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ABSTRACT


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Flightlessness in Diptera is discussed and incidence of wing reduction and loss in the Sphaeroceridae is reviewed. The genus Howickia Richards is particularly unique among genera which display flightlessness because it contains macropterous, brachypterous and apterous species, making it ideal for the study of the evolution of winglessness. This study illustrated, documented and phylogenetically analysed 26 Australian Howickia and Howickia-like species from the University of Guelph Insect Collection. COI data from sphaerocerids around the world as well as morphological data are used to determine outgroups for a morphology-based phylogenetic analysis. Results of the molecular analysis contentiously place Howickia within the strictly New World epandrial process group. Results of the morphological phylogenetic analysis establish one large clade and seven species groups. According to the phylogenetic analysis, wing loss has evolved independently at least three times in Australian Howickia. Several synonymies are suggested for consideration in a future revision.
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CHAPTER 1: INTRODUCTION

1.1 The evolution of flightlessness in Diptera

Wings and their associated musculature are energetically costly with insects’ metabolism during flight over 50-fold higher than at rest (Roff & Fairbank, 1990). In insect species with a short-winged and long-winged form, the short-winged trait is associated with earlier first reproduction, overall greater fecundity, and a longer lifespan (Roff, 1986; Roff & Fairbank, 1990). For these reasons, it is easy to understand how selective pressures would act against flight, and its associated structures, if it were not highly beneficial to an insect to disperse, find resources or mates and/or escape predators. Wing reduction and loss are common in Diptera living on other animals such as the blood-feeding obligate parasites of the families Hippoboscidae, Streblidae and Nycteribiidae. Parasites of endotherms are highly likely to evolve flightlessness because endotherms provide a consistent and persistent habitat which comes together with other similar habitats during mating, giving the parasites no reason to migrate (Roff, 1990; Wagner & Liebherr, 1992). Though wing reduction and loss are far less common in free-living members of the order there are still plenty of examples throughout several families, and researchers have found trends in the environments these species inhabit that could explain their flightless condition.

Roff (1990) found that insects living in alpine environments around the world displayed a higher than average rate of flightlessness. The crane fly genus Chionea are commonly called snow flies because they are often seen walking on top of snow. The entire genus is wingless, and this has often been attributed to cold temperatures in their habitats (Bezzi, 1917; Hackman, 1964; Roff, 1990). While it is difficult to vibrate wings at the rate required for lift in cold temperatures, Roff (1990) believed that the diet of these alpine flies as well as the composition of their habitat
also contributed to their wingless state. Many insects found at high altitudes are scavengers on fallout—bits of arthropods and plant material blown into their environments by strong winds. Roff (1990) believed the blanketing nature of this fallout combined with low rates of succession in alpine areas creates a persistent and consistent habitat that favours the loss of flight.

Marine habitats are another common location for flightless insects. Amongst the Diptera, the incidence of flightlessness in midges is extremely high in marine habitats compared to non-marine habitats (Roff, 1990). The ocean surface is a climactically consistent and extensive habitat, and insects in this environment can disperse by swimming or skating instead of flying. In Diptera, members of the nonbiting midge genus *Pontomyia* are exclusively marine species whose males use their vestigial non-membranous wings as paddles to skate on the water surface to find apterous females (Huang et al., 2014). The flightless midges do not have functional mouthparts and are extremely short-lived so finding food is not a concern.

There is a common belief that the flightless condition is more prevalent on oceanic islands than mainland. This theory began with Darwin (1876) who found what he believed was an inordinate number of flightless beetles on oceanic islands and hypothesized that winged morphs would suffer higher mortality than wingless morphs due to them being accidentently blown out to see or purposely leaving and being unable to reach and colonize a new land mass. While many in the scientific community accepted this explanation, other authors questioned its validity as there was not enough data to reinforce it. Roff (1990) pointed out that Darwin’s theory did not take scale into account and that the area of an island is significantly smaller than its perimeter where insects could be blown out to sea. When area and perimeter were considered, Roff (1990) showed that the chance of any insect being blown out to sea was extremely small, and that the
loss would not significantly affect a dynamic population of insects like it would an individual patch in a small, experimental setting.

The same theory regarding loss of winged individuals through straying from the main population has also been proposed as an explanation for flightless species at higher altitudes (Roff, 1990). While Roff (1990) did find a statistical correlation between flightlessness and increasing altitude in insects and agreed that straggling could significantly affect small insect populations in constricted areas such as mountain tops, he also pointed out that flightlessness had to have evolved before this process could take effect. Roff (1990) suggests that ultimately, the habitat must be stable enough for the costs of flight to outweigh its benefits and allow flightlessness to evolve in the first place. Habitat homogeneity and stability is currently the most widely accepted explanation for the evolution of flightlessness in insects (Perkins, 1913; Hackman, 1964; Roff, 1990).

The forest floor is one of the most common habitats of free-living flightless insects Perkins, 1913; Hackman, 1964; Roff, 1990). Roff (1990) found that flightlessness occurred at an above average level in woodlands in Orthoptera, Coleoptera and Lepidoptera. The leaf litter floor in woodlands is a homogenous habitat that is insulated from climactic extremes and has resources distributed relatively evenly amongst it and so it makes sense that flightlessness would be selected for in these environments (Roff, 1990). A large number of wingless flies in the families Dolichopodidae and Limoniidae live in the mountainous regions of Hawaii, and it has been theorized that the lack of predaceous ants at high elevations has allowed flightlessness to evolve (Hardy & Delfinado, 1973; Bickel, 2006). This theory was reinforced when the introduction of invasive, predaceous ants by humans to Hawaii was followed the extinction of the flightless dolichopodid *Emperoptera mirabilis* Grimshaw (Bickel, 2006). However, many flightless
Diptera do occupy the same habitats as ants, especially amongst the apterous sphaerocerids of Africa and Australia, and so while they may be a contributing factor, the lack of ants cannot fully explain the case of flightless Diptera in Hawaii. Instead, Perkins (1913) believed that flightlessness in Hawaiian insects could be explained in a similar way to that of flightless insects all over the world; by a forest floor habitat. In addition to the forest floor being a stable and persistent habitat, living in such a concealed environment makes flying away from predators ineffective, and instead favours running and jumping (Hackman, 1964). A terricolous habitat is one of the most common prerequisites for the evolution of flightlessness in free-living insects including Diptera.

Amongst Diptera, the family with perhaps the highest number of described flightless species may be the Sphaeroceridae, though this has not been formally quantified (S. Marshall, personal communication). While there is a significant number of flightless sphaerocerids around the world, Richards (1938, 1951a, 1951b, 1954, 1955b, 1957, 1960a, 1960b, 1963, 1965, 1966, 1968b) has described an unusually large number of genera with reduced or absent wings on mountains in Africa. Richards (1957) noted that the vast number of species in very restricted and relatively nearby ranges suggested sympatric origins. Hackman (1964) also addressed these African sphaerocerids and further discussed how speciation has likely taken place at a high rate among these apterous genera due to the genetic isolation that inevitably occurs when species are restricted to concealed and specialized niches such as under leaf litter and rocks at extreme elevations.

More recently, Roháček (2012) reviewed European sphaerocerid species with multiple wing states (polymorphic) and his own research into their probable evolution. Roháček noticed a distinct trend of many polymorphous species where the percentage of brachypterous specimens
in a population was directly related to latitude and elevation, where decreased latitude and increased elevation saw more brachyptery. This suggests that colder climates decrease the fitness of flight-capable specimens and favours flightless specimens. Another less well-studied factor that Roháček found largely influenced the development of flightlessness was humidity. The majority of polymorphic sphaerocerids that he studied were found in hypogean environments such as peatbogs and ravine leaflitter. Here, long wings inhibited specimens from penetrating deep layers of leaf litter and favoured brachyptery or aptery.

Through his observations, Roháček (2012) was able to draw conclusions regarding the evolutionary processes acting behind brachyptery and aptery. He found that in wing polymorphic species, preferred habitats of brachypterous and macropterous forms overlapped, allowing for genetic exchange and perpetuating multiple wing states. However, in dimorphic species, brachypterous and macropterous forms were more isolated due to their niche preferences. For example, the brachypterous form of *Crumomyia pedestris* was found in very humid, boggy areas where the larvae fed on dead snails, but the macropterous specimens were found in very arid, open areas, especially mammal burrows. This may be a case of parapatry where the different preferences may eventually lead to the evolution of two distinct species. Indeed, Roháček concluded that wing polymorphism was a transient stage in the evolution of brachypterous or apterous species. He also noted that this evolutionary process was likely slower in large regions in temperate zones where environmental conditions were more stable than say on a mountain top or island where species are more likely to be genetically isolated.

1.2 The Sphaeroceridae

The Sphaeroceridae are small, common and diverse group of flies associated with decaying organic matter. The common name, small dung flies, is misleading as only a small portion of
sphaerocerids are coprophages. Many species feed on carrion and decaying fungi, while the vast majority are associated with rotting vegetation (Roháček et al., 2011). The family contains some cosmopolitan species, but there is a much greater diversity of species living in highly specialized habitats such as animal burrows, the nests of social insects, inside of specific plants, deep inside of caves or leaf litter, on decaying seaweed, in subantarctic conditions, at high elevations and many more. This extreme adaptability has likely led to the enormous species richness and morphological diversity of the family (Roháček et al., 2011).

The study of Sphaeroceridae is an active field with every revision inevitably resulting in the description of more than double (usually much more) the existing species in a genus. In the World Catalogue of Sphaeroceridae (Roháček et al., 2001), the family consisted of five subfamilies containing 111 genera and 1339 described species. In the catalogue update (Roháček et al., 2011) the family contained 141 genera and 1550 species. Just after the catalog’s release, Kits and Marshall (2011) recognized Archiborborinae as a sixth subfamily of Sphaeroceridae. Today the Sphaeroceridae are made up of six subfamilies containing 158 genera and 1782 species [based on Paiero, 2018 plus publications since 2018]. The subfamily Limosininae is substantially larger and more diverse than any other subfamily, containing about 150 genera and 1650 described species, and it remains the most complex problem in the higher classification of sphaerocerids due to the vast physical diversity of its members (Roháček et al., 2011).

1.3 Wing loss and homoplasy in the Sphaeroceridae

The diversity and sheer number of Limosininae have made studying the relationships between genera very difficult, but this is highly compounded by wing loss and reduction (Roháček et al., 2011). For over a century systematists have noticed that flightless sphaerocerids have a surprisingly homogenous appearance. Just as a terricolous lifestyle selects against flight, it also
selects against other characters that would normally benefit flight-capable Diptera in more
traditional environments.

Halteres are gyroscopic organs normally used by flies to maintain balance while flying and, in
general, are reduced or lost in flightless Diptera (Bezzi, 1917; Hackman, 1964). Ocelli too,
which are normally used to sense changes in light and have been shown to contribute to
orientation during flight (Kalmus, 1945; Luk & Marshall, 2014), are often reduced or absent in
brachypterous and apterous flies. In many sphaerocerids there is often a marked reduction or loss
of chaetotaxy throughout the body, perhaps due to close quarters causing them to rub off or
hinder locomotion (Richards, 1951; Luk & Marshall, 2014). Thoracic morphology is distinctly
modified in apterous sphaerocerids, with an obvious reduction in the mid to posterior pleural
sclerites such as the anepimeron, the katatergite, the katepimeron, the meron and the
mediotergite (personal observation). This is related to the reduction in flight musculature. The
prosternum is also often broadened, likely due to enlarged leg muscles for running and jumping
(Hackman, 1964). The abdomen of flightless sphaerocerids is often short, broad, and sometimes
subpetiolate in its attachment to the thorax (Richards, 1951). This may allow the abdomen to be
better positioned for walking, allowing it to lift off the ground instead of hanging downwards
slightly as it does in most flying insects. In some species the abdomen is so petiolate that it is
difficult to distinguish from an ant, and many species are extremely beetle-like with their round,
shiny abdomen. This apparent mimicry appears in both winged and wingless flies, though it is
more common in wingless species. In many flightless species the abdomen is also well-
sclerotized, perhaps to avoid scratches as they navigate the forest floor (Luk & Marshall, 2014).
Together these terricolous modifications lead to many flightless sphaerocerids displaying striking
convergence as can be seen in Neotropical genera such as *Aptilotella* Duda, *Aptilotus* Mik, and
*Myrmolimosina* Marshall & Buck, several Afrotropical genera such as *Mesaptilotus* Richards, *Ocellipsis* Richards, *Pismira* Richards, and *Scutelliseta* Richards, and Australasian genera such as *Howickia* Richards, *Monteithiana* Richards, and *Bentrovata* Richards.

Many of the body parts affected by the loss of flight are normally highly diagnostic on a generic level, such as head and legs chaetotaxy and wing venation. This has created problems for systematists for as long as they’ve been describing apterous flies. Richards in particular struggled with the challenge of how much weight to give characters associated with aptery when faced with the numerous apterous sphaerocerids from Mount Elgon and the Ruwenzori Mountains in Africa (1951, 1960, 1966). He noted “There seem to be two viewpoints which must somehow be accommodated. First, it is sometimes suggested that apterous and brachypterous species, especially in families where the condition is common, should be placed in the most similar normal genus. There are even stronger grounds for doing this if species are known which are dimorphic… The second view to which I myself have hitherto adhered is that in the African Sphaeroceridae there are so many apterous species, often too highly modified for the winged ancestral stock to be guessed at with any certainty, that it is necessary to fit them into a number of genera” (Richards, 1966). In this same work Richards also noted that “male genitalia might here prove to be the best clue to the relationship… it seems to be the only way to reach a natural classification”, but that “the genital characters are not yet well enough known to place all the species in their logical position”. Sphaerocerids are now known for their character-rich terminalia and looking internally can give us a great deal more information about the origin of a species than external characters alone. Such is the case of *Aptilotus*, which is a genus first erected for a single apterous Palearctic species (*A. paradoxus* Mik), and later included two apterous Nearctic species which Richards believed were more closely related to macropterous Nearctic
species than to *A. paradoxus*. Marshall (1983) analysed the male terminalia of *A. paradoxus* and several new apterous, brachypterous and macropterous North American and Palaearctic species and found that, not only were they one related group (*Aptilotus*), but that most apterous species was more closely related to a macropterous species than other apterous species. Analysis of the terminalia of the numerous apterous species and genera around the world, especially in Africa and Australia, would undoubtably lead to similar synonymies, but is only possible with large, more complete collections of both winged and wingless specimens to compare. The Australian sphaerocerid collection at the University of Guelph insect collection is remarkably complete and with extensive curation and study should allow for advances to be made in flightless sphaerocerid taxonomy. However, African sphaerocerids have been far less extensively collected and both apterous and macropterous species should be targeted by sphaerocerid experts in the future to allow for meaningful comparison of the terminalia. Perhaps connections could even be seen between flightless Australian and African species.

### 1.4 Quantifying wing reduction and loss in the Sphaeroceridae

Though wing loss and reduction seems like a rare and anomalous trait for a fly, it is fairly common throughout the Sphaeroceridae. An exhaustive literature search was performed in order to quantify the degree of wing reduction and loss in the Sphaeroceridae (see Appendix 1). The wing states of each species were characterized using the following definitions from Hackman (1964) and Roháček (2012): Brachypterous species have reduced, blunt wings that are shorter than the abdomen, with at least the radial veins still distinct; stenopterous species are brachypterous but with very narrow wings; micropterous species have a small vestigial appendage of varying shape, with at most the traces of radial veins; dimorphic species have two distinct wing states in both sexes, usually macropterous (fully winged) and brachypterous;
polymorphic species have more than two wing states in both sexes including macropterous and varying degrees of brachyptery; apterous species may have a scale-like vestige with or without bristles, or have nothing at all. Where possible, the state of the halteres and ocelli were noted as well as any habitat information from label data. A “?” means that the data was not discussed in the species description.

A total of 225 described species of sphaerocerids that display some degree of wing loss were found (Appendix 1). There are 134 described apterous species of sphaerocerids in 22 genera, of which 19 species have females that are apterous and males that are brachypterous. Approximately 85% of wingless or wing reduced sphaerocerids belong in the subfamily Limosininae, which is to be expected as it is by far the largest subfamily. Only a single species belonging to Sphaerocerinae, three species belonging to Copromyzinae and 27 species belonging to Archiborborinae display reduced or lost wings. The small subfamilies Tucminae and Homalomitrinae contain only macropterous species.

Almost all reduced wing or wingless sphaerocerids are terricolous (found living on the ground or in the soil) and were mainly collected in leaf litter. Many species were noted in damp environments such as in peatlands or wet moss and litter. There are 122 species recorded as occurring at high altitudes (1500 m and higher), and this number is likely higher since many species were recorded in mountainous regions but lack elevation data. Five species were even recorded under stones, which may be due to a lack of litter at extreme elevations. Four of these species are found at the highest range of elevations recorded (from 3200-4300 m), while one is found on beaches which would also lack leaf litter. There are 22 species found on small islands, three of which occurred on subantarctic islands. Three species are found exclusively in caves.
The loss of halteres is highly correlated with wing reduction and loss. Halteres are absent in 169 species and small or reduced in 26 species, 15 of which had sessile halteres. A sessile haltere is probably a transition state to full loss and would likely no longer act as a gyroscopic organ as they would not be able to freely oscillate. *Howickia* is the only genus in which apterous species occur with normal halteres, and only five of the 17 described apterous or reduced winged species have lost halteres. Perhaps the halteres are serving another unseen purpose in this group for them to retain an organ that is so strongly selected against in the rest of the reduced winged species of the family.

Ocelli appear less strongly selected against than halteres in reduced wing species. They are absent in 40 species and reduced in 67 species. Many descriptions either did not discuss ocelli or only mentioned if they were present and it was not possible to know if they were reduced, though it is likely that the ocelli were not abnormal if the authors failed to mention them.

### 1.5 The collection of flightless sphaerocerids

Historically, flightless flies have been poorly represented in collections due to the nature of their collection. Large quantities of flies can be efficiently caught using Malaise traps and so these have been favoured collection methods of dipterists. However, flightless flies are best collected with pan traps or Berlese funnels, which were more often used by entomologists looking for ground-dwelling insects such as beetles and ants. Over time dipterists have taken note of the unique apterous specimens found in pan traps and began to target them.

Richards made one of the largest efforts in describing wingless sphaerocerids, describing dozens of apterous Afrotropical and Australasian genera from the 1930’s to the 1970’s, often from pan trap residues of other entomologists. Papp (1976) began soil trapping for apterous flies after noting many new species in soil trap residues from other researchers, and the lack of
terricolous sphaerocerids in the Hungarian Natural History Museum. Steve Marshall began making a point of looking for wingless species as well as their closest winged relatives in the late 1970’s while sampling the páramo in Ecuador (personal communication). While his collection of apterous Andean flies is significant, the majority of Marshall’s efforts towards apterous sphaerocerids has been focussed in Australia and New Zealand over the last 25 years which, combined with the specimens he sorted out of Stewart Peck’s residues, has resulted in the largest collection of wingless sphaerocerids from the Australian region in existence. This extraordinarily rich collection of apterous, brachypterous and macropterous species allows an opportunity to link apterous specimens to their winged ancestors and study the evolution of winglessness.

1.6 The genus Howickia

The genus Howickia Richards is a strictly Old World taxon with described species occurring in mountainous regions of Thailand, Nepal, India and Pakistan, with the highest concentration of described species from Australia and New Zealand. Prior to the revision of the New Zealand species (Marshall et al., 2014), Howickia only included a single apterous species from New Zealand. Marshall et al. (2014) suspected that the unique characters originally supporting the monophyly of Howickia were simply the result of wing loss, and that if examined more closely it would prove to be a synonym of another macropterous genus. This presumption was correct, and a revision of the New Zealand Howickia resulted in the synonymy of a mainly macropterous genus, Biroina Richards with Howickia, along with the description of 14 additional apterous species, and two fully winged species. Howickia was newly defined on the basis of characters of the male terminalia. Based on these results it was presumed that many of the Australian sphaerocerids in the University of Guelph Insect Collection would belong to Howickia, including many, if not all, of the apterous species.
1.6.1 Taxonomic history of *Howickia*

Hutton (1901) described *Apterina trilineata* Hutton, an apterous sphaerocerid from New Zealand with halteres and no ocelli. Richards (1951) decided *A. trilineata* was morphologically distinct enough to warrant putting it into its own genus, *Howickia* Richards.

In 1925, Duda described *Biroella* Duda as a subgenus of *Leptocera* Olivier based on *Limosina myrmecophila* Knab & Malloch 1912. In 1973, Richards recognized that the name *Biroella* was preoccupied by a grasshopper and changed it to *Biroina* Richards. He described 15 new species of *Biroina* at this time, two which were apterous and included in *Biroina* “based on general appearance”: *B. dodo* Richards from Australia and *B. myersi* Richards from New Zealand. He also erected three new genera for other brachypterous and apterous Australian sphaerocerids based on differences in ocelli, orbital setae and prosternum shape: *Monteithiana* Richards, *Bentrovata* Richards, and *Otwayia* Richards. In 1979, Papp erected the monotypic Australian genus *Apterobiroina* Papp distinct from previous apterous genera due to its wide, quadrangular prosternum.

Marshall (1989) elevated *Biroina* to genus level and listed all 15 species in the Australasian/Oceanian Diptera catalog. Papp (1995) described three species of Oriental *Biroina* (from Thailand, Pakistan, India and Nepal). Roháček et al. (2001) listed all 18 species in the World Catalog of Sphaeroceridae. Marshall et al. (2011) mentioned that *Biroina* was under revision and would likely be synonymized with *Howickia*. Marshall et al. (2014) redefined *Howickia*, synonymized it with *Biroina* based mainly on characters of the male terminalia, and newly described 14 apterous species as well as two macropterous species. They also suggested *Apterobiroina* may belong to the redefined *Howickia*. 

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1.6.2 Biology and natural history of *Howickia*

Except for biological and habitat data as noted on specimen labels, little is known of the natural history of *Howickia*. In general, the vast majority of sphaerocerids are microbial grazers on decaying plant matter (Marshall and Richards, 1987; Roháček et al., 2001). Most of the *Howickia* specimens in the University of Guelph Insect Collection have been collected in pan or pitfall traps baited with dung, carrion or fungus, and many winged specimens were collected in flight interception traps. Australian *Howickia* have been collected at a wide range of elevations from sea level to 1500m, though most specimens in the University of Guelph Insect Collection were found from 500-1200m. Described species of *Howickia* from Thailand, Nepal, India and Pakistan have been found in mountainous regions from 600-2800 m. Some series of collections taken at regular intervals throughout the day suggest *Howickia* are equally attracted to baited pans during the dawn, day, dusk and night.

On a collecting trip to Australia in 2016, Dr. Marshall noted that baited traps attract nearby *Howickia* specimens quite quickly and take relatively few specimens after the first hour. This could imply that *Howickia* are not travelling long distances for food, which aligns with some hypotheses for the evolution of aptery. Roff (1990) suggested that habitat homogeneity selects for flightlessness, especially habitats in which the climate is relatively stable and resources are distributed evenly. He believed that these habitats were more efficiently traversed on foot rather than by flight, and the inhabitants would have little incentive to leave. Roff (1990) suggested that leaf litter was an example of such a habitat, and many of the flightless *Howickia* specimens in the University of Guelph Insect Collection were found in terricolous forest environments. One would assume standard Berlese funnel extractions of leaf litter would be a profitable method of collecting specimens, though there is only a single specimen label that mentions using one (*H.*
*cynthia*, Renison Bell, 5 km NW, Berlese rainforest litter, 180m, 1 May 1987, N.I. Platnick, et al. (1#m, DEBU)). This suggests that a wealth of *Howickia* material awaits in Berlese residues from Australian weevil and spider collectors.

*Howickia myrmecophila* (Knab & Malloch) was so named because it was originally found in the presence of ants; however, this was likely a coincidence, as there are no further records of this species associated with ants (Richards, 1973). Dr. Geoff Monteith documented *H. myrmecophila* riding the backs of the scarab beetle *Cephalodesimius arminger*, and in the burrows of these beetles (Richards, 1973). He also documented one specimen of *H. subsinuata* bred from the beetle burrow. It may be that the flies are feeding on the beetle’s feces, but this is only speculation. Dr. Steve Marshall has collected and photographed *H. myrmecophila* in a wide variety of habitats, including debris on concrete steps, suggesting that this species is a common generalist (personal communication).

1.6.3 Relationships to other genera

There is not much known about the relationship of *Howickia* to other sphaerocerid genera. This is in part due to the limited taxonomic work on sphaerocerids in and around Australia, especially southeast Asia. Most of the Australasian sphaerocerid taxonomy has not been updated in almost 50 years since Richards tackled it, and current revisionary work may help elucidate relationships between the genera.

In their revision of the *Howickia* of New Zealand, Marshall et al. (2014) noted that fully winged *Howickia* are externally similar to *Paralimosina* Papp species, which also have posteroventral hypandrial lobes that are lacking in any New World taxa. This suggests that the ventral hypandrial lobe may characterize an Old World clade including *Paralimosina* and related genera. They also noted that *Paralimosina* differs from *Howickia* in their mid tibial chaetotaxy,
distiphallic structures and female terminalia. The relation of *Paralimosina* to *Howickia* is worth looking into further.

### 1.6.4 The current state of the Australian *Howickia*

In their revision of the New Zealand fauna, Marshall et al. (2014) redefined *Howickia* by the hypandrial structure of the male terminalia which consists of a main Y-shaped branch, a ventral hypandrial lobe, and a posterodorsal hypandrial apodeme (Fig. 2.4). Other probable apomorphies Marshall et al. (2014) included were telescoping female terminalia, a heavily sclerotized abdomen, a small but posteriorly prolonged basiphallus, a simple and tubular distiphallus at least in basal half, a posteromedially concave male sternite five, a strongly sinuate R$_{2+3}$ in winged forms, a mid tibia with paired anterodorsal-posterodorsal setae distally and proximally, and only an apical bristle ventrally, and a petiolate palpus. A revision of the Australian *Howickia* remains a necessary task, and that is what I had originally intended to do.

The more Australian sphaerocerids that I sorted through at the University of Guelph, the clearer it became that external characters listed by Marshall et al. (2014) as probable apomorphies were not going to work for the Australian *Howickia*. There were other specimens with matching mid tibial chaetotaxy, a sinuate R$_{2+3}$, and telescoping female terminalia that when dissected, did not match the defining hypandrial structure of *Howickia*. On top of this, there were flies with a feebly sinuate R$_{2+3}$ that did have the *Howickia* hypandrium. The Australian *Howickia* were not currently reliably identifiable using external characteristics.

The Australian sphaerocerid fauna is complicated with many small genera that seem to share external characteristics with *Howickia*. Richards’ (1973) key to the genera and subgenera of the Sphaeroceridae of Australia, New Zealand and New Guinea is non-functional and inconsistent, with the same characters appearing in sequential couplets, and most couplets containing
noncommittal descriptors such as “rarely so”, “nearly always”, “more or less”, and “relatively” that do not allow certain diagnoses by users. Richards (1973) key notably struggles to distinguish between Howickia, Pleuroseta Richards, Popondetta Richards, Pterogramma Spuler and Acuminiseta. A revision of Pterogramma (Smith & Marshall, 2004) revealed that it is a strictly New World genus, and that the “Pacific Pterogramma” were a distinct undescribed genus which included many previously described “Pterogramma” and several undescribed species which they were preparing to revise. Papp (2008) described one new species from that group in a new genus, Pseudopterogramma Papp, and included a single previously described “Pterogramma” species from Papua New Guinea. He never provided a definition or diagnostic characters, and never addressed the other Australasian species that Smith & Marshall (2004) had specifically stated belonged in that group. These undescribed Pseudopterogramma of Australia are externally very similar to Howickia with identical mid tibial chaeototaxy and a short, sinuate R_{2+3}.

There are currently 14 described species of Howickia from Australia with descriptions in Richards (1973). Unfortunately, most species are vaguely defined and poorly, if at all, illustrated as this was before it became conventional to thoroughly analyse and describe terminalia. This creates a problem for anyone looking to revise the genus and describe new species, as it makes the likelihood of describing synonyms very high. Dr. Marshall had photographed and made notes on several types during his visits to Australia, which were useful in putting names to some of the species in the University of Guelph Insect Collection, but I still needed to see several species. The Australian museums that the types were deposited in were reluctant to ship type material for examination, which is typical as the delicate material is easily damaged during transportation. They were willing to send me external photos of type specimens, which proved useful in some cases for putting names to a few more species at the University of Guelph, but many species did
not have unique identifying characters easily visible from habitus photos. This, combined with
the fact that the only reliable method we currently have for identifying many Australian
*Howickia* is through dissection of the male terminalia, made the prospects of a full revision
bleaker.

The Australian sphaerocerid collection at the University of Guelph is massive and spans more
than 20 mostly unsorted drawers. Hui Dong of the Shenzhen & Chinese Academy of Sciences
visited the University of Guelph Insect Collection in 2008 and joined Dr. Marshall’s effort in
identifying and sorting the Australian *Howickia* as part of her doctoral thesis. Dong ultimately
had to focus her research on Chinese species but managed to sort much of the material
tentatively identified as *Howickia* at the time and sorted it into recognizable species. Dong also
correctly determined the previously described species for which the characteristics were distinct
enough and the descriptions adequate to allow proper determination (*H. myrmecophila*, *H.
subsinuata*, and *H. trivittata*), and illustrated the genitalia of many of her recognized species.
Unfortunately, these recognized species were not sufficiently labelled, and it was difficult to
match the drawings to the corresponding flies. I examined all the partially sorted material and
found several more cryptic new species within. I had 26 recognizable species, about half of
which were apterous, one which was brachypterous, and the other half were macropterous. The
vast majority (16 drawers) of the Australian sphaerocerids in the University of Guelph Insect
Collection remain unsorted and undoubtably contained many more undescribed species.

I had still not come any closer to finding definitive external characters that could be used to
easily identify *Howickia*. In fact, I had come further as some of my recognized Australian
species challenged most of the probable apomorphies of the group. A proper revision of the
Australian *Howickia* was going to be a much larger project than I initially thought. It would
require addressing all of the described Australian species and genera that could potentially belong to *Howickia*, redescribing the existing Australian *Howickia* (many of which remained unidentifiable), sorting the remaining massive University of Guelph Insect Collection of Australian sphaerocerids, and ideally addressing the *Howickia* at other Australian museums. The fact remains that this is a really interesting group with a roughly equal number of apterous and macropterous species, and even some transitional brachypterous species. The Australian *Howickia* are the perfect group with which to study the evolution of winglessness using phylogenetics, whether or not they are fully revised and described.

1.7 Objectives & Hypotheses

1.7.1 Objectives

This study will illustrate and document a group of recognized species of Australian *Howickia* from the University of Guelph Insect Collection, including macropterous, brachypterous and apterous species. Molecular and morphological data will be used to determine genera most closely related to *Howickia* in order to inform outgroups for phylogenetic analysis. Phylogenetics will be used to analyse the evolution of winglessness in group of Australian *Howickia* species. This study will look at the number of times winglessness has evolved in this group of *Howickia* and investigate possible reasons for this evolution based on trends in the evolution of wing loss in the rest of the Sphaeroceridae. Based on the results of the phylogenetic analyses, species groups will be defined and help contribute to the later revision of the Australian *Howickia*.

1.7.2 Hypotheses

The following hypotheses regarding the evolution of winglessness in Australian *Howickia* were tested using phylogenetic analyses:
1) If flightlessness has evolved multiple times in the Australian *Howickia*, then I would expect some apterous species to be more closely related to macropterous species than to other apterous species.

2) If the dispersal ability of flightless *Howickia* is severely limited, then I would expect the apterous species on mainland Australia, Tasmania, and Lord Howe Island to represent independent evolutionary transitions to winglessness.

3) If speciation occurs at a higher rate in flightless species living in concealed habitats, then I would expect to see multiple morphologically similar apterous species occupying the same geographic range which are more related to one another than any other species.

**CHAPTER 2: MATERIALS AND METHODS**

**2.1 Species concepts**

Without completing a full revision in which every described specimen that is currently *Howickia* or could possibly be *Howickia* is considered, formally describing any perceived new species would be irresponsible as it could be a synonym. The formal descriptions are best saved for a later complete revision of the Australian *Howickia*. Instead, I have used recognized species as operational taxonomic units (OTUs) with manuscript names. OTUs allow me quantify characters and study the relationships among and surrounding this diverse and fascinating group without a complete and formal revision. Perceived undescribed species are referred to in the text and figures with their names in quotations marks; these names refer to manuscript names and are not considered published under the rules of the International Commision on Zoological Nomenclature. Where it was possible to match recognized species with previously described species I have done so, and those names are not in quotations. Several species first treated as
Howickia were later identified as described species in other genera. The current names of those described species are used throughout this work and possible synonymies are discussed in the comments section of the species accounts.

2.2 Species documentation

The majority of recognized species used in this study are from the University of Guelph Insect Collection (DEBU). While sorting miscellaneous drawers of sphaerocerids which had previously been borrowed from the Australian National Insect Collection (ANIC) I recognized another new apterous species (“H. discoloris”) which was not present in DEBU. This species was included to increase the number of apterous species in my analysis.

All 26 recognized species were documented photographically in species plates with a standard set of character informative images. Plates included the following images when possible: a head shot, a lateral habitus shot, images of the male terminalia including a ventral shot of sternite 5, a lateral and posterior shot of the epandrium, and a lateral shot of the internal structures, images of the female terminalia including a ventral shot of the hypoproct, a dorsal shot of the epiproct and a shot of the spermathecae. Occasionally some images were not available for certain species and this is specified in the species plate captions. All species considered in this work have the hypandrial structure that defines Howickia including the Y-shaped main part, the posterodorsal apodeme and the ventral hypandrial lobe. The ventral hypandrial lobe is often translucent and very delicate (in Clade 1 species) and is often lost in dissections so it is not always present in photos here.

Each OTU is listed in section 4.1 along with the type information of previously described species, the etymology of the given manuscript name if it is a perceived new species, and comments on identification, similar species, and/or locality where available and appropriate. For
previously described species the comment section includes discussion of how I determined the identification. A list of specimens examined is provided for each OTU in Appendix 2.

2.3 Specimen preparation

Most specimens were collected in pan traps and stored in alcohol for a time before they were critical point dried and point-mounted. Terminalia were prepared for examination by separating whole abdomens from mounted specimens. Male abdomens were cleared in hot 10% potassium hydroxide (KOH) for 20 to 30 minutes, neutralized in glacial acetic acid for an equal amount of time, and rinsed in deionized water. Specimens with very dark and heavily sclerotized abdomens were soaked in 3% hydrogen peroxide for 15-20 minutes to lighten them for photography. Female abdomens were delicate and often poorly sclerotized, and the KOH method often resulted in over-clearing, so most were enzymatically cleared according to Yau and Marshall (2015) with trypsin (0.5%) ethylenediaminetetraacetic acid solution in 2 ml vials at room temperature for at least 24 hours and then rinsed in deionized water. Cleared abdomens were transferred to glycerin in concavity slides for microscopic further dissection and examination. Male terminalia were photographed whole before the internal parts were dissected out and photographed. Due to the nature of the Howickia hypandrium being extremely well-secured to the epandrium, the dissection of internal parts for photographic documentation often meant sacrificing the external dissection. I felt that this sacrifice was justified in order to obtain a clear and permanent photograph and only did so if there was more than a single male specimen in the collection. All dissected parts were stored in glycerin in microvials pinned below specimens after examinations.
2.4 Photography and illustrations

Most whole specimen images were taken using a Canon DSLR mounted on a Stackshot system (Cognisys Inc., Michigan USA) and stacked using Helicon Focus (Helicon Soft Ltd., Kharkiv Ukraine). The head and habitus shots of “H. discoloris” and “H. parasubsinuata” were taken through a dissecting microscope with a Google Pixel 2 cellphone camera since the lab camera system was out of order for a time. Genitalia photographs were taken using a Nikon Coolpix 4500 mounted on a Zeiss compound microscope and stacked using Zerene Stacker (Zerene Systems LLC, Washington USA). Photos were visually enhanced in Adobe Photoshop CC 15 (Adobe, California USA). Species plates were assembled and edited using Inkscape: Open Source Scalable Vector Graphics Editor (Inkscape project, New York USA).

Scanning electron microscopy (SEM) was used to illustrate the texture of the frons of H. kentia which could not be clearly seen under a dissection microscope. A cleaned specimen, including the paper point, was placed on carbon tape adhered to stubs and then coated with a layer of gold-palladium using an Emitech K50 sputter coater. Photographs were taken with a Hitachi S-570 scanning electron microscope at the Department of Food Science, University of Guelph.

2.5 Outgroup determination

Before the set of Howickia and Howickia-like species could be phylogenetically analysed appropriate outgroups had to be determined in order to properly polarize characters. Since almost nothing was known about the relationships of Howickia to other sphaerocerid genera, a combination of morphological and molecular evidence was the best method for finding outgroups for my morphological phylogenetic analysis.
2.5.1 Morphology-based outgroups

Marshall et al. (2014) first noted the superficial similarity of Paralimosina Papp 1973 to Howickia due mainly to the posteroventral hypandrial lobes, however, they also noted the very different male and female terminalia, wing venation and mid tibia chaetotaxy. I further investigated this relationship to determine if Paralimosina would make a suitable outgroup by comparing external and internal morphology of male and female Paralimosina species to my recognized Howickia species.

I also further investigated the relationship between Howickia and the entirely undescribed or incorrectly placed Australian species belonging in Pseudopterogramma Papp 2008, which were previously treated as Pterogramma Spuler 1923 prior to the review of Smith and Marshall (2004). These flies are easily confused with Howickia due to their shared bright colours, mid tibia with paired proximal and distal anterodorsal-posterodorsal setae and short, sinuate wing vein R_{2+3}.

2.5.2 Molecular-based outgroups

A dataset of sequenced global sphaerocerids and their associated cytochrome c oxidase subunit I (COI) data from the Barcode of Life Data Systems (BOLD) was created by Valerie Levesque-Beaudin of the Centre for Biodiversity Genomics at the University of Guelph. This dataset contained 17567 specimens. I examined the 2253 photos available from this dataset and identified several Howickia and Howickia-like species. These species were loaned from the Centre for Biodiversity Genomics in order to confirm their identifications. Australian Howickia species identified were Howickia capitalis Richards, H. myrmecophila, “H. parasubsinuata”, “H. spina”, H. subsinuata, H. trivittata, and one unknown Tasmanian species. Two Howickia species from New Zealand were also identified, including one apterous species.
A data subset was created of Barcode Index Number (BIN) representatives which contained 1569 specimens. A parsimony analysis was conducted on this molecular data in TNT version 1.1 (Goloboff et al., 2008) using a New Technology search (using ratchet, tree-drifting, tree-fusing, and sectorial search). Trees were viewed in FigTree version 1.4.4 (A. Rambaut, 2009) and visually enhanced in Inkscape (Inkscape project, New York USA). The resulting trees were examined to determine the closest relatives to the identified Howickia in order to find potential outgroups for the morphological phylogenetic analysis.

Many specimens in the dataset were not identified past family level and it is worth noting that there were no identified specimens belonging to the genera deemed most morphologically similar to Howickia, Paralimosina and Pseudopterogramma.

2.6 Morphological phylogenetic analysis

Once the outgroups were determined through molecular and morphological evidence, the species were initially scored based on 54 morphological characters. Characters were chosen based on a combination of those used in previous sphaerocerid matrices (Smith & Marshall, 2004; Luk & Marshall, 2014; Yau & Marshall, 2018; Paiero, 2018) as well as unique and relevant characters to Howickia. Care was taken to not include traits related to aptery such as those surrounding halteres, ocelli and the state of wings as to prevent the appearance of relation due to homoplasy. The morphological interpretations and terminology used in this work follow Cumming and Wood (2009). Distiphallic terminology was adapted from Marshall (1985) and Luk and Marshall (2014), with the addition of some new terms for structures of the Howickia distiphallus. General chaetotaxy and wing venation of Howickia can be seen labelled in Figures 2.1-2.4. Fully labelled terminalia morphology can be seen in Figures 17.1-17.9.
Due to the results of the analysis of the first matrix, a second matrix was made using only a single morphology-based outgroup. This is further discussed in section 4.3.2. The second matrix scored the species on 44 morphological characters which were modified from the first matrix to suit only the single outgroup and *Howickia*.

Mesquite version 3.51 (Maddison & Maddison, 2018) was used for the construction of the character matrices (Tables 1 and 2). The matrices were analyzed in TNT version 1.1 (Goloboff et al., 2008) using a traditional search. The resulting trees were optimized using Winclada (Nixon, 1999) and visually enhanced in Inkscape (Inkscape project, New York USA).

CHAPTER 3: RESULTS AND DISCUSSION

3.1 Species accounts

Species accounts are presented in alphabetical order.

*Apterobiroina australis* (Papp, 1979)

(Figs. 4.1-4.9)

*Apterobiroina australis* Papp, 1979e: 370-372; Roháček et al., 2001: 117.

**TYPE MATERIAL.** Holotype male. **Victoria:** Mount Buller, Mirimbah, 10 Aug 1972, P. Zwick (MHNG).

**PARATYPES.** **Victoria:** Mount Buller, Mirimbah, 10 Aug 1972, P. Zwick. (3#m); Warburton, near Donna Buang, Cement Creek, 4 Jul 1972, P. Zwick (2#m, 1#f). 2 male paratypes are in the Hungarian Natural History Museum, the rest are in Geneva.
COMMENTS. The surstylus and cercus in a type photo sent to me by the Muséum d'Histoire Naturelle indisputably identify the specimens in the University of Guelph Insect Collection as \textit{A. australis}.

Papp (1979) distinguished \textit{Apterobiroina} from \textit{Howickia} only by the presence of two orbital setae, small ocelli a lack of pruinose lines on the frons and a wide quadrangular prosternum. Papp also never dissected a specimen. It is well established that chaetotaxy reduction, ocelli reduction and loss, and prosternum changes are all highly variable in flightless species and should not be used to justify generic status. The male terminalia of \textit{A. australis} are consistent with \textit{Howickia} and the genera will be officially synonymized in a later revision of the Australian \textit{Howickia}.

\textit{Australimosina flaviterga} (Richards, 1973)

(Figs. 5.1-5.9)


\textit{Acuminiseta flaviterga} (Richards), Marshall, 1989b: 602; Roháček et al., 2001: 111.

\textit{Australimosina flaviterga} (Richards), Papp, 2008: 135-136.


COMMENTS. The type was examined by S. Marshall in 1999, who noted that the wing of the holotype has distinct strong pigment lines along the veins, but the paratypes have uniformly brown wings. Richards (1973) illustrated a paratype, and Papp (2008) based his species concept off Richards’ illustrations. Papp’s illustrations of the male terminalia leave no doubt that this is the same species as Richards’ paratype, however this may not be the same species as the holotype.

Richards did not provide a diagnosis for Australian Acuminiseta, and regarding A. flaviterga only remarked that “this species does not run down very well to the subgenus Acuminiseta but seems better placed there than in Limosina” with no explanation. Roháček et al. (2001) noted that Acuminiseta Duda is a paraphyletic group and true Acuminiseta probably only occur in Africa. Papp (2008) did not discuss why he placed A. flaviterga in a new genus and gave zero diagnosis. The terminalia morphology is consistent with Howickia and should be formally synonymized in a later revision of the Australian Howickia. The holotype which is distinctly different from the paratypes as mentioned above should be examined thoroughly before synonymizing Australimosina and Howickia.

*Bentrovata regalis* (Richards, 1973)

(Figs. 6.1-6.12)


**TYPE MATERIAL.** Holotype female. **Western Australia:** Kings Park, Perth, in alcohol ex leaf litter, Sept 1957, G. Bornemissza (ANIC) (Apparently misplaced).
PARATYPES. Western Australia: Kings Park, Perth, in alcohol ex leaf litter, Sept 1957, G. Bornemissza (2#m, 1#f, ANIC); Kings Park, Perth, 1952-57 (1#m, ANIC); Kings Park, Perth, 9 Jun 1952 (1#f, ANIC). (All types apparently misplaced).

COMMENTS. The yellow thorax and black thorax morphs appear together, but the yellow morph seems far less common with a collection ratio of 1 yellow for every 3 black. *H. regalis* is sympatric with *H. apricitas*.

The yellow thorax morph is almost an exact match to Richards’ (1973) description of *Bentrovata regalis* with the yellow head and thorax, frons somewhat darker with five lines of silvery pubescence, ocelli small, prosternum mostly linear but with a narrow triangular posterior section, wings and halteres absent, and abdomen black. However, in Richards’ few illustrations of the male terminalia sternite 5 is simple without combs, while the University of Guelph specimens have two small posteromedial combs, and the surstylus is more crescent-shaped while the University of Guelph specimens’ is broadly rounded. Richards’ illustrations have not proven to be extremely accurate, especially overall surstylar shapes (compare our photos of *H. subsinuata, H. trivittata* and *H. nitidipleura*), and so I am treating the University of Guelph specimens as *B. regalis* here. Both Richards’ species and the University of Guelph specimens have only been recorded in Western Australia. Unfortunately, the types of *B. regalis* have been misplaced from the Australian National Insect Collection and so photos were not available for comparison.

Richards distinguished *Bentrovata* from *Monteithiana* only by the presence of a single orbital setae instead of two, silvery pruinose stripes on the frons, and the curved hind margin of the scutellum. These slight differences in morphology are highly variable between species and should not be used to separate genera. He distinguished *Bentrovata* from *Howickia* by the lack of
halteres and presence of ocelli, which are both traits known to be highly variable in flightless Diptera and should also not be used to divide these genera. The terminalia of Bentrovata regalis is consistent with Howickia and the genera should be formally synonymized in a later revision. Ideally the types of B. regalis are located and compared with specimens in the University of Guelph collection before this synonymy.

“Howickia acus” sp. n.

(Figs. 7.1-7.6)

ETYMOLOGY. The species epithet is derived from the Latin acus, “hair-pin, needle, pin”, in reference to the very long hair-pin-shaped postgonite and needle-like enlarged setae of the surstylus.

COMMENTS. Some “H. acus” specimens were observed to be slightly brachypterous with their wings not surpassing their abdomens. This is the only known species of Howickia which has been documented with slight brachyptery.

“Howickia apricitas” sp. n.

(Figs. 8.1-8.9)

ETYMOLOGY. The species epithet comes from the Latin apricitas, “sunniness, warmth of the sun”, referring to the bright, sunny yellow colour of the species’ head and thorax.
COMMENTS. “H. apricitas” is sympatric with B. regalis and easily distinguished by the lack of stripes on the frons of “H. apricitas”.

“Howickia bractea” sp. n.

(Figs. 9.1-9.10)

ETYMOLOGY. The species epithet is from the Latin bractea, “gold leaf, thin metal”, referring to the thin, golden leaf-shaped lamellae on the male cercus.

COMMENTS. “H. bractea” appears externally similar to Monteithiana cynthia but can be distinguished by lack of microtrichosity on the scutum (except marginally), and the bare sections of the frons inside of the interfrontal plates. M. cynthia has a uniformly microtrichose scutum and frons. “H. bractea” is also a Victorian species, while H. cynthia is Tasmanian. “H. bractea” is known only from a single locality and date.

“Howickia croca” sp. n.

(Figs. 10.1-10.9)

ETYMOLOGY. The species epithet is from the Latin crocus, “filament of a crocus/stamen”, referring to the stamen-shaped spermathecae and ducts.

COMMENTS. “H. croca” appears externally and internally similar to H. cynthia and both species are from Tasmania. However, “H. croca” can easily be distinguished by the presence of its haltere, the male sternite 5 with a posteromedial comb, and the surstylus with a large, claw-like posteroventral setae.

“Howickia discoloris” sp. n.

(Figs. 11.1-11.9)
ETYMOLOGY. The species epithet is from the Latin *discaloris*, “variegated, of different colours”, referring to the two-toned head and legs of this species.

COMMENTS. “*H. discoloris*” is a very distinct species with four dark stripes on the frons, a bicoloured gena, and a rather horizontally elongated eye. The male terminalia are very similar to other apterous Tasmanian species.

“Howickia flagella” sp. n.

(Figs. 12.1-12.9)

ETYMOLOGY. The species epithet is from the Latin *flagellum*, “arm, tentacle”, and refers to the tentacle-like surstyli,

COMMENTS. “*H. flagella*” is similar in colour, size and overall shape to *Apterobiroina australis*, but can be easily distinguished by its microtrichose scutum and lack of haltere.

*Howickia hardyina* (Richards, 1973)

(Figs. 13.1-13.9)

*Leptocera (Biroina) hardyina* Richards, 1973: 347.


TYPE MATERIAL. Holotype male. New South Wales: Mount Wilson, Blue Mountains, emerged from agaric, 29 Jun 1957, D.K. McAlpine (AMSA)

PARATYPES. New South Wales: Mount Wilson, Blue Mountains, 14 Apr 1959, D.K. McAlpine (1#f, AMSA); Katoomba, 31 Dec 1957, G.H. Hardy (1#f, AMSA).
**COMMENTS.** Identified based on Richards’ description of the male mid femoral comb of 7 setae, and the male mid tibial comb along its entire length. *H. hardyina* is very similar to *Australimosina flaviterga*. The males of both species are entirely brown, have a mid femur with a basal comb, a mid tibia with a comb along almost its entire length, and a poorly sclerotized T1+2. They can be distinguished by the fact that the mid femoral comb of *A. flaviterga* has 8-10 setae, where *H. hardyina*’s has 7, the male sternite 5 of *H. hardyina* has an anterior sclerotized band where *A. flaviterga* does not, and the posteroventral enlarged seta on the surstylus of *H. hardyina* is short and thorn-like, whereas in *A. flaviterga* it is elongated and curved anteriorly.

The females are currently indistinguishable, as Richards did not illustrate the females *A. flaviterga* he originally described and noted that the specimens that were somewhat variable and possibly included two or 3 similar species. Papp (2008) only examined a single male *A. flaviterga*. The females included here are assumed to be *H. hardyina* as they were collected with the males.

**“Howickia kentia” sp. n.**

(Figs. 14.1-14.11)

**ETYMOLOGY.** The species epithet is a reference to the Kentia palm, the world’s most popular palm tree for its low maintenance and beauty. The Kentia is endemic to moist lowland and submontane forests of Lord Howe Island, just like *H. kentia*, and is listed as vulnerable on the IUCN Red List due to its severely limited range.

**COMMENTS.** This is the only species of Sphaeroceridae known from Lord Howe Island. “*H. kentia*” is a highly autapomorphic species with robust chaetotaxy, no ocelli, reduced eyes, a bumpy frons, and a spoon-like appendage on the surstylus. There is no date on the specimens collected by T. Kingston, but the labels are clearly aged.
“Howickia manta” sp. n.

(Figs. 15.1-15.9)

ETYMOLOGY. The species is named for the male’s manta ray-shaped ventral hypandrial lobe.

COMMENTS. “H. manta” is another brown Howickia from Tasmania, but can males be distinguished from “H. spina” by its well sclerotized T1+2, from “H. pertusa” by its lack of large abdominal follicles, and from “H. acus” by its single pair of dorsocentral setae and significantly smaller eye:gena ratio. Males of “H. acus” also have a distinct large and obviously protruding postgonite when viewed laterally, lack a posteromedial comb on the male sternite 5, and are often brachypterous. This species is currently only known from a single locality and date.

“Howickia monteithi” sp. n.

(Figs. 16.1-16.9)

ETYMOLOGY. The species is named in honour of Geoff Monteith, whose sampling provided a significant portion of the material that made this study possible.

COMMENTS. “H. monteithi” is a common and extremely autapomorphic species with the basiphallus extremely reduced the postgonites expanded and apically fused.

Howickia myrmecophila (Knab & Malloch, 1912)

(Figs. 17.1-17.9)

Limosina myrmecophila Knab & Malloch, 1912a: 236.

Leptocera (Biróella) myrmecophila (Knab & Malloch), Duda, 1925: 76.

Leptocera (Biroina) myrmecophila (Knab & Malloch), Richards, 1973: 330.

Howickia myrmecophila (Knab & Malloch), Marshall et al., 2014.

**TYPE MATERIAL.** Holotype female. **New South Wales:** Otford, A. M. Lea (USNM).

**PARATYPES.** None.

**COMMENTS.** This is a large, attractive, and common fly. One female was found gravid with 35 eggs.

*Howickia nitidipleura* (Richards, 1973)

(Figs. 18.1-18.9)


Howickia nitidipleura (Richards), Marshall et al., 2014.

**TYPE MATERIAL.** Holotype male. **New South Wales:** National Park, 14 Oct 1956, D.K. McAlpine (AMSA).

**PARATYPES. New South Wales:** National Park, 14 Oct 1956, D.K. McAlpine (1#m, 1#f); National Park, 3 Nov 1956, D.K. McAlpine (1#f); National Park, 10 Sept 1955, D.K. McAlpine (1#f); National Park, 13 Apr 1957, D.K. McAlpine (1#f); National Park, 30 Aug 1957, D.K. McAlpine (1#m); National Park, 31 Aug 1957, D.K. McAlpine (1#m); Otford, 4 Apr 1954, D.K. McAlpine (1#m); Otford, 3 Mar 1962, D.K. McAlpine (1#f); Otford, 3 Feb 1962, D.K. McAlpine (1#f); Otford, 10 Feb 1962, D.K. McAlpine (2#m, 1#f); Otford, 4 Apr 1958, D.K. McAlpine (1#f); Otford, 8 Dec 1960, D.K. McAlpine (2#m); Mount Wilson, Blue Mountains, 2
Mar 1957, D.K. McAlpine (1#m); Mount Wilson, Blue Mountains, 23 Mar 1961, D.K.
McAlpine (1#m); Wentworth Falls, Blue Mountains, 20 Feb 1959, D.K. McAlpine (1#f);
Minnamurra Falls, 23 Oct 1962, D.K. McAlpine (1#f); near Gosford, Mooney Mooney Creek, 9
Nov 1957, D.K. McAlpine (1#f). All paratypes in AMSM except for 1 female and 1 male in
BMNH.

COMMENTS. *H. nitidipleura* could be confused with *Popondetta kurandensis* due to their large
size, faintly maculated wings, robust, black bodies and yellow heads, but *H. nitidipleura* has
black forelegs while *P. kurandensis* has yellow forelegs.

“*Howickia parasubsinuata*” sp. n.

(Figs. 19.1-19.9)

ETYMOLOGY. This species was recognized and named by Hui Dong due to its likeness to *H.
subsinuata*.

COMMENTS. This species is externally indistinguishable from *H. subsinuata*. Males can be
distinguished if the fifth sternite, surstylus or postgonite are visible. Sternite 5 of “*H.
parsubsinuata*” has a very small posteromedial comb flanked by two large setae, where as the
sternite 5 of *H. subsinuata* has a much larger comb flanked by two setulae, and a distinct shining
anterior sclerotized band. The postgonite of *H. subsinuata* is “boot-shaped” while it is narrower
and scoop-like in “*H. parasubsinuata*”. The surstylus of “*H. parasubsinuata*” has a broad
anterior lobe that is a flat, bald plate, whereas the surstylus of *H. subsinata* has setae on its
narrow anterior lobe. Females must be dissected for diagnosis. The spermathecae of *H.
subsinuata* are striated and broadly ovate, whereas they are narrow cylinders with pits on the
surface in “*H. parasubsinuata*”. Only male *H. subsinuata* were present in Tasmania so
Tasmanian females were illustrated for that species, and male specimens from Carnarvon National Park were largely “H. parasubsinuata” so females from that locality were illustrated for that species.

**Howickia percostata** (Richards, 1973)

(Figs. 20.1-20.9)

*Leptocera (Biroina) percostata* Richards, 1973: 342.


**PARATYPES.** **New South Wales:** Monga, 19 Jul 1962, D.H. Colless (1#f, ANIC); Brown Mountain, Bega district, 8 Mar 1963, D.H. Colless (1#f, ANIC); Clyde Mountain, near Braidwood, 2400 ft, 25 Feb 1961, D.J. McAlpine (1#f, AM).

**COMMENTS.** Specimens here were identified as *H. percostata* based on Richards’ description of the ventral comb of the mid femur and holotype photos.

“**Howickia pertusa**” sp. n.

(Figs. 21.1-21.9)

**ETYMOLOGY.** The species epithet is derived from the Latin *pertusa*, “leaky, perforated”, in reference to the large translucent follicles around the male’s abdominal setae.

**COMMENTS.** “*H. pertusa*”, “*H. acus*” and “*H. spina*” were always collected together, and the females collected simultaneously cannot be distinguished. I dissected several females that
appeared the most different morphologically, but internally they were also indistinguishable. The female postabdomen is illustrated with “H. pertusa” because it was the most numerous species collected. The character values for “H. pertusa” in the character matrices (Tables 1 and 2) were also used for “H. acus” and “H. spina”. The visible translucent follicles around every abdominal seta (easily visible on sternite 5 in Fig. 21.3) make the males of this species distinct from all other known species.

“Howickia polacornis” sp. n.

(Figs. 22.1-22.10)

ETYMOLOGY. The species epithet is derived from the Latin pola, “little”, and cornis, “wing”, in reference to the reduced wings.

COMMENTS. “H. polacornis” is known only from a single locality and date. This is the only known brachypterous species of Australian sphaerocerid, though the brachypterous Otwayia sabina which was not examined here may belong to Howickia. The silvery pruinose lines on the frons of O. sabina would easily distinguish it from “H. polacornis”.

“Howickia pruinosa” sp. n.

(Figs. 23.1-23.10)

ETYMOLOGY. The species epithet is derived from the Latin pruinosa meaning “frosted” in reference to fine white microtrichosity covering this species.

COMMENTS. “H. pruinosa” is known only from a single locality and date. This species is similar in appearance to the black morph of B. regalis, but the white microtrichosity covering it easily distinguished it.
“H. spina” sp. n.
(Figs. 24.1-24.9)

ETYMOLOGY. The species epithet is derived from the Latin spina, “spike, thorn, prickle”, in reference to the large thorn-like setae of the surstylus.

COMMENTS. “H. spina”, “H. pertusa”, and “H. acus” were always collected together. The females collected simultaneously lack any tergite modification and are extremely similar. I cannot definitively say what species they belong to, and so both “H. pertusa” and “H. spina” must show strong sexual dimorphism. See comments under “H. acus” to distinguish “H. spina” from similar species.

*Howickia subsinuata* (Richards, 1973)
(Figs. 25.1-25.9)

*Leptocera (Biroina) subsinuata* Richards, 1973: 331.


TYPE MATERIAL. Holotype male. **Australian Capital Territory**: Black Mountain, malaise trap, 10 May 1963, I.F.B. Common (ANIC).

PARATYPES. **Australian Capital Territory**: Black Mountain, malaise trap, 10 May 1963, I.F.B. Common (2#f, ANIC); Black Mountain, light trap, 19 Dec 1962, I.F.B. Common (1#f, ANIC); Mt. Gingera, 3 Dec 1964, E.B. Britton (1#f); Mount Majura, 2 Apr 1963, D.H. Colless (1#m, 1#f, ANIC); Ginninderra Falls, 28 Feb 1962 (1#f, ANIC). **New South Wales**: Minnamurra Falls, 31 Jan 1962, D.H. Colless (1#f, ANIC); Otford, 12 Oct 1957, D.K. McAlpine

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Howickia trivittata (Richards, 1973)

(Leptocera (Biroina) trivittata Richards, 1973: 340.)


Howickia trivittata (Richards), Marshall et al., 2014.


PARATYPES. New South Wales: Katoomba, 27 Sept 1959, G.H. Hardy (1#f); Blue Mountains, Springwood, 30 Jan 1956, D.K. McAlpine (1#f); Blue Mountains, below Govett’s Leap, 7 Dec 1956, D.K. McAlpine (1#f). Queensland: Lamington national park, Binna Burra, 31 Jan 1961, D.K. McAlpine (1#m). All paratypes in AMSA except one female in BMNH.

COMMENTS. Currently externally indistinguishable from “H. parasubsinuata”. See comments under “H. parasubsinuata” to distinguish these species. The list of specimens examined above contains both species. Only male H. subsinuata have been collected in Tasmania and Victoria.
COMMENTS. A distinctive little fly with a very short R_{2+3}, a boldly striped frons, a yellow gena and visibly large, round, posteriorly protruding male cerci.

“Howickia wamini” sp. n.

(Figs. 27.1-27.9)

ETYMOLOGY. For years this species was sorted as “western Australian Minilimosina” in the University of Guelph collection- wamini for short.

COMMENTS. “H. wamini” is currently the only macropterous Howickia recognized from Western Australia. It is unique in having 4 equally long interfrontal setae.

Monteithiana cynthia (Richards, 1973)

(Figs. 6.1-6.9)


PARATYPES. Cynthia Bay, Lake St. Clair, 7-8 Feb 1967, G. Monteith (1#f, QMBA).

COMMENTS. Specimens in the University of Guelph Insect Collection were identified as Monteithiana cynthia with the help of type photos graciously taken by Geoff Thompson of the Queensland Museum. The red head with dark occipital and antennae regions, lack of halteres, uniform microtrichosity of the frons and scutum along with the locality leave no doubt that this is M. cynthia. The mid tibia with paired anterodorsal-posterodorsal setae, hypandrial structure and distiphallic structure place this species within Howickia. Specimens and the type photos of the type species of Monteithiana, H. dealata, were also examined. Unfortunately, only a single male
was available for dissection and was too translucent to see details of the distiphallus, but it appears superficially similar to *M. cynthia*.

Richards distinguished *Monteithiana* from apterous *Biroina* by the absence of halteres, but it is well established that halteres are commonly altered flightless Diptera, and their presence or absence should not define a genus. Richards distinguished *Monteithiana* from his single New Zealand *Howickia* species by the presence of 2 orbital setae in *Monteithiana* and zero in *Howickia*, but it is also well established that chaetotaxy is often reduced and lost in flightless species. Internally all of the species in these genera are alike and should be formally synonymized, as suggested by Marshall et al. (2014). Ideally another male *M. dealata* is dissected and illustrated before *Monteithiana* is formally synonymized with *Howickia*.

**Popondetta kurandensis** (Richards, 1973)

(Figs. 29.1-29.10)


**PARATYPES.** Kuranda, 17, 20 May 1958, D.K. McAlpine (5#F, 3 AM, 2 BMNH).

**COMMENTS.** When justifying the subgeneric status of *Popondetta*, Richards only noted the prosternum being “broadly rectangular or more triangular, a character which normally occurs only in a number of brachypterous species” but also mentioned that “in fully winged forms it is known in *Biroina*...” and so Richards never actually distinguished *Popondetta* from *Biroina*
(now *Howickia*). His key to the genera and subgenera of the Sphaeroceridae of Australia, New Zealand, and New Guinea, fails to distinguish between these genera as well. The couplet diagnosing *Biroina* says “Vein R_{2+3} usually strongly bisinuate; wings often maculated or at least strongly clouded; mesoscutum and scutellum with scaly tomentum, scutellum flat and not longer than semicircular; mid tibia usually with more than 1 set of paired dorsal bristles, mid basitarsus sometimes with distinct ventral bristles, legs rarely much variegated; prosternum more or less triangular.” The second part of that couplet leading to diagnosing *Popondetta* immediately after says “Vein R_{2+3} rarely so strongly bisinuate; other characters not present in combination…”. The couplet diagnosing *Popondetta* reads “Prosternum broadly triangular or rectangular; postervertical bristles absent; face centrally rather protruding; 3^{rd} antennal segment and little pointed, aristal subapical; mesoscutum granulate.”. In the description of *Popondetta*, Richards says the wings can be maculated and vein R_{2+3} can be weakly or rather strongly sinuate, and so the species he has placed in *Popondetta* would actually key out to *Biroina* (*Howickia*) in his own key. The only character mentioned that strikes me as unique from *Howickia* is the face centrally protruding.

These specimens in the University of Guelph Insect Collection were identified as *Popondetta kurandensis* based on Richards description and type photos taken by S. Marshall. This is a large and distinct species with a bright yellow head and forelegs, a robust black body, a sinuate R_{2+3} and a centrally protruding face. Richards did not illustrate the terminalia, and when I dissected male and female, I found them consistent with other *Howickia*. *Popondetta* should likely be synonymized with *Howickia*, but the type species from New Guinea, *P. vittigera* (not present in the University of Guelph collection), should be examined first.
3.2 Outgroup results

3.2.1 Morphology-based outgroups

*Paralimosina* species described and illustrated in Roháček, 1983 and 1988 as well as physical specimens present in the University of Guelph Insect Collection were examined in order to further investigate the relationship between this genus and *Howickia*. The two genera were superficially similar, but the terminalia were extremely similar. The distiphallus of *Howickia* seems to come in two forms; a complex form, and a simple tube-form. The complex *Howickia* distiphalli and those of *Paralimosina* were both similar to those of *Pullimosina* Roháček as described by Marshall (1985). *Howickia* with a complex distiphallus tend to have a dorsal saddle sclerite (DS) with large lateral lobes, a median ventral process (VP) with is narrow and extends past the lateral lobes of the dorsal saddle, and dorsal and ventral paired apical processes (DPP and VPP respectively). The dorsal paired processes tend to be membranous in *Howickia* and often appears bumpy or bubbly in appearance, while the ventral paired processes tend to be well sclerotized, at least basally, and are sometimes fused into one U-shaped sclerite. *Howickia* with a complex distiphallus also often have an unpaired medial tube-shaped sclerite (MTS) which appears to arise from the distal end of the saddle sclerite. All of these sclerites can be observed in many *Paralimosina* species. *Howickia* and *Paralimosina* both lack the basal sclerite present in *Pullimosina*, and appear to lack the median ventral process described by Marshall (1985), though it could be homologous to the median tube-shaped sclerite. The remarkable similarity of the terminalia of *Howickia* and *Paralimosina* leave no doubt that they are close relatives, but the presence of a posterodorsal hypandrial apodeme in *Howickia* separate them from *Paralimosina*. Female *Paralimosina* also lack the telescoping terminalia present in *Howickia*. 
There were few series of identified and described species of *Paralimosina* in the University of Guelph collection and so *Paralimosina fucata* Rondani was used as the outgroup in the phylogenetic analysis since it was the most well represented identified species.

The most externally similar Australian flies to *Howickia* that I came across when sorting seemed to belong to *Pseudopterogramma*. There are currently no described species of Australian *Pseudopterogramma*, though several undescribed species I came across were consistent with Smith & Marshall’s (2004) and Papp’s (2008) descriptions. One particularly common species was used in this study and its morphology was compared to *Howickia* to determine if it would make a good outgroup for the phylogenetic analysis.

As discussed in section 1.3.3, *Pseudopterogramma* are extremely similar to *Howickia* externally with similar wing venation, identical mid tibial chaetotaxy, and similar bright colours often seen in *Howickia*. Internally, however, the undescribed species I examined was extremely different from *Howickia*. The distiphallus of the *Pseudopterogramma* species only consisted of two sclerites: a single, narrow ventral rod with serrations medially, and a membranous whip-like sclerite dorsally which was bifurcated apically. The *Pseudopterogramma* species also lacked the posterodorsal apodeme and ventral hypandrial lobe seen in the hypandrium of *Howickia* species. I decided to include this species as an outgroup, though I no longer think this genus is closely related to *Howickia*.

The hind tibia of the *Pseudopterogramma* species has a small preapical, anteroventral spur-like seta and long exserted dorsal seta at 2/3, which is also described in the Oriental species in Papp (2008). This character would an easy way to diagnose the group and distinguish it from *Howickia* if it is present in all species and should be further investigated in undescribed Australian species.
3.2.2 Molecular-based outgroups

The parsimony analysis of the global sphaerocerid CO1 data from BOLD produced 4 equally parsimonious trees (L= 31335, Ci=3, Ri=58). The differences between the trees were not significant and the Howickia-group and surrounding groups never differed so only the first tree is presented in Figures 1.1 and 1.2. The resulting tree including all BIN representatives of the global Sphaeroceridae from BOLD is presented in Figure 1.1. Figure 1.2 is a close up of the main Howickia group and the groups nearest to it with genera and species names applied where available.

In every tree, the main group of identified Howickia came out within the Epandrial Process Group (EPG). The EPG is a well-established New World group containing Aptilotella Duda, Archiceroptera Papp, Bitheca Marshall, Bromeloecia Spuler, Pterogramma Spuler, Robustagramma Marshall and Rudolfina Roháček. This group is characterized by having a finger-like process extending medially from the right margin of the epandrium (Marshall & Cui, 2005). Species in the EPG are also defined by the presence of three or more interfrontal setae, a scutellum with only two pairs of setae, the wing vein cell cup absent, a narrow alula with a straight hind margin, a mid tibia with at least one anterodorsal seta on the basal 1/3, one anterodorsal seta at 1/2, a pair of anterodorsal and posterodorsal setae at the apical ¾, and a mid tibia with an apical ventral seta. The exception to this diagnosis is the “boliviensis” group, which is currently unplaced and lack the epandrial finger (Paiero, 2018). Interestingly, Howickia species with an anterodorsal seta at ½ on their mid tibia, including H. myrmecophila and H. nitidipleura actually meet the criteria for the EPG, except for their lack of an epandrial finger, which is not diagnostic as it has been secondarily lost in some members. The externally diagnostic characters of the EPG are all subject to homoplasy and their presence in some
*Howickia* species does not mean they belong in the EPG, but it is worth noting due to the results of this molecular analysis.

Yau and Marshall (2017) found that the epandrial process was variable within the genus *Bromeloecia*, forming a bridge from the right to the left of the epandrium in some species, and almost absent in others. They suggested that the epandrial finger may be subject to rapid change. If *Howickia* really is part of the EPG, perhaps the unique structure of the hypandrium in *Howickia* is in part derived from the epandrial process seen in the EPG. The bridge formed by the epandrial process in some species of *Bromeloecia* vaguely resembles the broad, asymmetrical main part of the hypandrium in *Howickia*, especially in how high on the side of the epandrium it is attached. If the epandrial process really is subject to rapid evolution, then this is not impossible, though it is still unlikely given the geographic distance between established members of the EPG and *Howickia*.

Many species of *Howickia* closely resemble members of the EPG with their robust, well sclerotized bodies, and colourful, often patterned heads. Some apterous *Howickia* are almost identical to *Aptilotella* species, though this was historically thought to be due to the homoplasy of aptery. Though it isn’t usual, some members of the EPG have telescoping terminalia like *Howickia*. The *sororcula* and *enigmata* groups of the *Archiceroptera* genus complex along with *Bitheca* all have telescoping terminalia. Still, it is unlikely that *Howickia* belongs to the EPG given the geographic distance between them. The male terminalia of *Howickia* does not closely resemble that of any known EPG members, though this isn’t necessarily proof that they are not relatives. Within the extremely unique and complicated distiphalli of *Pterogramma* species, Smith & Marshall (2014) found no homologous sclerites at taxonomic levels above species group.
*Howickia* did not come back monophyletic in the parsimony analysis. Species in the *subsinuata* species group including *H. subsinuata*, “*H. parasubsinuata*” and another very similar looking but undescribed species, come out together, but very far away from the remainder of *Howickia* (Fig. 1.1). This suggests that the *subsinuata* group does not belong in *Howickia*. There was some concern about the inclusion of this group based on morphology since they are the only *Howickia* species with 3 dorsocentrals. Species in the *subsinuata* groups also have a very weak ventral hypandrial lobe (just an indistinct small membrane in its palace) and a fairly uniform distiphallus that is basally narrow and distally greatly expanded into a striated membranous sac. The analysis also shows *H. myrmecophila* very far derived from the main *Howickia* group. *H. myrmecophila* clearly shows all the diagnostic characters of the genus including the hypandrial structure, mid tibial chaetotaxy, highly sinuate R$_{2+3}$ and telescoping female terminalia, and its placement in these results could be problematic for the monophyly of *Howickia*. However, the paraphyly of *Howickia* here may reflect poor phylogenetic signaling of the COI gene. Ekrem et al. (2010) compared the value of 5 genes in phylogenetic signaling of Chironomidae and found that COI showed the weakest phylogenetic signal, while CAD showed the strongest. Characteristics Ekrem et al. (2010) found that contribute to the poor phylogenetic signal of COI were low number and variation of parsimony-informative sites and a high degree of fourfold degenerative sites. Similarly, Winterton et al. (2007) and Winkler et al. (2009) found that CAD was significantly more phylogenetically-informative than COI in Diptera. Paiero (2018) also found paraphyly in the phylogeny of Sphaeroceridae that was not supported by morphology when using COI. The wide availability of COI data for many species thanks to DNA barcoding makes its use in phylogenetic analysis very appealing, but the results should be taken with a grain of salt. Further analyses including a greater number of genes demed more phylogenetically-
informative in Diptera could help elucidate whether *Howickia* is a monophyletic group and whether the the *H. subsinuata* group belongs in the genus. The inclusion of a greater number of *Howickia* species as well as genera suspected to belong within the genus such as *Popondetta, Monteithiana* and *Bentrovata* would also be useful in future analyses.

Genera that came out as sister groups to *Howickia* in this parsimony analysis were *Bromeloecia* and *Pterogramma*. Of the two identified *Pterogramma* closest to the *Howickia* group, one specimen from Argentina appeared to belong to the *Pterogramma sublugubrinum* species-group, while the other specimen from Costa Rica was very similar to *Pterogramma madare* Spuler. For this reason, *P. substitutum* Richards 1961 (representative of the groundplan of the *P. sublugubrinum* group) and *P. madare* were used as outgroups in the morphological phylogenetic analysis. *Bromeloecia abundantia* Yau & Marshall is the most common species of *Bromeloecia* and was also chosen as an outgroup. *P. madare* and *P. substitutum* were coded in the matrix based on descriptions and illustrations from Smith & Marshall (2004), and *B. abundantia* was coded based on its description and illustrations from Yau & Marshall (2018).

### 3.3 Phylogenetic analyses

#### 3.3.1 Characters used in the phylogenetic analysis using all determined outgroups

The character states were scored as plesiomorphic (0), apomorphic (1), or multistate (1-3). All characters are treated as unordered.

**Head**

1. Ground colour: (0) black-brown; (1) yellow-orange or red-orange
2. Orbital setae: (0) 2; (1) 1
3. Outer vertical: (0) present; (1) absent
4. Face: (0) broad and concave; (1) with prominent tubercle

Thorax

5. Katepisternal seta(e): (0) 1 seta; (1) 2 setae

6. Scutal microtrichosity: (0) uniform; (1) bare, at least medially

7. Scutellar setae: (0) basal seta 0.4-0.6x the length of apical seta; (1) basal and apical setae subequal; (2) basal seta 1.5x the length of apical seta.

8. Dorsocentral setae: (0) 2; (1) 1; (2) 3

9. Pleuron: (0) uniformly coloured; (1) posteroventral corner of anepisternum, and usually also the ventral point of anepimeron and anterodorsal corner of katepimeron/meron paler than surrounding pleuron; (2) anepimeron darker than surrounding pleuron.

10. Fore femur: (0) without long golden hairs; (1) anterodorsally with 2 long ventrally bent golden hairs at base

11. Mid tibia- proximal setae: (0) a single anterodorsal proximal seta; (1) paired anterodorsal-posterodorsal setae; (2) 3 unpaired setae

12. Mid tibia- additional seta(e) above main proximal seta(e): (0) none; (1) a single anterodorsal seta; (2) 1 pair of anterodorsal-posterodorsal setae; (3) 2 pairs of anterodorsal-posterodorsal setae

13. Male mid tibial comb(s): (0) absent; (1) 1 comb; (2) 2 combs

14. Male mid femoral comb(s): (0) absent; (1) present

15. Mid basitarsus with distinct ventral seta at least in female (often reduced in male): (0) no; (1) yes
16. Hind tibia: (0) without setae; (1) with a small preapical, anteroventral spur-like seta and long exsrted dorsal bristle at 2/3

17. R\(_{4+5}\): (0) straight or distally gently curved upwards (not raised after r-m); (1) slightly sinuate; (2) abruptly upturned at 2/3 its length to meet costa

18. Costa: (0) not bypassing R\(_{4+5}\); (1) significantly bypassing R\(_{4+5}\) by 4-6 vein widths; (2) scarcely bypassing R\(_{4+5}\) by 1-2 vein widths

Abdomen

19. Tergal microtrichosity: (0) uniformly finely microtrichose, at least medially; (1) T1+2 microtrichose, the remaining tergites bare; (2) entirely bare or with one or more tergites with thin anterior line of microtrichosity.

20. Tergal desclerotization: (0) All tergites sclerotized; (1) T1+2 at least partially desclerotized in males.

Male postabdomen

21. S5: (0) not excised; (1) posteromedially excised; (2) asymmetrically excised; (3) posteromedially protruding

22. S5: (0) not desclerotized; (1) posteromedially desclerotized; (2) with desclerotized medial patch

23. S5: (0) without anterior sclerotized band; (1) with anterior sclerotized band

24. S5: (0) without comb(s); (1) with posteromedial comb(s)

25. Synsternrite 6+7: (0) entirely connected; no separate sclerites; (1) posteromedially with 1 or 2 sclerites separated from main body

26. Epandrial process: (0) finger-like; on right side of epandrium; (1) absent
27. Epandrium shape: (0) ball-shaped; rounded, not much tapering dorsally, generally as wide as tall; (1) narrower dorsally than ventrally; (2) entirely narrow

28. Epandrium texture: (0) smooth; (1) with a rippled texture, at least posteroventrally

29. Ventral hypandrial lobe: (0) absent; (1) present

30. Ventral hypandrial lobe: (0) absent or translucent and membranous; (1) at least partially dark and well-sclerotized; (2)

31. Posterodorsal hypandrial apodeme: (0) absent; (1) present

32. Cercus: (0) well differentiated from subanal plate; (1) not well differentiated from subanal plate; usually small and rounded or triangular with 1 or 2 long setae; (2) not well differentiated from subanal plate, small posteriorly projecting knobs

33. Surstylus: (0) deeply bilobed or trilobed; (1) shallowly lobed, or a single lobe with a greatly enlarged posterior bristle; (2) one broad lobe, usually with many large ventral setae, rarely bare

34. Surstylus: (0) without claw-like setae; (1) with at least 1 large claw-like setae

35. Basiphallus: (0) short with no epiphallus, or with epiphallus only as long as the width of the distiphallus; (1) with a long epiphallus extending at least 3X the width of the distiphallus

36. Postgonite: (0) short and distally narrowing; usually equal to or shorter than surstylus; (1) long and narrow, extending beyond surstylus; (2) short and entirely broad; usually equal to or shorter than surstylus

37. Postgonite: (0) not ventrally broadly rounded and bending anteriorly in a scoop-like fashion; (1) ventrally broadly rounded and bending anteriorly in a scoop-like fashion
38. Ejaculatory apodeme: (0) a small finger-like process with a circular bulb; (1) teardrop-shaped; (2) long and cylindrical with an irregular bulb

39. Distiphallus: (0) Distally not expanded or less than 2X the basal width; (1) Distally greatly expanded to almost 3X the basal width.

40. Ventrobasal sclerite: (0) small, U-shaped; (1) absent

41. Whip-like sclerite: (0) absent; (1) with a long, distally bifurcate whip-like sclerite arising dorsally from the base of the distiphallus

42. Dorsal saddle sclerite: (0) paired, present as lateral sclerites; (1) fused into a single saddle-shaped sclerite; (2) absent; (3) entirely fused and not discernable from surrounding sclerites

43. Finger-like sclerites: (0) present; (1) absent

44. Ventral sclerite(s): (0) paired; (1) absent; (2) a single, well-sclerotized rod; (3) entirely fused and not discernable from surrounding sclerites

45. Median ventral process: (0) absent or not a single rod; (1) medially serrated; (2) distally extending dorsally and around the apex of the distiphallus; (3) articulating or fused with ventral paired process

46. Ventral paired process: (0) absent; (1) broad, fused U-shaped or unfused paired lobes, articulating with the MVP; (2) entirely fused and not discernable from other sclerites

47. Median tube-shaped sclerite: (0) absent or fused, not discernable; (1) present

48. Dorsal paired process: (0) absent; (1) smooth or striated; (2) dorsally cellular in appearance

Female postabdomen

49. Telescoping female terminalia: (0) absent; (1) present
50. Spectacles-shaped sclerite: (0) not visible; (1) well-sclerotized

51. Epiproct: (0) uniformly sclerotized; (1) medially desclerotized

52. Spermathecae: (0) smooth; (1) striated

53. Spermathecae: (0) spherical or wider than long; (1) broadly ovate; (2) elongate

54. Spermathecae: (0) without invagination(s); (1) with invaginations
Table 1. Character state matrix with *Bromeloeia abundantia, Paralimosina fucata, Pseudopterogramma* sp., *Pterogramma madare* and *Pterogramma substitutum* as outgroups. The plesiomorphic state is indicated by (0), apomorphic state(s) are (1-2), and unknown or unavailable data is indicated by (?). All characters are treated as unordered.

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3.3.2 Results of initial phylogenetic analysis

Analysis of the character matrix including *Bromeloecia abundantia, Paralimosina fucata, Pterogramma madare* and *Pterogramma substitutum* as outgroups produced a single most parsimonious tree (Fig. 3.1) (length 213, consistency index 38, retention index 68).

In this analysis *Howickia* is rendered paraphyletic by *Paralimosina fucata*. The large clade including all of my *Howickia* and *Howickia*-like species as well as *P. fucata* is only supported by two synapomorphies; the presence of a ventral hypandrial lobe (29) and a long, cylindrical ejaculatory apodeme (38). A cylindrical ejaculatory apodeme is highly homoplastic amongst the Sphaeroceridae, and while it does separate *Paralimosina fucata* and *Howickia*-like species from the other outgroups in this analysis, it does not provide good support for *Paralimosina* rendering *Howickia* paraphyletic. The presence of a ventral hypandrial lobe is a good synapomorphy that certainly provides evidence for a close relationship between *Paralimosina* and *Howickia*.

Despite the large amount of homoplasy within the large *Howickia-Paralimosina* group, there are several recognizable groups. About half of the *Howickia* species cluster into Clade 1 defined by a non-discernable, fused median ventral process (44) and the lack of a median tube-shaped sclerite (47). Almost all species in this group have the simple, tubular distiphallus in which all or most of the ancestral sclerites have fused. *H. monteithi* is the only species in this clade that retains a distinct dorsal saddle sclerite (42). Other synapomorphies of Clade 1 include a single dorsocentral (8) and a translucent ventral hypandrial lobe (30).

The *croca* species group is an apterous Tasmanian group comprising “*H. croca*”, “*H. discoloris*” and *Monteithiana cynthia*. Synapomorphies supporting this groups are a pleuron with the posteroventral corner of the anepisternum paler than the surrounding pleuron (9), the lack of any additional setae above the main proximal setae (12) and tergites bare or mainly bare of
microtrichosity (19). The presence of *M. cynthia* within this group also further supports the synonymy of *Monteithiana* with *Howickia*.

Monophyly of the *flaviterga* species group is supported by the descleritization of T$_{1+2}$ (20). This group contains *Australimosina flaviterga*, *H. hardyina* and “*H. spina*”. Species in the group are all brown flies with tergites bare of microtrichosity except for T$_{1+2}$, with the complex ancestral distiphallus with a bubbly-looking paired dorsal process, and invaginated spermathecae. The presence of *Australimosina flaviterga* within this group further supports the synonymy of this monotypic genus with *Howickia*.

The *percostata* species group contains *H. percostata*, “*H. pertusa*” and “*H. wamini*” and its monophyly is supported by a single-lobed surstylus (33) and a scoop-like postgonite (37) which has also separately evolved in “*H. parasubsinuata*”. Species in this group are also uniformly brown.

The *myrmecophila* species group contains *H. myrmecophila* and *H. nitidipleura* and is characterized by the basiphallus being posteroventrally extended into a long epiphallus (35). These flies are large and showy with maculated wings, yellow heads, and bodies with a shiny, dark, patent leather appearance.

The *subsinuata* species group comprises of *H. subsinuata* and “*H. parasubsinuata*”. These species are indistinguishable using external morphology and are often found together. They are the only species of *Howickia* with three dorsocentras (8) and a distally greatly enlarged distiphallus (39). Externally flies in this species group are dark brown, the antennal region is yellow-orange, the frons has five silvery pruinose stripes and the mid tibia have two additional pairs of anterodorsal-posterodorsal setae.
The *regalis* species group contains *Bentrovata regalis* and “*H. apricitas*”. The species are Western Australian in distribution and sympatric. The species appear related due to a suite of characters including one orbital seta (2), the basal scutellar seta longer than the apical seta (7), a male sternite five that is asymmetrically excised (21) and broadly ovate spermathecae (53). Species in this group are also apterous, lacking halteres, and often have yellow heads and thoraces with black abdomens. The presence of *B. regalis* in this group is further evidence for its synonymy with *Howickia*.

The *flagella* species group is an apterous mainland group that comprises “*H. flagella*”, *Apterobiroina australis*, and “*H. bractea*”. The synapomorphies that define the *flagella* species-group are a narrow epandrium (27) and a posteriorly projecting knob-like male cercus (32). Members also share tergites bare or mostly bare of microtrichosity (19), a short, broad postgonite (36), and striated spermathecae (52).

In this analysis *Paralimosina fucata* appears between the more ancestral *Howickia* with the complicated distiphallus quite similar to *Paralimosina*, and the more derived *Howickia* of Clade 1 with a simple, fused distiphallus. *Paralimosina fucata* appears highly derived and apomorphic with a long list of characters separating it from other *Howickia*, and three apomorphies; a mid tibia with three unpaired proximal setae (11), the median ventral process extending dorsally to the apex of the distiphallus (45) and well-sclerotized spectacles-shaped sclerites (50). Characters 11 and 50 are characters used to define *Paralimosina* as a genus. In this interpretation *Paralimosina fucata* has secondarily lost the posterodorsal hypandrial apodeme (31), which seems unlikely for such a significant trait present in the rest of the *Howickia* and *Howickia*-like species. The apomorphies defining *Paralimosina* listed above and the absence of a posterodorsal hypandrial apodeme suggest that *Paralimosina* is distinct from *Howickia*. Adding the highly
morphologically-dissimilar species such as *Pterogramma, Bromeloecia* and *Pseudopterogramma* as outgroups in this analysis required me to attempt to homologize a lot of structures and add characters unique to those genera to attempt to distinguish them from the other species. This likely contributed to the analysis interpreting *P. fucata* to be more similar to the Clade 1 *Howickia* than the remaining *Howickia* and *Howickia*-like species. For these reasons I decided to run a subsequent analysis including only *P. fucata* as the outgroup and removing the traits that were irrelevant to *Paralimosina* and *Howickia*.

### 3.3.3 Characters used in the phylogenetic analysis using *Paralimosina fucata* as an outgroup

The character states were scored as plesiomorphic (0), apomorphic (1), or multistate (1-2). All characters are treated as unordered.

**Head**

1. Ground colour: (0) black-brown; (1) yellow-orange or red-orange
2. Orbital setae: (0) 2; (1) 1
3. Outer vertical: (0) present; (1) absent

**Thorax**

4. Katepisternal seta(e): (0) 2 setae; (1) 1 seta
5. Scutal microtrichosity: (0) uniform; (1) bare, at least medially
6. Scutellar setae: (0) basal seta 0.4-0.6x the length of apical seta; (1) basal and apical setae subequal; (2) basal seta 1.5x the length of apical seta. (0) basal and apical setae subequal; (1) basal seta 0.4-0.6x the length of apical seta; (2) basal seta 1.5x the length of apical seta.
7. Dorsocentral setae: (0) 2; (1) 1; (2) 3

8. Pleuron: (0) uniformly coloured; (1) posteroventral corner of anepisternum, and usually also the ventral point of anepimeron and anterodorsal corner of katepimeron/meron paler than surrounding pleuron; (2) anepimeron darker than surrounding pleuron.

9. Mid tibia- proximal setae: (0) 3 unpaired setae; (1) paired anterodorsal-posterodorsal setae

10. Mid tibia- additional seta(e) above main proximal seta(e): (0) none; (1) a single anterodorsal seta; (2) 1 pair of anterodorsal-posterodorsal setae; (3) 2 pairs of anterodorsal-posterodorsal setae

11. Male mid tibial comb(s): (0) absent; (1) 1 comb; (2) 2 combs

12. Male mid femoral comb(s): (0) absent; (1) present

13. Mid basitarsus with distinct ventral seta at least in female (often reduced in male): (0) no; (1) yes

14. R_{4+5}: (0) slightly sinuate; (1) straight or distally gently curved upwards (not raised after r-m)

15. Costa: (0) not bypassing R_{4+5}; (1) significantly bypassing R_{4+5} by 4-6 vein widths; (2) scarcely bypassing R_{4+5} by 1-2 vein widths

Abdomen

16. Tergal microtrichosity: (0) T1+2 microtrichose, the remaining tergites bare; (1) uniformly finely microtrichose; (2) entirely bare or with one or more tergites with thin anterior line of microtrichosity
17. Tergal desclerotization: (0) All tergites sclerotized; (1) T1+2 at least partially desclerotized in males

Male postabdomen

18. S5: (0) not excised; (1) posteromedially excised; (2) asymmetrically excised

19. S5: (0) not desclerotized; (1) posteromedially desclerotized; (2) with desclerotized medial patch

20. S5: (0) without anterior sclerotized band; (1) with anterior sclerotized band

21. S5: (0) without comb(s); (1) with posteromedial comb(s)

22. Epandrium shape: (0) ball-shaped; rounded, not much tapering dorsally, generally as wide as tall; (1) narrower dorsally than ventrally; (2) entirely narrow

23. Epandrium texture: (0) smooth; (1) with a rippled texture, at least posteroventrally

24. Ventral hypandrial lobe: (0) at least partially dark and well-sclerotized; (1) absent or translucent and membranous

25. Posterodorsal hypandrial apodeme: (0) absent; (1) present

26. Cercus: (0) not well differentiated from subanal plate; usually small and rounded or triangular with 1 or 2 long setae; (1) well differentiated from subanal plate; (2) not well differentiated from subanal plate, small posteriorly projecting knobs

27. Surstylus: (0) deeply bilobed or trilobed; (1) shallowly lobed, or a single lobe with a greatly enlarged posterior bristle; (2) one broad lobe, usually with many large ventral setae, rarely bare

28. Surstylus: (0) with at least 1 large claw-like setae; (1) without claw-like setae
29. Basiphallus: (0) short with no epiphallus, or with epiphallus only as long as the width of the distiphallus; (1) with a long epiphallus extending at least 3X the width of the distiphallus

30. Postgonite: (0) long and narrow, extending beyond surstylus; (1) short and entirely broad; usually equal to or shorter than surstylus

31. Postgonite: (0) not ventrally broadly rounded and bending anteriorly in a scoop-like fashion; (1) ventrally broadly rounded and bending anteriorly in a scoop-like fashion

32. Distiphallus: (0) Distally not expanded or less than 2X the basal width; (1) Distally greatly expanded to almost 3X the basal width.

33. Dorsal saddle sclerite: (0) present; (1) entirely fused and not discernable from surrounding sclerites

34. Median ventral process: (0) a single, well-sclerotized rod; (1) entirely fused and not discernable from surrounding sclerites

35. Median ventral process: (0) distally extending dorsally and around the apex of the distiphallus; (1) articulating or fused with ventral paired process

36. Ventral paired process: (0) absent; (1) broad, fused U-shaped or unfused paired lobes, articulating with the MVP; (2) entirely fused and not discernable from other sclerites

37. Median tube-shaped sclerite: (0) present; (1) absent or fused, not discernable

38. Dorsal paired process: (0) smooth, striated or absent; (1) dorsally bubbly in appearance

Female postabdomen

39. Telescoping female terminalia: (0) absent; (1) present

40. Spectacles-shaped sclerite: (0) well-sclerotized; (1) not visible
41. Epiproct: (0) uniformly sclerotized; (1) medially desclerotized
42. Spermathecae: (0) smooth; (1) striated
43. Spermathecae: (0) spherical or wider than long; (1) broadly ovate; (2) elongate
44. Spermathecae: (0) without invagination(s); (1) with invaginations
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**Table 2.** Character state matrix using *Paralimosina fucata* as an outgroup. The plesiomorphic state is indicated by (0), apomorphic state(s) are (1-2), and unknown or unavailable data is indicated by (?). All characters are treated as unordered.
3.3.4 Results of subsequent phylogenetic analysis

Analysis of the character matrix including only *Paralimosina fucata* as an outgroup produced two equally parsimonious trees (Figs. 3.2, 3.3) (length 154, consistency index 38, retention index 65). The trees differed only slightly in whether “*H. pruinosa*” arose before or after the *regalis* species group.

In this analysis *Howickia* and the *Howickia*-like species that are likely synonyms are recovered as a monophyletic group distinct from *P. fucata*. Characters supporting the monophyly of *Howickia* are a single katepisternal seta (4), a mid tibia with paired anterodorsal-posterodorsal setae (9), wing vein R_{4+5} straight or distally gently curved upwards (14), a posterodorsal hypandrial apodeme (25), the median ventral process of the distiphallus fused or articulating with the ventral paired process (35), telescoping female terminalia (39), no spectacles-shaped sclerites (40) and a medially desclerotized epiproct (41). Characters 4, 14, and 41 are plesiomorphic in the Sphaeroceridae and, while they do separate *P. fucata* and *Howickia* in this analysis, they do not provide strong evidence for their monophyly like the rest of the characters above. Clade 1 and all of the species groups discussed in the initial analysis all remain and are similarly supported.

This analysis more accurately reflects the relationship between *Paralimosina* and *Howickia* than the previous analysis. Though the genera share many traits in common, the traits that separate them are strong characters unlikely to have been secondarily gained and lost in species currently treated as *Paralimosina* and *Howickia*, and this research suggests that *Paralimosina* does not occur in Australia.
3.4 The evolution of winglessness in *Howickia*

Phylogenetic results show that winglessness has evolved at least three separate times; in Tasmania (*croca* species group), on Lord Howe Island ("*H. kentia*"), and on the mainland (*regalis* species group, "*H. pruinosa*” and *flagella* species group) (Fig. 3.2). It is very likely that winglessness has evolved multiple times on the mainland since the species in Western Australia are widely geographically separated from those in Queensland, Victoria and New South Wales. Apteronous species “*H. kentia*”, “*H. croca*”, “*H. discoloris*” and *M. cynthia* retain the more complex ancestral distiphallus, suggesting their ancestor was an ancestral winged *Howickia*, while the remaining species fit into Clade 1 with a simple, tubular distiphallus. Brachyptery also appears to have independently evolved in “*H. polacornis*”.

Apterous *Howickia* with overlapping ranges often have similar appearances, likely due to shared ancestry. All species in the *croca* species group share a red-orange head and a shiny black body, while species in the *regalis* species group share a yellow head and thorax with a black abdomen. It may be that these species evolved sympatrically in a similar fashion to Richards’ apterous sphaerocerids in mountainous regions of Africa. Speciation is likely higher among apterous species due to the genetic isolation that would occur when species are restricted to concealed and specialized niches where gene flow is limited. All apterous species of *Howickia* and similar genera appear to live on the forest floor and are most often collected in pan traps or sifted in litter.

“*Howickia kentia*” is a unique looking apterous species distinct from all other apterous species treated here in that its facial chaetotaxy is very robust. In all other species the facial chaetotaxy was very fine, reduced and even lost. Perhaps fortification of chaetotaxy is another method to prevent the abrasion of setae that would inevitably accompany a terricolous lifestyle.
The microtrichosity and setulae on the scutum and abdomen of “H. kentia” are also denser and longer than in most other apterous species. Roháček (2012) notes that dense and long leg and body chaetotaxy in sphaerocerids is strongly advantageous to survival in humid environments. He does not explain further, but perhaps it creates a barrier between the fly’s body to keep moisture out of the spiracles or prevent the moisture from lowering the body temperature. These characteristics suggest that “H. kentia” is found in a more humid environment than other apterous Howickia, and it would be interesting the investigate this further.

CHAPTER 4: CONCLUSION

The Sphaeroceridae may have the highest incidence of flightlessness of any dipteran family with 12.5% of described species displaying some form of wing reduction. Among the genera displaying brachyptery or aptery, Howickia is one of the few genera which includes a roughly equal number of both macropterous and apterous species, along with brachyptery, which has made it an ideal group with which to study the evolution of winglessness. The taxonomy of Howickia is complicated by a number of small and poorly defined Australasian genera. Historically the striking morphological autapomorphies that come with flightlessness has led taxonomists astray and caused them to place apterous species in their own genera. Today the use of terminalia characters has allowed many apterous species to be placed with their macropterous relatives. This is the case here with Apterobirolina, Bentrovata, and Monteithiana, which are suggested here as synonyms of Howickia. It is very likely that all wingless sphaerocerids in Australia belong to the genus Howickia.
Macropterous genera *Australimosina* and *Popondetta* are also suggested synonyms of *Howickia* which were likely placed in separate genera due to the fact that terminalia were not thoroughly illustrated when many of these genera were first described. The male terminalia of sphaerocerids are often considered taxonomic roadmaps because of their rich characters. Contrary to this trend, it was shown here that the male terminalia of *Howickia* are actually strikingly uniform, with either a complex but uniform distiphallus similar to *Paralimosina*, or a very simple and tubular distiphallus. This makes morphology-based phylogenetic analysis slightly more difficult and certainly more dependent on external characters, but the analyses here still managed to show several well-defined species groups which will be useful in a revision. A complete revision of the Australian *Howickia* is still a necessary task, and there are still several thousand unsorted Australian sphaerocerids at the University of Guelph Insect Collection which are likely to yield a number of undescribed *Howickia*.

Several species of Australian *Howickia* have severely restricted ranges and may be of interest to conservation biologists. The small and concealed nature of apterous sphaerocerid’s ranges make them particularly vulnerable to extinction due to habitat degradation and loss. “*Howickia kentia*” has only ever been collected in a very small range on Lord Howe Island and specimen labels have provided no information on the behavior or life history of this unique species. The highly reduced eyes and absence of ocelli suggests that their life history differs from the rest of the Australian *Howickia* and it would be interesting to learn more about this apterous species.

During initial specimen sorting it became very obvious how poor the overall state of sphaerocerid taxonomy in southeast Asia is, with some genera such as *Acuminiseta* lacking definitive diagnoses. Genera similar to *Howickia* such as *Paralimosina* and *Pseudopterogramma* are in need of complete revisions, which would undoubtably clear up the diagnosis of *Howickia*.
There are also several wingless African genera described by Richards lacking thorough illustrations which should be more closely examined and compared to *Howickia* for possible relatedness.

The Limosininae are vast in number and diversity, making their higher classification one of the most complex problems in sphaerocerid taxonomy today. The unexpected paraphyly of *Howickia* as well as its placement within the epandrial process group in the analysis of COI data here requires further investigation. A multigene analysis of the Sphaeroceridae with multiple definitively identified representatives from each genus would be a massive undertaking that would undoubtably help unravel the higher classification of the Limosininae and give further support to or refute the placement of *Howickia* in the EPG. Including multiple genes that have been shown to be phylogenetically-informative in Diptera such as CAD and COII is essential due to evidence that COI is less informative in the Sphaeroceridae.
REFERENCES


Richards, O.W. (1960b) Diptera (Sphaeroceridae) from south Chile. Proceedings of the Royal Entomological Society of London (B), 30, 57-68.


**FIGURES**

**Fig. 1.1.** One of four most parsimonious trees resulting from the parsimony analysis of the COI data of the BIN representatives of the global Sphaeroceridae from BOLD. The highlighted section includes the main *Howickia* group and its closest relatives.
**Fig. 1.2.** A closer look at the section of the parsimony analysis of the COI data of the BIN representatives of the global Sphaeroceridae from BOLD including the main *Howickia* group and its closest relatives (highlighted section in Fig. 1.1). Genus and species were included where possible.
Fig. 2.1. Head and thoracic chaetotaxy and important wing veination. "Howickia apricitas" sp. n. (left), Howickia myrmecophila (Knabb and Malloch) (right).
Fig. 2.2-2.3. Mid tibial chaetotaxy. 2.2, typical arrangement of macropterous species; typical arrangement of apterous species.
Fig. 3.1 Optimized characters on the most parsimonious tree produced by the phylogenetic analysis of the study set of Australian *Howickia* and *Howickia*-like species using *Bromeloechia abundatia*, *Paralimosina fucata*, *Pterogramma madare*, *Pterogramma substitutum* and *Pseudopterogramma* sp. as outgroups (length 213, consistency index 38, retention index 68). Solid dots indicate nonhomoplasious changes and open dots indicate homoplasies. Character numbers and their states are indicated above and below the dots, respectively. An asterisk (*) beside a species name symbolizes that it is macropterous. Species distributions are in bold letters beside their names. Australian Capital Territory was included in New South Wales due to its geographic location.
Fig. 3.2 Optimized characters one of the two most parsimonious tree produced by the phylogenetic analysis of the study set of Australian *Howickia* and *Howickia*-like species using only *Paralimosina fucata* as an outgroup (length 154, consistency index 38, retention index 65). Solid dots indicate nonhomoplasious changes and open dots indicate homoplasies. Character numbers and their states are indicated above and below the dots, respectively. An asterisk (*) beside a species name symbolizes that it is macropterous. Species distributions are in bold letters beside their names. Australian Capital Territory was included in New South Wales due to its geographic location.
Fig. 3.3 Optimized characters one of the two most parsimonious tree produced by the phylogenetic analysis of the study set of Australian *Howickia* and *Howickia*-like species using only *Paralimosina fucata* as an outgroup (length 154, consistency index 38, retention index 65). Solid dots indicate nonhomoplasious changes and open dots indicate homoplasies. Character numbers and their states are indicated above and below the dots, respectively.
Figs. 4.1-4.6. *Apterobiroina australis* Papp. 4.1, male habitus, left lateral; 4.2, head; 4.3, terminalia, ventral; 4.4, epandrium, left lateral; 4.5, epandrium, posterior; 4.6, phallus and associated structures; left lateral.
Figs. 4.7-4.9. *Apterobiroina australis* Papp. 4.7, female terminalia, dorsal; 4.8, female terminalia, ventral; 4.9, spermathecae.
Figs. 5.1-5.6. *Australimosina flaviterga* Richards. 5.1, male habitus, left lateral; 5.2, head; 5.3, terminalia, ventral; 5.4, epandrium, left lateral; 5.5, epandrium, posterior; 5.6, phallus and associated structures; left lateral. Abbreviations: DPP = distal paired process, DS = dorsal saddle sclerite, MTS = medial tube-shaped sclerite, MVP = medial ventral process, VPP = ventral paired process. Habitus and head photos by James Lumbers of the Australian National Insect Collection.
Figs. 6.1-6.6. *Monteithiana regalis* Richards. 6.1, female yellow thorax morph habitus, left lateral; 6.2, yellow thorax morph head; 6.3, female black thorax morph habitus, left lateral; 6.4, black thorax morph light head; 6.5, spermathecae; 6.6 black thorax morph dark head.
Figs. 6.7-6.12. *Monteithiana regalis* Richards. 6.7, terminalia, ventral; 6.8, epandrium, left lateral; 6.9, epandrium, posterior; 6.10, phallus and associated structures; left lateral; 6.11, female terminalia, dorsal; 6.12, female terminalia, ventral. Figs. 5.7-5.10. *Howickia kentia* sp. n. 5.7, female terminalia, dorsal; 5.8, female terminalia, ventral; 5.9, spermathecae; 5.10, head; 5.11, surstylus.
Figs. 7.1-7.6. “Howickia acus” sp. n. 7.1, male habitus, left lateral; 7.2, head; 7.3, terminalia, ventral; 7.4, epandrium, left lateral; 7.5, epandrium, posterior; 7.6, phallus and associated structures; left lateral. Abbreviations: DPP = distal paired process, DS = dorsal saddle sclerite, MTS = medial tube-shaped sclerite, MVP = medial ventral process, VPP = ventral paired process.
Figs. 8.1-8.6. “Howickia apricitas” sp. n. 8.1, male habitus, left lateral; 8.2, head; 8.3, terminalia, ventral; 8.4, epandrium, left lateral; 8.5, epandrium, posterior; 8.6, phallus and associated structures; left lateral.
Figs. 6.6-6.8. “Howickia apricitas” sp. n. 8.7, female terminalia, dorsal; 8.8, female terminalia, ventral; 8.9, spermathecae.
Figs. 9.1-9.6. “Howickia bractea” sp. n. 9.1, female habitus, left lateral; 9.2, head; 9.3, terminalia, ventral; 9.4, epandrium, left lateral; 9.5, epandrium, posterior; 9.6, phallus and associated structures.
Figs. 9.7-9.10. “Howickia bractea” sp. n. 9.7, female terminalia, dorsal; 9.8, female terminalia, ventral; 9.9, spermathecae; 9.10, male epandrium, posteroverentral.
Figs. 10.1-10.6. “Howickia croca” sp. n. 10.1, female habitus, left lateral; 10.2, head; 10.3, terminalia, ventral; 10.4, epandrium, left lateral; 10.5, epandrium, posterior; 10.6, phallus and associated structures; left lateral. Abbreviations: DPP = distal paired process, DS = dorsal saddle sclerite, MTS = medial tube-shaped sclerite, MVP = medial ventral process, VPP = ventral paired process.
Figs. 10.7-10.9. “Howickia croca” sp. n. 10.7, female terminalia, dorsal; 10.8, female terminalia, ventral; 10.9, spermathecae.
Figs. 11.1-11.6. “Howickia discoloris” sp. n. 11.1, male habitus, left lateral; 11.2, head; 11.3, terminalia, ventral; 11.4, epandrium, left lateral; 11.5, epandrium, posterior; 11.6, phallus and associated structures; left lateral. Abbreviations: DPP = distal paired process, DS = dorsal saddle sclerite, MTS = medial tube-shaped sclerite, MVP = medial ventral process, VPP = ventral paired process.
Figs. 11.7-11.9. “Howickia discoloris” sp. n. 11.7, female terminalia, dorsal; 11.8, female terminalia, ventral; 11.9, spermathecae.
Figs. 12.1-12.6. *Howickia flagella* sp. n. 12.1, male habitus, left lateral; 12.2, head; 12.3, terminalia, ventral; 12.4, epandrium, left lateral; 12.5, epandrium, posterior; 12.6, phallus and associated structures; left lateral.
Figs. 12.7-12.9. “Howickia flagella” sp. n. 12.7, female terminalia, dorsal; 12.8, female terminalia, ventral; 12.9, spermathecae.
Figs. 13.1-16.6. Howickia hardyina Richards. 13.1, male habitus, left lateral; 13.2, head; 13.3, terminalia, ventral; 13.4, epandrium, left lateral; 13.5, epandrium, posterior; 13.6, phallus and associated structures; left lateral. Abbreviations: DPP = distal paired process, DS = dorsal saddle sclerite, MTS = medial tube-shaped sclerite, MVP = medial ventral process, VPP = ventral paired process.
Figs. 14.7-14.9. *Howickia kentia* sp. n. 14.1, male habitus, left lateral; 14.2, head; 14.3, terminalia, ventral; 14.4, epandrium, left lateral; 14.5, epandrium, posterior; 14.6, phallus and associated structures; left lateral. Abbreviations: DPP = distal paired process, DS = dorsal saddle sclerite, MVP = medial ventral process, VPP = ventral paired process.
Figs. 15.7-15.9. “Howickia manta” sp. n. 15.1, male habitus, left lateral; 15.2, head; 15.3, terminalia, ventral; 15.4, epandrium, left lateral; 15.5, epandrium, posterior; 15.6, phallus and associated structures; left lateral. Abbreviations: DPP = distal paired process, DS = dorsal saddle sclerite, MVP = medial ventral process, VPP = ventral paired process.
Figs. 15.7-15.9. “Howickia manta” sp. n. 15.7, female terminalia, dorsal; 15.8, female terminalia, ventral; 15.9, spermathecae.
Figs. 16.7-16.9. *Howickia monteithi* sp. n. 16.1, male habitus, left lateral; 16.2, head; 16.3, terminalia, ventral; 16.4, epandrium, left lateral; 16.5, epandrium, posterior; 16.6, phallus and associated structures; left lateral. Abbreviations: DS = dorsal saddle sclerite, MVP = medial ventral process.
Figs. 16.7-16.9. “Howickia monteithi” sp. n. 16.7, female terminalia, dorsal; 16.8, female terminalia, ventral; 16.9, spermathecae.
Figs. 17.1-17.6. *Howickia myrmecophila* Knabb & Malloch. 17.1, male habitus, left lateral; 17.2, head; 17.3, terminalia, ventral; 17.4, epandrium, left lateral; 17.5, epandrium, posterior; 17.6, phallus and associated structures; left lateral. Abbreviations: DPP = distal paired process, DS = dorsal saddle sclerite, MTS = medial tube-shaped sclerite, MVP = medial ventral process, VPP = ventral paired process.
Figs. 17.7-17.9. Howickia myrmecophila Knabb & Malloch. 17.7, female terminalia, dorsal; 17.8, female terminalia, ventral; 17.9, spermathecae. Abbreviations: T8 = tergite 8, S8 = sternite 8.
Figs. 18.1-18.6. *Howickia nitidipleura* Richards. 18.1, male habitus, left lateral; 18.2, head; 18.3, terminalia, ventral; 18.4, epandrium, left lateral; 18.5, epandrium, posterior; 18.6, phallus and associated structures; left lateral.
Figs. 18.1-18.9. *Howickia nitidipleura* Richards. 18.7, female terminalia, dorsal; 18.8, female terminalia, ventral; 18.9, spermathecae.
Figs. 19.1-19.6. *Howickia parasubsinuata* sp. n. 19.1, male habitus, left lateral; 19.2, head; 19.3, terminalia, ventral; 19.4, epandrium, left lateral; 19.5, epandrium, posterior; 19.6, phallus and associated structures; left lateral.
Figs. 20.1-20.6. *Howickia percostata* Richards. 20.1, male habitus, left lateral; 20.2, head; 20.3, terminalia, ventral; 20.4, epandrium, left lateral; 20.5, epandrium, posterior; 20.6, phallus and associated structures; left lateral.
Figs. 20.7-20.9. Howickia percostata Richards. 20.7, female terminalia, dorsal; 20.8, female terminalia, ventral; 20.9, spermathecae.
Figs. 21.7-21.9. “Howickia pertusa” sp. n. 21.1, male habitus, left lateral; 21.2, head; 21.3, terminalia, ventral; 21.4, epandrium, left lateral; 21.5, epandrium, posterior; 21.6, phallus and associated structures; left lateral.
Figs. 22.1-22.6. *Howickia polacornis* sp. n. 9.1, male habitus, left lateral; 9.2, head; 9.3, terminalia, ventral; 9.4, epandrium, left lateral; 9.5, epandrium, posterior; 9.6, phallus and associated structures; left lateral. Abbreviations: DPP = distal paired process, DS = dorsal saddle sclerite, MTS = medial tube-shaped sclerite, MVP = medial ventral process, VPP = ventral paired process.
Figs. 22.7-22.10. *Howickia polacornis*” sp. n. 22.7, female terminalia, dorsal; 22.8, female terminalia, ventral; 22.9, spermathecae; 22.10, male cercus, surstylus and subependrial sclerite.
Figs. 23.1-23.6. “Howickia pruinosa” sp. n. 23.1, female habitus, left lateral; 23.2, head; 23.3, terminalia, ventral; 23.4, epandrium, left lateral; 23.5, epandrium, posterior; 23.6, phallus and associated structures; left lateral.
Figs. 23.7-23.9. “Howickia pruinosa” sp. n. 23.7, female terminalia, dorsal; 23.8, female terminalia, ventral; 23.9, spermathecae.
Figs. 24.1-24.6. “Howickia spina” sp. n. 24.1, male habitus, left lateral; 24.2, head; 24.3, terminalia, ventral; 24.4, epandrium, left lateral; 24.5, epandrium, posterior; 24.6, phallus and associated structures; left lateral. Abbreviations: DPP = distal paired process, DS = dorsal saddle sclerite, MTS = medial tube-shaped sclerite, MVP = medial ventral process, VPP = ventral paired process.
Figs. 25.1-25.6. *Howickia subsinuata* Richards. 25.1, male habitus, left lateral; 25.2, head; 25.3, terminalia, ventral; 25.4, epandrium, left lateral; 25.5, epandrium, posterior; 25.6, phallus and associated structures; left lateral.
Figs. 25.7-25.9. *Howickia subsinuata* Richards. 25.7, female terminalia, dorsal; 25.8, female terminalia, ventral; 25.9, spermathecae.
Figs. 27.1-27.6. “Howickia wamini” sp. n. 27.1, male habitus, left lateral; 27.2, head; 27.3, terminalia, ventral; 27.4, epandrium, left lateral; 27.5, epandrium, posterior; 27.6, phallus and associated structures; left lateral.
Figs. 27.7-27.9. “Howickia wamini” sp. n. 27.7, female terminalia, dorsal; 27.8, female terminalia, ventral; 27.9, spermathecae.
Figs. 29.1-29.6. Howickia kurandensis Richards. 29.1, male habitus, left lateral; 29.2, head; 29.3, terminalia, ventral; 29.4, epandrium, left lateral; 29.5, epandrium, posterior; 29.6, phallus and associated structures; left lateral. Abbreviations: DPP = distal paired process, DS = dorsal saddle sclerite, MVP = medial ventral process, VPP = ventral paired process.
Figs. 29.7-29.10. *Howickia kurandensis* Richards. 29.7, female terminalia, dorsal; 29.8, female terminalia, ventral; 29.9, spermathecae; 29.10, distiphallus. Abbreviations: DPP = distal paired process, DS = dorsal saddle sclerite, MTS = medial tube-shaped sclerite, MVP = medial ventral process, VPP = ventral paired process.
## APPENDIX

### Appendix 1.

Described species of Sphaeroceridae with wing reduction and loss. Wing state, haltere state, ocelli state, distribution and habitats are recorded. Unavailable information is marked with a “?”.  

<table>
<thead>
<tr>
<th>Subfamily</th>
<th>Genus</th>
<th>Species</th>
<th>Original Description</th>
<th>Wing State</th>
<th>Halteres</th>
<th>Ocelli</th>
<th>Locality/Region</th>
<th>Habitat(s)</th>
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<td>Archiborborinae</td>
<td>Antrops</td>
<td><em>biflavus</em></td>
<td>Kits &amp; Marshall, 2013</td>
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<td>present</td>
<td>Neotropical</td>
<td>3000 m</td>
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<td>Archiborborinae</td>
<td>Antrops</td>
<td><em>bucki</em></td>
<td>Kits &amp; Marshall, 2013</td>
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<td>absent</td>
<td>present</td>
<td>Neotropical</td>
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<td>present</td>
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<td>Marshall &amp; Smith, 1995</td>
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<td>miradorensis</td>
<td>Marshall &amp; Smith, 1995</td>
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<td>quadricercus</td>
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<td>Collin, 1930</td>
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<td>present</td>
<td>Palaearctic</td>
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<td>island</td>
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<td>selkerki</td>
<td>Enderlein, 1938</td>
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<td>present</td>
<td>Neotropical</td>
<td>island, terricolous, near streams, ferns</td>
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<td>venosa</td>
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<td>absent</td>
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<td>Afrotropical</td>
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<td>kabare</td>
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<td>mwenga</td>
<td>Richards, 1960a</td>
<td>apterous</td>
<td>absent</td>
<td>absent</td>
<td>Afrotropical</td>
<td>forest litter, 1900 m</td>
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<td>uvira</td>
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<td>absent</td>
<td>absent</td>
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<td>Marshall, 1984</td>
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<td>normal</td>
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<td>Smith &amp; Marshall, 2004</td>
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<td>damp forest</td>
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<td>Nearctic</td>
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<td>Halidae, 1836</td>
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<td>wide range including mammal burrows and caves</td>
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<td>normal</td>
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<td>forest litter</td>
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<td><em>cribratum</em></td>
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<td>reduced in brachypterous forms</td>
<td>normal</td>
<td>Palaeartic</td>
<td>forest litter</td>
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<td>absent</td>
<td>small</td>
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<td>Richards, 1968b</td>
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<td>small</td>
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<td>forest litter</td>
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<td><em>caledoniana</em></td>
<td>Richards, 1968b</td>
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<td>N/A</td>
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<td>small</td>
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<td>absent</td>
<td>small</td>
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<td>small</td>
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<td>Richards, 1968b</td>
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<td>absent</td>
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<td>Afrotropical</td>
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<td>small</td>
<td>Afrotropical</td>
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<td>small</td>
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<td>small</td>
<td>Afrotropical</td>
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<td>peregrina</td>
<td>Richards, 1968b</td>
<td>apterous</td>
<td>absent</td>
<td>small</td>
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<td>forest litter, 1400-1800 m</td>
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<td>Richards, 1968b</td>
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<td>small</td>
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<td>river forest litter</td>
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<td>Enderlein, 1908</td>
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<td><em>manicata</em></td>
<td>Richards, 1927</td>
<td>sometimes slightly brachypterous</td>
<td>normal</td>
<td>normal</td>
<td>Palaeartic</td>
<td>small mammal burrows, leaf-litter, moss</td>
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<td><em>pseudonivalis</em></td>
<td>Dahl, 1909</td>
<td>polymorphic</td>
<td>reduced in brachypterous forms</td>
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<td>small mammal burrows</td>
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<td><em>corrivalis</em></td>
<td>Villeneuve, 1918</td>
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<td>reduced in brachypterous forms</td>
<td>?</td>
<td>Palaeartic</td>
<td>litter and moss, mountain forests</td>
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<td><em>triseta</em></td>
<td>Richards, 1965</td>
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<td>small</td>
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<td><em>fuscana</em></td>
<td>Richards, 1965</td>
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<td>Afrotropical</td>
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<td>Richards, 1966</td>
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<td>normal</td>
<td>normal</td>
<td>Afrotropical</td>
<td>terricolous, 1600 m</td>
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<td>Richards, 1965</td>
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<td>absent</td>
<td>normal</td>
<td>Afrotropical</td>
<td>under stone, 4300 m</td>
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Appendix 2.

List of specimens examined for each species considered.

*Apterobiroina australis* (Papp, 1979)

**SPECIMENS EXAMINED. Victoria:** Warburton, Cement Creek, 200m, 28 Apr-7 May 1978, S. Peck (2#m, 1#f, 1 unknown, DEBU); Aucheron Gap, 16 km S of Warburton, carrion, 750m, 28 Apr-7 May 1978, S. Peck (5#m, 4#f, 1 unknown, DEBU); Photos of holotype.

*Australimosina flaviterga* (Richards, 1973)

**SPECIMENS EXAMINED. New South Wales:** Mount Wilson, 33°31’S, 150°22’E, pans, 17-21 Mar 1999, S.A. Marshall (5#m, DEBU). **Victoria:** Mount Donna, Buang, 1200m, 28 Apr-7 May 1978, S. and J. Peck (1#m, DEBU).

*Bentrovata regalis* (Richards, 1973)

**SPECIMENS EXAMINED. Western Australia:** Walpole National Park, Tingle Tree, forest, dung cup traps, 18 Jun-29 Jul 1980, S. and J. Peck (106#m, 150#f, 1 unknown, DEBU); Walpole National Park, Peaceful Bay, pan trap, coast sand heath, 17 Jun-13 Jul 1980, S. and J. Peck (1#f, DEBU); Pemberton, Gloucester Tree, karri, dung cup traps, 5-9 Jul 1980, S. and J. Peck (22#m, 22#f, DEBU); The Cascades, jarrah forest, dung cup traps, 7-13 Jul 1980, S. and J. Peck (13#m, 8#f, DEBU); Augusta, Bonarup State Forest, karri forest, dung cup traps, 19-22 Jul 1980, S. and J. Peck (9#m, 17#f, DEBU); Boranup Forest, ~25 km N of Augusta, 34°09’52S, 115°04’34E, karri forest, pans, 20-23 Nov 2003, S.A. Marshall (1#m, 1#f, DEBU); Augusta, Leeuwin Naturaliste National Park, forest, dung traps, The Spring Trail, 19-22 Jul 1980, S. and J. Peck (10#m, 12#f, DEBU); Augusta, Leeuwin, 22 Nov 2003, S.A. Marshall (1#f, DEBU); Coronation Road, 33 km SW of Manjinup, jarrah forest, dung traps, 14-17 Jul 1980, S. and J. Peck (11#m,
11#f, DEBU); Stirling Range National Park, Toolbrunup Trail, mini carrion traps, 10 Jun 1980, S. and J. Peck (10#m, 4#f, DEBU); Stirling Range National Park, GoldHoles, heath, carrion traps, 8-15 Jun 1980, S. and J. Peck (8#m, 7#f, 1 unknown, DEBU); Nannup, Barrabup Pool, forest, dung traps, 10 Jun 1980, S. and J. Peck (3#m, DEBU); Quininup, 29 km SSE Manjinup, karri forest, dung traps, 13-16 Jul 1980, S. and J. Peck (8#m, 11#f, DEBU); Windy Harbor, 27 km S of Northcliffe, coast heath, dung cup traps, 8-12 Jul 1980, S. and J. Peck (2#m, 1#f, DEBU); Sues Bridge, 50 km SW of Nannup, marri forest, dung cup traps, 24-26 Jul 1980, S. and J. Peck (3#m, 3#f, DEBU); Wrenwood Cottages, 10 km N of Augusta, 35°15’S, 115°01’E, paperbark grove, pans, 20-23 Nov 2003, S.A. Marshall (3#f, DEBU); Forth River, 45 km SE of Northcliffe, Chesapeake Road, forest, heath, dung cups, 1980, S. and J. Peck (1#m, DEBU); Fernhook Falls, ~30 km N of Walpole, Deep River shoreline, dune pans, 26-27 Nov 2003, S.A. Marshall (9#m, 12#f, DEBU); Albany, Two People Bay Reserve, heath, dung cup traps, 9-14 Jun 1980, S. and J. Peck (5#m, 7#f, DEBU); Mount Frankland, ~30 km N of Walpole, pans, 26 Nov 2003, S.A. Marshall (1#f, DEBU); Walpole, tingle tree forest, dung pans in leaf litter, 28-30 Nov 2003, S.A. Marshall (1#f, DEBU); Northcliffe Park, 1 km E, karri forest, dung traps, 13-16 Jul 1980, S. and J. Peck (5#m, 5#f, DEBU); Margaret River, Rosa Brook Road, marri forest, dung cup traps, 22-26 Jul 1980, S. and J. Peck (1#m, 1#f, DEBU); Porongurup National Park, karri, dung trap, 8-16 Jun 1980, S. and J. Peck (1#f, DEBU).

“H. acus” sp. n.

SPECIMENS EXAMINED. Tasmania: Cuckoo Falls, ~4 km E of Scottsdale, along Falls Road, along creek, pans/ some dung, 14 Dec 2003, S.A. Marshall (12#m, DEBU); Waratah, 8 km SW, 41°29’04S, 145°27’41E, rainforest, dung pans, 20-21 Dec 2003, S.A. Marshall (1#m,
DEBU); Mount William, Stumpys Bay, dry heath pans, 12-13 Dec 2003, S.A. Marshall (1#m, DEBU).

“Howickia apricita” sp. n.

SPECIMENS EXAMINED. Western Australia: Walpole National Park, Tingle Tree, forest, dung cup traps, 18 Jun-29 Jul 1980, S. and J. Peck (28#m, 33#f, DEBU); Walpole National Park, Collier Road, forest, mini carrion traps, 19 Jun-4 Jul 1980, S. and J. Peck (2#m, 6#f, DEBU); Walpole National Park, Hilltop Road, forest, dung cup traps, 20 Jun-4 Jul 1980, S. and J. Peck (6#f, DEBU); Pemberton, Gloucester Tree, karri, dung cup traps, 5-9 Jul 1980, S. and J. Peck (1#m, 3#f, DEBU); Wrenwood Cottages, 10 km N of Augusta, 35°15’S, 115°01’E, paperbark grove, pans, 20-23 Nov 2003, S.A. Marshall (2#m, 3#f, DEBU); Northcliffe Park, 1 km E, karri forest, dung traps, 13-16 Jul 1980, S. and J. Peck (2#m, 1#f, DEBU); Boranup Forest, ~25 km N of Augusta, 34°09’52S, 115°04’34E, karri forest, pans, 20-23 Nov 2003 (1#m, DEBU); Mount Frankland, ~30 km N of Walpole, pans, 26 Nov 2003, S.A. Marshall (1#m, DEBU); Walpole, tingle tree forest, dung pans in leaf litter, 28-30 Nov 2003, S.A. Marshall (1#f, DEBU).

“Howickia bracteata” sp. n.

SPECIMENS EXAMINED. Victoria: Mount Donna, Buang, 1200m, 28 Apr- 7 May 1978, S. and J. Peck (27#m, 25#f, DEBU).

“Howickia croca” sp. n.

SPECIMENS EXAMINED. Tasmania: Waratah, 8 km SW, 41°29’04S, 145°27’41E, rainforest, dung pans, 20-21 Dec 2003, S.A. Marshall (2#m, 3#f, DEBU).

“Howickia discoloris” sp. n.
**SPECIMENS EXAMINED. Tasmania:** Weldborough, 41°09’50S, 147°53’51E, *Nothofagus* forest, litter, 22-27 May 1993, J. Trueman et al. (17#f, 19#m, ANIC); 41°08S, 148°07E, near Peters Link Road, dry sclerophyll, 20-25 Feb 1993, J. Trueman et al. (5#f, 9#m, ANIC); Florentine, 29.2km WNW Maydena, on Eleven Road, *Nothofagus*, 460 m, 1-6 Feb 1980, A. Newton and M. Thayer (1#f, ANIC).

**“Howickia flagella” sp. n.**

**SPECIMENS EXAMINED. Queensland:** Lamington National Park, Binna Burra, *Nothofagus* grove, carrion, 900m, 23 Jun- 7 Jul 1978, S. and J. Peck (38#m, 33#f DEBU). **New South Wales:** Kyogle, *Nothofagus* forest, 1000m, 9 Jul 1978, S. and J. Peck (17#m, 22#f, DEBU); Gibraltar Range, 29°31’S, 152°22’E, volcanic, pitfall trap, 950m, 23 Sep 1999, J. Holt (3#m, 2#f, DEBU); Wiangaree, 33 km NE, near Tweed Valley lookout, 1000m, 13 Jun- 24 Aug 1982, S. and J. Peck (1#m, DEBU); Wiangaree, 32 km NE, Wiangaree State Forest, *Nothofagus* litter, 1000m, 24 Aug 1982, S. and J. Peck (1#m, 2#f, 1 unknown, DEBU).

**Howickia hardyina (Richards, 1973)**

**SPECIMENS EXAMINED. Victoria:** Mount Donna, Buang, 1200m, 28 Apr- 7 May 1978, S. and J. Peck (13#m, 15#f, DEBU).

**“Howickia kentia” sp. n.**

**SPECIMENS EXAMINED. New South Wales:** Lord Howe Island, Mount Gower, leaf litter, 100m, T. Kingston (4#m, 3#f, DEBU); Lord Howe Island, Intermediate Hill, carrion trap, 50-200ft, 19-30 Apr 1980, S. and J. Peck (1#m, 1#f, DEBU).

**“Howickia manta” sp. n.**
**SPECIMENS EXAMINED. Tasmania:** Mount William, Stumpys Bay, dry heath pans, 12-13 Dec 2003, S.A. Marshall (23#m, 37#f, DEBU).

“*Howickia monteithi*” sp. n.

**SPECIMENS EXAMINED. Queensland:** Malanda, Malanda Falls Reserve, rainforest, fungi, 730m, 22 Jul 1982, S. Peck (2#m, 4#f, DEBU); Malanda, 14 km SW, Mount Hypipamee National Park, rainforest, carrion trap, 960m, 24 Jul-2 Aug 1982, S. and J. Peck (2#m, 1#f, DEBU); Atherton, Lake Eacham, Wright’s Creek, leaf litter and soil, 720m, 31 Jul 1982, S. and J. Peck (3#m, 1#f, DEBU); Maleny, 7 km SE, Mary Cairncross Park, rainforest, flight interception trap, 18 Jun-15 Aug 1982, S. and J. Peck (1#m, 4#f, DEBU); Mossman, 20 km SW, Mount Lewis National Park, carrion trap, 1000m, 10 Jul-1 Aug 1982, S. and J. Peck (4#m, 1#f, DEBU); Cooyar, 8 km N, *Araucaria* vine, flight interception trap, 300m, 18 Jun-19 Aug 1982, S. and J. Peck (3#f, DEBU); Mount Bartle Frere, west side, carrion trap, 30 Jul-4 Aug 1982, S.J. Peck (1#m, DEBU); Mount Bartle Frere, Gourka Road, 17°23’S, 145°25°E, autom. dung trap (night), 750m, 28-30 Nov 1998, Monteith and Cook (3#m, 2#f, DEBU); Mount Bartle Frere, west base, 17°23’S, 145°25°E, autom. dung trap (dusk), 750m, 28-30 Nov 1998, Monteith and Cook (1#f, DEBU); Wiangree, 16 km NE, Sheep Station Creek, rainforest, 600m, 13 Jun-24 Aug 1982, S. and J. Peck (1#f, DEBU); Yungaburra, 16 km NE, on Gillies Road, NE of Atherton, rainforest, flight interception trap, 800m, 24 Jun-3 Aug 1982, Peck (1#m, DEBU); Paluma Paluma Dam Road, rainforest, flight interception trap, 850m, 22 Jun06 Aug 1982, S. Peck (1#m, DEBU); Millaa Millaa, 19 km NW, near the Crater, Nelson RG, flight interception trap, 1080m, 24 Jun-2 Aug 1982, S. and J. Peck (2#m, 1 unknown, DEBU); Ingham, 40 km W, near Wallaman Falls, rainforest flight interception trap, 600m, 22 Jun-7 Aug 1982, S. and J. Peck (1#m, DEBU); Kuranda State Forest, 3 km N of Kuranda, rainforest, flight interception trap,
360m, 25 Jun-3 Aug, 1982, S. Peck (2#f, DEBU); Cardwell, 30 km NW, Kirrama State Forest, rainforest, flight intercept trap, 800m, 23 Jun-8 Aug 1982, S. and J. Peck (1#m, DEBU); near Innisfail, Palmerston N. Park, carrion trap, 2-5 Aug 1982, S. and J. Peck (1#f, DEBU); Lamington National Park, Binna Burra, Nothofagus grove, carrion, 900m, 23 Jun-7 Jul 1978, S. and J. Peck (1#m, DEBU); Mount Glorious, malaise trap, 27 Apr-26 Oct 1989, A. Hiller (9#m, 11#f, DEBU); Mount Glorious, malaise trap, 26 Oct-6 Dec 1989, A. Hiller (3#m, 1#f, DEBU); Millstream Conservation Park, adjacent, 17°32’S, 145°29’E, open forest, autom. dung trap (day), 1040m, 4-5 Feb 1999, G.B. Monteith (4#m, 1#f, DEBU); Millstream Conservation Park, 17°32’S, 145°29’E, wet sclerophyll, fish, dung or fungus trap, 1040m, 3-5 Feb 1999, Monteith and Cook (17#m, 19#f, DEBU); The Millstream, 10 km NNE Ravenshoe, 17°32’S, 145°31’E, wet sclerophyll, dung trap, 1050m, 14-17 Apr 1999, G.B. and S.R. Monteith (16#m, 3#f, DEBU); Charmillin Creek, 17°42’S, 145°31’E, autom. dung trap, 5:30am-6.15pm, 900m, 2-5 Dec 1998, Monteith and Cook (9#m, 8#f, DEBU); Charmillin Creek, 17°42’S, 145°31’E, autom. dung trap, 6:15pm-7:15pm, 900m, 2-5 Dec 1998, Monteith and Cook (3#m, 1#f, DEBU); Millstream Retreat, 17°32’S, 145°31’E, wet sclerophyll, fungus trap, 1020m, 14-17 Apr 1999, G.B. and S.R. Monteith (4#f, DEBU); Kjellberg Road, St. For. boundary, 17°32’S, 145°35’E, rainforest, fungus pitfall, 920m, 8-9 Feb 1999, Monteith and Cook (17#m, 5#f, DEBU); Kjellberg Road turnoff, 17°32’S, 145°36’E, rainforest, dung pitfall, 740m, 6-9 Feb 1999, G.B. Monteith (2#m, 1#f, DEBU); Longlands Gap, three ways road junction, 17°28’S, 145°29’E, wet sclerophyll, dung trap, 1060m, Monteith and Cook (9#m, 7#f, DEBU); Vine Creek, Majors Mountain, 17°41’S, 145°32’E, rainforest, dung pitfall, 1060m, 4-6 Feb 1999, Monteith and Cook (12#m, 7#f, DEBU); Lake Euramoo, 17°10’S, 145°38’E, rainforest, dung pitfall, 700m, 10-11 Feb 1999, D.J. Cook (3#m, 4#f, DEBU); Mount Finnigan, summit, 15°51’S, 145°17’E rainforest,
dung trap (day), 1100m, 21 Nov 1998, G.B. Monteith (1#m, 2#f, DEBU); Mount Finnigan, summit, 15°51’S, 145°17’E rainforest, dung trap (night), 1100m, 21 Nov 1998, G.B. Monteith (1#f, DEBU); Arthur Baillie Road, 17°41’S, 145°31’E, autom. dung trap (night), 1000m, 6-8 Feb 1999. D.J. Cook (1#m, 1#f, DEBU); Brisbane Forest Park, Enoggera Creek at Scrub Road, 200m, 27°25’42S, 152°50’33E, malaise, 30 Oct-2 Nov 1995, Gaimari and Irwin (1#m, DEBU); Bare Rock, 2 km N of Mount Cordeaux, 28°2’42S, 152°23’E, pitfall traps, 1100m, 31 Dec 1993-20 Feb 1994, G.B. Monteith (1#m, DEBU); Mount Kooroomool, 7 km S of summit, dung trap (day), 1050m, 3 Dec 1998, G.B. Monteith (2#m, 3#f, DEBU); Mount Kooroomool, 7 km S of summit, dung trap (dusk), 1050m, 3 Dec 1998, G.B. Monteith (4#m, 5#f, DEBU); Mount Kooroomool, 7 km S of summit, dung trap (night/dawn), 1050m, 3 Dec 1998, G.B. Monteith (2#f, DEBU); Ravenshoe, 9.5 km N, 17°32’S, 145°29’E, wet sclerophyll, dung trap, 1060m, 14-17 Apr 1999, G.B. and S.R. Monteith (5#m, 2#f, DEBU); Ravenshoe, 9 km N, 17°32’S, 145°29’E, wet sclerophyll, fish or fungus pitfall, 1060m, 3-5 Feb 1999, Monteith and Cook (13#m, 8#f, DEBU); Ravenshoe, 2 km SW, 17°37’S, 145°28’E, open forest, autom. dung trap (dawn), 880m, 9 Feb 1999, G.B. Monteith (1#m, DEBU); Ravenshoe, 4 km SSE, 17°39’S, 145°30’E, open forest, dung trap, 930m, 4-6 Feb 1999, Monteith and Cook (2#m, 1#f, DEBU); Ravenshoe, 3 km NE, 17°32’S, 145°31’E, wet sclerophyll, dung pitfall, 1080m, 3-5 Feb 1999, Monteith and Cook (4#f, DEBU); Ravenshoe, 3 km SW, 17°38’S, 145°28’E, open forest, fungus or fish pitfall, 860m, 7-8 Feb 1999, Monteith and Cook (2#m, DEBU); Malanda, 3.5 km S, 17°23’S, 145°36’E, rainforest, dung pitfall, 6-9 Feb 1999, G.B. Monteith (16#m, 18#f, DEBU); Tully River, causeway above dam, wet sclerophyll, dung traps, 750m, 3-5 Dec 1998, D.J. Cook, (1#m, DEBU); Cheelonga Creek, Evelyn, 17°31’S, 145°32’E, rainforest, dung trap, 1080m, 15-17 Apr 1999, G.B. and S.R. Monteith (5#m, 3#f, DEBU); Mount Murray Prior,
16°56'S, 145°51'E, dung traps, 7-8 Dec 1998, G.B. Monteith (3#m, 2#f, DEBU); Cape Tribulation, transect site 8, 166°5'S, 145°26'E, 6am-6pm, 18 Nov 1999, G.B. Monteith (1#m, DEBU); Springbrook, pan traps, 9-10 Mar 1999, S. A. Marshall (2#f, DEBU); Millaa Millaa Falls, 17°30'S, 145°37'E, rainforest, dung pitfall, 800m, G.B. Monteith (1#m, 3#f, DEBU); Kauri Creek, 1 km SW, 17°9'S, 145°35'E, rainforest, fungus pitfall, 10-11 Feb 1999, Monteith and Cook (1#m, DEBU); Atherton, Tablelands, Lake Eacham, Chambers Lodge, dung, 6-8 Apr 1999, S.A. Marshall (1#m, DEBU); Mount Hugh nelson, south base, rainforest, dung pitfall, 1080m, 7-9 Feb 1999, G.B. Monteith (14#m, 6#f, DEBU); Bunya Mountains National Park, Westcott Camp, 26°51’51S, 151°34’81E, dung pans, 12-13 Oct 2002, S.A. Marshall (5#m, 3#f, DEBU); Bunya Mountains National Park, 26°52’S, 151°34’E, dung pans, 8 Oct 2002, S.A. Marshall (5#m, 5#f); Bunya Mountains National Park, 26°51’S, 151°31’E, pan trap and dung, 1000m, 28 Apr 1999, S.A. Marshall (6#m, 1#f); Mount Glorious, 27°19’54S, 152°45’29E, malaise, 3-9 Jan 1998, T. Hiller (1#m, 8#f, DEBU); Mount Glorious, 27°19’54S, 152°45’29E, malaise, 24-30 Dec 1997, T. Hiller (3#m, 5#f, DEBU); Sluice Creek, 17°32’S, 145°32’E, rainforest, dung trap, 1100m, 14-17 Apr 1999, G.B. and S.R. Monteith (3#m, 1#f, DEBU); Sluice Creek, 17°32’S, 145°32’E, rainforest, autom. dung trap (day), 1140m, 4-5 Feb 1999, D.J. Cook (5#m, 2#f, DEBU); Arthur Baillie Road, 17°41’S, 145°31’E, autom. dung trap (day), 1000m, 6-8 Feb 1999, D.J. Cook, (1#m, 2#f, DEBU); Arthur Baillie Road, 17°41’S, 145°31’E, autom. dung trap (night), 1000m, 6-8 Feb 1999, D.J. Cook, (1#m, 2#f, DEBU); Atherton, Tablelands, Lake Eacham, Chambers Lodge, dung, 6-8 Apr 1999, S.A. Marshall (6#m, 8#f, DEBU); Mount Hypipamee National Park, dung, 11-17 Apr 1999, S.A. Marshall (6#m, 1#f, DEBU); The Millstream, 10 km NNE Ravenshoe, 17°32’S, 145°31’E, wet sclerophyll, fungus trap, 1050m, 14-17 Apr 1999, G.B. and S.R. Monteith (1#f, DEBU); Cheelonga Creek, Evelyn,
17°31’S, 145°32’E, rainforest, dung trap, 1080m, 15-17 Apr 1999, G.B. and S.R. Monteith
(5#m, 3#f, DEBU); Maalan State Forest, Ravenshoe Road, 17°35’S, 145°36’E, rainforest, fungus
trap, 840m, 6-9 Feb 1999, Monteith and Cook (10#m, 1#f, DEBU); New South Wales: Coffs
Harbour, 8 km N, Bruxner Park, rainforest, flight interception trap, 140m, 12 Jun- 25 Aug 1982,
S. Peck, (1#m, DEBU).

_Howickia myrmecophila_ (Knab & Malloch, 1912)

**SPECIMENS EXAMINED: Queensland:** Lamington National Park, Binna Burra, _Nothofagus_
grove, carrion, 900m, 23 Jun- 7 Jul 1978, S. and J. Peck (16#m, 10#f, DEBU); Lamington
National Park, Binna Burra, creek bed, pans/ dun, 7 Oct 2002, S.A. Marshall (17#m, 7#f, 1
missing abdomen, DEBU); Mount Glorious, malaise trap, 26 Oct- 5 Dec 1989, A. Hiller (7#f,
DEBU); Springbrook, pan traps, 9-10 Mar 1999, S. A. Marshall (21#m, 15#f, DEBU); Bunya
Mountains National Park, 26°51’S, 151°31’E, pan trap and dung, 1000m, 28 Apr 1999, S.A.
Marshall (12#m, 8#f); Bunya Mountains National Park, Westcott Camp, 26°51’51S,
151°34’81E, dung pans, 12-13 Oct 2002, S.A. Marshall (6#m); Bunya Mountains National Park,
26°51’S, 151°34’E, dung pans, 8 Oct 2002, S.A. Marshall (2#m, 2#f); Maleny, 7km SE, Mary
Cairncross Scenic Reserve, rainforest, 900m, 18 Jun- 15 Aug 1982, S. and J. Peck (12#m, 6#f);
Bunya Mountains, 60 km NE of Dalby, _Auracaria_ forest, 900m, 17 Jun- 19 Aug 1982, S. and J.
Peck (3#m, 2#f); New South Wales: Mount Kaputar National Park, 30°12’S, 159°09’E, dung,
800m, 24-30 Mar 1999, S.A. Marshall (3#m, 1#f); Mount Kaputar National Park, 30°12’S,
159°09’E, dung, 1200m, 29-30 Mar 1999, S.A. Marshall (12#m, 13#f); Mount Kaputar National
Park, 30°12’S, 159°09’E, dung, 1300m, 28-30 Mar 1999, S.A. Marshall (18#m, 8#f); Mount
Kaputar National Park, 30°12’S, 159°09’E, dung in litter, 1500m, 24-30 Mar 1999, S.A.
Marshall (11#m, 8#f); Warrumbungle National Park, dung traps, dry forest, 25-27 Mar 1999,
S.A. Marshall (1#m, 1#f); Warrumbungle National Park, lookout, sweeping, 26 Mar 1999, S.A. Marshall (2#f); Gibraltar Range, 29°31’S, 152°22’E, volcanic, pitfall trap, 950m, 23 Sep 1999, J. Holt (1#m); Wiangaree, 33 km NE, near Tweed Valley lookout, rainforest, 1000m, 13 Jun-24 Aug 1982, S. and J. Peck (3#f); Wiangree, 16 km NE, Sheep Station Creek, rainforest, 600m, 13 Jun-24 Aug 1982, S. and J. Peck (#3m, 1#f, DEBU); Jenolan Caves, 20 Mar 1999, S.A. Marshall (1#m, DEBU); Kyogle, *Nothofagus* forest, 1000m, 8 Jul 1978, S. and J. Peck (1#f, DEBU); Kyogle, *Nothofagus* forest, 1000m, 9 Jul 1978, S. and J. Peck (17#m, 15#f, DEBU); Royal National Park, Sydney, carrion trap, rainforest, 5-14 Jun 1978, S. and J. Peck (9#m, 3#f, DEBU); Bruxner Park. N of Coff’s Harbour, 9-13 Jul 1978, S. and J. Peck (1#m, DEBU); Acacia Plateau, dry rainforest, 1000m, 23 Jan 1995, B.J. Sinclair (1#m, DEBU); Dorrigo National Park, Rosewood Creek, 23 Jan 1995, B. J. Sinclair (1#m, DEBU); Mossvale, Barrengarry Mountain, rainforest, 600m, 9 Jun-29 Aug 1982, S. and J. Peck; Blue Mountain National park, Blackheath, 13 Mar 1999, S.A. Marshall (6#m, 4#f, DEBU); Victoria: Acheron Gap, 16 km N of Warburton, *Nothofagus* grove, carrion, 750m, 28 Apr-7 May 1978, S. and J. Peck (1#m, 3#f, DEBU); Mount Donna, Buang, 1200m, 28 Apr-7 May 1978, S. and J. Peck (6#m, 11#f, DEBU); Australia Capital Territory: Black Mountain, carrion trap, dry sclerophyll, 11-18 Apr 1978, S. and J. Peck (8#m, 5#f, 1 missing abdomen, DEBU); Tasmania: Cradle Mountain National Park, Dove Lake, dung pans in button grass, 920m, 16-17 Dec 2003, S.A. Marshall (7#m, 2#f); Mount William, Stumpys Bay, dry heath pans, 12-13 Dec 2003, S.A. Marshall (15#m, 6#f); Chauncy Vale, 4 km E of Bagdad, creek bed pans, 9-10 Dec 2003, S.A. Marshall (1#m, 2#f); Scottsdale, 20 km W, dry forest, dung pans, 14 Dec 2003, S.A. Marshall (4#m, 3#f); Waratah, 8 km SW, 41°29’04S, 145°27’41E, rainforest, dung pans, 20-21 Dec 2003, S.A. Marshall (1#m)
**Howickia nitidipleura** (Richards, 1973)

**SPECIMENS EXAMINED. Queensland:** Mount Kooroomool, 7 km S of summit, dung trap (day), 1050 m, 3 Dec 1998, G.B. Monteith (22#m, 17#f, DEBU); Mount Kooroomool, 7 km S of summit, dung trap (dusk), 1050 m, 3 Dec 1998, G.B. Monteith (14#m, 22#f, DEBU); Mount Kooroomool, 7 km S of summit, dung trap (night/dawn), 1050 m, 3 Dec 1998, G.B. Monteith (10#m, 14#f, DEBU); Vine Creek, Majors Mountain, 17°41’S, 145°32’E, rainforest, dung pitfall, 1060 m, 4-6 Feb 1999, Monteith and Cook (18#m, 27#f, DEBU); Bellenden Ker, top station, 17°16’S, 145°51’E, autom. dung traps, 5:30am-6:15pm, 1500 m, 30 Nov-2 Dec 1998, G.B. Monteith (12#m, 26#f, DEBU); Mount Hugh nelson, south base, rainforest, dung pitfall, 1080 m, 7-9 Feb 1999, G.B. Monteith (7#m, 8#f, DEBU); Mount Bartle Frere, top camp, 17°24’S, 145°49’E, dung trap, 2-5:30pm, 29 Nov 1998, G.B. Monteith (2#m, 2#f, DEBU); Mount Bartle Frere, west side, carrion trap, 30 Jul-4 Aug 1982, S.J. Peck (1#m, DEBU); Charmillin Creek, 17°42’S, 145°31’E, autom. dung trap, 5:30am-6:15pm, 900 m, 2-5 Dec 1998, Monteith and Cook (1#m, 2#f, DEBU); Charmillin Creek, 17°42’S, 145°31’E, autom. dung trap, 6:15pm-7:15pm, 900 m, 2-5 Dec 1998, Monteith and Cook (1#m, 1#f, DEBU); Tully River, causeway above dam, wet sclerophyll, dung traps, 750 m, 3-5 Dec 1998, D.J. Cook, (3#f, DEBU); Sluice Creek, 17°32’S, 145°32’E, rainforest, autom. dung trap (day), 1140 m, 4-5 Feb 1999, D.J. Cook (1#m, 2#f, DEBU); The Millstream, 10 km NNE Ravenshoe, 17°32’S, 145°31’E, wet sclerophyll, dung trap, 1050 m, 14-117 Apr 1999, G.B. and S.R. Monteith (2#m, DEBU); The Millstream, 10 km NNE Ravenshoe, 17°32’S, 145°31’E, rainforest, fish pitfall, 1040 m, 3-5 Feb 1999, Monteith and Cook (2#m, 3#f, DEBU); Arthur Baillie Road, 17°41’S, 145°31’E, autom. dung trap, 1000 m, 6-8 Feb 1999, D.J. Cook (1#m, DEBU); Mount Finnigan, summit, 15°51’S, 145°17’E rainforest, dung trap (day), 1100 m, 21 Nov 1998, G.B. Monteith (2#f, DEBU); Mossman, 20 km SW,
Mount Lewis National Park, carrion trap, 1000m, 10 Jul-1 Aug 1982, S. and J. Peck (6#m, 15#f, DEBU); Malanda, 14 km SW, Mount Hypipamee National Park, rainforest, carrion trap, 960m, 24 Jul-2 Aug 1982, S. and J. Peck (2#m, 3f, DEBU).

“Howickia parasubsinuata” sp. n.

SPECIMENS EXAMINED. See list of specimens examined for H. subsinuata, which includes both species.

Howickia percostata (Richards, 1973)

SPECIMENS EXAMINED. New South Wales: 8’ ton top 8’ton House, 1250ft, 16 Jul 1978, S. and J. Peck (32#m, 77#f, DEBU); Kyogle, Nothofagus forest, 1000m, 9 Jul 1978, S. and J. Peck (3#m, 1#f, DEBU); Bateman’s Bay, carrion trap, 29 May-3 Jul 1978, S. and J. Peck (3#m, 7#f, DEBU); Royal National Park, Sydney, rainforest, carrion trap, 5-14 Jun 1978, S. and J. Peck (2#m, 11#f, DEBU); Kaputar National Park, 30°12’S, 159°09’E, dung, 800m, 24-30 Mar 1999, S.A. Marshall (1#m, DEBU); Victoria: Lind National Park, 21 km W of Cann River, carrion trap, 500m, 18-25 May 1978, S. and J. Peck (15#m, 12#f, DEBU); Mallacoota National Park, temperate rainforest, cal., 21-26 May 1978, S. and J. Peck (50#m, 49#f, DEBU); Mount Donna, Buang, 1200m, 28 Apr 1978, S. and J. Peck (1#m, 1#f, DEBU).

“Howickia pertusa” sp. n.

SPECIMENS EXAMINED. Tasmania: Cuckoo Falls, ~4 km E of Scottsdale, along Falls Road, along creek, pans/ some dung, 14 Dec 2003, S.A. Marshall (86#m, DEBU); Waratah, 8 km SW, 41°29’04S, 145°27’41E, rainforest, dung pans, 20-21 Dec 2003, S.A. Marshall (5#m, DEBU); Weldborough Rainforest, pans, 11-13 Dec 2003, S.A. Marshall (3#m, DEBU); Hellyer...
Gorge, 41°16′24″S, 145°36′55″E, rainforest, pans, 18-20 Dec 2003, S.A. Marshall (9#m, DEBU); Scottsdale, 20 km W, near creek, dung pans, 13-14 Dec 2003, S.A. Marshall (22#m, DEBU).

“Howickia polacornis” sp. n.

SPECIMENS EXAMINED. Tasmania: Waratah, 8 km SW, 41°29′04″S, 145°27′41″E, rainforest, dung pans, 20-21 Dec 2003, S.A. Marshall (19#m, 18#f, DEBU).

“Howickia pruinosa” sp. n.

SPECIMENS EXAMINED. Queensland: Bare Rock, 2 km N of Mount Cordeaux, 28°2′0″S, 152°23′0″E, pitfall traps, 1100 m, 31 Dec 1993-20 Feb 1994, G.B. Monteith (1#m, 3#f, DEBU).

“How. spina” sp. n.

SPECIMENS EXAMINED. Tasmania: Cuckoo Falls, ~4 km E of Scottsdale, along Falls Road, along creek, pans/ some dung, 14 Dec 2003, S.A. Marshall (53#m, DEBU); Chauncy Vale, 4 km E Bagdad, creek bed pans, 9-10 Dec 2003, S.A. Marshall (5#m, DEBU); Waratah, 8 km SW, 41°29′04″S, 145°27′41″E, rainforest, dung pans, 20-21 Dec 2003, S.A. Marshall (33#m, DEBU); Cradle Mountain National Park, Dove Lake, dung pans in button grass, 920m, 16-17 Dec 2003, S.A. Marshall (3#m, DEBU); Mount William, Stumpys Bay, dry heath pans, 12-13 Dec 2003, S.A. Marshall (2#m, DEBU); Weldborough Rainforest, pans, 11-13 Dec 2003, S.A. Marshall (11#m, DEBU); Hellyer Gorge, 41°16′24″S, 145°36′55″E, rainforest, pans, 18-20 Dec 2003, S.A. Marshall (3#m, DEBU); Scottsdale, 20 km W, near creek, dung pans, 13-14 Dec 2003, S.A. Marshall (1#m, DEBU).

Howickia subsinuata (Richards, 1973)
SPECIMENS EXAMINED. Queensland: Tolga Scrub, 17°15’S, 145°29’E, rainforest, fish pitfall, 760m, 3-6 Feb 1999, Monteith and Cook (24#m, 13#f, DEBU); Hann Tablelands Radar Station, 15°55’S, 145°15’E, dung trap, 2-6pm, 950m, 26 Nov, 1998, G.B. Monteith (10#m, 4#f, DEBU); Hann Tablelands, 3km SSW of tower, 16°57’S, 145°15’E, open forest, dung trap, 26-27 Nov, 1998, G.B. Monteith (1#m, DEBU); Eungella National Park, Fern Flat Campground, dung pans, 20-24 Apr 1999, S.A. Marshall (9#m, 7#f, DEBU); Hartley’s Creek, 4 km S, 15°41’S, 145°35’E, rainforest, dung pitfall, 5m, 3-11 Feb 1999, Monteith and Cook (#1m, DEBU); Wondecla, 2km SSE, 17°26’S, 145°24’E, open forest, dung pitfall, 910m, 3-6 Feb, 1999, Monteith and Cook (13#m, 5#f, DEBU); Baldy Mountain Road, 17°21’S, 145°25’E open forest, dung pitfall, 860m, 3-6 Feb 1999, Monteith and Cook (1#m, DEBU); Conway National Park, Arlie Beach, Mount Rooper Trail, pans and dung, 2-3 Apr 1999, S.A. Marshall (8#m, 3#f, DEBU); Lake Euramoo, 17°10’S, 145°38’E, rainforest, dung pitfall, 700m, 10-11 Feb 1999, D.J. Cook (1#m, DEBU); Mill Creek, 17°30’S, 145°27’E, open forest, dung trap, 940m, 2-6pm, 26 Nov 1998, G.B. Monteith (22#m, 6#f, DEBU); Mill Creek, above, 17°30’S, 145°27’E, open forest, dung, fungus, or rotten bait, 1030m, 5-6 Feb 1999, Monteith and Cook (26#m, 9#f, DEBU); Emerald Hill near Mareeba, 16°58’S, 145°26’E, dung trap, 390m, 18-19 Apr 1999, G.B. Monteith (23#m, 8#f, DEBU); Mareeba, 8km N, 17°S, 145°26’E, flight interception trap, 6 Feb 1997 (5#m, 4#f, DEBU); Millstream Conservation Park, adjacent, 17°32’S, 145°29’E, open forest, autom. dung trap (day), 1040m, 4-5 Feb 1999, G.B. Monteith (2#m, 1#f, DEBU); Millstream Conservation Park, 17°32’S, 145°29’E, wet sclerophyll, fish pitfall, 1040m, 3-5 Feb 1999, Monteith and Cook (3#m, 2#f, DEBU); Nipping Gully, site 2, 25°40’S, 151°26’E, rainforest, dung trap, 200m, 18-19 Dec 1998, G.B. Monteith (16#m, 12#f, DEBU); Burnett River, Gayndah, 25°37’S, 151°36’E, wallaby dung trap, 8-11 Oct 1998, G.B. Monteith (13#m,
Brisbane Forest Park, 27°25′5″S, 152°50′13″E, malaise over creek, 13-19 Dec, 1997, N. Power (2#m, 3#f, DEBU); Brisbane Forest Park, 27°25′5″S, 152°50′13″E, malaise in dry sclerophyll, 29 Nov-5 Dec 1997, N. Power (3#m, 2#f, DEBU); Brisbane Forest Park, 27°25′41″S, 152°50′15″E, Scrub Creek Road, yellow pans, 29 Sep-3 Oct 2002, C.R. Nelson (1#m, 1#f, DEBU); Ravenshoe, 9.5 km N, 17°32′S, 145°29′E, wet sclerophyll, dung trap, 1060m, 14-17 Apr 1999, G.B. and S.R. Monteith (1#m, DEBU); Ravenshoe, 9 km N, 17°32′S, 145°29′E, wet sclerophyll, fish or fungus pitfall, 1060m, 3-5 Feb 1999, Monteith and Cook (12#m, 2#f, DEBU); Ravenshoe, 7 km NW, 17°34′S, 145°31′E, wet sclerophyll, dung pitfall, 1000m, 3-5 Feb 1999, Monteith and Cook (1#f, DEBU); Ravenshoe, 4 km SSE, 17°39′S, 145°30′E, open forest, fungus pitfall, 930m, 4-6 Feb 1999, Monteith and Cook (9#m, 4#f, DEBU); Ravenshoe, 3 km SW, 17°38′S, 145°28′E, open forest, fungus or fish pitfall, 860m, 7-8 Feb 1999, Monteith and Cook (10#m, 3#f, DEBU); Ravenshoe, 3 km SE, 17°38′S, 145°30′E, open forest, fungus pitfall, 960m, 4-6 Feb 1999, Monteith and Cook (2#m, DEBU); Ravenshoe, 3 km NW, 17°35′S, 145°28′E, open forest, dung trap, 920m, 15-16 Apr 1999, G.B. and S.R. Monteith (14#m, 17#f, DEBU); Ravenshoe, 3 km SW, 17°38′S, 145°28′E, open forest, autom. fungus trap (day), 1000m, 7-8 Feb 1999, G.B. and S.R. Monteith (1#f, DEBU); Ravenshoe, 3 km SW, 17°39′S, 145°21′E, open forest, dung trap), 860m, 3-5 Feb 1999, Monteith and Cook (3#m, DEBU); Ravenshoe, 3.5 km SSW, 17°29′S, 145°22′E, open forest, dung trap, 920m, 17-18 Apr 1999, G.B. and S.R. Monteith (1#f, DEBU); Ravenshoe, 2 km SW, 17°37′S, 145°28′E, open forest, autom. dung trap dusk, 880m, 8-9 Feb 1999, G.B. Monteith (2#m, 2#f, DEBU); Ravenshoe, 2 km SW, 17°37′S, 145°28′E, open forest, autom. dung trap night, 880m, 8-9 Feb 1999, G.B. Monteith (2#m, 3#f, DEBU); Ravenshoe, 16 km NW on road, 17°30′S, 145°23′E, open forest, dung trap, 940m, 17-18 Apr 1999, G.B. Monteith (10#m, 14#f, DEBU); Ravenshoe, 3 km NW, 17°35′S, 145°28′E, open forest, dung trap, 920m, 15-16 Apr 1999, G.B. and S.R. Monteith (14#m, 17#f, DEBU); Ravenshoe, 3 km SW, 17°38′S, 145°28′E, open forest, autom. fungus trap (day), 1000m, 7-8 Feb 1999, G.B. and S.R. Monteith (1#f, DEBU); Ravenshoe, 3 km SW, 17°39′S, 145°21′E, open forest, dung trap), 860m, 3-5 Feb 1999, Monteith and Cook (3#m, DEBU); Ravenshoe, 3.5 km SSW, 17°29′S, 145°22′E, open forest, dung trap, 920m, 17-18 Apr 1999, G.B. and S.R. Monteith (1#f, DEBU); Ravenshoe, 2 km SW, 17°37′S, 145°28′E, open forest, autom. dung trap dusk, 880m, 8-9 Feb 1999, G.B. Monteith (2#m, 2#f, DEBU); Ravenshoe, 2 km SW, 17°37′S, 145°28′E, open forest, autom. dung trap night, 880m, 8-9 Feb 1999, G.B. Monteith (2#m, 3#f, DEBU); Ravenshoe, 16 km NW on road, 17°30′S, 145°23′E, open forest, dung trap, 940m, 17-18 Apr 1999, G.B. Monteith (10#m, 14#f, DEBU); Flaggy
Creek, 3.5 km SSW, 17°29’S, 145°22’E, open forest, dung trap, 920m, 17-18 Apr 1999, G.B. and S.R. Monteith (3#m, 8#f, DEBU); Flaggy Creek, 4 km S, 17°29’S, 145°23’E, dry open forest, dung trap, 930m, 17-18 Apr 1999, G.B. and S.R. Monteith (1#m, 5#f, DEBU); Flaggy Creek, 3.5 km SSW, 17°29’S, 145°22’E, open forest, dung trap, 920m, 17-18 Apr 1999, G.B. and S.R. Monteith (4#m, 2#f, DEBU); Archer Creek, 17°39’S, 145°21’E, open forest, autom, dung trap, night, 700m, 8-9 Feb 1999, G.B. Monteith (18#m, 8#f, DEBU); Archer Creek, 17°39’S, 145°21’E, open forest, autom, dung trap, dusk, 700m, 8-9 Feb 1999, G.B. Monteith (8#m, 12#f, DEBU); Archer Creek, 17°39’S, 145°21’E, open forest, dung pitfall, 700m, 8-9 Feb 1999, G.B. Monteith (1#m, 7#f, DEBU); Carnarvon National Park, Mount Moffatt, 25°4’S, 148°3’E, dung traps, 9-11 Oct 2002, S.A. Marshall (49#m, 65#f, DEBU); Carnarvon National Park, Mount Moffatt, Consuelo Tabelands Gate, dung traps, 11 Oct 2002, S.A. Marshall (15#m, 14#f, DEBU); Carnarvon National Park, Mount Moffatt Section, base camp, dung pans, 11-12 Oct 2002, S.A. Marshall (15#m, 26#f, DEBU); Carnarvon National Park, Mount Moffatt, Angelina Creek, 25°3’58S, 148°3’9E malaise over creek, 675m, 9-10 Oct 2002, S.A. Marshall (3#m, 4#f, DEBU); Carnarvon National Park, Carnarvon Creek, 24°57’S, 148°6’E, dung traps in moss, 11 Oct 2002, S.A. Marshall (1#f, DEBU); Carnarvon National Park, Mount Moffatt Section, top camp, dung traps, 11 Oct 2002, S.A. Marshall (1#m, DEBU); Carnarvon National Park, One Mile Creek, dung pans, 9-10 Oct 2002, S.A. Marshall (10#m, 15#f, DEBU); Carnarvon National Park, Mount Moffatt section, Maranoa River, east branch, near Top Moffat Camp, 10-13 Oct 2002, J.M. Cumming (12#m, 1#f, DEBU); Tumoulin, 2.5 km NW, 17°33’S, 145°26’E, open forest, dung pitfall, 980m, 4-5 Feb 1999, D.J. Cook (1#m, 2#f, DEBU); Crater Lake National Park, Lake Barrine, 17°28’S, 145°23’E, sweep, 10 Apr 1999, S. A. Marshall (1#m, DEBU); Mount Hypipamee National Park, dung, 11-17 Apr 1999, S.A. Marshall (9#m,
Bunya Mountains National Park, 26°51’S, 151°31’E, pan trap and dung, 1000m, 28 Apr 1999, S.A. Marshall (1#f, DEBU); Granite Gorge, 17°3’S, 145°21’E, open forest, dung trap, 480m, 14-18 Apr 1999, G.B. and S.R. Monteith (2#m, 2#f, DEBU); Bally Knob, summit, 17°39’S, 145°30’E, dry open forest, intercept trap, 6 Dec 1998- 6 Feb 1999, 1100m, Monteith and Cook (6#m, 2#f, DEBU); Kjellberg Road, St. For. boundary, 17°32’S, 145°35’E, rainforest, fungus pitfall, 920m, 8-9 Feb 1999, Monteith and Cook (1#m, DEBU); Kjellberg Road turnoff, 17°32’S, 145°36’E, rainforest, dung pitfall, 740m, 6-9 Feb 1999, G.B. Monteith (8#m, 2#f, DEBU); Shipton’s Flat, 15°48’S, 145°14’E, rainforest, autom. dung trap (day), 220m, 19-22 Nov 1998, G.B. Monteith (1#m, 1#f, DEBU); Longlands Gap, three ways road junction, 17°28’S, 145°29’E, wet sclerophyll, dung trap, 1060m, Monteith and Cook (3#m, DEBU); Buchan Point, 1 km NW, 16°44’S, 145°39’E, open forest, fish pitfall, 3-11 Feb 1999, Monteith and Cook (2#m, DEBU); Mount Glorious, 27°19’54’S, 152°45’29’E, malaise, 24-30 Jan 1989, A. Hiller (1#m, DEBU); Mount Glorious, 27°19’54’S, 152°45’29’E, malaise, 3-9 Jan 1998, T. Hiller (2#m, 2#f, DEBU); Mount Glorious, 27°19’54’S, 152°45’29’E, malaise, 24-30 Dec 1997, T. Hiller (2#m, 3#f, DEBU); Mount Glorious, malaise trap, 27 Apr- 26 May 1989, A. Hiller (8#m, 13#f, DEBU); Cooyar, 8 km N, Araucaria vine, flight interception trap, 300m, 18 Jun- 19 Aug 1982, S. and J. Peck (3#m, 8#f, DEBU); Atherton, Lake Barrine, bark, funnel litter, 750m, 29 Jul 1982, S. Peck (1#m, DEBU); Atherton, Lake Eacham, Wright’s Creek, leaf litter and soil, 720m, 31 Jul 1982, S. and J. Peck (1#f, DEBU); Prosperpine, 19 km E, Brandy Creek, rainforest, 21 Jun- 10 Aug 1982, S. and J. Peck (1#f, DEBU); Kenilworth, 7km SW, Yabba Creek, rainforest litter, 150m, 15 Aug 1982m S. and J. Peck (1#f, DEBU); Cooktown, Keatings Gap, rainforest, dun trap, 100m, 28-31 Jun 1982, S. and J. Peck (2#m, 2#f, DEBU); Malanda, 14 km SW, Mount Hypipamee National Park, rainforest, carrion trap, 960m, 24 Jul- 2 Aug 1982, S. and J. Peck
(1#m, 3f, DEBU); Malanda, Malanda Falls Reserve, rainforest, flight interception trap, 730m, 26-29 Jul 1982, S. Peck (1#f, DEBU); Mossman, 20 km SW, Mount Lewis National Park, rainforest, flight interception trap, 900m, 26 Jun-1 Aug 1982, S. and J. Peck (1#f, DEBU); Gin Gin, 64 km N, 18 km W of Bulburin State Forest, Granite Creek, rainforest, flight interception trap, 200m, 19 Jun-14 Aug 1982, Peck (1#f, DEBU); Shute Harbour, 5 km E, carrion, vine0thicket, 2m, 11 Aug 1982, S. Peck (3#m, DEBU); Kholo, 14 Dec 1972, Colbo (1#f, DEBU); Victoria: Malla-coola National Park, temperate rainforest, 21-26 May 1978, S. and J. Peck (1#m, DEBU); Australia Capital Territory: Tidbinbilla Park, near Canberra, Aug 26-27 1972, J.F. McAlpine (1#m, DEBU); New South Wales: Warrumbungle National Park, dry forest, dung traps, 500m, 25 Mar 1999, S.A. Marshall (12#m, 28#f, DEBU); Warrumbungle National Park, 30°14’S, 149°01’E, sweep lookout, 26 Mar 1999, S.A. Marshall (1#m, DEBU); Mount Kaputar National Park, 30°12’S, 150°09’E, dung, 1200m, 29-30 Mar 1999, S.A. Marshall (15#m, 13#f, DEBU); Blue Mountains, Blackheath, Hat Hill, pans, 18-22 Mar 1999 S.A. Marshall (1#m, 1#f, DEBU); Quorrobolong Cessnock Farm, study site, 32°55’38S, 151°23’35E, ex. carrion trap (day 6), 14 Jan 2010, S.A. Marshall (7#m, 10#f, DEBU); Tasmania: Waratah, 8 km SW, 41°29’04S, 145°27’41E, rainforest, dung pans, 20-21 Dec 2003, S.A. Marshall (1#m, DEBU); Cuckoo Falls, ~4 km E of Scottsdale, along Falls Road, along creek, pans/ some dung, 14 Dec 2003, S.A. Marshall (1#m, DEBU); Scottsdale, 20 km W, near creek, dung pans, 13-14 Dec 2003, S.A. Marshall (7#m, 12#f, DEBU); Scottsdale, 20 km W, dry forest, dung pans, 13-14 Dec 2003, S.A. Marshall (#m, DEBU); Mount William, Stumpys Bay, dry heath pans, 12-13 Dec 2003, S.A. Marshall (1#m, DEBU); Chauncy Vale, 4 km E of Bagdad, creek bed pans, 9-10 Dec 2003, S.A. Marshall (1#f, DEBU).

*Howickia trivittata* (Richards, 1973)
SPECIMENS EXAMINED. Queensland: Atherton, Lake Eacham, Wright’s Creek, rainforest, carrion trap, 720m, 31 Jul 1982, S. and J. Peck (14#m, 30#f, DEBU); Atherton, Lake Eacham, Wright’s Creek, rainforest, leaf litter and soil, 720m, 31 Jul 1982, S. and J. Peck (1#m, 1#f, DEBU); Atherton, Tablelands, Lake Eacham, Chambers Lodge, dung, 6-8 Apr 1999, S.A. Marshall (1#f, DEBU); Malanda, 14 km SW, Mount Hypipamee National Park, rainforest, carrion trap, 960m, 24 Jul-2 Aug 1982, S. and J. Peck (8#m, 15#f, DEBU); Malanda, Malanda Falls Reserve, rainforest, flight interception trap, 730m, 26-29 Jul 1982, S. Peck (6#m, 18#f, DEBU); Malanda, 3.5 km S, 17°23’S, 145°36’E, rainforest, dung pitfall, 6-9 Feb 1999, G.B. Monteith (1#m, DEBU); Mossman, 20 km SW, Mount Lewis National Park, rainforest, flight interception trap, 900m, 26 Jun-1 Aug 1982, S. and J. Peck (2#f, DEBU); Mossman, 20 km SW, Mount Lewis National Park, carrion trap, 1000m, 10 Jul-1 Aug 1982, S. and J. Peck (13#m, 24#f, DEBU); Mossman, 20 km SW, Mount Lewis National Park, dung trap, 1000m, 10 Jul-1 Aug 1982, S. and J. Peck (17#m, 17#f, DEBU); Cooyar, 8 km N, Araucaria vine, flight interception trap, 300m, 18 Jun-19 Aug 1982, S. and J. Peck (1#f, DEBU); Mount Bartle Frere, west side, carrion trap, 30 Jul-4 Aug 1982, S. and J. Peck (5#m, 17#f, DEBU); Bulahdelah, 11 km NE, O’Sullivan’s Gap Reservation, flight interception trap, sclerophyll, 50m, 11 Jun-27 Aug 1982, S. Peck (1#m, 1#f, DEBU); Mount Glorious, malaise trap, 27 Apr-26 Oct 1989, A. Hiller (6#m, 9#f, DEBU); Mount Glorious, malaise trap, 26 Oct-6 Dec 1989, A. Hiller (1#m, 1#f, DEBU); Mount Glorious, 27°19’54S, 152°45’29E, malaise, 24-30 Jan 1998, T. Hiller (2#m, 2#f, DEBU); Lamington National Park, Binna Burra, Nothofagus grove, carrion, 900m, 23 Jun-7 Jul 1978, S. and J. Peck (1#m, 1 uknown, DEBU); Lamington National Park, Binna Burra, creek bed, pans/dung, 7 Oct 2002, S.A. Marshall (8#m, 7#f, DEBU); Yunnaburra, 16 km NE, on Gillies Road, NE of Atherton, rainforest, flight intercept trap, 800m, 24 Jun-3 Aug 1982, Peck
(1#m, 4#f, DEBU); Eungella National Park, Fern Flat Campground, dung pans, 20-23 Apr 1999, S.A. Marshall (4#m, 8f, DEBU); Brisbane Forest Park, 27°25′41S, 152°50′15E, Scrub Creek Road, malaise, 29 Sep- 3 Oct 2002, C.R. Nelson (2#m, 1#f, DEBU); Brisbane Forest Park, Enoggera Creek at Scrub Road, 200m, 27°25′42S, 152°50′33E, malaise, 30 Oct-2 Nov 1995, Gaimari and Irwin (1#f, DEBU); Brisbane Forest Park, 27°25′5S, 152°50′13E, malaise in dry sclerophyll, 29 Nov- 5 Dec 1997, N. Power (1#f, DEBU); Brisbane Forest Park, 27°25′5S, 152°50′13E, malaise over creek, 13-19 Dec 1997, N. Power (1#m, DEBU); Carnarvon National Park, Carnarvon Creek, 24°57′S, 148°6′E, dung traps in moss, 11 Oct 2002, S.A. Marshall (1#f, DEBU); Tolga Scrub, 17°15′S, 145°29′E, rainforest, fungus pitfall, 760m, 3-6 Feb 1999, Monteith and Cook (1#m, DEBU); Mill Creek, above, 17°30′S, 145°27′E, open forest, rotten bait or fish or fungus pitfall, 940m, 5-9 Feb 1999, Monteith and Cook (2#m, 2#f, DEBU); Mill Creek, 4km S, 17°29′S, 145°23′E, dry open forest, dung trap, 930m, 17-18 Apr 1999, G.B. and S.R. Monteith (1#f, DEBU); Mill Creek, above, 17°30′S, 145°27′E, open forest, dung pitfall, 1000m, 5-6 Feb 1999, G. B. Monteith (1#f, DEBU); Vine Creek, Majors Mountain, 17°41′S, 145°32′E, rainforest, fish pitfall, 4-6 Feb 1999, Monteith and Cook (2#f, DEBU); Bellenden Ker, top station, 17°16′S, 145°51′E, dung traps, 1500m, 30 Nov-2 Dec 1998, G.B. Monteith (1#m, 4#f, DEBU); Millstream Conservation Park, adjacent, 17°32′S, 145°29′E, open forest, autom. dung trap (day), 1040m, 4-5 Feb 1999, G.B. Monteith (1#m, DEBU); Millstream Conservation Park, 17°32′S, 145°29′E, wet sclerophyll, fungus trap, 1040m, 3-5 Feb 1999, Monteith and Cook (2#m, 1#f, DEBU); Kjellberg Road, St. For. boundary, 17°32′S, 145°35′E, rainforest, fungus pitfall, 920m, 8-9 Feb 1999, Monteith and Cook (2#m, DEBU); Granite Gorge, 17°3′S, 145°21′E, open forest, dung trap, 480m, 14-18 Apr 1999, G.B. and S.R. Monteith (1#m, DEBU); Ravenshoe, 3 km SE, 17°38′S, 145°30′E, open forest, fungus trap, 960m, 15-18 Apr 1999, G.B.
and S.R. Monteith (5#m, 3#f, DEBU); Ravenshoe, 4 km SSE, 17°39’S, 145°30’E, open forest, fungus pitfall, 930m, 4-6 Feb 1999, Monteith and Cook (2#m, 3#f, DEBU); Ravenshoe, 9 km N, 17°32’S, 145°29’E, wet sclerophyll, fish or fungus pitfall, 1060m, 3-5 Feb 1999, Monteith and Cook (8#m, 8#f, DEBU); Ravenshoe, 16 km NW on road, 17°30’S, 145°23’E, open forest, dung trap, 940m, 17-18 Apr 1999, G.B. Monteith (1#m, 1#f, DEBU); Ravenshoe, 7 km NW, 17°34’S, 145°31’E, wet sclerophyll, dung pitfall, 1000m, 3-5 Feb 1999, Monteith and Cook (2#f, DEBU); The Millstream, 10 km NNE Ravenshoe, 17°32’S, 145°31’E, rainforest, pitfall trap, 1040m, 6 Dec 1998-5 Feb 1999, Cook and Monteith (1#f, DEBU); Ravenshoe, 9.5 km N, 17°32’S, 145°29’E, wet sclerophyll, dung trap, 1060m, 14-17 Apr 1999, G.B. and S.R. Monteith (1#f, DEBU); BLANK For., Ravenshoe Road, 17°35’S, 145°36’E, rainforest, fungus pitfall, 840m, 5-9 Feb 1999, Monteith and Cook (1#f, DEBU); Noosa Park, Tanglewood Trail, 26°24’S, 153°06’E, dung trap in sand, 5-7 Mar 1999, S.A. Marshall (1#f, DEBU); Longlands Gap, three ways road junction, 17°28’S, 145°29’E, wet sclerophyll, dung trap, 1060m, Monteith and Cook (2#m, 4#f, DEBU); **New South Wales:** Macksville, 30 km S, Ingalla State Forest, 12 Jun-26 Aug, wet sclerophyll, flight interception trap, 40m, Peck (2#f, DEBU); Bateman’s Bay, 3 km N, flight interception trap, wet sclerophyll, 50m, 9 Jun-30 Aug 1982, S. and J. Peck (1#m, DEBU); Bateman’s Bay, carrion trap, 29 May-3 Jul 1978, S. and J. Peck (5#m, 7#f, DEBU); Royal National Park, Sydney, rainforest, cation trap, 5-14 Jun 1978, S. and J. Peck (6#m, 8#f, 1 unknown, DEBU); 8’ ton top 8’ton House, 1250ft, 16 Jul 1978, S. and J. Peck (2#m, DEBU); Gibraltar Range, 29°31’S, 152°22’E, volcanic, pitfall trap, 850m, 23 Sept 1999, J. Holt (5#m, 11#f, DEBU); **Australian Central Territory:** Black Mountain, carrion trap, 700m, 11-18 Apr 1978, S. and J. Peck (2#m, 13#f, DEBU); Black Mountain, dry sclerophyll, carrion trap, 700m, 11-18 Apr 1978, S. and J. Peck (3#m, 2#f, DEBU).
“Howickia wamini” sp. n.

SPECIMENS EXAMINED. Western Australia: Peaceful Bay, Ficifolia Road and Nut Road, dry heath pans, 12-13 Dec 2003, S.A. Marshall (4#m, 11#f, DEBU).

Monteithiana cynthia (Richards, 1973)

SPECIMENS EXAMINED. Tasmania: Waratah, 8 km SW, 41°29’04S, 145°27’41E, rainforest, dung pans, 20-21 Dec 2003, S.A. Marshall (1#m, 1#f, DEBU); Strahan, 6 km SE, 30 Apr 1987, N.I. Platnick, et al. (3#m, DEBU); Strathgordon, 10 km SW, just N of Mount Sprent, 200k, 26 Apr 1987, N.I. Platnick, et al. (1#m, DEBU); Mount Rufus, Lake Saint Clair National Park, 29 Apr 1987, N.I. Platnick, et al. (1#m, DEBU); Renison Bell, 5 km NW, Berlese rainforest litter, 180m, 1 May 1987, N.I. Platnick, et al. (1#m, DEBU).

Popondetta kurandensis (Richards, 1973)

SPECIMENS EXAMINED. Queensland: Millaa Millaa Falls, 17°30’S, 145°37’E,, rainforest, dung pitfall, 800m, G.B. Monteith (3#f, DEBU); Lake Euraumo, 17°10’S, 145°38’E, rainforest, dung pitfall, 700m, 10-11 Feb 1999, D.J. Cook (1#f, DEBU); Kauri Creek, 1 km SW, 17°9’S, 145°35’E, rainforest, fungus pitfall, 10-11 Feb 1999, Monteith and Cook (4#m, 3#f, DEBU); Mount Murray Prior, 16°56’S, 145°51’E, dung traps, 7-8 Dec 1998, G.B. Monteith (4#m, 3#f, DEBU); Mount Hugh nelson, south base, rainforest, dung pitfall, 1080m, 7-9 Feb 1999, G.B. Monteith (5#m, DEBU); Mount Hypipamee National Park, dung, 11 Apr 1999, S.A. Marshall (2#m, 2#f, DEBU); Kjellberg Road, St. For. boundary, 17°32’S, 145°35’E, rainforest, fungus pitfall, 920m, 8-9 Feb 1999, Monteith and Cook (6#m, 1#f, DEBU); Lake Eacham, Chambers Lodge, 19°35’S, 143°19’E, pan traps, 6-8 Apr 1999, S.A. Marshall (7#m, 2#f, DEBU); Lake Barrine National Park, Crater Lake, sweeping, 10 Apr 1999, S.A. Marshall (4#m, DEBU).