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First occurrence of Ibacinae (Eucrustacea: Decapoda: Scyllaridae) from the Eocene of Pakistan

Denis Audo[a, b]

[a]UMR CNRS 6118 Géosciences, Université de Rennes I, Campus de Beaulieu, avenue du général Leclerc, 35042 Rennes cedex, France. E-mail: denis.audo@edu.mnhn.fr

[b]Muséum national d'Histoire naturelle, Centre de Recherche sur la Paléobiodiversité et les Paléoenvironnements (CR2P, UMR 7207), Sorbonne Universités, MNHN, UPMC, CNRS, 57 rue Cuvier F-75005 Paris, France.

Abstract

The fossil record of slipper lobsters (Scyllaridae) is very poor, even though the earliest species of the modern slipper lobsters (Neoscyllaridae) are known from the Early Cretaceous. Among the clades "subfamilies" of slipper lobsters, perhaps the most remarkable is Ibacinae (currently monogeneric), which contains species with a very wide carapace (cephalothoracic shield) and very deep incisions. Fossil species assigned to Ibacinae were reported from the Oligocene and Pleistocene. However, a recent reappraisal of Scyllaridae phylogeny revealed that the genus to which these two fossil occurrences belong is not closely allied to Ibacinae. Therefore Ibacinae was left with no known fossil record until the present study. The present study describes a new species which can be confidently assigned to Ibacinae (closely allied to *Ibacus*) from the Ypresian (early Eocene) from the Ghazij formation in Shaisuro, Dera Ghazi Khan District, Pakistan. This new species, ?*Ibacus mazariorum* corresponds to the oldest recorded occurrence of Ibacinae. The Ghazij formation was deposited on the north-western margin of the India-Pakistan plate during a critical period, shortly before the collision between of the India-Pakistan plate with Asia. Consequently, it is possible that *Ibacus*, and closely allied species may have remained in the same biogeographic area since Eocene. Considering the extant and fossil distribution of Ibacinae, additional fossil discoveries may be found in existing collections and fossiliferous outcrops from Neotethys, Indian and Pacific oceans.

Keywords: Achelata; *Ibacus*; Ypresian; Ghazij formation; distribution range; Neotethys.

Introduction

Slipper lobsters (Scyllaridae) are easy to recognize decapod crustaceans: contrary to almost all other crustaceans, their antennae do not have a long flagellum, but a rather short flagellum formed of a few podomeres (Holthuis 1991; Lavalli & Spanier 2012; Haug *et al.* 2016). Besides, in the case of modern species, (Neoscyllarida Haug, Audo, Charbonnier, Palero, Petit, Abi Saad & Haug, 2016: a clade recently erected to distinguish modern slipper lobsters and their closest fossil relatives), the antenna is even more peculiar: very wide, flattened, and asymmetrical. These antennae resemble a shovel, hence, Scyllaridae are sometimes called

“shovel-nosed lobster”. However, contrary to what this name implies, antennae are probably not used in burying, but rather to protect antennulae, to steer the animal during swimming and to flip upside-down opponents during antagonistic behaviour (Spanier & Weihs 1992; Lavalli *et al*. 2007).

Scyllaridae have a quite poor fossil record compared to other decapod crustaceans (Audo & Charbonnier 2012). Their known fossil diversity is rather low, discontinuous stratigraphically and geographically (see supplementary material table 1).

Based upon the available fossil evidence, we know that slipper lobsters have diverged from other achelates as early as the Late Jurassic (Haug *et al.* 2009). Witnesses of the evolution of slipper lobsters (with a mosaic of primitive and derived characters) are discovered as late as Late Cretaceous (Haug *et al.* 2016; Charbonnier *et al.* 2017), but the diversification of Neoscyllaridae occurred earlier, no later than the Early Cretaceous (see supplementary material table 1). This diversification gave rise to at least five clades (see phylogenetic tree in Yang *et al.* 2012). Four of these clades correspond to the subfamilies defined by Holthuis (1985): Arctidinae Holthuis, 1985, Scyllarinae Latreille, 1825, Theninae Holthuis, 1985 and Ibacinae Holthuis, 1985. The fifth clade is formed by *Evibacus* Smith, 1869 + *Parribacus* Dana, 1852, formerly assigned to Ibacinae (Holthuis 1985), but which are more closely related to Scyllarinae and Theninae than to *Ibacus* Leach, 1815 (Yang *et al.* 2012). Among these aforementioned clades or “subfamilies”, at least three are known in the fossil record (supplementary material table 1): (1) Arctidinae and (2) Scyllarinae which supposedly first occur in Early Cretaceous; (3) the unnamed clade containing *Parribacus* and *Evibacus*, which is represented in the fossil record by two species of *Parribacus* in Oligocene (Glaessner 1965) and Pleistocene (Hu & Tao 1996), both previously assigned to Ibacinae. Theninae has not yet been identified in the fossil record. With the exclusion of *Parribacus* from Ibacinae, it appears that no true Ibacinae was discovered in the fossil record before the present study. This situation is slightly surprising as Ibacinae could have been easily identified since it contains the most remarkable species, with the widest and most flattened (in proportion) carapaces (cephalothoracic shields).

The present study investigates a fossil from the Ypresian of Pakistan, which displays characters typical of Ibacinae, closely matching those of *Ibacus*, and assesses its significance: this discovery improves our knowledge of Scyllaridae fossil diversity and of the minimum age of Ibacinae.

Geological context

The studied specimen was collected from the Ghazij formation in Shaisuro (Fig. 1), 150 km south-west of Dera Ghazi Khan, Punjab Province (Collins & Morris 1978). The Ghazij formation crops out over several hundreds of kilometres near the suture zone between India-Pakistan plate and Asia (Clyde *et al.* 2003). This formation has an interesting origin: it was deposited on the north-western margin of the India-Pakistan plate about 50-56 MA ago (Ypresian, early Eocene), at a time when India-Pakistan plate was just beginning its collision with Asia (Clementz *et al.* 2011; note that the timing of this collision is still poorly constrained: Zhu *et al.* 2005). This important collision is probably recorded by the formation. Indeed, the formation was initially deposited under marine conditions, then in paralic conditions and the sedimentation at the top of the formation is of terrestrial origin (Clyde *et al.* 2003). In this context, it is very likely that this variation in the sedimentation is a direct result of the collision between India-Pakistan plate and Asia and of the uplifting of the Ghazij formation.

Surprisingly, the specimen described herein was labelled as coming from the "top of the Ghazij shales, Shaisuro" (handwritten on the label placed with the specimen), and the locality is referred by Collins & Morris (1978: p. 961) as "top of the Ghazij formation". As explained in Clyde *et al.* (2003), the Ghazij formation ends up with sedimentation of terrestrial origin, so a marine slipper lobster is unlikely to come from the upper most part of the Ghazij formation. Rather, it may come from the top of the green shales, in the lower part of the Ghazij formation. The shales mentioned on the label may represent the uppermost part of the Ghazij formation in Shaisuro (opposed to the top of the whole Ghazij formation), which may explain the confusion. Unfortunately, no information is available on the precise horizon of the Ghazij formation from which this specimen comes from. No information can be gathered from the specimen itself either, as it is preserved in a nodule, and the surrounding sediment was removed.

The Ypresian of Shaisuro has also yielded 6 specimens of the brachyuran *Glyphithyreus wetherelli* (Bell, 1858) (Collins & Morris 1978). In addition, three other brachyuran species are reported from Ghazij formation in other outcrops, *Laeviranina sinuosa* Collins & Morris, 1978, *Pyromaia inflata* Collins & Morris, 1978, *Pakicarcinus orientalis* (Collins & Morris, 1978) (Collins & Morris 1978; Charbonnier *et al.* 2013).

Material and Methods

This study is based on the sample NHMUK In.48229 housed in the palaeontological collections of the Natural History Museum, London, United Kingdom (NHMUK). This specimen was collected by Ernest Sheppard Pinfold F.G.S., who was a geologist of the Attock Oil Company (Claire Mellish, pers. comm. 2017). The fossil is preserved in three dimensions within a concretion and was probably only minimally flattened during diagenesis.

The specimen was imaged in cross-polarized light (Bengtson 2000; Haug *et al.* 2011) and with image stacking to enhance the contrast and ensure the whole specimen is in focus. In addition, the dorsal aspect of the specimen was imaged at two slightly diverging angles to produce stereo pairs with an exaggerated stereographic effect (Fig. 2A).

The morphological terminology follows that used by Holthuis (1985), except that the term "ridge" is replaced by "carina".

Abbreviations: CL= Carapace Length, measured from the posterior margin of ocular incision to the posterior margin (parallel to median line); CW= Carapace width, measured as the maximum width, perpendicular to median line.

Systematic palaeontology

"Class" **Malacostraca** Latreille, 1802

"Order" **Decapoda** Latreille, 1802

"Suborder" **Pleocyemata** Burkenroad, 1963

Achelata Scholtz and Richter, 1995

"Family" **Scyllaridae** Latreille, 1825

Neoscyllarida Haug, Audo, Charbonnier, Palero, Petit, Abi Saad and Haug, 2016

"Subfamily" **Ibacinae** Holthuis, 1985

"Genus" ?***Ibacus*** Leach, 1815

Type Species. — *Ibacus perroni* Leach, 1815, by monotypy.

Original diagnosis (Leach 1815). — *Shell* broader than long, subdepressed, on each side very deeply fissured; *eyes* inserted at the anterior margin; *peduncle* thick, recurved, acuminated towards its extremity. *External pedipalpes* with the two first joints externally crested; second joint internally, with many fissures; *flagrum* tripartite; the last segment many-jointed. *Legs* ten, short; two anterior pair abruptly thicker than the others; fifth pair pair didactyle; thumb short. *Tail* with five membranaceous lamellæ, which are crustaceous at their base. *Interior antennæ* three-jointed, terminated by two many-jointed setæ: *external antennæ* squamiform, four-jointed. *[sic]*

Emended diagnosis (Holthuis 1985: rearranged from key to genera). — Exopods of all maxillipeds with a multi-articulate flagellum; Carapace strongly depressed, with a deep cervical incision in the lateral margin. Mandible with a simple or two-segmented palp ("subfamily" Ibacinae); orbits anteriorly open, placed on the anterior margin of the carapace. Cervical incision usually open, at least at the base. Carapace without posteromedian tooth. Atlantic and Indo-West Pacific; Dorsal surface of the body smooth and punctate, not tuberculate, sometimes pubescent. Carapace with postrostral and branchial carinae distinct. Distance between the orbits as long as or shorter than the distance separating each orbit from the nearest anterolateral angle. Fifth abdominal somite with posteromedian spine. Mandibular palp consisting of a single segment. (Note that the key originally included biogeographic characters which are herein preserved).

?*Ibacus mazariorum* nov. sp.

Fig. 2

Diagnosis. — Carapace (cephalothoracic shield) dorsoventrally flattened; narrow concave frontal margin framed by a pair of spines; U-shaped ocular incisions, with converging axis, opening on the anterior margin; short postorbital and long branchial carinae aligned; anterior submedian carina present.

Description (Figs 2B, 2D).

Outline of carapace. — Carapace (cephalothoracic shield) dorsoventrally flattened, subovate in outline in dorsal aspect (CL= *ca* 20.4 mm, CW= *ca* 36.1 mm; lateral margin poorly preserved); narrow concave frontal margin framed by a pair of spines; ocular incision

U-shaped, opening on the anterior margin, orientated slightly obliquely, their axis converging anteriorly; lateral margin eroded; cervical incision indistinct if present, possibly reaching a small tubercle (intercervical carina?); postcervical incision, if any, not visible; posterior margin poorly preserved, straight between branchial carina and median line.

Carapace grooves and carina. — cervical groove indistinct, separating the short postorbital carina from the long branchial carina, not cutting median carina (no separation between postrostral carina and posterior postrostral carina); branchiocardiac groove shallow, extending longitudinally along the median carina; postcervical groove shallow, joined to branchiocardiac groove, probably cutting median carina (isolating posteriorly the intestinal carina); postrostral and posterior postrostral carinae merged into a single median carina extending on the posterior 2/3 of the carapace, forming four long crests, first three successively longer, last crest shorter; short intestinal carina intercalated between median carina and posterior margin; thin and raised orbital carina surrounding ocular incision; short, raised postorbital carina, about 1/8 as long as branchial carina; tubercle slightly posterior and outward of postorbital carina, possibly representing a short intercervical carina; long, straight and raised branchial carina, extending parallel to median line to the posterior margin; raised anterior submedian carina, slightly longer than postorbital carina, subdivided into two crests, lying subparallel to median line, at equal distance from postorbital and median carinae; raised posterior carina, parallel to posterior margin, not preserved medially.

Carapace ornamentation. — carapace smooth medially, visibily ornamented laterally with pits, which may correspond to the erosion of tubercles (see Charbonnier *et al.* 2014: 333, for typical example of variations due to the preservation).

Etymology. — dedicated to the Mazari tribe, which inhabits the area where the fossil was discovered.

Type Material. — Holotype NHMUK In.48229, by monotypy (Fig. 2).

Geographic and Stratigraphic Range. — Ghazij formation, Shaisuro, Mazari tribal area, *ca* 150 km south-west of Dera Ghazi Khan, Punjab Province, 28° 27’ N., 69° 50’ E. Ypresian stage, Eocene (locality 3 in Collins & Morris 1978).

Discussion. — ?*Ibacus mazariorum* nov. sp. is ascribed to Neoscyllarida based upon its wide, dorsoventrally flattened carapace with marked branchial and median carina and large ocular incisions placed on the anterior margin. Similar disposition, with a large carapace can also be

found in polychelidan lobsters, brachyurans and stomatopods. However, the disposition of carina and grooves in these taxa is completely different, notably, because they do not possess any anterior submedian carina, neither have a branchial groove extending along the median carina as much as in ?*Ibacus mazariorum* nov. sp. As a whole, the whole pattern of grooves and carinae on the carapace is only compatible with some genera of slipper lobsters (Scyllaridae). Within Scyllaridae, such a wide carapace is only documented in the Neoscyllarida, other groups having more elongated carapaces. More precisely, the ocular incisions (or orbits) which open anteriorly, are nearer to each other than to the anterolateral angle, the raised branchial and postrostral carinae are diagnostic of *Ibacus* Leach, 1815 (Holthuis 1985). However, due to the fragmentary condition of this fossil, it is not possible to verify if this species has the typical deep cervical incision of *Ibacus*. It is therefore more reasonable to assign this species with some doubts to *Ibacus*. ?*Ibacus mazariorum* is the only known fossil species with distinct affinities with *Ibacus*. It is easily distinguished from all other species of *Ibacus* by its particularly narrow frontal margin, narrower than the ocular incision width, wider in all other species.

Discussion

Minimum age of Ibacinae

?*Ibacus mazariorum* is the only known occurrence of a representative of Ibacinae. This occurrence proves that Ibacinae already diverged from their nearest Scyllaridae relatives before the early Eocene. This new data may help calibrate the divergence time between the "subfamilies" of Scyllaridae for future works similar to that proposed by Palero *et al.* (2009).

Distribution range of Ibacinae and *Ibacus* in past and extant environments

?*Ibacus mazariorum* is either a representative of *Ibacus* or a very close relative to this genus. The distribution range of *Ibacus* is currently limited to the Indian ocean and West-Pacific (Holthuis 1985, Holthuis 1991). ?*Ibacus mazariorum* used to live on the north-western margin of India-Pakistan plate, in the Neotethys ocean. Its distribution matches that of extant species of *Ibacus*. It is undoubtedly a case of phylogenetic conservatism of the distribution range. However, with only one specimen in one locality, it is not possible to know if the size of the distribution range varied for *Ibacus* and its closest relatives.

As a result, we may have better chances to complete our poor knowledge of fossil Ibacinae by investigating existing collections and fossiliferous outcrops from Mediterranean Sea,

Neotethys, Indian and Pacific oceans. Besides, at the time, the nearby Mediterranean part of Neotethys was still connected to the Eastern Neotethys (Golonka 2002). Therefore, it is surprising that Ibacinae does not occur in present-day Mediterranean sea. .

Conclusions

1. ?*Ibacus mazariorum* is the only known occurrence of a fossil Ibacinid;
2. ?*Ibacus mazariorum* completes our knowledge about fossil Scyllaridae, a group with a particularly poor fossil record.
3. This species belongs to *Ibacus* Leach, 1815, or is a very closely allied species;
4. It used to live in the same biogeographic area as modern Ibacinae (*Ibacus*);

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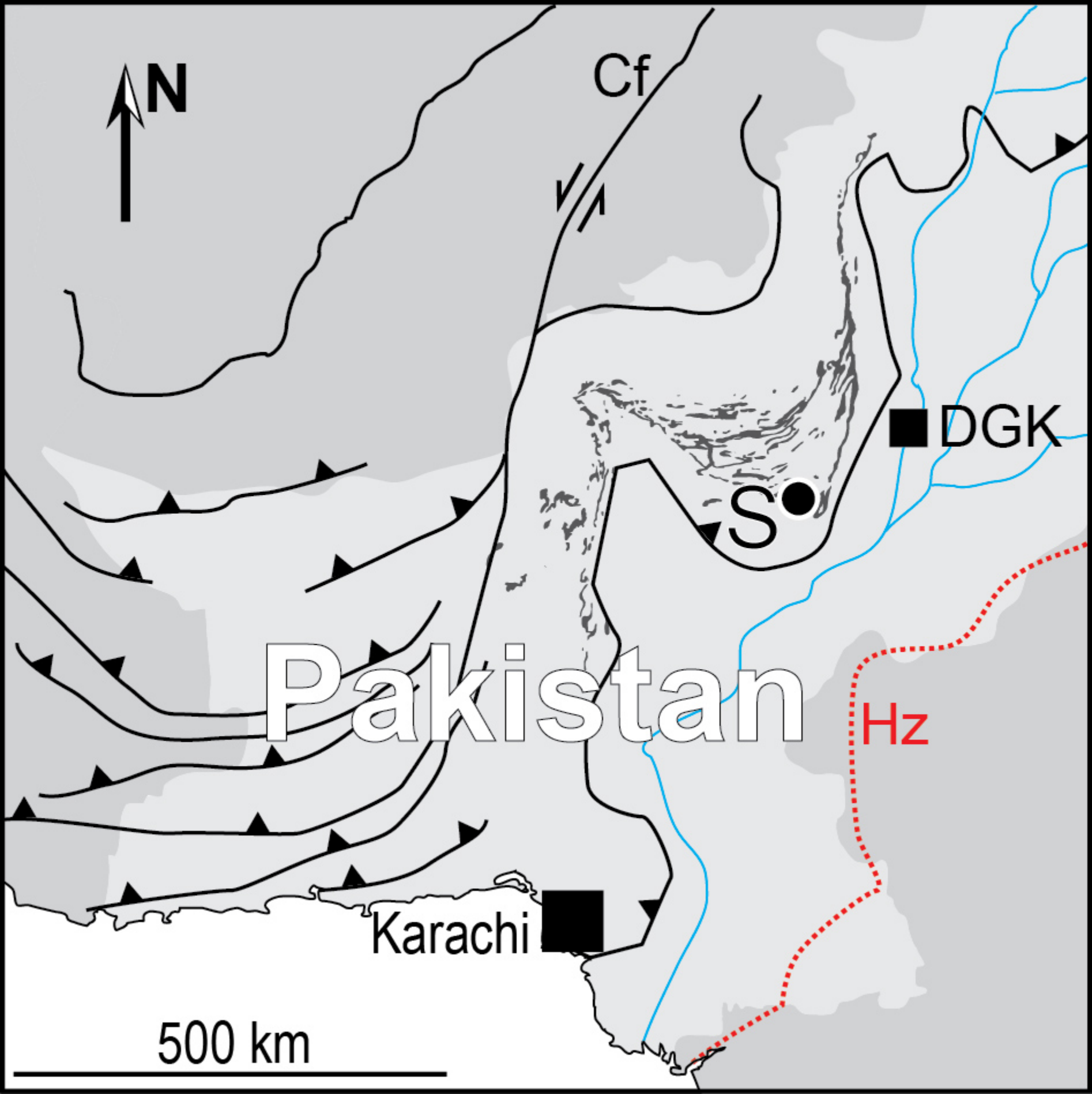
Figures

Figure 1

Situation of Shaisuro outcrop in Pakistan. Ghazij formation in dark grey, from Clyde et al. (2003); position of Shaisuro (circle) from Collins & Morris (1978); faults and hinge zone from Yin (2006). Abreviations: Cf= Chaman fault, DGK= Dera Ghazi Khan, Hz= Hinge zone; S= Shaisuro.

Figure 2

?*Ibacus mazariorum* nov. sp. from the Ypresian of Shaisuro. **A**, holotype in dorsal view, stereopair, cross-polarized light; **B**, interpretative line-drawing of dorsal view; **C**, frontal view, cross-polarized light; **D**, interpretative line-drawing of frontal view. Abbreviations: a= branchiocardiac groove, asmc= anterior submedian carina, bc= branchial carina, c= postcervical groove, e_1e= cervical groove, ei?= cervical incision, fm= frontal margin, ic?= intercervical carina, inc= intestinal carina, mc= median carina, o= ocular incision, oc= orbital carina, po= postorbital carina, poc= posterior carina. Scale bars: 10 mm. Pictures: D. Audo, © NHMUK.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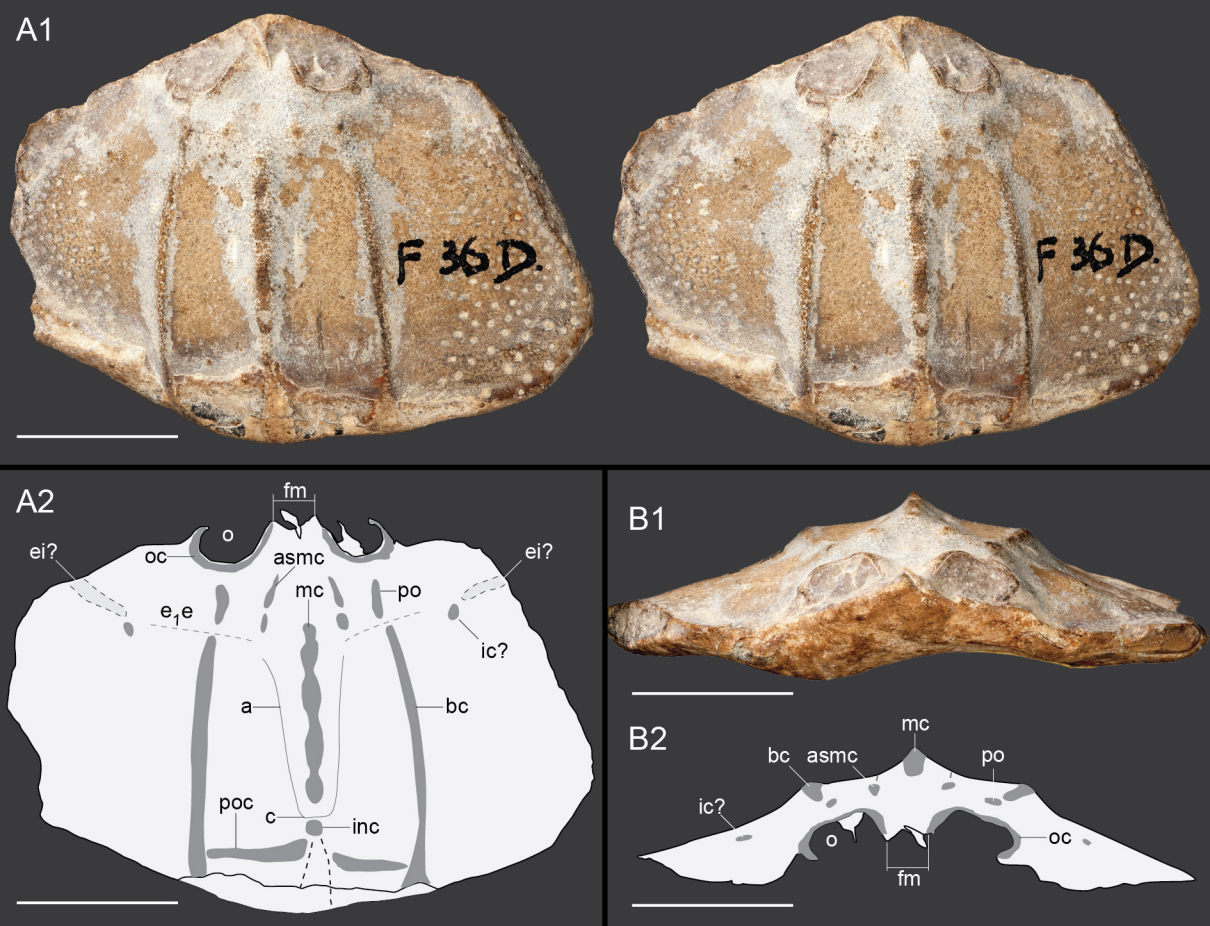
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	Age	Occurrence	References
Scyllaridae Latreille, 1825			
Sister taxa to Neoscyllarida Haug *et al.*, 2016			
Cancrinos Münster, 1839			
Cancrinos claviger Münster, 1839	Kimmeridgian-Tithonian	Bavaria, Germany	Haug *et al.* (2009)
Paracancrinos Haug *et al.*, 2016			
Paracancrinos libanensis (Garassino & Schweigert, 2006)	Late Cretaceous (Cenomanian)	Hadjoula, Lebanon	Haug *et al.* (2016)
Charbelicaris Haug et al., 2016			
Charbelicaris maronites Haug *et al.*, 2016	Late Cretaceous (Cenomanian)	Hadjoula, Lebanon	Haug *et al.* (2016)
Neoscyllarida† Haug *et al.*, 2016			
Arctidinae† Holthuis, 1985			
Acanthoscyllarides †† Audo & Charbonnier, 2012			
A. peterpani †† Audo & Charbonnier, 2012 (Nisto)	Late Cretaceous (Cenomanian)	Hadjoula, Lebanon	Audo & Charbonnier (2012)
Scyllarides † Gill, 1898			
S. bolcensis †† De Angeli and Garassino, 2008	Eocene (Ypresian)	Monte Postal, Italy	De Angeli & Garassino (2008)
S. koenigii †† (Bell, 1858)	Eocene (Ypresian)	Sheppey Island, United Kingdom	Förster (1984)
S. punctatus †† Woods, 1925	Early Cretaceous (Albian)	Folkestone, United Kingdom	Förster (1984)
S. tuberculatus †† (König, 1825)	Eocene (Ypresian)	London Clay Formation, United Kingdom	Quayle (1987)
Ibacinae† Holthuis, 1985			
Ibacus † Leach, 1815			
?*I. mazariorum* †† nov. sp.	Eocene (Ypresian)	Ryukyu Group, Taiwan	This study
Scyllarinae† Latreille, 1825			
Biarctus † Holthuis, 2002			
B. vitiensis † (Dana, 1852)	Late Pleistocene - Recent	Vitilevu, Fiji Island	Förster (1984)
Scyllarella †† Rathbun, 1935			
S. aspera †† Rathbun, 1935	Paleocene	Alabama, United States of America	Förster (1984)
S. gardneri †† (Woods, 1925)	Early Cretaceous (Albian)	Folkestone, United Kingdom	Förster (1984)
S. gibbera †† Rathbun, 1935	Paleocene	Alabama, United States of America	Förster (1984)
Scyllarus † Fabricius, 1775			
S. junghumi †† Böhm, 1922	Miocene	Java, Indonesia	Förster (1984)
S. mantelli †† Desmarest, 1822 (*Nomen dubium*)	?	United Kingdom	Desmarest (1822)
Unplaced at subfamily level			
Llajassus †† Nyborg & Garassino, 2017			
L. caesius (Squires, 2000)	Eocene (Lutetian)	Llajas Formation, United States of America	Nyborg & Garassino (2017)
Palibacus †† Förster, 1984			
P. praecursor (Dames, 1886)	Cenomanian	Hakel and Hadjoula, Lebanon	Förster (1984)
Parsacus †† Garassino *et al.*, 2014			
P. eocenicus Garassino et al., 2014	Eocene	Baba-Heydar, Shar-e-Kurd area, Iran	Garassino *et al.* (2014)
?*P cristatus* †† Förster, 1984 (Nisto)	Eocene	Bolca, Italy	Haug & Rudolf (2015)

Previously assigned to Ibacinae			
Parribacus † Dana, 1852			
P. japonicus † Holthuis, 1960	Neogene (Pleistocene) - Recent	Ryukyu Group, Taiwan	Hu and Tao (1996)
P . sp.†† Glaessner, 1965	Oligocene	Bad Iwonicz, Poland	Glaessner (1965)

Supplementary material

Table 1

Table 1: List of fossil slipper lobsters (Decapoda: Scyllaridae). Only postlarvae (nisto) and adults are included. Scyllaridae undoubtedly also occur in the fossil record as larvae. These larvae, the phyllosoma stages (Palero *et al.* 2014), are even more common than adults (Carolin Haug pers. comm. 2017). Unfortunately, the phyllosoma stages have a common morphology in all Achelata Scholtz & Richter, 1995. So it is often difficult, especially on fossil, to know if they correspond to Scyllaridae or to the more abundant Palinuridae Latreille, 1802. Note that *Scyllarella manleyi* Feldmann & Schweitzer, 2017 does not appear in this list because it is herein considered as a more recent synonym of *Llajassus caesis* (Squires, 2001). Indeed, *S. manleyi* holotype corresponds to a specimen which was convincingly ascribed to *Llajassus caesius* by Nyborg & Garassino (2017).

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