

# Systematics of Chaetognatha under the light of molecular data, using duplicated ribosomal 18S DNA sequences

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## Abstract

While the phylogenetic position of Chaetognatha has become central to the question of early bilaterian evolution, the internal systematics of the phylum are still not clear. The phylogenetic relationships of the chaetognaths were investigated using newly obtained small subunit ribosomal RNA nuclear 18S (SSU rRNA) sequences from 16 species together with 3 sequences available in GenBank. As previously shown with the large subunit ribosomal RNA 28S gene, two classes of Chaetognatha SSU rRNA gene can be identified, suggesting a duplication of the whole ribosomal cluster; allowing the rooting of one class of genes by another in phylogenetic analyses. Maximum Parsimony, Maximum Likelihood and Bayesian analyses of the molecular data, and statistical tests showed (1) that there are three main monophyletic groups: Sagittidae/Krohnittidae, Spadellidae/Pterosagittidae, and Eukrohnidae/Heterokrohnidae, (2) that the group of Apheroglossa without Pterosagittidae (Sagittidae/Krohnittidae) is monophyletic, (3) the Spadellidae/Pterosagittidae and Eukrohnidae/Heterokrohnidae families are very likely clustered, (4) the Krohnittidae and Pterosagittidae groups should no longer be considered as families as they are included in other groups designated as families, (5) suborder Ctenodontina is not monophyletic and the Flabellodontina should no longer be considered as a suborder, and (6) the Syngonata/Chorismogonata and the Monophragmophora/Biphragmophora hypotheses are rejected. Such conclusions are considered in the light of morphological characters, several of which are shown to be prone to homoplasy.

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## 1. Introduction

Chaetognaths constitute a small marine phylum of approximately 120 nominal species. They have been known to zoologists since at least the 18th century (Slabber, 1778). In the last few decades, their relationships within the metazoans have been strongly debated because of embryological and morphological features shared with the two main branches of Bilateria, the deuterostomes and the protostomes (see Hyman, 1959; Nielsen, 2001). Classical phyloge-

netic molecular markers such as small subunit ribosomal RNA nuclear 18S (SSU rRNA) sequences or intermediate filaments did not help convincingly to define the Chaetognatha affinities, due to the long-branch attraction artefact (Erber et al., 1998; Halanych, 1996; Mallatt and Winchell, 2002; Telford and Holland, 1993; Wadah and Satoh, 1994). Finally, while a *Hox* gene survey suggested a basal position among the Bilateria (Papillon et al., 2003), the analyses of the mitochondrial genomes of *Spadella cephaloptera* (Papillon et al., 2004) and *Paraspadella gotoi* (Helfenbein et al., 2004) supported close relationships with the protostomes.

Chaetognaths, commonly named arrow worms owing to their shape and high swimming velocity, are found in coastal and open waters. Most species are planktonic

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although a few are benthic. Chaetognaths are not metameric and display a very simple body plan divided into three regions: head, trunk, and tail. Their body bears a tail fin and one or two pairs of lateral fins, and is built around a hydroskeleton, which together with four longitudinal muscles plays a major role in locomotion (Duvert and Salat, 1979). The main internal organs, with the exception of nervous system and muscles, are the gut and ovaries in the trunk, and the testes in the tail segment. All extant species display this almost invariant organization, and this homogeneity has led to great difficulties in resolving an internal classification of the phylum.

Ritter-Zahony (1911), as well as Hyman (1959), recognized 6 genera: *Sagitta*, *Pterosagitta*, *Spadella*, *Eukrohnia*, *Heterokrohnia* and *Krohnitta*. This classification was followed until Tokioka (1965a) proposed a new systematics of Chaetognatha (Fig. 1A). The class Sagittoidea (extant species) was divided into two orders: the Phragmophora (presence of a transverse musculature, namely the phragmes, and of various kinds of glandular structures on the body surface) and the Aphragmophora (absence of a transverse musculature, and few glandular structures). Two families composed the Phragmophora: Spadellidae (genus *Spadella*) and Eukrohniidae (genera *Eukrohnia*, *Heterokrohnia*, and *Bathyspadella*). Tokioka suggested two suborders for the Aphragmophora: Flabellodontina and Ctenodontina, owing to the number of set of teeth and shape of teeth and hooks. The first suborder (Flabellodontina) only comprised the Krohnittidae family (*Krohnitta*), because of highly spe-

cialized features (only an anterior teeth-row, teeth stouter than in Ctenodontina and arranged in a fan shape and hooks curved abruptly), while the families Pterosagittidae (*Pterosagitta*) and Sagittidae (nine genera) belonged to the second suborder (Ctenodontina). In a following work, Tokioka (1965b) suggested that the Aphragmophora was not a natural group, and that the Ctenodontina were closer to the Phragmophora than to the Flabellodontina. In approximately the same way as Alvarino (1963), he also decided to split the genus *Sagitta*, described by Ritter-Zahony (1911), into nine new genera and gathered them into the Sagittidae. Bieri (1991a) followed this classification, and even proposed new genera of Sagittidae, to make more homogenous groupings. However, as with Salvini-Plawen (1986), Bieri's systematic system omitted the Aphragmophora suborders Ctenodontina and Flabellodontina of Tokioka.

Following the discovery of several new deep benthoplanktonic chaetognaths, another slight modification of Tokioka's hypothesis was proposed by Casanova (1985) (Fig. 1B). In this new classification, the Phragmophora was split into two orders: the Monophragmophora (*Spadellidae* and *Eukrohniidae*, with transverse muscles in trunk only) and the Biphragmophora (the new *Heterokrohniidae* family, with transverse muscles in both trunk and tail). Each of these orders belonged to new subclasses of the Sagittoidea: the Syngonata (with ducts between the genital glands in trunk and tail) included the Biphragmophora, and the Chorisomogonata (without such ducts) contained the Monophragmophora and Aphragmophora (Casanova, 1985).

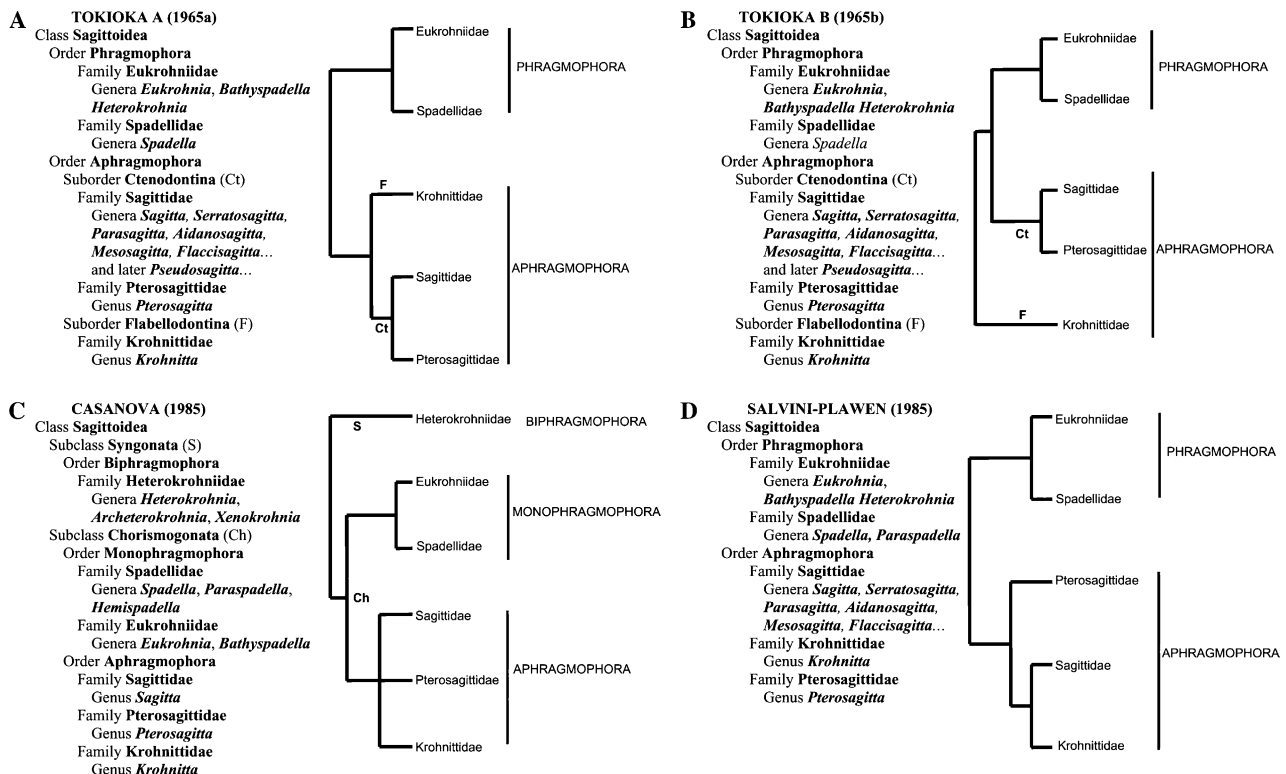


Fig. 1. Main hypotheses of chaetognaths systematics based on morphological criteria. (A) Tokioka A (Tokioka, 1965a), (B) Tokioka B (Tokioka, 1965b), (C) Casanova (1985), (D) Salvini-Plawen (1986). Ch, Chorisomogonata; Ct, Ctenodontina; F, Flabellodontina; S, Syngonata.

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