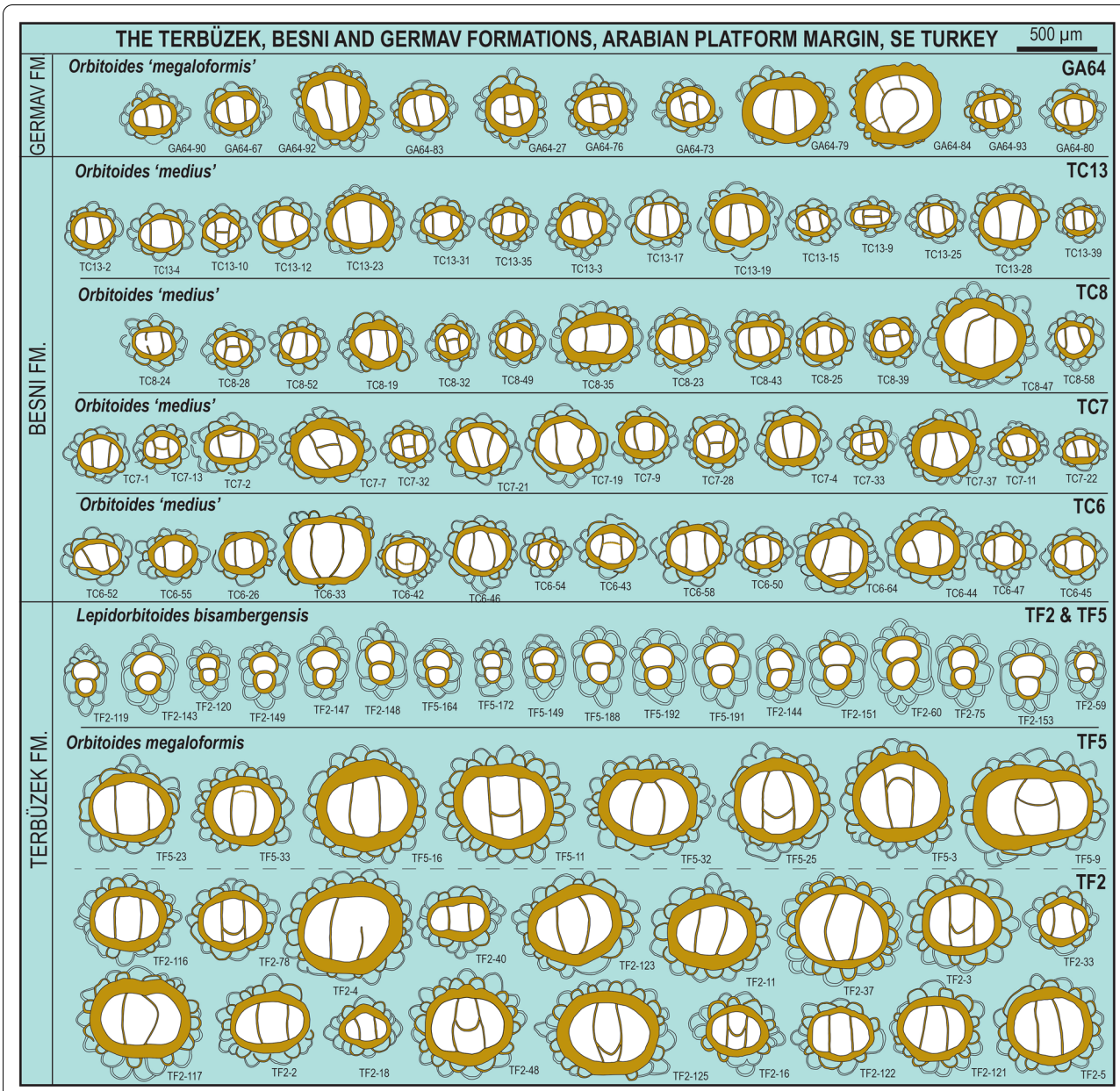

Fig. 19 Line drawings of the embryonic–nepionic stages of *Orbitoides* (and *Lepidorbitoides*) from the Terbüzek, Besni and Germav and formations, SE Turkey, Arabian Platform margin

of our flat to biconcave specimens (*O. pamiri*) with *O. medius* from the upper Campanian of Oman (Kayğılı et al. 2021) is given in Fig. 21. Both species have similar morphometric values for the size of the embryon and number of epi-embryonic chamberlets (Table 1). *O. medius* differs from *O. pamiri* in having biconvex tests, numerous lateral chamberlets and a thinner equatorial layer.

Based on the above data, we assert that biconvex and flat to biconcave *Orbitoides* populations from the upper Maastrichtian of Central Sakarya Basin and Taurides do not belong to the main *Orbitoides* evolutionary lineage. We think that *O. 'medius'* and *O. pamiri* represent offshoots from the main lineage in the Maastrichtian (Fig. 23), forming side-lines to the main lineage. These offshoots probably took place at levels corresponding to *L. minor* and/or *L. socialis* in the Maastrichtian since the record of the genus until the level with *L. bisambergensis* appears to be consistent with the species succession of *O. medius–O. megaloformis–O. gruenbachensis* in the Tethys. Well-dated Campanian deposits in two

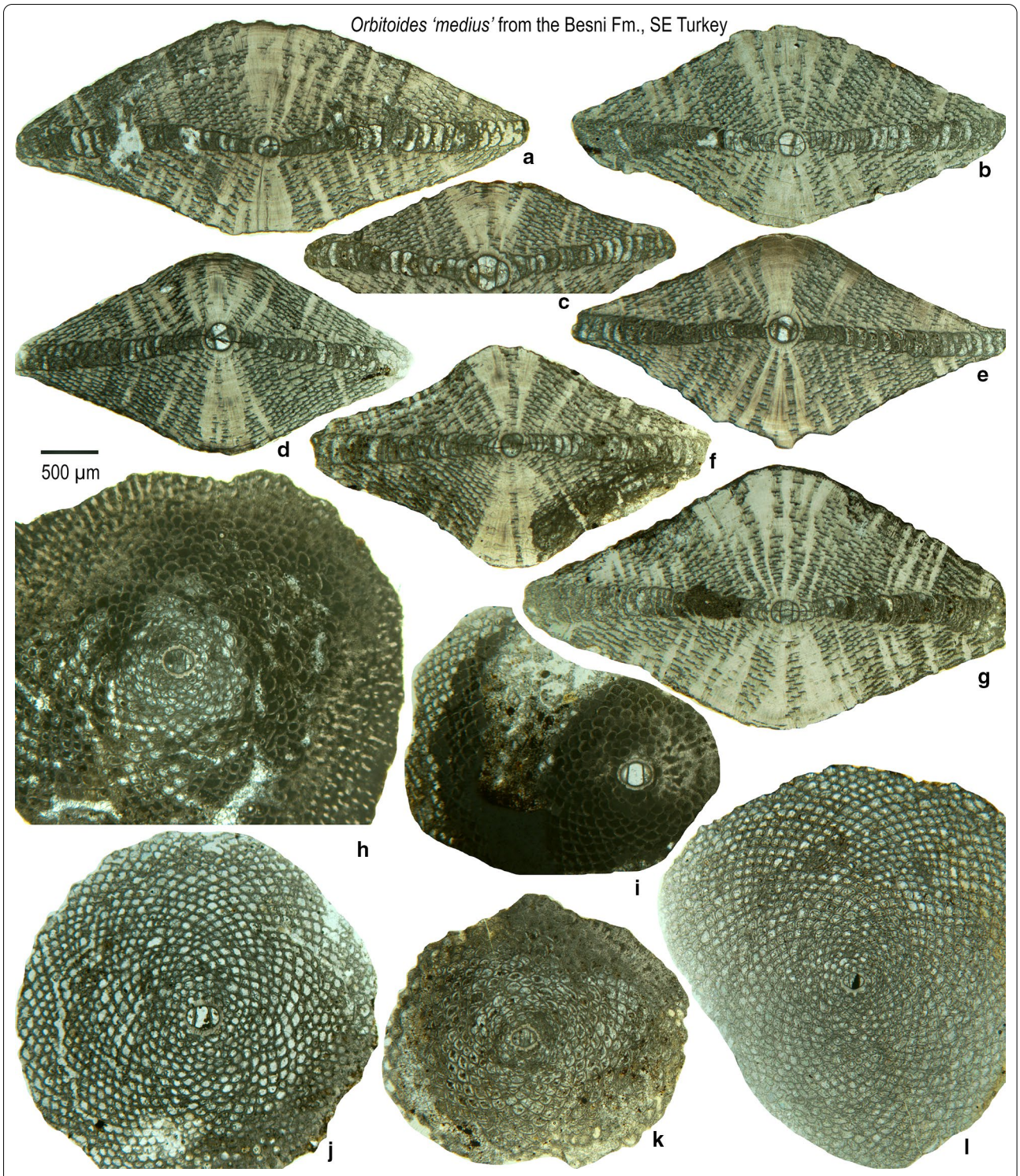

Fig. 20 Axial (**a**–**g**) and equatorial (**h**–**l**) sections of *Orbitoides 'medius'* from the Besni Formation in SE Turkey. Note the biconvex test with numerous cycles of lateral chamberlets and thick polar piles, and a thick equatorial layer. **a** TC7-47. **b** TC7-48. **c** TC7-43. **d** TC7-50. **e** TC7-44. **f** TC13-48. **g** TC13-47. **h** TC13-40. **i** TC8-78, **j** TC8-79. **k** TC13-43. **l** TC8-81

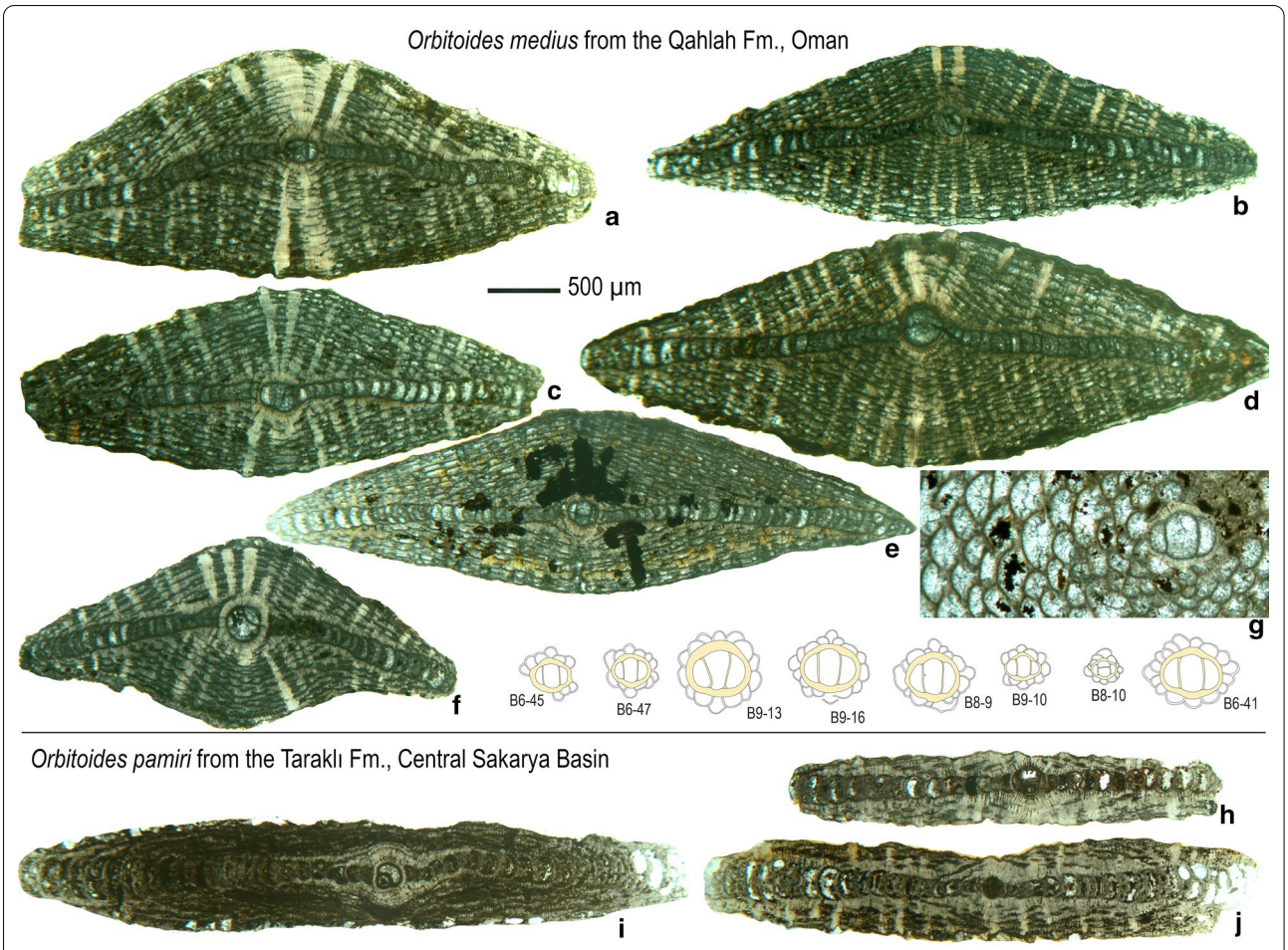

Fig. 21 Comparison of the axial and near axial sections of the upper Campanian *Orbitoides medius* from the Qahlah Formation from Oman (**a–f**) and *O. pamiri* from the upper Maastrichtian Taraklı Formation (**h–j**). An equatorial section of *O. medius* is shown in (**g**). Line drawings of the embryonic-nepionic stages of some *O. medius* specimens are also illustrated. Note that specimens from the Qahlah Formation are invariably biconvex and consist of numerous cycles of lateral chamberlets, whereas those from the Taraklı Formation (*O. pamiri*) are flat to biconcave with few cycles of lateral chamberlets. Refer to Kayğılı et al. (2021) for the detailed description of *O. medius* from Qahlah Formation. **a** B6-10. **b** B6-20. **c** B6-11. **d** B6-14. **e** B6-22. **f** B6-19, **g** B8-8. **h** EPB5-5. **i** EPB5-2. **j** EPB5-20

localities in Turkey yielded data consistent with this scheme. *Helicorbitoides voigti* van Gorsel and *Pseudosiderolites vidali* (Douvillé) recorded from the Tonya Formation in NE Turkey are associated with *O. medius* (Özcan et al. 2019), and *O. megaloformis* (Erdem et al. 2021), consistent with the record at the Campanian type section at Aubeterre. Caus et al. (1996) reported an *O. gruenbachensis* population from Maurens (Spain) associated with *L. bisambergensis*. This population does not contain *O. medius*-type embryons. We think that these inconsistent variations and widespread and common occurrence of flat to biconcave tests in at least two geographically separate regions in Turkey cannot simply be explained by environmentally induced morphological changes.

The principle of nepionic–embryonic acceleration demonstrated in many orbitoidal groups (Drooger, 1993) is also applicable in *Orbitoides* as recorded from single and separate sections from the late Santonian–Maastrichtian time interval in Western Europe. Nonetheless, our data also imply the significance of test features not only related with the equatorial layer but also lateral layers and overall test morphology in general. The biconvex specimens from the upper Maastrichtian of the Haymana Basin in Central Turkey were provisionally assigned to *O. 'medius'* because of their great resemblance to this species on the morphometric grounds (Özcan & Özkan-Altıner, 1997) and their distinction as a separate species from *O. pamiri* requires a detailed study.

Fig. 22 Equatorial sections of *O. gensacicus* (**a–b**) and *O. 'medius'* (**c–e**) from the Simsima Formation in the Buraymi region, Oman. **a** B28-27. **b** B32-9. **c** B32-20. **d** B32-8. **e** B28-50

Conclusions

The hypothesis that a distinct separate lineage of Maastrichtian *Orbitoides* occurs in addition to the classic lineage formed by progressive evolution of key biometric characteristics (notable E and Li + li) is supported by:

1. In Maastrichtian-aged sediments of the Besni Formation of Southeastern Turkey, *Orbitoides* biometrically similar to *O. medius* occur, overlying the Terbüzek Formation with *O. megaloformis*, and underlying the Germav Formation with *O. megaloformis* and possible *O. apiculatus*. We refer to such forms with the informal name *O. 'medius'*, to indicate that whilst they are very similar to *O. medius* in morphometric terms they represent a distinctively young retrograde or perhaps long-lived lineage that requires further study.
2. Within the Taraklı Formation of the Central Sakarya Basin, large biconvex specimens, with relatively large, complex embryons, referable to *O.* ex. interc. *gruenbachensis–apiculatus*, occur alongside flat-biconcave *Orbitoides*, with relatively small simple embryons in the biometric range of *O. medius.* We refer these to the overlooked species *O. pamiri* on the distinctive combination of morphology and embryon size and complexity.
3. Limited records of probable *O. 'medius'* occurring alongside *O. apiculatus* are also known from the Maastrichtian sediments of the Haymana Basin of Central Turkey.

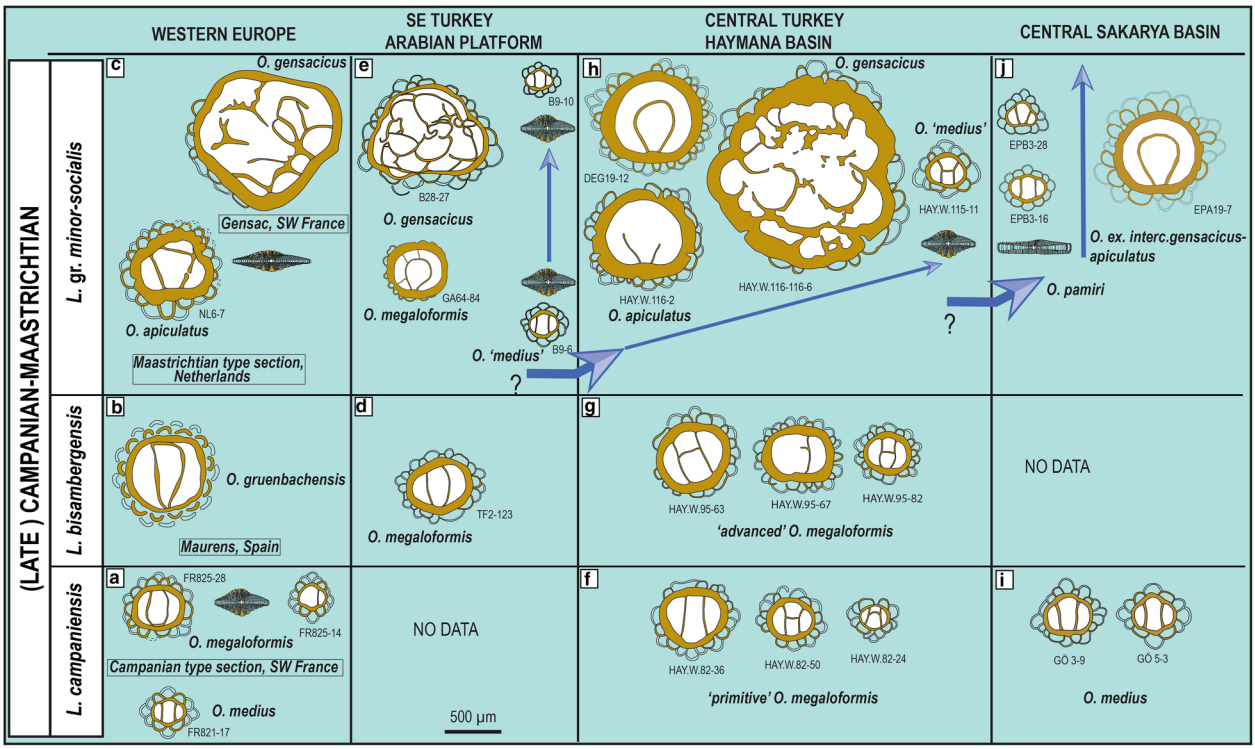

Fig. 23 Panel showing the tentative relations of *Orbitoides* species from the late Campanian to late Maastrichtian along the Arabian Plate margin, Turkey and Western Europe. Arrows show possible offshoots from the main *Orbitoides* lineage in the Maastrichtian, represented by *O. 'medius'* and *O. pamiri*. *Orbitoides gensacicus* from Gensac is not into scale. Data from Campanian and Maastrichtian type sections and from Gensac (SW France) are from van Hinte (1966b) and Eggink and Baumfalk (1983). The *O. gruenbachensis* population from Maurens, Spain is from Caus et al. (1996). The prefix 'GÖ' is for *Orbitoides medius* populations from the upper Campanian of the Central Sakarya Basin (unpublished data of EÖ and AOY). Details of samples HAY.W.82, 95, 115, 116 from the Haymana Basin are given in Özcan and Özkan-Altıner (1997)

4. *O. medius* is known from the Campanian Qahalah Formation of Oman, whilst the overlying Maastrichtian Simsima Formation yields *O. 'medius'*.

The recognition of *O. 'medius'* in undoubtedly Maastrichtian strata invites investigation of past records of *O. medius*. For example, this species has often been reported from Maastrichtian strata in the Middle East (e.g. Payandeh et al. 2019; Rahaghi, 1976; Schlagintweit et al. 2016) and Italy (Chiocchini et al. 2012). These records need to be re-examined to assess whether (i) these occurrences can be verified as *O. medius*; and (ii) if they are genuine Maastrichtian records.

Retrograde evolution within *Orbitoides* has been reported previously from the Caribbean bioprovince. There Mitchell (2005) reports the occurrence in uppermost Maastrichtian strata of a form he terms "*Orbitoides* cf. *megaloformis*". Biometrically, this taxon would appear very similar to *O. megaloformis* from typically upper Campanian strata (Fig. 7). This could be a further example of parallel lineages of *Orbitoides* occurring in the Maastrichtian, although it should be noted that the Caribbean is a separate bioprovince from the Mediterranean and Arabian Tethys (Goldbeck, 2007).

The recognition of multiple lineages of Maastrichtian *Orbitoides* requires the integration of both morphometric analysis of embryon features coupled with consideration of external morphologies, that can be demonstrated not be simply ecophenotypic. Hence, a combination of morphometric and typological approaches can be beneficial for recognising the speciation of Late Cretaceous *Orbitoides* and identifying parallel evolutionary lineages.

Appendix

Taxonomic list of the calcareous nannofossils recognised in the samples from Epçeler and Dereköy sections. All the references below are reported in http://www.mikrotax.org/Nannotax3

Arkhangelskiella cymbiformis Vekshina, 1959.

Biscutum constans (Górka, 1957) Black in Black and Barnes, 1959.

Biscutum ellipticum (Górka, 1957) Grün in Grün and Allemann, 1975.

Ceratolithoides aculeus (Stradner, 1961) Prins and Sissingh in Sissingh, 1977

Chiastozygus Gartner, 1968.

Cribrocorona gallica (Stradner, 1963) Perch-Nielsen, 1973.

Cribrosphaerella ehrenbergii (Arkhangelsky, 1912) Deflandre in Piveteau, 1952.

Cyclagelosphaera reinhardtii (Perch-Nielsen, 1968) Romein, 1977.

Eiffellithus gorkae Reinhardt, 1965.

Eiffellithus turriseiffelii (Deflandre in Deflandre and Fert, 1954) Reinhardt, 1965.

Lithraphidites quadratus Bramlette and Martini, 1964.

Lithraphidites praequadratus Roth, 1978

Markalius inversus (Deflandre in Deflandre and Fert, 1954) Bramlette and Martini, 1964.

Microrhabdulus decoratus Deflandre, 1959.

Micula concava (Stradner *in* Martini and Stradner, 1960) Verbeek, 1976.

Micula praemurus (Bukry, 1973) Stradner and Steinmetz, 1984.

Micula staurophora (Gardet, 1955) Stradner, 1963.

Micula swastica Stradner and Steinmetz, 1984.

Prediscosphaera cretacea (Arkhangelsky, 1912) Gartner, 1968.

Prediscosphaera ponticula (Bukry, 1969) Perch-Nielsen, 1984.

Retecapsa angustiforata Black, 1971.

Retecapsa crenulata (Bramlette and Martini, 1964) Grün in Grün and Allemann, 1975.

Russellia bukryi Risatti, 1973.

Zeugrhabdotus Reinhardt, 1965.

Watznaueria barnesiae (Black in Black and Barnes, 1959) Perch-Nielsen, 1968.

Watznaueria fossacincta (Black, 1971) Bown in Bown and Cooper, 1989.

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Authors' contributions
EÖ: conceptualization, methodology, investigation, sampling in Turkey and Oman, supervision, and writing original draft. AOY: sampling in Turkey, investigation, and resources. RC: investigation (study of calcareous nannofossils) and visualisation. SK: investigation (study of larger forams). AIO: field work in Central Sakarya Basin and sample collection. MDS: conceptualization and writing original draft. JP: conceptualization and writing original draft. İAA: sampling in Oman. ÜE: sampling in Central Sakarya Basin. All the authors read and approved the final manuscript.

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Availability of data and materials
All thin sections and oriented sections are deposited in the Palaeontology Section of the Department of Geological Engineering (İstanbul Technical University).

Declarations

Competing interests
We report no potential conflict of interest.

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