

TESTING PHYLOGENETIC RELATIONSHIPS OF FLOIAN (ORDOVICIAN) GRAPTOLITE RECORDS FROM ARGENTINA THROUGH CLADISTIC ANALYSIS

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Abstract. The analysis of two-stiped dichograptids, largely of baltograptid and expansograptid taxa of the family Didymograptidae from the Floian of northwestern Argentina, provides insight into the evolutionary relationships of this group. The important proximal end characters clearly cluster the baltograptids with the derived genera *Didymograptus* and *Aulograptus*. One of the analyses provides the information that the genera *Cymatograptus* and *Expansograptus* share a common ancestor but are not closely related to the two-stiped *Kiaerograptus* and related taxa. Likewise, with the exception of some controversial taxa, the families Tetragraptidae and Didymograptidae can be readily differentiated, supporting previous interpretations that they represent monophyletic clades. Although the present analyses are poorly supported, they provide hypotheses that could be further tested based on new data on isolated dichograptid taxa based on isolated or relief-preserved material.

Key words. Graptolites. Ordovician. Floian. Argentina. Phylogeny.

Resumen. EXPLORANDO LAS RELACIONES FILOGENÉTICAS DE LOS REGISTROS DE GRAPTOLITOS DEL FLOIANO (ORDOVÍCICO) DE ARGENTINA MEDIANTE ANÁLISIS CLADÍSTICO. El análisis de los dichograptidos de dos estipes, principalmente taxones de baltograptidos y expansograptidos de la familia Didymograptidae, del Floiano del noroeste de Argentina, permite establecer relaciones evolutivas para este grupo. Los caracteres del extremo proximal resultan importantes para agrupar claramente a los baltograptidos con los géneros derivados *Didymograptus* y *Aulograptus*. Uno de los análisis indica también que los géneros *Cymatograptus* y *Expansograptus* comparten un ancestro común, aunque no se hallan cercanamente relacionados con otros taxones de dos estipes, como el género *Kiaerograptus* y los taxones relacionados. A excepción de algunos taxones controversiales, las familias Tetragraptidae y Didymograptidae se diferencian notablemente a través de este análisis, justificando las interpretaciones previas de que ambas constituirían clados monofiléticos. Aunque los análisis presentados se encuentran pobremente soportados, proveen hipótesis que podrían ser comprobadas a la luz de mayor información proveniente de taxones de dichograptidos aislados o conservados en relieve.

Palabras clave. Graptolitos. Ordovícico. Floiano. Argentina. Filogenia.

GRAPTOLITES are understood as a nearly extinct group of hemichordates. A modern phylogenetic analysis adding morphological data drawn from the extant hemichordates *Cephalodiscus* and *Rhabdopleura* together with data on the major orders of graptolites revealed that the genus *Rhabdopleura* shares a number of synapomorphies with the graptolites. Thus, *Rhabdopleura* can be interpreted as an extant graptolite (Mitchell *et al.*, 2013) and used as a model for the understanding of graptolite anatomy and evolution. It is widely accepted that planktic graptolites appeared near the beginning of the Ordovician, originating from a benthic ancestor belonging to the order Dendroidea. The first planktic

species belongs to the genus *Rhabdinopora* Eichwald, 1855, of the family Anisograptidae and this group rapidly diversified during the Tremadocian (Bulman, 1970; Maletz, 1992; Cooper *et al.*, 1998). However, many relationships among graptolite clades remain uncertain due to lack of information about the proximal structure.

Graptolites have been traditionally described and taxonomically classified based on the general organization of their tubarium and the specific morphology of their stipes. However, many of these characters can be demonstrated as of polyphyletic nature (Bulman, 1970; Cooper and Fortey, 1982). As a result, a number of genera (and even families) of

graptolites, like *Tetragraptus* Salter, 1863 or *Didymograptus* M'Coy, 1851, were based on a limited number of morphological characteristics of their tubaria, some of which are strongly homoplastic and therefore are of questionable value for understanding the phylogeny of this fossil group. Rickards *et al.* (1977) carried out one of the pioneering works on graptolite phylogeny by producing the first synthesis of the Silurian and Early Devonian graptolite radiation, but this was before any cladistic analyses were produced. More recently, Cooper and Fortey (1982, 1983) and Mitchell (1987) focused on the characteristics of the proximal end of the colonies as the basis of phylogenetic systematics, where ancestor-descendant relationships may be inferred.

A major problem of the classification of graptolites is the frequently low number of morphological features related to the stipes or other tubarium features used in the analyses. The characters are often highly homoplastic and this fact limits their usefulness for understanding the phylogenetic relationships within this fossil group (Fortey and Cooper, 1986; Maletz, 2014). Thus, seemingly synapomorphic characters turn out to be homoplastic as is the case of the virgellar spine on the sicula (Maletz, 2010).

Most Ordovician graptolite genera are now defined on the basis of their proximal development patterns and thecal morphology (Cooper and Fortey, 1982; Williams and Stevens, 1988), following the idea that graptolites that share distinctive proximal end characters belong to monophyletic groups (Cooper and Fortey, 1982, 1983; Mitchell, 1986). Mitchell *et al.* (2007) proposed a phylogenetic classification for the order Diplogrptoidea based on the investigation of different morphological characters from the distal part, thecae, and the proximal development of several groups of biserial graptolites. Melchin *et al.* (2011) also studied the phylogenetic relationships of the biserial and monograptid graptolites from the Upper Ordovician–Lower Silurian. More recently, Maletz (2014) provided a comprehensive proposal for a taxonomic approach to the classification of the Pterobranchia (Cephalodiscida and Graptolithina). The author used a combination of phylogenetic systematics and traditional approach systematics, supported by cladistic analyses as a practical solution for the classification of the Graptolithina.

CLADISTIC ANALYSES

Phylogenetic systematics has largely replaced evolutionary taxonomic classification schemes, and uses cladistic analyses to recognize monophyletic groups that reflect the natural evolutionary process (Wiley, 1981). Cladistics produces a strict and exhaustive phylogeny, with binary branching trees, in which each taxon is defined as a clade, while evolutionary taxonomy produces a phylogeny that considers subjectively the morphology and which has a fixed hierarchy where the taxa are not always grouped in clades (Henning, 1975) and may not be monophyletic. The monophyletic nature of some graptolite taxa was tested in this paper. This principle means that the higher taxa include all the descendants of a common ancestor by evaluating previously selected characters and following the parsimony criterion, where the tree layout with the lowest number of steps is regarded as the best phylogenetic hypothesis for further discussion. However, in most of the cases the monophyly concept was not clearly represented and some problematic points appeared in the phylogenetic analysis that we discuss later.

The early phylogenetic analyses of graptolites used manually produced trees and stated an order of importance of the most significant characters. They applied the cladistic representation to address questions about phylogenetic relationships and classification problems between the taxa of the superfamily Dichograptacea and the family Glossograptidae (Fortey and Cooper, 1986; Maletz and Mitchell, 1996).

Several authors tried to understand the phylogenetic relationships of dichograptid graptolites by considering mainly characters of the proximal end of the colonies (Cooper and Fortey, 1982, 1983). This focus on the important characteristics of the proximal end of the graptolite tubarium favoured the introduction of new taxa such as the subgenera *Didymograptellus* Cooper and Fortey, 1982 and *Pendeograptus* Bouček and Přibyl, 1951, among others. More recently, proposals applying cladistic analysis to graptolite taxonomy emerged as a tool to explain and solve the phylogenetic relationships and evolution of the group.

Fortey *et al.* (2005) analyzed the origin and phylogenetic relationships of early biserial graptolites. The authors obtained a strict consensus tree and supported the discussion of the origins and phylogenetic relationships among diplograptids and glossograptids. Before carrying out the cladis-

tic analysis, they obtained new information from the proximal end of graptolites based on relief material, and their analysis included a greater number of such characters in comparison to those concerning the distal part of the tubarium and the thecal morphology. Similar studies including a majority of older –Early Ordovician– taxa are more scarce. However, a recent cladistic analysis of Tremadocian graptolites from China by Li *et al.* (2007) resulted in a consensus tree considering several evolutionary characters at the generic level. Some of the genera considered by these authors and additional taxa occurring in northwestern Argentina were used to gain a better understanding of the relationships of Ordovician graptolites. However, we prefer to work at the species level to corroborate evolutionary hypotheses, especially the monophyly of the two-stiped taxa and their relationships with other groups, as for example the Family Tetragraptidae.

Another comprehensive cladistic analysis to improve understanding of the phylogenetic relationships of Early to Middle Ordovician planktic graptolites was conducted recently by Maletz *et al.* (2009). The cladogram structure indicated several monophyletic groups, which were defined as orders, while the Dichograptoida was shown as a paraphyletic group. The interpretation of the resulting tree topology allowed the authors to validate previous qualitative assumptions, and contribute to the systematic classification of the group by producing a new classification for the planktic Graptoloidea. The authors defined sub-clades that appear within the suborder Pan-Glossograptina and superorder Pan-Sinograptina using the cladistic analysis. Some characters have demonstrated a stronger influence than others in the resulting classification, as they are more conservative, and consequently of greater phylogenetic importance. The authors related the low resolution within the individual taxonomic units to the limited number of species that they included in each group for the analysis. Recently, Maletz (2014) used a combination of traditional Linnaean taxonomy supported by cladistic analyses as a practical solution in the classification of Graptolithina.

The main purpose of this work was to test the hypothesis about graptolite relationships using the cladistic analysis to explain the evolutionary relationships between didymograptids or two-stiped taxa from the Early–Middle Ordovician and between this group and other taxa such as the

members of family Tetragraptidae. An additional goal was to study the phylogenetic importance of the different characters used in this work. Two main analyses were carried out to test the monophyly of the two-stiped taxa and others related taxa. The first analysis included the two-stiped taxa plus the tetragraptids and a number of multi-branched taxa. To explore the ancestor-descendent relationship of the two-stiped taxa, a second analysis was conducted including several more species of two-stiped taxa, and excluding the clade of tetragraptids. Some multi-branched taxa were used as outgroup in this analysis. The position of the taxa in the trees was analysed to observe their relationships, but excluding some controversial taxa that are discussed below. This paper also contributed to the knowledge of the evolutionary history of the graptolites, especially from northwestern Argentina and South America, helping to improve the graptolite database for future phylogenetic studies.

Institutional abbreviations. CEGH-UNC, collection of Cátedra de Estratigrafía y Geología Histórica, Universidad Nacional de Córdoba, Córdoba, Argentina; GSC, Type Collection Invertebrates and Fossil Plants of the Geological Survey of Canada; IANIGLA-PI, Paleoinvertebrate collection of Instituto Argentino de Nivología, Glaciología y Ciencias Ambientales, Mendoza, Argentina; LO, Collection of the Department of Geology, Lund University, Sweden; NIGP, Nanjing Institute of Geology and Palaeontology, China.

METHODS

In order to improve the resolution of the resulting trees (Figs. 1–2), a large number of Early Ordovician species was included in the current study. In addition to the data obtained from the material from northwestern Argentina, bibliographic information was also incorporated to complete the matrixes (Tabs. 1,3). In this analysis, we used phylogenetically important characters of the proximal end characters related to the distal part of the colonies (Fig. 3). The terms dichograptids, didymograptids, tetragraptids, ballograptids and expansograptids do not refer to any specific taxonomic level. They are used informally as commonly done in the literature (*e.g.*, Maletz *et al.*, 2009; Maletz, 2014 and references therein) to describe general groups of taxa based on morphological characters without attempting a taxonomic interpretation.

The matrix shown in Table 1 was constructed using the Mesquite software (Maddison and Maddison, 2011). It includes 33 taxa, largely species of the families Tetragraptidae and Didymograptidae, and 24 morphological characters with 59 separate states (see Tab. 2). Despite the limited number of characters used in this work it is important to highlight that the analysed data constitute a contribution to the graptolite database, and monophyletic relationships between different groups were established. Eighteen characters are binary and six are multi-state characters. Two multi-state characters are considered as ordered. Sixteen of the characters are associated with the proximal end, four with the thecal morphology and four with the stipe development. Most of the samples for character evaluation were collected from different stratigraphic sections located in the Sierra de Aguilar, Los Colorados, Cuesta de Toquero, La Quiaca, Pascha-Incamayo and Santa Victoria areas of northwestern Argentina (Toro, 1994, 1999; Toro and Maletz, 2007, 2008) and in a few cases morphological evaluation of characters had to be based on previously published

descriptions. Due to the impossibility of recovering chemically isolated material, the matrix was supplemented with literature data regarding tubarium and proximal end characters, based on carefully established synonymies. The number of taxa compared to the number of characters may still have limited the resolution of the internal structure of the resulting trees, but provides a considerable improvement over previous analyses.

This first analysis allowed observation of the relationships of two-stiped taxa to other taxa such as tetragraptids. The majority consensus tree is shown in Figure 1. In this tree, some relationships result controversial. As the majority tree takes the solution present in 50% of the trees, we decided to make a second analysis where a strict consensus tree was obtained that takes into consideration the solution present in all the cladograms (Fig. 2). In order to improve the resolution of the tree obtained in the analysis based on Table 1, another similar search was conducted, but at this time mostly didymograptid taxa were incorporated to the matrix presented in Table 3. Taxa such as *Pendeo-*

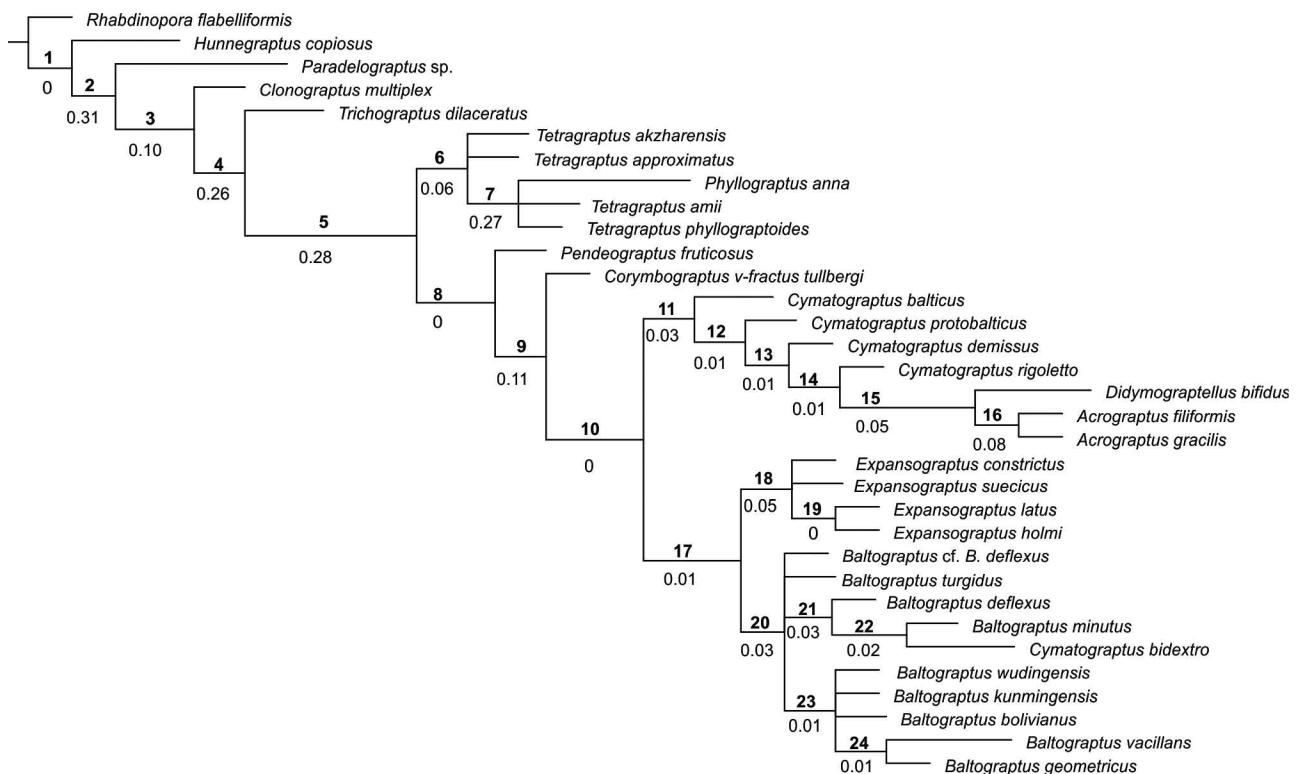


Figure 1. Majority consensus tree (50%) under implied weight (K=1) showing the synapomorphies for all taxa. Bold type number indicate node numbers and the number under branches indicate relative Bremer support values.

graptus fruticosus (Hall, 1858) and *Corymbograptus v-fractus tullbergi* (Monsen, 1937) that appeared in a controversial position were not included in the second analysis. It is expected that the quantification of valuable phylogenetic characters together with the selection of most of two-stiped specimens would help to clarify the relationships among these taxa. For this purpose, the matrix was designed using 29 taxa and 22 morphological characters with 54 states (Tabs. 3–4). *Rhabdinopora flabelliformis* (Eichwald, 1840) was chosen as outgroup taxon because it is interpreted as closely related to the other taxa but forms a basal taxon in relation to the whole group. Multi-branched species commonly recorded in the study area, such as *Hunnegraptus copiosus* Lindholm, 1991, and *Paradelograptus* sp. Erdtmann, Maletz and Gutiérrez Marco, 1987, were also included in the second phylogenetic analysis, and the species

Kiaerograptus supremus Lindholm, 1991, *Kiaerograptus kiaeri* (Monsen, 1925), *Didymograptus artus* Elles and Wood, 1901, *Xiphograptus lofuensis* (Lee, 1961) and *Aulograptus climacograptoides* (Bulman, 1931) were added from other sources for a more comprehensive analysis.

The phylogenetic analysis was performed using TNT software (Goloboff *et al.*, 2008). The data matrix was analysed using the implied weight method (IWA) and a $K=1-30$ range was explored for this analysis (Goloboff, 1993). Weighting of the characters means that the evidence in a specific tree is measured. The more consistent characters will be weighted, reducing the weight of the most homoplastic characters. The adjusted weight is a concave function of the homoplasy, being K the concavity constant; for this reason different K values for each analysis were chosen (see Goloboff, 1993, for more details about this

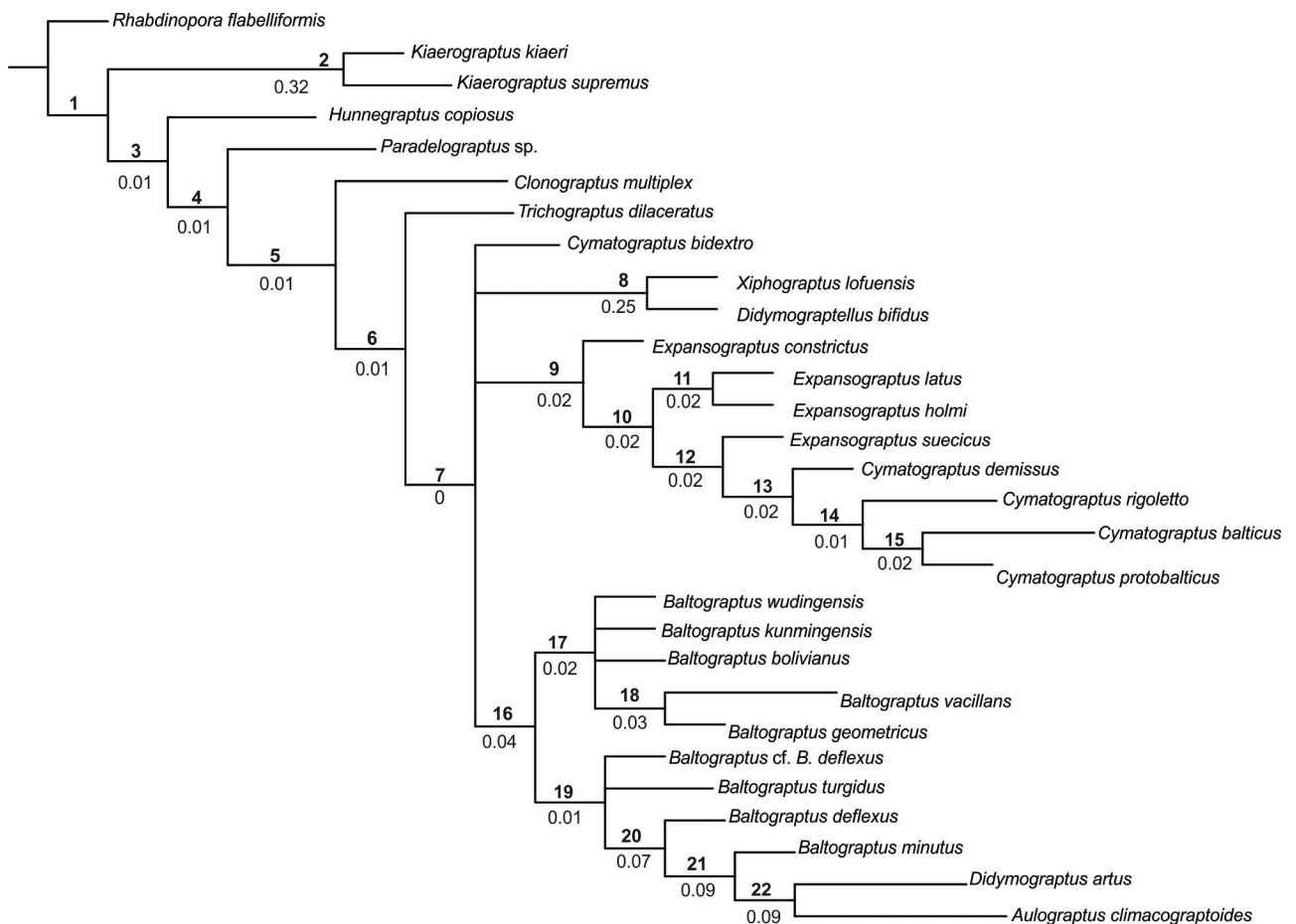


Figure 2. Strict consensus tree under implied weight ($K=2$) for two-stiped taxa. Bold type number indicate node numbers and the number under branches indicate relative Bremer support values.

TABLE 1. All taxa matrix.

Taxa	0	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23
Rhabdinopora flabelliformis	0	0	0	0	0	0	0	1	1	0	0	?	0	0	0	0	0	0	0	0	0	1	0	1
Clonograptus multiplex	1	1	0	0	0	1	0	0	1	2	1	?	0	0	1	0	0	0	0	0	1	3	1	0
Expansograptus suecicus	1	1	0	0	0	1	0	0	2	2	1	1	0	0	1	1	0	2	0	0	1	3	1	0
Expansograptus holmi	1	1	0	0	0	1	0	0	2	1	1	0	0	0	1	1	0	2	0	0	1	3	1	0
Expansograptus constrictus	1	1	0	0	0	1	0	0	2	2	1	0	0	0	1	1	0	2	0	0	1	3	1	0
Expansograptus latus	1	1	0	0	0	1	0	0	2	1	1	0	0	0	1	1	0	2	0	0	1	3	1	0
Cymatograptus bidextro	1	1	0	1	1	1	0	0	1	0	0	0	0	0	1	1	0	2	0	0	1	1	1	0
Cymatograptus demissus	1	1	0	0	0	1	0	0	2	2	1	1	0	0	1	1	0	2	1	0	1	1	1	0
Cymatograptus rigoletto	1	1	0	0	0	1	0	0	2	2	0	1	0	0	0	1	0	2	1	0	1	1	1	0
Cymatograptus protobalticus	1	1	0	0	0	1	0	0	2	3	2	1	0	0	1	1	0	2	1	0	1	1	1	0
Cymatograptus balticus	1	1	0	0	0	1	0	0	3	3	1	2	0	0	1	1	0	2	1	0	1	1	0	0
Baltograptus geometricus	1	1	1	0	0	1	0	0	2	1	0	0	0	0	1	1	0	2	0	0	1	1	1	0
Baltograptus vacillans	1	1	1	0	1	1	0	0	2	1	2	0	0	0	1	1	0	2	0	0	1	1	0	0
Baltograptus turgidus	1	1	1	0	0	1	0	0	2	2	1	0	0	0	1	1	0	2	1	0	1	2	1	0
Baltograptus cf. B. deflexus	1	1	1	0	0	1	0	0	1	0	1	0	0	0	1	1	0	2	0	0	1	2	1	0
Baltograptus deflexus	1	1	1	1	0	1	0	0	2	1	1	0	0	0	1	1	0	2	0	0	1	2	1	0
Baltograptus minutus	1	1	1	1	0	1	0	0	1	0	1	0	0	0	1	1	0	2	0	0	1	0	1	0
Baltograptus bolivianus	1	1	1	0	0	1	0	0	2	1	0	1	0	0	1	1	0	2	0	0	1	2	1	0
Baltograptus kunmingensis	1	1	1	0	0	1	0	0	2	1	0	0	0	0	1	1	0	2	0	0	1	2	1	0
Baltograptus wudingensis	1	1	1	0	0	1	0	0	2	1	0	0	0	0	1	1	0	2	0	0	1	2	1	0
Corymbograptus v-fractus t.	1	1	0	0	0	1	0	0	2	3	1	2	0	1	1	1	0	2	0	1	1	1	1	0
Tetragraptus phyllograptoides	1	1	0	0	0	1	0	0	2	2	1	?	0	1	1	1	0	1	0	1	1	4	1	0
Tetragraptus approximatus	1	1	0	0	0	1	0	0	2	2	1	1	0	1	1	1	0	1	0	1	1	3	1	0
Tetragraptus amii	1	1	0	0	0	1	0	0	3	1	0	0	0	1	1	1	0	1	0	1	1	4	1	0
Tetragraptus akzharensis	1	1	0	0	0	1	0	0	3	3	0	?	0	1	1	1	0	1	0	1	1	3	1	0
Acrograptus gracilis	1	1	0	0	0	1	1	1	1	0	0	0	0	0	0	1	0	2	1	0	1	1	1	0
Acrograptus filiformis	1	1	0	0	0	1	1	1	1	0	0	0	0	0	0	1	0	2	1	0	1	1	1	0
Paradelograptus sp.	1	1	0	0	0	1	1	1	0	0	0	0	0	1	0	0	1	0	0	1	1	1	0	0
Trichograptus dilaceratus	1	1	0	0	0	1	?	0	1	1	2	0	0	0	0	1	0	0	0	0	1	1	1	0
Pendeograptus fruticosus	1	1	0	0	0	1	0	0	2	3	1	2	0	1	1	1	0	1	0	1	1	0	1	0
Phyllograptus anna	1	1	0	0	0	1	0	0	2	0	0	?	1	1	1	1	0	1	1	1	1	5	1	0
Didymograptellus bifidus	1	1	0	0	0	1	0	1	1	0	0	0	1	0	1	1	0	2	1	0	1	0	1	0
Hunnegraptus copiosus	0	1	0	0	1	1	1	0	2	0	0	0	0	0	0	0	0	0	0	0	1	3	0	0

methodology). Both analyses were performed with a heuristic search of the most parsimonious trees. The search was performed using 1000 random trees, saving 10 trees per replicate, using the exchange algorithm (swapping) TBR (tree bisection reconnection). To assess the support of the branches of the obtained trees relative Bremer support was used (Bremer, 1994; Goloboff and Farris, 2001).

RESULTS

In the IWA analysis the homoplastic characters are weighted with a low value (Goloboff, 1993). The first char-

acter analysis for all taxa resulted in a number of phylogenetic trees that represent hypothetical evolutionary relationships between the studied species. The tree topology with $K=1$ was selected and 32 trees with a $\text{fit}=12.14$ were obtained for all the trees. The majority consensus tree has a consistency index (CI) of 0.36, a retention index (RI) of 0.60, the rescaling index was 0.22 and the index of homoplasy (HI) was 0.64, indicating a moderate amount of homoplasy. The branches of this tree present low relative Bremer support values.

In the second analysis, including a majority of the two-

TABLE 2. Coding characters for the all taxa analysis.

C0. Sicular bitheca (Maletz et al., 2009): (0) present; (1) absent.
C1. Bithecae along stipes (Maletz et al., 2009): (0) present; (1) absent.
C2. Origin of the Theca 1' (Maletz, 1994): (0) prosicula; (1) metasicula.
C3. Position of first dicalycal theca (Cooper and Fortey, 1983): (0) Th 1 ² (isograptid type); (1) Th 1' (artus type).
C4. Development mode (Cooper and Fortey, 1982; Maletz, 1994): (0) dextral; (1) dextral and sinistral.
C5. Nematularia (Erdtmann, 1982; Zeballo et al., 2005): (0) present; (1) absent.
C6. Metasicular shape (Maletz et al., 2009): (0) expanded; (1) parallel sided.
C7. Prosicular length (Carlucci, 2008): (0) proportionally short; (1) proportionally long.
C8. Sicula aperture width (mm) (Maletz et al., 2009): (0) <0.15; (1) between 0.15 and 0.25; (2) between 0.25 and 0.50; (3) >0.50.
C9. Sicula length (mm) (Maletz et al., 2009): (0) <1.5; (1) between 1.5 and 2; (2) between 2 and 2.5; (3) between 2.5 and 3.5.
C10. Sicula length/width ratio (Maletz et al., 2009): (0) between 2.9 and 5; (1) between 5 and 7.6; (2) >7.6.
C11. Sicular free wall length (mm) (Maletz et al., 1991): (0) between 0 and 0.50; (1) between 0.50 and 1; (2) >1.
C12. Presence of virgella (Maletz et al., 2009): (0) absent; (1) present.
C13. Sicular rutellum (Maletz et al., 2009): (0) absent; (1) present.
C14. Proximal branching style (Maletz et al., 2009): (0) asymmetric; (1) symmetric.
C15. Branching pattern (Maletz et al., 2009): (0) irregular; (1) regular.
C16. Thecal morphology (Bulman, 1970; Erdtmann et al., 1987; Jackson and Lenz, 2003): (0) dichograptid thecae; (1) kinnegraptid thecae.
C17. Maximum number of stipes (Maletz et al., 2009): (0) more than 4; (1) 4; (2) 2.
C18. Thecal overlap (Maletz et al., 2009): (0) uniform; (1) increasing distally.
C19. Thecal rutellum (Maletz et al., 2009): (0) absent; (1) present.
C20. Presence of dissepiments (Maletz et al., 2009): (0) present; (1) absent.
C21. Stipe attitude (Bulman, 1970): (0) pendent; (1) declined; (2) deflexed; (3) horizontal; (4) reclined; (5) scandent.
C22. Stipe width (Cooper and Fortey, 1982): (0) uniform; (1) variable.
C23. Branching (Maletz et al., 2009): (0) dichotomous; (1) cladial.

stiped taxa, the tree topology with K=2 was selected and 3 most parsimonious trees (fit=8.82) were obtained for all the trees. The strict consensus tree has a CI of 0.38, a RI of 0.54,

a rescaled index of 0.20 and an HI of 0.62. The values of these indices indicate a moderate amount of homoplasy. There is a polytomy at the base of the didymograptid branch

TABLE 3. Two-stiped taxa matrix.

Taxa	0	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21
Rhabdinopora flabelliformis	0	0	0	0	0	0	0	1	1	0	0	?	0	0	0	0	0	0	0	1	0	1
Clonograptus multiplex	1	1	0	0	0	1	0	0	1	2	1	?	0	1	0	0	0	0	1	3	1	0
Expansograptus suecicus	1	1	0	0	0	1	0	0	2	2	1	1	0	1	1	0	1	0	1	3	1	0
Expansograptus holmi	1	1	0	0	0	1	0	0	2	1	1	0	0	1	1	0	1	0	1	3	1	0
Expansograptus constrictus	1	1	0	0	0	1	0	0	2	2	0	0	0	1	1	0	1	0	1	3	1	0
Expansograptus latus	1	1	0	0	0	1	0	0	2	1	1	0	0	1	1	0	1	0	1	3	1	0
Cymatograptus bidextro	1	1	0	1	1	1	0	0	1	0	0	0	0	1	1	0	1	0	1	1	1	0
Cymatograptus demissus	1	1	0	0	0	1	0	0	2	2	1	1	0	1	1	0	1	0	1	1	1	0
Cymatograptus rigoletto	1	1	0	0	0	1	0	0	2	2	0	1	0	0	1	0	1	1	1	1	1	0
Cymatograptus protobalticus	1	1	0	0	0	1	0	0	2	3	2	1	0	1	1	0	1	1	1	1	1	0
Cymatograptus balticus	1	1	0	0	0	1	0	0	3	3	1	2	0	1	1	0	1	1	1	1	0	0
Baltograptus geometricus	1	1	1	0	0	1	0	0	2	1	0	0	0	1	1	0	1	0	1	1	1	0
Baltograptus vacillans	1	1	1	0	1	1	0	0	2	1	2	0	0	1	1	0	1	0	1	1	0	0
Baltograptus turgidus	1	1	1	0	0	1	0	0	2	2	1	0	0	1	1	0	1	1	1	2	1	0
Baltograptus cf. B. deflexus	1	1	1	0	0	1	0	0	1	0	1	0	0	1	1	0	1	0	1	2	1	0
Baltograptus deflexus	1	1	1	1	0	1	0	0	2	1	1	0	0	1	1	0	1	0	1	2	1	0
Baltograptus minutus	1	1	1	1	0	1	0	0	1	0	1	0	0	1	1	0	1	0	1	0	1	0
Baltograptus bolivianus	1	1	1	0	0	1	0	0	2	1	0	1	0	1	1	0	1	0	1	2	1	0
Baltograptus kunmingensis	1	1	1	0	0	1	0	0	2	1	0	0	0	1	1	0	1	0	1	2	1	0
Baltograptus wudingensis	1	1	1	0	0	1	0	0	2	1	0	0	0	1	1	0	1	0	1	2	1	0
Paradelograptus sp.	1	1	0	0	0	1	1	1	0	0	0	0	0	0	0	1	0	0	1	1	0	0
Trichograptus dilaceratus	1	1	0	0	0	1	?	0	1	1	2	0	0	0	1	0	0	0	1	1	1	0
Didymograptellus bifidus	1	1	0	0	0	1	0	1	1	0	0	0	1	1	1	0	1	1	1	0	1	0
Hunnegraptus copiosus	0	1	0	0	1	1	1	0	2	0	0	0	0	0	0	0	0	0	1	3	0	0
Kiaerograptus supremus	0	0	0	0	0	1	1	0	3	1	1	0	0	1	1	0	1	0	1	1	0	0
Kiaerograptus kiaeri	0	0	0	0	0	1	1	0	3	0	0	?	0	1	1	0	1	0	1	1	0	0
Xiphograptus lofuensis	1	1	0	0	0	1	0	1	2	0	0	0	1	1	1	0	1	1	1	3	1	0
Aulograptus climacograptoides	1	1	2	0	0	1	0	0	2	1	1	0	0	1	1	2	1	0	1	0	0	0
Didymograptus artus	1	1	2	1	?	1	1	0	2	0	0	?	0	1	1	0	1	1	1	0	1	0

(Fig. 2: node 7), indicating that the phylogenetic relationships of the didymograptids have not been fully resolved and need further attention. However, the splitting of two clades within the didymograptids can be considered as an interesting and important result from the point of view of graptolite classification. One of them includes the species of the genera *Expansograptus* Bouček and Přibyl, 1951, and *Cymatograptus* Jaanusson, 1965, and the other one includes the species of the genus *Baltograptus* Maletz, 1994. Relative Bremer support for IWA shows a low support values for all the nodes. In both cladograms, anisograptids represent the ancestral group, chosen a priori as outgroup, from which the derived planktic graptolites evolved.

Phylogenetic relationship for two-stiped taxa and multi-branched taxa

The IWA (K=1) for all taxa shows a cladogram with two major clades (Fig. 1). One of the clades in the obtained tree includes most species of the genus *Tetragraptus* and also *Phyllograptus anna* Hall, 1865. The second clade includes most of the two-stiped taxa plus *Pendeograptus fruticosus* and *Corymbograptus v-fractus tullbergi*. *Rhabdinopora flabelliformis* (Fig. 3.4, 11) and *Hunnegraptus copiosus* (node 1) are stem to the rest of the taxa in the tree. *Paradelograptus* sp. (node 2), *Clonograptus multiplex* (Nicholson, 1868) (node 3) and *Trichograptus dilaceratus* (Herrmann, 1885) (node 4) share the synapomorphy 'presence of sicular bitheca' (0¹)

TABLE 4. Coding characters for two-stiped taxa analysis.

C0. Sicular bitheca (Maletz et al., 2009): (0) present; (1) absent.
C1. Bithecae along stipes (Maletz et al., 2009): (0) present; (1) absent.
C2. Origin of the Theca 1 ¹ (Maletz, 1994): (0) prosicula; (1) high in the metasicula; (3) low in the metasicula.
C3. Position of first dicalyca theca (Cooper and Fortey, 1983): (0) Th 1 ² (isograptid type); (1) Th 1 ¹ (artus type).
C4. Development mode (Cooper and Fortey, 1982; Maletz, 1994): (0) dextral; (1) dextral and sinistral.
C5. Nematularia (Erdtmann, 1982; Zeballo et al., 2005): (0) present; (1) absent.
C6. Metasicular shape (Maletz et al., 2009): (0) expanded; (1) parallel sided.
C7. Prosicula length (Carlucci, 2008): (0) proportionally short; (1) proportionally long.
C8. Sicular aperture width (mm) (Maletz et al., 2009): (0) <0.15; (1) between 0.15 and 0.25; (2) between 0.25 and 0.50; (3) >0.50.
C9. Sicular length (mm) (Maletz et al., 2009): (0) <1.5; (1) between 1.5 and 2; (2) between 2 and 2.5; (3) between 2.5 and 3.5.
C10. Sicular length/width ratio (Maletz et al., 2009): (0) between 2.9 and 5; (1) between 5 and 7.6; (2) >7.6.
C11. Sicular free wall length (mm) (Maletz et al., 1991): (0) between 0 and 0.50; (1) between 0.50 and 1; (2) >1.
C12. Presence of virgella (Maletz et al., 2009): (0) absent; (1) present.
C13. Proximal branching style (Maletz et al., 2009): (0) asymmetric; (1) symmetric.
C14. Branching pattern (Maletz et al., 2009): (0) irregular; (1) regular.
C15. Thecae morphology (Bulman, 1970; Erdtmann et al., 1987; Jackson and Lenz, 2003): (0) dichograptid thecae; (1) climacograptid (geniculate) thecae.
C16. Maximum number of stipes (Maletz et al., 2009): (0) more than 4; (1) 4; (2) 2.
C17. Thecal overlap (Maletz et al., 2009): (0) uniform; (1) increasing distally.
C18. Presence of dissepiments (Maletz et al., 2009): (0) present; (1) absent.
C19. Stipe attitude (Bulman, 1970): (0) pendent; (1) declined; (2) deflexed; (3) horizontal.
C20. Stipes width (Cooper and Fortey, 1982): (0) uniform; (1) variable.
C21. Proximal dicalyca thecae (Bulman, 1970): (0) 3; (1) 1.

(Fig. 3.12), being a paraphyletic group that stems the family Tetragraptidae, the species *Phyllograptus anna* and the two-stiped species. This group (node 5) is supported by the synapomorphies: 'sicular aperture width' (8²), 'sicular rutellum' (13¹) (Fig. 3.8), 'maximum number of stipes' (17¹) and 'thecal rutellum' (19¹).

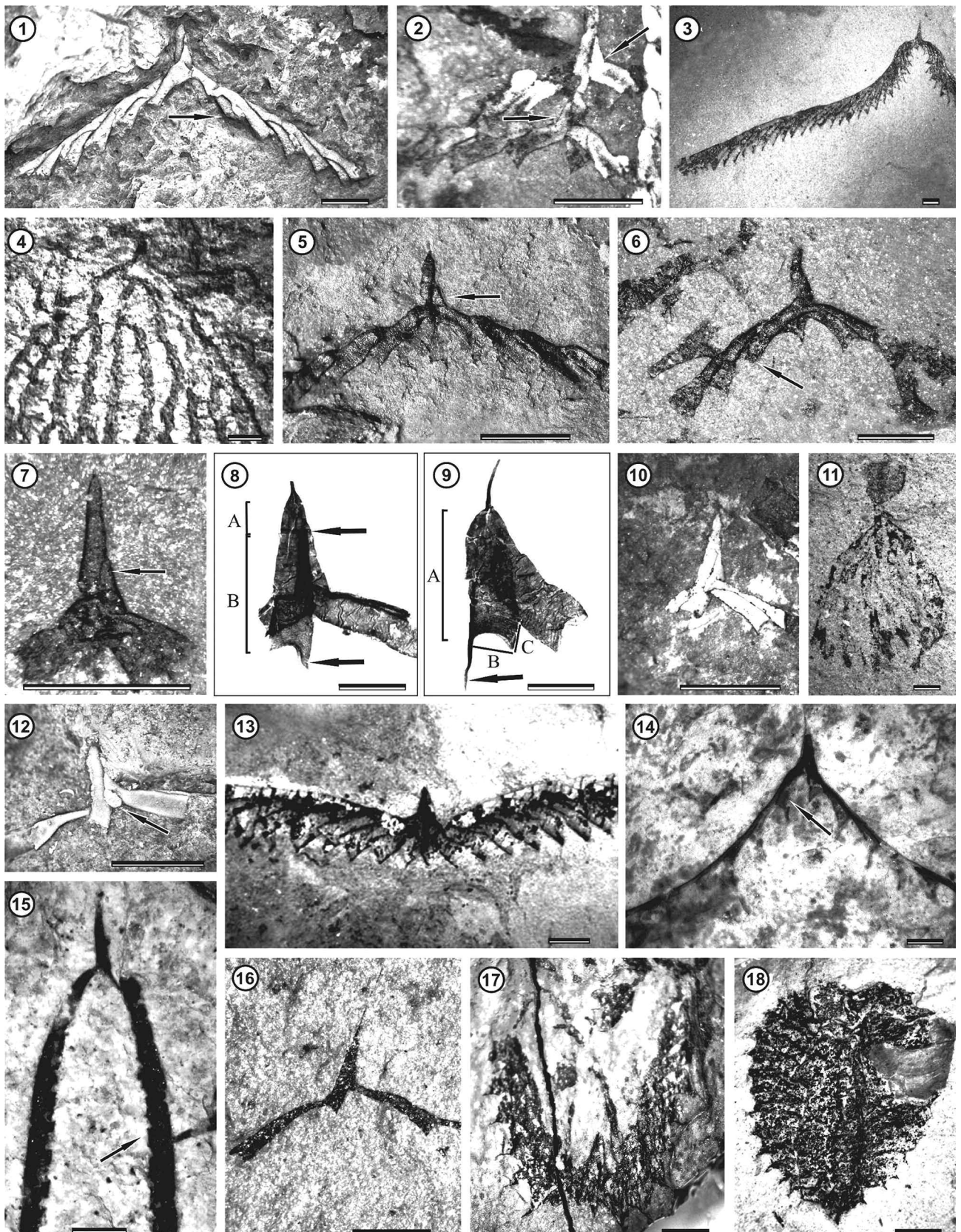
The synapomorphy 'stipe attitude' (21³) supports the node (6) with a trichotomy that groups *Tetragraptus* and *Phyllograptus anna*. However, *Tetragraptus phyllograptoides* Strandmark, 1902, *Tetragraptus amii* Elles and Wood, 1902 and *P. anna* (Fig. 3.18) are grouped and supported by the state change of synapomorphy (21⁴) (node 7). *Tetragraptus approximatus* Nicholson, 1873, is separated by the autapomorphies 'sicular free wall length' (11¹) and *Tetragraptus akzharensis* Tzaj, 1969, by the autapomorphies 'sicular apertural width' (8³) and 'sicular length' (9³). *Phyllograptus anna* shows the autapomorphies 'sicular length' (9⁰), 'presence of virgella' (12¹), 'thecal overlap' (18¹), and 'state change of stipe attitude' (21⁵). *Tetragraptus amii* shows the autapomorphies 'sicular apertural width' (8³) and 'sicular length' (9¹).

The didymograptids are grouped (node 10) by the state change of the synapomorphies 'sicular rutellum' (13⁰) and 'thecal rutellum' (19⁰). *Pendeograptus fruticosus* and *Corymbograptus v-fractus tullbergi* are excluded, being the stem of this clade. Although these two taxa share the synapomorphies 'sicular length' (9³) and 'sicular free wall length' (11²) with

the didymograptids (nodes 8 and 9), they are separated because of the 'loss of the sicular' (13⁰) and 'thecal rutellum' (19⁰); this issue is discussed in detail later. The two-stiped taxa are divided into two clades (node 10), one of these including *Baltograptus* and *Expansograptus* (node 17), and the other *Acrograptus* Tzaj, 1969, and *Didymograptellus* associated with species of *Cymatograptus* (node 11). The *Baltograptus* clade and the genus *Expansograptus* are grouped by the two synapomorphies 'sicular free wall length' (11⁰) and the 'stipe attitude' (21²).

The clade including the genera *Cymatograptus*, *Didymograptellus* and *Acrograptus* (node 11) appears as a sister group to the *Baltograptus* and *Expansograptus* clade. The three taxa are connected by the characters of the 'prosicular length' (7¹), 'sicular apertural width' (8¹), 'sicular length' (9⁰) and 'sicular free wall length' (11⁰) (node 15). A dichotomy separating *Didymograptellus bifidus* (Hall, 1865) from *Acrograptus filiformis* (Tullberg, 1880) (Fig. 3.16) and *Acrograptus gracilis* (Törnquist, 1890) is shown. The supporting synapomorphy of the node 16 is the metasicular shape (6¹). At the same time, the last mentioned three species (*Didymograptellus bifidus*, *Acrograptus filiformis* and *A. gracilis*), are sister to *Cymatograptus rigoletto* (Maletz, Rushton and Lindholm, 1991) (node 14) by the synapomorphy 'sicular length/ width ratio' (10⁰). *Cymatograptus demissus* (Törnquist, 1901) joins the group (node 13) by the 'sicular length'

Figure 3. Illustration of some of the characters used for the cladistic analysis. **1**, *Kiaerograptus supremus*, Krapperup core, Sweden LO 5970T, holotype, exhibiting bithecae along stipes. **2, 5**, *Cymatograptus bidextro*, Los Colorados area, Argentina; **2**, IANIGLA-PI 1798, two specimens showing sinistral development in obverse (upper) and reverse (lower) views; **5**, IANIGLA-PI 1813, specimen with dextral *artus* type of development and declined stipe attitude; the arrow indicates the position of dicalycal theca th1¹. **3, 7**, *Baltograptus turgidus*, Santa Victoria area, Argentina; **3**, CEGH-UNC 17553, complete mature specimen showing deflexed stipe attitude; **7**, IANIGLA-PI 1824, proximal end exhibiting metasicular origin of th1¹. **4**, *Rhabdinopora flabelliformis parabola*, Salar del Rincón, Argentina, CEGH-UNC 24884, multiramous specimen demonstrating presence of dissepiments. **6, 10**, *Baltograptus geometricus*; **6**, IANIGLA-PI 1825, Santa Victoria, Argentina, arrow indicates the dicalycal theca th1² (isograptid type of development); **10**, CEGH-UNC 24895, Los Colorados area, Argentina, juvenile specimen showing expanded metasicular shape. **8**, *Acrograptus* sp., Cow Head Group, western Newfoundland, Sweden, GSC 138209, isolated proximal end showing: **A**, prosicular length; **B**, metasicula, arrows indicating prosicular origin of the th1¹ and rutellum on sicular. **9**, *Didymograptellus bifidus*, GSC 133430, Cow Head Group, western Newfoundland, Sweden, juvenile specimen showing: **A**, sicular aperture width; **C**, sicular free wall length, arrow indicating virgellar spine. **11**, *Rhabdinopora proparabola*, Dayangcha, Jilin, China, NIGP 163138, complete specimen exhibiting nematularium. **12**, *Paradelograptus* sp. 1, GSC 118739, Artic Canada, proximal end with sicular bitheca; **14**, *Paradelograptus* sp. 2, CEGH-UNC 24900, Huancar, proximal portion of the tubarium with details of the kinnegraptid thecae. **13**, *Expansograptus constrictus*, CEGH-UNC 7541, Los Colorados area, Argentina, specimen showing horizontal stipe attitude with proximal reflection and dichograptid thecal morphology. **15**, *Aulograptus climacograptoides*, IANIGLA-PI 1008, Cuesta de Toquero, Argentina, showing pendent stipe attitude and climacograptid (geniculate) thecal morphology. **16**, *Acrograptus filiformis*, CEGH-UNC 4985, Río Cajas Creek area, proximal portion showing parallel sided metasicula and asymmetric proximal branching style. **17**, *Tetragraptus* sp., CEGH-UNC 24925, Santa Victoria area, Argentina specimen exhibiting reclined stipe attitude. **18**, *Phyllograptus anna*, CEGH-UNC 11268, Chamarra Creek, Los Colorados area, Argentina, complete specimen showing scandent stipe attitude. **1–7, 10–18**, scale bar= 1 mm; **8–9**, scale bar= 0.5 mm.



(9²); then *Cymatograptus protobalticus* (Monsen, 1937) by the 'sicular free wall length' (11¹) (node 12) and finally they are grouped with *C. balticus* (Tullberg, 1880) by the synapomorphy 'thecal overlap' (18¹).

Expansograptus species are grouped (node 18) by a trichotomy due to the state change of the synapomorphy 'stipe attitude' (21³) and it includes *Expansograptus constrictus* (Hall, 1865) (Fig. 3.13), *Expansograptus suecicus* (Tullberg, 1880), *Expansograptus latus* (Hall, 1907) and *Expansograptus holmi* (Törnquist, 1901) (node 19).

The *Baltograptus* clade (node 20) is supported by the synapomorphy 'origin of the theca 1' (2¹) (Fig. 3.7). It could be considered hypothetically as a monophyletic group, but *C. bidextro* is located in this group. Additionally, a polytomy appears at the base of this clade (Fig. 1) showing the group as polyphyletic. This polytomy separates *Baltograptus* cf. *B. deflexus* (= *B. sp. nov.* in Toro and Maletz, 2007; = *B. sp. cf. B. deflexus sensu* Maletz and Ahlberg, 2011; = '*B. cf. B. deflexus*' in Toro and Vento, 2013) and *Baltograptus turgidus* (Lee, 1974) from the other *Baltograptus* species. *Baltograptus deflexus* (Elles and Wood, 1901) and *Baltograptus minutus* (Törnquist, 1879) are separated by the position of the first 'dicalyca theca' (3¹) together with *Cymatograptus bidextro* Toro and Maletz, 2008 (Fig. 3.2, 5) (node 21). *Baltograptus minutus* and *C. bidextro* share the synapomorphies: 'sicular apertural width' (8¹) and the 'stipe attitude' (21¹) (node 22) but their relationship is uncertain (Fig. 1) because the taxon *C. bidextro* was described and identified as a member of the genus *Cymatograptus* (Toro and Maletz, 2008). However, the relationship of *C. bidextro* with the genus *Baltograptus* is not supported in the second analysis, where it appears in the basal polytomy of the didymograptids, indicating a questionable relationship to the genus *Cymatograptus* (Fig. 2). Although *Baltograptus minutus* and *Cymatograptus bidextro* share an *artus* type of development (Fig. 1), *C. bidextro* differs from the group of baltograptids by the prosicular origin of the first theca. The other baltograptids such as *Baltograptus wudingensis* (Lin, 1979 in Mu *et al.*, 1979), *Baltograptus kunningensis* (Ni, 1979 in Mu *et al.*, 1979), *Baltograptus bolivianus* (Finney and Branisa, 1984), *Baltograptus vacillans* (Tullberg, 1880) and *Baltograptus geometricus* (Törnquist, 1901) (Fig. 3.6) are grouped (node 23) by the synapomorphy 'sicular length/ width ratio' (10⁰). Also, the two last taxa (node 24) share the synapomorphy 'stipe attitude' (21¹).

Phylogenetic relationship for most two-stiped taxa

The presence of two stipes tubaria cannot be taken as a defining synapomorphic character because it is an easy achievement through the loss of subsequent branching. Thus, it is not surprising that *Kiaerograptus supremus* (Fig. 3.1) and *K. kiaeri* are clearly separated (node 2) from the other two-stiped taxa in this analysis (Fig. 2). They are grouped by the following synapomorphies: 'sicular apertural width' (8³), 'proximal branching style' (13¹), 'branching pattern' (14¹) and 'maximum number of stipes' (16¹) and are also united by the retention of the bithecae as a symplesiomorphic character. The other taxa are separated by the 'absence of bithecae along the stipes' (1¹) (node 1). *Hunnegraptus copiosus* is separated and the rest of the taxa are united by the synapomorphy 'absence of sicular bitheca' (0¹) (node 3). *Paradelograptus* sp. is separated (node 4) and the other taxa are associated by a node (5) that shows the synapomorphies 'metasicular shape' (6⁰) and 'stipe width' (20¹). *Clonograptus multiplex* is separated and the other species are united by the branching pattern (14¹). In the same way, *Trichograptus dilaceratus* is separated (node 6) and a node (7) groups the remaining taxa by the character 'maximum number of stipes' (16¹). This node shows a polytomy and *Cymatograptus bidextro* is separated by the autapomorphies 'position of the first dicalyca theca' (3¹) and the 'development mode' (4¹). A node (8) groups *Didymograptellus bifidus* and *Xiphograptus lofuensis* by the following synapomorphies: 'prosicula length' (7¹), 'presence of virgella' (12¹) (Fig. 3.9) and 'thecal overlap' (17¹). The third node in the polytomy associates species of the genera *Expansograptus* and *Cymatograptus*, except *C. bidextro* (node 9) by the character states 'sicular length' (9²) and 'stipe attitude' (19³). *Expansograptus constrictus* is separated (node 10) and *E. latus* and *E. holmi* are grouped (node 11) by the character state change 'sicular length' (9¹). *Expansograptus suecicus* is associated with species of the genus *Cymatograptus* (node 12) by the synapomorphy 'sicular free wall length' (11¹) (Fig. 3.9). The *Cymatograptus* species are grouped (node 13) by the 'stipe attitude' (19¹) and *C. balticus* and *C. protobalticus* stay together (node 15) by the synapomorphy 'sicular length' (9³). These last two species and *C. rigoletto* are grouped by the synapomorphy 'prosicula length' (7¹) (node 14).

Another node (16) in the polytomy groups the species of the genus *Baltograptus* together with *Didymograptus artus*

and *Aulograptus climacograptoides* by the character 'origin of the theca 1'' (2¹). Although this clade could be hypothetically considered as a monophyletic group, several polytomies are shown within it, highlighting the overriding importance of the proximal end characters, the isograptid and *artus* type proximal developments. A polytomy (node 17) groups *B. wudingensis*, *B. kunmingensis*, *B. bolivianus* together with *B. geometricus* and *B. vacillans* by the synapomorphy 'sicular length' (9¹). *Baltograptus geometricus* and *B. vacillans* (node 18) also share the character 'stipe attitude' (19¹) and all species share the isograptid development (Fig. 3.10). The next branch groups (node 19) the remaining *Baltograptus* species by the synapomorphy 'sicular length/width ratio' (10¹). *Baltograptus* cf. *B. deflexus* and *B. turgidus* are separated, and *B. deflexus*, *B. minutus*, *D. artus* and *A. climacograptoides* (Fig. 3.15) are associated (node 20) through the position of the 'first dicalyca theca' (1¹) (*artus* type proximal development). Finally, *B. minutus*, *D. artus* and *A. climacograptoides* (node 21) share the synapomorphy 'stipe attitude' (19⁰) but the last two species mentioned before (node 22) are grouped by the synapomorphy 'origin of theca 1'' (2²).

DISCUSSION

Graptolite taxonomists recognize that all characters cannot be weighted equally due to the presence of a considerable amount of homoplasy (Fortey and Cooper, 1986). Thus the implied weight method was used to reduce the impact of homoplasies and the trees obtained are discussed below.

The most remarkable characteristic of the tree in Figure 1, that also includes the outgroup *Rhabdinopora flabelliformis*, is the subdivision into two major clades. One of them is the monophyletic group comprising the species of *Tetragraptus* and *P. anna*, while the other clade includes two-stiped taxa, such as the genera *Baltograptus*, *Expansograptus* and *Cymatograptus* and the species *P. fruticosus* together with *Corymbograptus v-fractus tullbergi*. The presence of the genera *Tetragraptus* and *Phyllograptus* Hall, 1858 in the same clade is a consistent result according to the proposal of Maletz *et al.* (2009); however, in this paper *P. fruticosus* is included in the Superorder Pan Tetragraptia. In our work we considered the use of the families Tetragraptidae and Didymograptidae even though the position of the taxon *P.*

fruticosus is controversial and further work on the genus *Pendeograptus* is necessary to solve the problem.

In both cladograms (Figs. 1–2), *R. flabelliformis* was chosen as the outgroup because it represents the most ancestral taxon from which all other planktic graptolites originated, following the phylogenetic analyses performed previously by several authors (Fortey and Cooper, 1986; Maletz *et al.*, 2009). However, *Hunnegraptus copiosus* is separated from the rest of the anisograptid taxa by the presence of a sicular bitheca but lacking thecal bithecae, and it was recently included in the Anisograptidae by Maletz (2014).

It is important to point out that in our analysis *Clonograptus multiplex*, *Paradelograptus* sp., and *Trichograptus dilaceratus* are stem to the clades mentioned above, and they share the character of possessing more than two stipes, this being a plesiomorphic state of the mentioned character. The early separation of *Paradelograptus* sp. and *Trichograptus dilaceratus* from the families Tetragraptidae and Didymograptidae could indicate that they belong to a different clade, rather than being considered ancestral of the tetragraptids and didymograptids. This is coherent with the proposal of Maletz *et al.* (2009), who included them in the Suborder Sinograptia. More recently, Maletz (2014) referred *Paradelograptus* to the family Sigmagraptidae.

The tetragraptids are shown here as a monophyletic group which could have evolved from a multiramous ancestor in the Dichograptina (cf. Maletz, 2014). The Tetragraptidae was defined as a monophyletic group (Maletz *et al.*, 2009), which contradicts the notion of Maletz and Mitchell (1996) that isograptids originated from a reclined tetragraptid ancestor (Maletz, 2014) in which case the Tetragraptidae would have to be understood as a paraphyletic taxon. The origin of this clade is associated with several synapomorphies including the four-branched tubarium, whose phylogenetic importance would be related to the maximum number of distal dicalyca thecae as suggested by Maletz *et al.* (2009). In this analysis, *Tetragraptus akzharensis*, *T. approximatus*, *T. amii* and *T. phyllograptoides* are grouped together. The latter two species are associated with *Phyllograptus anna*, indicating that this species –and with the phyllograptid clade– evolved from a taxon related to the genus *Tetragraptus*.

Fortey and Cooper (1986) argued that the subfamily Tetra-

graptinae is a sister group of the subfamily Dichograptinae, and can be included in the family Dichograptidae, while Carlucci (2008) indicated that tetragraptids are monophyletic, and a sister group of glossograptids. Carlucci (2008) classified tetragraptids as a separate order (Pan-Tetragrapt), which also includes *Phyllo-graptus typus* Hall, 1858. Fortey and Cooper (1986) included the genus *Phyllograptus* in the order Virgellina and later (Maletz *et al.*, 2009; Maletz, 2014) suggested its inclusion in the Tetragrapt, on the basis of the proximal development. Even though this genus has a dorsal virgella as does *Xiphograptus* Cooper and Fortey, 1982, the origin of this character evolved independently in each of these genera (*sensu* Maletz *et al.*, 2009; Maletz, 2010).

The interpretations of the phylogenetic relationships of the genus *Pendeograptus* are controversial. The genus may have originated from pendent bryograptids and anisograptids according to Erdtmann (1985). Other authors postulated that this genus is not related to *Bryograptus* Lapworth, 1880, since the latter possesses sicular and thecal bithecae (Spjeldnaes, 1963; Li *et al.*, 2007; Maletz *et al.*, 2010). In a cladistic analysis conducted by Maletz *et al.* (2009), the authors emphasized that *Pendeograptus fruticosus* should be included in the order Tetragrapt and also highlighted its close relationship to the genus *Corymbograptus* Obut and Sobolevskaya, 1964, because of the similarities of their proximal ends (Maletz, 1994). According to our results, *P. fruticosus*, together with *Corymbograptus v-fractus tullbergi* are shown as stem of the didymograptid clade (Fig. 1). This result shows a controversial position for the taxa *Corymbograptus v-fractus tullbergi* and *P. fruticosus* in the phylogenetic tree, and is not in agreement with the phylogenetic analysis of Maletz *et al.* (2009) and the interpretation of Maletz (2014) including both taxa in the family Tetragraptidae. Future analysis considering a larger number of taxa and probably additional morphological information of the genera *Pendeograptus* and *Corymbograptus* may be needed to clarify their possible relationships to the didymograptids.

Fortey and Cooper (1986) classified the dichograptids as a subfamily within the superfamily Dichograptidae. This situation is quite different from the interpretation of Maletz *et al.* (2009), who obtained a resulting tree with low support in which the relationship between stem reclinatids, dichograptids (in the traditional classification) and Tetragrapt

is uncertain. The tubarium characteristics of the dichograptids suggest that this group may have arisen following several phylogenetic pathways and for this reason polytomies are present in the tree (Fortey and Cooper, 1986).

According to our analysis (Fig. 1), didymograptids together with the controversial taxa *Pendeograptus fruticosus* and *Corymbograptus v-fractus tullbergi* are shown as a large clade and as a sister group of the tetragraptids. The node that groups the two-stiped taxa is formed by several uniting characters as mentioned above, although the resulting tree includes several internal polytomies. Some of the most important characters in the didymograptid clade (Fig. 1) are the maximum number of stipes, reduced to two and the lack of sicular and thecal rutelli. In the subsequent analysis including mostly two-stiped taxa (Fig. 2), a clade comprising the *Baltograptus* species and derived ones can be observed. Although this clade includes several polytomies, the whole group stands out as a monophyletic taxon, from which the *Baltograptus* species with *artus* proximal end development, such as *B. deflexus* and *B. minutus*, as well as *Didymograptus artus* and *Aulograptus climacograptoides* may have evolved. Maletz (1994) suggested that *D. artus* descended from a common ancestor in the genus *Baltograptus* and this hypothesis is also supported in our work. The genus *Baltograptus* is a clear example that characters such as the stipe attitude do not have great phylogenetic significance because the same character may vary even within a single species (e.g., *Baltograptus vacillans*, Maletz, 1994).

In the other clade, *Didymograptellus bifidus* is found together with the genera *Acrograptus* and *Cymatograptus* (Fig. 1). This clustering suggests a monophyletic origin for the mentioned taxa and the clade represents a sister group to the genus *Baltograptus* and *Expansograptus*. Bulman (1970) suggested a polyphyletic origin for the genus *Didymograptus* and grouped the two-stiped taxa together, without considering other characters such as the stipe attitude or the proximal end features. According to the phylogenetic analysis herein a monophyletic origin of *Expansograptus* and *Cymatograptus* (excluding *C. bidextro*) is recognized. These genera are contemporary and the analysis suggests that they could have evolved from a common ancestor. According to Maletz (2014) the genera *Aulograptus*, *Baltograptus*, *Cymatograptus*, *Didymograptus* and *Expansograptus* are grouped in the family Didymograptidae, a small family of two-stiped dichograpt-

tids with a fairly symmetrical disposition of the stipes, a large sicula with a relatively small prosicula and simple thecae along the stipes, and certainly originated from a multi-ramous ancestor, but details are not available.

The inclusion of the genus *Acrograptus* (Fig. 1) as sister group to the genus *Didymograptellus* may show the limitations of the analysis. Maletz (2014) included *Acrograptus* in the Sinograptina and especially in the family Sigmagraptidae based on the development of the proximal end. A relationship to *Didymograptellus* is unlikely comparing the development of the sicula and the lack of a virgellar spine in *Acrograptus*. A correct placement of *Acrograptus* would only be possible by including more taxa of the Sigmagraptidae in the analysis, enhancing the relevance of the sigmagraptine proximal end development in such analysis.

The characters 'prosicular length', 'sicular apertural width', 'sicular length' and 'sicular free wall length' (Fig. 3.8–9) would group *D. bifidus* along with the two *Acrograptus* species. The tree obtained here (Fig. 1) shows that the two genera could have originated from an ancestor belonging to the genus *Cymatograptus* such as *C. rigoletto*. However, *D. bifidus* is grouped with *Xiphograptus lofuensis* in Figure 2. According to Maletz et al. (2009) *Didymograptellus* is a sister taxon of *Acrograptus* with a common ancestor with *X. lofuensis* and *Pterograptus elegans* Holm, 1881. This relationship is again based on the prosicular width.

Observing the two-stiped taxa tree (Fig. 2), *Didymograptellus bifidus* is associated with *Xiphograptus lofuensis* because of the presence of a dorsal virgellar spine. In general, the genus *Xiphograptus* shows a wide variation in tubarium shape, in addition to the changes in the prosicular size. Its origin is uncertain, but according to Maletz (1998) it could have originated from the genus *Expansograptus*. According to our results, *X. lofuensis* alongside *Didymograptellus* is separated from the clade as part of a polytomy and both of these taxa are not considered as members of the expansograptids. They were classified as members of the Family Pterograptidae by Maletz (2014), suggesting completely different phylogenetic relationships compared with our results; he postulated an origin of *Didymograptellus* independent from all other didymograptid taxa.

The *Baltograptus* clade is supported by the plesiomorphic character 'origin of the theca 1¹', which is the diagnostic character of this genus due to the lower metasicular

origin of theca 1¹. Even though the resolution within this clade is low, as suggested by the polytomies, it is important to mention that *B. minutus* and *B. deflexus* are grouped together by the presence of an *artus* type proximal end development, unlike other species of the same genus in which an isograptid proximal development is found. The plesiomorphic character state 'isograptid proximal development' is a highly conservative development type in the Dichograptina and is the most frequently observed development in all members of this clade.

Cymatograptus bidextro is clustered with the genus *Baltograptus* due to the *artus* type proximal end development (Fig. 1). However, in the tree of Figure 2, this taxon is separated as part of a polytomy, and it is associated to the other taxa only by sharing the maximum number of two-stipes. As a result of these two very different positions in the phylogenetic trees, the origin and position of *C. bidextro* remains uncertain until new studies are conducted, and it is not possible to support or to reject its inclusion in the genus *Cymatograptus* (see Toro and Maletz, 2008).

Cooper and Fortey (1983) proposed the idea that the *artus* proximal end development might have originated independently in at least three separate lineages. In one group, *artus* development is derived from an ancestor with isograptid development, while according to these authors the origin is uncertain for the other lineages. As more taxa with *artus* type proximal development have been discovered since the research made by Cooper and Fortey (1983), the situation is even more complex and multiple originations of an *artus* type proximal development must be postulated (see also *Xiphograptus artus* in Maletz, 2010). The separation of *C. bidextro* from the remaining taxa of the genus *Cymatograptus* cannot be explained yet through the tree topologies obtained in this work. The relationship between *C. bidextro* and *B. minutus* (Fig. 1) is controversial due to the fact that *C. bidextro* differs from baltograptids by the prosicular origin of the first theca. Because of the unclear results and the idea of obtaining a better resolution of graptolite phylogeny a second analysis emphasizing the two-stiped taxa was carried out (Fig. 2). As result of this analysis *C. bidextro* is not included in the group of baltograptids due to the origin of the first theca and it is separated from the other *Cymatograptus* taxa because of the '*artus* type proximal end' character.

The different states of the stipe attitude may have evolved several times, therefore introducing a high degree of homoplasy. It was postulated that this would also be the case in the pendent taxa (Maletz, 1994). This study supports the same hypothesis because pendent taxa, such as *Pendeograptus fruticosus*, *Baltograptus minutus* and *Didymograptellus bifidus*, are located in different positions on the cladogram. This fact may be explained as a plesiomorphic character (ancestral trait) that is homologous in several groups.

CONCLUSIONS

The results obtained from this analysis were the first attempt at understanding the phylogenetic relationships of the graptolite fauna present in northwestern Argentina. It supports the hypothesis that morphological characters of the proximal end could be more important to explain the evolution of graptolites, but also reveals problems that still remain to be resolved between some of the taxa involved in this study.

Even though the majority consensus tree for all taxa shows two major clades (the traditional families Tetragraptidae and Didymograptidae), their monophyly is not completely supported since *Pendeograptus fruticosus* and *Corymbograptus v-fractus tullbergi* are controversial taxa, and more research is necessary to understand the evolutionary process leading to these taxa.

The analysis of the two-stiped taxa shows them as a hypothetical monophyletic group and the genus *Baltograptus* also appears as a potentially monophyletic clade, which together with the genera *Expansograptus* and *Cymatograptus* would share a common ancestor. However, additional morphological information is needed to solve remaining polytomies in both analyses.

Even though the support values for both trees were low and some taxa remain as problematic, the contribution to the knowledge of the evolutionary history of the graptolites and database for future phylogenetic works is highlighted here.

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