TWO SALENIOID ECHINOIDS IN THE DANIAN OF THE MAASTRICHT AREA

by J. F. GEYS

ABSTRACT. Two species of salenioid echinoids, *Salenia minima* Agassiz and Desor, 1846 and *Hyposalenia heliophora* (Agassiz and Desor 1846) from the Danian strata in the Maastricht area, are described and discussed. Biometrical parameters are statistically treated and compared with those of some other salenioids. It is shown that both species are probably good index fossils for strata of Danian age.

PREVIOUS systematic treatments of the Danian echinoderm fauna in the Maastricht area were made exclusively by investigators studying the Cretaceous Maastricht Chalk. Lambert (1911) was the first to study the echinoid fauna of the Maastricht Cretaceous as a whole. The fauna was systematically revised by Smiser (1935). Both these authors essentially studied the important collections of the Koninklijk Belgisch Instituut voor Natuurwetenschappen in Brussels (K.B.I.N.). The so-called post-Maastrichtian (or Danian) echinoids from the Maastricht area, are less well represented in these collections, which may explain why the characteristic Danian species were not revised by both these authors. The collections of the K.B.I.N., as well as those of the Natuurhistorisch Museum at Maastricht (N.H.M.M.), were revised by M. Meijer. Unfortunately, his results were only partly published, but Meijer (1965) was the first to draw attention to the important differences between the echinoid faunas of the Houthem Formation (post-Maastrichtian) and the underlying chalk beds (Ma to Md), belonging to the Maastricht Chalk. As a result he separated his 'zone III' from the echinoid assemblages of the Maastricht Chalk, and he presumed that this zone was of Dano-Montian age. Meijer's view proved to be correct when Moorkens (1972) correlated the post-Maastrichtian Geulhem Chalk (Houthem Formation) with the Ciply Tuffaceous Chalk, which had been previously correlated with the type Danian at Fakse (Denmark) by Rasmussen (1965).

Two of the most characteristic species from the post-Maastrichtian Houthem Formation in the Maastricht area are discussed in this paper. They occur in the Ciply Tuffaceous Chalk, in the vicinity of Mons (Belgium), but they are absent in overlying and in underlying strata. In the Maastricht area, both species seem to be confined to strata which Felder (1975) termed the Geulhem Chalk of the Houthem Formation. A correlation between the Geulhem Chalk and the Ciply Tuffaceous Chalk is thus confirmed.

The specimens studied belong to the collections of the Natuurhistorisch Museum at Maastricht (N.H.M.). In some specimens, a few dimensions were measured by means of calipers (absolute error: 0·1 mm). Statistical calculations were carried out, using the formulas and symbols proposed by Till (1974).

The following abbreviations are used:

D: ambital diameter of the test III-5;
h: total height of the test;
ds: diameter of the apical system, taken between the centres of the distal borders of ocular III and genital 5;
dp: diameter of the peristome III-5.

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SYSTEMATIC DESCRIPTIONS

Class ECHINOIDEA Leske, 1778
Subclass EUECHINOIDEA Bronn, 1860
Superorder ECHINACEA Claus, 1876
Order SALENIOIDA Delage and Herouard, 1903
Family SALENIIDAE Agassiz, 1838
Subfamily SALENIINAE Agassiz, 1838
Genus SALENIA Gray, 1835
(= *Cidarelle* Desmoulins, 1835; = *Bathysalenia* Pomel, 1838)

Type species. Cidarites scutigera Münster *in* Goldfuss 1826, by original designation.

Salenia minima Agassiz and Desor, 1846

Plate 29, figs. 1–4

*.1846 *Salenia minima*, Agassiz and Desor, p. 342.
.1850 *Salenia minima*, d'Orbigny, p. 273.
.1857 *Salenia minima*, Desor, p. 151.
1857 *Salenia minima*, Bosquet, no. 839.
1859 *Salenia minima*, Binkhorst van den Binkhorst, p. 120.
.1864 *Salenia minima*, Cotteau, pp. 171–173, pl. 1040, figs. 1–10.
1879 *Salenia minima*, Ubaghs, p. 228.
1881 *Salenia minima*, Mourlon, p. 125.
.1910 *Salenia minima*, Lambert and Thiery, p. 211.
.1935 *Salenia minima*, Mortensen, p. 369, fig. 195*d*.
v.1965 *Salenia minima*, Meijer, p. 23.
.1979 *Salenia minima*, Geys, p. 320.
non 1935 *Salenia minima*, Smiser, p. 28, pl. 2, fig. 6*a–d*.

Type locality. Ciply, Hainaut, Belgium. Ciply Tuffaceous Chalk, Danian.

Studied specimens from the Maastricht area (Geulhem Chalk). Vroenhoven, Belgian Limburg: 88 specimens; Geulhem, Dutch Limburg: 18 specimens.

Dimensions. D: 1·7–9·2 mm; h: 0·9–6·0 mm; h/D ratio: 0·48–0·70; ds: 1·7–6·8 mm; ds/D ratio: 0·60–1·00; dp: 0·8–4·8 mm; dp/D ratio: 0·36–0·63.

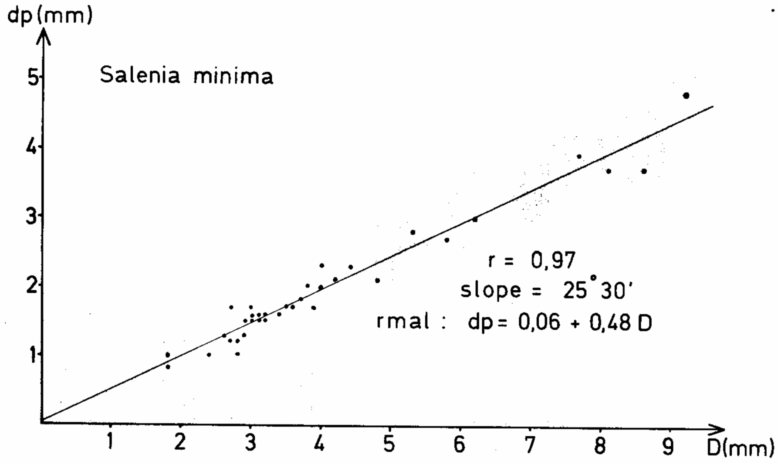
Description. The adoral side of the test is flat; the peristome is circular to subpentagonal, not sunken. Gill slits are very small. The perignatic girdle consists of small, spatulate auricles, not in contact with each other, and low arcuate apophyses.

The apical system is large and covers most of the aboral side of the test in young specimens. It is slightly convex and consists of eleven smooth plates, separated by distinct sutures. Sutural depressions are very small or absent. The ocular plates are triangular and a little concave. The genital plates and the suranal plate are nearly flat. The genital pores have an excentric position in the genital plates, being nearer to the apex. The madreporite can easily be distinguished by its irregular, more or less triangular poriferous depression. The periproct is oval or subtrigonal.

Each ambulacral series shows ten to twelve crenulate, non-perforate primary tubercles. The ambulacra are straight. The bigeminate character of its plates is very regular. The tubercles are close together and extrascrobicular granulation is almost completely absent. The axes of the pore pairs have an inclination of about 45°.

Interambulacral tubercles are crenulate, non-perforate. Five of them make a series. The areoles are smooth, large, and close together. Sometimes they are confluent, in the vicinity of the ambitus. A ring of six to eight scrobicular tubercles surrounds them on all but the adradial sides. Interradial extrascrobicular surfaces are coarsely granulated.

Variability. dp, ds, and h were plotted against D. Some parameters and the reduced major axis lines (rmal) were computed for each of these graphs, using the formulas proposed by Till (1974).



TEXT-FIG. 1. dp–D plot of *Salenia minima*, with reduced major axis line (rmal).

a. The rmal of the dp–D plot is given by

dp = 0·06 + 0·48 D (1) (Text-fig. 1).

The 95% confidence intervals of intercept and slope are respectively

$1{\cdot}96\ s_a(D/dp) = \pm 0{\cdot}16$ mm (2)
$1{\cdot}96\ s_b(D/dp) = \pm 0{\cdot}04$ (3).

From (1) and (2) one can conclude that the origin of the plot is included in the confidence band of the rmal, and that the dp/D ratio can be considered constant. Moreover, the slope (b = 0·48 ± 0·04) does not differ significantly from the mean dp/ratio (= 0·50), as follows from (1) and (3). The relative size of the peristome is not influenced by over-all size or age of the specimen.

b. The rmal of the h–D plot is given by

h = −0·31 + 0·68 D (4) (Text-fig. 2)

The 95% confidence intervals of intercept and slope are respectively

$1{\cdot}96\ s_a(D/h) = \pm 0{\cdot}13$ mm (5)
$1{\cdot}96\ s_b(D/h) = \pm 0{\cdot}03$ (6).

Obviously the origin is not included in the confidence band of the rmal, as follows from (4) and (5). (6) indicates that the slope (b = 0·68 ± 0·03) differs significantly from the mean h/D ratio (= 0·59). One can thus conclude that the h/D ratio is not constant, though the relationship between h and D is linear. Larger specimens tend to be less flattened than smaller individuals.

c. The rmal of the ds–D plot is given by

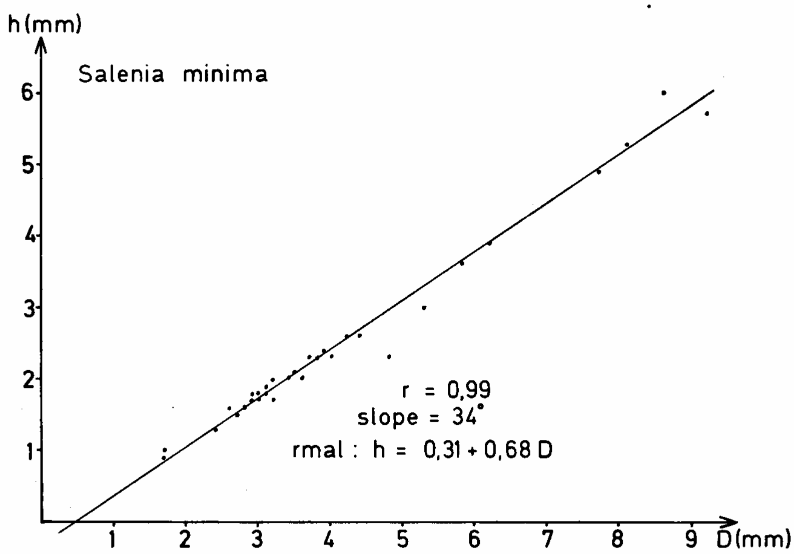
ds = 0·62 + 0·64 D (7) (Text-fig. 3),

with 95% confidence intervals of intercept and slope respectively

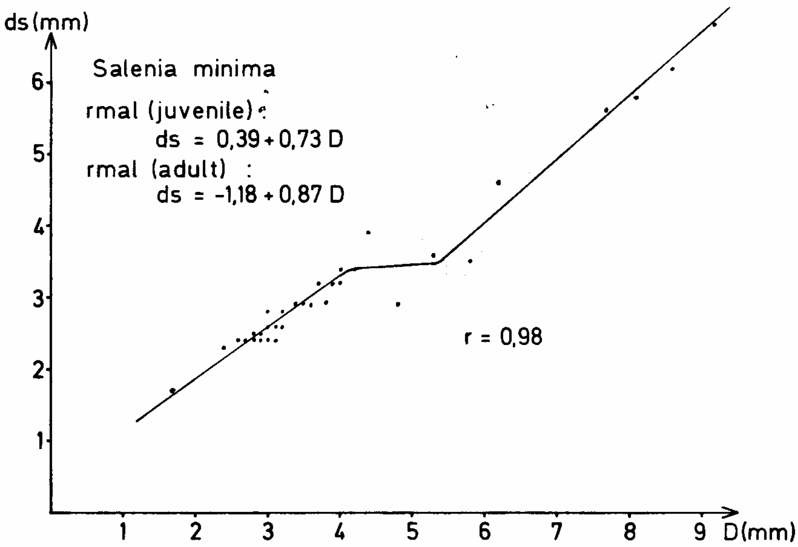
$1{\cdot}96\ s_a(D/ds) = \pm 0{\cdot}18$ mm (8)
$1{\cdot}96\ s_b(D/ds) = \pm 0{\cdot}02$ (9).

On one hand, one can conclude from (7) and (8) that the origin is not included in the confidence band of the rmal; on the other, (7) and (9) indicate that the slope (b = 0·64 ± 0·02) differs significantly from the mean ds/D ratio (= 0·82). Larger individuals are shown to have a relatively smaller apical system than smaller individuals. This could be put as follows: the apical system seems to grow less fast than the entire animal.

The relationship is clearly linear for specimens with D > 4·5 mm and for specimens with D < 4·5 mm



TEXT-FIG. 2. h–D plot of *Salenia minima* with reduced major axis line (rmal).



TEXT-FIG. 3. ds–D plot of *Salenia minima*, with reduced major axis line (rmal).

separately, but not for the population as a whole. This is clearly demonstrated by computing the rmal for both partial populations separately.

For large specimens (D > 4·5 mm) one obtains

$$ds = -1{\cdot}18 + 0{\cdot}87\,D$$

with 95% confidence intervals

$$1{\cdot}96\,s_a(D/ds) = \pm 0{\cdot}61 \text{ mm}$$
$$1{\cdot}96\,s_b(D/ds) = \pm 0{\cdot}04.$$

For small specimens (D < 4·5 mm) one obtains analogously

$$ds = 0{\cdot}39 + 0{\cdot}73\,D$$

with 95% confidence intervals

$$1{\cdot}96\,s_a(D/ds) = \pm 0{\cdot}23 \text{ mm}$$
$$1{\cdot}96\,s_b(D/ds) = \pm 0{\cdot}07.$$

From these equations we can conclude that the intercept is significantly different in large and small individuals. The difference in slope between the rmals of both populations is much less important. It seems as if the rate of growth of the apical system is drastically reduced when the specimens attain 4 to 5 mm over-all diameter. After crossing the D = 5 mm threshold, the rate of growth of the apical system seems to be more or less restored.

Discussion. Salenia minima is superficially similar to other small salenioids, such as *Salenidia pygmaea* (Hagenow 1940) and *Salenidia maestrichtensis* (Schlüter 1892). The lack of sutural depressions in its smooth apical system makes *Salenia minima* easy to recognize.

Smiser (1935) confused *Salenia minima* and *Goniopygus minor*. What he figured as *Salenia minima* is in fact a *Goniopygus minor* Sorignet, 1850. This error is discussed in a forthcoming paper of mine (Geys 1981).

A very similar species to *Salenia minima* has been described from the Danian of Denmark: *Salenidia danica* Ravn, 1928. Both species probably differ in the structure of their ambulacra and in the shape of their ocular plates.

For both *Salenidia pygmaea* and *Salenidia maestrichtensis* h–D, ds–D, and dp–D plots were statistically analysed, respectively by Nestler (1965) and by Geys (1979). A comparison with *Salenia minima* is instructive. The flattening in shape of larger, hence older specimens, as demonstrated in *Salenia minima*, exists in *Salenidia pygmaea* but not in *Salenidia maestrichtensis*. The relative shrinking of the peristome, demonstrated in *Salenidia pygmaea* and *Salenidia maestrichtensis*, is not indicated in *Salenia minima*. The growth of the apical system, however, shows similar patterns in all three of the species. Very small, very young specimens have apical systems covering the complete adapical surface. In *Salenidia maestrichtensis* a non-linear relationship between D and ds was demonstrated. For *Salenidia maestrichtensis* it was established that the beginning of the final linear segments in its d–D plot (D > 4·5 mm) coincides with the attainment of sexual maturity. It is not clear whether the same is true for *Salenia minima*.

Subfamily HYPOSALENIINAE Mortensen, 1934
Genus HYPOSALENIA Desor, 1856
(= *Peltastes* Agassiz, 1838, *non Peltastes* Rossi, 1807; *Peltosalenia* Quenstedt, 1874)

Type species. Echinus acanthoides Desmoulins 1837, by subsequent designation of Mortensen (1935).

Hyposalenia heliophora (Agassiz and Desor, 1846)

Plate 29, figs. 5–8

v*.1846 *Salenia heliophora*, Agassiz and Desor, p. 342.
v.1850 *Salenia heliophora*, d'Orbigny, p. 273.
v.1856 *Hyposalenia heliophora*, Desor, p. 148.
1857 *Hyposalenia heliophora*, Bosquet, no. 842.
v.1864 *Peltastes heliophorus*, Cotteau, pp. 122–124, pl. 1029, figs. 1–7.

1874 *Peltastes heliophorus*, Cotteau, p. 642.
1879 *Hyposalenia heliophora*, Ubaghs, p. 228.
1881 *Hyposalenia heliophora*, Mourlon, p. 125.
.1892 *Peltastes* cf. *heliophorus*, Schlüter, pp. 152–154.
.1910 *Peltastes heliophorus*, Lambert and Thiery, p. 209.
v.1928 *Hyposalenia heliophora*, Lambert and Jeannet, p. 203.
.1935 *Peltastes* cf. *heliophorus*, Kongiel, p. 31, pl. 2, fig. 5*a–c*.
.1935 *Hyposalenia heliophora*, Mortensen, p. 344, fig. 188*g*.
.1939 *Hyposalenia heliophora*, Kongiel, p. 20, pl. 3, figs. 19–21.
.1966 *Hyposalenia heliophora*, Fell and Pawson, p. U379, fig. 277-1*j*.
v.1966 *Hyposalenia heliophora*, Meijer, p. 23.
.1979 *Hyposalenia heliophora*, Geys, p. 320.

Type Locality. Maastricht, Dutch Limburg, the Netherlands. Geulhem Chalk, Houthem Formation, Danian.

Other occurrences. Ciply, Hainaut, Belgium: Ciply Tuffaceous Chalk, Danian (Agassiz and Desor 1846). Ciply, Hainaut, Belgium: Malogne Gravel, Danian (Cotteau 1874). Berlin, Germany: 'Geschiebe', reworked in Pleistocene (Schlüter 1892). Gora Puławska, Poland: Siwak, Lower Danian (Kongiel 1935, 1939).

Studied specimens from the Maastricht area (Geulhem Chalk). Vroenhoven, Belgian Limburg: 41 specimens; Geulhem, Dutch Limburg: 225 specimens.

Dimensions. Forty specimens, chosen at random, were measured. D: 1·7–12·0 mm; h: 1·0–7·5 mm; h/D ratio: 0·5–0·7; ds: 1·6–7·7 mm; ds/D ratio: 0·62–1·00; dp: 0·6–5·2 mm; dp/D ratio: 0·26–0·58.

Description. The adoral side is slightly convex, the peristome a little sunken. The peristome is distinctly decagonal and shows rather large gill slits. These slits are surrounded by low, blunt ridges. The auricles are short, rectangular, and spatulate. They are not in contact over the perradial suture.

The apical system is large and pentagonal, covering most of the adapical surface. It is conically convex and consists of eleven plates, separated by very fine, hardly visible sutures. Real sutural depressions are absent. The ocular plates are pentagonal, with more or less straight distal margins. The genital plates are hexagonal, the suranal plate is pentagonal. All the plates are covered by a conspicuous sculpture of ridges and furrows, which radiate from the centres of the plates, and which are perpendicular to the sutures. The genital pores have a central position in the plates. The periproct is oval or subtrigonal. It is situated between the apex and genital plate 5, so that the test is symmetrical with respect to the III-5 plane.

Ambulacral series consist of twelve or thirteen crenulate, non-perforate primary tubercles. The tubercles just below the ambitus are the largest in size. From there upwards, their size diminishes abruptly. The ambulacra are straight. The plates are very regularly bigeminate. The poriferous zones are uniserial throughout. The pores of each pair are separated by a low ridge. The axes of the pore pairs have an inclination of 45° below, and less than 45° above, the ambitus. Very small scrobicular tubercles, or granules, surround the primaries.

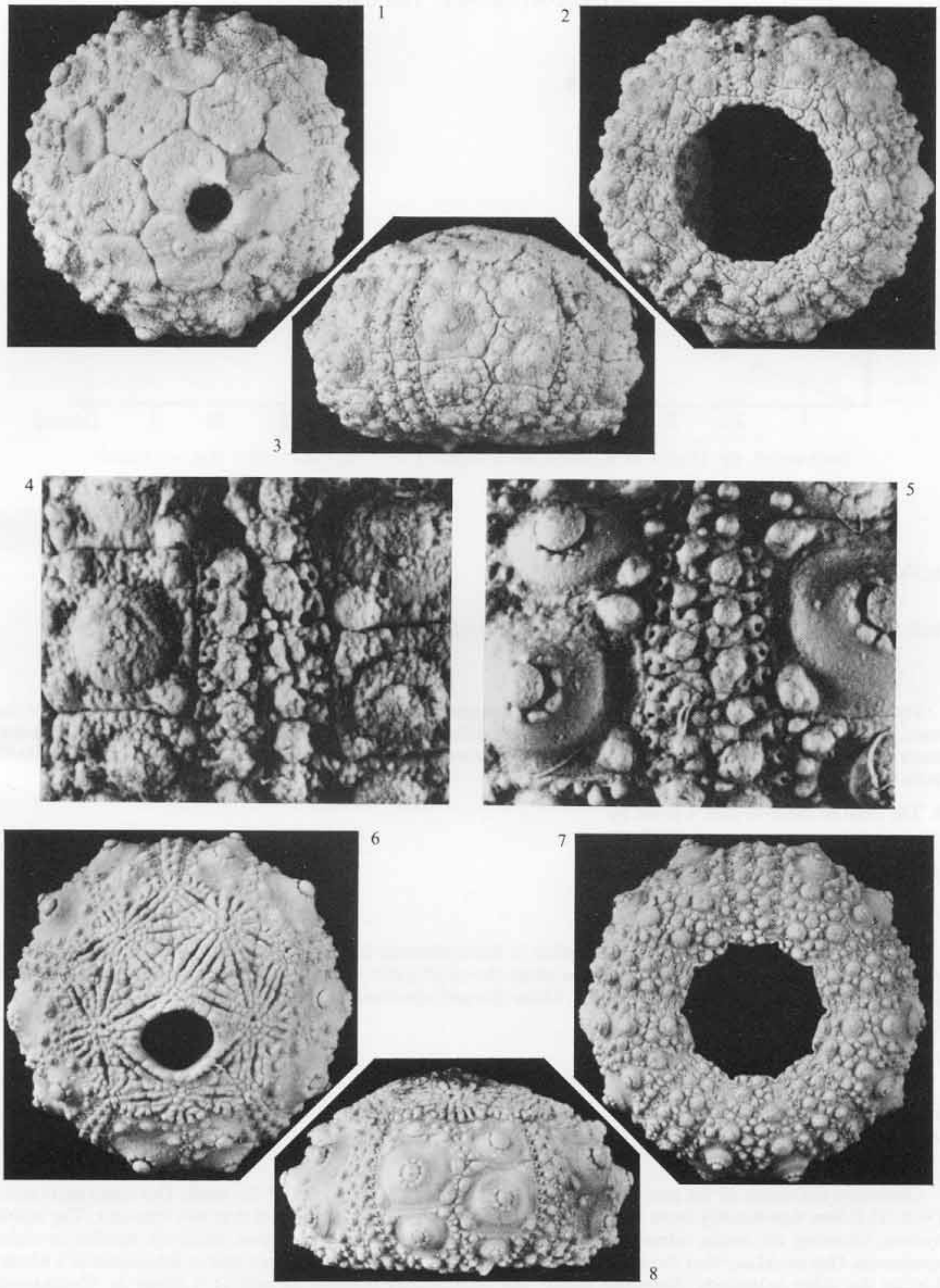
The interambulacral tubercles are crenulate, non-perforate. There are four or five in each series. The areoles are smooth, large, and confluent. Scrobicular rings are hence discontinuous. Granulation is coarse on the interradial miliary surfaces.

Variability. dp, ds, and h were plotted against D. Reduced major axis lines (rmal) and some parameters were computed for each of these graphs.

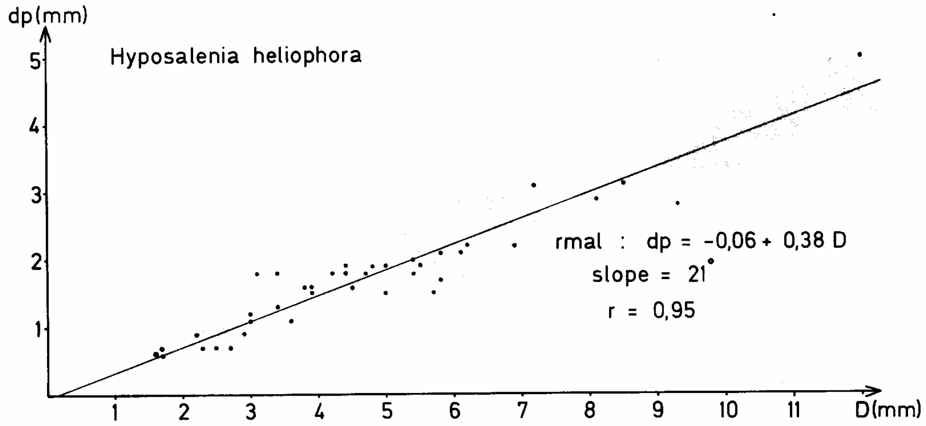
EXPLANATION OF PLATE 29

Figs. 1–4. *Salenia minima* Agassiz & Desor; NHMM-MM 895; Vroenhoven, Belgian Limburg; Geulhem Chalk. 1, adapical view, ×4. 2, adoral view, ×4. 3, lateral view, ×4. 4, detail of ambulacrum at the ambitus, ×12.

Figs. 5–8. *Hyposalenia heliophora* (Agassiz & Desor); NHMM-MM 899; Geulhem, Dutch Limburg; Geulhem Chalk. 5, detail of ambulacrum at the ambitus, ×12. 6, adapical view, ×4. 7, adoral view, ×4. 8, lateral view, ×4.



GEYS, salenioid echinoids



TEXT-FIG. 4. dp–D plot of *Hyposalenia heliophora*, with reduced major axis line (rmal).

a. The rmal of the dp–D plot is given by

$dp = -0{\cdot}06 + 0{\cdot}38\ D$ (text-fig. 4)

with 95% confidence intervals of intercept and slope, respectively

$1{\cdot}96\ s_a(dp/D) = \pm 0{\cdot}19$ mm

$1{\cdot}96\ s_b(dp/D) = \pm 0{\cdot}04$.

From these equations can be concluded that the origin of the plot is included in the confidence band of the rmal, and that the mean dp/D ratio ($= 0{\cdot}37$) does not differ significantly from the slope ($b = 0{\cdot}38 \pm 0{\cdot}04$). Hence, there is no difference in relative size of the peristome, between young (small) and old (large) specimens. The dp/D ratio is constant.

b. The rmal of the h–D plot is given by

$h = 0{\cdot}16 + 0{\cdot}57\ D$ (text-fig. 5)

with 95% confidence intervals

$1{\cdot}96\ s_a(h/D) = \pm 0{\cdot}11$ mm

$1{\cdot}96\ s_b(h/D) = 0{\cdot}01$.

The origin of the plot is clearly not included in the confidence band of the rmal. Moreover, the mean h/D ratio ($= 0{\cdot}62$) differs significantly from the slope ($b = 0{\cdot}57 \pm 0{\cdot}01$). Though the relationship between h and D is linear, the h/D ratio is not constant. Older (larger) specimens are slightly more flattened than young (small) ones.

c. The rmal of the ds–D plot is given by

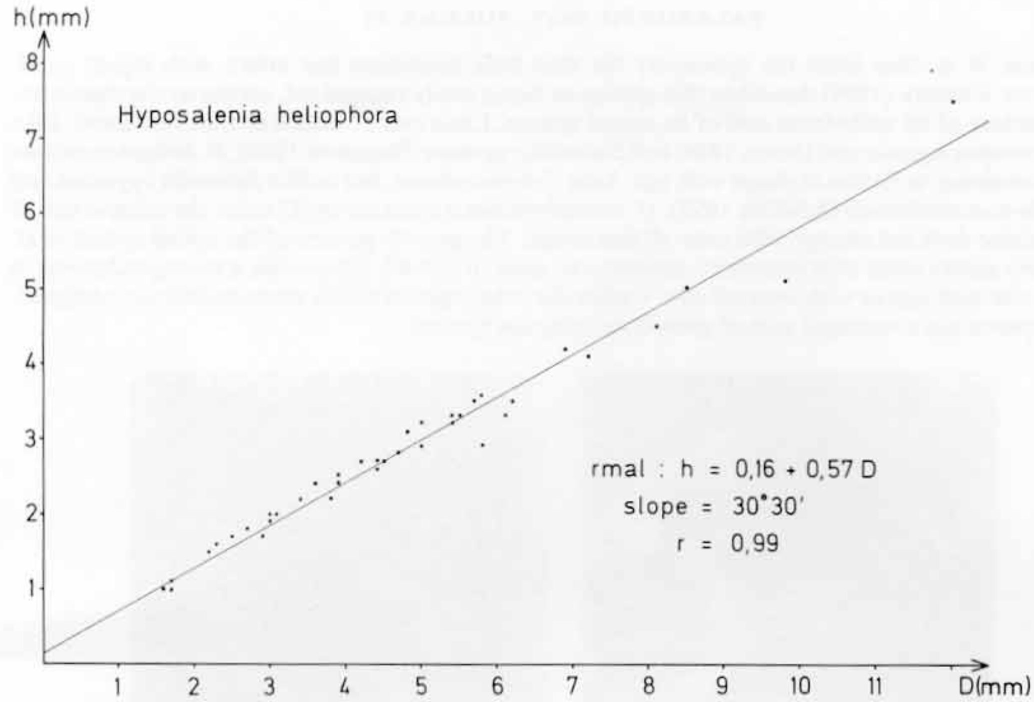
$ds = 0{\cdot}60 + 0{\cdot}62\ D$ (Text-fig. 6)

with 95% confidence intervals

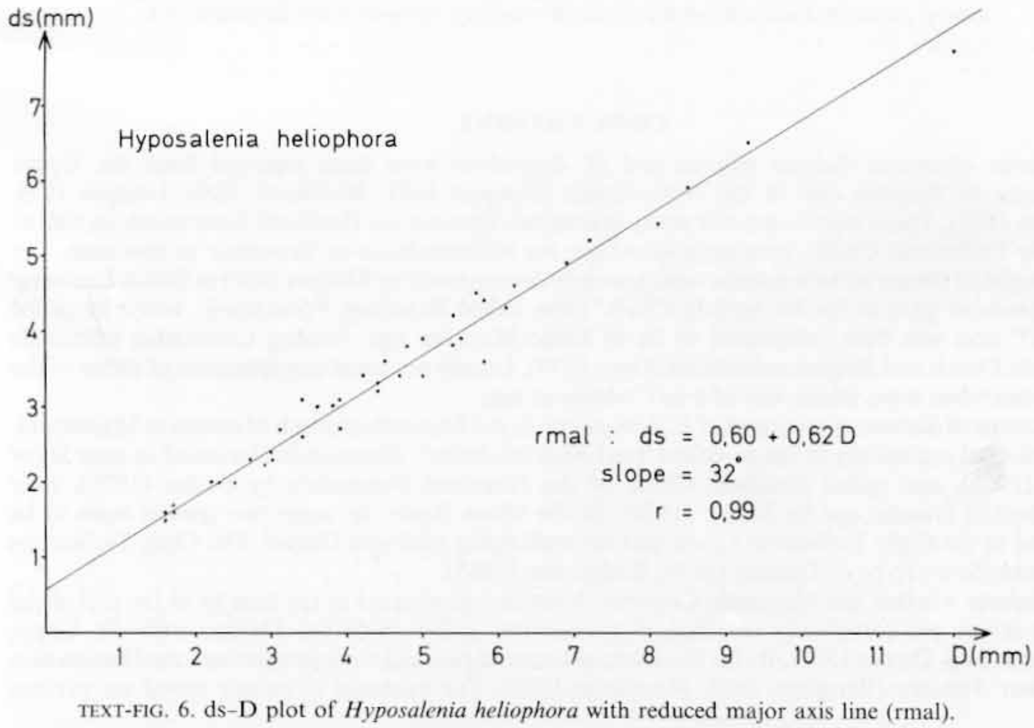
$1{\cdot}96\ s_a(ds/D) = \pm 0{\cdot}12$ mm

$1{\cdot}96\ s_b(ds/D) = \pm 0{\cdot}01$.

Obviously the origin of the graph is not included in the confidence band of the rmal. The mean ds/D ratio ($= 0{\cdot}78$) differs significantly from the slope ($b = 0{\cdot}62 \pm 0{\cdot}01$). The ds/D ratio is thus not constant. The apical system, covering the entire adapical surface in very young individuals, grows relatively smaller in older specimens. One could say that the apical system has a rate of growth less fast than that of the animal as a whole. Unlike the other salenioids, discussed above, the relationship between ds and D is linear in *Hyposalenia heliophora*.

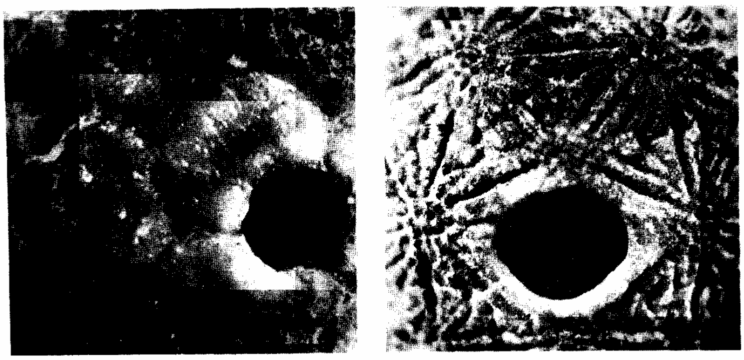


TEXT-FIG. 5. h–D plot of *Hyposalenia heliophora* with reduced major axis line (rmal).



TEXT-FIG. 6. ds–D plot of *Hyposalenia heliophora* with reduced major axis line (rmal).

Discussion. It is clear from the synonymy list that little confusion has arisen with repect to *H. heliophora*. Cotteau (1864) describes this species as being easily recognized, owing to the characteristic structure of its ambulacra and of its apical system. Little can be added to that statement. Like *Salenia minima* Agassiz and Desor, 1846, and *Salenidia pygmaea* (Hagenow 1840), *H. heliophora* shows a slight tendency to flatten in shape with age. Like *Salenia minima*, but unlike *Salenidia pygmaea* and *Salenidia maestrichtensis* (Schlüter 1892), *H. heliophora* has a constant dp/D ratio: the relative size of its peristome does not change with over-all size or age. The growth pattern of the apical system in *H. heliophora* shows some characteristics, common to most, if not all, Salenioids: a strong reduction in relative size with age or with over-all size. Unlike the other species which were statistically analysed, *H. heliophora* has a constant rate of growth in its apical system.



a *b*

TEXT-FIG. 7. Detail of the apical system, with periproct, suranal plate and surrounding genital plates in *Salenia minima* (*a*) and *Hyposalenia heliophora* (*b*). Enlarged, ×8.

CONCLUSIONS

On various occasions *Salenia minima* and *H. heliophora* have been reported from the Upper Cretaceous in Belgium and in the Netherlands (Bosquet 1857; Binkhorst 1859; Ubaghs 1879; Mourlon 1881). These reports are not really erroneous, because the Houthem Formation, as well as the Ciply Tuffaceous Chalk, were included within the Maastrichtian or 'Senonian' at that time. The stratigraphical ranges of both species were precisely documented by Meijer (1966) in Dutch Limburg: the 'uppermost part of the Maastricht Chalk' (now called Houthem Formation), which he called 'zone III' and was then considered to be of Dano-Montian age. Among Cretaceous salenioids in various Dutch and Belgian collections (Geys 1979), I could not trace any specimen of either of the species described here, which was of true Cretaceous age.

Specimens of *Salenia minima* and of *H. heliophora*, in the Natuurhistorisch Museum at Maastricht, were collected exclusively in the so-called 'post-Maastrichtian'. These strata, included in zone III of Meijer (1966), and called Geulhem Chalk of the Houthem Formation by Felder (1975), were considered of Danian age by Meijer (1959). In the Mons Basin the same two species seem to be restricted to the Ciply Tuffaceous Chalk and the underlying Malogne Gravel. The Ciply Tuffaceous Chalk was shown to be of Danian age by Rasmussen (1965).

The debate whether the Mesozoic–Cenozoic boundary is situated at the base or at the top of the Danian is not yet completely resolved. Some authors still include the Danian with the Upper Cretaceous (e.g. Davies 1975). By far the most widespread point of view is to include the Danian into the Lower Tertiary (Berggren 1963; Moorkens 1972). The evidence is mainly based on various palaeontological arguments: foraminifera and calcareous nannoplankton (Čepek and Moorkens 1979), ostracods (Deroo 1966), brachiopods (Kruytzer and Meijer 1958). Both *Salenia minima* and *H. heliophora* seem to be index fossils for Danian strata. Their presence in Maastrichtian or in Montian deposits has not yet been demonstrated.

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