Crassiangulina variacornuta sp. nov. from the late Llandovery and its bearing on Silurian and Devonian acritarch taxonomy

BASTIEN WAUTHOZ1, KEN J. DORNING2 and ALAIN LE HÉRISSÉ3

Key words. – Acritarch, Balonia, Crassiangulina variacornuta sp. nov., Crassiangulina spp., Biometry, Morphological variability, Silurian, Telychian

Abstract. – Crassiangulina variacornuta sp. nov., a new distinctive species of acritarch, with a short stratigraphical range within the Telychian (Silurian), is recorded from low latitude areas of Balonia (Belgium, England and Sweden) and from high latitude areas of Gondwana (Algeria, Brazil, Libya and Saudi Arabia). Therefore, the new species has good potential to be an international biostratigraphic marker for the Upper Llandovery. It has so far only been recorded in depositional environments where the sediments settled below storm wave base. The genus Crassiangulina JARDINÉ et al., 1972 is emended to incorporate the new species and to include triangular and other polygonal acritarchs with solid processes. The emended genus includes the type species Crassiangulina tesselita JARDINÉ et al., 1972 emend., C. grotesca CRAMER et al. 1976 comb. nov. et emend., and C. variacornuta sp. nov. A biometric study of 138 specimens of C. variacornuta sp. nov. from two sections in England and one section in Belgium and its statistical treatment show the biological consistency of the studied population and point to differences between the mean measurements between the sections, because of taphonomic or environmental factors. This emphasises the need to unravel the morphological variations of acritarch species along the genotypic, ecophenotypic, chronotypic and taphonotypic axes of morphological variability.

Crassiangulina variacornuta sp. nov. du Llandovery supérieur et son rôle dans la taxonomie des acritarches au Silurien et Dévonien

Mots clés. – Acritarche, Balonia, Crassiangulina variacornuta sp. nov., Crassiangulina spp., Biométrie, Variabilité morphologique, Silurien, Telychien


INTRODUCTION

Crassiangulina variacornuta sp. nov., a new species of veryhachiid acritarch with highly variable and solid processes is recorded on two major Silurian palaeocontinents : Balonia (assembled Avalonia and Baltica) and Gondwana. Crassiangulina variacornuta sp. nov. is extensively studied from three sections (fig. 1). The Sheinton Brook section is situated just west of the northernmost part of the Wenlock Edge, in the Welsh Borderlands. The Gullet Quarry section is in the central part of the Malvern Hills. The Steenkerke Borehole was drilled in the westernmost part of the Brabant Massif, Belgium.

Crassiangulina variacornuta sp. nov. is recorded and described from the Visby Beds in Gotland (Sweden), from the Qusaiba Member of the Qalibah Formation (Saudi Arabia) and from the Tianguá Formation of the Serra Grande Group of the Parnaiba Basin (Brazil). Finally it was recorded in subsurface sediments in Algeria and Libya.

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3Laboratoire de Paléontologie et Stratigraphie du Paléozoïque, Université de Bretagne occidentale, 6 avenue Le Gorgeu, 29285 Brest cedex, France. Manuscrit déposé le 13 novembre 2001 ; accepté après révision le 20 septembre 2002.
The fauna of the Pentamerus Beds generally belongs to the Pentamerus Community [Ziegler et al., 1968a] though Stricklandia lens ultima is recorded towards the top. The fauna of the Hughley Shales is typical of the Clorinda Community. This suggests a general deepening of the water column from the bottom to the top of the section [Ziegler et al., 1968b].

During the Telychian, the environment at Sheinton Brook was fully marine, most probably a quiet middle to outer shelf. To the west, the area was protected by the inundated Long Mynd high [Bridges, 1972].

The Pentamerus Beds contain graptolites indicative of the M. turriculatus Biozone [Ziegler et al., 1968b] consistent with the record of the acritarch Dactylofusus estillis (in ?Eupoikilofusus spinata) Cramer and Diez, 1972 [Hill, 1974b]. The brachiopod Eocoelia intermedia is recorded near the base of the Hughley Shales [Ziegler et al., 1968b] indicating a C3 to C4 age, equivalent to the crispus graptolite Biozone. Moreover, conodonts at the base of the Hughley Shales are characteristic of the staurognathoides Biozone [Aldridge, 1972]. The griestoniensis graptolite Biozone has been proved for the top of the Hughley Shales in the northeast part of Wenlock Edge [Ziegler et al., 1968b]. Overall, this evidence suggests that this section is early to mid Telychian in age.

Gullet Quarry, Malvern Hills, England. SO 7612 3811

The Wyche Formation consists of alternating shales, siltstones and sandstones. Thin lenticular shelly limestone lags are present, as separate limestone beds and at the base of some of the sandstones.

The depositional environment is normal marine and apparently faces a cliff or steep slope to the east, with the deposition taking place in relatively quiet waters as indicated by the dominant mudstones, with important tidal ebb currents and some storm surges [Bridges, 1972].

The shelly fauna is abundant and includes brachiopods of the Costistricklandia Community, described by Ziegler et al. [1968a]. The record of Costistricklandia lirata alpha and Eocoelia curtissi suggests a mid Telychian age [Ziegler et al., 1968b]. Conodonts recorded are referable to the Petrospathodus celloni conodont Biozone [Aldridge, 1972], suggesting an early to mid Telychian age for the section.

Steenerkerke 50E-134 borehole, Brabant Massif, Belgium

The Steenerkerke borehole was drilled to a depth of 342 m in Silurian rocks of the Lust Formation [Verniers et al., 2002] in the Brabant massif, near Steenkerke, Belgium. The sedimentary facies consists of muddy to silty turbidites with a gradual upward decrease in interbedded silty or sandy layers. Van Grootvel [1990] interprets it as a turbidite set characterized by an upward trend to dominating d- and e-Bouma intervals. He further suggests that the sedimentary environment of the borehole can be interpreted as a middle-fan in deep water. Graptolite and chitinozoan evidence suggests that the investigated part of the borehole is Telychian in age [Van Grootvel et al., 1998]. Graptolite assemblages from 330 m to 252 m are indicative of the crispus Biozone. Chitinozoans from 338 m to 252 m suggest an early to mid Telychian age for the section.

GEOLOGICAL SETTING

Sheinton Brook, Wenlock Edge, Shropshire, England. SJ 6116 0310

The Pentamerus Beds consist of approximately 150 m of blue-grey silty mudstones with sporadic thinly bedded shelly limestones and sandstones. They pass up to the Hughley Shales (also cited as Purple Shales in the literature). The contact between these units is somewhat gradational, and confused by silty bands at this locality. The Hughley Shales consist of 40 m to 50 m of purple to brown mudstones and silty mudstones with thin sandy limestones and calcareous siltstones [Ziegler et al., 1968b].

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Visby Beds, Gotland, Sweden

The lower Visby Beds consist of 9 m of alternating marl and nodular limestone. The upper Visby Beds (12 m) are characterised by the increasing thickness of the limestone beds [Le Hérissé, 1989 and references therein].

The sedimentation environment of the lower Visby Beds is fully marine and took place in quiet waters under wave base. This is the deepest and most offshore environment recorded in Gotland. The upper Visby Beds were deposited in a very similar environment though affected by storm wave action. The first reefs appear in the uppermost part of the Visby Beds [Le Hérissé, 1989 and references therein].

The lower Visby Beds are attributed to the latest Telychian, corresponding to levels equivalent to the *cremlulata* graptolite biozone. The upper Visby Beds are classically reported to the base of the Wenlock.

Qusaiba Member, Qalibah Formation, Saudi Arabia

The Qusaiba Member consists of up to 1000 m of mudstones passing up to siltstones and sandstones of the Sharawra Member. The Formation shows important lateral variations [Al-Hajri and Owens, 2000].

The environmental setting is fully marine, probably that of a pro-delta passing to a delta front [Al-Hajri and Owens, 2000].

The Qusaiba Member covers nearly all the Llandovery. Its upper limit corresponds to the Llandovery-Wenlock boundary. Le Hérissé [2000, see fig. 2, p. 59] documents 7 acritarch assemblages covering the whole Qusaiba Member. These assemblages are compared to chitinozoan biozones and the acritarch assemblages of Hill and Dorning [1984].

Tianguá Formation, Serra Grande Group, Parnaiba Basin, Brazil

The Tianguá Formation consists of 270 m of shales and sandstones. The lower part yields dark bioturbated carbonaceous mudstones passing up to light grey sandstones intercalated by dark shales and siltstones. The upper part consists of dark bioturbated shales with siltstone intercalations [Grahn, 1992].

The lower part of the Tianguá Formation was probably deposited in an offshore to lower shoreface environment. The sandstone dominated part displays a regressive phase leading to a delta front environment. The upper part witnesses the return of deeper facies [Grahn, 1992]. Open marine conditions prevailed with intermittent influx from fluvial discharges [Le Hérissé et al., 2001].

A recent investigation of the Tianguá Formation for chitinozoans, acritarchs, spores and cryptospores indicates a late Aeronian to middle Telychian age [Le Hérissé et al., 2001].

**MATERIAL AND METHODS**

Sheinton Brook

Sixteen samples were collected in the Sheinton Brook section out of four outcrops. Outcrops 1 (7 samples), 3 (1 sample) and 4 (1 sample) yielded rocks of the Pentamerus Beds. Outcrop 5 (7 samples) yielded rocks of the overlying Hughley Shales. All samples were processed in the palynological laboratory of the Laboratoire de Paléobotanique, Paléopalynologie et Micropaléontologie, Université de Liège, Belgium by Marcela Giraldo-Mezzatesta in October - November 2000.

All samples tested positively for CaCO₃. For each sample, 25 grams of rock were processed in 10 % HCl then they were left a fortnight in 40 % HF. The residue was then oxidised in 65 % HNO₃ for 1 minute, sieved through a 10 µm mesh, bathed 10 minutes in hot 25 % HCl to clean the residue, rinsed again and sieved through a 10 µm mesh.

Gullet Quarry

Eighteen samples were collected from the Gullet Quarry section by Ken J. Dorning and Andy Evans. All samples were processed in the old palynology laboratory of the Centre for Palynological Studies on F floor of the St. George’s building on Mappin Street, University of Sheffield by Andy Evans and Ken J. Dorning. All samples tested positively for CaCO₃. For each sample, 40 grams of rock were processed in 10 % HCl, decanted, digested in 40 % HF. The residue was then oxidised in 5 % HNO₃ for 10 minutes, decanted and centrifuged at 2000 rpm in a Zinc Chloride 2.0 g solution for 10 minutes and sieved through 64 µm and 7 µm nylon bolting cloth using warm water. Both the coarse and fine residues were then strew mounted on glass coverslips and mounted on 76 x 76 glass microslides using Petrophyx 154.

Steenkerke

Palynological slides were prepared from the 17 collected samples to study acritarchs from a depth of –340 m to –252 m. All samples were processed in the palynological laboratory of the Laboratoire de Paléobotanique, Paléopalynologie et Micropaléontologie, Université de Liège, Belgium by Bastien Wauthoz in December 1998 and January 1999.

No sample tested positively for CaCO₃. For each sample, 25 grams of rock were processed in 40 % HF for a fortnight. The residue was oxidised in Schulze solution (1 g of KClO₃ in 25 ml of 65 % HNO₃) for 6 hours, sieved through a 12 µm mesh, bathed 10 minutes in hot 25 % HCl to clean the residue, rinsed again and sieved through a 12 µm mesh.

Figured specimens and additional slides from Gullet Quarry are housed in the ML palynology collections of the Palynology Research Facility, University of Sheffield. Figured specimens and additional slides from Sheinton Brook and Steenkerke are housed in the collection of the Laboratoire de Paléobotanique, Paléopalynologie et Micropaléontologie végétal, Université de Liège.

**Biometric study**

Two measures were taken on 138 suitably preserved specimens from the 14 samples from Steenkerke, from the 5 samples from Gullet Quarry and from the 7 samples from Sheinton Brook. Only specimens that displayed little or hardly any deformation were included in the study. The measurements (Annexe 1) represent the height and width of specimens. The height is the distance from the 'notched' process (see § Systematic Palaeontology) up to the contact with the eilyma at half the distance from the other processes. The width is the distance between the other two processes. The following abbreviations are used in this analysis: SH for Sheinton Brook, GQ for Gullet Quarry and STK for Steenkerke.
The statistical analysis explores the different distribution in height and width for each locality and also for the total studied population. It uses basic statistics (minimum, mean, maximum, standard deviation, skewness and kurtosis), frequency histograms, Shapiro-Wilks W-normality test, correlation coefficient (r), analysis of variance (ANOVA), t-test for independent samples and scatterplots.

RESULTS

Palynological results

Sheinton Brook

All samples for Sheinton Brook yielded a rich and diverse acritarch assemblage. The acritarch colour ranges from pale yellow to orange, consistent with low geothermal alteration in this area previously recorded in the Wenlock [Dorning and Bell, 1987]. The acritarch assemblage contains occasional reworked acritarchs, mostly of Ordovician age, which range in colour from orange-brown to dark brown with rare grey and dark grey.

Dactylofusa estillis CRAMER and DIEZ 1972 is present in slides from outcrops 1, 3 and 4, but it is absent in samples from outcrop 5 where Crassiangulina variacornuta sp. nov. is found.

Gullet Quarry

The acritarch assemblages are rich and diverse. The acritarch colour ranges from pale yellowish brown to brown, indicating a slightly higher geothermal alteration than at Sheinton Brook. Some reworked Ordovician acritarchs are present. Only samples 5e, 18a and c and 4b and c yielded Crassiangulina variacornuta sp. nov. They are all situated in the lower 10 m of the section.

Steenkerke

The acritarch yield is often poor and rarely diverse. The acritarch colour ranges from pale brownish yellow to brown, indicating a slightly higher geothermal alteration than at Sheinton Brook. Some reworked Ordovician acritarchs are present. Only samples 5e, 18a and c and 4b and c yielded Crassiangulina variacornuta sp. nov. They are all situated in the lower 10 m of the section.

Visly Beds

The acritarch assemblages are described in Le Hérissé [1989]. Crassiangulina variacornuta sp. nov. is recorded in several localities of the north west coast (undescribed material).

Qusaiba Member

The acritarch assemblages are described in Le Hérissé [2000] and Le Hérissé et al. [1995]. Crassiangulina variacornuta sp. nov., as Crassiangulina cf. tesselita, occurs in the highly diversified assemblages 5 and 6 in the Telychian part of the Member.

Tianguá Formation

Palynological information is found in Le Hérissé et al. [2001]. Crassiangulina variacornuta sp. nov., as Crassiangulina cf. tesselita, occurs together with Crassiangulina grotesca CRAMER et al. 1976 comb. nov. et emend. Their association seems to be restricted to the early to middle Telychian transition.

Results of the biometric study of Crassiangulina variacornuta sp. nov.

The basic statistics for each locality and for the total studied population are found in table I (and see fig. 3).

<table>
<thead>
<tr>
<th>Sample</th>
<th>n</th>
<th>min</th>
<th>mean</th>
<th>max</th>
<th>s.d.</th>
<th>skew</th>
<th>kurt</th>
</tr>
</thead>
<tbody>
<tr>
<td>Total pop.</td>
<td>138</td>
<td>12.0</td>
<td>17.8</td>
<td>28.0</td>
<td>2.66</td>
<td>0.85</td>
<td>1.16</td>
</tr>
<tr>
<td>SH</td>
<td>47</td>
<td>14.0</td>
<td>19.2</td>
<td>28.0</td>
<td>2.89</td>
<td>0.88</td>
<td>0.74</td>
</tr>
<tr>
<td>GQ</td>
<td>42</td>
<td>13.0</td>
<td>17.2</td>
<td>22.5</td>
<td>2.07</td>
<td>0.47</td>
<td>-0.02</td>
</tr>
<tr>
<td>STK</td>
<td>49</td>
<td>12.0</td>
<td>17.0</td>
<td>22.5</td>
<td>2.34</td>
<td>0.51</td>
<td>0.07</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Sample</th>
<th>n</th>
<th>min</th>
<th>mean</th>
<th>max</th>
<th>s.d.</th>
<th>skew</th>
<th>kurt</th>
</tr>
</thead>
<tbody>
<tr>
<td>Total pop.</td>
<td>138</td>
<td>14.0</td>
<td>19.5</td>
<td>28.0</td>
<td>2.75</td>
<td>0.57</td>
<td>0.40</td>
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<tr>
<td>SH</td>
<td>47</td>
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<td>21.1</td>
<td>28.0</td>
<td>2.53</td>
<td>0.80</td>
<td>0.74</td>
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<td>GQ</td>
<td>42</td>
<td>14.0</td>
<td>19.6</td>
<td>27.0</td>
<td>2.58</td>
<td>0.81</td>
<td>1.17</td>
</tr>
<tr>
<td>STK</td>
<td>49</td>
<td>14.0</td>
<td>18.4</td>
<td>25.5</td>
<td>2.48</td>
<td>0.59</td>
<td>0.17</td>
</tr>
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</table>

TABLE I. – Biometric measurements of Crassiangulina variacornuta sp. nov. for the total population and for each locality. Minimum, mean and maximum values, standard deviation, skewness and kurtosis are given for both measurements.

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The distributions for height and width in the total population are significantly not normal (W_H = 0.96, p < 0.001 and W_W = 0.97, p = 0.004) though not two peaked (fig. 2). The skewness is always positive (table I) indicating a distortion towards higher values.

There is a significant correlation between height and width in STK and SH samples (respectively r = 0.80 and r = 0.81), whilst there is none in the GQ samples (r = 0.48).

The ANOVA test is significant for both height and width (p < 0.001, see table II). The t-tests indicate that the measures are statistically not equivalent between pairs of samples other than for the height when comparing GQ and STK samples (p-value = 0.721, see table III and fig. 3).

Inspection of the scatterplots shows there is a clear overlapping of the 95% confidence interval ellipse and that most observations plot together (fig. 4).

**DISCUSSION OF THE BIOMETRIC STUDY OF CRASSIANGULINA VARIACORNUTA SP. NOV.**

The distributions, though not normal, are apparently biologically consistent because they show a bell shape and are not two-peaked (fig. 2). The positive distortion in skewness is probably because of the mesh size used to sieve the residues during laboratory procedures, that has the effect of limiting the smaller size of the specimens in the slides.

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The correlation between height and width in specimens from the Steenkerke and Sheinton Brook samples may suggest a possible growth pattern, variations in nutrient availability, or depositional sorting. There is no satisfactory explanation for the absence of correlation in the Gullet Quarry locality, but hypotheses could include one or more of insufficient sampling, relative proximity to the shoreline, rapidly changing environmental conditions.

The t-tests indicate that there is a statistically significant difference between the means of the samples. This feature may be interpreted as the consequence of the differences in thermal alteration. The Steenkerke samples display the highest alteration and the lowest mean for both measures. The Sheinton Brook samples display the lowest alteration and the highest means. This interpretation is somewhat shaded by the similarity in the values of the means of the height in Steenkerke and in Gullet Quarry samples. In order to accept this interpretation, a non-linear shrinking of eilyma versus temperature is needed, with a relatively rapid shrinkage at low temperatures, followed by an additional slower size reduction at higher temperatures. This is not unreasonable, given the variation in translucency is also apparently non-linear as suggested by Brooks and Dorning [1997].

Another interpretation is that the larger specimens in Sheinton Brook indicate a more favourable environment. It appears that brachiopod communities are not very different between Sheinton Brook (Stricklandia to Clarinda Community) and Gullet Quarry (Stricklandia Community) though the Gullet Quarry environment was apparently somewhat shallower. Topographical and current pattern distributions are different [Bridges, 1975], which may account further for the biometric differences.

Other interpretations are based on the distribution of specimens in the scatterplots (fig. 4). The GQ specimens occupy a more dispersed morphospace that may suggest a more or less stressful environment in Gullet Quarry, perhaps linked to the nearshore environment.

**TABLE II.** – Results from the ANOVA. The value of F-Snedecor, the degrees of freedom (df) and the statistical significance (p-level) are given.

<table>
<thead>
<tr>
<th>Measure</th>
<th>F (df)</th>
<th>p-level</th>
</tr>
</thead>
<tbody>
<tr>
<td>Height</td>
<td>12.033</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Width</td>
<td>13.522</td>
<td>&lt;0.001</td>
</tr>
</tbody>
</table>

**TABLE III.** – Results from the t-Student test. The value of t, the degree of freedom (df) and the statistical significance (p-level) are given.

<table>
<thead>
<tr>
<th>Measure</th>
<th>t</th>
<th>df</th>
<th>p-level</th>
</tr>
</thead>
<tbody>
<tr>
<td>SH : GQ</td>
<td>-3.863</td>
<td>87</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>GQ : STK</td>
<td>0.358</td>
<td>89</td>
<td>0.721</td>
</tr>
<tr>
<td>STK : SH</td>
<td>-4.195</td>
<td>94</td>
<td>&lt;0.001</td>
</tr>
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</table>

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SYSTEMATIC PALAEONTOLOGY

Genus Crassiangulina JARDINÉ et al., 1972 emend.

Type-species: Crassiangulina tesselita JARDINÉ et al., 1972.

Diagnosis: The vesicle is hollow, triangular to polygonal in outline. The eilyma is unilayered, laevigate to slightly ornate. The processes are located at each corner of the vesicle and are generally distinct. They are composed of one to many solid elements. If many elements, they are fused together or not. The processes are generally heteromorphic. Sometimes differences are so slight that processes may appear homomorphic.

Remarks: On some specimens, the processes are as simple as a thickening of the eilyma that does not produce a clearly distinct process. The vesicle wall is scabrate to granulate. Most of the specimens appear to be triangular in outline, even in species that include polygonal specimens.

Comparison: Arkonia BURMANN 1970 has hollow processes freely communicating with the vesicle. The surface bears distinctive costae.

Dateriocradus LOEBLICH and TAPPAN 1971 has hollow irregularly branched processes, with branching often of more than one order, at the corners of the vesicle.

Frankea BURMANN 1970 has hollow processes freely communicating with the vesicle. The processes split into unbranched pinnae. Moreover, Le Hérissé has observed bilayered specimens [Servais, 1993, p. 80-81, but also see Vecoli et al., 1999].

Onondagaella CRAMER 1966 has hollow processes freely communicating with the vesicle. One of the processes bears a solid plug, which is interpreted as a fixing structure by Le Hérissé [1989].

Triangulina CRAMER 1964 is bilayered and has hollow processes.

Veryhachium DEUNFF 1954 has simple acuminate hollow processes freely communicating with the vesicle.

Discussion: The emendation of Crassiangulina JARDINÉ et al. 1972 is proposed in order to group into one genus triangular and polygonal acritarchs with a solid process at each vesicle corner. This avoids the need to create a monospecific genus in a grouping of forms that displays clear differences in process building but not in process structure (i.e. all species have solid processes).

Crassiangulina grotesca (CRAMER et al.) comb. nov. et emend.

Holotype: pl. 2, fig. 27, Cramer et al. [1976] (see also this work pl. III, fig. 24).

Locus typicus: sample 6548A04, San Pedro Formation, Torrestio, Spain.

Emended description: The vesicle is hollow and triangular in outline. The eilyma is laevigate. The sides of the vesicle taper gradually to the solid processes. Each process is distributed at one corner of the vesicle and is composed of a basall thickening, from which emerge a crown of filamentous elements.

PLATE I. – All specimens are Crassiangulina variacornuta sp. nov. (x 1000) from the Shiento Brok section. Captions give the slide number and England Finder reference for each specimen.

1. holotype, slide 56502, D40/2; 2. paratype, slide 54654, J4/1; 3. paratype, slide 56489, J54/2; 4. paratype, large specimen with inner darker body and solid elements on the vesicle surface, slide 56490, W39/4; 5. specimen with hardly developed right process, slide 56454, D36/0; 6. specimen with granulolate eilyma, slide 56454, W42/0; 7. specimen with torn off notched process, slide 56454, X48/1; 8. elongated specimen, slide 56487, V54/2; 9. specimen with twisted notched process, slide 56487, Z48/1; 10. large specimen with hardly developed processes, slide 56488, R53/0; 11. large specimen with solid elements on the vesicle surface, slide 56488, F53/1; 12. specimen with inner darker body, slide 56489, K42/2; 13. specimen with torn off notched process, slide 56489, R41/2; 14. slide 56489, T32/0; 15. slide 56489, X32/0; 16. specimen with twisted notched process, slide 56490, D46/2; 17. specimen with torn off notched process, slide 56490, F39/4; 18. specimen with simple processes, slide 56490, M39/4; 19. specimen with simple processes, slide 56490, M39/1; 20. note that the process to the right is a simple thickening of the eilyma, slide 56490, U48/1; 21. elongated specimen with well developed processes, slide 56490, V40/0; 22. slide 56490, W34/4; 23. small specimen with hardly developed processes, slide 56402, U37/2; 24. specimen with torn off notched process, slide 56492, X40/4.

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CRASSIANGULINA VARIACORNUTA SP. NOV.
Dimensions: total diameter of the vesicle: 30-35 µm, length of filamentous elements: 10-12 µm.

Remarks: in the Tiangu Formation, some specimens display filamentous elements that form a circular net around the basal thickening [Le Hérisse et al., 2001]. No excystment structure has been observed.

Stratigraphical and geographical distribution: San Pedro Formation (Ludlow), Province of Leon, Spain [Cramer et al., 1976]; Qalibah Formation (Telychian), Saudi Arabia [Le Hérisse, 2000]; Mudawwara Formation (Telychian), Hashemite Kingdom of Jordan [Keegan et al., 1990]; Tiangu Formation (late Aeronian to mid Telychian), Parnaiba Basin, Brazil [Le Hérisse et al., 2001].

Crassiangulina tesselita Jardiné et al. 1972 emend.

1964 Acritarch ? sp. 2 Cramer, p. 336, pl. V, fig. 6, text-fig. 40 : 2

1972 Crassiangulina tesselita Jardiné et al., p. 295, pl. I, figs. 1 and 2

1974 Crassiangulina tesselita Jardiné et al., p. 115, no figs.

1988 Crassiangulina tesselita Streel et al., p. 117, pl. 21, fig. 2

1996 Crassiangulina tesselita Vardóna et al., no figs.

Holotype: pl. I, fig. 1 – Collection ELF R. E. nº 1697 Jardiné et al. [1972].

Locus typical: sondage Tesselit nº 101, carotte 42, 2148 m, formation de Gazelle, bassin d’Illizi, Algérie.

Emended description: the vesicle is hollow, triangular to polygonal in outline. The eilyma is laevigate to scabrate. There are three to eight processes, one at each corner of the vesicle. Each process is a more or less distinct subspherical thickening rarely composed of more than one element (always verrucate).

Dimension: 22 to 40 µm.

Crassiangulina variacornuta sp. nov.

1974a Veryhachium sp. 1 Hill, p. 203, pl. 29, fig. 4 (unpublished Ph.D. thesis)

1995 Crassiangulina cf. tesselita LE HÉRISSE, AL-TAYYAR et al., p. 56, pl. 1, fig. 7

1997 Crassiangulina cf. tesselita Rubinstein, p. 608, pl. 1, fig. 4

2000 Crassiangulina cf. tesselita LE HÉRISSE, p. 70, pl. 6, fig. e

2001 Crassiangulina cf. tesselita LE HÉRISSE et al., p. 27-28, no fig.

2001 Avalonella variacornuta Wauthoz and Dorning, p. 74, no fig. nomen nudum

Derivatio nominis: from varius, a, um (different, varié – diverse, different) and cornutus, a, um (cornu – horned)

Holotype: specimen SH56 (56491) D40/2 (plate I, fig. 1)

Paratypes: specimens SH51 (56454) Y48/1, SH54 (56489) J52/4, SH55 (56490) W39/4, GQ18c (18/-64µm/c) V48/3, GQ18c (18/-64µm/c) X34/4, GQ4c (4/-64µm/c) V32/4, GQ5e (5/-64µm/e) S33/1, STK274.5 (53216) K62/1, STK283 (53218) V68/0, STK332.5 (53246) Q50/0 and STK336 (53247) T60/3 (respectively plate I, fig. 2-4; plate II, fig. 1-4; plate III, fig. 1-4).

Locus typical: base of the Hughley Shales in the stream section of Sheinton Brook (SJ 61280303), Shropshire, England.

Material: a total of more than 150 specimens from all sections.

Description: the vesicle is subtriangular in outline. Each of the three sides can be concave, straight or convex. The vesicle is dorso-ventrally flattened to form a somewhat inflated subtriangular cushion. The eilyma is generally laevigate and about 1 µm thick. The processes are stiff and apparently solid. They are composed of several to numerous verrucate, clavate and bacular elements. These elements can be fused together or more or less separated. Each process overlaps a corner of the triangle, with the overlapping being asymmetrical to the bisecting line. The processes are heteromorphic and usually different from each other though sometimes two processes can be very similar. One of the processes is always composed of an elongated verruca with or without other elements fused to it (referred to as the ‘notched’ process). This process is generally simpler than the other two because it is formed by fewer elements. It is more clearly differentiated from the vesicle than the other two processes. This notched process shows a solid outgrowth extending into the vesicle, generally surrounded by a ring of thinner eilyma. On some specimens, this process is absent, leaving a concave curved split. Rarely, some elements that can be interpreted as a fourth process are present on the eilyma.

Dimensions: height from ‘notched’ process to eilyma: 12 to 28 µm (mean: 17.8 µm), width between the other two processes: 14 to 28 µm (mean: 19.5 µm). Holotype: height = 24.0 µm, width = 22.5 µm.

Remarks: This species differs from C. tesselita Jardiné et al. emend. in having complex processes that are not subpherical. It differs from C. grotesca comb. nov. et emend. by the absence of filamentous elements crowning the basal thickenings at each vesicle angles. The process variability in specimens from Gotland and Brazil can be compared to that observed in specimens from England and Belgium [Le Hérisse, unpublished data; Le Hérisse et al., 2001].

The concave split observed in the place of the notched process may be interpreted as an excystment structure.
The acquisition of new morphological characters developed by the *Crassiangulina* complex, with the high degree of morphological variability in the process building of *C. variacornuta* sp. nov., may relate to variations in marine conditions, including nutrient supply and relative sea level fluctuations. It is possible that this variability is somehow related to major changes in global relative sea level, possibly associated with the early Llandovery and latest Llandovery transgressions [Beck and Strother, 1997; Johnson, 1996]. Le Hérissé et al. [2001] associated the presence of the *Crassiangulina* group with the flooding of continental margins, implying renewed oligotrophic conditions, and/or climatic changes in northern Brazil.

There is probable provincialism within the group during Silurian times, with *Crassiangulina grotesca* apparently restricted to Gondwana. On the other hand, *C. variacornuta* sp. nov. shows a high cosmopolitanism with records spread across two major palaeocontinents, Balonia and Gondwana. No *Crassiangulina* species are currently known from Laurentia and other palaeocontinents.

*Crassiangulina* disappears from the fossil record during the mid to late Devonian to reappear at the Devonian-Carboniferous boundary. Here the group is only represented by *Crassiangulina tessellata*, which shows less process variability but a much more complex vesicle shape, even though triangular forms are still dominant. This could be interpreted as a Lazarus phenomenon driven by ecological parameters.

**BIOSTRATIGRAPHY AND ECOLOGY OF **

*Crassiangulina variacornuta* sp. nov. has been recorded at stratigraphical horizons apparently equivalent to the *crispus* graptolite Biozone in the sections from Balonia. In Gullet Quarry, the studied samples all belong to strata equivalent to the *crispus* to *griestoniensis* graptolite biozones. In Sheinton Brook, the Pentamerus Beds are devoid of *C. variacornuta* sp. nov. [Hill, 1974a and this work], which first appears in the Hughley Shales. Moreover, Hill [1974a] did not record it in the overlying Bulidwas Formation. It therefore spans the interval equivalent to part or possibly all of the interval represented by the *crispus* to *griestoniensis* graptolite biozones in this section. In the type Llandovery area in south Wales, Hill [1974b] and Hill and Dorning [1984] did not record *C. variacornuta* sp. nov. Only limited information constrains the latest record in the Telychian, though *C. variacornuta* sp. nov. has not been recorded from the highest Llandovery strata or type Wenlock Series.
[Dorning, 1981; Hill, 1974a; Swire, 1993]. In Belgium, C. variacornuta sp. nov. is recorded in the Steenkerke borehole (crispus graptolite Biozone). It is, however, absent from the underlying strata in the 83W–44 Kortrijk (Lust Brewery) borehole that records a graptolite fauna indicative of the guerichii Biozone [Van Grootel et al., 1998]. Younger strata were not investigated in this area. In Gotland, C. variacornuta sp. nov. is recorded from the uppermost Llandovery up to near the Llandovery–Wenlock boundary. It is absent from Wenlock strata [Le Hérissé, 1989].

In the Qusaiba Member (Saudi Arabia), Crassiugulina variacornuta sp. nov. is recorded in assemblages 5 and 6. They cover an interval corresponding to the S. solituddina–A. hemeri, A. hemeri and A. macclurei chitinozoan biozones of Paris et al. [1995]. This is equivalent to an interval spanning the turriculatus, crispus and gries Johnseni graptolite biozones. C. variacornuta sp. nov. is absent from the uppermost Llandovery assemblage. The acritarch assemblage of the Tianguá formation (Brazil) is very similar to that of the Qusaiba Member. The age of the formation is late Aeronian to mid Telychian [Le Hérissé et al., 2001]. However, Le Hérissé notes that the close similarity between the Tianguá assemblage and assemblage 6 of the Qusaiba Member would more likely point to a mid Telychian age. Other records on Gondwana (Libya and Algeria) are presently of no use to further constrain the biostratigraphic framework of C. variacornuta sp. nov. However, they all fall within the late Llandovery–early Wenlock interval which is consistent with the other stratigraphic information.

From all the evidence, it appears that Crassiugulina variacornuta sp. nov. is limited to Telychian strata. On Balonia, the base of its biostratigraphical range seems well constrained and does not extend to strata below the crispus graptolite Biozone. On Gondwana, the base of its biostratigraphical range seems to be strata equivalent to the turriculatus graptolite Biozone. There is no evidence that the biostratigraphical range of C. variacornuta sp. nov. extends into the Wenlock on both palaeocontinents.

Crassiugulina variacornuta sp. nov. is recorded in different environments. In Gullet Quarry, it is found within a Stricklandia Community on a rather steep topography [Bridges, 1972]. In Sheinton Brook, it appears at the transition between the Pentamerus Beds (Pentamerus to Stricklandia brachiopod Community) and the Hughley Shales (Clorinda brachiopod Community). In the Steenkerke Borehole, C. variacornuta sp. nov. is found in deep water turbidites of the Brabant Massif. This record is not necessarily conclusive because the acritarch assemblage displays a mix of autochthonous, paraautochthonous and reworked specimens. It is probable that C. variacornuta sp. nov. was brought in together with other paraautochthonous particles including socolcodons and fragments of Hoegklintia spp.

In Gotland, it is found in a quiet offshore environment under storm wave base. In Gondwana C. variacornuta sp. nov. occurs in the pro-deltaic setting of the Qusaiba Member. It is associated with transgressive events indicated by increased diversity. The Tianguá Formation records fully marine offshore to lower shoreface conditions with intermittent influx from fluvial discharges.

Overall this indicates that C. variacornuta sp. nov. occurs in quiet, relatively deep, shelf environments (Stricklandia to Clorinda brachiopod Communities), mostly below storm wave base, associated with diverse acritarch assemblages, characteristic of the Telychian oceanic Snipklint Primo Event in Balonia. Moreover, the appearance of the species seems related to the flooding of the shelf during transgressive phase and the concurrent return of oligotrophic conditions. The greater size of specimens in Sheinton Brook, if not attributed to taphonomic processes, may suggest that sheltered protected marine palaeoenvironments were favourable to C. variacornuta sp. nov.

CONSEQUENCES FOR ACритARCH TAXONOMY

The classification of acritarchs is based on morphological features, because of the lack of understanding of their biological affinities. Therefore, the quality of the descriptions and the understanding of the characteristic morphological features of a taxon are the keystone of its applicability. Any set of taxonomic entities are theoretically just as good as any other, as far as morphology is concerned. In order to work, a taxonomy that is appropriate to be applicable is needed.

If only a few specimens of Crassiugulina variacornuta sp. nov. were available, closely resembling the holotype, then the chances are that specimens SH55: F39/4, GQ: P48/1, STK287: J30/4 or STK314: Q58/4 (respectively pl. I fig. 17; pl. II fig. 5, pl. III fig. 10 and 16) would be placed in another taxon. Indeed, some morphological criteria (such as the extent of the process around the vesicle angle) would allow their separate recognition. Taxonomic problems would arise with some ‘intermediate’ specimens such as SH51: Y39/3, SH55: U48/1, GQ18c: S36/1 or STK278: R58/3 (respectively pl. I fig. 5 and 20; pl. II fig. 7, pl. III fig. 21). Their position between the two ‘end members’ would not be easily assessed. Further problems would arise for specimens with large and well developed processes, including SH55: W39/4, GQ4c: X38/3 or STK283: V68/0 (respectively pl. I fig. 4; pl. II fig. 21, pl. III fig. 2).

Examination of a large population of specimens has permitted the recognition of the high degree of variability and of many side forms (or end members) of Crassiugulina variacornuta sp. nov. Moreover, the statistical treatment of the height and width measurements has confirmed that there was only one biometric entity.

Mean, standard deviation and asymmetry coefficients have defined the biometric range of the species. Should this kind of information be available for closely similar taxa, similarities and differences could be tested in order to assess whether two taxa are similar or not. This demonstrates the usefulness of biometrics and statistics in taxonomy.

Some statistical tests have shown differences between samples that otherwise would have been missed. The lack of correlation between height and width in Gullet Quarry was revealed by the correlation coefficient. In addition, the use of t-tests indicated significant differences between the means of each locality. Even when they are not easily interpretable, these differences tell us about the variability of a taxon.

Conceptually, any fossil taxon has four axes of morphological variability: the first is the variability allowed by the genes at a particular time, or genotype; the second is the variability due to environmental stress, or ecophenotype; the
third is the variability of features through time as the taxon evolves, or chronotype, and fourth is the variability due to taphonomic agents styled as taphonotype. Most probably, the chronotype also includes an expression of the genes. It is, however, interesting to separate it from genotype because the chronotype is useful to refine biostratigraphical schemes (see remarks on *Polygonium polygonale* Eisenack emend. Le Hérissé 1989 in Le Hérissé [1989]).

Probably the apparent variability in process shape in *Crassiangulina variacornuta* sp. nov. can be attributed to the genotype because process shape does not show clear differences between the localities. Each locality has specimens with simple processes, specimens with large elaborate processes and intermediate specimens.

Based on our observations, it appears that the absence of the notched process is more frequent in deeper water environments. It may therefore be an ecophenotypic variable. The presence of curved splits seems to be taphonomic since it is only recorded in the Steenkerke specimens. Moreover it does not seem to have any preferred location (see pl. III fig. 9 and 12) as would be expected for a biological structure (e.g. excystment curved split). Whether this structure is due to the higher thermal maturity or to current strength cannot be assessed. Since the studied material is limited to a short time span, it cannot be estimated whether *C. variacornuta* sp. nov. shows some chronotypic variability or not.

Only in defining these four axes of morphological variability correctly and thoroughly, can the understanding of the characteristic morphological features of old and new taxa be attained and made totally applicable. A way to achieve these goals is defining the morphospace [Foote, 1991, 1993; Gould, 1991].

Understanding the morphospace occupation of a particular taxon through time enables the definition of possible chronotypes which will refine biostratigraphical schemes. The definition of ecophenotype depends on the quantification of morphospace occupation in different environments. Application in palaeoenvironmental studies requires this quantification in order to test the assessment to a particular environment. Understanding the morphological variations implied by taphonomic degradation (chemical corrosion, bacterial feeding, compression and shearing, heating, etc.) will require studies in different geological contexts. Definition of discrete taphonotypes will help to decipher the burial context and to define the limits of a study, as implied by the preservation state. Assessment of the genotypic characteristics is critical to stabilise the taxonomy. However, because of the rather simple morphology of acritarchs there is no straightforward way to assess it. Ideally, only characters showing little ecophenotypic, chronotypic or taphonotypic variation should participate in the definition of the genotype.

**CONCLUSIONS**

The genus *Crassiangulina* Jardiné et al. 1972 is emended together with the type-species *Crassiangulina tesselita* (Jardiné et al.). *Crassiangulina (=Antruwjadna) grotesca* (Cramer) comb. nov. et emend. is included in the genus, as is *Crassiangulina variacornuta* sp. nov. that includes the species cited as *C. cf. tesselita*, mainly documented in Gondwana.

The group of *Crassiangulina* spp. acquires a high morphological variability soon after its appearance during the early Silurian. This is not surprising, given the high morphological diversity that acritarchs show during the late Llandovery [Beck and Strøther, 1997; Le Hérissé, 2000]. *C. grotesca* comb. nov. et emend. is restricted to temperate Gondwana during most of the Silurian. *C. tesselita* emend. is similarly restricted to Gondwana in the Devonian.

*Crassiangulina variacornuta* sp. nov. has the potential to be a good biostratigraphical and environmental marker on an international scale. In all studied sections it is limited to the Telychian. It also appears to be most frequently found in quiet marine shelf environments deposited below storm wave base, equivalent to the *Stricklandia* and *Clorinda* depth communities of Ziegler [1965].

The biometric and statistical analyses show the studied population of *C. variacornuta* sp. nov. forms a biologically consistent entity. The difference in mean size between the sections is tentatively explained by difference in thermal alteration between sections, although a palaeoenvironmental explanation is possible.

The variability of *C. variacornuta* sp. nov. is tentatively compared to the four axes of morphological variability (genotypic, ecophenotypic, taphonotypic and chronotypic). The variability in process building, similar in the three sections, is very probably genotypic. The absence of notched process, more frequent in deeper environments, seems to be ecophenotypic. Finally, the presence of a curved split, limited to Steenkerke samples, seems to be a taphonotypic variable, and does not have any taxonomic relevance. The short stratigraphic interval covered by the samples does not allow the determination of any chronotype.

This study assesses the importance of studying (and figuring) a large population of a single acritarch species in order to understand its morphological variations, and how these relate to the four axis of morphological variability. This is not only useful to understand the taxonomy of the genus, but also to reveal the true potential of the taxon as a palaeoontological and geological tool.

**Acknowledgements.** – Samples from Gullet Quarry were collected by Ken J. Dorming and Andy J. Evans in October 1993. the Steenkerke material comes from the Service Géologique de Belgique, collected by Bastien Wauthoz and Michel Vanguestaing in 1996. Sheinton Brook was first sampled for acritarchs by Paul J. Hill [Hill, 1974a], with the section recollected in detail by Ken J. Dorming and Bastien Wauthoz in September 2000.

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ANNEXE

ANNEXE 1 : MEASUREMENTS TAKEN ON SPECIMENS OF CRASSIANGULINA VARIACORNUTA SP. NOV.

Each specimen is given a case name, slide reference and England-finder position on the slide, height and width measures and a locality abbreviation (GQ: Gullet Quarry section, STK: Steenkerke borehole, SH: Shinestone Brook section).

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