Diversity and distribution of fiddler crabs (Crustacea: Brachyura: Ocypodidae) around the Arabian Sea

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ABSTRACT

Nine species of fiddler crabs (Crustacea: Ocypodidae: Gelasiminae) are known from the Arabian Sea and adjacent waters (Red Sea, Gulf of Aden, Gulf of Oman and Arabian/Persian Gulf): five species of *Austruca*, one *Cranuca*, two *Gelasimus* and one *Tubuca*. *COI* sequence data matches morphological species boundaries and shows high connectivity within each. The fauna is highly endemic, with three species of *Austruca* confined to this region: *A. albimana*, *A. iranica* and *A. sindensis*, and four other species are restricted to the Indian Ocean. *Austruca albimana* and *A. iranica* speciated locally and now have narrowly overlapping ranges in Oman. Our results confirm the westernmost distributions of *Austruca annulipes* and *Tubuca alcocki* are Pakistan and the Red Sea, respectively. A key for the nine species is also provided to help identification.

Key words: Fiddler crabs, *Austruca*, *Cranuca*, *Gelasimus*, *Tubuca*, Mitochondrial cytochrome c oxidase subunit I (*COI*), Barcodes.

BACKGROUND

Spanning more than half of the tropics, the Indo-West Pacific (IWP) is the largest and most diverse marine biogeographic region, recognized as a unit partly because many species range across its vast extent, from East Africa to the remote islands of Polynesia. Understanding diversification in this vast region relies in part on documenting the ranges, connectivity, and relationship of species. Genetic evidence is especially illuminating and reveals narrower ranges and cryptic diversity in some taxa, while confirming region-wide panmixia in others (Bickford et al. 2007; Teske et al. 2008; Lourenço et al. 2017). A major task today is to reevaluate species diversity and distributions established via morphology in the past, using integrative taxonomic methods.

The western Indian Ocean (WIO) is perhaps the most heterogeneous part of the IWP and genetic scrutiny, especially, has led to the recognition of greater diversity and more complex distributional patterns (DiBattista et al. 2015). The Arabian Sea and adjacent waters (Red Sea, Gulf of Aden, Gulf of Oman, Arabian/Persian Gulf) (Fig. 1) stand out as especially complex, with great regional and seasonal fluctuations in temperature, productivity, oxygenation, etc. This regional heterogeneity has led to substantial differences in the biota across this relatively small area, and both regional and local endemism, especially in the Red Sea, Gulf of Aden, and Oman (DiBattista et al. 2016; Wehe and Fiege 2002; Wells 2000).

Currently 49 species of fiddler crabs are recognized in the IWP region (Crane 1975; Shih et al. 2016 2018 2019; Shih and Poupin 2020), and the diversity is as high as 23 species around the Coral Triangle (also known as the Malay Archipelago or the Indo-Australian Archipelago = IAA; Lohman et al. 2011). However, only 13 species are recorded from the WIO (from eastern Africa to western Indian subcontinent), with an additional questionable record of *Tubuca paradussumieri* (Bott, 1973) from Madagascar (Shih et al. 2018: 49). The genus *Cranuca* and seven species, viz. *Austruca albimana* (Kossmann, 1877), *A. iranica* (Pretzmann, 1971), *A. occidentalis* (Naderloo, Schubart & Shih, 2016), *A. sindensis* (Alcock, 1900), *Cranuca inversa* (Hoffmann, 1874), *Paraleptuca chlorophthalmus* (H. Milne-Edwards, 1837) and *Tubuca urvillei* (H. Milne-Edwards, 1852), are endemic to this area.

In the northern part of the WIO, the Arabian Sea (including the coastal areas of Yemen, Oman, Pakistan and western India) and adjacent waters (including the Red Sea, Gulf of Aden, Gulf of Oman, and Arabian/Persian Gulf) (Fig. 1), nine species of

fiddler crabs have been reported, viz. *Austruca albimana*, *A. annulipes* (H. Milne-Edwards, 1837), *A. iranica*, *A. sindensis*, *A. variegata* (Heller, 1862), *Cranuca inversa*, *Gelasimus hesperiae* (Crane, 1975), *G. tetragonon* (Herbst, 1790) and *Tubuca alcocki* Shih, Chan & Ng, 2018 (Shih et al. 2009 2018 2021; Naderloo et al. 2010; Saher et al. 2014; Naderloo 2017). Most studies of fiddler crabs in this region have focused on taxonomy and distribution, with a few on molecular phylogenetics (e.g. Shih et al. 2009 2018), population genetics (Shih et al. 2015; Odhano et al. 2018), larval development (Hashmi 1968; Ghory and Siddiqui 2006; Al-Aidaroos 2013), behavior and ecology (Mokhlesi et al. 2011; Saher and Qureshi 2012 2017).

Studies of fiddler crabs around the Arabian Sea are comparatively few compared with other areas of the IWP, especially East Asia, Southeast Asia and Australia. In this study we assess each species in this fauna based on combined morphological and genetic evidence, update their distribution based on the literature and new specimens, and provide a key to the fauna. We also discuss genetic connectivity and origin of the fauna.

MATERIALS AND METHODS

Specimens of fiddler crabs collected from the Arabian Sea and adjacent waters (including the Red Sea, Gulf of Aden, Gulf of Oman and Arabian/Persian Gulf) (Table 1; Figure 1) were preserved in 70% to 95% ethanol and deposited in the Centre of Advanced Study in Marine Biology, Annamalai University (CASAU), Parangipettai, Tamil Nadu, India; the Zoological Collections of the Department of Life Science, National Chung Hsing University, Taichung, Taiwan (NCHUZOOL) and the Zoological Reference Collection, Raffles Museum of Biodiversity Research, National University of Singapore (ZRC). Specimens deposited in Muséum National d'Histoire naturelle, Paris, France (MNHN); Museo Zoologico dell'Università di Firenze, Italy (MZUF); the Naturhistorisches Museum, Wien, Austria (NHMW); Steinhardt National Collections of Natural History, Tel Aviv University, Israel (TAU); and Florida Museum of Natural History, University of Florida, Florida, USA (UF) were also examined. The following abbreviations are used: CW = carapace width, CL = carapace length. In the synonymy of each species, only the references to the original description, relevant revisions and records from around the Arabian Sea are included.

Genomic DNA was isolated from muscle tissue using kits (see Shih et al. 2016 for details). A portion of the *COI* gene was amplified with polymerase chain reaction

(PCR) using the primers LCO1490, HCO2198 (Folmer et al. 1994), COL14 (Roman and Palumbi 2004), COL6, COH6 (Schubart 2009) and ICOUB (Huang et al. 2021), or the newly designed primers LCOB (5'-CAAAYCATAAAGAYATYGG-3'), HCOex (5'-GCTCATACTACAAATCCTAAA-3'), HCOex2 (5'-GCTCANACTACAAATCCTAA-3') and HCOex3 (5'-GCTCANACTACRAATCCTA-3'). PCR conditions for the above primers were 40 cycles of denaturation for 50 s at 94°C, annealing for 70 s at 45–47°C, and extension for 60 s at 72°C, followed by extension for 10 min at 72°C. Sequences were obtained by automated sequencing (Applied Biosystems 3730, USA) and deposited into GenBank (Table 1).

Additional sequences of *COI* from related *A. occidentalis* from eastern Africa as well as *A. variegata* from the eastern Indian Ocean were downloaded from GenBank or sequenced from specimens with the same methods. A neighbor-joining (NJ) tree was generated with MEGA (vers. 11, Tamura et al. 2021), using the Kimura (1980) 2-parameter (K2P) model with the complete deletion option. K2P distances among specimens were also calculated in MEGA.

RESULTS

Molecular analyses of *COI*

Specimens of eight of the nine species of fiddler crabs recorded from the region were represented among the specimens studied, and *COI* sequences were successfully generated from 65 specimens representing all eight species (Table 1; Fig. 4).

Morphological and genetic identifications were fully congruent; there was no evidence for cryptic species in the region. Intra-specific variation was small, <0.8% (K2P) for all species. There was no pattern of geographic differentiation across the areas sampled, including samples from the eastern Indian Ocean and western Pacific Ocean, for species for which samples were available there. Interspecific divergences were all >10%, lowest between *G. hesperiae* and *G. tetragonon*.

TAXONOMY

Family Ocypodidae Rafinesque, 1815

Subfamily Gelasiminae Miers, 1886 (sensu Shih et al. 2016)

Genus *Austruca* Bott, 1973

Austruca albimana (Kossmann, 1877)

(Fig. 2A, B)

Gelasimus annulipes var. *albimana* Kossmann, 1877: 53 (type locality: Red Sea); Crane 1975: 298.

Uca annulipes – Nobili 1906a: 312; Nobili 1906b: 150; Maccagno 1928: 35, fig. 20; Hornby 1997: 14 [part?].

Uca (*Celuca*) *lactea annulipes* – Crane 1975: 298, 611 [part]; Lewinsohn 1977: 61.

Uca lactea albimana – Price et al. 1987: 456.

Uca albimana – Yamaguchi 1994: 153; Shih et al. 2009: 376; Shih et al. 2013: 643.

Uca annulipes albimana – Apel and Türkay 1999: 133; Simões et al. 2001: 86.

Uca (*Paraleptuca*) *albimana* – Ng et al. 2008: 241.

Uca (*Austruca*) *albimana* – Naderloo et al. 2010: 4, figs. 1a–l, 4a, 6a, b; Naderloo et al. 2015: 409; El-Sayed et al. 2016: 7, pls. 3A, B, 4A, D, G, J.

Austruca albimana – Shih et al. 2016: 153, 168; Naderloo 2017: 412, figs. 37.10, 37.13a; Baakdah 2018: 51; AAJ Kumar 2019: 53, figs. 2g–i, 3a–d; Sasaki 2019: 12423.

Austruca (*Austruca*) *albimana* – Rosenberg 2019: 734.

Material examined: **Egypt**: 2 ♂♂ (15.3, 15.2 mm) (NCHUZOOL 13242), Nabq-El Arwashie, Sinai, Red Sea, coll. S. Barbaresi et al., 14 Oct. 2004. **Saudi Arabia**: 3 ♂♂ (10.4–12.1 mm) (NCHUZOOL 15085), 1 ♀ (9.7) (NCHUZOOL 15002), 1 ♀ (11.8 mm) (NCHUZOOL 15003), Al Darb (17°26'53.4"N, 42°17'03.3"E), coll. A. J. Kumar, 25 Apr. 2017. **Oman**: 1 ♂ (11.8 mm) (UF 7790), Bar al Hikman Peninsula, coll. V. Bonito and G. Paulay, 22–24 Jan. 2005; 1 ♂ (17.2 mm) (UF 7789), Bar Al Hikman Peninsula, coll. V. Bonito and G. Paulay, 22–24 Jan. 2005; 1 ♂ (not measured) (UF 58686), Bandar Al Khiran sand flat (23.50856ºN, 58.73186ºE), coll. S. Brown, D. Uyeno, G. Koblasova and M. Cherneva, 26. Jan. 2020.

Distribution: Egypt (Red Sea), Saudi Arabia (Red Sea), Eritrea, Djibouti, Yemen (including Socotra), Oman and UAE.

Remarks: Because the Red Sea is semi-enclosed, *Austruca albimana* was thought to be endemic to this area (Shih et al. 2009). However, Naderloo et al. (2010) and Naderloo (2017) extended its distribution to the southern coast of the Gulf of Oman and the Arabian/Persian Gulf (Oman and UAE). Comparisons of *COI* sequences from specimens from central Oman (Barr al Hikman) and the Red Sea demonstrate genetic connectivity across this area (Fig. 4).

Austruca annulipes (H. Milne Edwards, 1837)

(Fig. 2C, D)

Cancer vocans minor Herbst, 1782: 81, pl. 1 (10) [nomen oblitum]; Shih et al. 2021: 208, fig. 1A.

Gelasimus annulipes H. Milne Edwards, 1837: 55, pl. 18 (10–13) (type locality: mer des Indes" (= Indian Ocean)) [nomen protectum]; Kossmann 1877: 53; Kingsley 1880: 148, pl. 10(22) [part]; Alcock 1900: 353; Chhapgar 1957: 508, pl. 13j–o.

Uca (*Celuca*) *lactea annulipes* – Crane 1975: 298, 611, figs. 18A–C, 19I–N, 20D–F, 24N–O, 27I, J, 29D, 32L, M, 41A, 54I, II, 69D, pls. 39A–D, 40C, D [part].

Uca annulipes – Tirmizi and Ghani 1996: 105, fig. 40; Shih et al. 2009: 376; Shih et al. 2013: 643; Saher et al. 2014: 672.

Uca (*Paraleptuca*) *annulipes* – Ng et al. 2008: 241.

Uca (*Austruca*) *annulipes* – Naderloo et al. 2010: 7, figs. 2a–h, 3a–e, 4b, 12a–c; Trivedi et al. 2015: 27.

Uca lactea annulipes – Trivedi et al. 2012: 17, 20, fig. 3c; Beleem et al. 2014: 420, 422, pl. 2.

Austruca annulipes – Shih et al. 2016: 153, 168, fig. 8A; Trivedi et al. 2018: 53; Beleem et al. 2019: 15; Sasaki 2019: 12424; Shih et al. 2021: 212, fig. 2; Pati et al. 2022: 526, fig. 12A–D.

Austruca lactea – Beleem et al. 2019: 15.

Austruca (*Austruca*) *annulipes* – Rosenberg 2019: 734.

Material examined: **Pakistan**: 3 ♂♂ (15.5–20.8 mm) (NCHUZOOL 15088), backwater mangrove area, Sandspit, Karachi, coll. N. U. Saher, 10 Dec. 2020. **India**: 2 ♂♂ (13.5, 14.6 mm) (ZRC 2016.0191), Narayan Sarovar, Gulf of Kachchh, Gujarat, coll. 26 Mar. 2015; 12 ♂♂ (7.2–14.7 mm), 8 ♀♀ (5.6–9.8 mm), 1 ovig. ♀ (11.4 mm) (NCHUZOOL 15086), Dongri, Uttan, Mira Bhayandar, Maharashtra, coll. H.-N. Chen

et al., 16 Mar. 2010; 6 ♂♂ (8.2–10.6 mm), 2 ♀♀ (6.5, 9.6 mm) (NCHUZOOL 15087), Mumbai, coll. H.-N. Chen et al., 17 Mar. 2010.

Distribution: Pakistan, India, Myanmar, Thailand, Malay Peninsula, Singapore, Indonesia, Borneo, Vietnam, and China (Hainan).

Remarks: *Austruca annulipes* was thought to be widely distributed in the IWP (Crane 1975; Naderloo et al. 2010). However, Shih et al. (2013) showed the specimens from eastern Africa represent a different species (as "*Uca* aff. *annulipes*"), later described as *Uca occidentalis* Naderloo, Schubart & Shih, 2016 (Naderloo et al. 2016). *COI* sequences show minimal genetic divergence suggesting good connectivity across the remainder of the species' range from Pakistan to China (Fig. 4). Saher et al. (2014) noted that *A. iranica* and *A. annulipes* are sympatric in Pakistan, confirmed with *COI* data here.

Austruca iranica (Pretzmann, 1971)

(Fig. 2E, F)

Gelasimus lacteus – Alcock, 1900: 355.

Uca annulipes – Stephensen 1946: 189; Pretzmann 1971: 481; Al-Ghais and Cooper 1996: 419, figs. 7, 8; Hornby 1997: 14 [part?]; Tirmizi and Ghani 1996: 105 [part; not fig. 40]; Mokhlesi et al. 2011: 245.

Uca annulipes iranica Pretzmann 1971: 481, pl. 5, figs. 11, 12 (type locality: Bandar-Abbas, Iran).

Uca (*Celuca*) *lactea annulipes* – Crane 1975: 298, 611 [part].

Uca annulipes iranica – Apel and Türkay 1999: 133.

Uca iranica – Shih et al. 2009: 376; Naderloo et al. 2013: 450; Shih et al. 2013: 643.

Uca (*Austruca*) *iranica* – Naderloo et al. 2010: 14, figs. 6c–f, 7a, 8a, 9a–k; Naderloo and Türkay 2012: 54; Saher et al. 2014: 669, figs. 1–4; Naderloo et al. 2015: 409.

Austruca iranica – Shih et al. 2016: 153, 168, fig 8C; Naderloo 2017: 413, figs. 37.11, 37.13b; Trivedi and Vachhrajani 2017: 82, figs. 4, 5; Trivedi et al. 2018: 54; Beleem et al. 2019: 15; Sasaki 2019: 12429; Pati et al. 2022: 527.

Austruca (*Austruca*) *iranica* – Rosenberg 2019: 734.

Material examined: **Oman**: 1 ♂ (13.8 mm) (UF 7791), Bar Al Hikman Peninsula, coll. V. Bonito and G. Paulay, 22–24 Jan. 2005; 1 ♀ (10.8 mm) (UF 7752), Bar Al

Hikman Peninsula, coll. V. Bonito et al., 24 Jan. 2005. **Iran**: 1 ♂ (16.4 mm) (NCHUZOOL 15090), Qeshm I., Hormozgan Prov., coll. Jun. 2008; 2 ♂♂ (12.4, 14.0 mm), 1 ♀ (13.8 mm) (NCHUZOOL 13245), 1 ovig. ♀ (12.1 mm) (NCHUZOOL 13247), Gavbandi, Hormozgan, coll. E. Kamrani, Jul. 2008; 3 ♂♂ (13.4–16.4 mm) (NCHUZOOL 13248), 1 ♀ (11.0 mm) (NCHUZOOL 13246), Qeshm I., Hormozgan Prov., coll. E. Kamrani, Jul. 2008; 6 ♂♂ (12.8–15.7 mm), 2 ♀♀ (12.4, 13.9 mm) (NCHUZOOL 15089), Dokohak, Qeshm I, Hormozgan Prov., coll. E. Kamrani, 23 Jan. 2013. **Pakistan**: 1 ♂ (18.7 mm), 1 ♀ (15.2 mm) (NCHUZOOL 15091), Sandspit, Karachi, Sindh, coll. 6 Mar. 2013.

Distribution: Oman, Iran, Pakistan and northwestern India.

Remarks: Although *A. iranica* was thought to be restricted to the Arabian/Persian Gulf (Shih et al. 2009), this is unlikely as the Gulf is young and was dry land during the last glacial maximum at 18,000 year BP (Lambeck 1996). Later studies showed its distribution extended eastward to the Gulf of Oman, Pakistan and northwestern India (Naderloo et al. 2010; Saher et al. 2014; Naderloo 2017; Trivedi and Vachhrajani 2017). Here we record this species from the Arabian Sea coast of Oman, a new western distributional limit, where it co-occurs in the same coastal mangrove with *A. albimana*. *COI* sequence data shows good connectivity across the distribution of the species (Fig. 4).

Austruca sindensis (Alcock, 1900)

(Fig. 2G, H)

Gelasimus inversus var. *sindensis* Alcock 1900: 356 (type locality: Karachi, Pakistan).

Uca (*Amphiuca*) *inversa sindensis* – Crane 1975: 107, 599, figs. 69j, pl. 16E–H.

Uca sindensis – Collins et al. 1984: 318, figs. 2, 3a–e, h, 4a, b, f, h; Apel and Türkay 1999: 134; Mokhlesi et al. 2011: 245; Saher and Qureshi, 2012: 124; Naderloo et al. 2013: 450; Shih et al. 2013: 643; Beleem et al. 2014: 422; Saher et al. 2014: 672.

Uca (*Paraleptuca*) *sindensis* – Ng et al. 2008: 241; Naser et al. 2010: e87 (pp. 1, 2), fig 2; Naderloo and Türkay 2012: 54; Naderloo et al. 2015: 409; Trivedi et al. 2015: 27.

Austruca sindensis – Shih et al. 2016: 153, 168, fig 8G; Naderloo 2017: 414, figs. 37.12, 37.13c; Odhano et al., 2018: 313; Trivedi et al. 2018: 54; Beleem et al. 2019: 15; Sasaki 2019: 12439; Pati et al. 2022: 528.

Austruca (*Sinduca*) *sindensis* – Rosenberg 2019: 734.

Material examined: **Iraq**: 2 ♂♂ (16.1 mm, broken) (ZRC 2010.0103), Khur Al-Zubair. **Iran**: 1 ♀ (12.9 mm) (NCHUZOOL 15092), Qeshm I. Hormozgan, coll. Jun. 2008; 1 ♂ (16.3 mm), 3 ♀♀ (10.8–11.7 mm) (NCHUZOOL 13576), Qeshm I. Hormozgan, coll. E. Kamrani, Jul. 2008; 11 ♂♂ (6.9–12.3 mm) (NCHUZOOL 13645), Bandar Abbas, Hormozgan, coll. E. Kamrani, 3 Feb. 2013. **Pakistan**: 2 ♂♂ (12.1–12.9 mm), 2 ♀♀ (9.3–11.2 mm) (NCHUZOOL 13643), Sonmiani, Balochistan, coll. N. U. Saher, 14 May 2012; 8 ♂♂ (9.2–12.0 mm) (NCHUZOOL 13644), Sonmiani, Balochistan, coll. N. U. Saher, 9 Feb. 2013; 2 ♂♂ (18.7–19.0 mm), 2 ♀♀ (14.3–15.8 mm) (NCHUZOOL 13641), Sandspit, Karachi, Sindh, coll. N. U. Saher, 14 May 2012; 9 ♂♂ (10.2–17.4 mm) (NCHUZOOL 13642), Sandspit, Karachi, Sindh, coll. N. U. Saher, 6 Mar. 2013.

Distribution: Kuwait, Iraq, Iran, Pakistan and western India.

Remarks: *Austruca sindensis* was described from Karachi, Pakistan (Alcock 1900) and later reported from adjacent areas, including Kuwait, Iraq, Iran and western India (Shih et al. 2015; Trivedi et al. 2018; Beleem et al. 2019). There are no records of this species from the southern coasts of the Arabian/Persian Gulf and the Gulf of Oman (Naderloo 2017).

Austruca variegata (Heller, 1862)

Gelasimus variegatus Heller, 1862: 521 (type locality: Madras, India); Kingsley 1880: 154; Crane 1975: 326.
Gelasimus perplexus – Heller 1865: 38, pl. 5(4); A. Milne-Edwards 1873: 274.
Uca triangularis – Kappalli et al. 2012: 967; Supriya et al. 2017: 647.
Uca (*Celuca*) *triangularis bengali* Crane 1975: 286, figs. 24I, J, 32N, O, 59A, 68C, 101 [part].
Austruca bengali – Shih et al. 2016: 153 [part]; Trivedi et al. 2018: 54.
Austruca triangularis – Trivedi et al. 2018: 54 [part].
Cranuca inversa – Trivedi et al. 2018: 54.
Austruca variegata — Sasaki 2019: 12442; Shih et al. 2019: 4, figs. 1a–c, 2, 3a, b, 4a–d, 5a–d, 6a–c, f, 7a, b, e, 8a–d, 9.

Material examined: Lectotype, ♂ (CW 16.7 mm, PL 24.7 mm) (NHMW 25656; original Novara label, #74 = AN.1866.II.74.; labeled as "*Gelasimus perplexus* M.

Edw."), Madras, India, coll. Johann Zelebor.

Distribution: Southwestern and eastern India, Sri Lanka and Bangladesh.

Remarks: *Austruca variegata* ranges mostly along the Bay of Bengal. This species has been frequently misidentified, as *A. bengali*, *A. perplexa*, *A. triangularis* and *Cranuca inversa* (see Shih et al. 2019). Shih et al. (2019) resurrected this species with morphological and molecular evidence. Although no specimens from western Indian were examined for our study, this species is recorded from the area by Kappalli et al. (2012) and Supriya et al. (2017) as "*Uca triangularis*", and its distribution appears to extend to the Laccadive Sea (Shih et al. 2019).

Genus *Cranuca* Beinlich & von Hagen, 2006

Cranuca inversa (Hoffmann, 1874)

(Fig. 3A, B)

Gelasimus inversus Hoffmann 1874: 19, pl. 4 (23–26) (type locality: Nossi-Faly, Madagascar); Kingsley 1880: 155.

Uca inversa – Pocock et al. 1903: 213, 216; Nobili 1906a: 312; Nobili 1906b: 151; Maccagno 1928: 26, fig. 13; Collins et al. 1984: 318, 324, figs. 3f, g, 4c–e, g; Yamaguchi 1994: 164; Al-Ghais and Cooper 1996: 421; Hornby 1997: 14; Apel and Türkay 1999: 134; Simões et al. 2001: 86; Hogarth and Beech 2002: 24, 1 unnumbered fig.; Naderloo et al. 2013: 450; Shih et al. 2013: 643.

Uca (*Amphiuca*) *inversa inversa* – Crane 1975: 105, 599, figs. 39G, 69I, pl. 16A–D; Lewinsohn 1977: 63.

Uca inversa inversa – Frasen et al. 1997: 150; Price et al. 1987: 456.

Uca (*Cranuca*) *inversa* – Beinlich and von Hagen 2006: 10, fig. 5a; Ng et al. 2008: 240; Naderloo and Türkay 2012: 53; Naderloo et al. 2015: 409; El-Sayed et al. 2016: 9, pls. 3C, D, 4B, E, H, K.

Cranuca inversa – Shih et al. 2016: 153, 169, fig 9A; Naderloo 2017: 416, fig. 37.13d, 37.14; Baakdah 2018: 51; AAJ Kumar 2019: 54, figs. 2j, 3e–g; Rosenberg 2019: 734; Sasaki 2019: 12443.

Material examined: **Egypt**: 1 ♂ (17.4 mm) (TAU SLR 1475), Nabq, Sinai, coll. 19 May 1968; 1 ♀ (18.1 mm) (NCHUZOOL 13623), Nabq-El Arwashie, Sinai, coll. S.

Barbaresi et al., 14 Oct. 2004. **Saudi Arabia**: 4 ♂♂ (16.5–19.9 mm) (NCHUZOOL 15093), Al Darb (17°26'53.4"N, 17°26'53.4"N), coll. A. J. Kumar, 25 Apr. 2017.

Distribution: South Africa to Somalia, Madagascar, Egypt (Red Sea), Saudi Arabia (Red Sea), Eritrea, Yemen, Oman, UAE and Iran.

Remarks: The southernmost record of this species from Natal, South Africa (Crane 1975) needs to be substantiated; confirmed records extend southward to Kosi Bay (near the Mozambican border) (Peer et al. 2015). The northernmost record is from Qeshm Island, Iran along the northern coast of the Arabian/Persian Gulf (Naderloo 2017). *COI* data confirm connectivity of populations between the Red Sea and the East African coast (Fig. 4).

Genus *Gelasimus* Latreille, 1817

Gelasimus hesperiae (Crane, 1975)

(Fig. 3C, D)

?*Gelasimus tetragonon* var. *spinicarpa* Kossmann, 1877: 52 (type locality: Red Sea); Crane 1975: 80; Rosenberg 2013:494.

Gelasimus cultrimanus – Kingsley 1880: 140, pl. 9(7) [part].

Gelasimus marionis – Kingsley 1880: 141, pl. 9(8) [part].

Uca Marionis – Nobili 1906a: 314.

Uca Marionis var. *nitida* – Nobili 1906a: 314.

Gelasimus marionis – Chhapgar 1957: 509, pl. 13p, q, s, t, v, w.

Gelasimus marionis nitidus – Chhapgar 1957: 510, pl. 13r, u.

Uca (*Thalassuca*) *vocans hesperiae* Crane, 1975: 89, 92, figs. 64E, EE (type locality: Zanzibar, Tanzania).

Uca vocans – Yamaguchi 1994: 180.

Uca vocans forma *excisa* – Al-Ghais and Cooper 1996: 421.

Uca vocans hesperiae – Frasen et al. 1997: 152.

Uca hesperiae – Apel and Türkay 1999: 134.

Uca (*Gelasimus*) *hesperiae* – Ng et al. 2008: 240; Naderloo et al. 2015: 409.

Uca (*Gelasimus*) *vocans* – Trivedi et al. 2015: 27.

Gelasimus hesperiae – Shih et al. 2016: 151, 169, fig 7C; Naderloo 2017: 416, figs. 37.13f, 37.16; Trivedi et al. 2018: 54; Sasaki 2019: 12447.

Gelasimus vocans – Trivedi et al. 2018: 54; Beleem et al. 2019: 15; Pati et al. 2022: 528, fig. 13A, B.

Gelasimus (*Gelasimus*) *hesperiae* – Rosenberg 2019: 734.

Material examined: **Eritrea**: 2 ♂♂ (21.0, 22.0 mm), 1 major chela (SMF 5645), Sahil, Massaua, selten überspülte Schlickzone mit Salicornia-artigem Bewuchs (15°36'37.1"N, 39°28'16.1"E), coll. E. Rüppell, Jan.-Mar. 1827. **Djibouti**: 1 ♂ (18.5 mm) (MNHN-IU-2011-5608), 1 ♂ (20.3 mm) (MNHN-IU-2011-5607), Mission Gravier, coll. 3 Feb. 1904. **India**: 4 ♂♂ (13.7–18.2 mm), 1 ovig. ♀ (15.8 mm) (NCHUZOOL 15094), 5 ♂♂ (14.2–19.4 mm), 3 ovig. ♀♀ (13.5–15.9 mm) (NCHUZOOL 15095), 3 ♂♂ (12.5–13.1 mm), 2 ♀♀ (9.3–8.5 mm) (CASAU-CR-1012), Kali R. estuary, Karwar, Karnataka, coll. M. Prema, 4 Feb. 2021.

Distribution: South Africa to Somalia, Eritrea, Djibouti, Yemen, Oman, UAE, India, Sri Lanka, Bangladesh, Myanmar, western Thailand, Malaysia (western Malay Peninsula), Singapore and Indonesia (West Sumatra).

Remarks: *Gelasimus tetragonon* var. *spinicarpa* was established by Kossmann (1877: 52) on three males from the Red Sea. One syntype (Leiden Museum cat. no. 1493, CL 12 mm, major propodus 23 mm) was identified as a species of the *Gelasimus vocans* complex by Crane (1975: 80), although the other two syntypes were not examined (Fransen et al. 1997: 152). Based on location, these Red Sea specimens would fall within Crane's *G. vocans herperiae*. Rosenberg (2013) called attention to a potential homonymy between *Uca spinicarpa* Rathbun, 1900 and *Gelasimus tetragonon* var. *spinicarpa* Kossmann, 1877, if both were in *Uca*. However, as these species are now considered to be in their original genera, no homonymy exists and *G. spinimana* is an available names, and potential senior synonym of *G. hesperiae*. Morphological examination and sequencing of Red Sea topotypical samples is needed to assess this synonymy.

The type locality of *Gelasimus hesperiae* is Tanzania (Zanzibar), with additional records from Madagascar, Eritrea, Sri Lanka, western Malay Peninsula and even Sulawesi in Crane (1975: 597). In the WIO, its distribution is extended southward to South Africa (Mngazana) (Peer et al. 2015) and eastward to Mumbai, western India (Chhapgar 1957). *COI* data shows high connectivity between sampled areas in W India and Thailand.

Gelasimus tetragonon (Herbst, 1790)

(Fig. 3E, F)

Cancer tetragonon Herbst 1790: 257, pl. 20 (110) (type locality: unknown).

Gelasimus tetragonon – Kossmann 1877: 52; Kingsley 1880: 143, pl. 9(11); Shih et al. 2016: 151, 169, fig 7F; Naderloo 2017: 418, figs. 37.13e, 37.18; Trivedi et al. 2018: 54; Sasaki 2019: 12450.

Uca tetragonon – Nobili 1906a: 313; Nobili 1906b: 151; Maccagno 1928: 22, figs. 7, 8; Price et al. 1987: 456; Apel and Türkay 1999: 134.

Uca (*Thalassuca*) *tetragonon* – Crane 1975: 77–81, 596, figs. 37D, 63A, B, 81F, 82E, pl. 13; Lewinsohn 1977: 59; Sakai 1999: 38, plate 20D (holotype).

Uca tetragonon – Yamaguchi 1994: 177, 184.

Uca (*Gelasimus*) *tetragonon* – Ng et al. 2008: 240; Naderloo et al. 2015: 409; El-Sayed et al. 2016: 10, pls. 3E, F, 4C, F, I, L.

Gelasimus (*Mesuca*) *tetragonon* – Rosenberg 2019: 734.

Material examined: **Egypt**: 2 ♂♂ (19.8–32.5 mm), 1 ♀ (21.1 mm) (NCHUZOOL 15096), Nabq-El Monqata, coll. S. Barbarest et al. 13 Oct. 2004. **Eritrea**: 1 ♂ (15.3 mm) (TAU EGg 3972), Dahlak Archipelago, coll. Apr. 1972.

Distribution: WIO (Kenya, Somalia, Eritrea, Egypt (Red Sea), Saudi Arabia (Red Sea), Yemen, Oman, UAE, India), eastern Indian Ocean and West Pacific Ocean (with eastern end Gambier Islands, French Polynesia).

Remarks: *Gelasimus tetragonon* is widely distributed in the IWP (Crane 1975). In the northwestern Indian Ocean, there are records from the Red Sea to the southern coasts of the Gulf of Oman and the Arabian/Persian Gulf, but not from northern coast of the Arabian/Persian Gulf to western India (Crane 1975; Naderloo 2017; Trivedi et al. 2018; Beleem et al. 2019). *COI* data shows high connectivity between sampled areas from the Red Sea to China.

Genus *Tubuca* Bott, 1973

Tubuca alcocki Shih, Chan & Ng, 2018

(Fig. 3G, H)

Gelasimus dussumieri H. Milne Edwards, 1852: 148, pl. 4(12) [part]; Alcock 1900:

361; Chhapgar 1957: 510, pl. 14a–f; Chandy 1973: 402.
Gelasimus acutus – Alcock 1900: 360.
Gelasimus urvillei – Alcock 1900: 362.
Uca (*Deltuca*) [*coarctata*] *urvillei* – Crane 1975: 35, 58–61, figs 8B, 9E, pl. 9C, D [part].
Uca (*Deltuca*) *urvillei* – Hogarth 1986: 222; Price et al. 1987: 456, 464; Krishnan 1992: 471.
Uca (*Deltuca*) *dussumieri* – Krishnan 1992: 471.
Uca urvillei – Tirmizi and Ghani 1996: 103, fig. 39; Saher 2008: 21, fig. 2.2, pl. 2.1; Odhano et al. 2015: 170, figs. 1, 2.
Uca (*Tubuca*) *urvillei* – Beinlich and von Hagen 2006: 10, 14, 25, fig. 7f, k; Ng et al. 2008: 242.
Uca dussumieri – Trivedi et al. 2012: 17, 20, fig. 3e; Beleem et al. 2014: 422.
Uca (*Tubuca*) *acuta* – Trivedi et al. 2015: 27.
Uca (*Tubuca*) *dussumieri* – Trivedi et al. 2015: 27.
Tubuca urvillei – Shih et al. 2016: 159, 174 [part], fig. 12A; Baakdah 2018: 51; AAJ Kumar 2019: 54.
Tubuca alcocki Shih, Chan & Ng, 2018: 49, figs. 3, 4A, C, 5A–D, 6, 7A, C, E, G (type locality: Ranong, Thailand); Beleem et al. 2019: 15; Sasaki 2019: 12507.
Tubuca dussumieri – Beleem et al. 2019: 15; Pati et al. 2022: 529.
Tubuca acuta – Beleem et al. 2019: 15.
Tubuca (*Tubuca*) *alcocki* – Rosenberg 2019: 735.

Material examined: Holotype: ♂ (CW 30.1 mm, CL 17.9 mm; PL 58.2 mm) (ZRC 2017.1278), Ranong mangroves, Thailand, coll. H.-T. Shih et al., 27 May 2012. Paratypes: 2 ♂♂ (CW 22.4–29.9 mm), 1 ♀ (CW 25.1 mm) (NCHUZOOL 13661), 1 ♂ (CW 29.5 mm) (NCHUZOOL 14896), 13 ♂♂ (CW 14.7–31.2 mm), 4 ♀♀ (CW 19.9–24.1 mm), 1 ovig. ♀ (CW 25.7 mm) (NCHUZOOL 14905), same data as holotype; 1 ♂ (CW 24.6 mm), 1 ovig. ♀ (CW 14.8 mm) (ZRC 2017.1279), Kamphuan mangroves, Ranong, Thailand, 9 Sep. 2000; 1 ♂ (CW 24.0 mm) (ZRC 2001.2347), Ranong, Thailand, coll. P. Clark, 7 Nov. 2001.

Saudi Arabia: 2 ♂♂ (19.1, 22.9 mm) (NCHUZOOL 14904), Al Darb (17° 26'53.4" N; 17°26' 53.4" N), coll. A. J. Kumar, 25 Apr. 2017. **Pakistan**: 2 ♂♂ (32.6, 33.9 mm), 1 ♂ (broken) (NCHUZOOL 15097), Sandspit, Karachi, coll. N. U. Saher, 10 Dec. 2020. **India**: 1 ♂ (CW 17.7 mm) (NCHUZOOL 14925), 1 ♂ (CW 19.0 mm) (NCHUZOOL 14899), 1 ♂ (CW 12.6 mm) (NCHUZOOL 14901), 1 ♀ (CW 17.5 mm) (NCHUZOOL 14902), 13 ♂♂ (CW 9.9–18.2 mm), 3 ♀♀ (CW 11.4–17.9 mm), 1 ovig. ♀ (CW 19.9 mm) (NCHUZOOL 14903), Mumbai, coll. H.-N. Chen et al., 17 Mar.

2010; 1 ♀ (CW 22.6 mm) (NCHUZOOL 14900), Diu mangroves, coll. K. Wong, 20 Mar. 2010; 3 ♂♂ (13.4–14.4 mm) (NCHUZOOL 15098), 1 ♂ (16.2 mm) (NCHUZOOL 15099), 2 ♂♂ (16.5–13.1 mm), 2♀♀ (14.5–9.8 mm), (CASAU-CR-1014), Sunkeri mangroves, Karwar, Karnataka, coll. M. Prema, 4 Feb. 2021.

Distribution: Western Saudi Arabia, Pakistan, India, Bangladesh and western Thailand.

Remarks: The two species of *Tubuca* recorded from the WIO, *T. urvillei* and *T. alcocki,* are sister species with allopatric distributions. The former is restricted to the southwestern Indian Ocean, while the latter ranges widely in the northern Indian Ocean (Shih et al. 2018), their ranges separated around the Somali Peninsula. *COI* data shows genetic homogeneity across the range of this species from the Red Sea to Thailand (Fig. 4).

A key to the genera and species of fiddler crabs in northwestern Indian Sea

1. Front narrow; outer surface of major cheliped manus with tubercles. 2
– Front wide; outer surface of major cheliped manus smooth.....4
2. Outer major cheliped dactylus with groove; major carpus with delimited anterodorsal area flattened; major chela equally likely to be left or right; orbital floor often with tubercles, ridge or mound..... ***Tubuca*** **(*T. alcocki*)**
– Outer major cheliped dactylus without groove; major carpus without delimited anterodorsal area flattened; major chela on right side >90% of the time; orbital floor without sculpture. .....3 (***Gelasimus***)
3. Outer surface of major cheliped manus with small tubercles; fingers narrow and thick; outer pollex without groove; female with carapace sides pilose toward posterior. ..... ***G. tetragonon***
– Outer surface of major cheliped manus with large tubercles; fingers broad and flat; outer pollex with one groove; female carapace sides lacking pile. ..... ***G. hesperiae***
4. Major cheliped with large subdistal tooth on cutting edge of dactylus. . ***Cranuca*** **(*C. inversa*)**
– Major cheliped without large subdistal tooth on cutting edge of dactylus. ..... 5 (***Austruca***)
5. Major cheliped without oblique granular ridge on inner surface of palm; immovable finger without subdistal tooth on cutting edge. 6
– Major cheliped with oblique granular ridge on inner surface of palm; immovable finger with distinct subdistal tooth on cutting edge. 7
6. Anterolateral angles of carapace acute, directed laterally; major cheliped with fingers slender, without large proximal tooth on cutting margin of fingers. .... ***A. sindensis***
– Anterolateral angles of carapace broadly triangular, directed anteriorly; major

cheliped with fingers broad, large proximal tooth on each cutting margin of finger. ***A. variegata***

7. Major chela with supramarginal groove adjacent to lower border on outer surface of palm. ..... ***A. annulipes***

– Major chela without supramarginal groove adjacent to lower margin of palm.. 8

8. Carapace with lateral margins nearly straight; major chela without large proximal tooth on cutting margin of fingers. .....*A. iranica*

- Carapace with lateral margins slightly converging distally; major chela with large proximal tooth on each cutting margin of finger. .....*A. albimana*

DISCUSSION

Integrative taxonomy of fiddler crabs

Sequence data, especially the use of the DNA barcode gene *COI*, is leading to a broad reevaluation of species and diversity. Many species that were thought to be well-defined and understood based on morphology have turned out to be complexes of cryptic species (Knowlton 1993, Rocha et al. 2021, Shih et al. 2018). A major task today is to reassess species diversity in all groups based on integrative methods that incorporate sequence data. *COI* sequence data in the fiddler crab species studied confirmed morphological species boundaries, revealing no cryptic species.

Interspecific divergences in *COI* were >10% (K2P) across all species (Table 2), indicating that they are well differentiated. The large genetic differences reflect the independent origin of most of these species and their sympatric occurrence. Fiddler crabs with less divergence tend to be sister species that retain an allopatric distribution. Most if not all (see below) Arabian species have their sister species outside the region. Contrasting examples of closely related allopatric species pairs and complexes include *Austruca citrus* Shih & Poupin, 2020 and *A. perplexa* (H. Milne Edwards, 1852) (≥ 1.29%, Shih and Poupin, 2020); *Gelasimus excisus* (Nobili, 1906) (= *Gelasimus neocultrimanus* (Bott, 1973)) and *Gelasimus jocelynae* Shih, Naruse & Ng, 2010 (≥ 4.77%, recalculated from Shih et al. 2010); *Minuca rapax* (Smith, 1870) and *M. virens* (Salmon & Atsaides, 1968) (≥ 3.29%, Thurman et al. 2018); the *Minuca burgersi* complex (3.77%–4.78% (mean p-distance), Thurman et al., 2021); *Paraleptuca splendida* (Stimpson, 1858) and *P. crassipes* (White, 1847) (≥ 2.49%, Shih et al. 2012); *Paraleptuca boninensis* (Shih, Komai & Liu, 2013) and *P. splendida* (≥ 2.33%, Shih et al. 2013); and *Tubuca alcocki* Shih, Chan & Ng, 2018 and *T. urvillei* (H. Milne Edwards, 1852) (3.78%, Shih et al. 2018), although the distance between *Austruca bengali* (Crane, 1975) and its sister species, *A. variegata*

(Heller, 1862) (Shih et al., 2019), is larger (≥ 13.7%). In contrast, the lowest divergence among sympatric fiddler crabs is between *Austruca iranica* and *A. sindensis* (10.75%). The large genetic distances among species are also useful for identification of specimens without distinguishing morphological taxonomic characters, e.g., damaged specimens, females, juveniles, and larvae (Chu et al. 2015), or in environmental samples.

Biogeography and speciation

Related species often have narrowly allopatric ranges suggestive of their origin through geographic speciation. The spatial scale of diversification varies across taxa from groups that show connectivity across the IWP, through those with subbasinal ranges, to those that show island or archipelago-scale endemism (Paulay and Meyer 2002: Fig. 4). Fiddler crabs typically have subbasinal ranges and often speciated on this scale (Shih et al. 2013 2019; Naderloo et al. 2016). The ranges of species in the northwest Indian Ocean fit with this pattern. Three of the nine species are endemic to this area and four others are restricted to areas within the Indian Ocean. None of the endemics are more finely restricted to the Red Sea, Gulf of Aden, or Oman, areas that each have substantial local endemism.

Oman straddles one of the steepest environmental gradients in the ocean. The meeting of the Arabian Sea and Gulf of Oman has been called “one of the sharpest biotic transitions known in marine biogeography” (Schils and Wilson 2006). Fiddler crabs follow this pattern with the distribution of four species terminating in this area, two of which may have speciated here.

Austruca albimana and *A. iranica* are closely related species (Shih et al. 2009 2016) that formed within the NW Indian Ocean, demonstrating that this area is large enough to allow in situ diversification for fiddler crabs (cf. Hoareau et al. 2013). These two species were thought to have narrowly allopatric ranges across the Gulf of Oman (Naderloo et al. 2016). We encountered the two species microsympatrically in the same coastal mangrove around Bar Al Hikman on the Arabian Sea coast of Oman, representing a westward range extension of *A. iranica*. Their co-occurrence demonstrates that these putative sister species coexist and thus have become full biological species.

Austruca, composed of small- to medium-sized species (CW about 15 mm; Shih et al. 2016), is the most diverse genus in the Indian Ocean, with five species in the area, viz. *A. albimana*, *A. annulipes*, *A. iranica, A. sindensis* and *A. variegata*. In

contrast, the largest IWP fiddler crab genus, *Tubuca*, composed of medium- to large-sized species (CW about 15–35 mm) that are diverse in the West Pacific (Shih et al. 2016), is represented only by *T. alcocki*.

Based on their distributions (Fig. 1, Table 3), the nine species of fiddler crabs of this region can be grouped into endemic, "western", "eastern" and widespread species (cf. Apel and Türkay 1999).

Austruca albimana, *A. iranica* and *A. sindensis* appear to be endemic to this area, the first with a westward the other two with an eastward distribution. The restriction of these species may reflect a preference for the extreme temperature and salinity environments of this area or habitat isolation to sporadic mangroves limiting dispersal (Queiroga and Blanton 2005; López-Duarte et al. 2011; Shih et al. 2015). The first two species form a robust clade with *A. annulipes* and *A. occidentalis* (Shih et al. 2016). The distributions of *A. albimana* and *A. iranica* narrowly overlap in south Oman, those of *A. iranica* and *A. annulipes* in Pakistan, while *A. occidentalis*, distributed from southern Somalia to South Africa (Naderloo et al. 2016), is narrowly separated from the others by the Somali Peninsula. A similar separation around the Somali Peninsula is shown by the sister species *Tubuca alcocki* and *T. urvillei* (Shih et al. 2018), showcasing this area as an important biogeographic boundary.

Cranuca inversa is a "western" species, with a range extending from Oman to southeastern Africa (Crane 1975). *Gelasimus hesperiae* and *G. tetragonon* are widely distributed species in the Indian Ocean and IWP, respectively (Crane 1975), both extend through the southwestern Indian Ocean. Ocean currents in the western WIO (Shenoi et al. 1999) might influence the larval dispersal of this species which need further studies..

Tubuca alcocki, *A. variegata* and *A. annulipes* belong to "eastern" species that range toward the eastern Indian Ocean or even the West Pacific (Shih et al. 2009 2018 2019), with their westernmost records in the Red Sea, western India and Pakistan, respectively (Table 3). The distribution of these three species in northwestern India Ocean may have been facilitated by currents in the WIO (Shenoi et al. 1999), but further experimental studies are necessary.

CONCLUSIONS

In this study, nine species of fiddler crabs from the Arabian Sea and adjacent waters are reported. Species were confirmed by morphology with support from their *COI* sequences, with interspecific divergences all > 10%. The fauna is highly endemic, with *Austruca albimana*, *A. iranica* and *A. sindensis* confined to this region. Other species can be grouped into "western" species (*Cranuca inversa*), "eastern" species (*Tubuca alcocki*, *A. annulipes* and *A. variegata*) and widely distributed species (*Gelasimus hesperiae and G. tetragonon*).

Acknowledgements: This study was supported by a grant from the Ministry of Science and Technology (MOST 108-2621-B-005-002-MY3), Executive Yuan, Taiwan, to HTS. We wish to express thanks to Peter K. L. Ng (ZRC), Gianna Innocenti (MZUF), Laure Corbari and Paula Martin-Lefèvre (MNHN), Bella S. Galil (TAU) and Ehsan Kamrani (Hormozgan University, Iran) for providing specimens used in this study; and Min-Wan Chen for measuring specimens and doing part of the molecular work. GP thanks NSF DEB 1856245 for funding. We also acknowledge two anonymous referees who helped improve the manuscript.

Authors' contributions: HTS conceived this study, performed the molecular analysis, and drafted the manuscript. MP, AJK, NUS, SR, SO and GP collected and processed the samples, participated in the discussion and drafted the manuscript. All authors read and approved the final manuscript.

Competing interests: The authors declare that they have no conflict of interest.
Availability of data and materials: Sequences generated in the study were deposited into the GenBank database (accession numbers in Table 1).
Consent for publication: Not applicable.
Ethics approval consent to participate: Not applicable.

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Table 1. Specimens and *COI* haplotypes of the fiddler crabs from the Arabian Sea and adjacent waters. The numbers within brackets following localities correspond to those in Fig. 1. *, sequences are shorter and not included for further analyses (see "Molecular analyses of *COI*"). See MATERIALS AND METHODS for abbreviations of museums and universities.

	Locality	Sample size	Catalogue no. of NCHUZOOL (unless indicated)	Haplotype	Access. no.
Austruca albimana	Egypt: Sinai: Nabq - El Arwashie; Ras Mohammed [1]	2	13242	AaL1	AB471906
	Saudi Arabia: Al Darb [4]	2	15002, 15003	AaL3, AaL4	xxx, xxx
	Oman: Bar Al Hikman Peninsula [9]	1	UF7790	AaL2	xxx
Austruca annulipes	Pakistan: Sandspit: backwater mangrove area [11]	3	15088	Aan1, Aan2, Aan3	xxx, AB491160, xxx
	India: Dongri, Uttan, Mira Bhayandar, Maharashtra [14]	1	15086	Aan4	xxx
	India: Mumbai [14]	1	15087	Aan5	xxx
	Thailand: Phuket	1	13257	Aan2	AB491160
	Malaysia: Tioman	1	13243	Aan6	AB471907
	China: Sanya, Hainan	1	13244	Aan6	AB471907
Austruca iranica	Oman: Bar Al Hikman Peninsula [9]	2	UF7791, UF7752	Ai1	AB471909
	Iran: Gavbandi, Hormozgan [6]	2	13245, 13247	Ai2, Ai3	AB471908, AB471910
	Iran: Qeshm I., Hormozgan [8]	2	13246, 13248	Ai1, Ai4	AB471909, AB471911
	Pakistan: Sandspit, Karachi, Sindh [11]	2	15091	Ai5, Ai6	xxx, xxx
Austruca occidentalis	South Madagascar	1	ZRC THH04-30	Ao1	AB813669
	South Madagascar	1	ZRC THH04-30	Ao1	
	Kenya: Ngomeni Bay	1	MZUF 4297	Ao2	
	Madagascar	1	UF14433	Ao2	
Austruca sindensis	Iraq: Khur Al-Zubair [5]	2	ZRC 2010.0103	As2	LC015060
	Iran: Bandar Abbas [7]	6	13645	As1, As2, As5	AB813673, LC015060, LC015063
	Iran: Qeshm I., Hormozgan [8]	4	13576	As1, 2	AB813673, LC015060
	Pakistan: Sonmiani, Balochistan [10]	1	13643; 13644	As1, As2, As3,	AB813673, LC015060, LC015061
	Pakistan: Sandspit, Karachi, Sindh [11]	4	13641	As1, As2, As3, As4,	AB813673, LC015060, LC015061, LC015062
	Pakistan: Sandspit, Karachi, Sindh [11]	6	13642	As1, , As2	AB813673, LC015060
Austruca variegata	India: Tamil Nadu	3	ZRC 2001.0853	Av1	LC465131
	India: Tamil Nadu	3	ZRC 2001.0853	Av2, Av3, Av4	LC465140, LC465141,

					LC465142
	India: Tamil Nadu	3	ZRC 2018.1375	Av5	LC465143, LC465144, LC465145
	India: West Bengal	2	ZRC 2017.0917	Av3, Av6	LC465146, LC465146
Cranuca inversa	Egypt: Sinai: Nabq [1]	1	TAU SLR 1475	Ci1	LC087973
	Egypt: Sinai: Nabq - El Arwashie; Ras Mohammed [1]	1	13623	Ci2	xxx
	Saudi Arabia: Al Darb [4]	2	15093	Ci3, Ci4	xxx, AB813674
	Somalia: Giumbo	1	MZUF 711	Ci4	AB813674
	Kenya: Gazi	1	MZUF 1024	Ci4	AB813674
	Tanzania: Dar es Salaam	1	13255	Ci5	AB471917
Gelasimus hesperiae	Djibouti [3]	1	MNHN-IU-2011-5608	—*	
	W India: Karnataka: Karwar: Kali river sangam [15]	4	15094, 15095	Gh1, Gh2, Gh3, Gh4	xxx, AB535423, xxx, xxx
	Thailand: Phuket	2	ZRC 2000.1056, ZRC 2001.1071	Gh5, Gh2	AB535422, AB535423
Gelasimus tetragonon	Egypt: Sinai: Nabq - El Monqata [1]	1	15096	Gt1	AB535431
	Eritrea: Dahlak Archipelago [2]	1	TAU EGg 3972	Gt2	xxx
	Madagascar: Belaza, Sarodrano	1	ZRC THH04-17	Gt3	LC053377
	Taiwan: Penghu	1	13304, 14678	Gt1	AB535431
Tubuca alcocki	Saudi Arabia: Al Darb [4]	2	14904	Ta1, Ta2	LC150445, xxx
	Pakistan: Sandspit [11]	3	15097	Ta1	LC150445
	India: Diu [13]	1	14900	—*	
	India: Mumbai [14]	6	14899, 14901, 14902, 14903, 14925	Ta1	LC150445
	W India: Karwar: Sunkeri [15]	3	15098, 15099	Ta1	LC150445
	Thailand: Ranong	1	ZRC 2017.1278 (holotype)	Ta1	LC150445
Total		78			

Table 2. Matrix of percentage pairwise nucleotide divergence with Kimura 2-parameter (K2P) distances based on cytochrome c oxidase subunit I (*COI*) within and between eight species of fiddler crabs from around the Arabian Sea and related species (see Table 1). Values of the range are shown in parentheses.

	Intraspecific	Interspecific								
	Nucleotide divergence	*A. albimana*	*A. annulipes*	*A. iranica*	*A. sindensis*	*A. albimana*	*A. variegata*	*C. inversa*	*G. hesperiae*	*G. tetragonon*	*T. alcocki*
Austruca albimana	0.49 (0–0.76)										
Austruca annulipes	0.39 (0–0.77)	14.02 (13.84–14.6)									
Austruca iranica	0.31 (0–0.61)	11.89 (11.45–12.38)	11.7 (11.51–12.08)								
Austruca sindensis	0.1 (0–0.15)	14.43 (14.06–14.83)	12.35 (12.09–12.66)	11.07 (10.75–11.49)							
Austruca albimana	0.13 (0–0.46)	17.31 (16.64–17.84)	14.47 (14.19–14.77)	14.35 (13.98–14.75)	15.41 (15.3–15.49)						
Austruca variegata	0.42 (0–0.92)	11.77 (11.53–12.26)	12.47 (11.96–13.09)	13.94 (13.48–14.45)	13.64 (13.47–13.86)	14.32 (13.99–14.77)					
Cranuca inversa	0.25 (0–0.61)	18.86 (18.42–19.63)	16.67 (16.33–16.92)	18.11 (17.48–18.49)	17.27 (16.9–17.5)	18.15 (17.5–18.71)	15.9 (15.76–16.15)				
Gelasimus hesperiae	0.35 (0–0.77)	15.53 (15.16–15.92)	16.63 (16.15–17.14)	18.14 (17.97–18.58)	19.4 (19.3–19.71)	16.2 (15.98–16.57)	16.59 (16.33–16.92)	15.79 (15.01–16.18)			
Gelasimus tetragonon	0.15 (0–0.3)	15.28 (15.02–15.41)	17.5 (16.97–17.98)	18.82 (18.41–19.03)	18.66 (18.51–18.71)	17.09 (16.57–17.17)	15.18 (14.65–15.42)	17.24 (16.75–17.55)	11.16 (10.9–11.45)		
Tubuca alcocki	0.02 (0–0.15)	18.37 (18.07–18.87)	17.8 (17.56–18.17)	16.13 (16–16.4)	18.8 (18.79–18.99)	16.8 (16.41–17.21)	14.48 (14.12–14.7)	16.19 (15.93–16.51)	16.3 (15.99–16.59)	15.89 (15.56–15.95)	

Table 3. Distribution of fiddler crabs in the Arabian Sea and adjacent waters. Species marked with an * are endemic to this area.

species	Red Sea	Gulf of Aden	SE Oman	Arabian /Persian Gulf	Gulf of Oman	Pakistan	W India
**Austruca albimana*	*	*	*	*	*		
Cranuca inversa	*	*		*	*		
Gelasimus tetragonon	*	*		*	*		
Gelasimus hesperiae	*	*		*	*		*
Tubuca alcocki	*	*				*	*
**Austruca iranica*			*	*	*	*	*
**Austruca sindensis*				*	*	*	*
Austruca annulipes						*	*
Austruca variegata							*

Figure legends:

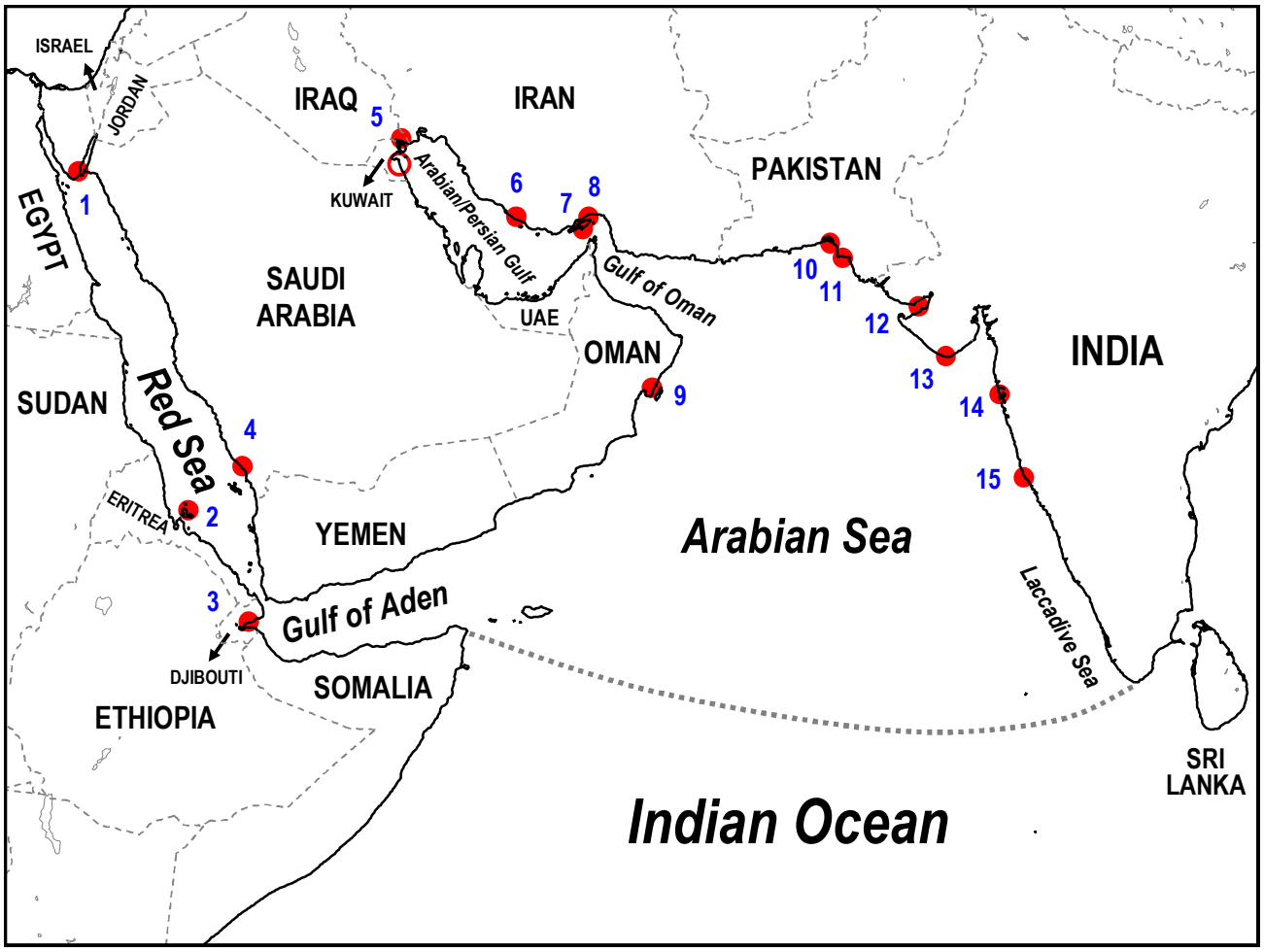
Fig. 1. Collection sites for specimens in this study (filled circles) and an additional literature record (empty circle) (see Table 1). Dash line on the Indian Ocean represents the border of the Arabian Sea.

Fig. 2. Dorsal view of carapace and frontal view of major cheliped. *Austruca albimana* (A, B, NCHUZOOL 13242, CW 15.2 mm, Egypt); *A. annulipes* (C, NCHUZOOL 13642, CW 17.4 mm, Pakistan; D, NCHUZOOL 15088, CW 19.4 mm, Pakistan); *A. iranica* (E, F, NCHUZOOL 15090, CW 16.4 mm, Iran); *A. sindensis* (G, H, NCHUZOOL 13642, CW 17.4 mm, Pakistan).

Fig. 3. Dorsal view of carapace and frontal view of major cheliped. *Cranuca inversa* (A, B, NCHUZOOL 15093, CW 19.9 mm, 18.7 mm, Saudi Arabia); *Gelasimus hesperiae* (C, D, MNHN-IU-2011-5608, CW 20.3 mm, Djibouti); *G. tetragonon* (E, F, NCHUZOOL 15096, CW 32.5 mm, Egypt); *Tubuca alcocki* (G, NCHUZOOL 14904, CW 19.1 mm, Saudi Arabia; H, NCHUZOOL 15097, CW 33.9 mm, Pakistan).

Fig. 4. *COI* neighbor-joining tree for fiddler crabs studied, with bootstrap support values (only >50% shown).

Fig. 1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JORDAN
IRAQ
IRAN
PAKISTAN
KUWAIT
Arabian/Persian Gulf
EGYPT
SAUDI ARABIA
UAE
Gulf of Oman
OMAN
INDIA
SUDAN
Red Sea
ERITREA
YEMEN
Arabian Sea
Gulf of Aden
Laccadive Sea
DJIBOUTI
SOMALIA
ETHIOPIA
SRI LANKA
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Fig. 2

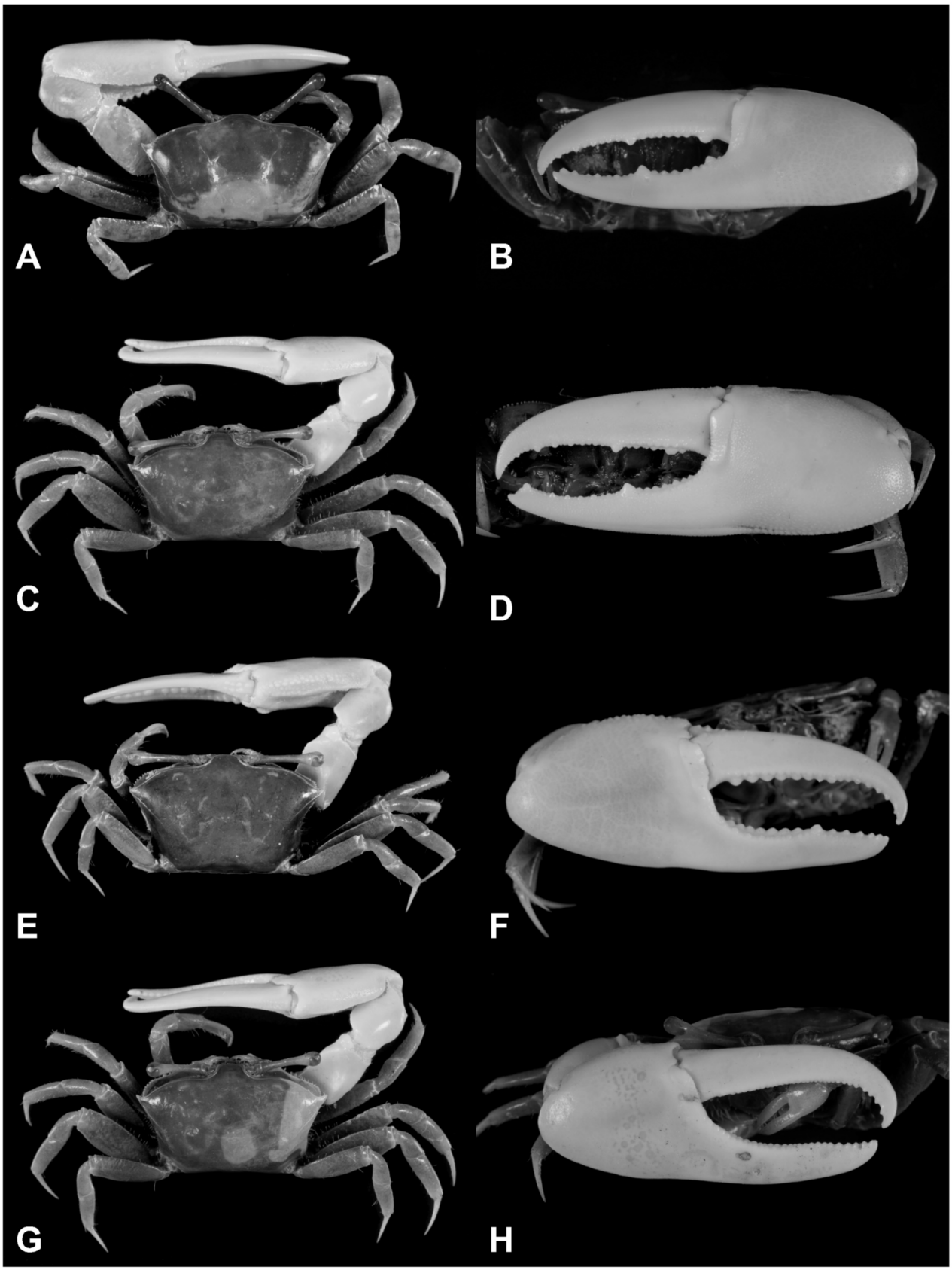
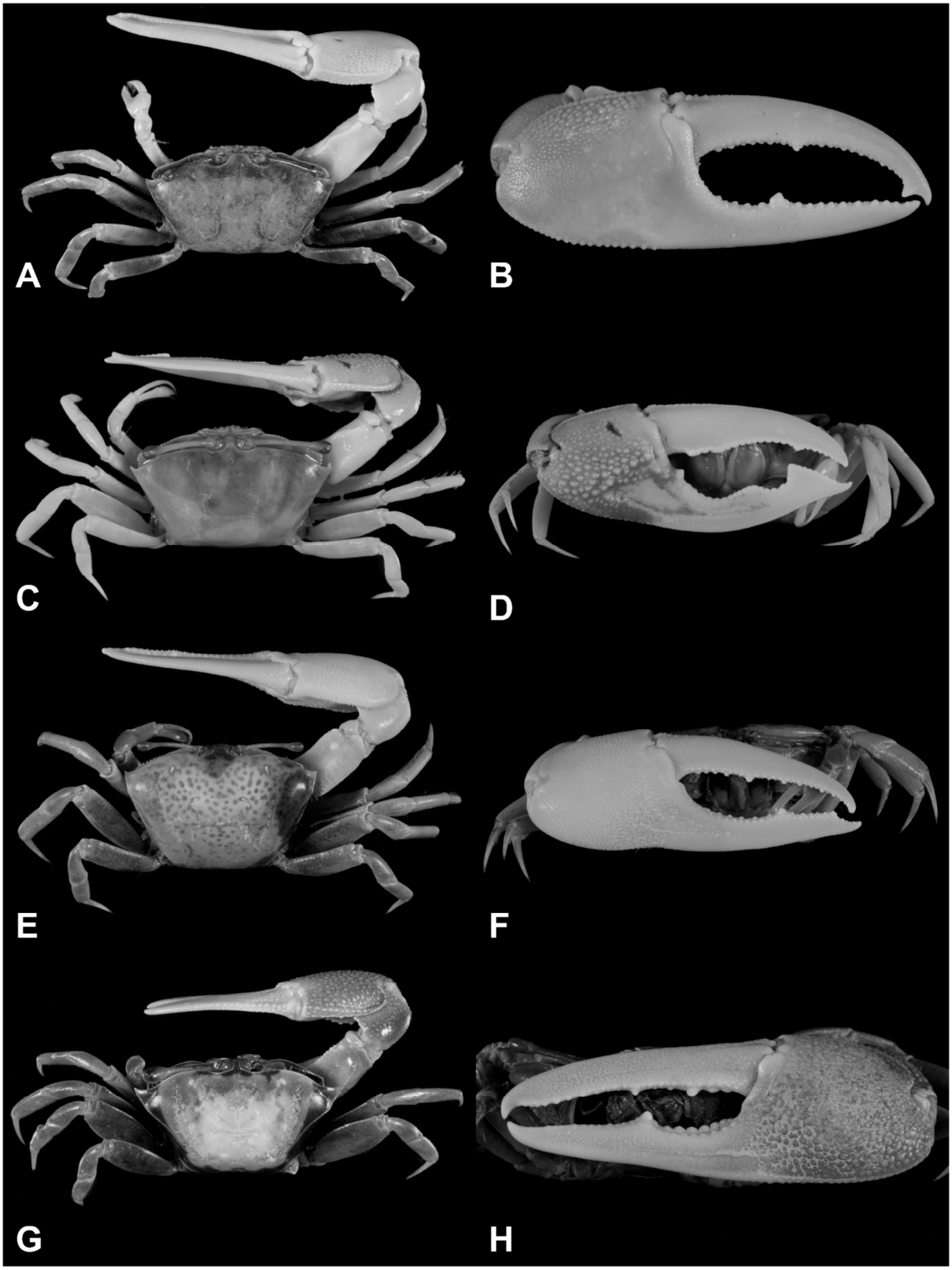
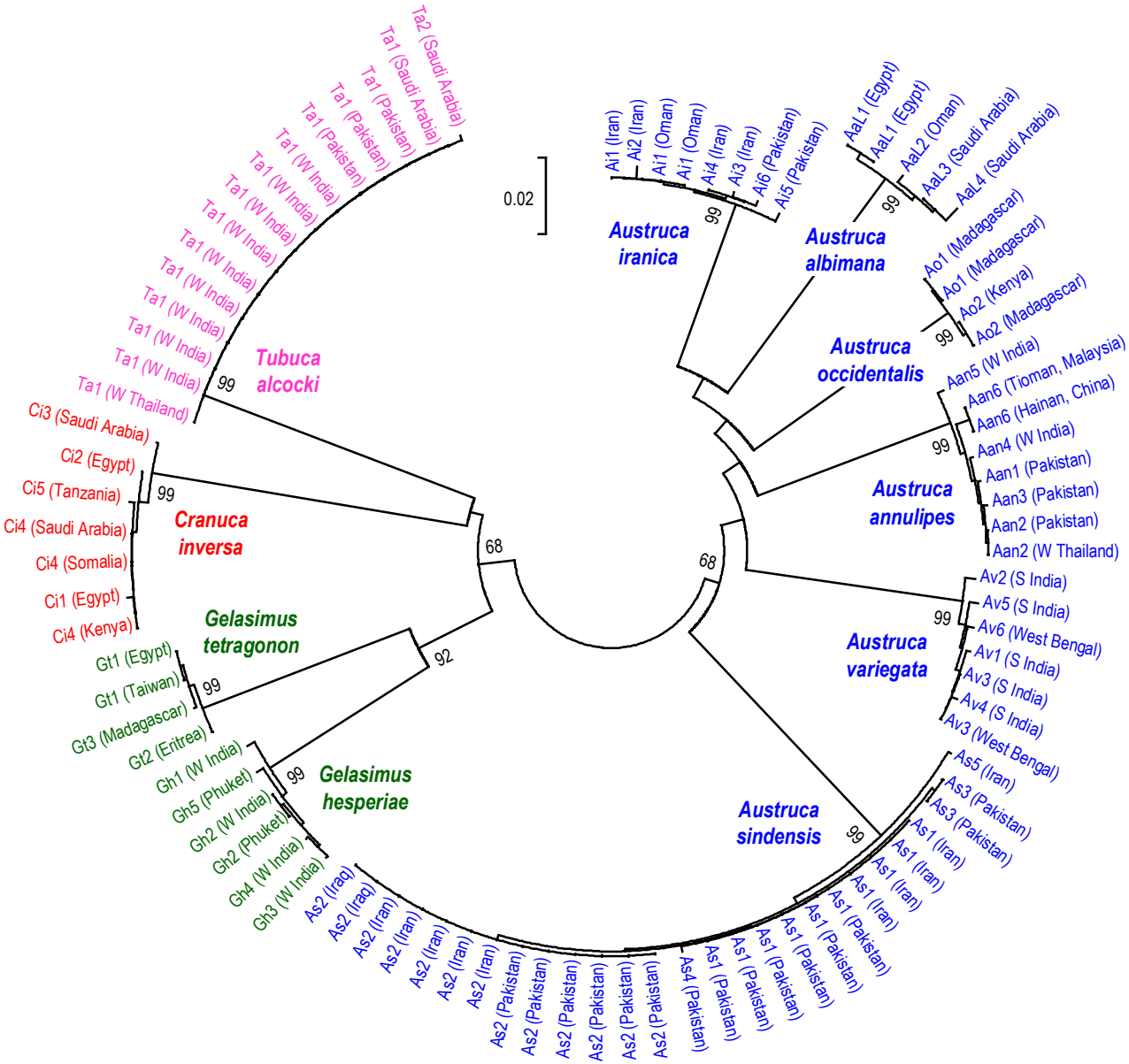


Fig. 3




0.02
Tubuca alcocki
Cranuca inversa
Gelasimus tetragonon
Gelasimus hesperiae
Austruca iranica
Austruca albimana
Austruca occidentalis
Austruca annulipes
Austruca variegata
Austruca sindensis
Ta2 (Saudi Arabia)
Ta1 (Saudi Arabia)
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Ta1 (Pakistan)
Ta1 (W India)
Ta1 (W India)
Ta1 (W India)
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Ta1 (W India)
Ta1 (W Thailand)
Ci3 (Saudi Arabia)
Ci2 (Egypt)
Ci5 (Tanzania)
Ci4 (Saudi Arabia)
Ci4 (Somalia)
Ci1 (Egypt)
Ci4 (Kenya)
Gt1 (Egypt)
Gt1 (Taiwan)
Gt3 (Madagascar)
Gt2 (Eritrea)
Gh1 (W India)
Gh5 (Phuket)
Gh2 (W India)
Gh2 (Phuket)
Gh4 (W India)
Gh3 (W India)
Ai1 (Iran)
Ai2 (Iran)
Ai1 (Oman)
Ai1 (Oman)
Ai4 (Iran)
Ai3 (Iran)
Ai6 (Pakistan)
Ai5 (Pakistan)
AaL1 (Egypt)
AaL1 (Egypt)
AaL2 (Oman)
AaL3 (Saudi Arabia)
AaL4 (Saudi Arabia)
Ao1 (Madagascar)
Ao1 (Madagascar)
Ao2 (Kenya)
Ao2 (Madagascar)
Aan5 (W India)
Aan6 (Tioman, Malaysia)
Aan6 (Hainan, China)
Aan4 (W India)
Aan1 (Pakistan)
Aan3 (Pakistan)
Aan2 (Pakistan)
Aan2 (W Thailand)
Av2 (S India)
Av5 (S India)
Av6 (West Bengal)
Av1 (S India)
Av3 (S India)
Av4 (S India)
Av3 (West Bengal)
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Fig. 4