WRINKLE-LAYER STRUCTURES IN JURASSIC AMMONITES

by JOHN RALPH SENIOR

ABSTRACT. Wrinkle-layer structures are recorded from Jurassic graphoceratid ammonites. They are compared with similar structures in Palaeozoic ammonoids.

THERE are in the geological literature many reports of shell surface structures in the ammonoids, some of which refer to the characteristic wrinkle-layer structure in the Palaeozoic forms; these have been reviewed recently by House (1970). Among such reports are two records in Jurassic ammonites: *Ammonites amaltheus* Schlotheim. (*Amaltheus margaritatus* [de Montfort].) Quenstedt 1846, p. 61. *Ammonites turneri* J. Sowerby. (*Euasteroceras turneri* [J. Sowerby].) Quenstedt 1858, p. 96.

Barrande (1877, pp. 1182–9) reviewed these examples, concluding that the structures were the result of ventral spiral ornament on the ostracum in both cases; although the recent review by Walliser (1970) indicates that the shell structure as illustrated in *Amaltheus margaritatus* may be a form of wrinkle-layer structure.

Other than the example figured by Walliser (1970, pl. 4, fig. 5) these reports have not been confirmed in the intervening century, and this has led to the mistaken assumption that wrinkle-layer structures are entirely absent from Jurassic (and Cretaceous) ammonites; it is significant that Arkell and others, in the ammonoid volume of the *Treatise on Invertebrate Paleontology* (Moore 1957), failed to mention wrinkle-layer structures in connection with Mesozoic ammonoids, especially as the structure is well displayed in the Triassic forms (Mojsisovics 1893).

During a study of a Bajocian ammonite family, the Graphoceratidae, over 60 individual ammonites, both macroconchs and microconchs referred to in future as [M] and [m] respectively, have been mechanically dissected in order to help determine their ontogenies. It was found that most of these specimens showed a thin shell layer, up to 0·75 mm thick at 13 mm diameter, superimposed on the dorsal ostracum of the previous whorl, and a few showed a similar layer to be at least locally present in an interior ventral position (text-fig. 1). The positioning of these shell layers in the Graphoceratidae appears to correspond exactly with that of the dorsal and ventral wrinkle-layers (Runzelschicht and Ritzensteifen respectively) in the Palaeozoic goniatites.

WRINKLE-LAYER STRUCTURES IN PALAEOZOIC AMMONOIDS

The term wrinkle-layer was first brought into English usage by Foord and Crick (1897, p. xx), to explain finely striate or ridged surface textures found not infrequently on goniatite shells. These structures, which are known in the literature under various names (reviewed by House 1970), are first seen fairly early in the goniatite ontogeny (about 5 mm diameter), and are more or less continuously present until the adult

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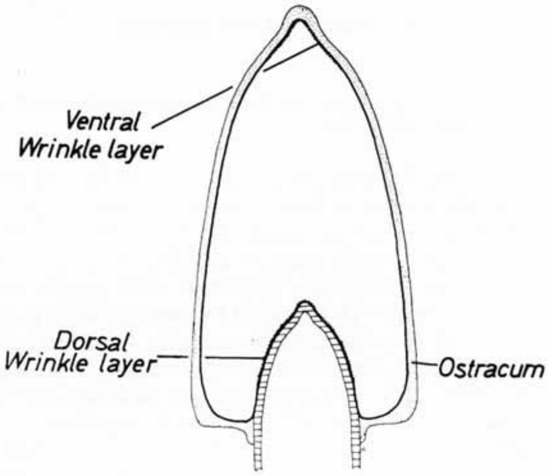
body-chamber. The surface ornament of these layers is fairly distinctive, consisting of closely spaced continuous fine striae or ridges, usually well oriented into radial or spiral patterns (or a combination of both), producing a wrinkle-like surface texture. The form and extent of the wrinkle-layer has been shown by House to vary from group to group in the Palaeozoic ammonoids.



TEXT-FIG. 1. Diagram showing the indicated continuity between the dorsal and ventral wrinkle-layer structure, based on a specimen of *Staufenia sinon* (Bayle) [M], Schwäbischen Alb, south-west Germany.

WRINKLE-LAYER STRUCTURES IN THE GRAPHOCERATIDAE

In the Graphoceratidae dorsal wrinkle-layer structures with surface ornament appear early in the ammonite ontogeny, and have been observed at diameters less than 2 mm at about one and a half volutions, shortly after the nepionic constriction, which occurs at approximately 0·90 mm diameter (*c.* 360° forward of the prosuture). At this early stage the surface of the shell layer has a moderately strong pustulate ornament, which forms a sub-spiral or sub-radial pattern, the former being the more common type (Pl. 14, figs. 1–5). After approximately 40 mm diameter the surface ornament of the dorsal layer is seen to fade gradually, leaving a thin, fairly uniform, undulating layer with growth lines, seen in some specimens to continue to the adult body-chamber (Pl. 13, figs. 1–3 and text-fig. 2). It seems likely that the occurrence of dorsal wrinkle-layer structures at larger diameters (over 60 mm diameter) should be quite common and the probable reason for their apparent rarity (Table 1) is the difficulty of recognizing a thin largely unornamented layer, which could easily be destroyed or overlooked when the ammonite is examined.

Ventral wrinkle-layer structures in the Graphoceratidae are more seldom seen and are rather specialized in ornament type. It appears from the many medial sections taken from different species in the Graphoceratidae that this ventral layer is probably continuous with the dorsal layer (see text-fig. 1), but is largely unornamented except in the immediate venter area, where spiral and radial ornament is seen, usually as negative impression on the internal mould (Pl. 13, figs. 4 and 5). This localized ventral ornament is very pronounced and continuous except immediately orad of each septum; the reason

TABLE 1. Showing the distribution of wrinkle-layer structures at present known in the Graphoceratidae. Dimensions in millimetres

		Dorsal wrinkle-layer	*Diameters observed*	*Ventral wrinkle-layer*	*Diameters observed*
Graphoceras v-scriptum (S. Buckman)	M	X	4·20	—	—
	m	X	3·50	—	—
G. concavum (J. Sowerby)	M	X	3·85	—	—
	m	X	4·10	—	—
G. impolita (S. Buckman)	M	X	3·36–11·37	—	—
Brasilia bradfordensis (S. Buckman)	M	X	4·25	—	—
B. baylii (S. Buckman)	M	X	3·41	—	—
	m	?	6·37	—	—
Ludwigia gigantea (S. Buckman)	M	?	10·27	—	—
L. murchisonae (J. Sowerby)	M	X	3·00	—	—
	m	—	—	—	—
L. haugi Douvillé	M	X	1·30	X	36·00
	m	?	10·25	—	—
L. sp. nov.	m	X	2·18	—	—
Leioceras comptum comptum	M	X	6·24	—	—
(Reinecke)	m	X	2·25	—	—
L. comptum bifidatum (S. Buckman)	M	X	4·37–13·30	—	—
	m	X	3·50	—	—
L. uncinatum (S. Buckman)	M	X	2·70–3·46	—	—
	m	X	1·45–8·77	X	15·60
L. opalinoides (Mayer)	M	X	3·72	—	—
	m	—	—	—	—
L. opalinum (Reinecke)	M	X	3·25–108·00	—	—
	m	—	—	—	—
L. costosum (Quenstedt)	M	X	3·62	—	6·00
	m	—	—	—	—
L. lineatum (S. Buckman)	M	X	5·10–24·95	X	65·00
	m	X	2·88	X	9·33
Staufenia staufensis (Oppel)	M	X	7·20	X	30·70–170·00
S. sinon (Bayle)	M	X	1·85–6·27	X	57·75
	m	X	3·17	—	—

for this seems obscure. It may be the result of interference by the mural portion of each septum, or of additional effects, such as shell dissolution by cameral fluids during life; though the former seems the more plausible, since the 'etching' is localized in effect. The ornament of the ventral wrinkle-layer structure appears to be more persistent throughout conch development and has been seen to diameters of 140 mm, but does not appear until the second or third whorls (at approximately 9 mm diameter), coinciding with keel development.

Ventral wrinkle-layer structures, as described above should not be confused with the secondary ostracum features—*connellen* of Hölder (1958, p. 22), which form indentations in the *ostracum* of the keel.

Two pattern types have so far been discerned in the ornament of the dorsal shell layer in the Graphoceratidae; the first, typified by *Graphoceras impolita* (S. Buckman) [M], consisting of semicircular, flat-topped, pustules (Pl. 14, figs. 3 and 4); the pustules in the second being elliptical and rounded in shape, as in *Leioceras uncinatum* (S. Buckman) [m] (Pl. 14, figs. 1 and 2).

The distribution of known wrinkle-layer structures in the Graphoceratidae at the present time is indicated in Table 1.

These shell structures in the Graphoceratidae, when compared with those seen in Palaeozoic and Triassic ammonoids, show some differences, particularly in the type of surface ornament. The lack of definite organization in the discontinuous pustulate ornament of the Jurassic ammonites, described here, contrasts with the stronger organization (usually near radiate or prorsiradiate, and to a lesser extent spiral) of the continuous characteristic elevations ('wrinkles') associated with the Palaeozoic and early Mesozoic ammonoids (excepting, for example, House, pl. B, fig. 2). Although there are these superficial differences in surface ornament, the shell layer seen in these Jurassic ammonites appears to be equivalent to the goniatite wrinkle-layer, certainly both appear to have been deposited in a similar manner and position and probably had the same

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EXPLANATION OF PLATE 13

Figs. 1–3. *Leioceras opalinum* (Reinecke) [M]. 1, 2, an almost complete specimen from Burton Bradstock, Dorset, showing the position of formation of the dorsal wrinkle-layer, adoral of the aperture. Walton Collection, SM J51394. 3, another specimen with a partly broken aperture, showing dorsal wrinkle-layer position on the posterior part of the body-chamber. S. Buckman collection, SM J6358; figured by Buckman (1888, p. 35, pl. 13, figs. 1, 2) as *Lioceras opalinum* (Reinecke), and later described by the same author (1899, p. xlv) as a syntype of *Cypholioceras opaliniforme* S. Buckman. Specimen from Harefield Hill, Gloucestershire. 1 × 1; 2 × 3; 3 × 1.

Figs. 4, 5. *Leioceras lineatum* (S. Buckman) [m]. Ornament of the ventral wrinkle-layer, on whorl section at diameters of *c.* 25 mm and 33·70 mm respectively. HU 121.J.1. Both × 3.

Fig. 6. *Graphoceras concavum* (J. Sowerby) [m]. Internal mould, showing the impression of the dorsal wrinkle-layer ornament, of the whorl previous. HU 121.J.2. × 28.

EXPLANATION OF PLATE 14

Figs. 1, 2. *Leioceras uncinatum* (S. Buckman) [m]. Scanning electron micrographs showing the semi-spiral ornament on an isolated fragment of the dorsal wrinkle-layer, removed at 2·67 mm diameter. 1, a complete fragment of the layer, the venter being situated midway, running parallel to the upper edge. 2, an enlargement of part of the ornament. Specimen from the Scissum bed, Burton Cliff, Dorset. HU 121.J.3. 1 × 60; 2 × 115.

Figs. 3, 4. *Graphoceras impolita* (S. Buckman) [M]. Dorsal wrinkle-layer surface ornament, at 3·36 mm diameter, showing a sub-radial pattern of truncated pustulae, enlarged in the scanning electron micrograph of fig. 3. Concavum Zone, Horn Park, Beaminster, Dorset. HU 121.J.4. 3 × 110; 4 × 30.

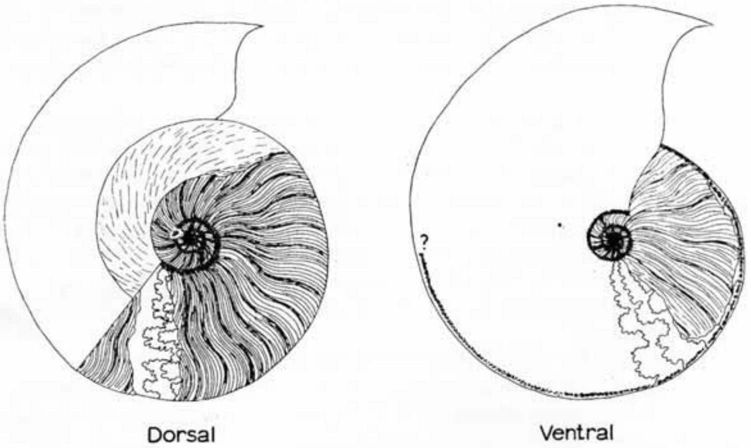
Fig. 5. *Staufenia sinon* (Bayle) [M]. Dorsal wrinkle-layer ornament at 1·87 mm diameter. Scheffhau, Bonndorf, Schwäbischen Alb, south-west Germany. HU 121.J.5. × *c.* 25.

Figs. 6, 7. *Nautilus pompilius* Linne ♂. Showing the ornament of the secondary nacreous layer, on the callus in the body-chamber. Photographs taken from a latex rubber replica. Rabaul district, New Guinea. 6 × 7·50; 7 × 35.

function. The surface ornament of this layer in the graphoceratids fits into classes Id and II (sculpture elements arranged and partially arranged, respectively), in the scheme devised by Walliser (1970, p. 119).

SECRETION AND FUNCTION OF THE WRINKLE-LAYER STRUCTURE

It appears that this shell layer was deposited in the body-chamber of the ammonite, just adoral of the aperture (text-fig. 2); this being well illustrated by an example of *Leioceras opalinum* (Reinecke) [M] (Pl. 13, figs. 1 and 2), where a thin shell layer is seen



TEXT-FIG. 2. Diagram illustrating wrinkle-layer structures in the Graphoceratidae; Dorsal—*Leioceras opalinum* (Reinecke) [M] (pl. 13, figs. 1 and 2), Ventral—*Staufenia staufensis* Oppel [M], Schwäbischen Alb, south-west Germany.

superimposed on the venter of the previous whorl just in front of the aperture; another macroconch specimen of the same species (Pl. 13, fig. 3), with the aperture partially broken away, shows clearly the position where the dorsal layer was deposited. The site of the secondary shell layer deposition in these Jurassic ammonites corresponds exactly with that in the Palaeozoic goniatites (House 1970).

The function of this layer in the fossil cephalopods can best be seen in connection with the supposed homology with secondary shell structures in the recent *Nautilus*. The thin nacreous layer which is secreted in the *Nautilus* body-chamber has been considered to be the exact analogue of the wrinkle-layer structures in the ammonoids (Suess 1870, House 1970), and has the probable function of smoothing out the effects of any minor irregularities on the ostracum of the previous whorl; this layer is deposited from a very localized part of the mantle, a fact substantiated by the inability of the mantle to completely eradicate the effects of larger irregularities, such as calcareous serpulid tubes. The very thin dark brown conchiolin layer ('Black-layer') which is deposited well outside the body-chamber by the mantle fold prior to the deposition of the nacreous layer, entirely envelopes all the surface of the periostracum of the previous whorl (including the serpulids), and extends just below the level of new callus formation; indicating that this layer probably acts as a 'primer' layer on the periostracum before new shell secretion is possible. All the three processes of conch development, conchiolin deposition, secretion of the main shell and the deposition of the secondary nacreous layer occur simultaneously at different parts of the mantle. Two of these shell processes are readily identifiable in the Graphoceratidae and other ammonoids, the exception being the absence of the 'Black-layer', an absence which cannot be simply explained, as material of similar composition is frequently preserved in the material studies, as siphon apparatus. An added attraction of considering the secondary nacreous layer as homologous with wrinkle-layer type structures is the presence of natural surface ornament, especially on some interior callus areas of *Nautilus* (Pl. 14, figs. 6 and 7). There is therefore no need to postulate dissolution of the periostracum as has been done by some authors (Miller 1947, p. 20).

The function of smoothing out the minor irregularities on the ostracum, if applied to the Graphoceratidae, must have been very effective with those species having only minor ostracum ornament, for example, *Leioceras opalinum* (Reinecke), but only partially effective with more coarsely ribbed forms, such as *Ludwigia haugi* Douvillé. There are indications in other Mesozoic ammonite groups that these secondary shell layers achieve greater thicknesses than of those seen in the Graphoceratidae; an example of this in *Douvilleiceras* is figured by Casey (1962, p. 264, text-fig. 93); where an apparently thick layer (termed by Casey the dorsal-shield) nullifies the extreme effect of the coarse ornament.

The inference made by Walliser (1970) that the surface ornament of the wrinkle-layer '. . . may have served for better attachment of the whole mantle . . .' apparently cannot be applied to the Graphoceratidae, as in that group of ammonoids the dorsal surface ornament fades considerably at larger dimensions.

DISCUSSION

The structures here described in the Graphoceratidae were initially thought to be the result of secondary dissolution of the ostracum during diagenesis, an idea rendered invalid by the available evidence. This thin dorsal layer can under favourable circumstances be isolated from the shell (?periostracum) of the previous whorl (Pl. 14, fig. 1), also resulting in a corresponding patterned surface on the internal mould (Pl. 13, fig. 6). Amongst specimens dissected, some of the inner whorls of the south German material were partially preserved as pyritic moulds and the dorsal wrinkle-layer structures in these is always seen as a negative impression. In such a position it would be unlikely that immediate postmortem dissolution of the shell would have occurred and hence diagenetic infill of the camerae may preserve the original surface. Hence it is thought that the wrinkle-layer is not a dissolution phenomenon.

It seems surprising that despite the vast amount of research on Mesozoic ammonite faunas, the structures here described have not been reliably recorded before; the probable reason for this is that exhaustive ontogenetic research in Mesozoic ammonoids is a fairly recent advance from the classical presentation of ammonite palaeontology. It is to be expected that as other Mesozoic ammonite groups are restudied in great detail more examples of wrinkle-layer structures will emerge. The author has already noted its presence in some Middle Jurassic perisphinctids.

Repositories. The material here described is deposited in the Sedgwick Museum, Cambridge (SM) and collections of the Geology Department, Hull (HU).

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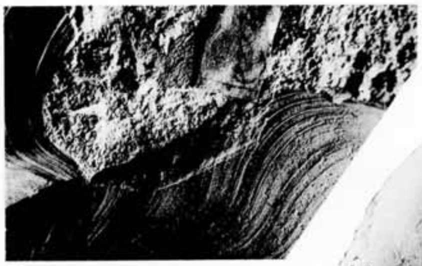

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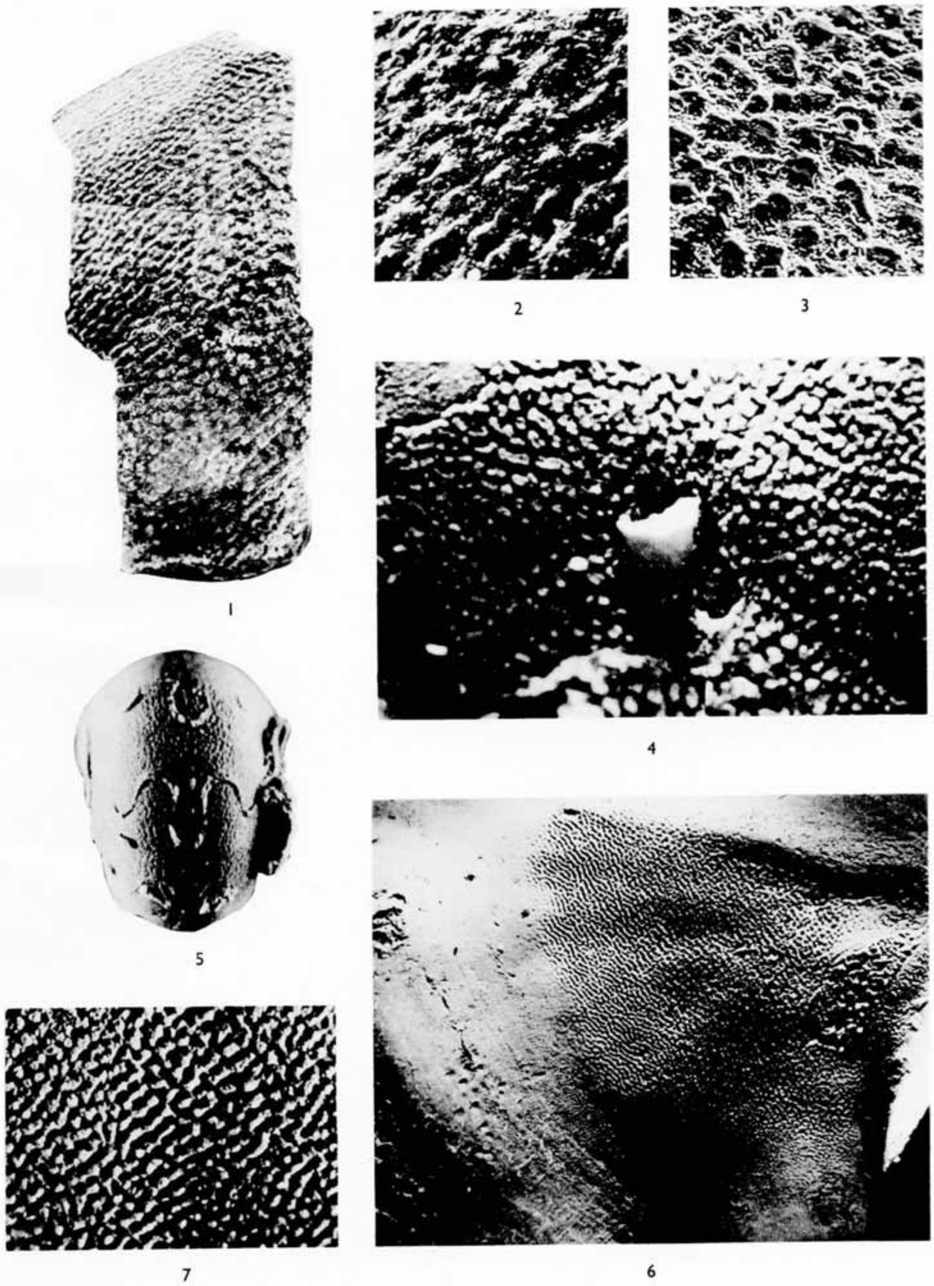

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