Sedimentology (1990) **37**, 287–301

In situ accretion mechanism of concavo-convex lacustrine oncoids ('swallow nests') from the Oligocene of the Mainz Basin, Rhineland, FRG

REINHOLD R. LEINFELDER* *and* CHRISTOPH HARTKOPF-FRÖDER†

**Institut für Geologie und Paläontologie, Universität Stuttgart, Böblinger Str. 72, D-7000 Stuttgart, and*
†Geologisches Landesamt Nordrhein-Westfalen, Postfach 1080, D-4150 Krefeld, FRG

ABSTRACT

Oligocene oncoids from the lacustrine Süßwasserschichten of the Mainz Basin exhibit a pustular surface and a characteristic cavity on their undersides, which gave rise to their designation as 'swallow nests'. Oncoids grew *in situ*, under low-energy conditions during a pause in sedimentation. Three features indicate that they were never overturned: (1) oncoids can be placed in a stable position on a smooth surface; (2) laminae, which are mostly concentric around the entire oncoids, display polar thickenings on the upper side during all growth stages of oncoids; (3) the depression is always situated on the stable side of oncoids. Development of this cavity is favoured by unionid shells, in the stable position, serving as oncoid nuclei, but occurs also under flat nuclei. It is interpreted as a product of reduced growth of cyanobacteria due to oligophotic conditions, on a fine-grained substrate, and is considered as diagnostic of the *in situ* growth of oncoids.

Oncoid cortices are mainly formed by a *Scytonema*-like cyanobacterium, whose carbonaceous organic remnants are occasionally preserved. Growth stages of individual oncoids were image-processed and compared by means of shape parameters. Due to optimum growth conditions, cyanobacteria try to occupy the entire available space; hence, oncoids tend to achieve a spherical form even during *in situ* growth. Renewed background sedimentation triggered the formation of pustular surfaces and finally caused the cessation of cyanobacterial growth.

INTRODUCTION

Both marine and freshwater oncoids are common throughout the geological record, yet the mechanism of their growth and, hence, their meaning for palaeoenvironmental reconstruction is still far from understood. According to the classical interpretation, oncoids are considered to be indicative of a certain level of water turbulence, necessary for at least occasional overturning, in order to enable phototrophic microbial growth to occur on all sides of oncoids (e.g. Logan, Rezak & Ginsburg, 1964; Radwańsky & Szulczewski, 1966; Dahanayake, 1977, 1983; Flügel, 1978). However, starting with Pia (1933), some authors considered an *in situ* growth of oncoids more likely. *In situ* growth of modern oncoids has been occasionally reported from lakes, lake margins and sabkhas (Jones & Wilkinson, 1978; Casanova, 1985; Dahanayake, Gerdes & Krumbein, 1985), as well as from rivers or streams (Golubic & Fischer, 1975; Leinfelder & Hartkopf, 1988; Hartkopf-Fröder, Hiss & Leinfelder, 1989). Freytet & Plaziat (1965) presented a fossil example of *in situ* growth of entire oncoids.

However, such observations were widely ignored by the majority of authors dealing with palaeoenvironmental reconstructions. Even in low-energy settings oncoid growth commonly continues to be explained by at least occasional overturning of oncoids, be it through high-energy events or through flipping over by swimming or vagile organisms (e.g. Ott, 1980; Ratcliffe, 1988; Toomey, Mitchel & Lowenstein, 1988).

Oncoids from the Oligocene Mainz Basin exhibit a set of distinct, regular yet polar features, among which a concave depression or groove is most characteristic

and, together with their pustular surface, led to the historical name 'swallow nests' ('Schwalbennester', Wagner, 1954; Rothausen & Sonne, 1984) (Figs 1 & 2).

Similar oncoids can be found in many fossil and modern sites (e.g. some of the specimens in Pia, 1933; Freytet & Plaziat, 1965; Bijma & Boekschoten, 1985). In our opinion, such oncoid shapes cannot be explained by the widely held view of growth under agitation. By means of qualitative and quantitative description, evaluation of geometric growth patterns, microstructural analysis and considerations of the sedimentological context, we propose an *in situ* growth mechanism which could be used to interpret ancient oncoid occurrences. Morphometric description of oncoids using digital image processing is used to facilitate comparison with other oncoid occurrences.

GEOLOGICAL FRAMEWORK

The Mainz Basin is the western offshoot of the Upper Rhine Graben and represents a faulted block bordered by the Rhenish Massif in the North, the Upper Palaeozoic and Triassic of the Nahe region in the West and the western main fault of the Rhine Graben in the East. In relation to the Rhine Graben, the area represents an elevated block since the late Oligocene. Deposition of Tertiary sediments within the basin is largely controlled by tectonic movements in the Upper Rhine Graben and the basin itself.

Lacustrine Eocene clays constitute the oldest known Tertiary sediments in this region. They unconformably overlie Lower Permian deposits. The first transgression took place in the early Oligocene and culminated with the deposition of the marine middle Oligocene fine-grained Rupelton Formation in the basin centre and the Lower Meeressand Formation at the nearshore areas. Due to an increasing isolation from the North Sea Basin and the Paratethys, salinity decreased gradually, finally resulting in a freshwater environment. This last phase of the first transgressive sequence is represented by the upper Oligocene Süßwasserschichten.

After a short period of depositional stillstand, and even partial erosion, a second transgression reached the Mainz Basin, leading to the deposition of upper Oligocene and lower/middle Miocene limestones and marls. As a result of several small-scale marine ingressions, salinity oscillated from brackish-marine to freshwater. The second transgressive cycle terminates in the middle Miocene. From the upper Miocene onward the area is characterized by fluviatile sedimentation. A detailed account on the geology and stratigraphy of the Mainz Basin is given by Rothausen & Sonne (1984).

The oncoids described in this paper occur in the upper part of the lacustrine Süßwasserschichten. As no outcrops exist, little is known about the spatial facies distribution of the approximately 40 m thick unit. The beds consist mainly of greenish grey to light bluish grey marls with brownish mottles and a few, thin limestone horizons. Locally, fine sands and milky vein quartz gravels are intercalated, transported into the basin by rivers draining the Rhenish Massif. The fauna (e.g. freshwater ostracods and very rare molluscs) and flora (e.g. the freshwater green alga *Pediastrum*, and a rich charophyte flora of fairly low diversity) indicate a freshwater environment, a conclusion which is also supported by isotope data (Rothe, Hoefs & Sonne, 1974; Rothausen & Sonne, 1984). Marls and micritic limestones with abundant charophytes suggest low-energy accumulation in shallow lakes, which locally even dried up as evidenced by root horizons and rare black pebbles. A late Oligocene (Chattian/early Arvernian) age is deduced from some isolated micromammalian remains washed into a lake (Bahlo & Tobien, 1982).

Apparently, oncoid distribution is restricted to one horizon with three main occurrences (Fig. 1), which were mapped by Wagner (1935, 1954). An attempt to excavate the oncoid horizon was only partially successful, the oncoid layer was found at a depth of

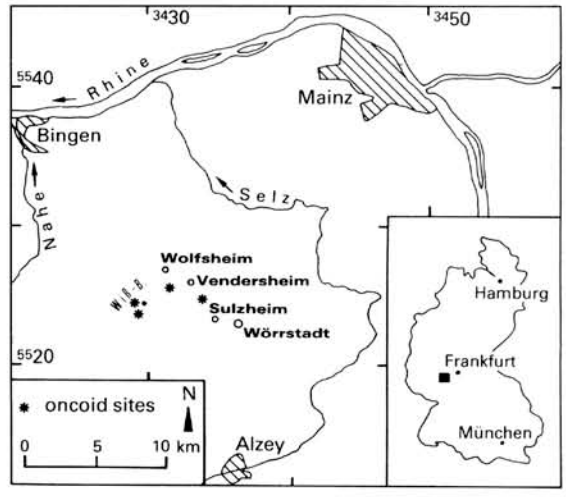

Fig. 1. Location of the Mainz Basin and occurrences of the 'swallow-nest' freshwater oncoids from the Oligocene Süßwasserschichten.

1 m. The whitish to (rarely) brownish oncoids are rather densely packed within the green, marly matrix. The greenish marls above and below the oncoid layer contain only scattered specimens of ostracods. Marly sediment which is preserved in pockets and voids between oncoid pustules (see below) contains very frequent smooth-shelled ostracods and rare, strongly recrystallized charophyte oogonia in addition to silt-sized detrital quartz. However, the oncoids were partially turned and imbricated as a result of solifluction which is widespread in the Mainz Basin. Nevertheless, in several dry drillings (up to a depth of 7 m), the oncoid horizon was found in a presumably undisturbed position. Although an auger with only 70 mm diameter was used, the 'swallow-nests' were detected in each borehole. This indicates that the dense population of oncoids is a primary feature and not artificially produced by solifluction.

MATERIALS AND METHODS

A representative sample of 120 oncoids, which covered the entire spectrum of oncoid sizes (between 7 and 88 mm, average 40 mm) and shapes, was studied. The length, breadth and height were measured. Thereafter, the oncoids were cut in their length/height plane and outline drawings of the nucleus and 3–4 characteristic concentric laminae were made. The upper, lower and lateral cortex thicknesses for each growth stage, and the depth of the concave depression were measured. By means of digital image processing, the perimeter and area for each growth stage was calculated, both for the entire oncoids and for their upper and lower cortices (Fig. 2).

The numerical perimeter and areal measurements were used to determine the 'relative sphericity' of entire oncoids and respective growth stages. To determine the 'relative sphericity' we use the D-parameter ('structural density'), defined by Schmidt-Kittler (1984, 1986) as

$$D = C^2/(4\pi \times A),$$

where C is the perimeter of the area and A the area. The 'structural density' is of paramount importance for quantifying and comparing the complicated occlusion pattern of fossil mammal teeth (op. cit.), but can be generally used for quantitative comparison of the shape of irregular, yet similar areas. D gives a relation of the measured irregularly shaped area with the area of a circle defined by the same perimeter as the irregular area. Hence, the more similar the processed area is to a circle, the closer D is to 1. D values were calculated for all discriminated growth stages of the oncoids. D values are similar to a theoretical approach to measure sphericity of gravels given by Wadell (1932) and hence are labelled here as 'relative sphericity'.

The 'relative sphericity' is dependent only on the area and perimeter of an outline. It does not express polar growth of an area. To quantify actual polar growth on the upper side of oncoids, we define a hemisphericity index H for individual growth stages ($H1$–$H4$):

$$H = A\,\mathrm{hem}/A_s,$$

where A_s is the measured area of an upper cortex growth stage, A hem is the area of a half-circle defined by a radius which equals the height of the measured upper cortex area (CT_s), i.e. $A\,\mathrm{hem} = 1/2\,CT_s^2\,\pi$. With this we obtain

$$H = (CT_s^2\,\pi)/(2\,A_s),$$

where $H = 1$ indicates (two-dimensional) hemispherical growth, $H > 1$ indicates columnar growth, and $H < 1$ indicates pillow-like growth.

Measurements were evaluated with the aid of a spread sheet computer program. Some important numerical values are given in Table 1; D and H measurements are shown in Figs 8 and 9.

Further investigations include microfabric and microfloral analysis, based on, partly EDTA-etched,

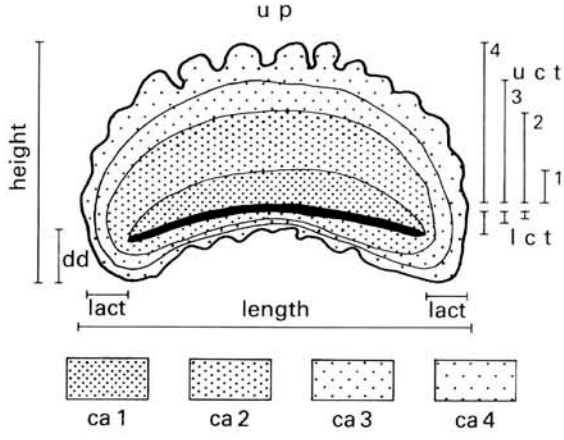

Fig. 2. Schematic diagram of a typical 'swallow nest' with designation of performed length, outline and area measurements and definition of descriptive terms: lact, lct, uct = lateral, lower and upper cortex thickness, respectively; dd = depth of basal depression; ca 1, 2, 3, 4 = cortex areas: growth stage 1 is represented by ca 1, growth stage 2 by ca 1 + 2, etc.

thin-section studies and measurements of light intensities underneath the oncoids.

OBSERVATIONS

General construction of oncoids

Despite the large number of specimens examined, and despite their occurrence at different sites, the oncoids are of fairly uniform morphology (Table 1; Figs 3 and 4): 75% exhibit the concave depression or groove. Nuclei were almost always composed of a single unionid valve whose convex side, with the exception of one oncoid, points to the upper side of the oncoid, which is also the side exhibiting the thicker cortex. In all cases, unionid shells were found dissolved by diagenesis, leaving an open or a partly to completely collapsed biomould. No fragmented shells were found. Breaking open the oncoids reveals the fine bivalve growth lines as an imprint pattern on the nucleus mould wall; hence, shells did not suffer from any abrasion. Despite dissolution of the aragonitic shell, the curved plane corresponding to the position of a collapsed unionid mould can be always detected (Figs 4 and 5). Two oncoids exhibit a nucleus composed of a straight branch fragment of calcified wood, one had a gastropod shell as core, two exhibited mud pebble cores and very few specimens lacked a distinct nucleus altogether.

The nucleus is always situated in the lower portion of the oncoid, i.e. the upper cortices are always much thicker than the lower ones (up to three times thicker). The lower cortex is extremely thin or lacking in the centre of the oncoid, normally resulting in the development of the typical groove or depression. The lateral cortices are slightly thicker than the lower ones (Table 1).

With very few exceptions (such as small specimens) oncoids can be placed in a stable position on a smooth surface. This also applies to those 25% of oncoids which do not exhibit a basal depression or hollow.

Except for a few specimens (all <10–20 mm in diameter) oncoids exhibit a rough warty surface. These small domes and mamillae may cause bizarre protrusions or, within the basal hollow may occasionally hang like microstalactites from the roof.

Geometry and fabric on oncoid cortices

The fabric of the oncoid cortices is very uniform throughout all the samples examined. Cortices consist of alternating light and dark laminae normally 0·5–1 mm (rarely up to 2 mm) thick (Fig. 5). In the outer part of the cortex, which is commonly lighter than the rest, lamination is less distinct. Lamination results mainly from varying contents of preserved organic matter.

The geometric arrangement of the laminae is extremely similar in almost all specimens. The first laminae are developed only on the upper side of the oncoids. Consecutive laminae coat the entire oncoid but are always thicker on the upper side. This results in a more or less hemispherical doming of the oncoid's shape. However, the ratios of upper versus lower

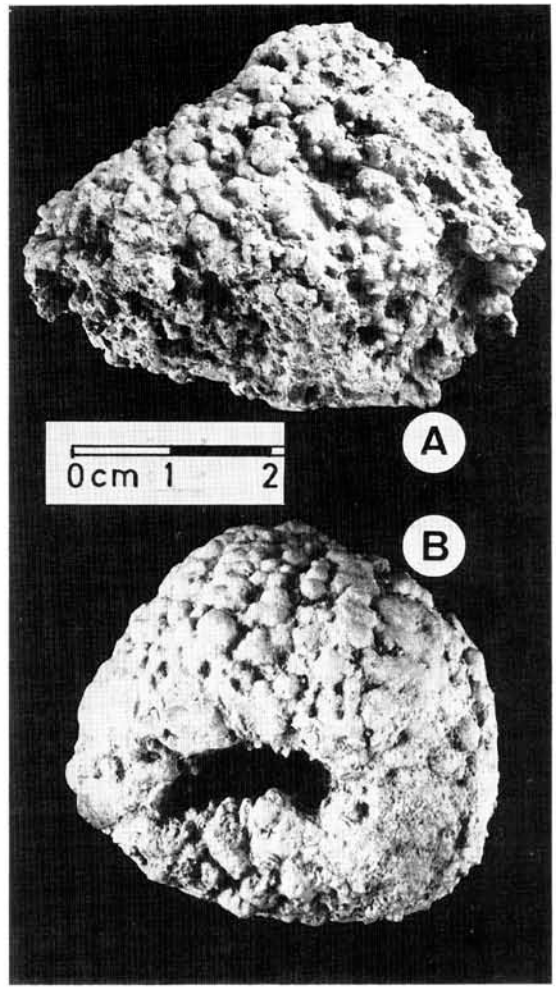

Fig. 3. Typical appearance of the 'swallow-nest' oncoids. (A) Lateral view of pustular surface; (B) basal view, displaying the characteristic concave groove.

Table 1. Linear measurements (mm) of 'swallow-nest' oncoids.

	Length	Breadth	Height	Length v. breadth	Breadth v. height	Length v. height	Depth of groove	UC thickness	LC thickness	Lat. C thickness	UC v. LC thickness	UC v. Lat. C thickness
Min.	7·0	7·0	4·5	1·00	0·48	0·65	1·00	6·65	0	1·40	1·07	0·90
Max.	88·0	56·0	49·5	2·51	2·44	3·33	15·50	32·60	15·70	19·50	10·00	4·50
Mean	40·4	28·7	24·3	1·39	1·21	1·68	5·50	15·20	5·27	8·40	3·58	1·87
SD	15·3	10·3	9·3	0·22	0·27	0·41	3·03	5·54	3·23	3·31	2·00	0·68
	38%	36%	37%	16%	23%	25%	55%	36%	61%	39%	56%	36%
n	114	112	101	110	99	100	85	88	83	88	81	88

UC = upper cortex, LC = lower cortex, Lat. C = lateral cortex.
Note polarity of all oncoid cortices and occurrence of a concave depression or groove in 75% of measured oncoids.

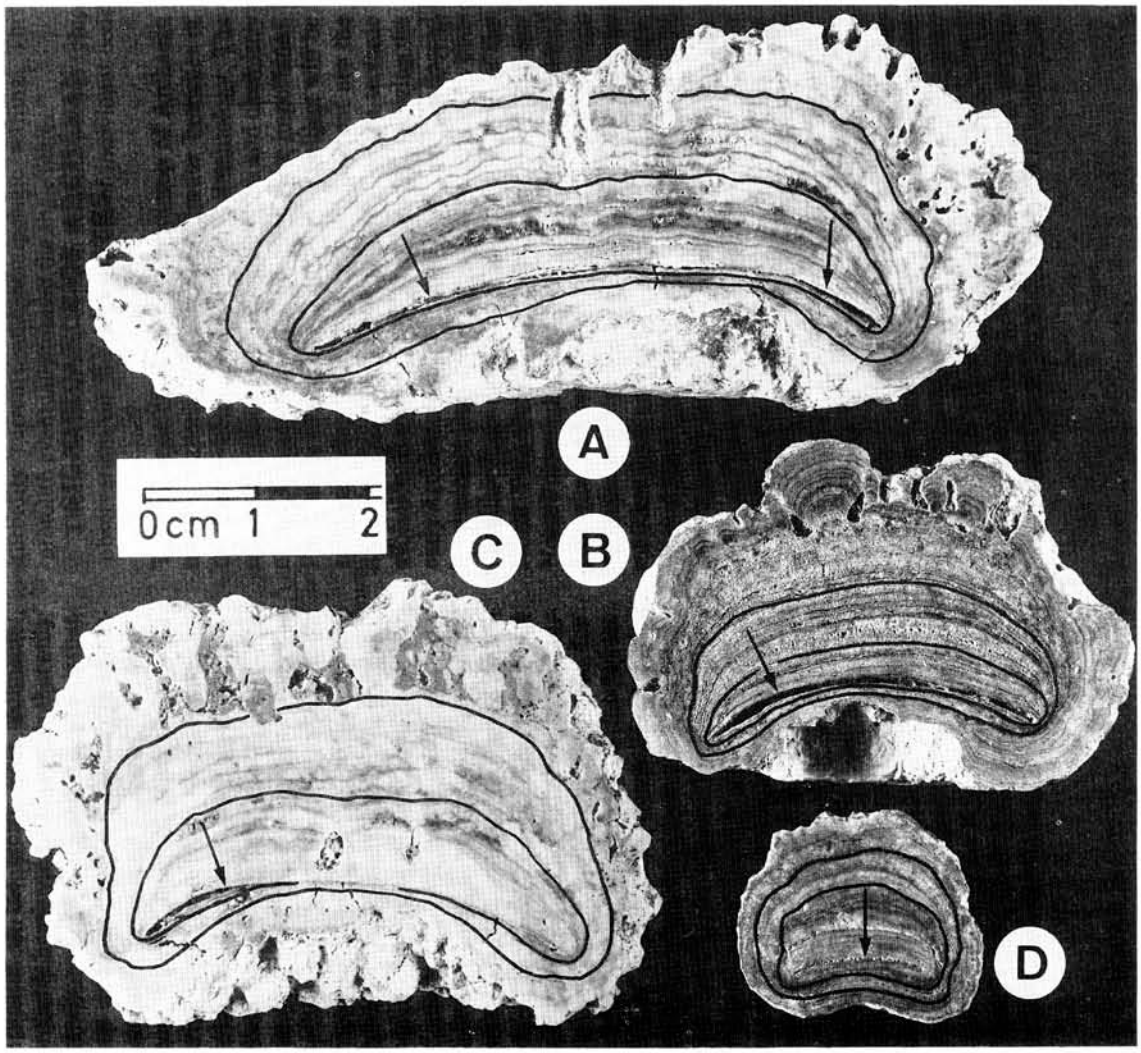

Fig. 4. Set of 'swallow-nest' oncoids cut in their length–height plane and line drawings outlining growth stages. Black arrows: position of leached freshwater bivalve nuclei. The specimens shown span the shape variation of oncoids: (A) laterally accentuated growth; (B), (C) normal shape; (D) small specimen.

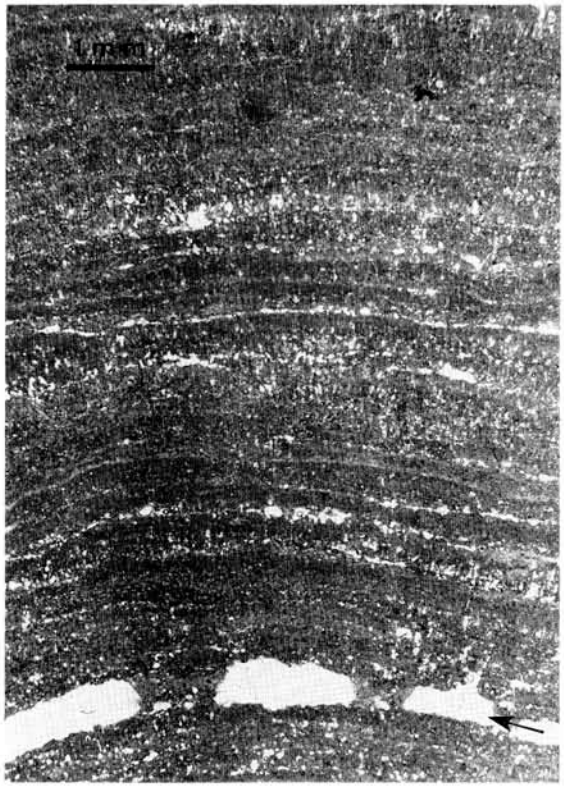

Fig. 5. Thin section of part of a 'swallow nest'. Note biomould of dissolved, aragonite-shelled bivalve nucleus (arrow) and regular cortex fabric composed of organic-rich, tangential laminae and thicker layers structured by fine radial voids.

cortex thicknesses and ratios of upper versus lower cortex areas decrease in most cases towards older growth stages, so that oncoids become increasingly equidimensional (see below). During most of the growth of the oncoids, laminae are smooth or only slightly crinkled. Columnar growth occurs only in a very few cases within inner laminae.

During the last stages of oncoid growth, this pattern changes completely. The outer few millimetres of the cortex are mostly characterized by dome-shaped, colloform and even branching colloform growth of laminae, leading to the above described mamillate surface (Fig. 6).

The trend in geometry change during oncoid growth can be quantified by the performed morphometric measurements: ratios of both upper versus lower cortex thicknesses and cortex areas for subsequent growth stages reveal that the polar character of growth was constantly diminishing to increase again during the last growth stage (Fig. 7). *D* and *H* values for consecutive growth stages of oncoids (Figs 8 and 9) monitor the degree of sphericity of oncoids: at the start of growth sphericity was very low (mean *D* value 2·44, mean *H* value 0·2), due to almost exclusive flat pillow-like upwards growth. In almost all samples sphericity then increases continuously (*D* mean = 1·53; *H* mean = 0·35), which is related to the development of a hemispherical structure. The later growth stages exhibit two trends. Most oncoids increase their sphericity slightly (both *D* and *H* values closer to 1) despite the formation of a pustular surface whose structure alone would raise the *D* value. This increase in structural density is, however, overcompensated by increasing equidimensionality, resulting from a lowering of the rate of upward growth. One third of the oncoids, however, exhibit an increase in the structural density, caused by continuing high upwards growth or by the development of a highly pustular surface. Eighty percent of oncoids showing a final decrease in *D* are larger than 42 mm, whereas *c.* 60% of those exhibiting an increase in *D* are shorter than 42 mm. In larger specimens where four different growth stages could be measured, 75% show an increase in *D*. This indicates that only after a certain equidimension in shape is reached, oncoids tend to intensify the development of their pustular outline.

Radially orientated vugs up to 8 mm long and 4 mm wide commonly cross-cut the regular oncoid fabric. Sharp truncation of pre-existing laminae indicates boring activity, possibly from boring polychaete worms. Ostracod-harbouring marl is occasionally preserved as infill of borings (Fig. 4). Borings are more frequent in the outer, mamillate parts of oncoids than further inside. Boreholes are commonly situated between warts and truncate their margins. However, upward doming of laminae within the warts clearly evidences that wart formation was due to algal/cyanobacterial growth and not an effect of bioerosion by borers. Broad domal growth of laminae occurs very rarely in interior parts of oncoids. Laminae in warts on the lower surface of oncoids may have truncated margins along an irregular surface. These truncations are not due to boring activity but might possibly indicate dissolution due to CO_2 production during decay of organic material.

A typical feature of the 'swallow-nest' oncoids is the numerous irregularly elongate, radially arranged voids, about 0·5 mm long, 0·1–0·3 mm wide, which are not filled by later cements. They give the oncoids a somewhat spongy, highly porous appearance and seem to be caused by the decay of cyanobacterial

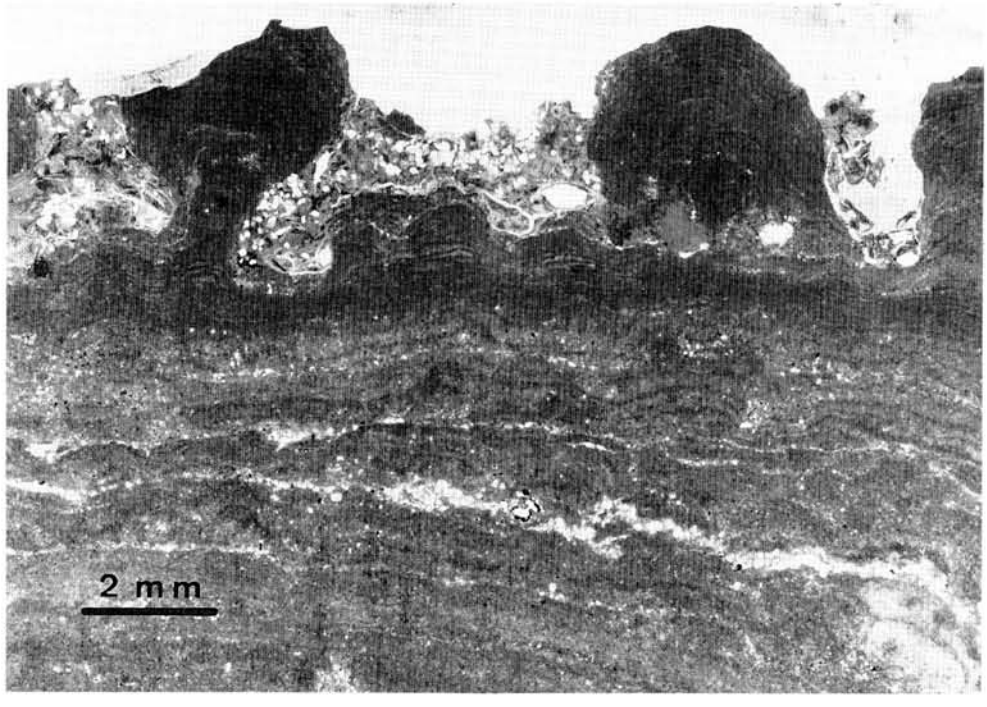

Fig. 6. Thin section of pustules formed on outer oncoid cortex. Pustules are formed by colloform growth of cortex laminae. Quartz silt and ostracod shells are stored between pustules.

filament bundles (see below). Less frequent are laminae-parallel, tangential voids up to 30 mm long and 0·5 mm wide. In some cases they can, with interruptions, be traced around the entire oncoid, resulting in partial to almost complete *in situ* detachment of parts of the oncoid cortex. In a few cases, tangential voids of different laminae are interconnected by irregular radial cracks. Tangential voids and cracks are partly or completely filled with irregular, mostly dog-tooth-like, phreatic cements. Hence, this interrelated void–crack system seems to be caused by desiccation due to subaerial exposure, fabric-bound dissolution and later recementation.

Cyanobacterial structures

The oncoids obviously represent microbialites, i.e. they are derived from algal or cyanobacterial activity. Besides the occurrence of smooth to crinkled to colloform microbial laminae, a variety of radial 'filaments' (*sensu* Krumbein, 1977) is preserved. These fine, up to 10 μm thick, spar-filled radial tubules commonly branch outward, which is characteristic for growth of cyanobacteria and many other algae. Commonly, neighbouring radial tubules coalesce to pass into the above-mentioned irregular radial voids, which give the oncoids their spongy character and might be interpreted as fenestrae derived from oxidation of organic matter.

Under the SEM both radial and tangential calcified tubules are visible, measuring about 5–8 μm in diameter (Fig. 10). These tubules are lined by bladed to equant, rhomb-shaped micritic to microsparitic crystals, which are coarsest along the direct lineation of the tubule (presumed filament mould).

Dissolving the carbonate of an uncovered thin-section with a 2·5% EDTA-solution reveals remainders of cyanobacterial filaments, preserved as carbonaceous organic matter, in their original arrangement (Fig. 11). However, dissolving a cortex fragment of the outer part of the oncoids mostly yields abundant material of hyphae of fungi. Their Recent and hence endolithic character is obvious from the good cellular preservation of the mycelium and the fungal vesicles. From this organic felt it is rather difficult to discern the fossil cyanobacterial material, due to similarities

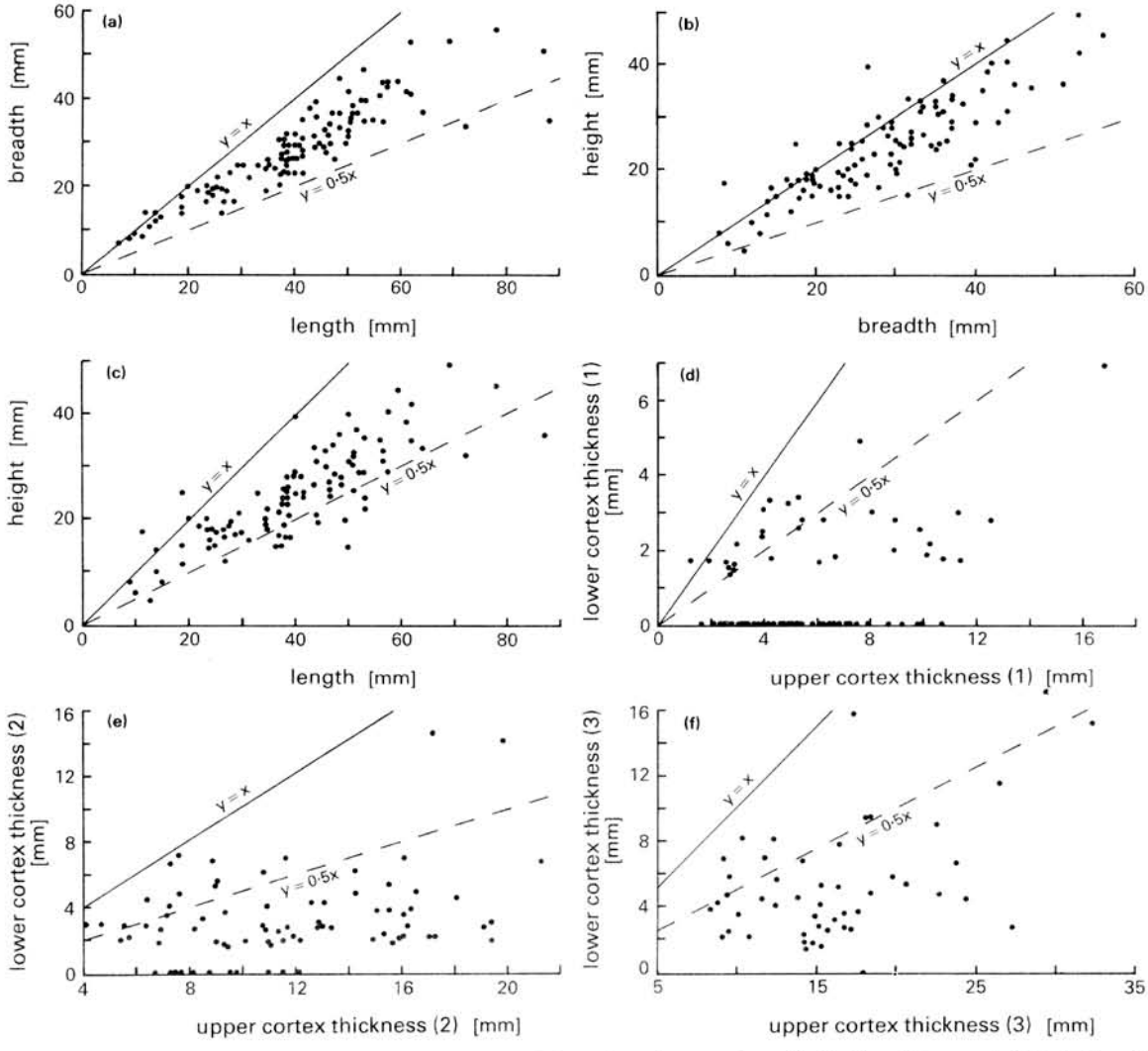

Fig. 7. Plots of linear measurements of 'swallow-nest' oncoids. (a) Length versus breadth, (b) breadth versus height, (c) length versus height. The similarities of ratios indicate that oncoids represent one single population. (d–f) Upper versus lower cortex thicknesses for oncoids with three growth stages discriminated. Many oncoids first exhibit only upward growth (d); dominance of upward growth is characteristic during all growth stages (1–3), yet this eccentricity decreases towards older growth stages. cf. Fig. 2 for definition of terms.

in both size and shape of fragments of modern fungal hyphae and fossil cyanobacterial filaments.

Cyanobacterial filaments from etched thin sections are best preserved in the middle to inner part of oncoid cortices. They commonly show branching and slightly undulous growth. Layers displaying radially orientated filaments alternate with laminae composed of partly interwoven, tangentially growing tubules. The latter laminae are thinner and much more densely packed with cyanobacterial filaments than the radially structured ones and correspond to the described dark cortical layers. Radial filaments clearly grow out from the tangential ones, occasionally by paired branchings. Apart from dominance of radial growth, orientation of filaments is fairly irregular; undulous, flagellate and obliquely growing threads occur as well (Fig. 11). Filament diameters measured from etched thin sections mostly range between (5–) 7·5–8·5 (–10) μm; at

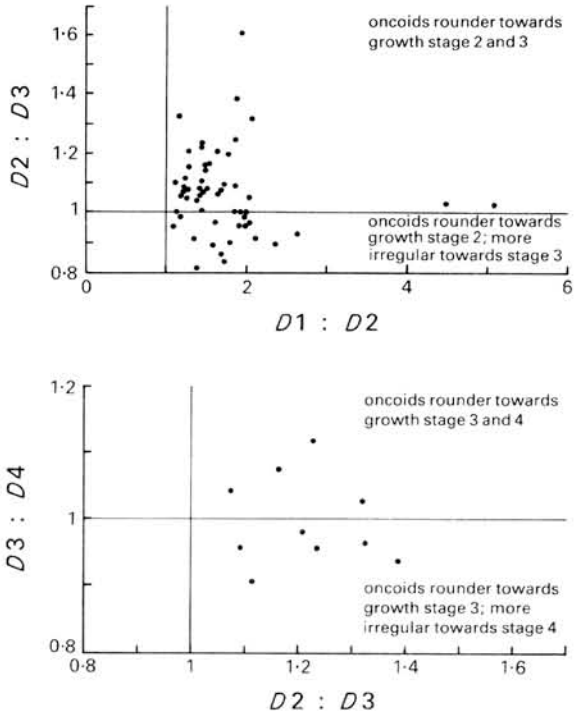

Fig. 8. Ratios of relative sphericity (D values) for all growth stages of oncoids, calculated from image-processed measurements of perimeter and areas of oncoid growth stages. A ratio of two consecutive D values >1 indicates increase in relative sphericity (cf. Schmidt-Kittler, 1984). All oncoids increase in roundness towards growth stage 2; then one-third of oncoids show a slight decrease in relative sphericity due to more pillow-like growth and pustule formation. For further explanation see text.

places where branching takes place, values up to 16 μm may occur.

Similar diameters and flagellate growth, both in the radially orientated and prostrate filaments, suggest a monospecific origin for the preserved tubules. Reticulate filament arrangement (horizontal versus radial threads), the frequent, often paired branchings, the filament diameters and the overall micritic structure of the laminae are comparable with the extant cyanobacterium *Scytonema*, although exact taxonomic determination is not possible due to the lack of preserved diagnostic features such as the existence of heterocysts and the 'false' nature of the branchings (cf. Golubic, 1976a, b; Monty, 1976; Pentecost, 1984). Reticulate filament arrangement in freshwater oncoids is also commonly ascribed to the oscillatorian cyanobacterium *Schizothrix calcicola*, which exhibits more irregular and much finer filaments than the material described here (cf. Riding & Voronova, 1982; Pentecost, 1984).

DISCUSSION

Both their peculiar shape and their occurence within clearly low-energy sediments precludes an interpretation of the 'swallow nests' as being created by frequent or occasional turnover. Even interpreting them as being initially stable (growth on upper surface), and then commonly overturned (middle cortex), then again stable (outer cortex) is improbable, since laminae (even in the outermost layers) are developed without interruptions around the entire cortex and always show growth polarity. Only very few, small oncoids, which do no exhibit unionid cores, show some slightly discordant laminae.

The unionid nucleus

As mentioned earlier, all unionid nuclei are positioned concave downside, thus defining the stable oncoid side as the lower and the side with prominent cyanobacterial growth as the upper side.

This implies the following.

(a) All unionid values were positioned concave downwards before encrustation.

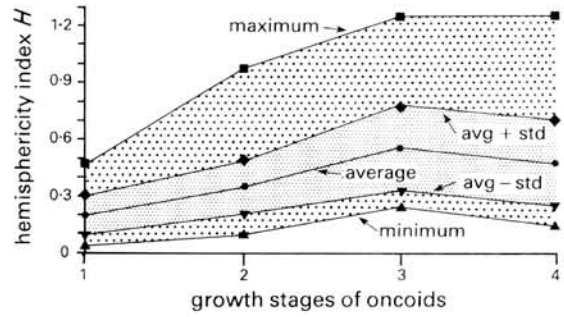

Fig. 9. Hemisphericity of the upper cortical part of oncoids as expressed by the shape parameter H. H values are calculated from image-processed line drawings and defined as the ratio of the area of an upper cortex growth stage versus the area of a half circle exhibiting a radius equal to the vertical thickness of the upper cortex growth stage. Below 1, an increase in H indicates a growth tendency towards a hemispherical shape; a decrease in H indicates return to a more pillow-like form (caused by pronounced lateral growth). Values greater than 1 mirror dominant upwards growth of the entire oncoid. Densely stippled area represents majority of oncoids, widely stippled area includes maximum and minimum values. avg = average values; std = standard deviation values.

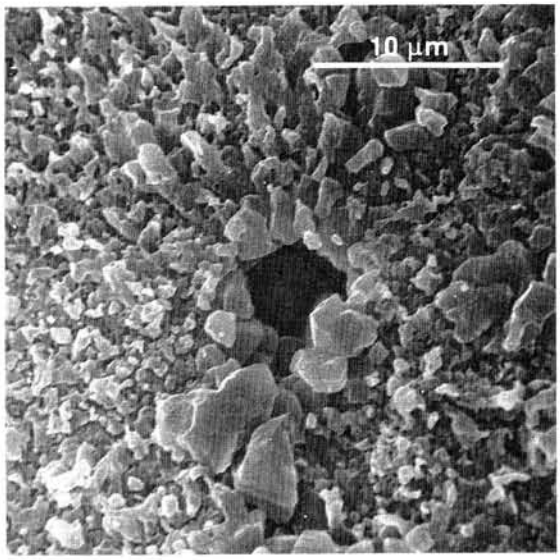

Fig. 10. SEM photograph of cyanobacterial filament ghosts: an empty thread is surrounded by bladed to rhombic, microsparitic, then micritic crystals.

(b) Development of a concave basal hollow is predetermined by the concave downward position of unionid shells, yet it does not always depend on this. Oncoids with straight wood fragments as cores also exhibit a basal, though less pronounced depression. Hence, both the basal hollow and the greater thickness of the upper cortex are primary features apparently resulting from growth of cyanobacteria.

(c) Oncoids were never overturned. Otherwise a cavity should develop on the surface facing the convex side of the shell and the thickening/thinning pattern of cortical layers should be opposite from the time of overturning onwards or, if commonly overturned, polar growth should stop.

Cyanobacterial growth under low light intensities

The problem arises of how to interpret *in situ* algal or cyanobacterial growth on lower sides of immobile oncoids.

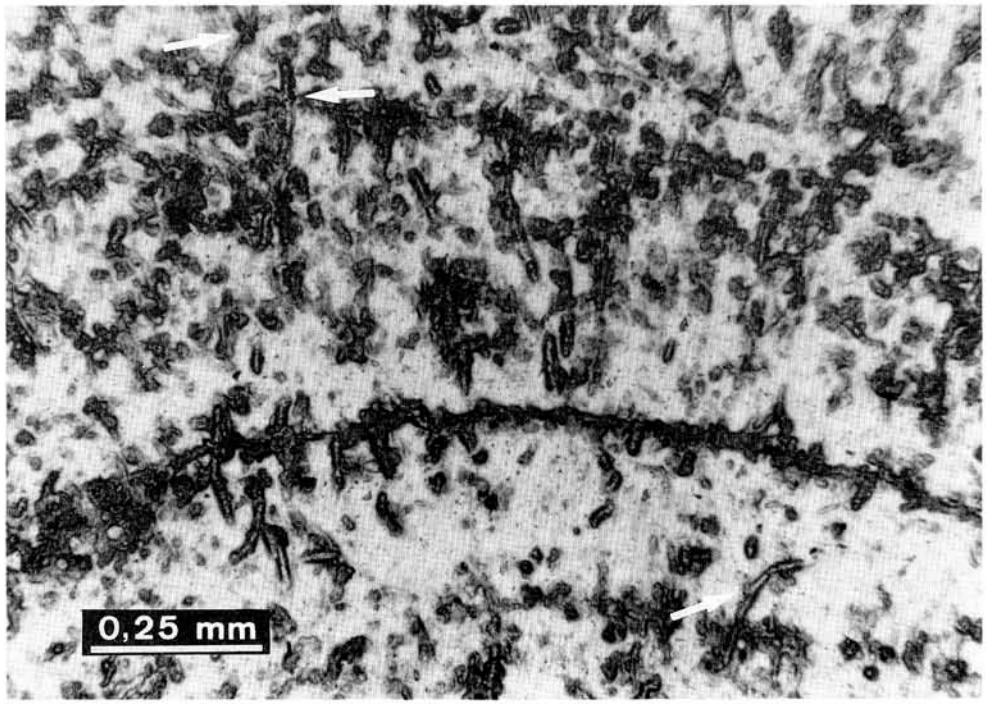

Fig. 11. Organic filament material yielded by dissolving the carbonate of a thin section with EDTA-solution. The thin section is, for preservational purposes, coated with a cover spray, which makes filaments appear erroneously thick. Original dimension, reticulate pattern and branching type (arrows) indicate a *Scytonema*-like cyanobacterium.

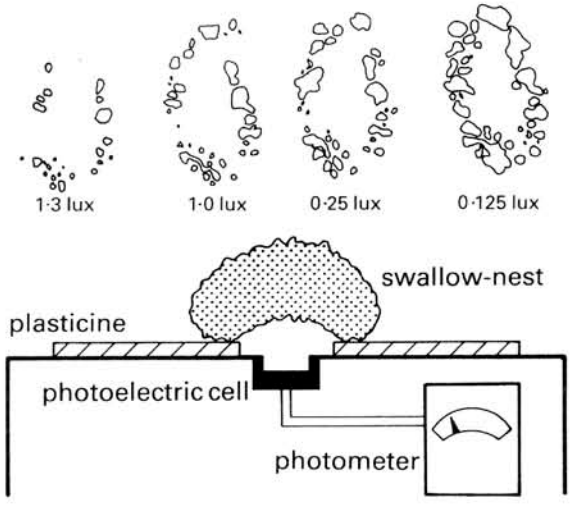

Fig. 12. Below: equipment for light-intensity tests under oncoids. Plasticine substrate serves to simulate certain sinking of oncoids into the original muddy substrate. Above: drawings of imprints of pustular oncoid base on plasticine floor, and related light intensities measured in oncoid depression: oncoids were pressed into plasticine with increasing pressure to simulate sinking into firm (left), semi-firm and very unconsolidated (right) muddy substrate.

Measurements from gravelly oncoid deposits from a Recent creek in Münsterland, FRG, revealed that sufficient light reached the lower surfaces of oncoids, due to diffusely reflected light, to allow phototrophic algal growth (Hartkopf-Fröder & Leinfelder, unpublished data).

Golubic & Fischer (1975) mention concave downward oncoid shapes from Recent creek deposits and consider that maximum growth of the responsibile oligophotic cyanobacterial community took place in the protected zone at the lower outer margin of the oncoids, whereas growth was zero in the centre of the lower surface due to complete darkness. Hence, this peculiar shape is interpreted by the authors as being a result of poor illumination.

It is tempting to apply this interpretation to the Oligocene 'swallow-nests' because when placed on a firm bottom (so as to simulate a semi-firm ground caused by a pause in background sedimentation) with their stable side down, all oncoids (even the flat-based ones) actually allow some light to penetrate to their lower surface due to their mamillate character and the spaces left between warts. The light intensity was measured in the basal hollow by means of a photometer. The measured light intensities (Fig. 12) are sufficient for reduced growth of cyanobacteria on the lower sides of oncoids. Even when simulating a certain degree of sinking into a surrounding muddy substrate by slightly pressing oncoids into a plasticine floor, some light still reaches the lower surface of oncoids due to their mammilate structure (Fig. 12).

As mentioned earlier, many ostracods were trapped and preserved within spaces between oncoid mamillae and in the cavity of the lower surface. In the normal part of the sequence, ostracods are always present, yet in minor amounts. Probably, as a result of a pause in sedimentation, ostracod shells were concentrated on the bottom yielding a light-coloured, sand-sized substrate which could easily scatter light to lower surfaces of oncoids.

Many cyanobacteria can live either phototrophically or heterotrophically or a combination of both (Krumbein, 1977, 1983; Gerdes, Krumbein & Holtkamp, 1985; Gerdes & Krumbein, 1987; also for further references). Hence, illumination insufficient for higher algae will still enable cyanobacterial growth, albeit at lower rates.

Interpretation of growth morphology

Oncoid shapes are commonly taken as an indication for distinct environments. Nickel (1983) combined characteristics of internal cortex structures, morphologies and general shape of Eocene freshwater oncoids to relate oncoid types to certain fluvial and lacustrine settings. Spheroidal oncoids are generally attributed to fluvial channels and bottom lags of alluvial ponds, whereas more irregular forms occur preferentially in shallow parts of ponds and lakes. Similar conclusions were drawn by Freytet & Plaziat (1965, 1982) for Tertiary oncoids of southern France. In Quaternary oncolites from the East African Rift System, oncoids exhibit different morphologies in different hydrodynamic settings which can be discriminated by statistical measurements of the oncoids' lengths, breadths and heights, and the thicknesses of the upper, lower and lateral oncoid cortices (Casanova, 1985). Here, too, fluvial oncoids are more spherical than lacustrine ones. Additionally, cortices on opposite sides of oncoids are of different thickness.

However, these results cannot be simply transferred to other situations. Recent oncoids from a water-poor creek in northern Germany are fairly flat and hence partly plot in areas occupied by the lacustrine oncoids in Casanova's study (Hartkopf-Fröder & Leinfelder, unpublished observation). On the other hand, similar plots from the swallow nests would plot among

Casanova's fluvial oncoids. In particular, the length to breadth ratio is very similar in both examples.

Hence, quantitative description of oncoids based on ratio determination of length to breadth, length to height and upper to lower cortical thickness may be useful for objectively discriminating different oncoid populations, keeping in mind that different populations are not necessarily related to different environmental settings. Such measurements reveal that the 'swallow nests' can be considered as one statistical population. Their length to breadth and breadth to height ratios are rather regular, exhibiting a low standard deviation. Length to height ratios are slightly more heterogenous. Ratios of upper versus lower cortex thickness vary largely, exhibiting a mean value of 3·58, which according to Casanova (1985) is typical for zero energy. The ratio of upper to lateral cortical thickness is more homogenous, with a mean value of 1·87, thus matching Casanova's lacustrine oncoids situated in the deeper parts of lakes (Fig. 7; Table 1).

Numerical measurements, particularly the determination of relative sphericity and hemisphericity for subsequent growth stages, help interpret growth mechanisms of the 'swallow nests' and should facilitate comparison with other oncoid occurrences. Since immobility of oncoids is evident by the above described facts, it is obvious that the observed decrease–increase pattern of the relative sphericity (*D* values) for subsequent growth stages is not due to a primary movement of oncoids combined with stabilization during later growth stages, but rather to the dynamics of *in situ* cyanobacterial growth. The tendency to achieve a hemispherical growth form during early growth stages corresponds with the bloom in cyanobacterial growth.

Optimum conditions led to a high vegetative reproduction and ramification of filaments, thus resulting in rather equal growth all over the upper surface of the oncoids. This style mostly ceased during the last growth stages, resulting in a slightly more pillow-like growth due to decrease in upwards growth in favour of a more pronounced lateral growth of the upper cortical zones.

The question arises whether the growth characteristics were driven by environmental changes or were solely due to the internal growth mechanisms of cyanobacteria. This problem might be solved by determining why mamillae developed in the final stage of oncoid growth. The warts of the 'swallow-nest' oncoids display the same microfabric and the same filament remains as the interior cortex parts. Hence, their development is not due to an environment-controlled shift in the calcifying microbial association, which in many modern and ancient microbialites accounts for mamillae development (e.g. Park, 1977; Nickel, 1983; Leinfelder, 1985; Leinfelder & Hartkopf, 1988). On the other hand, Leinfelder (1985) suggested that environmental change might cause a shift only in the associated non-calcifying microbial elements of a calcifying algal/cyanobacterial community, which could also change the calcification pattern and related morphology of the cortex and hence might lead to formation of mamillae. Actually, in the 'swallow nests' lamination is denser in the pustules and *Scytonema*-like filament remnants are less common, which might represent lower growth rates due to the deterioration of growth conditions. However, the rarity of *Scytonema* remnants in the mamillate structures may also be due to a greater oxidation of organic structures in the marginal parts of the oncoids during diagenesis.

Schneider (1977), Schneider, Schröder & Le-Campion-Alsumard (1983) and Toomey *et al.* (1988) describe cauliflower-like mamillate surfaces from both lacustrine and marine algal/cyanobacterial carbonates related to biological corrosion, competitive with cyanobacterial growth. Biological abrasion may even result in a furrow-like pattern. Settling of the carbonate decomposers only occurs when crusts are several millimetres thick. In caverns, caused by broadening outwards colloform growth, microbial deterioration of the organic matter may even cause inorganic solution of carbonate due to a locally raised CO_2 content (op. cit., Golubic, 1962). Occasional corrosional structures on the lower side of the 'swallow nests' and frequent borings show that such processes played a certain role in the formation of mamillae. However, they did not create the warts but rather overprinted the pre-existing mamillate fabric.

Oscillatorian cyanobacteria have the ability to form larger, millimetre-high morphological structures by clumping and gliding over each other, resulting in bundle- or tuft-like concentrations of 'filaments' (Walter, Bauld & Brock, 1976; Horodyski, 1977). This process is directed by phototaxis and enables continuation of cyanobacterial growth after a depositional event. Fine sediment particles which fall on oscillatorian mats can be transported laterally by contraction waves similar to the gliding process (Jarosch, 1962). Hence, detrital particles may concentrate in certain areas, thereby preventing cyanobacterial growth (cf. Freeman, Rosell & Obrador, 1982). Such processes may lead to a mamillate surface. The accumulation of detrital material between warts in the 'swallow nests'

demonstrates that in the present case this was the main process responsible for mamillae formation. Incipient mamillae formation in inner cortex areas occurs in some oncoids. In some of these cases, detrital material may be preserved between the mamillae, indicating that the development of warts occurred concomitantly with the detrital sedimentation, which seems also true for the formation of pustules on the exterior side of oncoids.

CONCLUSIONS

The Oligocene 'swallow-nest' oncoids from the Mainz Basin developed in a low-energy lacustrine environment characterized by slightly marly, ostracod- and charophyte-bearing clays. The development of the oncoids which are concentrated in one level represent a pause in background sedimentation.

All oncoids are remarkably similar with respect to their morphology, unionid bivalve nucleus and internal structures. Consequently, growth sequences are identical among all oncoids. Cyanobacteria started growing on disarticulated, concave downwards, densely packed unionid valves. Since lacustrine unionid shells are paper thin and very lightweight, even very moderate energy would have been sufficient to create such shell beds.

Shell beds of disarticulated, concave down unionid shells may occur both in the deeper water of large lakes and in the very shallow parts of small lakes, the latter of which always exhibit stillwater characteristics due to insufficient fetch for possible creation of wind-driven waves. In contrast, the shore zone of large lakes is often characterized by reworked, broken shells (Hanley & Flores, 1987). The 'swallow nests' apparently developed in the shallow zone of a small stillwater lake, since a few oncoid specimens show desiccation features and since the host beds occasionally exhibit root horizons.

After initial settlement of cyanobacteria on and under bivalve shells, growth conditions were then at a maximum to allow predominantly upwards radiating growth with tendency towards a hemisphere-like shape. This may have taken place in a few tens of years. Although change in growth direction of cyanobacteria is commonly diurnal (e.g. Golubic & Fischer, 1975; Monty, 1976), the dense/spongy couplets of laminae are normally considered as annual (Ott, 1980; Pentecost, 1978; Casanova & Lafont, 1985).

Appearance of pustules may indicate that growth rates ceased during the last stage of oncoid formation, due to a certain increase in detrital background sedimentation. Detrital particles were possibly transported to and stored in pockets between mamillae by cyanobacteria. Hence, formation of warts is an equilibrium process between cyanobacterial thriving and background sedimentation slightly higher than optimum for growth of cyanobacteria. Pustule formation was subsequently modified by boring organisms, widening the interstices between initial pustules. Bioabrasion and chemical corrosion played a minor role, but are evidenced by occasional furrows on the lower sides of oncoids. On the lower sides of oncoids, tubercles might be in part a reaction to diminishing available space caused by the concave structure. Above all, they increased surface area and directed themselves towards the entrance points of the diffuse light, thus resulting in optimum usage of the scarce light intensities at lower oncoid sides.

Statistical numerical measurements and image processing of oncoid parameters are valuable tools for describing and comparing different oncoids or growth stages, discriminating oncoid populations and, above all, interpreting growth mechanisms. They do, however, not directly delineate the depositional environments. Of special importance for interpreting growth mechanisms are sequences of upper versus lower and upper versus lateral cortex thicknesses, as well as the structural densities of outlines, hemisphericity, and growth factors of different growth stages. In the case of the swallow nests, the latter showed that increase in sphericity is also possible by *in situ* growth of cyanobacteria rather than movement and overturning in a fairly turbulent environment.

Oncoids displaying morphologies similar to the 'swallow nests', i.e. with a partly concave surface, are occasionally mentioned or drawn from both fluvial (Freytet & Plaziat, 1965, 1982; Golubic & Fischer, 1975; Jaffrezo, 1977; Ott, 1980; Nickel, 1983; Casanova, 1985; Scholz, 1986) and lacustrine deposits (Freeman *et al.*, 1982; Colom, 1983; Dean & Eggleston, 1984; Bijma & Boekschoten, 1985), yet they represent exceptional specimens in otherwise 'normal-shaped' oncoids. Such oncoid deposits are in most cases interpreted as being commonly overturned. A subrecent example exists in the swamps of the Orontes River, Middle East (Kinzelbach, 1985). Here, the unionid freshwater bivalve *Leguminaia wheatleyi* is encrusted from both sides by calcified cyanobacterial crusts. Again, the upper side is much better developed, which led the author to compare them with the 'swallow nests' of the Mainz Basin. We consider concavo-convex, 'swallow-nest'-type oncoids as good

indicators for *in situ* growth of these oncoids. However, spherical to ovoid oncoids, which normally form under frequent to occasional overturning, may also grow *in situ*, provided a coarse substrate reflects sufficient light to their undersides (Leinfelder & Hartkopf, 1988; Hartkopf-Fröder *et al.*, 1989). If mixing of oncoids from different sources can be excluded, the occurrence of a few 'swallow nests' within otherwise ovoid oncoids might indicate that parts or the entire oncoid population grew *in situ*.

ACKNOWLEDGMENTS

We would like to thank Ch. Wilhelm and G. Hausner, Institute of Botany, Mainz, for helpful discussions concerning cyanobacteria and fungi. R. Kinzelbach, Institute of Zoology, Darmstadt, kindly supplied us with modern, unionid-cored, oncoids from the Middle East. N. Schmidt-Kittler, Institute of Geosciences, Mainz, stimulated us to use his digital image processing methods. The students G. Ritschel, C. Gad and K. Thein performed most of the measurements and digitizing. Our thanks are particularly due to V. P. Wright, Cardiff, who made very helpful comments and suggestions on an earlier draft of this paper and who patiently improved our English. We also thank S. Golubic, W. E. Krumbein and J. Casanova for their thoughtful reviews, which improved the final form of the paper.

REFERENCES

BAHLO, E. & TOBIEN, H. (1982) Bestandsaufnahme der Säugetiere im "prä-aquitanen" Tertiär des Mainzer Beckens. *Mainz. Geowiss. Mitt.*, **10**, 131–157.

BIJMA, J. & BOEKSCHOTEN, G J. (1985) Recent bryozoan reefs and stromatolite development in brackish inland lakes, SW Netherlands. *Senckenbergiana marit.*, **17**, 163–185.

CASANOVA, J. (1985) Les oncolites du rift est-africain: morphométrie et paléoenvironnements. *Actes 110e congrès national des sociétés savantes, Montpellier, 1985, sciences*, **6**, 345–357.

CASANOVA, J. & LAFONT, R. (1985) Les cyanophycées encroûtantes des eaux courantes du Var (France). *Verh. Int. Ver. Limnol.*, **22**, 2805–2810.

COLOM, G. (1983) *Los lagos del Oligoceno de Mallorca*. Gràfiques Miramar S.A., Palma de Mallorca, 167 pp.

DAHANAYAKE, K. (1977) Classification of oncoids in the Upper Jurassic carbonates of the French Jura. *Sediment. Geol.*, **18**, 337–353.

DAHANAYAKE, K. (1983) Depositional environments of some Upper Jurassic oncoids. In: *Coated Grains* (Ed. by T. M. Peryt), pp. 377–385. Springer-Verlag, Berlin, 655 pp.

DAHANAYAKE, K., GERDES, G. & KRUMBEIN, W.E. (1985) Stromatolites, oncolites and oolites biogenically formed *in situ*. *Naturwissenschaften*, **72**, 513–518.

DEAN, W.E. & EGGLESTON, J.R. (1984) Freshwater oncolites created by industrial pollution, Onondaga Lake, New York. *Sediment. Geol.*, **40**, 217–232.

FLÜGEL, E. (1978) *Mikrofazielle Untersuchungsmethoden von Kalken*. Springer-Verlag, Berlin, 454 pp.

FREEMAN, T., ROSELL, J. & OBRADOR, A. (1982) Oncolites from lacustrine sediments in the Cretaceous of northeastern Spain. *Sedimentology*, **29**, 433–436.

FREYTET, P. & PLAZIAT, J.-C. (1965) Importance des constructions algaires dues à des Cyanophycées dans les formations continentales du Crétacé supérieur et de l'Eocène du Languedoc. *Bull. Soc. géol. Fr.*, **7**, 679–694.

FREYTET, P. & PLAZIAT, J.-C. (1982) Continental carbonate sedimentation and pedogenesis—Late Cretaceous and Early Tertiary of Southern France (Ed. by B. H. Purser). *Contrib. Sedimentol.*, **12**, 1–213.

GERDES, G. & KRUMBEIN, W.E. (1987) Biolaminated deposits. *Lect. Notes Earth Sci.*, **9**, 1–183.

GERDES, G., KRUMBEIN, W.E. & HOLTKAMP, E.M. (1985) Salinity and water activity related zonation of microbial communities and potential stromatolites of the Gavish Sabkha. In: *Hypersaline Ecosystems* (Ed. by G. M. Friedman & W. E. Krumbein), pp. 238–266. Springer-Verlag, Heidelberg, 484 pp.

GOLUBIC, S. (1962) Zur Kenntnis der Kalkinkrustation und Kalkkorrosion im Seelitoral. *Schweiz. Zeitschr. Hydrol.*, **24**, 229–243.

GOLUBIC, S. (1976a) Organisms that build stromatolites. In: *Stromatolites* (Ed. by M. R. Walter). *Devel. Sedimentol.*, **20**, 113–126.

GOLUBIC, S. (1976b) Taxonomy of extant stromatolite-building cyanophytes. In: *Stromatolites* (Ed. by M. R. Walter). *Devel. Sedimentol.*, **20**, 127–140.

GOLUBIC, S. & FISCHER, A.G. (1975) Ecology of calcareous nodules forming in Little Connestoga Creek near Lancaster, Pennsylvania. *Verh. Int. Ver. Limnol.*, **19**, 2315–2323.

HANLEY, J.H. & FLORES, R.M. (1987) Taphonomy and paleoecology of nonmarine mollusca: indicators of alluvial plain lacustrine sedimentation, upper part of the Tongue River member, Fort Union Formation (Paleocene), Northern Powder River Basin, Wyoming and Montana. *Palaios*, **2**, 479–496.

HARTKOPF-FRÖDER, C., HISS, M. & LEINFELDER, R.R. (1989) Holozäne Süßwasserkalke im Alme und Aftetal südlich von Büren (Kreis Paderborn, Nordrhein-Westfalen). *Münster. Forsch. Geol. Paläont.*, **69**, 261–289.

HORODYSKI, R.J. (1977) *Lyngbya* mats at Laguna Mormona, Baja California, Mexico: comparison with Proterozoic stromatolites. *J. sedim. Petrol.*, **47**, 1305–1320.

JAFFREZO, M. (1977) *Guides geologiques regionaux. Pyrenées orientales, Corbières*. Masson, Paris, 191 pp.

JAROSCH, R. (1962) Gliding. In: *Physiology and Biochemistry of Algae* (Ed. by R. A. Lewin), pp. 573–581. Academic Press, New York, 929 pp.

JONES, F.G. & WILKINSON, B.H. (1978) Structure and growth of lacustrine pisoliths from Recent Michigan Marl Lakes. *J. sedim. Petrol.*, **48**, 1103–1110.

KINZELBACH, R. (1985) Zur Entstehung der Zoozönose des Rheins. *Mainzer naturwiss. Arch. (Beih.)*, **5**, 5–49.

KRUMBEIN, W.E. (ed.) (1977) Cyanobakterien—Bakterien oder Algen? 1. *Oldenburger Symposium über Cyanobakterien*

1977. Taxonomische Stellung und Ökologie. 130 pp, Littmann, Oldenburg.

KRUMBEIN, W.E. (1983) Stromatolites—The challenge of a term in space and time. *Precambrian Res.*, **20**, 493–531.

LEINFELDER, R.R. (1985) Cyanophyte calcification morphotypes and depositional environments (Alenquer Oncolite, Upper Kimmeridgian?, Portugal). *Facies*, **12**, 253–274.

LEINFELDER, R.R. & HARTKOPF, C. (1988) *In-situ*-Wachstum rezenter und tertiärer Süßwasseronkoide aus dem Münsterland und dem Mainzer Becken (extended abstract). *Bochum. geolog. geotechn. Arbeiten*, **29**, 113–116.

LOGAN, B.W., REZAK, R. & GINSBURG, R.N. (1964) Classification and environmental significance of algal stromatolites. *J. Geol.*, **72**, 68–83.

MONTY, C. (1976) The origin and development of cryptalgal fabrics. In: *Stromatolites* (Ed. by M. R. Walter). *Devel. Sedimentol.*, **20**, 193–249.

NICKEL, E. (1983) Environmental significance of freshwater oncoids, Eocene Guarga Formation, Southern Pyrenees, Spain. In: *Coated Grains* (Ed. by T. M. Peryt), pp. 308–329. Springer-Verlag, Berlin, 655 pp.

OTT, E. (1980) Großonkoide und Algen-Festkalke in der Amper. In: *W. Grottenthaler, Geologische Karte von Bayern, 1:25 000, Erläuterungen zun Blatt Nr. 7833 Fürstenfeldbruck*, 37–42, Geol. LA, Munich.

PARK, R.K. (1977) The preservation potential of some recent stromatolites. *Sedimentology*, **24**, 485–506.

PENTECOST, A. (1978) Blue-green algae and freshwater carbonate deposits. *Proc. Roy. Soc. B*, **200**, 43–61.

PENTECOST, A. (1984) *Introduction to Freshwater Algae.* Kingprint Ltd, Richmond, 247 pp.

PIA, J. (1983) Die rezenten Kalksteine. *Z. Kristall. Miner. Petrogr., Abt. B, Ergänzbd.*, **1**, 1–420.

RADWAŃSKY, A. & SZULCZEWSKI, M. (1966) Jurassic stromatolites of the Villány Mountains (Southern Hungary). *Ann. Univ. Sci. Budapest Rolando Eötvös Nominatae, Sect. Geol.*, **9**, 87–107.

RATCLIFFE, K.T. (1988) Oncoids as environmental indicators in the Much Wenlock Limestone Formation of the English Midlands. *J. geol. Soc. London*, **145**, 117–124.

RIDING, R. & VORONOVA, L. (1982) Recent freshwater oscillatoriacean analogue of the Lower Palaeozoic calcareous alga *Angulocellularia. Lethaia*, **15**, 105–114.

ROTHAUSEN, K. & SONNE, V. (1984) Mainzer Becken. *Sammlung geologischer Führer*, **79**, Borntraeger, Berlin, Stuttgart, 203 pp.

ROTHE, P., HOEFS, J. & SONNE, V. (1974) The isotopic composition of Tertiary carbonates from the Mainz Basin: an example of isotopic fractionations in 'closed basins'. *Sedimentology*, **21**, 373–395.

SCHMIDT-KITTLER, N. (1984) Pattern analysis of occlusal surfaces in hypsodont herbivores and its bearing on morpho-functional studies. *Proc. Koninklijke Nederlandse Akad. Wetenschap. B*, **87**, 453–480.

SCHMIDT-KITTLER, N. (1986) Evaluation of occlusal patterns of hypsodont rodent dentitions by shape parameters. *Neues Jb. Geol. Paläont. Abh.*, **173**, 75–98.

SCHNEIDER, J. (1977) Carbonate construction and decomposition by epilithic and endolithic micro-organisms in salt- and freshwater. In: *Fossil Algae* (Ed. by E. Flügel), pp. 248–260. Springer-Verlag, Berlin, 375 pp.

SCHNEIDER, J., SCHRÖDER, H.G. & LECAMPION-ALSUMARD, T. (1983) Algal micro-reefs—coated grains from freshwater environments. In: *Coated Grains* (Ed. by T. M. Peryt), pp. 248–298. Springer-Verlag, Berlin, 655 pp.

SCHOLZ, H. (1986) Beiträge zur Sedimentologie und Paläontologie der Oberen Süßwassermolasse im Allgäu. *Jb. Geol. Bundesanstalt*, **129**, 99–127.

TOOMEY, D.F., MITCHELL, R.W. & LOWENSTEIN, T.K. (1988) "Algal biscuits" from the Lower Permian Herington/Krider Limestones of southern Kansas–northern Oklahoma: Paleoecology and paleodepositional setting. *Palaios*, **3**, 285–297.

WADELL, H. (1932) Volume, shape and roundness of rock particles. *J. Geol.*, **40**, 443–451.

WAGNER, W. (1935) *Geologische Karte von Hessen, Blatt-Nr. 6114 Wörrstadt 1:25 000,* Darmstadt.

WAGNER, W. (1954) Oberoligozäne Süßwasserbildungen des Mainzer Beckens bei Vendersheim in Rheinhessen. *Jb. Mitt. oberrhein. geol. Ver. N.F.*, **36**, 12–19.

WALTER, M.R., BAULD, J. & BROCK, T.D. (1976) Microbiology and morphogenesis of columnar stromatolites (*Conophyton, Vacerrilla*) from hot springs in Yellowstone National Park. In: *Stromatolites* (Ed. by M. R. Walter). *Devel. Sedimentol.*, **20**, 273–310.

(Manuscript received 5 January 1989; revision received 25 September 1989)