# An outline for the classification of Phylum Mollusca in taxonomic databases

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This is un unpublished document summarizing the options taken by the taxonomic editors for the higher classification units (below phylum, above superfamily) of the Mollusca, for the European Register of Marine Species and later the World Register of Marine Species.

#### Rationale

#### 1. Class and above issues.

The naming of molluscan classes and their acceptation as monophyletic units remains relatively unchallenged. The most unstable issue is the treatment of the "aplacophoran" classes as one class (Aplacophora with two subclasses), as two distinct classes or as a stem group of the Mollusca which would leave them paraphyletic (thus "unassigned" to a class in the options taken here, see below).

Groupings of classes into clades is highly controversial (for a review of competing hypothesis see Steiner & Dreyer (2003) Molecular phylogeny of Scaphopoda (Mollusca) inferred from 18S rDNA sequences: support for a Scaphopoda–Cephalopoda clade. — *Zoologica Scripta*, 32, 343–356). It will be considered here that this is irrelevant for the context of databases, so classes will be treated as an unresolved polytomy within Phylum Mollusca.

#### 2. Below class and above superfamily.

Conceptual issues – There is an overwhelming trend in the scientific community to consider the cladistic system as the sole acceptable criterion for a classification of living organisms. An alternative is to accept and name both monophyletic and paraphyletic groups considering that classification and phylogenetic reconstruction are two distinct endeavours each one with its own rationale (the evolutionary classification, see Ashlock, 1979: *Systematic Zoology* 28, 441-450), but this view is at this time out of fashion.

There are two basic problems in elaborating a classification which would reflect phylogeny adequately.

(a) We don't know the phylogeny, we only have phylogenetic hypothesis in which branching patterns may vary according to the which characters are considered, to which taxa are sampled and/or to which kind of analysis is performed. When this happens results are not "robust" and should not be used to alter a classification in use until they become unambiguous.

(b) The essence itself of phylogenetic history (once accepted as correct and not subject to change with new research) makes that its translation into a classification with ranks is not straightforward. Evolutionary patterns are highly asymmetrical: within any particular group, one or more lineages achieved some evolutionary novelty and underwent more and more diversification, threfore leaving behind a paraphyletic group sharing the common ancestor and the ancestral morphology.

(2.1.) One possibility of escape is to abandon ranks, leaving only names of nested clades (the option taken in Bouchet & Rocroi, 2005). This is not desirable because (1) hierarchical levels are uneasy to follow after a number of branchings and (2) ranking of higher categories is brings information to quantify how deep the diversification is going (an information not contained in the number of terminal taxa nor in the number of branching events). It does not matter whether this is done in the form of Linnean classification (Class, Order, Family...) or just with hierarchical numbers.

(2.2.) The option taken here is to collect unplaced taxa in an informal group, which is child of the containing group and is named "unassigned [name of containing taxon]".

These convenience or "placeholder" classification units are used either when no warranted phylogenetic results can be used, or where a well supported phylogeny leaves behind a number of taxa aside to a monophyletic crown group.

\* When skipping a rank, the omitted rank in this draft is the **least inclusive rank** (e.g. in Gastropods, rank Neritimorpha as a subclass, Order omitted), considering that the branching of Neritimorpha from Caenogastropoda is more remote than the branching between "orders" within the Caenogastropoda. An alternative would be to skip the more inclusive one, considering that the classification proceeds by grouping objects into higher categories (thus starting from species up), not by splitting large sets of objects into smaller sets. Opinions welcome.

Taxon searches should arrive into explanatory notes for rejected but well known taxa e.g. Archeogastropoda indicating that this is currently distributed in Patellogastropoda, Vetigastropoda, Cocculiniformia, Neritimorpha.

#### 3. Below Superfamily.

Subfamilies and tribes should be listed in the database under the appropriate family. The genera may be either listed as direct child-taxa of the family, or distributed in the different subfamilies. The latter option is tenable where there is a comprehensive phylogenetic scheme and where all genera can be placed, but for the users' convenience it should be avoided that some genera be direct child-taxa of the family, and other listed under a subfamily.

#### Contents

(2 = class, 3 = subclass, 4 = infraclass, 5 = order, 6 = suborder, 7 = infraorder, 8 = SPF, 9 = Family).

#### 2. Class Solenogastres.

Supraspecific classification is based on Salvini-Plawen (1978: *Zoologica*, Stuttgart, 44, 1-315); see also García –Álvarez & Salvini-Plawen (2007: *Iberus* 25, 73-143).

#### 5. (Order) Pholidoskepia

- 5. (Order) Neomeniamorpha
- 5. (Order) Cavibelonia
- 5. (Order) Sterrofustia

#### 2. Class Caudofoveata.

#### 5. (Order) Chaetodermatida

There is a debate over whether these should be subclasses of a Class Aplacophora or a separate classes. The phylogenetic relationships of aplacophoran molluscs are not unambiguously resolved although the data at hand (see Haszprunar 2000: *American Malacological Bulletin* 15, 115-130, and Glaubrecht, Maitas & Salvini-Plawen, 2005: *Mitteilungen aus der Museum für Naturkunde in Berlin* – Zoologische Reihe 81, 145-166) would support a relationship like

(Solenogastres(Caudofoveata(Polyplacophora(Conchifera)))) making Aplacophora paraphyletic. For this reason, *contra* the Aculiferan hypothesis of Scheltema (1993: *Biological Bulletin* 184, 57-78) and in agreement with the European school of Salvini-Plawen, the two taxa will be maintained as classes in the classification, without the need for further subdivisions above superfamily.

#### 2. Class Monoplacophora.

The only classification problem with modern monoplacophorans is the discussion around using Monoplacophora Odhner, 1940 vs. Tryblidiida. Monoplacophora sl. as defined in Runnegar & Jell (1976) would include three orders among which Tryblidiida. Problems arise from the ambiguous position of some paleozoic fossil taxa which could be monoplacophorans or gastropods, or (worse) stem-group gastropods derived from monoplacophorans, thus making Monoplacophora paraphyletic. Preference for the name Tryblidiida follows Waller's (1998) conclusion that these are the sister-group to all other Conchifera, thus escaping being paraphyletic.

Giribet et al. (2006: *Proceedings of the National Academy of Sciences* 103, 7723-7728) claimed that the monoplacophoran *Laevipilina* is recovered within a branch containing polyplacophoran taxa in an analysis including several nuclear and mitochondrial sequences. This result is based on a very small specimen and it is premature to introduce such a major change in the classification before this is replicated.

**5. (Order) Tryblidiida** Lemche, 1957 (to accomodate all Recent monoplacophorans)

#### 2. Class Polyplacophora.

Classification of chitons based on the conclusions of Okusu et al. 2003: *Organisms, Diversity & Evolution* 3, 281-302, mostly where supporting morphological conclusions of Sirenko 1993: *Ruthenica* 3: 97-117 (otherwise this molecular dataset does strange things with the outgroups and thus may not be taken as the basis for drastic changes in classification).

**4.** (Subclass) Neoloricata Bergenhayn, 1955 (added here, not considered in the studies above which include only members of the Neoloricata) Often listed as Order which would downgrade included taxa to Suborder and Infraorder respectively: opinions welcome.

#### (5) unassigned Neoloricata

9. Callochitonidae (suggested as sister-group to the Lepidopleurida by Okusu et al. but this needs more support before being integrated in the classification).

#### 5. (Order) Lepidopleurida (clade).

5. (Order) Chitonida (clade).

6. (Suborder) Acanthochitonina (possible clade).

6. (Suborder) Chitonina (clade).

The results in Okusu et al. (2003) are not conclusive enough to dismiss the clade Acanthochitonina as defended in Sirenko (1993) and from sperm morphology by Buckland-Nicks (1995: *Mémoires du Muséum National d'Histoire Naturelle* 166, 129-153). At the most, if the phylogeny of Okusu et al. is correct, this clade will need to be divided in two monophyletic units (then ranked as two distinct suborders), one around *Acanthochitona* and one around *Mopalia* (not Ischnochitonina because *Ischnochiton* belongs to the clade Chitonina).

#### 2. Class Gastropoda.

Gastropod classification is to be taken from Bouchet & Rocroi (2005: *Malacologia* 47 (1-2): 397 pp), with ranks added above superfamily and with every change or update justified in a note to the taxon entry.

Colour code black = taken directly from Bouchet & Rocroi (2005), Fuchsia = ranks added straightforward from B&R scheme (in both case details down to superfamily are omitted here, will be transcribed from B&R), Red = added or departing from B&R

The initial split **Eogastropoda/Orthogastropoda** proposed by Ponder & Lindberg, 1997 is not retained, following Bouchet & Rocroi, 2005: 271 note 14: challenged in Colgan *et al.* 2003). For this reason all ranks go up one step from Ruud Bank's draft for *Fauna Europaea*.

Keeping "Prosobranchia" as a subclass is a contentious issue, *maxime* if we derive the classification from Bouchet & Rocroi (2005) who reject it. Anyway every effort should be made to keep at the same rank (here subclass) the Heterobranchia and the Caenogastropoda which are supposed to be sister-groups.

#### 3. (Subclass) Patellogastropoda (clade)

**3. (Subclass) Vetigastropoda** (clade; would be rendered paraphyletic if Colgan et al. 2003 are correct in proposing Patellogastropoda as a derived clade of some Vetigastropoda). There has been much recent debate around Vetigastropod phylogeny, especially Kano (2008: *Zoologica Scripta* 37, 1-21) and Williams, Karube & Ozawa (2008: *Zoologica Scripta* 37, 483-506). Their conclusions should be followed in the draft classification, most of them were already foreseen in Bouchet & Rocroi (2005). Mainly:

- Kano does not believe that Anatomidae should be separated from Scissurellidae and suggests that this result was induced by contamination or mislabelling.

- The distribution of traditional Trochoideans in families and subfamilies may be updated with these results.

9. Family Ataphridae Cossmann, 1915 [= Trochaclididae

Thiele, 1928; = Acremodontinae Marshall, 1983; = Parataphrinae Calzada, 1989]

9. Family Pendromidae Warén, 1991 [= Trachysmatidae Thiele, 1925, based on erroneously identified genus]

**8. SPF Fissureloidea** Fleming, 1822

8. SPF Haliotoidea Rafinesque, 1815

8. SPF Lepetelloidea Dall, 1882

8. SPF Lepetodriloidea McLean, 1988

**8. SPF Neomphaloidea** McLean, 1981 (has been given higher rank

in some older classifications)

8. SPF Pleurotomarioidea Swainson, 1840

8. SPF Scissurelloidea Gray, 1847 (with the sole family

Scissurellidae following Kano (2008) *contra* Geiger & Thacker (2005: *Molluscan Research* 25, 47-55)).

8. SPF Seguenzioidea Verrill, 1884

9. Family Seguenziidae Verrill, 1884

9. Family Chilodontidae Wenz, 1938

SF Chilodontinae Wenz, 1938

SF Calliotropinae Hickman & McLean, 1990 (nota:

Kano (2008) claims that "the eucycline trochids" belong here but his taxon sampling belongs to Calliotropinae *sensu* Bouchet & Rocroi, 2005).

SF Cataeginae McLean & Quinn, 1987

#### **8. SPF Trochoidea** Rafinesque, 1815

9. Family Trochidae Rafinesque, 1815

SF Trochinae Rafinesque, 1815

SF Cantharidinae Gray, 1857

SF Monodontinae Gray, 1857 [= Gibbulinae

Stoliczka, 1868] (both ranked as tribes of the Trochinae in Bouchet & Rocroi, 2005, elevated to subfamily following Williams et al. (2007)).

	SF Halistylinae Keen, 1958
	SF Lirulariinae Hickman & McLean, 1990
	SF Stomatellinae Gray, 1840 [= Stomatiidae
Carpenter, 1861]	
	SF Umboniinae H. Adams & A. Adams, 1854
(1840)	
	9. Family Calliostomatidae Thiele, 1924 (1847)
	9. Family Solariellidae Powell, 1951 [= Minoliinae Kuroda,
Hobo & Oyama 10711	-

Habe & Oyama, 1971]

9. Family Turbinidae Rafinesque, 1815 (withdrawn

superfamily rank *contra* Bouchet & Rocroi (2005), placed as family of the Trochoidea following Williams et al. (2008); the character of calcareous operculum is given less and less importance, which makes sense, cf. the Naticidae).

SF Turbininae Rafinesque, 1815

SF Moelleriinae Hickman & McLean, 1990

SF Prisogastrinae Hickman & McLean, 1990

SF Skeneinae W. Clark, 1851 [= Delphinoideinae

Thiele, 1924] (should be pruned of many genera which go to the Seguenzioidea according to Kano (2008); he may be right but for the purpose of the database I would leave these genera in Skeneidae until somebody formally assigns them to a seguenzioid family in the literature).

SF Tegulinae Kuroda, Habe & Oyama, 1971

SF Margaritinae Thiele, 1924 (moved from

Trochidae to Turbinidae following Williams et al. 2007)

8. Family Liotiidae Gray, 1850

8. SPF Angarioidea Gray, 1857 formally raised to superfamily

level by Williams et al. (2008). The same suggest that something similar may be done in the future for *Arene*, but Bouchet & Rocroi (2005) note that Areneinae McLean, 2001, introduced in a congress abstract, is not an available family-level name.

9. Family Angariidae Gray, 1857 [= Delphinulidae]

**8. SPF Phasianelloidea** Swainson, 1840, formally raised to

superfamily level by Williams et al. (2008).

8. Family Phasianellidae Swainson, 1840

8. Family Colloniidae Cossmann, 1917

3. (Subclass) Cocculiniformia (clade, once some families are moved to Vetigastropoda).
3. (Subclass) Neritimorpha (clade)

\* **Clade Apogastropoda** *sensu* Ponder & Lindberg, 1997 = [Caenogastropoda + Heterobranchia], skipped; used in *Tree of Life* but neither in Bouchet & Rocroi nor in *Southern Synthesis*).

\* Clade Sorbeoconcha (should include [Cerithioidea + Campaniloidea + all Hypsogastropoda], see definition in Ponder & Lindberg, 1997: 225, not only [Cerithioidea + Campaniloidea] as suggested by the indent pattern in Bouchet & Rocroi). Neotaenioglossa Haller, 1892 suggested in Ruud Bank's draft for *Fauna Europaea* is not retained because it would need severe emendation to remove Pyramidellids, Cerithioids, etc.. and therefore would be too far from Haller's concept if it were to fit the concept of Sorbeoconcha. Despite being cladistically valid, the taxon Sorbeoconcha is also skipped because (1) ten years after its publication, the name still sounds unfamiliar to most and (2) it is not very helpful in the classification scheme because it includes the bulk of Caenogastropoda (only keeping out small stem groups Abyssochrysidae, Provannidae, and the architaenioglossate taxa)..

Apogastropoda and Sorbeoconcha, like Thiele's taxa, even if not in the hierarchy should be given an entry (as "alternate representation") indicating which families compose them.

# 3. (Subclass) Caenogastropoda (clade, sister group of Heterobranchia in *Tree of Life*)

# (5.) Unassigned Caenogastropoda

- 9. Family Abyssochrysidae
- 9. Family Provannidae
- **8.** SPF Ampullarioidea
- 8. SPF Cyclophoroidea
- 8. SPF Viviparoidea
- 8. SPF Cerithioidea
- 8. SPF Campaniloidea
- 8. SPF Triphoroidea
- **8.** SPF Epitonioidea
- **8.** SPF Eulimoidea

Informal Group Ptenoglossa is not used, because correctly stated as artificial by Ponder & Lindberg, 1997; this avoids pulling apart Cerithioidea + Campaniloidea from Triphoroidea in the scheme.

Architaenioglossa is not used, it is shown as unsupported by Harasewych et al. (1998: *Zoologica Scripta* 27, 361-372) and it is just as informative to use the three superfamilies.

Clade Hypsogasropoda is cladistically correct and should be given an entry as "alternate representation" but is skipped to avoid introducing too many levels in ranking. It includes the three following orders:

**5. (Order) Littorinimorpha** (clade until further notice, published evidence for them being monophyletic is scanty). *Tree of Life* (based on Ponder & Lindberg, 1997 and on Strong, 2003) may be more realistic in using only Neogastropoda as a clade and unresolved superfamilies of Hypsogastropoda for what is here the Littorinimorpha. This may be the least robust point in our Gastropod classification.

#### 5. (Order) Neogastropoda (clade)

#### 8. SPF Muricoidea

- 9. Family Muricidae
- 9. Family Babyloniidae
- 9. Family Mitridae
- 9. Family Cystiscidae
- 9. Family Marginellidae
- 9. Family Costellariidae
- 9. Family Harpidae
- 9. Family Pleioptygmatidae
- 9. Family Strepsiduridae

- 9. Family Turbinellidae
- 9. Family Volutidae
- 9. Family Volutomitridae

The treatment of Volutidae and others in Muricoidea is not very intuitive, it was first proposed by Ponder & Warén (1988) where these and also Buccinoidea (separate in Bouchet & Rocroi, 2005)) were placed in a very comprehensive Muricoidea.

8. SPF Buccinoidea

- 9. Family Columbellidae
- 9. Family Buccinidae
- 9. Family Fasciolariidae
- 9. Family Melongenidae
- 9. Family Nassariidae
- 8. SPF Pseudolivoidea
  - 9. Family Pseudolividae
- 8. SPF Olivoidea
  - 9. Family Olividae
- 8. SPF Cancellarioidea
  - 9. Family Cancellariidae
- 8. SPF Conoidea
  - 9. Family Conidae
    - 9. Family Terebridae
    - 9. Family Turridae

Malacolog goes back to the intuitive, traditional "Turridae" with subfamilies Clathurellinae, Cochlespirinae, Crassispirinae, Daphnellinae, Drilliinae, Mangeliinae, Oenopotinae, Strictispirinae, Taraninae, Turrinae and Zonulispirinae. Should we do this *contra* Taylor, Kantor & Sysoev (1993: Bulletin of the Natural History Museum, Zoology series, 59, 125-170)?

3. (Subclass) Heterobranchia (clade, ranked as sister group of Caenogastropoda in *Tree of life*)
 (4.) unassigned Heterobranchia (informal group, equivalent to infraclass): these are the

stem-group ("lower") Heterobranchia, and controversial taxa belonging to Heterobranchia but not placed consensually. "Heterostropha" not used, it is paraphyletic and such a heterogeneous group that it is just as informative to have loose superfamilies, but could have an explanative entry.

9. Families Cimidae, Orbitestellidae, Tjaernoeiidae, Xylodisculidae,

Omalogyridae, Rissoellidae, Glacidorbidae).

#### 8. SPF Architectonicoidea

9. Family Architectonicidae

#### 8. SPF Mathildoidea

9. Family Mathildidae

Is there a profound reason for Bouchet & Rocroi (2005) keeping Architectonicidae and Mathildidae in separate superfamilies? *Southern Synthesis* (chapter written by J. Healy), and Gary in *Malacolog*, keep them together, and these two families are so similar that they share virtually every character except spire height.

- 8. SPF Valvatoidea
- 8. SPF Pyramidelloidea
- 8. SPF Acteonoidea
- 8. SPF Ringiculoidea
- 8. SPF Siphonarioidea (if the phylogenetic hypothesis of Grande

et al. (2004) is accepted, it will be more parsimonious to accept siphonarids as

Opisthobranchs rather than to declare Opisthobranchs polyphyletic).

**4. (Infraclass) Opisthobranchia (informal group**, may be a clade when limited to the groups below and supplemented with *Siphonaria*)

(5.) "Group" Acochlidiacea given rank of Order as in Fauna of Australia (by Robert Burn)

**5. (Order) Cephalaspidea** (clade, monophyletic when removing Actaeonoidea, Ringiculoidea, Cylindrobullida)

**5. (Order) Umbraculida** (clade; Grande et al. (2004) use the name **Tylodinoidea** for this clade and found it to be the sister clade to the Cephalaspidea (Acteonoidea etc.. excluded)

5. (Order) Thecosomata

#### 5. (Order) Gymnosomata

Klussmann-Kolb & Dinapoli (2006: *Journal of Zoological Systematics and Evolutionary Research* 44(2), 118-129) brought convincing evidence that Gymnosomata and Thecosomata are sister-groups, so that Pteropoda can be considered as a clade (skipped here to avoid too many ranks), and that Pteropoda is sister-group to the Aplysiomorpha.

**5. (Order) Anaspidea** (clade). We use Anaspidea, which dates from Fischer, 1883 but originally also included Oxynoidae here excluded, preferred to Aplysiomorpha which dates from Pelseneer, 1906 but originally also included the Gymnosomata.

#### 5. (Order) Sacoglossa

9. Family Cylindrobullidae (controversial but Jensen's

(1996) placement in the Sacoglossa is the most sensible option in a working classification)

# **5.** (Order) Pleurobranchomorpha (clade)

**5. (Order) Nudibranchia** (probable clade)

Contrary to previous version, **Nudipleura** (clade; this is [Pleurobranchiomorpha + the nudibranchs]) is skipped because (1) we are already short of ranks at this level of the tree and (2) it is useful to keep such a well-known nale as Nudibranchia at its traditional Order level, as long as it is tenable. The concept of Nudipleura is nevertheless correct and has been given strong support by Grande et al. (2004) against the traditional grouping Notaspidea = [Umbraculida + Pleurobranchiomorpha] permanently ruled out).

Based on molecular data (Grande et al., 2004), the Nudibranchia were challenged to be a polyphyletic group, with Pleurobranchomorpha being the sister to the Anthobranchia. Conversely, Wägele & Willan (2000) found strong morphological evidence for the monophyly of Nudibranchia. Four years later, there does not seem to be any additional evidence that Nudibranchia are not monophyletic so they are retained as a valid taxon until convincingly challenged.

**6.** (Suborder) Euctenidiacea (clade; this includes the dorid-like nudibranchs and is named Nudibranchia (Anthobranchia) in Grande et al. (2004). Opinions welcome on which name to use.

**6.** (Suborder) Dexiarchia (clade, includes clades [Pseudoeuctenidiacea + Cladobranchia] in the working scheme of Bouchet & Rocroi but one rank will be skipped to avoid multiplication of hierarchical levels; for this reason Pseudoeuctenidiacea is given equal rank to the three infraorders of the Cladobranchia. There remains a suite of families of uncertain affinities, which are grouped in an artificial group of "unassigned Dexiarchia").

(7.) unassigned Dexiarchia

7 (Infraorder) Pseudoeuctenidiacea (clade)

7 (Infraorder) Euarminida (clade)

7. (Infraorder) Dendronotida (clade)

7. (Infraorder) Aeolidida (clade)

**4.** (**Infraclass**) **Pulmonata** (**informal group**). As it is still not clear whether the pulmonates (excluding Siphonarioidea and maybe some other groups) are monophyletic or not, the name should be preserved in the classification with the same rank as Opisthobranchia)

#### (5.) unassigned Pulmonata

- 8. SPF Amphiboloidea
- 8. SPF Trimusculoidea
- 8. SPF Ellobioidea
- 8. SPF Otinoidea

The Otinoidea were included in the Systellommatophora by Haszprunar & Huber (1990) and Nordsieck (1993a), and so placed in *Southern Synthesis*. However, according to the cladistic analyses of Barker (2001) and Dayrat & Tillier (2002) they are not related to the Systellommatophora.

The supposed clade Eupulmonata = [Ellobioidea + Trimusculoidea + Stylommatophora + (maybe) Otinoidea and Systellommatophora ] (used in *Southern Synthesis* as Order) is omitted due to current controversy. Barker (2001) and Dayrat & Tillier (2002) support a monophyletic group (Geophila) including the Systellommatophora [=

Onchidioidea+Veronicelloidea] and Stylommatophora, whereas H. Nordsieck (1993a) considered the Ellobioidea the sister-group of the Stylommatophora. Conversely, the molecular phylogenetic analysis of Dutra-Clarke et al. (2001) and Grande et al. (2004) has Eupulmonata polyphyletic, with (tentatively!) Ellobioidea as sister-group of all other Euthyneura.

5. (Order) Systellommatophora (clade)

**5. (Order) Hygrophila** (clade) (this is what is left of the basonmatophores when removing the controversial groups Amphiboloidea and Siphonarioidea)

## **5. (Order) Stylommatophora** (clade)

- 6. (Suborder) Elasmognatha (clade)
- 6. (Suborder) Orthurethra (clade)
- 6. (Suborder) Sigmurethra (informal group)

#### 2. Class Bivalvia.

note added june 2010: The bivalve classification will be adjusted to: **Bieler R.**, Carter J. G. & Coan E.V. (in press). Classification of bivalve families. In: Bouchet, P. & Rocroi, J.-P., Nomenclator of bivalve families. *Malacologia*, 52(2). so that the following comments, written prior to 2008, will become irrelevant.

The outline of bivalve classification essentially follows essentially Bieler & Mikkelsen (2006: *Zoological Journal of the Linnean Society* 148, 223–235), and details down to the family level to be transcribed from there unless otherwise noted. The previous draft was based on Giribet & Wheeler (2002: *Invertebrate Biology* 121, 271-324) which is essentially similar but the newer paper has the advantage of following the same rationale as Bouchet & Rocroi for the Gastropods, and of giving ranks and details down to the family level.

#### 3. (Subclass) Protobranchia

5. (Order) Nuculoida (clade)
8. SPF Nuculoidea
8. SPF Pristiglomoidea
5. (Order) Solemyoida (clade)
8. SPF Solemyoidea

# 8. SPF Maizanelloidea 9. Family Nucinellidae 5. (Order) Nuculanoida (clade) 8. SPF Nuculanoidea

The traditional subclass Protobranchia holds together with characters (the protobranch gills, the taxodont hinge in Nuculoidea and Nuculanoidea) which are plesiomorphic in Bivalves. There is debatable evidence that Nuculanoidea form a clade with lamellibranch bivalves rather than with the other protobranchs (Giribet & Wheeler, 2002). Pending further studies the three groups could be maintained as unassigned superfamilies of the Bivalvia but it is just as useful to keep Protobranchia with rank of subclass as long as it is not demonstrated to be polyphyletic (note that *Tree of Life* still uses Protobranchia with equal rank to Pteriomorpha, Paleoheterodonta, Heterodonta...). Internal relationships are not straightforward, there are not so many taxa so just go directly to superfamily rank. *Xenoturbella* to be ousted from here, with a note about Israelsson's hypothesis (1999: *Proceedings of the Royal Society* 266B, 835-841.

(clade Autolamellibranchiata (including all lamellibranchiate bivalves) is valid but skipped in classification scheme to avoid multiplication of ranks).

#### 3. (Subclass) Pteriomorpha (clade)

5. (Order) Arcoida (clade)
5. (Order) Mytiloida (clade)
5. (Order) Pterioida (probable clade)
(5) Unassigned Pteriomorpha

8. SPF Pinnoidea
8. SPF Limoidea
8. SPF Pectinoidea
8. SPF Plicatuloidea
8. SPF Dimyoidea
8. SPF Anomoiidea
8. SPF Ostreoidea

Results of Giribet & Wheeler (2003) indicate that Ostreoidea (as currently defined i. e. including pectinids) is polyphyletic, and that Limoidea + Pectinoidea + Anomioidea may form a clade (this makes sense). Since those results are still tentative and await a more extensive sampling of the pteriomorph taxa, there are two possibilities for the classification, maintain provisionally orders as in the *Treatise* and in *Southern Synthesis*, or use superfamilies as unassigned to order. The weakly supported but likely clade Pterioida is maintained.

(clade Heteroconchia = [Palaeoheterodonta + Heterodonta] skipped)

3. (Subclass) Paleoheterodonta (clade)

# 5. (Order) Trigonioida

## 5. (Order) Unionoida

This is an unexpected but well supported clade, reflected straightforward in the classification.

#### 3. (Subclass) Heterodonta

4. (Infraclass) Archiheterodonta Giribet in Taylor et al., 2007

#### 5. (Order) Carditoida

8. SPF Carditoidea

8. SPF Crassatelloidea

An unexpected but apparently well supported finding in Campbell (2002: Denver Annual Meeting of G.S.A., paper 236-4), Giribet & Wheeler (2003) and Dreyer et al. (2003) is that Astartidae and Carditidae are sister-groups to the remaining Heterodonta, may derive from fossil *Eodon* and may form together a clade. This has been given so much support in subsequent, independent studies (e.g. Bieler & Mikkelsen, 2006; Taylor et al., 2007: *Zoologica Scripta* 36, 587-606).

#### 4. (Infraclass) Euheterodonta

#### (5.) Unassigned Euheterodonta

- **8.** SPF Thyasiroidea
- 8. SPF Lucinoidea (excluding Thyasiridae and Ungulinidae)
- 8. SPF Solenoidea
- **8.** SPF Hiatelloidea
- 8. SPF Galeommatoidea
- 8. SPF Gastrochaenoidea
- 8. SPF Cardioidea
- 8. SPF Tellinoidea
- 8. SPF Sphaerioidea
- 8. SPF Myoidea
- 8. SPF Pholadoidea
- 8. SPF Dreissenoidea
- **8.** SPF Gaimardioidea
- 8. SPF Mactroidea
- 8. SPF Ungulinoidea
- 8. SPF Corbiculoidea
- 8. SPF Chamoidea
- 8. SPF Veneroidea
- 9. Families Glossidae, Hemidonacidae, Glauconomidae,

Trapezidae, Arcticidae, Vesicomyida, Kelliellidae.

#### 5. (Order) Anomalodesmata

- 8. SPF Pholadomyoidea
- 8. SPF Cuspidarioidea
- 8. SPF Pandoroidea
- 8. SPF Poromyoidea
- 8. SPF Thracioidea
- 8. SPF Verticordioidea

Current results in bivalve phylogeny indicate that Anomalodesmata are probably a monophyletic group (Dreyer et al., 2003; Taylor et al., 2007) but nested within Euheterodonta. This provides support to what is proposed by Giribet & Wheeler (2003) to merely merge Anomalodesmata into Heterodonta s.l. (note that *Tree of Life* still uses Anomalodsmata with equal rank to Pteriomorpha, Paleoheterodonta, Heterodonta...). It is helpful to reflect that these superfamilies go together and therefore keep the name Anomalodesmata as an order of the Euheterodonta. To be consistent, the same rank should be assigned to the other documented branches (e.g. Thyasiroidea, Lucinoidea, Solenoidea+Hiatelloidea, Tellinoidea) recognized in Taylor et al., and also to the crown group they name Neoheterodontei. The option taken here is to leave unresolved superfamilies until orders are formally named in the literature. There is compelling evidence that the traditional order Myoida is polyphyletic, so that its components figure here as unassigned superfamilies of the Euheterodonta, *contra* Bieler & Mikkelsen (2006).

## 2. Class Scaphopoda.

The following division follows Steiner & Dreyer (2003: Zoologica Scripta, 32, 343-356).

**5. (Order) Gadilida** (clade)

6. (Suborder) Entalimorpha (rank added here)

6. (Suborder) Gadilimorpha (rank added here)

# 5. (Order) Dentaliida (clade)

These two clades seem unambiguously supported by both molecular and morphological data; traditionally ranked as orders although why not subclass? Opinions welcome, decisions on this extend to other cases like the archeogastropod groups.

# 2. Class Cephalopoda.

The outline of cephalopod classification essentially follows the authoritative treatment in *Tree of Life* (Young R.E., Vecchione M. & Mangold K.M. 1995-2004). This draft is the translation of their phylogenetic scheme into a classification with the same rationale as for the other classes.

3. (Subclass) Nautiloidea (clade)

3. (Subclass) Coleoidea (clade)

# 4. (Infraclass) Decapodiformes (clade)

# (5.) Unassigned Decapodiformes

**8.** Bathyteuthoidea (clade, unranked in *Tree of Life*, here ranked as superfamily reflecting that the included genera *Bathyteuthis* and *Cthenopteryx* are now in separate families but have been considered long in the same family (e.g. Naef, 1921) and that molecular data confirm their close relationship one to another (Carlini, 1998: Ph.D. thesis cited in *Tree of Life* page).

9. Family Idiosepiidae (contains the sole genus *Idiosepius* Steenstrup, 1881, a tiny (< 1 cm) cephalopod of uncertain phylogenetic placement, sometimes included in Sepiida e.g. Nesis, 1987)

# 5. (Order) Myopsida (clade)

5. (Order) Oegopsida (contins most squids except Loliginidae)

5. (Order) Spirulida (monospecific clade)

**5.** (Order) Sepiida (clade; spelled Sepioidea in *Tree of Life*; Sepiolida Fioroni, 1981 is considered a suborder therein by *ToL*).

Relationships between the above clades are considered unresolved by the authors of ToL page, thus discarding the taxon Teuthida Naef, 1916 = [Myopsida + Oegopsida].

# 4. (Infraclass) Octopodiformes (clade)

5. (Order) Octopoda (clade; explicitly ranked as order in Tree of Life)

# 6. (Suborder) Cirrata

# 6. (Suborder) Incirrata

**5. (Order) Vampyromorpha** (monospecific clade; explicitly ranked as order in Tree of Life).