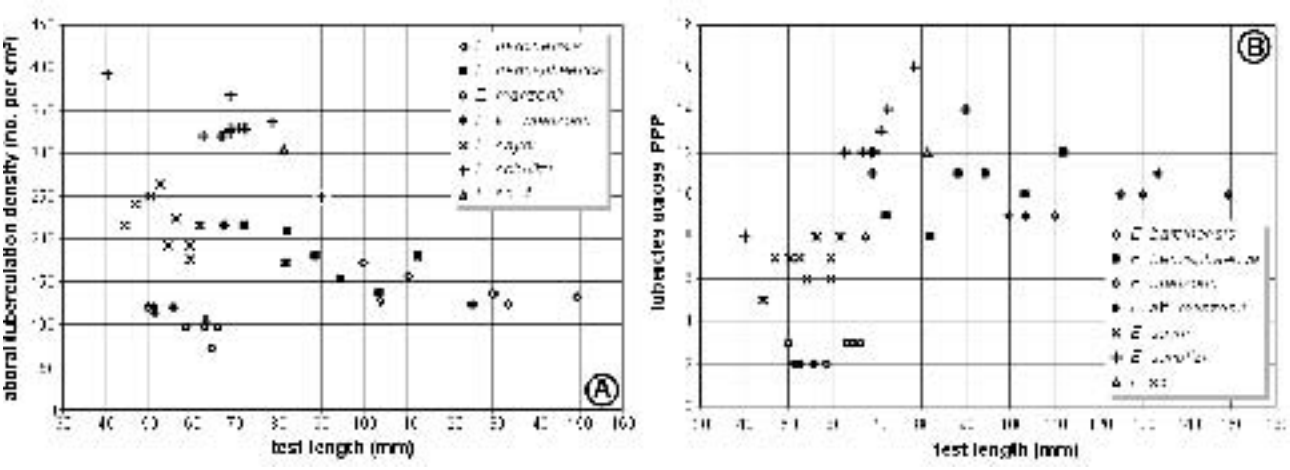

Figure 48: Morphometric comparison between the discussed *Echinolampas* species: Variation of aboral tubercle density (A; counted in the interporiferous zones of the petals I or V) and number of tubercles across the interporiferous zone of the posterior paired petals (B). Again, a distinct allometric component (see fig. 4.4) is evident. However, separation of the individual taxa is relative straightforward (e.g. large difference between *E. sayni* and *E. schultzi*,...).

Occurrence:

Austria: Early to Late Badenian (Langhian to Early Serravallian)
- Vienna Basin: Hof am Leithagebirge, NÖ ([NHMW]); Hornstein (=Szarvkö), Bgld (Vadász, 1915; [MAFI]); Mannersdorf, NÖ ([NHMW]); Müllendorf (Mühlendorfer Kreide AG quarry), Bgld ([NHMW]); Schrattenberg, NÖ ([NHMW])
- Styrian Basin: Retznei (Weissenegg Fm., Lafarge quarry), Styria ([coll. Meindl])

Paratethys (non-Austrian occurrences): Early to Late Badenian (Langhian to Early Serravallian)
- Great Hungarian Basin (Pannonian Basin): ? Budapest, Pest, Hungary (Kókay et al., 1984); ? Budapest-Rákos, Pest, Hungary (Mihály, 1969)
- Fore-Carpathian Basin: Niechobrz, south-eastern Poland [Szörényi, 1953 (locality is of Early Badenian age, see discussion in Bitner & Pisera, 2000: 7-8)]
- Transylvanian Basin: Gârbova de Sus (= Felsö-Orbó), Romania (Vadász, 1915; [MAFI]); Livezile (= Ùrháza, = Vládháza), Alba, Romania (Vadász, 1915); ? Moldoveneşti (= Várfalva), Cluj, Romania (Vadász, 1915); ? Pietroasa (= Csegez), Romania (Vadász, 1915); region east of Taşad, Romania (Paucă, 1936)

Mediterranean: ? Burdigalian to Serravallian
- Western Mediterranean: Ploaghe, Province Sassari, Sardinia (Lovisato, 1910); Viloví dans le Penedés, Catalogne, Spain (Lambert, 1906a, 1927a)
- Eastern Mediterranean: Gubba Cyrenaica, Lybia (Taviani, 1939)

Atlantic Ocean: Middle ? Miocene
- Iberian Atlantic coast: Alro dos Buxos, Trafaria, Portugal (de Loriol, 1896); Cazal das Rolas, Portugal (de Loriol, 1896); De Forno do Tijolo à Pragal, Portugal (de Loriol, 1896); Marvilla, Portugal (de Loriol, 1896); Palma, north of Alcacer do Sal, SW Portugal (de Loriol, 1896)

Echinolampas hemisphaerica (Lamarck, 1816)

(Figs. 43.2, 44, 45; Pl. 51, Figs. 1-2)

#	1829	*Clypeaster Linkii* nobis – Goldfuss: 133; pl. 42, figs. 4a-c
	1835	*E.*[*chinolampas*] *hemisphæricus* Ag. (*Clypeaster hemisph*. Lam.)– Agassiz: 187
	1835	*E.*[*chinolampas*] *Linkii* Ag. (*Clypeaster Link*. Goldf.) – Agassiz: 187
?	1836	*Clypeaster hemisphæricus*. – Grateloup: 146-147; No. II/7
pp	1847a	[*Echinolampas*] *hemisphæricus* Agass. – Agassiz & Desor: 165
	1847a	[*Echinolampas*] *Linkii* Agass. – Agassiz & Desor: 166
	1848	*Echinolampas hemisphæricus* (Ag.) – Gras: 52
	1852	*E.*[*chinolampas*] *hemisphæricus* (Ag.) – Gras: 47
	1857	*E.*[*chinolampas*] *hemisphæricus*, Ag. – Pictet: 210
	1857	*E.*[*chinolampas*] *Linkii*, Ag. – Pictet: 210
pp	1858	*Echinolampas hemisphaericus* Agass. – Desor: 307
	1858	[*Echinolampas*] *Linkii* Agass. – Desor: 309
?	1864	*Echinolampas hemisphæricus*, Lamarck – Wright: 480-481
	1869	*Echinolampas hemisphæricus* Lamarck (*Clypeaster*) – des Moulins: 315
	1869	*Echinolampas hemisphaericus* Lam. var. *Linki* Goldf. – Fuchs: 194
	1869a	*Echinolampas hemisphaericus* Lamarck sp. Varietas *Linkii* Goldfuss. – Laube: 183
pp	1869a	*Echinolampas hemisphaericus* Lamarck sp. Varietas *Rhodensis* Laube. – Laube: 183
	1870	*Echinolampas hemisphaericus* var. *Linki* Goldf. – Laube: 314
pp	1870	*Echinolampas hemisphaericus* var. *Rhodensis* Lbe. – Laube: 314
	1871	*Echinolampas hemisphaericus* Lamarck. Varietas *Linkii* Goldfuss. – Laube: 65, 66; pl. 18, fig. 3
pp	1871	*Echinolampas hemisphaericus* Lamarck. Varietas *Rhodensis* Laube. – Laube: 65, 66; pl. 18, fig. 2
?	1873	*Echinolampas hemisphaericus*, Lamk – Manzoni: 10-11, 19
	1875	*Clypeaster hemisphaericus* Lmck. – Quenstedt: 494-495
	1877	*Echinolampas hemisphaericus* Lam. var. *Linki* Goldf. – Karrer: 312
	1877	*Echinolampas haemisphaericus* Lam. var. *Linkii* Goldf. – Lóczy: 63
	1879	*Echinolampas hemisphæricus*, Lamck. – Hermite: 252

non 1880a *Echinolampas hemisphaericus* Lk. – Manzoni: 186, pl. 1, figs. 1-3 [specimens from the Pliocene of Castelarquato belong to *E.* (*Macrolampas*) *hoffmanni* Desor according to Borghi (1994: 7); specimens from the "Molassa serpentinosa" were referred to *E. italica* by Lambert (1906a: 93)]
1881 *Echinolampas hemisphæricus*, Lamk. – Manzoni: 174
1882a *Echinolampas hemisfericus*, Agas. – Mazzetti: 123
1883 *E. Linkii* – Pomel: 62
1883 *E. hemisphæricus* – Pomel: 62
1887b *Echinolampas hemisphaericus*, Lamarck, var. *Rhodi*, Laube. – Koch: 269
1887b *Echinolampas Laurillardi*, Agissiz. – Koch: 269
1888b *Echinolampas haemisphaericus*, var. *Rodi*, Lbe – Nemes: 22, 32
pp 1891 *Echinolampas hemisphæricus* (Lamarck), 1816. – Gregory: 605-606
1894 *Echinolampas hemisphaericus* var. *Rodi* Laube. – Mártonfi: 153
non 1897 *Echinolampas hemisphaericus* Lmk. sp. – Vinassa de Regny: 152 [= *E.* (*Macrolampas*) *hoffmanni* Desor fide Borghi (1994: 7)]
1899 *Echinolampas hemisphaericus* Lmk. sp., var. *Linkii* Goldf. – Roth von Telegd: 95
1906 *Echinolampas hemisphaericus* Lam. var. *Linkii*, Goldfs. – Vadász: 329, 331-332
pp v 1915 *Echinolampas hemisphaericus* Lam. sp. – Vadász: 206-209; fig. 94
? 1915 *Echinolampas angustipetalus* n. sp. – Vadász: 215; fig. 101; pl. 10 (4), fig. 4
1931 *Echinolampas hemisphaericus* Lam. – Janoschek: 83, 84
1939 *Echinolampas hemisphaericus* Lam. sp.– Kapounek: 72
non 1953 *Echinolampas hemisphaericus* (Lamarck), 1816. – Szörényi: 34, 84-85; pl. 3, figs. 2, 2a-b [misidentified *Conolampas* species]
1965 [*Echinolampas*] *hemisphaerica* Lamarck 1816 (*Clypeaster*) – Roman: 283
1969 *Echinolampas hemisphaericus* Lamarck – Mihály: 256
1969 *Echinolampas lecointrae* Lambert – Mitrović-Petrović: 122; pl. 1, figs. 1, 1a-b
1969 *Echinolampas italicus* Lambert – Mitrović-Petrović: 123; pl. 2, figs. 1, 1a
1969 *Echinolampas wrighti* Gregory – Mitrović-Petrović: 123; pl. 2, figs. 2, 2a
1970 *Echinolampas hemisphærica* (Lamarck) – Montenat & Roman: 116-117
1974 *Echinolampas* (*Echinolampas*) *hemisphaerica* (Lamarck) 1816 – Chavanon: vol.1: 184-186; vol. 2: 147-148; figs. 120-16, 169-171; pl. 12, figs. 7a-b
1974a *Echinolampas hemisphericus* – Rose: 345; fig. 3
? 1974b *Echinolampas hemisphericus* – Rose: 353; fig. 3
? 1980 *Echinolampas hemisphaerica* (Lamarck) – Challis: 149-152; pl. 49, figs. a-c, pl. 50, fig. a [pl. 51, figs. a-c depict a specimen from Martignas, Gironde France, which undoubtedly belongs to *E. hemisphaerica*, for the records from the Messinian of Malta see discussion below]
1984 *Echinolampas hemisphaeicus* Lamk. – Kókay et al.: 288
1985 *Echinolampas hemisphaericus* Lamarck, 1816 – Mihály: 244
1997 *Echinolampas laurillardi* Agassiz – Majcen et al.: 106; pl. 5, fig. 1
pp 1998 *Echinolampas hemisphaerica* (Lamarck, 1816) – Philippe: 86-90; pl. 17, figs. 4, 6-8
? 2001 *Echinolampas hemisphaerica* – Néraudeau et al.: 52; tab. 1
v. 2001 *Echinolampas hemisphaericus* (Lamarck) – Schmid et al.: 23

Type-material:
The provenance and current whereabouts of Lamarck's (1816) material is unknown. Subsequent publications do not agree on a single type region. Two regions, the Rhône Basin (more specifically the region of Tricastin) and the Aquitaine Basin (the area of Dax, Landes and Bordeaux, Gironde) are cited.

Material:
Badenian (Langhian-Early Serravallian) – Brunn am Steinfeld, NÖ, Austria
NHMW: 1 specimen (NHMW 2002z0181/0016)
Badenian (Langhian-Early Serravallian) – Kalksburg, Wien, Austria
NHMW: 3 specimens (NHMW 1904.VIII.50, 1904.VIII.53, 2002z0181/0020)
Badenian (Langhian-Early Serravallian) – Neckenmarkt (Galgenberg), Bgld, Austria
NHMW: 1 specimen (NHMW 2002z0181/0017)
Badenian (Langhian-Early Serravallian) – Ritzing, Bgld, Austria
NHMW: 1 specimen (NHMW 1973/1615/180a)
Late Badenian (Early Serravallian) – Müllendorf (Mühlendorfer Kreide AG quarry), Bgld, Austria
NHMW: 4 specimens (NHMW 1997z0178/1744, 1997z0178/1758, 2002z0181/0009-10)

Foreign material for comparison:
Burdigalian – Martignas, Gironde, France
NHMW: 1 specimen (NHMW C 6041)
Early Badenian (Langhian) – Kovácsszénnája (= Kovacéna), Baranya, Hungary
MAFI: 1 specimen [MAFI Ech 436 (reference material of Vadász, 1915)]
Badenian (Langhian-Early Serravallian) – Budatétény, Budapest, Hungary
NHMW: 1 specimen (NHMW 1997z0178/2424)
Late Badenian (Early Serravallian) – Buituri (= Bujtur), Romania
MAFI: 1 specimen [MAFI Ech 267 (reference material of Vadász, 1915; specimen very poor, determination tentative at best)]

Dimensions: see Tab. 10

Description:
Size and shape: The test is large and has an oval, antero-posteriorly elongated outline. Test width ranges from 88.6 to 93.2 % of TL with a mean of 91.5 % in the studied specimens, but test width may range up to 97 % TL in other areas/time slices [Rhône Basin (Philippe, 1998), Aquitaine Basin (Chavanon, 1974)]. The anterior margin is rounded, the posterior margin distinctly rostrate. The maximum width lies posterior of the apical disc, about 62 to 66 % of TL from the anterior margin. In profile the test is domed, nearly hemispherical, the maximum height coinciding with the posterior part of the apical disc. Test height ranges from 39.0 to 51.7 % TL, with a mean of 45.0 %. The ambitus is rounded and tumid.
Apical disc: The apical disc lies slightly anterior of the centre, about 42 to 43 % TL from the anterior margin. The apical disc is monobasal with four circular gonopores. The madreporite is pentagonal and crowded with numerous small madreporic pores. The gonopores lie at the apices of the madreporite. The ocular plates are small, bearing a small, circular ocular pore each.

Ambulacra: Adapically the ambulacra are petaloid, moderately broad, straight and only slightly closed distally. The frontal petal extends about 60 to 72 % of the corresponding test radius, the anterior paired petals about 68 to 80 (mean 73) % and the posterior paired petals about 70 to 80 %. In contrast to the other petals, the poriferous zones within the anterior paired petals are not of equal length. The anterior poriferous zones (IIb and IVa) are shorter than the posterior ones (IIa and IVb) extending about 80 to 94 % of the length of the petal. Poriferous zones Ib, IIa, IVb and Va are distinctly arched, whereas the other poriferous zones are nearly straight. The ambulacral pores in the petals are conjugated anisopores, which are strongly conjugated and slightly oblique. The interporiferous zones within the petals are distinctly inflated and up to four times as wide as a single poriferous zone. The poriferous zones are slightly depressed.

Adorally the ambulacra form slightly depressed phyllodes. They consist of four series of unipores in each ambulacrum. Two adradial series consisting of large, closely spaced unipores with rather large attachment area and two perradial series consisting of smaller, slightly elongated unipores, which are more widely spaced. The two buccal pores are slightly larger than the other phyllodal pores. In the adoral third of the phyllodes there is a double row of shallow pits running along the central suture. These are interpreted as sphaeridial pits.

Interambulacra: Adapically the interambulacra are slightly inflated between the petals. On the aboral surface they are covered with small, crenulate, perforate tubercles which are deeply sunken and closely spaced. The areoles are inclined towards the margin of the test. On the oral side the interambulacra are slightly inflated and form small, inflated bourrelets in interambulacra 2 and 3 adorally. There is no "naked zone" along the central suture between peristome and periproct in interambulacrum 5, as reported in other species of *Echinolampas*.

Peristome: The peristome lies slightly anterior of the centre, about 42-44 % TL from the anterior margin. It is oval to subpentagonal and transversely elongated. It is moderately large, being usually 13-16 % TW in width.

Periproct: The periproct is situated inframarginally in interambulacrum 5 and lies nearly completely on the oral surface. It is large, about 15 to 16 % TW wide and has an oval, transversely elongated shape.

Differential diagnosis (see Figs. 43, 45-48)**:**

As outlined above, *E. hemisphaerica* is characterised by its subpentagonal, rostrate outline, high, globose profile, distinctly inflated interporiferous zones of the petals, weakly developed bourrelets, and relatively wide poriferous zones.

For the difference to *E. schultzi* see below under that species.

For the difference to *E. sayni* see below under that species.

E. sp. 1, from the Badenian (Langhian-Early Serravallian), differs from *E. hemisphaerica* by its more elongated distinctly oval outline, smaller peristome and periproct and much more sunken poriferous zones.

E. barcinensis, a co-occurring species, differs from *E. hemisphaerica* by its much lower profile, lower test height (Fig. 44), distinctly less rostrate shape, larger periproct, less inflated petals and less sunken poriferous zones. Additionally, the number of tubercles across the interporiferous zone is distinctly lower.

E. manzonii and *E.* aff. *manzonii*, both from the Early Badenian (Langhian) differ from *E. hemisphaerica* by their very unequal poriferous zones in the paired petals (among other features, but this is the most easily recognised).

E. hoffmanni Desor in Agassiz & Desor, 1847 from the Pliocene of Sicily and Northern Italy has many similarities with the present species. According to Borghi (1994: 7) the two species might be closely related. When the measurements provided by Borghi (1994) are compared with those obtained from the *E. hemisphaerica* from the Central Paratethys it becomes evident that the Pliocene *E. hoffmanni* is less elongated (TW mean 97.6 % TL vs. 91.5 % TL in *E. hemisphaerica*) and has a smaller peristome (peristome width mean 10.7 % TL vs. 12.7 % TL) and periproct (periproct width mean 12.2 % TL vs. 14.7 % TL). These examples illustrate that albeit the two are obviously very similar it is possible to distinguish them. Due to the limited information available it is currently impossible to decide whether these differences might represent shifts due to different environmental conditions or if they represent differences at species level.

Discussion:

Roman (1965: 283) included the following species and subspecies into the synonymy of *E. hemisphaerica*: *E. linkii* (Goldfuss, 1826), var. *rhodensis* Laube, 1869, *E. subhemisphaerica* Pomel, 1887, *E. pomeli* Peron & Gauthie in Cotteau et al., 1891, *E. deydieri* Lambert, 1913, var. *cyrenaica* Desio, 1929, var. *bardiensis* Desio, 1929 and tentatively var. *cubensis* Palmer in Sanchez Roig, 1949. Unfortunately he did not provide a formal synonymy or discussed his reasons for synonymising the species with *E. hemisphaerica*. Following Lambert (1906a: 90-93; 1927a: 24) he excludes var. *maxima* de Loriol, 1896 from the synonymy and states that it belongs into the synonymy of *E. barcinensis* Lambert, 1906.

This species was re-described in detail by Philippe (1998: 86-90), who gave an extensive synonymy and revised all *Echinolampas* species reported from the Rhône Basin earlier. He also included *E. sayni* Lambert, 1913a into the synonymy of *E. hemisphaerica*, an opinion with which the present author does not agree with (see below under that species). The Austrian material fits rather well with the French material of *E. hemisphaerica* [both from the Rhône Basin (Philippe, 1998) and the Aquitaine Basin (Chavanon, 1974); see e.g. Fig. 44) and one can confidently regard them as conspecific. The quite variable morphology of this species, the uncertainty about its provenance and lack of a sufficient description during most of the 19th century led to the establishing of many junior synonyms of this species. Moreover, there are a number of similar and/or related other species on the originality of which there is no common agreement (e.g. *E. hoffmanni*, …). Recently Néraudeau et al. (1999: 356) even made the extant Western African *E. rangii* des Moulins, 1869 a junior synonym of *E. hemisphaerica*. Néraudeau et al. (1999) state that this is based on "biometric and statistical" analysis, but neither data nor analysis are presented.

Records of *E. hemisphaericus* from the Upper Coralline Limestone (Messinian, see Kienel et al., 1995) by Wright (1864), Rose (1974b) and Challis (1980, and records therein) are doubtful. The Maltese specimens described and figured by Challis (1980) have much lower profiles and test heights than usually observed in *E. hemisphaerica*, and are also less anteroposteriorly elongated. They show large similarities with the species *E. barcinensis* discussed above. Records of *E. hemisphaerica* from the *Globigerina* Limestone (Aquitanian to Langhian; see Mazzei, 1985 and references therein) by Cotteau (1913a) remain to be confirmed.

Laube (1869a, 1871) established a new subspecies (variety) of *E. hemisphaerica*, namely var. *rhodensis*, based on Pliocene material from the Island of Rhodes. Additionally he attributed specimens from the Badenian of Sóskut to this subspecies. The latter, however, is not conspecific with the material from Rhodes, but belongs to *E. hemisphaerica*. Laube's subspecies *rhodensis* is here elevated to species rank and is probably the senior synonym of *E. orbignyi* Desor, 1876, a species also based on Pliocene material from Rhodes. The latter was considered a probable junior synonym of *E. hoffmanni* by Borghi (1994) based on comparison of biometric data of specimens from the Pliocene of Northern Italy, Sicily and the measurements of *E. orbigny* from Rhodes given by Airaghi (1930). To fully resolve the relation between those three species, the Miocene species *E. hemisphaerica* and the extant *E. rangii* more refined investigations are necessary.

Occurrence:

Austria: Early ? to Late Badenian (Langhian-Early Serravallian)
- Vienna Basin: Baden, NÖ (Goldfuss , 1829; Desor, 1858); Brunn am Gebirge, NÖ (Laube, 1869a, 1871; Manzoni, 1873); Brunn am Steinfeld, NÖ ([NHMW]); Kalksburg, Vienna (Fuchs, 1869; Laube, 1869a, 1871; Manzoni, 1873; Karrer, 1877; Gregory, 1891; [NHMW]); Müllendorf (Mühlendorfer Kreide AG quarry), Bgld (Kapounek, 1939; [NHMW]); Vienna (Agassiz & Desor, 1847a; Pictet, 1857); Vienna Basin (Lóczy, 1877; Roman, 1965)
- Eisenstadt-Sopron Basin: Großhöflein, Bgld (Laube, 1869a, 1871; Manzoni, 1873); St. Margarethen (Kummer quarry), Bgld (Schmid et al., 2001)
- Oberpullendorf Bay: Neckenmarkt, Bgld (Janoschek, 1931; [NHMW]); Ritzing, Bgld (Quenstedt, 1875; [NHMW]);

Paratethys (non-Austrian occurrences): Early to Late Badenian (Langhian-Early Serravallian)
- Eisenstadt-Sopron Basin: Sopron, Györ-Moson-Sopron, Hungary (Lóczy, 1877)
- Great Hungarian Basin (Pannonian Basin): Bia, Pest, Hungary (Lóczy, 1877; Vadász, 1915); Budapest-Gyakorló, Hungary (Kókay et al., 1984; Mihály, 1985); Budapest Rákos, Hungary (Vadász, 1906, 1915; Mihály, 1969); Budatétény (= Tétény), Budapest, Hungary (Laube, 1869a, 1871; Manzoni, 1873; Lóczy, 1877; Vadász, 1915; [NHMW]); Kovácsszénnája (= Kovacéna), Baranya, Hungary (Vadász, 1915); Paptelek, Romania (Vadász, 1915); Sóskut, Hungary (Laube, 1869a, 1871; Gregory, 1891)
- Fore-Carpathian Basin: not recorded [earlier records (Szörényi, 1953; Roman, 1965) are erroneous]
- Transylvanian Basin: Buituri (= Bujtur), Romania (Koch, 1887b; Nemes, 1888b; Mártonfi, 1894; ? Vadász, 1915); Cacovalerii (= Cacova), Romania (Koch, 1887b); Gârbova de Sus (= Felsö-Orbó), Romania (Koch, 1887b); Minişu des Sus (= Felménes), Romania (Lóczy, 1877); Moldoveneşti (= Várfalva), Cluj, Romania (Koch, 1887b); Pietroasa (= Csegez), Romania (Roth von Telegd, 1899; Vadász, 1915)
- Styrian Basin: Slovenia (Majcen et al., 1997)
- Zala, Sáva and Dráva Basins: Derventa and Ugljevik, Bosnia & Herzegovina (Mitrović-Petrović, 1969)

Mediterranean: Burdigalian to Tortonian, ? Messinian*
- Western Mediterranean: Bologna, Italy (Manzoni, 1881); Corsica, France (Roman, 1965); Eastern Algeria (Roman, 1965); Montese, Italy (Mazzetti, 1882a); Isère, France (Gras, 1848, 1852; Gregory, 1891); Santa Ponsa de Ferrerias, Menorca, Spain (Hermite, 1879); Sardinia, Italy (Roman, 1965); Sierra de Las Atalayas, near Alicante, Valenica, Spain (Montenat & Roman. 1970)
- Central Mediterranean: Calabria, Southern Italy (Roman, 1965); Cyrenaica, Libya (Roman, 1965; Rose, 1974a); ? Greensand, Maltese Islands (Gregory, 1891); ? Upper Coralline Limestone, Maltese Islands (Wright, 1864; Laube, 1871; Gregory, 1891; Wigglesworth, 1964; Rose, 1974b; Challis, 1984)
- Eastern Mediterranean: Anatolia, Turkey (Roman, 1965); Cyprus (Manzoni, 1873; Gregory, 1891); Egypt (Roman, 1965); Turkey (Gregory, 1891)
- Rhône Basin: Burdigalian: Secteur es étangs (Fos-sur-Mer, Istres, Saint-Mitre-les-Ramparts), France (Philippe, 1998); Bordure sud des Alpilles (Fontvieille), France (Philippe, 1998); Bassin de Mus-Sommières (environs de Sommières), France (Philippe, 1998); Secteur de Montpellier (Celleneuve, Juvignac), France (Philippe, 1998); Bassin d'Avignon (les Angeles, Barbentane), France (Philippe, 1998); Vallée du Jabron (Châteauneuf-Miravail), France (Philippe, 1998); Bassin de Vairéas-Visan [Baumes-de-Transit; Chamaret, Grignan ?, Montségur-sur-Lauzon, St. Paul-trois-Châteaux (Agassiz & Desor, 1847a; Desor, 1858; Wright, 1864; Laube, 1871; Manzoni, 1873; Gregory, 1891), Saint-Restitut; Solérieux], France (Philippe, 1998); Sillon préalpin [Bassin de Crest: Cerst; Vercors: Bouvante, Oriol-en-Royans, Pont-en-Royans, Saint-Jean-en-Royans (Agassiz & Desor, 1847a; Gras, 1848, 1852; Desor, 1858; Wright, 1864; Laube, 1871; Manzoni, 1873)], France (Philippe, 1998)
- Tortonian: Bassin d'Aix (Rognes), France (Philippe, 1998); Bordure Sud-Luberon (Ansouis, Cadenet, Cucuron, Vaugines), France (Philippe, 1998)

Atlantic Ocean: Early Miocene
- Aquitane Basin: Bordelaise, France (Roman, 1965); Dax, Landes, France (Grateloup, 1836; Agassiz & Desor, 1847a); Faluns bleus de Narosse, near Dax, France (Grateloup, 1836; Desor, 1858; Wright, 1864; Chavanon, 1974); Landes, France (Manzoni, 1873; Gregory, 1891; Roman, 1965); Leognan, Gironde, France (Chavanon, 1974); Martignas, Gironde, France (Chavanon, 1974; Challis, 1980; [NHMW]); Martigues, Landes, France (Agassiz & Desor, 1847a; Desor, 1858; Wright, 1864; Laube, 1871; Manzoni, 1873; Gregory, 1891)
- Caribbean: ? Cuba [Roman, 1965 (Late Oligocene or Early Miocene)]
- Iberian Atlantic coast: Portugal (Roman, 1965)

* concerning the occurrences from the Messinian of the Maltese Islands see above under "Discussion"

Echinolampas manzonii Pomel, 1883

(Figs. 49, 50; Pl. 52, Figs. 1-3)

	1855	*Echinolampas Richardi*, Desmarest. – Wright: 124-125 [misidentified *E. manzonii* according to Gregory (1891) and Challis (1980)]
	1864	*Echinolampas Laurillardi*, Agassiz. – Wright: 480 [misidentified *E. manzonii* according to Gregory (1891) and Challis (1980)]
	1880a	*Echinolampas depressa* Gray. – Manzoni: 186-187, pl. 1, figs. 4-15
	1881	*Echinolampas depressa*, Gray. – Manzoni: 174
.	1882	*Echinolampas angulatus*, Mérian. – de Loriol: 13-16; pl. 2, figs. 1-10; pl. 2, figs. 1-2
non	1882	*Echinolampas angulatus*, Mérian. – de Loriol: 17-18; pl. 2, figs. 11, 11a-b
	1882a	*Echinolampas depressus*, Gray. – Mazzetti: 123
*	1883	*E. Manzonii* (*E. depressa* Manz. non Gray) – Pomel: 62
	1891	*Echinolampas manzoni*, n. sp. – Gregory: 606-607
?	1900	*Echinolampas angulatus* Mérian. – Verri & de Angelis d'Ossat: 259
	1907	*Echinolampas angulatus* Mérian. – Nelli: 263-265.
	1908a	*Echinolampas angulatus* Mérian. – Stefanini: 451-453; no. 10.
	1908b	*Echinolampas angulatus* Mér. – Stefanini: 79-83; pl. 13 [1], figs. 10-13
pp	1913a	*Echinolampas scutiformis* Leske, var. *angulatus* Merian. – Cottreau: 23, 64, 111-112; pl. 11, figs. 7, 7a
non	1913a	*Echinolampas scutiformis* Leske, var. *angulatus* Merian. – Cottreau: 64, 111-112; pl. 12, figs. 8-10
v.	1915	*Echinolampas angulatus* Mér. sp. – Vadász: 217
	1941	*Echinolampas angulatus* Mérian. – Meznerics: 90-91; pl. 2, fig. 6; pl. 3, fig. 1

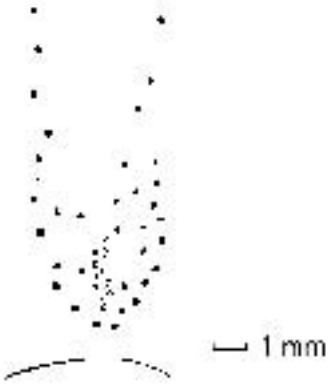

Figure 49: Phyllode I of *Echinolampas manzonii* Pomel, 1883 (Hartl Fm., Eisenstadt, Bgld; Wanzenböck coll. W4).

#	1953	*Echinolampas atrophus podoloicus* n. ssp. – Szörényi: 34-35, 85-86; pl. 6, figs. 4, 4a-b
	1965	[*Echinolampas*] *manzonii* Pomel 1883 – Roman: 289
	1974b	*Echinolampas manzonii* – Rose: 353; fig. 3
	1975	*Echinolampas manzoni* Gregory, non Pomel – Rose: 79, tab. 12
	1980	*Echinolampas manzoni* Gregory – Challis: 156-158; pl. 55, figs. a-c; pl. 56, fig. b
	2000	*Echinolampas* – Piller: 87
?	2001	*Echinolampas manzonii* – Néraudeau et al.: 52; tab. 1
v.	2003	*Echinolampas manzonii* Pomel – Kroh et al.: 92

Type-material:
Echinolampas manzonii Pomel, 1883:
Lectotype: the specimen figured by Manzoni (1880a) on plate 1, figures 14-15 (Gregory, 1891: 607); current whereabouts unknown
Locus typicus: Colline di Bologna, Italy
Stratum typicum: Molassa serpentinosa
Age: Miocene
Remarks: Gregory (1891: 607) designated Manzoni's (1880a) figure (pl. 1, fig. 14) as type. Additionally, he designated a specimen ("Brit. Mus., 24,621") from the British Museum of Natural History as type. This specimen, however, comes from a "nodule seam" of the *Globigerina* Limestone [probably either from the Burdigalian Qammieh conglomerate bed of Rose et al., 1992 (=Qolla I-Bajda conglomerate bed of Challis, 1980; = C_1 phosphate conglomerate of Pedley et al., 1976) or the Langhian Xwieni conglomerate bed of Challis, 1980 and Rose et al., 1992 (= C_2 phosphate conglomerate of Pedley et al., 1976), or from one of the subsidiary phosphate conglomerate horizons within the Upper *Globigerina* Limestone of an unnamed locality in Malta (written comm. Andrew B. Smith, 20.05.2003). Thus that specimen is not available for lectotype selection, as it was not part of Manzoni's original material and Gregory's action is therefore invalid.

Echinolampas atrophus podoloicus Szörényi, 1953:
Holotype: the specimen figured by Szörényi (1953: pl. 6, figs. 4, 4a-b); collection of the University Lwów, Ukraine [not seen]
Locus typicus: Podjarków, near Lwów, Western Ukraine
Biozone: Lower lagenid zone
Age: Early Badenian (Langhian), Middle Miocene (written comm. Anna Wysocka & Andrzej Radwański, 02.04.2004)
Remarks: Szörényi gave No. 1 as the inventory number of the sole specimen of this species. The same number (1), however, is listed under *Fibularia sandalina* and *Scutella paulensis* too.

Material:
Early Badenian (Langhian) – Eisenstadt (Hartl Fm., Hartl hill), Bgld, Austria
NHMW: 9 specimens (NHMW 1859.L.799; 1997z0178/1717a; 2003z0009/0001-7)
MAFI: 1 specimen [MAFI Ech 265 (reference material of Vadász, 1915)]
Wanzenböck coll.: 7 specimens (W1-W6, W18)
Early Badenian (Langhian) – Eisenstadt (Hartl Fm., shooting ground), Bgld, Austria
Wanzenböck coll.: 1 specimen (W19)

Dimensions (in mm)**:**

Inv. No.	TL	TW	TH	Remarks
NHMW 1997z0178/1717a	52.7	47.6	20.3	
NHMW 2003z0009/0001	52.9	48.7	25.5	
NHMW 2002z0009/0002	67.1	59.4	~26	deformed
W1	49.5	44.9	20.4	
W2	58.1	46.2	20.9	deformed
W3	47.5	40.2	23.3	
W4	63.4	52.5	24.2	deformed
W5	57.5	50.9	31.6	

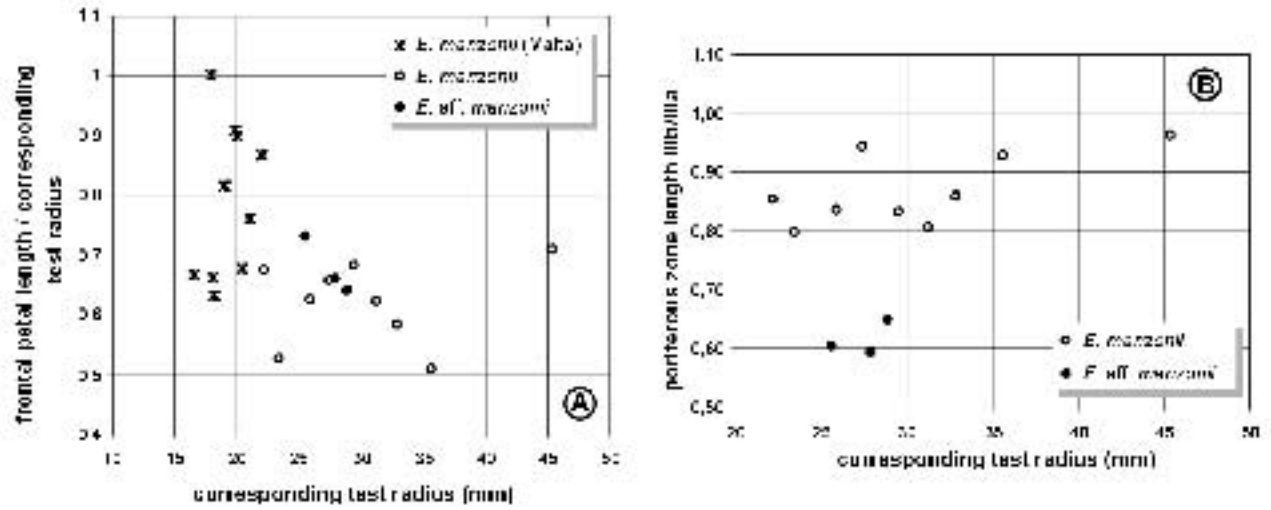

Figure 50: Morphometric comparison between *Echinolampas manzonii* and *E.* aff. *manzonii*: Variation of relative length of the frontal petal (A) and inequality of the poriferous zones within the frontal petal (B). Note the large variability of frontal petal length, especially when specimens from the Maltese Islands are considered (data provided by courtesy of M. Gatt, Rabat, Malta). The inequality of the poriferous zones is much more pronounced in *E.* aff. *manzonii* (also in the other petals, not shown here).

Description:
Size and shape: The test is of medium size, antero-posteriorly elongated and distinctly rostrate. The anterior margin is rounded, the posterior margin bluntly pointed. The maximum width lies posterior of the apical disc, about 60 % of TL from the anterior margin. In profile the test is domed, the maximum height coinciding with the position of the apical disc. The ambitus is rounded and tumid. The oral surface is strongly depressed around the peristome. The test width ranges from 79.5 to 96.1 % TL (mean = 87.3 %), the test height from 35.9 to 55 % TL (mean = 43.5 %).
Apical disc: The apical disc lies slightly anterior of the centre, about 40 to 45 % TL from the anterior margin. The apical disc is monobasal with 4 large, circular gonopores. The madreporite is pentagonal and crowded with numerous small madreporic pores. The gonopores lie at the apices of the madreporite. The ocular plates are small, bearing a small, circular ocular pore each.
Ambulacra: The ambulacra are petaloid and relatively narrow. The ambulacral pores within the petals are elongate isopores, outside the petals they are small, slit-shaped unipores. The frontal petal is the shortest and extends about 50-70 % of the corresponding test radius. The anterior paired petals extend about 65-75 % of the corresponding test radius. The posterior paired petals are longest (referring to the absolute values) and extend about 60-70 % of the corresponding test radius. The poriferous zones of all petals are strongly unequal. In the frontal petal this is not very pronounced, poriferous zone IIIb being about 80-96 % of IIIa. In the anterior and posterior paired petals, this is strongly expressed, IIb/IVa are about 47 to 67% of IIa/IVb (anterior paired petals) and Ia/Vb are 47 to 69% of Ib/Va (posterior paired petals). Adorally the ambulacra form distinct phyllodes. These consist of large rounded unipores. The shape of the phyllodes is shown in Fig. 49.
Interambulacra: The interambulacra are slightly inflated between the petals. On the oral surface the interambulacra are slightly inflated and form weak bourrelets between the phyllodes. A weakly developed, granular "naked zone" is present along the central suture adorally in interambulacrum 5.
Peristome: The peristome lies slightly anterior of the centre, about 44 % TL from the anterior margin. It lies in a depression and is oval (transversely elongated) to slightly subpentagonal. It measures 9 x 5 mm in a 52 mm TL specimen.
Periproct: The periproct is situated inframarginally in interambulacrum 5. It is large (11 x 6 mm long in a 52 mm TL specimen), distinctly rostrate and has an oval, transversely elongated shape.

Differential diagnosis (see Figs. 43, 45-48, 50)**:**
This species differs from *E. richardi* Desmarest in Brongniart, 1829 [= *E. laurillardi* Agassiz & Desor (obj. syn.)] by its greater inequality of the poriferous zones of the paired petals (Gregory, 1891: 607), especially in the posterior paired petals, the more elongated shape and stronger developed rostrum.

E. manzonii is very similar to *E. scutiformis* (Leske, 1778) and the species have been synonymised by some authors (e.g. Stefanini, 1908a: 451-453; Cottreau, 1913a: 111-112), whereas others considered these two species as clearly separated (e.g. Gregory, 1891: 607; Challis, 1980: 158). Consequently there is considerable confusion and it is often unclear which references belong into the synonymy of these species. Gregory (1891: 607) stated that the same characters that distinguish *E. manzonii* from *E. laurillardi*, distinguishes it also from *E. scutiformis*. Comparing the present material from Austria to French specimens of *E. scutiformis* from St. Restitute (Drôme) and Martigues in the collection of the NHMW (1849.V.43, 1852.II.1519 and 1858.XL.452) and to the detailed description and illustrations by Philippe (1998: 93-98; text-figs. 2a-f, 3a-f; pl. 18, figs. 1-9) it is apparent that the two species are different. Based on this material, the following differences can be observed: The petals are distinctly longer in *E. scutiformis* (extending between 72-78 % of the corresponding test radius in the frontal petal, 70-78 % in the anterior paired petals and 64-80 % in the posterior paired petals); the inequality of the poriferous zones is less pronounced in *E. scutiformis* (the anterior poriferous zone extends usually 69-74 % of the posterior poriferous zone in the anterior paired petals and the posterior poriferous zone extends about 74-76 % of the anterior poriferous zone in the posterior paired petals); the periproct lies fully on the oral side in *E. scutiformis*, whereas it is distinctly inframarginal in *E. manzonii*. Furthermore, the oral interambulacra are less swollen between the ambulacra in *E. scutiformis* and the test is less rostrate.

E. aff. *manzonii* differs from *E. manzonii* by its even more asymmetric frontal petal, where poriferous zone IIIb is only 60 to 65% of IIIa, whereas in *E. manzonii* IIIb is 80-96 % of IIIa. Additionally, the posterior poriferous zones of the posterior paired petals are usually shorter in *E.* aff. *manzonii* than in *E. manzonii*.

Discussion:
Contrary to the statement of Gregory (1891: 606, footnote) and later usage by Rose (1975) and Challis (1980) *E. manzonii* Pomel, 1883 is a valid name according to the ICZN rules (Article 12.2.1).

This species is characterised by strong inequality of the poriferous zones in the petals, its oval, elongated outline and the distinct rostrum.

According to Philippe (1998: 98) *E. angulata* Mérian in Agassiz & Desor, 1847 is a junior synonym of *E. scutiformis* (Leske, 1778), since the specimens corresponding to the diagnosis of Mérian are subadult specimens of *E. scutiformis*. The specimens from Camerino (Italy) erroneously attributed to *E. angulata* by de Loriol (1882: 13-18), belong to *E. manzonii*, on account of the structure of their petals. However, since de Loriol referred also to the type specimens of *E. angulata* Mérian this led to some confusion. Therefore, it is very difficult to judge whether or not a record of either species belongs into the synonymy of this species or the very similar *E. scutiformis*, unless accompanied by a description and illustrations (the synonymy list is restricted to such records where a decision was possible). Hence, the distribution data given below may not represent the total temporal and spatial distribution.

The Austrian material was compared with material from the C1 and C2 phosphate conglomerate horizons in the *Globigerina* Limestone of Malta (Early Burdigalian and Langhian respectively). The Maltese material is very similar to the Austria specimens, but usually smaller. Due to the fact that the relative length of the petals decreased during growth, the petals of the smaller Maltese specimens usually extend farther to the margin. The Maltese specimens also show an even larger variation in test height (biometric data of Maltese specimens provided by Michael Gatt, Mdina, Malta).

E. manzonii was placed into the genus *Miolampas* by Pomel (1883: 62) together with the extant *E. depressa* Gray, 1851. This genus was subsequently placed into the synonymy of *Echinolampas* by Kier (1962: 112). While the author does not propose to resurrect the genus *Miolampas*, *E. manzonii* should be referred to this genus in case it is re-established in future. *Miolampas* Pomel, 1883 [type-species: *E. depressa* Gray, 1851, by subsequent designation (Lambert, 1918: 44)] and the similar genus *Planilampas* Mortensen, 1948a [type-species: *E. sternopetala* Agassiz & Clark, 1907, by original designation; Mortensen (1948a) included also a new species, *P. keiensis*, in this genus] differ from typical *Echinolampas* by their strong inequality of the poriferous zones (especially in ambulacrum III) and the different nature of the aboral tuberculation (tubercles very closely spaced with areoles nearly touching in *Echinolampas*, *vs*. widely spaced tubercles with an average distance of *c*. one times the primary spine tubercle diameter in species formerly attributed to *Miolampas* or *Planilampas*). Kier (1962) does not give any specific reasons for

synonymising these two genera with *Echinolampas* besides the general remark that "... all these sections and subgenera are based on characters too variable to be of generic distinction." (KIER, 1962: 107).

The subspecies *E. atrophus podolicus* established for a single specimen from the Early Badenian of the Western Ukraine by SZÖRÉNYI (1953) is placed into the synonymy of *E. manzonii*. Her description and illustrations provide no features which would be suited to confidently separate her subspecies from *E. manzonii*. In *E. atropus* LAMBERT, 1906 from the Middle Miocene of Menora (Balearic Islands) the poriferous zone Ia, IIb, IVa, and Vb are almost completely reduced, with only a single pore pair developed adapically according to LAMBERT (1906a: 94). Thus the latter is well differentiated from both *E. manzonii* and SZÖRÉNYI's subspecies.

Little is known of the ecology of similar extant species (*E. depressa*, *E. keiensis*, *E. sternopetala*). According to SERAFY (1979) and MOOI (1990b: 696) *E. depressa* lives in relatively coarse carbonate sand composed of fragments of calcareous algae, based on substrate collected together with the specimens and gut content. MOOI (1990b: 696) observed that the gut content of museum specimens supports MORTENSEN's (1948a) suggestion that *Echinolampas* feeds mainly on foraminifers. While *E. depressa* was reported also from shallower habitats (30 to 310 m, SERAFY, 1979) *E. keiensis* and *E. sternopetala* are known up till now only from deeper settings [245 to 400 m (MORTENSEN, 1948a) and 100 to 500 m respectively (SHIGEI, 1986)].

Occurrence:

Austria: Early Badenian (Langhian)

Eisenstadt-Sopron Basin: Eisenstadt (Hartl Fm., Hartl hill), Bgld (VADÁSZ, 1915; KROH et al. 2003; [NHMW]); Eisenstadt (Hartl Fm., Johannesgrotte), Bgld (PILLER, 2000)

Paratethys (non-Austrian occurrences): Early Badenian (Langhian)

Great Hungarian Basin (Pannonian Basin): Kemence, Pest, Hungary (MEZNERICS, 1941); Márkháza, Nógrád, Hungary (MEZNERICS, 1941); Sámsonháza, Hungary (MEZNERICS, 1941)

Fore-Carpathian Basin: Pod'yarkov (= Podjarków), near Lwów, western Ukraine (SZÖRÉNYI, 1953)

Mediterranean: Burdigalian to Langhian; records from the Messinian and Early Pliocene (NÉRAUDEAU et al. 2001, based on ROMAN & SOUDET, 1990) need to be substantiated

Western Mediterranean: Italy: Campobono, region of Camerino (pp DE LORIOL, 1882); ? Città di Castello (VERRI & DE ANGELIS D'OSSAT, 1900); ? Dogana (VERRI & DE ANGELIS D'OSSAT, 1900; NELLI, 1907); La Vignaccia, near Piedebovigliana, region of Camerino (pp DE LORIOL, 1882); ? Monte Cedrone (VERRI & DE ANGELIS D'OSSAT, 1900; NELLI, 1907); ? Monte S. Maria Tiberina (VERRI & DE ANGELIS D'OSSAT, 1900); St-Ilario region of Camerino (pp DE LORIOL, 1882)

Central Mediterranean: Maltese Islands: Qammieh conglomerate bed (= Qolla I-Bajda conglomerate bed, = C_1 phosphate conglomerate) and Xwieni conglomerate bed (= C_2 phosphate conglomerate) (WRIGHT, 1864; GREGORY, 1891; pp STEFANINI, 1908a; pp STEFANINI, 1908b; pp COTTREAU, 1913a; ROMAN, 1965; ROSE, 1974b, 1975; CHALLIS, 1980) records from the Blue Clay (WRIGHT, 1864) and Greensand (WRIGHT, 1855) are dubious according to CHALLIS (1980) and need to be confirmed; Italy: Maserna, Emilia (pp STEFANINI, 1908b); Molassa di Serra di Guidoni, Bologna (MANZONI, 1881; GREGORY, 1891; pp STEFANINI, 1908b); Montese (Molassa serpentinosa), Colline Bologne (MANZONI, 1880a; MAZZETTI, 1882a; pp STEFANINI, 1908b; ROMAN, 1965); Paullo, Emilia (pp STEFANINI, 1908b); Salto, Emilia (pp STEFANINI, 1908b); San Marino (MANZONI, 1880a; NELLI, 1907); S. Maria Vigliana (Molassa serpentinosa) (MANZONI, 1880a; pp STEFANINI, 1908b; NELLI, 1907)

Echinolampas aff. *manzonii* POMEL, 1883

(Fig. 51; Pl. 52, Fig. 4-6)

Material:

Early Badenian (Langhian) – Stotzing (sandpit Mayer), Bgld, Austria

WANZENBÖCK coll.: 2 specimens (W7, W17)

? Early Badenian (Langhian) – Eisenstadt (Hartl Fm., Hartl hill), Bgld, Austria

NHMW: 1 specimen (NHMW 1997z0178/1717b)

Dimensions (in mm)**:**

Inv. No.	TL	TW	TH
NHMW 1997z0178/1717b	52.7	47.5	19.7
W7	51.4	47.8	22.8
W17	55.9	~55	~20

Description:

Size and shape: The test is of medium size, with oval, anteroposteriorly elongated outline. The anterior margin is rounded, the posterior margin bluntly pointed. The maximum width lies subcentrally. In profile the test is arched, the maximum height coinciding with the position of the apical disc. The ambitus is rounded and tumid, albeit less tumid than in *E. manzonii*. The oral surface is depressed around the peristome.

Apical disc: The apical disc lies slightly anterior of the centre, about 45 % TL from the anterior margin. The apical disc is monobasal with 4 large, circular gonopores. The madreporite is pentagonal and crowded with numerous small madreporic pores. The gonopores lie at the apices of the madreporite. The ocular plates are small, bearing a small, circular ocular pore each.

Ambulacra: The ambulacra are petaloid and relatively narrow. The ambulacral pores within the petals are elongate isopores, outside the petals they are small, slit-shaped unipores. The frontal petal is the shortest and the posterior paired petals longest. They extend about 65-70 % of the corresponding test radius. The poriferous zones of all petals are strongly unequal. In the frontal petal IIIb is about 60 to 65 % of IIIa. In the anterior and posterior paired petals, this is even more strongly expressed, IIb/IVa are about 42 to 54% of IIa/IVb (anterior paired petals) and Ia/Vb are 35 to 45% of Ib/Va (posterior paired petals). Adorally the ambulacra form distinct phyllodes consisting of large rounded unipores.

Interambulacra: The interambulacra are slightly inflated between the petals. The bourrelets between the phyllodes are very weakly expressed.

Peristome: The peristome lies slightly anterior of the centre, about 45 % TL from the anterior margin. It lies in a shallow depression and has an oval, transversely elongated shape.

Periproct: The periproct lies inframarginally, very close to the posterior margin. In specimen W17, however, it lies fully on the oral side, but that may in part be due to the distortion of the test by sedimentary compaction. It has an oval, transversely elongated shape and it is moderately rostrate.

Differential diagnosis:

For the difference between this species and *E. manzonii* see above under that species. From the other *Echinolampas* species discussed in this work this species differs by the pronounced inequality of its poriferous zones.

E. scutiformis (LESKE, 1778) differs by its higher, slightly conical profile and distinctly lesser inequality of its poriferous zones.

Discussion:

Only two specimens from a private collection and a single specimen from the Hartl Fm., Eisenstadt tentatively referred to