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Ankumia van Veen, 1932 (*nomen dubium*): pathological moult retention in the Cytherellidae (Platycopida: Ostracoda)

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ABSTRACT – The monotypic genus *Ankumia* is associated with the rich cytherellid fauna described by van Veen (1932) from the Upper Cretaceous (late Maastrichtian) rocks of South Limburg, The Netherlands. The type species (*A. bosqueti* van Veen, 1932) is redescribed because the genus possesses the enigmatic combination of cytherellid (posterior sex-dimorphism and R/L overlap) and eridostracan (several concentric bands) characters. As no holotype was designated, the redescription is based on a detailed SEM examination of the syntypes in the Bonnema/van Veen composite collection. Most syntypes show that the outer layer of coarse, concentric, rings, which form an oblique cone, are retained moults of a species of cytherellid. The point of retention in the early instars is along the posteroventral margin, contrary to the dorsal position of successive lamellae in eridostracan *Cryptophyllus*. Other syntypes possess the typical lateral outline of adult species of Cytherellidae. The ontogeny of each individual of retained moults ('*Ankumia*') has a nine-instar pattern, with a growth increment between successive moults about 1.15, slightly less than that (about 1.20) observed by Shaver (1953) for *Cytherella bullata*. The name *Ankumia* is abandonned, and a new combination proposed for the previous type species, *Platella bosqueti* (van Veen, 1932). *J. Micropalaeontol*. **22**(1): 85–99, July 2003.

INTRODUCTION

The classificatory position of the genus *Ankumia* within the Ostracoda was a paradox when first proposed by van Veen (1932) and remains so some 70 years later. The type species – *Ankumia bosqueti* van Veen, 1932 – was described as part of the rich cytherellid fauna of the Upper Cretaceous (late Maastrichtian) rocks of South Limburg, The Netherlands. Both van Veen (1932), the first to demonstrate sexual dimorphism in *Cytherella* (van Veen, 1928), and Bonnema (1932), emphasized the cytherellid characters (posterior sex-dimorphism and R/L overlap) of *Ankumia*. However, both authors also realized that the morphology of *Ankumia* is unusual for a cytherellid, in that the type species is characterized by a thick, heavy shell consisting of several concentric rings in the form of an oblique cone, the apex of which lies in a posteroventral position. They pointed out that these concentric bands are somewhat like those observed in *Eridoconcha* Ulrich & Bassler, 1923, from the Ordovician, Silurian and Devonian, but when the bands are absent due to exfoliation, an external pit shows the place of muscle attachment, as in many *Cytherella* species.

The genus *Ankumia* has been discussed under the Cytherellidae in several bibliographic works, such as van den Bold (1946), Howe & Laurencich (1958), Reyment (1961) and Coryell (1963). Its absence in other compilations, namely Pokorny (1958, 1978), and van Morkhoven (1962–63), however, may reflect a perception of the questionable status of the genus. Bless & Massa (1982, p. 28) have suggested that *Ankumia* van Veen, 1932 may belong to the Cryptophyllidae, a family referred to the Eridostraca, a group of multilamellar crustaceans. At present, some opinions hold that the Eridostraca are part of the ostracod group Palaeocopida (Schallreuter, 1968, 1977; Warshauer & Berdan, 1982); others, that they may be an extinct group of marine branchiopods (Schmidt, 1941, Jones, 1968, Langer, 1973, Adamczak, 1976). It is worth noting that *Ankumia* has remained monotypic, as neither the type species, nor any other species belonging to the genus have been described beyond the type area of South Limburg.

In view of the confusion that surrounds the genus, a reassessment of the type species has been long overdue. Therefore, the purpose of this paper is to revisit and examine the type species of *Ankumia* van Veen, (*A. bosqueti* van Veen, 1932), in order to evaluate the validity of the genus.

All type specimens figured in this paper are deposited in the palaeontological collections of the Netherlands Institute of Applied Geoscience TNO – National Geological Survey, Utrecht (previously the Rijks Geologische Dienst, Haarlem), under the prefix BvV-O.

The following abbreviations are used in reference to the specimens: C, carapace; LV, left valve; RV, right valve; R/L, right valve overlapping left valve; F, female; M, male; AMS, adductor muscle scar. All measurements (L, length; H, height; W, width) are in micrometres.

LOCALITIES

The material examined came from the three localities cited by van Veen (1932) in the Maastricht region: Bemelen, Geulem and Jekertal (Fig. 1). Thus, all three places of origin are in the type area of the Maastrichtian Stage, and constitute the type locality (ICZN, 1999, Article 73.2.3) for *Ankumia bosqueti* van Veen, 1932. Bemelen is sited about 5 km east of Maastricht. Geulhem (current spelling) is sited about 6.7 km northeast of Maastricht, and 0.5 km north of the Geulhemmerberg Cretaceous/Tertiary (K/T) boundary section (Brinkhuis & Smit, 1996). Jekertal (also spelt Jekerdal) refers to the valley of the River Jeker, which joins the River Maas, at Maastricht. Presumably the Jekertal locality refers to the rocks formerly exposed along the Albert Canal near Kanne, about 5 km SSW of Maastricht. The nearest exposure of these rocks is at the quarry of the ENCI Nederland BV cement factory, 3.6 km due south of Maastricht (Jagt *et al.*, 1996).

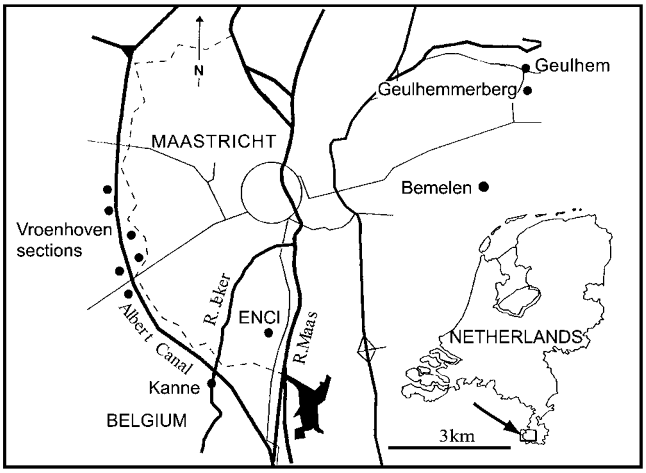

Fig. 1. Locations of sections (black dots) in the Maastrichtian type area mentioned in the text (in part after Jagt *et al.*, 1996, fig. 1).

STRATIGRAPHY

All three type localities lie within the upper part of the Maastricht Formation (*sensu* Felder, 1975). Van Veen (1932) collected the Jekertal sample from (translated) 'the third Bryozoan layer of Staring' within Uhlenbroek's (1912) unit Mc, and she collected the Bemelen sample from (translated) 'the first Bryozoan layer' within his unit Md. The Geulem sample was collected from an unspecified layer within Md. In current lithostratigraphic terms (Felder, 1975; Fig. 2), units Mc and Md are the penultimate and last members of the Maastricht Formation respectively, namely the Nekum Chalk Member (Mc; between the Laumont and the Caster horizons), and the Meerssen Chalk Member (Md; between the Caster and the Vroenhoven horizons). Biostratigraphically, Hokfer (1966) referred the Mc unit to his K foraminiferal Zone, and the Md unit to his L and M foraminiferal Zones. Verbeek (1977) assigned both the Mc and Md units in the ENCI quarry to his latest Maastrichtian *Micula murus* nannofossil Zone.

Van Veen (1932) also mentioned two other levels for unfigured specimens of *Ankumia bosqueti*, one from (translated) 'the third Bryozoan layer of Ubaghs (1879)' at Valkenburg (i.e. near the base of the Nekum Chalk Member; Nuyts, 1990), and the other from (translated) 'the younger layers of the Kunrade coral limestone' (i.e. above the Romontbosch Horizon, near the base of the Emael Member; Robaszynski *et al.*, 1985, fig. 33, p. 53).

In this paper, the stratigraphic position of the bryozoan layers cited by Van Veen (1932) is shown in descending order within the Nekum and Meerssen members, after Nuyts (1990, fig. 2). Their precise levels within these members of the Maastricht Formation are unknown. Any finer resolution would be equivocal, because the lateral extent of hardgrounds is often limited by the palaeo-relief (see Roep & Smit, 1996).

The position of the K/T boundary in the Maastrichtian type area was positioned at the Vroenhoven Horizon (at the top of the Meerssen Chalk Member; Felder, 1975), between the Maastricht and Houthem Formations. More recent studies (Brinkhuis & Smit, 1996) suggest that it occurs within the Meerssen Chalk Member, at the Berg en Terblijt Horizon. This would place the uppermost unit of this member (IVf-7 of Felder, 1975) in the Danian. Results from Sr isotope stratigraphy (Vonhof & Smit, 1996) suggest that the 20 m of calcarenites between the Laumont and the Berg en Terblijt horizons were deposited in 200 ka before the K/T boundary event.

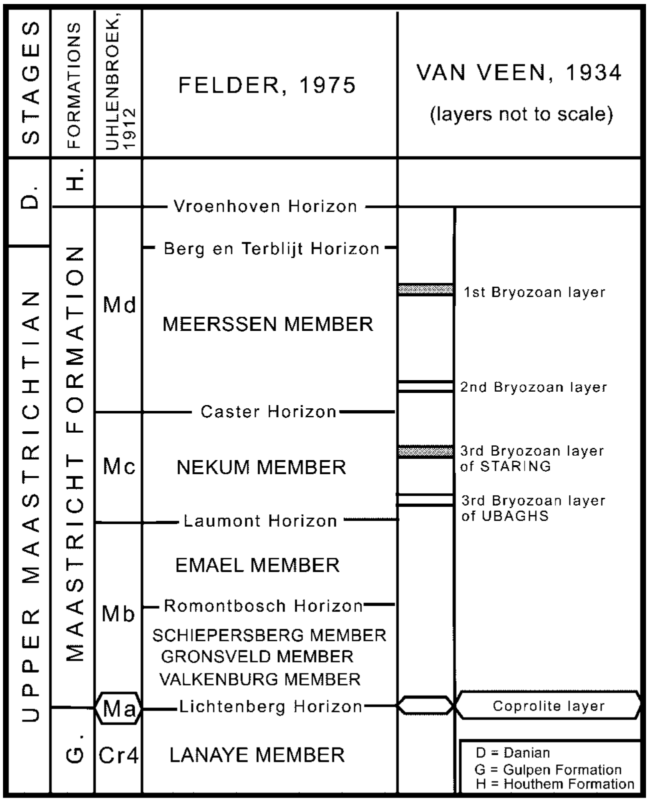

Fig. 2. Stratigraphy of the Maastricht Formation (in part after Nuyts, 1990, fig. 2; data from Uhlenbroek (1912), Felder (1975) and van Veen (1934)). The localities of *Ankumia bosqueti* van Veen, 1932 (in stipple) correspond to the bryozoan horizons, whose precise levels (within each member of the Maastricht Formation) are unknown.

MATERIAL

Van Veen (1932) illustrated ten specimens from the type series of *Ankumia bosqueti*, of which she considered six to be females (pl. 24, figs 1–18), and four she regarded as males (pl. 25, figs 1–14). She designated neither a holotype, nor syntypes (or any other catagory used in the meaning of syntype e.g. 'cotype' or 'type'). Therefore, according to the latest (fourth) edition of the International Code of Zoological Nomenclature (ICZN, 1999, Article 73.2),

> 'all the specimens of the type series are automatically syntypes if neither a holotype [Art. 72.1] nor a lectotype [Art. 74] has been fixed. When a nominal species-group taxon has syntypes, all have equal status in nomenclature as components of the name-bearing type'.

Dr Leendert Witte (Netherlands Institute of Applied Geoscience TNO – National Geological Survey, Utrecht) selected 24 specimens (syntypes) from the type series of *Ankumia bosqueti* van Veen, 1932 from the Bonnema/van Veen composite collection for the purpose of the present study. Van Veen probably combined the specimens of the earlier Bonnema collection with those of her collection (L. Witte, pers. comm.). Of the 24 specimens made available for study, 23 (10 LV, 9 RV, 4C) are mounted in five slides, and one specimen is a thin section. The available material includes four (probably five) of the specimens originally figured in her plate 24, together with 19 others selected from the type series. Their distribution on the slides is listed below. The position of a specimen on each slide is designated by a number after the oblique line.

Slide BvV-O.47, contains four primary type specimens illustrated by van Veen (1932, pl. 24), taken from two localities. Three came from Jekertal [found in Staring's 3rd bryozoan layer; Mc] viz., BvV-O.47/01, LV (pl. 24, figs 5–8); BvV-O.47/02, RV (pl. 24, figs 15–16); BvV-O.47/04, LV (pl. 24, figs 9–11). One came from Geulen [Md], BvV-O.47/03, C (pl. 24, figs 12–14). Van Veen (1932) regarded all the specimens figured on pl. 24 as females. The stratigraphic unit Mb, marked in pencil on the slide, is inconsistent with the units Mc and Md specified by van Veen (1932). It appears reasonable to accept the published information as correct.

Slide BvV-O.814 contains nine specimens (BvV-O.814/01 to /09) from Bemelen [1st bryozoan layer; Md], and Md is marked in pencil on the slide. In addition, a thin-sectioned specimen from the same locality was made available.

Slide BvV-O.1078 contains a very small specimen (C *Ankumia* unfigured; L=275; 3rd instar) from Jekerdal [3rd bryozoan layer; Mc].

Slide BvV-O.1286 contains eight specimens (BvV-O.1286/01 to /08) from Jekerdal [2nd bryozoan layer; Md on slide]. One specimen (BvV-O.1286/03), a RV of '*Ankumia*', is identical to the one illustrated by van Veen (pl. 24, figs 1–4), which she recorded in the plate explanation as coming from the 1st bryozoan layer in the Md of Bemelen.

Slide FO-93-012 contains one specimen (RV, '*Ankumia*' unfigured) taken from a cased borehole (Bor. 62A-233?) at 86–88 m in Cr3c Unit (Uhlenbroek, 1912) of the Gulpen Formation. It was donated to the Rijks Geologische Dienst, Haarlem, by J. Meessen, 14 January 1974. To my knowledge, *Ankumia* has not been found stratigraphically below Mc in the upper part of the Maastricht Formation. The presence of a specimen in the Gulpen Formation may be questioned, as it could be the result of down-hole contamination.

PREVIOUS WORK

Bonnema (1932) published illustrations, and an informal description, of specimens taken from his and van Veen's joint collection of Cretaceous ostracods of South Limburg, under the name *Cytherella* (?) n. sp. He noted (Bonnema, 1932, p. 289) that this species, 'to be described shortly by Miss van Veen', is related to the genus *Cytherella* by its posterior sex-dimorphism and R/L overlap. However, he thought that the species was remarkable because the valves, in his words (Bonnema, 1932, pp. 289, 290)

> … have concentric bands, somewhat like those observed in *Eridoconcha* from the Ordovician, Silurian and Devonian. Moreover, the carapace has a thick wall composed of two layers, the exterior of which decays much more easily than the interior, so that usually only the latter is still present. This occurs also in some species of *Cytherella*. Curiously enough, the carapace then greatly resembles that of an Ordovician *Bollia*.

After van Veen's (1932) work was published, Bonnema (1933) referred both the specimens with concentric bands and those which he compared to *Bollia*, to the type species of *Ankumia* (*A. bosqueti* van Veen, 1932).

As a prelude to the diagnosis of *Ankumia*, van Veen (1932, p. 359) provided a step-by-step explanation which led to the proposal of the new genus, and the fact that the plural personal pronoun 'we' was used in this part of the text suggests the influence of her mentor, Professor Bonnema. In order to understand the paradoxical nature of the genus, this explanation is paraphrased here. The material consisted of a large number of individual valves and a few carapaces which, on the basis of their form and sexual dimorphism, were first thought to have belonged to a new species of *Cytherella*. Because the valves possessed a lobe around the muscle scar field, which is a characteristic for *Bollia*, the new species was given the provisional (MS) name *Cytherella bolliaformis.*

The Bonnema/van Veen samples also included some valves with concentric bands which, to these authors, looked quite different from ostracod valves, and more closely resembled the shells of bivalves, or brachiopods. One such valve[1], placed under *Cytherella bolliaformis*, was externally covered in part by a $CaCO_3$ layer initially thought to be a post-mortem feature. Closer investigation demonstrated that this layer, where it was preserved best, showed concentric bands. The authors concluded (1) the $CaCO_3$ layer was not a post-mortem feature, but was a residual of a layer that originally covered the complete external parts of the shell, and (2) the shell shows two significant layers, of which the outer layer is, in many cases, lost.

On the basis of this examination van Veen recognized that this species was characterized by valves with two layers, and the inner layer clearly shows structures developed by an ostracod, related to *Cytherella*, *Cytherelloidea* and *Terquemia* species. She regarded the morphology of the outer layer of concentric bands extraordinary, but comparable to that described by Ulrich & Bassler (1923) in the diagnosis of their genus *Eridoconcha*. However, she noted some major morphological differences in the position of greatest width, and in the outline in end view. The position of greatest width is in the middle of the carapace in *Eridoconcha*, and in the posteroventral part of the carapace in her specimens. The end view of *Eridoconcha* is heart-shaped in outline, due to a prominent umbo, whereas the end view in her specimens, is triangular due to the broad ventral part of the carapace.

This preliminary discussion culminated in the diagnosis of the new genus *Ankumia* (van Veen, 1932, p. 360); translated here as:

> The shell is very thick walled, the right valve is larger than the left valve, the valves are built up by two different layers, of which the outer layer in many cases is lost by dissolution. The surface shows coarse, concentric rings; each valve is *Patella*-like, and after dissolution of the outer layer *Bollia*-like. The

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[1] No figures were cited, but her description indicates, at least to me, that the valve was illustrated, and it is recognized here as the syntype BvV-O47-04 (van Veen, 1932, pl. 24, figs 9–11; Pl. 1, fig. 1, this paper).

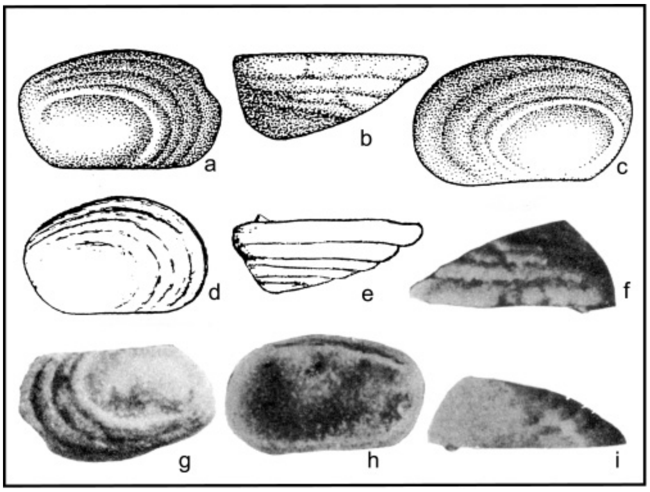


Fig. 3. Illustrations of *Ankumia bosqueti* van Veen, 1932: (**a–c**) adapted from Coryell (1963, pl. 13, figs 1–3); (**d**, **e**) reprinted by permission of Louisiana State University Press from Howe & Laurencich (1958, p. 49); (**f–i**) scanned images from Reyment (1961, p. Q388, figs 310, 3a, 3b, 3c, 3d). Reproduced with permission from van Veen (1932, pl. 24, figs 1, 2, 3, 16). Magnification c. × 38.

> sexual dimorphism resembles mostly *Cytherelloidea*, as females show two posterior cavities in each valve.

The interpretation of the surface sculpture of the valves of *Ankumia* has been a fundamental problem to the present day (Fig. 3). According to van Veen (1932) and subsequent authors (van den Bold, 1946; Howe & Laurencich, 1958; Reyment, 1961; Coryell, 1963) the valves consist of two layers.

1. An outer ('chalky') layer of coarse, concentric rings, which form an oblique cone, the apex of which lies in a postero-ventral position. Hence van Veen's comparison of its shape to that of the limpet gastropod *Patella*. The width of a complete carapace is equal or exceeds the length.
2. An inner layer exposed when the outer layer is lost (or 'completely dissolved'). In lateral outline it has a rounded anterior; an obliquely truncate posterior; convex dorsal margin, and a slightly concave ventral margin, which strongly resembles *Cytherella* with an external pit at the place of muscle attachment.

Therefore any attempt to elucidate the classificatory relationship of *Ankumia* requires a detailed study of its carapace morphology, and of the outer ('chalky') layer of coarse, concentric structures, in particular. The fact that all previous studies of this genus were made prior to the advent of Scanning Electron Microscope (SEM) techniques, now accepted as routinue by present-day standards, makes the need to revisit the genus all the more necessary.

Furthermore, the problem that besets the taxonomy of *Ankumia* is compounded by one of nomenclature because the provisional MS name *Cytherella bolliaformis*, which normally would be regarded as a *nomen nudum*, has been unwittingly made available by its entry in the *Catalogue of Ostracoda* (American Museum of Natural History, 1952–). The nomenclatural problem, and the measures taken to overcome it, are presented in more detail below.

METHODS

Fourteen specimens were selected for SEM examination. Of these, eight were of the typical '*Ankumia* shell type' (i.e. bearing an 'outer layer of coarse, concentric rings') and six were of the '*Cytherella* shell type' (i.e. 'inner layer with an external pit at the place of muscle attachment'). All measurements (L, H, W) were computed (to the nearest micrometre) directly from the SEM photographs (Table 1). The seven remaining specimens, all '*Cytherella* shell type', were measured (to the nearest 125 μm) under a binocular light microscope (Table 2). Examination of the SEM photographs suggested that the '*Ankumia* shell-type' specimens are actually retained moults of a cytherellid. This observation led me to study the ontogenetic growth of successive instars for each '*Ankumia* shell-type' specimen, by measuring the size (L) of instars for the ten individuals available. The ontogenetic methods that Shaver (1953) used to study the growth relationships and moult stage morphology of *Cytherella bullata* Alexander, 1932 (Late Cretaceous, Campanian, Texas, USA) have been followed, but on a more limited scale. The dimensions (L), the percentage increases for each instar (i.e. growth index, GI), and the percentages of the total L attained by each instar (%L) are shown in Tables 3 (Jekerdal) and 4 (Bemelen). These localities are treated separately because the possibility of ecophenotypic differences cannot be ruled out, even though the few specimens, on which the data are based, does not allow this to be demonstrated statistically.

The observation that the '*Ankumia* shell-type' specimens are retained moults of a cytherellid, requires a brief review of the subject of moult retention in Ostracoda generally.

Specimen	L	H	W	H/L	W/L	Remarks	Locality
O 47/01 LV	828	506	834	0.61	1.01	Pl. 2, figs 1–3; pl. 24, figs 5–8	Jekerdal, Mc
O 47/04 LV	748	444		0.59		Pl. 1, fig. 1; pl. 24, fig. 9	Jekerdal, Mc
O 814/01 LV	733	449		0.61		Pl. 2, figs 7, 8	Bemelen, Md
O 814/02 LV	377	225		0.60		Pl. 2, figs 6, 9, 12; 5th instar	Bemelen, Md
O 814/06 LV	656	404		0.62		Pl. 2, fig. 14	Bemelen, Md
O 1286/01 RV	796	465		0.58		Pl. 2, figs 4, 5	Jekerdal, Mc
O 1286/02 LV	796	477		0.60		Pl. 2, figs 10, 11	Jekerdal, Mc
O 1286/03 RV	768	468		0.61		Pl. 2, fig. 13; pl. 24, figs 1–4 ?	Bemelen ?, Md
FO 93-012 RV	417	267		0.64		instars 1–6; unfigured	
O 1078 C	275	192	200			instar 3; unfigured	Jekerdal, Mc

Table 1. Dimensions '*Ankumia* shell-type' specimens

Ankumia van Veen, 1932 (*nomen dubium*)

Specimen	L	H	W	H/L	W/L	Remarks	Locality
O 47/02 RVF	766	467		0.61		Pl. 1, fig. 4; pl. 24, figs 15, 16	Jekerdal, Mc
O 47/03 CF	680	408		0.60		Pl. 1, fig. 5; pl. 24, figs 12–14	Geulen, Md
O 814/03 LVM	625	350		0.56		Pl. 1, fig. 2	Bemelen, Md
O 814/04 RVM	667	375		0.56		Pl. 1, fig. 3	Bemelen, Md
O 814/05 RV	667	375		0.56			Bemelen, Md
O 814/07 RV	658	358		0.54			Bemelen, Md
O 814/08 LV	608	333		0.55		Fig. 5, 1	Bemelen, Md
O 814/09 RV	658	358		0.54		Fig. 5, 2	Bemelen, Md
O 1286/04 LV	625	375		0.60			Jekerdal, Mc
O 1286/05 LV	608	337		0.55			Jekerdal, Mc
O 1286/06 RV	667	367		0.55			Jekerdal, Mc
O 1286/07 CF	675	383	400	0.57	0.59		Jekerdal, Mc
O 1286/08 CM	700	400	358	0.57	0.51		Jekerdal, Mc

Table 2. Dimensions '*Cytherella* shell-type' specimens

Instar	O1286-1			O1286-2			O47/1			O47/4	O1078
	RV Lat Length	G.I	%L	LV Lat Length	G.I.	%L	LV Lat Length	G.I.	%L	LV Lat Length	
9 Adult	796	12.9	100	796	13.6	100	828	14	100		
8 A-1	705	13	88.6	701	14.7	88.1	726	16.2	87.7	747	
7 A-2	624	16	78.4	611	16.4	76.8	625	17.3	75.4	unmeasured	
6 A-3	538	13.7	67.6	525		66	533	15.9	64.4	unmeasured	
5 A-4	473	15.6	59.4				460	17.6	55.6	unmeasured	
4 A-5	409		51.4				391		47.2		
3 A-6											275
2 A-7											
1 A-8											

Table 3. Moult-stages of '*Ankumia* shell-type' specimens from Jekerdal

Instar	O1286-3			814-1		814-2			O814-6		
	RV Lat Length	G.I.	%L	LV Lat Length	%L	LV Lat Length	G.I.	%L	LV Lat Length	G.I.	%L
9 Adult	768	16.4	100	733[a]	100				656	14.7	100
8 A-1	660	13.8	86.4	unmeasured					572	13.9	87.2
7 A-2	580	16	74.4	unmeasured		483[a]	15.6		502	16.2	76.5
6 A-3	500	15.7	65.4	502	68.5	418[a]	10.9		432		65.9
5 A-4	432		60	434	59.2	377	14.6				
4 A-5				unmeasured		329	11.5				
3 A-6				unmeasured		295	11.7				
2 A-7				unmeasured		264	12.3				
1 A-8						235					

a, estimated.

Table 4. Moult-stages of '*Ankumia* shell-type' specimens from Bemelen

MOULT RETENTION IN OSTRACODA

Like other arthropods, ostracods go through a series of ecdyses in which the old exoskeleton is shed to allow for the growth of the body, from the nauplius stage to a fully developed adult. This moult cycle is a complex process controlled by several hormones. The timing in the release of the ecdysteroids (moulting hormones), or the peptide (moult-inhibiting) hormone, may interrupt the process of ecdysis (Greenaway, 1998, in Anderson, 1998). Such hormonal changes may be induced by environmental stimuli, temperature being of primary importance (Skinner, 1985; Aiken & Waddy, 1992). Recent experimental results from aquarium cultures of the isolated effect of temperature on the ontogenetic development of the ostracod *Krithe praetexta praetexta* (Sars) showed that the population structures move faster towards the later ontogenetic stages with higher temperature and vice versa (Majoran *et al.*, 2000). However, although the results of this aquarium experiment affected the stadia between instars, ecdysis still continued. To my knowledge, the phenomenon of ostracods continuing to moult without ecdysis has not been observed in the laboratory.

Moult retention in fossil and extant ostracod species is recognized where the earlier (or earliest) instar covers part of the external surface of the next instar, and the succession of instars forms a multilamellar carapace. The process is somewhat similar to the pharate ('cloaked') stage that occurs in insects, where a new cuticle is covered ('cloaked') by an old one that has not been discarded (Hales, 1998, in Anderson, 1998). Citations of ostracods that have retained their moults are rare because of the atypical (accidental, pathological) nature of the phenomenon. Moult retention in ostracods should not be confused with the 'nesting' (or 'cupping') of instars, where the oldest (i.e. largest) instar is in the external position, e.g. *Paraparchites humerosus* Ulrich & Bassler, 1906 as reported by Scott (1959); undetermined cypridids, as figured by Mandelstam & Schneider (1963, figs 43–45) and *Theriosynoecum conopium* Wakefield & Athersuch (1990, pl. 17 (38), figs 3, 4). This phenomenon is clearly a product of a post-mortem sedimentological process.

Among Recent ostracod species, true moult retention has been reported by Rome & Goreux (1960, p. 191) for *Candona candida* (Muller) and *Cypridopsis obesa* Sars, and by Sandberg & Plusquellec (1974, p. 15, pl. 4, figs 1, 4, 7), for *Cyprideis americana*, in one small valve marked by deep grooves and posterior distortion caused by the 'unintentional' retention of the valve of the last juvenile instar. The latter is attached along the posterior and posterodorsal margins.

In most cases, the retention of moults is usually fixed along the dorsal margin, especially with straight-hinged (palaeocopid) ostracods, e.g. *Ectodemites plummeri* from the Pennsylvanian of Illinois (Cooper, 1945), *Amphissites tener omphalotus* Becker, 1964 from the Late Devonian, Frasnian of Belgium (Becker, 1968), and the beyrichiacean species *Craspedobolbina* (*Mitrobeyrichia*) *clavata* (Kolmodin) from the Silurian of Gotland (Martinsson, 1962, fig. 24 A, B). Platycopid specimens of moults retained along the dorsal margin include the species *Hypotetragona aequitalis* Peterson, 1964 and *H. harrietensis* (Coryell & Malkin, 1936) from the Middle Devonian of Michigan (Peterson, 1964, pp. 863, 864).

Ordovician ostracods showing the phenomenon of moult retention were first described as *Primitia tolli* Bonnema, 1909, a species which Öpik (1935) referred to his proposed genus *Conchoprimitia*. The positions of earlier moults (retained or exfoliated) on the carapace of *Conchoprimitia tolli*, and related species, are marked by a distinct groove (Öpik, 1935). Hessland (1949) later restricted *Conchoprimitia* for non-sulcate species with two grooves, and introduced two genera to include species with one groove: *Conchoprimites* for those with a sulcus and *Conchoides* for those without sulcus. Henningsmoen (1953) and Jaanusson (1957), recognizing the multilamellar characteristics of these genera, placed both *Conchoprimites* and *Conchoides* into synonomy with *Conchoprimitia* Öpik 1935, because they regarded moult retention in these taxa as an 'accidental' or pathological phenomenon.

Apart from *Conchoprimitia*, all the examples cited above involve the retention of only one moult. Some two-grooved species of this genus indicate the retention of two or three moults. None appear to belong to the original concept of Adamczak (1961) Eridostraca, which included the multilamellar, relatively small-sized, carapaces of *Eridoconcha*, *Cryptophyllus* and *Aberroconcha*. The classification of Eridostraca is unresolved; this suprageneric taxon may represent a polyphyletic grouping of pathological ostracods and marine branchiopods (Jones, in Diaz Saravia & Jones, 1999).

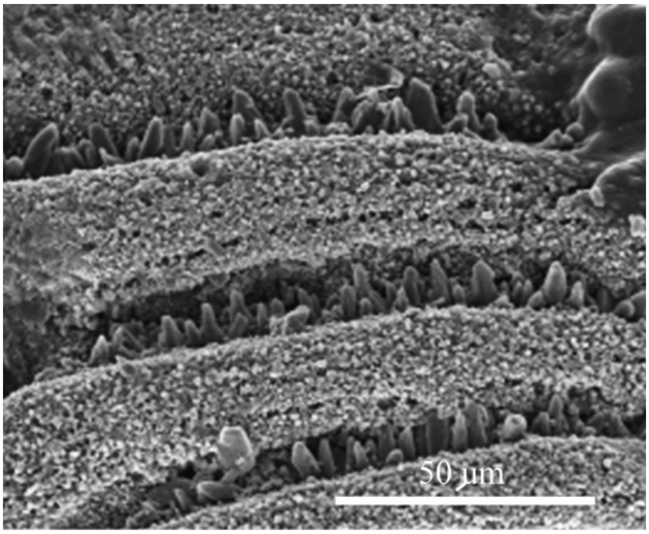


Fig. 4. The state of preservation of *Platella bosqueti* (van Veen, 1932). Diagenetic calcite crystals are visible in the gaps between the exposed parts (i.e. the bands) of successive instars, which in turn show borings possibly made by endolithic algae. Paralectotype C, a female LV, BvV-O47-01; from the Nekum Chalk Member of the Maastricht Formation, Jekerdal. Figured on Pl. 2, figs 1–3 (van Veen, 1932, pl. 24, figs 5–8).

MOULT STAGE MORPHOLOGY FOR *ANKUMIA*

The SEM examination of the eight '*Ankumia* shell-type' specimens illustrated in Plates 1 and 2 clearly demonstrates that they are retained moults of a single species of a cytherellid genus. The specimens from Jekerdal are generally larger than those from Bemelen. Tables 3 and 4 show the L measurements of the instars within each specimen that can be matched, by trial and error; they suggest a nine instar growth pattern (A-8 to A), characteristic for the Cytherellidae. An average growth index (GI) for 23 values, based on the increments between A-4 and A (the three values for the earlier moults were excluded as they only constituted one per instar) was calculated to be about 1.15. This growth index is slightly less than the *c.* 1.20 value observed by Shaver (1953) for *Cytherella bullata.* The point of retention is in the posteroventral area, where the width of the carapace rapidly increases throughout ontogeny. Therefore, the edges of each moult form a series of parallel lines along the ventral margin (Pl. 2, figs 6, 12) that superficially resembles those that define the edges of the lamellae along the dorsal margin of *Cryptophyllus* (Jones, 1962, pl. 1, fig. 8).

The largest specimen (O47-01), a LV (828 L), is presumed to be an adult. Instars A-1 to A-4 are retained; the latter bears the impression of the outline of the missing instar A-5, from which its L dimension can be measured (Pl. 2, fig. 1). The part of A-4 that was covered by the now exfoliated A-5 shows no trace of the punctae that are present on the exposed parts (i.e. the bands) of A-4 and successive instars (A-3 to A). It does bear, however, the impression of the lower half of the biserial pattern of stigmata that is typical of the AMS of Cytherellidae (Pl. 2, fig. 2). The position of the AMS would appear to correspond to one where it may have been present in the A-2 instar. Diagenetic calcite crystals are visible in the gaps between the exposed parts (i.e. the bands) of successive instars (Fig. 4). In ventral view the greatest width in the posterior half of the valve (417W) is estimated twice this value for the complete carapace (834W), and possibly more, with the additional thickness of the four missing juvenile instars (Pl. 2, fig. 3).

A smaller specimen (O47-04), a LV (747 L), presumably within the lower end of the observed size (L) range of the adult, show the remains of four retained moults (A-3 to A) at the posterior end (Pl. 1, fig. 1). In lateral view, the anterior and central surface of the carapace is closely comparable to that of *Cytherella*. A shallow, adductorial depression in the dorsocentral area contains a biserial AMS which is identical to that of Cytherellidae. The depression extends obliquely, slightly posterior and ventral to the AMS, and ends as a small pit (possibly marking the position of the AMS of an earlier instar). Punctae are distributed regularly around the dorsal and anterior borders of the valve, and locally, around the adductorial depression. As mentioned above, van Veen referred this specimen to her provisional MS species *Cytherella bolliaformis*, a name now available in the *Catalogue of Ostracoda*.

The smallest specimen (O 1078, unfigured), a C (275 L, 200W) with two early moults, is probably at the A-6 stage. It is extremely wide in comparison to H, a characteristic of juvenile cytherellids. Shaver's (1953) study of the moult stage morphology of *C. bullata* Alexander, 1932 demonstrated that the earliest instars are very wide, and the relative width generally decreases with age.

The earliest instars are also retained in a specimen (O 814-02) of a LV, but only the size (L) of the first five moults can be measured with confidence (Pl. 2, figs 6, 9, 12). A comparison of these dimensions with those of the later moults of the other specimens (Table 4) suggests that they belong to the A-8 to A-4 stages. The anterior end of the specimen is broken, and the size (L) of two larger retained moults (A-3; A-2) has been estimated. The first moult (A-8) is slightly larger (235 L) than that of the average size for *Cytherella bullata* (216 L, about 25% that of the female adult), and possesses a well-developed posteroventral swelling. Its surface is covered uniformly with distinct punctae (4–5 µm wide) which may have served as normal pore canals. The anterodorsal part of the moult is missing, and demonstrates a lack of punctae in that part of the next moult (A-7) that would have been covered, had the first moult been complete. Punctae are present on the exposed surface of the A-7 moult and of each successive moult. Views of the ventral margin show the edge of each successive moult forms a series of parallel lines (Pl. 2, figs 6, 12), the significance of which is discussed below. Internally, a low ridge somewhat obscured by diagenetic calcite, is present in the centrodorsal part of the valve. This structure is probably the expression of the adductorial pit, and possibly the movement of its site during ontogeny. Traces of a contact list can be seen along the free margin.

Internal examination of an adult specimen (O 1286-01) of a RV revealed a contact groove in the posterior half (Pl. 2, fig. 5); however, this feature is destroyed by strong recrystallization in the anterior half. Neither this specimen, nor any other specimen examined (Fig. 5), appear to possess the tooth and socket structure at the ends of the hinge line, described by van Veen (1932) and mentioned in Reyment's (1961) diagnosis of *Ankumia*.

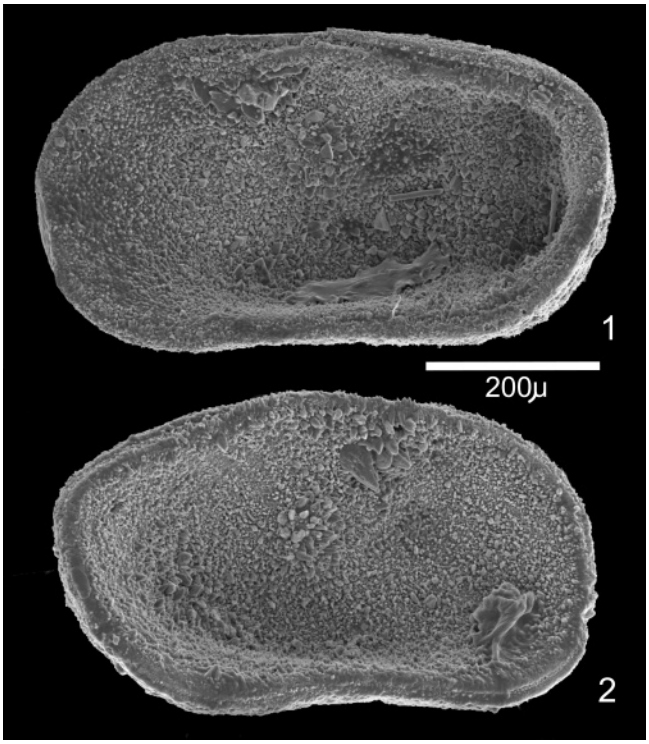


Fig. 5. *Platella bosqueti* (van Veen, 1932) from Bemelen. Internal views of syntypes. **1**, Female right valve O814-09; **2**, male left valve O814-08; magnification × 110.

DISCUSSION

It is a useful exercise to consider changes in carapace shape (dorsal and lateral outline) and other features of successive moults during a normal ontogeny, with ecdysis, and an abnormal one, without ecdysis. Shaver's (1953) study of the moult stage morphology of *Cytherella bullata* Alexander, 1932 showed that the earliest instars, in lateral view, are relatively higher in the anterior, with the line of greatest height 'moving' posteriorly with age. In dorsal view, they are relatively wider in the posterior, with the line of greatest width 'moving' anteriorly with age. The adult female reverses this trend. Such changes in the shape of successive moults would have occurred after ecdysis and before complete calcification of the cuticle (intermoult stage). The '*Cytherella* shell-type' syntypes within the *Ankumia* type series (Pl. 1, figs 2–5) show a carapace shape (dorsal and lateral outline) consistent with those of adult specimens of other species of *Cytherella*. In lateral outline they have a rounded anterior; an obliquely truncate posterior; convex dorsal margin, and a slightly concave ventral margin, with an external pit at the place of muscle attachment. It is of interest that of the thirteen '*Cytherella* shell-type' specimens examined, ten were disassociated valves, and three were carapaces.

In the case of the '*Ankumia* shell-type' syntypes within the *Ankumia* type series (Pl. 1, fig. 1; Pl. 2, figs 1–14), the absence of ecdysis appears to inhibit changes in shape. The shape of the posteroventral swelling of each juvenile moult is constrained by the shape of the previous one. As the size of the posteroventral swelling becomes progressively larger in successive moults, the shape of the feature remains much the same. It forms the heavy, cone-shaped structure described by van Veen (1932) as '*Patella*-

like', and by Howe & Laurencich (1958) as 'oblique'. The additional weight, after the calcification of each retained moult, would have compounded the stress-levels of the pathogenic animal. It is of interest that nine of the ten '*Ankumia* shell-type' specimens examined were disassociated valves; only one carapace (O 1078) was found, and this was a small specimen (275 L), probably of instar 3.

The series of parallel lines formed by the edges of each moult resemble those that define the edges of the lamellae of the eridostracan *Cryptophyllus*. Such a comparison is superficial because in '*Ankumia* shell-type' specimens the parallel lines are on the ventral margin, whereas in *Cryptophyllus* they are along the dorsum. An '*Ankumia* shell-type' specimen can easily be misinterpreted if it is figured, in lateral view, with the ventral margin uppermost (e.g. Reyment, 1961, fig. 310. 3a). In this case, the posteroventral swelling is superficially accepted as a dorsal umbo. For this reason, the comparison with *Cryptophyllus* suggested by Bless & Massa (1982) is invalid.

NOMENCLATURAL PROBLEM AND SOLUTION

At present, the availability of the name *Cytherella bolliaformis*, obfuscates any attempt to revise the species *Ankumia bosqueti*. It is clear that van Veen's concept of *Ankumia bosqueti* included those specimens she *first thought* belonged to a separate species of *Cytherella*. Unfortunately, she allowed what presumably was a provisional MS name (*Cytherella bolliaformis*) to appear in print. Normally, the name would be regarded as a *nomen nudum*, but its entry in the *Catalogue of Ostracoda* has made it available. I discussed this problem, and its consequent ramifications with Professor W. D. L. Ride (Chairman, Editorial Committees 3rd and 4th Editions International Code of Zoological Nomenclature) who kindly prepared the following statement:

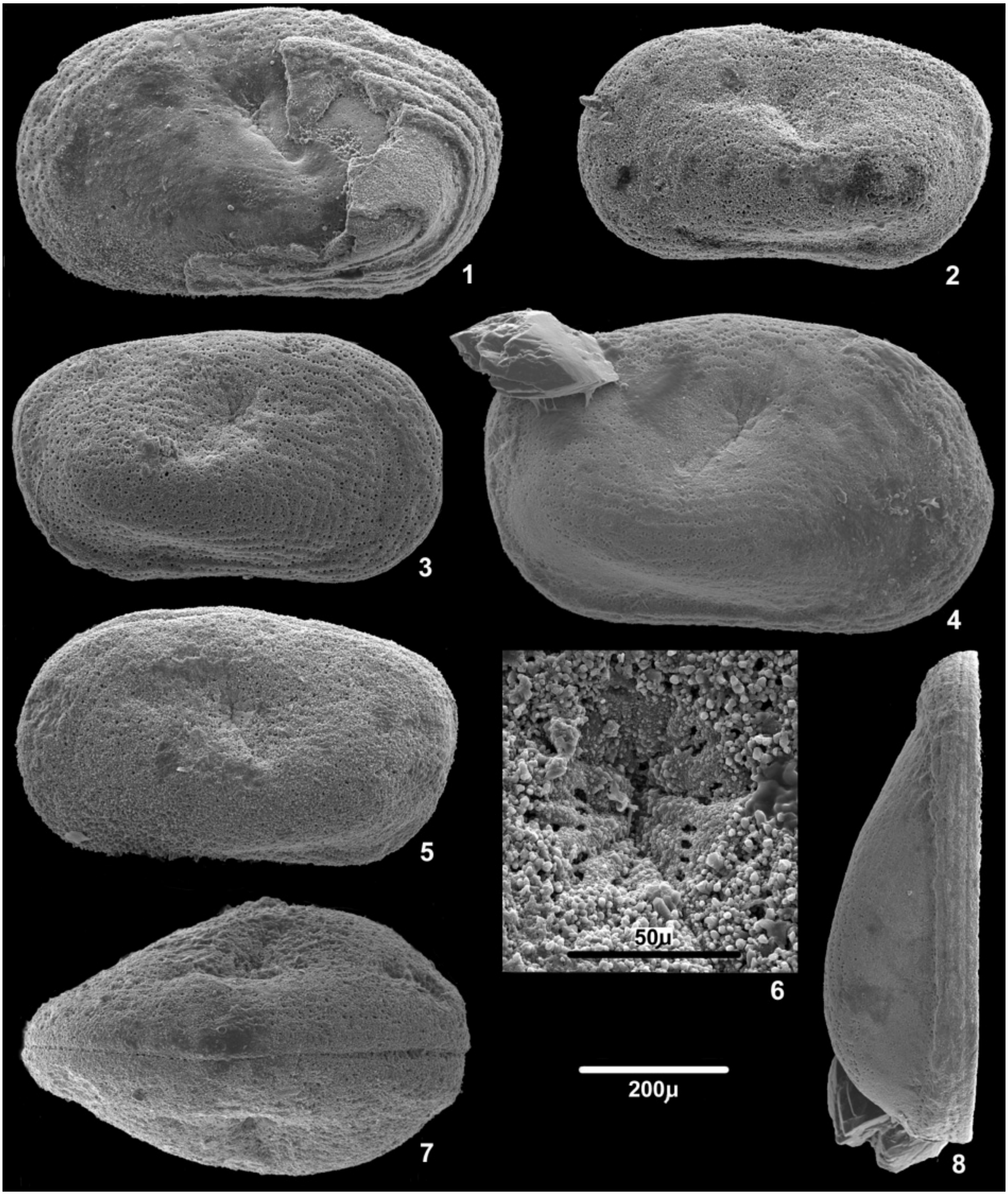
> *Nomenclatural considerations*: The name *Cytherella bolliaformis* was made available in an anonymous and undated entry in the *Catalogue of Ostracoda* (1952 –). The description is contained in two paragraphs by van Veen (1932, p. 360) and form part of her discussion of the new genus *Ankumia* which she proposed in the 1932 work.
>
> From van Veen's (1932) work it is clear that she did not intend to establish the name *bolliaformis.* However, the editors of the *Catalogue of Ostracoda* clearly recognize the taxon as valid. The introduction to the *Catalogue* and its *Supplements* state that it "extracts the original type descriptions of new taxa, stipulated emendations; and new names for homonyms … Description and diagnosis are given verbatim, except for editorial changes as follows: … (4) to remove inapplicable content." No mention is made of the inclusion of *nomina nuda* or otherwise unavailable names. Thus it is clear that the anonymous author(s) recognized the taxon omitting the explanatory part of van Veen's text describing the new species *Ankumia bosqueti* van Veen, 1932, in which she placed the specimens which she previously had regarded as '*bolliaformis*' (presumably in MS).
>
> Those specimens had been figured earlier in 1932 by J. H. Bonnema, as "*Cytherella (?)*n. sp. figs 4, 5." A reference is given by van Veen (1932), to Bonnema's earlier citation in the synonymy of *A bosqueti* (including citation of the numbered figures) – so there is no doubt that all three works refer to the same specimens and the same "taxon".
>
> Although the authorship of the work in which the name *Cytherella bolliaformis* was published post-1950 is anonymous and might be thought to be unavailable on that account (ICZN Art. 14), because the name, and the conditions that make it available are attributed wholly to van Veen, the name is not anonymous and is available from that work (ICZN Art.50.1.1).
>
> *Possible nomenclatural actions*: If on taxonomic grounds it is considered that the action of the anonymous authors of the *Catalogue* in recognizing the taxon (and its name *C. bolliaformis*) is not justified, and the original intention of van Veen should be confirmed, the following alternative remedies are available:
>
> 1. An application might be made to the International Commission on Zoological Nomenclature for the suppression of the name *Cytherella bolliaformis* van Veen (1952) for the purposes of synonymy and homonymy. The name would be totally unavailable for zoological nomenclature. The generic name *Ankumia* (type species *A. bosqueti)* would be unaffected.
>
> 2. Since the syntypes of *Cytherella bolliaformis* are within the syntypical series of *Ankumia bosqueti* van Veen, 1932, an identical specimen from the syntypes for both names might be selected as the lectotype of both. Both names would then be objective synonyms and *C. bolliaformis,* the junior synonym would be permanently invalid. The genus *Ankumia* would remain available if it were decided on taxonomic grounds that *Ankumia bosqueti* (as defined by its lectotype) is generically separable from the type species of *Cytherella.*
>
> Of the alternatives, alternative 2 is suggested as being the better because it will occasion no delay in reaching finality because it requires only publication by a reviser to take effect. Alternative 1 would require the Commission to take action under the Plenary Power with mandatory requirements of publication by the Commission as well as periods for discussion and voting.

Accepting alternative 2, I have selected an identical specimen from the syntypes for both names *Ankumia bosqueti* van Veen, 1932, and *Cytherella bolliaformis* van Veen, 1952 as the lectotype of both. This specimen is a female LV with retained moults, BvV-O47-04, figured here as Plate 1, fig. 1, and originally figured by van Veen (1932), as pl. 24, figs 9–11. As both names would now be objective synonyms, *C. bolliaformis*, the junior synonym, would be rendered permanently invalid.

SYSTEMATIC DESCRIPTION

Superfamily **Cytherelloidea** Sars, 1866
Family **Cytherellidae** Sars, 1866
Genus *Platella* Coryell & Fields, 1937

Type species. *Platella gatunensis* Coryell & Fields, 1937, p. 3, by original designation.



Explanation of Plate 1.

figs 1–8. *Platella bosqueti* (van Veen, 1932). Type material of *Ankumia bosqueti* van Veen, 1932 from Bemelen (figs 2, 3), Jekerdal (figs 1, 4) and Geulen (figs 5, 6). **fig. 1.** Female left valve O 47-04 lectotype selected here for both *Ankumia bosqueti* van Veen, 1932 and *Cytherella bolliaformis* van Veen, 1952 (pl. 24, figs 9–11, van Veen, 1932). **fig. 2.** Male left valve O814-03. **fig. 3.** Male right valve O814-04. **figs 4, 8.** Female right valve O47-02 paralectotype A (pl. 24, figs 15, 16, van Veen, 1932), external and ventral views. **figs 5, 6, 7.** Female carapace O47-03 paralectotype B (pl. 24, figs 12–14, van Veen, 1932), external left view, adductor muscle scar and dorsal views.

Remarks. The genus *Platella* was proposed for cytherellids ornamented by strong pits covering the entire shell surface. Some ostracod specialists (e.g. van Morkhoven, 1962; van den Bold, 1967) have challenged the validity of *Platella*, placing it into synonymy with *Cytherella* Jones, 1849. Others (e.g. Munsey, 1953; Marlière, 1958; Puri, 1960; Bate, 1963, 1972;

Dingle, 1981; Weaver, 1982; Ainsworth, 1986) have sought to retain the genus. McKenzie *et al.* (1991, p. 138) also chose to recognize *Platella* 'as ecologically useful since the characteristic surface punctation indicates relatively warm ambient temperatures'. In this paper, I regard the characteristics of the cytherellid-like specimens of *Ankumia bouqueti* – subquadrate lateral outline, shallow adductorial sulcus, and above all, the configuration of the pits (arranged in rows, subparallel to the free margin, and depressed between fine striae) – as indicating a closer relationship to *Platella*, than to either *Cytherella* Jones, 1849 and *Cytherelloidea* Alexander, 1929.

Platella bosqueti (van Veen, 1932)

(Pl. 1, figs 1–8; Pl. 2, figs 1–14; Fig. 5)

1932 *Cytherella?* sp. nov. Bonnema: 290, figs 2–6.
1932 *Cytherella bolliaformis* van Veen: 359, no figure designated (*nomen nudum*).
1932 *Ankumia bosqueti* van Veen: 360, pl. 24, figs 1–18, pl. 25, figs 1–14.
1933 *Ankumia bosqueti* Bonnema: 35, 36, figs 32, 33.
1946 *Ankumia bosqueti* van den Bold: 20.
1952 *Cytherella bolliaformis* van Veen: *Catalogue of Ostracoda* (name made available).
1958 *Ankumia bosqueti* Howe & Laurencich: 49, 2 figs.
1961 *Ankumia bosqueti* Reyment: Q383, fig. 310.3a–d.
1963 *Ankumia bosqueti* Coryell: 148, 149.
1958 *non Cytherelloidea bosqueti* (Marsson, 1880) Howe & Laurencich: 261

Revised diagnosis. A species of *Platella* with an oblique sulcus and a swollen, ventral lobe extending from the posterior, at the position of the greatest width, obliquely to the anteroventral margin of the valve. Surface covered with fine inosculating low ridges and parallel rows of fine punctae. Pathological individuals with retained moults develop a wedge-shaped outline in dorsal view.

Lectotype. The female LV with retained moults (BvV-O47-04) figured by van Veen (1932, p. 360) in pl. 24, figs 9–11, taken from the Bonnema/van Veen collection, Utrecht; lectotype here designated, and re-figured in Plate 1, fig. 1. This specimen is also the lectotype of *Cytherella bolliaformis* van Veen, 1932 (objective synonym) here designated, and refigured in Plate 1, fig. 1.

Figured paralectotypes. A. Female RV, BvV-O47-02; Plate 1, figs 4, 8 (van Veen, 1932, pl. 24, figs 15, 16); **B.** Female carapace, BvV-O47-03; Plate 1, figs 5–7 (van Veen, 1932, pl. 24, figs 12–14); **C.** Female LV, BvV-O47-01; Plate 2, figs 1–3 (van Veen, 1932, pl. 24, figs 5–8); **D.** Female RV, BvV-O1286-03; Plate 2, fig. 13 (van Veen, 1932, pl. 24, figs 1–4; Bonnema, 1932, figs 2–4; 1933, fig. 33)**,** taken from the Bonnema/van Veen collection, Utrecht.

Material studied. 24 syntypes from the type-series (Bonnema/van Veen collection).

Type locality and horizon. All three localities cited by van Veen (1932) in the Maastricht region: Bemelen, Geulem and Jekertal, South Limburg, The Netherlands, constitute the type locality (ICZN, 1999, Article 73.2.3). The upper part of the Maastricht Formation: the Nekum Chalk Member (Mc) at Jekertal, and the Meerssen Chalk Member (Md) at Bemelen and Geulem. Late Maastrichtian, Late Cretaceous. [K, L and M foraminiferal Zones of Hokfer (1966): *Micula murus* nannofossil Zone of Verbeek (1977)]. The locality of the lectotype and paralectotypes A and C is Jekertal, the locality of paralectotype B is Geulem, and paralectotype D comes from Bemelem.

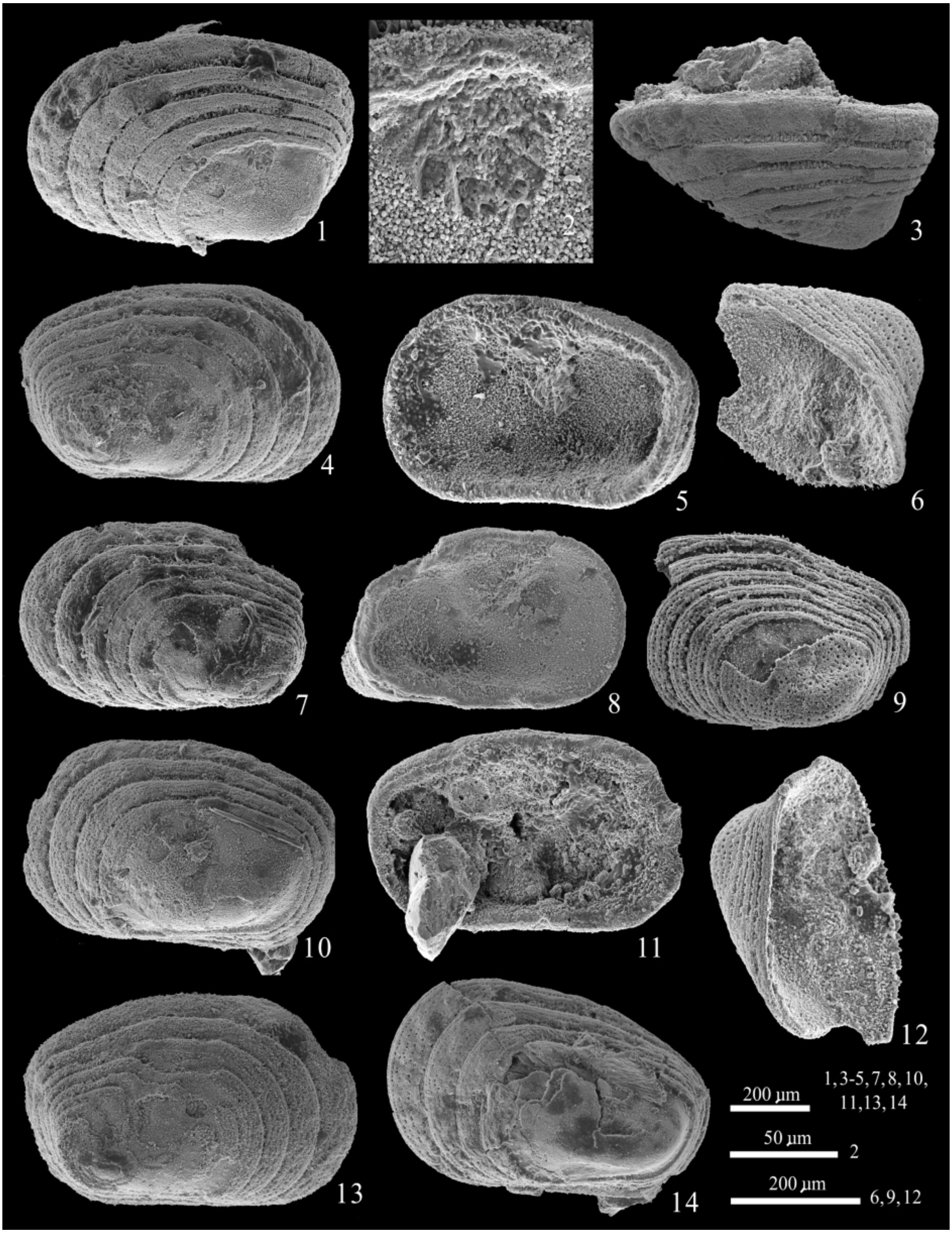
Description. Outline subquadrate in lateral view; greatest height in anterior half (male), and in mid-length position (female), dorsal margin gently convex, anterior extremity slightly below mid-height position, ventral margin concave (more marked in males), posterior margin obliquely truncated with extremity above mid-height position. RV slightly larger than LV, with slight stragular overlap on the anterodorsal margin. Adductorial depression shallow, obliquely extending from dorsocentral area, posteroventrally. AMS pattern biserial, a double column of stigmata. Ventral lobe, swollen, extending from the posterior, at the position of the greatest width, obliquely to the anteroventral margin of the valve. Shell thick, surface covered with fine inosculating low ridges, and parallel rows of fine punctae (normal pore canals). In dorsal view, outline pear-shaped, with greatest width in the posterior half of carapace; wedge-shaped in pathological individuals with retained moults.

Internally, the larger RV appears to have a continuous holosolenic contact groove, which receives the continuous marginal selvage of the smaller LV. Hinge structure adont, bipartite (*sensu* Adamczak, 1968, p. 91), with straight posterior part.

Dimensions. Tables 1 and 2 list the dimensions of '*Ankumia* shell-type' and '*Cytherella* shell-type' specimens, respectively.

Remarks. The growth of diagenetic calcite tends to obscure the internal surface of the valves, especially in the areas of high relief, e.g. in the expression of the adductorial sulcus in the centrodorsal part. Therefore, internal features are difficult to interpret. With these apprehensions, I suggest (1) the hinge structure shows no evidence cardinal teeth, and (2) females appear to possess two posterior internal brood cavities (Fig. 5, 1) as in the genus *Cytherelloidea*. Externally, two types of punctae are recognized. (1) those that are ± circular, 3 to 4 µm in diameter, and arranged in parallel rows between the inosculating low ridges, which are interpreted as the openings of normal pore canals, and (2) those that have no definite shape, 4 to 5 µm wide, not organized in a particular pattern, and are even present on the stigmata of the AMS; which may be of diagenetic origin, or borings by endolithic algae (see Bathurst, 1975, p. 382). Neither type of punctae are filled with micrite.

Comparisons. *Platella bosqueti* (van Veen, 1932) appears morphologically close to *Cytherella foveata* van Veen, 1932 (p. 341), a species referred by Marlière (1958) to the genus *Platella,* which is present at all three *P. bosqueti* localities. It can also be compared to *Cytherelloidea*? *dubia* van Veen, 1932 (p. 355) from the Jekertal (Mc) locality. From van Veen's illustrations, these



Explanation of Plate 2.

figs 1–14. *Platella bosqueti* (van Veen, 1932). Type material of *Ankumia bosqueti* van Veen, 1932 from Bemelen (figs 6–14) and Jekerdal (figs 1–5). **figs 1–3.** Left valve, O 47-01, paralectotype C external view (pl. 24, fig. 5, van Veen, 1932), adductor muscle scar, ventral view (pl. 24, fig. 6, van Veen, 1932). **figs 4, 5.** Right valve, O 1286-1 external, internal view. **figs 6, 9, 12.** Left valve O 814-2 posteroventral, external, ventral view. **figs 7, 8.** Left valve O 814-01, external view, internal view. **figs 10, 11.** Left valve O 1286-02, external view, internal view. **fig. 13.** Right valve, O1286-03 paralectotype D (pl. 24, fig. 1, van Veen, 1932). **fig. 14.** Left valve O814-06.

species are much thinner than *Platella bosqueti*, and a closer comparison would require an examination of their syntypes, which is beyond the scope of this paper. McKenzie *et al.* (1991) pointed out that van Veen's figures of *Ankumia* lack the wide marginal flange of *Geelongella*, and are not as compressed as their genus. *Platella bosqueti* possesses a prominent ventral lobe which gives the posterior, ventral and anterior parts of the valve margin a superfical flange-like appearance, that is not comparable to the distinctive *Geelongella* flange. Moreover, *Platella bosqueti* is considerably more obese than the two known species of *Geelongella,* and possesses punctation over the entire surface of the valves, that is characteristic of the genus, but not present in *Geelongella.*

PALAEOECOLOGY

Palaeoecological interpretation of van Veen's (1932) ostracod faunas in the upper part of the Maastricht Formation can be attempted firstly, by extrapolating what is presently known of the ecology of living ostracods, and secondly, by deducing the depositional environment from the associated fauna, the preservation of the fossil ostracods, the sedimentology and geochemistry of the rocks themselves.

In the first case, Kornicker's (1963) study of the environmental factors of water depth, salinity, substrate and temperature that influenced the distribution of cytherellids living in the Bimini Islands, Bahamas, is particularly relevant for the palaeoecological interpretation of their Cretaceous ancestors. Furthermore, many of the palaeoecological inferences drawn from the Upper Maastricht Formation (see below) suggest that the Bahaman location is a comparable scenario.

The Recent Bahaman analogue, when extrapolated into latest Maastrichtian time of the type Maastricht region, suggests that *Platella bosqueti* and the other cytherellid species described by van Veen (1932) – *P. foveata*, *Cytherella contracta*, *C. plana*, *C. sulcata*, *C. ubaghsi*, *Cytherelloidea biloculata*, *C. binkhorsti*, *C. spinigera* and *C.*? *dubia* – lived in a marginal, shallow, warm, (sub)tropical sea. They crawled on, and burrowed into, a substrate of bioclastic fine-grained sediment, oolite, coral rock, and hardground. The water depth was less than 17 m deep, and most species lived at depths less than 6 m deep, at temperatures between 24°C and 32°C. The association of the cytherellids with a rich bairdiid fauna in the Nekum Chalk Member at Jekertal (ten cytherellid species, twelve bairdiid species), and in the Meerssen Chalk Member at Belemen (eight cytherellid species, four bairdiid species) is indicative of a salinity in the upper part of the euhaline range (35.85–39.40‰). However, the Meerssen Chalk Member at Geulem contained six cytherellid species and no bairdiids, which is possibly indicative of a hyperhaline (40.00–46.50‰) environment.

The validity of the above Bahaman/Maastricht comparison depends upon the taphonomy of the cytherellid fauna of the Nekum and Meerssen Chalk Members, that is the degree to which the fauna represents a biocoenose. Important evidence to determine the amount of post-mortem transport of the fossil ostracods is to be found in their state of preservation, the associated fauna, the sedimentology and geochemistry. Although the '*Ankumia*' material examined here consists of only 23 specimens collected from three localities, and the composite sample is subject to collecting bias, some generalizations can still be made. The fact that most (83%) of the specimens are disarticulated valves indicates a high energy facies, and the rarity of juveniles suggests that these were winnowed from the original biocoenose.

Bless *et al.* (*in* Robaszynski *et al.*, 1985), in their synthesis of the palaeoecology of the Maastricht Formation, noted that a major change from Boreal to Tethyan influences took place at the end of the Mb (=Emael Member; Fig. 2) just before the deposition of the Nekum Chalk Member. This change is marked by a rapid increase in fossil diversity (both in numbers and taxa), the first appearance of characteristic Tethyan larger foraminiferids (e.g. *Siderolites*, *Orbitoides*), the serpulid *Sclerostyla mosae* and the first rudist bivalves. These authors (*in* Robaszynski *et al.*, 1985, fig. 34) linked this palaeobiogeographical change with a relative decrease in water depth, a shift from offshore to nearshore deposition, a relative increase in the water temperature, a relative higher level of water energy, and a distinct increase in the number of hardgrounds. Bless *et al.* (*in* Robaszynski *et al.*, 1985, p. 57) regarded the abundance of broken fossils, and of hermatypic corals, bryozoans, serpulids and calcareous algae as indicative of a very shallow marine shelf with a maximum depth of less than about 50 m, i.e. the inner part of the sublittoral zone. Bless (*in* Robaszynski *et al.*, 1985) has suggested that the predominance of ornamented ostracods in the upper part of the Maastricht Formation (his Ostracod Ecozone 13) indicates, in relative terms, a high energy facies in a shallow environment.

More details of the palaeoecology of the Nekum and Meerssen Chalk Members of the Maastricht Formation are contained in more recent contributions to the knowledge of the K/T boundary section (*in* Brinkhuis & Smit, 1996). Particular emphasis has been placed on the Meerssen Chalk Member, which is closer to the K/T boundary. Roep & Smit (1996) have studied the sedimentology of this unit, which represents an infill of palaeorelief by high stand carbonate sands, deposited by episodic storm-wave activity in about 20–40 m water depth. In a microfacies analysis of the unit, Zijlstra *et al.* (1996) recognize seven (tempestite) cycles deposited during precession periods of, on average, about 20 ka. These periods were characterized by variations of storm energy and of deposition rate. Sr isotope stratigraphy (Vonhof & Smit, 1996) suggest that the 20 m of calcarenites between the Laumont and the Berg en Terblijt horizons were deposited in 200 ka before the K/T boundary event.

With the K/T boundary positioned at the Berg en Terblijt Horizon, it is tempting to speculate that the presence of the pathological *Platella bosqueti* in the latest Maastrichtian is somehow related to K/T boundary events. The process of ecdysis would have been interrupted by hormonal changes induced by some unknown environmental stimuli in the south Limburg area during the last 200 ka of Cretaceous time. This was the time of massive eruptions of the Deccan Trap basalt lavas, and mantle degassing would have released many trace elements that would have been injurious to the extant biota. It is possible that the presence of such an element would have triggered hormonal change(s) in *Platella bosqueti*, as in any other susceptible species with a genetic abnormality.

Ankumia van Veen, 1932 (*nomen dubium*)

CONCLUSIONS

1. The genus *Ankumia* (type species *A. bosqueti* van Veen, 1932) is demonstrably a pathological case of moult retention within a single cytherellid species,and is therefore, discarded as an artificial (invalid) taxon.
2. The same lectotype has been selected for both *Ankumia bosqueti* van Veen, 1932 and *Cytherella bolliaformis* van Veen, 1952, because this action does not violate the original concept of the type series. Thus, both names are objective synonyms.
3. As *Cytherella bolliaformis* van Veen, 1952 is the junior synonym, *Ankumia bosqueti* van Veen, 1932 becomes the valid species, which is here referred to the genus *Platella*.
4. The new combination, *Platella bosqueti* (van Veen, 1932), is now based on the original concept of the type series, and includes both retained, and single adult, moults.
5. *Platella bosqueti* lived during the last 200 ka of Cretaceous time in ecological conditions similar to those of the cytherellids that live in the Bimini Island area at the present day.
6. As the genus *Ankumia* has remained monotypic (for 70 years), the type species being confined to the Late Maastrichtian type area of South Limburg, the 'taxon' appears to be a microfacies product that is unique to the local sedimentary and environmental events of that region.
7. As the process of ecdysis would have been interrupted by hormonal changes induced by some unknown environmental stimuli, it is tempting to speculate that the presence of this pathological ostracod taxon in the Latest Maastrichtian is somehow related to the K/T boundary events.

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