Chapter 1
Taxonomy and Systematics of African Fruit Flies (Diptera: Tephritidae)

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Abstract Work on the taxonomy of African fruit flies began with basic descriptions and alpha taxonomy to understand dipteran and/or insect diversity, and they were based upon material collected from isolated locations in Africa. Only later were more detailed taxonomic studies and descriptions initiated largely due to recognition of the economic impact some fruit fly pests had on horticultural crops. Taxonomic research was largely driven by the work of two entomologists at that time: Mario Bezzi (Italy) and Kenneth Munro (South Africa). In the latter part of the twentieth century and the first decades of this century, more comprehensive publications became available dealing both with generic revisions and higher classification. Again the greatest focus was on those groups comprising fruit flies of economic significance, including studies dealing with cryptic species. Considerable progress was also made with descriptions of other tephritid groups, although they received far less attention and it is expected that numerous new species await description. These taxonomic studies form the basis of studies on the phylogenetic relationships amongst the taxa, using both morphological and molecular data. Increasingly, greater attention is being given to putting this information into a larger evolutionary framework, in particular with respect to host plant associations.

Keywords Afrotropical • Species • Phylogeny • Descriptions

1 Introduction

Correctly naming an organism (by which we mean providing a scientific name and making it available as per the requirements set out by international codes) is a key prerequisite for any subsequent biological research or management activity involving that organism. Providing correct names and descriptions is, however, not a straightforward matter. Scientific species names should represent biological entities

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S. Ekesi et al. (eds.), *Fruit Fly Research and Development in Africa - Towards a Sustainable Management Strategy to Improve Horticulture*,
DOI 10.1007/978-3-319-43226-7_1

with unique characteristics reflecting their behaviour, ecological requirements and interactions with the environment, that allow them to be clearly differentiated from other entities. What exactly constitutes and defines this differentiation is a point of discussion and has led to numerous species concepts (de Queiroz 2007; Wilkins 2009; Hart 2010; Richards 2010; Hausdorf 2011). Nevertheless, for any practical application, there needs to be agreement on (a) the name that unambiguously identifies a particular species so that all can refer to the same species using the same name, and (b) what organisms and populations can be considered to be included under that name. While the first aspect is governed by clear rules, set out by international commissions on nomenclature (in the case of animals, the International Commission on Zoological Nomenclature; ICZN 1999, 2012) and largely followed by the majority of users, the second point leads to more controversy. Opinions and arguments for or against including particular organisms or populations under the same scientific name, or applying different names, is often a point of lengthy discussion. While these may be the biological equivalents of 'councils on the gender of the angels' for the majority of species, it does have far reaching implications when it concerns pest species. An obvious example of this, with relevance to African fruit flies, is the identity of the invasive species *Bactrocera invadens* Drew, Tsuruta and White, and whether this is identical to the oriental fruit fly, *Bactrocera dorsalis* (Hendel) or actually represents a different species (Drew and Romig 2013; Schutze et al. 2014a). Next to naming and describing species, understanding the relationships between species is the next most important consideration in research. Closely related species may share a number of characteristics such as similar host range, demographic characteristics, symbiotic relationships, adjacent or overlapping geographical distribution etc. Systematic and phylogenetic studies, unraveling the interrelationships between species within a larger group (genus, tribe, subfamily, family) provide a stable classification for known species but also a solid framework for further studies. This paper will present past and current developments both in the field of alpha taxonomy and systematic and phylogenetic research on African tephritid fruit flies. In particular, we will highlight the advent and implications of using novel techniques such as genetic markers, and the added advantages of integrated approaches.

2 Historical Account

2.1 *Early Taxonomy*

The earliest taxonomic descriptions of African fruit flies date back to the late eighteenth and early nineteenth centuries. These descriptions were mainly based upon material collected at trading posts along the African coastline and include species described by the German entomologist, Wiedemann, from specimens collected at the Cape of Good Hope Peninsula in South Africa and the Danish settlement of

Christiansborg in current-day Ghana (Wiedemann 1818, 1819, 1824, 1830; see Pont 1995 for review). Others were collected during organized expeditions. For example, during the German African Society Expedition to the southern Congo Basin, the naturalist, von Homeyer, collected fruit flies which were later described by Karsch, the curator of the Zoological Museum in Berlin (Karsch 1887; reviewed by Evenhuis 1997). In addition, species of Afrotropical origin, but also occurring in the Mediterranean Region, were described at that time (such as the earliest known species, the olive fruit fly, *Bactrocera oleae*, originally described by Rossi from Tuscany, Italy [Rossi 1790]). Throughout much of the nineteenth century, specimens housed in private or institutional natural history collections were the main source material for descriptions of African fruit flies, often as part of larger studies of insect diversity. These include Walker's endeavors to describe the entomological holdings of the British Museum (reviewed by Evenhuis 1997) and the studies of Loew on African Diptera (Loew 1852, 1861, 1862).

Only at the start of the twentieth century did more focused research begin to describe the tephritid fruit flies of Africa. There were two main reasons for this. Firstly, the economic impact of some fruit fly species on horticultural crops was recognized. Secondly, observations of the first invasive species in other continents triggered a search for control measures including potential classical biological control agents in the pest's country of origin. For example, Lounsbury, a government entomologist in the Cape Colony (part of current-day South Africa) and the initiator of biological control measures against invasive pests in Africa, was one of the first entomologists to collect fruit flies and have them identified by specialists such as Coquillett from the United States National Museum (Coquillett 1901). The Hawaii Board of Commissioners of Agriculture and Forestry became interested in the use of natural enemies to limit the economic damage caused by the Mediterranean fruit fly (medfly), *Ceratitis capitata* (Wiedemann), a species of African origin and invasive in Hawaii. In 1912, they engaged the services of an Italian entomologist, Silvestri, to visit Africa in search of natural enemies of *C. capitata* in its natural range. Silvestri spent almost a full year exploring several West African countries (Silvestri 1913). In addition to the natural enemies he reared, he also collected a number of fruit fly species amongst which some were new to science (Bezzi 1912, 1913; Silvestri 1913). This was the first in a series of expeditions in search of natural enemies during the twentieth century (Bianchi 1937; Bianchi and Krauss 1937; Van Zwaluwenburg 1937; Clausen et al. 1965) that resulted in large collections of known and new species with the associated biological data on their host plants. Similar local collections of flies emerging from infested fruits supplemented these data. The most noteworthy of these was the programme established by van Someren at the then Coryndon Museum (now National Museums of Kenya) in Nairobi, Kenya. In addition to these programmes with applied objectives, there were also a number of field expeditions organized by different institutions to document the rich biodiversity found in particular African ecosystems. Two taxonomists specializing in Tephritidae, Bezzi (Italy) and Munro (South Africa), examined much of this material. Together their research spanned a period of almost eighty years (1908–1984) and they described approximately 68 % of all known African tephritid species

(Cogan and Munro 1980; Norrbom et al. 1999). In addition to alpha taxonomy Munro also embarked on larger review papers on the transition genera between Tephritinae and Trypetinae (e.g. Munro 1947), and a series of papers with biological notes on host plant range, larval feeding behaviour, infestation rates and phenology (Munro 1925, 1926, 1929).

2.2 Comprehensive Revisions

From the 1980s onwards, more comprehensive publications became available that focused on taxonomic revisions of particular higher taxa at the genus (Freidberg 1985, 1991, 1999; Freidberg and Hancock 1989; Freidberg and Merz 2006) or higher level (Freidberg and Kaplan 1992, 1993; Munro 1984; Hancock 1984, 1985, 1986, 1990, 1999, 2000, 2005, 2012; Hancock et al. 2003). Most recently the focus has shifted to providing thorough revisions of the African representatives of economically important genera, in particular the frugivorous groups within the tribe Dacini that attack the fresh fruits of both commercial and wild host plants (De Meyer 1996, 1998, 2000, 2001; De Meyer and Copeland 2001, 2005, 2009; De Meyer and Freidberg 2005, 2006; White 2006; White and Goodger 2009; White et al. 2003) and closely related genera (De Meyer 2006, 2009; De Meyer and Freidberg 2012). Unrelated frugivorous groups, such as *Munromyia* Bezzi (Adramini), have also been revised recently (Copeland 2009; Copeland et al. 2004). Some of these revisions coincided with local, national or regional surveys (Copeland et al. 2005; De Meyer et al. 2012, 2013; Hancock 2003; Hancock et al. 2003) or biological studies (Copeland et al. 2002, 2006, 2009) that provided new material and data. These studies aimed to incorporate all available specimens to achieve, as much as possible, a global view on intraspecific variability, and resulted in extensive descriptions and redescriptions. In addition, these studies provided a summary of all known information regarding occurrence, distribution and reliability of host plant data.

2.3 Current Status

The current taxonomy of African fruit flies has advanced significantly. As a result of the taxonomic studies described in Sect. 2.2, the majority of genera that contain frugivorous species, which comprises approximately two-fifths of all the fruit fly species recorded from the Afrotropical region, have been revised over the last 20 years. This has provided, and still does, a sound basis for all subsequent research in the fields of ecology and biogeography, but also in applied research on fruit fly control. Most of the information from these revisions is also publicly available through dedicated websites (e.g. http://projects.bebif.be/fruitfly/index.html) and also more general websites (e.g. Global Biodiversity Information Facility [www.gbif.org];

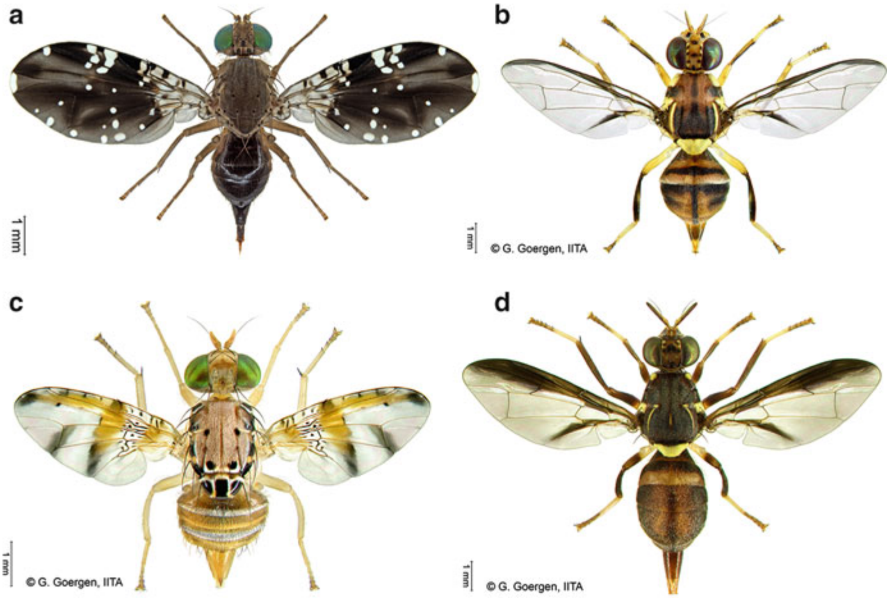

Fig. 1.1 Habitus images of African fruit flies (**a**) *Pseudafreutreta diaphasis* (Bigot); (**b**) *Bactrocera dorsalis* (Hendel); (**c**) *Ceratitis cosyra* (Walker); (**d**) *Dacus bivittatus* (Bigot) (All images copyright and courtesy of Georg Goergen)

Encyclopedia of Life [www.eol.org]). It has also enabled the development of modern multi-entry and electronic identification tools (Virgilio 2016; Virgilio et al. 2014), providing easy-to-use tools with different filters and levels with which to identify specimens, and hyperlinks to associated data.

However, non-frugivorous groups have received far less attention. Most of the tephritids belonging to the subfamily Tephritinae infest flower heads and attack particular plant families: Asteraceae, Acanthaceae, Lamiaceae and Verbenaceae (Freidberg and Han 2012) (Fig. 1.1a). Others, are saprophagous, leaf or stem miners, or gall formers (Norrbom et al. 1999). In Africa, approximately 600 species are known but numerous undescribed species are thought to exist. Besides some larger genera, like *Campiglossa* Rondani and *Trupanea* Schrank, the majority are grouped under about 130 different genera of which half only contain one or two described species. This makes identification, even to genus level, difficult. Some information is available but it is dispersed over numerous articles published over the last 30 years. Other non-frugiverous species are found in the subfamily Trypetinae for which Hancock (1986) provided a key to the Afrotropical genera (excluding the Dacini). There have subsequently been keys published for Afrotropical genera in several tribes: Trypetini (Hancock 2005); Schistopterini (Freidberg 2002); Tephritini (Merz 1999 [*Tephritis* Latreille group]; Merz and Dawah 2005 [*Campiglossa* group]). Other than these there are no comprehensive keys available for the majority of the other genera. However, a genus-level key is currently under development within the framework of the Manual of Afrotropical Diptera (http://afrotropicalmanual.org/), which will include all genera occurring in Africa. This is expected to drastically improve the identification process.

Despite the lack of a comprehensive key to genus level, keys to species level for a number of particular genera have been revised over the past decades. This includes genera within the subtribe Gastrozonina, a group that breed in bamboo but are closely related to the main frugivorous tephritids. They were revised by Hancock (1999) with keys to genus and species level. Within the Trypetinae, species-level keys are available for the genera *Conradtina* Enderlein, *Celidodacus* Hendel and *Coelotrypes* Bezzi, all within the tribe Adramini (Hancock 1986). For the Tephritinae, recent keys have been established for species in the genera: *Cryptophorellia* Freidberg and Hancock (Freidberg and Hancock 1989); *Tanaica* Munro (Merz and Dawah 2005); *Deroparia* Munro, *Euryphalara* Munro, *Xenodorella* Munro (Hancock 2000); *Oedaspis* Loew (Freidberg and Kaplan 1992); *Elgonina* Munro, *Gymnosagena* Munro, *Marriottella* Munro (Freidberg and Merz 2006); *Afreutreta* Bezzi, *Cosmetothrix* Munro and *Tarchonanthea* Freidberg and Kaplan (Freidberg and Kaplan 1993). Also within the Tephritinae the genus *Dicheniotes* Munro (tribe Tephrellini) has been revised and a key for all species provided by Hancock (2012), while the genus *Manicomyia* Hancock (also tribe Tephrellini) was revised by Freidberg and Han (2012). Several other groups within the Tephritinae are also under evaluation at this moment.

3 Cryptic Species and Population Genetics

Although one of the simplest definitions of a species is quoted as “a species is what a competent taxonomist says it is” (Regan (1926) as quoted in Froese (1999)), the truth is usually more complicated. As indicated in the introduction, establishing what exactly represents a species, is a complicated matter and myriad theories exist. For this reason, there are currently more than 20 different species concepts (Mayden 1997). Without going into the details of the philosophical, evolutionary and phylogenetic aspects of the debate (see Kunz 2012 for a recent review with regard to species and the principles of taxonomic classification), taxonomists traditionally work with the concept of morphological species, i.e. a number of individuals or populations that are similar in morphological (and/or anatomical) appearance and that can be separated from another species by discrete but consistent differences in morphology. However, this approach has been shown to have its limitations, especially in the case of cryptic species where closely related species are very similar morphologically, but demonstrate distinctly different biological traits (in particular pre- and postzygotic incompatibility). With species of economic significance this can have important consequences. If a morphologically assigned pest species actually consists of a complex of biologically distinct species that vary in host range, geographic spread, developmental physiology and ecology, then this will have very significant impacts on any proposed management plan. With regard to African fruit fly pests, two groups of economic importance were recently the subject of a coordinated research project to elucidate this issue. The project was initiated by the joint FAO/IAEA Insect Pest Control Section (De Meyer et al. 2015a) and entitled 'resolution of cryptic species complexes of tephritid pests to overcome constraints to SIT (sterile insect technology) applications and international trade'. Firstly, the specific status of *B. invadens* (Fig. 1.1b) was studied in relation to closely related species in the *B. dorsalis* species complex as defined by Drew and Hancock (1994). Secondly, within the genus *Ceratitis* MacLeay the so-called FAR complex (Barr and McPheron 2006; Barr and Wiegmann 2009; Barr et al. 2006), comprising *Ceratitis fasciventris* (Bezzi), *Ceratitis anonae* Graham and *Ceratitis rosa* Karsch (the Natal fruit fly), was studied in detail. In both cases an integrative approach was applied, using different diagnostic approaches to independently investigate whether consistent differences or similarities could be detected. These different approaches included adult and larval morphology, morphometrics, chemical ecology (pheromones and cuticular hydrocarbons), cytology, molecular markers, developmental physiology and pre- and postzygotic compatibility. A review was presented by Schutze et al. (2014a) for *B. invadens*, concluding that this should be considered as a junior synonym of *B. dorsalis*. Several other species of the *dorsalis* complex were also placed in synonymy (Schutze et al. 2014b). In contrast, the study on the FAR complex indicated that these three taxa should be considered as separate species (De Meyer et al. 2015b). For *C. rosa*, there is a strong indication that it actually consists of two different species that are morphologically very similar and can occur in sympatry, but that have different ecological requirements and biological traits that separate them (De Meyer et al. 2015b; Virgilio et al. 2013).

In addition to these two cryptic species complexes, it is possible that there are other cryptic species complexes present in Africa. Recent research on molecular diversity (Barr et al. 2012) and population genetics (Virgilio et al. 2015a) of the mango fruit fly, *Ceratitis cosyra* (Walker) (Fig. 1.1c) indicate that there is high intraspecific variability and a genetic structuring within this species. Morphological differences had been described previously (De Meyer 1998) but do not seem to be directly correlated with the genetic differences observed. Other species, such as the melon fly, *Zeugodacus cucurbitae* (Coquillett), show some differences in biology but are very homogenous with regard to morphology and genetic markers (Virgilio et al. 2010; De Meyer et al. 2015c). The same seems to be the case for other cucurbit feeders such as *Dacus bivittatus* (Bigot) (Fig. 1.1d) and *Dacus punctatifrons* (Karsch). However, the number of population genetic studies is limited and there is a need for more thorough revision with better geographic coverage.

4 Higher Phylogeny

Korneyev (1999a) provided a rather robust ground plan for the phylogenetic relationships between Tephritidae and other families within the superfamily Tephritoidea. Evolutionary developments in larval feeding strategies (from saprophagous life styles in the more primitive tephritoids to specialized phytophagous feeding habits), in conjunction with the key innovation of the tephritid ovipositor and, possibly, oviposition-meditated bacterial transfer (to better exploit food resources; Behar et al. 2008) have played a major role in tephritoid phylogeny and radiation in the Tephritidae (Diaz-Fleischer et al. 1999). Although a phylogenomic study combining morphological and molecular characteristics largely confirmed Tephritoidea as a superfamily (Wiegmann et al. 2011), the interrelationships amongst the families did partially deviate from the phylogeny proposed by Korneyev (1999a).

Within the family Tephritidae, the phylogenetic relationships amongst the major higher taxa are becoming clearer due to several studies investigating morphological (Korneyev 1999b) and genetic (Han and McPheron 1999; Han et al. 2006; Han and Ro 2009; Krosch et al. 2012; Virgilio et al. 2015b) data. Nevertheless, the classification is still not completely stable. The assignment of genera to higher taxa is in a state of flux and several genera remain unplaced in the currently accepted classification (Norrbom et al. 1999). Recently, joint phylogenetic studies of fruit flies and other organisms, such as microbionts, have been conducted which may provide valuable insights regarding the relationships between these higher taxa (Mazzon et al. 2008, 2010; Morrow et al. 2015).

Only a few publications have dealt specifically with phylogenetic relationships within African representatives of particular genera. With respect to frugivorous species the genus *Ceratitis* and the species groups within this genus have been studied (Barr and McPheron 2006; Barr and Wiegmann 2009; Barr et al. 2006; De Meyer 2005; Erbout et al. 2011), as have the interrelationships within the genus *Dacus* Fabricius (Hancock and Drew 2006; Virgilio et al. 2009; White 2006). In both cases, there is to a greater or lesser extent an incongruence between morphological and molecular data. Han and Ro (2005) already demonstrated that it is very difficult to identify phylogenetic signals in groups like these because of the limited number of informative characters. In genera with a relatively speciose fauna and morphological uniformity, such as *Dacus*, the homoplasy of character states is extremely high, resulting in unstable subgeneric divisions (White 2006). Only for genera with a restricted number of species, can a more stable phylogeny be produced (e.g. De Meyer and Freidberg 2005).

5 Taxonomy and Host Plant Relationships

Being phytophagous leads to close relationships between fruit flies and their host plants. The fact that some fruit flies (or Tephritoidea in general) have made the transition to feed upon living plant tissue in their larval stage (cf. the saprophagous lifestyle of related groups) has led to novel resource use and, at least in the case of Tephritidae, to evolutionary diversification and radiation (Diaz-Fleischer et al. 1999). Examples range from extreme specialization to unprecedented polyphagy. As phylogenetic reconstructions reflect an evolutionary process of species diversification throughout time, it is expected that host plant relationships will also be reflected in the phylogeny. With respect to the frugivorous tephritids of Africa, some genera have a stenophagous or olighophagous host range at the genus level; the best known examples are *Perilampsis* Bezzi, *Capparimyia* Bezzi and *Neoceratitis* Hendel. The genus *Perilampsis* comprises 17 species restricted to the Afrotropical region. Host plants are known for eight species and they all come from the Loranthaceae (De Meyer 2009); larval development takes place in the seeds, rather than the pulp of the berries (De Meyer 2009). Strangely enough the same niche (seed feeders in berries of Loranthaceae) is occupied by another ceratitidine genus, *Ceratitella* Malloch, in Asia and Australia (Hardy 1967; Hancock et al. 2000) but the actual phylogenetic affinity between these genera remains to be studied. Representatives of the genus *Capparimyia*, a predominantly Afrotropical genus (with only one representative from the Mediterranean region and the Middle East), feed on flower buds and fruits of Capparidaceae, including commercially grown capers (De Meyer and Freidberg 2005). *Neoceratitis* is also a predominantly Afrotropical genus (with one species from Asia) for which all confirmed host records belong to the plant genus *Lycium* L. (Solanaceae). Only the tomato fruit fly, *Neoceratitis cyanescens* (Bezzi), a species occurring in Madagascar and other islands in the Western Indian Ocean, has been reported from other Solanaceae (De Meyer and Freidberg 2012).

Other genera with larger numbers of species are not necessarily restricted to a single plant genus or family. However, groups within the fruit fly genera can be associated with particular hosts. For example, White et al. (2003) indicated that, within the genus *Trirhithrum* Bezzi, some species with morphological similarities were associated with Rubiaceae while other species with different morphological similarities were associated with Araceae; within this genus other species were known to have a large diversity of host plants. The genus *Dacus* also shows particular associations between species groups and hosts. Munro, in his biological notes on Tephritidae, observed two groups within the genus *Dacus*, i.e. those species infesting Cucurbitaceae and those species infesting Asclepiadaceae (now part of Apocynaceae) (Munro 1925). White (2006) subsequently summarized all host records available, demonstrating the presence of three biological groups, i.e. species feeding on Cucurbitaceae, Apocynaceae and Passifloraceae respectively. However, subgeneric classifications based solely on morphological characters do not seem to reflect the host plant associations of the three biological groups. Virgilio et al. (2009) provided a molecular phylogeny for a subset of species which more clearly reflected the host plant relationship. This study supports the argument for developing an integrated approach in systematic research, especially for groups that are characterized by high homoplasy in character states and high morphological similarity with few informative characters.

Other tephritid genera show a more complex pattern of host plant associations. The Afrotropical genus *Ceratitis* comprises about 100 species, amongst which are some of the most destructive pest species in Africa (White and Elson-Harris 1994). The genus includes representatives of both specialist feeders and generalists. In order to categorize the niche breadth of host plant utilization, we can differentiate monophagy (attacking a single species), stenophagy (attacking several species belonging to the same genus), oligophagy (attacking species of different genera belonging to the same family) and polyphagy (attacking representatives of several, unrelated, families) (White et al. 1999). All these different feeding types can be found in the genus *Ceratitis* (De Meyer 2005). Phylogenetic analyses indicate that stenophagous species form monophyletic clusters based on the host plant genus that they attack, e.g. *Solanum*, *Strychnos* or *Podocarpus* (De Meyer 2005; Erbout et al. 2011). The exact mechanism driving this monophyletic clustering is not clear. However, the host plant genera that support monophyletic clusters of stenophagous fruit fly species are generally not infested by generalist feeders. The same applies to some of the monophagous species like *C. flexuosa* (Walker) (De Meyer et al. 2002). In addition, these hosts are known for having secondary metabolites that could influence the development and fitness of fruit fly larvae (Erbout et al. 2009). It is possible that the phylogenetic pattern that is being observed reflects an evolutionary process whereby new pathways were selected to allow larvae to survive in hostile or toxic environments, followed by a radiation process resulting in a number of closely related species exploiting the same genus of host plant.

Acknowledgements Some of the research presented was funded through successive grants from the Belgian Science Policy (BELSPO Action 1 projects) and with support from the Joint Experimental Molecular Unity (JEMU). I would also like to thank Dr Georg Goergen (International Institute of Tropical Agriculture, Cotonou, Benin) for allowing me to include some of his habitus images of fruit flies.

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