AUTECOLOGY AND TAXONOMY OF TWO UPPER CRETACEOUS CRANIACEAN BRACHIOPODS

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Surlyk, F.: Autecology and taxonomy of two Upper Cretaceous craniacean brachiopods. *Bull. geol. Soc. Denmark,* vol. 22, pp. 219–243. Copenhagen, November, 12th 1973.

The two Upper Cretaceous brachiopods *Isocrania costata* (Sowerby) and *Isocrania egnabergensis* (Retzius) are closely related and have often been confused in the literature. However, on the basis of a large material it is shown that both species are well defined and easily distinguished.

I. egnabergensis occurs in the near-shore Campanian calcarenites of Scania, Sweden, whereas *I. costata* seems to be restricted to the off-shore Upper Campanian and Maastrichtian chalks of northern Europe. Both species settled and cemented onto small hard substrates and have correspondingly minute attachment surfaces on the ventral valve. During the ontogenetic growth of the brachiopod, the diminutive substrate lost its function and the brachiopod attained a free-living mode of life, for which its disc-like shape is ideal. *I. egnabergensis* is very often strongly worn around the dorsal umbo, but the worn area is commonly delimited by a growth line and the margins of the valves are normally well preserved. It is suggested that the wear occurred before the death of the animal and corresponds to the high-energy habitat. In contrast *I. costata* is always extremely well preserved but a large proportion of the shells has been bored by predaceous gastropods. The comparison of closely related species from different biotopes is of great significance in palaeoecology because in this way it is possible to test and refine the arguments while overgeneralized conclusions can be avoided.

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Isocrania costata (Sowerby) and *Isocrania egnabergensis* (Retzius) belongs to the notorious group of "difficult" fossils. They have been confused again and again in the literature and *I. costata* has often been demoted to the rank of a junior synonym of *I. egnabergensis.* Practically all errors are due, however, to the lack of stratigraphically collected material from well-known localities and to uncritical quotation of earlier authors. Type material is unknown for both species.

I. egnabergensis is the only costate craniacean brachiopod from the large quarry of Ignaberga where the holotype came from and a very large topotypical material has been obtained. *I. costata* is well figured (J. Sowerby 1823 pl. 35 fig. 6) and the type locality was said to be Orglandes (near Valognes, Normandy, France). Topotypical material has been obtained also for *I. costata.* A very large material from the Maastrichtian chalk of Denmark and northern Germany has been investigated and this material undoubtedly belongs to *I. costata.* The taxonomical study showed that *I. costata* and *I. egnabergensis* are two closely related but well defined and easily distinguishable species. It has not been attempted to give full synonym lists or geographical and stratigraphical distributions for the two species. The terminology in general follows Williams et al. (1965). An exception is that the valves are called ventral and dorsal valve respectively as it seems very awkward to use the terms pedicle and brachial valves for at group of brachiopods which in no known developmental stage possess a pedicle and which do not have a brachidium.

Autecology

Isocrania costata (Sowerby). Pl. 1, figs. 1–11, 16–19

Facies. – *I. costata* is very abundant in the off-shore facies of the coccolithic white chalk. Less commonly it is found in more shallow-water calcsiltites – the so-called tuffaceous chalks of the Netherlands and the Normany, France.

Material and preservation. – Almost all specimens of *I. costata* have been collected by washing of large-scale bulk samples of chalk (technique described by Surlyk, 1972). A total of about 300 individuals have been obtained in this way from the Danish chalk. Further material has been obtained in the same way from the chalk of Hemmoor (north Germany), England and Normandy (France) and from the collections of A. Rosenkrantz (Copenhagen) and the Mineralogical Museum of Copenhagen. In total the material comprises about 500 individuals. The number of individuals is reached by adding whichever is the greater number of dorsal or ventral valves to the number of whole shells in the samples, which gives the minimum number of individuals; this is in contrast to the term specimen which covers all dorsal or ventral valves of whole shells.

The preservation is extremely good. There has been found absolutely no signs of wear (some of the larger valves in older collections are sometimes worn but almost without exception these specimens have been collected on the beach from chalk cliff-falls which have suffered a little reworking by the sea). Neither are there any differences in the preservation of different size-classes, minute juveniles of 0.5 mm in diameter being just as well

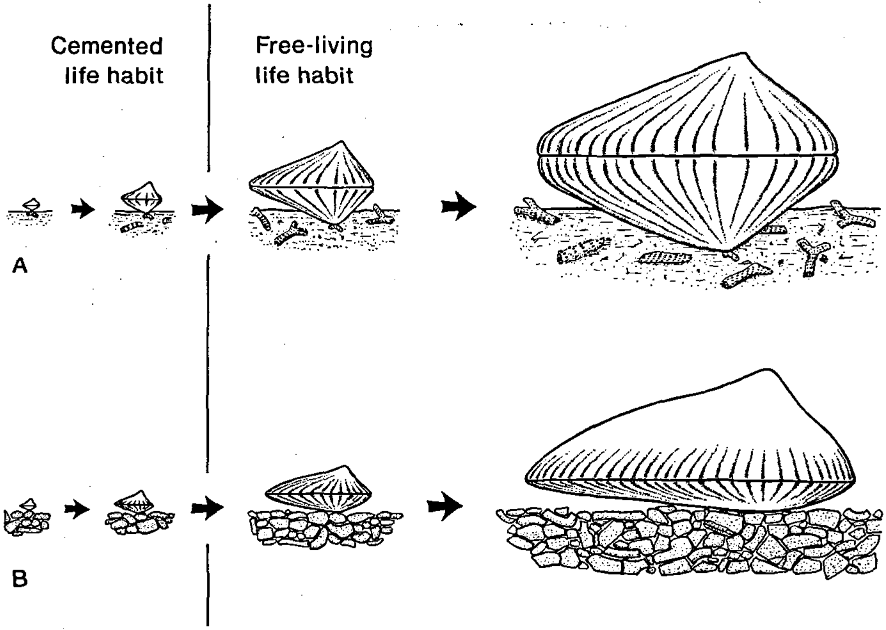


Fig. 1. Ontogeny and change in life habit of *Isocrania costata* (A) and *I. egnabergensis* (B). Both species settled as larvae onto small hard substrates. During the ontogenetic growth the small substrates lost their function and both species attained a free living mode of life. A circular, disc-like outline was developed by both brachiopods for reasons of stability and *I. costata,* which lived on relatively soft chalk bottom, developed in addition a conical ventral valve to keep the commissure above the surface of the sediment.

preserved as the largest adults. Bivalved juveniles are not uncommon, whereas bivalved adults are very rare.

Mode of life. – The early stages in the development of the recent *Crania anomala* (Müller) were described by Rowell (1960). He mentioned that the free swimming stages of the young *Crania* are unknown and explained the apparent absence of the larvae from the plankton by their having a short free-swimming life. They become attached earlier in their life history than other inarticulate brachiopods. A population sampled by Rowell at the end of April, shortly after the spring spawning, showed a very high proportion of individuals less than 1.5 mm maximum diameter. A third of these young individuals ranged in diameter from 0.2–0.3 mm. The development stage of the majority of these was that of the third pair of filaments. No attached specimens were found smaller than 0.2 mm.

The chalk samples after washing are sieved into three fractions: $>$ 1 mm,

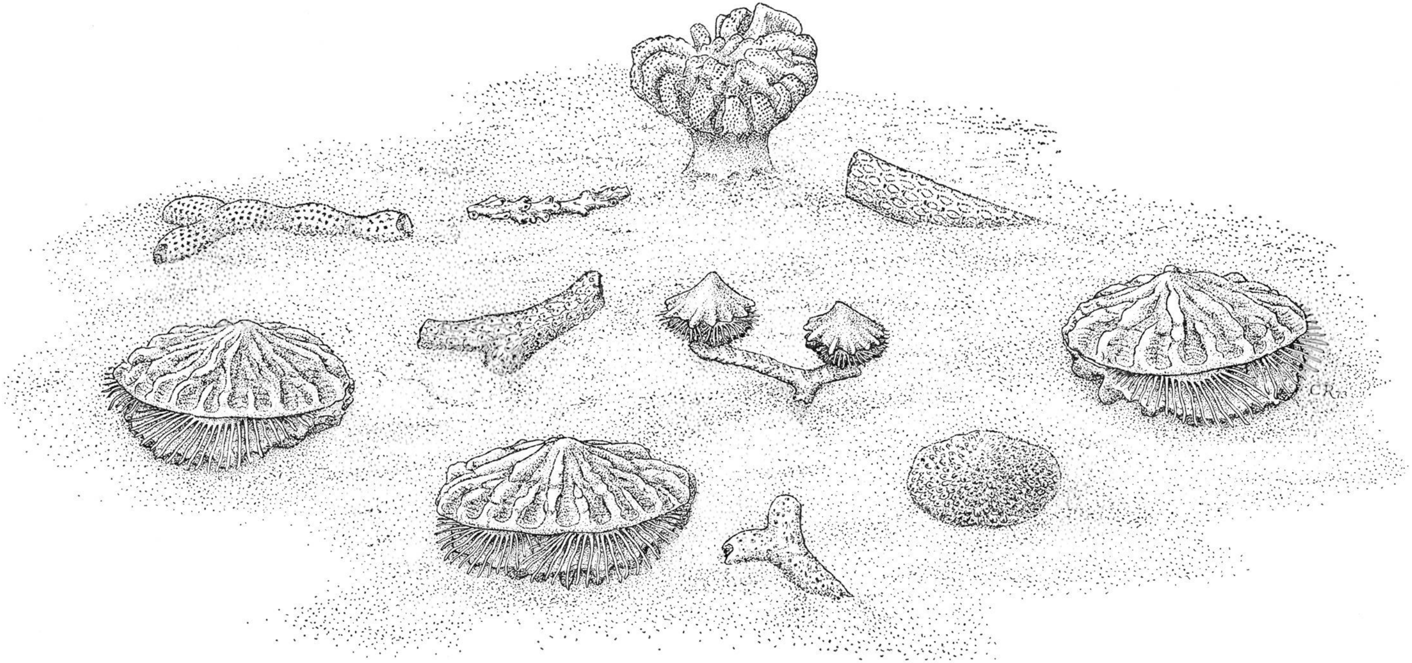


Fig. 2. Habitat and mode of life of *Isocrania costata.* This species is specialized for a free living life habit on the relatively soft chalk sea bottom. The larvae settled onto small, hard substrates e.g. bryozoans, but a free living mode of life was attained early in ontogeny. The fossils of the coccolithic ooze have mainly been drawn on the basis of the washing residue of sample Lindholm 8.

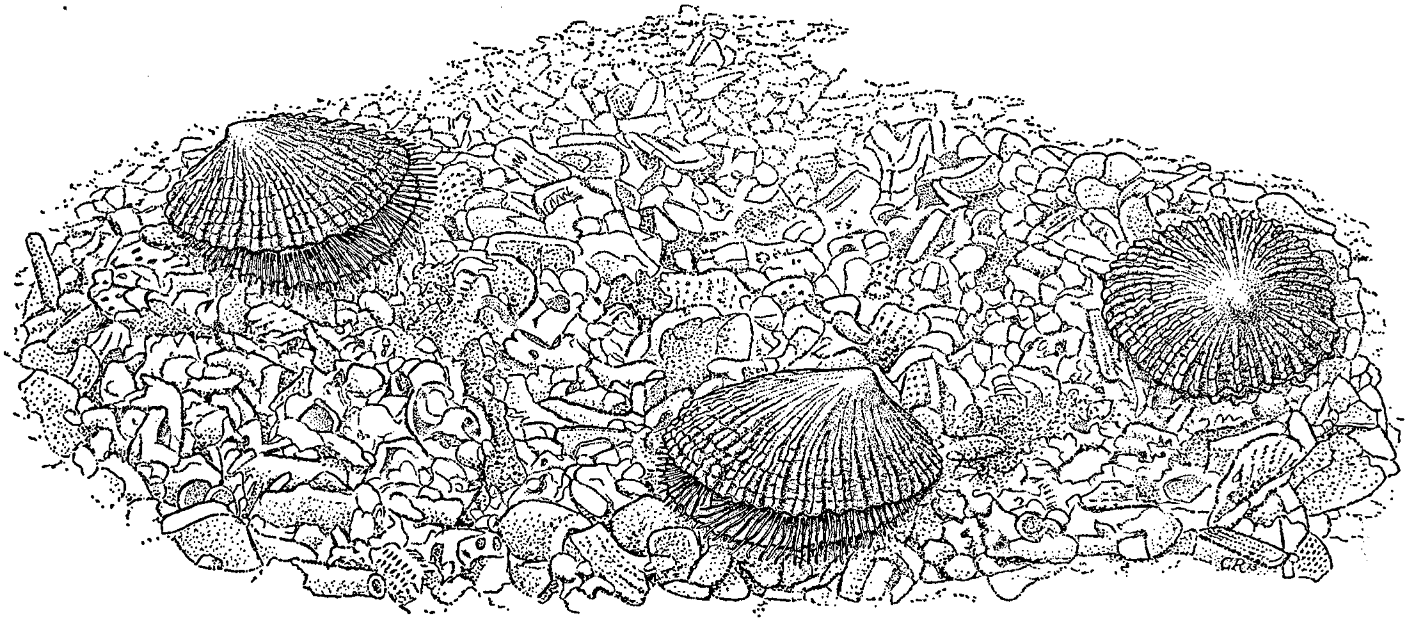


Fig. 3. Habitat and mode of life of *Isocrania egnabergensis*. This species seems to be restricted to the near shore skeletal sands of the Campanian Stage. The larvae settled onto small carbonate grains but rapidly became free living. The sediment and the fossils have been drawn on the basis of actual specimens from Ignaberga, Scania, Sweden.

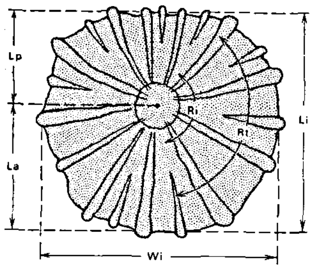
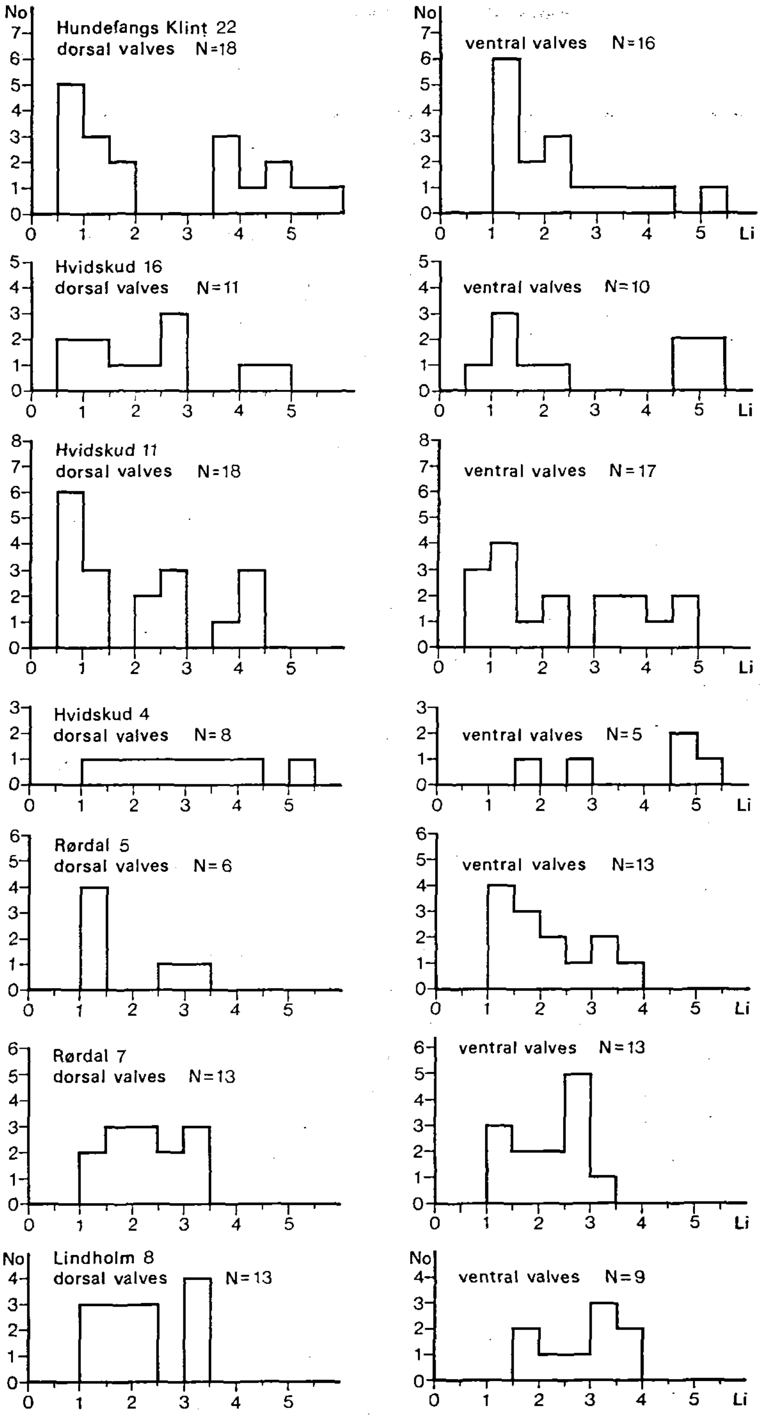


Fig. 4. Scheme of measurements. Li = length excluding the ribs; La = length from the umbo to the anterior margin; Lp = length from the umbo to the posterior margin; R*i* = initial number of ribs; Rt = total number of ribs.

0.5–1.0 mm and 0.25–0.5 mm. The latter fraction is not picked for brachiopods as they are indeterminate in this size. Minute *I. costata* are, however, quite common at a size of about 0.5 mm in length and it seems reasonable to assume that *I. costata* larvae settled at the same size and stage of development as the recent *Crania anomala. I. costata* settled onto the small hard substrates, notably delicate cheilostome and cyclostome Bryozoa, which had a scattered distribution on the chalk sea-floor. This position, very close to the uppermost soft layer of the chalk at the sediment water interface, is extremely dangerous to the small suspension feeding juvenile brachiopods and results in a very high juvenile mortality (Surlyk 1972). *I. costata* has no pedicle and its commissure was parallel to the attachment surface. It thus lived even closer to the sediment surface than the rest of the brachiopod fauna with which it competed for space on the small substrates. This drawback in the earliest stages may explain why *I. costata,* although common throughout the Maastrichtian chalk, never occurs in greater numbers.

If, however, the young *I. costata* succeeded in surviving the first dangerous period it ultimately benefitted by changing to another mode of life. During the phylogenetic evolution leading to *I. costata* a very small attachment surface was developed in combination with a ventral valve with a shape of a low cone. This shape is most unusual among craniaceans, where the ventral valve is normally flat and cemented to the substrate by the whole surface. Thus, during the growth of *I. costata* the minute original substrate lost its function and the brachiopods attained a free living life habit. The disc-like shape would seem to be ideal for reasons of stability (fig. 1; see also Surlyk 1972 fig. 4), but a brachiopod with the shape of a flat disc would constantly run the risk of having its filter apparatus clogged by cal-

Fig. 5. Size-frequency histograms of dorsal and ventral valves of *Isocrania costata* from 7 samples. *I. costata* only occurs in rather small numbers but the general tendency in almost all samples is a bimodal distribution. Hundefangs Klint 22, Hvidskud 16 and Hvidskud 11 are from bottom, middle part and top of zone 3 respectively. Rørdal 5 is from the top of zone 7. Rørdal 7 is from the bottom of zone 8 and Lindholm 8 is from the top of zone 8. Measurements in mm.


No
Hundefangs Klint 22
dorsal valves N=18
ventral valves N=16
Hvidskud 16
dorsal valves N=11
ventral valves N=10
Hvidskud 11
dorsal valves N=18
ventral valves N=17
Hvidskud 4
dorsal valves N=8
ventral valves N=5
Rørdal 5
dorsal valves N=6
ventral valves N=13
Rørdal 7
dorsal valves N=13
ventral valves N=13
Lindholm 8
dorsal valves N=13
ventral valves N=9
0 1 2 3 4 5
Li

careous mud put in suspension by passing vagile animals. Thus the low cone shape of the ventral valve was developed in order to elevate the commissure above the surface of the mud. The overall shape of *I. costata* is therefore a compromise between two different adaptive traits, the one leading to increased stability in the free living way of life and the other preventing the lophophore from being clogged by calcareous mud.

Population structure. – It was demonstrated by Surlyk (1972) that the population structures of the chalk brachiopods are closely correlated with their mode of life. Thus every major ecological group of brachiopods has a size-frequency distribution of a specific shape. A number of size-frequency distributions have been constructed on the basis of populations of *I. costata* from several samples (fig. 5). Although *I. costata* only occurs in small numbers the general tendency of the distributions reflects the mode of life remarkably well. The size-frequency distributions all show a pronounced bimodality with a peak corresponding to the very early juvenile mortality and a peak corresponding to the adult mortality. Thus the mortality reaches a minimum when the free living life habit is attained. This growth-mortality pattern occupies a very characteristic position in relation to the main ecological groups of brachiopods found in the Danish chalk (Surlyk 1972). Here the most important group comprises minute pedunculate brachiopods which were adapted to a life on the small hard substrates very close to the surface of the sediment. This group has strongly right-skewed size-frequency distributions and thus very high juvenile mortalities. Another ecological group comprises medium-sized hemispherical, secondarily free living brachiopods. This group has a bell-shaped or slightly left-skewed distribution with a very insignificant juvenile mortality. The juveniles of the free living larger brachiopods run the same risk as the juveniles of the minute pedunculate brachiopods as they are in all respects very closely alike. A rather large size would appear to be necessary for the free living mode of life, and it takes some years of growth to attain this size. It was therefore of great importance that the animals belonging to this group rapidly passed through the vulnerable small growth stages and reached their final size and shape as soon as possible. The initial growth rate of these species must therefore have been much greater than that of the small species, a fact that again influenced the size-

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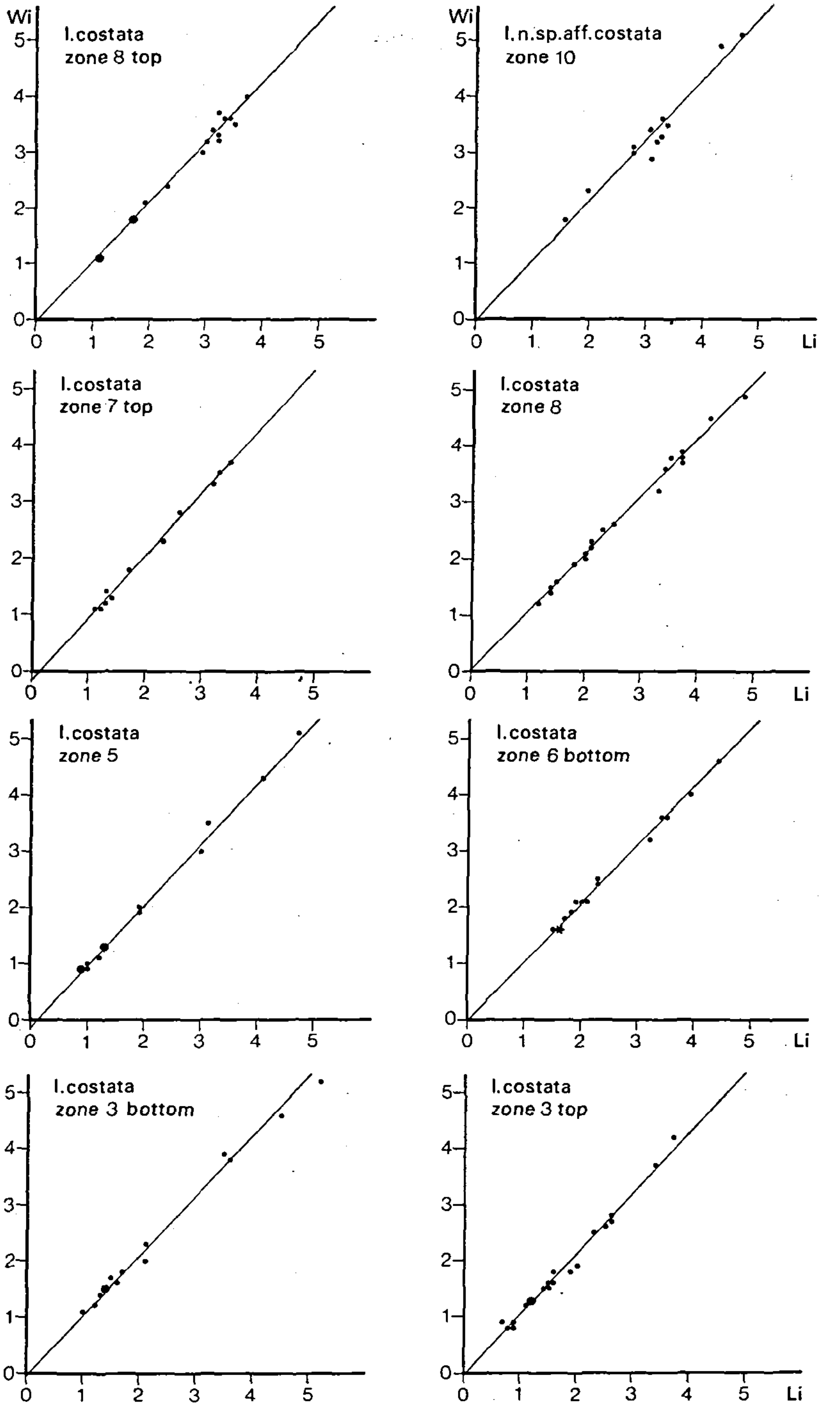
Fig. 6. Length-width diagrams of *Isocrania costata* from 8 samples arranged in stratigraphical order. The small dots correspond to one specimen whereas the larger dots correspond to two specimens. All measurements in mm. A regression analysis (least square method) has been made (equations shown in table 1). The equations are practically identical and no systematic changes can be detected. Thus the general shape of *I. costata* has remained unchanged throughout the Maastrichtian.


Wi
Li
I.costata
zone 8 top
I.n.sp.aff.costata
zone 10
I.costata
zone 7 top
I.costata
zone 8
I.costata
zone 5
I.costata
zone 6 bottom
I.costata
zone 3 bottom
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zone 3 top
0
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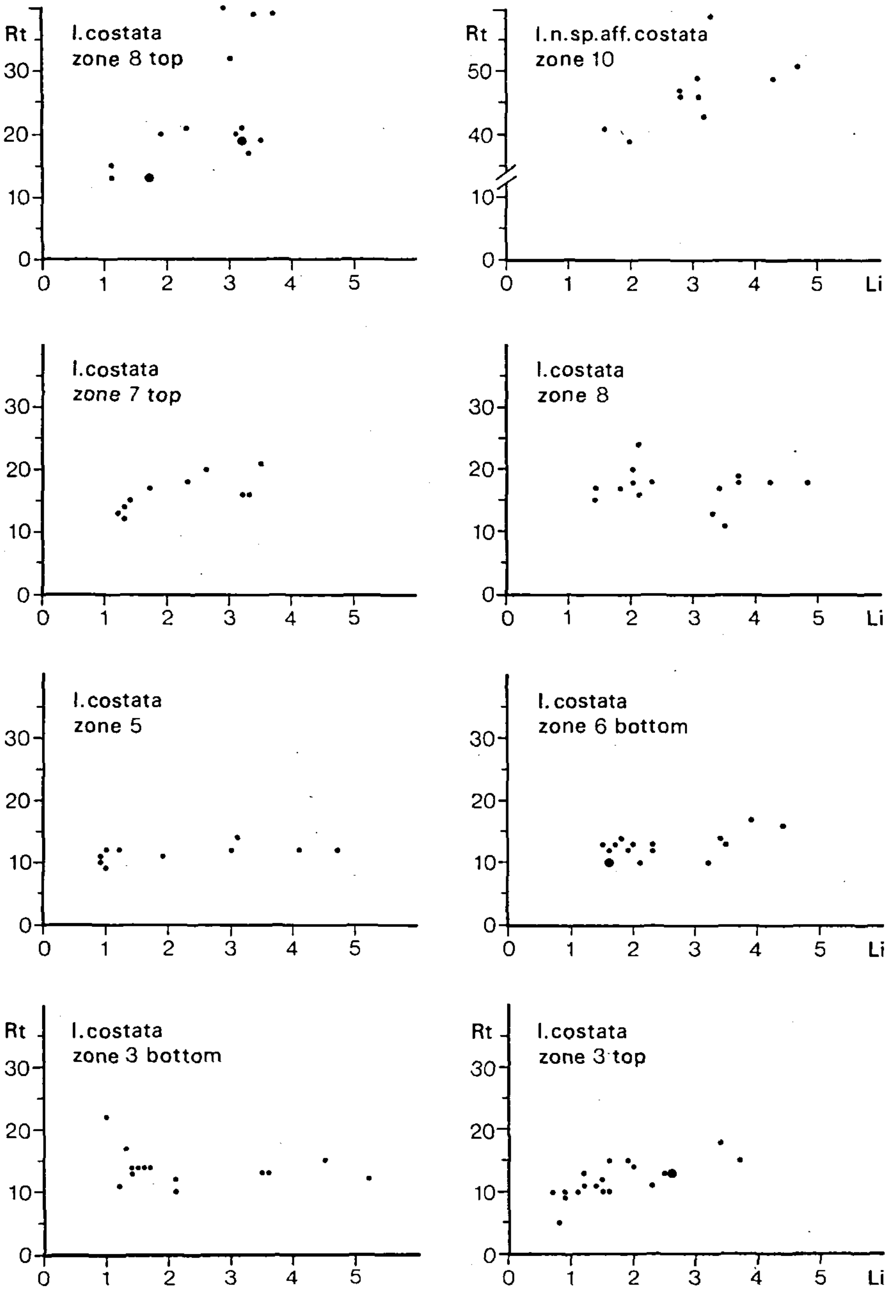

Fig. 7. The total number of ribs (Rt) in relation to length (Li) by *Isocrania costata* from 8 samples (same as in fig. 6), arranged in stratigraphical order. The number of ribs is rather constant in zones 3–5. From zones 7 to 8 top there is a steady increase in number of ribs and in zone 10 the species has changed so much that a new species is formed by phyletic speciation. The small dots correspond to one specimen and the larger dots to two specimens. The measurements are in mm.

Table 1. Regression lines, correlation coefficients, and size of the populations figured in fig. 6, 8 and 9.

I. costata, zone 3 bottom	Wi = 0.0758 + 1.0137 Li;	r = 0.9962;	N = 14
I. costata, zone 3 top	Wi = -0.0863 + 1.1053 Li;	r = 0.9927;	N = 20
I. costata, zone 5	Wi = -0.1425 + 1.1047 Li;	r = 0.9978;	N = 13
I. costata, zone 6 bottom	Wi = 0.0142 + 1.0328 Li;	r = 0.9973;	N = 16
I. costata, zone 7 top	Wi = -0.1530 + 1.0997 Li;	r = 0.9971;	N = 11
I. costata, zone 8	Wi = 0.0255 + 1.0319 Li;	r = 0.9961;	N = 19
I. costata, zone 8 top	Wi = 0.0433 + 1.0755 Li;	r = 0.9912;	N = 16
I. n.sp. aff. *costata,* zone 10	Wi = 0.0271 + 1.0752 Li;	r = 0.9762;	N = 12
I. costata, Dronningestolen	Wi = -0.1322 + 1.1011 Li;	r = 0.9961;	N = 85
I. egnabergensis, Ignaberga	Wi = 0.0641 + 0.9812 Li;	r = 0.9874;	N = 41
I. costata, Dronningestolen	Lp = 0.4192 + 0.4852 La;	r = 0.8977;	N = 33
I. egnabergensis, Ignaberga	Lp = 0.7552 + 0.2546 La;	r = 0.6727;	N = 37

mortality pattern. The bimodal size-frequency distribution of *I. costata* can thus be considered a variant of the bell-shaped curve characteristic of the hemispherical secondarily free living brachiopods. The juvenile peak in the *I. costata* curve only reflects the greater initial risk of the cemented juveniles as compared to the pedunculate juveniles of the other group.

Distribution in the sediment. – As *I. costata* is not a very common brachiopod only little is known of its distribution in the sediment. It is, however, never found in aggregations and it is presumably completely randomly distributed. Experiments with an airbrasive unit (see Surlyk 1972 pl. 5, fig. a) have shown that *I. costata* is rarely found lying horizontally in the chalk. It is often tilted and the two valves have moved several mm or even cm apart. This is due to the burrowing activity of the benthic infauna of the chalk. Bivalved specimens of *I. costata* are not uncommon among juveniles (1 mm or less in diameter, but are extremely rare among adults). In the few bivalved adult specimens (pl. 1, figs. 17–19) the individual valves are displaced in respect to each other. Due to the slow sedimentation of the chalk the adductors of adult individuals presumably disintegrated before burial and only in rare cases, e.g. if the brachiopod was pressed down into the sediment by vagile epifauna, was the whole shell buried before disintegration of the adductors. Later bioturbation is then responsible for the slight mutual displacement of the two valves.

Frequency and competition. – *I. costata* belongs to a group of brachiopods which occurs in almost all samples of chalk but never in large quantities. The largest number found in a single sample is 23 individuals (sample Hvidskud 11 (10 kg), position showed in Surlyk 1972 fig. 14). Normally, however, 10 kg of chalk contain 1–15 individuals. Nevertheless it is remarkable that in some horizons it is the most common brachiopod. This is most characteristic in the benthos poor chalk of zones 7 and 8, whereas it is rare in the benthos richest parts of the Danish chalk – zones 4–5 and 10 (see Surlyk 1972 fig. 3). These differences in frequency must be seen in connection with the supposed mode of life. As a larva *I. costata* is able to use the very small hard substrates available in the chalk e.g. bryozoans, serpulids, oyster spat etc. It shares this adaptation with the large group of minute pedunculate brachiopods characteristic of the chalk (see Surlyk 1972 fig. 5), but in contrast to this group *I. costata* changes during ontogeny to another life habit, namely free living. The chalk of zones 7 and (partly) 8 is very poor in benthonic organisms and pedunculate brachiopods only occur in a number of a few hundreds per 10 kg, whereas the chalk of e.g. zone 4 yields several thousands per 10 kg of chalk. In the benthos rich parts of the chalk *I. costata* never exceeds 1 % of the total brachiopod fauna but in the benthos poorest horizons it often constitutes more than 10 % of the brachiopod fauna and also increases in absolute numbers. This is due with little doubt to its change in life habit. There was strong competition among the minute brachiopods over the scattered substrates but *I. costata* only needed a hard substrate for a short period. As soon as it had reached a certain size it was large enough to "float" freely on the surface of the sediment and thus to avoid the strong inter- and intraspecific competition over the rare hard substrates (fig. 1).

Enemies. – A rather large number of *I. costata* has been killed by boring gastropods (Surlyk 1972 fig. 24c). The shape of the holes bored by these predators suggests that this was mainly the work of muricid gastropods and to a smaller degree of naticid gastropods. The holes normally lie around the umbonal part of the shell (fig. 12).

Isocrania egnabergensis (Retzius). Pl. 2 figs. 1–10

Facies. – *I. egnabergensis* seems to be almost restricted to near-shore carbonate sands. It is especially common at its type locality Ignaberga (Scania, Sweden), where the 17 m thick sequence of medium and coarse grained calcarenites rests on quartz sand close to a horst structure of bedrock. Throughout the calcarenites small pebbles of gneiss, granite etc. occur and at a single horizon these pebbles form a conglomerate. Upwards the grain size increases to a coarse and very fossiliferous calcarenite (Lundegren 1934).

Material and preservation. – 900 valves and shells from the type locality Ignaberga and a few valves from Ullstorp and Ivö Klack, also in Scania. The preservation of the dorsal and the ventral valves is different. The ventral valve is normally well preserved with little or no sign of wear (pl. 2, figs. 8–9). In contrast the dorsal valves are often badly worn in a circular area around the umbo whereas the margins are very well preserved. The worn area is often delimited by a growth ring in such a way that the entire surface lying between the umbo and that growth ring is perfectly smooth as if sandblown. A major reason for the difference in wear and wear pattern of the dorsal valves seem to be that the wear occurred before the death of the animal and was caused by current-swept sand. Another reason is the difference in morphology of the two valves. The dorsal valve has a rather pointed umbo and furthermore is rather thin in that part of the shell whereas the ventral valve has a flat umbo and has a short median septum situated between the anterior adductors. These two differences both favour preservation of the ventral valves. Correspondingly there are preserved approximately 2.6 times as many ventral as dorsal valves.

The relative number of bivalved shells is considerably larger in this species than in *I. costata* and the valves are almost never mutually displaced, but cover each other completely (pl. 2, figs. 1–2). The calcarenites of Ignaberga were laid down in an area swept by strong currents such as were capable of polishing the dorsal valves, but when deposition occurred it was so rapid that the shells were buried before the adductor muscles were disintegrated and the shells thus remained tightly together during and after burial. The calcarenites are not strongly bioturbated like the white chalk and the valves normally lie parallel to bedding (pl. 6, fig. 1).

Mode of life. – Juvenile specimens of *I. egnabergensis* are extremely rare in the calcarenites of Scania and it is only possible to get and idea of the first developmental stages by comparison with better known related craniacean brachiopods. Due to the close relationship with *I. costata* it is suggested that *I. egnabergensis* also settled onto small hard substrates such as bryozoans or fragmentary grains of other fossils at a size of about 0.3 mm in maximum length.

The preferred biotope seems to have been a bottom with rather coarse skeletal sand laid down in an area with considerable current action. The bottom was probably rather firm and the fines have been winnowed to a variable degree by the currents.

During the ontogenetic growth of *I. egnabergensis* the ventral valve took on a flatly rounded shape. The attachment surface was very small and only in rare cases have imprints of the minute substrates been observed. Thus, the life habit changed from firmly cemented to free living at an early stage in ontogeny. As the sediment is coarse grained and almost free of mud there was minimal risk of clogging the lophophore with mud placed in suspension by currents or passing animals. The need for elevating the commissure above the sediment was therefore not as great as for *I. costata* in the chalk biotope. Consequently another adaptive trait leading to increased stability was more important and this resulted in a flat circular disc shape (fig. 1).

The ventral valve not only has an ideally stable form but it is also heavier than the dorsal valve, indicating that the species even might have been able to live in bottom areas with more or less rapidly shifting sands.

In some horizons at Ignaberga the calcareous sands are cross bedded in 0.25 m thick sets. Thus not only the fragmentation and wear of the skeletal grains, but also the sedimentary structures point towards a bottom with occasional strong currents.

Population structures. – In contrast to the *I. costata* material that of *I. egnabergensis* has been collected not by washing of bulk samples, but by normal hand collecting. Thus only a general idea of the size distribution could be obtained. Further, and more important, the fossils have not necessarily been buried at the place where they lived. However, since a large part of the fossils seem to be confined to the particular facies at Ignaberga, since they are often well preserved and since they seem to be well adapted to the biotope, it may be argued that the transport was only local involving short distances. The assemblages are thus found generally where the animals lived. The most important loss of information has been through the destruction of the smaller fossils during transport and wave action, whereas diagenetic effects seem to be negligible.

The material of *I. egnabergensis* from Ignaberga is almost totally composed of adult of near-adult individuals. But on account of the information loss no biological inferences can be drawn from this population structure.

Distribution in the sediment. – *I. egnabergensis* reaches its maximum abundance in the upper, coarser parts of the Ignaberga succession. Here it occurs in great quantities on certain bedding planes probably in life position, with an orientation parallel to bedding (pl. 6, fig. 1). The unchanged orientation is possibly due to the limited bioturbation of the sediments.

Competition. – The rest of the brachiopod fauna at Ignaberga mainly comprises large sized pedunculate forms adapted to totally different modes of life. It may therefore be assumed that *I. egnabergensis* met with rather limited competition in the fight for space on the small substrates, the main obstacles for prolonged life being on the contrary strong currents. When it grew older and changed to a free living life habit, competition for space presumably played an unimportant role.

The great diversity of the fauna and the often strong current action suggests that food was of minor importance as a limiting factor for *I. egnabergensis.*

Enemies. – In contrast to *I. costata* only very few specimens of *I. egnabergensis* have been bored by predaceous gastropods. No other signs of predation have been found despite careful examination of all 900 specimens available.

Conclusions

The presence of two very specialized but almost identical craniacean brachiopod species in two very different biotopes provides an important way of testing conclusions drawn from observations on each of the two occurrences.

Thus it could be inferred with some justification that *I. costata* was able to live on the chalk sea bottom because of the lack of stronger currents there. Immediately the question arises: How could *I. egnabergensis* live on current swept bottoms at Ignaberga? This way of testing and refining arguments seems to be of great significance in palaeoecology. Every deduction on the palaeoecology of a species in a given biotope should be checked by examining and comparing closely related forms from other biotopes. In this way the often very generalized statements which appear repeatedly in palaeoecology can be reduced.

Taxonomy

Isocrania costata (Sowerby 1823)
Pl. 1, 3, 4, 5, 6, fig. 2

1823 *Crania costata:* J. Sowerby, vol. 4 without pagination, pl. 35 fig. 6
1828 *Crania costata:* Hoeninghaus, pl. 1 fig. 11
1840 *Crania costata:* Goldfuss, p. 294, pl. 162 fig. 11
1842 *Crania costata:* Hagenow, p. 530–531, pl. 9 fig. 1
1850 *Crania costata:* Dixon, p. 354, pl. 27 figs. 4–5
1852 *Crania Egnabergensis* Retzius: Davidson, p. 11–13 (partim), pl. 1 figs. 10–11, non figs. 8–9, 12–14
1894 *Crania costata:* Posselt, p. 15–17, pl. 1 figs. 1–4
pars 1909 *Crania ignabergensis* Retzius: Nielsen, p. 147–149
1972 *Isocrania costata:* Surlyk, figs. 5, 24

Holotype. – Sowerby vol. 4, pl. 35, fig. 6. The actual type specimen cannot be traced and must be presumed lost (E. F. Owen, personal communication 1972). The figure of the type specimen is very good and it is therefore not considered necessary to select a neotype. The type locality was said to be Orglandes (near Valognes, Normandy, France). In this area several small outliers of Maastrichtian calcarenites and -siltites occur. Additional material has been obtained from two of these localities (coll. E. Voigt, Hamburg). The specimens from Port Fiolet correspond particularly well with the figure of the holotype.

According to Sherborn (1894) the book "Genera of Recent and fossil shells" was published at intervals between 1822 and 1834(?); forty-two parts were issued, but considerable trouble has been caused by the difficulty of fixing the dates of the separately published parts of the book. From the original donation books of the Linnean Society, Sherborn succeeded in finding the dates of appearance of all 42 parts. The genus *Crania* was issued in part 12 (Newton 1891 p. 321) and part 12 was published in 1823 (Sherborn 1894). Thus the actual plate and the date of publication is known and only the problem of authorship has to be solved. J. and G. B. Sowerby were co-authors of the entire book, but the work was commenced by J. Sowerby who died in 1822 (Keen 1971).

The issue in the University Librarary of Copenhagen containing *Crania costata* is labelled as vol. 4 and on its front cover is written "The genera of Recent and fossil shells by James Sowerby vol. 4". This indication together with the data of publication both lead to J. Sowerby as the author of the species.

Diagnosis. – Small, free living *Isocrania* with subrectangular to circular outline. Both valves have a low conical shape and an ornamentation of 10–35 strong, radiating ribs. New ribs are formed by intercalation. The umbo is placed somewhat posterior to the centrum of the valves. The limbus is wide and pustulose in both valves. Anterior adductor close together in both valves.

Description. – Outline. The outline is subrectangular to perfectly circular. Normally the shell is somewhat wider than long (fig. 6).

Dorsal valve. The dorsal valve is of low conical shape. The protegulum is smooth, pointed and circular in outline (pl. 3). The first ribs are formed at a length of about 0.5 mm. The number of primary ribs varies between 10 and 30 (fig. 10). New ribs are formed by intercalation and their number may increase to about 35. There is, however, a pronounced increase in number of ribs through the Maastrichtian (fig. 7). The ribs are strong and prominent and protrude somewhat beyond the valve margin (pl. 1). The anterior and posterior ribs are straight whereas the lateral ribs curve slightly in a posterior direction. The surface of the valve between the ribs is in rare cases smooth but has normally a sculpture consisting of coarse radially directed spines (pl. 5). The anterior adductor scars are situated close to each other. The posterior adductors are separated by a septumlike extension of the limbus and are also limited anterio-laterally by such extensions. The limbus is wide and finely pustulose; also the anterior parts of the disc may have a finely pustulose sculpture. The impressions of the mantle canal system show to a variable degree.

Ventral valve. The outline and sculpture is similar to the dorsal valve. The only exterior difference is the protegulal node which is flat and in rare cases shows imprints of the tiny substrates (pl. 4, figs. 1–4, pl. 5, fig. 1). The scars of the anterior adductors are drop-shaped and converge anteriorly towards the midline of the valve. The scars of the posterior adductors are

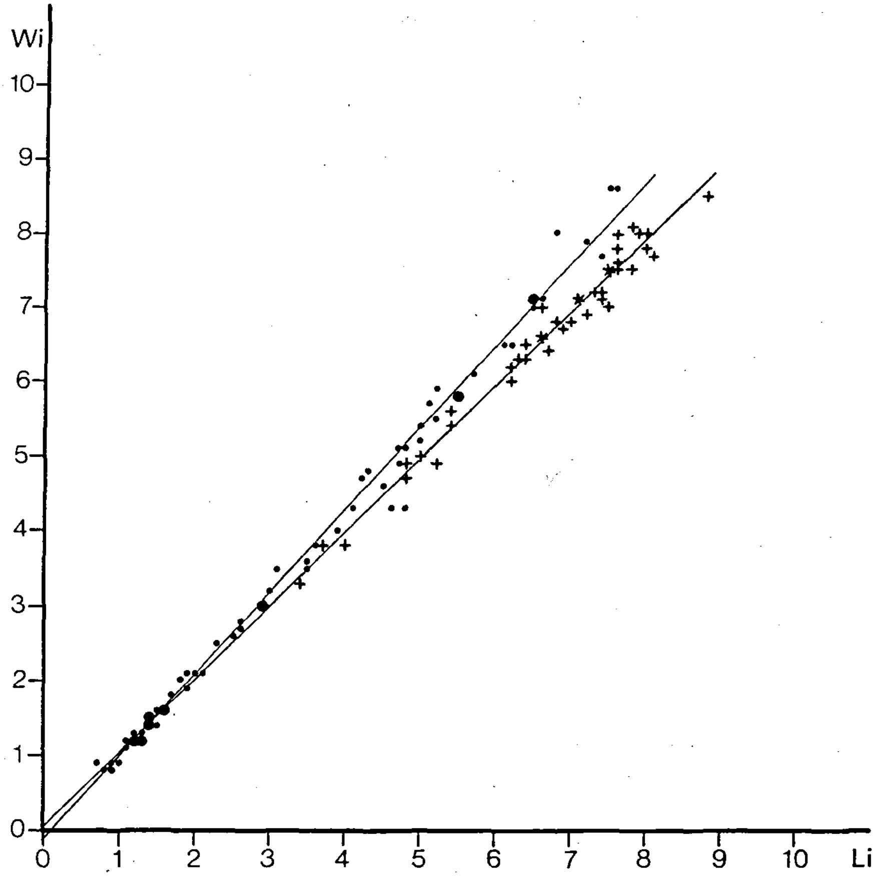

Fig. 8. Composite length-width diagram for both *I. costata* (dots) and *I. egnabergensis* (crosses). *I. costata* is generally wider than long and *I. egnabergensis* longer than wide. The population of *I. costata* is from Dronningestolen, Møns Klint and the population of *I. egnabergensis* is from Ignaberga, Scania. Measurements in mm. The large dots correspond to two specimens of *I. costata* and the asterisks correspond to two specimens of *I. egnabergensis*. A regression analysis (least square method) has been made (equations shown in table 1). An F-test shows that the variances of the two regression lines are equal ($P > 20\,\%$). A t-test of the slopes gave $t = 4.4723$ with 122 degrees of freedom, which is very highly significant ($P < 0.1\,\%$).

oval and have the same size and position as in the dorsal valve. A pointed septum is situated between the anterior adductors. Otherwise the sculpture of the interior is similar to the dorsal valve.

Affinities. – *I. costata* is closely related to *I. egnabergensis* (Retzius) but it is smaller, has significantly fewer and stronger ribs (fig. 11) and has a more rounded outline. *I. barbata* (Hagenow) has a more variable and irregular

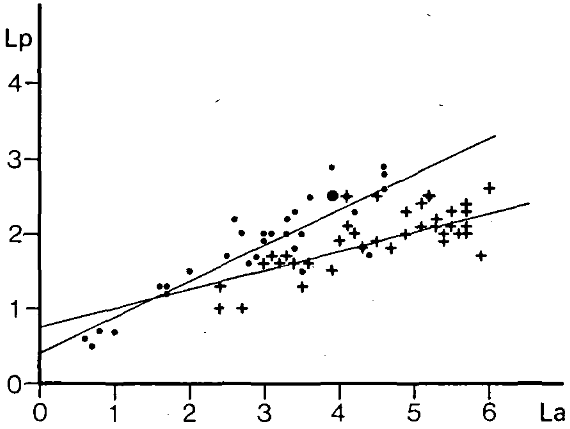

Fig. 9. Diagram showing the relation between anterior length (La) and posterior length (Lp) (fig. 4) of *I. costata* (dots) and *I. egnabergensis* (crosses). The diagram demonstrates clearly that the umbo is more posteriorly situated by *I. egnabergensis* than by *I. costata*. The material of *I. costata* is from Dronningestolen, Møns Klint and the material of *I. egnabergensis* is from Ignaberga, Scania. Measurements in mm. A regression analysis (least square method) has been made (equations shown in table 1). An F-test shows that the variances of the two regression lines are equal ($P > 20\ \%$). A t-test of the slopes gave $t = 3.6150$ with 66 degrees of freedom, which is very highly significant ($P < 0.1\ \%$).

shape, a larger attachment surface and a much larger number of ribs. Throughout the Campanian and Maastrichtian Stages closely related forms appear but little is known of their morphology and especially their stratigraphical occurrence. One of the more characteristic forms is often mentioned in the literature as *I. paucicostata* (Bosquet). It differs from *I. costata* in that the umbo is more posteriorly situated and the ribs are more curved in a posterior direction, protruding further beyond the shell margin. Its stratigraphical range is not known but it seems to be most common in uppermost Maastrichtian and possibly younger horizons. In the Campanian chalk of Norfolk, England forms of *Isocrania* intermediate between *I. egnabergensis* and *I. costata* are common together with a variety of *I. paucicostata* with extremely long, free ribs. In the Maastrichtian of Normandy, France, which is the type area for *I. costata,* several forms occur where the small grains between the large primary ribs are ordered radially and form a large number of irregular thin ribs. In some cases these ribs become almost as strong as the primary ribs and thus approach the *egnabergensis* type of ornamentation. A number of specimens showing all these variable ribbing patterns is shown of pl. 1, figs. 9–15. However, their correct taxonomic position can only be determined when larger stratigraphically collected populations are available. The finely ribbed forms belong together with the youngest Danish forms to a new species of *Isocrania* which will be described elsewhere.

Stratigraphy. – The stratigraphical occurrence is only well known in the Maastrichtian of Denmark, north Germany and east England. In Denmark it occurs in all 10 zones of Surlyk (1970). It is most numerous in zones 3, 7 and especially 8, whereas it is rare to very rare in zones 9 and 10 which are by far the best exposed. As demonstrated above (fig. 7) there is a phyletic trend towards a larger number of ribs in *I. costata.* In the uppermost Maastrichtian (zone 10) the species has changed so much that a new species of *Isocrania* is formed by phyletic speciation. The rare occurrences of *I. costata* in zone 10 may therefore better be regarded extreme morphological variants of the new species.

In Hemmoor (north Germany) *I. costata* is common in the highest part of the succession (top of *Belemnitella junior* Zone ≈ Surlyk's zones 8–9) and it occurs sporadically in the lowest parts of the quarry (bottom of the *Belemnella occidentalis* Zone ≈ Surlyk's zone 6). In England it occurs in the Upper Campanian *Belemnitella mucronata* Zone and in the Maastrichtian at Trimingham.

Material. – Denmark: Zone 1: 1 individual, zone 2: 2, zone 3: 80, zone 4: 23, zone 5: 28, zone 6: 2, zone 7: 34, zone 8: 81, zone 9: 20, zone 10: 10 (zones 1, 2 and 6 are badly exposed or only known from borings).

Hemmoor (north Germany): 53 individuals. In addition numerous specimens have been examined in the collections of the Mineralogical Museum (Copenhagen); the British Museum (Natural History); the Sedgwick Museum, Cambridge; E. Voigt, Hamburg; and A. Rosenkrantz, Copenhagen.

Isocrania egnabergensis (Retzius 1781)
Pl. 2

1731 Numulus minor rarissimus: Stobaeus, pl. 1 fig. 3
1781 *Crania Egnabergensis:* Retzius, p. 75, pl. 1 figs. 4–7
1826 *Crania striata,* Lam.: Nilsson, P. 327–328, pl. 2 fig. 4
1828 *Crania striata,* Defr.: Hoeninghaus, p. 10–11, fig. 10
1840 *Crania striata* Defr.: Goldfuss, p. 294, pl. 162 fig. 10
? 1866 *Crania Ignabergensis:* Schloenbach, p. 326–328, pl. 40 figs. 23–24
1885 *Crania Ignabergensis:* Lundgren, p. 30 (partim), pl. 1 fig. 10, non fig. 11
1953 *Crania egnabergensis:* Wind, p. 79
1958 *Crania egnabergensis:* Carlsson, p. 24, pl. 3 figs. 2–3, non fig. 4
non 1965 *Isocrania egnaburgensis:* Rowell in Williams et al., H 290, fig. 180, 1
non 1969 *Crania ignabergensis:* Kruytzer, p. 30–34, fig. 12

Holotype. – Numulus minor rarissimus, p. 31 and fig. 3 in Kilianus Stobaeus (1731). The actual holotype is presumably lost (Carlsson 1958), but a very large material has been obtained from the well exposed type locality Ignaberga. In the days of Stobaeus only small quarries existed at Ignaberga; they are now abandoned or incorporated in the two large quarries – the old and the new quarry of Ignaberga (Lundegren 1934). The strata exposed at Ignaberga all correspond to a rather short period belonging to the upper part of the Lower Campanian (Christensen 1969).

Name. – The species name was spelt *egnabergensis* by Retzius in 1781. It was corrected to *ignabergensis* by later authors to agree with the spelling of the name of the type locality Ignaberga. The correct spelling was exhumed by Wind (1953) and since then the name has been spelt *egnabergensis* by Carlsson (1958) and Rosenkrantz (1964). Most recently Kruytzer (1969) in an elaborate discussion argues that the correct spelling is *ignabergensis* because at the time of Retzius' travel the village was spelt Ignaberga. While the latter statement is probably correct the conclusion is wrong. It is irrele-

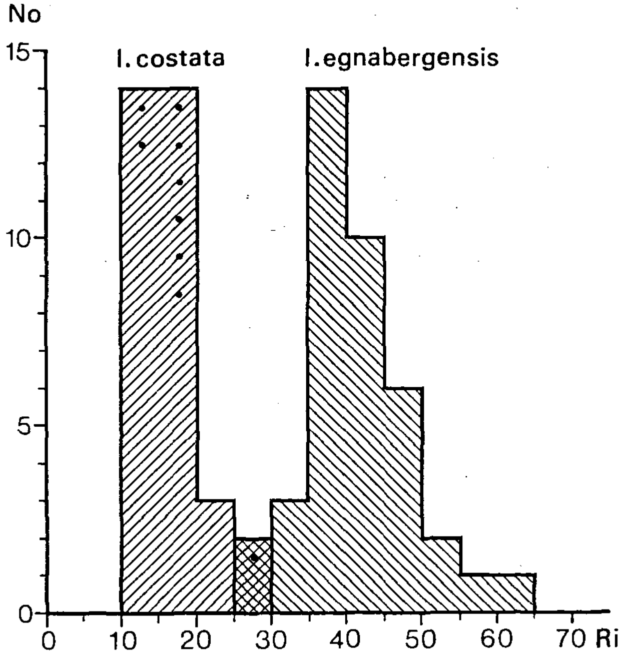

Fig. 10. Frequency histogram showing the number of initial (primary) ribs by *I. costata* (10–30 ribs) and by *I. egnabergensis* (25–65 ribs). The dots corresponds to dorsal valves, whereas the rest is ventral valves. The material of *I. costata* is from Dronningestolen, Møns Klint and the material of *I. egnabergensis* is from Ignaberga, Scania.

vant how the type locality is or was spelt for the naming of a species. Furthermore, in a footnote Retzius specially referred to the actual locality, stating that the name had been wrongly spelt by earlier authors, and adding a general warning against misspelling Swedish names. The spelling *egnabergensis* is not a slip of the pen or a printers error as the same spelling is used throughout the paper. It would indeed appear from the footnote that Retzius had given the spelling careful consideration. The correct name is therefore *egnabergensis* and conflicts in no way with the International Code of Zoological Nomenclature, article 32 (a) (ii).

Diagnosis. – Medium sized free living *Isocrania* with subrectangular outline. The anterior margin is wider than the posterior. The dorsal valve has a low conical shape whereas the ventral valve has a flatly rounded profile. The ornamentation consists of 30–70 fine radial ribs which curve gently in a posterior direction (fig. 11). New ribs are formed by intercalation. The umbo is placed close to the posterior margin. The attachment surface is small. The limbus is wide and strongly pustulose in both valves. The anterior adductor scars in the dorsal valve are large and rather widely spaced.

Description. – Outline. The outline is subrectangular but the anterior margin is wider than the posterior. The anterior and posterior as well as the lateral margins are often rather straight. The length is slightly larger than the width (fig. 8).

Dorsal valve. The dorsal valve is of a low conical shape. The protegulum is pointed and smooth and situated close to the posterior margin, but the area round the umbo is often strongly worn so that details of the young shell are difficult to see. The first ribs are formed at a length of about 0.5 mm. The number of primary ribs varies between 25 and 65 but most commonly 35–40 (fig. 10). New ribs are formed by intercalation and the number increases to about 50 with about 70 as a maximum (fig. 11). The thin, delicate, closely spaced ribs curve gently in a posterior direction and protrude slightly over the shell margin (pl. 2). The scars of the posterior adductors are drop shaped with the pointed end in an anterio-lateral direction. The anterior adductors are oval and somewhat smaller, but the distance between their centres is practically the same as for the posterior adductors. The impressions of the mantle canal system are rather weak. The limbus is wide and strongly pustulose; outwards it is sharply limited by a thin smooth area along the valve margin.

Ventral valve. The outline and sculpture resemble the dorsal valve, but the profile is flatly rounded and the protegulal node is flat. Both anterior and posterior adductor scars are oval or, rarely, drop shaped. The anterior scars are much smaller and somewhat closer to the midline than the posterior

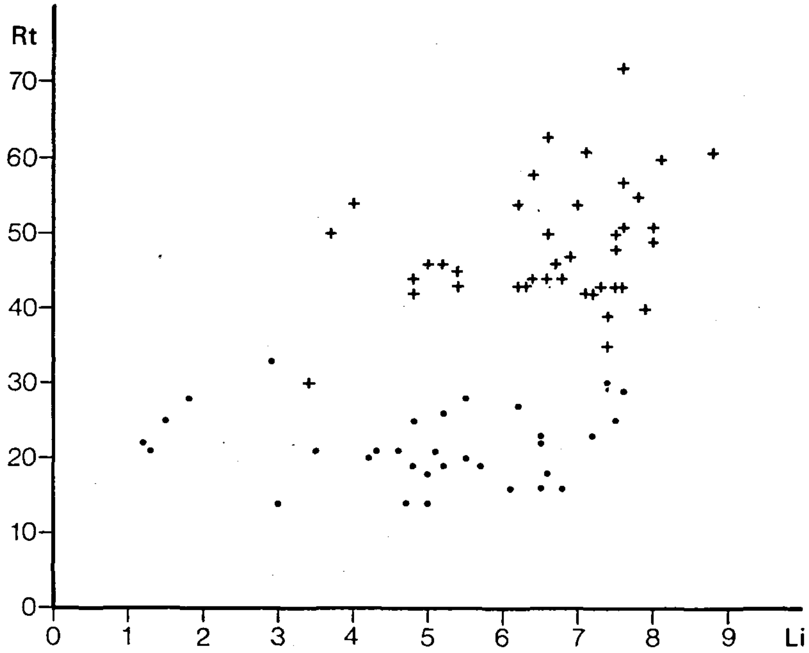

Fig. 11. Relation between total number of ribs (Rt) and length (Li) by *I. costata* (dots) and *I. egnabergensis* (crosses). The material of *I. costata* is from Dronningestolen, Møns Klint and the material of *I. egnabergensis* is from Ignaberga, Scania. Measurements in mm.

scars. There is a prominent, short septum between the anterior adductors. The impression of the mantle canal system is rather distinct. The valve margin is as in the dorsal valve.

Affinities. – *I. egnabergensis* is closely related to *I. costata* (Sowerby), but has a much larger number of closely spaced ribs (fig. 11). Furthermore, it is larger, has a less rounded shape and the dorsal scars of the anterior ad-

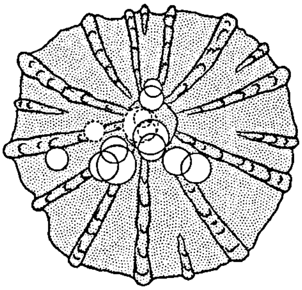

Fig. 12. Gastropod borings from 14 specimens of *I. costata* from Vitmunds Nakke, Møns Klint superimposed on one valve to show the concentration of borings around the umbo. Stippled outlines correspond to unfinished borings.

ductors are larger and more widely spaced than in *I. costata*. Another difference is the width/length ratio. *I. costata* is slightly wider than long, whereas *I. egnabergensis* is slightly longer than wide (fig. 8). Furthermore the umbo is situated closer to the posterior margin in *I. egnabergensis* than in *I. costata* (fig. 9). *I. barbata* (Hagenow) is even closer to *I. egnabergensis* than *I. costata* but is more irregular in outline, has a larger number of ribs and has a larger and very irregular attachment surface.

In the Campanian of Norfolk, England intermediate forms between *I. costata* and *I. egnabergensis* occur. They differ from the latter in having fewer ribs, smaller size, thinner valves, and a more rounded outline. The forms from Normandy, France mentioned under *I. costata* are also close to *I. egnabergensis* but they consistently have few regularly distributed ribs which are stronger than the large number of intercalated ribs. Moreover the specimens are smaller, have a thinner shell and a more rounded outline. Forms very close to *I. egnabergensis* and from the same type of facies occur in the Maastrichtian of Holland (see e.g. Kruytzer 1969 fig. 12). They differ from *I. egnabergensis* only in the more anterior position of the umbo, in the spinulose sculpture between the ribs and in a circular outline. Tentatively I would suggest that this form is an Upper Maastrichtian off-shoot of the *I. costata* line rather than a direct descendent of *I. egnabergensis*, corresponding to the stratigraphical increase in number of ribs by *I. costata* (fig. 7).

Stratigraphy. – *I. egnabergensis* is only well known from the upper part of the Lower Campanian in Scania, Sweden. However, the specimens figured by Schloenbach (1866) from the German Lower Campanian seem to be correctly identified.

Material. – 900 valves from Ignaberga, and a few valves from Ullstorp and Ivö Klack, all localities in Scania, Sweden.

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Dansk sammendrag

De to inarticulate branchiopoder *Isocrania costata* (Sowerby) og *Isocrania egnabergensis* (Retzius) findes almindeligt i henholdsvis skrivekridt fra Maastrichtien i Danmark og biokalkarenit fra øvre Nedre Campanien i Skåne. De to arter er stærkt specialiserede med små eller næsten manglende cementations-flader på ventralskallen i modsætning til andre craniaceer, der har en totalt cementeret ventralskal. *I. costata*'s skaller har begge ligesom dorsalskallen hos *I. egnabergensis* en lav kegleform. Ventralskallen hos *I. egnabergensis* er fladt afrundet i profil. Derudover har *I. egnabergensis* lidt større og tykkere skaller, og lidt større forreste muskelaftryk. Trods den stærke specialisering og det næsten ens udseende findes de to arter i to vidt forskellige facies, som de synes at være begrænsede til. Aflejringsmiljøet har været totalt forskelligt i de to biotoper. Skrivekridthavbunden er karakteriseret af yderst langsom sedimentation (i forhold til det enkelte dyrs levetid), af relativt dybt vand, af en total bioturbation og formodentlig af en blød overflade dækkende mere konsolideret og bæredygtigt sediment i nogle få millimeters dybde. Omvendt er de skånske kalkareniter aflejret i ganske lavt vand, hvor der herskede kraftige strømme (stærkt slid af korn, udvaskning af fine bestanddele, krydslejring).

I. costata slog sig efter et kort fritsvømmende larvestadium ned på meget små hårde substrater umiddelbart ved sedimentets overflade. Hvis dette meget risikable tidlige fastsiddende stadie blev heldigt overstået skiftede arten livsform. Substratet var nu så lille, at det var uden betydning og arten blev derfor fritlevende. Udfra en rent stabilitetsmæssig betragtning er *I. costata*'s skiveform ideel for en fritlevende brachiopod, men risikoen for tilslamning er overmåde stor. For at imødegå denne tilslamning udvikledes en kegleformet ventralskal, og således blev skalranden hævet over sediment overfladen. *I. costata's* specialisering skal ses som et kompromis mellem to adaptive tendenser: én gående mod forøget stabilitet og en anden, der forhindrer lophophoren i at blive slammet til i kalkmudder.

I. egnabergensis slog sig også ned på små hårde substrater, nemlig små strømslidte kalkkorn. Bunden har været forholdsvis hård og risikoen for tilslamning ringe. Den største fare har vel været at blive knust ved transport af stærk strøm. Tidligt skiftede arten livsform til fritlevende, idet substratet blev alt for lille. På grund af sedimentets grovkornethed var behovet for at løfte skalranden for at undgå tilslamning ringere end for *I. costata* i skrivekridt biotopen. Følgelig blev den anden adaptive tendens, der ledte mod forøget stabilitet, den vigtigste, og det resulterede i en flad, circulær ventralskal.

Eksemplet er valgt som en overordentlig betydningsfuld måde til at teste palæøkologiske konklusioner. Udfra studiet af *I. costata* og det miljø den levede i kunne det således hævdes at den kunne leve løstliggende umiddelbart på sedimentoverfladen på grund af fraværet af kraftigere strøm. Dette vil umiddelbart føre til modspørgsmålet: Hvordan kunne den nært beslægtede *I. egnabergensis* leve i de strømsvøbte miljøer i Skånes Kridt. Enhver deduktion om en arts palæøkologi på en bestemt biotop bør checkes ved at undersøge og sammenligne nært beslægtede arter fra andre biotoper. På denne måde kan de ofte overordentlig generelle udsagn der ses igen og igen i palæøkologisk litteratur forhåbentlig reduceres.

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Plate 1

Isocrania costata (Sowerby), figs. 1–11, 16–19. All specimens ×3. Figs. 1–8 and 17–19 are all from Dronningestolen, Møns Klint. Figs. 1–4: ventral valves; figs. 5–8: dorsal valves; fig. 9–11: ventral valves from Port Fiolet, Normandy, France (the type area of *I. costata*); fig. 16: ventral valve from Dixon's collection (British Museum no. B 484); the specimen is said to be from the Turonian of Sussex, but the general appearance suggests an Upper Campanian or Maastrichtian age. Fig. 17: bivalved specimen, dorsal view; fig. 18 a–b: bivalved specimen, dorsal and ventral views; fig. 19 a–b: bivalved specimen, dorsal and ventral views. *Isocrania* n.sp. aff. *costata*, figs. 12–15. All specimens from Chef du Pont, Normandy, France. All Specimens ×3; figs. 12, 14–15: dorsal valves; fig. 13: ventral valve. (Figs. 1–8, 17–19 are housed in the Mineralogical Museum, Copenhagen under MMH 12837–12847. Figs. 9–15 are housed in the Department of Palaeontology, University of Hamburg under nos 1673–1679).

Plate 1


1a


1b


2a


2b

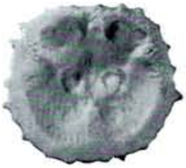

3a

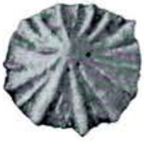

3b


4a


4b


5a


5b


6a


6b


7a


7b


8a


8b


9


10


11


12


13


14


15


16a


16b


17


18a


18b


19a


19b

Plate 2

Isocrania egnabergensis (Retzius). All specimens ×3, from Ignaberga, Scania, Sweden. Fig. 1 a–b: bivalved specimen, ventral and dorsal views. Note the small attachment surface on fig. 1 a. Fig. 2 a–b: bivalved specimen, ventral and dorsal views. Note the small attachment surface on fig. 2 a. Figs. 3–7: dorsal valves. Figs. 8–10: ventral valves. All specimens are housed in the Mineralogical Museum, Copenhagen under nos 12848–12857.


1a


1b


2a


2b


3a


3b


4a


4b


5a


5b


6a


6b


7a


7b


8a


8b


9a


9b


10a


10b

Plate 3

Juvenile dorsal valves of *Isocrania costata* from samples Hvidskud 11 (figs. 1–4, 6) and Hemmoor 79 ob. (fig. 5). *Fig.* 1: ×63 (MMH 12858); fig. 2: ×66 (MMH 12859); fig. 3: ×37 (MMH 12860); fig. 4: ×35 (MMH 12861); fig. 5: ×28 (Kma 22); fig. 6: ×19 (MMH 12862). All specimens from Hemmoor are housed in the Niedersächsisches Landesamt für Bodenforschung in Hannover.

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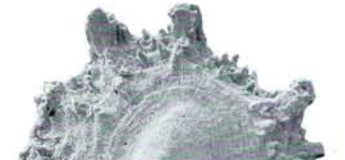

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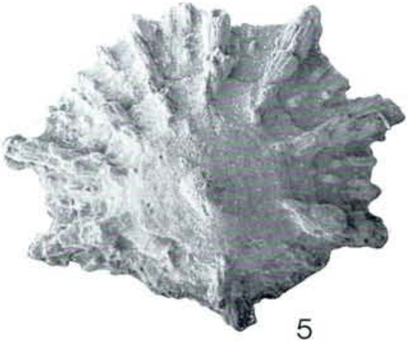

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Plate 4

Juvenile ventral valves of *Isocrania costata* (figs. 1–4). Fig. 1: ×63, Hvidskud 11 (MMH 12863); fig. 2: ×42, Hvidskud 11 (MMH 12864); fig. 3: ×30, Hvidskud 11 (MMH 12865); fig. 4: ×27, Hemmoor 140 u. (Kma 23); fig. 5: smooth, slightly corroded dorsal valve of *I. costata,* ×15, Hemmoor 140 u. (Kma 24); fig. 6: almost smooth dorsal valve of *I. costata,* ×21, Hemmoor 140 u. (Kma 25). Smooth dorsal valves as the one on fig. 5 will normally be referred to the genus *Crania.* The existence of specimens as the one on fig. 6 shows, however, that they may be pathological specimens of *I. costata.*


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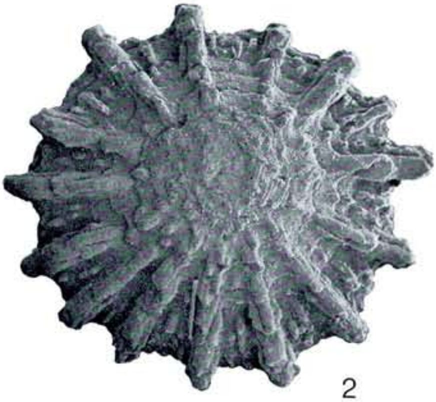
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Plate 5

Fig. 1: detail of attachment surface on ventral valve of *I. costata,* Hvidskud 11, ×142 (MMH 12866); fig. 2: as fig. 1, ×66 (MMH 12867); fig. 3: detail of ornamentation of *I. costata,* Hemmoor 79 ob. (Kma 26), ×66; fig. 4: as fig. 3, Hemmoor 140 u. (Kma 27), ×72; fig. 5: as fig. 3, Hvidskud 11, ×93 (MMH 12868); fig. 6: as fig. 3, Hvidskud 11, ×96 (MMH 12869).


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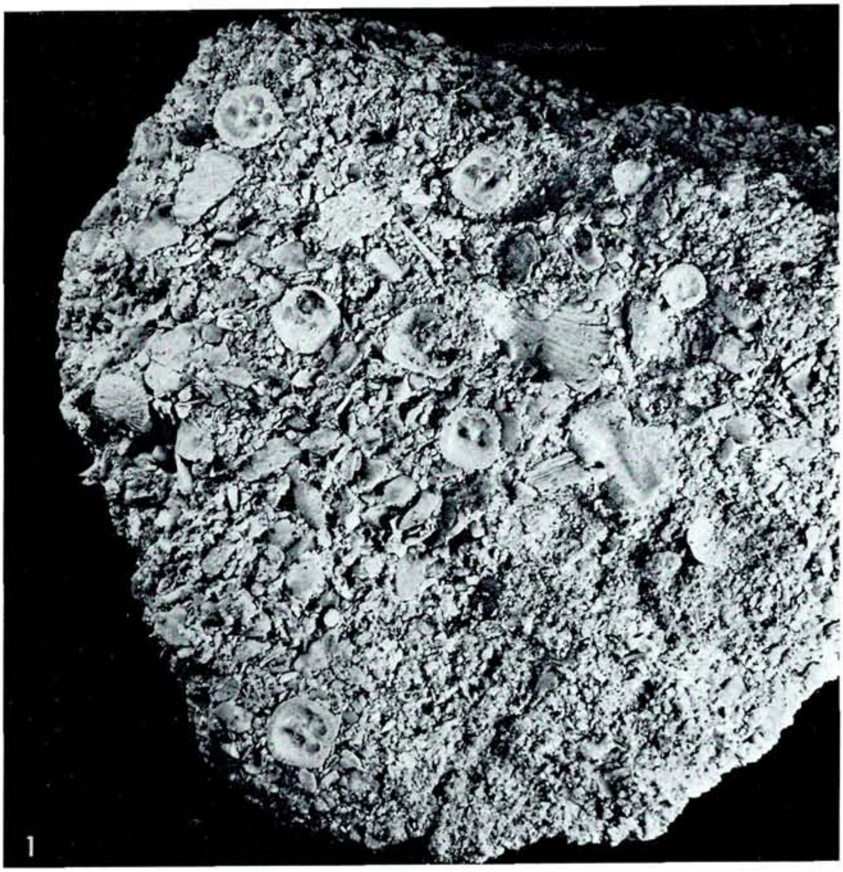
Plate 6

Fig. 1: Slab of calcarenite from Ignaberga, Scania, Sweden. Six ventral valves and one dorsal valve of *Isocrania egnabergensis* in life position, ×1.2 (MMH 12870). Fig. 2: protegulal node of dorsal valve of *I. costata,* Hemmoor 140 u. (Kma 28). Note tiny thallophyte borings, ×77. Fig. 3: detail of fig. 1 showing a ventral valve of *I. egnabergensis* from Ignaberga in life position, ×2.4.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