

# Review of data for a morphological look on Xenacoelomorpha (Bilateria incertae sedis)

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**Abstract** Recent investigations by means of high-tech morphology, evo-devo studies and molecular data suggest that the taxon Xenacoelomorpha (Nemertodermatida and Acoela plus *Xenoturbella*), formerly considered as primitive flatworms (Plathelminthes) or even bivalve Mollusca, represents either a quite plesiomorphic grouping as the earliest bilaterian offshoot or but is a substantially reduced and simplified sidebranch of ambulacralian Deuterostomia. Herein, I provide a compilation and review of the current morphological data and possible interpretations of the various character states. Phenotypic and genotypic data suggest monophyly of Xenacoelomorpha. There is no specific similarity between xenacoelomorphs and deuterostome larvae, and reduction appears improbable in free-living and predatory animals. Accordingly, Xenacoelomorpha are more likely similar to Urbilateria rather than degenerated and simplified coelomate deuterostomes. If so, the ground pattern of Bilateria has been retained only partially in the remaining main bilaterian clades (Nephrozoa) after the deviation of the Xenacoelomorpha, namely the nervous system in the Deuterostomia and the body

cavity conditions in the acoelomate Lophotrochozoa (particularly Platyzoa), Gastrotricha and cycloneurialian Ecdysozoa.

**Keywords** Xenacoelomorpha · Urbilateria · Phylogeny

## Introduction

Up to the 1990s, the acoelomorph “turbellarians” have been regarded as primitive members of the phylum Plathelminthes (e.g. Ehlers 1985; Ax 1996) and even critical voices (e.g. Smith et al. 1986) held this view. However, more recent analyses of morphological (in particular, ultrastructural, immunocytochemical, ontogenetic and evo-devo data (Tables 1A–O and 2, also Haszprunar 1996a, b; Nielsen 2010) and in particular several independent and increasingly complex molecular data sets (Baguña and Riutort 2004a, b; Tables 1P and 2) have established the assumption that the Acoelomorpha are not to be included in the Plathelminthes, but represent a phylum proper (but see e.g., Tyler 2001 for a contrary view).

As most recently reviewed by Hejnol (2015a) and Nakano (2015), the phylogenetic position of the simply structured marine worm *Xenoturbella bocki* Westblad 1949 has been controversially discussed since its discovery. Most morphological data claimed a position among the most basal Bilateria, either as a phylum for its own or together with the Acoelomorpha (Table 3). However, certain phenotypic characteristic suggests deuterostome affinities (e.g. Obst et al. 2008). A period of about 10 years of assumed molluscan affinities was based on erroneously selected sequences (Norén and Jondelius 1997) and erroneously interpreted morphological, gametogenic and ontogenetic data (Israelsson 1997, 1999a, b; Israelsson and Budd 2005).

A number of authors have claimed a close affinity between Acoelomorpha and *Xenoturbella*, and a unifying taxon,

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“I can see no other escape from this dilemma . . . than that some of us should venture to embark on a synthesis of facts and theories, albeit with second-hand and incomplete knowledge of some of them - and at the risk of making fools of ourselves”.

Erwin Schrödinger (1944) in the preface of “What is Life”

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**Table 1** Ultrastructural, immunochemical and evo-devo studies on Acoela

| Organ/genera investigated                                 | Character studied                    | Methods applied        | Reference                    |
|---|--------------------------------------|------------------------|------------------------------|
| <b>A. Whole body</b>                                      |                                      |                        |                              |
| <i>Convoluta</i>  | Whole body                           | LM, cytochemistry, TEM | Pedersen 1964, 1965          |
| <i>Oligochoerus</i>                                       | Whole body, sperm                    | TEM                    | Klima 1967                   |
| <i>Hesilicium</i>   | Whole body                           | LM, TEM                | Crezée and Tyler 1976        |
| <i>Convoluta</i>  | Whole body                           | LM                     | Drobysheva 1979              |
| <i>Solenofilomorpha</i>                                   | Mitochondria, anaerobiosis           | TEM                    | Duffy and Tyler 1984         |
| <i>Solenofilomorpha, Otocelis</i>                         | Mitochondria, anaerobiosis           | TEM                    | Rieger et al. 1990           |
| Acoela  | Whole body, review                   | LM, TEM                | Rieger et al. 1991           |
| <i>Isodiametra pulchra</i>                                | Whole body, review                   | LM, TEM                | Achatz et al. 2013           |
| <b>B. Epidermis, ciliation</b>                            |                                      |                        |                              |
| 6 genera  | Epidermis, pulsatile bodies          | TEM                    | Dorey 1965                   |
| <i>Symsagittifera</i>                                     | Subepidermal glands                  | TEM                    | Oschman 1967                 |
| <i>Paratomella</i>  | Tips of epidermal cilia              | LM, TEM                | Tyler 1973                   |
| <i>Childia</i>  | Epidermal ciliary root system        | TEM                    | Hendelberg and Hedlund 1974  |
| <i>Mecynostomum, Symsagittifera</i>                       | Epidermis                            | TEM                    | Bedini & Papi 1974           |
| 5 genera of Solenofilomorphidae                           | Anatomy, epidermis                   | LM, TEM                | Crezée 1975                  |
| <i>Childia</i>  | Epidermal ciliary root system        | TEM                    | Hendelberg 1976, 1981        |
| 7 genera of 5 families                                    | Epidermal ciliation                  | TEM                    | Tyler 1979                   |
| <i>Convoluta, Kuma</i>                                    | Rhabdites                            | TEM                    | Smith et al. 1982            |
| <i>Archaphanostoma</i>                                    | Ciliogenesis                         | TEM                    | Tyler 1984a                  |
| <i>Diopisthoporus, Paratomella, Convoluta, Hesilicium</i> | Epidermis, cilia                     | TEM                    | Tyler 1984b                  |
| <i>Paratomella, Isodiametra</i>                           | Epidermis, parenchyma                | TEM                    | Smith and Tyler 1985b        |
| <i>Diopisthoporus, Isodiametra</i>                        | Ciliary root system                  | TEM                    | Smith et al. 1986            |
| <i>Pseudactinoposthia</i>                                 | Epidermal ciliation                  | TEM                    | Rohde et al. 1988b           |
| 6 genera  | Epidermal ciliation                  | TEM                    | Raikova 1989b                |
| <i>Isodiametra</i>  | Ciliary root system                  | TEM                    | Smith 1990                   |
| <i>Paratomella</i>  | Epidermis, pulsatile bodies          | TEM                    | Ehlers 1992a                 |
| <i>Paratomella</i>  | Whole body                           | TEM                    | Ehlers 1992b                 |
| <i>Anaperus</i>   | Epidermis, pulsatile bodies          | TEM                    | Ehlers 1992c                 |
| 6 genera  | Epidermis                            | TEM                    | Raikova 1992                 |
| <i>Isodiametra</i>  | Epidermis, collar receptors, muscles | TEM, phalloidin        | Pfistermüller and Tyler 2002 |
| <i>Isodiametra, Haplogonaria</i>                          | Epidermis, muscles                   | TEM, phalloidin        | Tyler and Hooge 2004         |
| <b>C. Frontal glands</b>                                  |                                      |                        |                              |
| <i>Convoluta</i>  | Frontal glands                       | TEM                    | Klauser et al. 1985          |
| <i>Diopisthoporus</i>                                     | Frontal glands                       | TEM                    | Smith and Tyler 1985a        |
| <i>Diopisthoporus, Otocelis, Patatomella</i>              | Frontal glands                       | TEM                    | Smith and Tyler 1986         |
| <i>Paratomella</i>  | Frontal glands                       | TEM                    | Ehlers 1992d                 |
| <b>D. Pulsatile bodies</b>                                |                                      |                        |                              |
| 6 genera  | Pulsatile bodies, epidermis          | TEM                    | Dorey 1965                   |
| <i>Isodiametra</i>  | Pulsatile bodies                     | TEM                    | Tyler et al. 1989            |
| <i>Paratomella</i>  | Pulsatile bodies, epidermis          | TEM                    | Ehlers 1992a                 |
| <i>Anaperus</i>   | Pulsatile bodies, epidermis          | TEM                    | Ehlers 1992c                 |
| <b>E. Musculature</b>                                     |                                      |                        |                              |
| <i>Convoluta, Oxyposthia</i>                              | Nervous and muscle system            | TEM                    | Lagutenko et al. 1989        |
| <i>Anaperus</i>   | Musculature                          | TEM                    | Ehlers 1994                  |
| <i>Paratomella</i>  | Musculature                          | TEM, phalloidin        | Tyler and Hyra 1994          |
| 8 genera of 6 families                                    | Musculature                          | Phalloidin             | Tyler and Hyra 1998          |
| <i>Isodiametra</i>  | Musculature, brain                   | TEM, phalloidin        | Tyler and Rieger 1999        |

**Table 1** (continued)

| Organ/genera investigated  | Character studied   | Methods applied                            | Reference                                       |
|--|---|--|---|
| <i>Isodiametra</i> [ <i>Convoluta</i> ]  | Live photo, myogenesis  | LM, TEM phalloidin                         | Ladurner and Rieger 2000                        |
| <i>Neochildia</i>  | Cleavage, musculature   | Blastomere labelling, phalloidin           | Henry et al. 2000                               |
| 24 genera of 11 families   | Musculature   | Phalloidin                                 | Hooge 2001                                      |
| <i>Anaperus</i> , <i>Childia</i> , <i>Faerlea</i> ,<br><i>Paraphanostomum</i> , <i>Avagina</i><br><i>Isodiametra</i> | Nervous and muscle system                                     | ICC  | Reuter et al. 2001a, b                          |
| <i>Convolutriloba</i>  | Epidermis, collar receptors, muscles                          | TEM, phalloidin                            | Pfistermüller and Tyler 2002                    |
| 5 genera of 4 families   | Musculature   | TEM phalloidin                             | Gschwentner et al. 2003                         |
| <i>Paraphanostoma</i> , <i>Childia</i>   | Whole mounts, musculature                                     | LM, phalloidin                             | Hooge 2003                                      |
| 14 genera of 3 families  | Musculature, H3, 18S rRNA                                     | Phalloidin, phylogenetics                  | Tekle et al. 2004                               |
| <i>Childia</i>   | Whole mounts, musculature                                     | LM, phalloidin                             | Hooge and Tyler 2005                            |
| <i>Childia</i>   | Copulatory muscles  | Phalloidin, CLSM                           | Raikova et al. 2006                             |
| <i>Convolutriloba</i>  | Budding, systematics, axes,<br>muscle and nervous system      | Molecular phylogenetics ICC,<br>phalloidin | Sikes and Bely 2008                             |
| <i>Symsagittifera</i>  | Myogenesis, neurogenesis                                      | Phalloidin                                 | Semmler et al. 2008                             |
| 8 genera   | Musculature, nervous system,<br>sperm, sagittocysts, genitals | TEM, ICC, phalloidin                       | Achatz et al. 2010                              |
| <i>Symsagittifera</i>  | Muscle  | Phalloidin                                 | Chiodin et al. 2011                             |
| <i>Isodiametra</i>   | Nervous system, musculature,<br>statocyst                     | Phalloidin, ICC, LM, TEM                   | Achatz and Martinez 2012                        |
| <i>Convoluta</i> , <i>Isodiametra</i> ,<br><i>Symsagittifera</i> , <i>Convolutriloba</i>                             | Sperm, statocyst, nervous system,<br>sagittocyst, musculature | LM, TEM, ICC 5-HT, phalloidin              | Achatz and Martinez 2012, Achatz<br>et al. 2013 |
| <i>Symsagittifera</i>  | Live, symbiosis, regeneration,<br>muscle and nervous system   | LM, TEM, ICC, phalloidin CLSM              | Bailly et al. 2014                              |
| <i>Haplogonaria</i>  | Musculature   | Phalloidin, CLSM                           | Hooge & Tyler 2015                              |
| <b>F. Sagittocysts</b>   |   |  |   |
| <i>Symsagittifera</i> , <i>Sagittifera</i>   | Sagittocysts, copulatory organs                               | SEM, TEM                                   | Mamkaev and Kostenko 1991                       |
| <i>Convoluta</i> , <i>Praesagittifera</i> ,<br><i>Symsagittifera</i> , <i>Amphiscolops</i>                           | Sagittocysts  | TEM  | Yamasu 1991                                     |
| <i>Convolutriloba</i>  | Sagittocysts  | TEM  | Gschwentner et al. 1999                         |
| <i>Symsagittifera</i>  | Function of sagittocysts                                      | LM   | Gschwentner et al. 2002                         |
| <i>Convolutriloba</i>  | Symbiotic algae, sagittocysts                                 | SEM, TEM                                   | Hirose and Hirose 2007                          |
| <i>Convoluta</i> , <i>Isodiametra</i> ,<br><i>Symsagittifera</i> , <i>Convolutriloba</i>                             | Sperm, statocyst, nervous system,<br>sagittocyst, musculature | LM, TEM, ICC 5-HT, phalloidin              | Achatz and Martinez 2012, Achatz<br>et al. 2013 |
| <b>G. Parenchyma</b>   |   |  |   |
| <i>Amphiscolops</i> , <i>Convoluta</i>   | Parenchyma, regeneration                                      | LM, experiments                            | Hanson 1967                                     |
| <i>Anaperus</i>  | Parenchyma  | LM, TEM                                    | Boguta and Mamkaev, Yu.V 1972                   |
| <i>Oxyposthia</i> , <i>Convoluta</i> , <i>Anaperus</i>   | Parenchyma  | TEM  | Mamkaev and Markosova 1979                      |
| <i>Isodiametra</i>   | Parenchyma  | TEM  | Smith 1981                                      |
| <i>Paratomella</i> , <i>Isodiametra</i>  | Parenchyma, epidermis   | TEM  | Smith and Tyler 1985b                           |
| <i>Symsagittifera</i> [ <i>Convoluta</i> ]   | Parenchym, regeneration                                       | TEM  | Hori et al. 1999                                |
| <i>Oxyposthia</i>  | Peripheral parenchyma   | TEM  | Markosova and Mamkaev 2000                      |
| <i>Convoluta</i>   | Parenchym   | TEM  | Gazizova et al. 2013                            |
| <b>H. Digestive system</b>   |   |  |   |
| <i>Oxyposthia</i> , <i>Convoluta</i><br><i>Aphanostoma</i>   | Gut syncytium   | TEM  | Ivanov and Mamkaev 1977                         |
| <i>Oxyposthia</i>  | Gut, feeding, digestion                                       | TEM  | Mamkaev and Markosova 1981,<br>1986             |
| <i>Diopisthoporus</i> ,<br><i>Solenofilomorpha</i>   | Pharynx   | TEM  | Doe 1981  |
| <i>Actinoposthia</i>   | Digestive system (with lumen!)                                | TEM  | Raikova 1987a, b                                |
| <i>Oxyposthia</i>  | Gut, digestion  | TEM  | Markosova 1987                                  |
| <i>Convoluta</i>   | Gut, digestion  | TEM  | Markosova 1989                                  |
| <i>Myopea</i> , <i>Solenofilomorpha</i>  | Pharynx   | TEM  | Todt and Tyler 2006                             |

**Table 1** (continued)

| Organ/genera investigated  | Character studied  | Methods applied                            | Reference                     |
|--|--|--|-------------------------------|
| <i>Hofstenia, Convoluta, Conapet Proporus, Paratomella</i>           | Pharynx  | TEM, phalloidin                            | Todt 2009                     |
| I. Nervous and sensory system  |  |  |                               |
| <i>Symsagittifera</i>  | Statocyst  | LM, TEM                                    | Ivanov et al. 1972            |
| <i>Anaperus, Symsagittifera, Diatomovora</i>                         | Nervous system   | LM, review                                 | Mamkaev and Ivanov 1970       |
| <i>Anaperus, Symsagittifera, Convoluta, Diatomovora, Aphanostoma</i> | Nervous system anatomy                                     | LM   | Mamkaev and Kotikova 1972     |
| <i>Symsagittifera</i>  | Statocyst  | LM, TEM                                    | Ferrero 1973                  |
| <i>Symsagittifera, Mecynostomum</i>                                  | Ciliary receptors  | LM, TEM                                    | Bedini et al. 1973            |
| <i>Convoluta</i>   | Eye  | LM, TEM                                    | Popova and Mamkaev 1986       |
| <i>Convoluta, xxxxx</i>  | Epidermal sensillae  | LM, TEM                                    | Popova and Mamkaev, Yu.V 1987 |
| <i>Convoluta, Oxyposthia</i>   | Nervous and muscle system                                  | TEM  | Lagutenko et al. 1989         |
| <i>Otocelis</i>  | Eye  | TEM  | Lanfranchi 1990               |
| <i>Actinoposthia, Aphanostoma</i>                                    | CA-neuric system   | ICC  | Joffe 1991                    |
| <i>Symsagittifera</i>  | Nervous system, morphogenesis of statocyst                 | LM, TEM                                    | Ferrero and Bedini 1991       |
| <i>Convoluta, Praesagittifera, Symsagittifera, Amphiscolops</i>      | Eye  | TEM  | Yamasu 1991                   |
| <i>Symsagittifera</i>  | Nervous system   | TEM  | Bedini and Lanfranchi 1991    |
| <i>Haploposthia, Actinoposthia, Anaperus, Aphanostoma</i>            | Nervous system, ciliary receptors                          | TEM  | Raikova 1989a, 1991           |
| <i>Anaperus, Childia, Actinoposthia, Mecynostomum</i>                | Nervous system   | TEM, ICC 5-HT<br>ICC-FMRFamide             | Reuter et al. 1998            |
| <i>Isodiametra</i>   | Musculature, brain   | TEM, phalloidin                            | Tyler and Rieger 1999         |
| <i>Symsagittifera</i>  | Nervous system   | ICC GABA                                   | Bedini et al. 2001            |
| <i>Ferlea, Avagina, Paraphanostoma</i>                               | Nervous system   | ICC GYIRF, 5-HT                            |                               |
| 27 genera in 12 families   | Nervous system   | Review, ICC anti-tubulin                   | Raikova et al. 2001           |
| <i>Anaperus, Childia, Faerlea, Paraphanostomum, Avagina</i>          | Nervous and muscle System                                  | ICC  | Reuter et al. 2001a, b        |
| <i>Isodiametra</i>   | Epidermis, collar receptors, muscles                       | TEM, phalloidin                            | Pfistermüller and Tyler 2002  |
| <i>Paraphanophora</i>  | Nervous system   | TEM, ICC                                   | Raikova et al. 2004a          |
| <i>Hofstenia, Proporus, Conaperta,</i>                               | Receptors of mouth and pharynx                             | TEM  | Todt and Tyler 2007           |
| <i>Convoluta Convolutriloba</i>                                      | Regeneration of nervous system                             | ICC 5-HT                                   | Gaerber et al. 2007           |
| 7 genera   | Nervous system anatomy                                     | ICC 5-HT, FMRFamid                         | Kotikova and Raikova 2008     |
| <i>Convolutriloba</i>  | Budding, systematics, axes, muscle and nervous system      | Molecular phylogenetics<br>ICC, phalloidin | Sikes and Bely 2008           |
| <i>Symsagittifera</i>  | Myogenesis, neurogenesis                                   | Phalloidin                                 | Semmler et al. 2008           |
| <i>Convolutriloba</i>  | Neurogenesis   | ICC  | Hejnoj and Martindale 2008c   |
| 11 genera in 9 families  | Nervous system   | ICC review                                 | Semmler 2009                  |
| <i>Symsagittifera</i>  | Nervous + sensory system, neoblasts                        | 3D, TEM, ICC                               | Bery et al. 2010              |
| 8 genera   | Musculature, nervous system, sperm, sagittocysts, genitals | TEM, ICC, phalloidin                       | Achatz et al. 2010            |
| <i>Symsagittifera</i>  | Neurogenesis, SoxB2  | ICC, gene expression                       | Semmler et al. 2010           |
| <i>Isodiametra</i>   | Nervous system, musculature statocyst                      | Phalloidin, ICC, LM, TEM                   | Achatz and Martinez 2012      |
| <i>Convoluta, Isodiametra, Symsagittifera, Convolutriloba</i>        | Sperm, statocyst, nervous system, sagittocyst, musculature | LM, TEM, ICC 5-HT, phalloidin              | Achatz et al. 2013            |
| <i>Symsagittifera</i>  | Neuroglobins in nervous system                             | ICC, molecular phylogeny                   | Lechauve et al. 2013          |
| <i>Symsagittifera</i>  | Nervous system, brain                                      | TEM, ICC,                                  | Bailly et al. 2013            |
| <i>Symsagittifera</i>  | Nervous system, <i>elav</i> -gene                          | ICC, genomics                              | Perea-Atienza et al. 2015     |
| Acoela   | Nervous system review                                      | LM, TEM, ICC                               | Hejnoj 2015b                  |
| J. Genital system  |  |  |                               |

**Table 1** (continued)

| Organ/genera investigated   | Character studied   | Methods applied           | Reference                       |
|---|---|---------------------------|---------------------------------|
| <i>Convoluta</i>  | Genital system  | TEM                       | Mamkaev and Drobysheva 1971     |
| <i>Philocelis</i>   | Genital system  | TEM                       | Brüggemann 1985a, b, 1986       |
| <i>Symsagittifera</i> , <i>Sagittifera</i>  | Sagittocysts, copulatory organs                               | SEM, TEM                  | Mamkaev and Kostenko 1991       |
| <i>Childia</i>  | Copulatory muscles  | Phalloidin, CLSM          | Raikova et al. 2006             |
| 6 genera of 5 families  | Female genitals   | LM, TEM, phalloidin       | Petrov et al. 2006              |
| <i>Childia</i>  | Copulatory apparatus  | TEM, phalloidin           | Tekle et al. 2007b              |
| 6 genera of 5 families  | Genital system, sklerotized organs                            | TEM                       | Petrov 2007a, b                 |
| <i>Haplogonaria</i>   | Genital system  | LM, phalloidin, CLSM      | Hooge & Tyler 2015              |
| <b>K. Sperm</b>   |   |                           |                                 |
| <i>Oligochoerus</i>   | Sperm, whole body   | TEM                       | Klima 1967                      |
| <i>Anaperus</i>   | Sperm cells, Golgi complex                                    | TEM                       | Silveira 1967                   |
| <i>Childia</i>  | Spermatogenesis   | TEM, negative staining    | Henley 1968; Henley et al. 1968 |
| <i>Childia</i>  | Spermatogenesis   | TEM, negative staining    | Costello et al. 1969            |
| <i>Anaperus</i> , <i>Polychoerus</i>  | Sperm   | TEM, negative staining    | Henley and Costello 1969        |
| <i>Haploposthia</i> , <i>Paraphanostoma</i> ,<br><i>Convoluta</i>                             | Sperm, spermatogenesis  | TEM                       | Hendelberg 1969, 1974           |
| <i>Symsagittifera</i>   | Sperm morphology  | TEM                       | Bedini & Papi 1970              |
| <i>Convoluta</i>  | Sperm morphology  | TEM                       | Mamkaev and Ivanov 1970         |
| <i>Childia</i> , <i>Polychoerus</i>   | Sperm   | TEM                       | Henley 1974                     |
| <i>Haploposthia</i> , <i>Paraphanostoma</i> ,<br><i>Convoluta</i>                             | Sperm   | TEM                       | Hendelberg 1974                 |
| 6 genera of 6 families  | Sperm   | TEM                       | Hendelberg 1977, 1981           |
| <i>Convoluta</i>  | Spermiogenesis  | TEM                       | Boyer and Smith 1982            |
| <i>Amphiscolops</i> ,<br><i>Pseudactinoposthia</i>  | Spermiogenesis  | TEM                       | Rohde et al. 1988a              |
| <i>Aphanostoma</i> , <i>Actinoposthia</i> , ^,<br><i>Baltalimania</i> , <i>Symsagittifera</i> | Sperm   | TEM                       | Raikova and Justine 1994        |
| <i>Paratomella</i>  | Spermiogenesis  | TEM, ICC                  | Raikova et al. 1997             |
| <i>Actinoposthia</i>  | Sperm   | TEM                       | Justine et al. 1998             |
| <i>Actinoposthia</i> , <i>Symsagittifera</i>  | Sperm   | TEM                       | Raikova et al. 1998a            |
| <i>Convoluta</i>  | Sperm   | TEM ICC anti-tubulin      | Raikova and Justine 1999        |
| 27 genera in 12 families  | Sperm   | TEM, review               | Raikova et al. 2001             |
| 7 genera  | Sperm   | ICC anti-tubulin          | Raikova 2002                    |
| 10 genera of 5 families   | Sperm   | TEM                       | Petrov et al. 2004              |
| <i>Childia</i>  | Sperm, ontogeny, musculature                                  | Phalloidin, phylogenetics | Tekle et al. 2006               |
| <i>Chilida</i> , <i>Eumecynostomum</i> ,<br><i>Philocelis</i> , <i>Mecynostomum</i>           | Sperm   | TEM, ICC anti-tubulin     | Tekle et al. 2007a, b           |
| <i>Archaphanostoma</i>  | Spermatogenesis   | TEM                       | Zabotin and Golubev 2009        |
| 8 genera  | Musculature, nervous system,<br>sperm, sagittocysts, genitals | TEM, ICC, phalloidin      | Achatz et al. 2010              |
| <i>Isodiametra</i>  | Spermatogenesis, testis                                       | TEM                       | Boone et al. 2011b              |
| <i>Otocelis</i> , <i>Symsagittifera</i> ,<br><i>Amphiscolops</i> ,<br><i>Archaphanostoma</i>  | Spermatogenesis   | TEM                       | Zabotin and Golubev 2011        |
| <i>Convoluta</i>  | Spermatogenesis   | TEM                       | Chernova et al. 2012            |
| <b>L. Ovary, oogenesis</b>  |   |                           |                                 |
| Not specified   | Egg shell formation   | TEM                       | Thomas et al. 1985              |
| <i>Isodiametra</i>  | Oocytes   | TEM                       | Smith et al. 1988               |
| <i>Symsagittifera</i>   | Formation of egg layers                                       | TEM                       | Falleni and Gremigni 1989       |
| <i>Symsagittifera</i>   | Oogenesis   | TEM                       | Falleni and Gremigni 1990       |
| <i>Isodiametra</i>  | Oocytes, egg formation  | TEM                       | Chandler et al. 1992            |

**Table 1** (continued)

| Organ/genera investigated   | Character studied  | Methods applied                          | Reference  |
|---|--|--|--|
| <i>Childia</i>  | Oogenesis  | TEM                                      | Stricker et al. 1992                             |
| <i>Paratomella</i>  | Ovary  | TEM, cytochemistry                       | Falleni et al. 1995                              |
| <i>Actinoposthia</i>  | Oogenesis  | TEM, cytochemistry                       | Raikova et al. 1995                              |
| <i>Waminoa</i>  | Symbiosis, oocytes                                       | LM, TEM                                  | Barneah et al. 2007                              |
| <i>Convoluta</i>  | Oogenesis  | TEM                                      | Chernova et al. 2012                             |
| <i>Archaphanostoma</i> , <i>Otocelis</i> ,<br><i>Symsagittifera</i> , <i>Amphiscolops</i> | Oogenesis  | TEM                                      | Zabotin and Golubev 2014                         |
| <b>M. Cleavage, ontogeny</b>  |  |  |  |
| <i>Archaphanostoma agile</i> ,<br><i>Diopisthoporus brachypharyngeus</i>                  | Cleavage   | LM                                       | Apelt 1969b                                      |
| <i>Anaperus</i>   | Cleavage   | LM                                       | Boguta 1972                                      |
| <i>Childia</i>  | Regulative cleavage                                      | LM, deletion experiments                 | Boyer 1971                                       |
| <i>Symsagittifera</i> , <i>Oxyposthia</i>   | Cleavage   | LM                                       | Gureeva 1985, Gureeva and Mamkaev 1985a, b, 1989 |
| <i>Neochildia</i>   | Cleavage   | Fluorescence microscopy                  | Boyer et al. 1996; 2001                          |
| <i>Neochildia</i>   | Cleavage   | Blastomere labelling                     | Henry et al. 2000                                |
| <i>Otocelis</i>   | Ontogeny of genital system                               | LM                                       | Kozloff 2000                                     |
| <i>Neochildia</i>   | Cleavage, musculature                                    | Blastomere labelling phalloidin          | Henry et al. 2000                                |
| <i>Isodiametra</i> [ <i>Convoluta</i> ]   | Live photo, myogenesis                                   | LM, TEM phalloidin                       | Ladurner and Rieger 2000                         |
| <i>Neochildia</i>   | Ontogeny, POU genes                                      | LM, gene expression, ICC                 | Ramachandra et al. 2002                          |
| <i>Convolutriloba</i>   | Ontogeny, gene expression                                | ICC, evo-devo                            | Hejnlol and Martindale 2008a, b                  |
| <i>Symsagittifera</i>   | Myogenesis, neurogenesis                                 | Phalloidin                               | Semmler et al. 2008                              |
| <i>Convolutriloba</i>   | Regeneration, ontogeny                                   | LM, TEM, ICC, evo-devo                   | Sikes 2009                                       |
| Acoela  | Ontogeny, evo-devo review                                | LM, TEM, ICC                             | Hejnlol 2015a                                    |
| <b>N. Regeneration, neoblasts = stem cells, budding</b>                                   |  |  |  |
| <i>Convoluta</i>  | Regeneration of nervous system                           | LM cholinesterases                       | Boguta 1976                                      |
| <i>Convoluta</i> , <i>Oxyposthia</i>  | Regeneration of gut                                      | LM autoradiography                       | Drobysheva 1983, 1986                            |
| <i>Convoluta</i>  | Regeneration   | TEM                                      | Hori et al. 1999                                 |
| <i>Convolutriloba</i>   | Fission  | LM-DIC                                   | Åkesson et al. 2001                              |
| <i>Convolutriloba</i>   | Neoblasts = stem cells                                   | ICC BrdU, TEM                            | Gschwentner et al. 2001                          |
| <i>Convolutriloba</i>   | Regeneration of nervous system                           | ICC 5-HT                                 | Gaerber et al. 2007                              |
| <i>Convolutriloba</i>   | Budding, systematics, axes, muscle and nervous system    | Molecular phylogenetics, ICC, phalloidin | Sikes and Bely 2008                              |
| <i>Isodiametra</i>  | Neoblasts  | ICC BrdU, <i>piwi-1</i>                  | De Mulder et al. 2009                            |
| <i>Isodiametra</i>  | Neoblasts  | ICC BrdU                                 | Bely and Sikes 2010                              |
| <i>Symsagittifera</i>   | Neurosensory system, neoblasts                           | 3D, TEM, ICC,                            | Bery et al. 2010                                 |
| <i>Symsagittifera</i>   | Nervous system, regeneration                             | ICC AchE,                                | Bery and Martinez 2011                           |
| <i>Isodiametra</i>  | Regeneration   | LM, TEM, phalloidin, EdU                 | Perea-Atienza et al. 2013                        |
| <i>Symsagittifera</i>   | Regeneration, live, symbiosis, muscle and nervous system | LM, TEM, ICC, phalloidin CLSM            | Bailly et al. 2014                               |
| <i>Hofstenia</i>  | Regeneration, <i>Wnt</i> , <i>Bmp</i>                    | Evo-devo, phylogenetic                   | Srivastava et al. 2014                           |
| <b>O. Symbiosis</b>   |  |  |  |
| <i>Symsagittifera</i>   | Symbiotic algae  | TEM                                      | Sarfatti and Bedini 1965                         |
| <i>Symsagittifera</i>   | Symbionts  | TEM                                      | Oschman and Gray 1965                            |
| “ <i>Convoluta convoluta</i> ”  | Symbiotic diatome algae                                  | LM                                       | Apelt 1969a                                      |
| <i>Amphiscolops</i>   | Symbiotic dinoflagellates                                | TEM                                      | Taylor 1971                                      |
| “ <i>Convoluta</i> ” (???)  | Symbionts  | TEM                                      | Stoecker et al. 1989                             |
| <i>Amphiscolops</i>   | Symbiotic dinoflagellates                                | TEM, SEM                                 | Lopes and Silveira 1994                          |
| <i>Convolutriloba</i>   | Symbiotic algae, sagittocysts                            | SEM, TEM                                 | Hirose and Hirose 2007                           |

**Table 1** (continued)

| Organ/genera investigated  | Character studied                    | Methods applied              | Reference                       |
|--|--------------------------------------|------------------------------|---------------------------------|
| <i>Waminoa</i>   | Symbiosis, oocytes                   | LM, TEM                      | Barneah et al. 2007             |
| P. Genotypic characters, molecular analyses                            |                                      |                              |                                 |
| <i>Convoluta, Baltalimania</i>   | Chromosomes, karyotype               | LM                           | Birstein 1990                   |
| <i>Convoluta, Amphiscolops</i>   | 18S rRNA                             | Phylogenetics                | Katayama et al. 1993, 1996      |
| <i>Isodiametra, Praesagittifera</i>                                    | 18S rRNA                             | Phylogenetics                | Carranza et al. 1997            |
| <i>Paratomella, Simplicomorpha, Symsagittifera, Haplogonaria</i>       | 18S rRNA                             | Phylogenetics                | Ruiz-Trillo et al. 1999         |
| <i>Aphanostoma, Neochilida, Philomecynostomum</i>                      | 28S rRNA                             | Phylogenetics                | Litvaitis and Rohde 1999        |
| <i>Symsagittifera</i>  | EF-1 $\alpha$                        | Phylogenetics                | Berney et al. 2000              |
| <i>Childia, Aphanostoma, Symsagittifera</i>                            | EF-1 $\alpha$                        | Phylogenetics                | Littlewood et al. 2001          |
| 21 genera of 10 families   | 18S rRNA, systematics                | Phylogenetics                | Hooge et al. 2002               |
| <i>Paratomella</i>   | 18S rRNA, Cox1, Cytb, Hox genes      | Phylogenetics                | Baguña et al. 2002              |
| <i>Paratomella, Symsagittifera</i>                                     | Myosin heavy chain II, 18S rRNA      | Phylogenetics                | Ruiz-Trillo et al. 2002         |
| <i>Convoluta</i>   |                                      |                              |                                 |
| <i>Neochilida</i>  | Ontogeny, <i>POU</i> genes           | LM, Evo-devo, ICC            | Ramachandra et al. 2002         |
| <i>Anaperus, Childia, Paratomella</i>                                  | 18S + 28S rRNA                       | Phylogenetics                | Telford et al. 2003             |
| <i>Convoluta, Symsagittifera, Amphiscolops</i>                         | Lack of <i>let-7</i> RNA             | Phylogenetics                | Pasquinelli et al. 2003         |
| <i>Paratomella</i>   | Mitochondrial genome                 | Phylogenetics                | Cook et al. 2004                |
| <i>Symsagittifera</i>  | Hox genes                            | Phylogenetics                | Ogishima and Tanaka 2006        |
| <i>Childia, Symsagittifera</i>   | Micro-RNAs                           | Phylogenetics                | Sempere et al. 2006, 2007       |
| <i>Isodiametra</i>   | Regeneration <i>Wnt</i> , <i>Bmp</i> | Evo-devo                     | Hrouda 2007                     |
| <i>Hofstenia</i>   | Molecular taxonomy                   | Phylogenetics                | Hooge et al. 2007               |
| <i>Actinoposthia, Anaperus, Childia, Mecynostomum, Paratomella</i>     | 18S + 28S rRNA                       | Phylogenetics                | Wallberg et al. 2007            |
| 5 genera   | EST-data                             | Phylogenetics                | Philippe et al. 2007            |
| Acoelomorpha   | Phylogeny                            | Review                       | Deutsch 2008                    |
| <i>Convolutriloba</i>  | Many genes                           | Evo-devo                     | Hejnlol and Martindale 2008a, b |
| <i>Actinoposthia, Anaperus, Childia, Mecynostomum, Paratomella</i>     | 18S + 28S rRNA                       | Phylogenetics                | Wallberg 2009                   |
| <i>Isodiametra, Neochilida</i>   | Neoblasts, <i>piwi</i> -like gene    | Evo-devo, phylogenetics      | Egger et al. 2009               |
| <i>Paratomella, Convoluta, Childia, Paraphanostoma, Symsagittifera</i> | 13 nuclear genes                     | Phylogenetics                | Paps et al. 2009                |
| <i>Convolutriloba</i>  | Hox genes                            | Evo-devo, phylogenetics      | Hejnlol and Martindale 2009     |
| <i>Convolutriloba</i>  | 28S and 18S rDNA, COI, Hox           | Phylogenetics                | Sikes 2009                      |
| <i>Isodiametra</i>   | Neoblasts                            | ICC BrdU, <i>piwi-1</i>      | De Mulder et al. 2009           |
| <i>Symsagittifera, Isodiametra</i>                                     | Hox genes                            | Evo-devo, phylogenetics      | Moreno et al. 2009, 2010        |
| <i>Symsagittifera</i>  | Neurogenesis, SoxB2                  | ICC, gene expression         | Semmler et al. 2010             |
| <i>Symsagittifera</i>  | Mitochondrial genome                 | Gene order, phylogenetics    | Mwinyi et al. 2010              |
| <i>Convolutriloba</i>  | Hox genes                            | Evo-devo                     | Sikes and Bely 2010             |
| <i>Symsagittifera</i>  | Muscle molecule                      | Gene-expression <i>SrTrp</i> | Chiodin et al. 2011             |
| 126 species  | Morphology, 18S + 28S rRNA, COI      | Phylogenetics                | Jondelius et al. 2011           |
| Xenacoelomorpha  | Hox genes                            | Phylogenetics, review        | Moreno et al. 2011              |
| 5 genera   | EST data, mRNA,                      | Phylogenetics                | Philippe et al. 2011            |
| <i>Symsagittifera</i>  | GNE gene                             | Phylogenetics                | De Mendoza and Ruiz-Trillo 2011 |
| <i>Isodiametra</i>   | <i>Hedgehog</i> pathway              | Exposure experiments         | Bowie et al. 2012               |
| <i>Isodiametra</i>   | Mesodermal genes                     | Evo-devo, gene expression    | Chiodin et al. 2013             |

**Table 1** (continued)

| Organ/genera investigated | Character studied                     | Methods applied                         | Reference                    |
|---------------------------|---------------------------------------|---|------------------------------|
| <i>Symsagittifera</i>     | Neuroglobins in nervous system        | ICC, phylogeny                          | Lechauve et al. 2013         |
| <i>Symsagittifera</i>     | Mitochondrial genome                  | Gene order, phylogenetics               | Bernt et al. 2013            |
| <i>Hofstenia</i>          | Regeneration, <i>Wnt</i> , <i>Bmp</i> | Evo-devo, phylogenetics                 | Srivastava et al. 2014       |
| <i>Symsagittifera</i>     | Nervous system, <i>elav</i> -gene     | ICC, genomics                           | Perea-Atienza et al. 2015    |
| <i>Convolutriloba</i>     | Mouth-anus                            | Evo-devo, <i>brachyury</i> , <i>cdx</i> | Hejnal and Martín-Durán 2015 |

(1) In all papers prior to 1991, *Symsagittifera* is usually referred as *Convoluta* as is *Isodiametra* prior to 2005. (2) Papers dealing solely with the symbiosis of *Symsagittifera roscoffensis* or other sagittiferids are not listed herein

*COI* cytochrome oxidase I, *ICC* immunocytochemistry, *LM* light microscopy, *NGS* next-generation sequencing, *SEM* scanning electron microscopy, *TEM* transmission electron microscopy, *5-HT* serotonin

Xenacoelomorpha, has been proposed. A (weak) majority of recent molecular analyses (Tables 1P, 2B and 3B) place Xenacoelomorpha as sister-taxon to the deuterostome Ambulacraria (Echinodermata and Hemichordata). However, several molecular analyses and in particular Hox-gene-conditions suggest Xenacoelomorpha again as a basal bilaterian offshoot below the nephrozoan level of organization close to Urbilateria.

During the last two decades, many new data on Xenacoelomorpha have been accumulated usually not considered by the molecular studies. Thus, the present contribution wants to outline the phenotypic characteristics of Xenacoelomorpha and discusses possible ways of interpretations of these data. The recent excellent review on acoels by Achatz et al. (2013) is taken as a starting point; thus, the discussion focuses in particular on new data, respectively, of Nemertodermatidae and *Xenoturbella*. The current “new phylogeny” of the remaining bilaterian groups (i.e. Nephrozoa) into Deuterostomia and Protostomia with Lophotrochozoa (including the platyzoan phyla) and Ecdysozoa is accepted, and I will apply this terminology throughout this contribution.

## Character review

A recent review on the taxonomy and nomenclature of Xenacoelomorpha has been provided by Tyler and Schilling (2011) which is used herein as the systematic framework. For review, I provide first chronologically arranged tables on phenotypic studies within the three main taxa, Acoela, Nemertodermatida and *Xenoturbella*. I restrict this review mainly to “high-tech morphology” provided by electron microscopy, immunocytochemistry usually combined with confocal laser scanning microscopy (CLSM) on gene expression methodologies (“evo-devo”) and molecular data.

## Character analysis

### A general and cladistic view on “reduction”

Xenacoelomorpha lack a significant number of characters present in most other bilaterian supergroups. Many authors have regarded these conditions as “reduction of ...” However, a reasoning like “one cannot fully exclude the possibility of reduction” without any point of evidence, i.e. either direct retained traces, e.g. during ontogeny or by phylogenetic analyses, clearly is insufficient in this respect and should not be regarded as a scientific argument.

For instance, there is a long-lasting controversy, whether small, acoelomate “worms” are primitive or but derived within the Bilateria. In fact, certain (all?) interstitial, acoelomate polychaetes are probably derived from larger, coelomate ancestors by progenesis (Westheide 1987; Rieger 1985, 1994a, b; Rieger and Ladurner 2001, 2003; Andrade et al. 2015). However, such an assumption, i.e. the progenetic derivation of a taxon, needs points of evidence, namely shared features with larvae or juveniles of other coelomate taxa. If such points of evidence are not provided, the assumption of “secondary reduction” is simply an unsound speculation.

The matter becomes worse, if the term “reduced” is applied to a description. “Reduction” never is a fact, but always an (probabilistic) hypothesis on an evolutionary process. I also want to remind that applied terms (e.g. apical organ, eye, gut) to any structure are always far from being “just descriptive”. In contrast, each of these terms reflects a concept or a hypothesis, it may be on function or homology (Haszprunar 2011). Accordingly, statements like “acoelomorphs have a reduced excretory system” in my view is a purely speculative wording, the correct description of the fact is “acoelomorphs entirely lack an excretory system composed of ultrafiltration cells”, regardless whether one interprets this fact as a plesiomorphic character or but a secondary loss.



**Table 2** Ultrastructural, immunocytochemical, evo-devo and specific genotypic studies on Nemertodermatida

| Taxa investigated   | Character studied                              | Methods applied         | Reference                           |
|---|--|-------------------------|-------------------------------------|
| <b>A. Morphology</b>  |  |                         |                                     |
| <i>N. spp., F. apelti</i>   | Spermatogenesis                                | TEM                     | Tyler and Rieger 1975               |
| <i>Nemertoderma</i> sp.   | Adhesive organs                                | TEM                     | Tyler 1976                          |
| <i>N. spp., F. apelti</i>   | Sperm, epidermis                               | TEM                     | Tyler and Rieger 1977               |
| <i>N. bathycola</i> and <i>westbladi</i> , <i>M. stichopi</i>           | Spermatogenesis                                | TEM                     | Hendelberg 1977, 1981               |
| <i>F. apelti</i> , <i>N. sp.</i>  | Epidermis, cilia                               | TEM                     | Tyler 1984b                         |
| Not specified   | Egg shell formation                            | TEM                     | Thomas et al. 1985                  |
| <i>F. sp.</i> , Gen.nov.  | Epidermis, muscles                             | TEM                     | Smith and Tyler 1985a, b            |
| <i>F. cf. apelti</i>  | Frontal glands                                 | TEM                     | Smith and Tyler 1986                |
| <i>F. cf. apelti</i>  | Food-gathering organ                           | TEM                     | Tyler 1986                          |
| <i>N. sp., Ne. elongatus</i>  | Oocytes  | TEM                     | Smith et al. 1988                   |
| <i>N. sp. B</i>   | Frontal glands, epidermis                      | TEM                     | Ehlers 1992d                        |
| <i>M. stichopi</i>  | Epidermis, epibiotic bacteria                  | TEM                     | Lundin and Hendelberg 1995          |
| <i>M. stichopi</i>  | Epidermis, pulsatile bodies                    | TEM                     | Lundin and Hendelberg 1996          |
| <i>M. stichopi</i> , <i>N. westbladi</i> , <i>N. cf. bathycola</i>      | Epidermal ciliary root system                  | TEM                     | Lundin 1997                         |
| <i>M. stichopi</i> , <i>M. sp.</i> , <i>N. westbladi</i>                | Epidermal symbiotic bacteria                   | TEM                     | Lundin 1998b                        |
| <i>M. stichopi</i>  | Spermatogenesis                                | TEM                     | Lundin and Hendelberg 1998          |
| <i>N. westbladi</i> , <i>M. stichopi</i>                                | Nervous system: 5-HT, FMRFamid                 | ICC                     | Raikova et al. 2000a, b             |
| <i>St. psammicola</i>   | Musculature                                    | Phalloidin              | Hooge 2001                          |
| <i>N. westbladi</i> , <i>M. stichopi</i>                                | Nervous and muscle system                      | ICC                     | Reuter et al. 2001a, b              |
| Nemertodermatida  | All characters                                 | Morpho-cladistics       | Lundin and Sterrer 2001             |
| <i>N. westbladi</i>   | Cleavage                                       | LM                      | Jondelius et al. 2004               |
| <i>N. westbladi</i>   | Nervous system: GYIRFamid                      | ICC                     | Raikova et al. 2004b                |
| <i>F. cf. apelti</i> , <i>Ne. elongatus</i> , <i>St. cf. psammicola</i> | Neoblasts                                      | ICC                     | Smith et al. 2009                   |
| <i>St. psammicola</i>   | Pharynx  | TEM, phalloidin         | Todt 2009                           |
| <i>N. westbladi</i> , <i>F. apelti</i> ,                                | Testes, spermatogenesis                        | TEM                     | Boone et al. 2011a, b               |
| <i>M. stichopi</i>  | Live photos, cleavage, ontogeny nervous/muscle | LM, ICC                 | Børve and Hejnlø 2014               |
| <i>M. stichopi</i>  | Evo-devo of gut                                | NGS                     | Børve and Hejnlø 2011               |
| <i>N. westbladi</i> , <i>M. stichopi</i>                                | Live photos, muscular system                   | LM, phalloidin          | Meyer-Wachsmuth et al. 2013         |
| Nemertodermatida  | Ontogeny, evo-devo review                      | LM, TEM, ICC            | Hejnlø 2015a                        |
| Nemertodermatida  | Nervous system review                          | LM, TEM, ICC            | Hejnlø 2015b                        |
| <b>B. Molecular analyses</b>  |  |                         |                                     |
| <i>N. bathycola</i> and <i>westbladi</i> , <i>M. stichopi</i>           | 18S rDNA                                       | Phylogenetics           | Jondelius et al. 2002               |
| <i>N. bathycola</i> , <i>N. westbladi</i>                               | 18S rRNA, Cox1, Cytb, Hox genes                | Phylogenetics           | Baguña et al. 2002                  |
| <i>M. stichopi</i>  | 18S, 28S rRNA                                  | Phylogenetics           | Telford et al. 2003                 |
| <i>N. westbladi</i>   | Mysosin heavy chain II                         | Phylogenetics           | Ruiz-Trillo et al. 2004             |
| <i>N. westbladi</i>   | Hox and Parahox genes                          | Phylogenetics           | Jiménez-Guri et al. 2006            |
| 7 species of 5 genera   | 18S, 28S rDN                                   | Phylogenetics           | Wallberg et al. 2007; Wallberg 2009 |
| <i>N. westbladi</i> , <i>M. stichopi</i>                                | 13 nuclear genes                               | Phylogenetics           | Paps et al. 2009                    |
| <i>N. westbladi</i>   | Globin genes                                   | Phylogenetics           | Hoffmann et al. 2012                |
| <i>M. stichopi</i>  | Phylogenomic EST-data                          | Phylogenetics           | Ryan et al. 2013                    |
| 9 new species of 20   | H3, 18S + 28 S rRNA                            | Taxonomy, phylogenetics | Meyer-Wachsmuth et al. 2014         |
| <i>N. westbladi</i>   | Regeneration, <i>Wnt</i> , <i>Bmp</i>          | Evo-devo, phylogenetics | Srivastava et al. 2014 (Fig. S4)    |

*F* Flagellophora, *M* Meara, *N* Nemertoderma, *Ne* Nemertinoidea, *St* Sterreria, *COI* cytochrome oxidase I, *ICC* immunocytochemistry, *LM* light microscopy, *NGS* next-generation sequencing, *SEM* scanning electron microscopy, *TEM* transmission electron microscopy, *5-HT* serotonin

**Table 3** Phenotypic and specific genotypic studies on *Xenoturbella*

| Taxa investigated                     | Character studied  | Methods applied  | Reference                               |
|---------------------------------------|--|--|---|
| <b>A. Morphology</b>                  |  |  |   |
| <i>X. bocki</i>                       | Whole body   | LM   | Westblad 1949                           |
| <i>X. bocki</i>                       | Epidermis, statocyst                                     | LM   | Reisinger 1960                          |
| <i>X. bocki</i>                       | Extracellular matrix of body cavity                      | TEM  | Pedersen and Pedersen 1986              |
| <i>X. bocki</i>                       | Epidermis, cilia   | LM, TEM, SEM   | Franzén and Afzelius 1987; Franzén 1989 |
| <i>X. bocki</i>                       | Epidermis  | TEM  | Pedersen and Pedersen 1988              |
| <i>X. bocki</i>                       | Epidermis, cilia   | TEM  | Smith 1990                              |
| <i>X. bocki</i>                       | Statocyst  | LM, TEM  | Ehlers 1991                             |
| <i>X. bocki</i>                       | Subepidermal musculature                                 | TEM  | Ehlers and Sopott-Ehlers 1997a, b       |
| <i>X. bocki</i>                       | Egg  | LM   | Israelsson 1997                         |
| <i>X. bocki</i>                       | Epidermal cilia  | TEM  | Lundin 1998a, b                         |
| <i>X. bocki</i> , <i>X. westbladi</i> | Larva (highly erroneous)                                 | LM   | Israelsson 1999a, b                     |
| <i>X. westbladi</i>                   | Nervous system, muscle system                            | TEM, 5-HT, FaRP-ICC<br>phalloidin-fluorescence         | Raikova et al. 2000a, b                 |
| <i>X. bocki</i>                       | Live, epidermis, pulsatile bodies                        | TEM  | Lundin 2000b, 2001                      |
| <i>X. bocki</i>                       | Ontogeny (highly erroneous)                              | TEM  | Israelsson 2001                         |
| <i>X. bocki</i>                       | Nervous system   | LM, SALMFamid-2-ICC                                    | Stach et al. 2005                       |
| <i>X. bocki</i> , <i>X. westbladi</i> | Eggs   | LM, TEM, BrdU-ICC                                      | Israelsson and Budd 2005                |
| <i>X. bocki</i> , <i>X. westbladi</i> | Gastrodermis, phagocytosis,<br>muscle cells, DNA content | LM, TEM, ICC fluorescence<br>microscopy                | Israelsson 2006                         |
| <i>X. westbladii</i> , <i>X. sp.</i>  | Live photo, ecology, behaviour<br>feeding, regeneration  | Observations, community<br>analysis, SEM gut content   | Åkerman 2004                            |
| <i>X. bocki</i> , <i>X. westbladi</i> | Gastrodermis with endosymbiotic<br>chlamydiae            | LM, TEM; molecular phylogenetics<br>rDNA               | Israelsson 2007a                        |
| <i>X. bocki</i> , <i>X. westbladi</i> | Statocyst  | LM, TEM  | Israelsson 2007b                        |
| <i>X. bocki</i> , <i>X. westbladi</i> | Uptake dissolved organic matter                          | Various experiments                                    | Israelsson 2008                         |
| <i>X. bocki</i>                       | Live photos  | LM, SEM  | Telford 2008                            |
| <i>X. westbladi</i>                   | Nervous system   | TEM, 5-HT, FaRP-ICC                                    | Raikova 2008                            |
| <i>X. bocki</i>                       | Sperm ultrastructure                                     | TEM  | Obst et al. 2008                        |
| <i>X. bocki</i>                       | Endosymbiotic bacteria                                   | LM, TEM, molecular phylogenetics,<br>PCR-cloning, FISH | Kjeldsen et al. 2010                    |
| <i>X. westbladi</i>                   | Life photo   | LM   | Nielsen 2010                            |
| <i>X. bocki</i>                       | Nervous system   | 5-HT catabolic pathway                                 | Squires et al. 2010                     |
| <i>X. bocki</i>                       | Larva  | TEM  | Obst et al. 2011a                       |
| <i>X. bocki</i>                       | Spermatozoa  | LM, TEM  | Obst et al. 2011b                       |
| <i>X. bocki</i>                       | Larva, hatchling   | LM, TEM  | Nakano et al. 2013                      |
| <i>X. bocki</i>                       | Regeneration, <i>Wnt</i> , <i>Bmp</i>                    | Evo-devo, phylogenetics                                | Srivastava et al. 2014                  |
| <i>X. bocki</i>                       | Nervous system: genomics, EST                            | ICC, NGS   | Perea-Atienza et al. 2015               |
| <i>X. bocki</i>                       | Review   | Phylogenetics  | Nakano 2015                             |
| <b>B. Molecular analyses</b>          |  |  |   |
| <i>X. bocki</i>                       | 18S rDNA   | Prey (!) phylogenetics                                 | Norén and Jondelius 1997                |
| <i>X. bocki</i>                       | 18S rDNA   | Phylogenetics  | Gee 2003; Bourlat et al. 2003, 2006     |
| <i>X. bocki</i>                       | Mitochondrial genome                                     | Phylogenetics  | Perseke et al. 2007                     |
| <i>X. bocki</i>                       | Cox1, Cox2, Hox-genes                                    | Phylogenetics  | Telford 2008                            |
| <i>X. bocki</i>                       | Hox-genes  | Phylogenetics  | Fritsch et al. 2008                     |
| <i>X. bocki</i>                       | Feeding ecology  | Gut content barcoding                                  | Bourlat et al. 2008                     |
| <i>X. bocki</i>                       | Mitochondrial genome                                     | Phylogenetics  | Bourlat et al. 2009                     |
| <i>X. bocki</i>                       | EST-data   | Phylogenetics  | Witek 2009                              |
| <i>X. bocki</i>                       | 13 nuclear genes   | Phylogenetics  | Paps et al. 2009                        |
| <i>X. bocki</i>                       | Endosymbiotic bacteria                                   | Symbiont phylogenetics,<br>PCR-cloning, FISH           | Kjeldsen et al. 2010                    |

**Table 3** (continued)

| Taxa investigated          | Character studied                     | Methods applied                 | Reference                        |
|----------------------------|---------------------------------------|---------------------------------|----------------------------------|
| <i>X. bocki</i>            | COI-gene                              | Phylogenetics                   | Obst et al. 2011b                |
| <i>X. bocki</i>            | Phylogenomic                          | Phylogenetics                   | Philippe et al. 2011             |
| <i>X. bocki</i>            | GNE gene                              | Phylogenetics                   | De Mendoza and Ruiz-Trillo 2011  |
| <i>X. bocki</i>            | Globin genes                          | Phylogenetics                   | Hoffmann et al. 2012             |
| <i>X. bocki</i>            | Mitochondrial genome                  | Phylogenetics                   | Bernt et al. 2013                |
| <i>X. sp.1, sp.2, sp.3</i> | COI-gene                              | DNA barcoding                   | Rouse et al. 2013                |
| <i>X. bocki</i>            | Mitochondrial genome                  | Phylogenetics                   | Sorimachi et al. 2014            |
| <i>X. bocki</i>            | Regeneration, <i>Wnt</i> , <i>Bmp</i> | Evo-devo, phylogenetics         | Srivastava et al. 2014 (Fig. S4) |
| <i>X. bocki</i>            | <i>Pitx</i>                           | Phylogenetics, nodal signalling | Grande et al. 2014               |

According to Rouse et al. (2013), the two nominal species share the same COI sequence and thus may be conspecific

COI cytochrome oxidase I, ICC immunocytochemistry, LM light microscopy, SEM scanning electron microscopy, TEM transmission electron microscopy, 5-HT serotonin

### Size and locomotion

Most acoelomorphs are small worms of the 1–2-mm range, some sagittiferids with photosynthetic endosymbionts reach several millimetres, and *Hofstenia* species may exceed 20 mm. With the exception of *Oligochoerus* and few further freshwater species, they are marine inhabitants, and the overwhelming majority of species live in benthic or interstitial microhabitats. Only few of them (mostly again Sagittiferidae with photosymbiotic endosymbionts) are “flatworms” in a morphological sense, most species exhibit a cylindrical body shape.

*X. bocki* reaches up to 40 mm body length, but the closely related *Xenoturbella westbladi* is reported to be much smaller (max. 15 mm, Israelsson 1999a); however, the species identity of the latter is doubtful, (Rouse et al. 2013). Despite the large size, there is no flattening of the body of both *Xenoturbella* species by dorsoventral muscles as typically seen in flatworms. It is not possible to state whether this reflects enlargement such as in the acoel genus *Hofstenia*, which reaches more than 20 mm length, or reflects plesiomorphic conditions.

*Xenoturbella* and acoelomorphs share a mode of locotion by muco-ciliary gliding, which is the most efficient way of locomotion in small “worms” (Martin 1978).

### Epidermis

#### Ciliation

All Xenacoelomorpha share a polyciliary epidermis, monociliary cells are not present except for receptor cells. Rieger (1976, 1986a) has strongly emphasized the importance of the monociliary condition as a plesiomorphic feature in primitive metazoans and within the Bilateria. This assumption is widely accepted for non-bilaterian Metazoa, where only a few cases of multiciliary conditions (namely in the

Ctenophora, but also in certain Cnidaria) are reported. However, concerning the Bilateria, the situation is less clear: accepting plesiomorphic monociliary conditions and emergence of the polyciliary condition probably is due to multiple parallelism. But in certain cases (e.g. oweniid polychaetes or phoronids) character reversal by means of cytological “progenesis” (retaining of the monociliary condition during cell differentiation) may have also happened in evolution.

#### Ciliary ultrastructure

The epidermal cells of both acoelomorph taxa bear numerous cilia with a highly specific fine structure. Both, the ciliary tips with a formation of a “shoulder” and an apical electron-dense plate and the ciliary rootlet system, which interconnects adjacent cilia, are unique in their details and have been interpreted by several authors as one of the major synapomorphies of the two subgroups (Tables 1B and 2A).

*Xenoturbella* exhibits quite similar features in the ciliary system suggesting direct homology and thus monophyly of Xenacoelomorpha (latest review Nielsen 2010). However, according to Pardos (1988), similar ciliary tips (but not the respective root system) are also present in enteropneust hemichordates. Accepting the basal position of Acoelomorpha and *Xenoturbella* (see below), this appears to be a plesiomorphic feature for Bilateria and thus for Deuterostomia. Since the functional significance of the shoulder type is entirely unknown, a possible parallel development cannot be substantiated.

#### “Pulsatile bodies”

Several authors have investigated the fine structure of the so-called pulsatile bodies in the epidermis of the Acoelomorpha (Tables 1D and 2A). These structures are now generally considered to be degenerating epidermal cells. Very similar

epidermal structures are also found in *Xenoturbella* (Lundin 2000b, 2001), and it is probable that the so-called phagositized cells in the gut epithelium described by Israelsson (2006) are likewise degenerating gastrodermal cells.

The “pulsatile bodies” are a unique feature of Xenacoelomorpha and thus are likely a synapomorphy of the phylum.

### Cuticle

All acoelomorphs and *Xenoturbella* show a microvillous body surface; a true cuticle is never present. According to Rieger (1984), this is a primitive condition for Bilateria in general being retained in most deuterostomes and many lophotrochozoan phyla (Platyzoa, Nemertea, Phoronida) as well.

## Muscle system and body cavity

### Muscle anatomy

The application of specific staining methods (phalloidin coupled with fluorescent dyes versus f-actin) combined with confocal laser scanning microscopy (CLSM) have provided highly significant data on the muscle systems of small metazoans. In the Acoelomorpha, the muscle system of the body wall shows high variability, which is group-specific (Tables 1E and 2A). Hooge (2001) has interpreted this high variability, which contrasts with a much more uniform pattern in other plathelminths or other “worm” taxa, as a primitive character applying Mamkaev’s (1986) “principle of initial morphological diversity”. If so, the mesenchymate (versus epithelial) character of the acoelomorph body wall musculature would be plesiomorphic for Bilateria. On the other hand, this high variability makes direct reconstruction of a distinct plesiomorphic pattern of muscle fibres for Acoelomorpha or for Bilateria as a whole difficult. Data on the muscle system of planula larvae of Cnidaria are scarce (e.g. Boelsterli 1977) and in particular for anthozoans not available at present. Adult conditions in Cnidaria and Ctenophora include epithelial and mesenchymate (and even cross-striated) muscle cells; thus, outgroup comparison is not conclusive.

### Muscle ultrastructure

The mesenchymate (versus epithelial) type of muscles of the body wall probably is correlated with the acoelomate body cavity of the Acoelomorpha (the name refers to the lack of the gut lumen in most acoels, however) and in *Xenoturbella*.

Based on outgroup comparison with the Cnidaria, Rieger (1986a), Rieger and Lombardi (1987) and Rieger and Ladurner (2003) have advocated the primitiveness of myoepithelia in Bilateria. With the same argument, but now

focused on the Acoelomorpha, fibre muscle cells appear to be plesiomorphic in Nephrozoa.

### Body cavity

Rieger (1981) and Rieger et al. (1991) have thoroughly reviewed the high variability of the fine structure of the body cavity in acoelomorphs, and “Mamkaev’s (1986) principle” (high variability reflects plesiomorphy) might again be applied. However, the small size makes it likely that the body cavity of acoelomorphs and also of Urbilateria originally was not at all “parenchymous” as often quoted, but contained mainly muscle and nerve cells and (at best) only a few parenchymous cells between epidermis and gastrodermis.

## Digestive system

All Acoelomorpha and *Xenoturbella* have a gut forming a cul-de-sac and being devoid of a true hindgut system. The name Acoela (and Acoelomorpha accordingly) is based on the fact that the majority of species have a multinuclear, amoeboid and lumen-less gut which feeds by phagocytosis. Earlier authors considered this feature to be intermediate between protozoans and metazoans and regarded the Acoela as kingpins of metazoan evolution (see historical review by Smith and Tyler 1985b). However, *Xenoturbella*, the Nemertodermatida and the acoel *Paratomella* species, which represent one of the earliest subclades of the Acoela (Ehlers 1992b; Hooge et al. 2002; Hooge and Tyler 2006), both have cellular guts; thus, the “acoel” condition of the gut clearly is a derived one.

The position of the gut opening of the Acoelomorpha once more shows remarkable variability, which again may reflect their basic nature. Certain species, which nourish by endosymbiotic bacteria, diatoms or dinoflagellates, entirely lack a mouth opening, and by outgroup comparison, this condition is clearly derived. In some species, the gut opening is anteriorly placed, a mid-ventral opening is present in the majority of species and *Xenoturbella*, and certain species show a truly posterior gut opening. It is difficult to explain an evolutionary trend from anterior to posterior position in a predatory animal; the opposite way makes much more sense. von Salvini-Plawen (1978) has proposed a possible evolutionary scenario of Urbilateria out of a planula-like ancestral organization, and it is interesting to note that the latter have a posterior gut opening too, although these larvae are predominately lecithotrophic.

## Nervous system

No other bilaterian group shows higher principal variability with respect to the nervous system rather than the Acoelomorpha, and again “Mamkaev’s (1986) principle” might be applied. Thanks to recent thorough ultrastructural

and immunocytochemical studies of several representatives of the Acoela (Table 11) and Nemertodermatida (Table 2), the details of the acoelomorph nervous system are quite well known as is the case in *Xenoturbella* (Table 3).

### Neuroanatomy

Rieger et al. (1991) have thoroughly reviewed the neuroanatomical conditions in Acoelomorpha. They concluded that the most primitive neural condition of Acoelomorpha is reflected by a simple, basi- to subepithelial plexus. The more recent immunocytochemical studies by Raikova (2002; Raikova et al. 2004a, b; Raikova 2008) and by Achatz and Martinez (2012) revealed that an anteriorly placed ring containing serotonin and RF-amides such as present in *Nemertoderma* species may be added to the above characteristic. Acoelomorphs show various forms of neural concentrations usually with an anteriorly situated nervous centre (“commissural brain”). However, based on immunocytochemical studies, the latter are entirely differently structured (total lack of serotonergic or RF-amidergic nerve cells) and thus cannot be homologized with any “cerebral ganglion” or “brain” of other bilaterians. The “statocyst ganglion” is more likely interpreted as a synapomorphic condition of Acoelomorpha (Raikova et al. 1998a, b; Reuter et al. 1998, 2001a, b; Raikova 2008).

Also, the various longitudinal neural cords are probably autapomorphies of the respective acoelomorph clades. Basiepithelially positioned, plexus-like nervous systems are typical for Cnidaria (outgroup), adult lophophorates and larval trochozoans and are generally present in basic deuterostomes such as Echinodermata or Hemichordata. Also *Xenoturbella* shows a basiepithelially placed, neural plexus. In addition, Achatz and Martinez (2012) stated that the axial nervous system of acoelomorphs does not develop by exhibiting a staggered pattern of conserved regulatory genes as in other bilaterians but by a nested pattern of these genes. Thus, it is likely that this type of nervous system represents the plesiomorphic condition in the Bilateria. Accordingly, the occurrence of a cerebral ganglion, respectively, of a true central nervous system is an evolutionary (synapomorphic?; cf. Ghysen 2003 for review) event within the Bilateria (in fact only Protostomia), but no feature of Urbilateria.

The presence of large (12–13  $\mu\text{m}$ ) GYIRF-amidergic neurons associated with the basal parts of the longitudinal cords in *Nemertoderma* and acoels and the lack of serotonergic neurons in the anterior ring constitute further neural synapomorphies of Acoelomorpha (Reuter et al. 2001a, b; Raikova et al. 2001, 2004a, b).

### Stomatogastric nervous system

The unique lack of a stomatogastric nervous system in the Acoelomorpha and *Xenoturbella* (Raikova et al. 1998a, b;

2000a, 2000a, b; 2001; 2004a, 2004a, b; Raikova 2008) is more difficult to interpret. In the Cnidaria, true ganglionic neurons are restricted to the gastrodermis, whereas the epidermis contains primary sensory cells alone. In contrast, Protostomia and Deuterostomia show epidermal and gastrodermal neurons.

From the functional point of view, it seems unlikely that the stomatogastric system of primitively predatory organisms has been “reduced” in evolution. However, the gastrodermis is also a main muscular system in Cnidaria, whereas the musculature in Acoelomorpha and *Xenoturbella* is subdermally placed and entirely independent of the gut. At present stage of knowledge, it seems most probable that the nephrozoan nervous system unites and amplifies the two previous stages of neural level of organization.

### Sensory systems

It is interesting to note that a sensory “apical organ”, which is typical for planula larvae of Cnidaria and of the majority of early stages in the remaining Bilateria except the Ecdysozoa has not been found in any acoelomorph or in *Xenoturbella*. The “apical organ”—better called a “frontal organ”—of the Acoelomorpha is mainly a glandular rather than a sensory structure and represents probably a synapomorphy of the phylum (Smith and Tyler 1985b; 1988; Rieger et al. 1991; Ehlers 1992a).

Although many species live in shallow waters, Nemertodermatida (see review by Sterrer 1998) are entirely devoid of photoreceptive organs. In contrast, several acoel species have subepidermal eye spots, but according to Hooze et al. (2002), they all belong to a single, most derived clade of the Acoela (Sagittiferidae *sensu lato*). In addition, the fine structure of the sagittiferid eyes (e.g. Popova and Mamkaev 1986; Yamasu 1991) differs entirely from those in other bilaterians concerning both the sensory (lack of microvillous or ciliary photoreceptive membranes) and the pigment cells (with a vacuole containing light-reflecting platelets). In addition, Lanfranchi (1990) described a multicellular, epidermal eyespot in *Otocelis rubropunctata* (Otocelidae) again with specific fine structure. Since a “cerebral ganglion” is not present (see above), none of these eye types can be called “cerebral” and both have probably be independently evolved. Although *Pax-6* could be detected in a cDNA library of *Convoluta pulchra* (Baguña and Martinez, letter 9 July 2004), it is not expressed during ontogeny of sagittiferid eyes (Martindale personal communication; August 2008). Accordingly, it is very likely that the Acoelomorpha originally lacked eyes and that the eyes (as organs) have been independently evolved.

Already diploblastic metazoans show photoreception and certain cnidarian taxa have developed even true eyes, but there is a long-lasting discussion, whether Urbilateria had eyes (e.g. Arendt and Wittbrodt 2001). A good part of this discussion

mismatches photoreception (a biochemical respectively physiological process), photoreceptive cells (with some specific structural characters), photoreceptor organ respectively eyes (consisting at least of two cell types) and the various genes involved in these structures. Considering the acoelomorph and outgroup conditions as outlined above, it is likely that “Urbilateria” (and probably already diploblasts or even poriferans) already had certain photoreceptive cells with a distinct mode of development including *Pax-6* and *sine oculis* (e.g. Bebenek et al. 2004). In contrast, true eyes—as organs—are probably the result of multiple parallel evolutionary events (e.g. von Salvini-Plawen and Mayr 1977; Meyer-Rochow 2000; von Salvini-Plawen 2008).

Most species of Nemertodermatida and Acoela show anteriorly situated statocysts. These are unusual because several, freely movable (but non-flagellar) statoconial cells with an intracellular statolith are found within the statocyst's vesicle (Ferrero 1973; Ferrero and Bedini 1991; Ehlers 1991). In Nemertodermatida, there are always two statoconial cells, whereas one is present in acoel species. Similar conditions have been described once more in *Xenoturbella* (Ehlers 1991; Israelsson 2007b), where several, monoflagellate statoconial cells are present, and in the “commissural sac” of certain Mollusca-Solenogastres (Haszprunar 1986) with again non-flagellate statoconial cells. Whereas the latter probably is due to convergence, the similarities between the statocysts of *Xenoturbella* and Acoelomorpha might be caused by common inheritance.

### Excretory features

All Acoelomorpha, even freshwater inhabitants such as *Oligochoerus limnophilus* (cf. Klima 1967), are entirely devoid of ultrafiltration cells and of respective organs; they may be represented by protonephridial or metanephridial excretory systems. This contrasts not only sharply with the conditions in the true Plathelminthes (protonephridia without any exception), but likewise with those of nearly all other free-living bilaterians. The only notable exception among the latter are the Nematoda (and the endoparasitic Nematomorpha), where an apomorphic glandular excretory system is present, and again *Xenoturbella*, which lacks excretory systems at all.

Outgroup comparison with Cnidaria and Ctenophora suggests the lack of ultrafiltration cells a plesiomorphic character of the Bilateria. Once more, these conditions contradict a progenetic derivation from a more complicated bilaterian ancestor: The larvae of protostomes (if present) usually have protonephridia, whereas larvae of deuterostomes mostly show metanephridial excretory systems. Recently, ultrafiltration systems have also been detected in Broyzoa (Gruhl et al. 2009) and Brachiopoda (Kuzmina and Malakhov 2015) so that certain ecdysozoan taxa (Nematoda, Nematomorpha, many

insects) remain the only groups where an original ultrafiltration system has been entirely replaced.

### Reproductive features

#### *Asexual reproduction*

Most primitive metazoan taxa (Porifera, Placozoa, Cnidaria) show high regeneration ability and reproduce substantially by asexual processes (fission, budding, asexual swimmers, etc.). Accordingly, this feature might be plesiomorphic for Metazoa. Also, many acoelomorphs show asexual reproduction and again a high diversity of the respective processes is exhibited (see reviews by Ax and Schulz 1959; Åkesson et al. 2001; Reuter and Kreshchenko 2004). As reviewed by Rieger (1986a, b) and more recently by Reuter and Kreshchenko (2004) asexual reproduction has also been reported from true Plathelminthes, particularly from the basic Catenulida and Macrostromida. However, one should generally consider that high regeneration ability and asexual reproduction are closely related features. Indeed, summarizing all reports on asexual reproduction in Acoelomorpha or Macrostromida (and also basic Deuterostomia), the result is “occasionally” respectively “in certain clades”. Therefore, I conclude that high regeneration ability probably was a feature of Urbilateria, but it remains uncertain, whether asexual reproduction was predominant.

#### *Gender*

All Acoelomorpha are hermaphrodites suggesting hermaphroditic Urbilateria as likely, although the outgroup analysis is not unequivocal (Porifera are hermaphrodites, Cnidaria include hermaphrodites and gonochoristic species). The fertilization mode generally depends on size and the possibility of clonal reproduction. If small size and (mainly) sexual reproduction is accepted as plesiomorphic for Bilateria, internal fertilization of the few (and thus precious) eggs is the logical consequence.

#### *Genital apparatus*

Once more the Acoelomorpha exhibit substantial variation and diversity concerning their genital systems. Outgroup comparison with Porifera and Cnidaria show a non-gonad condition respectively-free gametes to be plesiomorphic, and there are several taxa in Acoelomorpha (reviewed by Rieger et al. 1991) showing this condition. The same is true at least for the “ovary” of Gnathostomulida and Gastrotricha, and the agonadial condition for both sexes is again found in *Xenoturbella*. Accordingly, a true gonad with an epithelial wall proper was not present in Urbilateria, but was evolved by parallelism in Protostomia and Deuterostomia respectively.

### Sperm and mode of fertilization

The ultrastructure and immunocytochemistry of sperm of Acoelomorpha have been thoroughly studied by several authors throughout the last decades. The shared biflagellate condition of sperm cells of Acoela and most Plathelminthes seems nowadays to be due to convergence, since spermatogenesis is entirely different in both taxa (Raikova et al. 1997; 2001; Raikova and Justine 1999; Raikova 2002). The acoel sperm shows also several further apomorphic features (Raikova 2002; Petrov et al. 2004). The genuine monoflagellate condition in the sperm of Nemertodermatida clearly is plesiomorphic for Acoelomorpha (Tyler and Rieger 1975; Lundin and Hendelberg 1998), and if internal fertilization is accepted as plesiomorphic for Bilateria, this is also true for their introsperm.

The sperm of *Xenoturbella* reflects ectaquatic fertilization and resembles those of enteropneust deuterostomes (Obst et al. 2008). However, this type of sperm is widely present among the Metazoa and no special synapomorphic structure could be detected.

### Cleavage

Contrary to Plathelminthes and other trochozoan Protostomia with a spiral-quartet cleavage type, the Acoelomorpha show a spiral-duet cleavage (e.g. Bresslau 1904; Apelt 1969b; Jondelius et al. 2004). Whereas most earlier authors regarded the acoelomorph condition as a “modified spiral cleavage”, recent investigations have emphasized the principal differences in the two cleavage types (see Tables 1, 2 and 3 and a recent review by Hejnal 2015b) with respect to many details. It is of particular importance that the acoelomorph spiral-duet cleavage is regulative like the radial cleavage of diploblasts, lophophorates and deuterostomes. Indeed, *Xenoturbella* shows a radial rather than a spiral type of cleavage (Hejnal 2015a). In contrast, the spiral-quartet cleavage and the various cleavage types among the Ecdysozoa are highly determinative or show even constant cell numbers (eutely). Based on outgroup comparison, a regulative cleavage type appears plesiomorphic for Bilateria, whereas the spiral-duet type is more likely another synapomorphy of Acoelomorpha.

### Mode of development

Without exception, Xenacoelomorpha show direct development. In addition, none of the adult body plans of histozoan (i.e. with true nervous and muscle tissues) non-Bilateria, i.e. Cnidaria (polyp) or Ctenophora, can be directly homologized with the acoelomorph adult, and the only comparable stage is the planula larva of Cnidaria. Indeed, certain anthozoan planula larvae (e.g. *Protopalathoa* sp.; cf. Babcock and Ryland 1990) already show bilateral symmetry according to a more

benthic mode of life, and these may act as functional models of the evolutionary process from planula-like diploblasts to bilaterian, acoelomorph-like triploblasts. If Urbilateria had direct development, all types of bi- or multiphasic life cycles among the Bilateria are secondary in origin.

The latter conclusion somewhat contrasts the ideas of Pasquinelli et al. (2003), who based their considerations on the fact that *let-7*, a gene which directs larval or juvenile to adult cell fate transitions, is found throughout the Bilateria, but is entirely lacking in Acoela and in basal metazoans such as Porifera and Cnidaria. Since *let-7* is also found in direct developers such as nematodes, but lacking in groups with biphasic life cycles (Porifera, Cnidaria), a correlation with complex life cycles appears a non-justified assumption.

### Stem cells (neoblasts)

Whereas the omnipotent stem cells (neoblasts) in true Plathelminthes have been studied by many authors in depths, there is a single study on neoblasts in the acoelomorphs (Gschwentner et al. 2001), namely the sagittiferid acoel *Convolutriloba longijissura*, member of a genus which shows an extreme amount of asexual reproduction by fission or budding. Thus, it remains to be verified whether or not the conditions reported for *Convolutriloba* are typical for Xenacoelomorpha as a whole. But even if so, the presence of an extensive stem cell system in Cnidaria suggests this condition as plesiomorphic for Bilateria.

### Acoelomorph affinities and significance of *Xenoturbella*

Clear dissimilarities between *Xenoturbella* and Acoelomorpha are found in size, which is usually 1–2 mm for Acoelomorpha (but up to 20 mm in the acoel *Hofstenia*) and 20–40 mm for *Xenoturbella*. Size may be correlated with the different sperm type (introsperm versus ectaquatic sperm). It is interesting to note that the quite large *Hofstenia* species show a highly unusual, anteriorly placed male gonopore and copulatory organ (Hooge et al. 2007). As outlined, Acoelomorpha show a spiral-duet cleavage, whereas *Xenoturbella* exhibits radial cleavage, both types are regulative, however.

On the other hand, the character analysis presented above has revealed a remarkable degree of similarity between the Acoelomorpha and *Xenoturbella*, both share the following:

1. A polyciliary, glandular epidermis with a distinct type of cilium with respect to both ciliary tip and rootlet-system
2. “Pulsatile bodies” as a special type of epidermal regeneration
3. An acoelomate body cavity mainly filled with muscle cells
4. A sac-like gut with ventral or posterior opening

5. An intraepidermal nerve plexus without any true, paired (serotonergic and RF-amidergic) cerebral ganglion
6. The lack of stomatogastric nerve system
7. The lack of a sensory apical organ
8. A statocyst vesicle with free statoconial cells having an intracellular statolith
9. The entire lack of ultrafiltration excretory systems
10. The lack of a true gonadal epithelium, no female genital opening

Although many of these similarities are probably plesiomorphic, in particular, the characters 1, 2, 6, 7 and 8 represent synapomorphies of a clade Xenacoelomorpha, a hypothesis which is also supported by most recent molecular analyses (most recently reviewed by Nakano 2015).

None of the morphological characteristics is finally decisive for the current two alternative placements of Xenacoelomorpha either at the base of the Bilateria or as a sister group to ambulacrarian Deuterostomia (Echinodermata and Hemichordata) (Fig. 1). The latter hypothesis, however, requires the assumption of many reductions, which are hard to envision because Xenacoelomorpha are free-living predators (with few exceptions among derived taxa of Acoela). Moreover, the deviation of Xenacoelomorpha by simple progenesis of a larval or juvenile deuterostomian (ambulacrarian) ancestor is not possible: (1) Deuterostomes generally have epithelial musculature, particularly in early ontogeny (Rieger and Lombardi 1987), a simple progenetic origin

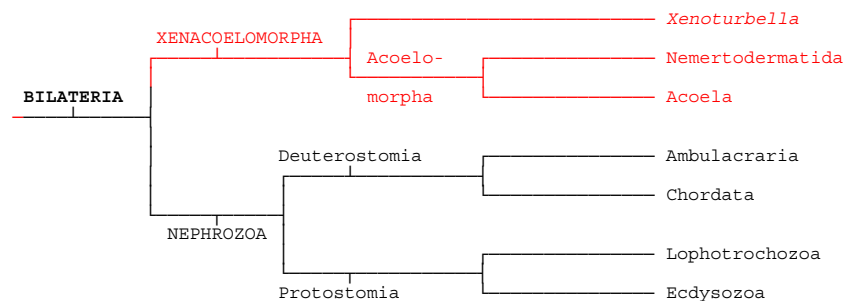
of Xenacoelomorpha with fibrous muscles is thus unlikely. (2) The entire lack of an apical organ, which is present in all ambulacrarian larval types, additionally contradicts the progenesis-hypothesis. (3) Ambulacrarian larvae show a well-developed and functional metanephridial excretory system. It is very unlikely that predators, which take up a high amount of proteins and thus are faced with extensive ammoniac waste, will omit an already present ultrafiltration system. If so, the forthcoming genome of *Symsagittifera roscoffensis* should not content genes (e.g. nephrin) which are correlated with an ultrafiltration system. (4) Deuterostome larvae develop coelomatic cavities very early in ontogeny. Again it is hard to assume that no trace of such a cavity have been remained in Xenacoelomorpha. (5) Finally, and bridging morphology with the molecular level of organization, the low number of acoelomorph Hox-genes (Cook et al. 2004; Moreno and Martínéz 2010), which is similar to cnidarians (e.g. DuBuc et al. 2012) compared with the much higher number inferred for the common ancestor of proto- and deuterostomes (Butts et al. 2008) additionally suggests an early xenacoelomorph offshoot rather than a reduced deuterostome lineage.

Accordingly, I favour the hypothesis of a position of Xenacoelomorpha at the basis of Bilateria.

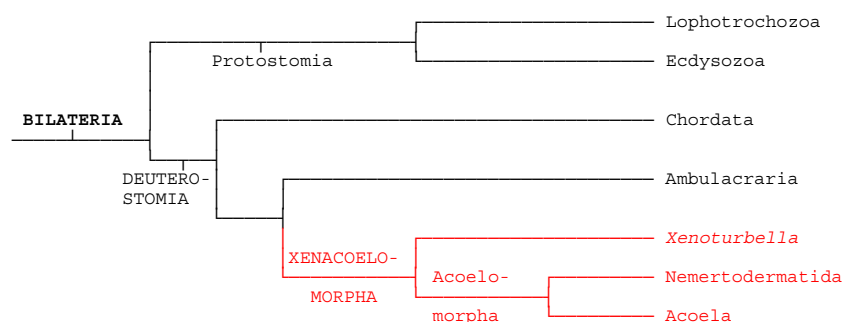
There are several data-sets in particular concerning *Xenoturbella* and Nemertodermatida, which are still urgently needed to confirm (or reject) this point of view: (1) development and organogenesis (including evo-devo studies on various gene-expressions), (2) data on the Hox-genes in particular

**Fig. 1** Hypothesis A

HYPOTHESIS A



HYPOTHESIS B





of *Xenoturbella*, (3) more whole genomes (a) to check for genes for e.g. ultrafiltration systems and (b) to infer additional molecular rare genomic events, which may be useful for phylogenetic reconstructions.

### Acoelomorpha and Urbilateria

Based on the assumption of basal Acoelomorpha and to summarize the character analysis executed above, Urbilateria (i.e. the hypothetical stem species of Bilateria including Acoelomorpha) probably has the following characteristics:

Urbilateria was a small (1–2 mm), benthic worm which moved by muco-ciliary gliding provided by highly specialized polyciliary cells and mucous cells of the epidermis enabling muco-ciliary gliding along the seafloor. The latter possibly regenerated by means of “pulsatile cells”. Below the epidermis was a fibrous muscle system consisting of a grid of outer ring, diagonal and inner longitudinal muscles, otherwise, only few parenchymous cells filled the acoelomate body cavity. Urbilateria probably was a predatory organism, the gut of which was a simple, cellular cul-de-sac with the gut opening posteriorly situated. The nervous system still was represented by a basiepithelial plexus (see e.g. the recent reviews by Schierwater et al. 2009 and Northcutt 2012); true ganglia were lacking, but (contrary to Acoelomorpha) a stomatogastric system was already present. Whereas photoreceptive cells probably occurred, the presence of true eyes is unlikely, and even if so, these eyes were certainly not “cerebral”. Urbilateria entirely lacked ultrafiltration cells and excretory organs. Regeneration ability certainly was high, but it is uncertain, whether or not asexual reproduction was of great importance. Concerning sexual reproduction true gonads (i.e. a gonadial epithelial wall) were lacking, the gametes rested freely in the body cavity (Extavour 2008). Internal fertilization was likely present by means of a copulatory system and introsperm, the yolky eggs respectively zygotes were shed by (regenerative) rupture of the body wall. Cleavage was regulative and development was direct without any true larval stage.

This scenario clearly rejects all historical variants of the enterocoel theory, i.e. the assumption of a large, coelomate (e.g. Dewel 1999; Rieger et al. 2004) or even segmented bilaterian ancestor as for instance proposed by Balavoine and Adoutte (2003; but see Seaver 2003 for contrary view). It also rejects all ideas on a planktic or biphasic Urbilateria (e.g. Rieger 1994a, b; Nielsen 1985, 2012, 2013). On the other hand, it supports (though varies) ideas summarized historically under the “planula-theory” (e.g. von Salvini-Plawen 1978). The latter assumption is further supported by recent evo-devo result showing the Cnidaria (in particular, the Anthozoa) as originally bilaterian animals (e.g. Matus et al. 2006).

This renewed proposal on the various features makes Urbilateria much simpler and much more similar to the diploblastic level of evolution than competing models. It avoids the

extra-assumptions of substantial reductions in Xenacoelomorpha and thus is as such more parsimonious than the deuterostome hypothesis.

As a consequence, one may identify several major evolutionary events after the split off of the Acoelomorpha. Interpreting these characters as synapomorphies, the monophyly of Deuterostomia and Protostomia under the exclusion of Acoelomorpha is likely. Erwin and Davidson (2002) have created the term “PDA” (protostome-deuterostome ancestor), but in the light of excluding the Acoelomorpha, this again is misleading.

Both, protostomes and deuterostomes (for the exceptional *Xenoturbella* see above) show identically structured and highly specialized ultrafiltration weirs in their excretory systems consisting of a meandering slit-system bridged by a thin, ladder-like diaphragm and covered/underlain by an extracellular matrix. This type of ultrafiltration weir occurs in protonephridial cyrtocytes or solenocytes, arthropod nephrocytes, molluscan rhogocytes or coelomate podocytes (see Haszprunar (1996b) for homology of these cell-types) and appears the most probable synapomorphy of both superclades. Accordingly, I follow the proposal of Jondelius et al. (2002) to name the clade including all Bilateria except the Acoelomorpha Nephrozoa.

Based on results of developmental gene-expression (“evo-devo”), several authors (e.g. Sprecher and Reichert 2003; Holland et al. 2013) considered the cerebral brain of protostomes and deuterostomes as monophyletic. However, identical gene-expression is a prerequisite but is not a conclusive argument for homology (see the “homocrazy” debate, e.g. Nielsen and Martinez 2003; Svensson 2004); therefore, this assumption needs further support. The same is true for a common basic photoreceptor type (Arendt and Wittbrott 2001).

It should be noted that the so-called zootype (e.g. Deutsch and LeGuyader 1998; Schierwater and DeSalle 2007; Erwin 2009), i.e. the summary of all assumptions concerning the original genetic equipment, particularly the Hox-Parahoxgenes of the Bilateria, actually refers only to Nephrozoa (Cook et al. 2004; Jiménez-Guri et al. 2006; Baguña et al. 2008). It remains to be studied, how far the current assumption of a zootype as a general genetic concept for the last common ancestor of Proto- and Deuterostomia is already present in the Acoelomorpha.

Accepting the Acoelomorpha as the earliest bilaterian offshoot not only strongly influences our understanding of Urbilateria but also has high significance for the rooting of character states of the remaining bilaterian superclades within the Nephrozoa, i.e. the Deuterostomia, Ecdysozoa and Lophotrochozoa. This mainly concerns among others the small body size coupled with ciliary movement, an acoelomate body cavity with fibrous muscles, internal fertilization and direct development. Accordingly, large body size, coelomatic cavities, epithelial musculature, true brains,

aquatic fertilization and bi- or multiphasic life cycles or even larval planktotrophy have been evolved several times.

## Outlook

A clear statement of caution at the end of this review: phylogenetics always is a matter of probabilities according to the current stage of knowledge. No doubt that this will not be the last word on Urbilateria or on *Xenoturbella* and Acoelomorpha. However, if this article will stimulate further research on Xenacoelomorpha as the most primitive clade of the Bilateria—even in order to show me wrong—then I have reached my aim.

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