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The heterobranch subgenus *Trochactaeon* (*Trochactaeon*) in the Campanian (Late Cretaceous) of the northern Arabian Platform and its paleoenvironmental and paleobiogeographic implications

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Non-technical Summary.—The Late Cretaceous gastropods from Turkey have been insufficiently studied. We herein present a taxonomic study of the subgenus *Trochactaeon (Trochactaeon)* from the upper part of the Karababa Formation (Karababa-C member) at the Saytepe section in southeastern Turkey. The Upper Cretaceous fossil-bearing Karababa Formation, cropping out in southeastern Turkey, yields a remarkable assemblage of acteonellid gastropods and rudist bivalves. The subgenus *Trochactaeon*, a very successful and widespread taxon within the heterobranch gastropod family Acteonellidae, dominated acteonellid assemblages throughout the Late Cretaceous. This is the first record of *Trochactaeon (Trochactaeon) giganteus subglobosus* from Turkey. It is from a single lower Campanian bed in the upper part of the Karababa Formation of the Gölbaşı region (south of Adıyaman), corresponding to the northwestern part of the Arabian Platform. This record complements information on the temporal and spatial distribution of *Trochactaeon* at the southern margin of the Tethyan Ocean during the last part of the Cretaceous Period. This discovery increases the documented diversity of the paleofauna from the Upper Cretaceous succession in southeastern Turkey and provides new insights into the paleoenvironment of the carbonate ramp of the northern Arabian plate, and the paleobiogeography of Campanian gastropods in general.

Abstract.—Acteonellids were one of the most significant groups of marine macro-invertebrates in the Late Cretaceous biota of the Tethyan Realm. They were common faunal elements associated with Cretaceous carbonate platform communities most notable for their abundance of rudist frameworks and thrived in coeval lagoons. The Upper Cretaceous fossil-bearing Karababa Formation, cropping out in southeastern Turkey, yields a remarkable assemblage of acteonellid gastropods and rudists. Cretaceous gastropods from sedimentary successions in Turkey barely have been studied over the past 80 years. The subgenus *Trochactaeon*, a very successful and widespread taxon of heterobranch gastropods within the family Acteonellidae, dominated acteonellid assemblages throughout the Late Cretaceous. In the present work, we present the first record of *Trochactaeon* (*Trochactaeon*) *giganteus subglobosus* from Turkey. It is from a single lower Campanian bed in the upper part of the Karababa Formation of the Gölbaşı region (south of Adıyaman), corresponding to the northwestern part of the Arabian Platform. This record complements information on the temporal and spatial distribution of *Trochactaeon* at the southern margin of the Tethyan Ocean during the last part of the Cretaceous Period. This discovery increases the documented diversity of the paleofauna from the Upper Cretaceous succession in southeastern Turkey and provides new insights into the paleoenvironment of the carbonate ramp of the northern Arabian plate, and the paleobiogeography of Campanian gastropods in general.

Introduction

The Cenomanian–Maastrichtian time span is marked in the Tethyan realm by paleogeographic and paleoenvironmental changes that had a profound effect on the gastropod biodiversity (Sohl, 1987). Members of Acteonellidae Gill, 1871, which are firmly nested within the Heterobranchia, represent some of the most important components of marine communities during the Cretaceous (Kollmann, 2014). From the gastropod point of view, and more particularly from that of the acteonellids, the Late Cretaceous is marked by great diversification of representatives of the family Acteonellidae (Sohl and Kollmann, 1985; Kollmann, 2014). The currently known European record of acteonellid gastropods is relatively abundant and diverse, especially in the Upper Cretaceous strata of the Eastern Alps (Kollmann, 1967). However, records of Cretaceous gastropods from Turkey are very rare and they are usually limited to a few specimens. Cretaceous strata of the Adıyaman area of southeastern Turkey comprise a relatively thick succession that is superbly exposed and relatively fossiliferous (Fig.1.1). These strata form an important sedimentary archive for understanding of the paleogeography of the northern Arabian Platform, which formed part of an extensive carbonate platform on the southern

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margin of the Tethys Sea (Yılmaz et al., 2018). Thus, any new addition to the faunas of poorly known regions, such as northern Arabia, provides new and interesting material for paleobioegeographical analyses.

Until we began our exploration and study on Cretaceous gastropods of Turkey, only a few nominate gastropod taxa had been known. For many years, a Late Cretaceous gastropod assemblage found in northwestern Anatolia and described by Stchepinsky (1942) was the only assemblage known from the entire area. Cretaceous rocks are widespread in southeastern Turkey, however only echinoderm remains, belemnitellids, venerid bivalves, and rudist faunas have been described (Özer, 1992; Farinacci and Manni, 2003; Hoşgör and Kostak, 2012; Mülayim et al., 2018; Hoşgör and Yılmaz, 2019).

During the Late Cretaceous, the Gaziantep, Adıyaman, and Mardin-Derik region was located at the southern margin of the Tethys Sea, prior to its closure (Hoşgör and Yılmaz, 2019). Shallow marine carbonate successions deposited in the area record several successive transitions from outer shelf to inner shelf and platform conditions (Yılmaz et al., 2018). The Upper Cretaceous Karababa Formation forms the upper part of the Mardin Group, a thick succession of mostly carbonate Cretaceous rocks known from outcrops and the subsurface in southeastern Turkey (Çelikdemir et al., 1991). Here, we provide the first record of a remarkable mollusk assemblage from an isolated outcrop of bioclastic limestones of the Karababa Formation (Fig. 1.2).

Knowledge of Cretaceous gastropods from the northern Arabian Platform has been restricted to general descriptions of faunal contents of Cretaceous strata presented by Conrad (1852), Blankenhorn (1890, 1927), Böhm (1900), and Delpey (1940). *Trochactaeon* is an extinct genus of acteonellid gastropods that had significant occurrences in the circum-equatorial Tethyan belt (Albian–Maastrichtian). Distribution and diversity patterns of acteonellids in the Cretaceous have been well studied (e.g., Kollmann, 1967, 2014; Sohl and Kollmann, 1985; Kowalke and Bandel, 1996). The Late Cretaceous paleogeography of the European, North African, and southwest Asian branches of the Tethyan Realm also allowed a wide geographical dispersal of the Acteonellidae, especially from the time of sea-level rise in the Cenomanian and onwards. The discovery presented here provides additional information and extends the known geographical distribution of *Trochactaeon* beyond

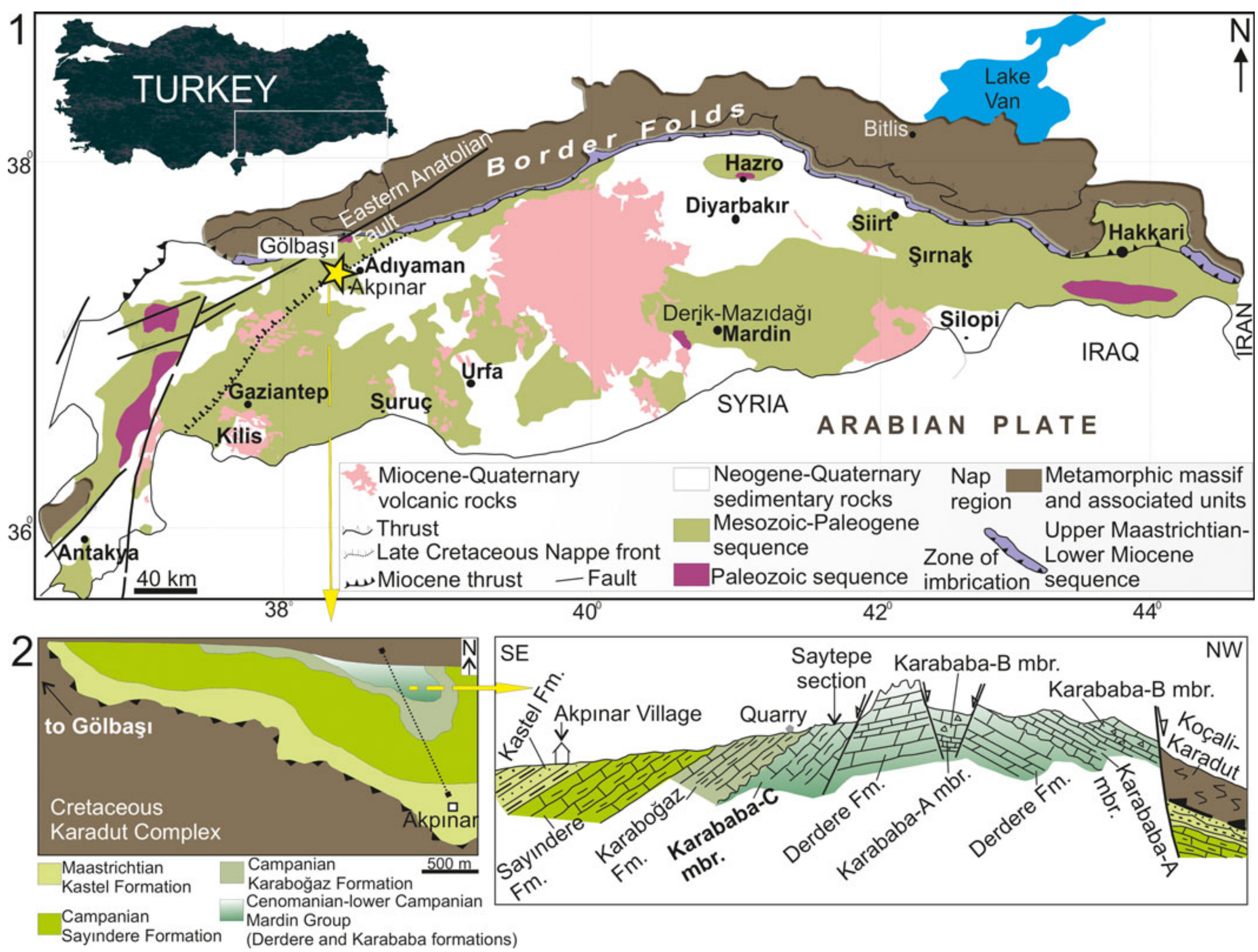

Figure 1. (**1**) Geological map of southeast Turkey (Hoşgör and Yılmaz, 2019). (**2**) Regional geological map of Akpınar Village near the Gölbaşı area showing the location of the studied outcrops and the cross section.

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Europe, indicating that it had a larger paleogeographical distribution than was previously thought. Previously, the '*Trochactaeon*' assemblage was also widely recorded in the southern ranges of the Greater Caucasus and Europe through field-work studies mainly concerning biostratigraphic analysis of depositional architecture for the Upper Cretaceous successions (Pčelintsev, 1953; Pokorný, 1959; Kollmann, 1967; Czabalay, 1973; Akopjan, 1976). This paper deals with the taxonomic description, stratigraphic and geographic ranges, and the paleoenvironmental significance of *Trochactaeon* (*Trochactaeon*) *giganteus subglobosus* (Münster, 1844) in the Adıyaman area (SE Turkey).

Geological setting

The Karababa Formation is exposed in extensive outcrops in the Antakya, Adıyaman, Diyarbakır, and Şırnak regions in southeastern Turkey, where it forms the upper part of the Mardin Group carbonates, which are part of the Arabian platform succession (Fig. 1.1). Numerous studies have been carried out on the Karababa Formation, including microfacies and sequence stratigraphy, geochemistry, and reservoir characterization (Çelikdemir et al., 1991; Cater and Gillcrist, 1994; Yılmaz et al., 2018). However, there is little information about macrofossil assemblages of this formation in SE Turkey. The age of the Karababa Formation has been reported in the literature as late Coniacian to early Campanian, based on biostratigraphic studies of benthic and planktonic foraminifera (Çoruh et al., 1997; Mülayim et al., 2016; Yılmaz et al., 2018).

The Karababa Formation is subdivided into three informal members designated by the letters A, B, and C from base to top. The Karababa-A member is a dark brownish gray, very fine-grained limestone. It contains abundant organic matter and pelagic foraminifera. The conformably overlying Karababa-B member, which was deposited in a shallower-water environment than the Karababa-A member, is composed of calcareous packstones/wackestones that are rich in pelagic foraminifera. The overlying Karababa-C member is a bioclastic limestone that is partly dolomitized (Yılmaz et al., 2018). The depositional succession of these members within a shallow marine sequence has been described from several exploration wells (Mülayim et al., 2016). Few outcrop studies have been published on the Karababa Formation, and these consider only the biostratigraphic aspects of a limited number of sections (Mülayim et al., 2016; Yılmaz et al., 2018). The Karababa Formation is unconformably (or conformably in some localities) underlain by the Derdere Formation (Cenomanian–Turonian) and unconformably overlain by the Karaboğaz and Sayındere formations (Campanian) (Fig. 1.2).

Saytepe section.—The Saytepe section was measured in the Karababa Formation (C-member) (Fig. 2). The base of the section consists of 15-m-thick, medium-bedded limestones, in which macro- and microfossils are absent. These limestones pass upward into rudist-bearing limestones interbedded with algal limestones (∼40 m thick). Three rudist levels can be distinguished, from bottom to top (Fig. 2.2). The first (lower) rudist level (40–50 cm thick, yellowish gray) consists of rare radiolitid valves and valve fragments. Some left valve transverse sections show a single row of radial canals like those seen in *Joufia serbica* (Milovanović, 1956), which recently was described by Özer et al. (2021), and radiolitid right valves (? *Sauvagesia* sp.) (Fig. 2). The second rudist level (60–70 cm thick, dark gray) is composed mainly of hippuritid right valves, usually exposed as transverse and slightly oblique sections scattered in a wackestone–packstone texture showing diagenetic effects (dolomitization, compaction, and micritization). Very sparse radiolitids are also present. *Vaccinites loftusi* (Woodward, 1855) is abundantly represented, but some specimens resemble *Pironaea* sp. (Munujos et al., 2016). The third level (50–60 cm thick, gray) is directly above the previous rudist level and consists of radiolitids exposed in transversal, oblique, and radial right-valve sections and abundant fragments. *Biradiolites bulgaricus* Pamouktchiev, 1967, *Biradiolites* sp., *Bournonia* cf. *B. dinarica* Slišković, 1983, *Durania* sp., and *Radiolites* sp. can be identified. This level is composed of packstones–wackestones that include radiolitid fragments, some of which are very thick. The right valve transverse sections of radiolitids represent isolated scattered individuals in life position, but abundant disoriented and reworked radiolitid fragments also are present. The distribution of these rudist species in the Mediterranean area (Steuber, 2002) suggests a Campanian age for the rudist fauna.

The uppermost part of the 15-m-thick sequence is characterized by the occurrence of acteonellid assemblages (Fig. 2.1, 2.2). The upper part of the Karababa Formation comprises mainly monospecific acteonellids, *Trochactaeon* (*Trochactaeon*) *giganteus subglobosus* (Münster, 1844) at the Saytepe locality. At this site, the thickness of the shell beds was measured, and the preserved parts of the shells were internal molds. The available top bedding surface of the acteonellid shell beds at this site was recorded in a packstone–grainstone bed (Fig. 2.1).

Material and methods

Preserved specimens of *Trochactaeon* described herein were collected from above the rudist-bearing limestone assigned to the Karababa Formation (C-member) in the Gölbaşı valley near Besni (37.75472°N, 37.7513938°E; topographical map sheet 1:25,000; M39-c) in the Adıyaman region. The studied stratigraphic section was measured on a bed-by-bed scale, for a total thickness of 70 m (Fig. 2). Stratigraphic and microfacies analyses were performed at the Sedimentology Laboratory of the Department of Geological Engineering, Middle East Technical University (METU), Ankara, Turkey. Microfacies determinations were carried out by a point-counting/visual estimation method on thin sections with a James Swift point-counting apparatus and an Olympus CX31 polarizing microscope, based on the principles of microfacies analysis of Flügel (2010).

The *Trochactaeon* bed yielded enough isolated and complete specimens to illustrate the diversity of their internal morphology. The descriptions and measurements in the systematic paleontology section follow Kollmann (1967) and Sohl and Kollmann (1985). The classification used in this work follows Bouchet et al. (2017). The synonymies contain only the most recent references, as well as those of importance to the discussion. All linear measurements are given in millimeters.

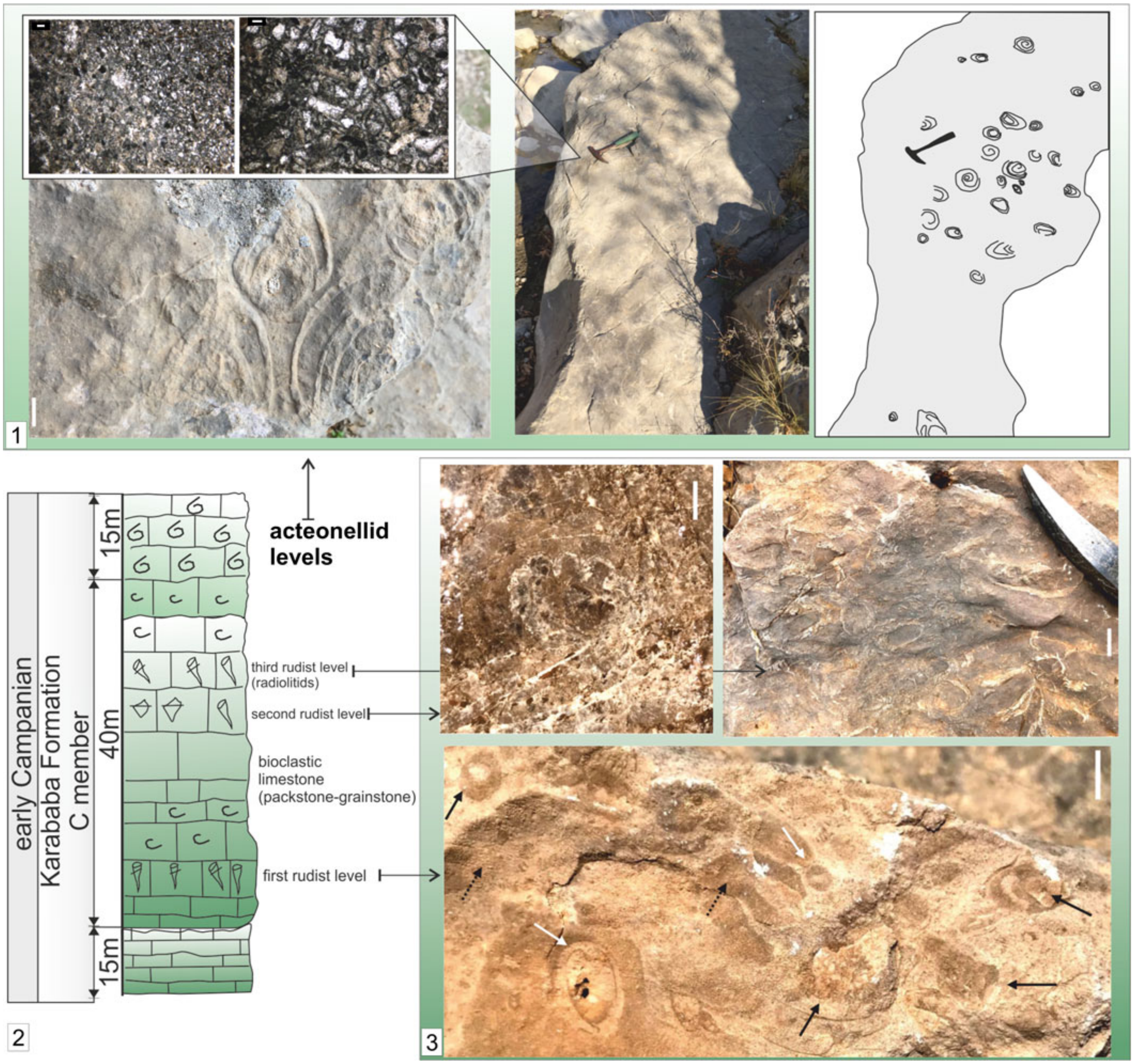

Figure 2. (**1**) Field views of lithofacies in the Saytepe section, acteonellid assemblage slabs, and photomicrographs of the packstone–grainstone microfacies; scale bars = 100 μm. (**2, 3**) First rudist level showing the left valve transverse sections of *Joufia serbica* (white arrows), indeterminable radiolitid right valve transverse and oblique sections (black arrows), and radiolitid right valve fragments (dashed black arrows). Second rudist level showing the right valve transverse sections of *Vaccinates loftusi*. Note diagenetic effects. Third rudist level consists mainly of radiolitid transverse, oblique, and radial right valve sections. Scales are hammer and 10-mm scale bars.

The rudists are embedded in limestone, therefore they were identified in the field and from field photographs (Fig. 2). They have undergone some diagenetic alteration (e.g., dolomitization, recrystallization, dissolution, and compaction).

Repositories and institutional abbreviation.—Most of the fossil specimens, as well as any additional material illustrated here, are stored in the Sedimentology Laboratory of the Department of Geological Engineering, Middle East Technical University (METU), Ankara, Turkey. Figured specimens are designated in the descriptions by the prefix METUGM (Middle East Technical University Geology Museum).

Systematic paleontology

Class Gastropoda Cuvier, 1795
Subclass Heterobranchia Burmeister, 1837
Superfamily Acteonoidea d'Orbigny, 1843
Family Acteonellidae Gill, 1871
Genus *Trochactaeon* Meek, 1863
Subgenus *Trochactaeon* Meek, 1863

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Type species.—Acteonella renauxiana d'Orbigny, 1842, by original designation; Turonian, France.

Diagnosis.—Subgeneric diagnosis rephrased from Kollmann (1967) and Sohl and Kollmann (1985): the greatest shell width is above mid-height, and the spire comprises less than half of the total shell height. The aperture is narrow, parietal lip smooth; columella with three plaits, one as a high palatal ridge.

Trochactaeon (*Trochactaeon*) *giganteus subglobosus*
(Münster, 1844)
Figures 3, 4.3

1844 *Tornatella subglobosa* Münster, p. 49, pl. 177, fig. 13a, b.
1959 *Acteonella* (*Trochactaeon*) *gigantea subglobosa* Pokorný, p. 959, textfig. 1, pl. 1, fig. 3.
1967 *Trochactaeon* (*Trochactaeon*) *giganteus subglobosus* Kollmann, p. 240, pl. 3. figs. 15, 19, pl. 8. figs. 53–55, pl. 9, figs. 56, 57.
1973 *Trochactaeon* (*Trochactaeon*) *giganteus subglobosus*; Czabalay, p. 293, pl. 5, fig. 1, pl. 6, fig. 2.
1998 *Trochactaeon* (*Trochactaeon*) *giganteus subglobosus*; Forner and Calzada, p. 31, pl. 1, fig. 2.

Holotype.—An internal mold (Nr.751/1), Santonian–lower Campanian (Kollmann, 1967), Hieflau, Austria (Eastern Alps).

Description.—Recrystallized, moderately large shells, approximately spherical shape, low-spired with apical angle >120° (Fig. 4). Aperture proportionally broad, columella thick, columellar lip only slightly expanded and bearing three plaits, low palatal ridge occurs within penultimate whorl, axial whorl section broad and inclined. Outer lip opisthocline at ~30° to shell axis.

Material and measurements.—The largest of the measured specimens (measurements in mm) is shown in Figure 3.5 (H: 155, MW: 135) (H: Height, MW: Maximum width, in mm). A small specimen is shown in Figures 3.3 and 4.3 (H: 70.4; MW: 68.5). The other four specimens available for measurement are illustrated in Figures 3.1 and 4.3 (H: 110.8; MW: 96), Figure 3.6 (H: 70; MW: 75), Figure 3.4 (H: 71; MW: 62), and Figure 3.2 (H: 145; MW: 105).

Remarks.—The majority of Cretaceous acteonellids from Europe, Caucasas, and Arabia (and in the present study) are preserved as recrystallized shells. The family Acteonellidae was created by Gill (1871) and its distinctive characters were presented and discussed in detail by Pčelintsev (1953), Kollmann (1967), Akopjan (1976), and Sohl and Kollmann (1985). The internal characters are best seen in axial sections cut through the center of the columella and these include the most diagnostic features of acteonellids. The results of numerous twentieth century works saw a progressive accumulation of data on the recrystallized shells of the genus *Trochactaeon*. Kollmann (1967) and Sohl and Kollmann (1985) discussed the taxonomy of the *Trochactaeon* group in detail and recognized four subgenera. The subgenus *Trochactaeon* differs from the other three subgenera by the greater width of the shell in relation to its height and the relatively large anterior expansion of the aperture.

The subgenus *Neocylindrites* differs from the other subgenera by its high subcylindrical shell and strong whorl overlap. In this regard, it is similar to the subgenus *Mexicotrochactaeon*, which is distinguished by presence of a parietal fold or ridge in addition to the columellar folds. The incision above the first columellar plate is rather narrow in all subgenera of *Trochactaeon*, but in the subgenus *Mexicotrochactaeon* the incision is broad and terminated by the parietal plait. The subgenus *Sevanella* differs from the other subgenera in having a deep spiral depression in the median part of its whorls and a sculpture of fold-like nodes. They are all heavily nodose shells with laterally depressed whorls. Based on the published descriptions, *Trochactaeon* (*Trochactaeon*) is proposed to have evolved from *T.* (*Neocylindrites*) during the upper part of the Cenomanian (Sohl and Kollmann, 1985). In general, Cenomanian species such as *T.* (*Trochactaeon*) *matensis* (Fittipaldi, 1900) and *T.* (*Trochactaeon*) *pseudocylindraceus* (Pčelintsev, 1953) remain morphologically close to *T.* (*Neocylindrites*), in which the whorls are only slightly inflated (Sohl and Kollmann, 1985).

Pokorný (1959) distinguished three subspecies of *Trochactaeon giganteus*: *T. giganteus giganteus* (Sowerby, 1832), *T. giganteus ventricosus* Hojnos, 1921, and *T. giganteus subglobosus* Münster, 1844. In their general review, Kollmann (1967) and Sohl and Kollmann (1985) accepted only two of these: *T. giganteus giganteus* Sowerby and *T. giganteus subglobosus* Münster, and included *T. giganteus ventricosus* in the synonymy of *T. giganteus subglobosus*. The differences between *Trochactaeon giganteus subglobosus* and *T. giganteus giganteus* have been discussed in detail by Kollmann (1967). *Trochactaeon giganteus giganteus* has a large size, but never reaches the width found in *Trochactaeon giganteus subglobosus*. In large forms of *T. giganteus giganteus*, the side walls in the upper section of the shell are almost cylindrical adapically and gradually converge in the lower section, whereas in *T. giganteus subglobosus* they are strongly curved and almost spherical.

Most of the inner whorls have been crushed and a few also have been recrystallized. The Turkish specimens strongly resemble *T.* (*T.*) *giganteus subglobosus* as figured and described by Kollmann (1967) from the upper Coniacian to lower Campanian of the Eastern Alps and by Czabalay (1973) from the Ugod Formation of Hungary in having the same size, general internal outline, and columellar plications (columellar folds) (Fig. 4). The stratigraphically closest species with similar morphology is *Trochactaeon* (*Trochactaeon*) *goldfussi* (d'Orbigny, 1850) from the Santonian–Campanian Ugod Formation (Czabalay, 1973, p. 294, pl. 5, fig. 1, pl. 6, fig. 2). This species differs from *T.* (*T.*) *giganteus subglobosus* by having weaker columellar folds.

Discussion

Paleoenvironmental and ecologic significance.—Throughout the Cretaceous, several climatic shifts occurred, leading to a transition from a greenhouse to a cool greenhouse world. It is generally agreed that the warmest temperatures in the tropical realm occurred during the Late Cretaceous (Cenomanian–

Figure 3. (**1–6**) *Trochactaeon* (*Trochactaeon*) *giganteus subglobosus* (Münster, 1844), axial sections, METUGM 2218-01-06, specimens from Saytepe section. All scale bars represent 10 mm.

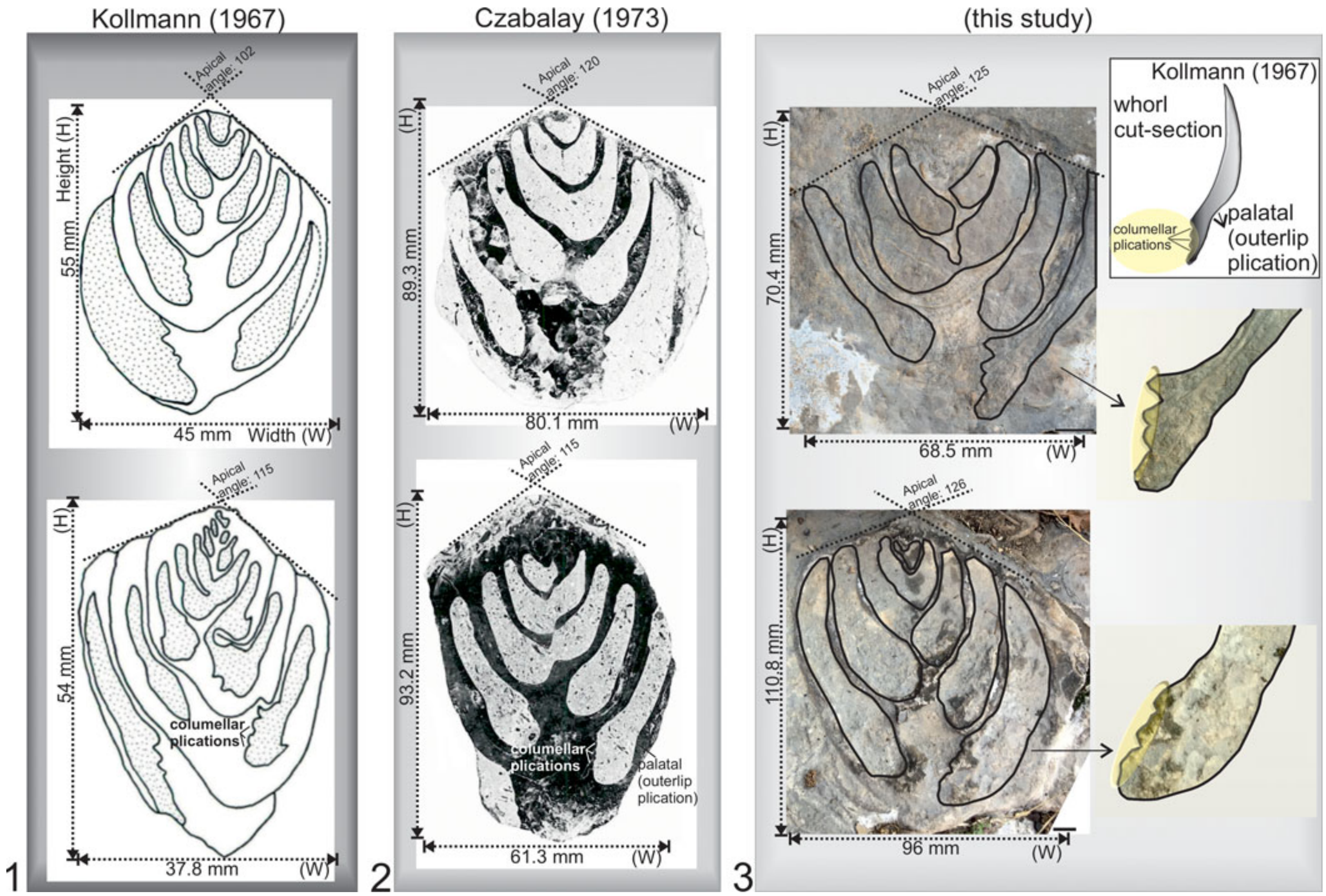

Figure 4. Morphologic features of *Trochactaeon* (*Trochactaeon*) shells in longitudinal cross-section, highlighting the plication (fold) of the palatal (outer lip) and the columellar folds.

Coniacian), and that temperatures declined sharply during the Maastrichtian (Hay, 2008). The Campanian (84.2–72.1 Ma) is the longest stage of the Late Cretaceous and a key interval, encompassing the transition from the 'hot greenhouse' of the Middle Cretaceous to the 'cool greenhouse' of the Maastrichtian (O'Connor et al., 2020). Within the tropical belt, zones of slightly hypersaline, nutrient-depleted water facilitated development of the rudist facies and their typical gastropods (Kiel, 2002; Kollmann, 2014). The life habit of the acteonellid gastropod genus *Trochactaeon* is generally accepted as mobile epifaunal (Sohl and Kollmann, 1985). A remarkable size increase in the comparatively short time range of this genus may reflect high nutrient environments due to favorable climatic conditions (Kollmann, 2014).

The Karababa limestone typically consists a patchwork of slightly variant, highly fossiliferous facies, dominated by biopelmicrites/sparites (wacke- and packstones), bio-micrites, pellets, and pack- grainstones (Fig. 2.1). Characteristic facies fossils include bivalves (hippuritids and radiolitids), gastropods, echinoid fragments, ostracodes, dasyclad algae, and foraminifers. Hippuritids and radiolitids are usually found as isolated individuals in the Saytepe section (Fig. 2.2). They appear to have toppled over but may have been transported and deposited not far from their original environment. The paleoecological and facies characteristics indicate that the rudist-bearing limestones were deposited on a gently sloping mid-carbonate ramp on the northern shelf of the Arabian platform.

Trochactaeon (*T.*) *giganteus subglobosus* formed monospecific populations that lived in the upper part of the Saytepe section. Sanders et al. (1997) and Kollmann (2005) have shown that *Trochactaeon* inhabited the proximal inner shelf, where it formed mostly monospecific assemblages. The nearly monospecific shell beds of the late Coniacian–early Santonian *Trochactaeon* assemblage from the Gosau deposits described by Kollmann (1965) have been interpreted as deposited in brackish to shallow-marine environments with fluctuating salinity. Salinity is an important issue because acteonellids sometimes have been stated to indicate brackish conditions. Acteonellids and nerineids are reported to have a certain tolerance for reduced salinity (Waite et al., 2008). *Trochactaeon* (*Trochactaeon*) presumably had a broader salinity tolerance, ranging from 5–10 ppm to 30–40 ppm (Sohl and Kollmann, 1985).

At most levels, the benthic fauna is impoverished, with diversity values from very low to low. However, low diversity is a result of stress conditions, which can be created by a number of environmental parameters. The low species diversity indicates a somewhat restricted environment (Fürsich et al., 2009). The low diversity together with individual abundances in the molluscan assemblages are features that are characteristic of brackish-water faunas (Fürsich et al., 1995). The simple trophic structure of the studied molluscan assemblage with a predominance of *T.* (*T.*) *giganteus subglobosus* may confirm high stress conditions.

The *Trochactaeon* gastropod fauna can be well correlated with the fauna of the Gosau deposits in Austria, Hungary, and Romania, which occurred in the late Turonian to Campanian (Czabalay, 1983; Wagreich and Faupl, 1994). Furthermore, associations of *Trochactaeon* with *Radiolites* and *Nerinea* in the Gosau Group at Brandenberg/Tyrol more likely indicate shallow-marine lagoonal conditions (Herm et al., 1979; Kowalke, 2005). In addition, the Turonian deposits of Amman (Jordan), which are composed of bioclastic limestone with cherty bands and layers, host several acteonellid species including *Trochactaeon (Mexicotrochactaeon) marjense* Mustafa and Bandel, 1992, and *T.* (*Neocylindrites*) *lamarcki* (Sowerby, 1832). According to Mustafa and Bandel (1992), these species are typical of carbonate-dominated lagoonal settings. Hence, tropical lagoonal environments along the coasts of the Tethys Ocean seem to have been the preferred habitat of Acteonellidae (Mustafa and Bandel, 1992). On the other hand, Rashwan et al.

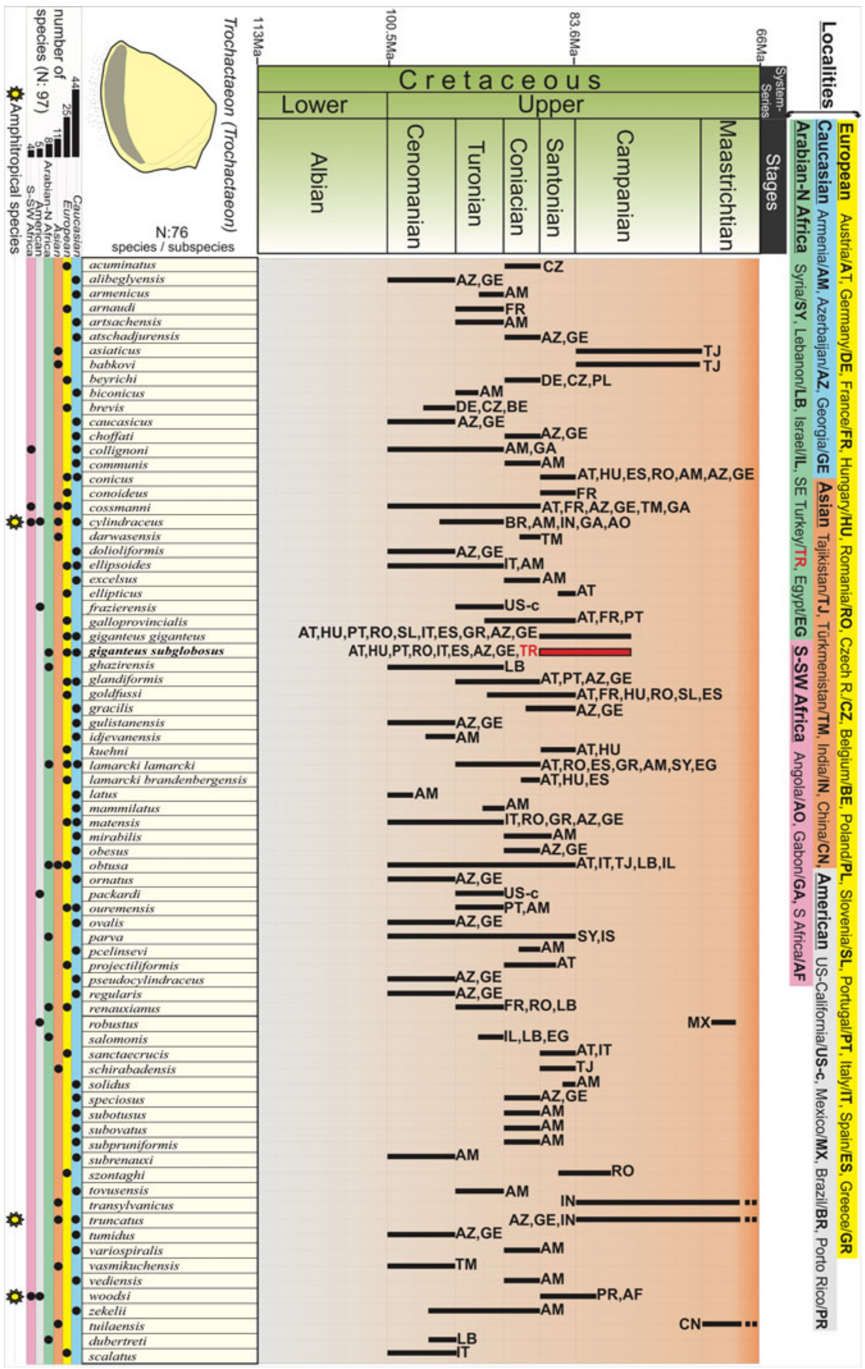

Figure 5. Stratigraphic range of *Trochactaeon* (*Trochactaeon*) species and subspecies during the Cretaceous (primary data sources are: Kollmann, 1967; Czabalay, 1973; Akopjan, 1976; Sohl and Kollmann, 1985; Kowalke and Bandel, 1996; Forner and Calzada, 1998; Kollmann, 2014).

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(2022) interpreted *Trochactaeon* shell concentrations as shallow nearshore warm-water accumulations in response to storm activity in the upper Turonian of Egypt.

Paleobiogeographical implications.—Upper Cretaceous shallow-water carbonates from the Tethys Ocean were accreted in the Mediterranean area and constitute the best archive of the endemic or amphitropical fauna that prevailed in this vast ocean during the Late Cretaceous (Kauffman, 1973; Sohl, 1987; Christensen, 1997; Squires, 2011, 2018; Steuber et al., 2016). *Trochactaeon* (*Trochactaeon*) is a widespread taxon recorded in Europe, Caucasia, Asia, America, south-southwestern Africa, and Arabia–northern Africa (Fig. 5). The stratigraphic range of *T.* (*Trochactaeon*) is also remarkable, covering nearly 35 million years from the Cenomanian to Maastrichtian (Fig. 5). The species of the nominate subgenus *T.* (*Trochactaeon*) rapidly and continuously diversified from the first appearance in the Cenomanian through Turonian stages (Sohl and Kollmann,

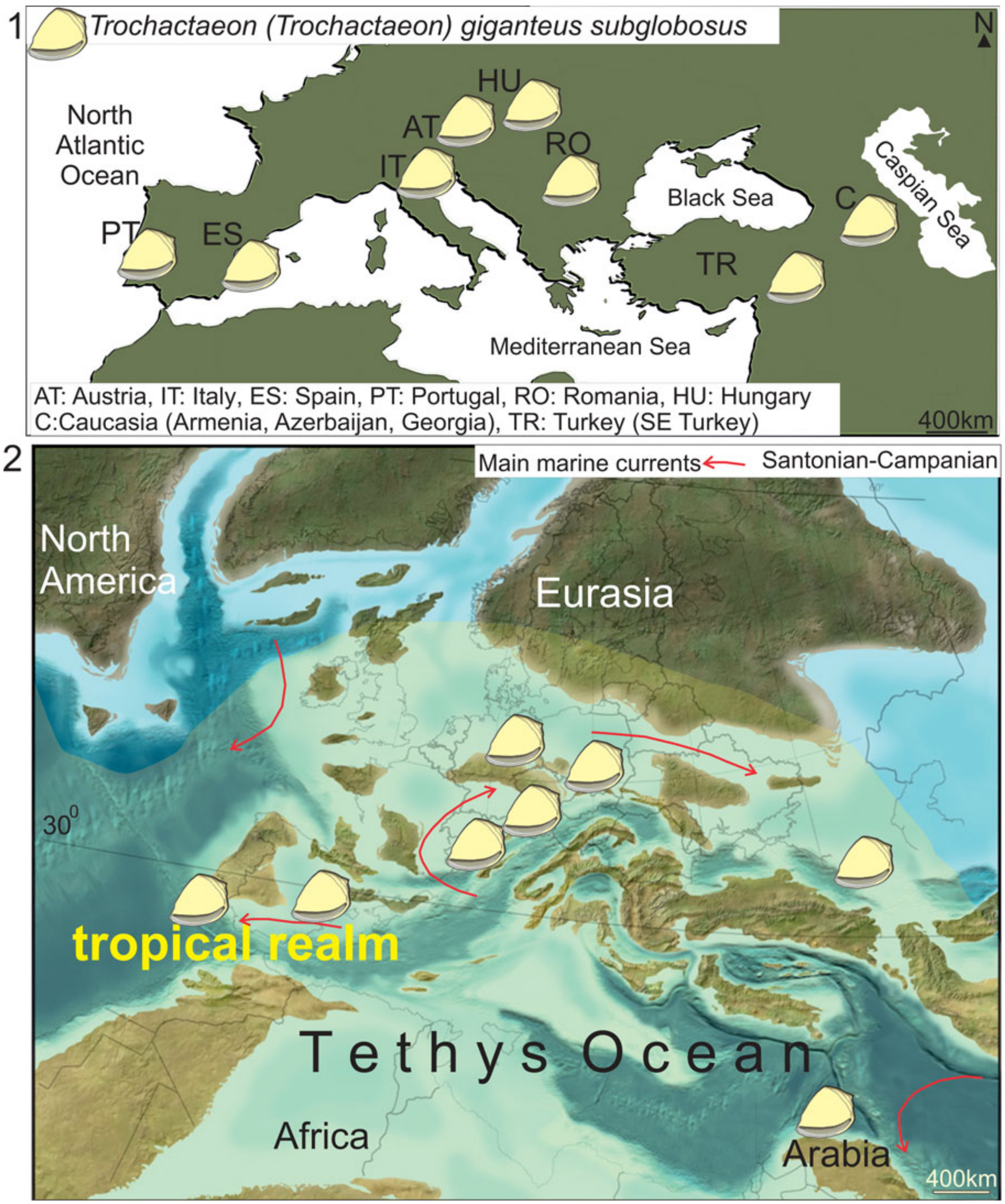

Figure 6. (**1**) Geographic and (**2**) paleobiogeographic distributions of *Trochactaeon* (*Trochactaeon*) *giganteus subglobosus* (Münster, 1844). Main ocean currents are based on Poulsen et al. (2001) and Callapez et al. (2015); paleogeographic map after Blakey (2012).

1985). The number of species/subspecies increased regularly from the Cenomanian to the Santonian (Fig. 5), while the highest numbers were reached in the Coniacian and Santonian stages (Sohl and Kollmann, 1985). Diversity decreased further throughout the Campanian and Maastrichtian stages (Kollmann, 2014).

Acteonellid assemblages have rarely been studied in the Late Cretaceous of the Arabian platform. The presence of *T.* (*Trochactaeon*) *renauxianus* (d'Orbigny, 1842), *T.* (*Trochactaeon*) *obtuse* (Zekeli, 1852), and *T.* (*Trochactaeon*) *lamarcki lamarcki* in the Cenomanian to Santonian shallow marine carbonate deposits of Syria, Lebanon, Israel, and Egypt extends the paleobiogeographical distribution of the subgenus into the Upper Cretaceous of Arabia–North Africa (Böhm, 1900; Blanckenhorn, 1927; Delpey, 1940; Sohl and Kollmann, 1985) (Fig. 5). The distribution of *T.* (*T.*) *giganteus subglobosus* was restricted to the Santonian to early Campanian of Austria, Hungary, Portugal, Romania, Italy, Spain, and the Caucasus and is regarded as a good indicator of a prevailing tropical climatic conditions (Pokorný, 1959; Kollmann, 1967; Czabalay, 1973; Sohl and Kollmann, 1985; Forner and Calzada, 1998) (Fig. 6). The subspecies *T.* (*T.*) *giganteus subglobosus* recorded herein expands the early Campanian distribution of the subspecies to the southern Tethys, which is much farther south than previously reported.

Trochactaeon (*Trochactaeon*) species are not recorded from the Coniacian to Santonian of the Americas (Fig. 5). In contrast, they occur in Europe, Caucasia, Asia, southern–southwestern Africa, and Arabia–northern Africa areas during this time (Fig. 5). Amphitropical distribution patterns are relatively common among diverse groups of tropical realm gastropods, particularly in carbonate platforms that were extensive in geographical latitude (i.e., South Africa and North/South America or Caucasia and Africa) during the Late Cretaceous (Squires, 2011). Amphitropic *Trochactaeon* (*Trochactaeon*) species achieved such a distribution no earlier than the late Cenomanian (Fig. 5).

Cenomanian–Campanian strata are characterized by high biological diversity of the acteonellid, nerineid, oyster, inoceramid, belemnite, and echinoid assemblages (Pčelintsev, 1953; Dobrov and Pavlova, 1959; Akopjan, 1976; Sohl and Kollmann, 1985; Christensen, 1997; Mamedalizade, 2019). At that time, several shared species from the Caucasus migrated from northern regions to southern Europe via to the Crimea region. The oceanic circulation pattern within the Mediterranean area was probably dominated by a westward surface current directed toward the central Atlantic along its southern margin, and an eastward surface current along its northern margin (Poulsen et al., 2001; Callapez et al., 2015). These oceanic currents would have aided dispersal of the acteonellid subgenus *Trochactaeon* (*Trochactaeon*) and many other invertebrate groups across the shallow carbonate shelves along the margins of the Tethys (Fig. 6.2).

Conclusion

During the Late Cretaceous, the subgenus *Trochactaeon* (*Trochactaeon*) had a very wide geographic distribution. It has been recorded throughout Europe, Caucasia, Asia, North America, and part of the Arabian Plate. Thus, *Trochactaeon* (*Trochactaeon*) species or subspecies were mainly a Tethyan Realm subspecies, with a significant extension towards the southern Tethys along the northern Arabian plate margin. The new discovery in Turkey therefore extends the distribution of the subspecies *T.* (*T.*) *giganteus subglobosus* into the southern Tethys in the Late Cretaceous. Preserved specimens of *Trochactaeon* described herein lie near the top of the Karababa-C member with the rudist fauna suggesting a Campanian age for the Saytepe section. Discovery of *T.* (*T.*) *giganteus subglobosus* in the Karababa Formation greatly expands the paleobiogeographic range of the subspecies and allows us to propose an early Campanian age for the upper part of this formation. Future work on the Karababa Formation offers great potential for the discovery of additional exceptionally preserved fossils in the Upper Cretaceous of SE Turkey that will help further refine the paleobiogeographic and stratigraphic distributions of acteonellid gastropods.

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Declaration of competing interests

The authors declare none.

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