Phylogeny of Harpacticoida (Copepoda): Revision of "Maxillipedasphalea" and Exanechentera

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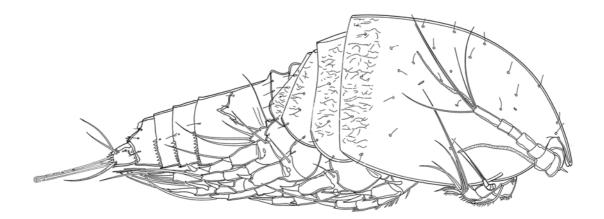
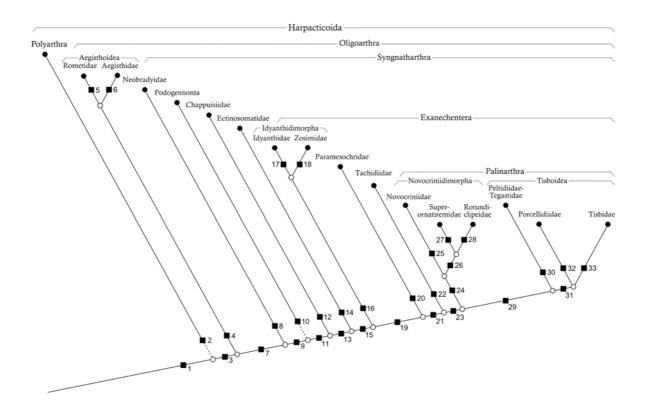


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DIAGRAM OF PHYLOGENETIC RELATIONSHIPS WITHIN HARPACTICOIDA



SUMMARY

- A hypothesis of phylogenetic relationships within Harpacticoida is presented as a result of the application of Phylogenetic Systematics and cladistic computer analysis.
- The result of the cladistic analysis of the data matrix of the taxa of Oligoarthra (16 taxa) and 3 outgroup taxa and 72 characters was one minimum length cladogram of a length of 154 (indices: CI = 0.57; RI = 0.77; RC = 0.44).
- The diagram of the phylogenetic relationships within Harpacticoida shows the same relationships as obtained from the cladistic analysis. Only the assumed evolution of the oral cone and the maxilliped is different in the two techniques.
- Hierarchical presentation of the phylogenetic system of Harpacticoida:

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Harpacticoida Sars, 1903
Polyarthra Lang, 1944
    Longipediidae Sars, 1903
    Canuellidae Lang, 1944
Oligoarthra Lang, 1944
    Aegisthoidea Giesbrecht, 1892
       Rometidae Seifried & Schminke, 2003
       Aegisthidae Giesbrecht, 1892
    Syngnatharthra Seifried & Schminke, 2003
       Neobradyidae Olofsson, 1917
       N.N. 1
          Podogennonta Lang, 1944
          N.N. 2
              Chappuisiidae Chappuis, 1940
              N.N. 3
                 Ectinosomatidae Sars, 1903
                 Exanechentera Lang. 1944
                     Idyanthidimorpha tax. nov.
                        Idvanthidae Lang, 1944
                        Zosimidae tax. fam.
                     N.N. 4
                        Paramesochridae Lang, 1944
                        N.N. 5
                           Tachidiidae Sars, 1909
                           Palinarthra tax. nov.
                               Novocriniidimorpha tax. nov.
                                  Novocriniidae Huys & Iliffe, 1998
                                  N.N. 6
                                      Superornatiremidae Huys, 1996
                                      Rotundiclipeidae Huys, 1988
                               Tisboidea Stebbing, 1910
                                  Peltidiidae Sars, 1904
                                  Tegastidae Sars, 1904
                                  N.N. 7
                                      Porcellidiidae Boeck, 1865
                                      Tisbidae Stebbing, 1910
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- Oligoarthra is monophyletic. Many autapomorphies support this hypothesis. The groundpattern of Oligoarthra is completed here. Some character states that are traditionally considered as plesiomorphic within Oligoarthra could be described as secondarily evolved or apomorphic within Oligoarthra (e.g. the separated first pedigerous somite, 2 egg-sacs, 2 proximal setae on the cutting edge of the mandible, the 2-segmented endopod of the mandible, setation of P5 within Podogennonta). Sometimes a different character state as hitherto maintained has to be assumed for the groundpattern of Oligoarthra; e.g. an allobasis and a 3-segmented endopod of maxilla is the plesiomorphic condition; the strong claw (I) of the maxilla is not fused with the endite of the basis and the praecoxa and the coxa of the maxilliped are fused to a syncoxa in the groundpattern of Oligoarthra.
- "Maxillipedasphalea" (Aegisthidae, Chappuisiidae, Darcythompsoniidae, Ectinosomatidae, Neobradyidae, Phyllognathopodidae) is polyphyletic and therefore not maintained here. Darcythompsoniidae and Phyllognathopodidae are integrated in Podogennonta.
- A cladistic analysis demonstrates: *Neocervinia* and *Pseudocervinia* are synonyms of *Cervinia* and *Brotskayaia* is a synonym of *Expansicervinia*.
- "Neobradyoidea" (Chappuisiidae, Darcythompsoniidae, Neobradyidae, Phyllognathopodidae) is polyphyletic and therefore not maintained here.
- *Paramesochra australis* belongs to Ameiridae (Podogennonta) as *Psammoleptomesochra australis*.
- Ectinosomatoidea is synonymized with Ectinosomatidae, as both taxa embrace the same species.
- The monophyly of Exanechentera is confirmed. The exanechenteran species share a bevelled antennal endopod, a bulge at the proximal border of the mandibular gnathobase and the claw with the pointed end of the male antennule. Thompsonulidae is excluded from Exanechentera and is transferred to Podogennonta. Novocriniidae, Paramesochridae, Rotundiclipeidae, and Superornatiremidae are integrated in Exanechentera.
- Idyanthidimorpha tax. nov. contains Zosimidae tax. fam. and Idyanthidae. They mainly share the displaced coxal setae of the maxilliped, the morphology of the P1 and the sexual dimorphism of P2.
- Lang (1944) established Idyanthinae. Idyanthinae is excluded from Tisbidae *sensu strictu* and is raised to family rank. The species of Idyanthidae are mainly characterised by the elongated exopod of the maxillula, the characteristic endopod of P1, and the lack of the inner setae of the P2 enp-3 in male. *Dactylopia* together with *Idyanthe*, *Idyella*, *Idyellopsis*, *Styracothorax*, and *Tachidiella* represents the taxon Idyanthidae. *Tachidiopsis* is excluded from Idyanthidae and transferred to Neobradyidae mainly on the basis of the shape and arrangement of the syncoxal setae of the maxilliped, and the sexual dimorphism in P2 and P3. *Tachidiopsis bozici*, *T. ibericus*, *T. laubieri*, *T. parasimilis*, and *T. sarsi* are moved from *Tachidiopsis* to *Marsteinia*. Styracothoracidae is synonymized with Idyanthidae, as *Styracothorax gladiator* has the autapomorphies of Idyanthidae. *Neoscutellidium* is excluded from Idyanthidae and is transferred to Cholidyinae (Tisbidae *sensu strictu*).
- *Zosime*, *Peresime*, and *Pseudozosime* are excluded from Idyanthidae and are combined in Zosimidae tax. fam. This monophyletic species group is characterised by many autapomorphies.
- Idyanthopsis psammophila belongs to Paramesochridae as Diarthrodella psammophila.
- As Harpacticidae was integrated in Podogennonta, "Tachidioidea" is polyphyletic and therefore not maintained here.
- The monotypic Euterpinidae is synonymized with Tachidiidae, as *Euterpina acutifrons* has all autapomorphies of Tachidiidae.
- The taxon Palinarthra tax. nov consists of Novocriniidimorpha tax. nov. (Novocriniidae Superornatiremidae Rotundiclipeidae) and Tisboidea (Peltidiidae Tegastidae -

Porcellidiidae - Tisbidae *sensu strictu*). The species of Palinarthra mainly share the oral cone, the elongated and narrow gnathobase mandible and praecoxal arthrite of the maxillula, the ornamentation of the distal syncoxal endite of the maxilla, and the short syncoxa of the maxilliped. Novocriniidimorph species share at least 13 autapomorphies. Tisboidea is mainly characterised by the proximally displaced fused praecoxal endites of the maxilla, the elongated enp-2, exp-1 and exp-2 of P1, and the rounded small exp-3 of P1 with the transformed spines.

- Clytemnestridae is synonymized with Peltidiidae, because the eight species of *Clytemnestra Goniopsyllus* belong to an advanced taxon within Peltidiidae. A complete revision of Peltidiidae Tegastidae on species level is needed to clarify whether Tegastidae is either the sister taxon of Peltidiidae or a monophyletic taxon within Peltidiidae probably related to *Clytemnestra Goniopsyllus*.
- The hypothesis of oligomerization in Oligoarthra, i.e. the reduction in the number of segments of the appendages and the body and additionally their ornamentation was tested and confirmed in general.
- In the evolution of Harpacticoida it is rare but possible, that a character state evolves resembling a formerly reduced state. For some character states it could be shown that it is not the recovered plesiomorphic state, but a new state resembling the plesiomorphic one. These rare evolutionary events lead mainly to the reappearance of segments, setae and aesthetascs.
- Every segment and almost all setae could be homologised in all examined adult species of Harpacticoida. The homology of setae of antenna, maxillula, maxilla, and maxilliped is completed here.
- First steps towards the characterisation of the evolution of Harpacticoida are made.