

# The Ordovician acritarch genus *Coryphidium*

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**Abstract:** The acritarch genus *Coryphidium* Vavrdová 1972 is one of the most frequently recorded acritarch taxa in the Ordovician. The original diagnoses, stratigraphical ranges and geographical distribution of all *Coryphidium* species are critically evaluated in a review of published literature supplemented by studies of material from the British Isles, Belgium, the Czech Republic, Germany, Spain, Morocco, Algeria, Tunisia, Lybia and China, including sections from type areas. The taxonomic concept of the genus is here rationalized: the genus *Coryphidium* is emended and the informal category of coryphid acritarchs is introduced to include all morphotypes with the characteristic vesicle shape of the two genera *Coryphidium* and *Vavrdovella* Loeblich and Tappan 1976. Nine of the previously described species can be attributed to the genus, and two other species possibly belong to it. The attribution to *Coryphidium* of the species *C. sichuanense* Wang and Chen 1987 is rejected here. Intraspecific variability is very important and the attribution of *Coryphidium* specimens at the specific level is sometimes difficult. The genus is found in all palaeoenvironments from nearshore to offshore settings and apparently does not occupy specific palaeoecological niches. *Coryphidium* is very useful biostratigraphically and palaeobiogeographically. The review indicates that the genus first appears in the uppermost Tremadocian *Araneograptus murrayi* graptolite Biozone and is common through the upper Lower Ordovician and the Middle Ordovician, while Upper Ordovician occurrences might be the result of reworking. Palaeogeographically, *Coryphidium* is an indicator of the peri-Gondwanan acritarch "palaeoprovince" during the Early/Middle Ordovician.

**Keywords:** acritarchs, biostratigraphy, palaeogeography, Ordovician

**Résumé :** Le genre d'acritarches *Coryphidium* Vavrdová 1972 est un des taxon d'acritarches le plus fréquemment trouvés dans l'Ordovicien. Les diagnoses originales, les extensions stratigraphiques et les distributions géographiques de toutes les espèces de *Coryphidium* sont critiquement évaluées sur base d'une revision de littérature et d'études de matériel des Iles Britanniques, de Belgique, d'Allemagne, de la République Tchèque, d'Espagne, du Maroc, de l'Algérie, de la Tunisie, de Lybie et de Chine, y compris de coupes géologiques des régions types. La conception du genre est révisé : le genre *Coryphidium* est emendé et la catégorie informelle des acritarches coryphides est introduite pour inclure tous les morphotypes avec la forme caractéristique du corps central des deux genres *Coryphidium* et *Vavrdovella* Loeblich and Tappan 1976. Neuf des espèces décrites précédemment peuvent être attribuées au genre, et deux autres espèces appartiennent peut-être au genre. L'attribution au genre *Coryphidium*

de l'espèce *C. sichuanense* Wang and Chen 1987 est rejetée ici. La variation intraspécifique est importante et l'attribution de spécimen de *Coryphidium* au niveau spécifique est parfois difficile. Le genre est trouvé dans tous les paléoenvironnements de milieux proximaux à distaux et apparemment il n'occupe pas des niches paléocéologiques particulières. *Coryphidium* est très utile biostratigraphiquement et paléobiogéographiquement. La révision montre que le genre apparaît pour la première fois dans la biozone à graptolites à *Araneograptus murrayi* du Trémacodien supérieur et qu'il est fréquent dans la partie supérieure de l'Ordovicien Inférieur et dans l'Ordovicien Moyen, tandis que la présence dans l'Ordovicien Supérieur peut être dû à du remaniement. Paléogéographiquement *Coryphidium* est un indicateur de la "paléoprovince" péri-Gondwanienne pendant l'Ordovicien Inférieur/Moyen.

Mots-clés : acritarche, biostratigraphie, paléogéographie, Ordovicien

## 1. Introduction

The acritarch genus *Coryphidium* and its type species, *Coryphidium bohemicum*, are important Ordovician acritarch taxa, being widely reported from numerous localities on the periphery of the Gondwanan supercontinent since their original description by Vavrdová (1972). The easily recognizable specimens of this genus are characterized by a rounded-square central body, with an ornament of ridges, and with the processes being concentrated at the four corners of the vesicle.

The genus is biostratigraphically and palaeobiogeographically significant. Brocke et al. (1995), Molyneux and Leader (1997) and Li et al. (2003), for example, considered *Coryphidium* and some of its species to be very useful for regional or international biostratigraphical correlations, while Vecoli (1999) erected the informal acritarch assemblage biozone *Arbusculidium filamentosum-Coryphidium bohemicum* of late Arenig age, that proved to be useful for regional correlation in the subsurface of the Algerian Sahara. Li (1989) and Servais et al. (2003) considered the genus to be one of the three taxa that define the peri-Gondwanan acritarch 'palaeoprovince'. Furthermore, Ghavidel-Syooki (1990) and Vavrdová (1997) described a '*Coryphidium bohemicum* province' and a '*Coryphidium bohemicum* acritarch bioprovince', respectively.

Several of the more frequently recorded and biostratigraphically most useful Ordovician acritarch taxa from the periphery of Gondwana have been reviewed in recent years. *Frankea* was revised by Servais (1993), *Dicrodiacrodium* by Servais et al. (1997), *Arkonina* and *Striatotheca* by Servais (1997), *Ampullula* by Brocke (1998), *Aureotesta* and *Marrocanium* by Brocke et al. (1998) and *Arbusculidium filamentosum* by Fatka and Brocke (1999). So far, however, the genus *Coryphidium*, has not been reviewed in detail, although it is commonly used for dating sedimentary rocks or determining palaeogeographical affinities.

The aim of the present paper is to review all published data concerning this important genus, in order to rationalize its taxonomy and to understand its relationship to *Vavrdovella* Loeblich and Tappan 1976, a genus of similar morphology. This study also attempts to review the biostratigraphical distribution of the genus in order to underline its potential for international correlations. In addition, all occurrences of the genus are plotted on a recent palaeogeographical reconstruction in order to understand better its palaeobiogeographical distribution.

## 2. The genus in its taxonomical context

### 2.1. The acritarch subgroup *Coryphomorphitae*

Vavrdová (1972) described the genus *Coryphidium* and its type species *C. bohemicum*, from the Klabava Shales of ‘Arenig age’ in Bohemia. The original diagnoses and descriptions of both the genus and its type species are short and clear, although Vavrdová’s (1972) diagnosis of *C. bohemicum*, based on thirty specimens is also relatively wide and allows the attribution of a great number of morphotypes to the species. Unfortunately, the exact location of the outcrop and of the type level was not indicated. The age indication (‘Arenig’) also remained vague and the precise biostratigraphy of the type level is still not precisely known to the present day. According to Martin (1982), the acritarchs described by Vavrdová (1965, 1966, 1973, 1976) from the locality ‘U Starého hradu’, south east of Klabava near Rokycany, including the type material of *Coryphidium bohemicum*, are from the *Tetragraptus* cf. *pseudobigsbyi* graptolite Biozone of Kraft (1977). Martin cites as a ‘pers.comm.’ from Vavrdová as the authority for this. The the *Tetragraptus* cf. *pseudobigsbyi* graptolite Biozone replaced the *Tetragraptus reclinatus abbreviatus* Biozone, which has been correlated with the British *Isograptus gibberulus* Biozone (Cooper and Fortey, 1982, fig. 2).

The original diagnosis (see Systematic Palaeontology section) highlights the characteristic features of the genus by a polyhedral central body with rounded angles, the vesicle wall with an ornament of fine ribs, and the processes concentrated at the corners of the vesicle. The original generic diagnosis also states that the processes are conical, proximally open and distally heteromorphic. For *C. bohemicum*, Vavrdová (1972) added some precision regarding the distance between ribs (spaced about 2 µm) and the number of processes (40-60), but there is no significant difference between the original diagnoses of the genus and the type species.

One year later, Vavrdová (1973) described another new acritarch genus to which she gave the name *Tetradineum* not realising that the name had already been used for an extant dinoflagellate genus (Klebs 1912). Vavrdová (1976) subsequently changed the name of her new genus to *Tetraniveum*, but in the meantime Loeblich and Tappan (1976) had introduced the name *Vavrdovella* as a replacement for *Tetradineum* Vavrdová 1973 (it was Alfred R. Loeblich Jr. who alerted Milada Vavrdová to the fact that *Tetradineum* Vavrdová 1973 was a junior homonym of the extant dinoflagellate genus). According to Fensome et al. (1990), *Vavrdovella* Loeblich and Tappan 1976 is the senior synonym of *Tetraniveum* Vavrdová 1976.

The diagnosis of the new genus ‘*Tetradineum*’ *sensu* Vavrdová 1973 (now *Vavrdovella*) was rather short: "vesicle differentiated into central body of variable outline and conical processes which are restricted to four or more areas symmetrically arranged. Processes are essentially simple, homomorph, distally pointed. Vesicle wall laevigate to microgranulate". This genus remains monospecific, its type species being *V. areniga* (Vavrdová 1973) Loeblich and Tappan 1976. According to its original diagnosis, the genus has the same central body shape as *Coryphidium*, but does not display the fine ribs on the vesicle wall that are characteristic of the latter genus. Furthermore, the processes of *Vavrdovella* are always simple, while those of *Coryphidium* are defined as heteromorphic and with complex branching.

Following the common use of acritarch subgroups in the 1960s (e.g. Downie et al., 1963), Vavrdová (1973) created a new subgroup, the ‘*Coryphomorphitae* incertae sedis’ (sic), with the following diagnosis: "Acritarchs having spherical to polyhedral vesicles, processes or other sculpture elements concentrated on several (more than two) areas adjoining corners of the central body. Other parts of vesicle laevigate or with different sculpture (granulate,

echinate, striate). Processes are numerous, homomorph or heteromorph" (Vavrdová, 1973, p. 285-287). Vavrdová (1973) created this new subgroup to include the two genera *Coryphidium* and *Tetradineum* (now *Vavrdovella*).

## 2.2. *Coryphidium* and *Vavrdovella* : a single taxonomic entity ?

The use of acritarch subgroups was abandoned by most acritarch workers in the 1970s, when an alphabetical arrangement of genera and species, first suggested by Loeblich (1970), was generally adopted instead. It is thus not surprising that the subgroup Coryphomorphae has not been commonly used following its introduction. However, as defined by Vavrdová (1973), this subgroup can be regarded as a distinct morphological entity, clearly distinguishable by the characteristic, pillow-shaped vesicles of its constituent genera and the tendency for the processes to be concentrated at the corners.

Although Vavrdová (1972, 1973) indicated the possibility of polyhedral vesicles, most specimens attributed to the two genera by Vavrdová and other authors have quadrangular, pillow-shaped vesicles with rounded corners and concave, straight or convex sides. Although the distinction between Vavrdová's two genera is straightforward according to their original diagnoses, the classification scheme is not without problems. Large populations usually display a range of morphological variability and it is possible to observe specimens that are intermediates between *Coryphidium* and *Vavrdovella*, or to put it another way, specimens that do not correspond to either *Coryphidium* or *Vavrdovella* as originally diagnosed. For example, specimens with heteromorphic processes but without ridges on the central body do not correspond with the original diagnosis of *Coryphidium* because of the absence of ridges, but neither do they correspond with the original diagnosis of *Vavrdovella* because the processes are not simple and sharp-pointed. Similarly, specimens with ridges on the central body, but with simple, distally pointed processes cannot be attributed to either *Coryphidium* or *Vavrdovella* as originally defined, although such specimens clearly belong to the subgroup Coryphomorphae. Thus, whereas the Coryphomorphae as a super-generic category is fairly well constrained and understood, and while some species of the constituent genera are similarly well defined, it is nevertheless sometimes difficult to make an attribution at the generic level. It is therefore useful to propose here the informal term of 'coryphids' or 'coryphid acritarchs' to designate morphotypes with the characteristic vesicle shape of the *Coryphomorphae sensu* Vavrdová (1973).

## 2.3. Historical review of the description of "coryphid" acritarchs

In this section, the history and the evolution of the taxonomic concepts of the 'coryphid' acritarchs are briefly summarized in order to clarify the different classification models and to explain the current problematic taxonomic situation.

The first formal description of a specimen that can clearly be attributed to the coryphids was included in Burmann's (1970) investigation of the 'late Llanvirn' *D. purchisoni* graptolite Biozone (now Darriwilian) of Rügen, Baltic Sea, Germany. Burmann (1970, p. 309; pl. 7, fig. 7) described a new species with the typical coryphid body outlines as '*Baltisphaeridium obtusatum* sp.n.' It is not sure if she observed more than one specimen. This species cannot be referred to *Coryphidium* because the characteristic ribs of *Coryphidium* are not cited in its diagnosis nor figured on the drawing, but neither can it be referred to *Vavrdovella* because the processes are not simple and pointed distally. However,

from a revision of material from this locality (Servais 1994, this study), it is clear that this morphotype can be attributed to the coryphids.

Martin et al. (1970, pl. 1, fig. 3) figured a specimen as 'indéterminé forme A' from the 'Caradoc' of Ombret, in the Belgian Condroz Inlier. This specimen is also clearly a coryphid acritarch, and possibly reworked. The age of these sediments has now been reconsidered and the formation can be attributed to the early-middle Caradoc (Verniers et al., 2003 ; Owens and Servais, in press, fig. 2).

On the basis of eight specimens, which were probably also reworked, Martin (1974) described the genus *Octogonium* from the lower Llandovery of the Deerlijk Formation (Brabant Massif, Belgium). The diagnosis of the genus and of its type species *O. vanguardinii* includes the presence of fine ribs ("fines rides subparallèles aux côtés ... ") as well as furcate distal process terminations, which clearly indicate that *Octogonium* is a junior synonym of *Coryphidium*. It is not clear, however, if the species *O. vanguardinii* is a junior synonym of *C. bohemicum*, as indicated in Martin's (1974, p. 63) 'Addendum', because *C. bohemicum* is described as having heteromorphic processes, whereas *O. vanguardinii* is not. In a subsequent paper, Martin (1977, p. 23) also placed *O. vanguardinii* in synonymy with *C. bohemicum*. Meanwhile, Rauscher (1974a, 1974b) had identified the species *C. bohemicum* from in the Ordovician of France.

The formal description of a second species of *Coryphidium* by Cramer et al. (1974) introduced additional taxonomic problems. Cramer et al. (1974) reported *C. bohemicum* and the new species *Coryphidium elegans* from the 'Upper Arenigian to Lower Llanvirnian' of the Tadla Basin, Morocco. Cramer et al. (1974) provided a long but imprecise description of *C. elegans*. The location of the material was precisely indicated (borehole BJ-109, depth 360 m), but Cramer et al. (1974) gave no indications of the number of observed specimens.

*Coryphidium elegans* was described as having "solid, slender" processes that "vary from flexible spines to hairs ; (that) occasionally ... may show some kind of tiny knob at the extreme distal termination". The holotype (Cramer et al. 1974, pl. 27, fig. 16) and the paratypes (partly republished in Cramer and Díez 1976) display essentially homomorphic, simple processes that are not furcate. *Coryphidium elegans* is therefore clearly distinguished from *C. bohemicum*, but at the same time it exemplifies the problem of generic definition that arose with the description of *Vavrdovella* (i.e. *Tetradinium* Vavrdová 1973) as a separate entity. Thus, although *Coryphidium elegans* is a typical coryphid acritarch, it does not fit the original diagnosis of *Coryphidium*, as it does not have heteromorphic, furcate processes but neither does it fit the diagnosis of *Vavrdovella*, because of its sculpture of ribs parallel to the vesicle sides. In fact, *C. elegans* could be considered as a transient between *Coryphidium* and *Vavrdovella* with ribs of the first and the processes of the second.

The taxonomy became more confused with the publication by Cramer and Díez (1976) of a further seven new species of *Coryphidium*, also from borehole BJ-109. All the holotypes of the new species were described from one sample (depth 510 m). Cramer and Díez (1976) indicated this level and the material of Cramer et al. (1974) to be of 'Late Arenig' age, an interpretation that was confirmed subsequently by chitinozoans ( Soufiane and Achab, 1993).

Cramer and Díez (1976) provided a first bibliographical listing for *C. bohemicum*, from which Martin's (1974) publication was omitted. However, the specimens of Martin et al. (1970) and *?Baltiphaeridium obtusatum* Burmann were placed in synonymy with *C. bohemicum*, which would make that Burmann's (1970) taxon the senior synonym.

The description of the seven new species of *Coryphidium* and comparison with the two previously described species is problematical. In their fig. 2, Cramer and Díez (1976) illustrated diagrammatically nine *Coryphidium* species described from the Arenic of Morocco: *C. bohemicum* Vavrdová 1972, *C. elegans* Cramer et al. 1974, and the new species *C. almohadillum*, *C. australe*, *C. barakum*, *C. miladae*, *C. minutum*, *C. ramiferum*, and *C.*

*tadlanum* (some of the adjectival specific epithets are corrected here, according to the recommendations of the International Code of Botanical Nomenclature, I.C.B.N., article 60 ; see Systematic Palaeontology section).

The diagnoses of Cramer and Díez's (1976) seven new species of *Coryphidium* stated that all had a similar morphology to *Coryphidium elegans*, but that they could be distinguished from that species and from each other by the presence or absence of ridges and by the nature of the processes. Thus, *Coryphidium almohadillum* and *C. barakum* correspond to the original diagnosis of *Coryphidium* in so far as they have ridges on the vesicle, but could be distinguished from *C. bohemicum* and *C. elegans* by their shorter processes. *Coryphidium ramiferum* also has the morphological features of *Coryphidium*, with the ribs on the vesicle and processes that branch into a crown, and might be distinguished from *C. bohemicum*, *C. elggans*, *C. almohadillum* and *C. barakum* by the morphology and distribution of its processes. However, neither *Coryphidium australe* nor *C. miladae* agree with the original diagnosis of also *Coryphidium* (both species have no ridges on the vesicle wall), nor with that of *Vavrdovella* (both species have no processes with complex distal terminations). The two remaining species, *Coryphidium minutum* and *C. tadlanum*, also lack ridges and therefore these too do not correspond to the original diagnosis of *Coryphidium*.

All the species introduced by Cramer et al. (1974) and Cramer and Díez (1976) display typical coryphid morphology, but problems arise because these authors did not indicate how many specimens each of their species was based upon, nor did they discuss the range of variability within each species. The lack of any evidence for discussion of variability within *Coryphidium* species described by Cramer and Díez (1976) is a major impediment to understanding their relationship to each other and to *Coryphidium bohemicum* and *C. elegans*. Some of Cramer and Díez's (1976) species are very similar to others. For example, it is virtually impossible to distinguish *Coryphidium almohadillum* from *C. barakum* on the basis of their diagnoses or illustrations (both species are characterized by very short processes, with overlapping dimensions and morphologies), and *Coryphidium australe* closely resembles *C. miladae* (both lack ridges on the vesicle wall and have similar processes). It is quite possible that each pair represents only a single species, and indeed possible the whole population of coryphid acritarchs described by Cramer et al. (1974) and Cramer and Díez (1976) from Morocco has been over-split because these authors did not take sufficient account of intraspecific variability when describing their material.

More recently, a further three species have been described. *Coryphidium sichuanense* Wang and Chen 1987 from the lower Cambrian of southern China has none of the characteristics of coryphid acritarchs and its attribution to *Coryphidium* is rejected here. The specimens of Wang and Chen (1987) might be better attributed to *Michrhystridium* sp.

Ghavidel-Syooki (1990) recorded *Coryphidium bohemicum* and *C. elegans* from the Ordovician of Iran, but also erected the new species '*Coryphidium persica*' (*persica* is here corrected to *persianum*, on the grounds that the specific epithet is based on a geographical name, Persia, I.C.B.N., article 60). Ghavidel-Syooki (1990) made no mention of ridges on the vesicle and it is not possible to observe such structures on the illustrated specimens. The new species was characterized by a "translucent membrane connected to the body by a set of filose process elements". The presence of membranes within the genus *Coryphidium* has not been recorded previously, and therefore the species is here only questionably attributed to the genus. Moreover, the species remains invalid, because Ghavidel-Syooki (1990) did not indicate a holotype among the four illustrated specimens (I.C.B.N., article 37).

The third species, *Coryphidium longispinosum*, with relatively long processes, was described by Garo (1991) from the Lower Ordovician of Yunnan Province. There is no indication in the original diagnosis whether the species has an ornament of (fine) ribs, and the photograph of the holotype is too poor to resolve this question. Hence, it is not clear if the

holotype of *C. longispinosum* corresponds with the diagnoses of *Coryphidium* or *Vavrdovella*. In this paper, the species *longispinosum* is therefore only questionable attributed to the genus *Coryphidium*.

Finally, some authors have described *Coryphidium* morphotypes in open nomenclature. Molyneux and Leader (1997) for example, described three morphotypes that were considered useful for regional biostratigraphy of British sections.

### 3. Material and methods

The material analysed in this study is from Belgium, the Czech Republic, Germany, England and Wales, Spain, Morocco, Algeria, Tunisia, Lybia and China. All localities were investigated by the authors in previous studies, to which the reader is referred for more detailed geological descriptions.

The Belgian material is from Llanvirnian (Darriwilian) levels of the Rigenée Formation in the Brabant Massif, previously investigated by Martin (1969) and Servais (1991) and more recently dated using chitinozoans by Samuelsson and Verniers (2000), and from the early Llanvirnian (middle Darriwilian) Huy formation of *D. artus* graptolite Biozone age in the Condroz Inlier, previously investigated by Servais and Maletz (1992). For the review of the stratigraphy of these localities, see Verniers et al. (2001).

German localities investigated here are in the Ebbe Anticline of the Rhenish Massif, western Germany, and boreholes on the island of Rügen, Baltic Sea. Material from the Ebbe Anticline was previously studied by Maletz and Servais (1993), and acritarchs from the Ordovician sequence of Rügen have been described in several papers, including those of Burmann (1970), Servais (1994) and Servais and Molyneux (1997). For a detailed review of the stratigraphy of the Ebbe anticline and the Rügen boreholes, see Samuelsson et al. (2002) and Servais et al. (2001), respectively.

Two samples from the Czech Republic were provided by M. Vavrdová to the senior author in 1990, including part of the sample from which the genus *Coryphidium* was originally described (a sample from the locality 'U Starého hradu' at Klabava near Rokycany). The second sample comes from the 'Llanvirnian' of 'Krusna Horá' near Beroun, mine 'Gabriela'-K3. The first sample is from the upper part of the Klabava Formation, and the second sample from the lower part of the Sárka Formation, but the precise positions and ages of the two samples are unknown. For a recent review of the regional stratigraphy of the area, see Kraft and Kraft (2003).

The Moroccan samples investigated here come from the borehole Boujad-109 of the Tadla Basin. Two samples from depths 360 m and 511 m were made available to M. Vanguetaine (Liège University, Belgium) in 1982. Soufiane and Achab (1993) indicated a late Arenig age for depths between 481 and 512 m (see biostratigraphy chapter).

The Spanish material reinvestigated for this study was previously analysed by Mette (1989) and restudied by Servais and Mette (2000).

British specimens of *Coryphidium* are from the Lower-Middle Ordovician (Tremadocian-Darriwilian) succession of the English Lake District (Rushton and Molyneux, 1989 ; Copper and Molyneux, 1990 ; Cooper et al., 2004), from the correlative succession of the Isle of Man (Molyneux 1999 ; Chadwick et al. 200x), and from south Wales (Molyneux, 1987). The Lake District material formed the basis of the analysis by Molyneux and Leader (1997). Additional specimens have been recorded from north Wales in unpublished thesis work (Booth, 1979) and from the Upper Ordovician (Caradoc) of the Welsh Borderland, where they were considered to be reworked (Turner, 1982).

Well preserved palynological assemblages containing relatively abundant specimens of *Coryphidium* from the subsurface of the Algerian Sahara (borehole NL-2) and of the Ghadamis Basin of southernmost Tunisia (boreholes ST-1, TT-1) and northwestern Libya (borehole A1-70) were previously analysed by Vecoli (1999 and unpublished data) and Vecoli et al. (2004), and are reconsidered for the present study. Age attributions were based on palynological grounds and indirect correlations (e.g., late Arenig age of the Algerian Sahara material) as well as on the basis of co-occurring chitinozon index-species (ornensis chitinozoan Biozone, late Arenig, in the A1-70 borehole of the Ghadamis Basin ; Vecoli and Quintavalle, unpublished).

The Chinese material is from different sections analysed in papers by Li and coworkers. For a complete list of the localities investigated by Li, see Li et al. (2002).

#### 4. Systematic palaeontology

##### 4.1. Original and emended diagnosis of the genus *Coryphidium*

As indicated above, some species attributed to *Coryphidium* do not comply with the original diagnosis of Vavrdová (1972). Therefore, the diagnosis is here emended to include all coryphid acritarchs that display the sculptural ridges on the vesicle wall, but also a wider range of process morphologies, including both branched and simple processes. The emended diagnosis allows the inclusion of all morphotypes with simple, distally unbranched processes, namely the specimens attributed to *Coryphidium elegans*.

Group Acritarcha *Incertae Sedis* Evitt 1963

Genus *Coryphidium* Vavrdová 1972 emend. nov. Servais, Li, Molyneux and Vecoli

*Type species. Coryphidium bohemicum* Vavrdová 1972

*Original diagnosis* (Vavrdová 1972, p. 84): "Acritarchs with polyhedral main body, angles rounded. Wall thin, single-layered, in places sculptured with very fine ribs. Numerous processes, equal in length, symmetrically distributed at angles of polyhedron and adjoining edges. Processes are conical, proximally opened, distally heteromorphic (truncate, bifurcate, plurifurcate)".

*Emended diagnosis* : Quadrangular, pillow-shaped vesicle with rounded corners. Sides of the vesicle concave, convex or straight. Sculptural ridges mostly more or less parallel to the sides, covering almost the entire vesicle wall ; some ridges may extend diagonally across the vesicle from corner to corner. Numerous processes, which in some cases tend to be concentrated at the corners of the vesicle but in others are distributed more widely and at random across the surface of the vesicle. The processes are of various length and morphology: being simple and sharp-tipped, or distally branched or truncated.

*Comparison* : *Coryphidium* is readily distinguished from all other acritarch genera. *Vavrdovella* has a similar vesicle outline, but it never has the sculptural ridges parallel to the vesicle sides, that are characteristic of *Coryphidium*. In addition, *Vavrdovella* has so far only been described with simple, distally tapering processes. Although it is a characteristic feature of the type species and certain other *Coryphidium* morphotypes, the concentration of processes at the corners of the vesicle is not always marked, and other species and



morphotypes of *Coryphidium* have more random and widespread process distributions across the vesicle. It is also possible to find intermediates between *Coryphidium* with processes concentrated at the four corners of the vesicle and *Acanthodiacrodium* with a typical diacromorph process distribution (processes concentrated at two opposing poles of the vesicle), for example *Acanthodiacrodium? dilatatum* Molyneux in Molyneux and Rushton 1988 and *Acanthodiacrodium? sp. 1* in Servais and Molyneux (1997). Such specimens are possible transients between diacromorph acritarchs, dominant in assemblages throughout the Tremadocian, and coryphid acritarchs, which first appear in the late Tremadocian. Such transients have been reported in several studies of late Tremadocian acritarchs, including Martin (1996), Brocke (1997), Servais and Molyneux (1997), Connery and Higgs (1999), Servais and Mette (2000), Vanguetstaine and Servais (2002) and Breuer and Vanguetstaine (2004).

#### 4.2. Bibliographical review of *Coryphidium* species

Based on previous attributions to the genus *Coryphidium*, and following the emended diagnosis, nine species are currently considered to belong to the genus. These nine species are, in alphabetical order :

*C. almohadillum* Cramer and Díez 1976  
*C. australe* Cramer and Díez 1976  
*C. barakum* Cramer and Díez 1976  
*C. bohemicum* Vavrdová, 1972  
*C. elegans* Cramer et al. 1974  
*C. miladae* Cramer and Díez 1976  
*C. minutum* Cramer and Díez 1976  
*C. ramiferum* Cramer and Díez 1976  
*C. tadlanum* Cramer and Díez 1976

The two questionable species (one of which is technically invalid as a holotype has not been selected) are:

*C. ? longispinosum* Gao 1991  
*C. ? persianum* Ghavidel-Syooki 1990 (invalid species)

The original diagnoses of all 11 species are included here. The taxonomic position is discussed and all species are briefly described. The stratigraphical and palaeogeographical distribution of all species is summarized, based on a review of all literature citations. Bibliographical lists are included for all 11 species. It is important to understand that these bibliographical lists are not to be considered as synonymy lists, however.

The following abbreviations are used in the bibliographical lists:

-: determination correct, according with the original description  
?: determination questionable  
non: determination not accepted  
\*: no specimens illustrated (determination impossible to control)  
pp: pro parte

*Coryphidium almohadillum* Cramer and Díez 1976

*Coryphidium almohadilla* n.sp. - Cramer and Díez 1976, p. 204, text-fig. 2 : 3, pl. 23 : figs. 8, 11.

*Coryphidium almohadilla* Cramer and Díez 1976. - Eisenack et al. 1979, p. 77.

?*Coryphidium almohadilla* Cram. and Díez. - Kalvacheva 1979, p. 1399, pl. 1 : fig. 12.

*Coryphidium almohadilla* Cramer and Díez 1976. - Downie 1984, text-fig. 4 : 34.

\**Coryphidium* cf. *almohadilla* Cramer and Díez 1976. - Mette 1989, p. 7.

\**Coryphidium almohadillum* Cramer and Díez 1976. - Fensome et al. 1990, p. 155.

\**Coryphidium almohadillum*. - Fensome et al. 1991, p. 3.

*Coryphidium* sp. cf. *C. almohadillum* Cramer and Díez 1976. - Connery and Higgs 1999, p. 136, 150, pl.2 : fig. 8.

non *Coryphidium almohadilla* Cramer and Díez 1976 (misspelling). – Xu 1999, p. 65, 75, pl. 1 : fig. 14.

\**Coryphidium* cf. *almohadillum* Cramer and Díez 1976. – Maziane et al. 2000, p. 62, 65, 67-68.

*Coryphidium* cf. *almohadillum* Cramer and Díez 1977 (sic). - Todd et al. 2000, p. 830.

*Holotype* : Cramer and Díez 1976, p. 204, pl. 23 : fig. 8.

*Type locality and type level* : Boujad, Tadla Basin, Morocco, borehole BJ-109, depth 510 m.

*Original diagnosis* (Cramer and Díez 1976): "Species of *Coryphidium* of a similar morphology to that of *C. elegans*, but distinguished from it in that *C. almohadilla* has numerous fine rugulae. These are arranged in a regular pattern and parallel to the sides of the body. Furthermore, it displays a dense cover of small mainly aculeate elements which in their majority are located on the crests of the rugulae. A few of the elements may be capitate, but most are sharp-tipped".

*Nomenclatural note* : Following Fensome et al. (1990), *Coryphidium almohadilla* is corrected here to *C. almohadillum* (I.C.B.N., Article 60).

*Remarks* : This is clearly a species of *Coryphidium*, its main diagnostic characteristic being very short processes. Cramer and Díez (1976) indicated that the process length could be up to 2  $\mu\text{m}$ , but was generally 1  $\mu\text{m}$  or less. The species is very close to *C. barakum*, which also has very short processes (elements up to 3  $\mu\text{m}$  according to Cramer and Díez, 1976 ; with pinnae smaller than 0.5  $\mu\text{m}$  on branched processes).

*Biostratigraphical and palaeobiogeographical distribution* : There have been few records of *C. almohadillum* since its original description. The determination of Kalvacheva (1979) at the specific level is questionable. Specimens with very short processes occur close to the Tremadoc-Arenig boundary in Ireland (Connery and Higgs 1999).

*Coryphidium australe* Cramer and Díez 1976

*Coryphidium australe* n. sp. - Cramer and Díez 1976, p. 205, text-fig. 2 : 5; pl. 23 : figs. 5-6.

*Coryphidium australe* Cramer and Díez 1976. - Eisenack et al. 1979, p. 79.

\**Coryphidium australe* Cramer et Díez. - Smith 1981, p. 143.

- Coryphidium australe* Cramer and Díez 1976. - Turner 1982, p. 122-123, 125, pl. 17 : fig. 4.  
*Coryphidium australe* Cramer and Díez 1976. - Albani et al. 1985a, p. 50-51, 58, 60; pl. 6, fig. 10.  
 \**Coryphidium australe*. - Fang 1986, p. 135.  
 ?*Coryphidium australe* Cramer and Díez 1976. - Albani 1989, p. 5, 7, 13, pl. 1 : figs. 18-19.  
*Coryphidium australe*. - Li 1990, p. 142, 147, 157, pl. 3 : fig. 12, pl. 5 : fig. 5.  
 \**Coryphidium* aff. *australe* Cramer et Díez. - Vavrdová 1990b, p. 242.  
 \**Coryphidium australe* Cramer and Díez 1976. - Fensome et al. 1990, p. 155.  
 \**Coryphidium australe*. - Fensome et al. 1990, p. 9.  
 \**Coryphidium australe* Cramer et Díez 1976. - Servais 1991, p. 240.  
*Coryphidium australe*. - Reitz 1994, p. 664, pl. 1 : fig. 21.  
*Coryphidium australe* Cramer et Díez 1976. - Li and Yuan 1998, p. 274, 277, 285, pl. 4 : figs. 9, 10, 14.  
 \**Coryphidium australe* Cramer et Díez 1976. - Rubinstein et al. 1999, p. 271-272, 274.  
*Coryphidium* cf. *australe* Cramer and Díez 1976. - Brocke et al. 2000, p. 37, pl. 2 : fig. 1.  
 \**Coryphidium australe* Cramer et Díez 1976. - Rubinstein and Toro, 2001, p. 426, 428, 431.

*Holotype* : Cramer and Díez 1976, p. 205, pl. 23 : fig. 20.

*Type locality and type level* : Boujad, Tadla Basin, Morocco, borehole BJ-109, depth 510 m.

*Original diagnosis* (Cramer and Díez 1976) : "Species of *Coryphidium* of a similar morphology to that of *C. elegans*, but distinguished from it in that *C. australe* has no rugulae, and has no filose elements. It shows instead a dense cover of plump, short processes. These processes are cylindrical to columnar and may have a few denticulate branches at about half height. They may be sharp-tipped, flat-capitate, or expanded by distal dichotomy".

*Remarks* : This species was described as having no ridges on the vesicle, and therefore it does not correspond with the original diagnosis of *Coryphidium*. Several authors have described and/or illustrated this morphotype with its characteristic plump, short processes, but without clearly visible ridges. It is possible that poorly preserved specimens of *C. bohemicum*, on which the fine details of the distal process ornamentation is no longer visible, have been described as *C. australe*.

*Biostratigraphical and palaeobiogeographical distribution*: As with *C. almohadillum*, there have been few records of *C. australe* since its original description. It occurs in several European and Chinese localities. Most records are of poorly preserved material.

#### *Coryphidium barakum* Cramer and Díez 1976

- Coryphidium baraka* n. sp. - Cramer and Díez 1976, p. 205, text-fig. 2 : 5, pl. 23 : figs. 5-6.  
*Coryphidium baraka* Cramer and Díez 1976. - Eisenack et al. 1979, p. 81.  
 ?*Coryphidium baraka* Cramer et Díez 1976. - Marhoumi et al. 1982, p. 139, pl. 1 : figs. 21-22.  
 \**Coryphidium* cf. *baraka* Cramer and Díez 1976. - Mette 1989, p. 7.  
 ?*Coryphidium baraka* Cramer et Díez 1976. - Albani 1989, p. 5, 13, pl. 1 : figs. 20, 23, 25.  
 \**Coryphidium barakum* Cramer and Díez 1976. - Fensome et al. 1990, p. 155.  
 \**Coryphidium barakum*. - Fensome et al. 1990, p. 9.  
 ?*Coryphidium baraka* Cramer and Díez 1976. - Reitz and Höll 1991, p. 331, pl. 1, fig. 7.

\**Coryphidium* cf. *baraka* Cramer and Díez 1976. - Reitz and Höll 1992, p. 199.  
\**Coryphidium barakum* Cramer and Díez 1976. –Quintavalle et al. 2000, p. 6, 9.

*Holotype* : Cramer and Díez 1976, p. 204, pl. 23 : fig. 8.

*Type locality and type level* : Boujad, Tadla Basin, Morocco, borehole BJ-109, 510 m.

*Original diagnosis* (Cramer and Díez, 1976) : "Species of *Coryphidium* of a similar morphology to that of *C. elegans*, but distinguished from it in that *C. baraka* has a dense cover of rugulae which are arranged in a regular pattern parallel to the sides of the body. The filose elements are numerous, small and short; they vary from aculeate to flagellate, or capitate; some are even bi- or trifurcated distally, with very short pinnae (< 0,5µ)".

*Nomenclatural note* : Following Fensome et al. (1990), *Coryphidium baraka* is corrected here to *C. barakum* (I.C.B.N., Article 60).

*Remarks* : This species clearly belongs to *Coryphidium*. It also fits into the diagnosis of *C. bohemicum*. In the original description Cramer and Díez (1976) only compared the species with *C. elegans*, but not with the type species *bohemicum*. The authors differentiated the new species because of its very short processes (< 0.5 µm). However, this is also the main characteristic feature of *C. almohadillum*, from which *C. barakum* is very difficult to distinguish.

*Biostratigraphical and palaeobiogeographical distribution* : It is not clear whether the specimens of *C. barakum* recorded since the original description truly represent the species. All later citations are questionable and/or the specimens were not illustrated.

#### *Coryphidium bohemicum* Vavrdová 1972

?*Baltisphaeridium* cf. *cristatum*. - Downie and Ford 1966, p. 322, pl. 17 : fig. 7.

Indéterminé Forme A. - Martin et al. 1970, p. 346, pl. 1 : fig. 3.

?*Baltisphaeridium* cf. *cristatum* Downie (*in* Downie and Ford 1966). - Lister et al. 1969, p. 98.

?*Baltisphaeridium obtusatum* sp.n. – Burmann 1970, p. 309, pl. 7 : 7.

*Acanthodiacrodium* sp. - Rauscher 1971, p. 292, 296, pl. 1, fig. 7.

*Coryphidium bohemicum* sp. nov. - Vavrdová 1972, p. 84-85, text-fig. 4, pl. 1 : figs. 1-2.

*Coryphidium bohemicum* Vavrdová 1972. - Rauscher 1974a, p. 79, 162, pl. 3 : figs. 21-22, 27-28, pl. 9 : figs. 17-18.

*Coryphidium bohemicum* Vavrdová. - Rauscher 1974b, pl. 1 : fig. 19.

*Coryphidium bohemicum* Vavrdová. - Vavrdová 1974, p. 173-174, text-fig. 1 : 18.

\**Coryphidium bohemicum* Vavrdová 1972. - Cramer et al. 1974, p. 184.

?*Octogonium vanguetainii* nov. sp. – Martin 1974, p. 9, 23-24, 31, 43, 46-47, 63, text-fig. 10, pl. 4 : figs. 119, 121.

*Coryphidium bohemicum* Vavrdová 1972. - Eisenack et al. 1976, p. 145-146.

?*Baltisphaeridium obtusatum* Burmann 1970. - Eisenack et al. 1976, p. 103.

?*Baltisphaeridium obtusatum* n.sp. (sic); Burmann 1976, table 1: 74.

\**Coryphidium bohemicum*. – Vavrdová 1976, p. 62.

*Coryphidium bohemicum* Vavrdová 1972. - Cramer and Díez 1976, p. 203, text-fig. 2 : 1.

\**Coryphidium bohemicum* Vavrdová 1972. - Díez and Cramer 1977, p. 5, 30.

- \**Coryphidium bohemicum* Vavrdová. - Vavrdová 1977, p. 111.
- \**Coryphidium bohemicum* Vavrd. 1972. - Fournier-Vinas and Donnot 1977, p. 125.
- Coryphidium bohemicum* Vavrdová, M., 1972. - Martin 1977, p. 23-24, pl. 4 : fig. 30, pl. 5 : fig. 4.
- Coryphidium bohemicum* Vavrdová 1972. - Fournier-Vinas 1978, p. 266, pl. 2, figs. 32-34.
- \**Coryphidium bohemicum* Vavrd. - Vavrdová 1978, p. 72.
- Coryphidium bohemicum* Vavrdová 1972. - Martin in Dean and Martin 1978, p. 7, 10-11, pl. 2 : figs. 1-2, 5, pl. 3 : fig. 25.
- Coryphidium bohemicum* Vavrdová 1972. - Martin and Rickards 1979, p. 191, pl. 1 : fig. 4.
- Coryphidium bohemicum* Vavrdová 1972. - Turner and Wadge 1979, p. 407, 411, pl. 18 : figs. 1-3.
- \**Coryphidium bohemicum* Vavrdová 1972. - Molyneux 1979, p. 417-419.
- \**Coryphidium* cf. *bohemicum* Vavrdová 1972. - Molyneux 1979, p. 416-417.
- \**Coryphidium bohemicum* Vavrdová. - Xing 1980, p. 438.
- Coryphidium bohemicum* Vavrdová 1972. - Cocchio 1981, p. 74-75, 98; pl. 2 : fig. 18.
- \**Coryphidium* cf. *bohemicum* Vavrdová 1972. - Cocchio 1981, p. 7.
- \**Coryphidium bohemicum*. - Barca et al. 1981, p. 384.
- Coryphidium bohemicum* Vavrdová 1972. - Cocchio 1982, p. 28; pl. 1 : fig. 19.
- \**Coryphidium bohemicum* Vavrdová 1972. - Martin 1982, p. 32-33.
- \**Coryphidium bohemicum*. - Vavrdová 1982a, p. 148, 152.
- \**Coryphidium bohemicum* Vavrdová. - Vavrdová 1982b, p. 338.
- Coryphidium* cf. *bohemicum* Vavrdová 1972. - Marhoumi et al. 1982, p. 139; pl. 1 : fig. 23.
- \**Coryphidium bohemicum* Vavrdová 1972. - Turner 1982, p. 122-123, 125.
- Coryphidium bohemicum* Vavrdová 1972. - Downie 1984, text-fig. 4 : 23.
- \**Coryphidium bohemicum* (Vavrd.). - Fournier-Vinas 1985, p. 809.
- \**Coryphidium bohemicum* Vavrdová 1972. - Albani et al. 1985b, p. 12.
- \**Coryphidium bohemicum* Vavrdová. - Vavrdová 1986, p. 356.
- \**Coryphidium bohemicum* Vavrdová 1972. - Vanguetstaine 1986, p. 74.
- Coryphidium bohemicum* Vavrdová 1972. - Fang 1986, p. 132, 135-136, 139-140, 146-147, 157, pl. 4 : fig. 2.
- Coryphidium bohemicum* Vavrdová 1972. - Li 1987, p. 616, 630, pl. 72 : figs. 5, 9.
- \**Coryphidium* aff. *bohemicum*. - Trythall et al. 1987, p. 35.
- pp *Coryphidium bohemicum* Vavrdová 1972. - Molyneux 1987, p. 324, figs. 14-18, ? 20.
- Coryphidium bohemicum* Vavrdová 1972. - Arriaga e Cunha and Vanguetstaine 1988, p. 72, pl. 1 : fig. 9.
- Coryphidium* cf. *bohemicum* Vavrdová 1972. - Arriaga e Cunha and Vanguetstaine 1988, p. 72, pl. 1 : fig. 10.
- \**Coryphidium bohemicum* 1972. - Vavrdová 1988, p. 8.
- \**Coryphidium bohemicum* Vavrdová 1972. - Mette 1989, p. 7.
- Coryphidium bohemicum*. - Vavrdová 1989, p. 404-405, text-fig. 1 : L2.
- Coryphidium bohemicum* Vavrdová 1972. - Albani 1989, p. 5, 13-14, pl. 1 : figs. 21-22.
- Coryphidium* aff. *bohemicum* Vavrdová 1972. - Rushton and Molyneux 1989, p. 271-273, text-fig. 4 : C, E-G, I, L.
- Coryphidium* cf. *bohemicum* Vavrdová 1972. - Steemans 1989, p. 302, fig. 145, pl. 2 : fig. 7.
- \**Coryphidium bohemicum* Vavrdová. - Vavrdová 1990b, p. 242-243.
- \**Coryphidium* aff. *bohemicum* ? Vavrdová 1972. - Cooper and Molyneux 1990, p. 151-152.
- Coryphidium bohemicum* Vavrdová. - Li 1990, p. 142, 147, 157, 159, pl. 3 : fig. 10.
- \**Coryphidium bohemicum* Vavrdová 1972. - Fensome et al. 1990, p. 155.
- Coryphidium bohemicum* Vavrdová 1972. - Ghavidel-Syooki 1990, pl. 4 : figs. 5-8.
- \**Coryphidium bohemicum*. - Fensome et al. 1991, p. 9.

- ?*Coryphidium bohemicum* Vavrdová 1972. - Reitz and Höll 1991, p. 331; pl. 1 : figs. 8-9.
- \**Coryphidium bohemicum* Vavrdová 1972. - Herbosch et al. 1991, p. 203.
- Coryphidium bohemicum* Vavrdová 1972. - Servais 1991, p. 240, pl. 1 : fig. 2.
- \**Coryphidium bohemicum* Vavrdová. - Gao 1991, p. 446-449, 455.
- \**Coryphidium bohemicum* Vavrdová (misspelling). - Gao 1991, p. 447.
- \**Coryphidium* cf. *bohemicum* Vavrdová (misspelling). - Gao 1991, p. 454.
- \**Coryphidium* aff. *bohemicum* Vavrdová 1972. - Millward and Molyneux 1992, pp. 81, 83, 85.
- \**Coryphidium bohemicum*. - Reitz and Höll 1992, p. 199.
- Coryphidium bohemicum* Vavrdová 1972. – Maletz and Servais 1993, p. 131, 133, 134, fig. 5 : 1-2.
- Coryphidium bohemicum* Vavrdová 1972. - Tongiorgi et al. 1994, p. 596-597, 599, 603, pl. 2 : fig. 2.
- \**Coryphidium bohemicum* Vavrdová 1972. -Tongiorgi et al. 1995, p. 15-17.
- Coryphidium bohemicum* Vavrdová. - Li and Yuan 1995, p. 61, pl. 1 : figs. 6-8.
- Coryphidium bohemicum* Vavrdová 1972. – Yin 1995, p. 50-51, pl. 18 : figs. 10-11.
- Coryphidium bohemicum* Vavrdová. - Xu et al. 1995, p. 291, pl. 1 : fig. 2.
- \**Coryphidium bohemicum*. - Cooper et al. 1995, p. 190-191.
- \**Coryphidium* aff. *bohemicum*. - Cooper et al. 1995, p. 190.
- \**Coryphidium bohemicum*. - Martin 1996, p. 5-6.
- \**Coryphidium bohemicum* ?. - Molyneux 1996, p. 546-547.
- \**Coryphidium* sp. aff. *C. bohemicum*. – Molyneux 1996, p. 546-548.
- Coryphidium bohemicum* Vavrdová 1972. – Ghavidel-Syooki 1997, p. 390, 402, pl. 3 : fig. 3.
- Coryphidium bohemicum* Vavrdová 1972. - Vavrdová 1997, p. 33-35, fig. 4 F, fig. 5 D.
- Coryphidium bohemicum* ?. – Molyneux and Leader 1997, p. 81, 83-85, 87-88, 90-93, pl. 1 : figs. 7-11.
- Coryphidium* sp. aff. *C. bohemicum*. – Molyneux and Leader 1997, p. 81, 83-85, 87-88, 90-93, pl. 1 : figs. 12-15.
- \**Coryphidium bohemicum*. – Servais and Fatka 1997, p. 622.
- \**Coryphidium bohemicum* Vavrdová 1972. – Tongiorgi et al. 1998, p. 186.
- Coryphidium bohemicum* Vavrdová 1972. – Li and Yuan 1998, p. 274, 277, pl. 4: figs. 11-13.
- Coryphidium bohemicum* Vavrdová 1972. – Connery and Higgs 1999, p. 136, 142, 146, 148, pl. 2, fig. 4.
- Coryphidium bohemicum*. – Molyneux 1999, p. 31, fig. 3b.
- Coryphidium* aff. *bohemicum*. – Molyneux 1999, p. 31, fig. 3g.
- Coryphidium bohemicum* Vavrdová 1972. – Vecoli 1999, p. 1, 12-13, 15, 19, 24, 37-38, 68, 80; pl. 5, fig. 9.
- \**Coryphidium bohemicum* Vavrdová 1972. – Vecoli et al. 1999, 331, 334, 338-339.
- Coryphidium bohemicum* Vavrdová 1972. – Xu 1999, p. 65, 75, pl. 1 : fig. 9.
- Coryphidium bohemicum* Vavrdová 1972. – Quintavalle et al. 2000, p. 5-6, 9, pl. 1 : fig. 8.
- \**Coryphidium bohemicum* Vavrdová 1972 *sensu stricto*. – Brocke et al. 2000, p. 32.
- \**Coryphidium bohemicum* group. – Brocke et al. 2000, p. 31-32.
- Coryphidium* cf. *bohemicum* Vavrdová 1972. – Maziane et al. 2000, p. 62, 65, 67, pl. 1 : fig. 9, pl. 2 : fig. 1.
- Coryphidium bohemicum*. - Todd et al. 2000, p. 829-830, 832, fig. 10d.
- Coryphidium bohemicum* Vavrdová 1972. – Li et al. 2002, p. 97-99, 101, pl. 1 : fig. 7.
- Coryphidium* cf. *C. bohemicum* Vavrdová 1972. – Rubinstein and Toro, p. 426-428, 431, 434, pl. 1 : fig. 4.
- \**Coryphidium bohemicum*. – Li et al. 2003, p. 96-98.
- \**Coryphidium bohemicum*. – Rubinstein 2003, p. 125.

*Holotype* : Vavrdová 1972, p. 84, pl. 1 : figs. 1-2, text-fig. 4.

*Type locality and type level* : Klabava near Rokycany (Czechoslovakia), Klabava Shales.

*Original diagnosis* (Vavrdová 1972) : "Outline rhombic, octagonal or sub-polygonal, sides convex, straight or concave. Wall single-layered, with microrugulate to microstriate sculpture. Ribs are positive, closely spaced (about 2 microns), parallel to edges, diminishing towards angles. Numerous conical processes (usually from 40 to 60 in number) are heteromorphic, proximally opened. Distally processes are closed, truncated, bifurcate, plurifurcate (both ombrellate and roset-(*sic*)like), lacinate, filled at their terminations. The distribution of processes is symmetrical, with an obvious concentration to the angles".

*Remarks* : As indicated in the bibliographical list, *Coryphidium bohemicum* has been recorded from numerous localities in over 80 publications. Vavrdová's (1972) diagnosis is rather wide and allows inclusion of many morphologies. The specimens attributed to *C. bohemicum* and illustrated in previous publications therefore show a wide range of process morphologies. Usually, *C. bohemicum* was distinguished from *C. elegans*, the second most recorded species, on the basis of the different process shape (more complex branching for *bohemicum*, more simple and tapering processes for *elegans*), although it is difficult to draw a limit between these two extreme morphologies. Some authors strictly followed the definition of Vavrdová (1972) and used the term *Coryphidium bohemicum* Vavrdová 1972 *sensu stricto* (e.g. Brocke et al. 2000), while others accepted some morphological variation (e.g. Molyneux and Leader 1997).

*Biostratigraphical and palaeobiogeographical distribution* : *C. bohemicum* has very widely been reported from numerous localities in the Lower and Middle Ordovician of peri-Gondwana. A detailed review of its distribution is provided in the biostratigraphy and palaeobiogeography chapters.

*Coryphidium elegans* Cramer et al. 1974

*Coryphidium elegans* n.sp. - Cramer et al. 1974, p. 182-184, 189, pl. 27 : figs. 12-19.

*Coryphidium elegans* Cramer, Allam, Kanes and Díez 1974. - Cramer and Díez 1976, p. 201-204, pl. 23 : 1-2, 21, 25, text-fig. 2 : 2.

*Coryphidium elegans* Cramer, Allam, Kanes and Díez 1974. - Eisenack et al. 1976, pp. 147-148.

\**Coryphidium elegans* Cramer, Allam, Kanes and Díez 1974 ; Díez and Cramer 1977, p. 10, 30.

?*Coryphidium elegans* Cram. et al. - Kalvacheva 1979, p. 1399, pl. 1 : fig. 10.

\**Coryphidium elegans* Cram. et al. - Molyneux 1979, pp. 417, 419.

\**Coryphidium elegans* Cram. et al. - Kalvacheva 1980, p. 196.

? *Coryphidium* cf. *elegans* Cram. et al. 1974. - Cocchio 1981, pp. 76-77, 98, text-fig. 50.

\**Coryphidium* cf. *elegans* Cramer, Allam, Kanes and Díez 1974. - Cocchio 1982, pp. 28, 31.

\**Coryphidium elegans* Cramer, Allam et al. 1974. - Turner 1982, pp. 122-123, 125.

*Coryphidium elegans* Cramer et al. 1974. - Downie 1984, text-fig. 4 : 18.

?*Coryphidium elegans* Cramer, Allam, Kanes and Díez 1974 ; Tongiorgi et al. 1984, p. 669, pl. 2, figs. 14, 15.

\**Coryphidium elegans*. - Baudelot and Fournier-Vinas 1984, p. 10.

- \**Coryphidium elegans* (Cram. , ...). - Fournier-Vinas 1985, p. 809.
- \**Coryphidium elegans* Cramer, Allam, Kanes and Díez 1974. - Albani et al. 1985b, p. 12.
- \**Coryphidium* cf. *elegans* Cramer, Allam, Kanes and Díez 1974. - Albani et al. 1985b, p. 13.
- \**Coryphidium elegans* Cramer, Hallam, Kanes and Díez 1974 [sic]. - Albani et al. 1985b, p. 14
- Coryphidium elegans* Cramer et al. 1974. - Fang 1986, pp. 130, 132, 135, 139-141, 147, 157, pl. 4 : fig. 1.
- ? *Coryphidium* aff. *elegans* Cramer, Allam, Kanes and Díez. - Mette 1989, p. 3, 8, pl.1 : 24, pl. 2 : 12, 13, 15.
- \**Coryphidium elegans*. - Mette 1989, p. 3-5, 8.
- Coryphidium elegans* Cramer, Allam, Kanes and Díez 1974 ; Albani 1989, p. 5, 14, 16, pl. 1 : figs. 26-29.
- ?*Coryphidium elegans* Cramer et al. – Li 1990, p. 142, 147, 157, pl. 2 : fig. 11.
- ?*Coryphidium* cf. *elegans* Cramer et al. 1974. - Cooper and Molyneux 1990, fig. 3 : p, q.
- \**Coryphidium elegans* Cramer et al. 1974. - Cooper and Molyneux 1990, p. 152.
- Coryphidium elegans* Cramer et al. 1974. – Ghavidel-Syooki 1994, pl. 4 : figs. 10-12.
- \**Coryphidium elegans* Cramer et al. 1974. - Fensome et al. 1990, p. 155.
- \**Coryphidium elegans*. - Fensome et al. 1991, p. 31.
- \**Coryphidium elegans* Cramer, Allam, Kanes and Díez 1974. - Millward and Molyneux 1992, p. 81, 83, 85.
- Coryphidium elegans* Cramer et al. 1974. - Tongiorgi et al. 1994, p. 596-597, 599, 603, pl. 2 : fig. 6.
- Coryphidium elegans* Cramer et al. 1974. – Ghavidel-Syooki 1994, pl. 4 : figs. 11-12.
- Coryphidium elegans* Cramer et al. 1974. – Ghavidel-Syooki 1995, pl. 1 : fig. 8.
- \**Coryphidium* cf. *elegans*. - Cooper et al. 1995, p. 190.
- Coryphidium* cf. *elegans* Cramer et al. 1974. – Martin 1996, 6-7, 12, pl. 1 : fig. 16.
- Coryphidium* sp. aff. *C. elegans*. – Molyneux 1996, p. 546-548.
- \**Coryphidium elegans*. – Ghavidel-Syooki 1997, p. 390.
- Coryphidium* sp. aff. *C. elegans*. – Molyneux and Leader 1997, p. 81, 83-93, pl. 1 : figs. 1-6.
- Coryphidium elegans* Cramer, Allam, Kanes and Díez 1974. - Connery and Higgs 1999, p. 136, 142, 144, 150, pl. 2, fig. 5.
- Coryphidium* sp. cf. *elegans* Cramer, Allam, Kanes and Díez 1974. - Connery and Higgs 1999, p. 136, 142, 144, pl. 2, fig. 6.
- Coryphidium* sp. aff. *elegans* Cramer, Allam, Kanes and Díez 1974 *sensu* Molyneux and Leader 1997. - Connery and Higgs 1999, p. 136, 142, pl. 2, fig. 8.
- Coryphidium elegans* Cramer, Allam, Kanes and Díez 1974. - Quintavalle et al. 2000, p. 6, 9, pl. 1 : fig. 11.
- Coryphidium elegans* Cramer and Díez 1976 (sic). – Brocke et al. 2000, p. 28, 31-32, 37, pl. 2 : fig. 2.
- Coryphidium bohemicum*. - Todd et al. 2000, p. 829-830, fig. 10c.

*Holotype* : Cramer et al. 1974, p. 184, pl. 27 : fig. 16.

*Type locality and type level* : Boujad, Tadla Basin, Morocco, borehole BJ-109, 360m.

*Original diagnosis* (Cramer et al. 1974). "Central body hollow, subsquare with rounded corners. The vesicles are plate-like in form, much flatter than wide. The vesicle is covered by a combination of short filose sculptural elements and short, non-accidental, low rugulae. The distribution of these sculptural elements show areas of preference : the filose sculptural elements are concentrated at the corners of the body (each corner shows about the same



sculptural density), and the rugulae are more abundant on the central portions of the body walls. The sculptural complexity, quantity, and size has been found to be quite variable from specimen to specimen in the same sample. The filose sculptural elements are essentially solid, slender and vary from flexible spines to hairs; occasionally they may show some kind of tiny knob at the extreme distal termination. These elements are up to about one micron thick (about one-half micron is normal) and up to ten microns long (but generally they are shorter : three to five microns is normal). At their bases they are a bit wider : up to three microns; they taper rapidly. The rare knobs are about one micron in diameter in all directions. The rugulate elements are about one micron both high and wide, two or three microns apart and of variable length. Generally they are about ten microns long. The vesicle wall is about one micron thick. Mode of opening not known; no endodermal structures observed.

*Remarks* : *Coryphidium elegans* is the second most frequently recorded species after *C. bohemicum* with citations in over 30 publications. The rather long diagnosis indicates that most specimens have long (up to 10  $\mu\text{m}$ ), simple processes with undivided distal tips, which differentiate this species from Vavrdová's (1972) *C. bohemicum*. On the other hand, however, the presence of simple processes makes an emendation of the generic diagnosis necessary. The specimens attributed to *C. elegans* in literature also show a wide range of process morphologies, but usually the name *C. elegans* was given to specimens with longer processes than those of *C. bohemicum*.

*Biostratigraphical and palaeobiogeographical distribution* : *C. elegans* has also been reported from numerous localities in the Lower and Middle Ordovician of Europe and southern China (see biostratigraphy and palaeobiogeography chapters).

*Coryphidium ? longispinosum* Gao 1991

*Coryphidium longispinosum* (sp. nov.). - Gao Lianda 1991, p. 446, 451, 454, 455, pl. 2, fig. 10.

*Holotype* : Gao Lianda 1991, p. 451, pl. 2 : fig. 10.

*Type locality and type level* : Wuding (Yunnan Province, China), Hongshiyuan Formation, sample W-3.

*Translation of the original description and of the comparison.*

Original diagnosis (translated from Chinese): The vesicle is more or less sub-quadrate, sometimes circular in outline. The wall is thick and yellowish brown in color. The corners are round and the four sides are concave, tending to go inside (*sic*). The surface of the vesicle has long appendices, which are more frequent at the corners. The bases of the appendices are not in contact. Length of the appendices: 8-20 $\mu$ ; the distal end of the spines is round or tapering. Central body diameter : 25-26 $\mu$ .

Comparison : The new species based on samples collected from the Yunnan province is similar in outline to *C. bohemicum* established from the early Ordovician (Arenigian stage) of Czechoslovakia, Bohemia, by Vavrdová (1972, p. 84-85, pl. 1 : fig. 1-2).

The difference is that the vesicle of the latter (*C. bohemicum*) is quadrate and has round corners, and some very fine lines are parallel to the four sides. At the corners and the four sides, a lot of densely distributed, small conical spines (2-3 $\mu$ ) are present.

*Remarks* : It is not clear if this species really belongs to *Coryphidium*. There is no evidence from the illustration of the holotype for the presence of the structural ridges, and neither are such structures mentioned in the diagnosis. On the contrary, in the comparison with *C. bohemicum*, Gao (1991) indicates that the latter species differs from *longispinosum* in displaying "fine lines". We therefore only questionably attribute Gao's (1991) new species to *Coryphidium*. The species has never been recorded since its original description, although a great number of other workers have analysed samples from the same area and stratigraphical interval (Li et al. 2003).

*Coryphidium miladae* Cramer and Díez 1976

*Coryphidium milada* n.sp. - Cramer and Díez 1976, p. 205, text-fig. 2 : 6, pl. 23, figs. 9, 14, 22, 23.

*Coryphidium milada* Cramer and Díez 1976. - Eisenack et al. 1979, p. 83.

\**Coryphidium* cf. *milada* Cr. and Díez. - Kalvacheva 1982a, p. 1103.

?*Coryphidium* cf. *milada* Cramer and Díez 1969 (sic). - Kalvacheva 1982b, pl. 1 : fig. 7.

?*Coryphidium* cf. *milada* Cr. and Díez (sic). - Kalvacheva 1982b, pl. 2 : fig. 7.

\**Coryphidium* cf. *milada* Cr. and Díez (sic). - Kalvacheva 1982b, p. 18.

?*Coryphidium milada* Cramer and Díez 1976. - Tongiorgi et al. 1984, p. 669, pl. 2 : fig. 16.

\**Coryphidium milada* (Cr.Díez). - Fournier-Vinas 1985, p. 809.

?*Coryphidium* cf. *C. milada* Cramer and Díez 1976. - Albani et al. 1985a, p. 50, 51, 60, pl. 6, fig. 9.

?*Coryphidium milada* Cramer e Díez 1976. - Albani et al. 1985b, p. 12, pl. 3, figs. 14, 15.

\**Coryphidium* cf. *milada* Cr. and Díez. - Kalvacheva 1986, p. 40.

?*Coryphidium milata* Cramer et al. 1967 (sic). - Fang 1986, p. 132,133, 147, pl. 4 : figs. 3, 4.

\**Coryphidium milada*. - Fang 1986, p. 135, 139, 140.

*Coryphidium milada* Cramer and Díez 1976. – Albani 1989, p. 5, 16, pl. 2 : figs. 2-3.

\**Coryphidium* cf. *milada* Cramer and Díez 1976. – Mette 1989, p. 7.

?*Coryphidium milada*. - Vavrdová 1990b, p. 243.

\**Coryphidium miladum* Cramer and Díez 1976. - Fensome et al. 1990, p. 155.

\**Coryphidium miladum*. - Fensome et al. 1991, p. 61.

?*Coryphidium milada*. – Reitz 1994, p. 664, pl. 1, fig. 20.

*Coryphidium miladae* Cramer and Díez 1976. – Tongiorgi et al. 1994, p. 596, 598-599, 603, pl. 2 : fig. 5.

*Coryphidium miladae* – *Coryphidium tadla* group. – Rubinstein et al. 1999, p. 270-272, 274, pl. 3 : figs. 3, 7, pl. 5 : fig. 4.

\**Coryphidium miladae* – *Coryphidium tadla* group *sensu* Rubinstein *in* Rubinstein et al. 1999. – Rubinstein and Toro 2001, p. 426, 428.

*Holotype* : Cramer and Díez 1976, p. 205, pl. 23 : fig. 9.

*Type locality and type level* : Boujad, Tadla Basin, Morocco, borehole BJ-109, 510m.

*Original diagnosis* (Cramer and Díez, 1976). "Species of *Coryphidium* of a similar morphology to that of *C. elegans*, but distinguished from it in that *C. milada* is smooth or has no distinct rugulate sculpture and that its filose elements are few, and rather widely spaced. These elements are in the form of thin bacula; some of them are sharp-tipped, others bifurcated distally, and still others truly club-shaped".

*Nomenclatural note* : *C. milada* is here corrected to *C. miladae*, since Milada is a personal name, the genitive inflection must be *miladae* (I.C.B.N., Article 60).

*Remarks* : As discussed above in the discussion of *C. australe* and *C. tadlanum*, two other of the seven 'new' *Coryphidium* species of Cramer and Díez (1976) are readily undistinguishable. *C. miladae* and *C. tadlanum* are diagnostified and illustrated in the publication of their original description with very close morphologies. Rubinstein in Rubinstein et al. (1999) created the informal "*Coryphidium miladae* – *Coryphidium tadlum* group". She presented a first synonymy list including both taxa from the original description of Cramer and Díez (1976) and the specimens determined as *C. milada* and *C. tadla* by Tongiorgi et al. (1984). We agree with Rubinstein that "no essential difference can be detected" between these two taxa (see also discussion below).

*Biostratigraphical and palaeobiogeographical distribution* : Perhaps because of its imprecise original description, *C. miladae* has only been reported from a few localities. Its distribution does not differ from that of the other species of the genus (see biostratigraphy and palaeobiogeography chapters).

#### *Coryphidium minutum* Cramer and Díez 1976

*Coryphidium minutum* n.sp. - Cramer and Díez 1976, p. 205, text-fig. 2 : 7, pl. 23 , figs. 7, 10.

*Coryphidium minutum* Cramer and Díez 1976. - Eisenack et al. 1979, p. 85.

?*Coryphidium minutum* Cramer et Díez 1976. - Marhoumi et al. 1982, p. 139, pl.1, figs. 19-20.

\**Coryphidium* cf. *minutum* Cr. and Díez. - Kalvacheva 1982a, p. 1103.

\**Coryphidium* cf. *minutum* Cr. and Díez ; Kalvacheva 1982b, p. 18.

\**Coryphidium* cf. *C. minutum* Kramer e Díez 1976 (sic). - Albani et al. 1985b, p. 14.

\**Coryphidium minutum* (Cr. Díez). - Fournier-Vinas 1985, p. 809.

\**Coryphidium* cf. *minutum* Cr. and Díez ; Kalvacheva 1986, p. 40.

? *Coryphidium minutum* Cramer et Díez 1976. - Molyneux, p. 324, text-fig. 19.

?*Coryphidium* cf. *minutum* Cramer and Díez 1976 ; Arriagha e Cunha and Vanguestaine 1989, p. 72, 74, pl. 1 : fig. 11.

\**Coryphidium* cf. *minutum* Cramer and Díez 1976. – Mette 1989, p. 7.

*Coryphidium minutum* Cramer and Díez 1976. – Albani 1989, p. 5, 16, pl. 2 : fig. 1.

\**Coryphidium minutum* Cramer and Díez 1976. - Fensome et al. 1990, p. 156.

\**Coryphidium minutum*. - Fensome et al. 1991, p. 62.

?*Coryphidium minutum* Cramer and Díez 1976. - Reitz and Höll 1991, p. 331, 334, pl. 2 : fig. 4.

\**Coryphidium minutum* Cramer and Díez 1976. - Reitz and Höll 1992, p. 199.

*Coryphidium minutum* Cramer and Díez 1976. – Tongiorgi et al. 1994, p. 596, 598-599, 603, pl. 2 : fig. 3.

*Coryphidium minutum* Cramer and Díez 1976. – Ghavidel-Syooki 2001, p. 20, pl. 3 : fig. 8.

*Holotype*. Cramer and Díez 1976, p. 205, pl. 23 : fig. 7.

*Type locality and type level*. Boujad, Tadla Basin, Morocco, borehole BJ-109, 510m.

*Original diagnosis* (Cramer and Díez 1976). "Species of *Coryphidium* of a similar general morphology to that of *C. elegans*, but distinguished from it in that *C. minutum* is entirely

smooth and displays a sculpture consisting of numerous tiny filose elements. These vary from aculeate to flagellate. Some are capitate".

*Remarks* : The original diagnosis of this species indicates that it lacks ridges ("entirely smooth") and so it should not be included in the genus *Coryphidium*. The processes of this morphotype are very small ("filose elements"). Coryphid acritarchs with such small processes have been recorded by several authors. The boundaries between *C. minutum* and other species with very small processes (*C. almohadillum*, *C. barakum*) are not clear. The processes are very similar, but some species have ridges/striations on the vesicle.

*Biostratigraphical and palaeobiogeographical distribution* : Perhaps because the original description of this species is not very precise, and the distinction between this and other taxa not clearly defined, *C. minutum* has not been recorded many times. Similarly to other species, its distribution falls within the biostratigraphical and palaeobiogeographical ranges of the genus *Coryphidium* (see biostratigraphy and palaeobiogeography chapters).

*Coryphidium ? persianum* Ghavidel-Syooki 1990 (invalid species)

*Coryphidium persica* n.sp. – Ghavidel-Syooki 1990, p. 172, pl. 4 : figs 1-4.

\**Coryphidium persica*. – Ghavidel-Syooki 1997, p. 390.

*Holotype*. No holotype has been designated, but four specimens were illustrated (Ghavidel-Syooki 1990, p. 172, pl. 4 : fig. 1-4). It is not clear where the type material is deposited.

*Type locality and type level*. Upper part of the Zard Kuh Formation, type level not precisely indicated.

*Original diagnosis* (Ghavidel-Syooki 1990). "Central body is typically quadrate to subquadrate with rounded corners. The vesicle is covered by a translucent membrane. The membrane is square shape that it is connected to the body by a set of filose processal elements. The filose processal elements are slender, solid and vary from flexible spines to hairs. This species ranges from 50-60 microns (including membrane and body). The body is 25 to 30 microns and the membrane is 10 to 15 microns. No endodermal structure and no mode of opening is recognizable".

*Remarks* : This species was described in its original diagnosis as lacking the ridges characteristic of the genus *Coryphidium*. In addition, the presence of a membrane is inconsistent with the original and emended diagnoses of the genus (membranes have never been reported so far).

As no holotype has been designated, the species is currently invalid (Art. 37. of the I.C.B.N.). The name has corrected here from *Coryphidium persica* to *C. persianum*, following recommendation 60 D of the I.C.B.N. (the specific epithet is derived from a geographical name, "Persia").

*Biostratigraphical and palaeobiogeographical distribution* : The species has only been recorded so far from the upper part of the Zard Kuh Formation in southern Iran.

*Coryphidium ramiferum* Cramer and Díez 1976

*Coryphidium ramiferum* n.sp. - Cramer and Díez 1976, p. 206, text-fig. 2 : 8, pl. 23, figs. 16, 24.

*Coryphidium ramiferum* Cramer and Díez 1976. - Eisenack et al. 1979, p. 87.

\**Coryphidium ramiferum* Cramer and Díez 1976. - Fensome et al. 1990, p. 156.

\**Coryphidium ramiferum*. - Fensome et al. 1991, p. 82.

*Holotype*. Cramer and Díez 1976, p. 206, pl. 23 : fig. 16.

*Type locality and type level*. Boujad, Tadla Basin, Morocco, borehole BJ-109, 510m.

*Original diagnosis* (Cramer and Díez 1976) : "Species of *Coryphidium* of a similar general morphology to that of *C. elegans*, but distinguished from it in that *C. ramiferum* has an indistinct sculpture of widely spaced rugulate elements and bears numerous ramified processes. These processes are short and plump and branch into a crown some about palmate pinnae of varying length".

*Remarks* : Clearly belonging to the genus *Coryphidium*, this species is characterized by processes with a typical crown-like distal termination. It has never been recorded since its original description.

*Biostratigraphical and palaeobiogeographical distribution* : The species is so far only known from the type-level in the Tadla Basin, Morocco.

*Coryphidium tadlanum* Cramer and Díez 1976

*Coryphidium tadla* n.sp. - Cramer and Díez 1976, p. 206, text-fig. 2 : 9, pl. 23, figs. 3, 4, 15, 18, 19.

*Coryphidium tadla* Cramer and Díez 1976. - Eisenack et al. 1979, p. 89.

\**Coryphidium tadla* Cramer and Díez 1976. – Fournier-Vinas 1978, p. 266.

?*Coryphidium tadla* Cramer and Díez 1976. – Cocchio 1981, p. 75, 98, text-fig. 49.

\**Coryphidium tadla* Cramer and Díez 1976. – Cocchio 1982, p. 28.

\**Coryphidium tadla* (Cr. Díez). – Fournier-Vinas 1985, p. 809.

\**Coryphidium tadla*. – Fang 1986, p. 135.

*Coryphidium tadla* Cramer and Díez 1976. – Albani 1989, p. 5, 16-17, pl. 2, figs. 4-5.

\**Coryphidium tadlum* Cramer and Díez 1976. - Fensome et al. 1990, p. 156.

\**Coryphidium tadlum*. - Fensome et al. 1991, p. 97.

*Coryphidium miladae* – *Coryphidium tadla* group. – Rubinstein et al. 1999, p. 270-272, 274, pl. 3 : figs. 3, 7, pl. 5 : fig. 4.

\**Coryphidium miladae* – *Coryphidium tadla* group *sensu* Rubinstein *in* Rubinstein et al. 1999. – Rubinstein and Toro 2001, p. 426, 428.

*Coryphidium tadla* Cramer, Allam, Kanes and Díez 1974. - Quintavalle et al. 2000, p. 6, 9, pl. 1 : fig. 7.

*Holotype*. Cramer and Díez 1976, p. 206, pl. 23 : fig. 16.

*Type locality and type level*. Boujad, Tadla Basin, Morocco, borehole BJ-109, 510m.

*Original diagnosis* (Cramer and Díez 1976). "Species of *Coryphidium* of a similar general morphology to that of *C. elegans*, but distinguished from it in that *C. tadla* has no rugulae and practically all the filose processes are capitate ; furthermore, only a few of them dichotomize at the extreme end of the processes. The distal expansions are often clearly elongated and spoon-shaped. The filose elements are markedly more abundant than in *C. elegans*".

*Nomenclatural note* : *Coryphidium tadla* is corrected here into *C. tadlanum*, because the locality where the new species is found (Tadla) is a geographical name (I.C.B.N., Article 60).

*Remarks* : This original diagnosis of this species describes it as lacking the rugulae (ridges/striations), which is inconsistent with the original diagnosis of the genus. However, although Cramer and Díez (1976) mentioned the absence of rugulae in the diagnosis, on the holotype (Cramer and Díez 1976, pl. 23, fig. 4), the fine ridges are clearly visible on the vesicle wall. *Coryphidium tadlanum* was placed in synonymy with *C. miladae* by Rubinstein in Rubinstein et al. (1999).

*Biostratigraphical and palaeobiogeographical distribution* : The species is so far only known from the type-level in the Tadla Basin, Morocco.

#### 4.3. Morphological variation within *Coryphidium* species and its taxonomic treatment

From a review of the literature, and in particular from a critical analyses of the diagnoses in Cramer et al. (1974) and Cramer and Díez (1976), it appears that most species of *Coryphidium* are not clearly defined and that it can be difficult to distinguish between them. In addition, none of the authors that have erected new taxa have discussed in detail the morphological characteristics that allows a distinction of the newly defined species from all previously described taxa. In particular, the descriptions of the seven new species of Cramer and Díez (1976) are almost impossible to understand, because the original diagnoses correspond with neither with the text-figures, nor with the microphotographs in the plate.

The bibliographical review of *Coryphidium* shows that many authors have had difficulties in assigning their specimens to published species. Several authors have used open nomenclature, including "cf." and "aff.", in their determinations. Vecoli (1999) considered *Coryphidium australe* from *C. miladae* as "possibly conspecific". Rubinstein in Rubinstein et al. (1999) has noted that it is impossible to distinguish *Coryphidium miladae* from *C. tadlanum*. In addition, as indicated above, it is also difficult to distinguish *C. almohadillum* and *C. barakum*, both species being described with very short ornaments (shorter than 1  $\mu\text{m}$  and 0.5  $\mu\text{m}$ , respectively). *Coryphidium minutum* is also very similar to these two latter species, but Cramer and Díez (1976) erected a new species for this morphotype, because they did not observe the fine ridges with the optical microscope.

In summary, nine species can currently be considered to be validly published species of the genus *Coryphidium*. Two other species, *C. ? longispinosum* and *C. ? persianum* possibly belong to it, although the latter species is not valid. The nine *Coryphidium* species (*C. almohadillum*, *C. australe*, *C. barakum*, *C. bohemicum*, *C. elegans*, *C. miladae*, *C. minutum*, *C. ramiferum*, *C. tadlanum*) all have the body outline typical of coryphid acritarchs, and all have vesicles of about the same size (length of the sides between 20 and 35  $\mu\text{m}$ ). They always show fine ridges (also called rugulae) on their wall, which are parallel to the vesicle border and that cover the entire body. These ridges are not always clearly visible or have not always been described, however, which might be the result of preservation or simply due to observation techniques.

The nine *Coryphidium* species show a wide morphological variability which is expressed mainly in process length and structure. So, whereas *C. bohemicum* is described as having heteromorphic processes of varying degrees of complexity, the diagnosis of *C. elegans* states that it has simple, distally tapering processes with sharp-pointed tips. Nevertheless, both Vavrdová (1972) and Cramer et al. (1974) accepted a wide variability for their species in the diagnoses. The seven other species of Cramer and Díez (1976) are also distinguished on the basis of different process types and sizes. If we accept a wide variation of process lengths and structures of *C. bohemicum*, all specimens could fall within the diagnosis of this species and all other taxa could be considered as junior synonyms of the type species. If, however, we consider every variation as taxonomically significant, we could consider all species as separate taxonomic entities.

The problem is how to deal taxonomically with the morphological variability exhibited between *Coryphidium* species. Servais and Eiserhardt (1995) indicated that transients may exist between previously described, clearly distinguishable taxa in the galeate acritarch plexus. Based on this study, Servais and Molyneux (1997, p. 118-119) discussed the taxonomical treatment of variability in acritarch morphotypes, including the galeates, and indicated that the great morphological variability of acritarchs presents a taxonomic problem. If the variability is discontinuous, it is straightforward to identify two different morphotypes as two separate taxa, and so, for example, to erect two separate species. However, if a continuous variability exists between two end-members of a larger population, it is usually not possible to draw limits between the morphotypes, and it is therefore very difficult, if not impossible, to define separate taxa. As indicated by Servais and Molyneux (1997), acritarch taxonomy needs to maintain a balance between two opposing tendencies. On the one hand, acritarch morphotypes that grade from one to the other ought to be included in the same taxon. On the other hand, different morphologies may provide information that is useful to earth science, especially for biostratigraphy, palaeobiogeography or palaeoecology. If the different morphotypes are subsumed into the same taxon, the biostratigraphical or other information could be lost.

Although material from several localities and regions has been analysed for the present study, it is not possible to make clear distinctions between the species defined in the literature, and it is sometimes difficult to attribute a species name to a specimen. However, it is clear that some morphotypes are biostratigraphically useful, at least at a local or regional scale. As our view of the genus is not complete, we have therefore avoided making new taxonomic decisions, and we retain the existing taxonomy, despite the inherent.

## **5. Palaeoecology and palaeobiology**

It is difficult to judge the biological significance of the morphological variability of acritarchs and to determine which aspect of variability is phenotypic and which is genotypic. As Palaeozoic acritarchs are usually considered to represent the cysts of organic-walled microphytoplankton, it is interesting to compare their morphological variability with that of Recent dinoflagellate cysts. In the last decade, studies on the formation of dinoflagellate cysts in culture experiments has shown that the morphology of the resting cysts is controlled by both temperature and salinity (Kokinos and Anderson 1995, and references therein). The results indicate that process length and process structure are salinity and temperature dependent. Short-spined dinoflagellate cysts are usually related to low salinity environments, and long processes can be related to higher salinities.

From these results of experiments on cultured dinoflagellate cysts, and also from palaeontological observations (e.g. Turon 1982, Ellegaard 2000), it appears that process

length provides a quantifiable record of past salinity levels. The models that arise from these observations can possibly be applied to Cenozoic sediments, but it will probably be more difficult to establish relationships between process length and salinity in older rocks. Interestingly, Cramer and Díez (1976, p. 203) wrote that "*Coryphidium* might indicate paleosalinities which are slightly higher than normal (i.e. normal = oceanic)", although they provided no arguments to support for this interpretation.

As yet, it is not possible to indicate the palaeoecological attributes of the genus *Coryphidium* and its species. Li et al. (2004) observed the genus in all samples and from all localities along an inshore-offshore transect in the Early-Middle Ordovician of the Yangtze Platform, southern China. *Coryphidium* is present from nearshore environments, displaying very low overall diversities (less than 10 acritarch species recorded), across the platform to offshore environments with the highest diversities (with about 40 acritarch species). Although quantitative studies, including biometrical studies of the processes, have not been completed at the specific level, it seems that *Coryphidium* morphotypes do not change across the Yangtze Platform. Specimens that can be attributed to *C. bohemicum* (displaying a large variety of processes up to 5 µm) have been recorded on both the carbonate platform (e.g. Li 1987) and in nearshore environments (e.g. Li and Yuan 1995).

## 6. Biostratigraphy

### 6.1. Stratigraphical distribution of the type material of *Coryphidium*

*Coryphidium* has been recorded in some 100 publications, from numerous localities in Europe, North Africa, Asia, Newfoundland and Argentina. However, only a few samples have been precisely dated by means of other fossil groups (graptolites, chitinozoa, trilobites, etc.).

Although attributed to the Arenig, Vavrdová's (1972) type material has never been dated precisely. The sample is considered to come from the upper part of the Klabava Formation from a level equivalent to the regional *Tetragraptus reclinatus abbreviatus* graptolite Biozone. This regional biozone is now renamed *Azygograptus ellesi* – *Tetragraptus reclinatus abbreviatus* graptolite Biozone (Kraft and Kraft 1999, 2003). According to the discussion in Martin (1982), this zone should correspond to the combined *Isograptus gibberulus* and *Didymograptus hirundo* graptolite Biozones in the British Isles (see also Tongiorgi and Di Milia 1999, fig. 1). *C. bohemicum* has been recorded from several stratigraphical levels by Vavrdová (1972, 1974, 1976, 1977, 1982a, 1982b, 1986, 1988, 1989, 1990a, 1990b, 1997), ranging from the regional *Corymbograptus v-similis* graptolite Biozone (equivalent of the upper part of the British *varicosus* graptolite Biozone) to the Upper Ordovician; the higher occurrences are considered to be the result of reworking (Vavrdová 1982). In the Czech Republic, *Coryphidium* is thus considered to range from the lower (but not lowermost) Arenig through the lower Llanvirn.

The type material of Cramer et al. (1974) and Cramer and Díez (1976) is from the borehole Boujad (BJ) 109, from depths of 360 m (Cramer et al. 1974) and 510 m (Cramer and Díez (1976)). Parts of this borehole have been dated by Soufiane and Achab (1993) using chitinozoans. A late Arenig age can clearly be attributed to the sample from 510 m, based on the presence of *Desmochitina bulla* between 512 and 481 m, but the sample from 360 m, which contained the holotype of *C. elegans*, is from an interval that is not dated by chitinozoans, and may be of late Arenig or younger age.

### 6.2. Biostratigraphically controlled occurrences of *Coryphidium*



It is not surprising that the genus was considered for many years to be typical of the Arenig and Llanvirn (e.g. Martin 1982), because most occurrences are from that time interval. Precisely dated occurrences in the Arenig and Llanvirn are available from China, Avalonia, the southern European – North African border of peri-Gondwana, and Argentina.

In southern China the genus has been recorded from the Chinese *D. deflexus* and *A. suecicus* graptolite biozones of late Yushmanian (late early Arenig) age (e.g. Li 1987) up to the Chinese *D. murchisoni* Biozone of late Darriwilian (late Llanvirn) age (e.g. Li et al. 2000). As in the Czech Republic, the genus has not yet been recorded in China from the lowermost Arenig.

Several sections from Avalonia that have yielded *Coryphidium* are dated by means of other fossil groups. The occurrence in the Wabana Group of Newfoundland ("western Avalonia") indicates a probable early Arenig age ("*D. extensus* Zone" according to Dean in Dean and Martin 1978). The stratigraphical range of *Coryphidium* in Belgium is now better constrained due to recent graptolite and chitinozoan studies. The occurrence in the Villers-la-Ville Formation in the Brabant Massif (Martin 1977) is now considered to be of middle Arenig age (Samuelsson and Verniers 2000), while the age of the Rigenée Formation in the Brabant Massif, which also yielded *Coryphidium* (Servais 1991), is now considered to span the latest Arenig and early Llanvirn, but certainly includes the early Llanvirn *D. artus* biozone (Maletz and Servais 1997, Samuelsson and Verniers 2000). *Coryphidium* specimens are also found in the Caradoc (e.g. Martin et al. 1970) and in the Lower Devonian (Steemans 1989) of Belgium, but these occurrences are considered to be the result of reworking. In Germany, *Coryphidium* is found at levels that are clearly dated as being of early and middle Llanvirn (Darriwilian), *D. artus* and *D. murchisoni* graptolite Biozone age (Burmans 1970, Maletz and Servais 1993, Servais 1994, Servais et al. 2001).

Occurrences of *Coryphidium* spp. in the Lake District of northwest England are generally well dated by graptolite faunas that occur in the same beds (Cooper et al., 2004). The earliest specimens of *Coryphidium*, including the morphotype *Coryphidium* aff. *elegans* of Molyneux and Leader (1997) are from the Watch Hill Formation of the Skiddaw Group, which is correlated with the latest Tremadocian *Araneograptus murrayi* Biozone based on the presence of the eponymous graptolite species. The *murrayi* Biozone of the Lake District is equivalent to the *Araneograptus murrayi* and *Hunnegraptus copiosus* graptolite biozones of the Baltoscandian succession. *Coryphidium* aff. *elegans* ranges into the overlying Hope Beck Formation, reaching a level that is probably in the lowest Arenig *Tetragraptus phyllograptoides* graptolite Biozone. Specimens assigned to *Coryphidium bohemicum* appear in the Hope Beck Formation, reaching a level that is probably in the lowest Arenig *Tetragraptus phyllograptoides* graptolite Biozone or in the overlying *Didymograptus varicosus* graptolite Biozone, and range into the upper Arenig *Isograptus victoriae* graptolite Biozone in the Kirk Stile Formation, if not higher. The *Coryphidium* aff. *bohemicum* morphotype of Molyneux and Leader (1997) occurs in the upper part of the Kirk Stile Formation, at a level assigned to the upper Arenig *Isograptus gibberulus* and *Aulograptus cucullus* biozones. *Coryphidium* aff. *bohemicum* occurs at the same locality as graptolites of the highest Arenig *cucullus* Biozone in the northern Lake District. Specimens of *Coryphidium* also occur in the lower Llanvirn *Didymograptus artus* Biozone in the Lake District (Booth, 1979). Booth (1979) recorded specimens of *Coryphidium*, assigned to *Coryphidium bohemicum* and *Coryphidium elegans*, from sections along the southern shore of the Menai Straits from Bangor to Caernarvon in North Wales. The beds in these sections comprise the lowest part of the Nant Ffrancon Group, ranging here from middle Arenig to Llanvirn in age. Molyneux (1987) recorded poorly preserved specimens assigned to *Coryphidium bohemicum* from the *Stapeleyella abyfrons* and *Bergamia rushtoni* trilobite biozones of the Fennian (upper Arenig) Pontyfenny Formation in south Wales, and a specimen assigned to

*Coryphidium minutum* from the lower (but probably not lowest) Arenig Allt Cystanog Member of the Ogof Hên Formation. Turner (1982) recorded *Coryphidium australe*, *C. bohemicum* and *C. australe* from the type Caradoc Series of the Ordovician in the Welsh Borders, where they were considered to be reworked.

Independently dated occurrences of *Coryphidium* from North Africa are from the borehole NI2 in northern Algeria (Vecoli 1999) and from borehole A1-70 in the Ghadamis Basin in NW Libya (Vecoli and Quintavalle, unpublished). These levels were dated with chitinoans as belonging to the late Arenig.

Recent studies from Argentina (Rubinstein et al. 1999, Rubinstein and Toro 2001) indicate the occurrence of *Coryphidium* sp. in the *Tetragraptus akzharensis* graptolite Biozone of early (but not earliest) Arenig age, and of the *Coryphidium miladae-tadlanum* group, *Coryphidium* cf. *C. bohemicum* and *Coryphidium australe* in the *Didymograptellus bifidus* graptolite Biozone of middle Arenig age.

Most of the other occurrences of *Coryphidium* are not precisely dated, and age information is generally only provided by the accompanying acritarch assemblages. Records of "Arenig-Llanvirn" *Coryphidium* occurrences include those of Marhoumi et al. (1982) from Morocco, Smith (1981) and Maziane et al. (2000) from Ireland, Arriagha e Cunha and Vanguetaine (1988) from Portugal, Rauscher (1974a, 1974b), Fournier-Vinas and Donot (1977), Fournier-Vinas (1978) and Cocchio (1981, 1982) from France, Reitz and Höll (1991, 1992) and Reitz (1994) from Austria, Albani et al. (1985b) from Hungary, Tongiorgi et al. (1984), Albani et al. (1985a) and Albani (1989) from Sardinia (Italy), Kalvacheva (1979, 1980, 1982a, 1982b, 1986) from Bulgaria, Ghavidel-Syooki (1990, 1997, 2001) from Iran, and Tongiorgi et al. (1994) and Quintavalle et al. (2000) from Pakistan.

### 6.3. First appearance of the genus *Coryphidium*

Of great interest for international correlations is the First Appearance Datum (FAD) of the genus *Coryphidium*, which is now established as being in the late Tremadocian. The first occurrence of *Coryphidium* in sections in the British Isles is in the *messauoudensis-trifidum* acritarch assemblage (Cooper et al., 2004), at a level that correlates with the late Tremadoc *Araeograptus murrayi* graptolite Biozone (see above).

Servais and Mette (2000) reinvestigated the *messauoudensis-trifidum* acritarch assemblage of the Barriga Shale Formation in south-western Spain. *Coryphidium* morphotypes, which can not be attributed to species, are present in this formation, although in very low numbers, in the late Tremadocian *Araneograptus murrayi* and *Hunnegraptus copiosus* graptolite biozones.

Preliminary results from new investigations in northwestern Argentina also indicate that the first appearance of *Coryphidium* in that area is in strata correlated with the *Araneograptus murrayi* Biozone (Rubinstein and Toro 2002, Rubinstein 2003).

Specimens of *Coryphidium* are also present in the *messauoudensis-trifidum* acritarch assemblage of the uppermost Jalhay Formation in the Stavelot Inlier, Belgium, that can also be dated as being of late Tremadocian age (Vanguetaine and Servais, 2002). However, *Coryphidium* has not been recorded from the *messauoudensis-trifidum* assemblage in the Varnkevitz Formation from the subsurface of the island of Rügen (Servais and Molyneux 1997).

In summary, the genus *Coryphidium* appears in the late Tremadocian, but most records are from Arenig and younger strata, this might reflect the relatively few studies on acritarchs from latest Tremadocian strata. Most records are from Arenig and Llanvirn sequences on the periphery of the Gondwana supercontinent. The last occurrence of the genus is not precisely

known, because records from the Upper Ordovician are generally attributed to reworking (e.g. Vavrdová 1982, Turner 1982).

#### 6.4. Stratigraphical significance of *Coryphidium* morphotypes

Although taxonomical problems clearly exist, and although the boundaries between the different species are difficult to draw (see above), it appears that different morphotypes may have a stratigraphical significance, that may be useful, at least at a local or regional level. The first *Coryphidium* specimens in the late Tremadocian do not yet display the complex morphology characteristic of the classical *bohemicum* morphotype that was described by Vavrdová (1972). In the late Tremadocian, the first coryphids have been attributed to morphological transients between the genera *Acanthodiacrodium* and *Coryphidium* (e.g. Servais and Mette, 2000). In the latest Tremadocian and lowest Arenigian, specimens of *Coryphidium* always display relatively short processes with usually undivided distal ends. Morphotypes comparable to Vavrdová's (1972) holotype appear to be typical for middle Arenig levels. Such specimens with clearly heteromorphic processes and a well differentiated sculpture of ribs on the vesicle wall have been recognised all around the Gondwanan margin in levels that can be attributed to the middle Arenigian. In the late Arenigian, such morphotypes become rare, but variability is great, as documented in Cramer and Díez (1976). In the Llanvirnian, specimens attributable to still exist. They have a more rounded vesicle with usually plump processes, as described by Burmann (1970) as *Baltisphaeridium obtusatum*.

In most areas where *Coryphidium* has been found, complete sections from the late Tremadocian into the early Llanvirn are not observed, so that the evolution of the morphology of the genus is not fully understood. Nevertheless, the observation of different morphotypes in the sections of England and Wales lead to the understanding of a stratigraphical succession of morphotypes that seems to have a stratigraphical significance at a local scale.

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### 7. Palaeobiogeography

As indicated by previous authors, *Coryphidium* is very important from a palaeobiogeographical point of view. Li (1989) observed the genus in his assemblages from South China together with the genus *Striatotheca* and the species *Arbusculidium filamentosum*, that all were considered typical for assemblages described from western and southern Europe and northern Africa. Therefore, Li (1989) attributed his South Chinese assemblages to the 'palaeoprovince' that was then named "Mediterranean province", following Vavrdová's (1974) distinction of two 'palaeoprovinces' in Europe. Li (1989) redefined this province by the presence of the three taxa *Coryphidium*, *Striatotheca* and *Arbusculidium filamentosum*. This province was subsequently renamed peri-Gondwanan acritarch 'palaeoprovince' (for a full historical overview, see Servais et al. 2003). The genus *Coryphidium* and in particular the type species were considered palaeobiogeographically so significant that Ghavidel-Syooki (1990) and Vavrdová (1997) described a '*Coryphidium bohemicum* province' and a '*Coryphidium bohemicum* acritarch bioprovince', respectively.

The comprehensive literature revision presented in the present work allows to provide a detailed plotting of all *Coryphidium* occurrences on a palaeobiogeographical reconstruction. Text-figure 1 clearly illustrates that *Coryphidium* is present all around the southern margin of

the supercontinent of Gondwana. From the occurrences on the Yangtze Platform in southern China at almost equatorial position in western Gondwana, the genus is distributed all around the southern part of Gondwana, including high latitudes, and the distribution continues towards lower latitudes on the eastern side of the supercontinent, where the genus is recorded from localities such as Argentina. The genus was never recorded from the continents located at low latitudes, such as Laurentia, Siberia and Baltica, but also not from Lower-Middle Ordovician successions of northern Gondwana, such as Australia or North China.

Occurrences from southern China were recorded by many authors working in successions of the Yangtze Platform, including Fang (1986), Li (1987, 1990, 1991), Li and Yuan (1995, 1997, 1998), Yin (1995), Tongiorgi et al. (1995), Brocke et al. (2000), Li et al. (2002, 2004). Tongiorgi et al. (1994) and Quintavalle et al. (2000) observed *Coryphidium* from Pakistan, while Ghavidel-Syooki (e.g. 1990, 1997, 2001) and Martin (1996) recorded the genus from Iran and Turkey respectively.

The North African occurrences include the localities analysed in Morocco (Cramer et al. 1974 ; Cramer and Díez 1976 ; Marhoumi et al. 1981), Algeria, Tunisia and Lybia (e.g. Vecoli 1999).

The genus was largely recorded from localities of peri-Gondwanan Europe, including successions in Spain (Mette 1989, Servais and Mette, 1990), Portugal (Arriagha e Cunha and Vanguetaine 1988), France (Rauscher 1974a, 1974b, Fournier-Vinas and Donot 1977, Fournier-Vinas 1978, and Cocchio 1981, 1982), the Czech Republic (Vavrdová 1972, 1974, 1976, 1977, 1982a, 1982b, 1986, 1988, 1989, 1990a, 1990b, 1997), Austria (Reitz and Höll 1991, 1992, Reitz 1994, Hungary (Albani et al. 1985b), Italy (Tongiorgi et al. 1984, Albani et al. 1985a, Albani 1989) and Bulgaria (Kalvacheva 1979, 1980, 1982a, 1982b, 1986)

*Coryphidium* was also recorded from numerous localities of Avalonia, including Newfoundland (e.g. Dean and Martin 1978), Ireland (Smith 1981, Connery and Higgs 1999, Maziane et al. 2000, and Todd et al. 2000), the United Kingdom (Downie and Ford 1966, Lister et al. 1969, Molyneux 1979, Turner and Wadge 1979, Turner 1982, Downie 1984, Rushton 1985, Molyneux 1987, Trythall et al. 1987, Rushton and Molyneux 1989, Cooper and Molyneux 1990, Millward and Molyneux 1992, Cooper et al. 1995, Molyneux 1996, Molyneux and Leader 1997, and Molyneux 1999), Belgium (Martin et al. 1970, Martin 1974, 1977, Vanguetaine 1986, Servais 1991, Servais and Maletz 1992) and the Avalonian parts of Germany (Burmman 1970, 1976, Maletz and Servais 1993, Servais 1994)

The South American occurrences on eastern Gondwana include the localities investigated in Argentina by Rubinstein et al. 1999, Rubinstein and Toro 2001, and Rubinstein 2003)

## 8. Conclusion

The attempt of this paper is to provide a comprehensive review of the acritarch genus *Coryphidium* Vavrdová 1972. Based on a revision of published literature supplemented by studies of material from the British Isles, Belgium, the Czech Republic, Germany, Spain, Morocco, Algeria, Tunisia, Lybia and China, the original diagnoses, stratigraphical ranges and geographical distribution of all *Coryphidium* species are critically evaluated. *Coryphidium* is emended and the informal category of coryphid acritarchs is introduced to include all morphotypes with the characteristic vesicle shape of the two genera *Coryphidium* and *Vavrdovella* Loeblich and Tappan 1976. Nine of the previously described species clearly belong to *Coryphidium*, while two other species possibly belong to it. However, the attribution to *Corphydium* of the species *C. sichuanense* Wang and Chen 1987 is rejected

here. *Coryphidium* seems to occur in all palaeoenvironments from nearshore to offshore settings and therefore does not seem to be palaeoecologically significant. Palaeogeographically, however, *Coryphidium* is of very great importance, as it is an indicator of the peri-Gondwanan acritarch 'palaeoprovince' during the Early/Middle Ordovician.

*Coryphidium* is also very useful biostratigraphically. The genus first appears in the uppermost Tremadocian *Araneograptus murrayi* graptolite Biozone and is common through the upper Lower Ordovician and the Middle Ordovician, while Upper Ordovician occurrences might be the result of reworking. The different morphotypes observed within the genus also appear to have a biostratigraphical importance, but this significance is limited because intraspecific variability is very high.

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## Plate 1.

Scale bar = 10µm.

- Fig. 1.** *Coryphidium* cf. *barakum*. Borehole BJ 109, Morocco -511 m, slide 20541, EF: J34/3.  
**Fig. 2.** *Coryphidium* cf. *almohadillum*. Borehole BJ 109, Morocco -511 m, slide 20541, EF: N31.  
**Fig. 3.** *Coryphidium* cf. *bohemicum*. Borehole BJ 109, Morocco -511 m, slide 20541, EF: M32/4.  
**Fig. 4.** *Coryphidium* cf. *bohemicum*. Borehole BJ 109, Morocco -511 m, slide 20541, EF: M33.  
**Fig. 5.** *Coryphidium* cf. *elegans*. Borehole BJ 109, Morocco -511 m, slide 20541, EF: F34/4.  
**Fig. 6.** *Coryphidium* cf. *bohemicum*. Borehole BJ 109, Morocco -511 m, slide 20541, EF: J37/1.  
**Fig. 7.** *Coryphidium* cf. *barakum*. Borehole BJ 109, Morocco -511 m, slide 20541, EF: P34.  
**Fig. 8.** *Coryphidium* cf. *bohemicum*. Borehole BJ 109, Morocco -511 m, slide 20541, EF: T31/4.  
**Fig. 9.** *Coryphidium* cf. *bohemicum*. Borehole BJ 109, Morocco -511 m, slide 20541, EF: O31.  
**Fig. 10.** *Coryphidium* cf. *miladae*. Borehole BJ 109, Morocco -511 m, slide 20541, EF: P34/2.  
**Fig. 11.** *Coryphidium* cf. *bohemicum*. Borehole BJ 109, Morocco -511 m, slide 20541, EF: M45.  
**Fig. 12.** *Coryphidium* cf. *miladae*. Borehole BJ 109, Morocco -511 m, slide 20541, EF: O44/1.

## Planche 1.

Barre d'échelle = 10µm.

- Fig. 1.** *Coryphidium* cf. *barakum*. Sondage BJ 109, Maroc -511 m, lame 20541, EF : J34/3.  
**Fig. 2.** *Coryphidium* cf. *almohadillum*. Sondage BJ 109, Maroc -511 m, lame 20541, EF : N31.  
**Fig. 3.** *Coryphidium* cf. *bohemicum*. Sondage BJ 109, Maroc -511 m, lame 20541, EF : M32/4.  
**Fig. 4.** *Coryphidium* cf. *bohemicum*. Sondage BJ 109, Maroc -511 m, lame 20541, EF : M33.  
**Fig. 5.** *Coryphidium* cf. *elegans*. Sondage BJ 109, Maroc -511 m, lame 20541, EF : F34/4.  
**Fig. 6.** *Coryphidium* cf. *bohemicum*. Sondage BJ 109, Maroc -511 m, lame 20541, EF : J37/1.  
**Fig. 7.** *Coryphidium* cf. *barakum*. Sondage BJ 109, Maroc -511 m, lame 20541, EF : P34.  
**Fig. 8.** *Coryphidium* cf. *bohemicum*. Sondage BJ 109, Maroc -511 m, lame 20541, EF : T31/4.  
**Fig. 9.** *Coryphidium* cf. *bohemicum*. Sondage BJ 109, Maroc -511 m, lame 20541, EF : O31.  
**Fig. 10.** *Coryphidium* cf. *miladae*. Sondage BJ 109, Maroc -511 m, lame 20541, EF : P34/2.  
**Fig. 11.** *Coryphidium* cf. *bohemicum*. Sondage BJ 109, Maroc -511 m, lame 20541, EF : M45.  
**Fig. 12.** *Coryphidium* cf. *miladae*. Sondage BJ 109, Maroc -511 m, lame 20541, EF : O44/1.

## Plate 2.

Scale bar = 10µm.

**Fig. 1.** *Coryphidium elegans*. Klabava Formation, Krusna Hora, “Gabriela mine”, Czech Republic, slide No. 22497, EF: E42/3.

**Fig. 2.** *Coryphidium* cf. *bohemicum*. *A. suecicus* graptolite zone, Meitan Formation (Honghuayan section), Guizhou Province, southeastern China. Sample No. AF1048, slide 1, EF: V29.

**Fig. 3.** *Coryphidium bohemicum*. Borehole ST1, Tunisia. Sample 1554, slide 10, EF: P39/2.

**Fig. 4.** Teratological specimen of ?*Coryphidium* sp., devoid of processes. Borehole BJ 109, Morocco -511m EF: Q36.

**Fig. 5.** *Coryphidium* cf. *elegans*. *U. austrodentatus* graptolite zone, Meitan Formation (Honghuayan section), Guizhou Province, southeastern China. Sample No. AF1093, slide 1, EF: L41/1.

**Fig. 6.** *Coryphidium* cf. *elegans*. *U. austrodentatus* graptolite zone, Meitan Formation (Honghuayan section), Guizhou Province, southeastern China. Sample No. AF1093, slide 2, EF: T39/1.

**Fig. 7.** *Coryphidium* cf. *elegans*. *U. austrodentatus* graptolite zone, Meitan Formation (Honghuayan section), Guizhou Province, southeastern China. Sample No. AF1093, slide 2, EF: V34/3.

## Planche 2.

Barre d'échelle = 10µm.

**Fig. 1.** *Coryphidium elegans*. Formation de Klabava, Krusna Hora, « Gabriela Mine », République Tchèque, lame no 22497, EF : E42/3.

**Fig. 2.** *Coryphidium* cf. *bohemicum*. Zone à graptolites *A. suecicus*, Formation de Meitan (section de Honghuayan), Province de Guizhou, sud-est de la Chine. Échantillon no AF1048, lame 1, EF : V29.

**Fig. 3.** *Coryphidium bohemicum*. Sondage ST1, Tunisie. Échantillon 1554, lame 10, EF : P39/2.

**Fig. 4.** Spécimen tératologique de ? *Coryphidium* sp., sans processus. Sondage BJ 109, Maroc -511 m, EF : Q36.

**Fig. 5.** *Coryphidium* cf. *elegans*. Zone à graptolites *U. austrodentatus*, Formation de Meitan (section de Honghuayan), Province de Guizhou, sud-est de la Chine. Échantillon no AF1093, lame 1, EF : L41/1.

**Fig. 6.** *Coryphidium* cf. *elegans*. Zone à graptolites *U. austrodentatus*, Formation de Meitan (section de Honghuayan), Province de Guizhou, sud-est de la Chine. Échantillon no AF1093, lame 2, EF : T39/1.

**Fig. 7.** *Coryphidium* cf. *elegans*. Zone à graptolites *U. austrodentatus*, Formation de Meitan (section de Honghuayan), Province de Guizhou, sud-est de la Chine. Échantillon no AF1093, lame 2, EF : V34/3.

**Figure 1.** Palaeogeographical distribution of the genus *Coryphidium* in the Early–Middle Ordovician. Palaeogeographical reconstruction adopted from Li and Servais (2002), modified after Li and Powell (2001). Legend of selected locations (for explanations and complete list of locations see Text): **1.** Yangtze Platform, South China; **2.** Karakorum and Chitral, Pakistan; **3.** Alborz Mts, Iran; **4.** Taurus Mts, Turkey; **5.** West Balkan Mts, Bulgaria; **6.** Bakony Mts, Hungary; **7.** Sierra Morena, Spain, and Barrancos, Portugal; **8.** Sahara subsurface, Lybia, Tunisia, Algeria; **9.** Tadla Basin, Morocco; **10.** Bohemia, Czech Republic; **11.** Rügen Island, Germany; **12.** English Lake District, Isle of Man and Wales, United Kingdom; **13.** Random and Bell Islands, Newfoundland; **14.** Eastern Cordillera, Argentina.

**Figure 1.** Distribution paléogéographique du genre *Coryphidium* dans l’Ordovicien inférieur et moyen. Réconstitution paléogéographique d’après Li et Servais (2002), modifiée d’après Li et Powell (2001). Légende des localités (pour plus d’explications et la liste complète des localités, voir le Texte) : **1.** Plateforme Yangtze, sud de la Chine ; **2.** Karakorum et Chitral, Pakistan ; **3.** Alborz Mts., Iran ; **4.** Taurus Mts, Turquie ; **5.** West Balkan Mts, Bulgarie ; **6.** Bakony Mts, Hongrie ; **7.** Sierra Morena, Espagne, et Barrancos, Portugal ; **8.** Sahara, Libya, Tunisie, Algérie ; **9.** Bassin de Tadla, Maroc ; **10.** Bohême, République tchèque ; **11.** Île de Rügen, Allemagne ; **12.** English Lake District, Angleterre ; Isle of Man et Pays de Galles, Royaume Uni ; **13.** Îles de Random et Bell, Terre-Neuve ; **14.** Cordillère Orientale, Argentine.









