New Early Cenozoic ghost shrimps (Decapoda, Axiidea, Callianassidae) from Pakistan and their palaeobiogeographic implications

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KEY WORDS
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Callianassidae,
Cenozoic,
Kirthar Range,
Sindh,
Pakistan,
Ranikot Group,
palaeobiogeography,
new combinations,
new species.

ABSTRACT

A new set of Paleocene and Eocene decapod crustaceans is described from the Kirthar Range of Pakistan. Two new ghost shrimps (Crustacea, Decapoda, Callianassidae) are described: *Neocallichirus khadroensis* Hyžný & Charbonnier, n. sp. from the Paleocene (Danian, Khadro Formation) of Gawar Band, Ranikot District, and *Neocallichirus lakhraensis* Hyžný & Charbonnier, n. sp. from the Early Eocene (Ypresian, Lakhra Formation) of Rbod Nala, Jhirak District. Both new species exhibit chelipeds which are morphologically surprisingly close to extant *Neocallichirus karumba* (Poore & Griffin, 1979) from the Indo-West Pacific. A group of species sharing this same cheliped morphology is provisionally called the "*karumba* group" based on *Neocallichirus karumba*, best documented species.

The "*karumba* group" encompasses seven fossil species: the two new Pakistani species, *Neocallichirus tuberculatus* (Lőrenthey *in* Lőrenthey & Beurlen, 1929) n. comb. from the Eocene of Hungary, *Neocallichirus borensis* Beschin, De Angeli, Checchi & Mietto, 2006 from the Eocene of Italy, *Neocallichirus birmanicus* (Noetling, 1901) n. comb. from the Miocene of Myanmar, *Neocallichirus dijki* (Martin, 1883) from the Miocene of Java and Philippines, and the subfossil *Neocallichirus maximus* (A. Milne-Edwards, 1870) from Thailand. Based upon the extant and fossil occurrences, it is difficult to reconstruct migration pattern of the "*karumba* group". For now, it can be concluded, that at the genus level, a relative homogeneity of the ghost shrimps is observed between the Eastern and the Western Tethyan regions, as already suggested by Merle *et al.* (2014) for the assemblage of volutid gastropods from the Lakhra Formation.

RÉSUMÉ

Nouvelles callianasses (Decapoda, Axiidea, Callianassidae) du Cénozoïque inférieur du Pakistan et leurs implications paléobiogéographiques.

Un nouvel ensemble de crustacés décapodes est décrit dans le Paléocène et l'Éocène des montagnes du Kirthar au Pakistan. Deux nouvelles espèces de callianasses (Crustacea, Decapoda, Callianassidae) sont décrites : *Neocallichirus khadroensis* Hyžný & Charbonnier, n. sp. du Paléocène (Danien, Formation Khadro) de Gawar Band, District de Ranikot, et *Neocallichirus lakhraensis* Hyžný & Charbonnier, n. sp. de l'Éocène basal (Yprésian, Formation Lakhra) de Rbod Nala, District de Jhirak. Ces deux nouvelles espèces montrent des chélipèdes qui sont morphologiquement très proches de l'actuel *Neocallichirus karumba* (Poore & Griffin, 1979) de l'Indo-Ouest Pacifique. Un groupe d'espèces partageant la même morphologie de chélipèdes est provisoirement appelé le « groupe *karumba* », fondé sur *Neocallichirus karumba*, espèce la mieux connue. Le « groupe *karumba* » englobe sept espèces fossiles : les deux nouvelles espèces pakistanaises, *Neocallichirus tuberculatus* (Lőrenthey *in* Lőrenthey & Beurlen, 1929) n. comb. de l'Éocène de Hongrie, *Neocallichirus borensis* Beschin, De Angeli, Checchi & Mietto, 2006 de l'Éocène d'Italie, *Neocallichirus birmanicus* (Noetling, 1901) n. comb. du Miocène du Myanmar (Birmanie), *Neocallichirus dijki* (Martin, 1883) du Miocène de Java et des Philippines, et le subfossile *Neocallichirus maximus* (A. Milne-Edwards, 1870) de Thaïlande. D'après les occurrences actuelles et fossiles, il est difficile de reconstituer les modalités de migration du « groupe *karumba* ». Il est juste possible d'observer, au niveau générique, une relative homogénéité des callianasses entre les régions téthysiennes occidentale et orientale, comme cela a été déjà suggéré par Merle *et al.* (2014) à partir de l'assemblage de gastéropodes volutidés de la Formation Lakhra.

MOTS CLÉS
Crustacea,
Decapoda,
Axiidea,
Callianassidae,
Cénozoïque,
chaîne du Kirthar,
Sindh,
Pakistan,
Groupe Ranikot,
paléobiogéographie,
combinaisons nouvelles,
espèces nouvelles.

INTRODUCTION

Callianassid and ctenochelid ghost shrimps belong to major components of many Cenozoic shallow marine decapod crustacean assemblages (Hyžný & Klompmaker 2015), which reflects the fact that ghost shrimps often live in high densities (Ziebis *et al.* 1996; Stamhuis *et al.* 1997; Bishop & Williams 2005). Until now, however, only a single fossil ghost shrimp species has been known from Pakistan, namely *Neocallichirus wellsi* Schweitzer, Feldmann & Gingerich, 2004 (recently tentatively reassigned to *Balsscallichirus* Sakai, 2011 by Hyžný 2016) from the Upper Eocene (Priabonian) of the Drazinda Formation. Herein, two new ghost shrimps are described from the Paleocene (Danian) and Lower Eocene (Ypresian) rocks of Kirthar Range extending the known fossil Pakistani ghost shrimp occurrences substantially. Both new taxa are morphologically surprisingly close to extant *Neocallichirus karumba* (Poore & Griffin, 1979) from the Indo-West Pacific. Moreover, the same cheliped morphotype is known also from the Eocene of Hungary (Lőrenthey & Beurlen 1929) and Italy (Beschin *et al.* 2006), documenting broad geographic distribution of the lineage during the Early Cenozoic.

REVIEW OF FOSSIL DECAPODS OF PAKISTAN

Fossil decapod crustaceans from Pakistan have been the subject of only few studies in the past (Stoliczka 1871; Noetling 1897; Glaessner 1933). Collins & Morris (1978) provided synopsis of all fossil decapod crustaceans previously reported from the area and described two new genera and eight new species. Later, Glaessner & Secrétan (1987) described new crabs from the Eocene of the Sulaiman Range. Schweitzer *et al.* (2004) re-evaluated the known decapod crustacean fauna from the Middle and Late Eocene of Pakistan and reported new occurrences of hermit crabs, ghost shrimps, and panopeid crabs. Most of these previous studies concerns only fossil crabs collected in northern Pakistan. More recently, Charbonnier *et al.* (2013) reported fossil decapod crustaceans collected during the late 1970s from the middle Eocene (Lutetian, Domanda Formation) of Rakhi Nala, Sulaiman Range, northern Pakistan. They also included crustaceans from the Paleocene (Thanetian? Bara Formation) exposed in the Lakhra Dome, Kirthar Range, southern Pakistan. These latter occurrences constituted the first report of Paleocene decapod crustaceans in southern Pakistan (Sind, Karachi Arc). The current work enlarges the study of Charbonnier *et al.* (2013) and includes new fossil ghost shrimps from southern Pakistan both collected in the Khadro (Danian, Ranikot District) and the Lakhra (Ypresian, Jhirak District) formations. Together with ghost shrimps also some indeterminate brachyuran material has been collected.

GEOLOGICAL SETTING

The term "Ranikot" series was introduced by Blanford (1876) to designate the "infra-nummulitic" rocks well exposed in the area of the Ranikot Fort, about 75 km NE of Hyderabad, Sindh, southern Pakistan. Vredenburg (1909) subdivided the Ranikot Group into "Lower Ranikot" (detritic) mostly exposed in the Laki Range, and the "Upper Ranikot" (carbonaceous) exclusively exposed in the Lakhra Dome and Jhimpir area (Fig. 1). In the southern Kirthar Range, the Ranikot Group is conformably capped by the Early Eocene limestones of the Laki Formation (Cheema *et al.* 1977; Shah 2009).

The Laki Range is an east-vergent fold-thrust belt that extends along a North-South axis between Thano Bhula Khan and Sehwan Sharif. It represents the western margin of the Indian subcontinent (Bannert *et al.* 1992) and this region has been highly uplifted, faulted and folded during the Pliocene to the present (Schelling 1999). In the Ranikot area, the cores of both Ranikot and Gorbandi anticlines expose the Paleocene shales, sandstones, and limestones of the Ranikot Group, and Late Cretaceous rocks at some places. The Blanford's Ranikot Group is now divided into three formations in ascending order: Khadro, Bara, and Lakhra. The fossil crustaceans reported here come from the Khadro and Lakhra formations. The 2012 and 2014's field seasons led in collaboration with colleagues of the University of Sindh (Jamshoro) have allowed us to collect new fossil data from these formations (Charbonnier *et al.* 2013; Merle *et al.* 2014; Rage *et al.* 2014), including crustaceans that are described herein.

The Gawar Band area (25°53'48.44"N, 67°49'58.49"E) in the Laki Range offers a detailed section of the Khadro Formation although the contact between the Khadro Formation and the Late Cretaceous Pab Formation is not visible there. The fossil crustaceans reported here come from greenish sandstones, situated two metres above an indurated brownish sandstone showing a high concentration of *Cardita beaumonti* d'Archiac & Haime, 1853 (now *Baluchicardia beaumonti*). According to Blanford (1879) and Shah (2009), these *Cardita beaumonti* beds marks the base of the Khadro Formation which is considered as early Danian in age (Cheema *et al.* 1977).

The Rbod Nala section (24°59'43.36"N, 68°10'42.46"E), Jhirak District, is about 100 km SSE of Ranikot, and it is situated along the Indus River near Jhimpir. Sample collecting was made possible due to a project of artificial drainage for agriculture purpose. This incision has preserved a fresh and detailed section of the lower part of the Lakhra Formation.

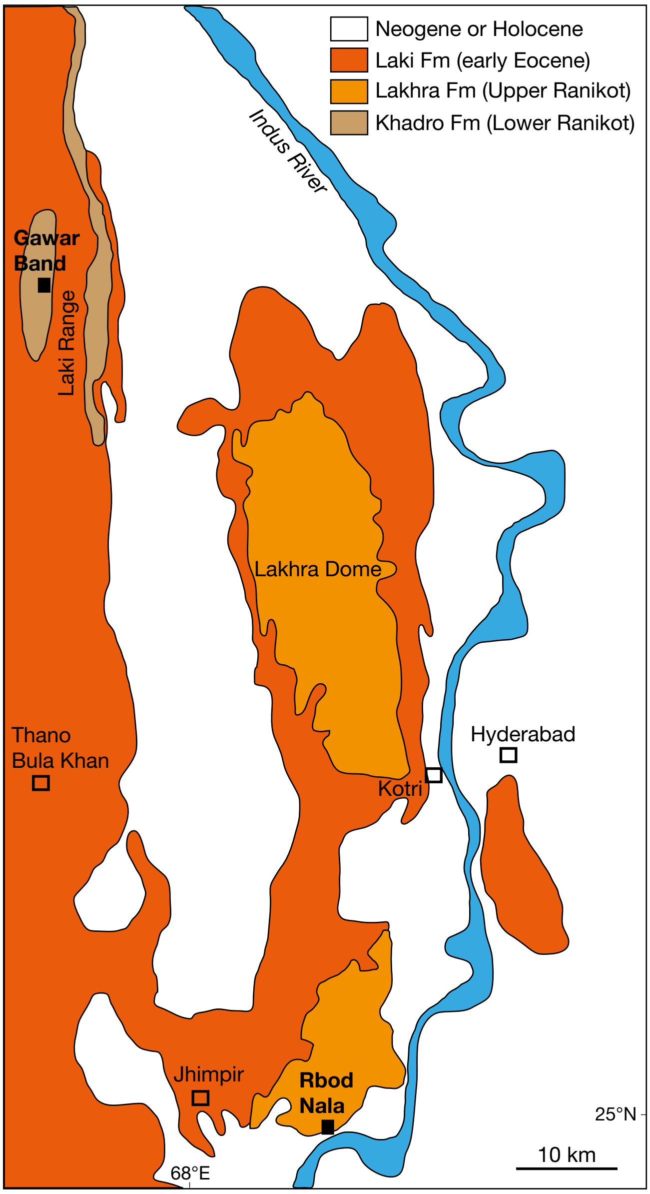

Fig. 1. — Simplified geological map (adapted from Hunting Survey Corporation, Ltd. 1961) of the Southern Kirthar Range, Southern Pakistan, showing the location of the fossil localities (Gawar Band and Rbod Nala). Line drawing: G. Métais.

The Lakhra is generally considered as entirely Thanetian in age on the basis of larger foraminifers (Williams 1959; Hunting Survey Corporation Ltd 1961; Cheema *et al.* 1977). However, Wakefield & Monteil (2002) challenged the age of the Lakhra Formation on the basis of foraminiferal and palynological data obtained from the Duljan-1 well-core, situated between the central and lower portions of the Indus Basin, about 100 km NE of Jhimpir. These authors have suggested that the formation probably straddles de Paleocene/Eocene boundary. The fossil material reported here comes from the lower part of the Rbod Nala section, about 10 metres above the conformable contact with the Bara Formation. Pending additional biostratigraphic calibration (in preparation), we can reasonably consider that the yielding crustacean beds are either latest Paleocene or earliest Eocene in age.

MATERIAL AND METHODS

In the Ranikot District, the fossilized decapod crustaceans found in the Khadro Formation comes from greenish sandstones with intercalations of green sandy clays. They are preserved in sandy nodules and mainly correspond to isolated cheliped elements, which is in accordance with the usual ghost shrimp preservation (Bishop & Williams 2005; Hyžný & Klompmaker 2015). The nodule-rich horizons are overlain by a bed containing a monospecific assemblage of *Baluchicardia beaumonti* (d'Archiac & Haime, 1853), i.e. *Cardita beaumonti* bed of earlier authors (e.g. Douvillé 1928, 1929).

In the Jhirak District, the fossil decapods found in the Lakhra Formation comes from the bioclastic sandstones and are associated with abundant and diversified molluscan fauna (Merle *et al.* 2014). They are preserved as internal molds or as slightly recrystallized isolated carapaces (brachyurans) and chelipeds (ghost shrimps).

Remains of ghost shrimp chelae were cleaned, measured and photographed dry using normal light. The length (measured at the upper margin) and maximum height of propodus was measured using a vernier calliper; measurements were evaluated in graphs.

For comparative purposes, extant material of *Neocallichirus karumba* (male NHMW 21937 and female NHMW 21938) has been examined and photographed immersed in alcohol.

The type and figured material of newly described taxa is housed at the Centre for Pure and Applied Geology of the University of Sindh (Jamshoro, Pakistan) and a copy (plastotype) of this material is housed at the Muséum national d'Histoire naturelle, Paris (collection de Paléontologie).

ABBREVIATIONS

Institutional abbreviations

CPAG	Centre for Pure and Applied Geology, University of Sindh, Jamshoro, Pakistan;
MCZ	Museo Civico "G. Zannato", Montecchio Maggiore (Vicenza), Italy;
MFGI	Hungarian Geological and Geophysical Institute, Budapest, Hungary;
MNHN.F	Collection de Paléontologie, Muséum national d'Histoire naturelle, Paris, France;
NHMW	Natural History Museum, Vienna, Austria.

Other abbreviations

RAN	Ranikot;
I	invertebrates;
P1-P5	first to fifth pereiopods (chelipeds);
mpl	major P1 propodus length;
mph	major P1 propodus height.

SYSTEMATIC PALAEONTOLOGY

Class MALACOSTRACA Latreille, 1802
Order DECAPODA Latreille, 1802
Infraorder AXIIDEA Saint Laurent, 1979
Family CALLIANASSIDAE Dana, 1852

Subfamily CALLICHIRINAE Manning & Felder, 1991

Genus *Neocallichirus* Sakai, 1988

TYPE SPECIES. — *Neocallichirus horneri* Sakai, 1988, by original designation.

INCLUDED FOSSIL SPECIES. — See Garassino *et al.* (2011) and Hyžný & Karasawa (2012) for updated lists.

COMMENTS. — The genus was erected by Sakai (1988), but because of its rather broad original diagnosis, it underwent numerous reconsiderations. As a consequence, taxonomic composition of *Neocallichirus* is complex, and was partly discussed by Hyžný & Karasawa (2012). Interestingly, Sakai himself has used several different concepts of the genus since its first description (Sakai 1988: 61; 1999: 84; 2005: 160; 2011: 451; see also Manning & Felder 1991: 779). The identification of the genus in the fossil record has been discussed by several authors (Schweitzer & Feldmann 2002; Schweitzer *et al.* 2004, 2006; Hyžný & Hudáčková 2012; Hyžný & Karasawa 2012), however, the revision of all fossil taxa treated at one time under *Neocallichirus* is still pending. As already noted previously (Hyžný & Hudáčková 2012; Hyžný & Karasawa 2012), the genus *Neocallichirus* as usually recognized in the fossil record may represent a mixture of several closely allied genera.

Because the fossil material described herein is morphologically close to *Callianassa karumba* currently classified within *Neocallichirus* (Sakai 1999, 2005, 2011; Dworschak 2008), we treat our new material as remains of representatives of this genus. However, it should be noted that *N. karumba* exhibits important differences from the type species of *Neocallichirus* (Dworschak 2008: 83). Because generic reconsideration of *Callianassa karumba* is beyond the scope of the present contribution, two new fossil species described herein are treated tentatively as *Neocallichirus*.

Neocallichirus khadroensis Hyžný & Charbonnier, n. sp.
(Figs 2; $5A_3$, C_2, D_3; 6I)

"fragments of chelae of an *Uca* or *Cardisoma*" – Stoliczka 1871: 2, pl. 1, figs 3-10.

ETYMOLOGY. — The specific epithet refers to the Khadro Formation where the type material was collected.

TYPE MATERIAL. — Holotype (CPAG.RAN.I.55, cast MNHN.F.A52405); 8 paratypes (CPAG.RAN.I.56-I.63, casts MNHN.F.A52406-A52413).

TYPE LOCALITY. — Gawar Band section (25°53'48.44"N, 67°49'58.49"E), Ranikot District, Sindh, Pakistan.

TYPE AGE. — Paleocene, Danian (Khadro Formation, Lower Ranikot Group).

STRATIGRAPHIC RANGE. — Danian (Pakistan) – Aquitanian? (India).

DIAGNOSIS. — Ghost shrimp with major P1 merus with spinose lower margin and large proximal hook; major P1 manus (palm) rectangular with tuberculated lateral surfaces and distal margin with large notch and/or prominent tooth just below the articulation with dactylus; major P1 dactylus approximately as long as manus (palm) with two blunt proximal spines on its upper margin and occlusal margin strongly armed with a stout and blunt tooth with three apices proximally followed with a broad gap, additional large tooth and several small teeth decreasing in size distally.

MEASUREMENTS (IN MM). — CPAG.RAN.I.55 (holotype): mpl = 21.2, mph = 23.4; CPAG.RAN.I.56 (paratype): mpl = 23, mph = 25; CPAG.RAN.I.57 (paratype): mpl = 15.2, mph = 17.5; CPAG.

Fig. 2. — *Neocallichirus khadroensis* Hyžný & Charbonnier, n. sp. from the nodules of the Gawar Band section (Danian, Khadro Formation), Ranikot District, Sindh, Pakistan: **A**, holotype CPAG.RAN.I.55, major left male P1 chela (propodus with articulated dactylus) showing occlusal margin of dactylus, outer view; **B**, paratype CPAG.RAN.I.56, major right male P1 propodus showing fixed finger with smooth occlusal margin, inner view; note a smaller major right P1 propodus; **C**, paratype CPAG.RAN.I.57, major left male P1 chela (propodus with articulated dactylus), inner view; **D**-**F**, paratype CPAG.RAN.I.58, major right male P1 propodus in outer (**D**), frontal (**E**) and inner (**F**) views; **G**, paratype CPAG.RAN.I.61, major left male P1 propodus, outer view; **H**, **I**, paratype CPAG.RAN.I.59, major right female P1 propodus with broken fixed finger in outer (**H**) and inner (**I**) views; **J**, paratype CPAG.RAN.I.63, major right P1 merus, outer view; **K**, paratype CPAG.RAN.I.62, major left male P1 propodus, inner view; **L**, paratype CPAG.RAN.I.60, major left male P1 propodus preserved in a sandy nodule, outer view. Photographs: L. Cazes and P. Loubry. Scale bar: 10 mm.

RAN.I.58 (paratype): mpl = 22.8, mph = 27.2; CPAG.RAN.I.60 (paratype): mpl = 13.7, mph = 18.3; CPAG.RAN.I.61 (paratype): mpl = 17.4, mph = 21.7; CPAG.RAN.I.62 (paratype): mpl = 18.3, mph = 22.4. Additionally 19 specimens deposited under collective number CPAG.RAN.I.76 were measured and evaluated graphically (Fig. 3A).

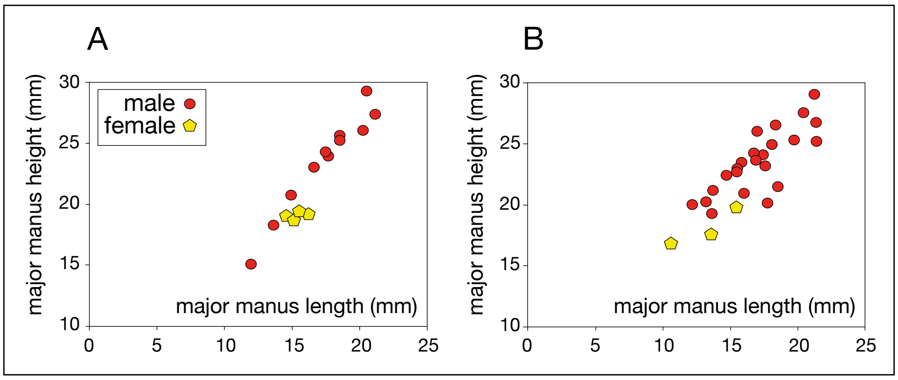

FIG. 3. — Measurements of major propodus in fossil ghost shrimps from Gawar Band and Rbod Nala sections, Pakistan: **A**, measurements in *Neocallichirus khadroensis* Hyžný & Charbonnier, n. sp.; **B**, measurements in *Neocallichirus lakhraensis* Hyžný & Charbonnier, n. sp. Graphs: M. Hyžný.

DESCRIPTION

Major P1

Merus approximately two times longer than high, with longitudinal keel running along the midline of the outer lateral surface, upper margin slightly convex and smooth, lower margin armed with prominent spines and large proximal hook. Carpus poorly preserved, distal portion unknown. Propodus stout, manus (palm) quadrate in outline or slightly higher than long, upper and lower margins parallel to each other, upper margin keeled and smooth, lower margin keeled and strongly serrated, distal margin usually with large notch and prominent tooth just below the articulation with dactylus; both outer and inner lateral surfaces covered with densely packed tubercles, tuberculation usually not reaching the upper third of the lateral surface, largest tubercles positioned close to the articulation with dactylus; inner propodal surface with large setal pits positioned at the upper margin distally; fingers approximately as long as manus (palm) or slightly longer; fixed finger slender, incurved distally, tip bent slightly upward, occlusal surface edentulous. Dactylus long and deep, upper margin with two spines proximally, occlusal surface strongly armed with a stout and blunt tooth with three apices proximally followed with a broad gap, additional large tooth and several small teeth decreasing in size distally, tip of dactylus hooked.

Minor P1, P2-P5, other appendages, carapace and pleon

Unknown.

COMMENTS

Stoliczka (1871: 2) described and figured some isolated chelae as remains "apparently one of the Grapsidae, an *Uca* or *Cardisoma*, or some other allied genus." In fact, the description and figures fully conform with *Neocallichirus khadroensis* Hyžný & Charbonnier, n. sp. as described herein. Stoliczka (1871: 2) reported this material from "a yellowish brown argillaceous rock between Soojapoor and Badra, south of Mhurr in Kutch". The age of the outcrops is not specified and might be Aquitanian after Biswas (1992).

Comparison of *N. khadroensis* Hyžný & Charbonnier, n. sp. with related species is given under comments of *Neocallichirus lakhraensis* Hyžný & Charbonnier, n. sp.

Neocallichirus lakhraensis Hyžný & Charbonnier, n. sp.
(Figs 4; 5A$_2$, B$_2$, C$_3$, D$_2$, E$_2$; 6H)

ETYMOLOGY. — The specific epithet refers to the Lakhra Formation from which the type material has been collected.

TYPE MATERIAL. — Holotype (CPAG.RAN.I.64, cast MNHN.F.A52414); 8 paratypes (CPAG.RAN.I.65-I.72, casts MNHN.F.A52415-A52422).

TYPE LOCALITY. — Rbod Nala section (24°59'43.36"N, 68°10'42.46"E), Jhirak District, Sindh, Pakistan.

TYPE AGE. — Eocene, Ypresian (Lakhra Formation, Upper Ranikot Group).

STRATIGRAPHIC RANGE. — Ypresian (Pakistan).

DIAGNOSIS. — Ghost shrimp with major P1 ischium with spinose lower margin; major P1 merus with spinose lower margin and large bifid proximal hook; major P1 manus (palm) rectangular with tuberculated lateral surfaces and ridge along the fixed finger, distal margin with large notch and/or prominent serrated tooth just below the articulation with dactylus; major P1 dactylus approximately as long as manus (palm) or longer with two blunt proximal spines on its upper margin and occlusal margin strongly armed with peg-shaped teeth decreasing in size distally; minor P1 carpus elongated, approximately 2.5 times longer than high, fingers without armature.

MEASUREMENTS (IN MM). — CPAG.RAN.I.64 (holotype): mpl = 17.6, mph = 24.2; CPAG.RAN.I.65 (paratype): mpl = 16.7, mph = 23; CPAG.RAN.I.66 (paratype): mpl = 15.6, mph = 19.4; CPAG.RAN.I.68 (paratype): mpl = 15.2, mph = 18.7; CPAG.RAN.I.71 (paratype): mpl = 12, mph = 15.1; CPAG.RAN.I.72 (paratype): mpl = 18.6, mph = 25.7. Additionally nine specimens deposited under collective number CPAG.RAN.I.77 were measured and evaluated graphically (Fig. 3B).

DESCRIPTION

Major P1

Ischium longer than high with spinose lower margin. Merus approximately two to three times longer than high, with longitudinal keel running along the midline of the outer lateral surface; lower half of the lateral surface tuberculated; upper margin slightly convex and smooth, lower margin armed with prominent spines and large bifid proximal hook. Carpus distinctly higher than long, upper margin straight, proximo-lower margin serrated; articulation with propodus distinctly

FIG. 4. — *Neocallichirus lakhraensis* Hyžný & Charbonnier, n. sp. from the Rbod Nala section (Ypresian, Lakhra Formation), Jhirak District, Sindh, Pakistan: **A**, **B**, paratype CPAG.RAN.I.65, major right male P1 chela (propodus with articulated dactylus) in outer (A) and inner (B) views; **C**, paratype CPAG.RAN.I.68, major right female P1 propodus with broken fixed finger, outer view; **D**, **E**, holotype CPAG.RAN.I.64, major right male P1 chela (propodus with articulated dactylus) in outer (**D**) and inner (**E**) views; **F**, paratype CPAG.RAN.I.66, major right female P1 chela (propodus with articulated dactylus), outer view; **G**, **H**, paratype CPAG.RAN.I.72, male with left major P1 cheliped showing propodus, carpus and merus (**G**) and right minor P1 cheliped showing merus, carpus, propodus and dactylus (**H**); **I**, paratype CPAG.RAN.I.70, major right P1 ischium with articulated merus and fragmentary carpus, outer view; **J**, paratype CPAG.RAN.I.71, major right male P1 cheliped (merus, carpus, propodus, dactylus), outer view**;** **K**, paratype CPAG.RAN.I.69, major left female P1 cheliped (dactylus, propodus, carpus, merus, ischium) with associated remains of P2 and P3. Photographs: L. Cazes and P. Loubry. Scale bar: 10 mm.

shorter than the entire length of proximal margin. Propodus stout, manus (palm) approximately as long as high, or higher than long; upper and lower margins parallel to each other, or slightly converging distally; upper margin keeled and smooth, lower margin keeled and strongly serrated, distal margin with large notch accompanied with a tooth, or only with a large triangular serrated tooth, just below the articulation with dactylus; both outer and inner lateral surfaces covered with unevenly spaced tubercles, inner surface containing fewer tubercles; fingers approximately as long as manus (palm) or distinctly longer; fixed finger slender with tuberculated ridge along its lateral surface, tip bent slightly upward, occlusal surface edentulous or armed with small teeth and with one blunt tooth at the midlength. Dactylus long and deep, upper margin with two spines proximally, occlusal surface strongly armed with peg-shaped teeth decreasing in size distally, tip of dactylus hooked.

Minor P1
Merus approximately 2.5 times longer than high, poorly preserved. Carpus approximately 2.5 times longer than high, upper and lower margins parallel to each other, proximo-lower border rounded. Propodus elongated, manus (palm) slightly longer than high, upper and lower margins parallel to each other; fixed finger approximately as long as manus (palm), occlusal surface edentulous. Dactylus long and slender, as long as fixed finger, not armed.

P2
Merus slender, longer than high. Carpus triangular in outline, diverging distally. Propodus approximately as long as high; fingers short.

P3
Poorly preserved.

P4-P5, other appendages, carapace and pleon
Unknown.

Comments
Neocallichirus lakhraensis Hyžný & Charbonnier, n. sp. differs from *N. khadroensis* Hyžný & Charbonnier, n. sp. by the arrangement of the teeth on the occlusal surface of the P1 dactylus (Fig. 5A$_{2,3}$) and the presence of well-developed granulated ridge along the fixed finger which is lacking in *N. khadroensis* Hyžný & Charbonnier, n. sp. Especially females of *N. lakhraensis* Hyžný & Charbonnier, n. sp. possess well-developed longitudinal ridge on the fixed finger (Figs 4F; 5D$_2$).

Morphologically, both above discussed species are remarkably similar to extant *N. karumba* (see comparisons in Fig. 5). Outline of the major P1 merus is virtually identical, as well as its armature and tuberculation (Fig. 5C$_{1-3}$). *Neocallichirus karumba*, however, possesses large elongated setal pores on the lateral surface of dactylus, at least in large males; such setal pores are missing in the material from Pakistan. Major difference which can be considered as taxonomically important on the species level is the development of the tooth below the articulation with dactylus and the tuberculation in the area of the notch. These characters are different in all three taxa. Large tubercles serving as bases of the tufts of setae on the propodal surface close to articulation with dactyli are present invariably in all specimens of *N. karumba* figured by Dworschak (2008), but they are absent in two new species described herein.

From fossil species, *N. khadroensis* Hyžný & Charbonnier, n. sp. and *N. lakhraensis* Hyžný & Charbonnier, n. sp. are rather close to *Callianassa tuberculata* Lőrenthey *in* Lőrenthey & Beurlen, 1929, from the Middle Eocene of Hungary and *N. borensis* Beschin, De Angeli, Checchi & Mietto, 2006, from the Late Eocene (Priabonian) of Italy (Fig. 6A-C). Both species shares with the Pakistani material general shape of propodus, tuberculation at the base of the dactylus and lateral surfaces of propodus. *Neocallichirus borensis* has several large tubercles in a row with setal pores on their tops, and in this respect it is very close to *N. karumba*, but differs from *N. khadroensis* Hyžný & Charbonnier, n. sp. and *N. lakhraensis* Hyžný & Charbonnier, n. sp. *Callianassa tuberculata*, herein considered congeneric with all above mentioned species, shares with *N. lakhraensis* Hyžný & Charbonnier, n. sp. similar armature of the dactylus, but differs in rather restricted tuberculation of the propodus and possession of large setal pores on the dactylus (Fig. 5D$_2$). Additionally, there is *Callianassa maxima* A. Milne-Edwards, 1870 (Fig. 6J-L), known only from a single (and apparently lost, see Sakai 1999: 103) subfossil specimen from Thailand (see Dworschak 2008: 75 for more details on other possible occurrences), which demonstrates a mixture of above mentioned characters including strong tuberculation and well-developed tooth-formula on the occlusal surface of dactylus. The species has been treated as *Neocallichirus* by Sakai (2011) and Hyžný & Karasawa (2012) and has confusing taxonomic history which does not need to be repeated here (for details see Dworschak 2008: 75, and Sakai 2011: 459).

There is one more fossil ghost shrimp reported from the Early Cenozoic of Pakistan, and hence *Neocallichirus wellsi* from the Drazinda Formation (Priabonian) of Domanda region (NW Frontier Province, Pakistan). *Neocallichirus wellsi* differs substantially from both new species from Pakistan with rectangular propodus converging distally with proportionately short fingers, distinctly longer carpus and merus with dissimilar armature on its lower margin (Schweitzer *et al.* 2004: fig. 4a-f).

PALAEOBIOLOGY

Sexual dimorphism

Sexual dimorphism expressed in the morphology of chelipeds (P1) is known in several ghost shrimp taxa (Hyžný & Klompmaker 2015, and references therein). Based on the comparison with the variations in extant *Neocallichirus karumba*, sexual dimorphism can be observed in the material

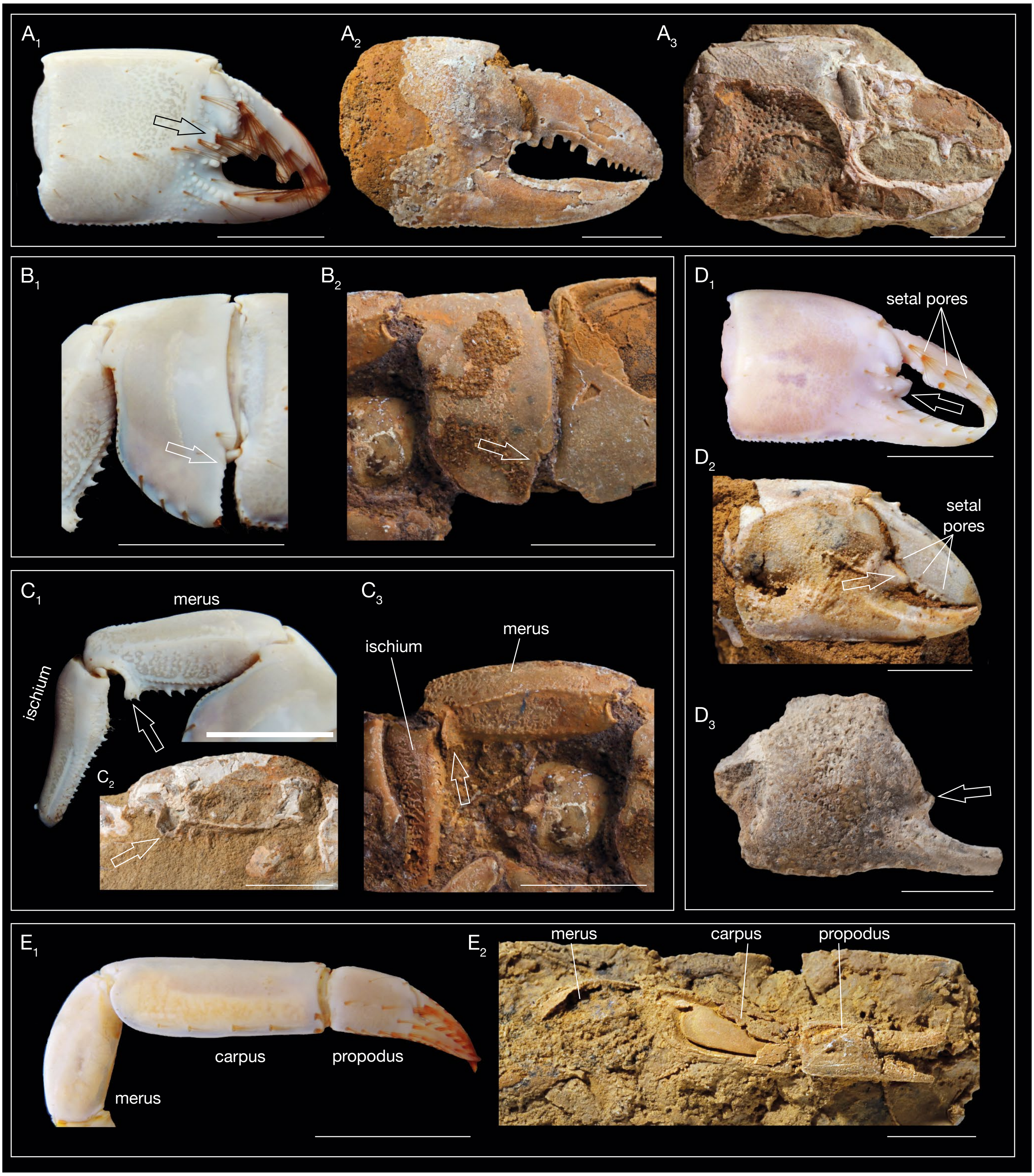

Fig. 5. — Comparison of extant and extinct *Neocallichirus* chelipeds: **A**, major male P1 chela of *Neocallichirus karumba* (Poore & Griffin, 1979) (**A$_1$**), *N. lakhraensis* Hyžný & Charbonnier, n. sp., holotype CPAG.RAN.I.64 (**A$_2$**) and *N. khadroensis* Hyžný & Charbonnier, n. sp., holotype CPAG.RAN.I.55 (**A$_3$**); **B**, major P1 carpus of *N. karumba* (**B$_1$**) and *N. lakhraensis* Hyžný & Charbonnier, n. sp., paratype CPAG.RAN.I.69 (**B$_2$**); **C**, major P1 merus of *N. karumba* (**C$_1$**), *N. khadroensis* Hyžný & Charbonnier, n. sp., paratype CPAG.RAN.I.63 (**C$_2$**) and *N. lakhraensis* Hyžný & Charbonnier, n. sp., paratype CPAG.RAN.I.69 (**C$_3$**); **D**, major female P1 chela of *N. karumba* (**D$_1$**), *N. lakhraensis* Hyžný & Charbonnier, n. sp., paratype CPAG.RAN.I.66 (**D$_2$**) and *N. khadroensis* Hyžný & Charbonnier, n. sp., paratype CPAG.RAN.I.59 (**D$_3$**); **E**, minor P1 cheliped of *N. karumba* (**E$_1$**) and *N. lakhraensis* Hyžný & Charbonnier, n. sp., paratype CPAG.RAN.I.72 (**E$_2$**). Specimens of *N. karumba* are deposited under NHMW 21937 (male) and NHMW 21938 (female). Photographs of extant specimens (immersed in alcohol): M. Hyžný; photographs of fossil specimens: L. Cazes and P. Loubry. Scale bars: 10 mm.

of two newly described species. Most of the specimens of *N. khadroensis* Hyžný & Charbonnier, n. sp. represent large males with typical notch at the base of the fixed finger just below the articulation with dactylus (Figs 2; 3A). Females do not possess such a well-pronounced notch (incision *sensu* Dworschak 2008); instead they have only a well-developed tooth (Fig. 2H, I). These differences are in accordance with observed sexual dimorphism in *N. karumba* (Dworschak 2008: figs 5c, d, k, l). Similarly, two morphotypes in the material of *N. lakhraensis* Hyžný & Charbonnier, n. sp. are observed and correspond to sexual dimorphs of *N. karumba* as figured by Dworschak (2008). Whereas large males typically exhibit notch at the base of the fixed finger, females have a well-developed tooth instead (Fig. 4C, F, K). Although in smaller specimens of *N. karumba* (total length less than 40 mm) the sexual dimorphism expressed in the morphology of chelipeds is difficult to determine, larger specimens clearly exhibit two morphotypes corresponding to males and females. As noted by Dworschak (2008: 83), only largest males show a deep notch in the propodus below the dactylus articulation. Interestingly, nearly all studied fossil specimens from Pakistan belonged to large individuals with estimated total length 8-12 cm, thus, the sexual dimorphic characters are observable in all of them.

Size of ghost shrimps

Because of the fossorial habits and difficulties in catching living animals (Kneer *et al.* 2013; Dworschak 2015), it is hard to estimate the maximum length of extant ghost shrimps. Dworschak (2015) noted that adult ghost shrimp body ranges from about 1.5 cm to approximately 16 cm (length from tip of the rostrum to end of the telson). Hyžný & Klompmaker (2015) assume that because large specimens have a greater fossilization potential, the fossil record can provide insight into the debate. In fact, the material of *Neocallichirus khadroensis* Hyžný & Charbonnier, n. sp. and *N. lakhraensis* Hyžný & Charbonnier, n. sp. represents remains of exceptionally large ghost shrimps. Based on extrapolation from the data of *N. karumba* (assuming the growth rate was the same for the fossil taxa discussed herein), it is estimated that largest specimens of *N. khadroensis* Hyžný & Charbonnier, n. sp. and *N. lakhraensis* Hyžný & Charbonnier, n. sp. were up to 12 and 11 cm long, respectively. The largest specimen of *Neocallichirus tuberculatus* n. comb. (Fig. 6E) could belong to even longer animal reaching total length exceeding 18 cm. Similarly long was probably also an individual to which the chela of *N. maximus* belonged (Fig. 6J-L). According to Milne-Edwards (1870), the chela was more than 6 cm long (including the fixed finger) and approximately 3.5 cm high and is therefore of similar size as the largest *N. tuberculatus* n. comb.

In *N. karumba*, the development of tuberculation on chelipeds is correlated with size. Large specimens of *N. karumba* (total length exceeding 40 mm) shows more tubercles on the lateral surfaces of the propodus than smaller ones (Dworschak 2008). Nearly all specimens of *N. khadroensis* Hyžný & Charbonnier, n. sp. and *N. lakhraensis* Hyžný & Charbonnier, n. sp. belonged to exceedingly large individuals and indeed, all of them are tuberculated. The prevalence of large specimens in the studied samples is not surprising given the higher fossilization potential of larger specimens (Hyžný & Klompmaker 2015).

PALAEOBIOGEOGRAPHY

Distribution of the "*karumba* group"

Schweitzer *et al.* (2004) noted that the genus *Neocallichirus* appears to have occupied a Tethyan distribution in its early history, with localities in Pakistan (Schweitzer *et al.* 2004), Italy (Beschin *et al.* 2002) and southern California (Schweitzer & Feldmann 2002). As noted above, the generic concept of *Neocallichirus* is rather broad and the genus as recognized in the fossil record may well represent a mixture of several distinct genera (Hyžný & Hudáčková 2012). Hyžný & Karasawa (2012: table 1) doubted attribution of many fossil taxa to *Neocallichirus*, although without detailed discussion on the issue. The revision of all fossil *Neocallichirus* species is strongly needed.

Here the discussion on the palaeobiogeography is provided only for taxa sharing the same cheliped morphology (and assumed to be a monophyletic grouping). This group of species are provisionally called the "*karumba* group" based on *Neocallichirus karumba*, the best documented species in the group.

Neocallichirus khadroensis Hyžný & Charbonnier, n. sp. from the Danian of Pakistan and probable Aquitanian of India is the oldest representative of the "*karumba* group" as recognized herein. *Neocallichirus lakhraensis* Hyžný & Charbonnier, n. sp. is known only from the Ypresian of Pakistan. *Neocallichirus tuberculatus* n. comb. is known from the Middle Eocene of Hungary (Lőrenthey & Beurlen 1929). Its occurrence suggests that the "*karumba* group" was widespread across much of the Western Tethys during the Middle Eocene. In the Late Eocene, the lineage was still present in the Western Tethys, as *Neocallichirus borensis* from the Priabonian of Italy witnesses (Beschin *et al.* 2006). This species is known only by propodi with dactyli. Propodus is quadrate or higher than long and the lateral surfaces of the propodus are tuberculated at the base of the fixed finger. There is a row of tubercles topped with setal pores on the outer lateral surface at the articulation with dactylus similarly as there is in *Neocallichirus karumba*.

Callianassa birmanica Noetling, 1901, was described from the Miocene of Myanmar. Noetling (1901: pl. 24, figs 3-5) figured several isolated propodi with broken fixed fingers. They are distinctly higher than long and strongly tuberculated. Just below the articulation with dactylus there is a notch with a tooth above it. Based on these characters, close relationship to *Neocallichirus karumba* is postulated and a new combination is proposed, *Neocallichirus birmanicus* n. comb.

Neocallichirus dijki (Martin, 1883), originally described as *Callianassa*, is known from the Miocene of Java and the Philippines (Martin 1883-1887; Smith 1913; Karasawa *et al.* 2008) and was transferred to *Neocallichirus* based on the similarities to *Neocallichirus karumba* by Karasawa *et al.* (2008). Both, *N. birmanicus* n. comb. and *N. dijki* suggests further spreading of the "*karumba* group" from its centre of origin further eastwards.

Subfossil *Neocallichirus maximus* has been reported from Thailand and extant *Neocallichirus karumba* is known from Australia (Queensland), Papua New Guinea, Taiwan, Singapore, Indonesia, Thailand, and India (Dworschak 2008). Today, the "*karumba* group" is spread across large areas of the Indo-West Pacific.

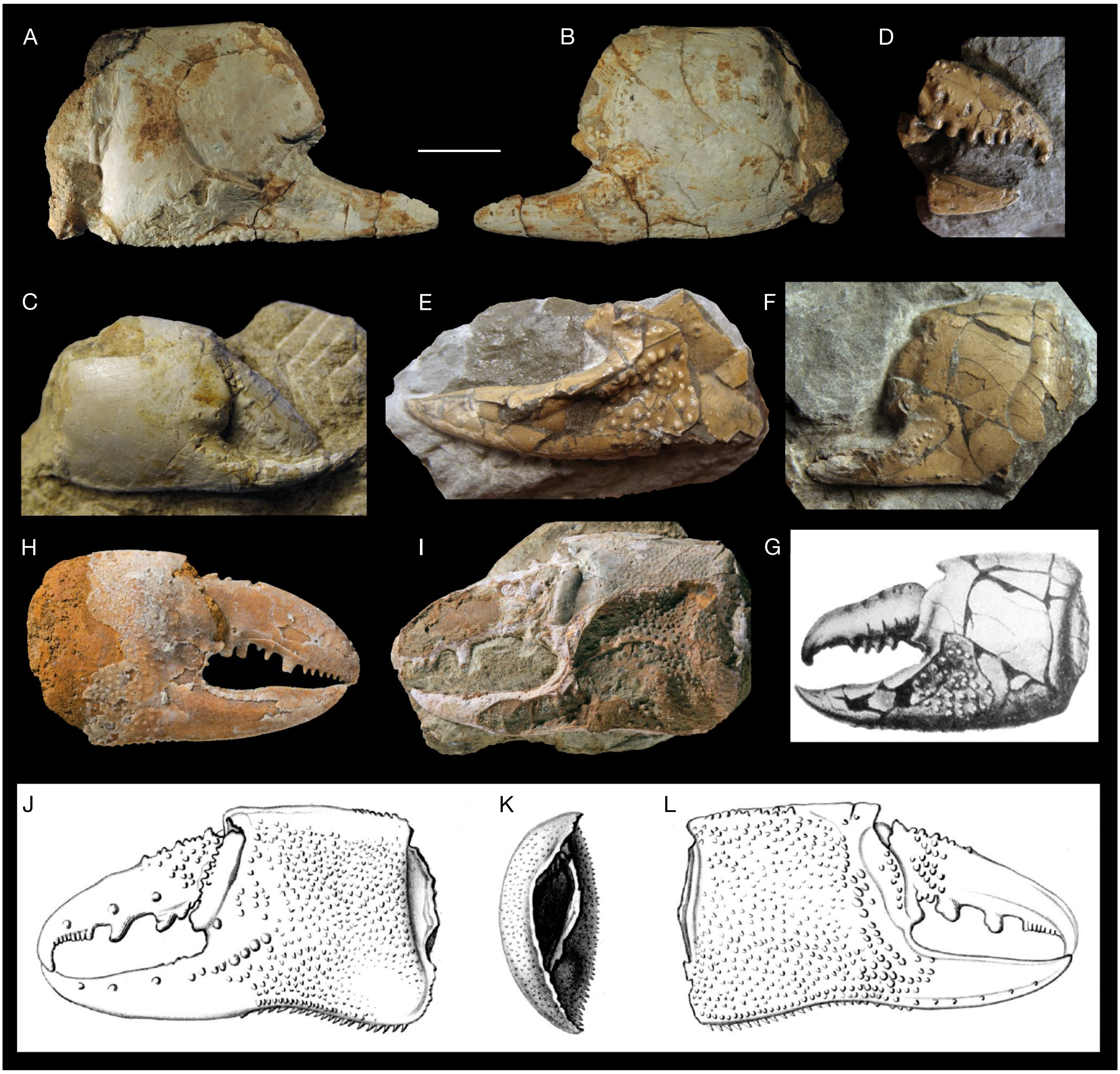

Fig. 6. — **A**-**C**, *Neocallichirus borensis* Beschin, De Angeli, Checchi & Mietto, 2006; **A**, **B**, holotype MCZ 2423; **C**, MCZ 2427; **D**-**G**, *Neocallichirus tuberculatus* (Lőrenthey *in* Lőrenthey & Beurlen, 1929) n. comb.; **D**-**F**, syntypes MFGI E.9465; **H**, *Neocallichirus lakhraensis* Hyžný & Charbonnier, n. sp., holotype CPAG.RAN.I.64; **I**, *Neocallichirus khadroensis* Hyžný & Charbonnier, n. sp., holotype CPAG.RAN.I.55; **J**-**L**, *Neocallichirus maximus* (A. Milne-Edwards, 1870). Photographs: M. Hyžný (A-F), and L. Cazes and P. Loubry (H-I). Scale bar: A-I, 10 mm. J-L, not to scale.

MAIN CONCLUSIONS

The fossil record is full of gaps and it is difficult to reconstruct migration pattern of the "*karumba* group". The oldest occurrence (Paleocene of Pakistan) and all known Miocene occurrences (Java and Philippines) largely overlap with extant distribution of the "*karumba* group". Today, however, there are no representatives of the group in the Mediterranean, although during the Eocene they were present in the area as suggested by Hungarian and Italian occurrences. Interestingly, if the Pakistani occurrences were not known, the oldest occurrence of the group would be in the circum-Mediterranean area and would match the "Go East!" scenario of Harzhauser *et al.* (2007, 2008) or concept of hopping biodiversity hotspots of Renema *et al.* (2008). The latter authors postulated relocation of the centres of biodiversity during the last 40 million years in the Eastward direction from the Western Tethys to Indo-Australian Archipelago. However, oldest occurrences of the "*karumba* group" in the Eastern Tethys may suggest gradual contraction of the centre of origin rather than its relocation. Similarly, the richest Early Eocene assemblage of volutid gastropods recently reported from the Lakhra Formation

(Merle *et al.* 2014) may suggest the same. At present, we do not consider the data presented herein are sufficient to resolve this issue; more research is needed to test which concept of the two mentioned above is better in explaining the observed distribution pattern of the "*karumba* group". For now, it can be concluded, that at the genus level, a relative homogeneity of the ghost shrimps is observed between the Eastern and the Western Tethyan regions, as already suggested by Merle *et al.* (2014) for volutid gastropods.

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