sides of the pores facing each other; interporal area is crossed by a narrow ridge of stereom, which links the two pores). In the adapical third of the anterior poriferous zones of the anterior paired petals the pores are distinctly reduced in size. In the posterior poriferous zones and in both poriferous of the posterior paired petals this is not the case (Fig. 78.D). The posterior paired petals are usually between 70 and 85 % of the length of the anterior ones. In juveniles and sub-adult specimens (TL ~ 15 mm) they can be even shorter (~ 65 %). Anterior paired petals extending about 60 to 70 % of the corresponding test radius, while the posterior paired petals extend about 50 %. The anterior paired petals diverge at an angle of about 85 to 115°, the posterior ones at about 50 to 75°. Neither, anterior nor posterior petals are confluent (Figs. 78.C-D).

Ambulacra II, III and IV are sparsely tuberculated ambitally and bear vertically elongated, slit-shaped unipores. On the oral side ambulacra I and V form broad, naked peri-plastronal areas bearing few secondary and miliary tubercles. The pores in these areas are antero-posteriorly elongated, slit-shaped unipores. Five ambulacral plates extend into the subanal fasciole, bearing four enlarged pores on each side (Fig. 80.C-D). Adorally all ambulacra form small phyllodes consisting of five to six slit-shaped unipores with an extensive attachment area in each ambulacrum (Fig. 80.A).

Interambulacra: Aborally the interambulacra are strongly inflated between the petals. Aboral tuberculation is very dense and homogenous. The tubercles become larger towards the ambitus and on the oral side. On the plastron the tubercles are arranged in a fan-shaped pattern, radiating from an elevation in the posterior part of the plastron. The plastron belongs to the holamphisternous type (Figs. 79.A-D) and forms a strong keel along its central suture. The labrum is short, T-shaped, slightly wider than long and projects slightly into the peristome. Usually it does not extend beyond the first ambulacral plate of the adjacent ambulacra (Fig. 80.A). In a single specimen, however, it extends to the second ambulacral plate (Fig. 80.B). According to Turner & Norlund (1988) this atypical condition may occur in *Brissopsis* species which are usually characterised by a labrum that does not extend beyond the first ambulacral plates.

Plastron width is relatively variable. In the material from the type-locality it increases during ontogeny due to allometric growth. In the smallest specimens (TL ~ 15 mm) it ranges from 33 to 37 % of TW and increases to 41 % in the largest speci-

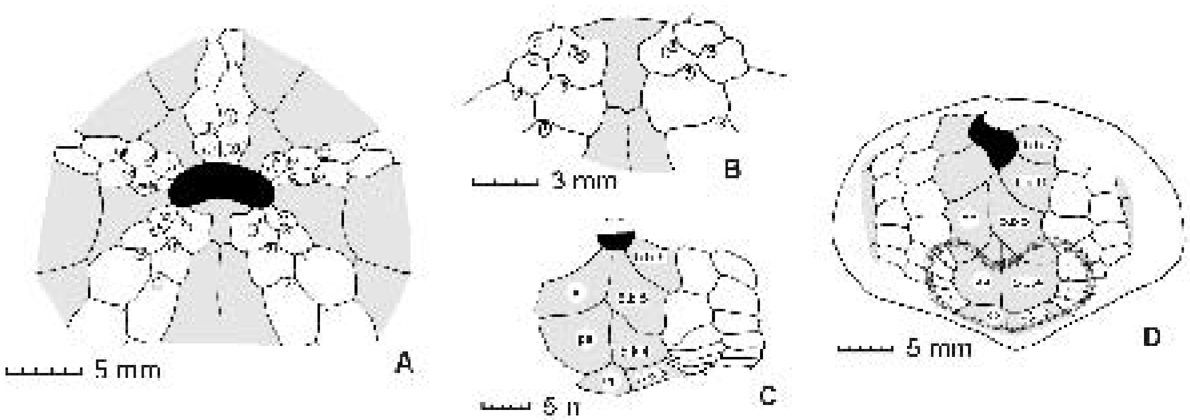

Figure 80: *Brissopsis ottnangensis* Hoernes, 1875: labrum shape, typical condition (A: Badenian, Devínska Nová Ves, Slovak Republic, SNM z24181), rare condition with labrum extending to 2nd ambulacral plate on each side (B: Badenian, Devínska Nová Ves, Slovak Republic, SNM z24180), anal plating (C: Ottnangian, Ottnang, OÖ, Austria, NHMW 1997z0178/0520; D: Badenian, Retznei, Styria, Austria, NHMW 2004z0098/0002). Interambulacra shaded, poorly visible sutures omitted or stippled, subanal fasciole dotted. Numbering of anal and preanal plates follows the Lovénian system; Abbreviations: ep = episternal plate, pa = preanal plate, an = anal plate.

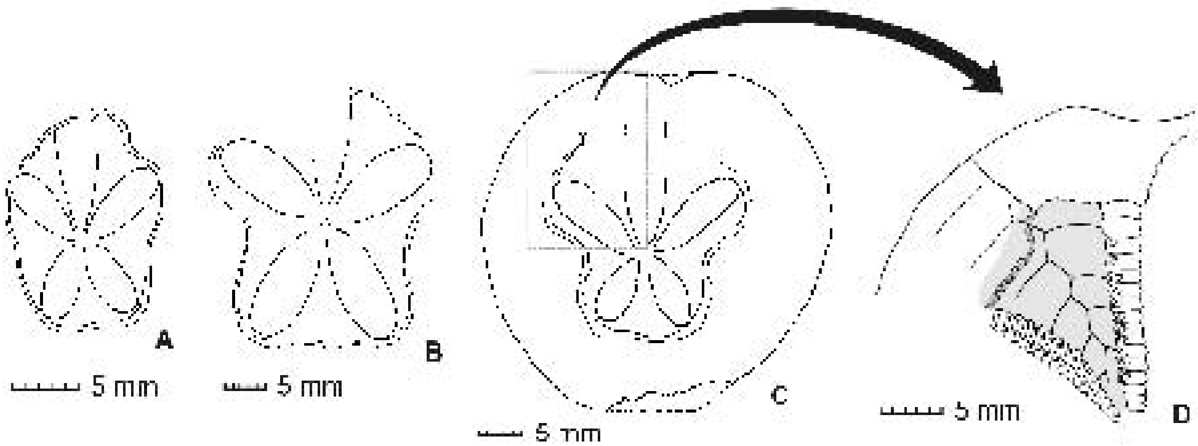

Figure 81: *Brissopsis ottnangensis* Hoernes, 1875: peripetalous fasciole shape (A: Badenian, Devínska Nová Ves, Slovak Republic, SNM z24179; B: Badenian, Devínska Nová Ves, Slovak Republic, SNM z24182; C-D: A: Badenian, Kalksburg, Vienna, Austria, NHMW 1981/55/12).

mens. In specimens from the Badenian of Devínska Nová Ves a markedly narrower plastron (~ 30 % of TW in 30 mm specimens) is observed.

The shape and number of the preanal and anal plates is similar to the condition observed in *B. atlantica* by TURNER & NORLUND (1988: fig. 3 A), both in material from the type locality Ottnang (Fig. 80.C) and in younger (Badenian) specimens (Fig. 80.D). There is only one pair of preanal plates (plates 5.a.4, 5.b.4), and the first anal plates (5.a.5, 5.b.5) are distinctly elongated vertically, tapering and form only a narrow portion of the periproctal margin.

Peristome: The peristome is situated anteriorly on the oral side of the test, about 15 to 25 % of TL from the anterior margin. It is kidney-shaped and measures 2.5 *vs*. 7 mm in a 40 mm TL specimen. The labrum is only slightly projecting.

Periproct: The periproct lies high on the posterior face of the test. It is nearly circular in shape but poorly preserved in most available specimens. In some specimens, especially in smaller ones it is partially visible in aboral view due to the obliquely truncated posterior end.

Fascioles: Both peripetalous and subanal fascioles are present. They belong to the orthofasciole type (*sensu* NÉRAUDEAU & al. 1998b). The peripetalous fasciole is indented between the anterior and posterior paired petals (Figs. 81.A-C) and has a distinct kink in interambulacra 2 and 3 (Fig. 81.D). The subanal fasciole is kidney shaped (Fig. 80.D).

Differential diagnosis:

Brissopsis crescenticus WRIGHT, 1855 from the Early Miocene of Malta differs from this species by its confluent petals, with distinctly laterally flexed petal tips, much less strongly diverging posterior petals, and more elongated outline [based on topotypic material collected from the Lower *Globigerina* Limestone in Malta; see also CHALLIS, 1980; the material from the Burdigalian of the Rhône Basin attributed to *B. crescenticus* by PHILIPPE (1998) is not typical of that species, if at all conspecific].

The Pliocene to extant *B. atlantica* MORTENSEN, 1907, which is the descendant of *B. crescenticus* according to MORTENSEN (1951), likewise differs by its confluent posterior petals and laterally flexed anterior petals (among other features; compare MORTENSEN, 1913; BORGHI, 1997; LACOUR & NÉRAUDEAU, 2000).

The extant *B. elongata* MORTENSEN, 1907 from the Caribbean and the South Atlantic differs by its confluent posterior petals, different arrangement of the anal and preanal plates and straight labrum margin (compare TURNER & NORLUND, 1988).

The Late Miocene to extant species *Brissopsis lyrifera* (FORBES, 1841) is very similar to *B. ottnangensis* and the latter species certainly belongs into the *Brissopsis lyrifera* – group as identified and characterised by LACOUR & NÉRAUDEAU (2000). Main differences to *B. lyrifera* are the shape of the individual petals (more lanceolate in *B. lyrifera*, wider and more lobate in *B. ottnangensis*), fasciole shape and overall test shape [extant *B. lyrifera* are more elongated (TW of ~ 85-91% TL) than *B. ottnangensis*] (compare data and illustrations found in MORTENSEN, 1951; BORGHI, 1997; LACOUR & NÉRAUDEAU, 2000).

The Cuban species *B. aguayoi* SÁNCHEZ ROIG, 1952 from the Oligocene to Miocene and *B. jimenoi* COTTEAU, 1875 from the Miocene differ by their strongly confluent posterior and laterally flexed anterior petals (compare KIER, 1984). Likewise the three known fossil Australian *Brissopsis* species *B. tatei* HALL, 1907, *B. australis* MCNAMARA et. al. 1986, and *B. praeluzonica* FELL, 1964 are also easily distinguished by the same petal configuration as the Cuban species (see MCNAMARA et. al. 1986).

Discussion:

Brissopsis duciei WRIGHT, 1855 from the Burdigalian to Messinian of Malta (see CHALLIS, 1980) is very similar to *B. ottnangensis* in many aspects. It differs from the present species by its more diverging anterior petals (up to 120°, even in large specimens), more circular outline (TW ranging from 96 to 103 % TL), and less strongly indented peripetalous fasciole in interambulacra 1 and 4. Unfortunately no specimens have been available for direct comparison. It is also unclear how the Burdigalian specimens of *B. duciei* look like, as all illustrations depict specimens from the Messinian Upper Coralline Limestone. In any case the two species seem to be closely related and further investigations involving material from the Burdigalian of Malta are necessary to see if the two forms might be end-members of a species with broader intraspecific variation.

Brissopsis specimens from the Badenian of Austria differ from *B. ottnangensis* from the type-area by its slightly more diverging anterior (~ 90-115°) and slightly less diverging posterior (50-60°) paired petals. Yet these features show considerable variation in the "population" from the type-locality too and the overlap is large. Moreover, the different preservation hampers comparison and distorts metric features (Ottnangian specimens come from pelitic sediments, are deformed and usually lack the original test; Badenian specimens, in contrast come from carbonates and retain the original shell). The key features used for the differentiation of extant *Brissopsis* species (petal shape and structure, labrum shape, number and shape of the preanal and anal plates, shape of the fascioles and number of ambulacral plates extending into the subanal fasciole) are identical in the material from both time slices. Thus they are treated as conspecific here.

VADÁSZ (1915) identified this species with *B. consobrinus* LAMBERT, 1909 from the "Helvétien" (? Middle Miocene) of Sardinia, which is indeed extremely similar to the present taxon. Without knowledge on the plating pattern, width of the plastron and other features not mentioned by LAMBERT an attribution to that species can only be tentative.

Several of the *Brissopsis* species and subspecies of BOTTO-MICA (1896) are similar to *B. ottnangensis*. All of them are, however, based on internal moulds and plating patterns, plastron structure and shape of the fascioles are unknown. Because of this lack of information it is impossible to judge their relation to *B. ottnangensis* without re-examination of BOTTO-MICA's material.

Occurrence:

Austria: Eggenburgian (Early Burdigalian) to Late Badenian (Early Serravallian)

M o l a s s e Z o n e: Antiesenhofen, near Schärding/Inn, OÖ ([NHMW]); borehole Eisenhub 2, OÖ (SCHAFFER & GRILL, 1951); Großwiesenhardt, near St. Marienkirchen, OÖ ([NHMW]); Haller Schlier, Pfarrkirchen, OÖ ([NHMW]); Mechters, near St. Pölten, NÖ (ABEL, 1904); Ort, near Bad Füssing, OÖ (WEIDLINGER, 2003); Ottnang, OÖ (HOERNES, 1875a, b; KITTL, 1886; COMMENDA, 1900; TOULA, 1914; VEIT, 1943; SCHAFFER & GRILL, 1951; SIEBER, 1956; PAPP & THENIUS in KÜHN, 1962; STOJASPAL, 1975; RUPP et al., 1991; [GBA]; [NHMW]); Pichl, WNW of Wels, OÖ (SUESS, 1891); Pielach river, south of Völlerndorf, NÖ ([NHMW]); Platt, near Zellerndorf, NÖ (SIEBER, 1935; KROH, 2003b); St. Pölten, NÖ (ABEL, 1904; [NHMW]); Schlierfazies der Innviertler Serie, OÖ (TOLLMANN, 1985)

V i e n n a B a s i n: Bad Vöslau, NÖ ([NHMW]); borehole at Aderklaa (Badenian, "Walbersdorfer Fazies"), NÖ (VEIT, 1943); borehole at Oberlaa (Badenian, "Walbersdorfer Fazies"), Vienna (VEIT, 1943); Gainfarn, NÖ (KROH, 2002b; [NHMW]); Kalksburg, Vienna ([NHMW]); Steinberggebiet, near Zistersdorf, NÖ (SIEBER, 1953a)

E i s e n s t a d t - S o p r o n B a s i n: Forchtenau, Bgld (VENDL, 1930); Mattersburg, Bgld (VENDL, 1930); Walbersdorf, near Mattersburg, Bgld (HOERNES, 1884; TOULA, 1884; KITTL, 1886; PROCHÁZKA, 1892a; SCHAFFER, 1897; HOERNES, 1903; VENDL, 1930; JANOSCHEK in SCHAFFER, 1943, 1951; RÖGL & MÜLLER, 1976; [GBA])

Lavant Basin: Mühldorf im Lavanttal, Ktn (Wank & Stojaspal, 1980; Wank, 1981)
Styrian Basin: Retznei (Weissenegg Fm., Lafarge quarry Rosenberg), Styria ([NHMW]); Weitendorf, Styria ([NHMW]); Wetzelsdorf, near Preding, Styria (Holler, 1900; [NHMW]); area Wildon-Leibnitz, Styria (Dreger, 1913)

Paratethys (non-Austrian occurrences): ? Oligocene, Ottnangian (Late Burdigalian) to Late Badenian (Early Serravallian)
Bavarian Molasse Basin: Mitterdorf, near Griesbach, Bavaria ([NHMW])
Molasse Zone: Ostrava (= Ostrau), Czech Republic (Kittl, 1886; Schaffer, 1897); Židlochovice, Moravia, Czech Republic (Cicha, 1978)
Vienna Basin: Devínska Nová Ves (brickyard), Slovak Republic (Schaffer, 1897; Abel, 1902; Hoernes, 1903; Schaffer, 1908; Toula, 1915; Janoschek in Schaffer, 1943; Tomašových, 1998; [NHMW]); Dubovce, *c.* 7 km ESE Holíč, Slovak Republic (Cicha et al., 1967); Radošovce, *c.* 9 km ESE Holíč, Slovak Republic (Cicha et al., 1967); Strachotín, c. 11 km N Mikulov, Czech Republic (Pospíchalová in Kroh, 2003b)
Eisenstadt-Sopron Basin: Sopron, Györ-Monson-Sopron, Hungary (Vendl, 1930)
Styrian Basin: Ferental ("Schlier" facies), probably Slovenia (Meznerics, 1936); Jahring ("Schlier" facies), probably Slovenia (Meznerics, 1936)
Great Hungarian Basin (Pannonian Basin): Etes (= Ettes), Nógrád, Hungary (Vadász, 1915); Fót Fm. and Garáb Schlier Fm., Nógrád, Hungary (Hámor, 1985); Györ, Györ-Monson-Sopron, Hungary (Vendl, 1930); Karacs-Lapujtö (= Lapujtö), Nógrád, Hungary (Vadász, 1915); Köalja-hegy, near Sajóvárkony, Borsod-Abaúj-Zemplén, Hungary (Jaskó, 1940); ? Letkés, Pest (Vadász, 1915); Mogyoród, near Fót, NW Budapest, Pest, Hungary (Horusitzky, 1927; Kroh, 2003b [NHMW]); Sajóvárkony, Borsod-Abaúj-Zemplén, Hungary (Jaskó, 1940); Vaszar, Baranya, Hungary (Vadász, 1915); Zagyvapálfalva (= Pálfalva), Nógrád, Hungary (Vadász, 1915)
Nowy Sącz Basin: Niskowa, western solpes of the Nowy Sącz depression, Poland (Bałuk, 1970)
Transcarpathian Basin: Hlinné, eastern Slovak Republic (Seneš, 1955; Cicha et al., 1967)
Transylvanian Basin: Chechiş, Romania (Givulescu & Duşa, 1960); Coştei (= Kostéj), Timiş, Romania (Givulescu & Duşa, 1960); Gârbova de Sus (= Felsö-Orbó), Romania (Vadász, 1915); Ilteu, Romania (Givulescu & Duşa, 1960); Lăpugiu des Sus (= Felsölapugy, = Lapugy), Hunedoara, Romania (Vadász, 1915); Tărăţel (= Cerecel), Romania (Vadász, 1915; Givulescu & Duşa, 1960); Tusa (= Tusza), Romania (Givulescu & Duşa, 1960);
Zala, Sáva and Dráva Basins: La'sko (formerly Tüffer; "Schlier" facies), Slovenia (Hoernes, 1903)

Mediterranean: ? Miocene
Western Mediterranean: ? Colline di Bologna, Italy (Manzoni, 1879); ? Ponti, near Camerino, Italy (de Loriol, 1882)

Brissopsis sp.

	1855	*Brissopsis* – Rolle: 354
	1871	*Brissopsis* – Stur: 562, 563
?	1880	Stacheln von *Brissopsis* – Rzehak: 302
	1884	*Brissopsis* sp. – Bittner: 457
	1893	*Brissopsis* sp. – Toula: 288
	1894	*Brissopsis* – Dreger: 74
	1913b	*Brissopsis* – Schaffer: 58
	1927a	*Brissopsis* – Schaffer: 82
	1936	*Brisopsis* (?) sp. – Paucă: 143
	1938	*Spatangus* cfr. *euglyphus* Laube 1867 – Poljak: 199-200; pl. 8, fig. 2 [misidentified *Brissopsis* sp.]
	1939	*Brissopsis* sp. – Kapounek: 78
	1939	*Brissopsis* sp. – Langer: 353
	1943	*Brissopsis* – Schaffer: 518
	1951	*Bryssopsis*– Janoschek in Schaffer: 575
	1952	*Brissopsis* sp. – Flügel et al.: 178
	1965	*Brissopsis* – Kollmann: 516
	1977	*Brissopsis* sp. – Ebner & Gräf: 161
	1981	*Brissopsis* sp. – Halmai: 105
	1987	*Brissopsis* sp. – Krainer: 150
	1990	*Brissopsis* sp. – Friebe: 245, 254
v.	2001	*Brissopsis* sp. – Schmid et al.: 13

Material:
Ottnangian (Late Burdigalian) – Antiesen river, near Antiesenhofen, near Schärding/Inn, OÖ, Austria
NHMW: 10 specimens (NHMW 1971/1485k-l, 1985/67/24-25, ../23a+b, 1989/83/36-38, ../40, 2003z0090/0001)
Ottnangian (Late Burdigalian) – Antiesenhofen, near Schärding/Inn, OÖ, Austria
NHMW: 11 specimens (NHMW 2003z0090/0006)
Ottnangian (Late Burdigalian) – Großwiesenhardt, near St. Marienkirchen, OÖ, Austria
NHMW: 9 fragments (NHMW 1986/101/24a+b, ../25a+b, 2003z0090/0003)
Ottnangian (Late Burdigalian) – St. Marienkirchen, OÖ, Austria
NHMW: 1 specimen (NHMW 1988/40/20)
Early Badenian (Langhian) – Gainfarn, NÖ, Austria
NHMW: 3 specimens (NHMW 2004z0154/0002, ../0006)

Discussion:
The records listed here either lack sufficient information to allow specific determination or are based on fragmentary material that is poorly preserved.

Occurrence:

Austria: Ottnangian (Late Burdigalian), Early to Late Badenian (Langhian-Early Serravallian)
Molasse Zone: Antiesenhofen, near Schärding/Inn, OÖ ([NHMW]); Gaindorf, NÖ (Schaffer, 1913b); Großwiesenhardt, near St. Marienkirchen, OÖ ([NHMW]); Ottnang, OÖ (Schaffer, 1943); Ravelsbach, NÖ (Schaffer, 1913b)
Vienna Basin: deep well Eichhorn 1, E of Zistersdorf, NÖ (Janoschek in Schaffer, 1951); Gainfarn, Nö ([NHMW]); Jungenberg, near Bisamberg, Vienna (Langer, 1939)
Eisenstadt-Sopron Basin: St. Margarethen (Kummer quarry), Bgld (Kapounek, 1939; Schmid et al., 2001); Walbersdorf, Bgld (Schaffer, 1927a)
Styrian Basin: Retznei (Lafarge quarry), Styria (Friebe, 1990); Spielfeld, Styria (Rolle, 1855; Stur, 1871); Teufelsberg, near St. Veit an der Drann, Styria (Dreger, 1894); Wagna (brickyard), Styria (Kollmann, 1965); Weitendorf, Stmk (Flügel et al., 1952; Ebner & Gräf, 1977; Krainer, 1987)

Paratethys (non-Austrian occurrences): Ottnangian (Late Burdigalian) to Late Badenian (Early Serravallian)
Molasse Zone: ? Židlochovice (= Groß-Seelowitz), Moravia, Czech Republic (Rzehak, 1880); Kralice nad Oslavou (= Kralitz), Moravia, Czech Republic (Toula, 1893)
Vienna Basin: Devínska Nová Ves, Slovak Republic (Schaffer, 1927a)
Great Hungarian Basin (Pannonian Basin): Fót, Hungary (Halmai, 1981)
Transylvanian Basin: region east of Taşad, Beiuş Basin, Romania (Paucă, 1936)

Zala, Sáva and Dráva Basins: Dráva valley, near Melling, E of Maribor (Marburg), Slovenia (Stur, 1871); La'sko (formerly Tüffer) ("Schlier" facies), Slovenia (Bittner, 1884); Dolje, Popov Dol, Croatia (Poljak, 1938)

Genus *Meoma* Gray, 1851

Type-species: *Meoma grandis* Gray, 1855; by original designation (Pomel, 1869: 131).
Diagnosis: Test ovate, with slight anterior sulcus; high profile; apical disc ethmolytic, with four gonopores; genital plate 2 projects beyond posterior oculars; ambulacrum III narrow and weakly sunken aborally, with small, simple isopores; paired ambulacra petaloid, narrow and prominently sunken; petals relatively straight with narrow interporal zone, extending to near ambitus; anterior petals strongly divergent; periproct large, on short, steeply undercut posterior face; peristome transversely elongated, kidney-shaped with projecting labrum; labral plate short and wide, not extending beyond first ambulacral plate; plastron fully tuberculated, ovate in outline, formed of sternal and episternal plates; episternal plates not strongly tapered to rear; spines and tubercles within peripetalous fasciole often slightly larger, but tubercles not sunken; peripetalous fasciole indented in interambulacra 1 and 4; subanal fasciole bilobed, well-developed only in juvenile, in adult only the adoral portion remains (modified from Kier, 1984; and Smith "*The Echinoid Directory*", 13.05.2004).
Distribution: Middle Eocene to Miocene – circumtropical, and temperate regions of Australia and New Zealand
Remarks: *Meoma* has similarities to *Macropneustes*, but can be distinguished by its deeply sunken, narrow petals and the shape of the peripetalous fasciole (indented in interambulacra 1 and 4)

According to Chesher (1969, 1970: 755) *Brissus cruciatus* Agassiz (in Agassiz & Desor, 1847), the type-species of *Schizobrissus* Pomel, 1869, is based on a single, poorly preserved specimen, that cannot be determined confidently even at family level. He thus concluded that *Schizobrissus* cannot be regarded a recognisable taxon. [According to Philippe (1998: 197) no other material was ever recorded from the type-locality, the Island of Capri (Thyrrenian Sea)].

Fischer's (1966) subdivision of *Meoma* into three subgenera was based mainly on the extent of the subanal fasciole. Yet Kier & Grant (1965: fig. 13) and Chesher (1969) showed that this feature is ontogenetically controlled and shows strong intraspecific variation in some species. In recent papers (e.g. Chesher, 1970; Kier, 1984; Žítt, 1985; McNamara et al., 1986) this subdivision was not used.
Ecology and biogeography: Modern species of *Meoma* inhabit clean, coarse sand or shell grit between 2 and 200 metres depth (Kier, 1984; Hendler et al., 1995). They are often associated with turtle grass beds and/or patch reefs and are non-selective or selective deposit feeders. *M. ventricosa* lives buried, with up to 4 cm of sediment above their apex. Most animals, however, are not completely buried, or just barely so. Specimens found within turtle grass beds live epibenthic and cover themselves with shell fragments and leaves of sea grass (Kier & Grant, 1965: 48). *M. ventricosa* is preyed upon the sea-star *Oreaster reticulatus* (Linné), sea turtles, stingrays, bony fish and cassid gastropods (Kier & Grant, 1965; Chesher, 1969; Gladfelter, 1978).

Within one year specimens of *M. ventricosa* can reach 88 mm TL and grow to 134 mm in four years. The largest known specimens are up to 200 mm in TL and come from open sand areas or deeper water (Chesher, 1969).

All extant species occur in the tropical zone (Caribbean and central East Pacific), but one species occurs in the Oligocene of southern Australia (McNamara et al., 1986) and the Oligocene to Early Miocene of New Zealand (Henderson, 1975). Additionally there are numerous records of *Meoma* from the Miocene of the Mediterranean.

Meoma locardi (Cotteau in Locard, 1877)

(Fig. 82; Pl. 74, Figs. 1-2)

*	1877	*Linthia locardi*, Tournouer, 1874 – Cotteau in Locard: 288-289; pl. 12, figs. 1-2
	1909	*Macropneustes saheliensis* (Pomel). – Stefanini: 58-60; pl. 1 (5), figs. 1-2
v.	1915	*Schizobrissus cruciatus* Ag. – Vadász: 228-229; text-fig. 118
	1995	*Meoma* (*Schizobrissus*) *locardi* (Cotteau, 1877) – Lachkhem & Roman: 15-16; pl. 5, fig. 1
	1998	*Meoma* (*Schizobrissus*) *locardi* (Tournouer in Cotteau, 1877) – Philippe: 194-195; pl. 21, figs. 10-14

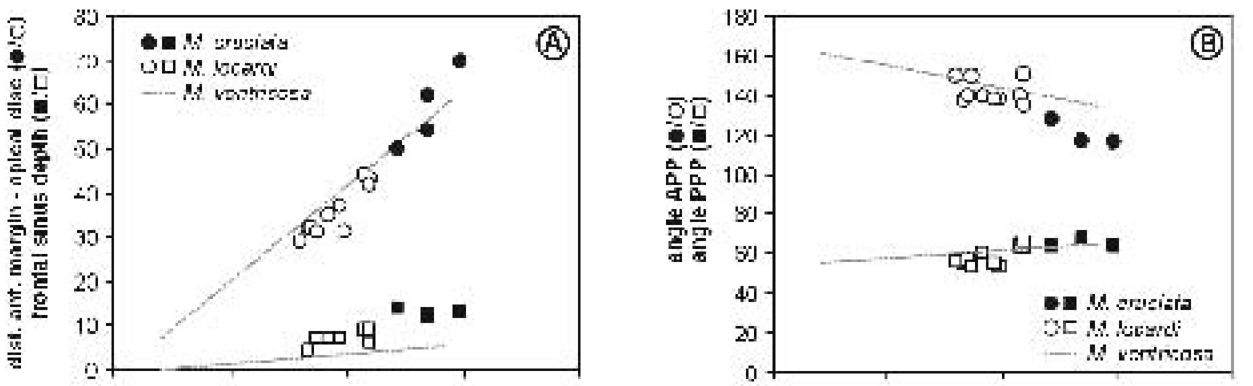

Figure 82: Ontogenetic changes in *Meoma*: distance between anterior margin and apical disc (A, circles), depth of the frontal sinus (A, rectangles), divergence of the anterior (B, circles) and posterior paired petals (B, rectangles). The grey, hatched line represents the degree of ontogenetic change present in extant *Meoma ventricosa* (based on Kier & Grant, 1965 and additional material in the NHMW collection). Data on the fossil specimens based on NHMW material and culled from the literature (Cotteau, 1877; Lambert, 1909; Stefanini, 1909; Vadász, 1915; Lachkhem & Roman, 1995; Philippe, 1998), attribution to *M. locardi* and *M. cruciata* represents the opinion of the respective authors. Note that the distinction between those two species seems to be based mainly on test length. Changes in the four features reported to be relevant for the distinction of the two species could also be interpreted as growth-related changes within a single species similar to those observed in extant *M. ventricosa* (see text).

Material:
Badenian (Langhian-Early Serravallian) – "Gallenegg", near Zagorje ob Savi (formerly Sagor, Krain), Slovenia
NHMW: 1 specimen, only aboral surface preserved (NHMW C.1967)
Badenian (Langhian-Early Serravallian) – Trbovlje (formerly Trifail), Slovenia
GBA: 1 partial internal mould (no inv. no.)
Late Badenian (Early Serravallian) – Mátraszölös (formerly Mátraszöllös), Nógrád, Hungary
MAFI: 1 specimen, with poorly preserved oral surface [MAFI Ech 157 (figured specimen of Vadász, 1915)]

Dimensions (in mm)**:**

Inv. No.	TL	TW	TH
GBA specimen	> 90	94	~54
MAFI Ech 157	110	100	~50
NHMW C.1967	122	106	40

Description:
Size and shape: The test is large, antero-posteriorly elongated with a roughly oval to slightly heart-shaped outline. The anterior margin shows a distinct frontal notch (depth 9 mm in the smallest and 14 mm in the largest specimen). In profile the test is low conical to highly domed, with a steep anterior slope. Posterior end obliquely truncated. The maximum height lies around the apical disc.
Apical disc: The apical disc is ethmolytic with 4 large, circular gonopores. It lies anterior of the centre, about 45 % TL from the anterior margin.
Ambulacra: The paired ambulacra are petaloid adapically. The petals are deeply sunken, subequal in length and bear many closely spaced elongate isopores. The interporiferous zone is narrow, barely reaching the width of a single poriferous zone in the widest, central part of the petals. The paired petals are straight (PPP), respectively slightly flexed anteriorly (APP), and extend about 55 to 60 % of the corresponding test radius. The anterior paired petals form an obtuse angle of around 128° in the largest, 135° in the middle and 140° in the smaller specimen (measured in planar aboral view). The posterior paired petals form an acute angle of about 50 to 65°. Ambulacrum III is nonpetaloid, and is increasingly depressed from the apex to the margin, where it forms a deep frontal sinus. The pores are poorly preserved and very small.
Interambulacra: The interambulacra are inflated between the petals, forming rounded keels between them. Other details are obliterated.
Peristome: Not preserved.
Periproct: Not preserved.
Fascioles: Not preserved.

Discussion:
Despite the poor preservation of the oral side of all three specimens the aboral side provides enough features to identify them with *Meoma locardi*.

Only three specimens of this species were available from the whole Central Paratethys. Although not coming from Austria they are discussed here to give some remarks on the systematics of this species.

Traditionally two species of *Meoma* have been recorded from the Miocene of the Mediterranean area: *M. cruciata* (Agassiz in Agassiz & Desor, 1847) and *M. locardi* (Cotteau in Locard, 1877) [sometimes also attributed to Tournouër, because Cotteau (1877) used a name proposed to him in a letter from that man; yet according to the ICZN Cotteau, 1877 is the correct author]. The problems around the name *cruciata* were outlined by Chesher (1969, 1970; see above) and obviously this name has to be considered as *nomen dubium* [holotype unrecognisable at family level (according to Chesher, 1970); type-locality imprecisely known, no topotypic material available]. Interestingly the holotype was never figured and its whereabouts are unknown [Cotteau (1877: 290) was not able to find it, nor anyone else, as far as I am aware of]. A plaster cast ("moulage" T.75) of the holotype is housed in the collection of the Museé d'Histoire Naturelle de Neuchâtel (Lambert & Jeannet, 1928: 198, T.75).

Most authors (e.g. Cotteau, 1877; Lachkhem & Roman, 1995; Philippe, 1998; ...) distinguished the two species on base of the depth of the frontal notch (deeper in *cruciata*), the position of the apical disc (more anterior in *locardi*) and the shape and divergence of the anterior paired petals (anterior flexed and strongly divergent in *locardi*, straight and less strongly divergent in *cruciata*). Both forms have the same temporal and spatial distribution and Lachkhem & Roman (1995:16) stated that "It is astonishing that two species of the same kind coexist in the same layer [in Melilla, Morocco], but it is also the case in Corsica, in the Rhône Basin and undoubtedly also in Sardinia. This could be attributed to sexual dimorphism, which is difficult to prove or they could be sympatric species." [translated from the French text]. Usually specimens larger than 115 mm TL were classified as *cruciata*, while smaller ones were named *locardi*. Opinions on specimens close to this "critical point", vary [e.g. the record of Vadász (1915), who calls his specimen *cruciata*, was placed into the synonymy list of *locardi* by Lachkem & Roman (1995:15-16) and then again in cf. *cruciata* by Philippe (1998: 197)].

In this context the description of the morphological changes occurring during the ontogeny of *Meoma ventricosa* by Kier & Grant (1965: 38-47, figs. 8-14; plate 9) is very elucidating. According to them the following changes occur during the growth from 22 to 160 mm TL: a) the test becomes lower, more angular, and the depth of the frontal notch increases, b) the petals become depressed, c) the posterior truncation tilts, so that the periproct becomes visible in oral view, d) the posterior petals become much longer (slightly exceeding the anterior petals in the largest specimens, f) the petals become narrower, g) the petals become curved, h) the divergence of the anterior paired petals decreases (from 162 to 135°) and that of the posterior ones increases (from 56 to 65°), i) the peristome becomes smaller relative to overall size and the labrum extends anteriorly, j) the spines become more equal in size and proportionally shorter, k) the subanal fasciole becomes discontinuous, l) the apical disc moves posteriorly towards the centre, m) genital pores appear at stage between 40 and 60 mm TL.

From the data provided by Kier & Grant (1965) it is evident that the features used as diagnostic on species level in the fossil *Meoma* species of the Mediterranean are entirely size related (Fig. 82). This can indeed be demonstrated by plotting, e.g. the anterior paired petal divergence against test length (Fig. 82.B, circles). It is thus doubtful to consider *M. locardi* and *M. cruciata* as two different species, and it is likely that they rather correspond to different growth stages of a single species. Yet the present author hesitates to synonymise them without having examined the type material of either species.

M. saheliensis (Pomel, 1887) was placed into the synonymy of *M. locardi* by Lachkem & Roman (1995:15-16) and Philippe (1998: 194). *M. lata* (Wright, 1855) from the Messinian of Malta is also highly similar to the present species (see Wright, 1855; Challis, 1980).

Occurrence:

Paratethys (non-Austrian occurrences): Badenian (Langhian-Early Serravallian)
Great Hungarian Basin (Pannonian Basin): Mátraszölös, Nógrád, Hungary (Vadász, 1915; [MAFI])
Zala, Sáva and Dráva Basins: "Gallenegg", near Zagorje ob Savi (formerly Sagor), Slovenia ([NHMW]); Trbovlje (formerly Trifail), Slovenia ([GBA])

Mediterranean: Burdigalian to Messinian, ? Pliocene
Western Mediterranean: Algeria (Cotteau et al., 1891); Corsica, France: Santa Manza (Cotteau in Locard, 1877);

Morocco: Idorhotsene, Melilla (Lachkhem & Roman, 1995); Rhône Basin, France: les Baux, Barbentane, Gordes, Goult and Villeneuve-lès-Avignon (Philippe, 1998); Reggio Emilia, Italy: Serra die Guidoni, Montese, Salto and Semelano (Stefanini, 1909); Sardinia, Italy: Santa-Lucia, near Pozzomaggiore (Cotteau, 1895), Cagliari and Is Mirrionis (Lambert, 1909)

Family Spatangidae Gray, 1825
Genus *Spatangus* Gray, 1825

Type-species: *Spatangus purpureus* Müller, 1776; by subsequent designation (ICZN, opinion 209, p. 385, 8th May 1954; see also ICZN, opinion 608, 21 March 1961).
Diagnosis: Test chordate, with shallow or moderately deep frontal notch; domed aboral and flattened oral surface; apical disc ethmolytic, with four gonopores; ambulacrum III narrow with small, simple isopores; paired ambulacra petaloid and flush with test; anterior paired petals flexed anteriorly, rudimentary pore-pairs in adapical half of anterior column; other pore-pairs large and conjugate; Posterior petals expanding adapically and converging distally; periproct on short steeply undercut posterior face; peristome transversely elongated, kidney-shaped, with projecting labrum; labrum anvil-shaped, in broad contact with sternal plates; sternal plates near-symmetrical, relatively broad and fully tuberculate; plastron formed of sternals and episternals; episternals not contracting towards posterior; aboral tuberculation heterogeneous with scattered coarse tubercles (not sunken in camellae); well-developed subanal fasciole, bilobed or shield-shaped; No other fascioles developed (modified from Smith *"The Echinoid Directory"*, 13.05.2004).
Distribution: ? Eocene, Oligocene to Recent – cosmopolitan (Fischer, 1966)
Remarks: There are more than 80 nominal species in the subgenus *Spatangus* (*S.*) (compare Lambert & Thiéry, 1909-1925 and Kier & Lawson, 1978) alone, most of which were reported from Miocene deposits of Europe. Classification of *Spatangus* species is notoriously difficult and hence the synonymy of many species is rather complicated. Due to the fact that most of the ancient species were based upon criteria as overall test shape, arrangement of primary tubercles and the like, there are many synonymous species. Mortensen (1951) considered the following features to be useful in specific determination within the genus (for extant species): 1) shape of the subanal plastron; 2) presence of primary tubercles outside the petals; 3) test profile (including test height); 4) shape of the posterior end; 5) the number of pore pairs within the subanal fasciole; and 6) presence of a keeled sternum. A recent investigation by Néraudeau et al. (1998a) showed that especially the shape of the subanal fasciole (1), the abundance of primary tubercles within the adapical interambulacra (2), depth of the frontal sinus (3) and the plastron architecture (4) are important to distinguish the two *Spatangus* species [*S. purpureus* (Müller) and *S. subinermis* Pomel] present in the Pliocene to Holocene of the Northern Mediterranean Sea. During the investigations done on the Neogene echinoids of Austria the plastron architecture and distribution of primary tubercles proved to be most useful to classify the different species.

***Spatangus austriacus* Laube, 1869**

(Figs. 83, 84, 85.A, C, 86.A-B; Pl. 75, Figs. 1-3, Pl. 76, Figs. 1-4)

* v pp 1869a *Spatangus austriacus* Laube. – Laube: 184
v pp 1870 *Spatangus austriacus* Lbe. – Laube: 314
v pp 1871 *Spatangus austriacus* Laube. – Laube: 73; pl. 19, fig. 2, 2a
non 1879 *Spatangus austriacus*, Laube. – Manzoni: 160; pl. 2, figs. 10-15; pl. 3, figs. 19-22; pl. 4, figs. 40-41 [fide Mazzetti (1882b), Airaghi (1908: 256), Stefanini (1908b: 112), Lambert (1924 in Lambert & Thiéry, 1909-1925: 462)]
non 1880a *Spatangus austriacus* Laube. – Manzoni: 185, 188
non 1881 *Spatangus austriacus*, Laube. – Manzoni: 174
non 1882b *Spatangus Austriacus*, Laube. – Mazzetti: 129
non 1882 *S.*[*patangus*] *austriacus* Laub. – Pantanelli: 45 [book review]
non 1883 *S.*[*patangus*] *austriacus* Laub. – Mazzetti & Pantanelli: 66
? 1884 *Spatangus austriacus* Laub. – Coppi: 191, no. 281
? 1887 *Spatangus austriacus* Laube – Neviani: 194, 208, no. 208
? non 1887b *Spatangus austriacus*, Laube. – Koch: 270
? 1887 *Spatangus austriacus*, Laube. – Parona: 307
? 1897 *Spatangus austriacus* Laube. – Angelis d'Ossat: 291, 292-293
pp 1897 *Spatangus austriacus*, Laube – Cotteau: 194
non 1897 *Spatangus austriacus* Laube. – Vinassa de Regny: 155
non 1901 *Spatangus austriacus* Lbe. – Airaghi: 215-216; pl. 27 (9), fig. 8 [= *S. taramellii* Airaghi, 1908; fide Airaghi (1908: 255)]
non 1908b *Spatangus austriacus* Laube. – Stefanini: 109-112
v. 1912a *Spatangus Austriacus* Laube. – Schaffer: 191-192; text-fig. 3; pl. 59, fig. 1-3; pl. 60, fig. 7
? non 1930 *Prospatangus austriacus* Laube. – Vendl: 50
non 1936 *Spatangus austriacus* Laube – Paucă: 143, 197; pl. 2, figs. 1-2
non 1938 *Spatangus austriacus* Laube 1871 – Poljak: 197-198; pl. 10, fig. 2
? non 1953 *Prospatangus austriacus* (Laube), 1871. – Szörényi: 37-38, 88-89; pl. 8, figs. 3, 3a-b
? 1963 *Spatangus austricacus* Laube – Comaschi Caria: 27-29
? 1967 *Spatangus austriacus* Laube – Menesini: 149-151; pl. 48 (3), figs. 1, 1a
v. 1971a *Spatangus austriacus* Laube, 1871 – Steininger: 595; pl. 2, fig. 3; pl. 3, fig. 5
1971b *Spatangus austriacus* Laube – Steininger: 119
1971c *Spatangus austriacus* Laube – Steininger: 129
1974 *Spatangus austriacus* Laube – Thenius: 47
? non 1979 *Spatangus austriacus* Laube, 1871 – Mączyńska: 31-32, pl. 3, figs. 1-2; pl. 4, fig. 1; pl. 5, figs. 1-2
? non 1988 *Spatangus austriacus* Laube, 1871 – Mączyńska: 62; pl. 4, figs. 4a-f
non 1996 *Spatangus austriacus* – Machalski: 26
non 1997 *Spatangus austriacus* Laube – Majcen et al.: 106; pl. 5, fig. 2
v. 1998 *Spatangus austriacus* Laube – Schultz: 120; pl. 54 fig. 3
v. 1999 *Spatangus austriacus* – Harzhauser & Kroh: 221

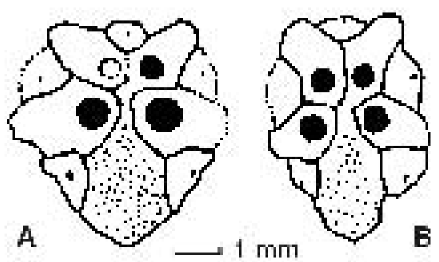

Figure 83: *Spatangus austriacus* Laube, 1869: apical disc (A: paralectotype, NHMW 26.IV.726; B: lectotype: NHMW 1866.I.1286; both from Bayersdorf, near Maissau, NÖ). Poorly visible sutures and genital pores omitted or stippled.

v.	1999	*Spatangus austriacus* Laube, 1871 – Kroh & Harzhauser: 160-161; pl. 1, figs. 1-2; pl. 3, fig. 3
v non	2001	*Spatangus austriacus* (Laube) – Schmid et al.: 13; pl. 1, fig. 5
v.	2002	*Spatangus austriacus* – Lukeneder & Harzhauser: 462
non	2004	*Spatangus austriacus* Laube, 1871 – Radwański & Wysocka: 385, 386; pl. 6, figs. 1a-b

Type-material:
<u>*Spatangus austriacus* Laube, 1869</u>:
Lectotype: NHMW 1866.I.1286, figured by Laube (1871: 73; pl. 19, fig. 2); Naturhistorisches Museum Wien, Geologische Abteilung
Paralectotype: NHMW 26.IV.726, figured by Laube [1871: 73; pl. 19, fig. 2a (erroneously labelled 1a at the plate)]; Naturhistorisches Museum Wien, Geologische Abteilung
Locus typicus: Bayersdorf, near Maissau, NÖ, Austria
Stratum typicum: Zogelsdorf Fm.
Age: Late Eggenburgian (Early Burdigalian), Early Miocene
Remarks: Laube (1869a: 184; 1871: 73) mentioned also an additional specimen from the Badenian of Großhöflein (= Nagyhöflány), Bgld, Austria (then belonging to Hungary), which was located at the Museum of Pest (probably the Hungarian National Museum). Unfortunately, neither Vadász (1915: 237) nor the present author were able to locate that specimen. It is, however, very likely that this specimen is not conspecific with the others, since *S. austriacus* is restricted to the Eggenburgian (see below).

Material:
Late Eggenburgian (Early Burdigalian) – Bayersdorf (Zogelsdorf Fm.), near Maissau, NÖ, Austria
NHMW: 2 specimens [NHMW 1866.I.1286 (**lectotype**) and 26.IV.726 (paralectotype)]
Late Eggenburgian (Early Burdigalian) – Eggendorf, NÖ, Austria
NHMW: 1 specimen (NHMW 1998z0048/0095)
Late Eggenburgian (Early Burdigalian) – Eggenburg (Kalvarienberg, Zogelsdorf Fm.), NÖ, Austria
IPUW: 1 specimen (no inventory no.)
Late Eggenburgian (Early Burdigalian) – Grübern (Zogelsdorf Fm.), near Maissau, NÖ, Austria
NHMW: 17 specimens (NHMW A2254, 1914.VII.19a-j; 2002z0159/0002-7)
IPUW: 3 specimens (no inventory no.)
Late Eggenburgian (Early Burdigalian) – Unternalb (Retz Fm., Hungerfeld), near Retz, NÖ, Austria
NHMW: 4 specimens (NHMW 1999z0049/0001, NHMW 1999z0049/0004)

Dimensions (in mm)**:**

Inv. No.	TL	TW	TH
NHMW 1866.I.1286 (LT)	80.4	77.2	34.4
NHMW 26.IV.726 (PLT)	>75	>50	34.5
NHMW 1998z0048/0095	48.7	51.6	17.4
NHMW 1999z0049/0001	124.1	~115	53.3
NHMW 1914.VII.19a	89.6	87.6	>31
NHMW 1914.VII.19b	78.5	76.5	~ 27
NHMW 1914.VII.19c	66.0	64.2	> 18
NHMW 1914.VII.19d	62.8	60.2	22.4
NHMW 1914.VII.19e	55.3	53.1	18.3
NHMW 1914.VII.19i	54.2	>47	>18.5
NHMW 1914.VII.19j	44.5	42.0	14.4
NHMW 2002z0159/0005	57.2	~55.5	30.2
NHMW 2002z0159/0006	70.6	64.4	21.9

Description:
<u>Size and shape</u>: Test large to very large, heart-shaped and slightly elongated antero-posteriorly. The anterior margin is rounded with a distinct frontal notch, which increases in depth during growth. The posterior margin is bluntly pointed to transversely truncated. Maximum width coincides with the position of the apical disc. In profile the test is arched to wedge-shaped with a steep anterior slope and a gentle posterior slope. The anterior end is rounded, the posterior low and obliquely truncated. Slightly posterior of the apical system there is a distinct kink in lateral view. The maximum height lies posterior of the apical disc in interambulacrum 5, about one-third of the distance apical disc-posterior margin from it. The oral side is flattened, with a sunken peristome and inflated plastron. The test width ranges from 92.2 to 97.7 % TL (Mean=95.6 %), the height from 31.0 to 52.8 % TL (Mean=38.2 %).
<u>Apical disc</u>: The apical disc lies slightly anterior of the centre, about 42 to 45 % TL from the anterior margin. It is ethmolytic with four large gonopores, the anterior ones of which are slightly smaller (Figs. 83.A-B).
<u>Ambulacra</u>: Ambulacrum III nonpetaloid, slightly depressed, increasingly so towards the anterior margin. The pores are strongly oblique, minute partitioned isopores, lying in small depression in the centre of each plate. The interporiferous zone is wide and bears only secondary and miliary tubercles. The paired ambulacra are petaloid, depressed and moderately closed distally. The anterior paired petals form an obtuse angle of about 130 to 145°, the posterior paired petals an acute angle of about 60° (ranging from 57 to 64°). The anterior paired petals are flexed anteriorly distally, the posterior paired petals slightly laterally at their distal tips. The petals are broad and show allometric growth [i.e. width 10.9 to 11.2 % TL in subadult specimens (TL 50-65 mm), 9.9 to 10.4 %TL (TL ~ 80 mm) in adult specimens and 9.3 % in the largest specimen available (TL = 124.1)]. Their shape changes from lobate in subadult to lanceolate in adult specimens. They extend two third to three quarter of the corresponding test radius. Within the petals the pores are elongated isopores. The poriferous zones are slightly depressed, whereas the interporiferous zones, which are about 2 (subadult specimens) to 2.5 (large specimens) times as wide as a single poriferous zone, are slightly inflated. The pores of the uppermost 5 to 8 plates in the anterior plate row of ambulacra II and IV are minute partitioned isopores. Outside the petals only minute microunipores are present, except in the phyllodes where large teardrop- to slit-shaped unipores with extensive periporal area are found.

Adorally well developed phyllodes are present, bearing 7 pores in ambulacrum III, 11 to 12 in each of the anterior paired ambulacra and 7 to 8 in the posterior paired ambulacra. Ambulacra I and V form moderately broad peri-plastronal areas lacking primary tubercles. In many subadult specimens the ambulacral plates are distinctly inflated on the oral side (e.g. Pl. 75, Fig. 3; Pl. 76, Fig. 3b).
<u>Interambulacra</u>: Adapically the interambulacra are slightly inflated between the petals. They bear few crenulate, perforate primary tubercles with inclined areoles, which are arranged in chevron-shaped groups (Fig. 85.A, C) at the adapical border of each plate in the interambulacra 1, 4 and 5. In the interambulacra 2 and 3 the primary tubercles are situated along the borders of ambulacrum III and along the adapical plate borders in the posterior plate rows (2a and 3b). Towards the margin of the test the primary tubercles are less numerous and smaller. The remaining surface of the interambulacra is covered by small, evenly distributed, crenulate perforate secondary tubercles with inclined areoles.

Adorally the interambulacra are densely covered with crenulate, perforate primary tubercles. ly few secondary and miliary tubercles are scattered among them. The tubercles increase in size from the margin towards the peristome. On the sternum and on the first pair of episternal plates the tubercles are arranged in a fan-shaped pattern radiating from a posterior elevation on the sternum respectively central elevation on the