coll: M. A. Carriker, Jr., Det. M. A. Carriker, Jr., Host: 16573). 1 specimen ex *Colinus leucopogon decorates*: COLOMBIA: 1 female (Casacora, Dept. Magdalena, May 18, 1942, Coll: M. A. Carriker, Jr., Det. Carriker, Host: 2739).

***G. leucurus*** Emerson, 1952

**25 specimens (9 males, 16 females): FMNH:** 1 specimen ex White-tailed Ptarmigan: USA: 1 female (Anchorage, Alaska, March 25, 1961, Det. K. C. Emerson). **OSEC:** 2 specimens ex *Lagopus leucurus*: USA: 1

male, 1 female (Silver Plume, Colo., Sept. 10-1963, Coll: J. T. Polhemus, Det. K. C. Emerson). 5 specimens (paratypes) ex *Lagopus leucurus*: USA: 1 male, 4 females (Willow Creek, Talkeetna Mts., Alaska, Aug. 22-1950, Coll: R. B. Williams, Det. K. C. Emerson, Host: Lot 50-11773, KCE Paratypes #64, 65). 2 specimens ex *Lagopus leucurus*: USA: 1 male, 1 female (Juneau, Alaska, 28-Aug-1963, Det. K. C. Emerson, OK 1839(4)). 2 specimens ex *Lagopus leucurus*: CANADA: 1 male, 1 female (George Creek, Alberta, 1956, Coll: D. A. Boaq, Det. K. C. Emerson, OK 1830(5)). 2 specimens ex *Lagopus leucurus*: USA: 1 male, 1 female (Silver Plume, Colo., Sept. 10-1963, Coll: J. T. Polhemus, Det. K. C. Emerson, OK 1833(6)). **USNM:** 3 specimens ex *Lagopus leucurus*: USA: 2 males, 1 female (Silver Plume, Colo., Sept. 10-1963, Coll: J. T. Polhemus). 2 specimens ex *Lagopus leucurus*: CANADA: 2 females (George Creek, Alberta, 1956, Coll: D. A. Boaq, Det. K. C. Emerson). 1 specimen ex *Lagopus leucurus*: CANADA: 1 female (George Creek, Alberta, 1956 19 X, Host: BYV-654). 5 specimens (paratypes) ex *Lagopus leucurus*: USA: 2 males, 3 females (Willow Creek, Talkeetna Mts., Alaska, Aug. 22-1950, Coll: R. B. Williams, Det. K. C. Emerson, Host: Host #263; Lot 50-11773; USNM Type # 61191).

***G. corpulentus*** Kellogg & Mann, 1912

**20 specimens (10 males, 10 females): OSEC:** 4 specimens ex *Canachites canadensis*: USA: 2 males, 2 females (Dillingham, Alaska, 21 July 1964, Coll: L. Ellison, Det. K. C. Emerson, OK 1796, Host: SG 48-64). 2 specimens ex *Canachites canadensis*: USA: 1 male, 1 female (Sterling, Alaska, 11 July, 1965, Coll: L. Ellison, Det. K. C. Emerson, Host: SG 24-65). **SMPM:** 4 specimens ex *Canachites canadensis*: CANADA: 2 males, 2 females (Thunder Bay Co., Ontario, 10 Oct., 1966, Coll: J. Wieb). **USNM:** 2 specimens ex *Canachites canadensis*: USA: 2 males (Plot 3, Delta Creek, Alaska, 12-xi-67, Host: 03121167 cat# 8698). 3 specimens ex *Canachites canadensis*: USA: 2 males, 1 female (Dillingham, Alaska, 21 July 1964, Coll: L. Ellison, Host: SG 48-64). 4 specimens ex *Canachites canadensis*: USA: 1 male, 3 females (Homer, Alaska, 26 Oct. 1963, Coll: L. Ellison, Host: SG 79-63). 1 specimen ex *Canachites canadensis*: CANADA: 1 female (Knob Lake, Quebec, Sept. 30-1953, Coll: Francis Harper, Host: F.H. 1435; Lot 54-895).

***G. merriamanus*** Packard, 1873

**20 specimens (10 males, 10 females): OSEC:** 2 specimens ex *Dendragapus obscurus richardsonii*: CANADA: 1 male, 1 female (George Creek, Alberta, 1956, Coll: D. A. Boaq, Det. K. C. Emerson, OK 1774). 3 specimens (neoparatypes) ex Grouse: USA: 2 males, 1 female

(Missoula Co., Mont., 8-8-1923, Coll. Rich, A.P. #2348, #3269, Det. K. C. Emerson, KCE: 55, 59). 4 specimens (neoparatypes) ex Grouse: USA: 1 male, 3 females (Ravalli Co., Mont., 4-10-1923, Coll: Rich; A.P. #2348, Det. K. C. Emerson, KCE: 56, 57, 58, 60). 2 specimens ex *Dendragapus obscurus*: USA: 1 male, 1 female (Ravalli Co., Mont., Sept.25.1949, Coll: W. L. Jellison, Det. K. C. Emerson, OK 1777 (11), OK 1781(4)). 1 specimen (paratype) ex Ruffed Grouse: USA: 1 female (Newton Ranch Springs, Colorado, 9-3-31, Det. K. C. Emerson, KCE 52, Host: No. 7155A). **USNM:** 2 specimens ex *Dendragapus obscurus richardsonii*: CANADA: 1 male, 1 female (George Creek, Alberta, 1956, Coll: D. A. Boaq). 6 specimens ex Blue grouse: USA: 4 males, 2 females (Ravalli Co., Mont., 9-26-1949, Coll: Jellison; A.P. 26941).

***G. ithaginis*** Clay, 1940

**20 specimens (10 males, 10 females): FMNH:** 2 specimens ex Blood Pheasant: NEPAL: 1 male, 1 female (Uring Ghang, Nuwakot Dist., 3 Sept. 1968, Host: NP-1158). **OSEC:** 2 specimens ex *Ithaginis cruentus*: NEPAL: 1 male, 1 female (Uring Ghang, Nuwakot Dist., 1 Sept. 1968, Det. K. C. Emerson, OK 3960, Host: NP-1142). 2 specimens ex *Ithaginis cruentus*: NEPAL: 1 male, 1 female (Gatlang, Rasuwa Dist., 29 April, 1968, Det. K. C. Emerson, OK 3963(1), Host: #15014). 2 specimens ex *Ithaginis cruentus*: NEPAL: 1 male, 1 female (Sankhuwa Sabha District, East Nepal, 26 July 1973, Det. K. C. Emerson, OK 12570(2), Host: HE 0608C). **SMPM:** 2 specimens ex *Ithaginis cruentus*: NEPAL: 1 male, 1 female (Sankhuwa Sabha District, East Nepal, 14 July 1973, Host: HE 0828). 2 specimens ex Blood Pheasant: NEPAL: 1 male, 1 female (Uring Ghang, Nuwakot Dist., 6 Sept. 1968, Host: NP-1181). **USNM:** 4 specimens ex *Ithaginis c. cruentus*: INDIA: 1 male, 3 females (Sikkim, Dec. 1925, Coll: Meinertzhagen, Det. Clay, Host: Female 3751). 1 specimen ex Blood Pheasant: NEPAL: 1 male (Uring Ghang, Nuwakot Dist., 3 Sept. 1968, Host: NP-1158). 1 specimen ex *Ithaginis cruentus*: NEPAL: 1 male (Sankhuwa Sabha District, East Nepal, 30 July 1973, Host: HE 0612C). 2 specimens ex *Ithaginis cruentus*: NEPAL: 1 male, 1 female (Sankhuwa Sabha District, East Nepal, 21 July 1973, Host: HE 0601C).

***G. chrysolophi*** Clay, 1940

**20 specimens (10 males, 10 females): OSEC:** 10 specimens ex Indian pheasant: USA: 5 males, 5 females (Kipu Kauai, Hawaii, 15 July 1978, Coll: Haas, Det. K. C. Emerson, OK 17268, OK 17269, OK 17270, OK 17271, OK 17272). **USNM:** 10 specimens ex Indian pheasant: USA: 5

males, 5 females (Kipu Kauai, Hawaii, 15 July 1978, Coll: Haas, Det. K. C. Emerson).

***G. dissimilis*** Denny, 1842

**21 specimens (10 males, 11 females): FMNH:** 2 specimens ex *Gallus g. gallus*: THAILAND: 1 male, 1 female (Nakhon Phanom, Nakae Kanluang, Kho Mt., 25 July 1954, Coll: Elbel, Det. Robert. E. Elbel, Host: B30927, RE 3924). 2 specimens ex *Gallus g. gallus*: SIAM: 1 male, 1 female (Nakhon Phanom, Nakae Kanluang, Kho Mt., Coll: Elbel-Boonsong, Det. K.C. Emerson, Host: B30927; RE 3924). **OSEC:** 2 specimens ex *Gallus gallus spadiceus*: THAILAND: 2 females (Phu Lam Lo Mt., Koksathon, Dansai, Loei, 30-Mar-54, Coll: R.E. Elbel & B. Lekaqul, Det. K. C. Emerson, OK B-22723, Host: RE. 3533). 2 specimens ex *Gallus lafayetii*: CEYLON: 1male, 1 female (Ceylon, Det. K.C. Emerson, OK: 3901(5), 3908(1)). 2 specimens ex *Gallus sonneratii*: INDIA: 1 male, 1 female (India, Det. K.C. Emerson, OK 3910 (6)). 3 specimens ex *Gallus gallus spadiceus*: THAILAND: 2 males, 1 female (Loei, Dansai, Koksathon Ban Nam Yen, Phak Khi Nak Mt., 14 Mar. 1955, Coll: R. E. Elbel, Det. K.C. Emerson, Host: RE 4926). **SMPM:** 1 specimen ex Chicken (domestic): FORMOSA: 1 male (Hsin Hua Tai-nan Hsien, 18-1-61, Host: 14032, 14034). 2 specimens ex *Gallus gallus murghi*: NEPAL: 1 male, 1 female (Madhu-ban, Bara District, 6 Jan. 1968, Host: NP-295). 1 specimen ex *Gallus gallus*: CUBA: 1 female (Habana, Coll: I. Perez Viqueras, Det. R. D. Price (1962)). **USNM:** 2 specimens ex *Gallus g. gallus*: MALAYSIA: 1 male, 1 female (Malaya, Sungei Buloh, 9 May 1956, Det. KCE, Host: R-45282). 2 specimens ex *Gallus g. gallus*: THAILAND: 1 male, 1 female (Nakhon Phanom, Nakae Kanluang, Kho Mt., 25 July 1954, Coll: Elbel-Boonsong, Det. K.C. Emerson, Host: B30927; RE 3924).

***G. cervinicornis*** Giebel, 1874

**27 specimens (10 males, 17 females): OSEC:** 12 specimens ex *Lophura nycthemera jonesi*: THAILAND: 6 males, 6 females (Loei, Dansai, Koksathon Ban Nam Yen, Phak Khi Nak Mt., 15 Mar. 1955, Coll: R.E. Elbel, Det. K. C. Emerson, OK 3825, Host: RE 4941). 3 specimens ex *Lophura nycthemera*: THAILAND: 2 males, 1 female (Petchabune Thung-Salung luang, 27 Nov. 67, Det. K. C. Emerson, OK: 10700(1), 10698(5), 10699(4), Host: S. No. XIE-815). 4 specimens ex *Gennasus nycthemerus rufipes*: NEPAL: 2 males, 2 females (Namkham, 75 miles N of Lashia, 4.ii.1945, Coll: H. S. Fuller, Det. K. C. Emerson, OK: 3821(7), 3820(2), 3822(3), 3823(6), Host: B.M. 1947-321 (137). **USNM:** 1 specimen ex *Gennasus nycthemerus rufipes*: NEPAL: 1 female

(Namkham, 75 miles N of Lashia, 4.ii.1945, Coll: H. S. Fuller, Host: B.M. 1947-321 (137)). 7 specimens ex *Lophura nycthemera jonesi*: THAILAND: 7 females (Loei, Dansai, Koksathon Ban Nam Yen, Phak Khi Nak Mt., 15 Mar. 1955, Coll: R.E. Elbel, Host: RE 4941).

***G. sinensis*** Emerson & Stojanovich, 1964

**16 specimens (8 males, 8 females): OSEC:** 4 specimens (paratypes) ex *Syrmaticus mikado*: FORMOSA: 2 males, 2 females (Formosa, 1 Feb. 1962, Det. K. C. Emerson, OK #647(4), OK #649(2), Host: PF-10939). 4 specimens (paratypes) ex *Syrmaticus mikado*: FORMOSA: 2 males, 2 females (Formosa, Wa-sheh, 31 Oct. 1961, Det. K. C. Emerson, OK #650(1), OK # 648(3), Host: PF-12432). **USNM:** 8 specimens (paratypes) ex *Syrmaticus mikado*: FORMOSA: 4 males, 4 females (Formosa, 1 Feb. 1962, Det. K. C. Emerson, Host: PF-10939).

***G. assimilis*** Piaget, 1880

**30 specimens (15 males, 15 females): BMNH:** 4 specimens ex *Francolinus clappertoni gedgei*: KENYA/UGANDA: 2 males, 2 females (Mt. Elgon, May 1908, Coll: Meinertzhagen, Host: Male 3573). 2 specimens ex *Francolinus coqui*: BENCHUANALAND: 1 male, 1 female (Bechuanaland, 19.vii.1956, Host: Brit. Mus. 1957-219). 2 specimens ex *Pternistis swainsoni*: SOUTH RHODESIA: 1 male, 1 female (Bulawayo, 7.xi.1972, Coll: S. Irwin, Host: Brit. Mus. 1973-39). 2 specimens ex *Francolinus ahantensis*: GHANA: 1 male, 1 female (29.iv.1963, Coll: F. R. Allison, Det. T. Clay, Host: Brit. Mus. 1963-341). 2 specimens ex *Francolinus sephaena*: SOUTH AFRICA: 1 male, 1 female (Nr. Newington, E. Transvaal, 19.vii.1957, Coll: F. Zumpt, Host: (47) Brit. Mus. 1958-76). 2 specimens ex *Francolinus bicalcaratus*: CAMEROUN: 2 females (Yaounde, 1955, Coll: J. Mouchet). 2 specimens ex *Ptilopachus p. petrosus*: GUINEA-BISSAU: 1 male, 1 female (Portuguese Guinea, May 1897, Coll: Meinertzhagen, Host: Female 3614). **FMNH:** 2 specimens ex *Francolinus coqui*: BECHUANALAND: 1 male, 1 female (Bebeete, 19.vii.1956, Host: (35)). **OSEC:** 4 specimens ex *Francolinus e. erckelii*: ETHIOPIA: 2 males, 2 females (Ethiopia, K. C. Emerson Collection). 1 specimen ex *Francolinus squamatus tetraoninus*: ETHIOPIA: 1 female (Ethiopia, K. C. Emerson Collection OK 3791). 4 specimens ex *Francolinus c. castaneicollis*: ETHIOPIA: 2 males, 2 females (Ethiopia, K. C. Emerson Collection). 3 specimens ex *Pternistis l. leucoscepus*: ETHIOPIA: 3 males (Ethiopia, K. C. Emerson Collection).

***G. antennatus*** Clay, 1940

**15 specimens (6 males, 9 females): BMNH:** 2 specimens ex *Pternistis leucoscepus infuscatus*: KENYA: 1 male, 1 female (Isiolo, Jan. 1955, Coll: Meinertzhagen, Det. Clay, Host: 20464). 11 specimens ex *Pternistis l. leucoscepus*: SOMALILAND: 4 males, 7 females (Somaliland, Feb. 1949, Coll: Meinertzhagen, Det. Lyal, Host: 18724). **OSEC:** 2 specimens ex *Pternistis leucoscepus infuscatus*: EAST AFRICA: 1 male, 1 female (Kenya Colony, Det. K. C. Emerson, OK 3786).

***G. dispar*** Burmeister, 1838

**33 specimens (14 males, 19 females): BMNH:** 5 specimens ex *Perdix hodgsiniae caragenae*: PAKISTAN/INDIA: 5 females (Ladak, June 1925, Coll: Meinertzhagen, Det. MJM 07, Host: Male 3650). 2 specimens ex *Alectoris g. graeca*: YUGOSLAVIA: 1 male, 1 female (Jugoslavia, Makedonija, 5.1.1956, Host: Brit. Mus. 1958-661). 2 specimens ex *Perdix perdix*: USA: 1 male, 1 female (Lincoln, 21.x.1963, Eskgrove Lab., Host: Brit. Mus. 1964-102). 6 specimens ex *Pternistis afer humboldii*: ZIMBABWE: 2 males, 4 females (Zambesi (Zoo), June 1937, Coll: Meinertzhagen, Host: Male 8342; Lice: [Stragglers]). **FMNH:** 2 specimens ex *Perdix p. perdix*: CANADA: 2 males (Vancouver, B. C., 1932, Det. K. C. Emerson). 1 specimen ex Chuckar: USA: 1 female (Ithaca, N.Y., Mar. 26. 1952, Coll: Dickerman, Det. K. C. Emerson). **INHS:** 1 specimen ex Hungarian Partridge: USA: 1 male (Yountville, Calif., 1949). **OSEC:** 2 specimens ex *Alectoris graeca chukar*: NEPAL: 1 male, 1 female (Geling, Mustang Dist., 22 May 1970, Det. K. C. Emerson, OK 3886, Host: NP-3953). 2 specimens ex *Perdix perdix*: USA: 1 male, 1 female (Timpie, Tooele Co., Utah, 16 Apr 1965, Coll: R.E. Elbel, Det. K. C. Emerson, Host: E&E Bir). 1 specimen ex *Alectoris graeca chukar*: NEPAL: 1 male (Himalayas, K. C. Emerson Collection 2202). 1 specimen ex *Alectoris graeca saxatilis*: GERMANY: 1 female (Germany, K. C. Emerson Collection, OK 2200(2)). **SMPM:** 2 specimens ex *Perdix perdix*: USA: 1 male, 1 female (Timpie, Tooele Co., Utah, 16 Apr 1965, Coll: R.E. Elbel, Det. R. D. Price). 2 specimens ex *Perdix p. perdix*: SWEDEN: 1 male, 1 female (Tynaberga, 7.3.1955, Host: 146). **USNM:** 2 specimens ex *Alectoris graeca chukar*: NEPAL: 1 male, 1 female (Geling, Mustang Dist., 22 May 1970, Host: NP-3953). 2 specimens ex *Alectoris rufa hisponica*: SPAIN: 1 male, 1 female (Salamanca, 1-iv-49, Coll: KCE - from skin).

***G. securiger*** Nitzsch, 1866

**20 specimens (10 males, 10 females): BMNH:** 13 specimens ex *Alectoris b. barbara*: MOROCCO: 6 males, 7 females (Morocco, Coll: Meinertzhagen, Host: 121-85). **OSEC:** 4 specimens ex *Alectoris barbara koenigi*: CANARY ISLANDS: 1 male, 3 females (Tenerife, Det. K. C. Emerson, OK 4006, 4009). 2 specimens ex *Alectoris barbara spatyi*:

TUNISIA: 2 males (Tunisia, Det. K. C. Emerson). **USNM:** 1 specimen ex *Alectoris barbara koenigi*: CANARY ISLANDS: 1 male (Tenerife, Det. K. C. Emerson).

***G. ortygis*** Denny, 1842

**38 specimens (18 males, 20 females): BMNH:** 2 specimens ex *Colinus virginianus*: USA: 1 male, 1 female (Stillwater, Oklahoma, xii-1948, Det. K. C. Emerson, Hopkins Collection). 2 specimens ex *Colinus virginianus*: USA: 1 male, 1 female (Tall Timbers Res. St., Leon Co. Fla., x.1968, Det. F. E. Kellogg, Host: TT10-68-137; Brit. Mus. 1969-408). 3 specimens ex *Colinus virginianus*: USA: 2 males, 1 female (Washington, D.C., 1889, Coll: Meinertzhagen, Host: Male 3243). **INHS:** 6 specimens ex Bobwhite: USA: 3 males, 3 females (Oliver, Ill., July 23, 1932, Coll: Dozier + Park, Det. Malcomson (1936)). **OSEC:** 2 specimens ex *Colinus virginianus*: USA: 1 male, 1 female (Raleigh, N.C., 18 Feb. 1897, Coll: C. S. Brimley, Det. K. C. Emerson, OK 2045). 2 specimens ex *Colinus virginianus*: USA: 1 male, 1 female (State College, Miss., 24 Dec. 1935, Coll: R. L. Bowen, Det. K. C. Emerson, OK 2054). 2 specimens ex *Colinus virginianus*: USA: 1 male, 1 female (Raleigh, N.C., 18 Feb. 1897, Coll: C. S. Brimley, Det. K. C. Emerson, OK 2046(3)). 2 specimens ex *Colinus virginianus*: USA: 1 male, 1 female (State College, Miss., 14 Dec 1935, Coll: R. L. Bowen, Det. K. C. Emerson, OK 2052(4)). 1 specimen ex Bobwhite quail: USA: 1 female (Greenleaf Lake, Muskogee Co., OK, Aug. 11, 1967, Coll: C.W.J. Det. D. C. Arnold). **SMPM:** 5 specimens ex *Colinus virginianus*: USA: 3 males, 2 females (Ames, Iowa, 15 Mar 1935, Coll: F. Hamerstrom, Det. R. D. Price (1961), Host: Aut. #4546; Louse: V-3360). 1 specimen ex Bobwhite quail: USA: 1 male (Jackson, S. Carolina, 30 April 1959, Coll: H. W. Kale). **USNM:** 10 specimens ex Mexican quail: USA: 13 males, 7 females (Columbus, Ohio, 1932, Coll: J. S. Hine (3-15-17), Host: Bish. #7228; U. S. Bur. Entomology (CNS)).

***G. tibetanus*** (Eichler, 1950)

**21 specimens (11 males, 10 females): OSEC:** 10 specimens ex *Tetraogallus tibetanus aquilonifer*: NEPAL: 5 males, 5 females (E. Nepal, Sankhuwa Sabha Dist., 10 Aug. 1973, Det. K. C. Emerson, OK: 12967(6), 12968, 12970(4), 12971, 12972, Host: HE 0743C). 1 specimen ex *Tetraogallus tibetanus*: NEPAL: 1 male (Himalayas, Oct 1888, Det. K. C. Emerson, OK 4024(1)). **USNM:** 10 specimens ex *Tetraogallus tibetanus aquilonifer* NEPAL: 5 males, 5 females (E. Nepal, Sankhuwa Sabha Dist., 10 Aug. 1973, Host: HE 0743C).

*G. ammoperdix* Clay, 1940

**30 specimens (15 males, 15 females): BMNH:** 3 specimens (paratypes) ex *Ammoperdix g. griseogularis*: PAKISTAN: 3 females (Peshawur, iii-1937, Coll: Meinertzhagen, Det. Clay, Host: 9475). 2 specimens ex *Ammoperdix heyi*: ISRAEL: 1 male, 1 female (Ein-Gedi, 24.iv.1959, Host: 738; Brit. Mus. 1959-405). 20 specimens (paratypes) ex *Ammoperdix g. griseogularis*: AFGHANISTAN: 11 males, 9 females (Afghanistan, May 1937, Coll: Meinertzhagen, Det. Clay, Host: 10243, 10266). **OSEC:** 4 specimens ex *Ammoperdix g. griseogularis*: AFGHANISTAN: 2 males, 2 females (Laghman, E. Afghanistan, 10.2.1968, Coll: Klockenhoff, Det. Klockenhoff, OK 18270, "compared with types", Host: 701). 1 specimen ex *Ammoperdix h. heyi*: PALENSTINE: 1 male (Palestine, Det. K. C. Emerson, OK 3784 (2)).

*G. retractus* Le Souëf, 1902

**9 specimens (4 males, 5 females): BMNH:** 2 specimens ex *Synoicus australis*: AUSTRALIA: 1 male, 1 female (Greens Beach, Tasmania, 28.8.1961, Coll: R. H. Green, Host: Brit. Mus. 1962-186). 2 specimens ex *Synoicus australis*: AUSTRALIA: 1 male, 1 female (Nr. Bridport, Tasmania, 5.vii.1962, Coll: B. C. Mollison, Det. T. Clay, Host: Brit. Mus. 1963-147). **OSEC:** 1 specimen ex *Synoicus ypsilophorus*: NEW GUINEA: 1 female (Western Highlands, Korgua, 24-Jun-63, Coll: H. Clissold, Det. K. C. Emerson, OK 21619, Host: BBM-NG 28201). 1 specimen ex *Synoicus ypsilophorus*: NEW GUINEA: 1 male (Western Highlands, Mur Mur, 14-Jun-63, Coll: H. Clissold, Det. K. C. Emerson, OK 21594, Host: BBM-NG 28113). 1 specimen ex *Synoicus ypsilophorus raalteni*: TIMOR: 1 male (Timor, Dec. 1904, Coll: Meinertzhagen, Det. K. C. Emerson, OK 4002(2), Host: Female 3616). 2 specimens ex *Synoicus* australis: AUSTRALIA: 2 females (Kingston, Tasmania, 30.I.1962, Coll: B. C. Mollison, Det. K. C. Emerson).

*G. soueefi* Clay, 1940

**8 specimens (2 males, 6 females): BMNH:** 1 specimen ex *Coturnix ussuriensis*: RUSSIA: 1 male (Ussutii, Chabarowsk, Eisenbahn, 25.ix.11, Coll: E. Borsow, Det. MJM 09, Host: 1912-373, Pres. by Hon. N. C. R.). 1 specimen ex *Coturnix coromandelica*: NO LOCATION: 1 female (Cambridge Museum, L. Harrison, Mallophaga Collection, Det. MJM 09, BM.1934-570). **OSEC:** 1 specimen ex *Coturnix chinensis*: PHILIPINES: 1 female (Philippine Islands, Dalton Pass, Nueva Vigcaya, 16.08N 120.55E, 24-Feb-68, Coll: GL Alcasid, Det. K. C. Emerson, Host: 8E 1364). 1 specimen ex *Coturnix chinensis*: PHILIPINES: 1 female (Philippine Islands, Dalton Pass, Nueva Vigcaya, 16.08N 120.22E, 24-

Jan-68, Coll: GL Alcasid, Det. K. C. Emerson, OK 21196, Host: 8E 1387). 3 specimens ex *Coturnix chinensis*: PHILIPINES: 3 females (Philippine Islands, Dalton Pass, Luzon, 6 Jan. 1967, Det. K. C. Emerson, OK 17288(1), OK 17245(2), OK 17244, Host: 7E-0159). **USNM:** 1 specimen ex *Excalfactoria chinensis*: MALAYSIA: 1 male (Malaya, Selangor, Kuala Lumpur, Apr. 14.1948, Coll: R. Traub & C. Philip, Det. E.W.S., Host: RT-8024; Lot 48-19015).

***G. biordinatus*** Clay, 1940

**26 specimens (13 males, 13 females): OSEC:** 2 specimens ex *Megapodius freycinet*: PAPUA NEW GUINEA: 1 male, 1 female (Papua, Jumbora, 22 Sept. 1963, Coll: H. Clissold, Det. K. C. Emerson, Host: BBM-NG 28842). 2 specimens ex *Megapodius* freycinet: PAPUA NEW GUINEA: 1 male, 1 female (New Guinea, Ambunti, 10 May 1963, Coll: P. Temple, Det. K. C. Emerson, OK 3780(1), Host: BBM-NG 22579). 2 specimens ex *Megapodius freycinet*: MALAYSIA: 1 male, 1 female (Meugalvus Isl., Sabah. East Malaysia, 2 June 1983, Coll. M. A. Marin, Det. K. C. Emerson, OK 21762(3)). 3 specimens ex *Megapodius freycinet*: INDONESIA: 2 males, 1 female (Halmahera Isl., 20 Sept. 1981, Coll: Paul M. Taylor, K. C. Emerson, OK 21807(5), OK 21806(7), OK 21808(4)). 1 specimen ex *Megapodius freycinet*: INDONESIA: 1 female (Halmahera Isl., 30 Sept. 1981, Coll: Paul M. Taylor, K. C. Emerson Collection, Host: A 1541). **USNM:** 4 specimens ex *Megapodius freycinet*: INDONESIA: 2 males, 2 females (Halmahera Isl., 20 Sept. 1981, Coll: Paul M. Taylor, Det. K. C. Emerson). 1 specimen ex *Megapodius laperousi senax*: PALAU: 1 male (Palau, 3-8.xi.1931, Coll: W. F. Coultas, Det. R. A. Ward, Host: AMNH 331877). 1 specimen ex *Megapodius freycinet*: INDONESIA: 1 male (Halmahera Isl., 28 April 1981, Coll: Paul M. Taylor, Det. K. C. Emerson, Host: A-623). 3 specimens ex Bush Fowl: PAPUA NEW GUINEA: 1 male, 2 female (Papau?, New Britain, Gaulim, 27 Oct. 1962, Coll: H. Clissold, Host: B-63916). 1 specimen ex *Megapodius freycinet cumingii*: PHILIPINES: 1 female (Philippine Islands, Canigaran, Pureto, Princesa, Palawan, 12-iv-1947, Det. K. C. Emerson). 6 specimens ex *Megapodius freycinet*: NO LOCATION: 3 males, 3 females (Det. MJM 09, Host: BBM-NG 21619).

***G. major*** (Piaget, 1880)

**20 specimens (10 males, 10 females): FMNH:** 2 specimens ex Bush Fowl: PAPUA NEW GUINEA: 2 males (Papua, New Britian, Gaulim, 27 Oct. 1962, Coll: H. Clissold, Det. K.C. Emerson, Host: B-63916). 3 specimens ex *Megapodius l. laperousi*: ASUCION: 3 males (Asucion Isl., 6.II.1909, Det. R. A. Ward, Host: (Male) AMNH 539274; Skin). 1

specimen ex *Megapodius freycinet*: SOLOMON ISLANDS: 1 female (Guadalcanal, Espéranue, July 18-1945, Coll: AJ. Nicholson, Host: Lot 45-19132). 1 specimen ex *Megapodius freycinet*: INDONESIA: 1 female (Halmahera Isl., 20 Sept 1981, Coll: Paul M. Taylor, K.C. Emerson Collection). **OSEC:** 2 specimens ex *Megapodius freycinet*: PAPUA NEW GUINEA: 1 male, 1 female (Papua, Buka Bara, 21 Sept. 1963, Coll: P. Shanahan, Det. K. C. Emerson, OK 3782, Host: BBM-NG 28811). 4 specimens ex *Megapodius f. freycinet*: INDONESIA: 1 male, 3 females (Halmahera Isl., 30 Sept 1981, Coll: Paul M. Taylor, Det: K.C. Emerson, OK 21907 (8)). 2 specimens ex *Megapodius nicobariensis sanghirensis*: INDONESIA: 2 females (Sangi Isl., Det. K.C. Emerson, OK 3967(3)). 2 specimens ex *Megapodius freycinet*: PAPUA NEW GUINEA: 1 male, 1 female (Papua, Cape Kileton, 17 Oct. 1963, Coll: H. Clissold, Det. K.C. Emerson, OK 3970(5), Host: BBM-NG 29236). 1 specimen ex *Megapodius freycinet*: MALAYSIA: 1 male (Meugalvus Isl., Sabah, East Malaysia, 2 June 1983, Coll: M. A. Marin, Det. K.C. Emerson). 2 specimens ex *Megapodius affinis decollates*: NEW GUINEA: 1 male, 1 female (New Guinea, Det. K.C. Emerson, 3977 (10), OK 3978(7)). 1 specimen ex *Megapodius freycinet*: INDONESIA: 1 female (Halmahera Isl., 20 Sept 1981, Coll: Paul M. Taylor, Det. K.C. Emerson, OK 21796 (9)).

***G. fissus*** (Rudow, 1869)

**24 specimens (12 males, 12 females): BMNH:** 3 specimens ex *Alectura l. lathami*: AUSTRALIA: 1 male, 2 females (New South Wales, Host: RM (Meinertzhagen) 3069). **OSEC:** 2 specimens ex *Aepypodius arfakianus*: PAPUA NEW GUINEA: 1 male, 1 female (Papua Mt. Bosavi, S. Highlands Dist., 11 June 1973, Det. K. C. Emerson, Host: 103362). 8 specimens ex *Aepypodius arfakianus*: PAPUA NEW GUINEA: 4 males, 4 females (New Guinea, Mt. Missim, 6 Oct. 1962, Coll: H. Clissold, OK: 3940(5), 3941(4), 3942(3), 3943(2), Host: BBM-NG 20641). **USNM:** 1 specimen ex *Alectura lathami*: AUSTRALIA: 1 male (E. Australia, Coll: K. C. Emerson, from skin). 10 specimens ex *Aepypodius arfakianus*: PAPUA NEW GUINEA: 5 males, 5 females (New Guinea, Mt. Missim, 6 Oct. 1962, Coll: H. Clissold, Host: BBM-NG 20641).

***G. crassipes*** (Piaget, 1888)

**12 specimens (6 males, 6 females): OSEC:** 6 specimens ex *Aepypodius arfakianus*: NEW GUINEA: 3 males, 3 females (New Guinea, Mt. Missim, 6 Oct. 1962, Coll: H. Clissold, Det. K. C. Emerson, OK 3845, OK 3844(3), Host: BBM-NG 20641). 4 specimens ex *Alectura lathami*: AUSTRALIA: 2 males, 2 females (East Australia, Det. K. C. Emerson, OK 3850(4), OK 3849(5), OK 3852(6)). **USNM:** 2 specimens ex *Aepypodius arfakianus*: NEW GUINEA: 1 male, 1 female (New Guinea, Mt. Missim, 6 Oct. 1962, Coll: H. Clissold, Host: BBM-NG 20641).

***G. australis*** Emerson & Price 1986

**13 specimens (6 males, 7 females): OSEC:** 5 specimens (paratypes) ex *Leipoa ocellata*: AUSTRALIA: 1 male, 4 females (Renmark, S. Australia, 6 Jan 1984, Coll: David Booth, Det. Emerson & Price, Host: B-37829; Paratype #1747, 1749, 1750, 1754). 2 specimens (paratypes) ex *Leipoa ocellata*: AUSTRALIA: 1 male, 1 female (Remark, S. Australia, 23 Oct 1983, Coll: David Booth, Det. Emerson & Price, Paratype #1748, 1753). 1 specimen ex *Leipoa ocellata*: AUSTRALIA: 1 male (Murray Scrubs, S. Australia, early 1900's, Det. Emerson & Price, Host: B 8348). 1 specimen (paratype) ex *Leipoa ocellata*: AUSTRALIA: 1 male (Murray Scrubs, S. Australia, early 1900's, Det. Emerson & Price, Host: B 8348, Paratype #1751). **SMPM:** 2 specimens (paratypes) ex *Leipoa ocellata*: AUSTRALIA: 1 male, 1 female (Renmark, S. Australia, 6 Jan 1984, Coll: David Booth, Det. Emerson & Price, Host: B-37829). **USNM:** 2 specimens (paratypes) ex *Leipoa ocellata*: AUSTRALIA: 1 male, 1 female (Murray Scrubs, S. Australia, early 1900's, Det. Emerson & Price, Host: B 8348).

***Goniocotes* Burmeister, 1838**

***Gon. diplogonus*** Nitzsch, 1866

**8 specimens (4 males, 4 females): OSEC:** 8 specimens ex *Tragopan satyra*: NEPAL: 4 males, 4 females (Kaldapeh Slope, nr. Melumchi, 23 Nov. 1969, Det. K. C. Emerson, OK 10925, OK 10926Host: NP-3397).

***Gon. gallinae*** (De Geer, 1778)

**9 specimens (4 males, 5 females): OSEC:** 6 specimens ex Poultry: THAILAND: 3 males, 3 females (Khon kaen, Nov. 20-1963, K. C. Emerson Collection, OK 10937 OK 10935, Host: No. 46; Lot 64-11537). 2 specimens ex Hen: THAILAND: 1 male, 1 female (Nakhon Raichasima, Nov. 24-1963, K. C. Emerson Collection, Host: No. 65). 1 specimen ex Chicken: USA: 1 female (Stillwater, OK, Payne Co., Nov. 11, 1956, Det. D. C. Arnold, CMCP-9AB).

***Gon. haplogonus*** Nitzsch, 1866

**10 specimens (5 males, 5 females): OSEC:** 2 specimens ex *Lophophorus impeyanus*: NEPAL: 1 male, 1 female (Dhukphu, Sindu Palchok Dist., 10 August 1969, Det. K. C. Emerson, OK 10941, Host: NP-2976). 2 specimens ex *Lophophorus impeyanus*: NEPAL: 1 male, 1 female (Thodung, Jiri Ramechap Dist., 12 Oct. 1963, Det. K. C. Emerson, OK 10940, Host: NP-3301). 2 specimens ex *Lophophorus impejanus*: NEPAL: 1 male, 1 female (Langtang Valley, 13 May 1969, Det. K. C. Emerson, OK 10949, Host: NP-2556). 2 specimens ex *Lophophorus impejanus*: NEPAL: 1 male, 1 female (Langtang Valley, 12 May 1969, Det. K. C. Emerson, OK 10950, Host: NP-2540). **USNM:** 2 specimens ex *Lophophorus impeyanus*: NEPAL: 1 male, 1 female (Thodung, Jiri Ramechap Dist., 12 Oct. 1963, Host: NP-3301).

***Gon. pallidomaculatus*** Piaget, 1880

**9 specimens (3 males, 9 females): OSEC:** 2 specimens ex *Arborophila rufogularis*: THAILAND: 1 male, 1 female (Doi Pha Hom Pok, Cheingmai, 5 Nov. 1965, Det. K. C. Emerson, OK 20053, Host: MAPS 1877). 2 specimens ex *Arborophila brunneopectus erythrophrys*: BORNEO: 1 male, 1 female (N. Borneo, Jrus Madi Mt., Pampang Ulu Kaingarak, 19 July 1963, Coll: US Army-Brit. Col. Off. Med. Res. Unit, Det. K. C. Emerson, Host: R40009; RT-8-19606). 2 specimens ex *Arborophila brunneopectus brunneopectus*: SIAM: 1 male, 1 female (Loei, Dansai, Koksathon Banmaed, 24 Mar 1954, Coll: Elbel, Det. K. C. Emerson, Host: RE 3462; RT B-22703). 1 specimen ex *Arborophila orientalis sumatrana*: SUMATRA: 1 female (Sumatra, K. C. Emerson Collection, OK 20058). 1 specimen ex *Arborophila brunneopectus erythrophrys*: BORNEO: 1 female (N. Borneo, 19 July 1953, Det. K. C. Emerson, OK 10978, Host: RT B-19709). 1 specimen ex *Arborophila javanica*: INDONESIA: 1 female (Indonesia, Tjibodas Gn. Gede, W. Java, 17 Dec 1970, Det. K. C. Emerson, Host: XIE 171, 070-21535).

***Gon. parviceps*** (Piaget, 1880)

**10 specimens (5 males, 5 females): OSEC:** 2 specimens ex *Pavo muticus imperator*: SIAM: 1 male, 1 female (PhuKho Mt. Kanluang Nakae, Nakhon Phanom, Coll. Elbel, K. C. Emerson, Host: B30924, RE 3912). 6 specimens ex *Pavo muticus*: THAILAND: 3 males, 3 females (Nansa, Ban Phahang, 8 Dec. 1961, Coll: Mr. Kittithonglongya, Det. K. C. Emerson, Host: V139). 2 specimens ex *Pavo imperator*: SIAM: 1 male, 1 female (Kho Mt., Nakhon Phanom, Nakae Kanluang, 11 July 1954, Det. K. C. Emerson, OK 2400).

***Gon. reticulatus*** Kéler, 1939

**4 specimens (2 males, 2 females): OSEC:** 2 specimens ex *Lophura leucomelana*: THAILAND: 1 male, 1 female (Khao Soi Dao Tai, Chanthaburi, 3 Mar. 1966, Det. K. C. Emerson, Host: MAPS 2322). 2 specimens ex *Lophura leucomelana*: THAILAND: 1 male, 1 female (Khao Soi Dao Tai, Chanthaburi, 18 Mar. 1966, Det. K. C. Emerson, Host: Maps 2347).

**OUTGROUP:**

***Physconelloides*** Ewing, 1927

***P. montana*** Carriker 1961

**10 specimens (5 males, 5 females): SMPM:** 5 specimens ex *Geotrygon montana*: PERU: 2 males, 3 females (Dept. Madre de Dios, Cerro de Pantiacolla, 17 Nov 1985, Coll: DH Clayton, Host: 1127). 1 specimen ex *Geotrygon montana*: PERU: 1 male (Dept. Cuzco, 20km NW Pilcopata, 21 Dec 1985, Coll: DH Clayton, Host: B66#). 4 specimens ex *Geotrygon montana*: PERU: 2 males, 2 females (Dept. Madre de Dios, Cerro de Pantiacolla, 1030m above Rio Palotoz, 29 Aug 1985, Coll: DH Clayton).

***Campanulotes*** Kéler, 1939

***C. bidentatus*** (Scopoli, 1763)

**11 specimens (6 males, 5 females): BMNH:** 11 specimens ex Domestic pigeon: CUBA: 6 males, 5 females (Boqueran, 8-19-30, Coll: H. S. Peters, Host: Bish#15300; 1234; A.G.).

***Heptapogaster*** Carriker, 1936

***H. temporalis*** Carriker, 1936

**13 specimens (6 males, 7 females): BMNH:** 13 specimens ex *Crypturellus cinereus*: BRAZIL: 6 males, 7 females (Brasil, Rondonia, Cachoeira, Nazare, W. Bank Rio Jiparana, 5 Nov 1986, Coll: T Peterson, Host: DFS, 86-1266).

**Table 2.7.** Data Matrix: Characters 1-14

| Character | 001 | 002 | 003 | 004 | 005 | 006 | 007 | 008 | 009 | 010 | 011 | 012 | 013 | 014 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 1. *Goniodes pavonis* | 2 | 1 | 1 | 1 | 1 | 3 | 3 | 2 | 2 | 2 | 1 | 1 | 1 | 2 |
| 2. *G. curvicornis* | 2 | 2 | 3 | 1 | 3 | 3 | 3 | 1 | 1 | 2 | 2 | 1 | 1 | 2 |
| 3. *G. spinicornis* | 2 | 2 | 2 | 1 | 1 | 3 | 3 | 1 | 1 | 2 | 1 | 1 | 1 | 1 |
| 4. *G. megaceros* | 2 | 2 | 2 | 1 | 1 | 3 | 3 | 1 | 1 | 2 | 1 | 1 | 1 | 1 |
| 5. *G. eurygaster* | 2 | 2 | 2 | 1 | 1 | 3 | 3 | 2 | 2 | 2 | 2 | 1 | 1 | 2 |
| 6. *G. coronatus* | 2 | 2 | 2 | 3 | 3 | 1 | 1 | 3 | 4 | 1 | 3 | 3 | 1 | 3 |
| 7. *G. processus* | 2 | 1 | 1 | 2 | 2 | 3 | 3 | 3 | 3 | 2 | 4 | 3 | 1 | 3 |
| 8. *G. wilsoni* | 2 | 1 | 1 | 1 | 3 | 3 | 3 | 3 | 3 | 2 | 1 | (12) | 2 | 2 |
| 9. *G. numidae* | 1 | 2 | 2 | 1 | 2 | 3 | 3 | 3 | 3 | 1 | 1 | 1 | (12) | 2 |
| 10. G. *hopkinsi* | 1 | 2 | 2 | 2 | 2 | 3 | 3 | 3 | 3 | 1 | 1 | 1 | 2 | 2 |
| 11. *G. gigas* | 1 | 1 | 1 | 1 | 1 | 3 | 3 | 3 | 3 | 1 | 2 | (23) | 2 | 2 |
| 12. *G. bituberculatus* | 3 | 1 | 2 | 2 | 2 | 1 | 1 | 2 | 2 | (12) | 2 | 1 | (12) | 2 |
| 13. *G. lagopi* | 3 | 1 | 2 | 1 | 1 | 1 | 1 | 2 | 2 | 2 | 2 | 1 | 2 | 2 |
| 14. *G. columbianus* | 3 | 1 | 2 | 1 | 2 | 3 | 3 | (12) | (12) | (12) | 2 | 1 | 1 | 2 |
| 15. *G. leucurus* | 3 | 1 | 2 | 1 | 2 | 3 | 3 | (12) | (12) | (12) | 2 | 1 | (12) | 2 |
| 16. *G. corpulentus* | 3 | 1 | 2 | 1 | 1 | 1 | 1 | (23) | (23) | (12) | (23) | 1 | 1 | 2 |
| 17. *G. merriamanus* | 2 | 1 | 2 | 1 | 1 | 1 | 1 | 1 | 2 | (12) | 3 | (13) | 2 | 2 |
| 18. *G. ithaginis* | 2 | 2 | 2 | (12) | (12) | 3 | 3 | (23) | (23) | (23) | 3 | 1 | 1 | 2 |
| 19. *G. chrysolophi* | 2 | 2 | 2 | (12) | (12) | 3 | 3 | 3 | 3 | 2 | 3 | (13) | 1 | 2 |
| 20. *G. dissimilis* | 3 | 2 | 2 | 1 | 1 | 3 | 3 | 3 | 4 | 2 | 3 | (13) | 1 | 2 |
| 21. *G. cervicornis* | 3 | 2 | 1 | 2 | 1 | 3 | 3 | (23) | (23) | 2 | 3 | 3 | 2 | (12) |
| 22. *G. sinensis* | 3 | 1 | 2 | 2 | 1 | 3 | 1 | (23) | (23) | 2 | 3 | 3 | 2 | (12) |
| 23. *G. assimilis* | 2 | 3 | 3 | (13) | (13) | 1 | 1 | 2 | 2 | 1 | 2 | 1 | (12) | 2 |
| 24. *G. dispar* | 2 | 3 | 3 | (13) | (13) | 3 | 3 | 2 | 2 | 1 | (23) | 1 | 1 | 2 |
| 25. *G. securiger* | 2 | 3 | 3 | (13) | (13) | 3 | 3 | 2 | 2 | 1 | (23) | (13) | 1 | (23) |
| 26. *G. ortygis* | 2 | 3 | 2 | 3 | 3 | 1 | 1 | (12) | (12) | 2 | 2 | 1 | 2 | (12) |
| 27. *G. tibetanus* | 2 | 1 | 2 | (13) | (13) | 3 | 3 | 2 | 2 | 1 | 3 | 1 | (12) | (12) |
| 28. *G. ammoperdix* | 2 | 1 | 2 | 3 | 3 | 3 | 3 | 1 | 1 | 2 | 2 | 1 | 1 | (12) |

**Table 2.7.** Data Matrix: Characters 1-14 (Cont.)

| Character | 001 | 002 | 003 | 004 | 005 | 006 | 007 | 008 | 009 | 010 | 011 | 012 | 013 | 014 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 29. *G. antennatus* | 2 | 3 | 3 | 1 | 3 | 3 | 3 | 3 | 3 | 1 | 2 | 2 | 2 | 3 |
| 30. *G. retractus* | 2 | 3 | 3 | 3 | 3 | 2 | 2 | 3 | 3 | 1 | 3 | (12) | 1 | 3 |
| 31. *G. soueefi* | 2 | 3 | 3 | 3 | 3 | 2 | 2 | 3 | 3 | 1 | 3 | (12) | 1 | (13) |
| 32. *G. biordinatus* | 1 | 2 | 2 | 1 | 1 | 3 | 3 | 2 | 2 | 2 | 2 | 1 | 1 | 2 |
| 33. *G. major* | 1 | 2 | 2 | 1 | 1 | 3 | 3 | 2 | 2 | 2 | 1 | 1 | 1 | 1 |
| 34. *G. fissus* | 1 | 2 | 2 | (12) | (12) | 3 | 3 | 2 | 2 | (12) | 2 | 1 | 1 | (12) |
| 35. *G. australis* | 1 | 2 | 2 | 1 | 1 | 3 | 3 | 1 | 1 | 2 | 2 | 1 | 1 | 1 |
| 36. *G. crassipes* | 1 | 2 | 2 | 1 | 1 | 3 | 3 | 2 | 2 | 2 | 3 | 1 | 1 | 1 |
| 37. *Goniocotes diplogonus* | 2 | 1 | 2 | 1 | 1 | 3 | 3 | 2 | 2 | 2 | 3 | 2 | 1 | 2 |
| 38. *Gon. gallinae* | 1 | 2 | 2 | 1 | 1 | 3 | 3 | 2 | 2 | 2 | 3 | (12) | 1 | 1 |
| 39. *Gon. haplogonus* | 2 | 2 | 2 | 1 | 1 | 3 | 3 | (23) | (23) | 1 | 3 | (12) | 1 | (12) |
| 40. *Gon. pallidomaculatus* | 2 | 2 | 2 | 1 | 1 | 3 | 3 | 2 | 2 | 2 | 1 | 1 | 1 | (12) |
| 41. *Gon. parviceps* | 3 | 1 | 2 | 2 | 1 | 3 | 2 | (12) | (12) | 2 | 1 | 1 | 1 | 1 |
| 42. *Gon. reticulatus* | 1 | 2 | 2 | 1 | 1 | 2 | 1 | 2 | 2 | 1 | 2 | 1 | 1 | 1 |
| 43. *Physconelloides montana* | 1 | 2 | 2 | 2 | 2 | 3 | 3 | (23) | (23) | 2 | 4 | (12) | 1 | 3 |
| 44. *Campanulotes bidentata* | 2 | 3 | 3 | 1 | 1 | 3 | 3 | 1 | 1 | 2 | 2 | 1 | 1 | 2 |
| 45. *Heptapsogaster temporalis* | 2 | 3 | 2 | 1 | 1 | 3 | 3 | 1 | 1 | 2 | (12) | 1 | 1 | 1 |

**Table 2.7.** Data Matrix: Characters 15-28

| Character | 015 | 016 | 017 | 018 | 019 | 020 | 021 | 022 | 023 | 024 | 025 | 026 | 027 | 028 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 1. *Goniodes pavonis* | 1 | 1 | 1 | 3 | 1 | 2 | 1 | 1 | 1 | 3 | 2 | 3 | 4 | 4 |
| 2. *G. curvicornis* | 1 | 1 | 1 | 3 | 1 | 2 | 1 | 1 | 1 | 3 | 2 | 2 | 3 | 3 |
| 3. *G. spinicornis* | 1 | 1 | 1 | 2 | 1 | 2 | 1 | 1 | 1 | 2 | 2 | 2 | 3 | 2 |
| 4. *G. megaceros* | 1 | 1 | 1 | 2 | 1 | 2 | 1 | 1 | 1 | 1 | 2 | 2 | 3 | 2 |
| 5. *G. eurygaster* | 1 | 1 | 1 | 2 | 1 | 2 | 1 | 2 | 1 | 1 | 2 | 2 | 3 | 3 |
| 6. *G. coronatus* | 1 | 2 | 1 | (12) | 2 | 2 | 1 | 2 | 1 | 3 | 1 | 2 | 2 | 2 |
| 7. *G. processus* | 1 | 2 | 2 | 1 | 1 | 3 | 2 | 2 | 2 | 2 | 2 | 3 | 4 | 4 |
| 8. *G. wilsoni* | 1 | 2 | 2 | (12) | 1 | 3 | 2 | 2 | 1 | 2 | 2 | 2 | 3 | 3 |
| 9. *G. numidae* | 1 | 1 | 2 | 1 | 1 | 2 | 1 | 1 | 1 | (23) | 2 | 2 | 3 | 3 |
| 10. *G. hopkinsi* | 1 | 2 | 2 | 1 | 1 | 2 | 1 | 1 | 2 | (23) | 1 | 2 | 3 | 3 |
| 11. *G. gigas* | 1 | 2 | (13) | 3 | 1 | 1 | 1 | 2 | 1 | 2 | 2 | 1 | 2 | 2 |
| 12. *G. bituberculatus* | 1 | 1 | 1 | 3 | (12) | 1 | 1 | 2 | 3 | (12) | (12) | 1 | 2 | 3 |
| 13. *G. lagopi* | 1 | (12) | 1 | 3 | 1 | 1 | 1 | 2 | 1 | 1 | 2 | 1 | 1 | 2 |
| 14. *G. columbianus* | 1 | 2 | (12) | 3 | 1 | 1 | 1 | 2 | 3 | (12) | 1 | 1 | 1 | 2 |
| 15. *G. leucurus* | 1 | 1 | 2 | 3 | 1 | 1 | 1 | 2 | 3 | (12) | 1 | 1 | 1 | 2 |
| 16. *G. corpulentus* | 1 | (12) | (12) | 3 | (12) | 1 | 1 | 2 | 3 | 1 | 1 | 1 | 1 | 2 |
| 17. *G. merriamanus* | 1 | 2 | 1 | 3 | 2 | 1 | 1 | 1 | 1 | 1 | 2 | 1 | 1 | 2 |
| 18. *G. ithaginis* | 1 | 1 | 1 | 4 | (12) | 1 | 1 | 2 | (12) | (12) | (12) | (12) | 1 | 2 |
| 19. *G. chrysolophi* | 1 | (12) | 3 | 4 | (12) | 1 | 1 | 2 | 3 | (12) | (12) | (12) | 1 | 2 |
| 20. *G. dissimilis* | 1 | 2 | 1 | 2 | 1 | 1 | 1 | (12) | 1 | 1 | 2 | (12) | 1 | 1 |
| 21. *G. cervicornis* | 1 | 2 | 3 | 3 | 1 | 1 | 1 | 1 | 1 | (23) | 2 | 1 | 2 | 3 |
| 22. *G. sinensis* | 1 | 2 | 3 | (23) | 1 | 1 | (12) | 2 | 1 | (13) | 2 | 2 | 2 | 3 |
| 23. *G. assimilis* | 1 | 2 | (12) | 1 | 1 | 1 | 1 | 2 | 3 | 1 | 2 | 1 | 1 | 2 |
| 24. *G. dispar* | 1 | 2 | 2 | 4 | 1 | 1 | 1 | 2 | 3 | 1 | 2 | 1 | 1 | 2 |
| 25. *G. securiger* | 1 | 2 | (13) | 4 | (12) | 1 | 1 | 2 | 3 | 1 | 2 | 1 | 1 | 2 |
| 26. *G. ortygis* | 1 | 1 | 1 | 1 | 1 | 1 | 1 | (12) | 1 | 1 | (12) | 1 | 1 | 2 |
| 27. *G. tibetanus* | 1 | 2 | 2 | 4 | (12) | 1 | 1 | 1 | 3 | 1 | 2 | 1 | 1 | 2 |
| 28. *G. ammoperdix* | 1 | 1 | 1 | (13) | 1 | 1 | 1 | 2 | 1 | 1 | 2 | 1 | 1 | 2 |

**Table 2.7.** Data Matrix: Characters 15-28 (Cont.)

| Character | 015 | 016 | 017 | 018 | 019 | 020 | 021 | 022 | 023 | 024 | 025 | 026 | 027 | 028 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 29. *G. antennatus* | 1 | 2 | 1 | (12) | 1 | 1 | 1 | 1 | 1 | 1 | 2 | 1 | 1 | 2 |
| 30. *G. retractus* | 1 | 2 | (12) | 2 | 1 | 1 | 1 | 2 | 1 | 1 | 1 | (12) | 1 | 2 |
| 31. *G. soueefi* | 1 | 2 | 1 | 1 | 1 | 2 | 1 | 2 | 1 | (12) | 1 | 2 | 2 | 2 |
| 32. *G. biordinatus* | 1 | 1 | 1 | (23) | 1 | (12) | 1 | 1 | (12) | 1 | 2 | 2 | 1 | 3 |
| 33. *G. major* | 1 | 1 | 1 | (23) | 2 | 2 | 1 | 1 | 2 | 2 | 2 | 3 | 4 | 3 |
| 34. *G. fissus* | 1 | 1 | 1 | (13) | (12) | (12) | 1 | 2 | (23) | 1 | 2 | (12) | 2 | 2 |
| 35. *G. australis* | 1 | 1 | 1 | (12) | (12) | (12) | 1 | 2 | 1 | 1 | 2 | 2 | 4 | 4 |
| 36. *G. crassipes* | 1 | 1 | 1 | 3 | 1 | (12) | 1 | 1 | 2 | 1 | 1 | 1 | 1 | 3 |
| 37. *Goniocotes diplogonus* | 1 | 1 | 1 | (23) | (12) | 1 | 1 | 1 | 3 | 1 | 1 | 1 | 3 | 3 |
| 38. *Gon. gallinae* | 1 | 1 | 1 | (23) | (12) | 1 | 1 | 1 | 3 | 1 | 1 | 1 | 2 | 2 |
| 39. *Gon. haplogonus* | 1 | 1 | 1 | (23) | 2 | 1 | 1 | 1 | 3 | 1 | 1 | 1 | 2 | 2 |
| 40. *Gon. pallidomaculatus* | 1 | 1 | 1 | (23) | 1 | 2 | 2 | 1 | 1 | 1 | (12) | 2 | 2 | 2 |
| 41. *Gon. parviceps* | 1 | 1 | 1 | 3 | 1 | 2 | 2 | 1 | 1 | 1 | (12) | 2 | 3 | 4 |
| 42. *Gon. reticulatus* | 1 | 1 | 1 | 3 | 1 | 1 | 1 | 1 | 1 | 1 | 2 | 2 | 3 | 4 |
| 43. *Physconelloides montana* | 2 | 2 | 1 | 3 | 1 | 1 | 1 | 1 | 3 | 1 | (12) | 1 | 4 | 4 |
| 44. *Campanulotes bidentata* | 1 | 1 | 1 | 3 | 2 | 3 | 1 | 1 | 2 | 1 | 2 | 2 | 1 | 1 |
| 45. *Heptapsogaster temporalis* | 2 | 1 | 1 | 3 | 1 | 1 | 1 | 1 | 3 | 1 | 1 | 4 | 2 | 4 |

**Table 2.7.** Data Matrix: Characters 29-42

| Character | 029 | 030 | 031 | 032 | 033 | 034 | 035 | 036 | 037 | 038 | 039 | 040 | 041 | 042 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 1. *G. pavonis* | 2 | 2 | 2 | 3 | 2 | 3 | 3 | 1 | 1 | 2 | 3 | 2 | 1 | 2 |
| 2. *G. curvicornis* | 2 | 1 | 1 | 3 | 1 | 3 | 3 | 1 | 1 | (12) | (34) | 2 | 1 | 2 |
| 3. *G. spinicornis* | (12) | (12) | 3 | 2 | 2 | 1 | 1 | 1 | 3 | 2 | 3 | 2 | 1 | 2 |
| 4. *G. megaceros* | (12) | (12) | 3 | 2 | 2 | 1 | 1 | 1 | 1 | 2 | 3 | 2 | 1 | 2 |
| 5. *G. eurygaster* | 2 | 2 | 3 | 3 | 2 | 3 | 3 | 1 | 1 | 1 | 1 | 2 | 1 | 3 |
| 6. *G. coronatus* | 1 | 1 | 3 | 1 | 1 | 1 | 1 | 3 | 3 | 2 | 2 | 1 | 1 | 2 |
| 7. *G. processus* | (12) | (12) | 3 | 3 | 2 | 3 | 3 | 1 | 1 | 2 | 1 | 2 | (12) | 2 |
| 8. *G. wilsoni* | (12) | (12) | 1 | 2 | 2 | 3 | 3 | 1 | 1 | 2 | 1 | 2 | 1 | 2 |
| 9. *G. numidae* | 2 | 2 | 3 | 3 | 2 | 3 | 3 | 3 | 3 | (13) | 2 | 2 | 2 | 2 |
| 10. *G. hopkinsi* | 2 | 2 | 3 | 3 | 2 | 3 | 3 | 1 | 1 | 2 | 2 | 1 | 2 | 2 |
| 11. *G. gigas* | 1 | 1 | 1 | 1 | 1 | 4 | 4 | 1 | 1 | 1 | 1 | 2 | 2 | 1 |
| 12. *G. bituberculatus* | (12) | (12) | 1 | 3 | 1 | 3 | 2 | 1 | 1 | 1 | 1 | 2 | 1 | 2 |
| 13. *G. lagopi* | 1 | 1 | 1 | 1 | 1 | 3 | 2 | 1 | 1 | 1 | 1 | 2 | 1 | 2 |
| 14. *G. columbianus* | (12) | (12) | 1 | 2 | 1 | 3 | 2 | 1 | 1 | 1 | 1 | 2 | 1 | 2 |
| 15. *G. leucurus* | (12) | (12) | 1 | 2 | 1 | 3 | 2 | 1 | 1 | 1 | 1 | 2 | 1 | 2 |
| 16. *G. corpulentus* | (12) | (12) | 1 | 2 | 1 | 3 | 2 | 1 | 1 | 1 | 1 | 2 | 1 | 2 |
| 17. *G. merriamanus* | (12) | (12) | 1 | 3 | 1 | 3 | 3 | 1 | 1 | 1 | 1 | 2 | 2 | 2 |
| 18. *G. ithaginis* | (12) | (12) | 1 | 1 | 1 | 3 | 2 | 1 | 1 | 1 | 1 | 2 | 1 | 2 |
| 19. *G. chrysolophi* | 2 | 2 | 2 | 1 | 1 | 3 | 2 | 1 | 1 | 1 | 1 | 2 | 1 | 2 |
| 20. *G. dissimilis* | 1 | 1 | 2 | 2 | (12) | 2 | 2 | 3 | 3 | 1 | 1 | (12) | 1 | 2 |
| 21. *G. cervicornis* | 1 | 1 | 1 | 3 | 1 | 2 | 2 | 1 | 3 | 1 | 1 | 2 | 2 | 2 |
| 22. *G. sinensis* | 2 | 2 | 2 | 3 | 1 | 1 | 1 | 1 | 1 | 1 | 2 | 2 | 2 | 2 |
| 23. *G. assimilis* | (12) | (12) | 1 | 1 | 1 | 2 | 2 | 1 | 1 | 1 | 1 | 2 | 2 | 3 |
| 24. *G. dispar* | (12) | (12) | 1 | 1 | 1 | 2 | 2 | 1 | 1 | 1 | 1 | 2 | 2 | 3 |
| 25. *G. securiger* | (12) | (12) | 1 | 1 | 1 | 2 | 2 | 1 | 1 | 1 | 1 | 2 | 2 | 2 |
| 26. *G. ortygis* | (12) | (12) | 1 | 3 | 1 | 3 | 2 | 1 | 1 | 1 | 1 | 2 | 2 | 2 |
| 27. *G. tibetanus* | (12) | (12) | 1 | 1 | 1 | 2 | 2 | 1 | 1 | 1 | 1 | 2 | 2 | 2 |

**Table 2.7.** Data Matrix: Characters 29-42 (Cont.)

| Character | 029 | 030 | 031 | 032 | 033 | 034 | 035 | 036 | 037 | 038 | 039 | 040 | 041 | 042 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 28. *G. ammoperdix* | 1 | 1 | 1 | 3 | 1 | 3 | 2 | 1 | 1 | 1 | 1 | 2 | 2 | 2 |
| 29. *G. antennatus* | 1 | 1 | 1 | 2 | 1 | 3 | 2 | 4 | 4 | 1 | 1 | 2 | 1 | 2 |
| 30. *G. retractus* | 1 | 1 | 2 | 3 | 1 | 3 | 2 | 4 | 1 | (12) | 1 | 2 | 2 | 3 |
| 31. *G. soueefi* | 1 | 1 | 2 | 2 | 1 | (12) | 1 | 4 | 4 | 2 | 3 | 2 | 2 | 3 |
| 32. *G. biordinatus* | 1 | 1 | 2 | 3 | 1 | 1 | 1 | 1 | 1 | 2 | 2 | 2 | 2 | 1 |
| 33. *G. major* | (12) | (12) | 3 | 3 | 2 | 1 | 1 | 1 | 1 | 2 | 3 | 2 | 2 | 1 |
| 34. *G. fissus* | 1 | 1 | 2 | 2 | 1 | 3 | 3 | 1 | 1 | (12) | 2 | 2 | 2 | 1 |
| 35. *G. australis* | 1 | 1 | (23) | (23) | 1 | 1 | 1 | 2 | 2 | 2 | (13) | 2 | 1 | 2 |
| 36. *G. crassipes* | 2 | 2 | 2 | 3 | 1 | 3 | 2 | 4 | 1 | 1 | 1 | 2 | 2 | 1 |
| 37. *Goniocotes diplogonus* | 1 | 2 | 1 | 1 | 2 | 2 | 2 | 1 | 1 | 1 | 1 | 2 | 2 | 1 |
| 38. *Gon. gallinae* | 1 | 1 | 1 | 1 | 1 | 2 | 2 | 1 | 3 | 1 | 1 | 2 | 2 | 1 |
| 39. *Gon. haplogonus* | 1 | 1 | 1 | 1 | 1 | 3 | 1 | 1 | 1 | 1 | 1 | 2 | 1 | 1 |
| 40. *Gon. pallidomaculatus* | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 2 | 3 | 2 | 1 | 1 |
| 41. *Gon. parviceps* | 1 | (12) | 1 | 1 | 1 | 1 | 2 | 1 | 3 | 2 | (12) | 1 | 1 | 2 |
| 42. *Gon. reticulatus* | (12) | (12) | 1 | 1 | 2 | 3 | 2 | 1 | 1 | 1 | 1 | 2 | 2 | 3 |
| 43. *Physconelloides montana* | 2 | 2 | 2 | 2 | 2 | 5 | 5 | 3 | 3 | 2 | 4 | 2 | 1 | 1 |
| 44. *Campanulotes bidentata* | 1 | 1 | 2 | 2 | 1 | 1 | 1 | 2 | 2 | 2 | 3 | 2 | (12) | 1 |
| 45. *Heptapsogaster temporalis* | 2 | 2 | 3 | 1 | 2 | 3 | 2 | 1 | 1 | 3 | 1 | 2 | 1 | 2 |

**Table 2.7.** Data Matrix: Characters 43-56

| Character | 043 | 044 | 045 | 046 | 047 | 048 | 049 | 050 | 051 | 052 | 053 | 054 | 055 | 056 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 1. *G. pavonis* | - | 5 | 1 | - | 6 | 2 | 1 | 1 | 2 | 5 | 3 | 2 | 1 | 1 |
| 2. *G. curvicornis* | - | 5 | 1 | - | 7 | 5 | 2 | 2 | 2 | 5 | 3 | 2 | 1 | 1 |
| 3. *G. spinicornis* | - | 5 | (13) | - | 6 | 2 | 1 | 1 | 2 | 5 | 3 | 2 | 1 | 1 |
| 4. *G. megaceros* | - | 5 | 1 | - | 6 | 2 | 1 | 1 | 2 | 5 | 3 | 2 | 1 | 1 |
| 5. *G. eurygaster* | - | 1 | 3 | - | 2 | 2 | 1 | 1 | 1 | 1 | 1 | - | 1 | - |
| 6. *G. coronatus* | - | 4 | 4 | - | 4 | 5 | 2 | 2 | 5 | 1 | 1 | - | 1 | - |
| 7. *G. processus* | - | 5 | 1 | - | 4 | 7 | 2 | 2 | 2 | 5 | 1 | - | 1 | - |
| 8. *G. wilsoni* | - | 3 | 3 | - | 2 | 2 | 1 | 1 | 1 | 1 | 2 | 1 | 1 | - |
| 9. *G. numidae* | - | 3 | 3 | - | 2 | 2 | 1 | 1 | 2 | 1 | 2 | 1 | 2 | - |
| 10. *G. hopkinsi* | - | 3 | 3 | - | 1 | 2 | 1 | 1 | 2 | 1 | 2 | 1 | 2 | - |
| 11. *G. gigas* | 3 | - | - | 2 | - | - | 1 | 1 | 1 | 1 | 1 | - | 1 | - |
| 12. *G. bituberculatus* | - | 5 | 1 | - | 6 | 1 | 1 | 1 | 2 | 5 | 1 | - | 1 | - |
| 13. *G. lagopi* | - | 5 | 1 | - | 6 | 1 | 1 | 1 | 2 | 5 | 1 | - | 1 | - |
| 14. *G. columbianus* | - | 5 | 1 | - | 6 | 1 | 1 | 1 | 2 | 5 | 1 | - | 1 | - |
| 15. *G. leucurus* | - | 5 | 1 | - | 6 | 1 | 1 | 1 | 2 | 5 | 2 | 1 | 2 | - |
| 16. *G. corpulentus* | - | 5 | 1 | - | 6 | 1 | 1 | 1 | 2 | 5 | 1 | - | 1 | - |
| 17. *G. merriamanus* | - | 2 | 3 | - | 2 | 5 | 2 | 2 | 1 | 5 | 1 | - | 1 | - |
| 18. *G. ithaginis* | - | 5 | 1 | - | 6 | 1 | 1 | 1 | 2 | 5 | 1 | - | 1 | - |
| 19. *G. chrysolophi* | - | 5 | 1 | - | 6 | 1 | 1 | 1 | 2 | 5 | 1 | - | 1 | - |
| 20. *G. dissimilis* | - | 2 | 3 | - | 2 | 5 | 2 | 2 | 2 | 5 | 1 | - | 1 | - |
| 21. *G. cervicornis* | - | 5 | 3 | - | 6 | 4 | 2 | 2 | 2 | 5 | 3 | 2 | 1 | 2 |
| 22. *G. sinensis* | - | 5 | 3 | - | 6 | 5 | 2 | 2 | 2 | 5 | 3 | 1 | 1 | 1 |
| 23. *G. assimilis* | - | 3 | 3 | - | 4 | 5 | 2 | 2 | 1 | 1 | 1 | - | 1 | - |
| 24. *G. dispar* | - | 3 | 3 | - | 4 | 1 | 2 | 1 | 1 | 1 | 1 | - | 1 | - |
| 25. *G. securiger* | - | 3 | 3 | - | 4 | 1 | 2 | 1 | 1 | 1 | 1 | - | 1 | - |
| 26. *G. ortygis* | - | 2 | 3 | - | 4 | 5 | 2 | 2 | 1 | 5 | 1 | - | 1 | - |
| 27. *G. tibetanus* | - | 5 | 1 | - | 4 | 1 | 1 | 1 | 2 | 5 | 1 | - | 1 | - |
| 28. *G. ammoperdix* | - | 2 | 3 | - | 4 | 1 | 1 | 1 | 1 | 5 | 1 | - | 1 | - |

**Table 2.7.** Data Matrix: Characters 43-56 (Cont.)

| Character | 043 | 044 | 045 | 046 | 047 | 048 | 049 | 050 | 051 | 052 | 053 | 054 | 055 | 056 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 29. *G. antennatus* | - | 2 | 3 | - | 4 | 5 | 2 | 2 | 2 | 5 | 1 | - | 1 | - |
| 30. *G. retractus* | - | 1 | 3 | - | 2 | 5 | 1 | 2 | 1 | 2 | 1 | - | 1 | - |
| 31. *G. soueefi* | - | 1 | 3 | - | 2 | 5 | 1 | 2 | 1 | 2 | 1 | - | 1 | - |
| 32. *G. biordinatus* | 1 | - | - | 5 | - | - | 2 | 2 | 1 | 1 | 1 | - | 1 | - |
| 33. *G. major* | 1 | - | - | 1 | - | - | 1 | 1 | 1 | 1 | 1 | - | 1 | - |
| 34. *G. fissus* | 2 | - | - | 5 | - | - | 2 | 2 | 2 | 1 | 1 | - | 1 | - |
| 35. *G. australis* | - | 5 | 1 | - | 7 | 1 | 2 | 1 | (12) | 5 | 2 | 1 | 1 | - |
| 36. *G. crassipes* | 1 | - | - | 5 | - | - | 2 | 2 | 1 | 1 | 1 | - | 1 | - |
| 37. *Goniocotes diplogonus* | 2 | - | - | 5 | - | - | 2 | 2 | 1 | 1 | 1 | - | 1 | - |
| 38. *Gon. gallinae* | 2 | - | - | 5 | - | - | 2 | 2 | 1 | 3 | 1 | - | 1 | - |
| 39. *Gon. haplogonus* | 2 | - | - | 5 | - | - | 2 | 2 | 1 | 3 | 1 | - | 1 | - |
| 40. *Gon. pallidomaculatus* | 1 | - | - | 5 | - | - | 2 | 2 | 1 | 1 | 1 | - | 1 | - |
| 41. *Gon. parviceps* | - | 5 | 2 | - | 7 | 5 | 3 | 2 | 5 | 5 | 3 | 3 | 3 | 2 |
| 42. *Gon. reticulatus* | - | 2 | 2 | - | 5 | 1 | 2 | 2 | 1 | 1 | 1 | - | 1 | - |
| 43. *Physconelloides montana* | 2 | - | - | 1 | - | - | 1 | 1 | 1 | 1 | 1 | - | 1 | - |
| 44. *Campanulotes bidentata* | 3 | - | - | 1 | - | - | 1 | 1 | 1 | 1 | 1 | - | 1 | - |
| 45. *Heptapsogaster temporalis* | - | 5 | 2 | - | 7 | 5 | 2 | 2 | 1 | 5 | 1 | - | 1 | - |

**Table 2.7.** Data Matrix: Characters 57-70

| Character | 05 | 05 | 05 | 06 | 06 | 06 | 06 | 06 | 06 | 06 | 06 | 06 | 60 | 07 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | 7 | 8 | 9 | 0 | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 0 |
| 1. *G. pavonis* | 2 | 2 | 1 | 1 | 1 | 3 | 2 | 3 | 2 | 3 | 3 | 1 | 2 | 2 |
| 2. *G. curvicornis* | 1 | 3 | 1 | 1 | 3 | 3 | 3 | 3 | 2 | 1 | 3 | 1 | 1 | 2 |
| 3. *G. spinicornis* | 2 | 1 | 4 | 1 | 3 | 3 | 3 | 3 | 1 | (12) | 3 | 1 | 2 | 2 |
| 4. *G. megaceros* | 2 | 1 | 4 | 1 | 3 | 3 | 3 | 3 | 1 | (12) | 3 | 1 | 2 | 2 |
| 5. *G. eurygaster* | - | 1 | 4 | ? | 2 | 4 | 1 | 2 | 2 | 3 | 3 | 2 | 2 | 2 |
| 6. *G. coronatus* | - | 1 | 1 | 1 | 1 | 4 | 3 | 3 | 2 | 2 | 2 | (12) | 2 | 1 |
| 7. *G. processus* | - | 1 | 1 | 1 | 3 | 4 | 1 | 3 | 2 | 3 | 3 | 1 | 2 | 1 |
| 8. *G. wilsoni* | - | 1 | 1 | 1 | 1 | 2 | 2 | 2 | 2 | 3 | 3 | 1 | 2 | 2 |
| 9. *G. numidae* | - | 2 | 1 | 1 | 3 | 2 | 2 | 2 | 2 | 3 | 3 | 1 | 2 | 2 |
| 10. *G. hopkinsi* | - | 2 | 1 | 1 | 3 | 2 | 1 | 2 | 2 | 2 | 2 | 1 | 2 | 2 |
| 11. *G. gigas* | - | 1 | 1 | 3 | 3 | 1 | - | 1 | 2 | 2 | 2 | 1 | 2 | 2 |
| 12. *G. bituberculatus* | - | 1 | 2 | 1 | 3 | 3 | 2 | 3 | 2 | (23) | (13) | 2 | 2 | 2 |
| 13. *G. lagopi* | - | 1 | 1 | 1 | 3 | 3 | 2 | 3 | 2 | 2 | 3 | 2 | 2 | 2 |
| 14. *G. columbianus* | - | 1 | 2 | 1 | 3 | 3 | 2 | 3 | 2 | 3 | 3 | 2 | 2 | 2 |
| 15. *G. leucurus* | - | 1 | 2 | 1 | 3 | 3 | 2 | 3 | 2 | 3 | 3 | 2 | 2 | 2 |
| 16. *G. corpulentus* | - | 1 | 2 | 1 | 3 | 3 | 2 | 3 | 2 | 2 | (23) | 2 | 2 | 2 |
| 17. *G. merriamanus* | - | 1 | 2 | 1 | 3 | (34) | 2 | 3 | 2 | 3 | 3 | 2 | 2 | 2 |
| 18. *G. ithaginis* | - | 1 | 1 | 1 | 3 | 3 | 2 | 3 | 2 | 2 | (23) | 2 | 2 | 1 |
| 19. *G. chrysolophi* | - | 1 | 1 | 1 | 3 | 3 | 2 | 3 | 2 | 2 | (23) | 2 | 2 | 2 |
| 20. *G. dissimilis* | - | 1 | 2 | ? | 1 | 3 | 2 | 3 | 2 | 2 | 2 | 1 | 2 | 1 |
| 21. *G. cervicornis* | 1 | 1 | 2 | 3 | 3 | 4 | 2 | 3 | 2 | 3 | 3 | 2 | 2 | 2 |
| 22. *G. sinensis* | 1 | 1 | 4 | 1 | 3 | 3 | 2 | 3 | 2 | 3 | 3 | 1 | 2 | 2 |
| 23. *G. assimilis* | - | 1 | 1 | 1 | 3 | 4 | 1 | 3 | 2 | 3 | 3 | 1 | 2 | 1 |
| 24. *G. dispar* | - | 1 | 1 | 1 | 3 | 4 | 1 | 3 | 2 | 3 | (23) | 1 | 2 | 1 |
| 25. *G. securiger* | - | 1 | 1 | 1 | 3 | 4 | 1 | 2 | 2 | 3 | (23) | 1 | 2 | 1 |
| 26. *G. ortygis* | - | 1 | 2 | 1 | 3 | 4 | 1 | 3 | 2 | 3 | 3 | 1 | 2 | 2 |
| 27. *G. tibetanus* | - | 2 | 2 | 1 | 3 | 3 | (12) | 3 | 2 | 3 | (23) | 1 | 2 | (12) |
| 28. *G. ammoperdix* | - | 1 | 1 | 1 | 1 | 4 | 1 | 3 | 2 | 2 | 2 | 2 | 2 | 2 |

**Table 2.7.** Data Matrix: Characters 57-70 (Cont.)

| Character | 057 | 058 | 059 | 060 | 061 | 062 | 063 | 064 | 065 | 066 | 067 | 068 | 069 | 070 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 29. *G. antennatus* | - | 1 | 1 | 1 | 1 | 4 | 1 | 3 | 2 | 3 | 3 | 1 | 2 | 2 |
| 30. *G. retractus* | - | 1 | 4 | 1 | 1 | 4 | 1 | 3 | 2 | 2 | 3 | 2 | 2 | 2 |
| 31. *G. soueefi* | - | 1 | 2 | 1 | 3 | 4 | 1 | 3 | 2 | 2 | 3 | 1 | 2 | 2 |
| 32. *G. biordinatus* | - | 4 | 4 | 1 | 3 | 1 | - | 1 | 1 | 2 | 3 | 1 | 1 | - |
| 33. *G. major* | - | 4 | 4 | 3 | 3 | 1 | - | 1 | 2 | 2 | 2 | 2 | 1 | - |
| 34. *G. fissus* | - | 1 | 1 | 1 | 1 | 1 | - | 1 | 2 | 2 | 1 | 2 | 1 | - |
| 35. *G. australis* | - | 2 | 1 | 1 | 2 | 4 | (12) | 3 | 1 | 1 | (23) | 1 | 2 | - |
| 36. *G. crassipes* | - | 4 | 4 | 3 | 3 | 1 | - | 1 | (12) | 2 | 2 | 2 | 1 | - |
| 37. *Goniocotes diplogonus* | - | 1 | 1 | 1 | 1 | 1 | - | 1 | 1 | (12) | (12) | 1 | 1 | - |
| 38. *Gon. gallinae* | - | 1 | 1 | 1 | 1 | 1 | - | 1 | 1 | 1 | 1 | - | 1 | - |
| 39. *Gon. haplogonus* | - | 1 | 1 | 1 | 1 | 1 | - | 1 | 1 | 1 | 1 | - | 1 | - |
| 40. *Gon. pallidomaculatus* | - | 4 | 4 | 1 | 1 | 1 | - | 1 | 1 | 1 | 1 | - | 1 | - |
| 41. *Gon. parviceps* | 1 | 3 | 1 | 1 | 1 | 3 | 3 | 3 | 1 | 1 | (12) | 1 | 2 | 1 |
| 42. *Gon. reticulatus* | - | 4 | 4 | 3 | 3 | 1 | - | 1 | 1 | (12) | 1 | - | 2 | 2 |
| 43. *Physconelloides montana* | - | 1 | 1 | 1 | 1 | 1 | - | 1 | 1 | 3 | 3 | 1 | 1 | - |
| 44. *Campanulotes bidentata* | - | 1 | 1 | 1 | 1 | 1 | - | 1 | 1 | 2 | 2 | 2 | 1 | - |
| 45. *Heptapsogaster temporalis* | - | 1 | 1 | 1 | 1 | 5 | (12) | 3 | 1 | 2 | 1 | 3 | 1 | - |

**Table 2.7.** Data Matrix: Characters 71-84

| Character | 071 | 072 | 073 | 074 | 075 | 076 | 077 | 078 | 079 | 080 | 081 | 082 | 083 | 084 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 1. *G. pavonis* | 2 | 2 | 3 | 1 | 3 | 1 | 2 | 3 | 1 | 2 | 1 | 1 | 2 | 2 |
| 2. *G. curvicornis* | 2 | 2 | (23) | 1 | (23) | 1 | 2 | 2 | 2 | 3 | 2 | 2 | 2 | 1 |
| 3. *G. spinicornis* | (12) | 2 | 3 | 1 | 3 | 1 | 1 | (12) | 2 | 3 | 1 | 3 | 1 | 1 |
| 4. *G. megaceros* | (12) | 2 | 3 | 1 | 3 | 1 | 1 | (12) | 1 | 3 | 1 | 3 | 1 | 1 |
| 5. *G. eurygaster* | 2 | 1 | 3 | 1 | 1 | 1 | (12) | 2 | 1 | 1 | 3 | 3 | 1 | 1 |
| 6. *G. coronatus* | 2 | 2 | 2 | 2 | 3 | 4 | 2 | (23) | 1 | 2 | 2 | 2 | 2 | 2 |
| 7. *G. processus* | (12) | 1 | 2 | 2 | (23) | (23) | (12) | 2 | 2 | 3 | 1 | 3 | 2 | 4 |
| 8. *G. wilsoni* | 2 | 1 | (23) | 1 | 3 | 3 | 2 | 3 | 1 | 1 | 2 | 2 | 2 | 2 |
| 9. *G. numidae* | 2 | 1 | 3 | 2 | (23) | (23) | 2 | 3 | 2 | 2 | 1 | 1 | 2 | 2 |
| 10. *G. hopkinsi* | 2 | 1 | 3 | 1 | (23) | (23) | 1 | 1 | 2 | 2 | 1 | 1 | 1 | 1 |
| 11. *G. gigas* | 2 | 1 | 2 | 1 | 3 | 3 | 1 | 2 | 1 | 1 | 1 | 1 | 2 | 2 |
| 12. *G. bituberculatus* | 2 | 1 | 3 | 2 | 3 | 3 | (12) | 2 | 2 | 3 | 1 | 2 | 2 | 2 |
| 13. *G. lagopi* | 2 | 2 | 2 | (12) | 3 | 1 | 1 | 2 | 2 | 3 | 1 | 2 | 2 | 1 |
| 14. *G. columbianus* | 2 | 1 | (12) | 2 | (23) | (23) | 2 | (23) | 2 | 3 | 1 | 2 | 2 | 2 |
| 15. *G. leucurus* | 2 | 1 | 3 | (12) | (23) | (23) | (12) | (23) | 2 | 3 | 1 | 2 | 2 | 2 |
| 16. *G. corpulentus* | 2 | 1 | 3 | (12) | (23) | (23) | (12) | (23) | 2 | 3 | 1 | 2 | 2 | 2 |
| 17. *G. merriamanus* | (12) | 1 | (23) | 1 | (23) | (23) | 1 | 2 | 2 | 3 | 1 | 1 | 2 | 1 |
| 18. *G. ithaginis* | 2 | 1 | 2 | 2 | (23) | (23) | 1 | 2 | 1 | 1 | 2 | 2 | 3 | 3 |
| 19. *G. chrysolophi* | 2 | 1 | 3 | 1 | (23) | (23) | 1 | 2 | 1 | 3 | 1 | 2 | 2 | 3 |
| 20. *G. dissimilis* | (12) | ? | (23) | 1 | 2 | 2 | 1 | (12) | 2 | ? | 2 | 2 | 1 | 1 |
| 21. *G. cervicornis* | 2 | 1 | (23) | 2 | (23) | (23) | (12) | (123) | 2 | 3 | 2 | 2 | 2 | 1 |
| 22. *G. sinensis* | 2 | 2 | (12) | 1 | 3 | 1 | (12) | 2 | 2 | 3 | 1 | 2 | 1 | 1 |
| 23. *G. assimilis* | 2 | 1 | (23) | 2 | (23) | (23) | (12) | (23) | 1 | 1 | 2 | 2 | 1 | 1 |
| 24. *G. dispar* | 2 | 1 | 3 | 1 | (23) | (23) | 2 | 3 | 1 | 1 | 2 | 2 | 1 | 1 |
| 25. *G. securiger* | 2 | 1 | 3 | 1 | (23) | (23) | 2 | (23) | 1 | 1 | 2 | 2 | 1 | 1 |
| 26. *G. ortygis* | 2 | 1 | 2 | 1 | 3 | 3 | 2 | (23) | 1 | 1 | 2 | 2 | 1 | 1 |
| 27. *G. tibetanus* | 2 | 1 | 3 | 2 | (23) | (23) | (12) | (12) | 2 | 3 | 2 | 3 | 1 | 1 |
| 28. *G. ammoperdix* | 2 | 1 | (23) | (12) | 3 | 3 | 2 | (23) | 1 | 1 | 2 | 2 | 3 | 3 |

**Table 2.7.** Data Matrix: Characters 71-84 (Cont.)

| Character | 07 1 | 07 2 | 07 3 | 07 4 | 07 5 | 07 6 | 07 7 | 07 8 | 07 9 | 08 0 | 08 1 | 08 2 | 08 3 | 08 4 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 29. *G. antennatus* | 1 | 1 | (23) | 2 | (23) | (23) | 1 | 2 | 2 | 1 | 2 | 2 | 1 | 1 |
| 30. *G. retractus* | 2 | 1 | 2 | 2 | 2 | 2 | 2 | (23) | 1 | 1 | 1 | 2 | 1 | 1 |
| 31. *G. soueefi* | 2 | 1 | 3 | 2 | 2 | 2 | 2 | 3 | 1 | 2 | 1 | 1 | 1 | 3 |
| 32. *G. biordinatus* | 1 | 2 | 1 | 1 | (23) | 1 | 1 | (12) | 1 | 1 | 2 | 2 | 1 | 1 |
| 33. *G. major* | 1 | 1 | 1 | 1 | 4 | 4 | 1 | 1 | 2 | 1 | 3 | 3 | 1 | 1 |
| 34. *G. fissus* | 1 | 1 | 3 | 1 | (23) | (23) | (13) | 1 | 1 | 1 | 3 | 3 | 1 | 1 |
| 35. *G. australis* | 1 | 2 | 3 | 1 | 2 | 1 | 3 | 1 | 1 | 3 | 2 | 3 | 2 | 3 |
| 36. *G. crassipes* | 1 | 1 | - | 1 | 1 | 1 | 3 | 1 | 2 | 1 | 2 | 2 | 3 | 3 |
| 37. *Goniocotes diplogonus* | (12) | 2 | 3 | 1 | 3 | 4 | 2 | (23) | 2 | 2 | 2 | 2 | 3 | 3 |
| 38. *Gon. gallinae* | 1 | 1 | 3 | 1 | 4 | 4 | (12) | (12) | 2 | 1 | 2 | 2 | 2 | 2 |
| 39. *Gon. haplogonus* | 1 | 2 | 1 | 1 | 3 | (12) | 1 | 1 | 2 | 1 | 2 | 2 | 1 | 1 |
| 40. *Gon. pallidomaculatus* | (12) | 2 | 1 | 1 | 3 | 4 | 1 | (12) | 2 | 1 | 2 | 2 | 1 | 1 |
| 41. *Gon. parviceps* | 1 | 1 | 3 | 1 | 4 | 4 | 3 | 1 | 2 | 3 | 1 | 2 | 1 | 1 |
| 42. *Gon. reticulatus* | 2 | 2 | 3 | 1 | 2 | 4 | 2 | (23) | 2 | 1 | 2 | 2 | 2 | 2 |
| 43. *Physconelloides montana* | 1 | 1 | 2 | 2 | 1 | 1 | 2 | 3 | 2 | 1 | 2 | 2 | 1 | 1 |
| 44. *Campanulotes bidentata* | 1 | 2 | 3 | 2 | (23) | 1 | 3 | (12) | 2 | 1 | 2 | 2 | 1 | 1 |
| 45. *Heptapsogaster temporalis* | (12) | 1 | 3 | 1 | (14) | (14) | 2 | (23) | 2 | 2 | 2 | 2 | 4 | 4 |

**Table 2.7.** Data Matrix: Characters 85-98

| Character | 08 5 | 08 6 | 08 7 | 08 8 | 08 9 | 09 0 | 09 1 | 09 2 | 09 3 | 09 4 | 09 5 | 09 6 | 09 7 | 09 8 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 1. *G. pavonis* | 3 | 3 | 3 | 1 | 1 | 2 | 2 | 3 | 4 | 1 | 3 | 3 | 3 | 1 |
| 2. *G. curvicornis* | 1 | 1 | 3 | 1 | 1 | 3 | 3 | 3 | 3 | 1 | 3 | 3 | (13) | 1 |
| 3. *G. spinicornis* | 1 | 1 | 3 | 1 | 1 | 1 | 3 | 3 | 3 | 2 | 3 | (23) | 1 | 1 |
| 4. *G. megaceros* | 1 | 1 | 3 | 1 | 1 | 3 | 3 | 1 | 1 | 1 | 3 | (23) | 1 | 1 |
| 5. *G. eurygaster* | 1 | 1 | 4 | 1 | 1 | 1 | 1 | (34) | (34) | 1 | 2 | 2 | 1 | 1 |
| 6. *G. coronatus* | 1 | 1 | 1 | 1 | 1 | 2 | 2 | 2 | 4 | 1 | 2 | 2 | 1 | 1 |
| 7. *G. processus* | 3 | 3 | 3 | 1 | 2 | 2 | 2 | 4 | 4 | 2 | 3 | 3 | 1 | 2 |
| 8. *G. wilsoni* | 3 | 3 | 1 | 1 | 1 | 2 | 2 | 2 | 4 | 1 | 3 | 3 | 1 | 2 |
| 9. *G. numidae* | 3 | 3 | 3 | 1 | 1 | 2 | 2 | 4 | 4 | 2 | 3 | (23) | (12) | (12) |
| 10. *G. hopkinsi* | 3 | 3 | 3 | 1 | 1 | 2 | 2 | 4 | 4 | 2 | 3 | 3 | 1 | 2 |
| 11. *G. gigas* | 3 | 3 | 3 | 1 | 1 | 2 | 2 | 2 | 2 | 1 | 2 | (23) | 2 | 1 |
| 12. *G. bituberculatus* | 1 | 3 | (13) | 2 | 2 | - | 1 | 1 | 1 | 1 | (23) | 2 | (12) | 1 |
| 13. *G. lagopi* | 1 | 1 | 3 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 2 | 2 | 1 | 1 |
| 14. *G. columbianus* | 3 | 3 | 3 | 2 | 2 | (12) | (12) | 2 | 2 | 2 | (23) | 2 | 1 | 1 |
| 15. *G. leucurus* | 1 | 3 | (13) | 2 | 2 | (12) | (12) | 2 | 2 | 2 | (23) | 2 | 1 | 1 |
| 16. *G. corpulentus* | 1 | 3 | (13) | 2 | 2 | (12) | (12) | 2 | 2 | 1 | (23) | 2 | 1 | 1 |
| 17. *G. merriamanus* | 1 | 1 | 3 | 1 | 2 | 1 | 1 | (12) | (12) | 1 | 2 | 2 | 1 | 1 |
| 18. *G. ithaginis* | 3 | 3 | 3 | 2 | 2 | (12) | (12) | (23) | (23) | 2 | 3 | 2 | 1 | 1 |
| 19. *G. chrysolophi* | 3 | 3 | 3 | 2 | 2 | 2 | 2 | (23) | (23) | 2 | 3 | 2 | 1 | 1 |
| 20. *G. dissimilis* | 1 | 1 | 3 | 2 | 2 | 3 | 3 | 1 | 1 | 2 | 2 | 2 | 1 | 1 |
| 21. *G. cervicornis* | 1 | 1 | (13) | 1 | 2 | 2 | 2 | 1 | 2 | 2 | (23) | 3 | 1 | (12) |
| 22. *G. sinensis* | 1 | 1 | 3 | 1 | 2 | 2 | 1 | 1 | 2 | 2 | 2 | (23) | 1 | (12) |
| 23. *G. assimilis* | (13) | (13) | 3 | 2 | 2 | 1 | 1 | 2 | 2 | 1 | (23) | 2 | 1 | 1 |
| 24. *G. dispar* | (13) | (13) | 3 | 2 | 2 | (12) | (12) | (23) | (23) | 1 | (23) | 2 | 1 | 1 |
| 25. *G. securiger* | (13) | (13) | 3 | 2 | 2 | (12) | (12) | (23) | (23) | 1 | (23) | 2 | 1 | 1 |
| 26. *G. ortygis* | 1 | 1 | 3 | 2 | 2 | 1 | 1 | 2 | 2 | 1 | 2 | 2 | 1 | 1 |
| 27. *G. tibetanus* | (13) | (13) | 3 | 2 | 2 | (12) | 2 | (23) | 4 | 2 | (23) | 2 | (13) | 1 |
| 28. *G. ammoperdix* | 3 | 3 | 3 | 2 | 2 | 2 | 1 | 2 | 2 | 1 | 1 | (23) | 2 | 1 |

**Table 2.7.** Data Matrix: Characters 85-98 (Cont.)

| Character | 08 5 | 08 6 | 08 7 | 08 8 | 08 9 | 09 0 | 09 1 | 09 2 | 09 3 | 09 4 | 09 5 | 09 6 | 09 7 | 09 8 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 29. *G. antennatus* | (13) | (13) | 3 | 2 | 2 | 3 | 3 | (12) | (12) | 1 | 2 | (23) | 1 | 2 |
| 30. *G. retractus* | 3 | 3 | 3 | 2 | 2 | 3 | (13) | 2 | 2 | 1 | 3 | 3 | 1 | 2 |
| 31. *G. soueefi* | (13) | (13) | 3 | 2 | 2 | 3 | (13) | 2 | 2 | 1 | 3 | 3 | 1 | 2 |
| 32. *G. biordinatus* | 1 | 1 | 3 | 2 | 2 | 3 | 3 | (23) | (23) | 1 | (23) | 2 | 1 | 1 |
| 33. *G. major* | 1 | 1 | 3 | 2 | 2 | 3 | 3 | (34) | (34) | 2 | (23) | 2 | 1 | 1 |
| 34. *G. fissus* | 1 | 1 | 3 | 2 | 2 | 1 | 1 | (23) | (23) | 1 | (23) | 2 | (13) | 1 |
| 35. *G. australis* | 2 | 2 | (13) | 1 | 2 | 3 | 2 | 2 | 3 | 1 | (12) | 2 | (13) | 1 |
| 36. *G. crassipes* | 1 | 1 | (13) | 1 | 1 | 3 | 3 | 2 | 2 | 1 | ? | 3 | 1 | 2 |
| 37. *Goniocotes diplogonus* | 2 | 2 | (13) | 1 | 1 | 3 | 3 | (12) | (12) | 2 | 2 | 3 | 3 | 2 |
| 38. *Gon. gallinae* | 1 | 1 | 3 | 1 | 1 | 3 | 3 | 1 | 1 | 2 | 2 | (23) | 3 | 1 |
| 39. *Gon. haplogonus* | 1 | 1 | 1 | 1 | 1 | 3 | 3 | 1 | 1 | 2 | 2 | (23) | 3 | 1 |
| 40. *Gon. pallidomaculatus* | 3 | 3 | 1 | 1 | 1 | 3 | 3 | 2 | 2 | 2 | 2 | 2 | 3 | 1 |
| 41. *Gon. parviceps* | 1 | 2 | 1 | 1 | 1 | 3 | 3 | (12) | (12) | 2 | 2 | 2 | 2 | 1 |
| 42. *Gon. reticulatus* | 1 | 1 | 2 | 1 | 1 | 3 | 3 | (12) | (12) | 2 | 2 | 1 | (13) | 1 |
| 43. *Physconelloides montana* | 1 | 1 | 1 | 2 | 2 | 3 | 3 | 4 | 4 | 2 | 2 | 2 | 1 | 1 |
| 44. *Campanulotes bidentata* | 1 | 1 | 1 | 1 | 1 | 3 | 3 | 1 | 1 | 2 | 1 | 2 | 2 | 1 |
| 45. *Heptapsogaster temporalis* | 1 | 1 | 3 | 2 | 2 | 4 | 4 | (12) | (12) | 2 | 1 | 2 | 3 | 1 |

**Table 2.7.** Data Matrix: Characters 99-112

| Character | 09 | 10 | 10 | 10 | 10 | 10 | 10 | 10 | 10 | 10 | 10 | 11 | 11 | 11 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | 9 | 0 | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 0 | 1 | 2 |
| 1. *G. pavonis* | 1 | 1 | 2 | 1 | 2 | 1 | 2 | 1 | 1 | 1 | 1 | 1 | 1 | 3 |
| 2. *G. curvicornis* | 1 | 1 | 2 | 1 | 2 | 1 | 6 | 4 | 2 | 2 | 2 | 1 | 1 | 3 |
| 3. *G. spinicornis* | 1 | 1 | 3 | 1 | 2 | 1 | 2 | 3 | 2 | 1 | 1 | 1 | 1 | 3 |
| 4. *G. megaceros* | 1 | 1 | 3 | 1 | 2 | 1 | 2 | 3 | 2 | 1 | 1 | 3 | 2 | 3 |
| 5. *G. eurygaster* | 1 | 1 | 2 | 1 | 2 | 2 | 2 | 3 | 2 | 2 | 2 | 1 | 1 | 2 |
| 6. *G. coronatus* | 1 | 1 | 2 | 1 | 2 | 1 | 2 | 3 | 2 | 1 | 1 | 1 | 1 | 2 |
| 7. *G. processus* | 2 | 1 | 1 | 1 | (45) | (45) | 2 | 3 | 2 | 2 | 2 | 4 | 4 | 2 |
| 8. *G. wilsoni* | 2 | 1 | 3 | 1 | 2 | 2 | 4 | 4 | 2 | 3 | 3 | 1 | 1 | 3 |
| 9. *G. numidae* | 2 | 1 | (23) | (12) | 1 | 1 | 4 | 4 | 2 | 3 | 3 | 1 | 1 | 2 |
| 10. *G. hopkinsi* | 2 | 1 | 1 | 1 | 1 | 1 | 4 | 4 | 2 | 3 | 3 | 1 | 1 | (34) |
| 11. *G. gigas* | 1 | 1 | (12) | 1 | (45) | (45) | 2 | 2 | (23) | 4 | 3 | 5 | 5 | (23) |
| 12. *G. bituberculatus* | 1 | 3 | (15) | 1 | (45) | (45) | 4 | 5 | (34) | 4 | 1 | 6 | 6 | (23) |
| 13. *G. lagopi* | 1 | 1 | 5 | 1 | (45) | (45) | 4 | 5 | 3 | 4 | 1 | 6 | 6 | 3 |
| 14. *G. columbianus* | (12) | 3 | (15) | 1 | 5 | 5 | 4 | 5 | (34) | 3 | 3 | 6 | 6 | (23) |
| 15. *G. leucurus* | (12) | 3 | (15) | 1 | 5 | 5 | 4 | 5 | (34) | 4 | 1 | 6 | 6 | (23) |
| 16. *G. corpulentus* | (12) | 3 | (15) | 1 | 5 | 5 | 4 | 5 | (34) | 4 | 1 | 6 | 6 | (23) |
| 17. *G. merriamanus* | 1 | 1 | 5 | 1 | 5 | 5 | 4 | 4 | 3 | 4 | 1 | 6 | 6 | 3 |
| 18. *G. ithaginis* | (12) | (23) | 5 | 1 | 4 | 5 | 4 | 5 | (34) | 4 | 1 | 6 | 5 | (23) |
| 19. *G. chrysolophi* | (12) | (23) | (15) | 1 | 5 | 5 | 4 | 5 | (34) | 4 | 1 | 6 | 6 | (23) |
| 20. *G. dissimilis* | (12) | (23) | 5 | 1 | 5 | 5 | (34) | (34) | 2 | 4 | 4 | 4 | 4 | 2 |
| 21. *G. cervicornis* | 1 | 1 | 1 | 1 | (45) | (45) | 4 | 5 | 3 | 4 | 2 | 6 | 6 | 3 |
| 22. *G. sinensis* | 1 | 1 | 5 | 1 | 5 | 5 | 2 | 4 | (34) | 4 | 1 | 6 | 6 | 3 |
| 23. *G. assimilis* | 2 | 2 | (12) | 1 | 5 | 5 | 2 | 4 | (34) | 2 | 2 | 6 | 5 | 3 |
| 24. *G. dispar* | (12) | 1 | (12) | 1 | 4 | 5 | 2 | 4 | (34) | 4 | 2 | 7 | 6 | 3 |
| 25. *G. securiger* | (12) | 1 | (12) | 1 | 5 | 5 | 2 | 4 | (34) | 4 | 2 | 7 | 6 | 3 |
| 26. *G. ortygis* | 1 | 1 | 2 | 1 | 5 | 5 | 2 | 4 | (34) | 4 | 1 | 6 | 6 | 3 |
| 27. *G. tibetanus* | (12) | (23) | (15) | 1 | 5 | 5 | 2 | 4 | (34) | 4 | 2 | 7 | 7 | 3 |
| 28. *G. ammoperdix* | 2 | 2 | 5 | 1 | 5 | 5 | (24) | 4 | (34) | 3 | 3 | 5 | 5 | 3 |

**Table 2.7.** Data Matrix: Characters 99-112 (Cont.)

| Character | 09<br>9 | 10<br>0 | 10<br>1 | 10<br>2 | 10<br>3 | 10<br>4 | 10<br>5 | 10<br>6 | 10<br>7 | 10<br>8 | 10<br>9 | 11<br>0 | 11<br>1 | 11<br>2 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 29. *G. antennatus* | 2 | 1 | 5 | 1 | 5 | 5 | 2 | 4 | 3 | 4 | 3 | 6 | 6 | 2 |
| 30. *G. retractus* | 2 | 2 | 5 | 1 | (45) | 5 | 2 | 4 | 3 | 3 | 1 | 6 | 5 | 3 |
| 31. *G. soueefi* | 2 | 1 | 6 | 1 | (45) | 5 | 2 | 4 | 3 | 3 | 3 | 6 | 5 | 3 |
| 32. *G. biordinatus* | 1 | 1 | 2 | 2 | 3 | 3 | (34) | (34) | (23) | 3 | 2 | 5 | 5 | 3 |
| 33. *G. major* | 1 | 1 | 2 | (12) | (23) | (23) | (34) | (34) | (23) | 3 | 2 | 1 | 1 | 3 |
| 34. *G. fissus* | (12) | 1 | (25) | 2 | 3 | 3 | 2 | 4 | (23) | 3 | (12) | 5 | 5 | 3 |
| 35. *G. australis* | (12) | 1 | 2 | 1 | 3 | 3 | 2 | 4 | (23) | 1 | 1 | 6 | 6 | (12) |
| 36. *G. crassipes* | 1 | 1 | 2 | 2 | 2 | 2 | 2 | 2 | 2 | 1 | 1 | 1 | 1 | 3 |
| 37. *Goniocotes diplogonus* | 1 | 1 | 2 | 1 | (12) | (12) | 6 | 6 | 2 | 1 | 1 | 1 | 1 | 3 |
| 38. *Gon. gallinae* | 1 | 1 | 6 | 1 | (12) | (12) | 6 | 6 | 2 | 1 | 1 | 1 | 1 | 2 |
| 39. *Gon. haplogonus* | 2 | 1 | 2 | 1 | (12) | (12) | 6 | 6 | 2 | 1 | 1 | 1 | 1 | 2 |
| 40. *Gon. pallidomaculatus* | 1 | 1 | 2 | 1 | 2 | 2 | 6 | 6 | 2 | 1 | 1 | 5 | 5 | 2 |
| 41. *Gon. parviceps* | 1 | 1 | 2 | (12) | 2 | 2 | 7 | 6 | 2 | 2 | 1 | 1 | 1 | 2 |
| 42. *Gon. reticulatus* | 1 | 1 | 2 | 1 | 1 | 1 | 6 | 6 | 2 | 1 | 1 | 1 | 1 | 2 |
| 43. *Physconelloides montana* | 1 | 1 | 2 | 3 | 1 | 1 | 6 | 6 | 2 | (12) | (12) | 1 | 1 | (12) |
| 44. *Campanulotes bidentata* | 1 | 1 | 2 | 1 | (45) | (45) | (23) | (23) | 2 | 3 | 3 | 6 | 6 | 2 |
| 45. *Heptapsogaster temporalis* | 2 | 1 | 6 | 2 | 1 | 1 | 4 | 4 | 2 | 4 | 3 | 1 | 1 | (23) |

**Table 2.7.** Data Matrix: Characters 113-126

| Character | 113 | 114 | 115 | 116 | 117 | 118 | 119 | 120 | 121 | 122 | 123 | 124 | 125 | 126 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 1. *G. pavonis* | 3 | 2 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 3 | 5 | 5 | 5 | 2 |
| 2. *G. curvicornis* | 2 | 2 | 1 | 1 | (12) | 1 | 1 | 1 | 1 | (12) | (12) | (12) | 5 | 1 |
| 3. *G. spinicornis* | 1 | 2 | 3 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 4 | 5 | 5 | 2 |
| 4. *G. megaceros* | 1 | 2 | 2 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 5 | 5 | 5 | 2 |
| 5. *G. eurygaster* | 2 | 2 | 2 | 1 | 1 | 1 | 1 | 1 | 2 | 3 | (25) | 5 | 5 | 2 |
| 6. *G. coronatus* | 2 | 2 | 1 | 1 | 1 | 1 | 1 | 3 | 4 | 3 | 1 | 1 | 5 | 1 |
| 7. *G. processus* | 2 | 2 | 2 | 1 | 1 | 2 | 1 | 1 | 1 | 3 | 2 | (12) | (15) | 1 |
| 8. *G. wilsoni* | 2 | 2 | 2 | (12) | 1 | 2 | 1 | 1 | 2 | (23) | 4 | 4 | (15) | 1 |
| 9. *G. numidae* | (23) | 2 | 2 | 2 | (12) | 3 | 2 | 3 | 3 | 1 | 4 | 4 | (145) | 1 |
| 10. *G. hopkinsi* | (34) | 2 | 2 | 2 | 2 | 1 | 2 | 3 | 3 | 3 | 4 | 4 | (15) | 1 |
| 11. *G. gigas* | (23) | 2 | 2 | 2 | 2 | 1 | 2 | 2 | 3 | 3 | 4 | 2 | (235) | 1 |
| 12. *G. bituberculatus* | (23) | (12) | 2 | 1 | (12) | 3 | 1 | 5 | 5 | (13) | (12) | (12) | 5 | 1 |
| 13. *G. lagopi* | 2 | 1 | 2 | 2 | 2 | 3 | 1 | 5 | 5 | (13) | 1 | 1 | (15) | 1 |
| 14. *G. columbianus* | 1 | (12) | 2 | 1 | (12) | 3 | 2 | 5 | 5 | 1 | (12) | (12) | 5 | 1 |
| 15. *G. leucurus* | 1 | (12) | 2 | 1 | (12) | 3 | 2 | 5 | 5 | (12) | (12) | (12) | 5 | 1 |
| 16. *G. corpulentus* | 1 | (12) | 2 | 1 | (12) | 3 | 2 | 5 | 5 | (12) | (12) | (12) | 5 | 1 |
| 17. *G. merriamanus* | 2 | 1 | 2 | (12) | (12) | 1 | 1 | 5 | 5 | (13) | (12) | 1 | 5 | 1 |
| 18. *G. ithaginis* | (23) | (12) | 2 | 1 | (12) | 3 | 2 | 5 | 5 | 3 | (12) | (12) | 5 | 1 |
| 19. *G. chrysolophi* | (23) | (12) | 2 | (12) | (12) | 3 | 2 | 1 | 2 | 3 | (12) | (12) | 5 | 1 |
| 20. *G. dissimilis* | 2 | (12) | 1 | (12) | 2 | 3 | 1 | (12) | (12) | 3 | 1 | 1 | (15) | 1 |
| 21. *G. cervicornis* | 2 | (12) | 1 | (12) | (12) | (23) | 1 | 5 | 3 | 3 | 1 | 1 | (15) | 1 |
| 22. *G. sinensis* | 2 | (12) | 1 | (12) | (12) | 3 | 2 | 5 | 4 | 3 | 2 | 2 | (15) | 1 |
| 23. *G. assimilis* | 2 | (12) | 3 | (12) | (23) | 1 | 1 | 4 | 4 | (13) | 1 | 1 | 5 | 1 |
| 24. *G. dispar* | 2 | (12) | (23) | (12) | 2 | 3 | 1 | 5 | 3 | 3 | 1 | 1 | 5 | 1 |
| 25. *G. securiger* | 2 | (12) | (23) | (12) | 2 | 3 | 2 | 5 | 3 | 3 | 1 | 1 | (15) | 1 |
| 26. *G. ortygis* | 2 | 1 | 2 | (12) | (12) | 3 | 1 | 5 | 5 | (13) | 1 | 1 | 5 | (12) |
| 27. *G. tibetanus* | 2 | (123) | (23) | (23) | (23) | 3 | 2 | 5 | 5 | 3 | 1 | 1 | (15) | (12) |
| 28. *G. ammoperdix* | 2 | (34) | (12) | 1 | 1 | 3 | 1 | 6 | 6 | (13) | 1 | 1 | 5 | 1 |

**Table 2.7.** Data Matrix: Characters 113-126 (Cont.)

| Character | 113 | 114 | 115 | 116 | 117 | 118 | 119 | 120 | 121 | 122 | 123 | 124 | 125 | 126 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 29. *G. antennatus* | 2 | 1 | 1 | 1 | 1 | 1 | 1 | 6 | 6 | 4 | (25) | 1 | (12) | 1 |
| 30. *G. retractus* | 3 | (12) | 1 | 1 | 1 | (13) | 1 | 6 | 6 | (13) | 1 | 1 | 1 | 1 |
| 31. *G. soueefi* | 3 | (12) | 2 | 1 | 1 | 3 | 1 | 6 | 6 | 1 | (12) | 1 | 1 | 1 |
| 32. *G. biordinatus* | 2 | (12) | 3 | 1 | (12) | 3 | 1 | 6 | ? | 1 | 1 | 1 | 5 | 1 |
| 33. *G. major* | 2 | 2 | 2 | 1 | (12) | (13) | 1 | 4 | 4 | 1 | (12) | 1 | 5 | 1 |
| 34. *G. fissus* | 2 | 1 | (13) | (12) | 2 | (13) | 1 | 4 | 4 | 1 | 4 | (12) | 5 | 2 |
| 35. *G. australis* | (12) | (1234) | (123) | (12) | 2 | (13) | 1 | 5 | 5 | 1 | (12) | (12) | 5 | 2 |
| 36. *G. crassipes* | 2 | 2 | 4 | 1 | 1 | 1 | 1 | 6 | 6 | 3 | 1 | 1 | 5 | 1 |
| 37. *Goniocotes diplogonus* | 2 | 1 | 4 | (12) | (12) | 4 | 1 | 6 | 6 | 1 | 1 | 1 | 5 | (12) |
| 38. *Gon. gallinae* | 2 | 2 | 2 | (12) | (12) | 4 | 1 | 6 | 6 | 1 | 1 | 1 | 5 | 2 |
| 39. *Gon. haplogonus* | 2 | (12) | 2 | (12) | (12) | 4 | 1 | 6 | 6 | 1 | 1 | 1 | 1 | 2 |
| 40. *Gon. pallidomaculatus* | 2 | 2 | 5 | 2 | 2 | 4 | 1 | 6 | 6 | 1 | 1 | 1 | 5 | 2 |
| 41. *Gon. parviceps* | 2 | (23) | 3 | (23) | 2 | 1 | 1 | 6 | 6 | 1 | (25) | (25) | 5 | 1 |
| 42. *Gon. reticulatus* | 2 | 2 | 3 | (23) | 2 | (14) | 1 | 6 | 6 | 1 | 1 | 1 | 5 | 2 |
| 43. *Physconelloides montana* | (12) | 1 | 2 | 1 | 1 | (13) | 1 | 3 | 3 | 3 | 1 | 1 | (15) | 1 |
| 44. *Campanulotes bidentata* | 2 | 1 | 1 | 1 | (12) | (23) | 1 | 6 | 6 | 1 | 1 | 1 | (15) | 3 |
| 45. *Heptapsogaster temporalis* | (23) | (34) | 4 | (12) | 2 | 1 | 1 | 6 | 6 | 2 | 3 | (12) | (12) | 1 |

**Table 2.7.** Data Matrix: Characters 127-140

| Character | 127 | 128 | 129 | 130 | 131 | 132 | 133 | 134 | 135 | 136 | 137 | 138 | 139 | 140 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 1. *G. pavonis* | 2 | 1 | 3 | 2 | 2 | 3 | 2 | 1 | 2 | (13) | (12) | 2 | 3 | 3 |
| 2. *G. curvicornis* | 2 | 2 | 1 | 2 | 2 | 3 | 2 | 2 | 2 | (13) | (12) | 2 | 3 | 3 |
| 3. *G. spinicornis* | 1 | 2 | 3 | 1 | 2 | 2 | 2 | 2 | 2 | (12) | (12) | 2 | 3 | 3 |
| 4. *G. megaceros* | 1 | 2 | 3 | 1 | 2 | 2 | 2 | 2 | 2 | (13) | (12) | 2 | 3 | 3 |
| 5. *G. eurygaster* | 2 | 1 | 1 | 1 | 3 | 3 | 1 | 1 | 2 | 1 | (12) | 2 | 3 | 3 |
| 6. *G. coronatus* | 1 | 1 | 3 | 1 | 3 | 3 | 2 | 2 | 2 | 1 | (12) | 2 | 3 | 3 |
| 7. *G. processus* | 1 | (12) | (12) | 2 | 2 | 3 | 1 | 1 | (23) | (13) | (12) | 2 | 2 | (23) |
| 8. *G. wilsoni* | 1 | (12) | (12) | 2 | 4 | 2 | 2 | 2 | 2 | (13) | (12) | 2 | 2 | 3 |
| 9. *G. numidae* | 3 | 1 | 2 | 2 | 4 | 2 | 1 | 2 | 2 | 1 | 1 | 2 | (23) | 3 |
| 10. *G. hopkinsi* | 1 | 1 | 1 | 2 | 4 | 2 | 1 | 1 | 2 | 1 | 1 | 2 | (23) | (23) |
| 11. *G. gigas* | 1 | 1 | 1 | 1 | 2 | 2 | 1 | 1 | 4 | (12) | (12) | 1 | 2 | 2 |
| 12. *G. bituberculatus* | 1 | 1 | 1 | 2 | (23) | 3 | 2 | 1 | 2 | 1 | 1 | 2 | 2 | 3 |
| 13. *G. lagopi* | 1 | 1 | 1 | 2 | 2 | 3 | 2 | 1 | 2 | 1 | 1 | 2 | 2 | 3 |
| 14. *G. columbianus* | 1 | 1 | 1 | 2 | 2 | 3 | 2 | 1 | 2 | 1 | 1 | 2 | 2 | 3 |
| 15. *G. leucurus* | 1 | 1 | 1 | 2 | 2 | 3 | 2 | 1 | 2 | 1 | 1 | 2 | 2 | 3 |
| 16. *G. corpulentus* | 1 | 1 | 1 | 2 | 2 | 3 | 2 | 1 | 2 | 1 | 1 | 2 | 2 | 3 |
| 17. *G. merriamanus* | 1 | 1 | 1 | 2 | (23) | 3 | 2 | 1 | (12) | 1 | 1 | 2 | 2 | 3 |
| 18. *G. ithaginis* | 1 | (12) | 1 | 2 | 2 | 3 | 1 | 1 | 2 | 1 | 1 | 2 | 2 | 3 |
| 19. *G. chrysolophi* | 1 | (12) | (12) | 2 | 2 | 3 | 1 | 1 | 2 | 1 | 1 | 2 | 2 | 3 |
| 20. *G. dissimilis* | 1 | 1 | 1 | ? | 3 | 3 | 1 | 1 | 1 | 1 | 1 | 2 | 4 | (23) |
| 21. *G. cervicornis* | 1 | 1 | 1 | 2 | 2 | 3 | 1 | 1 | 1 | 2 | 1 | 2 | 2 | (23) |
| 22. *G. sinensis* | 1 | 1 | 1 | 2 | (23) | 3 | - | 1 | 2 | 2 | 1 | 2 | 4 | 3 |
| 23. *G. assimilis* | 1 | 2 | 2 | 2 | 2 | 3 | 2 | 1 | (13) | 1 | 1 | 2 | (34) | 3 |
| 24. *G. dispar* | 1 | 1 | 1 | 2 | 2 | 3 | 2 | 2 | (13) | 1 | 1 | 2 | (34) | 3 |
| 25. *G. securiger* | 1 | 1 | 1 | 2 | 2 | 3 | 1 | 1 | (13) | 1 | 1 | 2 | (34) | 3 |
| 26. *G. ortygis* | (12) | 2 | 2 | 1 | 3 | 3 | 2 | 2 | 2 | 1 | 1 | 2 | (24) | 3 |
| 27. *G. tibetanus* | (12) | 1 | 1 | 2 | 2 | 3 | 1 | 1 | 2 | 1 | 1 | 2 | (34) | 3 |
| 28. *G. ammoperdix* | 1 | 2 | 2 | 1 | 2 | 2 | 1 | 1 | 2 | 1 | 1 | 1 | 2 | 3 |

**Table 2.7.** Data Matrix: Characters 127-140 (Cont.)

| Character | 12<br>7 | 12<br>8 | 12<br>9 | 13<br>0 | 13<br>1 | 13<br>2 | 13<br>3 | 13<br>4 | 13<br>5 | 13<br>6 | 13<br>7 | 13<br>8 | 13<br>9 | 14<br>0 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 29. *G. antennatus* | 1 | 2 | 2 | 1 | (23) | (23) | 1 | 1 | (13) | 1 | (12) | 2 | (24) | 3 |
| 30. *G. retractus* | 1 | 1 | 1 | 1 | (23) | (23) | 2 | 1 | 2 | 3 | 1 | 2 | 4 | 2 |
| 31. *G. soueefi* | 1 | 1 | 1 | 1 | (23) | 3 | 2 | 2 | (12) | 3 | 1 | 2 | 4 | 3 |
| 32. *G. biordinatus* | 1 | - | - | 1 | 3 | 3 | 1 | 1 | 2 | (13) | (12) | 1 | 1 | 2 |
| 33. *G. major* | 1 | 1 | 1 | 1 | 3 | 3 | 1 | 1 | 2 | (13) | 1 | (12) | 3 | 3 |
| 34. *G. fissus* | 1 | 2 | 2 | 1 | 3 | 3 | 1 | 1 | 2 | (13) | 1 | 2 | (23) | 2 |
| 35. *G. australis* | 2 | 1 | (12) | 2 | (23) | (13) | 2 | 1 | 2 | (13) | 1 | 2 | 2 | 1 |
| 36. *G. crassipes* | 1 | 1 | 1 | 1 | 3 | 3 | 1 | 1 | 3 | (13) | 1 | (12) | 2 | 3 |
| 37. *Goniocotes diplogonus* | (12) | 1 | 1 | 1 | 3 | 3 | 2 | 2 | (24) | 1 | 2 | (12) | 1 | (23) |
| 38. *Gon. gallinae* | 2 | (23) | (23) | 1 | 3 | 3 | 2 | 2 | (24) | 1 | 2 | (12) | 1 | (23) |
| 39. *Gon. haplogonus* | 2 | (12) | (12) | 1 | 3 | 3 | 2 | 2 | (24) | 1 | (12) | 2 | (23) | 3 |
| 40. *Gon. pallidomaculatus* | 2 | (13) | (13) | 1 | 3 | 3 | 2 | 2 | (24) | 1 | (12) | 2 | (23) | 2 |
| 41. *Gon. parviceps* | 1 | 2 | 2 | 2 | 3 | (23) | 2 | 2 | (24) | 1 | (12) | 2 | (23) | (23) |
| 42. *Gon. reticulatus* | 2 | 1 | 1 | 1 | 3 | 3 | 2 | 2 | (24) | 2 | (12) | 2 | 3 | (23) |
| 43. *Physconelloides montana* | 1 | 1 | 1 | 1 | 3 | 3 | 1 | 1 | 2 | 3 | 1 | 1 | 4 | 3 |
| 44. *Campanulotes bidentata* | 3 | 1 | 1 | 1 | 3 | 3 | 2 | 2 | 2 | (12) | 1 | (12) | (23) | 3 |
| 45. *Heptapsogaster temporalis* | 1 | 1 | 1 | 1 | 2 | 2 | 2 | 2 | (12) | 1 | 1 | 2 | 4 | 3 |

**Table 2.7.** Data Matrix: Characters 141-154

| Character | 14 | 14 | 14 | 14 | 14 | 14 | 14 | 14 | 14 | 15 | 15 | 15 | 15 | 15 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 0 | 1 | 2 | 3 | 4 |
| 1. *G. pavonis* | 1 | 1 | 1 | 2 | 1 | 1 | 3 | 3 | 1 | 3 | 3 | 2 | 1 | 3 |
| 2. *G. curvicornis* | 1 | 1 | 1 | 2 | 1 | 1 | 3 | 3 | 1 | 3 | 3 | 1 | 1 | 1 |
| 3. *G. spinicornis* | 1 | 1 | 1 | 2 | 1 | 1 | 3 | 3 | 2 | 3 | 3 | 2 | 1 | 1 |
| 4. *G. megaceros* | 1 | 1 | 1 | 2 | 1 | 1 | 3 | 3 | 1 | 3 | 3 | (12) | 1 | (13) |
| 5. *G. eurygaster* | 1 | 1 | 1 | 2 | 1 | 1 | 3 | 3 | 1 | (13) | 3 | 3 | 1 | (13) |
| 6. *G. coronatus* | 1 | 1 | 1 | 1 | 1 | 1 | 3 | 1 | 1 | 2 | 3 | 1 | 1 | 1 |
| 7. *G. processus* | 2 | - | 1 | 1 | 1 | 2 | 1 | 1 | 1 | 3 | 3 | 3 | 1 | 1 |
| 8. *G. wilsoni* | 1 | 1 | 1 | 1 | (34) | 3 | 4 | 3 | 1 | 3 | (23) | 2 | 1 | 1 |
| 9. *G. numidae* | (12) | 1 | 1 | 1 | 2 | 3 | 4 | 3 | 2 | 1 | (23) | 2 | 1 | 1 |
| 10. *G. hopkinsi* | 1 | 1 | 1 | 2 | 2 | 3 | 4 | 3 | 1 | 2 | (23) | 2 | 1 | 1 |
| 11. *G. gigas* | 2 | - | 1 | 1 | 1 | 2 | 3 | 1 | 1 | 2 | 3 | 3 | 1 | 1 |
| 12. *G. bituberculatus* | 2 | - | 1 | (12) | 1 | (12) | 1 | 1 | 2 | (23) | 3 | 3 | 1 | 2 |
| 13. *G. lagopi* | 2 | - | 1 | (12) | 1 | (12) | 1 | 1 | 1 | 1 | 3 | 3 | 1 | 1 |
| 14. *G. columbianus* | 2 | - | 1 | (12) | 1 | (12) | 1 | 3 | 1 | 2 | 3 | 2 | 1 | (12) |
| 15. *G. leucurus* | 1 | 2 | 1 | 2 | 1 | (12) | 1 | 3 | 1 | (13) | 3 | 3 | 1 | (12) |
| 16. *G. corpulentus* | 1 | 2 | 1 | 1 | 1 | 2 | 1 | 3 | 1 | (12) | 3 | 2 | 1 | 1 |
| 17. *G. merriamanus* | 2 | - | 1 | (12) | 1 | (12) | 1 | 1 | 1 | 2 | 3 | 1 | 1 | 1 |
| 18. *G. ithaginis* | 1 | 2 | 1 | 1 | 1 | 2 | 1 | 3 | 1 | (24) | 3 | 2 | 1 | 3 |
| 19. *G. chrysolophi* | 1 | 2 | 1 | 1 | 1 | 2 | 1 | 3 | 1 | (23) | 3 | 2 | 1 | 3 |
| 20. *G. dissimilis* | 2 | - | 1 | 1 | 1 | 2 | 1 | 1 | 1 | 2 | 3 | 1 | 1 | 1 |
| 21. *G. cervicornis* | (12) | 2 | 1 | 1 | 1 | (12) | (13) | 1 | 1 | 3 | 3 | 3 | 1 | 1 |
| 22. *G. sinensis* | 2 | - | 1 | 1 | 1 | 2 | 1 | 1 | 1 | 1 | (13) | 1 | 1 | 1 |
| 23. *G. assimilis* | (12) | (12) | 1 | (12) | 1 | 2 | 1 | 2 | 1 | (23) | (13) | 2 | 1 | 3 |
| 24. *G. dispar* | 1 | (12) | 1 | 1 | 1 | 2 | 1 | 3 | 1 | (23) | (13) | 2 | 1 | 3 |
| 25. *G. securiger* | 1 | (12) | 1 | 1 | 1 | 2 | 1 | 3 | 1 | (24) | 3 | 2 | 1 | 3 |
| 26. *G. ortygis* | 1 | 1 | 1 | 1 | 1 | (12) | 1 | 1 | 1 | 2 | (13) | 2 | 1 | 1 |
| 27. *G. tibetanus* | 1 | (12) | 1 | 1 | 1 | 2 | 1 | 3 | 1 | (245) | (13) | 3 | 1 | (13) |
| 28. *G. ammoperdix* | 1 | 3 | 2 | 1 | 1 | (12) | 1 | 1 | 1 | 2 | (13) | 1 | 1 | 1 |

**Table 2.7.** Data Matrix: Characters 141-154 (Cont.)

| Character | 14<br>1 | 14<br>2 | 14<br>3 | 14<br>4 | 14<br>5 | 14<br>6 | 14<br>7 | 14<br>8 | 14<br>9 | 15<br>0 | 15<br>1 | 15<br>2 | 15<br>3 | 15<br>4 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 29. *G. antennatus* | 2 | - | 1 | 1 | 1 | 2 | 1 | 1 | 1 | 1 | (13) | 3 | 1 | 1 |
| 30. *G. retractus* | 2 | - | 1 | 1 | 1 | 2 | 1 | 1 | 1 | 2 | 3 | (12) | (12) | 2 |
| 31. *G. soueefi* | 2 | - | 1 | 1 | 1 | 2 | 1 | 1 | 1 | 1 | 3 | (12) | (12) | 2 |
| 32. *G. biordinatus* | 1 | 4 | 3 | 2 | 1 | 2 | 3 | 3 | 1 | 1 | 3 | 1 | 1 | 1 |
| 33. *G. major* | 1 | (14) | 3 | 2 | 1 | 2 | 3 | 3 | 1 | 1 | 3 | 1 | 1 | 1 |
| 34. *G. fissus* | 1 | (12) | 1 | 2 | 1 | 2 | 1 | 2 | 1 | 6 | 3 | 3 | 1 | 1 |
| 35. *G. australis* | 1 | 1 | 1 | 1 | 1 | 3 | 3 | 3 | 1 | 3 | 3 | (12) | 1 | 1 |
| 36. *G. crassipes* | 2 | - | 1 | 2 | 1 | (12) | 1 | 1 | 1 | 1 | 3 | 3 | 1 | 1 |
| 37. *Goniocotes diplogonus* | 1 | (14) | 3 | 1 | 1 | (12) | 3 | 1 | 1 | 3 | 4 | 3 | 1 | 1 |
| 38. *Gon. gallinae* | 1 | (14) | 3 | 1 | 1 | 2 | 3 | 1 | 1 | (13) | 3 | 3 | 1 | 1 |
| 39. *Gon. haplogonus* | 2 | - | (13) | 1 | 1 | 1 | (23) | 1 | 1 | 3 | 4 | 3 | 1 | (12) |
| 40. *Gon. pallidomaculatus* | 1 | (14) | 3 | (12) | 1 | (12) | 3 | 1 | 1 | (12) | 4 | 1 | 1 | 1 |
| 41. *Gon. parviceps* | 1 | (14) | 3 | 1 | 1 | (12) | 3 | 3 | 1 | 1 | 4 | 3 | 3 | 1 |
| 42. *Gon. reticulatus* | 1 | (14) | (13) | 1 | 1 | 2 | 3 | 1 | 2 | (13) | 3 | 1 | 3 | 1 |
| 43. *Physconelloides montana* | 1 | 2 | 1 | 1 | 1 | (12) | 1 | 3 | 1 | 2 | (12) | 3 | 1 | 1 |
| 44. *Campanulotes bidentata* | 1 | 1 | 1 | 1 | 1 | (12) | (13) | 3 | 2 | 1 | 3 | 3 | 1 | 1 |
| 45. *Heptapsogaster temporalis* | 2 | - | 1 | 1 | 1 | 1 | 1 | 3 | 2 | (12) | 4 | 1 | 2 | 2 |

**Table 2.7.** Data Matrix: Characters 155-168

| Character | 15 | 15 | 15 | 15 | 15 | 16 | 16 | 16 | 16 | 16 | 16 | 16 | 16 | 16 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | 5 | 6 | 7 | 8 | 9 | 0 | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 |
| 1. *G. pavonis* | 1 | 1 | 2 | 3 | 2 | 1 | 1 | 1 | 1 | 1 | 1 | 2 | 2 | 2 |
| 2. *G. curvicornis* | 1 | 1 | 1 | 1 | 2 | 1 | 2 | 1 | 1 | 1 | 1 | 2 | 2 | 2 |
| 3. *G. spinicornis* | 2 | 2 | 1 | (135) | 1 | 2 | 1 | 1 | 1 | 1 | 1 | 2 | 2 | 1 |
| 4. *G. megaceros* | 2 | 1 | 2 | (13) | 1 | 2 | 1 | 1 | 1 | 1 | 1 | 2 | 2 | 2 |
| 5. *G. eurygaster* | 2 | 1 | 2 | 4 | 1 | 2 | 1 | 1 | 2 | 1 | 1 | 2 | 2 | 2 |
| 6. *G. coronatus* | 2 | 2 | 2 | 1 | 1 | 2 | 1 | 1 | 2 | 1 | 2 | (12) | 1 | 1 |
| 7. *G. processus* | 2 | 2 | 2 | 5 | 1 | 2 | 2 | 1 | 2 | 1 | 2 | 2 | 1 | 1 |
| 8. *G. wilsoni* | 2 | 1 | 2 | 5 | 2 | 2 | 4 | (12) | 2 | 1 | 1 | 2 | (12) | 1 |
| 9. *G. numidae* | 2 | 2 | 2 | (13) | 2 | 2 | 4 | 2 | 2 | 1 | 1 | 2 | 1 | 1 |
| 10. *G. hopkinsi* | 2 | 2 | 2 | (13) | 2 | 2 | 4 | 1 | 2 | 1 | 1 | (12) | 1 | 1 |
| 11. *G. gigas* | 2 | 2 | 2 | 1 | 1 | 2 | 1 | 1 | 3 | 1 | 2 | (12) | (12) | 1 |
| 12. *G. bituberculatus* | 2 | 2 | 2 | 5 | 2 | 2 | 1 | 1 | 2 | 1 | 2 | 2 | (12) | 1 |
| 13. *G. lagopi* | 2 | 2 | 2 | 5 | 1 | 2 | 1 | 1 | 2 | 1 | 2 | 2 | (12) | 1 |
| 14. *G. columbianus* | 2 | 2 | 2 | 3 | 1 | 2 | 1 | 1 | 1 | 1 | 2 | 2 | (12) | 1 |
| 15. *G. leucurus* | 2 | 2 | 2 | 5 | 1 | 2 | 1 | 1 | 1 | 1 | 1 | 2 | 2 | 1 |
| 16. *G. corpulentus* | 2 | 2 | 2 | 3 | 1 | 2 | 1 | 1 | 1 | 1 | 2 | 2 | 2 | 1 |
| 17. *G. merriamanus* | 2 | 2 | 2 | (13) | 1 | 2 | 1 | 1 | 1 | 1 | 1 | (12) | (12) | 1 |
| 18. *G. ithaginis* | 1 | 1 | (23) | 4 | 1 | 2 | 1 | 1 | 2 | 1 | 2 | 2 | (12) | 1 |
| 19. *G. chrysolophi* | 1 | 1 | (23) | 4 | 1 | 2 | 1 | 1 | 2 | 1 | 2 | 2 | (12) | 1 |
| 20. *G. dissimilis* | 1 | 2 | 3 | (13) | 1 | 2 | 1 | 1 | 1 | 1 | 2 | 2 | 1 | 1 |
| 21. *G. cervicornis* | 1 | 1 | 3 | (13) | 1 | 2 | 1 | 1 | (12) | 1 | (12) | (12) | (12) | 1 |
| 22. *G. sinensis* | 1 | (12) | 3 | (13) | 1 | 2 | 1 | 1 | 1 | 1 | 1 | (12) | (12) | 1 |
| 23. *G. assimilis* | 2 | 1 | 2 | 4 | 1 | 2 | (12) | 1 | (12) | 1 | 2 | 2 | (12) | 1 |
| 24. *G. dispar* | 2 | 1 | (23) | (34) | 1 | 2 | 1 | 1 | (12) | 1 | 2 | 2 | 1 | 1 |
| 25. *G. securiger* | 2 | 1 | (23) | (34) | 1 | 2 | 1 | 1 | (12) | 1 | 2 | 2 | (12) | 2 |
| 26. *G. ortygis* | 2 | 1 | 2 | 5 | 1 | 2 | 3 | 1 | (12) | 1 | (12) | 2 | 2 | 1 |
| 27. *G. tibetanus* | 2 | (12) | (23) | (34) | 1 | 2 | 2 | 1 | (12) | 1 | 2 | 2 | 1 | 1 |
| 28. *G. ammoperdix* | 1 | 1 | 1 | 1 | 1 | 2 | 1 | 1 | (12) | 1 | 2 | (12) | 1 | 1 |

**Table 2.7.** Data Matrix: Characters 155-168 (Cont.)

| Character | 155 | 156 | 157 | 158 | 159 | 160 | 161 | 162 | 163 | 164 | 165 | 166 | 167 | 168 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 29. *G. antennatus* | (12) | 2 | 2 | 1 | 1 | 2 | 1 | 1 | (23) | 1 | 2 | 2 | 2 | 1 |
| 30. *G. retractus* | 2 | 2 | 2 | (13) | 1 | 2 | 1 | 1 | 4 | 1 | 2 | 1 | 2 | 1 |
| 31. *G. soueefi* | 1 | 2 | 3 | (13) | 1 | 2 | 1 | 1 | 4 | 1 | 2 | 1 | 2 | 1 |
| 32. *G. biordinatus* | 1 | 2 | (12) | (13) | 1 | 2 | 1 | 1 | 2 | 1 | 2 | 1 | 1 | 1 |
| 33. *G. major* | 2 | 2 | (12) | (13) | 1 | 2 | 1 | 1 | 2 | 1 | 1 | (12) | 1 | 1 |
| 34. *G. fissus* | 2 | 2 | 2 | 3 | 2 | 2 | 1 | 1 | (23) | 1 | (12) | 2 | 1 | 2 |
| 35. *G. australis* | (12) | 2 | 2 | (15) | 2 | 2 | 3 | 2 | (23) | 1 | 1 | (12) | 2 | 1 |
| 36. *G. crassipes* | 1 | 2 | (12) | 5 | 1 | 2 | (13) | 1 | 5 | 2 | 3 | (12) | 1 | 1 |
| 37. *Goniocotes diplogonus* | 3 | 1 | 1 | (12) | (12) | 2 | 1 | 1 | 5 | 2 | 3 | (12) | 1 | 1 |
| 38. *Gon. gallinae* | 3 | 1 | 2 | (13) | 1 | 2 | 1 | 1 | 5 | 2 | 3 | (12) | 1 | 1 |
| 39. *Gon. haplogonus* | 3 | 1 | (12) | (12) | 1 | 2 | 1 | 1 | 5 | 2 | 3 | (12) | 1 | 2 |
| 40. *Gon. pallidomaculatus* | (23) | 1 | (12) | (12) | (12) | 2 | 1 | 1 | 5 | 2 | 3 | (12) | 1 | 1 |
| 41. *Gon. parviceps* | (23) | 1 | (12) | (13) | 1 | 2 | 1 | 1 | 5 | 2 | 3 | 1 | 1 | 1 |
| 42. *Gon. reticulatus* | (23) | 1 | (12) | 1 | 1 | 2 | 1 | 1 | 5 | 2 | 3 | 2 | 2 | 1 |
| 43. *Physconelloides montana* | 2 | 2 | 2 | (13) | 1 | 2 | 1 | 1 | 4 | (12) | 1 | 2 | 1 | 1 |
| 44. *Campanulotes bidentata* | 1 | 1 | 3 | 3 | 1 | 2 | 1 | 1 | 1 | 3 | (12) | (12) | 1 | 1 |
| 45. *Heptapsogaster temporalis* | 3 | 1 | (23) | 3 | 1 | 2 | 3 | 1 | (45) | 1 | 1 | (12) | 2 | 1 |

**Table 2.7.** Data Matrix: Characters 169-182

| Character | 169 | 170 | 171 | 172 | 173 | 174 | 175 | 176 | 177 | 178 | 179 | 180 | 181 | 182 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 1. *G. pavonis* | 1 | 1 | 2 | 1 | 2 | 2 | 1 | 1 | 2 | 2 | 1 | 3 | 3 | 2 |
| 2. *G. curvicornis* | 2 | 2 | 1 | 1 | 2 | 3 | 1 | 1 | 3 | 2 | 1 | 3 | 3 | 2 |
| 3. *G. spinicornis* | 2 | 1 | 2 | 1 | 2 | 3 | 1 | 2 | 2 | 1 | 2 | 3 | 3 | (12) |
| 4. *G. megaceros* | 1 | 1 | 2 | 1 | 2 | 1 | 1 | 2 | 2 | 1 | 1 | 3 | 3 | 1 |
| 5. *G. eurygaster* | 1 | 1 | 2 | 1 | 2 | 1 | 1 | 2 | 2 | 1 | 2 | 3 | 3 | 2 |
| 6. *G. coronatus* | 2 | 1 | 2 | 1 | 2 | 3 | 1 | 1 | 3 | 1 | 2 | 1 | 3 | 1 |
| 7. *G. processus* | 2 | 1 | 1 | 1 | 2 | 2 | 1 | 2 | 2 | 1 | (12) | 3 | 3 | (12) |
| 8. *G. wilsoni* | 2 | 1 | 1 | 1 | 3 | 2 | 1 | 4 | 3 | (12) | 1 | 3 | 3 | (12) |
| 9. *G. numidae* | 2 | 1 | 1 | 1 | 2 | 2 | 1 | 4 | 3 | 1 | 1 | 3 | 3 | 2 |
| 10. *G. hopkinsi* | 2 | 1 | 1 | 1 | 2 | 2 | 1 | 4 | 3 | 1 | (12) | 3 | 3 | 2 |
| 11. *G. gigas* | 2 | 1 | 1 | 1 | 2 | 1 | 1 | (14) | (23) | 1 | 1 | 3 | 3 | 2 |
| 12. *G. bituberculatus* | 2 | 1 | 1 | 2 | 1 | 1 | 2 | 1 | 2 | 1 | 1 | 2 | (23) | (12) |
| 13. *G. lagopi* | 2 | 1 | 1 | 1 | 1 | 1 | 2 | 1 | (23) | 2 | 2 | 2 | (23) | (12) |
| 14. *G. columbianus* | 2 | 1 | 1 | 1 | 1 | (13) | (13) | 1 | 2 | 1 | 1 | 1 | (23) | 1 |
| 15. *G. leucurus* | 2 | 1 | 1 | 1 | 1 | (13) | 1 | 1 | 2 | (12) | 2 | 2 | (23) | 2 |
| 16. *G. corpulentus* | 2 | 1 | 1 | 1 | 1 | (13) | 1 | 1 | 2 | (12) | 2 | (23) | (23) | (12) |
| 17. *G. merriamanus* | 2 | 1 | 1 | 1 | 1 | 3 | 1 | 1 | 2 | 1 | 2 | 3 | 3 | (12) |
| 18. *G. ithaginis* | 2 | 1 | 1 | 1 | 1 | (123) | 1 | 1 | 2 | (12) | 2 | (23) | (23) | (12) |
| 19. *G. chrysolophi* | 2 | 1 | 1 | 1 | 1 | (123) | 1 | 1 | 2 | (12) | 2 | 2 | (23) | 2 |
| 20. *G. dissimilis* | 2 | 1 | 1 | 1 | 1 | 3 | 3 | 1 | 2 | 1 | 1 | (12) | 3 | (12) |
| 21. *G. cervicornis* | 2 | 1 | 1 | 1 | 1 | 3 | (13) | 1 | 2 | 1 | 2 | 1 | 3 | 2 |
| 22. *G. sinensis* | 2 | 1 | 1 | 1 | 1 | 3 | (13) | 1 | 2 | (12) | (12) | 2 | 3 | 2 |
| 23. *G. assimilis* | 2 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 2 | 1 | 2 | 1 | (23) | (12) |
| 24. *G. dispar* | 2 | 1 | 1 | 1 | 1 | 1 | 1 | 4 | 2 | (12) | (12) | (23) | 3 | 2 |
| 25. *G. securiger* | 3 | 2 | 1 | 1 | 1 | 1 | 1 | 4 | 2 | 1 | 1 | (12) | (23) | 2 |
| 26. *G. ortygis* | 2 | 1 | 1 | 1 | 1 | 1 | 1 | 4 | 2 | 1 | (12) | 1 | 2 | (12) |
| 27. *G. tibetanus* | 2 | 1 | 1 | 1 | 1 | (13) | (13) | 1 | 2 | (12) | 2 | (23) | (23) | 2 |
| 28. *G. ammoperdix* | 2 | 1 | 1 | 1 | 1 | 1 | 1 | 4 | 2 | 1 | 2 | 1 | 3 | 1 |

**Table 2.7.** Data Matrix: Characters 169-182 (Cont.)

| Character | 169 | 170 | 171 | 172 | 173 | 174 | 175 | 176 | 177 | 178 | 179 | 180 | 181 | 182 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 29. *G. antennatus* | 2 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 2 | 1 | (12) | 2 | 2 | 2 |
| 30. *G. retractus* | 2 | 1 | 1 | 1 | 1 | 2 | 2 | 3 | 3 | 1 | (12) | (12) | (23) | (12) |
| 31. *G. soueefi* | 2 | 1 | 1 | 1 | 1 | 2 | 2 | 3 | 3 | 1 | 1 | 3 | 2 | (12) |
| 32. *G. biordinatus* | 2 | 1 | 1 | 1 | 2 | 1 | 1 | 2 | 2 | 1 | (12) | 2 | 3 | (12) |
| 33. *G. major* | 2 | 1 | 1 | 1 | 2 | 3 | 1 | 1 | 1 | 1 | 1 | 3 | 3 | (12) |
| 34. *G. fissus* | 4 | 1 | 1 | 2 | 1 | 2 | 2 | 1 | (12) | (12) | (12) | 3 | 2 | (12) |
| 35. *G. australis* | 2 | 1 | 1 | (12) | 1 | 1 | (12) | 1 | 2 | 1 | 1 | 2 | (23) | 2 |
| 36. *G. crassipes* | 2 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 2 | 1 | 1 | 2 | 2 | 1 |
| 37. *Goniocotes diplogonus* | 2 | 1 | 2 | 1 | 3 | 2 | 1 | 1 | 2 | 1 | 1 | 3 | 3 | 2 |
| 38. *Gon. gallinae* | 2 | 1 | 2 | 1 | 3 | 2 | 1 | 1 | 2 | 1 | 1 | (23) | 3 | 1 |
| 39. *Gon. haplogonus* | 2 | 1 | 2 | 1 | 3 | 3 | 1 | 1 | (23) | 1 | 1 | 3 | 3 | (12) |
| 40. *Gon. pallidomaculatus* | 2 | 1 | 2 | 1 | 3 | 1 | 1 | 1 | 1 | 1 | 1 | (12) | 3 | 1 |
| 41. *Gon. parviceps* | 2 | 1 | 2 | 1 | 3 | 1 | 1 | 2 | 2 | 1 | 1 | 3 | 3 | 2 |
| 42. *Gon. reticulatus* | 2 | 1 | 2 | 1 | 3 | 1 | 1 | 1 | (12) | 1 | 1 | 2 | 3 | 1 |
| 43. *Physconelloides montana* | 2 | 1 | 1 | 1 | 1 | 3 | 1 | 2 | 2 | 1 | 1 | (23) | 3 | 1 |
| 44. *Campanulotes bidentata* | 2 | 1 | 1 | 1 | 1 | 1 | 1 | 2 | 2 | 1 | 1 | (12) | (23) | 1 |
| 45. *Heptapsogaster temporalis* | 2 | 1 | 2 | 1 | 1 | 3 | 3 | 2 | 2 | 1 | 1 | 3 | 1 | 2 |

**Table 2.7.** Data Matrix: Characters 183-196

| Character | 183 | 184 | 185 | 186 | 187 | 188 | 189 | 190 | 191 | 192 | 193 | 194 | 195 | 196 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 1. *G. pavonis* | 2 | 2 | 1 | 2 | 2 | 2 | 2 | 1 | 3 | 3 | 2 | 1 | 1 | 1 |
| 2. *G. curvicornis* | 2 | 2 | 1 | 2 | (12) | (12) | 1 | 1 | 3 | 3 | 2 | 1 | 1 | 1 |
| 3. *G. spinicornis* | 2 | 2 | 2 | 2 | (23) | 3 | 1 | 1 | 3 | 3 | 4 | 2 | 1 | 2 |
| 4. *G. megaceros* | 2 | 1 | 2 | 2 | 1 | 2 | 1 | 1 | 3 | 3 | 2 | 1 | 1 | 2 |
| 5. *G. eurygaster* | 2 | 2 | 2 | 2 | 1 | 2 | (12) | 1 | 2 | 3 | 2 | 2 | 2 | (12) |
| 6. *G. coronatus* | (23) | 1 | 3 | 3 | 1 | 2 | 1 | (12) | 1 | - | - | 2 | 1 | (23) |
| 7. *G. processus* | 2 | 1 | 2 | 2 | 2 | 2 | 1 | 2 | 3 | 3 | 3 | 2 | 1 | 3 |
| 8. *G. wilsoni* | (23) | 1 | (12) | 2 | 2 | 2 | 1 | 1 | 3 | 3 | 2 | 2 | 1 | 1 |
| 9. *G. numidae* | 2 | 2 | (12) | (12) | 3 | 1 | 1 | 1 | 3 | 3 | 2 | 1 | 3 | (13) |
| 10. *G. hopkinsi* | 2 | (12) | (12) | 2 | 2 | 2 | 1 | 2 | 1 | - | - | 1 | 3 | 2 |
| 11. *G. gigas* | 2 | 1 | (12) | (23) | 2 | 2 | 1 | 2 | 3 | 3 | 2 | 2 | 1 | 3 |
| 12. *G. bituberculatus* | 2 | 1 | 1 | (23) | 2 | 2 | 1 | 1 | 1 | - | - | 1 | 2 | 2 |
| 13. *G. lagopi* | 2 | 1 | (23) | (23) | 2 | 2 | 1 | 1 | 2 | 3 | - | 2 | 1 | 3 |
| 14. *G. columbianus* | 2 | 1 | 3 | 3 | 2 | 2 | 1 | 2 | 2 | (12) | - | 2 | 1 | 3 |
| 15. *G. leucurus* | 2 | 1 | (23) | (23) | 2 | 2 | 1 | 2 | 1 | - | - | 2 | 1 | 2 |
| 16. *G. corpulentus* | 2 | 1 | 3 | 3 | 2 | 2 | 1 | 2 | 2 | (12) | - | 2 | 1 | 2 |
| 17. *G. merriamanus* | 2 | 1 | 2 | (23) | 2 | 2 | 1 | 1 | 3 | 3 | 2 | 2 | 1 | 3 |
| 18. *G. ithaginis* | 2 | 1 | 3 | (23) | 2 | 2 | 1 | 2 | 2 | (12) | - | 2 | 1 | 3 |
| 19. *G. chrysolophi* | 2 | 1 | 3 | (23) | 2 | 2 | 2 | 2 | 1 | - | - | 2 | 1 | 3 |
| 20. *G. dissimilis* | 2 | 1 | 3 | 3 | 2 | 2 | 1 | 1 | 1 | - | - | 2 | 2 | 3 |
| 21. *G. cervicornis* | 2 | (12) | (12) | (23) | (12) | 2 | 1 | 1 | 1 | - | - | 2 | 1 | 3 |
| 22. *G. sinensis* | 2 | 1 | 2 | 2 | 2 | 2 | 1 | 1 | 3 | 3 | 2 | 2 | 1 | 3 |
| 23. *G. assimilis* | 2 | 1 | (23) | (23) | 2 | 2 | 1 | 2 | 1 | - | - | 2 | 1 | 3 |
| 24. *G. dispar* | 2 | 1 | 3 | 3 | 2 | 2 | 2 | 1 | 1 | - | - | 2 | 1 | (23) |
| 25. *G. securiger* | 2 | 1 | (23) | (23) | 2 | 2 | 2 | (12) | 1 | - | - | 2 | 1 | (23) |
| 26. *G. ortygis* | 2 | 1 | 2 | 2 | 2 | 2 | 1 | (12) | 1 | - | - | 2 | 1 | 3 |
| 27. *G. tibetanus* | 2 | 1 | (23) | (23) | 2 | 2 | 2 | 2 | 3 | 2 | 2 | 2 | 1 | 3 |
| 28. *G. ammoperdix* | 2 | 1 | (23) | (23) | 2 | 2 | 1 | (12) | 1 | - | - | 2 | 1 | 3 |

**Table 2.7.** Data Matrix: Characters 183-196 (Cont.)

| Character | 18 3 | 18 4 | 18 5 | 18 6 | 18 7 | 18 8 | 18 9 | 19 0 | 19 1 | 19 2 | 19 3 | 19 4 | 19 5 | 19 6 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 29. *G. antennatus* | 2 | 1 | 2 | 2 | 2 | 2 | 1 | 2 | 3 | 3 | 2 | 2 | 1 | 3 |
| 30. *G. retractus* | 3 | 1 | 2 | (23) | 2 | 2 | 1 | 2 | 1 | - | - | 2 | 1 | (12) |
| 31. *G. soueefi* | 3 | 1 | 2 | (23) | 2 | 2 | 1 | 2 | 1 | - | - | 2 | 1 | (12) |
| 32. *G. biordinatus* | (23) | 1 | (12) | (23) | 2 | 2 | 1 | 1 | 3 | 3 | 2 | 2 | (12) | 1 |
| 33. *G. major* | (23) | 1 | (23) | 3 | 2 | 2 | 1 | 1 | 3 | 3 | 2 | 2 | 1 | 1 |
| 34. *G. fissus* | 2 | 1 | (23) | 3 | 2 | 2 | 1 | 2 | 3 | 3 | 2 | 2 | 1 | (23) |
| 35. *G. australis* | 2 | 1 | 2 | 2 | 2 | 2 | 1 | 1 | 3 | 3 | 2 | 2 | 1 | 1 |
| 36. *G. crassipes* | 2 | 1 | 2 | (23) | 2 | 2 | 1 | 1 | 3 | 3 | 2 | 2 | 1 | 1 |
| 37. *Goniocotes diplogonus* | (14) | 1 | (12) | (23) | 2 | 3 | 1 | 1 | 3 | 4 | 5 | 2 | 1 | 1 |
| 38. *Gon. gallinae* | (13) | 1 | (12) | (23) | 2 | 2 | 1 | 1 | 2 | (23) | 1 | 2 | 1 | 1 |
| 39. *Gon. haplogonus* | (13) | 1 | (12) | 2 | 2 | 2 | 1 | 1 | 3 | 4 | 5 | 2 | 1 | 1 |
| 40. *Gon. pallidomaculatus* | (23) | 1 | (23) | (23) | 2 | 2 | 1 | 1 | 2 | 1 | - | 2 | 1 | 1 |
| 41. *Gon. parviceps* | 2 | 1 | (13) | (13) | 2 | 2 | 1 | 1 | 3 | 4 | 5 | 2 | 1 | 1 |
| 42. *Gon. reticulatus* | 2 | 1 | (13) | (13) | 2 | 2 | 1 | 1 | 3 | (23) | 2 | 2 | 1 | (12) |
| 43. *Physconelloides montana* | 2 | 1 | (23) | (23) | 2 | 2 | 1 | (12) | 3 | 3 | 4 | 2 | 1 | (12) |
| 44. *Campanulotes bidentata* | (13) | 1 | 2 | 2 | 2 | 2 | 1 | (12) | 1 | - | - | 2 | 1 | 1 |
| 45. *Heptapsogaster temporalis* | (14) | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 3 | 4 | 5 | 1 | 1 | 2 |

**Table 2.7.** Data Matrix: Characters 197-210

| Character | 197 | 198 | 199 | 200 | 201 | 202 | 203 | 204 | 205 | 206 | 207 | 208 | 209 | 210 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 1. *G. pavonis* | 1 | 1 | 3 | 3 | 3 | 2 | 3 | 3 | 2 | 1 | 1 | 1 | - | - |
| 2. *G. curvicornis* | 1 | 1 | 3 | 3 | 2 | 2 | 2 | 3 | 2 | 1 | 1 | 2 | 3 | 2 |
| 3. *G. spinicornis* | 1 | 1 | 2 | 3 | 3 | 3 | 3 | 3 | 3 | 1 | 1 | 1 | - | - |
| 4. *G. megaceros* | 1 | 1 | 3 | 3 | 3 | 3 | 3 | 3 | 2 | 1 | 1 | 1 | - | - |
| 5. *G. eurygaster* | 1 | 1 | 3 | 4 | 3 | 3 | 2 | 2 | 2 | 2 | 1 | 1 | - | - |
| 6. *G. coronatus* | 1 | 1 | 3 | 3 | 2 | 1 | (23) | 1 | 1 | 1 | 1 | 1 | - | - |
| 7. *G. processus* | 1 | 1 | 3 | 2 | 2 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | - | - |
| 8. *G. wilsoni* | 1 | 2 | 3 | (34) | 3 | 3 | 3 | 1 | 2 | 3 | 1 | 1 | - | - |
| 9. *G. numidae* | 1 | 2 | 2 | 3 | 3 | 3 | 3 | 3 | 3 | 3 | 1 | 2 | 2 | 1 |
| 10. *G. hopkinsi* | 1 | 2 | 3 | 3 | 3 | 3 | 3 | 3 | 3 | 3 | 1 | 2 | 2 | 1 |
| 11. *G. gigas* | 2 | 1 | 3 | 3 | 3 | 2 | 3 | 1 | 2 | 1 | 1 | 2 | 2 | 2 |
| 12. *G. bituberculatus* | 1 | 1 | 1 | - | 2 | 3 | 3 | 3 | 3 | 1 | 1 | 1 | - | - |
| 13. *G. lagopi* | 1 | 1 | 3 | 4 | 4 | 3 | 3 | 3 | 2 | 1 | 1 | 1 | - | - |
| 14. *G. columbianus* | 1 | 1 | 1 | - | - | 3 | 2 | 3 | 2 | 1 | 1 | 1 | - | - |
| 15. *G. leucurus* | 1 | 1 | 1 | 2 | 3 | 3 | 2 | 2 | 2 | 2 | 2 | 1 | - | - |
| 16. *G. corpulentus* | 1 | 1 | 2 | 1 | 2 | 2 | 2 | 2 | 2 | 2 | 2 | 1 | - | - |
| 17. *G. merriamanus* | 1 | 1 | 3 | 2 | 3 | 3 | 2 | 2 | 2 | 4 | 4 | 1 | - | - |
| 18. *G. ithaginis* | 1 | 1 | 2 | 1 | 2 | 3 | 3 | 1 | 2 | 2 | 2 | 1 | - | - |
| 19. *G. chrysolophi* | 1 | 1 | 2 | 1 | 2 | 3 | 3 | 2 | 3 | 2 | 2 | 1 | - | - |
| 20. *G. dissimilis* | 1 | 1 | 3 | 2 | 2 | 2 | 2 | 2 | 2 | 4 | 4 | 1 | - | - |
| 21. *G. cervicornis* | 2 | 1 | 3 | 2 | 2 | 2 | 3 | 3 | 3 | 2 | 2 | 1 | - | - |
| 22. *G. sinensis* | 1 | 1 | 3 | 3 | 2 | 3 | 3 | 2 | 2 | 1 | 1 | 1 | - | - |
| 23. *G. assimilis* | 1 | 1 | 3 | 3 | 2 | 3 | 3 | 2 | 3 | 1 | 1 | 1 | - | - |
| 24. *G. dispar* | 1 | 1 | 3 | 4 | 2 | 3 | 3 | 3 | 3 | 2 | 2 | 1 | - | - |
| 25. *G. securiger* | 1 | 1 | 3 | 1 | 2 | 3 | 3 | 3 | 3 | 2 | 2 | 1 | - | - |
| 26. *G. ortygis* | 1 | 1 | 3 | 4 | 2 | 3 | 3 | (12) | 2 | 2 | 2 | 1 | - | - |
| 27. *G. tibetanus* | 1 | 1 | 3 | 3 | 3 | 4 | 4 | 3 | 3 | (12) | (12) | 2 | 1 | 1 |
| 28. *G. ammoperdix* | 1 | 1 | 3 | 2 | 2 | 2 | 2 | 1 | 2 | 1 | 1 | 1 | - | - |

**Table 2.7.** Data Matrix: Characters 197-210 (Cont.)

| Character | 197 | 198 | 199 | 200 | 201 | 202 | 203 | 204 | 205 | 206 | 207 | 208 | 209 | 210 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 29. *G. antennatus* | 2 | 1 | 3 | 3 | 2 | 3 | 2 | 1 | 2 | 1 | 1 | 1 | - | - |
| 30. *G. retractus* | 1 | 1 | 3 | 2 | 2 | 2 | 2 | 1 | 1 | 4 | 4 | 1 | - | - |
| 31. *G. soueefi* | 1 | 1 | 1 | 2 | 2 | 2 | 2 | 1 | 2 | ? | 1 | 1 | - | - |
| 32. *G. biordinatus* | 1 | 1 | 3 | (23) | 2 | 2 | 2 | 1 | 1 | 1 | 1 | 1 | - | - |
| 33. *G. major* | 1 | 1 | 3 | 2 | 2 | 2 | 2 | 2 | 2 | 1 | 1 | 1 | - | - |
| 34. *G. fissus* | 1 | 1 | 3 | 3 | 2 | 3 | 3 | 2 | 2 | 1 | 1 | 1 | - | - |
| 35. *G. australis* | 1 | 1 | 3 | 2 | 2 | 3 | 2 | 1 | 2 | 1 | 1 | 2 | 1 | 1 |
| 36. *G. crassipes* | 1 | 1 | 3 | 2 | 1 | 2 | 2 | 1 | 1 | 1 | 1 | 1 | - | - |
| 37. *Goniocotes diplogonus* | 1 | 1 | 3 | 2 | 2 | 2 | 2 | 2 | 2 | 1 | 1 | 1 | - | - |
| 38. *Gon. gallinae* | 1 | 1 | 3 | 2 | 1 | 2 | 2 | 1 | 1 | 1 | 1 | 1 | - | - |
| 39. *Gon. haplogonus* | 1 | 1 | 3 | 3 | 2 | 2 | 2 | 2 | 2 | 1 | 1 | 1 | - | - |
| 40. *Gon. pallidomaculatus* | 1 | 1 | 3 | 2 | 2 | 2 | 2 | 2 | 2 | 1 | 1 | 1 | - | - |
| 41. *Gon. parviceps* | 1 | 1 | 3 | 3 | 3 | 3 | 3 | 3 | 3 | 1 | 1 | 1 | - | - |
| 42. *Gon. reticulatus* | 1 | 1 | 3 | 3 | 2 | 3 | 3 | 1 | 2 | 1 | 1 | 1 | - | - |
| 43. *Physconelloides montana* | 1 | 1 | 3 | 2 | 2 | 1 | 2 | 1 | 2 | 1 | 1 | 1 | - | - |
| 44. *Campanulotes bidentata* | 1 | 1 | 3 | 2 | 2 | (12) | (12) | (12) | (12) | 1 | 1 | 1 | - | - |
| 45. *Heptapsogaster temporalis* | 1 | 1 | 3 | (12) | (12) | 1 | 2 | 1 | 2 | 1 | 1 | 1 | - | - |

**Table 2.7.** Data Matrix: Characters 211-224

| Character | 21 1 | 21 2 | 21 3 | 21 4 | 21 5 | 21 6 | 21 7 | 21 8 | 21 9 | 22 0 | 22 1 | 22 2 | 22 3 | 22 4 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 1. *G. pavonis* | 2 | 2 | 3 | 2 | 2 | 1 | 1 | 3 | 1 | 3 | 1 | 1 | 1 | 1 |
| 2. *G. curvicornis* | 2 | 2 | 3 | 2 | 2 | 1 | 1 | (13) | 1 | 1 | - | 2 | 1 | 1 |
| 3. *G. spinicornis* | 1 | 3 | 3 | (23) | 2 | 1 | 1 | 3 | 1 | 1 | 3 | 2 | 2 | 1 |
| 4. *G. megaceros* | 1 | 1 | 3 | 2 | (12) | 1 | 1 | 3 | 1 | 1 | 1 | 2 | 2 | 1 |
| 5. *G. eurygaster* | 1 | 1 | 3 | 2 | 2 | 1 | 2 | 1 | (13) | 1 | 1 | 3 | 2 | 2 |
| 6. *G. coronatus* | 2 | 2 | 3 | 2 | 2 | 3 | 1 | 2 | 3 | 3 | 1 | 4 | 1 | 2 |
| 7. *G. processus* | 1 | 1 | 3 | 2 | 2 | (12) | 1 | 2 | 3 | 1 | 1 | 1 | 1 | 2 |
| 8. *G. wilsoni* | 4 | 3 | 3 | 1 | 2 | (12) | 1 | (12) | (23) | 1 | 1 | 2 | 1 | 3 |
| 9. *G. numidae* | 3 | 3 | 3 | (123) | (12) | 1 | (12) | (12) | 3 | 1 | 3 | 2 | 2 | 3 |
| 10. *G. hopkinsi* | 3 | 3 | 3 | 2 | 1 | 1 | (12) | (12) | 3 | 1 | 1 | 2 | 2 | 3 |
| 11. *G. gigas* | (34) | (34) | 3 | 3 | (12) | (12) | 1 | 2 | (13) | 1 | 1 | 2 | 1 | 2 |
| 12. *G. bituberculatus* | 1 | 1 | 3 | (23) | (12) | (12) | 1 | 2 | (13) | 1 | 1 | (12) | 1 | 2 |
| 13. *G. lagopi* | 1 | 1 | 3 | 2 | (12) | 1 | 1 | 2 | (13) | 1 | 1 | (12) | 1 | 2 |
| 14. *G. columbianus* | 1 | 1 | 3 | 3 | (12) | 1 | 1 | 1 | (14) | 4 | 1 | - | 2 | 2 |
| 15. *G. leucurus* | 1 | 1 | 3 | 3 | 2 | 1 | 1 | 2 | (13) | 1 | 1 | - | 1 | 2 |
| 16. *G. corpulentus* | 1 | 1 | 3 | (123) | 2 | 1 | 1 | 2 | 3 | 1 | 1 | - | 2 | (23) |
| 17. *G. merriamanus* | 1 | 1 | 3 | (23) | 2 | (12) | 1 | (12) | (13) | 1 | 1 | 5 | 1 | 2 |
| 18. *G. ithaginis* | 1 | 1 | 3 | (23) | 2 | 1 | (13) | 2 | (13) | 4 | 1 | - | 2 | 2 |
| 19. *G. chrysolophi* | 1 | 1 | 3 | (23) | 2 | 1 | (13) | 2 | (13) | 3 | 1 | - | 2 | 2 |
| 20. *G. dissimilis* | (12) | (12) | 3 | 3 | 2 | (12) | 1 | 2 | (13) | 1 | 1 | (12) | 1 | 2 |
| 21. *G. cervicornis* | (12) | (12) | 3 | (12) | 2 | 1 | 1 | 2 | (23) | 2 | 1 | - | 2 | 2 |
| 22. *G. sinensis* | 1 | 1 | 3 | (23) | 2 | 1 | 1 | 2 | (23) | 1 | 1 | - | 2 | 2 |
| 23. *G. assimilis* | 1 | 1 | 3 | 3 | 2 | 1 | 1 | 1 | (23) | 3 | 1 | - | 2 | 2 |
| 24. *G. dispar* | 1 | 1 | 3 | (23) | 2 | 1 | 3 | 1 | (23) | 1 | - | - | 1 | 2 |
| 25. *G. securiger* | 1 | 1 | 3 | 3 | 2 | 1 | 1 | 1 | (23) | 1 | - | - | ? | 2 |
| 26. *G. ortygis* | 1 | 1 | 3 | (23) | 2 | 3 | 1 | 1 | (23) | 3 | 1 | - | 2 | 2 |
| 27. *G. tibetanus* | 1 | 1 | 3 | 3 | 2 | (12) | 1 | (12) | (23) | 1 | - | - | (12) | 2 |
| 28. *G. ammoperdix* | 1 | 1 | 3 | (23) | 2 | 3 | 1 | 1 | (23) | 3 | - | - | 1 | 2 |

**Table 2.7.** Data Matrix: Characters 211-224 (Cont.)

| Character | 211 | 212 | 213 | 214 | 215 | 216 | 217 | 218 | 219 | 220 | 221 | 222 | 223 | 224 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 29. *G. antennatus* | 1 | 1 | 3 | 3 | 2 | (12) | 1 | (12) | (23) | 1 | 1 | 5 | 2 | 2 |
| 30. *G. retractus* | (14) | (14) | 3 | 2 | 2 | 3 | 3 | (12) | 2 | 3 | 2 | - | 1 | 2 |
| 31. *G. soueefi* | 1 | 1 | 3 | 2 | 2 | 3 | 3 | (12) | 2 | (12) | 2 | - | 1 | 2 |
| 32. *G. biordinatus* | 3 | 5 | 3 | (12) | 2 | 3 | 1 | 2 | 1 | 1 | 2 | - | 2 | 2 |
| 33. *G. major* | 1 | 1 | 3 | 2 | 2 | 2 | 1 | 2 | 1 | 1 | 2 | - | (12) | 2 |
| 34. *G. fissus* | 1 | 1 | 3 | 3 | 2 | (12) | 1 | 2 | 1 | (12) | 2 | - | 2 | 2 |
| 35. *G. australis* | 1 | 1 | (23) | 2 | 1 | 1 | 2 | 3 | 1 | 1 | - | - | 2 | 2 |
| 36. *G. crassipes* | (14) | (14) | (23) | 2 | 2 | (12) | 1 | 2 | 1 | 1 | 2 | - | (12) | 2 |
| 37. *Goniocotes diplogonus* | (23) | (23) | 3 | 1 | 2 | 1 | 1 | 2 | 1 | 3 | 3 | 6 | 2 | 2 |
| 38. *Gon. gallinae* | (12) | (12) | 3 | (12) | 2 | 1 | 1 | 2 | 1 | 1 | 3 | 6 | 2 | 2 |
| 39. *Gon. haplogonus* | 3 | 3 | 3 | 1 | 2 | 3 | 1 | 2 | 3 | 2 | 3 | 6 | 2 | 3 |
| 40. *Gon. pallidomaculatus* | (23) | (23) | 3 | 2 | 2 | 1 | 1 | 2 | 1 | 1 | 3 | 6 | 2 | 2 |
| 41. *Gon. parviceps* | 2 | 2 | 3 | 1 | 2 | 1 | 1 | 2 | 3 | 1 | 3 | 6 | 1 | 2 |
| 42. *Gon. reticulatus* | (34) | (34) | 3 | 2 | 2 | 1 | (12) | 2 | 1 | 1 | 3 | 6 | 2 | 2 |
| 43. *Physconelloides montana* | (23) | (23) | 3 | (12) | 2 | 1 | (12) | 2 | 1 | 1 | 2 | 6 | 2 | 2 |
| 44. *Campanulotes bidentata* | 1 | 1 | 2 | 1 | 2 | 3 | 3 | 2 | (13) | 1 | 3 | 6 | 2 | 2 |
| 45. *Heptapsogaster temporalis* | 1 | 1 | 2 | 1 | 2 | 1 | 2 | 2 | 2 | 2 | 3 | 7 | 2 | 4 |

**Table 2.7.** Data Matrix: Characters 225-238

| Character | 22 5 | 22 6 | 22 7 | 22 8 | 22 9 | 23 0 | 23 1 | 23 2 | 23 3 | 23 4 | 23 5 | 23 6 | 23 7 | 23 8 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 1. *G. pavonis* | 2 | 2 | 2 | 3 | 1 | 1 | 2 | 3 | 2 | 1 | 2 | 1 | 2 | 2 |
| 2. *G. curvicornis* | 2 | 2 | 2 | 2 | 1 | 1 | 1 | 3 | 2 | 1 | 2 | 1 | 2 | 2 |
| 3. *G. spinicornis* | 2 | 1 | 1 | 2 | 1 | 1 | 2 | 3 | 3 | 1 | 2 | 1 | 1 | 2 |
| 4. *G. megaceros* | 2 | 1 | 1 | 2 | 1 | 1 | 2 | 3 | 3 | 1 | 2 | 1 | 1 | 2 |
| 5. *G. eurygaster* | 2 | 1 | 1 | 2 | 1 | 1 | 1 | 2 | 3 | - | - | 2 | 1 | 1 |
| 6. *G. coronatus* | 3 | 1 | 1 | 4 | 1 | 1 | 1 | 2 | 1 | - | - | 2 | 1 | 2 |
| 7. *G. processus* | 3 | 1 | 1 | 2 | 1 | 1 | 1 | 3 | 3 | 1 | 2 | 2 | (12) | (12) |
| 8. *G. wilsoni* | 3 | (12) | 1 | 1 | 2 | 1 | 1 | 3 | 1 | - | 1 | 2 | 2 | 1 |
| 9. G. numidae | 5 | 2 | 2 | 1 | 2 | 1 | 1 | 2 | 3 | 1 | 1 | 2 | 2 | 3 |
| 10. *G. hopkinsi* | 5 | 2 | 2 | 1 | 2 | 1 | 1 | 3 | 3 | 1 | 1 | 2 | 1 | 1 |
| 11. *G. gigas* | 2 | 1 | 2 | 1 | 1 | 1 | 1 | 3 | 2 | 1 | 2 | 2 | 1 | 2 |
| 12. *G. bituberculatus* | 2 | 1 | 1 | 3 | 1 | 1 | 2 | 2 | 2 | 2 | 2 | 2 | 2 | 3 |
| 13. *G. lagopi* | 2 | 1 | 1 | 3 | 1 | 1 | 2 | 2 | 2 | 1 | 2 | 2 | 1 | 2 |
| 14. *G. columbianus* | 2 | 1 | 1 | 3 | 1 | 1 | 2 | 2 | 2 | 1 | 2 | 2 | 2 | 3 |
| 15. *G. leucurus* | 2 | 1 | 1 | 3 | 1 | 1 | 2 | 3 | 2 | 1 | 2 | 2 | 2 | 3 |
| 16. *G. corpulentus* | 2 | 1 | 1 | 3 | 1 | 1 | 2 | 2 | 2 | 2 | 2 | 2 | 2 | 3 |
| 17. *G. merriamanus* | 2 | 1 | 1 | 3 | 1 | 1 | 2 | 2 | 2 | 1 | 2 | 2 | (12) | 2 |
| 18. *G. ithaginis* | 2 | 1 | 1 | 3 | 1 | 1 | 2 | 2 | 2 | 1 | 2 | 2 | 2 | 3 |
| 19. *G. chrysolophi* | 2 | 1 | 1 | 3 | 1 | 1 | 2 | 2 | 2 | 1 | 2 | 2 | 2 | 3 |
| 20. *G. dissimilis* | 2 | 1 | 1 | 3 | 1 | 1 | 2 | 2 | 2 | 1 | 2 | 1 | 2 | (12) |
| 21. *G. cervicornis* | 2 | 1 | 1 | 3 | 1 | 1 | 2 | 3 | 2 | 1 | 2 | 2 | 2 | 1 |
| 22. *G. sinensis* | 2 | 1 | 1 | 3 | 1 | 1 | 2 | 3 | 2 | 1 | 2 | 2 | 2 | 1 |
| 23. *G. assimilis* | 2 | 1 | 1 | 1 | 2 | 1 | (12) | 2 | 3 | 1 | 1 | 2 | 2 | 3 |
| 24. *G. dispar* | 2 | 1 | 1 | 1 | 2 | 1 | (12) | 2 | 3 | 1 | 2 | 2 | 2 | 3 |
| 25. *G. securiger* | 2 | 1 | 1 | 2 | 1 | 4 | 2 | 2 | 3 | 1 | 1 | 2 | 2 | (13) |
| 26. *G. ortygis* | 2 | 1 | 1 | 1 | 1 | 1 | 1 | 2 | 3 | 1 | 1 | 2 | 2 | 2 |
| 27. *G. tibetanus* | (23) | 1 | 1 | 1 | 1 | 1 | 2 | 3 | 2 | 1 | 2 | 2 | (12) | 1 |
| 28. *G. ammoperdix* | 2 | 1 | 1 | 2 | 1 | 1 | 2 | 2 | 2 | 1 | 2 | 1 | 2 | 2 |

**Table 2.7.** Data Matrix: Characters 225-238 (Cont.)

| Character | 225 | 226 | 227 | 228 | 229 | 230 | 231 | 232 | 233 | 234 | 235 | 236 | 237 | 238 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 29. *G. antennatus* | 2 | 1 | 1 | 2 | 1 | 1 | (12) | 3 | 3 | 3 | 1 | 1 | 2 | 2 |
| 30. *G. retractus* | 2 | 1 | 1 | 2 | 1 | 1 | 1 | 2 | 2 | 1 | 2 | 1 | 1 | 2 |
| 31. *G. soueefi* | 2 | 1 | 1 | 2 | 2 | 1 | 1 | 2 | 2 | 1 | 2 | 1 | 1 | 2 |
| 32. *G. biordinatus* | 4 | 1 | 1 | 1 | 2 | 3 | 2 | 1 | 3 | 1 | 1 | 1 | 1 | 2 |
| 33. *G. major* | 4 | 1 | 1 | 2 | 1 | 2 | 2 | 2 | 2 | 1 | 1 | 1 | 1 | 2 |
| 34. *G. fissus* | 4 | 1 | 1 | 1 | 2 | (23) | 1 | 2 | 3 | 1 | 1 | (12) | 2 | 3 |
| 35. *G. australis* | 4 | 1 | 1 | 2 | 1 | 2 | 1 | 2 | 2 | 1 | 1 | 2 | (12) | (23) |
| 36. *G. crassipes* | 4 | 1 | 1 | 1 | 2 | 2 | 1 | 1 | 3 | 1 | 1 | 1 | 1 | 2 |
| 37. *Goniocotes diplogonus* | 2 | 2 | 2 | 1 | 2 | 4 | 2 | 1 | 3 | 1 | 1 | 1 | 2 | 2 |
| 38. *Gon. gallinae* | 2 | 2 | 2 | 1 | 2 | 1 | 2 | 1 | 3 | 1 | 1 | 1 | 1 | 2 |
| 39. *Gon. haplogonus* | 4 | 2 | 2 | 1 | 2 | 1 | 1 | 1 | 3 | 1 | 1 | 1 | 1 | 2 |
| 40. *Gon. pallidomaculatus* | 2 | 2 | 2 | 1 | 2 | 1 | (12) | 1 | 3 | 1 | 1 | 1 | 1 | 2 |
| 41. *Gon. parviceps* | 4 | 2 | 2 | 3 | 1 | 1 | 1 | 2 | 2 | 1 | 2 | 1 | 1 | 2 |
| 42. *Gon. reticulatus* | 4 | 2 | 2 | 2 | 1 | 1 | 1 | 1 | 3 | 1 | 1 | 1 | 1 | 2 |
| 43. *Physconelloides montana* | 4 | 2 | 2 | 1 | 1 | 1 | 1 | 1 | 3 | 1 | 1 | 1 | 1 | 2 |
| 44. *Campanulotes bidentata* | 4 | 2 | 2 | 1 | 1 | (12) | 2 | 1 | 3 | 1 | 1 | 1 | 1 | 2 |
| 45. *Heptapsogaster temporalis* | 1 | 1 | 2 | 3 | 1 | 1 | 2 | 3 | 2 | 1 | 2 | 1 | 1 | 1 |

**Table 2.7.** Data Matrix: Characters 239-252

| Character | 239 | 240 | 241 | 242 | 243 | 244 | 245 | 246 | 247 | 248 | 249 | 250 | 251 | 252 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 1. *G. pavonis* | 2 | 1 | 3 | 1 | 1 | 2 | 3 | 1 | - | 5 | 6 | 8 | 8 | 2 |
| 2. *G. curvicornis* | 2 | 1 | 2 | 1 | 1 | (12) | 1 | 1 | - | 1 | 2 | 2 | 2 | 2 |
| 3. *G. spinicornis* | 2 | 2 | 1 | 2 | 1 | 1 | 3 | 1 | - | 5 | 8 | 8 | 8 | 2 |
| 4. *G. megaceros* | 2 | 1 | 1 | 2 | 1 | 1 | 3 | 1 | - | 5 | 8 | 9 | 8 | 2 |
| 5. *G. eurygaster* | 1 | 2 | 2 | 2 | 1 | 2 | 1 | 1 | - | 9 | 9 | 9 | 8 | 7 |
| 6. *G. coronatus* | 4 | 1 | 1 | 1 | 1 | 4 | 1 | 1 | - | 2 | 2 | 4 | 4 | 1 |
| 7. *G. processus* | 2 | 2 | 4 | 2 | 1 | 2 | 1 | 1 | - | 4 | 4 | 8 | 8 | 1 |
| 8. *G. wilsoni* | 2 | 2 | 4 | 2 | 2 | 2 | 1 | 1 | - | 5 | 5 | 8 | 9 | 2 |
| 9. *G. numidae* | 4 | 2 | 2 | 2 | 2 | 2 | 1 | 1 | - | 7 | 7 | 8 | 9 | 4 |
| 10. *G. hopkinsi* | 4 | 2 | (34) | 2 | 2 | 2 | 1 | 1 | - | 6 | 7 | 8 | 9 | 3 |
| 11. *G. gigas* | 3 | 1 | 3 | 1 | 1 | 5 | 1 | 1 | - | 5 | 5 | 9 | 9 | 1 |
| 12. *G. bituberculatus* | 4 | 1 | 1 | 1 | 2 | 5 | 1 | 2 | 1 | 3 | 5 | 6 | 5 | 1 |
| 13. *G. lagopi* | 4 | 1 | 3 | 1 | 2 | 5 | 1 | 2 | 1 | 2 | 4 | 5 | 4 | 1 |
| 14. *G. columbianus* | 4 | 1 | 2 | 1 | 2 | 4 | 1 | 2 | 2 | 1 | 1 | 2 | 2 | 1 |
| 15. *G. leucurus* | 4 | 1 | 3 | 1 | 2 | 2 | 1 | 2 | 2 | 2 | 3 | 5 | 4 | 1 |
| 16. *G. corpulentus* | 4 | 1 | 3 | 1 | 2 | 2 | 1 | 2 | 3 | 2 | 3 | 4 | 4 | 1 |
| 17. *G. merriamanus* | 4 | 1 | 3 | 1 | 2 | 5 | 1 | 2 | 1 | 2 | 3 | 4 | 4 | 1 |
| 18. *G. ithaginis* | 4 | 1 | 2 | (13) | 2 | 2 | 1 | 2 | 3 | 4 | 4 | 6 | 6 | 2 |
| 19. *G. chrysolophi* | 4 | 1 | 2 | 1 | 2 | 2 | 1 | 2 | 3 | 2 | 3 | 5 | 5 | 1 |
| 20. *G. dissimilis* | 4 | 1 | 3 | (13) | 2 | 6 | 1 | 2 | 2 | 3 | 4 | 6 | 6 | 1 |
| 21. *G. cervicornis* | 3 | 1 | 1 | 1 | 2 | 1 | 1 | 1 | - | 5 | 6 | 8 | 8 | 2 |
| 22. *G. sinensis* | 3 | 1 | 2 | 1 | 2 | 5 | 1 | 1 | - | 3 | 5 | 6 | 6 | 1 |
| 23. *G. assimilis* | 2 | 2 | ? | (23) | 2 | 1 | 2 | 1 | - | 4 | 4 | 6 | 5 | 4 |
| 24. *G. dispar* | 2 | 2 | 2 | 2 | 2 | 2 | 1 | 2 | 2 | 3 | 4 | 5 | 5 | 3 |
| 25. *G. securiger* | 2 | 2 | 2 | (23) | 2 | 2 | 1 | 2 | 1 | 3 | 4 | 4 | 5 | 3 |
| 26. *G. ortygis* | 3 | 1 | 3 | 2 | 2 | 2 | 1 | 2 | 2 | 1 | 2 | 3 | 3 | 1 |
| 27. *G. tibetanus* | 3 | 2 | 2 | (23) | 2 | 2 | 1 | 2 | 1 | 4 | 6 | 7 | 6 | 3 |
| 28. *G. ammoperdix* | 2 | 2 | 3 | (23) | 2 | 2 | 1 | 2 | 2 | 2 | 2 | 4 | 3 | 2 |

**Table 2.7.** Data Matrix: Characters 239-252 (Cont.)

| Character | 239 | 240 | 241 | 242 | 243 | 244 | 245 | 246 | 247 | 248 | 249 | 250 | 251 | 252 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 29. *G. antennatus* | 2 | 2 | 3 | 2 | 2 | 2 | 1 | 1 | - | 5 | 4 | 6 | 6 | 3 |
| 30. *G. retractus* | 4 | 1 | 3 | (13) | 1 | 5 | 1 | 2 | 1 | 1 | 2 | 4 | 4 | 0 |
| 31. *G. soueefi* | 4 | 1 | 3 | (13) | 1 | 5 | 1 | 2 | 1 | 1 | 0 | 0 | 2 | 9 |
| 32. *G. biordinatus* | 1 | 2 | (23) | (12) | 1 | 2 | 1 | 1 | - | 3 | 2 | 3 | 2 | 5 |
| 33. *G. major* | 3 | 2 | (23) | (12) | 1 | 2 | 1 | 1 | - | 5 | 5 | 6 | 5 | 5 |
| 34. *G. fissus* | 2 | 2 | (23) | 1 | 1 | 2 | 1 | 1 | - | 4 | 4 | 4 | 4 | 7 |
| 35. *G. australis* | 4 | 2 | 1 | (12) | 1 | 2 | 1 | 1 | - | 4 | 6 | 5 | 6 | 5 |
| 36. *G. crassipes* | 1 | 2 | 3 | (12) | 1 | 2 | 1 | 1 | - | 1 | 1 | 1 | 1 | 5 |
| 37. *Goniocotes diplogonus* | 3 | 2 | 2 | (23) | 1 | 1 | 1 | 1 | - | 0 | 0 | 1 | 1 | 3 |
| 38. *Gon. gallinae* | 3 | 2 | 2 | (23) | 1 | 1 | 1 | 1 | - | 0 | 1 | 0 | 1 | 3 |
| 39. *Gon. haplogonus* | 3 | 2 | 2 | (23) | 1 | 5 | 1 | 1 | - | 1 | 1 | 1 | 1 | 4 |
| 40. *Gon. pallidomaculatus* | 3 | 2 | 2 | (23) | 1 | 1 | 1 | 1 | - | 0 | 0 | 1 | 1 | 2 |
| 41. *Gon. parviceps* | 3 | 2 | 2 | (23) | 1 | 1 | 1 | 1 | - | 1 | 2 | 3 | 2 | 0 |
| 42. *Gon. reticulatus* | 3 | 2 | 2 | (23) | 1 | 1 | 1 | 1 | - | 1 | 1 | 1 | 1 | 4 |
| 43. *Physconelloides montana* | 3 | 1 | - | - | 1 | - | 1 | 1 | - | 1 | 1 | 1 | 1 | 3 |
| 44. *Campanulotes bidentata* | 3 | 2 | (23) | (12) | 1 | 4 | 1 | 1 | - | 0 | 0 | 1 | 1 | 1 |
| 45. *Heptapsogaster temporalis* | 1 | 1 | - | - | 1 | 1 | 1 | 1 | - | 0 | 0 | 0 | 0 | 5 |

**Table 2.7.** Data Matrix: Characters 253-262

| Character | 25<br>3 | 25<br>4 | 25<br>5 | 25<br>6 | 25<br>7 | 25<br>8 | 25<br>9 | 26<br>0 | 26<br>1 | 26<br>2 |
|---|---|---|---|---|---|---|---|---|---|---|
| 1. *G. pavonis* | 6 | 8 | 8 | 8 | 8 | 9 | 9 | 5 | 9 | 8 |
| 2. *G. curvicornis* | 6 | 2 | 2 | 3 | 2 | 3 | 2 | 3 | 3 | 2 |
| 3. *G. spinicornis* | 8 | 9 | 9 | 9 | 9 | 8 | 8 | 5 | 9 | 8 |
| 4. *G. megaceros* | 8 | 9 | 9 | 9 | 9 | 8 | 8 | 8 | 9 | 8 |
| 5. *G. eurygaster* | 9 | 9 | 9 | 9 | 9 | 9 | 8 | 6 | 8 | 8 |
| 6. *G. coronatus* | 3 | 2 | 3 | 3 | 2 | 3 | 3 | 2 | 3 | 3 |
| 7. *G. processus* | 4 | 6 | 6 | 6 | 6 | 5 | 6 | 4 | 7 | 6 |
| 8. *G. wilsoni* | 4 | 7 | 9 | 8 | 8 | 7 | 8 | 5 | 7 | 9 |
| 9. *G. numidae* | 6 | 7 | 8 | 8 | 9 | 7 | 8 | 4 | 6 | 8 |
| 10. *G. hopkinsi* | 6 | 6 | 7 | 7 | 8 | 6 | 8 | 2 | 6 | 8 |
| 11. *G. gigas* | 4 | 6 | 6 | 6 | 6 | 7 | 8 | 5 | 7 | 7 |
| 12. *G. bituberculatus* | 0 | 5 | 5 | 5 | 5 | 5 | 5 | 9 | 6 | 5 |
| 13. *G. lagopi* | 6 | 3 | 3 | 3 | 3 | 4 | 4 | 2 | 4 | 3 |
| 14. *G. columbianus* | 5 | 1 | 2 | 1 | 2 | 2 | 2 | 2 | 3 | 2 |
| 15. *G. leucurus* | 6 | 3 | 3 | 3 | 3 | 4 | 4 | 2 | 4 | 3 |
| 16. *G. corpulentus* | 5 | 3 | 3 | 3 | 3 | 4 | 3 | 2 | 4 | 3 |
| 17. *G. merriamanus* | 5 | 2 | 2 | 3 | 3 | 3 | 2 | 2 | 3 | 3 |
| 18. *G. ithaginis* | 6 | 4 | 4 | 4 | 4 | 5 | 5 | 2 | 5 | 4 |
| 19. *G. chrysolophi* | 5 | 3 | 3 | 3 | 3 | 4 | 4 | 2 | 4 | 3 |
| 20. *G. dissimilis* | 5 | 3 | 4 | 3 | 4 | 4 | 5 | 3 | 4 | 4 |
| 21. *G. cervicornis* | 6 | 7 | 5 | 7 | 6 | 7 | 6 | 1 | 7 | 6 |
| 22. *G. sinensis* | 6 | 5 | 4 | 5 | 5 | 6 | 5 | 3 | 5 | 5 |
| 23. *G. assimilis* | 6 | 3 | 3 | 3 | 3 | 4 | 4 | 2 | 4 | 4 |
| 24. *G. dispar* | 6 | 3 | 3 | 3 | 3 | 4 | 4 | 2 | 4 | 4 |
| 25. *G. securiger* | 6 | 2 | 3 | 3 | 3 | 3 | 4 | 1 | 3 | 3 |
| 26. *G. ortygis* | 4 | 1 | 2 | 2 | 2 | 2 | 3 | 1 | 2 | 3 |
| 27. *G. tibetanus* | 7 | 5 | 5 | 5 | 5 | 6 | 6 | 4 | 5 | 5 |
| 28. *G. ammoperdix* | 5 | 3 | 3 | 2 | 2 | 3 | 3 | 1 | 3 | 3 |

**Table 2.7.** Data Matrix: Characters 253-262 (Cont.)

| Character | 253 | 254 | 255 | 256 | 257 | 258 | 259 | 260 | 261 | 262 |
|---|---|---|---|---|---|---|---|---|---|---|
| 29. *G. antennatus* | 5 | 3 | 3 | 3 | 3 | 5 | 5 | 3 | 5 | 4 |
| 30. *G. retractus* | 3 | 1 | 2 | 2 | 2 | 2 | 2 | 3 | 4 | 4 |
| 31. *G. soueefi* | 2 | 1 | 0 | 1 | 0 | 6 | 5 | 1 | 0 | 4 |
| 32. *G. biordinatus* | 7 | 3 | 3 | 3 | 2 | 3 | 2 | 3 | 3 | 2 |
| 33. *G. major* | 8 | 5 | 5 | 4 | 4 | 5 | 4 | 3 | 5 | 4 |
| 34. *G. fissus* | 8 | 2 | 3 | 3 | 3 | 4 | 4 | 4 | 4 | 3 |
| 35. *G. australis* | 8 | 4 | 5 | 5 | 5 | 5 | 5 | 4 | 5 | 5 |
| 36. *G. crassipes* | 7 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 0 |
| 37. *Goniocotes diplogonus* | 6 | 0 | 0 | 1 | 1 | 0 | 1 | 1 | 1 | 0 |
| 38. *Gon. gallinae* | 5 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 |
| 39. *Gon. haplogonus* | 7 | 0 | 0 | 2 | 2 | 1 | 1 | 1 | 1 | 1 |
| 40. *Gon. pallidomaculatus* | 5 | 0 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 0 |
| 41. *Gon. parviceps* | 6 | 4 | 3 | 4 | 3 | 3 | 3 | 2 | 4 | 2 |
| 42. *Gon. reticulatus* | 6 | 1 | 2 | 1 | 2 | 1 | 2 | 1 | 1 | 1 |
| 43. *Physconelloides montana* | 6 | 1 | 2 | 1 | 1 | 0 | 1 | 1 | 1 | 1 |
| 44. *Campanulotes bidentata* | 4 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 |
| 45. *Heptapsogaster temporalis* | 7 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 1 | 0 |

# FIGURES

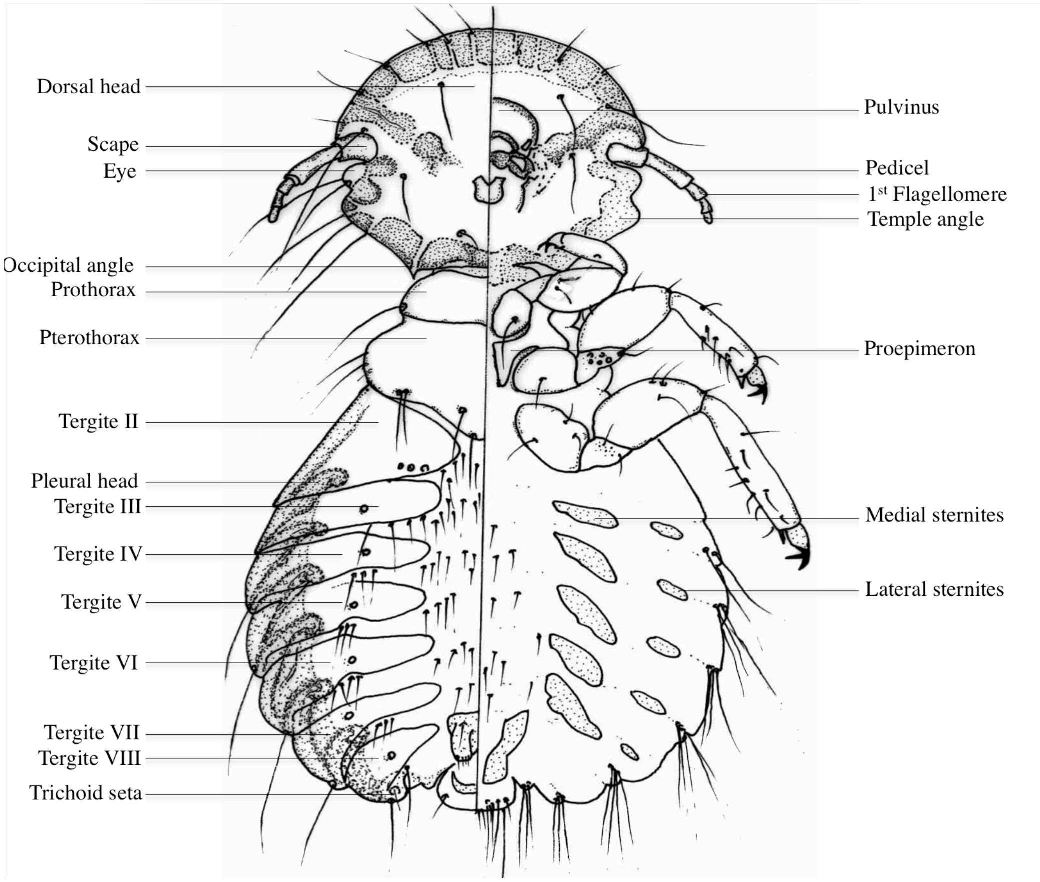


**Figure 2.1.** Generalized morphology of *Goniodes*, based on a male specimen. Dorsal view on the left, ventral view on the right.

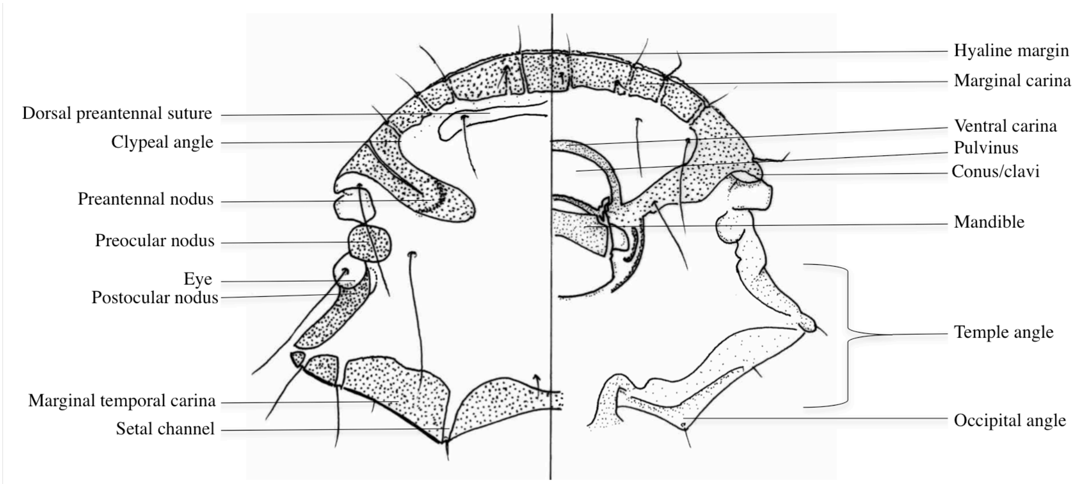


**Figure 2.2.** Generalized head morphology in *Goniodes*

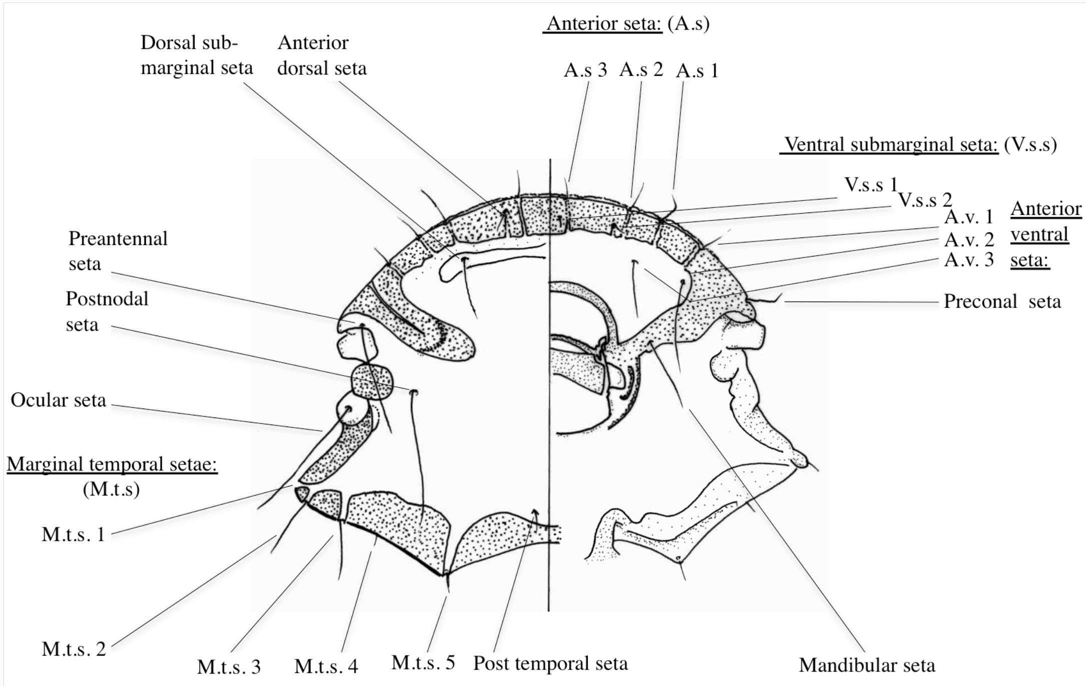


**Figure 2.3.** Generalized setal distribution in *Goniodes*

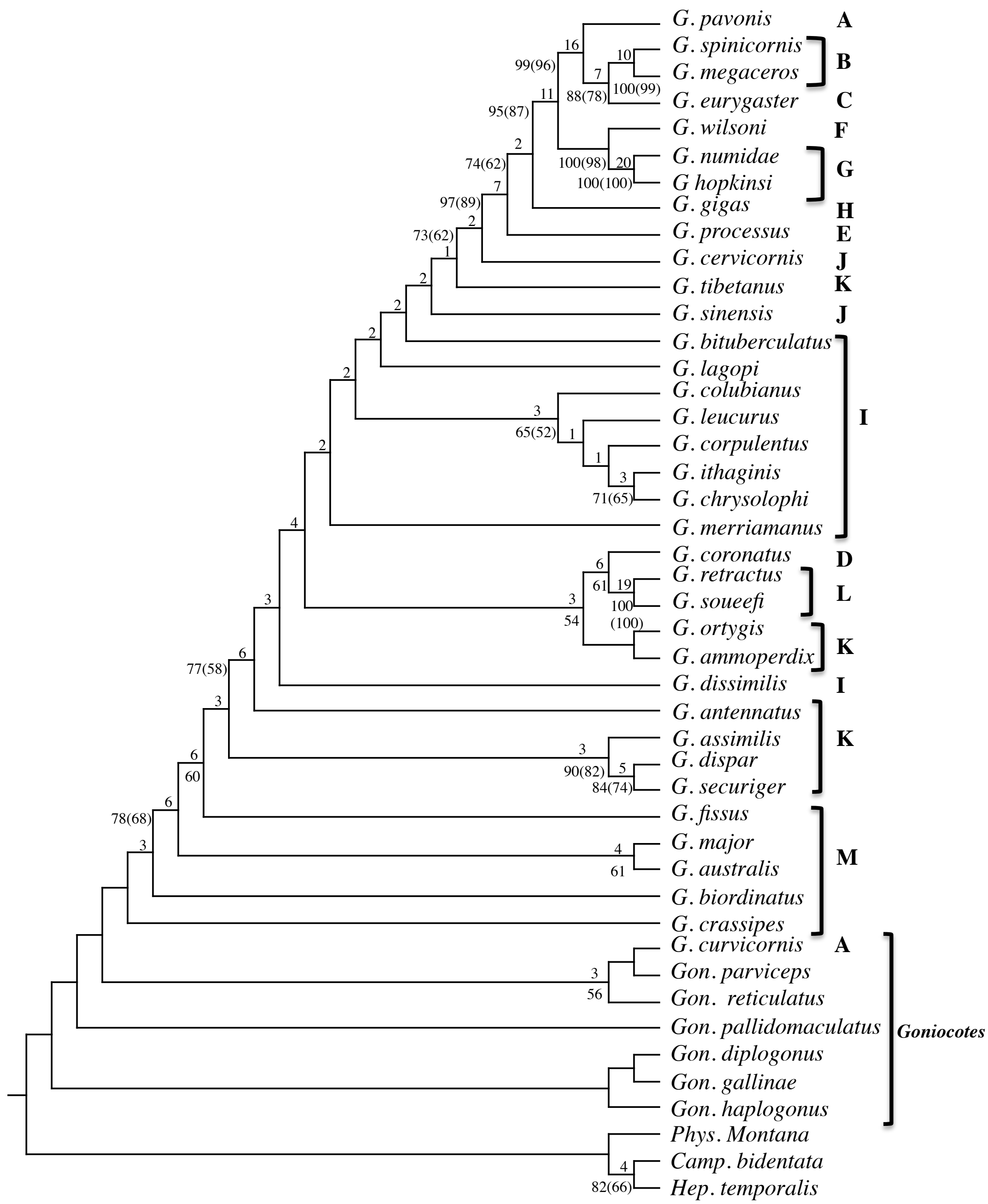


**Figure 2.4.** Consensus (50%) of 5 most parsimonious trees from the analysis. Support indicated above nodes are Bremmer,, below nodes are Jackknife with bootstrap values in brackets. Clay's (1940) intragenric groups are provided in bold to the right of species names.

## CHAPTER 3:

## A taxonomic revision of the Sub-Saharan members of the ischnoceran louse genus *Goniodes* Nitzsch, 1818 (Insecta: Phthiraptera: Ischnocera)

### ABSTRACT

African species of the feather louse genus *Goniodes* are reviewed and the the 31 species are placed in 8 intrageneric groups following an earlier revision by Theresa Clay. An additional 5 species from 3 intrageneric groups that are incidental or introduced to Africa are also briefly discussed. This revision provides an extensive review of the taxonomic and nomenclatural histories, host associations of each species, and concludes with an discussion of the current status of each species. The intrageneric groups, including the component species with their type hosts are: Group F – *G. wilsoni* ex *Afropavo congensis*; Group G – *G. numidae* ex *Numida m. meleagris*, *G. hopkinsi* ex *Guttera edouardi seth-smithi*, *G. meyi* ex *Numida meleagris meleagris*, *G. klockenhoffi* ex *Numida meleagris reichenowi*, *G. reichenowii* ex *Numida meleagris reichenowi*, *G. plumiferae* ex *Guttera plumifera schubotzi*, *G. schoutedenii* ex *Guttera edouardi verreauxi*, *G. inaequalis* ex *Guttera edouardi barbata*; Group H – *G. gigas* ex *Gallus gallus*, *G. agelastes* ex *Agelastes meleagrides*, *G. bifurcus* ex *Guttera pucherani pucherani*, *G. zairensis* ex *Guttera plumifera schubotzi*, *G. gutterae* ex *Guttera plumifera plumifera*, *G. phasidus* ex *Phasidus niger*; Group I – *G. emersoni* ex *Francolinus psilolaemus*; Group K – *G. assimilis* ex *Francolinus capensis*, *G. ammoperdix* ex *Ammoperdix griseogularis*, *G. antennatus* ex *Francolinus leucoscepus leucoscepus*, *G. oreophilus* ex *Francolinus psilolaemus elgonensis*, *G. scleroptilus* ex *Francolinus*

*levaillantoides jugularis*, *G. isogenos* ex *Francolinus africanus africanus*, Group L – *G. soueefi* ex *Coturnix chinensis australis*, *G. astrocephalus* ex *Coturnix coturnix coturnix*, *G. moucheti* ex *Francolinus nobilis*, *G. lootensi* ex *Coturnix chinensis adansonii*. Species introduced or incidental to Sub-Saharan Africa include: Group A – *G. pavonis* introduced via its type host *Pavo cristatus*; Group B – *G. meinertzhagenii* introduced via its type host *Pavo cristatus*; Group K – *G. dispar* introduced via its type host *Perdix perdix* (*Perdix cinerea*) to Robben Island, South Africa, and also known from single specimen collected from zoo specimen of *Francolinus afer cranchii* in Zimbabwe, *G. securiger* incidental in Sub-Saharan Africa via its type host *Alectoris barbara barbara*, *G. dissimilis* ex *Gallus gallus* incidental in Sub-Saharan Africa via domestic chickens.

## INTRODUCTION

*Goniodes* Nitzsch 1818, is one of the most speciose genera of chewing lice with approximately 100 recognized species, parasitic on 132 galliforms (Tables 2.3-2.4). *Goniodes* is a typical "body louse" (Clay 1949; Clay and Rothschild 1952), stocky with a broad abdomen and a relatively large flattened head. This "niche-determined" morphological type designation has no formal taxonomic standing or significance, as they often contain distantly related forms (Clay and Rothschild 1952, but also see Johnson *et al*. 2012). The body lice contain genera such as *Goniodes* and *Physconelloides* (on pigeons and doves, Columbiformes). *Goniodes*, like many other Ischnocera, has a conservative morphology, which complicates taxonomic work and makes identification difficult. This situation is exacerbated by the fact that morphological similarity might also be due to convergence (Johnson *et al*. 2012; Mey 1994; Smith 2000, 2001). A few species in Clay's (1940) group L have longer elongate bodies reminiscent of wing lice, and although the adaptive significance of this trend is unknown, it might, in combination with a small body size, be indicative of an increased ability to escape preening, and/or an adaptive radiation on a the host (Johnson *et al*. 2012).

There is little consensus on classification for *Goniodes*. As is the case for so many other Ischnoceran genera, the genus is characterized by a complicated taxonomic history with the complex schemes proposed by Kéler (1939, 1957) and Eichler (1963) on the one hand juxtaposed by the conservative approach of Hopkins and Clay (1952) and Price *et al*. (2003) on the other. Even the precise status of the family Goniodidae is still disputed, although it is widely recognized as a monophyletic group (Ledger, 1980; Lyal 1985; Mey, 1997). Historically, however, there has been great hesitation to separate genera, species groups, and species by some workers, which is indicative of the broad generic concept employed (Mey 2003). And the fact, that for most goniodids even well-defined species and species groups tend to grade into each other with new species descriptions (Smith 2000). The highly variable appearance and sexual dimorphism of the antennae and male genitalia, combined with a reliance on host associations, has led to the description of numerous taxa often times based on only a few specimens (Clay 1940; Ledger 1980; Mey 2003; Tendeiro 1988).

As such a better understanding of both the classification and relationships of *Goniodes* depends on sound taxonomic revisions in the framework of the morphospecies concept (Mey 2003). The taxonomic framework proposed for *Goniodes* is still Clay's seminal monograph published in 1940. She divided the genus into 13 intrageneric groups based on louse morphology, without consideration of the host associations. These informal groupings are problematic because the larger groups are amalgams including both Old and New World species. Tendeiro (1959, 1965, 1988) described many new genera and species often times from very small numbers of specimens. Given the lack of material for many of these species and the controversy surrounding the status of many others, this is obviously a difficult task. Many species and groups are defined by long, rather ambiguous, diagnoses containing a combination of small and superficial characters (Clay unpublished: 2). For the African species Tendeiro (1954b, 1954d, 1955b, 1960, 1988) contributed much, largely following Eichler (1963) and Kéler's (1957) classification, but the generic status of many of these taxa is questionable (Ledger 1980). Many of the features Tendeiro used to diagnose species are either difficult to discern or apparently convergent including the crop teeth (his scaly gular plates) and coloration (see discussion Group H), while others are at best tenuous and difficult to discern. In addition much of his work was published in Portuguese or French, making it largely inaccessible to most workers.

In combination, the complicated taxonomic histories of many taxa, a general lack of material for many species, a lack of active workers in Africa, and the widely differing morphological nomenclature employed make it difficult to start resolving some of these issues and gain a better understanding of the phylogenetic relationships between the taxa involved. An obvious precondition for any phylogenetic work is "sound" taxonomy (Mey 2003; Minelli 1993). Given the state of *Goniodes* taxonomy, a revision is not only warranted, but in light of Ledger (1980), an urgent outstanding need. Here I utilize established conventions and modern taxonomic methods (ICZN 2000; Winston 1999), accepted phthirapteran nomenclature (Price *et al*. 2003), and standardized morphological terminology (Mey 1994; Smith 2000, 2001) to define, describe, and illustrate, the Sub-Saharan species of *Goniodes*. These are divided into 6 groups following Clay (1940) with a discussion of each group. I have made every attempt to acquire multiple adult representatives of each species and wherever possible the type material. When a species is known from more than one host species specimens from all available host were sought. Some of Tendeiro's species were described from small series and I have not yet seen them, others type specimens have deteriorated to the point that they are useless for comparison and all but destroyed. Given the renewed efforts to better understand both the African avifauna and their Phthiraptera (Marks *et al*. 2004; Meyer *et al*. 2008; Weckstein *et al*. 2009) additional well-preserved specimens might become available through further collecting; and as such I recognize such species as valid. In cases where only a single sex was available, I use measurements from the original descriptions. Sometimes characters are obscured by debris on the slide, and in such cases, I used the original descriptions and illustrations. In cases where very few specimens were available I include measurements from the original description to illustrate the range of variation.

At the outset I have to offer a caveat that I am in full agreement with Clay (1940) that *Goniodes* as currently defined: *contains a large number of species of diverse form, which fall into a number of more or less well-defined groups. These however, cannot be considered to be of generic value, as there occur species, which are intermediate between the groups and connect up the whole range of species, with one or two exceptions into a definable genus. The generic separation of these groups would merely obscure natural relationships of the species, and would in no way clarify the classification*. As such I follow a very conservative approach in the belief that a cautionary approach will go far in preventing the mistakes of the past. I feel this approach is warranted given that an initial survey of 3000+ specimens of *Goniodes* from six museums (K. C. Emerson Entomology Museum, Oklahoma State University, Stillwater (OSEC); University of Minnesota Insect Collection, St. Paul (SMPM); Field Museum of Natural History, Chicago (FMNH); United States National Museum of Natural History, Washington, D. C (NMNH); The Natural History Museum, London (BMNH); and Musee Royal de L´Afrique Central, Tervuren (RMCA) revealed 22 new host records from 12 host genera from all parts of the world. This includes the first *Goniodes* recorded from the monotypic Southeast Asian galliform genera *Anurophasis* and *Calloperdix* (see Table 2.1). This confirms Ledger's assessment that there are many new species of *Goniodes* yet to be described (1980). Given that most host species, in general, harbor a unique louse species, and that this survey included holdings from only six museums, the potential for new species and expansion of *Goniodes* is astounding.

## MATERIALS & METHODS

Specimens were examined with a Leica compound microscope equipped with phase contrast. Morphological terminology follows Mey (1994) and Smith (2000, 2001). A variety of measurements were made using a ocular micrometer and each description section of the species accounts include the following measurements (Abbreviations included) in millimeters: TW – temple width; HL – head length at midline; CI – cephalic index (HL/TW); PW – prothorax width; MW – metathorax width; AWV – abdomen with at segment V; GL – Male genitalia length; PL – Male penis length; and TL – total length.

For brevity generic and group features are not repeated in the species descriptions.

If two or more specimens of the same sex were examined the range of measurements are provided, if three or more individuals were measured the mean is also provided in parentheses following the range. If only a single specimen was available for examination, measurements from the type description were used to indicate morphometric variability.

Host nomenclature and classification follows Dickinson (2003) and Madge and McGowan (2002). Specimens utilized were obtained from the following collections (acronyms follow Evenhuis and Samuelson 2007): BMNH – The Natural History Museum, London, United Kingdom; FMNH – Field Museum of Natural History, Chicago, Illinois, USA; INHS – Illinois Natural History Survey, Champaign, Illinois, USA; OSEC – K. C. Emerson Museum, Oklahoma State University, Stillwater, Oklahoma, USA; SMPM – University of Minnesota Insect Collection, St. Paul; Minnesota, USA; USNM – United States National Museum of Natural History, Washington, D. C.; RMCA – Musee Royal de L´Afrique Central, Tervuren, Belgium.

In the materials section the number of host individuals from which lice were examined is shown in parentheses. **Material examined:** Total # of lice (# of Males, Females). MUS ex *Host* (Author) (Host Order: Host Family) – Host Common Name: COUNTRY: # of lice Male, Female, nymph (Place/City, Date, Coll.).

ISCHNOCERA Kellogg

PHILOPTERIDAE Burmeister

***GONIODES* Nitzsch, 1818**

*Goniodes* Nitzsch, 1818: 293. Genotype by subsequent designation (Johnston and Harrison, 1911: 326). Type species: *Goniodes pavonis* = *Pediculus pavonis* L.

*Archigoniodes* Conci, 1946: 77. Type species: *Goniodes wilsoni* Clay.

*Archigoniodes* Eichler, 1945, 1946 = *nomen nudum* (Hopkins and Clay, 1952).

*Archigoniodes* Eichler, 1945, 1946 *apud* Conci 1946: 76-78. Type species: *Goniodes wilsoni*

Clay.

*Archigoniodes (Archigoniodes)* Conci, 1952: 176. Type species: *Goniodes wilsoni* Clay.

*Archigoniodes (Clayarchigoniodes)* Conci, 1952: 178. Type species: *Goniodes extraneus* Clay.

*Astrocotes* Kéler, 1939b: 109. Type species: *Goniocotes astrocephalus* Burm.

*Astrodes* Kéler, 1939b: 113. Type species: *Goniocotes coronatus* Giebel.

*Aurinirmus* Tendeiro, 1983c: 116. Type species: *Aurinirmus arfakianus* Tendeiro.

*Claygoniodes* Conci, 1946: 77. Type species: *Goniodes extraneus* Clay.

*Clayarchigoniodes* Conci, 1952: 178. Type species: *Goniodes extraneus* Clay.

*Clayarchigoniodes* Tendeiro, 1955a: 788. Type species: *Goniodes hopkinsi* Clay.

*Dictyocotes* Kéler, 1939: 153. Type species: *Goniocotes haplogonus* Nitzsch.

*Euligoniodes* Mey, 1997: 29. Type species: *Goniodes ocrea* Piaget.

*Gonocephalus* Nitzsch *apud* Kéler, 1939: 130. Type species: *Goniodes chelicornis* Denny.

*Gonotyles* Kéler, 1939: 48. Type species: *Goniodes cervinicornis* Giebel.

*Homocerus* Kéler, 1939: 117. Type species: *Goniocotes macrocephalus* Taschenberg.

*Keleria* Tendeiro, 1954b: 94. Type species: *Goniodes fimbriatus* Neumann.

*Kelerigoniodes* Conci, 1946: 76. Type species: *Goniodes processus* Kellogg and Paine.

*Leipoiella* Mey, 1986: 526. Type species: *Leipoiella maoriana* Mey.

*Lobicrotaphus* Mey, 1997: 35. Type species: *Goniocotes discogaster* Taschenberg.

*Maleoicus* Mey, 1997: 24. Type species: *Goniocotes minor* Piaget.

*Maleophilus* Mey, 1997: 23. Type species: *Goniocotes major* Piaget.

*Margaritenes* Kéler, 1939: 132. Type species: *Goniodes eurygaster* Piaget.

*Megatheliella* Mey, 1986: 530. Type species: *Goniodes leipoae* Emerson and Price.

*Oulocrepis* Kéler, 1939: 97. Type species: *Goniodes dissimilis* Denny.

*Solenodes* Kéler, 1939: 101. Type species: *Goniodes dispar* Burm.

*Stenocrotaphus* Kéler, 1939: 124. Type species: *Goniocotes gigas* Taschenberg.

*Weelahia* Mey, 1997: 33. Type species: *Goniocotes fissus* Rudow.

*Zlotorzyckella* Eichler and Vasjukova, 1981: 232. Type species: *Goniodes chelicornis* Denny.

A thorough characterization of the *Goniodes* is difficult, especially given the size of the genus, but based on Chapter 2, and the literature the genus can be characterized as follows: Relatively large Ischnocera with circumfasciate heads; head usually as wide, or even wider, than it is long. General morphology as in Figures 2.1-2.3; marginal carina (clypeal margin) complete (uninterrupted), flattened and anteriorly rounded usually with prominent clypeal angles. Trabeculae undeveloped and usually represented by membranous lobes. Clavi of variable size and shape present, either membranous or sclerotized. Antennae may be sexually monomorphic or dimorphic, but the 2$^{nd}$ and 3$^{rd}$ flagellomere is not modified or greatly reduced in the male. Frequently with a deep indentation between the temple and eye, the former usually expanded, protruding laterally forming an angle. Temporal angle usually with a ventral process showing a small terminal seta or thorn-like microseta in at least one, but usually both sexes. The occipital margin (*angles faciaux sensu* Tendeiro (1988)) extends posteriorly to varying degrees forming an angle with an apical seta or thorn-like microseta. Typically 2 + 2 enlarged temporal macrosetae, but up to 8 in some species. Marginal temporal seta (m.t.s) 1 and 3 well developed, m.t.s 2 is usually a microseta.

Thorax variable in shape and size. Posterolateral margin of prothorax rounded, not angular or extended. Pterothorax lacking lateral indication of meso-metathoracic suture, always with a trichoid seta *sensu* Smith (2000) located in a pit on the integument. Ventral pterothoracic setae (meso- and metasternal seta *sensu* Clay (1940)) absent or present. Lateral to latero-posterior margin of pterothorax with 2 distinct pairs of setae on either side.

Segment II of the abdomen large and with the postero-lateral margin free and sometimes extended. In some cases there are fusion between the second segment and the pterothorax as in *G. spinicornis* (Clay unpublished: 3). Tergal plates II-VIII usually widely separated often with additional sclerotized structures (tergal or intertergital thickenings *sensu* Clay (1940)). Sternites in the form of lateral, never central plates; and variable in shape and size; often constricted; or divided into 2 or more additional plates, with the medial pairs usually larger, and lateral ones progressively smaller. Pleurites broad and variable, but with complicated re-entrant heads extending anteriorly into preceding tergite. Pleural heads extending antero-medially to varying degrees, and can terminate lateral, medial or level, relative to the spiracle of the preceding tergite.

Segment VIII with a trichoid seta *sensu* Smith (2000), similar to that on the pterothorax, located in a pit on the integument.

Male abdomen with nine segments (II-X), of which segment IX is greatly reduced appearing as a lateral rudiment on either side; genital opening dorsal, usually bearing setae on the anterior and posterior margins. Male genitalia highly variable, often very simplified. Female abdomen with eight segments II-VIII ($8^{th}$ composed of true segments IX and X); tergal plate VIII usually continuous across the segment; vulva either terminal or at the level of segment VII, variable in form.

For brevity, generic and group features are not repeated in species descriptions. From here, I provide only the diagnostic characters pertinent to define the genus as it pertains to the sub generic groups of African species that serve to distinguish them, both as groups and as species from one another. Key characters are for both sexes unless otherwise indicated.

## Sub-Saharan species groups and species descriptions

### Group F

*Archigoniodes (Archigoniodes) sensu stricto* Tendeiro, 1988: 66. Type-species *G. wilsoni* Clay.

*Archigoniodes* Conci, 1946: 178 (sub genus).

*Archigoniodes* (Conci) Tendeiro, 1955: 787 (genus).

*Archigoniodes* Eichler in Conci, 1946: 178 – *nomina nudum* (Hopkins 1947: 98).

### *1. G. wilsoni* Clay

(Figures 1.1-1.3; Clay, 1938: 6 – Figures 5-9; Conci, 1952: 177 – Figure 1; Tendeiro, 1988: Plate XXXV (photo 1 and 2), XXXVI (photos 1 and 2), XXXVII (photos 1 and 2).

*G. wilsoni* Clay, 1938: 5.

*Archigoniodes wilsoni* Eichler 1945 (*nomen nudum*).

*Archigoniodes (Archigoniodes) wilsoni* Conci 1946: 77.

*Archigoniodes wilsoni* Tendeiro 1955a: 779; 1988: 66.

**Type Host**: *Afropavo congensis* Chapin, 1936 (Galliformes: Phasianidae) – Price *et al*. 2003: 186.

**Diagnosis and General Description:** Large species (Males: 3.08-3.26 mm; Females: 4.81-5.31 mm). Head round (length = width) with frons convex and apically rounded; many long setae on the head and thorax. Temples monomorphic and not expanded; coni thickened and extended posteriorly in both sexes. Antennae sexually dimorphic. No ventral pterothoracic seta. Pleurites broad with anterior pleural head nearly level with spiracle.

**Male:** Head round with large overhanging and pointed coni. Marginal carina wide, with a 17-18 seta and 1 sub median ventral seta + others, on each side. Antennae with scape short and robust, lacking process. Pedicel shorter than the flagellomeres combined; 1$^{st}$ flagellomere long and slightly asymmetrical, with small posteromedial hyaline expansion. Dorsal surface with numerous microseta. Dorsal submarginal and pre-antennal setae larger; postnodal setae very short. Eyes large and prominent with an ocular macroseta. Marginal temporal carina, not very wide, but unites with the postocular nodus, and with distinct setal channels. Occipital angles acute elongated, and triangular with an apical microseta.

Thorax as wide as the head. Prothorax with 5-9 lateral macroseta on the posterior third and 2-3 dorsal setae on the posterior margin. Pterothorax trapezoid with 19-20 lateral macrosetae and a row of shorter setae on posterior margin.

Abdomen pear-shaped; widest at segment IV; characterized by dorsal tergal combs on segments IV and V. Segment VIII reduced; segment XI very narrow and posteriorly rounded. Tergites distinct, wide; but less sclerotized compared to other African species. Tergites linguiform and medially reduced by setal insertions in segments II-VIII. Posterolateral end of segment II terminating in a distinct elongated point. Indistinct, weakly sclerotized inter-tergal plates present; very small in segments II-V; more elongate in segments VI-VI. Pleural heads III-VIII sclerotized, extending into the preceding segment by large anterior heads forming tripartite bulges. Small lateral sternites. Posterior margin of terminal segment rounded, anterior margin of genital opening sclerotized with numerous spine-like seta; and with more than 2 long macrosetae on each side.

Abdominal chaetotaxy, laterally with 2 macroseta on segments II-IV; 3 on segments IV-VIII; dorsally with 18-20 macrosetae on segment II; 22-26 on III; 28-30 on IV (central 18 thicker and forming a tergal comb); 29 on segment V (central 15 on each side forming a tergal comb); 23 on VI (central 8 forming a loose tergal comb); 16 on VII; 9 on VIII (lateral 7-8 longer); and none on segment XI. Few minute microsetae scattered ventrally. Male genitalia with lengthened basal plate and one paramere shorter than the other, similar to *G. numidae*.

Measurements:  TW 1.14-1.19(1.17); HL 0.93-0.97 (0.94); CI 0.80-0.81 (0.81); PW 0.78-0.82 (0.80); MW 1.15-1.25 (1.19); AWV 1.66-1.75 (1.70); GL 0.82-1.49 (1.26); TL 3.08-3.26 (3.19).

**Female:** Head wider than the male, with pre-antennal region, and coni longer. Wide marginal carina. Fewer dorsal setae. In addition to the sub-marginal, preantennal, and post nodal setae the marginal carina with 4 macrosetae each side. Fewer ventral sub marginal setae than male. Antennae filliform with pedicel longer than scape.

Thorax as in male, but with only 4 lateral setae on the prothorax; and 8-11 lateral and 2-3 setae on the posterior margin of the pterothorax.

Abdomen oval-shaped, considerably larger than that of male. Pleurites somewhat wider than male; sternites similar. Intertergal plates present, but indistinct and only visible in phase. Lacking bifid structure associated with genital region. Genital opening terminal, lacking marginal setae.

Abdominal chaetotaxy; lateral and dorso-lateral seta on the posterior margin of segment II: 2-3 on each side; III: 6-9; IV: 8; V: 8-9; VI: 10; remaining segments shown in Clay (1938: Figure 9). Dorsally segment II: 5 each side; III has 10; IV 7-9; V 7; VI has 4; VII = 4; VIII = 6. Ventrally segments II-IV have 1 central seta each side; V-VII have 2 central seta each side; VIII has 1 central set and numerous minute spines on each side; terminal segment as shown in Clay (1938: Figure 9).

Measurements:  TW 1.27-1.39 (1.33); HL 1.08-1.15 (1.13); CI 0.83-0.89 (0.85); PW 0.90-0.99 (0.95); MW 1.28-1.38 (1.35); AWV 2.02-2.15 (2.07); TL 4.81-5.13 (4.98).

**Discussion:** This monotypic group is similar to Group G especially in the appearance of the coni, the position of the male genital opening, female vulval margin, the distinctive cheatotaxy of the head and thorax, and the presence of tergal combs. According to Clay (1940) it lacks intertergital plates, however I agree with Tendeiro (1988) that they are present, although indistinct. As such, the best way to distinguish this taxon from Group G is the form and number of sternites; the number of tergal combs; and the generally weak sclerotization of the abdomen. See Tendeiro (1955a) and Conci (1946, 1952) for discussion regarding status and subgeneric status of *Archigoniodes* and *Clayarchigoniodes*, which includes species from Group F and G.

**Type material:** RMCA holotype, paratypes (4), Jar in slide cabinet (~160 specimens); BMNH paratypes.

**Material studied:** 8 specimens (4 males, 4 females): 2 specimens (NMNH) ex *Afropavo congensis* (Chapin, 1936)(Galliformes: Phasianidae) – Congo Peafowl: **CONGO**: 1 male, 1 female (no place, no date, Coll: Meinertzhagen, Host: 10606). 2 specimens (OK 4026) ex *Afropavo congensis* (Chapin, 1936)(Galliformes: Phasianidae) – Congo Peafowl: **BELGIAN CONGO**: 1 male, 1 female (Tshuapa, 1956, Coll: R. P. Lootens). 2 specimens (RMCA) ex *Afropavo congensis* (Chapin, 1936)(Galliformes: Phasianidae) – Congo Peafowl: **BELGIAN CONGO**: 1 male, 1 female (Tshuapa, Ikela, 26.x.1955, Coll: P. Lootens). 2 specimens (RMCA) ex *Afropavo congensis* (Chapin, 1936) (Galliformes: Phasianidae) – Congo Peafowl: **BELGIAN CONGO**: 1 male, 1 female (Tshuapa, 1956, Coll: R. P. Lootens).

**Additional material: BMNH**: 5 males, 4 females (paratypes) ex *Afropavo congensis*: CONGO: (Congo, vii. 1937, BMNH 14555, Meinertzhagen Collection, Host: Male 10621). 1 female ex *Afropavo congensis*: CONGO: Tshuapa, Ikela, 26.x.1955, Coll: P. Lootens, Brit. Mus.1956-168). 1 male ex *Afropavo congensis*: BELGIAN

CONGO: Tshuapa, Coll: R. P. Lootens. 1956, Brit. Mus. 1959-105). 2 females ex *Afropavo congensis* (Skin 260). **RMCA:** 2 males, 2 females (paratypes) (RMCA) ex *Afropavo congensis*: CONGO: (Congo, Coll. Mus. Congo, 10606). 2 males, 1 female ex *Afropavo congensis*: BELGIAN CONGO: (Inkongo (Lusambo), 1938, Coll: Rev. Wilson). 1 female ex *Afropavo congensis*: BELGIAN CONGO: (Bokungu, Basoka, 10-18-1950, Coll: Dupuis). 2 females, 2 males ex *Afropavo congensis*: BELGIUM: (Zoo – Anvers, 4.8.1961, Coll: P. L. G. Benoit).

## Group G

*Archigoniodes* Eichler in Conci, 1946: 178 – *nomina nudum* (Hopkins 1947: 98).

*Keleria* Tendeiro, 1954b: 94.

*Archigoniodes (Clayarchigoniodes*) Conci, 1952: 178.

*Clayarchigoniodes* (Conci) Tendeiro, 1955a: 788.

*Archigoniodes (Clayarchigoniodes)* Tendeiro, 1988: 33.

This group contains medium and large species (Males: 2.68-4.20mm; Females 4.45- 4.80mm) with monomorphic temples that are only slightly expanded. Coni are variable being either small and membranous, or large and sclerotized. Antennae sexually dimorphic, with the 1$^{st}$ flagellomere in the male elongated with a variable lateral hyaline extension, and the scape without a process. In the female the pedicel is considerably longer than scape. Always with more than 2-3 elongated temporal setae on each side. Numerous elongated macrosetae on the lateral margins of the head and pterothorax, more so in males. Prothorax with 2-4 large lateral setae in both sexes, with ventral pterothoracic setae absent. Pleurites broad and thickened. Males with tergal combs, variable, but usually on tergites IV, V, or VI. Intertergal plates usually present between segments VI-VII or III-VII in the male; between segments II-VII in the female. Sternites form two irregular plates each side of the abdomen. No bifid structure in the female, vulva terminal lacking marginal setae. Male genital opening modified and sclerotized to varying extends.

The overall similarity between the general characters and habitus (specifically in *G. gigas*) and *G. wilsoni* in Group F, and in general with species in Group H leads me to agree with Clay (1940) that none of these have generic value.

### *2. G. numidae* Mjöberg

(Figures 1.4-1.5; Clay 1940: 29 – Figures 18a-c,19a-b, 20a-b; Tendeiro 1988: Plate X (photos 1 and 2), XI (photos 1 and 2), XII (photos 1 and 2), XIII (photos 1 and 2), XIV (photos 1 and 2), XV (photo 1), XL (photos 1 and 2), XV (photo 2), XVI (photos 1 and 2), XVII (photos 1 and 2); Kéler 1952: 39 – Figures 16-18)

*G. numidae* Mjöberg, 1910b: 102.

*Goniodes fimbriatus* Neumann, 1913: 629 – Emerson, 1972: 76; Price *et al*. 2003: 184.

*Archigoniodes numidae intermediae* Tendeiro, 1988a: 4 – Price *et al*., 2003: 185.

*Goniodes perlatus* Clay, 1940a: 31 – Hopkins and Clay 1952: 157; Emerson, 1972: 76; Price *et al*. 2003: 185.

*Archigoniodes (Clayarchigoniodes) numidae* Conci, 1946: 77.

*G. fimbriatus* synonymy by Ledger, 1980: 101; Emerson, 1972.

*Clayarchigoniodes fimbriatus* Tendeiro, 1956: 129.

*Keleria fimbriatus* Tendeiro, 1954a: 312; 1954b: 94.

*G. perlatus* Emerson, 1972a.

*Stenocrotaphus perlatus* Kéler, 1952.

*Keleria perlata* Tendeiro, 1954a; 1955b: 151.

**Type Host**: *Numida m. meleagris* (Linnaeus, 1758)(Galliformes: Numidae) – Hopkins and Clay, 1952: 157; Price *et al.* 2003: 185.

**Hosts**: *N. m. galeatus* (Pallas, 1767)(Galliformes: Numidae) – West African Guineafowl – Clay, 1940a: 31; Tendeiro, 1956: 129; Price *et al.* 2003: 184.

*N. m. intermedia* Neumann, currently *Numida m. meleagris* (Linnaeus,1758) (Galliformes: Numidae) – Helmeted Guineafowl – Price *et al.* 2003: 185.

*N. m. major* (W. L. Sclater, 1924), currently *Numida m. meleagris* (Linnaeus, 1758)(Galliformes: Numidae) – Helmeted Guineafowl – Clay, 1940a: 32; Price *et al.* 2003: 185.

*N. m. callewaerti* (Grote, 1936), currently *N. m. galeatus* (Pallas, 1767) (Galliformes: Numidae) – West African Guineafowl – Clay 1940a: 31.

*N. m. maxima* (Boulton, 1934), currently *Numida meleagris marungensis* (Schalow,1884)(Galliformes: Numidae) – Tufted Guineafowl – Clay 1940a: 32.

*N. m. coronatus* (Gurney,1868)(Galliformes: Numidae) – Natal Helmeted Guineafowl – Clay 1940a: 32.

*N. m. mitrata* (Pallas, 1764)(Galliformes: Numidae) – Tufted Guineafowl – Clay 1940a: 32.

*N. m. damarensis* (Peters, 1934), currently *Numida meleagris papillosus* (Reichenow, 1894)(Galliformes: Numidae) – Damara Tufted Guineafowl – Clay 1940a: 32.

**Diagnosis and General Description:** Distinguished from *G. hopkinsi* by shape of the coni in both sexes, the antennae, genital openings, and male genitalia. From *G. klockenhoffi* by the shape of the abdomen in males, the wider carinas; and overall tergite shape. Note the large, square sternal plates in segment III-VI.

**Male:** Head, squat, much wider than long, slightly wider at temples; with approximately 8 macrosetae of varying lengths on the temples. Dorsal surface scattered with minute spine-like setae. M.t.s 1 a macrosetae. Antennae with scape enlarged compared to Female, pedicel elongate, and distal post-axial angle of 1$^{st}$ flagellomere elongated at a right angle to the 2$^{nd}$ flagellomere as a distally rounded process *sensu* Clay (1940); or 1$^{st}$ flagellomere somewhat triangular (*sensu* Neumann (1913) and Tendeiro(1954)) - this character is highly polymorphic in specimens and often both conditions are present in a single specimen. Tendeiro (1955) thought, and I agree, that this might be an artifact of preservation. Thorax with posterior margin of prothorax with 3-4 seta; lateral margin of pterothorax with 12-16 macro setae and 9-12 on the posterior dorsal margin.

Abdomen, short and broad, widest at segment IV; with intertergital plates (between segments II-VIII = 6 plates) and double sternal plates. Dorsal margin of genital opening elongated into a sclerotized bilobed process (pear-like) with a sclerotized posterior margin with setae. Abdominal chaetotaxy; tergal combs - some setae internal margin of tergite IV, a more defined group on V and a weak group on VI. Genitalia with an elongated basal plate terminating in simple pointed parameres of unequal length. Similar to *G. wilsoni*.

Measurements: (n = 21) TW 1.29-1.76 (1.40); HL 0.86-1.18 (0.95); CI 0.63-0.71 (0.68); PW 0.70-0.98 (0.81); MW 1.13-1.51 (1.27); AWV 1.53-2.12 (1.81); GL 0.80-1.98 (1.17); TL 2.66-4.28 (3.05);

**Female:** Head as in male, with filiform antennae; coni a little longer, marginal carina with only 2 elongate ventral submarginal setae. Thorax as in male, but with fewer setae on lateral (~10-12) and posterior (~2-4) margins of pterothorax

Abdomen, large and more elongated than male; with elongate tergal plates present (II-IX = 7 strips); posterolateral corner of segment II is prolonged into a point. Abdominal chaetotaxy: Dorsally II-V: 2 lateral, 4-5 median, + 2 central (elongate and anterior); VI-VII: 2-3 lateral, 2-5 median, + 2 elongate and central. Ventrally II-VIII: 2 central; with + 2 in VI-VII (= 4). Segment II: no laterals; III 4-5; IV-VIII 5-9.

Measurements: (n = 27) TW 0.90-1.78 (1.57); HL 0.64-1.23 (1.11); CI 0.63-0.83 (0.71); PW 0.56-1.01 (0.92); MW 0.76-1.58 (1.41); AWV 1.10-2.61 (2.22); TL 2.13-5.20 (4.56).

**Discussion:** Holotype (M. Meinertzhagen Coll. #7638) and paratypes (40 Males, 15 Females) for *G. perlatus* in BMNH. In the material from *Numida* there is at least 1 maybe 2 additional species related to *G. fimbriatus* and *G. perlatus* according to Clay (1940: 32). Hopkins and Clay (1952: 157) recognize *G. perlatus* as a valid species, but states that it might be a synonym of *G. numidae*, whose status they could not assess at that time. They further state that the types for *G. perlatus* are in the BMNH (Hopkins and Clay 1952: 157). RMCA holds the holotype and paratypes (4) for *G. fimbriatus* and *G. numidae intermediae;* BMNH the holotype for *G. perlatus*. Clay (1940) describes *G. perlatus*, and Ledger (1980) based on Clay (1940) places *G. fimbriatus* in *G. numidae*.

Tendeiro (1985) places *G. perlatus* in *G. numidae*, and concludes that the form *G. perlatus* broadly occurs in eastern and southern Africa, while the form *G. fimbriatus* predominates in West Africa (Tendeiro 1987). *Goniodes numidae* is thus a highly polymorphic species with a variable morphology which might be subject to selection based on aridity. This must influence sclerotization, the assumption being that drier conditions leads to an increase in sclerotization thereby reducing evaporation. The polymorphism found in this species is confirmed by Clay (1940:32), there is at least one and possibly 2 species more related to *G. fimbriatus* and *G. perlatus* (currently both included in *G. numidae*) in her material. Tendeiro's sub-species lend further support (1988).

**Material studied:** 48 specimens (21 Males, 27 Females): 4 specimens (BMNH) ex *Numida meleagris major* (W. L. Sclater, 1924), currently *Numida m. meleagris* (Linnaeus, 1758)(Galliformes: Numidae) – Helmeted Guineafowl: **UGANDA**: 2 males, 2 females (Buganda, Coll: Meinertzhagen, Host: 116871). 2 specimens (BMNH) ex *Numida meleagris major* (W. L. Sclater, 1924), currently *Numida m. meleagris* (Linnaeus, 1758) (Galliformes: Numidae) – Helmeted Guineafowl: **UGANDA**: 1 male, 1 female (Coll: Meinertzhagen, Host: III). 2 specimens (BMNH) ex *Numida meleagris major* (W. L. Sclater, 1924), currently *Numida m. meleagris* (Linnaeus, 1758) (Galliformes: Numidae) – Helmeted Guineafowl: **UGANDA**: 1 male, 1 female (Coll: Meinertzhagen, Host: XXXI). 2 specimens (BMNH) ex *Numida meleagris marunguensis* (Schalow, 1884)(Galliformes: Numidae) – Tufted Guineafowl: **ZAMBIA**: 2 females (N.W. Rhodesia, 1939, Coll: unknown, Host 13333; BM 1951-171 in Meinertzhagen Collection). 2 specimens (BMNH) ex *Numida meleagris coronata* (Gurney, 1868)

(Galliformes: Numidae) – Natal Helmeted Guineafowl: **SOUTH AFRICA**: 1 male, 1 female (Vryburg, Cape Province, 11-vii-1934, Coll. Unknown, Hopkins Collection). 4 specimens (BMNH) ex *Numida meleagris* (Linnaeus, 1758)(Galliformes: Numidae) – Helmeted Guineafowl: **BELGIAN CONGO**: 2 males, 2 females (Vallée Akangaru, xi-1939, Coll: A. Lestrade, Host: Brit. Mus. 1951-546). 4 specimens (BMNH) ex *Guttera edouardi chapini* (White, 1943)(Galliformes: Numidae) – Chapin's crested Guineafowl: **ANGOLA**: 1 male, 4 females (Benguella, Oct. 1901, Coll: Meinertzhagen, Host: 3140). 2 specimens (BMNH) ex *Numida meleagris galeata* (Pallas, 1767)(Galliformes: Numidae) – West African Guineafowl: **SIERRA LEONE**: 1 male, 1 female (Oct. 1904, Coll: Meinertzhagen, Host: 3128 Male). 3 specimens (BMNH) ex *Numida meleagris sabyi* (Hartert, 1919)(Galliformes: Numidae) – Morrocan Helmeted Guineafowl: **MAROCCO**: 2 males, 1 female (Coll: Meinertzhagen, Host: 12550). 1 specimen (FMNH) ex *Numida meleagris major* (W. L. Sclater, 1924), currently *Numida m. meleagris* (Linnaeus, 1758)(Galliformes: Numidae) – Helmeted Guineafowl: **UGANDA**: 1 male (Buvuma Island, 1948, Coll: unknown). 1 specimen (INHS) ex *Numida meleagris major* (W. L. Sclater, 1924), currently *Numida m. meleagris* (Linnaeus, 1758) (Galliformes: Numidae) – Helmeted Guineafowl: **UGANDA**: 1 female (Buvuma Island, 1948, Coll: unknown). 2 specimens (MINN) ex *Numida meleagris* (Linnaeus, 1758) (Galliformes: Numidae) – Helmeted Guineafowl: **SOUTH AFRICA**: 2 males (Bloemfontein Dist., 1 May 1994, Coll: G. Kopij, Host: 94.A.37). 4 specimens (NMNH) ex *Numida meleagris* (Linnaeus, 1758)(Galliformes: Numidae) – Helmeted Guineafowl: **SOUTH AFRICA**: 2 males, 2 females (Union of South Africa: Ndumu, Zululand, Dec.16. 1958, Coll: O. G. Babcock, Host: B.12). 1 specimen (NMNH) ex *Numida* *meleagris major* (W. L. Sclater, 1924), currently *Numida m. meleagris* (Linnaeus, 1758) (Galliformes: Numidae) – Helmeted Guineafowl: **UGANDA**: 1 female (Buvuma Island, 1948, Coll: unknown). 1 specimen (NMNH) ex *Numida meleagris galeata* (Pallas, 1767) (Galliformes: Numidae) – West African Guineafowl: **SENEGAL**: 1 male (from skin, Coll: K. C. Emerson). 1 specimen (NMNH) ex *Numida meleagris mitrata* (Pallas, 1764) (Galliformes: Numidae) – Tufted Guineafowl: **MADAGASCAR**: 1 female (Tanosy, Ft. Dauphin Dist., Nov. 12-1948, Coll: H. Hoogstraal, Host: Lot 52-1033). 2 specimens (OK) ex *Numida meleagris major* (W. L. Sclater, 1924), currently *Numida m. meleagris* (Linnaeus, 1758)(Galliformes: Numidae) – Helmeted Guineafowl: **UGANDA**: 1 male, 1 female (Buvuma Island, 1948, Coll: unknown). 6 specimens (OK) ex *Numida meleagris major* (W. L. Sclater, 1924), currently *Numida m. meleagris* (Linnaeus, 1758) (Galliformes: Numidae) – Helmeted Guineafowl: **UGANDA**: 1 male, 5 females (Busoga, 11-viii-37, Coll: unknown, Host: 4 (KCE #62)). 4 specimens (RMCA) ex *Numida meleagris* (Linnaeus, 1758)[Galliformes: Numidae) – Helmeted Guineafowl: **BELGIAN CONGO**: 2 males, 2 females (Vallée Akangaru, xi-1939, Coll: A. Lestrade).

### ***3. G. hopkinsi*** **Clay**

(Figures 1.6; Clay 1940: 27 – Figure 16, 17a-c; Tendeiro 1988: Plate XXIX (photo 1), XXX (photo 1 and 2).

*Goniodes hopkinsi* Clay, 1940a: 26.

*Archigoniodes:* subgen *Clayarchigoniodes* Conci 1946: 77.

*Keleria hopkinsi* Tendeiro 1954a: 313; 1954b: 94, 105.

*Clayarchigoniodes hopkinsi* Tendeiro, 1956: 129.

**Type Host**: *Guttera edouardi seth-smithi* (White, 1943)(Galliformes: Numidae) - Clay 1940a: 28; Price *et al*. 2003: 184.

**Hosts:** *G. e. sclateri* Reinchenow, currently *Guttera pucherani sclateri* (Reichenow, 1898)(Galliformes: Numidae) – Sclater's Crested Guineafowl – Clay 1940a: 28.

*G. e. pallasi* Stone, currently *Guttera pucherani verreauxi* (Elliot, 1870) (Galliformes: Numidae) – Lindi Crested Guinefowl – Clay 1940a: 28.

*G. e. edouardi* (Hartlaub, 1867)(Galliformes: Numidae) – Zambesi Crested Guineafowl – Clay 1940a: 28.

*G. pucherani* (Hartlaub, 1861)(Galliformes: Numidae) – Kenya Guineafowl – Clay 1940a: 28.

*Guttera verreauxi* Tendeiro 1956: 129.

**Diagnosis and General Description***:* Resembles *G. wilsoni* in enlarged coni; antennae; cheatotaxy; male genitalia, and female terminal segment. Differs in shape of the head and coni, and in the details of female terminal segment. From *G. numidae* by the form of the coni in both sexes, male antennae, and absence of intertergal plates in segments II-V.

**Male:** Head sclerotized, coni elongated and pointed posteriorly; scape not enlarged compared to female; pedicel elongated; 1$^{st}$ flagellomere with hyaline process parallel to the 2$^{nd}$. Thorax see Clay (1940: Figure 16)

Abdomen, short and round; intertergal plates between VI and VII only; IV and V with tergal combs; sternites as two, sometimes 3 plates; genital opening simpler and less sclerotized that *G. numidae*.

Measurements: (n = 3) TW 1.10-1.36 (1.27); HL 0.89-1.00 (0.94); CI 0.68-0.81 (0.74); PW 0.65-0.76 (0.70); MW 0.96-1.14 (1.06); AWV 1.30-1.68 (1.52); GL 0.52-0.72 (0.60); TL 2.68-3.31 (3.01);

**Female:** Head as in male, but larger, and with coni different. Thorax as in male, with fewer setae - laterally with 6-9, and posterior margin with approximately 3. Abdomen as in *G. numidae*; II-IX with intertergital plates; this is however variable, sometimes with intertergital plates on II-VII; or II-VIII. Abdominal chaetotaxy: dorsally II-VII as in *G. numidae*, but III-IV with more median setae 5/6-8. Ventral as in *G. numidae*. II-V 2 lateral, 4-5 median, and 2 long central. Segments VI-VII have 2-3 lateral, 3-5 median, and 2 long central. Ventrally II-VIII has 2 central except for VI-VII that have 4 central. Segment II no pleural, III 4-5 each side, IV-VIII 5-8 each side (Clay 1940:30). Genitalia as in *G. numidae*.

Measurements: (n = 9) TW 1.49-1.65 (1.57); HL 1.10-1.20 (1.15); CI 0.72-0.75 (0.73); PW 0.76-0.93 (0.86); MW 1.20-1.45 (1.31); AWV 1.51-2.30 (2.08); TL 3.57-5.06 (4.62).

**Discussion:** Male holotype #261, paratypes (9 males, 15 females) in BMNH – Clay 1940a: 28; Hopkins and Clay 1952: 154.

**Material studied:** 12 specimens (3 males, 9 females): 2 specimens (BMNH) ex *Guttera pucherani* (Hartlaub, 1861)(Galliformes: Numidae) – Kenya Guineafowl: **TANGANYIKA**: 1 male, 1 female (Tanganyika Territory, no date, Coll: R. E. Moran, Hopkins Collection; "on dry skin"). 1 specimen (BMNH) ex *Guttera edouardi* (Hartlaub, 1867)(Galliformes: Numidae) – Crested Guineafowl: **ZIMBABWE**: 1 male (S. Rhodesia: Chitsa, 13.vi.1950, Coll: unknown, Host: Brit.Mus.1956-353). 1 specimen

(BMNH) ex *Guttera plumifera schubotzi* (Reichenow, 1912)(Galliformes: Numidae) – Schubotz's Plumed Guineafowl: **CONGO**: 1 female (no date, Coll: Meinertzhagen, Host: 12561). 4 specimens (BMNH) ex *Guttera edouardi sclateri*, currently *Guttera pucherani sclateri* (Reichenow, 1898)(Galliformes: Numidae) – Sclater's Crested Guineafowl: **CAMEROON**: 4 females (Cameroons, 1898, Coll: Meinertzhagen, Host: Male 3635). 2 specimens (NMNH) ex *Guttera pallosi seth-smithi*, currently *Guttera pucherani verreauxi* (Elliot, 1870)(Galliformes: Numidae) – Lindi Crested Guineafowl: **EAST AFRICA**: 1 male, 1 female (East Africa, Budango Forest, Unjoro, 1912, Coll: C. E. Akeley, prep R. C. Simpson, Host: 388709). 2 specimens (OK) ex *Guttera edouardi seth-smithi* (White, 1943)(Galliformes: Numidae –Seth-Smith's crested Guineafowl: **UGANDA**: 2 females (Budango, no date, Coll: unknown, #54 K. C. Emerson).

**Additional material: BMNH:** 2 males, 2 females (paratypes) ex *Guttera edouardi seth-smithi*: UGANDA: (Budongo, Hopkins Collection XVI, XIX, Det. Tendeiro). 1 male, 1 female ex *Guttera edouardi sclateri*: CAMEROONS: (Cameroons, Det. Tendeiro (1985)). 1 Female ex *Guttera e. edouardi*: ZIMBABWE: (S. Rhodesia, 3003, Det. Tendeiro (1985). 1 female ex *Guttera e. edouardi*: NYASALAND (Nov. 1906, Coll: Meinertzhagen, Female 3144, Det. Tendeiro 1985). 1 male ex *Guttera edouardi pucherani*: TANGANYIKA: (Coll: Meinertzhagen 10899, Det. Tendeiro 1985).

### *4. G. meyi* Tendeiro 1987(Tendeiro 1988a: 44)

(Tendeiro 1988: Plates XVIII (photos 1 and 2), XIX (photos 1 and 2)

*Archigoniodes meyi* Tendeiro 1988a: 44 – Price *et al*. 2003: 185.

*Archigoniodes*: subgen *Clayarchigoniodes* (Tendeiro 1988: 44).

**Type Host**: *Numida meleagris meleagris* (Linnaeus, 1758)(Galliformes: Numidae) – Price *et al*. 2003: 185.

**Diagnosis and General Description***:* Males of this species has not been seen original description in Tendeiro (1988).

**Female:** Head narrower than male. Coni sclerotized and somewhat curved with posteromedial margin denticulate. Crop teeth present and distinct. Occipital angles acute and appears longer than in males. Prothorax with 3 lateral macro setae; pterothorax with 10-11. Abdomen very wide, and round. Tergite II large and triangular, III-VIII broad and linguiform, medially rounded, progressively shorter from anterior to posterior. Segments II-VIII with sternites present, medially clavate; larger in II-VI.

Measurements: (n = 2) TW 0.34-0.44; HL 0.66-0.81; CI 1.84-1.94; PW 0.55-0.66; MW 0.74-0.92; AWV 1.01-1.23; TL 2.23-2.44.

**Discussion:** BMNH has holotype, allotype, and paratypes. Original description is based on 2 shed cases ex *Numida meleagris meleagris*: YEMEN: (Dec. 1948) Coll: Meinertzhagen 18054).

### *5. G. klockenhoffi* Tendeiro 1987– (Tendeiro, J. 1988a: 47)

(Tendeiro 1988: Plates XX (photos 1 and 2), XXI (photos 1 and 2))

*Archigoniodes klockenhoffi* Tendeiro, 1988a: 47 – Price *et al*., 2003: 184.

*Archigoniodes:* subgen *Clayarchigoniodes* (Tendeiro 1988: 47).

**Type Host**: *Numida meleagris reichenowi* (Ogilvie-Grant, 1894)(Galliformes: Numidae) – Price *et al*. 2003: 184.

**Male:** Description based on Tendeiro (1988). Head wider than long, with expanded temples. Preantennal region short. Marginal carina broadly rounded, with 4 marginal setae; dorsal setae elongated; extending past posterior margin of the head. Two short ventral setae. Coni relatively short and not very robust, directed outwards and backwards, with the postero-lateral border denticulate. Antennae with the scape relatively short and robust; pedicel as long as the flagellomeres combined. $1^{st}$ flagellomere asymmetrical, with a short posterior hyaline expansion. Dorsal surface with scattered setae; those located posteromedially very small, rare or absent rare posterolaterally areas. 6-10 setae irregularly arranged on temporal and occipital margins. Posterior temporal carinas convergent meeting the posterior margins of preantennal nodes and ventral carina. Sclerotized areas in dorsal gular region, apparently corresponding to the post-occipital suture *sensu* Symmons (1952). Gular plates distinct, dark and sculptured. Marginal temporal carina broad, meeting post-ocular nodus, with well defined setal insertions. Occipital angles triangular, with a very short apical setae.

Thorax narrower than head. Prothorax with three anterior, spine like setae, 5-6 elongated lateral setae in the posterior third, and 3-4 setae on posterior margin. Pterothorax laterally rounded, with 19 elongated lateral setae and a row of setae on posterior margin.

Abdomen pear shape and posteriorly truncate. Maximum width at segments IV-V. Tergites granular medially. Segment II triangular, segments III-V broad and rounded; medially narrowed in VI-VIII; with the posterior margin very slightly indented in segments II-V by setal insertions; no indentations on segments VI -VIII. Sternites present on segments II-VII (similar to female) elongated, narrowed laterally, broader medially, especially on segments V-VII. Aneterior margins of segments IV-VI indented by setal insertions. Sternites with medial plates large and robust, densely granular, slightly constricted in the lateral third of segments IV-VII, those on segment VIII smaller and joined (4 out of 5 times) or seperated. As for the sub-genital plates; the lateral sternal plates are small, elliptical, and slightly constricted in segments V-VII or V-VIII. Pleurites very sclerotized with wider pleural heads in segments III-VII, primarily on the postero lateral margin in segment II. Abdominal chetotaxy with medial setae somewhat compressed in segments IV-V, forming clumps, but not distinct tergal combs.

**Female:** Description based on Tendeiro (1988: 47). Head more elongate than in the male. Marginal carina with four seta on each side. Coni as in the male, but more elongate. Antennae filiform with elongated pedicel. No dorsal setae. Eyes very large. Post-nodal setae apparently absent. Sclerotized areas in dorsal gular region, apparently corresponding to the post-occipital suture *sensu* Symmons (1952). Gular plates triangular and larger than those of male. Occipital angles more prominent than in males.

Thorax as in the male. Pterothorax with 14-15 slightly elongated lateral setae. Abdomen oval, broad, and much larger than the male. Tergite on segment II triangular; those on segment III to VIII, linguiform, broad, and medially rounded, with no indentations on the posterior margin. Interterigital plates clavate, medially broad; not indented, and present on segments II-VIII, with the posterior ones shorter/smaller. Medial sternites quadrangular in segment III; pear-shaped and laterally constricted on segments IV-VII. Lateral sternites large ovals in segment II; elliptical in segments III-V; and constricted in segments VI-VII.

**Material:** 1 specimen (paratype) ex *Numida meleagris major*: KENYA: 1 male (Isiolo, Jan. 1956, #20481); 2 specimens (paratypes) ex *Numida meleagris reichenowi*: KENYA: 2 males (Kenya, #12558). 2 specimens (paratypes) ex *Guttera edouardi pucherani*: (Tanga, T. T. viii. 1913, Meinertzhagen 3141).

### *6. G. reichenowii* Tendeiro 1987 – (Tendeiro, J. 1988a: 52)

(Tendeiro 1988: Plates XXII (photos 1 and 2), XXIII (photos 1 and 2))

*Archigoniodes reichenowii* Tendeiro, 1988a: 52 – Price *et al*., 2003: 185-186.

*Archigoniodes:* subgen *Clayarchigoniodes* (Tendeiro 1988: 52).

**Type Host**: *Numida meleagris reichenowi* (Ogilvie-Grant, 1894)(Galliformes: Numidae) – Price *et al*. 2003: 185-6.

**Diagnosis and General Description:** Only 2 specimens seen. Description partly based on the original by Tendeiro (1988).

**Male:** Head smaller than *G. klockenhoffi*. Head wider than long with the temples expanded. Prenatennal area short. Marginal carina widely rounded. Temple carina relatively wide 17-18 marginal setae, and 2-3 shorter ones in a single anterior row. Coni short, thick, directed outwards and backwards, with the postero-lateral edge rounded and not denticulate. Antennae relatively short with a robust scape; pedicle thick, as long as the 3 flagellomeres combined. 1st flagellomere short, robust, and asymmetrical, with a short postero-internal hyaline expansion. 2nd and 3rd flagellomeres less robust. Dorsal surface scattered with short microsetae: 7-8 irregular setae on each side; concentrated anterior to the occipital angle and posterior temporal marginal carina. Post-nodal setae very short. Eyes large, round, and very prominent, with an elongated ocular seta.

Marginal temporal carina bands forming a rectangle; converging and joined with the hypostome and the pre-antennal nodes. Sclerotized gular plates sculptured. Medial posterior areas patterned. Anterior temples very short. Temporal angles somewhat rectangular; slightly bulged and anteriorly warped. Temporal marginal carinas wide; uniting with highly sclerotized post-ocular nodes and pre-ocular nodes. Temporal marginal carinas with 10-11 macrosetae inserted at well-defined tubules. Occipital angles triangular, prominent, acute, with a very short apical microsetae.

Thorax narrower than the head. Pterothorax wide, broadly rounded laterally, with 12-13 elongated lateral setae and a row of short setae on the posterior margin.

Abdomen pear shaped, very broad, truncated posteriorly, with maximum width at segment IV. Tergopleural plates densely granular on the medial two-thirds. Segment II ia broadly triangular; segments III-VI linguiform without internal narrowing and indentations towards medial ends; segments VII-VIII has straight anterior margins with posterior margins indented by setal insertions – in some cases almost completly and rarely completely. Pleural heads capitate. Interterigital plates nearly indiscernible in segment II, but well sclerotized in segments III-VII: thin and elongated in segments III-V; thick and squat in segment VI, shorter, and unindented in segment VII. Apical segment trapezoid; with rounded posterior angles. Tergal chaetotaxy has a row of short macrosetae along posterior margin of tergites, increasing in number medially; but doesn't form tergal combs on segments IV and V. Medial sternal plates granular; large and sclerotized on segments III-VI; smaller on segment VII, and very small on segment VIII; the medial sternal plates are large and oval on segment II; oblong and smaller on segments III-VIII. Genital margin widened posteriorly, almost touching posteriorly; with outer edges parallel. Genitalia as in *G. numidae*; with a densely denticulate genital sac.

**Material:** 1 specimen ex *Numida meleagris reichenowi* (Ogilvie-Grant, 1894) (Galliformes: Numidae), KENYA: 1 male (Tsavo River, 26.5.1913, Coll: Bayer, Det. Tendeiro).

**Discussion:** Female unknown. Male holotype in the collection of RMCA.

***7. G. plumiferae*** Tendeiro 1987– (Tendeiro, J. 1988a: 54)

(Tendeiro 1988: Plates XXIV (photos 1 and 2), XXV (photos 1 and 2), XXVI (photos 1 and 2), XXVII (photos 1 and 2))

*Archigoniodes plumiferae* - Tendeiro, J. 1988a. – Price *et al*., 2003: 185.

*Archigoniodes:* subgen *Clayarchigoniodes* (Tendeiro 1988: 54).

**Type Host**: *Guttera plumifera schubotzi* (Reichenow, 1912)(Galliformes: Numidae) – Schubotz's Plumed Guineafowl – Price *et al*. 2003: 185.

**Diagnosis and General Description:** The male specimen this species is based on was lost and the photos in Tendeiro (1988) are designated the iconotype. The female holotype is damaged and as such the following description is based on Tendeiro (1988).

**Male:** Head somewhat rectangular, wider than long, temples not expanded; 0.96mm long by 1.31 mm wide, cephalic index = 1.36. Preantennal area short. Marginal carina wide nearly reaching the ventral carina with the internal border rounded. Marginal carina with 14-15 setae on each side. Coni rounded, with the antero-lateral border rounded and prominent; prolonged as a square sclerotized expansion, and with the posterior margin tilted/slanted. Antennas absent in the specimens studied. Dorsal surface covered by numerous scattered microsetae. Eyes large,semicircular; protruding. Post-nodal setae short. Anterior temples very short. Marginal temporal carina rounded with 9 elongate marginal temporal setae; extending from the posterior temples to the base of the anterior temples; and with prominent cannuculi (setal insertions). Temporal marginal carinas sclerotized bands dark; converging anteriorly; extending from the temporal marginal carinas to the hypostome and the pre-antennal nodus. Gular plates prominent sclerotized and ovoid. Occipital angles forming a large triangular posterior process; weakly sclerotized and with a very short apical microsetae.

Thorax narrower than the head. Prothorax with 4 lateral macro setae. Pterothorax with 11-13 elongated lateral setae and a row of short setae on the posterior margin extends prominently over the abdomen.

Abdomen pear-shaped, wide, with maximum width at segment IV. Tergopleural plates partially granular, broad and triangular in segment II. Large and medially linguiform in segments III-V; tapered in segments VI-VIII. Posterior margin with little or no indentations and with a postero-medial reentrant position to segment IV and V. Interterigital plates are small, oblong, and present on tergites II-VII. Terminal segment rectangular with posterior margin forming a low arch, with long and medium dorsal macrosetae. Sternites with thick internal plates, squat, grainy and very densely sclerotized in segments III-VII; smaller in segments II and VIII, with the antero-internal reinforcements narrow and capitate; lateral sternal plates absent in all segments.

Abdominal chaetotaxy: No sternal setae. Dorsal chetotaxy has short seta arranged along the posterior border of tergopleural plates; many more on the internal side of tergites III and IV and, especially, on tergite V; or they (setae) group together in tight bunches. Genital plate elongate, forming a horseshoe-shaped square in anterior extremities. Genitalia same as in *G. numidae*; with parameres very thin.

**Female:** Head as in the male. Marginal carina with four seta on each side. Coni very robust, more elongated and prominent than those of male; rounded, with the antero-lateral border rounded and prominent; prolonged as a square sclerotized expansion, and with the posterior margin tilted/slanted. Antennae filliform, with elongated pedicel. No scattered microsetae on dorsal surface. Marginal temporal carinas bend more medially than in the Male. Occipital angles more elongated than in the male.

Thorax as in the male. Pterothorax with 8 slightly elongated lateral setae. Abdomen oval shaped and wide. Tergopleural plates triangular in segment II; linguiform in segment III-VIII with the posterior margin unindented. Intergital plates clavate; thick; more elongated than in male, present on segments II-VII. Lateral sternal plates absent in all segments. Abdominal chaetotaxy, dorsally includes 2 lateral setae on segment II; and central setae in segments II-VIII, fewer in number than in II. Vulval margin as in *G. hopkinsi*.

**Discussion:** As stated above the male this species description is based on was lost. The female holotype (ex *Guttera plumifera schubotzi*: CONGO: (Moga, 7/3/1964, Coll: Prigogine, Det. Tendeiro) is desiccated and damaged beyond recognition and considered destroyed. Further collecting might yield additional specimens and as such I retain this species as valid.

***8. G. schoutedenii*** Tendeiro 1987– (Tendeiro, J. 1988a: 59)

(Tendeiro 1988: Plates XXXI (photos 1 and 2), XXXII (photos 1 and 2), XLIII (photos 1 and 2), XLIV (photos 1 and 2), XLVII (photos 1 and 2))

*Archigoniodes schoutedenii* - Tendeiro, J. 1988a. – Price *et al*., 2003: 186.

*Archigoniodes*: subgen *Clayarchigoniodes* (Tendeiro 1988, 58).

**Type Host**: *Guttera edouardi verreauxi* (Elliot) = *Guttera pucherani verreauxi* (Elliot, 1870)(Galliformes: Numidae) – Lindi Crested Guineafowl – Price *et al*. 2003: 186.

**Diagnosis and General Description:** Some specimens in the type series is desiccated and in poor shape. However there is a reasonably complete male and female available. The following description is based on these specimens and Tendeiro's original description and photos (1988).

**Male:** Head wider than long, temples not expanded. Preantennal region relatively short. Internal border of marginal carina rounded. Marginal carina very broad band, extending posteriorly to the buccal apparatus, with 15 elongated + 5 medium marginal setae, plus some small dorsal micro setae. Coni robust, rounded, highly sclerotized dorsally, with the antero-lateral border rounded and prominent; prolonged as a square sclerotized expansion, and with the posterior margin tilted/slanted. Antennae relatively short and robust: the scape short; pedicle slightly elongated, as long as 3 flagellomeres combined. The 1$^{st}$ flagellomere is short, cylindrical, with an posteromedial hyaline expansion. Dorsal surface scattered short with microsetae. Eyes large, rounded, bulging with a ocular macrochete. Post-nodal seta short. Anterior temples very short. Temporal angles rounded, slightly more prominent than the eyes: with 8-9 marginal macrosetae, extending anteriorly from the temples to the base of the occipital angles.

Marginal temporal carinas well sclerotized and converging forward, extending to the hypostome and medially to the posterior of the pre-antennal nodes. Gular plates irregular, and not very sclerotized. Temporal marginal carinas wide (as in *G. plumiferae)* uniting with post-ocular nodes posteriorly. Occipital angles forming a large triangular posterior process; weakly sclerotized and with a very short apical microsetae.

Thorax much narrower than the head. Prothorax with 3-4 lateral setae. Pterothorax with 12-14 elongated lateral setae and a row of small marginal setae on the posterior margin on each side.

Abdomen pear-shaped, wide, with maximum width at segment IV. Tergopleural plates partially granular; broad, triangular in segment II; regularly linguiform in segment III, with reentrant pleural heads in segments IV-V and tapered in segments VI-VIII. Intergital plates in segments III-VII; very small in segments III-V; small in segment VI and relatively small in segment VII. Sternites with thick squat, grainy and very densely sclerotized internal sternal plates in segments III-VII; smaller in segment VII, and with antero-internal reinforcements capitate: medial sternal plates on segments VII and VIII. Abdominal chaetotaxy with **t**ergal setae more numerous on the medial side of tergite IV and; especially, V, or they form tergal combs; looser on segment IV and tighter in segment V. Genital plate relatively wide posteriorly, tapering towards the anterior end. Genitalia as in *G. numidae*.

**Female**: Head as in the male, with marginal carina less wide and with only 4 macrosetae each side. Dorsal surface without scattered microsetae. Coni more robust than males; with the posterior margin tilted/slanted. Marginal temporal carinae bands more pronounced medially and gular plates more sclerotized than in the male.

Thorax as in the male. Pterothorax with 8-10 elongate lateral setae. Abdomen oval shaped and wide. Tergite triangular in segment II; linguiform and thick in segment III-VIII with the posterior margin not indented. Intertergal plates present on segments II-VII; long, thick, clavate, and wider medially. Lateral sternal plates larger and ovoid in segment II; small and elongate in segments III-VIII; can be fragmented or not in segments VI-VIII in the females studied. Tergopleural plate IX as in *G. hopkinsi*; bifid; with the anterior margin short, thick and rounded; and the posterior edge relatively short, slightly curved, fused to the opposite side. External sub-genital plates thick, wider in the middle, with elongate and thick inner plates.

Abdominal chaetotaxy, dorsally includes an elongated lateral seta on segment II; 2 on segment III, and 3 on segments IV-VIII. Short tergal setae on segments V-VIII and elongate central setae on segments II-VIII.

**Material:** 1 specimen (holotype) ex *Guttera edouardi verreauxi* (Elliot) = *Guttera pucherani verreauxi* (Elliot, 1870)(Galliformes: Numidae): CONGO: 1 male (see original). 1 specimen (allotype) ex *Guttera edouardi verreauxi* (Elliot) = *Guttera pucherani verreauxi* (Elliot, 1870)(Galliformes: Numidae): CONGO: 1 female (see original). 1 specimen (paratype) ex *Guttera edouardi verreauxi* (Elliot) = *Guttera pucherani verreauxi* (Elliot, 1870)(Galliformes: Numidae): CONGO: 1 male (Bokalakala, 7-6-1958 Nkele). Paratype female (same as paratype male above) and pre-imago paratype same as before are destroyed. Other nymph paratypes are in good shape.

### ***9. G. inaequalis*** Tendeiro 1987 – (Tendeiro, J. 1988a: 63)

(Tendeiro 1988: Plates XXXIII (photos 1 and 2), XXXIV (photos 1 and 2)

*Archigoniodes inaequalis* - Tendeiro, J. 1988a.– Price *et al*., 2003: 184.

*Archigoniodes:* subgen *Clayarchigoniodes* (Tendeiro 1987, 63).

**Type Host**: *Guttera edouardi barbata* (Ghigi) = *Guttera pucherani barbata* (Ghigi, 1905)(Galliformes: Numidae) – Malawi Crested Guineafowl – Price *et al*. 2003: 184.

**Diagnosis and General Description:** Specimens of this species has not been seen and the description is based on the original by Tendeiro (1988). Very large species that differ from all others in this group in: 1) the male having intertergal plates in segments II-V; ribbon-shaped, thin, and very elongated in segment II merging with the opposite side. They are also very elongate and filiform in segments III-VII. 2) the Female by the absence of these structures – reflected in the specific ephiphet (Latin *inaequalis*, e, unequal, dissimilar).

**Male:** Head wider than long, slightly expanded temples, with 0.95mm long by 1.25mm wide. Pre-antennal region not very elongated. Marginal carina broadly rounded and relatively wide with 4 marginal setae; 12-13 elongate marginal setae and 2 short ventral setae. Coni triangular, short, with ventral sub-marginal extensions. Scape relatively short and not robust. Pedicel is shorter than the three flagellomeres combined. 1$^{st}$ flagellomere slightly asymmetrical, with a short postero-medial hyaline expansion. Eyes rounded, with an ocular macrochete. Dorsal surface scattered with microseta, especially in the posterior half; rare in anterior half, post-nodal setae short. Marginal temporal carina converge slightly anteriorly. Gular plates slightly sclerotized. Marginal temporal carinae wide, with 9 macro setae extending to the base of occipital angles, which are triangular and with a very short apical microseta. Thorax narrower than head. Prothorax with 3-5 postero lateral macroseta and a row of setae on the posterior margin.

Abdomen pear-shaped, relatively wide, and truncate posteriorly. Maximum width at segment IV. Tergites densely granular medially, triangular and thick in segment II. Wide, linguiform with square medial ends in segments III-V. Those in segments III-IV narrowed on the postero medially, irregularly tapered in segments VI-VIII, and shorter on segment VIII. In general, the posterior edges is slightly indented, except in segment VIII which is not. Intertergal plates ribbon-like, thin and very elongated in segment II, where opposite ones might meet medially. Very elongated and filiform in segments III-VII. Tergites IV and VI with dense tufts of numerous bristles. Segments III-VII with large oblique medial sternal plates (see photos), those on III-V rectangular; those on VI-VII ovoid; the ones on segment VIII separated by small sub-genital plates. Lateral sternal plates on segments III-VIII small, with posterior ones either constricted or divided into two. Pleural heads relatively large as in *G. hopkinsi*.

**Female:** Head as in the male; with an elongated dorsal seta and four setae on each side. Coni more robust than the male. Antennae filiform, with the elongated pedicel. Dorsal surface without microsetae. Post-nodal setae very short. Occipital angles acute, and longer than in the male. Thorax as in the male.

Abdomen oval shaped, wide, and larger than the male. Tergite II as in male; tergites III-VII wide, rounded medially; the posterior edge unindented; progressively shorter from the posterior to anterior. Intertergal plates absent in all segments. Medial sub-sternal plates rectangular with rounded medial edge; pear-shaped in segment III; constricted in the medial third in segments IV-VII. Lateral sternal plates oval, large in segment II;  elliptical in segment III; and constricted or divided into two or three fragments in the remaining segments.  Posterior end as in the photo.

**Discussion:**  Holotype and allotype in the holdings of the BMNH.

## Group H

*Stenocrotaphus* Kéler 1939: 124.

Medium to large species (Males: 2.68-4.20mm; Females: 4.45- 4.80mm.); with monomorphic temples, somewhat expanded.  Coni monomorphic usually membranous, variably developed, either rounded or pointed; the tip slightly denticulate, or serrate. Antennae either monomorphic, or dimorphic; if similar the pedicel is considerably larger than scape, which has no appendage.  Ventral pterothoracic setae absent.  Pleurites broad. No bifid structure in female; vulva at level of segment VIII with setae concentrated at the lateral corners; no spinous process.  Male genital opening as in Group G.

Group H is similar to G in the presence of both lateral and medial sternites and the terminal segment of the females.  The strongly developed crop teeth (Tendeiro's scaly gular plates) and the coloration (incidentally also similar to Group G), are most probably convergent; these characters are linked to ecology and do not indicate phylogenetic similarity, they also found in *Goniocotes* and *Lipeurus* species occurring on the Numidae. These species cannot, however, be included in Group G with the other *Goniodes* from the Numidae owing to the absence of the distinctive cheatotaxy and intertergal plates, and the differences in the female vulva.  The anterior margins of the temporal carinas are very weakly sclerotized (See Smith 2000:81 for the condition here is to the extreme).

Prothorax with 1-2 more or less elongated lateral setae. Pterothorax with 2-3 lateral setae, 2 more postero medial, 1 medial setae. Ventral pterothoracic setae absent. Pleural heads large and sclerotized. Tergal and pleural plates apparently merged in adults, with a grainy texture, laterally darker; those on segments II and III partially fused in males, separated in females. Intertergal plates and tergal combs absent. Females without bifid structure associated with the internal genitals, genital opening with setae concentrated laterally.

### ***10. G. gigas*** Taschenberg

(Figures 1.7-1.9; Clay 1940: 34 – Figures 21, 22; Kéler 1939: 126 – Figures 67, 68; Tendeiro 1988: Plates I (photo 1), IV (photo 1), XLII (photos 1 and 2).

*G. gigas* Taschenberg, O. 1879. 52: 104.

*Goniocotes gigas* (Taschenberg, O. 1879: 104)- *nom. nov.* for *G. hologaster* Denny – Clay 1940a: 33; Price *et al.*, 2003: 184.

*Goniocotes abdominalis* – (Piaget, 1880: 238) – Clay 1940a: 32; Hopkins and Clay, 1952: 150; Price *et al.* 2003: 182.

*Goniocotes hologaster* – (Denny, 1842: 56 and 153), *nec G. hologaster* (Burmeister) 1938 – Clay 1940a.

*Goniocotes hologaster* – (Denny, 1842: 56 and 153)(*Goniocotes, nec Goniodes hologaster* (Nitzsch) 1818) – Hopkins and Clay 1952: 154; Price *et al.* 2003: 184

*Stenocrotaphus gigas* (Kéler 1939, 125), Tendeiro 1954a: 314, 1954b: 73; Tendeiro 1955c: 505, 545; Tendeiro 1956: 129.

**Type Host**: *Gallus gallus* (Linnaeus, 1758) (Galliformes: Phasianidae) – Red

Junglefowl – Price *et al*. 2003: 184.

*Gallus domesticus* = *Gallus gallus domesticus* (Linnaeus, 1758) (Galliformes: Phasianidae) – Domestic Chicken – Clay 1940a: 33; Hopkins and Clay 1952: 150, 154; Tendeiro 1955c: 505; Tendeiro 1956: 129.

**Hosts**: *Guttera e. edouardi* (Hartlaub, 1867)(Galliformes: Numidae) – Zambesi Crested Guineafowl – Clay, 1940a: 36; Price *et al*. 2003: 184.

*G. e. sethsmithi* Neumann (White, 1943) (Galliformes: Numidae) – Seth-Smith's Crested Guineafowl – Clay 1940a: 36.

*G. e. sclateri* Reichenow = *Guttera pucherani sclateri* (Reichenow, 1898) – Sclater's Crested Guineafowl – Clay 1940a: 36.

*G. p. plumifera* (Cassin, 1857)(Galliformes: Numidae) – Cameroon plumed Guineafowl– Clay, 1940a: 36; Price *et al*. 2003: 184.

*G. pucherani* (Hartlaub, 1861) (Galliformes: Numidae) – Kenya Guineafowl – Clay 1940a: 36.

*Numida m. meleagris* (Linnaeus, 1758)(Galliformes: Numidae) – Helmeted Guineafowl – Clay, 1940a: 36; Price *et al*. 2003: 184.

*Numida m. major* Hartlaub = *Numida meleagris major* (W.L.Sclater, 1924)(Galliformes: Numidae) – Uganda Tufted Guineafowl – Clay 1940a: 35.

*N. m. mitrata* (Pallas, 1764)(Galliformes: Numidae) – Zambesi Helmeted Guineafowl – Clay 1940a: 35.

*N. m. rikwae* Reichenow = *Numida meleagris marungensis* (Schalow, 1884) (Galliformes: Numidae) – Angola Helmeted Guineafowl – Clay 1940a: 35.

*N. m. coronata* (Gurney, 1868)(Galliformes: Numidae) – Natal Helmeted Guineafowl – Clay 1940a: 36.

*N. m. callewaerti* Chapin = *Numida meleagris galeatus* (Pallas, 1767) (Galliformes: Numidae) – Guinea Helmeted Guineafowl – Clay 1940a: 36.

*N. m. galeata* (Pallas, 1767)(Galliformes: Numidae) – Guinea Helmeted Guineafowl – Clay 1940a: 36; Tendeiro 1956: 129.

*N. m. reichenowi* (Ogilvie-Grant, 1894)( Galliformes: Numidae) – East African Helmeted Guineafowl – Clay 1940a: 36.

*Guttera verreauxi* Tendeiro 1956: 129.

**Diagnosis and General Description:** Although originally described from the domestic chicken the true host of this species is the guinea fowl (*Numidae*). This species and *agelastes* are not closely related to any other, except general similarity in certain characters to the preceding species from Numidae. *See* Tendeiro 1988: 20.

**Male:** Head with thick marginal carina and temples barely expanded; preantennal nodus terminating medially in circular sclerotized structure. Elongated pedicel with 1st flagellomere simple and unmodified (Fig. 21). Thorax with shape and dorsal cheatotaxy as in female (Clay 1940, Figure 22).

Abdomen broadly rounded, with posterior margins of the two halves of the first tergal plate (II) fused to the anterior margins of the second (III). With medial and lateral sternal plates on segments III-VII. Abdominal chaetotaxy, dorsally II: 2-3 lateral, 18-20 medial, 2-3 central; III. Genital opening resembling that of *G. hopkinsi*. Genitalia with thickened elongated basal plate and somewhat flattened parameres reaching a considerable distance below the distal termination of the mesosome.

Measurements: (n = 19) TW 0.98-1.23(1.12); HL 0.88-1.13 (1.00); CI 0.85-0.94 (0.89); PW 0.63-0.76 (0.68); MW 0.88-1.10 (0.96); AWV 1.67-2.10 (1.83); GL 1.10-1.36 (1.25); TL 2.85-3.55(3.25);

**Female:** Head as in male, but larger, and with antennae comparatively shorter. Thorax as shown in Clay (1940, Figure 22). Abdomen large; with tergite IX partially divided into two antero-posteriorly, the most posterior portions each side fusing centrally as in *G. fimbriatus* (Clay 1940, Figure 22). See Clay (1940: 33) for abdominal chaetotaxy.

Measurements: (n = 21) TW 1.17-1.36 (1.27); HL 1.03-1.23 (1.13); CI 0.82-0.94 (0.89); PW 0.70-0.88 (0.76); MW 0.98-1.13 (1.06); AWV 1.83-2.18 (2.05); TL 3.65-4.38 (4.06).

**Discussion:** *G. gigas* was originally described from *Gallus domesticus*, its true hosts are the Numidae (Clay 1940a: 33). Holotype of *G. hologaster* is a female in the Denny Collection. A lectotype (Male #1) and paratypes (2 males, 3 females) of *G. abdominalis* is in the BMNH; paratypes slide #134 in the Leiden Museum includes 1 male and 1 female according to Clay 1940a: 36. Types of *G. abdominalis* and *G. hologaster* are in the BMNH according to Hopkins and Clay (1952: 150, 154). There is material collected from *Numida meleagris* and *Guttera plumifera* in both the Denny and Piaget Collections located at the *BMNH* according to Clay (1940).

**Material studied:** 40 specimens (19 Males, 21 Females). 2 specimens (BMNH) ex *Guttera edouardi seth-smithi* Neumann (White, 1943) (Galliformes: Numidae) – Seth-Smith's Crested Guineafowl: **UGANDA**: 2 females (Bustimla, viii-1946, Coll: R.G.C. van Someren). 4 specimens (BMNH) ex *Guttera edouardi seth-smithi* Neumann (White,

1943) (Galliformes: Numidae) – Seth-Smith's Crested Guineafowl: **KENYA**: 2 males, 2 females (no place, no date, Coll: Meinertzhagen, Host: 10854). 2 specimens (BMNH) ex *Numida meleagris* (Linnaeus, 1758)(Galliformes: Numidae) – Helmeted Guineafowl: **SOUTH AFRICA**: 1 male, 1 female (Pretoria, 24.iv.1966, Coll: M. S. Markus, Host: Brit.Mus.1966-334.4). 6 specimens (BMNH) ex *Numida meleagris sabyi* (Hartert, 1919)(Galliformes: Numidae) – Morrocan Helmeted Guineafowl: **MARROCO**: 3 Males, 3 females (no place, Dec. 1938, Coll: Meinertzhagen, Host: 12513 "Hatched under fowl"). 4 specimens (INHS) ex Domestic hen = *Gallus gallus domesticus* (Linnaeus, 1758) (Galliformes: Phasianidae): **USA**: 2 males, 2 females (Rushville, IL, July 9, 1905, Coll: Anna T. Walken). 3 specimens (NMNH) ex *Numida meleagris major* (W.L.Sclater, 1924) (Galliformes: Numidae) – Uganda Tufted Guineafowl: **UGANDA**: 3 Males (Busuli, Duyanda, 1940, Coll: G. H. E. Hopkins). 2 specimens (NMNH) ex *Numida meleagris* (Linnaeus, 1758)(Galliformes: Numidae) – Helmeted Guineafowl: **SOUTH AFRICA**: 1 Male, 1 Female (Union of South Africa, Ndumu, Zululand, Dec.16.1958, Coll: O. G. Babcock, Host: B.12). 5 specimens (NMNH) ex Guinea fowl ()() – Common name: **USA**: 1 Male, 4 Females (Bexar Co. Texas, 2-xii-66, Coll: unknown). 3 specimens (MINN) ex *Gallus gallus* (Linnaeus, 1758) (Galliformes: Phasianidae) – Red Junglefowl: **CUBA**: 2 Males, 1 Female (Habana, no date, Coll: I. Perez Viqueras). 4 specimens (MINN) ex *Numida meleagris* (Linnaeus, 1758)(Galliformes: Numidae) – Helmeted Guineafowl: **SOUTH AFRICA**: 2 Males, 2 Females (Kruger National Park, no date, Coll: unknown). 2 specimens (OK) ex *Numida meleagris* (Linnaeus, 1758)(Galliformes: Numidae) – Helmeted Guineafowl: **SOUTH AFRICA**: 1Male, 1 Female (RSA: Bloemfontein Dist., 1-May-94, Coll: G. Kopij, Host: 94.A.37/39). 1

specimen (OK) ex *Numida meleagris galeata* (Pallas, 1767)(Galliformes: Numidae) – Guinea Helmeted Guineafowl: **SENEGAL**: 1 Male (det. K. C. Emerson). 1 specimen (OK) ex *Numida meleagris major* (W.L.Sclater, 1924) (Galliformes: Numidae) – Uganda Tufted Guineafowl: **UGANDA**: 1 Female (Buvuma Island, 1948, Coll: unknown). 1 specimen (OK 3944(4)) ex *Guttera pucherani* (Hartlaub, 1861)(Galliformes: Numidae) – Kenya Guineafowl: **SOMALIA**: 1 Female (Somaliland, no date, Coll; unknown).

### ***11. G. agelastes*** Clay

*G. agelastes* Clay, T. 1940a. 110: 36.

*Goniocotes abdominalis* var. *latifasciata* Piaget, 1885: 44 *nec* Piaget, 1883 (Incorrect reference in Harrison, 1916: 81 – Clay 1940a: 36.

*Goniocotes latifasciatus* – (Piaget, 1885: 44) (*nec* 1880) – Hopkins and Clay, 1952: 155; Price *et al*. 2003: 184.

*Stenocrotaphus* (Tendeiro 1987, 31).

**Type Host**: *Agelastes meleagrides* (Bonaparte, 1850)(Galliformes: Numidae) – White-breasted Guineafowl – Hopkins and Clay 1952: 150, 155; Price *et al*. 2003: 184.

**Diagnosis and General Description:** No material from this species has been seen and the following description is based on those of Clay (1940), the original Piaget (1855:44), and that of Tendeiro (1988:31). This species is distinguished from *G. gigas* by the wider marginal carina and the cheatotaxy of the genital region with *G. agelastes* having more and bigger setae on the lateral vulval margins, and more spine-like setae anterior to this. Measurements fall within the range of *G. gigas*.

Piaget (1855:44) states; *the coni is very traingular, the antenna filliform, the pedicel is as long as the 1st flagellomere, large round eye with an ocular seta. Temples expanded with 2 macro setae and blunt occipital angle. Temporal carina follows outside margin.*

**Discussion**: Holotype, a female in the Piaget Collection (Slide #55) located at the BMNH, is labeled *Goniocotes abdominalis* var. *latifasciata* (Clay 1940: 36). Also see (Hopkins and Clay 1952: 150).

***12. G. bifurcus*** Tendeiro

(Tendeiro 1988: Plates II (photos 1 and 2), III (photos 1 and 2))

*G. bifurcus* Tendeiro, J. 1988a. 149: 23.

*Stenocrotaphus bifurcus* – (Tendeiro, J. 1988a: 23) – Price *et al*., 2003: 183.

*Stenocrotaphus* (Tendeiro 1987, 23).

**Type Host**: *Guttera edouardi pucherani* = *Guttera pucherani pucherani* (Hartlaub, 1861)(Galliformes: Numidae) – Kenya Guineafowl – Price *et al*. 2003: 183.

**Diagnosis and General Description:** Species not seen, description based on original by Tendeiro 1988. Species similar to *G. gigas* with antennas monomorphic. In Males filiform with the 1st flagellomere without any projection or only a mere vestige of asymmetry. G. *bifurcus* is distinguised by the very round head, the antennae being more slender and very elongated, the post antennal area of the head less dark/sclerotized, the abdomen narrower anteriorly, the plural heads being bifurcated, and very oblique sternal plates on segments III-VII. Overall the species is weakly sclerotized, and relatively large, Males 2.98 mm 1.51 mm.

**Male:** Head round, slightly wider than long, without exapanded temples, with 1.02 mm by 1.12 mm, cephalic index, 1.10. Preantennal area short. Marginal carina broadly rounded. Marginal carina very wide, especially medially. Coni short and membranous. Antennae filiform, slender, very elongated, the scape relatively short and not robust; pedicel almost as long as 3 flagellomeres combined; all flagellomeres approximately the same length, relatively elongated, the 1$^{st}$ without any protrusion or even simple vestige of asymmetry. Post antennal area a little darker (more sclerotized) than *G. gigas*. Eyes relatively large, with an ocular seta. Anterior temples very short and not very prominent, the temporal angles with three macrosetae, tapering towards the middle of the temples medium widely twisted/sinuous and oblique posteriorly. Posterior temporal carina extensions and gular scaly plates absent. Temporal marginal carina dark and reaching the post-ocular nodules. Occipital angles not very prominent with a short microseta. Narrow thorax. Prothorax retangular with a lateral elongated seta. Pterothorax prominent on the abdomen, with two lateral setae on each side. Other setae broken in the male seen.

Abdomen pear-shaped, narrower anteriorly, with the maximum width at segment IV. Tergite very broad in segment II, merged, as in males of other species in *Stenocrotaphus*, with the rectangular tergite of segment III; tergites IV-VIII linguiform; with bifurcated pleural heads on segments III-VII. Terminal segment prominent, narrow, with a concave/convex/broadly rounded posterior border. Intertergal plates absent. Sternites very slanted in segments III-VII.

Abdominal chaetotaxy; laterally a macroseta on II; 2 on III-VII (1-2 on tergite III in our specimen), and a row of medial elongated setae and macrosetae on segments II-

VII.  Tergal combs absent.  Genitalia simple with a narrow basal plate, fringed parameres and a weakly developed genital sac with relatively coarse denticulations.

**Discussion:** Female of this species unknown.  Male holotype in the collection of the BMNH.

***13. G. zairensis*** Tendeiro 1987 – (Tendeiro, J. 1988a: 25)

(Tendeiro 1988: Plates IV (photo 2), V (photos 1 and 2), VI (photo 1))

*Stenocrotaphus zairensis* – Tendeiro, J. 1988a. 149: 25 – Price *et al*., 2003: 186.

*Stenocrotaphus* (Tendeiro 1987: 25).

**Type Host**: *Guttera plumifera schubotzi* (Reichenow, 1912)(Galliformes: Numidae) – Schubotz's Plumed Guineafowl – Price *et al*. 2003: 186.

**Diagnosis and General Description:** The holotype of this species is desiccated and damaged.  Description based on the original by Tendeiro (1988).  Very large species, Male, 3.83mm long by 9.2 mm wide.  Head as wide as long, narrow at the temporal angles, with 1.17 mm long by 1.17 mm wide (1.32 mm at the lateral cones), cephalic index (1.13) 1.00.  Pre-antennal area relatively short.  Frons broadly rounded.  Marginal carina very wide, reaching the immediate vicinity of the mouthparts.  Coni very large, membranous, colorless, triangular, with the antero-medial border rounded with a slightly denticulate apical tip.  Antennae relatively elongate; scape very robust, as long as the pedicel.  Pedicel elongated, filiform, slightly curved inwards, as long as the 3 flagellomeres combined.  1st flagellomere short, asymmetrical, with a protuberance on postero-medial edge.  Post-antennale area brown, much darker than the anterior = sclerotized.  Eyes very large, elliptical, with an ocular macrochete.  Anterior temples very short. Temples rounded with 2 very short micro setae, 2 macrosetae and 1 short spine-like seta. Medial temporal carina and gular scaly plates absent. Temporal marginal carina very dark (sclerotized), laterally joining the pre-and post-ocular nodes. Occipital angles prominent rounded, with a short apical microsetae.

Thorax much narrower than the head. Prothorax rectangular, with an elongated lateral seta. Pterothorax prominent on the abdomen, with two elongate lateral setae, two medial setae and a central seta on each side,.

Abdomen pear-shaped, short, narrowed anteriorly and greatly expanded in the posterior third, with maximum width at level of segments IV-V. Tergites on segments II and III partially fused, with segment II globose and large, the others being linguiform, with the pleural heads capitate. Intertergal plates absent. Protruding rounded apical segment. Sternites with medial plates elongated, slanted in segments III-VII; lateral sternal plates absent.

Abdominal chaetotaxy; tergal chetotaxy includes, on each side: 1 lateral seta on tergite III; and two elongated setae on tergites IV-V. As well as 3-4 central setae on tergite II; 5-6 in tergite III ; 5-7 in IV; 4-5 in tergite V; 3-4 in tergite VI; , 3 in tergite VII; and 0-1 in tergite VIII; tergal combs absent.

Genitalia with the basal plate relatively broad and with large lateral reinforcements, narrowing towards the paramera, the mesosome lyriforme and the genital sac with two pairs of anterior slecrites strongly sclerotized and with coarse denticulations.

**Material:** Holotype male ex *Guttera plumifera schubotzi* (Reichenow, 1912)(Galliformes: Numidae): CONGO: 1 male (Ubanjo).

**Discussion:** Male holotype from the collection of the RMCA is damaged, female unknown.

***14. G. gutterae*** Tendeiro 1987– (Tendeiro, J. 1988a: 27)

(Figures: Tendeiro 1988: Plates 1 (photo 2), VI (photo 2), VII (photos 1 and 2), VIII (photo 1))

*Stenocrotaphus gutterae* –Tendeiro, J. 1988a. 149: 27 – Price *et al*., 2003: 184.

*Stenocrotaphus* (Tendeiro 1987, 27).

**Type Host**: *Guttera plumifera plumifera* (Cassin, 1857)(Galliformes:Numidae) – Cameroon Plumed Guineafowl – Price *et al*. 2003: 184.

**Male:** Very large species, with head, 4.07mm long and 1.99 mm wide. Head almost as long as wide. Temples not expanded 1.17mm on 1.21mm; cephalic index, 1.03. Pre-antennale region short. Frons broadly rounded. Marginal carina very wide, especially medially. Coni membranous, triangular, with a rounded tip. Antennae elongate, with a robust scape, as long as the pedicel and 1$^{st}$ flagellomere combined. Pedicel in relation extends to nearly as long the three flagellomeres combined. 1$^{st}$ flagellomere short, bent inwards with a robust projecting protuberance on the outer third of its posterior border,that bears the 2$^{nd}$ and 3$^{rd}$ flagellomere, the latter being longer. Post antennal region brown, sclerotized, much darker than the anterior. Eyes very large, rounded, with an ocular macrochete. Anterior temples very short, rounded, with the temporal angles rounded each with a short spine + 2 macroseta separated by a micro setae. Medial temporal carinae and gular plates absent. Marginal temporal carinae with sclerotized (darker) portions anteriorly reaching the post-ocular nodes. Protruding occipital angles, with a apical spine-like setae.

Thorax much narrower than the head. Prothorax rectangular, with 1-2 lateral setae of medium length. Pterothorax prominent on the abdomen, with, on each side, two long lateral setae almost juxtaposed, two elongate middle setae and an elongated central seta.

Abdomen pear-shaped; narrowed anteriorly; with the maximum width at segment IV. Tergites of segments II and III partially fused; those of segment III globular, followed by regularly linguiform ones with the pleural heads capitate, more sclerotized along the medial third of the anterior edges. Apical segment very prominent, ovoid, encircled by a narrow marginal band. Intertergal plates absent. Sternites with medial plates oblique/slanted and elongated in segments II-VII. Lateral sternal plates absent.

Abdominal chaetotaxy includes; on each side; an elongated lateral seta on tergite III, 2 on tergites III-VII and 3 on tergite VIII; as well as four central setae, on each side. Tergal combs absent. Genitalia with relatively enlarged basal plate, and with large lateral reinforcements, the parameres elongated, the mesosome bulb-shaped with antero-lateral spikes, and the genital sack without sclerites but very coarsely denticulate.

**Discussion:** Holotype in collection of the BMNH.

***15. G. phasidus*** Tendeiro 1987 – (Tendeiro, J. 1988a: 29))

(Figures: Tendeiro 1988: Plates VIII (photo 2), IX (photos 1 and 2)

*Stenocrotaphus phasidus* – Tendeiro, J. 1988a. 149: 29 – Price *et al*., 2003: 185.

*Stenocrotaphus* (Tendeiro 1987, 29).

**Type Host**: *Phasidus niger* (Cassin) = *Agelastes niger* (Cassin, 1857) (Galliformes: Numidae) – Black Guineafowl – Price *et al*. 2003: 185.

**Diagnosis and General Description:** The holotype of this species, a female is damaged. Males unknown. The following description is based on the holotype and original description by Tendeiro (1988). Very large species, with Female 4.22mm long and 2.08mm wide. This species is similar to *S. agelastes* (Clay 1940), a parasite of *Agelastes meleagridis*, in the shape of the head, especially the width of the marginal carinas and coni. It differs from the description and iconography of *Goniocotes abdominalis var. latifasciata*, Piaget (1885) in the marginal bands broader, the pre-antennal region more elongated, the temporal angles thicker and much less prominent compared to the eyes, and the temples on average longer and more oblique.

**Female:** Head somewhat hexagonal, wider anterior to the antennas, being 1.12mm long by 1.21mm wide (1.36mm at the lateral cones). Cephalic index, (1.21) 1.08. Preantennal region relatively elongated. Frons broadly rounded. Marginal carina very wide, especially medially; constricted clypeal angles. Prominent coni, membranous and rounded ventral surface; directed outside and pointed dorsally. Antennae filiform, with a relatively elongated scape more robust than the pedicel; pedicel elongate, filiform, and as long as the 3 flagellomeres combined. A pair of sclerotized structures (dark dorsal spots); lateral and anterior to the mandibles. Post-antenal area darker than the anterior. Eyes wide, with an elongated ocular seta. Anterior temples very short, overlapping the postero-internal corner of the eyes. Temporal angles rounded, as prominent as the eyes, with two spines, alternating with 2 macroseta. Medial temporal carinae and gular plates absent. Marginal temporal band dark. Prominent buldging occipital angles with a short microseta.

Thorax much narrower than the head. Prothorax rectangular, with an elongated lateral seta. Pterothorax prominent on the abdomen with two elongated "meta lateral" setae (and presumably, a "meta-center", seta not visible in the specimen studied).

Abdomen oval, wide, with maximum width in segment V. Tergites rounded in segment II; linguiform in the following segments; wide, with pleural heads narrowing anteromedially; more pronounced in segments III-IV. Sternal plates apparently absent. Spiracular plates sickle-shaped and sclerotized. Tergal chetotaxy includes, on each side; a elongate lateral seta on tergite III; with 2 on the following tergites, and a row of elongated central setae on all segments.

Measurements: (n = 1) TW 1.18; HL 1.13; CI 0.96; PW 0.72; MW 0.96; AWV 1.89; TL 3.93.

**Discussion:** The holotype (1 specimen ex *Phasidus niger*: CONGO: 1 Female (holotype) (Stanleyville, A. Pilette, B. L. G. Benoit) from the collection of the RMCA is damaged and as such the descriptions and measurements are based on this specimen and the original description provided by Tendeiro (1988).

## Group I

Species large to medium (Males 1.90-4.10mm., Females 2.40-4.48mm.); Temples sexual dimorphic. Only slightly, or not at all, expanded in males; always more expanded in the female. Coni partly membranous in both sexes, and developed to a greater or lesser extend. Antennae sexually dimorphic. Male scape may have no process, a small un-sclerotized process, or a large sclerotized thickened process; 1st flagellomere produced distally at right angles to the 2nd. In the female, the pedicel is either shorter or equal to the length of the scape. Ventral pterothoracic seta absent. Pleurites without pronounced pleural heads between marginal band and spiracle. Bifid structure absent in Female; the vulval margin has setae concentrated at lateral corners, and a spinous process is present in the genital region. Male genital opening unmodified. Group I contains a relatively homogenous assemblage of species, which cannot always be separated from those in Group K, the two groups merging into each other. The coni in groups I, J, and K are diverse in shape, and in I and K, and some species of J, are membranous, and apt to be distorted and indistinct in specimens treated with "caustic potash" (Clay 1940).

### ***16. G. emersoni*** Tendeiro

(Figures: Tendeiro 1965: Photos 30-35)

*G. emersoni* Tendeiro, J. 1965b. (Ser. 4) 2: 67.

**Type Host**: *Francolinus psilolaemus* (Gray, G. R., 1867)(Galliformes: Phasianidae) – Moorland Francolin – Price *et al*. 2003: 184.

**Diagnosis and General Description:** Description based on original by Tendeiro (1965). Species distinguished by sexual dimorphism of temples and antennas, in the absence of ventral pterothoracic setae, the absence of pleural heads between the marginal band and the spiracles, the abscence of an bifid abdominal struture in the female, the presence of a spinous process in the genital area of female and unmodified male genital opening. This species falls in Group I of Clay according to Tendeiro (original description). The general shape of the head, in Males and Females, is very similar to

*Goniodes bituberculatus*, a species that also lacks the posterior protuberance on the scape and in which the Male genitalia have very short parameres. Among the *Goniodes* in group I with a posterior protuberance on the scape, *G. ocellatus* has a very short protuberance. In *G. sectus* it is broad and buldging, while in *G. crosso* it is thick and distally pointed; in *G. chloropus* it is thin, next to a very wide marginal carina.. The male genitalia in *G. emersoni* is very different from all of these species. In *G. isogenos* the antennae are monomorphic (Kéler, 1952) which distinguishes it from *G. emersoni*.

**Male:** Head as long as wide, temples not expanded. Marginal carina thin. Coni acute. Antennae robust, very long, with the scape expanded, and with a pronounced posterior tooth-like protrusion with a spine-like seta on the outer edge; 1st flagellomere with long projection on the posteromedial corner, curved inwards. Eyes very prominent. Temple rounded, not prominent, narrowing inward postreriorly; occipital angle rounded, protruding slightly posteriorly. Thorax as long as the head. Abdomen very broad, pear-shaped, with pleural heads. Male genitalia characterized by: 1) long, broad basal plate, 2) long, relatively robust parameres, and 3) a short pseudopenis.

Measurements: (n = 5) TW 0.70-1.04 (0.83); HL 0.67-0.87 (0.72); CI 0.72-0.96 (0.87); PW 0.48-0.55 (0.52); MW 0.67-0.80 (0.76); AWV 1.09-1.53 (1.38); GL 1.06 ( ); TL 2.26-2.55 (2.45).

**Female:** Head much wider than long, broader posteriorly, with temporal angles projected outwards (medially) and the occipital angle projecting a little more posteriorly than in males. Thorax as in the male. Abdomen oval, wider. Pleural heads present. Spinous process present on the female genitalia, pronounced and pointing posteriorly.

Measurements: (n = 3) TW 1.14-1.20 (1.16); HL 0.79-0.91 (0.83); CI 0.69-0.76 (0.72); PW 0.54-0.55 (0.55); MW 0.80-0.82 (0.81); AWV 1.45-1.57 (1.50); TL 2.73-2.95 (2.84).

**Discussion:** Types in the collection of the BMNH collected from skin. Description based on original by Tendeiro (1965). Also see Ledger (1980:102).

## Group K

Large to small species (Males 1.60-4.20mm., Females 2.05-3.90mm.). Temples monomorphic and usually expanded. Coni partly membranous in both sexes, and developed to a greater or lesser extend. Antennae sexually dimorphic; male scape without thickened process, 1st flagellomere produced distally as a minute tubercle, or as a process laying either parallel or at right angles to the 2nd flagellomere; female pedicel is either shorter or equal in length to the scape. Ventral pterothoracic setae absent. Plural heads absent, except in *G. isogenos*. Bifid structure absent. Vulva with setae concentrated at lateral corners; spinous process present except in *G. extraneus*. Male genital opening unmodified. This group contains a diverse collection of species that according to Clay (1940) cannot be further divided into groups. Females cannot be separated those of Group I, nor can certain species in this group be separated from those in Group L.

### ***17. G. assimilis*** – Piaget

(Clay 1940: 81 – Figures 56-57a-b)

*G. assimilis* Piaget, E. 1880.: 248; Harrison, 1916 Parasitology 9: 75.

*Goniodes pternistis* – (Bedford, 1929: 520); Bedford 1932 18(1): 331 – Clay 1940a: 81; Hopkins and Clay, 1952: 157; Price *et al*. 2003: 185.

*Goniodes assimilis* Bedford 1932 18(1): 330.

*Solenodes assimilis* Kéler 1939, 220; Kéler 1952 72:42; Tendeiro 1954a: 303, Tendeiro 1956: 128.

**Type Host**: *Francolinus capensis* (Gmelin, 1789)(Galliformes: Phasianidae) – Cape Francolin – Clay 1940a: 8; Price *et al*. 2003: 183.

**Hosts**: *F. a. afer* (Müller, 1776)(Galliformes: Phasianidae) – Bare-throated Spurfowl – Clay, 1940a: 84; Price *et al*. 2003: 183.

*F. a. nyanzae* (Conover, 1929) = *Francolinus afer cranchii* (Leach, 1818) (Galliformes: Phasianidae) – Cranch's Spurfowl – Clay 1940a: 84.

*F. a. intercedens* (Reichenow, 1909) = *Francolinus afer cranchii* (Leach, 1818) (Galliformes: Phasianidae) – Cranch's Spurfowl – Clay 1940a: 84.

*F. a. humboldtii* (Peters) = *Francolinus afer cranchii* (Leach, 1818) (Galliformes: Phasianidae) – Cranch's Spurfowl – Clay 1940a: 84.

*F. a. harterti* (Reichenow, 1909)( Galliformes: Phasianidae) – Usumbura Vermiculated Red-throated Francolin – Clay 1940a: 84.

*F. ahantenis* (Temminck, 1854)(Galliformes: Phasianidae) – Ahanta Francolin – Ledger, 1980: 102; Price *et al*. 2003: 183.

*F. b. bicalcaratus* (Linnaeus, 1766) (Galliformes: Phasianidae) – Double-spurred Francolin – Clay, 1940a: 84; Tendeiro, 1956: 128; Price *et al*. 2003: 183.

*F. b. ogilviegranti* (Bannerman, 1922) (Galliformes: Phasianidae) – Double-spurred Francolin – Clay 1940a: 84.

*F. castaneicollis* (Salvadori, 1888)(Galliformes: Phasianidae) – Chestnut-naped Francolin – Price *et al*., 2003: 183.

*F. c. clappertoni* (Children and Vigors, 1826) (Galliformes: Phasianidae) – Clapperton's Francolin – Clay 1940a: 83; Price *et al*. 2003: 183.

*F. c. gedgii* (Ogilvie-Grant, 1891) (Galliformes: Phasianidae) – Clapperton's Francolin – Clay 1940a: 83.

*F. c. heuglini* (Neumann, 1907) (Galliformes: Phasianidae) – Clapperton's Francolin – Clay 1940a: 84.

*F. c. sharpii* (Ogilvie Grant, 1892) (Galliformes: Phasianidae) – Clapperton's Francolin – Clay 1940a: 84 .

*F. coqui* (Smith, A. 1836) (Galliformes: Phasianidae) – Coqui Francolin – Ledger , 1980: 102; Price *et al*. 2003: 183.

*F. e. erckelii* (Rüppell, 1835) (Galliformes: Phasianidae) – Erckel's Francolin – Clay, 1940a: 84; Price *et al*. 2003: 183.

*F. e. pentoni* (Praed) = *F. e. erckelii* (Rüppell, 1835) (Galliformes: Phasianidae) – Erckel's Francolin – Clay 1940a: 84.

*F. h. hildebrandti* (Cabanis, 1878) (Galliformes: Phasianidae) – Hildebrandt's Francolin – Clay, 1940a: 84; Price *et al*. 2003: 183.

*F. h. altumi* (Fisher and Reichenow, 1884) (Galliformes: Phasianidae) – Hildebrandt's Francolin – Clay 1940a: 84.

*F. icterorhynchus* (Heuglin, 1863)( Galliformes: Phasianidae) – Heuglin's Francolin – Price *et al*. 2003: 183.

*F. icterorhynchus dybowski* Dusalet = *F. icterorhynchus* (Heuglin, 1863) (Galliformes: Phasianidae) – Heuglin's Francolin – Clay 1940a: 84.

*F. leucoscepus* (Gray, G. R., 1867)(Galliformes: Phasianidae) – Yellow-necked Spurfowl – Ledger, 1980: 102; Price *et al*. 2003: 183.

*F. leucoscepus infuscatus* (Cabanis) = *F. leucoscepus* (Gray, G. R., 1867)(Galliformes: Phasianidae) – Yellow-necked Spurfowl - Clay, 1940a: 84; Price *et al*. 2003: 183.

*F. levaillantii* (Valenciennes, 1825)(Galliformes: Phasianidae) – Red-winged Francolin – Ledger, 1980: 102; Price *et al*. 2003: 183.

*F. levalliantoides* (Smith, A., 1836)(Galliformes: Phasianidae) – Orange River Francolin – Ledger, 1980: 102; Price *et al*. 2003: 183.

*F. natalensis* (Smith, A., 1833) (Galliformes: Phasianidae) – Natal Francolin – Ledger, 1980: 102; Price *et al*. 2003: 183.

*F. sephaena* (Smith, A., 1836) (Galliformes: Phasianidae) – Crested Francolin – Price *et al*. 2003: 183.

*F. sephaena zambesiae* (Mackworth-Praed, 1920) (Galliformes: Phasianidae) – Zambesi Crested Francolin – – Clay, 1940a: 84.

*F. squamatus* (Cassin, 1857)(Galliformes: Phasianidae) – Scaly Francolin – Price *et al*. 2003: 183.

*F. squamatus maranensis* (Mearns, 1910) (Galliformes: Phasianidae) – Scaly Francolin – Clay, 1940a: 84.

*F. swainsonii* (Smith, A., 1836) (Galliformes: Phasianidae) – Swainson's Spurfowl – Clay, 1940a: 81, 84; Hopkins and Clay 1952: 157; Price *et al*. 2003: 183, 185.

*Ptilopachus p. petrosus* (Gmelin, 1789)(Galliformes: Phasianidae) – Stone Partridge – Clay 1940a: 84; Price *et al*. 2003: 183.

**Diagnosis and General Description:** Following Clay 1940:81, Piaget (1880:246) separates *G. truncates* (=*flaviceps*), *G. dispar*, and *G. assimilis* by the presence or absence of an appendage (pleural head) on the lateral bands of the abdominal segments. All these species, however, possess this anterior re-entrant portion of the pleurite on segments II-VIII, although in slightly immature specimens it appears to be absent. Bedford, when describing *pternistis* and *sceroptilus*, must have based his comparisons on Piaget's key, and thus separated the *Goniodes* occurring on *Pternistis* from *G. assimilis* Piaget by the fact that that in the former "the bands on all the segments have an appendage" while in the latter "only the lateral bands on the last segment have an appendage"; whereas in reality there appears to be no difference between specimens from *Pternistis swainsoni* and the types of *G. assimilis*.

This species found on a large number of species of *Francolinus* and *Pternistis* is distinguished from *G. dispar* by the shape of the head, the tergites, and the characters of the Male genitalia and Female genital region.

There are no females of *assimilis* in the Piaget collection, nor have any been examined from the type host, except 2 females in the Bedford collection labeled *G. assimilis* from *Francolinus capensis*; these however are quite distinct from the Females from the species of *Francolinus* and *Pternistis* mentioned below, and do not seem to differ in any way from a Female of *G. scleroptilus* lent through the kindness of the late Mr. Bedford. The following description is taken from specimens from *Francolinus clappertoni gedgii*.

**Male**: Head with expanded temples bearing the lateral spine on a small transparent process; antennae with scape not greatly enlarged, and distal post-axial angle in 1st flagellomere prolonged into a short rather transparent process parallel to the 2nd flagellomere (Clay 1940, figure 56). Thorax as shown in Clay (1940, Figure 56). Abdomen with terminal segments as shown in Clay (1940, figure 57a). Genitalia as shown in Bedford's figure of *G. pternistes* (1929, figure 21).

Measurements (n = 15) TW 0.86-1.38 (1.01); HL 0.64-0.79 (0.73); CI 0.30-0.83 (0.72); PW 0.38-0.50 (0.43); MW 0.52-0.71 (0.62); AWV 1.04-1.26 (1.15); GL 0.51-0.98 (0.73); TL 1.95-2.42 (2.18);

**Female:** Head similar to that of male in shape, but somewhat larger and with filliform antennae. Thorax as in male. Abdomen more elongated than in male with tergal plates the same. There are no pediculate spines on the vulval margin, and the spinous process on the genital region is weakly sclerotized and easily overlooked (Clay 1940, fig 57b).

Measurements: (n = 15) TW 0.96-1.43 (1.15); HL 0.75-0.92 (0.82); CI 0.53-0.78 (0.72); PW 0.43-0.59 (0.48); MW 0.61-0.81 (0.69); AWV 1.09-1.68 (1.34); TL 2.33-3.19 (2.70).

**Discussion:** Remarks: Lecto (M #6) + M para in Piaget Coll. BMNH designated by Clay 1940a: 84. Types in BMNH – Hopkins and Clay 1952: 150 ***BMNH lecto para***

**Material studied:** 30 specimens (15 Males, 15 Females). 4 specimens (BMNH) ex *Francolinus clappertoni gedgei* (Ogilvie-Grant, 1891) (Galliformes: Phasianidae) – Clapperton's Francolin: **UGANDA**: 2 Males, 2 Females (Mt. Elgon, May 1908, Coll: Meinertzhagen, Host: Male 3573). 2 specimens (BMNH) ex *Francolinus coqui* (Smith,

A. 1836) (Galliformes: Phasianidae) – Coqui Francolin: **BOTSWANA**: 1 Male, 1 Female (Bechuanaland, 19.vii.1956, Coll: unknown, Host: Brit. Mus. 1957-219). 2 specimens (BMNH) ex *Pternistis swainsoni* = *Francolinus swainsonii* (Smith, A., 1836) (Galliformes: Phasianidae) – Swainson's Spurfowl: **ZIMBABWE**: 1 Male, 1 Female (S. Rhodesia: Bulawayo, 7.xi.1972, Coll: S. Irwin, Host: Brit. Mus. 1973-39). 2 specimens (BMNH) ex *Francolinus ahantensis* (Temminck, 1854)(Galliformes: Phasianidae) – Ahanta Francolin: **GHANA**: 1 Male, 1 Female (no place, 29.iv.1963, Coll: F. R. Allison, Host: Brit. Mus. 1963-341). 2 specimens (BMNH) ex *Francolinus sephaena* (Smith, A., 1836) (Galliformes: Phasianidae) – Crested Francolin: **SOUTH AFRICA**: 1 Male, 1 Female (Nr. Newington, E. Transvaal, 19.vii.1957, Coll: F. Zumpt, Host: (47) Brit. Mus. 1958-76). 2 specimens (BMNH) ex *Francolinus bicalcaratus* (Linnaeus, 1766) (Galliformes: Phasianidae) – Double-spurred Francolin: **CAMEROUN**: 2 Females (Yaounde, 1955, Coll: J. Mouchet). 2 specimens (BMNH) ex *Ptilopachus p. petrosus* (Gmelin, 1789)(Galliformes: Phasianidae) – Stone Partridge: **GUINEA-BISSAU**: 1 Male, 1 Female (Portuguese Guinea, May 1897, Coll: Meinertzhagen, Host: Female 3614). 2 specimens (FMNH) ex *Francolinus coqui* (Smith, A. 1836) (Galliformes: Phasianidae) – Coqui Francolin: **BOTSWANA**: 1 Male, 1 Female (Bebeete, 19.vii.1956, Coll: unknown, Host: (35)). 4 specimens (OK) ex *Francolinus e. erckelii* (Rüppell, 1835) (Galliformes: Phasianidae) – Erckel's Francolin: **ETHIOPIA**: 2 Males, 2 Females (det. K.C. Emerson). 1 specimen (OK 3791) ex *Francolinus squamatus tetraoninus* (Blundell and Lovat, 1899) = *Francolinus squamatus schuetti* (Cabanis, 1880) (Galliformes: Phasianidae) – Scaly Francolin: **ETHIOPIA**: 1 Female (det. K.C. Emerson). 4 specimens (OK) ex *Francolinus c. castaneicollis* (Salvadori, 1888)(Galliformes: Phasianidae) – Chestnut-naped Francolin: **ETHIOPIA**: 2 Males, 2 Females (det. K.C. Emerson). 3 specimens (OK) ex *Pternistis l. leucoscepus = Francolinus leucoscepus* (Gray, G. R., 1867)(Galliformes: Phasianidae) – Yellow-necked Spurfowl: **ETHIOPIA**: 3 Males (det. K.C. Emerson).

### *18. G. ammoperdix* Clay

Figures: Clay 1940: 94 – Figures 63 a-b, 64 a-b)

*G. ammoperdix* Clay, T. 1940a. 110: 93.

**Type Host**: *Ammoperdix griseogularis* (Brandt, J. F., 1843)(Galliformes: Phasianidae) – See-see Partridge – Clay 1940a: 95; Hopkins and Clay 1952: 150; Price *et al*. 2003: 182.

**Hosts**: *Ammoperdix heyi* (Temminck, 1825) (Galliformes: Phasianidae) – Sand Partridge – Price *et al*. 2003: 182.

*Ammoperdix heyi cholmleyi* (Ogilvie-Grant, 1897) (Galliformes: Phasianidae) – South Egyptian Sand Partridge – Clay 1940a: 95.

*A. h. nicolli* (Hartert, 1919) (Galliformes: Phasianidae) – North Egyptian Sand Partridge – Clay 1940a: 95.

**Diagnosis and General Description:** This species does not closely resemble any other species, and is distinguished by the shape of the head and narrow marginal carina in both sexes; by the genitalia of the male and the cheatotaxy of the genital region of the female. Extralimital (Ledger 1980: 102)

**Male**: Head with narrow marginal carina and temples not, or only very little expanded. Scape somewhat enlarged, and distal prolongation of the 1$^{st}$ flagellomere short and at right angles to 2nd flagellomere (Clay 1940 Figure 63a). Thorax with prothoracic lateral margin diverging and with postero-lateral angle in the form of a small protuberance. Lateral margins of pterothorax flattened and diverging posteriorly. Abdomen elongate, oval in shape; segment X small with flattened posterior margin (Clay 1940, Figure 64a). Genitalia see Clay (1940, figure 63b).

Measurements: (n = 15) TW 0.60-0.69 (0.66); HL 0.52-0.58 (0.56); CI 0.81-0.88 (0.84); PW 0.41-0.48 (0.45); MW 0.50-0.59 (0.55); AWV 0.85-1.06 (0.97); GL 0.36-0.65 (0.54); TL 1.70-1.99 (1.87).

**Female:** Head similar to that of male in shape but tends to be wider across the temples. Thorax as in male. Abdomen more elongate than that of male; spinous process on the genital region is long and pointed; pediculate spines are absent, and there is a continuous row of setae on the vulval margin (Clay 1940, Figure 64b).

Measurements: (n = 15) TW 0.74-0.84 (0.79); HL 0.58-0.65 (0.62); CI 0.76-0.80 (0.78); PW 0.45-0.53 (0.48); MW 0.55-0.67 (0.61); AWV 0.95-1.22 (1.10); TL 2.10-2.48 (2.29).

**Discussion:** Holotype (Male #9475), paratypes (18 Males, 20 Females) in the Meinertzhagen Collection of the BMNH (Clay 1940: 95; Hopkins and Clay 1952: 150).

**Material studied:** 30 specimens (15 Males, 15 Females). 3 specimens (BMNH) ex *Ammoperdix g. griseogularis spatyi* = *Ammoperdix griseogularis griseogularis* (Brandt, J. F., 1843)(Galliformes: Phasianidae) – See-see Partridge: **PAKISTAN**: 3 Females (Peshawur, iii-1937, Coll: Meinertzhagen, Host: 9475). 2 specimens (BMNH) ex *Ammoperdix heyi* (Temminck, 1825) (Galliformes: Phasianidae) – Sand Partridge: **ISRAEL**: 1 Male, 1 Female (Ein-Gedi, 24.iv.1959, Coll: unknown, Host: 738; Brit. Mus.

1959-405). 20 specimens (BMNH) ex *Ammoperdix g. griseogularis* (Brandt, J. F., 1843)(Galliformes: Phasianidae) – See-see Partridge: **AFGHANISTAN**: 11 Males, 9 Females (no place, May 1937, Coll: Meinertzhagen, Host: 10243, 10266). 4 specimens (OK 18270) ex *Ammoperdix g. griseogularis* (Brandt, J. F., 1843)(Galliformes: Phasianidae) – See-see Partridge: **AFGHANISTAN**: 2 Males, 2 Females (Laghman, E. Afghanistan, 10.2.1968, Coll: Klockenhoff, Host: 701). 1 specimen (OK 3784 (2)) ex *Ammoperdix h. heyi* (Temminck, 1825) (Galliformes: Phasianidae) – Sand Partridge: **PALENSTINE**: 1 Male (no additional data).

### *19. G. antennatus* Clay

(Figures: Clay 1940: 85 – Figures 58a-b)

*G. antennatus* Clay, T. 1940a. Genera and species of Mallophaga occurring on gallinaceous hosts. – Part II. Goniodes. Proc. Zool. Soc. London (Ser. B) 110: 84.

**Type Host**: *Francolinus l. leucoscepus* (Gray, G. R., 1867)(Galliformes: Phasianidae) – Yellow-necked Spurfowl – Clay 1940a: 85; Price *et al*. 2003: 183.

**Diagnosis and General Description:** Following Clay 1940: 84 this species resembles *G. assimilis* in general, but is distinguished by the prolongation of the distal post-axial angle of 1st flagellomere lying at right angles to the 2nd flagellomere, and not parallel as in *assimilis* and by the genitalia of the Male.

**Male:** Head with broad marginal carina and temples widely expanded; the scape enlarged to a greater extent than in *G. assimilis*, and with prolongation of 1st flagellomere larger and at right angles to the 2nd (Clay 1940, Figure 58a). Thorax as in *G. assimilis*.

Abdomen similar to that of *G. assimilis* but somewhat larger, and lacking the central setae on sternites II-III. See Clay 1940: 84 for abdominal cheatotaxy. Tergal seta not divisible into lateral and central groups, although the outer and central setae are somewhat longer and stouter than the intermediate seta. Genitalia with broad, evenly thickened basal plate and widely curved parameres (Clay 1940, Figure 58b).

**Measurements:** (n = 6) TW 1.03-1.10 (1.07); HL 0.79-0.80 (0.79); CI 0.73-0.77 (0.74); PW 0.47-0.49 (0.48); MW 0.69-0.71 (0.70); AWV 1.43-1.55 (1.49); GL 0.91-1.03 (0.99); TL 2.61-2.71 (2.67)

**Female:** Unknown (Clay 1940), but specimens listed below were located in various museums collections. Measurements (n = 9): TW 1.13-1.19 (1.16); HL 0.87-0.91 (0.90); CI 0.76-0.79 (0.77); PW 0.48-0.52 (0.49); MW 0.71-0.74 (0.73); AWV 1.39-1.53 (1.49); TL 2.88-3.04 (2.95).

**Discussion:** Holotype (Male #3643) and 2 Male paratypes are in the Meinertzhagen Collection of the BMNH (Clay 1940a: 85; Hopkins and Clay 1952: 150).

**Material studied:** 15 specimens (6 Males, 9 Females). 2 specimens (BMNH) ex *Pternistis leucoscepus infuscatus* = *Francolinus leucoscepus* (Gray, G. R., 1867)(Galliformes: Phasianidae) – Yellow-necked Spurfowl: **KENYA**: 1 Male, 1 Female (Isiolo, Jan. 1955, Coll: Meinertzhagen, Host: 20464). 11 specimens (BMNH) ex *Pternistis l. leucoscepus* = *Francolinus l. leucoscepus* (Gray, G. R., 1867)(Galliformes: Phasianidae) – Yellow-necked Spurfowl: **SOMALIA**: 4 Males, 7 Females (no place, Feb. 1949, Coll: Meinertzhagen, Host: 18724). 2 specimens (OK 3786) ex *Pternistis leucoscepus infuscatus* = *Francolinus leucoscepus* (Gray, G. R., 1867)(Galliformes:

Phasianidae) – Yellow-necked Spurfowl: **KENYA**: 1 Male, 1 Female (East Africa: Kenya Colony, no date, no collector).

***20. G. oreophilus*** Clay

(Figures: Clay 1940: 77 – Figure 52 a-b, 53 a-b)

*G. oreophilus* Clay, T. 1940a. Genera and species of Mallophaga occurring on gallinaceous hosts. – Part II. *Goniodes*. Proc. Zool. Soc. London (Ser. B) 110: 77.

**Type Host**: *Francolinus shelleyi theresae* Meinertzhagen = *Francolinus psilolaemus theresae* (Meinertzhagen, R., 1937) currently *Francolinus psilolaemus elgonensis* (Ogilvie-Grant, 1891)(Galliformes: Phasianidae) – Elgon Francolin – Price *et al*. 2003: 185.

**Hosts:** *F. j. jacksoni* (Ogilvie-Grant, 1891)(Galliformes: Phasianidae) –Jackson's Francolin – Clay, 1940a: 79; Price *et al*. 2003: 185.

*F. j. pollenorum* (Meinertzhagen, R., 1937) = *F. j. jacksoni* (Ogilvie-Grant, 1891) (Galliformes: Phasianidae) – Jackson's Francolin – Clay 1940a: 79.

**Diagnosis and General Description:** Following Clay 1940:77 *G. oreophilus* is a large darkly marked (heavily sclerotized ) species distinguished by the shape of the head in both sexes, by the large flattened genitalia of the Male, and by the characters of the terminal segments of the abdomen of the Female.

**Male:** Head and thorax as shown in Clay (1940, figure 52b) with temples widely expanded and with the small process bearing the ventro-lateral temple seta apparent; scape enlarged, and distal post-axial angle of 1st flagellomere prolonged to a considerable extent. Abdomen with inner margin of tergal plates straight; segment X large, rounded, and protruding with thickened marginal band (Clay 1940, figure 53a). Genitalia unique and unlike any other species of *Goniodes* see Clay (1940, figure 52a).

**Measurements:** (n = 9) TW 1.21-1.43 (1.30); HL 0.82-0.96 (0.88); CI 0.64-0.75 (0.68); PW 0.54-0.65 (0.60); MW 0.83-1.00 (0.92); AWV 1.68-2.06 (1.83); GL 0.95-1.22 (0.91); TL 3.05-3.75 (3.31).

**Female:** Head of similar to that of male, but wider across the temples. Thorax as in male. Abdomen large and rounded, with form and cheatotaxy of terminal segments as shown in Clay (1940, Figure 53b). Abdominal cheatotaxy as in Clay (1940: 78).

**Measurements:** (n = 10) TW 1.30-2.14 (1.50); HL 0.85-0.96 (0.92); CI 0.43-0.67 (0.62); PW 0.55-0.65 (0.62); MW 0.85-0.99 (0.93); AWV 1.58-1.93 (1.79); TL 3.10-3.78 (3.52).

**Discussion:** Holotype (Male #6589), paratypes (8 Males, 8 Females) in the Meinertzhagen Collection of the BMNH (Clay 1940a: 79, Hopkins and Clay 1952: 157).

### *21. G. scleroptilus* Bedford

(Figures Clay 1940: 86 – Figure 59a-b; Kéler 1952: 47 – Figure 20 a-c)

*G. scleroptilus* – Bedford, G. A. H. 1929. Anoplura (Siphunculata and Mallophaga) from South African hosts. Ann. Rept. Dir. Veter. Serv. and Anim. Ind., Un. So. Afr. 15: 520.

*Solenodes* Keler 1939: 220.

**Type Host**: *Francolinus gariepensis jugularis* Büttikofer (*Scleroptila g. jugularis*) = *Francolinus levaillantoides jugularis* (Büttikofer,1889)(Galliformes:

Phasianidae) – Angola Orange River Francolin – Clay 1940a: 86; Hopkins and Clay 1952: 158.

*Francolinus levallliantoides jugularis* Büttikofer, 1889)(Galliformes: Phasianidae) – Angola Orange River Francolin – Price *et al*. 2003: 186.

**Diagnosis and General Description:** The host of this species was originally given as *gariepensis pallidor*, but was corrected to *gariepensis jugularis* in Bedford 1932: 331.

**Male:** As described by Kéler 1952: 47.

**Female:** See Clay 1940.

**Measurements:** (n = 1) TW 1.26; HL 0.92; CI 0.72; PW 0.56; MW 0.79; AWV 1.63; TL 1.23.

**Discussion:** Type host originally given as *F. g. pallidior*, but corrected to *F. g. jugularis* by Bedford, 1932: 331 (Clay 1940a: 86; Hopkins and Clay 1952: 158).

***22. G. isogenos*** Nitzsch,

(Figures: Kéler 1939: 130 – Figure 69)

*G. isogenos* – Nitzsch, (in Giebel, C. 1866. Die im zoologischen Museum der Universität Halle aufgestellten Epizoen nebst Beobachtungen über dieselben. Zeit. Gesamt. Naturwiss. 28: 388)

*Stenocrotaphus isogenos* (Kéler 1939: 128) also see Kéler 1952:42

**Type Host:** *Francolinus a. africanus* (Stephens, 1819) (Galliformes: Phasianidae) – Grey-winged Francolin – Clay 1940a: 91; Hopkins and Clay 1952: 154; Price *et al*. 2003: 184).

**Diagnosis and General Description:** According to Ledger 1980: 42… *the status is open. Clay saw only a single Female and placed it in her group K; Kéler (1952:42) says as it does not have dimorphic antennae it should be in his genus Stenocrotaphus (Clay's group H)* (Ledger 1980: 42). However, Clay (1940) also states that *G. isogenos* Females are distinct from other *Goniodes* from *Francolinus* and *Pternistis* in the form of the pleurites and genital region. She declines to describe the species as she only had a single Female and in the belief that Kéler, who examined the original types, will deal with it in his paper (1939) on the *Goniodes* from the Halle collection.

**Measurements:** Male (n = 3) TW 1.08-1.70 (1.49); HL 1.75-2.02 (1.84); CI 1.03-1.87 (1.31); PW 1.29-1.38 (1.32); MW 1.85-1.88 (1.86); AWV 1.29-1.43 (1.38); GL 0.84-0.92 (0.87); TL 2.48-2.76 (2.58).

**Measurements:** Female (n = 8) TW 1.04-1.10 (1.06); HL 2.02-2.10 (2.05); CI 1.88-1.98 (1.93); PW 1.13-1.38 (1.32); MW 1.63-1.98 (1.88); AWV 1.28-1.53 (1.45); TL 2.52-2.88 (2.78).

## Group L

Small species (Males 1.80-2.60mm., Females = 2.40-2.85mm.). Temples monomorphic and usually expanded. Coni partly membranous in both sexes, and developed to a greater or lesser extend. Antennae may be sexually mono, or dimorphic. If dimorphic; Males without process on the scape and with 1$^{st}$ flagellomere prolonged distally at right angles to the 2$^{nd}$. In Female, the pedicel is either shorter or of equal length to the scape. Ventral pterothoracic setae absent. Pleurites similar to those in Group K, with plural heads sometimes present. Bifid Structure absent. Vulva margin with setae concentrated laterally, spinous process present in genital region. Male genital opening unmodified. The species in this group are unusual in appearance, with an elongated abdomen and accompanying elongation and thickening of the pleurites (Ledger 1980: 103). However, general characters of the Male and Female genital region, as well as the head, thorax, and abdomen are very similar to those found in *G. keleri* in Group K, "*thus making a generic separation unsatisfactory, as it merely obscures this relationship and does not simplify the general classification* (Clay 1940: 97).

### ***23. G. soueefi*** Clay

(Figures: Clay 1940: 97 – Figure 66 b, 68 a)

*G. soueefi* – Clay, T. 1940a. Genera and species of Mallophaga occurring on gallinaceous hosts. – Part II. *Goniodes*. Proc. Zool. Soc. London (Ser. B) 110: 100 1940a. Genera and species of Mallophaga occurring on gallinaceous hosts. – Part II. *Goniodes*. Proc. Zool. Soc. London (Ser. B) 110: 100.

*Goniodes elongates* – (Piaget (partim) 1885: 52) *nec* Piaget 1880 – Clay 1940a: 100; Hopkins and Clay, 1952: 153; Price *et al*. 2003: 184.

*Goniodes longus* – (Le Souëf, 1902b: 90) *nec* Rudow 1869 – Clay 1940a: 100; Hopkins and Clay, 1952: 155; Price *et al*. 2003: 185.

**Type Host**: *Coturnix chinensis australis* (Gould) – Clay 1940a: 100; Hopkins and Clay, 1952: 155; 158; Price *et al*. 2003: 184, 186.

**Hosts:** *C. chinensis lineatula* (Rensch) (L.)[Gall.: Phasian.] – Clay, 1940a: 100.

*C. chinensis lineata* (Rensch) - Price *et al*. 2003: 185.

*C. chinensis* - Price *et al*. 2003: 186.

**Diagnosis and General Description:** According to Clay (1940: 100) *G. soueefi* can be distinguished from *G. retractus* by the greater length of the prolongation of the distal post-axial angle of the 1st flagellomere of the Male and by the longer and more pointed occipital angles.

**Male:** Head and thorax as shown in Clay (1940, figure 68a) and characterized by the form of the 1st flagellomere and occipital angles. Thorax as shown in Clay (1940, Figure 68a). Abdomen, in general similar to *G. retractus* but somewhat narrower. According to Clay (1940) the only specimen she examined, Piaget's male, is in extremely poor condition, but, as far she can determine the pleurites, cheatotaxy (except that there appear to be fewer dorsal seta), and characters of the posterior segments of the abdomen are as in *G. retractus*. The genitalia appear to be of the same general type as those of *G. keleri* and *G. astrocephalus*.

**Measurements:** (n = 2) TW 0.44-0.57; HL 0.50-0.51; CI 1.13; PW 0.26-0.32; MW 0.37-0.46; AWV 0.56-0.70; GL 0.48-0.51; TL 1.81-2.13;

**Female:** Clay (1940) saw no females from the type-host and her description, followed here, was based on specimens from *Coturnix chinensis*. Head with shape as in male, but somewhat larger and antennae filiform. Thorax as in male, but broader. Abdomen with general characters as in the male, but broader and more elongated. Posterior segments shown in Clay (1940, figure 66b).

Abdominal of segments II-VII as shown for the male of *G. retractus*, except that segments II-IV have fewer dorsal seta. Chetoataxy of posterior segments as shown in Clay (1940, figure 66b).

**Measurements:** (n = 6) TW 0.29-0.60 (0.46); HL 0.29-0.61 (0.49); CI 0.97-1.13 (1.07); PW 0.20-0.34 (0.27); MW 0.27-0.51 (0.39); AWV 0.43-0.90 (0.63); TL 2.40-3.40 (2.79).

**Discussion:** Piaget (1855: 53) mentions 2 Females from *Francolinus capensis* but these are not in the Piaget Collection in the BMNH (Clay 1940a: 100). Host record *Francolinus capensis* is in error; Types of *Goniodes elongatus* – (Piaget (partim) 1885: 52) *nec* Piaget 1880); and *G. soueefi* in BMNH.

**Material studied:** 8 specimens (2 Males, 6 Females). 1 specimen (BMNH) ex *Coturnix ussuriensis* ()() – Common name: **RUSSIA**: 1 Male (Ussutii, Chabarowsk, Eisenbahn, 25.ix.11, Coll: E. Borsow, Host: 1912-373). 1 specimen (BMNH) ex *Coturnix coromandelica* ()() – Common name: **UNKNOWN**: 1 Female (place unknown, date unknown, Coll: unknown, Cambridge Museum "L. Harrison, Mallophaga", Host: BM.1934-570 L. Harrison Coll.). 1 specimen (NMNH) ex *Excalfactoria chinensis* ()() – Common name: **MALAYSIA**: 1 Male (Malaya, Selangor, Kuala Lumpur, Apr. 14.1948, Coll: R. Traub and C. Philip, E.W.S., Host: RT-8024; Lot 48-19015). 1 specimen (OK) ex *Coturnix chinensis* ()() – Common name: **PHILLIPINES**: 1 Female (Dalton Pass, Nueva Vigcaya, 16.08N 120.55E, 24-Feb-68, Coll: GL Alcasid, Host: 8E 1364). 1 specimen (OK 21196) ex *Coturnix chinensis* ()() – Common name: **PHILLIPINES**: 1 Female (Dalton Pass, Nueva Vigcaya, 16.08N 120.22E, 24-Jan-68, Coll: GL Alcasid, Host: 8E 1387). 3 specimens (OK 17288, 17245, 17244) ex *Coturnix chinensis* ()() – Common name: **PHILLIPINES**: 3 Females (Dalton Pass, Luzon, 6 Jan. 1967, Coll: unknown, Host: 7E-0159).

### *24. G. astrocephalus* Burmeister

(Figures: Kéler 1939: 110 – Figures 57, 58)

*G. astrocephalus* – Burmeister, H. 1838. Mallophaga Nitzsch. Handbuch der Entomologie, Berlin, 2: 431.

*Goniodes paradoxus* Nitzsch 1818: 294 *nom. nud.* – Clay 1940a: 100.

*Goniodes paradoxus* Stephens 1829: 333 – Clay 1940a: 100.

*Goniodes paradoxus* Burmeister 1838: 432 *nec* Stephens, 1829 – Clay 1940a: 101.

*Goniocotes astrocephalus* (Burmeister, H. 1838: 431) – Clay 1940a: 101; Price *et al*., 2003: 183.

*Goniocotes asterocephalus* Nitzsch 1874(2): 182 – Clay 1940a: 101.

*Goniodes elongatus* – (Piaget, 1880: 281 partim ) – Clay 1940a: 101; Hopkins and Clay, 1952: 153; Price *et al*. 2003: 184.

*Goniocotes gracilis* – (Taschenberg, 1882: 71) *nom. nov.* for *Goniocotes asterocephalus* Piaget 1880 *nec* Burmeister 1838 – Clay 1940a: 101; Hopkins and Clay, 1952: 154; Price *et al*. 2003: 184.

*Astrocotes astrocephalus* (Kéler 1939, 109).

**Type Host:** *Coturnix c. coturnix* (Linnaeus, 1758)(Galliformes: Phasianidae) – Common Quail – Clay 1940a: 102, Hopkins and Clay 1952: 153; Price *et al*. 2003: 183, 184.

**Hosts:** *C. c. africana* (Temminck and Schlegel, 1849)(Galliformes: Phasianidae) – African Quail – Clay 1940a: 102.

*Coturnix coromandelica* (Gmelin, 1789) (Galliformes: Phasianidae) – Rain Quail – Clay, 1940a: 102; Price *et al*. 2003: 183.

*Coturnix d. delegorguei* (Delegorgue, 1847)(Galliformes: Phasianidae) – Harlequin Quail – Clay, 1940a: 102; Price *et al*. 2003: 183.

*Picus major* – Clay 1940a: 102 in error.

*Ortyx virginianus* – Clay 1940a: 102.

**Diagnosis and General Description:** According to Clay (1940: 101) it is evident from Piaget's description and figures of *Goniocotes asterocephalus* (1880:226 + plate xix. Fig 1) that he had nymphs, further verified by two immature individuals of *G. astrocephalus* in the Piaget collection labeled *Gc. Asterocephalus* N. As a result Piaget described mature specimens from *Coturnix coturnix* as a new species i.e *G. elongatus*. Taschenberg 1882:71 considered Piaget's *G. elongatus* synonym to *G. asterocephalus* Burmeister, but assumed that Piaget's *G. asterocephalus* was a different species, naming it *G. gracilis*. Meanwhile Piaget obtained a Male specimen from *Excalfactoria* (*Coturnix*) *chinensis australis*, which he considered conspecific with Female *G. elongatus* from the type host *Coturnix coturnix* and as that Male had sexually dimorphic antennae, he (1885:52) maintains that *G. elongatus* is distinct from *G. astrocephalus*. He however had two species, one represented only by a Male, (*G. soueefi*), the other by a Female (*G. astrocephalus*). *G. astrocephalus* has been placed in *Goniocotes* by previous authors according to Clay based on the absence of sexual dimorphism of the antennae, a character, she considers of little generic importance. Especially since *G. retractus, G. souefi,* and *G. astrocephalus*, all closely related species, have both the presence and absence of such sexual dimorphism. *G. astrocephalus* in general resembles both *G. retractus* and *G. souefi* and is distinguished from them by the absence of sexual dimorphism of the antennae of the Male and by a shorter and less acute occipital angel in the Female.

**Male:** Head narrow with elongated pre-antennal region and temples but little expanded. Antennae simple and unmodified. Thorax as in *G. retractus*. Abdomen similar to that of *G. retractus*, but somewhat narrower and more elongate. Cheatotaxy as in *G. retractus,* but there tend to be somewhat fewer dorsal seta according to Clay (1940). Genitalia are similar to those of *G. keleri*, but differ in some details (see Clay 1940, figure 68b).

**Measurements:** (n = 11) TW 0.43-0.55 (0.51); HL 0.51-0.66 (0.56); CI 1.03-1.24 (1.10); PW 0.26-0.30 (0.28); MW 0.37-0.47 (0.42); AWV 0.54-0.74 (0.63); GL 0.47-0.64 (0.54); TL 1.79-2.14 (1.96);

**Female:** Head similar in shape to that of male but larger. Thorax as in male. Abdomen generally the same shape as that of the male. Abdominal chaetotaxy; ventral cheatotaxy as in male. On the dorsal surface, segment II has no lateral and 4 central seta; III has 1 lateral and 4 central seta; segments IV-VIII have 2 lateral and 4 central seta. The cheatotaxy of the posterior segments and genital region as in *G. souefi*, but there tend to be fewer seta at the lateral corners of the vulva (Clay 1940).

**Measurements:** (n = 10) TW 0.52-0.70 (0.63); HL 0.58-0.71 (0.65); CI 1.01-1.11 (1.04); PW 0.31-0.38 (0.34); MW 0.45-0.58 (0.52); AWV 0.76-1.08 (0.89); TL 2.33-3.22 (2.70).

**Discussion:** Lectotype (Female #158) of *G. elongates* in the Piaget Collection at the BMNH designated as such by Clay (1940: 102). Types of *Goniodes elongates*

(Piaget, 1880: 281 partim ) and *Goniodes gracilis* are in the collection of the BMNH according to Hopkins and Clay (1952: 153, 154).

### ***25. G. moucheti*** Tendeiro

(Figures: Tendeiro 1960c: 102 – Figures 5-6, photos 37-38)

*G. moucheti* Tendeiro, J. 1960c. Études sur les Mallophages africains. Junta Invest. Ultramar, Estudos, Ensaios e Docum. 65: 99.

**Type Host**: *Francolinus nobilis* (Reichenow, 1908)(Galliformes: Phasianidae) – Handsome Francolin – Price *et al*. 2003: 185.

**Diagnosis and General Description:** Following the original description by Tendeiro (1960c) *G. moucheti* based on its morphology belongs in Clay's Group L (1940). The temples are expanded and similar in both sexes; the coni partly membranous and more or less developed; antennas dimorphic, in Males without any protuberance on the scape, and with a small tubercle (*G. securiger*) or an expansion paralell or at right angles with the 1st and 2nd flagellomere. And the Female has the vulva (the exception was *G. extraneus*) with setae concentrated at the corners and a lateral spinous process in the genital area. This group is largely the genus *Solenodes* (Kéler 1939) with the exception of *G. isogenos* Nitzsch 1866; with no sexual dimorphism in the antennae, and which was placed in the genus *Stenocrotaphus* by Kéler (1939).

It is distinguished from *G. temporalis* (Kéler) considered *G. extraneus* by Clay (1940) by the fact that the temporal setae occurs on a well defined temple process in both sexes, the 1st flagellomere of the Male antennae has a pointed expansion and Male genitalia has an elongated basal plate and sclerotized paramera of uneven length. It is much smaller than *G. assimilis* with the 1st flagellomere of the Male antennae having a small expansion parallel to the 2nd. *Goniodes scleroptilus* Bedford, is also much smaller and the temples are not as expanded. In addition, Males of other species described in the group K - and indeed, all other known forms of the genus *Goniodes* - do not possess the antennal characters so typical for *G. moucheti* especially with regard to the process on the 1st falgellomere.

**Male:** Head with marginal carina very wide, with four short and equal anterior setae; a large dorsal submarginal seta, and 2 short submarginal ventral spines. Clavi buldging. Antennae: scape short, robust. Pedicel elongated; longer than the 2nd and 3rd flagellomeres combined; 1st flagellomere with a big postero-internal expansion sacculate (sac-like) very characteristic. Dorsal anterior pre-and post-nodal antennal seta shorter than the dorsal temporal setae. Eyes very prominent, with an ocular macrochete. Temporal angle projected outside, with a thorn on a small prominence. Temporal marginal band very wide, with 2 + 1 marginal temporal macrochete, a spinule and a temporal submarginal spine. Proeminent facial angle, with a spine.-occipital edge Sub linear.

Thorax much shorter than the head. Prothorax with a lateral macrochete. Pterothorax with 2 lateral macrochetes, 2 meta lateral macrochetes and 1 metacentrale seta.

Abdomen pear-shaped or pyriform, very wide, with its maximum width in back. Tergopleurales plates with a forward extension, those of anterior segments has inner edges straight. Dorsal chaetotaxy includes a core group of 2-4 setae and lateral groups, with denser bristles. Male genitalia has narrow and elongated basal plate; narrow parameres.

**Measurements:** (n = 1) TW 1.42; HL 0.93; CI 0.65; PW 0.60; MW 0.91; AWV 1.88; GL 1.62; TL 3.35.

**Female:** Head as in male with filiform antennae, the pedicel longer than the 2nd and 3rd falgellomeres combined. 1st Flagellomere and 2nd flagellomere nearly equal in length. Thorax as in the male. Abdomen oval, wider, more elongated than in males. Subgenital plate with a spinous process leading medially and back. Vulva angular, with a row very short strong spines; laterally with tufts of short bristles.

**Measurements:** (n = 1) TW 1.28; HL 0.97; CI 0.76; PW 0.62; MW 0.92; AWV 1.73; TL 3.46.

**Materials: BMNH** 2 specimens (paratypes) ex *Francolinus nobilis*: CONGO: 1 male, 1 female (Kivu, Coll: J. Mouchet, no. 289, Brit. Mus. 1963-509).

### ***26. G. lootensi*** Tendeiro

(Figures: Tendeiro 1960c: 109 – Figures 7-9, photos 31, 33)

*G. lootensi* Tendeiro, J. 1960c. Études sur les Mallophages africains. Junta Invest. Ultramar, Estudos, Ensaios e Docum. 65: 107.

**Type Host**: *Coturnix chinensis adansonii* (Verreaux and Verreaux, 1851) = *Coturnix adansonii* (Verreaux and Verreaux, 1851) (Galliformes: Phasianidae) – Blue Quail – Price *et al*. 2003: 185.

**Diagnosis and General Description:** As per Tendeiro (1960c) this is a small species, sexual dimorphism pronounced the Male with 1.79-1.88mm long and 0.63mm wide, and the Female, 2.73-2.98mm by 0.83-0.93mm. It is placed in Group L (Clay 1940) based on its elongated abdomen, the antennae having an expansion on the 1st flagellomere and the condition of the pleural heads. It can be distinguished from other species in the group by the characters of the Male genitalia and Female genital area, as well as the form of the head, thorax and abdomen. In these characters they represent species in group K spcifically *G. keleri*.

The L-group contains the species *G. retractus, G. soueefi* - both have the 1st flagellomere of the antennae of the Male prolonged distally in right angle to the 2nd; and *G. astrocephalus* with no sexual dimorphism for the antennae. Kéler (1939) established the genus *Astrocotes* for *G. astrocephalus* using the abscence of sexual dimorphism in the antennae; the wedge like body shape, a truncated terminal section as defining characters.

According to Tendeiro (1960c) the length of the Male indicated by Clay obviously comes a slip of the pen, while the one we studied, also a healthy adult is sclerotized, may represents an individual being smaller than average. In any case there is some discrepancy between the ratio total length / length of the head of Males, which is clearly superior to those of *G. lootensi* (3.60-3.66) in the specimen measured by Clay (4.26) and is lower in the copy that we studied (3.33). As such Tendeiro did not utilize morphometrics in describing this species.

Both species are distinguished: 1 - by the different profile of the head, with the anterior portion less develloped and the facial angle acute and long in our new species, short and buldging in *G. astrocephalus*; 2 - in the Male, by the different form of posterior half of the abdomen, in *G. lootensi* with pleura VII-VIII much more lopsided than the backward segments IX-X, VII still being slightly further back than the VIII, while in *G.*

*astrocephalus* the pleura VII-VIII are less lopsided backward, the VII being significantly less backwards, the VIII and located at the same level of IX, and 3 - in the Female by the presence of a posterior segment medially notched and lateral hooks to pleura IV-VIII (1 in segments IV-VI and 2 in segment VII) in *G. lootensi*, absent in *G. astrocephalus*.

**Male:** Head almost as wide as long, with very wide marginal carinas, thicker in fromt thick. With four short and equal anterior setae; a strong submarginal dorsal seta and 2 submarginal ventral spinules. Clavi strong, acute. Antennae: scape short, robust; pedicel slightly elongated, shorter than the 2nd and 3rd flagellomere combined. 1st flagellomere slightly asymmetrical, with the inner edge a little longer than the outer but without forming a true postero-medial protuberance. 2nd flagellomere squat, as long as wide. 3rd flagellomere a bit longer than the 1st. Anterior dorsal, antennal pre-and post-nodal setae long. Eye circular, very prominent, with an ocular macochete shorter than the temporal. Temporal angle slightly projected outside; with a macrochete and 2 short spines angled and a posterior macrochete. Posterior temple convex curved in front and abruptly behind, to form a long and acute facial angle, with a very short terminal spinule. Temporal band broad. Occipital edge convex, with a short seta on each side.

Thorax much shorter than the head. Prothorax very short, has the hind margin concave, with a lateral macrosetae. Pterothorax angled on the abdomen, with a seta + 2 lateral macrosetae, 1 seta + 1 macrochete metalateral and a seta metacentrale.

Abdomen elongated, relatively narrow, with thick pleura and very warped backward; those of segments VII-VIII largely exceeding segments IX-X; that it frame laterally; maximum width at level V of pleura. Tergopleural plates rounded with an anterior extension and having a seta tergale anterior, and 3 posterior on segment II. 3

posterior setae on segment III. 4 in segments IV-V; and 1 on segments VI-VII. Pleural chetotaxy includes a seta by the angle of segments III-V. 2 setae on segment VI. 2 macrochetes on segment VII and a macrochete in segment VIII, as well as two ventral setae in segments III-VII and 3 in segment VIII. Sternites III-VII with a seta progressively longer to the rear, and a spinule, it is absent in tergite VII.

Male genitalia has very long and narrow basal plate, followed by long very thin and pointed paramera, endomerale plate rounded, with little linear sclerotized sclerites.

**Measurements:** (n = 4) TW 0.47-0.48 (0.47); HL 0.50-0.51 (0.51); CI 1.06-1.09 (1.08); PW 0.27-0.28 (0.28); MW 0.37-0.39 (0.38); AWV 0.50-0.56 (0.53); GL 0.41-0.66 (0.57); TL 1.78-1.89 (1.82).

**Female:** Head as broad as long (slightly larger than the Male); antennas as in the male, with the 1st flagellomere symmetrical or slightly asymmetrical. Thorax as in the male. Abdomen more elongated than in the male, sternites also very drawn back, but those segments VII-VIII does not extend past the posterior segment, with a hook lateral to segments IV-VI and IX and 2 in segment VII. Posterior segment with a median notch. Subgenitale plate with a spinous process. Vulva concave, with a spine on each side of the midline.

**Measurements:** (n = 3) TW 0.60-0.63 (0.62); HL 0.60-0.64 (0.62); CI 0.98-1.03 (1.00); PW 0.34-0.37 (0.36); MW 0.49-0.51 (0.50); AWV 0.79-0.82 (0.81); TL 2.68-2.83 (2.77).

**Material studied: RMCA:** 14 specimens (holotype, allotype + 12 paratypes) ex *Excalfactoria adamsoni*: BELGIAN CONGO: 6 Males, 6 Females (Tshuapa, 15.vii.1957, Coll: R. P. Lootens). BMNH: 2 specimens (paratypes) ex *Excalfactoria* *adamsoni*: BELGIAN CONGO: 1 Male, 1 Female (Tshuapa, 15.vii.1957, Coll: R. P. Lootens, B.M. 1960-106 ).

**Discussion:** Placement in Group L by Tendeiro (1960c). Holotype, allotype, and paratypes (20) in the collection of RMCA. Nymphs designated in the type series are much less elongated and shaped more like other *Goniodes*, although they are very rectangular in appearance posteriorly. One set of slides contain paratypes are desiccated and all but destroyed. Nymph series of paratypes starting to degrade.

## Introduced and species incidental to Sub-Saharan Africa

### Group A

Large species (Males 3.60-3.80mm., females 3.80-4.70mm.). Temples not sexually dimorphic, not greatly expanded. Clavi thickened in both sexes, prolonged posteriorly in M and postero-laterally in F. Antennae sexually dimorphic. M, 1st segment enlarged and bearing a thickened process, 3rd segment with distal post-axial angel prolonged as narrow elongated process. F, 1st segment longer than 2nd, but shorter than combined lengths of segments II – IV (See Kéler, 1937 (1): 131) – (segment I, 0.186-0.122mm., Segments II-IV, .334-.338mm.). Meso- and metatarsal hairs present Pleurites broad, due to thickened area between marginal band of the pleurite and the spiracle being present. F w/ bifid structure associated w/ internal genital organs apparent in abdomen Vulva at the level of segment VII w/ hairs concentrated at the lateral corners, no spinous process present on the genital region. Anterior margin of M genital opening somewhat prolonged posteriorly and bilobed.

This group of large distinct species is introduced into Africa on *Pavo*.

### ***27. Goniodes pavonis*** (L.)

*Pediculus pavonis* Linnaeus, 1758: 613. Type host: *Pavo cristatus* L.

*Nirmus tetragonocephalus* Olfers, 1816: 90. Type host: *Pavo cristatus* L.

*Philopterus falcicornis* Nitzsch, 1818: 293. *Nomen novum* for *Pediculus pavonis* L.

Type host: *Pavo cristatus* L.

*Goniodes falcicornis* Nitzsch, 1818: 293. Type host: *Pavo cristatus* L.

**Type Host**: *Pavo cristatus* (Linnaeus, 1758)(Galliformes: Phasianidae) – Indian Peafowl.

**Hosts**: *P. muticus* (Linnaeus, 1766) (Galliformes: Phasianidae) – Green Peafowl

**Material studied**: 33 specimens (16 Males, 17 Females). 1 specimen (FMNH) ex *Pavo cristatus* (Linnaeus, 1758)(Galliformes: Phasianidae) – Indian Peafowl: **NEPAL**: 1 Female (Bhogbhawanpur Banke Dist., 3 April 1968, Coll: unknown, Host NP-452). 2 specimens (FMNH) ex *Pavo cristatus* (Linnaeus, 1758)(Galliformes: Phasianidae) – Indian Peafowl: **NEPAL**: 2 Males (Bhogbhawanpur Banke Dist., 5 April 1968, Coll: unknown, Host NP-460). 2 specimens (FMNH) ex Peacock: **USA**: 1 Male, 1 Female (Michigan, 28 May 1929, Coll: A. F. Franzen). 2 specimens (NMNH) ex *Pavo cristatus* (Linnaeus, 1758)(Galliformes: Phasianidae) – Indian Peafowl: **NEPAL**: 1 Male, 1 Female (Bhogbhawanpur Banke Dist., 31 March 1968, Coll: unknown, Host NP-425). 2 specimens (NMNH) ex *Pavo cristatus* (Linnaeus, 1758)(Galliformes: Phasianidae) – Indian Peafowl: **NEPAL**: 2 Males (Bhogbhawanpur Banke Dist., 6 April 1968, Coll: unknown, Host NP-482: Lewis Collection). 4 specimens (NMNH) ex *Pavo muticus* *imperator* (Delacour, 1949)(Galliformes: Phasianidae) – Indo-Chinese Green Peafowl: **THAILAND**: 2 Males, 2 Females (Nakhon Phanom, Nakae Kanluang, Kho Mt., 16 July 1954, Coll: Elbel and Boonsong, Host: B30924, RE 3912). 4 specimens (NMNH) ex *Pavo muticus imperator* (Delacour, 1949)(Galliformes: Phasianidae) – Indo-Chinese Green Peafowl: **THAILAND**: 2 Males, 2 Females (Nakhon Phanom, Nakae Kanluang, Kho Mt., 25 July 1954, Coll: R. E. Elbel, Host: B30924, RE 3912). 2 specimens (NMNH) ex Pea fowl ()() – Peacock: **USA**: 1 Male, 1 Female (Baton Rouge, LA., May 9, 1957, Coll: E. Cancienne, Host: No. 32418 (Lot 57-6363). 2 specimens (NMNH) ex. *Pavo cristatus* (Linnaeus, 1758)(Galliformes: Phasianidae) – Indian Peafowl: **USA**: 1 Male, 1 Female (Chicago Zool. Park, 18 Jan. 1967, Coll: Ursula Rowlatt, Host: 182-65). 1 specimen (OK) ex *Pavo cristatus* (Linnaeus, 1758)(Galliformes: Phasianidae) – Indian Peafowl: **NEPAL**: 1 Female (Bhogbhawanpur Banke Dist., 3 April 1968, Coll: unknown, Host NP-452). 1 specimen (OK) ex *Pavo cristatus* (Linnaeus, 1758)(Galliformes: Phasianidae) – Indian Peafowl: **NEPAL**: 1 Female (Bhogbhawanpur Banke Dist., 5 April 1968, Coll: unknown, Host NP-460). 1 specimen (OK #3991) ex *Pavo muticus imperator* (Delacour, 1949)(Galliformes: Phasianidae) – Indo-Chinese Green Peafowl: **THAILAND**: 1 Female (Nakhon Phanom, Nakae Kanluang, Kho Mt., 25 July 1954, Coll: R. E. Elbel, Host: B30924, RE 3912). 1 specimen (OK #3990) ex *Pavo muticus* (Linnaeus, 1766) (Galliformes: Phasianidae) – Green Peafowl: **THAILAND**: 1 Female (Nansa, Ban Phahang, 8 Dec. 1961, Coll: Mr. Kittithonglongya, Host. V139). 6 specimens (OK) ex *Pavo cristatus* (Linnaeus, 1758)(Galliformes: Phasianidae) – Indian Peafowl: **UNITED KINGDOM**: 3 Males, 3 Females (Bridgenorth, Shropshire, 11.viii.1934, Coll: Frances Pitt). 2 specimens (OK) ex Pea fowl ()() – Peacock: **USA**: 1

Male, 1 Female (Baton Rouge, LA., May 9, 1957, Coll: E. Cancienne, Host: No. 32418 (Lot 57-6363).

**Description**: **Male** (n = 16) TW 1.10-1.21 (1.16 ); HL 0.91-1.00 (0.95 ); CI 0.79-0.84 (0.82); PW 0.79-0.93 (0.87); MW 1.19-1.35 (1.28); AWV 2.00-2.30 (2.16); GL 0.83-1.58 (1.31); PL 0.48-0.53 (0.50); TL 3.55-4.30 (3.9);

**Female** (n = 17) TW 1.35-1.54 (1.44); HL 1.00-1.13 (1.06); CI 0.69-0.78 (0.74); PW 0.83-0.94 (0.91); MW 1.23-1.38 (1.33); AWV 2.18-2.48 (2.33); TL 4.03-4.70 (4.40);

**Discussion**: Neotype (M Meinertzhagen Coll. #8175) and neoparatypes (22M, 27 F) designated by Clay 1940: 7. The specimens in Clay 1940:7 is also neotypes for *G. falcicornis* (Nitzsch) – Clay and Hopkins 1950: 261.- BMNH n/type

## Group B

Large species (M = 3.48-5.22mm., F = 3.66-5.65mm.), with variable temple development: either similar in both sexes or not expanded; or with Female temples greatly expanded. Clavi distinct in both sexes, but scarcely developed in Male, elongated postero-laterally in Females. Antennae sexually dimorphic: Male with enlarged scape with a thickened process, 1st flagellomere with distal post-axial angel prolonged as narrow elongated process. Female, 1st segment longer than 2nd, but shorter than combined lengths of segments II – IV (See Kéler, 1937 (1): 131) – (segment I, .186-.122mm., Segments II-IV, .334-.338mm.). Meso- and metatarsal hairs present. Pleurites broad, due to thickened area between marginal band of the pleurite and the spiracle being present, or without inner thickened areas. Female with bifid structure; vulva nearly terminal with setae along posterior margin, not concentrated laterally, and no spinous process. Anterior margin of Male genital opening somewhat prolonged posteriorly and bilobed, or with margin not prolonged posteriorly.

This group is also introduced into Africa on *Pavo*

### ***28. G. meinertzhageni*** Clay

*G. meinhertzhageni* – Clay, T. 1940a. Genera and species of Mallophaga occurring on gallinaceous hosts. – Part II. *Goniodes*. Proc. Zool. Soc. London (Ser. B) 110: 9.

**Type Host**: *Pavo cristatus* (Linnaeus, 1758)(Galliformes: Phasianidae) – Indian Peafowl – Price *et al*. 2003: 185

**Description**: **Male** (n = 2) TW 1.01; HL 0.83-0.84; CI 0.81-0.83; PW 0.81-0.85; MW 1.13-1.19; AWV 2.00-2.04; GL 1.43-1.48; TL 3.73-3.79

**Female** (n = 6) TW 1.15-1.43 (1.26); HL 0.80-0.93 (0.85); CI 0.56-0.72 (0.68); PW 0.59-0.83 (0.67); MW 0.83-1.20 (0.96); AWV 1.45-2.06 (1.71); TL 2.85-4.08 (3.30);

**Discussion**: Remarks: Holo (M Meinertzhagen Coll. #4452), Para (2M, 1F) – BMNH. Types in BMNH – Hopkins and Clay 1952: 156

### Group K

Species large to small (M = 1.60-4.20mm., F = 2.05-3.90mm.); temples expanded and similar in both sexes; coni partly membranous in both sexes, and developed to a greater or lesser extend; antennae sexually dimorphic: Male scape without process, 1$^{st}$ flagellomere distally as a minute tubercle, or distinct process parallel to, or at right angle to the 2$^{nd}$ flagellomere. Female with pedicel either shorter or equal to scape. Ventral pterothoracic setae absent. Pleurites without thickened area between marginal band of pleurites and spiracle. Female bifid structure absent. Vulval margin with lateral concentrations of seta and spinous process. Male genital opening unmodified.

Introduced or incidental in Africa

### ***29. G. dispar*** Burmeister

*G. dispar* Burmeister, H. 1838. Mallophaga Nitzsch. Handbuch der Entomologie, Berlin, 2: 432

*Goniodes dispar* Nitzsch, 1818: 294 *nom. nud.* – Clay 1940a: 87

*Goniodes breviantennatus* – (Piaget, 1885: 50) – Clay 1940a: 87; Clay 1947: 546; Hopkins and Clay, 1952: 151; Price *et al.* 2003: 183

*Solenodes cypricus* – (Kéler, 1939b: 107) – Clay 1947: 546; Hopkins and Clay, 1952: 152; Price *et al.* 2003: 183

*Goniodes flaviceps* – (Rudow, 1869b: 28) – Clay 1940a: 87; Clay 1947: 546; Hopkins and Clay, 1952: 154; Price *et al.* 2003: 184; Tendeiro 1955c: 535

*Goniodes truncatus* – (Giebel, 1874: 194) – Clay 1940a: 87; Clay 1947: 546; Hopkins and Clay, 1952: 159; Price *et al.* 2003: 186; Tendeiro 1955c: 535

*Genocephalus* (Kéler 1937, 130)

*Solenodes truncatus* (Kéler 1939, 103)

*Solenodes dispar* Hopkins and Clay 1952:153

*Solenodes dispar flaviceps* Tendeiro 1955c: 535; Tendeiro 1956: 504

**Type Host**: *Perdix perdix* (*Perdix cinerea*) (Linnaeus, 1758)(Galliformes: Phasianidae) – Grey Partridge – Clay 1940a: 87; Price *et al.* 2003: 184

**Hosts**: *P. p. lucida* (Altum, 1894)(Galliformes: Phasianidae) – Eastern Grey Partridge – Clay 1940a: 89

*P. rubra* = *Alectoris rufa* (Linnaeus, 1758)(Galliformes: Phasianidae) – Red-legged Partridge – Clay 1940a: 90; Hopkins and Clay 1952: 159

*Alectoris chukar* (Gray, J. E., 1830)(Galliformes: Phasianidae) – Chukar – Clay, 1940a: 89; Price *et al*. 2003: 184

*A. graeca* (Meisner, 1804) (Galliformes: Phasianidae) – Rock Partridge - Price *et al*. 2003: 184

*A. graeca chukar* (J. E. Gray) = *A. graeca* (Meisner, 1804) (Galliformes: Phasianidae) – Rock Partridge – Clay, 1940a: 87, 89; Hopkins and Clay 1952: 151

*A. g. pallescens* (Hume, 1873) = *Alectoris chukar pallescens* (Hume, 1873) (Galliformes: Phasianidae) – Northern Chukar – Clay 1940a: 89

*A. g. phillbyi* Lowe = *Alectoris philbyi* (Lowe, 1934) (Galliformes: Phasianidae) Philby's Partridge – Clay 1940a: 89

*A. g. falki* (Hartert, 1917) = *Alectoris chukar falki* (Hartert, 1917) (Galliformes: Phasianidae) – Chukar – Clay 1940a: 89

*A. g. cypriotes* (Hartert, 1917) = *Alectoris chukar cypriotes* (Hartert, 1917) (Galliformes: Phasianidae) – Island Chukar – Hopkins and Clay 1952: 152

*Alectoris rufa rufa* (Linnaeus, 1758)(Galliformes: Phasianidae) – Red-legged Partridge – Clay, 1940a: 89; Hopkins and Clay 1952: 154, 159; Price *et al*. 2003: 184, 186

*Alectoris rufa hispanica* Tendeiro 1955c: 504, 536.

*A. chukar cypriotes* Hartert = *Alectoris chukar cypriotes* (Hartert, 1917) (Galliformes: Phasianidae) – Island Chukar – Clay 1940a: 89; Hopkins and Clay,1952: 152; Price *et al*. 2003: 184

*Phasianus veneratus reevesii* = *Syrmaticus reevesii* (Gray, J. E.1829)(Galliformes: Phasianidae) – Reeve's Pheasant = stragglers – Clay 1940a: 89

*Otis tetrax tetrax* Tendeiro 1955c: 536

**Material studied:** 33 specimens (14 Males, 19 Females). 5 specimens (BMNH) ex *Perdix hodgsiniae caragenae* (Meinertzhagen and Meinertzhagen, 1926)(Galliformes: Phasianidae) – Tibetan Partridge: **INDIA**: 5 Females (Ladak, June 1925, Coll: Meinertzhagen, Host: Male 3650). 2 specimens (BMNH) ex *Alectoris g. graeca* (Meisner, 1804) (Galliformes: Phasianidae) – Rock Partridge: **JUGOSLAVIA**: 1 Male, 1 Female (Makedonija, 5.1.1956, Coll: unknown, Host: Brit. Mus. 1958-661). 2 specimens (BMNH) ex *Perdix perdix* (Linnaeus, 1758)(Galliformes: Phasianidae) – Grey Partridge: **USA**: 1 Male, 1 Female (Lincoln, NE, 21.x.1963, Coll: Eskgrove Lab., Host: Brit. Mus. 1964-102). 6 specimens (BMNH) ex *Pternistis afer humboldii* = *Francolinus afer cranchii* (Leach, 1818)(Galliformes: Phasianidae) – Cranch's Spurfowl: **ZIMBABWE**: 2 Males, 4 Females (Zambesi (Zoo), June 1937, Coll: Meinertzhagen, Host: Male 8342). 2 specimens (FMNH) ex *Perdix perdix* (Linnaeus, 1758)(Galliformes: Phasianidae) – Grey Partridge: **CANADA**: 2 Males (Vancouver, B. C., 1932, Coll: unknown, det. K. C. Emerson). 1 specimen (FMNH) ex Chuckar = *Alectoris chukar* (Gray, J. E., 1830)(Galliformes: Phasianidae): **USA**: 1 Female (Ithaca, N.Y., Mar. 26. 1952, Coll: Dickerman). 1 specimen (INHS) ex Hungarian Partridge = *Perdix perdix* (Linnaeus, 1758)(Galliformes: Phasianidae): **USA**: 1 Male (Yountville, Calif., 1949, Coll: unknown). 2 specimens (MINN) ex *Perdix perdix* (Linnaeus, 1758)(Galliformes: Phasianidae) – Grey Partridge: **USA**: 1 Male, 1 Female (Timpie, Tooele Co., Utah, 16 Apr 1965, Coll: R.E. Elbel). 2 specimens (MINN) ex *Perdix perdix* (Linnaeus, 1758)(Galliformes: Phasianidae) – Grey Partridge: **SWEDEN**: 1 Male, 1 Female (Tynaberga, 7. 3. 1955., Coll: unknown, Host: 146). 2 specimens (NMNH) ex *Alectoris graeca chukar* = *A. graeca* (Meisner, 1804) (Galliformes: Phasianidae) – Rock Partridge: **NEPAL**: 1 Male, 1 Female (Geling, Mustang Dist., 22 May 1970, Coll: unknown, Host: NP-3953). 2 specimens (NMNH) ex *Alectoris rufa hisponica* =*Alectoris rufa hispanica* (Seoane, 1894)(Galliformes: Phasianidae) – North Iberian Red-legged Partridge: **SPAIN**: 1 Male, 1 Female (Salamanca, 1-iv-49, Coll: K. C. Emerson from skin). 2 specimens (OK 3886) ex *Alectoris graeca chukar* = *A. graeca* (Meisner, 1804) (Galliformes: Phasianidae) – Rock Partridge: **NEPAL**: 1 Male, 1 Female (Geling, Mustang Dist., 22 May 1970, Coll: unknown, Host: NP-3953). 2 specimens (OK) ex *Perdix perdix* (Linnaeus, 1758) (Galliformes: Phasianidae) – Grey Partridge: **USA**: 1 Male, 1 Female (Timpie, Tooele Co., Utah, 16 Apr 1965, Coll: R. E. Elbel, Host: EandE Bir). 1 specimen (OK 2202 (1)) ex *Alectoris graeca chukar* = *A. graeca* (Meisner, 1804) (Galliformes: Phasianidae) – Rock Partridge: **HIMALAYAS**: 1 Male (no data). 1 specimen (OK 2202 (2)) ex *Alectoris graeca saxatilis* (Bechstein, 1805)(Galliformes: Phasianidae) – Alpine Rock Partridge: **GERMANY**: 1 Female (no data).

**Description**: **Male** (n = 14) TW 0.80-0.90 (0.84); HL 0.59-0.69 (0.64); CI 0.74-0.79 (0.76); PW 0.37-0.51 (0.44); MW 0.52-0.71 (0.64); AWV 1.11-1.24 (1.17); GL 0.56-0.73 (0.65); TL 1.90-2.19 (2.03)

**Female** (n = 19) TW 0.79-1.23 (1.04); HL 0.70-0.84 (0.76); CI 0.71-0.89 (0.74); PW 0.45-0.56 (0.50); MW 0.65-0.83 (0.74); AWV 1.15-1.53 (1.36); TL 2.35-3.13 (2.76);

**Discussion:** Remarks: Lecto (M #24) para (4M, 4F) of *G. breviantennatus* in Piaget Coll. BMNH designated by Clay 1940a: 90 *BMNH* ***lecto para***

**Discussion:** Introduced on Robben Island South Africa (Madge 2002) and one specimen from *Pternistes* from Zimbabwe

### ***30. G. securiger*** Nitzsch

*G. securiger* Nitzsch, (in Giebel, C. 1866. Die im zoologischen Museum der Universität Halle aufgestellten Epizoen nebst Beobachtungen über dieselben. Zeit. Gesamt. Naturwiss. 28: 387)

**Type Host**: *Alectoris b. barbara* (Bonnaterre, 1792)(Galliformes: Phasianidae) – Barbary Partridge – Clay 1940a: 90; Hopkins and Clay 1952: 158; Price et al 2003: 186

**Material studied:** 20 specimens (10 Males, 10 Females). 13 specimens (BMNH) ex *Alectoris b. barbara* (Bonnaterre, 1792)(Galliformes: Phasianidae) – Barbary Partridge: **MORROCO**: 6 Males, 7 Females (no place, no date, Coll: Meinertzhagen, Host: 121-85). 1 specimen (NMNH) ex *Alectoris barbara koenigi* (Reichenow, 1899)(Galliformes: Phasianidae) – Reichenow's Barbary Partridge: **CANARY ISLANDS**: 1 Male (Tenerife, no date, no collector). 2 specimens (OK) ex *Alectoris barbara koenigi* (Reichenow, 1899)(Galliformes: Phasianidae) – Reichenow's Barbary Partridge: **CANARY ISLANDS**: 2 Females (Tenerife, no date, no collector). 1 specimen (OK 4006 (3)) ex *Alectoris barbara koenigi* (Reichenow, 1899)(Galliformes: Phasianidae) – Reichenow's Barbary Partridge: **CANARY ISLANDS**: 1 Male (Tenerife, no date, no collector). 1 specimen (OK 4009 (4)) ex *Alectoris barbara koenigi* (Reichenow, 1899)(Galliformes: Phasianidae) – Reichenow's Barbary Partridge: **CANARY ISLANDS**: 1 Female (Tenerife, no date, no collector). 2 specimens (OK) ex *Alectoris barbara spatyi* = *Alectoris barbara spatzi* (Reichenow, 1895)(Galliformes: Phasianidae) – Saharan Barabary Partridge: **TUNISIA**: 2 Males (no place, no date, no collector).

**Description**: **Male** (n = 10) TW 0.76-0.82 (0.79); HL 0.60-0.63 (0.61); CI 0.76-0.80 (0.78); PW 0.39-0.42 (0.40); MW 0.58-0.61 (0.60); AWV 0.94-1.03 (0.98); GL 0.22-0.54 (0.45); TL 1.82-1.93 (1.88);

**Female** (n = 10) TW 0.99-1.07 (1.03); HL 0.73-0.80 (0.76); CI 0.73-0.78 (0.74); PW 0.46-0.53 (0.49); MW 0.69-0.74 (0.72); AWV 1.17-1.40 (1.31); TL 2.31-2.80 (2.63);

**Discussion:** Occur in North Africa probably incidental in Sub-Saharan Africa… See Tendeiro 1955c: 535; Pictured in Kéler 1939 as *Solenodes truncatus*

### ***31. G. dissimilis*** Denny

*G. dissimilis* – Denny, H. 1842. Monographia anoplurorum Britanniae. Henry G. Bohn, London. xxvi + 262: 57 and 162

*Goniodes dissimilis* Nitzsch, 1818: 294 *nom. nud.* – Clay 1940a: 62

*Goniodes dissimilis bankiva* – (Piaget, 1880: 269) – Clay 1940a: 62; Hopkins and Clay, 1952: 151; Price *et al*. 2003: 184

*Oulocrepis dissimilis* (Kéler 1939, 97)

**Type Host**: *Gallus gallus* (Linnaeus, 1758)(Galliformes: Phasianidae) – Red Junglefowl – Price *et al*. 2003: 184

**Hosts**: *Gallus domestica* = *Gallus gallus domesticus* (Linnaeus,1758) (Galliformes: Phasianidae) – Domestic Chicken – Clay 1940a: 62

*Gallus domesticus* = *Gallus gallus domesticus* (Linnaeus, 1758)(Galliformes: Phasianidae) – Domestic Chicken – Hopkins and Clay 1952: 153

*G. gallus labouillei* = *Gallus gallus jabouillei* (Delacour and Kinnear, 1928)(Galliformes: Phasianidae) – Tonkin red junglefowl

*G. g. murghi* (Robinson and Kloss, 1920)(Galliformes: Phasianidae) – Indian Red Junglefowl

*G. lafayettii* (Lesson, 1831)(Galliformes: Phasianidae) – Ceylon Junglefowl – Clay, 1940a: 65; Price *et al*. 2003: 184

*G. sonneratti* (Temminck, 1813) (Galliformes: Phasianidae) – Grey Junglefowl – Price *et al*., 2003: 184

*G. gallus bankiva* (Temminck, 1813) (Galliformes: Phasianidae) – Javan Red Junglefowl – Clay 1940a: 62; Piaget, 1880: 269; Hopkins and Clay 1952: 151; Price *et al*. 2003: 184

**Material studied:** 21 specimens (10 Males, 11 Females). 4 specimens (FMNH) ex *Gallus g. gallus* (Linnaeus, 1758)(Galliformes: Phasianidae) – Red Junglefowl: **THAILAND**: 2 Males, 2 Females (Nakhon Phanom, Nakae Kanluang, Kho Mt., 25 July 1954, Coll: Elbel and Boonsong; Host: B30927; RE 3924). 1 specimen (MINN) ex Domestic chicken = *Gallus gallus domesticus* (Linnaeus, 1758)(Galliformes: Phasianidae) – Domestic Chicken: **TAIWAN**: 1 Male (Formosa, Hsin Hua Tai-nan Hsien, 18-1-61, Coll: unknown, Host: 14032, 14034). 2 specimens (MINN) ex *Gallus gallus murghi* (Robinson and Kloss, 1920)(Galliformes: Phasianidae) – Indian Red Junglefowl: **NEPAL**: 1 Male, 1 Female (Madhu-ban, Bara District, 6 Jan. 1968, Host:

NP-295). 1 specimen (MINN) ex *Gallus gallus* (Linnaeus, 1758)(Galliformes: Phasianidae) – Red Junglefowl: **CUBA**: 1 Female (Habana, no date, Coll: I. Perez Viqueras). 2 specimens (NMNH) ex *Gallus g. gallus* (Linnaeus, 1758)(Galliformes: Phasianidae) – Red Junglefowl: **MALAYSIA**: 1 Male, 1 Female (Malaya, Sungei Buloh, 9 May 1956, Host: R-45282). 2 specimens (NMNH) ex *Gallus g. gallus* (Linnaeus, 1758)(Galliformes: Phasianidae) – Red Junglefowl: **THAILAND**: 1 Male, 1 Female (Nakhon Phanom, Nakae Kanluang, Kho Mt., 25 July 1954, Coll: Elbel and Boonsong, Host: B30927; RE 3924). 2 specimens (OK B-22723) ex *Gallus gallus spadiceus* (Bonnaterre, 1792)(Galliformes: Phasianidae) – Burmese Red Junglefowl: **THAILAND**: 2 Females (Phu Lam Lo Mt., Koksathon, Dansai, Loei, 30-Mar-54, Coll: R.E. Elbel and B. Lekaqul, Host: RE. 3533). 2 specimens (OK 3901, 3908) ex *Gallus lafayetii* (Lesson, 1831)(Galliformes: Phasianidae) – Ceylon Junglefowl: **SRI LANKA**: 1 Male, 1 Female (Ceylon). 2 specimens (OK 3910) ex *Gallus sonneratii* (Temminck, 1813) (Galliformes: Phasianidae) – Grey Junglefowl: **INDIA**: 1 Male, 1 Female (India). 3 specimens (OK) ex *Gallus gallus spadiceus* (Bonnaterre, 1792)(Galliformes: Phasianidae) – Burmese Red Junglefowl: **THAILAND**: 2 Males, 1 Female (Loei, Dansai, Koksathon Ban Nam Yen, Phak Khi Nak Mt., 14 Mar. 1955, Coll: R. E. Elbel, Host: RE 4926).

**Description**: **Male** (n = 10) TW 0.77-0.85 (0.82); HL 0.68-0.76 (0.71); CI 0.85-0.90 (0.87); PW 0.44-0.52 (0.48); MW 0.63-0.76 (0.70); AWV 1.04-1.28 (1.16); GL 0.79-0.87 (0.82); TL 1.98-2.43 (2.21);

**Female** (n = 10) TW 1.03-1.12 (1.09); HL 0.78-0.88 (0.84); CI 0.75-0.79 (0.77); PW 0.50-0.60 (0.55); MW 0.70-0.86 (0.79); AWV 1.33-1.54 (1.47); TL 2.58-3.05 (2.89);

**Discussion:** Holotype (Male #101) for *G. dissimilis bankiva* is in the Piaget Collection of the BMNH.; Neotype (female) and neoparatypes (7 males, 5 females) of *G. dissimilis* designated as such by Clay (1940: 65) are also in the collection of the BMNH (Hopkins and Clay 1952: 151). This species is an introduction inot Africa likely on *Gallus gallus*.

## DISCUSSION

Many of the features Tendeiro used to diagnose species are either difficult to discern or apparently convergent including the crop teeth (his scaly gular plates) and coloration (see discussion Group H). The highly variable appearance of the antennae, sexual dimorphism thereof, and Male genitalia, combined with a reliance on host associations has led to the description of numerous taxa. Although "niche-determined" morphological type designation has no formal taxonomic standing or significance - they often contain distantly related forms (Cite, but also see Johnson *et al*. 2012).

Tendeiro described many new genera and species often times from very small numbers of specimens. Given the lack of material and the controversy surrounding the generic status of many of these species. For the African species Tendeiro (dates) contributed much in a series of works largely following Eichler and Kéler's classification; but the generic status of many of these taxa are questionable (Ledger 1980) in addition much of Tendeiro's work was published in Portuguese or French, making it largely inaccessible to most workers. Many of the features Tendeiro used to diagnose species are either difficult to discern or apparently convergent including the crop teeth (his scaly gular plates) and coloration (see discussion Group H). The highly variable appearance of the antennae, sexual dimorphism thereof, and Male genitalia, combined with a reliance on host associations has led to the description of numerous taxa….

Some of Tendeiro's species were described from small series and I have not yet seen them, others have deteriorated to the point that they are useless for comparison and all but destroyed. Sometimes characters are obscured by debris on the slide….

I disagree with Mey 2003 that … *I do not think it a good strategy when Phthiraptera taxa that are not (or only nearly) identical in the details of their biometry, form , or structure are thrown together while the available category of the subspecies remains unused (p. 131)*

"*As is the case in the columbiform Goniodidae many of the well-defined genera appear to grade into each other in light of new species descriptions. This is a recurring theme in the literature on goniodidae and more broadly the Ischnocera, which forced many authorities (Hopkins and Clay 1952) to accept only the broadest possible generic definitions. Ledger (1980) provides more specific account of some of these problems faced by taxonomists working on the Goniodidae, and it seems likely that further work on their phylogeny will require an extensive review of the taxonomic status of most, if not all, goniodid taxa"* (Smith 2000: 91)

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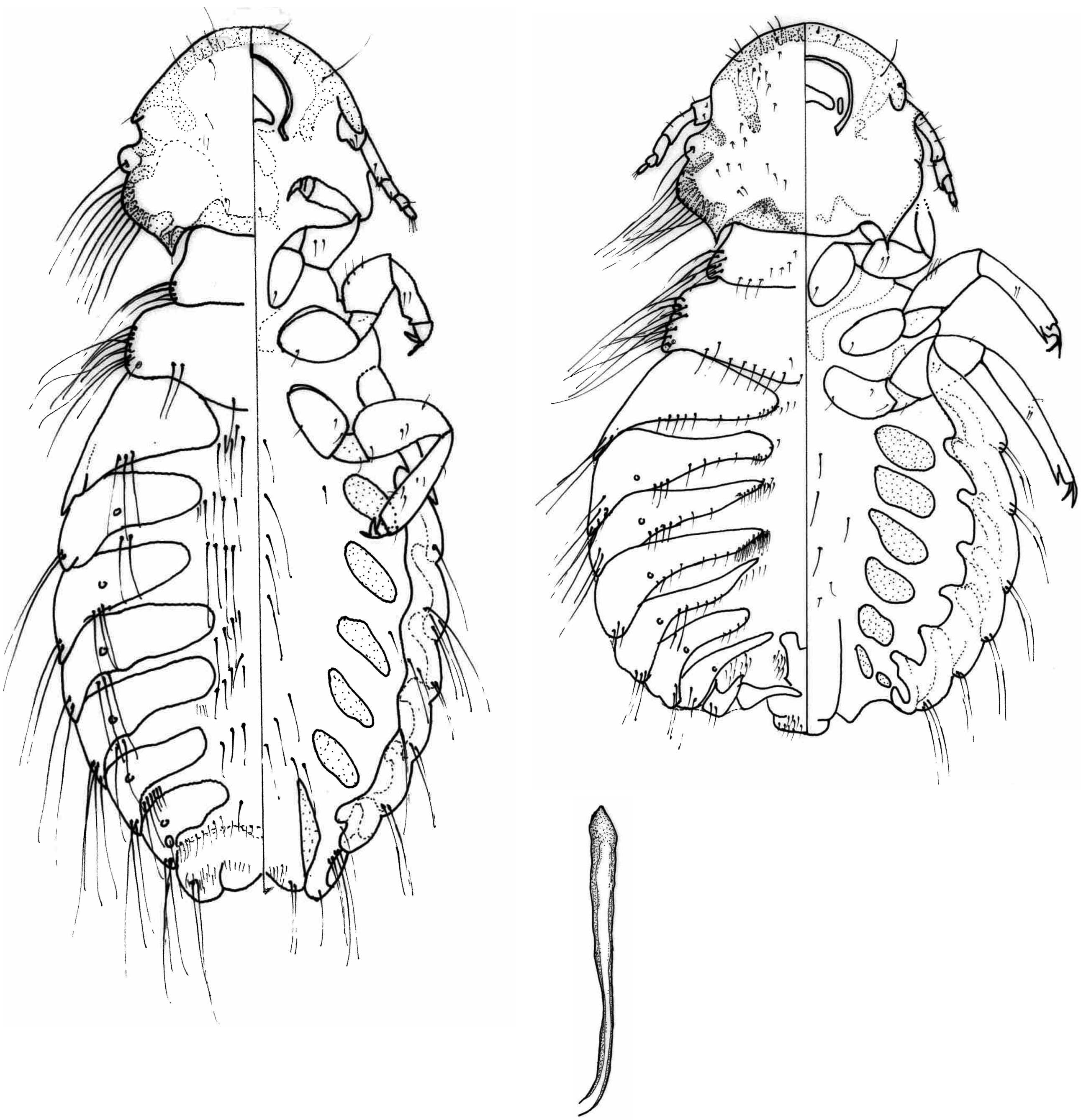
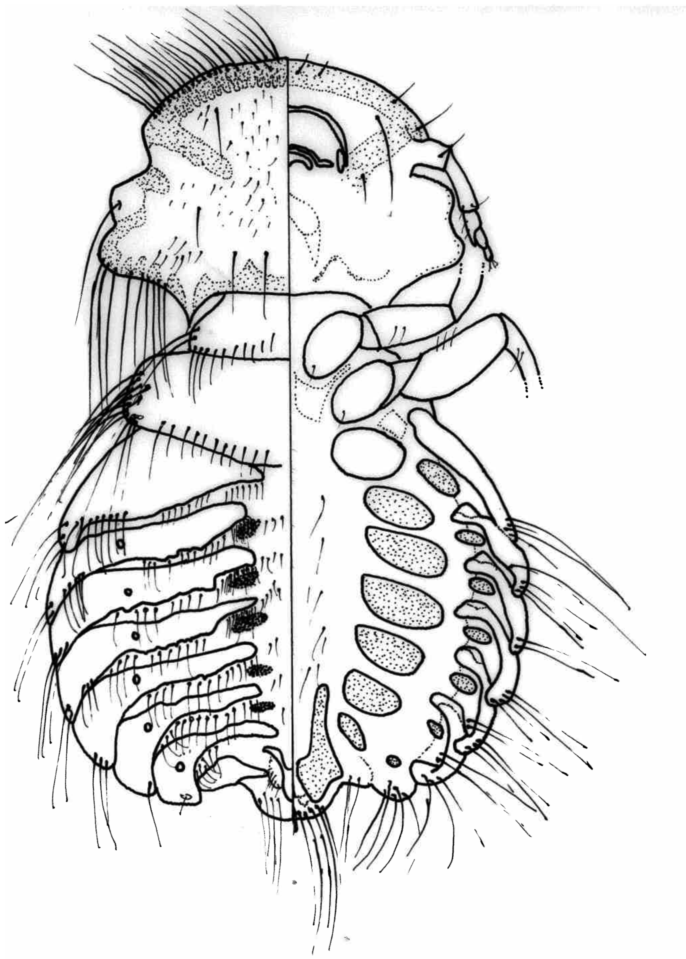
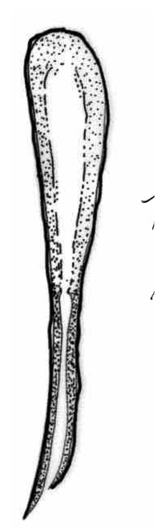
# FIGURES



**Figures 3.1-3.3.** *Goniodes wilsoni* 3.1 Female; 3.2 Male; 3.3 Male genitalia





**Figures 3.4-3.5.** *Goniodes numidae* 3.4 Male; 3.5 Male genitalia

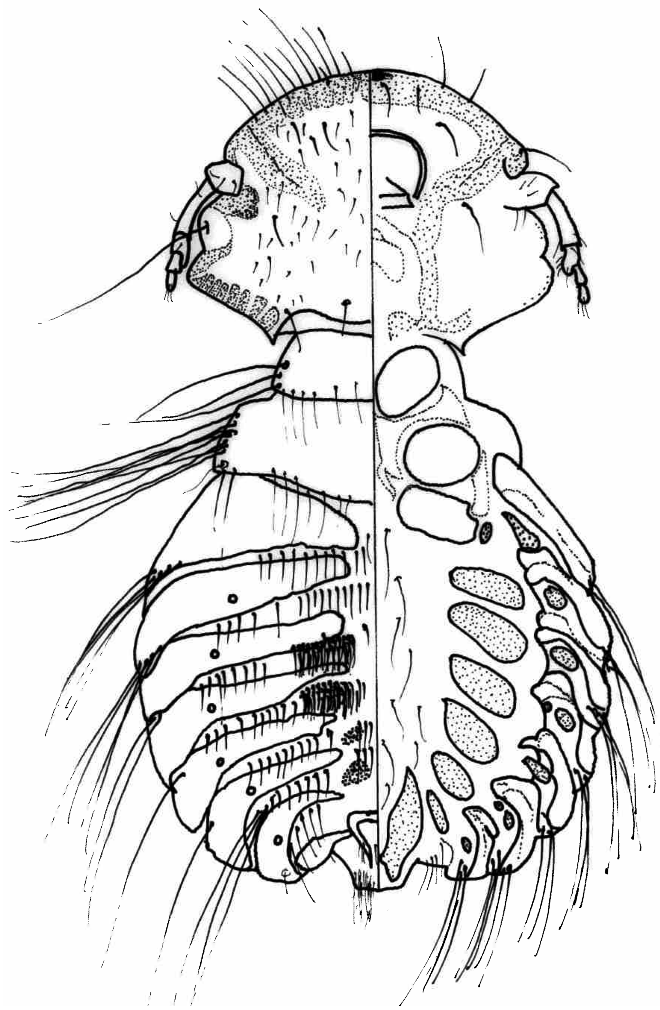
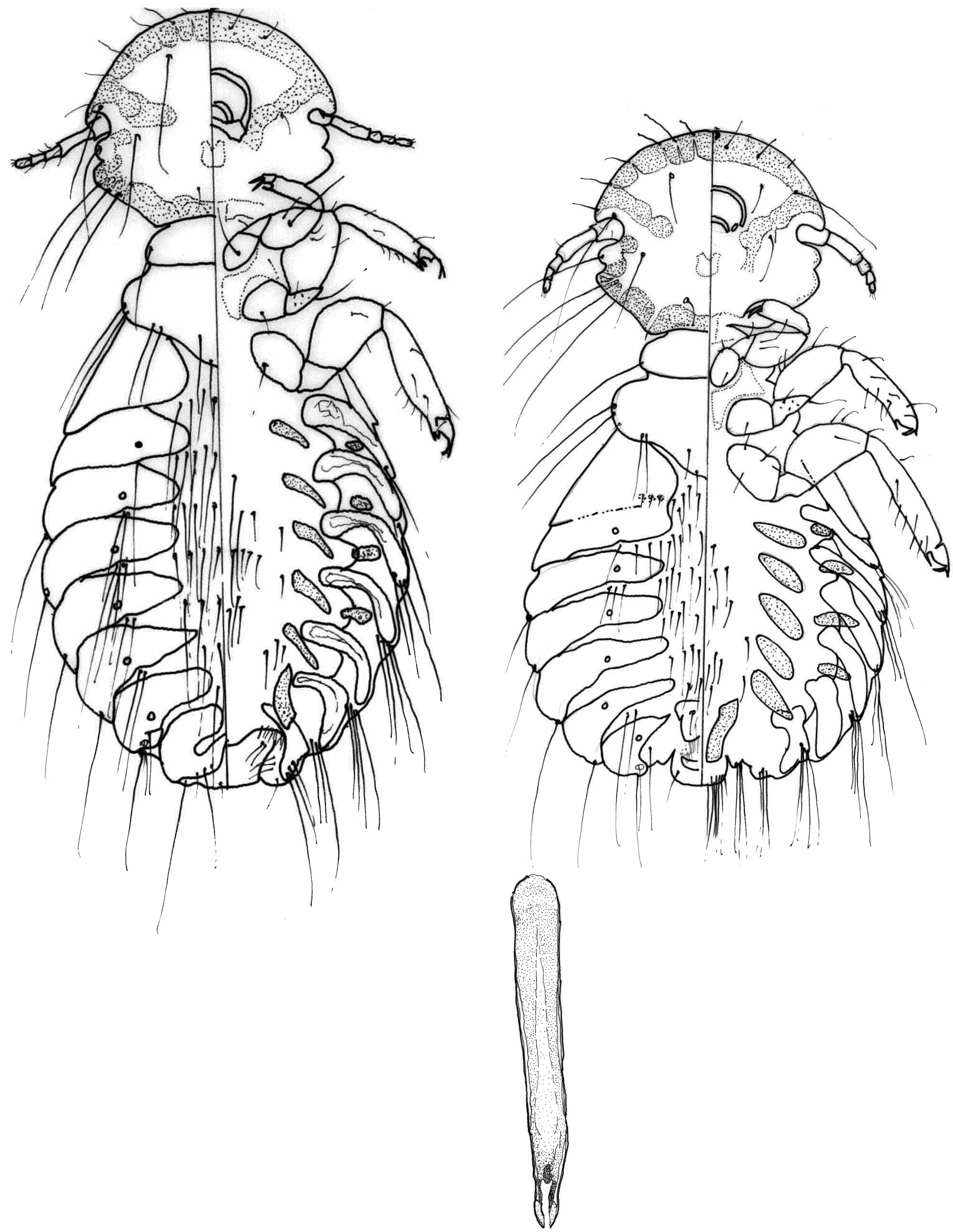


**Figure 3.6.** *Goniodes hopkinsi* Male



**Figures 3.7-3.9.** *Goniodes gigas* 3.7 Female; 3.8 Male; 3.9 Male genitalia

## CHAPTER 4:

## Type specimens of chewing lice (Insecta: Phthiraptera: Amblycera and Ischnocera) in the Royal Museum for Central Africa, Tervuren, Belgium.


### ABSTRACT

In keeping with the recommendations of the International Code of Zoological Nomenclature I present the first published listing of the Phthirapteran (Insecta) type material housed in the Royal Museum for Central Africa in Tervuren, Belgium. This annotated catalogue lists the primary and secondary types of 63 chewing lice taxa from the suborder Amblycera (families Menoponidae and Laemobothriidae) and Ischnocera (families Philopteridae and Trichodectidae), and includes data for 39 holotypes, 488 paratypes (including 23 allotypes), 7 metatypes, and 34 "type" specimens of unknown status. Taxa are listed alphabetically by specific epithet, original generic assignment, and (in parentheses) the current family designation. Also included are the author, year of description, and original citation, followed by the type, original collection and host data, any relevant taxonomic remarks, and its current taxonomic status.


### INTRODUCTION

The Royal Museum for Central Africa (RMCA) located in Tervuren, Belgium is an important African research institution despite a historic association with King Leopold II and colonialism (see Hochschild 1998; Vangroenweghe 1985; and Vellut 2005). With its research focus primarily on Africa the RMCA has especially strong holdings from central Africa assembled during the colonial periods of the Congo Free State (1885 to 1908) and the Belgian Congo (1908 to 1960), but contains materials from nearly every African country and island. The zoology collection alone contains approximately 10 million specimens of which nearly 60% are insects (RMCA 2009a, b). The phthirapteran collection contains type material from 62 species of Phthiraptera designated in taxonomic studies, the majority (52 species) described by João Leal da Silva Tendeiro (1916-1991). Lesser numbers result from the work of Stefan von Kéler (1897-1967) – 4 species, Theresa Rachael Clay (1915-1995) – 2 species, Günter Timmerman (1908-1979) – 2 species, Fábio Leche Werneck (1894-1961) – 1 species, and P. L. G. Benoit – 1 species). Taxa were described from material largely collected by various expeditions and "missions" in the Exploration des Parc Nationaux program of the Institut des Parcs Nationaux du Congo (De Coninck, pers. comm.).

Type specimens are the foundational units of zoological taxonomy. They represent the standards of reference that provide objectivity in nomenclature and are of great scientific value (Mayr and Ashlock 1991, Winston 1999). As such the International Commission in Zoological Nomenclature (1999) strongly recommends that lists of such type material be published (ICZN Recommendation 72F.4). The purpose of this paper is to provide such a listing of type material of the phthirapteran suborders Amblycera and Ischnocera, commonly known as the chewing lice (Johnson and Clayton 2003), currently in the collection of the RMCA. It is also another contribution to the growing list of similar Phthirapteran type catalogs (Abrahamovich *et al.,* 2006; Cardozo-de-Almeida *et al.*, 2003; Durden and Adams 2005; Tenorio 1979, Valim 2009) which in combination with the recent world checklist for chewing lice (Price *et al.*, 2003) plays an important role in ongoing efforts to better understand the nomenclature, taxonomy, and systematics of this historically neglected insect order (Mey 2003, Price *et al*., 2003).

## MATERIALS & METHODS:

For consistency, ease of taxon location, and indexing all type categories of Phthiraptera held in the RMCA are listed in alphabetical order. In addition to holotypes, information on paratypes, allotypes, and some material with no legal standing are included following Lavett Smith and Buerkli (1969) interpretation of the code as implemented by Valim (2009). I strongly agree with Lavett Smith and Buerkli (1969) that the practical value of including such materials "transcends the legalistic aspects of taxonomy" (p. 249). Nomenclature and classification for the chewing louse follow that presented in the recent world checklist by Price *et al.,* 2003. Host names and classification were updated following Dickinson (2003) for birds and Wilson and Reeder (2005) for mammals.

The following data are provided for each taxon following the annotation format used by Adams & Lewis (1995) and Durden & Adams (2005). The entry for each taxon starts with the specific epithet in bold followed by the original generic assignment (in bold) and current family (in parenthesis and regular font) on the same line. Subsequent sections are all indented starting with "**Description:**" which includes a complete citation of the original description i.e. Author, year, Title, *Journal* Volume (number): Pages, Illustrations, Photos). The next section lists the types in the collection including the "**Type category:**" Total # of lice (Location in collection) ex *Host* (Author) (Host Order: Host Family) – Host Common Name: COUNTRY: # of lice male, female, nymph

(Place/City, Date, Coll.), and is repeated as necessary. One or two additional sections "**Remarks:**" and "**Current Status:**" follow for some of the taxa. The former includes any pertinent, unusual, or notable information and/or inconsistencies related to the material, nomenclature, and literature associated with that specific taxon, whereas the latter includes the current status of the taxon in Price *et al*., (2003).

<u>Annotation Format</u>

***specific epithet, Generic assignment*** **(Family designation)**

**Description:** Author. (Year) Title. *Journal* Vol(#): pp; fig; photos.

**Category of type:** Total # of lice (Location in collection) ex *Host* (Author) (Host Order: Host Family) – Host Common Name: COUNTRY: # of lice male, female, nymph (Place/City, Date, Coll.); repeat if necessary…

**Current Status:** From Price *et al.,* 2003.

**Remarks:** Only for unusual or notable taxonomic situations.

## TYPE SPECIMENS WITH DISCUSSION

***aethiopicum, Coloceras*** **(Family Philopteridae)**

**Description:** Tendeiro, J. (1973) Estudos sobre os Goniodídeos (Mallophaga, Ischnocera) dos Columbiformes. XIV– Género *Coloceras* Taschenberg, 1882. *Revista de Ciências Veterinárias, Universidade de Lourenço Marques (Série A)* 6: 310; fig. 23; photos 64-72, 184, 210.

**Paratypes:** 7 specimens (Tervuren Box 24 Slide # 10-16) ex *Turtur afer afer* (L. 1766) (Columbiformes: Columbidae)—Blue-spotted Wood Dove: TOGO: 1

female, 1 nymph (Badou, 16 July 1969, Coll: Mission W. Verheyen); 1 female (Niantougou, 24 July 1969, Coll: Mission W. Verheyen); 1 nymph (Kolekope, 30 August 1969, Coll: Mission W. Verheyen); 1 nymph (Tetetou, 3 September 1969, Coll: Mission W. Verheyen); 1 male, 1 female (Togoville, 13 September 1969, Coll: Mission W. Verheyen). 6 specimens (Tervuren Box 24 Slide # 17-22) ex *Turtur abyssinicus delicatulus* (= *delicatula*), currently *Turtur abyssinicus* (Sharpe, 1902) (Columbiformes: Columbidae)—Black-billed Wood Dove: TOGO: 1 female, 1 nymph (Niantougou, 22 July 1969, Coll: Mission W. Verheyen); 1 female, 1 nymph (Togoville, 14 September 1969, Coll: F. Puylaert); 2 females (Aledjo, 1 December 1969, Coll: Mission W. Verheyen).

**Current Status:** Valid – Price *et al*. (2003: 163).

***afra, Bonomiella* (Family Menoponidae)**

**Description:** Tendeiro, J. (1980) Contributions a l'etude des Mallophages des Columbiformes Africains. *Musée Royal de l'Afrique Centrale (Tervuren), Sciences Zoologiques* 232: 48; fig. 12; photos 9-11.

**Holotype**: 1 specimen (Tervuren Box 24 Slide # 5) ex *Turtur afer afer* (L. 1766) (Columbiformes: Columbidae)—Blue-spotted Wood Dove: TOGO: 1 female (Togoville, 13 September 1969, Coll: Mission W. Verheyen).

**Current Status:** Valid – Price *et al*. (2003: 93).

***afra, Clayia* (Family Menoponidae)**

**Description:** Tendeiro, J., L. F. Mendes, and O. Baessa de Aguiar. (1994) Etudes sur les Mallophages (Insecta, Mallophaga) des Galliformes de l'Afrique Centrale. III. Nouvelles données sur les Amblycera et description de 12 espèces nouvelles de genre *Clayia* Hopkins, 1941. *Estudos, Ensaios e Documentos. Instituto de Investigação Científica Tropical* 159: 17; figs. 1-4.

**Holotype:** 1 specimen (Menoponidae Box 5 Slide # 1) ex *Pternistis afer cranchii*, currently *Francolinus afer cranchii* (Leach, 1818) (Galliformes: Phasianidae)— Cranch's Spurfowl: CONGO: 1 male (Ndwa, no date, Coll: Ngawe). **Paratypes**: 1 specimen (Menoponidae Box 5 Slide # 2) ex *Pternistis afer cranchii*, currently *Francolinus afer cranchii* (Leach, 1818) (Galliformes: Phasianidae)—Cranch's Spurfowl: CONGO: 1 female, designated allotype (Ndwa, no date, Coll: Ngawe). 34 specimens (Menoponidae Slide Box 5) ex *Pternistis afer*, currently *Francolinus afer* (Müller, 1776) (Galliformes: Phasianidae)—Red-necked Spurfowl: CONGO: 1 male (Bas-Congo, Mansadi June 1937, Coll: E. Dartevelle); 4 nymphs (Kunungu, May 1937 Coll: Dr. H. Schouteden); 1 nymph (Prés Teuka, Kando, 3 August 1937, Coll: G. F. de Witte); 1 male (Keseki, 1939, Coll: Nkele); 5 males, 2 females (Katombe, 9 December 1949, Coll: Van Assche); 1 male (Kasaji, Kivu, 24 January 1950, Coll: Fisher); 1 female (Kasaji, Kivu, 2 March 1950, Coll: Fisher); 2 males, 3 females (Kasaji, Kivu, 17 April 1950, Coll: Fisher); 1 male (Lusambo, 30 June 1950, Coll: Windmolders); 4 males, 1 female, 1 nymph (Prés Boma, Lokandu, October 1954, Coll: Mesmaechers); 1 male, 1 female (Ndwa, no date, Coll: Ngawe); 1 female, 1 nymph (Kunungu, no date, Coll: Dr. H. Schouteden); 2 females (Boma, no date, Coll: Dr. Dartevelle). 11 specimens (Menoponidae Slide Box 5) ex *Pternitis afer hartesti*, currently *Francolinus afer harterti* (Reichenow, 1909) (Galliformes: Phasianidae)— Usumbara Vemiculated Red-throated Francolin: BURUNDI: 2 females (Usumbara, 29 January 1926, Coll: H. Schouteden); 1 male (Usumbara, February 1926, Coll: H. Schouteden); 1 male (Usumbara, December 1926, Coll: H. Schouteden); CONGO: 2 males, 1 nymph (Kivu, Mufua, 11 April 1951, Coll: Prigogine); 3 males, 1 nymph (Uvira, no date, Coll: Pawels). 21 specimens (Menoponidae Slide Box 5) ex *Pternistis afer nyanzae*, currently *Francolinus afer cranchii* (Leach, 1818) (Galliformes: Phasianidae)—Cranch's Spurfowl: RUANDA: 5 males, 2 females, 4 nymphs (Astrida, February 1949, Coll: A. Fain); 4 males, 1 female, 2 nymphs (Nsinda, 8 May 1950, Coll: A. Lestrade); 1 male, 1 nymph (Buggesera, 5 October 1953, Coll: A. Lestrade); 1 female (Astrida, no date, Coll: Aureliaon).

**Current Status:** Valid – Price *et al*. (2003: 96).

***africana, Rallicola (Rallicola)*** **(Family Philopteridae)**

**Description:** Timmermann, G. (1958) Zwei neue Federlinge aus den Gattungen *Rallicola* und *Quadraceps*. *Bonner Zoologische Beiträge* 8 (3/4): 304; figs. 1, 1a.

**Paratypes:** 3 specimens (Philopteridae Box 4 Slide # 1-3) ex *Actophilornis africanus* (Gmelin, 1789) (Charadriiformes: Jacanidae)—African Jacana: BELGIUM CONGO: 3 unsexed specimens (Upemba, Mabwe lac, alt. 585m., 30 July 1947, Coll: G.F. de Witte).

**Current Status:** Valid – Price *et al*. (2003: 228).

***afropavo*, *Amyrsidea (Argimenopon)*** **(Family Menoponidae)**

**Description:** Benoit, P.L.G. (1962) Les Mallophages du paon congolais (*Afropavo congensis* Chapin). *Bulletins de la Société Royal de Zoologie d'Anvers* 26: 20; figs. 7-11.

**Holotype:** 1 specimen (Menoponidae Box 1 Slide # 1) ex *Afropavo congensis* Chapin, 1936 (Galliformes: Phasianidae)—Congo Peafowl: BELGIUM: 1 male (Jardin Zoologique d'Anvers, 13 October 1961, Coll: P.L.G. Benoit). **Paratypes**: 1 specimen (Menoponidae Box 1 Slide # 2) ex *Afropavo congensis* Chapin, 1936 (Galliformes: Phasianidae)—Congo Peafowl: BELGIUM: 1 female, designated allotype (Jardin Zoologique d'Anvers, 13 October 1961, Coll: P.L.G. Benoit). 36 specimens (Menoponidae Box 1 Slide # 3-31) ex *Afropavo congensis* Chapin, 1936 (Galliformes: Phasianidae)—Congo Peafowl: BELGIUM: 4 male, 6 female (Anvers Zoo, 13 October 1961, Coll: P.L.G. Benoit); 3 males, 11 females (Anvers Zoo, 4 August 1961, Coll: P.L.G. Benoit); BELGIUM CONGO: 4 unsexed (Lusambo, Inkongo, 22 April 1909, Coll: Rev. Wilson); 2 male, 1 female, 1 nymph (Tshuapa, Ikela, 26 October 1955, Coll: P. Lootens); 4 unsexed (Tshuapa, 10 May 1909, Coll: R. P. Lootens).

**Current Status:** Valid – Price *et al*. (2003: 86).

**Remarks:** Benoit (p. 20) gives collection data as, BELGIUM: Jardin Zoologique d'Anvers, 4 August 1961, Coll: P.L.G. Benoit. However the date on the actual slide is different: BELGIUM: Jardin Zoologique d'Anvers (Anvers Zoo), 13 October 1961, Coll: P.L.G. Benoit.

***alopochen, Trinoton*** **(Family Menoponidae)**

**Description:** Tendeiro, J. (1960). Etudes sur les Mallophages africains. *Junta de Investigações do Ultramar, Estudos, Ensaios e Documentos* 65 (1959): 73; photos 23, 24, 27, 29.

**Paratypes:** 2 specimens (Menoponidae Box 3 Slide # 82-83) ex *Alopochen aegyptiacus* (L. 1766) (Anseriformes: Anatidae)—Egyptian Goose: BELGIUM CONGO: 1 unsexed (Ganza, alt. 860 m., 30 May 1949, Coll. G. F. de Witte - no. 2645a); 1 female (Kaswabilenga, alt. 700 m., 30 October 1947, Coll: G.F. de Witte - no. 950a).

**Current Status:** Valid – Price *et al*. (2003: 138).

***ampullacea, Splendoroffula*** **(Family Philopteridae)**

**Description**: Kéler, S. v. (1955) Mallophaga. Zwei neue Arten der Gattung *Splendoroffula* Clay u. Meinertzhagen. *Annales Musée Royal de Congo Belge, Tervuren, Sciences Zoologiques* 36: 422; figs. 9, 10, 13; photos "Tafel II" 1, 6, 7.

**Paratypes**: 11 specimens (Philopteridae Box 4 Slide # 66-74) ex *Musophaga violacea rossae* currently *Musophaga rossae* Gould, 1852 (Musophagiformes: Musophagidae)—Ross's Turaco: BELGIUM CONGO: 2 females (R. Mubale, alt. 1480 m., 8 May 1947, Coll: G.F. de Witte - P.N.U. 382a: Host #413); 3m, 1f (R. Mubale, alt. 1480 m., 10 May 1947, Coll: G.F. de Witte - P.N.U. 378a: Host #444); 1m, 1f (R. Mubale, alt. 1480 m., 14 May 1947, Coll: G.F. de Witte -

P.N.U. no. 400a: Host #475); 3f (Gorges de la Pelenge, alt. 1150 m., 26 May 1947, Coll: G.F. de Witte - P.N.U. no. 552a: Host #553).

**Current Status:** Valid – Price *et al*. (2003: 238).

**Remarks:** Kéler (p. 422) assigns only subspecific status and later (Kéler, 1958) treats this taxa as both a species (p. 301) and a subspecies of *S. subtilis* (p. 311).

***angolensis, Colpocephalum*** **(Family Menoponidae)**

**Description:** Tendeiro, J. 1964. Mallophaga. *Ann. Mus. Roy. l' Afr. Cent. (Tervuren) Ser. Zool*. 132: 171, fig. (2-3) photos 1-3.

**Paratypes:** 102 specimens (Menoponidae 6 # Slide 7-36) ex *Gypohierax angolensis* (Gmelin, 1788) (Falconiformes: Accipitridae)—Palm-nut Vulture: CONGO: 52 males, 42 females, 8 nymphs (Lualaba, Kasongo, Maniema, November 1959, Coll: P.L.G. Benoit no.'s 236, 237, 240).

**Current Status:** Junior synonym of *Colpocephalum angolensis* Price and Beer, 1963 (Price and Emerson, 1967) accepted by Price *et al*. (2003: 97).

***anisorhamphos, Saemundssonia (Saemundssonia)*** **(Family Philopteridae)**

**Description:** Timmermann. G. (1951) Njungar um lúsaættkvíslina Sæmundssonia Tim. *Sérprentum úr Náttúrufræoingnum* 3(21): 142; fig. 2.

**Holotype**: 1 specimen (Philopteridae Box 4 Slide # 17) ex *Rynchops flavirostris* Vieillot, 1816 (Charadriiformes: Laridae)—African Skimmer: BELGIUM CONGO: 1 male (Mateba, April 1937, Coll: Dartevelle). **Paratypes**: 1 specimen (Philopteridae Box 4 Slide # 17) ex *Rynchops flavirostris* Vieillot, 1816

(Charadriiformes: Laridae)—African Skimmer, BELGIUM CONGO: 1 female, designated allotype (Mateba, April 1937, Coll: Dartevelle). 7 specimens (Philopteridae Box 4 Slide # 18) ex *Rynchops flavirostris* Vieillot, 1816 (Charadriiformes: Laridae)—African Skimmer: BELGIUM CONGO: 4 males 3 females (Mateba, April 1937, Coll: Dartevelle).

**Current Status:** Valid – Price *et al*. (2003: 232).

***balati, Mulcticola*** **(Family Philopteridae)**

**Description**: Tendeiro, J. (1962) Études sur les Mallophages. Observations aditionelles sur le genre *Multicola* (Ischnocera, Philopteridae), avec la description de quelques nouvelles espèces. *Do Boletim Cultural da Guiné Portuguesa* 17: 352; fig. 2; photos 5-8.

**Paratypes:** 3 specimens (Philopteridae Box 3 Slide #3-5) ex *Scotornis fossii fossii*, currently *Camprimulgus fosii fosii* Hartlaub, 1857 (Caprimulgiformes: Caprimulgidae)—Square-tailed Nightjar: CONGO: 3 females (Lualaba, Kasongo, Maniema, November 1959, Coll: P.L.G. Benoit - no. 54).

**Current Status:** Valid – Price *et al*. (2003: 198).

**Remarks:** Originally described by Tendeiro (1960: 188) as *Multicola* sp. 4 from *Scotornis fossii clarus*, which is currently *Camprimulgus clarus* Reichenow, 1892.

***basilewskyi basilewskyi, Sturnidoecus*** **(Family Philopteridae)**

**Description:** Tendeiro, J. (1964). Mallophaga. *Annales Musée Royal de l'Afrique Centrale (Tervuren), Series Zoologiques* 132: 194, fig. 11-14; photos 21-24.

**Holotype:** 1 specimen (Philopteridae Box 6 Slide # 51) ex *Textor cucullatus* subsp. currently *Ploceus cucullatus* (Müller, 1776) (Passeriformes: Ploceidae)—Village Weaver: CONGO: 1 male and allotype female (Maniema, Kasongo, Lualaba, November 1959, Coll: P.L. Benoit - no. 231). **Paratypes:** 1 specimen (Philopteridae Box 6 Slide # 51) ex *Textor cucullatus* subsp. currently *Ploceus cucullatus* (Müller, 1776) (Passeriformes: Ploceidae)—Village Weaver: CONGO: 1 female, designated allotype (Lualaba, Kasongo, Maniema, November 1959, Coll: P.L. Benoit - no. 231). 26 specimens (Philopteridae Box 6 Slide # 52-62) ex *Textor cucullatus* subsp. currently *Ploceus cucullatus* (Müller, 1776) (Passeriformes: Ploceidae)—Village Weaver: CONGO: 1 male, 7 female, 18 nymphs (Kasongo, November 1959, Coll: P.L.G. Benoit).

**Current Status**: Considered a junior synonym of *S. minor* Tendeiro, 1963 by Price *et al*. (2003: 242).

**Remarks:** Tendeiro (1963: 17) publishes the names *Sturnidoecus basilewskyi basilewskyi* and *Sturnidoecus basilewskyi minor*. The former is "*en publication*" and includes no formal description, only type specimens and photos, whereas the later is formally described. The specimens above correspond exactly to the type series published for *Sturnidoecus basilewskyi basilewskyi* (Tendeiro, 1963). This description (Tendeiro, 1964: 194) includes 3 extra specimens.

### ***benoiti, Coloceras*** **(Family Philopteridae)**

**Description:** Tendeiro, J. (1973) Estudos sobre os Goniodídeos (Mallophaga, Ischnocera) dos Columbiformes. XIV–Género *Coloceras* Taschenberg, 1882. *Revista de Ciências Veterinárias, Universidade de Lourenço Marques (Série A)* 6: 451; figs. 64, 70; photos 168-172, 246.

**Paratype:** 1 specimen (Tervuren Box 24 Slide # 31) ex *Turturoena iriditorques*, currently *Columba iriditorques* Cassin, 1856 (Columbiformes: Columbidae)—Western Bronze-naped Pigeon: CONGO: 1 female (Bakalokala, 18 November 1959, Coll: Nkele (no. 103441)).

**Current Status:** Valid – Price *et al*. (2003: 163).

***brazi, Pseudomenopon*** **(Family Menoponidae).**

**Description:** Tendeiro. J. (1965). Etudes sur les Mallophages. Observations sur le genre *Pseudomenopon* Mjöberg, 1910, avec description de six espèces et une sous-espèces nouvelles. *Revista dos Estudos Gerais Universitários de Moçambique (Série 4)* 2: 23; photos 6, 7, 24, 34, 45, 54.

**Holotype:** 1 specimen (Tervuren Box 23 Slide # 29) ex *Podica senegalensis petersii* Hartlaub, 1852 (Gruiformes: Heliornitidae)—African Finfoot: BELGIUM CONGO: 1 male (P.N.U., Ganza (alt. 860 m.), 13 June 1949, Coll: G.F. de Witte no. 2680a, host # 5143). **Paratypes:** 14 specimens Tervuren Box 23 Slide # 30-43) ex *Podica senegalensis petersii* Hartlaub, 1852 (Gruiformes: Heliornitidae)— Finfoot: BELGIUM CONGO: 4 males, 4 females (1 designated allotype), 6 nymphs (P.N.U., Ganza (alt. 860 m.), 13 June 1949, Coll: G.F. de Witte).

**Current Status:** Considered a junior synonym of *P. pilosum* (Scopoli, 1763) by Price (1974: 74) and accepted by Price *et al*. (2003: 135).

***carrikeri, Columbicola*** **(Family Philopteridae)**

**Description:** Tendeiro, J. (1965) Estudos sobre Malófagos. Revisao monográfica do género *Columbicola* Ewing (Ischnocera, Philopteridae). *Memórias da Junta de Investigações do Ultramar (Série 2)* 32(1962): 238; figs. 74-78; photos 99-104, 210; map 6, 2.

**Paratypes:** 3 specimens (Philopteridae Box 1) ex *Turtur chalcospilos erlangeri* currently *Turtur chalcospilos* (Wagler, 1827) (Columbiformes: Columbidae)—Emerald-spotted Wood-Dove: BELGIUM CONGO: 1 male, 2 female, (P.N.U., Kaziba, alt. 1140 m., 7 February 1948, Coll: G.F. de Witte – no. 1262a Bird no. 2326).

**Current Status:** Valid – Price *et al*. (2003: 166).

***clappertoni, Clayia*** **(Family Menoponidae)**

**Description:** Tendeiro, J., L. F. Mendes, and O. Baessa de Aguiar. (1994) Etudes sur les Mallophages (Insecta, Mallophaga) des Galliformes de l'Afrique Centrale. III. Nouvelles données sur les Amblycera et description de 12 espèces nouvelles de genre *Clayia* Hopkins, 1941. *Estudos, Ensaios e Documentos. Instituto de Investigação Científica Tropical* 159: 24; figs. 5-7.

**Holotype:** 1 specimen (Tervuren Box 20 Slide # 93) ex *Francolinus clappertoni* Children & Vigors, 1826 (Galliformes: Phasianidae)—Clapperton's Francolin: ETHIOPIE: 1 male (Riv. Robi, 21 December 1941, Coll: Debrasina).

**Current Status:** Valid – Price *et al*. (2003: 96).

***congensis, Clayia*** **(Family Menoponidae)**

**Description:** Tendeiro, J., L. F. Mendes, and O. Baessa de Aguiar. (1994) Etudes sur les Mallophages (Insecta, Mallophaga) des Galliformes de l'Afrique Centrale. III. Nouvelles données sur les Amblycera et description de 12 espèces nouvelles de genre *Clayia* Hopkins, 1941. *Estudos, Ensaios e Documentos. Instituto de Investigação Científica Tropical* 159: 26; figs. 8-9.

**Holotype:** 1 specimen (Tervuren Box 20 Slide #85) ex *Guttera plumifera schubotzi* Reichenow, 1912 (Galliformes: Numidae)—Schubotz's plummed Guineafowl: CONGO: 1 male (Lima, 20 December 1960, Coll: Lukala).

**Current Status:** Valid – Price *et al*. (2003: 96).

***galachrysiae, Quadraceps*** **(Family Philopteridae)**

**Description:** Tendeiro, J. (1964) Mallophaga. *Annales Musée Royal de l'Afrique Centrale (Tervuren), Sciences Zoologiques* 132: 201; fig. 18; photos 29, 31, 33.

**Holotype:** 1 specimen (Philopteridae Box 6 Slide # 24) ex *Galachrysia cinerea cinerea* currently *Glareola cinerea cinerea* Fraser, 1843 (Charadriiformes: Glareolidae)—Grey Pratincole: CONGO: 1 male (Lualaba, Kasongo, Maniema, 15 November 1959, Coll: P.L.G. Benoit - no. 56).

**Current Status:** Valid – Price *et al*. (2003: 224).

***gambensis, Trinoton*** **(Family Menoponidae)**

**Description:** Tendeiro, J. (1958) Etudes sur les Mallophages. Quelques Mallophages du Musée de Dundo (Angola). *Publications Culturais Companhia de Diamantes de Angola* 48: 96; figs. 10-13; photos 11-12.

**Holotype:** 1 specimen (Menoponidae Box 3 Slide # 86-87) ex *Plectropterus gambensis* (L., 1766) (Anseriformes: Anatidae)—Spur-winged Goose: BELGIUM CONGO: 1 male (Upemba, Mabure Lac, alt. 585 m., 6 August 1947, Coll: G.F. de Witte no. 702a (host no 1135)). **Paratypes:** 1 specimen (Menoponidae Box 3 Slide # 87) ex *Plectropterus gambensis* (L., 1766) (Anseriformes: Anatidae)—Spur-winged Goose: BELGIUM CONGO: 1 female, designated allotype (Upemba, Mabure Lac, alt. 585 m., 6 August 1947, Coll: G.F. de Witte no. 702a (Host no 1135)). 2 specimens (Menoponidae Box 3 Slide # 88-89) ex *Plectropterus gambensis* (L., 1766) (Anseriformes: Anatidae)—Spur-winged Goose: BELGIUM CONGO: 1 male 1 female (Upemba, Mabure Lac, (alt. 585 m.), 6 August 1947, Coll: G.F. de Witte no. 702a (Host no. 1135)).

**Current Status:** Valid – Price *et al*. (2003: 138).

**Remarks:** Tendeiro (1958: 96) states that the holotype, allotype, and paratypes should be British Museum of Natural History, London and the Centre de Zoologie de la Junta de Investigações do Ultramar, Lisbon, not the RMCA, Tervuren. In addition only 4 of the 5 specimens mentioned were found.

***grandiculus*, *Laemobothrion (Laemobothrion)*** **(Family Laemobothriidae)**

**Description:** Tendeiro, J. (1964). Mallophaga. *Annales Musée Royal de l'Afrique Centrale (Tervuren), Series Zoologiques* 132: 185, fig. 9-10; photos 17-20.

**Paratypes:** 14 specimens (Laemobothrion Box Slide # 40-46) ex *Buteo rufofuscus* (Forster, J. R. 1798) (Falconiformes: Accipitridae)—Jackal Buzzard: CONGO: 1 male, 9 females, 4 nymphs (Maniema, Kasongo, Lualaba, November 1959, Coll: P.L.G. Benoit no. 206).

**Current Status:** Considered a junior synonym of *L. maximum* (Scopoli, 1763) by Price and Emerson (1967: 251) and accepted by Price *et al*. (2003: 80).

***guineensis stactolaemae*, *Penenirmus*** **(Family Philopteridae)**

**Description:** Tendeiro, J. (1962) Etudes sur les Mallophages. Observations sur des Ischnocera africains, avec description de 12 espèces and 2 sous-espèces nouvelles. *Do Boletim Cultural da Guiné Portuguesa* 17: 699; photos 17-20.

**Holotype:** 1 specimen (Philopteridae Box 3 Slide # 51) ex *Stactolaema anchietae katangae* (Vincent, 1934) (Piciformes: Ramphastidae)—Anchieta's Barbet: CONGO: 1 male (Parc National de l'Upemba, Kenia, alt. 1700m., 10 March 1948, Coll: G.F. de Witte - no. 1408a. (Bird # 2598)). **Paratypes:** 1 specimen (Tervuren Box 23 Slide # 70) ex *Stactolaema anchietae katangae* (Vincent, 1934) (Piciformes: Rhamphastidae) —Anchieta's Barbet: BELGIUM CONGO: 1 female designated allotype Parc National de l'Upemba, Kenia (alt. 1700 m.), 10 March 1948, Coll: G.F. de Witte # 2598). 1 specimen (Tervuren Box 23 Slide # 69) ex *Stactolaema anchietae katangae* (Vincent, 1934) (Piciformes: Rhamphastidae)—

Anchieta's Barbet: BELGIUM CONGO: 1 female, (Parc National de l'Upemba, Mubale river (alt. 1480 m.), 14 May 1947, Coll: G.F. de Witte no. 384a # (bird #485)).

**Current Status:** *P. stactolaemae* Tendeiro, 1962. Elevated to species rank by Price *et al*. (2003: 211).

***gypohieracis, Craspedorrhynchus*** **(Family Philopteridae)**

**Description:** Tendeiro, J. (1955) Anotações parasitológicas. III. Duas novas espécies de Malófagos parasitas dos Falconiformes: *Craspedorrhynchus hopkinsi* n.sp., do peneireiro-cinzento, *Elanus caeruleus caeruleus* Desfontaines, *C. gypohieracis* n.sp., da aguia pesqueira *Gypohierax angolensis* (Gmelin), observacoes sobre o *C. spathulatus* (Giebel 1874). *Do Boletim Cultural da Guiné Portuguesa* 9: 803; figs. 6-8.

**Metatypes:** Metatypes designated by Tendeiro 1964: 193 (∴ collected from type locality by author & ∴ designated) 6 specimens (Philopteridae Box 2 Slide # 1-5) ex *Gypohierax angolensis* (Gmelin, 1788) (Falconiformes: Accipitridae)—Palm-nut Vulture: CONGO: 2 males, 2 females, 2 nymphs (Maniema, Kasongo, Lualaba, November 1959, Coll: P.L.G. Benoit # 238).

**Current Status:** Valid – Price *et al*. (2003: 169).

***kassaica, Clayia*** **(Family Menoponidae)**

**Description:** Tendeiro, J., L. F. Mendes, and O. Baessa de Aguiar. (1994) Etudes sur les Mallophages (Insecta, Mallophaga) des Galliformes de l'Afrique Centrale.

III. Nouvelles données sur les Amblycera et description de 12 espèces nouvelles de genre *Clayia* Hopkins, 1941. *Estudos, Ensaios e Documentos. Instituto de Investigação Científica Tropical* 159: 35; figs. 21-25.

**Holotype:** 1 specimen (Tervuren Box 20 Slide # 98) ex *Francolinus coqui kassaica* (= *Francolinus coqui kasaicus*) currently *Francolinus coqui coqui* (Smith, A. 1836) (Galliformes: Phasianidae)—Coqui Francolin: CONGO: 1 male (Kwango, Usambo, April 1953, Coll: Alvoet (host no. 53604)). **Paratypes:** 1 specimen (Tervuren Box 20 Slide # 98) ex *Francolinus coqui kassaica* (= *Francolinus coqui kasaicus*) currently *Francolinus coqui coqui* (Smith, A. 1836) (Galliformes: Phasianidae)—Coqui Francolin: CONGO: 1 female, designated allotype (Kwango, Usambo, April 1953, Coll: Alvoet (host no. 53604)).

**Current Status:** Valid – Price *et al*. (2003: 96).

***kenyensis, Clayia*** **(Family Menoponidae)**

**Description:** Tendeiro, J., L. F. Mendes, and O. Baessa de Aguiar. (1994) Etudes sur les Mallophages (Insecta, Mallophaga) des Galliformes de l'Afrique Centrale. III. Nouvelles données sur les Amblycera et description de 12 espèces nouvelles de genre *Clayia* Hopkins, 1941. *Estudos, Ensaios e Documentos. Instituto de Investigação Científica Tropical* 159: 39; figs. 26-30.

**Holotype:** 1 specimen (Tervuren Box 19 Slide # 53-58) ex *Pternistis leucoscopus infuscatus* currently *Francolinus leucoscepus* Gray, G. R. 1867 (Galliformes: Phasianidae)—Yellow-necked Spurfowl: KENYA: 1 male (Zinani River, 24 May 1913, Coll: Dr. Bayer). **Paratypes:** 5 specimens (Tervuren Box

19 Slide # 54-58) ex *Pternistis leucoscopus infuscatus* currently *Francolinus leucoscepus* Gray, 1867 (Galliformes: Phasianidae)—Yellow-necked Spurfowl: KENYA: 1 male, 3 females (one designated allotype), 1 nymph (Zinani River, 24 May 1913, Coll: Dr. Bayer).

**Current Status:** Valid – Price *et al*. (2003: 96).

***lootensi, Goniodes*** **(Family Philopteridae)**

**Description:** Tendeiro, J. (1960) Etudes sur les Mallophages africains. *Junta de Investigações do Ultramar, Estudos, Ensaios e Documentos* 65(1959): 107; figs. 7-9; photos 31, 33.

**Holotype:** 1 specimen (Philopteridae Box 5 Slide # 70) ex *Excalfactoria adansonii* currently *Coturnix adansonii* (Verreaux, J. & Verreaux, E. 1851) (Galliformes: Phasianidae)—Blue Quail: BELGIUM CONGO: 1male (Tshuape, 15 July 1957, Coll: R.P. Lootens no. 802A, (host no. 88264)). **Paratypes**: 19 specimens (Philopteridae Box 5 Slide # 70-78) ex *Excalfactoria adansonii* currently *Coturnix adansonii* (Verreaux & Verreaux, 1851) (Galliformes: Phasianidae)—Blue Quail: BELGIUM CONGO: 1 female (designated allotype), 18 unsexed (Tshuape, 15 July 1957, Coll: R.P. Lootens no. 802A, (host no. 88264)).

**Current Status:** Valid – Price *et al*. (2003: 185).

***lopesi, Sturnidoecus*** **(Family Philopteridae)**

**Description:** Tendeiro, J. (1963) Etudes sur les Mallophages. Observations sur des Ischnocera africains, avec description de 12 espèces et 2 sous-espèces nouvelles (suite et fin). *Do Boletim Cultural da Guiné Portuguesa* 18: 21; figs. 9-10; photos 28-30.

**Paratype:** 1 specimen (Tervuren Box 23 Slide # 77) ex *Textor cucullatus nigriceps* currently *Ploceus nigriceps* (Layard, E. L. 1867) (Passeriformes: Ploceidae)—Layard's Weaver: BELGIUM CONGO: 1 nymph (Parc National de l'Upemba, Mabwe, alt. 585 m., 4 January 1949, Coll: G.F. de Witte - no. 2189. (Bird number 4280)).

**Current Status:** Valid – Price *et al*. (2003: 243).

***lophocerus* subsp*, Chapinia* (Family Menoponidae)**

**Description:** Tendeiro, J. (1964). Mallophaga. *Annales Musée Royal de l'Afrique Centrale (Tervuren), Series Zoologiques* 132: 169.

**Paratypes:** 34 specimens (Menoponidae Box 11/3 Slide # 55-65) ex *Tockus fasciatus* (Shaw, 1811) (Bucertiformes: Bucerotidae)—African Pied Hornbill: CONGO: 11 males, 11 females, 12 nymphs (Maniema, Kasongo, Lualaba, 13 November 1959, Coll: P.L.G. Benoit no. 230).

**Current Status:** Considered valid as *Chapinia fasciati* Elbel, 1967 by Price *et al*. (2003: 94).

**Remarks:** This series designated paratypes for *Chapinia lophocerus* subsp (Elbel) by Tendeiro (1964: 169). Elbel later described *C. fasciati* (1967:12) but used only a single male specimen from Tendeiro's type series in his description. As such only that single specimen should be considered a valid paratype.

***machadoi, Eurytrichodectes*** **(Family Trichodectidae)**

**Description:** Werneck, F. L. (1958) Novo e inesperado tricodectídeo (Mallophaga). *Publications Culturais Companhia de Diamantes de Angola* 40: 143; figs. 1-7.

**Holotype:** 1 specimen (Trichodectidae Box Slide # 20) ex *Dendrohyrax (Heterohyrax) brucei bocagei* currently *Heterohyrax brucei* (Gray, 1886) (Hydracoidea: Procaviidae) (Shoshani, J. 2005: 87)—Yellow-spotted Hyrax: ANGOLA: 1 male (Distrito de Benguela, Cubal da Ganda, no date, Coll: Marco de Canavezes).

**Current Status:** Valid – Price *et al*. (2003: 256).

**Remarks:** According to Werneck (1958: 143) the RMCA collection also holds a female allotype.

***meinertzhageni meinertzhageni, Columbicola*** **(Family Philopteridae)**

**Description:** Tendeiro, J. (1959) Etudes sur les Mallophages. Sur deux espèces et trois sous-espèces nouvelles du genre *Columbicola* Ewing, parasites de Columbidés africains. *Do Boletim Cultural Guiné Portuguesa* 14 (56): 671; figs. 1-7.

**Paratypes:** 1 specimen (Philopteridae Box 1A Slide # 89) ex *Columba arquatrix arquatrix* currently *Columba arquatrix* Temminck, 1808 (Columbiformes:

Columbidae)—African Olive-Pigeon: BELGIUM CONGO: 1 male (Pelengue, alt. 1150 m., 16 June 1947, Coll: G.F. de Witte – no. 626a). 2 specimens (Philopteridae Box 1A Slide #85) ex *Streptopelia semitorquata* (Rüppell, 1837) (Columbiformes: Columbidae)—Red-eyed Dove: BELGIUM CONGO: 1 male, 1 female Det. T. Clay (Boma no. 317, 1951, Coll: unknown).

**Current Status:** Valid – Price *et al*. (2003: 167).

**Remarks:** The two specimens from *Streptopelia semitorquata* (Rüppell, 1837) are actually labeled *Columbicola clayae*. However neither the description for this species (Tendeiro, 1960: 599) nor Price *et al*. (2003: 166) records *C. clayae* from *S. semitorquata*. These specimens does however corresponds exactly with the paratypes recorded for *C. meinertzhageni* (Tendeiro, 1959: 671) and should be considered such.

***meinertzhageni parvus, Columbicola*** **(Family Philopteridae)**

**Description:** Tendeiro, J. (1959) Etudes sur les Mallophages. Sur deux espèces et trois sous-espèces nouvelles du genre *Columbicola* Ewing, parasites de Columbidés africains. *Do Boletim Cultural Guiné Portuguesa* 14 (56): 688; figs. 4, 6, 9.

**Paratypes:** 3 specimens (Philopteridae Box 1A Slide # 87) ex *Turtur chalcospilos* (Wagler, 1827) (Columbiformes: Columbidae)—Emerald-spotted Wood-Dove: BELGIUM CONGO: 1 male, 2 female (Kakongo, 1951, no. 399, Brit. Mus. 1951-546; generic determination dr. T. Clay).

**Current Status:** *C. parvus* Tendeiro, 1959 – elevated to species rank by Price *et al*. (2003: 167).

***mendesi, Pseudomenopon*** **(Family Menoponidae)**

**Description:** Tendeiro 1965: Études sur les Mallophages observations sur le genre Pseudomenopon Mjöberg, 1910, avec description de six espèces et une sous-espece nouvelles. *Estudos Gerais Universitários de Moçambique II (Série IV)* 1965: 32 synonomized into *P. concretum* by Price 1974a: 78.

**Paratypes:** 1 specimen (Tervuren Box 23 Slide # 45) ex *Porphyrio madagascariensis* (Latham, 1802) (Gruiformes: Rallidae)—African Swamphen: BELGIUM CONGO: 1 female (P.N.U., Mabwe (alt. 585 m.), 10 February 1949, Coll: G.F. de Witte no. 2 333a, host 4-382).

**Current Status:** Considered a junior synonym of *P. concretum* (Piaget 1880) by Price (1974: 78) accepted by Price *et al*., 2003: 135.

***nahani, Clayia*** **(Family Menoponidae)**

**Description:** Tendeiro, J., L. F. Mendes, and O. Baessa de Aguiar. (1994) Etudes sur les Mallophages (Insecta, Mallophaga) des Galliformes de l'Afrique Centrale. III. Nouvelles données sur les Amblycera et description de 12 espèces nouvelles de genre *Clayia* Hopkins, 1941. *Estudos, Ensaios e Documentos. Instituto de Investigação Científica Tropical* 159: 51; figs. 41-44.

**Holotype:** 1 specimen (Tervuren Box 19 Slide # 1) ex *Acentrortyx nahani* = *Francolinus nahani* Dubois, 1905 (Galliformes: Phasianidae)—Nahan's

Francolin: CONGO: 1 male (Lima, 17 February 1961, Coll: Lukala). **Paratypes**: 13 specimens (Tervuren Box 19 Slide # 2-12) ex *Acentrortyx nahani* = *Francolinus nahani* Dubois, 1905 (Galliformes: Phasianidae)—Nahan's Francolin: CONGO: 1 female, designated allotype (Lima, 17 February 1961, Coll: Lukala); 2 females, 9 nymphs (Lima, 17 February 1961, Coll: Lukala); 1 nymph (Lima, Kivu, 12 June 1960, Coll: Lukala). 1 specimen (Tervuren Box 19 Slide # 13) ex *Francolinus coqui lynesi*, currently*Francolinus coqui coqui* (Smith, A. 1836) (Galliformes: Phasianidae)—Coqui Francolin: CONGO: 1 nymph (Kivu, Kasaji, 4 January 1950, Coll: W. S. Fischer).

**Current Status:** Valid – Price *et al*. (2003: 96).

***numidae intermediae, Archigoniodes*** **(Family Philopteridae)**

**Description:** Tendeiro, J. (1988) Etudes sur les Goniodidés (Mallophaga, Ischnocera) des Galliformes. III–Espèces parasites des Numididés. *Estudos, Ensaios e Documentos*. *Instituto de Investigação Científica Tropical* 149: 41, plates 15 (photo 2), 16 (photo 1 & 2), 17 (photo 1 & 2), map 4.

**Holotype:** 1 specimen (Philopteridae Box 5 Slide # 11) ex *Numida ptilorhyncha*, currently *Numida meleagris meleagris* (L., 1758) (Galliformes: Numidae)—Saharan Helmeted Guineafowl: RUANDA: 1 male (Rubona, 30 March 1961, Coll: Delepierre). **Paratype:** 3 specimens (Philopteridae Box 5 Slide # 12-13) ex *Numida meleagris meleagris* (L., 1758) (Galliformes: Numidae)—Saharan Helmeted Guineafowl: URUNDI: 1 nymph (Usumbura, 29 January 1926, Coll: H. Schouteden); RUANDA: 2 nymphs (Katare, 1 August 1951, Coll: A. Lestrade).

**Current Status:** Considered a junior synonym of *Goniodes numidae* Mjöberg 1910 by Price *et al*. (2003: 185). Generic reassignment by Price *et al*. (2003: 147) following Hopkins and Clay (1952: 38).

***obliteratus, Columbicola*** **(Family Philopteridae)**

**Description:** Tendeiro, J. (1980) Contributions a l'etude des Mallophages des Columbiformes Africains. *Musee Royal de l'Afrique Centrale (Tervuren), Sciences Zoologiques* 232: 38; fig. 11; photo 8.

**Holotype:** 1 specimen (Tervuren Box 26 Slide # 70) ex *Aplopelia larvata simplex*, currently *Columba simplex* (Hartlaub, 1849) (Columbiformes: Columbidae)—Forest Dove: CONGO (= Zaire): 1 male (Muana, 14 February 1953, Coll: Prigogine (no. 64602)). **Paratypes:** 2 specimens (Tervuren Box 26 Slide # 71-72) ex *Aplopelia larvata simplex*, currently *Columba simplex* (Hartlaub, 1849) (Columbiformes: Columbidae)—Forest Dove: CONGO (= Zaire): 2 females, 1 designated allotype (Muana, 14 February 1953, Coll: Prigogine (no. 64602)).

**Current Status:** Valid – Price *et al*. (2003: 167).

***paleata, Degeeriella*** **(Family Philopteridae)**

**Description:** Tendeiro, J. (1958). Etudes sur les Mallophages. Sur deux espèces et trois sous-espèces du genre *Degeeriella* Neumann 1906 (Ischnocera, Philopteridae), parasites des Falconiformes. *Do Boletim Cultural da Guiné Portuguesa* 13(49): 29; fig. 2; photos 3-4.

**Paratype:** 1 specimen (Philopteridae Box 2 Slide # 45) ex *Gypohierax angolensis* (Gmelin, 1788)—Palm-nut Vulture: CONGO: 1 male (Maniema, Kasongo, Lualaba, November 1959, Coll: P.L.G. Benoit no. 237).

**Current Status:** Valid – Price *et al*. (2003: 174).

**Remarks:** This specimen designated a metatype by Tendeiro (1964: 200).

***phalloides, Amyrsidea (Argimenopon)*** **(Family Menoponidae)**

**Description:** Tendeiro, J. (1980) Etudes sur les Mallophages (Insecta, Mallophaga) des Galliformes de l'Afrique centrale. I–Genre *Amyrsidea* Ewing, 1927. *Garcia de Orta, Série Zoologica* 9(1-2): 86; plate 3 photos 1, 2.

**Holotype:** 1 specimen (Menoponidae Box10-2 Slide # 94) ex *Afropavo congensis* Chapin, 1936 (Galliformes: Phasianidae)—Congo Peafowl: BELGIUM CONGO: 1 male (Lusambo, Inkongo, 1938, Coll: Wilson). **Paratype:** 1 specimen (Menoponidae Box10-2 Slide # 95) ex *Afropavo congensis* Chapin, 1936 (Galliformes: Phasianidae)—Congo Peafowl: BELGIUM CONGO: 1 female, designated allotype (Lusambo, Inkongo, 1938, Coll: Wilson).

**Current Status:** Valid – Price *et al*. (2003: 87).

***phasida, Clayia*** **(Family Menoponidae)**

**Description:** Tendeiro, J., L. F. Mendes, and O. Baessa de Aguiar. (1994) Etudes sur les Mallophages (Insecta, Mallophaga) des Galliformes de l'Afrique Centrale. III. Nouvelles données sur les Amblycera et description de 12 espèces nouvelles de genre *Clayia* Hopkins, 1941. *Estudos, Ensaios e Documentos. Instituto de Investigação Científica Tropical* 159: 57; figs. 49-54.

**Holotype:** 1 specimen (Tervuren Box 20 Slide # 80) ex *Phasidus niger*, currently *Agelastes niger* (Cassin, 1857) (Galliformes: Numidae)—Black Guineafowl: CONGO: 1 male (Eturi, Epulu, no date, Coll: Station de Chasse). **Paratype:** 1 specimen (Tervuren Box 20 Slide # 81) ex *Phasidus niger*, currently *Agelastes niger* (Cassin, 1857) (Galliformes: Numidae)—Black Guineafowl: CONGO: 1 female, designated allotype (Eturi, Epulu, no date, Coll: Station de Chasse).

**Current Status:** Valid – Price *et al*. (2003: 96).

***phasidus, Stenocrotaphus*** **(Family Philopteridae)**

**Description:** Tendeiro, J. (1988) Etudes sur les Goniodidés (Mallophaga, Ischnocera) des Galliformes. III - Espèces parasites des Numididés. *Estudos, Ensaios e Documentos. Instituto de Investigação Científica Tropical* 149: 29; plate 8 photo 2, plate 9 photos 1-2; map 5.

**Holoype:** 1 specimen (Philopteridae Box 6 Slide # 67) ex *Phasidus niger*, currently *Agelastes niger* (Cassin, 1857) (Galliformes: Numidae)—Black Guineafowl: CONGO: 1 female (Stanleyville (=Kisangani), no date, Coll: A. Pitette).

**Current Status:** *Goniodes phasidus* (Tendeiro 1988). Generic reassignment by Price *et al*. (2003: 147) following Hopkins and Clay (1952: 338).

***plumiferae, Archigoniodes*** **(Family Philopteridae)**

**Description:** Tendeiro, J. (1988) Etudes sur les Goniodidés (Mallophaga, Ischnocera) des Galliformes. III–Espèces parasites des Numididés. *Estudos, Ensaios e Documentos. Instituto de Investigação Científica Tropical* 149: 54; plate 24 photos 1, 2, plate 25 photos 1, 2, plate 26 photos 1, 2, plate 27 photos 1, 2; map 7.

**Holotype:** 1 specimen (Philopteridae Box 5 Slide # 17) ex *Guttera plumifera schubotzi* Reichenow, 1912 (Galliformes: Numidae)—Schubotz's plummed Guinea-fowl: CONGO: 1 female (Moga, 7 March 1964, Coll: Prigogine).

**Notes:** Described in *Archigoniodes* Tendeiro, 1988a: 54. Male allotype (plate 24, photo 1) considered iconotype "celui-là au Musée Royal de l'Afrique Centrale".

**Current Status:** *Goniodes plumiferae* (Tendeiro 1988). Generic reassignment by Price *et al*. (2003: 147) following Hopkins and Clay (1952: 38).

***puylaerti, Turturicola*** **(Family Philopteridae)**

**Description:** Tendeiro, J. (1977) Description de deux espèces nouvelles du genre *Turturicola* Th. Clay et Meinertzhagen, 1937 (Mallophaga, Ischnocera). *Revue de Zoologie Africaine* 91(3): 705; figs. 1, 2; photos 1, 2, 3.

**Holotype:** 1 specimen (Tervuren Box 24 Slide # 82) ex *Streptopelia vinacea* (Gmelin, 1789) (Columbiformes: Columbidae)—Vinaceous Dove: CAMEROON: 1 male (Yagona, 24 November 1970, Coll: W. Verheyen and De Vree - no. 1176).

**Current Status:** Valid – Price *et al*. (2003: 246).

***reichenowii, Archigoniodes*** **(Family Philopteridae)**

**Description:** Tendeiro, J. (1988) Etudes sur les Goniodidés (Mallophaga, Ischnocera) des Galliformes. III–Espèces parasites des Numididés. *Estudos, Ensaios e Documentos. Instituto de Investigação Científica Tropical* 149: 52; plate 22 photos 1, 2, plate 23 photos 1, 2; map 4.

**Holotype:** 1 specimen (Philopteridae Box 5 Slide # 19) ex *Numida meleagris reichenowi* Ogilvie-Grant, 1894 (Galliformes: Numidae)—Reichenow's helmeted Guineafowl: KENYA: 1 male (Tsavo River, 26 May 1913, Coll: Bayer).

**Current Status:** *Goniodes reichenowii* (Tendeiro 1988). Generic reassignment by Price *et al*. (2003: 147) following Hopkins and Clay (1952: 38).

***ruwenzorornis, Splendoroffula*** **(Family Philopteridae)**

**Description:** Kéler, S. v. (1955) Mallophaga. Zwei neue Arten der Gattung *Splendoroffula* Clay u. Meinertzhagen. *Annales Musée Royal de Congo Belge, Tervuren, Sciences Zoologiques* 36: 412.

**Holotype:** 1 specimen (Philopteridae Box 4 Slide # 53) ex *Ruwenzorornis johnstoni kivuensis* Neumann, 1908 (Musophagiformes: Musophagidae)—Kivu Lorie: RUANDA: 1 male (Rutovu, fôret du Rugege, 2350 m., 20-23 January 1953, Coll: P. Basilewsky). **Paratypes:** 33 specimens (Philopteridae Box 4 Slide # 53-60) ex *Musophaga johnstoni kivuensis*, currently *Ruwenzorornis johnstoni kivuensis* Neumann, 1908 (Musophagiformes: Musophagidae)—Kivu Lorie RUANDA: 18 males, 5 females (1 designated allotype), 10 nymphs (Rutovu, fôret du Rugege, 2350 m., 20-23 January 1953, Coll: P. Basilewsky).

**Current Status:** Valid – Price *et al*. (2003: 238).

***ruwenzorornis turacina, Splendoroffula* (*Family Philopteridae*)**

**Description:** Kéler, S. v. (1958) The genera *Oxylipeures* Mjöberg and *Splendoroffula* Clay and Meinertzhagen (Mallophaga). *Deutsche Entomologische Zeitschrift, N. F.* 5(3/4): 308.

**Holotype:** 1 specimen (Philopteridae Box 4 Slide # 61) ex *Turacus schalowi schalowi*, currently *Tauraco schalowi* (Reichenow, 1891) (Musophagiformes: Musophagidae)—Schalow's Turaco: BELGIUM CONGO: 1 male (R. Mubale (alt. 1480 m.), 14 May 1947, Coll: G.F. de Witte). **Paratypes:** 2 specimens (Philopteridae Box 4 Slide # 62-63) ex *Turacus schalowi schalowi*, currently *Tauraco schalowi schalowi* (Reichenow, 1891) (Musophagiformes: Musophagidae)—Schalow's Turaco: BELGIUM CONGO: 2 females, 1 designated allotype (R. Mubale (alt. 1480 m.), 14 May 1947, Coll: G.F. de Witte).

**Current Status:** *S. turacina* Kéler 1958 – elevated to species rank by Price *et al*. (2003: 238).

**Remarks:** Originally described by Kéler (1955: 412) as *S. ruwenzorornis* and later treated as a subspecies (Kéler 1958: 308-309).

***savoi, Coloceras* (Family Philopteridae)**

**Description:** Tendeiro, J. (1973) Estudos sobre os Goniodídeos (Mallophaga, Ischnocera) dos Columbiformes. XIV–Género *Coloceras* Taschenberg, 1882.

*Revista de Ciências Veterinárias, Universidade de Lourenço Marques (Série A)* 6: 257; figs. 7, 16; photos 19-24, 177, 202.

**Paratypes:** 6 specimens (Tervuren Box 24 Slide # 72-77) ex *Columba guinea guinea* L., 1758 (Columbiformes: Columbidae)—Speckled Pigeon: TOGO: 5 females, 1 nymph (Borgou, 10 December 1969, Coll: Mission W. Verheyen).

**Current Status:** Valid – Price *et al*. (2003: 165).

***schoutedenii, Archigoniodes*** **(Family Philopteridae)**

**Description:** Tendeiro, J. (1988) Etudes sur les Goniodidés (Mallophaga, Ischnocera) des Galliformes. III–Espèces parasites des Numididés. *Estudos, Ensaios e Documentos*. *Instituto de Investigação Científica Tropical* 149: 59; plate 31 photos 1, 2, plate 32 photos 1, 2 ,plate XLIII photos 1, 2, XLIV photo 1, XLV photos 1, 2, XLVI photos 1, 2, XLVII photos 1, 2; map 6.

**Holotype:** 1 specimen (Philopteridae Box 5 Slide # 21) ex *Guttera edouardi schoutedeni*, currently *Guttera pucherani verreauxi* (Elliot, 1870 “d’apres Crowe 1978” according to Tendeiro) (Galliformes: Numidae)—Lindi Crested Guineafowl: CONGO: 1 male (Bsan-Kusu, 16 March 1954, Coll: Herroelen).

**Paratypes:** 10 specimens (Philopteridae Box 5 Slide # 22-8) ex *Guttera edouardi schoutedeni*, currently *Guttera pucherani verreauxi* (Elliot, 1870 “d’apres Crowe 1978”) (Galliformes: Numidae)—Lindi Crested Guineafowl: CONGO: 1 female, designated allotype (Nganda, 26 November 1957, Coll: Prigogine); 1 nymph (Léopoldville, Jardin Zoologique, July 1941, no collector), 2 nymphs (Bsan-Kusu, 16 March 1954, Coll: Herroelen), 1 male, 1 female, 2 nymphs (Bokala-kaba, 7

June 1958, Coll: Nkele), 2 *Stenocrotaphus* spp. nymphs (Bokala-kaba, 7 June 1958, Coll: Nkele).

**Current Status:** *Goniodes reichenowii* (Tendeiro 1988). Generic reassignment by Price *et al*. (2003: 147) following Hopkins and Clay (1952: 38).

***scotopeliae, Kurodaia (Conciella)*** **(Family Menoponidae)**

**Description:** Tendeiro, J. (1964) Mallophaga. *Annales Musée Royal de l'Afrique Centrale (Tervuren), Series Zoologiques* 132: 179; figs. 7-8; photos 9-10.

**Holotype**: 1 specimen (Menoponidae Box 3 Slide # 37) ex *Scotopelia peli* (Bonaparte, 1850) (Strigiformes: Strigidae)—Pel's Fishing-Owl: BELGIUM CONGO: 1 male (Tshuapa, 19 January 1954, Coll: P. Herroelen British Mus. 1959-105). **Paratypes:** 19 specimens (Menoponidae Box 3 Slide # 37-46) ex *Scotopelia peli* (Bonaparte, 1850) (Strigiformes: Strigidae)—Pel's Fishing-Owl: BELGIUM CONGO: 1 female, designated allotype (Tshuapa, 19 January 1954, Coll: P. Herroelen British Mus. 1959-105); CONGO: 1 male, 16 females, 1 nymph (Lualaba, Kasongo, November 1959, Coll: P.L.G. Benoit – no. 234).

**Current Status:** Valid – Price *et al*. (2003: 115).

**Remarks:** According to Tendeiro (1964: 179) the holotype and allotype should be in the collection of the British Museum of Natural History, London.

***smithi, Colpocephalum*** **(Family Menoponidae)**

**Description:** Clay, T. (1964) A new species of *Colpocephalum* Nitzsch (Mallophaga). *Proceedings of the Royal Entomological Society London (B)* 33 (1-2): 11; figs. 1; plate 1 figs. 1-3.

**Paratype:** 1 specimen (Menoponidae Box 14 Slide # 5) ex *Scopus umbretta umbretta* Gmelin J. F. 1789 (Ciconiiformes: Scopidae)—Hamerkop: BELGIUM CONGO: 1 male (Ganza, alt. 860 m., 7 June 1949, Coll: Mission G. F. de Witte P.N.U.).

**Current Status:** Valid – Price *et al*. (2003: 102).

***spenorhynchus*, *Colpocephalum* (Family Menoponidae)**

**Description:** Tendeiro, J. (1964) Mallophaga. *Annales Musée Royal de l'Afrique Centrale (Tervuren), Series Zoologiques* 132: 173, fig. 4; photos 4-6.

**Holotype:** 1 specimen (Menoponidae Box 6 Slide # 94) ex *Sphenorhynchus abdimii*, currently *Ciconia abdimii* Lichtenstein, 1823 (Ciconiiformes: Ciconiidae)—Abdim's Stork: CONGO: 1 male (Maniema, Kasongo, Lualaba, November 1959, Coll: P.L.G. Benoit). **Paratype:** 1 specimen (Menoponidae Box 6 Slide # 95) ex *Sphenorhynchus abdimii*, currently *Ciconia abdimii* Lichtenstein, 1823 (Ciconiiformes: Ciconiidae)—Abdim's Stork: CONGO: 1 male (Maniema, Kasongo, Lualaba, November 1959, Coll: P.L.G. Benoit).

**Current Status:** Considered a junior synonym of *Ciconiphilus quadripustulatus* (Burmeister 1838) by Price and Emerson (1967: 250) accepted by Price *et al*. (2003: 96).

**Remarks:** According to Tendeiro (1964: 132) only the male holotype should be in the RMCA collection.

***subcruzi, Clayia*** **(Family Menoponidae)**

**Description:** Tendeiro, J., L. F. Mendes, and O. Baessa de Aguiar. (1994) Etudes sur les Mallophages (Insecta, Mallophaga) des Galliformes de l'Afrique Centrale. III. Nouvelles données sur les Amblycera et description de 12 espèces nouvelles de genre *Clayia* Hopkins, 1941. *Estudos, Ensaios e Documentos. Instituto de Investigação Científica Tropical* 159: 70; figs. 66-67.

**Holotype:** 1 specimen (Tervuren Box 19 Slide # 45) ex *Guttera plumifera schubotzi* Reichenow, 1912 (Galliformes: Numidae)—Schubotz's plummed Guineafowl: CONGO: 1 male (Banguru, Bafwabaka, 12 March 1953, Coll: Abbelaos). **Paratypes:** 2 specimens (Tervuren Box 19 Slide # 45) ex *Guttera plumifera schubotzi* Reichenow, 1912 (Galliformes: Numidae)—Schubotz's plummed Guineafowl: CONGO: 1 male, 1 nymph (Banguru, Bafwabaka, 12 March 1953, Coll: Abbelaos).

**Current Status:** Valid – Price *et al*. (2003: 96).

**Remarks:** These specimens represent *Clayia* sp. (1) described from *Guttera plumifera plumifera* (Cassin, 1857) according to Emerson (1956).

***subtilis, Splendoroffula*** **(Family Philopteridae)**

Description: Kéler, S. v. (1955) Mallophaga. Zwei neue Arten der Gattung *Splendoroffula* Clay u. Meinertzhagen. *Annales Musée Royal de Congo Belge, Tervuren, Sciences Zoologiques* 36: 421.

**Paratypes:** 4 specimens (Philopteridae Box 4 Slide # 64-65) ex *Gallirex porphyreolophus chlorochlamys*, currently *Tauraco porphyreolophus chlorochlamys* (Shelley, 1881) (Musophagiformes: Musophagidae)—East African Purple-crested Lourie: MOZAMBIQUE: 2 males, 2 females (Dindiza, 29 June 1951, Coll: von Zumpt and Dias).

**Current Status:** Valid – Price *et al*. (2003: 238).

***tandani, Coloceras*** **(Family Philopteridae)**

**Description:** Tendeiro, J. (1973) Estudos sobre os Goniodídeos (Mallophaga, Ischnocera) dos Columbiformes. XIV–Género *Coloceras* Taschenberg, 1882. *Revista de Ciências Veterinárias, Universidade de Lourenço Marques (Série A)* 6: 445; figs. 63, 69; photos 162-167, 198, 245.

**Paratypes:** 4 specimens (Tervuren Box 24 Slide # 33-35) ex *Streptopelia semitorquata semitorquata* (Rüppell, 1837) (Columbiformes: Columbidae)—Red-eyed Dove: TOGO: 1 male, 2 females, 1 nymph (Togoville, 11 September 1969, Coll: F. Puylaert).

**Current Status:** Valid – Price *et al*. (2003: 165).

***textoris, Sturnidoecus*** **(Family Philopteridae)**

**Description:** Tendeiro, J. (1964) Mallophaga. *Annales Musée Royal de l'Afrique Centrale (Tervuren), Sciences Zoologiques* 132: 196; figs. 15-17; photos 25-28.

**Holotype:** 1 specimen (Philopteridae Box 6 Slide # 64) ex *Textor melanocephalus* currently *Ploceus melanocephalus* (L., 1758) (Passeriformes, Ploceidae)—Black-headed Weaver: CONGO: 1 male (Lualaba, Kasongo, Maniema 13 November 1959, Coll: P.L.G. Benoit – no. 53). **Paratypes:** 3 specimens (Philopteridae Box 6 Slide # 64-65) ex *Textor melanocephalus* currently *Ploceus melanocephalus* (L., 1758) (Passeriformes, Ploceidae)—Black-headed Weaver: CONGO: 2 males, 1 female (designated allotype) (Lualaba, Kasongo, Maniema 13 November 1959, Coll: P.L.G. Benoit – no. 53). 5 specimens (Tervuren Box 23 Slide # 79-83) ex *Textor melanocephalus duboisi* currently *Ploceus melanocephalus duboisi* Hartlaub, 1886 (Passeriformes: Ploceidae)—Dubois's Black-headed Weaver: BELGIUM CONGO: 2 males, 3 females (Parc National de l'Upemba, Mabwe, alt. 585 m., 17 February 1949, Coll: G.F. de Witte – no. 2344a. (Host #4428)).

**Current Status:** Valid – Price *et al*. (2003: 243).

***theresae, Coloceras*** **(Family Philopteridae)**

**Description:** Tendeiro, J. (1973) Estudos sobre os Goniodídeos (Mallophaga, Ischnocera) dos Columbiformes. XIV–Género *Coloceras* Taschenberg, 1882. *Revista de Ciências Veterinárias, Universidade de Lourenço Marques (Série A)* 6: 305; fig. 22; photos 59-63, 183, 209.

**Paratypes:** 9 specimens (Philopteridae Box 1) ex *Turtur tympanistria fraseri* currently *Turtur tympanistria* (Temminck, 1809) (Columbiformes: Columbidae) —Tambourine Dove: TOGO: 1 female (Anhové-Hové, 18 July 1968, Coll: Mission W. Verheyen), 1 nymph (Misahohé, 6 August 1969, Coll: F. Puylaert), 2 females (Misahohé, 10 August 1969, Coll: F. Puylaert), 1 nymph (Anhové-Hové, 12 December 1969, Coll: Mission W. Verheyen), 2 males, 2 females (Drogoegan, 2 December 1969, Mission W. Verheyen).

**Current Status:** Valid – Price *et al*. (2003: 165).

***timmermanni, Pseudomenopon*** **(Family Menoponidae)**

**Description:** Tendeiro. J. (1965). Etudes sur les Mallophages. Observations sur le genre *Pseudomenopon* Mjöberg, 1910, avec description de six espèces et une sous-espèces nouvelles. *Revista dos Estudos Gerais Universitários de Moçambique (Série 4)* 2: 41; photos 18, 19, 30, 40, 50, 59.

**Holotype:** 1 specimen (Tervuren Box 23 Slide # 66) ex *Actophilornis africana* = *Actophilornis africanus*) (Gmelin, 1789) (Charadriiformes: Jacanidae)—African Jacana: BELGIUM CONGO: 1 male (P.N.U., Mabwe (alt. 585 m.), 22 November 1948, no. 7972a Coll: G.F. de Witte Host # 3-896). **Paratype:** 1 specimen (Tervuren Box 23 Slide # 67) ex *Actophilornis africana* (sic *africanus*) (Gmelin, 1789) (Charadriiformes: Jacanidae)—African Jacana: BELGIUM CONGO: 1 female, designated allotype (P.N.U., Mabwe (alt. 585 m.), 22 November 1948, no. 7972a Coll: G.F. de Witte Host # 3-896)

**Current Status:** Considered a junior synonym of *P. lanceolatum* Tendeiro, 1965 by Price (1974: 82) accepted by Price *et al*. (2003: 136).

***tordoi, Kurodaia (Conciella)*** **(Family Menoponidae)**

**Description:** Tendeiro, J. (1964) Mallophaga. *Musée Royal de l'Afrique Centrale (Tervuren), Sciences Zoologiques* 132: 176; figs. 5-6; photos 7-8.

**Holotype:** 1 specimen (Menoponidae Box 3 Slide # 47) ex *Ciccaba woodfordi*, currently *Strix woodfordii* (Smith, A 1834) (Strigiformes: Strigidae)—African Wood-Owl: CONGO: 1 male (Lualaba, Kasongo, Maniema, November 1959, Coll: P.L.G. Benoit – no. 242). **Paratypes:** 8 specimens (Menoponidae Box 3 Slide # 47-50) ex *Ciccaba woodfordi* currently *Strix woodfordii* (Smith, 1834) (Strigiformes: Strigidae)—African Wood-Owl: CONGO: 1 male, 7 females (1 designated allotype) (Lualaba, Kasongo, Maniema, November 1959, Coll: P.L.G. Benoit – no. 242).

**Current Status:** Valid – Price *et al*. (2003: 115).

***transvaaliensis, Clayia*** **(Family Menoponidae)**

**Description:** Tendeiro, J., L. F. Mendes, and O. Baessa de Aguiar. (1994) Etudes sur les Mallophages (Insecta, Mallophaga) des Galliformes de l'Afrique Centrale. III. Nouvelles données sur les Amblycera et description de 12 espèces nouvelles de genre *Clayia* Hopkins, 1941. *Estudos, Ensaios e Documentos. Instituto de Investigação Científica Tropical* 159: 79; figs. 74-78.

**Paratype:** 1 specimen (Tervuren Box 20 Slide # 83) ex *Pternistis castaneiventer lehemanni*, currently *Francolinus afer castaneiventer* (Gunning & Roberts 1911) (Galliformes: Phasianidae)—Cape Red-necked Francolin: SOUTH AFRICA: 1 female, designated allotype (Transvaal, Onderstepoot (sic. = Onderstepoort), no date, Coll: Colback).

**Current Status:** Valid – Price *et al*. (2003: 96).

**Remarks:** According to Tendeiro *et al*. (1994: 79) there should also be a holotype male with same data.

***truncatum, Coloceras*** **(Family Philopteridae)**

**Description:** Tendeiro, J. (1973) Estudos sobre os Goniodídeos (Mallophaga, Ischnocera) dos Columbiformes. XIV–Género *Coloceras* Taschenberg, 1882. *Revista de Ciências Veterinárias, Universidade de Lourenço Marques (Série A)* 6: 242; figs. 5, 14, 15; photos 7-15, 176, 201.

**Paratypes:** 3 specimens (Philopteridae Box 1) ex *Streptopelia semitorquata erythrophrys*, currently *Streptopelia semitorquata* (Rüppell, 1837) (Columbiformes: Columbidae)—Red-eyed Dove: TOGO: 1 male (Azafi, 14 July 1968, Coll: Mission W. Verheyen); 1 female, 1 nymph (Evou, 16 July 1969, Coll: F. Puylaert).

**Current Status:** Valid – Price *et al*. (2003: 165).

***turturis, Hohorstiella*** **(Family Menoponidae)**

**Description:** Tendeiro, J. (1980) Contributions a l'etude des Mallophages des Columbiformes Africains. *Musee Royal de l'Afrique Centrale (Tervuren), Sciences Zoologiques* 232: 4; fig 1; photo 1.

**Holotype:** 1 specimen (Tervuren Box 25 Slide # 67) ex *Turtur afer afer* (L., 1766) (Columbiformes: Columbidae)—Blue-spotted Wood-Dove: TOGO: 1 female (Niantougou, 24 July 1969, Coll: Mission W. Verheyen).

**Current Status:** Valid – Price *et al*. (2003: 111).

***verheyeni, Turturicola*** **(Family Philopteridae)**

**Description:** Tendeiro, J. (1977) Description de deux espèces nouvelles du genre *Turturicola* Th. Clay et Meinertzhagen, 1937 (Mallophaga, Ischnocera). *Revue de Zoologie Africaine* 91: 707; figs. 3-4; photos plate II, 1-5.

**Holotype:** 1 specimen (Tervuren Box 24 Slide # 79) ex *Streptopelia vinacea* (Gmelin, 1789) (Columbiformes: Columbidae)—Vinaceous Dove: TOGO: 1 male (Niantougou, 22 July 1969, Coll: Mission W. Verheyen). **Paratype:** 1 specimen (Tervuren Box 24 Slide # 80) ex *Streptopelia vinacea* (Gmelin, 1789) (Columbiformes: Columbidae)—Vinaceous Dove: TOGO: 1 female, designated allotype (Niantougou, 22 July 1969, Coll: Mission W. Verheyen).

**Current Status:** Valid – Price *et al*. (2003: 246).

***whyteii, Clayia*** **(Family Menoponidae)**

**Description:** Tendeiro, J., L. F. Mendes, and O. Baessa de Aguiar. (1994) Etudes sur les Mallophages (Insecta, Mallophaga) des Galliformes de l'Afrique Centrale.

III. Nouvelles données sur les Amblycera et description de 12 espèces nouvelles de genre *Clayia* Hopkins, 1941. *Estudos, Ensaios e Documentos. Instituto de Investigação Científica Tropical* 159: 85; figs. 81-82.

**Holotype:** 1 specimen (Tervuren Box 20 Slide # 95) ex *Francolinus shelleyi whytei* Neumann, 1908 (Galliformes: Phasianidae)—Nyasa Shelley Francolin: CONGO: 1 female (Elizabethville, April 1926, Coll: H. Schouteden). **Paratype:** 1 specimen (Tervuren Box 20 Slide # 96) ex *Francolinus shelleyi whytei* Neumann, 1908 (Galliformes: Phasianidae)—Nyasa Shelley Francolin: CONGO: 1 nymph (Elizabethville, April 1926, Coll: H. Schouteden).

**Current Status:** Valid – Price *et al*. (2003: 96).

***wilsoni, Goniodes*** **(Family Philopteridae)**

**Description:** Clay, T. (1938) New species of Mallophaga from *Afropavo congensis* Chapin. *American Museum Novitates* 1008: 5; figs. 5-9.

**Holotype:** 1 specimen (Philopteridae Box 8 Slide # 1) ex *Afropavo congensis* Chapin, 1936 (Galliformes: Phasianidae)—Congo Peafowl: CONGO: 1 male (East Congo Forest, July 1937, Coll: Rev. T. H. Wilson). **Paratypes:** 3 specimens (Philopteridae Box 8 Slide # 2) ex *Afropavo congensis* Chapin, 1936 (Galliformes: Phasianidae)—Congo Peafowl: CONGO: 1 male, 2 females (East Congo Forest, July 1937, Coll: Rev. T. H. Wilson).

**Current Status:** Valid – Price *et al*. (2003: 186).

***wittei, Sturnidoecus*** **(Family Philopteridae)**

**Description:** Tendeiro, J. (1963) Etudes sur les Mallophages. Observations sur des Ischnocera africains, avec description de 12 espèces et 2 sous-espèces nouvelles (suite et fin). *Do Boletim Cultural da Guiné Portuguesa* 18: 46; figs. 19-20; photos 43-46.

**Holotype:** 1 specimen (Tervuren Box 23 Slide # 86) ex *Tchagra senegala armena* currently *Tchagra senegalus armenus* (Oberholser, 1906) (Passeriformes: Malaconotidae)—Black-crowned Tchagra: BELGIUM CONGO: 1 male (Parc national de l'Upemba, Mabwe lac, alt. 585 m., 28 July 1947, Coll: G.F. de Witte - no. 684a) (Bird # 1031)). **Paratypes:** 6 specimens (Tervuren Box 23 Slide # 86-91) ex *Tchagra senegala armena* currently *Tchagra senegalus armenus* (Oberholser, 1906) (Passeriformes: Malaconotidae)—Black-crowned Tchagra: BELGIUM CONGO: 6 females, 1 designated allotype (Parc national de l'Upemba, Mabwe lac, alt. 585 m., 28 July 1947, Coll: G.F. de Witte - no. 684a) (Bird # 1031)).

**Current Status:** Valid – Price *et al*. (2003: 243).

***zairensis, Clayia*** **(Family Menoponidae)**

**Description:** Tendeiro, J., L. F. Mendes, and O. Baessa de Aguiar. (1994) Etudes sur les Mallophages (Insecta, Mallophaga) des Galliformes de l'Afrique Centrale. III. Nouvelles données sur les Amblycera et description de 12 espèces nouvelles de genre *Clayia* Hopkins, 1941. *Estudos, Ensaios e Documentos. Instituto de Investigação Científica Tropical* 159: 87; figs. 83-86.

**Holotype:** 1 specimen (Tervuren Box 20 Slide # 88) ex *Guttera plumifera schubotzi* Reichenow, 1912 (Galliformes: Numidae)—Schubotz's plummed Guineafowl: CONGO: 1 female (Buta Uele, 19 December 1935, Coll: R.P. Hutsebaut).

**Current Status:** Valid – Price *et al*. (2003: 96).

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## APPENDIX A:

## There and Back Again: Switching Between Host Orders by Avian Body Lice (Ischnocera: Goniodidae)[1]


## ABSTRACT

Studies of major switches by parasites between highly divergent host lineages are important for understanding new opportunities for parasite diversification. One such major host switch is inferred for avian feather lice (Ischnocera) in the family Goniodidae, which parasitize two distantly related groups of birds: Galliformes (pheasants, quail, partridges, etc.) and Columbiformes (pigeons and doves). Although there have been several cophylogenetic studies of lice at the species level, few studies have focused on such broad evolutionary patterns and major host-switching events. Using a phylogeny based on DNA sequences for goniodid feather lice, we investigated the direction of this major host switch. Surprisingly, we found that goniodid feather lice have switched host orders, not just once, but twice. A primary host switch occurred from Galliformes to Columbiformes, leading to a large radiation of columbiform body lice. Subsequently, there was also a host switch from Columbiformes back to Galliformes, specifically to megapodes in the Papua-Australasian region. Our results further reveal that although morphologically diagnosable lineages are supported by molecular data, many of the existing genera are not monophyletic and a revision of generic limits is needed.



**Keywords**: ectoparasites, host-switching, phylogeny, coevolution, Galliformes, Columbiformes


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## INTRODUCTION

Cophylogenetic studies of parasitic lice (Insecta: Phthiraptera) have focused mainly on species level studies within orders or families of birds and mammals. These studies have revealed a variety of patterns from tight cospeciation (Hafner *et al*., 1994; Page *et al*., 1998; Clayton & Johnson 2003; Hughes *et al*., 2007) to a lack of significant congruence between host and parasite phylogenies (Johnson *et al*., 2002). Studies of coevolutionary history at higher taxonomic scales (across families or orders) are rare (but see Johnson *et al*., 2006). Understanding processes at these higher levels is important to determine whether species level processes, such as cospeciation, simply scale up to broader macroevolutionary patterns, or whether host shifts between major host lineages, have broad consequences for parasite diversification.

Among feather lice, such host-switching between families or orders of birds is thought to be rare because most genera of lice are confined to a single host family or order (Price *et al*., 2003). However, one such opportunity for exploring major host shifts lies within the body louse family Goniodidae. These lice parasitize two distantly related orders (Hackett *et al*., 2008), Galliformes (pheasants, quail, partridges, megapodes, etc.) and Columbiformes (pigeons and doves). The presence of related genera of lice on these hosts is likely the result of one or more major host-switching events. Lice in the family Goniodidae have a rounded body form and are generally confined to the belly and rump regions of the host, which is why they are often called "body" lice (Clay, 1949). These lice are closely related to body lice in the family Heptapsogasteridae (Smith, 2000; Cruickshank *et al*., 2001; Johnson *et al*., 2001), which are confined to the avian order

Tinamiformes (tinamous), an ancient lineage of South American birds that is closely related to the flightless ratites (ostriches, emus, rheas, cassowaries, and kiwis; Hackett *et al*., 2008).

Previous phylogenetic studies of the family Goniodidae have used both morphological (Smith, 2000) and molecular (Johnson *et al*., 2001) data for phylogeny reconstruction. The morphological study of Smith (2000), which used 62 morphological characters for 15 species of Goniodidae, failed to recover monophyly of either the lice parasitizing Galliformes or Columbiformes, suggesting multiple switching events between these host orders. In contrast, a molecular study by Johnson *et al*. (2001), which involved maximum likelihood analysis of two gene regions for 24 species of Goniodidae, recovered reciprocal monophyly for the lice parasitizing Galliformes, with respect to those parasitizing Columbiformes. These results supported previous work separating the family into Goniodinae (from Galliformes) and Physconelloidinae (from Columbiformes). The molecular phylogenetic tree suggested a single inter-ordinal host switch, but the direction of the switch was ambiguous. However, only three species of lice from Galliformes were included in the Johnson *et al*. (2001) study.

The goal of the current study was to expand both the taxon sampling and number of gene regions in a more detailed molecular phylogenetic study of Goniodidae. The ultimate purpose of this study was to further test whether lice from Galliformes and Columbiformes are reciprocally monophyletic, and provide further inferences regarding possible switching of lice between these host orders. We present analyses of DNA sequences from three gene regions (one nuclear and two mitochondrial) for expanded sampling of 89 taxa of Goniodidae.

## MATERIALS & METHODS

Lice were collected, stored, and prepared according to procedures described by Johnson *et al*. (2001). Species were identified from voucher specimen slides according to the generic level taxonomy of Price *et al*. (2003). However, we also applied generic names recognized by Tendeiro (1969a,b, 1973) for columbiform body lice as a potential subgeneric classification. DNA was extracted from individual lice using a Qiagen Tissue Extraction Kit and the exoskeleton was retained and slide mounted as a voucher specimen. Voucher slides are deposited in the Illinois Natural History Survey Insect Collection and in the Price Institute for Phthiraptera Research, University of Utah. Portions of the mitochondrial cytochrome oxidase I (COI, 379 bp) and nuclear elongation factor 1-a (EF1a, 347 bp) were amplified using primers and PCR protocols described by Johnson *et al*. (2001). Furthermore, a portion of the mitochondrial 16S ribosomal DNA gene (16S, 573 aligned bp) was amplified using the primers 16Sar and 16Sbr (Simon *et al*., 1994). PCR conditions were similar to those for COI and EF1a, though a 46ºC annealing temperature was used. PCR products were purified using a Qiagen PCR Purification Kit and sequenced using ABI BigDye fluorescent cycle sequencing kit. Sequences were run on an ABI 3730xl capillary sequencer (GenBank Accession Numbers AF278644, AF278646-AF278647, AF278652, AF278655, AF278659, AF278662-AF278665, AF278670, AF278673, AF278678-AF278679, AF320403-AF320404, AF348644-AF348647, AF348650, AF348654-AF348655, AF348657, AF348668, AF348837-AF348842, AF348844-AF348845, AF348847-AF348849,

AF348851-AF348853, AF414769, AF414772, AF414777, AF414780, AF414785, AF414787, AF414789, AF414805, and HQ332786-HQ333008).

For protein coding genes, sequences were aligned by eye according to codons. There were no observed codon indels. For 16S rDNA, sequences were aligned using ClustalX (Thompson *et al*., 1997). This alignment resulted in several regions that appeared to have ambiguous alignments with many indels. These regions were removed from analyses to avoid any confounding influence of problematic homology among sites in the alignment (98 bp total). For all analyses trees were rooted using *Strongylocotes orbiculatus*, a representative of the Heptapsogasteridae, which parasitizes tinamous (Aves: Tinamidae). Both morphological (Smith, 2000) and molecular (Cruickshank *et al*., 2001; Johnson *et al*., 2001) data indicate that Heptapsogasteridae is the sister taxon of Goniodidae.

To evaluate the stability of trees to method of analysis, we used parsimony (using PAUP*, Swofford, 2000), Bayesian inference (using MrBayes, Ronquist & Huelsenbeck, 2003), and maximum likelihood (Zwickl, 2006) reconstruction methods. For parsimony we conducted 100 random addition replicates of all three gene regions combined (1202 bp) with TBR branch swapping. We also conducted analyses of each gene separately to evaluate any major conflicts between gene regions. We used bootstrapping (Felsenstein 1985) to assess the stability of this tree to character re-sampling. We calculated consistency indices to evaluate and compare the relative substitution patterns of the three genes.

We conducted Bayesian analyses on three different partitioning schemes: 1) all data combined; 2) two-partitions (mtDNA and EF1a), and 3) three-partitions (COI, 16S, and EF1a). We used MrModeltest v2.3 (Nylander, 2004) to determine which model of molecular evolution was most appropriate for each partition and then chose among the three partitioning schemes using Bayes factors (see Brandley *et al*., 2005), calculated using the harmonic mean from the sump command within MrBayes (Huelsenbeck & Ronquist, 2001). We considered a difference of 2 *ln* Bayes factor > 10 the minimum value to discriminate between partitioning schemes. The Bayes factor analysis determined that the three-partition scheme is most appropriate and is thus the one presented here. The three-partition scheme had likelihood models set for the two mtDNA genes (COI and 16s) as GTR+I+G with a flat Dirichlet prior for state frequencies and for EF1a as HKY+I+G with the state frequencies fixed as equal. All model parameters except the topology and branch lengths were unlinked between partitions and were estimated from the data as part of the analysis. We ran two parallel runs for 10 million generations, each with four Markov chains, to ensure that our analyses were not stuck at local optima (Huelsenbeck & Bollback, 2001). Markov chains were sampled every 500 generations, yielding 20,000 parameter point estimates. We used these 20,000 point estimates minus the burn-in generations (500) to create a 50% majority-rule consensus tree and to calculate Bayesian posterior probabilities (PP), which we used to assess nodal support.

As an alternative assessment of phylogenetic support, we conducted a maximum likelihood bootstrap analysis using Garli v1.0 (Zwickl, 2006). We used a six parameter model with invariant sites and a gamma shape parameter for rate heterogeneity. Values of the parameters that best fit the data are estimated during the analysis. We performed 100 ML bootstrap replicates.

## RESULTS

Substantial variation between species was evident in each gene region, with COI (CI = 0.14) being the most variable, followed by 16S (CI = 0.23) and nuclear EF1a (CI = 0.45). Earlier studies of substitution rates in mitochondrial versus nuclear genes in lice, including Goniodidae, have shown a dramatically elevated substitution rate in mitochondrial as compared to nuclear genes (Johnson *et al*., 2003). Even very closely related species exhibit large divergences in mitochondrial genes with almost no divergence in EF1a. Thus, mitochondrial genes should be useful for resolving relationships among closely related species, whereas multiple substitution interferes with the ability of such genes to resolve deeper relationships. Even given these differences, parsimony trees from individual gene regions were broadly congruent (not shown). Results from a partition homogeneity test (Farris *et al*., 1994, 1995; Swofford 2000) comparing all three gene regions were not significant ($P = 0.22$), again indicating that data from these three gene regions were broadly concordant. Given that each gene fragment is less than 1000 bp, a combined analysis of all three genes should improve resolution and support.

Combined unweighted parsimony searches recovered only two most parsimonious trees (Figure 1). A consensus of these trees was highly resolved and revealed several notable groups of species. Among taxa parasitic on pigeons and doves (Columbiformes), support for several large clades was recovered. These included two large clades of *Physconelloides* species that primarily parasitize 1) small-bodied New World doves (*Columbina*, *Uropelia*, *Claravis*, and *Metriopelia*) and 2) New World mid-sized doves

(*Leptotila* and *Geotrygon*) and large bodied pigeons (*Patagioenas*). A monophyletic group of *Campanulotes* (*Saussurites*) parasitic on Australian phabine doves (*Phaps*, *Geophaps*, *Ocyphaps*, *Petrophassa*, *Geopelia*, *Leucosarcia*) was recovered, as was a large clade of *Coloceras* (*Coloceras*) species parasitic on a variety of Old World pigeons and doves. Among columbiform lice, the most basal split was between *Coloceras museihalense* a parasite of the Great Cuckoo-Dove (*Reinwardtoena reinwardtsi*) of New Guinea and all other species of lice on Columbiformes. Above this node, a group of four species (Subgenera: *Nitzschiella* and *Nitzschielloides*), was the sister taxon of the remaining columbiform lice. Although bootstrap support for some of these major clades, as well as more terminal species level relationships, is high (>75%), support for relationships among major groups within columbiform lice is relatively weak (<50%). This may to be due to relatively short branches in this region of the tree, as well as relatively high homoplasy in mitochondrial genes at these divergences.

Taxa parasitic on Galliformes (i.e. *Goniodes* and *Goniocotes*) for the most part formed a paraphyletic grade at the base of the tree, with lice from Columbiformes embedded within those from Galliformes. Interestingly, one louse species parasitic on Galliformes:Megapodidae (*Goniodes biordinatus* ex *Megapodius reinwardt*) is embedded within those parasitizing Columbiformes, making the lice from Columbiformes paraphyletic. Some of the relationships among the lice of Galliformes were relatively well supported by bootstrapping, including a sister relationship (75%) between *Goniocotes tallegallae* and all of the body lice of Columbiformes (including the *Goniodes biordinatus* ex *Megapodius*). However, in this tree neither *Goniodes* nor *Goniocotes* were monophyletic.

Despite the problem of high levels of multiple substitution in mitochondrial genes, results from Bayesian analyses (Figure 2) were quite similar to those of parsimony. In particular two large, but separate, clades of New World *Physconelloides* were recovered. However, unlike the parsimony trees, the Bayesian tree included the *Physconelloides* parasitic on New World mid-sized doves in the genus *Zenaida* in the same group as those from other New World mid-sized doves and pigeons (*Leptotila* and *Geotrygon*). There was high (100% posterior probability) support for a group of Australian *Campanulotes* (*Saussurites*) as well as for monophyly of a large clade, comprising the Old World *Coloceras* (*Coloceras*) species (see also Figure 3). The most basal splits among the columbiform lice were identical to those recovered by parsimony with *Coloceras museihalense* again being the sister taxon of all other lice parasitizing Columbiformes. Furthermore, as in the parsimony tree, the next node up the tree was the split between the group of four *Coloceras* (*Nitzschiella/Nitzschielloides*) species and all other columbiform lice, indicating that the most basal relationships within columbiform lice are stable to method of analysis. Relationships among the major clades of columbiform lice were relatively weakly supported by Bayesian posterior probabilities.

The tree recovered by Bayesian analysis also included a paraphyletic grade of galliform lice in which the lice of Columbiformes were embedded. In addition, *Goniodes* (*Homocerus*) *biordinatus* from *Megapodius reinwardt* (Galliformes: Megapodidae) was well embedded within the lice of Columbiformes. As in the parsimony tree, *Goniocotes* (*Aurinirmus*) *talegallae* from *Talegalla fuscirostris* (Galliformes: Megapodidae) was sister to the columbiform louse group (100% posterior probability). Some of the other relationships among the galliform lice were different than those recovered by parsimony, although many were strongly supported by Bayesian posterior probability (>95%). For example, monophyly of a group containing all the species sampled from the genus *Goniodes* (minus *Goniodes biordinatus*) was supported in the Bayesian tree. The results of the maximum likelihood bootstrap analysis were concordant with the Bayesian analysis. Most of the nodes strongly supported by Bayesian posterior probabilities also had strong maximum likelihood bootstrap support (Figures 2 and 3).

In general, the phylogeny reflects the traditional generic classifications of Goniodidae. However, several genera are not monophyletic in either the parsimony or Bayesian trees. In the past, there have been two main classification schemes of the Goniodidae of Columbiformes. One is more conservative, recognizing fewer genera (Hopkins & Clay, 1952; Price *et al*., 2003). The other, developed by Tendeiro (1969a,b, 1971, 1973), over several revisions of this group, split taxa into many more genera (which we have indicated with subgeneric designations in parentheses). In several cases, the splitting of taxa into additional genera by Tendeiro appears to be justified. For example *Coloceras* (*Coloceras*) forms a large well-supported clade that is separated from other groups that have been lumped under the genus *Coloceras* (Price *et al*., 2003): *Nitzschiella*, *Patellinirmus*, *Ancistrodes*. A subgroup of *Campanulotes*, distributed on Australian phabine doves, is separated from other *Campanulotes*, and placed by Tendeiro in the genus *Saussurites*. However, Tendeiro (1971) also places *Campanulotes flavus* in this genus, and this appears to be distantly related to the Australian *Campanulotes* (*Saussurites*). Consistent with Tendeiro's interpretation, *Campanulotes* (*Nitzschielloides*) is separated from other species in the genus *Campanulotes*.

Tendeiro (1980a, 1983) also recognized separate genera (*Homocerus* and *Aurinirmus*) for some of the species of goniodid lice occurring on megapodes. In our study these are represented by *Goniodes* (*Homocerus*) *biordinatus* and *Goniocotes* (*Aurinirmus*) *tallegallae*. In both trees, we find these separated from other members of *Goniodes* and *Goniocotes*, both having closer phylogenetic relationships with the lice of Columbiformes. Tendeiro (1980a) suggested that the species of *Homocerus* are closely related to *Coloceras* and *Patellinirmus*, and this is what we found for *Goniodes* (*Homocerus*) *biordinatus*, which fell between *Coloceras* (*Coloceras*) and *Coloceras* (*Patellinirmus*). Similarly, Tendeiro (1983) suggested that *Aurinirmus* is more closely related to columbiform lice in the genera *Saussurites* and *Auricotes* than to the lice of Galliformes, and in all our analyses *Goniocotes* (*Aurinirmus*) *tallegallae* was sister to the lice of Columbiformes, and not to other *Goniocotes*. Thus, the paraphyly of galliform goniodid lice based on our molecular data is in agreement with the taxonomic assessment of Tendeiro (1980a, 1983) based on morphology.

While the morphological differences used by Tendeiro to recognize additional genera within Goniodidae appear to largely reflect phylogenetic history, some of Tendeiro's genera still remain problematic. For example, subgenus *Nitzschiella* does not form a monophyletic group in either the parsimony or Bayesian tree. Furthermore, the subgenus *Saussurites* is not monophyletic, with the New World species being separated from the Australian taxa. Though taxon sampling of the large genus *Auricotes* is not high, this genus is also not monophyletic in either tree. Finally, Tendeiro recognized the genus *Physconelloides*; however, this genus also appears to involve at least three independent groups: one on Australian phabines, one on small New World ground doves, and one on larger New World doves and pigeons. Five species groups were recognized by Tendeiro (1980b) and Price *et al*. (1999) on the basis of morphology, and the monophyly of each of these groups is generally well supported in the molecular phylogeny.

In the Bayesian tree, recognition of *Homocerus* and *Aurinirmus* as distinct genera would make both *Goniodes* and *Goniocotes* monophyletic. However, the problem of distinguishing *Goniodes* and *Goniocotes* morphologically has long been recognized (Clay, 1951; Ledger, 1980), and our limited taxon sampling of these genera does not enable a more detailed assessment of their status. Further morphological and molecular work on the Goniodidae of Galliformes is needed.

## DISCUSSION

Phylogenetic analyses (parsimony and Bayesian inference) of sequences from mitochondrial COI and 16S and nuclear EF1a genes for parasitic lice in Goniodidae result in relatively well resolved and supported trees (Figures 1 and 2). At the highest level, these trees indicate host-switching between avian orders. Given that Galliformes (pheasants, quail, partridges, megapodes, etc.) and Columbiformes (pigeons and doves) are very distantly related (Hackett *et al*., 2008) the host distribution of lice in these phylogenies indicates a major switch from Galliformes to Columbiformes, given that columbiform lice are well embedded within those of Galliformes (Figure 3). More importantly, a host switch in the opposite direction (from Columbiformes to Galliformes) also appears to have happened more recently. Both parsimony and Bayesian trees place *Goniodes biordinatus* from *Megapodius reinwardt* (Galliformes: Megapodidae) well within the clade of lice from pigeons and doves. Unfortunately the exact relationship of this species within this clade is still unclear because of low support for basal relationships within the columbiform louse group, making it difficult to reconstruct the details of this switch.

Although morphologically similar species tended to form well-supported clades, most genera were not recovered as monophyletic in either the parsimony or Bayesian trees. *Physconelloides* was split into two (Bayesian) or three (parsimony) groups. The genus *Campanulotes*, which is largely recognized for its small size and morphological simplification, fell into three separate groups. Finally, representatives of the genus *Coloceras* were spread throughout the tree. Much of the paraphyly of *Coloceras* can be accounted for by recognition of the subgenera *Ancistrodes*, *Patellinirmus*, and *Nitzschiella* as distinct from *Coloceras*. However, the subgenus *Nitzschiella*, which was recognized as a distinct genus by Tendeiro (1969a) but not by Price *et al.* (2003), formed three (Bayesian) or four (parsimony) distinct groups; therefore, adopting the classification of Tendeiro still leaves unresolved taxonomic problems. It should be noted, however, that because support for relationships among major clades was low, monophyly of many of these genera cannot be completely ruled out. Note, however, that both methods of analysis identified the same major groups.

Several other important biogeographic and host association patterns are also evident in the phylogeny of this group (Figure 3). Species parasitic on New World hosts are largely split into two main groups. These are mainly comprised of lice in the genus *Physconelloides*, which Price *et al.* (1999) divided into five main groups. The monophyly of each of the four New World groups is supported, and the Bayesian tree recovers a clade containing three of these four groups (Figures 2 and 3). The New World species *Campanulotes frenatus*, from *Geotrygon frenata*, is not closely related to New World *Physconelloides* and seems to be an independent colonization of the New World. The large clade of *Coloceras* (*Coloceras*) occurs exclusively in the Old World including Australia. It is also widespread across distantly related lineages of pigeons and doves (Johnson, 2004), thus showing correlation with biogeography but not host phylogeny. Lice from Australian phabine doves also form three distinct clades, suggesting three independent radiations in Australia on this group of hosts. Interestingly, the Australian phabines are the only group of Columbiformes to host three different genera of body lice, which differ markedly in size. There are also species of non-phabine doves in Australia that independently colonized Australia from South-East Asia (e.g. *Macropygia*, *Ptilinopus*, *Ducula*). Lice from these non-phabine doves are separated from the three groups of phabine lice, suggesting that these birds may have carried their lice with them when they colonized Australia (Pereira *et al*. 2007).

The sister taxon to all columbiform lice is *Goniocotes talegallae*, which parasitizes a megapode (*Talegalla fuscirostris*) from New Guinea. Furthermore, the most basal split among columbiform lice occurs between *Coloceras* (*Nitzschiella*) *museihalense* from *Reinwardtoena reinwardtsi*, also from New Guinea. Together, this suggests that columbiform lice may have begun to radiate first in New Guinea, which is consistent with the origin of South East Asia and the Papua-Australian region of Columbiformes identified by Pereira *et al*. (2007), with subsequent rapid dispersal to other regions. This early radiation in the Papua-Australian region also appears to have facilitated the host-switch back to Galliformes, as *Megapodius* is distributed in Australia and New Guinea.

In conclusion, our results provide an example of how major host switches by parasites between distantly related groups of hosts can be important evolutionary events. As such, they provide novel opportunities for parasite diversification on these new hosts. The avian feather lice in the family Goniodidae have undergone two such major host shifts: one from Galliformes to Columbiformes and one back to Galliformes (in particular to megapodes) from Columbiformes. The first host switch provided an opportunity for these lice to radiate on pigeons and doves, in some cases with up to three genera on a single host. Given the lack of strong concordance between louse phylogeny and major host groups at deeper scales and the very short branches connecting major lineages of lice in this group, it seems likely that much of the early radiation of these lice was fostered by host-switching among existing columbiform lineages. In contrast, the more terminal relationships in the louse phylogeny are concordant with host phylogeny (Clayton & Johnson 2003; Johnson & Clayton, 2003), indicating a more recent history of cospeciation. Molecular dating of the louse and host phylogenies could aid in indicating when the first host-switch from Galliformes to Columbiformes occurred with respect to the radiation of Columbiformes.

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# TABLES

**Table A.1.** Specimens used in the present study

| Number | Extract code | Louse species | Host species | Host order | Country |
|---|---|---|---|---|---|
| 1 | Auaff.5.18.2004.13 | *Auricotes affinis* | *Ducula rufigaster* | Columbiform. | New Guinea |
| 2 | Aumar.5.18.2004.14 | *Auricotes* sp. | *Ducula bakeri* | Columbiform. | Vanuatu |
| 3 | Aurot.5.26.1999.1 | *Auricotes rotundus* | *Ptilinopus occipitalis* | Columbiform. | Philippines |
| 4 | Ausp.Chste.5.18.2004.11 | *Coloceras* (*Nitzschiella*) *stephanii* | *Chalcophaps stephani* | Columbiform. | New Guinea |
| 5 | Ausp.Dubic.2.9.2004.11 | *Auricotes lativenter* | *Ducula bicolor* | Columbiform. | Australia |
| 6 | Ausp.Ptriv.5.18.2004.12 | *Auricotes bellus* | *Ptilinopus rivoli* | Columbiform. | New Guinea |
| 7 | Cabid.2.9.2004.6 | *Campanulotes bidentatus* | *Columba palumbus* | Columbiform. | UK |
| 8 | Cacam.2.9.2004.8 | *Campanulotes* (*Nitzschielloides*) *campanulatus* | *Streptopelia picturata* | Columbiform. | Madagascar |
| 9 | Cacom.1.16.2001.4 | *Campanulotes compar* | *Columba livia* | Columbiform. | USA |
| 10 | Cadur.2.9.2004.4 | *Campanulotes* (*Saussurites*) *durdeni* | *Ocyphaps lophotes* | Columbiform. | Australia |
| 11 | Cafla.2.9.2004.2 | *Campanulotes* (*Saussurites*) *elegans* | *Phaps chalcoptera* | Columbiform. | Australia |
| 12 | Casp.Gehum.2.24.2004.4 | *Campanulotes* (*Saussurites*) sp. | *Geopelia humeralis* | Columbiform. | Australia |
| 13 | Casp.Geplu.2.24.2004.8 | *Campanulotes* (*Saussurites*) sp. | *Geophaps plumifera* | Columbiform. | Australia |
| 14 | Casp.Gesmi.4.26.2004.16 | *Campanulotes* (*Saussurites*) sp. | *Geophaps smithii* | Columbiform. | Australia |
| 15 | Casp.Lemel.2.24.2004.10 | *Campanulotes* (*Saussurites*) *flavus* | *Leucosarcia melanoleuca* | Columbiform. | Australia |
| 16 | Cccly.5.26.1999.2 | *Coloceras* (*Coloceras*) *clypeatum* | *Phapitreron amethystina* | Columbiform. | Philippines |
| 17 | Ccdor.2.9.2004.1 | *Coloceras* (*Nitzschiella*) *doryanus* | *Macropygia phasianella* | Columbiform. | Australia |
| 18 | Ccdor.7.1.1999.8 | *Coloceras* (*Nitzschiella*) *doryanus* | *Macropygia tenuirostris* | Columbiform. | Philippines |
| 19 | Ccgra.2.9.2004.3 | *Coloceras* (*Coloceras*) *grande* | *Phaps chalcoptera* | Columbiform. | Australia |
| 20 | Ccmus.4.26.2004.7 | *Coloceras* (*Nitzschiella*) *museihalense* | *Reinwardtoena reinwardtii* | Columbiform. | New Guinea |
| 21 | Ccset.3.21.2000.10 | *Coloceras* (*Coloceras*) *setosum* | *Treron waalia* | Columbiform. | Ghana |
| 22 | Ccsp.Chind.3.21.2000.4 | *Coloceras* (*Coloceras*) *neoindicum* | *Chalcophaps indica* | Columbiform. | Philippines |
| 23 | Ccsp.Chind.5.18.2004.1 | *Coloceras* (*Nitzschiella*) sp. | *Chalcophaps indica* | Columbiform. | Vanuatu |
| 24 | Ccsp.Cogui.2.10.1999.10 | *Coloceras* (*Coloceras*) *savoi* | *Columba guinea* | Columbiform. | South Africa |
| 25 | Ccsp.Colcm.5.18.2004.4 | *Coloceras* (*Nitzschiella*) sp. | *Columba leucomela* | Columbiform. | Australia |
| 26 | Ccsp.Copal.2.9.2004.7 | *Coloceras* (*Coloceras*) *damicorne* | *Columba palumbus* | Columbiform. | UK |
| 27 | Ccsp.Gecun.5.18.2004.8 | *Coloceras* (*Coloceras*) sp. | *Geopelia cuneata* | Columbiform. | Australia |
| 28 | Ccsp.Gehum.12.6.2004.8 | *Coloceras* (*Coloceras*) sp. | *Geopelia humeralis* | Columbiform. | Australia |
| 29 | Ccsp.Gepla.5.18.2004.7 | *Coloceras* (*Coloceras*) sp. | *Geopelia placida* | Columbiform. | Australia |
| 30 | Ccsp.Gesmi.5.18.2004.3 | *Physconelloides australiensis* | *Geophaps smithii* | Columbiform. | Australia |
| 31 | Ccsp.Henov.4.26.2004.4 | *Coloceras* (*Patellinirmus*) sp. | *Hemiphaga novaeseelandiae* | Columbiform. | N. Zealand |
| 32 | Ccsp.Lemel.2.24.2004.9 | *Coloceras* (*Coloceras*) sp. | *Leucosarcia melanoleuca* | Columbiform. | Australia |
| 33 | Ccsp.Loant.5.18.2004.2 | *Coloceras* (*Ancistrodes*) *furcatum* | *Lopholaimus antarcticus* | Columbiform. | Australia |
| 34 | Ccsp.Maruf.11.15.1999.4 | *Coloceras* (*Nitzschiella*) sp. | *Macropygia ruficeps* | Columbiform. | Borneo |
| 35 | Ccsp.Oclop.2.9.2004.5 | *Coloceras* (*Coloceras*) sp. | *Ocyphaps lophotes* | Columbiform. | Australia |
| 36 | Ccsp.Pealb.5.18.2004.6 | *Physconelloides australiensis* | *Petrophassa albipennis* | Columbiform. | Australia |
| 37 | Ccsp.Peruf.5.18.2004.9 | *Physconelloides* sp. | *Petrophassa rufipennis* | Columbiform. | Australia |
| 38 | Ccsp.Phleu.5.26.1999.4 | *Coloceras* (*Coloceras*) sp. | *Phapitreron leucotis* | Columbiform. | Philippines |
| 39 | Ccsp.Stcap.1.12.1999.5 | *Coloceras* (*Coloceras*) *chinense* | *Streptopelia capicola* | Columbiform. | South Africa |
| 40 | Ccsp.Stdct.12.6.2004.7 | *Coloceras* (*Coloceras*) *chinense* | *Streptopelia decaocto* | Columbiform. | USA |
| 41 | Ccsp.Stdec.11.15.1999.2 | *Coloceras* (*Nitzschiella*) *hilli* | *Streptopelia decaocto* | Columbiform. | Netherlands |
| 42 | Ccsp.Stpic.2.9.2004.9 | *Coloceras* (*Coloceras*) *hoogstraali* | *Streptopelia picturata* | Columbiform. | Madagascar |
| 43 | Ccsp.Stsem.4.26.2004.5 | *Coloceras* (*Coloceras*) sp. | *Streptopelia semitorquata* | Columbiform. | Ghana |
| 44 | Ccsp.Stvin.4.26.2004.2 | *Coloceras* (*Coloceras*) *chinense* | *Streptopelia vinacea* | Columbiform. | Ghana |
| 45 | Ccsp.Tuaby.4.26.2004.15 | *Coloceras* (*Coloceras*) *chinense* | *Turtur abyssinicus* | Columbiform. | Ghana |
| 46 | Ccsp.Tubre.3.21.2000.7 | *Coloceras* (*Nitzschiella*) *laticlypeatus* | *Turtur brehmeri* | Columbiform. | Ghana |
| 47 | Ccsp.Tutym.2.3.2001.6 | *Coloceras* (*Coloceras*) *theresae* | *Turtur tympanistria* | Columbiform. | Uganda |
| 48 | Ccste.5.18.2004.10 | *Coloceras* (*Coloceras*) sp. | *Chalcophaps stephani* | Columbiform. | New Guinea |
| 49 | Gdast.4.26.2004.10 | *Goniocotes* (*Goniodes*) *astrocephalus* | *Coturnix coturnix* | Galliformes | Russia |
| 50 | Gdcen.2.24.2004.7 | *Goniodes* (*Goniodes*) *centrocerci* | *Centrocercus urophasianus* | Galliformes | USA |
| 51 | Gdsp.Cacal.1.15.2000.2 | *Goniodes* (*Goniodes*) sp. | *Callipepla californica* | Galliformes | USA |
| 52 | Gdsp.Frafr.2.3.1999.12 | *Goniodes* (*Goniodes*) *isogenos* | *Francolinus africanus* | Galliformes | South Africa |
| 53 | Gdsp.Merei.2.24.2004.3 | *Goniod.* (*Homocerus*) *biordinatus* | *Megapodius reinwardt* | Galliformes | Australia |
| 54 | Gdsp.Phcol.2.24.2004.1 | *Goniodes* (*Goniodes*) *colchici* | *Phasianus colchicus* | Galliformes | USA |
| 55 | Gdsp.Ptpet.4.26.2004.3 | *Goniodes* (*Goniodes*) *assimilis* | *Ptilopachus petrosus* | Galliformes | Ghana |
| 56 | Gosp.Frafr.1.12.1999.12 | *Goniocotes* (*Goniocotes*) sp. | *Francolinus africanus* | Galliformes | South Africa |
| 57 | Gosp.Phcol.11.10.2001.2 | *Goniocotes* (*Goniocotes*) *chrysocephalus* | *Phasianus colchicus* | Galliformes | USA |
| 58 | Gosp.Tafla.4.26.2004.9 | *Goniocot.* (*Aurinirmus*) *talegallae* | *Talegalla fuscirostris* | Galliformes | New Guinea |
| 59 | Kobra.3.24.2001.1 | *Kodocephalon bradicephalum* | *Goura scheepmakeri* | Columbiform. | New Guinea |
| 60 | Kosub.4.26.2004.8 | *Kodocephalon suborbiculatum* | *Goura victoria* | Columbiform. | New Guinea |

**Table A.1.** (Cont.)

| Number | Extract code | Louse species | Host species | Host order | Country |
|---|---|---|---|---|---|
| 61 | Phcer.1.25.1999.10 | *Physconelloides ceratoceps* 4 | *L. verreauxi fulviventris* | Columbiform. | Mexico |
| 62 | Phcer.1.25.1999.11 | *Physconelloides ceratoceps* 4 | *L. verreauxi angelica* | Columbiform. | USA |
| 63 | Phcer.11.15.1999.9 | *Physconelloides ceratoceps* 3 | *Leptotila plumbeiceps* | Columbiform. | Mexico |
| 64 | Phcer.2.24.2004.5 | *Physconelloides ceratoceps* 3 | *Leptotila cassinii* | Columbiform. | Costa Rica |
| 65 | Phcer.9.29.1998.10 | *Physconelloides ceratoceps* 1 | *Leptotila jamaicensis* | Columbiform. | Mexico |
| 66 | Phcub.1.25.1999.2 | *Physconelloides cubanus* | *Geotrygon montana* | Columbiform. | Mexico |
| 67 | Pheme.2.9.2004.10 | *Physconelloides emersoni* | *Metriopelia melanoptera* | Columbiform. | Argentina |
| 68 | Pheur.1.16.2001.5 | *Physconelloides eurysema* 1 | *Columbina passerina* | Columbiform. | USA |
| 69 | Pheur.1.25.2000.1 | *Physconelloides eurysema* 3 | *Claravis pretiosa* | Columbiform. | Mexico |
| 70 | Pheur.1.25.2000.4 | *Physconelloides eurysema* 3 | *Columbina passerina* | Columbiform. | Mexico |
| 71 | Pheur.2.24.2004.6 | *Physconelloides eurysema* 1 | *Columbina minuta* | Columbiform. | Costa Rica |
| 72 | Pheur.5.18.2004.5 | *Physconelloides eurysema* 3 | *Columbina picui* | Columbiform. | Bolivia |
| 73 | Phgal.7.1.1999.1 | *Physconelloides galapagensis* | *Zenaida galapagoensis* | Columbiform. | Galapagos |
| 74 | Phrob.10.5.1999.11 | *Physconelloides robbinsi* | *Metriopelia ceciliae* | Columbiform. | Bolivia |
| 75 | Phsp.Cobuc.4.26.2004.13 | *Physconelloides eurysema* 3 | *Columbina buckleyi* | Columbiform. | Peru |
| 76 | Phsp.Cocru.4.26.2004.14 | *Physconelloides eurysema* 3 | *Columbina cruziana* | Columbiform. | Peru |
| 77 | Phsp.Comcs.4.26.2004.12 | *Physconelloides* sp. | *Patagioenas maculosa* | Columbiform. | Peru |
| 78 | Phsp.Cospe.4.19.1999.9 | *Physconelloides spenceri* 1 | *Patagioenas speciosa* | Columbiform. | Mexico |
| 79 | Phsp.Gefre.1.9.2001.16 | *Cam.* (*Saussurites*) *frenatus* | *Geotrygon frenata* | Columbiform. | Peru |
| 80 | Phsp.Gesap.3.24.2001.7 | *Physconelloides* sp. | *Geotrygon sapphirina* | Columbiform. | Peru |
| 81 | Phsp.Lemeg.1.25.2000.6 | *Physconelloides ceratoceps* 2 | *Leptotila megalura* | Columbiform. | Bolivia |
| 82 | Phsp.Urcam.10.12.1999.6 | *Physconelloides* sp. | *Uropelia campestris* | Columbiform. | Bolivia |
| 83 | Phspe.1.16.2001.6 | *Physconelloides spenceri* 2 | *Patagioenas fasciata* | Columbiform. | USA |
| 84 | Phspe.10.12.1999.3 | *Physconelloides spenceri* 2 | *Patagioenas fasciata* | Columbiform. | Peru |
| 85 | Phtal.4.19.1999.8 | *Physconelloides anolaimae* 1 | *Patagioenas subvinacea* | Columbiform. | Guyana |
| 86 | Phwis.9.29.1998.11 | *Physconelloides wisemani* | *Zenaida asiatica* | Columbiform. | USA |
| 87 | Phwol.4.24.1999.4 | *Physconelloides anolaimae* 2 | *Columba plumbea* | Columbiform. | Guyana |
| 88 | Phzen.2.24.2004.2 | *Physconelloides zenaidurae* | *Zenaida auriculata* | Columbiform. | Bolivia |
| 89 | Phzen.5.4.1999.2 | *Physconelloides zenaidurae* | *Zenaida macroura* | Columbiform. | USA |
| 90 | Sgorb.11.10.2001.10 | *Strongylocotes orbicularis* | *Crypturellus parvirostris* | Tinamiformes | Bolivia |

# FIGURES

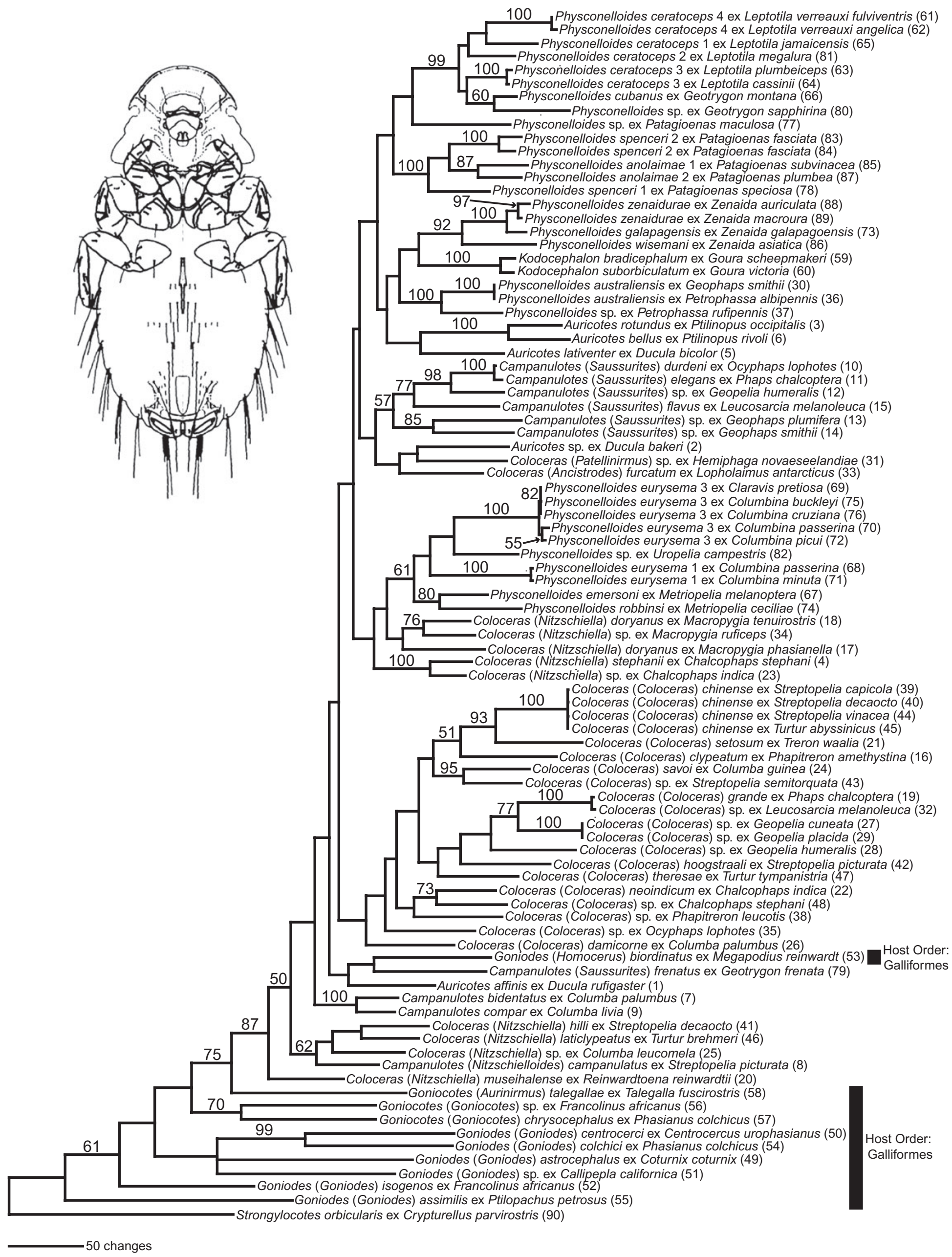


**Figure A.1.** Consensus of two trees (length = 5401, consistency index = 0.195, rescaled consistency index = 0.096) from unweighted parsimony analysis of cytochrome oxidase I, 16S, and elongation factor 1-α combined. Branch lengths are proportional to the number of reconstructed substitutions. Numbers associated with branches are from 1000 parsimony bootstrap replicates. Lice associated with the Order Galliformes are indicated by vertical bars, with all other ingroup taxa occurring on pigeons and doves (Columbiformes). Numbers after louse species names indicate potentially cryptic species (*sensu* Johnson *et al*., 2001). Names in parentheses are generic names for lice *sensu* Tendeiro (1969a, b, 1973) and are used here as tentative subgenera. Numbers in parentheses correspond to the specimen numbers given in Table A.1.

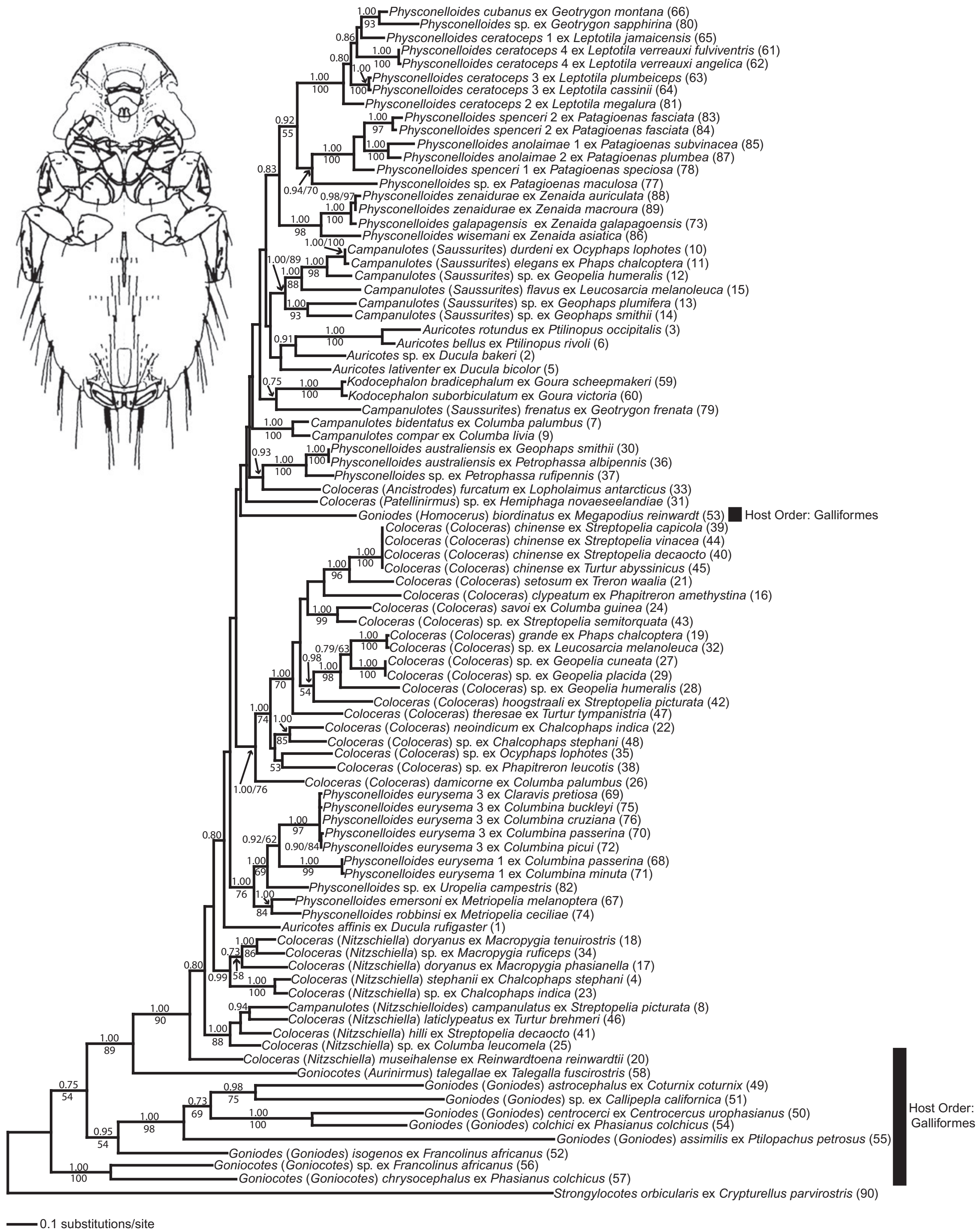


**Figure A.2.** Bayesian consensus tree from the three partition analysis scheme (cytochrome oxidase I, 16S, and elongation factor 1-α). Branch lengths are proportional to substitutions per site. Numbers associated with nodes are Bayesian posterior probabilities (above branches or slashes) and maximum likelihood bootstrap values (below branches or slashes). Other conventions follow those of Fig. A.1.

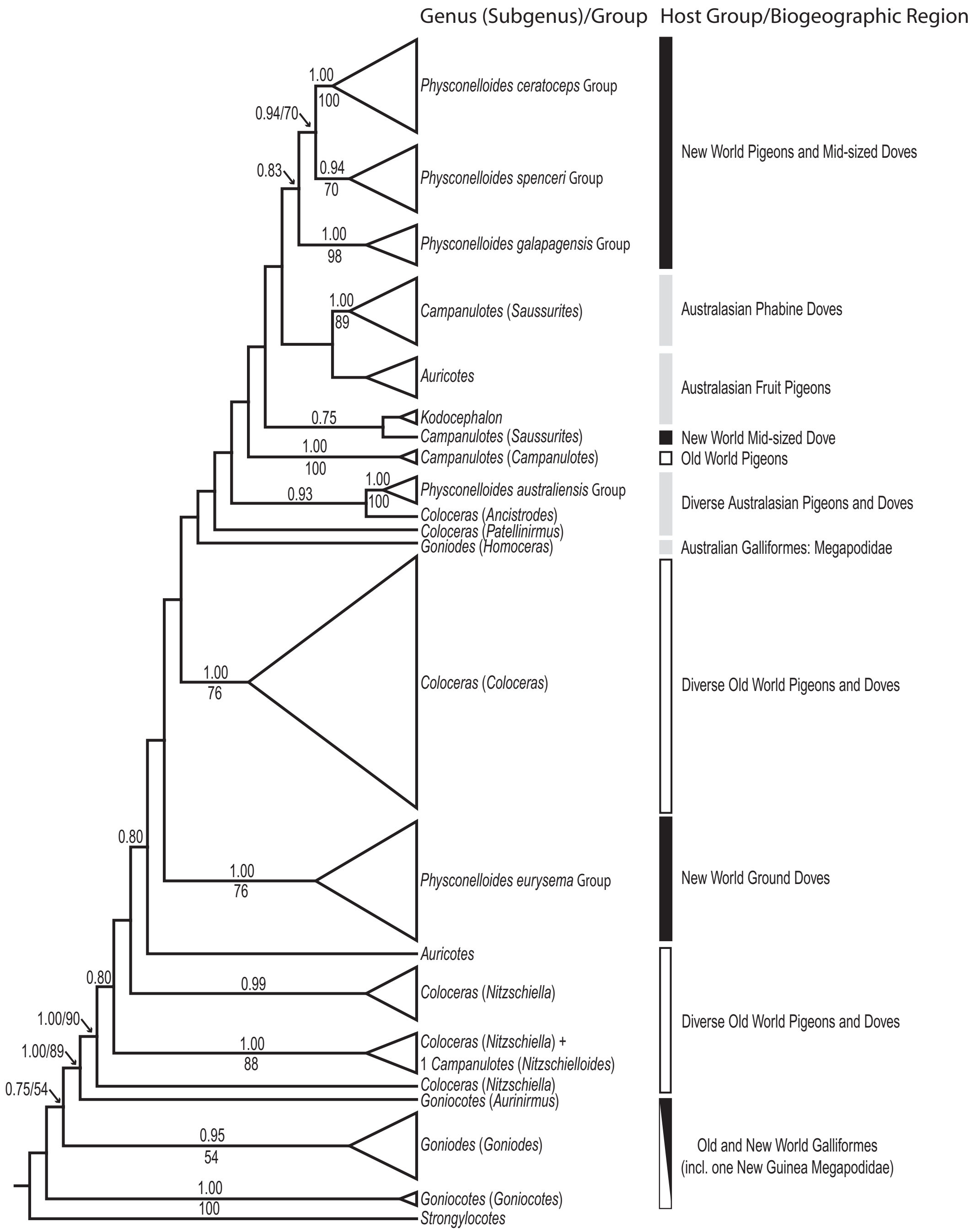


**Figure A.3.** Schematic phylogenetic tree of Goniodidae based on the Bayesian tree showing generic classification (subgenus or species group), biogeographic distribution (vertical), and host group. Shading of vertical bars corresponds to biogeographic region: Grey, Australasia; white, Old World; black, New World; white/black, lineages found in both the Old World and New World. Numbers above and below the branches or slashes are Bayesian posterior probability (> 0.75) and maximum likelihood bootstrap (> 50) values, respectively.