A REVIEW OF THE ORDOVICIAN ACritarchs
AUREOTESTA AND MARROCANIUM

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(12 figures, 1 table & 2 plates)

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ABSTRACT. The two monospecific Ordovician acritarch genera Aureotesta Vavrdová 1972 and Marrocanium Cramer et al. 1974 are investigated in well preserved assemblages from Bohemia, China and Morocco. A high variability is observed in each of the investigated samples and a gradual transition between the two taxa is documented. The differentiation of two distinct genera, as used up to the present, is no longer justified, because both morphotypes and transitional forms occur in the same population. The logical consequence of this observation is the classification of all specimens under one single taxon name: Aureotesta clathrata e mend. The extreme poles of the population are classified at the varietas level: Aureotesta clathrata var. clathrata and Aureotesta clathrata var. simplex. The easily discernible taxon Aureotesta clathrata is of great biostratigraphical and palaeobiogeographical importance. Its First Appearance Datum (FAD) is in the Corymbograpitus v-similis Biozone in Bohemia and in the Didymograpitus deflexus Biozone in South China. Palaeobiogeographically, its distribution is limited to the cold to temperate Gondwanan and peri-Gondwanan ("Mediterranean") "Palaeoprovence", located during the Early Ordovician at high latitudes in the southern hemisphere.

KEYWORDS: Ordovician, acritarchs, systematics, variability, biostratigraphy, palaeobiogeography.

RESUME. Les deux genres monospécifiques d’acritarches de l’Ordovicien Aureotesta Vavrdová 1972 et Marrocanium Cramer et al. 1974 ont été étudiés à partir d’assemblages bien préservés de Bohême, de Chine et du Maroc. Une très grande variabilité a été observée dans tous les échantillons analysés et une transition graduée entre les deux taxons est documentée. La différenciation de deux genres distincts, telle qu’utilisée jusqu’à présent, n’est plus justifiée, parce que les deux morphotypes et des spécimens intermédiaires ont été observés dans la même population. La conséquence logique de cette observation est de classer tous les spécimens sous un seul nom de taxon: Aureotesta clathrata e mend. Les pôles extrêmes de la population peuvent être classés au niveau de variété: Aureotesta clathrata var. clathrata et Aureotesta clathrata var. simplex. Le taxon Aureotesta clathrata est d’une grande importance biostratigraphique et paléobiogéographique. Sa première apparition est dans la Biozone à Corymbograpitus v-similis en Bohême et dans la Biozone à Didymograpitus deflexus en Chine du Sud. Sa distribution paléogéographique est limitée à la paléoprovence froide à tempérée de Gondwana et de péri-Gondwana, "paléoprovence méditerranéenne", située pendant l’Ordovicien inférieur dans les régions de hautes latitudes de l’hémisphère sud.

MOTS-CLES: Ordovicien, acritarches, systématique, variabilité, biostratigraphie, paléobiogéographie.

1. INTRODUCTION

The acritarch index of Fensome et al. (1990) gives a complete overview of the abundant literature on acritarchs and prasinophytes. In that catalogue, several hundred acritarch genera and several thousand acritarch species are listed.
According to the survey of Ordovician acritarch literature by Servais (1998), over 250 genera are available for the Ordovician acritarchs, and the number of species described and cited for this system is estimated to exceed 2000.

The description of many species and genera was based on a limited number of specimens. For the description of a new acritarch taxon, the detailed comparison with previously published taxa, the study of larger populations, and investigations of variability have commonly been neglected. Therefore, it appears highly probable that the number of taxa available in the acritarch literature is exaggerated. It seems that numerous acritarch species are actually probably synonyms.

Because acritarch classification is purely artificial, based mostly on arbitrarily selected morphographical criteria, and taking into consideration that acritarch taxa are of unknown biological affinity, it is evident that most of the parataxonomic acritarch species cannot be considered as biological entities.

Critical reviews of the literature and studies of large populations are needed to understand the taxonomic value of individual acritarch taxa. Such studies are also necessary to establish a hierarchy of the parameters used for differentiation at the generic, specific, and infraspecific level.

The present work is an attempt to understand the systematic position of two important Ordovician acritarchs which have been considered as separate genera up to the present: Aureotesta and Marrocanium.

The genus Aureotesta (type species A. clathrata) was first described by Vavrdová (1972, p.83-84) from the Arenig part of the Klabava Formation in Bohemia. According to the protologue, Aureotesta is characterized by a square to rectangular central body with an ornamentation of numerous delicate outgrowths forming a fine filamentous network (Fig. 1).

Cramer et al. (1974, p. 57-59) erected the new genus Marrocanium (type species M. simplex) from the late Arenig of the Tadla Basin in Morocco. According to the protological data, the central body is square to rectangular and a thin transparent web extends between the base of the processes (Fig. 2).

![Figure 1. Idealized specimen of "Aureotesta clathrata" Vavrdová 1972. Measurement parameters are the central body length (CBL), the central body width (CBW), the process length (PL), and the height of the filamentous outgrowths (FL).](image)

Both genera remain monospecific up to the present. They have been reported from numerous localities in Gondwana and peri-Gondwana. Today, the names Aureotesta and Marrocanium are of common use. Both taxa are generally considered as separate units at the species and genus level.

During studies on early Ordovician material from Bohemia, China, and Morocco, the authors of the present work investigated numerous specimens which are attributable to Aureotesta and Marrocanium. The material comes from sample areas which all provide well preserved and highly diversified acritarch assemblages. The results of these investigations reveal that those specimens which show the typical characters of Aureotesta clathrata (the filamentous network) and Marrocanium simplex (the transparent web) actually represent only two end-members of a large population. Numerous specimens of the population constitute the morphological intermediates between the end-members showing both the network and the web (Fig. 3).
A REVIEW OF THE ORDOVICIAN ACRITARCHS AUREOTESTA AND MARROCANIUM

Figure 2. Idealized specimen of "Marrocanium simplex" Cramer et al. 1974. Measurement parameters are the central body length (CBL), the central body width (CBW), the process length (PL), and the width of the transparent web (WW).

A high variability of these forms is observed in all investigated areas. The end-members and the transients between them are found in each of the analysed samples so that it is difficult and even impossible to attribute the investigated specimens to the taxa previously described by Vavrdová (1972) and Cramer et al. (1974).

From these observations the following questions arise: How should such transients be classified? Is it possible to differentiate the two end-members within a single population as separate taxa, and even as separate genera?

Because, according to Article 2 of the International Code of Botanical Nomenclature (Greuter et al., 1994), the basal rank in plant taxonomy is the species (species), it would perhaps be more appropriate to consider all observed specimens as a single species (species) and the extreme forms as varieties (varietas).

In the present work, the literature on Aureotesta and Marrocanium is completely reviewed and material from several localities, including material from the type-localities is investigated to clarify the taxonomic position of this plexus of forms.

Figure 3. Idealized specimen of a transitional specimen showing both the diagnostic characteristics of "clathrata" (filamentous outgrowths) and of "simplex" (transparent web).

2. MATERIALS AND METHODS

The type-locality of the genus Aureotesta is in the Bohemian Klabava Formation. This formation was re-investigated by the second author (O.F.). The following samples were analysed for the present study: sample KL-24 from the Drahous section near Rokycany (compare Fütka & Brecke, 1998, figs. 1 and 3); and samples MY-2 and MY-3 from the Myto section (compare Paris & Merigl, 1984). The first sample comes from the Tetraraptus-Azygograpthus grahotolite Biozone (Kraft & Kraft, 1993). The samples from the Myto section are dated by means of chitinoozans as belonging to the Desmochnitina bulla Biozone (Paris & Merigl, 1984; sample no 16).

Marrocanium was originally described by Cramer et al. (1974) from the borehole Boujad-109 in the Todla Basin, Morocco. The type level is at depth - 360 m. Two samples (depths -360 m and -511 m) of this core have been provided by the Office National de Recherches et d'Exploitations Pétrolières (ONAREP) to the third author (Th.S.). These levels have recently been re-dated as belonging to the late Arenig, Desmochnitina bulla chitinoozan Biozone (Soufiane & Achab, 1993).
The Chinese material was collected by the first author (R.B.) from the Dawan Formation, Yangtze Platform, Hubei Province, SE-China. The samples come from the Didymograptus deflexus, Azygograptus succicus, and Undulograptus sinodentatus/Didymograptus nexus graptolite Biozones. The investigated samples were collected from the two sections of Datianba and Wangjiazei (Brocke, 1997; Fatka & Brocke, 1998).

Further comparative material comes from the early Llanvirn (Didymograptus artus) Huy Formation in the Belgian Condroz Ridge (Servais & Maletz, 1992) and from the Llanvirn (Didymograptus artus and D. murchisoni Biozones) of the borehole Binz 1 from the Island of Rügen (comp. Servais & Katzung, 1993).

All samples were subjected to standard palynological preparation techniques and were sieved at 10 or 12 µm. The Belgian, German, and Moroccan material was oxidized with Schulze solution.

The Chinese material is stored in the collections of the Institut für Angewandte Geowissenschaften II at the TU Berlin. Bohemian samples are housed in the collection of the Univerzita Karlova at Prague. All Belgian, German, and Morrocan specimens are stored in the collections of the Services Associés de Paléontologie de l’Université de Liège.

3. STRATIGRAPHICAL CORRELATIONS

The material investigated in the present study comes from several areas which were located during the early Ordovician at high latitudes in the southern hemisphere. They belong to Gondwana (Morocco), peri-Gondwana (Belgium, Germany, and Bohemia), and the Yangtze Platform in South China. A stratigraphical correlation scheme of the early Ordovician biozones between the British Isles, Newfoundland, France, Bohemia, and South China is indicated in Fig. 4.

The Belgian and German levels are correlated with the British graptolite biozones. The Bohemian graptolite and chitinozoan biozones are indicated in column 4 and 5 in Fig. 4, respectively. There is no biozonation available for the Moroccan boreholes of the Tadla Basin, but the levels investigated in the present study can be correlated with the late Arenig Desmochitinula bulla chitinozoan Biozone (Sousiane & Achab, 1993). The studied samples from the Dawan Formation in southern China come from the Didymograptus deflexus, Azygograptus succicus, and the Undulograptus sinodentatus/Didymograptus nexus graptolite Biozones. They are approximately equivalent to the Didymograptus extensus and Didymograptus hirundo Biozones of the British Arenig (Fig. 4).

4. SYSTEMATIC PALAEONTOLOGY

INCERTAE SEDIS
Group Acritarcha Evitt 1963

Genus Aureotesta Vavrdová 1972 emend.

Type species. Aureotesta clathrata Vavrdová 1972.


Original diagnosis of Aureotesta. Acritarchs with hollow main body, outline polygonal. Low number of horn-like processes, proximally opened, distally closed, clathrate, taper gradually from corners. Extremely fine net of filamentose outgrowths envelops both main body and processes, diminishing towards their terminations (Vavrdová, 1972, p. 83).

Emended diagnosis. Central body polygonal in shape, generally square to rectangular or trapezoidal. Each corner bears a hollow, simple process, which is proximally open, slightly tapering to a distally closed tip. Central body wall smooth or with minor ornamentation of microgranulation. The central body and the processes are covered partly or completely by an envelope formed by a thin web and/or a network formed by fine anastomous filamentous outgrowths. These outgrowths are superficial and do not communicate with the vesicle cavity.

While Vavrdová (1972) did not mention the variability of her new genus Aureotesta in the description, idealizing the genus by mentioning only the filamentous network (reticulum) in her holotype, Cramer et al. (1974) noted in their "additional morphographic information" that Aureotesta bears a thin, transparent web, which appears together with the "raised reticulum". Vavrdová did not report this information in subsequent papers. She cited and figured her species Aureotesta clathrata numerous times (Vavrdová, 1972, 1974, 1976, 1977, 1982, 1986, 1988, 1989, 1990, 1993, 1995). Marrocanium
Figure 4. Stratigraphical correlation scheme of Early Ordovician biozones between the British Isles, Newfoundland, France, Bohemia, and South China.

was only mentioned (Vavrdová, 1977, 1978, 1986, 1988, 1990, 1993), but it was never figured.

Our observation confirms the information of Cramer et al. (1974). All assemblages indicate a very large variability between typical "Aureotesta" and typical "Marrocanium" specimens. It is surprising that Cramer et al. (1974) erected a further new genus, because it is obvious that they observed also the high variability of the specimens in the Moroccan material, which is reinvestigated in the present work.

The previous systematic position of this plexus of forms and the new taxonomic reconsideration are illustrated in Table 1. There is only one possible and logical consequence of our observation: the Aureotesta-Marrocanium plexus must be classified under a single taxon name at the genus and at the species level. Therefore, the single genus name Aureotesta is used. Marrocanium is a junior synonym. The species name to retain is clathrata, because it has priority, simplex being described two years later.

Comparison. The genus Aureotesta emend. is easily discernible in early Ordovician acritarch assemblages. Confusion with other taxa is almost impossible. It is distinguished from rectangular specimens of Vehryachium Deunff 1954 by its ornamentation of a reticulum and/or a web. This latter genus may show the same central body shape, but is always unornamented. Striatotheca Burmanna 1970 is rectangular and has a striate ornamentation on the vesicle wall. Barakella Cramer & Diez 1977 sometimes has a similar vesicle shape. This genus is heteropolar, however, its ornamentation of small filamentous outgrowths being limited to one pole.

*Aureotesta clathrata* Vavrdová 1972 emend.

Plate 1, figs. A-M; Plate 2, figs. A-K


**Original diagnosis.** Main body flat, thick-walled, outline square to rectangular with more or less straight sides. Four stout processes, conical with broad opened bases, are placed at corners of the
main body. Distally processes are closed, sharp-pointed. Numerous delicate outgrowths, distally irregularly branched and connected, form outer coat on both processes and main body. Height of outgrowth diminishes towards terminations of processes (Vavrdová 1972, p. 84).

**Emended diagnosis.** A rectangular to square species of *Aureoesta* showing numerous delicate outgrowths, distally irregularly branched and connected, forming an outer coat on both the processes and the central body and/or a thin web which envelopes the processes and the central body.

**Holotype.** Vavrdová, 1972: 83-84; Pl. 1; Figs. 5-6; Text-Fig. 3, MV 13.

The holotype of the species *Aureoesta clathrata* was figured in a photograph. Some details are unfortunately not clear on this photograph. Vavrdová (1972, Text-fg. 3) also included a schematized drawing from which it is not clear if the holotype bears only the filamentous network or additionally a transparent web. The holotype is relatively complete. Only one process is broken. Vavrdová indicated a length of "66 microns", which probably includes central body and processes. From the schematized drawing, it appears that the filamentous outgrowths forming the reticulum are slightly destroyed.

The evidence discussed below draws attention to transients with a reticulum and a web and specimens with only a web. Therefore, the holotype may only be typical of the extreme pole of the population which bears only a reticulum and no web. This is not in opposition to the International Code of Botanical Nomenclature, because the nomenclatural type is not necessarily the most typical or representative element of a taxon (I.C.B.N. Article 7.2).

**Type locality.** Vavrdová (1972) published this species from "Klava near Rankovy, Bohemia".

<table>
<thead>
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<th>Table 1.</th>
<th>The previous systematic position of the genera <em>Aureoesta</em> and <em>Marrocanum</em> and the taxonomical reconsideration proposed in the present study.</th>
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<td><strong>Genus level</strong></td>
<td><strong>Previous works</strong></td>
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<tr>
<td><em>Aureoesta</em></td>
<td><em>Marrocanum</em></td>
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<tr>
<td><strong>Species level</strong></td>
<td><strong>clathrata</strong></td>
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<td><strong>Variation level</strong></td>
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**Figure 5.** Drawing of a specimen of *Aureoesta clathrata* showing a well developed filamentous network covering the central body and the four processes. The gradual transition from the transparent web into the filamentous network is clearly visible on several parts of the specimen. Specimen from borehole Boujad-109; sample -511 m; slide 20541; England Finder graticule coordinates L53/4 - L54/3. The same specimen is figured in Plate 2, fig. 1.

**Figure 6.** Drawing of a specimen which typically constitutes a morphological transient between the "clathrata" and "simplex" poles, showing both the filamentous network and the transparent web. Specimen from borehole Boujad-109; sample -511 m; slide 20541; England Finder graticule coordinates G 44/3. The same specimen is figured in Plate 2, fig. 2.
A precise map indicating the exact locality was not provided by Vavrdová (1972) and was also not given in subsequent papers.

**Type level.** Vavrdová (1972) indicated the type level to be in the "Klabava shales (Arenig)".

Around the village of Klabava, the Klabava Formation is over 300 m thick. The exact level in the stratigraphic section and the precise age of Vavrdová's (1972) sample has never been published. **Discussion.** The species *Aureotesta clathrata* is emended here to include forms with a reticulum, those with a web, and those with a combination of both. The samples investigated in the present work include complete populations of all these forms.

Some specimens show a web on one side of the vesicle and a reticulum on the other. Sometimes a gradual transition between a network which is built up by the delicate filaments and the typical web is readily observed. Such specimens are neither attributable to *Aureotesta clathrata sensu* Vavrdová (1972) nor to *Marrocanium simplex sensu* Cramer *et al.* (1974).

The drawings of three specimens from one single level of the Moroccan subsurface (borehole Boujad-109, depth -501 m) illustrates clearly the wide variability of the specimens. Fig. 5 shows a specimen with a well developed reticulum covering both the processes and the central body. The gradual transition from the filamentous network to a small web is clearly visible on several parts of the specimen. Fig. 6 illustrates a specimen with a well developed web. This web partly passes into an anastomotic network. Fig. 7 shows a representative and typical specimen of the other ("Marrocanium") pole with only a transparent web, but no reticulum.

The investigation of assemblages which are poorly preserved and which produce few specimens (e.g., the Belgian and German material) does not allow this observation. This clearly illustrates that the study of a limited number of specimens may not give a complete view of a taxon.

It is evident that the observed populations represent a single entity, which should preferably be classified under a single species name. Therefore, all specimens are classified here as *Aureotesta clathrata* Vavrdová (1972) emend. The extreme poles of the population can then easily be classified

![Figure 7. Drawing of *Aureotesta clathrata var. simplex* showing a well developed transparent web, but no filamentous outgrowths. Specimen from borehole Boujad-109; sample - 511 m; slide 20542; England Finder graticule coordinates M-N 37. The same specimen is figured in Plate 2, fig. 3 at an infraspecific level. We propose the variety (varietas) clathrata for the pole presenting only a reticulum and the variety simplex for the specimens presenting only a web (compare Table 1).](image)

**Measurements.** Over 120 specimens have been measured in the present study (Fig. 8). The values of the central body length (CBL), the central body width (CBW), and the process length (PL) are measured for all specimens. The height of the filamentous network (FL) and/or the width of the transparent web (WW) was measured in all specimens which show these features.

<table>
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<th>Measurement</th>
<th>Value</th>
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<tr>
<td>CBL</td>
<td>18-42 μm</td>
</tr>
<tr>
<td>CBW</td>
<td>15-42 μm</td>
</tr>
<tr>
<td>PL</td>
<td>11-53 μm</td>
</tr>
<tr>
<td>FL</td>
<td>up to 9 μm</td>
</tr>
<tr>
<td>WW</td>
<td>up to 15 μm</td>
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The biometrical studies indicate that all data are reasonably well distributed in clusters. Only minor differences are observed between the different localities. They may be the result of numerous factors, which are impossible to determine with the present knowledge on acritarch affinities (palaeoenvironment, nutrient supply, water...
temperature, salinity, etc.). The clusters show clearly that there are no biometrical differences between the specimens with a reticulum, those with a web, and those showing both structures. Apparently, all specimens belong to a single population.

Preservation of specimens. Not only a great number of specimens is necessary to understand the variability of an acritarch species. The preservation of the assemblages is also very important for a detailed description and a clear understanding of each acritarch taxon.

The ornament structure in *Aureocystis clathrata* (the fine filamentous reticulum and the thin web) is very delicate. It is easily damaged when the preservation is poor. The observation of poorly preserved assemblages from Belgium and Germany clearly indicates that numerous structural details are no longer visible. In the material from the Huy Formation (comp. Servais & Maletz, 1992), for example, the appendices of most acritarchs are commonly broken, because the calcification rate is very high. It is evident from the well preserved Moroccan and perfectly preserved Chinese material that both the web (*simplex*) and the reticulum (*clathrata*) are ornament structures which were both present originally. It appears, however, that these primary structures were possibly altered later. Our observations indicate that in some specimens the delicate structures have been damaged. The web (*simplex*) sometimes shows an alteration, and is full of holes and crystal marks or is filamentary resembling the original structure of the reticulum.

*Aureocystis clathrata* var. *clathrata* Vavrdová 1972

Autonym

Plate 1, Figs. J-M

**Synonymy.** (numbers in bold refer to Figs. 9 and 11)

1972 *Aureocystis clathrata* sp. nov.; Vavrdová: 79, 83-84, Pl. 1, Figs. 5, 6; Fig. 3. (1)
1974 *Aureocystis clathrata*; Cramer and Diez: 141. (2)
1974 *Aureocystis clathrata* Vavrdová; Cramer *et al.*: 57-59, 63-64, Pl. 25, Figs. 1, 2, 4-9. (3)
1974 *Aureocystis clathrata* Vavrdová; Vavrdová: 174, (4)
1976 *Aureocystis clathrata* Vavrdová 1972; Eisenack *et al.*: 87. (5)
1976 *Aureocystis clathrata*; Vavrdová: 62. (6)
1977 *Aureocystis clathrata* Vavrdová; Cramer & Diez: Pl. 4, Fig. 13. (7)
1977 *Aureocystis clathrata* Vavrdová; Diez & Cramer: 7, 30. (8)
1977 *Aureocystis clathrata* Vavrdová; Vavrdová: 111, Pl. 3, Fig. 2 (note *Coryphidium bohemicum* as indicated in the plate explanation). (9)
1979 *Aureocystis clathrata* Vavrdová 1972; Cramer & Diez: 44, 68, 125, Fig. 3: 23. (10)
1982 *Aureocystis clathrata* Vavrdová 1972; Martin: 30, 36-38, Pl. 1, Fig. 5. (12)
1982 *Aureocystis clathrata* Vavrdová; Vavrdová: 338. (13)
1984 *Aureocystis clathrata* Vavrdová 1972; Downie: Fig. 4: 39. (14)
1986 *Aureocystis clathrata* Vavrdová. Vavrdová: 356. (15)
1988 *Aureocystis clathrata* Vavrdová 1972; Arriagha E Cunha & Vanguexainte: 72, 74, Pl. 1, Figs. 6-8. (16)
1988 *Aureocystis clathrata* Vavrdová; Vavrdová: 7, 8. (17)
1989 *Aureocystis clathrata*; Vavrdová: 405, Fig. 1, L 3. (18)
1989 *Aureocystis clathrata* Vavrdová 1972; Steemans: 223, 301, 331, 362, Pl. 2, Fig. 1; Figs. 91, 143, 219. (19)
1990 *Aureocystis* sp. [sic.]; Ghaived-Syooki: 217 (20)
1990 *Aureocystis clathrata* Vavrdová 1972; Fansome *et al.*: 79. (21)
1990 *Aureocystis clathrata*; Vavrdová: 241, 243. (22)
1991 *Aureocystis clathrata*; Fansome *et al.*: 18. (23)
1992 *Aureocystis clathrata*; Brocke: 16. (24)
1992 *Aureocystis clathrata* Vavrdová 1972; Dean & Martin: 198. (25)
1992 *Aureocystis clathrata* Vavrdová 1972; Servais & Maletz: 272. (26)
1993 *Aureocystis clathrata* Vavrdová; Servais: 149-150, 287, 292, 294, 297, Pl. 9, Fig. 12; Fig. 38. (27)
1993 *Aureocystis clathrata* Vavrdová 1972; Vavrdová: 128, Pl. 2, Figs. 2, 4. (28)
1995 *Aureocystis clathrata* Vavrdová, 1972; Vavrdová: 375: Pl. 6, Fig. 3. (29)
Figure 8. Scatter diagrams of central body length (CBL) against central body width (CBW) for specimens of *Aureotesta clathrata var. clathrata* (A), transitional specimens (B), and of *Aureotesta clathrata var. simplex* (C), and scatter diagrams of central body length (CBL) against process length (PL) for specimens of *Aureotesta clathrata var. clathrata* (D), transitional specimens (E), and of *Aureotesta clathrata var. simplex* (F).
Figure 9. Stratigraphical distribution of *Aureostemma clathrata* var. *clathrata*.
Diagnostic feature. A variety of *Aureogetes clathrata* in which the ornament consists only of a reticulum of fine filamentous outgrowths, and not a web.

Biometrical studies. 36 specimens from Bohemian sections and 17 specimens from the Moroccan subsurface are measured here (Fig. 8). The scatter diagrams of the CBL against the CBW and of the CBL against the PL show only minor differences between the populations of both areas. While the CBL and the CBW are nearly identical, the PL is slightly greater in the Moroccan specimens (Fig. 8 A and D). The height of the filamentous network is variable and is in relation to the preservation. This network is generally 4 to 5 μm high, but it may attain up to 9 μm.

Remarks. *Aureogetes clathrata* var. *clathrata* is one end-member of *A. clathrata*. This variety shows no web, but only a reticulum. In the Chinese samples, this variety is very rare, because most specimens present also a transparent web. In the Moroccan material, all transients are present. In the Bohemian sections, the variety *clathrata* is the dominant group.

The synonymy list presented here is based on a compilation of the literature. All references citing "*Aureogetes*" are included. More than half of these articles do not figure the species. It is not possible to check in the other references if the figured specimens are really belonging to the variety *clathrata*, because the photographs are generally not of a sufficient quality.

Stratigraphical range. The stratigraphical distribution of *Aureogetes clathrata* var. *clathrata* documented in the literature is illustrated in Fig. 9. The age of the samples providing *A. clathrata* var. *clathrata* is only poorly documented. Most of the occurrences are insecure, because only few are controlled by means of another fossil group. *Aureogetes clathrata* var. *clathrata* appears in the Arenig. First undisputed occurrences are in the *Corymbograpthus v-sinillos* Biozone in Bohemia (Vavrdová, 1993) and in the *Didymograptus deflexus* Biozone in South China (Brocke, 1992). The variety *clathrata* is present in the early Llanvirn *D. artus* graptolite Biozone of Belgium (Servais & Maletz, 1992; Servais, 1993) and in the *D. murchisoni* Biozone of Rügen, NE-Germany (Servais, 1993). Some of the younger occurrences have been interpreted as the result of a reworking (e.g., Vavrdová, 1989), so that the latest occurrence remains uncertain.

Palaeogeographical distribution. The palaeogeographical distribution of *Aureogetes clathrata* var. *clathrata* as documented in the published occurrences is illustrated in Fig. 10. All occurrences are from sections in peri-Gondwana, Gondwana, and the Yangtze Platform in southern China. The variety is absent from the Baltic area and has not yet been reported from Laurentia, Australia, or other parts of the globe.

*Aureogetes clathrata* var. *simplex* (Cramer, Kanes, Diez & Christopher 1974) comb. nov. emend.

Plate 2, Figs. C-G, J-K

Synonymy. (numbers in bold refer to Figs. 11 and 12)

1974 *Marrocanum simplex*; Cramer & Diez: 141. (2)
1976 *Marrocanum simplex* Cramer et al.; Eisenack et al.: 441. (3)
1977 *Marrocanum simplex* Cramer; Vavrdová: 111. (5)
1978 *Marrocanum simplex* Cramer; Vavrdová: 72. (6)
1979 *Marrocanum simplex* Cramer et al. 1974; Cramer & Diez: 51, 89, 126, Fig. 3: 138. (7)
1979 *Marrocanum simplex* Cramer et al.; Martin & Rickards: 191, 193, 196, Pl. 1, Figs. 5, 18. (8)
1979 cf. *Marrocanum simplex* Cramer et al.; Turner & Wadge: 407-408, Pl. 18, Fig. 7. (9)
1981 *Marrocanum simplex* Cramer et al.; Smith: 142, 143. (10)
1982 *Marrocanum simplex* Cramer et al.; Martin: 30, 33, 36-38, Pl. 1, Fig. 2. (11)
1982 *Marrocanum simplex* Cramer, Kanes et al. 1974; Turner: 122-123, 129, 132, Pl. 17, Fig. 1. (12)
1984 *Marrocanum simplex* Cramer et al. 1974; Downie; Fig. 4: 38. (13)
1985 *Marrocanum* sp.; Fournier-Vinas: 809, 811, Pl. 3, Figs. 6-8. (14)
1986 *Marrocanum simplex* Cramer; Vavrdová: 356. (15)
Figure 10. Palaeogeographical map of the Early Ordovician ( Arenigian), modified after Scotese & Denham (1988) and Torsvik & Trench (1991), showing the geographical distribution of *Aureoestula clathrata* var. *clathrata*. Numbers correspond to those listed in synonymy.

1988 *Marrocanium simplex* Cramer; Vavrdová: 8. (17)
1989 *Marrocanium simplex* Cramer et al. 1974;
Albani: 5, 19-20, Pl. 2, Figs. 23-24. (18)
1989 *Marrocanium simplex* Cramer; Li Jun: 3. (19)
1989 *Marrocanium simplex* Cramer et al. 1974;
Rushton & Molyneux: 271, 273, Fig. 5: A. (20)
1990 *Marrocanium simplex* Cramer et al. 1974;
Fensome et al.: 311. (21)
1990 *Marrocanium simplex*; Molyneux: 616, Fig. 1: 24. (22)
1990 *Marrocanium simplex* Cramer et al.;
Vavrdová: 241. (23)
1991 *Marrocanium simplex* Fensome: 90. (24)
1991 *Marrocanium simplex* Cramer, Kanes, Diez & Christopher, 1974; Ghavidel-Syokk: 151, 164,
174-175, 188, 190, 217, Pl. 8, Fig. 10, Pl. 10, Fig. 9. (25)
1991 *Marrocanium simplex* Cramer et al. 1974;
Servais: 241, 244, Pl. 1, Fig. 11, Fig. 8. (26)
1992 *Marrocanium simplex*; Brocke: 18. (27)
1992 *Marrocanium simplex* Cramer et al. 1974;
Millward & Molyneux: 81, 83. (28)
1992 *Marrocanium simplex* Cramer et al. 1974;
Ottone et al.: 100, 106, 111-112, Pl. 3, Fig. 4. (29)
1992 *Marrocanium simplex* Cramer et al. 1974;
Servais & Maletz: 272, Pl. 3, Fig. 6. (30)
1993 *Marrocanium simplex* Cramer, Kanes, Diez & Christopher, 1974; Di Milia et al.: 174. (31)
1993 *Marrocanium simplex* Cramer, Kanes, Diez & Christopher, 1974; Servais: 207-208, 282, 292,
294, 297, 301, Pl. 7, Fig. 4, Pl. 11, Fig. 8; Fig. 48.
(32)
1993 *Marrocanium simplex* Cramer et al. 1974;
Vavrdová: 128. (33)
1994 *Marrocanium simplex* Cramer et al.;
Tongiorgi et al.: 597, 599. (34)

Original description of *Marrocanium simplex*. Central body square to rectangular, dorsoventrally compressed, pillow-shaped. Each corner bears one veryhachid process of variable length, hollow at the base and solid distally. No difference in construction of body and vesicle was noticed. A thin, transparent web extends between the bases of the processes, with a radial outline that is roughly congruent with that of the central body. The surface
of this web and of the central body is psilate to microrugulate or scabrate (elements less than 0.5 micron high and wide). No endodermal structures observed; opening through a straight slit-pylome situated at a long edge of the central body (Cramer et al., 1974, p. 59).

**Diagnostic feature.** A variety of *Aureoestesa clathrata* in which the ornament consists only of a fine web, and not a reticulum of fine filamentous outgrowths.

**Biometrical studies.** Fig. 8 (C) and Fig. 8 (F) show the scatter diagrams of the CBL against the CBW and of the CBL against the PL of the specimens from the investigated samples of China and Morocco. All specimens are reasonably distributed in clusters, only minor differences are observed. The height of the web may be very important. In some Moroccan and Chinese specimens, it is over 10 µm high and may reach 15 µm.

**Remarks.** *Aureoestesa clathrata* var. *simplex* represents the second end-member, with specimens having only a thin web covering the processes and the central body. As for *Aureoestesa clathrata* var. *clathrata*, the synonymy list includes all references mentioning *Marrocanium*.

It is important to note, that the web is not only extending between the base of the processes as it was indicated in Cramer et al. (1974). It partly covers also the central body and forms an outer coat on both the processes and the vesicle.

**Stratigraphical range.** Fig. 11 illustrates the stratigraphical distribution of *Aureoestesa clathrata* var. *simplex* based on the published occurrences. As for *Aureoestesa clathrata* var. *clathrata*, most of the occurrences are insecure because few of them are controlled by means of another fossil group.

The stratigraphical distribution of *Aureoestesa clathrata* var. *simplex* is similar to that of *Aureoestesa clathrata* var. *clathrata*. The variety *simplex* first appears in the *Didymograptus deflexus* Biozone in Southern China. It is common in the late Arenig and still present in the early Llanvirn. Younger occurrences are not clearly documented.

**Palaeogeographical distribution.** The palaeogeographical distribution of *Aureoestesa clathrata* var. *simplex* is illustrated in Fig. 12. All occurrences are published from sections located in peri-Gondwana, Gondwana, and the Yangtze Platform in southern China. The variety is absent in the Baltic area and has not yet been reported from Laurentia and Australia.

**5. CONCLUSIONS**

The high variability of the specimens belonging to the taxa *Aureoestesa* Vavrdov 1972 and *Marrocanium* Cramer et al. 1974 observed in material from different areas, including the type localities, lead to the conclusion that all specimens belong to one population and should be classified under a single name: *Aureoestesa clathrata* emend. The extreme poles of this population are classified at the *varietas* level: var. *clathrata* and var. *simplex*.

The biometrical investigations in the present study indicate no major differences between the two varieties. Data vary only slightly from one investigated area to another.

*Aureoestesa clathrata* emend appears in the *Corymbograptus v-similis* graptolite Biozone in Bohemia and in the *Didymograptus deflexus* graptolite Biozone in China. It is abundant in the late Arenig sediments and ranges at least into the Llanvirn *Didymograptus murchisoni* Biozone.

Palaeogeographically, it is typical of the cold to temperate Gondwanan and peri-Gondwanan cold water realm, located during the early Ordovician at high latitudes in the southern hemisphere.

The present study illustrates that only a complete review (including the reinvestigation of the type material, variability studies, biometrics, etc.) may lead to a clear taxonomic understanding of an acritarch taxon. It reveals that studies of a limited number of specimens, or investigations on a single sample or a single outcrop area may give an incomplete view of a taxon. In the light of this evidence, it appears probable that numerous predefined acritarch taxa (genera and species), of which the original description was based on a few specimens only (or even on a single individuum), are actually very questionable.

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7. REFERENCES


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**PLATE 1**

Figures A-I, specimens of *Aureotesta clathrata* from the Dawan Formation, Datinba section, South China.

A. *Aureotesta clathrata*, slide DTBDW-16, England Finder Graticule Coordinates X54 ; magnification x 750.

B. *Aureotesta clathrata*, DTBDW-16xy, Z33 ; x 1000.

C. *Aureotesta clathrata*, DTBDW-16, P 56/4, x 1000.

D-E. *Aureotesta clathrata*, DTBDW-16, Z 50/2 ; x 1000. D: transmitted light ; E : reflected light.

F. *Aureotesta clathrata*, DTBDW-16, J 61/2, x 1000.

G. *Aureotesta clathrata*, SEM DTBDW-14 ; magnification x 1800.

H. *Aureotesta clathrata*, SEM DTBDW-14 ; magnification x 1000.

I. *Aureotesta clathrata*, SEM DTBDW-14 ; magnification x 5000.

Figures J-M, specimens of *Aureotesta clathrata* var. *claratha* from the Klabava Formation, Bohemia.

J. *Aureotesta clathrata* var. *claratha*, KL-24B, L 48/2 ; x 750.

K. *Aureotesta clathrata* var. *claratha*, KL-24A, S 50/4 ; x 750.

L. *Aureotesta clathrata* var. *claratha*, MY-2E, F 62/1 ; x 750.

M. *Aureotesta clathrata* var. *claratha*, MY-2B, V 60/3 ; X 750.
PLATE 2


A. *Aureotesta clathrata*, borehole Boujad-109; depth -511 m, slide 20541, England, Finder Graticule Coordinates L 53/4 - L 54/3; same specimen as in Text-fig. 5.

B. *Aureotesta clathrata*, Boujad-109, -511 m, 20541, G 44/3; same specimen as in Text-fig. 6.

C. *Aureotesta clathrata* var. *simplex*, Boujad-109, -511 m, 20541, M-N 37; same specimen as in Text-fig. 7.

D. *Aureotesta clathrata* var. *simplex*, Boujad-109, -360 m, 20539, E-F 35.

E. *Aureotesta clathrata* var. *simplex*, Boujad-109, -511 m, 20542, N 42/3.

F. *Aureotesta clathrata* var. *simplex*, Boujad-109, -511 m, 20542, Q 50/3.

H. *Aureotesta clathrata*, Boujad-109, -511 m, 20542, W 45/2.

I. *Aureotesta clathrata*, Boujad-109, -511 m, 20540, T 51.

J. *Aureotesta clathrata* var. *simplex*, Boujad-109, -511 m, 20541, H 38 - 39.

K. *Aureotesta clathrata* var. *simplex*, Boujad-109, -511 m, 20541, M 33/1.

Figure G. Specimen of *Aureotesta clathrata* from borehole Binz 1, Rügen Island, NE-Germany.

G. *Aureotesta clathrata* var. *simplex*, Binz 1, depth -5117,1 m, 22859, Z 37/2.

Magnification of all specimens x 750.