

A species-level supertree for stylophoran echinoderms

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The construction of supertrees from smaller, character-based cladograms permits simultaneous inclusion of a large number of taxa in a single analysis, summarizes patterns of relationships from many independent data sources, and highlights areas of conflict to be targeted by character matrix studies. The method is applied for the first time to stylophoran echinoderms (cornutes and mitrates). Published cladistic analyses of this problematic group are used to build a supertree of 77 species. Key areas of stylophoran phylogeny to be addressed by future studies include the systematic placement of several mitrate-like cornutes, the affinities of peltocystidan and lagynocystid mitrates, and the position of such bizarre-looking taxa as *Diamphidiocystis* and *Lobocarpus*. A strict consensus of 72,278 equally parsimonious supertree solutions shows cornutes to be paraphyletic relative to mitrates. *Lobocarpus* is either one of the most derived cornutes or the sister taxon to all mitrates, in agreement with its chimaera-like combination of cornute- and mitrate-like features. *Chinianocarpus* is basal to peltocystidan rather than to mitrocystitidan mitrates. *Nanocarpus*, an almost bilaterally symmetrical taxon previously allied to cornutes, is nested within mitrates as sister taxon to mitrocystitids plus anomalocystitids. *Diamphidiocystis* and *Lagynocystis* cause loss of phylogenetic resolution among derived mitrocystitids and basal anomalocystitids.

Key words: Echinodermata, Stylophora, Cornuta, Mitrata, source trees, supertree, strict consensus, parsimony.

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Introduction

Stylophorans are a palaeontological conundrum. They are among the most problematic of all extinct groups of metazoans. Their zoological affinities as well as morphological polarity have been debated for over thirty years, but no consensus has emerged (for a detailed review of the controversy, see Jefferies 1986). Irreconcilable phylogenetic and morpho-functional interpretations of these fossils as echinoderms (Ubaghs 1968, 1975, 1981; Philip 1979; Jollie 1982; Kolata and Jollie 1982; Paul and Smith 1984; Parsley 1988, 1991, 1994, 1997, 1998, 2000; Kolata et al. 1991; Sumrall 1997; Lefebvre et al. 1998; Ruta 1999a–c; David et al. 2000; Lefebvre 2000a) or as chordates (the so-called “calcichordates”; Jefferies 1981, 1986, 1991, 1997, 2001; Jefferies and Lewis 1978; Cripps 1988, 1989a, b, 1990, 1991; Daley 1992; Jefferies et al. 1996; Ruta 1997a, b; Ruta and Theron 1997; Jefferies and Jacobson 1998; Sutcliffe et al. 2000; Dominguez et al. 2002) have led to a flurry of research targeted at evaluating the various biological and systematic implications as well as evolutionary scenarios associated with each of the competing hypotheses (Peterson 1995; Bergström et al. 1998; Lefebvre et al. 1998; Lefebvre and Vizcaino 1999; Ruta 1999b, c; Lefebvre 2000a, b, 2001, 2003; Martí Mus 2002). At the same time, a large amount of new information and character revision have improved considerably the broad picture of stylophoran intrinsic relationships (Cripps 1991; Daley 1992; Parsley 1997, 1998; Ruta 1997a, 1999b; Ruta and Theron 1997; Lefebvre and Vizcaino 1999; Ruta and Jell

1999; Lefebvre 2001; Martí Mus 2002). Despite much recent progress and unusually fast rate of data accumulation (Mooi 2001), there is a dismaying lack of agreement about the higher-level systematic position of stylophorans. As Ubaghs (1994: 3) aptly put it, “La diversité de ces opinions et les critiques, souvent pertinentes, adressées à chacune d’elles (y compris la mienne) ... , suggèrent que le problème de la vraie nature des stylophores reste posé”.

A revision of stylophorans and of their putative allies among the diverse array of Palaeozoic, echinoderm-like groups (Paul and Smith 1984; Sumrall 1997) are timely to make sense of patterns of character distribution in primitive deuterostomes. This is especially important in the light of contributory new information from such diverse fields as developmental biology and palaeontology (e.g., Bromham and Degnan 1999; Donoghue et al. 2000; Peterson and Eernisse 2001). A stunning series of recent fossil discoveries from the Lower Cambrian of China have improved our understanding of basal chordate evolution. A multitude of spectacular and challenging new fossils have been proposed as stem gnathostomes, stem myopterygians (*sensu* Janvier 1981, i.e., the clade consisting of lampreys plus gnathostomes), or even stem craniates (e.g., Smith et al. 2001; Shu et al. 2003, and references therein). Together with recent advances in developmental biology, these new finds are slowly forcing a rethinking of long-established views about the nature and distribution of jaws, respiratory structures, sense organs, mineralized parts and paired appendages in basal chordates and deuterostomes (Janvier 1996a, b, 2001; Coates and Cohn

1998; Donoghue et al. 2000; Smith and Coates 2000; Donoghue and Aldridge 2001; Smith et al. 2001; Dominguez et al. 2002; Donoghue 2003). On casual judgement, attempts to integrate this new information with data on the enigmatic stylophorans seem unrealistic, given the highly controversial nature of the latter. However, comprehensive investigations of deuterostome and, more specifically, chordate and echinoderm evolution call for critical scrutiny of all lines of evidence (including problematic extinct groups), and for evaluation of additional, less frequently used data sources (e.g., degree of congruence between stratigraphical order of appearance of key taxa and sequence of phylogenetic branching events; see comments in Jefferies 1986; Smith et al. 2001; and Dominguez et al. 2002).

In this paper, I address stylophoran intrinsic relationships from the perspective of supertree building (Baum 1992; Ragan 1992), and consider all the species that have been included in cladistic analyses published over the last 15 years. I point out that the nature of the present work is chiefly methodological and does not aim to replace primary, character-based trees. It does, however, address the merits of a relatively new and still largely unexplored approach to phylogeny reconstruction (see Bininda-Emonds et al. 2002, Goloboff and Pol 2002 and Pisani et al. 2002 for detailed reviews). It also provides a framework for future character analyses of stylophorans through the erection of 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.

Supertrees

Terminology.—Component trees (i.e., primary, character-based cladograms) are also known as *source trees* (Pisani et al. 2002). The analyses from which they derive are *original* or *primary analyses*. The topology of each source tree is translated into its matrix representation, or *MR*. The combined matrix for all source trees is processed using a parsimony optimality criterion (*matrix representation using parsimony*, or *MRP*). The combined matrix includes simple binary coding for each node in each source tree. Taxa that are subtended by a given node are scored as “1”; a “0” score is given to taxa that do not descend from that node; if a taxon is not represented in a source tree, then it is scored as “?” (Bininda-Emonds et al. 2002; Pisani and Wilkinson 2002; Pisani et al. 2002). The MR “characters” (*matrix elements* of Pisani et al. 2002) are the nodal points of each source trees. MR processing yields one or more shortest trees, called *component coding-MRP supertrees*, or *CC-MRP supertrees* (Pisani et al., 2002). These can be combined into various types of consensus topologies.

Rationale.—Systematic studies that are based on primary character/taxon matrixes can rarely accommodate large taxon numbers. Computer memory limitations and accuracy

in tree search are often a major hurdle to jump and represent common problems with large data sets. The construction of all-encompassing matrixes is often impractical. For example, different data sources (morphology; molecules; physiology; behaviour) might be available for different clades within the same group of organisms. Therefore, it might be difficult to combine in the same matrix partially overlapping taxon sets that have been coded for rather heterogenous character types. Systematists encounter similar problems in analyses of combined fossil and living representatives of a group.

In many cases, however, it is desirable to produce detailed phylogenies, e.g., to infer large-scale macroevolutionary patterns or to analyze profiles of diversity and disparity through time (Bininda-Emonds et al. 1998, 1999, 2002). In these cases, supertrees provide a powerful means of collating information from smaller-scale, character-derived trees. Supertree construction overcomes several of the problems associated with very large taxon/character sets and has been applied to several organisms, both living (e.g., some orders of birds, mammals and plants) and fossils (e.g., dinosaurs) (reviews in Bininda-Emonds et al. 2002). The method offers several advantages. First, it allows multiple trees, consisting of partially or totally overlapping taxon sets, to be combined in a single, large-scale phylogeny. Second, it is unique in its ability to synthesize competing hypotheses of relationship for exceedingly numerous operational taxonomic units. Third, supertrees provide in many cases partial or full resolution for groups that are poorly resolved in one or more of the source trees. Fourth, conflicting positions of some groups or single species in the source trees often tend to cancel out in favour of a single, unambiguous placement in the supertree. A final aspect of supertree construction relates to their ability to generate, in some cases, groups that do not appear in any of the contributory cladograms (but see comments below). In these cases, supertrees call for a critical scrutiny of the evidence (characters) in support of such novel groups. Finally, supertrees might be used as simple tests of the ability of various nodes in the source trees to be retrieved in large scale analyses.

Limits.—Recent reviews (Bininda-Emonds et al. 1999; Goloboff and Pol 2002; Pisani et al. 2002) illustrate different systematists’ approaches to the rationale and limitations of supertree methods. Thus, Bininda-Emonds et al. (2002: 277) consider “... supertrees [to] provide a greater potential for complete taxonomic coverage based on a consensus of all phylogenetic information” (see also preceding section). Goloboff and Pol (2002), on the other hand, reason that supertrees could be used as phylogenetic hypotheses only if the strict or semistrict consensus topology of all CC-MRP solutions was resolved to a considerable extent. However, they point out that such resolved topology may be rarely found in analyses that include very large numbers of taxa. Matrix representation departs from standard phylogenetic analyses that employ primary characters (but see Bininda-Emonds and Sanderson 2001). Thus, the very use of an optimality criterion (parsimony or otherwise) might be considered to be

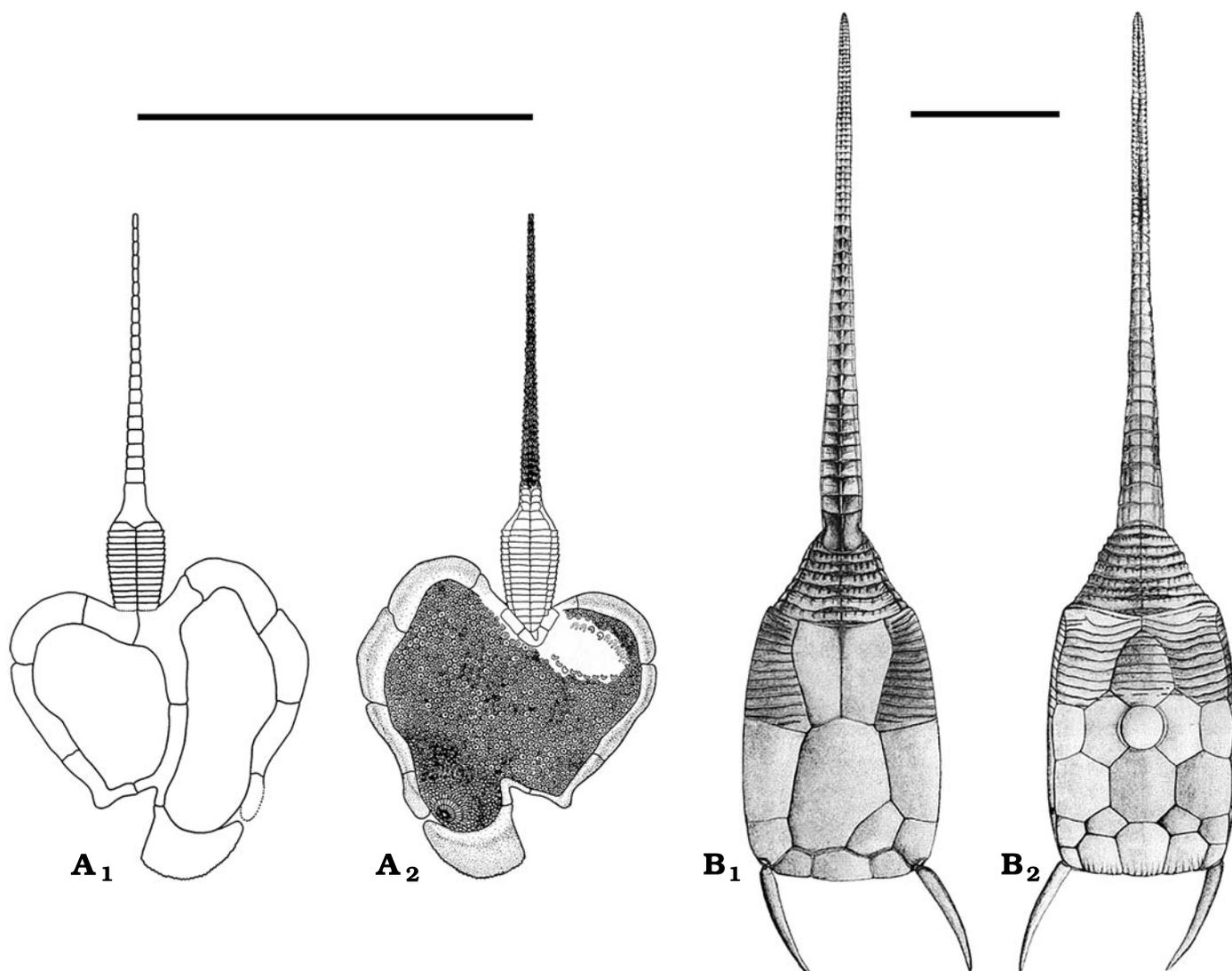


Fig. 1. Basic anatomical organization of stylophorans. **A.** The cornute *Flabelllicarpus rushtoni* (Lower Ordovician; England) in ventral (A₁) and dorsal (A₂) views (modified from Martí Mus 2002). **B.** The mitrate *Rhencystis latipedunculata* (Lower Devonian; Germany) in ventral (B₁) and dorsal (B₂) views (modified from Ruta and Bartels 1998). Scale bars 1 cm.

problematic, since it is unclear how this criterion actually operates in terms of selection of competing branching patterns.

One of the main problems associated with supertrees is that their overall topology is affected by that of the source trees. It has been shown that large, pectinate and/or fully resolved trees impact supertree shape to a greater extent than small, dichotomous and/or poorly resolved trees (Wilkinson et al. 2001; Bininda-Emonds et al. 2002; Goloboff and Pol 2002; Pisani et al. 2002). According to Bininda-Emonds and Bryant (1998), the influence of large source trees might be justified if they are more accurate and more informative than smaller-scale cladograms. Finally, the influence of source tree size and shape and degree of taxonomic overlap between source trees are still poorly explored (Bininda-Emonds et al. 1999, 2002; Pisani and Wilkinson 2002).

It is preferable to interpret supertrees as a summaries of the information related to component topologies, rather than as primary phylogenetic hypotheses. Inspection of supertrees (including novel branching patterns) enables systematists to explore possible, previously undetected character combinations in support of crucial nodes, and draws attention to areas of conflict among contributory cladograms.

Stylophoran morphology

Lefebvre and Vizcaino (1999), Ruta (1999a–c), David et al. (2000), Lefebvre (2000b, 2001) and Martí Mus (2002) provide succinct but comprehensive accounts of the basic anatomical organization of the two major groups of stylophorans,

the cornutes and the mitrates. Jefferies' (1986) book is the best detailed account of stylophorans as a whole, and includes most of the primary literature prior to 1986. More recent discussions include Lefebvre and Vizcaino (1999), Ruta (1999b, c), Jefferies (2001), Lefebvre (2001) and Martí Mus (2002). Only a brief overview of the group is necessary here.

Stylophorans are calcite-plated, marine metazoans found in Middle Cambrian to Upper Carboniferous sediments (Ubaghs 1967; Kolata et al. 1991), and with an almost worldwide distribution. Their body consists of a massive part, departing more or less significantly from a bilaterally symmetrical outline, and an elongate, usually distinctly tripartite appendage. These two regions are referred to as a theca or head, and as an aulacophore or tail, depending upon interpretations. The massive part shows a variable number of perforations, subcentral and marginal plates, peripheral spines, etc. The appendage resembles in several respects the arm of a crinoid (David et al. 2000; but see Philip 1979; Ubaghs 1981; and Jefferies 1986) in possessing basal ossicles covered by paired plates. Its proximal part (attached to the theca) bears telescopically arranged, tetramerous rings, except in primitive forms. Fig. 1 illustrates the main differences between the body organization of a cornute and that of a mitrate.

Previous phylogenetic work on stylophorans

Jefferies (1986) first undertook a large-scale (albeit manual) reconstruction of the pattern of character distribution among several cornute and mitrate species. Slight modifications of his phylogenetic scheme have been published in a number of subsequent papers (e.g., Jefferies 2001). Jefferies' work paved the way to the first detailed, computer-assisted analyses of stylophorans and to comprehensive revisions of the anatomy of a plethora of species, including several new taxa. Many areas of stylophoran phylogeny remain controversial (e.g., status of cornutes; position of peltocystidan and lagynocystid mitrates; affinities of mitrate-like cornutes). This is the result of different factors, including: (1) conflicting interpretations of skeletal features and contrasting hypotheses of thecal plate homology in cornutes and mitrates (Lefebvre et al. 1998; Lefebvre and Vizcaino 1999; Ruta 1999a, b; Lefebvre 2000a, b, 2001); (2) character selection as well as different regimes of character coding, ordering and weighting (e.g., Parsley 1997, 1998; Ruta 1997a, 1999c; Ruta and Theron 1997; Ruta and Jell 1999; Lefebvre 2001; Martí Mus 2002); (3) use of largely non-overlapping taxon samples in different analyses.

The paraphyletic status of cornutes relative to mitrates has been endorsed by several calcichordate workers (Jefferies et al. 1987; Cripps 1988, 1989a, b, 1991; Daley 1992; Woods and Jefferies 1992; Cripps and Daley 1994). More recently, a series of papers have challenged this hypothesis, based on a re-evaluation of skeletal homologies in cornutes and mitrates.

Such homologies support a topological and anatomical correspondence between the flat (ventral) surface of the cornute theca and the plano-concave surface of the mitrate theca (Lefebvre et al. 1998; Lefebvre and Vizcaino 1999; David et al., 2000; Lefebvre 2000a, b, 2001; see also Ruta 1999a, c and Martí Mus 2002). New character analyses (Lefebvre and Vizcaino 1999; Lefebvre 2001) place cornutes and mitrates as monophyletic sister groups. These are hypothesized to share a common ancestor that was perhaps phylogenetically close to the Middle Cambrian genus *Ceratocystis* (Ubaghs 1967; Jefferies 1969), usually regarded as the most basal known cornute (Jefferies 1986, 2001).

Large-scale phylogenetic analyses of cornutes include those of Cripps (1991), Daley (1992) and Martí Mus (2002). These studies differ in the placement of several basal, boot-shaped cornutes as well as some of the more bilaterally symmetrical forms.

Species-level interrelationships of mitrates have been examined by Jefferies (1986), Cripps (1990), Beisswenger (1994), Ruta (1997a, 1999b), Ruta and Theron (1997), Ruta and Jell (1999), and Lefebvre (2000b). Some of these studies focus on a large subset of mitrates, referred to as the anomalocystitids, which are characterized by the presence of a pair of movable, spine-like marginal plates (Lefebvre 2000b; but see also Jefferies 1986 and Craske and Jefferies 1989).

The only published large-scale studies of stylophoran relationships, comprehensive of both cornutes and mitrates, are those of Parsley (1997, 1998). In those works, mitrates are polyphyletic, their origins being rooted into two distinct sets of cornutes. Parsley's (1997, 1998) concept of Ankyroida, a clade including mitrates and mitrate-like cornutes, has been criticized and refuted by Lefebvre (2001) in the light of a revised interpretation of plate homologies across stylophorans. According to Lefebvre (2001, and references therein), the phylogenetic separation between cornutes and mitrates is much deeper than that proposed by the calcichordate theory, and may have occurred as early as the Middle–Upper Cambrian.

Materials and methods

The matrix representations of all stylophoran source trees have been constructed by hand using the program MacClade v. 3.0.1 (Maddison and Maddison 1992). The data set is available at <http://www.app.pan.pl/acta48/app.559-matrix.rtf> or upon request from the author. The combined matrix for all contributory cladograms consists of 77 stylophoran species coded for 369 matrix elements. An all-zero outgroup (implying grouping of taxa based exclusively on shared matrix elements) has been used to root the supertree (Bininda-Emonds et al. 2002). All original analyses have been reprocessed with PAUP* (Swofford 2002) to check the original results.

In the case of analyses yielding several equally parsimonious solutions, only the strict consensus of these has been used as a source tree. This applies also to those primary stud-

ies in which a 50 percent majority-rule consensus has been used (e.g., Lefebvre 2001). Analyses that were originally performed using programs other than PAUP have been reprocessed with the latter. For instance, Daley's (1992) study employed Hennig86, while Parsley's (1998) cladogram was generated with NONA (Goloboff 1993). Re-running such data sets with PAUP yields slightly different results. In these cases, matrix representations of both the new topologies and those retrieved in the original analyses have been considered. However, I point out that supertree shape is found to be largely unaffected either by the use of PAUP-derived trees only, or by the use of trees generated with programs other than PAUP.

In some analyses (e.g., Cripps 1991; Daley 1992), the group Mitrata as been used as a terminal operational taxonomic unit. In the matrix representation, I have replaced such supraspecific unit with an unresolved clade consisting of three species, *Chinianocarpos thorali*, *Peltocystis cornuta*, and *Lagynocystis pyramidalis*. These taxa represent the basalmost mitrocystitid, the basalmost peltocystidan and the only representative of the lagynocystids, respectively, in most previous studies (Jefferies 1986).

The use of statistical methods to assess branch support for supertrees is questionable (Goloboff and Pol 2002; Pisani and Wilkinson 2002), since it is not clear what support measures mean with respect to the position of taxa in each of the contributory trees. Reweighting methods are likewise of dubious significance, especially when source trees differ considerably in the amount of taxon overlap. Therefore, I have treated matrix elements as having equal weight.

PAUP search settings include 2,000 random stepwise additions followed by TBR (tree bisection-reconnection) branch-swapping searching, holding a single tree in memory at any one time. Searching on each tree with unlimited MAXTREES recovered the same island of trees. No shorter trees were recovered after employing the iterative re-weighting strategy proposed by Quicke et al. (2001).

Source trees.—I have considered only analyses (both manual and computer-assisted) published after 1986. Cripps' (1989b) study is not included in the supertree since it is superseded by Cripps (1989a, 1991) and by Cripps and Daley (1994). Likewise, Craske and Jefferies (1989) is superseded by Cripps (1990), whereas Parsley (1997) is superseded by Parsley (1998). Source trees include: Jefferies et al. (1987) on assorted cornutes; Cripps (1988, 1989a, 1991) on various groups of cornutes and large-scale analysis of cornutes (Cripps 1991 has been also reprocessed in PAUP); Cripps (1990) on several mitrocystitid mitrates; Daley (1992) on large-scale analysis of cornutes (also reprocessed in PAUP); Woods and Jefferies (1992) on assorted cornutes; Beisswenger (1994) on assorted mitrocystitid mitrates; Cripps and Daley (1994) on various groups of cornutes; Parsley (1998) on large-scale analysis of cornutes and mitrates (also reprocessed in PAUP); Ruta (1997a, 1999b), Ruta and Theron (1997) and Ruta and Jell (1999) on derived mitrocystitid as well as anomalocystitid mitrates; Lefebvre and Vizcaino

(1999), Lefebvre (2000b, 2001) on assorted stylophorans; Martí Mus (2002) on large-scale analysis of cornutes.

Results

PAUP* yielded 72,278 equally parsimonious CC-MRP solutions at 486 steps (C.I. = 0.7473, excluding uninformative characters; R.I. = 0.9206; R.C. = 0.699). From these, both a strict consensus (Fig. 2) and an agreement subtree (not shown here) were derived. The agreement subtree contains the largest set of taxa (68 out of 78; size of subtree = 87.2 percent) for which all most parsimonious solutions agree upon mutual relationships (i.e. such relationships are observed in each of the solutions), and from which unstable taxa have been removed (Swofford 2002; Kearney 2002). Such unstable taxa include the mitrates *Diamphidiocystis drepanon*, *Lagynocystis pyramidalis*, and *Vizcainocarpus dentiger*; the cornutes *Ceratocystis vizcainoi*, *Cothurnocystis courtessolei*, *Hanusia sarkensis*, *Prochauvelicystis semispinosa*, *Scotiaecystis collapsa*, and *Thoralicystis griffei*; and the enigmatic Upper Cambrian *Lobocarpus vizcainoi*, originally regarded as a cornute (Ubaghs 1999), but reinterpreted as a basal mitrate (Lefebvre 2000b; but see also remarks on *Lobocarpus* in Martí Mus 2002 and its possible interpretation by the latter author as a cornute, possibly related to *Milonicystis*).

Despite the large number of equally parsimonious solutions, the topology of the strict consensus is fairly well resolved (Fig. 2). The largest polytomy subtends seven mitrate-like cornute species (*Beryllia miranda*, *Domfrontia pissotensis*, *Hanusia obtusa*, *H. prilepensis*, *H. sarkensis*, *Prokopicystis mergli*, *Reticulocarpos hanusi*) and the problematic *Lobocarpus*, all of which appear to be adjacent to mitrates. Inspection of the agreement subtree shows that loss of phylogenetic resolution is caused solely by the unstable placement of *Lobocarpus* and *Hanusia sarkensis*. *Lobocarpus* shows a chimaera-like arrangement of cornute and mitrate features, and its affinities require reassessment. Considering its mixture of characters, it is noteworthy to find that, in the various CC-MRP solutions, the position of this taxon shifts from the node immediately basal to mitrates (in agreement with Lefebvre's 2000b hypothesis; see also Ubaghs 1999) to the node immediately distal to (*Lyticocarpus courtessolei* (*Amygdalotheca griffei*, *Milonicystis kerfornei*)) in partial agreement with Martí Mus' (2002) hypothesis. In the agreement subtree, the most basal clade of mitrate-like cornutes is represented by (*Lyticocarpus courtessolei* (*Amygdalotheca griffei*, *Milonicystis kerfornei*)). In increasing order of proximity to mitrates, other nearly bilaterally symmetrical cornutes include: (*Hanusia obtusa*, *H. prilepensis*), *Reticulocarpos hanusi*, *Beryllia miranda*, *Domfrontia pissotensis*, and *Prokopicystis mergli*. This arrangement is in good agreement with the topologies retrieved by Cripps (1991), Daley (1992), and Cripps and Daley (1994), but contrasts with the clear-cut separation between cornutes and mitrates advocated by Lefebvre (2000b,

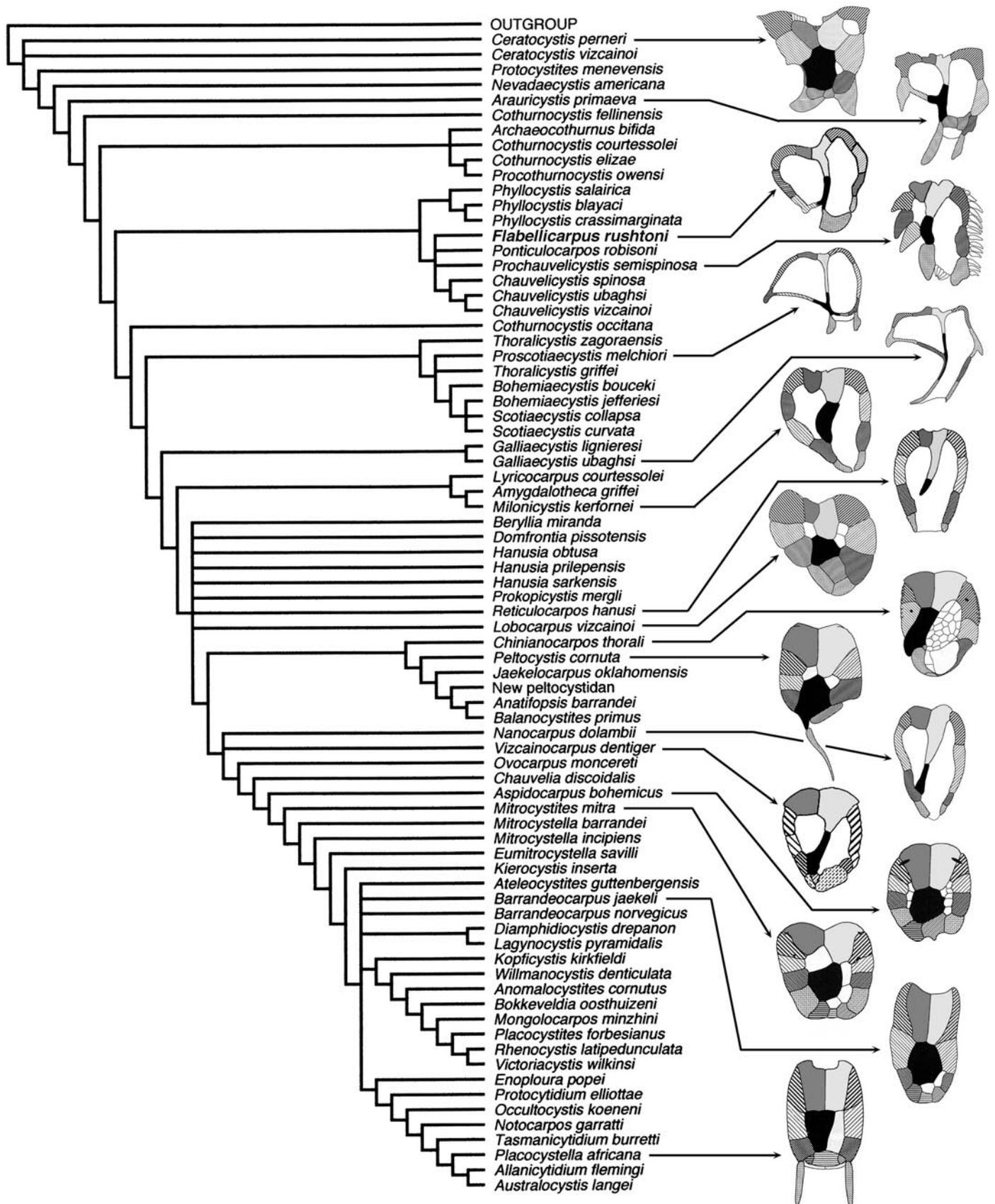


Fig. 2. Strict consensus supertree for styloporans. The lower thecal surfaces of representative taxa are not drawn to the same scale (modified from Lefebvre and Vizcaino 1999; Lefebvre 2000b, 2001; and Martí Mus 2002). See text for details.

2001). In addition, Lefebvre and Vizcaino (1999) treat *Prokopicystis* and *Reticulocarpos* as relatives of *Galliaecystis* and *Hanusia*, but place *Beryllia* and *Domfrontia* close to *Amygdalotheca* and *Nanocarpus*.

Another large, polytomous node subtends three mitrate species (*Ateleocystites guttenbergensis*, *Barrandeocarpus jaekeli*, *B. norvegicus*) and three mitrate clades (each of these is fully resolved in the strict consensus). Two of these clades correspond largely to Ruta's (1999b) "boreal" and "austral" anomalocystitid groups. The third clade, (*Lagynocystis pyramidalis*, *Diamphidiocystis drepanon*), has been retrieved in Parsley's (1997, 1998) analyses. These two species cause considerable loss of phylogenetic resolution in the strict consensus. This is hardly surprising, since Parsley's (1997, 1998) analyses conflict with the more traditional, basal position of *Lagynocystis* within mitrates (Jefferies 1986) and with the anomalocystitid affinities of *Diamphidiocystis* (Ruta 1999b). If both taxa are removed, then the sequence of branching events in the agreement subtree shows *Kierocystis inserta*, *Barrandeocarpus jaekeli*, *B. norvegicus*, and *Ateleocystites guttenbergensis* as progressively more closely related species (in that order) to the "boreal" and "austral" clades. This arrangement agrees broadly with Craske and Jefferies's (1989), Cripps' (1990), Ruta's (1997a, 1999b), Ruta and Theron's (1997) and Ruta and Jell's (1999) relationship schemes for derived mitrocystitids (including the genus *Barrandeocarpus*) and basal anomalocystitids. The supertree also resolves the conflicting positions of *Ateleocystites*, *Barrandeocarpus*, and *Kierocystis* in Ruta's (1999b) analysis (but see also discussion in Ruta and Jell 1999).

The strict consensus shows five additional, small polytomies. One of these affects the very basal portion of the mitrate clade. *Ovocarpus moncereti* and more derived mitrates form an unresolved trichotomy with the basal mitrocystitid *Vizcainocarpus dentiger* (an unstable taxon) and the mitrate-like cornute *Nanocarpus dolambii*. The second and third small polytomies are found within scotiaecystine cornutes (Cripps 1988, 1989b, 1991; Daley 1992; Cripps and Daley 1994), one of the most easily characterizable and most frequently retrieved cornute clades (Lefebvre and Vizcaino 1999; Lefebvre 2001; Martí Mus 2002). A basal trichotomy subtends *Proscotiaecystis melchiori*, *Thoralicystis griffei*, and more derived scotiaecystines. Within the latter, *Bohemiacystis jefferiesi* is collapsed in an unresolved node with *Scotiaecystis curvata* and *S. collapsa* (but see Lefebvre and Vizcaino 1999 and Martí Mus 2002 for different opinions on the separation between the two *Scotiaecystis* species). The fourth small polytomy subtends chauvelicystine cornutes. The monophyletic genus *Chauvelicystis* is collapsed in an unresolved tetrachotomy with *Flabelllicarpus rushtoni* (genus name amended from *Flabelllicystis*; Dr. Monica Martí Mus personal communication June, 2003), *Ponticulocarpos robisoni*, and *Prochauvelicystis semispinosa*. While this topology is largely congruent with those of Cripps (1991), Daley (1992), Cripps and Daley (1994), and Martí Mus (2002), the taxonomic membership of the chauvelicystine

clade is less inclusive than that proposed by Lefebvre and Vizcaino (1999), according to whom *Lyricocarpus* and *Milonicystis* also belong in the chauvelicystines. Finally, *Archaeochothurnus bifida* and *Cothurnocystis courtessolei* are collapsed in a polytomy with a clade consisting of *C. elizae* and *Procothurnocystis owensi*.

Discussion of results

Supertrees often include branching patterns that are absent in the source trees. Attempts to eliminate topological incongruence by deleting conflict-generating taxa from the matrix representation of a source tree might affect the output of supertree analysis, and yield supertrees that differ from those generated by combining source topologies with undeleted taxa (Bininda-Emonds et al. 2002; Pisani et al. 2002; and references therein). As an alternative solution, conflict-generating taxa may be collapsed in the supertree. Examples of novel branching patterns are evident in the stylophoran strict consensus of CC-MRP solutions as well as in the agreement subtree and are discussed briefly below.

Nanocarpus dolambii is one of several species of mitrate-like, nearly bilaterally symmetrical cornute species. If supported by character-based analyses, its position as sister taxon to the mitrocystitid-anomalocystitid clade would imply a re-evaluation of skeletal features traditionally used to separate cornutes from mitrates (Cripps 1989a, b, 1991; Ubahgs 1991; Cripps and Daley 1994; Ruta 1997a, 1999a, c; Lefebvre 2000a, b, 2001; Martí Mus 2002). Thecal similarities in cornutes and mitrates are not uncommon. It is perhaps significant that, apart from different proportions of certain marginal plates, the lower thecal surfaces of *Nanocarpus* and *Vizcainocarpus* are strikingly similar (Fig. 2). Evidence upon which the cornute-mitrate separation rests, and the close affinities of mitrate-like cornutes to mitrates, are often equivocal and theory-laden (Lefebvre and Vizcaino 1999; Ruta 1999c; Lefebvre 2000b, 2001; Martí Mus 2002). In contrast, Lefebvre and Vizcaino (1999) argue in favour of amygdalothecid affinities for *Nanocarpus*, and regard this taxon as a close relative of *Amygdalotheca*, *Beryllia*, and *Domfrontia*, which are placed in the family Amygdalothecidae. The latter is paired with Hanusiidae, which includes a heterogeneous assemblage of strongly asymmetrical and mitrate-like cornute genera (*Galliaecystis*, *Hanusia*, *Prokopicystis*, *Reticulocarpos*). In Martí Mus' (2002) analysis, *Nanocarpus* is placed in an unresolved clade with *Amygdalotheca*, *Prokopicystis*, and *Reticulocarpos*. In turn, this clade is paired with hanusiid amygdalothecidans *sensu* Lefebvre and Vizcaino (1999). The strict consensus supertree places hanusiids and amygdalothecids adjacent to mitrates, but these two families appear as slightly overlapping, polyphyletic arrays of species.

At the base of the supertree (Fig. 2), cothurnocystidans and other boot-shaped cornutes form a paraphyletic group. A close relationship between phyllocystines and chauvelicystines emerges, in partial agreement with the conclusions

of Cripps (1991), Cripps and Daley (1994) and Martí Mus (2002). Scotiaecystines are more derived than phyllocystines and chauvelicystines, but less derived than amygdalothecids and hanusiids. At the very base of the supertree, the sequence of cladogenetic events leads from massively built, Middle Cambrian taxa such as *Ceratocystis* and *Protocystites*, to late Cambrian and lower Ordovician boot-shaped taxa (*Nevadaecystis*, *Arauricystis*, *Cothurnocystis fellinensis*).

In the derived part of the supertree (Fig. 2), *Kierocystis* and *Barrandeocarpus* are progressively more closely related to the anomalocystitid mitrates (Craske and Jefferies 1989; Cripps 1990), and are more derived than *Eumitrocystella* (Beisswenger 1994; Ruta and Theron 1997; Ruta 1999b; Ruta and Jell 1999). The topology of the distal portion of the supertree reflects largely the hypotheses of Ruta (1999b) and Ruta and Jell (1999), since these are the only large-scale studies of anomalocystitids published thus far. The position of such genera as *Barrandeocarpus* (Ubaghs 1979; Ruta 1997b), *Kierocystis*, and *Kopfcystis* (Parsley 1991), although not generally agreed upon (Ruta 1999b), has important implications for tracing the ancestry of anomalocystitids from within mitrocystitids. The transition between the spine-less mitrocystitids and the spine-bearing anomalocystitids has been discussed in detail by Ruta (1997b), Ruta and Theron (1997), Ruta and Jell (1999), and Lefebvre (2000b). Ruta and Jell (1999) support a derived, spine-less condition for *Barrandeocarpus*, in contrast with the hypothesis of Craske and Jefferies (1989), Cripps (1990) and Beisswenger (1994) (but see also Ruta 1999b and Lefebvre 2000b). Among mitrates, the position of *Chinianocarpos* as sister taxon to peltocystidans and the clade (*Lagynocystis* + *Diamphidiocystis*) reflect largely Parsley's (1997, 1998) tree topology. The latter clade, however, is highly unstable and problematic, as discussed above.

Conclusions

Supertree construction identifies areas of stylophoran phylogeny that require additional investigation. In particular, the monophyletic versus paraphyletic status of cornutes relative to mitrates remains a pivotal issue, with broad implications for character polarity within the group. In this respect, the affinities of the mitrate-like cornutes are crucial, especially in the light of the character transformations that are hypothesized to have occurred at the cornute-mitrate transition by calcichordate workers. The highly unstable position and problematic affinities of such taxa as *Lobocarpus*, coupled with the non-uniform clustering of nearly bilaterally symmetrical taxa, imply a large amount of homoplasy in the thecal construction of stylophorans as a whole, and call for a new evaluation of thecal plate homologies.

The sequence of cladogenetic events in the basalmost portion of the stylophoran tree is in a state of flux. In particular, a highly asymmetrical and boot-shaped outline of the theca seems to have been retained, presumably as a plesio-

morphic condition, in the basal portions of several discrete cornute clades (cothurnocystines; scotiaecystines). Notable exceptions are the heart- or leaf-shaped thecal outlines of phyllocystines and chauvelicystines.

Higher-level mitrate interrelationships are changing rapidly. The conventional subdivision of mitrates into lagynocystids, peltocystidans, mitrocystitids and anomalocystitids needs revision, especially in the light of overall similarities in the thecal plating pattern of the basalmost members of the first three groups. A better understanding of the mitrocystitid-anomalocystitid transition must await reassessment of various spine-less taxa from the Upper Ordovician.

Finally, it is hoped that the present contribution will form the basis for constructive criticism of much current understanding of stylophoran interrelationships.

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