

The “new phylogeny”. What is new about it?¹

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Ideas about animal phylogeny have been evolving ever since HAECKEL (1866) drew his famous phylogenetic tree, which had only very broad information about the interrelationships of the phyla.

However, already in 1888, HATSCHEK (1888) created a classification with many of the names we see in modern discussions: Protaxonia or Coelenterata (now often called Diploblastica) for Spongia + Cnidaria + Ctenophora, and Heteraxonia or Bilateria for Zygoneura + Ambulacralia (a misspelling of Ambulacraria) + Chordonii (Tab. 1). He put much emphasis on the nervous system of the Zygoneura with a paired (or secondarily fused) ventral nerve cords and on the presence of trochophora-type larvae in several of the zygoneuran groups.

GROBBEN (1908) coined the terms Protostomia for HATSCHEK’s Zygoneura and Deuterostomia for Ambulacraria + Chordonii. This scheme is retained almost unaltered in most German textbooks until this day, for example, GROBBEN (1910), GROBBEN & KÜHN (1932), KAESTNER (1954/55), GRUNER (1980), AX (1995), and WESTHEIDE & RIEGER (2007), in some cases with slightly changed names. This must evidently be regarded as “the classical morphology-based bilaterian phylogeny”.

The first volume of HYMAN’s enormously influential series “The Invertebrates” (HYMAN 1940) had a chapter on classification, where she discussed various classificatory schemes, but it is clear, that she did not put much faith in a phylogeny (see also JENNER 2004). For practical purposes,

she arranged the bilaterians in three grades: Acoelomata, Pseudocoelomata and Eucoelomata. However, her accompanying diagram (HYMAN 1940, fig. 5) shows relationships which are in good accordance with HATSCHEK’s classical scheme, and the three names Acoelomata, Pseudocoelomata and Eucoelomata are not found in the drawing. Her books were much respected in the United States, and her practical arrangement of the bilaterian phyla in three groups has crept into many American college textbooks as a classification. However, the larger university level textbooks, such as the several editions of BARNES’ “Invertebrate Zoology” (BARNES 1974; RUPPERT & BARNES 1994; RUPPERT et al. 2004) and BRUSCA & BRUSCA’s “Invertebrates” (BRUSCA & BRUSCA 1990, 2003), have retained the classical arrangement of Protostomia + Deuterostomia.

Many American textbooks have earlier used HYMAN’s scheme or hybrids with both classifications indicated, but have now changed to Protostomia (= Lophotrochozoa + Ecdysozoa) + Deuterostomia, see for example, STRICKBERGER (1995, 2000), RAVEN & JOHNSON (1989), and RAVEN et al. (2008).

Also British textbooks, such as BARNES et al. (1988 and 2001) have now changed from a “phylogenetic lawn”, as inspired by WILLMER (1990), to the Protostomia-Deuterostomia classification.

Quite misleadingly, many papers on molecular phylogeny have called the phylogeny which uses the Protostomia-Deuterostomia division the “new phylogeny” as opposed to the “traditional morphology-based phylogeny”

Tab. 1. The traditional classification of the Bilateria proposed by HATSCHEK (1888) and GROBBEN (1908) corresponds in principle to modern classifications based on both morphology, for example NIELSEN (1995, 2001), and molecular biology, for example DUNN et al. (2008), whereas the classification called “the traditional morphology-based classification” in many molecular phylogenetic papers, here exemplified by the paper by ADOUTTE et al. (1999), and in many college-level American textbooks is based on a misinterpretation of HYMAN (1940).

HATSCHEK 1888	GROBBEN 1908	NIELSEN 1995	ADOUTTE et al. 1999
Heteraxonia = Bilateria	= Coelomata	Bilateria	Bilateria
Zygoneura	= Protostomia	Protostomia	Acoelomata
Ambulacralia	= Deuterostomia	Deuterostomia	Pseudocoelomata
Chordonii			Eucoelomata

¹ Contribution to the WILLI-HENNIG-Symposium on Phylogenetics and Evolution, University of Hohenheim, 29 September – 2 October 2009.

based on HYMAN's arrangement, for example ADOUTTE et al. (2000), HALANYCH (2004) and LARTILLOT & PHILIPPE (2008). The division of the Protostomia into Lophotrochozoa + Ecdysozoa was indeed new, but to describe HYMAN's arrangement as the traditional morphology-based phylogeny can in a friendly view only be seen as an unacceptable ignorance of the literature on animal morphology from over a century.

It can only be hoped that we will not again see the Acoelomata-Pseudocoelomata-Coelomata concept described as the "traditional, morphology-based phylogeny".

References

- ADOUTTE, A., BALAVOINE, G., LARTILLOT, N., LESPINET, O., PRUD'HOMME, B. & DE ROSA, R. (2000): The new animal phylogeny: reliability and implications. – Proceedings of the National Academy of Sciences of the United States of America, **97**: 4453–4456.
- AX, P. (1995): *Das System der Metazoa I*; Stuttgart (Gustav Fischer).
- BARNES, R. D. (1974): *Invertebrate Zoology*, 3rd ed.; Philadelphia (W. B. Saunders).
- BARNES, R. S. K., CALOW, P. & OLIVE, P. J. W. (1988): *The Invertebrates: A New Synthesis*; Oxford (Blackwell).
- BARNES, R. S. K., CALOW, P., OLIVE, P. J. W., GOLDING, D. W. & SPICER, J. I. (2001): *The Invertebrates. A Synthesis*, 3rd ed.; Malden, MA (Blackwell).
- BRUSCA, R. C. & BRUSCA, G. J. (1990): *Invertebrates*; Sunderland, MA (Sinauer).
- BRUSCA, R. C. & BRUSCA, G. J. (2003): *Invertebrates*, 2nd ed.; Sunderland, MA (Sinauer).
- DUNN, C. W., HEJNOL, A., MATUS, D. Q., PANG, K., BROWNE, W. E., SMITH, S. A., SEAVER, E. C., ROUSE, G. W., OBST, M., EDGECOMBE, G. D., SØRENSEN, M. V., HADDOCK, S. H. D., SCHMIDT-RHAESA, A., OKUSU, A., KRISTENSEN, R. M., WHEELER, W., MARTINDALE, M. Q. & GIRIBET, G. (2008): Broad phylogenomic sampling improves resolution of the animal tree of life. – *Nature*, **452**: 745–749.
- GROBEN, K. (1908): Die systematische Einteilung des Tierreichs. – *Verhandlungen der Kaiserlich-Königlichen Zoologisch-Botanischen Gesellschaft in Wien*, **58**: 491–511.
- GROBEN, K. (1910): CLAUD-GROBEN: *Lehrbuch der Zoologie*, 2nd ed.; Marburg (Elvert'sche Verlagsbuchhandlung).
- GROBEN, K. & KÜHN, A. (1932): *Lehrbuch der Zoologie*, 10th ed. (begründet von C. CLAUS); Berlin (Julius Springer).
- GRUNER, H.-E. (1980): *Lehrbuch der Speziellen Zoologie*, 4th ed. (begründet von A. KAESTNER), Band I: Wirbellose Tiere, 1. Teil; Stuttgart (Gustav Fischer).
- HAECKEL, E. (1866): *Generelle Morphologie der Organismen*. 2 vols.; Berlin (Georg Reimer).
- HALANYCH, K. M. (2004): The new view of animal phylogeny. – *Annual Review of Ecology, Evolution and Systematics*, **35**: 229–256.
- HATSCHKE, B. (1888): *Lehrbuch der Zoologie*, 1. Lieferung (pp. 1–144); Jena (Gustav Fischer).
- HYMAN, L. H. (1940): *The Invertebrates*, vol. 1. Protozoa through Ctenophora; New York (McGraw-Hill).
- JENNER, R. A. (2004): Libbie Henrietta Hyman (1888–1969): from developmental mechanisms to the evolution of animal body plans. – *Journal of Experimental Zoology (Molecular Development and Evolution)*, **302B**: 413–423.
- KAESTNER, A. (1954/55): *Lehrbuch der Speziellen Zoologie*, Teil I: Wirbellose, 1 Halbband; Jena (Gustav Fischer).
- LARTILLOT, N. & PHILIPPE, H. (2008): Improvement of molecular phylogenetic inference and the phylogeny of the Bilateria. – *Philosophical Transactions of the Royal Society of London, Series B*, **363**: 1463–1472.
- NIELSEN, C. (1995): *Animal Evolution: Interrelationships of the Living Phyla*; Oxford (Oxford University Press).
- NIELSEN, C. (2001): *Animal Evolution: Interrelationships of the Living Phyla*, 2nd ed.; Oxford (Oxford University Press).
- RAVEN, P. H. & JOHNSON, G. B. (1989): *Biology*, 2nd ed.; St. Louis (Times Mirror/Mosby College Publishing).
- RAVEN, P. H., JOHNSON, G. B., LOSOS, J. B., MASON, K. A. & SINGER, S. R. (2008): *Biology*, 8th ed.; Boston (McGraw-Hill).
- RUPPERT, E. E. & BARNES, R. D. (1994): *Invertebrate Zoology*, 6th ed.; Fort Worth (Saunders College Publishing).
- RUPPERT, E. E., FOX, R. S. & BARNES, R. D. (2004): *Invertebrate Zoology: A Functional Evolutionary Approach* (7th ed. of R. D. BARNES' *Invertebrate Zoology*); Belmont, CA (Brooks/Cole).
- STRICKBERGER, M. W. (1995): *Evolution*, 2nd ed.; Boston (Jones and Bartlett Publishers).
- STRICKBERGER, M. W. (2000): *Evolution*, 3rd ed.; Boston (Jones and Bartlett Publishers).
- WESTHEIDE, W. & RIEGER, R. (2007): *Spezielle Zoologie. Teil 1: Einzeller und Wirbellose Tiere*. 2nd ed.; Heidelberg (Elsevier, Spektrum).
- WILLMER, P. (1990): *Invertebrate Relationships. Patterns in Animal Evolution*; Cambridge (Cambridge University Press).

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Received and accepted as extended summary of oral presentation: 15 April 2010.