Stratigraphic record of *Eponides* Montfort 1808 (benthic Foraminifera) through the Paleocene carbonates of the northern Neotethys margin

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ABSTRACT: In the former northern Neotethys margin where Paleocene shallow-water limestone successions crop out (Austria, Turkey and Iran), morphotypes closely resembling *Eponides* have been recognized. These foraminifers are lamellar-perforated, with a trochospirally arranged set of trapezoidal chambers. We have tested their generic identification through a detailed architectural analysis of thin sections of carbonate rocks in which *Eponides*-like specimens have abundantly been recovered. This study shows the occurrence of bipartitor, arched septa and a pseudoumbilicus formed by the fusion of ventral ends of chambers. These features allow us to identify the specimens as *Eponides,* although the specific attribution has not been attempted. The evolutionary pattern displayed by the Late Cretaceous and Cenozoic *Eponides* and phylogenetically-related allies is briefly discussed.

Keywords: Benthic foraminifera, *Eponides*, Austria, Eastern Pontides, Yazd Block, Paleocene carbonates.

INTRODUCTION

The stratigraphic distribution of the foraminiferal genus *Eponides* Montfort is known to extend throughout the Eocene-Recent time interval (Baccaert 1987; Loeblich and Tappan 1987; Hottinger et al. 1991). According to our current knowledge *Eponides* and related taxa belong to a monophyletic lineage spanning from the Cretaceous to Recent times (Reiss 1960; Hauser and Grünig 1993). *Globorotalites* Brotzen characterizes the Late Cretaceous (Reiss 1959), whereas *Eponides* and *Poroeponides* (Terquem), which first appear in the Eocene and Miocene respectively, are still thriving in modern seas (Hottinger et al. 1991). Notwithstanding the supposed agglutinating nature of the *Globorotalites* test speculated by Hauser and Grünig (1993), the updated foraminiferal classification proposed by Hayward et al. (2020) would definitely consider this foraminifer as lamellar perforated like *Eponides* and *Poroeponides*, thus approving Reiss's (1959, 1960) first hypothesis.

There are several records of true *Eponides* (see discussion in Hottinger et al. 1991), or structurally-related specimens, in the geological literature recorded from levels not older than the Eocene (e.g., Loeblich and Tappan 1987). Given that the *Eponides* lineage starts at least from the Late Cretaceous, there is a consistent temporal gap in their history that spans, at least, through the entire Paleocene. In the present study we aim to fill this gap by presenting some interesting stratigraphic records of several specimens we have recognized in thin-sections of carbonate rocks and that are identifiable as *Eponides* as Hottinger et al. (1991) have suggested. These come from the Danian of Austria and the lower-middle Paleocene (SBZs 1-3) of Turkey and Iran, where ages have been constrained by means of planktonic (Schlagintweit et al. 2018; Sanders et al. 2019) or benthic (Consorti and Köroğlu 2019; Schlagintweit and Rashidi 2019) foraminifera. Paleogeographically, the study areas formerly belonged to the northern margin of the Neotethys ocean where most likely *Eponides* populations thrived successfully.

TAXONOMY AND SHELL STRUCTURE OF *EPONIDES*

For a long time, the genus *Eponides* remained an unclear issue mainly because it was equivocally described and illustrated under *Nautilus repandus* Fichtel and Moll 1798. Furthermore, its holotype, thought lost, was re-discovered after almost two centuries by Rögl and Hansen (1984; see also Cimerman and Langer 1991; Hottinger et al. 1991 and references cited therein). Once its nomenclature has been fixed as *Eponides repandus* (Fichtel and Moll), Hottinger et al. (1991) clarified the taxonomy of *Poroeponides lateralis* (Terquem) as well, which is considered a close relative of *Eponides*, whereas Hauser and Grünig (1993) added some critical information on *Globorotalites* along with other similar, non-phylogenetically related taxa.

We report here the main shell features of *Eponides* (*E. repandus* type-species) critical for thin section identification. For more details on the shell architecture of *Eponides, Poroeponides* and *Globorotalites*, a rich glossary of specific terms as well as a discussion on previous works on this topic, we recommend a careful reading of Reiss (1959, 1960), Rögl and Hansen (1984), Hottinger et al. (1991), Hauser and Grünig (1993), Hottinger (2006) and Parker (2009).

Eponides is a lamellar perforated medium-sized foraminifer. The perforation of the outer chamber wall is evident. Chambers are subtrapezoidal, trochospirally arranged; evolute on the dorsal side and involute on ventral side. The shell is markedly convex on the ventral side and slightly convex on the dorsal side. Chamber sutures are distinctly curved on the dorsal side, and radial or slightly curved on the ventral side (see also Hottinger 2006; fig. 61B). The main aperture is represented by a large interiomarginal arch. There may be supplementary apertures. The septal flap extends into a bipartitor, which is characterized by a marginal thickening and is positioned in front of the (previous) aperture. The ventral chamber prolongation bends distinctly and, fused with the previous chamber wall, it produces an externally visible pseudoumbilicus, and continues running through the adjacent whorl as an umbilical plate. The canal system is composed of a columellar spire. It is constrained between the umbilical plate, the bipartitor, and the preceding whorl, and is open to the exterior through the pseudoumbilicus of the last chamber. According to Hottinger et al. (1991), *Eponides* does not possess intraseptal interlocular canals.

STRATIGRAPHIC FRAMEWORK

The Paleocene shallow-water carbonate successions containing the studied specimens were described by Sanders et al. (2019), Schlagintweit and Rashidi (2019) and Consorti and Köroğlu (2019) (with references therein). We summarize the main stratigraphic setting in the following subchapters. According to Scotese (2014) their paleogeographic position can be referred to the northern margin of the western-central Neotethys Ocean (text-fig. 1).

Austria

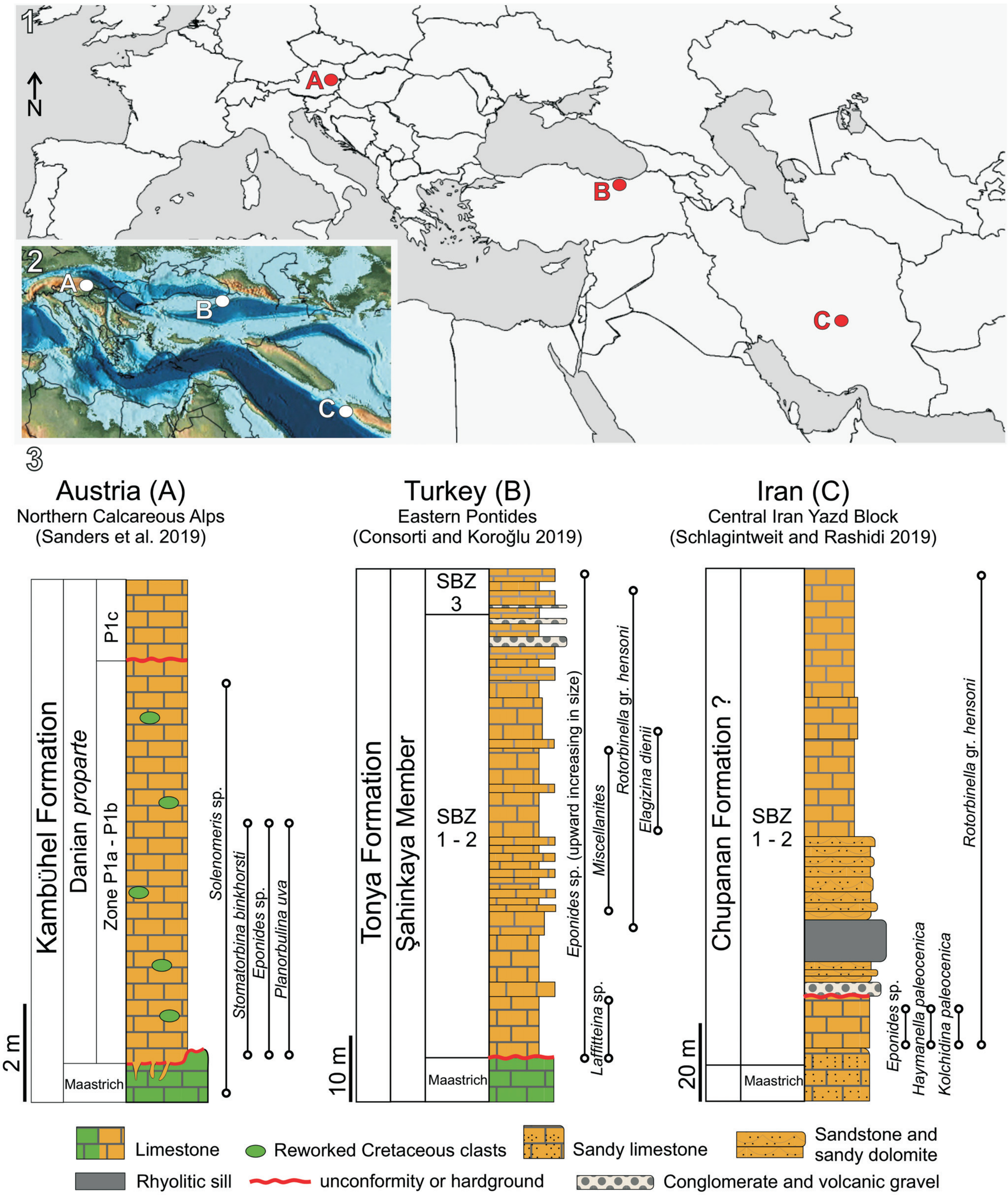
The carbonate succession studied herein crops out in the southeastern Austrian Alps (Northern Calcareous Alps). At this locality the Kambühel Formation records a discrete Cretaceous-Paleocene boundary in a shallow-water setting. The base of the section is represented by a benthic foraminiferal calcarenite with larger benthic foraminifera, among them *Siderolites calcitrapoides* Lamarck, *Orbitoides brinkae* Visser, *Lepidorbitoides socialis* Leymerie, *Hellenocyclina beotica* Reichel, *Sirtina ornata* (Rahaghi), *Daviesina fleuriausi* (d'Orbigny) and *Clypeorbis? ultima* Schlagintweit et al. (Schlagintweit et al. 2016) of the late Maastrichtian, referred to the Cretaceous foraminifer zone 3 (CF3) *Pseudoguembelina hariaensis* (Keller 2014). Maastrichtian rocks are topped by a subaerial exposure surface represented by a hardground**.** The hardground is followed by a carbonate facies of the early Danian zone P1a(1), suggesting a phase of non-deposition of about 0.5 m.y. duration. The early Danian records a depositional environment between shoreface and emersion. Shoreface limestones are rich in bryozoans, coralline algae, common planktonic foraminifera along with reworked Maastrichtian and older clasts. The benthic foraminiferal assemblage is represented by *Solenomeris* sp., *Stomatorbina binkhorsti* (Reuss), *Eponides* sp., *Planorbulina uva* Scheibner, and polymorphinids. The Danian succession is bothered by a short subaerial exposure marked by a hardground of about 1.5 m.y. duration (text-fig. 1); please see Sanders et al. (2019) and Schlagintweit et al. (2018) for additional information.

Turkey

The succession under investigation is part of the Şahinkaya Member at the Çalköy section, in the Eastern Pontides; northern Turkey (text-fig. 1). This sequence is approximately 100 meters thick and is represented by massive to well-bedded limestones. The section comprises a lower part, roughly 25 meters thick, of Maastrichtian wackestone to grainstones, including *Siderolites calcitrapoides*, *Canalispina iapygia* Robles-Salcedo et al., *Lepidorbitoides minor* (Schlumberger), *Orbitoides* cf. *gruenbachensis* Papp, *Orbitoides* cf. *media* (d'Archiac), *Sirtina orbitoidiformis* Brönnimann and Wirz, *Sirtina ornata*, *Clypeorbis mamillata* (Schlumberger), and a few planktonic foraminifera. There is a depositional hiatus, represented by an unconformity, between the Cretaceous and the overlying Paleocene, of about 2 m.y. duration. The Paleocene is about 75 meters thick and is represented by carbonates with oxidized bioclasts and some coral levels interested by vadose isopachous marine cements resulting from subaerial diagenesis. The rich foraminiferal assemblage comprises, among them, the genus *Miscellanites* with three species, *M. primitivus* (Rahaghi), *M. globularis* (Rahaghi) and *M. minutus* (Rahaghi); the genus *Elazigina* with *E. dienii* (Hottinger) and *E*. cf. *lenticula*, *Ornatononion moorkensi* (Hottinger) and *Rotorbinella* gr. *hensoni*. Their vertical distribution assigns the age to the Danian–lower Thanetian, respectively Shallow Benthic Zones 1 to 3 (Serra-Kiel et al. 1998; Hottinger 2014). More details can be found in Inan et al. (1999); Inan and Inan (2014); Köroğlu and Kandemir (2019) and Consorti and Köroğlu (2019).

Iran

The Kuh-e-Chah Torsh (or Mount Chah Torsh) section is placed in one of the Central Iranian tectonostratigraphic units called the Yazd Block (Wilmsen et al. 2015). It shows an almost continuous K–Pg succession of shallow-water limestones and dolostones interbedded with volcanic products and siliciclastic deposits in its lower part (text-fig. 1). In this section, the Upper Cretaceous is recorded by sandy limestones containing bryozoans, oysters, and the larger benthic foraminifera *Simplorbites gensacicus* (Leymerie), *Canalispina iapygia* Robles-Salcedo, Vicedo, Parente and Caus, *Sirelina orduensis* Meriç and Inan, *Sirtina ornata* (Rahaghi), *Orbitoides gruenbachensis* Papp, and rare *Omphalocyclus macroporus* (Lamarck) and *Solenomeris* sp. These deposits can be correlated with the Tarbur Formation of the Zagros Zone, which is Late Maastrichtian in age (Schlagintweit et al. 2016; Consorti and Rashidi 2018; Consorti et al. 2019). The upper Maastrichtian sediments display an increase in siliciclastic influx upwards, along with a decrease in the abundance of orbitoidal foraminifera. Above the last sample with larger foraminifera, an interval of sandy marls (0.8 m to 1.0 m) barren of fossils, possibly represents the K-Pg boundary interval. Upwards, mixed carbonatic-siliciclastic marine levels record a new transgression, and contain several benthic foraminifera, including *Rotorbinella* gr. *hensoni* Hottinger. The age of these beds can be assigned to the Danian (Hottinger 2014). These facies grade upward into a thick succession of grey carbonates with abundant foraminifera including, among them, *Eponides* sp., *Sistanites iranicus* Rahaghi, *Idalina sinjarica* Grimsdale, *Rotorbinella hensoni* (Smout), *Elazigina* cf. *dienii* (Hottinger), *Ankarella* sp., *Haymanella* sp. and *Kolchidina paleocenica* (Cushman), along with bryozoans and green algae. Based on the occurrence of Paleocene larger foraminifera, this succession is tentatively correlated with the Chupanan Formation of Wilmsen et al. (2015), and placed, in



TEXT-FIGURE 1
Geographic location (1) and paleogeographic position (2) of the studied Paleocene successions. Paleogeographic map taken from Scotese (2014). 3. Synthetic stratigraphic logs of the Maastrichtian-Paleocene shallow-water successions studied from Austria (A), Turkey (B) and Iran (C). SBZ: Shallow Benthic Zone of Serra-Kiel et al. (1998).

the Mount Chah Torsh section, into the SBZs 1 and 2; see Schlagintweit and Rashidi (2019) for more stratigraphic and paleontological information.

MATERIAL AND METHODS

This study refers exclusively to specimens studied in thin-sections. The Austrian samples labelled as KB- (for Kambühel) are deposited at the University of Innsbruck in the collection of D. Sanders. The two Iranian specimens illustrated in the present paper are deposited in the Geosciences Museum of Mashad (in the Geological Survey of North-Iran East territory) under the depository label thin section Gmm1395. We have also studied 57 thin sections (labelled CK 1–57) from the Turkish succession in the Eastern Pontides. The material is deposited in the Department of Geological Engineering, University of Recep Tayyip Erdogan (Rize).

For the micropaleontological analysis of *Eponides* and the identification of its shell elements we refer to the works and terminology of Hottinger et al. (1991) and Hottinger (2006).

RESULTS

Eponides-like specimens have been found in the Paleocene samples from the Eastern Pontides area of Turkey. These are mostly recovered as reworked, sometimes oxidized, bioclasts in the deposits related to the bioclastic sand shoal facies association (see Consorti and Köroğlu 2019). Some encrusting foraminifers are observed attached to these shells (see the arrow in pl. 1, fig. 3). Due to their copiousness, we had the chance to obtain several randomly oriented sections and some sub-axial and sub-equatorial highly-diagnostic cuts. The most complete specimens are biconvex with about 2.5 trochospiral whorls. In axial view these foraminifera clearly display a bipartitor, attached to the apertural face of, likely, the preceding chamber (see e.g., pl. 1, fig. 1, 6, 7, 8, 12). Some specimens also show a very distinct umbilical bending of the ventral chamber prolongation with the consequent production of a pseudoumbilicus (pl. 1, fig. 6, 8). The umbilical plate is evident and lies in front of the adjacent whorl (pl. 1, fig. 3, 8). The apertures are always represented by a large slit in interiomarginal position; bounded by the bipartitor at the upper part. Chambers in tangential view appear subtrapezoidal (pl. 2, fig. 9). Sub-equatorial centered views of sections passing through the dorsal area show markedly curved septa, like a scythe (pl. 1, fig. 9, 10, pl. 2, fig. 1, 4). Proloculus diameter is approximately 0.15 mm (range between 0.12 mm and 0.16 mm). There are 7–8 chambers in the first whorl and 4–5 chambers in the second. Chambers volume dramatically increase through ontogeny. In sub-equatorial sections passing through the ventral area (pl. 2, fig. 3, 5) a lamellar thickening, most probably related to the pseudoumbilicus, is observed. A set of radial septa branch out from the pseudoumbilicus towards the periphery of the shell. The entire shell is lamellar perforated; calcite crystals grow perpendicular to the outer surface. Pores occur on the outer shell wall and are relatively wide. Septa appear double-layered with an inner dark line resembling an intraseptal interlocular space (see e.g., pl. 2, fig. 3, 7). In terms of shell size there is a quite wide discrepancy among individuals. We have counted 23 specimens in which shell diameter can be measured with high confidence. The biggest ones are 1 mm in diameter (pl. 1, fig. 11, 12 and pl. 2, fig. 7), whereas the smaller individuals are between 0.5 mm and 0.6 mm in diameter.

Few individuals have been recovered from the base of the Danian succession in Austria (pl. 2, fig. 10, 12). These are biconvex with trochospirally arranged set of chambers. In sub-axial view they display the bipartitor, umbilical plate and, in sub-equatorial view, strongly curved septa. Shell mineralogy is lamellar-perforated with a double-layered appearance through the septa. Diameter of the shell ranges between 0.4 mm and 0.65 mm, approximately.

Shell geometry of the two specimens recovered at the base of the Paleocene carbonates from Iran (pl. 2, fig. 13, 17) is plano-convex. Sub-axial sections display a structure placed at the apertural face similar to the bipartitor. Umbilical termination of chambers bends over the ventral side like *Eponides*. Their coalescence is not marked whereas the umbilical area seems lacking any shell thickenings. The maximum diameter of these specimens is 0.5 mm. Shell is lamellar-perforated, double layered, whereas the thickness is comparatively small with respect those from Austria and Turkey.

DISCUSSION

The bipartitor is observed in all the studied specimens. Such occurrence, in combination with the other shell features, can be taken as a straightforward taxonomical diagnostic characteristic for *Eponides*: type-species *E. repandus* (Fichtel and Moll) (see Hottinger et al. 1991) and used to distinguish related genera (Hauser and Grünig 1993). A comprehensive specific assignment of the Paleocene specimens here presented is not discussed. In modern seas *Eponides* is represented by three species: *E. repandus*, *Eponides* cf. *E. concameratus* (Williamson) and *E. cribrorepandus* (Hottinger et al. 1991), although the latter is sometimes considered an ecophenotypic variation of *E. repandus* (Parker 2009). There are possibly more species in the modern ocean, but unfortunately there are no data to establish the molecular or taxonomic extension (see Pawlowski et al. 2013; Holzmann and Pawlowski 2017).

The genus *Poroeponides*, differently to *Eponides*, shows a cribrate aperture and lacks any interiomarginal communications. *Eponides* may have some supplementary apertures that are debatable under their specific taxonomic usage (Hottinger et al. 1991; Parker 2009; Förderer and Langer 2018). Supplementary apertures, however, have not been observed in our material. Samples from Turkey and Austria are biconvex and display all the diagnostic *Eponides* features including the pseudoumbilicus and the umbilical plate. In these individuals the septa are markedly curved and directly comparable with those of *Eponides repandus*. The Paleocene specimens further display a type of structure that convincingly resembles an intraseptal interlocular space, as in rotaliids (see e.g., Hottinger 2014; Consorti et al. 2017). According to Hottinger et al. (1991) such a canal system section does not occur in *Eponides*. A critical observation of the figures in Hottinger et al. (1991, 1993), Hauser and Grünig (1993), Hottinger (2006) and Förderer and Langer (2018) do not allow to verify such a statement as there are no views showing the inner septa. Thus, due to the 'rotaliid' nature, intraseptal interlocular spaces would be present in our *Eponides* individuals and may be also expected in modern representatives.

Further Paleocene *Eponides* can be found in Inan and Inan (2008; pl. 2C; Turkey), Consorti and Schlagintweit (2020; fig. 1C; Turkey); Schlagintweit et al. (2018; fig. 2I; Iran). A probable additional specimen is figured in Vicedo et al. (2019; fig. 15H; Oman) as *Gyroidina* sp.

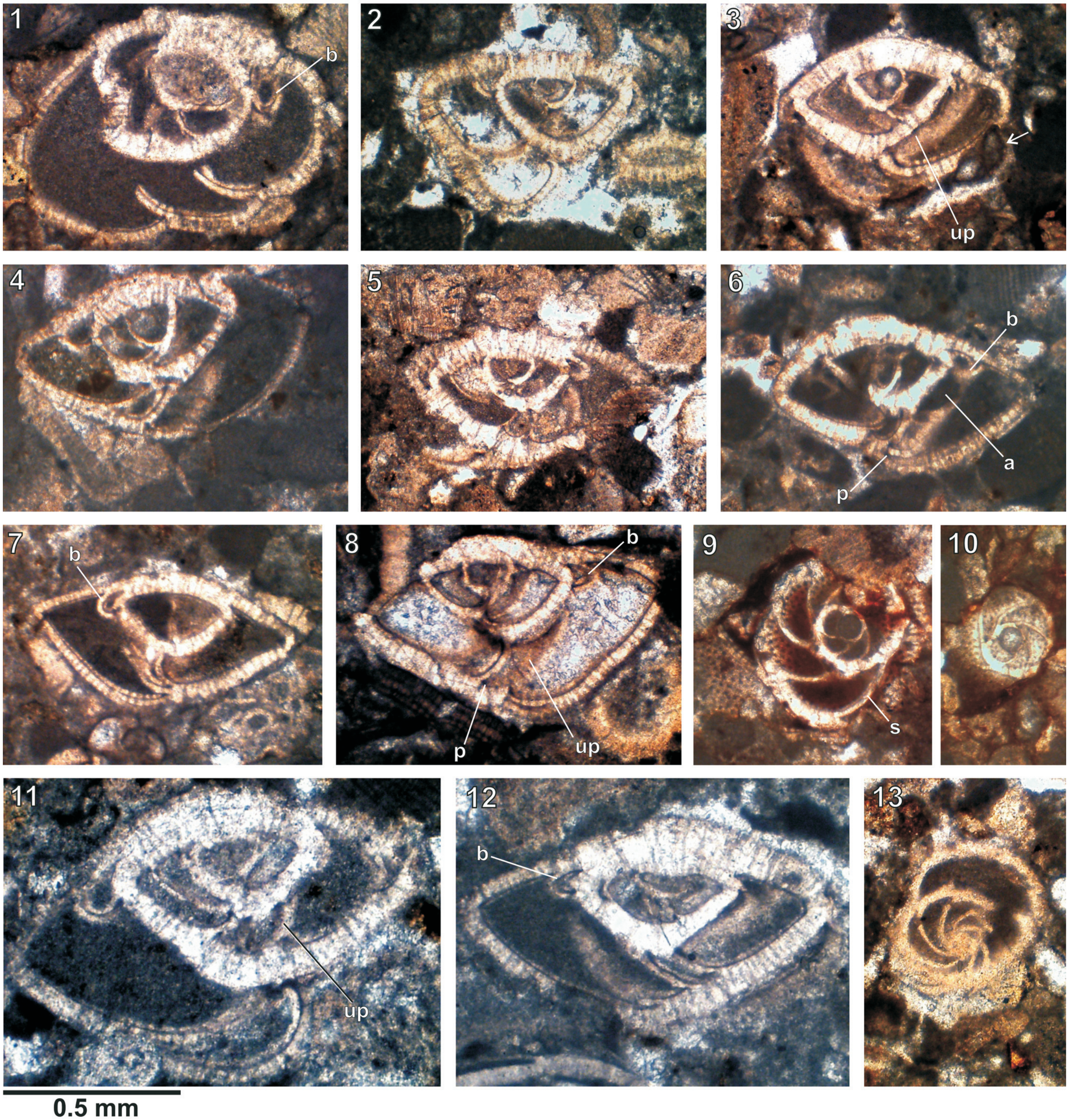


PLATE 1
Eponides from the Paleocene of Turkey, Eastern Pontides area.
Abbreviations: b= bipartitor, a=aperture, up= umbilical plate, p= pseudoumbilicus, s= septum.

1 Oblique section (CK-40)

2-8, 11-12 Sub-axial sections. Repository; 2=CK-21, 4 and 6=CK-32, 5=CK-54, 7=CK-55, 8=CK-56, 3 and 11= CK-50, 12=CK-57,

9-10 Centered sub-equatorial sections. Repository; 9=CK-41; 10=CK-32

13 Sub-equatorial section passing through the ventral area (CK-36)

A morphological ecophenotypic variability is common in *Eponides* and related genera (Hottinger et al. 1991; Hauser and Grünig 1993). The occurrence of supplementary apertures could be linked to such an effect (Parker 2009). Hottinger et al. (1991) instead placed supplementary apertures in relation with *E. cribrorepandus*. A shell diameter discrepancy, likely ecophenotypic, is observed in the Paleocene specimens from the shallow-water succession of the Eastern Pontides area. Here we have detected an upward stratigraphic trend of size-increase. The largest specimens (up to 1 mm in diameter) are recorded in the stratigraphic space referred to SBZ 3, whereas the smaller ones (roughly 0.5 mm in diameter) are frequent in SBZ 1 and 2. This leads to the conclusion that the genus *Eponides*, which supposedly appeared after K-Pg extinction event, follows Cope's rule during the Paleocene. A size-increase trend through geological time is common in foraminifera (Hottinger 2001). Examples include, among others, the genus *Caudammina* Montanaro-Gallitelli (see Kaminski and Gradstein 2005; Benedetti and Pignatti 2009), the dimensions and complexity of lepidocyclinid embryos (Benedetti et al. 2010) and the size of planktonic foraminifera (Arnold et al. 1995). Guex (2003) also explain Cope's rule based on the increase of involution of Jurassic lituolid Foraminifera and the elongation index of Cenozoic alveolinids. The tendency here reported in *Eponides* is thus a possible further evidence and is maybe also the reason why specimens from the Danian of Iran and Austria (this work) are smaller. Here we interpret this pattern as driven by the environmental K-Pg aftermath and related to the Upper Paleocene recovery of stable ecological niches in marine benthic communities (Hottinger 2001). Our sampling, however, refers to a discrete bulk of well-preserved individuals and further studies should be made in order to statistically characterize the lineage.

CONCLUSIONS

Eponides-like specimens have been reported from the Danian of Austria, Iran and from the Paleocene of Turkey in the Eastern Pontides area. The shell architecture of the foraminifers described in this work shows that there is an easy match with the morphological characters reported from the type species *Eponides repandus*. The specific occurrence of i) the bipartitor, placed at the apertural face, ii) the pseudoumbilicus and iii) sickle-shaped septa, confirm such hypothesis. Therefore, such records allow further information on the evolutionary history of early Cenozoic *Eponides* and phylogenetically related taxa. Our outcomes also reveal that the intraseptal interlocular space, discarded by previous workers, is obvious in fossil Paleocene *Eponides* and expected among the living representatives. A trend in size increase among adult shells through the stratigraphic interval SBZs 1-3 suggests that: (1) *Eponides* followed Cope's rule through the Paleocene; (2) the K-Pg extinction may have triggered the evolution of *Eponides* and related genera, the origin of which can be found in the Late Cretaceous genus *Globorotalites*.

ACKNOWLEDGMENTS

The constructive comments and corrections made by the journal reviewers Andrea Benedetti (Tivoli) and Mike Kaminski (KFUPM) have greatly improved the quality of this work.

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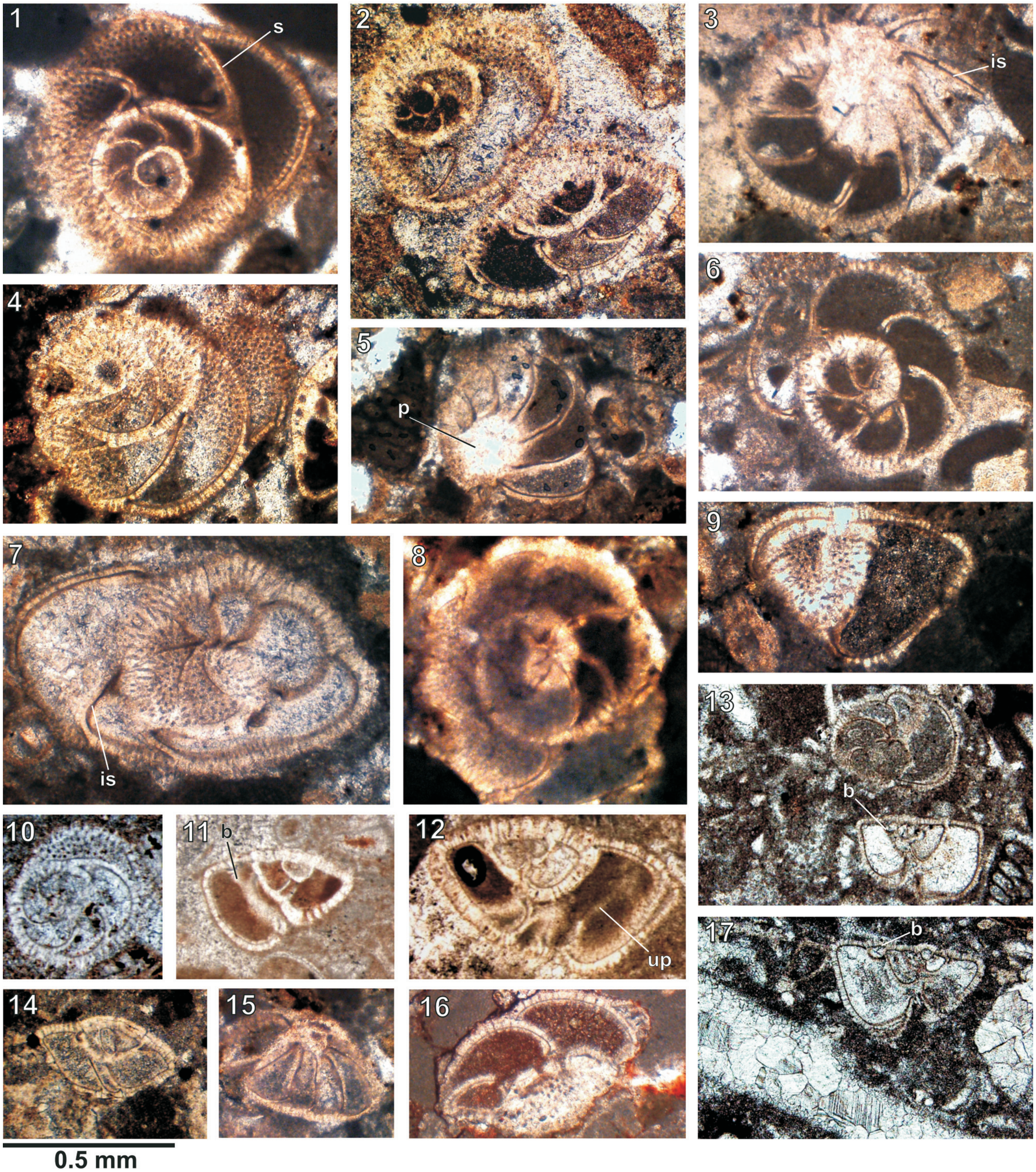

PLATE 2

Eponides from the Paleocene of Turkey, Eastern Pontides area (1-9, 14-16); from the Danian of Austria (10-12) and from the Danian of Central Iran, Yazd Block (13, 17).

Abbreviations: b= bipartitor, is= intraseptal interlocular space, up= umbilical plate, p= pseudoumbilicus, s= septum.

1, 3, 4-6, 8, 10, 16	Sub-equatorial sections. Repository; 1=CK-53, 3 and 6=CK-54, 4=CK-37, 5=CK-47, 8=CK-57, 10=KB-109, 16=CK-45,
2, 7	Oblique sections. Repository; 2=CK-37, 7=CK-55,
9, 14-15	Tangential sections. Repository; 9=CK-54, 14= CK-33, 15=CK-50
11-13, 17	Sub-axial sections. Repository; 11 and 12=KB-109, 13 and 17=Gmm1395

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