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Drosophilids (Diptera) from Mayotte island: an annotated list of species collected in 2013 and comments on the colonisation of Indian Ocean Islands

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Summary. The Indian Ocean Islands are a most interesting region for evolutionary studies of terrestrial organisms and, among insects, the Drosophilidae family occupies a privileged position. The Comoros archipelago was, up to now, the least explored place among all the islands. We present here the results of a collection on one of the four main islands, Mayotte. From 4500 collected flies, 25 species were distinguished. The biology, ecology and biogeography of each species are discussed. Considering the extant known species from all islands, five evolutionary scenarios are proposed, ranging from the invasive, cosmopolitan, man-transported species to endemic species restricted to a single island. Some species raise a puzzling problem: despite having a very narrow and specialised ecological niche, they are broadly distributed on most islands and also on the African mainland.

Résumé. Drosophilides (Diptera) de l'île de Mayotte : liste commentée des espèces collectées en 2013 et notes sur la colonisation des îles de l'Océan Indien. Les îles de l'océan indien sont extrêmement intéressantes pour les études de l'évolution des organismes terrestres, et chez les insectes, les Drosophiles ont reçu une attention particulière. Parmi toutes les îles, l'archipel des Comores était resté jusqu'à maintenant la région la moins bien explorée. Nous présentons ici les résultats d'une prospection de l'une de quatre principales îles, Mayotte. Parmi les 4500 Drosophiles collectées, 25 espèces ont été répertoriées. La biologie, l'écologie et la biogéographie de chacune de ces espèces sont discutées. Considérant l'état actuel de nos connaissances sur l'ensemble des îles, 5 scénario évolutifs sont proposés, allant des espèces cosmopolites invasives transportées par l'homme, jusqu'aux endémiques limitées à une seule île. Certaines espèces posent un problème particulier : en dépit d'une niche écologique très étroite et spécialisée, elles ont atteint une distribution géographique très large couvrant la plupart des îles et le continent Africain.

Keywords: Drosophila; biogeography; Afrotropical region; migration; invasive species; specialisation

Indian ocean islands have been known for a long time as a very interesting place for the study of speciation (Tsacas et al. 1981; Lachaise et al. 1996; Grimaldi et al. 2000; Cariou et al. 2009; Yassin & David 2010a; Yassin et al. 2012). These islands include the very large island of Madagascar, part of Africa that separated from the mainland about 80–90 million years ago (Vences et al. 2009). Several much smaller islands exist near Madagascar. The Seychelles archipelago has granitic islands and is also continental. All other islands have a volcanic origin, including Mauritius, Rodrigues, Réunion, the Comoros archipelago and the very small Scattered Islands. A comprehensive survey (Lachaise et al. 1996) indicated a total of 128 species of Drosophilidae, a family used extensively in evolutionary studies, in these islands. The least investigated place was Comoros, with only 31 known species. Moreover, Lachaise et al. (1996), following Tsacas et al. (1981), considered the Comoros archipelago as a single entity, and did not distinguish the four major islands, Grande Comore, Mohélie, Anjouan and Mayotte. The aim of this paper is to provide more specific information on the drosophilid fauna of Mayotte. An expedition to Mayotte was sponsored by the French CNRS and took place in January 2013. We present here the list of the 25 collected species with their abundance. We also present information on the biology and biogeography of each species and discuss the colonisation of these islands, distinguishing various evolutionary scenarios.

Material and methods

Three classical methods were implemented: attractive banana traps, sweeping with a net, and aspirating flies from an identified resource. Traps were made of plastic bottles with a lateral opening through which a piece of fermenting banana could be introduced (no yeast added). These traps were hung in shaded places and then visited regularly. Trapped flies were collected with an

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aspirator, kept alive in a vial and brought to our field laboratory for identification after anaesthesia and eventual establishment of cultures. The net technique is more general but sometimes less efficient than trapping. Sweeping over fallen fruits basically provided the same species as the traps. Sweeping in humid places without any obvious resource is more interesting since it provides unusual and rare species. Finally, direct aspiration was also implemented from some resources such as flowers or fungi on wood logs.

Results

Species abundance in different habitats

We explored numerous sites mostly in the northern part of the island. For the sake of simplicity, these habitats may be distributed in four groups as follows: (1) urban areas at low altitude; (2) wooden areas of secondary forest also at low altitude and not far from the ocean; (3) the Gouverneur track, a small road in forest with an elevation of 280–400 m asl; (4) the Mount Combani road, mostly in secondary forest, altitude around 200–400 m. The data are given in Table 1 in decreasing order of species abundance, for a total of 4502 collected flies. The table comprises 22 entries, but in a few cases species were not identified in the field but were later identified in laboratory cultures, so that the real number of collected species is 25.

Comments on species, according to the recent classification proposed by Yassin (2013)

Subfamily Drosophilinae

Tribe Colocasiomyini

Genus *Scaptodrosophila*

Species group *aterrima*

Scaptodrosophila caliginosa (Lamb 1914:341)

Although found only on flowers in the Afrotropical region, this species is widespread and known from almost all other islands, but it was not found in Comoros (Lachaise et al. 1996). Its broad distribution is puzzling because humans are unlikely to transport such a specialised species. In Mayotte the species was collected in the large flowers of *Hibiscus tiliaceus* along the sea shore, an ecological niche also found in the other islands.

Species group *brunnea*

Scaptodrosophila sp. 1

This small species is remarkable in the white tip of its scutellum. We collected already a similar species from Madagascar and Scattered Islands (Yassin et al. 2012). They are probably the same, new species.

Table 1. Abundance and distribution of the species collected on Mayotte. Four kinds of habitats are distinguished.

Species	rank	Total	%	Urban area	Forest, sea level	Gouverneur track	Mount Combani
S. *latifascieformis*	1	1337	29.70	175	237	620	305
D. nasuta	2	970	21.55	80	85	425	380
D. malerk otliana	3	591	13.13	40	351	95	105
D. yakuba	4	577	12.82		577		
Z. tuberculatus complex	5	569	12.64		154	400	15
Z. cf indianus	6	220	4.89	14	9	62	135
S. caliginosa	7	110	2.44		110		
M. fracticosta	8	32	0.71			32	
D. montium gr.	9	25	0.56	2		8	15
D. cf jucunda	10	14	0.31			14	
Microdrosophila sexsetosa	11	13	0.29	13			
D. simlulans	12	10	0.22	2	2	3	3
D. suma	12	10	0.22		10		
D. ananassae	14	5	0.11	4			1
D. melanogaster	15	4	0.09		1	2	1
H. sp	15	4	0.09			4	
Chymomyza sp	17	3	0.07			3	
S. gr. Eundo	17	3	0.07	2			1
M. sp	19	2	0.04			2	
S. cf bangi	20	1	0.02	1			
Z. ghesquieri	20	1	0.02		1		
D. sp	20	1	0.02		1		
Total	**22**	**4502**	**100 %**	**333**	**1538**	**1670**	**961**

C= Chymomyza; D=Drosophila; H=Hirtodrosophila; M=Mycodrosophila; S=Scaptodrosophila; Z=Zaprionus Location of the sampled sites: Urban area (Kangani): -12.732985, 45.186520; Forest, sea level: -12.777666, 45.104947; Gouverneur track: starting at -12.777138S, 45.215525E; Mount Combani: -12.786602S, 45.169357E.

Species group *latifasciaeformis*

***Scaptodrosophila latifasciaeformis* (Duda 1940:22)**

This small generalist species was very abundant everywhere. It is now a widespread cosmopolitan and its geographic origin is not clear, but it might be the Afrotropical region.

Species group *saba*

***Scaptodrosophila bangi* (Burla 1954:143)**

The species is abundant on the mainland and was also indicated by Lachaise et al. (1996) from Comoros, Madagascar and Réunion and by Yassin et al. (2012) from Glorioso Island.

Tribe Drosophilini

Genus *Drosophila*

***Drosophila* sp. 2.**

The only individual is a female of greyish colour in fairly poor condition. Molecular analyses might eventually help its identification.

Species group *spinipes*

***Drosophila suma* Burla 1954:200**

This black species breeds in flowers and is widespread in most islands and also on the mainland (David et al. 2011). It is remarkable in its unique feeding behaviour: the foretarsus of both sexes bears strong spines which are used for scratching the surface of the flowers; then the oozing liquid is ingested as a food. This species was already collected in flowers of *Ipomea* and *Crinum* (David et al. 2011). In Mayotte we found it on a third plant, the flowers of *Cucurbita* species, i.e. very large flowers with a yellow colour. These observations clearly show that the flower phenotype, size and colour are not important in the identification and use of a flower as a host. The smell may be more important. Another interesting characteristic of this species is its geographic distribution. Many studies show that species are endemic to one or two islands, revealing that colonisation of different places separated by large oceanic distances is not easy. *D. suma* is never very abundant and is not transported by modern man, but nonetheless is very broadly distributed in the Afrotropical region.

Subgenus *Drosophila*

Species group *immigrans*

***Drosophila nasuta* Lamb 1914:346**

This invasive species was also found in all habitats. It is native to the Oriental region, possibly India, but it was described in 1910 from the Seychelles (Lamb 1914) where it had been introduced by modern man. Its presence in all the Indian Ocean islands is a consequence of a human introduction (Bachtrog 2006).

Subgenus *Siphlodora*

***Drosophila jucunda* Lamb 1914:339 comb. nov.**

This species was described from the Seychelles and was considered as a strict endemic of this archipelago. We collected 14 individuals on fungi. Their phenotype is similar to that of *D. jucunda*, for which a large collection is available in the Paris museum. The identity requires further studies and a precise comparison. The Seychellian series was not collected on fungi, which suggests either that they are distinct species, or that their ecology is different.

Subgenus *Sophophora*

Species group *ananassae*

***Drosophila ananassae* Doleschall 1858:128**

This is another cosmopolitan species, easily transported by man and generally domestic. Surprisingly, we collected only five individuals on Mayotte.

***Drosophila malerkotliana* Parshad & Paika 1964:235**

This is an invasive cosmopolitan species and is widespread in most continents but native to India. It is found in great numbers in Madagascar, Réunion and the Seychelles but is absent from Mauritius (David et al. 1989) where only the close relative, *D parabipectinata*, is found. Such a possible competitive exclusion in nature between two related species is a rare event which deserves further investigation.

Species group *melanogaster*

***Drosophila melanogaster* Meigen 1830:85**

This domestic laboratory species is found all over the world and, native to tropical Africa, has been introduced by man in all continents (David & Capy 1988). We are not aware of any place in the world having suitable climatic conditions in which *D. melanogaster* does not occur. Thus we were very surprised to collect only four individuals of this species in our collection of 4500 individual flies. It appears to be rare in Mayotte. Moreover we expected *D. melanogaster* in domestic habitats at low altitude, but the four specimens were all collected in wild places. This suggests that the *D. melanogaster* population in Mayotte deserves more attention and especially a genetic comparison with African mainland flies.

***Drosophila simulans* Sturtevant 1919:153**

This close relative to *D. melanogaster* is abundant in all Indian Ocean islands. Indeed it was previously collected in

large numbers on Mayotte by Dr C. Montchamp (personal communication; Bastide et al. 2011). During the present expedition, we were surprised to collect only 10 individuals. This suggests that its abundance may shift seasonally.

Drosophila yakuba Burla 1954:161

This was the first described species closely related to *D. melanogaster* but restricted to the Afrotropical region (Burla 1954). Its domestic status also favours its transportation by man, and it was already known from Madagascar. It is however absent from Réunion, Mauritius and the Seychelles, and its discovery in Mayotte was thus a surprise. Moreover, it was very abundant, but only in a restricted habitat, unlike elsewhere on the African mainland and in Madagascar. It might be possible that, in Mayotte, *D. yakuba* occupies a special and restricted ecological niche, accompanied by some genetic specialisation. Obviously this problem deserves further study. Interestingly, about 45% of the flies harboured in their abdomen a dark elongated capsule corresponding to a melanised and killed larva of a parasitoid wasp (see Carton et al. 2005). The responsible parasitoid was further identified as *Leptopilina victoriae*, a widespread tropical species described from the Seychelles.

Species group *montium*

Species complex *bocqueti*

Drosophila chauvacae Tsacas 1984:431

This species was described from Grande Comore and it is also known from Madagascar. We isolated all females collected in Mayotte and finally succeeded in getting four isofemale lines, two of which were identified as *D. chauvacae* thanks to the male genitalia. *D. chauvacae* belongs to the *bocqueti* complex with two species on the African mainland, *D. bocqueti* Tsacas & Lachaise, 1974:204 and *D. burlai* Tsacas & Lachaise, 1974:200. The Mayotte strains were crossed with *D. chauvacae* from Madagascar and they produced hybrids very easily in F1 and F2: there is no doubt they belong to the same species. Crosses were also undertaken with the mainland species. With *D. burlai*, no hybrids could be obtained, while hybrids were quite easily obtained with *D. bocqueti*. But the F1 flies did not produce any progeny, due to a male sterility. We may conclude that *D. chauvacae* is a valid species close to *D. bocqueti*.

Species complex *bakoue*

Drosophila malagassya Tsacas & Rafael

Two strains of *D. malagassya* were available from Madagascar. *D. malagassya* belongs to the *D. bakoue* complex, which is widespread on the mainland. Crosses were undertaken between the two strains from Mayotte and the two strains from Madagascar, but with complex results. In all cases, the crosses were successful and produced a progeny, often in large number. But in about 50% of the crosses, no F2 was observed, even when there were many F1s. The direction of the cross might be important, for example Madagascar females and Mayotte males could produce F2 progeny while, in the reverse case, males F1 were completely sterile. It is clear that such a situation is difficult to explain and that more extensive studies are needed, including molecular analyses, crossing between single pairs and measuring male sterility frequency by dissection.

Genus *Hirtodrosophila*

Hirtodrosophila sp. 1

Four individuals belonging to a single species were collected on fungi but have not yet been identified.

Genus *Microdrosophila*

Subgenus *Oxystyloptera*

Microdosophila sexsetosa (Duda 1939:56)

This species was collected by sweeping on decaying plant material. It has been described from the African mainland but this was the first time it has been collected in the Indian Ocean islands.

Genus *Mycodrosophila*

Mycodrosophila fracticosta (Lamb 1914:329)

This mycophagous species was collected by aspiration from fungi growing on fallen trunks. It was described from the Seychelles and is also found in Madagascar and other islands.

Mycodrosophila sp. 1

We collected two specimens of a very small species, which is not yet identified.

Genus *Zaprionus*

Subgenus *Zaprionus*

Group *inermis*

Zaprionus ghesquierei Collart 1937:8

A small, widespread species that is generally not abundant. It was previously known only from Madagascar (Chassagnard & McEvey 1992).

Subgroup *tuberculatus*

This subgroup of seven species (Yassin & David 2010b) harbours five species in the Indian Ocean islands, and two

of them were expected in Mayotte, namely *Z. tuberculatus* Malloch 1932:11 and *Z. mascariensis* Tsacas & David 1975:379. Laboratory studies identified these two species, but *Z. mascariensis* was rare, while a related species, *Z. sepsoides* Duda 1939:20, was identified as being the dominant species. *Z. sepsoides* is abundant in Madagascar, but not known from the other islands. Its morphology is very close to *Z. mascariensis*, from which it is distinguished mostly by the length of the testis, *Z. mascariensis* having the longest (Tsacas et al. 1977; Yassin 2008). *Z. sepsoides* is probably native to the African mainland and may have been introduced by humans to Mayotte.

Group *vittiger*

Zaprionus indianus Gupta 1970:63

This species is native to the African mainland but a powerful invader that has been introduced in many subtropical and tropical countries (Yassin, Capy, et al. 2008). It was absent from the Seychelles at the beginning of the twentieth century (Lamb 1914) but is now very abundant there as well as in all other islands and even in the very small Scattered Islands (Yassin et al. 2012).

Zaprionus cf. *ornatus* sp. nov.

More interestingly, we also identified another related species in the same complex, a species mentioned by Lachaise et al. (1996) as *Z. megalorchis* Chassagnard & Tsacas 1993:185. Yassin and David (2010b) showed that *Z. megalorchis* from the mainland should be called *Z. ornatus* Séguy 1933:40. As we had laboratory cultures of this species from both Madagascar and the Congo, we could undertake hybridisation assays. The conclusion was without any ambiguity: the strains of Mayotte and Madagascar belong clearly to the same species, but they are different to the mainland strain with which they do not produce any hybrid. This new species remains to be described.

Discussion: the colonisation of the Indian Ocean Islands

The Drosophilid fauna of the Indian Ocean Islands (IOI) is now quite well known. Presumably many more species remain to be discovered and identified, but our extant knowledge reveals the complexity of the colonisation of these islands, their faunal exchanges and endemic speciation. Here we would like to discuss these various aspects and, for that, we identify five different cases, considering either that the same species exists in different islands, or that different but related species exist either between islands or between IOI and the African continent.

(a) Invasive, human-transported species

These often cosmopolitan species are quite numerous. In the *Drosophila melanogaster* subgroup, the two cosmopolitans *D. melanogaster* itself and *D. simulans* are well known and extensively investigated (David et al. 2004; Gibert et al. 2004). A surprising observation is that they seem rare in Mayotte. *D. yakuba*, already known from Madagascar, raises an interesting question: its apparent ecological specialisation suggests a possible ancient colonisation, independent of human activities. Three other species are generally found in great abundance: *D. malerkotliana* and *D. nasuta*, introduced from the oriental region, and *Scaptodrosophila latifasciaeformis*, which might be native to the Afrotropical region. Two species of *Zaprionus*, i.e. *Z. indianus* and *Z. tuberculatus*, are powerful invaders and abundant in all islands. There is however a problem concerning *Z. tuberculatus*, which seems to be absent from Madagascar. *Z. sepsoides*, a relative of *Z. tuberculatus*, is abundant in Madagascar and in Mayotte, and might be a competitor. Finally, worth mentioning is the rarity *of D. kikkawai* in the IOI, which seems to exist only in Madagascar and Réunion (David & Tsacas 1975).

(b) Non-invasive but widespread species in Africa

For the first time, *Microdrosophila sextosa* has been discovered in the IOI. This species seems also to be found in Uganda and the Côte d'Ivoire (Duda 1939; Burla 1954). It is very unlikely that such a rare species was transported and introduced by man. *Drosophila suma* raises exactly the same problem. In IOI it is known from Mauritius, Madagascar, Mayotte but it has also been observed in Congo, Kenya, etc. (David et al. 2011). This flower-breeding species has a very narrow, specialised ecological niche (David et al. 2011). It must have travelled by its own means but we do not understand how. Molecular analyses of various populations might help to solve this ecological mystery. A last case is the flower-breeding *Scaptodrosophila caliginosa*. This species seems to exist in all IOI, but it is also widespread on the African mainland (David & Tsacas 1981).

(c) Endemic species on several islands

The most interesting case is certainly *Z. mascariensis*. This well-defined species is found in Madagascar, Comoros, Mauritius and Reunion but not in Seychelles. It provides a clear evidence of faunistic (natural?) exchanges across islands. *D. chauvacae* and *D. malagassya* are other cases, revealing an exchange between Madagascar and Mayotte. Finally, *Scaptodrosophila caliginosa*, a flower-breeding species, is also found on several islands, but also widespread on African mainland (Tsacas et al. 1988). An exchange between Seychelles and another island is shown here for the first time, concerning *D. jucunda*.

Also worth mentioning is a collection of several individuals of *S. finitima* from Grande Comore by L. Tsacas in 1982 (Paris Museum). Previously this species was known only from the Seychelles.

(d) Related species endemic to a single island

This case corresponds probably to ancient colonisations of the various islands, followed by local speciation. Such is the case with *D. mauritiana* and *D. sechellia*. These species share with *D. simulans* a common ancestor which was probably in Madagascar. Two independent colonisations occurred, one of the Seychelles and the other of Mauritius, several hundred thousand years ago (Legrand et al. 2009, 2011). The other case concerns the *D. ercepeae* complex of the *ananassae* group. Four species are presently known, each endemic in a single island: *D. ercepeae* in Reunion, *D. merina* in Madagascar, *D. vallismaia* in the Seychelles and *D. comoriensis* in Grande Comore. This is a most interesting case of island speciation, although we do not know the geographic origin of the ancestor.

(e) Related species in IOI and African mainland

This case probably mostly corresponds to a common ancestor in Africa and to a propagule arriving in IOI (although the reverse scenario might be possible). A first case is *D. chauvacae*, closely related to *D. bocqueti* and *D. burlai* on the mainland. We have shown that *D. bocqueti* and *D. chauvacae* are sufficiently close to produce hybrids, but the F1 males are fully sterile. In *Zaprionus*, there are pairs of related species: one on the African continent, the other in Madagascar. One case is *Z. inermis–Z. cercus*. The other is *Z. ornatus* (ex. *megalorchis*) on the mainland and its relative (sp. nov.) found both in Madagascar and Mayotte.

Conclusions

Our knowledge of the Drosophilid fauna of IOI reveals the extreme complexity of evolutionary processes in islands and archipelagos. Not surprisingly, IOI flies often share relationships with African flies, although the overall species richness is much less, suggesting that natural colonisations are rare and unpredictable. We may also recall that there have been also some direct connections with Oriental places, for example India. One example is *D. ashburneri* of the *D suzukii* subgroup (Tsacas 1984). Another is the *ercepeae* complex of the *D ananasae* group. Another concerns the subgenus *Zaprionus* (Yassin, Araripe, et al. 2008). This clade, which now comprises more than 50 species (Yassin & David 2010b) originated from a common ancestor about 10 MA which arrived in Madagascar then spread on the African mainland with several comeback events.

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