

Stylophoran supertrees revisited

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Supertree analysis is a recent exploratory method that involves the simultaneous combination of two or more character-based source trees into a single consensus supertree. This method was recently applied by Ruta to a fossil group of enigmatic Palaeozoic forms, the stylophoran echinoderms. Ruta's supertree suggested that mitrates are polyphyletic and originated from paraphyletic cornutes. Re-examination of Ruta's data matrix strongly suggests that most source trees were based on dubious homologies resulting from theory-laden assumptions (calcichordate model) or superficial similarities (ankyroid scenario). A new supertree analysis was performed using a slightly corrected version of Ruta's original combined matrix; the 70% majority-rule consensus of 24,168 most parsimonious supertrees suggests that mitrates are monophyletic and derived from paraphyletic cornutes. A second new supertree analysis was generated to test the influence of the pruning of three taxa in some calcichordate source trees; the 70% majority-rule consensus of 3,720 shortest supertrees indicates that both cornutes and mitrates are monophyletic and derived from a *Ceratocystis*-like ancestor. The two new supertree analyses demonstrate the dramatic influence of the relative contributions of each initial assumption of plate homologies (and underlying anatomical interpretations), in original source trees, on the final topology of supertrees.

Key words: Echinodermata, Stylophora, Cornuta, Mitrata, Ankyroida, Calcichordata, supertree, Palaeozoic.

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Introduction

Supertree construction is a recent, valuable, exploratory tool for studies of large-scale macroevolutionary patterns. Supertrees combine the information contained in a set of smaller, less inclusive, character-based source trees (Bininda-Emonds and Sanderson 2001; Goloboff and Pol 2002; Pisani and Wilkinson 2002). The most widely used technique for supertree construction is the Matrix Representation with Parsimony (MRP), independently developed by Baum (1992) and Ragan (1992). This technique consists of the transformation of each source tree into a matrix representation (MR), reflecting both the original topology of the tree and group membership of included taxa (Baum 1992; Ragan 1992; Baum and Ragan 1993; Bininda-Emonds et al. 2002; Pisani and Wilkinson 2002; Pisani et al. 2002). Matrix elements are binary characters indicating for each node of each source tree, whether a given taxon is a member of the clade (coded as "1") or not (coded as "0"). Matrix representations of multiple source trees with non-identical taxon sets can be combined in a global "combined matrix", with missing entries (taxa absent in one or several source trees) scored as "?" (Pisani and Wilkinson 2002). Parsimony analysis of the combined matrix yields one or more most parsimonious trees: the MRP supertrees or component-coding supertrees (Pisani and Wilkinson 2002; Pisani et al. 2002). Ultimately, when several MRP supertrees are obtained, they can be processed using the consensus method to produce an MRP consensus supertree, which synthesises the information contained in each individual source tree. Consequently, MRP supertrees represent a relatively new, popular, and powerful tool for reconstructing large-scale phylogenies from multiple,

disparate, character-derived trees (Purvis 1995; Bininda-Emonds et al. 1999; Purvis and Webster 1999; Liu et al. 2001; Pisani and Wilkinson 2002). Recently, supertree reconstruction was also presented as one possible approach to reconstructing phylogenies of problematic clades, such as trypanosomatid protozoans (Stothard 2000) and stylophoran echinoderms (Ruta 2003).

Stylophorans are a class of relatively small, enigmatic, marine calcite-plated fossils, exclusively known from the Middle Cambrian to the upper Carboniferous (Ubaghs 1967; Derstler 1979; Kolata et al. 1991; Domínguez et al. 2002). All share the same basic organisation, with a delicate, tripartite appendage, inserted in a massive, flattened, asymmetrical theca (Fig. 1). Both the appendage and the theca are made of numerous skeletal elements, each consisting of a single crystal of calcite, showing the typical microstructure (stereom) of echinoderm plates (Ubaghs 1967; Smith 1990; Cripps 1991). Consequently, stylophorans exhibit some clear echinoderm-like features. However, they also lack other characters generally considered as apomorphies of the phylum (e.g., pentamerous radial symmetry). Their unusual morphology is at the heart of a long-lasting controversy concerning the interpretation of the appendage, and their systematic position within deuterostomes (e.g., Ubaghs 1961, 1967, 1981; Jefferies 1967, 1981, 1986; Philip 1979; Chauvel 1981; Kolata and Jollie 1982; Cripps 1991; Kolata et al. 1991; Ruta 1999a; David et al. 2000; Lefebvre 2000a, 2001, 2003a). The appendage was first interpreted as a pelmatozoan stem, and stylophorans were considered as primitive, aberrant echinoderms (Barrande 1887; Jaekel 1901; Bather 1913; Chauvel 1941; Caster 1952; Philip 1979; Kolata et al. 1991; Smith 2004). Later, the ap-

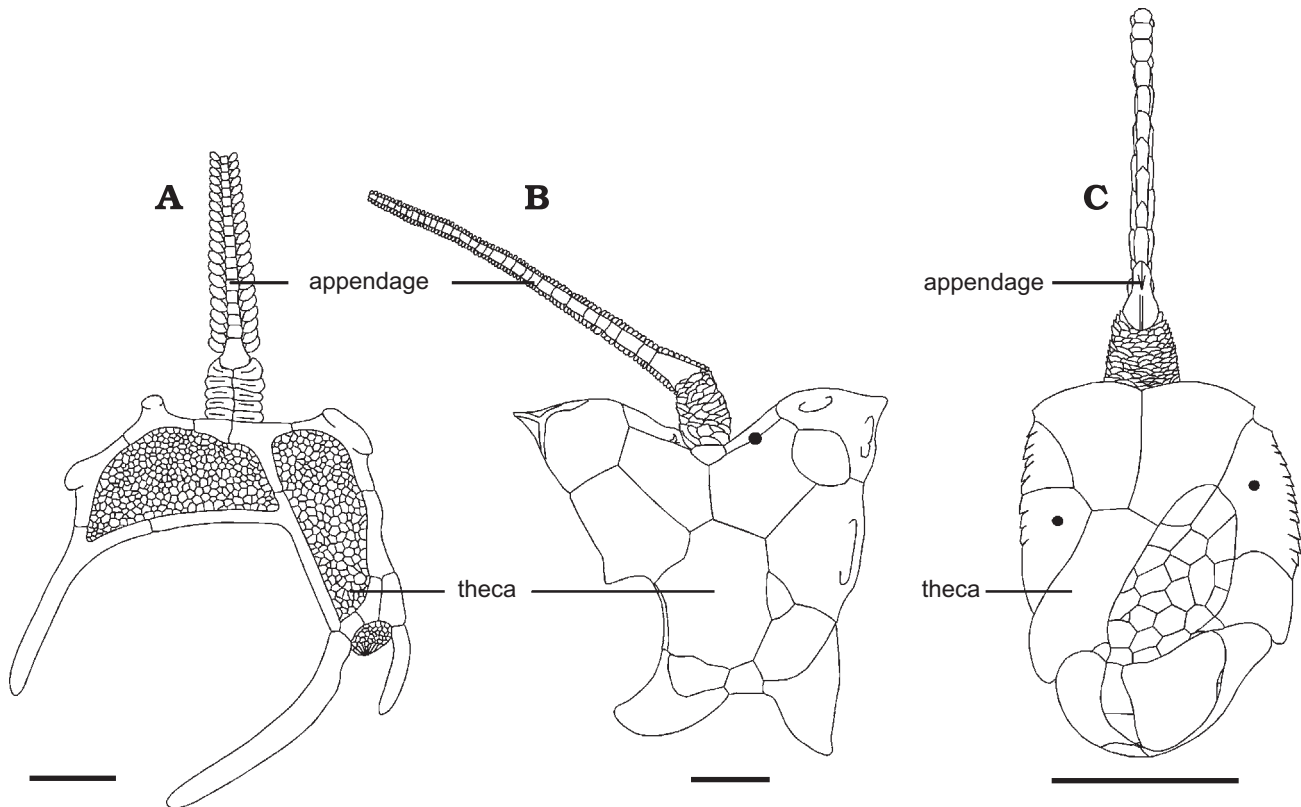


Fig. 1. Morphology of stylophorans; all reconstructions in lower aspect. **A.** The cornute *Cothurnocystis elizae* (Upper Ordovician, Scotland); redrawn and modified from Ubaghs (1967). **B.** The primitive stylophoran *Ceratocystis perneri* (Middle Cambrian, Bohemia); redrawn from Ubaghs (1967). **C.** The mitrate *Chinianocarpus thorali* (Lower Ordovician, Montagne Noire, France); redrawn from Jefferies (1986). Scale bars 5 mm.

pendage was compared to a chordate tail, and stylophorans were interpreted as echinoderm-like, but primarily primitive chordates, the “calcichordates” (Gislen 1930; Jefferies 1967, 1986; Cripps 1991; Daley 1992; Ruta and Theron 1997; Domínguez et al. 2002). More recently, the appendage was interpreted as equivalent to an ophiuroid or crinoid feeding arm, and stylophorans were considered either as relatively primitive (Ubaghs 1961, 1967; Nichols 1972; Parsley 1988), or highly derived echinoderms (Sumrall 1997; Dzik 1999; David et al. 2000). The systematic position of stylophorans within deuterostomes is beyond the scope of Ruta’s supertree and of this paper, both of which focus on phylogenetic relationships within stylophorans. However, the three contrasting interpretations have important consequences for anatomical reconstructions, and for assumptions when determining plate homologies within stylophorans.

The class Stylophora is traditionally subdivided into the two orders Cornuta and Mitrata (Gill and Caster 1960; Ubaghs 1967; Jefferies 1967; Parsley 1988; Cripps 1991; Ruta 1999a; Lefebvre 2001; Martí Mus 2002). Cornutes (Fig. 1A) are usually characterised by relatively rigid appendages, and asymmetrical thecae delimited by a narrow frame of delicate marginal elements (Ubaghs 1967; Parsley 1988; Lefebvre 2001; Martí Mus 2002). In contrast, mitrates (Fig. 1C) possessed a highly flexible appendage and more symmetrical thecae, comprised of larger, more massive marginals (Ubaghs 1967; Pars-

ley 1988; Lefebvre 2001). Cornutes and mitrates have long been considered as monophyletic groups of unknown affinities to each other (Jaekel 1918; Chauvel 1941; Caster 1952), or as sharing an unknown ancestor (Gill and Caster 1960; Ubaghs 1967, 1969). An alternative scenario, with mitrates deriving from paraphyletic cornutes, was proposed by Jefferies (1967, 1969). This phylogenetic hypothesis was essentially motivated by theoretical requirements of the “calcichordate model”, such as the assumption of putative soft parts inside the thecae of both cornutes and mitrates (Jefferies 1967, 1981, 1986). Similar theoretical premises obligated calcichordate workers to ignore clearly evident homologies within stylophorans, such as the very similar appendages of cornutes and mitrates, or their comparable plano-concave thecal surfaces (see Philip 1979; Ubaghs 1981; Chauvel 1981; Kolata et al. 1991; Parsley 1991, 1997, 1998; Lefebvre et al. 1998; Ruta 1999a; David et al. 2000; Lefebvre 2000a, 2001, 2003a, b). However, most authors initially followed Jefferies’ suggestion, and considered mitrates to have originated from nearly symmetrical cornutes close to *Phyllocystis* (Jefferies 1969), *Reticulocarpus* (Jefferies and Prokop 1972; Ubaghs 1975), *Amygdalotheca* (Derstler 1979), *Domfrontia* (Cripps 1988), *Prokopicystis* (Cripps 1989a, b, 1991; Daley 1992; Woods and Jefferies 1992; Cripps and Daley 1994), or *Nanocarpus* (Ubaghs 1991). In the only, large-scale, comprehensive cladistic analysis of stylophorans, Parsley (1997, 1998) sug-

gested that mitrates were polyphyletic, having derived from various groups of paraphyletic cornutes (see also Derstler 1979). Consequently, Parsley (1997, 1998) proposed to unify all mitrates and symmetrical cornutes within the monophyletic group Ankyroida, and to abolish the order Mitrata (see Ruta 1999b; Sumrall and Sprinkle 1999; Parsley 2000; Parsley et al. 2000). However, the monophyly of ankyroids was seriously questioned by Lefebvre (2001), who produced a critical review of Parsley's data matrix based on a detailed discussion on plate homologies. Finally, several recent cladistic analyses supported the monophyly of both cornutes and mitrates, and suggested that these two clades derived from a *Ceratocystis*-like ancestor (Lefebvre and Vizcaïno 1999; Lefebvre 2000b, 2001). *Ceratocystis perneri* (Fig. 1B), from the Middle Cambrian of Bohemia, is one of the oldest and most primitive known stylophorans. In this context, Ruta (2003) performed a species-level supertree analysis of stylophorans to investigate internal relationships within the class. Ruta (2003: 560) claimed that the supertree method could provide a "novel hypothesis that is independent of any assumption of skeletal plate homology, as well as of any anatomical orientation and systematic position of the group".

The aim of this paper is to show that the supertree analysis performed by Ruta (2003) cannot be independent of assumptions of skeletal plate homology, and is necessarily biased by underlying considerations on anatomical orientation and systematic position of the class.

Supertrees

Supertrees are consensus trees and, consequently, they favour groups (and topologies) that occur in most of the trees, even if contradicted by a few source trees (Goloboff and Pol 2002; Pisani and Wilkinson 2002). The underlying idea is that a group that is present in a large number of analyses is better supported than one that is seldom observed (but see Sumrall et al. 2001). In Ruta's analysis (2003), the majority of source trees (14 on 23, representing 52.9% of matrix elements) were produced by calcichordate workers. Other source trees were performed following either an echinoderm (7 trees on 23; 36.3% of matrix elements), or a "neutral" (neither calcichordate nor echinoderm) interpretation (2 trees on 23; 10.8% of matrix elements). Consequently, the resulting consensus supertree was inevitably strongly influenced by the most numerous source trees (and matrix elements), and reflected mostly phylogenetic analyses and the assumptions of calcichordate workers. In successive contributions of calcichordate workers, thecal plate homologies were relatively well-identified within each stylophoran order, but theoretical requirements of the model followed (e.g., homology of the plano-concave thecal surface of cornutes with the convex thecal surface of mitrates) prevented these authors to identify interordinal plate homologies (see Kolata et al. 1991; Lefebvre et al. 1998; Ruta 1999a; Lefebvre 2000a, 2001, 2003a; Martí Mus 2002). As a consequence, all calci-

chordate source trees including both cornutes and mitrates are based on a biased scheme of thecal plate homologies, resulting more from theory-laden considerations than from direct and descriptive anatomical comparisons (9 trees on 23; 40.9% of matrix elements).

Another consequence of the presence of a majority of calcichordate source trees is that their implied topology, with mitrates deriving from paraphyletic cornutes, will strongly affect the resulting topology of Ruta's consensus supertree (2003). In the calcichordate scenario, mitrates must derive from paraphyletic cornutes, not because of the observation of transitional forms, but because of the obligatory reconstruction of hypothetical "soft parts" inside the stylophoran theca (see Jefferies 1967, 1981, 1986; Jefferies and Lewis 1978; Cripps 1991; Cripps and Daley 1994). As pointed out by Cripps (1991: 345): "[...] a consequence of this procedure is that it denied *a priori* the possibility of cornute monophyly." Paraphyly of cornutes is also strongly supported in the two "ankyroid" source trees based on the phylogenetic analysis of Parsley (1997). Consequently, in Ruta's analysis (2003), most source trees support the paraphyly of cornutes (11 trees on 23, representing 60.4% of matrix elements), several source trees are "neutral" (focusing only on cornutes or on mitrates; 9 trees on 23; 30.6% of matrix elements), and very few support the monophyly of both cornutes and mitrates (3 trees on 23; 9% of matrix elements). Hence, the original source trees available for supertree construction by Ruta (2003) were strongly dominated by scenarios supporting the paraphyly of cornutes. This bias was artificially strengthened by Ruta (2003), who re-analysed using PAUP three large data sets, all supporting the paraphyly of cornutes, but originally processed with a different program (Cripps 1991; Daley 1992; Parsley 1997). In Ruta's supertree construction (2003), the topologies of these three source original trees, as well as their very similar new PAUP versions, were both included in the combined matrix.

Problems with MRD supertrees have been pointed out several times, and concern mostly differences in size, shape (topology), and overlap between the different source trees (Purvis 1995; Bininda-Emonds and Bryant 1998; Bininda-Emonds et al. 1999; Bininda-Emonds and Sanderson 2001; Goloboff and Pol 2002; Pisani and Wilkinson 2002). Simulations suggest that biases induced by differences in size and shape between source trees would apparently be negligible compared to those due to a weak overlap between source data (Bininda-Emonds and Sanderson 2001; Goloboff and Pol 2002). However, simulations also suggest that accuracy of supertrees could be greatly enhanced by the inclusion of one relatively large and comprehensive source study (Bininda-Emonds and Sanderson 2001). Stylophoran source trees used by Ruta (2003) are largely non-overlapping, most of them focusing exclusively on cornutes (e.g., Jefferies et al. 1987; Cripps 1991; Daley 1992; Cripps and Daley 1994; Martí Mus 2002), or on mitrocystitid mitrates (e.g., Cripps 1990; Beisswenger 1994; Ruta and Theron 1997; Ruta and Jell 1999; Ruta 1999c; Lefebvre 2000b). Consequently, the phylogenetic analysis of Parsley (1997), which provides one relatively com-

plete, large source tree including most stylophoran taxa (42 species on the 78 used in the supertree), certainly played a key role in the final topology of the supertree. However, as pointed out by Lefebvre (2001; see also comments in Ruta 1999b), the phylogenetic analysis of Parsley (1997) relies more on superficial similarities (symmetrical or asymmetrical aspects of thecae, number and/or function of some skeletal elements), rather than on rigorously established plate homologies. Consequently, the resulting tree of Parsley (1997) represents more a kind of phenogram (taxa grouped following similarities in shape), than an actual cladogram (groupings based on shared derived characters).

Most source trees included in Ruta's supertree (2003) were based on dubious and/or disputable plate homologies (ankyroid and calcichordate scenarios) supporting the same phylogenetic scenario (mitrates deriving from paraphyletic cornutes). The supertree being a consensus of the information included in the various source trees, the results obtained by Ruta (2003) are thus hardly surprising. The global topology of Ruta's consensus supertree (2003: fig. 2) is strongly influenced by the single comprehensive analysis of stylophorans (Parsley 1997; 2 trees on 23; 19.5% of matrix elements): (1) mitrates are polyphyletic and derive from paraphyletic cornutes; (2) *Chinianocarpos* is more closely related to peltocystids than to mitrocystitids; (3) peltocystids derive from a *Beryllia*-like cornute; (4) *Lagynocystis* is a derived anomalocystitid, closely related to *Diamphidiocystis*; and (5) mitrocystitids derive from a *Nanocarpus*-like cornute. Intra-ordinal relationships are more influenced by some smaller comprehensive studies focusing either on cornutes, or on mitrates. For example, the sister-group relationship between chauvelicystine and phyllocystine cornutes reflects the extensive works of calcichordate workers (Cripps 1988, 1991; Daley 1992; Cripps and Daley 1994). Monophyly of scotiaecystine cornutes is supported by several source trees (Cripps 1988, 1991; Daley 1992; Parsley 1997; Martí Mus 2002). Finally, the topology of anomalocystitid mitrates in the supertree of Ruta (2003) largely reflects the single comprehensive phylogenetic analysis focusing on this group (Ruta 1999c; see also Ruta and Jell 1999).

The basic assumption of supertree reconstruction (a group present in a large number of analyses is better supported than one that is seldom observed) is probably not correct in the case of stylophorans (see also discussion in Sumrall et al. 2001). The resulting topology, with mitrates deriving from paraphyletic cornutes, is based both on a theory-laden scenario ignoring thecal plate homologies between the two orders (calcichordate theory), and on the single comprehensive study of the group, focusing more on superficial similarities, rather than on homologies (Parsley 1997). Two consensus supertrees will be elaborated below, so as to demonstrate that the one produced by Ruta (2003) is strongly biased by initial assumptions about skeletal plate homologies, and by underlying theories on the anatomy and systematic position of stylophorans (chordates or echinoderms). The first supertree corresponds to a slightly modified version of Ruta's original one (2003). The main dif-

ferences stem only from the correction of some mistakes in the original data set, a few changes in source trees, and the suppression of reprocessed versions (using PAUP) of the three analyses reported twice in Ruta's combined matrix (Cripps 1991; Daley 1992; Parsley 1997). The second supertree is constructed using the same source data as the first, with one significant difference. In most calcichordate source trees, the order Mitrata was placed arbitrarily as a terminal operational unit, so as to determine derived character states (Jefferies et al. 1987; Cripps 1988, 1989b, 1991; Daley 1992; Cripps and Daley 1994). For the construction of his supertree, Ruta (2003) replaced the group Mitrata by the basalmost members of the three main mitrate suborders: *Chinianocarpos thorali* (mitrocystitids), *Lagynocystis pyramilis* (lagynocystids), and *Peltocystis cornuta* (peltocystids). The choice of these three taxa can be disputed (*Chinianocarpos* is a basal peltocystid following the phylogenetic analysis of Parsley 1997), and, more importantly, brings strong support to the calcichordate scenario, implying that mitrates derived *a priori* from paraphyletic cornutes (see Cripps 1991). In the construction of the second supertree, designed to test tree topologies actually based on observation and not on theoretical assumptions, the three mitrates *Chinianocarpos*, *Lagynocystis*, and *Peltocystis* were pruned from all calcichordate source trees focusing on cornutes.

Materials and methods.—The original combined matrix of Ruta (2003), available at <http://www.app.pan.pl/acta48/app.559-matrix.rtf>, was downloaded and matrix representations of each source tree were checked. Each source tree was replotted using PAUP from its matrix representation, and both its topology and included taxa were compared with those of the corresponding original analysis. Very few mistakes and/or problems were detected during the comparison of the original trees with their matrix representations. For example, the cornute *Ponticulocarpus robisoni*, which is mentioned as "Spence Shale cornute" (see Sumrall and Sprinkle 1999) in the original analysis of Parsley (1997), was not scored in the two corresponding matrix representations of Ruta (2003). Other differences concern the matrix representation of the unpublished analysis of Lee et al. (in press), which includes *Anatifopsis barrandei*, a new peltocystidan, and *Cothurnocystis elizae*, instead of *A. trapeziiformis*, *A. cocaban*, and *C. fellinensis*, respectively (see also Lefebvre et al. 2005). Almost all tree topologies reconstructed from matrix representations were found to be equivalent to the original ones, with the exception of the MR corresponding to the analysis of Cripps (1989a). Topology and included taxa for this matrix representation do not match any of the various trees produced by Cripps (1989a: fig. 23, 1989b: fig. 25). Consequently, this matrix representation was deleted from the combined matrix, and replaced by a new matrix representation elaborated from Cripps (1989b: fig. 25). The tree topology reconstructed from the matrix representation of the analysis of Ruta (1999c) is relatively close to, but definitely different from, any of his various original trees. In this case, differences probably result from the fact that Ruta

(2003) elaborated his matrix representation from an unpublished strict consensus tree of his analysis, rather than from any of his published trees, corresponding to the three most parsimonious solutions (Ruta 1999c: fig. 13, appendix 3), and to a 50% majority-rule consensus tree (Ruta 1999c: fig. 14a). Topologies derived from strict consensus trees were also preferred by Ruta (2003) to elaborate the matrix representations of the analyses performed by Cripps (1991) and Lefebvre (2001). Considering that all source trees included in Ruta's analysis (2003) were not necessarily strict consensus trees (e.g., Jefferies et al. 1987; Cripps 1990; Woods and Jefferies 1992; Beisswenger 1994; Ruta and Theron 1997; Lefebvre and Vizcaïno 1999), the matrix representations of the strict consensus trees of Cripps (1991) and Lefebvre (2001) were replaced in the combined matrix by the original, more informative corresponding trees figured by Cripps (1991: fig. 15; tree resulting from the successive weighting procedure), and Lefebvre (2001: fig. 22; 50% majority-rule consensus tree). Finally, so as to avoid redundant information, matrix elements corresponding to the analyses of Cripps (1991), Daley (1992), and Parsley (1997), re-generated by Ruta (2003), were deleted. Only matrix representations corresponding to original source trees have been preserved in the combined matrix.

The resulting combined matrix (A) comprises 78 stylophoran species (one more than in Ruta's (2003) original data set: *Anatifopsis trapeziiformis*), scored for 319 matrix elements (including 20 uninformative characters). The combined matrix A synthesises the information extracted from 20 original source trees, including 8 analyses (51.5% of informative matrix elements) supporting the paraphyly of cornutes (Jefferies et al. 1987: fig. 26; Cripps 1988: figs. 16, 17; Cripps 1989b: fig. 25; Cripps 1991: fig. 15; Daley 1992: fig. 15; Woods and Jefferies 1992: fig. 12; Cripps and Daley 1994: fig. 12; Parsley 1997: fig. 6), and three source data trees (13.4% of informative matrix elements) in favour of the monophyly of cornutes (Lefebvre and Vizcaïno 1999: fig. 27; Lefebvre 2000b: fig. 12; Lefebvre 2001: fig. 22). Several source trees are "neutral" (9 trees on 20; 35.1% of matrix elements), and focus exclusively on phylogenetic relationships within cornutes (Cripps and Daley 1994: fig. 16; Martí Mus 2002: fig. 11), or within mitrates (Cripps 1990: figs. 20, 22; Beisswenger 1994: fig. 9; Ruta 1997: fig. 9; Ruta and Theron 1997: figs. 23–25; Ruta and Jell 1999: fig. 15; Ruta 1999c: unpublished strict consensus tree; Lee et al. in press). A first parsimony analysis was performed using PAUP* (Swofford 2002) on combined matrix A. This matrix was exclusively based on original source trees available.

A second parsimony analysis was generated using a modified version of combined matrix A. Modifications concern the pruning of the three mitrate taxa *Chinianocarpus*, *Lagynocystis*, and *Peltocystis* in all calcichordate source analyses focusing on cornute phylogeny (see above). This deletion was made so as to eradicate the *a priori* paraphyly of this order, implied by the calcichordate model (Cripps 1991). The second combined matrix (B) comprises 78 stylophoran species, coded for 319 matrix elements (including 27 uninfor-

mative characters). In combined matrix B, "neutral" source trees are the most numerous (16 trees on 20; 71.3% of informative matrix characters), and focus exclusively on phylogenetic relationships within cornutes (Jefferies et al. 1987; Cripps 1988, 1989b, 1991; Daley 1992; Woods and Jefferies 1992; Cripps and Daley 1994; Martí Mus 2002) or within mitrates (Cripps 1990; Beisswenger 1994; Ruta 1997, 1999c; Ruta and Theron 1997; Ruta and Jell 1999; Lee et al. in press). Source data supporting either the paraphyly of cornutes (Parsley 1997), or their monophyly (Lefebvre and Vizcaïno 1999; Lefebvre 2000b, 2001) are represented by relatively comparable proportions of matrix elements in combined matrix B, 14.7% and 14% respectively. A second parsimony analysis was performed, using PAUP* (Swofford 2002) on combined matrix B.

Results and discussion.—Parsimony analysis of combined matrix A yielded 24,168 equally parsimonious shortest MRP supertrees at 403 steps (C.I. = 0.742, excluding uninformative characters; R.I. = 0.920; R.C. = 0.683). From these equally shortest solutions, a 70% majority-rule MRP consensus supertree A was derived (Fig. 2). Topology of the corresponding strict consensus tree is quite similar and is not illustrated here (it can be easily deduced by collapsing all more weakly supported nodes). A 70% majority-rule MRP consensus supertree is used here to express in more detail the results of the phylogenetic exploration. The main differences between the 70% majority-rule consensus supertree A and the strict consensus tree concern: (1) the possible monophyly of the clade uniting three derived cornutes (*Beryllia miranda*, *Lycocarpus courtessolei*, and *Reticulocarpus hanusi*); (2) within peltocystid mitrates, the possible monophyly of the clade (*Anatifopsis trapeziiformis* + *Balanocystites primus*); (3) the sister-group relationship between the cornute *Nanocarpus dolambii* and mitrates; and (4) the basal position of *Lagynocystis pyramidalis* within mitrates. Consequently, topology of consensus supertree A is relatively well-resolved (Fig. 2), and it is comparable in many respects to the consensus supertree generated by Ruta (2003: fig. 2). This topology results from the relatively similar combined matrices used in the two analyses. As in Ruta's analysis (2003), consensus supertree A shows mitrates deriving from paraphyletic cornutes. This first result is hardly surprising, given the large proportion of matrix elements supporting this scenario (51.5%), compared to those in favour of cornute monophyly (13.4%). Several clades outlined in the supertree of Ruta (2003) are confirmed in this new analysis, and reflect the influence of one or several source trees: the scotiaecystine cornutes (Cripps 1988, 1991; Daley 1992; Martí Mus 2002), the clade uniting phyllocystines and chauvelicystines (Cripps 1988, 1991; Daley 1992; Cripps and Daley 1994), the clade uniting *Chinianocarpus* and peltocystids (Parsley 1997), the two clades formed by austral and boreal anomalocystitids (Ruta and Theron 1997; Ruta 1999c; Ruta and Jell 1999). However, consensus supertree A (Fig. 2 herein) shows also some significant discrepancies with Ruta's super-

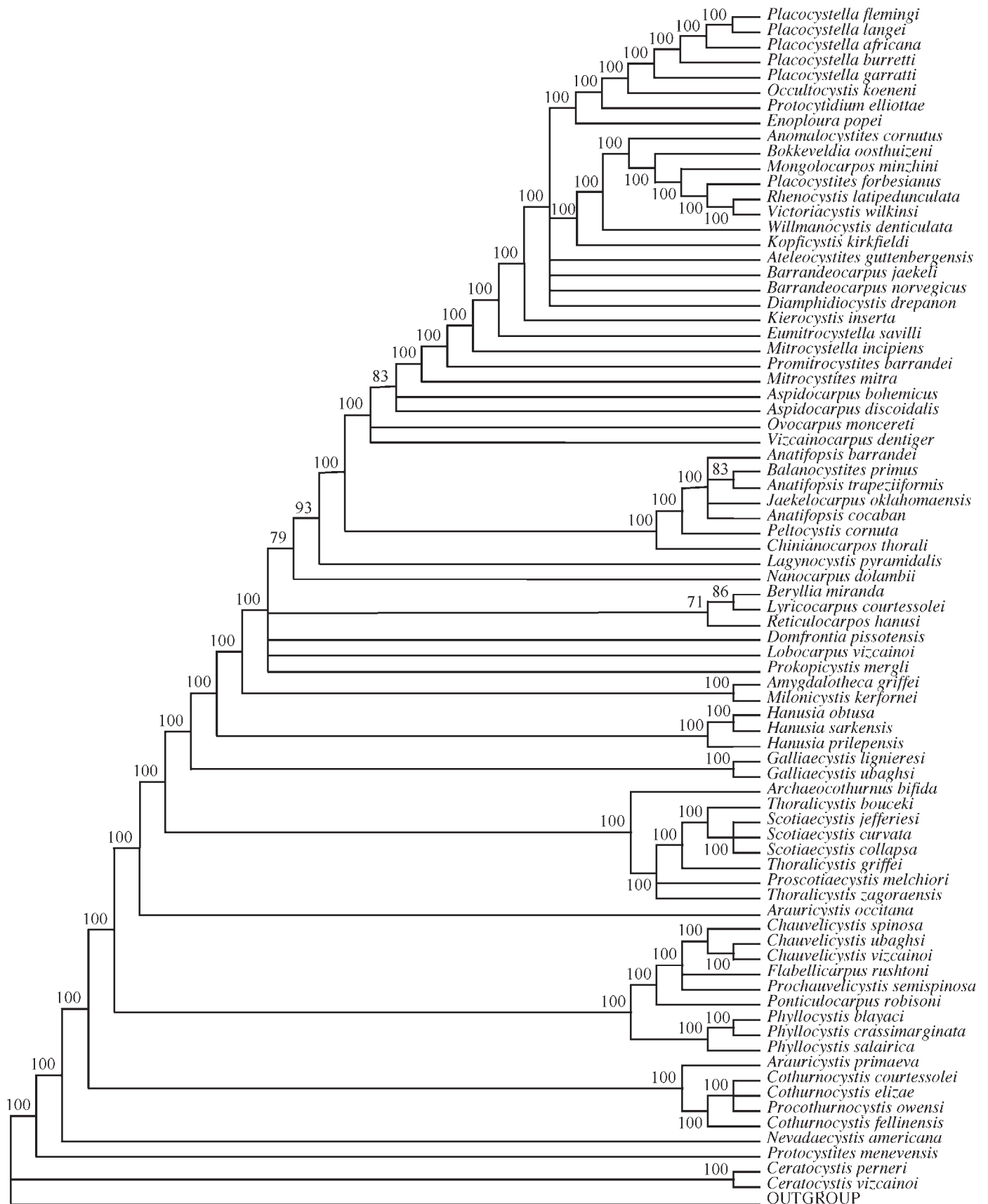


Fig. 2. 70% majority-rule consensus supertree A for stylophorans. See text for details.

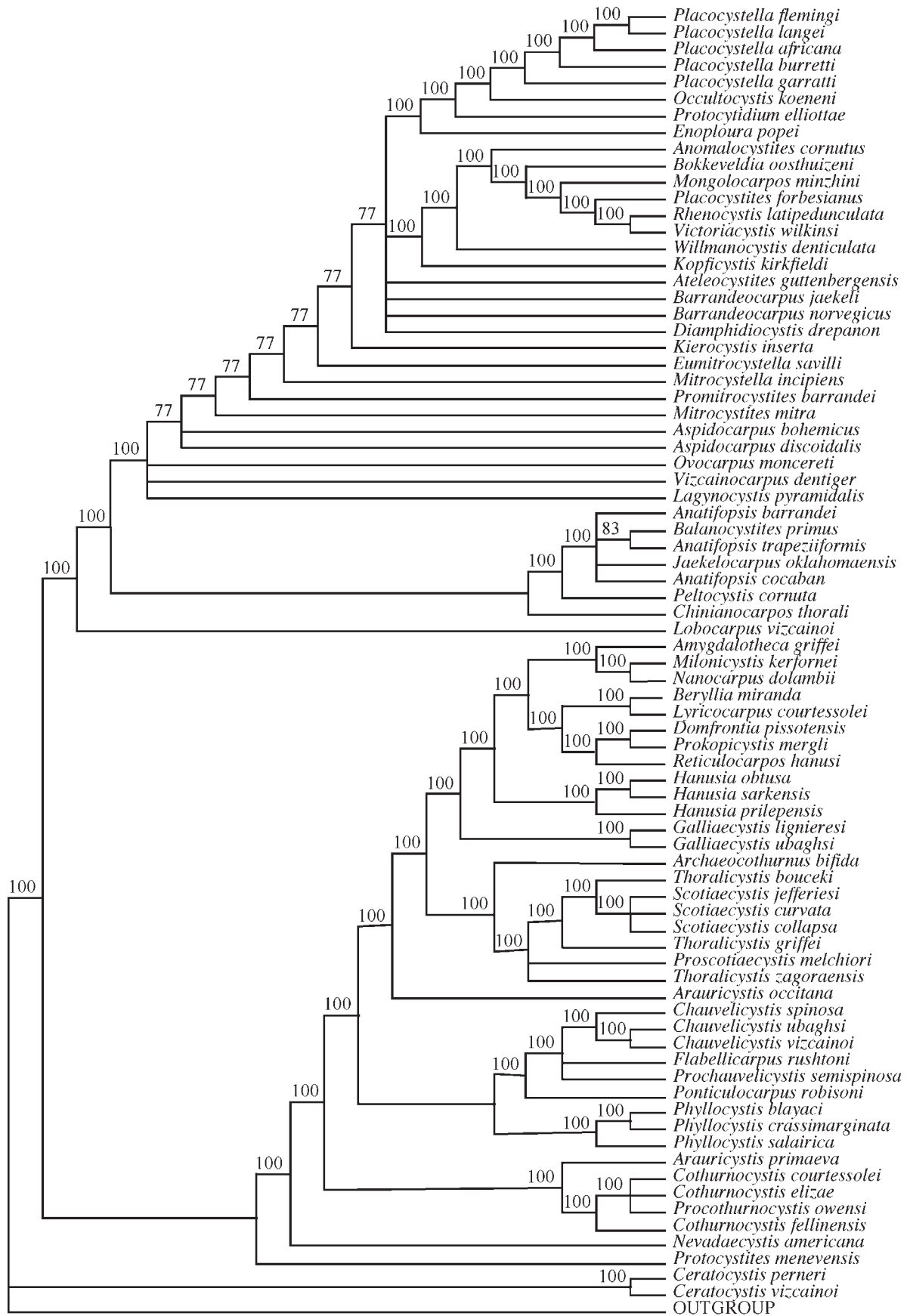


Fig. 3. 70% majority-rule consensus supertree B for stylophorans. See text for details.

tree (2003). One of the most striking differences concerns mitrates: they form a relatively well supported monophyletic group in supertree A, whereas they were polyphyletic in the consensus supertree of Ruta (2003: fig. 2). This difference probably results from the contrasted proportions of matrix elements related to the ankyroid scenario of Parsley (1997) in the two analyses: 19.5%, in the combined matrix of Ruta (2003), and 13.5% in combined matrix A. Following the ankyroid scenario, mitrates were polyphyletic and derived from paraphyletic cornutes (Parsley 1997, 1998). Consequently, the topology of consensus supertree A appears as more influenced by calcichordate source trees supporting both paraphyly of cornutes and monophyly of mitrates (7 trees on 20, representing 37.5% of matrix elements). Another significant difference with Ruta's (2003) supertree concerns the position of *Lagynocystis* as basalmost mitrate, and sister-group of the clade uniting peltocystids and mitrocystitids (Fig. 2). A basal position of *Lagynocystis* is only supported in three small echinoderm source analyses (Lefebvre and Vizcaïno 1999; Lefebvre 2000b, 2001), and is thus probably induced by the coding of *Lagynocystis* as one of the three basalmost mitrates by Ruta (2003: 563) in all calcichordate source trees dealing with cornutes. In the consensus supertree of Ruta (2003), *Lagynocystis* was a highly derived mitrocystitid mitrate, closely related to *Diamphidocystis*: this phylogenetic position of *Lagynocystis* was strongly influenced by the analysis of Parsley (1997). Other differences from the supertree generated by Ruta (2003) concern phylogenetic relationships within cornutes. For example, in Ruta's supertree (2003), the three species of the genus *Hanusia* form a large polytomy with several other cornutes, whereas they constitute here a well defined clade (Fig. 2). This difference certainly results from the recoding of the original source tree of Cripps (1989b). Some other differences concern: (1) cothurnocystines, which form a much better defined clade than in Ruta's (2003) supertree; (2) the more basal position of *Ponticulocarpus* within chauvelicystines, as suggested by Martí Mus (2002); and (3) the placement of *Archaeochothurnus* as sister-group of scotiaecystines, following Cripps (1991), rather than as sister-group of cothurnocystines, as suggested by Parsley (1997).

Parsimony analysis of combined matrix B yielded 3,720 equally parsimonious shortest MRP supertrees at 379 steps (C.I. = 0.752, excluding uninformative characters; R.I. = 0.922; R.C. = 0.693). From these equally shortest solutions, a 70% majority-rule MRP consensus supertree B was derived (Fig. 3). The topology of the corresponding strict consensus tree (not illustrated here) differs from that of supertree B in: (1) less resolution within peltocystid mitrates (absence of the clade uniting *Anatifopsis trapeziiformis* with *Balanocystites primus*), and (2) a large polytomy within basalmost mitrocystitid mitrates. Consensus supertree B is relatively well resolved, and its global topology is clearly distinct from those of both Ruta's (2003: fig. 2) supertree, and consensus supertree A (Fig. 2). Contrary to the two other supertrees, supertree B suggests that both cornutes and mitrates constitute

monophyletic groups. This result is the direct consequence of the pruning of the three mitrate taxa *Chinianocarpos*, *Lagynocystis*, and *Peltocystis*, placed as terminal operational taxonomic units in all calcichordate source trees focusing on cornutes, and implying *a priori* the paraphyly of this stylophoran order (Cripps 1991). Supertree B (Fig. 3 herein) clearly demonstrates that the simple deletion of three taxa in some calcichordate source trees has dramatic consequences on the global topology of stylophoran phylogeny. This example shows that supertree topology can be drastically influenced by contrasting criteria of plate homologies, themselves related to acceptance of particular anatomical interpretations. Contrary to the situation in the two other supertrees, the combined matrix B contains comparable proportions of matrix elements supporting the two rival hypotheses of cornute paraphyly (14.7% of informative characters), and monophyly (14% of informative characters). However, the three small source trees supporting cornute monophyly (Lefebvre and Vizcaïno 1999; Lefebvre 2000b, 2001) apparently influenced more the global tree topology than the single, large analysis in favour of cornute paraphyly (Parsley 1997). Other differences from Ruta's supertree (2003) and supertree A (Fig. 2) concern phylogenetic relationships within mitrates. In supertree B, peltocystids are the sister-group of a clade uniting *Lagynocystis* and mitrocystitids, and *Lobocarpus* appears as the basalmost mitrate (Fig. 3). In the two other supertrees, *Lobocarpus* occurs in a large polytomy within "mitrate-like" cornutes (Fig. 2; see Ruta 2003). Its position as basal mitrate reflects the phylogenetic analysis of Lefebvre (2000b). Within cornutes, amygdalothecids (*sensu* Lefebvre and Vizcaïno 1999) form a relatively well defined clade, deriving from paraphyletic cothurnocystids (Fig. 3). However, topology of supertree B also resembles in many respects the situation in both Ruta's supertree (2003) and supertree A. Within mitrates, topologies are remarkably comparable in the three supertrees, as far as peltocystids (with *Chinianocarpos* as sister-group), and mitrocystitids (with the two well defined clades of austral and boreal anomalocystitids) are concerned. Within cornutes, cothurnocystids comprise the same three main monophyletic groups in supertree B as in supertree A: (1) cothurnocystines; (2) the clade uniting chauvelicystines and phyllocystines; and (3) scotiaecystines. This cornute topology is mostly influenced by the numerous and comprehensive studies made by calcichordate workers (Cripps 1988, 1991; Daley 1992; Cripps and Daley 1994). However, both the position of scotiaecystines as sister-group of amygdalothecids and the placement of *Arauricystis occitana* out of cothurnocystines more likely reflect the phylogenetic analysis of Martí Mus (2002; see also Daley 1992 for scotiaecystines).

Conclusions

Supertree analyses undoubtedly constitute a very powerful and useful tool to synthesise, in a single tree, very disparate data dispersed within several smaller, less inclusive analyses.

However, this consensus method relies on the hypothesis that the more frequently a topology is observed in the source data, the more probable it is that this topology is correct. This study shows that this basic assumption is not true for stylophorans: most available phylogenetic analyses are based either on erroneous homologies (calcichordate model), or on superficial similarities (ankyroid scenario). Consequently, Ruta's (2003) supertree analysis, which mostly reflects calcichordate and ankyroid source data, appears as a poorly grounded attempt to generate a full stylophoran phylogeny. The prerequisite for a meaningful supertree analysis of stylophorans would probably consist in taking into account only source trees based on a sound model of thecal plate homologies.

The present study also demonstrates that contrasting supertree topologies can be obtained with relatively small changes in the relative proportions of matrix elements supporting the various anatomical and/or homology models: polyphyletic mitrates deriving from paraphyletic cornutes (Ruta 2003: fig. 2), monophyletic mitrates deriving from paraphyletic cornutes (supertree A, Fig. 2), or cornutes and mitrates both monophyletic, and deriving from a *Ceratocystis*-like ancestor (supertree B, Fig. 3). Ruta's claim (2003: 560) that supertree analysis provided for stylophorans "[...] a novel hypothesis that is independent of any assumption of skeletal plate homology, as well as of any anatomical orientation and systematic position of the group [...]" is thus falsified. All calcichordate source trees are based on erroneous plate homologies, implied by incorrect respective anatomical orientations of cornutes and mitrates, resulting from their supposed systematic position (interpretation as primitive chordates).

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