

Three new bivalve genera from Triassic hydrocarbon seep deposits in southern Turkey

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Three new bivalve genera and species are described from Upper Triassic hydrocarbon seep deposits from the Kasımlar shales in the Taurus Mountains in southern Turkey. *Terzileria gregaria* and *Kasımlara kosuni* belong to the carditiid family Kalenteridae, and *Aksumya krystyni* belongs to the anomalodesmatan superfamily Pholadomyoidae. A single specimen is described in open nomenclature as *Kasımlara* sp. due to its significantly more angular shell profile compared to *K. kosuni*. The kalenterids *Terzileria* and *Kasımlara* narrow the stratigraphic gap between two seep-inhabiting “modiomorphid” clades: the Silurian–Devonian *Atavioconcha* and the Late Jurassic–Cretaceous *Caspiconcha*. This raises the questions whether these four genera are members of a single phylogenetic lineage that continuously inhabited deep-sea hydrocarbon seeps from the Silurian to the Cretaceous (the “single lineage hypothesis”), or are repeated offshoots of various lineages that convergently developed similar morphological adaptations to this habitat (the “repeated colonization hypothesis”). *Aksumya* represents the first anomalodesmatan genus that appears to be restricted to the seep environment, considering that all previous claims of seep-inhabiting anomalodesmatans are questionable.

Key words: Bivalvia, Pholadomyoidae, Kalenteridae, hydrocarbon seeps, Triassic, Taurus Mountains, Turkey.

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Introduction

Deep-sea hydrothermal vents and methane seeps harbor unique faunal associations relying on chemosynthetic primary production (Sibuet and Olu 1998; Van Dover 2000). These animals appear to have an evolutionary history largely independent of that of photosynthesis-based food chains and may be buffered from extinction events affecting shallow-water ecosystems (Tunnicliffe 1992; Little and Vrijenhoek 2003; Kiel 2015). Mollusks are a major constituent of this fauna at present-day vents and seeps, and have become a model group for studies on their physiology, adaptations, and biogeography (Childress et al. 1986; Peek et al. 1998; Distel et al. 2000; Lorion et al. 2013; Kiel 2016; Johnson et al. 2017). Due to the strong link of these faunas to geological features, Earth's history and the fossil record play a major role in understanding their evolution (Campbell and Bottjer 1995; Tunnicliffe et al. 1996; Kiel and Little 2006; Johnson et al. 2010; Vrijenhoek 2013).

Paramount to linking Recent taxa to their fossil counterparts, and hence to understand their evolutionary history and phylogenetic relationships, is a proper documentation and identification of the fossil species. The Cenozoic fossil

record of mollusks especially in hydrocarbon seeps is relatively well known (Squires and Goedert 1991; Amano and Kiel 2007; Saether et al. 2010; Amano and Jenkins 2011; Kiel and Amano 2013; Kiel and Taviani 2017; and references therein) and also the number of Late Jurassic to Cretaceous seep faunas is increasing (Kaim et al. 2008, 2014, 2017; Kiel 2013; Hryniewicz et al. 2017a; and references therein). Beyond the Late Jurassic, however, the fossil record of seeps and especially of properly described seep-inhabiting mollusks, is sparse (Jakubowicz et al. 2017; Hryniewicz et al. 2017b). The purpose of the present contribution is to describe three new bivalve genera from recently reported Upper Triassic seep deposits in southern Turkey, and to briefly discuss their evolutionary implications.

Institutional abbreviations.—NRM, Swedish Museum of Natural History, Stockholm, Sweden.

Material and methods

The sources of the present material are limestone deposits from the Kasımlar Basin in the Anamas Akseki Autochthon

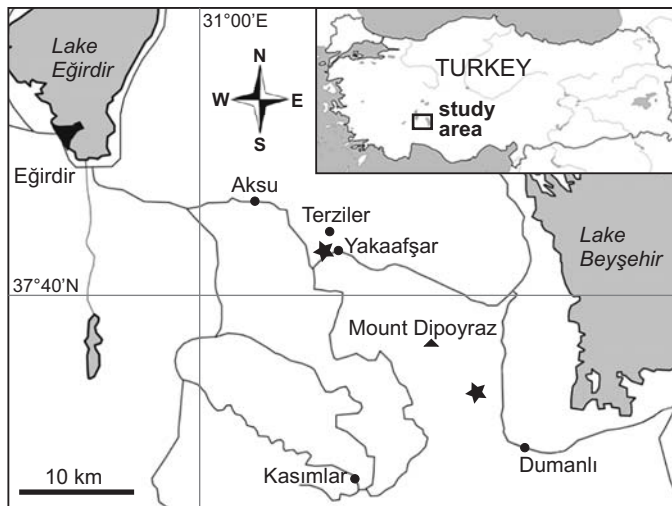


Fig. 1. Locality map of the Late Triassic seep deposits (stars), in southern Turkey, where the here described bivalves were found (from Kiel et al. 2017).

in the Taurus Mountains in southern Turkey (Fig. 1; Kiel et al. 2017). These sites were first mentioned in the literature in a report on their brachiopods (Ager et al. 1978). The Kasımlar Basin is interpreted as a small ocean basin partially bordered by carbonate platforms and filled by “deeper water” (cf. Lukeneder et al. 2012), siliciclastic sediments known as Kasımlar Formation or Kasımlar shales (Gutnic et al. 1979). Within these siliciclastics, three seep deposits were found on a slope on the north side of the road just West of the village of Yakaafşar, at the turnoff to Terziler, referred to as Terziler I–III, and two were found about six km NW of the village of Dumanlı, referred to as Dumanlı I and II, during field work in 2015. Further material was collected by Leopold Krystyn (Vienna, Austria) in 1973 from the same area as the Terziler I–III localities; this site is here referred to as “Leo’s Terziler seep deposit”. The seep deposits were dated by conodonts that were etched from the carbonates; the Dumanlı sites are dated as middle to late early Norian based on *Epigondolella triangularis*, the Terziler sites are dated as late Carnian based on *Quadralella polygnathiformis* (Tekin 1999; Chen et al. 2015; Kiel et al. 2017). A more detailed description of these sites and their fauna can be found in Kiel et al. (2017).

The specimens were extracted from the rock matrix using hammer and chisel in the field, and a pneumatic micro-hammer in the lab. The material is housed in the paleontological collection of the Swedish Museum of Natural History in Stockholm (NRM); figured specimens are numbered Mo184051–184074. All specimens except polished surfaces were coated with ammonium chloride prior to photography.

Systematic paleontology

Class Bivalvia Linnaeus, 1758

Clade Archiheterodonta Giribet in Taylor et al. 2007

Order Carditida Dall, 1889

Family Kalenteridae Marwick, 1953

Genus *Terzileria* nov.

Etymology: For the village of Terziler, near the type locality.

Type species: *Terzileria gregaria* sp. nov.; see below.

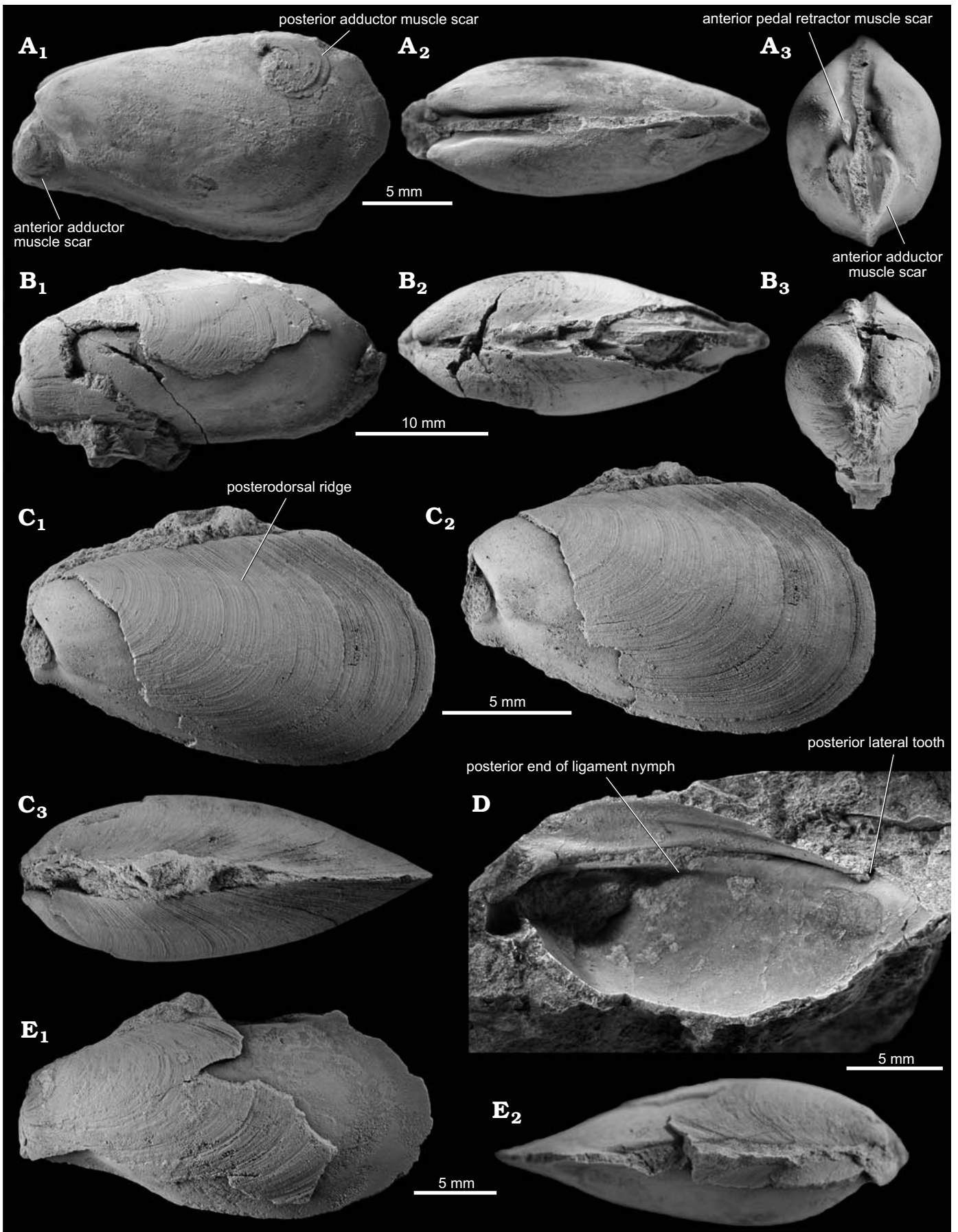
Species included: The type species and possibly also the “permophorid” reported from a Norian, Late Triassic seep deposit in eastern Oregon, USA (Peckmann et al. 2011).

Diagnosis.—Modioliform shell, subterminal umbones, elongate-lenticular escutcheon, shell surface with growth lines and faint posterodorsal groove; hinge plate edentulous, ligament nymph short and close to shell margin, elongate posterior lateral tooth quite distinct in left valve but less so in right valve; anterior adductor muscle scar deep, oval to almost round, positioned at anterior end of shell; anterior pedal retractor scar not fused with adductor muscle scar; pallial line entire and running close to ventral shell margin, no sinus; posterior adductor muscle scar round with projection (probably fused posterior pedal retractor scar) on anteroventral side.

Remarks.—Most similar to *Terzileria* is the Permian *Netschajewia* Likharev, 1925, with its modioliform outline, edentulous hinge plate, and the elongate posterior lateral tooth being stronger in the left valve. *Terzileria* differs from *Netschajewia* by having an elongate-lenticular escutcheon (lacking in *Netschajewia*) and a more-or-less evenly convex globosity of the shell, whereas *Netschajewia* has a distinct broad ridge running from the umbo to the posteroventral margin (Murchison et al. 1845). The available descriptions and illustrations of the type species of *Netschajewia* (i.e., *Pleurophorus modioliformis* King in de Verneuil and Murchison, 1844 = *Mytilus pallasi* de Verneuil in Murchison et al., 1845) did not discuss or show the anterior pedal retractor muscle scar, the posterior adductor muscle scar and the possible presence of a pallial sinus (Murchison et al. 1845; King 1850; Newell 1957; Chavan 1969).

Also very similar to *Terzileria* is the Jurassic–Cretaceous seep-restricted genus *Caspiconcha* Kelly in Kelly et al. 2000. They differ by the following features: (i) in *Caspiconcha* the anterior adductor muscle scar is in a more dorsal position than in *Terzileria*; (ii) in *Caspiconcha* the anterior adductor muscle scar and the pedal retractor scar are fused, whereas in *Terzileria* they are separated; (iii) in *Terzileria* the pallial line is closer to the shell margin than in *Caspiconcha*;

Fig. 2. The kalenterid bivalve *Terzileria gregaria* gen. et sp. nov. from the late Carnian, Late Triassic Terziler III seep deposit in southern Turkey. →
A. Mo184051, holotype, internal mold, left valve (A₁), dorsal (A₂) and anterior (A₃) views. **B.** Mo184052, paratype, specimen with shell partially preserved, left valve (B₁), dorsal (B₂) and anterior (B₃) views. **C.** Mo184053, paratype, small specimen with shell preserved on most of posterior side, left valve (C₁), the same at slightly different angle (C₂), dorsal view (C₃). **D.** Mo184054, fragmentary but articulated specimen, interior of the dorsal side, showing the edentulous hinge. **E.** Mo184055, paratype, large specimen showing outer shell surface of the anterior half of the shell; left valve (E₁) and dorsal view (E₂).



(iv) secondary pallial attachment scars tend to be found in the anterior half of the shell in *Caspiconcha*, whereas in *Terzileria* they tend to occur more posteriorly (Kelly et al. 2000; Kiel et al. 2010; Jenkins et al. 2013, 2018).

The type species of *Kalentera* Marwick, 1953 is similar in shell outline, the lateral tooth in the left valve and the shape of the anterior adductor muscle scar (Marwick 1953; Chavan 1969) but is clearly distinct from *Terzileria* by having cardinal teeth. Other species of *Kalentera* are more trapezoidal in outline and have a distinctive angular ridge running from umbo to the posteroventral corner (Grant-Mackie 1979; Covacevich et al. 1991; Damborenea 2004).

The genus *Healeyia* Hautmann, 2001 has a similarly shaped pallial line, anterior adductor muscle scars and a separated pedal retractor scars, but clearly differs from *Terzileria* by its strong and sharp diagonal keel running from the umbo to the posteroventral margin, and by its thicker hinge plate (Hautmann 2001). Similar to *Terzileria* regarding modioliform shell and subterminal umbo is the Late Triassic *Myoconcha* (*Pseudomyoconcha*?) *auriculata* Broili, 1903 as figured in Hautmann (2001), but it differs from *Terzileria* by having fine radial ribs on the shell surface. *Myoconcha* Sowerby, 1824 has a narrower and more pointed anterior margin than *Terzileria*, and possesses cardinal teeth, whereas *Terzileria* is edentulous (Chavan 1969). The Late Triassic *Ouamouia grantmackie* Campbell, 1984 from New Caledonia and New Zealand is more bean-shaped than *Terzileria* (by having a broader anterior margin and a less wide posterior margin), has a much stronger hinge plate that features cardinal teeth, a smaller anterior adductor muscle scar, and fine radial striation on the anteroventral shell surface (Campbell 1984). The type species of *Triaphorus* Marwick, 1953, *Triaphorus zealandicus* (Trechmann, 1917), also has a broader anterior margin and a narrower posterior margin compared to *Terzileria*, and possesses cardinal teeth (Chavan 1969; Damborenea 2004). Most other kalenterid genera differ from *Terzileria* by possessing cardinal teeth (i.e., *Permophorus*, *Celtoides*, *Pseudopermophorus*, *Curionia*, *Myoconcha*, and *Pseudomyoconcha*; see Chavan 1969).

The new genus *Kazimlara* described below from the same seep deposits differs by being much more inflated, having a much smaller anterior adductor muscle scar, and by showing a lateral curvature of the shell that is not seen in *Terzileria*.

Stratigraphic and geographic range.—Late Triassic hydrocarbon seep deposits in Turkey and possibly also in Oregon.

Terzileria gregaria sp. nov.

Figs. 2, 3.

2017 *Caspiconcha*-like bivalve; Kiel et al. 2017: fig. 4B, C.

Etymology: For its gregarious occurrence at the type locality.

Type material: Holotype: Mo184051, an internal mold showing features of the pallial line and muscle attachment scars. Paratypes: Mo184052–184060 from type locality.

Type locality: The Terziler III seep deposit, southern Turkey.

Table 1. Measurements (in mm) of *Terzileria gregaria* sp. nov.

Specimen number	Locality	Length	Height	Width
Mo184051	Terziler III	21.5	12	8
Mo184052	Terziler III	28	13	11
Mo184053	Terziler III	16.5	10	6.5
Mo184055	Terziler III	25	13	9
Mo184056	Terziler III	25	14	9
Mo184057	Terziler III	20	11	8.2
Mo184058	Terziler III	23.3	12.5	9
Mo184060	Terziler III	25	14	9.5
Mo184075	Terziler III	28	15.7	11.2
Mo184076	Terziler III	25	13	10.5
Mo184077	Terziler III	24	11.5	8.5
Mo184078	Terziler III	19	10	7.2
Mo184079	Terziler III	19	10	7.8
Mo184080	Leo's Terziler site	33	15	13

Type horizon: Late Carnian, Late Triassic seep deposits of the Kasimlar shales.

Material.—The type material and 75 specimens from Terziler III; five specimens from Terziler II; one specimen from Leo's Terziler seep deposit; see Table 1 for measurements.

Diagnosis.—As for genus.

Description.—Shell elongate modioliform, largest specimen 33 mm long; length:height ratio about 1.7–2.0; moderately inflated, width:length ratio about 0.38–0.40; beak subterminal, prosogyrate; shell surface smooth except for fine growth increments; escutcheon elongate-lenticular and marked by a sharp ridge; ligament nymph short, slightly less than 1/3 of shell length, close to shell margin, indicating external ligament; short, heart-shaped lunule. Posterodorsal margin very gently convex, posterior end well rounded, ventral margin gently convex, anterior margin truncate and pointing anteroventrally. Anterior adductor muscle scars D-shaped, steeply deepening toward the anterior, terminating anteriorly at a triangular wall perpendicular to the anterior-posterior shell axis; concentric growth increments. Anterior pedal retractor scars elongate-oval, nearly parallel to anterior-posterior shell axis, positioned below and just anterior to the umbones. Pallial line close and subparallel to ventral and posterior shell margin with a distinct bulge just posterior to the anterior adductor muscle scar; reaches the posterior adductor scar at the center of its posterior margin; some specimens show strong secondary pallial attachment scars radiating toward the shell's interior, especially along the ventral and posterior margins. Posterior adductor scar positioned in the middle of the posterior half of the shell, roundish, with a sinuous indentation underneath the onset of the posterior pedal retractor scar, which projects spine-like from the anterior side of the dorsal margin of the adductor scar. The hinge plate is edentulous, the posterior lateral tooth is elongate, and is well-developed in the left valve but inconspicuous in the right valve.

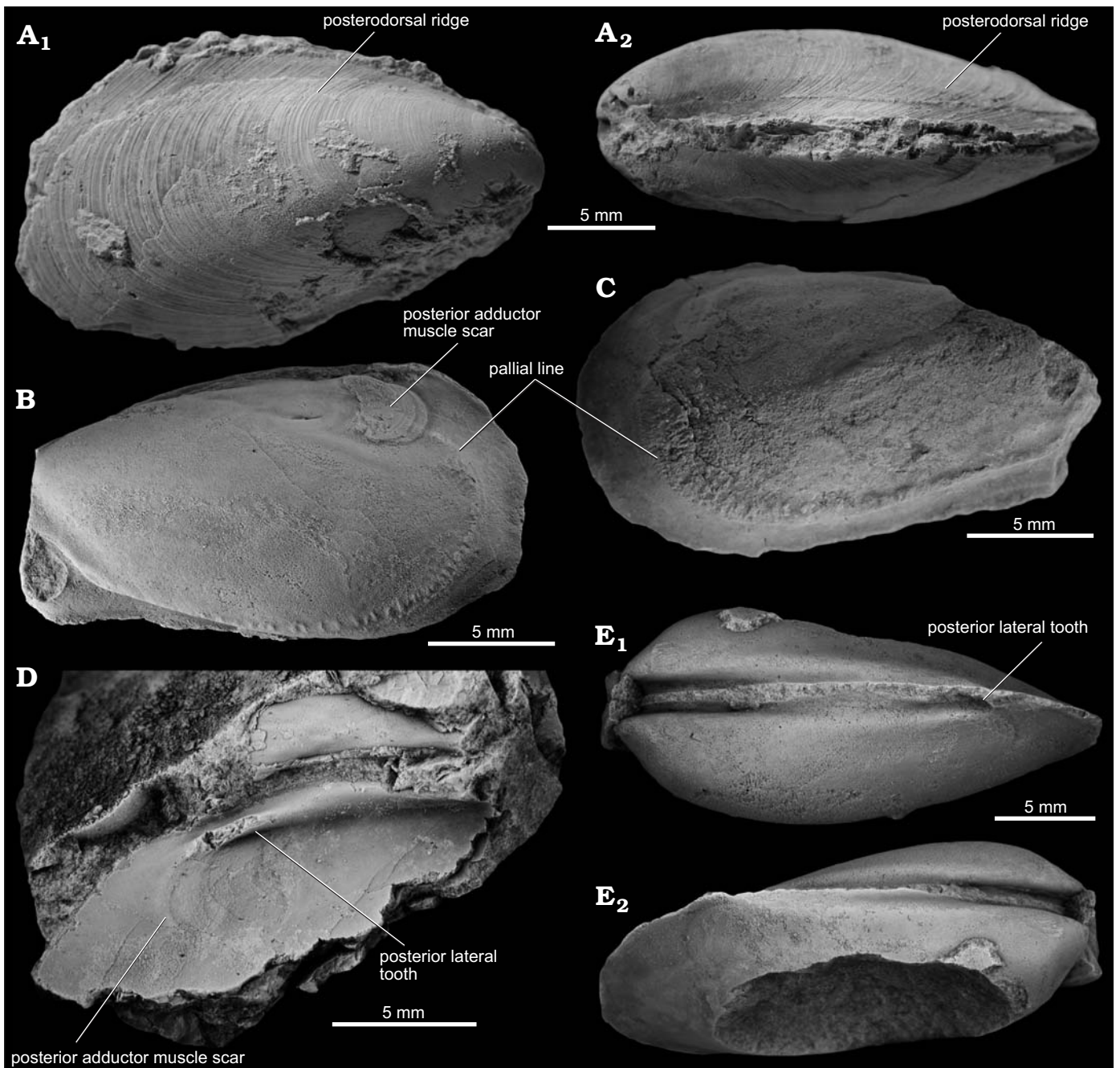


Fig. 3. The kalenterid bivalve *Terzileria gregaria* gen. et sp. nov. from the late Carnian, Late Triassic Terziler III seep deposit in southern Turkey. **A.** Mo184056, specimen with preserved shell showing irregular growth increments; right valve (**A₁**) and dorsal view (**A₂**). **B.** Mo184057, left valve of an internal mold, note mantle muscle scars along the pallial line. **C.** Mo184058, right valve of a specimen. **D.** Mo184059, shell fragment preserving the posterodorsal part of the inner shell surface of a left valve. **E.** Mo184060, internal mold showing the impression of the posterior lateral tooth in the left valve (**E₁**) and the lack of this feature in the right valve (**E₂**).

Remarks.—The “possible permophorid” reported from a Late Triassic seep deposit in Oregon, USA (Peckmann et al. 2011), might also belong to *Terzileria*, and differs from *T. gregaria* by being more elongate and having a broader anterior margin. The Early Jurassic *Myoconcha neuquena* Leanza, 1940 was recently discussed as an early member or possible ancestor of *Caspiconcha* (Jenkins et al. 2018). It could therefore, at least stratigraphically speaking, be a link between *Terzileria* and *Caspiconcha*. *Myoconcha neuquena*

differs from *T. gregaria* mainly by having the anterior pedal retractor and adductor muscle scars fused, by its oblique posterior adductor muscle scar with a much broader ventral extension, and by its thicker hinge plate (as shown in Griffin and Pastorino 2006: figs. 4-1, 4-2).

Stratigraphic and geographic range.—Late Carnian, Late Triassic seep deposits in the Kasımlar shales in southern Turkey.

Genus *Kasimlara* nov.

Etymology: For its occurrence in the Kasımlar shales in southern Turkey.

Type species: *Kasimlara kosuni* sp. nov.; see below.

Species included: The type species and *Kasimlara* sp. (described below).

Diagnosis.—Strongly inflated, laterally curved, modioliform shell with subterminal umbo, small but deep anterior adductor muscle scar, pallial line with very small, pointed sinus.

Remarks.—*Kasimlara kosuni* sp. nov. resembles the type species of *Healeyia*, *H. gonoides* (Healey, 1908) regarding shell outline, inflation, and the strong diagonal ridge (Hautmann 2001). But *H. gonoides* has a distinct anterior pedal retractor scar that is not apparent in *Kasimlara kosuni*, and although *K. kosuni* is only known from internal molds, it is obvious that its hinge plate is not as strong as in *H. gonoides*. Furthermore, the strong diagonal ridge across the shell surface has two strong keels in *H. gonoides* whereas *Kasimlara* sp. shows only one keel.

The main differences between *Kasimlara* and *Terzileria* described above are (i) the much smaller anterior adductor muscle scar in *Kasimlara*, (ii) the much stronger inflation of *Kasimlara*, (iii) the lack of lateral shell curvature in *Terzileria*, and (iv) the presence of a small pallial sinus in *Kasimlara*, which *Terzileria* lacks.

Stratigraphic and geographic range.—Late Triassic hydrocarbon seep deposits in Turkey.

Kasimlara kosuni sp. nov.

Figs. 4, 5.

2017 new genus of bivalve clade Modiomorphida; Kiel et al. 2017: fig. 4D.

Etymology: For Erdal Koşun (Antalya, Turkey).

Type material: Holotype: Mo184061, an internal mold of a large left valve. Paratypes: Mo184062–184064) from the type locality.

Type locality: The Terziler III seep deposit (southern Turkey).

Type horizon: Late Carnian, Late Triassic seep deposits of the Kasımlar shales.

Material.—The type material and three further specimens from the type locality; see Table 2 for measurements.

Diagnosis.—As for genus.

Description.—Strongly inflated, modioliform shell that is laterally curved to some degree, with the direction of curving differing between specimens; umbo subterminal, strong ridge running from umbo to posteroventral margin; anterior adductor muscle scar small but deep, cone-shaped pointing

Table 2. Measurements (in mm) of *Kasimlara kozuni* sp. nov., * incomplete.

Specimen number	Locality	L	H	W
Mo184061	Terziler III	57	26	11 (single)
Mo184063	Terziler III	20	9	10
Mo184064	Terziler III	21*	10	12.2
Mo184081	Terziler III	36	15	18
Mo184082	Terziler III	32*	21	19.5
Mo184083	Terziler III	29.5	13	8 (single)

toward the anterior; onset of pallial line posterior to anterior adductor muscle scar, distant from ventral margin and running subparallel to it; secondary pallial attachment scars occur as pits at the anterior side of the shell, along the ventral margin they are fine but numerous and strongly inclined anteriorly; very small pallial sinus, posterior adductor muscle scar indistinct, round; inner shell surface with fine radial striations close to the dorsal and ventral margins, and pustules in the area between. The largest specimen reaches 57 mm in length, 26 mm in height, and the single valve is 11 mm thick.

Remarks.—The lateral curvature of the shell is either to the left, as in the holotype (meaning that the commissure of the right valve is concave, that of the left valve is convex), whereas the two paratypes illustrated in Fig. 5 are curved to the right. I have not seen any specimen without lateral curvature.

Stratigraphic and geographic range.—Late Triassic hydrocarbon seep deposits in Turkey.

Kasimlara sp.

Fig. 6.

Material.—Mo184065, a single left valve from the Terziler II seep deposit (southern Turkey), late Carnian, Late Triassic of the Kasımlar shales.

Description.—Strongly inflated, mytiliform to modioliform shell that is laterally slightly curved, 35 mm long, 15 mm high, single valve 7 mm thick; posterodorsal margin straight, anterior margin evenly curved, reaching the ventral margin at the posterior end of the shell; ventral margin nearly straight; umbo subterminal, strong, angular ridge running from umbo to posteroventral margin; shell surface smooth except for commarginal growth increments.

Remarks.—Details of the anterior margin and of the internal features of the shell (hinge, pallial line, muscle scars) are unknown. The anterior side of the shell is more pointed than in *Kasimlara kosuni* and the ridge running from the umbo to the posteroventral margin has an angular profile, which differs from the more curved profile of this ridge in *Kasimlara kosuni*. Whether these differences fall within the phenotypic variation of *Kasimlara kosuni*, or if this specimen belongs to a separate species cannot be decided with the limited available material; hence the specimen is left in open nomenclature.

Clade Anomalodesmata Dall, 1889

Superfamily Pholadomyoidea Gray, 1847

Family uncertain

Genus *Aksumya* nov.

Etymology: Combined from the town Aksu near the type locality, and the bivalve genus *Mya*.

Type species: *Aksumya krystyni* sp. nov.; see below.

Species included: The type species and possibly also the “nuculanid”

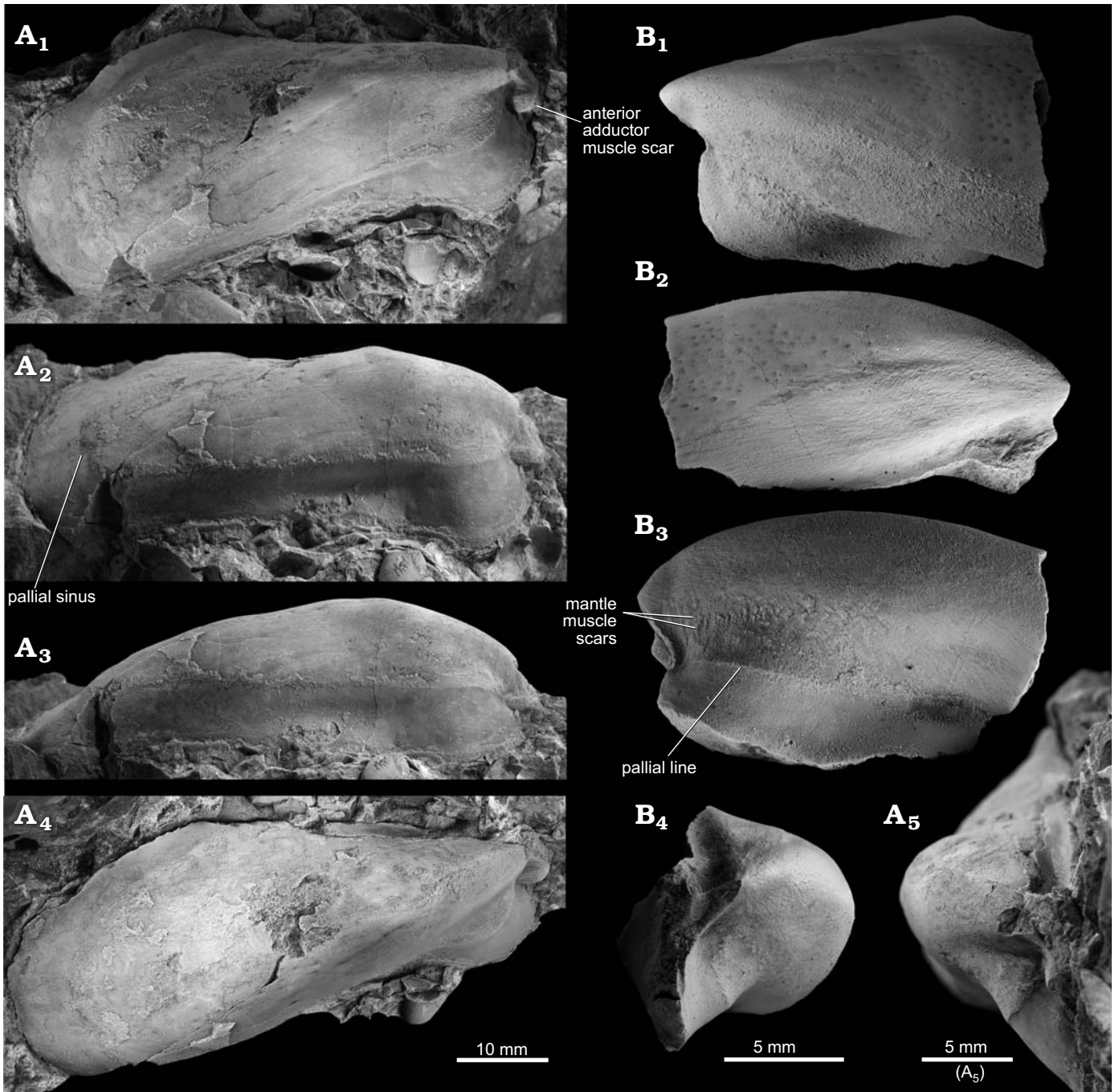


Fig. 4. The kalenterid bivalve *Kasimlara kosuni* gen. et sp. nov. from the late Carnian, Late Triassic Terziler III seep deposit in southern Turkey. **A.** Mo184061, holotype, large internal mold of right valve; lateral (A₁), lateral-ventral (A₂), ventral (A₃), lateral-dorsal (A₄), and anterior (A₅) views. **B.** Mo184062, internal mold of anterior part of left valve; showing tubercles (as pits in the mold) on the lateral side of the shell's interior (B₁), fine radial striation on the dorsal inner side of the shell (B₂), ventral view on the dorsal inner side of the shell (B₃), anterior side, note the strong inflation of the shell (B₄).

from a Norian, Late Triassic seep deposit in Oregon (Peckmann et al. 2011).

Diagnosis.—Shell nuculaniform with elongated, tapering posterior side, broad umbonal sulcus and sinuous ventral margin, surface sculpture of commarginal growth lines and fine pustules; hinge plate with two blunt teeth in each valve and a short and strong ligament nymph holding an calcified external ligament; shell interior with radial striation;

anterior adductor muscle scar roundish to quadrate, fused dorsally with anterior pedal retractor scar; pallial line entire and close to ventral margin, no pallial sinus.

Remarks.—Regarding its overall shell shape, muscle scar and hinge characters, and the fine pustules on the shell surface, *Aksumya* can safely be placed among the Pholadomyoidea. But assigning it to any of the currently recognized families is rather difficult. With some Paleozoic Grammysiidae

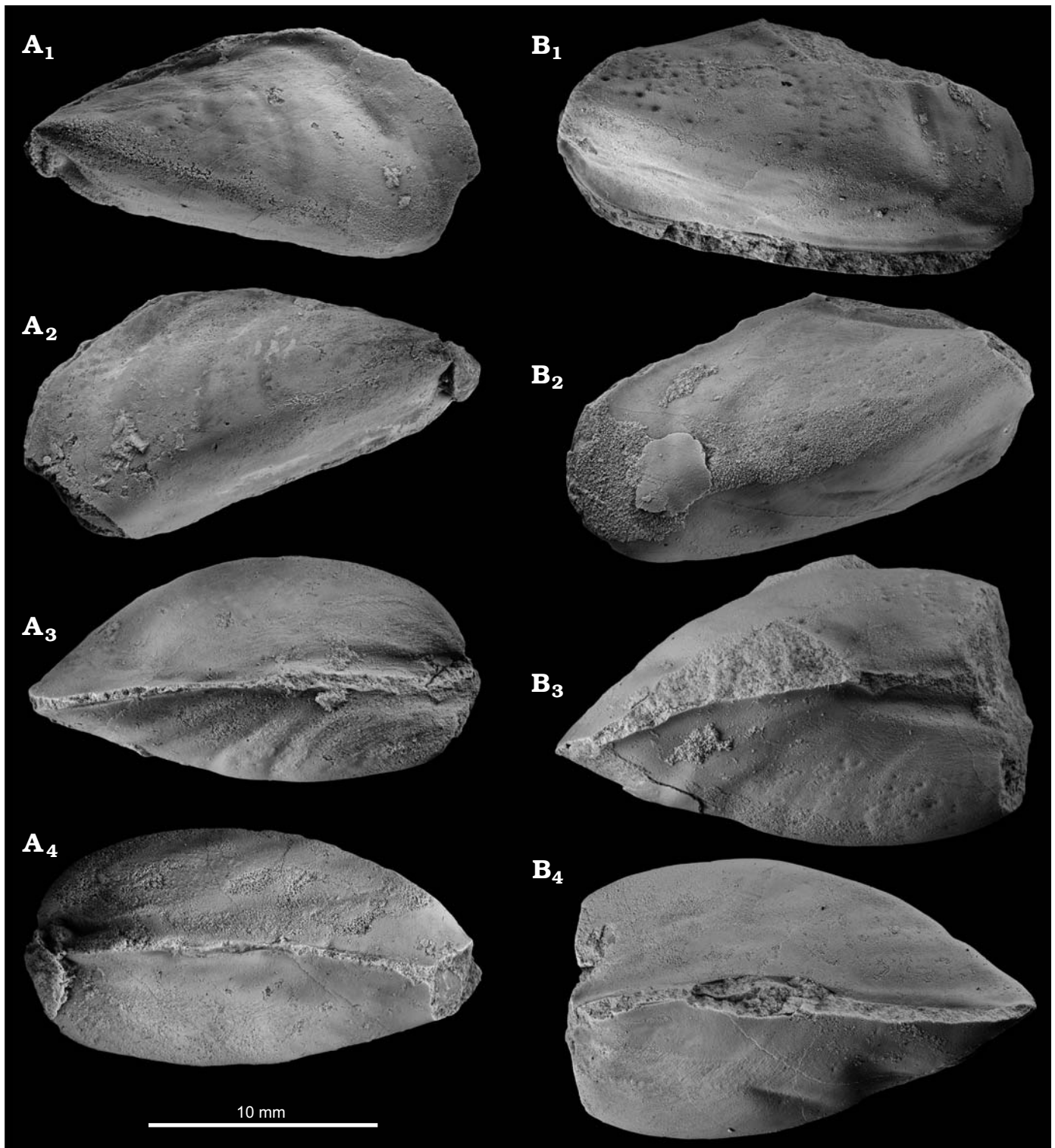


Fig. 5. The kalenterid bivalve *Kasimlara kosuni* gen. et sp. nov. from the late Carnian, Late Triassic Terziler III seep deposit in southern Turkey. **A.** Mo184063, internal mold of an articulated specimen; left (A_1) and right (A_2) valves, dorsal (A_3) and ventral (A_4) sides, showing the curvature of the shell. **B.** Mo184064, internal mold of articulated specimen; left (B_1) and right (B_2) valves, dorsal (B_3) and ventral (B_4) sides, showing the curvature of the shell; note the strong, healed predation scars on the posterior side of the left valve (B_1) and on the posteroventral side of the right valve (B_4).

(= Sanguinulitidae) it shares the broad umbonal sulcus and sinuous ventral margin, and possibly its hinge dentition (i.e., *Tellinomorpha*, cf. Morris and Dickins 1991). However, similar shell shapes are also found among the Mesozoic–Recent

Pholadomyidae (*Pachymya*, *Machomya*), and the hinge features shown here on polished surfaces and interpreted as teeth also resemble the pits for internal ligaments documented for *Pholadomya* (Newell 1969).

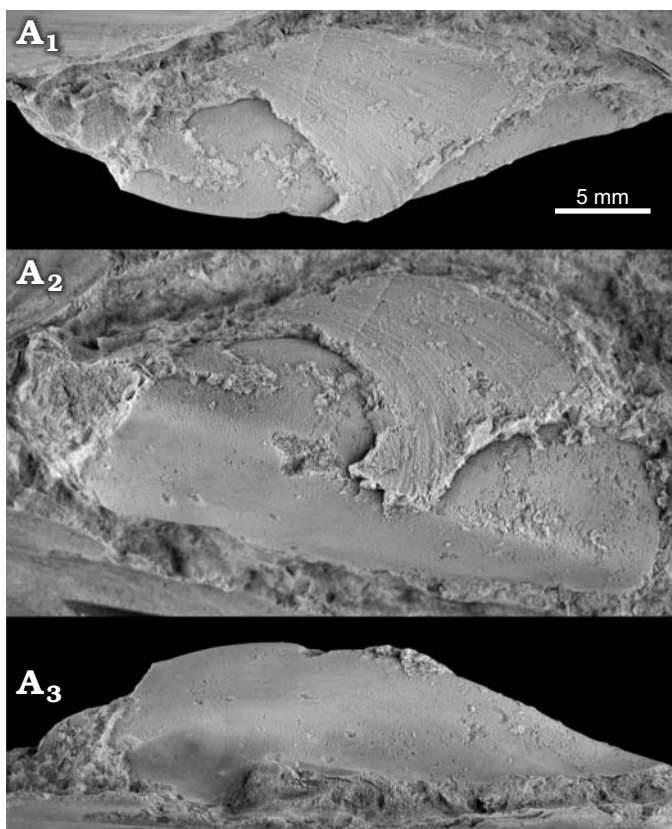


Fig. 6. The kalenterid bivalve *Kasimlara* sp. from the late Carnian, Late Triassic Terziler II seep deposit in southern Turkey. Mo184065, single left valve; view on the dorsal (A_1) and the ventral (A_3) sides, lateral view (A_2).

Almost identical regarding shell shape, external surface and hinge characters is the Viséan, early Carboniferous genus *Tellinomorpha* de Koninck, 1885 (type *T. cuneiformis* de Koninck, 1885). However, there are several reasons why I hesitate placing *Aksumya krystyni* in this genus: (i) *Tellinomorpha* is based on a single right valve with unknown internal features; (ii) the posterior siphonal area is broken in that single specimen, hence its length is unknown, and furthermore, it is demarcated by the upturn of the growth lines (cf. Morris and Dickins 1991) and this upturn is angular in *T. cuneiformis* but gently rounded in *Aksumya krystyni*; (iii) the only known specimen of *T. cuneiformis* is about 100 million years older than *Aksumya krystyni* and I find it unlikely that such decent-sized bivalves (exceeding 70 mm in length) should have remained unnoticed during such a long geologic time interval, spanning most of the Carboniferous, the well-sampled Permian, and half of the Triassic.

Among the Pholadomyidae, species of *Arcomya* Roemer, 1839 are less inflated, have much narrower gapes anterior and posterior of the umbones, the pallial line crosses the anteroventral margin obliquely, whereas it largely follows the ventral shell margin in *Aksumya*, and pallial line and posterior adductor muscle scar are more distant from the posterior margin than in *Aksumya*. In *Pachymya* Sowerby, 1826 the shell is more inflated posteriorly and also has pallial line and posterior adductor muscle scar more distant

from the posterior margin than *Aksumya*. *Machomya* de Loriol in de Loriol and Cotteau, 1868 has an anterior internal rib, whereas *Aksumya* has such a rib on the posterior side. Externally, shells of *Homomya* Agassiz, 1843 and of *Pleuromya* Agassiz, 1842 are quite similar, but both genera have a deep pallial sinus, which *Aksumya* lacks.

Stratigraphic and geographic range.—Late Triassic hydrocarbon seep deposits in Turkey and possibly also in Oregon.

Aksumya krystyni gen. et sp. nov.

Figs. 7–9.

2017 new genus of bivalve clade Anomalodesmata; Kiel et al. 2017: fig. 4A.

Etymology: For Leopold Krystyn (Vienna, Austria).

Type material: Holotype: Mo184067, a specimen with preserved shell surface. Paratypes: Mo184066, Mo184068–184074 from the type locality.

Type locality: Leo's Terziler seep deposit, southern Turkey.

Type horizon: Late Carnian, Late Triassic seep deposits of the Kasimlar shales.

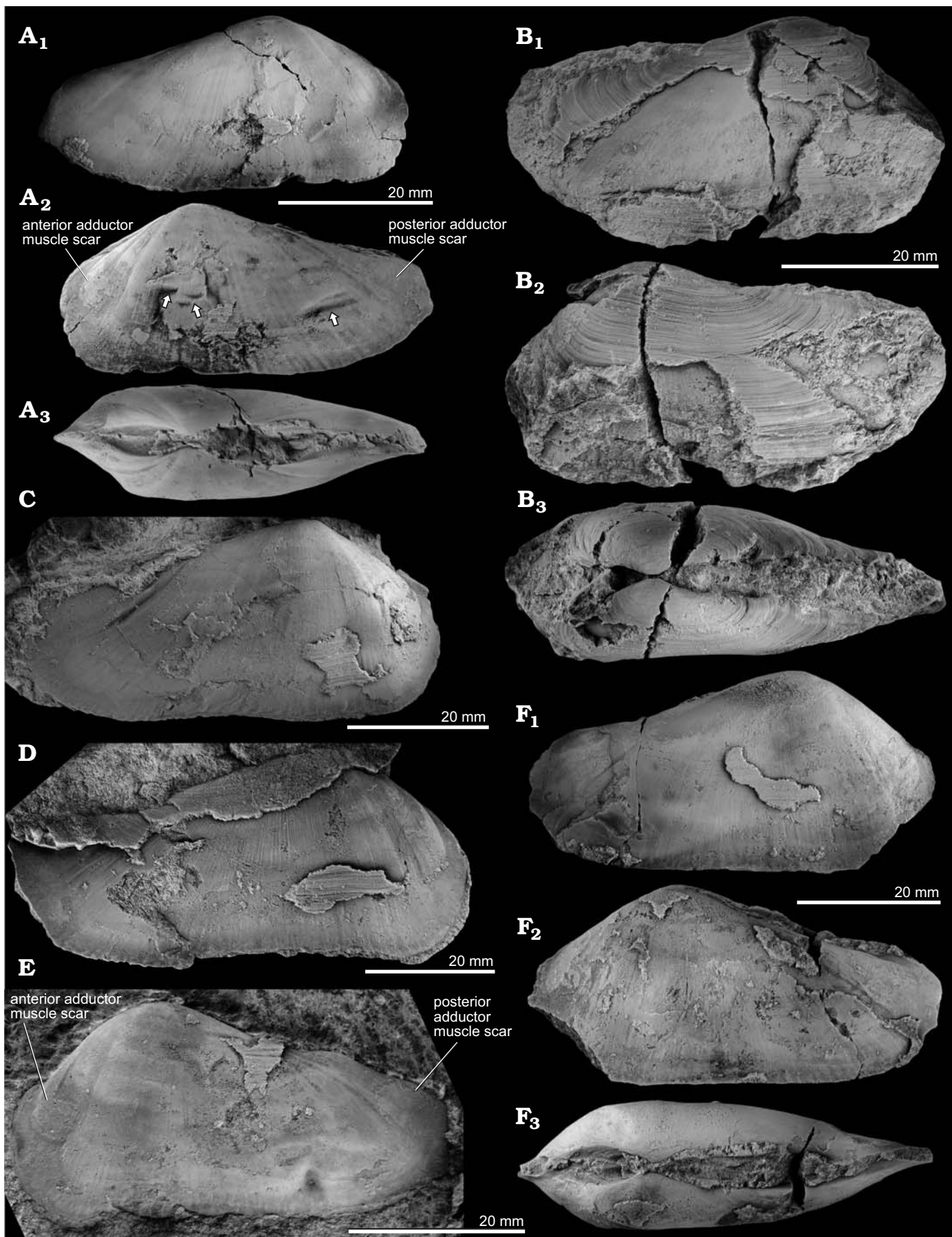
Material.—Ten specimens from the type locality, two from Terziler I, six specimens and many fragments from Terziler II, 14 specimens from Terziler III, 18 specimens and many fragments from Dumanlı I, 12 specimens and many fragments from Dumanlı II; southern Turkey, late Carnian, Late Triassic of the Kasimlar shales. See Table 3 for measurements.

Diagnosis.—As for genus.

Description.—Elongate nuculaniform shell, umbo slightly prosogyrate, positioned in the anterior half of the shell;

Table 3. Measurements (in mm) of *Aksumya krystyni* sp. nov., * incomplete.

Specimen number	Locality	Length	Height	Width
Mo184066	Leo's Terziler site	48	22	14.5
Mo184067	Leo's Terziler site	56	29	19.5
Mo184068	Leo's Terziler site	61	29	19
Mo184069	Leo's Terziler site	73	ca. 34	23
Mo184070	Leo's Terziler site	53	26	7 (single)
Mo184071	Leo's Terziler site	58.5	29	18
Mo184072	Leo's Terziler site	49*	28	18
Mo184084	Leo's Terziler site	64	35	22
Mo184085	Leo's Terziler site	52*	28	18
Mo184086	Leo's Terziler site	46	24	14
Mo184074	Terziler III	36*	18	15
Mo184087	Terziler III	38	19	12
Mo184088	Terziler III	22*	13	4 (single)
Mo184089	Terziler III	24	12	7
Mo184090	Terziler III	16	9	6
Mo184073	Dumanlı I	56*	35*	21
Mo184091	Dumanlı II	71	36	14
Mo184092	Dumanlı II	65*	41	21
Mo184093	Dumanlı II	79	36*	
Mo184094	Dumanlı II	65*	38	20
Mo184095	Dumanlı II	66.5	31	9 (single)



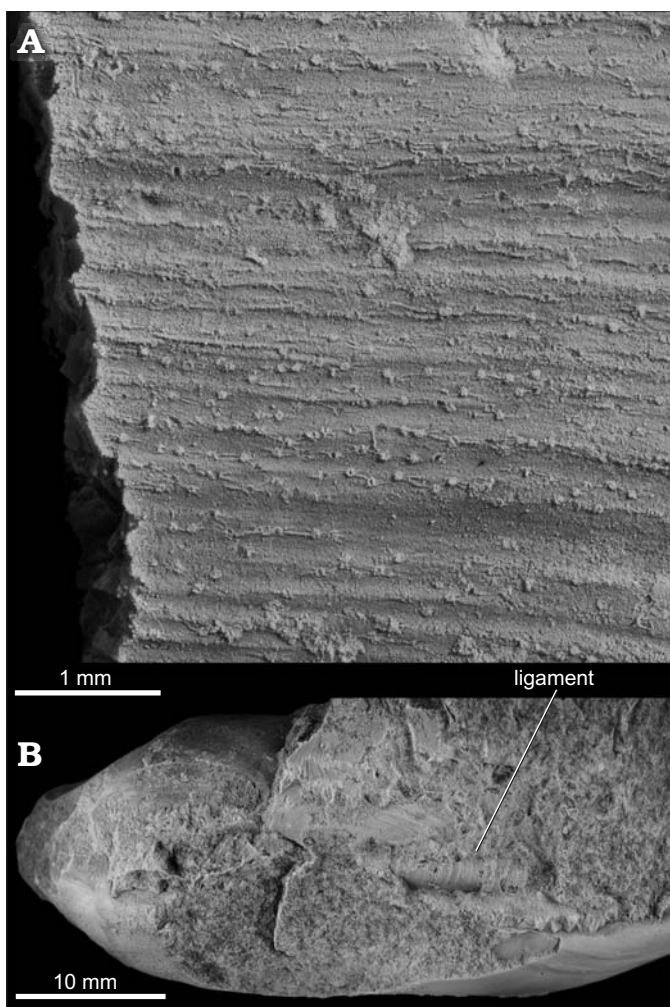


Fig. 8. The pholadomyoid bivalve *Aksumya krystyni* gen. et sp. nov. from the late Carnian, Late Triassic Leo's Terziler seep deposit in southern Turkey. **A.** Mo184067, holotype, close-up on the small shell spines. **B.** Mo184072, specimen with preserved ligament.

surface sculptured by commarginal growth lines and tiny, irregularly distributed spines; ligament at least partially external and calcified; anterodorsal margin running more-or-less straight down to about 2/5 of the shell height, anterior margin below rounded or truncate; ventral margin straight to slightly concave; anterior variable, ranging from broad and blunt, to tapering into a blunt, pointed, posteroventral end, to acute-rounded and pointing slightly upward. Shell moderately inflated, with broad and shallow sulcus running from the umbo to the ventral margin; escutcheon lanceolate, deep, bordered by a sharp ridge; largest specimen ca. 74 mm long. Entire inner shell surface covered by fine radial grooves; ventral margin of inner shell surface cren-

ulated; broad groove running from umbo to anterodorsal margin, bordering the anterior adductor muscle scar, which is indistinct, situated mostly below the midline of the shell, roundish to quadrate, and fused dorsally with the anterior pedal retractor scar; pallial line indistinct, onset apparently at the posteroventral margin of the anterior adductor muscle scar, running close to the ventral shell margin, no pallial sinus; posterior adductor muscle scar indistinct, roundish, situated in the posterodorsal corner of the shell, above a broad and shallow groove that radiates from about the middle part of the shell (anterior half of escutcheon) toward the posterior margin. Hinge plate narrow and short, with two blunt teeth in each valve; ligament nymph short and strong holding an external and calcified ligament

Remarks.—The “Nuculanid” from the early Norian, Late Triassic Greylock Butte seep deposits in Oregon, USA (Peckmann et al. 2011: fig. 3G) almost certainly also belongs to *Aksumya*. That species reaches 50 mm in length and is the most common mollusk ($n = 15$) at this *Halorella*-dominated seep deposit. It has a shorter and taller shell with a steeper and more angular anterior margin than *Aksumya krystyni* sp. nov.

Stratigraphic and geographic range.—Late Carnian to late early Norian (Late Triassic) seep deposits in the Kasımlar shales in southern Turkey.

Discussion

The presence of two distinct and new modiomorphid genera at the Upper Triassic seep deposits in the Kasımlar shales in southern Turkey had already been indicated in the initial report of these sites (Kiel et al. 2017) and they are here described as *Terzileria* and *Kasımlara*. They significantly increase the diversity of modiomorphid bivalves at seeps and shorten the stratigraphic gap between the Silurian–Devonian *Atavioconcha* (Jakubowicz et al. 2017; Hryniewicz et al. 2017b) and the Late Jurassic–Late Cretaceous *Caspiconcha* (Kelly et al. 2000; Kiel et al. 2010; Jenkins et al. 2013, 2018).

The phylogenetic relationships between members of the “modiomorphid” families Kalenteridae, Myoconchidae, and Modiomorphidae remain unclear (Hryniewicz et al. 2017b), and the distinctions between these groupings are indeed based on a rather limited set of characters (Chavan 1969). There are two general possibilities for the relationships among the seep-inhabiting genera *Atavioconcha*, *Terzileria*, *Kasımlara*, and *Caspiconcha*. The first possibil-

← Fig. 7. The pholadomyoid bivalve *Aksumya krystyni* gen. et sp. nov. from the late Carnian, Late Triassic, Leo's Terziler seep deposit in southern Turkey. **A.** Mo184066, paratype, internal mold of an articulated specimen with interior radial striations, right (A_1) and left (A_2) valves, note healed predation scars (arrows), dorsal view (A_3). **B.** Mo184067, holotype, specimen with preserved external surface, showing the overall outline of the shell; right (B_1) and left (B_2) valves, dorsal view (B_3). **C.** Mo184068, paratype, right valve with particularly strong ridge running from the middle of the dorsal margin to the anterodorsal corner of the posterior adductor muscle scar. **D.** Mo184069, paratype, right valve of a large specimen showing the projection on the anterodorsal side of the anterior adductor muscle scar. **E.** Mo184070, paratype, left valve, and predation marks on the posteroventral side. **F.** Mo184071, paratype, internal mold of articulated specimen, right (F_1) and left (F_2) valves, dorsal view (F_3).

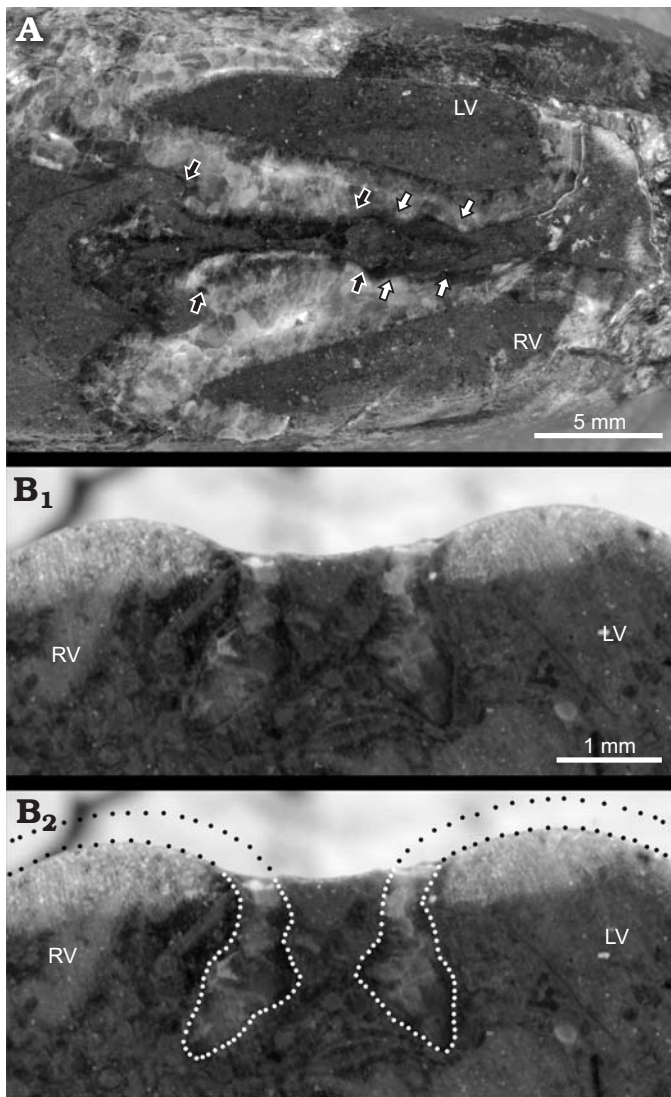


Fig. 9. The pholadomyoid bivalve *Aksumya krystyni* gen. et sp. nov. from the late Carnian, Late Triassic in southern Turkey; polished surfaces of cross sections showing hinge and nymph details. **A.** Mo184073 from Dumanlı I; cross section cut horizontally through the umbones, showing hinge (white arrows) and ligament nymph (black arrows). **B.** Mo184074 from Terziler III, vertical cross section showing hinge area just below umbo, seen from the anterior; white dotted line in B₂ indicates the hinge area, black dotted line indicates the inferred shell material of the umbones. Abbreviations: LV, left valve; RV, right valve.

ity, coined here the “single lineage hypothesis”, is that these four genera are members of a single lineage that has continuously inhabited hydrocarbon seeps from the Silurian to the Cretaceous. An analog from the more recent geologic record is the Bathymodiolinae, whose members have been living almost exclusively in deep-water reducing habitats such as hydrothermal vents, methane seeps, and large accumulations of organic matter since the Eocene (Kenk and Wilson 1985; Distel et al. 2000; Lorion et al. 2013; Kiel and Amano 2013). An interesting implication of this hypothesis is that this putative deep-water lineage would have survived the end-Permian mass extinction event, as did certain shallow-water representatives of the kalenterids (Damborenea 2004).

The second possibility, here coined the “repeated colonization hypothesis”, is that the four genera represent individual offshoots of one or several “modiomorphid” lineages that repeatedly developed similar morphological adaptations (cf. Hryniewicz et al. 2017b) to the methane-seep environments. This hypothesis raises interesting questions of its own: was there a single “source habitat” from these repeated colonization started, and why did this group that successfully colonized reducing habitats over the course of 350 million years, fail to colonize them again after the Cretaceous?

Chemosymbiosis is unknown from extant Anomalodesmata (Harper et al. 2006; Taylor and Glover 2010) and the alleged thraacid *Nipponothracia* from fossil seep deposits in Japan proved to be a lucinid (Kase et al. 2007; Kiel 2013). Recently, members of three genera of presumed anomalodesmatans (*Anhemia*, *Tambaquyra*, and *Maackia*) were reported from concretionary limestone deposits from the Permian of Brazil, which were interpreted as cold seep deposits (Matos et al. 2017). However, (i) the published field images and rock samples look unlike other, confirmed, seep deposits, (ii) the carbonates lack banded and botryoidal rim cements characteristic for seep carbonates (cf., Peckmann and Thiel 2004), and (iii) their carbon isotope signature is not very negative and is well within the range of septarian and other concretions resulting from the oxidation of organic matter (Irwin et al. 1977). Thus the interpretation of these “anomalodesmatans” as seep-inhabiting bivalves is not followed here. This makes *Aksumya* the first seep-inhabiting and probably seep-restricted genus of the Anomalodesmata.

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