geodiversitas

2021 • 43 • 24

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

Christos PSARRAS,
Efterpi KOSKERIDOU &
Didier MERLE

art. 43 (24) — Published on 2 December 2021
www.geodiversitas.com

PUBLICATIONS SCIENTIFIQUES

MUSÉUM NAL HIST NATURELLE

Geodiversitas est indexé dans / Geodiversitas *is indexed in:*
– Science Citation Index Expanded (SciSearch®)
– ISI Alerting Services®
– Current Contents® / Physical, Chemical, and Earth Sciences®
– Scopus®

Geodiversitas est distribué en version électronique par / Geodiversitas *is distributed electronically by:*
– BioOne® (http://www.bioone.org)

Les articles ainsi que les nouveautés nomenclaturales publiés dans *Geodiversitas* sont référencés par / *Articles and nomenclatural novelties published in* Geodiversitas *are referenced by:*
– ZooBank® (http://zoobank.org)

Geodiversitas est une revue en flux continu publiée par les Publications scientifiques du Muséum, Paris
Geodiversitas *is a fast track journal published by the Museum Science Press, Paris*

Les Publications scientifiques du Muséum publient aussi / *The Museum Science Press also publish:* ***Adansonia***, ***Zoosystema***, ***Anthropozoologica***, ***European Journal of Taxonomy***, ***Naturae***, ***Cryptogamie*** **sous-sections** ***Algologie***, ***Bryologie***, ***Mycologie, Comptes Rendus Palevol***

Diffusion – Publications scientifiques Muséum national d'Histoire naturelle
CP 41 – 57 rue Cuvier F-75231 Paris cedex 05 (France)
Tél. : 33 (0)1 40 79 48 05 / Fax : 33 (0)1 40 79 38 40
diff.pub@mnhn.fr / http://sciencepress.mnhn.fr

ISSN (imprimé / *print*) : 1280-9659/ ISSN (électronique / *electronic*) : 1638-9395

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

Christos PSARRAS
Efterpi KOSKERIDOU
National and Kapodistrian University of Athens, Faculty of Geology and Geoenvironment,
Department of Hist. Geology-Paleontology, Athens (Greece)
cpsarras@geol.uoa.gr
ekosker@geol.uoa.gr

Didier MERLE
CR2P (CNRS, MNHN, UPMC, Sorbonne Université),
Département Origines et Évolution, Muséum national d'Histoire naturelle,
case postale 38, 57 rue Cuvier, F-75231 Paris cedex 05 (France)
didier.merle@mnhn.fr

Submitted on 20 October 2019 | accepted on 24 April 2020 | published on 2 December 2021

urn:lsid:zoobank.org:pub:D36D1E14-73BE-4176-8024-F3673A65B8C1

Psarras C., Koskeridou E. & Merle D. 2021. — Late Miocene Conidae (Mollusca: Gastropoda) of Crete (Greece). Part 1: genera *Conilithes* Swainson, 1840 and *Conus* (*Kalloconus*) da Motta, 1991. *Geodiversitas* 43 (24): 1309-1339. https://doi.org/10.5252/geodiversitas2021v43a24. http://geodiversitas.com/43/24

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*) *asterousiaensis* 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* Erünal-Erentöz, 1958 and *Conus* (*Kalloconus*) *letkesensis* (Harzhauser & Landau 2016). *Conilithes antidiluvianus* (Bruguière, 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.

KEY WORDS
Conidae,
late Miocene,
Greece,
Crete Island,
ultraviolet light,
new species.

RÉSUMÉ
Les Conidae du Miocène supérieur de Crète (*Grèce*). *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*) *helladicus* 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* Erünal-Erentöz, 1958 et *Conus* (*Kalloconus*) *letkesensis* (Harzhauser & Landau 2016). *Conilithes antidiluvianus* (Bruguière, 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*) *helladicus* n. sp.). Deuxièmement, il révèle aussi d'étroites affinités avec l'assemblage de Conidés du Langhian de Paratethys (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 au Serravallien, 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; Zachariasse *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) Tylissos locality (Fig. 1[1]) is in the foothills of Psiloritis mountains and according to Delrieu (1990), Tylissos sand facies are covered by marls containing *Globorotalia miocenica mediterranea* Catalano & Sprovieri 1969.

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

3) Panassos 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.

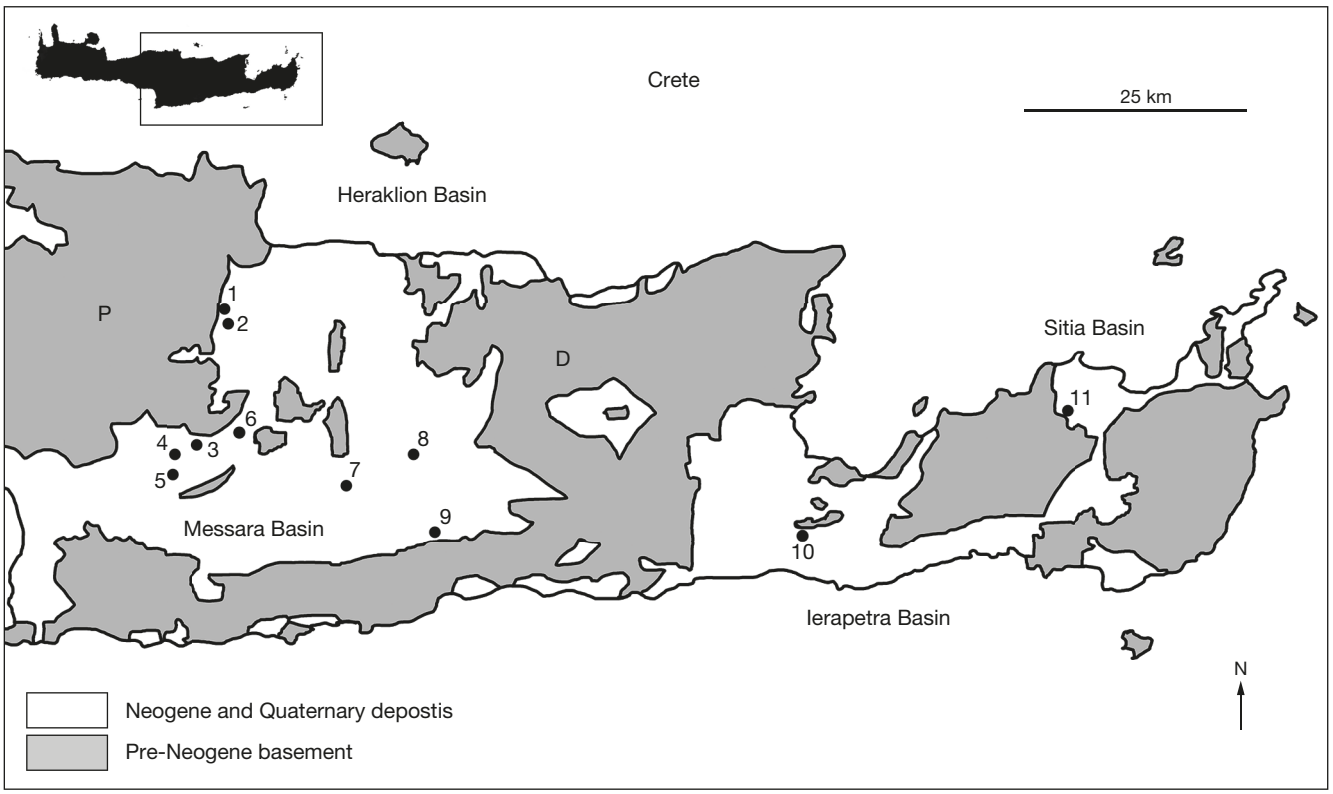

FIG. 1. — General sketch map of central and eastern Crete, showing the localities from where the material was collected. Grey coloured areas show the Upper Nappes and Lower Nappes combined as the pre-Neogene basement, while the Neogene and Quaternary are shown in white colour. Abbreviations: **P**, Psiloritis Mountains; **A**, Asterousia Mountains; **D**, Dikti Mountains. Localities shown in numbers: **1**, Tylissos; **2**, Keramoutsi; **3**, Panassos; **4**, Apomarma; **5**, Psalidha; **6**, Adhraktia; **7**, Tefeli; **8**, Partira; **9**, Filippi; **10**, Makrilia; **11**, Achladhia.

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 (Delrieu 1990).

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 spécifique 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

TABLE 1. — Shell measurements and ratios *Conilithes brezinae* (Hoernes & Auinger, 1879) from the Tortonian of Crete (Greece). Mean and standard deviation are computed from 39 specimens. The largest specimen comes from Adhraktia (MNHN.F.A72567).

	SL	MD	AH	HMD	AL	SA	LWA	LW	RD	PMD	RSH	SSFD	SSFd	PV
Largest specimen	27.8 mm	10.5 mm	18.2 mm	16.3 mm	18.2 mm	50.5°	32.6°	2.65	0.58	0.9	0.35	–	–	–
Mean	20.5 mm	8.2 mm	14 mm	12.5 mm	13.9 mm	53°	31.2°	2.51	0.59	0.89	0.32	2.32	3.86	0.69
Standard deviation	4.14	1.56	2.85	2.59	2.81	5.34	2.83	0.16	0.04	0.03	0.03	0.78	1.34	0.19

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 (Seraphsidae); Caze *et al.* 2011a, b (Lutetian gastropods and Ampullinidae, 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-70D 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 chresonymic 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 Paratethys by Harzhauser & Landau (2016). In this paper we will not repeat chresonymies and species descriptions given by those authors unless modified or challenged by our findings.

ABBREVIATIONS

Repository

NKUA	National and Kapodistrian University of Athens, Greece;
AMPG (IV)	Catalogue numbering of the Paleontology and Geology Museum of the National and Kapodistrian University of Athens, Greece;
MSNM	Museo di Storia Naturale di Milano, Italy;
MNHN.F	Muséum national d'Histoire naturelle, Paris, collection de paléontologie, France;
NHMW	Naturhistorisches Museum Wien, Austria;
MTA	Maden Tetkik ve Arama (The Mineral Research and Exploration General Directorate History of Nature Museum), Ankara, Turkey.
MPUM	Museo Paleontologico dell 'Universita di Modena, Italy.

Measurements

SL	shell length;
MD	maximum diameter;
AH	apertural height;
HMD	height of maximum diameter;
AL	apertural length;
SA	Spire angle;
LWA	length width ratio;
LW	length-width ratio;
RD	relative diameter (MD/AH);
PMD	position of maximum diameter (HMD/AH);
RSH	relative height of the spire {(SL-AH)/SL};
SSFD	subsutural flexure depth;
SSFd	subsutural flexure relative depth;
PV	position of the vertex (see also Harzhauser & Landau [2016]).

SYSTEMATIC PALAEONTOLOGY

Class GASTROPODA Cuvier, 1795
Subclass CAENOGASTROPODA Cox, 1960
Order NEOGASTROPODA Wenz, 1938
Superfamily CONOIDEA Fleming, 1822
Family CONIDAE Fleming, 1822

Genus *Conilithes* Swainson, 1840

TYPE SPECIES (by monotypy). — *Conus antidiluvianus* Bruguière, 1792. 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, this work) to Pliocene of Italy (Hall 1966; Janssen *et al.* 2014a, b) and other localities in France (Biot), Sicily, Turkey (Hatay Basin), and Syria (Erünal-Erentöz 1958; Janssen *et al.* 2014a).

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.

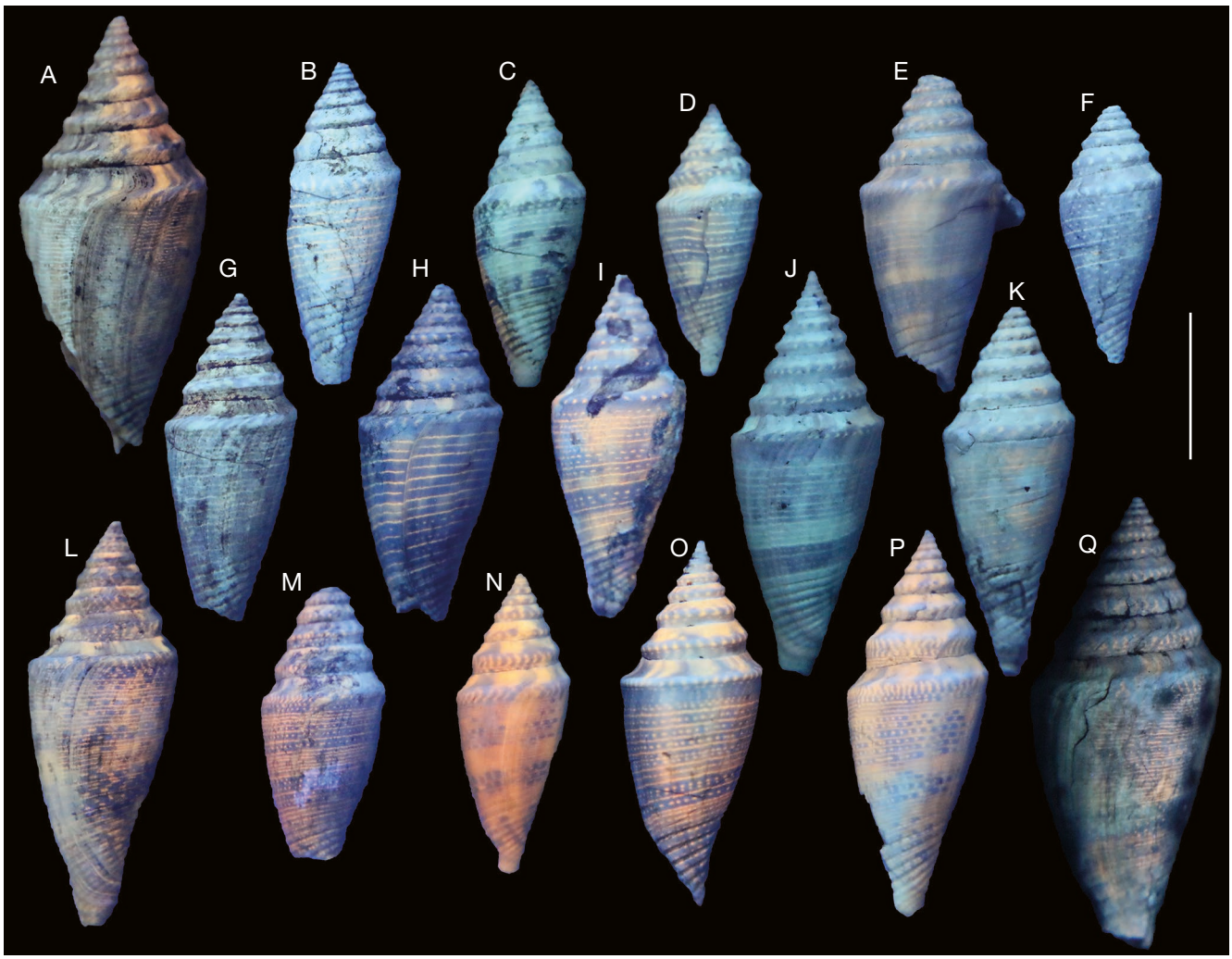

Fig. 2. — *Conilithes brezinae* (Hoernes & Auinger, 1879) specimens from the Tortonian of Crete (Greece), showing colour pattern variation under UV light in abapertural views: **A**, AMPG(IV) 2638, Panassos; **B**, AMPG(IV) 2610, Partira; **C**, MNHN.F.A72573, Crete; **D**, MNHN.F.A72579, Crete; **E**, MNHN.F.A72583, Crete; **F**, MNHN.F.A72570, Partira; **G**, AMPG(IV) 2637, Tefeli; **H**, AMPG(IV) 2629, Filippi; **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.

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, $5D_1$-D_3,$5E_1$-E_3, $5F_1$-F_3,$5G_1$-G_3, 5H.

Type material. — Syntype NHMW 1999z0077/0023a, illustrated in Hörnes (1851: pl. 5, fig. 8a), syntype NHMW 1999z0077/0023b, illustrated in Hörnes (1851: pl. 5, fig. 8b), syntype NHMW 1999z0077/0023c, illustrated in Hörnes (1851: pl. 5, fig. 8c), syntype NHMW 1999z0077/0023d, illustrated in Hörnes (1851: pl. 5, fig. 8d), syntype NHMW 1999z0077/0023e, 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

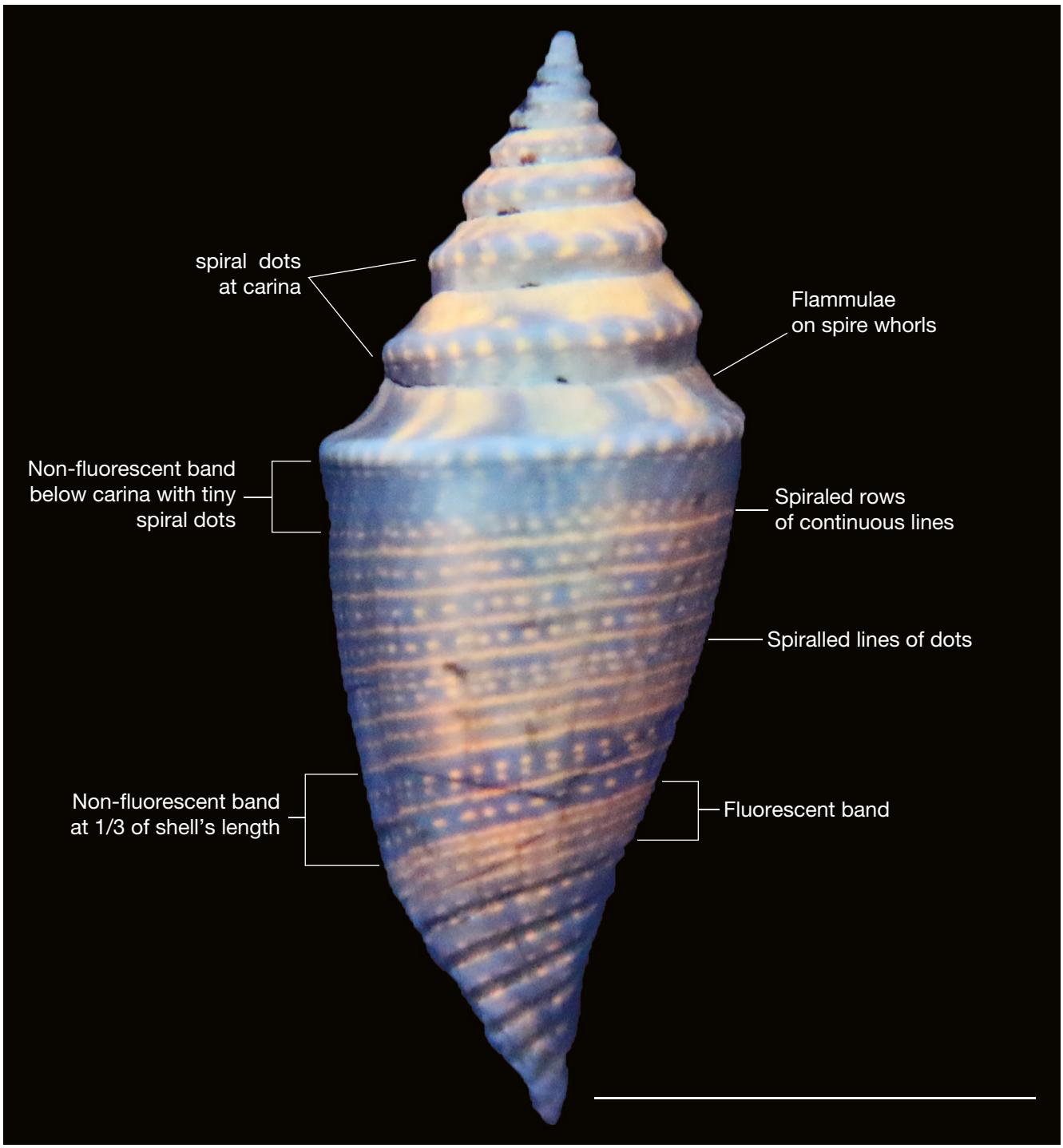

FIG. 3. — Elements constituting the colour patterns of *Conilithes brezinae* (Hoernes & Auinger, 1879), MNHN.F.A72565, Tortonian of Crete (Greece). Scale bar: 1 cm.

(commonly found in all of the shallow marine Tortonian Formations of Crete).

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,

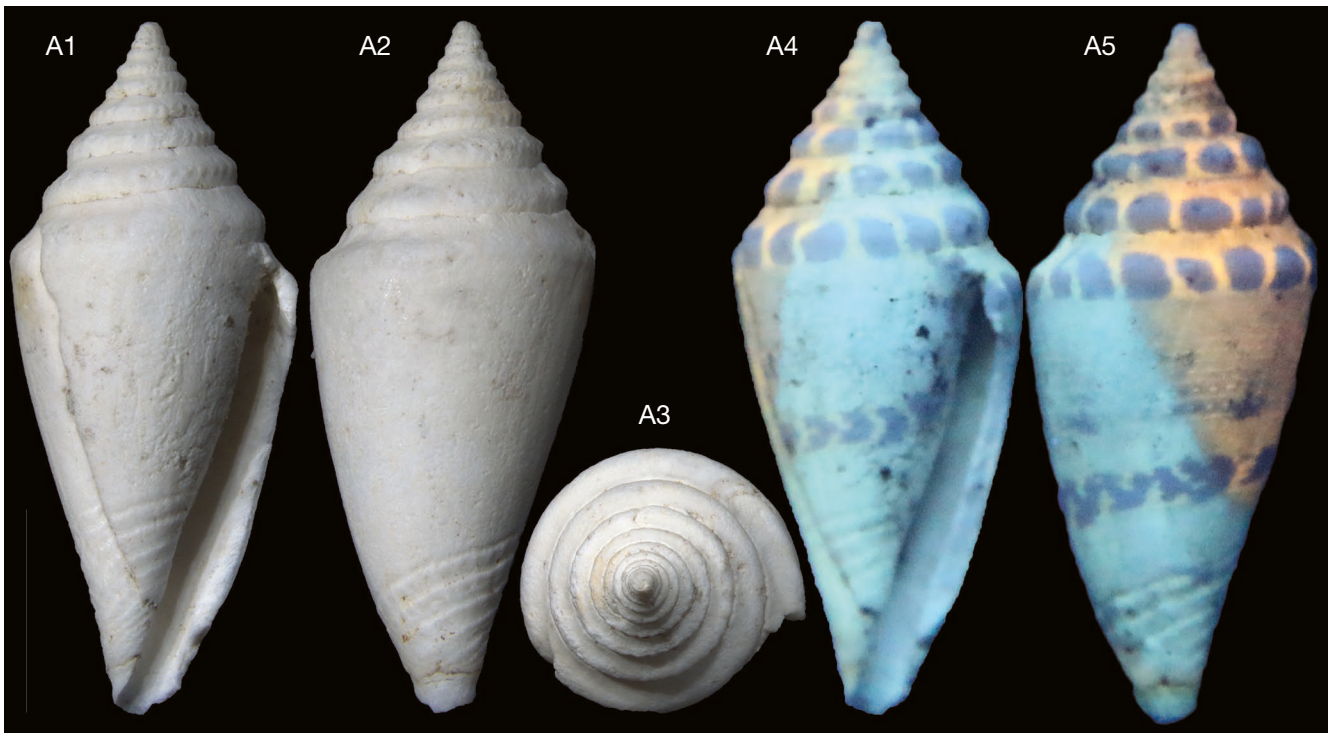

Fig. 4. — *Conilithes herodus* n. sp. paratype (MNHN.F.A72587) from the Tortonian of Crete (Greece), under natural light in apertural view (**A1**), abapertural view (**A2**), apical view (**A3**) and under UV light in apertural (**A4**) and abapertural view (**A5**). Scale bar: 0.5 cm.

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)

urn:lsid:zoobank.org:act:3817887E-22AC-45DB-8BF4-1C1083234F7A

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.F.A72585, MNHN.F.A72586; MNHN.F.A72587, MNHN.F.A72588, MNHN.F.A72589, MNHN.F.A72590, MNHN.F.A72591; Makrilia: MNHN.F.A72592; Tefeli: AMPG(IV) 2609.

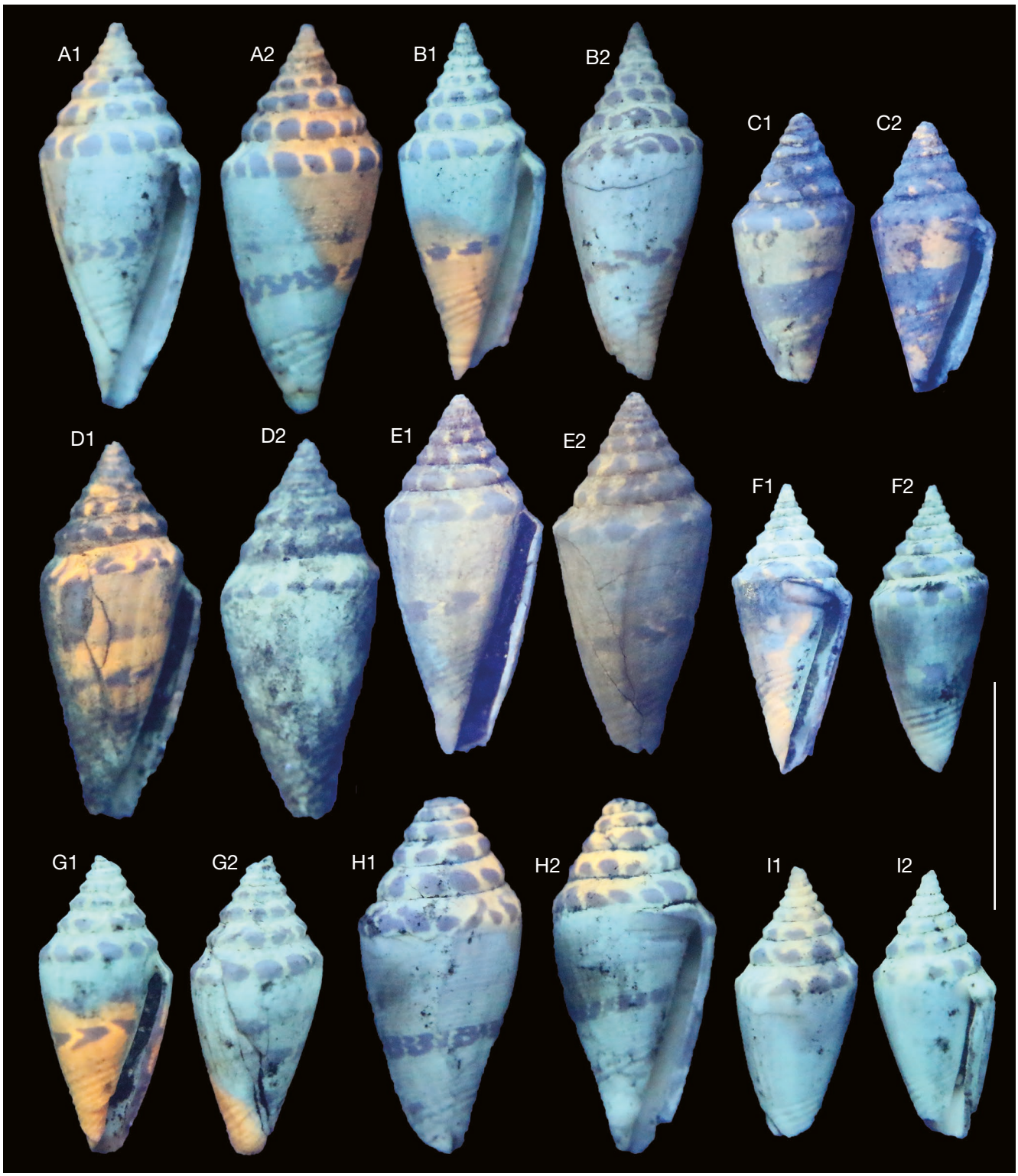

FIG. 5. — Variation of the colour pattern of *Conilithes herodus* n. sp. from the Tortonian of Crete (Greece): **A**, Paratype MNHN.F.A72587, Crete; **B**, Paratype MNHN.F.A72585, Crete; **C**, Paratype MNHN.F.A72592, Makrilia; **D**, Paratype MNHN.F.A72588, Crete; **E**, Holotype AMPG(IV) 2608, Tefeli; **F**, Paratype MNHN.F.A72586, Crete; **G**, Paratype MNHN.F.A72590, Crete; **H**, Paratype MNHN.F.A72589, Crete; **I**, Paratype MNHN.F.A72591, Crete. Scale bar: 1 cm.

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
Largest specimen	16.86 mm	7.21 mm	11.96 mm	10.26 mm	11.64 mm	58.8°	35.4°	2.34	0.61	0.86	0.29	2.5	2.33	0.54
Mean	14.4 mm	6.3 mm	10 mm	8.6 mm	9.9 mm	57.6°	33.5°	2.28	0.64	0.86	0.31	1.75	3.38	0.29
Standard deviation	2.08	0.84	1.56	1.47	1.62	3.54	2.65	0.12	0.03	0.04	0.03	–	–	–

TABLE 3. — Shell measurements and ratios for the specimen (MNHN.F.A72593) of *Conilithes* sp. from the Tortonian of Makrilia (Crete, Greece).

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).

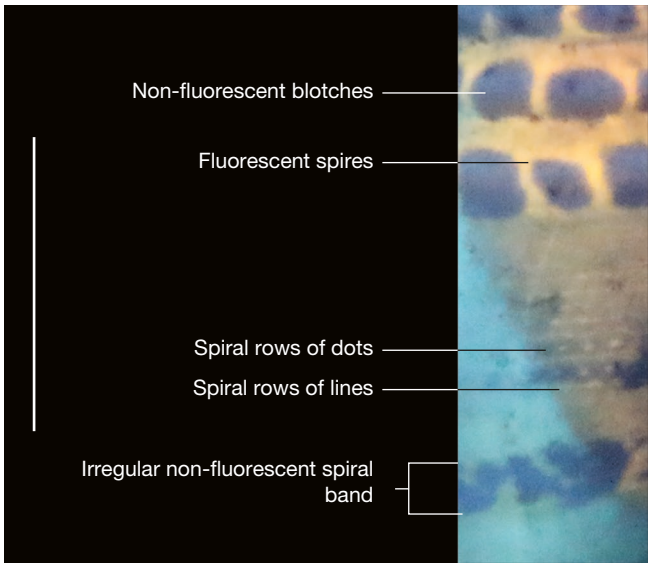

FIG. 6. — Elements constituting the colour pattern of *Conilithes herodus* n. sp., paratype (MNHN.F.A72587), Tortonian, Crete (see also Figs 4, 5A). Scale bar: 0.5 cm.

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.

Conilithes sp.
(Figs 7, 8; Table 3)

MATERIAL EXAMINED. — **Greece.** One specimen, MNHN.F.A72593 Makrilia 35°03'42.4"N, 25°43'19.0"E, Ierapetra graben, Makrilia Fm, Tortonian.

STRATIGRAPHIC RANGE. — Tortonian of Greece (Ierapetra Basin, Crete).

SHELL DESCRIPTION

Small-sized, conical shell. Protoconch multispiral (Fig. 7A7). Early spire whorls high, conical, beaded on carina, straight, with a coeloconoid outline (coeloconoid: approaching conical shape but with concave sides). Late spire whorls scalate, straight to convex, with a slightly coeloconoid outline. Carina beaded on the 5-6 early teleoconch whorls only (Fig. 7A).

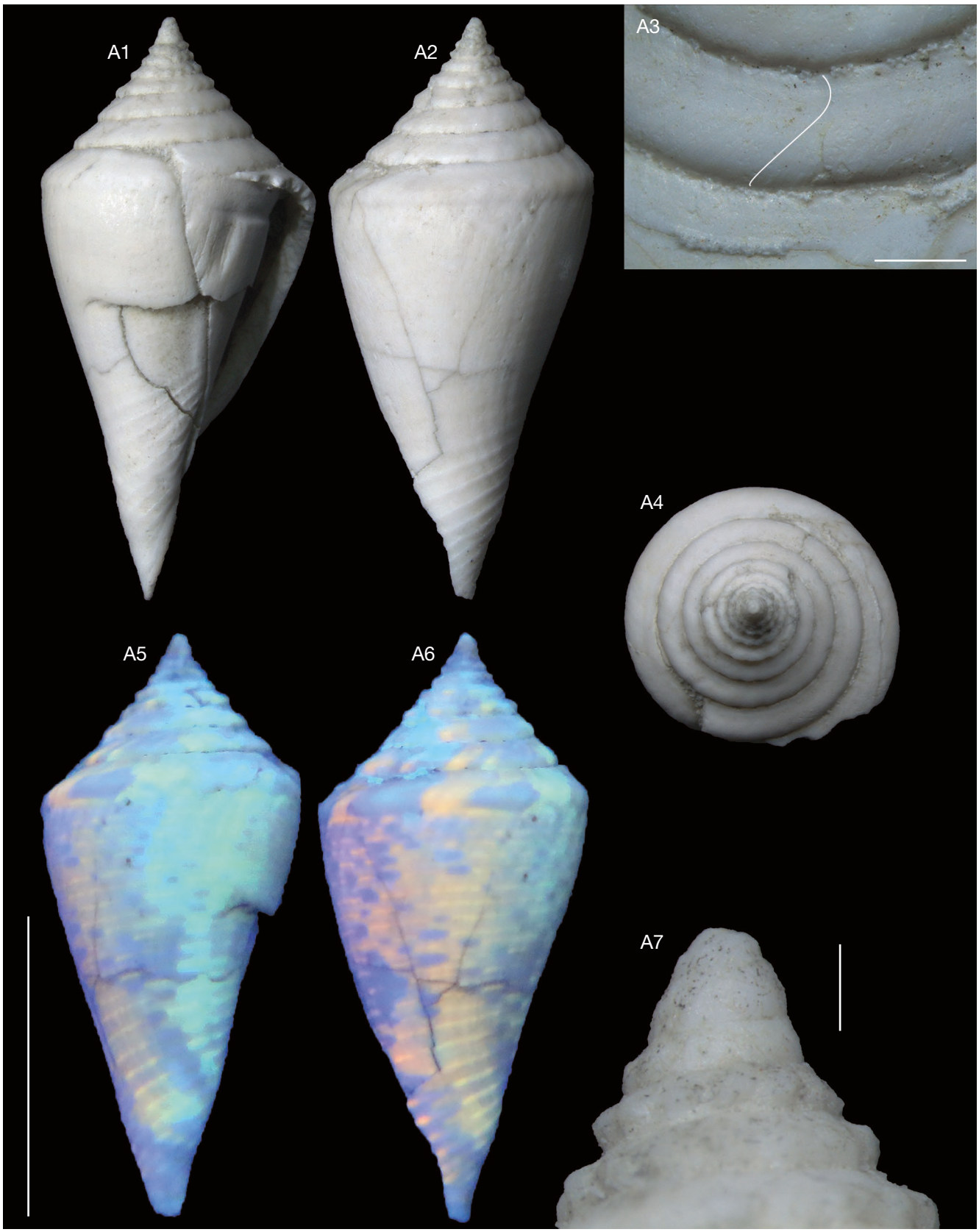

FIG. 7. — *Conilithes* sp. from the Tortonian of Crete (Greece), MNHN.F.A72593, Makrilia in apertural (**A1**, **A5**), abapertural (**A2**, **A6**) and apical (**A4**) views, under natural (**A1**-**A4**, **A7**) and UV light; **A3**, detail of the subsutural flexure (**white line**); **A7**, detail of the protoconch. Scale bars: A1-A2, A4-A6, 1 cm; A3, A7, 0.05 cm.

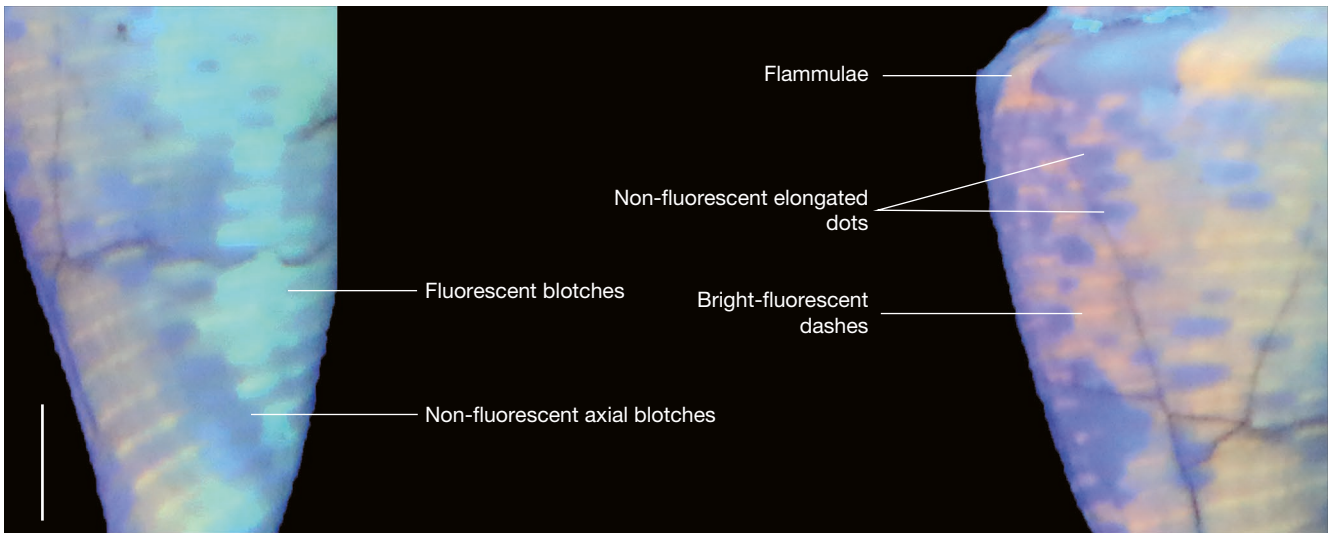

Fig. 8. — Elements constituting the colour pattern of *Conilithes* sp. (MNHN.F.A72593, Makrilia, Crete, Greece). Scale bar: 0.2 cm.

Table 4. — Shell measurements and ratios *Conilithes striatulus* (Brocchi, 1814) from the Tortonian of Crete (Greece). Mean and standard deviation are computed from 11 complete specimens. The largest comes from Panassos (AMPG(IV) 2640).

	SL	MD	AH	HMD	AL	SA	LWA	LW	RD	PMD	RSH	SSFD	SSFd	PV
Largest specimen	15.84 mm	8.17 mm	11.64 mm	10.22 mm	11.72 mm	74.20°	42.6°	1.94	0.7	0.88	0.27	2.33	4.4	0.47
Mean	13.8 mm	7.1 mm	10.4 mm	8.9 mm	10.5 mm	76.6°	33°	1.95	0.69	0.85	0.25	1.86	4.1	0.47
Standard deviation	2.28	0.82	1.74	1.66	1.9	6.38	3.33	0.14	0.05	0.04	0.03	0.42	0.85	0.1

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 sceptophorus* (Boettger, 1887) in the longer last whorl. It differs from *Conilithes antidiluvianus* (Bruguière, 1792) in the less pronounced shoulder and less elevated spire whorls. 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. 8I-J.

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 (MSNM i4672, 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 whorls of relatively medium height and robust outline. Spire whorls straight to coeloconoid, conical, with scalariform, slightly elevated spire whorls and angulated shoulders. Usual, faint spiral cords on early spire whorls, but no tubercles or beads. Subsutural flexure moderately deep, strongly curved, moderately asymmetrical. Maximum diameter on shoulder. Last whorl straight, conical.

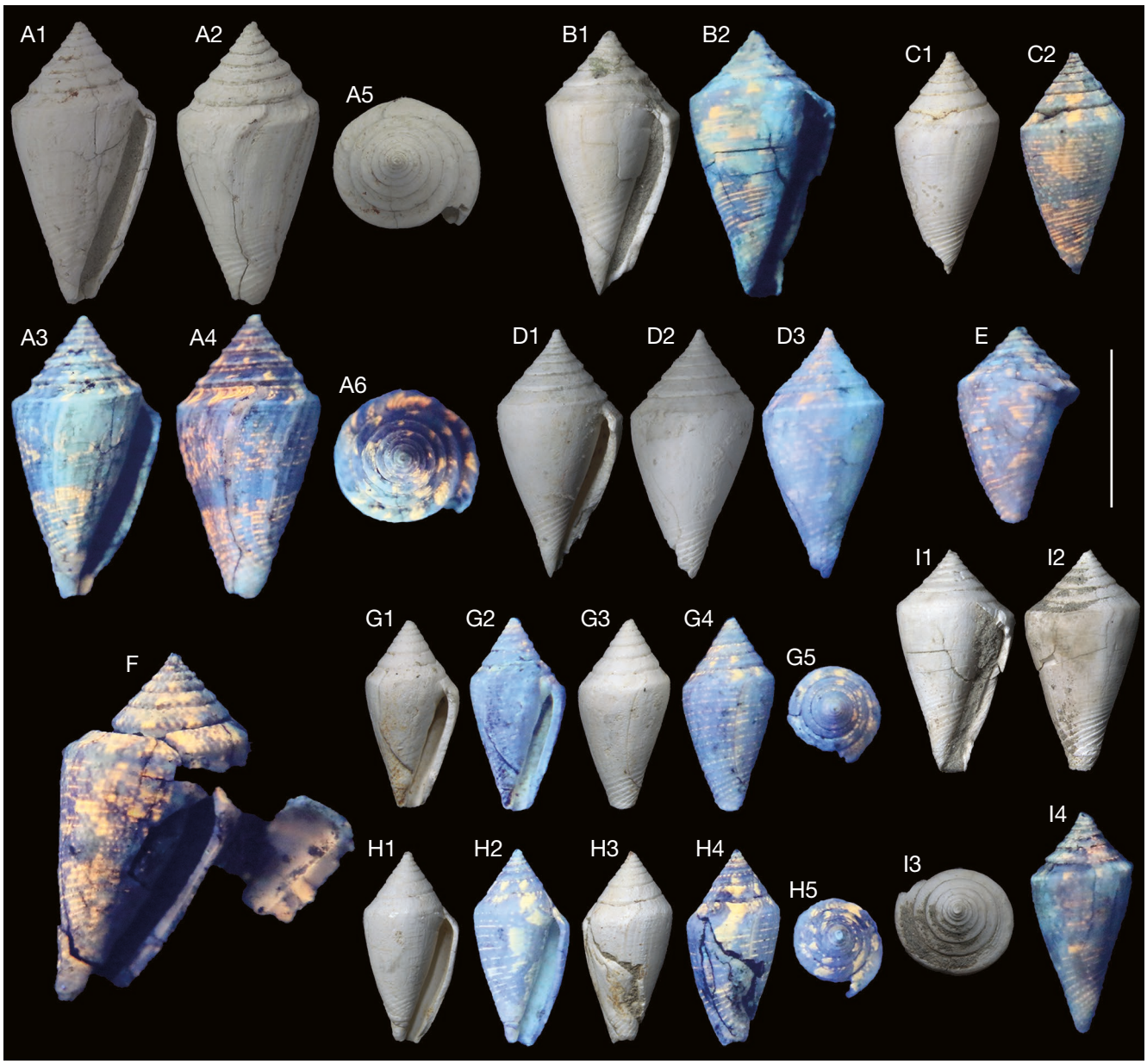

Fig. 9. — *Conilithes striatulus* (Brocchi, 1814) from Tortonian of Crete (Greece). Specimens shown in apertural, abapertural, and apical views under natural and UV light: **A**, AMPG(IV) 2640, Panassos; **B**, AMPG(IV) 2641, Panassos; **C**, MNHN.F.A72597, Crete; **D**, MNHN.F.A72601, Psalidha; **E**, AMPG(IV) 2643, Panassos; **F**, AMPG(IV) 2639, Panassos; **G**, MNHN.F.A72600, Crete; **H**, specimen MNHN.F.A72599, Crete; **I**, AMPG(IV) 2642, Panassos. Scale bar: 1 cm.

Aperture straight. Fasciole 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. The spiral rows of dots or dashes start at carina and continue along the length of 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 the shorter spire whorls and its more robust shell.

TABLE 5. — Shell measurements of *Conilithes antidiluvianus* (Bruguière, 1792), AMPG(IV) 2691, from the Tortonian of Makrilia (Crete, Greece).

	MD	SA	LWA
AMPG(IV) 2691 (broken specimen)	15.41 mm	68°	27.5°

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

Conus antidiluvianus Bruguière, 1792: 637.

Conospirus antediluvianus – Sacco 1893a; b: 39, pl. 4, fig. 35.

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

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

Conilithes antidiluvianus – Caze 2010: fig. 37B. — Harzhauser & Landau 2016: 46, figs 3C, $5J_1$-J_3, $5K_1$, $6A_1$-A_3.

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 (Erünal-Erentöz 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 Saccos' figure (Sacco 1893b: pl. 4, fig. 35) and the figured specimen by Caze (2010: fig. 23B).

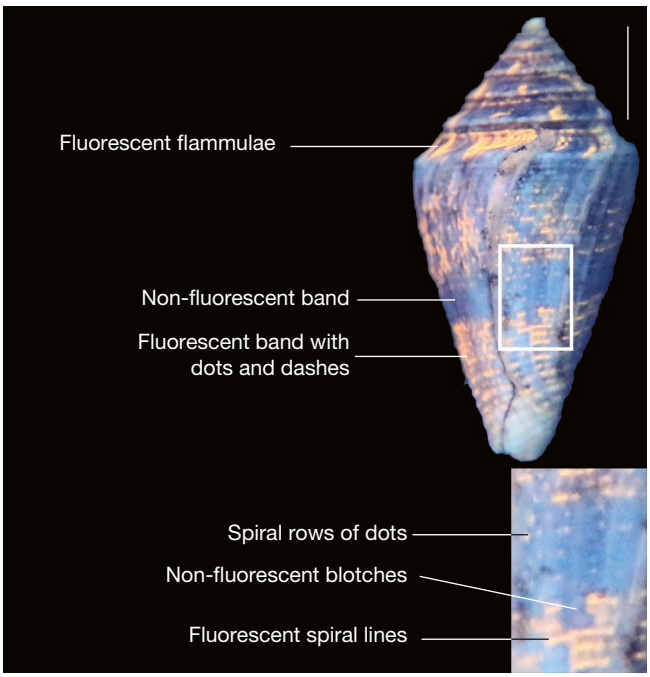

FIG. 10. — Elements constituting the colour pattern *of Conilithes striatulus* (Brocchi, 1814), AMPG(IV) 2640, Panassos, Crete, Greece. Same specimen as in the Fig. 9A. Scale bar: 0.2 cm.

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* (Bruguière, 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* n. sp., 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

Trovaoconus Tucker & Tenorio, 2009: 126. — *Conus venulatus* Hwass in Bruguière, 1792 (Recent: West-Africa) by original designation.

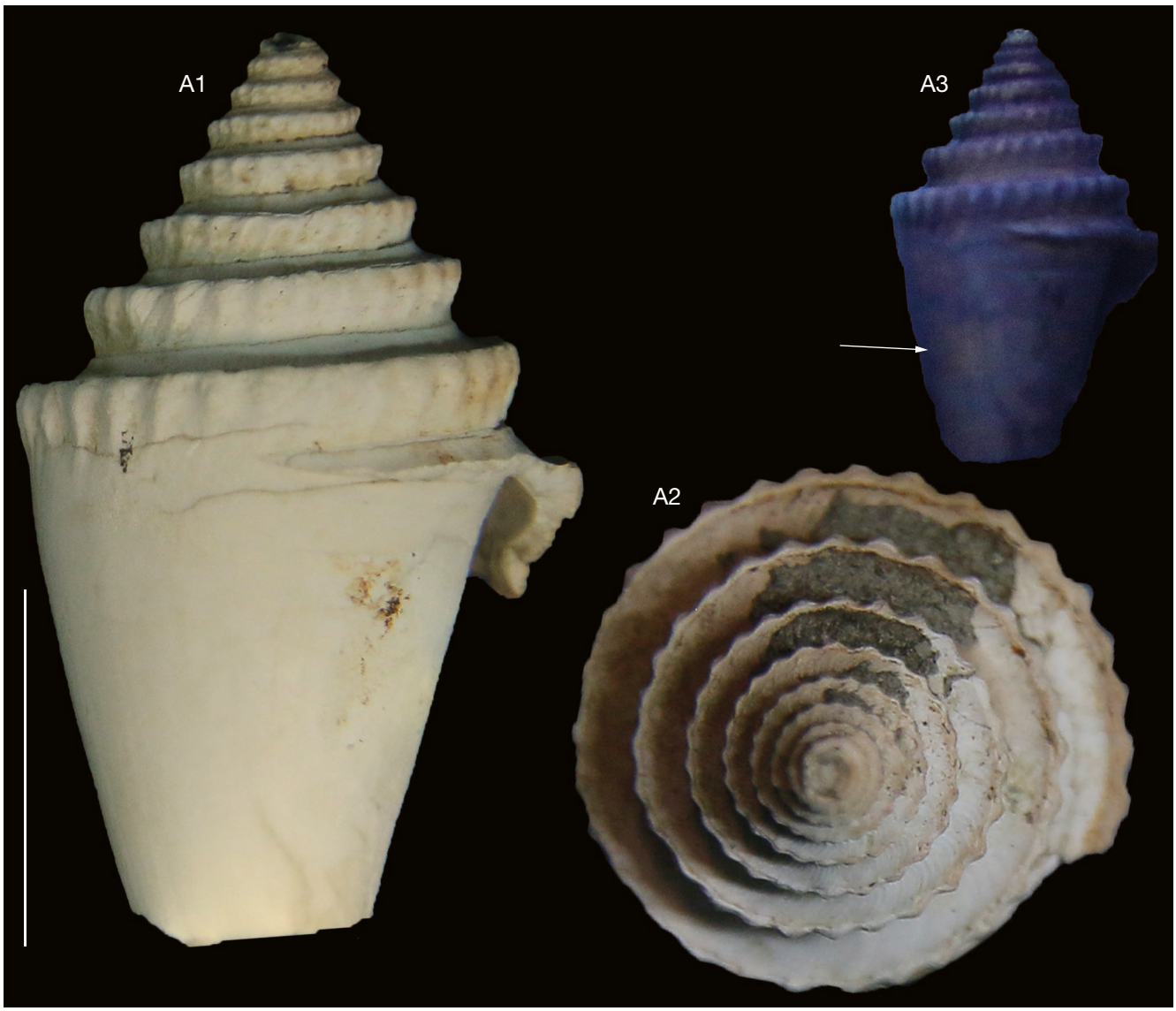

Fig. 11. — *Conilithes antidiluvianus* (Bruguière, 1792) from the Tortonian of Makrilia, Crete, Greece (AMPG(IV) 2691): a broken specimen, very faint pattern under UV light. The white arrow indicates the colour pattern. Scale bar: 1 cm.

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

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

Kalloconus neumayri – Harzhauser & Landau 2016: 64-65, tables 1, 2, figs 3O, 11C_1-C_3, 11D_1-D_2, 11E_1-E_2, 11F_1-F_2

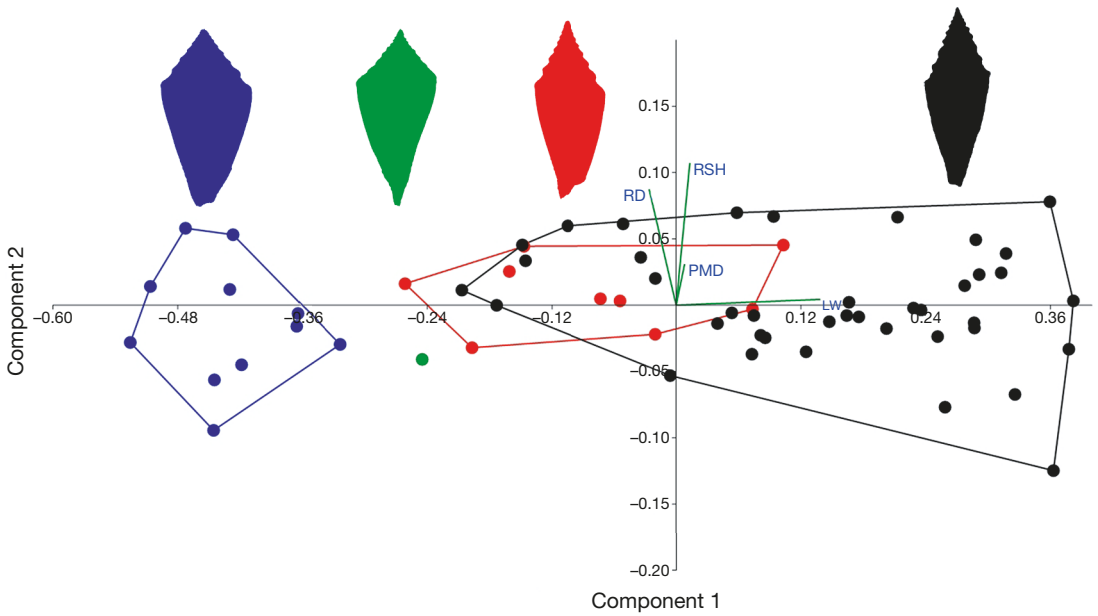

FIG. 12. — PCA graph with four species of *Conilithes* found in late Miocene localities of Crete, Greece. Dots, specimens and area colors: ●, *Conilithes herodus* n. sp.; ●, *Conilithes brezinae* (Hoernes & Auinger, 1879); ●, *Conilithes* sp.; ●, represent *Conilithes striatulus* (Brocchi, 1814). Abbreviations: **LW**, length width ratio; **RD**, relative diameter; **PMD**, position of maximum diameter; **RSH**, relative height of spire.

TABLE 6. — Shell measurements and ratios *Conus* (*Kalloconus*) *neumayri* Hoernes & Auinger, 1879 from the Tortonian of Crete (Greece). Mean and standard deviation are computed from 10 specimens. The largest specimen (MNHN.F.A72602) comes from Makrilia.

	SL	MD	AH	HMD	AL	SA	LWA	LW	RD	PMD	RSH	SSFD	SSFd	PV
Largest specimen	35.65 mm	24.27 mm	31.92 mm	26.5 mm	32.09 mm	129°	46°	1.47	0.76	0.83	0.11	–	–	–
Mean	26.8 mm	17.7 mm	24.4 mm	20.0 mm	24.2 mm	129°	41.3°	1.52	0.73	0.9	0.09	2.33	12.96	0.4
Standard deviation	5.16	3.53	4.5	3.89	4.52	5.51	3.38	0.08	0.04	0.09	0.01	1.31	9.83	0.22

TYPE MATERIAL. — One syntype NHMW 1999Z0077/0027 (figured specimen of Hoernes & Auinger 1879: pl. 1, fig. 17) and three other syntypes NHMW 1854/0035/0056 (including the figured specimen of Hoernes & Auinger (1879: pl. 1, fig 18).

TYPE LOCALITY. — Lăpugiu de Sus (Romania), middle Miocene (Langhian).

STRATIGRAPHIC RANGE. — Langhian of Paratethys (Vienna Basin, Transylvanian Basin [Harzhauser & Landau 2016]), Serravallian of Turkey (Karaman Basin [Landau *et al.* 2013]), Tortonian of Greece (Ierapetra and Messara Basins, Crete).

MATERIAL EXAMINED. — **Greece.** Filippi: Six specimens AMPG(IV) 2644-2649; Makrilia: two specimens MNHN.F.A72602, MNHN.F.A72603; Crete: two specimens MNHN.F.A72604, MNHN.F.A72605. All of them display colour patterns under UV light.

DESCRIPTION OF COLOUR PATTERN

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

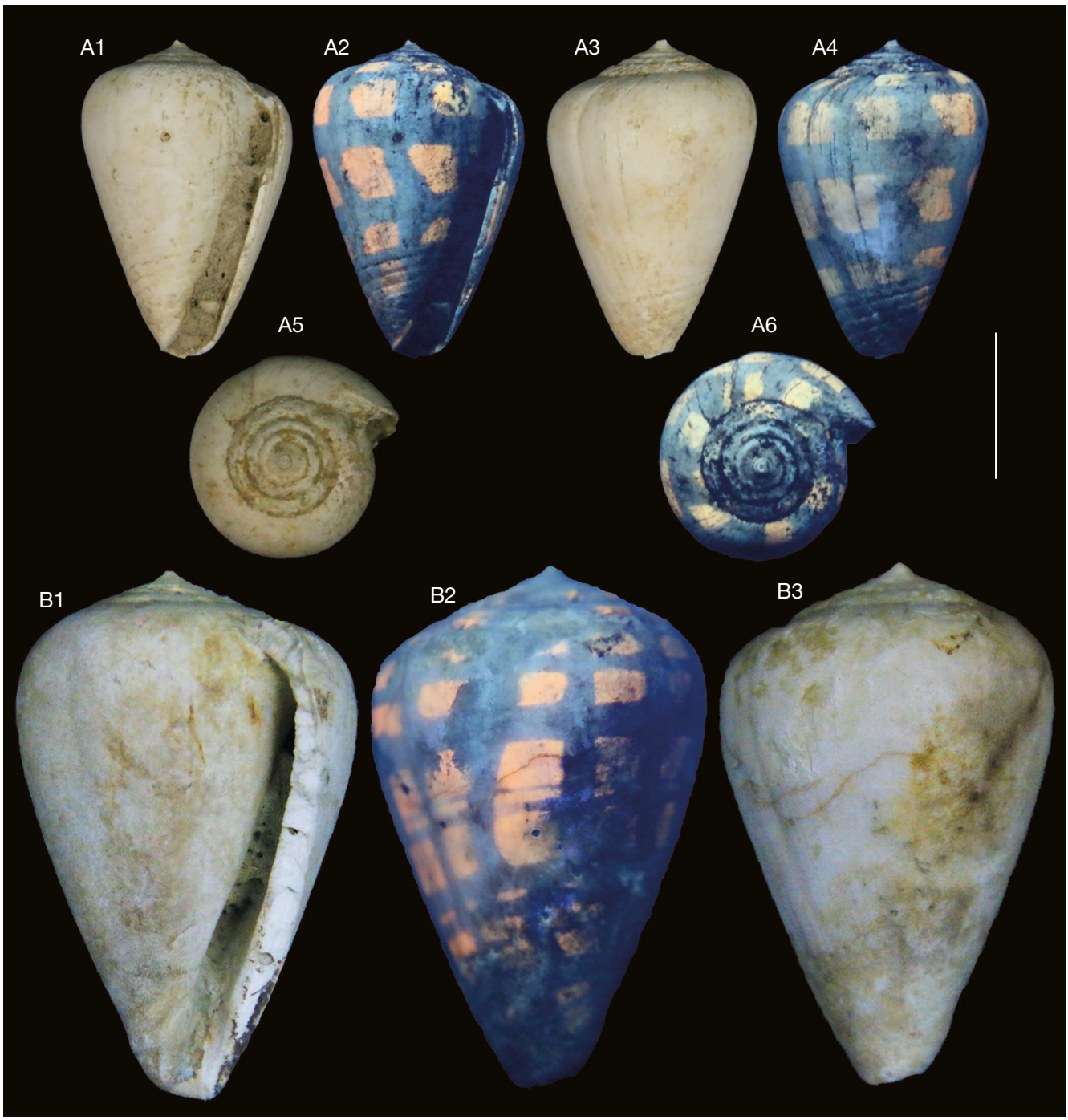

FIG. 13. — *Conus* (*Kalloconus*) *neumayri* Hoernes & Auinger, 1879 from the Tortonian of Crete (Greece) shown in natural light (**A1**, **A3**, **A5**, **B1**, **B3**) and under UV light: **A**, AMPG(IV) 2645, Filippi: small specimen with clear colour pattern of rectangular blotches; **B**, MNHN.F.A72602, Makrilia: a large-sized specimen and thin rectangular dots-dashes. Scale bar: 1 cm.

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*) *daciae* (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 Bałuk (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.

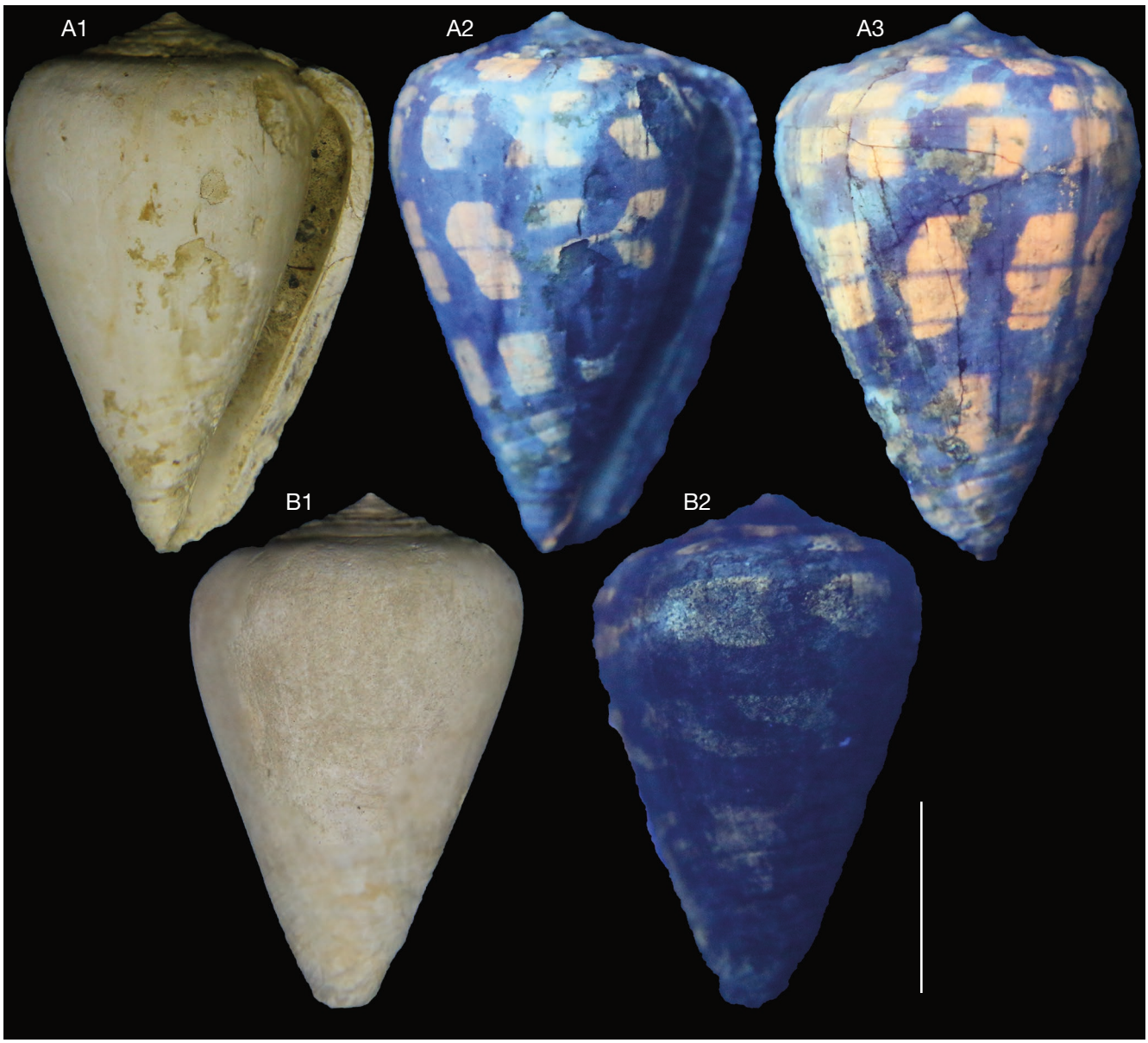

Fig. 14. — *Conus* (*Kalloconus*) *neumayri* Hoernes & Auinger, 1879 from Tefeli (Tortonian, Crete, Greece): **A**, AMPG(IV) 2646: a medium-sized specimen with an intermediate pattern of rectangular blotches that tend to form axial zig-zag stripes, disrupted by thin non-fluorescent spiral lines; **B**, AMPG(IV) 2648: a small-sized specimen with faint colour pattern of blotches unevenly separated by zig-zag non-fluorescent stripes. Scale bar: 1 cm.

Conus (*Kalloconus*) *hendricksi* (Harzhauser & Landau, 2016) (Figs 16, 17; Table 7)

Kalloconus hendricksi Harzhauser & Landau, 2016: 57-59, figs 3H, 3I, 8F_1-F_5, 8G_1-G_3, 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_1-F_5).

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-

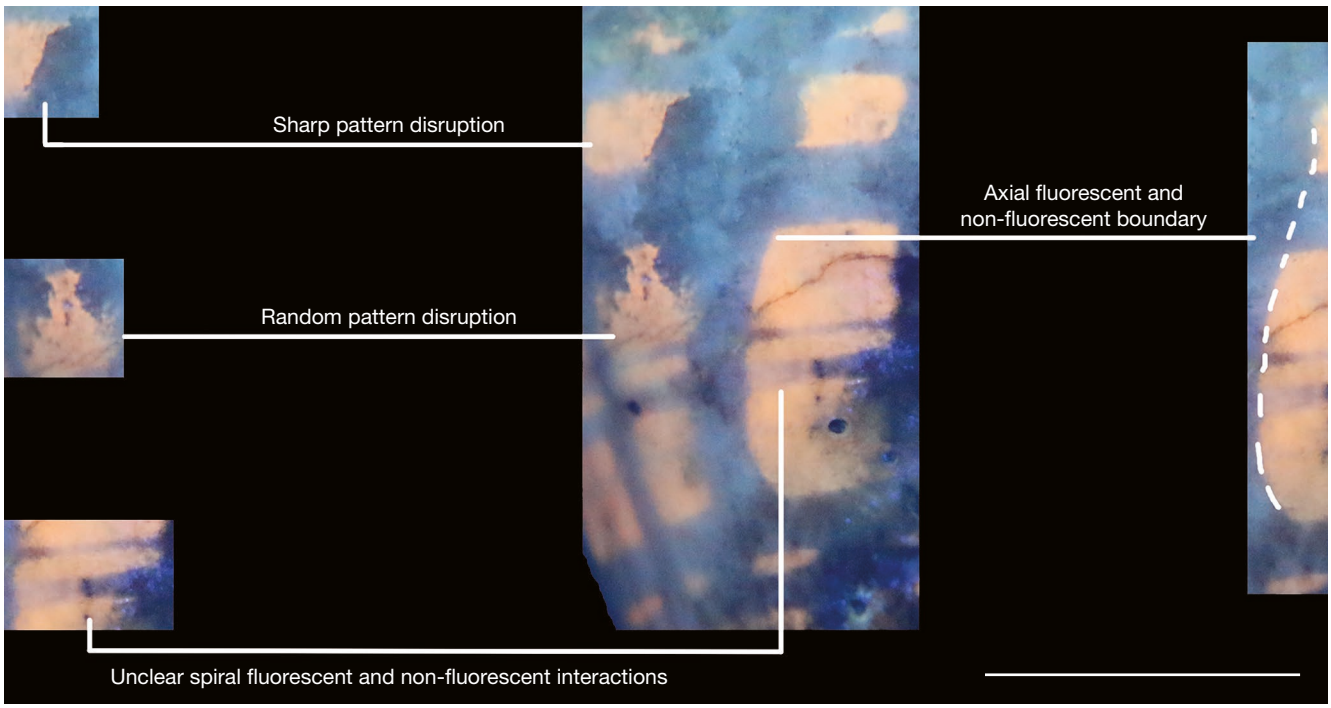

FIG. 15. — Pattern constituted of blotches in *Conus* (*Kalloconus*) *neumayri* Hoernes & Auinger, 1879 from the Tortonian of Crete (Greece). The elements of the colour pattern come from the specimen MNHN.F.A72602 (Fig. 13B2, Makrilia). Scale bar: 1 cm.

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	LWA	LW	RD	PMD	RSH	SSFD	SSFd	PV
Largest specimen	28.24 mm	17.07 mm	26.57 mm	22.33 mm	27.03 mm	146°	39.5°	1.65	0.64	0.84	0.06	–	–	–
Mean	15.8 mm	10.1 mm	14.6 mm	11.7 mm	14.6 mm	129.8°	42.6°	1.59	0.69	0.8	0.08	2.54	7.2	0.64
Standard deviation	3.5	2.41	3.46	3.02	3.53	14.4	4.08	0.11	0.04	0.05	0.04	–	–	–

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*) *berghausi* 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*) *berghausi*. 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 berghausi* 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 whorls (Fig. 16). In the study material, the pointed, early spire whorls are absent on adult specimens, possibly because of the destruction and erosion, of their early, pointed whorls (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 whorls of our Greek specimens, match with *Conus* (*Kalloconus*) *hendricksi*. For these reasons we attribute them to this species.

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

FIG. 16. — *Conus* (*Kalloconus*) *hendricksi* from the Tortonian of Crete (Greece): **A**, MNHN.F.A72610, ?Filippi: the largest specimen collected in abapertural and apical view (apertural view is destroyed). Notice the broken early spire whorls and the relatively equal distance of each spiral row of dots; **B**, MNHN.F.A72614, ?Filippi: a well-preserved specimen, with damaged early spire whorls, but with a well preserved last whorl; **C**, MNHN.F.A72628, ?Filippi: a small specimen with undamaged early spire whorls. Notice the coeloconoid shape of the spire that is missing in the larger specimens. 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 sutural 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*.

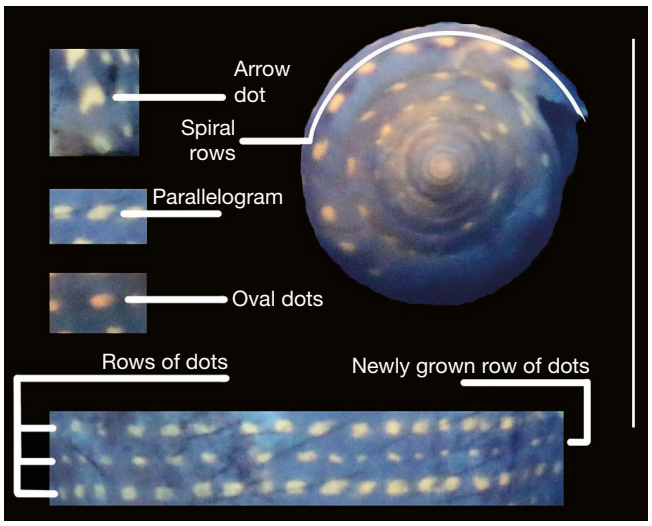

FIG. 17. — Pattern constituted of dots on *Conus* (*Kalloconus*) *hendricksi* (Harzhauser & Landau, 2016) from the Tortonian of Crete (Greece). Composite figure from the specimens (MNHN.F.A72610 and MNHN.F.A72628). Scale bar: 1 cm.

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*) *hendricksi*. In our opinion, the specimen illustrated by Hoernes & Auinger (1879) belongs to a different species.

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

urn:lsid:zoobank.org:act:796AC37E-AC9E-48FE-89B6-2C11F282F6B5

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 Greece (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 whorl. 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 Karaman 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* Erünal-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* Erünal-Erentöz, 1958**
(Figs 19, 20; Table 9)

Conus (*Dentroconus*) *gulemani* Erünal-Erentöz, 1958: 113, pl. 18, figs 5-6.

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.

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	4.96	12.47	5.8	0.14	0.07	0.03	0.03	1.14	1.84	0.16

Conus bitorosus – Caze *et al.* 2011a: 172, fig. 2L.

TYPE MATERIAL. — One syntype: MNHN.FA26722; 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 Ierapetra Basins, Crete).

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

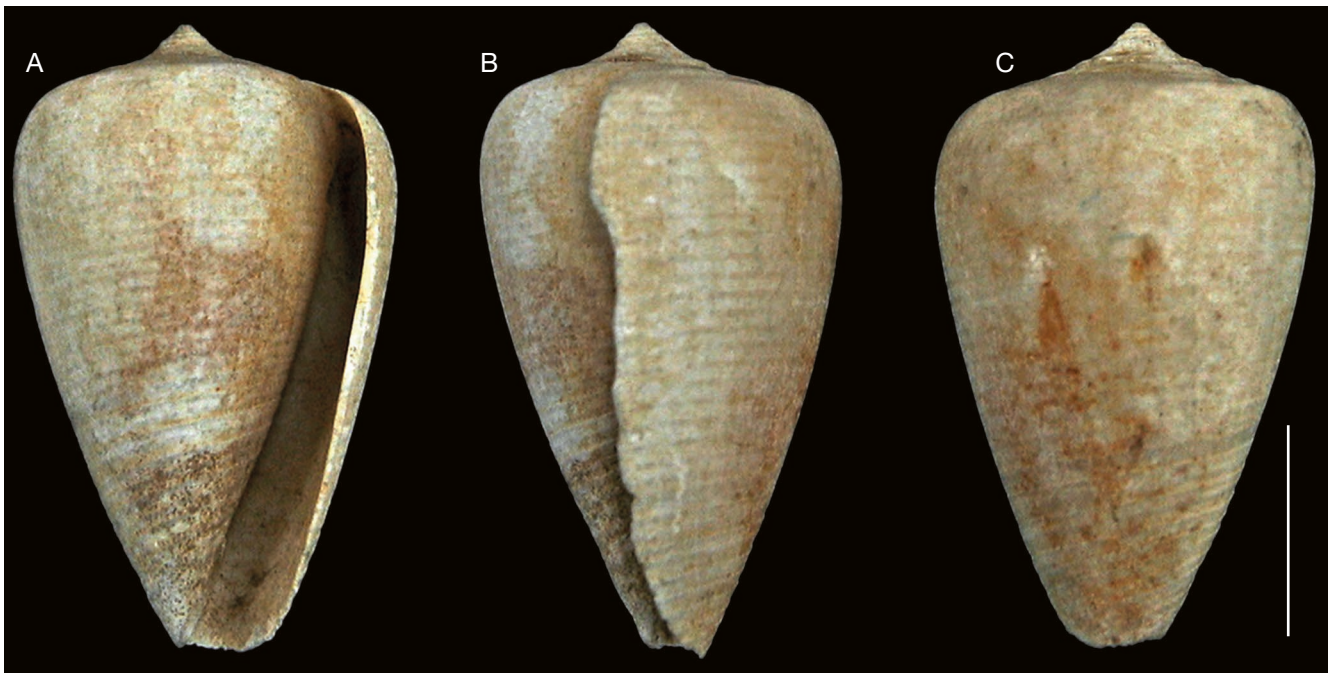

Fig. 19. — Syntype of *Conus* (*Kalloconus*) *gulemani* Erünal-Erentöz, 1958, MNHN.FA26722 (Serravallian, Zengen Köy S, Derebogazi, Karaman Basin, Turkey). Photos taken under natural light by J. Mouchart. Scale bar: 1 cm.

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	0.03	1.11	2.95	0.14

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.F.A26722; 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.F.A30841) from Makrilia as *Conus bitorosus* Fontannes, 1880. *Conus bitorosus*, 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

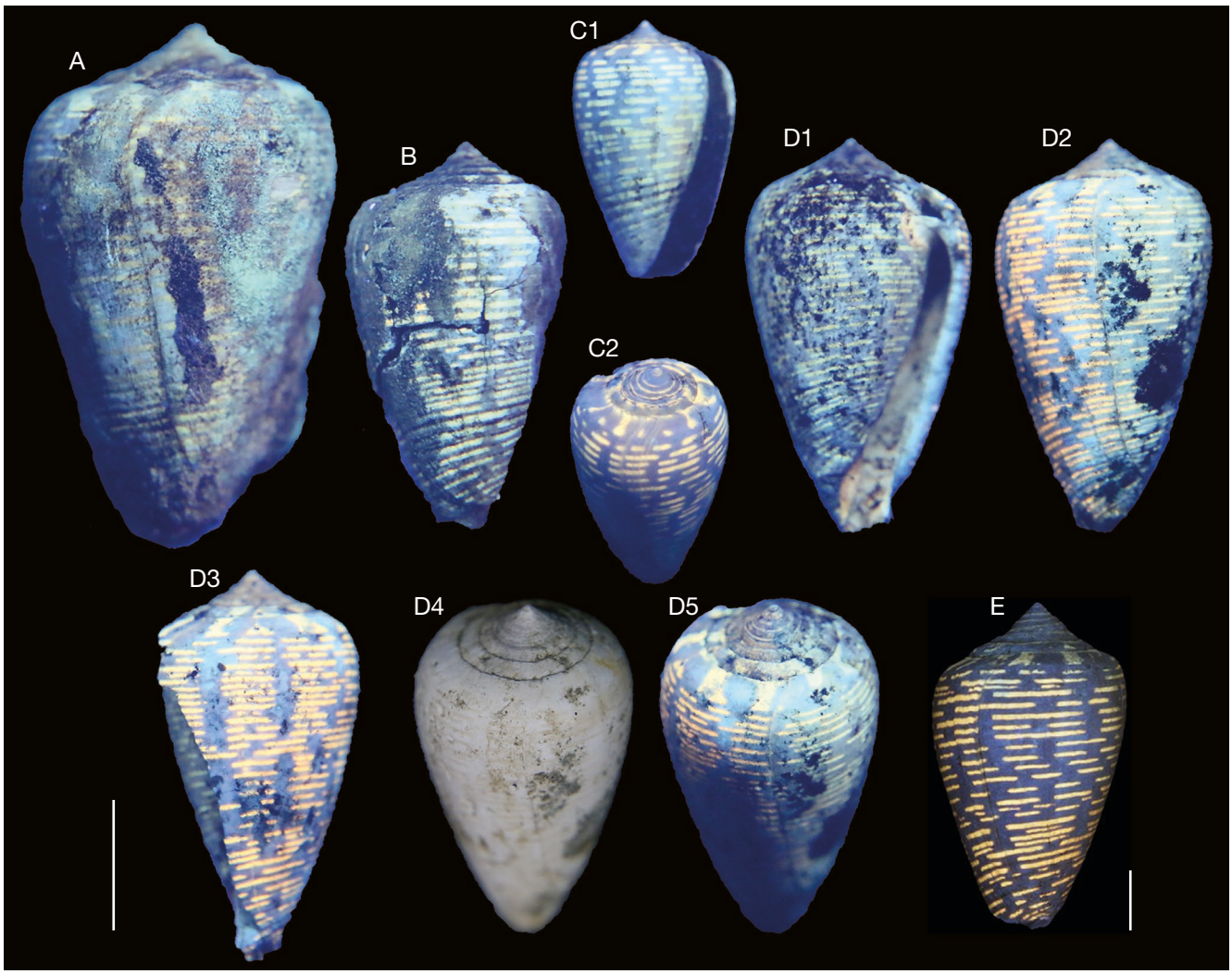

FIG. 20. — *Conus* (*Kalloconus*) *gulemani* Erünal-Erentöz, 1958 from the Tortonian of Crete (Greece): **A**, AMPG(IV) 2672, Filippi: a large specimen showing fade colour pattern under UV light, with patches covered by bryozoan colonies; **B**, AMPG(IV) 2664, Filippi: a specimen with solid colour pattern of mostly spiral lines; **C**, AMPG(IV) 2674, Filippi: a small specimen with its last whorl intact, showing this species' last whorl outline and subsutural flexure; **D**, AMPG(IV) 2675, Filippi: a specimen with clear colour pattern under normal and UV light, with clear axial non-fluorescent areas; **E**, MNHN.F.A30841 identified as *Conus bitorosus* by Caze *et al.* 2011a, Makrilia. Scale bars: 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, $10E_1$-E_3, $10F_1$-F_4, $10G_1$-G_4, $10H_1$-H_3.

Monteiroconus 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

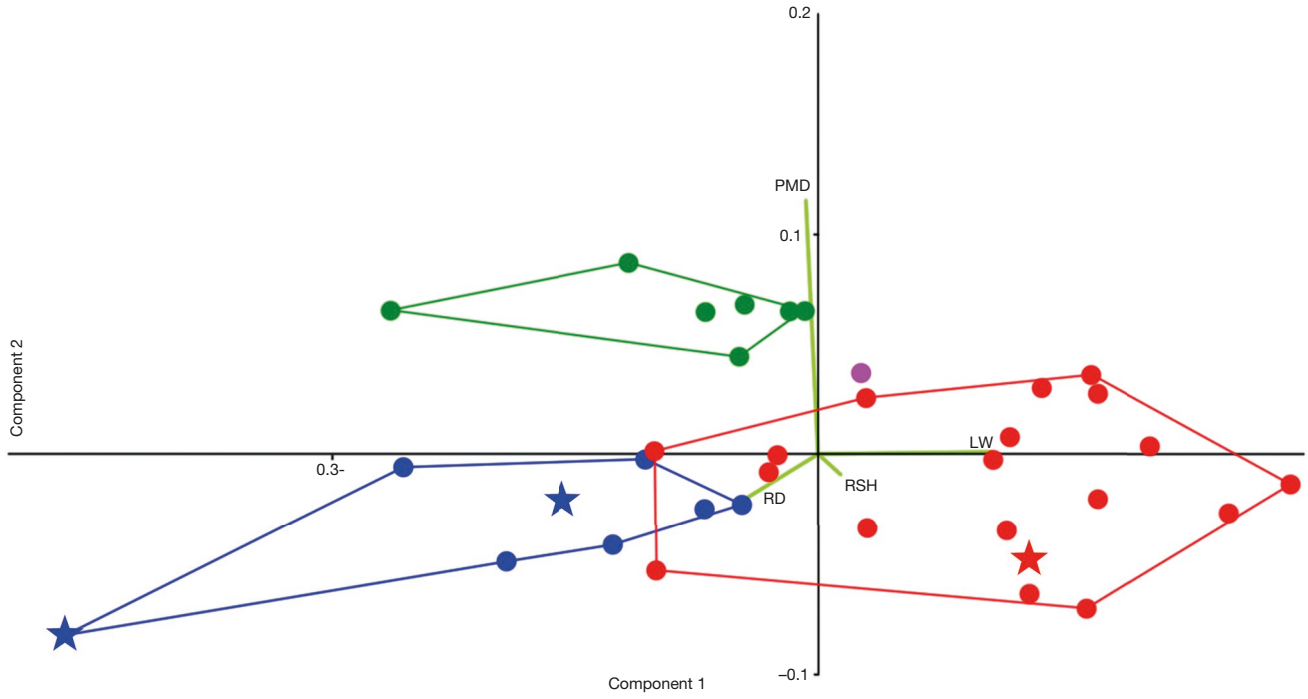

FIG. 21. — PCA graph with four species of *Conus* (*Kalloconus*) with similar colour pattern variations. Dots and area colors: ●, *Conus* (*Kalloconus*) *hungaricus* Hoernes & Auinger, 1879; ●, *Conus* (*Kalloconus*) *tietzei* Hoernes & Auinger, 1879; ●, *Conus* (*Kalloconus*) *gulemani* Erünal-Erentöz, 1958; ●, *Conus* (*Kalloconus*) *helladicus* n. sp.; ★, best preserved specimens from both species described herein. Abbreviations: **LW**, length width ratio; **RD**, relative diameter; **PMD**, position of maximum diameter; **RSH**, relative height of spire.

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

SL	MD	AH	HMD	AL	SA	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	SA	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	16.03	3.81	0.18	0.07	0.03	0.04			

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). Harzhauser & Landau (2016) described three darker bands on the last whorl of the Paratethyan *Conus* (*Kalloconus*) *letkesensis* (Harzhauser & Landau 2016: fig. 10F-H). These bands are not visible on the Cretan specimen. The presence of this species in the Tortonian Eastern Protomediterranean, is an addition to the important cohort of taxa common to both the Middle Miocene of the Paratethys and eastern Proto-Mediterranean. The typical Paratethyan Langhian assemblages (Harzhauser & Landau 2016) were found in the Proto-Mediterranean in the Serravallian of Turkey (Landau *et al.* 2013). This species is an example of the persistence of some taxa into the late Miocene of Eastern Proto-Mediterranean.

Conus (*Kalloconus*) *asterousiaensis* n. sp
(Figs 24, 25, 26, 27; Table 11)

urn:lsid:zoobank.org:act:CD6E9758-6E97-45B5-A8F0-1C900A4417A7

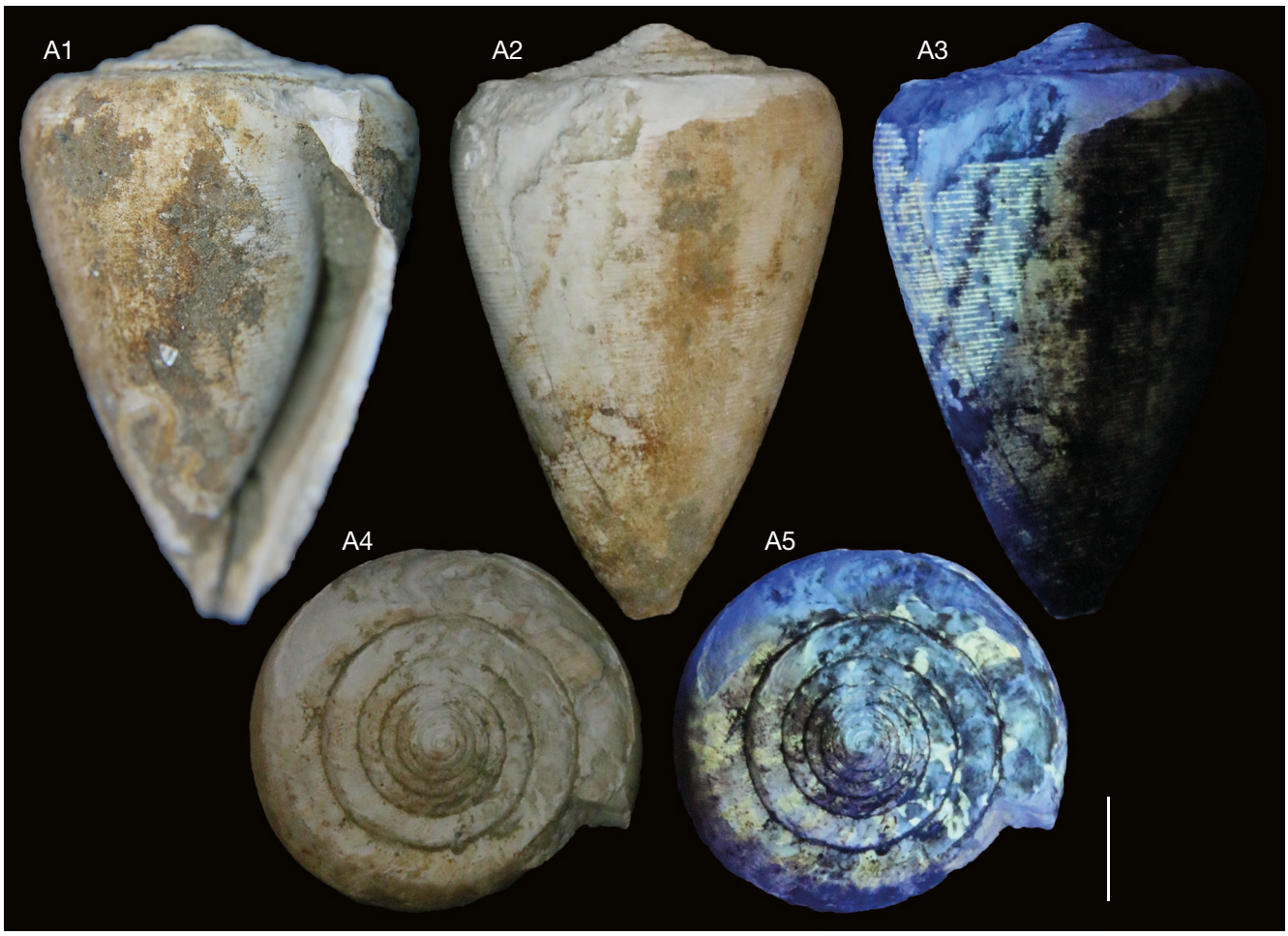

Fig. 22. — *Conus* (*Kalloconus*) *letkesensis* (Harzhauser & Landau, 2016) from Filippi, Crete (Greece). Specimen AMPG(IV) 2682 with small dense dashes and irregular flammulae on the spire. Specimen shown under natural light (**A1**-**A2**, **A4**) and UV light. Scale bar: 1 cm.

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.

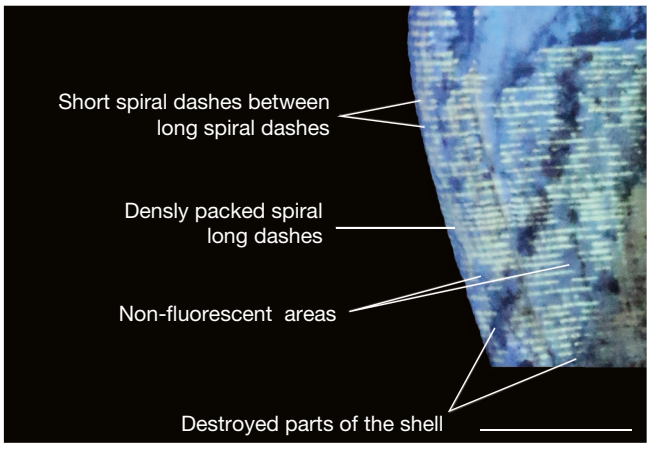

Fig. 23. — Pattern of the dashes on *Conus* (*Kalloconus*) *letkesensis* (Harzhauser & Landau, 2016). Dashed colour pattern is from AMPG(IV) 2682 (Fig. 22) from Filippi, Crete (Greece). Scale bar: 1 cm.

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

Fig. 24. — *Conus* (*Kalloconus*) *asterousiaensis* n. sp. from the Tortonian of Crete (Greece) on apertural, abapertural and apical views, under natural and UV light: paratype AMPG(IV) 2689, Tefeli: the largest specimen with faint colour pattern of dots and dashes; **B**, holotype AMPG(IV) 2683, Filippi: specimen in abapertural and apical view; **C**, MNHN.F.A72642, Crete; **D**, Paratype MNHN.F.A72644, Crete; **E**, MNHN.F.A72647, Crete. Scale bar: 1 cm.

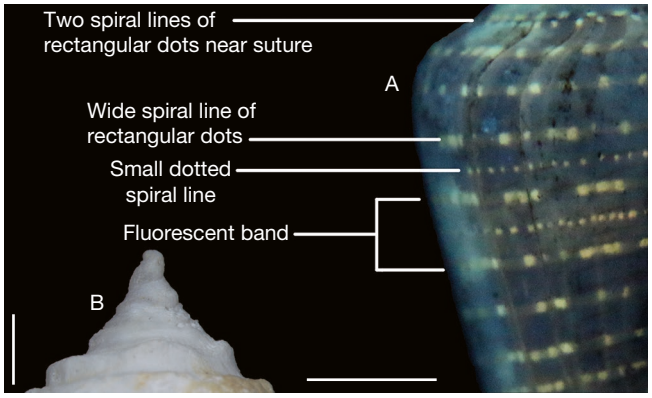

Fig. 25. — Elements constituting the colour pattern of *Conus* (*Kalloconus*) *asterousiaensis* n. sp. of from the Tortonian of Crete (Greece), with an example of this species' protoconch, shown under natural light: **A**, Paratype MNHN.F.A72644, Crete: Notice the two spiral lines of dots on both sides of the suture, the abrupt transitional pattern of dots in the dim fluorescent, axial lines. Notice the small spiral lines of dots and the fluorescent band on the centre of the shell's length; **B**, MNHN.F.A72647, Crete: this specimen has its multispiral protoconch preserved. Scale bars: A, 0.5 cm; B, 0.1 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

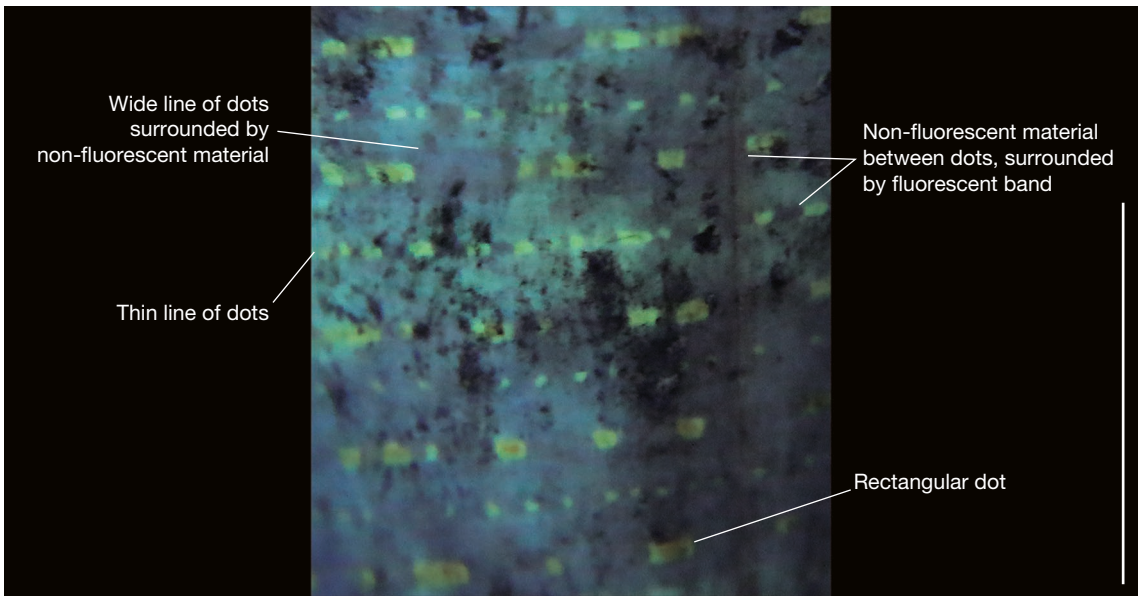

FIG. 26. — Colour pattern of *Conus* (*Kalloconus*) *asterousiaensis* n. sp. MNHN.F.A72642 from the Tortonian of Crete (Greece). Notice the large spiral line with the smaller dots at the centre of the line, surrounded by dim fluorescent material. The line is also surrounded by a fluorescent band. Scale bar: 1 cm.

TABLE 12. — Comparison of the Tortonian assemblage of *Conilithes* Swainson, 1840 and *Conus* (*Kalloconus*) da Motta, 1991 of Crete (Greece) with Neogene (Langhian to Pliocene) assemblages of neighbouring regions (Langhian of Italy (Sacco 1893a, b; Hall 1966), Paratethys (Harzhauser & Landau 2016), Turkey (Erünal-Erentöz 1958; Landau *et al.* 2013),Tortonian of Italy (Sacco 1893a, b), Pliocene of Italy (Sacco 1893a, b). In the column referring to this work (Crete, Greece), the number of examined specimens.

	Langhian		Serravallian	Tortonian		Pliocene
	Italy	Paratethys	Turkey	Italy	Crete, Greece	Italy
Conilithes brezinae (Hoernes & Auinger, 1879)	–	•	–	–	49	–
Conilithes herodus n. sp.	–	–	–	–	10	–
Conilithes sp.	–	–	–	–	1	–
Conilithes striatulus (Brocchi, 1814)	?	•	–	•	13	•
Conilithes antidiluvianus (Bruguière, 1792)	–	•	–	•	1	•
Conus (*Kalloconus*) *neumayri* Hoernes & Auinger, 1879	–	•	•	–	10	–
Conus (*Kalloconus*) *hendricksi* (Harzhauser & Landau, 2016)	–	•	•	•	39	–
Conus (*Kalloconus*) *helladicus* n. sp.	–	–	–	–	9	–
Conus (*Kalloconus*) *gulemani* Erünal-Erentöz, 1958	–	–	•	–	19	–
Conus (*Kalloconus*) *letkesensis* (Harzhauser & Landau, 2016)	–	•	–	–	1	–
Conus (*Kalloconus*) *asterousiaensis* n. sp.	–	–	–	*	17	–

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, quadrangular, 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 morphological 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 *Kalloconus*, 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

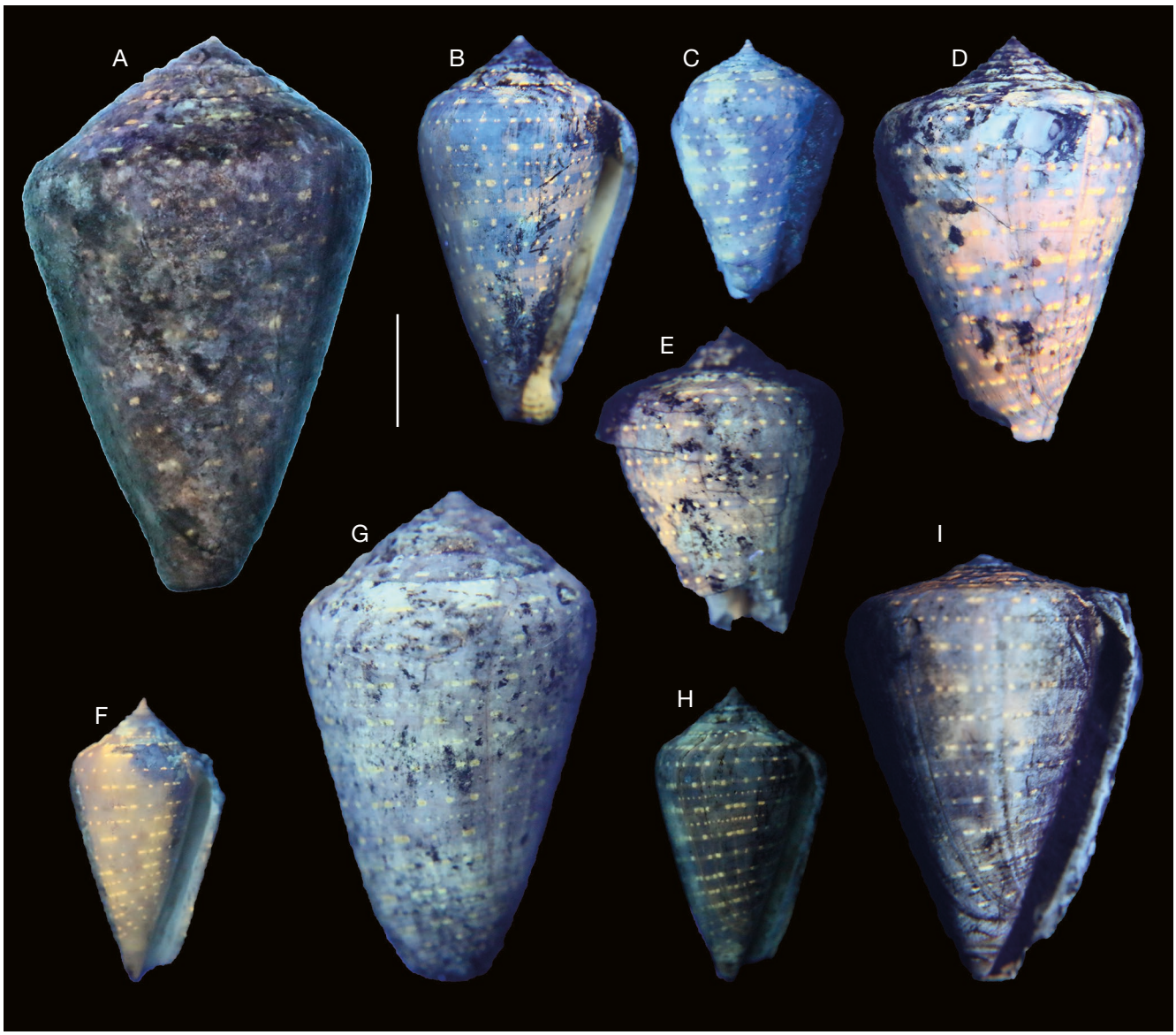

Fig. 27. — Morphological variation of shoulder and spire height in *Conus* (*Kalloconus*) *asterousiaensis* n. sp. from the Tortonian of Crete (Greece). Colour pattern of the specimens seems consistent, despite the fact that there is a wide variety in spire height and angulation of shoulder: **A**, Paratype AMPG(IV) 2689, Tefeli; **B**, AMPG(IV) 2688, Filippi; **C**, MNHN.F.A72645, Crete; **D**, AMPG(IV) 2684, Filippi; **E**, MNHN.F.A72648, Crete; **F**, MNHN.F.A72647, Crete; **G**, MNHN.F.A72642, Crete; **H**, Paratype MNHN.F.A72644, Crete; **I**, Holotype AMPG(IV) 2683, Filippi. Scale bar: 1 cm.

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*) *helladicus* n. sp. and *Conus* (*Kalloconus*) *asterousiaensis*) 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*) *helladicus* 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 only four 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.

Acknowledgements
We thank Giorgio Teruzzi from the Museo di Storia Naturale di Milano for providing figures of the type specimen, Astrinos Damianakis, a private collector from Panassos village for showing fossiliferous localities of Panassos, Manuel Jiménez-Tenorio from the Universidad de Cádiz for sharing his knowledge about Recent Conidae and the Museum of Mineralogy and Petrology of the National and Kapodistrian University of Athens, Faculty of Geology and Geoenvironment for being kind enough to let use their UV light. We thank Malcolm Symonds (Ashtead, UK) for greatly improving the English of the text. We are grateful to the reviewers, Bernard Manuel Landau and Jonathan R. Hendricks, for their constructive comments on the manuscript. This research is part of Psarras Christos' PhD thesis from the National and Kapodistrian University of Athens, Department of Historical Geology-Paleontology, faculty of Geology and Geoenvironment, Athens (Greece). The MNHN gives access to the collections in the framework of the RECOLNAT national Research Infrastructure.

REFERENCES

Abalde S., Tenorio M. J., Uribe J. E. & Zardoya R. 2019. — Conidae phylogenomics and evolution. *Zoologica Scripta* 48: 194-214. https://doi.org/10.1111/zsc.12329

Bachmeyer F. & Symeonidis N. 1978. — Eine fossile Seenadel (Syngnathidae) aus dem Obermiozän von Ierapetra, Insel Kreta (Griechenland). *Annalen des Naturhistorischen Museums in Wien, Serie A*, 81: 121-127.

Bałuk W. 1997. — Middle Miocene (Badenian) gastropods from Korytnica, Poland. Part III. *Acta Geologica Polonica* 47: 1-75.

Bellardi L. & Michelotti G. 1841. — Saggio orittographico sulla classe dei gasteropodi fossili dei terreni terziarii del Piemonte. *Memorie della Reale Accademia delle Scienze di Torino*, ser. 2, 3: 93-174.

Brocchi G. 1814. — *Conchiologia fossile subapennina, con osservazioni geologiche sugli Apennini e sul suolo adiacente*. Stamperia Reale, Milano, 1-2, 712 pp. https://doi.org/10.5962/bhl.title.11569

Bruguière M. 1792. — *Encyclopédie méthodique. Histoire naturelle des Vers*. Tome Ier. Impensis Panckoucke, Paris: 345-752. https://doi.org/10.5962/bhl.title.49857

Catalano R. & Sprovieri R. 1969. — Stratigrafia e micropaleontologia. dell intervallo tripolaceo, di torrente Rossi (Enna). *Atti della Accademia gioenia di scienze naturali in Catania* 7 (1): 513-27.

Cate J. M. 1972. — On the occurrence of the volutid subgenus *Eneata*. *Tulane Studies in Geology and Paleontology* 10 (1): 47-50.

Caze B. 2010. — *Intérêt systématique de l'étude des motifs colorés résiduels chez les mollusques du Cénozoïque d'Europe*. Thèse de doctorat, Muséum national d'Histoire naturelle, Paris, 558 p.

Caze B., Merle D., Pacaud J.-M. & Saint Martin J.-P. 2010. — First systematic study using the variability of the residual colour patterns: the case of the Paleogene Seraphsidae (Mollusca, Gastropoda, Stromboidea). *Geodiversitas* 32 (3): 417-477. https://doi.org/10.5252/g2010n3a4

Caze B., Merle D., Saint Martin J.-P. & Pacaud J.-M. 2011a. — Contribution of residual colour patterns to the species characterization of Caenozoic molluscs (Gastropoda, Bivalvia). *Comptes Rendus Palevol* 10: 171-179. https://doi.org/10.1016/j.crpv.2010.10.005

Caze B., Merle D., Le Meur M., Pacaud J.-M., Ledon D. & Saint Martin J.-P. 2011b. — Taxonomic implications of the residual colour patterns of ampullinid gastropods and their contribution to the discrimination from naticids. *Acta Palaeontologica Polonica* 56 (2): 329-347. https://doi.org/10.4202/app.2009.0084 https://doi.org/10.4202/app.2009.0084

Caze B., Merle D. & Schneider S. 2015. — UV Light reveals the diversity of Jurassic shell colour patterns: examples from the Cordebugle Lagerstätte (Calvados, France). *Plos One* 10 (6): 1-38. https://doi.org/10.1371/journal.pone.0126745

Children J. G. 1823. — Lamarck's genera of shells. *Quarterly Journal of Science, Literature and the Arts* (*London*), 14 (28): 298-322, pl. 5-6 [Gennaio 1823]; 15(29): 23-52, pl. 2-3 [Aprile 1823]; 15 (30): 216-258, pl. 7-8 [Luglio 1823]; 16 (31): 49-79, pl. 5 [Ottobre 1823]; 16 (32): 241-264, pl. 6 [Dicembre 1823]. https://www.biodiversitylibrary.org/bibliography/2259

Da Motta A. J. 1991. — *A Systematic Classification of the Gastropod Family Conidae at the Generic Level*. La Conchiglia, Roma, 48 p.

Davoli F. 1972. — Conidae (Gastropoda), *in* Montanaro E. (ed.), Studi monografici sulla malacologia miocenica modenense. Parte 1 – Molluschi tortoniani di Montegibbio. *Palaeontographia Italica* 68 (n.s. 38): 51-143.

Delrieu B. 1990. — *Évolution tectono-sédimentaire du Malevisi et du secteur d'Ano-Moulia au Miocène supérieur (bassin d'Héraklion, Crète centrale, Grèce)*. Mémoire de Géologie de 5ème de l'IGAL, 369 p.

Dermitzakis M. D. 1969. — Geological Researches of the Neogene Deposits of the Hierapetra Province in Crete. *Annales géologiques des Pays helléniques* 21: 342-484.

DESHAYES G. P. IN DESHAYES G. P. & MILNE-EDWARDS H. 1845. — *Histoire naturelle des animaux sans vertèbres, présentant les caractères généraux et particuliers de ces animaux, leur distribution, leurs classes, leurs familles, leurs genres, et la citation des principales espèces qui s'y rapportent ; précedée d'une introduction offrant la détermination des caractères essentiels de l'animal, sa distinction du végétal et des autres corps naturels ; enfin, l'exposition des principes fondamentaux de la zoologie*. Volume 11. Deuxième Édition. J.-B. Baillïère, Paris. https://doi.org/10.5962/bhl.title.63986

DOCKERY D. T. 1980. — Color patterns of some Eocene molluscs. *Mississippi Geology* 1 (1): 3-7.

DUDA T. F. JR & KOHN A. J. 2005. — Species-level phylogeography and evolutionary history of the hyperdiverse marine gastropod genus *Conus*. *Molecular Phylogenetics and Evolution* 34 (2): 257-272. https://doi.org/10.1016/j.ympev.2004.09.012

ERÜNAL-ERENTÖZ L. 1958. — Mollusques du Néogène des bassins de Karaman, Adana et Hatay (Turquie). Première thèse, 1ère partie. *Publications de l'Institut d'Études et de Recherches minières de Turquie*, C3: 1-232.

EICHWALD E. 1830. — *Naturhistorische Skizze von Lithauen, Volhynien und Podolien in Geognostisch-Mineralogischer, Botanischer und Zoologischer Hinsicht*. Voss, Wilna, 256 p.

ERÜNAL-ERENTÖZ L. 1958. — *Mollusques du Néogène des bassins de Karaman, Adana et Hatay (Turquie)*. Première thèse, 1ère partie. Publications de l'Institut d'Études et de Recherches minières de Turquie C3: 1-232.

FERRERO MORTARA E., MONTEFAMEGLIO L., NOVELLI M., OPESSO G., PAVIA G. & TAMPIERI R. 1984. — *Catalogo dei tipi e degli esemplari figurati della collezione Bellardi e Sacco II*. Museo Regionale di Scienze Naturali, Catalogo 7: 1-484.

FONTANNES F. 1880. — *Les invertébrés du bassin Tertiaires du sud-est de la France. Les Mollusques pliocènes de la vallée du Rhône et du Roussillon*. Volume I. *Gastéropodes des formations marines et saumâtres*. Georg, Lyon & F. Savy, Paris, 77-168, février 1880; 169-268, juin 1880. https://doi.org/10.5962/bhl.title.13209

FORTUIN A. R. 1977. — Stratigraphy and sedimentary history of the Neogene deposits in the Ierapetra Region, eastern Crete. *GUA Papers of Geology* 8: 1-164.

FORTUIN A. R. 1978. — Late Cenozoic history of eastern Crete and implications for the geology and geodynamics of the southern Aegean area. *Geologie en Mijnbouw* 57 (3): 451-484.

FRYDAS D. 2004. — Calcareous and siliceous phytoplankton stratigraphy of Neogene marine sediments in central Crete (Greece). *Revue de Micropaléontologie* 47: 87-102. https://doi.org/10.1016/j.revmic.2004.03.002

GONG Z., MATZKE N. J., ERMENTROUT B., SONG D., VENDETTI J. E., SLATKIN M. & OSTER G. 2012. — Evolution of patterns on Conus shells. *Proceedings of the National Academy of Sciences* 109 (5): E234-E241. https://doi.org/10.1073/pnas.1119859109

HALL C. A. JR 1966. — Middle Miocene *Conus* (class Gastropoda) from Piedmont, Northern Italy. *Bollettino della Società Paleontologica Italiana* 3 (2): 111-171.

HARZHAUSER M. & LANDAU B. 2016. — A revision of the Neogene Conidae and Conorbidae (Gastropoda) of the Paratethys Sea. *Zootaxa* 4210 (1): 001-178. https://doi.org/10.11646/zootaxa.4210.1.1

HENDRICKS J. R. 2009. — The genus *Conus* (Mollusca: Neogastropoda) in the Plio-Pleistocene of the southeastern United States. *Bulletins of American Paleontology* 375: 1-180.

HENDRICKS J. R. 2015. — Glowing seashells: diversity of fossilized coloration patterns on coral reef-associated cone snail (Gastropoda: Conidae) shells from the Neogene of the Dominican Republic. *Plos One* 10: e0120924. https://doi.org/10.1371/journal.pone.0120924

HENDRICKS J. R. 2018. — Diversity and preserved shell coloration patterns of Miocene Conidae (Neogastropoda) from an exposure of the Gatun Formation, Colón Province, Panama. *Journal of Paleontology* 92 (5): 1-34. https://doi.org/10.1017/jpa.2017.153

HOERLE S. E. 1976. — The genus *Conus* (Mollusca: Gastropoda) from the Alum Bluff group of Northwestern Florida. *Tulane Studies in Geology and Paleontology* 14 (1-2): 1-31.

HOERLE S. E. & VOKES E. H. 1978. — A review of the volutid genera *Lyria* and *Falsilyria* (Mollusca: Gastropoda) in the Tertiary of the Western Atlantic. *Tulane Studies in Geology and Paleontology* 14 (3): 105-130.

HOERNES R. 1878. — Ueber das Vorkommen des genus *Conus* in den marinen Neogen. *Ablagerungen der öster.-ungar. Monarchie. Verhandlungen der k.k. Geologischen Reichsanstalt* 9: 191-196.

HOERNES R. & AUINGER M. 1879. — Die Gasteropoden der Meeres-Ablagerungen der ersten und zweiten Miocänen Mediterran-Stufe in der Österreichisch-Ungarischen Monarchie. *Abhandlungen der Kaiserlich-Königlichen Geologischen Reichsanstalt* 12:1-52.

HÖRNES M. 1851. — Die fossilen Mollusken des Tertiär-Beckens von Wien. *Abhandlungen der Kaiserlich-Königlichen Geologischen Reichsanstalt* 3-4 (published in parts): 1-42, pls 1-5.

HWASS C. H. 1792. — Cone, *in* BRUGUIÈRE J.-P. (ed.), *Encyclopédie méthodique ou par ordre de matières. Histoire Naturelle des Vers*. Volume 1. Panckoucke, Paris: 586-757. https://www.biodiversitylibrary.org/page/8892574

INTERNATIONAL COMMISSION ON ZOOLOGICAL NOMENCLATURE 1999. — *International Commission on Zoological Nomenclature. Fourth ed., International Trust for Zoological Nomenclature*. The Natural History Museum, London, v-xxix, 306 p.

JANSSEN A. W., JANSSEN R., TRACEY S., VAESSEN L. M.B. & VOORT J. VAN DER 2014a. — History of a marine, Cainozoic gastropod taxon, *Conus antidiluvianus* Bruguière, 1792 and its nomenclatural implications. *Cainozoic Research* 14: 73-90.

JANSSEN A. W., JANSSEN R., TRACEY S., VAESSEN L. M.B. & VOORT J. VAN DER 2014b. — Case 3668 *Conus antidiluvianus* Bruguière, 1792 (Mollusca, Gastropoda, CONIDAE): proposed conservation of prevailing usage of specific name by setting aside the unidentifiable lectotype and replacing it with a neotype. *The Bulletin of Zoological Nomenclature* 71 (4): 223-229. https://doi.org/10.21805/bzn.v71i4.a11

KIENER L. C. 1845-1850. — *Spécies général et iconographie des coquilles vivantes : comprenant la collection du Muséum d'histoire naturelle de Paris, la collection Lamarck, celle du Prince Masséna (appartenant maintenant à M. M. Delessert) et les découvertes récentes des voyageurs*. Vol. 2. *Famille des Enroulées*. Vol. 2. *Genre Cone (Conus, Lam.)*. Paris, Rousseau & J. B. Baillière, 379 p. https://doi.org/10.5962/bhl.title.969

KOHN A. J. 1990. — Tempo and mode of evolution in Conidae. *Malacologia* 32 (1): 55-67.

KOSKERIDOU E. 1997. — *The Neogene Turritellids of Greece*. Gaia 3. Publications of the Department of Geology, NKUA, 210 p.

KOSKERIDOU E., GIAMALI C., ANTONARAKOU A., KONTAKIOTIS G. & KARAKITSIOS V. 2017. — Early Pliocene gastropod assemblages from the eastern Mediterranean (SW Peloponnese, Greece) and their palaeobiogeographic implications. *Geobios* 50 (4): 267-277. https://doi.org/10.1016/j.geobios.2017.06.003

KOVÁCS Z. & VICIÁN Z. 2013. — Badenian (middle Miocene) Conoidean (Neogastropoda) fauna from Letkés (N Hungary). *Fragmenta Palaeontologica Hungarica* 30: 53-100.

LANDAU B., HARZHAUSER M., BÜYÜKMERIÇ Y. & SILVA C. 2013. — Systematics and palaeobiogeography of the gastropods of the middle Miocene (Serravallian) Karaman Basin of Turkey. *Cainozoic Research* 1: 1-13.

LIGHTFOOT J. 1786. — [Shell description] *A Catalogue of the Portland Museum, Lately the Property of the Dowager Duchess of Portland, Deceased, which will be Sold at Auction, by Mr. Skinner & Co*. Privately published, London. https://doi.org/10.5962/bhl.title.69702

LINNAEUS C. 1758. — *Systema naturae per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis. 1 Editio decima, reformata*. Laurentius Salvius: Holmiae. https://doi.org/10.5962/bhl.title.7377

MARCOPOULOU-DIACANTONI A. & LOGOS E. 2004. — The occurrence of the *Metaxytherium cuvieri* Christol in the late Miocene sediments of Sitia, Crete. *Bulletin of the Geological Society of Greece* 36 (2): 764-771. https://doi.org/10.12681/bgsg.16808

MARSHALL J., KELLEY W. P., RUBAKHIN S. S., BINGHAM J.-P., SWEEDLER J. V. & GILLY W. F. 2002. — Anatomical correlates of venom production in *Conus californicus*. *The Biological Bulletin* 203: 27-41. https://doi.org/10.2307/1543455

MERLE D., BARRIER P., BRÉBION P., LAURIAT-RAGE A. & TSAGARIS S. 1988. — *Paléopeuplements et déformations synsédimentaires dans le Miocène supérieur du bassin d'Héraklion*. Museo Regionale di Scienze Naturali, Torino: 297-301.

MERLE D., PACAUD J.-M., KRILOFF A. & LOUBRY P. 2008. — Les motifs colorés résiduels des coquilles lutétiennes du bassin de Paris, *in* MERLE D. (ed.), *Stratotype lutétien*. Muséum national d'Histoire naturelle, Paris; Biotope, Mèze; BRGM, Orléans: 182-227.

MEULENKAMP J. E., DERMITZAKIS M., GEORGIADOU-DIKEOULIA E., JONKERS H. A. & BOGER H. 1979. — Field guide to the Neogene of Crete. *Publications of the Department of Geology and Paleontology, University of Athens*, Series A, 32: 1-32.

MICHELOTTI G. 1847. — Description des fossiles des terrains miocènes de l'Italie septentrionale. Ouvrage publié par la Société hollandaise des Sciences, et accompagné d'un atlas de 17 planches. *Natuurkundelige Verhandelingen van de Hollandsche Maatschappei van Wetenschappen te Haarlem*, Ser. 2, 3 (2): 1-408.

MIETHE A. & BORN A. 1928. — Die Fluorographie von Fossilien. *Paläontologische Zeitschrift* 9 (4): 343-356. https://doi.org/10.1007/BF03041560

MOFORIS L., KOSTOPOULOU S., PANAGOPOULOS G., PYLIOTIS I., TRIANTAPHYLLOU M., MANOUTSOGLOU E. & ZELILIDIS A. 2013. — Sedimentation processes and palaeogeographic evolution of Makrilia Pliocene deposits, SE Crete. *Bulletin of the Geological Society of Greece* 47: 216-225. https://doi.org/10.12681/bgsg.10929

MONTEIRO A., TENORIO M. J. & POPPE G. T. 2004. — *A Conchological Iconography. The family Conidae. The West African and Mediterranean species of* Conus. Conchbooks, Hackenheim, Germany, 102 p., 164 pls.

MUÑIZ SOLÍS R. 1999. — The genus *Conus* L., 1758 (Gastropoda, Neogastropoda) from the Pliocene of Estepona (Malaga, Spain). *Iberus: revista de la Sociedad Española de Malacología* 17: 31-90.

PACAUD J.-M. 2017. — *Trahaldia*, un nouveau genre de Columbellidae (Gastropoda: Neogastropoda) de l'Éocène moyen du bassin de Paris. *Xenophora Taxonomy* 16: 3-8.

PACAUD J.-M. & CAZES L. 2014. — Motif coloré résiduel préservé sur des coquilles du genre *Bullia* Gray *in* Griffith & Pidgeon, 1833 (Mollusca : Gastropoda) de l'Éocène moyen du bassin de Paris et des Etats-Unis. *Xenophora Taxonomy* 18: 16-22.

OLIVERA B. M., SEGER J., HORVATH M. P. & FEDOSOV A. E. 2015. — Prey-capture strategies of fish-hunting Cone snails: behavior, neurobiology and evolution. *Brain, Behavior and Evolution* 86: 58-74. https://doi.org/10.1159/000438449

OLSSON A. A. 1967. — *Some Tertiary Mollusks from South Florida and the Caribbean*. Paleontological Research Institution, Ithaca, 61 p.

PEDRIALI L. & ROBBA E. 2005. — A revision of the Pliocene naticids of Northern and Central Italy. I. The subfamily Naticinae except *Tectonatica*. *Rivista Italiana di Paleontologia e Stratigrafia* 111: 109-179. https://doi.org/10.13130/2039-4942/6279

PEREIRA DA COSTA F. A. 1866. — *Gasteropodes dos depositos Terciarios do Portugal*. Commissão Geologica de Portugal, Lisboa. [1° Caderno, i-x, 1-116 + 5 unnumbered pages of index, figure captions and errata, pls 1-15].

PINNA G. & SPEZIA L. 1978. — Catalogo dei tipi del Museo civico di storia naturale di Milano. V. I tipi dei gasteropodi fossili. *Atti della Società italiana di scienze naturali e del Museo civico di storia naturale di Milano* 119 (2): 125-180.

PUILLANDRE N., BOUCHET P., DUDA T. F., KAUFERSTEIN S., KOHN A. J., OLIVERA B. M., WATKINS M. & MEYER C. 2014. — Molecular phylogeny and evolution of the cone snails (Gastropoda, Conoidea). *Molecular Phylogenetics and Evolution* 78: 290-303. https://doi.org/10.1016/j.ympev.2014.05.023

RING U., BRACHERT T. & FASSOULAS C. 2001. — Middle Miocene graben development in Crete and its possible relation to large-scale detachment faults in the southern Aegean. *Terra Nova* 13 (4): 297-304. https://doi.org/10.1046/j.1365-3121.2001.00359.x

RÖCKEL D., KORN W. & KOHN A. J. 1995. — *Manual of the Living Conidae*. Vol. 1. The Indo-Pacific Region. Verlag Christa Hemmen, 517 p.

SACCO F. 1893a. — I molluschi dei terreni terziarii del Piemonte e della Liguria. Parte 13 [a]: (Conidae) (Fasciolo Primo). *Memorie della Reale Accademia delle Scienze di Torino*, series 2, 44: 1-54.

SACCO F. 1893b. — *I molluschi dei terreni terziarii del Piemonte e della Liguria. Parte 13 [b]: (Conidae e Conorbidae) (Fascicolo secundo)*. Clausen, Torino: 55-143.

SACHSE M. & MOHR B. A. R. 1996. — Eine obermiozäne Makro- und Mikroflora aus Südkreta (Griechenland), und deren paläoklimatische Interpretation. Vorläufige Betrachtungen. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen* 200 (1-2): 149-182. https://doi.org/10.1127/njgpa/200/1996/149

SAFAVI-HEMAMI H., GAJEWIAK J., KARANTH S., ROBINSON S. D., UEBERHEIDE B., DOUGLASS A. D., SCHLEGEL A., IMPERIAL J. S., WATKINS M., BANDYOPADHYAY P. K., YANDELL M., LI Q., PURCELL A. W., NORTON R. S., ELLGAARD L. & OLIVERA B. M. 2015. — Specialized insulin is used for chemical warfare by fish-hunting cone snails. *Proceedings of the National Academy of Sciences of the United States of America* 112: 1743-1748. https://doi.org/10.1073/pnas.1423857112

SMITH B. 1930. — Some Specific Criteria in Conus. *Proceedings of the Academy of Natural Sciences of Philadelphia* 82: 279-288. https://www.jstor.org/stable/4064076

SWAINSON W. 1840. — *A Treatise on Malacology; or, the Natural Classification of Shells and Shell Fish*. Longman, Orme, Brown; Green & Longmans, London. https://doi.org/10.5962/bhl.title.8027

SYMEONIDIS N. 1965. — Das Neogen von Ostkreta. *Annales géologiques des Pays helléniques* 16: 249-314.

SYMEONIDIS N. & KONSTANTINIDIS D. 1968. — Beobachtungen zu den Neogen – Ablagerungen des Zentralgebietes der Insel Kreta. *Annales géologiques des Pays helléniques* 19: 657-688.

THIELE J. 1929. — *Handbuch der systematischen Weichtierkunde*, Gustav Fischer, Jena, 3761 p.

TUCKER J. K. & TENORIO M. J. 2009. — *Systematic Classification of Recent and Fossil Conoidean Gastropods*. Hackenheim, Conchbooks, 296 p.

VOKES H. E. & VOKES E. H. 1968. — Variation in the genus *Orthaulax* (Mollusca: Gastropoda). *Tulane Studies in Geology and Paleontology* 6 (2): 71-79.

ZACHARIASSE W. J., VAN HINSBERGEN D. J.J. & FORTUIN A. R. 2011. — Formation and fragmentation of a late Miocene supradetachment basin in central Crete: implications for exhumation mechanisms of high-pressure rocks in the Aegean forearc. *Basin Research* 23: 678-701. https://doi.org/10.1111/j.1365-2117.2011.00507.x

Submitted on 20 October 2019;
accepted on 24 April 2020;
published on 2 December 2021.