ıtural inversion in a heteromorph ammonite an(˙ts ˙plication for septal formation

TER D. WARD AND GERD E. G. WESTERMANN

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The first known sutural inversion in ammonoids occurred in the adolescent stage of a late Cretaceous *Glyptoxoceras subcompressum* (Forbes). Inversion has affected all folioles and lobules which are convex adapically instead of adorally, but not the tie-points from which they are 'suspended' and which shape the principal saddle and lobes. The ventral median saddle is also normal due to its proximity to the siphuncle. The partially inverted sutures are also strongly approximated. This suggests that, in this instance, body advance was mainly by muscular pull against a negative pressure differential of cameral liquid to 'ambient' body pressure across the septal mantle, owing to insufficient liquid in the newly forming chamber. Conversely, a slightly positive pressure differential is inferred for normal ammonitic septum formation. In spite of reversal, the length of folioles and lobules remains constant, indicating the existence of a 'permanent' sinuous attachment band resembling the posterior aponeurosis of *Nautilus*, with tie-points for primary wall attachment.

Peter D. Ward and Gerd E. G. Westermann, Department of Geology, McMaster University, Hamilton, Ontario, L8S 4M1, Canada; 17th December, 1975.

ımonoid septal sutures (suture lines) share characteristics of convergent, pointed ıpical parts (lobe and saddle incisions) and ınded adoral parts (lobules and folioles). hough adapical and adoral curvature may eptionally be similar, the reversal of adoral l adapical curvatures has been unknown. ɘ alleged complete sutural inversion reted by Haas (1941) was challenged (Schindelf 1968) and shown to be erroneous due to ɔng assembly of the specimen (Westermann 2).

Ve have now recognized examples of partial ıral inversion in a recently found Upper taceous heteromorph ammonite. This abert specimen permits important inferences arding the two hypotheses of septal formaı recently advanced by Seilacher (1973, 5) and Westermann (1975: Fig. 7). While eeing in some essential parts, the two dels differ in the degree of flexibility and nogeneity attributed to the posterior or tal mantle and the role of the cameral ııd. Seilacher supposes that the septal mantle, after advancing by longitudinal muscular contraction (only) into its new position, has lost its crinkled shape stemming from the last septum and re-adheres smoothly and with more or less straight margin against the outer wall. Subsequently, the posterior mantle is pulled off the shell wall to which it has become attached in principle tie-points, resulting in adorally convex sinuses forming the beginning of the saddles. Several successive orders of tie-points are introduced as the pull-off and adoral arching of the contact line continues. The radial (centripetal) pull away from the wall is due to contraction of the 'subepithelial muscle system' of the septal mantle. The fluting of the septal mantle also requires peripheral expansion by a factor of two or more. The tie-points form the bases of the sutural incision and their subdivision, while the lobules and folioles correspond to the more or less arbitrary line of mantle detachment from the wall between them. This implies that the margin of the septal mantle, later producing the septal suture is, at least originally,

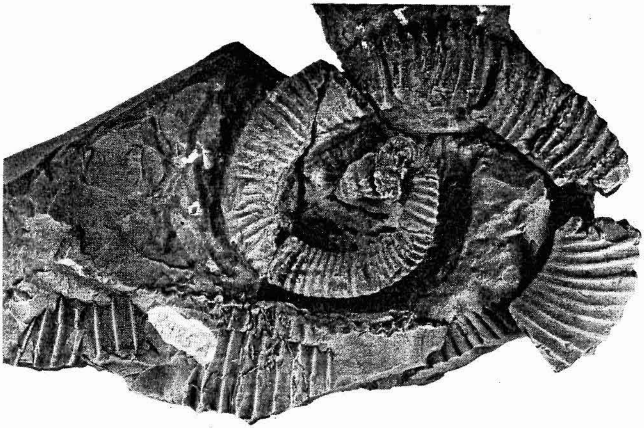

Fig. 1. The aberrant heteromorph *Glyptoxoceras subcompressum* (Forbes) with inverted septal sutures on early gyroconic growth stage (Fig. 2) from the Upper Cretaceous Haslam Formation of Vancouver Island, McM. K-985, ×1.

not differentiated and that, indeed, the septal mantle and the posterior part of the lateral mantle are structurally indistinct and functionally interchangeable. No significant part in shaping of the normal septum and suture is attributed to the liquid transferred behind the posterior mantle.

Westermann postulates the existence during growth of a slightly positive pressure differential of cameral liquid to body (under ambient water pressure) across the septal mantle. The liquid pressure, built up osmotically, acts in conjunction with muscular pull to advance and re-shape the septal mantle, in particular the adorally convex lobules and folioles. Saddles and lobes, lobules and folioles are merely the re-inflated, slightly modified replicates of the previous septal margin and correspond to a sinuous thickened mantle structure resembling the posterior aponeurosis of living *Nautilus*. This is the attachment band of the septal mantle which abounds in non-expandable collagenous fibres essentially with random orientation. Reattachment of the septal mantle occurs at first in tie-points as in Seilacher's model. However, the tie-points are postulated to lie along the well differentiated attachment band which is stiff enough to partially retain its curvature and control that of the septal mantle after separation from the previous septum. After re-inflation of lobules and folioles by the cameral liquid, the entire band attaches to the wall.

Description

The undistorted, almost complete specimen of *Glyptoxoceras subcompressum* (Forbes) was found by Ward in the late Santonian or early Campanian Haslam Formation, Elongatum Zone, on the Puntlege River, Vancouver Island, British Columbia (McMaster K-985; Fig. 1).

Glyptoxoceras subcompressum is a lytoceratine heteromorph with torticonic juvenile whorls followed by gyroconic adolescent and adult whorls. The septal suture is quadrilobate (formula E–L–U–I) and slightly asymmetrical throughout, in the manner of turrilitids and torticonic nostoceratids, even though most of the phragmocone is planispirally symmetric. Description and classification are being presented elsewhere by Ward.

Specimen K-985 differs from conspecific specimens (Geological Survey of Canada 89541, 83903, 77390) in the shape of several consecutive adolescent sutures on the early gyroconic growth stage (dorso-ventral height H = 5.9–6.4 mm); no marked differences can be detected on the juvenile and adult stages which thus appear completely normal. The gyroconic portion of the phragmocone has 16 septa: the first is normal; the second (H = 5.7 mm) is transitional, with similar curvature of incisions, lobules and folioles; the third to sixth septa are inverted, with sharp, acute adoral and rounded adapical curvatures, on

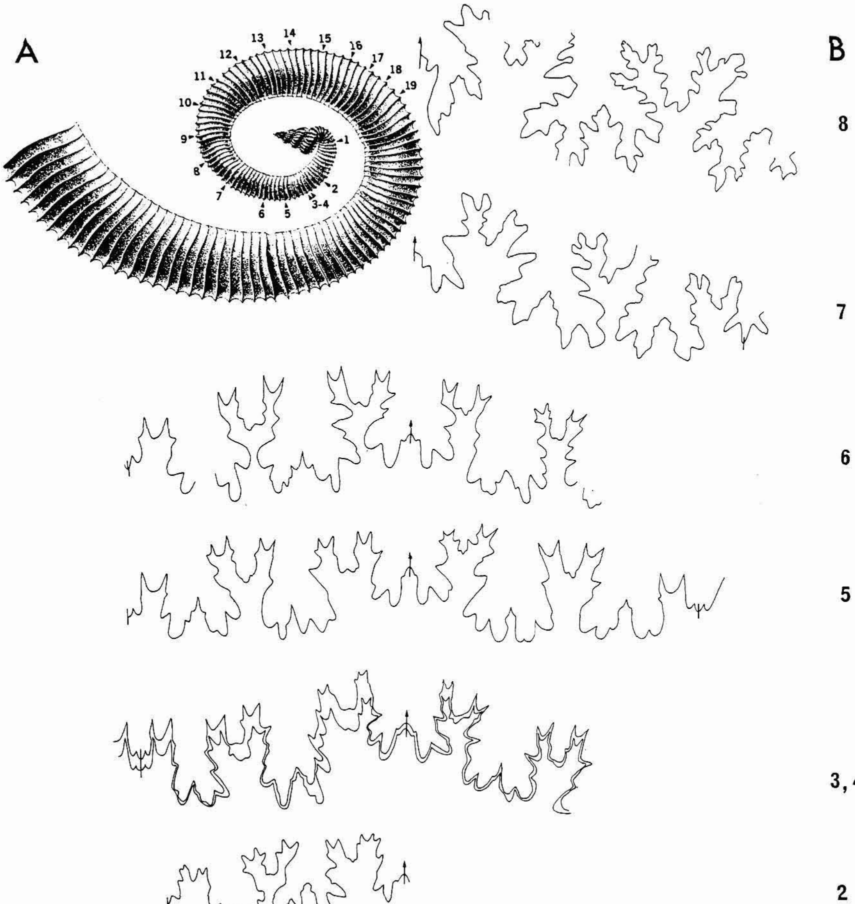

Fig. 2. Adolescent septal sutures of *Glyptoxoceras subcompressum* (Forbes), McM. K-985. □A. Reconstruction of the species (by Mr. M. Orsen) with positions of adolescent and adult sutures (Nos. 1–19) indicated. □B. Suture Nos. 2–8, spacing not to scale except for Nos. 3–4. Inversion occurs only in the approximated suture Nos. 2–6.

the narrow saddles as in the broad lobes, so that folioles and lobules appear to be hanging rather than arching in conventional orientation; the seventh and subsequent septa are again normal. Significantly, septal approximation is correlated with inversion, and the third and fourth sutures are so close that their septa may be partially in contact (Fig. 2:3, 4).

The inverted sutures differ from the normal sutures essentially only in the direction of inflation of lobules and folioles, being convex adapically instead of adorally, but little in the position of the incision bases (tie-point)

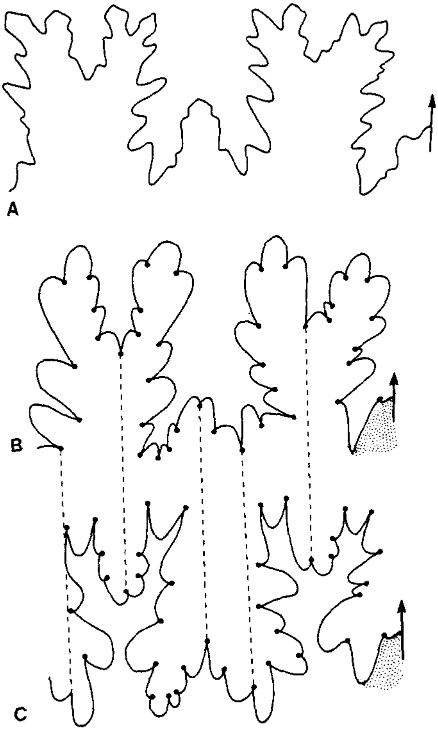

Fig. 3. Comparison of inverted and normal septal sutures, same species and growth stage. □A. Comparative suture of normal specimen (GSC) at similar diameter. □B. The same suture if reverted back to normal, assuming attachment at the same tie-points and reversal of the pressure differential across the posterior mantle, from the nautiloid to the ammonoid condition. □C. Part of suture No. 6 of *Glyptoxoceras subcompressum* (Forbes), McM. K-985, with postulated tie-points (solid circles) and constraints owing to the siphuncle (shaded).

between them. This can be demonstrated by the close resemblance of a normal suture with an inverted suture which has been modified simply by turning its lobules and folioles inside-out as if suspended from fixed tie-points. Merely the (latest or highest order) tie-points at the top of the saddles require minor shift or duplication. An exception is the ventral median saddle, situated above the siphuncle, which is not inverted (Fig. 3).

Implications for septal formation

Sutural inversion is restricted to adolescence and affects only (a) the convexity of lobules and folioles from adoral to adapical except for the ventral median saddle and (b) the spacing of the sutures (septa), i.e. becoming approximated. The position of the tie-points and the length (along curvature) of the individual lobules and folioles remain essentially unchanged. The changes in convexity and distance can both be explained as due to malfunctioning of the osmotic system related to the transfer of liquid into the space between the latest septum and the posterior mantle as the body advances. Except for a small growth increment in volume, the liquid probably originates from the latest chamber(s) which is being emptied concurrently with the new growth so that neutral buoyancy is maintained (cf. Denton & Gilpin-Brown 1973). However, the advance of the body against ambient water pressure at any depth requires that muscular pull is coordinated with volume and pressure regulation of the liquid; its pressure will closely approximate the 'ambient' body pressure. A slight pressure differential across the posterior mantle has to be compensated for by the longitudinal muscles of the mantle; a slightly negative differential of the liquid will result in adapically convex curvature of the septal mantle (as in nautiloids, but not possible to observe here) and of the non-attached parts of the mantle margin, i.e. lobules and folioles between tie-points. In normal ammonoids, the system appears to be balanced consistently more or less on the positive side with respect to liquid pressure, resulting in the common adoral convexity of septal and sutural curvatures. The osmotic pressure for liquid transfer in front of the latest septum was probably controlled by the same organ as the osmotic pressure differential across the ectosiphuncle in the chambers, i.e. the siphuncular cord (cf. Denton & Gilpin-Brown 1973 for living cephalopods). Thus, inability to build up sufficient liquid pressure behind the body will hinder body advance unless the process would occur very close to the ocean surface, i.e. against minimal ambient pressure, since chamber length (strictly its volume) depends on the volume of liquid available under near-ambient pressure. Concurrent and/or subsequent pull of the mantle muscles can only distort the shape of the posterior mantle, by advancing its periphery while the free parts bulge adapically. If the free parts include a stiffened peripheral attachment band with fixed-length intervals between tie-points, a series of adorally concave loops resembling the normal convex loops is produced. The results is a series of approximated and inverted sutures.

This abnormal case of sutural inversion is thus seen as evidence supporting the model of septal formation advanced by Westermann (1975), which assumes (permanent) structural modification of the mantle into a non-expandable and non-contractile septal part, its peripheral attachment band, and the longitudinal part. If the pressure differential across the septal mantle of a homogeneous mantle as inferred by the pull-off model were reversed, the folds and lobules would be reduced in height but they would not invert from convex to concave, retaining the same height. The presence of a 'permanent' attachment band for the septal mantle is also highly probable for reasons of analogy with living *Nautilius*, i.e. the posterior aponeurosis. On the other hand, the new formation in almost identical position of this essential mantle structure during each septum secretion is improbable.

The normality of the median saddle in the external (ventral) lobe within the otherwise inverted sutures is probably owing to its immediate proximity to the ventro-marginal siphuncle. Since the ammonite septum is prochoanitic, the siphuncular cord begins (or exits) within an invagination of the septal mantle which secretes the septal neck. This tight circular fold apparently can not be exfoliated and influences the mantle shape in its immediate vicinity.

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