A re-evaluation of extinct European crabs referred to the genus *Calappilia* A. Milne Edwards *in* Bouillé, 1873 (Brachyura, Calappidae)

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Key words – Brachyura, Calappidae, Paleogene, Neogene, reassessment.
A reassessment of extinct species, fourteen in all, found in Europe and attributed to *Calappilia* has been carried out. For each species a short diagnosis is provided, and where necessary, its systematic position is reconsidered. *Calappilia dacica lyrata* is here elevated to species rank, while *C. mainii* is reassigned to *Stenodromia* A. Milne Edwards *in* Bouillé, 1873 and *C. sexdentata* is considered to be a *nomen nudum*. Photographs are provided of all type specimens available to us; most of these had so far been known only from (partially inaccurate) line drawings. For the first time, well-preserved chelipeds are described for the genus, having been found in articulation with a carapace of *C. dacica*.

Contents

Introduction

The extinct genus *Calappilia* ranges in age from Early Eocene to Miocene, being represented by several widely distributed species across shallow-water inner shelves that are characterised by high levels of terrigenous deposition. This corresponds to the environment in which extant Calappidae live buried within the sediment (Bachmayer, 1962). The species referred to the genus do not constitute a homogeneous group, which means that generic assignment is less than straightforward for some of them. *Calappilia* has occasionally been confused with *Calappa* Weber, 1795 (see Beurlen, 1939; Bachmayer, 1962). In addition, Glaessner (1969) considered *Paracyclois* Miers, 1886 to be synonymous with *Calappilia*; this issue was discussed by Beschin *et al*. (2013) and is here reconsidered.

Up to now, European representatives of the genus included *C. verrucosa* A. Milne Edwards *in* Bouillé, 1873 (type species), *C. dacica* Bittner, 1893, *C. dacica lyrata* Lőrenthey *in* Lőrenthey & Beurlen, 1929, *C. gemmata* Beschin, Busulini, De Angeli & Tessier, 1994,

C. incisa Bittner, 1886, *C. mainii* Allasinaz, 1987, *C. matzkei* (Bachmayer, 1962), *C. minuta* Beschin, Busulini & Tessier, 2013, *C. perlata* Noetling, 1885, *C. scopuli* Quayle & Collins, 1981, *C. sexdentata* A. Milne Edwards *in* Bouillé, 1876, *C. subovata* Beschin, Busulini, De Angeli & Tessier, 2002, *C. tridentata* (Beurlen, 1939) and *C. vicetina* Fabiani, 1910 (see Busulini *et al.*, 2013).

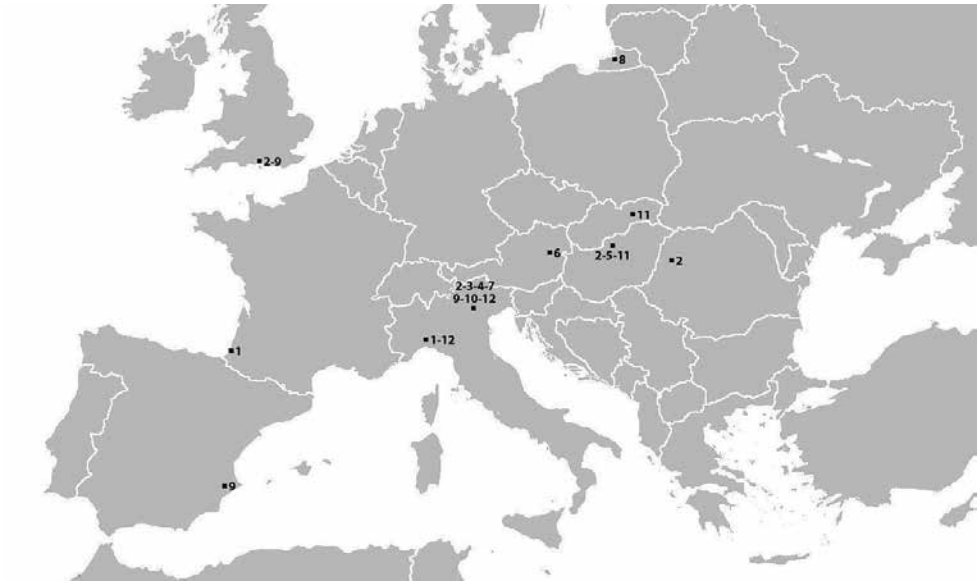

Fig. 1. Distribution of European species of *Calappilia* (each species is referred to its corresponding number in Table 1).

Table 1. List of European species of *Calappilia*, in alphabetical order, with indication of geographical and stratigraphical provenance; the numbers in the left-hand column are the ones indicated in Fig. 1 as well.

		Eocene	**Oligocene**	**Miocene**
1	*C. verrucosa* A.Milne Edwards, 1873	southwest France	northwest Italy	
2	*C. dacica* Bittner, 1893	Romania, Hungary, northeast Italy, England		
3	*C. gemmata* Beschin, Busulini, De Angeli & Tessier, 1994	northeast Italy		
4	*C. incisa* Bittner, 1886	northeast Italy		
5	*C. lyrata* Lőrenthey, 1929	Hungary		
6	*C. matzkei* (Bachmayer, 1962)			Austria
7	*C. minuta* Beschin, Busulini & Tessier, 2013	northeast Italy		
8	*C. perlata* Noetling, 1885	Kaliningrad (Russia)		
9	*C. scopuli* Quayle & Collins, 1981	England, eastern Spain, northeast Italy		
10	*C. subovata* Beschin, Busulini, De Angeli & Tessier, 2002	northeast Italy		
11	*C. tridentata* (Beurlen, 1939)	Slovakia	Hungary	
12	*C. vicetina* Fabiani, 1910		northeast and northwest Italy	

In the present survey we re-evaluate all of these taxa, by presenting brief diagnoses for each (on the basis of their types and, if these were not available, of their original description) and, where needed, a reconsideration of its systematic position. The types of most of these species were poorly documented, being often known exclusively from (occasionally inaccurate) line drawings. Here we supply photographs of all type specimens available to us, and document well-preserved chelipeds of the genus for the first time, on the basis of an articulated find of *C. dacica*.

The Eocene was the period of maximum development and distribution of the genus. Across Europe, ten species are known (Fig. 1; Table 1); six additional species have been recorded from the Eocene of America (United States, Caribbean Islands and Mexico), namely *C. bonairensis* Van Straelen, 1933, *C. brooksi* Ross & Scolaro, 1964, *C. diglypta* Stenzel, 1934, *C. hondoensis* Rathbun, 1930, *C. ocalanus* (Ross, Lewis & Scolaro, 1964) and *C. sitzi* Blow & Manning, 1996 (Table 2). None of these occurs at coeval levels in Europe. Other Eocene species have been described from Indonesia: *C. boehmi* Glaessner, 1929 [*nomen novum* in Glaessner (1929: 73) for *C. verrucosa* Böhm, 1922, *nomen preoccupatum*] and *C. borneoensis* Van Straelen, 1923) (Table 2). Schweitzer & Feldmann (2010) referred, albeit with a query, *Atelecyclus gorodinskii* Remy *in* Gorodiski & Remy, 1959, from the Eocene of Senegal, to *Calappilia*. However, Ossó & Domínguez (2013) have lately considered this to be better assigned to the family Montezumellidae Ossó & Domínguez, 2013.

There are only three Oligocene species in Europe, and a single one of Miocene age (Fig. 1; Table 1). Further extra-European records pertain to taxa species found in Miocene strata of New Zealand and South America, such as *C. maxwelli* Feldmann, 1993, *C.*? *chilensis* Feldmann, Schweitzer & Encinas, 2005 and *C. circularis* (Beurlen, 1958) (Table 2).

Institutional abbreviations – HNHM, Hungarian Natural History Museum (Természettudományi Múzeum), Budapest, Hungary; MCZ, Museo civico 'G. Zannato' di Montecchio Maggiore (Vicenza, Italy); MFGI, Hungarian Geological and Geophysical Institute, Budapest, Hungary; MGPD, Museo di Geologia e Paleontologia, Università di Padova, Italy; MNHN, Muséum national d'Histoire naturelle, Paris, France; MPMOV, Museo

Table 2. List of extra-European species of *Calappilia*, in alphabetical order, with indication of geographical and stratigraphical provenance.

	Eocene	**Oligocene**	**Miocene**
C. boehmi Glaessner, 1929	Java		
C. bonairensis Van Straelen, 1933	Bonaire Island (Dutch Caribbeans)		
C. borneoensis Van Straelen, 1923	Borneo		
C. brooksi Ross & Scolaro, 1964	Florida (USA)		
C.? *chilensis* Feldmann, Schweitzer & Encinas, 2005			Chile
C. circularis (Beurlen, 1958)			Brazil
C. diglypta Stenzel, 1934	Texas (USA)		
C. hondoensis Rathbun, 1930	California (USA), Mexico		
C. maxwelli Feldmann, 1993			New Zealand
C. ocalanus (Ross, Lewis & Scolaro, 1964)	Florida (USA)		
C. sitzi Blow & Manning, 1996	North Carolina (USA)		

paleontologico Maini di Ovada, Alessandria, Italy; MSNVR, Museo civico di Storia naturale di Verona, Italy; NHM, Natural History Museum, Department of Palaeontology, London, United Kingdom; SM, Sedgwick Museum, Cambridge University, Cambridge, United Kingdom.

Systematics

Higher-rank classification follows De Grave *et al.* (2009) and Schweitzer *et al.* (2010). Measurements (in mm): L = maximum carapace length; W = maximum carapace width; FoW = fronto-orbital width; Wp: posterior margin width.

Order Decapoda Latreille, 1802
Infraorder Brachyura Linnaeus, 1758
Section Eubrachyura de Saint Laurent, 1980
Subsection Heterotremata Guinot, 1977
Superfamily Calappoidea De Haan, 1833
Family Calappidae De Haan, 1833
Genus *Calappilia* A. Milne Edwards *in* Bouillé, 1873

Type species – *Calappilia verrucosa* A. Milne Edwards *in* Bouillé, 1873, by monotypy.

Diagnosis – Carapace convex, subcircular in outline, with narrow bilobed or triangular front; gastric and cardiac regions defined by sinuous longitudinal grooves, more or less incised; branchial regions very inflated in anterior part, being narrower posteriorly; greatest carapace width in anterior or middle part; posterolateral margins characterised by some spines, lacking wing-like projections covering pereiopods; dorsal carapace surface covered by numerous large tubercles. Differences amongst species depend above all on shape of front, development and number of posterolateral and posterior spines and number and distribution of tubercles (Table 3).

Remarks – As noted above, representatives of *Calappilia* are characterised by a carapace which is widest in the anterior or middle part and with posterolateral margins bearing variously developed spines. These features allow a clear differentiation from members of the genus *Calappa* Weber, 1795 which have maximum carapace width in the posterior half, at wing-like projections covering the pereiopods. However, a closer resemblance is seen to two other genera with a similar carapace outline, namely the modern *Cyclozodion* Williams & Child, 1989 and *Paracyclois* Miers, 1886 (Fig. 2).

Glaessner (1969) considered *Paracyclois* to be a junior synonym of *Calappilia*, but failed to provide an explanation for his choice. In contrast, Williams & Child (1989) maintained both genera, considering *Calappilia* nearer to *Calappa* than to *Paracyclois* but erecting *Cyclozodion* as a sort of intermediate between the last two. In their view, *Cyclozodion* displays juvenile features of *Calappa* in that greatest carapace width is situated anteriorly of the wing-like projection, even if this situation changes very rapidly during growth. *Cyclozodion* differs from *Paracyclois* in lacking spines on the ischium and merus of pereiopods 2-5. Morphological similarities among *Calappilia*, *Cyclozodion* and *Paracyclois* were emphasised not only by Williams & Child (1989), but also by Schweitzer & Feldmann (2000). In

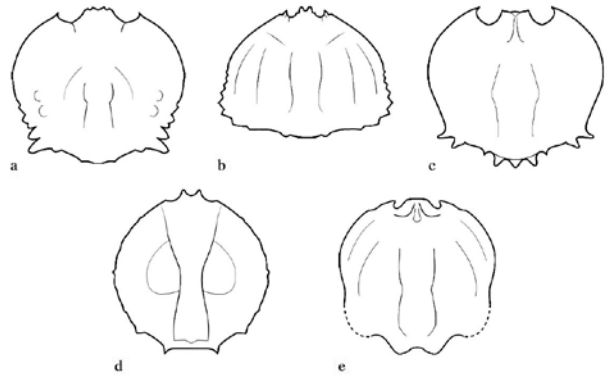

Fig. 2. Schematic carapace outlines: a – *Cyclozodion angustum*; b – *Calappa granulata*; c – *Paracyclois milneedwardsi*; d – *Calappilia verrucosa* (after A. Milne Edwards *in* Bouillé, 1873, pl. 4, fig. 3); e – *Stenodromia gibbosa*.

any case, *Cyclozodion* and *Paracyclois* can be distinguished from *Calappilia* in having a different fronto-orbital structure, shallower longitudinal grooves bordering the gastro-cardiac region, ill-defined protogastric lobes, weaker dorsal carapace ornamentation, a slightly trilobate posterior margin (*P. milneedwardsi* Miers, 1886 has three spines on the posterior margin) and, according to Williams & Child (1989), a different eye stalk structure. In short, we concur with Williams & Child (1989), Schweitzer & Feldmann (2000), De Grave *et al.* (2009) and Beschin *et al.* (2013) that these genera are distinct.

Calappilia verrucosa A. Milne Edwards *in* Bouillé, 1873

Pl. 1, figs. 1-3.

*1873 *Calappilia verrucosa* A. Milne Edwards *in* Bouillé, p. 8, pl. 4, fig. 3, 3a.
non 1922 *Calappilia verrucosa* Böhm, p. 527, pl. 63, fig. 9.
2003a *Calappilia verrucosa* A. Milne Edwards: De Angeli & Marangon, p. 101, text-fig. 1(2).
2003b *Calappilia verrucosa* A. Milne Edwards: De Angeli & Marangon, p. 190, text-figs. 3-5.

Type – Holotype, by monotypy, is MNHN.F.R03771 (a cast) (Pl. 1, fig. 1: W 16.0).

Other material examined – MCZ.2388 (Pl. 1, fig. 2: W 16.4; L 16.2; FoW 8.7) and MCZ.2389.

Diagnosis – Carapace subcircular in outline, strongly vaulted with narrow bilobed front; gastric and cardiac regions defined by deep, sinuous longitudinal grooves; branchial regions highly inflated anteriorly with well defined epibranchial lobe, becoming narrower posteriorly. Dorsal surface covered with large tubercles, larger on outer parts of carapace. Lateral margins regularly arched; each posterolateral margin bearing one strong spine. Posterior margin characterised by one pair of spines.

Remarks – A. Milne Edwards *in* Bouillé (1873, pl. 4, fig. 3a) also described a claw which he referred to this species; this has a very compressed and keeled dactylus with a large basal tooth, while the propodus is covered with large tubercles. Here we provide a photograph of a cast of a specimen that is labelled as the holotype; the differences between this and the original drawing are clear (Pl. 1, figs. 1, 3). For example, the

anterior portions of the carapace and the frontal margin, as described by A. Milne Edwards *in* Bouillé (1873), are now missing. Thus, this specimen may either have suffered subsequent damage, or not be the original at all.

Occurrence – The age of the type specimen, which was collected near the lighthouse at Biarritz (southwest France), is uncertain. Data with the holotype (cast in MNHN collections) show it to be of Eocene age; this is also the age indicated in some of the earliest studies (e.g., Noetling, 1885; Lőrenthey & Beurlen, 1929). Other authors referred it, with a query, to the Oligocene (Fabiani, 1910; Rathbun, 1930), or, more specifically, the Lower Oligocene (Rupelian) (Allasinaz, 1987; De Angeli & Marangon, 2003a, b). The complex geological structure of the Biarritz area and the lack of data on the level of provenance are not conducive to a reliable solution of this problem but we here assume an Eocene date of the type specimen to be correct. *Calappilia verrucosa* is also known from the Lower Oligocene of Alessandria, northwest Italy (De Angeli & Marangon, 2003a, b).

***Calappilia dacica* Bittner, 1893**

Pl. 1, figs. 4-6.

*1893 *Calappilia dacica* Bittner, p. 16, pl. 2, fig. 1.
1898 *Calappilia dacica* Bittner: Lőrenthey, p. 30, pl. 1, fig. 5.
1929 *Calappilia dacica* Bittner: Lőrenthey & Beurlen, p. 127, pl. 6, figs. 4-6.
1981 *Calappilia dacica* Bittner: Quayle & Collins, p. 739, pl. 104, figs. 6, 9.
1982 *Calappilia dacica* Bittner: Busulini *et al.*, p. 77.
2009a *Calappilia dacica* Bittner: Beschin *et al.*, p. 11, pl. 2, figs. 1-3.
2009 *Calappilia dacica* Bittner: De Angeli & Caporiondo, p. 26, fig. 3(8).
2010 *Calappilia dacica* Bittner: Beschin *et al.*, p. 18, pl. 2, figs. 6, 7.
2012 *Calappilia dacica* Bittner: Busulini *et al.*, p. 53, pl. 2, fig. 2.

Types – Bittner (1893) noted that the type series (two specimens) of his species was housed at Klausenburg (now Cluj-Napoca, Romania), but its current whereabouts is unknown. Unfortunately, it has not yet been traced in any of the main Romanian institutes (universities of Cluj-Napoca and Bucharest and Geological Museum of Romania) (Iuliana Lazăr, pers. comm., 2013).

Material examined – MCZ.1341 (Pl. 1, fig. 4: W 16.2; L 15.5; FoW 7.6), MCZ.1342, MCZ.3020, MCZ.3063–3084, MCZ.3234, MCZ.3235, MCZ.3355–3358. In addition, casts of specimens from Hungary (MFGI collections), as presented to us by Dr Pál Müller.

Diagnosis – Carapace weakly domed, slightly wider than long, with shallow longitudinal grooves. Front narrow, bilobed. Posterolateral margins convergent and lined by seven teeth (6th and 7th largest); wide arch joining posterolateral margin with posterior angle. Posterior margin with small marginal spine and wide median projection. Three tubercles, arranged in triangle, on each protogastric lobe; meso-metagastric lobe with four tubercles in two rows and one large tubercle; urogastric lobe with two median tubercles; one long tubercle surrounded by other smaller ones on anterior part of cardiac region and two pairs of tiny tubercles on posterior part. Branchial regions wide, 25-30 large tubercles concentric to lateral margins in addition to numerous smaller ones.

Remarks – Busulini *et al.* (1982) recorded an exceptional specimen with both chelipeds preserved in anatomical position (see Pl. 1, fig. 5 here). The current whereabouts of this specimen, collected by a member of the Società veneziana di Scienze naturali, is unknown. The merus, carpus and propodus are thick and stubby, their entire outer surface being covered with tubercles; the upper margin of the propodus is lined by large stout tubercles that do not constitute a sharp keel (as seen in species of *Calappa*); on the lower margin there are rows of numerous beads; the fixed finger is short and triangular, the dactylus stout and sickle shaped; both fingers are black in colour.

Occurrence – *Calappilia dacica* is a long-ranging species, first recorded from the Bartonian (Middle Eocene) of Romania (Bittner, 1893) and with subsequent records from the Upper Eocene of Hungary (Lőrenthey, 1898; Lőrenthey & Beurlen, 1929), the Middle Eocene (Bartonian) of southern England (Quayle & Collins, 1981) and Middle and Upper Eocene (Lutetian, Bartonian and Priabonian) of Veneto (Busulini *et al.*, 1982, 2012; Beschin *et al.*, 2009a, 2010; De Angeli & Caporiondo, 2009).

Calappilia gemmata Beschin, Busulini, De Angeli & Tessier, 1994

Pl. 1, figs. 7-9.

*1994 *Calappilia gemmata* Beschin, Busulini, De Angeli & Tessier, p. 167, text-fig. 3; pl. 2, figs. 1, 2.

Types examined – Holotype is MCZ.1427 (Pl. 1, fig. 7: W 14.0; L 13.0; FoW 6.0); paratypes are MCZ.1425, MCZ.1426 (Pl. 1, fig. 8: W 14.3) and MCZ.1428.

Diagnosis – Carapace subcircular in outline, strongly domed with shallow longitudinal grooves. Front bilobed, protruding. Anterolateral margins convex and posterolateral ones convergent. Three large teeth on posterior angle and three short, wide triangular projections on median part of posterior margin. Dorsal surface covered with tiny granules and some large, rounded tubercles, one on each protogastric and hepatic regions, one on mesogastric, metagastric and cardiac regions, six on each branchial region.

Remarks – General carapace shape, development of the teeth on the posterior angle, structure of the posterior margin and the ornament of few large tubercles allow this species to be compared with *C. tridentata* (see below). In dorsal carapace ornament, this species also shows some resemblance to *Nantocyclois eocenicus* Beschin, Busulini & Tessier, 2013.

Occurrence – Middle Eocene of Veneto, northeast Italy.

Calappilia incisa Bittner, 1886

Pl. 2, figs. 1-3.

*1886 *Calappilia incisa* Bittner, p. 48(5), fig. 3.
1982 *Calappilia* cf. *incisa* Bittner: Busulini *et al.*, p. 77.
1994 *Calappilia incisa* Bittner: Beschin *et al.*, p. 168, pl. 1, figs. 5, 6.

Types examined – Lectotype (here designated) is MSNVR.i3454 (Pl. 2, fig. 1: W 24.0; L 23.0); paralectotypes are MSNVR.i1950(?) and MSNVR.i1950a.

Other material examined – MCZ.1259 and MCZ.1446 (Pl. 2, fig. 2: W 22.5; L 21.6; FoW 8.8).

Diagnosis – Carapace subcircular in outline, strongly domed. Gastro-cardiac region defined by two narrow, sinuous longitudinal grooves, deeply sunken posteriorly. Posterolateral margins lined by seven teeth with basal tubercle above (6th one best developed). Posterior margin with three short, wide triangular projections (median one particularly well developed) and among them two tubercles protrude from intestinal region. Meso-metagastric lobe with two rows of three tiny tubercles and large median, elongated tubercle; each protogastric lobe with three small tubercles in transverse row and another larger posterior one; on posterior part of long cardiac region, three tubercles in triangle projecting on posterior margin. Highly developed branchial regions covered with large, elongated tubercles concentric to lateral margins.

Remarks – Bittner (1886) based his description on the best-preserved of three specimens in the type series; this is here designated lectotype. Bittner expressed doubts over the conspecificity of one of the other two specimens (most likely pertaining to MSNVR. i1950 – our own observation, 2013). We concur because its carapace outline, with regularly convex anterior and anterolateral margins and strongly re-entering posterolateral margins, and the dorsal tuberculation are reminiscent of *Mursiopsis pustulosus* Ristori, 1889 (Ristori, 1889; Allasinaz, 1987). The types of the present species lack the fronto-orbital region, but subsequently recovered individuals have allowed the description of the carapace to be complemented (see Pl. 2, fig. 2). The front is subtriangular, covered with small granules, and protrudes beyond the orbits; the orbital margin is swollen, with a small triangular upper-orbital tooth.

Occurrence – Middle Eocene of Veneto, northeast Italy.

Calappilia lyrata Lőrenthey *in* Lőrenthey & Beurlen, 1929

Pl. 2, figs. 5, 6.

*1929 *Calappilia dacica* var. *lyrata* Lőrenthey *in* Lőrenthey & Beurlen, p. 128, pl. 6, figs. 7, 8.

Types – Syntypes are MFGI.E9260 (Pl. 2, fig. 5: W 26.0; L 28.0), and the specimen labelled *Calappilia dacica lyrata* among the ones with the collective number MFGI.E9263.

Diagnosis – Carapace slightly longer than wide; front with median triangular rostrum with two tiny lateral spines; convergent posterolateral margins strongly concave and bearing strong posterior spine; posterior margin characterised by lateral spines and large median rounded projection. Shallow longitudinal grooves. On meso-metagastric lobe two large tubercles, surrounded by smaller ones; another large tubercle on cardiac region; 25-30 tubercles distributed over branchial regions.

Remarks – Lőrenthey (*in* Lőrenthey & Beurlen, 1929) described, as *Calappilia dacica* var. *lyrata*, some specimens (probably four) from the Upper Eocene of Budapest; some differences between the new variety and typical *C. dacica* were noted, but the author also emphasised characters that, in his opinion, joined the two. The original line drawings (Lőrenthey & Beurlen, 1929, pl. 6, figs. 7, 8) are very different from each other and probably are not really representative of these carapaces. They represent two specimens, realistically the ones whose measurements were given. Our reassessment of syntype MFGI.E9260 suggests that it is one of the specimen depicted by Lőrenthey & Beurlen (1929, pl. 6, fig. 7); as seen also in the drawing it is proportionally narrower than *C. dacica*, and the structure of the frontal, posterolateral and posterior margins and the distribution of tubercles on the dorsal surface do not match those of the latter species. Thus, we afford full species status to var. *lyrata*, but wish to defer designation of a lectotype to another occasion in view of the current incomplete reassessment of the type series.

Occurrence – Upper Eocene of Budapest (Hungary).

***Calappilia matzkei* (Bachmayer, 1962)**

Pl. 2, fig. 4.

*1962 *Calappa matzkei* Bachmayer, p. 43, pl. 3, fig. 1a-d.
1979 *Calappilia matzkei* (Bachmayer): Müller, p. 866.
1984 *Calappilia matzkei* (Bachmayer): Müller, p. 68.
1998 *Calappilia matzkei* (Bachmayer): Müller, p. 23.

Type – The sole specimen known, originally housed in a private collection at Neunkirchen (Niederösterreich, Austria), is probably lost (Müller, 1998) (Pl. 2, fig. 4: W 33.7; L 31.6).

Diagnosis – Carapace weakly transversely ovate and strongly vaulted, principally in posterior third, with deep longitudinal grooves. Front bilobed; lateral margins forming continuous arch beaded by tubercles, but posterolateral ornament incompletely preserved; posterior margin wavy. Anterior part of carapace with numerous large tubercles and scattered smaller ones; three larger tubercles in a line on meso-metagastric region; many small tubercles on protogastric and cardiac regions. Ornament scarce on posterior part of carapace. Original cuticle not preserved.

Remarks –Bachmayer (1962) stressed the morphological affinities between this species and *Calappa praelata* Lőrenthey *in* Lőrenthey & Beurlen, 1929, from the Miocene of Hungary. However, Müller (1998) expressed doubts over both the age and specific attribution of this specimen, considering it to be closely similar to the Eocene *Calappilia dacica*. Many features differentiate *C. matzkei* from the latter, such as the rounded general carapace outline which lacks a posterior projection, its convexity (particularly evident in the posterior third) and the distribution and development of tubercles (almost absent from the posterior half). With regard to age assignment, it appears inappropriate to reject Bachmayer's view without a restudy of the original material.

Occurrence – Upper Miocene of Austria.

Calappilia minuta Beschin, Busulini & Tessier, 2013
Pl. 2, fig. 7a, b.

*2013 *Calappilia minuta* Beschin, Busulini & Tessier, p. 124, pl. 2, fig. 5a-c.

Type examined – Holotype, by monotypy, is MCZ.3482 (Pl. 2, figs. 7a, b: W 11.5; L 9.5; FoW 6.0).

Diagnosis – Carapace small, vaulted, subcircular in outline. Anterolateral margins convex; posterolateral margins weakly concave with at least five triangular spines increasing in size and one tooth at side of posterior margin. Sinuous branchiocardiac grooves deeply sunken. Dorsal surface covered with isolated tubercles. Two longitudinal sets of two tiny tubercles on each protogastric lobe; one long ovate tubercle characterising meso-metagastric lobe and another one on cardiac region. Three series of tubercles concentric to lateral margins on each branchial region; best developed is intermediate one, composed of five elements.

Occurrence – Middle Eocene of Veneto, northeast Italy.

Calappilia perlata Noetling, 1885
Pl. 2, fig. 8.

*1885 *Calappilia perlata* Noetling, p. 125, pl. 2, fig. 1, 1a-e.

Type – The holotype was originally housed in the collections of the Albertus-Universität Königsberg (now Kaliningrad, Russia), but it was probably lost during the Second World War. It could not be found at the Bundesanstalt für Geowissenschaften und Rohstoffe (Berlin) where part of the Noetling Collection is registered; so far, we have not received any response on our query from the Museum für Naturkunde (Berlin).

Remarks – Noetling (1885) based his new species on a single individual (i.e., the holotype by monotypy), but he did hint at the existence of other specimens.

Diagnosis – Carapace strongly vaulted, principally in posterior part, and subpentagonal in outline. Anterolateral margins divergent and almost straight, with three large tubercles near lateral angle; posterolateral margins convergent and weakly convex with eight stout, yet weakly developed, spines (6^{th} one being strongest). Dorsal surface covered with fine granules, particularly abundant and thick in anterior portion of carapace, also covering tubercles. Median carapace regions with only few, small tubercles: five tiny ones on cardiac region forming rectangle with central granule (typical of species); branchial regions covered with many larger tubercles, better developed on inner and anterior parts. Type retaining ventral regions of carapace and thoracic sternites.

Occurrence – Eocene of former Samland, East Prussia, now Kaliningrad, Russia. The type comes from the so-called 'Bernsteinformation, Zone A1'. On the basis of palaeontological evidence Noetling (1885) dated this as Early Oligocene. Recent studies, however,

suggest an Eocene age, more precisely Middle (K-Ar dating; see Ritzkowski, 1997; Jagt *et al.*, 2006) or Late Eocene, on micropalaeontological assemblages (Perkovsky *et al.*, 2007).

Calappilia scopuli Quayle & Collins, 1981

Pl. 3, fig. 1.

*1981 *Calappilia scopuli* Quayle & Collins, p. 739, pl. 104, fig. 8.
1991 *Calappilia scopuli* Quayle & Collins: Vía Boada, p. 182, pl. 1, fig. 2.
2009b *Calappilia scopuli* Quayle & Collins: Beschin *et al.*, p. 71, pl. 3, fig. 4.
2012 *Calappilia scopuli* Quayle & Collins: Busulini *et al.*, p. 54, pl. 2, fig. 3.

Types – Holotype is NHM.61705; paratypes are NHM.61706 and SM.C84877.

Material examined – MCZ.3354 and MSNVR.78532 (Pl. 3, fig. 1: W 21.5; L 15.7).

Diagnosis – Carapace moderately vaulted, subcircular in outline. Posterolateral margins with three or four tubercles and four spines (3rd one being largest) and three spines on posterior margin. Front narrow, bilobed. Orbits close together and directed upwards. Urogastric lobe forming narrow bar. Dorsal surface covered with scattered granules. Median tubercles subdued and arranged in row: two on mesogastric lobe, one on urogastric lobe and on cardiac region. Two tubercles on each protogastric lobe forming transverse row of four elements. Two longitudinal rows of tubercles on each branchial region; tubercles near mesogastric lobe with slightly smaller tubercle above.

Occurrence – Middle Eocene of southern England (Quayle & Collins, 1981), eastern Spain (Vía Boada, 1991); Lower and Upper Eocene of Veneto, northeast Italy (Beschin *et al.*, 2009b; Busulini *et al.*, 2012).

Calappilia sexdentata A. Milne Edwards *in* Bouillé, 1876

*1876 *Calappilia sexdentata* A. Milne Edwards *in* Bouillé, p. 34.

Remarks – From Paleogene levels near Biarritz (southwest France), A. Milne Edwards *in* Bouillé (1876) recorded a second species of *Calappilia*, *C. sexdentata*, but failed to provide any illustrations. In addition, the whereabouts of the type is unknown. It was described as being larger than *C. verrucosa* (see above) and to be characterised by a wide carapace, swollen gastro-cardiac region, an entire anterolateral margin, a posterolateral margin with three large teeth, and a near-smooth dorsal surface.

Despite the fact that this form has been quoted on some occasions in comparisons with other species of *Calappilia* (see, for instance, Bittner, 1886, 1893; Allasinaz, 1987), *C. sexdentata* is here considered to be a *nomen nudum*.

Calappilia subovata Beschin, Busulini, De Angeli & Tessier, 2002

Pl. 3, figs. 2, 3.

*2002 *Calappilia subovata* Beschin, Busulini, De Angeli & Tessier, p. 13, text-fig. 8; pl. 2, fig. 4.

Type examined – Holotype, by monotypy, is MCZ.2269 (Pl. 3, fig. 2: W: 14.0; L: 11.2; FoW: 7.4).

Diagnosis – Carapace domed and ovate in outline. Front wide, bilobed. Anterolateral margins lined by tiny rounded teeth; posterolateral margins with six strong triangular teeth (3rd to 5th being best developed). On posterior margin three short, wide triangular projections. Longitudinal grooves weakly sunken. Branchial regions highly developed. Dorsal surface covered with numerous tiny granules and many large tubercles of various sizes, irregularly distributed. Large tubercle on mesogastric lobe and another one on urogastric lobe.

Occurrence – Middle Eocene of Veneto, northeast Italy.

***Calappilia tridentata* (Beurlen, 1939)**

Pl. 3, fig. 8.

*1939 *Calappa tridentata* Beurlen, p. 150, text-fig. 5, pl. 7, figs. 8-10.
2007 *Calappilia* sp.: Hyžný, p. 59, fig. 1f.
2010 *Calappilia tridentata* (Beurlen): Schweitzer *et al.*, p. 84.
2011 *Calappilia tridentata* (Beurlen): Hyžný, p. 166, fig. 1D.

Types – Syntypes are HNHM.M.59.4676, HNHM.M.59.4679, HNHM.M.59.4681 (Pl. 3, fig. 8: W 26,0) and HNHM.M.60.758 (M. Hyžný, pers. comm., 2013).

Diagnosis – Carapace subcircular, strongly domed in smallest specimens, more flattened in largest ones. Gastro-cardiac region defined by deep longitudinal grooves. Posterolateral margins highly convergent with two large triangular spines (first one being better developed); three pointed spines protruding from posterior margin. Stretched tubercles arranged in longitudinal lines characterise anterior half of carapace; ornament of posterior half very weakened.

Remarks – Beurlen (1939) described a set of specimens of varying sizes (the width of the largest one being in excess of 50 mm, the smallest about 18 mm) and noted some growth-related differences. The largest carapaces are flatter and the ornament is weaker. In view of this, we refrain from designating a lectotype, at least for the time being.
Beurlen (1939) assigned this species to *Calappa* on account of the regular ornament, but did consider it an intermediate between *Calappa* and *Calappilia* because it lacked the wing-like extention of the posterolateral margin, yet had posterior spines, a character that he regarded as primitive. We agree with Schweitzer *et al.* (2010) and Hyžný (2011) in referring the species to *Calappilia*.

Occurrence – Eocene of Slovakia (Hyžný, 2011); Oligocene of Hungary (Beurlen, 1939).

Calappilia vicetina Fabiani, 1910
Pl. 3, figs. 4, 5.

*1910 *Calappilia vicetina* Fabiani, pp. 4, 21, pl. 1, fig. 1a-c.
1987 *Calappilia vicetina* Fabiani: Allasinaz, p. 525, text-fig. 6; pl. 1, fig. 7.
? 2012 *Calappilia vicetina* Fabiani: Messina, p. 45, fig. 1.

Type examined – Neotype (here designated) is MGPD.23999 (Pl. 3, fig. 5: W 18.0; Wp 8.0).

Diagnosis – Carapace weakly domed, transversely ovate, with greatest width in anterior third. Longitudinal grooves sunken, making transverse profile trilobate. Twelve or thirteen spines, increasing in size, lining lateral margin. Posterolateral margin joining posterior one in large arch bearing single, barely visible, triangular spine. Posterior margin with large median projection in shape of dovetail with marginal spines and two smaller spines. Meso-metagastric lobe with row of three large tubercles. Five tubercles on cardiac region: two of them in row, others in triangle. Three series of large tubercles characterise each branchial region: medial one being clearest, with a few large, reniform tubercles.

Remarks – Only a single specimen of *C. vicetina* is housed in the MGPD collections (our own observation, 2013); according to its original label, it was collected in 1928 by Fabiani from Oligocene strata near San Gottardo dei Berici (Vicenza). These data and the size of specimen (W 18.0 mm; Wp 8.0 mm) show that it does not belong to the type series that was described by Fabiani (1910), which included a single damaged individual that lacked the frontal margin (W 38 mm; L 33 mm), plus a fragment, both collected near Nanto (Vicenza). In view of the fact that the type series is lost, specimen MGPD.23999 is here designated neotype of *C. vicetina*. Even if the carapace is incomplete, it does allow assessment of a limited set of specific features, such as the peculiar structure of the posterior margin and the reniform swellings on the median part of the branchial regions. In contrast, the line of tubercles on the gastric and cardiac regions is barely visible.

Messina (2012) described an exceptionally preserved specimen from the Lower Oligocene of the Vicenza area as *Calappilia vicetina*, but the carapace outline of that individual conforms better to *Calappa*. The carapace lacking lateral and posterior margins described as *C. vicetina* in Beschin & De Angeli (2012) from the Miocene of Veneto, cannot be attributed to *Calappilia* because the longitudinal grooves converge onto the intestinal region; it is closely similar to *Mursia lienharti* (Bachmayer, 1962) (see Müller, 1984) and some chelipeds attributed to the latter species were found in coeval levels of Veneto (Beschin & De Angeli, 2012).

Occurrence – Lower Oligocene of Vicenza, northeast Italy and Alessandria, northwest Italy.

Genus *Stenodromia* A. Milne Edwards *in* Bouillé, 1873

Type species – *Stenodromia gibbosa* A. Milne Edwards *in* Bouillé, 1873, by monotypy.

Diagnosis – Carapace convex, subcircular in outline, with narrow slightly protruding front; gastric and cardiac regions swollen and defined by very deep and broad longitudinal grooves; branchial regions inflated in anterior part, being narrower posteriorly; posterolateral margins characterised by few spiny protrusions; weakly tuberculate oblique keel developing from posterior branchial lobe to gastric region; dorsal carapace surface almost smooth.

Remarks – In the MNHN collection there is a cast of a specimen of *Stenodromia gibbosa* labelled as a syntype (MNHN.F.R03835) (Pl. 3, fig. 7: L 26.0). Only a single damaged specimen was considered in the original description of the species; the specimen housed in the Paris collections is clearly the one depicted by A. Milne Edwards *in* Bouillé (1873, pl. 4, fig. 4), making it the holotype by monotypy.

***Stenodromia mainii* (Allasinaz, 1987)**

Pl. 3, fig. 6.

*1987 *Calappilia mainii* Allasinaz, p. 523, text-fig. 2, pl. 1, figs. 2-6.

Types – Holotype is MPMOV.158M (Pl. 3, fig. 6: W 25.0; L 23.0); paratypes are MPMOV.1a, MPMOV.189, MPMOV.289 and MPMOV.162M.

Diagnosis – Carapace weakly convex and subcircular in outline, slightly longer than wide. Greatest width in posterior half, because of presence of well-developed posterolateral spines. Front narrow with slightly protruding subrectangular rostrum; orbits entire, circular, deep and rimmed. Lateral margins smooth without tubercles: anterolateral ones shorter and convex, posterolateral margins characterised first by wide concavity and secondly by two large protruding triangular spines. Two additional similar spines protruding at side of short convex posterior margin. Median carapace regions appearing keel like, defined by shallow sinuous longitudinal grooves. On either side two other oblique keels developing from posterolateral spines: inner one ending on protogastric lobe, outer one on epibranchial lobe.

Remarks – Allasinaz (1987) stressed the resemblance between *C. mainii* and members of the genus *Stenodromia*, noting the pyriform outline and subparallel dorsal keels. However, he decided not to refer the species to the latter genus in view of the differences that in his opinion characterised the structure of the posterior spines in *Stenodromia*, particularly a strong median spine as a projection of the intestinal region. Actually, A. Milne Edwards *in* Bouillé (1873), in his description of the type species, *S. gibbosa*, did not record either a strong posterior spine or a large intestinal region. Neither of these features is seen in the cast of the syntype of *S. gibbosa*, the sole known specimen, in which, unfortunately, the typical posterolateral teeth are not well preserved. *Stenodromia calasanctii* Vía Boada, 1959, from the Eocene of Spain, the only other species of the genus to date, is the best-known representative (Glaessner, 1969). It is smaller than the type species, has a different orbitofrontal structure, less developed dorsal keels with a lower number of pointed tubercles and a strong median posterior spine. Allasinaz (1987) probably considered the features of this species to be typical of *Stenodromia*.

Calappilia mainii therefore is more correctly placed in *Stenodromia* in view of the overall carapace shape, the development of longitudinal keels and posterolateral and posterior teeth. Allasinaz (1987) compared the species also with *C. sexdentata* (*nomen nudum*), the original description of which refers to three posterolateral/posterior teeth. The specimens studied by Allasinaz (1987) constituted a very heterogeneous group and a more detailed analysis of the type series would be needed to ascertain the correct attribution of all the specimens to the same species.

Occurrence – Lower Oligocene of Alessandria, northwest Italy.

Conclusions

The present survey of the genus *Calappilia* has allowed to clarify the differences among all European species referred to it, on the basis of their type series and, if not available, of the original descriptions. Results of this reassessment include the upgrading of *C. dacica lyrata* to full species status and the transfer of *C. mainii* to *Stenodromia*. We here present for the first time photographic documentation of some types of species that so far were known exclusively from the original illustrations that, at times, not fully corresponded to the real specimens. These include *C. verrucosa* (cast of the holotype), *C. incisa* (lectotype, here designated), *C. lyrata* (syntype) and *C. vicetina* (neotype, here designated). We also indicated that the type series of some species (i.e., *C. dacica*, *C. perlata* and *C. vicetina*) have probably been lost. We have found no additional published or unpublished material of *C. sexdentata*. In view of the fact that this 'taxon' has never been illustrated, it is here considered a *nomen nudum*.

During the Eocene *Calappilia* was already clearly differentiated, with a Tethyan and Atlantic distribution. Ten species of *Calappilia* are known from the Eocene in Europe (Table 1): six of these stem from western Veneto (Vicenza and Verona territories, northeast Italy). This abundance of species suggests that the genus originated in this part of the Tethys. Up to now four of these species appear to be endemic to this area, being known exclusively from Middle Eocene levels (*C. gemmata*, *C. incisa*, *C. minuta* and *C. subovata*). Two others (*C. dacica* and *C. scopuli*) have a wider distribution and are long-lived; their distribution confirms that there were connections between Peri-Tethyan basins during the Eocene. *Calappilia dacica*, first recorded from Middle Eocene levels in Romania (Bittner, 1893), occurs in coeval levels in southern England (Quayle & Collins, 1981) and in the Upper Eocene of Hungary (Lőrenthey & Beurlen, 1929). The same species is also known from the Lutetian and Priabonian of western (Beschin *et al.*, 2010) and eastern Veneto (Treviso territory; Busulini *et al.*, 2012). *Calappilia scopuli* is the oldest species of the genus and also the one with the longest range, having been recorded from all Eocene stages, with examples from the Middle Eocene of southern England, the Ypresian of western Veneto, the Priabonian of eastern Veneto and the Middle Eocene of Spain (Vía Boada, 1991; Busulini *et al.*, 2012; Beschin *et al.*, 2012). Other Eocene congeners comprise the type species, *C. verrucosa*, from southwest France, *C. lyrata* from the Upper Eocene of Hungary (Lőrenthey & Beurlen, 1929), *C. perlata* from the Middle (or Upper) Eocene of Kaliningrad (Russia) (Noetling, 1885) and *C. tridentata* from the Upper Eocene of Slovakia (Hyžný, 2011).

From Oligocene levels species of *Calappilia* have been recorded solely from Europe.

Calappilia verrucosa occurs in the Ligure-Piemontese Basin, *C. vicetina* of coeval rocks in Veneto and in the same basin, while *C. tridentata* occurs in Hungary. *Calappilia matzkei* from Austria is the sole known Miocene representative of the genus in Europe.

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Table 3. Key for identification of European species of *Calappilia*.

	carapace	**front**	**median regions**	**lateral regions**	**posterolateral margin**	**posterior margin**
C. verrucosa	subcircular, strongly domed	bilobed	deep longitudinal grooves; many small tubercles	very inflated anterior branchial region with large tubercles; well defined epibranchial lobe	one strong spine	one pair of spines
C. dacica	subcircular, weakly domed	bilobed	shallow longitudinal grooves; two rows of two tubercles and median larger one on gastric region; one elongate tubercle and two pairs of tiny tubercles on cardiac region	25-30 large tubercles	seven teeth and posterior concavity	small marginal spine; wide median projection
C. gemmata	subcircular, strongly domed	bilobed protruding	shallow longitudinal grooves; one large tubercle on mesogastric, metagastric and cardiac regions	few large tubercles (one protogastric, one hepatic, six branchial) and tiny granules	three large teeth on posterior angle	three short median triangular projections
C. incisa	subcircular, strongly domed	sub-triangular	deeply sunken posteriorly longitudinal grooves; pairs of small tubercles and few large median elongate ones on gastric region; three tubercles in triangle on cardiac region	many large elongate tubercles on very developed branchial region	seven teeth	three short triangular projections
C. lyrata	slightly longitudinally ovate, weakly domed	sub-triangular protruding	shallow longitudinal grooves; two large tubercles on gastric region; one large tubercle on cardiac region	25-30 large tubercles	concave margin with strong posterior spine	lateral spines; wide median projection
C. matzkei	slightly trans-versely ovate, strongly domed in posterior third	bilobed	deep longitudinal grooves; three large tubercles on gastric region; small tubercles on cardiac region	many large tubercles and scattered smaller ones on anterior part	*incompletely preserved*	wavy
C. minuta	subcircular, strongly domed	*unknown*	deeply sunken longitudinal grooves; four rows of two tubercles and median elongate one on gastric region; another one on cardiac region	three longitudinal series of tubercles on branchial region	weakly concave margin with at least five spines	one tooth on each side

C. perlata	subpentagonal, strongly domed	*unknown*	few small tubercles; five ones forming a centred rectancle on cardiac region	many tubercles covered with fine granules better developed on anterior parts	eight spines	*incompletely preserved*
C. scopuli	subcircular, moderately domed	narrow, bilobed; orbits close together and inclined upwards	deep longitudinal grooves; three large tubercles on gastric region; one large tubercle on cardiac region	transverse row of four tubercles on protogastric lobes; two rows of tubercles on branchial region and scattered granules; medial tubercles with slightly smaller tubercle above	three /four tubercles and four spines	three spines
C. subovata	transversely ovate, domed	wide, bilobed	shallow longitudinal grooves; two large tubercles on gastric region; many small tubercles on cardiac region	very developed branchial region covered with many tiny granules and tubercles	six strong triangular teeth	three short projections
C. tridentata	subcircular, domed in smallest specimens, more flattened in largest ones	triangular (?)	deep longitudinal grooves; line of large subdued tubercles on gastric region	stretched tubercles in lines in anterior branchial region	two large triangular spines	three spines
C. vicetina	trasversely, ovate, weakly domed	*unknown*	sunken longitudinal grooves; five large tubercles in line on gastric and cardiac region; three tubercles in triangle on cardiac region	three longitudinal series of tubercles on branchial region; medial tubercles very large and reniform	12/13 spines line the lateral margins and posterior concavity	dovetail median projection with four small spines

Plate 1

***Calappilia verrucosa* A. Milne Edwards *in* Bouillé, 1873**

Fig. 1. Cast of holotype (MNHN.F.R03771), Biarritz, southwest France.
Fig. 2. MCZ.2388, Alessandria, northwest Italy.
Fig. 3. Line drawing (from A. Milne Edwards *in* Bouillé, 1873, pl. 4, fig. 3).

***Calappilia dacica* Bittner, 1893**

Fig. 4. MCZ.1341, Parona (Verona, northeast Italy).
Fig. 5. Current whereabouts unknown (see text); frontal view and chelipeds, Arzignano (Vicenza, northeast Italy).
Fig. 6. Line drawing (from Bittner, 1893, pl. 2, fig. 1).

***Calappilia gemmata* Beschin, Busulini, De Angeli & Tessier, 1994**

Fig. 7. Holotype (MCZ.1427), Nogarole Vicentino (Vicenza, northeast Italy).
Fig. 8. MCZ.1426, frontal view, Nogarole Vicentino (Vicenza, northeast Italy).
Fig. 9. Line drawing (from Beschin *et al.*, 1994, text-fig. 3).

Scale bars equal 10 mm.


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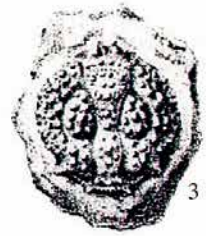
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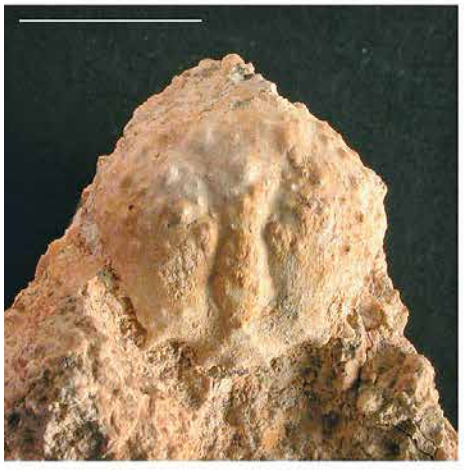
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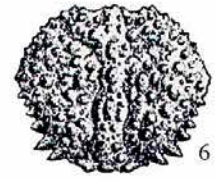
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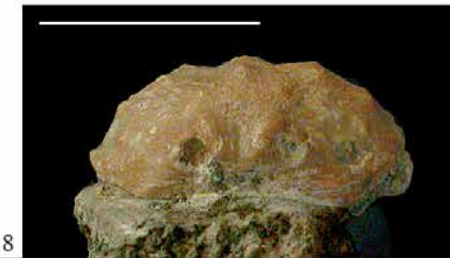
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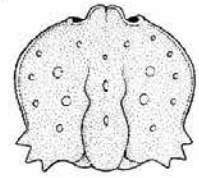
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Plate 2

***Calappilia incisa* Bittner, 1886**

Fig. 1. Lectotype (NSNVR.i3454), Avesa (Verona, northeast Italy).
Fig. 2. MCZ.1446, Nogarole Vicentino (Vicenza, northeast Italy).
Fig. 3. Line drawing (from Bittner, 1886, fig. 3).

***Calappilia matzkei* (Bachmayer, 1962)**

Fig. 4. Holotype (from Bachmayer, 1962, pl. 3, fig. 1), Niederösterreich (Austria).

***Calappilia lyrata* Lőrenthey in Lőrenthey & Beurlen, 1929**

Fig. 5. Syntype (MFGI.E9260), Budapest (Hungary).
Fig. 6. Line drawing (from Lőrenthey & Beurlen, 1929, pl. 6, fig. 7).

***Calappilia minuta* Beschin, Busulini & Tessier, 2013**

Fig. 7a, b. Holotype (MCZ.3482), Nanto (Vicenza, northeast Italy).

***Calappilia perlata* Noetling, 1885**

Fig. 8. Line drawing (from Noetling, 1885, pl. 2, fig. 1), Kaliningrad (Russia).

Scale bars equal 10 mm.


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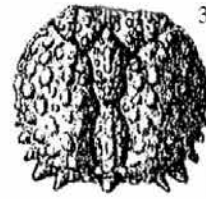
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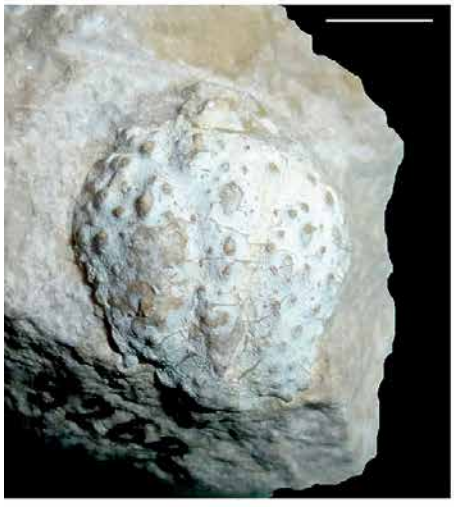
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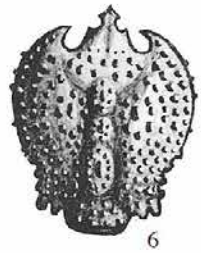
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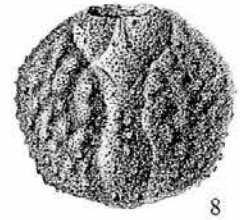
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Plate 3

***Calappilia scopuli* Quayle & Collins, 1981**

Fig. 1. MSNVR.78532, San Giovanni Ilarione (Verona, northeast Italy).

***Calappilia subovata* Beschin, Busulini, De Angeli & Tessier, 2002**

Fig. 2. Holotype (MCZ.2269), Arzignano (Vicenza, northeast Italy).
Fig. 3. Line drawing (from Beschin *et al.*, 2002, text-fig. 8).

***Calappilia vicetina* Fabiani, 1910**

Fig. 4. Line drawing (from Fabiani, 1910, pl. 1, fig.1b).
Fig. 5. Neotype (MGPD.23999), San Gottardo, (Vicenza, northeast Italy).

***Stenodromia mainii* (Allasinaz, 1987)**

Fig. 6. Holotype (MPMOV.158M), Ovada, (Alessandria, northwest Italy).

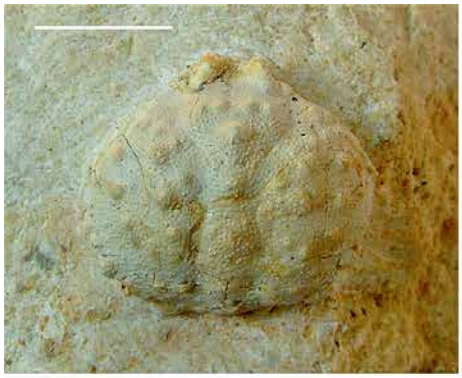
***Stenodromia gibbosa* A. Milne Edwards *in* Bouillé, 1873**

Fig. 7. Cast of holotype (MNHN.F.R03835), Biarritz (southwest France).

***Calappilia tridentata* (Beurlen, 1939)**

Fig. 8. Syntype (HNHM.M.59.4681), Budapest (Hungary).

Scale bars equal 10 mm.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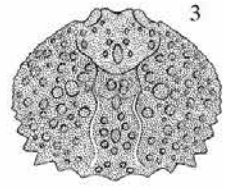
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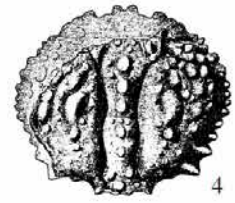
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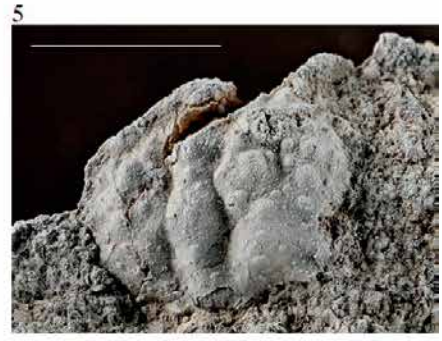

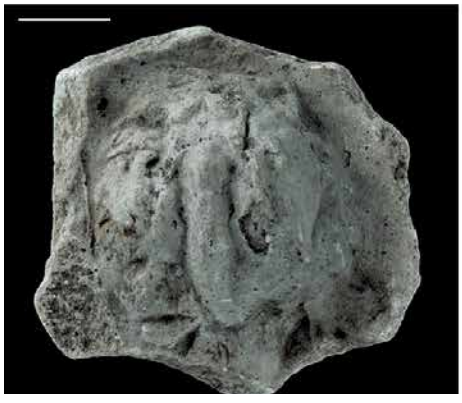
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