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Tanaidacean Phylogeny – the Second Step: the Basal Paratanaoidean Families (Crustacea: Malacostraca)

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> Abstract

Phylogenetic relationships between the basal (or less derived) families in the tanaidacean superorder Paratanaoidea are examined and their monophyly tested using evidence derived from external morphology. With the genus *Zeuxoides* from the superfamily Tanaidoidea as outgroup, monophyly is confirmed for the Paratanaidae, Pseudotanaidae, Pseudozeuxidae, and Typhlotanaidae. The subfamily Teleotanainae is raised to family status to accommodate the genus *Teleotanais*. The monophyly of Leptocheliidae s.str. is accepted but several taxa are not included, neither is monophyly verified for Heterotanainae and Leptocheliinae. Nototanaidae appears to be polyphyletic and is split into Nototanaidae s.str. and Tanaissuidae fam. nov. Cryptocopidae is recognized but with exclusion of the Iungentitanainae; otherwise, this family is left for later analysis, including more derived taxa. *Protanaissus*, *Leptochelia*, *Pseudoleptochelia* and *Pseudonototanais* all appear to be non-monophyletic and will need revisions, while *Antiplotanais*, *Grallatotanais*, *Metatanais*, and *Tangalooma* are considered 'floating' taxa, albeit close to existing family-level clades. Initial attempts to include the derived tanaidacean families proved inconclusive and this suggests that limited phylogenetic analyses of the Paratanaoidea are necessary. We here suggest a revised method – the 'Restricted taxa analysis' – for resolving difficult datasets of the 'many-taxa-few-characters' type. This study should be regarded as a platform for more comprehensive analyses and systematic conclusions for the Tanaidacea.

> Key words

Phylogenetic analysis, Tanaidacea, plesiomorphic Tanaidomorpha, Tanaissuidae, Teleotanaidae, Restricted taxa analysis.

1. Introduction

The phylogeny of the paratanaoid Tanaidacea was last revised in 2002 in the first explicit use of computer-assisted parsimony methods (Larsen & Wilson 2002). This was still weakly developed and incomplete (Larsen 2005) and even deemed controversial by some workers (Bamber 2005; Błażewicz-Paszkowycz 2007). The earliest phylogenies presented by Sieg (1984) employed the 'bauplan/ground-plan' principle that is no longer considered adequate for modern phylogenetic studies; in these, he abandoned the previous division of the Tanaidacea into Monokonophora and Dikonophora and divided it into three Recent suborders (Apseudomorpha, Neotanaidomorpha and Tanaidomorpha) and the extinct Anthracocaridomorpha. Sieg (1984) went further into the suborders with several phylogenies on the Apseudomorpha and inferred the least derived tanaidacean genus to be *Gigantapseudes* Gamô, 1984. He also resolved the more derived Apseudomorpha but not in an all-inclusive analysis (Sieg 1984). No other attempts have been made to revise the Apseudomorpha using phylogenetic methods.

Since the Neotanaidomorpha consists of only one family, phylogenetic treatment of this taxon is not dealt with in this paper. At the present time, a consensus exists that, in phenetic terms, it occupies a position intermediate between the Apseudomorpha and Tanaidomorpha (Lang 1956; Gardiner 1975; Sieg 1983; Kudinova-Pasternak 1985; Sieg 1988; Larsen & Wilson 2002).

The Tanaidomorpha is by far the largest suborder (currently containing 15 families, 127 genera and more than 75% of all known tanaidacean species) and it is where the highest diversity is found. The members of this taxon are also the smallest tanaidaceans, characterised by many setal reductions and segmental fusions that further complicate the systematics. Sieg (1984) provided an all-encompassing phylogeny of the Tanaidomorpha but the systematics changed continuously almost immediately following this publication. Sieg himself continued to make changes in the composition of the more derived families (Agathotanaidae, Anarthruridae and Leptognathiidae) and, despite that the Leptognathiinae and Typhlotanainae did not constitute monophyletic groups in his own phylogeny, he combined them in the family Leptognathiidae. That family was later the focus of multiple alterations and recombinations (Bird & Holdich 1984; Sieg 1986a,b) but, again, without phylogenetic analysis. The constant altering of the taxa and diagnoses of this family group resulted in confused systematics. Subsequent workers tended to use Leptognathiidae as a repository whenever they described a new tanaidacean that did not fit any established family. In the deep sea, this amounts to about 50% of all tanaidomorphan species. This unfortunate fact has haunted tanaidacean systematics ever since.

Of the two superfamilies in the Tanaidomorpha, Tanaoidea and Paratanaoidea, only the latter was affected substantially by Larsen & Wilson (2002); since then, the systematics have further changed rapidly with close to 40 new genera and hundreds of new species described. Again, many shifts in tanaidacean systematics have been introduced without phylogenetic analysis (Gutu & Heard 2002; Gutu 2006; Błażewicz-Paszkowycz 2007). Only two papers (Guerrero-Kommritz & Brandt 2005; Larsen & Shimomura 2008), one dissertation (McLelland 2008) and one conference poster (Błażewicz-Paszkowycz & Poore 2008) employed computer-assisted phylogenetic methods to the Tanaidacea. The study of Guerrero-Kommritz & Brandt (2005) was restricted to the Akanthophoreinae and the authors wisely abstained from making major systematic conclusions. The analysis by Larsen & Shimomura (2008) dealt only with the Nototanaidae s.str. (with leptocheliid outgroups) and had an equally restricted hypothesis. The poster of Blazewicz-Paszkowycz & Poore (2008) included the more derived, non-paratanaoid, taxa but did not resolve most of these. What was resolved operated with bootstrap support to as low as 53%, further highlighting the problems with homoplasy in tanaidacean phylogenies.

The present study is a follow-up on the Larsen & Wilson (2002) phylogenetic analysis, including all species in the character evaluation and is thus not restricted to the 'exemplar approach' as used there (i.e. use of one well-described species or the type species of a genus). On the other hand, this new analysis is limited to the 'basal' families in order to keep the ratio of taxa to characters low, a pragmatic approach that does not imply that there should be a strict relationship between number of characters and terminal taxa, i.e. full resolution of all family relationships is not intended. It should be regarded as the first of several new attempts to improve resolution and consistency in tanaidomorphan systematics. Yet, impeding or restricting analyses of tanaidacean phylogeny are the perceived lack of 'good' characters due to reductions, significant inter-taxa variation (as seen by current taxonomy), confusing setal forms and a multitude of homoplasies (Larsen & Wilson 2002; Guerrero-Kommritz & Brandt 2005). The conservative or convergent morphology of the numerous tanaidomorphan genera, particularly in the deep sea, remains an obstacle to phylogenetic resolution. The lack of knowledge about the male gender of many of these genera is a further complication. Males are especially unknown in species-rich deep-sea assemblages and, if they are of the natatory form, they generally remain listed as 'indeterminate'. In this paper a method, the 'Restricted taxa analysis' is suggested to help overcome these obstacles. Clearly, the identification and refining of testable characters remains an imperative and is ongoing.

2. Materials and methods

2.1. Ingroup

The ingroup is made up of 57 taxa, mostly genera or subgenera, from what are perceived to be the most basal to mid-level families in the paratanaoidean tree (see Tab. 1 for these and authorities). Fortunately, just prior to submission of this study, a paper describing two new relevant genera (*Antiplotanais*, Typhlotanaidae and *Catenarius*, Leptocheliidae) was published by Bamber (2008) but time constraints prevented the inclusion of the new *Leptochelia* species in the present analysis. All relevant species were included to produce a character scoring for each nominal genus as a terminal taxon but, as initial data from the character analysis revealed considerable polymorphism in certain genera (e.g. *Leptochelia*, *Pseudoleptochelia*, *Pseudonototanais* and *Protanaissus*) these were subdivided as necessary (see Tab. 1) into what appeared to be more 'natural' groups. Using several more realistic, polymorphism-light taxa was considered preferable to one clearly polyphyletic genus. The two subgenera of *Pseudotanais* G.O. Sars were also treated separately and this is supported by a recent study by McLelland (2008).

Tab. 1. Taxa included in the analysis. Existing taxa that did not appear in Larsen & Wilson (2002) are assigned to their appropriate family in column 3 in square brackets.

Taxa	**Authority & notes**	**Larsen & Wilson (2002) family**
Zeuxoides	Sieg, 1980; OUTGROUP	not applicable
Charbeitanais	Bamber & Bird, 1997	[Pseudozeuxidae]
Pseudozeuxo	Sieg, 1982	Pseudozeuxidae
Heterotanoides	Sieg, 1977	Pseudozeuxidae
Intermedichelia	Gutu, 1996	Leptocheliidae
Hargeria	Lang, 1973; treated separately from *Leptochelia*	Leptocheliidae
Heterotanais	G.O. Sars, 1882	Leptocheliidae
Leptochelia-I	Dana, 1849; does not include Bamber (2008) species	Leptocheliidae
Mesotanais	Dollfus, 1897	Leptocheliidae
Pseudoleptochelia-I	Lang, 1973; excludes *P. fairgo* and *P. filum*	Leptocheliidae
Pseudoleptochelia-II	Only for *P. filum* (Stimpson, 1853)	[Leptocheliidae]
Pseudonototanais-I	Lang, 1973; only for *P. werthi* (Vanhöffen, 1914)	Leptocheliidae
Pseudonototanais-II	Only for *P. ebriosus* Bamber & Bird, 1997	[Leptocheliidae]
Pseudonototanais-III	Only for *P. bransfieldensis* Sieg, 1986	[Leptocheliidae]
Bathytanais	Beddard, 1886	Paratanaididaae
Paratanais	Dana, 1852	Paratanaididae
Pseudobathytanais	Kudinova-Pasternak, 1970	Paratanaididae
Bathytanaissus	Bird & Holdich, 1989	Nototanaididae
Metatanais	Shiino, 1952	Nototanaididae
Nesotanais	Shiino, 1968	Nototanaididae
Nototanais	Richardson, 1906	Nototanaididae
Protanaissus-I	Sieg, 1982; type species *P. longidactylus* (Shiino) only	Nototanaididae
Protanaissus-III	Only for *P. makrothrix* Sieg, 1986	[Nototanaididae]
Protanaissus-IV	Only for *P. alvesi* Gutu, 1996	[Nototanaididae]
Paratyphlotanais	Kudinova-Pasternak & Pasternak, 1978	Nototanaididae
Peraeospinosus	Sieg, 1986	Nototanaididae
Tanaissus	Norman & Scott, 1906	Nototanaididae
Teleotanais	Lang, 1956 (see also Bamber 2008)	Nototanaididae
Typhlotanais	G.O. Sars, 1882; *T. aequiremis* (Lilljeborg, 1864) only	Nototanaididae
Typhlotanoides	Sieg, 1983	Nototanaididae
Akanthinotanais	(Sieg, 1977)	Pseudotanaididae
Mystriocentrus	Bird & Holdich, 1989	Pseudotanaididae
Pseudotanais	G.O. Sars, 1882; as subgenus	Pseudotanaididae
Parapseudotanais	Bird & Holdich, 1989	Pseudotanaididae
Cryptocope	G.O. Sars, 1882	Pseudotanaididae
Cryptocopoides	Sieg, 1976	Pseudotanaididae
Curtichelia	Kudinova-Pasternak, 1987	Pseudotanaididae
Iungentitanais	Sieg, 1976	Pseudotanaididae
Latitanais	Kudinova-Pasternak, 1987	Pseudotanaididae
Meromonakantha	Sieg, 1986	*incertae sedis*
Nototanoides	Sieg & Heard, 1985	*incertae sedis*
Antiplotanais	Bamber, 2008	n/a
Bathyleptochelia	Larsen, 2003	n/a
Catenarius	Bamber, 2008	n/a
Hamatipeda	Błażewicz-Paszkowycz, 2007	n/a
Grallatotanais	Gutu & Iliffe, 2001	n/a
Konarus	Bamber, 2006; also *Pseudoleptochelia fairgo* Bamber, 2005	n/a
Larsenotanais	Błażewicz-Paszkowycz, 2007	n/a
Leptochelia-II	Only for *L. elongata* Larsen & Rayment, 2002	n/a
Obesutanais	Larsen et al., 2006	n/a
Paranesotanais	Larsen & Shimomura, 2008	n/a
Protanaissus-II	Only for *P. floridensis* Larsen & Heard, 2004	n/a
Pulcherella	Błażewicz-Paszkowycz, 2007	n/a
Tangalooma	Bamber, 2008	n/a
Torquella	Błażewicz-Paszkowycz, 2007	n/a
Typhlamia	Błażewicz-Paszkowycz, 2007	n/a
Xeplenois	Bamber, 2005	n/a

2.2. Outgroup

The number of characters that can be directly compared between ingroup and outgroup taxa usually increases if the outgroup is closely related to the ingroup (Nixon & Carpenter 1993). Therefore, *Zeuxoides* Sieg, 1980 was chosen as the most suitable outgroup. This well-described genus also belongs to the Tanaidomorpha and is thus a 'close' outgroup. Because *Zeuxoides* belongs to the superfamily Tanaoidea, it is also considered basally derived in relation to the ingroup. The members of this genus are exclusively shallow-water dwelling, thus diminishing the issue of evolutionary tracks in shallow waters *contra* those in the deep-sea where different environmental conditions impinge and the more derived (apomorphic) groups predominate (Sieg 1983).

2.3. Data

The data matrix (Tab. 2) was developed from an Excel spreadsheet and reformatted for use in T.N.T. Many characters scored have been verified by personal observation by the authors, thus reducing bias from poorly described taxa, although some remain intractable. Others were scored based on literature data, mostly taxonomic descriptions. Some characters previously considered of phylogenetic importance (as in Larsen & Wilson 2002) were excluded or re-defined due to new observations. The data consist of 107 unordered characters, 100 parsimony-informative and seven outgroup-defining characters. Not all of the many morphological features peculiar to the outgroup taxon were formulated as characters, since most of them are invariable in the ingroup and thus not phylogenetically informative.

2.4. Analysis

Heuristic searches were performed on the data matrix using both T.N.T 1.1 (Goloboff et al. 2003, 2008) and PAUP* 4.0b-10 (Swofford 1999). Characters were analysed both with 'implied weighting' and 'unweighted' in T.N.T and 'unweighted' in the PAUP analysis. 'Unweighted' introduces the fewest ad hoc assumptions about character evolution (Allard & Carpenter 1996; Kluge 1997; Larsen & Wilson 2002). Both analyses were performed unrooted.

2.5. Settings

In T.N.T. the settings used were: Data format = 8 states; memory, maxtree = 10.000; collapsing rule min. length = 0; traditional search with 'Collapse trees after search' and 'Tree Bisection Reconnection' on; Traditional Search; 'retain 10 trees per round; 1000 replications. The consensus in T.N.T. is calculated from four shortest trees with a tree length of 525.

In PAUP, analysis employed the tree space search of Edgecombe et al. (2000), with 1000 replications of random starting trees and heuristic TBR branch swapping on a maximum of 10 trees per replication (i.e., PAUP* commands: *hsearch addseq=random randomize=trees nchuck=10 chuckscore=0 nreps=1000;*). PAUP found 20 shortest trees with a tree length of 670.

While there is an almost 100-step difference, the consensus topographies computed by these two programs are identical. We have no explanation for this apparent discrepancy at this time but suspect that the different algorithms of the programs to be responsible.

2.6. Branch support

The Bremer support (Bremer 1994) was used to estimate branch support and the values are given next to the branches in Fig. 1. The Bootstrap, Jackknife and other resampling support analyses are not considered reliable and were not used in this analysis (see Larsen & Wilson 2002 for review). The Bremer support analysis was performed only in T.N.T. using a '20 step suboptimal tree search', with a relative fit value of 1.00, values are given in absolute numbers.

2.7. The 'Restricted taxa analysis'

As our previous attempts to conduct an all-encompassing phylogenetic analysis of the Tanaidomorpha consistently failed to achieve fully resolved trees, mainly due to homoplasy, we here suggest a new approach to difficult datasets and suggest the name 'Restricted taxa analysis'. We applied this method here to alleviate the problems with poor resolution due to many taxa and few characters. The restricted taxa analysis works by building the phylogenetic analysis module by module. Initially, the analysis was carried out with only those less-derived paratanaoid families for which character-scoring was achievable for both females and males. After two monophyletic clades were established, further taxa were added and, as other clades emerged and 'floaters' identified, this step was repeated.

We intend to continue this incremental analysis of unresolved taxa/clades but excluding all but one taxon (genus) from those monophyletic families/clades previously established with confidence. The restricted number of taxa in the analysis should allow resolution of derived genera. Once resolution is achieved with newly-added taxa, a specific analysis of the clade (or clades) and its close outgroup taxa can be conducted to confirm or reject the hypothesised affiliation. A growing or expanding phylogeny will be built with repeated increments and 'floaters' kept within the analyses to establish if they can be ultimately assigned to a distinct clade or family.

3. Character description

All the following characters are based on female (or neuter) morphologies. Distinctive male characters have been scored for the relatively limited number of taxa with known males and used in establishing a 'groundplan' organization for those taxa (see above). They are, however, not used here in this more taxon-inclusive analysis.

Additional character-scoring procedures for the genera not covered in this analysis have identified many more potentially phylogenetically-useful characters, or refined those already identified. Yet other useful/discriminatory characters, such as pleopod setation patterns, cephalothorax-plate morphology and pereopod setal counts, were initially appraised in this analysis but set aside because of inadequacies in the published literature, inconsistent recording of features across all taxa, or were evident as homoplasies (as pertains to this analysis).

In some instances in the following list 'absent' may be inferred shorthand for a state "not showing the stated character" rather than meaning the lack of *any* 'characters' or features in the location. Future analyses will also split some of the more complex multistate characters and more fully address the issues of 'absence' and 'non-applicability' in scoring. The term 'spine', unless otherwise stated, refers to stiff, thickened setae.

0 **Pleon multiple pinnate setae** (0 = absent, 1 = present). In this character the state 'present' is only found in several Tanaidae genera, including the outgroup *Zeuxoides* (see Sieg 1980: fig. 46).

1 **Labium palp/process** (0 = absent, 1 = present). A labial palp is possessed by several Tanaidae genera, including the outgroup taxon *Zeuxoides* (see also Larsen & Wilson 2002: character 22; see Sieg 1980: fig. 40).

2 **Mandible setal row** (0 = absent, 1 = present). A setal row is possessed by several Tanaidae genera, including the outgroup *Zeuxoides*. It is best developed in the Apseudomorpha (see also Larsen & Wilson 2002: character 19; see Sieg 1980: fig. 7).

3 **Maxilliped coxa** (0 = absent, 1 = present). A maxilliped coxa is possessed by the Tanaidae; including the outgroup *Zeuxoides* (see also Larsen & Wilson 2002: character 30; see Sieg 1980: fig. 10).

4 **Maxilliped palp articles 3–4 double inner row of setae** (0 = absent [single row], 1 = present). A double setal row is possessed by several Tanaidae genera, including the outgroup *Zeuxoides* (see Bird 2008: fig. 3G).

5 **Pereopod ischio-basis** (0 = absent, 1 = present). The presence of an ischio-basis is seen in Tanaidae, including the outgroup *Zeuxoides*; usually described as absent, the ischial remnant is often clearly visible as a non-articulated terminal portion of the basis, with its concomitant setal group (see also Larsen & Wilson 2002: character 42; see Bird 2008: fig. 5E).

6 **Pereopod-6 setal comb** (0 = absent, 1 = present). A setal comb is possessed by the Tanaidae, including the outgroup *Zeuxoides*. Formed of blade-like setae on the infero-distal margin of this pereopod only (see Bird 2008: fig. 5J).

7 **Pleopod basal article outer setae** (0 = absent, 1 = present). Outer basal setae are possessed by the Tanaidae, including the outgroup *Zeuxoides*. Inner setae persist in the basal paratanaoid groups (see Sieg 1980: fig. 47).

8 **Compound eyes** (0 = absent, 1 = present). The presence of eyes helps inference of shallow-water/deep-water evolutionary tracks but can hinder analyses – as a homoplasy (see also Larsen & Wilson 2002: character 5).

9 **Cephalothorax narrower anteriorly** (0 = absent, 1 = present). This describes the 'pinched in' anterior part of the carapace in taxa as *Tanaissus* and *Nototanais* and is not merely the slight narrowing anterior of the eyes as seen in other groups (see Bird 2002: fig. 2A, B).

10 **Cephalothorax reduced, subtriangular** (0 = absent, 1 = present). Presence of this peculiar character state is exemplified by the deep-sea *Latitanais* and the '*Leptognathia*' *birsteini*/*microcephala*-group (see Bird 2007: fig. 17A).

11 **Pereon short and stout** (0 = absent, 1 = present). Although non-specific this character may assist discrimination between certain groups; exemplified by *Cryptocopoides* and *Obesutanais* (see Larsen et al. 2006: fig. 5A for the latter). See character 12 below.

12 **Pereonites 1–3 very short relative to pereonites 4–6** (0 = absent, 1 = present). This equates to characters 3 and 41 in Larsen & Wilson (2002) and the 'present' state is a substitute/equivalent for the possession of a single pair of marsupial plates. Presence seems to be restricted to the Pseudotanainae (see Bird & Holdich 1989: fig. 3A).

13 **Pereonite 1 trapezoidal (wider anterior)** (0 = absent, 1 = present). This pereonite form is seen at its

most extreme expression in some typhlotanaids such as *Torquella* (see Blazewicz-Paszkowycz 2007: fig. 40A,B), but further analysis is required to trace homoplasies.

14 Pereonite 1 hyposphenian/sternal spur (0 = absent, 1 = present). Spurs appear in several apparently un-related genera such as many typhlotanaids, *Cryptocopoides* and *Insociabilitanais* Larsen, 2005, and is certainly homoplasic; it may be ontogenetically dependent, as ovigerous females lack this feature (Lang 1953; Larsen 2005).

15 Pleon reduced (0 = absent, 1 = present). This character is not to be confused with others tied to the pleon (reduction in width, fusion etc.) and the 'present' state is restricted to *Pseudozeuxo* and *Charbeitanais* (see Bamber & Bird 1997: fig. 19B,E).

16 Pleonite lateral setae circumplumose (0 = absent, 1 = present). The large epimeral setae typified by presence on paratanaids (see also Larsen & Wilson 2002: character 8; see Larsen 2001: fig. 3A–C). The presence of simple setae is scored as 0 to avoid misinterpretations in the literature of the presence or absence of this type of seta.

17 Pleotelson flat, plate-like (0 = absent, 1 = present). The plate-like state is currently known only for the paratanaid *Xeplenois* (see Bamber 2005: fig. 53A, B).

18 Antennula articles, excluding minute cap-like, count (0 = three, 1 = four, 2 = five). Confusion and obfuscation of analyses can occur if the presence of a minute (cap-like) article is not recognised (Larsen & Wilson 2002: character 11). See character 21.

19 Antennula article 1 composite (0 = absent, 1 = present). The nature of the antennula articulation and possible alternative pathways to reduction in article count is helped by identifying this character. It almost always occurs (i.e. is <u>not</u> invariant) with a three-articled antennula (excluding minute cap-like article) and is recognised by the presence of two setal groups on the lateral margin, ostensibly marking the fusion of two previous articles (see Bird 2002: figs. 5A, 8A).

20 Antennula short penultimate article (0 = absent, 1 = article-2, 2 = article-3). The 'present' state is denoted by an article that is only about as long as broad, typified by many typhlotanaid genera (see Błażewicz-Paszkowycz 2007: fig. 14A).

21 Antennula terminal article minute, cap-like (0 = absent, 1 = present). This small article may have been overlooked in some descriptions and its evolutionary 'fate' is almost certainly fusion with the preceding article. It also occurs in more derived paratanaoid groups such as the Colletteidae (see Larsen 2001: fig. 17C).

22 Antennula article 3 subterminal aesthetascs (0 = absent, 1 = present). Subterminal aesthetascs may be a synapomorphy for those pseudozeuxid genera carrying it (see Sieg 1982a: fig. 1) but it need not be homologous with character 23, see below.

23 Antennula article 2 subterminal aesthetascs (0 = absent, 1 = present). The 'present' state is seemingly restricted to *Nototanoides* (also with 3-articled antennula); the evolutionary tracks of this and the preceding character require further investigation, along with patterns of article-fusion and amalgamation (see Sieg & Heard 1985: fig. 2).

24 Antennula article 3 with terminal spur (0 = absent, 1 = present). A terminal spur is known from the typhlotanaids *Meromonakantha* and *Paratyphlotanais* (see Błażewicz-Paszkowycz 2007: fig. 3A).

25 Antennula serrate distal setae (0 = absent, 1 = present). Serrate setae are confined to the paratanaids *Bathytanais* and *Pseudobathytanais* (see also Larsen & Wilson 2002: character 12; see Larsen & Heard 2001: fig. 1B).

26 Antenna multi-articled, count (0 = seven, 1 = six). Further antennal count states are evident (such as for *Agathotanais*) but are not required for this analysis (see also Larsen & Wilson 2002: character 14; see Sieg 1976: fig. 7).

27 Antenna article 2 larger or longer than article 3 (0 = absent, 1 = present). Scoring for 'presence' is dependent on the distinctly wider (bulkier) appearance of article-2 if not clearly longer than article-3 (see Larsen 2001: fig. 5B).

28 Antenna article 3 larger or longer than article 2 (0 = absent, 1 = present). The converse of the preceding character, a larger article 3 is seen in some pseudotanaids (see Sieg 1986a: fig. 100) and *Tangalooma*.

29 Antenna article 2 dorsal strong acute spine/apophysis (0 = absent, 1 = present). For this character 'presence' is typified by the condition in *Leptochelia* and excludes states where a simple spiniform seta is present (see Bamber & Bird 1997: fig. 11D).

30 Antenna article-2 dorsal stout broad-based spine (0 = absent, 1 = present). A broad spine is evident only in some *Pseudotanais* species. This character is here defined separately from the former to avoid further possible homoplasy influences (see Bird & Holdich 1989: fig. 4C).

31 Antenna article-2 ventral strong acute spine or apophysis with seta (0 = absent, 1 = spine, 2 = apophysis). For this character, 'presence' is typified by the condition in *Leptochelia*, state 2 by the condition in *Bathytanais* and *Pseudobathytanais* (see Larsen & Heard 2001: figs. 1D, 3A). The apophysis/spine in *Paratanais gaspodei* (see Bamber 2005: fig. 49C) is possibly homologous with the more extreme form of the two former paratanaid genera. This character excludes states where a simple spiniform seta is present.

32 Antenna article-3 dorsal strong acute spine/apophysis (0 = absent, 1 = present). The 'presence' character state is typified by that exhibited by *Leptochelia* and excludes states where a simple spiniform seta is present (see also LARSEN & WILSON 2002: character 13; see BAMBER & BIRD 1997: fig. 11D).

33 Antenna article-3 dorsal strong broad-based spine (0 = absent, 1 = present). This exists (as a probable homoplasy) in some *Pseudotanais* species and *Pseudobathytanais*. This character is difficult to discriminate from the not-always-adequate literature. Information of phylogenetic value may be lost here in our failure to discriminate between the various degrees of 'robustness' from the older descriptions. However, to avoid creating artificial homoplasy on the basis of poor descriptions, we have chosen to keep the character conservative. This is also to some extent applicable to character 28 (see BIRD & HOLDICH 1989: fig. 4C or LARSEN & HEARD 2001: fig. 1D).

34 Labial lobes pairs, count (0 = two, 1 = one). This character may be considered to be plesiomorphic in state 0 and apomorphic in state 1 as three pairs are present in the Neotanaidomorpha (see also LARSEN & WILSON 2002: character 21; see LARSEN & RAYMENT 2002: fig. 1F for illustration).

35 Mandible molar broad, grinding surface (0 = absent, 1 = present). The broad molars of many shallow-water genera such as *Zeuxoides*, *Leptochelia* and *Pseudoleptochelia* are surfaced with numerous rows of highly pectinate spines. As algal-grazing is a likely feeding method this character is not seen in deep-sea genera. It may be considered a 'sister-character' to the presence of eyes in this respect. For comparison with characters 35–36 see also LARSEN & WILSON 2002: character 17; see LANG 1973: fig. 2f,g).

36 Mandible molar piercing or crushing (0 = absent, 1 = broad nodulose, 2 = broad spinose, 3 = acuminate-armed, 4 = acuminate-simple). Molar shapes are highly diverse but some phylogenetic value is present, if not with some homoplasy, which is to be expected when feeding strategies are considered (see BŁAŻEWICZ-PASZKOWYCZ 2007: fig. 3D,E for state 1; GUTU 1996: fig. 43A for state 2; BIRD & HOLDICH 1989: fig. 1G,H for states 3 and 4).

37 Mandible right incisor bifid – points open/symmetrical, with distal crenation (0 = absent, 1 = present). The 'present' state is typified by the mandible seen in *Leptochelia* but is widespread in the paratanaoids (see BAMBER 2005: fig. 37D). Other incisor types are scored '0' but work is in progress to refine characters/states for this feature.

38 Mandible right incisor bifid – points closed/asymmetrical (0 = absent, 1 = present). The 'present' state is typified by *Pseudotanais*, where the bifid tip is almost closed (see BIRD & HOLDICH 1989: fig. 4F).

39 Mandible left incisor/lacinia broad, facing anterior (0 = absent, 1 = present). The 'present' state is somewhat restricted to the pseudotanaids and nototanaid genera (see BIRD & HOLDICH 1989: fig. 4E).

40 Maxillula palp distally bent (near or actual right-angle) (0 = absent, 1 = present). Consistently scoring the overall variation in maxillula palp shape is a near impossibility but this two-state character is defined by the definite near right-angle bend, exemplified by *Tanaopsis* (see LANG 1967: fig. 2I).

41 Maxillula endite terminal spines short (0 = absent, 1 = present). Although somewhat subjective, several paratanaoids (e.g. *Bathyleptochelia*, *Heterotanoides*, and *Teleotanais*) exhibit relatively stout and blunt maxillula spines that may be of phylogenetic value (see BAMBER & BIRD 1997: fig. 9A or LARSEN 2003: fig. 6E).

42 Maxilliped basis and endites both laterally expanded (0 = absent, 1 = present). This is an apparent synapomorphy within the Paratanaidae. It is not to be confused with flared endites in other taxa, see character 45 (see also LARSEN & WILSON 2002: character 33; see LARSEN 2001: fig. 3D).

43 Maxilliped basis fusion (0 = absent, 1 = present). The partial fusion state is not distinguished from the 'present' state in this analysis although it might prove to be of value in more detailed within-taxon analyses, where appropriate (see also LARSEN & WILSON 2002: character 31; see SIEG 1976: fig. 8).

44 Maxilliped endite fusion (0 = absent, 1 = present, 2 = present in part). For this character, the partial state is considered to be valid and appropriate (see also LARSEN & WILSON 2002: character 32), largely because it may be less prone to misinterpretation than the basal fusion states (see 43 above; see SIEG 1976: fig. 9).

45 Maxilliped endites distally expanded or flared (0 = absent, 1 = weak, 2 = strong, 3 = highly developed). Endite shape in the paratanaoids ranges from simple oblong to highly flared; the latter is typified by *Tanaopsis* (see also LARSEN & WILSON 2002: character 33; see LANG 1967: fig. 3A for state 3).

46 Maxilliped endite marginal articulated blunt teeth, count (0 = four, 1 = three, 2 = one, 3 = absent). These flat tooth-like spines are typical of the leptocheliids and their allied taxa although pointed forms also exist that may be phylogenetically distinct (see next characters 47–48, also LARSEN & WILSON 2002: character 34; see LARSEN & WILSON 1998: fig. 6F or BAMBER 2005: fig. 40H).

47 Maxilliped endite marginal articulated pointed spines, count (0 = five, 1 = four, 2 = three, 3 = one, 4 = absent). Pointed spines occur in several leptocheliid (or 'leptochelioid') genera, including the recently described Australian *Catenarius* (see BAMBER 2008: fig. 39H or LANG 1973: fig. 2I).

48 Maxilliped endite paired rounded spines/tubercles (marginal or submarginal) (0 = absent, 1 =

present). This form of endite armament may be evolutionarily derived from the previous character, but the form and location is distinctive and may have more precise phylogenetic value. Typified by many paratanaids, pseudotanaids and some nototanaids and typhlotanaids (see Larsen & Wilson 1998: fig. 7C or Sieg & Heard 1985: fig. 3). Another character is recognised in the possession of a single rounded cusp but this is not required for this analysis.

49 **Maxilliped endite large lateral seta** (0 = absent, 1 = present). This highly distinctive seta is linked to the presence of distal spines (characters 46 and 47) although some taxa such as *Heterotanoides* may have a similar (homologous?) seta in a sub-lateral location (see Bamber & Bird 1997: figs. 12D, 20E).

50 **Maxilliped basal setae, count** (0 = three or more, 1 = two, 2 = one, 3 = absent). Although some species show ontogenetic differences (i.e. larger individuals may have more setae than more juvenile individuals) when dealing with mature specimens this may have some value (see Larsen & Rayment 2002: figs. 3H, 6F).

51 **Maxilliped palp article-2 lateral seta** (0 = absent, 1 = present). This character has yet to prove its full usefulness, principally because inconsistency in the literature impedes comprehensive analysis (see Bamber & Bird 1997: fig. 17F).

52 **Maxilliped palp article-2 bifid/trifid/strongly pectinate spine** (0 = absent, 1 = present). This presence of a modified spine occurs in several genera and may be of phylogenetic value; typified by *Nototanoides* and several species of *Paratanais* (see Sieg & Heard 1985: fig. 3 or Gutu & Ramos 1995: fig. 7A,B).

53 **Maxilliped palp article-2 long seta (as long as articles 3–4)** (0 = absent, 1 = present). Presence of a long seta is typified by *Bathytanaissus* (see Bird & Holdich 1989: fig. 25L).

54 **Maxilliped palp article-2 medial setae, count** (0 = four or more, 1 = three, 2 = two). Character state 0 is a strong separator of taxa such as Tanaidae and Leptocheliidae from more 'apomorphic' groups, the larger number of setae being plesiomorphic (see Sieg 1980: fig. 47 for state 0).

55 **Maxilliped palp article-3 medial setae, count** (0 = five or more, 1 = three or four). As with the previous character, this can be considered to be a plesiomorphic/apomorphic split (see Larsen 2003: fig. 6G for state 0). Further resolution is required for analysis of groups such as the Anarthruridae, where three or four setae occur in the various genera (Bird 2004a).

56 **Cheliped-cephalothorax sclerite inserted dorsally (triangular)** (0 = absent, 1 = present). The cheliped-cephalothorax attachment has been the focus of much phylogenetic discussion in the Tanaidacea literature (see Larsen & Wilson 2002: character 38) and some revision of the character would increase its phylogenetic value significantly. As presented here, this differs somewhat from given by Larsen & Wilson (2002). Unfortunately, this character has not been recorded or illustrated for most of the 'older' taxa and even today many authors ignore this important feature. It is therefore presented here in a restricted form, although this character could be expanded to differentiate between: 1) the dorsally attached triangular sclerite, typical of many less-derived paratanaoids (plesiomorphic condition); 2) the postero-dorsally attached elongated sclerite (free basis margin present) seen in many derived paratanaoid genera and many taxa so far without family affiliations; 3) other conditions seen in agathotanaids and anarthrurids. The last are not relevant to this study where, in practice, all the taxa have either the triangular sclerite (see Larsen & Wilson 1998: fig. 7B) or a less distinctive posterodorsal attachment.

57 **Cheliped basis with suture ('pseudocoxa')** (0 = absent, 1 = present). The presence of a suture is shown only by *Nesotanais* (for *N. lacustris*). This condition is not homologous with the condition seen in the Agathotanaidae (see Shiino 1968: fig. 3A).

58 **Cheliped basis reaches pereonite-1** (0 = absent, 1 = present). The 'present' character state is seen in many less-derived paratanaoids (see Larsen 2001: fig. 16A), but in more apomorphic deep-sea groups the cheliped is pushed further anteriorly and little, if any, free basis posterior margin is evident.

59 **Cheliped carpus stout, rounded (as long as broad)** (0 = absent, 1 = present). Typified by *Tanaissus*, the rounded character state does not include merely short carpal forms (see Bird 2002: fig. 1D).

60 **Cheliped carpus cuff** (0 = absent, 1 = present). Typified within the basal paratanaoids by *Konarus* (see Bamber 2006: fig. 4A), it may be an analogous structure (in terms of function) to the carpal shield of more apomorphic groups such as *Stenotanais* Bird & Holdich, 1984, *Akanthophoreus* Sieg, 1986 and *Paraleptognathia* Kudinova-Pasternak, 1981.

61 **Cheliped chela forcipate** (0 = absent, 1 = present). A clear diastema between the fixed finger and dactylus defines the 'present' character state; seemingly confined within some Pseudotanainae females (see Bird & Holdich 1989: fig. 1E). This character does appear in other families but only in males (e.g. *Pseudonototanais*, *Tangalooma*).

62 **Cheliped fixed-finger crushing incisive margin** (0 = absent, 1 = present). Many basal paratanaoids and other taxa exhibit the character state of a raised, non-denticulate incisive margin (see Lang 1973: fig. 2k). This is difficult to score accurately in some instances where only literature-based data are used. Further refinement of characters expressing the fixed finger shape and dentition is in progress.

63 Cheliped dactylus crenations (0 = absent, 1 = present). Further analysis may revise this into more than one character to distinguish between true crenation and presence of nodules (see Larsen & Shimomura 2008: fig. 6D or Larsen & Shimomura 2009: fig. 2A).

64 Cheliped dactylus thin, strongly curved (0 = absent, 1 = present). The 'present' state is exemplified by *Tanaissus*; it is perhaps better expressed as a marked disparity in width of the dactylus and fixed finger, the latter usually deep and with highly convex incisive margin (see Sieg 1982b: fig. 6 or Bird 2002: fig. 1D).

65 Cheliped propodus ventral setae, count (0 = 3 or more, 1 = one or two). In broad terms, state 0 may define more plesiomorphic taxa than those exhibiting state 1, but this cannot be extrapolated to the one or two-setae states (see Sieg & Heard 1985: fig. 4 for state 0).

66 Cheliped carpus multiple dorsal setae (0 = absent, 1 = present). In most instances paratanaoids have few dorsal setae (none or just one proximal and one distal) but some taxa, including *Pseudoleptochelia* and *Peraeospinosus*, have many small setae distributed along the dorsal margin (see Błażewicz-Paszkowycz 2007: fig. 25A).

67 Cheliped carpus mid-ventral setae, count (0 = four or more, 1 = three, 2 = two, 3 = one, 4 = none). As with character 65, state 0 may define more plesiomorphic taxa than those exhibiting states 1, 2 or 3, but this cannot be extended to these latter states (see Sieg 1980: fig. 10 for state 0).

68 Cheliped merus ventral setae, count (0 = four or more, 1 = three, 2 = two, 3 = one). See previous character for carpal setae.

69 Pereopod 1 bayonet spines (0 = absent, 1 = present). Bayonet spines are not present in most of the basal paratanaoids but occur in *Paratyphlotanais* (see Bird 2004b: fig. 3A).

70 Pereopod 1 propodus with distoventral seta or spine (0 = absent, 1 = seta, 2 = spine). This is an attempt to distinguish between two basic setal types, although refinement of state 2 is likely in future analyses (see Sieg & Heard 1985: fig. 5 for state 1, Błażewicz-Paszkowycz 2005: figs. 3B, 18A for state 2). The presence of a spine is more frequent in the derived paratanaoidean genera.

71 Pereopod 1 dactylus/unguis clearly longer than propodus (0 = absent, 1 = present). A long dactylus/unguis is exemplified by *Intermedichelia* but is present in less extreme form in other leptocheliid genera (see also Larsen & Wilson 2002: character 44; see Gutu 1996: fig. 39A or Bamber 2005: fig. 45B).

72 Pereopod 1 unguis longer than dactylus (0 = absent, 1 = present). This is distinct from, and not correlated with, the previous pereopod-1 character (see also Larsen & Wilson 2002: character 44; see Larsen 2001: fig. 6A).

73 Pereopod 1 and pereopods 2–3 different in shape and setal arrangement (0 = absent/weak, 1 = moderate, 2 = strong). Somewhat subjective in scoring, the amount of differentiation between the first pereopods and the two succeeding pairs is an under-rated phylogenetic character (see Larsen & Shimomura 2008; fig. 7A–C for state 0 – *Paranesotanais*; Bamber & Bird 1997: fig. 21A–C for state 1 – *Charbeitanais*; Bird 2008: figs. 16C, 17C for state 2 – *Zeuxoides*).

74 Pereopods 2–3 merus simple, stout or short spines (0 = absent, 1 = present). These spines are distinguished from simple setae or bayonet spines – see below.

75 Pereopods 2–3 merus bayonet spines (0 = absent, 1 = present). Bayonet spines are straight, strong spiniform setae at least as long as the width of the article on which they arise. Typified by *Tanaissus* and most *Paratyphlotanais* species in this analysis (see Bird 2002: fig. 7B,C and Bird 2004b: fig. 3C), although more extreme forms are seen in genera not covered here.

76 Pereopods 2–3 carpus bayonet spines (0 = absent, 1 = present). See previous character; typified by *Akanthinotanais* but present elsewhere (see Bird & Holdich 1989: fig. 1A).

77 Pereopods 2–3 carpus blade-like spines (0 = absent, 1 = present). Presence is indicated by deep spines, typified by *Pseudotanais* (*Pseudotanais*) (see Bird & Holdich 1989: fig. 1B).

78 Pereopods 2–3 carpus spines, count (0 = none, 1 = one, 2 = two or more). This includes all spine types, excluding simple setae.

79 Pereopods 2–3 propodus distoventral seta or spine (0 = absent, 1 = seta, 2 = spine). This distinction is useful but yet more information is likely to be derived when a closer analysis of the setal types involved is carried out (see Larsen 2001: fig. 6B,C for state 1, Sieg & Heard 1985; fig. 5 for state 2).

80 Pereopods 2–3 carpus single distoventral spine only (0 = absent, 1= small, 2 = conical-robust, 3 = simple). Useful phylogenetic discrimination may be hidden in this character, state 1 seen in (for example) *Konarus* and *Heterotanais* and state 2 being typified by *Bathyleptochelia* (see Larsen 2003: fig. 7B).

81 Pereopods 2–3 carpus two distoventral spines only (0 = absent; 1 = present, one spine type; 2 = present, two spine types). This character seems to mark a condition distinct from others, where one or more spines are located in more dorsal (or at least medial) positions on the carpus; typified by *Nesotanais* (state 1) and several pseudotanaid genera (state 2) (see Shiino 1968: fig. 3E for state 1; Bird & Holdich 1989: fig. 22B for state 2).

Tab. 2. Basal paratanaoid data matrix. Polymorphisms are simplified: [01] = A, [02] = B, [12] = C, [13] = D, [23] = E, [24] = F, [34] = G, [124] = H, [234] = J.

	0		1		2		3		4	
Character	01234	56789	01234	56789	01234	56789	01234	56789	01234	56789
Taxon										
Zeuxoides	11111	11110	00000	00010	00000	00100	00000	10000	00000	01200
Heterotanais	00000	00010	00000	00001	00000	01101	00100	10100	00000	02401
Heterotanoides	00000	00010	00000	00001	00100	00A00	00000	01100	01000	0FF01
Mesotanais-I	00000	00000	00000	00001	0A000	0110A	00A00	0D100	0A000	0HJ01
Intermedichelia	00000	0001?	00000	00001	01000	01000	0100?	10100	00000	02400
Leptochelia-I	00000	00010	00000	00001	01000	01001	01100	10100	00000	01401
Hargeria	00000	00010	00000	00001	01000	01001	01100	10100	00000	04201
Pseudoleptochelia-I	00000	00010	00000	00001	0A000	01001	0AA00	10100	00000	0A401
Pseudonototanais-I	00000	00010	00000	00001	01000	0110A	00100	10100	11000	02401
Nesotanais	00000	0001?	00000	00001	00000	01A00	00001	10100	00012	144A0
Nototanais	00000	00011	00000	00001	00000	01100	00001	01100	00010	14400
Tanaissus	00000	00001	00000	00001	00000	01100	00001	0G101	A0011	24400
Peraeospinosus	00000	00000	00001	00001	10000	01100	00001	01000	00010	14410
Typhlotanais	00000	00000	00001	00001	10000	01100	00001	01000	00010	14410
Paratanais	00000	00010	00000	01010	2A000	01100	0B011	10100	00110	04410
Charbeitanais	00000	00011	00000	10001	00100	01100	00000	01100	00010	0FF01
Pseudozeuxo	00000	00011	00000	10001	00100	01100	00000	01100	00000	02401
Nototanoides	00000	00011	00000	00001	00010	01100	00001	10100	00012	14410
Grallatotanais	00000	00010	00000	00010	01000	01000	00000	10100	00000	03400
Konarus	00000	00010	00000	00001	01000	01000	00000	10100	00000	01401
Paranesotanais	00000	00010	00000	00001	00100	01100	00101	10100	00012	24400
Tangalooma	00000	00010	01000	00010	00000	01010	00001	01100	00000	?4400
Bathyleptochelia	00000	00011	00000	00001	10000	01100	00000	AA100	01000	01001
Catenarius	00000	00011	00000	00011	01000	01000	0000?	10?00	01000	04201
Bathytanaissus	00000	00001	00000	00001	00000	01100	00001	03101	10010	24410
Metatanais	00000	00010	01000	00001	10000	01100	0000?	01?00	00110	04400
Paratyphlotanais	00000	00000	00011	00001	10001	01100	00001	01000	00010	14400
Protanaissus	00000	00001	00000	00001	00000	01100	00001	04101	10010	24400
Teleotanais	00000	00011	00000	01010	00000	01000	00000	10010	010A0	04C01
Typhlotanaoides	00000	00000	01001	00001	10000	01000	00001	01000	00010	04410
Bathytanais	00000	00010	00000	01010	20000	11101	02011	10000	A0110	02400
Pseudobathytanais	00000	00010	000A0	0A011	B0000	11100	0B0A1	10100	00110	02400
Cryptocope	00000	00001	01001	00010	20000	01100	00000	03000	00010	04400
Cryptocopoides	00000	00000	01001	00010	20000	01100	00000	02000	00010	04400
Curtichelia	00000	00000	1000?	00010	00000	01100	00001	0C000	00010	04400
Iungentitanais	00000	00010	0100?	00010	00000	01000	00001	????0	01010	01401
Latitanais	00000	00000	1000?	00010	01000	01100	00001	02000	00010	04400
Akanthinotanais	00000	000AA	01100	00000	00000	010A0	00001	0G011	A001C	C4400
Mystriocentrus	00000	00001	01100	00000	00000	01000	00001	04011	10011	14400
Pseudotanais	00000	000A1	01100	00000	00000	010A0	A00A1	0J011	1001C	C44A0
Parapseudotanais	00000	00001	00100	00000	10000	01100	00001	04011	?0012	14400
Meromonakantha	00000	00000	00011	00001	10001	01100	00001	01100	00010	14410
Xeplenois	00000	00010	00000	01101	20000	01100	00011	01000	00100	02400
Hamatipeda	00000	00000	00011	00001	10000	01100	00000	01000	00010	1440A
Larsenotanais	00000	00000	00001	00001	10000	01100	00000	01A00	00010	14410
Pulcherella	00000	00000	00011	00001	10000	01100	00001	01000	00010	14410
Obesutanais	00000	00000	01001	00001	10000	01100	0000?	01000	00010	?4400
Torquella	00000	00000	00011	00001	10000	01100	00001	01000	00010	1441A
Typhlamia	00000	00000	00011	00001	10000	01100	00001	01000	00010	A441A
Antiplotanais	00000	00000	0100?	00001	10000	01?00	00001	01000	00010	14400
Protanaissus-II	00000	00011	00000	00001	00000	01100	00001	03??1	10010	14400
Protanaissus-III	00000	00000	00000	00001	00000	01100	00001	02101	10010	04400
Protanaissus-IV	00000	00001	00000	00001	00000	01100	0000?	02101	100?0	04400
Leptochelia-II	00000	00010	00000	00010	01000	01000	00000	10100	01000	0140?
Pseudoleptochelia-II	00000	0001?	00000	00001	11000	01100	0000?	A???0	??000	01401
Pseudonototanais-II	00000	00010	00000	00001	10000	01?01	00100	1A100	00010	02401
Pseudonototanais-III	00000	00010	00000	00001	10000	01?01	00101	00100	00000	02401
Mesotanais-II	00000	00001	00010	00001	A1000	01101	00000	03100	01000	04200

82 Pereopod-3 stouter than pereopod-2 (0 = absent, 1 = present). Restricted to a few disparate genera (e.g. *Tangalooma*, *Typhlotanoides*) the value of this character needs further analysis (see Bamber 2008: fig. 17F).

83 Pereopods 4–6 basis thicker than pereopods 1–3 basis (≥ 1.67 times longer than broad) (0 = absent, 1 = present). Homoplasy may affect this character in broad analyses but may have more value in more focused studies (see Błażewicz-Paszkowycz 2007: fig. 4).

Tab. 2. Continuation.

	5		6		7		8		9		10	
Character	01234	56789	01234	56789	01234	56789	01234	56789	01234	56789	01234	56
Taxon												
Zeuxoides	A1000	01010	00100	00000	10021	00021	0000A	11010	40000	00001	01100	20
Heterotanais	21000	01010	00100	10120	10020	00002	10011	11000	20200	00001	00100	11
Heterotanoides	20001	01010	00000	00220	10000	00001	000A0	11000	10100	00001	00100	A1
Mesotanais-I	1A0A0	01010	00000	101E0	1A0C0	00011	100AA	10000	2AAA0	00001	00100	1A
Intermedichelia	01000	01010	00100	10120	11120	0000C	00011	21010	10201	00001	00000	10
Leptochelia-I	0100A	01010	00100	A0110	1A021	00012	10011	11000	20000	00001	00100	1A
Hargeria	01001	010?0	00100	00110	10011	00012	10011	11000	20000	00001	00000	10
Pseudoleptochelia-I	A1000	11010	00100	AACD0	10021	000C2	AA011	11000	20100	00001	00100	1A
Pseudonototanais-I	1100A	01010	00100	10120	10020	00022	10000	10000	20100	00001	00100	11
Nesotanais	20001	1AA10	00000	10230	101C0	00022	010AA	10A00	30310	01001	00000	12
Nototanais	210A1	11010	00000	10230	10110	01022	01000	D0100	30310	00001	00000	12
Tanaissus	20001	10011	00011	10230	101C0	11022	00000	10A00	30310	01001	00000	12
Peraeospinosus	21001	10010	00000	11230	20111	00022	00011	23020	11310	01101	10000	C3
Typhlotanais	21001	10000	00000	10130	00100	00012	10011	13020	01310	01001	10000	13
Paratanais	21101	11010	00100	10230	101C1	00021	00001	22010	31310	01001	00000	12
Charbeitanais	20001	11010	00000	10230	20010	000C1	00000	10000	20200	01001	021??	03
Pseudozeuxo	10000	01010	00000	10130	10010	00011	10010	10000	20200	01001	021??	02
Nototanoides	20101	10010	00000	00230	10110	00022	00000	10000	31310	00001	00000	12
Grallatotanais	21000	01010	00000	10220	10010	00001	00010	20010	00100	00001	00000	11
Konarus	01000	01010	10100	10130	11120	00012	10011	11000	20100	00001	00100	11
Paranesotanais	20001	11010	00010	00230	10100	0000C	0000A	10000	31310	01001	10000	12
Tangalooma	200?0	010?0	00000	10130	10120	00012	10111	10000	C0200	02001	20100	02
Bathyleptochelia	100?0	01010	00100	10230	01020	00011	20010	10000	20100	01001	00100	11
Catenarius	01001	010?0	00100	11130	11011	00012	10011	10000	10100	00001	00000	10
Bathytanaissus	21011	10010	00001	10220	01121	00012	30000	10001	10310	03001	00000	12
Metatanais	31000	10010	00100	10430	20100	00022	C0000	20010	20300	01111	000??	?3
Paratyphlotanais	21001	10000	00000	1A23A	10101	A1021	00010	10100	31300	01001	10000	12
Protanaissus	31011	10010	00010	10230	11120	00021	01100	10100	20310	02001	00000	12
Teleotanais	2100A	010?0	00100	00220	1A000	00001	00011	10000	20100	00001	00100	CE
Typhlotanaoides	210?1	10010	00000	10230	10100	00011	10101	22020	00310	00001	10000	12
Bathytanais	2AA01	11010	00000	10230	11110	00001	00011	22010	31310	01001	A0000	12
Pseudobathytanais	02000	11000	00000	10230	10120	000C1	C000A	2D010	2A310	01001	00000	1E
Cryptocope	21001	10000	00000	10230	10100	00011	30000	10000	20300	01000	00010	02
Cryptocopoides	310?1	10000	00000	10230	10100	01011	0A000	30100	20300	02010	00011	A2
Curtichelia	21002	10000	00000	102?0	101??	??0??	????0	11000	E0300	02??0	10000	12
Iungentitanais	21002	01000	00000	10230	10000	00001	00000	10000	20200	02001	10000	12
Latitanais	E100C	A0000	00000	10230	1010A	00021	01000	10000	3A300	02100	00000	12
Akanthinotanais	EA0AC	10000	00000	10A30	10101	01022	01000	D0A00	20310	02001	00011	0E
Mystriocentrus	20011	10010	01000	10230	10111	00122	02000	10001	21310	02111	00011	03
Pseudotanais	E10AC	10010	0A000	10230	10101	00122	0B0A0	10001	1A310	02001	00011	0E
Parapseudotanais	31001	100?0	00000	10230	10110	00122	01010	10000	30310	02001	10011	12
Meromonakantha	21001	10000	00000	10230	10101	00022	00000	10010	20300	01001	00000	12
Xeplenois	20001	11000	00100	10230	10121	00021	00001	22010	11300	00001	10000	12
Hamatipeda	21001	10000	00000	10230	10101	00012	10011	200C0	21310	01001	10000	1E
Larsenotanais	21001	10010	00000	11230	10110	00012	10010	C3020	0A310	01001	00000	13
Pulcherella	21001	10000	00000	10230	10100	00001	0001A	13020	00310	01001	10000	12
Obesutanais	31001	100?0	00000	11130	10010	0001C	10011	12020	11310	01001	10010	13
Torquella	21001	10000	00000	10130	10101	000C2	AA011	C30C0	11310	0C111	10000	12
Typhlamia	E10?1	10000	00000	10230	10100	00012	AA01A	C3020	0A310	01001	10000	12
Antiplotanais	20001	10000	00000	11230	10120	00002	00010	11000	50310	01001	00000	13
Protanaissus-II	30001	11010	00010	10330	00021	00012	20000	10000	00300	02001	00000	12
Protanaissus-III	21002	100?0	00011	10230	11030	00011	20010	10000	30310	12001	00000	12
Protanaissus-IV	?1001	110?0	00001	10230	01130	00011	20011	10000	31310	12001	00000	12
Leptochelia-II	00000	11000	00000	10120	11021	00012	10111	10000	A0C10	01001	00?00	10
Pseudoleptochelia-II	110?0	010?0	00100	00220	10020	00012	10000	10000	10300	00001	00100	11
Pseudonototanais-II	110?0	010?0	00000	10130	10020	00012	10000	10000	20100	00001	00100	10
Pseudonototanais-III	11000	010?0	00000	10230	10020	00001	00000	10000	20100	00001	00100	1A
Mesotanais-II	11000	010?0	00001	10120	11010	00011	10010	10000	20110	00001	00100	10

84 Pereopods 4–6 basis stout (≤ 2.5 times longer than broad) (0 = absent, 1 = present). This is not necessarily correlated with the previous character and the same comments about homoplasy and further usefulness apply (see Larsen 2001: fig. 6D–F).

85 Pereopods 4–6 merus robust or bayonet spines (0 = absent, 1 = simple, 2 = robust, 3 = bayonet). Definition of spine types is partly compromised by overlap in shape, where the ‘robust’ form is typified by *Paratanais* (see Larsen 2001: fig. 6E) and ‘bayonet' by *Nototanais* and *Akanthinotanais* (see Sieg 1977: fig. 29).

86 Pereopods 4–6 carpus microtrichial field or 'prickly tubercle' (with or without microtrichia) (0 = absent, 1 = microtrichia, 2 = microtrichia, strong, 3 = prickly tubercle). Clinging-apparatus pereopod structures vary widely across tanaidacean groups and defining these states within the paratanaoid clade is an attempt to avoid self-defining categories as exemplified by *Bathytanais*, *Paratanais* and typhlotanaids (see Lang 1973: fig. 16E,D or Bird 2004b: fig. 9G for state 1; Larsen et al. 2006: fig. 6E,G for state 2). 'Prickly tubercles' (see Błażewicz-Paszkowycz 2007: fig. 12G,H) may occur outside of the Typhlotanaidae, as in *Pseudobathytanais gibberosus* Larsen & Heard, 2001.

87 Pereopods 4–6 carpus bayonet spines (0 = absent, 1 = present). Presence of bayonet spines is exemplified by *Nototanais* and *Akanthinotanais* (see Sieg 1986a: fig. 102).

88 Pereopods 4–6 carpus complex-denticulated, or hook-like, spines (0 = absent, 1 = complex, 2 = hooks). Complex-denticulated spines are exemplified by the paratanaid *Bathytanais* but clearly delimiting this character is problematical (see Larsen & Heard 2001: fig. 7D–F). Distinctive hook-like spines (often portrayed in a non-articulated form) seem to be restricted to some of the typhlotanaids such as *Pulcherella* and *Hamatipeda* (see Błażewicz-Paszkowycz 2007: figs. 19E, 28G). This character complements the previous character 86 in defining the pereopod clinging-apparatus.

89 Pereopods 4–6 carpus blade spine (0 = absent, 1 = present). Essentially the same structure as seen in character 77.

90 Pereopods 4–6 carpus spines, count (0 = one, 1 = two, 2 = three, 3 = four, 4 = five or more, 5 = none). This includes all spine types, and excludes simple setae.

91 Pereopods 4–6 dorsomedial pinnate setae (0 = absent, 1 = present). This character is scored '1' if a pinnate seta is on any (not necessarily all) of the posterior pereopods. It appears to be a valuable marker of taxa such as the Paratanaidae, Pseudotanaidae and Typhlotanaidae (see Larsen 2001: fig. 6D).

92 Pereopods 4–5 propodus distodorsal setae, count (0 = four or more, 1 = three, 2 = two, 3 = one). A consistent feature of many paratanaoid families is the presence of only a single seta above the propodus-dactylus articulation and the states 0 and 1 may indicate plesiomorphy.

93 Pereopods 4–5 propodus distodorsal seta modified (long/thick and/or pectinate) (0 = absent, 1 = present). Further investigation (ideally using SEM) would permit more accurate definition of probable variation in this character, typified by most nototanaids, pseudotanaids and typhlotanaids (see Bird & Holdich 1989: fig. 5D–E or Sieg & Heard 1985: fig. 6).

94 Pereopods 4–5 propodus distodorsal seta modified (long, slender) (0 = absent, 1 = present). Presence of this seta only occurs in *Intermedichelia* but it may justifiably represent an analogous form of long seta – in this instance being more slender and acuminate than in the previous character (see Gutu 1996: fig. 40A,B).

95 Pereopod-6 propodus with long distoventral setae (0 = absent, 1 = present). Present as an autapomorphy of a pair of species in *Protanaissus* (*P. alvesi* Gutu, 1996 and *P. makrotrichos* Sieg, 1986). See Gutu (1996: fig. 45D).

96 Pereopod-6 propodus distodorsal setae, count (0 = four or more, 1 = three, 2 = two, 3 = one). Generally, taxa with a single seta in this position on pereopods 4–5 have two on pereopod-6.

97 Pereopods 1–3 rod, or bone-like seta (0 = absent, 1 = present). Modified setae in this category are rather short and stiff, rod-like, sometimes with a weakly bifid tip. They may be overlooked in some instances and have been described as 'simple seta' in many older descriptions; often present in taxa such as *Torquella* and some other typhlotanaids (see Błażewicz-Paszkowycz 2007: fig. 25B).

98 Pereopods 4–6 rod, or bone-like seta (0 = absent, 1 = present). See character 97.

99 Pereopods 4–6 dactylus-unguis 'claw-like' (0 = absent, 1 = present). This character has been a diagnostic of the family Nototanaidae but has been a source of misleading phylogenetic decisions. A claw-like state (i.e. the dactylus and unguis are fused into a single article – 'claw') may be the dominant state in the basal paratanaoids and it is probable that a transverse row of minute setules can often be misinterpreted as an articulation. Similarly, in some taxa the 'claw' retains a fusion line that may often have been described as an articulation. In this analysis the state is recognised by the presence of a small unguis (i.e. definitely shorter than the dactylus) together with fusion (or the appearance of being unfused due to presence of setules/fusion line). See also Larsen & Wilson (2002: character 46); see Larsen (2001: fig. 6D–F).

100 Pereopods 4–6 unguis tip modified (0 = absent, 1 = present). Bifid or trifid unguis tips are largely restricted to a few genera, typified by *Paranesotanais*, *Curtichelia* and *Tangalooma* (see Bamber 2008: fig. 17G–I or Larsen & Shimomura 2008: fig. 7D,F).

101 Pleopod pairs, count (0 = five, 1 = three, 2 = one, 3 = none). The default character state of five pairs is supplemented by two other 'present' categories typified by the outgroup *Zeuxoides* (three pairs) and the *Pseudozeuxo*/*Charbeitanais* clade (one pair of reduced pleopods).

102 Pleopod basal article inner setae (0 = absent, 1 = present). The presence of an inner seta is common in the basal paratanaoid genera but may have been overlooked in some instances (see Bamber & Bird 1997: figs. 8E, 16D). This observation is also applicable to the following two characters.

103 Pleopod endopod setae all terminal (0 = absent, 1 = present). Explicitly, all setae are arranged in a more or less straight fringe at the ramus tip; typified by most species of *Pseudotanais* and some other genera such as *Cryptocope* (see Bird & Holdich 1989: fig. 7G).

104 Pleopod exopod setae all terminal (0 = absent, 1 = present). See comment for previous character.

105 Pleopod endopod inner/subterminal setae, count (0 = absent, 1 = one, 2 = two or more). The plesiomorphic condition (exhibited by the outgroup *Zeuxoides)* is represented by state 2; apart from *Teleotanais* (see Bamber 2008: fig. 20K) only the typhlotanaid *Peraeospinosus magnus* Kudinova-Pasternak, 1990 appears to possess this character state.

106 Uropod endopod articles, count (0 = five to seven, 1 = three to four, 2 = two, 3 = one). This character essentially distinguishes the leptocheliid genera from other paratanaoids (see also Larsen & Wilson 2002: character 51), although it is ontogenetically dependent (e.g. Masunari 1983; Bird & Bamber 2000; Larsen 2005).

4. Discussion

4.1. Overview

The systematic conclusions (see Tab. 4) are based on the strict consensus (see Fig. 1), derived from the analysis using unweighted characters. Tree statistics are given in Tab. 3. Based on the consensus and one of the most parsimonious trees from TNT (Fig. 2), most of the established families examined were monophyletic (but with a varying number of inferred modifications to the classification), i.e. the Paratanaidae, Pseudotanaidae s.str., Pseudozeuxidae, and Typhlotanaidae; these results were also supported by Błażewicz-Paszkowycz & Poore (2008). The genus *Teleotanais* Shiino, 1978 branches off early from the Paratanaoidea clade, with a high Bremer index for the remaining Paratanaoidea, and warrants its own family (see below). *Grallatotanais* is the next taxon branching off the Paratanaoidea tree. It is has some unusual features such as elongate pereopods 4–6 but may be a leptocheliid relative.

The rest of the Paratanaoidea falls into two clades. The first is a large and relatively unresolved clade representing the Leptocheliidae and allied genera, from *Heterotanoides* to *Catenarius* in Fig. 1. This is the sister group to a much larger and heterogeneous clade that incorporates all of the remaining families. In contrast to the apparent monophyly of the families mentioned previously, the Nototanaidae appears not to be monophyletic and is here represented by two clades, indicative of two separate families, the Nototanaidae s.str. and the Tanaissuidae fam. nov. (see below).

4.2. *Teleotanais*

This genus is differentiated from all other Paratanaoidea (these with Bremer support 5). Recently, Bamber (2008) assigned *Teleotanais* to a new subfamily, Teleotanainae, within the Paratanaidae, principally on the basis of finding circumplumose setae on the pleonal epimera. In most other respects this genus is unlike any paratanaid and appears more leptocheliid-like but with some plesiomorphic features (e.g. endopod with more than one inner seta); in contrast, it has the more apomorphic two-articled uropod endopod state. It is raised to family-level here (see below).

4.3. *Heterotanoides-Catenarius* clade

This is a large clade with eighteen taxa, all belonging to either the Leptocheliidae or Pseudozeuxidae as recognised by Larsen & Wilson (2002). Our resulting phylogeny (Figs. 1, 2) implies the existence of several subfamilies (or families) but not with the same composition as suggested by Larsen & Wilson (2002) although analysis with the inclusion of male characters does support separate Heterotanainae and Leptocheliinae. However, there are a number of taxa (e.g. *Mesotanais* and *Pseudonototanais* groupings) that do not fit into either of these subfamily-level clades so we abstain from drawing conclusions on subfamilies here. A 'restricted taxa analysis' of the Leptocheliidae using all species and male data will be helpful in resolving this situation, as these clarify and strengthen relationships such as between *Heterotanais* and *Pseudonototanais* (forcipate male chelae) and *Konarus* and some *Pseudoleptochelia* species (subchelate male chelae). The entire clade (possibly including *Teleotanais* and *Grallatotanais*) it is likely to be raised to the level of superfamily. Still, the monophyly of the 'old' Leptocheliidae is confirmed (as the *Pseudonototanais*-III-*Catenarius* clade) but the recently added genera (*Konarus*-*Catenarius* clade) seem to be paraphyletic relative to Leptocheliidae s.str., albeit a sister group. The genera *Leptochelia*, *Pseudonototanais*, and *Pseudoleptochelia* themselves appear to be paraphyletic and will also need further analysis.

Tab. 3. Tree statistics derived from PAUP 4.10b.

Tree length	525 (TNT) 670 (PAUP)
Consistency index (CI)	0.4358
Homoplasy index (HI)	0.7985
Retention index (RI)	0.6272
Rescaled consistency index (RC)	0.2734

Tab. 4. Systematic changes of the basal families within the Paratanaoidea.

Family	Monophyly (Bremer support)	Remarks
Cryptocopidae	Yes (25)	Without Iungentitanainae.
Leptocheliidae *sensu stricto*	Yes (1)	Possibly several clades and previous subdivision into Heterotanainae and Leptocheliinae is not discounted (in absence of male characters here).
Nototanaidae *sensu* Sieg, 1982	No	Divided into two groups.
Nototanaidae *sensu stricto*	Yes (1)	See Discussion. Bremer index would probably increase if male characters were included.
Pseudozeuxidae	Yes (5)	The close affinity with *Bathyleptochelia* can currently not be explained.
Paratanaidae	Yes (15)	The close affinity with *Metatanais* suggests that this genus is close to the Paratanaidae and an intermediate genus between Paratanaidae and the nototanaid/typhlotanaid group.
Pseudotanaidae *sensu stricto*	Yes (25)	Cryptocopidae taxa removed.
Typhlotanaidae	Yes (1)	Without *Antiplotanais?* Possibly with two subfamilies.
Tanaissuidae	Yes (2)	New family.
Teleotanaidae	Yes (5)	New family.

4.4. *Bathyleptochelia-Pseudozeuxo* clade

Although it clearly nests within the larger leptocheliid-allies clade, the Pseudozeuxidae is a well-supported clade. but is an apparent sister group to *Bathyleptochelia*. Its maxilliped and pereopod setation are typically 'leptocheliid' in appearance but it presents apomorphic characters with respect to the pleon-pleopods and uropods, as noted by Sieg (1982a). Subterminal aesthetascs on the antennula are shared by *Heterotanoides*, *Nototanoides* and *Paranesotanais* but only in the first taxon may this be homologous with Pseudozeuxidae. The inclusion of *Bathyleptochelia* with the pseudozeuxids in this clade is related to apparent homologies with respect to cephalothorax shape, maxilliped palp and pereopod-6 propodus setation. Further study is required to validate this, but currently *Bathyleptochelia* is not included in this family (see below).

4.5. *Latitanais-Cryptocope* clade

The family Cryptocopidae, recently reviewed and erected by McLelland (2008), is also confirmed in this analysis, within a larger clade with *Curtichelia* and *Latitanais*, as also found by him. We expect, however, that this clade will be heavily modified when the more derived taxa are included in the analysis (Larsen & Bird research in progress). However, as this analysis shows, we cannot accept the inclusion of *Curtichelia* or *Latitanais* within the Iungentitanainae (McLelland 2008) and consider that that subfamily might be restricted and elevated to an independent family in the near future. The *Curtichelia-Latitanais* clade will likely be affiliated with some of the more derived taxa currently in other families or without family designation.

4.6. *Xeplenois-Paratanais* clade

This family clade appears as the sister clade to the larger pseudotanaid-nototanaid-typhlotanaid group. The Paratanaidae commends itself by being one of the few families that has remained stable since its establishment and it is probably the only one which is uncontroversial. Paratanaids occur in both deep (*Bathytanais*, *Pseudobathytanais*) and shallow water (*Bathytanais*, *Paratanais*, *Xeplenois*) but the majority of species are from shallow water. Using this character matrix, we found no support for the subfamily division suggested by Larsen & Heard (2001), although we still consider it to be valid (detailed study with other known characters is required). Only *Metatanais* needs to be confirmed as a true member of this clade (see below).

4.7. *Meromonakantha-Peraeospinosus* clade

This analysis appears to confirm the monophyly of Typhlotanaidae, which, however, includes *Meromonakantha* and *Paratyphlotanais*, an outcome also shown by Błażewicz-Paszkowycz & Poore (2008). This monophyly conflicts with Błażewicz-Paszkowycz (2007), who removed several 'old' typhlotanaid genera from the Nototanaidae and re-established the Typhlotanaidae, but retained *Meromonakantha* and *Paratyphlotanais* in the former. More precise relationships *within* the typhlotanaid clade would likely be found with a focused analysis.

4.8. *Nototanais-Nototanoides* clade

The support for the original Nototanaidae is weak, but it appears as the sister clade to the Pseudotanaidae and a clade of other nototanaid genera (see below). It is comprised of genera possessing eyes and broad mandibular molars (even if not of the shallow-water 'grinding' type) as compared to the *Protanaissus-I-Protanaissus-III* clade (see below). Further study with male data may yet determine the validity or otherwise of this split. This family-level group is found in relatively shallow water (0–300 meters).

4.9. *Parapseudotanais-Mystriocentrus* clade

The Pseudotanaidae Sieg, 1976 was recently redefined (McLelland 2008) and split into two families Pseudotanaidae s.str. and Cryptocopidae and the present analysis fully supports this split (see below, under Cryptocopidae). The Pseudotanainae Sieg, 1976 now constitutes the whole family.

4.10. *Protanaissus-I-Protanaissus-III* clade

A well-defined clade that is composed of 'nototanaid' genera and is defined as a new family (see below). In the character analysis *Protanaissus* proved highly polymorphic and was split into its component species. It warrants further revision as *P. alvesi* Gutu, 1996 and *P. makrothrix* Sieg, 1986 as well as *P. floridensis* Larsen & Heard, 2004 are divergent from the type species *P. longidactylus* (Shiino, 1970). For example, *P. floridensis* appears to be phylogenetically positioned between *Protanaissus* s.str. and *Tanaissus* but cannot be included in either since it possesses eyes. Furthermore, it has unfused maxilliped endites (conflicting with *Tanaissus*) but lacks the elongated pereopod-1 dactylus/unguis (conflicting with *Protanaissus* s.str.). Work on resolving these anomalies, is in progress (Heard & Bird in prep.).

4.11. Floaters – *incertae sedis*

This category includes *Metatanais* Shiino, 1952, *Grallatotanais* Gutu & Iliffe, 2001, *Tangalooma* Bamber, 2008, and *Antiplotanais* Bamber, 2008. They are considered 'floaters' because they appear in the cladogram as singletons outside of any family-level clade, although this does not absolutely preclude their belonging to any of these. *Metatanais* appears to show several affinities with the Paratanaidae, but is rather poorly described (in the published literature) and contains a number of reduced features. *Metatanais* is probably a highly derived taxon closely related to the Paratanaidae but it has to be considered separate until either more detailed drawings are published or the male can be described. A similar rationale can be applied to *Antiplotanais* with regards to the Typhlotanaidae.

The former pseudotanaids *Curtichelia* Kudinova-Pasternak, 1987, *Iungentitanais* Sieg, 1977, *Latitanais* Kudinova-Pasternak, 1987 and *Paraiungentitanais* Sieg, 1977 (not included in the analysis due to incomplete description) were removed from Pseudotanaidae and included into the Cryptocopidae by McLelland (2008). However we do not consider this group to be monophyletic but neither do we consider these genera as floaters. The evidence provided by this analysis suggests that the subfamily Iungentitanainae may warrant its own family and the affinity of *Curtichelia* and *Latitanais* will be resolved with the inclusion in the analysis of the more derived paratanaoidean clades of Leptognathiidae and Colletteidae (see under Cryptocopidae).

4.12. General remarks

Tanaidacean systematics is still in a state of flux and previous attempts to construct an all-encompassing phylogeny have consistently failed due to conservative morphologies, homoplasy, and poorly described taxa. The low consistency index in our analyses (CI 0.4358) shows that many homoplasies are still present in the dataset.

We have high expectations to alleviate this situation by continuing to revise and improve character identification and expanding the character-taxon matrix by using the 'Restricted taxa analysis' (RTA) outlined above (see section 2.7.). Even if RTA failed to fully resolve the affiliation of all 38 genera of *incertae sedis* status (see Tab. 5), of which 31 were not treated in the present analysis, then RTA should at least reveal the closest neighbours of these taxa. Many other

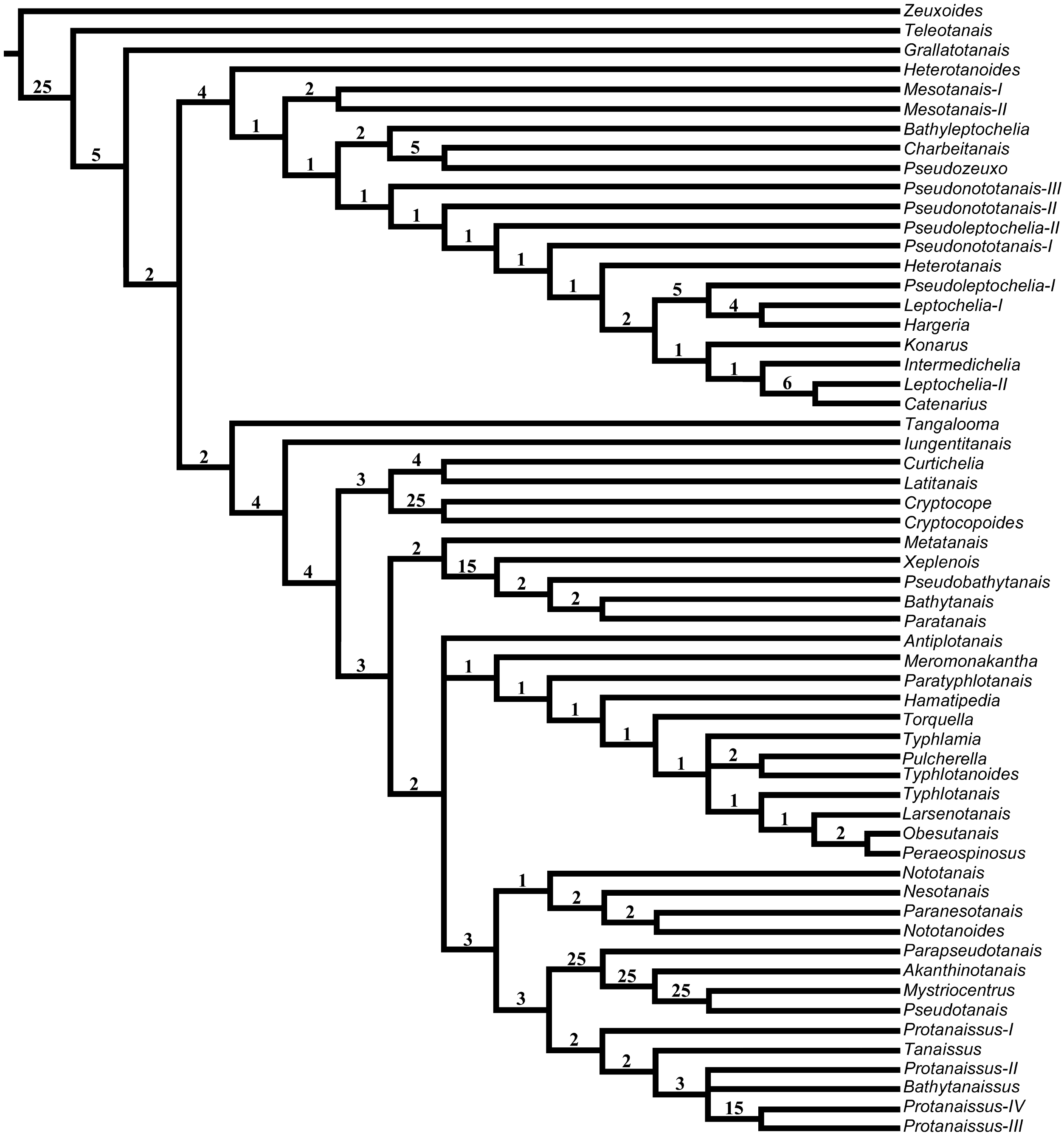

Fig. 1. Strict consensus of four trees resulting from analysis of the matrix in Tab. 2. Bremer support values are shown adjacent to the branches.

doubtfully assigned genera in the Colletteidae and other apomorphic (or 'repository') families could also be classified with more confidence, although it is probable that a residue of 'transitional' taxa will remain.

5. Systematics

The following classification provides details of three new, or recently defined, families derived from the present analysis as well as partially redefining and rediagnosing the other relevant families, whether affected by changes or not.

Teleotanaidae Bamber, 2008

Diagnosis, female. Eyes present. Circumplumose setae on epimera of pleonites 1–4. Antennula with four articles. Antenna with six articles, article-3 much longer than article-2, without robust dorsal setae. Molar process broad with heavy chitinized grinding surface.

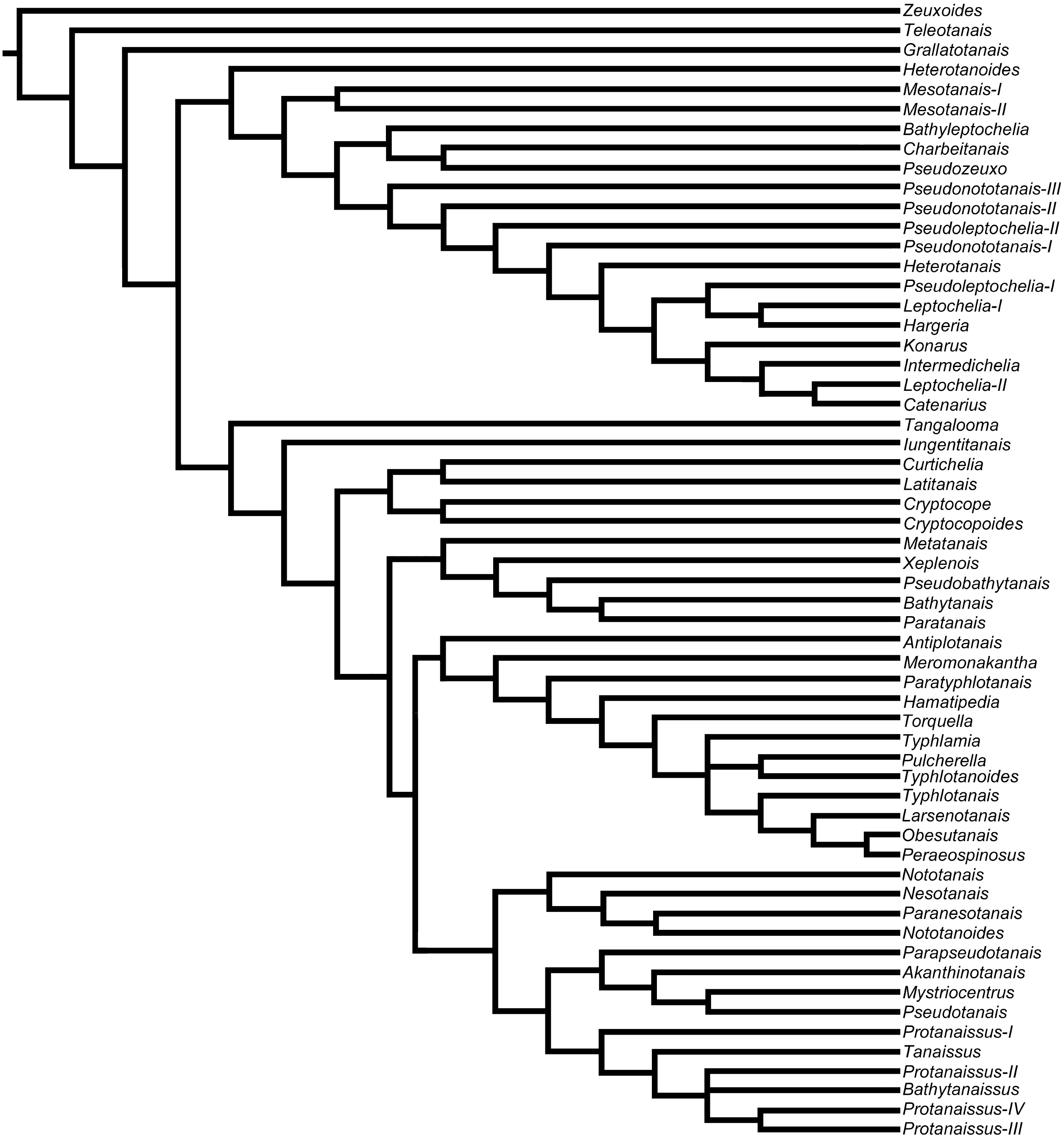

Fig. 2. One of four most parsimonious trees derived from T.N.T. analysis.

Labium with two pair of lobes. Maxillula endite with stout terminal spines. Maxilliped basis fused; endites not fused, narrower than basis, with pair of pointed spines and large lateral seta. Cheliped attachment via dorsally-inserted triangular sclerite. Marsupium with four pairs of oostegites. Pereopod 1–3 coxae present. Pereopod 4–6 coxae and clinging apparatus absent; propodus with three or more dorsodistal setae; dactylus and unguis claw-like. Pleopods well developed; basis with seta; endopod with one or two inner setae Uropod endopod with two articles; exopod with two articles.

Diagnosis, male. Unknown.

Genera included. *Teleotanais* Lang, 1956.

Remarks. Authority to this family has to be given to Bamber (2008) according to the International Code of Zoological Nomenclature, article 34. It is exclusively found in shallow water and seems to favor euryhaline habitats (Sieg & Heard 1983).

Tab. 5. Paratanaoidean genera currently without family designation as listed by the Tanaidacea website (Anderson et al. 2007).

Genus	Authority
Akanthophoreus	Sieg, 1986
Allodaposia	Sieg, 1986
Andrognathia	Sieg, 1983
Androtanais	Sieg, 1976
Armatognathia	Kudinova-Pasternak, 1987
Armaturatanais	Larsen, 2005
Bifidia	Sieg & Zibrowius, 1988
Chauliopleona	Dojiri & Sieg, 1997
Coalecerotanais	Larsen, 2003
Curtichelia	Kudinova-Pasternak, 1987
Dimorphognathia	Sieg, 1986
Exspina	Lang, 1968
Grallatotanais	Gutu & Iliffe, 2001
Insociabilitanais	Larsen, 2005
Iungentitanais	Sieg, 1977
Latitanais	Kudinova-Pasternak, 1987
Leptognathioides	Bird & Holdich, 1984
Metatanais	Shiino, 1952
Mimicarhaphura	Sieg, 1986
Monstrotanais	Kudinova-Pasternak, 1981
Nototanoides	Sieg & Heard, 1985
Parafilitanais	Kudinova-Pasternak, 1989
Paraiungentitanais	Sieg, 1977
Paraleptognathia	Kudinova-Pasternak, 1981
Pseudoarthrura	Larsen, 2005
Pseudomacrinella	Kudinova-Pasternak, 1990
Pseudoparatanais	Lang, 1973
Robustochelia	Kudinova-Pasternak, 1983
Robustognathia	Kudinova-Pasternak, 1989
Safaritanais	Kudinova-Pasternak, 1987
Salemia	Lang, 1971
Scoloura	Sieg & Dojiri, 1997
Singula	Błażewicz-Paszkowycz, 2005
Spinitanaopsis	(Larsen, 2003)
Stenotanais	Bird & Holdich, 1984
Tanabnormia	Gutu, 1986
Tanaopsis	G.O. Sars, 1896
Tangalooma	Bamber, 2008

Leptocheliidae *sensu* Lang, 1973

Diagnosis, female. Carapace with visible plates present (e.g. *Konarus*) or absent. Pereonites 1–3 not reduced. Pleon with five free pleonites. Antennula with three to four principal articles; minute terminal article often present in addition. Antenna with six articles, article-3 (and often article-2) with dorsal spine or apophysis. Molar process broad and with a heavily chitinized grinding surface. Labium with two pairs of lobes. Maxilliped basis and endites not fused; endites narrower than basis and with two to five (commonly three) flat or pointed spines and a large lateral seta. Cheliped attachment via dorsally-inserted triangular sclerite. Marsupium with four pairs of oostegites. Pereopods 1–3 coxa present. Pereopods 4–6 coxa absent; propodus with at least three dorsodistal setae; dactylus and unguis fused to a claw. Pleopods well developed; basal article with seta. Uropod endopod with three to six articles, exopod with one or two articles.

Diagnosis, male (where known)**.** Body shorter than in female. Eyes larger than in females. Antennula with more than four articles and flagellar articles with aesthetascs. Mouthparts reduced. Cheliped always significantly enlarged and elongated or with forcipate chela. Pleopods well developed.

Genera included. *Catenarius* Bamber, 2008; *Heterotanais* G.O. Sars, 1882; *Konarus* Bamber, 2006; *Leptochelia* Dana, 1849; *Pseudoleptochelia* Lang, 1973; *Pseudonototanais* Lang, 1973.

Remarks. It has been argued for inclusion into the family of the genera *Bathyleptochelia* Larsen, 2003; *Grallatotanais* Gutu & Iliffe, 2001; *Heterotanoides* Sieg, 1977; *Intermedichelia* Gutu, 1996; *Mesotanais* Dollfus, 1897; this could be justified here but, until a closer evaluation (including the many new leptocheliid species recently described by Bamber 2008) can be conducted these genera are excluded. The genus *Hargeria*, currently synonymised with *Leptochelia* s.str., is suppressed until future analyses prove this to be unsustainable.

Pseudozeuxidae Sieg, 1982

Diagnosis, female. Eyes present, Pereonites 1–3 not reduced. Pleon with five free but reduced pleonites. Antennula with three articles. Antenna with six articles, article-3 with one or two dorsal robust setae. Molar process broad. Labium with two pairs of lobes. Maxilliped basis and endites not fused endites narrower than basis, with two flat spines and large lateral seta. Cheliped basis attached via dorsally inserted triangular sclerite. Marsupium with four pairs of oostegites. Pereopod coxa present on pereopods 1–3 but absent on pereopods 4–6, pereopod 4–6 dactylus and unguis fused to a claw. Pleopods reduced to one vestigial pair on the first pleonite only; basis with seta. Uropod endopod with two articles although incomplete fusion may occur, exopod with two articles.

Diagnosis, male. Body not compressed but shorter than in female and with more elongate cephalothorax. Functional mouthparts retained.

Genera included. *Pseudozeuxo* Sieg, 1982; *Charbeitanais* Bamber & Bird, 1997.

Remarks. A correction to the drawing of the *Charbeitanais* pleopod (fig. 19E) in Bamber & Bird (1997) is required here: the most proximal seta is actually attached to the basal article, the single ramus bearing two setae; the annular structure (interpreted originally as the pleopod basis) is part of the pleon.

Cryptocopidae McLelland, 2008

Diagnosis (after McLelland 2008) (N.B. this largely distinguishes the taxon from the family Pseudotanaidae)**.** Eyelobes pigmented, rudimentary or absent. Pereon with six free pereonites none of which are reduced. Pleon with five free pleonites. Antennula with four articles. Antenna with six articles, second and third articles with simple setae. Mandible molar broad or narrow, with or without terminal ring of setae. Maxillula palp with two terminal setae and endite with five to ten spiniform setae. Maxilla rudimentary. Maxilliped bases completely or partially fused. Maxilliped endites completely unfused; with simple setae, cusps, or naked. Cheliped attached to carapace via a sclerite. Chelae not forcipate. Cheliped carpus with one or two inferior setae. Cheliped propodus less than 1.5 times longer than the carpus. Cheliped fixed finger with one or two inferior setae. Cheliped dactylus seta present or absent. Marsupium formed by one or possibly four pairs of oostegites*. Pereopods 4–6 merus with two setae and without fusion of dactylus and unguis to form a claw. Pleopods well developed, with terminal setae only, or rudimentary without setae. Uropod exopods with one or two articles. Uropod endopods with two articles. [*Currently, no species in the Cryptocopidae is known with certainty to have a marsupium consisting of one pair of oostegites.]

Subfamily: Cryptocopinae (Sieg, 1976)
Genera included: *Cryptocope* G.O. Sars, 1882.

Subfamily: Cryptocopoidinae McLelland, 2008
Genera included: *Cryptocopoides* Sieg, 1976.

Subfamily: Iungentitanainae McLelland, 2008
(see remarks)
Genera included: *Curtichelia* Kudinova-Pasternak, 1987; *Iungentitanais* Sieg, 1977; *Latitanais* Kudinova-Pasternak, 1987; *Paraiungentitanais* Sieg, 1977.

Paratanaidae Lang, 1949

Diagnosis, female. Plates apparent in carapace. Eyes present. Pereonites 1–3 not reduced. Pleonites 1–5 with circumplumose epimeral setae. Antennula with four articles and additional minute terminal article often only visible in SEM (Larsen 2000). Antenna with six articles, article three with dorsal spiniform setae, or with ventral apophysis. Mandible molar broad, with heavily chitinised grinding surface. Labium with one pair of lobes. Maxilliped basis partly fused and endites not fused endites broader than basis and with two flat setae, without lateral seta. Cheliped attachment via dorsally-inserted triangular sclerite. Marsupium with four pairs of oostegites. Pereopod 1–3 with coxa. Pereopod 4–6 without coxa; carpus with clinging apparatus present as strong spines (complex or not) but without microtrichial field; propodus with one (P4–5) or at least three (P6) strong setae; dactylus and unguis fused to a claw. Uropod endopod with two articles although incomplete fusion may occur, exopod with one or two articles.

Diagnosis, male (only known of *Paratanais*)**.** Body laterally compressed and significantly shorter than in female. Pereonites shorter and pleonites more developed than in female. Eyes large (> 20% of carapace). Antennula with more than seven articles, flagellar articles densely packed with aesthetascs. Mouthparts reduced. Pereopods without clinging apparatus. Pleopods well developed with plumose setae longer than on female.

Genera included. *Bathytanais* Beddard, 1886; *Pseudobathytanais* Kudinova-Pasternak, 1991; *Paratanais* Dana, 1852; *Xeplenois* Bamber, 2005.

Typhlotanaidae Sieg, 1984

Diagnosis. Eyes or eyelobes lacking. Antennula with three articles. Antenna with six articles. Mandible molar broad, nodulose. Maxilliped endite distal margin (usually) with two non-articulated processes or cusps. Cheliped basis attached dorsoposteriorly, with small sclerite. Marsupium of four pairs of oostegites. Pereopods 1–3 with coxa. Pereopods 4–6 without coxa; carpus often with clinging apparatus of microtrichial field (with or without prickly tubercle) and/or hooks; propodus with one (pereopod 4–5) or three (pereopod 6) dorsodistal setae; dactylus and unguis either fused or not fused but claw-like. Uropod rami with one or two articles.

Diagnosis male (where known)**.** Body laterally compressed, more so at mid-length, shorter than in female. Pereonites wider than long. Pleonites strongly developed. Antennula with more than five articles and many aesthetascs. Mouthparts reduced. Pereopods without clinging apparatus.

Genera included. *Hamatipeda* Błażewicz-Paszkowycz, 2007; *Larsenotanais* Błażewicz-Paszkowycz, 2007; *Meromonakantha* Sieg, 1986; *Obesutanais* Larsen et al., 2006; *Paratyphlotanais* Kudinova-Pasternak & Pasternak, 1978; *Peraeospinosus* Sieg, 1986; *Pulcherella* Błażewicz-Paszkowycz, 2007; *Torquella* Błażewicz-Paszkowycz, 2007; *Typhlamia* Błażewicz-Paszkowycz, 2007; *Typhlotanais* G.O. Sars, 1882; *Typhlotanoides* Sieg, 1983.

Remarks. The diagnosis of Typhlotanaidae (Błażewicz-Paszkowycz 2007) states that the family is lacking the cheliped sclerite (side piece), but this structure was present (albeit small) in all typhlotanaid taxa examined during this study.

Nototanaidae Sieg, 1976 s.str.

Diagnosis, female. Carapace with anterior narrowing. Eyes present. Pereonites 1–3 not reduced. Antennula with three articles. Antenna with six articles, article-3 with robust dorsal setae. Mandible molar broad, with heavy chitinized grinding surface. Labium with one pair of lobes. Maxilliped basis at least partially fused; endites not fused, narrower than basis, flared with or without medial setae and cusps/spines, without large lateral seta. Cheliped attachment via sclerite or basis with suture ('pseudocoxa'; *Nesotanais*). Marsupium of four pairs of oostegites. Pereopods 1–3 coxae present. Pereopods 4–6 coxae and clinging apparatus absent; propodus with one (P4–5) or at least three (P6) dorsodistal setae; dactylus and unguis fused to a claw. Pleopods well developed. Uropod endopod with two articles; exopod with one or two articles.
Diagnosis, male. Body often shorter than that of female but never laterally compressed. Cephalothorax usually more elongate and narrower anteriorly. Antennula with more than five articles and multiple aesthetascs on flagellar articles. Mouthparts reduced. Pleopods well developed. Uropod endopod with two or three articles.
Genera included. *Nesotanais* Shiino, 1978; *Nototanais* Richardson, 1906; *Nototanoides* Sieg & Heard, 1985; *Paranesotanais* Larsen & Shimomura, 2007.

Pseudotanaidae Sieg, 1976 s.str.

Diagnosis, female. Eyes absent, present or eyelobes only. Pereonites 1–3 reduced, short compared to width. Antennula with three articles. Antenna with six articles; articles 2–3 with or without broad-based spine. Mandibular molar acuminate or broad and spinose (piercing type); left mandible incisor/lacinia mobilis broad and pointed in an anterior direction. Labium with one pair of lobes. Maxilliped basis fused; endites fused or partly fused, flared, with or without pair of rounded spiniform processes, no lateral seta. Cheliped basis attached posterodorsally, via sclerite. Marsupium with only one pair of oostegites. Pereopod coxa present on all pereopods. Pereopods 4–6 carpus with or without blade-like ventral spine, without clinging apparatus; propodus with one (P4–5) dorsodistal long/strong modified seta, or two setae (P6); dactylus and unguis either fused or not but unguis always reduced, claw-like. Pleopods well developed, without basal seta and with terminal setae, or absent. Uropod endopod with two articles, exopod with one or two articles.
Diagnosis, male (only known from *Pseudotanais*)**.** Carapace shorter than in females. Antennula with six to seven articles and several aesthetascs. Cheliped only moderately larger than in female. Pleopod plumose setae generally longer than in female.
Genera included. *Akanthinotanais* Sieg, 1977; *Mystriocentrus* Bird & Holdich, 1989; *Parapseudotanais* Bird & Holdich, 1989; *Pseudotanais* G.O. Sars, 1882.

Tanaissuidae fam. nov.

Diagnosis, female. Cephalothorax narrower anteriorly. Pereonites 1–3 not reduced. Antennula with three articles. Eyes absent or present (*Protanaissus* in part). Mandibular molar acuminate or not but never 'crushing' ('piercing' type, *Protanaissus* in part); left mandible incisor/lacinia mobilis broad and pointed in an anterior direction. Maxilliped basis fused; endites fused (*Tanaissus*) or unfused, without tooth-like spines or lateral seta; highly flared or narrow (*Protanaissus*). Pereopods 4–6 with one (P4–5) or two (P6) long, thickened dorsodistal setae (*Bathytanaissus* with one P6 seta). Uropod with two endopod articles.
Diagnosis male (based only on *Tanaissus*; see Bird 2002)**.** Pereon and pleon generally more elongate than in female (or with extreme elongation of pereonites 2–4). Cephalothorax with more pronounced anterior narrowing. Antennula with two or three-articled peduncle and four or five articled flagellum (bearing aesthetascs). Mouthparts reduced, usually to rudimentary maxilliped. Cheliped more elongate than in female, with complex incisive margin on fixed finger.
Genera included. *Bathytanaissus* Bird & Holdich, 1989; *Protanaissus* Sieg, 1982; *Tanaissus* Norman & Scott, 1906.

Incertae sedis

Genera included. *Antiplotanais* Bamber, 2008; *Bathyleptochelia* Larsen, 2003; *Grallatotanais* Gutu & Iliffe, 2001; *Heterotanoides* Sieg, 1977; *Intermedichelia* Gutu, 1996; *Metatanais* Shiino, 1952; *Tangalooma* Bamber, 2008.

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