TERMS OF USE
This pdf is provided by Magnolia Press for private/research use.
Commercial sale or deposition in a public library or website is prohibited.

*Zootaxa* 3741 (2): 295–300
www.mapress.com/zootaxa/

Copyright © 2013 Magnolia Press

ISSN 1175-5326 (print edition)
**ZOOTAXA**
ISSN 1175-5334 (online edition)

**Correspondence**

http://dx.doi.org/10.11646/zootaxa.3741.2.8
http://zoobank.org/urn:lsid:zoobank.org:pub:1CEAA5B0-A327-4902-ABED-5CF5F445A10A

# Why *Drosophila* is not *Drosophila* any more, why it will be worse and what can be done about it?

JAROSLAV FLEGR
*Department of Philosophy and History of Science, Faculty of Science, Charles University, Vinicna 7, Prague, Czech Republic.*
*E-mail: flegr@cesnet.cz*

Formally, *Drosophila melanogaster* Meigen, 1830 is still *Drosophila*; however, it just waits for the first formal revision of the genus. On the basis of a 23 : 4 vote, the International Commission on Zoological Nomenclature rejected the proposal (Kim van der Linde et al., 2007) to make an exception to the rules and to switch the type of the genus *Drosophila* from *D. funebris* to *D. melanogaster* in order to retain for ever the name *Drosophila melanogaster* for the species that represents probably the most important model organism in many branches of biological research. The results of molecular taxonomic studies have shown that the correct name of this species should be *Sophophora melanogaster* rather than *Drosophila melanogaster* (O'Grady, 2010; van der Linde et al., 2010). Taxonomists and phylogeneticists are not concerned too much with this as *Drosophila/Sophophora melanogaster* represents for them just one of many millions of species. The nontaxonomists, i.e., the remaining approximately seven billion inhabitants of our planet, are in a worse situation. When they want to communicate precisely about the fly that eats their fruit, that is a vector of bacterial pathogens in food processing or healthcare facilities, that is a carrier of an interesting gene, or that is considered as the subject of a regulation or a rule to be formulated, they have a problem.

The genera like *Drosophila* are just a tip of the iceberg. In the past decade, i.e. after the advent of multigene or even whole-genome studies, molecular phylogenetics evolved from an amusing toy for molecular biologists searching for a “cheap publication” or for a simple project for a pregraduate or postgraduate student to a potent tool that can provide a reliable picture of the phylogeny of particular groups of organisms. With this advance, more and more biologists have been forced to admit that many traditional taxa, including the genera, were wrongly constructed and needed to be redefined or even abandoned. Molecular analyses often show that a particular clade *B* of a phylogenetic tree comprising species with a typical and distinct morphology is, in fact, an internal sub-clade of another clade, *A*, of the phylogenetic tree consisting of clades comprising, again, species with a typical and distinct morphology, but different from that of the species on clade *B*. Usually, this surprising result of the molecular analysis is sooner or later confirmed by a focused analysis of classical, e.g., morphological, traits. When the species of clade *A* were originally assembled into taxon *A* and species of clade *B* were originally assembled into taxon *B* of the same or higher taxonomic rank as taxon *A* then new results change the status of taxon *A* from monophyletic (holophyletic in Ashlock’s (1971) terminology) to paraphyletic (polyphyletic in Hennig’s (1966) terminology). Paraphyletic taxa violate the fundamental principle of the current, cladistic, taxonomy—any two species of a particular taxon should be more related to one another (should have a more recent common ancestor) than to any other species from a different taxon of the same or higher taxonomic level (Hennig, 1966).

This issue can be correctly resolved in two different ways. One possibility is to cancel the inserted taxon *B* while redirecting all its species to taxon *A*, despite the fact that they may differ from the remaining species more than other representatives of *A* do from members of a sister taxon of taxon *A*. When this solution is chosen and when clades *A* and *B* have the taxonomic rank of genus, the scientific name of the species of genus *B* should be changed. And if genus *B* was described and properly named earlier than the genus *A*, all genus *A* species rather than genus *B* species should be renamed In speciose genera like *Drosophila*, such change of the generic name could bring about various taxonomic problems. For example, lumping all drosophilas into one genus to allow *Drosophila melanogaster* to keep its name would result in four species ending up with the name *Drosophila serrata* and another four with the name *Drosophila carinata* (van der Linde & Yassin, 2010).

The other option is to keep both genera. In such a case, however, only a part of the original genus *A* would be retained and all groups of species of genus *A* that branched earlier than genus *B* would be classified into their own (new) genera and would be given new scientific names, despite the fact that the representatives of most new genera would look

*Accepted by A. Minelli: 8 Nov. 2013; published: 27 Nov. 2013*

TERMS OF USE
This pdf is provided by Magnolia Press for private/research use.
Commercial sale or deposition in a public library or website is prohibited.

quite similar and many traditional and widely used names of species (like *Drosophila melanogaster*) would have to be changed.

With the development of reliable molecular phylogenetic methods, more and more paraphyletic taxa will be identified and the taxonomists will be increasingly forced to make the choice between the two aforementioned bad options and the rest of mankind will have to reconcile with the fact that the names of important species may change from time to time. Everybody has to make peace even with the fact that being a member of the same taxon says very little about inner and outer similarity between species. The absence of outer similarity (the phenotypic similarity that is often just a result of convergence due to similar selective pressures) would probably be more readily accepted than the lack of inner similarity (the phenotypic similarity that is often a result of neutral evolution or of phylogenetic constraints). A taxonomic system that does not correctly reflect the inner similarity of the species would be similarly "useful" as would be a system based on the chemical composition of a homogenate of representatives of particular species or on the alphabetic order of the letters in their names (Mayr, 1982). Currently, knowing that the flies swarming in our cellar fall into the genus *Drosophila*, we can guess many physiological, morphological, and ecological properties of the organisms from their name. On the other hand, nothing might be possible to guess from a system that would not reflect the inner similarity of the species.

Of course, not every genus studied by molecular phylogenetic methods will turn out paraphyletic and, as such, needing to be cancelled out, renamed or modified. Todays' experiences, however, suggest that in large (speciose) genera, it might be more or less a rule. The reasons for this unfortunate situation could be in principle two. The worse alternative is that no rigorous system of formal rules exists that could be used for the construction of a taxonomic system that would reflect both the phylogenetic relationship and phenotypic similarity of its species. The second possibility is more favorable. It supposes that such a system of rules can be found; however, it should differ from the system that is now in use. In my opinion, the second possibility is more likely and, moreover, the cure can be relatively easy. Before its introduction, it would be quite useful to discuss why, so often, a phenotypically distinct group of species shows up to be an internal clade of a phenotypically distinct and uniform group of species instead of being a sister clade of them. The answer to this question is nontrivial and rather interesting.

It is highly probable that this phenomenon is related to the punctuational nature of biological evolution. If the evolution worked in a gradualistic way, as Charles Darwin and most of his 20th century successors supposed to be true, such a pattern would be relatively rare and a radically different phenotype of the members of an internal sub-clade of a clade might be caused only by radically different selection pressures resulting, for example, from switching to a radically different type of environment. Such a switch would, however, probably also occur in some species outside the inner clade and most of the new characters typical for the inner clade would have a nature of an evolutionary adaptation to a new environment or to a new life strategy. Therefore, the taxonomists would probably recognize the adaptive nature of the novelties observed and would not establish a separate taxon for a particular phenotypically distinct sub-clade. The current taxonomists would therefore be saved from solving the problem of how to deal with a paraphyletic taxon when some distinct clade of a species turns out to be an internal clade of a taxon of the same or even lower taxonomic rank.

Within the past three decades, the palaeontologists have provided an abundance of evidence that the evolution of most of multicellular species is not gradualistic but punctuational in nature (Eldredge & Gould, 1972; Eldredge et al., 2005; Gould, 2002; Hunt, 2010; Monroe & Bokma, 2010). A large survey of well-documented case studies in the Neogene fossil records found 52 instances of punctuational evolution and only two instances of gradualistic evolution (Jackson & Cheetham, 1999). Similarly, gradualistic evolution was identified in only 8 of 88 Ordovician trilobite lineages and only in one of 34 scallop lineages in the northern European Jurassic (Jablonski, 2000). Starting with Ernst Mayr, biologists suggested several genetic mechanisms that might explain the existence of punctuational evolution in multicellular or sexual species (Mayr, 1963). Some of these models suggest that the species are evolutionarily frozen under normal conditions and can only partly respond to the existing selection pressures (Carson, 1968; Flegr, 1998, 2010; Mayr, 1963; Templeton, 1980). Under some conditions, for example after peripatric speciation, they can turn to the plastic state in which they start to respond to selection; however, after some time, as a result of an accumulation of genetic polymorphism by frequency-dependent selection, the plastic species switches to the normal, frozen, state again and the adaptive evolution of the new species ends. Transient plasticity of a new species can lead to a radical phenotypic switch without any change to the environment and can be accompanied by a rapid radiation and diversification of the new species resembling the adaptive radiation. In the contrast with other (more frequent) types of speciation (e.g. vicariant, sympatric, parapatric), the speciation coupled with the switch from the frozen to plastic state can lead to such a prominent change in the phenotype or may even give origin to several new divergent phenotypes, so that the taxonomists most probably will establish a new genus or a new taxon of higher rank, e.g., a tribe or a family, for the new species and its descendants (Hörandl, 2006). For example, fifty highly diverse species of Hawaiian silverswords (trees, shrubs, mat-

TERMS OF USE
This pdf is provided by Magnolia Press for private/research use.
Commercial sale or deposition in a public library or website is prohibited.

plants, cushion plants, lianas) branched off inside the phenetically conservative genus *Raillardiopsis* (tarweeds) (Baldwin, Kyhos, Dvorak, & Carr, 1991) and all highly diversified genera of cacti (family Cactaceae) were found to nest within the previously recognised genus *Talinum* (family Portulacaceae) (Hershkovitz & Zimmer, 1997).

A biological species is often defined as a set of individuals sharing an identical gene pool throughout the period between two speciation events. Within a framework of punctuational theories, a genus can be defined as a set of individuals sharing a common exclusive ancestor in the period between two subsequent events of evolutionary plasticity (Flegr, 2013). Therefore, by the definition, species of the same genus evolve in the gradualist mode while evolution of distinct genera is mostly punctuational in nature. Only some (prominent morphological) characters can be recognised in fossils and therefore paleontological species correspond to neontological genera rather than species. This is probably the reason why the punctuational mode of evolution is so prevailing in the available paleontological record (Eldredge et al., 2005).

In a gradualistic world, paraphyletic taxa (except the species, whose paraphyletic nature is usually tolerated even by cladistics) would be relatively rare. Two related genera whose species share (within a particular genus) enough independently acquired traits to have convinced taxonomists to establish a separate genus for each of them, will most likely be monophyletic and will probably form sister taxa.

In contrast, in the punctuational world, the paraphyletic taxa will be relatively common as a species can switch from the frozen to the plastic state in any place of the phylogenetic tree. The origin of a new genus as a result of the switch of some frozen species to the plastic state will be most probably accompanied by the transition of the originally monophyletic (holophyletic) genus to the paraphyletic state (Zander, 2010), but see also Podani (2010b).

The problems with paraphyletic taxa do not only concern the genera but also the taxa of any taxonomic rank. In any rank-based taxonomy, a higher rank taxon is originally composed of species that shared the same unique combination of phenotypic characters. When a certain species of a particular taxon becomes so plastic that even these characters radically change and taxonomists separate this species and its descendants into a new taxon of the same or higher taxonomic rank, the taxon becomes paraphyletic. For example, when a species of a certain line of reptiles acquired the properties characteristic for birds, the taxon Reptilia became paraphyletic. Many taxonomists silently tolerate the traditional division of the superclass Tetrapoda into the classes Amphibia, Reptilia, Mammalia, and Aves and do not, for example, rewrite the corresponding Wikipedia chapters every morning (however, from time to time they do), only because they have already recognized the vainness of such activities –secondary school biology teachers are far much more numerous than theoretical taxonomists.

Which set of taxonomic rules suits best a taxonomic system to be developed for sorting the organisms that evolved in the punctuational rather than the gradualistic way? The one that is used today, with one important exception. The paraphyletic taxa, it means the taxa that include a common ancestor of all its species but not all descendants of this ancestor, should be tolerated in the taxonomic system (Hörandl, 2006; Hörandl & Stuessy, 2010; Podani, 2010a; Zander, 2010). A group of the descendants of such an ancestor can be reclassified into another taxon, *B* (or, usually, into several new taxa *B*, *C*, *D*, etc.) of the same taxonomic rank (Fig 1a), however, under the condition that just one member of taxon *B*, namely the common ancestor of taxon *B*, has the ancestor that is not a member of taxon *A*, and no member of taxon *B* has a descendant that is a member of taxon *A*. When the former criterion failed to be met, taxon *B* would be polyphyletic (Fig 1b); when the latter one failed to be met, taxon *A* would be polyphyletic (Fig 1c).

Cladists try to construct the taxonomic system on the basis of relationships (cladogenesis), while ignoring possibly parallel anagenesis (phenotypic similarity) of species. In doing this, they are forced to depart from a three-hundred-year-old system of formal ranks, to exclude all paleontological species, and to overlook the fact that (without a time machine) cladogenesis must be reconstructed solely on the basis of anagenesis. Further cladists must ignore the fact that many important clades originated not by branching, but by fusion of phylogenetic branches, and therefore the concept of relationship cannot be applied to real reticulated phylogeny. They often argue that the members of paraphyletic taxa have no inner similarity to each other—that the only thing they have in common is the absence of the evolutionary novelties that appeared in the common ancestor of the derived taxon *B*. This, however, would be true only in a gradualistic world where the number of differences between two species indicates the time passed from the moment of the emergence of their common ancestor. In the world of punctuational evolution, the number of such differences reflects the number of switches to plasticity in the edges connecting the two species. Therefore, any two members of paraphyletic taxon *A* are likely to have more traits in common than any of them has with any member of taxon *B*, even if some of them is a sister species of the ancestor of taxon *B*, i.e., if some of them is more related to members of taxon *B* than to any other member of taxon *A*. From the perspective of gradualistic evolutionary theories, which ruled for most of the 20th century and have strongly influenced even today's thinking of biologists, the principles of cladistic phylogenetics, including rejecting paraphyletic taxa, were absolutely legitimate. After the fall of the gradualistic paradigm and the discovery of the

TERMS OF USE
This pdf is provided by Magnolia Press for private/research use.
Commercial sale or deposition in a public library or website is prohibited.

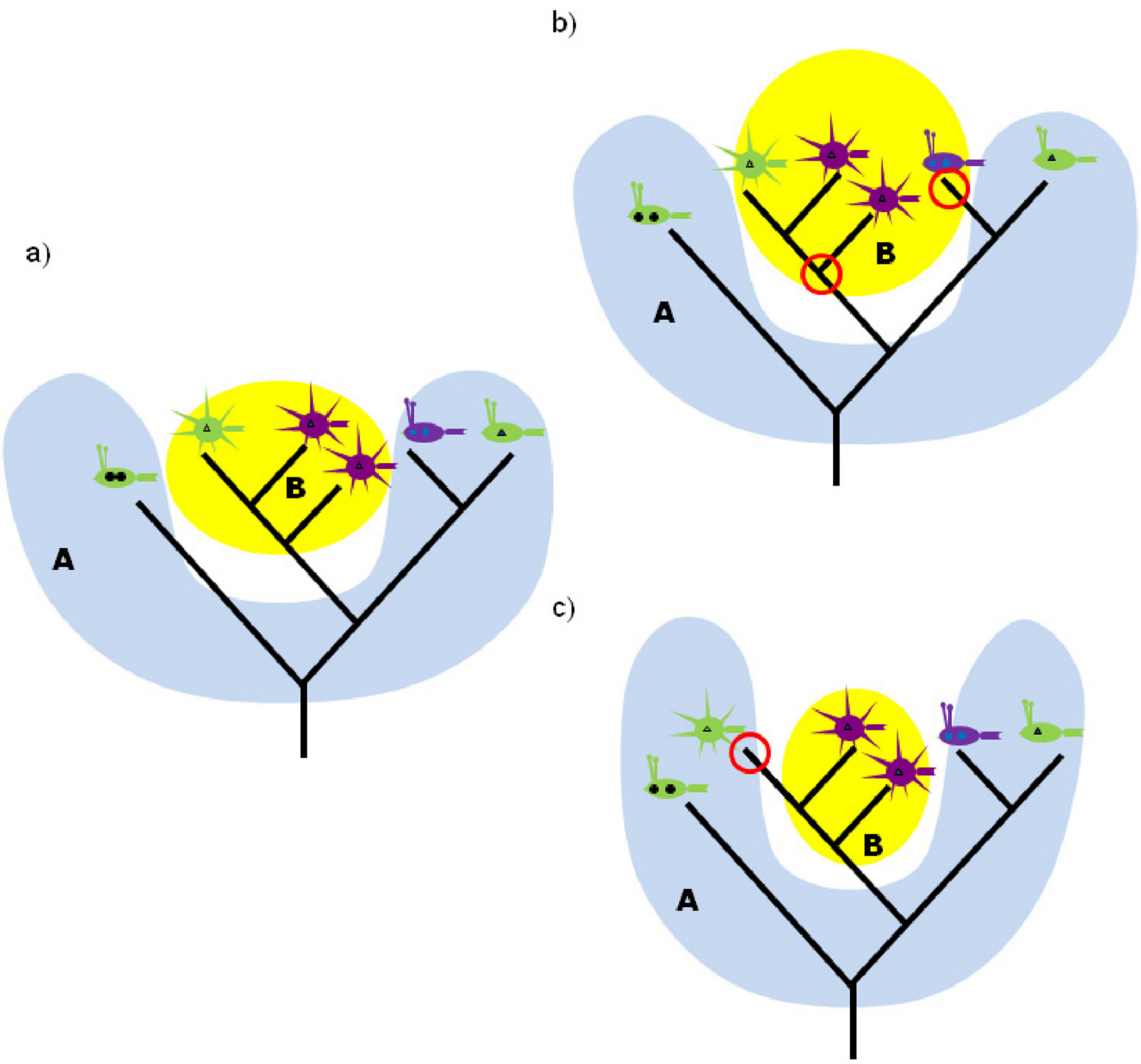

**FIGURE 1.** Correctly and incorrectly constructed taxonomic systems. A correctly constructed system (a) contains a paraphyletic taxon A and monophyletic, namely holophyletic, taxon B. System (b) contains paraphyletic taxon A and polyphyletic taxon B and system (c) contains paraphyletic taxon B and polyphyletic taxon A. The red circles indicate the places where the condition one (a) or the condition two (c) fails.

punctuational nature of adaptive evolution in multicellular (sexual) species, this element of cladistic taxonomy lost any theoretical backing. The advances in the modern molecular phylogenetic methods showed that the current system of cladistic taxonomic rules is not useful from the perspective of taxonomic practice either, because it results in the instability of the taxonomic system. Both the theoretical and practical reasons therefore suggest that our present system of taxonomic rules needs be modified. It is highly probable that the rehabilitation of the paraphyletic taxa would be a helpful step in this regard.

It is, of course, probable that most of the current theoretical taxonomists, who spent a large part of their active professional life fighting the fuzzy eclectic phylogenetics and taxonomy, would not be very enthusiastic about the recurrent more and more urgent suggestions of rehabilitating the paraphyletic taxa (Hörandl, 2006; Hörandl & Stuessy, 2010; Podani, 2010a; Zander, 2010). The change, fuelled by practical taxonomists who mostly use a 'wrong' eclectic taxonomy in their everyday practice anyway, will be probably slow and painful. It is, however, necessary to start the change as soon as possible. Otherwise, we might soon have to say farewell not only to drosophilas but to the whole taxonomic system.

Jaroslav Flegr
*Australopithecus sapiens*, possibly Reptilia, Pisces

TERMS OF USE
This pdf is provided by Magnolia Press for private/research use.
Commercial sale or deposition in a public library or website is prohibited.

**Acknowledgements**

I would like to thank to all three referees for their constructive suggestions and comments. This work was supported by project UNCE 204004 (Charles University of Prague).

## References

Ashlock, P.D. (1971) Monophyly and associated terms. *Systematic Zoology,* 20, 63–69.
http://dx.doi.org/10.2307/2412223

Baldwin, B.G., Kyhos, D.W., Dvorak, J. & Carr, G.D. (1991) Chloroplast DNA evidence for a North-American origin of the Hawaiian silversword alliance (Asteraceae). *Proceedings of the National Academy of Sciences of the United States of America,* 88, 1840–1843.
http://dx.doi.org/10.1073/pnas.88.5.1840

Carson, H.L. (1968) The population flush and its genetic consequences. *In:* Lewontin, R.C. (Ed.), *Population Biology and Evolution*. Syracuse University Press, Syracuse, pp. 123–137.

Eldredge, N. & Gould, S.J. (1972) Punctuated equilibria: an alternative to phyletic gradualism. *In:* Schopf, T.J.M. (Ed.), *Models in Paleontology*, San Francisco, pp. 82–115.

Eldredge, N., Thompson, J.N., Brakefield, P.M., Gavrilets, S., Jablonski, D., Jackson, J.B.C., Lenski, R.E., Lieberman, B.S., McPeek, M.A. & Miller III, W. (2005) The dynamics of evolutionary stasis. *Paleobiology,* 31, 133–145.
http://dx.doi.org/10.1666/0094-8373(2005)031[0133:tdoes]2.0.co;2

Flegr, J. (1998) On the "origin" of natural selection by means of speciation. *Rivista di Biologia-Biology Forum,* 91, 291–304. http://digital.casalini.it/10.1400/22749

Flegr, J. (2010) Elastic, not plastic species: frozen plasticity theory and the origin of adaptive evolution in sexually reproducing organisms. *Biology Direct,* 5, 2.
http://dx.doi.org/10.1186/1745-6150-5-2

Flegr, J. (2013) Microevolutionary, macroevolutionary, ecological and taxonomical implications of of punctuational theories of adaptive evolution. *Biology Direct,* 8, 1.
http://dx.doi.org/10.1186/1745-6150-8-1

Gould, S.J. (2002) *The Structure of Evolutionary Theory*. Belknap Press of Harvard University Press, Camridge, 1464 pp.

Hennig, W. (1966) *Phylogenetic Systematics*. University of Illinois Press, Urbana, 263 pp.

Hershkovitz, M.A. & Zimmer, E.A. (1997) On the evolutionary origins of the cacti. *Taxon,* 46, 217–232.
http://dx.doi.org/10.2307/1224092

Hörandl, E. (2006) Paraphyletic versus monophyletic taxa-evolutionary versus cladistic classifications. *Taxon,* 55, 564–570.
http://dx.doi.org/10.2307/25065631

Hörandl, E. & Stuessy, T.F. (2010) Paraphyletic groups as natural units of biological classification. *Taxon,* 59, 1641–1653.

Hunt, G. (2010) Evolution in fossil lineages: paleontology and the origin of species. *American Naturalist,* 176, S61–S76.
http://dx.doi.org/10.1086/657057

Jablonski, D. (2000) Micro- and macroevolution: scale and hierarchy in evolutionary biology and paleobiology. *Paleobiology,* 26, 15–52.
http://dx.doi.org/10.1666/0094-8373(2000)26[15:mamsah]2.0.co;2

Jackson, J.B.C. & Cheetham, A.H. (1999) Tempo and mode of speciation in the sea. *Trends in Ecology & Evolution,* 14, 72–77.
http://dx.doi.org/10.1016/s0169-5347(98)01504-3

Mayr, E. (1963) *Animal Species and Evolution*. Harvard University Press, Cambridge, 797 pp.

Mayr, E. (1982) *The Growth of Biological Thought*. Belknap Press of Harvard University Press, Cambridge, 974 pp.

Monroe, M.J. & Bokma, F. (2010) Punctuated equilibrium in a neontological context. *Theory in Biosciences,* 129, 103–111.
http://dx.doi.org/10.1007/s12064-010-0087-7

O'Grady, P.M. (2010) Whither *Drosophila*? *Genetics,* 185, 703–705.
http://dx.doi.org/10.1534/genetics.110.118232

Podani, J. (2010a) Monophyly and paraphyly: A discourse without end? *Taxon*, 59, 1011–1015.

Podani, J. (2010b) Taxonomy in evolutionary perspective An essay on the relationships between taxonomy and evolutionary theory. *Synbiologia Hungarica,* 6, 1–42.

Templeton, A.R. (1980) The theory of speciation via the founder principle. *Genetics,* 94, 1101–1038. Available from: http://www.ncbi.nlm.nih.gov/pmc/articles/PMC1214177/ (accessed 22 Nov. 2013)

TERMS OF USE
This pdf is provided by Magnolia Press for private/research use.
Commercial sale or deposition in a public library or website is prohibited.

van der Linde, K., Bächli, G., Toda, M.J., Zhang, W.-X., Katoh, T., Hu, Y.G. & Spicer, G.S. (2007) *Drosophila* Fallén, 1832 (Insecta, Diptera): proposed conservation of usage. *Bulletin of Zoological Nomenclature*, 64, 238–242.

van der Linde, K., Houle, D., Spicer, G.S. & Steppan, S.J. (2010) A supermatrix-based molecular phylogeny of the family Drosophilidae. *Genetics Research,* 92, 25–38.
http://dx.doi.org/10.1017/s001667231000008x

van der Linde, K. & Yassin, A. (2010) A fly by any other name. *New Scientist,* 206, 24–25. Available from: http://www.researchgate.net/publication/232804737_A_fly_by_any_other_name (accessed 22 Nov. 2013)

Zander, R.H. (2010) Taxon mapping exemplifies punctuated equilibrium and atavistic saltation. *Plant Systematics and Evolution,* 286, 69–90.
http://dx.doi.org/10.1007/s00606-010-0281-6