Reported occurrence: Late Badenian (Early Serravallian) of Minişu des Sus (= Felménes), Arad, Romania (Lóczy, 1877); Early Badenian (Langhian) of Mykolaiv (= Mikołajów) and Radziechów (= Radziejów), S of Lwów, western Ukraine (Szörényi, 1953); Badenian (Langhian-Early Serravallian) of the Vienna Basin (Lóczy, 1877)

Remarks: According to Vadász (1915: 108) the only known specimen of this species is lost. Thus the illustrations by Lóczy (1877) are the only information available (the description is very brief and lacks details). Unfortunately the Lóczy's drawing fits with a large number of juvenile echinaceans and the present author is neither able to associate *P. loczyi* with any other species, nor to confirm the its distinctiveness.

***Schizechinus delphinus* (Lambert, 1906)**

1887b *Psammechinus Duciei*, Wright. – Koch: 261
1915 *Psammechinus delphinus* Defr. sp. – Vadász: 110 [based on Koch's specimen]

Reported occurrence: Late Badenian (Early Serravallian) of Gârbova de Sus (= Gîrbova de Sus, = Felsö-Orbó), Romania (Koch, 1887b; Vadász, 1915)

Remarks: This species is usually attributed to Defrance, but was never published and clearly is a collection name and thus not valid according to the ICZN. It has recently been re-described by Philippe (1998) under the name *Psammechinus delphinus* (Defrance), but clearly belongs to the genus *Schizechinus* based on its tuberculation pattern (numerous subequal tubercles on the ambital interambulacra, arrangement of the small secondary tubercles).

Koch's records is based on a single worn fragment, which also forms the base of Vadász's record. At present it is unclear to whether the determination as *S. duciei* or as *S. delphinus* is correct, or whether it belongs to the contemporaneous *S. hungaricus*. The situation is complicated by the lack of a throughout revision of the genus *Schizechinus* involving all Mediterranean and Paratethyan species.

***Parasalenia fontannesi* (Cotteau, 1888)**

? 1977 *Parasalenia fontannesi* Cotteau, 1888 – Mączyńska: 195-196; pl. 3, figs. 1-5
non 1987 *Parasalenia fontannesi* Cotteau, 1888 – Mączyńska: 146, 148; pl. 2, fig.2 [misidentified diadematoid ambulacral plate]
? 1993 *Parasalenia fontannesi* Cotteau, 1888 – Mączyńska: 109; pl. 3, figs.1-3; pl. 6, figs. 1d-1f
? 1996 *Parasalenia fontannesi* Cotteau, 1888 – Mączyńska: 41; pl. 1, figs.8a-b, 9a-b

Reported occurrence: Badenian: Korytnica Clays, Poland (Mączyńska, 1977); Busko, Kików, Skowronno, Szczaworyż, and Żerniki, Central Poland (Mączyńska, 1993); Niechobrz near Rzeszów, Southern Poland (Mączyńska, 1996)

Remarks: The attribution of the material figured by Mączyńska (1977, 1993, 1996) to *Parasalenia fontannesi* is very doubtful. As no description is given in any of the cited papers, the records can only be judged by the illustration. The only features that the illustrated specimens have in common are the lateral deformation (clearly post-mortem) and their being juvenile echinaceans. What little can be made out of the tuberculation does not look like *Parasalenia* at all. *P. fontannesi* was recently re-described and very well illustrated by Philippe (1998). His figures clearly show that *P. fontannesi*, as extant *Parasalenia* species, is characterised by a large, imperforate primary tubercles with a huge mamelon on each plate and few, tiny secondary tubercles (see Philippe, 1998: pl. 6, figs. 7b-c). The Polish material doesn't even come close and has to be considered as misidentified. Besides, apart from the records of Mączyńska P. fontannesi was up till now only undoubtedly recorded from Aquitanian strata, while the Polish specimens are of Badenian (Langhian-Early Serravallian) age.

The ambulacral plate figured by Mączyńska (1987: pl. 2, fig. 2) does definitely not belong to *Parasalenia*, yet not even to an echinacean. The perforated, strongly crenulate primary tubercle in combination with the shape of the plate and the ambulacral pores is characteristic of a diadematoid.

P. fontannesi thus has to be considered absent from the Central Paratethys, until more convincing specimens are described.

***Parasalenia* sp.**

? 1993 *Parasalenia* sp. – Mączyńska: 109; pl. 3, figs.4-5
? 2004 *Parasalenia* sp. – Radwański & Wysocka: 385

Reported occurrence: Pińczów, Central Poland (Mączyńska, 1993); Świniary, Poland (Radwański & Wysocka, 2004)

Remarks: The ambulacral plate figured by Mączyńska (1993: pl. 3, fig. 5) again seems to belong to a diadematoid (tough not so clear as in the pervious case due to the poor preservation; see above under *P. fontannesi*). The worn corona figured by Mączyńska (1993: pl. 3, fig. 4a-b), could be a juvenile *Schizechinus* or a *Psammechinus*, but is certainly no *Parasalenia* (based on the tuberculation of the ambital interambulacra which never shows multiple subequal tubercles/enlarged secondary tubercles in *Parasalenia*).

"*Cyphosoma*" sp.

? 1893 *Cyphosoma*. – Toula: 289
? 1974 *Cyphosoma* Kalabis: 315

Reported occurrence: Kralice nad Oslavou (= Kralitz), Czech Republic (Toula, 1893)

Remarks: *Cyphsoma* is a junior synonym of *Phymosoma*, a genus ranging from the Late Jurassic to the Eocene. Toula's record is most probably based on a misidentified Miocene echinacean (e.g. *Schizechinus*).

***Salenia* ? sp.**

1893 Ocellarplättchen des Scheitelschildes (*Salenia* ?). – Toula: 288

Reported occurrence: Kralice nad Oslavou (= Kralitz), Czech Republic (Toula, 1893)

Remarks: *Salenia is a* Cretaceous genus, Toula's record probably refers to misidentified genital plates of cidaroids.

Cohort Irregularia Latreille, 1825
Order Echinoneoida Jensen, 1982
Suborder Echinoneina Clark, 1925
Family Echinoneidae Agassiz & Desor, 1847
Genus *Echinoneus* Leske, 1778

Type-species: *Echinoneus cyclostomus* Leske, 1778; by subsequent designation (Clark, 1917: 101).
Diagnosis: Test ovoid; ambulacra in groups of 3; pore pairs uniserially adapically, in groups of 3 adorally. Poriferous zones slightly sunken. Apical disc tetrabasal. Peristome oblique, irregular. Buccal membrane with small plates. Periproct infra-

marginal. Tubercles imperforate or perforate and noncrenulate (modified from Wagner & Durham, 1966; Donovan, 1993).
Distribution: Oligocene to Recent – circumtropical (from Wagner & Durham, 1966b and Donovan, 1993)

Echinoneus aff. *abnormalis* de Loriol, 1883

(Fig. 23; Pl. 48, Figs. 4-5)

v. 2004a *Echinoneus* – Kroh: 229
(Late Badenian: Müllendorf, Kreide AG quarry, Bgld)

Material:
Late Badenian (Early Serravallian) – Müllendorf (Mühlendorfer Kreide AG quarry), Bgld, Austria
NHMW: 1 specimen (NHMW 2002z0172/0001)
Wanzenböck coll.: 2 specimens (W23, W24)
Temel coll.: 1 specimen (casts of this specimen are housed at the NHMW 2002z0172/0002)

Dimensions (in mm)**:**

Inv. No.	TL	TW	TH
NHMW 2002z0172/0001	41.8	32.8	23.3
Temel coll.	21.0	15.7	9.9
Wanzenböck coll. W23	7.7	5.7	3.5
Wanzenböck coll. W24	18.9	15.0	9.3

Description:
Size and shape: Test ovoid, of small to medium size, ranging from 21 to 42 mm test length in the studied specimens. The maximum width lies centrally in large specimens. In small specimens it lies posteriorly, coinciding with line 1a-4b. Maximum height lies subcentrally. Test width ranging from 74.8 to 78.5 % TL in the studied material and test height from 47.1 to 55.7 %TL.
Apical disc: Apical disc situated slightly anteriorly, about 45 % TL away from the anterior margin. It is holectypoid with genital plate 5 still present (not reduced as in the tetrabasal apical disc of *E. abnormalis* or *E. cyclostomus*), similar to the condition in *Holectypus* (see Fig. 22.D and compare Melville & Durham, 1966: U228, fig. 170.6). The madreporite (G2) is strongly enlarged and bears numerous small madreporic pores. The other genital plates are rather small (see Fig. 22.C). Four small, circular genital pores are present.
Ambulacra: The ambulacra are nonpetaloid with small, closely spaced, slightly sunken, partitioned isopores adapically. Adorally the pores are less closely spaced, strongly oblique and arranged in weak arches of three (giving the poriferous zone a slightly undulating appearance). Around the peristome the pores are indistinct. The poriferous zones are slightly depressed and very narrow. The interporiferous zones are distinctly inflated adapically and are up to ten times as wide as a single poriferous zone. The tuberculation of the interporiferous zones is similar to that of the interambulacra.
Interambulacra: The interambulacra are densely covered by small perforate, noncrenulate primary tubercles (Fig. 23). Miliary and secondary tubercles are found on the ridges between the slightly sunken areoles of the primary tubercles. They are imperforate and noncrenulate. On the oral side the primary tubercles are up to twice as large as on the aboral surface.
Peristome: The peristome lies centrally on the oral side. It is irregularly oval to triangular and strongly oblique, elongated along the 2-V axis. It shows allometric growth and measures 4.5 x 2.4 mm in the 21.0 mm TL specimen and 6.4 x 4.5 mm in the 41.8 mm TL specimen.
Periproct: The periproct lies inframarginally in interambulacrum 5, just behind the peristome. It is teardrop-shaped and elongated antero-posteriorly. It is larger than the peristome, measuring 5.2 x 3.5 mm in the 21.0 mm TL specimen and ~9 x ~5.5 mm in the 41.8 mm TL specimen.

Discussion:
The studied specimens are closely similar to the extant species *E. abnormalis* (see de Loriol, 1883: 41; pl. 5, fig. 2, 2a-d; Mortensen, 1948a: 80-81). They differ, however, by the holectypoid nature of the apical disc and more numerous secondary and/or glassy tubercles (difficult to distinguish in the fossil specimens). The scarcity and moderate preservation of the material precludes both statistical and detailed morphological comparisons (e.g. plate patterns) of extant and fossil material.

Based on the perforated primary tubercles Lambert & Thiéry (1921: 331) established the genus *Koehleraster* for this species. Mortensen (1948a: 74, 81), however, was uncertain if this feature alone justified the generic distinction and tentatively placed the genus into the synonymy of *Echinoneus*.

E. abnormalis differs from *E. cyclostomus* Leske, 1778 by the presence of perforate tubercles instead of imperforate and by its less well developed glassy tubercles (Clark, 1925: 176; Mortensen, 1948a: 80-81).

This is the first record of the genus *Echinoneus* from the Miocene of the Central Paratethys. It is also one of the first fossil echinoneids with perforate tubercles. Those fossil species for which data on the tubercles are available [e.g. *E. melitensis*

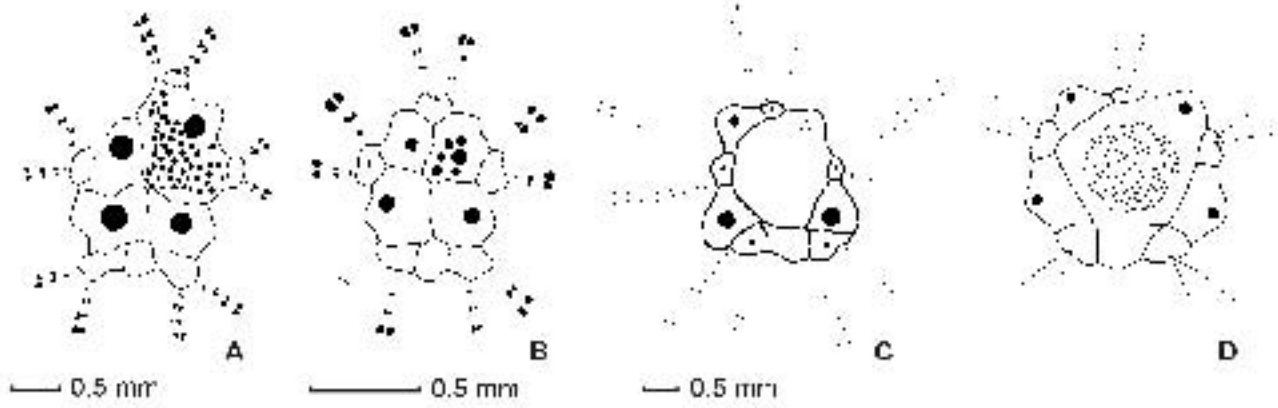

Figure 22: Comparison of the apical discs of *Echinoneus cyclostomus* Leske, 1778 (A: recent, Mauritius, NHMW coll.; drawn from SEM photograph), *Echinoneus abnormalis* de Loriol, 1883 (B: recent, Aldabra, Indian Ocean, BMNH-Zool. 1972.1.12.14; drawn from SEM photograph), *Echinoneus* aff. *abnormalis* de Loriol, 1883 [C: Late Badenian (Early Serravallian), Müllendorf (Kreide AG quarry), Bgld; NHMW 2002z0172/0001; camera lucida drawing], and *Holectypus depressus* (Leske, 1778) (D: redrawn from Wagner & Durham, 1966: U441, fig. 329/1c; scale unknown). Poorly visible sutures and pores stippled.

Figure 23: *Echinoneus* aff. *abnormalis* de Loriol, 1883: white arrows indicate perforate primary tubercles [Müllendorf (Kreide AG quarry), Bgld; NHMW 2002z0172/0001].

(Wright, 1864), see Challis (1980: 102-105) and Philippe (1998: 84-86); *E. thomasi* Peron & Gauthier in Cotteau et al., 1891, *E. artini* Gauthier in Fourtau, 1900 see Brighton (1929: 89)] have imperforate tubercles and were associated with *E. cyclostomus* recently (Challis, 1980; Philippe, 1998; Néraudeau et al., 1999; Néraudeau et al., 2001). Most fossil records of *Echinoneus* are, however, based on poorly preserved material and differential diagnoses provided by the authors are usually insufficient. Lambert (1928: 21) stated that: "La distinction des diverses espèces d'*Echinoneus* est souvent assez délicate, mais ce n'est pas une raison pour confondre avec l'espèce vivante, *E. cyclostomus* Leske, les diverses espèces du Miocène et l'Oligocène des Antilles." Mortensen (1948a) in contrast suggested that most fossil species might fall into the synonymy of *E. cyclostomus* because none of the "diagnostic" features allowed a differentiation without knowing the provenience of the material. Indeed material form the Oligocene to Pleistocene of the Caribbean studied by Donovan recently is reported to be morphologically indistinguishable from extant *E. cyclostomus* (Donovan, 1993: 382; Donovan & Veale, 1996: 633-635; Dixon & Donovan, 1998: 104; Donovan, 2001: 183, Simpson, 2001: 34).

Ecology:

Nearly nothing is known on the ecology of extant *E. abnormalis.* Most authors (e.g. Mortensen, 1948a) assumed a similar habitat as for *E. cyclostomus*. Ecological data on *E. cyclostomus* can be found in Mortensen (1948a: 75-80), Fontaine (1953), Kier & Grant (1965: 11-12, 26), Rose (1978: 299-306) and Hendler et al. (1995: 227-228). Generally, *E. cyclostomus* seems to be a cryptic, if not always really burrowing species. It is found in the shallow sublittoral of the tropical region (circumtropical) except at the west coasts of America, Africa and Australia. Usually it is associated with rocks or reef debris of coarse sand to gravel size and is often found attached to the underside of coral slabs. It can also be associated with coralline algal debris (Mortensen, 1948a). According to Hendler et al. (1995: 227-228) *E. cyclostomus* is common on reef flats and in other reef habitats. Fontaine (1953) and Rose (1978: 300) suggested that this species indicates the proximity of reefs and might, therefore, be useful in palaeoecological reconstruction. Sloan et al. (1979: 119) reported *E. abnormalis* from sand under coral heads and boulders in the shallow sublittoral of the lagoon of the Aldabra Atoll.

Both in extant environments (Kier & Grant, 1965: 12) and the fossil record (Zammit-Maempel, 1979: 9; Challis, 1980: 325; Boggild & Rose, 1984: fig. 2; Donovan & Veale, 1996: 632-635) the co-occurrence of *Echinoneus* with *Brissus* in biodetritic sediments close to reef-like structures was recorded. In the fossil Austrian occurrence (Müllendorf, Bgld) *Echinoneus* is also associated with a *Brissus* species and found within a bioclastic coralline algal wackestone.

Occurrence:

Austria: Late Badenian (Early Serravallian)
Vienna Basin: Müllendorf (Mühlendorfer Kreide AG quarry), Bgld (Kroh, 2004a; [NHMW])

Paratethys (non-Austrian occurrences): not recorded

Mediterranean: not recorded

Superorder Microstomata Smith, 1984
Series Neognathostomata Smith, 1981
Order Clypeasteroida Agassiz, 1872
Suborder Clypeasterina Agassiz, 1872
Family Clypeasteridae Agassiz, 1835
Genus *Clypeaster* Lamarck, 1801

Type species: *Echinus rosaceus* Linné, 1758, p. 665; by subsequent designation (des Moulins, 1835: 183).
Diagnosis: Medium-sized to large, test flattened to highly campanulate, margin rounded to flattened and inflated; peristome usually in deep infundibulum; oral surface flat to concave; petals variable, closed and rounded to open or sublyrate, with outer pores elongate, inner ones rounded, commonly connected by grooves; periproct usually inframarginal, rarely marginal, situated between 3rd and 4th, or 4th and 5th pair of coronal plates; buccal membrane naked, with imbedded irregular spicules; internal supports variable in abundance, consisting of thin laminae and pillars; wall of test sometimes double, separated by pillars (Durham, 1966).
Distribution: Late Eocene to Recent – circumtropical (Durham, 1966; Ali, 1983)
Remarks: *Clypeaster* is possibly the most diverse echinoid genus in the Cenozoic. In total more than 480 nominal species and/or subspecies have been established (Lambert & Thiéry, 1909-1925; Kier & Lawson, 1978). Several attempts were made to divide *Clypeaster* in subgenera or sections, resulting in 38 genus/sub-genus rank taxa. Variation in external test morphology and shape of the petals is very great, but no systematic basis for subgeneric grouping can be recognised according to Durham (1955: 118; 1966: U243). Thus these taxa were considered synonyms of *Clypeaster* by him.

The (palaeo-)biogeography of the genus *Clypeaster* was studied by Ali (1983), who postulated a Middle Eocene origin in south-western Europe, based on the report of two species from the Late Lutetian of Catalonia, Spain by Via & Padreny (1970). While being largely confined to the circum-Mediterranean Region in the Late Eocene, the Oligocene was a time of dispersal for this group and the genus *Clypeaster* reached Central America in the West and the Indo-Malayan region in the East. In the Miocene *Clypeaster* had its largest geographical distribution, finally reaching Australia in the Middle Miocene (McNamara & Kendrick, 1994). During the late Pliocene to Pleistocene the diversity of the genus *Clypeaster* was greatly reduced and although *Clypeaster* managed to gain a foothold again in the Mediterranean after the Messinian Salinity Crisis (Néraudeau et al., 1999; Rose & Wood, 1999), it vanished from this region during the Late Pliocene (Néraudeau et al., 2001). Today *Clypeaster* is found in the shallow sublittoral of the tropics, all around the world (for details see Mortensen, 1948b). In some regions the genus still reaches high diversities, as e.g. in the Caribbean, where ten (possibly eleven) species are reported, several of them co-occurring at single localities (Hopkins, 1988). The co-occurrence of several different clypeasteroid species at single localities may be explained by resource parti-

tioning (*Clypeaster rosaceous*, *C. subdepressus*, *Encope michelini* and *Leodia sexiesperforata* all facilitate different size fractions of the sediment; see TELFORD & MOOI, 1986, and TELFORD et al. 1987). Additionally, offset in spawning time might be a mechanism leading to reproductive isolation, but needs to be demonstrated for the Caribbean *Clypeaster* species. The distribution of the Caribbean *Clypeaster* species is at least partially controlled by temperature, only two species range beyond 30° N latitude (HOPKINS, 1988: 337, fig. 1). The biogeography of the extant clypeasteroids was discussed by GHIOLD & HOFFMAN (1984, 1985, 1986).

As already pointed out by numerous authors (e.g. KALABIS, 1949: 81) many nominally described species of *Clypeaster* are in fact junior synonyms, owing to the practice of describing new species based on single, often poorly preserved specimens (e.g. VADÁSZ, 1915; LOVISATO, 1909, 1910, 1911a, b, 1912a, b, 1913, 1914a, b), and incomplete knowledge of the literature and stratigraphy. The genus *Clypeaster* with its more than 480 nominal species (most of which were described from the Miocene of the Mediterranean region) is thus one of the best examples of taxonomic over-completeness.

One of the major problems in the systematics of this genus is the exceptional high intraspecific variability displayed by (at least some) *Clypeaster* species. Profile shape, outline, thickness of the test, tubercle densities, thickness of the margin, etc. can vary considerably within a single species, especially between populations from different habitats/sedimentary environments. Even the width and depth of the infundibulum and the (relative) length of the petals show a distinct degree of intraspecific variation. Yet, it is these features which were and are primarily used to distinguish the various species (also in the systematics of extant forms) in the genus *Clypeaster*. Attempts to employ the internal support system for classificatory purposes (CHECCHIA-RISPOLI, 1920, 1923; KALABIS 1935, 1937c; ROMAN, 1952) did until now not result in features that can be confidently employed for *Clypeaster* systematics. Although the internal structures can in some cases be revealed by x-ray images evaluation of the differences is very difficult. In the majority of the specimens, however, x-ray images are extremely difficult to prepare (due to low contrast between skeletal material and sedimentary infilling, differing test thickness,...) and thus variation of the internal support system within individual species is poorly known. While it might be possible to employ additional features (e.g. pedicellariae, …) for the definition of extant species, this is impossible for fossil forms. Therefore special care has to be taken when working with fossil species of this genus and apart from morphology temporal and spatial distribution of the taxa should also be taken into account.

Another potential problem in *Clypeaster* systematics is the ability of echinoids to form hybrids, even across genus boundaries (MORTENSEN, 1912; ONODA, 1943). Although not demonstrated to occur in the genus *Clypeaster* until now, hybridisation could be one possible explanation for the occurrence of intermediate forms between otherwise well distinguished species.

A further problem in *Clypeaster* systematics is our often inadequate knowledge of the type material of many species, its whereabouts, provenance and morphology. As stated above in the introduction, the author re-examined the material of species recorded from the Austrian Neogene, whenever possible. Special emphasis was also placed on the search for the material of the Naturhistorisches Museum Wien examined by MICHELIN during 1856 to 1857. This material comprises a large part of the reference specimens of MICHELIN's *Clypeaster* monograph. About 80 percent of the material could be located in the collections of the Naturhistorisches Museum Wien, including several types and figured specimens.

The synonymy lists include primarily Austrian and other Paratethyal references because these could either be evaluated by the original material or topotypic specimens. It is very difficult to evaluate the extremely high number of *Clypeaster* records in the geological and palaeontological literature of the Mediterranean region without seeing the material the records refer to. Similarly differential diagnoses are restricted to co-occurring taxa in the Paratethys and a few well-known Mediterranean forms. It would be impossible and also out of scope of this paper to give differential diagnoses to all the *Clypeaster* species reported from the Mediterranean Neogene (more than 250 species).

Notes to morphometry in the genus *Clypeaster*: A large number of measurements were made to improve and substantiate the morphological analysis of the Austrian *Clypeaster* species. During this a number of problems were encountered: a) measurements were often difficult or impossible due to inadequate preservation of many specimens. This hampered multivariate approaches, since most analyses exclude incomplete data sets; b) many potential informative features are very difficult to measure using simple distance measurement (e.g. inflation of the interporiferous zone, width of the infundibulum at the transition to the "normal" flattened oral surface, profile outline,…). A schematic drawing (Fig. 24) shows which variables were measured. The raw data can be found in Table 9.

Notes to clypeasteroid nomenclature: The term "infundibulum" is applied in at least two different ways in the literature. While some authors apply it only when the peristome lies in a concave, funnel-like, depression at the apex of the concavity near the centre of the oral surface (e.g. in *Clypeaster rosaceus*), others use it in all *Clypeaster* species, even when oral surface is flattened and horizontal all the way towards the edge of the peristome (e.g. *Clypeaster subdepressus*). Here it is used in the second sense (e.g. stating in the descriptions that there is a very narrow and shallow infundibulum in species like *C. campanulatus*, rather than saying there is none).

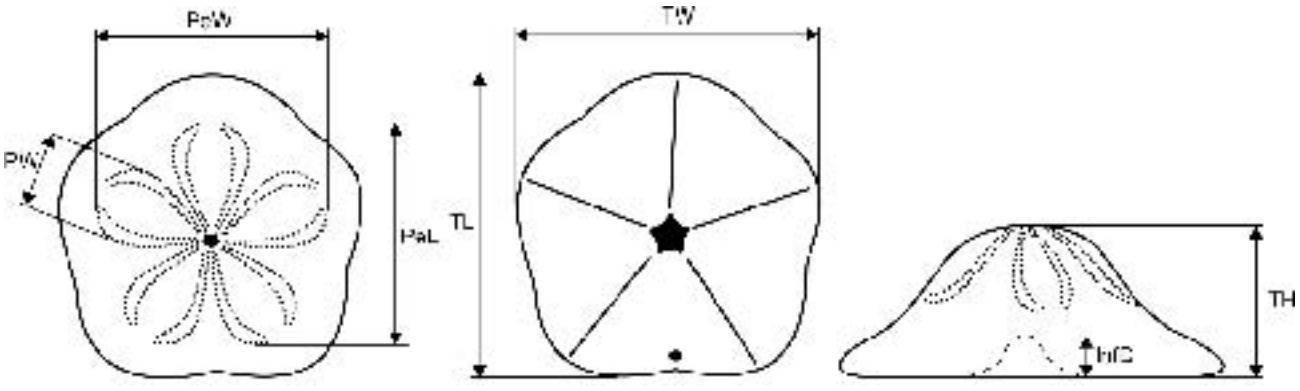

Figure 24: Schematic drawing of *Clypeaster* showing the variables measured.

Clypeaster calabrus Seguenza, 1880

(Pl. 31, Figs. 1-3; Pl. 32, Figs. 1-3)

	1868	*C. intermedius* – Karrer: 570 (footnote)
	1869	*Clypeaster intermedius* Dues. – Fuchs: 194
	1869a	*Clyp. intermedius* Desmoulins. – Laube: 183
	1870	*Clypeaster intermedius* Mich. – Laube: 314
pp	1871	*Clypeaster intermedius* Desmoulins. – Laube: 64-65 [Austrian material]
	1877	*Clypeaster intermedius* Desm. – Hilber: 261, 262
	1877	*Clypeaster intermedius* Desm. – Karrer: 170, 312
	1877	*Clypeaster intermedius* Desm. – Lóczy: 63
	1878	*Clypeaster intermedius* Desm. – Hilber: 553, 560, 563, 575
*	1880	C.[*lypeaster*] *intermedius* des Moulins, Var. *Calabra*. n. – Seguenza: 54; pl. 5, figs. 3, 3a-b
	1907	[*Clypeaster*] *intermedius* Desm. – Schaffer: 28
	1907	*Clypeaster intermedius* Desm. – Schaffer: 35
	1915	*Cl. excentricus* Vad. – Májer: 35, 88
	1915	*Cl. danubicus* Vad. – Májer: 35, 88
# v.	1915	*Clypeaster Scillae* Desm. var. *alienus* Vad. – Vadász: 129-131; fig. 23
v pp	1915	*Clypeaster crassus* Ag. – Vadász: 131-132; figs. 24
# v.	1915	*Clypeaster excentricus* n. sp. – Vadász: 133; fig. 26; pl. 11 (5), fig. 9
# v.	1915	*Clypeaster danubicus* n. sp. – Vadász: 134; fig. 27
v.	1915	*Clypeaster acclivis* Pomel. – Vadász: 136-137; fig. 29
pp	1925	*Clypeaster calabrus* – Checchia-Rispoli: 18, pl. 7, figs. 1, 1a-b, 2, 2a-b, 3; pl. 9, fig. 2; pl. 10, figs. 1, 1a-b, 2, 2a-b, 3; pl. 13, figs. 1, 1a-b, 2 [the specimen on pl. 9, fig. 2 was placed into *C. scillae* by Imbesi Smedile, 1959]
	1928	*Clypeaster intermedius* Desm. – Bobies: 48
?	1936	*Clypeaster intermedius* Désm. – Szörényi: 300-301; figs. 55-56 [abnorm 4-rayed specimen]
	1938a	*Clypeaster calabrus* Segu. – Kalabis: 2, 5, 7, 10
	1938b	Clypeaster scillae aff. var. *calabra* Segu. – Kalabis: 4-5, 8
	1938	*Clypeaster gregoryi* Lambert 1913 – Poljak: 181-182; pl. 5, fig. 1
	1939	*Clypeaster intermedius*. – Kapounek: 72
	1941	*Clypeaster acclivis* Pomel. – Meznerics: 87; pl. 1, figs. 1-2
#	1941	*Clypeaster epianthus* n. sp. – Meznerics: 87-88; pl. 2, fig. 1; pl. 3, fig. 2
#	1941	*Clypeaster kemencensis* n. sp. – Meznerics: 88; pl. 2, fig. 3; pl. 3, fig. 6
	1942	[*Clypeaster*] *intermedius* Desm. – Schaffer: 130
	1942	*Clypeaster intermedius* Desm. – Schaffer: 94
	1949	*Clypeaster intermedius* Desmoulins – Schouppé: 143
?	1958	*Clypeaster calabrus* Sequenza – Imbesi Smedile: 17-18; pl. 2, figs. 1, 1a-b, 2, 2a; pl. 3, fig. 1
non	1967	*Clypeaster calabrus* (Seguenza) – Marcopoulou-Diacantoni: 365-367; pl. 16, fig. 1; pl. 18, figs. 1-2
?	1968	*Clypeaster intermedius* Desm. – Flügel & Heritsch: 44; pl. 4, fig. 2
	1969	*Clypeaster grandiflorus* Bronn – Mitrović-Petrović: 128; pl. 10, fig. 2; pl. 11, figs. 1, 1a
	1975	*Clypeaster calabrus* (Seguenza, 1880). – Kalabis: 176
v.	1982	*Clypeaster scillae* Desmarest – Rögl et al.: 65; un-numbered fig. [misidentification]
v.	1998	*Clypeaster intermedius* Michl.– Schultz: 116; pl. 52b, figs. 7
	2001	*Clypeaster calabrus* Seguenza 1880 (Lambert, 1906) – Ventura & Zanfrà: 66

Type-material:

Clypeaster calabrus Seguenza, 1880:
Syntypes: Two syntypes, one of which is figured by Seguenza (1880: pl. 5, figs. 3, 3a-b); current whereabouts unknown
Locus typicus: Stilo, Calabria
Age: Early to ?Middle Miocene [Aquitanian according to Seguenza (1880: 54), "Elveziano" according to Checchia-Rispoli (1925: 18)]

Clypeaster danubicus Vadász, 1915:
Holotype: MAFI Ech 230, figured by Vadász (1915: fig. 27); housed at the Museum of the Hungarian Geological Survey
Locus typicus: Kemence, Pest, Hungary
Stratum typicum: Leitha limestone
Age: Late Badenian (Early Serravallian), Middle Miocene

Clypeaster excentricus Vadász, 1915:
Lectotype (designated by Boda, 1964: 205): MAFI Ech 126; housed at the Museum of the Hungarian Geological Survey
Paralectotype: MAFI Ech 435 from the Early Badenian of Gombhegy, Kemence, Hungary; and another specimen from Letkés, Hungary (not located)
Locus typicus: Kemence, Pest, Hungary
Stratum typicum: Leitha limestone
Age: Late Badenian (Early Serravallian), Middle Miocene

Clypeaster scillae alienus Vadász, 1915:
Syntype: MAFI Ech 123, figured by Vadász (1915: fig. 23); housed at the Museum of the Hungarian Geological Survey; second specimen mentioned by Vadász not located
Locus typicus: Gârbova de Sus (= Gîrbova de Sus, = Felsö-Orbó), Romania
Age: Late Badenian (Early Serravallian), Middle Miocene

Clypeaster epianthus Meznerics, 1941:
Holotype: specimen figured by Meznerics (1941: pl. 2, fig. 1; pl. 3, fig. 2); private collection of R. Streda; current whereabouts unknown
Locus typicus: Mátraszölös (= Mátraszöllös), Hungary
Age: Badenian (Langhian-Early Serravallian)

Clypeaster kemencensis Meznerics, 1941:
Holotype: specimen figured by Meznerics (1941: pl. 2, fig. 3; pl. 3, fig. 6); private collection of R. Streda; current whereabouts unknown
Locus typicus: Kemence, Hungary
Stratum typicum: Leitha limestone
Age: Late Badenian (Early Serravallian), Middle Miocene

Material:

Early ? Badenian (Langhian) – Rauchstallbrunngraben, near Baden, NÖ, Austria
NHMW: 3 specimens (NHMW 1978/2040/2, 1978/2040/6, 1978/2040/14)
Early Badenian (Langhian) – Stotzing (sandpit Mayer), Bgld, Austria
NHMW: 1 specimen (NHMW 2004z0093/0022)
Badenian (Langhian-Early Serravallian) – Brunn am Steinfeld, NÖ, Austria
NHMW: 2 specimens (NHMW 1859.LIV.1, 2003z0051/0001)
Badenian (Langhian-Early Serravallian) – Kalksburg, Vienna, Austria
NHMW: 21 specimens (NHMW 1866.XLVII.36, 1890.X.3-6,1890.X.61903.III.7, 1904.VIII.73-79, 1904.VIII.81, 2003z0049/0001 to 0006, 2003z0049/0030)
Badenian (Langhian-Early Serravallian) – Petersdorf, Styria, Austria
NHMW: 1 specimen (NHMW 1868.VIII.60)
Badenian (Langhian-Early Serravallian) – unknown locality, Austria

Species	Inventory No.	Location	TL	TW	TH	PeL	PeW	APP_W	Loc.[1]	InfD
C. calabrus	NHMW 2003z0049/0001	Kalksburg. W	140	124	44	96	85	26.9	2	-
C. calabrus	NHMW 2003z0049/0002	Kalksburg. W	156	138	50	-	-	-	-	18.0
C. calabrus	NHMW 2003z0049/0003	Kalksburg. W	137	117	47	95	81[2]	25.5	2	18.9
C. calabrus	NHMW 1904.VIII.76	Kalksburg. W	131	113	41	86	-	21.4	2	15.0
C. calabrus	NHMW 1890.X.5	Kalksburg. W	106	93	36	69	68	20.5	4	-
C. calabrus	NHMW 1904.VIII.73	Kalksburg. W	123	110	45	81	-	21.4	2	-
C. calabrus	NHMW 1904.VIII.75	Kalksburg. W	138	129	43	96[2]	89	25.9	2	-
C. calabrus	NHMW 1904.VIII.78	Kalksburg. W	107	93	35	-	-	18.8	4	15.3
C. calabrus	NHMW 1904.VIII.79	Kalksburg. W	101	92	-	-	-	-	-	-
C. calabrus	NHMW 2003z0049/0004	Kalksburg. W	135	115	47	-	-	-	-	20.3
C. calabrus	NHMW 1903.III.7	Kalksburg. W	129	109	31	-	-	-	-	-
C. calabrus	NHMW 1890.X.3	Kalksburg. W	131	121	46	84	78	23	2	-
C. calabrus	NHMW 2003z0049/0006	Kalksburg. W	131	108	44	-	75	25.8	4	17.6
C. calabrus	NHMW 1904.VIII.77	Kalksburg. W	130	120	45	80	73	20.8	2	-
C. calabrus	NHMW 2004z0112/0003	Müllendorf. Bgld	98	84	30	63	55	15.5	2	-
C. calabrus	NHMW 1997z0178/1753a	Müllendorf. Bgld	123	116	37	83	75	22.5	2	14.6
C. calabrus	NHMW 1997z0178/1753b	Müllendorf. Bgld	84	74	30	59	51	15.7	2	12.7
C. calabrus	NHMW 1868.VIII.60	Petersdorf. Bgld	123	107	37	-	-	27.1	4	15.7
C. calabrus	NHMW 1978/2040/6	Baden (RBG). NÖ	102	86	32	68	58	-	-	-
C. calabrus	NHMW 1978/2040/2	Baden (RBG). NÖ	116	97	38	71	60	19.6	4	-
C. campanulatus f. *acuminatus*	NHMW 1904.VIII.85	Kalksburg. W	147	133	62	104	96	30.7	4	12.1
C. campanulatus f. *acuminatus*	NHMW 1904.VIII.91	Perchtoldsdorf. NÖ	150	133	63	108	105	32.6	2	16.1
C. campanulatus f. *acuminatus*	NHMW A2736	Perchtoldsdorf. NÖ	148	133	66	115	108	36.3	4	-
C. campanulatus f. *aff. gibbosus*	NHMW 1857.38.23	Kalksburg. W	170	144	52	117	107	38.8	1	-
C. campanulatus f. *aff. reidii*	NHMW 1904.VIII.87	Kalksburg. W	152	138	63	113	-	32.8	2	15.9
C. campanulatus f. *aff. reidii*	NHMW 1890.X.8	Perchtoldsdorf. NÖ	134	126	60	103	98	28.8	2	-
C. campanulatus f. *campanulatus*	NHMW 1867.XXII.1	Hainburg. NÖ	-	132	60	99	97[2]	33.9	4	-
C. campanulatus f. *campanulatus*	NHMW 2003z0049/0008	Kalksburg. W	177	166	95	120	-	-	-	-
C. campanulatus f. *campanulatus*	NHMW 2003z0049/0007	Kalksburg. W	150	137	59	105	96	27.8	2	18.0
C. campanulatus f. *campanulatus*	NHMW 1978/2040/3	Baden (RBG). NÖ	154	134	60	99	93	30.6	2	-
C. campanulatus f. *campanulatus*	NHMW 1978/2040/4	Baden (RBG). NÖ	149	137	63	-	97	31.2	2	17.2
C. campanulatus f. *campanulatus*	NHMW 1976/1843/17	Baden (RBG). NÖ	140	122	60	98	90	28.8	2	17.9
C. campanulatus f. *campanulatus*	NHMW 1976/1843/16	Baden (RBG). NÖ	147	134	86[2]	107	100	31.8	4	16.5
C. campanulatus f. *partschi*	NHMW 1904.VIII.63	Kalksburg. W	147	140	52	102	97	27.6	2	-
C. campanulatus f. *partschi*	NHMW 1857.38.35	Kalksburg. W	151	140	50	94	88	25.9	2	-
C. campanulatus f. *partschi*	NHMW 2003z0049/0011	Kalksburg. W	147	139	51	101	101	28.8	4	14.6
C. campanulatus f. *partschi*	NHMW 1866.I.1274	Kalksburg. W	157	137	55	107	97	31.7	2	-
C. campanulatus f. *partschi*	NHMW 2003z0049/0012	Kalksburg. W	198	152	62[2]	128	108	34.5	2	-
C. campanulatus f. *partschi*	NHMW 2003z0049/0013	Kalksburg. W	186	165	64	-	-	31	2	-
C. campanulatus f. *partschi*	NHMW 2003z0049/0014	Kalksburg. W	161	146	59	-	-	-	-	17.1
C. campanulatus f. *partschi*	NHMW 2003z0049/0015	Kalksburg. W	153	143	54	96[2]	89	30.1	4	15.1
C. campanulatus f. *partschi*	NHMW A2740	Kalksburg. W	167	155	62	-	-	-	-	14.9
C. campanulatus f. *partschi*	NHMW A2744	Kalksburg. W	162	144	51	114	104	33	2	14.5
C. campanulatus f. *partschi*	NHMW 1857.38.31	Kalksburg. W	169	161	59	116	108	33.1	2	-
C. campanulatus f. *partschi*	NHMW 1904.VIII.66	Kalksburg. W	172	159	64	108	103	30	2	-
C. campanulatus f. *partschi*	NHMW 2003z0049/0009	Kalksburg. W	149	138	49	-	-	-	-	18.3
C. campanulatus f. *partschi*	NHMW 1904.VIII.69	Kalksburg. W	162	151	52	102	95	27.9	2	-
C. campanulatus f. *partschi*	NHMW 1904.VIII.68	Kalksburg. W	144	135	48	-	-	-	-	-
C. campanulatus f. *partschi*	NHMW 1858.XXV.39	Kalksburg. W	143	132	42	88	85	25	2	-
C. campanulatus f. *partschi*	NHMW 1858.III.132	Kalksburg. W	152	-	47	102	-	27.6	2	14.6
C. campanulatus f. *partschi*	NHMW 2003z0049/0010	Kalksburg. W	145	133	49	-	-	-	-	-
C. campanulatus f. *partschi*	NHMW 1858.III.18	Kalksburg. W	186	172	53	114	113	29.2	2	14.5
C. campanulatus f. *partschi*	NHMW 1857.38.29	Kalksburg. W	158	145	50	100	95	-	-	-
C. campanulatus f. *partschi*	NHMW 1858.III.19	Kalksburg. W	162	154	50	96	92	23.8	4	18.3
C. campanulatus f. *partschi*	NHMW 1857.38.30	Kalksburg. W	176	159	62	118	113	32.9	4	14.8
C. campanulatus f. *partschi*	NHMW 1857.38.26	Kalksburg. W	159	142	78	-	-	26.2	4	-
C. campanulatus f. *partschi*	NHMW 1904.VIII.88	Kalksburg. W	182	161	61	117	102	33.4	4	-
C. campanulatus f. *partschi*	NHMW 1857.38.32	Kalksburg. W	152	139	59	101	97	30	4	14.7
C. campanulatus f. *partschi*	NHMW 1904.VIII.71	Perchtoldsdorf. NÖ	150	134	52	102	92	31.8	4	-
C. campanulatus f. *partschi*	NHMW A2737	Kalksburg. W	162	147	52	98	91	24.3	4	-
C. campanulatus f. *partschi*	NHMW 2003z0049/0028	Kalksburg. W	162	149	60	-	-	29.4	2	-
C. campanulatus f. *portentosus*	NHMW 1978/2040/1	Baden (RBG). NÖ	148	141	64	100	103	28.2	4	-
C. campanulatus f. *portentosus*	NHMW 2003z0055/0002	Baden (RBG). NÖ	164	152	83	-	-	31.4	2	-

Table 9: Dimensions of the *Clypeaster* specimens used in the present study.

Species	Inventory No.	Location	TL	TW	TH	PeL	PeW	APP_W	Loc.[1]	InfD
C. campanulatus f. *pyramidalis*	NHMW 1905.VII.10	Leibnitz. Stmk	155	145	85	-	-	31.2	2	-
C. campanulatus f. *pyramidalis*	NHMW 1843.LIII.1	Baden (M). NÖ	167	153	84	121	119	34.8	2	-
C. campanulatus f. *pyramidalis*	NHMW 1904.VIII.83	Baden (RBG). NÖ	151	137	86	105	100	32.9	2	-
C. campanulatus f. *pyramidalis*	NHMW 1904.VIII.89	Baden (RBG). NÖ	148	134	70	-	-	29.5	4	-
C. scillae	NHMW 1978/2022/3	Aflenz. Stmk	87	73	33	57	51	14.3	4	-
C. scillae	NHMW 1978/2022/2	Aflenz. Stmk	85	70	35	59[2]	48	15.1	2	-
C. scillae	NHMW 1978/2022/1	Aflenz. Stmk	91	66	31	-	-	14	4	16.2
C. scillae	NHMW 1858.XII.8	Brunn/Steinfeld. NÖ	89	85	31	65	58	16.2	2	-
C. scillae	NHMW 2003z0056/0001	Eisenstadt. Bgld	92	73	35	60	50	14.6	4	13.7
C. scillae	NHMW 1869.I.664	Großhöflein. Bgld	98	82	-	69	55	16.7	2	-
C. scillae	NHMW 1867.XXII.2	Hainburg. NÖ	85	72	30	57	49	14.5	2	11.6
C. scillae	NHMW 1858.XV.56	Höflein. Bgld	92	72	35	-	-	-	-	-
C. scillae	NHMW 1868.VIII.42	Höflein. Bgld	91	74	42	-	-	-	-	-
C. scillae	NHMW 1852.II.1547	Šahy. SK	99	81	37	74	62	21.1	4	18.7
C. scillae	NHMW 1852.II.1548	Šahy. SK	92	77	36	-	-	-	-	-
C. scillae	NHMW 1904.VIII.74	Kalksburg. W	136	110	49	96	76	-	-	22.6
C. scillae	NHMW 1857.38.28	Kalksburg. W	98	77	40	66	54	-	-	-
C. scillae	NHMW 1865.XXXV.22	Kemence. HU	116	94	41	76	64	20.3	2	-
C. scillae	NHMW 1865.XXXV.16	Kemence. HU	55	44	15	33	28	-	-	-
C. scillae	NHMW 2003z0057/0001	Kemence. HU	86	67	35	-	-	14.3	4	15.0
C. scillae	NHMW 1865.XXXV.19	Kemence. HU	92	71	32	60	49	16.3	4	15.2
C. scillae	NHMW 2003z0057/0002	Kemence. HU	95	76	36	63	51	15.9	4	-
C. scillae	NHMW 1865.XXXV.21	Kemence. HU	78	62	28	52	42	12.8	2	15.6
C. scillae	NHMW 1865.XXXV.20	Kemence. HU	86	70	28	-	-	-	-	-
C. scillae	NHMW 1858.XXXIX.17	Kemence. HU	75	59	29	50	41	13.4	2	-
C. scillae	NHMW 1858.XXXIX.14	Kemence. HU	106	82	43	75	62	17.5	2	-
C. scillae	NHMW 1858.XXXIX.15	Kemence. HU	72	61	30	-	-	11.6	2	-
C. scillae	NHMW 1858.XXXIX.16	Kemence. HU	86	68	35	58	47	13.5	2	15.7
C. scillae	NHMW 1852.II.1546	Kemence. HU	88	75	30	-	-	-	-	-
C. scillae	NHMW 1885.XXXV.18	Kemence. HU	92	74	35	-	-	15	4	-
C. scillae	NHMW 1865.XXXV.17	Kemence. HU	47	38	15	29	24	7.8	2	7.6
C. scillae	NHMW 2003z0058/0001	Leibnitz. Stmk	97	78	28	63	50	14.5	2	-
C. scillae	NHMW 1978/2020/1	Mannersdorf. NÖ	106	88	40	73	57	21.2	2	>20
C. scillae	NHMW 1978/2020/3	Mannersdorf. NÖ	103	81	38	-	-	-	-	>16
C. scillae	NHMW 1978/2020/6	Mannersdorf. NÖ	112	87	35	78	-	18.5	4	-
C. scillae	NHMW 1978/2020/4	Mannersdorf. NÖ	108	85	40	73	56	17.1	4	-
C. scillae	NHMW 1978/2020/5	Mannersdorf. NÖ	116	88	42	81	-	17.9	2	18.7
C. scillae	NHMW 1978/2020/17	Mannersdorf. NÖ	96	76	32	63	52	15.6	2	-
C. scillae	NHMW 1978/2020/16	Mannersdorf. NÖ	106	89	36	72	61	16.8	4	-
C. scillae	NHMW 1978/2020/7	Mannersdorf. NÖ	112	86	39	77	-	17	2	17.7
C. scillae	NHMW 1978/2020/13	Mannersdorf. NÖ	78	63	31	52	42	13.5	4	15.9
C. scillae	NHMW 1978/2020/14	Mannersdorf. NÖ	81	63	34	-	-	-	-	-
C. scillae	NHMW 1978/2020/11	Mannersdorf. NÖ	97	74	34	65	51	16.2	4	16.2
C. scillae	NHMW 1978/2020/18	Mannersdorf. NÖ	83	65	27	56	44	14.7	2	15.7
C. scillae	NHMW 1978/2020/8	Mannersdorf. NÖ	94	73	66	-	-	15.5	4	-
C. scillae	NHMW 1978/2020/20	Mannersdorf. NÖ	91	74	24	57	47	15.1	4	14.5
C. scillae	NHMW 1978/2020/10	Mannersdorf. NÖ	101	78	36	-	-	19[2]	2	19.8
C. scillae	NHMW 1978/2020/12	Mannersdorf. NÖ	86	66	34	55	44	12.8	2	18.6
C. scillae	NHMW 1978/2020/9	Mannersdorf. NÖ	97	75	-	-	-	-	-	-
C. scillae	NHMW 1978/2020/19	Mannersdorf. NÖ	104	84	31	66	54	16.3	2	16.2
C. scillae	NHMW 1978/2020/15	Mannersdorf. NÖ	106	81	47	-	-	-	-	-
C. scillae	NHMW 2004z0072/0003	Mannersdorf. NÖ	82	67	30	53	44	13.4	4	16.6
C. scillae	NHMW A2328	Müllendorf. Bgld	99	79	34	67	55	18.5	2	15.0
C. scillae	NHMW 2003z0031/0006	Müllendorf. Bgld	66	55	19	-	-	12.8	4	9.2
C. scillae	NHMW 2004z0112/0007	Müllendorf. Bgld	85	70	31	59	50	15.6	2	-
C. scillae	NHMW 1997z0178/1745	Müllendorf. Bgld	111	89	39	78	62	20	2	14.9
C. scillae	NHMW 1976/1843/8	Baden (RBG). NÖ	108	89	33	70	61	16.6	4	17.4
C. scillae	NHMW 2004z0098/0006	Retznei. Stmk	57	48	23	39	33	10.7	2	10.7
C. scillae	NHMW 1978/2021/1	St. Nikolai. Stmk	93	78	35	-	-	-	-	-
C. scillae	NHMW 1978/2021/2	St. Nikolai. Stmk	98	77	29	-	-	15.9	2	-
C. scillae	NHMW 1868.I.Anhang	Gamlitz. Stmk	112	91	38	74	59	19.4	4	-

Abbreviations for variables: see Fig. 24; SK = Slovak Republic, HU = Hungary, RGB = Rauchstallbrunngraben, M = Mitterberg
Footnotes: 1 = Location of measurement; 2 = approximation

Table 9: Dimensions of the *Clypeaster* specimens used in the present study.