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Quaternary intertidal and supratidal crabs (Decapoda, Brachyura) from tropical America and the systematic affinities of fossil fiddler crabs

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Concentrations of fully articulated crabs are rare in the fossil record, especially for terrestrial and semi-terrestrial taxa, which tend to be represented by scarce, fragmentary and poorly preserved fossils due to preservational biases. A newly discovered fossiliferous locality at Bahía Bique, west of Panama City, Panama, yielded a collection of supratidal, intertidal and shallow subtidal invertebrates and vertebrates of mid-Holocene age. Notable discoveries include the first fossils of the sally lightfoot crab *Grapsus*, the first for the land crab *Cardisoma* in the Eastern Pacific and, remarkably, the most complete and abundant collection of fossil fiddler crabs, *Uca*, yet discovered. The abundance and exceptional preservation of fossil male, female, juvenile and adult individuals of *Uca* aff. *ornata* in eroded burrow infills suggest that rapid entombment and early diagenesis were crucial for their preservation. The habitat preference of extant *U. ornata* for soft muds of open intertidal mudflats indicates that part of Bahía Bique must have been a large estuarine mudflat with close proximity to freshwater influx, in contrast to the present-day gravel field where the fossils are found as *ex situ* boulders, cobbles and gravel-sized clasts eroded from rocks of the poorly known Pacific Muck. We examine the systematic relationships of fossil fiddler crabs from Bahía Bique via synthetic and cladistic approaches, and conclude that they were from an extinct population of the extant *Uca ornata*. The fidelity of living–death assemblages between the Bique faunule and extant faunas of the tropical Eastern Pacific confirm the Quaternary age of the assemblage, and stimulate a detailed discussion of the preservation and palaeoecology of terrestrial and semi-terrestrial crabs in tropical assemblages.

Keywords: Brachyura; Eubrachyura; Ocypodidae; palaeobiology; Panama; *Uca*

Introduction

The transition from fully aquatic to terrestrial or semi-terrestrial habitats is an infrequent event in most plant and animal groups. Higher crabs, or Eubrachyura, are one of the few marine groups that have successfully invaded land, although relatively recently in geological time. Unfortunately, the fossil record of terrestrial and semi-terrestrial crabs is fragmentary, and mostly represented by a handful of incomplete and poorly preserved fossils due to mechanical, chemical and/or biological biases (e.g. Donovan & Dixon 1998; Schweitzer *et al.* 2008; Baalbergen & Donovan 2013; Locatelli 2013; Luque *et al.* 2015; Serrano-Sánchez *et al.* 2016). A newly discovered fossiliferous locality at Bahía Bique, west of Panama City, Panama (Fig. 1), has yielded a large collection of supratidal, intertidal and shallow subtidal invertebrates (e.g. bivalves, gastropods, crabs, barnacles), vertebrates

(e.g. shark and ray teeth, catfish cranial and postcranial bones) and plant remains (wood fragments, mangrove roots) of Quaternary age (Portell *et al.* 2012; Hendy *et al.* in progress). This new assemblage includes representatives of two superfamilies of ‘higher’ true crabs that have colonized land: Grapsoidea MacLeay, 1838, and Ocypodoidea Rafinesque, 1815 (Brachyura: Eubrachyura: Thoracotremata). Among our findings is one of the few fossil records of the fiddler crab *Uca* Leach, 1814 (Ocypodoidea: family Ocypodidae) (Figs 2–4). This represents the most complete and abundant sample of fossil fiddler crabs worldwide, comprised of several hundred adult and juvenile, male, and female individuals, often with appendages articulated. The degree of preservation and articulation of these crabs suggest special preservational conditions, which lead to the remarkable and otherwise unlikely fossilization of remains of these semi-terrestrial crabs. Other terrestrial and semi-terrestrial crabs in the assemblage

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Figure 1. Localities on the Pacific Coast of Panama where fossil and extant specimens of *Uca ornata* (Smith, 1870) were discovered. **A, B,** Punta Chame, a muddy tidal flat; **A,** overview of the area; **B,** close-up showing dozens of extant male and female *U. ornata* feeding on the surface. **C, D,** Bahía Bique, a gravelly intertidal beach; **C,** view of the area; **D,** close-up showing the coarse substrate from which the re-worked fossils were collected.

include the sally lightfoot crab genus *Grapsus* Linnaeus, 1758 (Grapsoidae: Grapsidae), and the land crab genus *Cardisoma* Latreille, 1825 (Grapsoidae, Gecarcinidae).

Here, following the works of Rosenberg (2001) and Domínguez Alonso (2008), we place the fossil fiddler crabs from Bahía Bique in a phylogenetic framework via synthetic and cladistic approaches, and discuss the systematics, preservation, palaeobiology and the fidelity of living–death crab assemblages from the Quaternary of tropical America.

Geological setting

Deposits of late Pleistocene to Holocene age along Panama's Pacific coast are poorly known, although those on the Burica Peninsula (Chiriquí Province) are well described (Olsson 1942). The Pacific Muck, informally named by Thompson (1947), comprises a series of wave-

cut benches, raised beach, and shallow-water deposits reported from the Pacific coast of central Panama. The unit occurs at depth in Bahía de Panama, in the lower reaches of larger streams flowing into the Pacific near Panama City, and extends as far inland from the Pacific entrance of the Panama Canal as the Miraflores Locks (Thompson 1947; Pinilla *et al.* 2011). The Pacific Muck is regarded as Pleistocene–Holocene in age and seems to correlate with the Atlantic Muck exposed along the Caribbean coast of central Panama (Jones 1950; Woodring 1957; Pinilla *et al.* 2011).

This unit is exposed in Bahía Bique, a shallow embayment approximately 15 km west of Panama City and about 4 km west of Veracruz (Hendy *et al.* research in progress). In Bahía Bique, fossils from the Pacific Muck can be sampled *ex situ* as boulders, cobbles and gravel-sized clasts, winnowed on the extensive modern mudflat (Fig. 1C, D). These fossils are typically preserved within small, irregularly shaped, dark-coloured, siltstone or sandstone

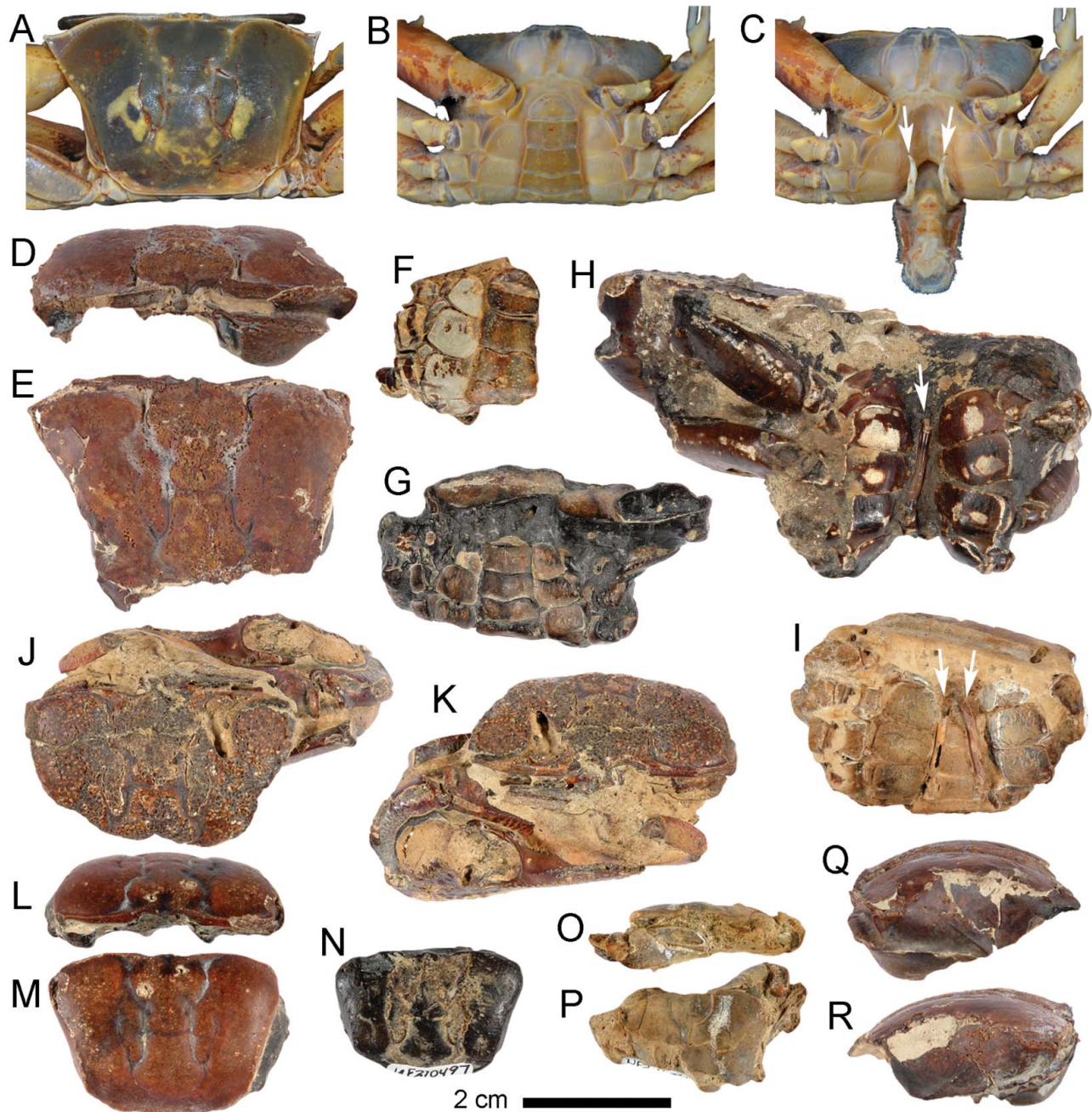


Figure 2. Recent and fossil male *Uca ornata* (Smith, 1870) from the Pacific Coast of Panama. **A–C**, Recent *U. ornata* specimen from Punta Chame; **A**, dorsal carapace showing asymmetric orbits; **B**, ventral view with pleon or ‘abdomen’ pressed against the thoracic sternum; **C**, ventral view with pleon or ‘abdomen’ extended posteriorly to reveal the gonopods (white arrows). **D–R**, fossil †*Uca* aff. *ornata* specimens from Bahía Bique; **D**, **E**, UF 212135, frontal (**D**) and dorsal (**E**) carapace with asymmetrical orbits; **F**, UF 220518, ventral carapace with pleon preserved; **G**, UF 210492, ventral carapace with pleon preserved; **H**, UF 206048, ventral carapace with right gonopod preserved (white arrow); **I**, UF 206069, ventral carapace with pleon eroded at the sides exposing the gonopods (white arrows); **J**, **K**, UF 211120, showing dorsal view of carapace and the right major cheliped (**J**) and frontal margin with right eyestalk preserved (**K**); **L**, **M**, UF 210341, frontal (**L**) and dorsal (**M**) carapace; **N**, UF 210497, dorsal carapace of small specimen; **O**, **P**, UF 206061, frontal (**O**) and dorsal (**P**) carapace of very small specimen with small right major cheliped (**O**); **Q**, **R**, UF 212135, left (**Q**) and right (**R**) lateral views of carapace. Specimens photographed dry and uncoated.

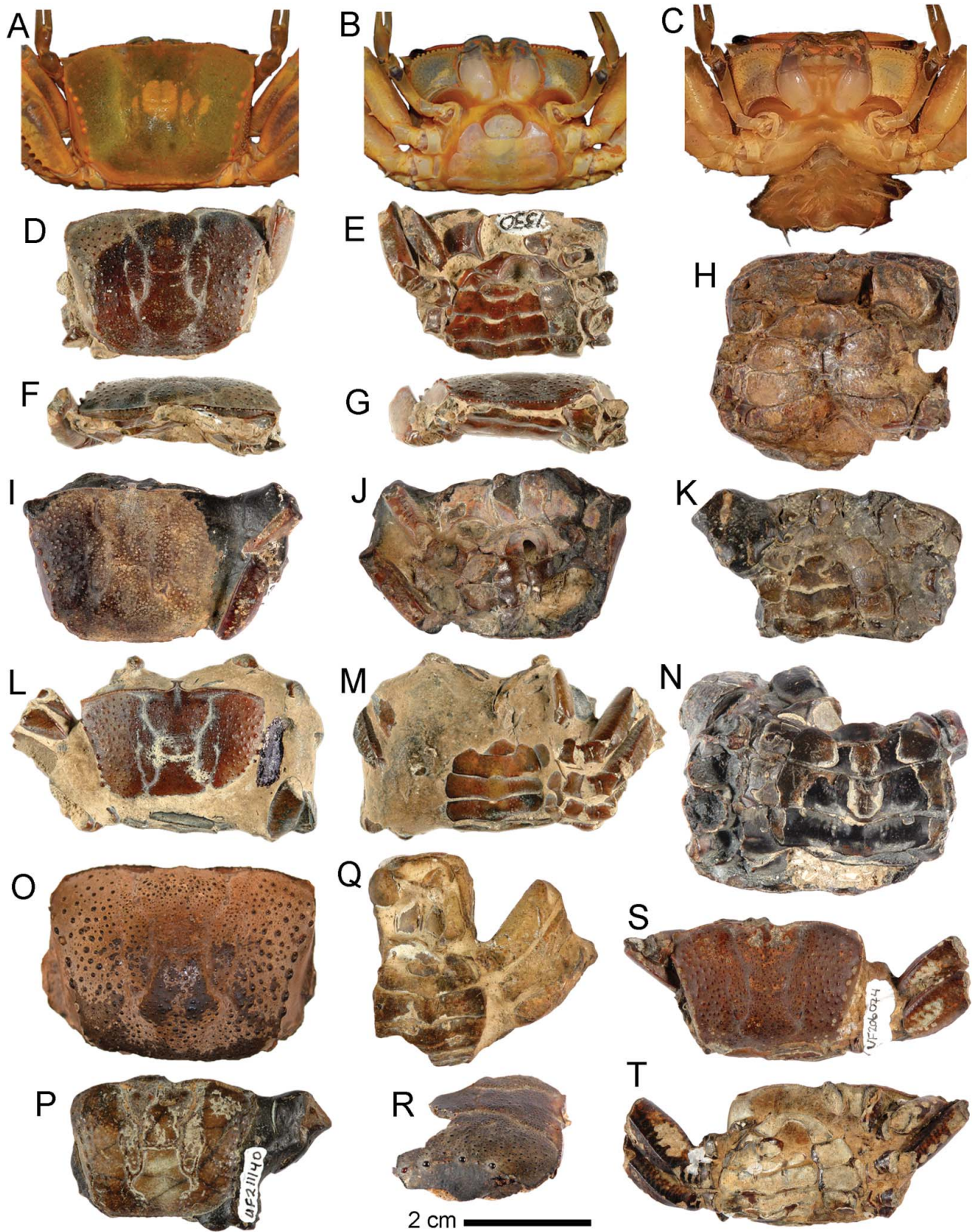


Figure 3. Recent and fossil female *Uca ornata* (Smith, 1870) from the Pacific Coast of Panama. A–C, Recent *U. ornata* specimen from Punta Chame; A, dorsal carapace; B, ventral view with pleon or ‘abdomen’ pressed against the thoracic sternum; C, ventral view with pleon extended posteriorly revealing the thoracic sexual openings. D–T, fossil †*Uca* aff. *ornata* specimens from Bahía Bique; D–G,

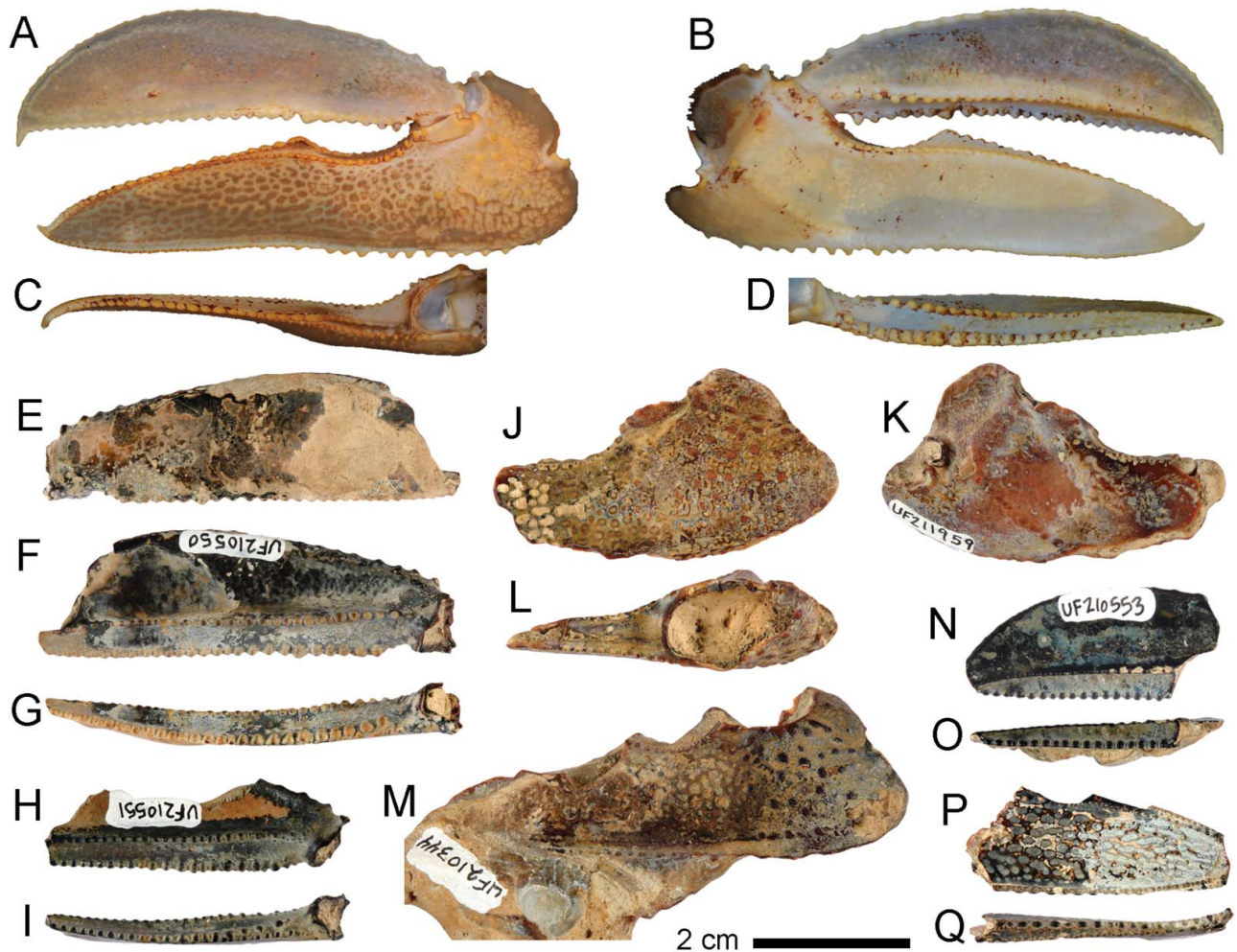


Figure 4. Major chelipeds of fossil and Recent *Uca ornata* (Smith, 1870) from the Pacific Coast of Panama. **A–D**, Recent *U. ornata* specimen from Punta Chame; **A**, outer (lateral) view of major cheliped showing the smooth dactylus, the pollex with shallow irregular fossae, and the granulated manus; **B**, inner (medial) view of major cheliped showing the smooth dactylus and pollex, and the robust palm with an oblique ridge; **C**, dorsal view of pollex occlusal margin; **D**, ventral view of dactylus occlusal margin. **E–Q**, Fossil *Uca* aff. *ornata* specimens from Bahía Bique; **E–G**, UF 210550, dactylus of right major cheliped showing the outer (**E**), inner (**F**), and occlusal (**G**) surfaces. **H, I**, UF 210551, dactylus fragment of right major cheliped showing the proximal end, inner (**H**) and occlusal (**I**) surfaces; **J–L**, UF 211959, propodus of left major cheliped showing the manus (**J**), the palm (**K**), and the propodus view of the occlusal surface (**L**); **M**, UF 210344, propodus of left major cheliped showing the manus and the proximal margin of the pollex; **N, O**, UF 210553, dactylus distal portion of right major cheliped showing the inner (**N**) and occlusal (**O**) surfaces; **P, Q**, UF 211965, pollex of right major cheliped showing the irregular fossae (**P**) and the occlusal surface (**Q**). Specimens photographed dry and uncoated.

concretions, many of which appear to be burrow in-fills, with most encrusted by Recent epibionts. The Bique faunule includes abundant molluscs and crustaceans, but also rare shark and ray teeth, catfish skulls and spines, turtle carapace fragments, wood fragments and mangrove

rhizophores. Most of the 28 species of molluscs are typical of intertidal muddy and sandy sediment, with some inhabiting nearby rocky substrates and mangrove forests (Hendy *et al.* research in progress). The crab fauna includes at least seven taxa that likely inhabited shallow subtidal to

LACMIP 14647, showing the dorsal (**D**), ventral (**E**), frontal (**F**), and posterior (**G**) carapace, the latter being granulated; **H**, UF 210297, showing the thoracic sexual openings; **I, J**, UF 210303, showing the dorsal (**I**) and ventral carapace and the third maxillipeds (**J**); **K, P**, UF 211140, ventral (**K**) and dorsal (**P**) carapace; **L, M**, LACMIP 14648, showing details of the rostrum and the dorsal ornamentation (**L**) and the pleon plus the reduced chelipeds (**M**); **N**, UF 211122, large ventral female; **O**, USNM 618320a, dorsal carapace; **Q**, UF 211129, showing the pleon and the third maxillipeds; **R**, UF 211132, right anterolateral margin, showing details of the granulation; **S, T**, UF 206074, dorsal (**S**) and ventral (**T**) views. Specimens photographed dry and uncoated.

intertidal and low supratidal zones, and represent a range of lifestyles and behaviours. We initially suspected that these fossils were dumped spoil from the excavations of Neogene rocks from the Panama Canal or nearby areas. However, no Miocene fossils were recognized in this assemblage. In fact, all of the identified fossil mollusc and crustacean species are extant, and their similarity in composition and relative abundance to the present-day death assemblages of the nearby coastline clearly suggest a Quaternary affinity. Radiocarbon dates from associated molluscs indicate that this fossil assemblage likely accumulated during the mid-Holocene (~5500 kyr BP).

Material and methods

Institutional abbreviations

LACMIP: Invertebrate Paleontology, Natural History Museum of Los Angeles County, Los Angeles, CA, USA; **UF:** Invertebrate Paleontology Division, Florida Museum of Natural History, University of Florida, Gainesville, FL, USA; **USNM:** United States National Museum, Smithsonian Institution, Washington, DC, USA.

Anatomical and phylogenetic abbreviations

Ca: carpus; **Ch:** cheliped; **CI:** consistency index; **Cx2–Cx4:** coxa of second to fourth pereiopods; **Da:** dactylus; **DaL:** dactylus maximum length; **DaW:** dactylus maximum width; **L:** carapace maximum length; **Lo:** left orbit; **MaW:** manus maximum width; **Me:** merus; **P2–P5:** second to fifth pereiopods; **Pr:** propodus; **PrL:** propodus maximum length; **PoW:** pollex maximum width; **RI:** retention index; **Ro:** right orbit; **TL:** tree length; **W1:** carapace maximum width; **W2:** carapace posterior margin width; †: fossil.

Material

A collection of 415 (374 measured) fossil specimens of †*Uca* aff. *ornata* (Figs 2–6), one †*Grapsus* aff. *grapsus* (Fig. 7A–G), and one †*Cardisoma* aff. *crassum* (Fig. 7I–K), deposited in the UF, together with two additional specimens of †*U.* aff. *ornata* deposited in the Invertebrate Paleontology collections of the LACMIP, and three specimens deposited in the Paleobiology collections of the USNM. *Ex situ* fossil fiddler crabs from Bahía Bique were first recognized in the 1970s (e.g. Fig. 3O), and in 2006 Mark Torchin's Lab (STRI, Panama) rediscovered the fossiliferous locality. The specimens that are the focus of this study were surface hand-collected by us from the winnowed clasts and concretionary burrow infills accessible during low tides in Bahía Bique during several field trips between 2008 and 2014 (Fig. 1C, D). Additional information about these specimens may be obtained at the FLMNH website <http://www.flmnh.ufl.edu/invertpaleo/search.asp>.

Measurements and photography

Measurements (in mm) estimated in dorsal carapace of males and females comprised: carapace maximum length (**L**); width of the left (**Lo**) and right (**Ro**) orbits; carapace maximum width (**W1**) and posterior margin width (**W2**) (Fig. 5A; Supplementary Dataset 1). Measurements (in mm) estimated in male major chelipeds comprised: dactylus maximum length (**DaL**) and width (**DaW**); manus maximum width (**MaW**); propodus maximum length (**PrL**); and pollex maximum width (**PoW**) (Fig. 5B; Supplementary Dataset 1). These measurements were estimated only on complete or nearly complete dorsal carapaces of †*Uca* aff. *ornata*, and male major chelipeds using digital callipers to 0.01 mm. When half or more of the posterior margin in males or females was preserved,

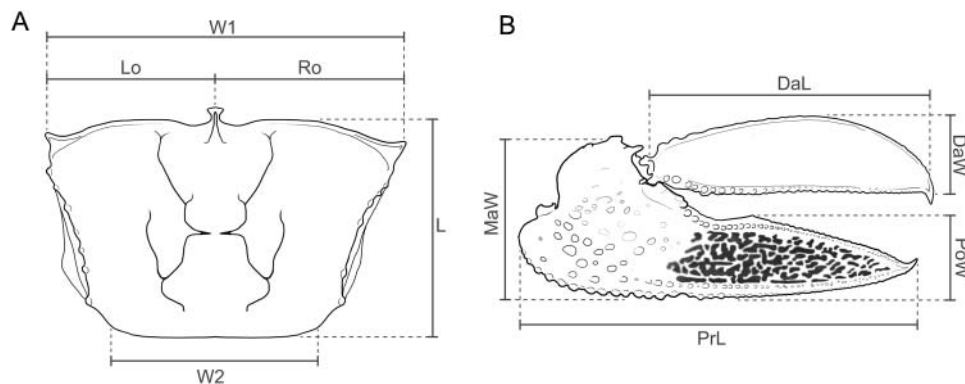


Figure 5. Measurements taken on fossil †*Uca* aff. *ornata* from Bahía Bique, Pacific Coast of Panama (see list of measurements in Supplementary Dataset 1). **A**, male dorsal carapace; **B**, male major cheliped. Abbreviations: DaL, dactylus maximum length; DaW, dactylus maximum width; L, carapace maximum length; Lo, left orbit; MaW, manus maximum width; PrL, propodus maximum length; PoW, pollex maximum width; Ro, right orbit; W1, carapace maximum width; W2, carapace posterior margin width.

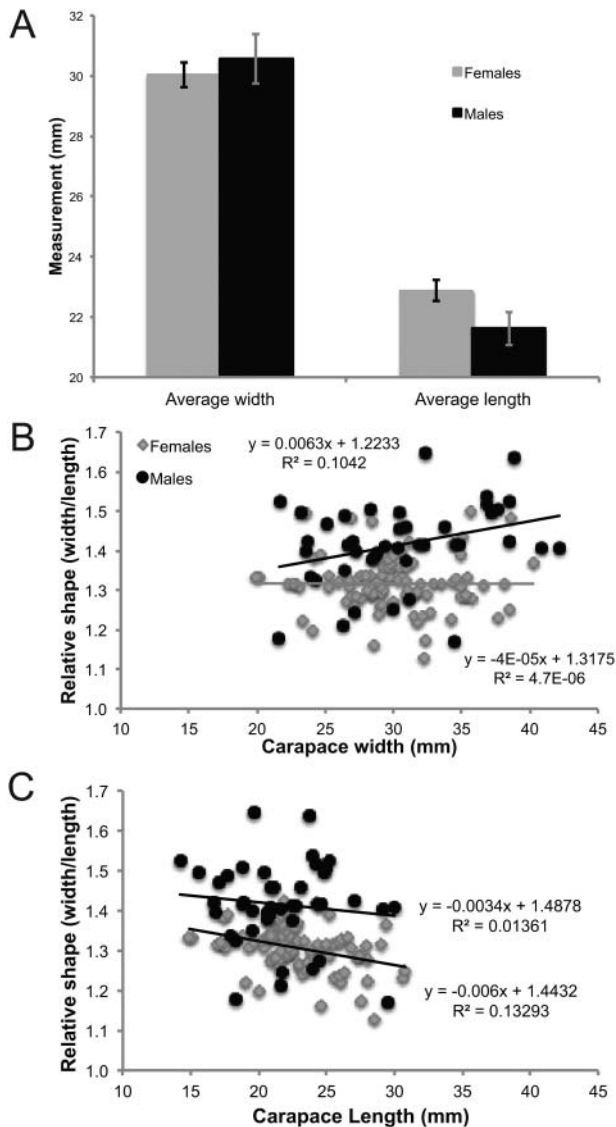


Figure 6. Carapace sizes and shapes in males and females of the fossil *†Uca* aff. *ornata*. **A**, average carapace width and length (\pm standard error) for males and females. Males and females do not differ in average width, but females are significantly longer than males (t-test $p = 0.0496$). **B**, carapace shape (width/length) of males and females versus carapace width. As males increase in carapace width, the shape of their carapace becomes more rectangular, while the shape of females remains constant as carapace width increases. **C**, carapace shape (width/length) of males and females versus carapace length. The sexes do not differ in relative shape with respect to carapace length.

the measurement of the intact half was doubled to estimate the total posterior width (W2). For the fronto-orbital margin, however, this estimation is only informative for females since they are bilaterally symmetrical (Supplementary Dataset 1), whereas males become asymmetrical as they grow, with a longer orbit and eyestalk always occurring on the same side as the major cheliped (Figs 2J–

K, 4). Thus, in males with incomplete fronto-orbital margins (W1), maximum width cannot be estimated. Handedness in males (right- or left-clawed) was noted when it could be determined.

Phylogenetic analysis

We reanalysed a modified dataset after Domínguez Alonso (2008) – constructed after Rosenberg (2001, appendix III) – as the backbone to examine the systematic placement of the fossil fiddler crabs from Bahía Bique in addition to traditional systematic taxonomy (Supplementary Dataset 1). Additional taxonomic units included in the analysis, besides the fossil *Uca* (*Uca*) from Bahía Bique, were the extant fiddler crabs *Uca* (*Leptuca*) *beebei* Crane, 1941, and *Uca* (*Leptuca*) *stenodactylus* (Milne Edwards & Lucas, 1843). Domínguez Alonso (2008) included *Uca* (*Afruca*) *tangeri* (Eydoux, 1835) as an outgroup in his analysis, but due to the currently recognized proximity between *Uca* and *Afruca* (e.g. Sturmbauer *et al.* 1996; Rosenberg 2001; Shih *et al.* 2016), we included it in the ingroup. Character 1 for *†U. ‘marinae’* was rescored since the state is likely not preserved in the fossils rather than being truly absent, as discussed below. Six behavioural characters included by Domínguez Alonso (2008) were excluded as they did not help to resolve the topology upon inclusion of the fossil material, for which no behavioural traits could be scored. The resulting dataset was created in Mesquite (Maddison & Maddison 2011) and consisted of 14 taxa – two outgroup and 12 ingroup – and 78 adult morphological characters (Supplementary Dataset 2). Missing character states were scored as (?) and inapplicable character states as (–). All characters were unordered and equally weighted. Fossil taxa such as *†Uca hamlini* Rathbun, 1926, *†U. oldroydi* Rathbun, 1926, and *†U. miocenica* Artal, 2008 were not included in our analyses due to the high number of missing characters, which do not help resolve the topology. Fossil specimens of *†U. (Afruca) tangeri* (de Gibert *et al.* 2013) were scored with the extant *A. tangeri*.

The phylogenetic analysis was conducted using the software PAUP* 4.0b10 (Swofford 2002) under branch-and-bound search analyses. Bremer support values were calculated in TNT 1.1 (Goloboff *et al.* 2008) under tree bisection reconnection (TBR) and retained sub-optimal trees by 30 steps. Bootstrap and jackknife values were calculated in TNT 1.1 after 1000 iterations each.

Data archiving statement

The data for this study are available in TreeBASE (<http://purl.org/phylo/treebase/phyloids/study/TB2:S19520>), Morphobank (<http://morphobank.org/permalink/?P2482>), and in the Supplemental material to this paper.

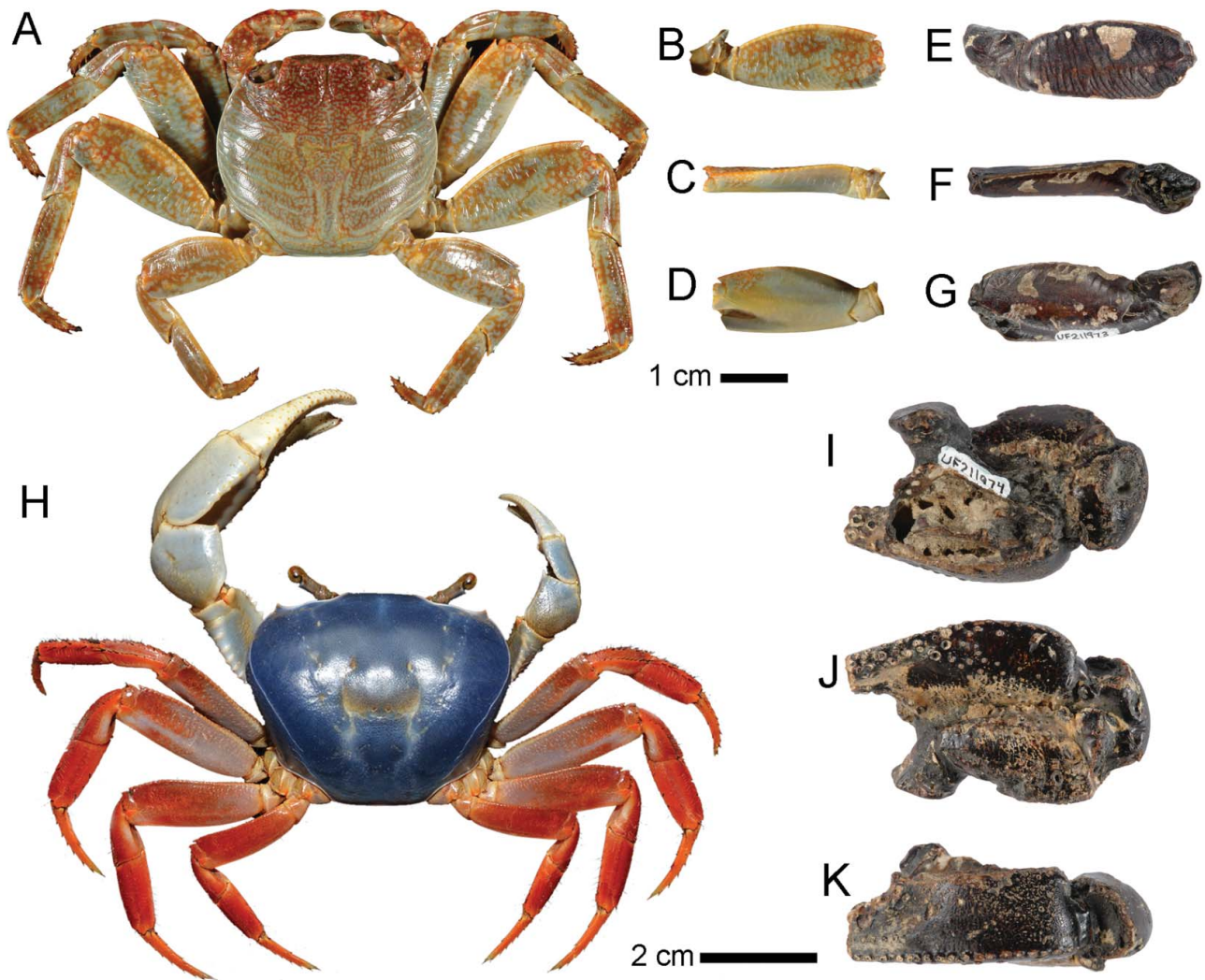


Figure 7. Fossil terrestrial and semi-terrestrial brachyuran crabs from Bahía Bique, Pacific Coast of Panama, associated with †*Uca* aff. *ornata*. **A–D**, extant *Grapsus grapsus* (Linnaeus, 1758); **A**, dorsal view; **B–D**, right merus of third pereiopod in dorsal (**B**), anterior (**C**), and ventral (**D**) views. **E–G**, fossil *Grapsus* aff. *grapsus* from Bahía Bique, UF 211973, right merus of third pereiopod in dorsal (**E**), anterior (**F**), and ventral (**G**) views. **H**, extant *Cardisoma crassum* Smith, 1870. **I–K**, fossil *Cardisoma* aff. *crassum* from Bahía Bique, UF 211974, left cheliped preserving an eroded propodus, merus, and carpus in dorsal (**I**), ventral (**J**), and lateral (**K**) views. Scale bars: 5 mm (A–G); 2 mm (H–K). Specimens photographed dry and uncoated.

Systematic palaeontology

Decapoda Latreille, 1802

Brachyura Latreille, 1802

Thoracotremata Guinot, 1977

Ocypodoidea Rafinesque, 1815

Family **Ocypodidae** Rafinesque, 1815

Genus *Uca* Leach, 1814

†*Uca* aff. *ornata* (Smith, 1870)

(Figs 2D–R, 3D–T, 4E–Q)

1870 *Gelasimus ornatus* Smith: 125, pl. 2, fig. 9, 9a.

1871 *Gelasimus ornatus* Smith; Smith: 91.

1877 *Gelasimus ornatus* Smith; Lockington: 147.

1880 *Gelasimus ornatus* Smith; Kingsley: 146.

1911 *Uca insignis* Rathbun [non *Acanthoplax insignis* H. Milne Edwards, 1852]: 551 [in part].

1918 *Uca insignis* Rathbun: 385 [in part].

1941 *Uca insignis* Rathbun; Crane: 173, fig 5.

1954 *Uca (Uca) insignis* Rathbun; Bott: 156 [in part].

1957 *Uca insignis* Rathbun; Crane: 71, fig 2.

1957 *Uca insignis* Rathbun; Garth: 106 [in part].

1968 *Uca insignis* Rathbun; von Hagen: 442 [in part].

1968 *Uca pizarri* von Hagen: 439, figs 14d, 15a, 16a, 20.

1970a *Uca pizarri* von Hagen; von Hagen: 220.

1970b *Uca pizarri* von Hagen; von Hagen: 22, 28, 48, 51.

- 1975 *Uca (Uca) ornata* (Smith); Crane: 150, pl. 21E–H, figs 26E, 31D, 39C, D, 45G, 65G, 99.
 1985 *Uca ornata* (Smith); Barnwell & Szelistowski: 85A.
 1985 *Uca (Uca) ornata* (Smith); von Prahl & Toro: 274.
 1995b *Uca ornata* (Smith); Hendrickx: 143.
 2001 *Uca ornata* (Smith); Rosenberg: 849, 860, fig 1A.
 2002 *Uca ornata* (Smith); Rosenberg: 162, fig 1C.
 2006 *Uca (Uca) ornata* (Smith); Beinlich & von Hagen: 25.
 2008 *Uca (Uca) ornata* (Smith); Domínguez Alonso: 665
 2008 *Uca marinae*†? Domínguez Alonso: 5, figs 3, 4 [in part].
 2012 *Uca ornata* (Smith); Perez *et al.*: 308.
 2012 *Uca ornata*† (Smith); Portell *et al.*: 268.
 2013 *Uca (Uca) ornata* (Smith); Thurman *et al.*: 16.
 2015 *Uca ornata*† (Smith); Luque *et al.*: 423.
 2017 *Uca ornata*† (Smith); Luque *et al.*: fig. 12R.

Description.

Dorsal carapace. Large for fiddler crabs (for measurements see Supplementary Dataset 1, and compare with Crane 1975), wider than long, trapezoidal in outline, slightly convex sagittally, less so transversely, carapace symmetrical in females and slightly asymmetrical in males, widest at fronto-orbital margin or between the anterolateral margins (Figs 2D, E, J–O, 3D, F, G, I, L, O, P, S). Fronto-orbital margin broad, consisting of a very short and narrow rostrum and very wide orbits (Figs 2D, E, J, K, 3I, L). Orbits well developed, directed forwards, somewhat sinuous, slightly concave axially and slightly convex distally, maximum width of the finely granulated supra-orbital margin greater than adjacent eyestalk, lacking supra-orbital fissures or spines, only bearing a short, triangular, forward-directed outer orbital spine (Figs 2D, E, J–M, 3F, L); sub-orbital margin with fused crenulations medially grading to separated crenulations laterally. Orbits in females equidimensional (Fig. 3F, L, S), whereas in males they are heterodimensional, with the longer orbit always on the same side as the major cheliped (Fig. 2D, E, J–M). Longer orbit in males, between 7% and 21% longer than the shorter orbit (Supplementary Dataset 1). Rostrum small, longer than wide, narrower than base of eyestalk, spatulate, directed downwards and slightly forward, depressed axially, positioned below the base of the eyestalks (Figs 2D, E, J, K, 3I, L). Anterolateral margins short, convex, with acute anterolateral angles, poorly differentiated from posterolateral margin in females, better defined in males, bearing between 3 and 5 relatively large, roundish, widely spaced blunt tubercles; posterolateral margin slightly longer than anterolateral margin, slightly convex, bearing between 4 and 5 relatively large, roundish, widely spaced blunt tubercles in males, and up to 10 tubercles in females. Junction between posterolateral and posterior margins marked by a concavity at level of coxa of pereopod 5 (Figs 2E, Q, R, 3O, R). Posterior margin

long, about 0.57 times as wide as carapace maximum width, slightly convex (Figs 2M, 3D, I, S); posterior margin in males tends to be smooth (Fig. 2A, M), whereas in females it may be beaded with about 10 to 15 small tubercles (Fig. 3G). Carapace lateral margins nearly vertical, unornamented, except from a low-relief ridge constituted by minute granules closely spaced and extending obliquely, anterodorsally to posteroventrally. Dorsal carapace verrucose to granulate in females (Fig. 3A, D, L, O), less so in males (Fig. 2A, D, E).

Ventral carapace. Pterygostome small, wider than long, sub-rectangular, anterior portion nearly straight, in contact with sub-orbital margin; posterior portion concave, to accommodate the coxa of cheliped; distal portion nearly straight; anterior portion rimmed, concave, grooved (Fig. 2D, E, H). Sternites with distal margins visible when pleon oppressed in both male and female (Fig. 2F, G; 3E, J, M, N, T). Sternites 1 to 3 small, fused, sub-triangular, broadening posteriorly; sternite 4 broad, trapezoidal in outline, faintly fused anteriorly with sternite 3, strongly concave axially, suture 4/5 mostly incomplete, only complete axially; sternites 5 to 7 large, well developed, smooth, about three times wider than long, separated from preceding sternites by incomplete sutures; episternites 5 to 7 well developed, small, sub-triangular in outline, nearly as long as corresponding sternite, wider anteriorly (Fig. 2F–I, 3H). Female gonopores sternal, located nearly axially in sternite 6, with well-developed vulvae and opercula (Fig. 3H). Coxae of pereopods never in contact with pleon. Pleonites unfused in both sexes, although strongly sexually dimorphic; pleonites 1–3 in females are shorter than pleonites 4–6, being slender in males (Fig. 2F, G), and much wider in females (Fig. 3E, J, M, N, T). Uropods or uropodal plates absent.

Appendages. Proximal portion of eyestalk preserved in one large male specimen (Fig. 2K), long, slender, smooth, broader at the base. In the same specimen, four, relatively large antennal segments were preserved. Third maxilliped endognathischium elongate, slightly less than twice its width, semi-rectangular in outline, internal margin slightly convex posteriorly, less so anteriorly, outer margin nearly straight anteriorly and concave posteriorly at contact with exognath (Fig. 3K, Q). Major cheliped in males hypertrophied, laterally compressed, extremely wide dorsoventrally (Fig. 4). Handedness of males could be determined in 114 specimens and was equally distributed (51% right-handed vs. 49% left-handed) (Supplementary Dataset 1). Dactylus of major cheliped at least three times longer than manus and nearly as long as pollex, strongly arched, higher at distal third, with maximum height about one-quarter its length, height diminishing sharply at the articulation with manus (Fig. 4E, F); dactylus with very smooth external and internal surfaces lacking ornamentation (Fig. 4E, F, N), ending distally in a

sharp, nearly conical tooth directed downward, meeting or slightly overlapping to the inside of a similar tooth on the pollex. Occlusal surface of dactylus constituted by a lower margin with evenly spaced, coarse and blunt tubercles, and a sub-parallel inner row of evenly spaced, single tubercles except at proximal portion, where tubercles are unevenly spaced, lacking a large tubercle on the inside edge of the dactyl; the middle tubercle row lacks median and sub-distal teeth (Fig. 4G–I, O). Propodus very large, about one-quarter longer than dactylus, constituted by broad, robust manus and long, high pollex (Fig. 4M). Pollex about as long as dactylus, height just sub-equal to dactylus, higher at posterior third, with maximum height about one-fourth the pollex length, tapering distally and ending in a sharp, conical, apical tooth directed upwards, with very smooth internal surface lacking ornamentation; external surface uneven, ornamented with shallow, irregular fossae extending from distal portion to contact with manus, but lacking tuberculation (Fig. 4M, P); two sub-parallel rows of evenly spaced tubercles on pollex occlusal surface and a third, sub-parallel row on the inner surface, the middle row may or may not present large median and sub-distal teeth, the inner row extends to the base of the dactyl. Manus of major propodus robust, broad, nearly as long as broad, constituting one-fourth the propodus length, large, spaced tubercles on the outer surface, small tubercles on the lower surface, bearing a groove outside the dactyl cusp (Fig. 4J, M). Palm of major propodus well developed, with an oblique ridge that extends from pollex lower margin to carpal cavity, and bears one well-developed tubercle, but lacking a parallel row of tubercles between the oblique ridge and the dactyl (Fig. 4K). Carpus nearly as long as pollex maximum height, apparently smooth surface throughout, usually eroded, so no spines have been recognized. Merus sub-cylindrical, much longer than wide, with anterodorsal margin bearing several small, roundish tubercles proximally, lacking a large convex flange and apparently with a single distal tooth near articulation with carpus; ventral margin bearing at least eight tubercles widely spaced (Fig. 2J). Male minor cheliped ischium with a large tubercle on the ventral anterior margin. Female chelipeds isochelous, equidimensional, short, with relatively long, straight pollex and dactylus (Fig. 3M). Male meri of P2–P5 bearing a large tooth in the posteroventral margin, lacking serration, dorsal margin serration absent; male meri of P3–P5 lacking distal or proximal serration on anteroventral margin.

Gonopods. Tube of large size, about half as long as carapace maximum length (Fig. 2H, I), slightly curved bordered by two flanges, finely granulated and both ending distally towards the pore; distal portion of gonopod poorly preserved. Basis with concavity to receive the articular condyle at the base of the tube. Tube flanges covered by fine granules.

Measurements. For measurements taken and list of measurements, see Fig. 5 and Supplementary Dataset 1. Of 404 specimens examined, 242 could be sexed and some measurements taken. Males and females differ slightly in size and shape. Overall, the carapaces of males were not significantly wider than females (average maximum width: males = 30.55 mm \pm 0.870 SE, females = 30.02 mm \pm 0.419 SE, t-test: $N_{\text{females}} = 96$, $N_{\text{males}} = 43$, $p = 0.52$), but were somewhat shorter (average carapace length: males = 21.62 mm \pm 0.553 SE, females = 22.87 mm \pm 0.341 SE, t-test: $N_{\text{females}} = 96$, $N_{\text{males}} = 43$, $p = 0.0496$) (Fig. 6). Males became more rectangular as they increased in size; males larger than average length (≥ 22 mm) were significantly wider than females of this size class (t-test, $N_{\text{females}} = 56$, $N_{\text{males}} = 18$, $p = 0.002$). Orbital length for the left and right sides of the carapace differed in males. The orbit of the major claw side was invariably longer than the orbit of the minor claw side. The absolute difference in orbit size between the two sides ranged from 0.54 mm to 2.80 mm, which represented 3 to 9% of total carapace width. Based on our small sample size of specimens with both orbits measurable ($N = 10$), there was no relationship between asymmetry in orbit length and body size (carapace length or width). However, there was a significant increase in asymmetry with body size when measurements of four extant individuals were included (Supplementary Dataset 1).

Geological range. Plio-Pleistocene?–Holocene to present.

Occurrence. Restricted to the tropical Eastern Pacific. Extant: El Salvador to northern Perú (Crane 1975; von Prah 1982; Hendrickx 1984; von Prah *et al.* 2011; Fiddler Crab Info Webpage http://www.fiddlercrab.info/u_ornata.html, data retrieved June 26, 2017). Fossil: Plio-Pleistocene? of Honduras (Domínguez Alonso 2008) and middle Holocene of Panama (herein).

Remarks. The only two extant species of heavy-clawed fiddler crabs in the Eastern Pacific are *Uca insignis* and *U. ornata*, and both occur in Panama. The fossil fiddler crabs from Bahía Bique, Panama, are identical to extant *U. ornata*, and differ from *U. insignis* in the presence of large teeth on the posteroventral margin of the merus of pereopods 2 to 4, the lack of large tubercles on the anterior margin of the merus of the major cheliped, the nature of the sub-orbital crenulations, and the large and widely spaced tubercles on the dorsolateral margins of the carapace (Supplementary Dataset 2).

Grapsoida MacLeay, 1838
 Family **Gecarcinidae** MacLeay, 1838
 Genus **Cardisoma** Latreille, 1828
Cardisoma aff. *crassum* Smith, 1870
 (Fig 7I–K)

Material. UF 211974.

Description. Major left cheliped of a large specimen, well preserved. Merus sub-triangular transversely, about twice as long as wide, somewhat stout, narrower at articulation with ischium and wider at articulation with carpus; dorsal and anteroventral margins strongly ornamented distally near articulation with carpus, less so proximally near articulation with ischium, with prominent conical tubercles, most worn down due to erosion; posterolateral and ventral surfaces smooth, with low-relief transverse terraces; anterolateral surface not exposed. Carpus stout, slightly longer than wide (maximum L = 19.7 mm; maximum W = 14.8 mm), wider proximally near articulation with merus and narrower near articulation with propodus, relatively smooth throughout, bearing several tubercles on the proximal posterodorsal margin. Propodus large and stout, incomplete, missing the dorsal margin; manus large, manus ventral surface is flattened and smooth, bearing several relatively large tubercles on the lower surface, extending from proximal portion near articulation with carpus to ventral portion of dactylus; palm smooth, but bearing a few tubercles extending from posterior mid palm to the ventral portion of dactylus; pollex broken, only posterior portion near manus preserved, inner tubercle row extends posterior to the base of dactyl, middle tubercle row apparently bearing large teeth, outer tubercle row present. Dactylus missing. Sex indeterminate, but probably corresponds to a large female major cheliped.

Measurements. Propodus maximum length = 31.7 mm; manus maximum width = 14.7 mm; max H = unknown.

Geological range. Mid-Holocene to present.

Occurrence. Extant: Tropical Eastern Pacific, from Baja California to Honduras, Panama, Colombia and Perú (Rathbun 1918; Smith 1870; Hendrickx 1984). Fossil: Bahía Bique, Pacific Coast of Panama (herein).

Remarks. In extant males and females of *Cardisoma crassum*, the chelipeds are heterochelous, but the major cheliped in males is noticeably hypertrophied with respect to the major cheliped in females. The diagnostic robust, short and stout manus of the cheliped, granulated and ornamented ventrally, support the affiliation with *Cardisoma crassum*, which is the only species of *Cardisoma* living today in the Tropical Eastern Pacific. *Cardisoma crassum* is a semi-terrestrial crab that lives in the supratidal zone, preferably in open fields, margins of streams and mangrove swamps commonly in lowland soils close to brackish and salt waters, where it constructs deep burrows used as permanent residence (Bright & Hogue 1972). Other fossil occurrences of the genus are restricted to the species †*C. guanhumii* Latreille, 1828, from the Pliocene–Holocene of Bermuda, Costa Rica, Jamaica and Puerto Rico (e.g. Rathbun 1919; Türkay 1978; Collins &

Donovan 1998; Donovan & Dixon 1998; Schweitzer *et al.* 2008; Collins *et al.* 2009; Luque 2017; Luque *et al.* 2017). Another species, †*C. planum* Rathbun, 1945, from the Pliocene of Fiji, cannot be assigned to the genus (Türkay 1978; Schweitzer *et al.* 2008). Thus, this is only the second species of the genus *Cardisoma* with a confirmed fossil record, and the first occurrence of fossil remains of the genus in the Eastern Pacific.

Family **Grapsidae** MacLeay, 1838

Genus ***Grapsus*** Lamarck, 1801

Grapsus* aff. *grapsus (Linnaeus, 1758)
(Fig 7E–G)

Material. UF 211973.

Description. Large merus of right pereiopod 4, twice as long as it is wide, with a short, thin, well-developed keel on outer margin, several perpendicular striations or terraces dorsally and rather smooth terraces ventrally; ischio-basis very short, about one-fifth as long as merus, with some striations posterodorsally. Sex indeterminate.

Measurements. Merus maximum length = 34.2 mm; merus maximum width = 15.7 mm.

Geological range. Mid-Holocene to present.

Occurrence. Extant: Tropical Eastern Pacific, from California to the Galapagos and northern Chile; Western Tropical Atlantic, from Florida and the Gulf of Mexico, to the Caribbean islands, Panama, Colombia, Venezuela, and Brazil (Hendrickx 1995a; Encyclopedia of Life <http://eol.org/pages/1021865/overview>, data retrieved 26 June 2017). Fossil: Bahía Bique, Pacific Coast of Panama (herein).

Remarks. Despite the fragmentary nature of the specimen, its characteristic pattern of terraces or striations on the leg are identical to those seen in *Grapsus grapsus* specimens (Schmalfuss 1978). Also known as sally light-foot crabs, they live in the splash zone and scrape algae from the rocks in the intertidal zone. Today, they can be found at Playa Bique, mainly where there are large rocks exposed to the waves. Intertidal and supratidal crabs are seldom preserved due to mechanical, chemical and biological biases, hence their rarity as fossils. To our knowledge, there are no fossil grapsids known to date; this represents, therefore the first fossil record for the genus worldwide.

Phylogenetic analysis

We used a modified version of the dataset of Domínguez Alonso (2008) – modified after Rosenberg (2001) – as the backbone to examine the systematic placement of the fossil *Uca* from Bahía Bique in addition to traditional

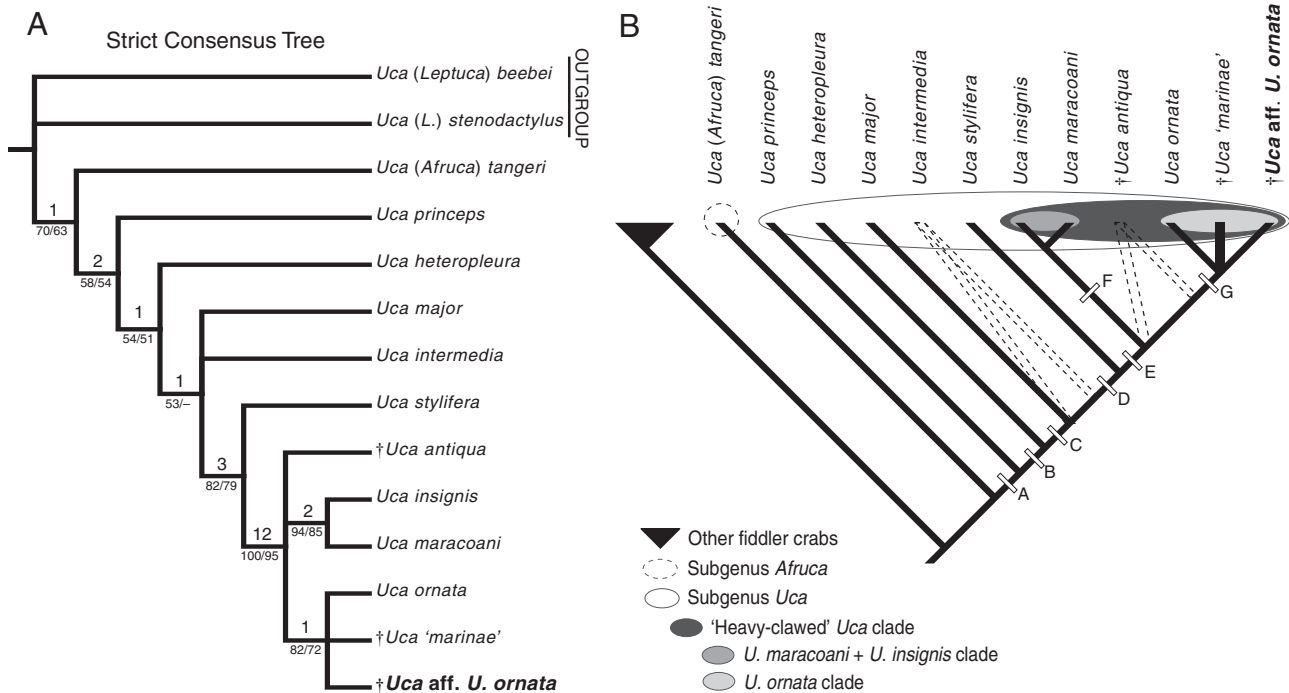


Figure 8. Phylogenetic analyses. **A**, strict consensus of nine equally most parsimonious trees. Tree length (TL) = 146 steps; consistency index (CI) = 0.57; retention index (RI) = 0.75. Bremer support indicated above branches, and bootstrap/jackknife values indicated below the branches from left to right, respectively. **B**, cladogram showing the different clades within *Uca* (white oval). Extant *Uca ornata* (Smith, 1870), †*U. 'marinae'*, and †*U. aff. ornata*, are recovered as a monophyletic clade with bootstrap and jackknife support of 82/72 respectively (light grey oval). *Uca maracoani* (Latreille, 1802), and *U. insignis* (Milne Edwards, 1852) are also recovered as a monophyletic clade with bootstrap and jackknife support of 94/85 respectively (grey oval), and these two clades together with †*U. antiqua* Brito, 1972, constitute a monophyletic clade with bootstrap and jackknife support of 100/95 respectively (dark grey oval). White dotted branches indicate the recovered phylogenetic position of terminals in soft polytomies under a strict consensus and majority rule consensus of nine equally most parsimonious trees. Terminals with dagger (†) known from fossils.

systematic taxonomy, since it is the most recent morphological phylogeny that incorporates fossil fiddler crabs (Supplementary Dataset 1). The resulting analysis yielded nine equally most parsimonious trees, with TL = 146 steps, CL = 0.562, and RI = 0.749. The following clades were recognized:

Clade A: all taxa within *Uca* were united by the synapomorphic rough dorsal margin of the outer major manus [Ch. 12 (0–1)] (Fig. 8). *Uca* was recovered as sister to the monotypic *Afruca*.

Clade B: this was the least inclusive of all clades of *Uca*, with *U. princeps* recovered as the sister taxon. Terminals in this clade are united by the absence of a gonopod thumb [Ch. 72 (1–0)]. Unfortunately, gonopodial traits are usually not preserved in fossils, so we cannot confirm their presence or absence on most fossil terminals.

Clade C: in our analysis, *U. heteropleura* was recovered as the sister taxon to this clade, which is united by the synapomorphic lack of serrations on anteroventral margin of the meri of pereopods 3 and 4 [Ch. 49 (1–0); 53 (1–0)].

Clade D: in the strict consensus, *U. major* and *U. intermedia* were recovered in a soft polytomy with this clade,

which is united by the presence of a large tooth at the major claw's carpus anterodorsal margin, the pits on the outer major pollex and the absence of dorsal serrations on the merus of pereopods 2 to 4 [Ch. 9 (0–1); 31 (0–1); 48 (1–0); 52 (1–0); 56 (1–0)].

Clade E: this was the best supported of all clades (Fig. 8B), and includes the heavy-clawed fiddler crabs within the *Uca maracoani* and *U. ornata* groups, and the extinct †*U. antiqua*. In the strict consensus, †*U. antiqua* was recovered in a soft polytomy with *U. maracoani* and *U. ornata* groups. They are united by the anterodorsal margin of major merus with a distal tooth, the inner tubercle row of major pollex extending to the dactyl's base, the major pollex narrower than the dactyl, and the major dactyl and pollex with thin sharp, inward spines [Ch. 6 (0–1); 24 (1–0); 27 (0–1); 28 (0–1)]. Extant members of this clade also share the presence of pile on the pereopods 2 to 5 [Ch. 34 (0–1); 35 (0–1); 36 (0–1); 38 (0–1) 39 (0–1); 41 (0–1); 42 (0–1); 43(0–1)]. Other synapomorphies that unite the clade are the lack of serrations on the posteroventral margin of the meri of pereopods 2 to 5 and the relatively flat carapace [Ch. 47 (1–0); 51 (1–0); 55 (1–0); 59 (1–0); 64 (0–1); 69 (0–1)].

Clade F: this comprises *Uca maracoani* + *U. insignis*. One of the two extant groups of heavy-clawed fiddler crabs, were united by the presence of pile on the manus of pereopod 2 and the carpi of pereopods 3–4 [Ch. 33 (0-1); 37 (0-1); 40 (0-1)].

Clade G: *Uca ornata* + †*U. aff. ornata* + †*U. 'marinae'*: the second clade of heavy-clawed fiddler crabs. Despite several missing characters in the fossil †*U. aff. ornata* and †*U. 'marinae'* from Panama and Honduras, their scored characters were identical to those in extant *U. ornata*, and therefore, the three terminals were recovered in a trichotomy in the strict consensus (Fig. 8A). The spine present in the posteroventral margin of pereopods 2 to 4 is a synapomorphy that sets them apart from other *Uca* terminals [Ch. 44 (0-1); 45 (0-1); 46 (0-1); 62 (1-0)].

Phylogenetic remarks

Placing the Bique material in a cladistic framework also allowed us to test the phylogenetic hypothesis of Domínguez Alonso (2008) regarding the placement of his fossil species, †*Uca 'marinae'*. The author described †*U. marinae* from the Plio-Pleistocene to Holocene of Honduras, Central America, and depicted it as the sister taxon of *Uca ornata* (Domínguez Alonso 2008, fig. 5). In his dataset, both taxa differed only on the presence of setae on the epibranchial region, scored as present in *U. ornata*, and absent in †*U. marinae* (Domínguez Alonso 2008, appendix 2, character 1). Other than that, the character states for †*U. 'marinae'* have identical scoring as extant and fossil *U. ornata*. A delicate feature like the epibranchial setae is unlikely to be preserved in fossil decapods, suggesting that the 'absence' of such setae in †*U. marinae* is due to poor preservation. In fact, none of the ~400 studied dorsal carapaces of male or female †*U. aff. ornata* from Panama preserves setae or pile on the epibranchial region or other parts of the body, unlike living individuals, reinforcing the hypothesis that the absence of setae in fossil taxa is just a preservational artefact. Based exclusively on the characters scored by Domínguez Alonso (2008) following the work of Rosenberg (2001), †*U. 'marinae'* and *U. ornata* are identical, suggesting that the former is a junior synonym of the latter. The only conspicuous difference between them is the presence on some specimens of large spines on the anterodorsal margin of the major merus in †*U. 'marinae'*, which are virtually identical to those seen in *U. insignis*. *Uca ornata*, *U. insignis*, and the extinct †*U. 'marinae'* have overlapping ranges, and it would not be surprising if *U. 'marinae'* is conspecific with either, especially since both *U. ornata* and *U. insignis* can be found in sympatry in extant communities (J. Christy, pers. obs. 2016). While the overall topology of our revised analysis is identical to that of Domínguez Alonso (2008), our phylogenetic results suggest that †*U. 'marinae'* might be, at

least in part, a junior synonym of *U. ornata*, although it could represent a mixture of specimens of *U. ornata* and *U. insignis*.

Discussion

Biology of extant and fossil *Uca ornata*

Uca ornata is one of the largest-bodied members of fiddler crabs. Males possess one hypertrophied claw (right or left, at random) with broad and flat fingers used in courtship and combat (Fig. 4). The reduction in height of the dactyl at the articulation with the manus in *U. ornata* may be the most extreme among fiddler crabs. This allows males to open their claws wider than most other species, which they do when they wave. The consequence is a relatively weak claw due to poor mechanical advantage (short in lever/long out lever) (J. Christy and B. Swanson, pers. obs.). *Uca ornata* is restricted to the tropical Eastern Pacific, ranging from El Salvador to northern Peru. It feeds on organic detritus contained in the soft (sometimes oozy) muds of open intertidal mudflats usually near the mouths of rivers (Crane 1975). This type of substrate provides the crabs with some support to their weight, particularly during courtship (Crane 1975). Today, the populations of *U. ornata* that we are aware of in Panama (J. Christy and J. Luque, pers. obs.) tend to be patchy and low density, consisting of only a few individuals (usually a dozen or less), and usually in sympatry with other fiddler crabs, including *U. saltitanta* Crane, 1941, *U. oerstedii* Rathbun, 1904, *U. festae* Nobili, 1901, *U. princeps* (Smith, 1870), and rarely with its closely related congener *U. insignis* (Milne Edwards, 1852). However, we recently discovered a dense population of *U. ornata* in Punta Chame with hundreds of individuals in a mangrove mudflat (J. Luque, J. Christy and K. Kerr, pers. obs., May 2015) (Fig. 1A, B), which is closer in density to what we observe in the Bique fossil faunule. The presence of †*Uca aff. ornata* in the Bique fossil assemblage indicates that the area was a large, sheltered intertidal mudflat, surrounded by mangroves, and with some freshwater influx during the mid-Holocene, rather than the pebbly beach we know today. It is not clear to us why no remains of other fiddler crab species have been found in the fossiliferous Bahia Bique assemblage.

Exceptional preservation of *Uca* and other fossils

The preservation of a concentration of fully articulated crabs is an unusual occurrence in the fossil record, and often thought to be the result of mass mortality events (e.g. Portell & Schindler 1991; Feldmann *et al.* 1999; Portell *et al.* 2003; Vega *et al.* 2007; Crawford *et al.* 2008; Maguire *et al.* 2016). Although fossils of taxa such as portunoid crabs are common and abundant, intertidal and supratidal decapods like land crabs and sally lightfoot

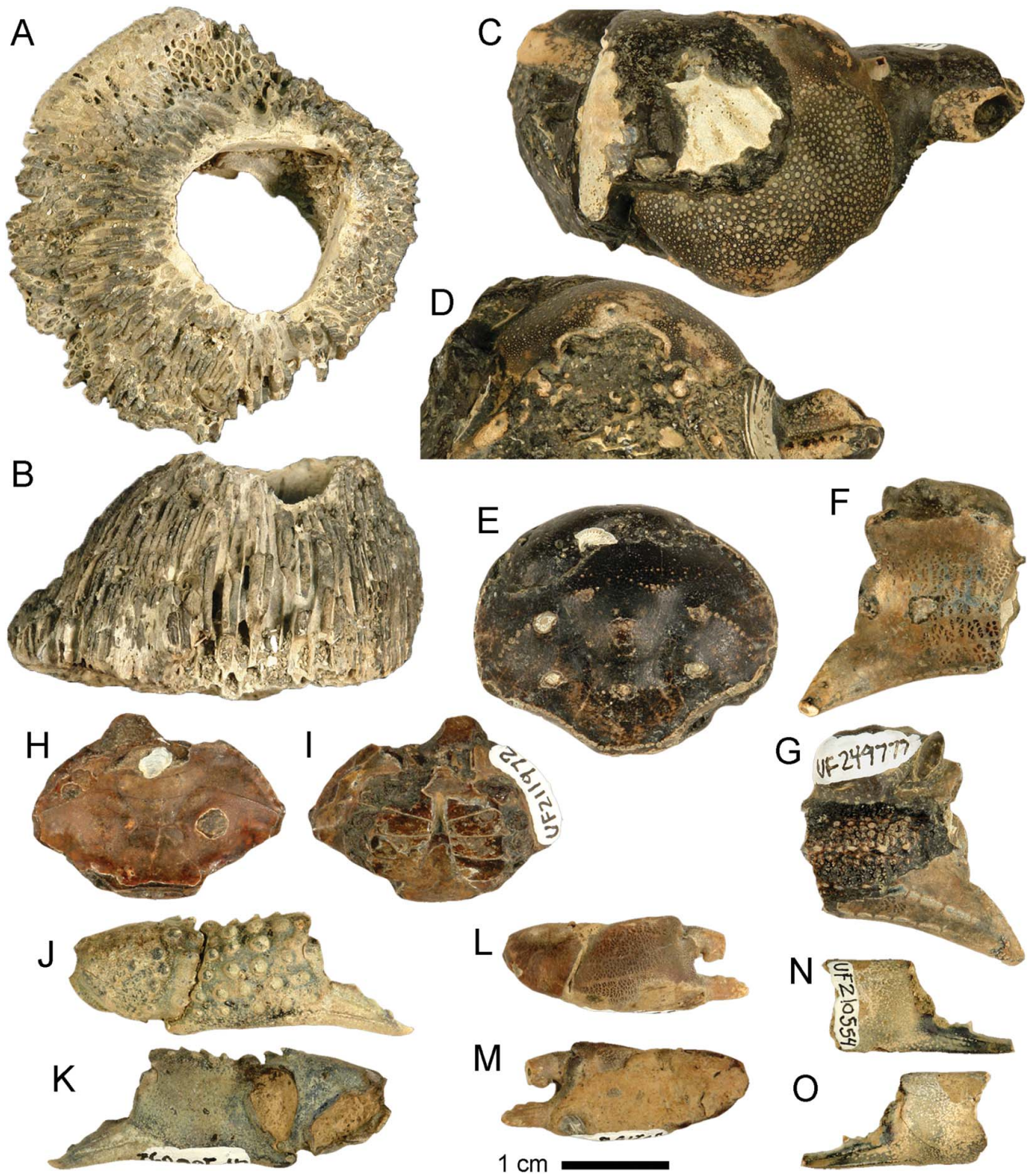


Figure 9. Remains of fossil intertidal to shallow subtidal barnacles and decapod crustaceans from Bahía Bique, Pacific Coast of Panama, associated with †*Uca* aff. *ornata*. **A, B**, Balanomorpha: Tetraclitidae: *Tetraclita squamosa* (Brugière 1789), UF 220523, apertural view of barnacle shell (**A**), right lateral view of shell (**B**). **C, D**, Brachyura: Leucosiidae: *Leucosilia* cf. *jurinii* (Saussure 1853), UF 249776, in dorsal (**C**) and posterior (**D**) views. **E–G**, Aethridae: *Hepatus* sp.; **E**, UF 249748, dorsal carapace; **F, G**, UF 249777, propodus of right cheliped in outer (**F**) and inner (**G**) views. **H, I**, Portunidae: *Callinectes* cf. *arcuatus* Ordway, 1863, UF 211972, dorsal (**H**) and ventral (**I**) juvenile male carapace. **J, K**, Eriphiidae: *Eriphia* aff. *squamata* Stimpson, 1859, UF 206092, outer (**J**) and inner (**K**) view of propodus and carpus of right cheliped. **L, M**, Xanthoidea? indet., UF 206092, outer (**L**) and inner (**M**) view of propodus and carpus of right cheliped. **N, O**, Decapoda indet., UF 210554, inner (**N**) and outer (**O**) view of propodus of left cheliped. Specimens photographed dry and uncoated.

crabs are extremely uncommon. Fiddler crabs are no exception, with only a few reported fossil species that are often based on fragmentary material (e.g. Rathbun 1919; Crane 1975; Artal 2008; de Gibert *et al.* 2013).

The carapaces of fiddler crabs are fragile, and their exuviae and carcasses are prone to rapid chemical, biogenic, and mechanical destruction. In more than 60 years of combined fieldwork digging thousands of extant fiddler crabs out of burrows by three of us (J. Christy, K. Kerr and J. Luque), we have found very few fiddler crab moults and corpses. Corpses found in their burrows are extremely rare; when found, they are rapidly decaying, but are not crushed. Moults, when encountered, are degraded, disarticulated, and break apart easily. Some fiddler crabs have been observed on the surface consuming their exuviae after moulting; a behaviour that adds to the preservation bias of their remains. The pH in the burrows of several species is slightly acidic (e.g. Mokhtari *et al.* 2015, 2016), aiding the disintegration of moults and corpses.

The remarkable preservation and abundance of hundreds of fiddler crabs in the Bahía Bique assemblage, including juveniles and adults of both sexes, and males with the major chelae closed and held along the anterior portion of the carapace, the pereopods often stacked laterally parallel to each other and the pleons pressed ventrally, indicate that several individuals were preserved in 'normal' positions within their burrow shafts or chambers, which is consistent with their presence as eroded burrow infills. No fossils have been identified in moulting position and no corpses are preserved in atypical or traumatic positions (Bishop 1986). Some of the specimens are found crushed dorsoventrally.

Unfortunately, since the Bique fossils are found *ex situ* and lack a clear stratigraphical context, we can only hypothesize about the potential events that could have led to their death and unusually good preservation. Tuffaceous deposits are in close proximity to the fossiliferous sediments at Bahía Bique, which presumably originated from the nearby volcanic peaks such as the Cerro Cabra (c. 2 km from Bahía Bique) and nearby features (e.g. Cerro Chame, Cerro Cermeno, Cerro Vacamonte and the Bono-Otoque Islands). These hills and mountains may have formed during a Quaternary volcanic phase, resulting in deposition of dacitic pyroclastic flows and airfall dated as late as 56 kyr BP (Defant *et al.* 1991; Hidalgo *et al.* 2011). Hendy *et al.* (in progress) have suggested that many of the Bique taxa could have been suffocated, killed and rapidly buried by a fine particulate Quaternary volcanic airfall (see also Kranz 1974; Heikoop *et al.* 1996; Crawford *et al.* 2008). This scenario seems quite plausible, although we have not found volcanic ashes directly associated with the fossil fiddler crabs, and thus no confirmed link between volcanic activity and their mortality.

Alternative scenarios that may explain the rapid burial and preservation of the fossil fiddler crabs include storms,

hurricanes, mudslides, or a massive river runoff due to an onland-flooding event. Each of these scenarios has the potential to dump suddenly enough sediment over the intertidal to bury the crabs while in their burrows, and crush several specimens dorsoventrally. Rapid accumulation of sediment also has the potential to change the chemistry of the water and sediment in the crabs' burrows, which would be necessary to facilitate the unusually good preservation observed. Another unusually well-preserved intertidal crab is *Ocypode quadrata* (Fabricius 1787) from the late Quaternary of Florida (Rathbun 1935; Portell *et al.* 2003; Luque *et al.* 2017). Like the fossil fiddler crabs from Bahía Bique, these Florida ocypodids are represented by hundreds of articulated specimens in relaxed or 'normal' positions. The crabs have been interpreted as carcasses in concretionary burrow infills, likely formed after rapid burial and saturation with calcium-rich freshwater (Portell *et al.* 2003). In both of these intertidal Quaternary assemblages, the events/processes that resulted in their death could have also played a role in their rapid preservation.

Other sporadic occurrences of crustaceans in the Bahía Bique taphocoenosis include the aethrid crab *Hepatus* sp. (Fig. 9E–G) and the portunid crab *Callinectes* cf. *arcuatus* Ordway, 1863 (Fig. 9H, I), shallow subtidal dwellers sometimes found in tidal pools. Crustaceans like the acorn barnacle *Tetraclita squamosa* (Brugière 1789) (Fig. 9A, B), and crabs like the purse crab *Leucosilia* cf. *jurinii* (Saussure 1853) (Fig. 9C, D), the stone crab *Eriphia* aff. *squamata* Stimpson, 1859 (Fig. 4J, K), and *Uca*, *Grapsus* and *Cardisoma* (Figs 2–4, 7), indicate intertidal foreshore to supratidal backshore habitats, respectively. All of the fossil crustaceans discovered in Bahía Bique are identical in morphology to extant species, which supports the idea that these fossils represent a Quaternary assemblage of reworked material from the Pacific Muck.

Conclusions

Regardless of the potential factors that led to the death and unusual preservation of fossil fiddler crabs from Bahía Bique, Panama, it must have: (1) occurred rapidly, (2) entombed the crabs while in their burrows, (3) deposited enough material to prevent escape, and (4) changed the geochemistry in the sediment fast enough to facilitate the preservation of the otherwise rare fiddler crab fossils.

The fidelity of living–dead mollusc and crustacean assemblages from Bahía Bique indicates that the fossil faunule represents a mixture of supratidal, intertidal and shallow subtidal taxa of Quaternary age. Radiocarbon dates on the bivalve *Saccostrea palmula* suggest an age of ~5000 kyr BP. It seems parsimonious to consider that the oyster and fiddler crab ages are approximately the same, although it is possible that they come from different time intervals within the Quaternary.

The new fossil fiddler crab material represents a large population of the extant *Uca ornata*. Our phylogenetic analysis suggests that *Uca 'marinae'*, supposedly from the Plio-Pleistocene of Honduras, is likely a junior synonym of *U. ornata* or *U. insignis*. The Panama and Honduras fossil occurrences overlap with the present biogeographical ranges of *U. ornata* and *U. insignis*, restricted to the Tropical Eastern Pacific and ranging from El Salvador to Northern Peru. The habitat preference of modern *Uca ornata* for soft muds of open intertidal mudflats indicates that part of Bahía Bique must have been a large estuarine mudflat near freshwater influx during the Quaternary (e.g. Fig. 1A, B), in contrast to the present gravel field where the fossils are found as *ex situ* boulders, cobbles and gravel-sized clasts eroded from rocks of the Pacific Muck (Fig. 1C, D).

In Bahía Bique, fiddler crabs are the most abundant macrofossils after bivalves and gastropods. Some sporadic remains of semi-terrestrial and shallow marine invertebrates (e.g. land crabs, portunid crabs) and vertebrates (e.g. shark and ray teeth, catfish remains) might correspond to carcasses present in the intertidal at the time of burial, or even re-worked material transported during the burial event. Remarkably, the faunule includes the first confirmed fossil record for the sally lightfoot crab genus *Grapsus*, the first fossil record of the land crab *Cardisoma* in the Eastern Pacific, and the most complete and abundant record of fossil fiddler crabs *Uca* worldwide.

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