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Monograph

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Late Miocene Conidae (Mollusca: Gastropoda) of Crete (Greece). Part 2

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Abstract. Late Miocene Conidae of Crete (Greece) have recently been evaluated for the genera *Conilithes* and *Conus* (*Kalloconus*). We continue this first inventory of the Miocene Conidae from Crete by discussing the genera *Conus* (*Lautoconus*), *Conus* (*Stephanoconus*), *Conus* (*Plagioconus*) and two species, not attributed to a subgenus of *Conus*. With the use of UV light, we recognized 17 species, of which five are new: *Conus* (*Lautoconus*) *ictini* sp. nov., *Conus* (*Lautoconus*) *lauriatragei* sp. nov., *Conus* (*Lautoconus*) *damianakisi* sp. nov., *Conus* (*Stephanoconus*) *moissettei* sp. nov. and *Conus davolii* sp. nov. Six species are first reported in the Late Miocene of Greece: *Conus* (*Lautoconus*) cf. *baldichieri* Borson, 1820, *Conus* (*Stephanoconus*) cf. *taurinensis* Bellardi & Michelotti, 1841, *Conus fuscocingulatus* Hörnes 1851, *Conus* (*Plagioconus*) *elatus* Michelotti, 1847 and *Conus* (*Plagioconus*) *aquensis* d'Orbigny, 1852. Six species are left in open nomenclature.

Keywords. Crete Island, Late Miocene, Conidae, ultraviolet light, new species.

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Introduction

Conidae Fleming, 1822 snails are carnivorous gastropods that prey mainly on bristle worms (Polychaeta), while some species hunt other gastropods or fish (Olivera *et al.* 2015; Safavi-Hemami *et al.* 2015). Their rich biodiversity, reaching more than 900 extant species, inhabits a wide range of depths in subtropical and tropical seas (e.g., Kohn 2014; Monnier *et al*. 2018; Abalde *et al.* 2019). Their fossil record starts from the Early Eocene (Duda & Kohn 2005) and it has been suggested that they radiated multiple times in the past (Kohn 1990), with the greatest radiation event happening in the Neogene. There

is little information on the Miocene Conidae of Greece, with limited references (Symeonidis 1965; Symeonidis & Kostantinidis 1968; Dermitzakis 1969; Merle *et al.* 1988; Koskeridou 1997; Koskeridou *et al.* 2017; Thivaiou *et al.* 2019) where they have often been misidentified. The unclear diversity of the Conidae of Greece has been tackled by Psarras *et al.* (2021), who revised the genera *Conilithes* Swainson, 1840 and *Conus* (*Kalloconus*) da Motta, 1991, using UV light to reveal their colour patterns. The diversity of colour patterns is helpful to distinguish many living species and is important for the identification of fossil conids (e.g., Hendricks 2015; Psarras *et al.* 2021 for the Miocene of Crete). In this work, we continue the systematic revision of the Tortonian Conidae from Crete by showcasing the subgenera *Conus* (*Lautoconus*) Monterosato, 1923, *Conus* (*Stephanoconus*) Mörch, 1852 and *Conus* (*Plagioconus*) Tucker & Tenorio, 2009.

Geological background

Crete is located in the southern part of the Aegean, interpreted as a horst structure in the forearc of the Hellenic plate (Meulenkamp *et al*. 1979; Zachariasse *et al*. 2011). Due to normal faults in N–S and E–W directions formed, the Upper nappes are acting as the basement's footwall, while the Neogene deposits are acting as the hanging wall. The specimens were collected from the Heraklion and Messara Basins in Central Crete, and the Ierapetra Basin and Sitia Graben in Eastern Crete. The Heraklion and Messara Basins are surrounded by the Psiloritis Mountains to the North-West, the Asterousia Mountain range to the South and Dikti Mountains to the East. The two basins are divided by the E-W striking Central Heraklion Normal Fault (CHNF) that was active between 9.7 and 7.36 Ma (Zachariasse *et al.* 2011). In the Ierapetra Basin, the Neogene deposits are deposited unconformably above the pre-Neogene series (Ring *et al.* 2001). The Apostoli Basin was shallow with lacustrine, brackish and shallow marine deposits during the Tortonian (Drinia 1998). The localities mentioned in Psarras *et al*. (2021) are also discussed herein (Fig. 1).

The localities Tylissos and Keramoutsi (Fig. 1.1–2) are situated on the eastern side of Psiloritis mountains and contain deposited faces of sand, covered by Tortonian marls, with *Globorotalia miocenica mediterranea* Catalano & Sprovieri, 1969 (Delrieu 1990). Panassos (35.130° N, 24.986° E) is on the mountain range SE of Psiloritis (Fig. 1.3), presenting a Tortonian malacofauna (Delrieu 1990; Koskeridou 1997), Late Tortonian–Early Messinian, based on recent data (Frydas 2004). Some species were collected S-E of Apomarma Village, along the construction of the new road, in sections no

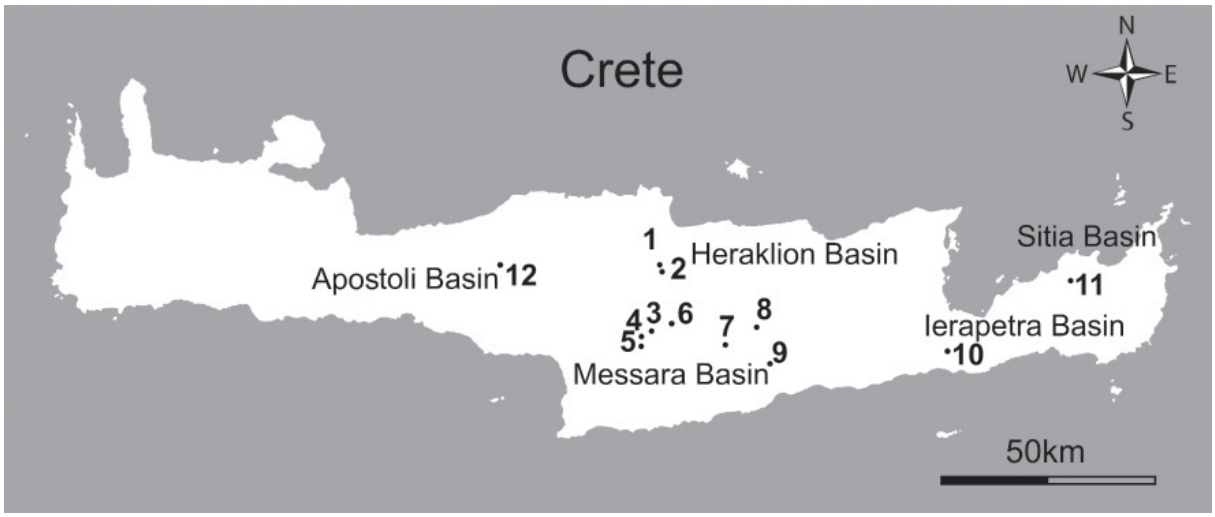

Fig. 1. General map Crete, showing the localities where the material was collected: 1 = Tylissos; 2 = Keramoutsi; 3 = Panassos; 4 = Apomarma; 5 = Psalidha; 6 = Adhraktia; 7 = Tefeli; 8 = Partira; 9 = Filippi; 10 = Makrilia; 11 = Achladhia; 12 = Voleones.

longer cropping out (Fig. 1.4). The area hosts a Tortonian fauna and is known in the literature under the name Aghia Irini (Delrieu 1990). The locality of Psalidha (35.085° N, 24.962° E; Fig. 1.5) hosts a rich Tortonian malacofauna associated with coral reefs (Symeonidis & Kostantinidis 1968; Delrieu 1990; Koskeridou 1997). Adhraktia (Fig. 1.6), a locality north of Panassos, and its Tortonian infralittoral assemblage have been studied by Delrieu (1990): Adhraktia-a. The area around Tefeli village (Fig. 1.7) hosts a rich shallow marine Tortonian malacofauna (Symeonidis & Kostantinidis 1968; Koskeridou 1997). The section at Partira (Fig. 1.8) points towards a Tortonian age, as the area is covered by the Tortonian deposits of the Kasteliana and Moulia Formations (Zachariasse *et al.* 2011). The succession cropping out at Filippi (35.035° N, 25.250° E; Fig. 1.9) contains a shallow marine Tortonian malacofauna (Symeonidis & Kostantinidis 1968) previously known for its richness in Conidae fossils (Psarras *et al.* 2021). In Makrilia (35.062° N, 25.722° E; Fig. 1.10) the lower to middle part of the section contains a Tortonian fauna (Dermitzakis 1969; Koskeridou 1997). The succession cropping out at Achladhia (Fig. 1.11) is characterised by a shallow marine Tortonian fauna (Koskeridou 1997; Marcopoulou-Diacantoni & Logos 2004). Voleones (Fig. 1.12) in the Apostoli Basin has been studied in the past by Symeonidis (1969), who dated the locality as Tortonian.

Material and methods

Material

We handpicked samples from four localities: Filippi, Panassos, Apomarma and Tefeli. For the other localities, we studied the historical collections of the National and Kapodistrian University of Athens (NKUA), and the Muséum national d'histoire naturelle, Paris, in particular the specimens collected during the 'Action spécifique du Muséum project' (1989–1990) on the Neogene of Crete. Most specimens from Partira and Tefeli were collected by one of us (E.K.). If the colour patterns of the fossil specimens are not clearly visible under UV light, the specimens can be bleached using sodium hypochlorite, so their patterns could be revealed (e.g., Caze *et al*. 2015). In this case, it was not necessary to bleach the specimens, as most of them already display a colour pattern under UV light.

Methods

Conidae from the Tortonian of Crete can be characterised by using a combination of morphological and colour pattern characteristics visible under UV light, as was observed on other well-preserved fossil gastropods (e.g., in older works: Olsson 1967; Vokes & Vokes 1968; Krueger 1974; Hoerle 1976, or recent works: Merle *et al.* 2008; Caze 2010; Caze *et al.* 2011a, 2011b, 2015; Landau *et al.* 2013; Hendricks 2015, 2018; Harzhauser & Landau 2016). When gastropods die, the pigments on the shell surface degrade, but don't totally disappear. By exposing the shells under ultraviolet light, their pigments become fluorescent, although their precise nature is most likely still unknown (Affenzeller *et al*. 2019). The contrast between fluorescent and non-fluorescent areas on the shell enhances the revelation of a residual colour pattern, almost similar to that of the shell surface, when the animal was alive. This method is very useful in the identification of the Cretan conids. Without disregarding the morphology of the shell, which is the primary characteristic for identification, the method of colour pattern identification is a useful addition to our 'researching artillery' that practically helps disentangle clusters of species which are conservative in shape (Marshall *et al.* 2002), but possess different colour pattern variations (Gong *et al.* 2012; Hendricks 2015). For the identification of species, we first studied specimens and subsequently grouped them into groups according to their morphology and colour pattern variations. Then, we did statistical analysis using Principal Component Analysis (PCA) graphs to verify our interpretations. By imputing measurements for each specimen, the program PAST computes the overall outline of each shell and groups specimens into a two-dimensional graph. The interpretation of such clusters usually displays species' morphological variation. The input of the data, here used, consists of different ratios of measurements concerning the length, diameter and the apertural height of each

shell. Despite some ratios having the same underlying measurements, the resulting graphs successfully display the differences between the group.

Photographs

We photographed with a CANON EOS-70D with an EFS 15–85mm image stabilizer ultrasonic lens, adding when necessary extra magnification 4 × lens. The figures were taken using decreased exposure levels (-2), in order to better capture the UV colours. Multiple photographs were taken at different focus points, which were then combined and blended into Photoshop. The UV photographs were taken under UV light with wavelength of 365 nm. The UV lights mostly used are two flashlights Convoy S2+, placed diagonally on both sides of the figured specimen. On both flashlights the original glass was replaced with a ZWB2 filter, which blocks any natural light emitted from the flashlight. The figures from MNHN were taken using two ATLAS MMT GmbH Fluotest Forte UV lamps, placed diagonally on both sides of the figured specimen. Also, we occasionally photographed specimens under a LEICA M165 C stereoscope, with a camera LEICA IC90 E.

Shell terminology

We follow the terminology of Smith (1930), Röckel *et al.* (1995) and Hendricks (2009), for the description of the shell's dimensions. The shell lengths are considered: large (> 80 mm), moderately large (55–80 mm), medium-sized (35–55 mm), moderately small (25–35 mm), small (15–25 mm) and very small (< 15 mm). For the subsutural flexure measurements, we used Harzhauser & Landau (2016), following their 45°-angled measurement style in order to compare the Cretan material with the Paratethys material. The identification of species has been done by using as many characteristics as possible, therefore all measurements are equally important. The subsutural flexure, even though it is variable at the intraspecific level and even differs in individuals, is an equally important tool for the description of a species. For the systematic arrangement we follow Puillandre *et al.* (2014, 2015) and refer to *Lautoconus*, *Stephanoconus* and *Plagioconus* as subgenera, as in Psarras *et al.* (2021). The colour patterns which show two to four different colours are called, according to Meinhardt (1998), "levels of pigmentation".

Measurements

We follow the terminology of Smith (1930), Röckel *et al*. (1995) and Hendricks (2009), and Harzhauser & Landau (2016). The measurements were taken from individual shells for comparison with other fossil Conidae from Europe. For the ratios we follow Harzhauser & Landau (2016), which we use for the PCA graphs.

Abbreviations

AH = apertural height
AL = apertural length
HMD = height of maximum diameter
LW = length-width ratio
LWA = last whorl angle
MD = maximum diameter
PMD = position of maximum diameter (HMD/AH)
PV = position of the vertex
RD = relative diameter (MD/AH)
RSH = relative height of the spire {(SL-AH)/SL}
SA = spire angle
SL = shell length
SSFD = subsutural flexure depth
SSFd = subsutural flexure relative depth

The measurements of the studied specimens can be found in the Supplementary file 1.

Repositories

AMPG (IV)	=	Catalogue numbering of the Paleontology and Geology Museum of the National and Kapodistrian University of Athens, Greece
HNHM	=	Hungarian Natural History Museum, Budapest, Hungary
MHNG	=	Muséum d'histoire Naturelle de la Ville de Genève, Switzerland
MNHN.F	=	Muséum national d'Histoire naturelle, Paris, collection de paléontologie, France
MOD	=	Museo Paleontologico dell 'Universita di Modena, Polo Museale dell'Università degli Studi di Modena e Reggio Emilia, Italy
MRSN	=	Museo Regionale di Scienze Naturali, Turin, Italy
MSNM	=	Museo di Storia Naturale di Milano, Italy
MTA	=	Maden Tetkik ve Arama (The Mineral Research and Exploration General Directorate History of Nature Museum), Ankara, Turkey
NHMW	=	Naturhistorisches Museum Wien, Austria
NKUA	=	National and Kapodistrian University of Athens, Greece

Results

Systematic palaeontology

Class Gastropoda Cuvier, 1795
Subclass Caenogastropoda Cox, 1960
Order Neogastropoda Wenz, 1938
Superfamily Conoidea Fleming, 1822
Family Conidae Fleming, 1822

Genus ***Conus*** (Linnaeus, 1758)

Type species

Conus marmoreus Linnaeus, 1758 (Recent: Indo-Pacific) by subsequent designation, Winckworth (1945: 139).

Subgenus ***Conus* (*Lautoconus*)** Monterosato, 1923

Type species

Conus mediterraneus Hwass in Bruguière, 1792 (Recent, Mediterranean Sea) by original designation.

Diagnosis

Moderately small to moderately large, turnip-shaped species. Medium-wide to wide shells and convex sides. Spire low to moderately high. Paucispiral protoconch. Early whorls ornamented with cords, which might persist on later spire whorls or appear as spiral threads. Subsutural flexure from very shallow to deep, usually moderately curved, moderately asymmetrical. colour pattern variable, displaying blotches, spiral rows of dots, dashes, and tents in multiple combinations.

Remarks

Puillandre *et al.* (2014, 2015) treated *Lautoconus* at the subgenus level. In this work we show two species that are large-sized (*Conus* (*Lautoconus*) *damianakisi* sp. nov. and *Conus* (*Lautoconus*) *lauriatragei* sp. nov.). The species of the subgenus display an intraspecific morphological variability, as it is here shown for more than one species. The colour patterns are also variable, displaying patterns such as blotches, spiral rows of dots, dashes and tents in multiple combinations (see Monnier *et al*. 2018). We

follow Harzhauser & Landau (2016) in excluding from this subgenus the species with tuberculate spire whorls. The oldest occurrence in Greece is reported from the early Miocene (Thivaiou *et al*. 2019) by an incomplete specimen (AMPG(IV) 2473). However, the attribution to *Lautoconus* seems doubtful and this specimen could possibly belong to *Conus* (*Eoconus*) Tucker & Tenorio, 2009 (see more in Tracey *et al*. 2017).

Conus* (*Lautoconus*) *eschewegi Pereira da Costa, 1866
Figs 2–3, 20, 40A; Table 1

Conus Eschewegi Pereira da Costa, 1866: 29, pl. 9 figs 18, 19a–b, 21, 23a–b (non figs 20, 22, 34).
Chelyconus taurorectus Sacco, 1893b: 67, pl. 6 fig. 35. **Syn. nov**.
Lautoconus quaqqaoides Harzhauser & Landau, 2016: 88–89, figs 17d, 20e–j. **Syn. nov**.

Conus (*Dendroconus*) *subraristriatus* – Hoernes & Auinger 1879: 23 (partim), pl. 1 fig. 20 (non *Conus* (*Lautoconus*) *subraristriatus* Pereira da Costa, 1866).
[Conus] D.[endroconus] Eschewegi var. *caelata* – Sacco 1893a: 13, pl. 1 fig. 24.
[Conus] D.[endroconus] Eschewegi var. *depressoastensis* – Sacco 1893a: 13, pl. 1 fig. 25.
Dendroconus pyruloides – Sacco 1893a: 13, pl. 1 fig. 26. — Ferrero-Mortara *et al.* 1984: 102, pl. 15 figs 9a–b, pl. 16 figs 7a–b.
Chelyconus deshayesi var. *mioantiqua* – Sacco 1893b: pl. 7 fig. 18. (non *Conus deshayesi* Bellardi & Michelotti, 1841).
Chelyconus taurorectus – Ferrero-Mortara *et al.* 1984: 117, pl. 8 fig. 4.
Conus taurorectus – Hall 1966: 161, pl. 20 figs 8, 13.
Conus (*Chelyconus*) *enzesfeldensis* – Symeonidis & Konstantinidis 1968: 671, pl. 7 fig. 17 (non *Conus* (*Lautoconus*) *enzesfeldensis* Hoernes & Auinger, 1879).
Conus eschewegi – Davoli 1972: 107, pl. 6 figs 1–16. — Muñiz Solís 1999: 73, fig. 9c–e.
Chelyconus rotundus – Kovács & Vicián 2013: 61, fig. 16 (non *Conus* (*Lautoconus*) *rotundus* Hoernes & Auinger, 1879).
Lautoconus belus – Kovács & Vicián 2013: 68, figs 4, 53–55 (non *Conus* (*Lautoconus*) *belus* d'Orbigny, 1852).
Lautoconus eschewegi – Kovács & Vicián 2013: 70, fig. 7.
Lautoconus pyrula – Kovács & Vicián 2013: 71, figs 7, 62–65 (non *Conus* (*Lautoconus*) *pyrula* Brocchi, 1814).
Varioconus pelagicus – Landau *et al.* 2013: 247–248, pl. 82 fig. 1a–b.

non *Lautoconus eschewegi* – Kovács & Vicián 2013: figs 56–61 (misidentification).
non *Conus* (*Lautoconus*) *eschewegi* – Harzhauser & Landau 2016: 76–77, figs 3v, 16a1–a2, 16b1–b3, 16c1–c2, 16d1–d2 (misidentification).

Type locality

Cacela Basin, Portugal (Tortonian).

Type material

Specimen illustrated by Pereira da Costa (1866: pl. 9 fig. 23a–b), selected as "lectotype" proposed by Sacco (1893a) [*perciò la specie del Da Costa si doveva o abolire o restringere in limiti più definiti, come io credetti di fare ponendone a tipo la fig. 23*]. Collection whereabouts are unknown (Harzhauser & Landau 2016).

Material examined

GREECE – **Crete** • 5 specs; Filippi; 35.035° N, 25.250° E; Efterpi Koskeridou leg.; AMPG(IV) 3694 to AMPG(IV) 3698 • 5 specs; Filippi; 35.035° N, 25.250° E; Nikolaos Symeonidis leg.; AMPG(IV) 3701 to AMPG(IV) 3705 • 2 specs; Filippi; 35.035° N, 25.250° E; 2017; Christos Psarras leg.; AMPG(IV) 3706 to AMPG(IV) 3707 • 2 specs; Achladhia; 1964; Nikolaos Symeonidis leg.; AMPG(IV) 3699 to AMPG(IV) 3700 • 2 specs; Partira; AMPG(IV) 3708 to AMPG(IV) 3709 • 5 specs; Tefeli; Efterpi Koskeridou leg.; AMPG(IV) 3710 to AMPG(IV) 3714 • 8 specs; 1990; Action spécifique du Muséum project (1989–1990) exped.; MNHN.F.A82973 to MNHN.F.A82980 • 1 spec.; Adhraktia; 1990; Action spécifique du Muséum project (1989–1990) exped.; MNHN.F.A82981.

Shell description

Small-medium-sized (SL: 39.57 mm) and elongated shell, with straight to cyrtoconoid spire outline. Spire convex, conical of variable height, ranging from nearly flat to low conical. Early spire whorls straight, striated. Late spire whorls convex, with impressed suture. Subsutural flexure very shallow, weakly curved, moderately asymmetrical (Fig. 40A). Shoulder rounded, with maximum diameter varying in position, from near shoulder to one fourth posterior part of last whorl. Last whorl slightly inflated. Aperture straight to slightly curved, widening considerably towards fasciole. Siphonal canal wide, straight. Fasciole twisted, slightly inflated in larger specimens. Spiral cords present along the anterior part of last whorl.

Description of colour pattern

The colour pattern on spire whorls consists of periodical, irregularly shaped dashes, sometimes parallel to the direction of shell growth. The colour pattern on the rest of the shell consists of spiral rows of fluorescent dashes, demarcated by non-fluorescent areas. Faintly fluorescent blotches appearing sporadically in some shells, surrounding the dashes and connecting axially arranged spiral dashes. Axially arranged spiral dashes tending to form vertical, diagonal, or zigzag axial formations (Fig. 3). Occasionally, a hint of a non-fluorescent band on middle whorl height, engulfing a spiral line of short dashes (seen clearly on Fig. 2E).

Remarks

The Cretan specimens differ from the other species of *Conus* (*Lautoconus*) herein, in the relatively slender morphology (Table 1), the low angled spire and the exquisite colour pattern of delicate spiral rows of dashes. We argue that the morphological variability recorded in the studied material is likely due to the different overall shape during development, with larger specimens having a more robust outline. Small specimens which are more elongated, could be interpreted as *Lautoconus pyruloides* (Sacco, 1893a) (Ferrero Mortara *et al.* 1984: pl. 15 fig. 9, pl. 16 fig. 7), but past researchers assigned them to *Conus* (*Lautoconus*) *eschewegi* (Hall 1966; Davoli 1972). In Greece, specimens studied by Symeonidis & Konstantinidis (1968) were assigned to *Conus enzesfeldensis* Hoernes & Auinger, 1879, a species considered a junior synonym of *Conus* (*Lautoconus*) *subraristriatus* Pereira da Costa, 1866. It is easily differentiated from the Cretan specimens, both in the morphology of its narrower shoulder and the different colour pattern of the widely spaced, continuous, narrow, spiral rows of dots and dashes (e.g., Harzhauser & Landau 2016). Harzhauser & Landau (2016) regarded Spanish Pliocene specimens described from Estepona (Muniz Solís, 1999) as *Conus* (*Lautoconus*) *eschewegi* Pereira da Costa, 1866. We disagree on that statement because Muñiz Solís' specimen (Muñiz Solís 1999: fig. 9c–e) and the Cretan specimens (Fig. 2F–G) have very similar morphologies. Harzhauser & Landau (2016) mentioned that Pereira da Costa had a "much too broad species concept". We disagree with that statement as well, because in the Cretan specimens there is also a spectrum of variability in morphology, with smooth to slightly angulated shoulder, flat to inflated spire whorls and a conical to concave spire. This variation

has also been shown in specimens of Davoli (1972: pl. 6 figs 1–16), indicating a wide morphological variation for this species.

Furthermore, in Davoli (1972: pl. 6 figs 1a–b, 11) the colour pattern is figured as spirally arranged, elongated dashes. Kovács & Vicián (2013) reported three species, *Lautoconus eschewegi* (Pereira da Costa, 1866), *Lautoconus belus* (d'Orbigny, 1852) and *Lautoconus pyrula* (Brocchi, 1814), from the middle Miocene of the Paratethys at Letkés (Hungary). These specimens are in fact conspecific (Harzhauser & Landau 2016). Additionally, they have a colour pattern variation of densely arranged rows of equally spaced, densely packed, short dashes (Kovács & Vicián 2013: figs 55–58, 62–65), a pattern different from the Cretan specimens and Davoli's (1972). Harzhauser & Landau (2016) identified

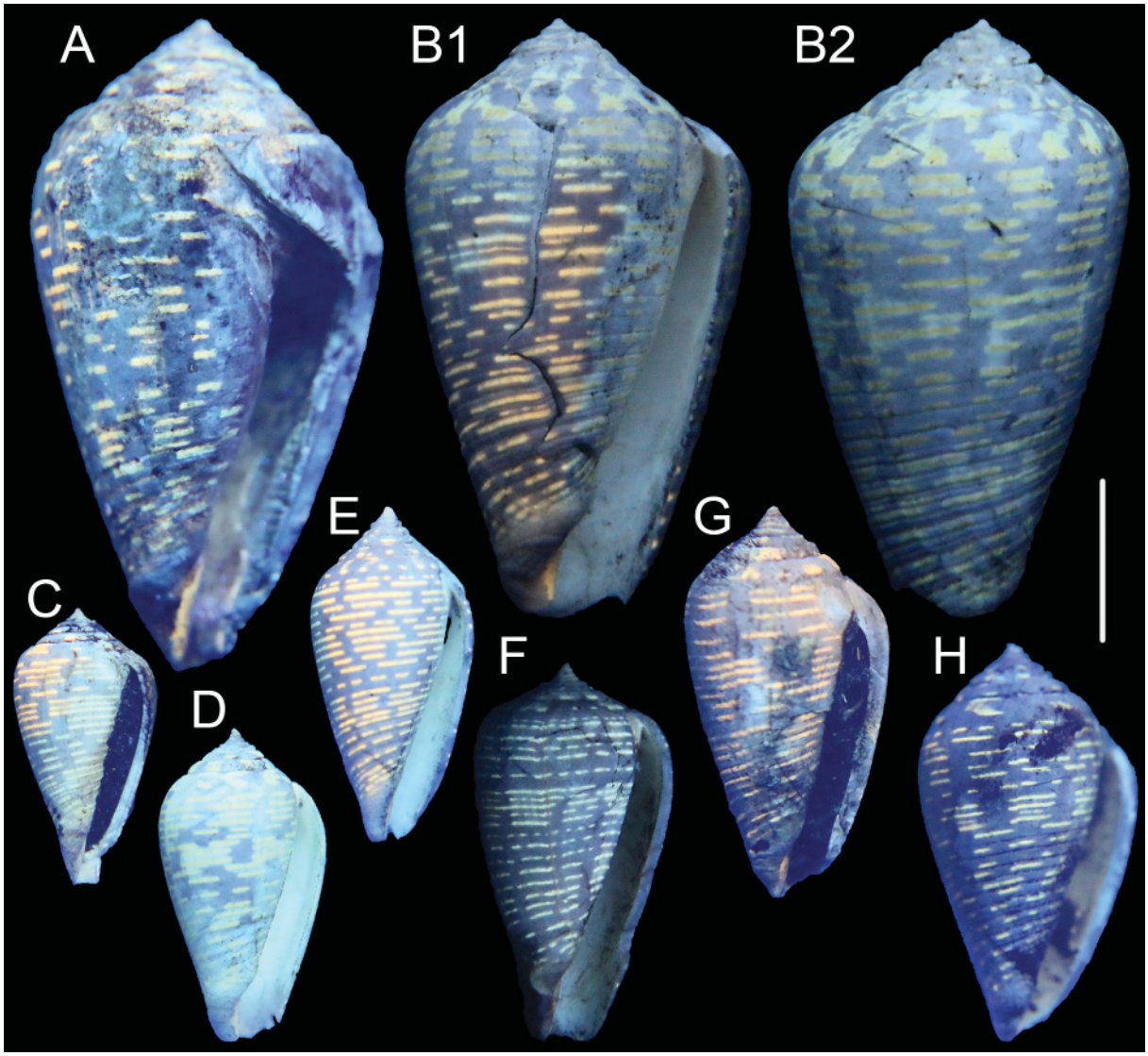

Fig. 2. *Conus* (*Lautoconus*) *eschewegi* Pereira da Costa, 1866 from the Tortonian of Crete (Greece) on apertural and abapertural views, under UV light, displaying morphological and colour pattern variations. **A**. Specimen MNHN.F.A82973, Crete. **B**. Specimen MNHN.F.A82974, Crete. **C**. Specimen AMPG(IV) 3702, Filippi. **D**. Specimen MNHN.F.A82980, Crete. **E**. Specimen MNHN.F.A82981. **F**. Specimen MNHN.FA82978, Crete. **G**. Specimen AMPG(IV) 3711, Tefeli. **H**. Specimen AMPG(IV) 3706, Filippi. Scale bar = 1 cm.

Table 1. Shell measurements and ratios of *Conus* (*Lautoconus*) *eschewegi* Pereira da Costa, 1866 from the Tortonian of Crete (Greece). Mean and standard deviation are computed from 31 specimens. The largest specimen is MNHN.F.A82973.

	SL	MD	AH	HMD	AL	SA	LWA
Largest specimen	39.57 mm	21.26 mm	32.91 mm	27.68 mm	33.22 mm	97.7°	38.9°
Mean	26.96 mm	16.26 mm	23.37 mm	19.23 mm	23.41 mm	106.7°	37.9°
Standard deviation	6.76	4.79	5.96	4.95	6.07	11.63	5.68
	LW	**RD**	**PMD**	**RSH**	**SSFD**	**SSFd**	**PV**
Largest specimen	1.86	0.65	0.84	0.17			
Mean	1.73	0.67	0.86	0.13	4.97	11.8	0.6
Standard deviation	0.17	0.07	0.08	0.03	1.27	3.33	0.24

those specimens as *Lautoconus eschewegi* (Pereira da Costa, 1866), but we consider the specimens in Kovács & Vicián (2013) as well as those of Harzhauser & Landau (2016: fig. 16c–d) to belong to another species, with a similar morphology as *Conus* (*Lautoconus*) *eschewegi* but with different colour pattern variations.

Hall (1966: pl. 20 figs 8, 13) mentioned *Conus* (*Lautoconus*) *taurorectus* Sacco, 1893b, a specimen from the collection of Sacco as *Conus deshayesi* var. *mioantiqua* (figured in Sacco 1893b: pl. 7 fig. 18), which shows a similar RD (≈ 0.74) (measured directly from Hall's figure 1966: pl. 20 fig. 13) and a similarly faint colour pattern to *Conus* (*Lautoconus*) *eschewegi*. We consider that specimen as a large-sized *Conus* (*Lautoconus*) *eschewegi*. Therefore, the lectotype figured by Hall (1966) and Ferrero Mortara (1984) (fixation of the lectotype (MRSN BS.038.05.052, Sacco coll.) by inference of 'holotype' (ICZN 1999: Art. 74.6) by Hall (1966: 161) is considered a junior synonym of *Conus* (*Lautoconus*) *eschewegi.*

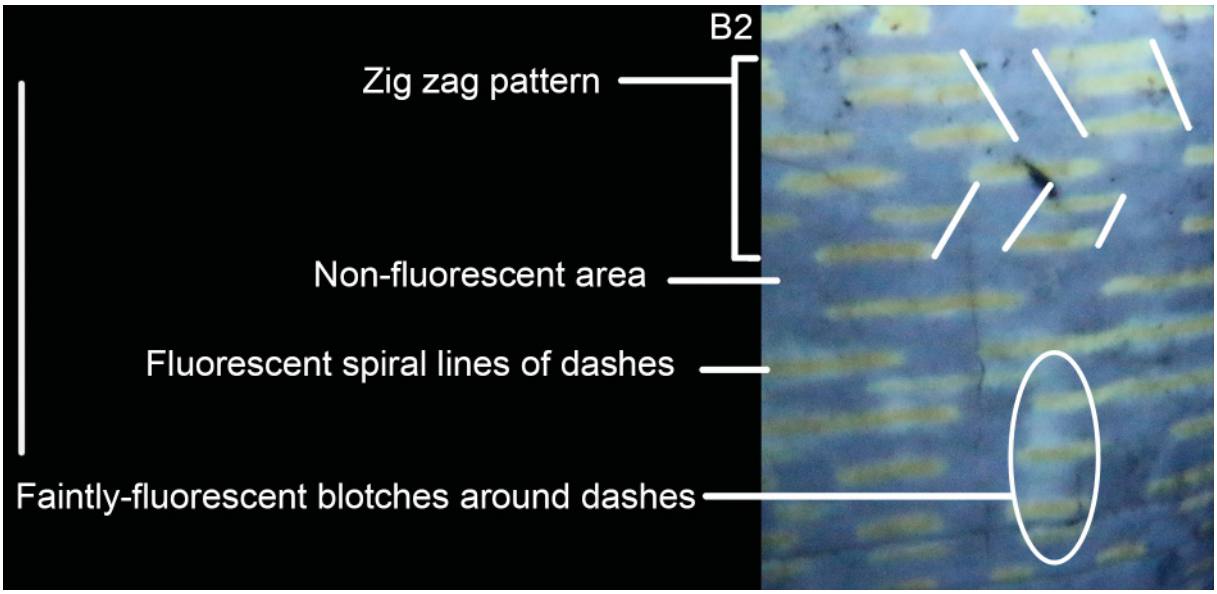

Fig. 3. Elements constituting the colour pattern of *Conus* (*Lautoconus*) *eschewegi* Pereira da Costa, 1866 (MNHN.F.A82974) from the Tortonian of Crete (Greece). Scale bar = 1 cm.

This species is related to *Conus* (*Lautoconus*) *quaqqaoides* Harzhauser & Landau, 2016, as both display similar colour patterns and an overall shell outline. The zig-zag patterns described (Harzhauser & Landau 2016: fig. 20h–j) are visible on some Cretan shells as well. The Greek specimens differ in the relatively higher spire whorls, a more inflated last whorl, straight aperture, as well as a shallower and less curved subsutural flexure. These differences, however, are minor and could be interpreted as different morphotypes of one species. Davoli's figures show a morphotype of *Conus* (*Lautoconus*) *eschewegi*, which is very similar to that of *Conus* (*Lautoconus*) *quaqqaoides* (Davoli 1972: pl. 5 figs 13, 16). Since both morphs are similar and present in Davoli's work (1972), we consider *Conus* (*Lautoconus*) *quaqqaoides* Harzhauser & Landau, 2016 as a junior synonym of *Conus* (*Lautoconus*) *eschewegi.* Landau *et al.* (2013: pl. 82 fig. 1) named a specimen as *Lautoconus pelagicus* (Brocchi, 1814), which is identical to the Cretan specimens. Additionally, the colour pattern of the Paratethyan *Conus* (*Lautoconus*) *pelagicus* described by Harzhauser & Landau (2016) is much different from that of the Turkish specimen of Landau *et al*. (2013). For this reason, we consider that Landau *et al.*'s specimen (2013) is not conspecific with the Paratethyan *Conus* (*Lautoconus*) *pelagicus* and most likely belongs to *Conus* (*Lautoconus*) *eschewegi*. The Mediterranean *Conus* (*Lautoconus*) *pelagicus* possibly possesses a similar colour pattern as *Conus* (*Lautoconus*) *eschewegi*, as inferred by the specimen of *Chelyconus pelagicus* var. *astensinflata* Sacco, 1893b, which shows a dashed pattern and no zonation (MRSN BS03805143, Annalaura Pistarino pers. comm.). More work needs to be done on the Italian Conidae using UV light to clarify the confusion. The Messinian fragment of Davoli (2003), named as *Conus eschewegi*, needs verification under UV light as it could belong to a different species.

Conus (*Lautoconus*) *steindachneri* Hoernes, 1879 is also a species similar to the Cretan specimens. Harzhauser & Landau (2016) described a colour pattern of spiral lines or long spiral dashes, very similar to the studied material. Furthermore, some of the adult Cretan specimens (Fig. 2B) show a similarity in morphology, but *Conus* (*Lautoconus*) *steindachneri* has a relatively wider shoulder width (*Conus* (*Lautoconus*) *steindachneri* RD = 0.72; Harzhauser & Landau 2016) and a deeper, strongly asymmetrical subsutural flexure. The Hungarian *Conus* (*Lautoconus*) *steindachneri* from Kovács & Balázs (2015: figs 91–92) are not similar to the Cretan specimens, as they have a very wide and slightly angulated shoulder.

The Pliocene *Conus deshayesi* Bellardi & Michelotti, 1841 has a similar morphology, but the colour pattern illustrated in Bellardi & Michelotti (1841) consists of densely spaced spiral rows of dashes, unlike the studied specimens.

Stratigraphic range

Burdigalian of Italy (Hall 1966); Langhian of Paratethys (Pannonian Basin) (Kovács & Vicián 2013; Harzhauser & Landau 2016); Serravalian of Turkey (Karaman Basin) (Landau *et al.* 2013); Tortonian of Portugal (Cacela Velha) (Pereira da Costa 1866), Italy (Po Basin) (Sacco 1893a; Davoli 1972) and Greece (Messara Basin) (Symeonidis & Kostantinidis 1968; this work); Pliocene of Spain (Estepona) (Muñiz Solís 1999). Reports from the Messinian (Davoli 2003) and Pliocene (Davoli 1972) of the Mediterranean are in need of confirmation.

Conus* (*Lautoconus*) *ictini sp. nov.
urn:lsid:zoobank.org:act:AF2A4A6E-63F0-4FC1-AE80-1C94537E2E4A
Figs 4–5, 20, 40B; Table 2

Conus (*Varioconus*) *pelagicus* – Landau *et al.* 2013: pl. 82 fig. 2a–b (non *Conus* (*Lautoconus*) *pelagicus* Brocchi, 1814).

Diagnosis

A species with smooth, low angled, conical spire whorls and bricked-wall-like colour pattern.

Etymology

Name taken after Ictinus (Latin translation of the ancient Greek Ἰκτῖνος), one of the two architects of the Parthenon.

Material examined

Holotype

GREECE – **Crete** • Tefeli; Messara Basin, Tortonian; Efterpi Koskeridou leg.; AMPG(IV) 3719.

Paratypes

GREECE – **Crete** • 1 spec.; same collection data as for holotype; AMPG(IV) 3720 • 1 spec.; same collection data as for holotype; AMPG(IV) 3718.

Other material

GREECE – **Crete** • 1 spec.; Filippi; 35.035° N, 25.250° E; 2017; Christos Psarras leg.; AMPG(IV) 3717 • 2 specs; Achladhia; 1964; Nikolaos Symeonidis leg.; AMPG(IV) 3715 to AMPG(IV) 3716.

Shell description

Moderately small to medium-sized (H. max: 42.68 mm), oval to olive-like shells, with smooth spire whorls. Spire conical, smooth, slightly elevated in some specimens. Early spire whorls coeloconoid in outline, individual sutural ramps straight to slightly convex. Late spire whorls convex, with straight outline. Suture incised. Subsutural flexure shallow, moderately curved, moderately asymmetrical (Fig. 40B). Shoulder rounded to slightly angulated. Maximum diameter right below shoulder. Last whorl elongated, smooth. Spiral cords on anterior part of last whorl. Fasciole twisted distinct, swollen.

Description of colour pattern

The residual colour of the last whorls consists of three levels of colouration. The first vivid colouration is made up of horizontally arranged, densely packed, evenly spaced, continuous spiral lines (Fig. 5) and vertical to diagonal, narrow, short lines that connect the spiral lines, creating a bricked-wall-like pattern (Fig. 5). This pattern is faded in many parts of the shell (Fig. 4B). Under natural light, though, the colour pattern is visible even without the help of UV light on the holotype as parallel, closely arranged lines (Fig. 4A1, A3). A second level of colour consists of fluorescent blotches on the last whorl and irregular flammulae on the spire whorls. The fluorescent blotches are often filling the rectangular areas between the spiral lines of the first level of colour (Fig. 4C–D). The third level consists of a non-fluorescent pattern bearing irregular blotches that overlaps the other patterns (Fig. 5).

Remarks

Morphologically (Table 2), this species is very similar to *Conus* (*Lautoconus*) *pelagicus* Brocchi, 1814. It differs slightly in the smoother spire whorls and a more inflated appearance (Fig. 4). The occurrence of this morphotype, at multiple localities and ages (Serravallian, Turkey (Landau *et al.* 2013) and Tortonian, Greece (this work)), is evidence for the existence of a separate species. *Conus* (*Lautoconus*) *ictini* sp. nov. has a distinct brick-like colour pattern, making it possible to distinguish it safely from other species under UV light. *Conus* (*Lautoconus*) *eschewegi* (Landau *et al.* 2013: pl. 82 fig. 1a–b, see Remarks above) displays multiple spiral dots and dashes, while *Conus* (*Lautoconus*) *ictini* sp. nov.

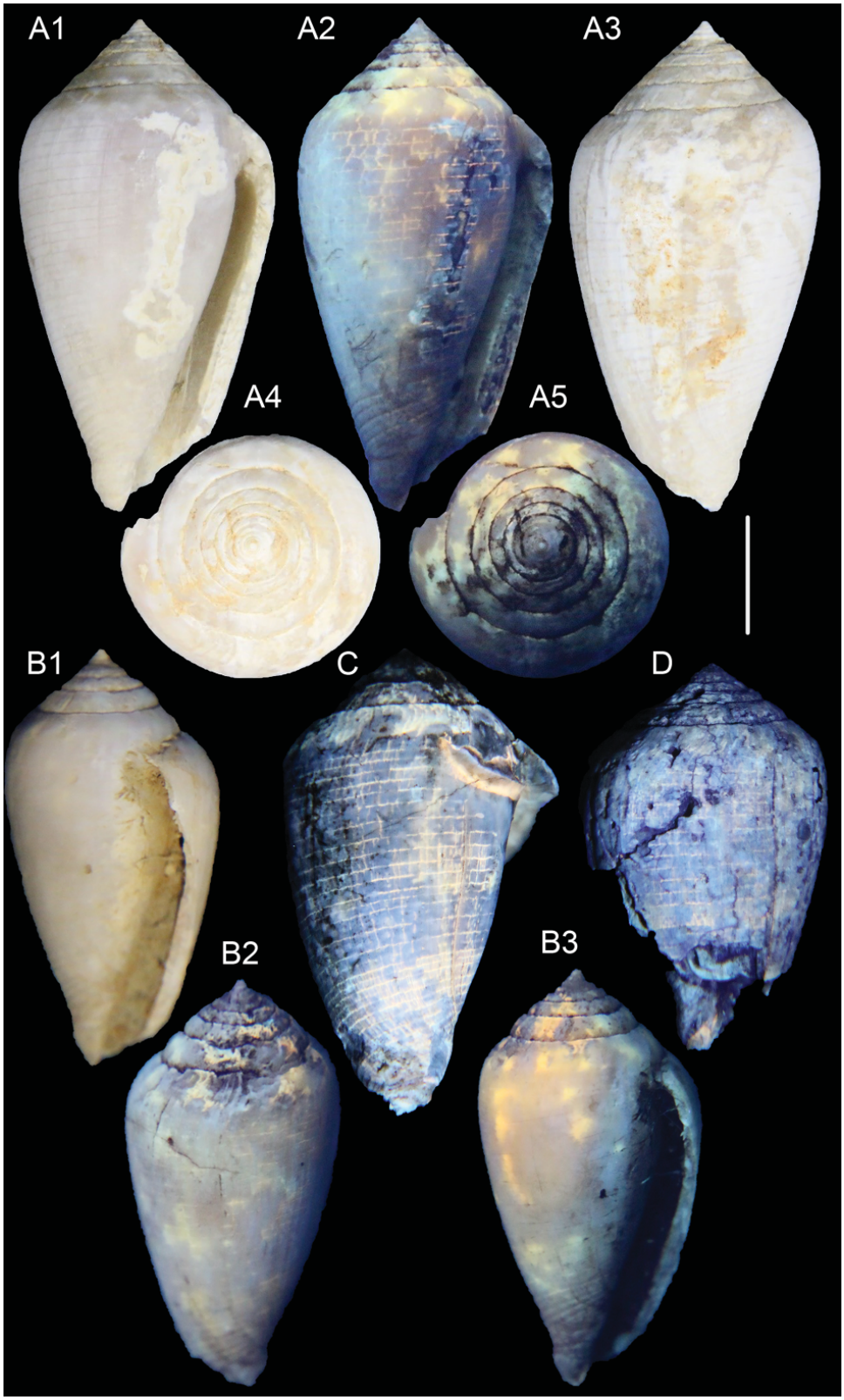

Fig. 4. *Conus* (*Lautoconus*) *ictini* sp. nov. from the Tortonian of Crete (Greece) on apertural, abapertural and apical views, under natural (A1, A3, A4, B1) and UV light. **A**. Holotype AMPG(IV) 3719, Tefeli. **B**. Paratype AMPG(IV) 3720, Tefeli. **C**. Paratype AMPG(IV) 3718, Tefeli. **D**. Specimen AMPG(IV) 3716, Achladhia. Scale bar = 1 cm.

Table 2. Shell measurements and ratios of seven specimens of *Conus* (*Lautoconus*) *ictini* sp. nov. from the Tortonian of Crete (Greece). The largest specimen is AMPG(IV) 3715.

	SL	**MD**	**AH**	**HMD**	**AL**	**SA**	**LWA**
Largest specimen	42.68 mm	23.22 mm	36.46 mm	28.53 mm	36.28 mm	95.4°	34°
Mean	40.53 mm	21.29 mm	33.86 mm	26.69 mm	34.09 mm	98.87°	34.47°
Standard deviation	1.87	2.40	2.27	1.77	1.90	9.41	1.84
	LW	**RD**	**PMD**	**RSH**	**SSFD**	**SSFd**	**PV**
Largest specimen	1.84	0.64	0.78	0.15	–	–	–
Mean	1.81	0.67	0.79	0.17	3.06	4.88	0.56
Standard deviation	0.14	0.07	0.03	0.02	1.19	0.18	0.25

bears multiple continuous spiral lines and vertical brick-like patterns. The colour pattern of *Conus* (*Lautoconus*) *ictini* sp. nov. is very similar to that of the extant *Conus* (*Quasiconus*) *melvilli* Sowerby, 1879, a species inhabiting the Arabian Peninsula (Moolenbeek & Coomans 1993).

Stratigraphic range

Serravallian of Turkey (Karaman Basin) (Landau *et al.* 2013) and Tortonian of Greece (Achladhia, Sitia Basin and Messara Basin, Crete).

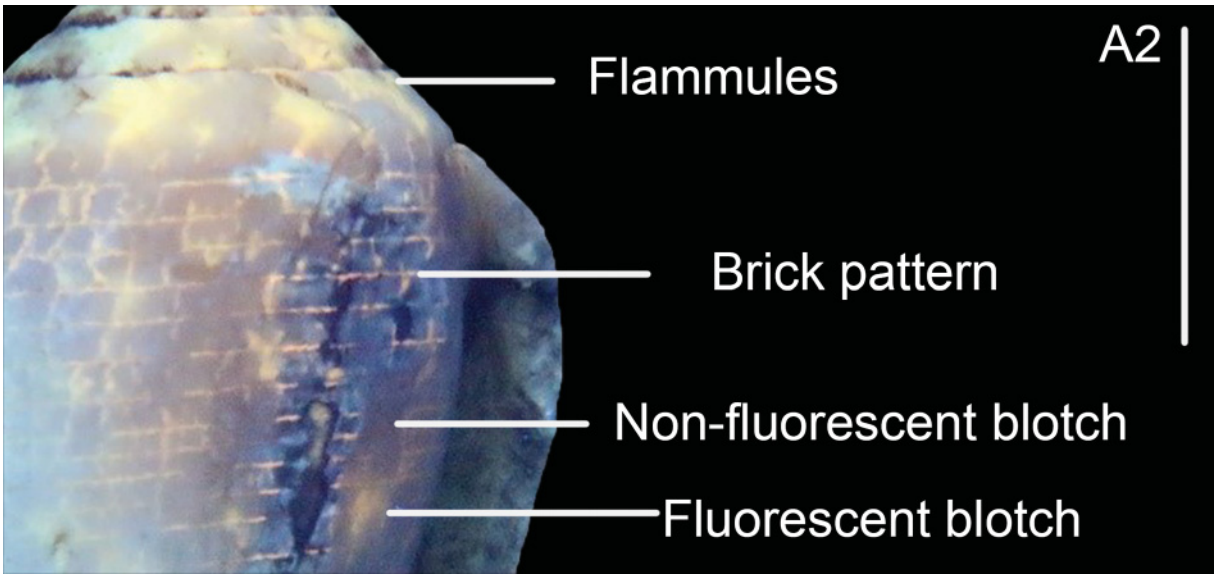

Fig. 5. Elements constituting the colour pattern of *Conus* (*Lautoconus*) *ictini* sp. nov, holotype AMPG(IV) 3719 from Tefeli Crete (Greece). Notice the axially arranged lines that connect the spiral lines. Scale bar = 1 cm.

***Conus* (*Lautoconus*)** sp. 1
Figs 6, 20, 40C; Table 3

Material examined

GREECE – **Crete** • 1 spec.; 1990; Action spécifique du Muséum project (1989–1990) exped.; MNHN.F.A82982.

Shell description

Medium-sized shell (SL: 35 mm, base broken) with low conical spire. Spire whorl outline conical. Early spire whorls conical, worn out. Later spire whorls conical, straight, slightly convex. Shoulder

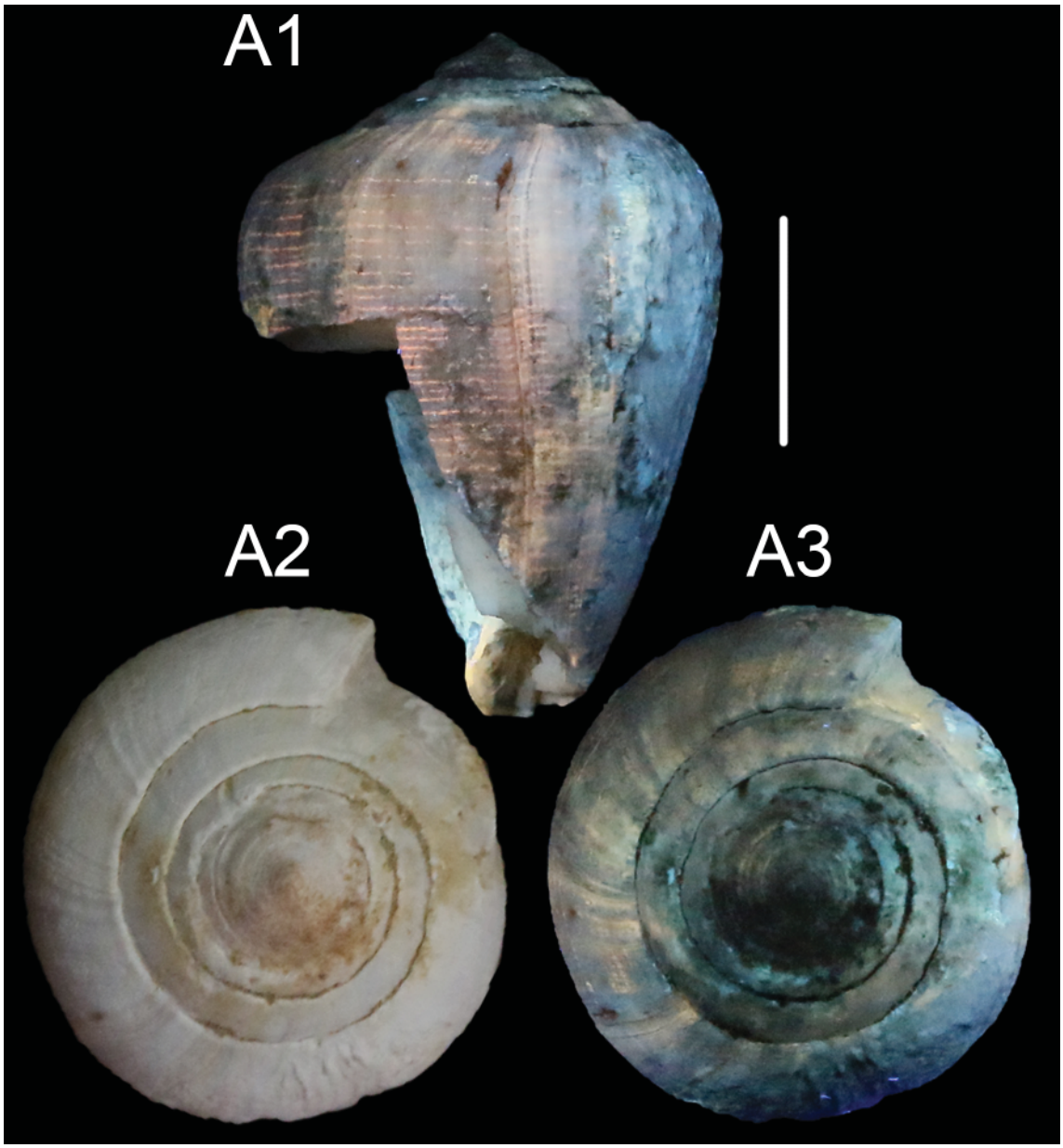

Fig. 6. *Conus* (*Lautoconus*) sp. 1 from the Tortonian of Crete (Greece), specimen MNHN.F.A82982, in abapertural and apical views, under natural (A2) and UV light. Scale bar = 1 cm.

Table 3. Shell measurements of one broken specimen of *Conus* (*Lautoconus*) sp. 1 (MNHN.F.A82982) from the Tortonian of Crete (Greece).

	SL	MD	AH	HMD	AL	SA	LWA
Largest specimen	–	23.06 mm	–	–	–	116.5°	35°
	LW	**RD**	**PMD**	**RSH**	**SSFD**	**SSFd**	**PV**
Largest specimen	–	–	–	–	3.86	9.33	0.75

smooth, with maximum diameter below shoulder. Suture channeled. Subsutural flexure very shallow, very weakly curved, nearly symmetrical (Fig. 40C).

Description of colour pattern

The colour pattern consists of closely related, delicate, elongated, wavy spiral rows of dashes. On the spires, the pattern consists of very thin axial flammulae, closely related to each other. The flammulae are vaguely connected with a spiral band, at the center of the sutural ramp.

Remarks

This species is very similar in morphology (Table 3) to *Conus* (*Lautoconus*) *ictini* sp. nov. It differs in the wider shoulder and the relatively lower conical spire outline. It can also be distinguished by its relatively shallower subsutural flexure relative depth (SSFd = 4.88 in *Conus* (*Lautoconus*) *ictini* sp. nov.). Moreover, it displays a very different colour pattern from the brick-like pattern of *Conus* (*Lautoconus*) *ictini* sp. nov. (Fig. 6). Another species with a similar colour pattern on the last whorl is *Conus* (*Leporiconus*) *suessi* Hoernes & Auinger, 1879 (see Harzhauser & Landau 2016), but *Conus* (*Lautoconus*) sp. 1 does not possess striate spire whorls. Therefore, it does not match the description of *Conus* (*Leporiconus*) *suessi*.

Stratigraphic range

Upper Tortonian Crete, Greece.

***Conus* (*Lautoconus*)** sp. 2
Figs 7–9, 20, 40D; Table 4

Conus (*Rhizoconus*) *ponderosus ponderosus* – Symeonidis 1965: pl. 63 figs 4, 4a. — Symeonidis & Konstantinidis 1968: pl. 80 figs 2, 2a. (AMPG(IV) 2768) (non *Conus* (*Lautoconus*) *ponderosus* (Brocchi, 1814)).

Material examined

GREECE – **Crete** • 1 spec.; Filippi; Messara Basin, Tortonian; 35.035° N, 25.250° E; 1964; Nikolaos Symeonidis leg.; AMPG(IV) 2768 • 41 specs; Achladhia; 1964; Nikolaos Symeonidis leg.; AMPG(IV) 3721 to AMPG(IV) 3761 • 29 specs; 1990; Action spécifique du Muséum project (1989–1990) exped.; MNHN.F.A82983 to MNHN.F.A83011 • 1 spec.; Filippi; AMPG(IV) 3762 • 6 specs; Filippi; Efterpi Koskeridou leg.; AMPG(IV) 3763 to AMPG(IV) 3768 • 1 spec.; Filippi; AMPG(IV) 3769 • 17 specs; Filippi; 2017; Christos Psarras leg.; AMPG(IV) 3770 to AMPG(IV) 3786 • 1 spec.; Panassos; 35.130° N, 24.986° E; 2017; Christos Psarras leg.; AMPG(IV) 3787 • 1 spec.; Filippi; AMPG(IV) 3788 • 2 specs; Tefeli; AMPG(IV) 3789 to AMPG(IV) 3790 • 11 specs; Tefeli; Efterpi Koskeridou leg.; AMPG(IV) 3791 to AMPG(IV) 3801.

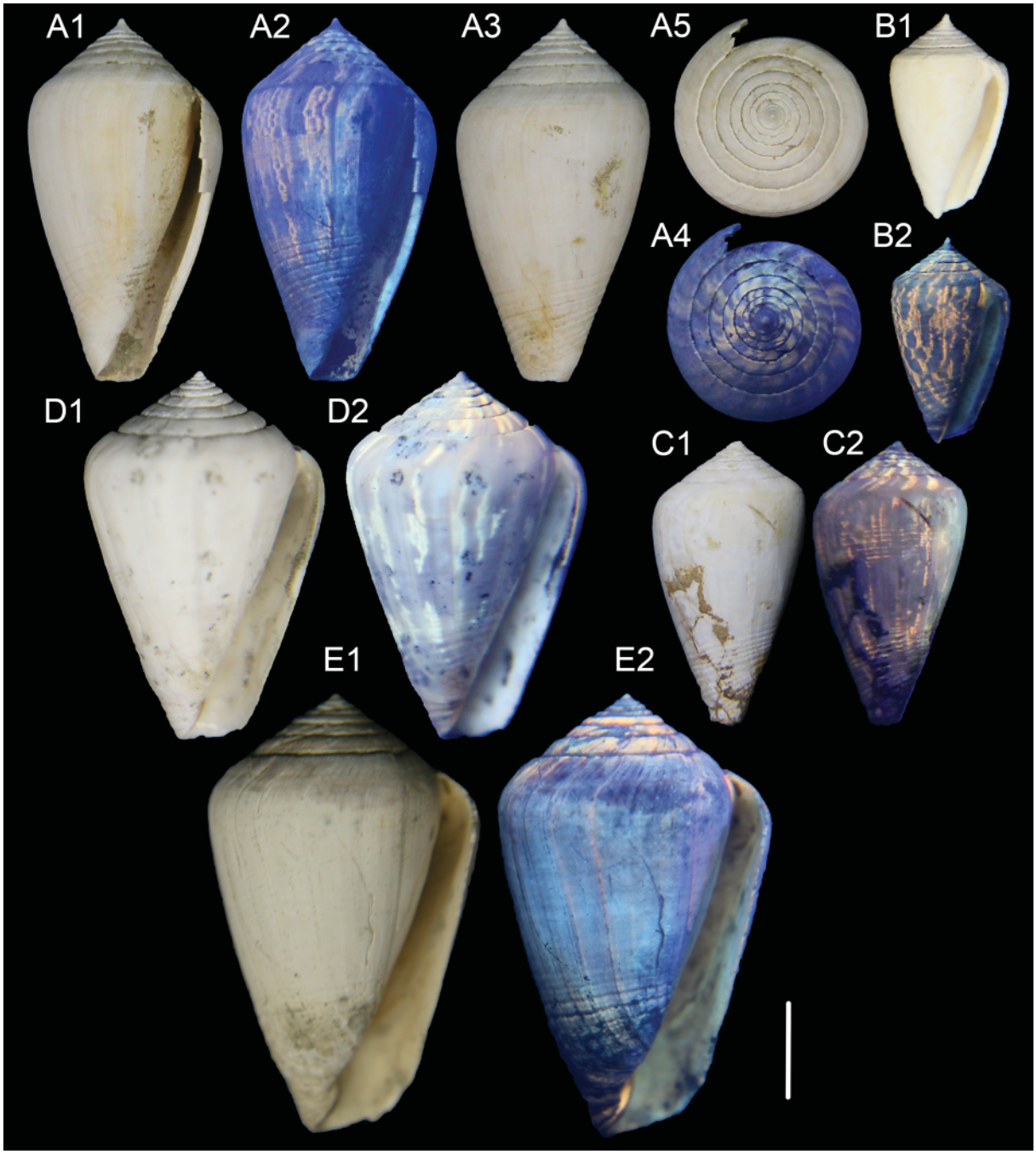

Fig. 7. Shell morphotypes of *Conus* (*Lautoconus*) sp. 2 from the Tortonian of Filippi, Crete (Greece) shown in apertural view under natural (A1, A3–A4, B1, C1, D1, E1) and UV light. **A**. Specimen AMPG(IV) 3771, Filippi: an elongate sample with relatively high LW. **B.** Specimen MNHN.F.A83004, Crete: a small specimen showing vivid colour pattern under UV light. **C**. Specimen AMPG(IV) 3786, Filippi: a specimen with unusual pattern of spiral dashes instead of bands. **D**. Specimen MNHN.F.A82996, Crete: a specimen with relatively low LW. **E**. Specimen AMPG(IV) 2768, Crete: Symeonidis & Kostantinidis's specimen with unclear colour pattern. Scale bar = 1 cm.

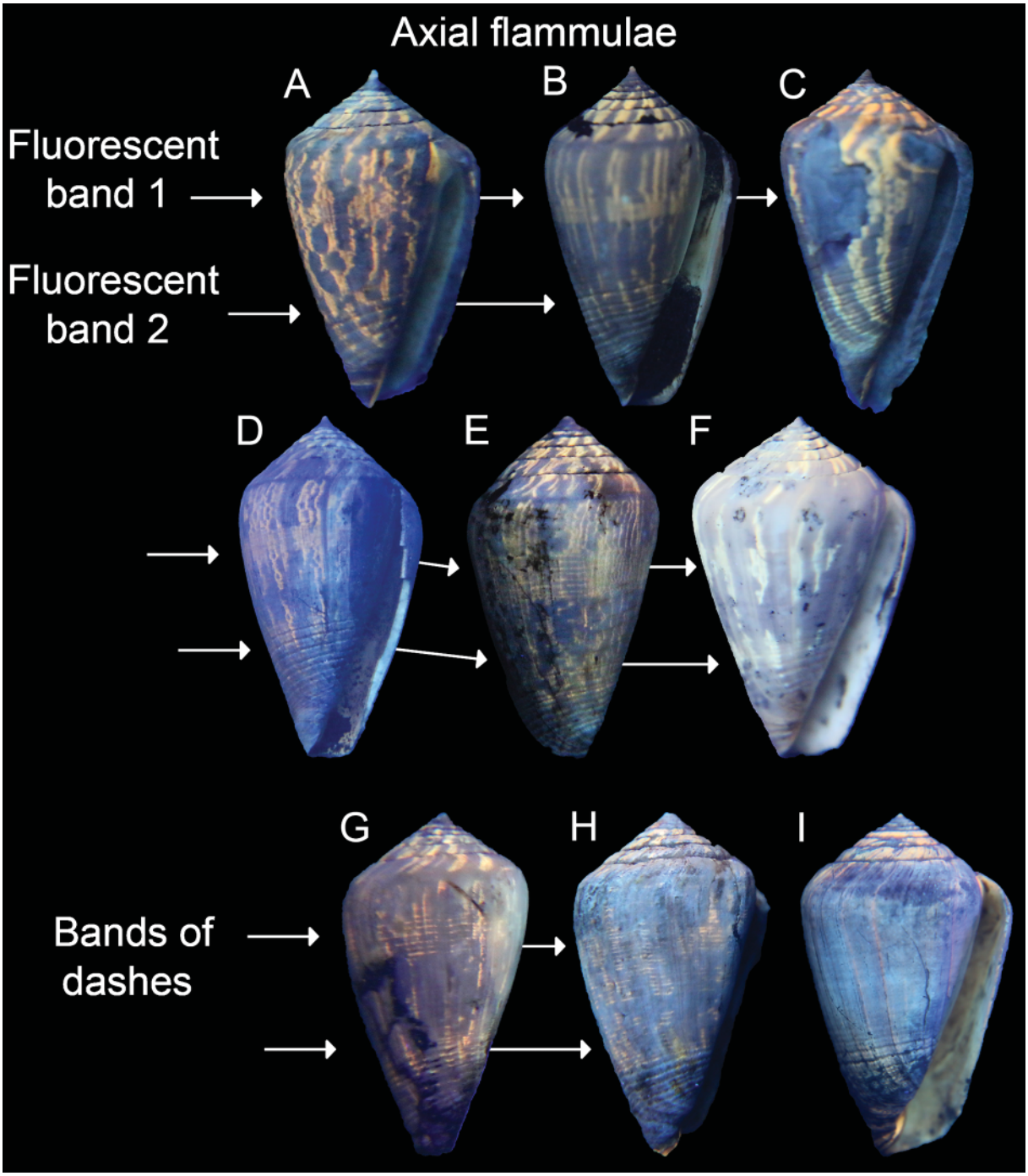

Fig. 8. Nine shells of *Conus* (*Lautoconus*) sp. 2 from the Tortonian of Crete (Greece) showing colour pattern variations in apertural view under UV light. **A**. Specimen MNHN.F.A83004, Crete. **B**. Specimen AMPG(IV) 3772, Filippi. **C**. Specimen MNHN.F.A83002, Crete. **D**. Specimen AMPG(IV) 3771, Filippi. **E**. Specimen AMPG(IV) 3770, Filippi. **F**. Specimen MNHN.F.A82996, Crete. **G**. Specimen AMPG(IV) 3786, Filippi. **H**. Specimen AMPG(IV) 3762, Filippi. **I**. Specimen AMPG(IV) 2768. Specimens are not to scale.

Shell description

Medium-sized shells (51.92 mm), with medium to low conical, straight to slightly coeloconoid spire. Early spire whorls faintly striate, highly pointed. Later spire whorls smooth, straight to slightly coeloconoid. Faint spiral grooves on spire whorls, diminishing on late spire whorls. Suture channelled. Subsutural flexure shallow, moderately curved, moderately asymmetrical (Fig. 40D). Shoulder rounded, with an angulation at suture height. Maximum diameter right below shoulder. Last whorl conical, with variable elongation of the last whorl, not constricted. Spiral grooves present on anterior third of last whorl. Aperture moderate, widening anteriorly. Fasciole indistinct, slightly twisted.

Description of colour pattern

The colour pattern consists of two levels of colouration. The first consists of yellow axial stripes on a non-fluorescent base. Those stripes are either continuous from the shoulder, where a non-fluorescent disruption exists (Fig. 8), until the anterior of the shell, or are not continuous, showing patterns of axial disruptions, convergences with other stripes, and divisions of individual stripes into more (Fig. 8A). The second level consists of two axial bands; the first one is placed just above the middle of the shell and the second one is placed on the anterior part of the shell, along with the last spiral groove. The bands are not always continuous or visible (Fig. 8B). In some shells, they resemble closely arranged, thin spiral dashes (Fig. 8E, G–H), some of them axially arranged (Fig. 8H).

Remarks

This species is the most common *Conus* (*Lautoconus*) in the Tortonian of Crete. The study of more than 100 specimens (Table 4) consistently shows the recurrence of the morphology and colour pattern

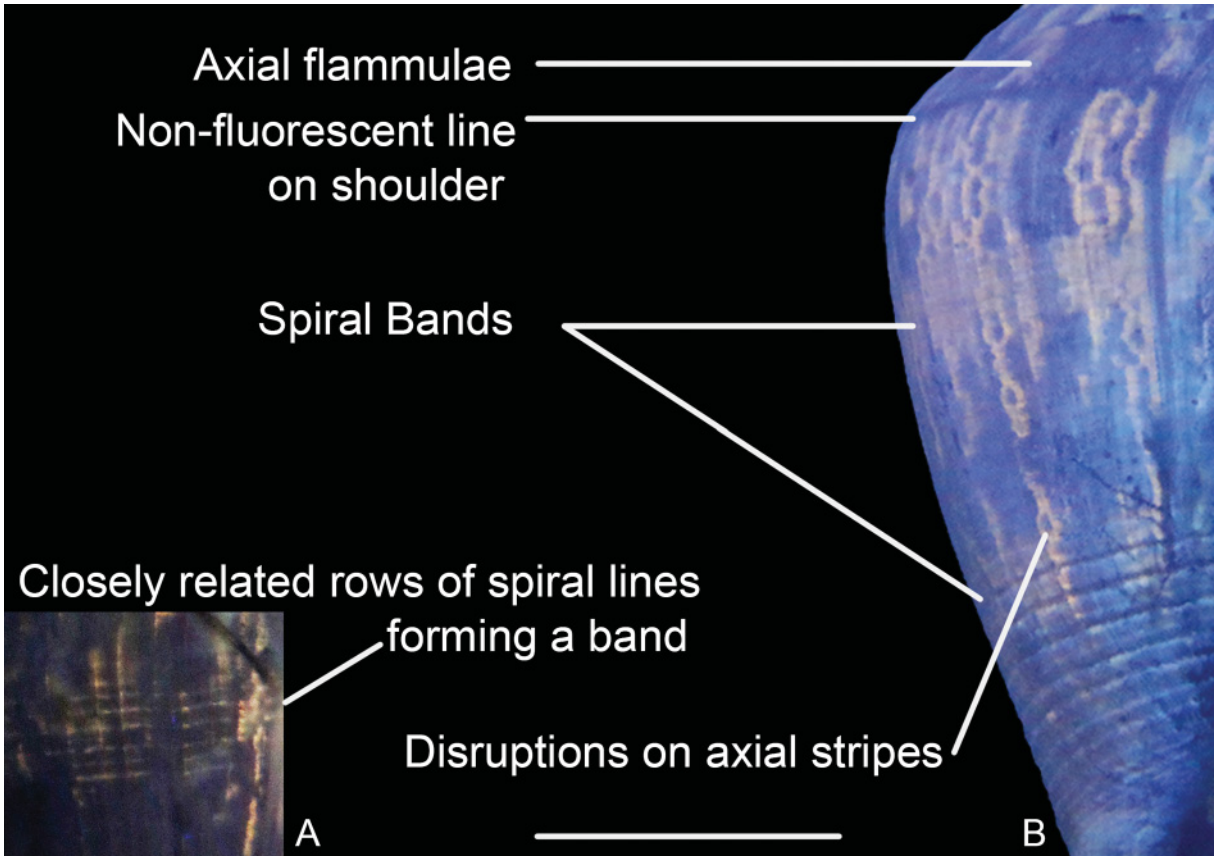

Fig. 9. Colour pattern elements of *Conus* (*Lautoconus*) sp. 2 from the Tortonian of Crete (Greece). **A**. Specimen AMPG(IV) 3786, Filippi. **B**. Specimen AMPG(IV) 3771, Filippi. Scale bar = 1 cm.

Table 4. Shell measurements and ratios of *Conus* (*Lautoconus*) sp. 2 from the Tortonian of Crete (Greece). Mean and standard deviation are computed for 109 of a total of 110 specimens. The largest specimen is AMPG(IV) 3753.

	SL	MD	AH	HMD	AL	SA	LWA
Largest specimen	51.92 mm	29.44 mm	44.85 mm	38.25 mm	44.66 mm	103.2°	37.3°
Mean	35.4 mm	20.23 mm	29.97 mm	25.09 mm	29.76 mm	103.51°	38.61°
Standard deviation	8.16	4.53	7.15	6.08	7.05	8.03	2.83
	LW	**RD**	**PMD**	**RSH**	**SSFD**	**SSFd**	**PV**
Largest specimen	1.76	0.66	0.85	0.14	–	–	–
Mean	1.75	0.68	0.84	0.15	2.61	6.74	0.62
Standard deviation	0.1	0.04	0.03	0.03	0.65	2.16	0.2

of this species (Fig. 8). From the Serravallian of Turkey, Erünal-Erentöz (1958: 121, pl. 20 figs 4–5) described *Conus* (*Chelyconus*) *pyrula* var. *mucronata*, but the binome *Conus mucronatus* is occupied by a recent species, described by Reeve (1843). The Turkish material displays a morphology similar to the Cretan specimens, with pointed early spire whorls, low conical late whorls and an angulated shoulder. As no colour pattern has been studied for that material, we cannot consider with certainty that the Cretan and the Turkish specimens belong to same species. The type specimen of the Pliocene *Conus bitorosus* var. *elatoastensis* Sacco, 1893 (Sacco 1893b), illustrated by Hall (1966: pl. 23 fig. 24), is very similar to *Conus* (*Lautoconus*) sp. 2, but we have not observed its colour pattern.

The shell morphology of the Pliocene *Conus* (*Lautoconus*) *ponderosus* Brocchi, 1814 resembles that of *Conus* (*Lautoconus*) sp. 2, but differs by lacking the early, pointed spire whorls, by the occurrence of spiral grooves on last whorl and by the frequent angulation on shoulder. Its colour pattern seems not preserved (Harzhauser & Landau 2016; Annalaura Pistarino pers. comm.). One syntype of *Conus* (*Lautoconus*) *conoponderosus* Sacco, 1893b (MRSN BS.038.05.082, Tortonian of Colli Tortonesi) was figured in Davoli (1972: pl. 4 fig. 19). It bears a similar morphology, but displays a lower spire and a stout last whorl differing from most of the specimens studied here. Its colour pattern was not observed. Despite the discussed differences in shell morphology, *Conus ponderosus* and *Conus conoponderosus* might be different morphotypes of a same species. Since we observed similar morphotypes from Crete, we cannot disregard the possibility of them being conspecific. Thus, we refrain from attributing the Cretan material to *Conus* (*Lautoconus*) *ponderosus*, *Conus* (*Lautoconus*) *conoponderosus* or *Conus elatoastensis*. Further examination needs to be done on the Italian types by using UV light in order to clarify whether the colour pattern allows distinguishing these species.

Conus (*Lautoconus*) *pyrula* Brocchi, 1814 differs from *Conus* (*Lautoconus*) sp. 2 by a more robust morphology and a weaker angulation on shoulder (Fig. 7). The colour pattern of *Conus* (*Lautoconus*) sp. 2 bears additional spiral bands (Figs 8–9), whereas that of *Conus* (*Lautoconus*) *pyrula* bears irregular, ochre-coloured longitudinal lines (see the description by Sacco 1893b). We examined Italian Pliocene specimens stored at the MNHN Paris (Vegga coll., MNHN.F.B32569), that are identified as *Conus pyrula* Brocchi, 1814 and we confirm that they display the colour pattern described by Sacco (1893b). *Conus* (*Lautoconus*) *steinabrunnensis* Sacco, 1893 (Sacco 1893b) from the Langhian of Austria bears large irregular blotches and flammulae on spire whorls (Harzhauser & Landau 2016), differing from the colour pattern of *Conus* (*Lautoconus*) sp. 2. *Conus* (*Lautoconus*) *steindachneri* Hoernes, 1879 from the Langhian of Austria has a colour pattern of numerous thin spirals (Harzhauser & Landau 2016), also differing from that of *Conus* (*Lautoconus*) sp. 2.

Stratigraphic range

Tortonian of Greece (Achladhia, Sitia Basin and Messara Basin, Crete) (this work).

***Conus* (*Lautoconus*)** sp. 3
Figs 10, 20, 40E; Table 5

Conus (*Chelyconus*) *clavatulus* – Caze 2010: fig. 33f (non *Conus clavatulus* d'Orbigny, 1852).

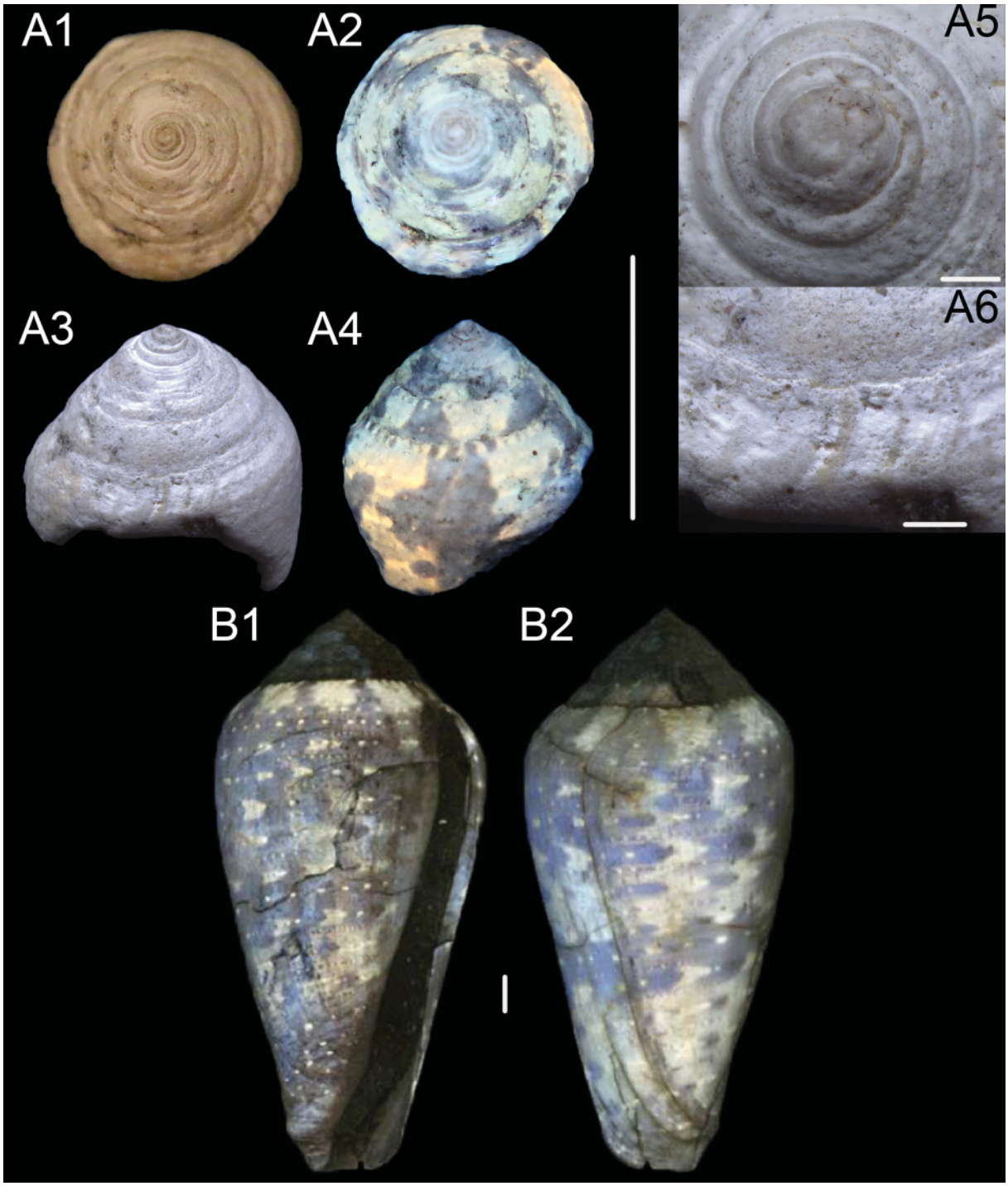

Fig. 10. *Conus* (*Lautoconus*) sp. 3 from the Tortonian of Crete, (Greece) on apertural, abapertural and apical views, under natural (A1, A3, A5, A6) and UV light. **A**. Specimen MNHN.F.A83012, Crete. **B**. Specimen MNHN.F.A30844, Voleones: figured of Caze (2010: fig. 33f) showing the colour pattern of this very large specimen under UV light. Scale bars: A1–A4, B1–B2 = 1 cm; A5 = 500 µm; A6 = 1 mm.

Table 5. Shell measurements and ratios for one specimen of *Conus* (*Lautoconus*) sp. 3, measured from Caze (2010: fig. 33). Subsutural flexure measurements are from the broken specimen MNHN.F.A83012.

SL	MD	AH	HMD	AL	SA	LWA
172.7 mm	83.6 mm	144.1 mm	126.5 mm	13.7 mm	96°	32°
LW	**RD**	**PMD**	**RSH**	**SSFD**	**SSFd**	**PV**
2.07	0.58	0.88	0.17	–	–	–
	MNHN.F.A83012			7.6	25	0.92

Material examined

GREECE – **Crete** • 1 spec.; Voleones; Tortonian; 1990; Didier Merle leg.; Action spécifique du Muséum project (1989–1990) exped.; MNHN.F.A30844 • 1 spec.; Action spécifique du Muséum project (1989–1990) exped.; MNHN.F.A83012.

Shell description

Large (estimated SL: 172.7 mm), elongate, sturdy shell. Spire whorl outline conical. Early spire whorls conical, later spire whorls conical, with slightly convex outline. Shoulder rounded, with maximum diameter just below shoulder. Suture slightly impressed. Subsutural flexure very shallow, very weakly curved, nearly symmetrical (Fig. 40E). Last whorl elongated, straight. Aperture straight. Apertural canal short, wide, fasciole twisted.

Colour pattern variation

Three levels of colouration are present in this species. The first one consists of two fluorescent bands, which are on the middle and anterior parts of the shell. The second one is a pattern of spirally arranged alterations of non-fluorescent and fluorescent dots. The third level is displayed between the spiral alterations of dots. It consists of a series of fluorescent, arrow-like blotches-tents, pointing in the opposite direction of the shell growth, alternated by non-fluorescent areas. The non-fluorescent areas might have one or two dots between the fluorescent arrows. Along with the second level of fluorescent dots, irregular fluorescent flammulae appear on the spire whorls.

Remarks

The colour pattern of the species is unique in the studied material. The relatively rounded spire whorls and the lack of tubercles on early spire whorls allow us to categorize it as an elongated *Conus* (*Lautoconus*). Caze (2010) identified this specimen (MNHN.F.A30844) (Fig. 10) as *Conus* (*Chelyconus*) *clavatulus* d'Orbigny, 1852, originally described from the early Miocene of Saubrigues (France). Hall (1966: pl. 23 figs 23–24) illustrated the type material (a syntype from the early Miocene of "Dax-Saubrigues", Aquitaine) of *Conus clavatulus* from the collection of Grateloup. The shell of this specimen resembles *Conus* (*Lautoconus*) sp. 3. *Conus subclavatus* d'Orbigny, 1852, another species of the early Miocene of the Aquitaine Basin, is known from a syntype (MNHN.F.A13055) of the d'Orbigny's collection and is rather similar to *Conus clavatulus*. Since the patterns of both species remain unknown, we refrain from attributing the Cretan specimens to one of these species. Additionally, *C.* (*Lautoconus*) sp. 3 differs from the figured specimens of Kovács & Vicián (2013) from the Langhian of Hungary, named *Varioconus clavatulus* (d'Orbigny, 1852), in the higher spire and the more angulated shoulder. Finally, this species is not *Conus* (*Lautoconus*) *ponderosus* Brocchi, 1814 as it has a slightly higher spire and more elongate last whorl.

Stratigraphic range

Tortonian of Greece (Voleones, Apostoli Basin, Crete).

Conus* (*Lautoconus*)** cf. ***baldichieri Borson, 1820
Figs 11–12, 20, 40F; Table 6

Material examined

GREECE – **Crete** • 1 spec.; Adhraktia; Messara Basin, Tortonian; 1990; Action spécifique du Muséum project (1989–1990) exped.; MNHN.F.A83013.

Shell description

Moderately large shell (31.14 mm). Early spire whorls coeloconoid, straight. Middle to late spire whorls convex, elevated, creating conical, bulbous outline. Subsutural flexure deep, strongly curved, strongly asymmetrical (Fig. 40F). Shoulder slightly angulated. Maximum diameter right below shoulder. Aperture narrow, widening towards siphonal canal. Last whorl straight to slightly inflated. Siphonal canal short, wide. Fasciole short, twisted.

Description of colour pattern

The colour pattern consists of three levels of colouration. The first one consists of continuous grouped spiral lines of dim-fluorescent colour (Fig. 12, dim fluorescent lines). The second one consists of continuous spiral lines of bright-fluorescent colour (Fig. 12, bright green coloured lines). Both patterns of lines are slightly wavy, and it is possible for the second one to overprint the first. The third level of colouration is a series of thin, wavy, fluorescent and axial lines (Fig. 12, axial lines). The lines are not always continuous, but are more prominent on the spire whorls. Some of the lines are linked one to another, turning into a pattern of axially entangled lines. The result of the three patterns reminds of vehicle tire tracks (Fig. 11A2).

Remarks

Ferrero Mortara *et al*. (1984: pl. 16 fig. 8) figured the 'holotype' of *Conus baldchieri* (in fact they made a fixation of a lectotype by inference of holotype, ICZN 1999: Art. 74.6)) regarded by Sacco (1893a) as *Lithoconus mercatii* var. *baldichieri*. The Cretan specimen attributed to *Conus* (*Lautoconus*) cf. *baldichieri* is similar to *Conus baldichieri* Borson, 1820 from the Pliocene of Italy, but differs in the less striated spire whorls, the less inflated shell, the more elongate last whorl and its shorter siphonal canal.

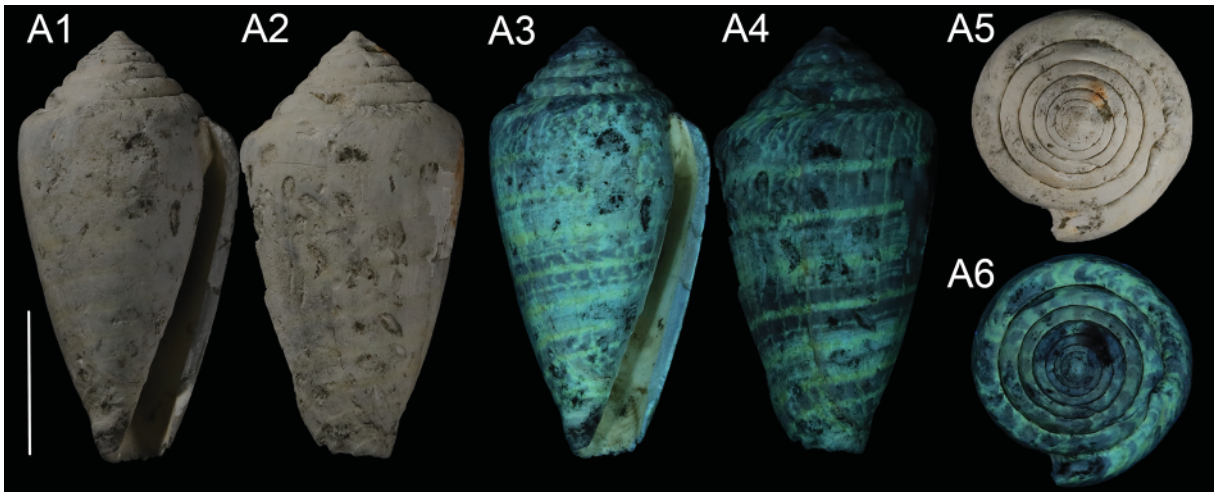

Fig. 11. *Conus* (*Lautoconus*) cf. *baldichieri* Borson, 1820 from the Tortonian of Crete (Greece) on apertural, abapertural and apical views, under natural (A1–A2, A5) and UV light. Specimen MNHN.F.A83013. Scale bar = 1 cm.

Table 6. Shell measurements and ratios of the specimen of *Conus* (*Lautoconus*) cf. *baldichieri* Borson, 1820 from the Tortonian of Crete (Greece).

SL	MD	AH	HMD	AL	SA	LWA
31.14 mm	16.22 mm	25.35 mm	21.08 mm	24.97 mm	88.2°	42°
LW	**RD**	**PMD**	**RSH**	**SSFD**	**SSFd**	**PV**
1.92	0.64	0.83	0.19	1.25	4.33	0.37

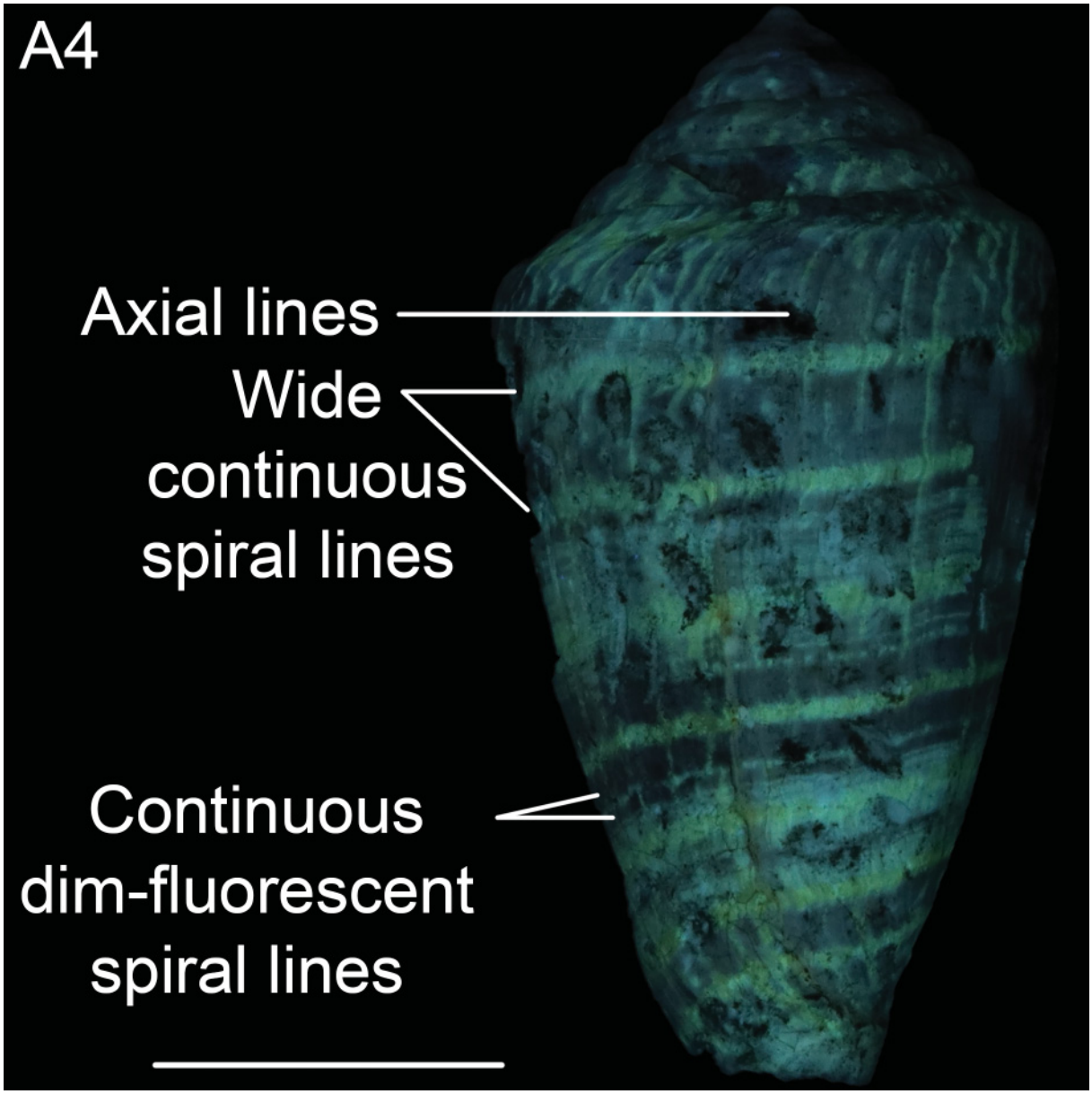

Fig. 12. Elements constituting the colour pattern of *Conus* (*Lautoconus*) cf. *baldichieri* Borson, 1820 from the Tortonian of Crete (Greece), specimen MNHN.F.A83013, shown under UV light. Scale bar = 1 cm.

As we have not studied this Italian specimen under UV light, we prefer leaving the Cretan specimen in open nomenclature.

Stratigraphic range

Tortonian of Greece (Messara Basin, Crete) (this work).

Conus* (*Lautoconus*) *lauriatragei sp. nov.
urn:lsid:zoobank.org:act:E76A5E2C-EFE3-49F8-9999-625B71E8F562
Figs 13–14, 20, 40G; Table 7

Conus (*Lautoconus*) sp. – Kovács & Vicián 2013: 73, fig. 73.

Etymology

Name taken after Agnès Lauriat-Rage who was responsible of the Action spécifique du Muséum project (1989–1990).

Material examined

Holotype

GREECE – **Crete** • Tylissos Est [Locality East of Tylissos village]; Heraklion Basin; 1990; Action spécifique du Muséum project (1989–1990) exped.; MNHN.F.A83014.

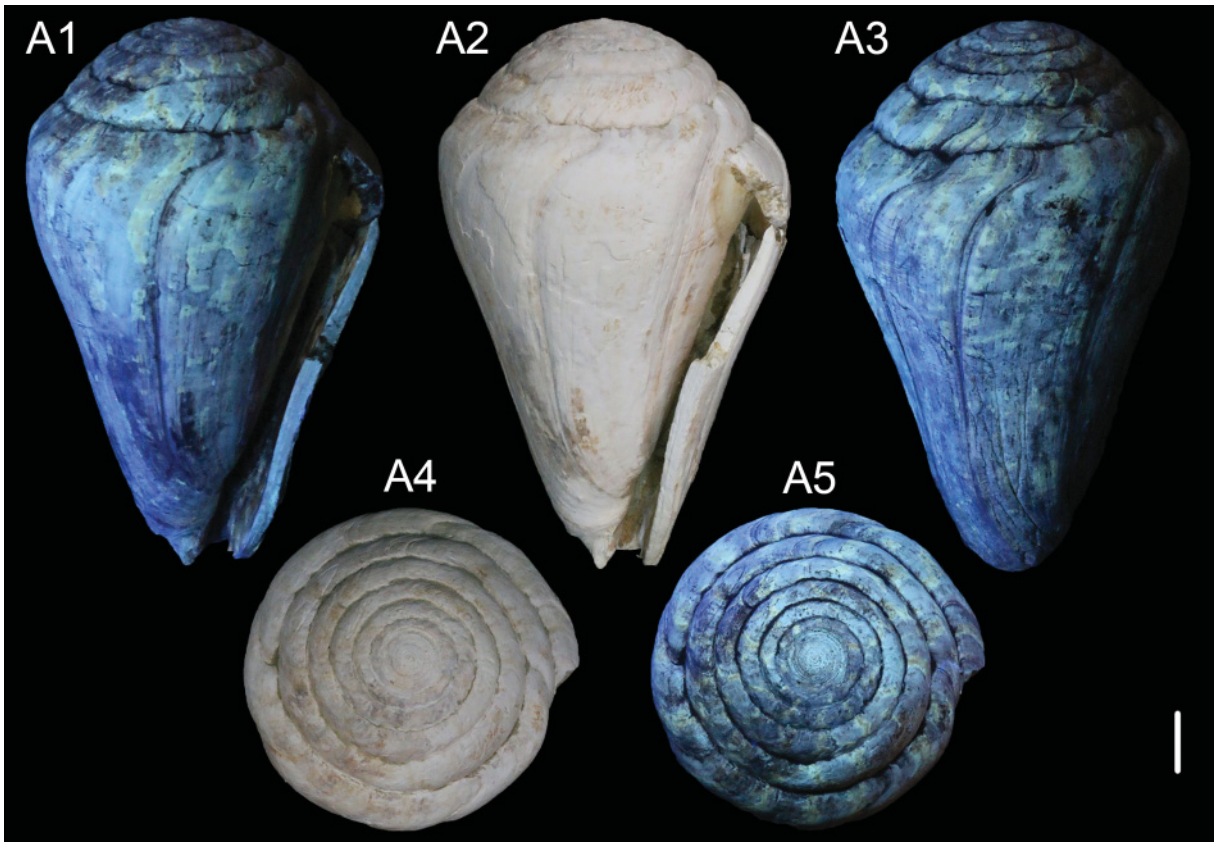

Fig. 13. *Conus* (*Lautoconus*) *lauriatragei* sp. nov,, specimen MNHN.F.A83014 from the late Miocene of Tylissos, Crete (Greece) in apertural, abapertural and apical views, under natural (A2, A4) and UV light. Scale bar = 1 cm.

Table 7. Shell measurements and ratios of *Conus* (*Lautoconus*) *lauriatragei* sp. nov. MNHN.F.A83014 from the late Miocene of Tylissos, Crete (Greece).

SL	MD	AH	HMD	AL	SA	LWA
83.84 mm	52 mm	72.42 mm	64.39 mm	71.12 mm	81°	38.5°
LW	**RD**	**PMD**	**RSH**	**SSFD**	**SSFd**	**PV**
1.61	0.79	0.9	0.14	1	5.549	0.304

Other material

HUNGARY – **Letkes** • Pannonian Basin; HNHM INV 2013.291.

Shell description

Large-sized shell (SL max.: l83.84 mm), with hemispherical-shaped spire and smooth shoulder. Early spire whorls convex, smooth, resulting in flat to convex outline. Later spire whorls strongly convex, elevated. Suture channelled, irregular. Subsutural flexure very deep, moderately curved, strongly asymmetrical (Fig. 40G). Shoulder smooth, with maximum diameter at shoulder. Aperture narrow, curved. Last whorl conical, straight to concave, narrowing slightly at centre of last whorl. Deeply carved growth lines on last whorl. Aperture not straight, wavy. Fasciole very small, to indistinct.

Description of colour pattern

Shell surface partly damaged (Fig. 13). The visible colour pattern consists of wide, axial flammulae on the spire whorls, that continue axially as ribbons on the body of the shell. The ribbons are connected with irregular fluorescent blotches (Fig. 14).

Remarks

This species is quite unusual in morphology (Table 7), being very large with a semi-circular spire outline species of *Conus* (*Lautoconus*) with a similar morphology occur today, such as *Conus* (*Lautoconus*) *regonae* Rolán & Trovão in Rolán, 1990 (see Tenorio *et al*. 2020: fig. 6d). Therefore, we are confident in assigning it to this subgenus. Other than the Cretan specimen, another specimen called *Conus* (*Lautoconus*) sp. (HNHM INV 2013.291; Kovács & Vicián 2013) has also been found in the Paratethys from the Pannonian Basin at Letkés, Hungary, and for us it could belong to the same species. Its colour pattern is not comparable to any of the Conidae studied herein. Despite not having at least

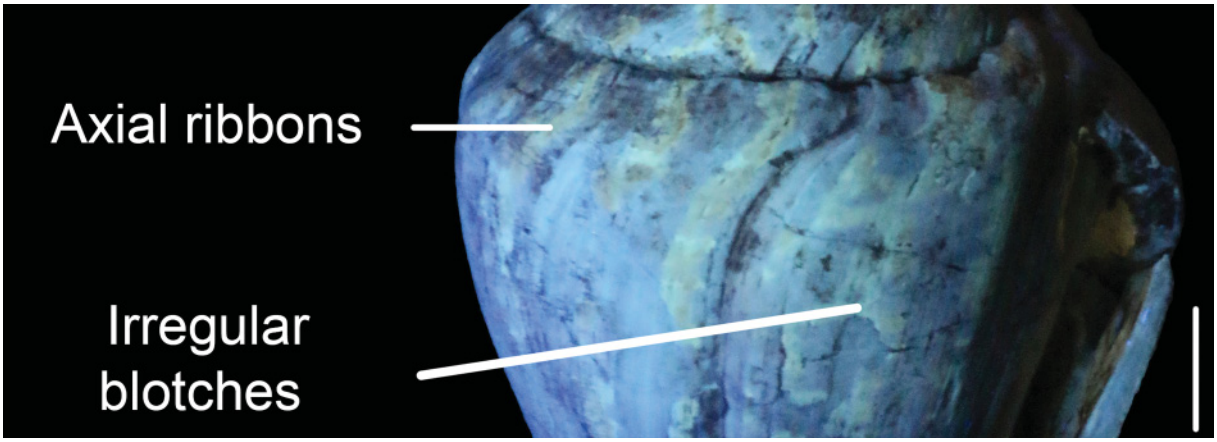

Fig. 14. Colour pattern of irregular blotches and axial ribbons on *Conus* (*Lautoconus*) *lauriatragei* sp. nov. MNHN.F.A83014 from the late Miocene of Tylissos, Crete (Greece). Scale bar = 1 cm.

three shells of this species found so far (Hendricks 2015), due to the unique morphology of this species we name it *Conus* (*Lautoconus*) *lauriatragei* sp. nov.

Stratigraphic range

Langhian of Hungary (Pannonian Basin, Kovács & Vicián 2013) and Tortonian of Greece (Heraklion Basin, Crete).

Conus* (*Lautoconus*) *damianakisi sp. nov.
urn:lsid:zoobank.org:act:BBAB551E-3B05-46E6-BC10-4234556D8EDC
Figs 15–16, 20, 40H; Table 8

Etymology

Named after Astrinos Damianakis, a private collector from Panassos village, who helped us during the material collection.

Material examined

Holotype

GREECE – **Crete** • Tefeli; Messara Basin, Tortonian; Efterpi Koskeridou leg.; AMPG(IV) 3802.

Paratypes

GREECE – **Crete** • 1 spec.; same collection data as for holotype; AMPG(IV) 3803 • 1 spec.; same collection data as for holotype; AMPG(IV) 3804.

Other material

GREECE – **Crete** • 1 spec.; same collection data as for holotype; AMPG(IV) 3805 • 1 spec.; Messara Basin, Tortonian; Efterpi Koskeridou leg.; AMPG(IV) 3806 • 1 spec.; Achladhia; 1964; Nikolaos Symeonidis leg.; AMPG(IV) 3807.

Shell description

Large shells (SL max.: 80.02 mm), with smooth, conical spire whorls and spiral cords. Spire whorls straight to slightly convex, with slightly concave outline in early spire whorls, straight to slightly convex in later spire whorls, with smooth to slightly elevated interactions of spire whorls, creating smooth, low conical to convex outline. Multiple spiral cords on top of spire whorls, with three to four on early spire whorls, up to ten on late spire whorls. Shoulder rounded. Maximum diameter below shoulder. Suture, channelled, not straight. Subsutural flexure moderately deep to shallow, moderately curved, strongly to moderately asymmetrical (Fig. 40H). Last spire whorl conical, straight. Aperture narrow, fasciole small, slightly twisted. Spiral grooves near anterior part of last whorl.

Colour pattern variation

The colour pattern on the spire whorls consists of thin flammulae, frequently very closely related to united, resulting in wide, fluorescent and comma shaped flammulae (Fig. 15, see apical views). The colour pattern of the last whorls consists of two levels of pigmentation. The first one consists of wide, dim-fluorescent spiral bands, interrupted by non-fluorescent, thin spiral, continuous bands or lines. The second level consists of very closely related, fluorescent dashes to continuous lines. The dashes tend to be on an axial synchronization with other spiral dashes-lines. The width of the spiral bands varies, as well as the number of interruptions of the spiral lines. Also, the length of the dashes varies as well, from almost dot-shaped dashes to continuous spiral lines (Fig. 16).

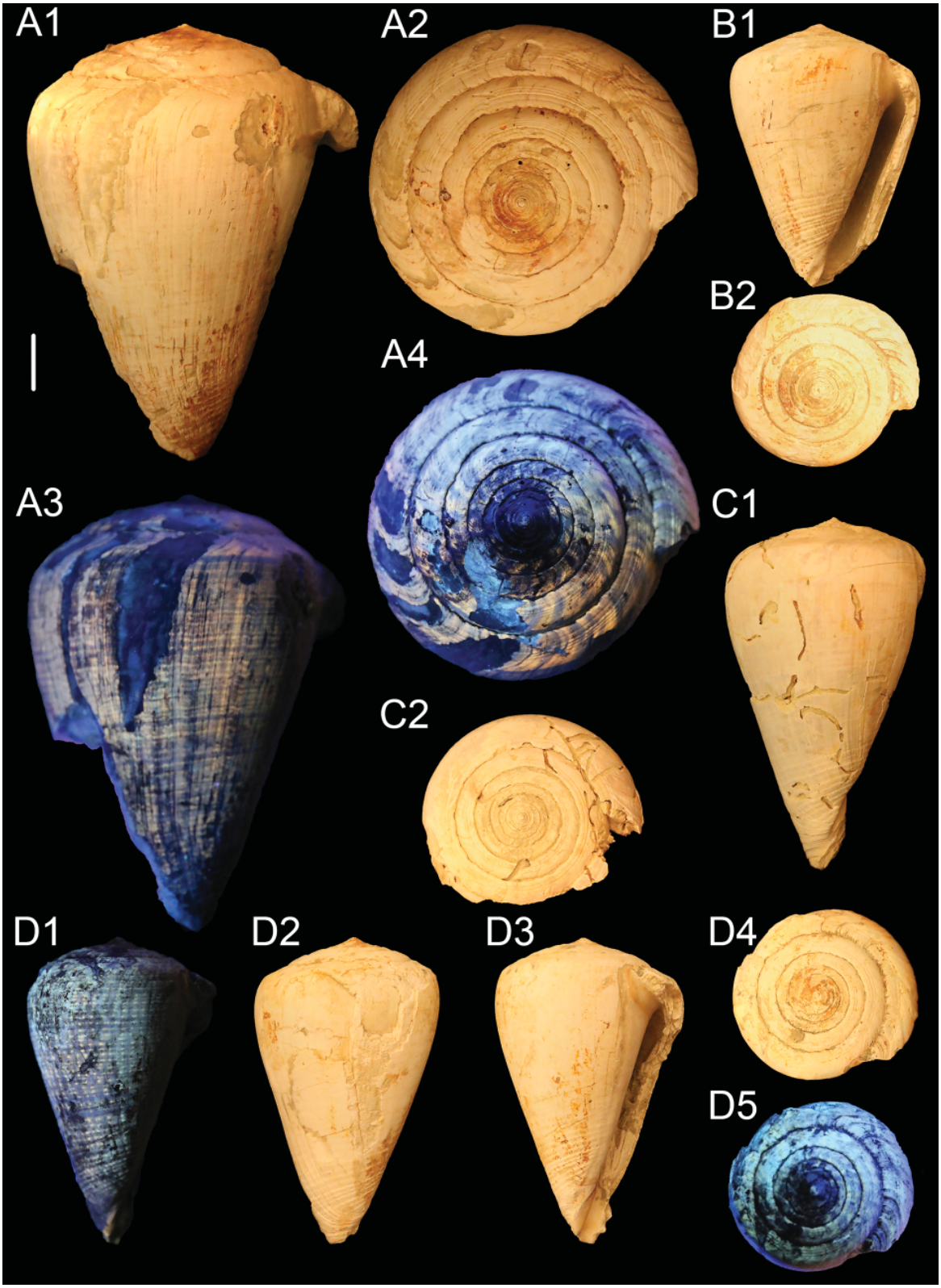

Fig. 15. *Conus* (*Lautoconus*) *damianakisi* sp. nov. from Tefeli, Crete (Greece), shown in apertural, abapertural and apical views, under natural (A1–A2, B1–B2, C1–C2, D2–D4) and UV light. **A**. Holotype AMPG(IV) 3802, Tefeli. **B**. Paratype AMPG(IV) 3804, Tefeli. **C**. Specimen AMPG(IV) 3806, Crete. **D**. Paratype AMPG(IV) 3803, Tefeli. Scale bar = 1 cm.

Table 8. Shell measurements and ratios of *Conus* (*Lautoconus*) *damianakisi* sp. nov., from the late Miocene of Tefeli, Crete (Greece). Mean and standard deviation are computed from seven partially damaged specimens, where possible.

	SL	MD	AH	HMD	AL	SA	LWA
Holotype	80.02 mm	61.13 mm	71.71 mm	60.95 mm	71.39 mm	150°	33°
AMPG(IV) 3804	44.4 mm	32.8 mm	39.22 mm	31.94 mm	40.11 mm	136°	41.8°
Mean	54.99 mm	36.64 mm	50.01 mm	42.06 mm	49.91 mm	137.6°	37.72°
Standard deviation	15.7	12.89	14.47	13.78	13.98	10.11	3.32
	LW	**RD**	**PMD**	**RSH**	**SSFD**	**SSFd**	**PV**
Holotype	1.31	0.86	0.85	0.1	1.14	3.56	0.14
AMPG(IV) 3804	1.35	0.82	0.8	0.1	1.33	6.38	0.31
Mean	1.53	0.73	0.83	0.09	1.61	5.08	0.27
Standard deviation	0.18	0.1	0.05	0.02	0.53	1.59	0.15

Remarks

The characters of the spire whorls and the colour pattern variation differentiate this species from the rest of the studied material. The specimens are similar in morphology (Table 8) to *Conus pseudo-textilis* Grateloup, var. *pliocenica* Erünal-Erentöz, 1958. The studied species differs from the variety of Erünal-Erentöz in the slightly concave sutural ramps. This difference is crucial, because the concave sutural ramps is shared between the specimens of Erünal-Erentöz and members of *Monteiroconus*, but not the members of *Lautoconus*.

Stratigraphic range

Tortonian of Greece (Heraklion Basin, Crete).

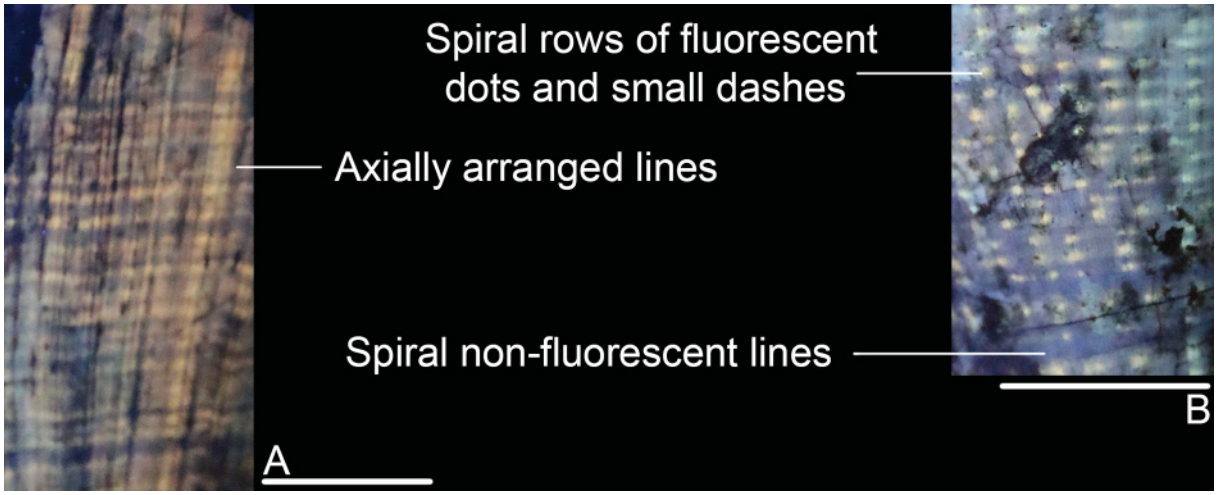

Fig. 16. Elements constituting the colour pattern of *Conus* (*Lautoconus*) *damianakisi* sp. nov. from the Tortonian of Tefeli, Crete (Greece). **A**. Part of the holotype AMPG(IV) 3802. **B**. Part of paratype AMPG(IV) 3803. Scale bars = 1 cm.

***Conus* (*Lautoconus*)** sp. 4
Figs 17, 20, 40I; Table 9

Conus (*Chelyconus*) *?pyrula* – Caze 2010: 63, fig. 37a1–a3 (non *Conus pyrula* Brocchi, 1814).

Material examined

GREECE – **Crete** • 1 spec.; Apomarma; Messara Basin; Tortonian; 1990; Action spécifique du Muséum project (1989–1990) exped.; MNHN.F.A83015.

TURKEY – **Antakya** • 1 spec.; Samandag; Antakya Basin; Piacenzian; MNHN.F.A31529.

Shell description

Medium-sized shell (SL max.: 29.43 mm). Early spire whorls conical to convex, of low to medium height. Later spire whorls conical in outline, with convex, smooth sutural ramp. Subsutural flexure moderately deep, strongly curved, moderately asymmetrical (Fig. 40I). Shoulder smooth at early spire whorls, slightly angulated at later spire whorls. Maximum diameter below shoulder. Last whorl conical, slightly widened. Aperture narrow, straight, widening towards slightly twisted fasciole. Shell smooth, except for two faded spiral cords near fasciole.

Colour pattern variation

The colour pattern on the spire whorls consists of irregular blotches. The colour pattern on the last whorl consists of two levels of colouration. The first one consists of fluorescent blotches. The second level consists of spirally arranged irregular rows of fluorescent dashes, interrupted by non-fluorescent tents. The tents can be either as small as dots, or small non-fluorescent dashes, or can be axially wide enough to unite with other tents and create an axial non-fluorescent area. The resulting pattern is variable and depends on the number of tents, as well as on the size of those tents. The Cretan specimen shows an axial unification of the tents, while the Turkish specimen displays a spiral unification of the tents, in the middle part of the last whorl.

We noticed that the specimen from Apomarma (MNHN.F.A83015) had different grades of erosion, with non-fluorescent areas being more resistant to erosion, than those being previously with colour patterns (see Fig. 17A4 in comparison to the right side of Fig. 17A3, where the shell is not so eroded). This might indicate that the substance enclosed in the shell structure, which is responsible for the pigments, is more prone to erosion than the non-pigmented areas.

Remarks

This species is placed in *Lautoconus*, as it has smooth early spire whorls and a convex sutural ramp. The Pliocene Turkish specimen identified by Caze (2010) as *Conus* (*Chelyconus*) *?pyrula* Brocchi, 1814 and the Cretan specimen of *Conus* (*Lautoconus*) sp. 4 share smooth and convex spire whorls with a slightly angulated shoulder (Fig. 17) and have a similar colour pattern. Thus, they very likely belong to the same species. The typical Pliocene *Conus pyrula* bears a colour pattern of axially arranged stripes. *Conus* (*Lautoconus*) sp. 4 differs from the Paratethyan species of *Conus* (*Lautoconus*) (Harzhauser & Landau 2016) in the presence of tents in its colour pattern. *Conus* (*Lautoconus*) sp. 5 (see below) has a similar colour pattern of tents, but it differs morphologically from this species in the smooth outline of the spire whorls and the olive-like morphological outline. As such, we consider these specimens as two separate species. Unfortunately, in lacking more specimens with similar morphological characteristics and colour pattern, we do not name this species. *Conus* (*Lautoconus*) sp. 4 has a very common shell outline and is not easily distinguishable from other species without the help of UV light. The colour pattern is also reminiscent of extant species of *Conus* (*Lautoconus*), such as the West African species *Conus* (*Lautoconus*) *saragasae* Rolán, 1986 (Tenorio *et al*. 2020).

The morphological outline of *Conus* (*Lautoconus*) sp. 4 can be compared with several *Conus* (*Stephanoconus*) species discussed in this work (e.g., *Conus* (*Stephanoconus*) cf. *taurinensis* Bellardi & Michelotti, 1841 and *Conus Conus* (*Stephanoconus*) *moissettei* sp. nov.). Both species, however, possess the tuberculate early spire whorls, lacking in *Conus* (*Lautoconus*) sp. 4. Furthermore, their colour pattern is not comprised of tents.

Stratigraphic range

Tortonian of Greece (Messara Basin, Crete) (this work) and Piacenzian (Pliocene) of Turkey (Antakya Basin, Samandag Fm.) (see Tarı *et al.* 2013 for the age).

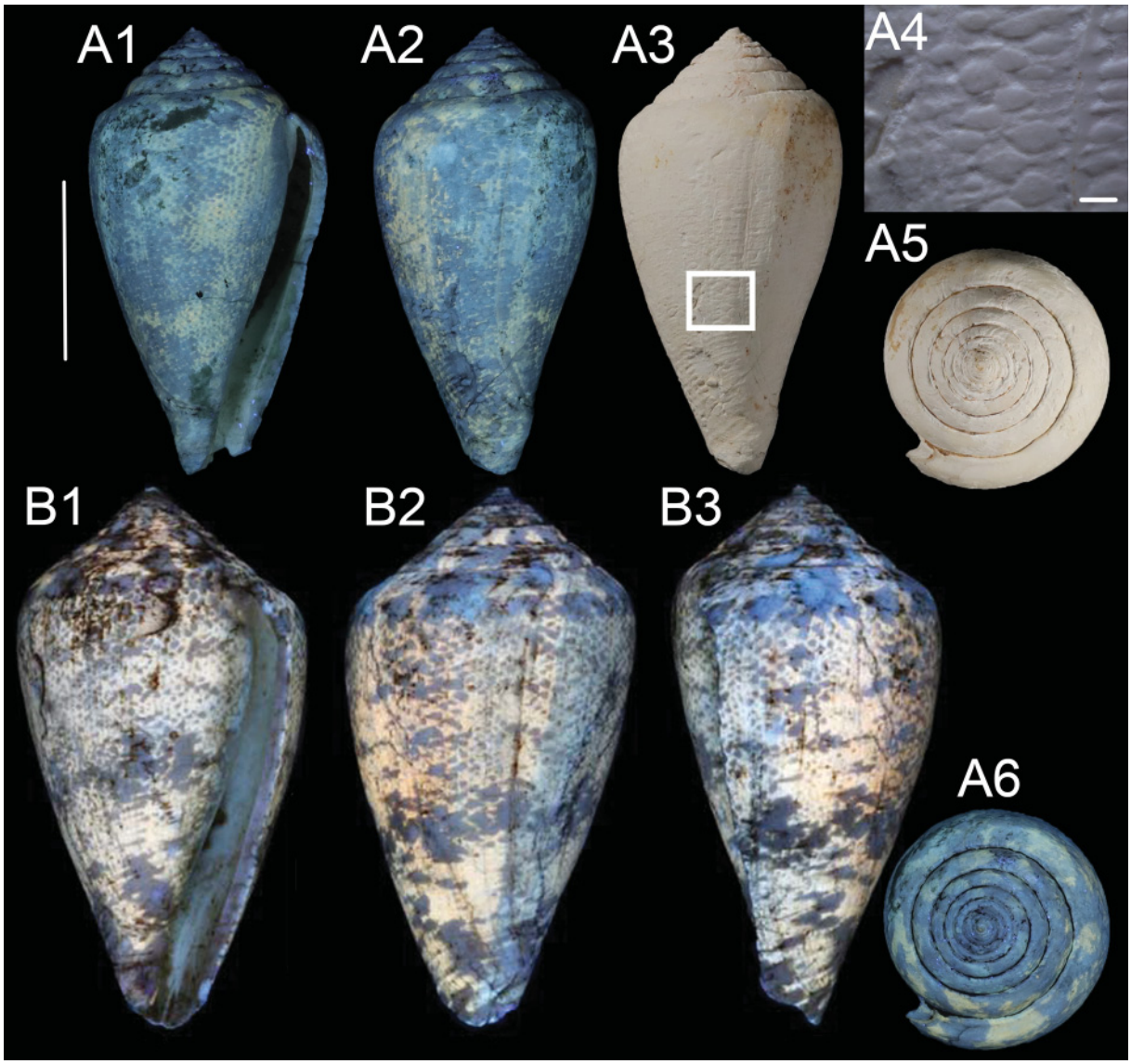

Fig. 17. *Conus* (*Lautoconus*) sp. 4 from the Tortonian of Crete (Greece) and the Piacenzian of Antakya (Turkey) (figure altered after Caze 2010), displayed under natural (A3–A5) and UV light. **A**. Specimen MNHN.F.A83015, Apomarma, displaying different grades of erosion (A3 box zoomed to A4). **B**. Specimen MNHN.F.A31529, Samandag (photo by Caze 2010). Scale bars: A1–A3, A5–B3 = 1 cm; A4 = 500 µm.

Table 9. Shell measurements and ratios of *Conus* (*Lautoconus*) sp. 4, from the late Miocene of Apomarma, Crete (Greece) and the Pliocene of Antakya (Turkey). Only two specimens are measured, the largest being the Turkish specimen, its shell size calculated from the figured specimen of Caze (2010).

	SL	MD	AH	HMD	AL	SA	LWA
MNHN.F.A31529	29.43 mm	16 mm	24.86 mm	20 mm	24.29 mm	98°	36°
MNHN.F.A83015	25.5 mm1	13.67 mm	21.22 mm	17.12 mm	21.51 mm	94.5°	35.7°
	LW	**RD**	**PMD**	**RSH**	**SSFD**	**SSFd**	**PV**
MNHN.F.A31529	1.84	0.64	0.80	0.16	–	–	–
MNHN.F.A83015	1.87	0.64	0.81	0.17	1.41	4.38	0.43

***Conus* (*Lautoconus*)** sp. 5
Figs 18–20, 40J; Table 10

Conus clavatulus – Davoli 1972: pl .4 figs 15–16 (non figs 5, 17 = *Conus davolii* sp. nov.) (non *Conus clavatulus* d'Orbigny, 1852).

Material examined

GREECE – **Crete** • 1 spec.; Filippi; Messara Basin, Tortonian; 35.035° N, 25.250° E; AMPG(IV) 3861.

Shell description

Moderately small (SL max.: 26.93 mm), biconical shell. Spire conical, straight. Early spire whorls straight to concave. Later spire whorls straight to convex, smooth. Suture moderately incised, undulated. Subsutural flexure very shallow, weakly curved, moderately asymmetrical (Fig. 40J). Last spire whorl with broad, straight to convex sutural ramp, continuing into smooth to subangulated shoulder and down to squished, rather sigmoidal last whorl. Maximum diameter right below shoulder. Aperture narrow, widening abapically. Siphonal canal long, straight. Fasciole indistinct. Faint spiral cords on quarter anterior part of last whorl.

Description of colour pattern

The colour pattern on the spire whorls consists of fluorescent irregular blotches and, inside those, randomly positioned, non-fluorescent tents. The tents continue until shoulder height. The colour pattern on the last whorl consists of two levels of pigmentation. The first pattern consists of amorphous, fluorescent blotches, disrupted by non-fluorescent tents. The second pattern consists of discontinuous, evenly distanced, spiral lines. The spiral lines are a series of alterations of fluorescent dots-dashes and non-fluorescent dashes. The second pattern, when overlapping the non-fluorescent tent level, displays only the fluorescent dots-dashes of the continuous spiral lines (Fig. 19).

Remarks

This species comprises only one specimen, partly broken (Table 10). Its biconical morphology is unique in the Greek collection. It could be compared with those studied by Davoli (1972) and named as ?*Conus clavatulus* d'Orbigny, 1852 (MOD n°5569 bis and MOD n°5610). These specimens have not been studied under UV light; therefore, we place them within *Conus* (*Lautoconus*) sp. 5. The specimen (AMPG(IV) 3861) is similar to several species of *Conus* described from the Paratethys, discussed in Harzhauser & Landau (2016) as *Leporiconus* Iredale, 1930. This species differs from the *Conus* (*Leporiconus*) in lacking tubercles on the early spire whorls. Also, the shell is smooth, except for the

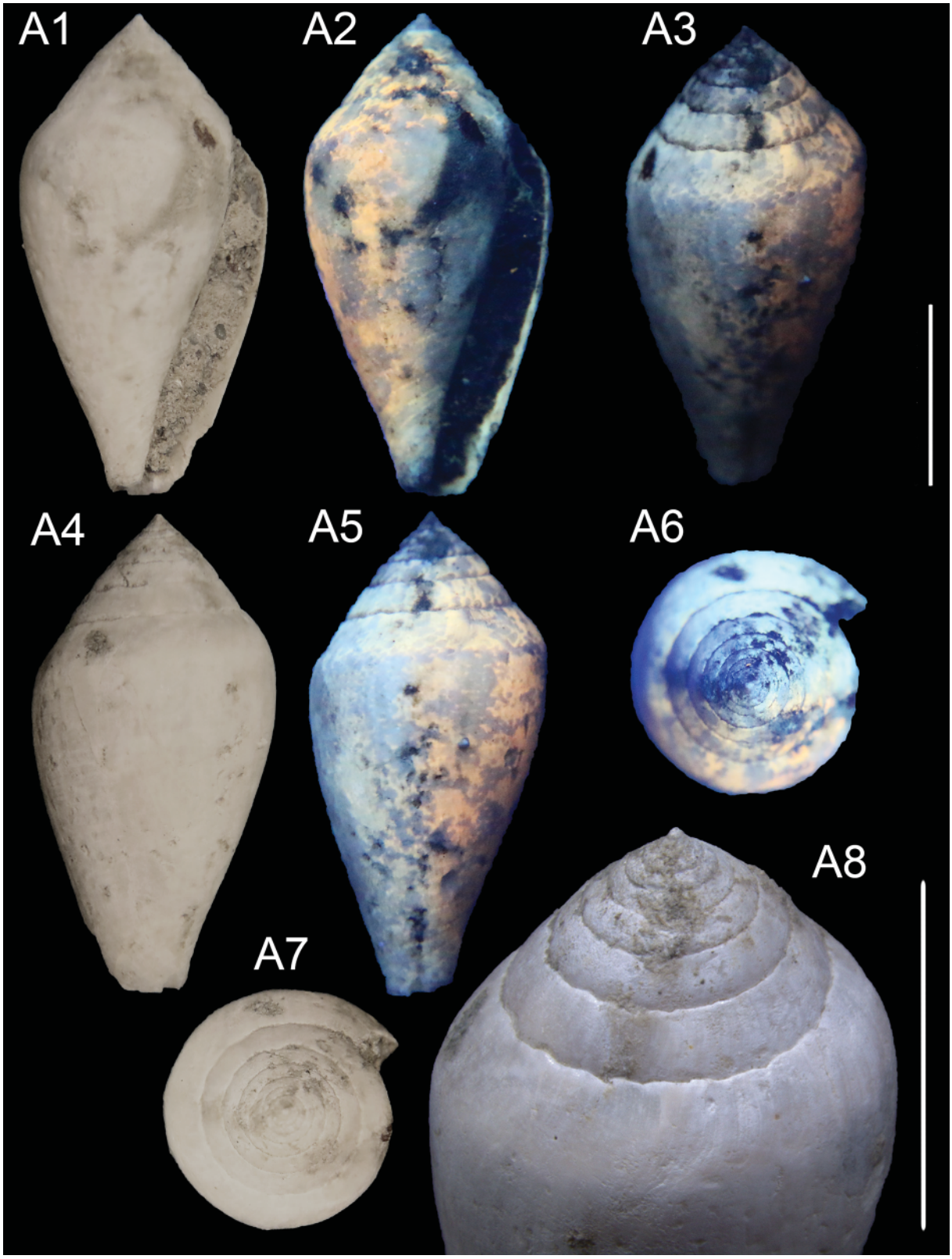

Fig. 18. *Conus* (*Lautoconus*) sp. 5, specimen from the Tortonian of Filippi, Crete (Greece), shown under natural (A1, A4, A7–A8) and UV light. **A**. Specimen AMPG(IV) 3861, Filippi: notice the shallow subsutural flexure in A8. Scale bars = 1 cm.

Table 10. Shell measurements and ratios of *Conus* (*Lautoconus*) sp. 5 from the Tortonian of Crete (Greece).

SL	MD	AH	HMD	AL	SA	LWA
26.93 mm	14.08 mm	20.8 mm	15.35 mm	20.55 mm	103°	30°
LW	**RD**	**PMD**	**RSH**	**SSFD**	**SSFd**	**PV**
1.91	0.68	0.74	0.23	5.67	7	0.67

faint spiral cords near the anterior part of the shell. For this reason, we prefer placing it into *Conus* (*Lautoconus*). The specimen has a morphology similar to *Conus mucronatolaevis* var. *permamillata* Sacco, 1893 (Sacco 1893b: pl. 6 fig. 33). Harzhauser & Landau (2016: fig. 35j) noticed that its colour pattern consists of a series of closely positioned lines of dots, a pattern very different from the Cretan material. *Chelyconus spongiopictus* Sacco, 1893 (Sacco 1893b: pl. 10 fig. 16) has a morphology of similar outline, but lacks the subangulated shoulder of the studied species. The colour pattern of irregular blotches and spiral lines of dots is similar to that of *Conus* (*Stephanoconus*) cf. *taurinensis* Bellardi & Michelotti, 1841. They are easily differentiated by the pyriform morphology of this specimen, with no tubercles and a not so inflated shoulder.

Stratigraphic range

?Tortonian of Italy from Montegibbio (Davoli 1972) and Greece (Messara Basin, Crete).

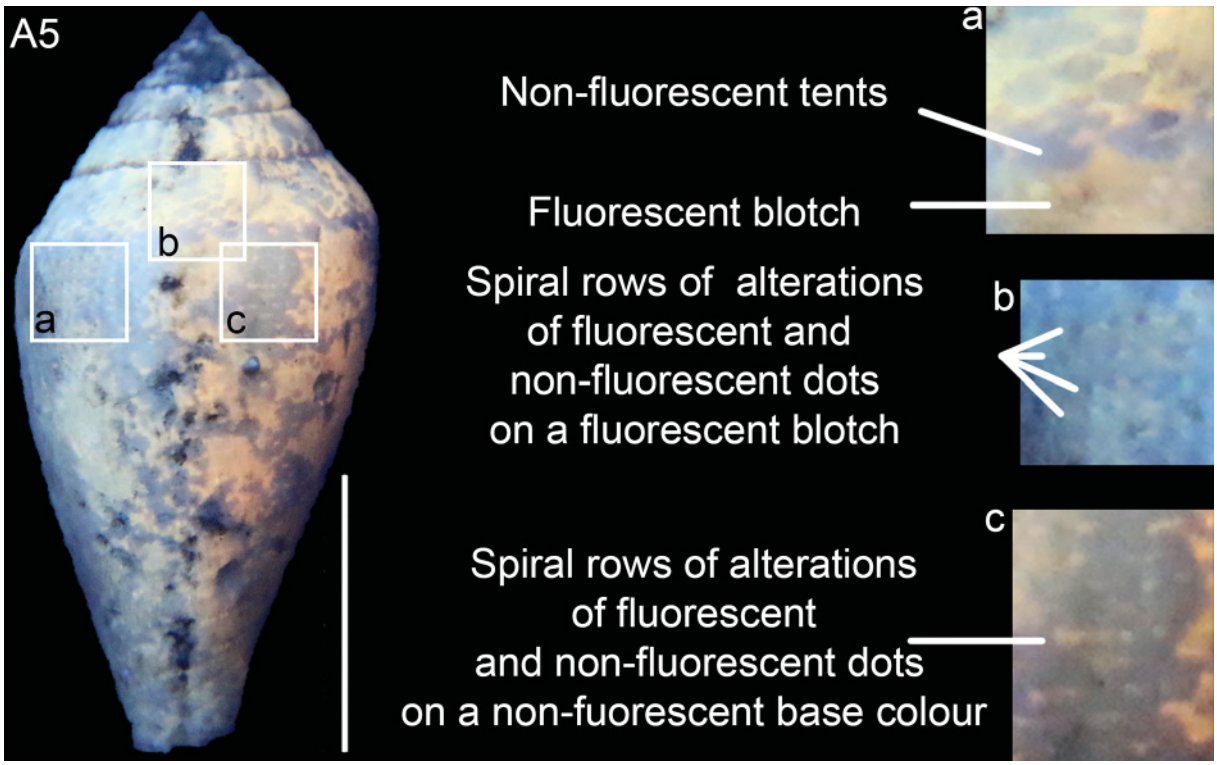

Fig. 19. Colour pattern elements of *Conus* (*Lautoconus*) sp. 5 from the Tortonian of Filippi, Crete (Greece). **A5**. Specimen AMPG(IV) 3861, on abapertural view. Scale bar = 1 cm.

Concluding remarks about Conus (Lautoconus)

Two species, *Conus* (*Lautoconus*) *eschewegi* Pereira da Costa 1866 and *Conus* (*Lautoconus*) *lauriatragei* sp. nov., are mentioned in the Paratethys and mainly from the Pannonian Basin. Eight species, *Conus* (*Lautoconus*) *eschewegi* Pereira da Costa 1866, *Conus* (*Lautoconus*) *ictini* sp. nov., *Conus* (*Lautoconus*) sp. 2, *Conus* (*Lautoconus*) sp. 3, *Conus* (*Lautoconus*) cf. *baldichieri*, *Conus* (*Lautoconus*) *damianakisi* sp. nov., *Conus* (*Lautoconus*) sp. 4 and *Conus* (*Lautoconus*) sp. 5 are present in the Proto-Mediterranean (see Table 18). *Conus* (*Lautoconus*) sp. 1 is a species found only in Crete. Finally, this species assemblage suggests a much stronger relationship with the Proto-Mediterranean faunas than with the Paratethyan faunas.

The PCA graph (Fig. 20) shows that the species are morphologically similar and point out the necessity of the colour patterns as an extra characteristic for their identification (Psarras *et al.* 2021).

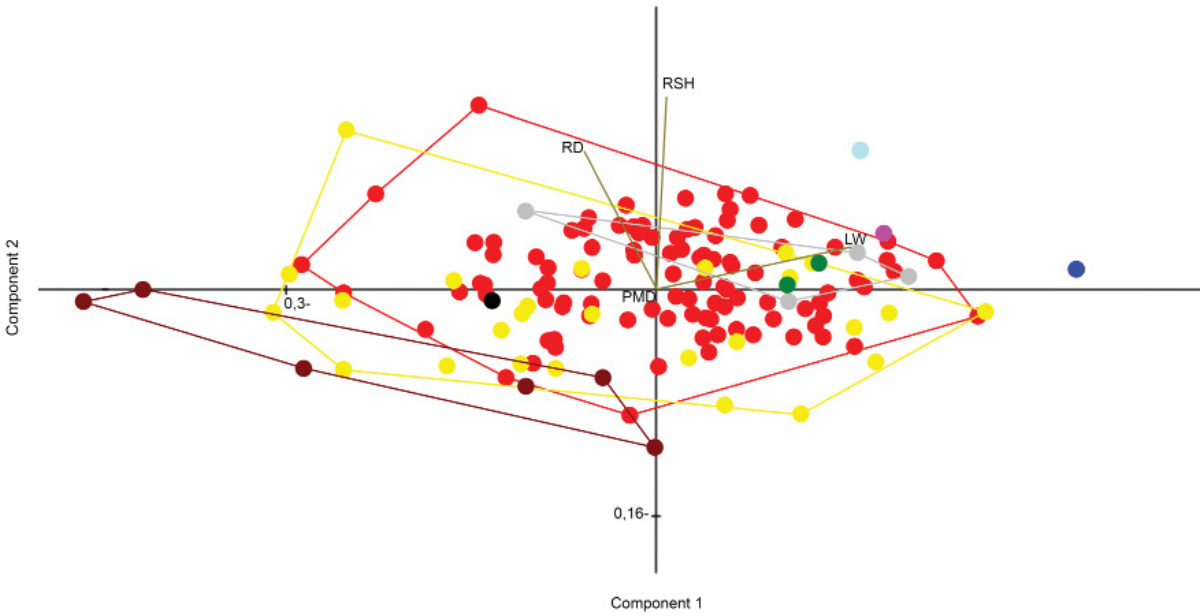

Fig. 20. PCA graph with nine species of *Conus* (*Lautoconus*) found in late Miocene localities of Crete (Greece). *Conus* (*Lautoconus*) sp. 1 is broken and cannot be included in the graph. Yellow dots = *Conus* (*Lautoconus*) *eschewegi* (Pereira da Costa, 1866); grey dots = *Conus* (*Lautoconus*) *ictini* sp. nov.; red dots = *Conus* (*Lautoconus*) sp. 2; blue dot = *Conus* (*Lautoconus*) sp. 3; black dot = *Conus* (*Lautoconus*) *lauriatragei* sp. nov.; brown dots = *Conus* (*Lautoconus*) *damianakisi* sp. nov.; purple dot = *Conus* (*Lautoconus*) cf. *baldichieri* Borson, 1820; green dots = *Conus* (*Lautoconus*) sp. 4; light blue dot = *Conus* (*Lautoconus*) sp. 5. Abbreviations: LW = length width ratio; PMD = position of maximum diameter; RD = relative diameter; RSH = relative height of spire.

Subgenus Conus (Stephanoconus) Mörch, 1852

Subgenus ***Conus* (*Stephanoconus*)** Mörch, 1852

Type species

Conus leucostictus Gmelin, 1791 accepted as *Conus regius* Gmelin, 1791 (type by subsequent designation Wenz 1943: 1469). Recent, tropical West Atlantic.

Descriptive comments

The nodules on the spire whorls occur on most extant species, except on *Conus* (*Stephanoconus*) *genuanus* Linnaeus, 1758 and can either fade out or persist in later spire whorls. Some species also have spiral ribs on the body whorl. The protoconch is multispiral. The colour pattern consists of spiral bands (two to three), axial blotches, spiral rows of small to large dots and dashes, in colours of shades brown, cream and white. All *Conus* (*Stephanoconus*) feed on Polychaeta have a similar radular morphology (Tucker & Tenorio 2009).

Remarks

According to Puillandre *et al*. (2015), the subgenus occurs in all tropical seas. The phylogenetic trees of Lin *et al*. (2021: fig. 2) and Torres *et al*. (2021: fig. 5), recently found *Conus genuanus* Linnaeus, 1758 in a clade of *Stephanoconus*. This species shares a similar colour pattern with the other species of the subgenus, but lacks nodules on the spire. Tucker & Tenorio (2009) noted that nodules are an important morphological element of this genus and, thus, did not find the connection of *Conus genuanus* to other species of this group plausible. Here, we follow Lin *et al.* (2021) and Torres *et al*. (2021) in including *Conus genuanus* in *Conus* (*Stephanoconus*).

Another point to investigate is the close phylogenetic relationship between *Conus* (*Stephanoconus*) *genuanus* Linnaeus, 1758 and *Conus* (*Stephanoconus*) *chiangi* Azuma, 1972, an Indo-Pacific species (Lin *et al*. 2021: fig. 2). Their phylogenetic proximity evidently points towards the closure of the Tethys Ocean, acting as a barrier and isolating the populations.

In Psarras *et al*. (2021), we considered that *Conus* (*Kalloconus*) *asterousiaensis* Psarras, Koskeridou & Merle, 2021 is very similar to *Conus genuanus*, both in morphology and colour pattern variations. The characters used to assign *Conus asterousiaensis* to *Conus* (*Kalloconus*) were the morphology of the conical smooth spire and the multispiral protoconch. This subgeneric attribution was done, but before the phylogenetic works of Lin *et al.* (2021) and Torres *et al*. (2021) became available, and *Conus* (*Stephanoconus*) *genuanus* has previously been included in other subgenera (e.g., in *Kalloconus* da Motta, 1991 by da Motta (1991) and in *Genuanoconus* Tucker & Tenorio, 2009 by Tucker & Tenorio (2009)). The colour pattern of *Conus asterousiaensis* is similar to that of most species of *Conus* (*Stephanoconus*), prompting us to consider it as a member of *Conus* (*Stephanoconus*).

Conus* (*Stephanoconus*)** cf. ***taurinensis Bellardi & Michelotti, 1841
Figs 21–25, 40K; Table 11

Conus sp. 1 – Caze 2010: p. 61 fig. 33c.
Conus aff. *clavatus* – Erünal-Erentöz 1958: pl. 19 fig. 5 [non *Conus clavatus* Lamarck, 1810].
Varioconus taurinensis – Landau *et al.* 2013: 251–252, pl. 41 figs 5–6, 10, pl. 42 fig. 13, pl. 82 figs 6–7.

Material examined

GREECE – **Crete** • 4 specs; 1990; Action spécifique du Muséum project (1989–1990) exped.; MNHN.F.A83016 to MNHN.F.A83019 • 4 specs; same collection data as for preceding; MNHN.F.A83020

to MNHN.F.A83023 • 8 specs; same collection data as for preceding; MNHN.F.A83024 to MNHN.F.A83031 • 1 spec.; same collection data as for preceding; MNHN.F.A83032 • 3 specs; same collection data as for preceding; MNHN.F.A83033 to MNHN.F.A83035 • 2 specs; same collection data as for preceding; MNHN.F.A83036 to MNHN.F.A83037 • 1 spec.; same collection data as for preceding; MNHN.F.A83038 • 1 spec.; same collection data as for preceding; MNHN.F.A83039 • 1 spec.; same collection data as for preceding; MNHN.F.A83040 • 3 specs; same collection data as for preceding; MNHN.F.A83041 to MNHN.F.A83043 • 3 specs; same collection data as for preceding; MNHN.F.A83044 to MNHN.F.A83046 • 3 specs; same collection data as for preceding; MNHN.F.A83047 to MNHN.F.A83049 • 1 spec.; same collection data as for preceding; MNHN.F.A83050 • 1 spec.; same collection data as for preceding; MNHN.F.A83051 • 1 spec.; same collection data as for preceding; MNHN.F.A83052 • 6 specs; same collection data as for preceding; MNHN.F.A83053 to MNHN.F.A83058 • 1 spec.; same collection data as for preceding; MNHN.F.A83059 • 1 spec.; same collection data as for preceding; MNHN.F.A83060 • 1 spec.; same collection data as for preceding; MNHN.F.A83061 • 6 specs; same collection data as for preceding; MNHN.F.A83062 to; MNHN.F.A83067 • 2 specs; same collection data as for preceding; MNHN.F.A83068 to MNHN.F.A83069 • 1 spec.; Psalidha; 35.085° N, 24.962° E; MNHN.F.A83070 • 1 spec.; Filippi; 35.035° N, 25.250° E; Efterpi Koskeridou leg.; AMPG(IV) 3808 • 5 specs; same collection data as for preceding; AMPG(IV) 3809 to AMPG(IV) 3813 • 1 spec.; same locality; 2017; Christos Psarras leg.; AMPG(IV) 3814 • 1 spec.; same collection data as for preceding; AMPG(IV) 3815 • 2 specs; same collection data as for preceding; AMPG(IV) 3816 to AMPG(IV) 3817 • 1 spec.; same locality; AMPG(IV) 3818 • 1 spec.; same collection data as for preceding; AMPG(IV) 3819 • 2 specs; same collection data as for preceding; AMPG(IV) 3820 to AMPG(IV) 3821 • 1 spec.; same collection data as for preceding; AMPG(IV) 3822 • 1 spec.; same locality; 2017; Christos Psarras leg.; AMPG(IV) 3823 • 1 spec.; Partira; Efterpi Koskeridou leg.; AMPG(IV) 3824 • 1 spec.; Tefeli; Efterpi Koskeridou leg.; AMPG(IV) 3825 • 2 specs; same collection data as for preceding; AMPG(IV) 3826 to AMPG(IV) 3827 • 4 specs; same collection data as for preceding; AMPG(IV) 3828 to AMPG(IV) 3831.

Shell description

Usually small to rarely medium-sized shells (SL max.: 52.5 mm) (Fig. 22). Spire elevated, conical. Outline of spire whorls variable in shape, with height, ranging from medium to high (Fig. 22). Early spire whorls elevated, convex, striate, creating straight to highly conical outline, tuberculated, with faint spiral cords on early sutural ramps. Later spire whorls smooth, elongate, convex, not always in symmetry to surrounding spire whorls, with late spire whorls usually inflated and more robust. Suture incised, slightly undulated. Subsutural flexure shallow, moderately curved, moderately asymmetrical (Fig. 40K). Shoulder smooth to weakly angular, with maximum diameter just below shoulder. Last whorl elongated, curved. Aperture narrow, widening slightly towards fasciole. Siphonal canal short, straight. Siphonal fasciole indistinct. Faint spiral grooves visible on one fifth anterior part of body.

Description of colour pattern

The colour pattern consists of two levels of colouration. The first one is a pattern of irregular blotches (Fig. 23) of variable size, sometimes with zig-zag boundaries (Fig. 22B) or non-continuous spiral bands on the middle and anterior parts of the shell (Fig. 22C, F, H). The pattern might continue on spire whorls as irregular, thin, flammulated blotches (Fig. 24). The second level consists of evenly arranged, spiral rows of wavy dashes and dots (Figs 23–24). The spiral rows start at the shoulder of the shell, continuing spirally towards the anterior part. The spiral rows exists in between the spiral grooves. On some specimens of exceptional preservation, the spiral lines of dashes and dots are better displayed as continuous fluorescent wavy lines, with interruptions of grey coloured oval dots (Fig. 24). These dots are visible even under natural light (Figs 21A, C, 23). When the lines cover the first pattern of irregular blotches, the second pattern is seen as bright-fluorescent (Fig. 24), while the grey coloured oval dots are

often presumed to be part of the base colour, which is not the case. Spiral rows are often not visible in shells of no exceptional preservation.

Remarks

The Cretan specimens are very similar to *Conus taurinensis* Bellardi & Michelotti, 1841. To our knowledge, the type specimens of *Conus taurinensis* Bellardi & Michelotti, 1841, discussed by Sacco (1893b), Hall (1966) and Ferrero Mortara (1984), are stored in the Museo Regionale di Scienze Naturali,

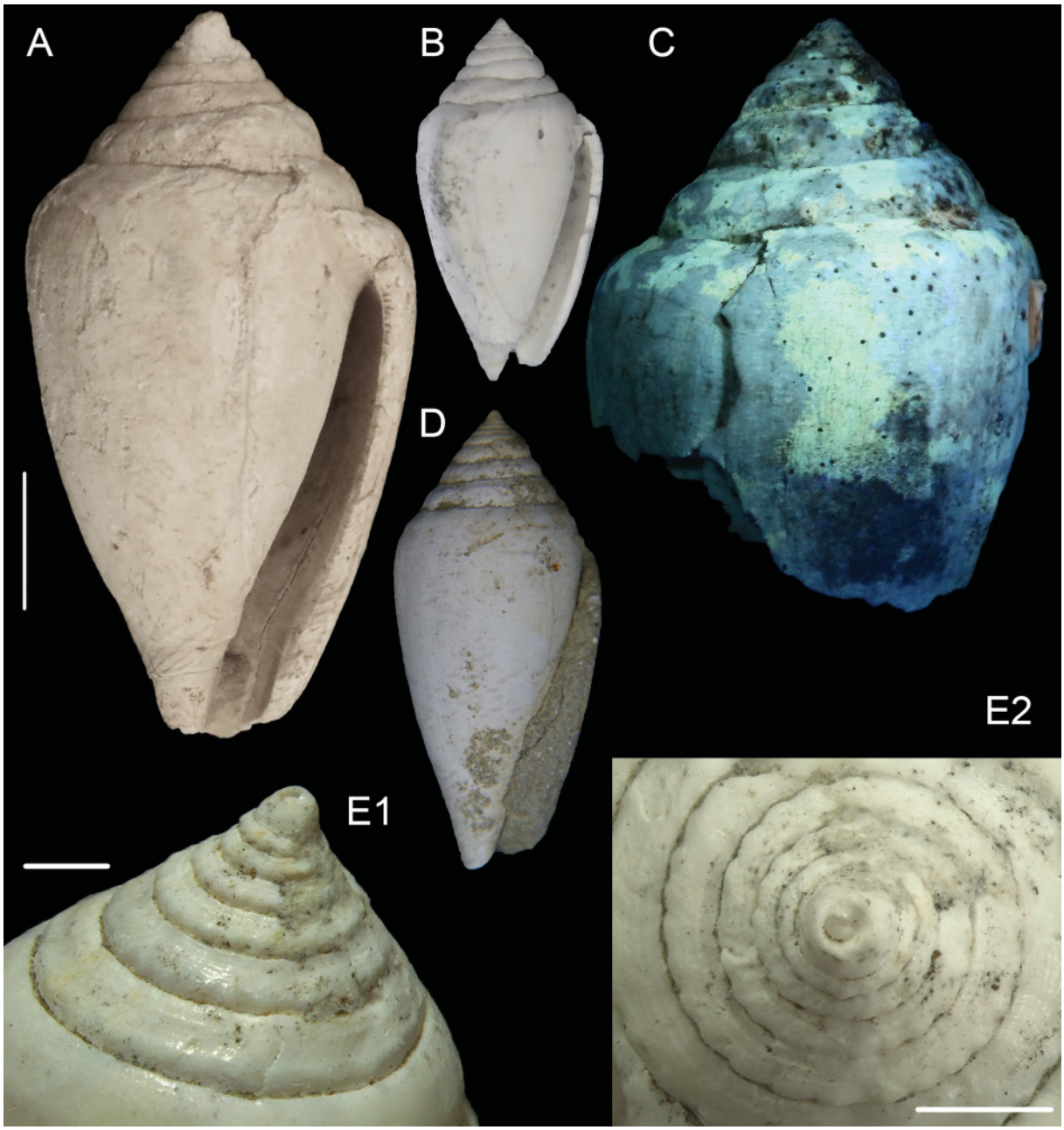

Fig. 21. *Conus* (*Stephanoconus*) cf. *taurinensis* Bellardi & Michelotti, 1841 from the Tortonian of Crete (Greece) in apertural and apical views, under natural and UV (C) light. **A**. Specimen AMPG(IV) 3808, Tefeli. **B**. Specimen MNHN.F.A83060. **C**. Specimen MNHN.F.A83070, Psalidha. **D**. Specimen AMPG(IV) 3815, Filippi, Crete. **E**. Specimen MNHN.F.A83051, Crete. Scale bars = 1 cm.

Turin, Italy (Annalaura Pistarino pers. comm.) (syntype MRSN BS.038.05.163), but no colour patterns are preserved. Hall (1966) stated that the type specimens of *Conus taurinensis* possess spiral cords on their last whorl. However, these specimens are very worn. Due to the bad preservation and the lack

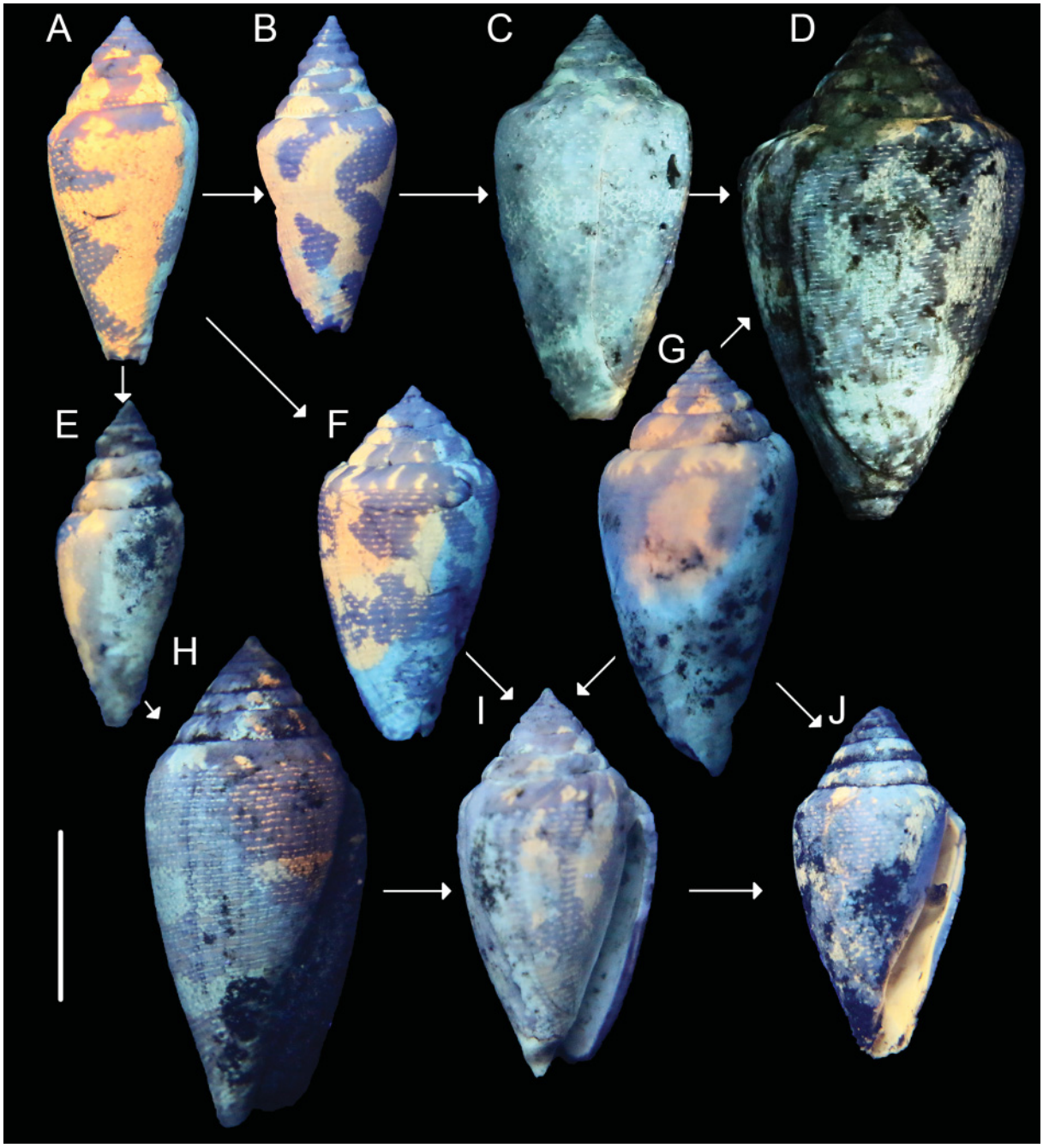

Fig. 22. Morphotypes of *Conus* (*Stephanoconus*) cf. *taurinensis* Bellardi & Michelotti, 1841 from the Tortonian of Crete (Greece) in apertural and abapertural views and under UV light. Arrows show the similarities of the morphotypes figured herein. **A**. Specimen MNHN.F.A83061. **B**. Specimen MNHN.F.A83024. **C**. Specimen MNHN.F.A83044. **D**. Specimen AMPG(IV) 3814. **E**. Specimen AMPG(IV) 3819. **F**. Specimen MNHN.F.A83052. **G**. Specimen AMPG(IV) 3818. **H**. Specimen AMPG(IV) 3815. **I**. Specimen MNHN.F.A83060. **J**. Specimen AMPG(IV) 3823. Scale bar = 1 cm.

of colour patterns of the type material of *C. taurinensis*, we refrain from attributing with certainty the Cretan specimens to this species until more topotypes with colour patterns are observed.

Erünal-Erentöz (1958) identified similar material from the Tortonian of the Adana Basin (Turkey) as *Conus* aff. *clavatus* Lamarck, 1810, a species originally described from the early Miocene (Aquitanian) of Dax, France. The type specimen of *Conus clavatus* Lamarck, 1810 (MHNG GEPI 46266, Lionel Cavin pers. comm.; Decrouez 1993) differs from the Turkish specimen, by the smooth and conical early spire whorls. Landau *et al.* (2013: pl. 12 figs 6–7) also figured one Turkish specimen as *Varionoconus taurinensis* (Bellardi & Michelotti, 1841), this time with a visible colour pattern which is identical to that of the Cretan specimens. We consider the specimens of both Erünal-Erentöz (1958) and Landau *et al.* (2013) as conspecific to *Conus* cf. *taurinensis.*

Stratigraphic range

Serravallian of Turkey (Karaman Basin) (Landau *et al.* 2013); Tortonian of Turkey (Adana Basin) (Erünal-Erentöz 1958) and Greece (Messara Basin and Heraklion Basin, Crete) (this work).

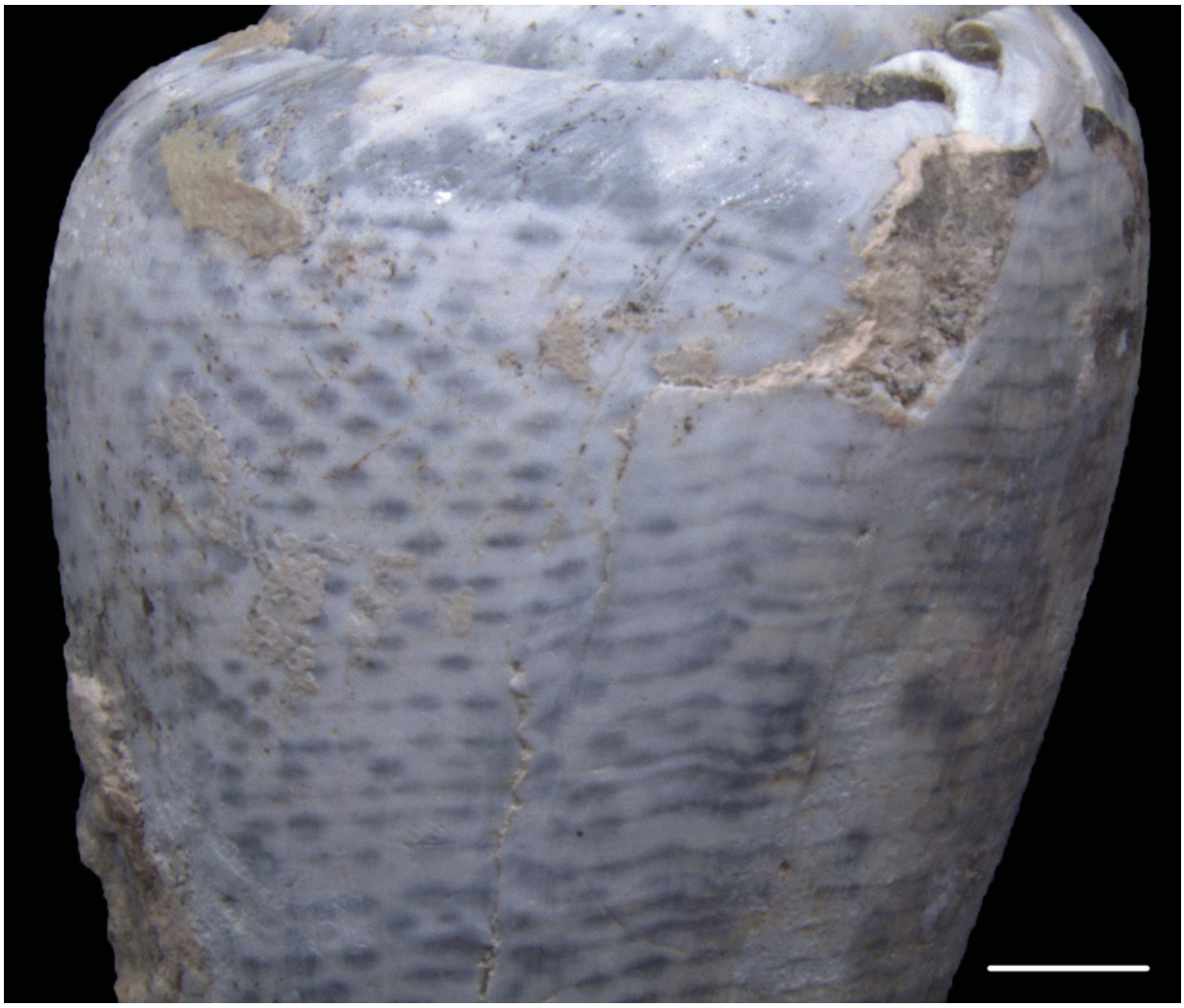

Fig. 23. *Conus* (*Stephanoconus*) cf. *taurinensis* Bellardi & Michelotti, 1841 from the Tortonian of Crete (Greece), showing excellent preservation under natural light. AMPG(IV) 3822: the continuous spiral pattern of dots and dashes, as well as the blotches on the spire whorls, are clearly visible. Scale bar = 2 mm.

Table 11. Shell measurements and ratios of *Conus* (*Stephanoconus*) cf. *taurinensis* Bellardi & Michelotti, 1841 from the Tortonian of Crete (Greece). Mean and standard deviation are computed from 79 specimens. The largest specimen is AMPG(IV) 3808.

	SL	MD	AH	HMD	AL	SA	LWA
Largest specimen	52.5 mm	28.44 mm	39.27 mm	31.05 mm	39.69 mm	80.3°	44°
Mean	21.6 mm	10.8 mm	16.4 mm	13.6 mm	16.5 mm	74.2°	36.5°
Standard deviation	7.24	4.24	5.64	4.64	5.51	11.55	3.64
	LW	**RD**	**PMD**	**RSH**	**SSFD**	**SSFd**	**PV**
Largest specimen	1.85	0.72	1.01	0.25	2	6.2	0.35
Mean	2.07	0.64	0.83	0.24	2.47	5.79	0.53
Standard deviation	0.15	0.04	0.05	0.04	0.67	1.80	0.19

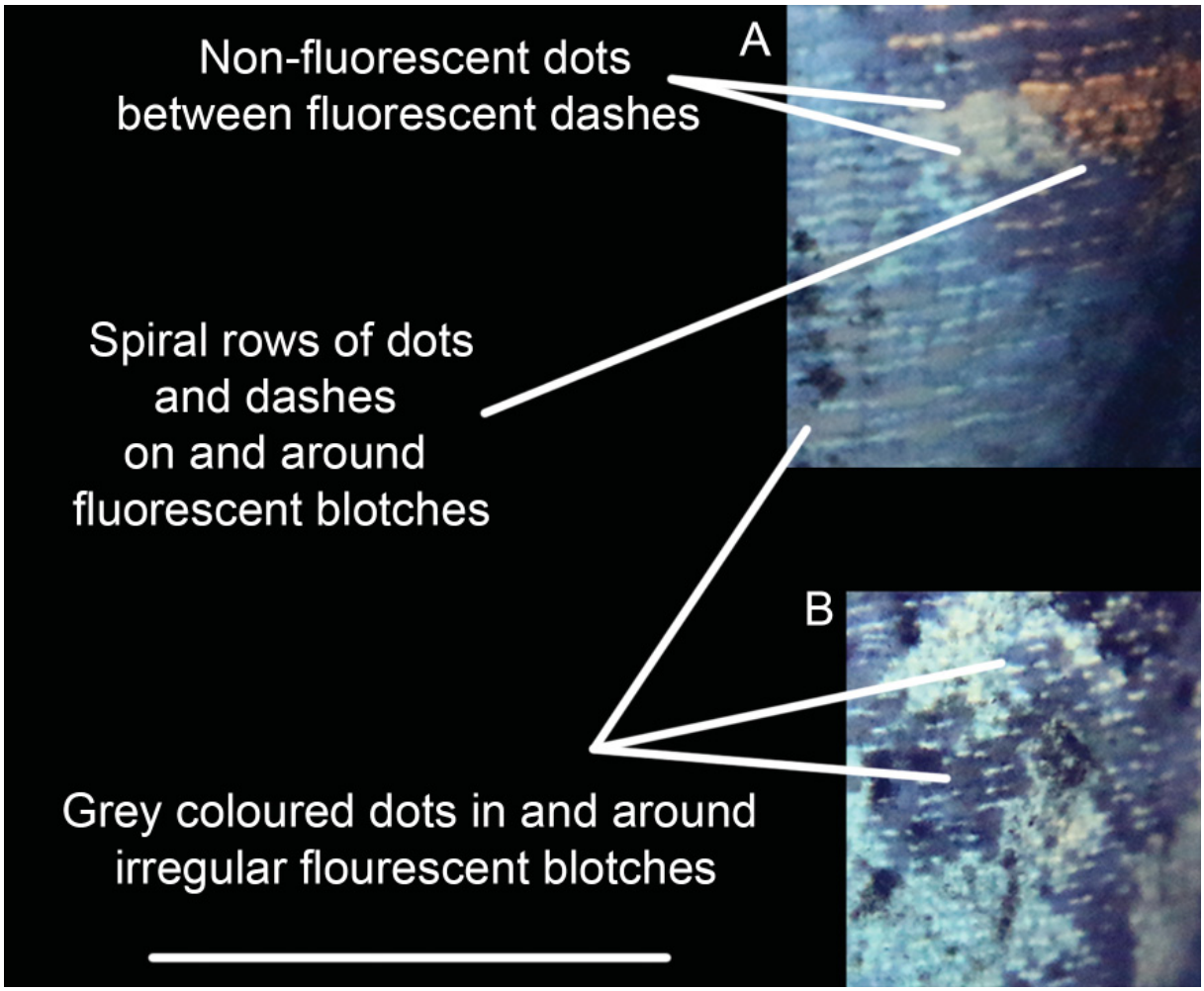

Fig. 24. *Conus* (*Stephanoconus*) cf. *taurinensis* Bellardi & Michelotti, 1841 from the Tortonian of Crete (Greece), showing a colour pattern variation under UV light. **A**. Specimen AMPG(IV) 3814. **B**. Specimen AMPG(IV) 3815. Scale bar = 1 cm.

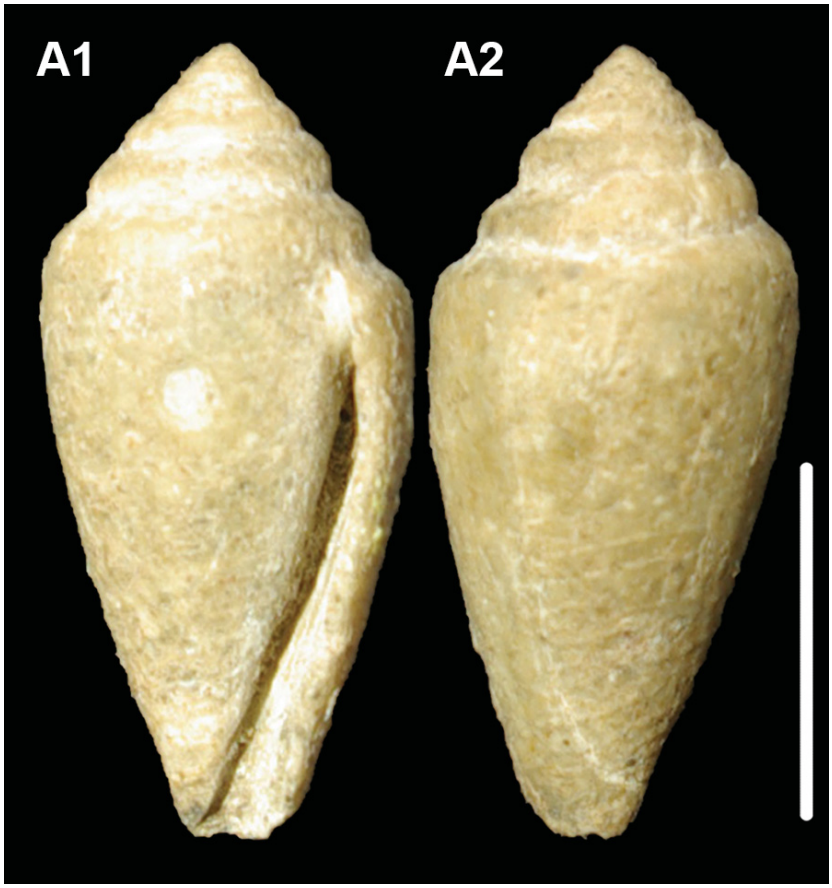

Fig. 25. *Conus* (*Stephanoconus*) *taurinensis* Bellardi & Michelotti, 1841, stored at the Museo Regionale di Scienze Naturali, Turin, syntype MRSN BS.038.05.163, Colli Torinesi (Italy), Burdigalian. Scale bar = 1 cm.

Conus* (*Stephanoconus*) *moissettei sp. nov.
urn:lsid:zoobank.org:act:057EF9CB-D76D-47D3-9545-699C1B7F5454
Figs 26–28, 40L; Table 12

Etymology

Species named after Pierre Moissette, member of the Action spécifique du Muséum project (1989–1990).

Material examined

Holotype

GREECE – **Crete** • Adhraktia; Messara Basin; 1990; Action spécifique du Muséum project (1989–1990) exped.; MNHN.F.A83071.

Paratypes

GREECE – **Crete** • 2 specs; same collection data as for holotype; MNHN.F.A83072, MNHN.F.A83073.

Other material

GREECE – **Crete** • 1 spec.; 1990; Action spécifique du Muséum project (1989–1990) exped.; MNHN.F.A83074 • 1 spec.; 1990; same collection data as for preceding; MNHN.F.A83075 • 1 spec.;

1990; same collection data as for preceding; MNHN.F.A83076 • 5 specs; 1990; same collection data as for preceding; MNHN.F.A83077 to MNHN.F.A83081.

Shell description

Small shells (SL max.: 24.17 mm). Early spire whorls elevated, convex to conical, tuberculated. Later spire whorls smooth, straight to convex, with channelled suture. Spire whorl outline conical to slightly coeloconoid in early spire whorls, conical to convex in later spire whorls. Subsutural flexure shallow,

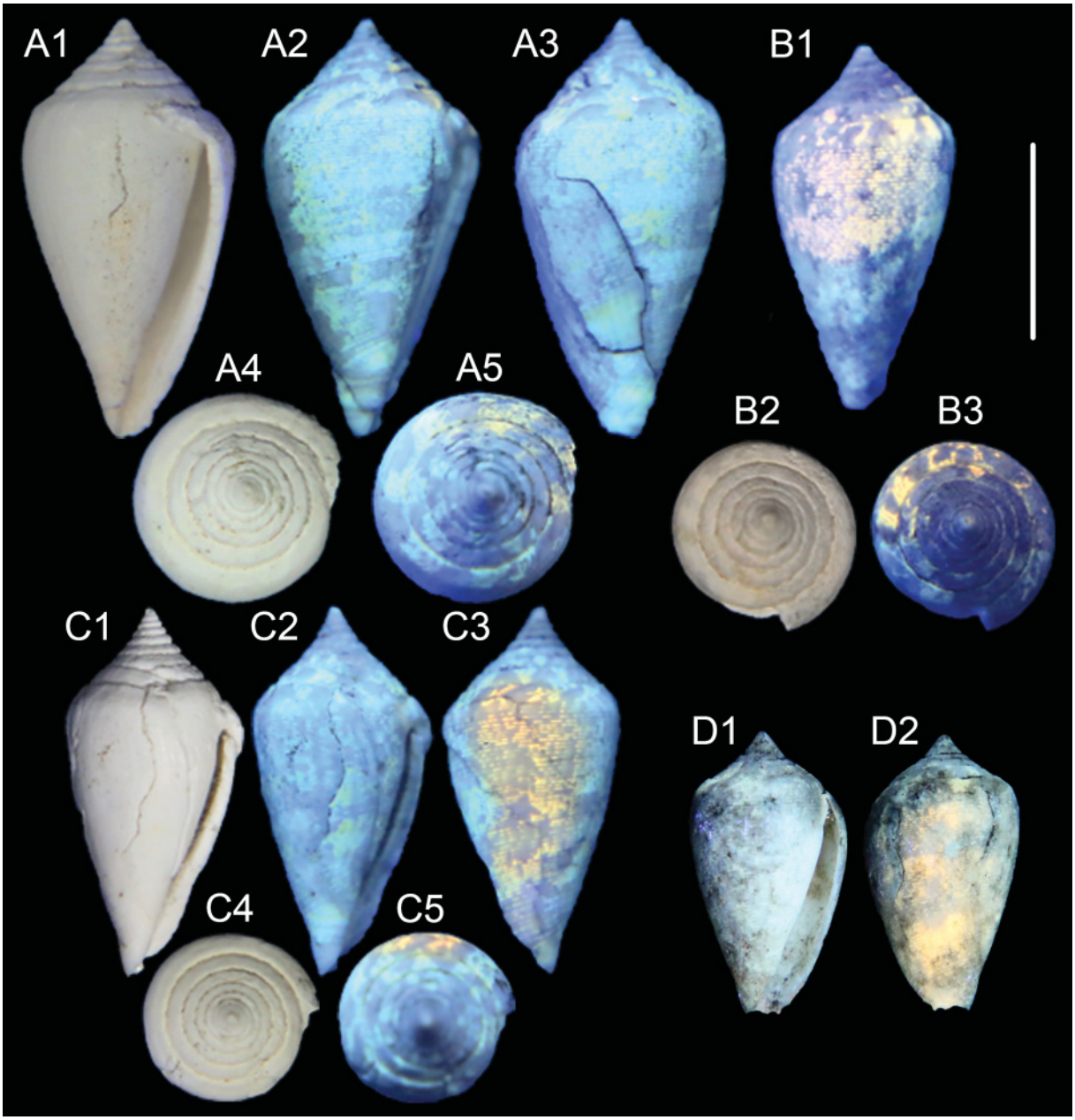

Fig. 26. *Conus* (*Stephanoconus*) *moissettei* sp. nov. from the Tortonian of Adhraktia, Crete (Greece) shown in apertural view under natural (A1, A4, B1, B4, C1, C4) and UV light. **A**. Holotype MNHN.F.A83071: the largest specimen showing a spectacular green fluorescent pattern. **B**. Paratype MNHN.F.A83072: paratype with orange colour pattern on abapertural view. **C**. Paratype MNHN.F.A83073: paratype with intact early spire whorls. **D**. MNHN.F.A83075, Crete. Scale bar = 1 cm.

moderately curved, moderately asymmetrical (Fig. 40L). Shoulder smooth, rounded to slightly angulated, with maximum diameter right below shoulder. Aperture of narrow to medium width, widening towards shell's anterior part. Last whorl straight to slightly widened below shoulder. Fasciole short, slightly twisted. No spiral grooves on last whorl.

Description of colour pattern

On the spire whorls, the colour pattern consists of irregular, bright-fluorescent flammulae. On the last whorls, the first colour pattern level consists of three, widely spaced, fluorescent spiral bands. The bands exist near the shoulder, at the middle and anterior parts of the last whorl. The second level consists of very closely arranged, spiral lines of dashes, which can vary from very long to dot-like dashes (Fig. 27). In between the dashes, non-fluorescent dashes exist, usually creating axially to diagonally spaced, non-fluorescent areas, in the form of blotches. The intensity of the fluorescent colours is not constant in the levels of patterns (Fig. 28). The first level is illuminated with a fade-fluorescent colour. The colour intensity of the second level is axially directed, from fade-fluorescent to bright-fluorescent in colour, creating axially arranged, bright-fluorescent areas of dashes, suppressed by non-fluorescent blotches. The non-fluorescent dashes, between the fluorescent ones, are visible when the second pattern overlaps the first.

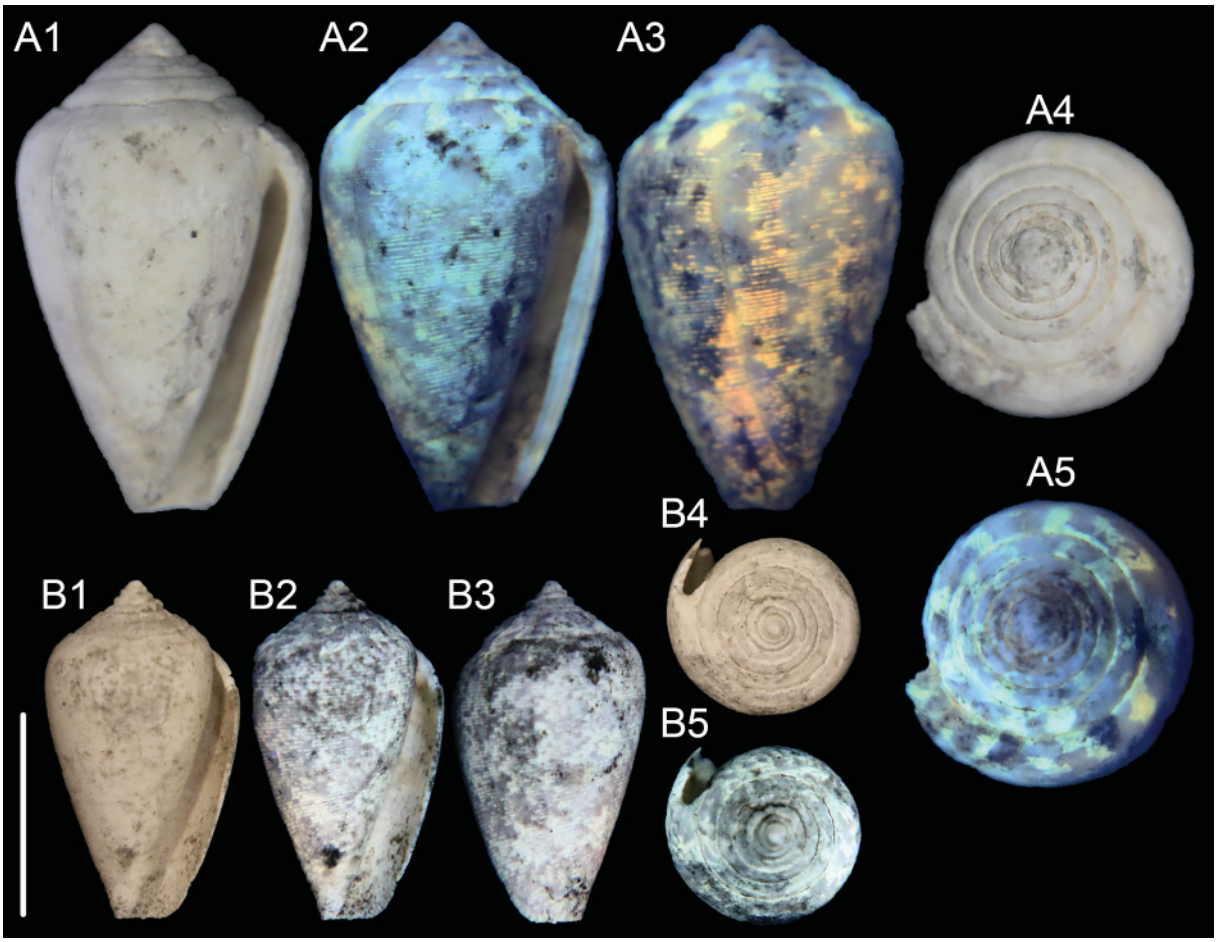

Fig. 27. Specimens of *Conus* (*Stephanoconus*) *moissettei* sp. nov. from the Tortonian of Crete (Greece), shown under natural (A1, A4, B1–B4) and UV light. **A**. Specimen MNHN.F.A83076, Crete: the largest specimen of the collection. **B**. Specimen MNHN.F.A83074, Crete. Scale bar = 1 cm.

Table 12. Shell measurements and ratios of *Conus* (*Stephanoconus*) *moissettei* sp. nov. from the Tortonian of Crete (Greece). Mean and standard deviation are computed from eight specimens. The largest specimen is MNHN.F.A83076.

	SL	MD	AH	HMD	AL	SA	LWA
Largest specimen	24.17 mm	14.5 mm	19.24 mm	15.1 mm	20.09 mm	96.8°	45.4°
Mean	17.32 mm	9.45 mm	13.62 mm	10.9 mm	14.13 mm	88.3°	41.66°
Standard deviation	4.03	2.46	3.31	2.92	3.46	8.91	2.64
	LW	**RD**	**PMD**	**RSH**	**SSFD**	**SSFd**	**PV**
Largest specimen	1.67	0.75	0.78	0.20	–	–	–
Mean	1.85	0.69	0.80	0.22	2.8	5.2	0.5
Standard deviation	0.15	0.05	0.04	0.02	–	–	–

Remarks

This species is identifiable from the rest of the studied specimens in the small size of the shells and the intricate colour pattern variation of dashes and bands. *Conus* (*Stephanoconus*) cf. *taurinensis* is distinguishable from this species by the early highly conical spire whorls, the smoother spire whorl outline, with less inflated sutural ramps and a different colour pattern. The shell shape of *Conus* (*Stephanoconus*) *moissettei* sp. nov. resembles a specimen of *Conus* (sensu lato) *vindobonensis* Hoernes & Auinger, 1879 (Harzhauser & Landau 2016: fig. 35e and discussion), but the Austrian species differs by a more elongated shell shape, a deeper subsutural flexure and spiral grooves on the anterior part of last whorl. Its colour pattern is not known.

Stratigraphic range

Tortonian of Greece (Crete) (this work).

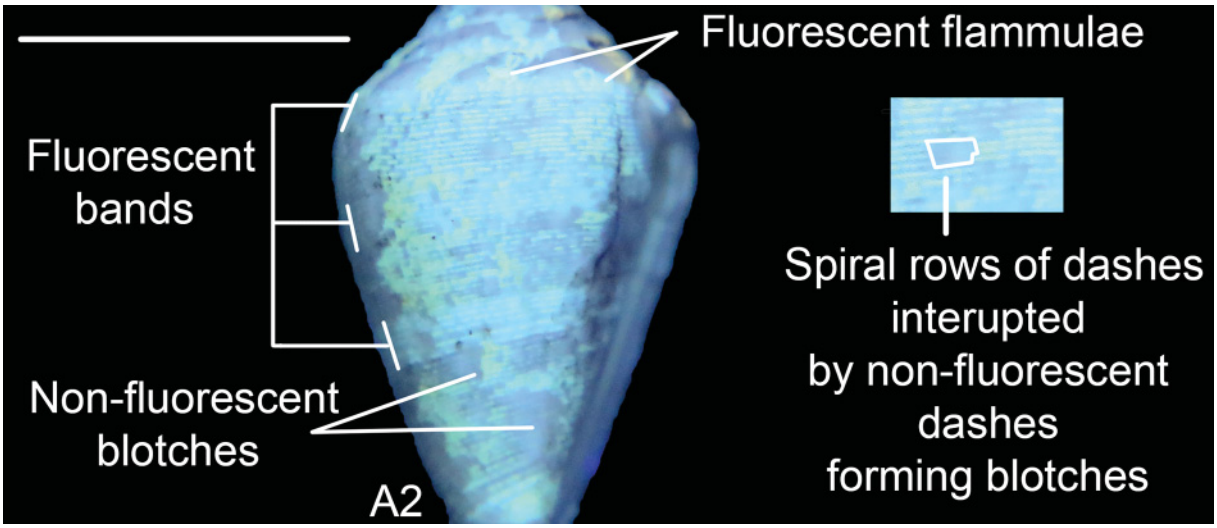

Fig. 28. Colour patterns of *Conus* (*Stephanoconus*) *moissettei* sp. nov., holotype (MNHN.F.A83071) from the Tortonian of Adhraktia Crete (Greece). Scale bar = 1 cm for the main shell, the orthogonal image on the right is enlarged by 150%.

Concluding remarks about Conus (Stephanoconus) Mörch, 1852

Here, this subgenus is identified in the Miocene of Europe for the first time. Three species are assigned to this subgenus: *Conus* (*Stephanoconus*) *asterousiaensis* (Psarras & Koskeridou & Merle, 2021), *Conus* (*Stephanoconus*) cf. *taurinensis* and *Conus* (*Stephanoconus*) *moissettei* sp. nov. The phylogenetic tree of Lin *et al*. (2021: fig. 2) points to *C. genuanus* and *C. chiangi* being closely related (see Remarks for *Conus* (*Stephanoconus*). The Cretan species represent a link between the West African and the Indo-Pacific species.

Subgenus Conus (Plagioconus) Tucker & Tenorio, 2009

Subgenus ***Conus* (*Plagioconus*)** Tucker & Tenorio, 2009

Type species (by original designation)

Conus elatus Michelotti, 1847. Burdigalian of Italy (Colli Torinesi) (Hall 1966); Langhian of Paratethys (see Harzhauser & Landau 2016 for more references); Tortonian of Italy (Sant'Agatha fossili, Stazzano, Montegibbio) (Sacco 1893a) and Greece (Messara Basin, Crete) (this work).

Diagnosis

Elongated last whorl, medium to high spire whorl height, beaded early spire whorls. Spiral sculpture on the ramp finely to distinctly striate. Subsutural flexure shallow (Tucker & Tenorio 2009). Deep-very deep, moderately-strongly asymmetrical, moderately-strongly curved, subsutural flexures (Harzhauser & Landau 2016).

Remarks

Tucker & Tenorio (2009) first described *Plagioconus* at genus level and were followed by Harzhauser & Landau (2016), who, in turn, proposed an emended description, according to their Paratethyan species. On the other hand, Puillandre *et al.* (2014, 2015) placed many genera of Conidae as subgenera under the genus *Conus*. Morphologically, this group of species can be included in the genus *Conus*, thus, we refer here to *Plagioconus* at the subgeneric level.

Conus* (*Plagioconus*) *elatus Michelotti, 1847
Figs 29, 36, 40O; Table 13

Conus elatus mihi Michelotti, 1847: 341, pl. 13 fig. 16–16'.
Conus Puschi mihi Michelotti, 1847: 340, pl. 14 fig. 6. **Syn. nov**.

Conus elongatus nobis – Borson 1820: 198, pl. 1 fig. 4 (non *Conus elongatus* Holten, 1802). — Hall 1966: 145, pl. 25 figs 6, 10–13. — Davoli 1972: pl. 6 figs 20, 23–24.
Conus Puschi – Hörnes 1851: 35, pl. 4 figs 6–7. — Hall 1966: pl. 27 figs 10, 14, 19.
Conus (*Leptoconus*) *elatus* – Sacco 1893a: 35, pl. 4 figs 15, 17, 21, 25.
Conus (*Chelyconus*) *puschi* – Symeonidis 1965: pl. 14 figs 1–3 (AMPG(IV) 3862, AMPG(IV) 3864, AMPG(IV) 3880).
? *Conus puschi* – Davoli 1972: 128, pl. 8 figs 17–20.
Conus (*Leptoconus*) *extensus* – Chira & Voia 2001: 156, pl. 2 fig. 1a–b (non *Conus* (*Plagioconus*) *extensus* Hörnes, 1851).
Plagioconus marii – Kovács & Vicián 2013: 81, figs 101–105 (non *Conus* (*Plagioconus*) *marii* (Sacco, 1893)) (non fig. 108 = *Conus* (*Plagioconus*) *austriaconoe* (Sacco, 1893)). — Kovács & Balázs 2015: 26, figs 50–51.
Plagioconus elatus – Tucker & Tenorio 2009: 11, pl. 6 fig. 5. — Harzhauser & Landau 2016: 132–133, figs 30h, 32a–b.

Plagioconus puschi – Kovács & Vicián 2013: 81, figs 106–107. —Landau *et al*. 2013: 245, pl. 39 fig. 5, pl. 41 fig. 13, pl. 42 fig. 7, pl. 81 fig. 9. — Harzhauser & Landau 2016: 139–141, figs 30j, 33a1–a3, 33b1–b3, 33c1–c3.

Type locality

Tortona, Italy (Tortonian).

Type material

The type specimens are lost (Hall 1966), probably destroyed during WWII (Manni 2005; Hall pers. comm.).

Material examined

GREECE – **Crete** • 19 specs; Achladhia; 1964; Nikolaos Symeonidis leg.; AMPG(IV) 3862 to AMPG(IV) 3880 • 2 specs; same collection data as for preceding; AMPG(IV) 3885 to AMPG(IV) 3886 • 2 specs; same collection data as for preceding; AMPG(IV) 3888 to AMPG(IV) 3889 • 1 spec.; Psalidha; 35.085° N, 24.962° E; Christos Psarras leg.; 2018; AMPG(IV) 3900 • 1 spec.; 1990; Action spécifique du Muséum project (1989–1990) exped.; MNHN.F.A83093.

Shell description

Medium-large-sized shells (SL max.: 82.8 mm). Spire whorls of medium height, conical to convex in outline in early spire whorls, coeloconoid in late spire whorls. Early spire whorls conical, convex, slightly elevated. Middle spire whorls convex, with straight to convex sutural ramp. Last two to three whorls widened, with straight or inflated, deep suture. Absence of ornamentation along the sutural ramp. Subsutural flexure deep to very deep, rarely moderately deep, usually moderately to rarely strongly curved, strongly asymmetrical (Fig. 40O). Shoulder smooth, with weak angulation near external part of sutural ramp, more angulated on last whorl. Aperture straight, relatively narrow. Fasciole carved by growth lines. Last whorl straight conical.

Description of colour pattern

The colour pattern faintly exists in some shells in the form of axial flammulae in the spire whorls, parallel to the subsutural flexure. On the last whorl, some shells present continuous axially arranged stripes united with the flammulae of the spire whorls. Due to the bad preservation of the specimens, some partially preserve their stripes in the form of axial blotches (Fig. 29H2).

Remarks

Michelotti (1847) identified two morphotypes of *Conus* for which he gave two names, *elatus* and *puschi* respectively. The two species were differentiated mainly by the presence or absence of a widened last whorl and the angulation at shoulder. This difference was later illustrated in Sacco (1893b) and by Hall (1966). Davoli (1972) figured some extreme morphs of *Conus elatus*, but he failed to identify *Conus puschi*, as noted by Harzhauser & Landau (2016). Additionally, morphotypes of the Paratethyan *Conus puschi* possess shallower subsutural flexures than *Conus elatus* (Harzhauser & Landau 2016). Taking all this into account, we tried to identify our specimens based on morphology, as the colour patterns are poorly preserved or non-existent. The material mostly comes from one locality (Achladhia) and was previously assigned to *Conus puschi* (Symeonidis 1965; Symeonidis & Kostantinidis 1968). We identified several large sized specimens with a widened shoulder and angulations at the shoulder (Fig. 29F–G), which can be considered as '*elatus*' morphs. We also found shells with smooth spire whorls and almost no angulation at the shoulder (Fig. 29A), which can be considered as '*puschi*' morphs. Due to the large number of specimens, we were able to see their morphological variability (Table 13). We identified some shells with intermediate morphologies of smooth dome-shaped spire whorls (Fig. 29B–C) and

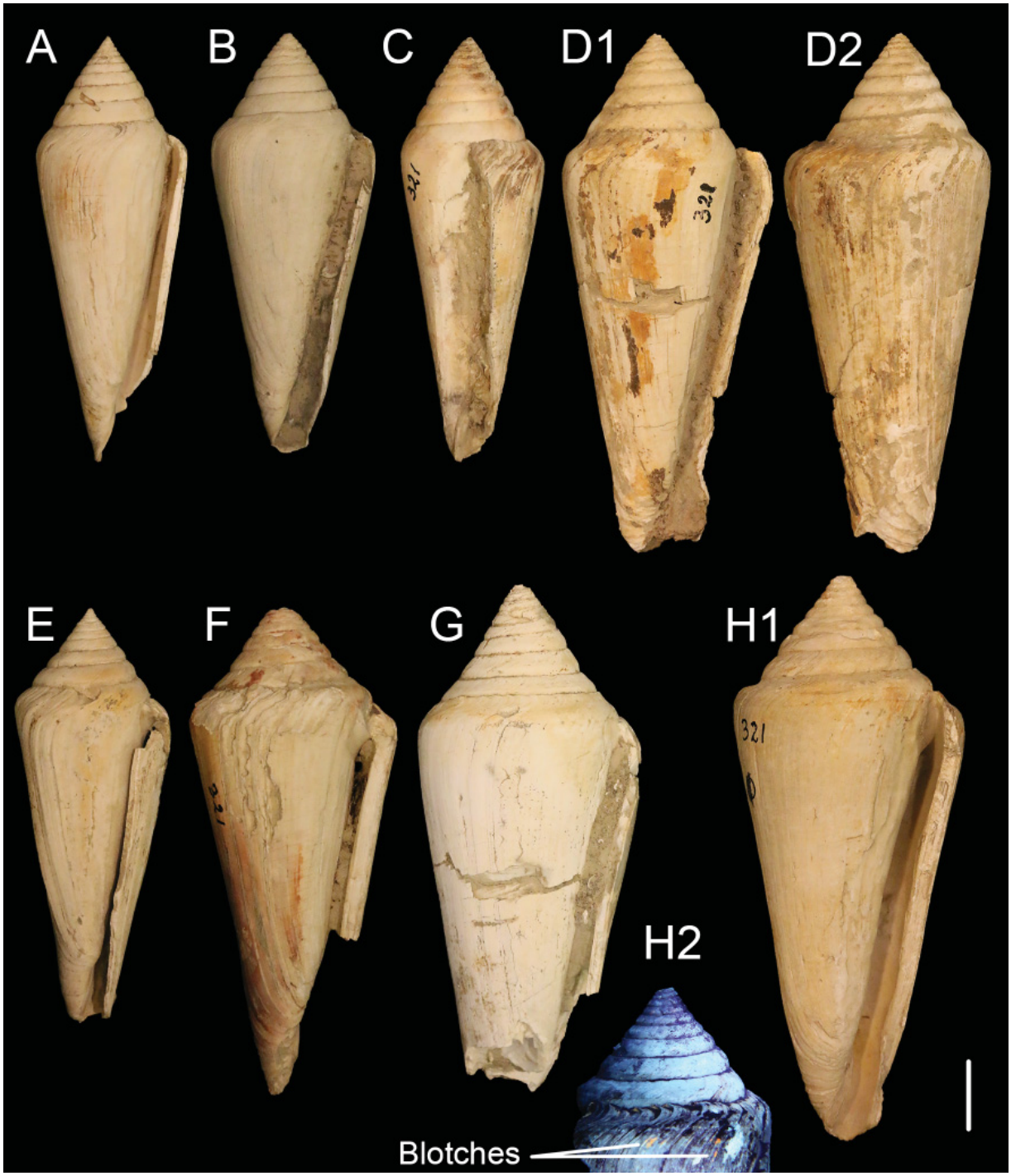

Fig. 29. *Conus* (*Plagioconus*) *elatus* Michelotti, 1847 from the Tortonian of Crete (Greece) on apertural and abapertural views under natural and UV (H2) light. **A**. Specimen AMPG(IV) 3875, Achladhia. **B**. Specimen AMPG(IV) 3867, Achladhia. **C**. Specimen AMPG(IV) 3876, Achladhia. **D**. Specimen AMPG(IV) 3865, Achladhia. **E**. Specimen AMPG(IV) 3864, Achladhia. **F**. Specimen AMPG(IV) 3863, Achladhia. **G**. Specimen AMPG(IV) 3900, Psalidha. **H**. Specimen AMPG(IV) 3862, Achladhia: Scale bar = 1 cm.

Table 13. Shell measurements and ratios of *Conus* (*Plagioconus*) *elatus* Michelotti, 1847 from the Tortonian of Crete (Greece). Mean and standard deviation are computed from 25 specimens. The largest specimen is AMPG(IV) 3862.

	SL	MD	AH	HMD	AL	SA	LWA
Largest specimen	82.8 mm	34.17 mm	66.87 mm	61.43 mm	66.74 mm	78.4°	22.2°
Mean	64.44 mm	22.94 mm	47.41 mm	40.75 mm	47.45 mm	68.59°	22.88°
Standard deviation	9.42	4.17	7.57	7.34	7.94	6.15	1.81
	LW	**RD**	**PMD**	**RSH**	**SSFD**	**SSFd**	**PV**
Largest specimen	2.42	0.51	0.92	0.19	1	5	0.43
Mean	2.14	0.40	0.75	0.17	1.12	5.45	0.26
Standard deviation	0.15	0.03	0.01	0.02	0.19	1.63	0.07

widened shoulder (Fig. 29D) and others with an angulated but normally arranged shoulder (Fig. 29H). Furthermore, the subsutural flexure was variable in individual shells, and some had shallower SSF than others. With this evidence, we consider the two morphs being the extremes of a single species.

The Cretan specimens could be compared to *Conus marii* Sacco, 1893 but they differ from the figured specimens of *Conus marii* illustrated by Hall (1966) and Harzhauser & Landau (2016) in the elevated and less inflated spire whorls.

Some of the studied specimens (Fig. 29A–D) are very similar to specimens of *Conus extensus* Partsch in Hörnes, 1856 illustrated by Chira & Voia (2001: pl. 2 fig. 1) and *Plagioconus marii* illustrated by Kovács & Vicián (2013: figs 101–105) and Kovács & Balázs (2015: figs 50–51). All of them display conical to slightly convex spires of medium height and are considered as conspecific to *Conus* (*Plagioconus*) *elatus* Michelotti, 1847.

Stratigraphic range

Burdigalian of Italy (Colli Torinesi) (Hall 1966); Langhian of Paratethys (Pannonian Basin (Kovács & Vicián 2013; Kovács & Balázs 2015), Transylvanian Basin (Chira & Voia 2001, see Harzhauser & Landau 2016 for more references); Tortonian of Italy (Sant'Agatha fossili, Stazzano, Montegibbio) (Sacco 1893a) and Greece (Messara an Sitia Basins, Crete) (this work).

***Conus* (*Plagioconus*)** sp.
Figs 30–31, 36, 40P–Q; Table 14

Conus (*Chelyconus*) *puschi* – Symeonidis & Konstantinidis 1968: pl. 7 fig. 3 (non fig. 17 = *Conus* (*Plagioconus*) *aquensis* d'Orbigny, 1852) (non *Conus elatus* Michelotti, 1847).

Material examined

GREECE – **Crete** • 4 specs; Achladhia; 1964; Nikolaos Symeonidis leg.; AMPG(IV) 3881 to AMPG(IV) 3884 • 1 spec.; same collection data as for preceding AMPG(IV) 3887 • 4 specs; Filippi; 35.035° N, 25.250° E; 2017; Christos Psarras leg.; AMPG(IV) 3890 to AMPG(IV) 3893 • 1 spec.; same locality as for preceding; Efterpi Koskeridou leg.; AMPG(IV) 3894 • 1 spec.; same locality as for preceding; AMPG(IV) 3895 • 2 specs; Panassos; 35.130° N, 24.986° E; 2017; Christos Psarras leg.; AMPG(IV) 3896 to AMPG(IV) 3897 • 2 specs; Psalidha; 35.085° N, 24.962° E; Christos Psarras leg.; 2018; AMPG(IV) 3898 to AMPG(IV) 3899 • 5 specs; same collection data as for preceding; AMPG(IV) 3901 to AMPG(IV) 3905 • 1 spec.; Tefeli; Efterpi Koskeridou leg.; AMPG(IV) 3906 • 1 spec.; 1990; Action

Table 14. Shell measurements and ratios of *Conus* (*Plagioconus*) sp. from the Tortonian of Crete (Greece). Mean and standard deviation are computed from 27 specimens. The largest specimen is AMPG(IV) 3896.

	SL	MD	AH	HMD	AL	SA	LWA
Largest specimen	76.1 mm	26.2 mm	57.4 mm	50.1 mm	57.2 mm	51.3°	19°
Mean	50.47 mm	24.92 mm	31.45 mm	34.25 mm	36.31 mm	54.54°	30.28°
Standard deviation	13.84	14.54	13.56	9.63	11.14	12.53	15.45
	LW	**RD**	**PMD**	**RSH**	**SSFD**	**SSFd**	**PV**
Largest specimen	2.91	0.46	0.87	0.25	–	–	–
Mean	2.83	0.48	0.91	0.26	1.60	5.80	0.37
Standard deviation	0.33	0.07	0.03	0.02	0.60	1.73	0.20

spécifique du Muséum project (1989–1990) exped.; MNHN.F.A83092 • 2 specs; Panassos; 35.130° N, 24.986° E; Didier Merle leg.; MNHN.F.A83094 to MNHN.F.A83095 • 1 spec.; 1990; Action spécifique du Muséum project (1989–1990) exped.; MNHN.F.A83096 • 1 spec.; Partira; 1990; Action spécifique du Muséum project (1989–1990) exped.; MNHN.F.A83097 • 1 spec.; Psalidha; 35.085° N, 24.962° E; Didier Merle leg.; MNHN.F.A83098.

Shell description

Medium-large-sized shells (SL max.: 76.1 mm). Spire whorls medium to high, with conical outline. Protoconch multispiral. Early spire whorls conical, slightly elevated and beaded, with angulated shoulder. Late spire whorls conical, flat to striated, with straight to convex sutural ramp. Suture incised, of variable depth. Subsutural flexure moderately deep (Fig. 40P) to deep (Fig. 40Q), moderately curved, strongly asymmetrical. Sutural ramp straight to slightly inflated and convex. Shoulder smooth to subangulated. Spiral angulation at shoulder, as separation of last whorl and sutural ramp. Aperture straight, narrow. Last whorl elongated, conical. Fasciole smooth, elongated, slightly twisted. Faint spiral cords at anterior part of last whorl.

Description of colour pattern

The first pattern level consists of an alteration of fluorescent spiral bands, on a non-fluorescent base colour, with one thin fluorescent band at the position of the maximum diameter, another wide fluorescent band near the shoulder of the shell, and, in some shells, a third smaller band present on half of the anterior part of the last whorl (Fig. 30B). The second level consists of rows of dots and dashes, which are axially or spirally arranged on the surface of the shell, on top of the first field. The colour pattern of the spire whorls consists of fluorescent flammulae of irregular width, usually continuing on the last whorl, as axial dots or dashes (Fig. 30G). The pattern is not consistent in all shells, as some shells under the UV light display either faded patterns (Fig. 30C), one pattern on the last whorl (Fig. 30B), or none at all (Fig. 30D).

Remarks

The Cretan specimens are mostly broken, but the remaining shell surfaces are in pristine condition, the beads on the spire whorls are visible and, most importantly, the colour patterns can be distinguished under UV light (Fig. 31). The specimens of *Conus* (*Plagioconus*) sp. display variable shoulder angulation height of the spire (Fig. 30; Table 14). The colour pattern is consistent, with fluorescent bands and occasional spiral or axial dots and dashes. Some of the studied specimens have previously been identified by Symeonidis & Kostantinidis (1968) as *Conus puschi*, here regarded as a synonym *Conus* (*Plagioconus*) *elatus* Michelotti, 1847. After studying the material, we noticed that the overall spire

outline of *Conus* (*Plagioconus*) sp. is more straight-sided, than *Conus* (*Plagioconus*) *elatus* Michelotti, 1847, which has a slightly inflated outline on the middle whorls. The spire of *Conus* (*Plagioconus*) *elatus* then continues to much more pronounced later spire whorls, which is not the case for *Conus* (*Plagioconus*) sp. Also, the shells of *Conus* (*Plagioconus*) *elatus* have almost no colour pattern (only flammulae and some blotches on the spire whorl), while the specimens of *Conus* (*Plagioconus*) sp. are much more flamboyant.

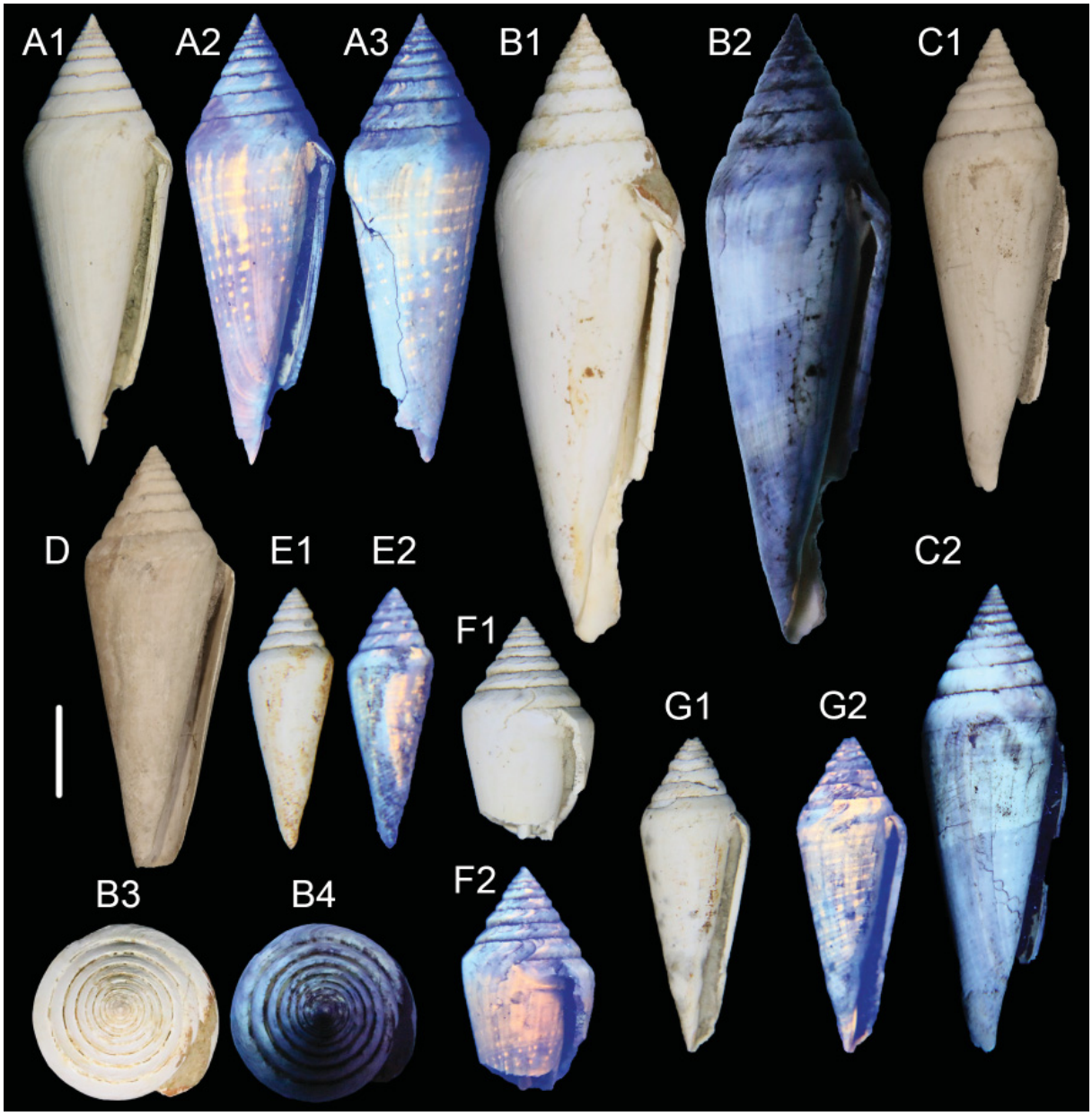

Fig. 30. *Conus* (*Plagioconus*) sp. from the Tortonian of Crete (Greece) in apertural, abapertural and apical views, under natural (A1, B1, B3, C1, D1, E1, F, G1) and UV light. **A**. Specimen AMPG(IV) 3901, Psalidha. **B**. Specimen AMPG(IV) 3890, Filippi. **C**. Specimen MNHN.F.A83095, Panassos. **D**. Specimen AMPG(IV) 3881, Achladhia. **E**. Specimen AMPG(IV) 3903, Psalidha. **F**. Specimen AMPG(IV) 3904, Psalidha. **G**. Specimen AMPG(IV) 3902, Psalidha. Scale bar = 1 cm.

Hall (1966) illustrated specimens of several varieties of other species and considered them as synonyms of *Conus aquensis* d'Orbigny, 1852. These specimens are a type specimen of *Conus oboesus?* var. *paucispirata* Sacco, 1893, a type specimen of *Conus oboesus*? var. *elatoides* Sacco, 1893, a type of *Conus puschi* var. *pseudobiconica* Sacco, 1893, a type specimen of *Conus pushi* var. *peracutolonga* Sacco, 1893 and a type specimen of *Conus elatus* var. *fusuloparva* Sacco, 1893. These specimens have the same conical, elongated spire whorls and angulation at the shoulder as *Conus* (*Plagioconus*) sp.

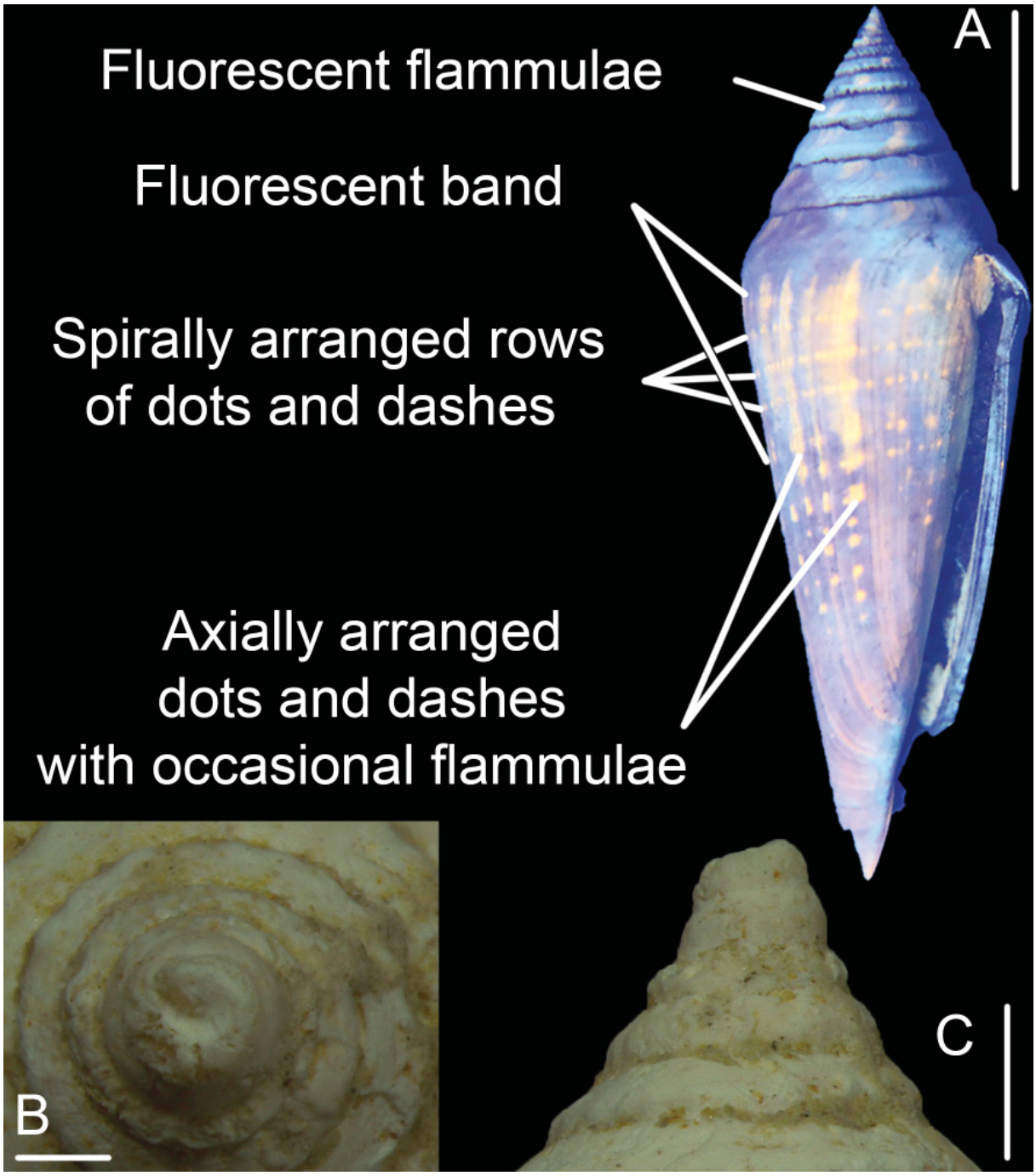

Fig. 31. *Conus* (*Plagioconus*) sp. from the Tortonian of Crete (Greece), displaying elements of colour pattern (A) and shape of the protoconch (B–C). **A**. Specimen AMPG(IV) 3901, Psalidha. **B–C**. Specimen AMPG(IV) 3891, Filippi. Scale bars: A = 1 cm; B = 500 μm; C = 1 mm.

As we had no access to their colour patterns, we cannot check the synonymy of Hall (1966). A comparison with the syntype (MNHN.F.A13061) of *Conus* (*Plagioconus*) *aquensis* (Fig. 32) from the early Miocene of the Aquitaine Basin shows that Hall's specimens possess more angulated shoulders, high conical spires and relatively narrower diameters (RD). Two specimens named as *Conus puschi* from Davoli (1972: pl. 8 figs 17a–b, 19) have an elongated spire similar to that of the studied specimens (Fig. 30B1–C2), but the spire whorls are not distinctly elevated and there is a slight angulation at the shoulder. We also wait for their colour pattern descriptions in order to compare to the Cretan specimens.

Stratigraphic range

Tortonian of Greece (Messara Basin and Sitia Basin, Crete (Symeonidis & Kostantinidis 1968; this work)).

Conus* (*Plagioconus*) *aquensis d'Orbigny, 1852
Figs 32–36; Table 15

Conus aquensis d'Orbigny, 1852: 11.

Conus antidiluvianus – Grateloup 1847: pl. 44 fig. 6 (non *Conilithes antidiluvianus* Bruguière, 1792).
Conus (*Chelyconus ?*) *aquensis* – Peyrot 1930: 103–104.
Conus (*Chelyconus*) *aquensis* – Peyrot 1931: pl. 4 figs 4, 7, 16, 19.
Conus (*Chelyconus*) *puschi* – Symeonidis & Kostantinidis 1968: pl. 7 fig. 13 (non *Conus* (*Plagioconus*) *elatus* Michelotti, 1847) (non fig. 3).
Conus (*Chelyconus*) sp. – Caze *et al*. 2010: fig. 5m1–m2.
Plagioconus puschi – Landau *et al.* 2013: pl. 81 fig. 9 (non *Conus* (*Plagioconus*) *elatus* Michelotti, 1847).
Plagioconus bellissimus – Harzhauser & Landau 2016: fig. 31f1–f2 only.

non *Conus aquensis* – Hall 1966: pl. 22 figs 2, 8, 13, 18–19, 23, 27. – Davoli 2003: pl. 1 figs 15a–b.

Type locality

Saint-Paul-lès-Dax.

Type material

Syntypes

FRANCE – **Dax** • 2 specs; Saint-Paul-lès-Dax; Aquitaine Basin; Aquitanian-Burdigalian; MNHN.F.A13061.

Other material

GREECE – **Crete** • 8 specs; Achladhia; 1964; Nikolaos Symeonidis leg.; AMPG(IV) 3907 to AMPG(IV) 3914 • 4 specs; Filippi; 35.035° N, 25.250° E; 2017; Christos Psarras leg.; AMPG(IV) 3915.

Shell description

Moderately large (SL max.: 67.4 mm), elongated shell. Early spire whorls beaded, elongated, with angulated shoulder. Beads absent after the 7th spire whorl, angulated shoulder smoother after the 5th spire whorl (Fig. 34). Delicate spiral cords on sutural ramp (Fig. 32). In some specimens, up to three spiral grooves can be seen, just under shoulder (Fig. 34). Maximum diameter just below shoulder. Suture incised, subsutural flexure shallow, moderately curved, strongly asymmetrical (Fig. 40). Last whorl straight to slightly inflated. Surface of subadult shells decorated with spiral grooves on all of shell's length, deeper grooves at anterior half of shell (Fig. 34). Spiral nodules present along last whorl in between

spiral grooves (Fig. 32B1), fading out on adult specimens (Fig. 32A1). Also, on adult specimens, spiral grooves present only along half to two thirds of anterior part of last whorl. Aperture narrow, straight, widened slightly on fasciole. Siphonal canal medium. Fasciole indistinct, slightly twisted.

Description of colour pattern

The colour pattern consists of flammulae and blotches on the spire whorls, sometimes aligned with the subsutural flexures. Flammulae continue until just below the shoulder. The colour pattern on the last whorl consists of fluorescent, densely spaced dots and dashes, organized axially and spirally. Fluorescent axial blotches also exist, uniting several dashes axially (Fig. 35). These fluorescent blotches are mainly present on the upper, middle and bottom parts of the last whorl, organised as faint spiral bands.

Remarks

The Cretan specimens are very similar to the syntypes of *Conus* (*Plagioconus*) *aquensis* d'Orbigny, 1852 originally described from the early Miocene of Aquitaine Basin, as they share similarly beaded early spire whorls, spiral grooves along the two thirds of the anterior part of the last whorl. The subsutural flexures are shallow and the colour pattern is identical. The species is easily recognised by the prominent beaded early to middle spire whorls (see Fig. 32B7), the grooved last whorl and the moderately elevated

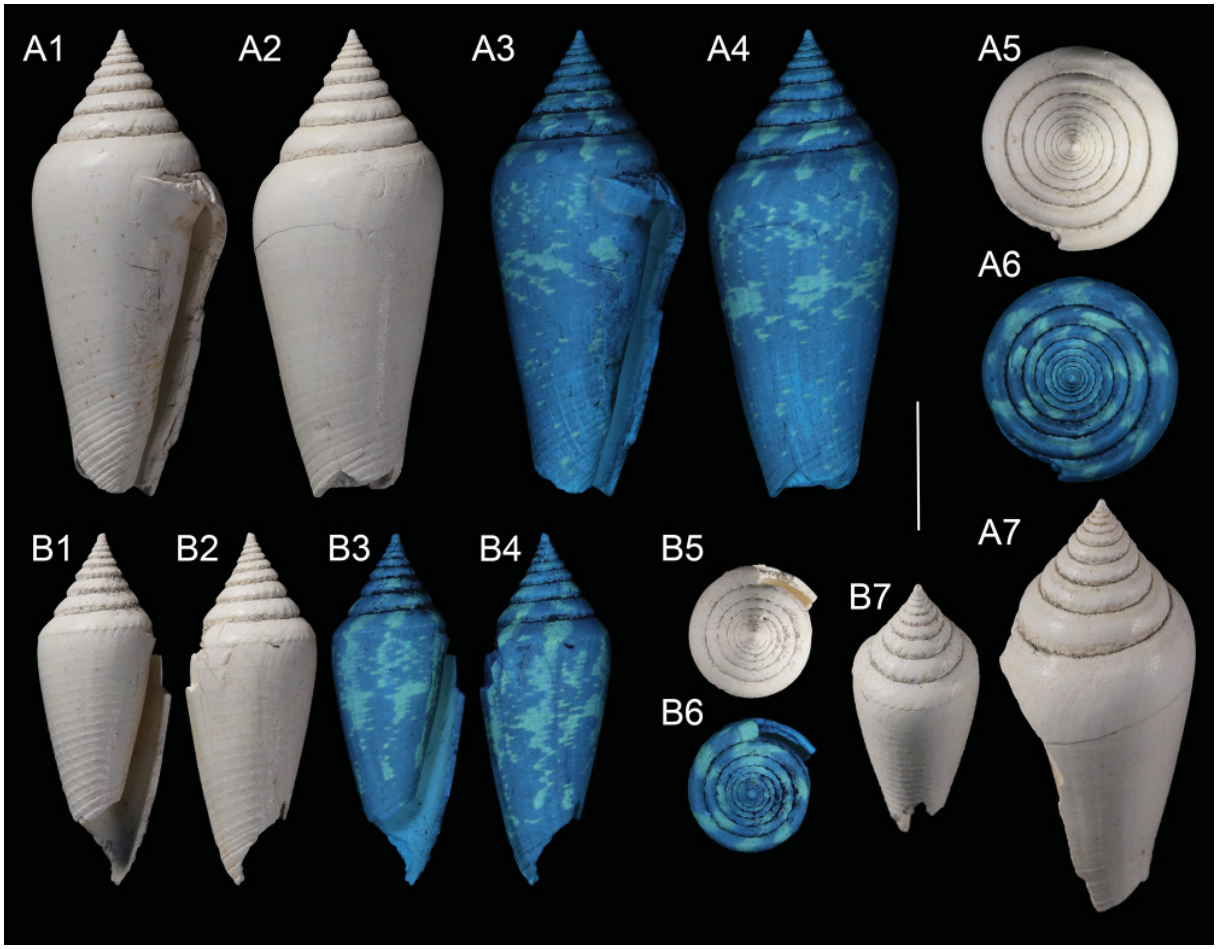

Fig. 32. Two syntypes of *Conus* (*Plagioconus*) *aquensis* d'Orbigny, 1852 from Saint-Paul-lès-Dax in the Aquitaine Basin, France, in apertural, abapertural and apical views, under natural (A1–A2, A5, A7, B1–B2, B5, B7) and UV light (MNHN.F.A13061). Scale bar = 1 cm.

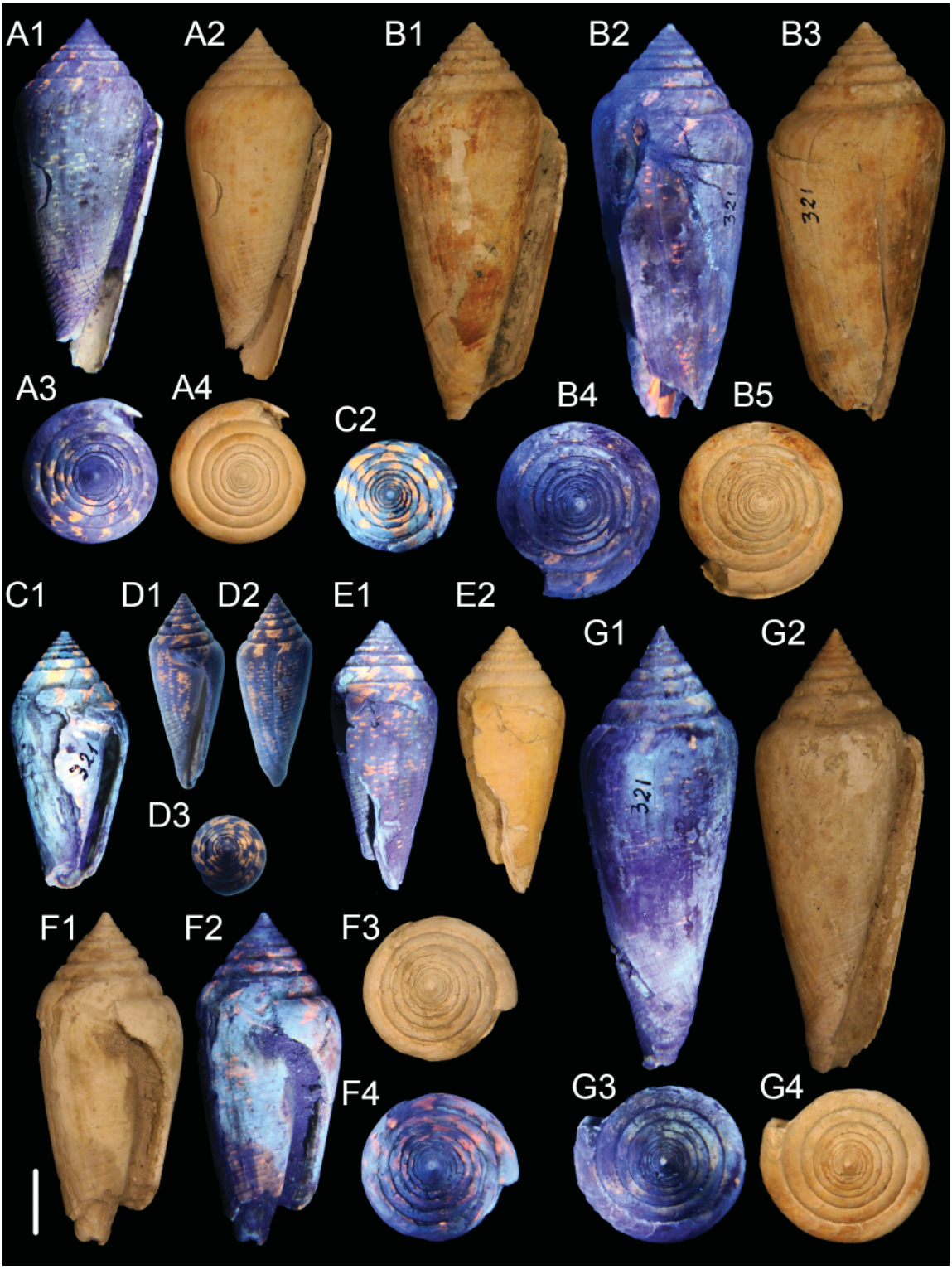

Fig. 33. *Conus* (*Plagioconus*) *aquensis* d'Orbigny, 1852 from the Tortonian of Crete (Greece) in apertural, abapertural and apical views, under natural (A2, A4, B1, B3, B5, E2, F1, F3, G2, G4) and UV light. **A**. Specimen AMPG(IV) 3909, Achladhia. **B**. Specimen AMPG(IV) 3908, Achladhia. **C**. Specimen AMPG(IV) 3913, Achladhia. **D**. Specimen AMPG(IV) 3915, Filippi. **E**. Specimen AMPG(IV) 3914, Achladhia. **F**. Specimen AMPG(IV) 3911, Achladhia. **G**. Specimen AMPG(IV) 3907, Achladhia. Scale bar = 1 cm.

spires (Table 15). The colour pattern of spiral dashes is also easily recognisable under UV light. *Conus* (*Plagioconus*) *aquensis* d'Orbigny, 1852 has been mistakenly named as *Conus antidiluvianus* by Grateloup (1847) from which it mainly differs in the convex spire whorls and the colour pattern (Janssen *et al*. 2014). d'Orbigny (1852) noticed the error and named this species *Conus aquensis*. Peyrot (1930) was the first who gave a detailed description of this species and figured some examples. The type specimen of *Conus burdigalensis* Mayer, 1858 (from Saucats near Bordeaux, Burdigalian, Mayer-Eymar coll. N 2741, whereabouts are unknown), figured in Hall (1966: pl. 27 fig. 11) is similar in morphology to *Conus* (*Plagioconus*) *aquensis*, but we have not studied the specimen's colour patterns. Landau *et al.* (2013:

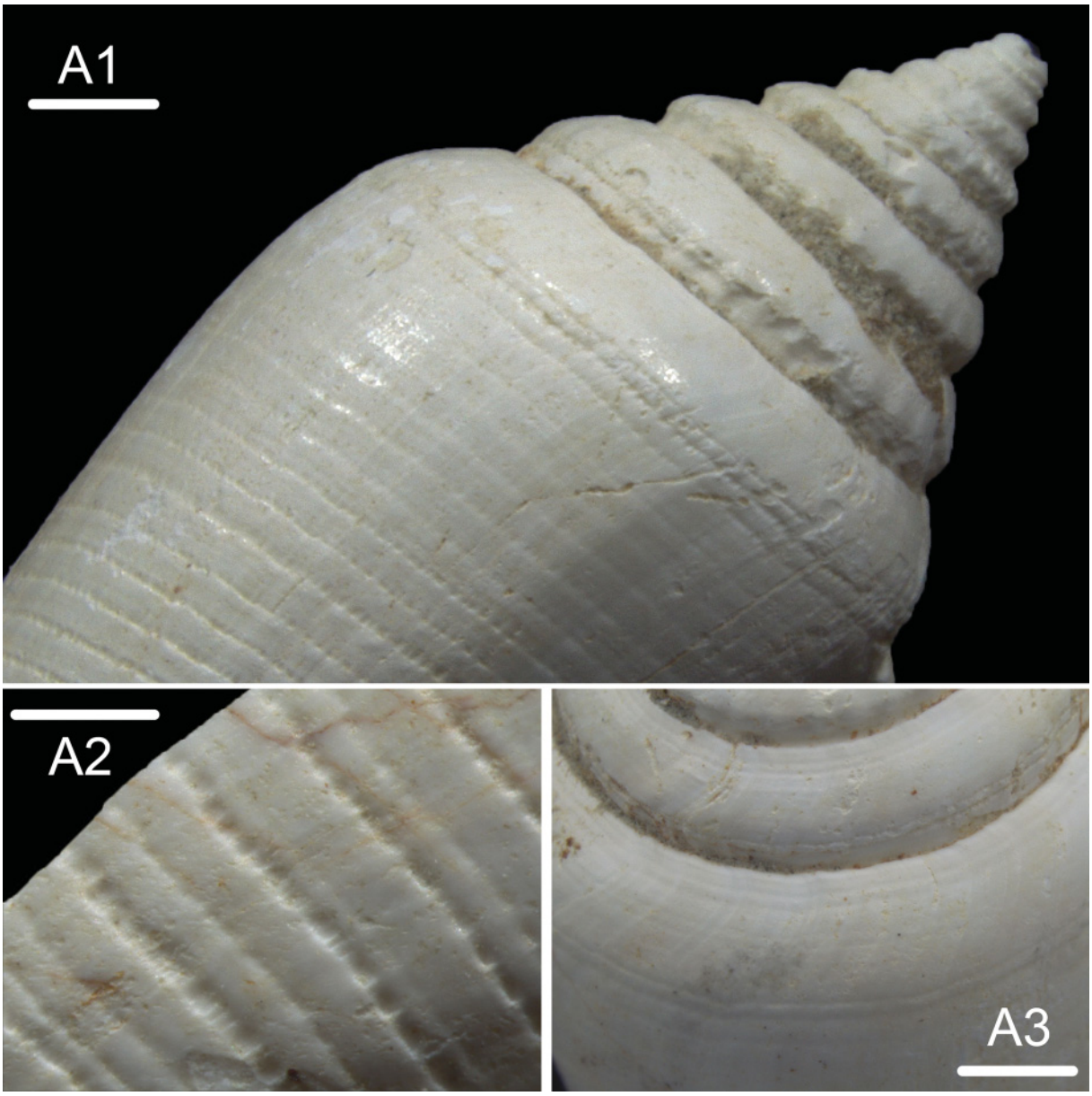

Fig. 34. *Conus* (*Plagioconus*) *aquensis* d'Orbigny, 1852 from the Tortonian of Filippi, Crete (Greece) (AMPG(IV) 3915), specimen in close-up. **A1**. Notice the beaded spire whorls, the three spiral cords on shoulder and the spiral grooves on the rest of the shell. **A2**. Notice the spiral grooves on last whorl. **A3**. Notice the delicate spiral cords on sutural ramp, as well as shallow subsutural flexure. Scale bars: A1, A3 = 2 mm; A2 = 1 mm.

Table 15. Shell measurements and ratios of *Conus* (*Plagioconus*) *aquensis* d'Orbigny, 1852 from the Tortonian of Crete (Greece). Mean and standard deviation are computed from nine specimens. The largest specimen is AMPG(IV) 3907.

	SL	MD	AH	HMD	AL	SA	LWA
Largest specimen	67.4 mm	25.8 mm	54.1 mm	47.5 mm	51.6 mm	71.4°	26°
Mean	50.2 mm	20.8 mm	42.4 mm	29.4 mm	33.2 mm	72.6°	25.8°
Standard deviation	14.7	4.3	10.9	9.5	10.6	5.7	2.7
	LW	**RD**	**PMD**	**RSH**	**SSFD**	**SSFd**	**PV**
Largest specimen	2.61	0.48	0.88	0.2	2.13	3.6	0.38
Mean	2.46	0.51	0.86	0.2	2.02	4.78	0.26
Standard deviation	0.15	0.03	0.01	0	0.23	2.39	0.1

pl. 81 fig. 9) identified one of their fossils as *Plagioconus puschi* (Michelotti, 1847) (RGM 777 891 (ex JvdV collection), Pınarlar Yaylası, Akpınar, Karaman Basin, Turkey). The colour pattern resembles the pattern described herein. The morphological characteristic of multiple spiral grooves on the anterior part of the shell are evident in their figure, they match those of *Conus* (*Plagioconus*) *aquensis.* For these reasons, we consider the Turkish specimens as *Conus* (*Plagioconus*) *aquensis*. Furthermore, Landau *et al.* (2013) compared a specimen from the Langhian of Romania attributed by Caze (2010) to *Conus* (*Chelyconus*) sp. (Caze 2010: fig. 5m1–2), which has a similar colour pattern. We studied this specimen (MNHN.F.A31836) and confirmed that the pattern is similar to *Conus* (*Plagioconus*) *aquensis*. The morphology of the spire is very similar to that of the type specimen, with beads on early spire whorls and a shallow subsutural flexure. The pattern is also similar to *Conus* (*Plagioconus*) *aquensis*, but the faint spiral and axial bands, underlying the spiral dashes, cover a larger portion of the shell. This pattern is considered here as a variation; therefore, the specimen (MNHN.F.A31836) is considered here as *Conus* (*Plagioconus*) *aquensis*. Harzhauser & Landau (2016) named a new species *Conus* (*Plagioconus*) *bellissimus*, but they showed the pattern of only one specimen out of four figured therein (fig. 31c–f). The shells figured (Harzhauser & Landau 2016) have a similar morphology to each other, except for

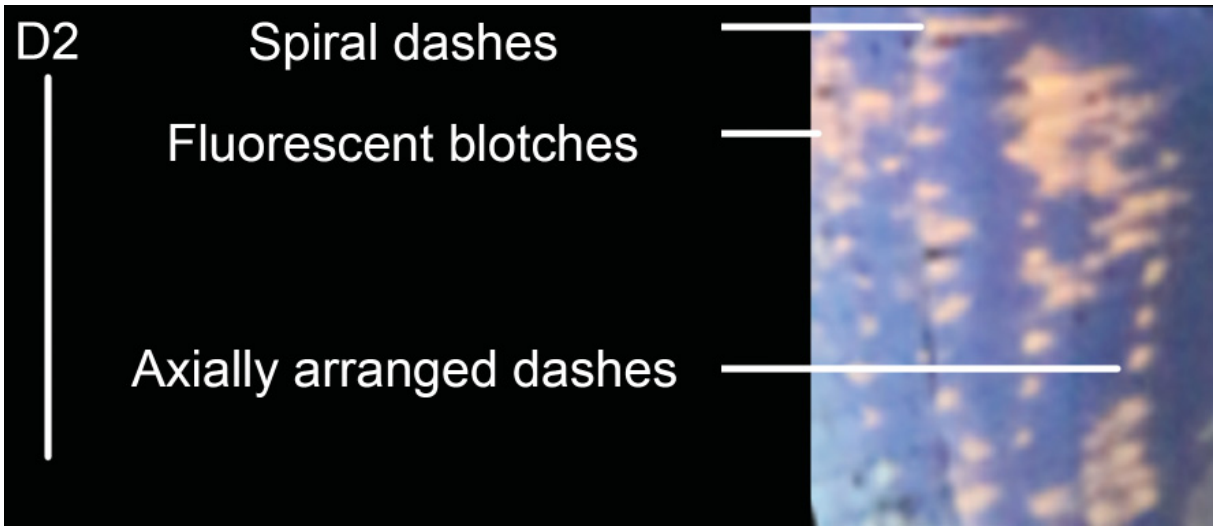

Fig. 35. Elements constituting the colour pattern of *Conus* (*Plagioconus*) *aquensis* d'Orbigny, 1852 from the Tortonian of Filippi, Crete (Greece). **D2**. Specimen AMPG(IV) 3915. Scale bar = 0.5 cm.

a specimen from the Langhian of Letkés in Hungary (private collection Anton Breitenberger), which is provided with its colour pattern, that has a more inflated sutural ramp and a shorter spire than the rest of the specimens shown by the authors (Harzhauser & Landau 2016). This specimen illustrated under UV light bears an outline and a colour pattern similar to that of specimen AMPG(IV) 3909, Achladhia, Crete. Additionally, the colour pattern of this Hungarian specimen is identical to that of the Turkish and Romanian ones illustrated by Landau *et al.* (2013).

Stratigraphic range

Aquitanian–Burdigalian of France (Aquitaine Basin) (d'Orbigny 1852; Mayer 1858); Burdigalian of Italy (Hall 1966); Langhian of Hungary (Pannonian Basin) (Harzhauser & Landau 2016) and Romania (Caze *et al*. 2010); Serravallian of Turkey (Karaman Basin) (Landau *et al.* 2013) and Tortonian of Greece (Sitia Basin and Messara Basin, Crete).

Concluding remarks about Conus (Plagioconus) (Tucker & Tenorio, 2009)

From the PCA graph (Fig. 36), it is evident that *Conus* (*Plagioconus*) sp. (Fig. 36, yellow colour) forms a distinct cluster, thus verifying our hypothesis of its existence. *Conus* (*Plagioconus*) *elatus* Michelotti, 1847 (Fig. 36, black colour) and *Conus* (*Plagioconus*) *aquensis* d'Orbigny, 1852 (Fig. 36, red colour) show a slight convergence in their morphology. The result does not consider the presence of beads and spiral grooves on *Conus* (*Plagioconus*), but overall, the species are clearly defined.

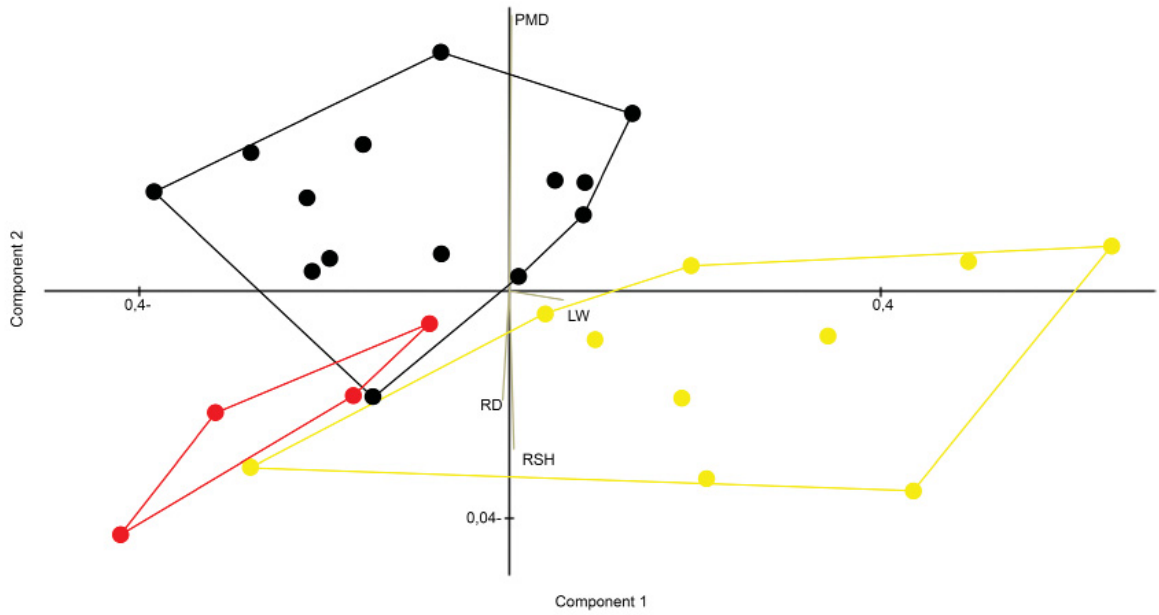

Fig. 36. PCA graph with three species of *Conus* (*Plagioconus*) found at late Miocene localities of Crete (Greece). Black dots = *Conus* (*Plagioconus*) *elatus* Michelotti, 1847; red dots = *Conus* (*Plagioconus*) *aquensis* d'Orbigny, 1852; yellow dots = *Conus* (*Plagioconus*) sp. Abbreviations: LW = length width ratio; PMD = position of maximum diameter; RD = relative diameter; RSH = relative height of spire.

Species not assigned to any subgenus

Conus davolii sp. nov.
urn:lsid:zoobank.org:act:CCB87343-51EE-4FD1-A3C9-9ABF2746B885
Figs 37–38, 40M; Table 16

Conus clavatulus – Davoli 1972: pl. 4 figs 5, 17 (non figs 15–16 = *Conus* (*Lautoconus*) sp. 4) (non *Conus clavatulus* d'Orbigny, 1852).
?*Varioconus olivaeformis* – Kovács & Balázs 2015: 31–32, figs 69–70 (non *Conus* (*Mioconus*) subgen. nov. *olivaeformis* (Hoernes & Auinger, 1879)).

Diagnosis

A small-sized, torpedo-shaped species with delicate pattern of spiral rows of dots and blotches.

Etymology

A species named after Davoli, who first figured that species.

Material examined

Holotype
GREECE – **Crete** • 1990; Action spécifique du Muséum project (1989–1990) exped.; MNHN.F.A83091.

Paratypes
ITALY • 2 specs; Collezione Coppi 382; MOD n.ro di Cat. 5524 [Davoli 1972: pl. 4 figs 5a–b, 17].

Shell description

Shell small (SL max.: 22.1 mm) and elongated. Early spire whorls worn out, straight, conical. Later spire whorls slightly convex, with conical outline. Subsutural flexure moderately deep, weakly curved, moderately asymmetrical (Fig. 40M). Suture slightly incised. Shoulder rounded, with maximum diameter below shoulder. Aperture narrow, straight, with long canal. Siphonal fasciole twisted. No spiral grooves on last whorls.

Description of colour pattern

The pattern consists of small fluorescent blotches, and evenly arranged fading spiral lines bearing dots at almost equal distances from each other (Fig. 38).

Remarks

Conus davolii sp. nov. is a characteristic torpedo-shaped species (Fig. 37), which has a very delicate colour pattern. Its morphology is unique in the Greek collection (Table 16). Two Italian specimens from the Tortonian of Montegibbio have been misidentified as *Conus clavatulus* d'Orbigny 1852 by Davoli (1972) (see remarks for *Conus* (*Lautoconus*) sp. 3). On the other hand, their rare torpedo-shaped morphology is similar to that of the Cretan specimen. Despite the fact that we did not study the patterns of the two specimens, the Italian specimens and the Greek specimen are morphologically conspecific. In view of this deduction and because of lack of more material from the type locality, we designate the two specimens figured by Davoli (1972: pl. 4 figs 5, 17) as the paratypes.

This species could be misinterpreted as a juvenile *Conus* (*Lautoconus*) *ictini* sp. nov. The morphology of this species is different from *Conus* (*Lautoconus*) *ictini* sp. nov., as the spire whorls are not straight, because there are no spiral grooves on the anterior part of the last whorl. The colour pattern is also different from *Conus* (*Lautoconus*) *ictini* sp. nov., as there is no brick-like pattern, but a dotted pattern

on the spiral lines. The species could be compared to *Conus praelongus* Hoernes & Auinger, 1879, but, morphologically, the spire of *Conus davolii* sp. nov. is not as elevated as in *Conus praelongus* (see Harzhauser & Landau 2016: fig. 34b–d). The colour pattern is different as well, with *Conus praelongus* bearing a dashed pattern.

Conus olivaeformis Hoernes & Auinger, 1879 is another species with a similar morphology. It differs in the shallow subsutural flexure, the subangulated shoulder and the inferred (Harzhauser & Landau 2016) colour pattern of densely spaced spiral dashes. The specimen of Kovács & Balázs (2015) is probably *Conus olivaeformis*, but without UV light results, we cannot be certain.

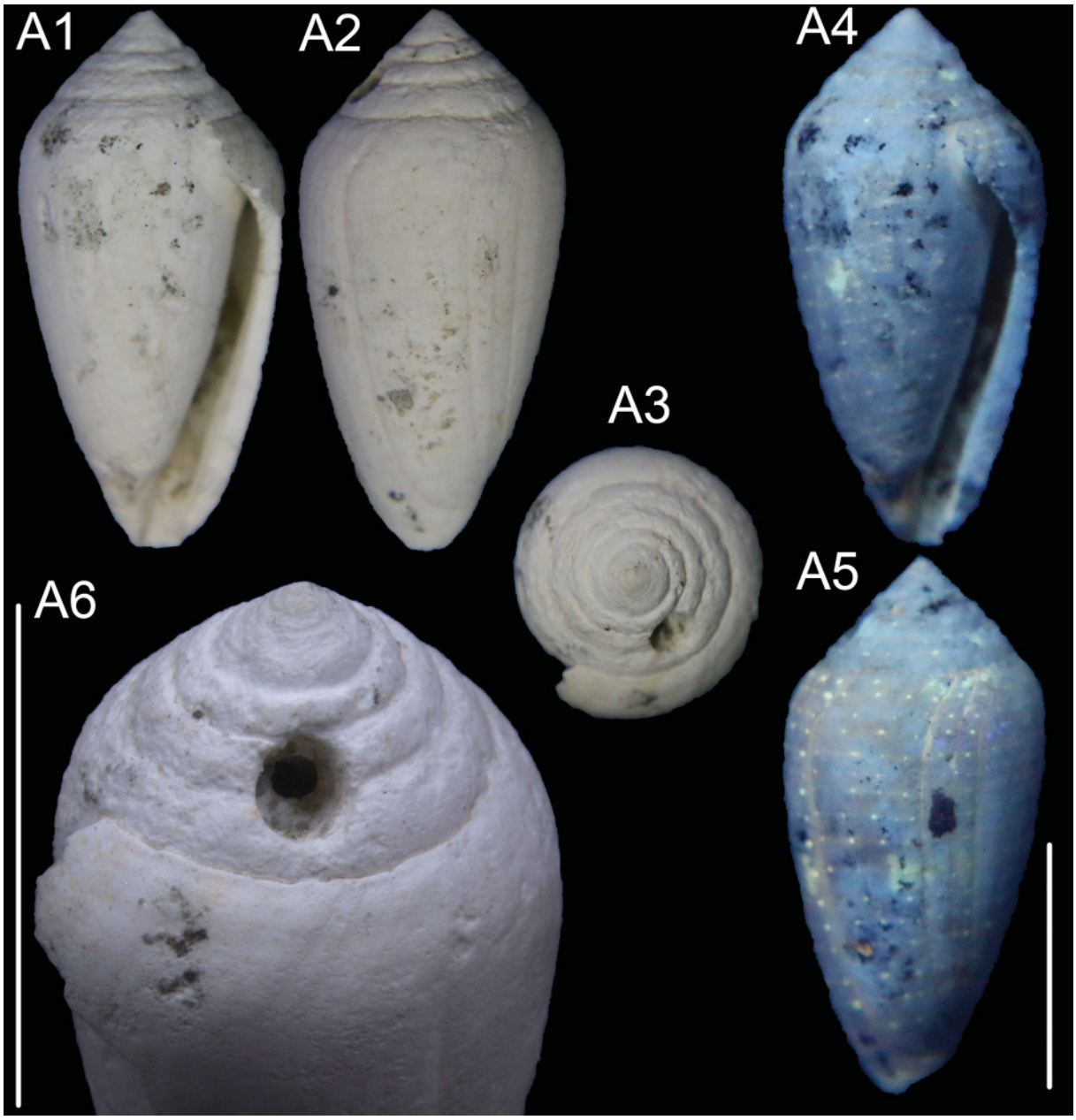

Fig. 37. *Conus davolii* sp. nov., holotype MNHN.F.A83091 from the Tortonian of Filippi, Crete (Greece), in apertural and abapertural views, under natural (A1–A3, A6) and UV light. Scale bars = 1 cm.

Table 16. Shell measurements and ratios of *Conus davolii* sp. nov., specimen MNHN.F.A83091 from the Tortonian of Filippi, Crete (Greece).

SL	MD	AH	HMD	AL	SA	LWA
22.1 mm	11.7 mm	18.4 mm	14.8 mm	18.2 mm	101°	44°
LW	**RD**	**PMD**	**RSH**	**SSFD**	**SSFd**	**PV**
1.89	0.64	0.80	0.17	1.82	12.5	0.56

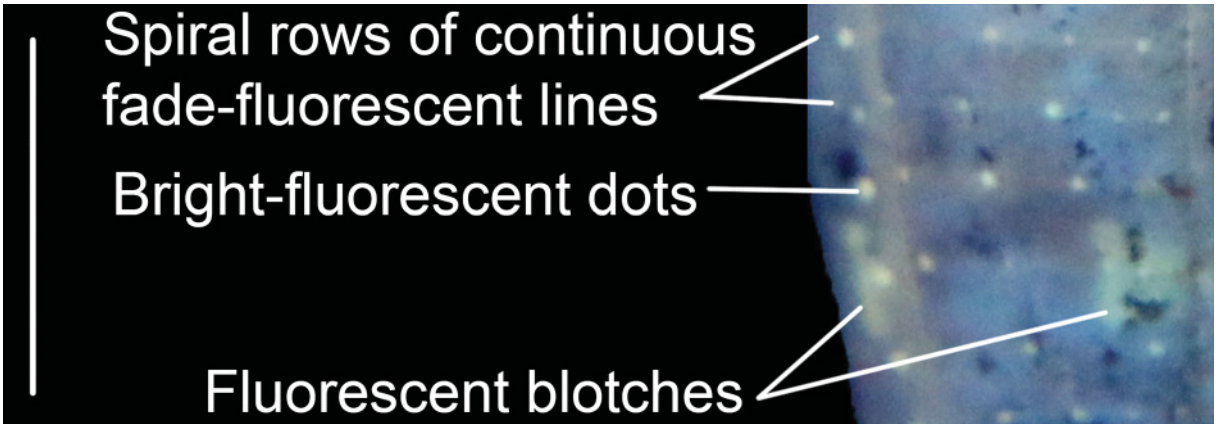

Fig. 38. Colour pattern of *Conus davolii* sp. nov., holotype MNHN.F.A83091 from the Tortonian of Filippi, Crete (Greece). Scale bar = 0.5 cm.

Conus davolii sp. nov. resembles the extant *Conus* (*Hermes*) *nussatella* Linnaeus, 1758, in the torpedo-shaped whorl and the colour pattern of spiral rows of continuous dashes and spots on them, with alternating blotches. The ridges on the last whorl are a feature not present on the studied specimen; therefore, we do not assign the studied species to *Conus* (*Hermes*) Montfort, 1810 and do not include this species to any subgenus until more material will have been studied.

Stratigraphic range

?Langhian of Hungary (Kovács & Balázs 2015); Tortonian of Greece (Messara Basin, Crete) and Italy (Montegibbio) (Davoli 1972).

Conus fuscocingulatus Hörnes, 1851
Figs 39, 40N; Table 17

Conus fusco-cingulatus Hörnes, 1851: 21 (partim), pl. 1 figs 5a–c.

Conus (*Chelyconus*) *fuscocingulatus* – Hoernes & Auinger 1879: 47, pl. 1 figs 10–11, ?13 (non fig. 12 = ? *Conus moravicus* Hoernes & Auinger, 1879, see Harzhauser & Landau 2016). *Conus* (*Dendroconus*) *ochreocingulata* – Sacco 1893a: 12 (unnecessary new name for *Conus fuscocingulatus* of Hoernes & Auinger 1879: pl. 1 figs 10–11). *Conus* (*Dendroconus*) *pötzleinsdorfensis* – Sacco 1893a: 12 (? unnecessary new name for nov. nom. pro *Conus fuscocingulatus* in Hoernes & Auinger 1879: pl. 1 fig. 13). *Conus basteroti* – Caze 2010: 61, fig. 33L (non *Conus basteroti* Mayer-Eymar, 1891).
Phasmoconus fuscocingulatus – Harzhauser & Landau 2016: 123, 125, figs 12, 17w–x, 29c–f.

Type material

Syntype

AUSTRIA – **Pötzleinsdorf** • NHMW 1846/0037/0055.

Material examined

GREECE – **Crete** • 9 specs; 1990; Action spécifique du Muséum project (1989–1990) exped.; MNHN.F.A83082 to MNHN.F.A83090 • 1 spec.; Achladhia; 1964; Nikolaos Symeonidis leg.; AMPG(IV) 3832 • 12 specs; Filippi; 35.035° N, 25.250° E; Efterpi Koskeridou leg.; AMPG(IV) 3833

Fig. 39. *Conus fuscocingulatus* Hörnes, 1851, specimen from the Tortonian of Crete (Greece), shown in apertural view under natural (A1, B1, B3, C1, C3) and UV light. **A**. Specimen AMPG(IV) 3832, Achladhia. **B**. Specimen AMPG(IV) 3833, Filippi. **C**. Specimen AMPG(IV) 3857, Tefeli. **D**. Specimen AMPG(IV) 3855, Tefeli. **E**. Specimen AMPG(IV) 3858, Tefeli. **F**. Specimen AMPG(IV) 3856, Tefeli. **G**. Specimen AMPG(IV) 3853, Tefeli. **H**. Specimen AMPG(IV) 3852, Tefeli. **I**. Specimen AMPG(IV) 3851, Tefeli. Scale bar = 1 cm.

to AMPG(IV) 3844 • 3 specs; same locality; 2017; Christos Psarras leg.; AMPG(IV) 3845 to AMPG(IV) 3847 • 3 specs; Partira; Efterpi Koskeridou leg.; AMPG(IV) 3848 to AMPG(IV) 3850 • 1 spec.; Tefeli; Efterpi Koskeridou leg.; AMPG(IV) 3851 • 6 specs; same collection data as for preceding; AMPG(IV) 3852 to AMPG(IV) 3857 • 1 spec.; same collection data as for preceding; AMPG(IV) 3858 • 2 specs; same collection data as for preceding; AMPG(IV) 3859 to AMPG(IV) 3860.

Description of colour pattern

The colour pattern on the last whorl consists of evenly spaced spiral rows of continuous lines. Between the spirals, very thin, wavy, mostly discontinuous spiral lines exist. The spiral rows, of continuous lines on spiral grooves, are just above every spiral groove. On the spire whorls, the spiral lines start near the shoulder of the shell, while the spiral line near the suture is partly covered by the growing shell. The lines are not always of the same width and vary from clear lines with specific boundaries to wavy, blurry lines.

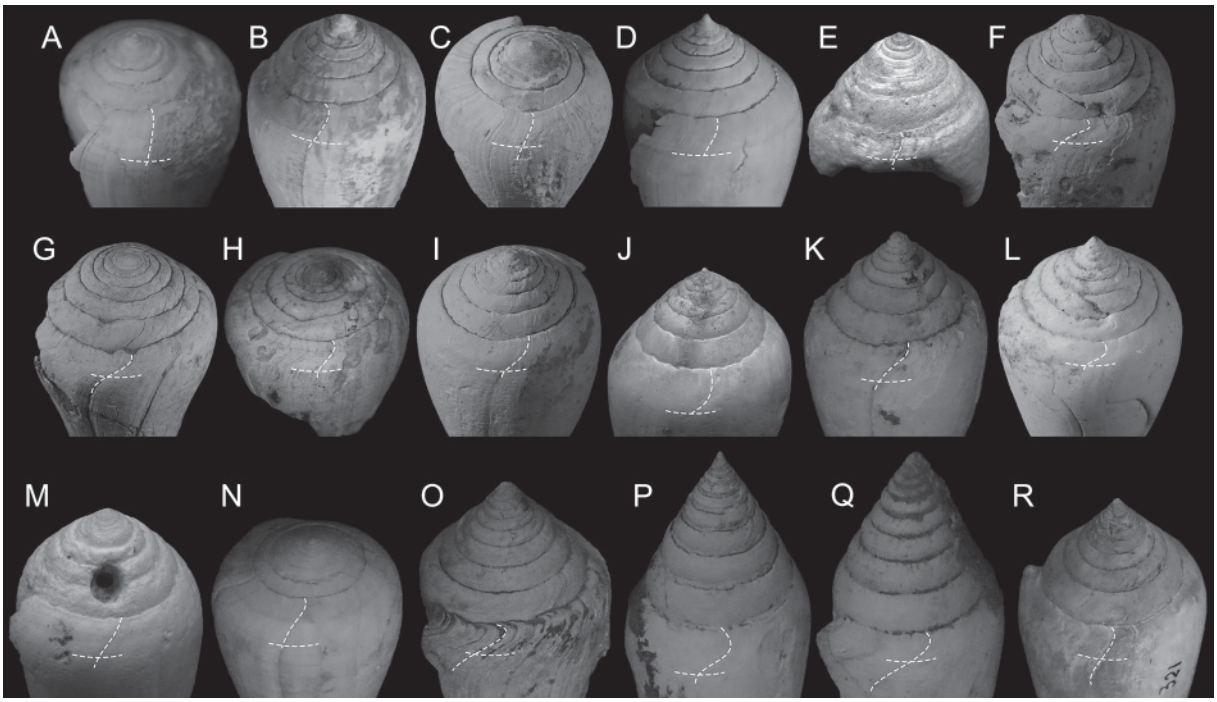

Fig. 40. Examples of subsutural flexures. **A**. *Conus* (*Lautoconus*) *eschewegi* Pereira da Costa, 1866 (MNHN.F.A82976). **B**. *Conus* (*Lautoconus*) *ictini* sp. nov. (AMPG(IV) 3719). **C**. *Conus* (*Lautoconus*) sp. 1 (MNHN.F.A82982). **D**. *Conus* (*Lautoconus*) sp. 2 (AMPG(IV) 3756). **E**. *Conus* (*Lautoconus*) sp. 3 (MNHN.F.A83012). **F**. *Conus* (*Lautoconus*) cf. *baldichieri* Borson, 1820 (MNHN.F.A83013). **G**. *Conus* (*Lautoconus*) *lauriatragei* sp. nov. (MNHN.F.A83014). **H**. *Conus* (*Lautoconus*) *damianakisi* sp. nov. (AMPG(IV) 3802). **I**. *Conus* (*Lautoconus*) sp. 4 (MNHN.F.A83015). **J**. *Conus* (*Lautoconus*) sp. 5 (AMPG(IV) 3861). **K**. *Conus* (*Stephanoconus*) cf. *taurinensis* Bellardi & Michelotti, 1841 (AMPG(IV) 3808). **L**. *Conus* (*Stephanoconus*) *moissettei* sp. nov. (MNHN.F.A83071). **M**. *Conus davolii* sp. nov. (MNHN.F.A83091). **N**. *Conus fuscocingulatus* Hörnes, 1851 (AMPG(IV) 3858). **O**. *Conus* (*Plagioconus*) *elatus* Michelotti, 1847 (AMPG(IV) 3862). **P**. *Conus* (*Plagioconus*) sp. (AMPG(IV) 3890). **Q**. *Conus* (*Plagioconus*) sp. (AMPG(IV) 3898). **R**. *Conus* (*Plagioconus*) *aquensis* d'Orbigny, 1852 (AMPG(IV) 3907). Not to scale.

Table 17. Shell measurements and ratios of *Conus fuscocingulatus* Hörnes, 1851 from the Tortonian of Crete (Greece). Mean and standard deviation are computed from 38 specimens.

	SL	MD	AH	HMD	AL	SA	LWA
Largest specimen	30.6 mm	19 mm	28.6 mm	23.9 mm	27.7 mm	126.4°	38.3°
Mean	17.17 mm	10.47 mm	15.88 mm	12.64 mm	15.64 mm	130.06°	41.74°
Standard deviation	4.65	2.84	4.17	3.49	4.21	13.82	3.63
	LW	**RD**	**PMD**	**RSH**	**SSFD**	**SSFd**	**PV**
Largest specimen	1.61	0.66	0.83	0.06	3.33	11	0.83
Mean	1.64	0.66	0.79	0.07	3.00	9.03	0.51
Standard deviation	0.10	0.04	0.03	0.03	0.30	0.92	0.09

Remarks

Harzhauser & Landau (2016) described the morphological variation of *Conus fuscocingulatus* and briefly characterised its colour patterns. We consider that our material belongs to this species and expand the colour pattern description. Our specimens show a diversity at the angulation (Fig. 39A, E) and width (Fig. 39D, F) of the shoulder, as well as at the height of the spire (Fig. 39B, G) (Table 17). Nevertheless, other characteristics such as the dense spiral cords and grooves on the anterior part of the last whorl, the shallow subsutural flexure (Fig. 40N), and the very clear colour pattern are indicative of the conspecificity of the specimens. Usually, the spire whorls of the specimens are eroded and only few beads and indistinct swellings are visible. From those characteristics, we could place this species in *Conus* (*Stephanoconus*) Mörch, 1852, but the colour pattern variation is clearly different from the patterns seen in extant *Conus* (*Stephanoconus*). We also disagree with the placement of this species in *Conus* (*Phasmoconus*), as this subgenus engulfs many species with radically different morphological and colour pattern variations (e.g., see Monnier *et al*. 2018). An extant species from Papua-New Guinea and the Solomon Islands, attributed to *Conus* (*Phasmoconus*) aff. *mucronatus* Reeve, 1843 by Monnier *et al*. (2018) displays a rather similar colour pattern, but differs from *Conus fuscocingulatus* Hörnes, 1851 by flammulae on its spire whorls, many discontinuous spiral rows and an angulate shoulder.

Stratigraphic range

Langhian of Paratethys (see Harzhauser & Landau 2016 for more details) and Tortonian of Greece (Messara and Sitia Basins) (this work).

Discussion

This work has focused on the subgenera *Lautoconus* Monterosato, 1923, *Stephanoconus* Mörch, 1852, and *Plagioconus* Tucker & Tenorio, 2009 as well as on two species of *Conus* not included in a subgenus. We found 17 species from the Tortonian of Crete, Greece (Table 18), of which five are considered as new (*Conus* (*Lautoconus*) *ictini* sp. nov., *Conus* (*Lautoconus*) *lauriatragei* sp. nov., *Conus* (*Lautoconus*) *damianakisi* sp. nov., *Conus* (*Stephanoconus*) *moissettei* sp. nov. and *Conus davolii* sp. nov.) Six are in open nomenclature (*Conus* (*Lautoconus*) sp. 1 to sp. 5 and *Conus* (*Plagioconus*) sp.) (Table 18). The Cretan assemblage shares four species with the Serravallian fauna of Turkey. With the middle Miocene of Central Proto-Mediterranean and the Atlantic, it shares at least three species and with the Paratethyan region it shares at least five species. At least three species seem to persist in the Pliocene of the Mediterranean (Table 18).

Psarras *et al*. (2021) studied the *Conus* (*Kalloconus*) and *Conilithes* and previously identified 11 species in the Tortonian of Crete, one of which was endemic to Crete. The presence of at least two more species

Table 18. Comparison of the Tortonian assemblage of *Conus* (*Lautoconus*), *Conus* (*Stephanoconus*) and *Conus* (*Plagioconus*) of Crete (Greece) with those of Neogene (Langhian to Pliocene) assemblages of neighbouring regions (Langhian of Italy (Sacco 1893a, 1893b; Hall 1966), Paratethys (Harzhauser & Landau 2016), Turkey (Erünal-Erentöz 1958; Landau *et al*. 2013), Tortonian of Italy (Sacco 1893a, 1893b; Davoli 1972), Tortonian of Crete (this work), Pliocene of Italy (Sacco 1893a, 1893b), Pliocene of Spain (Muñiz Solís 1999). **1**. *Conus* (*Lautoconus*) *eschewegi* Pereira da Costa, 1866. **2**. *Conus* (*Lautoconus*) *ictini* sp. nov. **3**. *Conus* (*Lautoconus*) sp. 1. **4**. *Conus* (*Lautoconus*) sp. 2. **5**. *Conus* (*Lautoconus*) sp. 3. **6**. *Conus* (*Lautoconus*) cf. *baldichieri*. **7**. *Conus* (*Lautoconus*) *lauriatragei* sp. nov. **8**. *Conus* (*Lautoconus*) *damianakisi* sp. nov. **9**. *Conus* (*Lautoconus*) sp. 4. **10**. *Conus* (*Lautoconus*) sp. 5. **11**. *Conus* (*Stephanoconus*) cf. *taurinensis* Bellardi & Michelotti, 1841. **12**. *Conus* (*Stephanoconus*) *moissettei* sp. nov. **13**. *Conus* (*Plagioconus*) *elatus* Michelotti, 1847. **14**. *Conus* (*Plagioconus*) sp. **15**. *Conus* (*Plagioconus*) *aquensis* d'Orbigny, 1852. **16**. *Conus davolii* sp. nov. **17**. *Conus fuscocingulatus* Hörnes, 1851). The number of studied Cretan specimens is indicated.

Species	Aquitanian	Burdigalian	Langhian	Serravallian	Tortonian			Pliocene		
	France	Italy	Paratethys	Turkey	Italy	Portugal	Crete, Greece	Italy	Spain	Turkey
1		•	•	•	•	•	31		•	
2				•			7			
3							1			
4		?					110			?
5							2			
6							1	?		
7			•				1			
8							7			•
9							1			•
10					?		1			
11				•			79			
12							8			
13		•	•		•		25			
14		?			?		27			
15	•		•	•			9			
16			?		•		1			
17			•				38			

endemic to Crete (*Conus* (*Lautoconus*) sp. 1 and *Conus* (*Stephanoconus*) *moissettei* sp. nov.) is interesting, as it either displays endemic species from Crete, or it indicates a taxonomic gap in the inventory of the Proto-Mediterranean Conidae. In essence, the description of residual colour patterns of the Conidae is crucial for a more precise assessment of the conid paleobiodiversity.

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