

THE PALAEOBIOLOGY OF THE CRETACEOUS IRREGULAR ECHINOIDS *INFULASTER* AND *HAGENOWIA*

by ANDREW S. GALE and ANDREW B. SMITH

ABSTRACT. The taxonomy of the infaunal holasteroids *Infulaster* and *Hagenowia* is revised in the light of new material from the Senonian Chalk of southern England. Investigation of the plating structure in *Hagenowia* permits a more precise definition of its species, and a better understanding of the evolution of the rostrum. The majority of structural modifications in the *Infulaster-Hagenowia* lineage were caused directly, or indirectly, by apical elongation and size reduction. A detailed study of test and ambulacral pore morphology, tuberculation, and spines, taken in comparison with living echinoids, allows reconstruction of the life habits of *Infulaster* and *Hagenowia*. The evolutionary changes are related to the adoption of a specialized method of feeding and an attempt to avoid predation.

THE echinoid genus *Hagenowia*, in which the apical part of the test is drawn out to form a rostrum, is the most bizarre of a wide range of holasteroids which inhabited the Upper Cretaceous Chalk Sea of north-west Europe. The ancestry of this genus was traced by Wright and Wright (1949) to *Infulaster*, and the evolutionary story further discussed and elaborated by Ernst and Schulz (1971).

The Upper Chalk in England falls into two distinct faunal provinces, the boundary of which ran approximately east-west through north Norfolk (Peake and Hancock 1961; Reid 1976; Rawson *et al.* 1978). *Infulaster* and *Hagenowia* have been regarded as characteristic members of the northern province fauna (where they occur commonly) and recorded hitherto only as occasional rarities in the south. *Hagenowia* is the most common fossil in one interval of the Yorkshire Upper Chalk and has been used there as a local zonal index in place of *Micraster coranguinum* (Rowe 1904; Wright and Wright 1942).

Collecting during recent years from the Senonian Chalk of south-east England has yielded abundant material of both genera and shows that they occur frequently at certain stratigraphical levels in at least part of the southern province. This material has provided much new information (particularly concerning the rostrum of *Hagenowia*) which has allowed a reappraisal of the taxonomy and phylogeny of *Infulaster* and *Hagenowia*.

Irregular echinoid lineages in the Chalk have provided a number of classical evolutionary stories, of which the best known is in *Micraster* (Rowe 1899). Progressive morphological changes in *Micraster* were interpreted by Nichols (1959) as adaptations to an increasing depth of burial. A similar explanation has been advanced for the *Infulaster-Hagenowia* story (Nichols 1959; Ernst and Schulz 1971). Our work suggests that changes in this lineage, particularly the development and modification of the rostrum, are related to the adoption of a specialized method of feeding, and avoidance of predation.

METHODS OF STUDY

Although the surface details of *Infulaster* and *Hagenowia* from southern England are often well preserved, the tests are invariably distorted by compactional crushing. For this reason, biometrical studies on the material have not been attempted.

In a detailed study of the rostrum of *H. elongata* (Nielsen) Schmid (1972) used a special technique to elucidate the plating structure. This took advantage of the naturally separate reflectivity of

individual plates, accentuated by gold coating. This method proved to be effective on *H. blackmorei* Wright and Wright, but unsuccessful on earlier members of the genus. To work out the plating arrangements of these, naturally weathered rostra were stained with black ink to pick out the sutures. Surface details of the echinoids, particularly tubercles and pores, were studied with the scanning electron microscope

Abbreviations used for museum collections are as follows: BMNH—British Museum (Natural History); IGS—Institute of Geological Sciences, London; MMH—Mineralogical-Geological Museum, Copenhagen.

STRATIGRAPHY

In this paper the usage of stages and zones within the Upper Chalk of England have been adopted from Rawson *et al.* (1978). Text-fig. 1 gives a generalized succession of all but the lowest Senonian in east Kent, and is based on the cliff sections between Dover and Kingsdown, and on the Isle of Thanet. The section is abstracted from detailed measurements made by one of us (A. S. G.) and gives only selected marker horizons, to which records of species are related.

Details of the distribution of *Infulaster* and *Hagenowia* in north-west Germany are taken from Ernst and Schulz (1971, 1974). In connection with this, it is important to note that the Turonian-Coniacian boundary in Germany is taken at a different level from that generally used in England, where the *Holaster planus*-*Micraster cortestudinarium* zonal junction is taken as the stage boundary (Rawson *et al.* 1978). The base of the Coniacian in the German sense probably falls within the basal few metres of the *coranguinum* Zone at Dover, on the basis of evidence from *Inoceramus* faunas.

SYSTEMATIC PALAEOLOGY

Order HOLASTEROIDA Durham and Melville, 1957

Family HOLASTERIDAE Pictet, 1857

Genus INFULASTER Desor, 1858

Type Species. *Cardiaster hagenowi* d'Orbigny 1853 (= *Spatangus excentricus* Woodward 1833; see Wright and Wright 1949, p. 455).

Diagnosis. Small to medium-sized holasterids, proportionately narrow and tall, with apex positioned anteriorly. Anterior ambulacrum set in a sulcus which runs from the apex to the transversely rounded peristome on the adoral surface. Paired ambulacra flush with test, non-petaloid. Apical system uninterrupted, elongated, with four genital pores. Periproct situated at summit of steep posterior truncation. Plastron metasternal, weakly keeled. Marginal fasciole present.

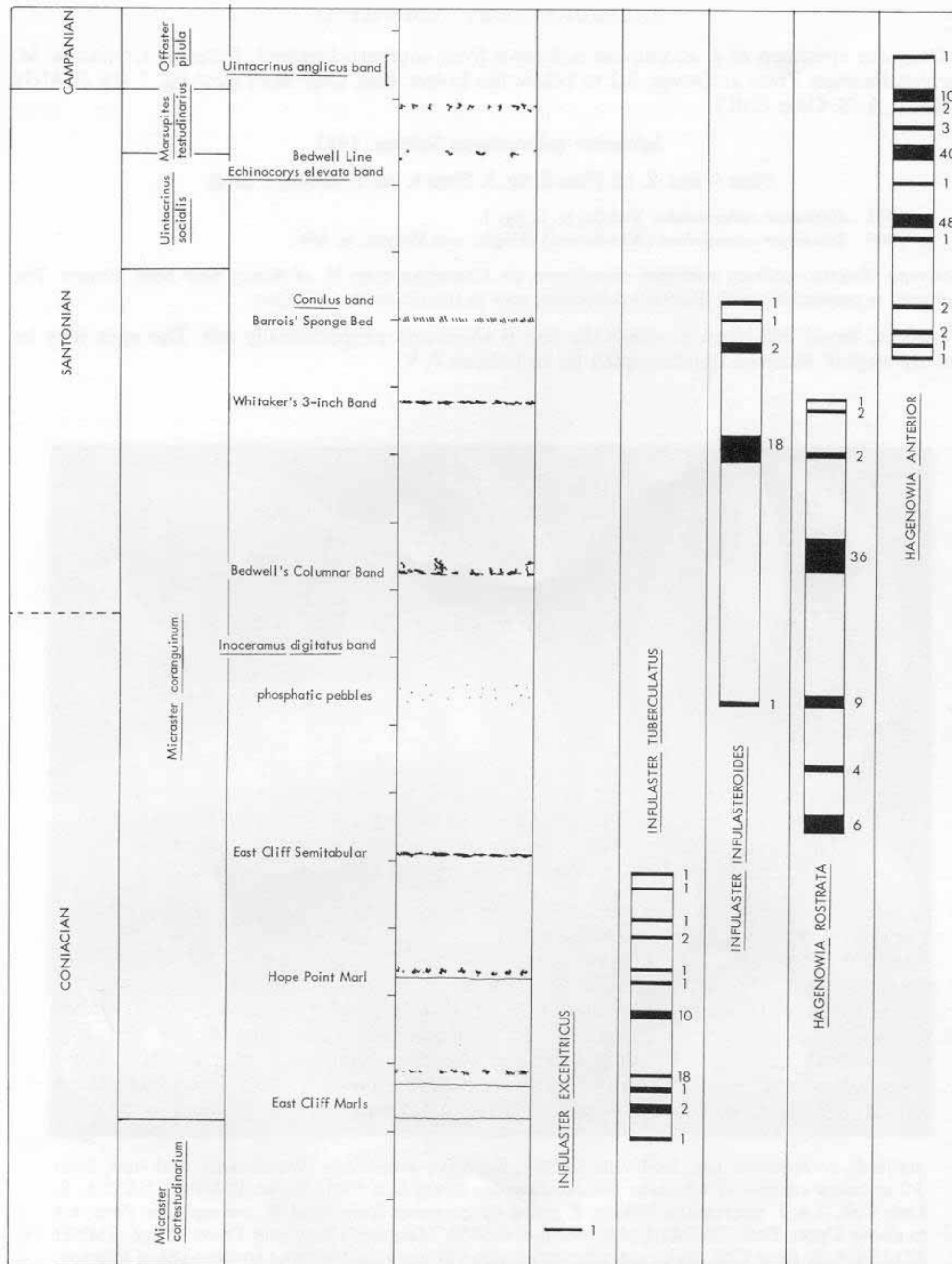
Remarks. The diagnosis given above essentially follows the description of *Infulaster* given by Wright and Wright (1949), with some elaboration.

Wright and Wright (1949) regarded *I. excentricus* as the only valid species of *Infulaster*, and placed *I. krausei* Desor, *I. borcharidi* Desor, *I. hagenowi* (d'Orbigny), and *I. tuberculatus* Valette in synonymy with it. *I. tuberculatus* is here considered to be a separate species, and its descendant, *Hagenowia infulasteroides* Wright and Wright is transferred to *Infulaster*. This species displays a number of features previously thought to be exclusive to *Hagenowia*, notably interruption of the pastron and elongation of the dorsolateral plate columns. *Infulaster* thus differs from *Hagenowia* only in its uninterrupted apical system and lack of a rostrum.

Infulaster excentricus (Woodward, 1833)

Text-fig. 2 (1)

Remarks. Large forms of *Infulaster* occur commonly in the Middle and Upper Turonian of the northern province in England (north Norfolk, Lincolnshire, Yorkshire) and in the eastern extension of the province in north-west Germany (Ernst and Schulz 1971), Poland (Nietsch 1921) and the Caucasus (Moskveena 1959). For these, the name *I. excentricus* is used provisionally, and it is not intended in this paper to revise and redescribe this material, which may include more than one species.



TEXT-FIG. 1. Generalized succession in the Senonian Chalk (lowest beds omitted) of the Kent coast, with selected marker bands only, showing the distribution of species of *Infulaster* and *Hagenowia*. Scale on left of column in 5 m intervals. Flints solid black.

Only one specimen of *I. excentricus* is known from southern England, from the Coniacian *M. cortestudinarium* Zone at Dover, 3·2 m below the Lower East Cliff Marl (text-fig. 2 (1); BMNH E76832, A. S. Gale Coll.)

Infulaster tuberculatus Valette, 1913

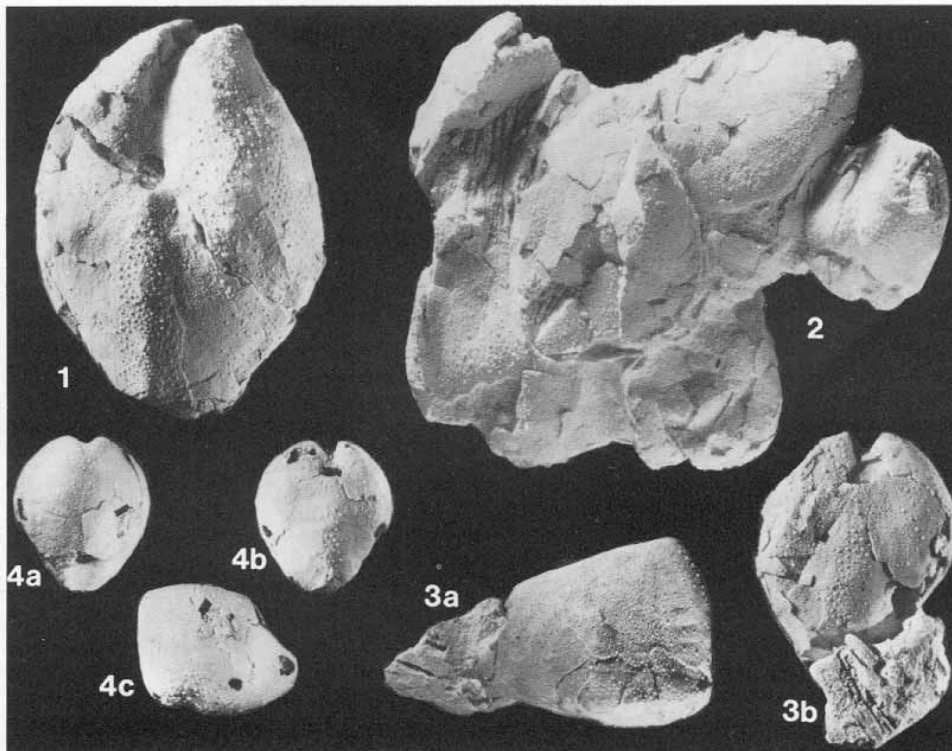
Plate 4, figs. 2, 11; Plate 5, fig. 3; Plate 6, fig. 5; text-fig. 2 (2-4)

1913 *Infulaster tuberculatus* Valette, p. 5, fig. 1.

p. 1949 *Infulaster excentricus* (Woodward) Wright and Wright, p. 456.

Holotype. Valette's solitary specimen came from the Coniacian zone H, of Rosoy near Sens, France. The specimen is presumably with Valette's collection, now in the University of Dijon.

Diagnosis. Small *Infulaster* in which the test is short and proportionally tall. The apex may be acutely angled. Plastron uninterrupted by ambulacra I, V.



TEXT-FIG. 2. *Infulaster* spp. from east Kent: 1, *Infulaster excentricus* (Woodward), oral view, from 3·2 m below summit of *Micraster cortestudinarium* Zone, East Cliff, Dover. BMNH E76832 A. S. Gale Coll. 2-4, *I. tuberculatus* Valette. 2, group of specimens from basal *M. coranguinum* Zone, 0·8 m above Upper East Cliff Marl, cliffs north-east of St. Margaret's Bay, near Dover, Kent. BMNH E76833, A. S. Gale Coll. 3a, b, oral and lateral views of individual without stratigraphical location, east of Dover, Kent. BMNH E10300 Cockburn Coll. 4a-c, dorsal, oral, and lateral views of specimen from 0·5 m below Lower East Cliff Marl, top of *M. cortestudinarium* Zone, East Cliff, Dover, Kent. BMNH E76834, A. S. Gale Coll. All specimens $\times 2$. Coated in ammonium chloride.

Remarks. Small *Infulaster* with lengths of 10–20 mm are common in the Lower *coranguinum* Zone of east Kent. These are almost invariably crushed and fragmentary, but the few well-preserved individuals show close similarities in shape with Valette's figures of *I. tuberculatus*. The species differs from *I. excentricus* in having a proportionally shorter test with a steep posterior slope in addition to the consistent difference in size. Many individuals are slightly inflated just posterior to the apex. Specimens from the higher part of the range of the species at Dover, although distorted, have acutely angled apices, and can only be distinguished from *I. infulasteroides* (Wright and Wright) by their uninterrupted plastrons.

Occurrence. At Dover the species occurs in the highest 1.5 m of the *M. cortestudinarium* Zone, and the basal 18 m of the *M. coranguinum* Zone (text-fig. 1). The species is most common just beneath a band of large flints about 1 m above the upper East Cliff Marl, where clusters of individuals are found. The type specimen came from the Coniacian H of Rosoy, a level equivalent to approximately the lower half of the *coranguinum* Zone.

Infulaster infulasteroides (Wright and Wright 1949)

Plate 4, fig. 2

1949 *Hagenowia infulasteroides* Wright and Wright, p. 470, figs. 17, 18.

1971 *Hagenowia infulasteroides* Wright and Wright; Ernst and Schulz, p. 138, pl. 13, figs. 1–4; text-fig. 6.

Types. The holotype is a flint steinkern from the Haldon Gravel of Devon (Wright and Wright 1949, fig. 17; BMNH E8403). A paratype, similarly preserved, comes from flint gravel at Lulworth, Dorset (BMNH E1709). Both were probably derived originally from the upper part of the *coranguinum* Zone. A second paratype, a crushed, incomplete test from the *coranguinum* Zone of the North Foreland, near Broadstairs, Kent (BMNH E33886, Rowe Coll.) almost certainly came from a level 2–4 m below Whitaker's 3-inch band, the only horizon at which the species is common in east Kent.

Diagnosis. Test with acutely angled apex. Plates of interambulacra 1 and 4 on sides of test elongated. Plastron interrupted by ambulacra I and V.

Remarks. This species is transferred from *Hagenowia* to *Infulaster* on account of its undivided apical system, and the absence of a rostrum. The general morphology and variation is well illustrated by Ernst and Schulz (1971).

Occurrence. In east Kent *I. infulasteroides* ranges from 10 m below Bedwell's Columnar Band, up to the base of the *Uintacrinus* Zone (text-fig. 1). It is only common 2–4 m below Whitaker's 3-inch band, where it occurs in clusters. *I. infulasteroides* is also known from the upper *coranguinum* Zone of Berkshire, Hampshire, Sussex and the Isle of Wight, and the *Uintacrinus* Zone of Hampshire. Ernst and Schulz (1971) record this species from the Middle Santonian of Lagerdorf.

Genus HAGENOWIA Duncan, 1889

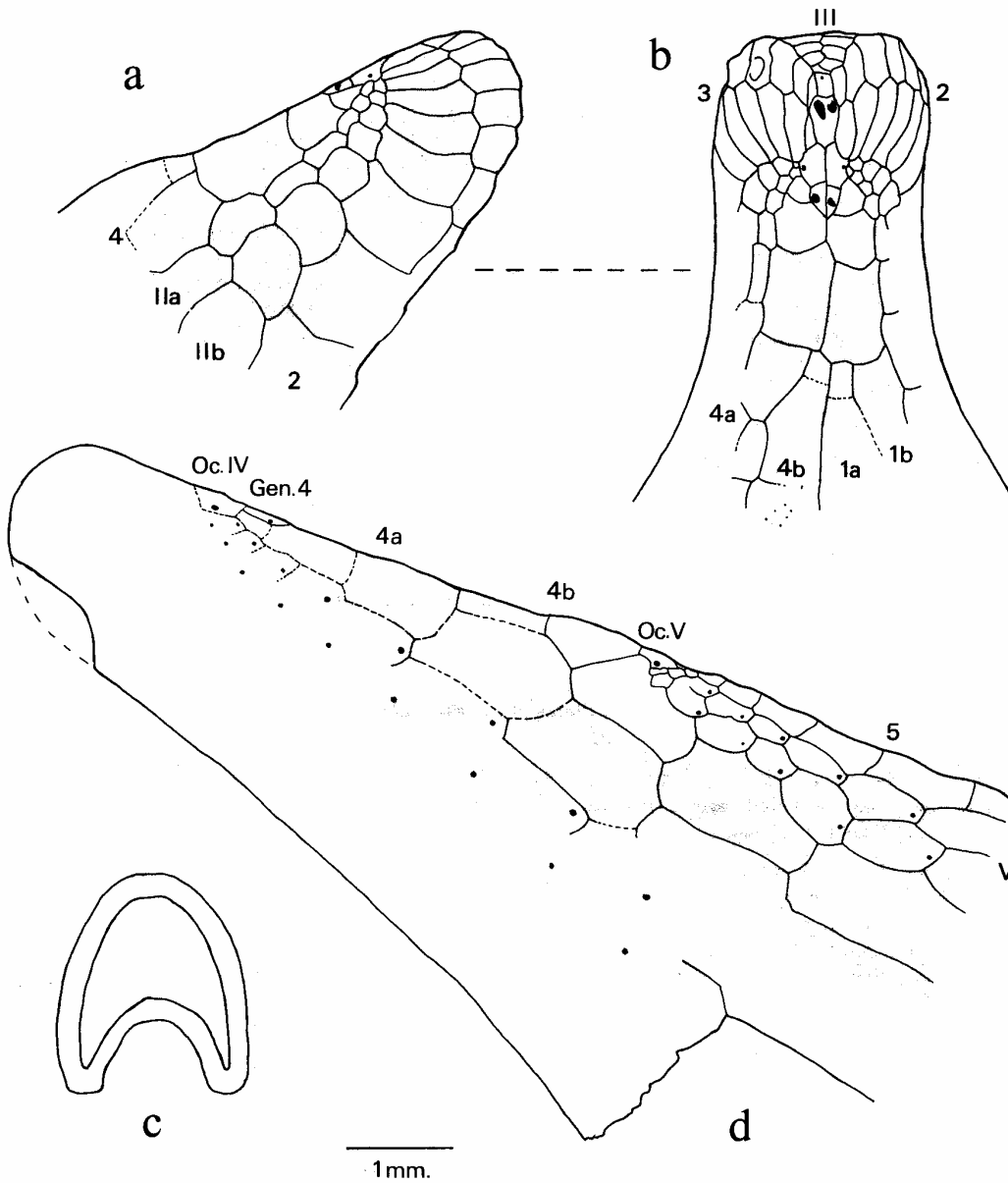
(= *Martinosigra* Nielsen, 1942)

Type species. *Cardiaster rostratus* Forbes 1852 by original designation.

Diagnosis. Small holasterids in which the apical part of the test is elongated antero-dorsally to form a tapering rostrum. Narrow, well-defined sulcus runs from apex of rostrum to circular peristome. Apical system disjunct, with two posterior oculars at base of rostrum separated from remainder of system (which is on rostral tip) by interambulacra 1 and 4. Two or four genital pores.

Longitudinally oval periproct is positioned at the summit of the posterior truncation. Plastron metasternal, keeled. Marginal fasciole.

Remarks. The diagnosis of *Hagenowia* is amended from that of Wright and Wright (1949), to exclude *I. infulasteroides* from the genus. The most important diagnostic feature of *Hagenowia* is



TEXT-FIG. 3. Plating structure and cross-sectional shape of the rostrum in *Hagenowia rostrata* (Forbes): *a* and *b*, dorsal and lateral views of a small individual from 1 m above Bedwell's Columnar Band, East Cliff, Dover. BMNH E76835, A. S. Gale Coll. *c*, cross-section of the rostrum, taken at the 3rd plate of interambulacral row 1*b*. Specimen from 1.5 m above Bedwell's Columnar Band, Ramsgate. BMNH E76836, A. S. Gale Coll. *d*, lateral view of specimen from 2 m above the East Cliff Semitabular, East Cliff, Dover. BMNH E76837, A. S. Gale Coll.

the separation of the apical system. Interruption of the plastron by ambulacra I and V is seen in all *Hagenowia* and is also present in *I. infulasteroides*.

Hagenowia rostrata (Forbes, 1852)

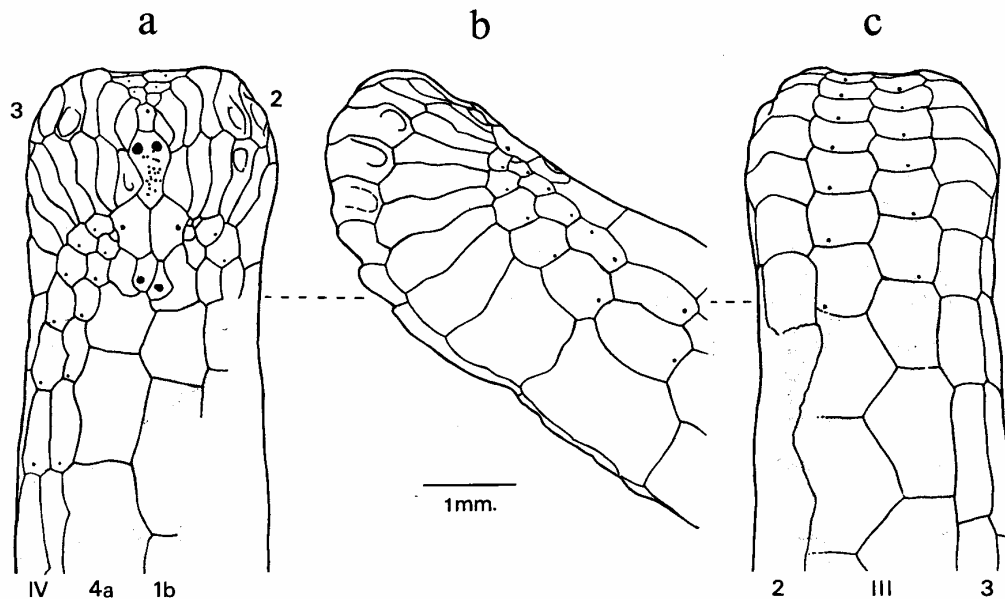
Plate 3, figs. 1-5; Plate 4, fig. 3; Plate 5, figs. 1, 2, 5; text-figs. 3, 4

- 1852 *Cardiaster rostratus* Forbes, p. 3, pl. 10, figs. 19-24.
 1858 *Infulaster rostratus* (Forbes); Desor, p. 348.
 1881 *Infulaster rostratus* (Forbes); Wright, p. 307, pl. 70, figs. 2, 3.
 1889 *Hagenowia rostrata* (Forbes); Duncan, p. 210.
 1942 *Martinosigra rostrata* (Forbes); Nielsen, p. 163.
 1949 *Hagenowia rostrata* (Forbes); Wright and Wright, p. 462, figs. 7, 8, 11, 12, non 9, 10.
 1971 *Hagenowia rostrata* (Forbes); Ernst and Schulz, p. 138, pl. 13, fig. 5; pl. 14, fig. 1; text-fig. 7.

Lectotype. A specimen figured by Forbes (1852, pl. 10, figs 19-21; IGS 38656) was taken as lectotype by Wright and Wright (1949). This came from the 'Chalk with Flints of Bostal Heath, near Plumstead' (Forbes 1852, p. 3), in south-east London, presumably from the upper part of the *coranguinum* Zone.

Diagnosis. Rostrum short, sharply tapering; plates of ambulacral rows IIa, IVb contiguous, not reduced; posterior side of rostrum broad, evenly rounded; sulcus deep; subanal protruberance double, asymmetrical.

Remarks. The plating arrangements of the rostrum is completely known only in this species of *Hagenowia* (text-figs. 3, 4). Oculars I and V are small, and positioned at the base of the rostrum. Together with ambulacra I and V, and interambulacrum 5, they are separated from the rest of the apical system along the dorsal margin of the rostrum by interambulacra 1 and 4 (text-fig. 3). The



TEXT-FIG. 4. Plating structure of the rostrum tip in *Hagenowia rostrata* (Forbes): a-c, Dorsal, lateral, and frontal views of large specimen from 3 m below Whitaker's 3-inch band, North Foreland, near Broadstairs, Kent. BMNH E76838, A. S. Gale Coll.

first two plates of interambulacral rows 1a and 4b meet along the dorsal margin of the rostrum above oculars I and V. The second plates are often slightly swollen in lateral profile and form a distinct, low protuberance at the base of the rostrum (e.g. Pl. 3, fig. 2b). 1a and 4b are occluded from the rostrum above this level by two or three plates of the outer rows, 1b and 4a.

Variations in test shape of *H. rostrata* is shown by a group of specimens from the upper *coranguinum* Zone of the Kent coast (Pl. 3, figs. 1-5). Low, depressed forms with relatively high anterior angles (Pl. 3, fig. 1) intergrade continuously through to tall individuals with steep sides and more upright rostra (Pl. 3, fig. 2). No stratigraphical separation of these forms is known to occur. Small individuals of *H. rostrata* have shorter, less well demarcated rostra (Pl. 3, fig. 4).

Ernst and Schulz (1971, p. 138, text-fig. 7, fig. 1) recorded a stratigraphically low 'early form' of *H. rostrata* from the (? Lower) Coniacian of Lagerdorf, north-west Germany. This has a short posterior slope, a short rostrum, and a flat profile to the base. A single specimen (Pl. 3, fig. 5) from the lowest horizon at which *Hagenowia* occurs at Dover, some 2 m above the East Cliff Semitabular flint (text-fig. 1) compares quite well in lateral profile with the figured Lagerdorf individual. The Dover specimen differs from other English examples of *H. rostrata* in having a broad, relatively shallow sulcus without narrow margins. In anterior profile, the sides of the test do not inflect sharply as the body passes into the rostrum.

Occurrence. On the Kent coast (text-fig. 1) *H. rostrata* is found in a succession of discrete bands in the *coranguinum* Zone, from the East Cliff Semitabular to Whitaker's 3-inch band. It occurs in the same zone throughout its outcrop in southern England, although precise details of horizon are seldom recorded. In northern France a solitary example was found 3 m below the equivalent of Whitaker's 3-inch band at Coquelles, near Calais (A. S. G. Coll.). In Yorkshire, Rowe (1904) used *H. rostrata* as a local index for the *M. coranguinum* Zone, which was subsequently formalized by Wright and Wright (1942). Recent study has shown that the species of *Hagenowia* common in the flintless chalk of the Yorkshire coast below the entry of *Uintacrinus* is, in fact, *H. anterior*. The only true *H. rostrata* we have seen from Yorkshire are from the flinty chalk with *Inoceramus involutus* of Little Weighton (Wrights' Coll.). In north-west Germany *H. rostrata* occurs in the Coniacian Chalk at Lagerdorf (Ernst and Schulz 1971, text-fig. 5; 1974, text-fig. 4a).

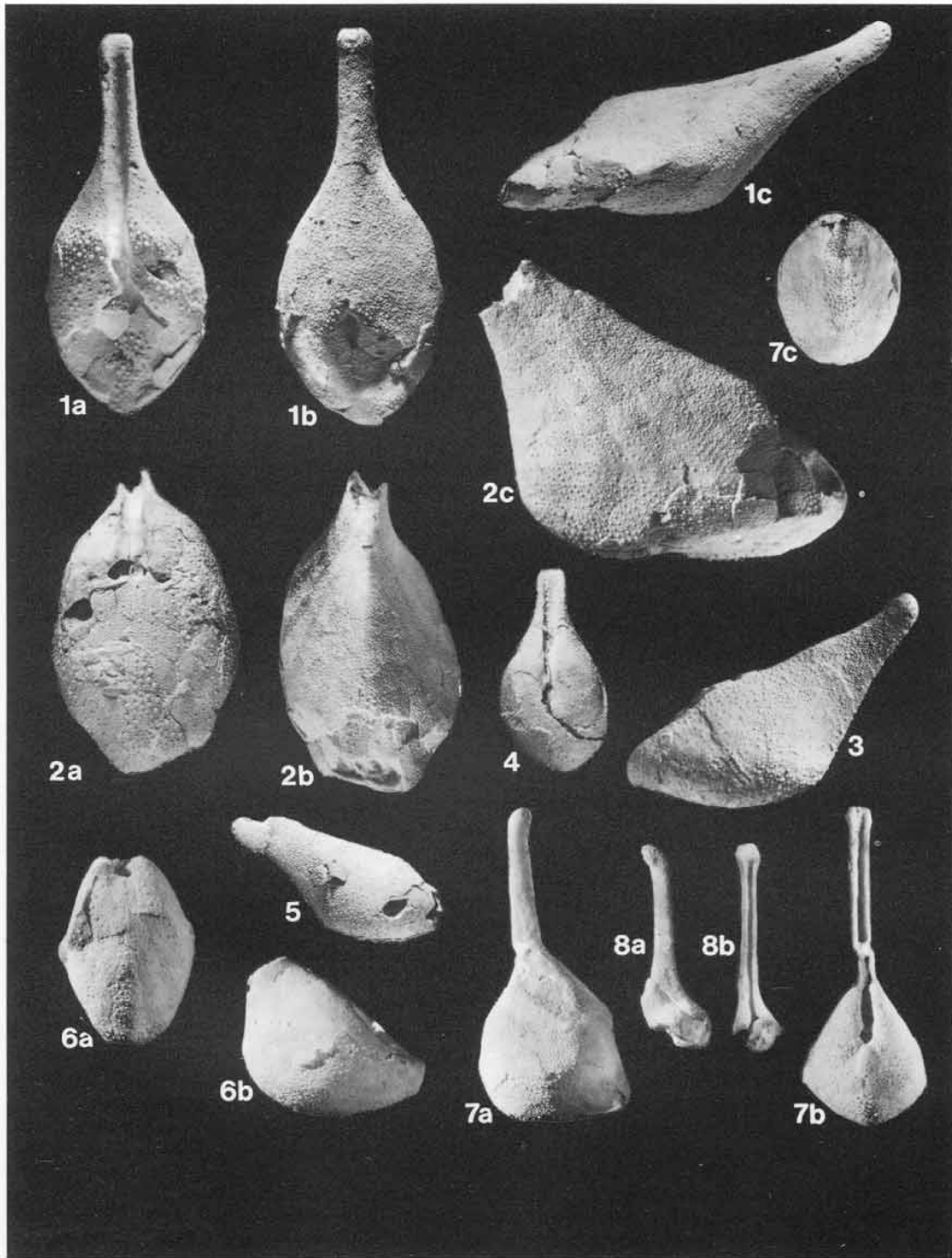
EXPLANATION OF PLATE 3

Figs. 1-5. *Hagenowia rostrata* (Forbes). *Micraster coranguinum* Zone, Kent coast. 1a-c, oral, dorsal, and lateral views of depressed specimen from 3 m beneath Whitaker's 3-inch band, North Foreland near Broadstairs. BMNH E76838, A. S. Gale Coll. 2a, b, oral and lateral views of high individual, with more vertical rostrum, retaining radioles on the base from 2 m above Bedwell's Columnar Band, same locality. BMNH E76848, A. S. Gale Coll. 3, lateral view of specimen, same horizon and locality. BMNH E76849, A. S. Gale Coll. 4, small individual with short rostrum, 1 m above Bedwell's Columnar Band, East Cliff, Dover. BMNH E76835, A. S. Gale Coll. 5, lateral view of specimen with poorly demarcated rostrum. 2 m above East Cliff Semitabular, East Cliff, Dover. BMNH E76850, A. S. Gale Coll.

Fig. 6a, b. *H. anterior* Ernst and Schulz. Oral and lateral views of body. The rostrum has broken off, and its base is bored. *Uintacrinus* Zone, Harding's Whiting Pits, Devizes Road, Salisbury Wilts. BMNH E35788, Blackmore Coll.

Figs. 7, 8. *H. blackmorei* Wright and Wright. 7a-c, lateral, frontal, and oral views of the holotype (body only). The rostrum belongs to *H. anterior* and has been artificially attached. Lower Campanian, probably lower *G. quadrata* Zone, West Harnham, near Salisbury, Wilts. BMNH E33916, Blackmore Coll. 8a, b, lateral and frontal views of rostrum from *Hagenowia* horizon, lower *G. quadrata* Zone, pit no. 3 of Gaster (1924), North Lancing, near Worthing, Sussex. I.G.S. no. Zm 2907.

All specimens $\times 2$. Coated with ammonium chloride.



GALE and SMITH, Cretaceous irregular echinoids

Hagenowia anterior Ernst and Schulz, 1971

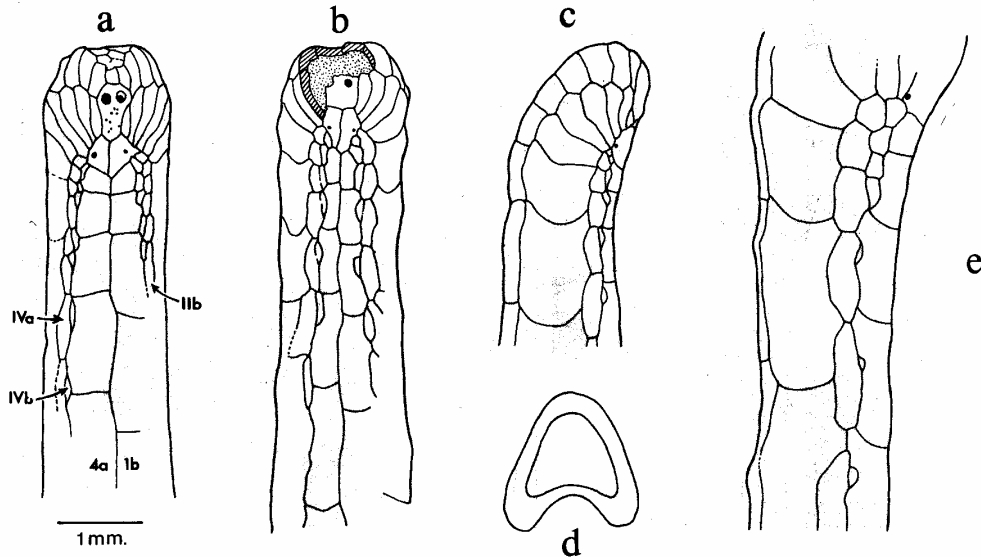
Plate 3, fig. 6; Plate 4, figs. 5, 10, 12; Plate 5, figs. 6, 8; Plate 6, figs. 2, 6, 8; text-fig. 5

1949 *Hagenowia rostrata* (Forbes); Wright and Wright, p. 462, figs. 9, 13.1971 *Hagenowia blackmorei* Wright and Wright, *anterior* Ernst and Schulz, p. 140, pl. 13, fig. 6; pl. 14, figs. 2, 3; text-fig. 8.

Types. The holotype is from the Middle Santonian *rogalae-westfalica* Zone of Lagerdorf, north-west Germany (Ernst and Schulz 1971, text-fig. 8, fig. 1; pl. 14, figs. 2, 3). The paratypes are from the same horizon and locality.

Diagnosis. Rostrum long and slender, cross-section triangular, posterior side evenly rounded; individual plates of ambulacral rows IIa, IVb small, separated by interambulacral rows 1a, 4b and ambulacral rows IIb, IVa in the rostrum; subanal protruberance single, narrow.

Remarks. The plating arrangement of all but the basal rostrum is known in this species (text-fig. 5). Individual plate rows are proportionately longer and narrower than in *H. rostrata*. At least six plates of interambulacral rows 1a, 4b meet along the dorsal margin of the rostrum (text-fig. 5b); these are variable in width. Plates of ambulacral rows IIa and IVb are small, and although the first few are usually in contact with each other, most are separated by 1a and 4b, and IIb, IVa (text-fig. 5A-C, E). The size and shape of these occluded plates is variable. In some individuals (e.g. text-fig. 5E) plates of IIa and IVb are locally separated by interambulacra 1a, 4b and 2a, 3b. Genitals 1 and 4 are absent.



TEXT-FIG. 5. Plating structure and cross-sectional shape of the rostrum in *Hagenowia anterior* Ernst and Schulz: a, dorsal view of rostrum from 5 m above Whitaker's 3-inch band, Kingsgate, Kent. BMNH E76839, A. S. Gale Coll. b, dorsal view of rostrum from basal 1 m. of *Marsupites* Zone, Minnis Bay, Kent. BMNH E76840, A. S. Gale Coll. c, lateral view of rostrum tip, mid *Uintacrinus* Zone, near Margate, Kent. BMNH E76841, A. S. Gale Coll. d, cross-section of rostrum, taken at 2nd/3rd plate of interambulacral row 1b, mid *Uintacrinus* Zone, near Margate. e, lateral view of rostrum, base of *Uintacrinus anglicus* band, Foreness Point, near Margate. BMNH E76842, A. S. Gale Coll.

Some variation in the attitude of the rostrum occurs in *M. anterior*, although the body shape is quite consistent. Lateral furrows on the sides of the test, just anterior to the periproct (Ernst and Schulz 1971, text-fig. 8, figs. 2, 3) are sometimes present. *H. anterior* is raised to specific rank on account of significant differences in rostral structure and body shape from *H. blackmorei*.

Occurrence. In east Kent the species first appears at 3.5 m above Whitaker's 3-inch band in the *coranguinum* Zone and ranges up into the *Uintacrinus anglicus* band in the lower *Offaster pilula* Zone (text-fig. 1). Levels of abundance occur in the mid *U. socialis* Zone and in the basal *Marsupites* Zone. Scattered records of this species exist from Dorset, Wiltshire, Hampshire, and the Isle of Wight (*Uintacrinus* Zone). In Yorkshire *H. anterior* occurs commonly in the flintless upper part of the *coranguinum* Zone and ranges up into the lower Campanian *I. lingua* Zone. At Lagerdorf the species ranges from the mid *rogalae-westfalica* Zone to the *Marsupites* Zone, with one doubtful earlier record from the *coranguinum-westfalica* zone (Ernst and Schulz 1971, 1974).

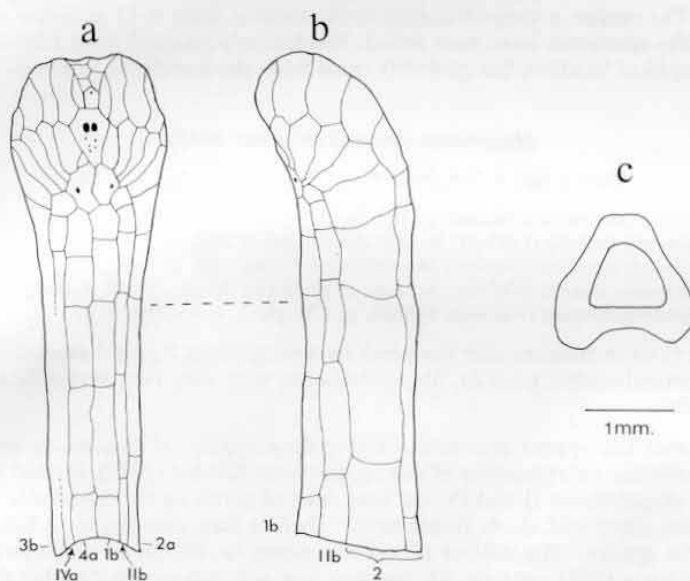
Hagenowia blackmorei Wright and Wright, 1949

Plate 3, figs. 7, 8; Plate 4, fig. 6; Plate 6, figs. 4, 7, 9; text-fig. 6

1949 *Hagenowia blackmorei* Wright and Wright, pp. 467-70, figs. 14-16.

1971 *Hagenowia blackmorei blackmorei* Wright and Wright; Ernst and Schulz, p. 140, text-fig. 2.

Types. The specimen chosen as holotype by Wright and Wright (1949, fig. 14) is from the Lower Campanian Chalk of East Harnham, near Salisbury, Wiltshire (BMNH E33916, Blackmore Coll.), probably from the *G. quadrata* Zone. However, as pointed out by C. J. Wood (*in* Ernst and Schulz 1971), the body and rostrum belong to two specimens of separate species, and have been artificially joined. The body belongs to the species



TEXT-FIG. 6. Plating structure and cross-sectional shape of the rostrum in *Hagenowia blackmorei* Wright and Wright: *a, b*, dorsal and lateral views of rostrum, based on specimen from 10 m. above *planoconvexa* bed, *G. quadrata* Zone, cliffs west of Newhaven, Sussex. BMNH E76843, A. S. Gale Coll. *c*, cross-section of rostrum 3 mm below tip, same horizon and locality.

characteristic of the lower *quadrata* Zone of southern England, and possesses the features of *H. blackmorei* as described by Wright and Wright. The rostrum is from an individual of *H. anterior* from the Santonian. The body alone is therefore selected as lectotype. The paratype is an internal and external mould in flint from the Haldon Gravel, Devon (Wright and Wright 1949, figs. 14, 15; BMNH E8404, Vicary Coll.).

Diagnosis. Rostrum slender, upright, well demarcated from body, equilaterally triangular in cross-section; interambulacral rows 1a, 4b form narrow dorsal ridge on rostrum, surface of ambulacral rows IIb, IVa slightly inset; sulcus shallow, with a gently concave floor; IIa, IVb not present in rostrum; body squarish in lateral profile, anterior part of base vertically below peristome; subanal protuberance single, small; posterior slope steep; fasciole noticeably oblique.

Remarks. The structure of the rostrum in this species (text-fig. 6) is similar to that in *H. elongata* (Nielsen) (Schmid 1972) but individual plates are less elongated and broader than in the Maastrichtian species. The dorsal ridge on the rostrum is broader and less sharply defined than in *H. elongata*, and genitals 2, 3 are not usually separated from oculars II, IV in *H. blackmorei*, as is invariably so in *H. elongata*. The latter species has only two, vertically situated, madreporic pores, whereas the number and arrangement of these is variable in *H. blackmorei*.

A few *Hagenowia* rostra are known from the Upper Campanian *Belemnitella mucronata* Zone of southern England (Wright and Wright 1949). These show affinities with both *H. blackmorei* and *H. elongata*, but lack the specialized madreporic pores of the latter and are referred to *H. cf. blackmorei*.

Occurrence. *H. blackmorei* appears to be restricted to the lower part of the *G. quadrata* Zone in southern England. Gaster (1924) used the term *Hagenowia* horizon for this level in Sussex. Collecting from the cliffs west of Newhaven in Sussex suggests that the species occurs only within the 12 m of chalk above the marl pair (*planoconvexa* bed) taken by Brydone (1914) as the base of the *G. quadrata* Zone. The species is only abundant in the interval from 9–11 m above this bed, where approximately fifty specimens have been found. Blackmore's material from East Harnham lacks detailed stratigraphical location, but probably came from the correlative horizon.

Hagenowia elongata (Nielsen, 1942)

Plate 4, figs. 4, 7–9; Plate 5, figs. 7, 9; Plate 6, figs. 1, 3, 10

1942 *Martinosigra elongata* Nielsen, p. 163, fig. 2.

1949 *Hagenowia rostrata* (Forbes); Wright and Wright, p. 462.

1950 *Hagenowia elongata* (Nielsen); Mortensen, p. 97, fig. 100.

1971 *Hagenowia elongata* (Nielsen); Schmid, in Ernst and Schulz, p. 141, text-fig. 2, el.

1972 *Hagenowia elongata* (Nielsen); Schmid, p. 179, pls. 1–4; text-figs. 1, 2.

Diagnosis. Plate rows in rostrum very long and narrow; genitals 2 and 3 separated from oculars II and IV by interambulacral rows 2a, 3b; madreporite with only two, vertically situated, pores; sulcus shallow, flat.

Remarks. Now that the rostral structures of preceding species of *Hagenowia* are known, it is necessary to modify the interpretation of this species from Schmid (1972). Instead of representing both plate rows of ambulacra II and IV, the four rows of plates on the dorsal side of the rostrum are IIb, IVa (outer rows) and 1b, 4a (inner rows). There is little else to add to Schmid's excellent description of the species. The outline of a body stated to belong to this species was shown by Ernst and Seibertz (1977, text-fig. 6), but this new material awaits detailed description and figuring.

Occurrence. Upper Lower Maastrichtian, Zone of *Belemnella occidentalis*, Denmark and north-west Germany.

PHYLOGENY

Wright and Wright (1949) suggested that *I. infulasteroides* arose from the 'small *I. excentricus*' of the *cortestudinarium* Zone (here *I. tuberculatus*) and subsequently gave rise to *H. rostrata*. They regarded *H. blackmorei* as a short-lived offshoot from *H. rostrata*, which itself survived into the Upper Campanian. Ernst and Schulz (1971, p. 141, text-fig. 2) modified this story only slightly, by placing the origin of *H. rostrata* near the point at which an *infulasteroides* lineage diverged from the main *Infulaster* stock. They retained separate *rostrata* and *blackmorei* lineages throughout the Santonian and Campanian. More recently, Ernst and Seibertz (1977, p. 563, text-fig. 6) showed the *H. rostrata* lineage as terminating within the Middle Santonian.

It is suggested here that only two lineages are recognizable in this group of echinoids.

1. *Infulaster* lineage: *I. excentricus* (*sensu lato*)—*I. tuberculatus*—*I. infulasteroides*
2. *Hagenowia* lineage: *H. rostrata*—*H. anterior*—*H. blackmorei*—*H. elongata*.

Since *Hagenowia* appeared before *I. tuberculatus* gave rise to *I. infulasteroides*, it is likely that the origins of this genus lay in the former species, probably during the mid-Coniacian. In this case, *I. infulasteroides* parallels rather than antecedes *Hagenowia* in the development of an acutely angled apex and an interrupted plastron.

Although the over-all changes in each of the lineages are progressive, individual species are in general well demarcated from both ancestor and descendant. No two species in either lineage are known definitely to overlap in stratigraphical order.

EVOLUTIONARY TRENDS

1. *Size*. In the *Infulaster* lineage there is a dramatic decrease in size from *I. excentricus*, which is characteristically between 40 and 50 mm in length, to *I. tuberculatus* (15–25 mm). With this change, the test became proportionately shorter and deeper. In late *I. tuberculatus* and in *I. infulasteroides* the apex of the test became more acutely angled resulting from an increase in the length of plate rows on the sides of the test.

2. *Rostrum*. In *Hagenowia* the apical system is separated into two parts to form a trivium and bivium. This was a direct consequence of the considerable elongation of the apical region.

In the earliest species, *H. rostrata*, oculars I and V are separated from genitals 1 and 4 by interambulacral rows 1 and 4 along the dorsal side of the rostrum. Plate rows 1a and 4b are occluded from the distal rostrum by rows 1b and 4a, which meet along the dorsal mid-line. Rostral plates are elongated, the sulcus is deep, and the body cavity within the rostrum is large. In profile, the rostral tip is only slightly enlarged.

In *H. anterior* the rostrum is better demarcated from the body and is relatively narrow. Plate rows are proportionately narrower and more plates per row are present in the rostrum. Plates of ambulacral rows IIa and IVb are typically diminutive while genitals 1 and 4 have been lost. In comparison with *H. rostrata*, the rostrum of *H. anterior* is more equilaterally triangular in cross-section and the rims of the sulcus, formed by interambulacral rows 2b and 3a, are distinctly thickened. The walls of the rostrum are also proportionally thicker and the body cavity smaller. The sulcus is significantly shallower.

The trend towards increasing slenderness and sharper demarcation of the rostrum is continued in *H. blackmorei*. Ambulacral rows IIa and IVb are lost completely from the part of the rostrum where the plating arrangement is known. Rostral plates are more elongate than in previous species. In cross-section, the rostrum is triangular and thickened at each corner while the body cavity is further reduced. Ambulacral plate rows IIa and IVb are slightly depressed. The sulcus is shallower than in *H. anterior* and its rims are parallel. The tip of the rostrum is broader than the shaft and the rostrum is more or less vertical in attitude.

Rostral development is most pronounced in *H. elongata*. Rostral plates are narrower and more elongate than in any of its predecessors. Interambulacral plate rows 2a and 3b always separate

genitals 2 and 3 from oculars II and IV. Only two vertically placed madreporic pores are present.

Summarizing these trends, there is a progressive increase in the slenderness and clearer demarcation of the rostrum. This is achieved through elongation and narrowing of plate rows, increasing the number of plates in each row present, and loss of plate rows. The rostrum adopts a more vertical attitude and is strengthened by the development of buttresses and by thickening of the walls. The body cavity within the rostrum is progressively reduced and genitals 1 and 4 are lost during evolution.

3. *Body.* The body of *H. rostrata* differs little from that of the ancestral *Infulaster*. During the evolution of *Hagenowia* there were five important changes to the structure of the body. Firstly, the plastron became interrupted in *I. infulasteroides* and in all species of *Hagenowia*. Secondly, the base became progressively more convex. Thirdly, the peristome moved from a basal to an anterior position with a vertical attitude. Fourthly, the posterior slope became more vertical and the fasciole more oblique. Finally there was a change from a double, asymmetrical sub-anal protruberance in *H. rostrata* to a single centrally placed protruberance in later species.

4. *Pore morphology.* The more important changes in pore morphology during the evolution of *Infulaster* and *Hagenowia* include the progressive loss of phyllode and dorso-lateral pores and the increasing differentiation of pores at the rostral tip. Three distinct regions of pores are recognizable and will be dealt with separately. Pore terminology is taken from Smith (1980a).

(a) *Phyllode pores.* In *Infulaster*, phyllode pores are relatively large isopores, rounded in outline, with an axially positioned neural canal in an adoral position. They are 300–350 μm in length in *I. excentricus* but only 180–250 μm in length in later species. Thirty such pores lie around the peristome in *I. excentricus* but only 20 to 22 are present in *I. tuberculatus* and *I. infulasteroides*. Similar phyllode pores are found in *H. rostrata* and *H. anterior*. *H. rostrata* has between 14 and 18 such pores while *H. anterior* has slightly fewer (the exact number cannot be ascertained in any of the specimens examined). *H. blackmorei* has only two small, circular unipores lacking any periporal ornament. These lie on either side of the anterior sulcus immediately above the peristome. There is no sign of pores in lateral and posterior ambulacra adjacent to the peristome.

(b) *Latero-dorsal pores.* In *Infulaster*, isopores of the posterior columns of ambulacra II and IV are twice as long as other latero-dorsal pores. These elongate isopores have no obvious neural

EXPLANATION OF PLATE 4

Bottom of micrograph adoral unless otherwise stated.

Fig. 1. *Infulaster infulasteroides*: latero-dorsal partitioned isopore from interambulacrum 5. BMNH E76851.

Fig. 2. *I. tuberculatus*: partitioned isopore with axially positioned neural canal near the apex of ambulacrum III. BMNH E76852.

Fig. 3. *Hagenowia rostrata*: partitioned isopore with axially positioned neural canal near the apex of ambulacrum III. BMNH E7684.

Fig. 4. *H. elongata*: simple unipore of ambulacrum III within the rostral sulcus. MM 12820.

Fig. 5. *H. anterior*: unipore with broad periporal area in ambulacrum III at the rostral head. Adoral to the right. BMNH E76844.

Fig. 6. *H. blackmorei*: unipore with broad periporal area in ambulacrum III at the rostral head. BMNH E76846.

Fig. 7. *H. elongata*: unipore in ambulacrum III at the rostral head.

Fig. 8. *H. elongata*: tuberculation on the lateral face of the rostrum. Apex to the left, dorsal ridge at top.

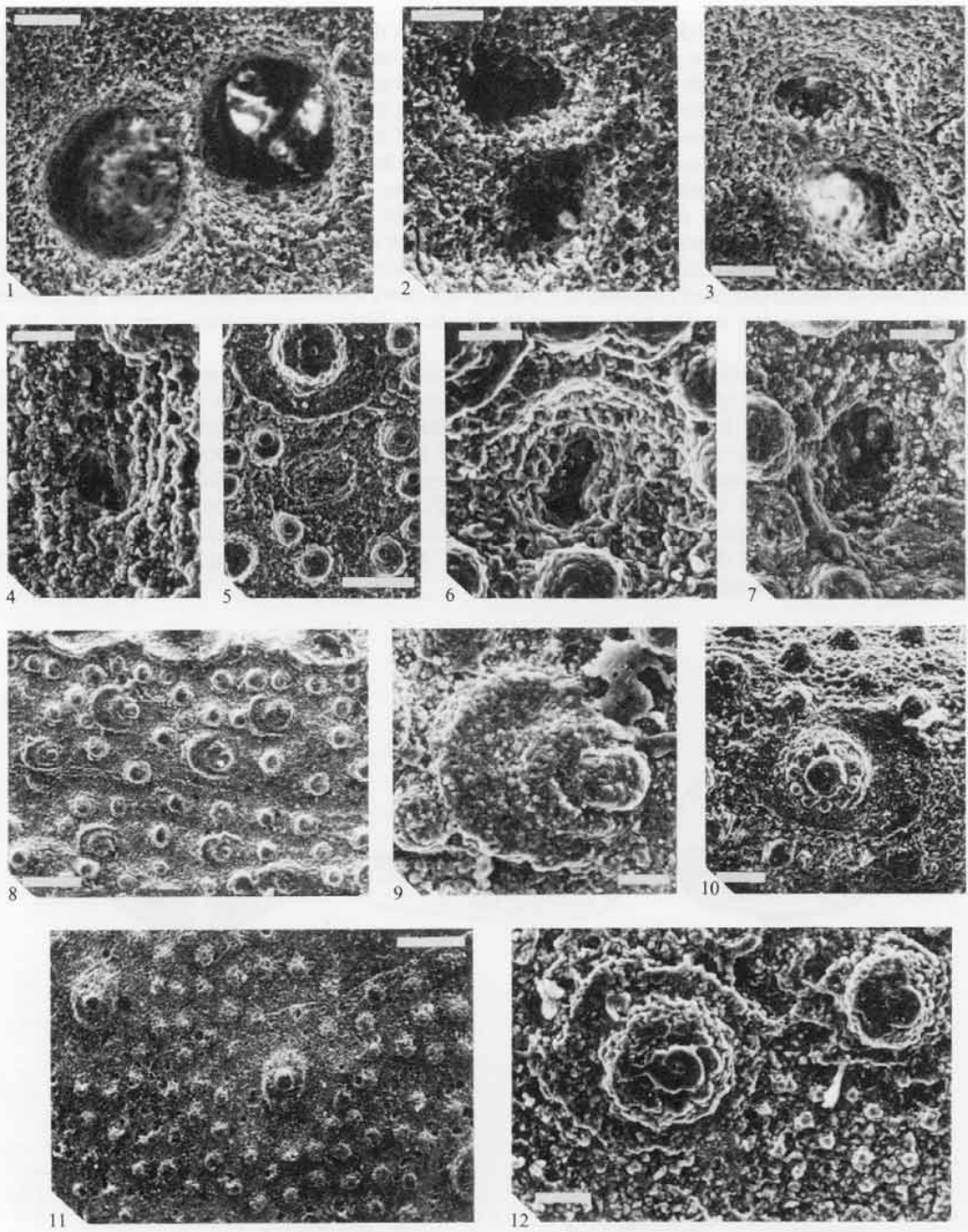
Fig. 9. *H. elongata*: enlargement of fig. 8 showing one tubercle.

Fig. 10. *H. anterior*: dorsal tubercle on rostrum showing enlarged areole and radially symmetrical crenulation.

Fig. 11. *I. tuberculatus*: latero-dorsal tubercles.

Fig. 12. *H. anterior*: latero-dorsal tubercles at the base of the rostrum.

Scale bar in figs. 1–4, 6, 7, 9, 12 = 100 μm ; figs. 5, 8, 10, 11 = 200 μm .

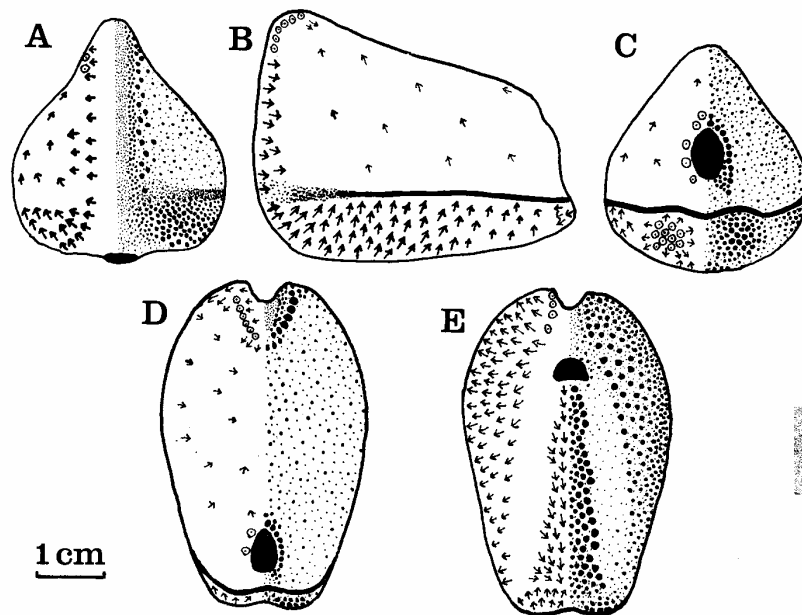


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canal and the interporal partition is more or less flush with the test surface and may be very broad. Other dorso-lateral pores are partitioned isopores with a small, laterally positioned neural canal (Pl. 4, fig. 1). All isopores are widely spaced and have no recognizable attachment area. Pores of *I. excentricus* are approximately twice the size of pores in later species.

Latero-dorsal pores vary tremendously in specimens of *H. rostrata*. In some of the larger specimens there are isopores, arranged as in *Infulaster*. One of these has elongate isopores of ambulacra IIb and IVa which are even larger than those in *I. excentricus*. The majority of specimens lack such elongate isopores and have small partitioned isopores in all columns. In other specimens, all latero-dorsal pores are reduced to unipores. Finally, one specimen has unipores in ambulacral columns IIb and IVa and small partitioned isopores in columns IIa and IVb. In *H. anterior* there are no pores in rostral plates of ambulacra II and IV but there are between three and five partitioned isopores in each column on the body above the fasciole. There are no latero-dorsal pores in *H. blackmorei*.

(c) *Ambulacrum III pores*. Pores in the frontal sulcus are similar in size and shape in the three species of *Infulaster* and in *H. rostrata*. These are partitioned isopores with axially aligned neural canals (Pl. 4, figs. 2, 3). Pores near the apex are identical with those within the sulcus. In later species of *Hagenowia*, pores in the sulcus are smaller than those at the apex. The 12 to 14 most adapical pores in *H. anterior* and *H. blackmorei* are unipores, circular in outline, and with a narrow central pore surrounded by a clear periporal area (Pl. 4 figs. 5, 6). Unipores in the sulcus are smaller with a reduced periporal area. In the apical unipores of *H. elongata*, the central pore is much larger and most of the periporal area is lost (Pl. 4, fig. 7). Unipores in the sulcus are minute and lack periporal ornament (Pl. 4, fig. 4).



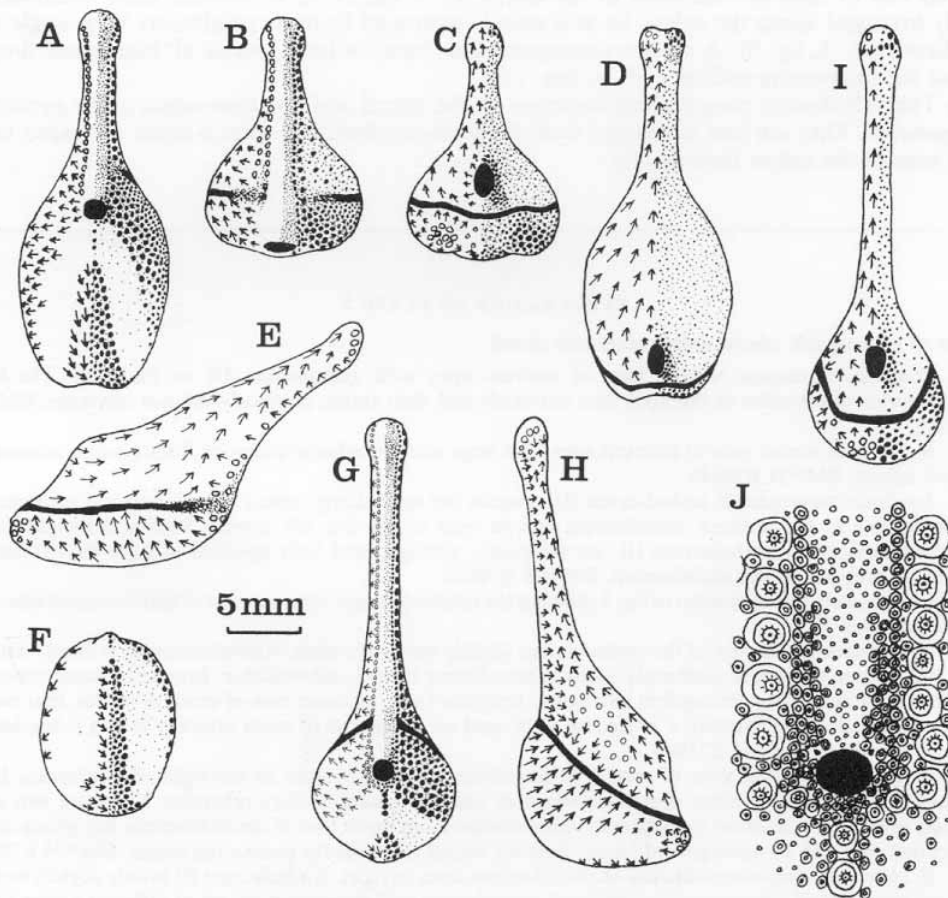
TEXT-FIG. 7. Tubercle arrangement in *Infulaster excentricus*. A—anterior: B—lateral: C—posterior: D—aboral: E—oral. Arrows on the left-hand side of diagrams show the direction of areole enlargement. Circles indicate radially symmetrical tubercles. Stippling on the right-hand side of diagrams indicates the size and arrangement of tubercles. The marginal fasciole appears as a black band.

5. *Tubercle arrangement.* Although some marked changes occur in the detailed arrangement of tubercles during the evolution of *Hagenowia*, all functionally distinct groups of tubercles were already developed in *I. excentricus*. The more important changes are outlined below.

(i) There is a slight reduction in the area of plastron tubercles in later species of *Hagenowia*. This is accompanied by a corresponding increase in the tubercle-free ambulacral zones on either side of the plastron. The plastron is extremely narrow in *H. blackmorei* (text-fig. 8F).

(ii) There is a relative increase in the area of ventro-lateral tubercles, which are best developed in *H. blackmorei*. This is a consequence of the increasing obliquity of the fasciole (which, in turn, arose from the progressive shift of the peristome).

(iii) Tubercles in the sub-anal region are radially arranged around two points in *Infulaster* and *H. rostrata* (text-figs. 7, 8). In *H. anterior* and *H. blackmorei*, sub-anal tubercles are radially arranged around a single point (text-fig. 8i).



TEXT-FIG. 8. Tubercle arrangement in *Hagenowia*. A-E, *H. rostrata*: A—oral; B—anterior; C—posterior; D—aboral; E—lateral. F-J, *H. blackmorei*: F—oral; G—anterior; H—lateral; I—posterior; J—arrangement at the base of the sulcus and surrounding the peristome. For explanation see text-fig. 7.

(iv) Latero-dorsal tubercles in *Infulaster* have an areole which is radially symmetrical or only weakly enlarged adapical (Pl. 4, fig. 11). In *Hagenowia* the areole becomes increasingly enlarged in an adapical direction, whilst crenulation is enlarged on the opposite side (Pl. 4, figs. 8-10, 12; text-fig. 8). Latero-dorsal tubercles are least dense immediately above the marginal fasciole and become progressively denser towards the dorsal ridge. Tubercle density over the dorsal surface increases progressively during evolution. There are between 1 and 3 tubercles per mm² in *I. excentricus* and *I. tuberculatus* and this increases to 4 or 5 tubercles per mm² in *I. infulasteroides*. A similar tubercle density is found laterally at the base of the rostrum in species of *Hagenowia*. On the rostrum itself, tubercle density increases to 8 to 10 tubercles per mm² in *H. blackmorei* and as much as 15 tubercles per mm² in *H. elongata* where there are four closely packed rows of tubercles.

(v) The parts of interambulacra 2 and 3 which form the outer zone of lateral walls of the anterior sulcus have relatively small and radially symmetrical tubercles (Pl. 5, figs. 3-9). There are three rather irregular rows of these tubercles above the marginal fasciole in *I. excentricus*. In *I. tuberculatus* and *I. infulasteroides* the interambulacral zones are narrower and there is only a single rather irregular row of tubercles marginal to the sulcus (Pl. 5, fig. 3). In *H. rostrata* these tubercles are linearly arranged along the sulcus lip and each is separated from its neighbours by a single row of miliaries (Pl. 5, fig. 5). A similar arrangement is found in later species of *Hagenowia* though without the intervening miliaries (Pl. 6, figs. 1-4).

(vi) Tubercle density progressively increases on the lateral and posterior edges of the peristome in *Hagenowia*. They are best developed in *H. blackmorei* where they form a dense U-shaped band at the base of the sulcus (text-fig. 8j).

EXPLANATION OF PLATE 5

Bottom of micrograph adoral unless otherwise stated.

Fig. 1. *Hagenowia rostrata*: ventral view of rostrum apex with ambulacrum III on the right. The large interambulacral tubercles at the apex face outwards and their spines obviously did not converge. BMNH E76845.

Fig. 2. *H. rostrata*: dorsal view of rostrum apex. The large interambulacral tubercles form a collar around the frontal sulcus. BMNH E76845.

Fig. 3. *Infulaster tuberculatus*: ambulacrum III towards the apex. Large apical interambulacral tubercles set perpendicular to the anterior ambulacrum can be seen in the top left corner. Smaller interambulacral tubercles, adjacent to ambulacrum III, are irregularly arranged and their spines would not have formed a protective arch above the ambulacrum. BMNH E76852.

Fig. 4. *I. tuberculatus*: enlargement of fig. 3 showing the relatively dense arrangement of variably sized tubercles in ambulacrum III.

Fig. 5. *H. rostrata*: stereo view of the rostral sulcus slightly below the apex. Ambulacrum III is deeply sunken and has denser and more uniformly sized tuberculation than *I. tuberculatus*. Interambulacral tubercles bordering the sulcus are arranged in two rather irregular rows, an inner row of small tubercles, that would have supported spines forming a protective arch, and an outer row of more laterally facing tubercles for excavating spines. BMNH E76845.

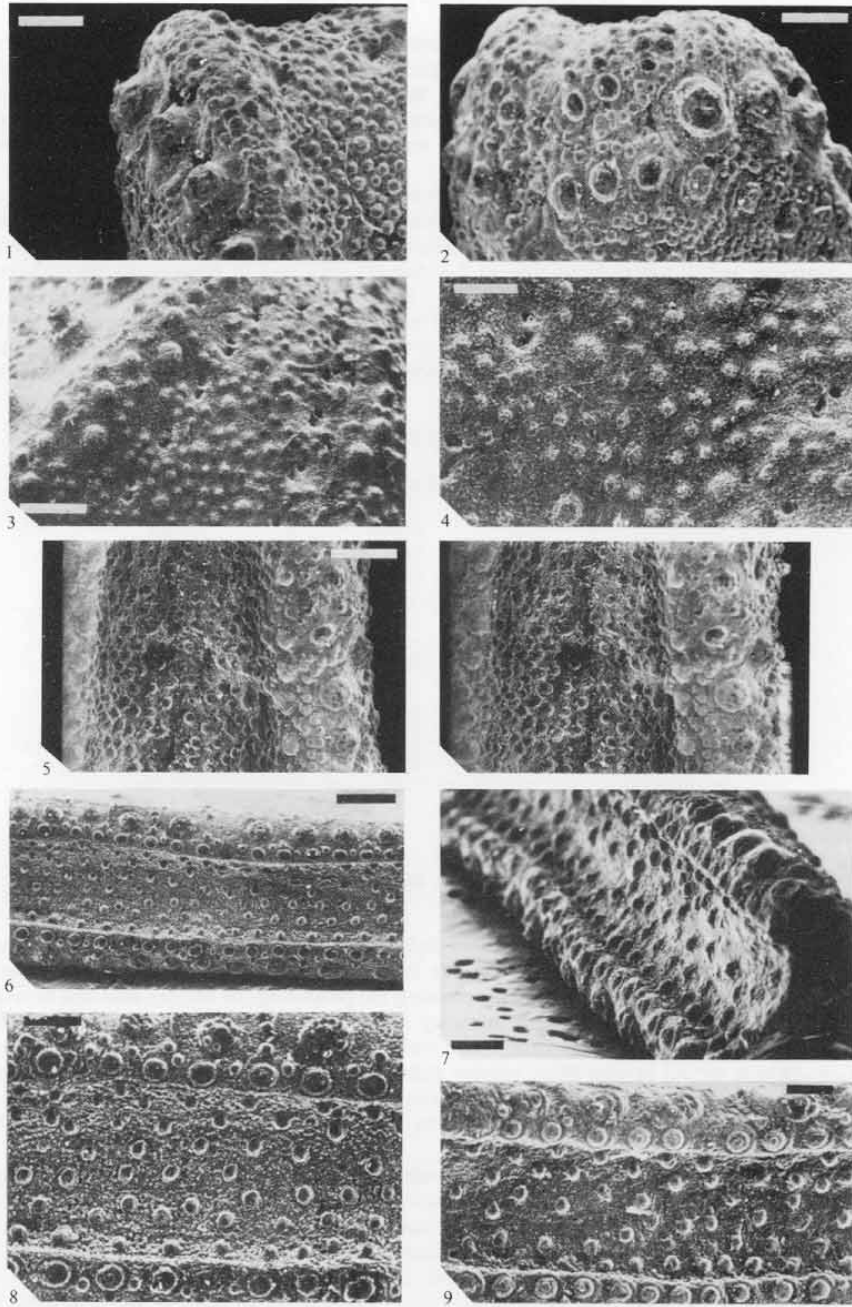
Fig. 6. *H. anterior*: ventral view of rostral sulcus about mid-length, apex to the right. Ambulacrum III is moderately sunken and rather sparsely covered in uniformly sized miliary tubercles. There are two well-defined rows of tubercles on the adjacent interambulacra, an inner row of small tubercles for spines of the protective arch and an outer row of larger, laterally facing tubercles for excavating spines. BMNH E76844.

Fig. 7. *H. elongata*: oblique ventral view of rostral sulcus, apex to right. Ambulacrum III is only slightly sunken and the two rows of adjacent interambulacral tubercles are well developed and set at different angles to the sulcus. MM 12820.

Fig. 8. *H. anterior*: enlargement of fig. 6.

Fig. 9. *H. elongata*: as fig. 7 but viewed perpendicular to the sulcus.

Scale bar in figs. 4, 7-9 = 200 μ m; figs. 1-3, 5, 6 = 400 μ m.



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(vii) The large tubercles of the anterior interambulacra found on either side of the frontal sulcus are arranged in two rather irregular rows with interspersed miliaries in species of *Infulaster*. With the development of the rostrum in *Hagenowia*, the areas of interambulacra which face towards the anterior are reduced and there is only a single row of these large tubercles on either side. Tubercles are rather irregularly arranged in *H. rostrata* but in later species they abut to form a well-defined row (Pl. 5, figs. 5-9; Pl. 6, figs. 1, 2).

(viii) The size and density of the miliaries which cover the floor and walls of the frontal sulcus vary amongst species (Table 1). Miliaries are largest in *I. infulasteroides* and *H. rostrata* and become progressively smaller in later species. Miliary density does not vary along the length of the sulcus in *I. excentricus* and *I. tuberculatus*, but in *I. infulasteroides* and in *Hagenowia* the miliaries are denser at the top of the sulcus, where they may reach densities equivalent to that found in the lateral fasciole (120 to 140 miliaries per mm²). There is a corresponding increase in the density of miliaries lying outside the sulcus near the head of the rostrum. This results in the development of a rather diffuse band of miliary tubercles that fades towards the dorsal surface of the rostrum.

TABLE 1. Size and density of miliary tubercles in ambulacrum III

Species	Adapical miliaries		Median miliaries	
	Size (μm)	Mean density (mm ⁻²)	Size (μm)	Mean density (mm ⁻²)
<i>Infulaster excentricus</i>	50-60	35	50-60	35
<i>I. tuberculatus</i>	60-70	50-55	50	50-55
<i>I. infulasteroides</i>	50-75	80	80-100	50-60
<i>Hagenowia rostrata</i>	60-75	75	80-90	40-50
<i>H. anterior</i>	50	100	60-70	60-70
<i>H. blackmorei</i>	40-50	130	50-60	70
<i>H. elongata</i>	40-50	140	50-60	60

FUNCTIONAL MORPHOLOGY

Size and Shape

1. *Size*. The marked reduction in the size of *Infulaster* in the early Coniacian could have had several possible advantages. A reduction in size increases the surface area to volume ratio. This eases the animal's respiratory demands by increasing the percentage of oxygen that can be obtained by direct diffusion. By reaching sexual maturity at an earlier stage, smaller species can have a shorter generation time. This could have arisen with the development of stable and highly suitable conditions, which would favour those species able to reproduce and multiply more rapidly. The reduction in size may also have been brought about by predatory pressures. Small animals with apical elongation would be much less obvious from the surface, when buried, than larger, semi-infaunal species.

2. *The anterior ambulacrum*. The anterior ambulacrum provides the main, if not sole, passageway for transferring sediment orally in Recent spatangoids (Smith 1980b). In certain species, spines of the anterior ambulacrum are specialized for mucous string feeding (Chesher 1963; Buchanan 1966). The sunken anterior ambulacrum in *Infulaster* and *Hagenowia* must also have provided an important pathway for sediment transportation. In *Infulaster* the anterior sulcus is deep but in *Hagenowia* it shallows progressively. This is accompanied by increasing development of the protective arch of spines covering the sulcus (see later, p. 36). The reduction in the depth of the

sulcus is linked to the development of rostrum. The sulcus decreases in depth as the rostrum increases in slenderness because of the reduction in internal volume. In *Hagenowia* the frontal channel is maintained as the sulcus shallows by the development of a dense grill of spines arching across ambulacrum III.

3. *The rostrum.* The development and elongation of the rostrum permitted *Hagenowia* to live buried within the sediment while maintaining contact with surface waters (Nichols 1959; Ernst and Schulz 1971). Via the rostrum, oxygenated water could be drawn into the burrow and the surface, organic-rich layer of sediment passed to the mouth. Because of its small size, *Hagenowia* cannot be said to have burrowed deeply. The oral surface of *H. blackmorei* could only have been about 3 cm below the surface, approximately the same level as postulated for *I. excentricus*. However, the rostrum presumably made *Hagenowia* less obvious from the surface since only the rostral tip would have disturbed the surface sediment and not the whole dorsal surface (text-fig. 11). Predation may have been an important selection pressure.

The rostrum, which is oblique in *H. rostrata*, becomes progressively more vertical in later species. Simultaneously it also develops a cross-section with thicker plates and buttressing. Early *Hagenowia* presumably needed an oblique rostrum to streamline their movement through the sediment and thus minimize the stresses applied to the thin-walled rostrum. In later species, as the rostrum became more robust, it could be held in a more vertical position.

4. *The anterior movement of the peristome.* In *Infulaster* the peristome lies on the oral surface near the anterior margin (text-fig. 7) but in *H. rostrata* it lies marginally at the base of the anterior sulcus and in *H. blackmorei* it has shifted to a frontal position (Pl. 3, fig. 7b). This change is thought to reflect an increasing dependence on sediment coming down the anterior sulcus. In Recent spatangoids, phyllode tube-feet are used to collect sediment from the floor of the burrow and transfer it to the mouth (Nichols 1959; Chesher 1969; Smith 1980a). This is also likely to have been true in *Infulaster*. Particles coming down the anterior sulcus would have landed on the floor of the burrow just in front of the peristome and within reach of the tube-feet. In *H. rostrata* the mouth lies at the base of the sulcus so that tube-feet would have been able to collect and transfer particles direct from the sulcus. In *H. blackmorei* the mouth is anterior and raised well above the floor of the burrow. Peristomial tube-feet are reduced and, because of their position, could only have been involved with sediment coming down the sulcus.

5. *The plastron.* The oral surface is relatively flat in *Infulaster* but becomes more or less keeled in *Hagenowia*. An arched or keeled plastron is found in Recent spatangoids which burrow in muddy or sandy substrata. Surface-dwelling spatangoids or spatangoids that burrow shallowly in sands or gravels have a flat plastron. A keeled or arched plastron may provide a better arrangement of tubercles and spines for efficient forward thrust.

6. *Sub-anal protruberances.* *Infulaster* has two clear bulges in the sub-anal region whereas *H. anterior* and *H. blackmorei* have only a single protruberance. In *H. rostrata* there are two sub-anal protruberances which are asymmetrical. Usually the right-hand bulge is larger and more prominent than the other. Devries (1953) showed that asymmetry in the test of spatangoids relates to the way in which the gut is coiled. This probably accounts for the asymmetry of the sub-anal region in *H. rostrata*.

The change from a double to a single sub-anal protruberance is probably linked with the development of asymmetry. Each bulge bore a tuft of spines (see p. 34). Whereas the test of *I. excentricus* was broad enough to have had two distinct tufts of sub-anal spines, later species had progressively narrower bodies. Presumably, as internal volume reduced, the gut became more tightly packed and any asymmetry this gave to the test was enhanced. In *Hagenowia* this made one of the tufts of spines larger and more posterior in position. The tuft of spines on the smaller bulge would therefore have become less important and was lost in later species.

Pore morphology

1. *Latero-dorsal pores and their tube-feet.* Pore morphology suggests that specialized respiratory tube-feet were present only in species of *Infulaster* and in some large forms of *H. rostrata*. By

comparison with extant species, these tube-feet were probably rather elongate with a central, partitioned region (see Smith 1980a). Respiratory tube-feet were best developed in the posterior columns of ambulacra II and IV. Other columns either had less elongate respiratory tube-feet or had thin-walled cylindrical tube-feet. The positioning of respiratory tube-feet presumably reflects the water-circulation pattern over the aboral surface.

The unipores and partitioned isopores in *H. rostrata* would have unspecialized sensory tube-feet. In later species of *Hagenowia*, aboral tube-feet are reduced and finally lost. This, at first glance, appears to be rather a strange adaptation for an infaunal echinoid. However, holasteroids, in general, show no modifications for protecting aboral tube-feet during burial. Respiratory tube-feet can function efficiently in infaunal spatangoids because of their sunken ambulacra and the curved arch of protective spines above them. Respiratory tube-feet in clypeasteroids and cassidulids function efficiently because of their extreme elongation (Smith 1980a). In *Infulaster*, respiratory tube-feet were neither extremely elongate, nor associated with sunken ambulacra nor a protective arch of spines. The tube-feet were able to play an effective part in gaseous exchange only because much of the dorsal surface remained uncovered. In *Hagenowia*, all but the extreme tip of the rostrum was covered, thus it became impossible for the tube-feet to function efficiently and they were quickly lost.

The change in efficiency of the respiratory tube-feet may be linked with the over-all reduction in body size that occurred. As more of the dorsal surface became covered by sediment, with apical elongation, respiratory tube-feet presumably became less efficient. To compensate for this, a reduction in body size took place so that a larger proportion of the total oxygen consumed could come from direct diffusion. In *Hagenowia*, body size is further reduced with the complete loss of latero-dorsal tube feet.

2. *Pores and tube-feet of the anterior ambulacrum.* Small isopores are found along the length of the anterior ambulacrum in species of *Infulaster* and in *H. rostrata*. Their similarity with the ambital isopores in other ambulacra and the fact that they are uniform in shape and size along the whole length of the ambulacrum (excluding phyllode pores) indicates that the associated tube-feet were sensory in function and terminated in a sensory pad rather than a disc. The pores diverge little as they pass inwards, and the accompanying ampullae were probably cylindrical (Smith 1980a). These tube-feet are likely to have actively probed the sediment in front of them as well as sensing the particles passing down the sulcus.

In later species of *Hagenowia*, isopores are replaced by unipores. Those in the sulcus are extremely small and, by comparison with Recent spatangoids, are likely to have borne small, non-extensible epithelial knobs which were chemosensory in function. Apical unipores differ both in size and shape. Similar broad-rimmed unipores in Recent holasteroids and spatangoids bear relatively large and extensible, sensory tube-feet (Smith 1980a). Such tube-feet are likely to have been important chemical and tactile sense organs and no doubt would have extended out of the funnel to probe the surrounding sediment.

The increase in pore size in apical unipores of *H. elongata* suggests that the associated tube-feet were more extensible than those of previous species. A larger pore means that a larger volume of coelomic fluid can pass in and out of the tube-feet rapidly.

3. *Phyllode pores and their tube-feet.* The isopores surrounding the peristome are much larger than isopores of other non-respiratory tube-feet in both *Infulaster* and *Hagenowia*. Phyllode tube-feet of Recent spatangoids and holasteroids are penicillate and work by mucous adhesion (Smith 1980a). Their broad disc requires the support of a large diameter stem. They are therefore associated with large, oval isopores or unipores. The arrangement of a few large pores around the peristome in *Infulaster* and *Hagenowia* indicates that their tube-feet also collected sediment by means of a mucous adhesive disc. However, the disc could not have been particularly broad, judging from the size of the isopores, and may not have been penicillate.

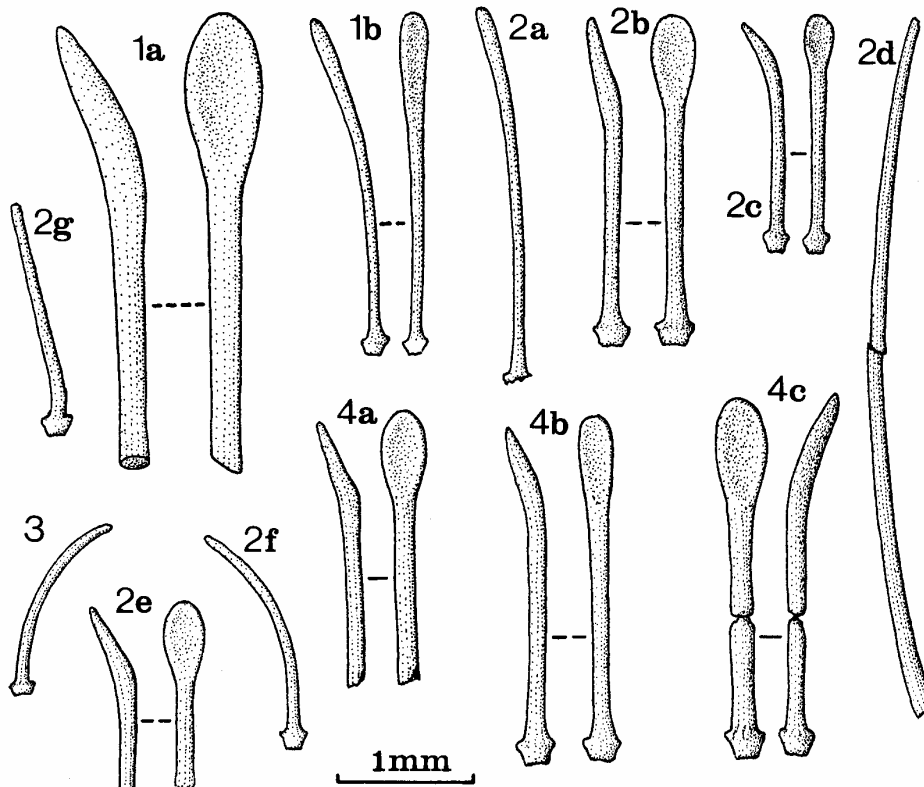
There are only two small unipores around the peristome of *H. blackmorei*. These are likely to have been associated with sensory tube-feet.

Spine morphology

A specimen of *I. infulasteroides* (BMNH E35766) and a specimen of *H. rostrata* (BMNH E76848) both retain a large number of different spines. Camera lucida drawings of these spines are given in text-fig. 9.

A large number of latero-dorsal spines lie near the dorsal ridge in the specimen of *I. infulasteroides*. These are about 1.75 mm in length and have a pronounced spatulate tip. The spatulate tip is set oblique to the straight shaft. Amongst these spatulate spines is a shaft, about 5 mm in length, with neither tip nor base preserved. The thinner, distal end tapers gently and is unspatulate. This gently curved spine almost certainly attached to one of the large interambulacral tubercles at the apex of the anterior sulcus.

Ventro-lateral spines, found below the marginal fasciole of *I. infulasteroides*, are spatulate and 2 to 2.5 mm in length. The spatulate tip is also set oblique to the shaft. On the plastron are three spatulate spines, none of which have their base preserved. Entire spines must be greater than 1.75 mm in length. On the oral surface there are two long and slender spines, one of which is broken



TEXT-FIG. 9. Spines of *Infulaster* and *Hagenowia*:

1. *I. excentricus* (BMNH E40770): a, latero-ventral spine; b, latero-dorsal spine.
2. *I. infulasteroides* (BMNH E35766): a, sub-anal spine; b, latero-ventral spine; c, latero-dorsal spine; d, apical spine; e, plastron spine; f, spine from the protective arch across the frontal sulcus; g, anterior excavatory spine.
3. *H. anterior* (BMNH E40158): spine from the protective arch across the frontal sulcus.
4. *H. rostrata* (BMNH E76848): a, latero-ventral spine; b, anal spine; c, plastron spine.

just below the milled ring, the other having no remnant of the spine base. The proximal end lies near the large tubercles of the sub-anal protruberance. Both spines are gently curved and are about 2.75 mm in length. The shaft becomes slightly broader distally, but does not appear to be spatulate.

In the anterior sulcus there are a number of non-spatulate spines. Most of those lying on the floor of the sulcus are small, slender, and strongly curved. They are about 1.5 mm in length and do not flatten distally. These are derived from the small interambulacral tubercles lining the outer margin of the sulcus, judging from the size and shape of the spine base. Stouter spines, about 1.75 mm in length, are found within the sulcus and on the adjacent interambulacra. The shaft is slightly bent a little above the milled ring, and tapers distally (the extreme tip is unfortunately not preserved). These spines are associated with the large interambulacral tubercles adjacent to the sulcus.

Plastron and latero-ventral spines of *H. rostrata* are similar to those of *I. infulasteroides*. In the specimen of *H. rostrata*, a number of stout, straight spines, up to 2.5 mm in length, are preserved within the periproct. Their tip is slightly flattened and is set slightly oblique to the shaft. These spines are probably associated with the large interambulacral tubercles which surround the periproct.

The spines in all species of *Infulaster* and *Hagenowia* are likely to be similar, judging from the similarity in tubercle structure and arrangement. The function of each group of spines is best discussed in conjunction with the structure of their tubercles. A reconstruction of the spine coverage in *I. infulasteroides* and *Hagenowia* is given in text-fig. 10. Spine posture is inferred from tubercle structure.

Tubercle structure and arrangement

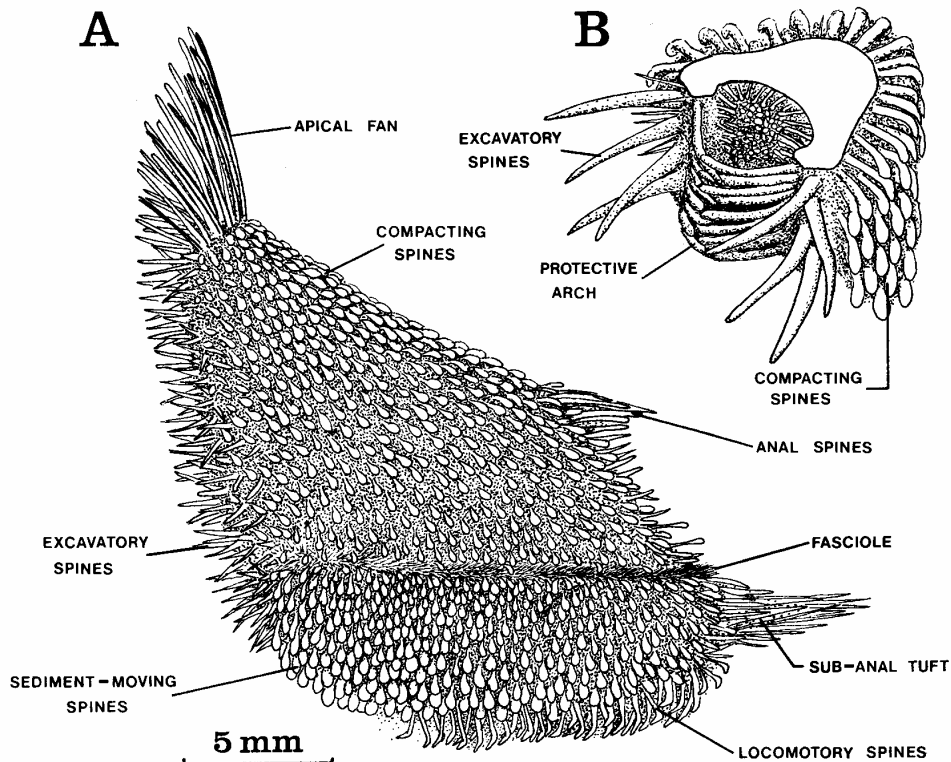
The shape and arrangement of tubercles can give information on spine posture and movement (Smith 1980b). There are a number of distinct areas of tubercles in *Infulaster* and *Hagenowia*, each of which bore spines with a specific function. Tubercle arrangement in *I. excentricus*, *H. rostrata*, and *H. blackmorei* is depicted in text-figs. 7 and 8. The following groups of tubercles can be distinguished.

1. *Plastron tubercles*. Plastron tubercles in both *Infulaster* and *Hagenowia* are closely spaced with only a few interspersed miliary tubercles. Largest tubercles lie laterally with smallest tubercles lying along the central ridge. Their areole is slightly enlarged on the meso-posterior side (text-figs. 7, 8) and platform crenulation is radially symmetrical. As in Recent spatangoids, the power stroke would have been towards the mid posterior, and plastron spines, with their spatulate tips, must have provided the main thrust for locomotion. However, plastron tubercles of Recent spatangoids have asymmetric crenulation and pronounced areole enlargement (Smith 1980b). The movement of plastron spines was probably more restricted and less effective in *Infulaster* and *Hagenowia* compared with Recent spatangoids. Radially symmetrical crenulation indicates that plastron spines were held more or less perpendicular to the test (Smith 1980b).

2. *Latero-ventral tubercles*. Tubercles found below the marginal fasciole in interambulacra 1-4 have their areole enlarged adambitally and towards the fasciole. Platform crenulation is either radially symmetrical or is slightly larger on the adoral side (opposite the direction of areole enlargement). These tubercles are denser on the anterior half but become more uniformly distributed in later species. They decrease in size and become more densely packed towards the fasciole.

This arrangement differs from that found in Recent spatangoids, where the areole is enlarged in a latero-posterior direction and crenulation is asymmetrical. (Smith 1980b). In spatangoids the associated spines lie oblique to the test and excavate sediment from beneath the animal with an oar-like action. Tubercle structure, in *Infulaster* and *Hagenowia*, indicates that, whereas oral spines were more or less perpendicular, adambital spines were inclined slightly downwards away from the fasciole. Areole enlargement suggests that spines pushed sediment outwards and upwards and were principally used in excavating and burrowing.

3. *Sub-anal tubercles*. Tubercles are radially arranged on each sub-anal bulge with large, radially symmetrical tubercles centrally, and smaller tubercles marginally (text-figs. 7 and 8). Marginal tubercles often have a slight areole enlargement on the side away from the centre. A similar tubercle



TEXT-FIG. 10. Spine posture and arrangement in *Infulaster* and *Hagenowia*. A, *Infulaster infulasteroides*, lateral view. B, *Hagenowia blackmorei*, cut-away section through the rostrum showing the anterior sulcus. The relative size of spines is based on specimen BMNH E35766, and spine posture and function is interpreted from tubercle structure.

arrangement in Recent spatangoids is associated with tufts of spines (Smith 1980b). *Infulaster* and *H. rostrata* must have had two sub-anal tufts of spines whereas later species of *Hagenowia* had only a single tuft. The upper spines of each tuft abut against the marginal fasciole. Mucus from the fasciole could easily have been transferred to the sub-anal spines. The sub-anal tuft of spines is used in constructing a tunnel, in spatangoids, with the aid of specialized tube-feet (Nichols 1959; Chesher 1968). *Infulaster* and *Hagenowia* lacked sub-anal, funnel-building tube-feet and were unlikely to have built an extensive tunnel. However, the spines alone may have been able to maintain a short sub-anal tunnel with the help of mucus from the fasciole. In spatangoids the sub-anal tunnel is used to remove water from the burrow (Chesher 1968).

4. *Anal tubercles*. Large tubercles are found around the dorsal and lateral edges of the periproct. They decrease in size away from the periproct and are most numerous dorsally and on either side immediately below the periproct. The crenulate platform is radially symmetrical. There may be slight areole enlargement on the anterior side. Beneath the periproct is a broad band of miliaries, extending to the fasciole. A similar arrangement of tubercles is found in Recent spatangoids, where a semicircle of longer spines surrounds the periproct. These maintain a space within the burrow for defaecation and prevent fouling of the aboral surface.

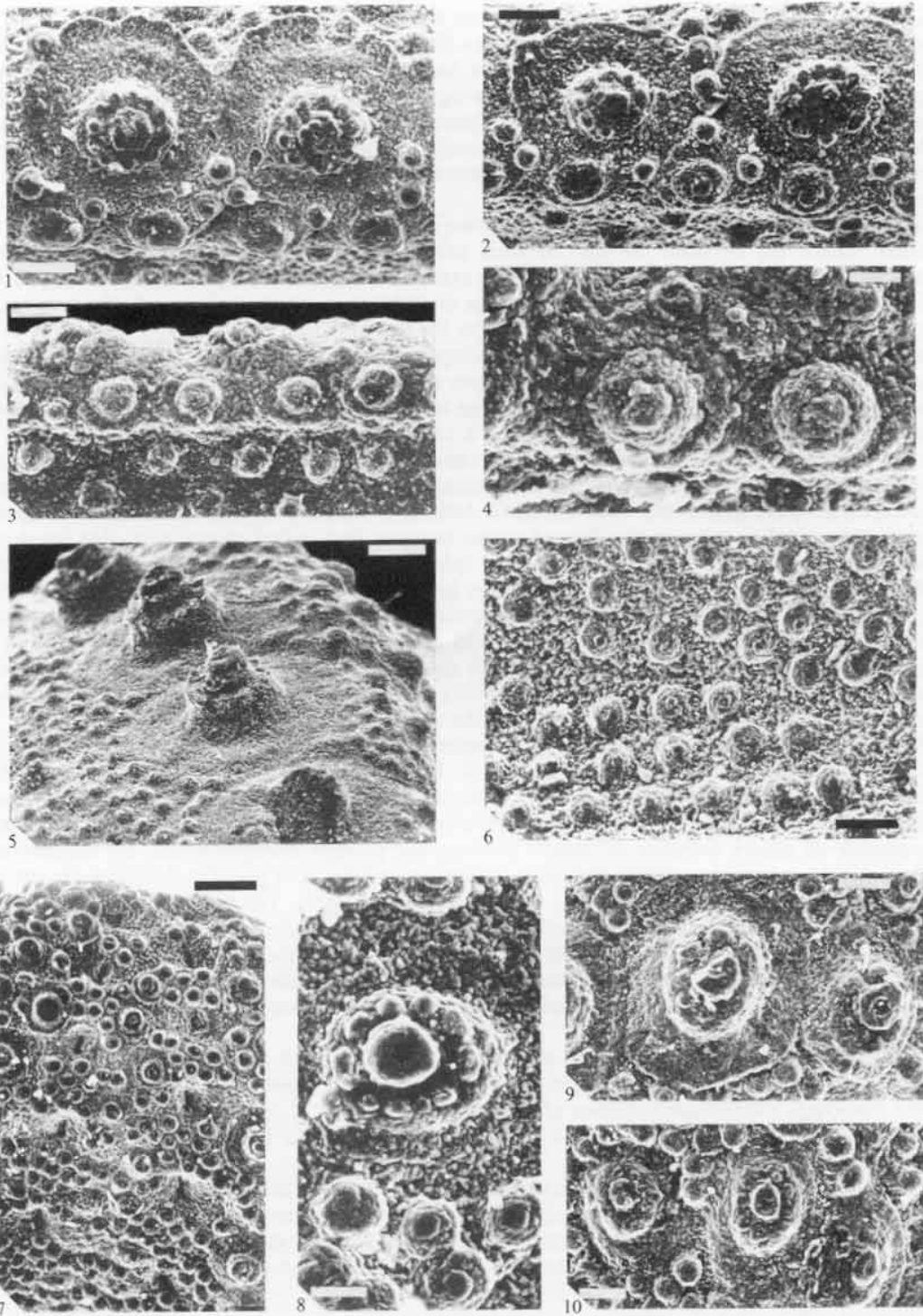
5. *Latero-dorsal tubercles*. Tubercles above the marginal fasciole have only a weak bilateral symmetry in *I. excentricus* and *I. tuberculatus*. This becomes much more pronounced in *Hagenowia* due to a marked enlargement of the areole on the anterior or adapical side (see text-fig. 8). Numerous miliaries occur between the tubercles. These tubercles support short, spatulate spines in *I. infulasteroides*. Similar spatulate spines, attaching to bilaterally symmetrical tubercles, are found in Recent spatangoids, where they are used for compacting the burrow walls, transporting sediment posteriorly, and moving the dorsal mucous coat (Smith 1980b). *I. excentricus* has a low aboral tubercle density but later species of *Infulaster* and *Hagenowia* have progressively denser tuberculation. The increased protection provided by a denser spine coverage is an adaptation for living infaunally. Tubercles are especially dense along the rostrum, presumably for compacting and maintaining an open passageway down into the burrow.

In *H. blackmorei*, tubercles just above the marginal fasciole have an adoral areole enlargement indicating that the spatulate tips of spines were tilted in opposite directions on either side of the fasciole, a situation common in Recent spatangoids for distributing mucus.

6. *Tubercles associated with the anterior sulcus*. There are two sets of interambulacral tubercles lying adjacent to the anterior sulcus. Firstly, there are small, radially symmetrical tubercles which form an inward-facing row along the lip of the sulcus (Pl. 4, figs. 5-9; Pl. 5, figs. 1-4). They are rather irregularly arranged in early species but become organized into a well-defined line in *Hagenowia*. The associated curved and non-spatulate spines would have formed an arched roofing to the anterior sulcus (text-fig. 10B). The increasing density and organization of these spines was partially due to the decreasing depth of the anterior sulcus and partially due to the increasing importance of the sulcus as a pathway for transporting sediment to the mouth. In *Hagenowia* the anterior shift of the peristome shows that more reliance was placed on sediment coming down the sulcus. The arch of spines would have maintained a clear frontal pathway and would have prevented sediment from the frontal wall of the burrow clogging or contaminating the stream of sediment passing down the anterior sulcus. They ensured that sediment could only enter the sulcus at the apex.

EXPLANATION OF PLATE 6

- Fig. 1. *Hagenowia elongata*: large interambulacral tubercles adjacent to the rostral sulcus that support excavating spines. Crenulation is radially symmetrical but the areole is enlarged laterally away from ambulacrum III. Smaller tubercles for protective arch spines can be seen towards the bottom. MM 12820.
- Fig. 2. *H. anterior*: interambulacral tubercles, as above but with intervening miliaries. BMNH E76844.
- Fig. 3. *H. elongata*: row of small interambulacral tubercles immediately adjacent to the frontal sulcus (bottom of micrograph) for spines forming a protective arch to the sulcus. MM 12820.
- Fig. 4. *H. elongata*: enlargement of fig. 3 showing the radially symmetrical areole and the lack of crenulation.
- Fig. 5. *Infulaster tuberculatus*: large apical interambulacral tubercles, ambulacrum III to the right. These have radially symmetrical areoles and crenulation and are not tilted. Their spines must have been held pointing away from ambulacrum III. BMNH E76852.
- Fig. 6. *H. anterior*: miliary tubercles near the apex of the rostral sulcus, apex to the sulcus. These are tilted adapically and laterally, away from the mid-line, suggesting that their spines had a meso-adoral power stroke. BMNH E76844.
- Fig. 7. *H. blackmorei*: adapical part of ambulacrum III showing dense, irregular arrangement of varying sized tubercles at the top of the sulcus. BMNH E76846.
- Fig. 8. *H. anterior*: large ambulacral tubercle adjacent to an apical ambulacrum III unipore. Crenulation is slightly stronger laterally (towards the pore) and the protective spine must have been gently curved. BMNH E76844.
- Fig. 9. *H. blackmorei*: large apical interambulacral tubercle with a radially symmetrical areole and slightly stronger crenulation towards ambulacrum III (top of micrograph). BMNH E76846.
- Fig. 10. *H. elongata*: large apical interambulacral tubercles. The areole is slightly border to the posterior (bottom of micrograph), crenulation is radially symmetrical. MM 12820.
- Scale bar in figs. 4, 8 = 40 μm ; figs. 1-3, 6, 9, 10 = 100 μm ; figs. 5, 7 = 200 μm .



GALE and SMITH, Cretaceous irregular echinoids

The other set of interambulacral tubercles are large and outward-facing (Pl. 5, figs. 5-9; Pl. 6, figs. 1-3). They form a single, well-defined row in *Hagenowia*. Platform crenulation is either radially symmetrical or is enlarged slightly on the side facing the sulcus. Their areole is enlarged in the opposite direction (text-fig. 8; Pl. 6, fig. 1) showing that the power stroke of the spine was directed away from the sulcus. These stout, pointed spines were probably used to loosen and excavate sediment of the anterior wall of the burrow. Recent spatangoids, such as *Echinocardium cordatum* (Pennant), have both an anterior arch of protective spines and adjacent excavating spines, and their tubercles and spines are rather similar.

The apical interambulacral tubercles and spines of *Infulaster* and *Hagenowia* are the largest they possess. There are between 16 and 20 such tubercles on the adapical plates of the anterior interambulacra. Their areoles are either radially symmetrical or are enlarged slightly to the posterior (Pl. 5, figs. 1-3; Pl. 6, figs. 5, 9, 10). Platform crenulation is more or less radially symmetrical though crenulation may be slightly enlarged on the anterior side (Pl. 6, fig. 9). Tubercles are so positioned that, were the spines to converge adapically to form a tuft, they would have to lie at a considerable angle to the tubercles and the plate surface. The structure of the tubercles, however, shows that spines were not set obliquely, forming an apical tuft, but probably formed a fan-shaped array. This fan of spines would have formed a collar to the anterior sulcus (text-fig. 10A). This arrangement is common to all species of *Infulaster* and *Hagenowia* and is also found in certain species of *Cardiaster*. As the apex is the most vulnerable part of the test in infaunal or semi-infaunal species, these apical spines may have acted as a deterrent to predators. The fan-shaped arrangement around the apical opening to the frontal sulcus suggests that apical spines were also involved in collecting sediment, either acting as a funnel or helping to cascade surface sediment into the sulcus.

Within ambulacrum III, small tubercles are interspersed with miliaries near the apex (Pl. 6, fig. 7), but in the sulcus ambulacral plates are covered almost entirely by uniformly sized miliaries (Pl. 6, fig. 6). A similar arrangement is found in *Micraster* but has not yet been reported in any Recent species (Smith, 1980b). In many Recent spatangoids, miliary tubercles of ambulacrum III bear short, straight spines with fleshy tips, usually well endowed with cilia and mucous glands. A similar type of spine was probably present in the sulcus of *Infulaster* and *Hagenowia*.

Several lines of evidence suggest that the anterior sulcus became increasingly important as a pathway for transferring sediment to the mouth. Evolutionary changes in the size and density of miliaries in the sulcus may therefore be related to an improved feeding mechanism. The progressive differentiation of a distinct band of dense miliaries at the apex of the sulcus may mark the increasing importance of ciliary currents or mucus binding for particle transportation. By concentrating miliary spines at the apex, where sediment entered the sulcus, it is possible that copious amounts of mucus could have been produced to enmesh particles loosely. The relatively few spines within the sulcus could then have transported a stream of mucus-bound sediment with relative ease. Tubercle and spine arrangement is highly distinctive in Recent, mucous string feeding spatangoids (Chesher 1963; Buchanan 1966; Smith 1980b) and very different from that in *Hagenowia*. *Hagenowia*, then, did not feed by means of a compact mucous string but may have had a much looser flow of weakly bound particles.

7. *Fascioles*. The marginal fasciole shows little change except that it becomes more sharply defined across the anterior interambulacra in later species of *Hagenowia*. The increasing obliquity of the fasciole is a direct consequence of the changing position of the peristome. The fasciole does not cross the anterior ambulacrum, as stated by Nichols (1959), but becomes more diffuse and peters out towards the sulcus.

Fascioles act as pumps, drawing oxygenated water through the burrow, and as a source of mucus. A dorsal mucous coat prevents finer particles falling between spines and clogging the burrow. Both *Infulaster* and *Hagenowia* are likely to have lived at least partially buried and the fasciole probably drew water down from the apex and over the central and posterior parts of the test.

PRESERVATION

Increased differentiation and strengthening of the rostrum in successive species of *Hagenowia* was accompanied by relative thinning of the body wall. This is reflected in the increased rarity of preservation of *Hagenowia* bodies in successively later species and the greater frequency of isolated rostra.

Bodies of *Hagenowia* are rarely bored or encrusted by the organisms which colonized much of the skeletal debris littering the chalk sea floor, and it is likely that once exhumed, the fragile tests fragmented rapidly leaving only the more durable rostra. The rostra often contain sponge crypts, and characteristic oval borings (500–1000 μm in length) with irregularly bevelled rims. Encrusters are extremely rare on *H. rostrata*, probably because they were too small to provide suitable substrata.

One preservational style occurs consistently in *Hagenowia*, in which the rostrum is lost, having broken away along plate sutures near its base (e.g. Pl. 3, fig. 2). The resulting irregular stump has, in some specimens been attacked by boring organisms (e.g. Pl. 3, figs. 6b, 7a). Such specimens frequently retain scattered spines on the sides and base of the body. Presumably these individuals remained in life orientation within the sediment after death, with the rostrum protruding above the sediment-water interface, which was stable for long enough to allow colonization by borers.

Two specimens of *Hagenowia* have repaired injury to the rostrum. In one specimen (BMNH E76849) the obliquely broken tip of the rostrum was sealed across, and new tubercles and genital pores developed. Such damage was probably the result of predation.

SELECTION PRESSURES AND MODE OF LIFE

The majority of structural changes in the *Infulaster/Hagenowia* lineage were caused, either directly or indirectly, by elongation of the apical region of the test, and to a lesser extent by the reduction in size. Apical elongation necessitated disruption of the apical system, plate elongation, loss of plate columns from the rostrum, and an increased slenderness of the rostrum. This increased slenderness in turn reduced the internal volume of the rostrum, which caused a decrease in depth of the sulcus, loss of two of the four gonads, and the change from extensible tube-feet with large ampullae, to small tube-feet with reduced ampullae. The slender rostrum required buttressing at the anterior and posterior margins, and an increasingly better organization of tubercles. The increase in obliquity of the fasciole was a consequence of the anterior and adapical movement of the peristome. The size reduction resulted in the change from a double to a single subanal bulge and in the interruption of the plastron.

Various features displayed by *Infulaster* and *Hagenowia* are interpreted as adaptations to an infaunal mode of life. The latero-ventral spines were specialized for excavating sediment from beneath the animal. In order for the fasciole and subanal tuft of spines to have functioned, these echinoids must have lived at least partially buried. Latero-dorsal spines modified for compacting sediment of the burrow walls are developed to immediately below the apex, as are the excavating spines and the protective arch of spines across the sulcus (text-fig. 10). This clearly implies that both *Infulaster* and *Hagenowia* lived within the sediment, with their apices at or just below the surface.

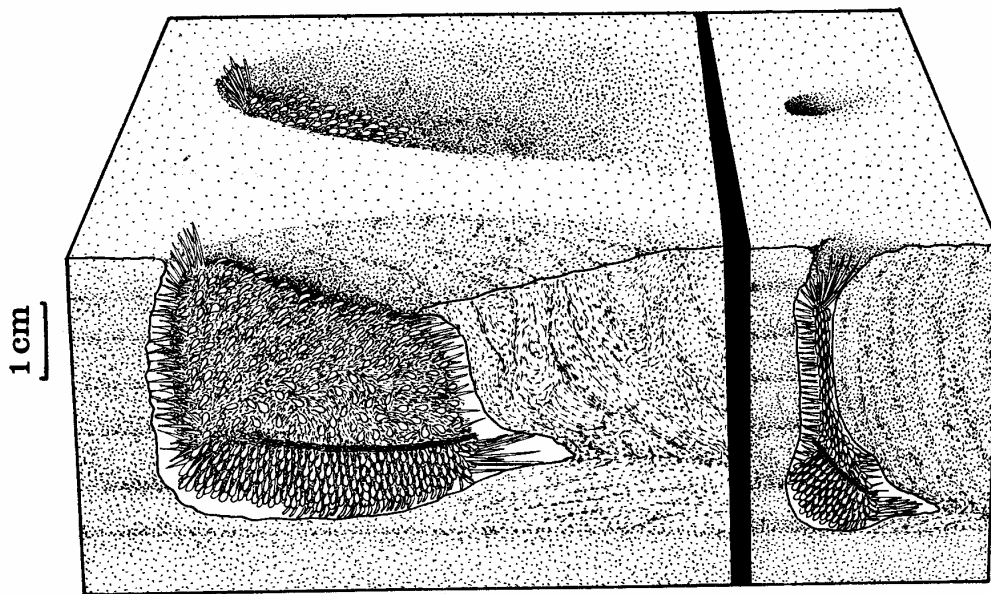
It is highly improbable that either genus could have burrowed more deeply, as funnel-building tube-feet are lacking, and the apical spines were held in a broad fan and not a tuft. Living within fine-grained sediments, they had to maintain direct contact with surface waters. This could only have been achieved by keeping the apex of the test at the surface.

I. excentricus has an almost flat dorsal surface, most of which must have remained exposed on the sea floor. Later species evolved to become less conspicuous, by apical elongation. In this way the bulk of the animal could be removed from the surface, with only a small apical part of the test visible. This apical elongation brought about the structural changes enumerated above. The loss of aboral respiratory tube-feet was probably an important factor in influencing the size reduction which occurred.

Other morphological changes accompany a change in feeding strategy. *Infulaster* used its phyllode tube-feet to pick up sediment around the mouth. Sediment coming down the frontal sulcus was not collected directly and probably formed only a small part of the animal's diet. *Hagenowia* came to rely much more heavily on sediment from the anterior sulcus and may have developed some sort of mucus binding to cope with this increased volume of sediment. Adaptations linked with this change in feeding strategy include the anterior movement of the peristome, loss of large phyllode tube-feet, and increasingly denser arch of spines across the sulcus and their extension to cover the peristome, the more extensible sensory tube-feet at the apex, and the increasing differentiation of miliaries within the sulcus.

All the morphological trends and specializations discussed are directly or indirectly concerned with adaptations for feeding or burial. The predominant pressures acting on the *Infulaster-Hagenowia* lineage were for increased efficiency in feeding and for increased protection by becoming less obvious at the surface. *I. excentricus* lived semi-infaunally with much of the dorsal surface exposed, and progressed leaving a clear furrow in its wake (text-fig. 11). In later species, as the dorsal surface became more oblique with apical elongation, less and less of the test remained exposed at the surface. In *H. blackmorei* only the very small apical head remained near the surface, the remainder of the body being fully covered (text-fig. 11). Only a small circular hole at the surface would have marked the position of this species.

It is not entirely correct to speak of an increasing depth of burial in the *Infulaster-Hagenowia* lineage, since the apex stays at the same level and the oral surface of *I. excentricus* lay at considerably greater depth than in many later species, because of the reduction in size. However, with apical elongation and the more vertical orientation of the rostrum, the oral surface was removed further from the sea floor. The most likely cause of this change is increasing predation, with selection



TEXT-FIG. 11. Mode of life of *Infulaster* and *Hagenowia*. Cut-away block sections showing the depth of burial of *Infulaster excentricus* (left-hand side) and *Hagenowia blackmorei* (right-hand side). Further back a second individual is illustrated to highlight the change in surface appearance with the development of apical elongation.

against those more obvious at the surface. Predation was a threat to *Hagenowia*, since regenerated rostra are known.

It is not clear whether the change in feeding habit resulted from a change in the nature of the sediment (e.g. the development of a surface layer richer in organic material or, conversely, an over-all reduction in organic content) or reflected a progressive adaptation to a constant sediment type. *Infulaster* and *Hagenowia* are both found in bands in apparently uniform pelagic chalk sequences. However, original subtle differences in the nature of the sediment may well have been obscured by bioturbation and diagenesis.

Hagenowia provides some indirect evidence as to the nature of the chalk sea floor. The presence of cutting and compacting spines on the rostrum implies that the sediment in which it lived was sufficiently cohesive to both require and allow such treatment. This is in accord with the suggestion made from other lines of evidence by Surlyk and Birkelund (1977) that the bottom was relatively stable, with only a superficial layer (a few millimetres thick) of easily resuspendible material.

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ANDREW S. GALE
Department of Geology
King's College, London
Strand
London WC2R 2LS

ANDREW B. SMITH
Department of Geology
University of Liverpool
P.O. Box 147
Liverpool L69 3RX