	1996	*Echinolampas* sp. – Mączyńska: 41; pl. 1, figs. 10a-b
v	1998	*Echinolampas laurillardi* Agassiz– Schultz: 118; pl. 53, fig. 2
v.	2002b	*Echinolampas* sp. – Kroh: 12
v.	2003a	*Echinolampas* ? sp. – Kroh: 165; pl. 4, fig. 15

Material:
Egerian (Chattian-Aquitanian) – Steyregg (sandpit Treul), OÖ (see Roetzel et al., 1991; Kaiser et al., 2001)
NHMW: 5 specimens (NHMW 2004z0092/0001-5)
Late Eggenburgian (Early Burdigalian) – Gauderndorf (Himmelreich), NÖ, Austria
NHMW: 1 specimen (NHMW A606)
Remark: locality not confirmed, attached sediment untypical
Late Eggenburgian (Early Burdigalian) – Limberg (Zogelsdorf Fm., Hengl quarry), NÖ, Austria
NHMW: 10 fragments (NHMW 2003z0002/0009)
Badenian (Langhian-Early Serravallian) – Baden, NÖ, Austria
NHMW: 13 test fragments (NHMW 1846.37.957, 1852.II.1616)
Badenian (Langhian-Early Serravallian) – Oslip, Bgld, Austria
NHMW: numerous test fragments (NHMW 2003z0083/0005)
Late Badenian (Early Serravallian) – Stiefingbach (old mill, Pesendorf 16), Styria Austria
NHMW: 1 specimen (NHMW 2004z0114/0002)
Late Badenian (Early Serravallian) – St. Margarethen, Bgld, Austria
NHMW: 1 test fragment (NHMW 1989/66/5)
Late Badenian (Early Serravallian) – St. Margarethen (Kummer quarry), Bgld, Austria
NHMW: 1 crushed specimen (NHMW 2004z0001/0045)

Foreign material:
Late Badenian (Early Serravallian) – Buituri (= Bujtur), 20 km S of Deva, Romania
NHMW: 1 test fragment (NHMW 1852.II.1603f)

Dimensions (in mm)**:**

Inv. No.	TL	TW	TH
NHMW 2004z0092/0001	45.8	48.1	25.6
NHMW 2004z0092/0002	~65	>54	>24

Discussion:
Being easily recognisable, the genus *Echinolampas* has been often reported in the geological/palaeontological literature of Austria. Records listed under the present heading either lack sufficient information to attach them to any of the species described above or are based on material too fragmentary or poorly preserved for specific determination.

Recently a number of *Echinolampas* specimens from the Egerian (Chattian-Aquitanian) of Steyregg, OÖ were obtained by the NHMW from a private collector (Josef Kastl, Linz). Despite their poor preservation (Figs. 53.A-C) the specimens are nonetheless very interesting as they represent one of the first records and the only available specimens of this genus from the Egerian (material from earlier records could not be traced). They are rather small (none of the specimens is larger than 65 mm in length), have an angular outline with subequal length and width, a concave oral side, marginal periproct (fully on the oral side) and long petals. They are not well enough preserved for specific determination.

The specimen (Figs. 52.A-C) figured as *Echinolampas laurillardi* by Schultz (1998) is problematic. The label accompanying the specimen states that it comes from Himmelreich, near Gauderndorf (Lower Austria) but the preservation and attached sediment are untypical for this locality. Neither is it similar to the sediment of any of the other Austrian localities where echinolampadids were recovered. The specimen could not associated with any of the species documented from the Central Paratethys. The combination of its small peristome with very weakly developed bourrelets, the dense aboral tuberculation, the relatively high test and weakly sunken poriferous zones, as well as the inframarginal periproct (also visible in posterior view) is unparalleled in the other species discussed here. It is thus likely that the specimen does not come from the Central Paratethys at all and is left in open nomenclature here.

Occurrence:
Austria: Egerian (Chattian-Aquitanian) to Late Badenian (Early Serravallian)
Molasse Zone: Eggenburg (Bahnhof), NÖ (Fuchs, 1903b); Eggenburg (Brunnstube), NÖ (Nebelsick et al., 1991a); Eggenburg, surroundings, NÖ (Fuchs, 1877); Eggenburg region (Zogelsdorf Fm.), NÖ (Nebelsick, 1989); Gauderndorf, NÖ (Steininger, 1971d; Schultz, 1998); Limberg (Hengl quarry) NÖ (Nebelsick et al., 1991b); Steyregg (sandpit Treul), OÖ (Roetzel et al., 1991; [NHMW]); Plesching (phosphoritic sand), OÖ (Grill, 1935)
Vienna Basin: Baden, NÖ ([NHMW]); Gainfarn, NÖ (Kroh, 2002b); Leitha Mts. (Tollmann, 1985); Mödling, NÖ (Karrer, 1877); Müllendorf, Bgld (Tollmann, 1955; Schaffer, 1961); Niederleis, NÖ (Kroh, 2003a); Steinabrunn, near Drasenhofen, NÖ (Sieber, 1958b);
Eisenstadt-Sopron Basin: Oslip, Bgld ([NHMW]); St. Margarethen, Bgld ([NHMW]); St. Margarethen (Kummer quarry), Bgld ([NHMW])
Styrian Basin: Stiefingbach (old mill, Pesendorf 16), Styria ([NHMW])

Paratethys (non-Austrian occurrences): Badenian (Langhian-Early Serravallian)
Great Hungarian Basin (Pannonian Basin): Hidas, Hungary (Roth von Telegd, 1899)
Transylvanian Basin: Buituri (= Bujtur), Romania ([NHMW])

Unconfirmed records of *Echinolampas* from the Central Paratethys

***Echinolampas italicus* Lambert, 1906**

1915 *Echinolampas italicus* Lamb. – Vadász: 212-213; fig. 98

Reported occurrence: Badenian of Livezile (= Ùrháza, =Vládháza), Alba, Romania (Vadász, 1915)

Remarks: The reference material of Vadász (1915) was not seen by the present author and from Vadász's description and illustrations it is not clear how this species might be differentiated from flat specimens of *E. hemisphaerica*.

***Echinolampas* aff. *italicus* Lambert, 1906**

1955 *Echinolampas* aff. *italicus* Lamb. – Tollmann: Tab. 5b

Reported occurrence: sandpit between Großhöflein and Kleinhöflein, Bgld, Austria (Tollmann, 1955)

Remarks: The name *E. italica* was proposed by Lambert (1906a) for *Echinolampas hemisphaerica* Manzoni (1880a): 186; pl. 1, figs. 1-3), non Lamarck (1816). This species has never again been reported from Austria and the material on which this record is based could not be traced. It is unclear to which of the species discussed above this record refers.

***Echinolampas dumasi* Cotteau, 1893**

v 1915 *Echinolampas Dumasi* Cott. – Vadász: 216; fig. 102; pl. 10 (4), fig. 5

Reported occurrence: Late Badenian (Early Serravallian) of Biatorbágy (= Bia), Pest, Hungary (Vadász, 1915)

Remarks: This record is based on a single specimen in the MAFI collection (Ech 243). It differs from the species discussed above by its strongly inflated oral side, its relatively narrow petals and its periproct which lies inframarginally to marginally. It can, nevertheless, not be ruled out that this specimen is simply an abnormally developed *E. hemisphaerica* and additional specimens are needed to settle this issue.

Echinolampas dacica Vadász, 1915 & *Echinolampas dacica humilis* Vadász, 1915

*	1915	*Echinolampas dacicus* n. sp. – Vadász: 211-212; fig. 97a; pl. 12 (6), fig. 5
*	1915	*Echinolampas dacicus* var. *humilis* Vad. – Vadász: 211-212; fig. 97b; pl. 12 (6), fig. 6

Reported occurrence: Badenia of Livezile (= Ùrháza, =Vládháza), Alba, Romania (Vadász, 1915)

Remarks: The differential diagnostic features to *E. hemisphaerica* outlined by Vadász (1915) do not allow a confident separation of the two species. It seems likely that *E. dacica* may turn out synonymous with *E. hemispherica*. Yet, without having seen the types or any other specimens attributed to this species the author hesitates to synonymise them.

Genus *Conolampas* Agassiz, 1883

Type-species: *Conoclypus sigsbei* Agassiz, 1878, by original designation.

Synonyms of *Conolampas*:
Pygasterides Lovén, 1888,p. 13. Type-species: *P. relictus* Lovén, 1888, p. 13, by monotypy.
Scutolampas Lambert, 1906, p. 33. Type-species: *Conoclypus plagiosomus* Agassiz, 1840b, p. 5 [*nomen nudum*], by original designation.
Hypsoheteroclypus Szörényi, 1953: p. 76. Type-species: *Hypsoclypus doma* Pomel, 1887, p. 163, by original designation.

Potential synonyms of *Conolampas*:
Hypsoclypus Pomel, 1869, p. 25. Type-species: *Galerites semiglobus* Lamarck, 1816, p. 311, by subsequent designation (Stefanini, 1907: 348).
Heteroclypeus Cotteau, 1891, p. 194. Type-species: *Galerites semiglobus* Lamarck, 1816, p. 311, by original designation.

Emended diagnosis: Large campanulate to bell-shaped echinolampadid with straight, long and distally open petals; outline circular to subpentagonal; apical disc monobasal, knob-shaped in some species; straight, narrow poriferous zones; periproct transversely elongated and inframarginal; bourrelets and phyllodes well developed; basicoronal plates of the interambulacra 1 and 4 exsert in adult specimens; aboral tuberculation sparse, rarely exceeding 100 primary tubercles/cm² in adult specimens; distance between aboral primary tubercles more than one times their diameter (Kroh & Mooi, in prep.).
Distribution: ? Oligocene of the Caribbean; Early Miocene to Pliocene of the Mediterranean; Recent: Caribbean area and Indo-Malayan regions (Kroh & Mooi, in prep.).

Discussion: Originally the fossil species of this genus were associated with the genus *Conoclypus* (Agassiz, 1840b: 5; Agassiz & Desor, 1847a: 167-168; Desor, 1858: 318-323,...) or *Conoclypeus* [Manzoni, 1880a: 187, 1881: 174; Mazzetti, 1882a: 123-125; *Conoclypeus* is a *nomen nudum* according to Durham et al. (1966: U633)] because of similarities in general test shape. Later these species were removed from the conoclypids and recognised as having affinities with the echinolampadids by Pomel (1869: 25, 62-63), mainly because of similarities in the poriferous zones and the shape of the periproct (Cotteau, 1891: 194). Munier-Chalmas (fide Stefanini, 1908c: 348), however, showed that there is no Aristotle's lantern in *C. semiglobosus* contrary to the "true" conoclypids. Based on this, and the presence of poriferous zones of unequal length within the petals, Stefanini (1908c) placed most of the Neogene taxa ascribed to the genera *Conoclypus*, *Hypsoclypus* and *Heteroclypeus* into the genus *Echinolampas*.

Subsequently the genera *Hypsoclypus* Pomel, 1869, *Heteroclypeus* Cotteau, 1891, *Scutolampas* Lambert, 1906 and *Hypsoheteroclypus* Szörényi, 1953 were established for species of this group, resulting in many discussions how to separate these genera and which species they should include. Part of these discussions resulted from the action of Lambert (1907a: 54), who invalidly designated *C. plagiosomus* Agassiz, 1840b as type species for *Hypsoclypus* Pomel, 1869. However, according to the ICZN-rules this is not possible since *C. plagiosomus* was not included in the original publication and, moreover, is a *nomen nudum* (see below). Another hotly disputed question was whether *C. plagiosomus* and *C. lucae* are synonyms and which of those two names has priority [Kier (1962: 112) showed that *Conoclypus plagiosomus* is a junior subjective synonym of *C. lucae*. Agassiz's (1840b: 5) *Conoclypus plagiosomus* is a *nomen nudum* since no description, definition or indication is given (ICZN 4th ed., 2000, Article 12.1.). In Agassiz & Desor (1847a: 168) both taxa (*plagiosomus* and *lucae*) are accompanied by a short description and are thus available names (ICZN 4th ed., Articles 11 and 12). Moreover, they count as simultaneously published. Desor (1858: 322) acting as "the first reviser" stated that *C. lucae* and *C. plagiosomus* are conspecific and gave preference to *C. lucae*, which is thus the valid name for the species (ICZN 4th ed., Article 24.2.). In the copy of Agassiz & Desor (1847a) in the NHMW-library, *ucæ* instead of *lucæ* is written on page 168, however, on page 361 the name is correctly spelled. Desor (1858: 322) acting as "the First Reviser" choose the spelling *lucae*, which is therefore the correct one (ICZN 4th ed., Article 32.2.1.). Initially Lambert (1907a: 54) also considered *C. lucae* and *C. plagiosomus* as synonyms, but treated them as different species later. This erroneous opinion of Lambert (1913a: 131-133), Lambert & Thiéry (1921: 376) and Lambert & Jeannet (1928: 124, 178) was based on a specimen labelled erroneously as coming from the "Helvétien" of La Couronne, France. According to Roman & Strougo (1988: 147) the specimen figured by Lambert (1913a: pl. 10, figs. 7-9) is of Eocene age and belongs to *Echinolampas africana* var. *fraasi* de Loriol, 1880.]. The action of Stefanini (1908c: 348), who designated *C. semiglobus* as type species, rendered the discussion of the differences between *Hypsoclypus* and *Heteroclypeus* futile, since the type-species of both taxa is identical due to this decision.

Kroh & Mooi (in prep.) showed that the type-species of the above mentioned genera, as well as a number of closely related species are congeneric with the extant species of the genus *Conolampas*, a deeper water echinolampadid. Main arguments for placing these species in *Conolampas* are the aboral tuberculation (compare Mooi, 1990a), which is very distinct from the tuberculation of *Echinolampas*, the exsert condition of basicoronal plates in the interambulacra 1 and 4 (in adult specimens) and the narrower, straight or divergent poriferous zones in the petals. In addition, the great size and general shape of the test, particularly the very low ambitus, and the nearly flat oral surface are identical with these features in other members of the genus *Conolampas* (Mooi, 1990a). Although not unique to *Conolampas*, the well developed bourrelets and phyllodes and tiny naked zone in the posterior interambulacrum are consistent with this genus.

Pygasterides Lovén, 1888 is a genus established for a species based on juvenile material of *Conolampas sigsbei* Agassiz, 1878 (compare Mortensen, 1948a).

Remarks: In the Miocene of the Mediterranean and Paratethys more than 20 species of this group were reported (Airaghi 1900; Stefanini, 1908c; Roman, 1965). This inflation of nominal taxa was caused by the variable gross morphology of this group and the praxis of basing species on minor variations in overall test morphology. However, specimens from single localities and narrow time horizons [e.g. specimens from the Early Badenian of the Vienna Basin or the Early Badenian of Pod'yarkov (= Podjarków), in the Ukraine] show a wide variation in gross test morphology. Szörényi (1953: 78-84) described and illustrated eight different "*Hypsoheteroclypus*" species from a single locality on base of a single specimen each; most of these specimens show minor variations in overall test morphology only and it is highly questionable whether all of these species are justified. The specimen Szörényi (1953: 84-85) determined as *Echinolampas hemisphaerica* also belongs to *Conolampas*.

Analysis of the Austrian material revealed four different morphotypes in two different geological horizons. One of these morphotypes is based on a single specimen [NHMW V.b.ß.k.12 (6983)] of unknown stratigraphic and doubtful geographic origin [the label states "(angeblich Nattheim) wahrscheinlich Steiermark"]. Nattheim is a locality in Germany famous for its beautiful Jurassic fossils but there are no marine sediments of the Neogene in this area. This specimen is similar to the specimens figured by Stefanini (1908c: pl. 13, fig. 1a-c) as *Echinolampas ugolinii* and differs from the other specimens by its longer petals, higher tubercle density, broader posterior paired petals and higher number of tubercles across the interporiferous zone. Since no other specimens similar to this one turned up in any Neogene deposit of the Central Paratethys, it is probably not from this area at all. Therefore it is excluded from further consideration. Most specimens come from the Early Badenian (Langhian) time-slice, where this genus was widely distributed throughout the Central Paratethys (Austria, Hungary and Ukraine). These specimens represent two morphotypes, which are very similar and differ mainly in their relative test height. The fourth morphotype is represented by a single specimen in the Austrian material and comes from Late Badenian (Early Serravallian) sediments. It differs from the Early Badenian morphotypes by its hemispherical profile, higher tuberculation density, shorter petals and even more inflated madreporite.

Four species of *Conolampas* are known today, only two of which co-occur (*C. diomedeae* and *C. malayana*). These two species are well separated by distinct morphological features (i.e. the length of the poriferous zones, which extend nearly up to the ambitus in *C. diomedeae*, whereas they extend only about 1/2 of the corresponding test radius in *C. malayana*). Mortensen (1948a) used the following morphological features to separate the extant species of *Conolampas*: 1) Respiratory pore morphology (isopores or anisopores); 2) Lengths of the petals (1/2-2/3 of the corresponding test radius or extending nearly to the ambitus; 3) position of the periproct; 4) position of the peristome; and 5) width of the petals.

Ecology and biogeography: Today four extant species of *Conolampas* are known, which occur at depths between 120 to 800 meters in the Caribbean (*C. sigsbei*), the Maldives (*C. murrayana*) and the Philippines (*C. diomedeae* and *C. malayana*) (Mooi, 1990a). As in *Echinolampas*, little is known on the biology of the extant species of *Conolampas*. For the Indo-Pacific species only the collection depths are known [*C. diomedeae*: 265 m (Mortensen, 1948a), 195-181 m (David & de Ridder, 1989); *C. malayana*: 245 to 400 m (Mortensen, 1948a); *C. murrayana*: 229 m (Mortensen, 1948a)]. *C. sigsbei*, from the Caribbean Sea and the eastern margin of the Gulf of Mexico, is better studied. It is found between 120 and 800 m as epibenthic browser on substrate composed of fine carbonate debris and small foraminifers. As it moves over the surface it leaves a trail as wide as its test (based on direct observations from submersibles by David Pawson and Charles Messing, in Mooi, 1990b: 698).

Predation scars can commonly be observed on specimens of this genus (Pl. 60, Fig. 2d). These scars consist of irregularly circular holes in the test, which are tentatively attributed to boring predation by cassid gastropods (for more information on drilling predation see Kowalewski & Nebelsick, 2003 and references therein). This genus is generally rather rare, and seems to be associated with slightly deeper habitats. It is usually found in limestone (rudstone) or coarse calcareous sandstone. An exception of this is a single specimen of *C. subpentagonalis* found in the sediments of the Hartl Formation (Eisenstadt, Austria), which was interpreted as very shallow, higher energy deposits (Kroh et al., 2003).

Conolampas subpentagonalis (Gregory, 1891)

(Pl. 58, Figs. 1, 3; Pl. 59, Figs. 1a-b; Pl. 60, Figs. 1-2)

.	1869a	*Conoclypus plagiosomus* Ag. – Laube: 183
	1870	*Conoclypus plagiosomus* Ag. – Laube: 314
	1871	*Conoclypus plagiosomus* Agassiz (Teste Wright). – Laube: 67-68; pl. 19, fig. 3
?	1877	*Conoclypeus* – Fuchs: 667
?	1878	*Conoclypus plagiosomus* Ag. – Hilber: 563, 575
* pp	1891	*Heteroclypeus subpentagonalis*, n. sp. – Gregory: 599-600
#.	1900	*Heteroclypus Nevianii*, n. f. – Airaghi: 177-178; pl. 1, figs. 5-6
?	1907	*Echinolampas plagiosomus* Ag. sp. – Vogl: 245, 306
v.	1915	*Echinolampas* (*Heteroclypeus*) *subpentagonalis* Greg. – Vadász: 201-202; text-fig. 91
v.	1915	*Echinolampas* (*Heteroclypeus*) *semiglobus* Lam. – Vadász: 203
	1915	*Echinolampas* (*Heteroclypeus*) *Nevianii* Air. – Vadász: 204-205; text-fig. 92
?	1926	*Echinolampas subpentagonalis* Greg. – Strausz: 213, 368
.	1938	*Heteroclypeus cotteaui* Lambert 1907 – Poljak: 194-195; pl. 9, figs. 1, 1a
?	1950	*Hypsoclypus subpentagonalis* Greg. – Szörényi: 145
? #	1950	*Hypsoclypus egregyensis* n.sp. – Szörényi: 143-145; pl. 1, fig. 6; pl. 2, figs. 1, 1a
? #	1953	*Hypsoheteroclypus plagiosomus corsicanus* n. ssp. – Szörényi: 28-29, 78-79; pl. 4, figs. 1, 1a-b
	1953	*Hypsoheteroclypus montesiensis* (Mazzetti), 1881, (Stefanini), 1907 – Szörényi: 30-31, 80-81; pl. 5, figs. 3, 3a-b
?	1953	*Echinolampas hemisphaericus* (Lamarck), 1816. – Szörényi: 34, 84-85; pl. 3, figs. 2, 2a-b
?	1962	*Echinolampas lucae* (Desor) – Kier: 111-113; text-fig. 93; pl. 30, fig. 5; pl. 31, fig. 1; pl. 32, fig. 1
	1963	*Conoclypus plagiosomus* Agassiz – Müller, 515; figs. 677B a-b
	1965	[*Echinolampas* (*Hypsoclypus*)] *egregyensis* Szörényi 1950 (*Hypsoclypus*) – Roman: 306
	1965	[*Echinolampas* (*Hypsoclypus*)] *nevianii* Airaghi 1900 (*Heteroclypus*) – Roman: 307
	1965	[*Echinolampas* (*Hypsoclypus*)] *subpentagonalis* Gregory 1891 (*Heteroclypeus*) – Roman: 308
	1981	*E. subpentagonalis* Greg. – Halmai: 106
v pp	2002	*Conoclypus* sp. – Kazár: 153; fig. 1
	2003b	*Echinolampas subpentagonalis* (Gregory, 1891) – Kroh: 251 [literature review]

Type-material:

Heteroclypeus subpentagonalis Gregory, 1891:

Holotype: the specimen figured by Laube (1871: pl. 19, fig. 3); Geological Survey of Austria. The holotype could not be located at the Geological Survey in Vienna. It is also not found in

the Catalogue of this institution dating back to the beginning of the second world war and has to be considered lost.
Type-area: Großhöflein, Bgld or Zirknitz, Styria (both Austria)
Age: presumably Early Badenian (Langhian), Middle Miocene

Heteroclypus nevianii Airaghi, 1900:
Holotype: specimen figured by Airaghi (1900: pl. 1, figs. 5-6); Museo civico di Milano, Italy [not examined]
Locus typicus: Vena presso Monteleone Calabro, Southern Italy
Age: Middle? Miocene

? *Hypsoheteroclypus plagiosomus corsicanus* Szörényi, 1953:
Holotype: the specimen figured by Szörényi (1953: pl. 4, figs.1, 1a-b); collection of the University Lwów, Ukraine, specimen no. 6 [not seen]
Locus typicus: Pod'yarkov (= 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: As in other species established by Szörényi (1953) the specimen number of the holotype is ambiguous. Specimen no. 6 is mentioned under *Scutella paulensis* as well as under this species.

Material:
Early Badenian (Langhian) – Eisenstadt (basal Hartl Fm.), Bgld, Austria
Wanzenböck coll.: 1 specimen
Early Badenian (Langhian) – Retznei [Weissenegg Fm., Lafarge quarry (formerly Perlmoser)], Styria, Austria
Wanzenböck coll.: 1 specimen (W15)
Early Badenian (Langhian) – Stotzing (sandpit Mayer), Bgld, Austria
NHMW: 1 specimen (NHMW 2003z0008/0001)
Wanzenböck coll.: 4 specimens (W8-W11)
Early ? Badenian (Langhian) – Ewitsch, Styria, Austria
NHMW: 1 specimen (NHMW 2002z0181/0005)
Badenian (Langhian-Early Serravallian) – Eisenstadt, Bgld, Austria [possibly from the so-called "Terebratelfundstelle", Großhöflein near Eisenstadt, based on adhering sediment; certainly not from Müllendorf (as the younger label states) or the Hartl Fm., Eisenstadt]
GBA: 1 specimen (no inventory no.)

Foreign material for comparison:
Ottnangian (Late Burdigalian) – Fót, Hungary
MAFI:2 specimens [MAFI Ech 242 (figured specimen of *E. subpentagonalis* in Vadász, 1915: fig. 91)], 268 (reference material of *E. subpentagonalis* in Vadász, 1915)]
Early Badenian (Langhian) – Mátraverebély, Nógrád, Hungary
MAFI:1 specimen [MAFI Ech 433 (reference material of *E. semiglobus* in Vadász, 1915)]

Dimensions: see Tab. 10

Description (based on the Austrian specimens)**:**
Size and shape: The test is large with up to 15 cm test length. The outline is subcircular to very slightly subpentagonal. Both anterior and posterior margin are rounded. The maximum width and height coincide with the position of the apical disc. In some specimens the maximum width may lie slightly posterior of the apical disc. The profile is low conical with slightly inflated slopes. The ambitus is thin and rounded and it lies very low on the test. The oral surface is nearly flat.
Apical disc: The apical disc lies subcentrally to slightly anterior of the centre. The apical disc is monobasal with four large, circular gonopores and five small ocular pores. The madreporite is pentagonal in outline and highly swollen (knob-shaped) and bears numerous small hydropores, as well as small tubercles.
Ambulacra: The ambulacra are semi-petaloid on the aboral surface. They consist of two slightly diverging rows of closely spaced conjugated anisopores in each ambulacrum. The adradial pores in each pair are large, slightly oblique and teardrop-shaped. Adapically the two poriferous zones of each ambulacrum converge towards each other and the apex, and both poriferous and interporiferous zones are distinctly depressed in this area. The poriferous zones of the "petals" are very slightly depressed. In the paired ambulacra, the poriferous zones are of slightly different length: They are longer in the posterior half of the anterior paired ambulacra (IIa and IVb) and the anterior half of the posterior paired ambulacra (Ib and Va). The frontal petal is slightly curved towards the left and extends about 65 to 80 % of the corresponding test radius (measured along the slope of the test, not in planar view). The anterior paired petals are similar in length to the frontal petal, the posterior paired petals are slightly longer (70-85 % TL). Outside the petals only minute unipores with sunken attachment area and adoral positioned neural canal are found. The tuberculation on the aboral interporiferous zones is not very dense; the spacing between the primary tubercles is about one and a half to two times their diameter. Miliary tubercles are loosely spread among them. In the poriferous zones, only small miliary tubercles are present, they are situated on the ridges between adjacent pore pairs. Halfway along the test height there are 5 to 6 primary tubercles across the interporiferous zones.
On the oral side the ambulacra are depressed around the peristome and form well developed phyllodes (Pl. 60, Fig. 2f). The poriferous zones bear small unipores with sunken attachment area and adorally positioned neural canal. The unipores of the phyllodes are slightly larger. The tuberculation of the ambulacra on the oral surface is very similar to those on the interambulacra. The phyllodes consist of three series of unipores in each half-ambulacrum. An "outer" or adradial series consisting of large, closely spaced unipores with rather large attachment area. An "inner" or perradial series consisting of smaller, slightly vertically elongated unipores, which are more widely spaced. Between those two a third series consisting of widely spaced unipores is found. The two buccal pores are of similar size as the pores from the adradial series, but distinctly elongated vertically. In the adoral third of the phyllodes there is a double row of shallow pits (sphaeridial pits) running along the central suture.
Interambulacra: Around the apex the interambulacra are distinctly inflated. The tuberculation on the aboral side is fairly homogenous. The primary tubercles are small and widely spaced. The mean distance between them is about one and a half to three times their diameters. Miliary tubercles are loosely spread among them. Directly at the ambitus the spacing of the primary tubercles becomes very tight suddenly, with the areoles of the tubercles nearly touching each other. On the oral side the spacing of the primaries is more widely again, except near the margin. Along the central suture of interambulacrum 5 there is a zone of especially widely spaced tubercles [similar to the "naked zone" Kier (1962) noted in many species of *Echinolampas*]. The primary tubercles of the oral side are about one and a half to two times larger than those of the aboral surface. Data on the tubercle density of both ambulacra and interambulacra can be found in Tab. 10. On the oral side the interambulacra are highly inflated around the peristome and along their interradial sutures, forming well developed bourrelets.
Peristome: The peristome lies centrally to slightly anterior of the centre. It is oval (transversely elongated) to slightly subpentagonal in shape. It is always smaller than the periproct, being about 10-11 % of TL wide. Inside the test, no auricles are present.
Periproct: The periproct is situated very close to the margin in interambulacrum 5, but lies fully on the oral surface. It is large, being 12-14 % of TL wide. The shape of the peristome is oval, transversely elongated.

Differential diagnosis:
C. semiglobus (Lamarck) from the Aquitanian of the Aquitaine Basin differs from this species by its broader petals, by its small

periproct (8-10% TW vs. 12-14 % TW in *C. subpentagonalis*), denser aboral tuberculation, higher number of tubercles across the interporiferous zones (10 to 12 vs. 5 to 6 in *C. subpentagonalis* and *C. elegans*), its more strongly developed floscelle and the presence of primary tubercles on the ridges between the respiratory pores (based on a specimen from the type region Dax, France housed at the NHMW under the number 1898.I.14)

C. lucae (Desor in Agassiz & Desor, 1847) [syn. *C. plagiosomus* (Agassiz in Agassiz & Desor, 1847)] from the Burdigalian of the Rhône Basin differs by its moderately arched profile (not at all conical as in *C. subpentagonalis* or *C. elegans*), lack of an inflated madreporite and long petals which abut only shortly before they reach the ambitus (based on the description and illustration in Philippe, 1998).

C. pignatarii (Airaghi, 1900) [syn. *C. hemsphaericus* (Gregory, 1891) and *C. melitensis* (Lambert & Thiéry, 1921)] from the Serravallian ? to Messinian of the Central Mediterranean differs from this species by its high (TH ~ 55 % TL), hemispherical profile, much broader petals and its smaller periproct (8-10% TW vs. 12-14 % TW in *C. subpentagonalis*) (based on the description of Stefanini, 1907).

Discussion:
This species differs from *C. elegans* mainly by its lower relative test height. In a scatter-plot of test length versus test height two groups, which align along two different regression lines can be observed (Fig. 54). Due to the fact that both this species and *C. elegans* are relatively rare and often deformed by compaction multivariate statistics proved to be problematic. A preliminary principal component analysis (in the following: PCA) with a reduced data set using the variables TL, TH, APP_ant, APP_post, APP_Cr, PPP_Cr, PPP_W, Tubs1 and Tubs2 (for an explanation of the variables see Fig. 55) was carried out. Unfortunately only eleven specimens could be used for the analysis, since the other cases had too many missing values. The PCA resulted in 3 factors controlling the variance in the data-set. The first factor had high loads of most variables except these concerning tubercle density and test height. The second factor was controlled by the tubercle density variables and the third factor by test height (see Fig. 56.B). A 3D-scatter plot of the resulting factors shows a separation of the data-set into two groups as assumed by the initial ad-hoc hypothesis based on careful examination of the specimens. The two point clouds lie very close together, partially overlapping, however, and the number of cases is very low, effectively limiting the success of this kind of analysis (Fig. 56.A). PCA's with even more reduced data-sets, facilitated more cases but gave no useful results due to the low number of variables employed (PCA calculated with SPSS 11.0.1).

Therefore another approach was used to test the separation of the two groups. Test length and height data from the examined specimens and from the specimens published in the literature on Central Paratethyan and Northern Italian specimens (Stefanini, 1907; Vadász, 1915; Poljak, 1938 and Szörényi, 1953) were used to generate a scatter-plot and calculate two regression lines (Fig. 54). These were tested using the method proposed by Zorn (1972: 373). The test shows a significant difference at a 99% confidence level (Z = 4.293; Tab. 11). The Kolmogorov-Smirnov-Test was employed to test if the distributions of TL and TH conform to normal distributions. Both variables show a normal distribution according to this test, but this might be an artefact due to the low number of cases (n=45). The independent sample t-test confirms that there is a significant difference between the two groups in the variable TH (Sign. = 0.003), but not in TL (Sign. = 0.185) (t-test calculated with SPSS 11.0.1).

Therefore, the two observed morphotypes are considered as distinct species for the time being, but this should be critically tested with more well preserved specimens. Unfortunately no data on the test height variability in the only common extant *Conolampas* species (*C. sigsbei*) is available in the literature.

Another possible explanation for the observed differences in relative test height would be the "flatness-rule" (German: "Flachheitsregel") of Ernst (1970: 54-60). According to this

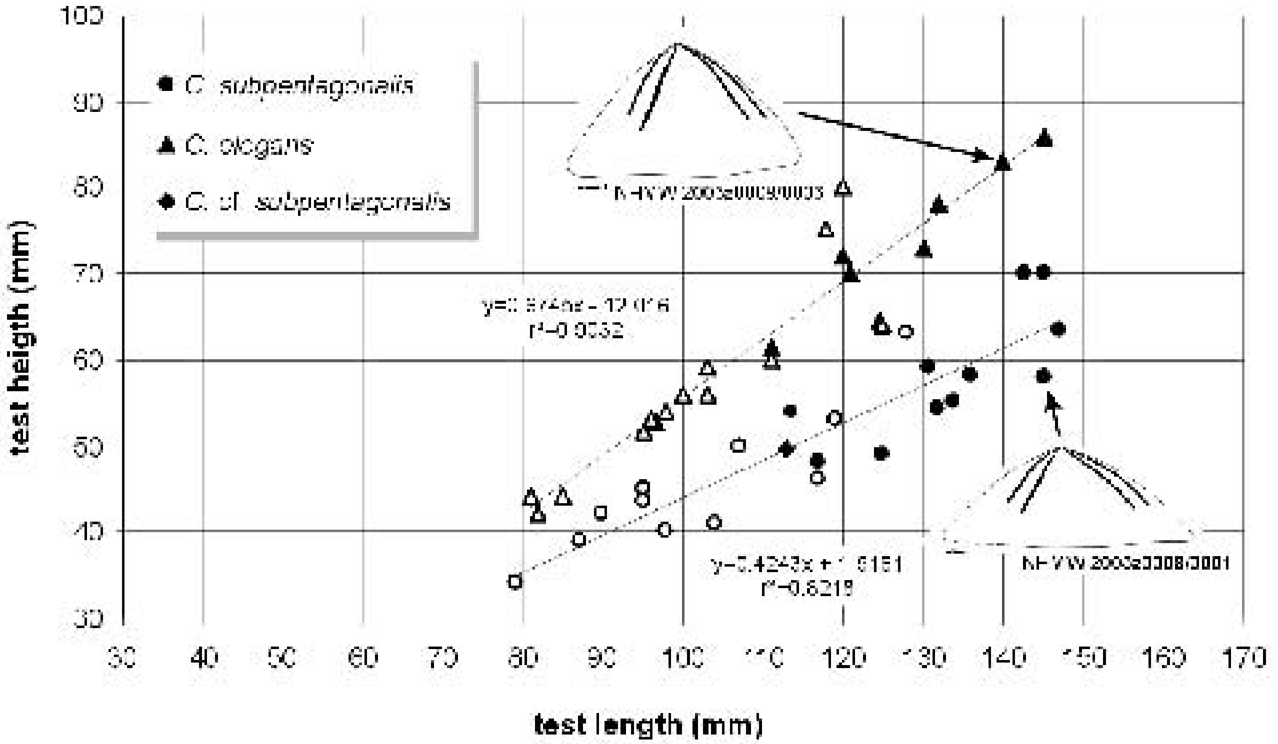

Figure 54: Scatter plot of test length versus test width in *Conolampas elegans* (Airaghi, 1900) and *C. subpentagonalis* (Gregory, 1891). Solid symbols mark specimens from Austria, open symbols literature data (Stefanini, 1908c; Vadász, 1915; Poljak, 1938; Szörényi, 1953).

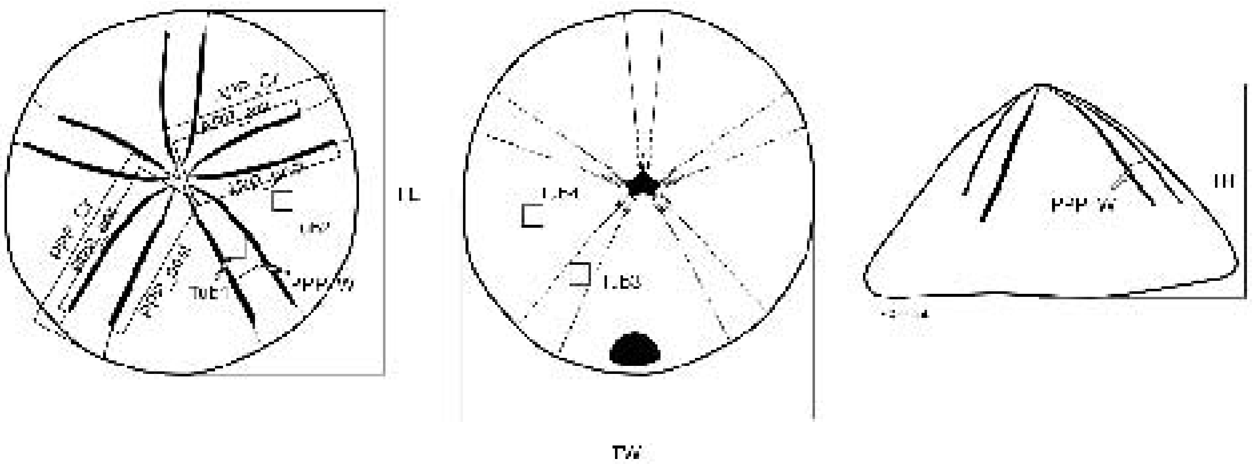

Figure 55: Schematic drawing of *Conolampas elegans* showing the variables used in the PCA of *Conolampas*. TL, TH, APP_ant, APP_post, APP_Cr, PPP_Cr, and PPP_W are linear measurements (note that the variables concerning the poriferous zones and the corresponding test radius were not measured in planar view; instead they were measured parallel to the test surface); Tubs1 to 4 are tubercle counts performed in the area indicated by the respective square or (in case of poor preservation of that area) on the respective location on the other half of the bilaterally symmetrical test.

theory the test height of epibenthic irregular echinoids is correlated with the amount of terrigenous material in the substrate (high morphotypes in pure limestone, low morphotypes in terrigenous sediments). Ernst observed this in six Late Cretaceous genera (*Galerites*, *Conulus*, *Echinocorys*, *Offaster*, *Cardiotaxis* and *Galeola*) in the chalk facies of Northern Europe. However, even Ernst was not sure how to interpret this phenomenon and did not treat it consistently in all these genera. In some he placed the higher and lower group in a single species, in others in different species. Moreover, in some of these genera these groups have only barely overlapping variation ranges and few intermediary forms (e.g. *Echinocorys*, see Ernst, 1970: fig. 5) as in the considered *Conolampas* material. Unfortunately, this "flatness-rule" was never tested with extant irregular echinoids. Although Ernst (1973a) did a lot morphometrics on extant Mediterranean echinoids these were mostly epibenthic regular echinoids (*Arbacia*, *Paracentrotus* and *Sphaerechinus*). In these the test height varies considerably between 35 to 65 % test diameter and seems to be controlled (at least partially) by water energy and turbulence. As the two morphotypes of *Conolampas* occur within the same layer and sediment type a correlation to sediment grain size and chemistry seems unlikely in the present case.

Nichols (1959: 405) discussed the possibility that the existence of high and low types might be related to water depth. This, however, seems to be unlikely in the case of *Conolampas*,

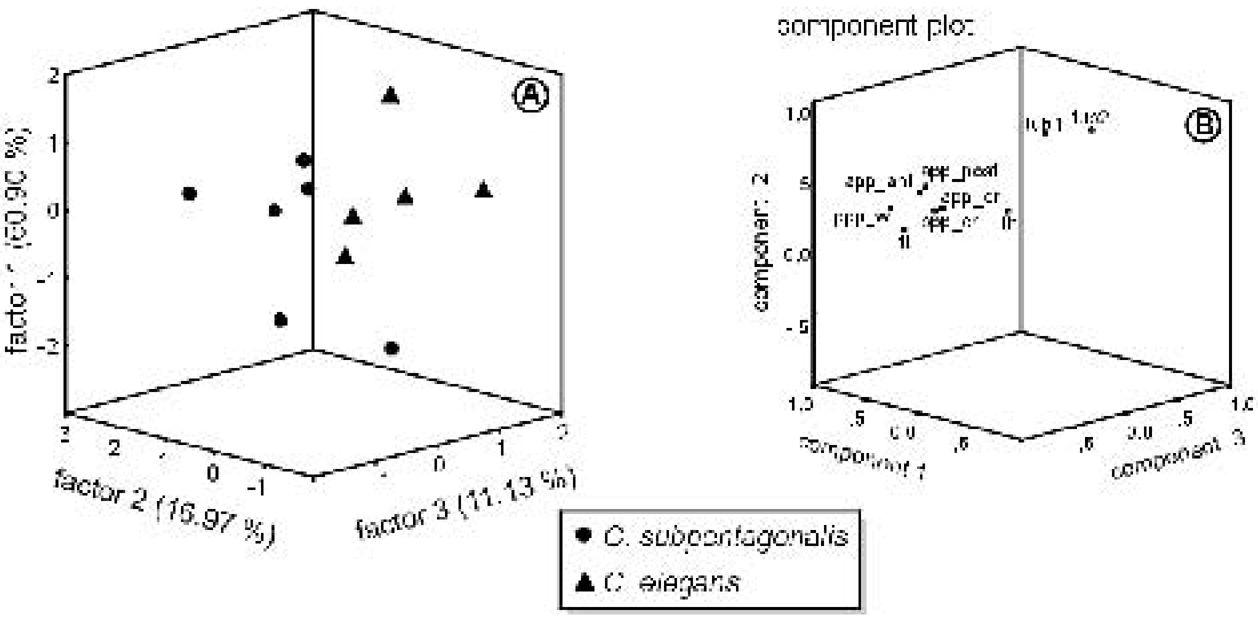

Figure 56: PCA of *Conolampas elegans* and *C. subpentagonalis*: 3-D scatter plot (A) of the three factors calculated by the PCA (percentages of variance explained by the individual factors is found in brackets behind the factor numbers) and component plot (B) showing the factor loading for the used variables (TL, TH, APP_ant, APP_post, APP_Cr, PPP_Cr, PPP_W, Tubs1 and Tubs2). Factors 1 to 3 explain 89 % of the variance in the present sample.

	n	b	r^2	SB
Conolampas elegans	22	0.6745	0.9032	0.04474127
Conolampas subpentagonalis	23	0.4243	0.8218	0.03734762
n=no. of specimens; b=gradient of the regression line; r^2=coefficient of determination; SB=standard deviation of r				

Table 11: Results of the comparison of the regression lines of test length versus test width in *Conolampas elegans* (Airaghi, 1900) and *C. subpentagonalis* (Gregory, 1891) after the method of Zorn (1972) (regressions calculated with MS Excel 97).

since the two morphotypes occur together in the same horizon in the outcrops Stotzing and Retznei.

It is widely agreed, that the Austrian morphotype belongs into a different species than the specimens from the Burdigalian of the Rhône Basin (Gregory, 1891; Roman, 1965; Philippe, 1998) and this could be confirmed by the present study. Unfortunately Laube's specimens were lost, among them the holotype of *C. subpentagonalis*, necessitating the proposal of a neotype.

Philippe (1998: 98-99) included *Heteroclypeus subpentagonalis* Gregory, 1891 into the synonymy of *Conolampas lucae* (Desor in Agassiz & Desor, 1847) [under the name *Echinolampas* (*Hypsoclypus*) *plagiosomus* (Agassiz, 1840b)], yet he explicitly excluded the material of Laube (1871). This action, however is not possible, since the type specimen of *H. subpentagonalis* is Laube's specimen (compare Gregory, 1891: 599-600).

Gregory (1891: 599-600) based the name *subpentagonalis* on the pentagonal shape shown by the figure in Laube (1871). Laube, however, stated explicitly that his specimens had a circular outline and several of the figures given in his work do not correspond exactly to the material on which they are based.

Occurrence:

<u>Austria</u>: Early Badenian (Langhian)

Vienna Basin: Stotzing (sandpit Mayer), Bgld (pp Kazár, 2002; [NHMW]); Vienna Basin (? Fuchs, 1877)

Eisenstadt-Sopron Basin: Eisenstadt (basal Hartl Fm., Hartl hill), Bgld ([NHMW]); Großhöflein, Bgld (Laube, 1869a, 1871; p. p. Gregory, 1891; Müller, 1963); Kleinhöflein (= Nagy-Höflány), Bgld (Vadász, 1915)

Styrian Basin: Ewitsch, Styria ([NHMW]); ? Kainberg, Styria (Hilber, 1878); Retznei (Weissenegg Fm., Lafarge quarry), Styria ([NHMW]); Zirknitz, Styria (Laube, 1869a, 1871; p. p. Gregory, 1891)

<u>Paratethys (non-Austrian occurrences)</u>: Ottnangian (Late Burdigalian) – Early Badenian (Langhian), ? Late Badenian (Early Serravallian)

Great Hungarian Basin (Pannonian Basin): Fót, Hungary (? Vogl, 1907; Vadász, 1915; Halmai, 1981; Kroh, 2003b; [MAFI]); ? Magyaregregy, Leányköi árok, Mecsek Mts., Hungary (Szörényi, 1950; Roman, 1965); Mátraverebély, Nógrád, Hungary (Vadász, 1915; [MAFI]); ? Fót (Somlyó Mt.), Hungary (Strausz, 1926; Kroh, 2003b)

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

Transylvanian Basin: Gârbova de Sus (= Felsö-Orbó), Romania (Vadász, 1915; Roman, 1965)

Zala, Sáva and Dráva Basins: surroundings of Beograd, Serbia (Roman, 1965); Donja Velešnja near Kostajnica, southern Croatia (Poljak, 1938); Donja Voča, in the Ivanšćica Mts., Croatia (Poljak, 1938); Giznik, Samobora Gora, Slovenian-Croatian border region (Poljak, 1938); Kirin, Petrova Gora, in Gliskom Pokuplju, Croatia (Poljak, 1938); Mesarski Brijeg, near Daruvara, Psunj Mts., Croatia (Poljak, 1938)

<u>Mediterranean</u>: Middle Miocene

Central Mediterranean: Vena presso Monteleone Calabro, southern Italy (Airaghi, 1900; Roman, 1965); ? *Globigerina* Limestone, Maltese Islands (Gregory, 1891; Roman, 1965)

Conolampas elegans (Airaghi, 1900)

(Pl. 57, Figs. 1-2; Pl. 58, Figs. 2, 4)

?	1880a	*Conoclypeus plagiosomus* Ag. – Manzoni: 187; pl. 2, figs. 23
?	1881	*Conoclypeus plagiosomus*, Ag. – Manzoni: 174
?	1882a	*Conoclypeus plagiosomus*, Agas. – Mazzetti: 123-124
?*	1882a	*Conoclypeus montesiensis*, Mazzetti. – Mazzetti: 124-125; Pl. 2, Fig. 3
*.	1900	*Heteroclyp<u>us</u> elegans*, n. f. – Airaghi: 176-177; pl. 1, figs. 3-4
.	1905a	*Heteroclyp<u>us</u> semiglobosus* (Lam.) Cott. – Airaghi: 214-216; figs. 1-2
.	1908c	*Echinolampas Montesiensis* (Mazzetti) Stef. – Stefanini: 370-375; pl. 13, figs. 3, 4a-b, 5a-b, 6
? v	1915	*Echinolampas* (*Heteroclypeus*) cfr. *elegans* Air. – Vadász: 203-204
# v.	1915	*Echinolampas* (*Heteroclypeus*) *hungaricus* n. sp. – Vadász: 205-206; text-fig. 93
	1938	*Hypsoclypus plagiosomus* Agassiz (*Conoclypeus*) 1840 – Poljak: 193-194
	1953	*Hypsoheteroclypus plagiosomus subpentagonalis* (Gregory), 1892, Szörényi – Szörényi: 29, 79-80; pl. 4, figs. 2, 2a-b
	1953	*Hypsoheteroclypus plagiosomus lamberti* (Checchia-Rispoli), 1917. Szörényi – Szörényi: 30, 80; pl. 5, figs. 1, 1a, 2a-b
?	1953	*Hypsoheteroclypus hungaricus* (Vadász), 1915. – Szörényi: 31-32, 81-82; pl. 3, figs. 3, 3a-b
	1953	*Hypsoheteroclypus pyramidalis* (Abich), 1859. – Szörényi: 32-33, 83; pl. 2, figs. 4, 4a-b
#	1953	*Hypsoheteroclypus vicinoconoideus* n.sp. – Szörényi: 33, 83-84; pl. 6, figs. 2, 2a-b
?	1955	*Echinolampas hungaricus* Vad<u>as</u> – Tollmann: Tab. 5b [probably refers to a specimen erroneously attributed to the locality Müllendorf in the GBA coll.]
	1965	[*Echinolampas* (*Hypsoclypus*)] *elegans* Airaghi 1901 (*Heteroclypus*) – Roman: 306
#	1965	[*Echinolampas* (*Hypsoclypus*)] *vadaszi* Roman (*nov. nom.*) – Roman: 309
	1993	*Conoclypus plagiosomus* Agassiz – Hiden: 17-18; fig.
v pp	2002	*Conoclypus* sp. – Kazár: 153; fig. 1

Type-material:

<u>*Heteroclypus elegans* Airaghi, 1900</u>:
Holotype: specimen figured by Airaghi (1900: pl. 1, figs. 3-4); Museo civico di Milano, Italy [not examined]
Locus typicus: Portotorres, Sardinia
Age: Middle ? Miocene