



<http://doi.org/10.11646/zootaxa.4137.1.9>

<http://zoobank.org/urn:lsid:zoobank.org:pub:4AA64424-FF21-4CAC-945B-1C9F08BCDC58>

Timeless standards for species delimitation

DALTON S. AMORIM^{1,29}, CHARLES MORPHY D. SANTOS², FRANK-THORSTEN KRELL³, ALAIN DUBOIS⁴, SILVIO S. NIHEI⁵, OTTO M.P. OLIVEIRA², ADRIAN PONT⁶, HOJUN SONG⁷, VANESSA K. VERDADE², DIEGO A. FACHIN¹, BRUNA KLASSA², CARLOS JOSÉ E. LAMAS⁸, SARAH S. OLIVEIRA⁹, CLAUDIO J. B. DE CARVALHO¹⁰, CÁTIA A. MELLO-PATIU¹¹, EDUARDO HAJDU¹¹, MÁRCIA S. COURI¹¹, VERA C. SILVA¹², RENATO S. CAPELLARI¹³, RAFAELA L. FALASCHI⁸, RODRIGO M. FEITOSA¹⁰, LORENZO PRENDINI¹⁴, JOSÉ P. POMBAL JR.¹¹, FERNANDO FERNÁNDEZ¹⁵, ROSANA M. ROCHA¹⁰, JOHN E. LATTKE¹⁰, ULISSES CARAMASCHI¹¹, MARCELO DUARTE⁸, ANTONIO CARLOS MARQUES⁵, ROBERTO E. REIS¹⁶, OLAVI KURINA¹⁷, DANIELA M. TAKIYA¹⁸, MARCOS TAVARES⁸, DANIEL SILVA FERNANDES¹⁸, FRANCISCO LUÍS FRANCO¹⁹, FABIANA CUEZZO²⁰, DENNIS PAULSON²¹, BENOIT GUÉNARD²², BIRGIT C. SCHLICK-STEINER²³, WOLFGANG ARTHOFER²³, FLORIAN M. STEINER²³, BRIAN L. FISHER²⁴, ROBERT A. JOHNSON²⁵, THIBAUT DOMINIQUE DELSINNE²⁶, DAVID A. DONOSO²⁷, PABLO RICARDO MULIERI²⁸, LUCIANO DAMIÁN PATITUCCI²⁸, JAMES M. CARPENTER¹⁴, LEE HERMAN¹⁴ & DAVID GRIMALDI¹⁴

¹*Departamento de Biologia, Faculdade de Filosofia, Ciências e Letras de Ribeirão Preto, Universidade de São Paulo, Av. Bandeirantes, 3900, 14040-901, Ribeirão Preto, SP, Brazil*

²*Centro de Ciências Naturais e Humanas, Universidade Federal do ABC, Rua Santa Adélia, 166, Bairro Bangu, 09210-170, Santo André, SP, Brazil*

³*Department of Zoology, Denver Museum of Nature & Science, 2001 Colorado Boulevard, Denver CO 80205-5798, U.S.A.*

⁴*Institut de Systématique, Évolution, Biodiversité, ISYEB – UMR 7205 – CNRS, MNHN, UPMC, EPHE, Muséum national d'Histoire naturelle, Sorbonne Universités, 57 rue Cuvier, CP 30, F-75005, Paris, France*

⁵*Departamento de Zoologia, Instituto de Biociências, Universidade de São Paulo, Rua do Matão, Travessa 14, n. 101, Cidade Universitária, São Paulo, SP, 05508-900, Brazil*

⁶*Oxford University Museum of Natural History, Parks Road, Oxford OX1 3PW, UK.*

⁷*Department of Entomology, Texas A&M University, Biological Control Facility, Room 118-119, College Station, TX 77843-2475, U.S.A.*

⁸*Museu de Zoologia da Universidade de São Paulo. Avenida Nazaré, 481, Ipiranga, 04263-000, São Paulo, SP, Brazil*

⁹*Departamento de Ecologia, Instituto de Ciências Biológicas, Universidade Federal de Goiás, Campus II. Prédio ICB1. Avenida Esperança, s/n, Campus Samambaia, 74690-900, Goiânia, Goiás, Brazil*

¹⁰*Departamento de Zoologia, Universidade Federal do Paraná, Caixa Postal 19020, 81531-980, Curitiba, PR, Brazil*

¹¹*Museu Nacional, Universidade Federal do Rio de Janeiro, Parque Quinta da Boa Vista s/nº, São Cristóvão, 20940-040 Rio de Janeiro RJ, Brazil*

¹²*Faculdade de Ciências Agrárias e Veterinárias de Jaboticabal, UNESP – Univ Estadual Paulista, Campus Jaboticabal, Departamento de Morfologia e Fisiologia Animal, Via de Acesso Professor Paulo Donato Castellane, s/n, Vila Industrial, 14884-900, Jaboticabal, SP, Brazil*

¹³*Instituto Federal do Triângulo Mineiro, 38064-790, Uberaba, MG, Brazil*

¹⁴*Division of Invertebrate Zoology, American Museum of Natural History, Central Park West at 79th St., New York, 10024-5192, U.S.A.*

¹⁵*Instituto de Ciencias Naturales, Universidad Nacional de Colombia, Carrera 30 No. 45 - 03, Bogotá D.C., Colombia*

¹⁶*Pontifícia Universidade Católica do Rio Grande do Sul. P.O. Box 1429, 90619-900 Porto Alegre, RS, Brazil*

¹⁷*Institute of Agricultural and Environmental Sciences, Estonian University of Life Sciences, Kreutzwaldi st 5D, 51014 Tartu, Estonia*

¹⁸*Departamento de Zoologia, Instituto de Biologia, Universidade Federal do Rio de Janeiro, Av. Carlos Chagas Filho 373, CCS, Bloco A, 21941-902, Rio de Janeiro, RJ, Brazil*

¹⁹*Laboratório Especial de Coleções Zoológicas, Instituto Butantan, Av. Dr. Vital Brasil, 1500, 05503-900 São Paulo SP, Brazil*

²⁰*INSUE – CONICET, Facultad de Ciencias Naturales e Instituto Miguel Lillo, Miguel Lillo 205 T4000JFE, San Miguel de Tucuman, Argentina*

²⁹*Slater Museum of Natural History, University of Puget Sound, Tacoma, WA 98416, USA.*

²²*School of Biological Sciences, The University of Hong Kong, Kadoorie Biological Sciences Building, Pokfulam Road, Hong Kong, PRC*

²³Molecular Ecology Group, Institute of Ecology, University of Innsbruck, Technikerstr. 25, 6020 Innsbruck, Austria

²⁴Department of Entomology, California Academy of Sciences, 55 Music Concourse Drive San Francisco, CA 94118, U.S.A.

²⁵School of Life Sciences, Arizona State University, Tempe, AZ 85282-4501, U.S.A.

²⁶Société d'Histoire Naturelle Alcide d'Orbigny, 57 rue de Gergovie, 63170 Aubière, France

²⁷Instituto de Ciencias Biológicas, Escuela Politécnica Nacional, Av. Ladrón de Guevara E11-253, Quito, Ecuador

²⁸División Entomología, Museo Argentino de Ciencias Naturales "Bernardino Rivadavia", Av. Angel Gallardo 470,- C1405DJR Buenos Aires Argentina

²⁹Corresponding author. E-mail: dsamorim@usp.br

The Original Controversy

Recently a new species of bombyliid fly, *Marleyimyia xylocopae*, was described by Marshall & Evenhuis (2015) based on two photographs taken during fieldwork in the Republic of South Africa. This species has no preserved holotype. The paper generated some buzz, especially among dipterists, because in most cases photographs taken in the field provide insufficient information for properly diagnosing and documenting species of Diptera.

Santos *et al.* (2016) expressed their dismay about this publication and that kind of practice in taxonomy. The approach taken by Marshall & Evenhuis (2015) was considered an undesirable, even dangerous, shortcut, showing disregard for robust taxonomic practices that have proven exceptionally useful for two and a half centuries. The benefits of having a name for an additional species, even of a beautiful insect, are far outweighed by the potential disadvantages that such taxonomic practice may cause for biology. Indeed, it is difficult to predict the scientific implications when traditional standards are abandoned. Precision in scientific communication in any paper, scientific journal, technical report, and everyday communication about the biological features—from biochemistry to behavior and conservation—of all taxa fundamentally depends on the quality and stability of the biological nomenclature. The same names given to different species or higher taxa, or different names given to the same taxon may cause major confusion and misinterpretation, and even huge losses of money if pest species are misidentified. Economically important *Bemisia* whiteflies, for instance, that were originally identified as one and, later, two species (Toscano *et al.* 1998), are now considered to form a complex involving “11 well-defined high-level groups containing at least 24 morphologically indistinguishable species” (De Barro *et al.* 2011). There is a lot at stake in a system with close to 2,000,000 species names and counting.

Marshall & Evenhuis's (2015) arguments in support of their position on the use of photographs instead of preserved holotype specimens are unconvincing and have been earlier addressed by Dubois (2009, 2010). Both Marshall and Evenhuis are experienced taxonomists and, hence, have a very clear understanding of the central role of physical holotypes in taxonomy. They are aware of the risks, and are clearly against generally abandoning proven standards. They nonetheless predict, however, that: (1) more digital photographs of unpreserved specimens are and will be available for taxonomic use; and (2) the trend of describing new species without preserved type specimens is “inevitable”. Why claim a trend to be “inevitable” and promote it through practice, if they do not want to encourage the practice by others?

Criticisms by Santos *et al.* (2016) were not directed against the use of modern technology in taxonomy. They addressed the pitfalls of the misuse thereof. The use of new technologies should, of course, be encouraged, but as a valuable addition, not as a substitute for the entire taxonomic process of collecting, preparing, comparing, describing, and delimiting species, that allows identifications (which are always hypotheses) to be double-checked. The existing obstacles to properly delimiting and identifying species are already complex enough even with holotypes at hand. While technology, such as digital imaging, improves many aspects of modern taxonomic practice (Santos *et al.* 2016), the major flaw in the argument by Marshall & Evenhuis (2015) is to confuse the issue of data sources with the issue of quality protocols. As sources of information, high-tech photos are welcome in taxonomy. Holotype specimens physically present in collections, however, represent quality protocols for a growingly complex system.

Marshall & Evenhuis (2015) stated that images of living specimens may provide information not discernible in preserved specimens. True, but minimally so. Photographs provide a very limited set of characters, lacking information available from holotype vouchers, such as sequences, internal anatomy etc. No image, even in 3-D, provides the data of a preserved specimen. It cannot be denied that the lack of a physical holotype creates a significant problem, since proper verifiability is hampered. Ironically, while Marshall & Evenhuis (2015) embrace

digital technology in taxonomic practice, their use of photographic holotypes makes it impossible to apply new technology to species like *Marleyimyia xylocopae*.

If Marshall & Evenhuis (2015) had simply referred to the new species as “*Marleyimyia* sp.” it would have been sufficient for documentation purposes. *Marleyimyia* “sp.” would avoid any potential connection with “taxonomic malpractice” (Krell & Wheeler 2015), as Marshall & Evenhuis (2015) themselves recognize. We seriously question any benefits of having a few more species names weighed against the problems delimiting species without preserved specimens. Van der Heyden (2015) has shown that it is possible to provide evidence for the existence of a new species using just a photograph without formally naming it, even if finding a journal for such a paper proved difficult (T. van der Heyden, pers.comm.).

Another fly without a preserved type

Löbl *et al.* (2016) also considered the arguments in Marshall & Evenhuis (2015) weak and “ill-founded.” In spite of the controversy with *Marleyimyia xylocopae*, a few months later another fly species was formally described without a physical type. In a recent paper revising the rare Nothybidae (Diptera: Schizophora), Lonsdale & Marshall (2016) described three new species of *Nothybus*, one of which, *N. absens*, was based merely on two photographs taken in the field.

Lonsdale & Marshall (2016, p. 14) argued: “The most serious criticism leveled against describing species without an extant type is that such a description is ‘non-science’.” We do not agree. Formal descriptions of new taxa without preserved specimens may be science, but sub-standard science. When a species is based on a superficial description and types cannot be traced, taxonomists relegate it to the status of “species inquirenda”. Lonsdale & Marshall claimed that “although the types are considered lost, the species are distinctive enough to make the designation of neotypes unnecessary” (Lonsdale & Marshall 2016, p. 3-4). Perhaps distinct enough for now, but this ignores future discoveries and ambiguities. They then stated, “if the character states in our description turn out to apply to multiple species distinguishable only by male genitalia, then a neotype will be necessary and can be easily designated” (p. 14). This presumes that another specimen will be found, and it bequeaths to other researchers the cost and effort of collecting the specimens and solving further identity problems of species like *Nothybus absens*. *Après nous le déluge*.

A Response to Marshall & Evenhuis

Marshall & Evenhuis (2016) wrote a rebuttal to critiques against photographic types which we feel needs a response. They acknowledged (p. 87) that the diagnosis/delimitation of a species is a scientific hypothesis and as such must be testable, capable of being verified or falsified based on subsequent observations and analyses. They also stated, “A description that points to [i.e., is based on] attributes visible in a photo is no different in this regard [as a testable hypothesis] than a description that points to attributes of a physical type specimen.” Further (p. 88): “...we maintain that the lack of a type specimen should not stand in the way of providing a name for a *thoroughly substantiated* and well-illustrated species” [italics ours]. We could not disagree more, for two reasons.

1. A specimen, as a standard of its species, has infinitely more fidelity than images thereof, whether or not the images are from high-resolution digital photography, scanning electron microscopy, CT scanning, or a portfolio of all the above. Like DNA sequences, imaging usually reveals new characters, but all of these techniques on their own are profoundly incomplete representations of the phenotype and genome of a specimen. A species is not “thoroughly substantiated” (Marshall & Evenhuis 2016) by a photo. Even DNA sequences alone are inappropriate surrogates for a type specimen.

2. Subsequent examination of an image is unlikely to find any new characters beyond what the pixels that were originally captured have already revealed. This makes it impossible to verify the status of a species known only from an image, the proper generic placement of a species after the generic system was revised, or its position in a phylogeny. A released or escaped type specimen cannot provide any additional, independent evidence that could test the hypotheses formulated on the basis of the first observation (the photo), as pointed out by Löbl *et al.* (2016). Limited testability results in sub-standard science. Constant discovery of new characters and species is why types

in museum collections are often the specimens most requested by researchers: modern new techniques better characterize species and variation. The taxonomists who designated types generations ago may have thought at the time that their descriptions and drawings were sufficient to characterize species, just like photos of *Marleymyia* and *Nothybus*. Thankfully, those taxonomists left types.

Marshall & Evenhuis (2016, p. 89) stated: “(...) [taxonomic] problems can only arise once new specimens have been collected and studied for additional characters.” The criticism by Löbl *et al.* (2016) is still entirely valid, not just because of unforeseen future problems but because history also informs us. New characters and character systems are *always* being discovered. Is there a described species for which new characters have *not* been subsequently found? Systematics, uniquely historical as it is, has evolved from quaint descriptions with contrived renderings to much more sophisticated concepts of species. Technology will provide future data from specimens that we cannot even predict. Thirty years ago Raman spectroscopy and laser ablation stable isotope analysis was inconceivable, let alone that it could determine (nondestructively) the composition of trace elements and molecules in a tiny fossil insect. Eventually our present concepts of species will be quaint too, but there will be types, the timeless standards for species delimitation.

Marshall & Evenhuis (2016) acknowledge the important practice of preserving voucher and type specimens, but they justify (p. 88–89) the surrogate use of photos by highlighting problems with type specimens. They counter the critique by Löbl *et al.* (2016), that photos can be manipulated, because types and other important specimens can also be manipulated, citing the chimeric hoaxes Piltdown Man and “*Archaeoraptor liaoningensis*”. Indeed, even Willi Hennig was misled by a forgery, a specimen of the living latrine fly *Fannia scalaris* inserted into an authentic piece of Eocene Baltic amber, later dubbed “Piltdown fly” (Grimaldi *et al.* 1994). But the crux is: all of these were exposed as hoaxes because the specimens could be re-examined. There is no such opportunity with just a photo of a carefully doctored specimen. Yes, some taxonomists have designated female specimens or juveniles as types in species requiring male genitalia for proper diagnosis, but with morphometrics, sequencing and other techniques specimens of different genders and stages can be associated. This does not mean that new techniques should necessarily establish new criteria for defining species, but they can if needed. You still need a specimen. The argument that photos are OK because type specimens are imperfect is fatal logic: If the actual specimen is imperfect, why would a superficial representation of it be as acceptable?

Further, Marshall & Evenhuis (2016, p. 88) stated that if a photo “is *good enough* for a taxonomist to use it as a proxy type, why would it be more subject to misinterpretation than a specimen?” [emphasis ours]. This is an appeal to authority, a “trust us” dismissal to which scientists are natural skeptics, and which begs questions: Who should be trusted to choose photos instead of preserved specimens. Any taxonomist? Just an experienced one? At what point does a novice become an authority? The 2005 report that the ivory billed woodpecker, *Campephilus principalis*—thought to be extinct for decades—was alive deep in Arkansas woods (Fitzpatrick *et al.*, 2005) was made by an experienced team of ornithologists who felt that grainy video footage was good enough to document their discovery. The footage was later thought to be of a pileated woodpecker, *Dryocopus pileatus* (Sibley *et al.* 2006). At what point does a photo become “good enough”? The elegance of the classic practice of type specimens is that it is objective and extraordinarily, perhaps even endlessly, informative. A few feathers from said woodpecker would have been nicer. Likewise, if Robb *et al.* (2013) had based their description of a new owl on actual samples, not just photos and recordings, taxonomic confusion could have been easily avoided.

A Good Example

Earlier this year, Skejo and Caballero (2016) published the description of a new species of pygmy grasshopper (family Tetrigidae), which was initially identified from a single photograph taken in the Philippines posted on Facebook. The authors immediately recognized it as a new species of the genus *Arulenus* Stål, 1877 and took the necessary steps to properly describe it as new. They tracked down the exact locality where the photograph was taken and purchased from an online dealer physical specimens matching the photo that were collected from the same locality. The authors collaborated with a local scientist in the Philippines in order to collect fresh specimens and also to obtain ecological information. They could have described a new species from the photo, but instead they chose the difficult, time-consuming path of proper taxonomic diligence, which eventually resulted in a preserved type specimen. Field photos can be a starting point for new expeditions and collecting efforts, but should not be an end point for a taxonomy without physical types.

Implications

Descriptions of new species without preserved name-bearing types have occurred in groups other than insects and have occasionally caused controversy (see, e.g., Nemésio 2009). Sometimes the lack of types was justified by the threatened status of the species (see Minter *et al.* 2014), although some would strongly disagree (e.g., Dubois 2003, 2009). In other cases, there have been attempts to designate living holotypes in the wild, although they could have been deposited in zoos (Gentile & Snell 2009). In some taxonomic groups, holotypes rapidly disintegrate whatever the preservation technique used, as in ctenophores (Matsumoto 1988). In any circumstances, what is a loophole left open in the system to address such particular situations or old descriptions by, e.g. Fabricius or Linnaeus, based on paintings (“Jones’ Icones”) (Santry *et al.* [without year]) or published illustrations, is now being used as an excuse to describe species without having a preserved holotype. In relying solely on Article 73.1.4 of the International Code of Zoological Nomenclature (1999) in support of their designation of the photographed holotype, Marshall & Evenhuis (2016) neglect Recommendation 73B, that “an author should designate as holotype a specimen actually studied by him or her, not a specimen known to the author only from descriptions or illustrations in the literature”. The spirit of the International Code of Zoological Nomenclature is willfully violated by a description based only on a photograph.

The “digital taxonomy age” of Lonsdale & Marshall (2016) and Marshall & Evenhuis (2015) brings up the risk of abandoning pivotal aspects of the tested and proven process of species name stability and verifiability. Yes, we do want high quality photos to be used in biodiversity studies. What we do not need is to create problems for the scientific community in the future. Damage to the nomenclatural system is hard to see at this stage but easy to predict. Experienced taxonomists may have judgment to select the few cases when species could be properly described based on photos—although even in such cases the future may prove them wrong. If we approve or even welcome photo-based descriptions, how are we going to deal with a potential wave of inevitably incomplete species descriptions based on photos?

Promoting taxonomy without preserved specimens can have much more severe unforeseen consequences. The acceptance that vouchers may be negligible can be construed as support for ongoing budget cuts at natural history museums (Dubois 2010, Connif 2016). Decision-makers who do not understand the fundamental role of taxonomy and systematics in the biological sciences are already dismantling the safe-house of taxonomy based on misguided arguments with detrimental consequences. Such collateral damage is especially untimely when society and governmental agencies need to be aware that proper biodiversity conservation efforts cannot be undertaken without huge amounts of high-quality taxonomic work (Santos *et al.* 2016).

In this sense, the “inevitable” quick-and-dirty taxonomy based on photos may give the impression that this is an easy-to-do branch of science. Systematics is in fact a non-trivial area of scientific research. Indeed, many scientists think of taxonomy as just about “naming new species”—as if species were self-evident Platonic entities waiting to be named. Taxonomy is about proposing scientific, verifiable hypotheses of delimitation of complex historical biological entities at different levels (species, clades of species, genera, or higher taxa), characterization of each portion of this system with as much information as possible, and providing unique names for the 2 million+ species and higher taxa in an unequivocal way. Indeed, as addressed by Dubois & Nemésio (2007: 16) and Dubois (2009: 28), the information carried by specimens, even a single one, is much more important and relevant than that carried by descriptions, photographs, drawings or paintings, and even DNA sequences. There is an immeasurable difference between having and not having a specimen available, because the information carried by a physical specimen is virtually endless, whereas all other sources of information are limited to the information chosen by the author of the description or to some limited aspects of Hennig’s “holomorph” of the specimen.

A transformation of the nature and purpose of natural history museums seems to be underway in the mind of some administrators and decision makers: from centers of knowledge development and provision of the past and present to entertainment centers largely devoid of scientific background. In a brief opinion piece published in *The New York Times*, Connif (2016, p. SR4) correctly synthesizes: “This view of the natural history museum as moribund is a terrible misunderstanding on many counts. Natural history museums do indeed store specimens from millions or even billions of years in the past. (...) Their collections, one museum director told me, are where ‘we have placed our entire three-dimensional record of the planet that sustains us’.” Collections from different times even add a fourth dimension to the record. Biodiversity research needs additional data, more collecting (especially in poorly known or threatened geographical areas), more specimens in museums, increased funding for

taxonomists, lab work, sophisticated training, and more positions in this area of science. This is what builds reliable conservation decisions and environmental model construction. Gathering great amounts of information—the so-called big-data initiatives (Lynch 2008)—and organizing it in databases has become the new standard in biodiversity studies (Kelling *et al.* 2009, Edmunds *et al.* 2013, Diniz-Filho *et al.* 2013). Such initiatives allow easy access to the results of museum-driven research and recognition of meta-patterns that emerge only from large verifiable datasets. Without preserved specimens such datasets are not verifiable and would not exist in the first place.

In recent times science has become increasingly integrative. New technology-based means of gathering information have added to taxonomic quality control and sophisticated methods of data analysis. In taxonomy, new sources of data—e.g., nano CT-scan (Arillo *et al.* 2015), evo-devo (Minelli 2015), 3D morphology (Khoury *et al.* 2015), transcriptome phylogeny (Peters *et al.* 2014), and cryopreservation centers—add to other sources of information and protocols that keep the biological system sound, including its nomenclature. But here again the new methods do not replace, but complement the traditional, tested methods and procedures (Schlick-Steiner *et al.* 2010).

The very basis for the entire biodiversity system and the corresponding worldwide communication is unequivocal identification. *More* information on species, not *less* information, is needed to speed up sound biodiversity research. Taxonomy without vouchers will lead us into a quagmire. The fact that there are ambiguities in the International Code of Zoological Nomenclature (1999)—designed for special cases—does not justify abandoning long proven taxonomic procedures—and indeed these ambiguities should be addressed in the future (see Dubois & Nemésio 2007). Editors and reviewers of the world's foremost zootaxonomical journal (Zhang 2014) should also aspire to keep the system reliable.

Disclaimer: The presence of one Commissioner of the ICZN amongst the authors of this paper does not mean that the opinions expressed in this paper are those of the ICZN. The Commissioner participated in writing this paper in the capacity of an active taxonomist, not as a commissioner.

References

- Arillo, A., Peñalver, E., Pérez-De La Fuente, R., Delclòs, X., Criscione, J., Barden, P.M., Riccio, M.L. & Grimaldi, D.A. (2015) Long-proboscid brachyceran flies in Cretaceous amber (Diptera: Stratiomyomorpha: Zhangsolvidae). *Systematic Entomology*, 40, 242–267.
<http://dx.doi.org/10.1111/syen.12106>
- Connif, R. (2016) Our natural history, Endangered. *The New York Times*, pp. SR4. Available from: http://www.nytimes.com/2016/04/03/opinion/ournatural-history-endangered.html?smid=fb-share&_r=0 (accessed 11 May 2016)
- De Barro, P.J., Liu, S.S., Boykin, L.M. & Dinsdale, A.B. (2011) *Bemisia tabaci*: a statement of species status. *Annual Review of Entomology*, 56, 1–19.
<http://dx.doi.org/10.1146/annurev-ento-112408-085504>
- Diniz-Filho, J.A.F., Loyola, R.D., Raia, P., Mooers, A.O. & Bini, L.M. (2013) Darwinian shortfalls in biodiversity conservation. *Trends in Ecology & Evolution*, 28, 689–695.
<http://dx.doi.org/10.1016/j.tree.2013.09.003>
- Dubois, A. (2003) The relationships between taxonomy and conservation biology in the century of extinction. *Comptes Rendus Biologies*, 326 (Supplement 1), S9–21.
[http://dx.doi.org/10.1016/S1631-0691\(03\)00022-2](http://dx.doi.org/10.1016/S1631-0691(03)00022-2)
- Dubois, A. (2009) Endangered species and endangered knowledge. *Zootaxa*, 2201, 26–29.
- Dubois, A. (2010) Nomenclatural rules in zoology as a potential threat against natural history museums. *Organisms Diversity and Evolution*, 10, 81–90.
<http://dx.doi.org/10.1007/s13127-010-0015-1>
- Dubois, A. & Nemésio, A. (2007) Does nomenclatural availability of nomina of new species or subspecies require the deposition of vouchers in collections? *Zootaxa*, 1409, 1–22.
- Edmunds, S.C., Hunter, C.I., Smith, V., Stoev, P. & Penev, L. (2013) Biodiversity research in the “big data” era: GigaScience and Pensoft work together to publish the most data-rich species description. *GigaScience*, 2, 14.
<http://dx.doi.org/10.1186/2047-217X-2-14>
- Fitzpatrick, J.W., Lammertink, M., Luneau Jr., M.D., Gallagher, T.W., Harrison, B.R., Sparling, G.M., Rosenberg, K.V., Rohrbaugh, R.W., Swarthout, E.C., Wrege, P.H., Swarthout, S.B., Dantzker, M.S., Charif, R.A., Barksdale, T.R., Remsen

- Jr., J.V., Simon, S.D. & Zollner, D. (2005) Ivory-billed woodpecker (*Campephilus principalis*) persists in continental North America. *Science*, 308 (5727), 1460–1462.
<http://dx.doi.org/10.1126/science.1114103>
- Gentile, G. & Snell, H. (2009) *Conolophus marthae* sp. nov. (Squamata, Iguanidae), a new species of land iguana from the Galápagos archipelago. *Zootaxa*, 2201, 1–10.
- Grimaldi, D., Shedrinsky, A., Ross, A. & Baer, N.S. (1994) Forgeries of fossils in “amber”: history, identification, and case studies. *Curator*, 37 (4), 251–274.
<http://dx.doi.org/10.1111/j.2151-6952.1994.tb01023.x>
- Hrycaj, S., Chesebro, J. & Popadić, A. (2010) Functional analysis of Scr during embryonic development in the cockroach, *Periplaneta americana*. *Developmental Biology*, 341, 324–334.
<http://dx.doi.org/10.1016/j.ydbio.2010.02.018>
- International Commission on Zoological Nomenclature [ICZN] (1999) *International Code of Zoological Nomenclature*. 4th Edition. International Trust for Zoological Nomenclature, London, 335 pp.
- Kelling, S., Hochachka, W.M., Fink, D., Riedewald, M., Caruana, R., Ballard, G. & Hooker, G. (2009) Data-intensive science: a new paradigm for biodiversity studies. *BioScience*, 59, 613–620.
- Khoury, B.M., Bigelow, E.M.R., Smith, L.M., Schlecht, S.H., Scheller, E.L., Andarawis-Puri, N. & Jepsen, K.J. (2015) The use of nano-computed tomography to enhance musculoskeletal research. *Connective Tissue Research*, 56, 106–119.
<http://dx.doi.org/10.3109/03008207.2015.1005211>
- Krell, F.T. & Wheeler, Q.D. (2014) Specimen collection: plan for the future. *Science*, 344, 815–816.
<http://dx.doi.org/10.1126/science.344.6186.815>
- Löbl, I., Cibois, A. & Landry, B. (2016) Describing new species in the absence of sampled specimens: a taxonomist’s own-goal. *Bulletin of Zoological Nomenclature*, 73, 83–86.
- Lonsdale, O. & Marshall, S.A. (2016) Revision of the family Nothybidae (Diptera: Schizophora). *Zootaxa*, 4098 (1), 1–42.
<http://dx.doi.org/10.11646/zootaxa.4098.1.1>
- Lynch, C. (2008) Big data: How do your data grow? *Nature*, 455, 28–29.
<http://dx.doi.org/10.1038/455028a>
- Marshall, S.A. & Evenhuis, N.L. (2015) New species without dead bodies: a case for photo-based descriptions, illustrated by a striking new species of *Marleyimyia* Hesse (Diptera, Bombyliidae) from South Africa. *Zookeys*, 525, 117–127.
<http://dx.doi.org/10.3897/zookeys.525.6143>
- Marshall, S.A. & Evenhuis, N.L. (2016) Proxy types, taxonomic discretion, and taxonomic progress: a response to Löbl *et al.* *Bulletin of Zoological Nomenclature*, 73, 87–92.
- Matsumoto, G.I. (1988) A new species of lobate ctenophore, *Leucothea pulchra* sp. nov., from the California Bight. *Journal of Plankton Research*, 10 (2), 301–311.
<http://dx.doi.org/10.1093/plankt/10.2.301>
- Minelli, A. (2015) Biological systematics in the Evo-Devo era. *European Journal of Taxonomy* 125, 1–23.
<http://dx.doi.org/10.5852/ejt.2015.125>
- Minteer, B.A., Collins, J.P. & Puschendorf, R. (2014) Avoiding (re)extinction. *Science*, 344, 260–261.
<http://dx.doi.org/10.1126/science.1250953>
- Nemésio, A. (2009) On the live holotype of the Galápagos pink land Iguana, *Conolophus marthae* Gentile & Snell, 2009 (Squamata: Iguanidae): is it an acceptable exception? *Zootaxa*, 2201, 21–25.
- Peters, R.S., Meusemann, K., Petersen, M., Mayer, C., Wilbrandt, J., Ziesmann, T., Donath, A. Kjer, K.M., Aspöck, U., Aspöck, H., Aberer, A., Stamatakis, A., Friedrich, F., Hünefeld, F., Niehuis, O., Beutel, R.G. & Misof, B. (2014) The evolutionary history of holometabolous insects inferred from transcriptome-based phylogeny and comprehensive morphological data. *BMC Evolutionary Biology*, 14, 52–69.
<http://dx.doi.org/10.1186/1471-2148-14-52>
- Robb, M.S., van den Berg, A.B. & Constantine, M. (2013) A new species of *Strix* owl from Oman. *Dutch Birding*, 35, 275–310.
- Santos, C.M.D., Amorim, D.S., Klassa, B., Fachin, D.A., Nihei, S.S., Carvalho, C.J.B., Falaschi, R.L., Mello-Patiu, C.A., Couri, M.S., Oliveira, S.S., Silva, V.C., Ribeiro, G.C., Capellari, R.S. & Lamas, C.J.E. (2016) On typeless species and the perils of fast taxonomy. *Systematic Entomology*, 41 (3), 511–515.
<http://dx.doi.org/10.1111/syen.12180>
- Santry, K., Joomun, S. & Phibbs, S. [without year] Jones’ Icones Online. Museum of Natural History, University of Oxford, Oxford, UK. Available from: <http://www.jonesicones.com/index.html> (accessed 17 Jun. 2016)
- Schlick-Steiner, B.C., Steiner, F.M., Seifert, B., Stauffer, C., Christian, E. & Crozier, R.H. (2010) Integrative taxonomy: a multisource approach to exploring biodiversity. *Annual Review of Entomology*, 55, 421–438.
<http://dx.doi.org/10.1146/annurev-ento-112408-085432>
- Sibley, D.A., Bevier, L.R., Patten, M.A. & Elphick, C.S. (2006) Comment on “Ivory-billed woodpecker (*Campephilus principalis*) persists in continental North America”. *Science*, 311, 1555a–1555a. [sic]
<http://dx.doi.org/10.1126/science.1122778>
- Skejo, J. & Caballero, J.H.S. (2016) A hidden pygmy devil from the Philippines: *Arulenus miae* sp. nov.—a new species serendipitously discovered in an amateur Facebook post (Tetrigidae: Discotettiginae). *Zootaxa*, 4067 (3), 383–393.

<http://dx.doi.org/10.11646/zootaxa.4067.3.7>

Toscano, N.C, Castle, S.J., Henneberry, T.J. & Prabhaker, N. (1998) Persistent silverleaf whitefly exploits desert crop systems. *California Agriculture*, 52, 29–33.

<http://dx.doi.org/10.3733/ca.v052n02p29>

Van der Heyden, T. (2015) “Wild shot” photographs of an apparently undescribed bug species of the tribe Anisocelini from Costa Rica (Hemiptera, Heteroptera, Coreidae). *Boletín de la Asociación Española de Entomología*, 39, 407–410.

Zhang, Z.-Q. (2014) Sustaining the development of world’s foremost journal in biodiversity discovery and inventory: *Zootaxa* editors and their contributions. *Zootaxa*, 3753 (6), 597–600.

<http://dx.doi.org/10.11646/zootaxa.3753.6.6>