



CHAPTER SIX

**AFROTROPICAL DIPTERA
– RICH SAVANNAS, POOR RAINFORESTS**

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INTRODUCTION

Africa (Fig. 6.1) is a hot continent that was levelled by prolonged Cretaceous and early Tertiary erosion, during which time little upheaval took place. There was no Pleistocene Ice Age in Africa, so aside from the equatorial peaks of mounts Ruwenzori, Kenya and Kilimanjaro, and the Atlas Mountains of North Africa, there are no recent glacial landforms. In tropical sub-Saharan Africa generally there are two vast biomes — equatorial rainforest (usually termed the Guineo-Congolian rainforest, Fig. 6.1: 1), mostly in the western lowlands — and savanna (Fig. 6.1: 2, 3) that occupies the greater part of the continent.

The dipteran fauna of the region bears the imprint of vast savanna evolution in the tropics and a complex vegetational biome history in the subtropical south (Mucina & Rutherford 2006). Biogeographically, the Afrotropics as currently perceived are limited northwards by the young Sahara Desert (Fig. 6.1: 17), which developed in the Pliocene and became hyper-arid in the Pleistocene (Maley 1996). The Sahara was previously an enormous savanna and grassland, which supposedly extended the range of Afrotropical Diptera much closer to the Mediterranean (e.g., Adams & Faure 1997). Vermilionidae in the Atlas Mountains and the Canary Islands (Stuckenberg 2000, Stuckenberg & Fisher 1999) and species of the asilid genus *Habropogon* Loew in countries bordering the Mediterranean (Londt 2000) are examples of isolated relicts of the fauna that predated aridification.

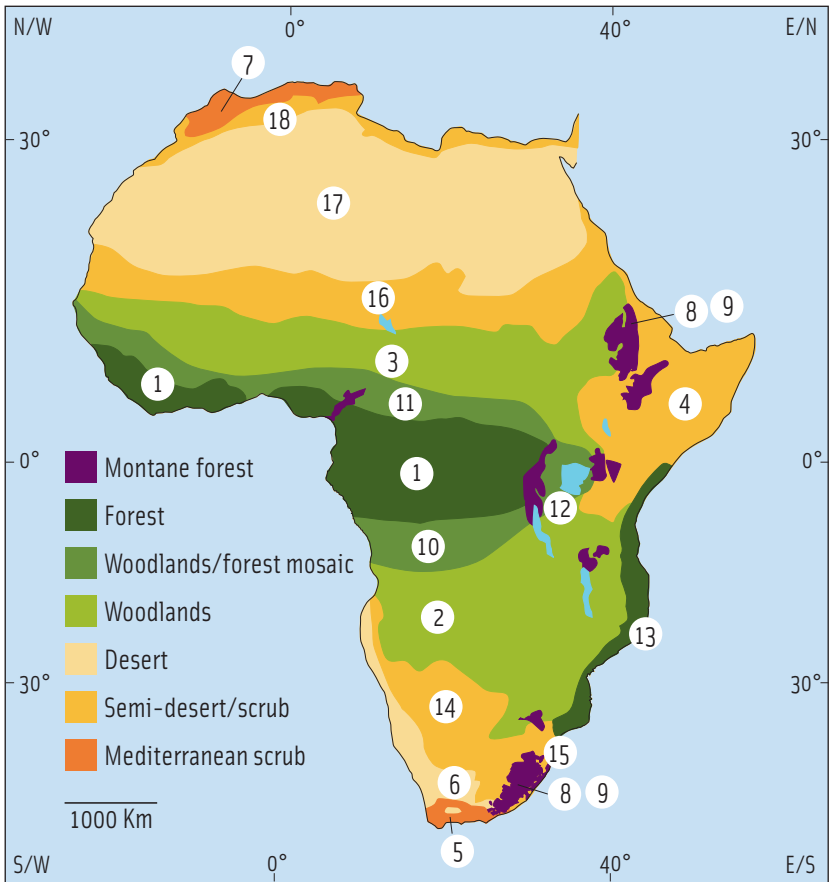


Figure 6.1. The phytochoria of Africa as defined by White (1983)
(after Clarke 2000a).

Regional centres of endemism:

1. Guineo-Congolian, 2. Zambezian, 3. Sudanian, 4. Somalia-Masai, 5. Cape,
6. Karoo-Namib, 7. Mediterranean, 8. Afro-montane archipelago-like regional centre of endemism.

Regions of extreme floristic impoverishment:

9. Afro-alpine archipelago-like region of extreme floristic impoverishment.

Regional transition zones:

10. Guineo-Congolian/Zambezia, 11. Guineo-Congolian/Sudania,
14. Kalahari-Highveld, 16. Sahel, 17. Sahara. 18. Mediterranean/Sahara.

Regional Mosaics:

12. Lake Victoria, 13. Zanzibar-Inhambane, 15. Tongoland-Pondoland.

1. Extent of the Afrotropical Region

The historical and contemporary use of the term 'Afrotropical Region' is worthy of comment, as is the true extent of this region. The concept of an 'Ethiopian Region' was first proposed by Sclater (1858), based on the distribution of birds, and was later adopted by Alfred Russell Wallace in his enduring work *The Geographical Distribution of Animals*, published in 1876. Wallace defined the Ethiopian Region as the area of continental Africa, Madagascar and its islands, and the Arabian Peninsula south of the Tropic of Cancer and further divided this region into four sub-regions: the West African, East African, South African and Malagasy sub-regions. Although our concept of these sub-regions has altered somewhat as more floristic and faunistic information has become available (Werger 1978 for review), the perceived extent of the region as a whole has little changed. Following the renaming of the political state formerly known as Abyssinia to Ethiopia in 1941, a great deal of confusion in the application of the term 'Ethiopian Region' ensued in the literature and numerous alternative terms began to appear, e.g., sub-Saharan Africa, Afrotropical Realm, etc. As a result of this, Crosskey & White (1977) proposed the replacement name 'Afrotropical Region' corresponding exactly to the Ethiopian Region as it was then known, and this term has become widely accepted and adopted by systematists and biogeographers alike.

Later, for convenience, Crosskey (1980: 27, 32) used the northern borders of the states of Mauritania, Mali, Niger, Chad and Sudan as the regional boundary between the Afrotropical and Palaearctic parts of continental Africa, and for the Arabian Peninsula the northern boundaries of the modern state of Yemen. Crosskey also included Madagascar in his concept of the Afrotropical Region, regarded as a separate zoogeographical region by some biogeographers, and the South Atlantic islands of Ascension, St. Helena, Tristan da Cunha and Gough, as well as the Cape Verde Islands, the Gulf of Guinea islands and the islands of the western Indian Ocean.

Recently, more extensive sampling of Diptera in the Arabian Peninsula, especially in Yemen, Oman and the United Arab Emirates, together with published studies of the Rhopalocera (Larsen 1984) and the Neuroptera (Hölzel 1998), have raised some interesting open questions in respect to the true extent of the Afrotropical Region in this important

transitional zone encompassing elements of Afrotropical, Palaeartic and Oriental faunas.

2. South African Complexities

South Africa has the most diverse and distinctive Diptera fauna in the Afrotropics. That country is ecologically complex, with 24 bioclimatic regions (Phillips 1959). South Africa has Africa's oldest mountains — the Cape Fold Mountains, which are part of a Triassic orogeny that predates the break-up of Gondwana — and the Great Escarpment, which was initiated in the east by the separation of Antarctica and southeastern Africa in the Early Jurassic (*ca.* 200 Mya). These mountains preserve endemic Gondwanan Blephariceridae, Psychodidae, Empididae, Africa's only tanyderid, and close-to-basal Chironomidae (Stuckenberg 1962). The Cape Floral Kingdom, *Capensis*, occurs in two famously diverse biomes with about 13,000 endemic plant species — these are the Fynbos shrubland of the Cape Fold Mountains and the Succulent Karoo (Taylor 1978). So much topographic, climatic and floristic diversity promoted radiation among the Diptera, and there are species-rich, systematically complex faunas of the families Asilidae, Bombyliidae, Empididae, Limoniidae, Mydidae, Nemestrinidae, Tabanidae, Therevidae and Vermileonidae. Recent studies prove flies to be important as pollinators in the Cape flora, and there are numerous and often remarkable examples of convergent adaptations of the mouth-parts for feeding in co-adapted flowers (e.g., Barraclough 2006b; Manning & Goldblatt 1995; Struck 1992, 1994).

3. Rostrum Elongation as a Notable Adaptation in the Diptera of the Cape Flora

The Fynbos flora is notable for its great taxonomic diversity and profuse flowering of nectar-bearing plants, many of which have nectaries recessed in tubular corollas. This resource evidently has produced a co-adaptive response among Diptera in that elongation of the proboscis has evolved. While such an adaptation is frequent in families such as Bombyliidae, Nemestrinidae and Tabanidae, other families among the Fynbos flies also present a long proboscis, which in some of these cases is unique in the families represented (Stuckenberg 1998). The following are notable examples:

Arthroteles Bezzi (Rhagionidae). The only rhagionid genus whose species have an elongate, slender proboscis, formed by lengthening of the labium. Its sister-group is the locally represented genus *Atherimorpha* White, in which the proboscis has the short, stout form normal in Rhagionidae.

Peringueyomyia barnardi Alexander (Tanyderidae). This endemic, monotypic genus has a very limited distribution in the Fynbos (Duxbury & Barraclough 1994); it is unique in the family in its elongate, slender head form; there is ventral, tubular extension of the head capsule, bearing small mouth-parts terminally.

Rhynchoheterotricha stuckenbergae Freeman (Sciaridae). The only Afrotropical sciarid with a very long proboscis. It is formed by a slender, tubular extension of the head capsule, bearing the mouth-parts at the apex.

Forcipomyia subgenus *Rhinohelea* de Meillon & Wirth (Ceratopogonidae). This contains two species of small midges with uniquely elongate mouth-parts, one of these collected from a flowering *Erica* species (B.R. Stuckenberg unpubl.).

Many other cases could be cited of Fynbos flies with less remarkable, but nevertheless unusual mouth-part elongation. In the rhinophorid genus *Phyto* Robineau-Desvoidy, progressive lengthening of the proboscis occurs in a group of closely-related species (Pape 1997) found in the southwestern Cape mountains.

In the montane environment of the Drakensberg escarpment in the east of the country, another rich flora is present, where a large variety of nectar-feeding flies occurs. Among these is a species of *Arthroteles* Bezzi, obviously derived from the main occurrence of the genus in the Cape mountains. Proboscis elongation is conspicuous among the Drakensberg dextine Tachinidae. In this grassland flora are many species of *Helichrysum* (Compositae), the conspicuous flowers of which attract these flies.

4. Namibia: Deserts and Arid Savannas

Extending along the Atlantic coast of Namibia and southern Angola is the spectacular Namib Desert, the oldest in Africa, the aridification of which began in the early Middle Miocene (*ca.* 16 Mya) (Barnard 1998). The aridification of the Namib Desert also impacted on the adjacent mountains (Namibian Escarpment and desert inselbergs). Among the Diptera are



Figure 6.2. The Gondwanan empidid genus *Homalocnemis* Philippi occurs in Chile and New Zealand; one species is recorded on the hyper-arid Namib Desert coast.

peculiar, highly-adapted desert mydids that survive through autogeny; the flies have vestigial mouthparts, and their larvae store nutrients for oogenesis (Wharton 1982). Adaptations to extreme xeric conditions are also demonstrated in the camillid genus *Katacamilla* Papp, recorded as breeding in dung in rock hyrax abodes and in arid bat caves in Namibia; eggs have been shown to survive extended periods of desiccation in a viable state, larval development being triggered by seasonal precipitation or the urine of bats and other cave-dwelling mammals (Barraclough 1998, Kirk-Spriggs *et al.* 2002). Some extraordinary discoveries of old lineages of Diptera were unexpected in the Namib Desert: a species of the empidid genus *Homalocnemis* Philippi (Fig. 6.2) was collected on a flowering succulent

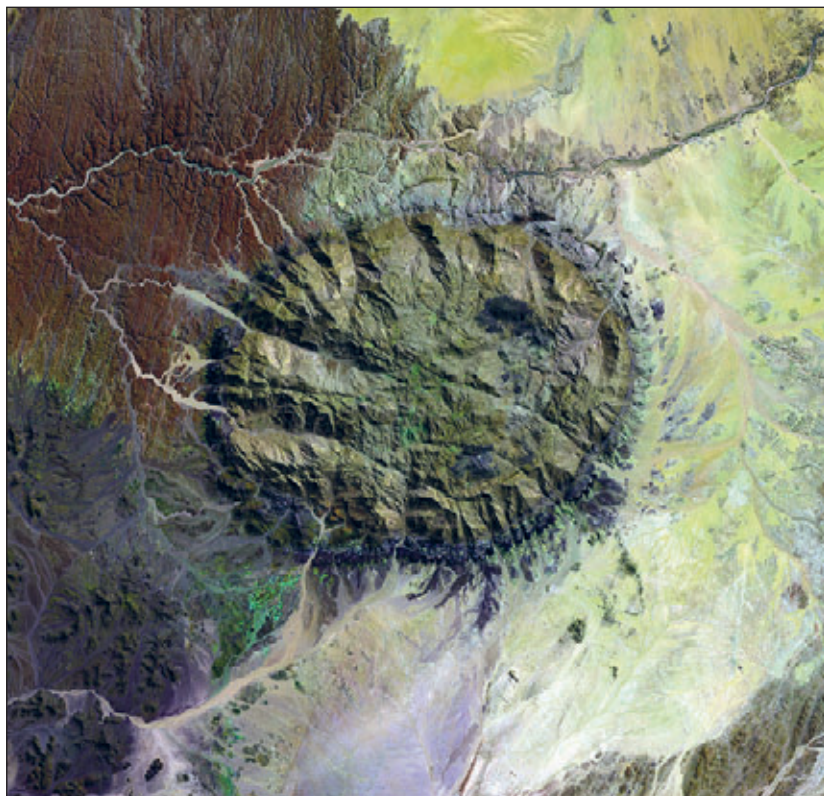


Figure 6.3. The Brandberg Massif is the most spectacular topographical feature of the Namibian landscape; covering an area of 650 km² and rising 1.8 km above the Namib penneplain it predates the break-up of Gondwana. With its largely succulent plateau flora and orographic rainfall, it has acted as a refugium for arid Gondwanan insects (NASA).

between the desert dunes and the beach — the other species of the genus occur in humid forests in Chile and New Zealand (Chvála 1991), and two species of the psychodid genus *Nemapalpus* Macquart were found in rock hyrax abodes in the arid highlands (Bethanie District and the Khomas Hochland) — elsewhere, the species of the genus occur in humid forests (Stuckenberg 1978). These flies must be solitary survivors of a Namibian mid-Tertiary woodland fauna. Other notable examples of flies restricted to the hyper-arid region of Namibia include *Orthactia deserticola* Lyneborg in the Therevidae (M. Hauser, pers. comm.), *Zumba antennalis* (Ville-neuve) in the Calliphoridae *sensu lato* (Kurahashi & Kirk-Spriggs 2006).

On the edge of the Namib Desert is the magnificent Brandberg Massif (Fig. 6.3); Namibia's highest mountain (highest peak Königstein 2,575 m.a.s.l.), which comprises a massive inselberg 650 km² in size, rising 1.8 km above the Namib peneplain. The Brandberg is a granitic ring complex, which pre-dates the break-up of Gondwana and thus also the change in continental climatic and environmental conditions that prevailed during the Plio-Pleistocene (Marais & Kirk-Spriggs 2000). Geologically, it consists of a series of alkali granites that intruded into the throat of an active volcano in the Early Cretaceous (*ca.* 300 Mya) (Miller 2000). The extensive undulating upland plateau (*ca.* 2000 m) exhibits a winter rainfall climate and associated flora, and shares floral elements with the Succulent Karoo biome of southern Namibia (Kirk-Spriggs 2003). The orographic rainfall, and vegetation of the Brandberg, coupled with its long isolation, has created refugia for Gondwanan faunal elements, and it has a relatively high proportion of endemic species as a result. Gondwanan elements have been identified in the coleopterous family Cerambycidae (Adlbauer 2000), and most strikingly, in the recent discovery of the genus *Alavesia* Waters & Arillo (Empidoidea), previously only known from Cretaceous amber (B. Sinclair, unpubl.). The Brandberg has been the subject of a dedicated floral and faunal biodiversity study and contributions on numerous dipterous families have appeared in the volume *Dâures — Biodiversity of the Brandberg Massif, Namibia* (Kirk-Spriggs & Marais 2000). Notable endemic species on the Brandberg are: the dolichopodid *Schistostoma brandbergensis* (Shamshev & Sinclair 2006), the vermilionid *Leptyoma (Perianthomyia) monticola* (Stuckenberg 2000), the mythicomyiid genus *Hesychastes* (Evenhuis 2001) and species *Psiloderoides dauresensis* (Kirk-Spriggs & Evenhuis 2008).

Namibia has two clearly-defined areas of endemism, the arid north-western escarpment, the origin of which was initiated by the slow continental break-up of west Gondwana 130–145 Mya (Barnard 1998), and parts of which still retain relict Gondwana land surfaces, and the southern winter-rainfall zone (Succulent Karoo biome, Gariep Centre), that is restricted to the southern coastal region bordering the Orange River (Irish 1994). Endemism is tangibly demonstrated in numerous groups of flora and fauna in these two areas (Barnard 1998, Simmons *et al.* 1998); studies of the Diptera occurring on the Namibian Escarpment have been few however. An example of an escarpment-restricted species is the endemic *Thoracites nigrifacies* Kurahashi (Calliphoridae *sensu lato*) (Kura-

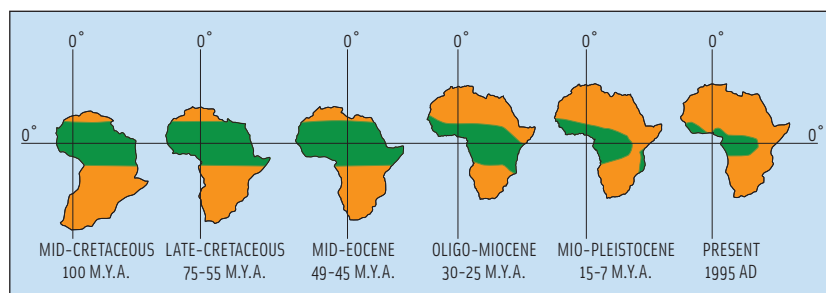


Figure 6.4. Inferred changes to the extent and distribution of forest cover in Africa since the mid-Cretaceous. Shoreline changes are not represented. Changes in the position and orientation of the African continent are due to continental drift
(after Clarke 2000b).

hashi & Kirk-Spriggs 2006). Examples of species apparently restricted to the Succulent Karoo of southern Namibia are more numerous and occur in the Vermilionidae (Stuckenberg 2000), Mythicomyiidae (Evenhuis 2000), Dolichopodidae (Grichanov *et al.* 2006), Calliphoridae *sensu lato* (Kurahashi & Kirk-Spriggs 2006), and Tephritidae (Hancock *et al.* 2001).

While the 'arid' savanna biome, which covers the greater part of Namibia, undoubtedly has a rich Diptera fauna and includes many species more widely distributed in the temperate south and more northerly tropical parts of Africa (e.g., Bombyliidae — Greathead 2000, 2006; Dolichopodidae — Grichanov *et al.* 2006), it has now been clearly demonstrated that the most species-rich area for Namibian Diptera is the 'mesic' savanna of the northeast of the country (Kavango and Caprivi Regions) (e.g., Calliphoridae *sensu lato* — Kurahashi & Kirk-Spriggs 2006; Tephritidae — Hancock *et al.* 2001, 2003; Lonchaeidae — McGowan 2005). Sampling in this region using Malaise trapping and other techniques has resulted in the single greatest increase in dipterous species now known to occur in the country (A.H. Kirk-Spriggs, pers. obs.).

5. The Rainforests

Africa is unusual in that its equatorial rainforests have had a history of radical disturbance due to Neogene climatic change (Maley 1996). Forest cover has changed dramatically since the Mid-Cretaceous (100 Mya), when forest covered the greater part of West Africa and what is today the western Sahara Desert (Fig. 6.4). By the Oligo-Miocene (30–25 Mya) these

forests formed a continuous forest belt which stretched across the African continent and from which forest cover has regressed to its present day extent (Clarke & Burgess 2000). This explains why many taxa occurring in the Eastern Arc Mountains of Kenya and Tanzania share affinities with taxa in the Guineo-Congolian rainforest (Clausnitzer 2003), and there are also strong floristic affinities between these now disjunctive regions that must pre-date the mid-Tertiary uplift of these mountains. The Eastern Arc Mountains do, however, exhibit interesting affinities with other regions, particularly Madagascar and the mountains of West Africa (Burgess *et al.* 2007). Much of the vast Congo Basin forest is rooted in sand (*sables ocres*) that was a dune desert in the Miocene, and it has been hypothesised that the present range of this forest is, therefore, relatively recent (Clarke 2000b). This instability is reflected in the equatorial rainforest fauna — it is remarkably low in diversity, and there is no evidence of a highly adapted canopy fauna (Meadows 1996). Consequently, there are few lowland rainforest endemics of systematic significance among the Diptera.

The current state of knowledge of canopy invertebrates in tropical forests was reviewed by Basset (2001). He lists eight studies specifically related to canopy invertebrates in the Guineo-Congolian rainforest: three studies in Cameroon (Basset *et al.* 1992, Dejean *et al.* 1992, Watt *et al.* 1997), two in Uganda (Corbet 1961; Wagner 1998, 1999, 2000), two in the Democratic Republic of Congo (as Zaïre) (Sutton & Hudson 1980, Wagner 1997), and one in Rwanda (Wagner 1997). Twenty percent of these studies have focus on the Coleoptera, and only one (Corbet 1961) is specifically related to the Diptera. Basset (2001) notes, however, that although often neglected in taxonomic studies, Diptera play a much more significant role in arboreal community interactions than implied by their usual designation as ‘tourists’ in the canopy. Indeed, if biomass and density of canopy invertebrates is considered worldwide, the Diptera rank fourth after the Blattodea, Hymenoptera and Coleoptera (Basset 2001).

In addition to the canopy studies noted above, Moran *et al.* (1994) studied the herbivorous insects on twelve species of evergreen broadleaved trees in a small relict forest in the Pondoland Centre in South Africa (Fig. 6.1: 15). They found the fauna to also be markedly depauperate as compared to that reported from native broadleaved trees from other parts of the world, despite the fact that the sampled forest included numerous endemic and rare tree species. In the more temperate south, Moran & Southwood (1982) undertook canopy fogging of trees in the Grahamstown and

Hogsback area of the Amathole Mountains of the Eastern Cape, South Africa. This study was primarily concerned with guild composition rather than an estimation of biodiversity. The late Harold Oldroyd (1957) observed that the Congo forest Tabanidae were inhabitants mainly of forest margins and the transitional zones between tropical forest and savanna (Fig. 6.1: 10, 11).

6. Afromontane Biome

Afromontane forest occurs in South Africa, on the eastern escarpment and other sites with orographic rain (Partridge & Maud 1987). In successive countries to the north, similar forests are scattered along the rift valley escarpments and on uplands and isolated mountains. The Ethiopian Highlands, which began to rise in the Tertiary (*ca.* 75 Mya), form a rugged mass of mountains in Ethiopia, Eritrea and northern Somalia in north-eastern Africa, reaching altitudes of 1,500–4,600 m.a.s.l. The opening of the series of rift valleys in the closing stages of the Pliocene divided these highlands, thus creating Africa's great salt lakes (e.g., Fig. 6.1: 12). This rifting gave rise to large, alkali basalt shield volcanoes in the Ethiopian and Virunga regions beginning about 25–29 Mya. The associated forests share a characteristic dipteran fauna whose patterns of endemism and cladogenesis suggest that the apparent ecological gaps between these forests may not in fact invariably be barriers to dispersal and faunal exchange. Species of the chamaemyiid genus *Leucopis* subgenus *Leucopella* Malloch have been shown to occur in the Great Rift Valley forests and the Ethiopian Highlands, but one species is restricted to the Arabian Peninsula (Gaimari & Raspi 2002). A similar distribution is exhibited by true examples of the curtonotid genus *Cyrtona* Séguy, species of which appear to have radiated along the Great Rift Valley forests and dispersed into coastal areas of South Africa (A.H. Kirk-Spriggs, unpubl.).

There may be a localised montane hot spot in the Cameroon area, where a still undescribed blepharicerid occurs (B.R. Stuckenberg, pers. obs.). This is supported by the fact that the Cameroon forests have been demonstrated as an area of endemism for birds (de Jong & Congdon 1993) and butterflies (Stuart *et al.* 2003). The Ruwenzori Massif in Uganda also has some remarkable Diptera, such as the endemic, monotypic psychodid genus *Eutonnoiria* Alexander, one of only three endemic genera of Psychodidae in Africa (Duckhouse & Lewis 1980).

7. Arid Coasts

While most of Africa has undergone ceaseless climate fluctuations, generating the expansion and contractions of forests and savannas over millennia, the continent's arid coasts have remained relatively stable (Barnard 1998). A study of the marine-littoral biogeography of the Diptera of the south-western and southern African seaboard (Kirk-Spriggs *et al.* 2001) has indicated that the distribution of coastal Diptera is largely influenced by the effects of the cold Benguela and warm Agulhas currents, and the associated primary production of kelp, and some interesting distributional patterns are illustrated for the Canacidae (as Tethinidae) and Sarcophagidae, as discussed by Kirk-Spriggs *et al.* (2001).

8. Savanna

Savanna (termed the Sudano-Zambeian Region, Fig. 6.1: 2 & 3) characterises much of the vast expanse of the flat landscape of tropical Africa around the Guineo-Congolian Region (Werger & Coetzee 1978). It varies from grassland to woodland with grasses, and it is an old biome with a highly adapted invertebrate fauna, which forms complex mosaics as exhibited, for example, in the chrysomelid beetle genus *Monolepta* (Kirk-Spriggs 2003, Wagner 2001). With the limited rainfall confined to the warmest months, the Diptera of the savanna are highly seasonal and also fire-adapted (Phillips 1965). The vast extent of this relatively homogeneous grassland is reflected in the wide distribution of many of the flies (e.g., Asilidae, Bombyliidae), with even small graminivorous acalyptrates, e.g., Chloropidae, ranging from Ethiopia to South Africa. Although great expanses of the African savanna remain poorly sampled and our knowledge is largely based on scattered records and type localities, centres of endemism in the grasslands are apparent. Poor sampling of African grasslands in general may be largely due to the misconception that such habitats are largely monotonous.

The environment has produced convergent adaptations of body form, colouring and behaviour among the smaller flies (B.R. Stuckenberg, pers. obs.). Ismay (2000) has noted, for example, the number of small species of Chloropidae in the Afrotropics that are bright yellow in colour with a distinct black, shining pleural spot. He notes that this similarity occurs in the chloropid genera *Arctuator* Sabrosky, *Conioscinella* Duda,

Oscinimorpha Lioy and *Pselaphia* Becker as occurring in Namibia, and in some Milichiidae, Phoridae and Hybotidae. Water-retaining cavities and rot holes in savanna trees are important breeding sites for taxa, and synchronous, wet-season flowering of trees provides a critical resource of nectar and pollen for many Diptera. The role of Diptera as pollinators of flowering trees is surely underestimated in Africa. Fogging of flowering *Acacia* trees in Namibia, for example, has revealed an extensive associated Diptera fauna, which is predominated by the Calliphoridae *sensu lato* (A.H. Kirk-Spriggs, pers. obs.). Radiation of the larger savanna mammals prompted diversification of the Oestridae, the greatest development having been in the Afrotropics and the Palaearctic Region — the two African rhinoceros species are hosts to the larvae of the two magnificent species of *Gyrostigma* Brauer, the future of which is looking increasingly precarious with the dwindling numbers of their hosts (Barraclough 2006a).

There have been few studies of insect canopy faunas in African savannas using modern fogging and mist-blowing techniques. The only published study is that of Krüger & McGavin (1997), who studied the insect fauna associated with *Acacia* species in Mkomazi Game Reserve in north-east Tanzania using a mist blower. They found canopy faunas to be highly diverse, and that the Coleoptera diversity paralleled that of other tropical areas. The Diptera component represented 1.0% of the biomass share. The National Museum of Namibia has also recently undertaken extensive canopy fogging of individual trees in the arid and mesic savanna biome of Namibia, but these studies remain unpublished.

9. Madagascar

Madagascar is an ancient fragment of Gondwana which separated from Pangea from the mid-Jurassic to the Early Cretaceous. The dominant biome during the Tertiary was probably monsoon rainforest, with drier forests and scrub in the west (de Wit 2003). The Madagascan Diptera encompass a remarkable mix of relationships. Two endemic Gondwanan relicts are the blepharicerid genus *Paulianina* Alexander and the acrocerid genus *Parahelle* Schlinger. Oriental and African relationships occur in many families, though few with South Africa. Some large families are poorly represented — there are few Bombyliidae (18 species in eight genera, 16 of which are endemic) and Empididae (although not officially recorded from Madagascar there are numerous species), and the Nemes-

trinidae are represented by only one species. Much of the fauna could still be unknown — the first vermilionid was discovered recently by Mike Irwin (Stuckenberg 2002), two species of Rhizophoridae await description (A.H. Kirk-Spriggs, pers obs.; T. Pape, unpubl.), at least 100 undescribed species of Lauxaniidae have been collected (B.R. Stuckenberg, pers. obs.), and additional families are likely to be recorded. With fewer than 2,500 recorded species, considerably more collection and study of Madagascar Diptera is obviously required, and is now being undertaken on a coordinated basis (see below).

10. Afrotropical Faunistics

The size, taxonomic composition and characteristics of the Afrotropical Diptera have received growing attention in recent decades. With the publication of the first comprehensive systematic synopsis of this fauna — *Catalogue of the Diptera of the Afrotropical Region* (Crosskey 1980) — it was possible to obtain statistical data on the taxa described or recorded to that date, as well as general information on distribution and biology. This was one of the best catalogues of its kind, and immediately became the basis for further dipterological studies. The total number of Afrotropical species recorded in that work was 16,318, in 95 families, of which 1,944 species were known from Madagascar and 14,669 species from the continental Afrotropical Region.

Growing concerns about the developing biodiversity crisis led to the publication of various synoptic overviews directed at assessments of the extent to which knowledge of the world's fauna in general was known. The first contemporary prediction of the probable number of insect species on Earth was that of Erwin (1982). He gave a figure of 30 million, based on his pioneering work on the canopy fogging of tropical rainforest trees. This prediction has since been substantially downscaled. Gaston (1991) took a 'taxonomist-based' approach, in which specialist systematists were asked to provide predictions of the probable number of described and undescribed species. From these tentative but possibly more reliable data he came up with a tangible figure of five million. Contributions relating to the Afrotropics began to appear. Estimations in respect to the South African insect fauna were provided for each insect order in the textbook *Insects of Southern Africa* (Scholtz & Holm 1985). The chapter on Diptera by Barraclough & Londt (1985) gives a total of 6,243 recorded species, al-

though the origin of these data remains unclear. Scholtz & Chown (1995) and Scholtz (1999) reviewed the same data for all the insect orders, and a synoptic analysis by Miller & Rogo (2001) covered a wide range of associated topics. It had been estimated by Barraclough that the true size of the dipteran fauna in the Afrotropics could be double what had already become known by 1985 (Scholtz & Chown 1995). Some of this literature was discussed by Kirk-Spriggs (2003) in an introductory study of African biogeographical patterns.

The most recent published review of the Afrotropical Diptera, by Irwin *et al.* (2003), appeared in the stupendous book *The Natural History of Madagascar* (Goodman & Benstead 2003). Drawing on the computerised *BioSystematic Database of World Diptera* online from the USDA/National Museum of Natural History, Smithsonian Institution (Thompson 2006), it could be reported that by early 2001, 19,051 valid fly species had been recorded in the Afrotropical Region. This represented about 13% of the world's fly species. Of these, 1,796 were known from Madagascar — a smaller total than that obtained from data in the 1980 *Catalogue*.

The present study attempts to revise data for the Afrotropical Diptera (Table 6.2). For this, the excellent resources of the *BioSystematic Database of World Diptera* have been invaluable. It must be stressed, however, that the accumulated taxonomic literature deals almost entirely with morphospecies, which can be recognised by traditional, usually morphological criteria (but with some interesting exceptions among black flies and mosquitoes, see below), and that no calculated projections of faunal size through standardised collecting techniques or rates of accumulation of taxa is available (but see Dikow *et al.* 2009). The true number of existing species, including cryptic and sibling ones, the recognition of which requires genetic or molecular studies, cannot even be guessed at. It is salutary to recall, for example, that whereas just over 120 species of *Anopheles* Meigen mosquitoes were recognised in 1987, later genetic studies showed the existence of species complexes within every taxon examined, leading to the estimation that the African anopheline fauna may actually attain 600 species (Coetzee 1999). Another startling example is provided by the vector of onchocerciasis in West Africa, once considered to be the species *Simulium damnosum* Theobald, which has since been shown by cytogenetic studies to be a complex of at least 40 species (Coetzee 1999). Such situations may be far more prevalent among Diptera than has been realised. A case in point is the tephritid genus *Ceratitis* MacLeay; it has

been reported that close study of apparently polyphagous species revealed the existence of species complexes involving undescribed stenophagous species (De Meyer 2001).

In our study we follow the approach of Gaston (1991) to estimate the number of undescribed species from the Afrotropical Region. Practising systematic authorities on each fly family were contacted and asked to confirm the number of described species provided through the *BioSystematic Database of World Diptera*, and also to predict the probable number of undescribed species likely to occur in the region. In the case of families for which no systematists are currently engaged in research, competent systematists, well-versed in the Afrotropical fauna, were asked to make such predictions. In the case of families for which the fauna is extremely poorly known, e.g., Cecidomyiidae, Phoridae and Sphaeroceridae, it was only possible to provide a highest and lowest estimation; this is why two figures must be provided for the Diptera of the Afrotropical Region as a whole — a lowest and highest estimation.

11. Estimate of Total Afrotropical Diptera Fauna

Irwin *et al.* (2003) discuss what they term the ‘discovery phase’, being the part of a timeline during which most species in a given environment are discovered and described. They note that this is quite advanced for most of the North American insect fauna and is virtually complete in the case of the best-documented insect fauna of Great Britain. The situation in the Afrotropics is markedly different. Table 6.2 provides details of the number of described species for each family known to occur in the Afrotropical Region, plus specialist estimates of the number of undescribed species. Figures presented in the table indicate the following:

It can be concluded that 19,689 species of Diptera are currently known from the Afrotropical Region, this representing an overall increase of 3,371 species in the past 26 years, since the publication of Crosskey’s (1980) *Catalogue*.

Specialist estimates of the overall number of undescribed species range from 29,961–37,930 (*mean*: 33,946). The range difference of 7,969 is largely due to the range-estimates given for three of the least known families, the Cecidomyiidae (5,000–10,000), Phoridae (2,000–3,000), and Sphaeroceridae (1,000–2,000). A round figure of 30,000 species at the lower end is therefore reasonable for general purposes.

Table 6.1. Numbers of described species of Diptera from the six zoogeographical regions of the world and the percentage of the world fauna. Data from Thompson (2006), unless otherwise stated.

Zoogeographical region	Number of known species	Percentage of known world fauna
Afrotropical Region*	19,689	13%
Palearctic Region	40,291	27%
Oriental Region	21,559	14%
Australasian/Oceanian Region	17,948	12%
Nearctic Region	21,356	14%
Neotropical Region	29,783	20%
Totals	150,626	100%

*Numerical data based on familial information provided in Table 6.2.

This estimate implies that $\frac{2}{3}$ to $\frac{1}{2}$ of the dipteran species might be known. If the total number of species added to the regional list from 1981–2006 is considered (3,371), this gives an average of 129 new species per year. Hypothetically, at that average rate of taxonomic growth it would take upwards of three centuries (231–289 years) to reach the end of the discovery phase.

12. Comparison to Other Zoogeographic Regions

The number of species known to occur in the six zoogeographical regions is here briefly reviewed, based on the revised figure for the Afrotropical Region presented above, and data from the *BioSystematic Database of World Diptera* (Thompson 2006) for the other regions. The number of genera from the six regions is not considered, as that taxonomic ranking is not necessarily definitive between regions. From data presented in Table 6.1 the Afrotropical Region accounts for a mere 13% of the species of Diptera known worldwide. This is rather a reflection of taxonomic effort than of actual numbers. Also, the geographical extent of each of the five regions varies enormously, with the Palearctic comprising a considerably greater proportion of landmass than the other five; the Oriental and Australasian/Oceanian regions comprising the least. It is not surprising, therefore, that the Palearctic Region accounts for 27% of the world spe-



Figure 6.5. The remarkable *Mormotomyia hirsuta* Austen, the only known species of the endemic family Mormotomyiidae, associated with bats in Kenya.

cies, being as it is the largest of the zoogeographic regions and having as it does the best-studied fauna. Predictive figures for the six regions may present a more plausible estimation of the world Diptera fauna.

13. Endemic Afrotropical Families

Four families of Diptera are now known to be endemic to the Afrotropical Region, *viz.* the Mormotomyiidae, Marginidae, Natalimyzidae and Glossinidae. A brief résumé of what is known for each of these families is provided below. McAlpine (1991) has intimated that aside from the Marginidae and Natalimyzidae to which he refers (as unknown family in the latter case), it may be assumed that further new dipterous families of limited diversity and distribution await discovery in the Afrotropics. Given the extremely limited distribution of the family Mormotomyiidae and the meagre distribution of the Marginidae in wet forests, these are the families of Diptera most at risk of extinction (McAlpine 1991).

Mormotomiidae (Fig. 6.5) — This family of truly remarkable flies comprises a single species, *Mormotomyia hirsuta* Austen, which was described from a single locality, Ukazzi Hill, Garissa District, Kenya. Flies were found to occur in a cave-like cleft about a yard wide, with its horizontal and oblique side-cracks inhabited by unidentified bats. Larvae were found to develop in the accumulated dung of bats, and to be saprophagous, either on the decaying organic matter itself or predacious on other inhabitants. Upon entering the cave at Ukazzi, H.B. Sharpe noted that the flies ‘came floating down from above like feathers’ (Austen 1936: 430); a behaviour later noted by van Emden (1950), who remarked that the fall of the flies is apparently much slowed by the long, shaggy, hair-like body setae and occurred in a slight spiral motion. As well as the disproportionately long legs, which abound in numerous ‘mummy-brown’ hair-like setae, the wings are drastically reduced to dysfunctional thin straps, and the halteres are entirely absent. Austen (1936) discussed the relationship of the family based on morphological characters. He believed it to be an acalyptrate fly ‘perhaps’ most closely related to the Sphaeroceridae (as Borboridae). Later van Emden (1950) described the immature stages (egg, third instar larva and puparium) and discussed relationships based on larval and adult morphology. He considered that the genus represents a well-founded family intermediate between the Scathophagidae (as Cordyluridae) and the Acalyptratae.

Natalimyziidae (Fig. 6.6) — This family was only formally described in 2006 (Barracough & McAlpine 2006), although it has been recognised as a distinct family for some forty years. The family is apparently widespread in Africa, with current records from South Africa (Western Cape, Eastern Cape, Kwazulu-Natal, Mpumalanga, Limpopo), Zimbabwe, Kenya and Nigeria. Although regarded as predominantly associated with grassland in South Africa, recent Malaise trapping in indigenous forest of the Eastern Cape has indicated that the family is also common in forests (A.H. Kirk-Spriggs, pers. obs.). Larvae have not yet been described, but appear to be micro-floral grazers in decaying grass (Miller 1984). Some 20 species are known from South Africa alone. The family is currently ascribed to the subfamily Sciomyzoidea and molecular studies are currently underway as part of the *FlyTree* Project (B. Wiegmann, unpubl.). The family was included in an identification key to the acalyptrate flies of southern Africa as ‘New family’ by Barracough (1995).

Marginidae — This family is one of the two endemic Afrotropical acalyptrate families described in the past few decades (McAlpine 1991). The description was based on two species of the monotypic genus *Margo*, namely: *M. aperta* from Chirinda Forest, near Mount Selinda in Zimbabwe, and *M. clausa* from near the coastal town of Manakara in Mada-



Figure 6.6. An undescribed species of the endemic family Natalimyziidae from the Eastern Cape, South Africa. The family was only described in 2006.

gascar. McAlpine (1991) discussed the systematic relationships of the family in some detail and suggested its placement in the Opomyzoidea. The occurrence of the species in both the continental Afrotropical Region and Madagascar suggests that additional species may await discovery in humid African forests. The immature stages remain unknown and molecular work is required to correctly determine superfamilial placement.

Glossinidae — *Tsetse* require no introduction and are well known due to their status as vectors of pathogens such as African trypanosomiasis (sleeping sickness) and its animal equivalent *Nagana*. Although the family is restricted to tropical Africa today, two Oligocene fossil species, *G. †oligocenus* Scudder and *G. †osborni* Cockerell, are known from the United States and are frequently used as examples of regional extinction events (Grimaldi 1992, Evenhuis 2006). The family was also recently found in Miocene European deposits (Wedmann 2000). Twenty-three species of the genus are extant in tropical Africa today and an extensive literature has developed related to their taxonomy, behaviour, habitat preferences, development, and role as disease vectors. They are readily distinguished from other blood-sucking flies by the hatchet-shaped discal cell of the wing and the multi-plumed arista.

14. Some Absent Families

Notable families absent from the Afrotropical fauna are the Atelestidae, Hilarimorphidae, Pseudopomyzidae, Spaniidae, Trichoceridae (Africa is the only continent without this family of lower Diptera) and Xylophagidae.

15. Largest Afrotropical Families

The three largest families of Diptera in the region are the Asilidae (1,643), the Bombyliidae (1,425) and the Limoniidae (1,034). These three families alone constitute almost 21% of the fauna – none of which is likely to double in numbers through future research. Other families with >500 described species are the Ceratopogonidae (913), Chironomidae (556), Culicidae (752), Dolichopodidae (738), Muscidae (932), Syrphidae (562), Tabanidae (815), Tachinidae (1,013), and Tephritidae (947). The total number of species for all 12 families mentioned here is 11,330, which is more than half (57.5%) of the fauna. Many of the smaller families could, therefore, be doubled by new species without markedly affecting the total estimate.

16. Least Known Families in the Afrotropics

The following families are regarded as least known (>1000 undescribed species predicted), and are ranked in order of importance, i.e., least known first. Figures for Madagascar are derived from Irwin *et al.* (2003), with Phoridae updated from Disney (2005).

Cecidomyiidae — gall midges are by far the least known family of Afrotropical Diptera. They are under-collected and under-studied. Most research has been directed to those species of agricultural importance or to species associated with particular plant hosts. Currently only 213 described species (3 in Madagascar!), representing only an estimated 2–4% of the true number of species (5,000–10,000).

Phoridae — scuttle flies are extremely diverse in the region and remain under-studied. Currently only 418 described species (18 in Madagascar), representing only an estimated 12–17% of the estimated number of species (2,000–3,000).

Sphaeroceridae — lesser dung flies are an enormous group which has received only limited attention. Currently only 321 described species (11

in Madagascar), representing only an estimated 14–24% of the estimated number of species (1,000–2,000). These estimations may be rather high, given that the distribution of dung-dependant flies in savannas is hardly known, particularly the dependence of species associated with the dung of indigenous species as opposed to domesticated species.

Ceratopogonidae — biting midges are also poorly known. Most recent research has focused on the *Culicoides* Latreille vectors of veterinary arboviruses. Currently 913 described species (12 in Madagascar), representing 31% of the estimated number of species (2000).

Mycetophilidae — fungus gnats are extremely prolific in tropical forests and in savanna in the wet season. Currently only 249 described species (a single endemic species in Madagascar), representing 11% of the estimated number of species (2000).

Sciaridae — dark-winged fungus gnats have been very poorly studied, but are known to be prolific in wet forest and savannas. Currently only 71 described species (6 in Madagascar), representing 3% of the predicted number of species (2000).

Dolichopodidae — Currently 738 described species (52 in Madagascar), representing 33–42% of the predicted number of species (1,000–1,500).

Tachinidae — Currently 1,013 described species (187 in Madagascar), representing 51% of the predicted number of species (2,000).

17. Notable Taxonomic Growth

Examples of productivity since 1980 by some individual specialists:

Asilidae: the largest Afrotropical family. Jason Londt has described 25% of the species. He enlarged the genus *Neolophonotus* Engel by 192 new species, or 76% of the present total of 253 species — this is currently the largest Afrotropical genus of Diptera.

Camillidae: Originally considered to be a minor Palaearctic family. David Barraclough increased the number of Afrotropical camillids from 1 genus and 2 species to 4 genera and 20 species, showing it to be primarily an African family.

18. Best Known and Collected Countries

The best known dipterous faunas are those for the modern states of South Africa, Namibia, Kenya, and Nigeria. This assumption is based on the

extent of Diptera material from these countries in European and African museums.

19. Possible Gondwanan Elements in the Afrotropical Diptera

It has been long known that South Africa has the most distinctive invertebrate fauna in the Afrotropics. Included are various taxa the phylogenetic relationships of which indicate them to be of ancient occurrence in this region (Kirk-Spriggs 2003, Stuckenberg 1962). The explanation for their presence has been that they are remnants of a fauna that diversified and dispersed across the Gondwanan landmass before its prolonged break-up into separate continental masses. These Palaeogenic elements thus have been termed 'Gondwanan', and their presence in South Africa is of great interest, especially as their distribution pattern concurs with a biogeographical situation also involving South America and Australia. Each of these three continents has essentially two insect faunas — a southern one, mostly associated with relatively temperate environments, the other mainly in more northerly, warmer or even tropical latitudes. These austral insect faunas have taxa in common and appear to share an evolutionary history that reflects continental drift. Two areas of such putative Gondwanan insects occur in the Afrotropics — namely, in South Africa and in Madagascar. They need to be considered separately.

South Africa has Africa's oldest mountains. They are of two kinds, with completely different origins. In the south of the country, extending more or less east-west, with a smaller interlocking north-south section in the west, is a series of elongate ranges, constituted by similar sedimentary rocks, known as the Cape Fold Mountains. They are part of an ancient orogeny that predated the break-up of Gondwana. At that time they were continuous with old mountains in south-eastern Australia, with the trans-Antarctic ranges, and even with a small range in the Buenos Aires Province of Argentina known as the Sierra de la Ventana. Recognition of this once enormous orogeny extending across Gondwana, was an insight by the South African geologist Alex L. Du Toit, whose landmark book *Our wandering continents; an hypothesis of continental drifting* (1937) provided the first elaboration of continental relationships and drift.

Also in South Africa is the eastern Great Escarpment, called the Drakensberg over much of its length. This was initiated as a result of the separation of Antarctica from southeastern Africa in the Jurassic, when a



Figure 6.7. Africa's only tanyderid, *Peringueyomyia barnardi* Alexander from the Cape Fold Mountains of South Africa.

new drainage system formed in the hinterland of the new South African coastline, flowing eastwards towards the expanding Indian Ocean. Extremely prolonged water erosion established by this drainage, operating throughout the Mesozoic and twice rejuvenated by Cenozoic episodes of continental uplift, created this escarpment in eastern South Africa. It was progressively eroded westward, until the presence of a massive, almost horizontal sequence of hard basaltic rocks retarded the rate of erosion and resulted in steep exposure of an underlying, very thick sequence of sediments. With permanent benefit of summer rains derived from the expanding, warm Indian Ocean, this escarpment could acquire and retain freshwater and terrestrial invertebrate faunas during much of the Mesozoic and Cenozoic (Partridge & Maud 1987).

All these mountains are preserved ancient landforms with a characteristic biota, which include putative Gondwanan Blephariceridae, Thaumaleidae, Psychodidae, Empididae, Africa's only tanyderid (Fig. 6.7), near-basal Chironomidae, and other flies with possible austral relationships. Among the more convincing cases are the following taxa:

Blephariceridae — all the South African species are in the genus *Elporia* Edwards, which belongs to the tribe Paltostomatini, the other genera of which are all Neotropical (Stuckenberg 2004). *Elporia* is probably the sister-group of the genus *Kelloggina* Williston, which is limited to the old coastal highlands of central and southern Brazil. Because of the strong cladistic support for blepharicerid classification, a good case can be made for a Gondwanan origin of *Elporia*.

Thaumaleidae — only two species of this small nematoceran family associated with mountain streams have been described from the Afrotropics (Sinclair & Stuckenberg 1995). One occurs in the Natal Drakensberg, the other in the Cape Fold Mountains. They constitute the endemic South African genus *Afrothaumalea* Stuckenberg, which is part of a monophylum of genera also occurring in Australasia and temperate South America. The closest relative of *Afrothaumalea* appears to be the Australian and southern Chilean genus *Niphtha* Theischinger (Sinclair & Stuckenberg 1995).

Psychodidae — the distinctive genus *Gondwanotrichomyia* Duckhouse was erected for two species limited to montane evergreen forests of eastern South Africa (Duckhouse 1980). Related species occur in Australia and Chile.

Rhagionidae — a genus with species of 'archaic' habitus, *Atherimorpha* White, has been recorded as well represented in South Africa (Nagatomi & Nagatomi 1990), inhabiting mesic montane grasslands and the fynbos flora of the Cape Fold Mountains. Although these species are classified as congeneric with evidently Gondwanan clades of *Atherimorpha* in southern South America and eastern Australia, this relationship has not yet been confirmed through morphological study. It was proposed first by Bezzi (1926), but may have been based on symplesiomorphies.

Empididae — the near-basal genus *Homalocnemis* Philippi (Fig. 6.2) was recorded from the edge of the Namib Desert by Chvála (1991); the genus is also recorded from Chile and New Zealand (see above). Other possible Gondwanan genera in the Empididae are discussed by Sinclair (2003).

Tabanidae — the endemic genus *Stuckenbergina* Oldroyd (1962) is the only Afrotropical member of the tribe Pangoniini. This tribe otherwise has a notable austral distribution, involving elements shared between South America and Australia. The two described South African species are associated with the Cape Fold Mountains.

Chironomidae — putative cases of Palaeogenic genera are discussed by Sæther & Ekrem (2003).

Simuliidae — distribution patterns and possible Gondwanan subgenera are discussed by Miranda-Esquivel & Coscarón (2003).

During the Gondwanan history of Madagascar, when this island was still united with Africa in the west and with India in the east — and when the compound Indian-Madagascan landmass was contiguous with the still united Australian + Antarctic continental sectors of Gondwana, which also had contact through western Antarctica to southernmost South America — the possibility of an evolution of a pan-austral insect fauna which dispersed variably over this huge area is entirely plausible (Wells 2003). Particularly significant in this regard is the recent remarkable expansion of knowledge of the palaeobotany of Antarctica (Hill & Scriven 1995). At the time when that continental area had a central position with contact to all of the other austral areas which later attained independent continental status with the break-up of Gondwana, Antarctica was not a frigid wilderness with scanty flora. Hill & Scriven stated that Antarctica was a key area in the development of the extant vegetation of the Southern Hemisphere, and that ancestors of the present austral flora were established there by the end of the Cretaceous. Angiosperms were present by the Mid-Cretaceous, and may have been invasive elements in Antarctica, possibly coming from South America *via* the Antarctic Peninsula. Madagascar + India could thus have shared faunal components that may have evolved and diversified in southern South America and Antarctica.

Expeditions to Madagascar in the late 1950s (by B.R. Stuckenberg) were directed at collecting Diptera in general, but with a special objective to search for what seemed to be the Gondwanan elements that were already known in South Africa. None of them could be found. Indeed, among the Diptera in Madagascar it was a blepharicerid genus well developed there, *Paulianina*, that was the only taxon for which a Gondwanan origin could at that time be plausibly postulated. This genus is the sister-group of the austral Neotropical — Australian genus *Edwardsina* Alexander, and the two genera together constitute the near-basal subfamily Edwardsiniinae. The biogeography of *Edwardsina* had long attracted attention, the genus having been considered a likely Gondwanan relict by earlier dipterists, such as R.J. Tillyard, A.L. Tonnoir, I.M. Mackerras and D.H.D. Edwards. *Paulianina* is classified in a different subfamily to that of the South African genus *Elporia* (Blepharicerinae), the sister-group of which may be the Brazilian *Kelloggina* (see above), so a separate explanation for the presence of Edwardsiniinae in Madagascar could be expected.

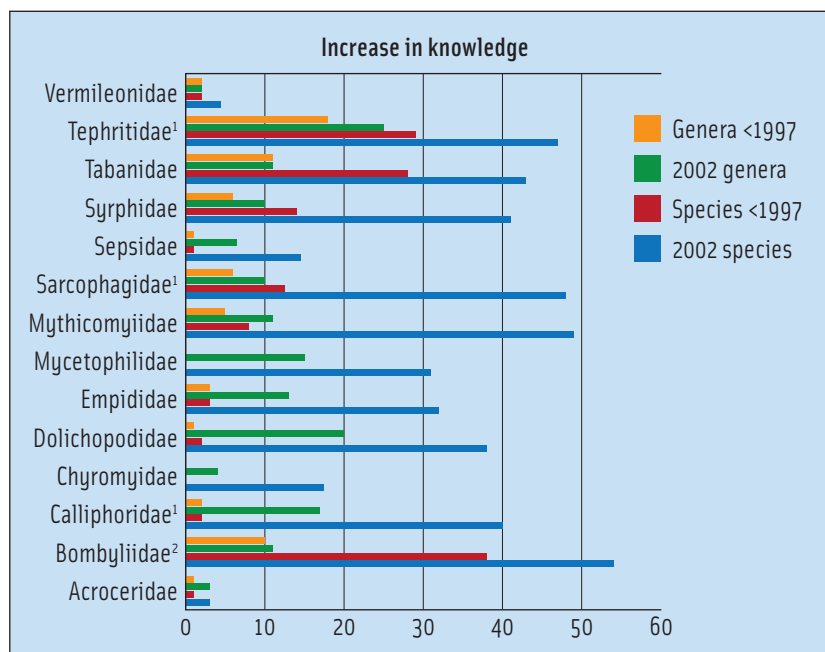


Figure 6.8. Examples of the increase in knowledge of 14 families of Diptera occurring in Namibia from 1997 to 2002. <1997 figures from Crosskey (1980). This increase has been due to dedicated sampling efforts using Malaise traps and other techniques, the field preparation of good quality material, and taxonomic efforts by specialist systematists.

¹species numbers reduced by 50%

²species numbers reduced by 75%

There is still one other record of blepharicerids in sub-Saharan Africa — two finds of immature stages of a still undescribed genus and species apparently in the blepharicerine tribe Paltostomatini, in West Africa. This taxon was recorded as a species of *Elporia* (Germain *et al.* 1967), but that assessment is probably erroneous, as the larval stages differ in having one additional pair of prolegs. Also in Madagascar is an undescribed blepharicerid not related to Edwardsiniinae (Paulian 1954). It is known only from river systems draining off the Andringitra Massif, and it was once thought to be possibly a member of the tribe Apistomyiini. Adults were found in 1958, but determination of its relationships among the Blepharicerinae has been inconclusive (Stuckenberg 2004). This species may have been derived from tropical sub-Saharan Africa, outside the range of *Elporia*.

20. Innovations in the Bioinventory of Africa's Diptera

If our knowledge of the Diptera of Africa is to improve, despite the all too apparent constraints of the new millennium, a new approach to the sampling and study of the African Diptera fauna must be adopted. To assess such changes in approach that need to be considered, it is useful to examine and assess some of the more recent innovative approaches that have been undertaken both within and from outside Africa.

Namibian bioinventory — as a developing African country, the Republic of Namibia is a good example of a sub-Saharan country whose recent bioinventory initiatives have resulted in a substantial increase in the number of Diptera known from that country (see Fig. 6.8). The use of Malaise traps and other modern techniques to sample the dipterous fauna in a range of habitat types and biomes, together with the field preparation of good quality material, has encouraged international specialists to work on the Namibian fauna, and numerous faunal reviews have, and continue to, appear as a result. Targeted biodiversity studies, such as the National Museum of Namibia's Marine-littoral Survey 1998 and Brandberg Biodiversity Project have also been widely regarded as benchmark studies.

An Arthropod Survey of Madagascar's Protected Areas (1998–2009) — initiated by Mike Irwin (University of Illinois of Urbana-Champaign) and chiefly funded through the Schlinger Foundation, this project involves the long-term monitoring of Diptera by use of Malaise traps in protected areas throughout the island of Madagascar. Traps are serviced by locals on a monthly basis and most traps being continually deployed for at least one year, thus enabling seasonal data to be analysed. The project has trained local Madagascans as sorters, but sorted material is managed and distributed by the California Academy of Sciences in San Francisco. At the termination of the sampling phase (2009), it may be several decades before this material can be fully processed, but it is already turning up numerous families not previously recorded from Madagascar and is making great strides in our knowledge of the Malagasy fauna.

United Arab Emirates Insect Project — initiated by Sheikh Tahnoon bin Zayed al Nahyan from Abu Dhabi, and run by Antonius van Harten, this project is restricted to the United Arab Emirates, but also includes available material from Yemen and Oman, collected by van Harten and others (see above). The project is now in its third year, and the first of a series of volumes entitled *The Arthropod Fauna of the United Arab Emir-*

ates was recently published (van Harten 2008), with contributions on 17 families of Diptera by specialist researchers. This coordinated project is doing much to better our understanding of this fascinating transitional region.

The following projects, programmes and initiatives are here suggested as especially suitable for bringing the bioinventory of Africa's Diptera fauna forwards.

A Manual of Afrotropical Diptera — the publication of such a manual, providing generic keys, taxonomic information and notes on immature stages and biology, in line with manuals produced for the other zoogeographical regions of the world, would do much to stimulate future interest in Afrotropical Diptera.

Catalogue of Afrotropical Diptera — it has been over 26 years since the publication of Crosskey's (1980) *Catalogue*. Although catalogues to various families of Diptera have appeared, which deal with the fauna on a world basis, there is now an urgent need for a new, fully up-dated Afrotropical catalogue, preferably with an on-line version.

Country faunal bioinventories — there is now a disproportionate amount of information available on the Diptera of South Africa and Namibia. If we are to gain better insight into the biological diversity and biogeography of Afrotropical Diptera it is necessary to undertake coordinated, long-term sampling using Malaise traps and specialist collection in other under-collected African countries.

Targeted biodiversity studies — multi-disciplinary studies of specific habitat types and biodiversity hotspots are urgently required, especially in threatened habitats. Examples of high priority areas are West African and Congo rainforests (especially Cameroon, Sierra Leone, Liberia, Côte d'Ivoire, and Ghana), the Eastern Arc Mountains, the Albertine Rift, the arid north-eastern regions of the Horn of Africa, the escarpments of South Africa, Namibia and Angola, the isolated inselbergs of Namibia and Angola, the Hoggar and Tibesti Mountains of the central Sahara and the Ethiopian Highlands. Recent steps towards an inventory of the species-rich and highly endemic biota of the Eastern Arc Mountains are currently being taken by the EU-funded network of excellence, *European Distributed Institute of Taxonomy*, Workpackage 7 (T. Pape, pers. comm.).

Table 6.2. Systematic list of known species of Afrotropical Diptera by family and specialist predictions of the number of undescribed species. Numbers of described species based on *BioSystematic Database of World Diptera* (Thompson 2006); emended by specialists [in brackets]. Figures and predictions based on data collected in 2006.

Estimations of undescribed species				
Family	Known species	Estimated No. undescribed species	Percentage of species known	Percentage of fauna awaiting description
Acroceridae ⁶	67	10+	87%	13%
Agromyzidae ²⁸	273	400+	41%	59%
Anisopodidae ⁴⁵	16	2+	89%	11%
Anthomyiidae ⁴⁴	66	20–25+	77%	23–27%
Anthomyzidae ⁷	23	100+	19%	81%
Apioceridae ⁴⁵	4	1+	80%	20%
Asilidae ²³	1,533[1643]	1,900+	46%	54%
Asteiidae ²⁴	15	15+	50%	50%
Athericidae ⁴⁵	22	8+	73%	27%
Aulacigastridae ⁶	4	2–3+	67%	33–43%
Bibionidae ⁴⁵	71	6+	92%	8%
Blephariceridae ⁴⁵	28	8+	78%	22%
Bombyliidae ¹⁵	1,425	300+	83%	17%
Braulidae ⁶	3	0	100%	0%
Calliphoridae ³⁷	207	50+	81%	19%
Camillidae ⁶	22	20–25+	52%	48–53%
Canacidae ⁴¹	25	42+	37%	63%
Carnidae ²⁵	6	5+	55%	45%
Cecidomyiidae ²⁶	213	5,000–10,000+	4%	96–98%
Celyphidae ⁴²	13[12]	7+	63%	37%
Ceratopogonidae ⁵	913	2,000+	31%	69%
Chamaemyiidae ³²	15[10]	40–50+	20%	80–83%
Chaoboridae ⁴⁵	8	6+	57%	43%
Chironomidae ⁴³	556	374+	60%	40%
Chloropidae ⁴	401	700+	36%	64%
Chyromyiidae ⁹	13[10]	70–100+	13%	88–91%
Clusiidae ⁶	10	15–20+	40%	60–67%
Coelopidae ⁶	5	0	100%	0%
Conopidae ⁶	160	40+	80%	20%

Estimations of undescribed species				
Family	Known species	Estimated No. undescribed species	Percentage of species known	Percentage of fauna awaiting description
Corethrellidae ⁴⁵	3	3+	50%	50%
Cryptochetidae ⁶	12	2+	86%	14%
Ctenostylidae ⁶	2	0	100%	0%
Culicidae ³⁸	752	752+	50%	50%
Curtonotidae ³⁵	25	50+	33%	67%
Diadocidiidae ⁴⁵	1	2+	33%	67%
Diastatidae ⁶	12	2–3+	86%	14–20%
Diopsidae ⁶	137	1233+	90%	10%
Dixidae ³¹	8	16+	33%	67%
Dolichopodidae ³⁶	738	1,000–1,500+	42%	58–67%
Drosophilidae ⁶	451	250+	64%	36%
Empididae ¹⁸	367	640+	36%	64%
Ephydriidae ⁴¹	339	578+	37%	63%
Fanniidae ⁸	13	3–6+	80%	20–30%
Glossinidae ⁴⁵	23	0	100%	0%
Heliomyzidae ¹²	62	80+	44%	56%
Hippoboscidae ⁴⁵	130	0	100%	0%
Keroplastidae ²	170	500+	25%	75%
Lauxaniidae ³²	91[90]	400+	18%	82%
Limoniidae ²⁷	1,034	1,500+	41%	59%
Loncheidae ²⁹	64	250+	20%	80%
Lonchopteridae ⁶	6	0	100%	0%
Lygistorrhinidae ⁴⁶	7	20+	26%	74%
Marginidae ⁶	3	1–2+	75%	25–40%
Micropezidae ⁶	65	15+	81%	19%
Milichiidae ¹³	63[67]	192–203+	26%	74–75%
Mormotomyiidae ³⁵	1	0	100%	0%
Muscidae ⁸	932	233–466+	80%	20–40%
Mycetophilidae ²	249	2,000+	11%	89%
Mydidae ³	200	200+	50%	50%
Mythicomyiidae ⁹	55	220+	20%	80%
Natalimyziidae ⁶	1	30–40	3%	97–98%
Nemestrinidae ⁶	51	30+	63%	37%

Estimations of undescribed species				
Family	Known species	Estimated No. undescribed species	Percentage of species known	Percentage of fauna awaiting description
Neminidae ⁶	7	2+	78%	23%
Neriidae ⁶	20	5+	80%	20%
Neurochaetidae ⁶	12	1–2+	92%	8–14%
Odiniidae ⁶	8	8–10+	50%	50–60%
Oestridae ¹⁶	35	8+	81%	19%
Opomyzidae ⁶	5	0	100%	0%
Periscelididae ⁶	10	5+	67%	33%
Phoridae ³⁴	418	2,000–3,000+	17%	83–88%
Piophilidae ⁶	7	0	100%	0%
Pipunculidae ¹	152	300+	34%	66%
Platypezidae ²	41	40+	41%	49%
Platystomatidae ⁴⁰	241[280]	70+	80%	20%
Psilidae ⁶	52	10+	84%	16%
Psychodidae ⁴⁵	299	199+	60%	40%
Ptychopteridae ⁶	9	1–2+	90%	10–18%
Pyrgotidae ³⁰	141	10+	93%	7%
Rhagionidae ⁴⁵	54	70+	80%	20%
Rhiniidae ³⁷	151	30+	83%	17%
Rhinophoridae ¹⁶	28	50+	36%	64%
Sarcophagidae ¹⁶	394	330+	54%	46%
Scathophagidae ⁸	4[5]	0	100%	0%
Scatopsidae ⁴⁷	43[45]	400+	10%	90%
Scenopinidae ¹¹	69[68]	46+	60%	40%
Sciaridae ²⁰	71	2,000+	3%	97%
Sciomyzidae ³³	64	35+	65%	35%
Sepsidae ¹⁴	131	131+	50%	50%
Simuliidae ²¹	210	60+	78%	22%
Sphaeroceridae ⁷	321	1,000–2,000+	24%	76–86%
Stratiomyidae ¹⁷	388	100–150+	80%	20–28%
Syrphidae ⁴⁰	593[562]	241+	80%	30%
Tabanidae ³⁹	815	50+	94%	6%
Tachinidae ⁶	1,013	1,000+	51%	49%
Tachiniscidae ⁶	2	0	100%	0%

Estimations of undescribed species				
Family	Known species	Estimated No. undescribed species	Percentage of species known	Percentage of fauna awaiting description
Tanyderidae ⁴⁵	1	0	100%	0%
Tephritidae ²²	947	100–200+	90%	10–17%
Tethinidae ⁴¹	23	41+	36%	64%
Thaumaleidae ⁴⁵	2	2+	50%	50%
Therevidae ¹⁰	147[160]	50+	76%	24%
Tipulidae ²⁷	374	200+	65%	35%
Ulidiidae ⁶	24	5+	83%	17%
Vermileonidae ⁴⁵	29	12	71%	29%
Xenasteiidae ⁶	2	0	100%	0%
Xylomyidae ⁴⁵	6	0	100%	0%

Sources of information:

- ¹ Marc De Meyer & Mihály Földvári (pers. comms.)
- ² Peter Chandler (pers. comm.)
- ³ Torsten Dikow (pers. comm.)
- ⁴ John Deeming (pers. comm.)
- ⁵ Rudy Meiswinkel (pers. comm.)
- ⁶ David Barraclough (pers. comm.)
- ⁷ Jindrich Roháček (pers. comm.)
- ⁸ Adrian Pont (pers. comm.)
- ⁹ Martin Ebejer (pers. comm.)
- ¹⁰ Martin Hauser (pers. comm.)
- ¹¹ Shaun Winterton (pers. comm.)
- ¹² Andrzej Woźnica (pers. comm.)
- ¹³ John Swann (pers. comm.)
- ¹⁴ Andrey Ozerov (pers. comm.)
- ¹⁵ David Greathead (pers. comm.)
- ¹⁶ Thomas Pape (pers. comm.)
- ¹⁷ Norm Woodley (pers. comm.)
- ¹⁸ Brad Sinclair (pers. comm.)
- ¹⁹ Neal Evenhuis (pers. comm.)
- ²⁰ Pekka Vilkkamaa (pers. comm.)
- ²¹ Douglas Craig (pers. comm.)
- ²² David Hancock (pers. comm.)
- ²³ Jason Londt (pers. comm.)
- ²⁴ Amnon Freidberg (pers. comm.)
- ²⁵ David Barraclough & Amnon Freidberg (pers. comms.)
- ²⁶ Netta Dorchin & Keith Harris (pers. comms.)
- ²⁷ Chen Young (pers. comm.)
- ²⁸ Michael von Tschirnhaus (pers. comm.)
- ²⁹ Iain MacGowan (pers. comm.)
- ³⁰ Valery Korneyev (pers. comm.)
- ³¹ Henry Disney (pers. comm.)
- ³² Stephen Gaimari & Ray Miller (pers. comm.)
- ³³ Lloyd Knutson (pers. comm.)
- ³⁴ Mikhail Mostovski (pers. comm.)
- ³⁵ Ashley Kirk-Spriggs (pers. obs.)
- ³⁶ Igor Grichanov (pers. comm.)
- ³⁷ Hiromu Kurahashi (pers. comm.)
- ³⁸ Maureen Coetzee (pers. comm.)
- ³⁹ John Chainey (pers. comm.)
- ⁴⁰ Andrew Whittington (pers. comm.)
- ⁴¹ Wayne Mathis (pers. comm.)
- ⁴² Ray Miller (pers. comm.)
- ⁴³ Pete Cranston (pers. comm.)
- ⁴⁴ Michael Ackland (pers. comm.)
- ⁴⁵ Brian Stuckenberg (pers. obs.)
- ⁴⁶ Heikki Hippa (pers. comm.)
- ⁴⁷ Jean-Paul Haenni (pers. comm.)

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