NHMW: 1 specimen (NHMW 2003z0050/0001, 2003z0050/0003 [specimen figured in Rögl et. al., 1982])
Late Badenian (Early Serravallian) – Müllendorf (Mühlendorfer Kreide AG quarry), Bgld, Austria
NHMW: 9 specimens (NHMW 1997z0178/1741, ../ 1746a-c, ../ 1753a-b, ../1755, 2004z0112/0003-4)
GBA: 3 specimens (no inventory numbers)

**Foreign material for comparison:**
Early Badenian (Langhian) – Kemence (Gombhegy), Pest, Hungary
MAFI: 2 specimens [MAFI Ech 126 and Ech 435 (**syntypes** of *Clypeaster excentricus* Vadász, 1915: 133, fig. 26, pl. 11 (5), fig. 9)]
Late Badenian (Early Serravallian) – Gârbova de Sus (= Gîrbova de Sus, = Felsö-Orbó), Romania
MAFI: 1 specimen [MAFI Ech 123 (**syntype** of *Clypeaster scillae alienus* Vadász, 1915: 129-131, fig. 23), Ech 134 (specimen figured as *Clypeaster acclivis* Pomel by Vadász, 1915: 136, fig. 29)]
Late Badenian (Early Serravallian) – Kemence, Pest, Hungary
MAFI: 2 specimens [MAFI Ech 230 (**holotype** of *Clypeaster danubicus* Vadász, 1915: 134, fig. 27), Ech 239 (specimen figured as *Clypeaster crassus* Ag. by Vadász, 1915: 131-132, fig. 24)]

**Dimensions:** see Tab. 9

**Description:**
Size and shape: The test is of medium to large size, elongated antero-posteriorly, with a pentagonal outline. The anterior margin is bluntly pointed, the posterior margin transversely truncated, distinctly indented and less thick than the anterior margin. The ambitus is moderately thick and may be tumid in some specimens, but is distinctly thinner than in *C. scillae*. The lateral margins are distinctly indented in interambulacra 1 and 4. There may be also marginal indentations in interambulacra 2 and 3 but they are usually less well developed. The maximum width lies anterior of the apical disc, where ambulacral columns IIa and IIIb reach the ambitus. In profile, the test has a trapezoid shape with a moderately domed petaloid area. The maximum height lies around the apical disc on the raised adapical parts of the interporiferous zones of the ambulacra. The oral surface is distinctly flattened, with a broad, moderately deep infundibulum.
Apical disc: The apical disc lies subcentrally and is slightly depressed. It belongs to the monobasal type with a large, central, subpentagonal madreporite and 5 circular gonopores.
Ambulacra: All five ambulacra are petaloid, straight and closing distally. The frontal petal is longest, the anterior paired petals shortest. The length of the petals ranges from 57 to 66 % of the corresponding test radius. The poriferous zones are slightly depressed and relatively wide. The pore pairs are conjugated anisopores. Adjacent pore pairs are separated by a narrow ridge with a single row of up to 8 primary tubercles. The interporiferous zones are strongly inflated and usually 2.4 to 2.7 times as wide as single poriferous zone at the widest point of the petals. They are crowded with primary tubercles similar to those on the interambulacra. On the oral surface shallow, simple unbranched food grooves are present in the axis of the ambulacra.
Interambulacra: The interambulacra are distinctly depressed adapically between the petals. They are crowded with perforate crenulate primary tubercles in sunken areoles. Between the primary tubercles, dense miliary tuberculation is present. Tubercle size and density increases towards the margin. Between the petals the tubercle density is usually low and the tubercles are slightly larger. On the oral surface tubercles are larger than on the aboral side and more closely spaced, their areoles nearly touching each other.
Peristome: The peristome is subcircular to very slightly oval and lies subcentrally on the oral side of the test in a moderately deep, broad infundibulum with gently sloping walls.
Periproct: The periproct is subcircular and lies inframarginally, about 3 to 4 mm away from the posterior margin.
Internal support system: unknown

**Differential diagnosis:**
For the difference to *C. barcinensis* ? Lambert, 1906, see above under that species.
*C. campanulatus* (Schlotheim, 1820) (and its phenotypes), a species occurring in the Badenian (Langhian-Early Serravallian) of the Paratethys, differs by its larger test height, broader petals, more strongly raised petaloid area, and thicker margin.
*C. folium* Agassiz in Agassiz & Desor, 1847, a species restricted to the Badenian (Langhian-Early Serravallian) in the Paratethys, is distinguished from this species by its lower test height, more elongated outline with deeper marginal indentations in the interambulacra, smaller and less raised petaloid area, and deeper food grooves.
*C. intermedius* des Moulins, 1837, an Early Miocene species of the Rhône Basin, differs from *C. calabrus* by its broader petals, less strongly inflated interporiferous zones, but more inflated interambulacra between the petals, deeper, more steep-walled infundibulum and less strong marginal indentations.
*C. latirostris* Michelin, 1861, a species occurring in the Late Eggenburgian (Early Burdigalian) of the Molasse Zone, is distinguished from this species by its subequal test length and width, lower test height, thin margin, slightly inflated interporiferous zones, and the broad, very shallow infundibulum.
For the difference to *C. neudorfensis* Lambert, 1927, see below under that species.
*C. scillae* des Moulins, 1837, a co-occurring species, differs from *C. calabrus* by its (usually) higher test, more elongated outline (see Fig. 25.A), more strongly raised petaloid area, thicker and more tumid margin, deeper, steep-walled infundibulum (Fig. 25.B) and less strong marginal indentations. High morphotypes of *C. calabrus* differ from *C. scillae* by their different profile: in *C. scillae* the whole aboral surface is inflated and the margin is thick; in *C. calabrus*, in contrast, only the petaloid area is inflated and the margin is relatively thin [compare e.g. the figure of "*C. danubicus*" in Vadász (1915: 134, fig. 7), which represents such a high morphotype of *C. calabrus*]. Additionally, *C. scillae* has an inflated oral surface with cushion-shaped interambulacra, whereas *C. calabrus* has a distinctly flattened surface.

**Discussion:**
The studied specimens are placed in the species *Clypeaster calabrus* Seguenza, 1880. The same is true for most of the specimens of the Badenian deposits of Austria formerly referred to *C. intermedius*, as already observed by Kalabis (1937a: 2, 7-8; 1949: 93-96). *C. intermedius* has recently been re-described and illustrated by Philippe (1998: 112-118) and it seems clear now that records from the Middle Miocene of the Paratethys are misidentifications.
Lambert (1906b) raised *C. intermedius calabra* Seguenza, 1880 to species rank and also associated *C. petaliferus* Seguenza, 1880 with that species. Cottreau (1913a: 58) rejected this and placed both *C. intermedius calabra* and *C. petaliferus* into the synonymy of *C. intermedius* des Moulins, 1837. Checchia-Rispoli (1925: 20) opposed Cottreau and insisted that both *C. calabrus* and *C. petaliferus* were distinct species. Lambert (1927a: 14) commented on Cottreau's action in the following way: «M. Cottreau réunit ces deux formes au *C. intermedius*; cette manière de voir peut être fondée, en ce qui concerne *C. petaliferus*, mais en ce qui concerne *C. calabrus* je ne saurais m'y rallier; sa forme est trop différente de l'espèce se rapprocherait plutôt *C. crassicostatus*.» ("Mr. Cottreau united these two forms with *C. intermedius*; while this opinion can be accepted, with regard to *C. petaliferus*, but with regard to *C. calabrus* I cannot endorse this; its form is too different from

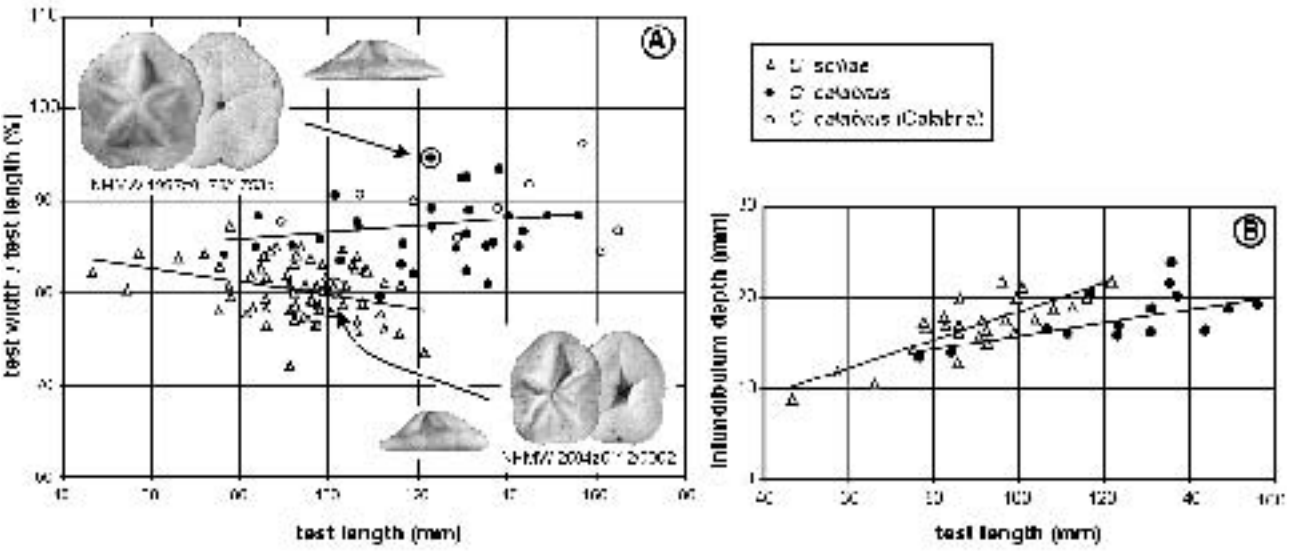


Figure 25: Morphometric comparison between *C. calabrus* Seguenza, 1880 and *C. scillae* des Moulins, 1837: Variation of relative test width (A) and infundibulum depth (B). Data of *C. calabrus* specimens from the type-area have been included in diagram A for comparison (from Seguenza, 1880 and Ventura & Zanfrà, 2001).

that species and would rather approach *C. crassicostatus."*). Kalabis (1949: 94, 97) discussed the different opinions expressed by former authors and concluded that since *C. intermedius* and *C. calabrus* did not coexist in any locality they represent an example of geographic speciation and have thus to be considered subspecies. I do, however, not support his view and, like Lambert, regard *C. calabrus* as distinct species for the following reasons: a) the two species are clearly separable and to my knowledge no intermediate forms with *C. intermedius* exist; b) the re-description of the type material of *C. intermedius* and additional material from the type region by Philippe (1998) give us a much better knowledge of the variation in *C. intermedius* than ever before and although the two species seem to be clearly related, they are well differentiated; c) the two species are, most probably, not contemporaneous (Middle Miocene records of *C. intermedius* are dubious, as are Early Miocene records of *C. calabrus*).

Another question is the relation between *C. calabrus* and *C. scillae*. Like Kalabis (1937b: 2, 1938b: 3-5 but see also the discussion in 1949: 96) I initially thought that *C. calabrus* and *C. scillae* could be the extreme morphotypes of a single species with strong morphological variation, probably related to the sediment grain size or other environmental factors. This observation was based on a large series of specimens from the Vienna Basin (Mannersdorf and Kalksburg, Austria) and the Pannonian Basin (Kemence, Hungary). Research on specimens from further localities and different palaeoenvironmental settings, however, suggests that this is not the case. Although, there is an environmental signal in test morphology, it is less strong than initially thought and seems to concern mostly test height and to a certain extent thickness of the margin. Moreover, the two species co-occur in several localities (e.g. Müllendorf, Austria), within the same sedimentary units, where they are well differentiated. I thus consider *C. calabrus* and *C. scillae* distinct species with slightly overlapping morpho-space (when all individuals of several time horizons and palaeoenvironmental settings are examined together; compare Fig. 25.A). Another, although, probably less likely possibility is that these two species have the ability to interbreed. Hybridisation is known to occur in many groups of the echinoids (Mortensen, 1912; Onoda, 1943; Lessios & Pearse, 1996; Lessios et al., 2001a, b; Rahman et al., 2001), probably even across genus boundaries (Mortensen, 1912) and the hybrids usually share features of both parent taxa.

The two species *Clypeaster epianthus* Meznerics, 1941 and *C. kemencensis* Meznerics, 1941 which have been established each on a single specimen of Mátraszölös respectively Kemence (both in Hungary) are placed into the synonymy of *C. calabrus* here. The type specimens were housed in a private collection and could not be located. Nevertheless it is clear from the descriptions and illustrations that they fall well within the variability of the species discussed here. Meznerics (1941) was correct in arguing that the two species cannot be placed into *C. scillae* or synonymous (*C. grandiflorus*, *C. crassus*, ...) species but failed to realise that Seguenza had already proposed a name for such forms. There are no features which would allow to differentiate these two species from *C. calabrus*.

**Occurrence:**

Austria: Badenian (Langhian-Early Serravallian)

Vienna Basin: Brunn am Steinfeld (Kalabis, 1938a; [NHMW]); Hainburg, NÖ (Kalabis, 1938b); Kalksburg, Vienna (Karrer, 1868; Fuchs, 1869; Laube, 1869a; Karrer, 1877; Schaffer, 1907; Kalabis, 1938a+b; Schaffer, 1942; Kalabis, 1975; Schultz, 1998; [NHMW]); Müllendorf (Mühlendorfer Kreide AG quarry), Bgld (Kapounek, 1939; Rögl et al., 1982; [NHMW]); Perchtoldsdorf, NÖ (Kalabis, 1938a+b); Rauchstallbrunngraben, Baden, NÖ (Laube, 1869a, 1871; Karrer, 1877; Schaffer, 1907; Bobies, 1928; Schaffer, 1942; Kalabis, 1975; [NHMW]); Rodaun, Vienna (Kalabis, 1938b); Vienna Basin (Lóczy, 1877)

Styrian Basin: Gamlitz, Styria (Hilber, 1877); Kainberg, Styria (Hilber, 1878); Petersdorf, Styria [NHMW]; Retznei near Ehrenhausen, Styria (Schouppé, 1949); St. Nikolai im Sausal, Styria (Hilber, 1878); Wildon, Styria (Hilber, 1878; ? Flügel & Heritsch, 1968)

Zala, Sáva and Dráva Basins: Kaznica, Croatia (Poljak, 1938); Vujići, Bosnia & Herzegovina (Mitrović-Petrović, 1969)

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

Molasse Zone: Podivín, Czech Republic (Kalabis, 1975)

Great Hungarian Basin (Pannonian Basin): Kemence (Gombhegy), Pest, Hungary (Májer, 1915; Vadász, 1915; [MAFI]); Kemence, Pest, Hungary (Vadász, 1915; Mezne-

RICS, 1941; [MAFI]); Mátraszölös, Hungary (? SZÖRÉNYI, 1936; MEZNERICS, 1941; KALABIS, 1975)

Transylvanian Basin: Gârbova de Sus (= Gîrbova de Sus, = Felsö-Orbó), Romania (VADÁSZ, 1915; [MAFI]); Minişu des Sus (= Felménes), Arad, Romania (LÓCZY, 1877)

Mediterranean: Early to Middle Miocene

Central Mediterranean: Belcastro, Calabria, Italy (pp CHECCHIA-RISPOLI, 1925; VENTURA & ZANFRÀ, 2001); Stilo, Calabria, Italy (SEGUENZA, 1880; ? IMBESI SMEDILE, 1958)

## *Clypeaster campanulatus* (SCHLOTHEIM, 1820)

(Pl. 22 to 27)

**Material:** see below under the respective formae

**Dimensions:** see Tab. 9

**Description:**

Size and shape: The test is of large size, with a subpentagonal outline. Test width varies between 85 to 95 % TL with very few exceptions (see Fig. 26.A). The margin of the test is moderately thick and rounded but not tumid (like e.g. in *C. scillae*). In aboral view the anterior margin is bluntly pointed and the posterior margin transversely truncated with only weak interambulacral indentations (if present at all). The maximum width lies anterior of the centre, where ambulacral columns IIa and IVb reach the ambitus. Profile outline and inflation of the petaloid area are extremely variable (see Plates 22 to 27 and Fig. 26.B). Consequently, the profile may be low and rounded to very high and pyramidal or even nearly hemispherical. The apex is usually somewhat flattened and coincides with the apical disc. The oral surface is distinctly flattened with a very narrow infundibulum.

Apical disc: The apical disc lies subcentrally and belongs to the monobasal type with a large, central, subpentagonal madreporite and 5 circular gonopores.

Ambulacra: Petals straight and open distally (IPZ width usually >7 mm distally). The frontal petal is usually the longest; the paired petals are more or less subequal in length, the posterior ones being a little bit longer than the anterior ones in some specimens. The length of the petals is quite variable and ranging from 63 to 75 % of the corresponding test radius. The poriferous zones are depressed and relatively wide. They are widest near the distal end of the petals. The pore pairs are conjugated anisopores. Adjacent pore pairs are separated by a narrow ridge with a single row of 2 to 15 primary tubercles (depending on position within the petal, size of the specimen and possibly also environmental parameters such as sediment grain size). The interporiferous zones are inflated, medially flattened and usually 2.5 to 3.5 times as wide as a single poriferous zone at the widest point of the petals. They are crowded with primary tubercles similar to those on the interambulacra. Outside the petals only minute microunipores are present, which are observable only in exceptionally preserved specimens/fragments. On the oral surface simple unbranched food grooves are present in the axes of the ambulacra.

Interambulacra: Adapically the interambulacra are slightly inflated between the petals, forming weak keels between them. They are crowded with perforate, crenulate primary tubercles

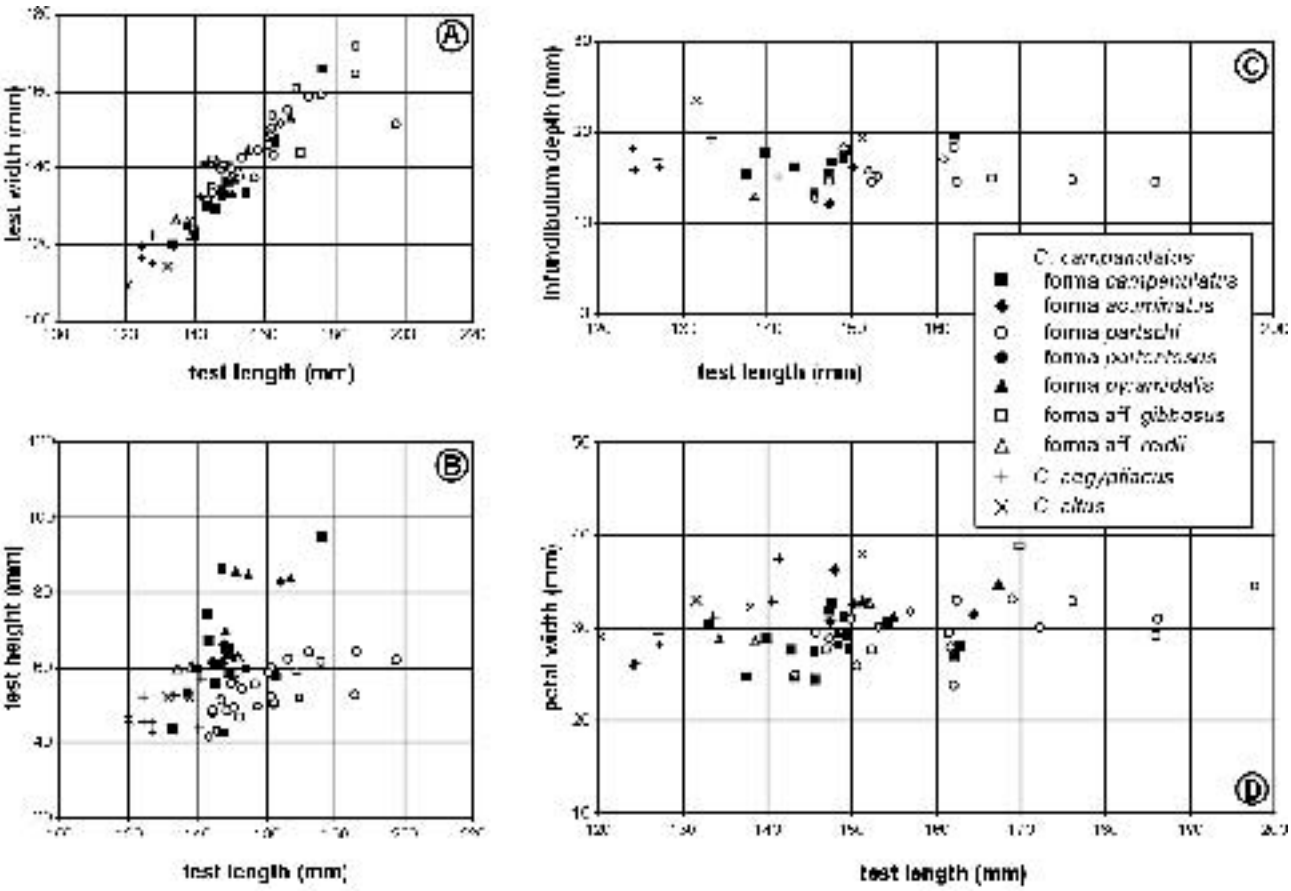


Figure 26: Morphological variation in the *Clypeaster campanulatus* group: test width (A), test height (B), infundibulum depth (C) and maximum petal width (D; measured in petals II or IV). Additionally, data of the nominal species *C. altus* from the Messinian of the Maltese Islands and *C. aegyptiacus* from the Pliocene of Egypt are included for comparison.

in sunken areoles. Between the primary tubercles, dense miliary tuberculation is present. Tubercle density and size is more or less homogenous on the aboral surface. On the oral surface tubercles are larger, more closely spaced and tubercle size increases towards the peristome. Adorally the interambulacra are flattened, producing an even surface, which is not inclined towards the peristome.

Peristome: The peristome is circular and lies centrally on the oral side of the test in a narrow and moderately deep infundibulum (see Fig. 26.C).

Periproct: The periproct is subcircular to very slightly oval, transversely elongated. Its diameter is about half or less that of the peristome. It lies inframarginally, usually about 5 to 6 mm away from the posterior margin.

Internal support system: The test of this species is double-walled in the marginal areas and reinforced by a moderately dense internal pillar system. The pillars are most abundant in the margin, in the central region around the lantern and in the interambulacra (see Pl. 26, Fig. 3).

**Differential diagnosis:**

*C. altus* Leske, 1778, from the Messinian of Malta differs by its longer and broader petals, thicker margin and broad infundibulum. Similarities in overall shape and profile occur but are considered to represent parallel adaptations to environmental conditions here.

For the difference to *C. barcinensis* ? Lambert, 1906 see above under that species.

*C. calabrus* Seguenza, 1880, a co-occurring species, differs by its very different profile, concave oral surface with broad infundibulum, narrower petals, much more inflated interporiferous zone, and deep marginal indentations.

*C. folium* Agassiz in Agassiz & Desor, 1847, from the Badenian (Langhian-Early Serravallian) of the Paratethys, is distinguished from this species by its flattened test with deep marginal indentations in the interambulacra, thinner margin, smaller petaloid area, broader infundibulum, and deeper food grooves.

*C. intermedius* des Moulins, 1837, an Early Miocene species of the Rhône Basin, differs from *C. campanulatus* (and its phenotypes) by its strongly different profile, lower test height, narrower petals, less strongly raised petaloid area, larger infundibulum, and thinner margin.

*C. latirostris* Michelin, 1861, a species occurring in the Eggenburgian (Early Burdigalian) of the Molasse Zone, is distinguished from this species by its subequal test length and width, lower test height, thin margin, only slightly inflated interporiferous zones, and the broad, very shallow infundibulum.

For the difference to *C. neudorfensis* Lambert, 1927, see below under that species.

*C. scillae* des Moulins, 1837, a co-occurring species, differs by its strongly different profile, concave oral surface with broad infundibulum, narrower petals, much more inflated interporiferous zone.

**Discussion:**

As outlined above in the introduction to the genus *Clypeaster*, this group is an outstanding example of taxonomic over-completeness. High intraspecific morphological variability and the use typological species concepts by earlier palaeontologists led to the recognition of an enormous number of species. In the Paratethys more than 50 nominal species were described (Michelin, 1861; Vadász, 1915; …). Although the genus *Clypeaster* can show high diversity in the modern tropics (e.g. the Caribbean, see Hopkins, 1988), 50 synchronous nominal species in an area slightly larger than the modern Mediterranean are unparalleled in modern times.

It is difficult to accept all these as biological species having evolved in different parts of the Paratethys as reproductively isolated groups. Furthermore, these groups are interconnected by transitional morphs which co-occur at single localities. Hence they cannot be interpreted as chronosubspecies (*sensu* Willmann, 1987) or as biological subspecies (as done by Kalabis, 1949) since at least some are clearly sympatric. Hybridization which is known to occur in a variety of echinoid groups (Mortensen, 1912; Onoda, 1943; Lessios & Pearse, 1996) may also be a possible factor.

As these numerous species can be relatively well characterised and differentiated from other *Clypeaster* species in the study area I decided to treat the *Clypeaster campanulatus* types as extreme morphologies of a single species. I do, however, not renounce describing the characteristic formae. Although being aware that these taxa do not accurately fit to the biological species concept, ecological information might be lost if these were treated as a single superspecies.

These formae are named according to the junior synonym of *C. campanulatus*, whose type material is closest to that particular phenotype. Care has to be taken, however, that only names of species synonymous of *C. campanulatus* are used. Other names like *reidii* Wright, 1855 are not available, since they probably represent other, distinct species are synonyms of other, distinct species [like here in the case of *reidii* Wright, 1855 which was shown to be a junior synonym of *C. altus* Leske, 1778 by Challis, 1980 (A comprehensive revision of the Maltese clypeasterids is still missing. It is possible that Challis (1980) overestimated the variability of *C. altus* and that *C. campanulatus* co-occurs with the former species there)]. It is interesting that clearly distinct species like *C. campanulatus* and *C. altus* both exhibit a large intraspecific variation and may indeed form very similar phenotypes [concerning profile outline and overall shape; Marcopoulou-Diacantoni (1967) for example, described a large number of species using various names from different regions and stratigraphic horizons. Many of the specimens on which her identifications are based, however, could also be interpreted as phenotypes of *C. altus,* the intraspecific variability of which was documented by Challis (1980)]. Addressing the subject of parallel evolution and development of similar phenotypes in different species of *Clypeaster* Rose & Poddubiuk (1987: 464) suggested that: "Individual species morphology may thus be of more obvious palaeoenvironmental than taxonomic or stratigraphic significance."

The records of *C. campanulatus* from the Burdigalian of the Rhône Basin by Lambert (1913a) and Philippe (1998) are unconvincing. Both records lack an illustration or description. Moreover, there are also no other undoubted Early Miocene records of this species. Records of *C. campanulatus* or its synonyms and formae from sediments of the Mediterranean area are difficult to evaluate, in many cases no other information besides the name of the taxon is given [e.g. *C. alticostatus* and *C. portentosus* in the Miocene of Cyprus (Cowper Reed, 1932, 1933; Henson et al., 1949)]. But also in better documented records it is often difficult to doubtlessly confirm the specific identity with the Paratethyan species *C. campanulatus*. Anyhow, the present work focuses on the records from the Paratethys where the reference specimens or at least material from the respective localities were seen by the author. Records of *C. campanulatus* from the Mediterranean area are omitted from the synonymy lists in most cases.

**forma *campanulatus* (Schlotheim, 1820)**
(Pl. 22; Figs. 1a-c)

| | | |
|---|---|---|
| | 1767 | unbekannte und bisher noch nicht beschriebene Versteinerung – Anonymus: 702-706 [first mention of the two *Clypeaster* specimens described and illustrated by Knorr & Walch] |
| . | 1771 | *Scutum angulare altum* – Walch: 215-217 |
| . | 1771 | [*Scutum angulare altum*] – Knorr: pl. IX.d., fig. 1. |
| * | 1820 | *Echinites campanulatus*. – Schlotheim: 323 |
| ? | 1868 | *Cl. altus* – Karrer: 570 (footnote) |
| ? | 1869 | *Clypeaster altus* Lam. – Fuchs: 194 |

| | | |
|---|---|---|
| | 1874 | *Clypeaster altus conicus* – Quenstedt: pl. 82, fig. 13 |
| pp | 1875 | *Scutum altum* – Quenstedt: 533-534 |
| | 1875 | *Scutum altum conicum* – Quenstedt: 534-538 |
| pp | 1875 | *Scutum altum campanulatum* – Quenstedt: 538-539 |
| ? | 1877 | *Clypeaster altus* Lam. – Karrer: 312 |
| pp | 1891 | *Clypeaster altus*, (Leske), 1778. – Gregory: 593-596 |
| ? | 1899 | *Clypeaster altus* Lmk. – Roth von Telegd: 95 |
| ? | 1907 | *Clypeaster altus* Lam. – Schaffer: 35 |
| # ? | 1915 | *Clypeaster hungaricus* n. sp. – Vadász: 155-156, figs. 47-48 [type material lost] |
| ? | 1915 | *Clypeaster agassizi* Sism. – Vadász: 162-165, figs. 54-55 [reference material lost] |
| # v. | 1915 | *Clypeaster periplanus* n. sp. – Vadász: 193-194, figs. 83-84 |
| # ? | 1915 | *Clypeaster periplanus* var. *subtilis* – Vadász: 194 [type material lost] |
| ? | 1937a | *Clypeaster campanulatus* Schloth. – Kalabis: 46 |
| | 1938b | *Clypeaster campanulatus* (Schlotheim) – Kalabis: 5-7, 8-10 |
| | 1938 | *Clypeaster campanulatus* Schlotheim 1920 – Poljak: 186-187; pl. 6, fig. 1 |
| ? | 1942 | *Clypeaster altus* Lam. – Schaffer: 94 |
| | 1949 | *Clypeaster campanulatus* (Schlotheim, 1820) – Kalabis: 42-54; 97-111 |
| | 1949 | *Clypeaster campanulatus campanulatus* (Schlotheim, 1820) – Kalabis: 42-46; 97-101; pl. 3, figs. 1-3 |
| | 1949 | *Clypeaster altus* Lambert – Schouppé: 143 |
| ? | 1967 | *Clypeaster campanulatus* Schlotheim, 1820 – Marcopoulou-Diacantoni: 367-368; pl. 12, fig. 1 |
| | 1969 | *Clypeaster suboblongus* Pomel – Mitrović-Petrović: 127; pl. 7, fig. 2; pl. 8, fig. 1 |
| | 1969 | *Clypeaster sequenzai* Vad. – Mitrović-Petrović: 133; pl. 19, figs. 1, 1a; pl. 20, fig. 1 |
| | 1981 | *Clypeaster reidii* Wright– Mitrović-Petrović: 179; figs. 9-10 |
| | 1984 | *Clypeaster sequenzai* Vadasz – Mitrović-Petrović: 233; pl. 13, figs. 2, 2a-b |
| # | 1990 | *Clypeaster gombosae* n. sp. – Mihály: 238-239, 240-241; pl. 2, fig.2; pl. 3, fig. 1; pl. 4, fig. 1 |
| v. | 2004 | *Clypeaster* – Harzhauser et al.: 82, fig. |

**Type-material:**
Clypeaster campanulatus (Schlotheim, 1820):
Syntypes: specimen figured by Knorr (1771: pl. IX.d., fig. 1) and an additional specimen mentioned by Walch (1771); collection of Mister Geinitz (donated by R. von Moll, Vienna); current whereabouts unknown [see also Anonymous (1767)]
Locus typicus: Baden, NÖ, Austria (probably from the quarries in the valley called Rauchstallbrunngraben)
Stratum typicum: "gelber Sandstein"
Age: Badenian (Langhian-Early Serravallian), Middle Miocene

*Clypeaster periplanus* Vadász, 1915:
Holotype: MAFI Ech 146 (Vadász, 1915: figs. 83-84); Museum of the Hungarian Geological Survey, Budapest
Locus typicus: Gârbova de Sus (= Felsö-Orbó), Romania
Age: Late Badenian (Early Serravallian), Middle Miocene

*Clypeaster gombosae* Mihály, 1990:
Holotype: MAFI Coll. Ech. 340; Museum of the Hungarian Geological Survey, Budapest
Locus typicus: Gomb-Hill, Kemence, Hungary
Stratum typicum: Sámsonháza Fm.
Age: Early Badenian (Langhian), Middle Miocene

**Material:**
Early ? Badenian (Langhian) – Rauchstallbrunngraben, near Baden, NÖ, Austria
NHMW: 7 specimens (NHMW 1952/14, 1976/1843/14 to 1976/1843/17, 1978/2040/3, 1978/2040/4), 7 casts ["Prägesteinkerne"] (NHMW 1836.XXIII, 1978/2040/8, 1978/2040/9, 1978/2040/12, 1978/2040/13, 1978/2040/15, 1978/2040/16)
Badenian (Langhian-Early Serravallian) – Brunn am Steinfeld, NÖ, Austria
NHMW: 1 specimen (NHMW 2003z0051/0002)
Badenian (Langhian-Early Serravallian) – Hainburg (*Halitherium*-locality), NÖ, Austria
NHMW: 1 specimen (NHMW 1867.XXII.1)
Badenian (Langhian-Early Serravallian) – Kalksburg, Vienna, Austria
NHMW: 2 specimens (NHMW 2003z0049/0007, 2003z0049/0008)
Badenian (Langhian-Early Serravallian) – Lugoj (surroundings of), Romania
NHMW: 1 specimen (NHMW 1873.XIV.41)
Late Badenian (Early Serravallian) – Gârbova de Sus (= Felsö-Orbó), Romania
MAFI: 1 specimen [MAFI Ech 146 (**holotype** of *Clypeaster periplanus* Vadász, 1915: 193-194, figs. 83-84)]
Late Badenian (Early Serravallian) – Müllendorf (quarry of the Mühlendorfer Kreidewerke AG), Bgld, Austria
NHMW: 6 specimens (NHMW 1997z0178/1747-1748, ../1750-1751, 2004z0112/0001, ../0006)

Transitional specimen *campanulatus* (Schlotheim, 1820) – *acuminatus* Desor in Agassiz & Desor, 1847:
Badenian (Langhian-Early Serravallian) – Rauchstall-brunngraben, near Baden, NÖ, Austria
NHMW: 1 specimen (NHMW 1978/2040/5)

Transitional specimens *campanulatus* (Schlotheim, 1820) – *partschii* Michelin, 1861:
Badenian (Langhian-Early Serravallian) – Kalksburg, Vienna, Austria
NHMW: 3 specimens (NHMW A2737, 2003z0049/0028 to 0029)

**Description:**
Morphotype with a strongly raised rounded petaloid area, the sides of which form a distinct angle with the marginal area outside the petals (in profile view). The area around the apical disc is somewhat flattened. The petals are narrower than in morphotypes where the whole aboral surface is inflated. Test height between 40 to 60 % TL.

**Remarks:**
This phenotype can easily be recognised by its distinct hat-like test profile. It is most common in the localities Rauchstall-brunngraben near Baden (where the type material of *campanulatus* comes from) and Müllendorf. Intermediate morphs connecting this form to *partschii* Michelin, 1861, *pyramidalis* Michelin, 1861 and *acuminatus* Desor in Agassiz & Desor, 1847 exist.

Some specimens of this phenotype from the type locality Rauchstallbrunngraben near Baden show an extremely thin and unusually sharp margin instead of the normally 5 to 10 mm thick margin. A section through such a specimen revealed that this was caused by postsedimentary compaction and leaching of the test (i.e. the specimens are "Prägesteinkerne"; see Fig. 27). The skeletal material is completely dissolved and partly replaced by an extremely thin layer of newly formed calcite (i.e. a pseudomorphosis). Therefore the extremely thin margin of these specimens does not have any value as specific character, it is caused postmortally by diagenesis. Kalabis (1938b: 6) reached a very similar explanation for this phenomenon, based on a large series of specimens from this locality.

Based on Vadász's description and illustrations *C. hungaricus* and *C. agassizi* are very similar to *C. campanulatus*. They fit

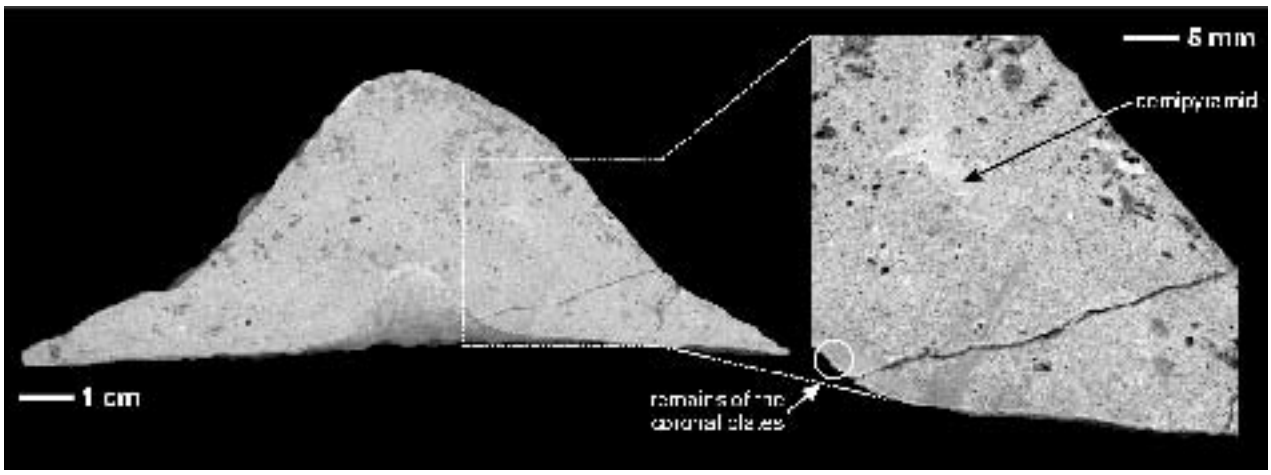


Figure 27: *Clypeaster campanulatus* (Schlotheim, 1820): vertical cross section of a "Prägesteinkern" from Rauchstallbrunngraben, near Baden, NÖ (NHMW 1978/2040/16; the original test is nearly completely leached, only traces remain)

best with material recovered from the locality Rauchstallbrunngraben, near Baden, the type locality of *campanulatus*. The type material of *hungaricus* and *agassizi* could not be located at the Museum of the Hungarian Geological Survey (where all other types of Vadász are kept) and is considered lost.

**forma *partschii* Michelin, 1861**
(Pl. 23; Figs. 1-2; Pl. 26, Fig. 1a-c)

| | | |
|---|---|---|
| * v. | 1861 | *Clypeaster Partschii*, Michelin – Michelin: 127-128; pl. 17, figs. 3; pl. 30, figs. a-f |
| | 1867 | *Clyp. Partschi* Mich. – Stache: 143 |
| v. | 1868 | *Clypeaster Partschi* Mich. – Karrer: 570 (footnote) |
| v. | 1869 | *Clypeaster Partschi* Michel. – Fuchs: 194 |
| v. | 1869a | *Clyp. Partschi* Michelin. – Laube: 183 |
| v. | 1870 | *Clypeaster Partschi* Mich. – Laube: 314 |
| v. | 1871 | *Clypeaster Partschi* Michelin. – Laube: 64 |
| v. | 1877 | *Clypeaster Partschi* Mich. – Karrer: 312 |
| ? | 1885 | *Clypeaster confusus* (*Partschii* antea, non Michelin) – Pomel: pl. B22, figs. 1-5 [fide Lambert, 1927a] |
| ? | 1885 | *Clypeaster paratinus* – Pomel: pl. B27, figs. 1-6 [fide Lambert, 1927a] |
| | 1906 | *Clypeaster Partschi*, Michelin. – Vadász: 331 |
| | 1907 | *Clypeaster Partschi* Mich. – Schaffer: 35 |
| v. | 1915 | *Clypeaster sardiniensis* Cotteau. – Vadász: 137-138; figs. 30 |
| # v. | 1915 | *Clypeaster sardiniensis* Cott. var. *ellipticus* Vad. – Vadász: 137-138; figs. 31 |
| v. | 1915 | *Clypeaster crassicostatus* Sism. – Vadász: 139-140; figs. 32-33 |
| # ? v | 1915 | *Clypeaster inflatus* n.sp. – Vadász: 142; figs. 35 |
| pp | 1915 | *Clypeaster campanulatus* Schloth. sp. – Vadász: 144-145 |
| # | 1915 | *Clypeaster campanulatus* Schl. var. *declinatus* Vad. – Vadász: 144-145, fig. 37a [type material lost] |
| # | 1915 | *Clypeaster campanulatus* Schl. var. *rotundus* Vad. – Vadász: 144-145, fig. 37b [type material lost] |
| # | 1915 | *Clypeaster campanulatus* Schl. var. *sphaericus* Vad. – Vadász: 144-145 [type material lost] |
| # | 1915 | *Clypeaster depressus* n. sp. – Vadász: 150-152, figs. 42-43 [type material lost] |
| # v. | 1915 | *Clypeaster Lambert* Lov. var. *extensus* n. var. – Vadász: 172-173, figs. 64-65 |
| | 1915 | *Clypeaster suboblongus* Pom. – Vadász: 183-184, fig. 74 |
| # v. | 1915 | *Clypeaster felménesensis* n. sp. – Vadász: 183-184, fig. 74 [subadult specimen] |
| v. | 1915 | *Clypeaster partschi* Mich. – Vadász: 186-187, figs. 76-77 |
| ? | 1915 | *Clypeaster petaliferus* Segu. – Vadász: 190-191, fig. 80 |
| ? # | 1915 | *Clypeaster gracilis* n. sp. – Vadász: 191-192, figs. 81-82 [type material lost] |
| v. | 1924b | *Clypeaster Partschi* Mich. – Schaffer: 478; fig. 594 |
| ? | 1931 | *Clypeaster Partschi* Michelin. – Lambert: 87 |
| | 1936 | *Clypeaster partschi* Michelin – Paucă: 143, 194-195; pl. 1, figs. 1-2 |
| | 1937a | *Clypeaster partschii* Mich. – Kalabis: 45, fig. 2 |
| | 1938a | *Clypeaster partschi* Michelin – Kalabis: 3, 6, 9, 11 |
| | 1938 | *Clypeaster partschi* Michelin 1863 – Poljak: 189-190 |
| | 1939 | *Clypeaster Partschi* Mich. – Kapounek: 72 |
| | 1942 | *Clypeaster Partschi* Mich. – Schaffer: 94 |
| | 1949 | *Clypeaster campanulatus partschi* Michelin, 1861 – Kalabis: 46-48; 101-104; pl. 4, figs. 1-2 |
| | 1953 | *Clypeaster partschi* Michelin, 1861. – Szörényi: 68-69 |
| | 1954 | *Clypeaster campanulatus partschi* Michel. – Sieber: pl. 10, fig. 4 |
| ? | 1969 | *Clypeaster sardiniensis* Cotteau – Mihály: 256 |
| | 1969 | *Clypeaster sardiniensis* Cott. – Mitrović-Petrović: 125; pl. 3, fig. 3; pl. 4, figs. 1, 1a |
| | 1969 | *Clypeaster olisiponensis* Mich. – Mitrović-Petrović: 130-131; pl. 14, fig. 2; pl. 15; figs. 1, 1a |
| | 1969 | *Clypeaster gibbosus* (Risso) M. de Serr. – Mitrović-Petrović: 133-134; pl. 20, fig. 2; pl. 21; figs. 1, 1a |
| non | 1970 | *Clypeaster* cf. *partschi* Michelin, 1861. – Marcopoulou-Diacantoni: 252; pl. 23, fig. 3 |
| | 1984 | *Clypeaster sardiniensis* Cott.– Kókay et al.: 288 |
| | 1984 | *Clypeaster reidii* Wright – Mitrović-Petrović: 222-223; pl. 2, fig. 2; pl. 3, figs. 1, 1a |
| | 1984 | *Clypeaster sardiniensis* Cotteau – Mitrović-Petrović: 230; pl. 10, figs. 1, 1a-b |
| v. | 2002b | *Clypeaster* gr. *altus* (Lamarck) – Kroh: 11 |

**Type-material:**
*Clypeaster partschii* Michelin, 1861:
Syntypes: sixteen specimens in the collection of the Naturhistorsiches Museum Wien [NHMW 1857.38.24, 1857.38.26, 1857.38.29, 1857.38.30 (probably the specimen figured by Michelin, 1861), 1857.38.31-35, 1858.III.16-19, 1858.III.132, 2003z0049/0007, 2003z0049/0010]
Locus typicus: Kalksburg, Vienna
Age: Badenian (Langhian-Early Serravallian), Middle Miocene
Remarks: All specimens are accompanied by hand-written labels of Michelin. Both the labels and the specimens bear corresponding numbers. There is, therefore, little doubt that these specimens represent Michelin's reference specimens.

*Clypeaster felménesensis* Vadász, 1915:
Holotype: Ech 149 (Vadász, 1915: fig. 74); Museum of the Hungarian Geological Survey, Budapest
Locus typicus: Minişu des Sus (= Felménes), Arad, Romania
Age: Late Badenian (Early Serravallian), Middle Miocene

*Clypeaster inflatus* Vadász, 1915:
Holotype: Ech 148 (Vadász, 1915: fig. 35); Museum of the Hungarian Geological Survey, Budapest
Locus typicus: Slatina-Timiş (= Temes-Szlatina), Romania
Age: Late Badenian (Early Serravallian), Middle Miocene

*Clypeaster lamberti extensus* Vadász, 1915:
Holotype: Ech 232 (Vadász, 1915: figs. 64-65); Museum of the Hungarian Geological Survey, Budapest
Locus typicus: Alsótold, Nógrád, Hungary
Age: Late Badenian (Early Serravallian), Middle Miocene

*Clypeaster sardiniensis ellipticus* Vadász, 1915:
Holotype: MAFI Ech 155 (Vadász, 1915: fig. 31); Museum of the Hungarian Geological Survey, Budapest
Locus typicus: Armeniş (= Örményes), Romania
Age: Late Badenian (Early Serravallian), Middle Miocene

**Material:**
Early Badenian (Langhian) – Gainfarn, NÖ, Austria
NHMW: 1 specimen (NHMW 2003z0003/20)
Early ? Badenian (Langhian) – Rauchstallbrunngraben, near Baden, NÖ, Austria
NHMW: 3 specimens (NHMW 1976/1843/22, 1978/2040/11, 1978/2040/7)
Badenian (Langhian-Early Serravallian) – Kalksburg, Vienna, Austria
NHMW: 44 specimens, among them the **syntypes** of *C. partschi* Michelin (see above under Type-material) (NHMW 1857.38.24, 1857.38.25, 1857.38.29 to 1857.38.31, 1857.38.33 to 1857.38.35, 1858.III.16 to 1858.III.19, 1858.III.132, 1858.XXV.39, 1866.I.1274, 1890.X.1, 1904.VIII.63, 1904.VIII.65 to 1904.VIII.69, 1904.VIII.86, A2738, A2740, A2744, 1997z0178/1672, 2003z0049/0009 to 0026)
Badenian (Langhian-Early Serravallian) – Perchtolsdorf, NÖ, Austria
NHMW: 3 specimens (NHMW 1904.VIII.70, A 2735, 2003z0052/0001)
Badenian (Langhian-Early Serravallian) – Steinebrunn, NÖ, Austria
NHMW: 1 specimen (NHMW 1859.XLV.628)
Badenian (Langhian-Early Serravallian) – Vöslau, NÖ, Austria
NHMW: 1 specimen (NHMW 2003z0053/0001)
Badenian (Langhian-Early Serravallian) – Kemence, Hungary
NHMW: 1 specimen (NHMW 1858.XXXIX.13)
MAFI: 1 specimen [MAFI Ech 132 (referred to as *Clypeaster crassicostatus* Sism. by Vadász, 1915: 139-140, figs. 32-33)]
Late Badenian (Early Serravallian) – Alsótold, Nógrád, Hungary
MAFI: 1 specimen [MAFI Ech 232 (**holotype** of *Clypeaster lamberti extensus* Vadász, 1915: 172-73, figs. 64-65)]
Late Badenian (Early Serravallian) – Armeniş (= Örményes), Romania
MAFI: 1 specimen [MAFI Ech 155 (**holotype** of *Clypeaster sardiniensis ellipticus* Vadász, 1915: 138, fig. 31)]
Late Badenian (Early Serravallian) – Biatorbágy (= Bia), Pest, Hungary
MAFI: 1 specimen [MAFI Ech 154 (referred to as *Clypeaster sardiniensis* Cott. by Vadász, 1915: 137-138)]
Late Badenian (Early Serravallian) – Gârbova de Sus (= Felsö-Orbó), Romania
MAFI: 1 specimen [MAFI Ech 262 (figured as *Clypeaster partschi* Mich. by Vadász, 1915: 186-187, figs. 76-77)]
Late Badenian (Early Serravallian) – Globu Craiovei (= Globukrajova), Romania
MAFI: 3 specimen [MAFI Ech 271 (**syntype** of *Clypeaster acuminatus robustus* Vadász, 1915: 149-150), Ech 272 and 278 (referred to as *Clypeaster sardiniensis* Cott. by Vadász, 1915: 137-138)]
Late Badenian (Early Serravallian) – Luncaviţa (= Lunkavica), Romania
MAFI: 1 specimen [MAFI Ech 277 (referred to as *Clypeaster sardiniensis* Cott. by Vadász, 1915: 137-138)]
Late Badenian (Early Serravallian) – Minişu des Sus (= Felménes), Arad, Romania
MAFI: 1 specimen [MAFI Ech 149 (**holotype** of *Clypeaster felménesensis* Vadász, 1915: 183-184, fig. 74)]
Late Badenian (Early Serravallian) – Müllendorf (quarry of the Mühlendorfer Kreidewerke AG), Bgld, Austria
NHMW: 2 specimens (NHMW 1997z0178/1752, 2004z0112/0005)

Transitional specimens *partschii* Michelin, 1861 – *acuminatus* Desor in Agassiz & Desor, 1847:
Badenian (Langhian-Early Serravallian) – Kalksburg, Vienna, Austria
NHMW: 2 specimens (NHMW 1857.38.26, 1857.38.27)
Late Badenian (Early Serravallian) – Minişu des Sus (= Felménes), Arad, Romania
MAFI: 1 specimen [MAFI Ech 280 (**syntype** of *Clypeaster acuminatus robustus* Vadász, 1915: 149-150)]
Late Badenian (Early Serravallian) – Slatina-Timiş (= Temes-Szlatina), Romania
MAFI: 1 specimen [MAFI Ech 147 (**syntype** of *Clypeaster acuminatus robustus* Vadász, 1915: 149-150, fig. 41)]

Transitional specimens *partschii* Michelin, 1861 – aff. *gibbosus* de Serres, 1829:
Early Badenian (Langhian) – Gamlitz (Unterer Gnaser Bruch), near Ehrenhausen, Styria, Austria
NHMW: 1 specimen (NHMW 1868.I.Anhang.2)
Badenian (Langhian-Early Serravallian) – Kalksburg, Vienna, Austria
NHMW: 3 specimens (NHMW 1904.VIII.84, 1904.VIII.92, 2003z0049/0027)

Transitional specimens *partschii* Michelin, 1861 – aff. *reidii* Wright, 1855:
Badenian (Langhian-Early Serravallian) – Kalksburg, Vienna, Austria
NHMW: 1 specimen (NHMW 1857.38.32)
Badenian (Langhian-Early Serravallian) – Perchtoldsdorf, NÖ, Austria
NHMW: 2 specimens (NHMW 1890.X.9, 1904.VIII.71)

**Description:**
This morphotype has a low test height and a gently arched profile. The petaloid area is moderately inflated and its sides are either flush with the surface outside the petalodium or they form a very weak angle. Test height between 29 to 37 % TL.