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Dictyoptychus Douvillé: Taxonomic Revision, Phylogeny and Biogeography

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Abstract: The late Campanian–Maastrichtian transgressive sequences of the southeastern Anatolia (northernmost part of the Arabian platform) and only one Maastrichtian limestone block within the ophiolitic association of the easternmost part of the Taurus Orogenic Belt contain very well-preserved specimens of *Dictyoptychus* Douvillé 1905. Study of Turkish specimens and also of those described in the literature reveals considerable ontogenic variability, hence need for revision of the species of the genus erected hitherto. *Dictyoptychus leesi* (Kühn 1929), *Dictyoptychus paronai* (Kühn 1929), *Dictyoptychus persicus* (Cox 1934), *Dictyoptychus euphratica* Karacabey-Öztemür 1979 and *Dictyoptychus orontica* Karacabey-Öztemür 1979 are accordingly re-interpreted to represent a single species synonymous with *Dictyoptychus morgani* (Douvillé 1904a). Despite similarities of the canal structure of the right valve of *Dictyoptychus striatus* (Douvillé 1910) with those of *Dictyoptychus morgani* (Douvillé 1904a), must remain problematic at present to include in latter species until its very distinctive radial ornamentation and inner margin structure of the right valve is clearly determined.

The phyologenetic relations between *Dictyoptychus* Douvillé 1905, *Eodictyoptychus* Skelton & El-Asa'ad 1992 and *Semailia* Morris & Skelton 1995 are investigated. *Dictyoptychus quadrizonalis* Özer 2005 and *Dictyoptychus vanensis* Özer 2005 are possibly the most primitive species of the genus. Similarities of the right valve canal structure imply derivation of *Dictyoptychus quadrizonalis* Özer 2005 from *Eodictyoptychus arumaensis* Skelton & El-Asa'ad 1992, as well as a possible link between *Dictyoptychus morgani* (Douvillé 1904), *Dictyoptychus vanensis* Özer 2005 and *Semailia smithi* Morris & Skelton 1995.

The limited biogeographic distribution of the genus within the Afro-Arabian plate indicates endemism together with *Eodictyoptychus* Skelton & El-Asa'ad 1992 and *Semailia* Morris & Skelton 1995.

Key Words: Rudists, *Dictyoptychus*, taxonomy, revision, phylogeny, biogeography

Dictyoptychus Douvillé: Taksonomik Revizyon, Filojeni ve Biyocoğrafya

Özet: Güneydoğu Anadolu'daki geç Kampaniyen–Mastrihtiyen transgresif istiflerinden ve Toros Orojenik Kuşağı'nın en doğusunda yeralan ofiyolit topluluğunda bulunan Mastrihtiyen kireçtaşı bloğundan derlenen çok iyi korunmuş *Dictyoptychus* Douvillé 1905 örneklerinin sağ kavkılarının farklı düzeylerinden yapılan enine kesitler ve günümüze değin yapılan tanımlamalar ontojenetik değişimlerin gözlenmesine ve bu nedenle bilinen türlerin revizyonlarının yapılmasına olanak sağlamıştır. Önceki çalışmalarda tanımlanmış olan *Dictyoptychus leesi* (Kühn 1929), *Dictyoptychus paronai* (Kühn 1929), *Dictyoptychus persicus* (Cox 1934), *Dictyoptychus euphratica* Karacabey-Öztemür 1979 ve *Dictyoptychus orontica* Karacabey-Öztemür 1979 türlerinin, *Dictyoptychus morgani* (Douvillé 1904a)'nin sinonimi olduğu kanıtlanmıştır. *Dictyoptychus striatus* (Douvillé 1910) türünün sağ kavkısındaki kanal yapısının *Dictyoptychus morgani* (Douvillé 1904a) ile benzerliğine karşın, sağ kavkısındaki çok belirgin boyuna süslemelerinin ve kavkı kenarındaki yapısının ayrıntılı olarak tanımlanmasına dek bu türe dahil edilebilmesi sorunlu gözükmektedir.

Dictyoptychus Douvillé 1905 cinsinin, *Eodictyoptychus* Skelton & El-Asa'ad 1992 ve *Semailia* Morris & Skelton 1995 cinsleriyle olan filojenetik ilişkisi incelenmiştir. *Dictyoptychus quadrizonalis* Özer 2005 ve *Dictyoptychus vanensis* Özer 2005, olasılıkla cinsin öncü türleridir. Sağ kavkının kanal yapısının benzerliği, *Dictyoptychus quadrizonalis* Özer 2005 türünün *Eodictyoptychus arumaensis* Skelton & El-Asa'ad 1992 türünden türediğini, *Dictyoptychus morgani* (Douvillé

1904), *Dictyoptychus vanensis* Özer 2005 ve *Semailia smithi* Morris & Skelton 1995 türleri arasında da bir bağlantının olduğunu işaret etmektedir.

Cinsin, *Eodictyoptychus* Skelton & El-Asa'ad 1992 ve *Semailia* Morris & Skelton 1995 ile birlikte Afro-Arabian plakasındaki sınırlı biyocoğrafik dağılımı endemizmi vurgulamaktadır.

Anahtar Sözcükler: Rudistler, *Dictyoptychus*, taksonomi, revizyon, filojeni, biyocoğrafya

Introduction

The first record of *Dictyoptychus* Douvillé 1905 from Turkey including two new species, *Dictyoptychus euphratica* and *Dictyoptychus orontica* was furnished by Karacabey-Öztemür (1979) from the Kahta-Adıyaman and Yayladağı-Antakya areas (Figure 1). Özer (1986, 1991, 1992a, b) added records of other, *Dictyoptychus leesi* (Kühn 1929) and *Dictyoptychus striatus* (Douvillé 1910), and documented a more extended geographical distribution of the genus in southeastern Anatolia. Two new species of the genus, *Dictyoptychus guadrizonalis* and *Dictyoptychus vanensis* were described by Özer (2005) and *Dictyoptychus paronai* (Kühn 1929) also determined from the one limestone block within the ophiolitic association of the easternmost part of the Taurus Orogenic Belt (Figure 1), in the Gevaş-Van area.

Despite of the presence of the genus in southeastern Anatolia, the specimens of the other genera of the family Dictyoptychidae Skelton in Skelton & Benton (1993) such as *Eodictyoptychus* Skelton & El-Asa'ad 1992 and *Semailia* Morris & Skelton 1995, have not yet been found in Turkey.

Variability of the canal shapes and the cardinal apparatus is studied in transverse sections cut at different levels in the right valves of specimens of *Dictyoptychus* Douvillé 1905, collected by the author from southeastern Anatolia.

The main objective of this study is to discuss and to revise the taxonomic status of the many species of the *Dictyoptychus* Douvillé 1905 described so far and also to analyse its phylogenetic relations with *Eodictyoptychus* Skelton & El-Asa'ad 1992 and *Semailia* Morris & Skelton 1995. The biogeographic distribution of the genus is also reviewed.

Geological Setting and Stratigraphy

The specimens of *Dictyoptychus* were found in the northernmostpart of the Arabian platform, around Kahta-Adıyaman (southeastern Anatolia) and in the Yayladağı-Antakya areas, and also in the easternmostpart of the Taurus Orogenic Belt, around Gevaş-Van area (Figure 1).

In the southeastern Anatolia, the lower autochthonous unit of the Arabian platform comprises Precambrian to Upper Cretaceous platform-type carbonates (Figure 2). The Kastel intracratonic basin formed over the autochthonous units during the Campanian and the allochthonous units were transported into the basin by gravity slides. The allochthonous units are giant nappe stacks of ophiolitic associations and sub-ophiolitic thrust sheets (Koçali and Karadut complexes).

The upper autochthonous units were deposited during the late Campanian–Maastrichtian–Early Paleocene, on top the ophiolitic nappes and Kastel Formation and consist of, from bottom to top, red-coloured siliciclastics with rudist limestone lenses (Terbüzek Formation), shallow-water carbonates with rudists (Besni Formation), and pelagic mudstones with bioclastic limestone lenses containing reworked rudist fragments (Germav Formation) (Righo de Righi & Cortesini 1964; Sungurlu 1974; Yalçın 1976; Perinçek 1979; Perinçek & Özkaya 1981; Şengör & Yılmaz 1981; Meriç *et al.* 1985; Özer 1986; Altıner 1989; Yılmaz & Yiğitbaş 1991; Yılmaz 1993; Yılmaz *et al.* 1993; Elmas & Yılmaz 2003; Özer *et al.* 2008). These units show lateral facies changes indicating diachronous transgressive sedimentation and are overlain by clastics of the Gercüş Formation and the carbonates of the Midyat Formation of Eocene age (Figure 2).

Well-exposed outcrops of late Campanian–Maastrichtian–Early Paleocene transgressive sequences are observed around Kahta-Adıyaman area where many specimens of *Dictyoptychus* were found in the Terbüzek and Besni formations (Figures 3 & 4). In the Alidamı locality, the rudist limestone lenses in reddish clastics of the Terbüzek Formation

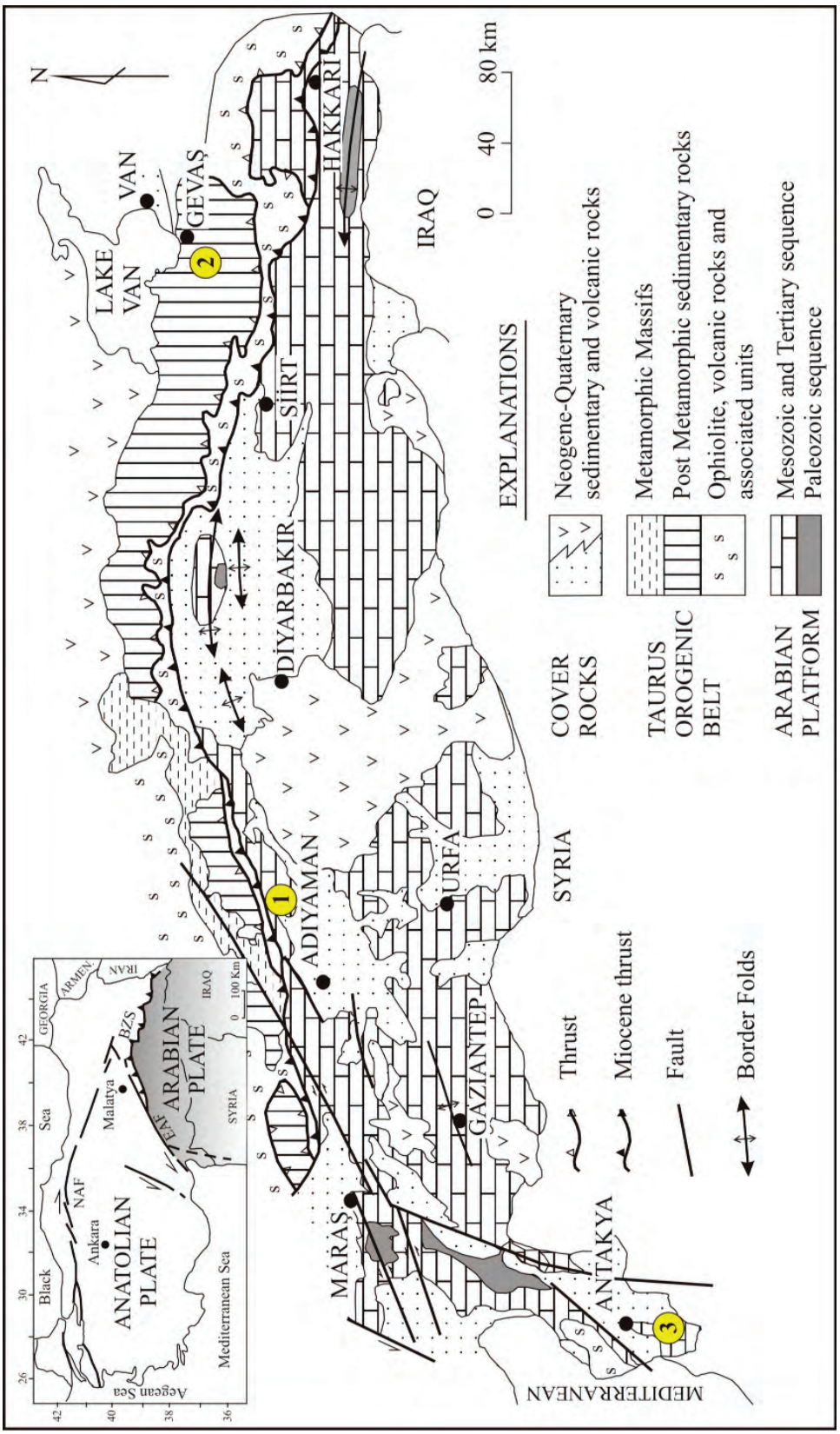

Figure 1. Generalized geological map of southeastern Anatolia (simplified from Perinçek 1979; Yilmaz 1993) showing the *Dictyoptychus* localities: 1– Kahta-Adıyaman, 2– Gevaş-Van, 3– Yayladağı-Antakya. BZS– Bitlis Suture Zone, EAF– East Anatolian Fault, NAF– North Anatolian Fault.

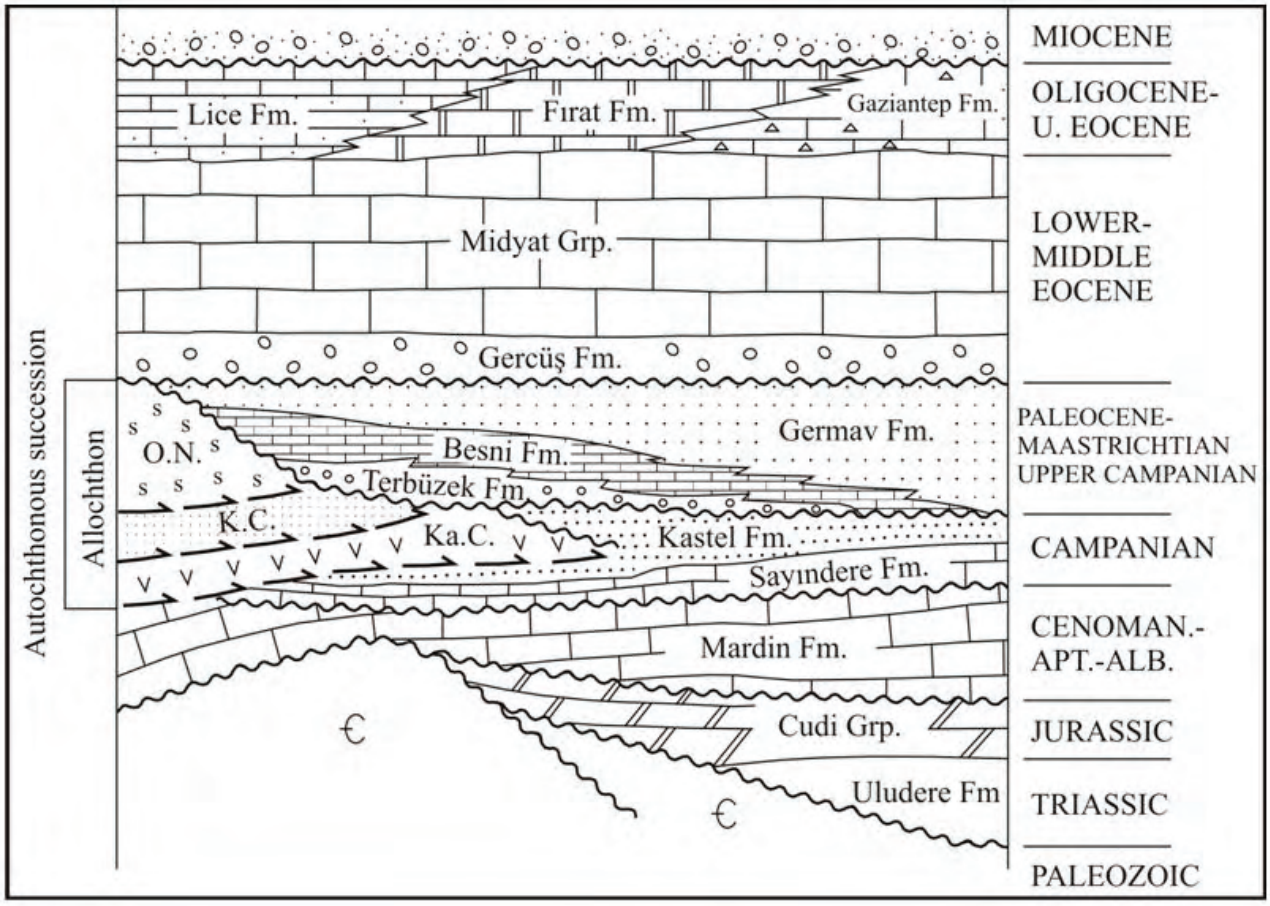

Figure 2. Generalized stratigraphic section of southeastern Anatolia showing the autochthonous-allochthonous units and also dictyoptychid-bearing late Campanian–Maastrichtian transgressive units (Terbüzek, Besni and Germav formations) (modified from Sungurlu 1974 and Perinçek 1979). Ka.C.– Karadut Complex, K.C.– Koçali Complex, O.N.– Ophiolitic nappes.

contain numerous, well-preserved and generally robust specimens of rudist such as *Vautrinia*, *Pseudosabinia*, *Pseudopolyconites*, *Paracaprinula*, *Vaccinites* and *Pironaea* besides *Dictyoptychus* (Karacabey-Öztemür 1979; Özer 1986, 2008; Özer *et al.* 2008; Steuber & Özer 2008; Steuber *et al.* 2009). New material recently collected from the rudist limestone lenses of the Alidamı section also include *Dictyoptychus quadrizonalis* and *Dictyoptychus vanensis* which were previously determined from the Gevaş-Van area by Özer (2005). The Maastrichtian age for the dictyoptychid-bearing limestones lenses of the Alidamı locality was accepted by Karacabey-Öztemür (1979) and Özer (1986, 1992a, b) based on the presence of typical benthic foraminifers in the rudist limestones (Meriç *et al.* 1985, 1987, 2001; Meriç & Görmüş 2001). However, Özcan (1993, 2007) identified some benthic foraminifers in the lowest limestone lens with rudists and suggested a late Campanian age. Recently, a late Campanian age was concluded by Schlüter *et al.* (2008), Steuber & Özer (2008) and Steuber *et al.* (2009) based on the Sr-isotope values from the rudist shells of the Alidamı locality. A very similar Campanian rudist association in transgressive sequences developed on top of ophiolites, also containing larger benthic foraminifers such as *Omphalocyclus* was reported from the United Arab Emirates by Morris & Skelton (1995).

Around Güzelsu (formerly Huni) and Eskikahta localities in the Kahta-Adıyaman area (Figures 3 & 4), the calcareous sandstones and clayey limestones

of the Besni Formation contain well-preserved specimens of *Dictyoptychus* and some hippuritids, radiolitids and large benthic foraminifers (especially *Loftusia*) (Özer 1986). A Maastrichtian age for the rudists of these localities was proposed by Özer (1986). This is confirmed by Sr-isotope values that indicate an early Maastrichtian age for these levels (Schlüter *et al.* 2008).

In the Gevaş-Van area (Figures 1 & 5), four rock units have been differentiated by Yılmaz *et al.* (1981); these are metamorphic rocks of the Bitlis Massif, ophiolite association, rocks of the transition zone between the ophiolite and metamorphic rocks, and the overlying sedimentary cover. The ophiolite association shows a wide distribution around the southern part of the Lake Van and contains fossiliferous and unfossiliferous limestone blocks around Yemişlik, Dilmetaş, İkizler and Aladüz villages and in the surroundings of Gevaş (Figure 5). In the Sivertan Hill (west of Dilmetaş village), only one limestone block contains abundant macrofossils (rudists, hermatypic corals, small *Cyclolites,* exogyrids, actaeonellids and gastropods), large benthic foraminifers (*Loftusia)* and form an anticlinal structure which allows logging of a measured stratigraphic section (Özer 1992c) (Figure 5). Two new species of *Dictyoptychus*, *D. guadrizonalis* and *D. vanensis* were described from the rudist collection and a Maastrichtian age was suggested for the Sivertan Hill limestone block by Özer (2005). The rudist and benthic foraminiferal associations of the Sivertan Hill section shows very close resemblances to those of the Simsima Formation, on the western margins of the Oman Mountains – United Arab Emirates (Skelton *et al.* 2000).

Taxonomy, Description and Revision

Class BIVALVIA Linné 1758

Subclass HETERODONTA Neumayr 1884

Order HIPPURITOIDA Newell 1965

Superfamily HIPPURITOIDEA Gray 1848

Family DICTYOPTYCHIDAE Skelton in Skelton & Benton (1993)

Genus *Dictyoptychus* Douvillé 1905

Type species *Polyptychus Morgani* Douvillé 1904a

Dictyoptychus morgani (Douvillé 1904a)

plate 1, figures 1–6; plate 2, figures 1–4; plate 3, figures 1–4; plate 4, figures 1–6; text-figure 7A

1904a *Polyptychus Morgani* n. gen. n. sp. Douvillé, p. 520, text-figures 1 and 2.

1904b *Polyptychus Morgani* n. gen. n. sp. Douvillé, Douvillé, p. 248, plate 33 bis, figures 1–5.

1905 *Dictyoptychus Morgani* (Douvillé), Douvillé, p. 178.

1910 *Polyptychus striatus* n. sp. Douvillé, p. 78, plate 7, figures 1–2.

1929 *Hippurites (Vaccinites) Paronai* nov. spec. Kühn, p. 25, plate 1, figure 1, text-figures 1–2.

1929 *Praeradiolites* (?) *Leesi* nov. spec. Kühn, p. 30, plate 2, figure 1, plate 3, figure 1.

1933 *Trechmanella morgani* (Douvillé), Cox, p. 388.

1933 *Trechmanella* sp., Cox, p. 382, text-figure 44/9.

1934 *Trechmanella persica* sp. nov. Cox, p. 43, plates 4–7, text-figures 1–27.

1934 ? *Trechmanella morgani* (Douvillé), Cox, p. 64, plate 8.

1937 *Anomoptychus morgani* (Douvillé), Kühn, p. 270.

1937 *Anomoptychus striatus* (Douvillé), Kühn, p. 271.

1937 *Anomoptychus persicus* (Cox), Kühn, p. 271.

1937 *Anomoptychus paronai* (Kühn), Kühn, p. 272–275, text-figure 1.

1937 *Anomoptychus leesi* (Kühn), Kühn, p. 275–280, text-figures 2–8.

1949 *Anomoptychus Paronai* Kühn, Tavani, p. 11.

1979 *Dictyoptychus orontica* n. sp. Karacabey-Öztemür, p. 35, plate 1, figures 1–3, plate 4, figure 1.

1979 *Dictyoptychus euphratica* n. sp. Karacabey-Öztemür, p. 37, plate 2, figures 1, 2, plate 3, figures 1, 2, plate 4, figures 2, 3.

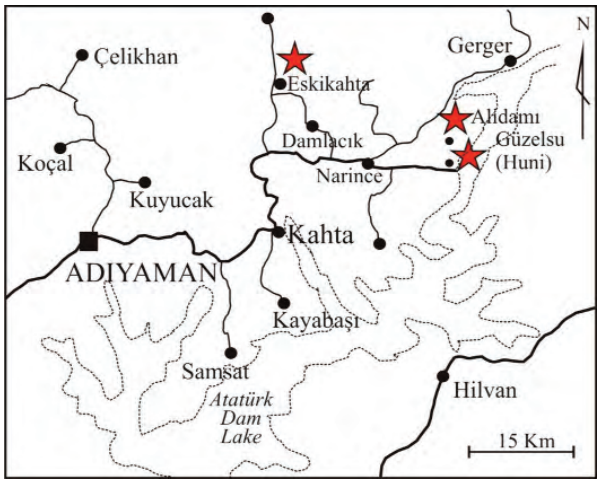

Figure 3. Location map of the Adıyaman area showing the *Dictyoptychus* localities: Alidamı, Güzelsu (Huni) and Eskikahta (red asterisks).

1986 *Dictyoptychus euphratica* Karacabey-Öztemür, Özer, p. 101, plate 2, figures 1, 2.

1986 *Dictyoptychus leesi* (Kühn), Özer, p. 101, plate 2, figure 3.

1986 *Dictyoptychus striatus* (Douvillé), Özer, p. 102, plate 3, figure 1.

1992 c *Dictyoptychus* cf. *euphratica* Karacabey-Öztemür, Özer, p. 77, plate 1, figure 4.

1992 *Dictyoptychus paronai* (Kühn), Pons *et al.*, p. 223, text-figure 5a, b.

1995 *Dictyoptychus morgani* (Douvillé), Morris & Skelton, p. 282, plate 1, figure 3.

2000 *Dictyoptychus morgani* (Douvillé), Skelton & Smith, p. 123.

2000 *Dictyoptychus persica* (Cox), Skelton & Smith, p. 123.

2005 *Dictyoptychus paronai* (Kühn), Özer, p. 243, figures 9 (1–4), 10.

Material. Numerous well-preserved specimens with both valves collected from Alidamı village (N 37° 55.722′; E 38° 54. 366′), Güzelsu (Huni) village (N 37° 54.480′ ; E 38° 52.478′) and Eskikahta (N 37° 57.257′; E 38° 39.210′) in the Kahta-Adıyaman and Sivertan Hill-Dilmetaş village (N 38° 17.754′; E 42° 57.083′) in the Gevaş-Van areas. Also, a few badly preserved specimens with two valves from the Yaylaçiftliği (N 35°. 54.551′; E 36°. 05.813′) in the Yayladağı-Antakya area.

Description. The specimens are characterized by the presence of the enlarged polygonal canals in the inner shell layer of the attached right valve. These canals present one, two or three rows approximately parallel to the whole periphery of the valve. The ventral margin of some specimens is very thin where the canals are absent. There is no trace of a ligamental ridge. The cardinal apparatus is situated generally in perpendicular position to the anterior margin. The posterior tooth is dorso-ventrally flattened in transverse section while the anterior one is rounded and robust. An accessory cavity separates the posterior tooth from the dorsal margin. The ridge-like tooth of the right valve is situated between the left valve teeth. The surface of the right valve is generally smooth, though fine growth lines can be observed. The radial bands are gently developed as two slight swellings.

The left valve is depressed conical with dorsally pointed eccentric apex and also cap-like in shape with an apex strongly inclined towards the dorsal margin. Because of the very thin outer layer (about 1 mm) of the left valve, the longitudinal sections of the radial canals, which are the one of the main characteristic features of the genus can be seen clearly at the eroded parts of the valve.

Variability. The study of the Turkish specimens and the literature reveals considerable variability in the external and internal features.

External Variability. The right valve is obtusely conical (about 50 to 100 mm in length) in the young forms but robust, curved conical to cylindro-conical and straightening out in the adults (i.e. horn-shaped), reaching to 395 mm in length (Table 1; Figure 6). The ornamentation of the valve is very simple and the surface is smooth; however, dense and fine growth lamellae are visible in places (Plate 4, Figures 3 & 4). Only the specimens determined as *D. striatus* show thin longitudinal costae separated by fine grooves (Douvillé 1910 and this study) (Plate 2, Figure 1). Two slight swellings represent the anterior and posterior radial bands in all of the specimens, although these seem to be more developed in the

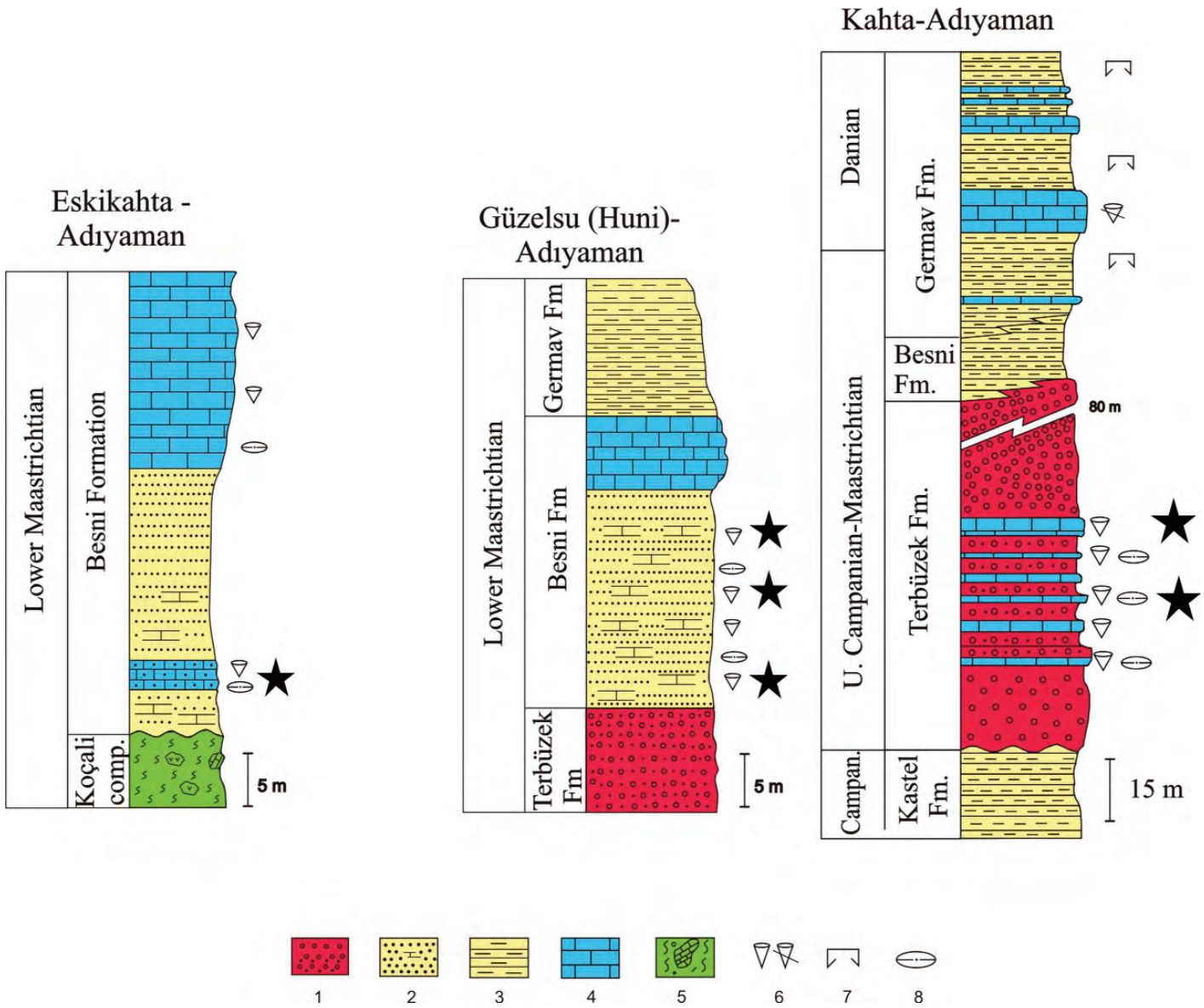

Figure 4. Measured stratigraphic sections of the Alidamı (after Meriç *et al.* 1985 and Özer 1986), Huni and Eskikahta localities (see for the locations to Figure 3) showing the *Dictyoptychus* levels (black asterisks). 1– conglomerates, sandy conglomerates, 2– sandstones, calcareous sandstones, 3– mudstones, 4– limestones, 5– ophiolitic complex, 6– rudists and fragments, 7– planktonic foraminifera, 8– benthonic foraminifera.

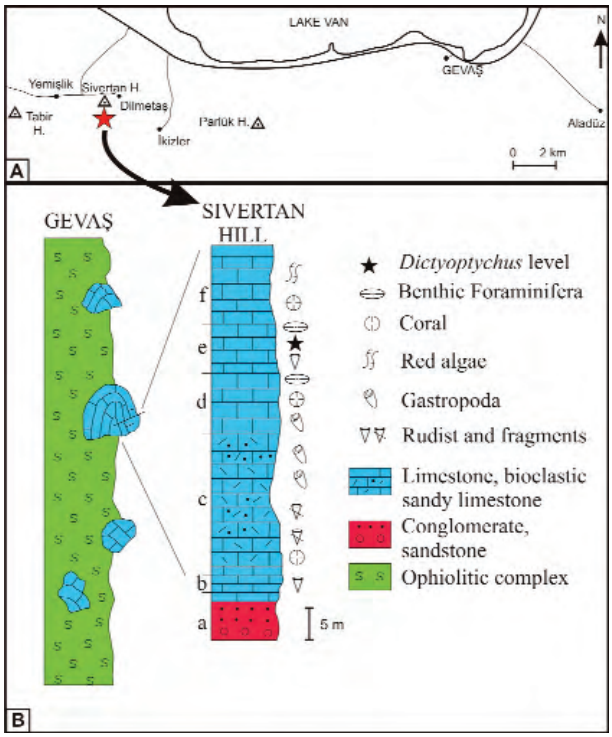

Figure 5. Location map of the Gevaş-Van area **(A)** showing the *Dictyoptychus* locality (red asterisk) and Sivertan Hill measured stratigraphic sections **(B)** (simplified from Özer 1992, 2005). a– greyish-green conglomerates and sandstones, b– rudist-bearing limestones, c– bioclastic sandy limestones, d– gastropod-bearing limestones, e– rudist-bearing limestones (especially *Dictyoptychus*) and f– dark-grey massive limestones with red algae.

specimen originally referred to *D. persicus*. The dorsally excentric pointed apex of the left valve can be strongly developed like in the form of a hook and inclined towards the dorsal margin (Plate 1, Figures 1 to 6; Plate 4, Figures 3 & 4; Plate 5, Figure 1).

Internal Variability. The structure of the enlarged polygonal canals in the inner shell layer of the right valve changes from young to adult stages. In the same of Turkish specimen, two rows of canals can be reduced to one row and the shape of the large polygonal canals can change from irregular to regular and sometimes elongated in cross-sectional shape (Plate 2, Figures 2 & 3; Plate 3, Figures 1 to 4; Plate 4, Figures 1, 2, 5 & 6). The polygonal canals of the species seem to be more variable, for example, it is possible to see from Douvillé's (1904a) and Cox's (1934) illustrations of their Iranian material that the variability of the large canals in the right valve of the revised *D. morgani* is even greater than that of Turkish specimens. The large specimens illustrated by Cox (1934, e.g., figure 3) show >4 rows in the ventral margin, while the holotype of the species shown in Douvillé (1904a, figure 2) does not contain thin part. This variation is consistent with an ontogenetic spread of canals around the ventral area and increase in their number. The wall of the enlarged canals is thick in the adults, while it is very thin in the young forms. The shape and the position of the cardinal apparatus also varies in sections from different levels in a single right valve (Plate 2, Figures 2 & 3; Plate 3, Figures 1 to 4). The commissural diameter of the right valve ranges from 80 x 60 to 205 x 173 mm, and the length of the right valve from 55 to 395 mm (Table 1). The thickness of the outer shell layer of the right valve reaches 15 mm in the adult forms.

Discussions and Revision. The transversal sections from different levels of the right valves collected from Turkey and also the study of literature reveals the controversial taxonomic position of the many determined known species of the genus as given in the above synoymy list, as follows:

Transverse sections from 25 mm below the commissure of the Turkish specimens originally assigned to *D. striatus* show the characters of the species indicated by Douvillé (1910, p. 78) such as very sparse enlarged polygonal canals and cardinal apparatus elongated approximately in a dorso-ventral direction (Plate 2, Figure 2) (Özer 1986). However, transverse section passing 50 mm below of the commissure in the same specimen present a canal structure and cardinal apparatus arrangement like those of *D. morgani* (Plate 2, Figure 3). Because of these similarities Turkish specimens are here accepted as *D. morgani*. But, due to the development of the radial striate external ornamentation described by Douvillé (1910) in *D. striatus* in contrast to other species of the genus, reveals a question needs further investigation.

Table 1. External features of right (RV) and left valves (LV) of *Dictyoptychus* species. Note the variability of the measurements and the other features.

species / external features		*Dictyoptychus morgani*						*D.striatus*	*D.quadrizonalis*	*D.vanensis*
		morgani	*orontica*	*leesi*	*paronai*	*persicus*	*euphratica*			
LV	depressed connical with dorsally excentic apex	+		+				+	+	+
	depressed cap-like in shape with strongly excentric apex		+		+	+	+		+	
	height (mm)	? 5–10	15	5–10	20–25	50	20–30	5	20	15
	ornamentation	smooth	growth lamellae	concentric growth lines	smooth	smooth	concentric growth lines	smooth	smooth	smooth
RV	regular conical	+		+				+		+
	conical. slightly uncurved towards ventral side		+		+	+	+		+	
	lenght (mm)	? 100	55	145–295	120–245	230–395	90	110–230–350	135–270	90
	diametre (mm)	120x100	80x60	190x145	190x112 150x120 150x90	205x173	95x80	190x80 150x100	95x70 190x130	105x80
	ornamentation	growth lamellae	dense, fine growth lamellae	smooth growth lamellae	smooth dense, fine growth lamellae	dense, fine growth lamellae	smooth / rare growth lines	dense, fine growth lamellae and longitudinal costae	smooth or fine growth lamellae	smooth
	radial bands	slightly developed	no structure	very slightly developed	slightly developed	two longitudinal swellings	very slightly developed	two longitudinal swellings	very slightly developed	very slightly developed

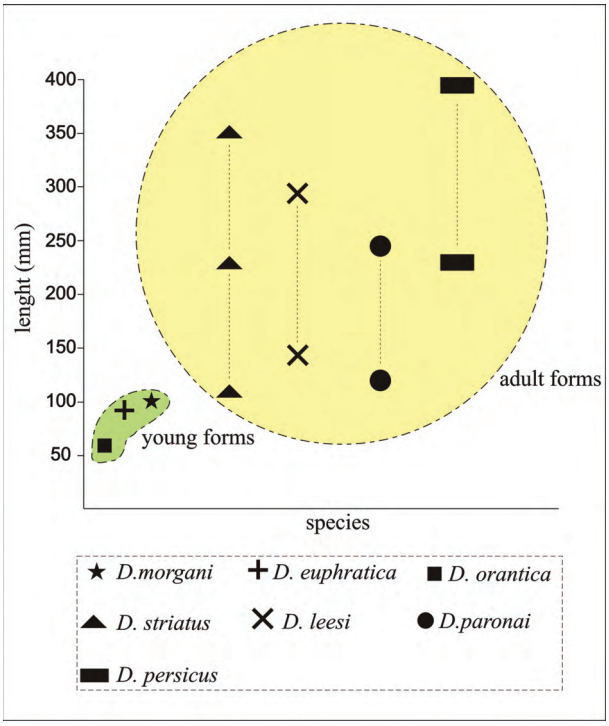

Figure 6. Graph showing the right valve lengths of the determined species of *Dictyoptychus*. Note two differents localisation of the measurements allowing to separation of young and adult forms.

The robust Turkish specimens referred to *D. leesi* show the same external features of both valves; especially with the surface of the left valve (Özer 1986), which is ornamented with sparse concentric lines as figured by Kühn (1929, plate 3, figure 1) and depressed left valve (Kühn 1937). But, the transversal sections of the right valves show a canal structure similar to that of *D. morgani*, although the walls of canals are relativly thicker than those the type specimen of *D. morgani*. Kühn (1937) also demonstrated and explained these features of the canals in erecting *D. leesi*.

The numerous right valve specimens referred to *D. paronai* show a canals with irregular outlines and of very different sizes, a small body cavity and a perpendicular position of the cardinal apparatus to the anterior margin in the transverse sections approximately 10 mm below the commissure (adult stage), as explained in the determination of the species by Kühn (1929, 1937), Pons *et al.* (1992) and Özer (2005). However, these features differ in the young stages of the valve presenting especially large canals with regular outlines as *D. morgani* (Plate 3, Figures 1 to 4).

The Iranian right valves referred to *D. persicus* also show enlarged polygonal canals (Cox 1934; Kühn 1937) similar to those of *D. morgani*; synonymy of the two species was already proposed by Skelton & Smith (2000).

The numerous well-preserved Turkish specimens with both valves referred to *D. euphratica* present a canal structure consisting of two or three rows of canals parallel to the periphery of the valve (Plate 4, Figures 5 & 6). Again, this is a typical feature of *D. morgani*. Some of the former specimens show two rows of canals just below the commissure, reducing to one row situated at the periphery, just like *D. orontica,* in the transverse sections cut 20 mm below of the commissure. A carefully study of some specimens, showing one row of canals, indicates also the presence of large canals like those of *D. morgani* towards the inner part of the inner shell layer (Plate 4, Figure 6). Turkish and Iranian specimens show that the variability of the large polygonal canals in the right valve of *D. morgani.*

The data implies that specimens previously referred to *D. leesi*, *D. paronai*, *D. persicus*, *D. euphratica* and *D. orontica* all belong a single species namely *Dictyoptychus morgani* (Douvillé 1904a). The ressemblances of Turkish specimens with the forms described by Douvillé (1910) as *D. striatus*, may suggest that this species synonymous with *D. morgani*. However, it seems problematic to include *D. striatus* in *D. morgani*, because of distinct development of radial ornamentation of the right valve of *D. striatus.* That needs further investigations to reveal the structure of the external ornamentation and also the inner margin of the right valve. The specimens originally determined as *D. morgani, D. euphratica* and *D. orontica* are here interpreted as relatively juvenile forms, and the others, adult forms of the same species. Variation in right valve lengths are also consistent with this interpretation (Figure 6).

Pons *et al.* (1992) regarded all species of the genus as probably synonymyous, though the need for more detailed descriptions as noted, a view echoed by Morris & Skelton (1995).

Dictyoptychus quadrizonalis Özer 2005

Plate 5, Figures 1–5; text-figure 7C

2005 *Dictyoptychus quadrizonalis* n. sp., Özer, 237–241, figures 4 (1–4), 5 (1, 2), 6.

Material. Two specimens with both valves (No. SV 88-19 and 20) and two specimens with only of right valves (No. SV 88-17 and 21) were collected from Sivertan Hill-Dilmetaş village (N 38° 17.754′ ; E 42° 57.083′) in the Gevaş-Van area. Two additional specimens with both valves (No. AD 12 and 13) were found from the Alidamı village (N 37° 55.722′ ; E 38° 54. 366′) in the Kahta-Adıyaman area.

Description. The right valve has an inner shell layer consisting especially of numerous canals smaller than those of *D. morgani* of fusiform, polygonal, rectangular, and small polygonal shape in section. The ligamental ridge is absent. The cardinal apparatus is robust and filled in all parts by small canals. The inner shell layer of the left valve consists of radial canals which can be seen in transverse section and in the eroded parts of the external layer of the left valve.

Discussions and Remarks. The diagnostic character of this species is the presence of numerous smaller canals in the right valve, which clear differentaties it from *D. morgani* and *D. vanensis* (Figure 7), but in this respect it resembles another genus of Dictyoptychidae, *Eodictyoptychus. E. arumaensis*, which is the only species of this genus currently known, has smaller canals in the right valve like *D. quadrizonalis*; however the specimens of the later consist only of radial canals in the left valve not numerous smaller canals as in *E.arumaensis*. This observation suggests a phylogenetic transition between *Dictyoptychus* and *Eodictyoptychus* as discussed below. Transverse sections at different levels of the right valves preserve the typical canal structure of the species in the inner shell layer (Plate 5, Figures 4 & 5).

Dictyoptychus vanensis Özer 2005

Plate 6, Figures 1–6; text-figure 7B

2005 *Dictyoptychus vanensis* n. sp., Özer, 241–243, figures 7 (1–4), 8.

Material. One specimen with both valves (No. SV 88-11), one specimen with right and partly preserved

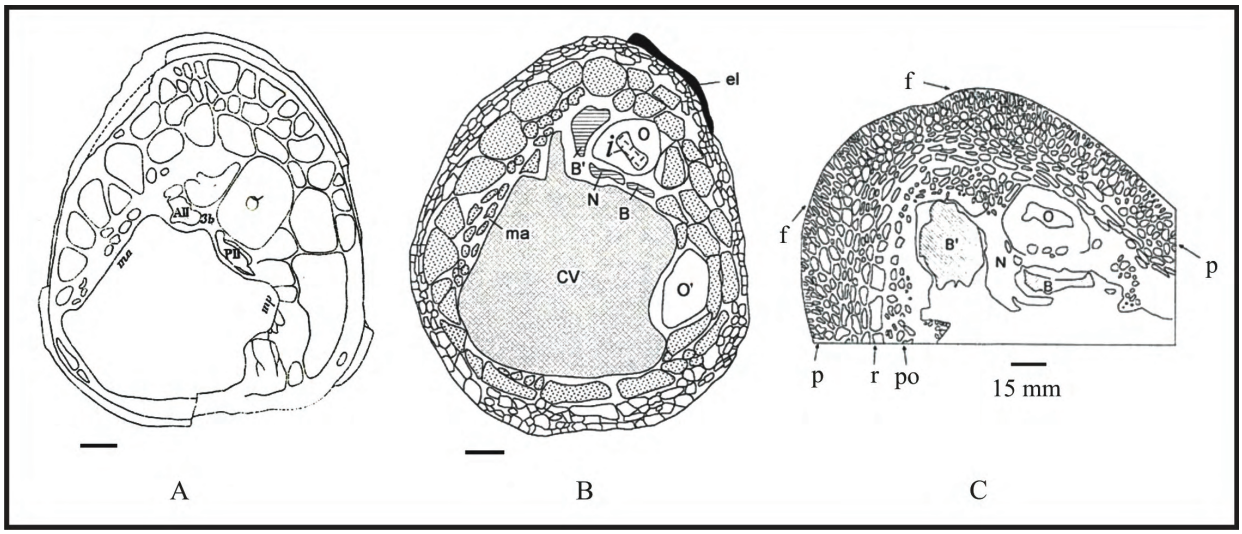

Figure 7. Transverse sections showing the canal structures of the inner shell layer of the right valve of *Dictyoptychus* species: **(A)** *D. morgani* (copy from Douvillé 1904a, figure 2), **(B)** *D. vanensis*, **(C)** *D. quadrizonalis* (copies from Özer, 2005, figures 8 and 6 respectively). Horizontal scale indicates 10 mm for A and B.

left valve (No. SV 88-12) and two specimens of right valves (No. SV 88-14 and 18) were collected from Sivertan Hill-Dilmetaş village (N 38° 17.754′ ; E 42° 57.083′) in the Gevaş-Van area. Two specimens of the right valves with partly preserved left valves (No. AD 18 and 20) were recently collected from the Alidamı section (N 37° 55.722′ ; E 38° 54. 366′) in the Kahta-Adıyaman area.

Description. The inner shell layer of the right valve consists of two differents types of canals from exterior to interior. In the exterior part are three to four rows of small, dense, and elongated, hexagonal and rectangular canals around the whole periphery of the valve. The interior part of the layer is characterized by large (maximum about 14 mm), polygonal and rectangular canals. In places, the little polygonal canals are present below these large canals, especially around the antero-dorsal side. There is no trace of a ligamental ridge. Central cavity occupies more than half of the valve section. The accessory cavities are well-developed. At the eroded parts of the thin outer shell layer of the left valve, the radial canal sections are observed.

Discussions and Remarks. This species has enlarged polygonal canals in the right valve, as in *D. morgani*, but also includes many smaller canals, in contrast to *D. morgani*, around the periphery of the valve outside the polygonal canals, which are clearly observed in the specimens from the type locality (Geveş-Van) and also those of Alidamı locality (Kahta-Adıyaman). Because of these characters, the species was interpreted as the most primitive species of *Dictyoptychus* (Özer 2005). The transverse sections from different levels of the right valve present no appreciable variability (Plate 6, Figures 5 & 6).

Phylogeny

The family Dictyoptychidae was created by Skelton in Skelton & Benton (1993) and its distinctive characters were presented and discussed in detail by Skelton & El-Asa'ad (1992) and Morris & Skelton (1995). According these authors, this was a replacement name for 'Trechmannellidae' Cox (1934, p. 65) necessitated because '*Trechmannella*' is a junior objective synonym of *Dictyoptychus*. This family consists of three genera *Dictyoptychus*, *Eodictyoptychus* and *Semailia*. The diagnostic characters of the family include a distinctive myocardinal organization with a dorso-ventrally flattened posterior tooth in the LV situated ventrally to a prominent accessory cavity, a canaliculate inner shell layer in both valves and absence of a ligament. *Dictyoptychus* has some similarities with the other two genera of the family suggesting phylogenetic relations as follows:

Based on the published descriptions *Eodictyoptychus* seems to be the oldest representative of the family (Figure 8). Although the original Campanian age assignment of the type material given by Skelton & El-Asa'ad (1992) was revised to Maastrichtian by Philip *et al.* (2002), other specimens later described from around the Qahlah/Simsima boundary by Morris & Skelton (1995) may still be of Campanian age. *Dictyoptychus* and *Semailia*, by contrast, have been recorded only from the late Campanian–Maastrictian of the Arabian platform (Morris & Skelton 1995; Steuber 2002). These stratigraphic data suggest that *Eodictyoptychus* is the ancestral genus of Dictyoptychidae.

The present study reveals that *Dictyoptychus* has three species namely *D. morgani*, *D. quadrizonalis* and *D. vanensis*. According to the features of the canaliculate inner shell layer of the right valve of these species (Figure 7), *Dictyoptychus* can be separated in two groups or branches (Figure 9): (1) forms with small canals include *D. quadrizonalis* and (2) forms with large canals contain *D. morgani, D. vanensis*. *D. striatus* may belong to second branche; however, it depends further detailed studies about the external radial ornamentation of the species.

D. quadrizonalis resembles *E. arumaensis* especially with respect to the numerous smaller canals in the inner shell layer of the right valve. However, this species differs clearly from it by the presence only of radial canals in the inner shell layer of the left valve, which is one of the important generic characters of *Dictyoptychus*, instead of numerous smaller canals as in *E. arumaensis.* This

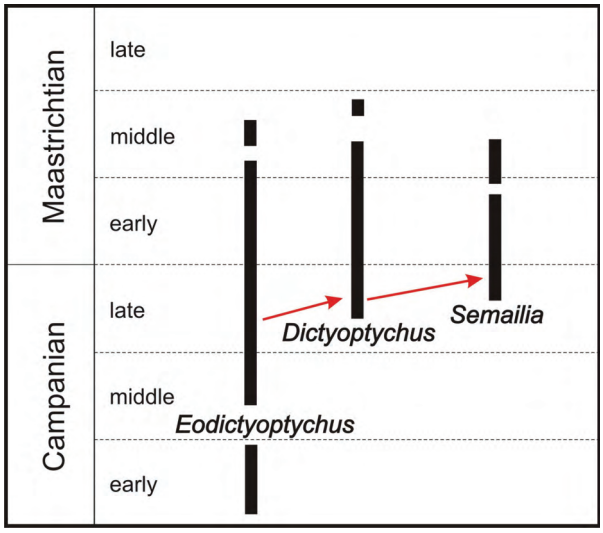

Figure 8. Phyletic model and stratigraphic distribution of dictyoptychid genera showing the relationships of *Dictyoptychus* with *Eodictyoptychus* and *Semailia.*

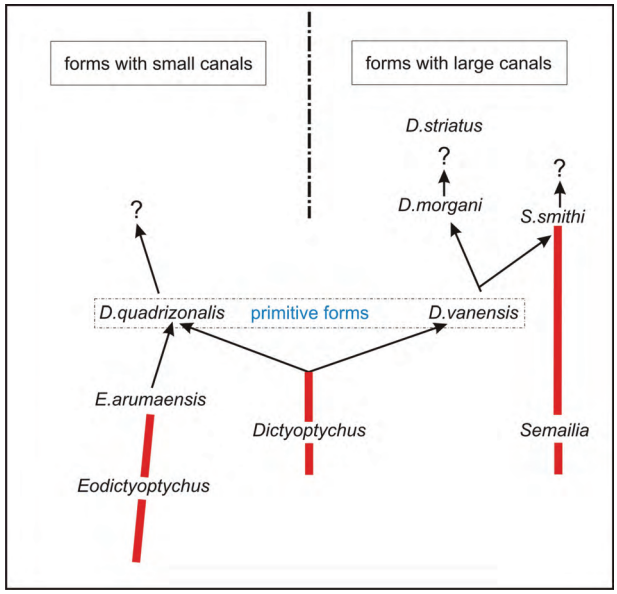

Figure 9. Hypothetical phylogram showing the relationships of *Dictyoptychus* species with *Eodictyoptychus* and *Semailia* respectively.

similarity implies derivation of *Dictyoptychus* from *Eodictyoptychus*. The present study shows that the late Campanian rudist fauna of the Kahta-Adıyaman area (Özer *et al.* 2008; Steuber *et al.* 2009), contains also the specimens of *D. quadrizonalis* and *D. vanensis.* Because of this, it is probable that this derivation was realised during the late Campanian (Figure 9).

D. vanensis shows a close similarity to *D. morgani* by the numerous enlarged polygonal canals in the inner shell layer of the right valve. But, it is distinguished from *D. morgani* by the continuation of three or four rows of smaller canals around the whole periphery, beside the enlarged polygonal canals of the right valve (Figure 7). However, the presence of enlarged polygonal canals in the right valve of *D. vanensis* suggests evidently the phylogenetic relation with *D. morgani.*

Semailia is clearly distinguished from *Eodictyoptychus* and *Dictyoptychus* by the strong shell carinae and irregular large polygonal canals in both valves. The phylogenetic status of *Semailia* remains uncertain. But, according to present knowledge its enlarged irregularly rounded polygonal canals in the thick inner shell layer of the right valve suggest a link with *Dictyoptychus*. In detail, the single species of the genus, *S. smithi* Morris & Skelton 1995, seems related by its large canals to *D. morgani* and *D. vanensis*.

These characters show that the *D. quadrizonalis* and *D. vanensis* are possibly the most primitive species of *Dictyoptychus*, as indicated by Özer (2005), consisting of two separate branches through the phylogenetic lineage of the genus.

Biogeography

Dictyoptychus shows a very limited geographic distribution within the Tethyan province as follows (Figure 10):

D. morgani was found in the Bakthyari (southwestern Iran) by Douvillé (1904a). *D. striatus* and *D. persicus* were based on material from around the Zardalal locality-Kirmanshah (western Iran) and Bakthyari (southwestern Iran) respectively (Douvillé 1910; Cox 1933, 1934). Khazaei *et al.* (2010) also reports the presence of *Dictyoptychus* specimens from the Maastrichtian of Tarbur Formation-Zagros region (southwestern Iran). Kühn (1929) described two new species of the genus as *D. leesi* and *D.*

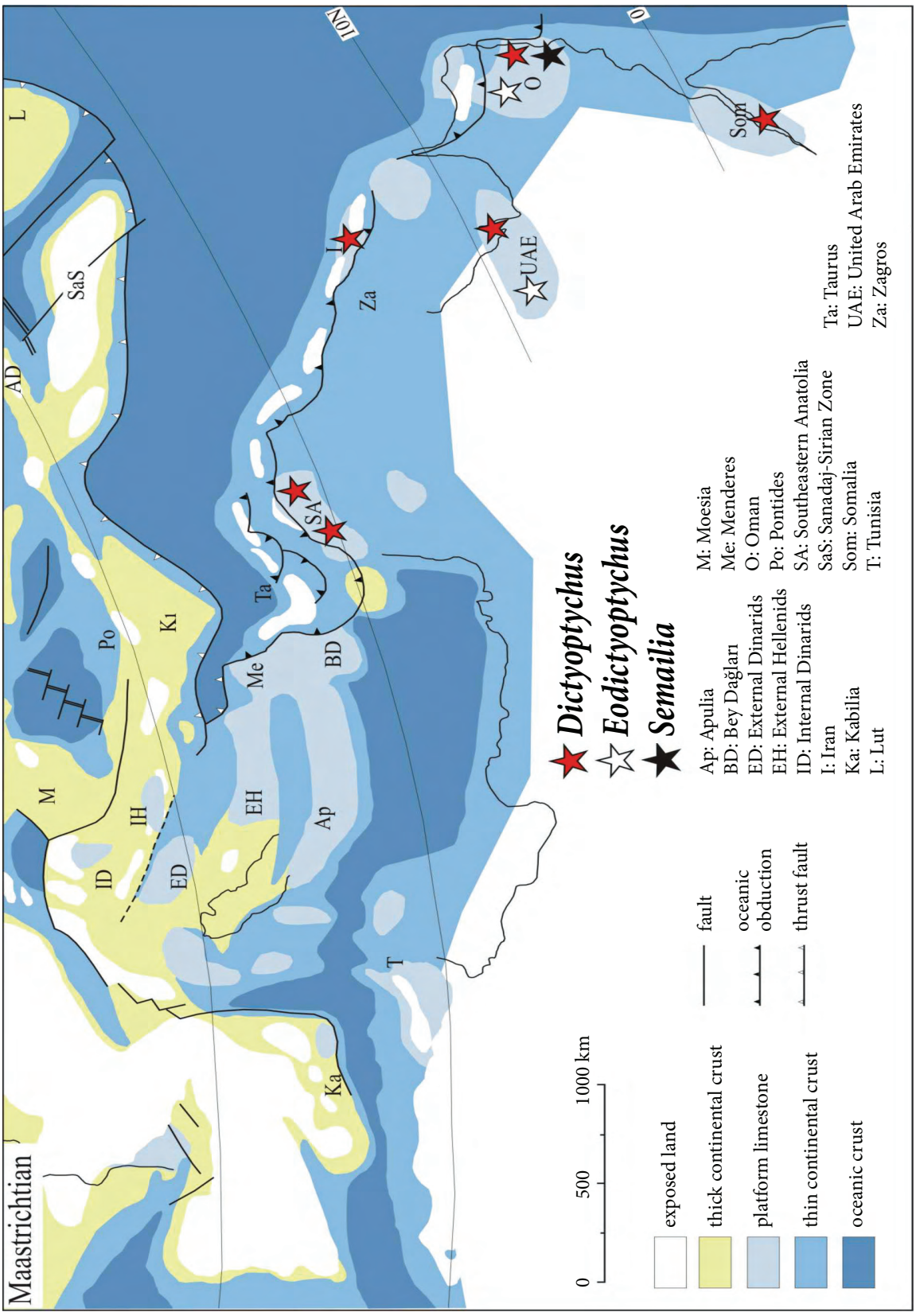

Figure 10. Campanian–Maastrichtian palaeogeographical reconstruction of the Mediterranean area (simplified after Dercourt *et al.* 1986) showing the local distribution of *Dictyoptychus* and also *Eodictyoptychus* and *Semailia* in the Afro-Arabian plate indicating endemism.

paronai from the Maastrichtian of the Oman Peninsula. *D. morgani* was also determined from the late Campanian–Maastrichtian of the Oman Peninsula and United Arab Emirates by Morris & Skelton (1995) and Skelton & Smith (2000).

D. paronai was found from the Maastrichtian of the locality Bur Hardag (northeast of Somalia) by Tavani (1949), and also Tisje section (northern Somalia) by Pons *et al.* (1992).

Numerous specimens of the genus were found around Kahta-Adıyaman and Yayladağı-Antakya areas in the southeastern Anatolia and two new species *D. euphratica* and *D. orontica*, were described by Karacabey-Öztemür (1979). *D. leesi* Kühn and *D. striatus* Douvillé were reported from the Maastrichtian of the Kahta-Adıyaman area by Özer (1986). The new locality of *Dictyoptychus* was discovered by Özer (1992c) in the Gevaş-Van araea (southeastern Anatolian orogenic belt) where two new species *D. quadrizonalis* and *D. vanensis* were described and *D. paronai* was also determined by Özer (2005).

The geographic distribution of *Dictyoptychus* indicates endemism localised on the Afro-Arabian plate. The presence of *Eodictyoptychus* in the Oman Peninsula and United Arab Emirates and *Semailia* in the Oman Peninsula (Skelton & El-Asa'ad 1992; Morris & Skelton 1995) substantiate this endemism.

Conclusions

Numerous specimens of *Dictyoptychus* were found in the late Campanian and early Maastrichtian levels of the transgressive sequences of the southeastern Anatolia and in the Maastrichtian limestone block of the ophiolitic association of the easternmost part of the Taurus orogenic belt in Turkey.

The variability of the external and internal features of the genus and careful study of the previous descriptions of the genus in the literature prompt the taxonomic revision of the many described species and also interpretation of the relationships of the genus with *Eodictyoptychus* and *Semailia* as follows:

- the transversal sections at the different levels of the right valves of the known species of the genus such as *D. striatus, D. leesi*, *D. paronai*, *D. persicus*, *D. euphratica* and *D. orontica* show considerable variability of the canal shapes and the cardinal apparatus from adults to young stages in the same specimen. All of the species, except *D. persicus,* were determined by Karacabey-Öztemür (1979) and Özer (1986, 2005) from the southeastern Anatolia. The restudy of these well-preserved specimens indicate this clear ontogenetic variability. The same observations were also indicated for some species such as *D. persicus* by Cox (1934), *D. leesi* by Kühn (1929) and *D. paronai* by Pons *et al.* (1992) and Özer (2005).
- *D. morgani* is characterized by the large polygonal canalicular structure of the attached right valve showing greater variability from the one row to the many rows of canals. *D. leesi*, *D. paronai*, *D. persicus*, *D. euphratica* and *D. orontica* show the same similar distinctive features of *D. morgani* indicating synonymy with the latter species. Only, *D. striatus* seems to be problematic to include in *D. morgani,* because of its radial ornamentation of the right valve, which is not observed in the latter species. So, the transfer of this species to the *D. morgani* remains open to question.
- the variabilities of the specimens show that the *D. morgani*, *D. euphratica* and *D. orontica* are the juvenil forms of the genus; while the others represent adult forms.
- the apex of the left valve of *D. morgani* changes from pointed to strongly inclined apex towards the dorsal margin.
- two new species determined by Özer (2005), *D. vanensis* and *D. quadrizonalis*, are conserved under the *Dictyoptychus* because of their very characteristic canal structure of the right valve.
- based on the canal structure of the right valve, *Dictyoptychus* are separated in two phylogenetic branches: (1) forms with small canals include *D. quadrizonalis* and (2) forms with large canals contain *D. morgani, D. vanensis* and probably *D. striatus.*

- *D. quadrizonalis* and *D. vanensis* are possibly the most primitive species of *Dictyoptychus*.
- the close similarities of the right valve canal structure indicate the phylogenetic relation and transition between *D. quadrizonalis* and its presumed ancestor, *E. arumaensis*.
- the presence of large canals in the right valves may be indicate the phylogenetic relation between *D. morgani*, *D. vanensis* and *S. smithi*.

The genus *Dictyoptychus* show a geographic distribution in Tethyan province, limited to the Afro-Arabian plate during the Campanian–Maastrichtian, between the environ 20° north and 10° south palaeolatitudes. *Eodictyoptychus* and *Semailia* show nearly the same distribution. This indicates the endemism of Dictyoptychidae.

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PLATE 1

Figures 1–6. *Dictyoptychus morgani* (Douvillé). Upper views of left valves (LV) illustrating the variability of the dorsally excentric apex and shape of the valve.

Figure 1. LV with pointed apex (black arrow). The longitudinal radial canals are clearly observed in the eroded parts of the thin external layer. No. AD 3-11. Alidamı-Kahta-Adıyaman. (*D. leesi* after Özer 1986). Scale bar is 40 mm.

Figure 2. Very depressed LV showing thin longitudinal radial canals in the transverse section around pointed apex (white arrow). No. EK 8. Eskikahta-Adıyaman. (*D. striatus* after Özer 1986). Scale bar is 40 mm.

Figure 3. LV is depressed cap-like in shape with an apex strongly inclined towards the dorsal margin. At the eroded parts of the thin external layer, radial canals of the internal layer can be observed (arrow). No. SV 88-26, Sivertan Hill-Gevaş-Van. (*D. paronai* after Özer 2005). Scale bar is 30 mm.

Figure 4–6. The apex of the LV is strongly developed and inclined towards the dorsal margin in the form of a hook. Note the variability of the shape and diameter of the valve (*D. euphratica* after Karacabey-Öztemür 1979 and Özer 1986). **(4)** No. AD 3-9, Alidamı-Kahta-Adıyaman. Scale bar is 10 mm. **(5)** No. HU 2-7, Güzelsu (Huni)-Kahta-Adıyaman. Scale bar is 5 mm. Note the longitudinal radial canals. **(6)** No. HU 2-9. Güzelsu (Huni)-Kahta-Adıyaman. Scale bar is 10 mm.

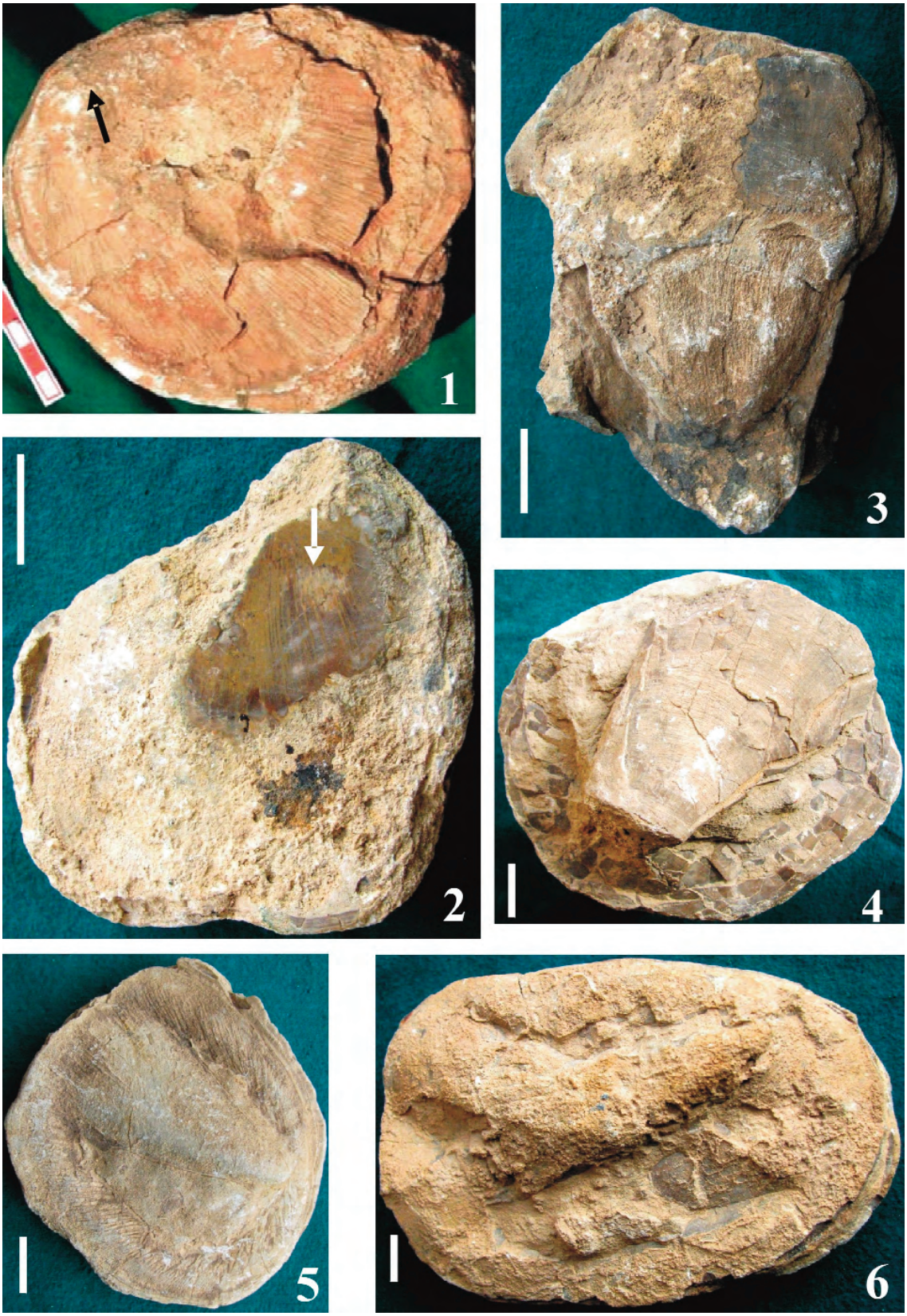
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PLATE 2

Figures 1–3. *Dictyoptychus morgani* (Douvillé).

Figure 1. Right valve (RV) showing the radial bands (Ab: anterior, Ib: inter, Sb: posterior bands) and thin longitudinal costae separated by fine grooove. Note very robust valve (scale bar is 20 mm). Black arrows indicate the transverse section lines of Figures 2 and 3. No. EK 8. Eskikahta-Adıyaman. (previously *D. striatus* after Özer 1986).

Figure 2. Transverse section of the RV passing approximately 25 mm below the commissure of the same specimen. See Figure 1 for section line. Scale bar is 20 mm. Note the perpendicular position of the cardinal apparatus to the anterior margin and sparse, enlarged and elongated large canals.

Figure 3. Transverse section passing approximately 25 mm below the previous section line (Figure 2) of the same specimen. See Figure 1 for section line. Scale bar is 20 mm. Compare the canal sections with Figure 2 and note the large canal sections showing close ressemblances those of *D. morgani*. The walls of the canals are very thick.

Figure 4. Field photograph showing conjoined specimens: **(A)** adult and **(B)** young forms of *Dictyoptychus morgani* Douvillé (previously *D. striatus* after Özer 1986) and **(C)** *Vaccinites vesiculosus* Woodward. Alidamı-Kahta-Adıyaman. Scale bar is 10 mm.

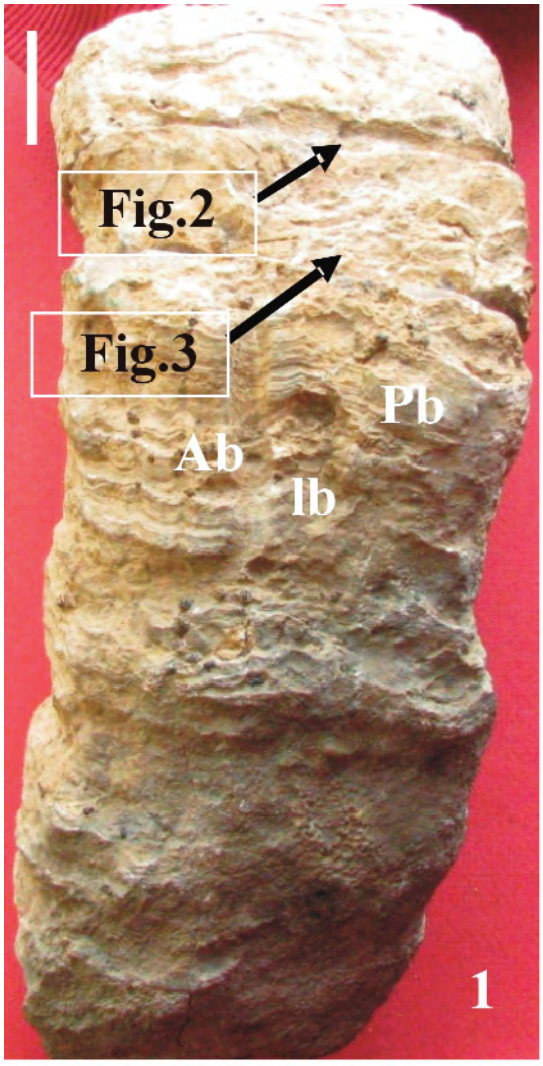
Fig.2
Fig.3
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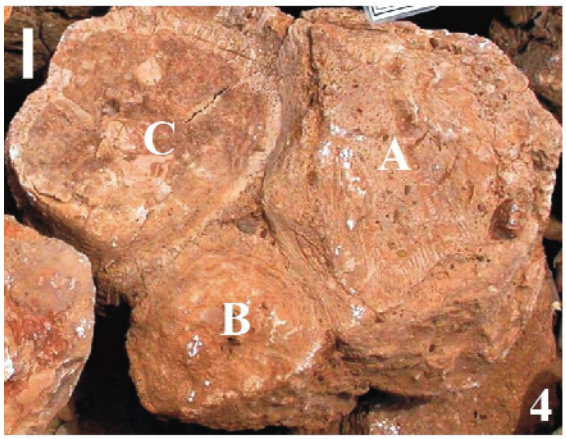
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PLATE 3

Figures 1–4. *Dictyoptychus morgani* (Douvillé). (formerly *D. paronai* by Özer 1992, 2005).

Figure 1. Transverse section of the RV passing 20 mm below the commissure. No. SV 88-28. Sivertan Hill-Gevaş-Van. Scale bar is 20 mm.

Figure 2. Transverse section passing approximately 10 mm below the previous section line (Figure 1) of the same specimen. Scale bar is 20 mm. Compare the canal sections and cardinal apparatus with those in Figure 1 and note the large canal sections showing close ressemblances those of *D. morgani*. The outlines of the canals can be clearly observed because of the very thick walls.

Figure 3. Transverse section of the RV passing 10 mm below the commissure. No. SV 88-13. Sivertan Hill-Gevaş-Van. Scale bar is 10 mm.

Figure 4. Transverse section passing approximately below 10 mm the previous section line (Figure 3) of the same specimen. Scale bar is 10 mm. Compare the cardinal apparatus and the large canal sections with those in Figure 3. Large canal sections show typical characteristics of *D. morgani*.


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PLATE 4

Figures 1–6. *Dictyoptychus morgani* Douvillé.

Figure 1. Transverse section of the RV passing 10 mm below the commissure. No. SV 88-14. Sivertan Hill-Gevaş-Van. Scale bar is 10 mm.

Figure 2. Transverse section passing approximately 10 mm below the previous section line (Figure 1) of the same specimen. Scale bar is 10 mm. Note the central cavity is much smaller than that of the previous section, and canal shapes are completely different.

Figures 3, 4. Both valves, anterior side. Note the dense and fine growth lamellae in the right valve and the variability of the left valve shape. (According to the left valve shape similar specimens were determined as *D. euphratica* by Karacabey-Öztemür 1979 and Özer 1986). No. HU 3-2 and No. HU 3-5. Güzelsu (Huni)-Kahta-Adıyaman. Scale bar is 10 mm.

Figure 5. Transverse section of the RV passing 10 mm below the commissure showing typical inner shell canal layer of *D. morgani* (formerly *D. euphratica* after Özer 1986). No. AD 3-4. Alidamı-Kahta-Adıyaman. Scale bar is 20 mm.

Figure 6. Transverse section of the RV passing 10 mm below the commissure showing mainly one row of canals like *D. orontica* Karacabey-Öztemür. However, careful observation indicates the presence also of other large canals in the inner shell layer showing similarity to *D. morgani*. No. AD 3-6. Alidamı-Kahta-Adıyaman. Scale bar is 20 mm.


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PLATE 5

Figures 1–5. *Dictyoptychus quadrizonalis* Özer.

Figure 1. Both valves, ventral side. The surface of the right valve is very smooth. Note very robuste conical right valve. Scale bar is 50 mm. Black arrow indicate the transverse section line of Figure 2. No. AD 12. Alidamı-Kahta-Adıyaman.

Figure 2. Transverse section of the RV passing 5 mm below the commissure showing the numerous smaller canals in the inner shell layer, same specimen. Cardinal apparatus is partly preserved. Scale bar is 30 mm. See Figure 1 for section line. Indicated area is shown in Figure 3.

Figure 3. Enlargement of the RV (indicated area in Figure 2) showing details of the canal organisation consisting of the smaller polygonal and rectangular canals. Scale bar is 30 mm.

Figure 4. Transverse section of the RV passing 5 mm below the commissure. No. SV 88-19. Sivertan Hill-Gevaş-Van. Scale bar is 10 mm.

Figure 5. Transverse section of the RV passing 15 mm below the previous section in Figure 4. Note the preservation of canal organisation. Scale bar is 10 mm.


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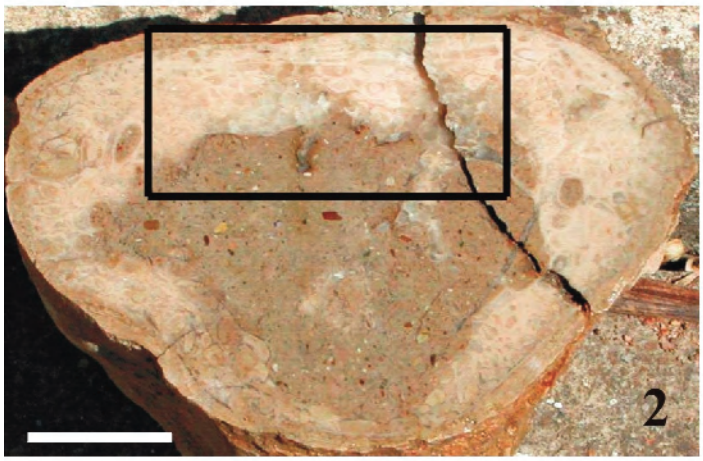
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PLATE 6

Figures 1–6. *Dictyoptychus vanensis* Özer.

Figure 1. Transverse section of the RV passing 5 mm below the commissure showing two canal types-small polygonal in the exterior, and large polygonal in the interior part of the inner shell layer. Indicated area is shown in Figure 3. No. AD 18. Alidamı-Kahta-Adıyaman. Scale bar is 10 mm.

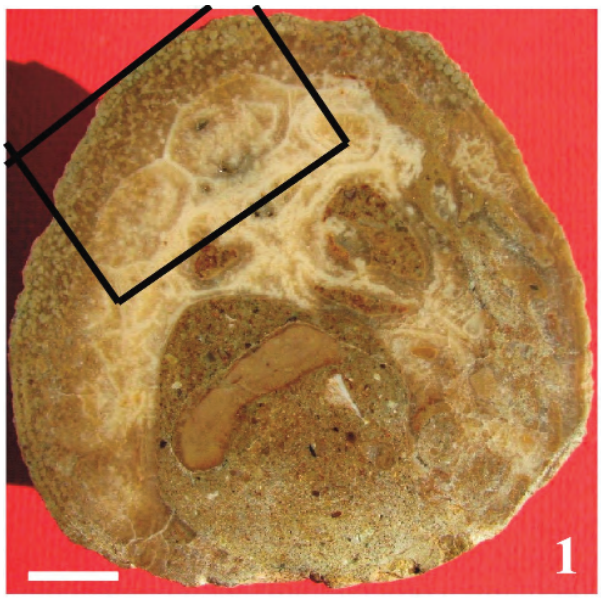
Figure 2. Enlargement of the RV (indicated area in Figure 1) showing details of the canal organisation consisting of the smaller and large polygonal canals. Same specimen. Scale bar is 5 mm.

Figure 3. Transverse section of the RV, the commissure unknown. Note the preservation of small and large polygonal canals. Indicated area is given in Figure 4. No. AD 20. Alidamı-Kahta-Adıyaman. Scale bar is 10 mm.

Figure 4. Enlargement of the RV (indicated area in Figure 3) showing details of the canal organisation. Same specimen. Scale bar is 10 mm. Compare with the ventral part of the transversal section of Figure 5.

Figure 5. Transverse section of the RV passing 10 mm below the commissure. No. SV 88-11. Sivertan Hill-Gevaş-Van. Scale bar is 10 mm.

Figure 6. Transverse section of the RV passing 10 mm below the previous section. Same specimen. Note the preservation of typical canal organisation. Scale bar is 10 mm.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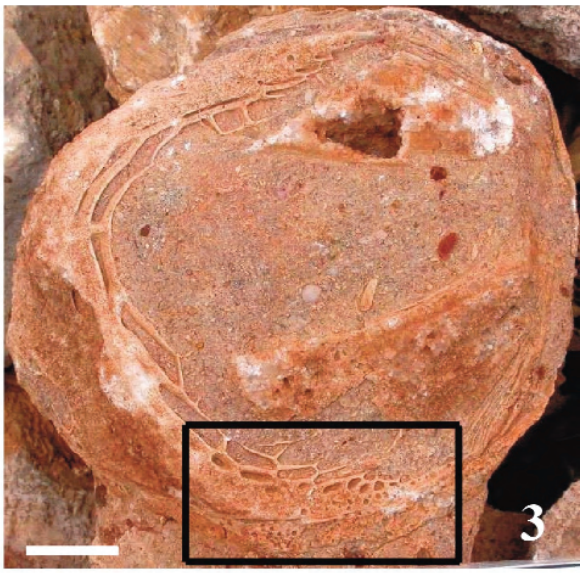
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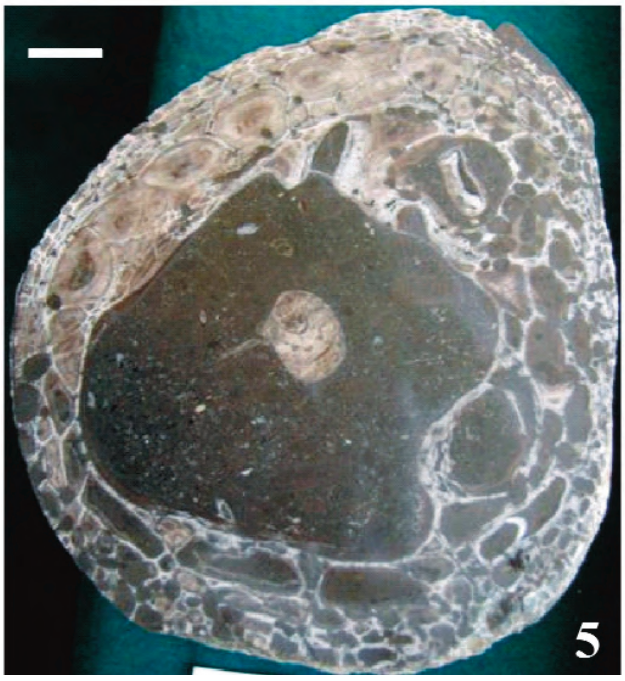
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