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The monophyly of *Magelona* F. Müller, 1858 (Polychaeta, Magelonidae): Comments on Meißner *et al.*'s (2023) reinstatement of *Octomagelona* Aguirrezabalaga, Ceberio & Fiege, 2001

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Abstract

The first published phylogenetic hypotheses involving members of the polychaete taxon Magelonidae Cunningham & Ramage, 1888, were reported by Mortimer *et al.* (2021), wherein results showed that for the two genera in the family, *Magelona* F. Müller, 1858, was paraphyletic relative to *Octomagelona* Aguirrezabalaga, Ceberio & Fiege, 2001. The only option to formally name at least some of the resultant phylogenetic hypotheses was to place *Octomagelona* into synonymy with *Magelona*, leaving the definition of Magelonidae redundant with that of a monophyletic *Magelona*. Meißner *et al.* (2023) subsequently described specimens as members of new species, *Octomagelona borowskii* Fiege, Knebelsberger & Meißner, 2023, and *O.* sp. cf. *O. borowskii*, with the view that *Octomagelona* should be maintained as distinct from *Magelona*. We present reasons why reestablishing the paraphyly of *Magelona* is scientifically unwarranted.

Key words: Nomenclature, paraphyly, phylogenetic hypotheses, specific hypotheses, systematics

Introduction

One of the consequences of Mortimer *et al.*'s (2021: fig. 17) phylogenetic inference involving members of Magelonidae Cunningham & Ramage, 1888, was to acknowledge that *Magelona* F. Müller, 1858, is paraphyletic relative to the monophyletic *Octomagelona* Aguirrezabalaga, Ceberio & Fiege, 2001 (Fig. 1). The only feasible nomenclatural solution was to synonymize *Octomagelona* with *Magelona* (cf. Rouse *et al.* 2022, Read & Fauchald 2024 *partim*), with the consequence that defining the name *Magelona* is redundant with the monotypic Magelonidae, insofar as both names refer to phylogenetic hypotheses causally accounting for the same set of characters. The formal definition of Magelonidae, and thus *Magelona*, is,

Magelonidae Cunningham & Ramage, 1888

Type genus. Magelona F. Müller, 1858, by monotypy.

Definition. A composite phylogenetic hypothesis (Fig. 1), causally accounting for (a) presence of a shovelshaped prostomium, (b) absence of nuchal organs, (c) presence of prostomial ridges, (d) ventral palps with (e) papillate surfaces, (f) presence of a burrowing organ, and (g) magelonid-like body regionation.

Contrary to Mortimer *et al.*'s (2021) definition of Magelonidae/Magelona, Meißner *et al.* (2023) reinstate Octomagelona as part of their descriptions of specimens from the Southeast Pacific, for which specific hypothesis O. borowskii Fiege, Knebelsberger & Meißner, 2023, is introduced, as well as O. sp. cf. O. borowskii from the Southeast Atlantic. Justification for this decision is presented in the authors' remarks regarding Octomagelona (Meißner *et al.* 2023: 21–22),

"Mortimer *et al.* (2021), considered *Octomagelona* a junior synonym of *Magelona* following their phylogenetic analysis based on morphological characters. We agree with these authors that the 'magelonid-like body regionation'

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FIGURE. 1. Strict consensus tree, modified from Mortimer *et al.* (2021: fig. 17), indicating a paraphyletic *Magelona* relative to *Octomagelona* (bold). The only viable solution to remove paraphyly was to make *Octomagelona* a junior synonym of *Magelona*; i.e., provide a formal definition of Magelonidae/*Magelona* as a phylogenetic hypothesis, wherein all less inclusive phylogenetic hypotheses are unnamed.

is an important synapomorphy for Magelonidae (Mortimer *et al.* 2021: 67 and abstract) but we regard the two different character states for the thoracic body region, i.e. the presence of eight versus nine thoracic chaetigers, as an easy to observe and taxonomically sufficient character to distinguish between the two genera. Therefore, we prefer to maintain *Octomagelona* as a valid genus for the time being and hope that studies of genetic markers will add significant information to characterize the two genera."

The goal of the present paper is to provide reasons why formal recognition of the name *Octomagelona* is neither scientifically valid nor systematically useful.²

The Objective of Systematics Means Negating Paraphyly

The most apparent problem is that recognizing *Octomagelona* results in *Magelona* once again being paraphyletic; an issue not acknowledged by Meißner *et al.* (2023). We will not argue the traditional defences that monophyly is preferred because it defines supraspecific taxa by way of synapomorphies, refers to all descendants derived from a common ancestor, or favours natural groups (e.g., Oosterbroek 1987, Schmidt-Lebuhn 2012, Zachos 2014). Rather, Mortimer *et al.* (2021) emphasize the importance of recognizing formal names of phylogenetic hypotheses as referring to explanatory accounts of specified characters of organisms, as mentioned in the previous section, which by default necessitates monophyly (Fitzhugh 2005, Fitzhugh 2006a, Fitzhugh 2006b, Fitzhugh 2008, Fitzhugh 2009, Fitzhugh 2012, Fitzhugh 2013, Fitzhugh 2014, Fitzhugh 2016a, Fitzhugh 2016b, Fitzhugh 2016c, Fitzhugh 2021). Too often discussions of mono- and paraphyly lay emphasis on *groups* of organisms rather than phylogenetic *hypotheses qua* past causal conditions of character origin/fixation and subsequent population splitting events.

Compounding the problem is that systematists are obliged to follow nomenclatural rules set forth by the International Codes of Nomenclature (e.g., International Commission on Zoological Nomenclature 1999) that impose ranks on formal names of specific and phylogenetic hypotheses, as well as requiring specific hypotheses to be recognized using binomial names, wherein a specific hypothesis must be conjoined to a phylogenetic hypothesis at the rank of genus, even though the two classes of hypotheses involve separate inferential actions (Fitzhugh 2009, 2013; Mortimer *et al.* 2021). Ideally, formal names of phylogenetic hypotheses should be in accordance with scientific principles, i.e., defined as explanatory accounts for specified characters (e.g., Fitzhugh 2008, Fitzhugh *et al.* 2015, Nogueira *et al.* 2010, Nogueira *et al.* 2013, Nogueira *et al.* 2017, Mortimer *et al.* 2021), thus ensuring monophyly, notwithstanding that the International Codes of Nomenclature are silent on the topic of paraphyly.

Forcing *Magelona* to be paraphyletic in order to recognize *Octomagelona* is a consequence of arbitrarily elevating a phylogenetic hypothesis to the rank of genus that is in fact subsumed under *Magelona*, as indicated in Fig. 1. This erroneously implies that phylogenetic hypotheses named *Magelona* and *Octomagelona* are epistemically equivalent, yet arbitrarily ignores all other unnamed phylogenetic hypotheses under either of those names (cf. Mortimer *et al.* 2021: fig. 17). *Octomagelona* is an artefact of a nomenclatural system that enables personal biases over scientific objectives. What is important to realize is that the *status* of the phylogenetic hypothesis originally named *Octomagelona* is not compromised by Mortimer *et al.*'s (2021) actions. The hypothesis still stands; it is simply no longer given a formal name, just as the multitude of other phylogenetic hypotheses under *Magelona* are not formally named.

Meißner *et al.* (2023) offer no scientifically credible argument for maintaining the formal name *Octomagelona*. Their reasoning appears to stem from the perspective that semaphoront distinctness is an important criterion. This is, however, at odds with the goal of scientific inquiry being the pursuit of causal understanding (Hanson 1958, Hempel 1965, Rescher 1970, Popper 1983, Popper 1992, Salmon 1984, Van Fraassen 1990, Strahler 1992, Mahner & Bunge 1997, Thagard 2004, Nola & Sankey 2007, Regt, Leonelli & Eigner 2009, Hoyningen-Huene 2013, Potochnik 2017, Potochnik 2020, Anjum & Mumford 2018, Currie 2018), which is echoed by Mortimer *et al.* (2021: **Methodological**

¹ Following the phylogenetic hypothesis of Mortimer *et al.* (2021; Fig. 1), the World Register of Marine Species (WoRMS) recognizes *Octomagelona* as a junior subjective synonym of *Magelona*, inclusive of type species *O. bizkaiensis* Aguirrezabalaga, Ceberio & Fiege, 2001 (Read & Fauchald 2024: https://www.marinespecies.org/aphia.php?p=taxdetails&id=914 on 2024-07-22). Contrary to that, however, WoRMS recognizes *O. borowskii* but does not acknowledge it as a member of *Magelona*.

² An updated Magelonidae phylogenetic analysis (Mortimer, Fitzhugh & Brasil, in prep.) will again provide an empirical basis for *Octomagelona* as a synonym of *Magelona*, inclusive of *O. borowskii* and *O.* sp. cf. *O. borowskii*.

considerations: The goal of scientific inquiry). To "distinguish between" *Magelona* and *Octomagelona* according to particular characters presumes genera are either concrete entities or mere class constructs. Both connotations are erroneous given that taxa are explanatory hypotheses (Mortimer *et al.* 2021 and references therein). Genera, like all supraspecific ranks, are largely arbitrarily applied to particular phylogenetic hypotheses in lieu of any number of unnamed phylogenetic hypotheses.

Meißner *et al.* (2023) state that the distinction between eight (*Octomagelona*) and nine thoracic chaetigers (paraphyletic *Magelona*) is "an easy to observe and taxonomically sufficient [*sic*] character to distinguish between the two genera." This is not a scientifically credible argument favouring a paraphyletic *Magelona*. To correctly say two genera are "distinguished" from one another is to articulate differences between respective phylogenetic hypotheses. Taxa cannot be distinguished on the basis of characters of organisms; eight versus nine chaetigers only distinguish semaphoronts (*sensu* Hennig 1966), not phylogenetic hypotheses. Emphasizing eight versus nine chaetigers as justification for *Octomagelona* is an a priori decision—a matter of personal inclination—not scientific necessity.

Meißner *et al.*'s (2023) statement that they "hope that studies of genetic markers will add significant [*sic*] information to characterize the two genera" will not resolve the problem they suggest exists. Emphasizing sequence data over other classes of characters is part of the reductionist attitude that has consumed much of systematics, incorrectly assuming that sequence data offer better opportunities to elucidate "true relationships" or offer "stronger support." The view that one should default to sequence data is based on the false premise that those data offer solutions to perceived problems that cannot be addressed with characters at higher levels of organization, typically morphological. This perspective overlooks the actual goal of systematics and evolutionary biology as a matter of scientific inquiry; that goal being to causally account for properties of organisms (Fitzhugh 2012, 2016b; Uller & Laland 2019), as opposed to attempting to "characterize" genera or other taxa. Systematics research is not accomplished through the reductionist agenda associated with sequence data. As aptly noted by Dupré & Nicholson (2018: 26–27),

"...it has become increasingly clear to many biologists, as well as philosophers, that reductionism is at best a severely limited approach to understanding living systems.... In a world of processes, reductionism makes little sense.... When we accept that the living world is a process world, we are able to understand why reductionism in biology, despite its countless limited successes in local and fixed contexts, can never fully succeed as a global explanatory enterprise, even in principle."

The scope of causality that is the purview of evolutionary biology and systematics precludes reducing all or most explanatory interest to the level of nucleotides or amino acids, or thinking sequence data offer any kind of enhancement to the objective of inquiry. Also typically neglected in systematics is that explaining shared nucleotides or amino acids is not so simple a matter as implementing computer algorithms with those characters (cf. Fitzhugh 2016b, 2021, regarding downward causation; discussed by Mortimer et al. 2021). Such algorithms imply that all sequence data are explained via genetic drift or neutrality, whereas the spectre of downward causation accounting for sequence data in relation to natural selection due to emergent properties at higher organizational levels is unrealistically ignored (Fitzhugh 2016b, Mortimer et al. 2021). Implying that sequence data are somehow more worthy of attention than other classes of characters typically derive from thinking the objective of systematics is to obtain phylogenetic trees (e.g., "the tree of life"), "the" phylogeny, and/or that the larger number of characters provided by sequence data is more favourable under the guise of improving "statistical consistency" (Felsenstein 1978, Felsenstein 2004, Swofford et al. 1996, Heath, Hedtke & Hillis 2008, Assis 2014, Brower 2018; e.g., Goto 2016, Tilic et al. 2020). The popularity of "tree thinking" in systematics (e.g., O'Hara 1988, O'Hara 1994, O'Hara 1997, Meisel 2010, Baum & Smith 2012, Jenner 2024) has also encouraged the view that sequence data are the preferred means to infer phylogenetic trees *sensu* topologies, yet too often ignores acknowledging the multitude of explanatory hypotheses implied by those trees. Statistical consistency is a notion only relevant to the continual (inductive) testing of hypotheses "in the long run," not the abductive inferences of those hypotheses (Peirce 1902, Peirce 1932: 2.774–777, Rescher 1978, Fitzhugh 2012, Fitzhugh 2016b, Mortimer et al. 2021). More sequence data does not equate with improved systematics results.

Morphological Considerations

One of the further justifications that Meißner et al. (2023) make for recognizing Octomagelona is description of the thoracic chaetae among members of Magelona bizkaiensis in the analysis by Mortimer et al. (2021: table S1, coding matrix character 31). Meißner et al. (2023) suggest that these chaetae were incorrectly described as bilimbate by Mortimer et al. (2021), rather than unilimbate "as stated in the original description," i.e., Aguirrezabalaga et al. (2001). There are several problems with this assertion. First, in the original description of members of *M. bizkaiensis*, it states that all thoracic chaetae are "long and limbate capillaries," similar in size and form, but gives no further information. However, the illustration (albeit reproduced at low resolution) of a thoracic chaeta by Aguirrezabalaga et al. (2001: fig 2C) appears bilimbate, particularly in the basal half, so it is unclear from the original description the nature of the chaetae. Furthermore, it has long been recognized (Jones 1963, 1971, 1977, 1978; Mortimer & Clarke 2024) that there is intraspecific variation in limbate chaetae among magelonids. For instance, members of the following species have been recorded to possess both uni- and bilimbate chaetae: M. papillicornis F. Müller, 1858; M. longicornis Johnson, 1901; M. pitelkai Hartman, 1944; M. riojai Jones, 1963; M. hartmanae Jones, 1978; M. debeerei Clarke, Paterson, Florence & Gibbons, 2010, and M. ekapa Mortimer & Clarke, 2024. Although further observations of variation within magelonid thoracic chaetae are much needed, and many authors have undervalued the importance of fully describing chaetae (Brasil 2003, Mortimer et al. 2021), variation is nevertheless present. Observations by the current authors (KM, ACB) suggest that when both uni- and bilimbate chaetae are present, variation may occur along the thorax, shifting from unilimbate in the anterior thorax to bilimbate in the posterior (e.g., members of *M. debeerei*), whilst in other cases bilimbate chaetae may predominate but with more slender unilimbate chaetae at the outer margin of a fascicle, as is noted among members of M. ekapa (Mortimer & Clarke, 2024: figs 5p, r). In their phylogenetic analysis, Mortimer et al. (2021: 44) state that "For some individuals, both unilimbate and bilimbate chaetae have been recorded, however, the predominant form in each case was coded..." Therefore, the presence of unilimbate chaetae in *M. bizkaiensis* as noted by Meißner et al. (2023) does not indicate that the coding was incorrect. The SEM image in Meißner et al. (2023: fig. 12L) is from chaetiger 1, where, as noted above, chaetae are often more slender and unilimbate chaetae may occur. This is something which should be verified towards the posterior thorax, as well as within an individual fascicle.

Meißner *et al.* (2023) describe members of *Octomagelona borowskii* as having thoracic capillaries that are partly bilimbate, with irregularly bilimbate chaetae also present. They (Meißner *et al.* 2023: 22) argue that it "remains to be evaluated whether irregularly indented limbation represents a natural character state or an artefact due to the effect of fixative or mechanical treatment during sampling." Whilst we are in agreement that this is a character that needs further investigation, it is something that has been noted before, e.g., Hartman (1944), Jones (1978), Bolívar & Lana (1986) and Brasil (2003). The character appears consistently among members of a species, whilst is absent among others, suggesting its validity.

The phylogenetic analysis of Mortimer *et al.* (2021) highlights several characters of importance in the recognition of magelonid species: (1) presence/absence of prostomial horns (in addition to their form, i.e., distinct or rudimentary); (2) relative dimensions of the prostomium; (3) morphology of anterior lamellae, including presence/ absence of superior dorsal lobes; (4) development of the anterior lamellae; (5) presence/absence of specialised chaetae on chaetiger 9; and (6) presence of lateral abdominal pouches. The notable morphological characters among individuals to which the phylogenetic hypothesis formerly named *Octomagelona* refer include (1') wider than long prostomia with rudimentary horns carrying one pair of prostomial ridges; (2') a large achaetous region; (3') filiform anterior lamellae in subchaetal position, without superior dorsal lobes; (4') rounded/bulbous anterior chaetigers; (5') anterior region which tapers from the achaetous region to "thoracic/abdominal" junction. These characters are, however, shared with members of some other magelonid species which possess nine anterior chaetigers. Not surprisingly, the phylogenetic analyses of Brasil (2003) and Mortimer *et al.* (2021) found *Magelona* paraphyletic relative to *Octomagelona*, and members of the latter genus closely related to members of species such as *M. variolamellata* Bolívar & Lana (1986), *M. equilamellae* Harmelin, 1964, *Magelona* sp. I of Uebelacker & Jones (1984), and *M. polydentata* Jones, 1963, on the basis of many shared morphological characters.

Unfortunately, the specimens of *Magelona borowskii* and *M*. sp. cf. *M. borowskii* were illustrated by Meißner *et al.* (2023: fig. 12) using SEM (the paratype SEMs being the main source to illustrate members of the species; no illustrations of the holotype are provided) and appear to have shrivelled during critical point drying, such that the overall conditions of the material make it very difficult to relate to members of other magelonid species. There are

specimens from Mexico, Australia and West Africa that are members of several undescribed magelonid species with eight anterior chaetigers awaiting description (Brasil, 2003; Mortimer *et al.*, 2021, Parapar *et al.*, 2021). These will undoubtedly be informative in future analyses.

Conclusion

There are no scientific justifications for reinstating the formal name *Octomagelona* and force *Magelona* to again be paraphyletic. Nomenclatural decisions are secondary to the goal of scientific inquiry as applied to biological systematics, not *vice versa*. It is critical to again emphasize Mortimer *et al.*'s (2021) discussion that since taxa are explanatory hypotheses, they are products of non-deductive reasoning known as abduction (Fitzhugh 2006a, 2012, 2016c, 2021; Mortimer *et al.* 2021), and as a consequence those hypotheses must take into account the requirement of total evidence (Fitzhugh 2006b, 2014). Consideration of all relevant characters is imperative, not just one or several characters deemed "distinctive" (limitations imposed by downward causation in relation to sequence data notwithstanding, cf. Fitzhugh 2016b, Mortimer *et al.* 2021). Just as important, specimens with "distinctive" characters cannot warrant formal names that result in paraphyly.

References

Aguirrezabalaga, F., Ceberio, A. & Fiege, D. (2001) *Octomagelona bizkaiensis* (Polychaeta: Magelonidae) a new genus and species from the Capbreton Canyon (Bay of Biscay, north-east Atlantic). *Journal of the Marine Biological Association of the United Kingdom*, 81, 221–224.

https://doi.org/10.1017/S0025315401003678

Anjum, R.L. & Mumford, S. (2018) *Causation in Science and the Methods of Scientific Discovery*. Oxford University Press, New York, New York, 278 pp.

https://doi.org/10.1093/oso/9780198733669.001.0001

Assis, L.C.S. (2014) Testing evolutionary hypotheses: from Willi Hennig to angiosperm phylogeny group. *Cladistics*, 30, 240–242.

https://doi.org/10.1111/cla.12048

- Baum, D.A. & Smith, S.D. (2012) *Tree Thinking: An Introduction to Phylogenetic Biology*. Roberts and Co., Greenwood Village, 476 pp.
- Bolívar, G.A. & Lana, P.C. (1986) Magelonidae (Annelida: Polychaeta) do litoral sudeste do Brasil. *Neritica*, 1, 131–147. https://doi.org/10.5380/rn.v1i3.41200
- Brasil, A.C. (2003) Filogenia de Magelonidae Cunningham & Ramage, 1888 (Annelida—Polychaeta) com base na morfologia externa. PhD thesis, Universidade Federal do Paraná, 113 pp.
- Brower, A.V.Z. (2018) Statistical consistency and phylogenetic inference: a brief review. *Cladistics*, 34, 562–567. https://doi.org/10.1111/cla.12216
- Clarke, D.T., Paterson, G.L.J., Florence, W.K. & Gibbons, M.J. (2010) A new species of *Magelona* (Polychaeta: Magelonidae) from southern Namibia. *African Natural History*, 6, 77–82.
- Currie, A. (2018) *Rock, Bone, and Ruin: An Optimist's Guide to the Historical Sciences*. The MIT Press, Cambridge, 372 pp. https://doi.org/10.7551/mitpress/11421.001.0001
- Dupré, J. & Nicholson, D.J. (2018) A manifesto for a processual philosophy of biology. *In*: Nicholson, D.J. & Dupré, J. (Eds.), *Everything Flows: Towards a Processual Philosophy of Biology*. Oxford University Press, Oxford, pp. 3–45. https://doi.org/10.1093/oso/9780198779636.001.0001
- Felsenstein, J. (1978) Cases in which parsimony or compatibility methods will be positively misleading. *Systematic Zoology*, 27, 401–410.

https://doi.org/10.1093/sysbio/27.4.401

Felsenstein, J. (2004) *Inferring Phylogenies*. Sinauer Associates Inc., Sunderland, Massachusetts, 664 pp. https://doi.org/10.1093/sysbio/27.4.401

Fiege, D., Licher, F. & Mackie, A.S.Y. (2000) A partial review of the European Magelonidae (Annelida: Polychaeta): Magelona mirabilis redefined and M. johnstoni sp. nov. distinguished. Journal of the Marine Biological Association of the United Kingdom, 80, 215–234.

https://doi.org/10.1017/S0025315499001800

Fitzhugh, K. (2005) The inferential basis of species hypotheses: the solution to defining the term 'species'. *Marine Ecology*, 26, 155–165.

https://doi.org/10.1111/j.1439-0485.2005.00058.x

Fitzhugh, K. (2006a) The abduction of phylogenetic hypotheses. *Zootaxa*, 1145 (1), 1–110. https://doi.org/10.11646/zootaxa.1145.1.1 Fitzhugh, K. (2006b) The 'requirement of total evidence' and its role in phylogenetic systematics. *Biology and Philosophy*, 21, 309–351.

https://doi.org/10.1007/s10539-005-7325-2

- Fitzhugh, K. (2008) Abductive inference: implications for 'Linnean' and 'phylogenetic' approaches for representing biological systematization. *Evolutionary Biology*, 35, 52–82. https://doi.org/10.1007/s11692-008-9015-x
- Fitzhugh, K. (2009) Species as explanatory hypotheses: refinements and implications. *Acta Biotheoretica*, 57, 201–248. https://doi.org/10.1007/s10441-009-9071-3
- Fitzhugh, K. (2012) The limits of understanding in biological systematics. *Zootaxa*, 3435 (1), 40–67. https://doi.org/10.11646/zootaxa.3435.1.2
- Fitzhugh, K. (2013) Defining 'species', 'biodiversity', and 'conservation' by their transitive relations. In: Pavlinov, I.Y. (Ed.), The Species Problem—Ongoing Problems. InTech, New York, New York, pp. 93–130. https://doi.org/10.5772/52331
- Fitzhugh, K. (2014) Character mapping and cladogram comparison versus the requirement of total evidence: does it matter for polychaete systematics? *Memoirs of Museum Victoria*, 71, 67–78. https://doi.org/10.24199/j.mmv.2014.71.07
- Fitzhugh, K. (2016a) Ernst Mayr, causal understanding, and systematics: an example using sabelliform polychaetes. *Invertebrate Biology*, 135, 302–313.
- https://doi.org/10.1111/ivb.12133
- Fitzhugh, K. (2016b) Sequence data, phylogenetic inference, and implications of downward causation. *Acta Biotheoretica*, 64, 133–160.

https://doi.org/10.1007/s10441-016-9277-0

- Fitzhugh, K. (2016c) Dispelling five myths about hypothesis testing in biological systematics. *Organisms Diversity & Evolution*, 16, 443–465.
 - https://doi.org/10.1007/s13127-016-0274-6
- Fitzhugh, K. (2021) Phylogenetic inference and the misplaced premise of substitution rates. *Acta Biotheoretica*, 69, 799–819. https://doi.org/10.1007/s10441-021-09412-4
- Fitzhugh, K., Nogueira, J.M.M., Carrerette, O. & Hutchings, P. (2015) An assessment of the status of Polycirridae genera (Annelida: Terebelliformia) and evolutionary transformation series of characters within the family. *Zoological Journal of the Linnean Society*, 174, 666–701. https://doi.org/10.1111/zoj.12259
- Goto, R. (2016) A comprehensive molecular phylogeny of spoon worms (Echiura Annelida): implications for morphological evolution, the origin of dwarf males, and habitat shifts. *Molecular Phylogenetics and Evolution*, 99, 247–260. https://doi.org/10.1016/j.ympev.2016.03.003
- Harmelin, J.G. (1964) Étude de l'endofaune des 'mattes' d'herbiers de *Posidonia oceanica* Delile. *Recueil des Travaux de la Station Marine d'Endoume*, 35, 43–105.
- Hartman, O. (1944) Polychaetous annelids from California, including two new genera and nine new species. *Allan Hancock Pacific Expeditions*, 10, 239–304.
- Hanson, N.R. (1958) Patterns of Discovery: An Inquiry into the Conceptual Foundations of Science. Cambridge University Press, New York, New York, 241 pp.
- Heath, T.A., Hedtke, S.M. & Hillis, D.M. (2008) Taxon sampling and the accuracy of phylogenetic analysis. *Journal of Systematics and Evolution*, 46, 239–257.
- https://doi.org/10.3724/SP.J.1002.2008.08016
- Hempel, C.G. (1965) Aspects of Scientific Explanation and other Essays in the Philosophy of Science. The Free Press, New York, New York, 505 pp.
- Hennig, W. (1966) Phylogenetic Systematics. University of Illinois Press, Urbana, Illinois, 263 pp.
- Hernández-Alcántara, P. & Solís-Weiss, V. (2000) Magelonidae from the Mexican Pacific and northern Gulf of Mexico, with the description of a new genus (*Meredithia*) and four new species. *In*: Reish, D.J. & Lana, P. (Eds.), *Proceedings of the 6th International Polychaete Conference, Curitiba, Brazil, 1998. Bulletin of Marine Science,* 67, pp. 625–644.
- Hoyningen-Huene, P. (2013) *Systematicity: The Nature of Science*. Oxford University Press, New York, New York, 287 pp. https://doi.org/10.1093/acprof:oso/9780199985050.001.0001
- International Commission on Zoological Nomenclature. (1999) *International Code of Zoological Nomenclature*. The International Trust for Zoological Nomenclature, London, 306 pp.
- Jenner, R.A. (2024) Lineage thinking in evolutionary biology: How to improve the teaching of tree thinking. *Science & Education*. [published online]
 - https://doi.org/10.1007/s11191-024-00531-1
- Johnson, H.P. (1901) The Polychaeta of the Puget Sound region. *Proceedings of the Boston Society for Natural History*, 29, 381–437, pls. 1–19.
- Jones, M.L. (1963) Four new species of *Magelona* (Annelida, Polychaeta) and a redescription of *Magelona longicornis* Johnson. *American Museum Novitates*, 2164, 1–31.
- Jones, M.L. (1968) On the morphology, feeding, and behavior of Magelona sp. Biological Bulletin, 134, 272-297.

https://doi.org/10.2307/1539604

Jones, M.L. (1971) Magelona berkeleyi n. sp. from Puget Sound (Annelida: Polychaeta) with a further redescription of Magelona longicornis Johnson and a consideration of recently described species of Magelona. Journal of the Fisheries Research Board of Canada, 28, 1445–1454.

https://doi.org/10.1139/f71-223

- Jones, M.L. (1977) A redescription of Magelona papillicornis F. Müller. In: Reish, D.J. & Fauchald, K. (Eds.), Essays on Polychaetous Annelids in Memory of Dr Olga Hartman. Allan Hancock Foundation, University of Southern California, Los Angeles, California, pp. 247–266.
- Jones, M.L. (1978) Three new species of *Magelona* (Annelida, Polychaeta) and a redescription of *Magelona pitelkai* Hartman. *Proceedings of the Biological Society of Washington*, 91, 336–363.
- Mahner, M. & Bunge, M. (1997) Foundations of Biophilosophy. Springer, New York, New York, 423 pp. https://doi.org/10.1007/978-3-662-03368-5
- Meisel, R.P. (2010) Teaching tree-thinking to undergraduate biology students. *Evolution: Education and Outreach*, 3, 621–628.

https://doi.org/10.1007/s12052-010-0254-9

Meißner, K., Schwentner, M., Götting, M., Knebelsberger, T. & Fiege, D. (2023) Polychaetes distributed across oceans examples of widely recorded species from abyssal depths of the Atlantic and Pacific Oceans. Zoological Journal of the Linnean Society, 199, 906–944.

https://doi.org/10.1093/zoolinnean/zlad069

- Mortimer, K. & Clarke, D.T. (2024) Untangling the Magelonidae (Annelida: Polychaeta) of southern Africa, including the description of a new species. *African Zoology*. [published online] https://doi.org/10.1080/15627020.2024.2311085
- Mortimer, K., Fitzhugh, K., dos Brasil, A.C. & Lana, P. (2021) Who's who in *Magelona*: phylogenetic hypotheses under Magelonidae Cunningham & Ramage, 1888 (Annelida: Polychaeta). *PeerJ*, 9, e11993. https://doi.org/10.7717/peerj.11993
- Müller, F. (1858) Einiges über die Anneliden fauna der Insel Santa Catharina an der brasilianischen Küste. Archiv für Naturgeschichte, 24, 211–220.
- Nogueira, J.M.M., Fitzhugh, K. & Rossi, M.C.S. (2010) A new genus and new species of fan worms (Polychaeta: Sabellidae) from Atlantic and Pacific Oceans the formal treatment of taxon names as explanatory hypotheses. *Zootaxa*, 2603 (1), 1–52.

https://doi.org/10.11646/zootaxa.2603.1.1

- Nogueira, J.M.M., Fitzhugh, K. & Hutchings, P. (2013) The continuing challenge of phylogenetic relationships in Terebelliformia (Annelida: Polychaeta). *Invertebrate Systematics*, 27, 186–238. https://doi.org/10.1071/IS12062
- Nogueira, J.M.M., Fitzhugh, K., Hutchings, P. & Carrerette, O. (2017) Phylogenetic analysis of the family Telothelepodidae Nogueira, Fitzhugh & Hutchings, 2013 (Annelida: Polychaeta). *Marine Biology Research*, 13, 671–692. https://doi.org/10.1080/17451000.2017.1283526
- Nola, R. & Sankey, H. (2007) *Theories of Scientific Method: An Introduction*. McGill Queen's University Press, Ithaca, New York, 240 pp.

https://doi.org/10.1017/UPO9781844653881

https://doi.org/10.2307/2992272

O'Hara, R.J. (1994) Evolutionary history and the species problem. *American Zoologist*, 34, 12–22. https://doi.org/10.1093/icb/34.1.12

- O'Hara, R.J. (1997) Population thinking and tree thinking in systematics. *Zoologica Scripta*, 26, 323–329. https://doi.org/10.1111/j.1463-6409.1997.tb00422.x
- Oosterbroek, P. (1987) More appropriate definitions of paraphyly and polyphyly, with a comment on the Farris 1974 model. *Systematic Biology*, 36, 103–108. https://doi.org/10.2307/2413263
- Parapar, J., Mortimer, K. Capa, M. & Moreira. J. (2021). On the systematics and biodiversity of the Palaeoannelida. *Diversity*, 13, 41.

https://doi.org/10.3390/d13020041

- Peirce, C.S. (1902) Reasoning. In: Baldwin, J.A. & Rand, B. (Eds.), Dictionary of Philosophy And Psychology: Prefatory Note. Text, Le-Z. Addenda: Indices. I. Greek Terms. II. Latin Terms. III. German Terms. IV. French Terms. V. Italian Terms. The Macmillan Company, New York, New York, pp. 426–428.
- Peirce, C.S. (1932) Collected Papers of Charles Sanders Peirce, Volume 2, Elements of Logic. Harvard University Press, Cambridge, Massachusetts, 535 pp.
- Popper, K.R. (1983) *Objective Knowledge: An Evolutionary Approach*. Oxford University Press, New York, New York, 395 pp.

Popper, K.R. (1992) Realism and the Aim of Science. Routledge, New York, New York, 420 pp.

O'Hara, R.J. (1988) Homage to Clio, or, toward an historical philosophy for evolutionary biology. Systematic Zoology, 37, 142–155.

- Potochnik, A. (2017) *Idealization and the Aims of Science*. University of Chicago Press, Chicago, Illinois, 252 pp. https://doi.org/10.7208/chicago/9780226507194.001.0001
- Potochnik, A. (2020) What constitutes an explanation in biology? In: Kampourakis, K. & Uller, T. (Eds.), Philosophy of Science for Biologists. Cambridge University Press, New York, pp. 21–35. https://doi.org/10.1017/9781108648981.003
- Read, G. & Fauchald, K. (Eds.) (2024). World Polychaeta Database. Magelonidae Cunningham & Ramage, 1888. World Register of Marine Species. Available from: https://www.marinespecies.org/aphia.php?p=taxdetails&id=914 (accessed 22 July 2024)
- de Regt, H.W., Leonelli, S. & Eigner, K. (2009) Focusing on scientific understanding. *In*: de Regt, H., Leonelli, S. & Eigner, K. (Eds.), *Scientific Understanding: Philosophical Perspectives*. University of Pittsburgh Press, Pittsburgh, pp. 1–17. https://doi.org/10.2307/j.ctt9qh59s
- Rescher, N. (1970) Scientific Explanation. The Free Press, New York, New York, 242 pp.
- Rescher, N. (1978) *Peirce's Philosophy of Science: Critical Studies in his Theory of Induction and Scientific Method*. University of Notre Dame Press, Notre Dame, 119 pp.
- Salmon, W.C. (1984) Scientific Explanation and the Causal Structure of the World. Princeton University Press, Princeton, New Jersey, 305 pp.
- Schmidt-Lebuhn, A.N. (2012) Fallacies and false premises—a critical assessment of the arguments for the recognition of paraphyletic taxa in botany. *Cladistics*, 28, 174–187. https://doi.org/10.1111/j.1096-0031.2011.00367.x

Strahler, A.N. (1992) Understanding Science: An Introduction to Concepts and Issues. Prometheus Books, Buffalo, 409 pp.

- Swofford, D.L., Olsen, G.J., Waddell, P.J. & Hillis, D.M. (1996) Phylogenetic inference. *In*: Hillis, D.M., Moritz, C. & Mable, B.K. (Eds.), *Molecular Systematics*. Sinauer Associates, Sunderland, Massachusetts, pp. 407–514.
- Thagard, P. (2004) Rationality and science. In: Mele, A. & Rawlings, P. (Eds.), Handbook of Rationality. Oxford University Press, Oxford, pp. 363–379.
- https://doi.org/10.1093/0195145399.003.0019
- Tilic, E., Sayyari, E., Stiller, J., Mirarab, S. & Rouse, GW. (2020) More is needed Thousands of loci are required to elucidate the relationships of the 'flowers of the sea' (Sabellida, Annelida). *Molecular Phylogenetics and Evolution*, 151, 106892. https://doi.org/10.1016/j.ympev.2020.106892
- Uebelacker, J.M. & Jones, M.L. (1984) Family Magelonidae. In: Uebelacker, J.M. & Johnson, P.G. (Eds.), Taxonomic guide to the polychaetes of the northern Gulf of Mexico. Vol. 3. Final report to the U.S. Department of the Interior, Minerals Management Service, contract 14-12-001-29091, report no. OCS Study 84-0049. Barry A. Vittor and Associates, Mobile, Alabama, pp. 7.1–7.29.
- Uller, T. & Laland, K.N. (2019) Evolutionary causation. In: Uller, T. & Laland, K.N. (Eds.), Evolutionary Causation: Biological and Philosophical Reflections. The MIT Press, Cambridge, pp. 1–12. https://doi.org/10.7551/mitpress/11693.003.0002
- Van Fraassen, B.C. (1990) The Scientific Image. Clarendon Press, New York, New York, 235 pp.
- Zachos, F.E. (2014) Paraphyly—again!? A plea against the dissociation of taxonomy and phylogenetics. *Zootaxa*, 3764 (5), 594–596.

https://doi.org/10.11646/zootaxa.3764.5.8