

Oligocene crabs (Decapoda: Brachyura) from the Asmari Formation in Yasuj area (SW Iran)

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ABSTRACT:

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New findings of crustacean decapod brachyurans from the Rupelian period (lower Oligocene) in Iran are presented in this study. In particular, *Lophoranina* sp. and *Palaeocarpilius* cf. *P. rugifer* Stoliczka, 1871, from the Rupelian strata were found in two previously unexplored localities, Abshar and Vezg near Yasuj in the southwestern region of Iran. The discovery contributes to fill the gap in the record of brachyuran decapod crustaceans in Iran during the Eocene and Miocene periods. The presence of both genera in the Oligocene of Iran suggests a certain degree of faunal similarity among brachyurans on both sides of the Tethys Realm.

Key words: Paleogene; Rupelian; Tethys; Brachyura; *Palaeocarpilius*; *Lophoranina*.

INTRODUCTION

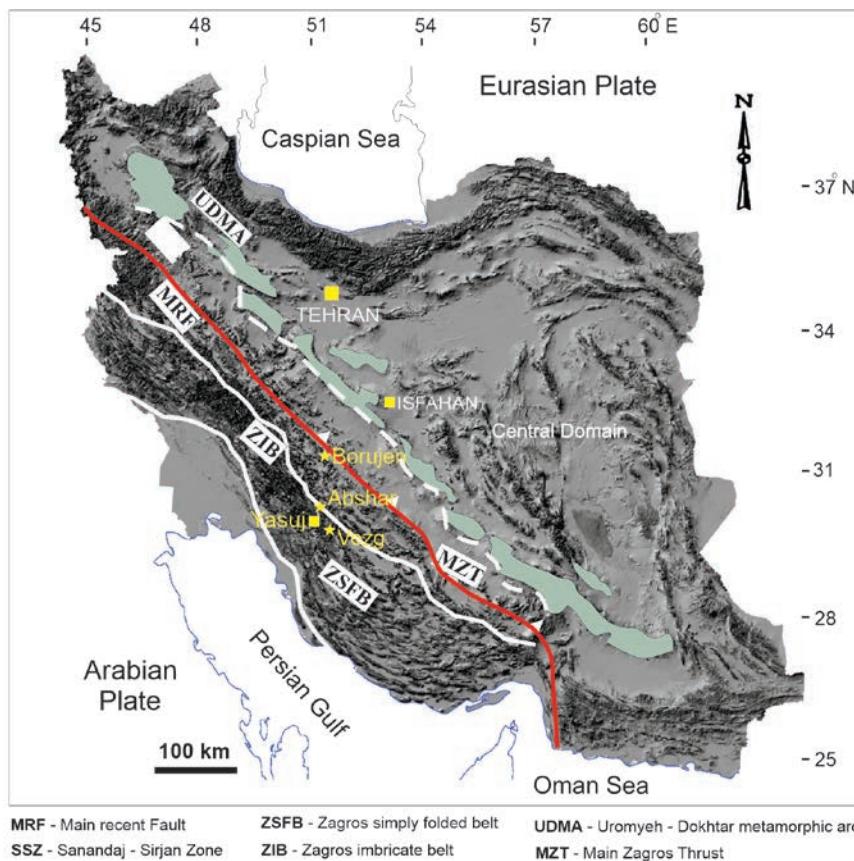
The presence of Paleogene brachyuran decapod crustaceans in Iran is poorly documented. Previous reports by Withers (1932) mention the remains of *Zanthopsis* M'Coy, 1849, and describe *Lophoranina persica* from Eocene deposits in western and southwestern Iran, respectively. In addition, Khodaverdi Hassan-Vand *et al.* (2016) report the occurrence of *Retrocypoda almelai* Vía Boada, 1959, in the middle Eocene of the Isfahan region, previously known only from the westernmost Tethys. Recently, Ossó *et al.* (2023) confirmed the presence of *Zanthopsis* in the lower Eocene of the same region, emphasizing its affinities with the western Tethys. This is in contrast to the extensive studies conducted on the Neogene brachyuran faunas of Iran (e.g., Glaessner 1933; Vega *et al.* 2010a, 2012; Heidari *et al.* 2012; Hyžný *et al.* 2021).

The aim of this paper is to present the first report of brachyuran decapod crustaceans from the

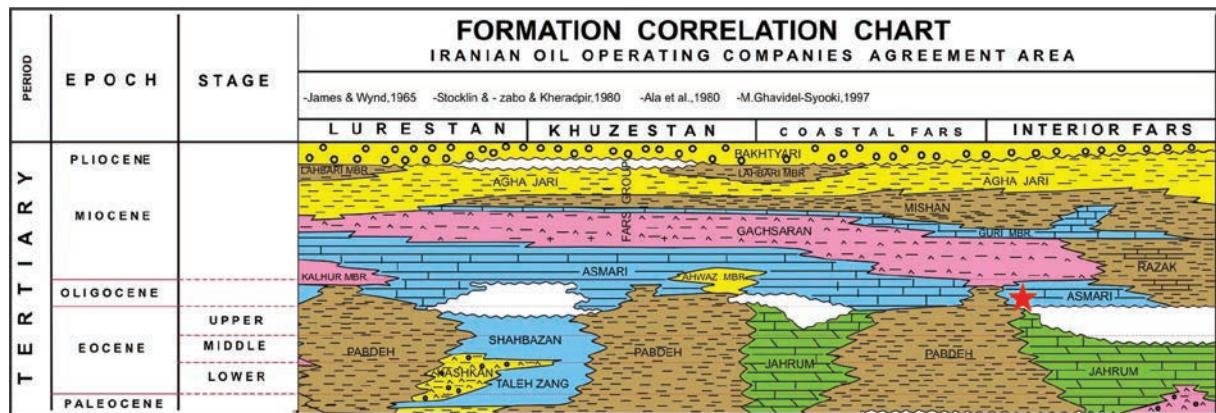
Asmari Formation in Iran and to discuss their paleobiogeographic implications. The discovery of brachyuran decapods in the Oligocene exposures of the Asmari Formation fills the gap in the faunal record between the early Paleogene and the Neogene in the region.

GEOLOGICAL SETTING

The Asmari Formation in SW Iran contains most of Iran's recoverable oil reservoirs, which are mainly trapped in large anticlines in the Zagros Mountains (McQuillan 1974). The Zagros fold-and-thrust belt is part of the Alpine-Himalayan system and extends from the NW Iranian border through SE Iran to the Strait of Hormuz (Heydari *et al.* 2003). In the type section at Tang-e Gel-e Tursch (Valley of Sour Earth) on the south-western flank of the Kuh-e Asmari Anticline, the Asmari Formation consists of 314 m of mainly limestones, dolomitic



Text-fig. 1. General map of Iran showing eight geological provinces (adapted from Heydari *et al.* 2003).

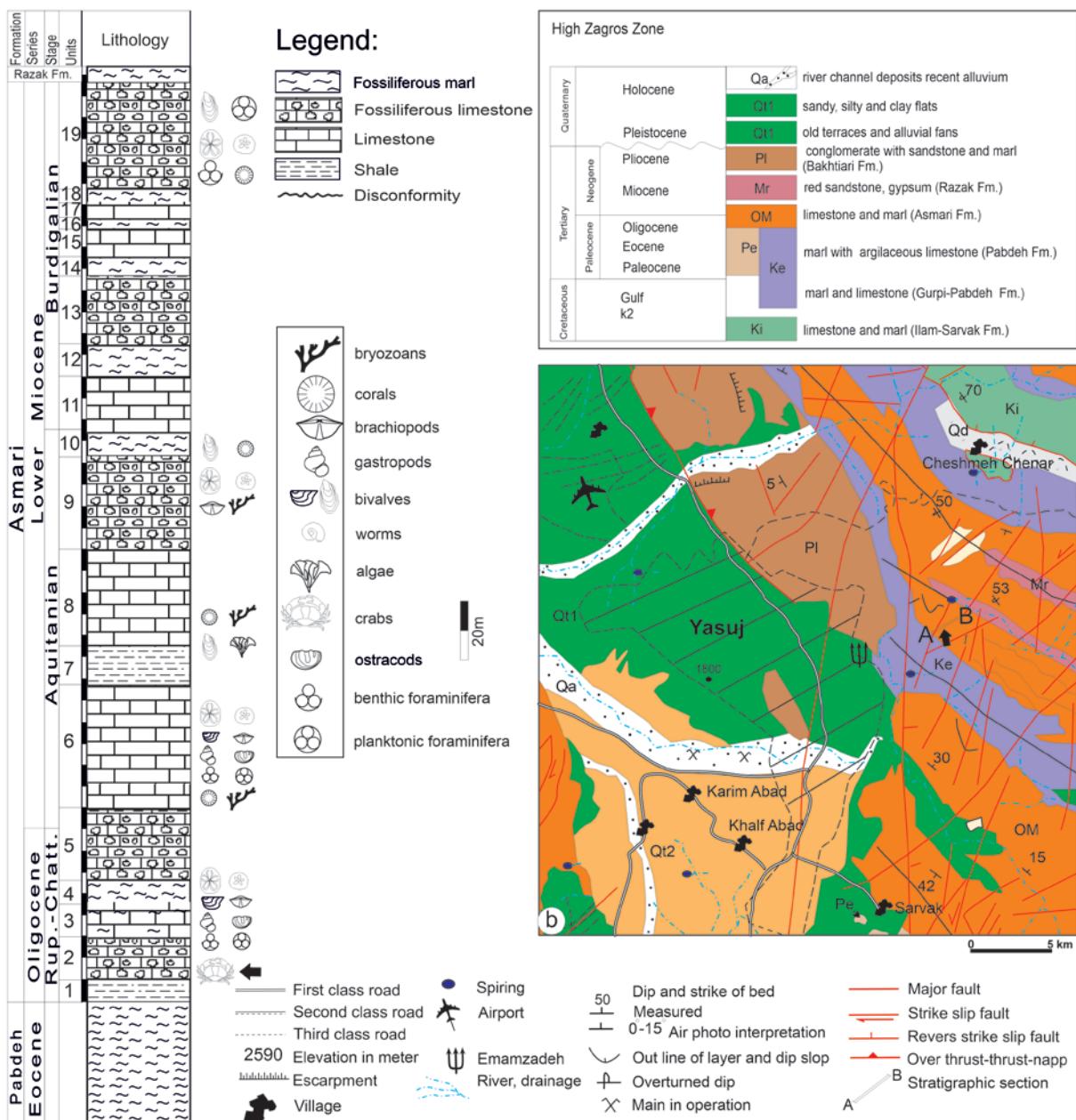


Text-fig. 2. Cenozoic stratigraphic correlation chart of the Iranian Sector of the Zagros Basin; modified from James and Wynd (1965). Red star indicates the study area.

limestones, and argillaceous limestones (James and Wynd 1965). An Oligocene (Rupelian) to early Miocene (Burdigalian) age has been assigned to the formation based mainly on foraminiferal zones and strontium isotope stratigraphy (Lees 1933; Thomas 1950; James and Wynd 1965; Wynd 1965; Adams and Bourgeois 1967; Adams 1969; Ehrenberg *et al.*

2007; Laursen *et al.* 2009; Van Buchem *et al.* 2010; Text-figs 1 and 2).

This study is based on two outcrop sections of the Asmari Formation at Abshar and Vezg (about 35 km apart) in the Zagros fold-and-thrust-belt (Text-fig. 1). The Abshar section ($30^{\circ}40'35.70''N$, $51^{\circ}37'40.67''E$) is located about 3 km northwest of the city of Yasuj.



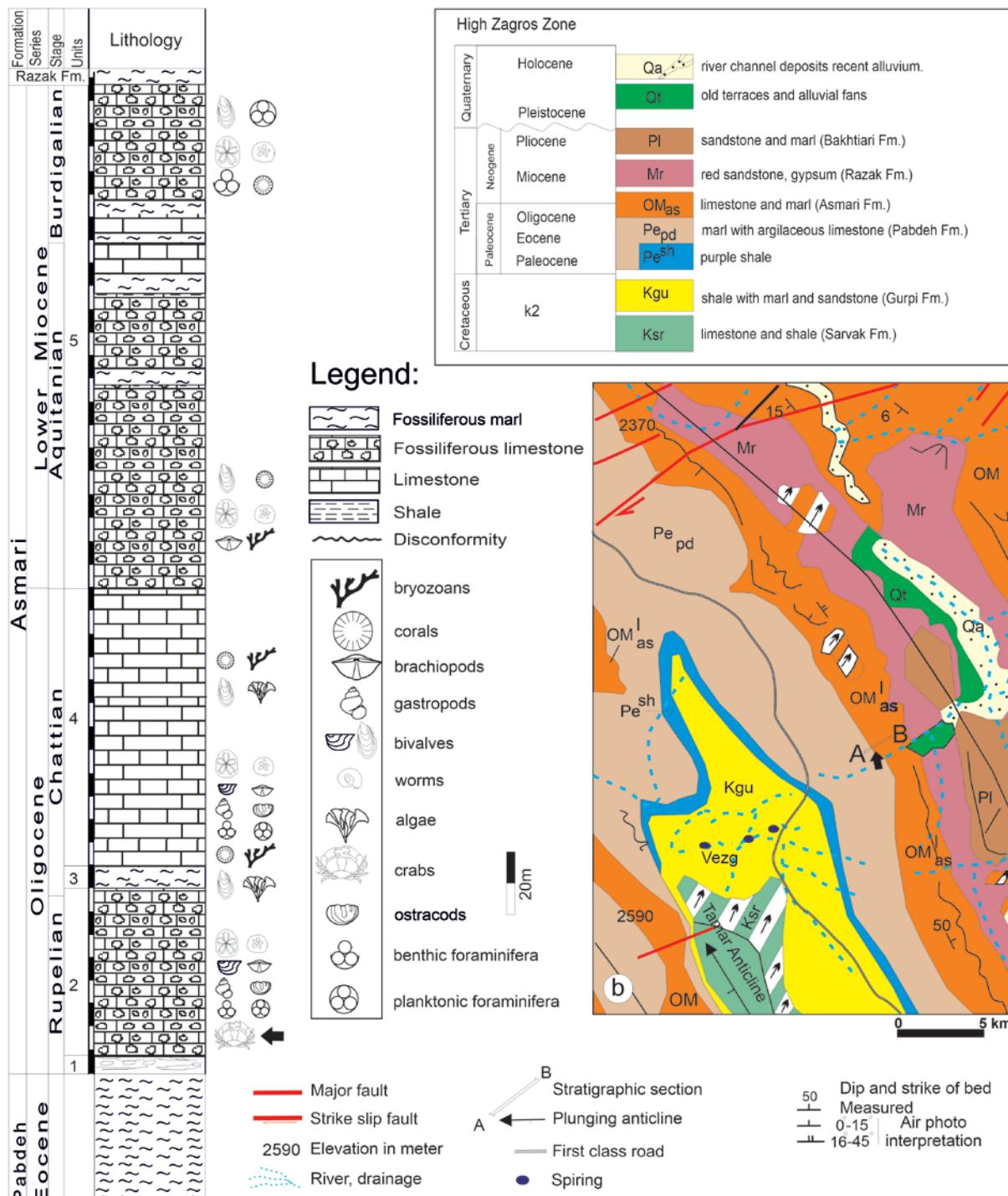
Text-fig. 3. Stratigraphical column of the Abshar section (left) and geological map of the study area (right); modified from Sedaghat and Shaverdi (1975).

The Vezg section ($36^{\circ}33'10.77''N$, $51^{\circ}40'43.13''E$) is located about 15 km southeast of the city of Yasuj (approximately 3 km northeast of Vezg village; Text-figs 3 and 4).

Abshar section

The thickness of the section measured at Abshar (Text-fig. 2) is 420 m, and consists of dolomitized

marly limestones of the Pabdeh Formation at the base overlain by the Asmari Formation. Here, the Asmari Formation is characterized by marls, limestones, marly limestones and dolomitic limestones. The contacts of the Asmari Formation and both the underlying Pabdeh Formation and the overlying Razak Formation are conformable (Text-fig. 3). *Lophoranina* beds occur in the fossiliferous limestones at the base of the Asmari Formation.

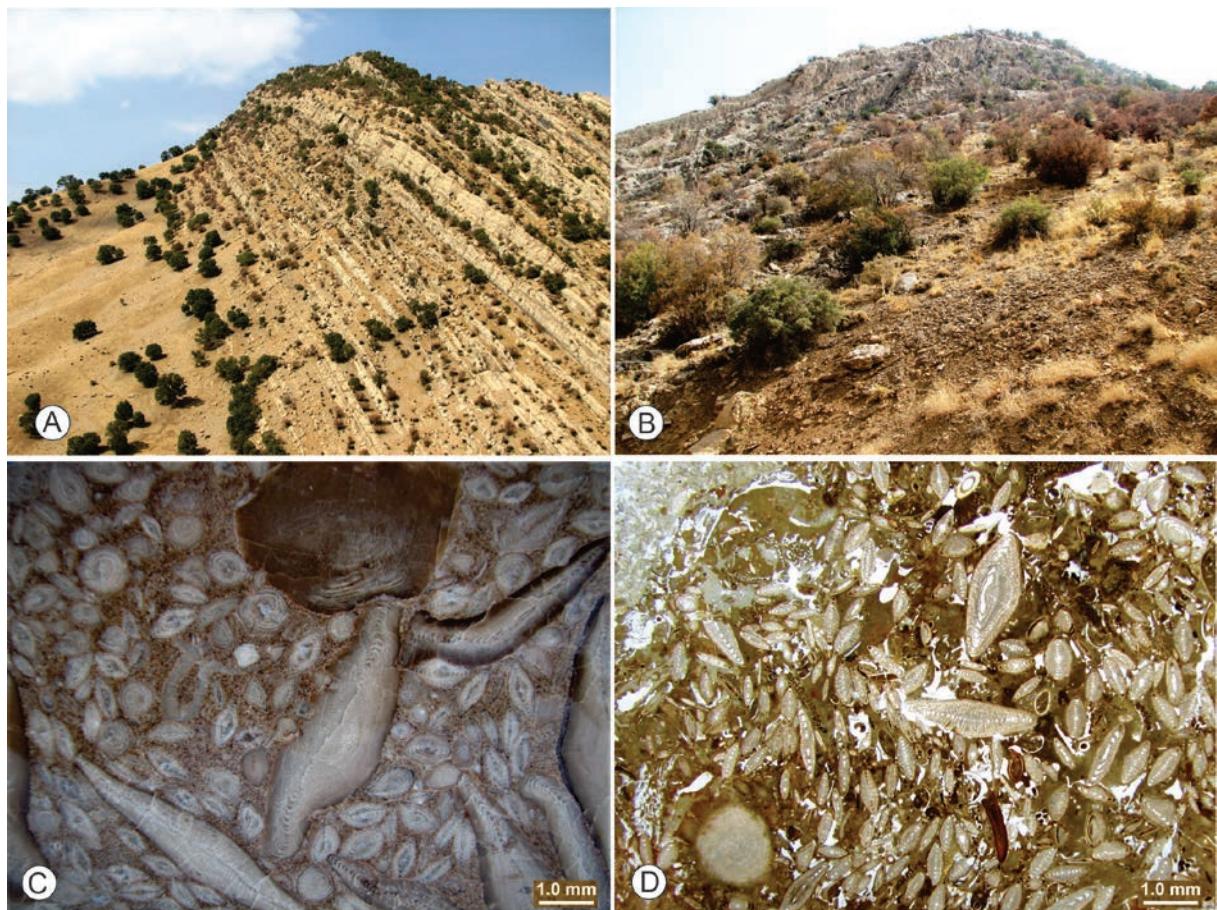


Text-fig. 4. Stratigraphic column of the Vezg section (left) (from Ansari 2005) and geological map of the study area (right); modified from Sedaghat and Shaverdi (1975).

Vezg section

The Asmari Formation is characterized by limestones, dolomitic limestones, marly limestones and

sandy limestones. Its contact with the underlying Pabdeh Formation is transitional and conformable, and the upper contact with the overlying Razak Formation is conformable. Deposits of the Asmari



Text-fig. 5. Vezg section. A – lower boundary of the Asmari Formation (limestone) with the Pabdeh Formation (shale and marl); B – upper boundary with the Razak Formation; C, D – thin sections showing benthic foraminifera (*Nummulites fichteli* Michelotti, 1841 and *Nummulites intermedius* Schaub, 1981) of the Abshar and Vezg sections, respectively.

Formation in this section are very well preserved with almost original characteristics and thicknesses due to minimal diagenesis, compaction and tectonism (Text-figs 4 and 5). The *Palaeocarpilius* bed occurs in the basal levels of the Asmari Formation.

MATERIAL AND METHODS

The studied material was recovered from the surface, as *ex situ*, in the basal units of the Asmari Formation in the Abshar and Vezg sections, and was photographed with a NIKON D5600 camera.

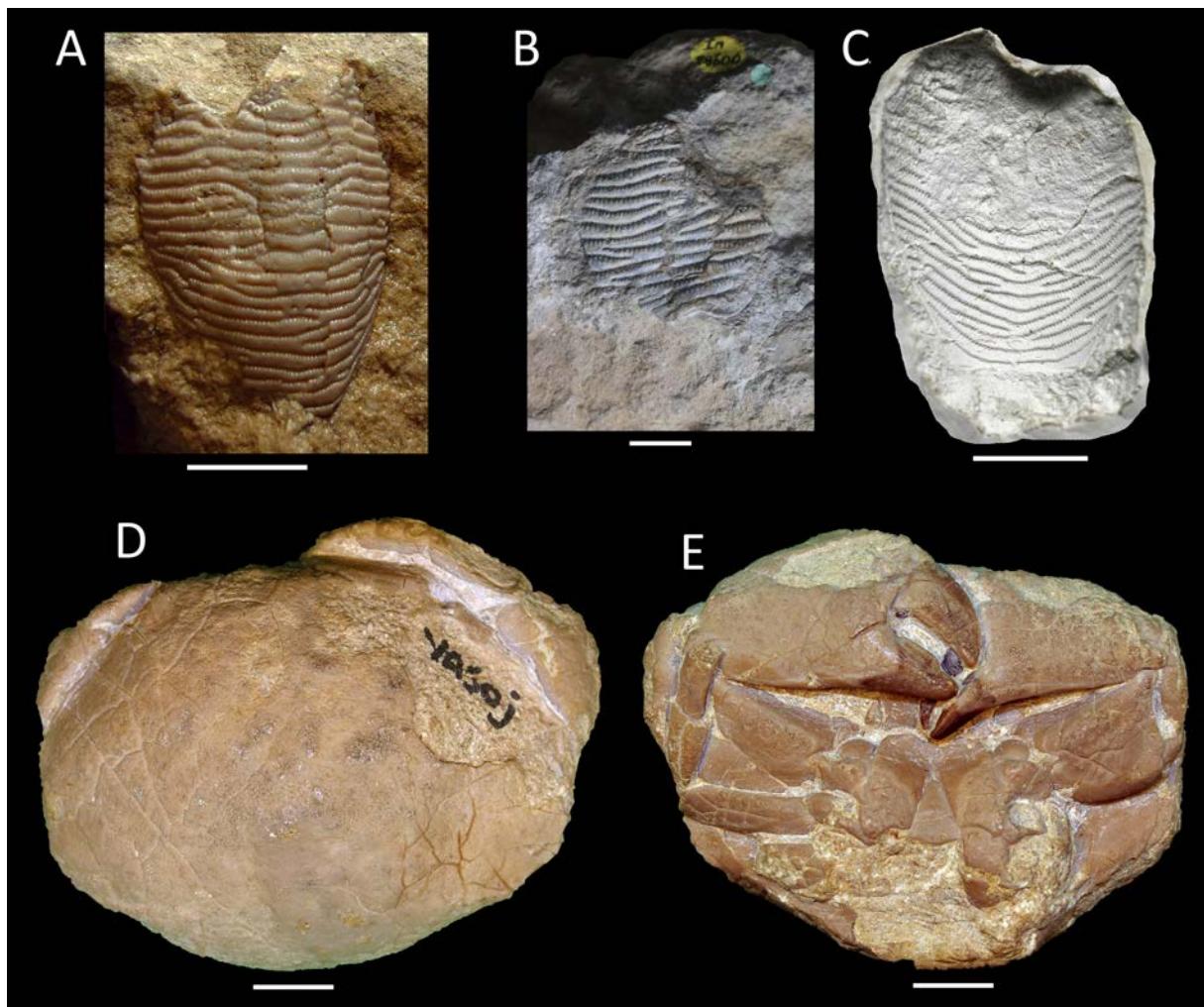
Repositories and abbreviations: UIGM – University of Isfahan Geology Museum, Isfahan, Iran; NHMUK – Natural History Museum, London, United Kingdom.

SYSTEMATIC PALAEONTOLOGY

- Order Decapoda Latreille, 1802
- Infraorder Brachyura Linnæus, 1758
- Superfamily Raninoidea De Haan, 1839
- Family Raninidae De Haan, 1839
- Subfamily Ranininae De Haan, 1839
- Genus *Lophoranina* Fabiani, 1910

TYPE SPECIES: *Ranina marestiana* König, 1825.

SPECIES INCLUDED (after Karasawa *et al.* 2014): *L. aculeata* (A. Milne-Edwards, 1881); *L. albeshtensis* Schweitzer, Feldmann and Lazăr, 2009; *L. aldrovandii* (Ranzani, 1820); *L. bakeri* (A. Milne-Edwards, 1872); *L. barroisi* (Brocchi, 1877); *L. bishopi* Squires and Demetrian, 1992; *L. bittneri* (Lörenthey, 1902); *L. cinquecrista* Feldmann, Schweitzer, Bennett, Fran-



Text-fig. 6. Eocene and Oligocene crabs from different areas discussed in text. **A** – *Lophoranina* sp., UIGM 1017, in dorsal view, from the Rupelian of Vezg section (SW Iran); **B** – *Lophoranina persica* Withers, 1932, NHMUK 28600, in dorsal view, from the Eocene of Borujen (SW Iran); **C** – *Lophoranina bakeri* (A. Milne-Edwards, 1863), NHMUK 23283, in dorsal view (latex cast of holotype), from the Eocene of Sindh (Pakistan); **D, E** – *Palaeocarpilius* cf. *P. rugifer* Stoliczka, 1871, UIGM 1016, from the Rupelian of Abshar section (SW Iran); in dorsal (D) and ventral view (E). Scale bar equals 10 mm (B and C photographed by Rich Howard NHMUK).

tescu, Resar and Trudeau, 2011; *L. cristaspina* Vega, Cosma, Coutiño, Feldmann, Schweitzer and Waugh, 2001; *L. georgiana* (Rathbun, 1935); *L. kemmelingi* Van Straelen, 1924 [imprint 1923]; *L. laevifrons* (Bittner, 1875); *L. levantina* Lewy, 1977; *L. maxima* Beschin, Busulini, De Angeli and Tessier, 2004; *L. persica* Withers, 1932; *L. porifera* (Woodward, 1866); *L. quinquespinosa* (Rathbun, 1945); *L. raynorae* Blow and Manning, 1996; *L. reussi* (Woodward, 1866); *L. rossi* Blow and Manning, 1996; *L. soembaensis* Van Straelen, 1938; *L. straeleni* Vía Boada, 1959; *L. tchihatcheffi* (A. Milne-Edwards, 1866); *L. toyosimai* Yabe and Sugiyama, 1935.

Lophoranina sp.
(Text-fig. 6A)

MATERIAL AND MEASUREMENTS: One dorsal carapace, partially preserved, embedded in limestone matrix. Carapace length = 29 mm; carapace width = 20.6 mm.

DESCRIPTION: Carapace longitudinally ovate in outline, longer than wide, L/W ratio about 1.35, maximum width at anterior third of carapace. Dorsal surface crossed by about twenty transverse parallel terraces with finely toothed upper margin; terraces slightly sig-

moidal in the first half of carapace, gently downward curved medially and strongly oblique laterally in the posterior half of the carapace; terraces randomly and irregularly bifurcated mainly in the posterior half of the carapace. Three terraces between branchiocardiac grooves straight, parallel. Regions undefined. Rostrum not preserved; post-frontal region incomplete, appears to be scabrously ornamented; remains of right orbit with visible supraorbital fissure and acute anteriorly directed outer orbital spine. Anterolateral margin with two anteriorly directed spines. Posterolateral and posterior margins with fine margins. Posterolateral corners rounded.

REMARKS: The Abshar specimen is confidently assigned to *Lophoranina* on the basis of its longitudinally ovate carapace crossed by the characteristic transverse dentate terraces, diagnostic of the genus. However, the lack of rostrum and post-frontal regions makes the specific placement of the reported specimen difficult.

Withers (1932, pp. 469, 470, 34, pl. 12, fig. 1) described *Lophoranina persica* from the Eocene beds of Borujen, also in SW of Iran (see Text-fig. 1). Comparison with the images of the holotype and the single specimen provided by the NHMUK (Text-fig. 6B) reveals clear differences between this species and the specimen examined here. Indeed, *Lophoranina persica*, a fragmentary specimen, has fewer terraces, which are much more widely spaced and more coarsely dentate than the Abshar specimen, and their posterolateral corners are also different.

Withers (1932, pp. 468, 469, pl. 12, figs 3–5) also redescribed *Lophoranina bakeri* from the Eocene of Sindh (Pakistan). Examination of images of a latex cast of the holotype from the NHMUK (Text-fig. 6C) shows similarities in the shape of its terraces and its dentition in the upper margin, as well as its posterolateral and posterior margins. However, this specimen of *Lophoranina bakeri* lacks the entire frontal and central portions of the anterior part of the carapace, making any comparison with the Iranian specimen inconclusive. The examination of the holotype of *Lophoranina tchihatcheffi* from the Eocene of Thrace (Turkey) in the collections of the MNHN (Paris, France) by one of us (AO, April 2023), shows some similarities with the studied specimen, especially regarding the post-frontal features and the shape of the fronto-orbital margin, but it differs in having the maximum width in the middle of the carapace, instead of in the anterior third as in the Iranian specimen; moreover, the eroded dorsal surface of the holotype prevents examination of the branchiocar-

diac grooves and the anterolateral spines, making the comparison results inconclusive (cf. Charbonnier and Garassino 2022, pp. 108, 109, fig. 201; <https://science.mnhn.fr/institution/mnhn/collection/f/item/b22421?listIndex=106>). *Lophoranina levantina*, from the middle Eocene of Israel, could not be studied because it was not possible to consult the work.

Lophoranina is one of the most species-rich genera of Raninidae (see Schweitzer *et al.* 2010, pp. 73, 74). Species characterization has usually been based on rostral and post-frontal characters, anterolateral spines and measurements, as well as the ambiguous shape and number of dorsal terraces. The Iranian specimen shows some similarities with several western Tethys species, such as the triangular and anteriorly directed first post-frontal terrace found in species such as *Lophoranina bittneri*, *L. laevifrons*, or *L. maxima* (see Beschin *et al.* 2011). However, given that the most diagnostic characters, such as the rostrum and the frontal and post-frontal regions, are not preserved in the Iranian specimen, we leave our specimen in open nomenclature.

Section Eubrachyura de Saint Laurent, 1980

Subsection Heterotremata Guinot, 1977

Superfamily Carpilioidea Ortmann, 1893

Family Carpiliidae Ortmann, 1893

Genus *Palaeocarpilius* A. Milne-Edwards, 1862

TYPE SPECIES: *Cancer macrochelus* Desmarest, 1822, by original designation.

SPECIES INCLUDED: *Palaeocarpilius aquitanicus* A. Milne-Edwards, 1862; *P. ignotus* A. Milne-Edwards, 1862 (finger only); *P. intermedius* Stubblefield, 1927; *P. laevis* Imaizumi, 1939; *P. macrochelus* (Desmarest, 1822); *P. mississippiensis* (Rathbun, 1935); *P. rugifer* Stoliczka, 1871; *P. valrovinensis* (De Gregorio, 1895).

Palaeocarpilius cf. *P. rugifer* Stoliczka, 1871

(Text-fig. 6D, E)

MATERIAL AND MEASUREMENTS: One weathered carapace showing dorsal and ventral sides. Carapace length = 53 mm; carapace width = 69 mm.

DESCRIPTION: Carapace transversely ovate, wider than long, L/W ratio about 0.75, maximum width beyond the posterior third; convex in both senses, appears smooth; regions not defined; short transverse ridges extending from the level of the epibranchial teeth. Front triangular, strongly deflexed, about 0.45

of carapace width. Fronto-orbital margin about 0.65 of carapace width. Orbita rounded, small. Anterolateral margins strongly convex, teeth not preserved. Posterolateral margin slightly concave. Posterior margin straight, slightly convex, about 0.37 of carapace width. Male thoracic sternum narrow; thoracic sternite 3 subtrapezoidal, depressed medially; sternite 4 subtrapezoidal, strongly divided longitudinally by sternopleonal cavity; sternite 5 subtrapezoidal, short, posteriorly directed. Episternites 4 and 5 inclined posteriorly. Suture 3/4 defined by weak transverse groove; suture 4/5 complete. Sternopleonal cavity deep, narrow, reaching suture 3/4. Telson of male pleon narrow, elongate, subtriangular, rounded tip. Chelipeds strong, distinctly heterochelous. Ischium appears to be fused with merus. Carpus robust. Right propodus very strong, distinctly subtrapezoidal, upper margin armed with remains of blunt spines; lower margin with longitudinal ridge; dactylus strong, curved, with proximal flattened molariform tooth; pollex strong, short, with medial flattened molariform tooth. Left propodus subtrapezoidal, elongated, longer and not as high as right propodus, proximal outer surface appears to bear remains of spines near carpo-propodial articulation; dactyli slender. Ambulatory leg relatively long and flattened.

REMARKS: Although the dorsal surface of the carapace of the Vezg specimen is weathered and eroded, its ovate outline, smooth and vaulted surface, strong heterochelous chelipeds and characteristic sternum allow us to assign it with confidence to the genus *Palaeocarpilius* (e.g., Beschin and De Angeli 2006, pp. 11–23, figs 1–5, t. 1–4). The lack of specific diagnostic characters, such as the anterolateral teeth or the spines of the upper margin of the palm of propodi, prevents us from counting them and thus blurs their specific placement.

However, if compared with the ubiquitous *Palaeocarpilius macrochelus*, present on both sides of the Tethys Realm during the middle Eocene to Oligocene, in northern Europe (see Smelror and Ossó 2016) and the Middle East (e.g., Aly 2019, fig. 4), some differences are evident. For example, *Palaeocarpilius macrochelus* has a carapace that is longitudinally more vaulted than the Iranian specimen, as well as a smoother outer side of the palms, while the studied specimen appears to have the remains of spines near the carpo-propodial articulation of the palm. This is also the case for species of some genera previously placed in the genus *Palaeocarpilius* (see Feldmann et al. 2011, t. 2).

On the contrary, another *Palaeocarpilius* spe-

cies, *P. rugifer*, already reported from the Oligocene of nearby regions such as India and Pakistan (e.g., Stoliczka 1871; Vega et al. 2010b), and also present in the lower Miocene of Iran (Hyžný et al. 2021), shows more morphological affinities with the described specimen. For example, its carapace seems to be less vaulted longitudinally than in other species, such as the Iranian specimen. Also, the studied specimen preserves some remains of spines at the proximal end of the left palm, near the carpo-propodial articulation (Text-fig. 6B), as does *Palaeocarpilius rugifer* (cf. Stoliczka 1871, pl. 5, 3). However, other diagnostic characters such as the rugose surface of the carapace, the spines in the upper and outer margins of the palms, or the three characteristic spines on the carpus (Stoliczka 1871, pl. 4, figs 1, 3, 6, pl. 5, figs 2, 3), cannot be observed due to the eroded state of the specimen. The assignment of our specimen to this species is therefore only tentative.

DISCUSSION

The genus *Lophoranina* has been found over a wide geographical range, from the Ypresian (early Eocene) to the Miocene, along the Tethys Sea (e.g., Beschin et al. 2011), the Pacific (Squires and Demetrio 1992), the Atlantic coast of North America (Blow and Manning 1996), in the Caribbean (Vega et al. 2001; Luque et al. 2017), and the Indo-Pacific (Yabe and Sugiyama 1935). Similarly, the genus *Palaeocarpilius* was present from the middle Eocene to the Miocene and was distributed throughout the Tethys Sea (e.g., Aly 2019 and references therein), Europe (see A. Milne-Edwards 1862; Smelror and Ossó 2016), the Atlantic coast of North America (see Rathbun 1935), and the Pacific Ocean (see Imaizumi 1939).

Interestingly, as it occurs in the Eocene (see Ossó et al. 2023), the fossil record of Oligocene brachyuran crabs in Iran is sparse compared to the nearby regions of India and Pakistan, which have a relatively rich fossil record of the same age (e.g., Stoliczka 1871; Glaessner 1933; Collins and Morris 1978; Schweitzer et al. 2004; Charbonnier et al. 2013). Most of the genera reported from these regions, such as *Galenopsis* A. Milne-Edwards, 1865, *Glypithyreus* Reuss, 1859, *Goniocypoda* Woodward, 1867, *Hepaticus* Bittner, 1875, *Laeviranina* Lörenthey in Lörenthey and Beurlen, 1929, *Liopsalis* Von Meyer, 1862, *Portunus* Weber, 1795, *Scylla* De Haan, 1833, as well as the aforementioned *Lophoranina*, and *Palaeocarpilius*, were also present in the western Tethys during the Paleogene.

Although scarce, the Oligocene brachyuran crab records from Iran, together with the Eocene records of *Lophoranina*, *Zanthopsis*, and *Retrocypoda* (see Ossó *et al.* 2023 and references therein), suggest a relative homogeneity of brachyuran faunas between the western and eastern sides of the Tethys Realm during the Paleogene. This similarity apparently persisted until the closure of the Tethys Seaway in the early Miocene (see Harzauser *et al.* 2007; Hyžný *et al.* 2021, and references therein).

CONCLUSIONS

Lophoranina and *Palaeocarpilius* were globally distributed and diversified in warm waters during the Eocene. Both genera experienced a decline towards the end of the Paleogene and, based on the available fossil record, were restricted to warm waters of the Indo-Pacific during the Miocene. The presence of these genera in the Oligocene beds of Iran helps to bridge the palaeobiogeographic gap of fossil crabs between India and Pakistan, and the western Tethys Realm during the Oligocene.

The findings, although limited to a few specimens, suggest a potential homogeneity of Paleogene brachyuran faunas on both sides of the Tethys Realm. However, further research and collection efforts in Iranian outcrops are needed to confirm this suggestion and to improve our understanding of the brachyuran fossil record in the region.

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REFERENCES

- Adams, C.G. and Bourgeois, E. 1967. Asmari biostratigraphy. Unpublished Report 1074, 74 pp. Geological and Exploration Division, Iranian Oil Operating Companies; Tehran.
- Adams, T.D. 1969. The Asmari Formation of Lurestan and Khuzestan provinces. Unpublished Report 1154, 93 pp. Geological and Exploration Division, Iranian Oil Operating Companies; Tehran.
- Aly, M.F. 2019. New occurrence of the brachyuran crab *Palaeocarpilius macrochelus* (Desmarest, 1822) from the Oligocene of the United Arab Emirates. *Annales de Paléontologie*, **106** (2), 102383.
- Ansari, H. 2005. Stratigraphy of the Asmari formation in north Fahlian area, southeast of Yasuj. Unpublished MSc thesis, 156 pp. University of Isfahan, Isfahan.
- Beschin, C., Busulini, A., De Angeli, A. and Tessier, G. 2004. The Eocene decapod crustacean fauna of the “Main” Quarry in Arzignano (Vicenza-NE Italy) with the description of a new species of Raninidae. *Lavori – Società Veneziana di Scienze Naturali*, **29**, 109–117.
- Beschin, C. and De Angeli, A. 2006. Il genere *Palaeocarpilius* A. Milne-Edwards, 1862 (Decapoda, Brachyura, Carpiliidae) nel Terziario del Vicentino (Italia Settentrionale). *Studi e Ricerche*, **13**, 11–23.
- Beschin, C., De Angeli, A. and Zorzin, R. 2011. Il genere *Lophoranina* Fabiani, 1910 (Crustacea, Decapoda, Brachyura, Raninidae) nel Terziario dei Lessini veronesi (Italia settentrionale). *Bollettino del Museo Civico di Storia Naturale di Verona, Geologia Paleontologia Preistoria*, **35**, 33–56.
- Bittner, A. 1875. Die Brachyuren des vicentinischen Tertiärganges. *Denkschriften der Kaiserlichen Akademie der Wissenschaften (Mathematisch-naturwissenschaftliche Klasse)*, **34**, 63–105.
- Blow, W.C. and Manning, R.C. 1996. Preliminary descriptions of 25 new decapod crustaceans from the Middle Eocene of the Carolinas, U.S.A. *Tulane Studies in Geology and Paleontology*, **29** (1), 1–26.
- Brocchi, P. 1877. Description de quelques Crustacés fossiles appartenant à la tribu des Raniniens. *Annales de la Société Géologique*, **8**, 1–6.
- Charbonnier, S. and Garassino, A. 2022. Fossil Decapod Crustacea in the historical collections, 292 pp. Mémoires du Muséum national d’Histoire Naturelle; Paris.
- Charbonnier, S., Garassino, A., Pasini, G., Métais, G., Merle, D., Bartolini, A., Brohi, I.A., Solangi, S.H., Lashari, R.A., Welcomme, J.-L. and Marivaux, L. 2013. Early Paleogene decapod crustaceans from the Sulaiman and Kirthar Ranges, Pakistan. *Annales de Paléontologie*, **99**, 101–117.
- Collins, J.S.H. and Morris, S.F. 1978. New Lower Tertiary crabs from Pakistan. *Palaeontology*, **21**, 957–981.
- De Gregorio, A. 1895. Description des faunes tertiaires de la Vénétie. Note sur certain Crustacés (Brachiopodes) Éocéniques (avec un catalogue de tous les Crustacés de la Vénétie cités par les auteurs). *Annales de Géologie et de Paléontologie*, **18**, 1–22.
- De Haan, W. 1833–1850. Crustacea. In: von Siebold, P.F. (Ed.), *Fauna Japonica sive Descriptio Animalium, quae in Itinerare per Japoniam, Jussu et Auspiciis Superiorum, qui summa in India Batava Imperium Tenent, Suscepito, Annis*

- 1823–1830, i–xvii, ix–xxi, ix–xvi, 1–243. Collegit, Notis, Observationibus et Adumbrationibus Illustravit. J. Müller et Co.; Leyden.
- Desmarest, A.G. 1822. Histoire naturelle des crustacés fossiles. Les crustacés proprement dits, 67–154. F.G. Levraut; Paris.
- Ehrenberg, S.N., Pickard N.A.H., Laursen, G.V., Monibi, S., Mossadegh, Z.K., Svånå, T.A., Aqrabi, A.A.M., McArthur, J.M. and Thirlwall, M.F. 2007. Strontium isotope stratigraphy of the Asmari Formation (Oligocene–Lower Miocene), SW Iran. *Journal of Petroleum Geology*, **30**, 107–128.
- Fabiani, R. 1910. Sulle specie di *Ranina* finora note ed in particolare sulla *Ranina aldrovandii*. *Atti della Accademia Scientifica Venetino Trentino Istriana*, **3**, 85–102.
- Feldmann, R.M., Schweitzer, C.E., Bennett, O.A., Frantescu, O.D., Resar, N. and Trudeau, A. 2011. New Eocene Brachyura (Crustacea: Decapoda) from Egypt. *Neues Jahrbuch für Geologie und Paläontologie Abhandlungen*, **262**, 323–353.
- Glaessner, M.F. 1933. New Tertiary crabs in the collection of the British Museum. *Annals and Magazine of Natural History*, Series 10, **12** (67), 1–28.
- Guinot, D. 1977. Propositions pour une nouvelle classification des Crustacés Décapodes Brachyours. *Comptes rendus hebdomadaires des séances de l'Académie des sciences, série D*, **285**, 1049–1052.
- Harzhauser, M., Kroh, A., Mandic, O., Piller, W.E., Göhlich, U., Reuter, M. and Berning, B. 2007. Biogeographic responses to geodynamics: A key study all around the Oligo-Miocene Tethyan Seaway. *Zoologischer Anzeiger – A Journal of Comparative Zoology*, **246** (4), 241–256.
- Heidari, A., Feldmann, R.M. and Moussavi-Harami, R. 2012. Miocene decapod crustacean from the Guri Member of the Mishan Formation, Bandar-Abbas, Southern Iran. *Bulletin of the Mizunami Fossil Museum*, **38**, 1–7.
- Heydari, E., Hassanzadeh, J., Wade, W.J. and Ghazi, A.M. 2003. Permian–Triassic boundary interval in the Abadeh section of Iran with implications for mass extinction. Part 1. Sedimentology. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **193**, 405–423.
- Hyžný, M., Bahrami, A., Yazdi, M. and Torabi, H. 2021. Decapod crustaceans from the lower Miocene Qom Formation of the Isfahan area, Central Iran. *Boletín de la Sociedad Geológica Mexicana*, **73** (3), A140521.
- Imaiizumi, R. 1939. *Palaeocarpilius laevis* sp. nov. from the Tappocho Limestone of Saipan Mariana Group. *Jubilee Publication in the Commemoration of Professor H. Yabe, M.I.A. Sixtieth Birthday*, **1**, 221–226.
- James, G.A. and Wynd, J.G. 1965. Stratigraphic nomenclature of Iranian oil consortium agreement area. *American Association of Petroleum Geologists Bulletin*, **49**, 2182–2245.
- Karasawa, H., Schweitzer, C.E., Feldmann, R.M. and Luque, J. 2014. Systematics and Phylogeny of the Raninoida (Crustacea: Brachyura). *Journal of Crustacean Biology*, **34**, 216–272.
- Khodaverdi Hassan-Vand, M., Bahrami, A., Yazdi, M., Ossó, Á., Safari, A., Martínez, J.L. and Vega, F.J. 2016. Occurrence of *Retrocypoda almeli* Via Boada, 1959 (Decapoda: Retroplumidae) in the Eocene of Central Iran. *Paleontología Mexicana*, **5**, 21–31.
- König, C.E. 1825. *Icones Fossilium Sectiles*, 4 pp. G.B. Sowerby; London.
- Latreille, P.A. 1802. Histoire naturelle, générale et particulière des Crustacés et des Insectes. Ouvrage faisant suite à l'histoire Naturelle générale et particulière, composée par Leclerc de Buffon, et rédigée par C.S. Sonnini, membre de plusieurs Sociétés savants, 476 pp. Dufart; Paris.
- Laursen, G.V., Monibi, S., Allan, T.L., Pickard, N.A., Hosseiney, A., Vincent, B., Hamon, Y., Van Buchem, F.S.P., Moallemi, A. and Druillion, G. 2009. The Asmari Formation revisited: changed stratigraphic allocation and new biozonation, 5 pp. First International Petroleum Conference and Exhibition. Shiraz, Iran.
- Lees, G.M. 1933. The reservoir rocks of Persian oil fields. *American Association of Petroleum Geologists Bulletin*, **17** (3), 229–240.
- Lewy, Z. 1977. *Ranina (Lophoranina) levantina* sp. nov. from the Middle Eocene of Israel. *Israel Journal of Earth Sciences*, **26**, 97–101.
- Linnæus, C. 1758. *Systema naturae per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis*, 1. Editio decima, reformata, 824 pp. Laurentii Salvii; Holmiae.
- Lörenthey, E. 1902. Neuere Beiträge zur Tertiären Dekapodenfauna Ungarns. *Mathematisch und Naturwissenschaftliche Berichte aus Ungarn*, **18**, 98–120.
- Lörenthey, E. and Beurlen, K. 1929. Die fossilen Decapoden der Lander der Ungarischen Krone. *Geologica Hungarica, Series Palaeontologica*, **3**, 1–420.
- Luque, J., Schweitzer, C.E., Santana, W., Portell, R.W., Vega, F.J. and Klompmaker, A.A. 2017. Checklist of fossil decapod crustaceans from tropical America, part I: Anomura and Brachyura. *Nauplius*, **25**, 1–85.
- M'Coy, F. 1849. On the classification of some British fossil Crustacea with notices of new forms in the university collection art Cambridge. *Annals and Magazine of Natural History*, (2) **4**, 161–179, 330–335.
- McQuillan, H. 1974. Fracture patterns on Kuh-e-Asmari Anticline, Southwest Iran. *American Association of Petroleum Geologists Bulletin*, **58**, 236–246.
- Michelotti G. 1841. Saggio storico dei rizopodi caratteristici dei terreni sopraccetacei. *Memorie di matematica e di Fisica della Società Italiana delle Scienze residente in Modena*, **22**, 253–302.
- Milne-Edwards, A. 1862. Monographie des Crustacés fossiles de la famille des Cancériens: *Annales des Sciences Naturelles (Botanique)*, Séries 4, **18**, 31–85.
- Milne-Edwards, A. 1863. Monographie des Crustacés de la fa-

- mille Cancériens. *Annales des Sciences Naturelles (Zoologie), Séries 4*, **20**, 273–324.
- Milne-Edwards, A. 1865. Monographie des Crustacés de la famille Cancériens. *Annales des Sciences Naturelles (Zoologie), Séries 5*, **3**, 297–351.
- Milne-Edwards, A. 1866. Asie Mineure, description physique de celle contrée. In: Tchihatcheff, P. de (Ed.), Paleontologie, 165 pp. L. Guerin; Paris.
- Milne-Edwards, A. 1872. Note sur quelques Crustacés fossiles appartenant aux genres *Ranina* et *Galenopsis*. *Annales des Sciences Géologiques*, **3**, 1–11.
- Milne-Edwards, A. 1881. Note sur quelques Crustacés fossiles des environs de Biarritz. *Annales des Sciences Géologiques*, **11** (2), 1–8.
- Ortmann, A. 1893. Die Decapoden-Krebse des Strassburger Museums. VI. Theil. Abtheilung: Brachyura (Brachyura genuina Boas) 1. Unterabtheilung: Majoidea und Cancroidea, 1. Section Portuninea. *Zoologische Jahrbücher, Abtheilung für Systematik, Geographie und Biologie der Thiere*, **7**, 23–88.
- Ossó, Á., Bahrami, A., Yazdi, M. and Mohammadrezaei, A. 2023. Presence of *Zanthopsis* M'Coy, 1849 (Crustacea: Decapoda: Brachyura) in the Early Eocene of Iran, and comments on the different species and/or morphotypes and their palaeobiogeography. *Annales de Paléontologie*, **109**, 102597.
- Ranzani, C. 1820. Osservazioni sopra un fossile dell'Aldrovandi chiamato Sepite. *Memorie di Storia Naturale*, **7**.
- Rathbun, M.J. 1935. Fossil Crustacea of the Atlantic and Gulf Coastal Plain. *Geological Society of America, Special Paper*, **2**, i–viii + 1–160.
- Rathbun, M.J. 1945. Decapod Crustacea. In: Ladd, H.S. and Hoffmeister, J.E. (Eds), Geology of Lau, Fiji. *Berniece P. Bishop Museum Bulletin*, **181**, 373–391.
- Reuss, A.E. 1859. Zur Kenntnis fossiler Krabben. Akademie der Wissenschaften Wien. *Denkschrift*, **17**, 1–90.
- Saint Laurent, M. de 1980. Sur la classification et la phylogénie des Crustacés Décapodes Brachyoures. I. Podotremata Guinot, 1977 et Eubrachyura sect. nov. *Comptes rendus hebdomadaires des Séances de l'Académie des Sciences*, **290**, 1265–1268.
- Schaub, H. 1981. Nummulites et Assilines de la Téthys Paléogène. Taxinomie, Phylogénie et Biostratigraphie. *Mémoires Suisses de Paléontologie*, **104**, 236 pp., **105**, Atlas I, **106**, Atlas II.
- Schweitzer, C.E., Feldmann, R.M., Garassino, A., Karasawa, H. and Schweigert, G. 2010. Systematic List of Fossil Decapod Crustacean Species. *Crustaceana Monographs*, **10**, 1–222.
- Schweitzer, C.E., Feldmann, R.M. and Gingerich P.D. 2004. New Decapoda (Crustacea) from the Middle and Late Eocene of Pakistan and a revision of *Lobonotus* A. Milne Edwards, 1864. *Contributions from the Museum of Paleontology, The University of Michigan*, **31** (4), 89–118.
- Schweitzer, C.E., Feldmann, R.M. and Lazar, I. 2009. Fossil Crustacea (excluding Cirripedia and Ostracoda) in the University of Bucharest Collections, Romania, including new species. *Bulletin of the Mizunami Fossil Museum*, **35**, 1–14.
- Sedaghat, M.E. and Shaverdi, T. 1975. Yasuj Geological map (1:100000), series sheet: 6351. Geological Survey and Mineral Exploration of Iran; Tehran.
- Smelror, M. and Ossó, Á. 2016. Paleogene fossils in erratic blocks from Averøy and Frei, Nordmøre, Norway. *Norges Geologiske Undersøkelse Bulletin*, **455**, 1–10.
- Squires, R.L. and Demetrian, R.A. 1992. Paleontology of the Eocene Bateque Formation, Baja California Sur, Mexico. *Natural History Museum of Los Angeles County Contributions in Science*, **434**, 1–55.
- Stoliczka, F. 1871. Observations of fossil crabs from Tertiary deposits in Sind and Kutch: Memoirs of the Geological Survey of India, *Palaeontologica Indica*, **14** (1), 1–16.
- Stubblefield, C.J. 1927. Lower Miocene Crustacea from Pemba Island. *Reports on the Paleontology of Zanzibar*, **1927**, 118–120.
- Thomas, A.N. 1950. The Asmari limestone of south-west Iran. In: Hobson, G.D. (Ed.), International Geological Congress, report of 18th session Great Britain 1948, Part IV, proceedings of section E, the geology of petroleum, 35–44. IGC Publication; Great Britain.
- Van Buchem, F.S.P., Allan, T.L., Laursen, G.V., Lotfpour, M., Moallemi, A., Monibi, S., Motiei, H., Pickard, N.A.H., Tahmasbi, A.R., Vedrenne, V. and Vincent, B. 2010. Regional stratigraphic architecture and reservoir types of the Oligo-Miocene deposits in the Dezful Embayment (Asmari and Pabdeh Formations), SW Iran. *Geological Society, London, special publications*, **329**, 219–263.
- Van Straelen, V. 1924 [imprint 1923]. Description des raniniens nouveaux des terrains tertiars de Bornéo. *Proceedings Koninklijke Nederlandse Akademie van Wetenschappen*, **26**, 777–782.
- Van Straelen, V. 1938. Crustacés Décapodes cénozoïques des Indes Orientales Néerlandaises. *Leidsche Geologische Mededeelingen*, **10** (1), 90–103.
- Vega, F.J., Cosma, T., Coutiño, M.A., Feldmann, R.M., Nyborg, T.G., Schweitzer, C.E. and Waugh, D.A. 2001. New Middle Eocene decapods (Crustacea) from Chiapas, Mexico. *Journal of Paleontology*, **75**, 929–946.
- Vega, F.J., Gholamalian, H. and Bahrami, A. 2010a. First record of Miocene crustaceans from Hormozgan Province, Southern Iran. *Palaontologische Zeitschrift*, **84**, 485–493.
- Vega, F.J., Gholamalian, H., Hassani, M.J., Sajadi, S.H. and Schaaf, P. 2012. Miocene Crustacea from northern Bandar Abbas, South Iran. *Neues Jahrbuch für Geologie und Paläontologie. Abhandlungen*, **265**, 221–234.
- Vega, F.J., Tiwari, J.K. and Bajpai, S. 2010b. Additions to *Palaeocarpilius rugifer* Stoliczka from the Oligocene of Kutch, western India. *Bulletin of the Mizunami Fossil Museum*, **36**, 45–49.

- Vía Boada, L. 1959. Decápodos fósiles del Eoceno español. *Boletín del Instituto Geológico y Minero de España*, **70**, 1–72.
- Von Meyer, H. 1862. Tertiaere Decapoden aus den Alpen, von Oeningen und dem Taunus. *Palaeontographica*, **10**, 147–178.
- Weber, F. 1795. Nomenclator entomologicus secundum Entomologian Systematicam ill. Fabricii: adjectis speciebus recens detectis et varietatibus, 171 pp. Carolum Ernestum Bohn.; Chilonii et Hamburgi.
- Withers, T.H. 1932. Some Eocene crabs from Persia and India. *Annals and Magazine of Natural History*, Serie 10, **9**, 467–472.
- Woodward, H. 1866. Note on a new species of *Ranina* (*Ranina porifera*) from the Tertiary strata of Trinidad. *Quarterly Journal of the Geological Society of London*, **22**, 591–592.
- Woodward, H. 1867. On a new species of shore-crab, *Gonio-cypoda Edwardsi*, from the lower Eocene of Hampshire. *Geological Magazine*, **4**, 529–531.
- Wynd, J.G. 1965. Biofacies of Iranian oil consortium agreement area. Unpublished report 1082, 212 pp. Iranian Oil Operating Companies; Tehran.
- Yabe, H., and Sugiyama, T. 1935. A new species of the genus *Ranina* (*Lophoranina*) from Haha-jima, Ogasawara Group (Bonin Islands), Japan. *Japanese Journal of Geology and Geography*, **12** (1–2), 1–4.

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