Late Miocene Conidae (Mollusca: Gastropoda) of Crete (Greece).
Part 1: genera *Conilithes* Swainson, 1840 and *Conus* (*Kalloconus*) da Motta, 1991

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ABSTRACT
Conidae is a diverse family of carnivorous marine gastropods. They rapidly diversified during the Miocene and now they inhabit tropical and subtropical seas. Here we attempt to provide the first inventory of fossil conids from the late Miocene of Crete (Greece). This paper deals with the genera Conilithes and Conus (Kalloconus) da Motta, 1991 and will be followed by papers presenting other genera of the family. Using UV light, we described the residual colour patterns of eleven species, of which three are new: Conilithes herodus n. sp., Conus (Kalloconus) helladicus n. sp and Conus (Kalloconus) asterosiaenius n. sp. One species is in open nomenclature: Conilithes sp.. Six species are first recorded in the late Miocene of Crete: Conilithes brezinae (Hoernes & Auinger, 1879), Conilithes striatulus (Brocchi, 1814), Conus (Kalloconus) neumayri Hoernes & Auinger, 1879, Conus (Kalloconus) hendricksi (Harzhauser & Landau, 2016), Conus (Kalloconus) gulemani Erünel-Erentöz, 1958 and Conus (Kalloconus) lekeseni (Harzhauser & Landau 2016). Conilithes antcidilivianus (Bruguère, 1792) is the only species already recorded by past Greek authors. Firstly, our study reveals that only two species are restricted to the late Miocene of Crete (Conilithes herodus n. sp. and Conus (Kalloconus) helladicus n. sp.). Secondly, we found deep relationships with the conid assemblage from the Langhian of Paratethys (six shared species). This result could be interpreted as a conid fauna, present and widely distributed since the Langhian-Serravallian in both the Paratethys and the eastern Proto-Mediterranean. This fauna disappeared from Paratethys during the Serravallian, but probably persisted in the eastern Proto-Mediterranean, as suggested by the relationships with the Serravallian of Turkey and the Tortonian of Crete (this work). On the other hand, the weak relationships with the late Neogene of Italy might be biased because, for the comparison with Italian faunas, we used works that illustrated Conidae without UV light.
RÉSUMÉ
Les Conidae du Miocène supérieur de Crète (Grece). Partie 1 : genres Conilithes Swainson, 1840 et Conus (Kalloconus) da Motta, 1991. Les Conidae forment une famille diversifiée de gastéropodes marins carnivores. Au cours du Miocène, ils se diversifient rapidement et actuellement, ils occupent principalement les mers tropicales et subtropicales. Dans ce travail, un premier inventaire des Conidae du Miocène supérieur de Crète est donné en se concentrant sur les genres Conilithes et Conus (Kalloconus). Il sera complété par des articles complémentaires sur les autres genres de la famille. En utilisant la fluorescence UV des pigments résiduels, nous décrivons les motifs colorés de onze espèces, parmi lesquelles trois sont nouvelles : Conilithes herodus n. sp., Conus (Kalloconus) belladicus n. sp. et Conus (Kalloconus) asterousiaensis n. sp. Une espèce est laissée en nomenclature ouverte : Conilithes n. sp. Six espèces sont signalées la première fois dans le Miocène supérieur de Crète : Conilithes brezinae (Hoernes & Auinger, 1879), Conilithes striatulus (Brocchi, 1814), Conus (Kalloconus) neumayri Hoernes & Auinger, 1879, Conus (Kalloconus) hendricksi (Harzhauser & Landau 2016), Conus (Kalloconus) gulemani Erínul-Erentiţă, 1958 et Conus (Kalloconus) lektosensis (Harzhauser & Landau 2016). Conilithes antiđiluvianus (Bruquiére, 1792) est la seule espèce déjà signalée par les anciens auteurs grecques. Premièrement, notre étude révèle que seules deux espèces sont restreintes au Miocène supérieur de Crète (Conilithes herodus n. sp. et Conus (Kalloconus) belladicus n. sp.). Deuxièmement, il révèle aussi d’êtroites affinités avec l’assemblage de Conidés du Langhian de Paratéthys (six espèces communes). Ce résultat suggère qu’une faune de Conidae, largement distribuée en Paratéthys et en Proto-Méditerranée au Langhien a disparu de Paratéthys et en Turquie, mais a persisté dans l’est de la Proto-Méditerranée en Turquie et en Crète (Grèce) jusqu’au Miocène supérieur (ce travail). Par ailleurs, les faibles relations avec le Néogène supérieur d’Italie pourraient être biaisées car les travaux disponibles présentent les conidés en lumière naturelle.

MOTS CLÉS
Conidae, Miocène supérieur, Grèce, Crète, fluorescence UV, espèces nouvelles.

INTRODUCTION
The Conidae snails are a family of marine gastropods with a remarkable biodiversity of more than 900 extant species. Conids are present in a variety of depths in subtropical and tropical seas (e.g., Hendricks 2015; Abalde et al. 2019). They are carnivorous, mainly hunting a specific prey (Kohn 1990). Most species eat polychaete worms, but some lineages eat other gastropods or even fish (Olivera et al. 2015; Safavi-Hemami et al. 2015).

The rich conid fossil record starts from the early Eocene (Duda & Kohn 2005). Kohn (1990) suggested multiple radiation events, but the Neogene is one of the greatest phases of radiation. Until now, Conidae from the Neogene of Greece have sporadically been identified and named as Conus sp., with the few exceptions of Symeonidis (1965), Symeonidis & Konstantinidis (1968), Dermitzakis 1969, Merle et al. (1988), Koskeridou (1997) and Koskeridou et al. (2017). Most of the cone shells were misidentified (Symeonidis 1965; Symeonidis & Konstantinidis 1968), leading to an unclear distribution of the Conidae fauna in the Eastern Mediterranean during the late Miocene. Here, we present the first systematic study of Conidae from the late Miocene of Crete (Greece) using UV light in order to reveal their colour patterns as an aid to their identification. An updated taxonomy of the conids found in the Tortonian of Crete is necessary for an accurate representation of the biodiversity of the family in the late Miocene of Eastern Mediterranean.

GEOLOGICAL BACKGROUND
The island of Crete today is a horst in the forearc of the Aegean region. N-S and E-W extension created normal faults where the footwall is the basement, and the hanging wall Neogene deposits overlie basement rocks of the Upper Nappes. Our study area is in Central Crete, in the Heraklion and Messara Basins (Meulenkamp et al. 1979; Zacharias et al. 2011) and in two localities from the Ierapetra Basin and Sitia Basin of Eastern Crete (Dermitzakis 1969). Three mountains, Psiloritis Mountains (P), Asterousia Mountains (A) and Dikti Mountains (D), surround the Heraklion and Messara Basins (Fig. 1). Ierapetra graben deposits are overlain on the pre-Neogene series unconformity (Ring et al. 2001). The localities where the fossils were found have been discussed in the past with Symeonidis’s work being of great importance for the study of late Miocene mollusc faunas (Symeonidis 1965; Symeonidis & Konstantinidis 1968).

1) Tyllissos locality (Fig. 1[1]) is in the foothills of Psiloritis mountains and according to Delrieu (1990), Tyllissos sand facies are covered by marls containing Globorotalia mirucenta mediterranea Catalano & Sprovieri 1969.

2) Keramoutsi locality (Fig. 1[2]) is south of Tyllissos, and as well as Tyllissos, its sandy sediments are covered by marls containing Globorotalia mirucenta mediterranea.

3) Papanos locality (Fig. 1[3]) is in the south-eastern foothills of Psiloritis, and hosts a rich Tortonian fauna (Delrieu 1990; Koskeridou 1997). Frydas (2004) has found Messinian sediments in the area, so we consider the locality as late Tortonian-early Messinian.
4) Apomarma locality (Fig. 1[4]) has been studied again by Delrieu (1990), named therein as Aghia Irini, and contains a rich Tortonian fauna. Part of the collection was extracted from sections of the new road, now covered and no longer accessible.

5) Psalidha locality (35°05′08.1″N, 24°57′46.0″E) (Fig. 1, 5) has been studied previously (Symeonidis & Konstantinidis, 1968; Merle et al. 1988; Koskeridou 1997), who found a rich Tortonian mollusc fauna beside coral reefs.

6) Adhraktia locality (Fig. 1[6]), just north of the village of Panassos, has been studied by Delrieu (1990) (Adhraktia-a), who found a Tortonian infralittoral mollusc fauna beside coral reefs.

7) Tefeli locality (Fig. 1[7]) bears a rich Tortonian mollusc fauna with many large-sized shells (Symeonidis & Konstantinidis 1968; Koskeridou 1997), pointing towards a shallow marine environment.

8) Partira section (Fig. 1[8]) is an area, which according to Zachariasse et al. (2011) is of Tortonian age and bears sediments of Kasteliana and Moulia Formations. A shallow marine mollusc fauna has also been found (CP and EK).

9) Filippi locality (35°02′07.2″N, 25°15′00.5″E) (Fig. 1[9]) bears sandy sediments, with a rich shallow marine mollusc fauna and was considered by Symeonidis & Konstantinidis as Tortonian in age (1968).

10) Makrilia locality (35°03′42.4″N, 25°43′19.0″E) (Fig. 1[10]) is of late Tortonian age (NN11a) based on planktonic foraminifera and calcareous nannoplankton (Fortuin 1977; Bachmeyer & Symeonidis 1978; Sachse & Mohr 1996).

11) Achladia locality (Fig. 1[11]) has been discussed in the past (e.g., Koskeridou 1997; Marcopoulou-Diacantoni & Logos 2004) and shows a shallow marine Tortonian fauna.

MATERIAL AND METHOD

MATERIAL
We handpicked samples from the Filippi, Panassos, Apomarma, Tefeli and Makrilia localities. For the other areas we use the historical collections of the National and Kapodistrian University of Athens (NKUA), and the collections of the Muséum national d’Histoire naturelle, Paris, particularly the material coming from the Action spécifigue du Muséum project (1989-1990) on the Neogene of Crete. The specimens were not bleached, as most of them revealed their colour pattern under UV light.

METHOD
The observation of colour patterns on fossil shells is difficult, as the degradation of the pigments happens quickly after the death of the animal and continues also during fossilisation. A solution to the problem is the use of ultraviolet light (UV), as the colour pattern of the fossil shells becomes visible with the exposure of wavelengths below 365 nm (Miethe & Born...
1928; Olsson 1967; Vokes & Vokes 1968; Cate 1972; Hoerle 1976; Hoerle & Vokes 1978; Dockery 1980). In the last fifteen years, many works have pointed out that the colour pattern of gastropods can be easily revealed and are important for their identification at species level (e.g., Pedriali & Robba 2005 (Naticidae); Merle et al. 2008 (Lutetian gastropods, Paris basin); Caze 2010 (Seraphisidae); Caze et al. 2011a, b (Lutetian gastropods and Amphullinidae, Paris Basin); Landau et al. 2013 (Serravallian gastropods, Turkey); Pacaud 2017 (Columbellidae); Pacaud & Cazes 2014 (Nassariidae, Paris Basin and United States); Caze et al. 2015 (Jurassic gastropods); Harzhauser & Landau 2016 (Conidae, Paratethys); Hendricks 2009, 2015, 2018 (Conidae Western Atlantic); the list is not exhaustive). Concerning the conids, zoologists have long been used the colour patterns to separate extant species, since their shells are conservative in shape and display few shell characters (Marshall et al. 2002; Hendricks 2015). According to Hall (1966), fossil cone shells, that are only observed under natural light and with superficially similar morphologies, have been often misidentified. Consequently, the study of their colour pattern is the best means for their identification at species level (Hendricks 2009, 2015, 2018).

Photographs
We used a CANON EOS-7D with an EFS 15-85 mm image stabilizer ultrasonic lens, using extra magnification × 4 lens. The UV figures were photographed under UV light with wavelength of 365 nm. Also, we occasionally used a LEICA M165 C, with a camera LEICA IC90 E.

Shell terminology
We follow Smith (1930), Röckel et al. (1995), Hendricks (2009), but mainly we used Harzhauser & Landau’s (2016) terminology for the subsutural flexure measurements. We follow the 45 angled measurement style of Harzhauser & Landau (2016) in order to compare the Greek specimens with the Paratethys material.

SYNONYMIC AND CHRESONOMIC LISTS
We provide the list of the synonyms. Concerning the chresonymic list, we concentrate on Greek references, because, for some species, the list could be very long. This group has received considerable attention recently; the middle Miocene eastern Mediterranean of the Karaman Basin, Turkey was revised by Landau et al. (2013), and the middle Miocene Parathys by Harzhauser & Landau (2016). In this paper we will not repeat chresonymics and species descriptions given by those authors unless modified or challenged by our findings.

**SYSTEMATIC PALAEONTOLOGY**

**Genus Conilithes** Swainson, 1840

| Type species (by monotypy). — Conus antidiluvianus Bruguère, 1792. Early-middle Miocene of Parathys (see Harzhauser & Landau 2016 for detailed references), Torontonian of Italy (Sant’Agatha Fossili, Stazzano, Montegibbio [Sacco 1893a]) and Greece (Ierapetra Basin, Crete, this work) to Pliocene of Italy (Sant’Agatha Fossili, Stazzano, Montegibbio [Sacco 1893a]) and Greece (Ierapetra Basin, Crete, this work) to Pliocene of Italy (Sant’Agatha Fossili, Stazzano, Montegibbio [Sacco 1893a]).

**Diagnosis.** — Biconic shell. Scalariform spire, angular, carinate shoulder, which often bears tubercles, but no spiral sculpture (Tucker & Tenorio 2009). Subsutural flexures deep, strongly curved, moderately asymmetrical (Harzhauser & Landau 2016). Beaded early teleoconch whorls.
Remarks
Based on our material, we show that the subsutural flexures are variable from shallow (e.g., *Conilithes brezinae* (Hoernes & Auinger, 1879)) to deep (e.g., mean SSFD of *Conilithes herodus* n. sp.). In addition, early teleoconchs whorls can be devoid of beads (e.g., *Conilithes striatulus* (Brocchi, 1814)) and rarely species display beads on their last whorls (e.g., *Conilithes* sp.). The stratigraphical range of the genus is Eocene to Pliocene of Europe (Proto-Mediterranean and Paratethys) and North America (Harzhauser & Landau 2016).

*Conilithes brezinae* (Hoernes & Auinger, 1879) (Figs 2, 3; Table 1)

*Conus* (*Leptoconus*) *brezinae* Hoernes & Auinger, 1879: 36.

*Conus* (*Leptoconus*) *brezinae* Hoernes, 1878: 195, nomen nudum.

*Conus* dujardini – Hörnes 1851: 40 (partim), pl. 5, figs 8a-f. — Symeonidis 1965: 290-291, pl. 63, figs 5-6. — Symeonidis & Konstantinidis 1968: pl. 81, figs 9-12. — Caze 2010: fig. 33D-E.

*Conus* (*Conospirus*) *dujardini* – Dermitzakis 1969: pl. 79, fig. 8.

*Conilithes brezinae* – Harzhauser & Landau 2016: 48-50, tables 1-2, figs 3F, 5D₁-D₃, 5E₁-E₃, 5F₁-F₃, 5G₁-G₃, 5H₁.

Type material. — Syntype NHMW 1999x0077/0023a, illustrated in Hörnes (1851: pl. 5, fig. 8a), syntype NHMW 1999x0077/0023b, illustrated in Hörnes (1851: pl. 5, fig. 8b), syntype NHMW 1999x0077/0023c, illustrated in Hörnes (1851: pl. 5, fig. 8c), syntype NHMW 1999x0077/0023d, illustrated in Hörnes (1851: pl. 5, fig. 8d), syntype NHMW 1999x0077/0023e, illustrated in Hörnes (1851: pl. 5, fig. 8e).

Type locality. — Steinebrunn (Austria). Middle Miocene (late Langhian).

Stratigraphic range. — Langhian Paratethys (see Harzhauser & Landau 2016 for detailed references) and Tortonian of Greece.

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Fig. 2. — *Conilithes brezinae* (Hoernes & Auinger, 1879) specimens from the Tortonian of Crete (Greece), showing colour pattern variation under UV light in abapertural views: A, AMPG(iv) 2638, Panassos; B, AMPG(iv) 2610, Partira; C, MNHN.F.A72573, Crete; D, MNHN.F.A72574, Crete; E, MNHN.F.A72583, Crete; F, MNHN.F.A72570, Partira; G, AMPG(iv) 2637, Tafeli; H, AMPG(iv) 2629, Filipo; I, MNHN.F.A72577, Crete; J, MNHN.F.A72567, Adhraktia; K, MNHN.F.A72582, Crete; L, AMPG(iv) 2611, Psalidha; M, AMPG(iv) 2620, Psalidha; N, AMPG(iv) 2614, Psalidha; O, MNHN.F.A72565, Crete; P, AMPG(iv) 2612, Psalidha; Q, AMPG(iv) 2788: figured specimen of Symeonidis & Konstantinidis (1968: pl. 81, fig. 10), Crete. Scale bar: 1 cm.
Material examined. — Greece. Crete (precise localities unknown), 17 specimens: MNHN.F.A72565, MNHN.F.A72566, MNHN.F.A72571 to MNHN.F.A72584 and AMPG(IV) 2788; Filippi, 11 specimens: AMPG(IV) 2624-2629, 2631, 2633-2636; Partira, four specimens: (three specimens MNHN.F.A72568 to MNHN.F.A72570 and one specimen AMPG(IV) 2610); Tefeli, three specimens: AMPG(IV) 2630, 2632, 2637; Adhraktia, one specimen: MNHN.F.A72567; Psalidha, 13 specimens: AMPG(IV) 2611-2623. All of them display colour patterns under UV light.

Description of the colour pattern

Main colour pattern of this species consists of flammulae on spire whorls (Fig. 3), dots on carina (Fig. 3) and a non-fluorescent band below carina with small to tiny spiral rows of dots (Fig. 3). On the last whorl, this species bears spiral lines of dots usually interspersed with continuous spiral lines.
on a non-fluorescent base colour. A non-fluorescent band on the anterior part of last whorl exists in most specimens (Fig. 2), surrounded by fluorescent bands (Fig. 3). The colour pattern variability of this species results from the ratio of the alternation between continuous spiral lines and other discontinuous lines making small dots (e.g., Fig. 2F, H), as well as the existence of one or two non-fluorescent bands at the last whorl (e.g., Fig. 2C, I, K). Minor pattern variations are the axial fluorescent bands and the existence of fluorescent bands, as a result of dots and lines coalescing.

Remarks
Symeonidis (1965), Symeonidis & Konstantinidis (1968), Dermitzakis (1969), Merle et al. (1988) and Koskeridou (1997) reported this species from Crete, under the name of Conus dujardini (Fig. 2Q). Harzhauser & Landau (2016) noted that the taxon Conilithes dujardini (Deshayes, 1845) had been used as a dumping ground for numerous Conilithes species. Harzhauser & Landau (2016) identified Conilithes brezinae and distinguished it from the Conilithes dujardini. The Cretan specimens are assigned to the species Conilithes brezinae, as they are morphologically identical. The specimens studied herein sometimes (one out of three specimens) possess 1-2 spiral grooves just under carina, but the grooves are not punctate, as in Conilithes exaltatus (Eichwald, 1830) (Harzhauser & Landau 2016). They possess a shallow subsutural flexure (Table 1), but since SSFD is a variable intraspecific character, we do not separate the material studied from the Paratethyan specimens (deep SSF, Harzhauser & Landau 2016). Harzhauser & Landau (2016) hypothesized the existence of this species in the Proto-Mediterranean (Harzhauser & Landau 2016) and with our material, we confirm their hypothesis. A specimen, first identified as Conilithes dujardini (Deshayes, 1845) from the Karaman Basin (Landau et al. 2013), has been identified by Harzhauser & Landau 2016 as Conilithes brezinae. Unlike Conilithes brezinae from Crete and Paratethys, the Karaman specimen possesses a colour pattern of irregular fluorescent blotches (Landau et al. 2013: 562, pl. 82, fig. 5). The horizontal non-fluorescent band, shared between the Karaman specimen and the Cretan specimens, is a pattern occurring in multiple extant and extinct Conus species (e.g., see herein Conilithes herodus n. sp. and Conilithes striatulus (Brocchi, 1814)). For these reasons, we prefer exclude that specimen from Conilithes brezinae until more specimens from Karaman are figured.

Conilithes herodus n. sp.
(Figs 4, 5, 6; Table 2)

Diagnosis. — Conilithes species with a colour pattern of large, non-fluorescent blotches and arch-like fluorescent areas on carina.

Type material. — Holotype AMPG(IV) 2608. — Paratypes, all Tortonian in age: Greece. Crete: MNHN.EA72585, MNHN.EA72586; MNHN.EA72587, MNHN.EA72588, MNHN.EA72589, MNHN.EA72590, MNHN.EA72591; Makritia: MNHN.EA72592; Tefeli: AMPG(IV) 2609.
**Type Locality.** — Tefeli, Tortonian, Crete, Greece.

**Stratigraphic Range.** — Tortonian of Greece (Ierapetra and Messara Basins, Crete).

**Etymology.** — Name taken from the Odeon of Herodes Atticus, in Athens, which bears many arched structures that look like the colour pattern of this species.
TABLE 2. — Shell measurements and ratios of Conilithes herodus n. sp. from the Tortonian of Crete (Greece). Mean and standard deviation are computed from nine specimens. Largest specimen is paratype MNHN.F.A72587.

| SL     | MD    | AH    | HMD   | AL    | SA    | LWA   | LW    | RD    | PMD   | RSH   | SSFD  | SSFd  | PV  |
|--------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-----|
| 19.6 mm| 9.27 mm| 14.83 mm| 13.4 mm| 15.26 mm| 78.6°| 40.5°| 2.11 | 0.63 | 0.9   | 0.24  | 2.21  | 6.15  | 0.18 |

SHELL DESCRIPTION
Small-sized and elongate shells. Protoconch not preserved. Spire with a maximum of ten spire whorls, high, conical with flat sutural ramp in early whorls, slightly concave in later spire whorls. Carina subangulated to angulated, with tubercles visible on early spire whorls, sometimes visible until 8th spire whorl. Subsutural flexure shallow, strongly curved, strongly to moderately asymmetrical. No spiral grooves below carina. Last whorl elongated, conical. Aperture straight, narrow, widening towards twisted fasciole. Growth lines not prominent, with spiral grooves visible on the anterior part of the shell, towards the anterior part of the last whorl.

DESCRIPTION OF COLOUR PATTERN
The colour pattern of the spire whorls consists of thin, axial or irregular fluorescent lines, engulfing angular or irregularly oval, non-fluorescent blotches on carina (Fig. 6). On the body of the shell, two spirally arranged, wide, fluorescent bands exist (Fig. 5), usually disrupted by a non-fluorescent band, with fluorescent blotches or dots. In most cases, the blotches create arrow like patterns (Figs 5G1, 6). Tiny lines of bright fluorescent dots (Fig. 6) are on the wide fluorescent bands and sometimes on the non-fluorescent base colour, also surrounded by fine thin, continuous, bright fluorescent spiral lines (Fig. 6).

REMARKS
The specimens described herein (Table 2), possess a subangulated to angulated shoulder, revealing a slight morphological variability. The colour pattern on the spire whorls is the most distinguishing character that separates it from the rest of the Conilithes species. The shell of this species is similar to Conilithes brezinae, but none possesses spiral cords below carina, as some Conilithes brezinae specimens do. The colour pattern is different, bearing blotches on spire whorls, two fluorescent bands and one non-fluorescent band in the middle of the last whorl. The similarity in colour pattern on the rest of the shell, bearing lines of dots and continuous spiral lines, suggests a close relation between the species. This species is also morphologically similar to Conilithes sceptophorus (Boettger, 1887), but it differs in its pattern described, consisted of axial zig-zag stripes (Harzhauser & Landau 2016). It differs from Conilithes allioni (Michelotti, 1847) in the more elongated spire, and from Conilithes eichwaldi Harzhauser & Landau, 2016 in the smooth shoulder, being more angulated on the Cretan specimens.
Fig. 7. — *Conilites* sp. from the Tortonian of Crete (Greece), MNHN.F.A72593, Makrilia in apertural (A1, A5), abapertural (A2, A6) and apical (A4) views, under natural (A1-A4, A7) and UV light; A3, detail of the subsutural flexure (white line); A7, detail of the protoconch. Scale bars: A1-A2, A4-A6, 1 cm; A3, A7, 0.05 cm.
Maximum diameter at angulated shoulder. Suture channelled. Subsutural flexure shallow, moderately curved, strongly asymmetrical (Fig. 7A3). Aperture narrow, straight. Last spire whorl straight, conical, narrow. Spiral grooves on the anterior part of last whorl. Fasciole indistinct.

**Description of Colour Pattern**

Colour pattern consists of thick flammulae on spire whorls. Colour pattern on last whorl consists of fluorescent blotches and closely related, bright fluorescent spiral lines-dashes, that are separated by non-fluorescent elongated dots and non-fluorescent axial blotches (Fig. 8).

**Remarks**

A species differing from *Conilithes brezinae* and *Conilithes herodus* n. sp. herein, in the strongly beaded early spire whorls (five or six) and the lower relative height of the spire (RSH) (Table 3). Also, the shallow subsutural flexure diverges from the other species of *Conilithes*, but this species cannot be included in the genus *Conasprella* Thiele, 1929 (type species by subsequent designation (Tucker & Tenorio 2009): *Conus pagoda* Kiener, 1847), as the last whorl of the shell lacks any sulci (Harzhauser & Landau 2016). It differs from *Conilithes allioni* (Michelotti, 1847) and *Conilithes sceptrophorus* (Boettger, 1887) in the longer last whorl. It differs from *Conilithes antidiiluvianus* (Bruquièr, 1792) in the less pronounced shoulder and less elevated spire whors. As we have only one specimen, we refrain from naming it.

**Conilithes striatulus** (Brocchi, 1814)

(Figs 9, 10; Table 4)

*Conus striatulus* Brocchi, 1814: 294, pl. 3, fig. 4.

*Conus (Chelyconus) striatulus* – Sacco 1893a: 93-96, pl. 9, figs 30-31, 34. — Muñiz Solís 1999: 61-63, fig. 81-F.

*Conus striatulus* – Pinna & Spezia (1978): 137, pl. 22, fig. 2-2.

**Type locality.** — Piacentino Piemontese, Italy. Pliocene.

**Type material.** — Lectotype figured in Brocchi (1814: pl. 3, fig. 4).

Fixation of the lectotype (MSNMI4672, Brocchi coll.) by inference of “holotype” (ICZN 1999: art. 74.6) by Pinna & Spezia (1978).

**Stratigraphic range.** — Early Miocene: Burdigalian of Italy (Colli Torinesi; Sacco 1893a); late Miocene: Tortonian of Italy (Stazzano; Sacco 1893a) and Greece (Messara Basin, Crete); Pliocene: Piacenzian of Italy (Piacentino; Sacco 1893a) and Spain (Estepona; Muñiz Solís 1999).

**Material examined.** — Greece. Psalidha, one specimen MNHN.F.A72601. Panassos: five specimens AMPG(IV) 2639-2643. Crete: seven specimens MNHN.F.A72594 to MNHN.F.A72600. All of them display colour patterns under UV light.

**Shell description**

Small-sized shells with spire whors of relatively medium height and robust outline. Spire whors straight to coeloconid, conical, with scalariform, slightly elevated spire whors and angulated shoulders. Usual, faint spiral cords on early spire whors, but no tubercles or beads. Subsutural flexure moderately deep, strongly curved, moderately asymmetrical. Maximum diameter on shoulder. Last whor straight, conical.
Aperture straight. Fasciolae indistinct. Spiral grooves on the anterior part of last whorl.

Colour pattern variation. — The colour pattern consists of fluorescent flammulae on the spire (Fig. 10). The last whorl bears a primary pattern of irregular, fluorescent blotches. The blotches can be axial flammulae that continue from the spire whorls, towards the anterior of the shell, or can be spirally arranged as bands, parallel to a second pattern of fluorescent spiral lines of dots and dashes, along the length of the shell. All patterns are occasionally disrupted by non-fluorescent blotches (Fig. 10). On some shells, a non-fluorescent band exists along the centre of the length of the shell, decorated with fluorescent spiral lines of dots or dashes (Fig. 10, non-fluorescent band).

Remarks
This species has been reported from the Miocene (Burdigalian and Tortonian) and the Pliocene of Italy (see Brocchi 1814: pl. 3, fig. 4; Sacco 1893a: pl. 9, fig. 30). The Greek material (Table 4) is very similar to the lectotype of Conus striatulus (MSNM i4672) coming from the Pliocene. Unfortunately, no colour pattern under UV light is visible on the lectotype (Giorgio Teruzzi, personal communication). Nevertheless, we do not observe any shell differences between the Greek specimens and the lectotype. Therefore, we consider them to belong to Conilithes striatulus. This species slightly differs from the other Conilithes species by its shorter spire whorls and its more robust shell.
**TABLE 5.** — Shell measurements of *Conilithes antidiluvianus* (Bruguère, 1792), AMPG(IV) 2691, from the Tortonian of Makrilia (Crete, Greece).

| MD    | SA  | LWA |
|-------|-----|-----|
| 15.41 mm | 68° | 27.5° |

*Conilithes antidiluvianus* (Bruguère, 1792)  
(Fig. 11; Table 5)

*Conus antidiluvianus* Bruguère, 1792: 637.

*Conospirus antidiluvianus* – Sacco 1893a: b: 39, pl. 4, fig. 35.

*Conus (Conospirus) antidiluvianus* – Dermitzakis 1969: pl. 78, fig. 7.

*Conus (Conilithes) antidiluvianus* – Muñiz Solís 1999: 69-71, fig. 8O-Q.

*Conilithes antidiluvianus* – Caze 2010: fig. 37B. — Harzhauser & Landau 2016: 46, figs 3C, 5J-5K, 6A-6J.

*Conus antidiluvianus* – Janssen et al. 2014a: 13, fig. 16; 2014b: 227.

**TYPE MATERIAL.** — Neotype: MSNM i28027, Badagnano, Rio dei Carbonari (Italy), designated by Janssen et al. (2014a), Pliocene.

**TYPE LOCALITY.** — Badagnano, Rio dei Carbonari, Piacenza Province, Italy (Pliocene, Piacenzian, Castell’Arquato Formation).

**STRATIGRAPHIC RANGE.** — Early-middle Miocene of Paratethys (see Harzhauser & Landau 2016 for detailed references), Tortonian of Italy (Sant’Agatha Fossili, Stazzano, Montegibbio [Sacco 1893a]) and Greece (Ierapetra Basin, Crete): Pliocene of Italy (Hall 1966; Janssen et al. 2014a, b), Greece (Heraklion Basin, Crete [Caze 2010]) and other localities in France (Biot), Sicily, Turkey (Hatay Basin) and Syria (Erínal–Errentió 1958; Janssen et al. 2014a).

**MATERIAL EXAMINED.** — Makrilia: one broken specimen AMPG(IV) 2691 displaying faint colour patterns under UV light.

**DESCRIPTION OF THE COLOUR PATTERN**

Colour pattern is absent on most of the specimen’s surface. There is a faint pattern of axially arranged, rectangular blotches along the posterior two-thirds of last whorl (Fig. 11A3).

**REMARKS**

The name of this species has been thoroughly discussed (Janssen et al. 2014a; b; Harzhauser & Landau 2016). This species is conspicuously absent from most of the localities studied herein, probably due to its deep-water habitat (Harzhauser & Landau 2016). Only one specimen has been recovered by us from the Makrilia Fm (Table 5; Fortuin 1978), found inside rubble. Recently Moforis et al. (2013) found Pliocene strata from Makrilia, but our specimen collected at the base of Makrilia Fm., is Tortonian in age. Dermitzakis (1969) has also reported this species from the Asari section (Ierapetra Basin) while Caze (2010) reported it from the Pliocene of Kavrochori village (Heraklion Basin). Despite the bad preservation of the colour pattern of our specimen, it resembles the well-preserved colour pattern of Sacco’s figure (Sacco 1893b: pl. 4, fig. 35) and the figured specimen by Caze (2010: fig. 23B).

**CONCLUDING REMARKS ABOUT CONILITHES**

*Conilithes dujardini* (Deshayes, 1845) had been thought to exist in Paratethys and Proto-Mediterranean seas during the Miocene. Past Greek researchers identified almost all *Conilithes* species (the exception is *Conilithes antidiluvianus* (Bruguère, 1792)) as *Conilithes dujardini* (e.g., Symeonidis 1965; Symeonidis & Konstantinidis 1968; Dermitzakis 1969). Harzhauser & Landau (2016) proved the presence of multiple *Conilithes* species for the Langhian-Serravallian of the Paratethys, describing six species. Herein, using ultraviolet light, we propose five species for the Tortonian of Crete, with three of them not present in Paratethys, thus revealing the diversity of this genus. The species are easily recognizable by their colour pattern variations. Despite their differences, the similarities of their patterns, such as the continuous spiral lines and spiral rows of dots-dashes, along with the spiral bands, show a close relation between these species. Morphological differences exist in most species, shown using principal components analysis, using the ratios LW, RD, RSH, and PMD (PCA, Fig. 12). Two of these species seem to have similar morphological variations, *Conilithes brezinae* and *Conilithes herodus*, suggesting a very close relationship.

**Genus Conus Linnaeus, 1758**

**TYPE SPECIES.** — *Conus marmoreus* Linnaeus, 1758 (Recent, Indo-Pacific) by subsequent designation by Children (1823: 107).

**Subgenus Kalloconus** da Motta, 1991

*Troacoconus* Tucker & Tenorio, 2009: 126. — *Conus venulatus* Hwass in Bruguère, 1792 (Recent: West-Africa) by original designation.
Psarras C. et al.

**Type species.** — *Conus pulcher* Lightfoot, 1786 (Recent, West Africa) by original designation.

**Diagnosis.** — Protoconch multispiral. Teleoconch squat to moderately elongate, obconic shells with broad and rounded shoulders. Spire whorls low to very low, smooth, convex. Subsutural flexure very shallow in small species - deep in larger species, moderately curved and moderately asymmetrical. Colour pattern consists mainly of spirally arranged spots and dashes in continuous spiral rows (Diagnosis following Tucker & Tenorio (2009) and Harzhauser & Landau (2016)).

**Remarks.**
Puillandre *et al.* (2014) considered *Kalloconus* at subgenus level and found a monophyletic group. Today *Kalloconus* is restricted to the tropical East Atlantic (West Africa), but its fossil record demonstrates that it also had a European distribution during the Miocene in the Proto-Mediterranean and Paratethys. *Conus (Kalloconus)* can be distinguished from *Conus (Monteiroconus)*, mainly by the lack of spiral cords on the whorls and by its straight, lightly concave whorls.

*Conus (Kalloconus) neumayri* Hoernes & Auinger, 1879 (Figs 13, 14, 15; Table 6)

*Conus (Lithoconus) neumayri* Hoernes & Auinger, 1879: 27, pl. 1, figs 17-18;
*Conus (Lithoconus) neumayri* – Hoernes 1878: 195, nomen nudum.

*Monteiroconus dacie* – Landau *et al.* 2013: pl. 81, fig. 6.

*Monteiroconus mercatti* – Landau *et al.* 2013: pl. 81, fig. 8.

*Kalloconus neumayri* – Harzhauser & Landau 2016: 64-65, tables 1, 2, figs 3O, 11C₂-C₃, 11D₁-D₂, 11E₁-E₂, 11F₁-F₂

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Fig. 11. — Conilithes antidiluvianus (Bruguière, 1792) from the Tortonian of Makrilia, Crete, Greece (AMPG(IV) 2691): a broken specimen, very faint pattern under UV light. The white arrow indicates the colour pattern. Scale bar: 1 cm.
The colour pattern consists of one layer displaying very large, polygonal-like, rectangular blotches, restricted axially and spirally (see axial fluorescent and non-fluorescent boundary, Fig. 15). Not all blotches are rectangular. Some have sharp, not straight disruptions, while others fade randomly to the non-fluorescent base colour. On large specimens (see Fig. 15), some blotches tend to faintly connect with each other with faintly fluorescent areas between blotches (see unclear spiral interactions, Fig. 15). The pattern is continuous from the anterior part of the last whorl to the spire (Fig. 13A6). Blotches might be narrow, separated by two non-fluorescent spiral bands, thus creating dash-like rows of blotches.

**Remarks**
This species is not common in Crete (Table 12), but is very easily recognizable under UV light. The colour pattern of large rectangular blotches is characteristic of the species. Moreover, the interactions between the blotches and the dash-like patterns are also characters of this species (Figs 13, 15; see also Harzhauser & Landau 2016: fig. 11E1, F1). The Greek specimens differ morphologically from the Paratethyan ones in the strongly asymmetrical subsutural flexure (Table 6; moderately asymmetrical on Harzhauser & Landau 2016), but we consider that this difference could result from a local variation.

Landau et al. (2013), in our opinion, misjudged the more extreme Conus (Kalloconus) neumayri pattern (e.g., Fig. 14). They consider this extreme pattern as that of Conus (Monteiroconus) daciae from the Karaman Basin, Turkey (see Landau et al. 2013; pl. 81, fig. 6a, b). The colour pattern described therein is identical with the pattern of Conus (Kalloconus) neumayri. Unfortunately, their assumption was not fixed in Harzhauser & Landau (2016), since they assumed that Conus (Kalloconus) neumayri shows no signs.
of dots or dashes, but bears only large rectangular blotches. Herein we show that this is not the case, because interactions between the blotches and dash-like patterns between blotches, are present in the colour pattern spectrum of this species (Figs 13, 15). We believe the specimen of Landau et al. (2013: pl. 81, fig. 6a, b) is *Conus (Kalloconus) neumayri*. Therefore, the pattern assigned to *Conus (Monteiroconus) dacie* (Harzhauser & Landau 2016) is not correct and is herein considered as undescribed.

Harzhauser & Landau (2016) rejected the synonymy of this species with *Conus (Monteiroconus) berghausi* Michelotti, 1847, as Hall (1966) and Baluk (1997) proposed. We agree that the shell morphology and colour patterns are different and are indicators of two species. *Conus (Monteiroconus) berghausi* dots are small compared to the blotches of *Conus (Kalloconus) neumayri*. Furthermore, morphologically, *Conus (Kalloconus) neumayri* is more elongate, with slightly striated spire whorls and a rounder shoulder.
Conus (Kalloconus) hendricksi
(Harzhauser & Landau, 2016)
(Figs 16, 17; Table 7)

Kalloconus hendricksi Harzhauser & Landau, 2016: 57-59, figs 3H, 3I, 8F, 8G, 8H.

?Conus berghausi – Davoli 1972: pl. 3, figs 12-13.

Kalloconus berghausi – Landau et al. 2013: pl. 81, fig. 1.

Type material. — Holotype: NHMW 1870/0033/0005a (see Harzhauser & Landau 2016: fig. 8F-8I).

Type locality. — Lăpugiu de Sus (Romania), Langhian.

Stratigraphic range. — Langhian of Paratethys (see Harzhauser & Landau [2016] for detailed references), Serravallian of Karaman Basin (Turkey), Tortonian of Italy (Montegibbio, see Davoli [1972]) and Greece (Messara Basin, Crete).

Material examined. — Filippi: Nine specimens AMPG(IV) 2651-2659; Filippi, Crete: 30 specimens (MNHN.F.A72606 to MNHN.F.A72635). All specimens display a colour pattern under UV light.

Description of colour pattern
The colour pattern consists of one layer of fluorescent, evenly arranged rows of dots. The dots are evenly spaced, evenly sized, differing in shape. Some dots have an oval shape; others are more rectangular to parallelogram, while a few are arrow-
like shaped (Fig. 17). The axial distance between individual rows does not change with the individual's growth. Newly developed spiral lines of dots are added to fill the gaps, seen as faded, tiny dots between two rows (Fig. 17). As a result, large specimens tend to have numerous rows of dots, while smaller specimens have less rows. The largest specimen has over 22 rows (abapical rows are not clearly visible), while younger have less than 15. On the spire whorls, there is one spiral row of dots, with most of those partly covered by the suture of the succeeding whorls (Fig. 16).

REMARKS
Recently, *Conus (Kalloconus) hendricksi* (Harzhauser & Landau 2016) has been separated from *Conus (Monteiroconus) bergbasi* Michelotti, 1847, a very similar species both in shell morphology and in colour pattern. The differences reported by these authors are the relative larger size, the squat, club-shaped shells with a prominent shoulder and the spiral cords on spire whorls of *Conus (Monteiroconus) bergbasi*. They stated that the specimens of *Conus (Kalloconus) hendricksi* are smaller and less club-shaped. According to Harzhauser & Landau (2016), we use the subgenus *Monteiroconus* da Motta, 1991 for *Conus bergbasi* because of the presence of spiral cords on spire whorls. The study material (Table 7) fits the *Conus (Kalloconus) hendricksi* shell morphology, on the constrained, defined shoulder and the smooth, coeloconoid early spire whors (Fig. 16). In the study material, the pointed, early spire whors are absent on adult specimens, possibly because of the destruction and erosion, of their early, pointed whors (Fig. 16A, B). This might cause confusion and misleading results in PCA analysis (see Harzhauser & Landau 2016). Thus, we refrain from using this method on the Greek material. Furthermore, *Conus (Kalloconus) hendricksi* has a consistent colour pattern (Harzhauser & Landau 2016). Harzhauser & Landau (2016) described 13-16 spiral lines of dots on the last whorl (*Conus (Kalloconus) hendricksi* paratype), with some of them bearing smaller dots. On the Greek specimens, we observe more lines of dots (22 rows visible), and we consider that this small difference probably results from a geographical variation of the character. Finally, the spiral dots on the spire whors of our Greek specimens, match with *Conus (Kalloconus) hendricksi*. For these reasons we attribute them to this species.

The specimen of *Conus (Monteiroconus) bergbasi* from the Karaman Basin (Turkey) figured by Landau et al. (2013)

**Table 7.** Shell measurements and ratios *Conus (Kalloconus) hendricksi* (Harzhauser & Landau, 2016) from the Tortonian of Crete (Greece). Mean and standard deviation are computed from 39 specimens. The largest specimen is the specimen MNHN.F.A72610.

|                  | SL   | MD   | AH   | HMD  | AL   | SA   | LW   | LD   | PMD  | RSH  | SSFD | SSFd | PV  |
|------------------|------|------|------|------|------|------|------|------|------|------|------|------|-----|
| Largest specimen | 28.24| 17.07| 26.57| 22.33| 27.03| 146° | 39.5°| 1.65 | 0.64 | 0.84 | 0.06 | –    | –   |
| Mean             | 15.8 | 10.1 | 14.6 | 11.7 | 14.6 | 129.8| 42.6 | 1.59 | 0.69 | 0.8  | 0.08 | 2.54 | 7.2 |
| Standard deviation | 3.5  | 2.41 | 3.46 | 3.02 | 3.53 | 14.4 | 4.08 | 0.11 | 0.04 | 0.05 | 0.04 | –    | –   |

**Fig. 15.** — Pattern constituted of blotches in *Conus (Kalloconus) neumayri* Hoernes & Auinger, 1879 from the Tortonian of Crete (Greece). The elements of the colour pattern come from the specimen MNHN.F.A72602 (Fig. 13B2, Makrilia). Scale bar: 1 cm.
displays a colour pattern which is identical to the study material. In their figure showing the colour pattern of the species (Landau et al. 2013: pl. 81, fig. 1), the last row of dots near the suture is near or above the shoulder. This means that this specimen has spiral rows of dots on its sutureal ramp, the characteristic pattern of *Conus (Kalloconus) hendricksi* and not flammulae, a pattern character described on *Conus (Monteiroconus) berghausi* by Harzhauser & Landau (2016). Therefore, we believe that the specimens from Karaman Basin are *Conus (Kalloconus) hendricksi* rather than *Conus (Monteiroconus) berghausi*.

The specimens figured by Davoli (1972: pl. 3, figs 12-13) bear a colour pattern identical to the Greek specimens. Furthermore, the morphology of coeloconoid early spire outline and the relatively smooth shoulder are characters, which allow us to differentiate from *Conus (Monteiroconus) berghausi*. The other shells figured in Davoli as *Conus berghausi* (Davoli 1972: pl. 3, figs 11, 17-25) could be either *Conus (Monteiroconus) berghausi* or *Conus (Kalloconus) hendricksi*. The uncertainty results from the unclear figured shell morphology and colour patterns of these specimens and for the time being, we refrain from assigning them to *Conus (Kalloconus) hendricksi*.
The specimen illustrated by Hoernes & Auinger (1879) and named as *Conus (Dendroconus) subraristriatus* Pereira da Costa, 1866 (Pereira da Costa 1866: 23 [partim]; pl. 1, fig. 21 [only]), was discussed by Harzhauser & Landau (2016). We do not agree with their conclusion that it belongs to *Conus (Kalloconus) hendricksi*, as the colour pattern consisting of dots encircled by white coloured bands is different from that of *Conus (Kalloconus) helladicus*. In our opinion, the specimen illustrated by Hoernes & Auinger (1879) belongs to a different species.

**Conus (Kalloconus) helladicus** n. sp.
(Fig. 18; Table 8)

*Kalloconus hungaricus* – Landau et al. 2013: pl. 37, figs 9-10, pl. 38, fig. 1.

**Diagnosis.** — A medium-sized shell, with almost flat spire whorls and a colour pattern bearing wide flammulae on spire whorls, with spiral rows of dashes on last whorl.

**Type material.** — Holotype: AMPG(IV) 2660, Psalidha (Fig. 18B). Three paratypes, MNHN.F.A72636 to MNHN.F.A72638, Crete (Fig. 18A, C, D).

**Type locality.** — Psalidha, 35°05'08.1"N, 24°57'46.0"E, Messara Basin, Tortonian, Crete, Greece.

**Stratigraphic range.** — Tortonian of Crete (Messara Basin, Crete).

**Etymology.** — As *Conus (Kalloconus) hungaricus* Hoernes & Auinger, 1879 was first found in Hungary, we propose *Conus (Kalloconus) helladicus* n. sp., a species found in Greece (*Hellas* in Greek).

**Other material examined.** — Greece. Tefeli: four specimens AMPG(IV) 2661–2662, 2676–2677; Crete: one specimen (MNHN.F.A72639). All of them display a colour patterns under UV light.

**Shell description**
Medium-sized, robust shells, with relatively low spired whorls. Early spire whorls coeloconoid. Last spire whorls, smooth, straight to concave, creating a low conical to flat outline. Suture impressed. Subsutural flexure shallow, weakly curved, moderately asymmetrical. Shoulder rounded, protruded, creating a bulky outline. Maximum diameter below shoulder. Last whorl straight. Aperture moderate, narrow near suture, straight. Apertural canal wide, fasciole twisted, demarcated from base and inner lip. There are two extreme forms. Form 1 consists of robust forms which are relatively wider in comparison to form 2 and have low angled spire whorls. Form 2 consists of relatively elongated forms with flat spire whorls. Intermediate forms also exist.

**Description of colour pattern**
The colour pattern consists of one layer of short and long, fluorescent, spiral dashes, arranged in evenly spaced spiral rows. The spire whorls display wide, fluorescent flammulae, with irregular boundaries on a non-fluorescent base colour. The flammulae do not connect with the colour pattern of the last whorl.

**Remarks**
This species shows some variations in the relative diameter of its spire whorls (Table 8). The difference between the elongated and robust forms is not very variable. However intermediate forms (Fig. 18B, C) between both forms (Fig. 18A, D) point towards the existence of a single species.

*Conus (Kalloconus) hungaricus* specimens sensu Landau et al. 2013: pl. 37, figs 9, 10, pl. 38, fig. 1) from the Kara-man Basin (Turkey) are more likely to be *Conus (Kalloconus) helladicus* n. sp., because of their flat spire whorls and their identical colour pattern.

*Conus (Kalloconus) hungaricus* Hoernes & Auinger, 1879 from Paratethys seems closely related to *Conus (Kalloconus) helladicus* n. sp., but the medium height, conical spire whorls and the subsutural flexure of *Conus (Kalloconus) hungaricus* (medium depth, moderately curved, see Harzhauser & Landau 2016) are characters separating both species. *Conus (Kalloconus) tietzei* Hoernes & Auinger, 1879 differs in the relatively angulated shoulder and the medium depth of the subsutural flexure (Harzhauser & Landau 2016). *Conus (Kalloconus) gulemani* Erünlal-Erentöz, 1958 bears a similar morphology and a colour pattern. The differences between both species exist on the spiral whorl height and the smoother shoulder of *Conus (Kalloconus) gulemani*. All these species seem to be very closely related, but the differential characters of *Conus (Kalloconus) helladicus* n. sp. caused us to consider the Greek material as a new species.

*Conus (Kalloconus) gulemani* Erünlal-Erentöz, 1958
(Figs 19, 20; Table 9)

*Conus (Dentroconus) gulemani* Erünlal-Erentöz, 1958: 113, pl. 18, figs 5-6.
Late Miocene Conidae (Mollusca: Gastropoda) of Crete (Greece)

Conus (Kalloconus) helladicus n. sp.

**Type Material.** — One syntype: MNHN.F.A72638; three or four syntypes, MTA, Ankara.

**Type Locality.** — Zengen Köy S, Dereboğazi (Karaman Basin, Turkey). According to Landau et al. (2013) the localities of the Karaman Basin are Serravallian in age.

**Stratigraphic Range.** — Serravallian (Karaman Basin, Turkey (Landau et al. 2013) and Tortonian of Greece (Messara and Iera- petra Basins, Crete).

**Material Examined.** — Greece: Psalidha: two specimens AMPG(IV) 2663, 2665; Tofeli: six specimens from AMPG(IV) 2676-2681. Filippi: nine specimens AMPG(IV) 2664, 2668-2675; Crete: two specimens (MNHN.F.A72640 and MNHN.F.A72641). All of them display colour patterns under UV light.

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**Fig. 18.** — Conus (Kalloconus) helladicus n. sp. from the Tortonian of Crete (Greece): A, Paratype MNHN.F.A72638: a solid club shaped shell with large relative diameter (form 1) and a distinct colour pattern; B, Holotype AMPG(IV) 2660, Psalidha: a low spired specimen with a relatively narrow diameter (form 2), with a distinct colour pattern; C, Paratype MNHN.F.A72636: a small-sized shell with large relative diameter (form 1); D, Paratype MNHN.F.A72637: a flat spired conid with slightly protruding early spire whorls (form 2). Scale bar: 1 cm.

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**Table 8.** — Shell measurements and ratios of Conus (Kalloconus) helladicus n. sp. from the Tortonian of Crete (Greece). Mean and standard deviation are computed from nine specimens, the largest being the holotype (AMPG(IV) 2660).

| SL    | MD   | AH   | HMD  | AL   | SA   | LWA  | LW   | RD   | PMD  | RSH  | SSFD | SSfd | PV   |
|-------|------|------|------|------|------|------|------|------|------|------|------|------|------|
|        |      |      |      |      |      |      |      |      |      |      |      |      |      |
| Largest specimen | 40.25 mm | 37.5 mm | 39.3 mm | 30.25 mm | 39.1 mm | 155° | 35° | 1.07 | 0.95 | 0.77 | 0.02 | 2.6 | 10.33 | 0.55 |
| Mean   | 33.2 mm | 24.8 mm | 30.9 mm | 24.8 mm | 31.1 mm | 143.3° | 42° | 1.35 | 0.8 | 0.8 | 0.07 | 3.15 | 7.22 | 0.5 |
| Standard deviation | 5.28 | 5.55 | 5.17 | 3.99 | 4.98 | 12.47 | 5.8 | 0.14 | 0.07 | 0.03 | 0.03 | 1.14 | 1.84 | 0.16 |
Shell description
Small-to-medium-sized shells. Spire whorls weakly convex, with strongly coeloconoid outline on early whorls, that decreases on later whorls. Spire height low to moderate. Spire low (Fig. 20D) to moderately high (Fig. 20E). Suture impressed. Subsutural flexure shallow, weakly curved, moderately asymmetrical. Maximum diameter below rounded shoulder. Last spire whorl slightly inflated, convex not straight. Aperture curved, widening towards fasciole. Canal moderately wide, fasciole twisted, inflated.

Description of colour pattern
The colour pattern consists of one layer of a series of closely related, spiral rows of dashes (Fig. 20B), disrupted randomly by non-fluorescent dots or small dashes. The non-fluorescent dots are slightly wider than the fluorescent spiral rows. Sometimes the dots are axially aligned, creating a synchronous, vertical disruption of the spiral rows. The dots on the spiral rows are not constant in numbers or distances and can be multiple or few. This results in a variety of colour patterns, with shells having mostly spiral rows of elongated dashes with very few interruptions (Fig. 20B), to patterns with multiple disruptions, resembling series of short fluorescent dashes (Fig. 20D).

Remarks
Erünal-Erentöz (1958) described Conus (Dendroconus) gulemani distinguishing it from the rest of her known Conidae by the relative narrower shoulder width, the coeloconoid spire whorls, and the colour pattern of spiral dashes. One syntype stored in the MNHN (MNHN.FA26722; Fig. 19) is very similar in morphology (Table 9) and colour pattern to the Greek specimens (Fig. 20). Therefore, we consider them conspecific with Conus (Kalloconus) gulemani.

Caze et al. (2011a) identified a specimen (MNHN.FA30841) from Makrilia as Conus bitorus Fontannes, 1880. Conus bitorus, however, has a straight conical spire whorl outline (see Fontannes 1880, pl. 8 fig. 12 and Sacco 1893b, pl. 10, fig. 19), whereas Conus (Kalloconus) gulemani has clearly a coeloconoid spire outline. As such, we believe that the specimen of Caze et al. (2011a) belongs to Conus (Kalloconus) gulemani.

The colour pattern of this species is similar to species like Conus (Kalloconus) hungaricus Hoernes & Auinger, 1879 and Conus (Kalloconus) tietzei Hoernes & Auinger, 1879, but both species differ from Conus (Kalloconus) gulemani by their shell morphology (Fig. 21). Conus (Kalloconus) hungaricus has club shaped shells, wider relative diameter of the last whorl and conical spire whorls. Conus (Kalloconus) tietzei has a more angulated shoulder and straight last whorl, which is slightly

Table 9. — Shell measurements and ratios of Conus (Kalloconus) gulemani Erünal-Erentöz, 1958 from the Tortonian of Crete (Greece). Mean and standard deviation are computed from 19 specimens. The largest specimen is AMPG(IV) 2672.

| SL        | MD        | AH        | HMD       | AL         | SA       | LWA      | LW        | RD        | PMD       | RSH      | SSFD     | SSfd     | PV       |
|-----------|-----------|-----------|-----------|------------|----------|----------|-----------|-----------|-----------|----------|----------|----------|----------|
| Largest specimen | 39.19 mm  | 25.8 mm   | 33.97 mm  | 26.82 mm   | 35.08 mm | 123°     | 35°       | 1.52      | 0.76      | 0.79     | 0.13     |          |          |
| Mean      | 28 mm     | 17.9 mm   | 25.5 mm   | 20.3 mm    | 25.7 mm  | 129.4°   | 43°       | 1.58      | 0.7       | 0.80     | 0.09     | 2.92     | 9.27     | 0.46     |
| Standard deviation | 5.56     | 4.09      | 5.1       | 4.07       | 5.29     | 11.53    | 4.43      | 0.1       | 0.04      | 0.03     | 0.31     | 0.11     | 2.95     | 0.14     |

Fig. 19. — Syntype of Conus (Kalloconus) gulemani Erünal-Erentöz, 1958, MNHN.FA26722 (Serravallian, Zengen Köy S, Derebogazi, Karaman Basin, Turkey). Photos taken under natural light by J. Mouchart. Scale bar: 1 cm.
more inflated in *Conus (Kalloconus) gulemani*. “*Dendroconus pyruloides* var. *planacutispira* (Sacco 1893a: pl. 1, fig. 27) is morphologically similar to our material, but it differs in the angle of the last whorl near the fasciole, a feature lacking in *Conus (Kalloconus) gulemani*. A species with an identical colour pattern, but with shorter spire whorls is *Conus (Kalloconus) pseudonivifer* Monteiro, Tenorio & Poppe, 2004 (Monteiro et al. 2004), an extant species from the Cape Verde islands. Because of these similarities, both species seem to be closely related.

*Conus (Kalloconus) letkesensis*
(Harzhauser & Landau, 2016)
(Figs 22, 23; Table 10)

*Kalloconus letkesensis* Harzhauser & Landau, 2016: 63, figs 3M, 10E1-E2, 10F1-F4, 10G1-G4, 10H1-H3.

*Monteirconus tietzei* – Kovács & Vicián 2013 (partim): 79, figs 92, 94.

**Type material.** — Holotype NHMW 2016/0006/0001. Paratype NHMW 2016/0006/0002.

**Type locality.** — Letkés (Hungary) – Middle Miocene (Langhian)

**Stratigraphic range.** — Langhian of Paratethys (Pannonian Basin, Letkés, Hungary), Tortonian of Greece (Messara Basin, Crete).

**Material examined.** — Greece. Filippi: 1 specimen AMPG(IV) 2682.

**Description of colour pattern**

The colour pattern consists of multiple, closely placed spirals of long and short, very thin, fluorescent dashes. Dashes are not of constant length, with some resembling dots, whereas others resemble continuous spiral lines. Short dashes are usually between long dashes, while there are areas of the shell with multiple long dashes, there are areas that do not have any fluorescent colour (Fig. 23). The colour pattern on the
spire whorls is partially destroyed on this specimen, but most likely consists of fluorescent flammulae (Fig. 22).

REMARKS
This species has a low spire and a broad, conical last whorl, with smooth shoulder and a flat-sided last whorl (Table 10). The colour pattern consists of delicate spiral rows of dashes. These characters are typical of Conus (Kalloconus) letkesensis (Harzhauser & Landau, 2016) and therefore we attribute our specimen to this species. The Greek specimen is larger than the Paratethyan specimens (largest Paratethyan: 40.9 mm, versus Greek specimen: 52.45 mm) and it displays a slightly different subsutural flexure (moderately curved in Harzhauser & Landau 2016).

TABLE 10. — Shell measurements and ratios Conus (Kalloconus) letkesensis (Harzhauser & Landau, 2016) from Filippi, Crete (Greece), AMPG(IV) 2682.

| SL  | MD   | AH   | HMD  | AL   | LWA  | LW  | RD  | PMD  | RSH  | SSFD | SSFd | PV  |
|-----|------|------|------|------|------|-----|-----|------|------|------|------|-----|
| 52.45 mm | 35.45 mm | 49.25 mm | 42 mm | 48.9 mm | 150° | 50° | 1.48 | 0.72 | 0.85 | 0.06 | 2   | 9   | 0.29 |

Table 11. — Shell measurements and ratios of Conus (Kalloconus) asterousiaensis n. sp. from the Tortonian of Crete (Greece). 17 specimens measured; the largest specimen AMPG(IV) 2689 comes from Tefeli.

| SL  | MD   | AH   | HMD  | AL   | LWA  | LW  | RD  | PMD  | RSH  | SSFD | SSFd | PV  |
|-----|------|------|------|------|------|-----|-----|------|------|------|------|-----|
| Largest specimen | 50.05 mm | 32.2 mm | 43.15 mm | 37.5 mm | 41.85 mm | 110° | 34° | 1.55 | 0.75 | 0.87 | 0.14 | 2.73 | 4.57 | 0.23 |
| Mean | 28.2 mm | 17.2 mm | 24.3 mm | 20.9 mm | 24.4 mm | 128.1° | 37.5° | 1.69 | 0.7 | 0.86 | 0.14 | 3.11 | 7.8 | 0.67 |
| Standard deviation | 10.52 | 7.47 | 9.36 | 8.36 | 9.48 | 10.03 | 3.81 | 0.18 | 0.07 | 0.03 | 0.04 |

Conus (Kalloconus) asterousiaensis n. sp. (Figs 24, 25, 26, 27; Table 11)
Conus raristriatus – Davoli 1972: 74, pl. 8, fig. 1a, b.

**Diagnosis.** — *Conus* (*Kalloconus*) of medium-large size, robust shell with conical spire, with colour pattern of spiral rows of quadrangular dots and fluorescent bands on spire whorls.

**Type Material.** — Holotype: AMPG(IV) 2683, Filippi; 1 paratype AMPG(IV) 2688, Filippi; 1 paratype AMPG(IV) 2689, Tefeli; 1 paratype MNHN.F.A72644, Crete.

**Type Locality.** — Filippi, 35°02’07.2”N, 25°15’00.5”E, Messara Basin, Tortonian, Crete, Greece.

**Stratigraphic Range.** — Tortonian of Greece (Messara Basin, Crete), and Italy.

**Etymology.** — Name taken from the Asterousia Mountain range south of the locality, Crete, Greece.

**Other Material Examined.** — Greece. Filippi: four specimens AMPG(IV) 2684-2687; Partira: one specimen MNHN.F.A72650; Tefeli: one specimen AMPG(IV) 2690; Crete: seven specimens MNHN.F.A72642 to MNHN.F.A72643 and MNHN.F.A72645 to MNHN.F.A72649. All specimens display a colour pattern under UV light.

**Shell Description.**

Medium-sized, stout shell. Spire straight to coeloconoid, highly conical to flat. Protoconch multispiral (Fig. 25B). Early spire whorls elevated, coeloconoid, smooth, with straight to convex outline. Later spire whorls straight to concave, with smooth, conical outline. Last spire whorl convex, slightly striate. Shoulder rounded to angulated. Maximum diameter

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![Figure 22](image-url) — *Conus (Kalloconus) letkesensis* (Harzhauser & Landau, 2016) from Filippi, Crete (Greece). Specimen AMPG(IV) 2682 with small dense dashes and irregular flammulae on the spire. Specimen shown under natural light (A1-A2, A4) and UV light. Scale bar: 1 cm.

![Figure 23](image-url) — Pattern of the dashes on *Conus (Kalloconus) letkesensis* (Harzhauser & Landau, 2016). Dashed colour pattern is from AMPG(IV) 2682 (Fig. 22) from Filippi, Crete (Greece). Scale bar: 1 cm.
just below shoulder. Subsutural flexure shallow, moderately to weakly curved, strongly asymmetrical. Last whorl conical, straight. Aperture narrow, straight, widening near siphonal canal. Siphonal canal wide, short. Fasciole short, twisted. There are two extremes of a form. The first extreme form (form 1, Fig. 27A, G) consists of conical spire whorls of medium height and rounded shoulder. The second extreme form (form 2, Fig. 27I) consists of relatively flat spire whorls and angulated shoulder. Intermediate forms also exist (Fig. 27B, D, E).

**Description of Colour Pattern**

Colour pattern on spire whorls consists of two rows of regularly arranged, quadrangular to rectangular dots, near carina and near suture, respectively. Flammulae are visible on some specimens (Fig. 24B4). The colour pattern on last whorl consists of three layers. The first layer consists of two fluorescent bands, one on the middle of the last whorl and another near the anterior part of the shell (Fig. 25). The
second layer consists of multiple, continuous spiral lines, equally distant on individual shells. The lines are not always constant in width. Usually, the thin lines are surrounded by wider lines. The colour of the lines is dim-fluorescent or non-fluorescent. Inside those, there are bright, quadran-
gular, sharply edged, fluorescent dots alternated with non-
fluorescent areas (Fig. 26). The dots are usually as wide as the corresponding line, but sometimes the dots are engulfed by the dim-fluorescent material of the line (Fig. 26). The lines overlap the pattern of the bands (Fig. 25). One specimen shows a third layer of pattern that consists of axially arranged, fluorescent blotches, placed on top of the bands and lines, with dots preserved on top of all other patterns (Fig. 27C).

REMARKS
The Greek specimens present two extreme forms (Fig. 27A, G, I), that are connected with intermediate shell forms (Fig. 27B, D, E), therefore we regard them as one species. Morphological characters like the subsutural flexure, the smooth spire whorls and the conical straight last whorl characterize this species (Table 11). Despite the morpho-
logical variability, the colour pattern remains constant to all shells (Fig. 27). Accordingly, we consider that this species displays a wide variability in spire height and angulation of shoulder, but bears a stable colour pattern variation. The Greek specimens are attributed to the subgenus Kalloco-
nus, because of the lack of the spiral sculpture, a concave conical spire outline, a wide last whorl and broad shoulder.

A syntype of Conus raristriatus Bellardi & Michelotti, 1841, from the Tortonian of Sant’Agata Fossili (BS.038.05.133), was illustrated by Bellardi & Michelotti (1841: pl. 5, figs 8-9) and later figured by Ferrero Mortara et al. (1984). The illustration shows a colour pattern of evenly distanced spiral lines, but no spiral rows of dots as on Conus (Kalloconus) asterousiaensis n. sp. As such, the
syntype suggests that *Conus raristriatus* and *Conus (Kalloconus) asterousiaensis* n. sp. belong to two different species. However, a Tortonian specimen figured by Davoli (1972: pl. 8, fig. 1a, b, specimen no. 5545 housed in the Museo Paleontologico dell’Universita di Modena) and named *Conus raristriatus* displays a shell shape very similar to the morphotypes of *Conus (Kalloconus) asterousiaensis* n. sp. (see Fig. 27B, F, H). In addition, under natural light the Italian specimen figured by Davoli seems to be displaying similarities of colour pattern (discontinuous spiral lines) with the Greek specimens. For this reason, we consider it conspecific with the Greek material.

*Conus (Kalloconus) asterousiaensis* n. sp. could also be compared to *Conus (Lautoconus) subraristriatus* Pereira da Costa, 1866. They differ morphologically, mainly in the cyrtoconoid, more elongate and higher spire. In terms of colour pattern variations, both species possess the spirally arranged rows of dots and dashes, with fluorescent bands. The difference is that *Conus (Lautoconus) subraristriatus* does not exhibit any pigmentation between the fluorescent bands (Landau et al. 2013; Harzhauser & Landau 2016), whereas *Conus (Kalloconus) asterousiaensis* n. sp. possesses colour patterns along the whole length of the last whorl.

The colour pattern of *Conus (Kalloconus) asterousiaensis* n. sp. is similar to that of the extant species *Conus genuanus* Linnaeus, 1758. This West African species could be related to *C. (K.) asterousiaensis* n. sp. and suggests a Proto-Mediterranean origin of some West African conids.
CONCLUSION

The study using UV light of the conid genera Conilithes and Conus (Kalloconus) from the late Miocene of Crete (Greece) reveals a high species diversity from the tropical environment of the Proto-Mediterranean. The collection of the NKUA actually contains a much more diverse variety of fossil Conidae than the one described by past research collectors, because they could not differentiate species in natural light. In this work, we recognize eleven species, among which one is left in open nomenclature (Conilithes sp.), three are new (Conilithes herodus n. sp., Conus (Kalloconus) belladuce n. sp. and Conus (Kalloconus) asteriouseni) and six are recorded for the first time in the late Miocene of Crete (Table 12). We compare this assemblage with those of the Miocene and Pliocene neighbouring regions (Italy, Turkey and Paratethys; Table 12). First, only two species (Conilithes herodus n. sp., Conus (Kalloconus) belladuce n. sp.) are endemic from the late Miocene of Crete. Secondly, we found strong relationships with the Langhian of Paratethys (six shared species), whereas three species are shared with the Serravallian of Turkey (Karaman Basin) and four only with the Tortonian of Italy. This result could be interpreted as a fauna, present and widely distributed since the Langhian-Serravallian in both the Paratethys and the eastern Proto-Mediterranean (Landau et al. 2013). This fauna disappeared from the Paratethys during the Serravallian (= Sarmatian), because of strong environmental changes due to the disconnection from the Proto-Mediterranean (Landau et al. 2013), but probably persisted in the eastern Proto-Mediterranean, as suggested by the faunas of the Serravallian of Turkey and the Tortonian of Crete (this work). However, the weak relation of the Cretan fauna with the late Neogene of Italy could be biased, because, for the comparisons with Italian faunas, we use works that figured Conidae in natural light, as no recent works used UV light to study conids. Consequently, this disparity of information between the Paratethys and Italy could be another reason why we found more affinities with the Langhian of Paratethys than with the Tortonian of Italy.

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