Lousy Phylogenies: Phthiraptera Systematics and the Antiquity of Lice

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Phthiraptera (parasitic lice) comprise about 5,000 described species present in four suborders (Fig. 1): Anoplura (colloquially known as sucking lice), Rhynchophthirina (a monogeneric group found on elephants and warthogs), Ischnocera and Amblycera. Phthirapteran monophyly is supported by 19 apomorphies, the most significant of which include haploid reduction in primary spermatogonia, the presence of a basal hydropile in the egg, dorsoventral compression of the head and loss of the dorsal tentorial arms.

Every conceivable relationship between the four phthirapteran suborders has been proposed at some time. Historically the chewing lice (Amblycera, Ischnocera and arguably Rhynchophthirina) had been subsumed under the name 'Mallophaga', which was awarded ordinal status along with the Anoplura. Morphological data supporting the monophyly of 'Mallophaga' was proposed by KIM & LUDWIG (1978, 1982), although these results were controversial (HAUB 1980).

LYAL (1985) conducted a detailed review of the morphological data that define basal louse relationships. His study confirmed the monophyly of all four suborders, although ischnoceran monophyly was the least well supported. The subordinal phylogeny established by LYAL (1985) confirmed that 'Mallophaga' are paraphyletic and form a grade within Phthiraptera. Significant synapomorphies given by LYAL (1985) defining these relationships are (1) for Rhynchophthirina + Anoplura: head 'fixed' in relation to thorax, loss of anterior tentorial pits and partial transfer of antennal muscle attachment site to dorsum of head; (2) for Rhynchophthirina + Anoplura + Ischnocera: development of saucer-shaped antennal sensilla, partial occlusion of occipital foramen by a connective tissue septum and development of spiracular glands.

Recent molecular evidence supports LYAL's (1985) phylogeny. Using nuclear genes CRUICKSHANK et al. (2001), JOHNSON & WHITING (2002) and most recently BARKER et al. (2003) have investigated phthirapteran basal relationships. All but CRUICKSHANK et al.'s (2001) results are completely congruent with those of LYAL (1985), and the discrepancies in CRUICKSHANK et al.'s study are likely to be the result of an over-reliance on a relatively short fragment of the faster evolving EF1-α gene (SMITH et al. in press).

Familial relationships within each of the suborders are slightly less problematic, with the notable exception of the Ischnocera.

Anopluran lice exclusively parasitise mammals and have a significant medical and veterinary importance. In part, this explains why they are the best-studied suborder of Phthiraptera. Between 1920 and 1935 Gordon Ferris provided the foundation for modern taxonomic work on the Anoplura, and when republished as a monograph FERRIS (1951) recognized 6 families. In the light of new species descriptions this was expanded to 15 (KIM & LUDWIG 1978). Apomorphies for Anoplura include the development of piercing stylets from the hypopharynx and labium, fusion of the pronotum to the mesonotum, and reduction of the meso- and metathoracic terga. A generic level morphological phylogeny for Anoplura was proposed by KIM (1988). Molecular studies on anopluran relationships are ongoing, but for the moment BARKER et al. (2003) provides an initial account of anopluran relationships using 18S rRNA.

Rhynchophthirina comprise just three species in a single genus. The subordinal status of this taxon was awarded by FERRIS (1931) on account of the peculiar morphology of its members. Both monophyly and high rank are supported by morphological (LYAL 1985) and molecular (BARKER et al. 2003) data. Notable apomorphies for Rhynchophthirina include an anterior prolongation of the head into a rostrum with mandibles terminal and rotated 180°, and extension of the pretarsal apodeme into the femur without a tibial muscle bundle.

Amblyceran classification has been the subject of several detailed studies, most notably by CLAY (1970), who did much to stabilise their familial groupings. CLAY (1969) also considered possible relationships of genera in the largest amblyceran family, the Menoponidae. This study has been considerably expanded by MARSHALL (2003), who provides the most comprehensive study of amblyceran relationships to date covering generic level relationships for almost all taxa that parasitise birds and Australasian marsupials. Her study is broadly consistent with the available molecular studies, although the latter are few in number and largely confined to terminal clades of the amblyceran tree. Significant apomorphies for Amblycera include the development of an antennal fossa concealing the antennae and the presence of a pedunculate first flagellar segment.

Ischnocera form the largest suborder of Phthiraptera and their basal systematics is the subject of intense debate. HOPKINS & CLAY (1952) recognize just 3 families while EICHLER (1963) accepts 21. Based on both molecular and morphological data the most recent studies on Ischnocera recognize at least three monophyletic groups (LYAL 1985; MEY 1994; SMITH 2000, 2001; SMITH et al. in press). These are the Trichodectidae (sensu HOPKINS & CLAY 1952) restricted to mammalian hosts, the Heptapsogasteridae (sensu SMITH 2000) present on tinamiform birds and the Goniodidae (sensu SMITH 2000) of Galliformes and Columbiformes. A fourth group, the Philopteridae (sensu EICHLER 1963) comprise some 70 % of ischnoceran species and are present on almost all families of birds. It is generally accepted that this is a miscellaneous collection of genera and is almost certainly para- or polyphyletic. Despite being the subject of several extensive phylogenetic studies there is little consensus about basal ischnoceran relationships (SMITH et al. in press). Indeed, even the monophyly of the Ischnocera is weakly supported with no unequivocal morphological apomorphies defining this clade. Character convergence, multiple substitutions at high divergences, and ancient radiation over a short period of time have contributed to the problem of resolving ischnoceran phylogeny with the data currently available. A monotypic taxon (the Trichophilopteridae) represented by a single species present on Madagascan primates (Lemuridae and Indridae) may be related to the avian 'Philopteridae'. This species bears a number of significant morphological characters that are apparently intermediate between the 'Philopteridae' of birds and the Trichodectidae of mammals. Consequently the affinities of this genus are unclear, and it has been variably placed amongst both these groups or in an independent family within Ischnocera (SMITH 2001).

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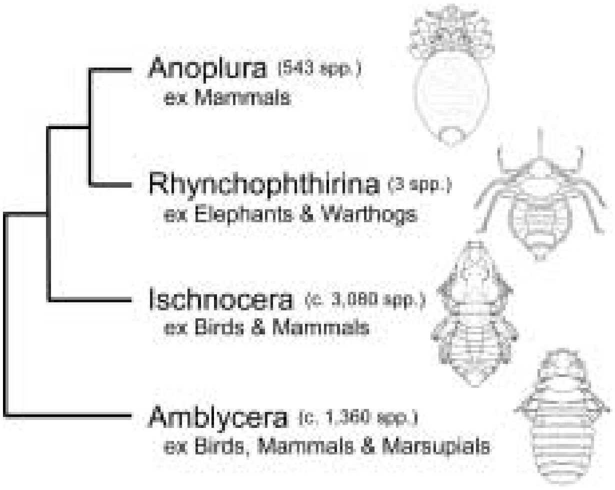

Fig. 1. The four suborders of Phthiraptera and their species content, host range, and phylogenetic relationships.

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Thysanoptera Phylogeny – the Molecular Future

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The monophyly of the Thysanoptera is strongly supported by a number of morphological characters including the protrusible arolium on the pretarsus and the asymmetric mouthparts (right mandible is absent). Molecular analyses also strongly support the monophyly of the Thysanoptera (CRESPI et al. 1996).

The current classification of Thysanoptera consists of approximately 5500 species in two suborders, Tubulifera and Terebrantia, and nine families, with Phlaeothripidae alone constituting the Tubulifera. The only recent attempt to assess the phylogeny of the order as a whole (MOUND et al. 1980) raises several questions about the relationships of the families within the order that are unresolved with morphological methods. One such question was that of the evolutionary origins of the Phlaeothripidae, which possesses so many autapomorphic characters that it could either be sister taxon to the remaining eight families (i.e., to Terebrantia) or it could be derived from the subfamily Panchaetothripinae, making the Thripidae paraphyletic (see Fig. 1). The former hypothesis is supported by many apomorphic characters that suggest that Phlaeothripidae may be independently evolved from the Protothysanoptera, and several synapomorphic characters that are shared by all of the Terebrantian families (MOUND et al. 1980). The latter hypothesis is based on a number of apparent synapomorphies uniting Phlaeothripidae and Panchaetothripinae to the exclusion of the remaining families (as well as the remaining Thripidae). Some of the questions relating to the relationships of the thysanopteran families were subsequently addressed using molecular methods by CRESPI et al. (1996), who used frag-