

Phylogenetic analysis of the Echinoderidae (Kinorhyncha: Cyclorhagida)

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Abstract

The phylogeny of the kinorhynch family Echinoderidae is analyzed using morphological characters and parsimony as the optimization criterion. Thirty-six characters were coded in a matrix with eleven echinoderid terminals, representing all echinoderid genera and six non-echinoderid outgroup taxa. The ingroup includes *Polacanthoderes martinezi* and *Cephalorhyncha liticola*, newly described in a separate paper. The resulting most parsimonious trees support *Polacanthoderes* as the most basal echinoderid genus, followed by an unresolved clade with non-monophyletic *Fissuroderes* and monophyletic *Cephalorhyncha* and *Echinoderes*.

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Introduction

Even though the kinorhynchs have been known for a reasonable amount of time, the group's internal relationships remain a puzzle. Only few studies have dealt with kinorhynch phylogeny (Neuhaus 1994, 1995; Adrianov and Malakhov 1996, 1999; Kristensen 2002; Neuhaus and Higgins 2002), all of them based on theoretical considerations and discussions; thus, kinorhynch relationships have never been analyzed using modern numerical methods. The present study represents the first attempt to understand kinorhynch phylogeny using morphological data analyzed under a cladistic approach. The analyses focus on the relationships within the family Echinoderidae.

The family Echinoderidae was originally erected by Bütschli (1876) to contain the single kinorhynch species, *Echinoderes dujardini* Claparède, 1863. For some time, the derived higher-taxon names Echinoderida or

Echinodera were treated as synonymous with the name “Kinorhyncha” that had been introduced by Reinhard (1885, 1887) and now applies to the whole phylum. Present-day kinorhynch taxonomy was founded by Zelinka (1896) who discriminated between the two main clades, Homalorhagida and Cyclorhagida. Echinoderidae was assigned to the latter, and considered as closely related to Centroderidae Zelinka, 1896. Until the mid 1920s, more than 70 years after the first kinorhynch had been recorded by Dujardin (1851), only few species had been formally described. Then the known kinorhynch biodiversity increased dramatically with the publication of Zelinka's (1928) monumental “Monographie der Echinodera”, in which he described a total of 48 new species, and several new genera. In his classification, Zelinka assigned four genera to Echinoderidae. Unfortunately, two of these genera, *Habroderes* and *Habroderella*, were mostly based on specimens that have since turned out to be juveniles of *Echinoderes*, and most of the corresponding names are considered as nomina dubia today. The two species of the fourth genus

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recognized by Zelinka, *Echinoderella*, have been assigned to *Echinoderes* as well. Hence, the family Echinoderidae became monogeneric again for some time, containing *Echinoderes* only (for further historic overview of kinorhynch classification, see Higgins 1971). Recently, the genera *Cephalorhyncha* and *Fissuroderes* have been added to Echinoderidae (Neuhaus and Blasche 2006); thus, the family comprises three genera today.

In a separate paper in the present issue of ODE (Sørensen 2008), a new echinoderid genus and species, and a new species of *Cephalorhyncha* are described. Character states of these new taxa have been included in the present paper's data matrix, together with selected character states of other known echinoderid species, in order to analyze the relationships within the diverse family Echinoderidae.

Material and methods

Morphological traits of 17 terminal taxa were coded in a character state matrix (Table 1). The matrix includes 36 characters, 32 of them bistate and 4 multistate, resulting in a total of 76 character states. All characters were coded as non-additive, except for character 5 which was ordered. Detailed descriptions of all characters and character states are given below.

Outgroup taxa selected for the analysis are the homalorhagid *Paracentrophyes quadridentatus* (Zelinka, 1928) and five cyclorhagid non-echinoderid species: *Antygomonas paulae* Sørensen, 2007; *Campyloderes macquariae* (Johnston, 1938); *Dracoderes abei* Higgins & Shirayama, 1990; *D. orientalis* Adrianov & Malakhov,

1999; and *Zelinkaderes brightae* Sørensen, Heiner, Ziemer & Neuhaus, 2007. The following 11 echinoderid species, representing all known echinoderid genera, were selected as ingroup taxa: *Polacanthoderes martinezi* Sørensen, 2008; *Cephalorhyncha liticola* Sørensen, 2008; *C. asiatica* (Adrianov, 1989); *C. nybakkeni* (Higgins 1986); *Fissuroderes higginsii* Neuhaus & Blasche, 2006; *F. novaezealandia* Neuhaus & Blasche, 2006; *F. papai* Neuhaus & Blasche, 2006; *F. rangi* Neuhaus & Blasche, 2006; *F. thermoi* Neuhaus & Blasche, 2006; *Echinoderes spinifurca* Sørensen, Heiner & Ziemer, 2005; and *E. truncatus* Higgins, 1983.

All character codings are based either on published descriptions or on personal observations. Documentation of most previously unreported character traits is included in the character descriptions below. The main literature sources for character codings per species are as follows. *Paracentrophyes quadridentatus*: Higgins (1983), Neuhaus (1995). *Campyloderes macquariae*: Higgins (1967), Neuhaus (2004). *Antygomonas paulae*: Sørensen (2007). *Dracoderes abei*: Higgins and Shirayama (1990). *Dracoderes orientalis*: Adrianov and Malakhov (1999). *Zelinkaderes brightae*: Sørensen et al. (2007). *Polacanthoderes martinezi*: Sørensen (2008). *Cephalorhyncha liticola*: Sørensen (2008). *Cephalorhyncha asiatica*: Adrianov (1989), Adrianov and Malakhov (1999), Neuhaus and Blasche (2006). *Cephalorhyncha nybakkeni*: Higgins (1986a), Neuhaus and Blasche (2006). All five species of *Fissuroderes*: Neuhaus and Blasche (2006). *Echinoderes spinifurca*: Sørensen et al. (2005). *Echinoderes truncatus*: Higgins (1983), Sørensen (2006).

Most species included in the data matrix were examined with a light microscope; all except the species

Table 1. Morphological character state matrix for analysis of relationships among selected kinorhynch species

Species	Character	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	1	1	1	2	2	2	2	2	2	2	2	2	2	2	3	3	3	3	3	3	3	
		1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	
<i>Paracentrophyes quadridentatus</i>		1	0	0	0	0	0	0	0	0	–	–	–	–	1	1	–	–	0	0	–	1	–	–	–	–	–	–	–	0	–	–	0	0	0	0	0	
<i>Campyloderes macquariae</i>		–	1	0	0	0	0	0	0	1	0	1	1	1	1	1	0	0	0	1	1	0	0	1	1	1	1	0	0	–	–	0	0	0	0	0	0	
<i>Antygomonas paulae</i>		0	2	0	0	0	0	0	0	1	1	1	1	1	1	1	0	0	0	1	1	0	0	?	1	1	1	0	0	–	–	0	0	0	0	0	0	
<i>Zelinkaderes brightae</i>		0	2	0	0	2	0	0	0	1	1	0	0	0	1	1	1	0	0	0	1	1	0	0	1	0	0	0	0	0	–	–	0	0	0	0	0	
<i>Dracoderes abei</i>		1	1	0	1	0	0	0	1	0	2	0	1	1	1	0	0	1	1	0	0	0	–	1	1	0	0	1	0	0	–	–	0	0	0	0	0	0
<i>Dracoderes orientalis</i>		1	1	0	?	0	0	0	1	0	2	0	1	1	1	0	0	1	1	0	0	0	–	1	0	0	0	0	0	?	–	–	0	0	0	0	0	0
<i>Polacanthoderes martinezi</i>		0	2	0	2	0	0	0	1	0	–	0	0	0	0	0	0	1	0	0	0	0	1	1	1	0	0	0	1	1	0	–	–	0	1	0	0	0
<i>Cephalorhyncha liticola</i>		0	2	1	2	1	1	?	1	1	2	0	0	0	0	0	0	1	0	1	0	1	1	1	0	0	0	1	1	0	–	–	0	0	0	0	0	0
<i>Cephalorhyncha asiatica</i>		0	2	0	2	1	1	1	1	1	2	0	0	0	0	0	0	1	0	1	0	1	1	1	0	0	0	1	1	1	1	1	0	0	0	0	0	0
<i>Cephalorhyncha nybakkeni</i>		0	2	1	?	1	1	1	1	1	2	0	0	0	0	0	0	1	0	1	0	1	?	?	0	0	0	1	0	1	1	?	0	0	0	0	0	0
<i>Fissuroderes higginsii</i>		?	2	0	2	0	0	0	1	1	2	0	0	0	0	0	0	1	0	1	0	1	1	1	0	0	0	1	1	1	0	1	1	0	1	1	1	1
<i>Fissuroderes novaezealandia</i>		?	2	0	?	0	0	0	1	1	2	0	0	0	0	0	0	0	1	0	1	0	1	1	1	0	0	0	1	0	1	0	1	p	0	p	p	p
<i>Fissuroderes papai</i>		?	2	0	?	0	0	1	1	1	2	0	0	0	0	0	0	1	0	1	0	1	1	1	0	0	0	1	1	1	1	0	0	0	0	0	0	0
<i>Fissuroderes rangi</i>		0	2	0	?	0	0	0	1	1	2	0	0	0	0	0	0	1	0	0	0	1	1	1	0	0	0	0	0	1	1	0	0	p	0	0	0	0
<i>Fissuroderes thermoi</i>		?	2	0	2	0	0	0	1	1	2	0	0	0	0	0	0	1	0	1	0	1	1	1	0	0	0	1	0	1	0	1	1	0	1	1	1	1
<i>Echinoderes truncatus</i>		0	2	0	2	2	0	0	1	1	2	0	0	0	0	0	0	1	0	1	0	1	1	1	0	0	0	1	0	0	–	–	0	0	0	1	0	0
<i>Echinoderes spinifurca</i>		0	2	0	2	2	0	0	1	1	2	0	0	0	0	0	0	1	0	1	0	1	1	1	0	0	0	1	0	0	–	–	0	0	0	0	0	0

? = missing data; – = inapplicable character state; p = character state coded as polymorphic.

of *Fissuroderes*, *Dracoderes orientalis*, *Cephalorhyncha asiatica* and *C. nybakkeni* were examined with SEM as well. Specimens of *Fissuroderes* and *C. asiatica* were loaned from the Museum für Naturkunde, Berlin, Germany. Specimens of *Paracentrophyes quadridentatus* were collected from muddy sediment at 42 m depth outside of Kaldbak Fjord on the Faroe Islands (62°04'01"N 06°46'23"W) and kindly provided by Prof. R.M. Kristensen. The author collected specimens of *Campyloderes macquariae* from intertidal aggregations of the coralline alga *Corallina officinalis* in Kaldbak Fjord, Faroe Islands (62°03'28"N 06°49'40"W). Specimens of *Dracoderes abei* were collected at the species' type locality in Tanabe Bay, Japan (Higgins and Shirayama 1990). Detailed information from SEM examinations of *Antygomonas paulae*, *Zelinkaderes brightae*, *Echinoderes spinifurca* and *E. truncatus* is given in Sørensen (2007), Sørensen et al. (2007), Sørensen et al. (2005) and Sørensen (2006), respectively.

The terminology used for the main body regions and segments follows Neuhaus and Higgins (2002) and Neuhaus and Blasche (2006). Hence, the adult kinorhynch body is divided into a head, a neck, and a trunk consisting of segments 1–11. This terminology and numbering is gradually getting accepted by most researchers, and I prefer to use it here and in future contributions. Character states of most characters are exemplified in Fig. 1; additional character states for specific taxa are illustrated in Figs. 2–6.

The data set was analyzed with PAUP* version 4.0 (Swofford 2002) and TNT 1.1 (Goloboff et al. 2003), using branch-and-bound search algorithms (= implicit enumeration in TNT).

Character descriptions

1. Size of outer oral styles: 0 = all outer oral styles of similar size; 1 = size alternating between larger and smaller. The outer oral styles are uniform in size in most kinorhynch species (e.g. Fig. 2B and D), whereas in *Paracentrophyes quadridentatus* and *Dracoderes abei* the size alternates between larger and smaller styles (Fig. 2A and C). Outer oral styles are absent in *Campyloderes macquariae*; thus, the character was coded as inapplicable for this taxon.
2. Number of placids in neck: 0 = 7 placids; 1 = 14 placids; 2 = 16 placids. The character refers to the number of placids, or introvert closing plates, that are located in the neck region.
3. Shape of anterior corners of placids: 0 = angular; 1 = rounded. Whereas most kinorhynchs possess rectangular placids with angular anterior corners, *Cephalorhyncha liticola* and *C. nybakkeni* exhibit characteristic, clearly rounded corners resulting in less rectangular appearance of the placids (Higgins 1986a).
4. Number of trichoscalids: 0 = 14 trichoscalids; 1 = 7 trichoscalids; 2 = 6 trichoscalids. Trichoscalids are small, modified sensorial head appendages with a featherlike appearance (Fig. 2E and F). They are located in the posteriormost introvert ring (ring 07), but usually they are not attached to the same radii as the scalids in the six more anterior rings. Instead, their exact location is often related to another kind of structures, the trichoscalid plates, which are small plates attached to the placids of the neck (Figs. 1A and B, 2F). However, trichoscalid plates can be missing in some species, e.g. in *Antygomonas paulae* (Fig. 2E). In some kinorhynch species, e.g. in *A. paulae*, *Campyloderes macquariae* and *Zelinkaderes brightae*, the number of trichoscalids almost exceeds the number of placids, whereas species of Echinoderidae apparently possess six trichoscalids only.
5. Midventral fissure on segment 2: 0 = complete; 1 = partial; 2 = absent [ordered]. This character refers specifically to the condition of the midventral fissure or plate joint on the second trunk segment. The fissure can be complete and distinct as in most taxa in the data set (Fig. 3A and B) but also completely absent as in species of *Echinoderes* (Figs. 1B, 3D) and *Zelinkaderes*. A special condition is present in species of *Cephalorhyncha*, in which a partial fissure is evident on the anterior part of the segment only (Fig. 3C). The latter condition likely represents an intermediate stage between a complete fissure and the absence of any kind of cuticular joint. Hence, the character states of this character have been treated as an ordered, bi-directional transition series as follows: fissure complete ↔ fissure partial ↔ fissure absent.
6. Appearance of sternal plates on third trunk segment: 0 = sternal plates on third segment with angular corners at anterior margin, sternal plates similar on following segments; 1 = sternal plates on third segment with rounded corners and with oblique anterior segment margins. Sternal plates are most often rectangular with almost angular corners (Figs. 1B, 3A, B and D). Especially the sternal plates on segments 3–10 follow this pattern in most genera. However, the sternal plates of segment 3 in *Cephalorhyncha liticola* and *C. asiatica* differ (Fig. 3C), as the anterior segment margins are oblique, which gives the plates a trapezoidal rather than rectangular shape. The special appearance of the sternal plates in this segment is also stressed by the anterior pachycycli that do not meet the midventral line at right angles as the anterior pachycycli do on the following seven segments (Fig. 3C).
7. Composition of terminal trunk segment: 0 = of one tergal and two sternal plates; 1 = of two tergal and

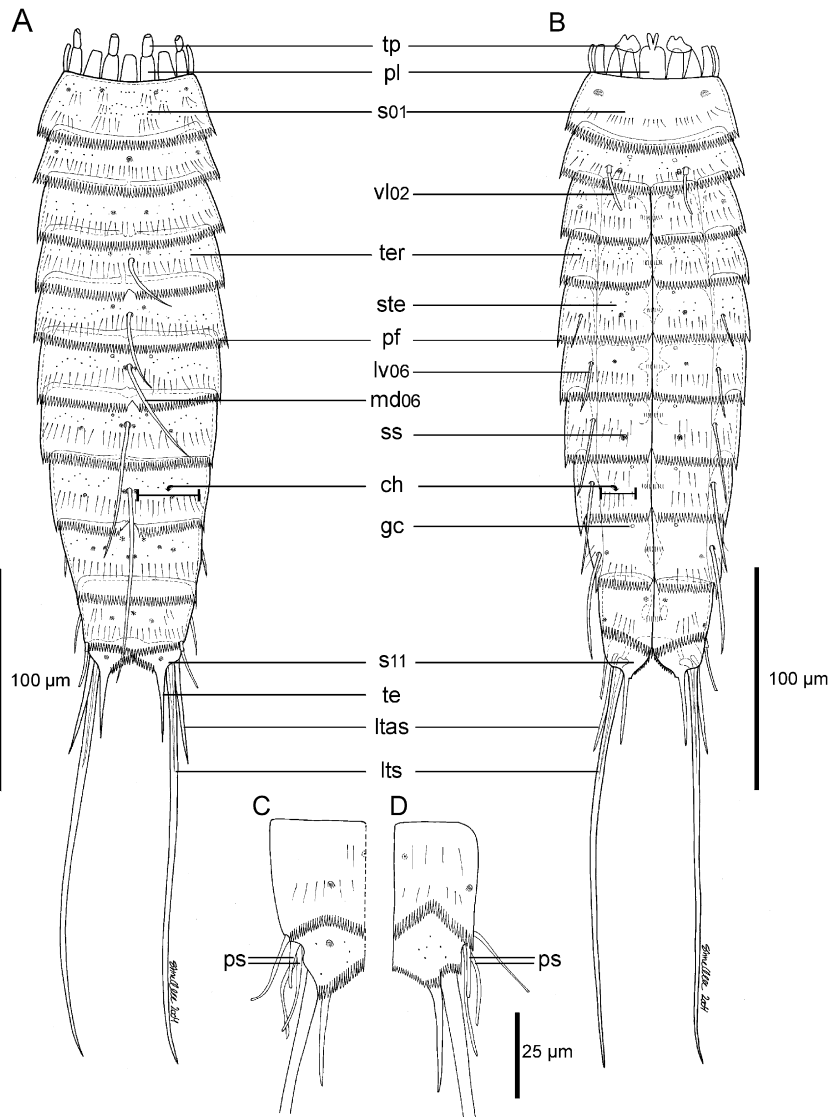


Fig. 1. Line drawings of one selected echinoderid species, *Echinoderes spinifurca*, exemplifying most of the characters used in the phylogenetic analysis. (A) Female, dorsal view. (B) Female, ventral view. (C) Male, segments 10 and 11, dorsal view. (D) Male, segments 10 and 11, ventral view. *Abbreviations:* ch = cuticular hairs; gc = type 1 gland cell outlet; ltas = lateral terminal accessory spine; lts = lateral terminal spine; lv = lateroventral spine; md = middorsal spine; pf = pectinate fringe; pl = placid; s = segment; ps = penile spines; ss = sensory spot; ste = sternal plate; te = tergal extension; ter = tergal plate; tp = trichoscalid plate; vl = ventrolateral spine. Double digits denote respective segment number.

two sternal plates. The terminal trunk segment can have either one or two tergal plates. According to Neuhaus and Blasche (2006), two tergal plates on segment 11 are present in *Fissuroderes papai*, *Cephalorhyncha asiatica* and *C. nybakkeni*. In *C. liticola* there is no clear indication of a middorsal fissure on segment 11, but that is difficult to examine in this very small species, hence this character was coded as uncertain for this taxon.

8. Termination of last trunk segment: 0 = segmental plates rounded posteriorly; 1 = segmental plates forming posterior extensions. The tergal and sternal

plates of the terminal segment can either be rounded posteriorly, without extensions (Fig. 4A and B), or form conspicuous posterior extensions (Figs. 1A, 4C and D).

9. Secondary pectinate fringe: 0 = absent; 1 = present. This character refers to the presence or absence of a secondary pectinate fringe or fringes on the anterior part of each segment.
10. Appearance of cuticular hairs: 0 = scale-like; 1 = leaf-like; 2 = acicular. The morphology of cuticular hairs differs between genera, and some phylogenetic significance has been suggested (Sørensen 2006).

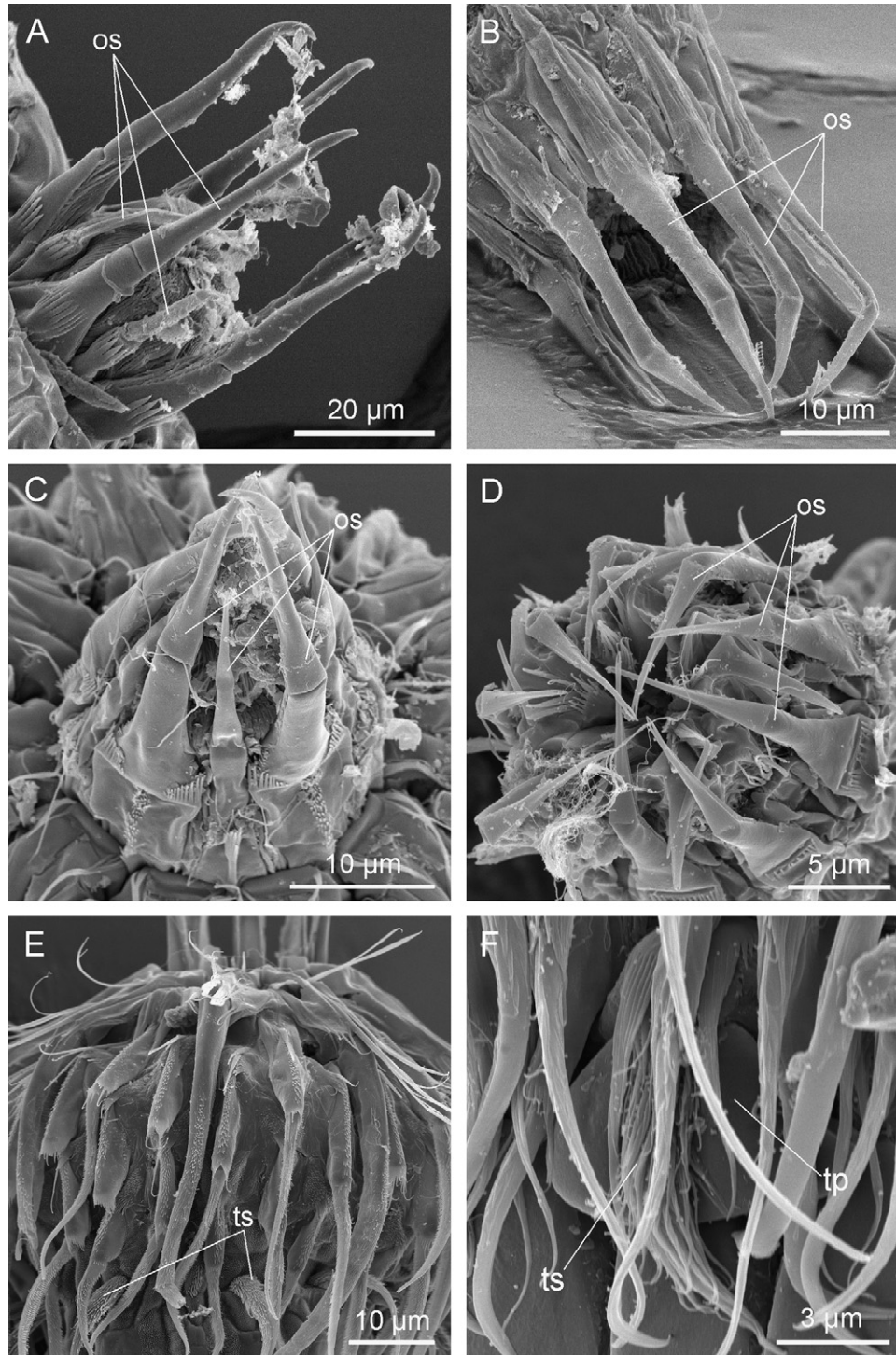


Fig. 2. Scanning electron micrographs illustrating selected traits in the mouth cone and introvert used in the phylogenetic analysis. (A) *Paracentrophyes quadridentatus*, outer oral styles. (B) *Antygomonas paulae*, outer oral styles. (C) *Dracoderes abei*, outer oral styles. (D) *Echinoderes spinifurca*, outer oral styles. (E) *A. paulae*, ventrolateral view showing introvert sections 1 and 10. (F) *E. spinifurca*, trichoscalid in introvert section 10. *Abbreviations:* os = outer oral styles; tp = trichoscalid plate; ts = trichoscalid.

In the taxa included in the present analysis we find either very small scale-like hairs (Fig. 5B), larger leaf-like hairs (Fig. 5A and D), or regular acicular hairs (Figs. 1A and B, 5C, 6B–D). *Polacanthoderes*

martinezi lacks cuticular hairs; thus the character was coded as inapplicable for this taxon.

11. Middorsal spine on segment 1: 0 = absent; 1 = present. Characters 11–16 concern the presence or

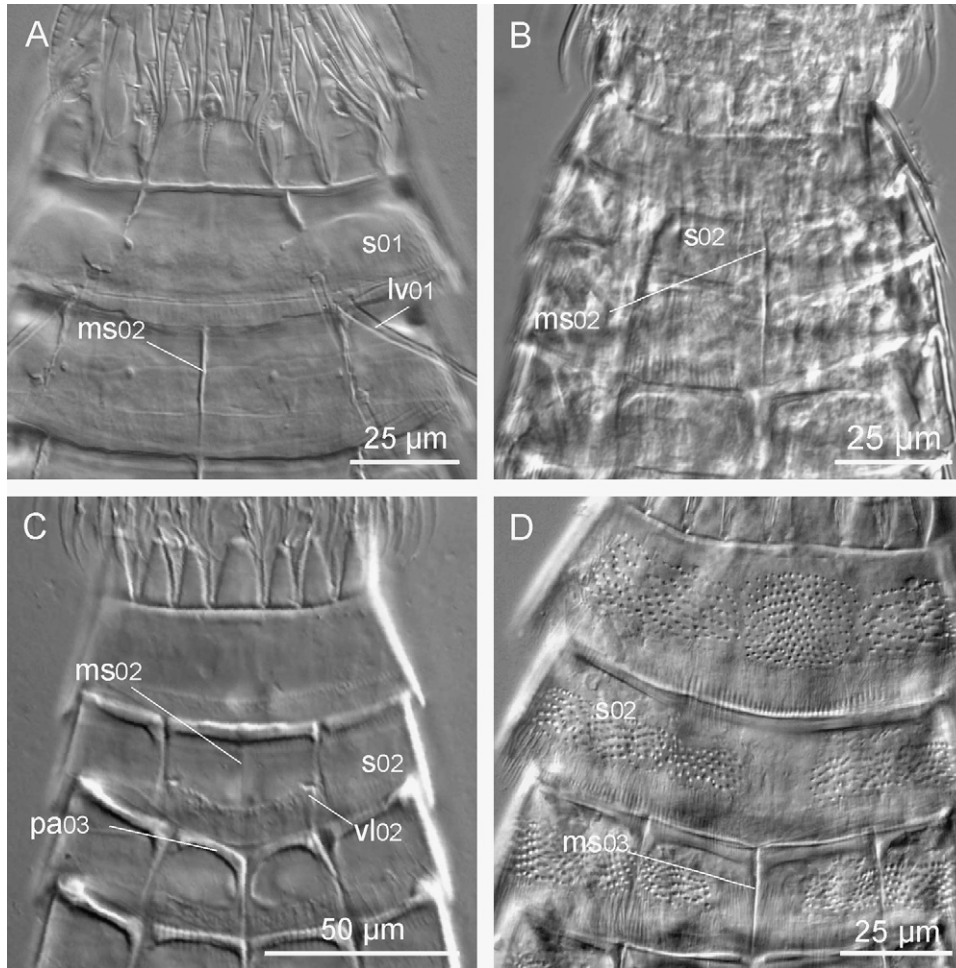


Fig. 3. Light microscope photos illustrating selected traits in anterior trunk segments. (A) *Campyloderes macquariae*, introvert and segments 1 and 2, ventral view. (B) *Fissuroderes thermoii*, segments 1–4, ventral view. (C) *Cephalorhyncha asiatica*, segments 1–3, ventral view. (D) *Echinoderes truncatus*, segments 1–3, ventral view. Abbreviations: lv = lateroventral spine; ms = middorsal articulation; pa = pachycyclus; s = segment; vl = ventrolateral spine. Double digits denote respective segment number.

absence of middorsal acicular spines (Figs. 1A, 6B, D and F). *Paracentrophyes quadridentatus* and all other homalorhagid kinorhynch species lack spines in any position on segments 1–9; hence characters 11–14 were coded as inapplicable for *P. quadridentatus*. Since all ingroup taxa possess middorsal spines on segments 4–8, characters concerning these segments would have been uninformative, therefore have not been included.

12. Middorsal spine on segment 2: 0 = absent; 1 = present. See char. 11.
13. Middorsal spine on segment 3: 0 = absent; 1 = present. See char. 11.
14. Middorsal spine on segment 9: 0 = absent; 1 = present. See char. 11.
15. Middorsal spine on segment 10: 0 = absent; 1 = present. See char. 11.
16. Middorsal spine on segment 11: 0 = absent; 1 = present. See char. 11.
17. Location of middorsal spines: 0 = on posterior segment margin; 1 = mesially. In some species the middorsal spine clearly is attached through a cuticular perforation more or less mesially on the segment (Figs. 1A, 6B and D), whereas in other species the spine is attached near the posterior segment margin (Fig. 6E and F).
18. Alignment of middorsal spines: 0 = spines located in exactly middorsal positions; 1 = spines alternatingly offset to lateral of midline. In most cyclorhagid kinorhynchs, the middorsal spines are located exactly on the animal's dorsal midline (Figs. 1A, 6D and F). In species of *Dracoderes*, however, the middorsal spines are alternatingly slightly offset to lateral of this midline (Fig. 6B; see also Higgins and Shirayama 1990; Adrianov and Malakhov 1999).
19. Ventrolateral acicular spines on segment 2: 0 = absent; 1 = present. Ventrolateral acicular spines are found in many echinoderid species (Figs. 1B,

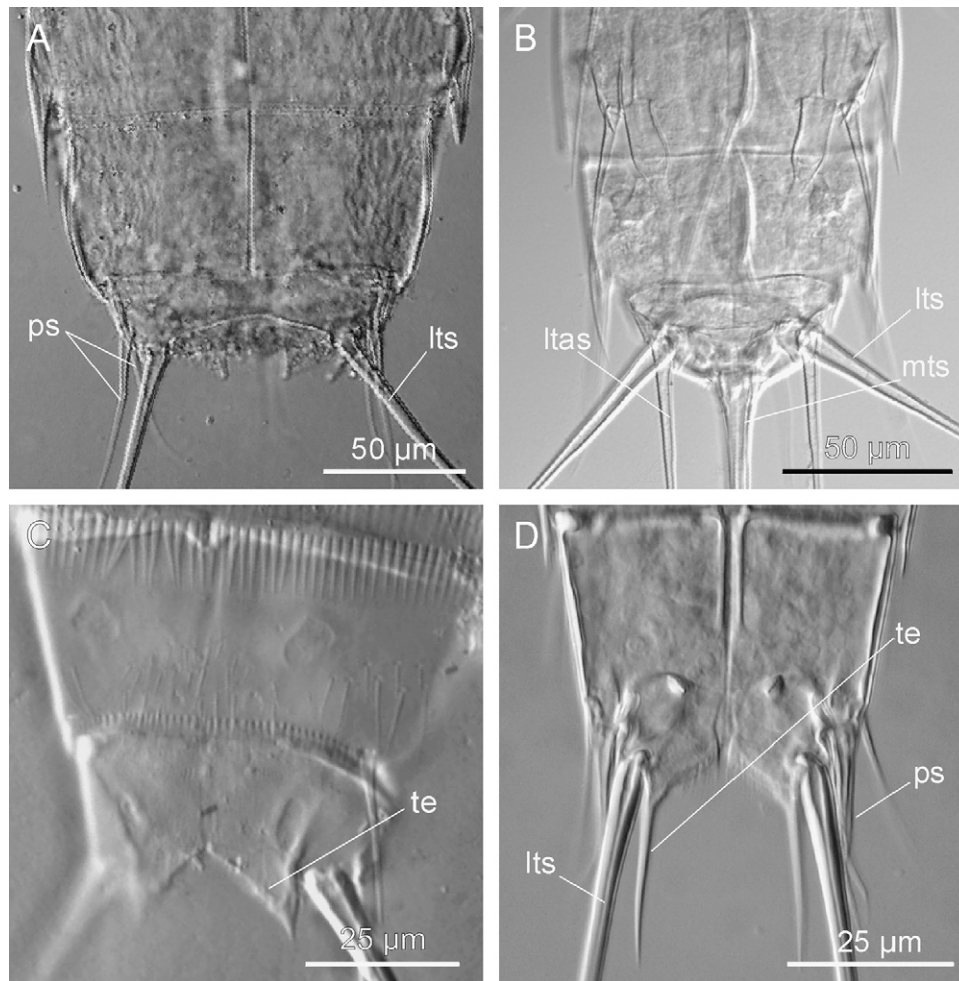


Fig. 4. Light microscope photos illustrating selected traits in posterior trunk segments. (A) *Paracentrophyes quadridentatus*, segments 10 and 11, ventral view. (B) *Antygomonas paulae*, segments 9–11, ventral view. (C) *Cephalorhyncha asiatica*, segments 10 and 11, dorsal view. (D) *Echinoderes spinifurca*, segments 10 and 11, ventral view. *Abbreviations:* ltas = lateral terminal accessory spine; lts = lateral terminal spine; mts = midterminal spine; ps = penile spines; te = tergal extension.

3C, 6C). *Paracentrophyes quadridentatus*, like other homalorhagids, has no such spines on segments 1–10; thus the character was coded as inapplicable for this taxon. *Campyloderes macquariae* and *Antygomonas paulae* do have lateral spines, but not on the sternal plates (Fig. 6G); ventrolateral spines are absent from segment 2 in species of *Dracoderes* and *Polacanthoderes martinezi* as well.

20. Midterminal spine: 0 = absent; 1 = present. A midterminal spine is present in the adult stage of most cyclorhagid species (Figs. 4B, 6H), except in species of *Dracoderes* and Echinoderidae. *Paracentrophyes quadridentatus* was originally reported as possessing a midterminal spine (Higgins 1983), but new, yet unpublished examinations of the terminal appendages in this species show that it has a minute midterminal process only, and that the unpaired medial spine should be interpreted as a middorsal spine (Pardos, pers. comm.). Hence, the character was coded as absent for *P. quadridentatus*.

21. Lateral terminal accessory spines: 0 = absent; 1 = present. Character state 1 was assigned where lateral terminal accessory spines are present at least in one of the sexes (Figs. 1A and B, 4B, 6H).

22. Sexual dimorphism in appearance of lateral terminal accessory spines (ltas): 0 = ltas present in both sexes; 1 = ltas present in females only. In echinoderid kinorhynch species, lateral terminal accessory spines are present in females only (Fig. 1), whereas these spines are present in both sexes in other species, e.g. in *Campyloderes macquariae* and *Antygomonas paulae*. This character was coded as inapplicable for taxa without lateral terminal accessory spines in either sex (see character 21). Only the female is known for *C. nybakkeni*; hence the character was coded as uncertain for this taxon.

23. Male penile spines: 0 = absent; 1 = present. Flexible penile spines are found in males of *Paracentrophyes quadridentatus* (Fig. 4A), *Dracoderes abei* and all echinoderid species (Figs. 1C and D, 4D), whereas

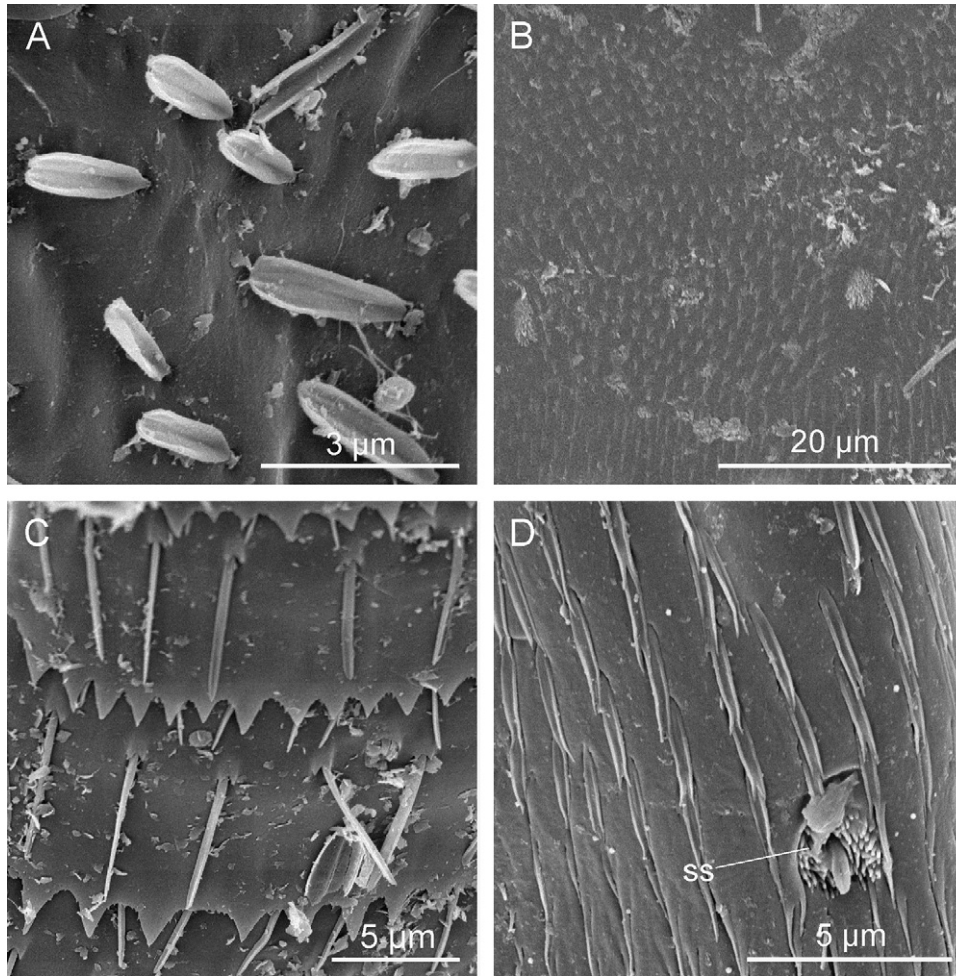


Fig. 5. Scanning electron micrographs illustrating different character states of cuticular hairs. (A) *Antygomonas paulae*, leaf-like cuticular hairs. (B) *Paracentrophyes quadridentatus*, scale-like cuticular hairs. (C) *Dracoderes abei*, acicular cuticular hairs. (D) *Zelinkaderes brightae*, leaf-like cuticular hairs. Abbreviation: ss = sensory spot.

they are absent in other cyclorhagid genera, e.g. *Zelinkaderes*, *Antygomonas* and *Campyloderes*. Only one female is known for *Cephalorhyncha nybakkeni*; hence the character was coded as uncertain for this taxon.

24. Lateroventral spines on segment 2: 0 = absent; 1 = present. Characters 24–28 concern the presence or absence of lateroventral and lateral accessory acicular spines (Fig. 1B). *Paracentrophyes quadridentatus* and all other homalorhagid kinorhynch species lack spines in any position on segments 1–9; hence characters 24–28 were coded as inapplicable for *P. quadridentatus*. Characters concerning lateroventral spines on segments 6 and 7 were not included in the analysis, as they would have been non-informative.
25. Lateroventral spines on segment 3: 0 = absent; 1 = present. See char. 24.
26. Lateroventral spines on segment 4: 0 = absent; 1 = present. See char. 24.
27. Lateroventral spines on segment 5: 0 = absent; 1 = present. See char. 24.
28. Lateral accessory spines on segment 8: 0 = absent; 1 = present. See char. 24.
29. Type 1 gland cell outlets with large funnel-shaped subcuticular structures: 0 = absent; 1 = present. Special, funnel-shaped subcuticular structures are found associated with type 1 gland cells in certain species of *Fissuroderes* (in *F. novaezealandia* only in females) and *Cephalorhyncha* (Neuhaus and Blasche 2006). Such structures have not been found in any species of *Echinoderes*, nor in *Polacanthoderes martinezi* or *Cephalorhyncha liticola*.
30. Location of type 1 gland cell outlets with large funnel-shaped subcuticular structures: 0 = ventromedial on segment 7; 1 = ventromedial on segment 8. The funnel-shaped subcuticular structures do not appear in the same segment in all species (Neuhaus and Blasche 2006). Character 30 was coded as inapplicable for taxa without such

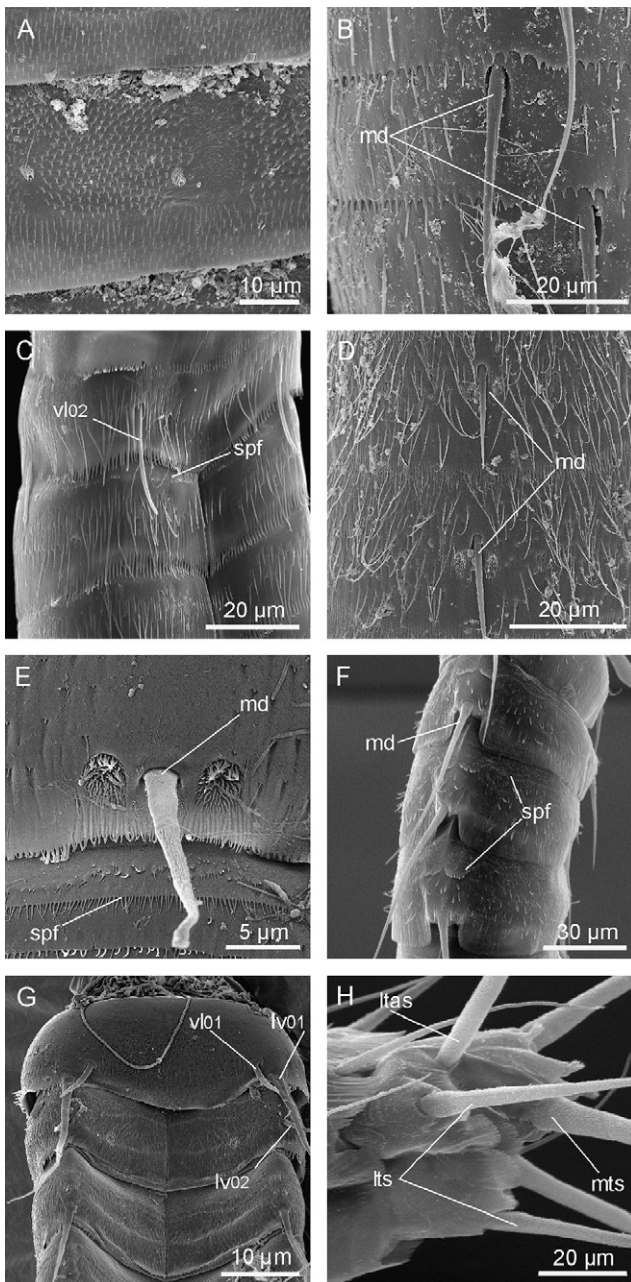


Fig. 6. Scanning electron micrographs illustrating selected traits used in the phylogenetic analysis. (A) *Paracentrophyes quadridentatus*, sternal plate on segment 6. (B) *Dracoderes abei*, segments 5 and 6, middorsal view. (C) *Echinoderes spinifurca*, segments 2–5, ventrolateral view. (D) *E. truncatus*, segments 6 and 7, middorsal view. (E) *Campyloderes macquariae*, attachment of middorsal spine on trunk segment 1. (F) *Antygomonas paulae*, segments 3–5, dorsal view. (G) *C. macquariae*, segments 1–3, ventral view. (H) *A. paulae*, segment 11, ventral view. *Abbreviations:* ltas = lateral terminal accessory spine; lts = lateral terminal spine; lv = lateroventral spine; md = middorsal spine; mts = midterminal spine; spf = secondary pectinate fringe; vl = ventrolateral spine. Double digits denote respective segment number.

structures associated with type 1 gland cell outlets (see character 29).

31. Sexual dimorphism in presence/absence of large funnel-shaped subcuticular structures associated with type 1 gland cell outlets: 0 = funnel-shaped structures present in both sexes; 1 = funnel-shaped structures present in females only. The character was coded as inapplicable for taxa without funnel-shaped subcuticular structures associated with type 1 gland cell outlets (see character 29). Only the female is known for *Cephalorhyncha nybakkeni*; hence character 31 was coded as uncertain for this taxon.
32. Midlateral type 2 gland cell outlets on segment 5: 0 = absent; 1 = present. Characters 32–36 concern the presence and location of type 2 gland cell outlets. In some taxa, the positions of the outlets show sexual dimorphism. In these cases the corresponding characters were coded as polymorphic. Type 2 gland cell outlets can be present in more segments/positions than represented in characters 32–36, but only positions that produced informative characters were included in the matrix.
33. Laterodorsal type 2 gland cell outlets on segment 6: 0 = absent; 1 = present. See char. 32.
34. Midlateral type 2 gland cell outlets on segment 6: 0 = absent; 1 = present. See char. 32.
35. Midlateral type 2 gland cell outlets on segment 8: 0 = absent; 1 = present. See char. 32.
36. Midlateral type 2 gland cell outlets on segment 9: 0 = absent; 1 = present. See char. 32.

Results

Parsimony analysis of the data set in TNT produced 8 most parsimonious trees, whereas analysis in PAUP produced 24 most parsimonious trees of 60 steps, all with a consistency index (CI) of 0.6667 and a rescaled consistency index (RC) of 0.5098. The trees from the two analyses produce identical strict consensus trees and character optimizations (Fig. 7). The difference in number of trees occurs because TNT discards trees with collapsed nodes, whereas these trees are maintained in PAUP. Hence, the 8 fully resolved trees found by TNT were also among the 24 trees produced in PAUP, whereas the remaining 16 PAUP trees contained polytomies. The strict consensus tree produced by the two analyses is shown in Fig. 7; selected character state transformations are indicated on the branches. *Paracentrophyes quadridentatus* branches off most basally in the tree, followed by a clade with *Antygomonas paulae*, *Campyloderes macquariae* and *Zelinkaderes brightae*. This clade is supported by the development of a secondary pectinate fringe (char. 9), among other traits.

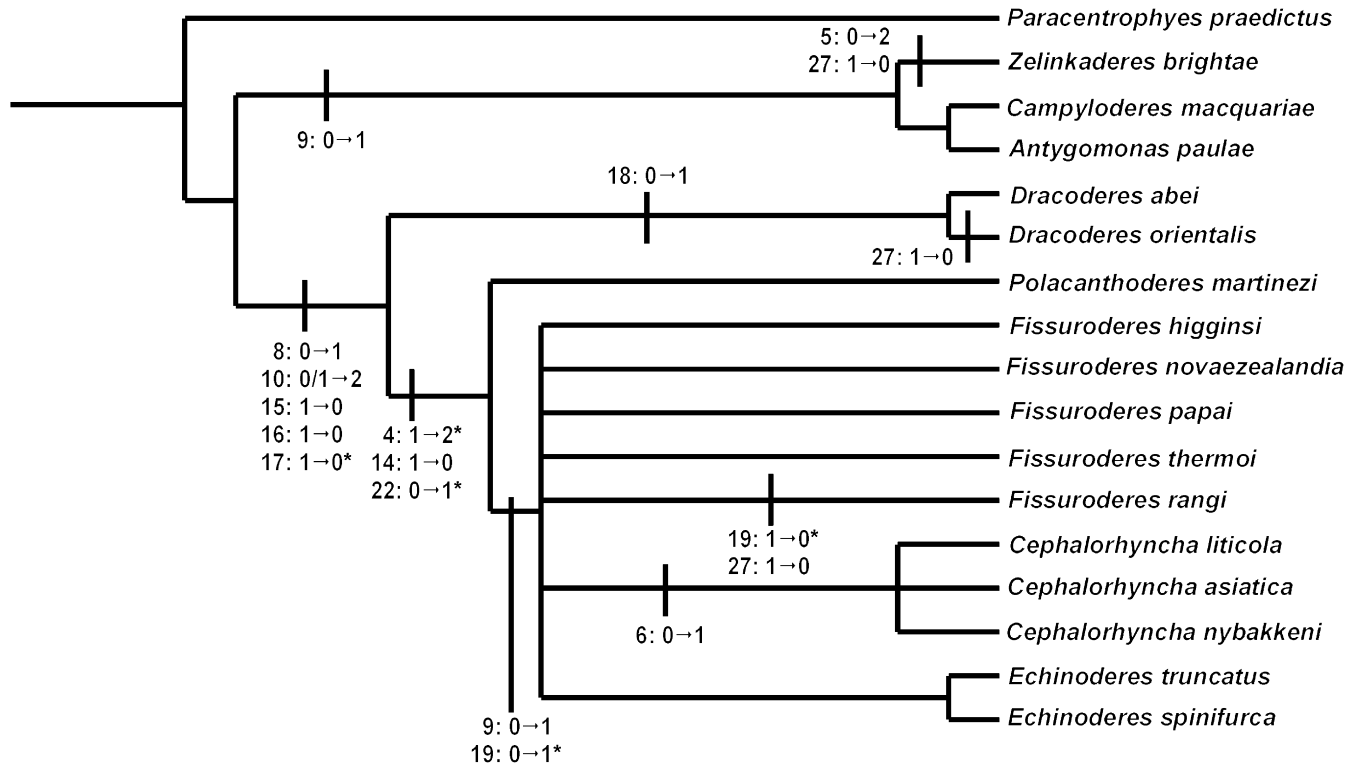


Fig. 7. Strict consensus tree of 60 steps, obtained after branch-and-bound searches in PAUP* and TNT. Selected character transformations indicated at internodes; those marked with an asterisk could not be optimized unambiguously, hence were optimized manually through equivocal cycling and evaluation of the possible solutions.

The two species of *Dracoderes* form the next clade branching off, which constitutes the sister taxon to the monophyletic Echinoderidae. Dracoderid monophyly is supported by the shift from aligned to alternately offset middorsal spines (char. 18). The sister-group relationship between *Dracoderes* and Echinoderidae is supported by several characters, including: termination of tergal and sternal plates on segment 11 in posteriorly pointing projections (char. 8), modification of cuticular hairs from either scale-like or leaf-like to acicular hairs (char. 10), loss of middorsal spine on segments 10 and 11 (chars. 15, 16), and displacement of the middorsal spines from near the posterior segment margin to more mesial positions (char. 17). Character 17 could not be optimized unambiguously, hence its optimization was done manually after equivocal cycling.

The next clade, identical to Echinoderidae, is supported by the following characters transformations: number of trichoscalids reduced from 7 to 6 (char. 4), and loss of middorsal spine on segment 9 (char. 14). Character 3 could not be optimized unambiguously, but it was assumed that the number of trichoscalids has undergone reductions from 14 in the most basal taxa, through 7 as displayed in *Dracoderes abei*, to 6 as found in all echinoderids. Another possible autapomorphy for Echinoderidae is the presence of lateral terminal accessory spines being restricted to females only

(char. 22), but this character could not be optimized unambiguously due to the complete absence of these spines in species of *Dracoderes*.

Within Echinoderidae, *P. martinezi* branches off as the first taxon. Its sister clade of all remaining echinoderids is supported by the development of secondary pectinate fringes (char. 9) and ventrolateral spines on segment 2 (char. 19).

Relationships among this latter clade of Echinoderidae excluding *Polacanthoderes* cannot be resolved. Monophyly for the genera *Cephalorhyncha* and *Echinoderes* is supported in all trees, but the included species of *Fissuroderes* branch off in positions varying among the different most parsimonious trees, either basally at the branch leading to *Cephalorhyncha* or on the branch leading to a clade consisting of *Cephalorhyncha*, *Echinoderes* and other species of *Fissuroderes*.

Discussion

The Echinoderidae

Analyses of the morphological data set (Table 1) support monophyly of Echinoderidae as defined by Neuhaus and Blasche (2006) (Fig. 7). The clade comprising the genera *Fissuroderes*, *Cephalorhyncha*

and *Echinoderes* is rooted by *Polacanthoderes*; hence Echinoderidae can be extended, without jeopardizing its monophyly, to comprise the latter genus as well.

As stated in the Results section, evaluation of echinoderid synapomorphies reveals that the family is supported essentially by the loss of a middorsal spine on segment 9, and by a decline in the number of trichoscalids to a total of 6. According to the analyses' character optimization, the presence of middorsal spines on most segments is interpreted as the plesiomorphic condition within Cyclorhagida. This agrees with earlier suggestions (Higgins 1990; Adrianov and Malakhov 1996), and supports interpretation of the loss of middorsal spine 9 as synapomorphic for species of Echinoderidae. If the loss of middorsal spines on segments 2 and 3 in species of *Zelinkaderes* is taken as a convergent reduction, loss of middorsal spines on these segments can also be considered as echinoderid synapomorphies. However, these characters could not be optimized unambiguously in the present analysis, which is probably due to limited taxon sampling. Reductions of middorsal spines as echinoderid synapomorphies are furthermore supported by the ontogeny, as the youngest juvenile stages often possess middorsal spines on most segments, and spine numbers are reduced with the following molts (Zelinka 1928; Higgins 1977; Sørensen et al. 2000). Hence, even though the character traits are based on secondary losses, it seems reasonable to consider them as echinoderid synapomorphies.

The other proposed echinoderid synapomorphy, the reduction of trichoscalids to a number fixed at 6, appears to be well-supported as well. Information on the exact number of trichoscalids is missing for several kinorhynchs (both echinoderids and non-echinoderid species), but in most reports and descriptions that include data on echinoderid trichoscalids or at least trichoscalid plates, their number seems to be fixed at 6, in two dorsal pairs and a ventral one (e.g. Higgins 1964, 1978, 1982, 1983, 1985, 1986b; Higgins and Rao 1979; Huys and Coomans 1989; Nebelsick 1993; Pardos et al. 1998; Sørensen et al. 2005; Sørensen 2006). The only exceptions are *Echinoderes brevispinosus* and *E. riedli* which, according to the illustrations, have 8 and 10 trichoscalid plates, respectively (Higgins 1966), whereas *E. aureus* and *E. sensibilis* apparently have 4 only (Adrianov et al. 2002a, b). However, nothing suggests that these latter four otherwise typical *Echinoderes* species should be very basal within the genus; hence I consider these exceptions as convergent specializations.

Another possible autapomorphy for Echinoderidae is the presence of lateral terminal accessory spines in females only. This conspicuous sexual dimorphism is expressed in all species of *Fissuroderes*, *Cephalorhyncha* and *Polacanthoderes*, and in addition in a great majority of species in *Echinoderes*. Lateral terminal accessory spines are present in both sexes of most other

cyclorhagid species, which probably constitutes a cyclorhagid synapomorphy. However, lateral terminal accessory spines are lacking in species of *Dracoderes*, which disables the attempts to optimize character 22 (sexual dimorphism in appearance of lateral terminal accessory spines) unambiguously. *Dracoderes* is very likely a potential sister taxon to Echinoderidae, even though the limited taxon sampling for the present study does not allow us to state so conclusively. The lateral terminal accessory spines in species of *Dracoderes* have obviously been lost secondarily, but since we are unable to say whether lateral terminal accessory spines would have been present in *Dracoderes* females only or in both sexes, we cannot say whether the character state is autapomorphic for Echinoderidae only, or synapomorphic for Echinoderidae + Dracoderidae.

The taxonomic definition of Echinoderidae has usually followed the diagnosis by Higgins (1990): Kinorhynchs with 16 distinct placids (the midventral one broadest) that articulate with the first trunk segment; segments 1 and 2 consisting of complete cuticular rings, segments 3–11 with one tergal and two sternal plates; midterminal spine absent in adults but present in at least some juvenile stages; middorsal spines in some adults and all juvenile stages; subdorsal spines, if present, found on segment 2 only; cuspidate spines absent; and outer oral styles consisting of two segments. However, when Neuhaus and Blasche (2006) described *Fissuroderes* and assigned this genus and *Cephalorhyncha* to Echinoderidae, that required emendation of the family diagnosis. Most of the traits listed by Higgins (1990) could be retained, but characterization of the trunk segments had to be revised to a first trunk segment consisting of a closed ring, and segments 3–10 consisting of one tergal and two sternal plates, whereas the morphology of segments 2 and 11 remained variable. Furthermore, Neuhaus and Blasche (2006) omitted the criterion of 'subdorsal spines found on segment 2 only'.

Most, if not all, of the listed diagnostic traits can probably be considered as symplesiomorphies, and none of the echinoderid autapomorphies listed above is included in the diagnosis. This is not a big problem, as diagnoses for taxonomic entities often have a phenetic origin and are created mostly for identification purposes. However, it is urgent to stress that a group's taxonomy should reflect its phylogeny; hence the diagnostic characters listed above can never serve to define the clade Echinoderidae, but only as a guideline during identification of specimens. Therefore, the autapomorphic characters traits that define Echinoderidae at present are solely the loss of middorsal spine on segment 9 (and probably segments 2 and 3), the reduction of trichoscalids to a number of 6, and perhaps the occurrence of lateral terminal accessory spines in females only.

Internal relationships of Echinoderidae

The resulting tree (Fig. 7) shows *Polacanthoderes* as the most basal echinoderid genus. However, the analyses failed to find a solution for the relationships above *Polacanthoderes*, because no exact positions could be established for the included species of *Fissuroderes*. This genus was proposed by Neuhaus and Blasche (2006), with the formation of a complete midventral fissure between the sternal plates of segment 2 as an important autapomorphy. The condition of the second trunk segment, and in particular the development/loss of sternal plates and midventral fissure, are obviously pivotal for understanding the internal echinoderid relationships. In the present analysis, character 5 deals with this transformation; it is the only additive multi-state character in the matrix (Table 1). Character states were assigned based on the assumption that the partially developed midventral fissure, as displayed in species of *Cephalorhyncha* (Fig. 2C), constitutes an intermediate state between the complete-fissure and no-fissure conditions. No a priori assumptions were made about the polarity of these character states, because objective character polarization should be done only by outgroup comparison or comparison with the most basal ingroup taxa. Based on the presence of a midventral fissure in segment 2 in five of the six outgroup taxa, the analyses suggest by simple outgroup comparison that the presence of a fissure is a basal kinorhynch trait, and hence plesiomorphic for Echinoderidae. Consequently, this trait cannot support monophyly of *Fissuroderes*. No other potential synapomorphies for all species of *Fissuroderes* are currently known. Neuhaus and Blasche (2006) suggest the presence of type 1 gland cell outlets with a conspicuous funnel-shaped subcuticular structure in a ventromedial position of segment 7 (char. 30) as being synapomorphic for *F. higginsi*, *F. thermo* and *F. novaezealandia*. This suggestion is supported in a majority of the most parsimonious trees obtained in the present analyses, but since the remaining two species of the genus, *F. papai* and *F. rangi*, do not possess this trait, it cannot be autapomorphic for the genus. In spite of the missing synapomorphies, I consider it as premature to reject possible monophyly of the genus, but the analyses clearly show that exploration for new reliable and consistent characters is needed.

As stated above, the analyses propose the presence of a midventral fissure in segment 2 as a plesiomorphic condition within Kinorhyncha. This stands in contrast to hypotheses of Neuhaus and Blasche (2006) as well as of Neuhaus (1994) and Neuhaus and Higgins (2002), who suggested that the condition of the second trunk segment in species of *Echinoderes* displays the most ancestral condition within kinorhynchs. Their argumentation is built on comparison with species of priapulids and loriciferans, the most likely kinorhynch sister group.

However, Priapulids and loriciferans are non-segmented animals without any traces of differentiated plates like those found in kinorhynchs (for more detailed information on priapulid morphology see, e.g., Adrianov and Malakhov 1999; for loriciferans see Kristensen 1991). Based on this similarity, Neuhaus and Blasche (2006) suggested that “This character [tube-like cuticle without any cuticular plates] is supposed to be retained, e.g., in species of *Echinoderes* ...” (Neuhaus and Blasche 2006, p. 47). This reasoning makes perfect sense, but still I would dare to propose some counter arguments to their hypothesis. First, I do not agree that absence of tegumental plates in priapulids and species of *Echinoderes* can be homologized straight away. The absence of tegumental plates in priapulids is most probably narrowly tied to the lack of segments; hence, in phylogenetic terminology, the character ‘tegumental plates’ would become inapplicable for taxa without segmentation. This argument is also supported by the fact that many animal species from various phyla possess a ‘tube-like cuticle without any cuticular plates’, but their overall trunk morphology can hardly be directly compared with the condition in the second trunk segment in species of *Echinoderes*. Secondly, by comparing species of various kinorhynch groups it becomes evident that all species of the Homalorhagida and most non-echinoderid cyclorhagid species possess a midventral fissure on segment 2. Admittedly, our current knowledge of kinorhynch phylogeny is still extremely limited, but it appears reasonable to assume that Kinorhyncha basally splits into the clades Homalorhagida and Cyclorhagida, and that Echinoderidae is an ingroup within the latter (e.g. Higgins 1990; Adrianov and Malakhov 1996, 1999; Kristensen 2002). If one can accept this assumption, the most parsimonious solution would obviously be to consider the midventral fissure of segment 2 as a basal kinorhynch trait, and to interpret its loss as apomorphic for *Echinoderes* (and *Cephalorhyncha*).

The basal taxa

Nothing conclusive can be said about the basal taxa in the analyses (Fig. 7), due to the limited taxon sampling. The position of *Dracoderes*, however, can and should be addressed. The genus is currently assigned to the monogeneric family Dracoderidae Higgins & Shirayama, 1990, but its obvious resemblance with species of Echinoderidae raises the question whether *Dracoderes* should be included in the latter family. This would be supported by the presence of tergal and sternal extensions of the terminal segment, by modification of cuticular hairs from either scale-like or leaf-like to acicular hairs, loss of middorsal spines on segments 10 and 11, and by displacement of the remaining middorsal

spines from positions near the posterior segment margin to more mesial positions. The most conspicuous autapomorphic trait for species of *Dracoderes* is the alternating lateral displacement of the middorsal spines (Fig. 6B; see also Higgins and Shirayama 1990). However, this trait is obviously an apomorphic modification of the regular, medially aligned pattern of middorsal spines found in all other cyclorhagids; hence this specialty does not serve as an argument not to include *Dracoderes* in Echinoderidae (or any other family). Then again, it should be stressed that the position of *Dracoderes* remains unresolved, and even if it turned out to be inseparably related to Echinoderidae, it would still be the most basal taxon in that family. Hence, whether *Dracoderes* should be placed in Echinoderidae or in a family of its own would be a taxonomic question, rather than a phylogenetic one. Since the present phylogenetic study has not presented any new, conclusive answers to this question, I see no reason not to maintain the current taxonomy and keep *Dracoderes* in the family Dracoderidae.

Conclusions

Cladistic analyses of Echinoderidae assign the genus *Polacanthoderes* to this family, and confirm the generic placement of *Cephalorhyncha liticola*. They support the monophyly of Echinoderidae and suggest the following synapomorphies for the family: loss of middorsal spine on segment 9, and perhaps on 2 and 3 as well; reduction of trichoscalids to a number of 6; and possibly the presence of lateral terminal accessory spines in females only. However, the characters ‘loss of middorsal spines on segments 2 and 3’ and ‘lateral terminal accessory spines present in females only’ could not be optimized unambiguously. According to the analyses, *Polacanthoderes* can be considered as the most basal taxon in Echinoderidae. Monophyly is supported for *Cephalorhyncha* as well as *Echinoderes*, whereas none of the most parsimonious trees yielded a monophyletic *Fissuroderes*. Due to the varying positions of species of *Fissuroderes*, the relationship between these and the genera *Cephalorhyncha* and *Echinoderes* could not be established.

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