

Spider crabs of the Western Atlantic with special reference to fossil and some modern Mithracinae

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Spider crabs are well-known from modern oceans and are also common in the western part of the Atlantic Ocean. When spider crabs (Majoidea) appeared in the Western Atlantic in deep time and when they became diverse, hinges on their fossil record. By reviewing their fossil record, we show that (1) spider crabs first appeared in the Western Atlantic in the Late Cretaceous, (2) they became common since the Miocene, and (3) most genera are found in the Caribbean region starting in the Miocene. Furthermore, taxonomic work on some modern and fossil Mithracinae was conducted. Specifically, *Maguimithrax* gen. nov. is erected to accommodate the extant species *Damithrax spinosissimus*, while *Damithrax* cf. *D. pleuracanthus* is recognized for the first time from the fossil record (late Pliocene–early Pleistocene, Florida, USA). Furthermore, two new species are described from the lower Miocene coral-associated limestones of Jamaica (*Mithrax arawakum* sp. nov. and *Nemausa miocenica* sp. nov.). Spurred by a recent revision of the subfamily, two known species from the same deposits are refigured and transferred to new genera: *Mithrax donovani* to *Nemausa*, and *Mithrax unguis* to *Damithrax*. The diverse assemblage of decapods from these coral-associated limestones underlines the importance of reefs for the abundance and diversity of decapods in deep time. Finally, we quantitatively show that these crabs possess allometric growth in that length/width ratios drop as specimens grow, a factor that is often insufficiently taken into account while describing and comparing among taxa .

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Abstract

Spider crabs are well-known from modern oceans and are also common in the western part of the Atlantic Ocean. When spider crabs (Majoidea) appeared in the Western Atlantic in deep time and when they became diverse, hinges on their fossil record. By reviewing their fossil record, we show that (1) spider crabs first appeared in the Western Atlantic in the Late Cretaceous, (2) they

became common since the Miocene, and (3) most genera are found in the Caribbean region starting in the Miocene. Furthermore, taxonomic work on some modern and fossil Mithracinae was conducted. Specifically, *Maguimithrax* gen. nov. is erected to accommodate the extant species *Damithrax spinosissimus*, while *Damithrax* cf. *D. pleuracanthus* is recognized for the first time from the fossil record (late Pliocene–early Pleistocene, Florida, USA). Furthermore, two new species are described from the lower Miocene coral-associated limestones of Jamaica (*Mithrax arawakum* sp. nov. and *Nemausa miocenica* sp. nov.). Spurred by a recent revision of the subfamily, two known species from the same deposits are refigured and transferred to new genera: *Mithrax donovani* to *Nemausa*, and *Mithrax unguis* to *Damithrax*. The diverse assemblage of decapods from these coral-associated limestones underlines the importance of reefs for the abundance and diversity of decapods in deep time. Finally, we quantitatively show that these crabs possess allometric growth in that length/width ratios drop as specimens grow, a factor that is often insufficiently taken into account while describing and comparing among taxa.

Introduction

Modern spider crabs (Majoidea) range in size from a few millimeters to more than a meter in carapace length. Long, slender legs and a pyriform to triangular shape give many of them a spider-like appearance. They occur in nearly all oceans (e.g., Griffin, 1966), and many of them have been found to decorate themselves for camouflage (e.g., Wicksten, 1993; Guinot, Tavares & Castro, 2013). Today, spider crabs are very diverse with nearly 1000 species worldwide (Ng, Guinot & Davie, 2008; De Grave et al., 2009). More than 125 species have been found in the

fossil record (De Grave et al., 2009; Schweitzer et al., 2010), with the oldest species known from the mid-Cretaceous of Europe (Breton, 2009; Klompmaker, 2013). Collins, Portell & Donovan (2009) provided an overview of fossil decapods, including majoids, known from the Caribbean region. Since then, various new fossil majoid occurrences and new fossil species have been reported for the Western Atlantic (e.g., Collins et al., 2010; Collins & Donovan, 2012; Feldmann et al., 2013; Frantescu, 2013; Varela, 2013; Collins, Garvie & Mellish, 2014; Stepp, 2014).

The Mithracinae (or Mithracidae sensu Windsor & Felder, 2014) are spider crabs that do not decorate themselves, and are found in (sub)tropical waters from intertidal to 450 m depth, mainly as reef- and rubble dwellers (Windsor & Felder, 2014). Recently, the family was revised extensively using morphological and molecular analyses resulting in numerous redefinitions and the resurrection and erection of four genera (Windsor & Felder, 2014). As for the Western and Eastern Pacific, the Mithracinae are well-known from the Western Atlantic with over 30 species (e.g., Rathbun, 1925; Abele & Kim, 1986; Felder et al., 2009; Windsor & Felder, 2014), the latter authors (p. 154) suggesting it is an “amphi-American” group. Although their fossil record is decent, with 19 species known from the fossil record (Schweitzer et al., 2010), additional research is required because representatives of many extant genera have a scarce fossil record.

Here, we review the fossil record of spider crabs in the Western Atlantic to elucidate their occurrences through time and their paleobiogeography. Furthermore, various fossil and modern members of the Mithracinae are described or reassigned, and growth of these majoids is studied.

Materials & Methods

We compiled data on all fossil majoid occurrences known from the Western Atlantic (defined here: Argentina to Canada) determined to the genus- and species-levels based on the literature and previously unreported material from the FLMNH Invertebrate Paleontology Collection.

For the systematics part, the length and width of crab carapaces were measured with digital calipers accurate to 0.03 mm. Institutional abbreviations for specimens: FSBC: Fish and Wildlife Research Institute, St. Petersburg, Florida, USA; UF: Florida Museum of Natural History at the University of Florida, Gainesville, Florida, USA. Modern UF specimens are housed in Invertebrate Zoology (IZ); fossil specimens in Invertebrate Paleontology (IP).

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Results

Spider crab distribution in the Western Atlantic

Genera and species known today (15/19 or 79%, 13/31 or 42%, resp.) are well-represented in the dataset (Table S1) on fossil spider crabs because most taxon occurrences (108/117 or 92%) are Neogene and Quaternary in age. Spider crabs in this part of the world first appeared the late Late Cretaceous (Rathbun, 1935; Feldmann et al., 2013), which is younger than the mid-Cretaceous occurrences in Europe (Breton, 2009; Klompmaker, 2013). They become increasingly better represented towards the Recent on the genus- and family-levels (Fig. 1). All modern majoid families (sensu De Grave et al., 2009) are represented except for the Hymenosomatidae that do not have a fossil record. Most taxa are found in the Caribbean region as opposed to in higher latitudes (Fig. 2).

Discussion

All modern majoid families (sensu De Grave et al., 2009) are represented in Figure 1 except for the Hymenosomatidae that do not have a fossil record. This is likely to be related to their small size and weakly calcified exoskeleton (e.g., Ng & Jeng, 1999; Guinot, 2011; Tavares & Santana, 2015; note that Guinot argued that the family does not belong to the Majoidea). Conversely, the Epialtidae and Majidae (especially Mithracinae) are well-represented, being markedly larger and better calcified, comparatively. The results show that historical diversification of the Mithracinae in the Americas helps to explain their abundance there today.

Although the pattern that most majoid taxa are found in the Caribbean region (Fig. 2) is consistent with the modern latitudinal diversity gradient for decapods, including Brachyura (e.g.,

Abele, 1982; Steele, 1988), much more research has been done in the (sub)tropical Western Atlantic region and exposures may be more numerous. However, fossil decapods from the eastern coast of the USA have received considerable attention (e.g., Rathbun, 1935; Roberts, 1962; Blow & Manning, 1996; Blow, 2003; Feldmann et al., 2013; Frăntescu, 2013), but less research has been done on fossil decapods from Brazil and other South American countries south of the Caribbean region (e.g., Aguirre-Urreta, 1990; Casadío et al., 2005; Martins-Neto & Dias Júnior, 2007; Távora, Paixão & Da Silva, 2010). More fossil decapods – including spider crabs – are expected to be present in those regions.

The spider crabs *Mithrax arawakum* sp. nov. and *Nemausa miocenica* sp. nov. erected below add to the number of species known from the lower Miocene limestones at the Duncans Quarry in Jamaica. Portell & Collins (2004) reported on 16 decapod species from these limestones, a unique crab fauna from the Miocene of the Caribbean because 9/14 genera were unknown until then from that region. As for another diverse decapod assemblage in the Caribbean (Collins & Morris, 1976), this fauna is also associated with corals. Cenozoic, coral-associated fauna from Europe are also speciose (e.g., Müller, 1984; Jakobsen & Collins, 1997; Beschin et al., 2007; Gatt & De Angeli, 2010; Beschin, Busulini & Tessier, 2015) as are such decapod faunas from the Mesozoic (e.g., Collins, Fraaye & Jagt, 1995; Fraaije, 2003; Krobicki & Zatoń, 2008; Klompmaker, 2013; Klompmaker, Ortiz & Wells, 2013; Robins, Feldmann & Schweitzer, 2013). Moreover, a significant correlation exists between reef abundance and decapod diversity throughout the Mesozoic (Klompmaker et al., 2013). The assemblage from the Duncans Quarry underlines the importance of reefs for the abundance and diversity of decapods in deep time.

139

140 **Systematic Paleontology**

141


142 Order Decapoda Latreille, 1802

143 Infraorder Brachyura Linnaeus, 1758

144 Section Eubrachyura De Saint Laurent, 1980

145 Superfamily Majoidea Samouelle, 1819

146 Family Majidae Samouelle, 1819

147 Subfamily Mithracinae  Leay, 1838

148

149 *Maguimithrax* gen. nov.

150

151 *Etymology*.—Contraction of the family name of Tobey Maguire, the actor in three Spider-Man
152 movies (2002, 2004, 2007), and *Mithrax*.

153

154 *Type species*.—*Maia spinosissimus* Lamarck, 1818, by present designation, gender masculine,
155 extant.

156

157 *Species included*.—*Maguimithrax spinosissimus* (Lamarck, 1818).

158

159 *Material*.—UF 12474 (1♀), 11447 (1♂), 11457 (1♀), 31157 (1♂, 1♀), 11388 (1♂, 1♀), all
160 FLMNH IZ collection.

161

Diagnosis.—Carapace slightly longer than wide to about equally wide as long in large specimens (l/w ratio = $\sim 1.09 - 0.97$) (Fig. 3), maximum reported width without spines 167 mm, rounded to diamond-shaped, without angled transition from antero- to posterolateral margin, covered with spines laterally and tubercles more axially. Upper orbital margin with four to five spines including strong outer orbital spine and axialmost spine; four suborbital spines including two spines on antennal article, axialmost one strongest. Lateral margin bears six spines, anteriormost ones with accessory spines at anterior bases, fifth and sixth spines weaker. Gastric, cardiac, and uro-metagastric regions surrounded by pronounced grooves; other regions less delineated. Chelipeds and other appendages spinose dorsally, less so to smooth ventrally; cheliped propodus with tubercles or spines on upper margins and two to four tubercles on inner side.

Remarks.—Verrill (1908), Rathbun (1925), and Wagner (1990) all noted that young specimens of *D. spinosissimus* are close to *Nemausa acuticornis* and *N. cornuta*. There are indeed many similarities between *Nemausa* and *D. spinosissimus* including the spinose character of the carapace and appendages, a comparable third maxilliped (see Windsor & Felder, 2014: fig. 4), a longer than wide carapace in younger individuals (Fig. 4), and a similar groove and region structure of the carapace. Not surprisingly, *D. spinosissimus* has been placed in *Nemausa* (Coelho & Torres, 1990). Several differences exist compared to *Nemausa* as currently defined. The carapace is more rounded to diamond-shaped compared to the pyriform carapaces of *Nemausa* so that the point of maximum width is reached more anteriorly; *D. spinosissimus* bears six lateral spines, whereas *Nemausa* bears five such spines; and the spine at the lateral angle is very strong in *Nemausa* compared to other lateral spines, but it is less prominent than others in

D. spinosissimus. Molecular phylogenetics support the assertion that *D. spinosissimus* does not fit within *Nemausa* (Windsor & Felder, 2014).

The species has been assigned to *Mithrax* as well (e.g., Provenzano & Brownell, 1977; Wagner, 1990). However, *Mithrax* as currently defined is markedly different in that (1) the third maxilliped endopod merus distomesial margin has a deep, angular excavation at the articulation with the palp in *D. spinosissimus*, whereas this merus exhibits no pronounced concavity in *Mithrax* (cf. Windsor & Felder, 2014); (2) the ornamentation on the carapace is more varied in *Mithrax*, consisting of more granules; (3) the propodus bears tubercles and spines in the examined specimens of *D. spinosissimus*, but it is smooth in *Mithrax*; and (4) molecular phylogenetics separates *D. spinosissimus* from *Mithrax* (Windsor & Felder, 2014).

Most recently, the latter authors assigned the species to *Damithrax*. However, it should be noted that *D. spinosissimus* is much more spinose on the dorsal carapace than other species of *Damithrax* (e.g., Desbonne & Schramm, 1867: pl. 8; Rathbun, 1925: pl. 135), including the type species. Moreover, the propodus is not smooth in *D. spinosissimus* unlike in other species of the genus, and specimens across a considerable size range (< 75 mm carapace width) are slightly longer than wide or about equally wide as long, unlike the diagnosis of the genus. Not surprisingly, the species plots as a sister taxon to all other modern *Damithrax* spp. (Windsor & Felder, 2014: fig. 2); the latter authors also indicated that this taxon “is somewhat the outlier” (p. 155). Finally, all three of the discussed genera possess a lateral angle, whereas this area is much more rounded in *D. spinosissimus*. Thus, *D. spinosissimus* fits better in a new genus:

Maguimithrax gen. nov.

Detailed descriptions of the species and ontogenetic variations were detailed by Rathbun (1925), Williams (1984), and Wagner (1990) that need no repeat here. Sexual dimorphism is

evident in that larger males ($> \sim 60$ mm carapace width based on the studied material) exhibit a pronounced tooth on the occlusal surface of the dactylus, whereas females do not bear such a tooth.

Stratigraphic and geographic range.—Extant only, North Carolina – Venezuela (Williams, 1984; Wagner, 1990).

Damithrax Windsor & Felder, 2014

Type species.—*Mithrax pleuracanthus* Stimpson, 1871, extant.

Species included.—*Damithrax hispidus* (Herbst, 1790) [= *Maia spinicineta* Lamarck, 1818; *Mithrax laevimanus* Desbonne in Desbonne & Schramm, 1867; *Mithrax depressus* A. Milne-Edwards, 1875 (part); *Mithrax caribbaeus* Rathbun, 1920; *Mithrax carribbaeus*, Ng et al., 2008 (incorrect spelling)]; *Damithrax pleuracanthus* (Stimpson, 1871); *Damithrax tortugae* (Rathbun, 1920); *Damithrax unguis* (Portell & Collins, 2004).

Emended diagnosis.—Carapace wider than long [for large specimens, about equally long as wide for small specimens], overall shape pyriform; dorsal surface smooth to tuberculate, not obviously setose; [five] lateral spines or teeth, first two commonly with accessory spine, lateral angle with single spine; posterior margin tuberculate. Rostral horns blunt, sparsely setose, tips not converging, not reaching [far] beyond first movable article of antenna. Antenna fused basal

article very broad, forming floor of orbit, bearing two or three blunt marginal spines or teeth, anteriormost the largest, decreasing posteriorly (third often very low, or not developed), anterior two visible in dorsal view. Orbit complete, dorsal margin weakly armed behind strong pre-ocular tooth, eyestalk protected above by single blunt dorsal tooth or tubercle separated by closed fissure from two or three blunt post-ocular teeth or tubercles. Third maxilliped endopod merus distomesial margin deeply, angularly excavated at articulation with palp. Cheliped greater than or equal to carapace length; merus dorsal surface spinous, spines not laminar; carpus varied from smooth to rough; propodus smooth; dactylus with enlarged proximal tooth when mature, opposed margins of fingers otherwise crenulate. Pereiopods two to five (ambulatory legs) decreasing in size anterior to posterior; articles finely setose; merus dorsal surface bearing large tubercles and spines, ventral surface with one to six tubercles or spinules; carpus dorsal surface spinous; propodus without spination; dactylus strong, approximately half length of propodus, dactylar lock well developed. (adapted after Windsor & Felder, 2014, changes in brackets)

Remarks.—The diagnosis of Windsor & Felder (2014) mentioned that the carapace is wider than long. While this generally applies to large specimens, small specimens can be about equally long as wide or even slightly longer than wide (Fig. 5).

Damithrax unguis (Portell & Collins, 2004)

Figures 5, 6

2004 *Mithrax unguis* sp. nov.; Portell & Collins, 2004: p. 117, fig. 1.6.

253

254 *Locality*.—FLMNH-IP XJ015: Duncans Quarry 01, Trelawny Parish, Jamaica (18.4710, -
255 77.5796 WGS 84).

256

257 *Stratigraphic horizon*.—lower Miocene, Montpelier Formation (uppermost unit) (Mitchell, 2004;
258 Portell & Collins, 2004).

259

260 *Material*.—Holotype: UF 106697; Paratypes: UF 73089, 73165, 103955, 106768, 106772,
261 111483; Topotypes: UF 112783–112785, 112795, 112942, 112946, 113010, 113011, 113117,
262 113586, 113587, 113675, 113677, 255051–255054. All internal molds, some RTV silicone
263 rubber casts of external molds.

264

265 *Diagnosis*.—Pyriform carapace, l/w ratios vary from ~0.90 for the largest specimens, ~1.00 for
266 small specimens. Short rostrum with two small spines downturned, slightly longer than axialmost
267 inner orbital spine. Four usually single spines (second one may have accessory small spine
268 anteriorly in some specimens) on anterolateral margin excluding outer orbital spine. Forwardly
269 directed shallow orbit with spines on the upper orbital margin: four upper orbital spines
270 including outer orbital spine with center two converging; suborbital margin with three spines,
271 axialmost one strongest. Smaller orbital spines less pronounced in small specimens. Tubercular
272 gastric and branchial regions.

273

274 *Description*.—See Portell & Collins (2004: p. 117).

275

276 *Measurements*.—Table S2.

277

278 *Remarks*.—Portell & Collins (2004) erected *Mithrax unguis* based on early Miocene specimens
279 from the Duncans Quarry, Trelawny Parish, Jamaica. The generic placement was reassessed here
280 because of the revision of extant Mithracinae by Windsor & Felder (2014). Given the close
281 similarity to *Damithrax hispidus*, as was also indicated by Portell & Collins (2004), and a
282 reasonable fit with the current generic diagnosis of *Damithrax*, *Mithrax unguis* is transferred to
283 *Damithrax*. The species cannot be retained in *Mithrax* because of the non-spinose character on
284 the dorsal carapace not including the lateral margins. The species differs from *D. hispidus*, *D.*
285 *pleuracanthus*, and *D. tortugae* in that the rostrum is sharp instead of blunt and the *D. unguis*
286 seems to have sharper upper orbital spines. Moreover, the length/width ratios separate *D. unguis*
287 from *D. hispidus* (Fig. 5).

288 Portell & Collins (2004) had a limited number of specimens available and showed
289 measurements for three of them. With additional collecting, preparation, and identification, many
290 new specimens became available allowing for the investigation of ontogenetic variation within
291 the species. As was quantitatively shown for several fossil crab species (e.g., Klompmaker,
292 Feldmann & Schweitzer, 2012; De Jesús Gómez-Cruz, Bermúdez & Vega, 2015; see below),
293 width grows faster relative to the length resulting in a decline of length/width ratios (Figs. 5, 6);
294 similar morphometric results were also obtained for ghost shrimp claws recently (e.g.,
295 Klompmaker et al., 2015). Such allometric growth is especially important for genera of
296 Mithracinae that are currently diagnosed, in part, based on carapace length/width ratios (Windsor
297 & Felder, 2014). For *D. unguis*, one could postulate that width is greater than length for some,
298 width is (sub)equal to length, and even length is greater than width for the smallest specimens.

Therefore, providing a range of l/w ratios along with specimen sizes for diagnoses and descriptions seems even more useful.

Stratigraphic and geographic range.—lower Miocene, Jamaica.

Damithrax cf. *D. pleuracanthus*

Figures 7–10

Locality.—FLMNH-IP SO001: MacAsphalt Shell Pit, Sarasota County, Florida, USA (27.3666, -82.4520 WGS 84).

Stratigraphic horizon.—late Pliocene–early Pleistocene, spoil.

Material.—Single carapace (UF 29057), cuticle.

Diagnosis.—See Williams (1984: p. 334, 335).

Description.—Carapace pyriform, about as long as wide (l/w ratio = 1.01), maximum width at ~61% of carapace length, weakly convex longitudinally and moderately so transversely. Rostrum with two forward projections, only bases preserved; with blunt triangular axial projection oriented downward and posteriorly, with rims. Orbits directed anterolaterally, about as wide as tall, deep, with seven spines around orbit: two spines on antennal segment of which the

axialmost one is strongest, separated by a notch and then followed by weak spine more laterally; upper orbital margin with four spines including strong outer orbital spine and stronger axialmost spine; two weak spines in between. Circular antennal holes between axialmost suborbital spine and rostral spines. Anterolateral margin with four spines (excluding outer orbital spine), third spine weakest, last spine at transition from antero- to posterolateral margin, oriented laterally. Posterolateral margin more rounded than anterolateral margin, with single small spine just posterior to previous spine. Posterior margin with convex protrusion axially, exhibiting row of tubercles and granules continuing onto posterolateral margin. Frontal region including epigastric region with double row of tubercles. Hepatic regions small, at lower level compared to gastric region, with single anterolateral spine. Protogastric regions bulbous, with major tubercle laterally and less pronounced one axially. Mesogastric region with tubercle on process; base swollen, divided into three regions, central region oval. Uro- and/or protogastric region small, wider than long. Cardiac region pentagonal to triangular, with concave margins, about equally long as wide, tubercular. Branchial regions confluent. Intestinal region not delineated, with two strong tubercles. Cervical groove moderately deep, with two slits axially, V-shaped overall but rounded axially, bends more laterally near anterolateral margin. Shallow groove extends from cervical groove near base hepatic region to below outer orbital spine. Grooves around cardiac and uro- and/or metagastric regions. Dorsal carapace surface of cuticle with very small pits, armed with tubercles all over, more granules posteriorly; row of five tubercles midway gastric region. Ventrolateral sides below anterolateral margins contain small spines. Of hardened parts: most of ventral surface, abdomen, and appendages lacking.

Measurements.—Excluding spines and rostrum: 13.9 mm long, 13.8 mm wide.

345

346 *Remarks.*—The specimen is very well-preserved and is ascribed to *Damithrax* sp. because of the
 347 close similarity to extant species, notably *Damithrax hispidus*, *D. pleuracanthus*, and *D.*
 348 *tortugae*. These modern species were synonymized by Wagner (1990), but Windsor & Felder
 349 (2009) resurrected them based on molecular evidence and supported by morphological characters
 350 of the appendages. Ornamentation on the dorsal carapace, as was used by Rathbun (1925), was
 351 rejected by Windsor & Felder (2009) because of ontogenetic variability (accessory spines and
 352 tubercles become more apparent with age), especially within *D. pleuracanthus*. Ontogenetic
 353 variability of tubercles on the dorsal carapace was also found for *D. hispidus* in that the largest
 354 specimen (75.4 mm carapace width) exhibits fewer tubercles compared to small specimens (<
 355 ~30 mm carapace width) (pers. obs. AAK). Windsor & Felder (2009) suggested that
 356 ornamentation on the merus and carpus of the cheliped can be used to distinguish between *D.*
 357 *hispidus*, *D. pleuracanthus*, and *D. tortugae*. The FLMNH IZ collection contained sufficient
 358 specimens of *D. hispidus* and *D. pleuracanthus* to verify identifications. Indeed, specimens of *D.*
 359 *pleuracanthus* contain more tubercles on the carpus but ornamental differences were difficult to
 360 verify for the merus. While large specimens of *D. hispidus* (> ~35 mm carapace width) often
 361 contained two spines on the inner side of the merus, smaller specimens (< ~23 mm carapace
 362 width) often contained only a single tubercle, much like similar-sized specimens of *D.*
 363 *pleuracanthus* (Table S3). An additional character to distinguish the two species is
 364 ornamentation on the dorsal carapace: tubercles appear better developed on the branchial and
 365 gastric regions of *D. pleuracanthus* relative to *D. hispidus* (Figs. 8–10). These differences are
 366 confirmed for slightly larger specimens from Rathbun (1925: pls. 146.1, 150.1), whereas *D.*
 367 *tortugae* appears to have even coarser dorsal tubercles (Rathbun, 1925: pl. 147.2). Additionally,

a row of small tubercles is present along the posterolateral margin in *D. pleuracanthus*, but is absent in *D. hispidus* for the examined size range (Fig. 9). Thus, we argue that ornamentation on the dorsal carapace can be used to distinguish among modern species for similar-sized specimens. The fossil specimen conforms best to *D. pleuracanthus* in terms of coarseness of the tubercles and the presence of a row of small tubercles along the posterolateral margin. Given the lack of chelipeds to confirm species placement and some minor differences that may represent intraspecific variability (e.g., less robust anterolateral spines in the fossil specimen), the ascription is with some query. Nevertheless, this is the first record of this species in the fossil record. The results in Windsor & Felder (2009) and herein suggest that the ascription of fossil specimens to *D. hispidus* (e.g., Collins & Morris, 1976; Morris, 1993; Collins, Donovan & Dixon, 1996; Varela & Rojas-Consuegra, 2011) may need to be revisited.

Stratigraphic and geographic range.—late Pliocene—early Pleistocene to Recent, North Carolina – Venezuela – Bermuda (Williams, 1984, see also Tavares & Albuquerque, 1993).

Mithrax A. Milne-Edwards, 1875

Type species.—*Cancer aculeatus* Herbst, 1790 (see Windsor & Felder, 2014), extant.

Species included.—*Mithrax aculeatus* (Herbst, 1790) [= *Cancer spinosus* Herbst, 1790; *Cancer aculeatus* Fabricius, 1793; *Mithrax pilosus* Rathbun, 1892; *Mithrax verrucosus* H. Milne-Edwards, 1832; *Mithrax plumosus* Rathbun, 1901; *Mithrax trispinosus* Kingsley, 1879]; *Mithrax*

391 *armatus* Saussure, 1853 [=*Mithrax orcutti* Rathbun, 1925]; *Mithrax arawakum* sp. nov.; *Mithrax*
 392 *bellii* Gerstaecker, 1857; *Mithrax besnardi* Melo, 1990; *Mithrax braziliensis* Rathbun, 1892;
 393 *Mithrax caboverdianus* Türkay, 1986; *Mithrax clarionensis* Garth, 1940; *Mithrax hemphilli*
 394 Rathbun, 1892; *Mithrax leucomelas* Desbonne in Desbonne & Schramm, 1867; *Mithrax*
 395 *tuberculatus* Stimpson, 1860.

396

397 *Diagnosis*.—See Windsor & Felder (2014: p. 162, 163).

398

399

400 *Mithrax arawakum* sp. nov.

401 Figure 11

402

403 *Etymology*.—Named in honor of the Arawak natives, who settled the island of Xaymaca
 404 (Jamaica).

405

406 *Type material*.—UF 112682 (holotype, internal mold), UF 112941 (paratype, external mold +
 407 cast).

408

409 *Type locality*.—FLMNH-IP XJ015: Duncans Quarry 01, Trelawny Parish, Jamaica (18.4710, -
 410 77.5796 WGS 84).

411

412 *Type horizon*.—lower Miocene, Montpelier Formation (uppermost unit) (Mitchell, 2004; Portell
 413 & Collins, 2004).

414

415 *Material*.—No material known other than type specimens.

416

417 *Diagnosis*.—Carapace pyriform, slightly longer than wide (l/w ratio = 1.03 for holotype). Short
 418 rostrum with two small spines downturned. Orbits directed forward, with at least four distinct
 419 spines around orbit: one long spine at angle of suborbital margin near rostral horns, other such
 420 spines not preserved; a slender and long outer orbital spine; a small central upper orbital spine;
 421 and a large projection on upper margin near rostral horns. Anterolateral margin with four strong
 422 spines (excluding outer orbital spine), middle two with small spine at anterior base; last spine at
 423 transition from antero- to posterolateral margin, oriented laterally. Posterolateral margin more
 424 rounded than anterolateral margin, with single small spine just posterior to previous spine.
 425 Frontal region with two longitudinal rims connecting to rostral spines and tubercular epigastric
 426 regions. Cervical groove deep and wide, U-shaped. Branchiocardiac groove strongest around
 427 cardiac region, weaker more laterally. Dorsal carapace surface armed with tubercles, granules,
 428 and spines (especially on branchial regions), not very densely so.

429

430 *Description*.—Carapace pyriform, slightly longer than wide (l/w ratio = 1.03 for holotype),
 431 maximum width at ~65% of carapace length, weakly convex longitudinally and moderately so
 432 transversely. Short rostrum with two small spines downturned. Orbits directed forward, wider
 433 than tall, not very deep, at least four distinct spines around orbit: one long spine with a smaller
 434 spine axially at angle of suborbital margin near rostral horns, other such spines not preserved
 435 (may be broken); a slender and long outer orbital spine; a small central upper orbital spine; and a
 436 large projection on upper margin near rostral horns. Single small spine present below orbit.

Anterolateral margin with four strong spines (excluding outer orbital spine), middle two with small spine at anterior base; last spine at transition from antero- to posterolateral margin, oriented laterally. Posterolateral margin with single small spine just posterior to previous spine. Posterior margin with convex protrusion axially, with row of granules adjacent to convexity. Frontal region with two longitudinal rims connecting to rostral spines and tubercular epigastric regions. Hepatic regions small, at lower level compared to gastric region, with single strong anterolateral spine. Protogastric regions bulbous, with major tubercle laterally and less pronounced one axially. Mesogastric region with tubercle on process; base swollen, divided into three regions. Uro- and/or protogastric region small, appears as a laterally elongated tubercle. Cardiac region pentagonal, about equally long as wide, tubercular. Branchial regions weakly divided; epi- and mesobranchial regions confluent, tubercular; metabranchial separated from others, with spines, tubercles, and granules. Intestinal region not delineated, with two strong tubercles. Cervical groove deep and wide, U-shaped, bends more laterally near anterolateral margin to continue on ventral carapace, where it bends forward. Short groove extends from cervical groove near base hepatic region to outer orbital spine. Branchiocardiac groove strongest around cardiac region, weaker more laterally, not expressed to very weak on ventral carapace. Dorsal carapace surface armed with tubercles, granules, and spines (especially on branchial regions), not very densely so; row of five tubercles midway gastric region. Of hardened parts: most of ventral surface, abdomen, cuticle, and appendages lacking.

Measurements.—Excluding spines and rostrum: 14.0 mm long, 13.6 mm wide (UF 112682); length not measurable, 13.0 mm wide (UF 112941).

Remarks.—The species appears to fit best in *Mithrax* because (a) the carapace being about equally long as wide (l/w ratio = 1.03); (b) dorsal ornamentation with tubercles, granules, and spines (although less obvious than in most *Mithrax* spp.); and (c) orbit weakly produced and with two spines on upper margin excluding outer orbital spine.

The new species differs from all other congeners. The carapaces of *M. aculeatus*, *M. armatus*, *M. bellii*, *M. besnardi*, and *M. hemphilli* exhibit a dense cover of granules (Rathbun, 1925: pls. 138.3, 139, 140, 142, 144; Garth, 1946: pl. 66, 1958: pl. 40.2; Melo, 1990; pers. obs. AAK FLMNH IP collection for *M. aculeatus*), whereas granules are much less abundant in the new species. Additionally, *M. besnardi* has a higher number of spines on the upper orbital margin (four excluding outer orbital spine instead of two). For *M. braziliensis*, Rathbun (1892) mentioned that the regions of this species are weakly defined, unlike the present species. Moreover, the upper orbital margin bears two small spines, whereas the new species bears one small and one larger one excluding the outer orbital spine. Although the ornamentation on the dorsal carapace of *M. caboverdianus* seems comparable (tubercles and spines with some interspersed granules) to the new species, the similar-sized holotype in Turkey (1986) (15.3 mm long) appears somewhat longer than wide (l/w ratio = 1.09) relatively (1.03 for *Mithrax arawakum* sp. nov.), but more specimens are needed to confirm this potential difference. Distinct rostral spines are missing in *M. caboverdianus*, but are present in *Mithrax arawakum* sp. nov. Additionally, the cardiac region in *M. caboverdianus* appears wider. The upper orbital margin contains more spines in *M. clarionensis* and the spines on the lateral margin are less prominent for a similar-sized specimen (Garth, 1940: pl. 15). *Mithrax leucomelas* was never figured and the specimen was already lost when Desbonne & Schramm (1867) erected the species. The description suggests that this species is different from the new species because *M. leucomelas* is

said not to be spinose, the anterolateral margins are only slightly toothed, and the lateral angle does not bear a spine, unlike the specimens herein. Lastly, the new species is less tubercular than *M. tuberculatus* for a similar-sized specimen (Rathbun, 1925: pl. 151.1). Moreover, the rostral horns of *M. tuberculatus* are blunt; they are sharp in the new species.

This taxon is of special importance because it constitutes the oldest confirmed record of fossil *Mithrax*. The early Miocene record of *Mithrax* sp. from Cuba (Varela, 2013) is based on a fixed finger, which may not be sufficient for a genus ascription in the light of the recent revision (Windsor & Felder, 2014). The same applies to other appendage fragments attributed to *Mithrax* sp. as well as incomplete carapaces (see Table S1).

The holotype is an internal mold, whereas the paratype is an external mold. Since the size of the two specimens is similar, the ornamentation can be compared. The cast of the external mold shows ornamentation that is largely the same to that of the internal mold, but some granules appear larger (those near the posterior margin).

Stratigraphic and geographic range.—lower Miocene, Jamaica.

Nemausa A. Milne-Edwards, 1875

Type species.—*Pisa spinipes* Bell, 1836, subsequent designation, extant.

Species included.—*Nemausa acuticornis* (Stimpson, 1871); *Nemausa cornuta* (Saussure, 1857) [= *Nemausa rostrata* A. Milne-Edwards, 1875]; *Nemausa donovani* (Portell & Collins, 2004);

506 *Nemausa miocenica* sp. nov.; *Nemausa sinensis* (Rathbun, 1892); *Nemausa spinipes* (Bell, 1836)
507 [= *Mithrax mexicanus* Glassell, 1936].

508

509 *Diagnosis*.—See Windsor & Felder (2014: p. 163, 164), but note that the now included fossil
510 species and *N. sinensis* all have a tubercular rather than spinous character on the dorsal surface.

511

512 *Remarks*.—*Mithrax donovani* (Figure 12) is moved to *Nemausa* because the carapace is longer
513 than wide in *Nemausa*, whereas the carapace length is subequal to the width or wider than long
514 in the diagnosis of *Mithrax* (see Windsor & Felder, 2014). The small size of the specimen (6.7
515 mm maximum width, 8.0 mm preserved length excluding rostrum) suggests that not all
516 characters may have fully developed yet (anterolateral spines, dorsal ornamentation, length/width
517 trajectory), so the ascription to this genus is preliminary until better preserved material is
518 discovered.

519 As for other spider crabs studied herein, ontogenetic change in the length/width ratios is
520 evident for *Nemausa* as well (Fig. 13). The relationship for the species with the most specimens
521 available, *N. acuticornis*, is best explained by a logarithmic trend line, suggesting that
522 length/width ratios change faster in smaller specimens.

523

524

525 *Nemausa miocenica* sp. nov.

526 Figure 13, 14

527

528 *Etymology*.—After the epoch during which the holotype lived (Miocene).

529

530 *Type material*.—Holotype and sole specimen, UF 113651 (internal mold with some cuticle,
531 external mold + cast).

532

533 *Type locality*.—FLMNH-IP XJ015: Duncans Quarry 01, Trelawny Parish, Jamaica (18.4710, -
534 77.5796 WGS 84).

535

536 *Type horizon*.—lower Miocene, Montpelier Formation (uppermost unit) (Mitchell, 2004; Portell
537 & Collins, 2004).

538

539 *Material*.—No material known other than type specimen.

540

541 *Diagnosis*.—Length/width ratio pyriform carapace = 1.19; orbital margins with seven spines, one
542 long spine at angle of suborbital margin near rostral horns and two additional, smaller spines on
543 same margin; anterolateral margin of carapace with four strong spines, anteriormost two with
544 small spine at anterior base; mesogastric region flattened, anterior part not defined.

545

546 *Description*.—Carapace pyriform, length/width ratio = 1.19, maximum width at 59% of carapace
547 length, moderately convex longitudinally and transversely. Rostrum incompletely preserved, but
548 with bases of two diverging spines. Orbits anterolaterally directed, wider than tall, deepest in
549 most lateral part, seven spines around orbit: one long spine at angle of suborbital margin near
550 rostral horns and two additional, smaller spines on same margin, separated by notch that marks
551 boundary between antennal segment and rest of suborbital structure; one strong outer orbital

spine with elongated base; three supraorbital spines, one closest to rostrum strongest. Anterolateral margin with four strong spines (excluding outer orbital spine), anteriormost two with small spine at anterior base; last strong spine at transition from antero- to posterolateral margin, directed laterally. Posterolateral margin more rounded than anterolateral margin, with single spine just posterior to previous spine. Gastric and hepatic regions mostly undifferentiated; epigastric regions appear as tubercles; base of mesogastric region swollen, anterior part not defined; uro- and/or metagastric region small, wider than long, sandwiched between mesogastric and cardiac regions. Cardiac region hexagonal. Branchial and intestinal regions confluent. Cervical groove deepest axially; curves around base mesogastric region, then becomes shallower and bends transversely to intersect lateral margin between first and second anterolateral spines. Branchiocardiac groove only defines lateral parts of cardiac region, does not reach lateral margin. Dorsal carapace surface armed with larger and smaller tubercles; row of five pronounced tubercles midway gastric region; other strong tubercles present on epigastric, branchial, and cardiac regions. Of hardened parts: ventral surface, abdomen, and appendages missing; rostral spines largely missing.

Measurements.—Excluding spines and rostrum: 27.7 mm long, 23.3 mm wide, and 14 mm tall (as preserved).

Remarks.—The anterolateral spines are about equally prominent on the cast and the internal mold. The bases of the rostral spines and many of the orbital spines are much better visible on the cast, which is not surprising given the delicate nature of spines, having the tendency to break easily on the internal mold. Perhaps surprisingly, the small tubercles on the dorsal carapace are

not as numerous on the cast, yet another example that ornamentation with and without the cuticle can differ (see Lörenthey & Beurlen, 1929; Klompmaker, Hyžný & Jakobsen, 2015). Here, the difference can at least in part be explained by the fact that still some cuticle is present near/in those tubercles in the external mold, leading to the absence or less obvious tubercles on the cast.

Nemausa acuticornis is consistently more differentiated in the gastric region (e.g., center mesogastric region better defined and outlined: Fig. 14; Rathbun, 1925: pl. 136.1; Felder et al., 2014: fig. 7C). Moreover, Figure 15 shows and Rathbun (1925: p. 391) mentioned that the suborbital margin of *N. acuticornis* contained only one pronounced spine between the outer orbital spine and the spines on the antennal segment, whereas this specimen bears two distinct spines there. Finally, *N. acuticornis* is relatively wider for specimens of the same size (Fig. 13).

Nemausa cornutus exhibits more spinose ornamentation on the carapace (Rathbun 1925: pl. 137.3 and 137.4) even though the specimens are larger (larger specimens tend to have weaker ornamentation compared to younger specimens from the same species in the Mithracinae). Moreover, the specimens in Rathbun (1925: pl. 137.3 and 137.4) are narrower (Fig. 13), although more specimens are needed to statistically test this difference.

Nemausa sinensis has a lower l/w ratio (1.03 [Garth, 1958: pl. 41.1], 1.06 [Rathbun, 1892: pl. 38.2]) compared to *N. miocenica* sp. nov. (1.19) (Fig. 13). Furthermore, stronger tubercles are present on *N. sinensis*.

Very few specimens of *N. spinipes* are figured, with Rathbun (1925) showing the best image. *Nemausa spinipes* has a better defined mesogastric region (Rathbun, 1925: pl. 136.4) and all anterolateral spines are single and not associated with smaller spines as in the specimen under study. The same author also showed a very strong tubercle on the posterior part of the

mesogastric region, not seen in the specimen under study; and two instead of one tubercle are present around the location where the mesogastric process would be.

Nemausa donovani is different in that the mesogastric region is outlined entirely and a distinct elevation is seen in the center of the posterior part of this region, both unlike in the new species. This is unlikely related to ontogeny because the mesogastric features appear stable throughout ontogeny in a congeneric species (Fig. 15). Although anterolateral spines become more prominent throughout ontogeny in *Nemausa* (*N. acuticornis*, Fig. 15), the difference between *N. donovani* and *N. miocenica* sp. nov. is much greater, supporting the hypothesis that these are two separate species. Furthermore, *N. miocenica* sp. nov. bears a denser ornamentation of tubercles, which may only in part be explained by ontogeny (Fig. 15) because even the smallest specimen of *N. acuticornis* bears distinct tubercles on the branchial regions, whereas these regions are nearly smooth in *N. donovani*, unlike for *N. miocenica* sp. nov.

Stratigraphic and geographic range.—lower Miocene, Jamaica.

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Supplemental Information

Tables S1–S3 can be found at...

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Figure legends

Figure 1. Stratigraphic ranges of families and genera of spider crabs (Majoidea) in the Western Atlantic. Grey bars represent probable occurrences based on modern or bracketing fossil occurrences for that taxon. Chart arranged stratigraphically and by family. The Hymenosomatidae have no fossil record and the Priscinachidae are only known from Europe thus far. The ranges of families are derived from genera; genus names that were uncertain (aff., ?[genus], or “[genus]”) were not used. Timescale produced with TSCreator 6.4 (<http://www.tscreator.org>).

Figure 2. Genus-level diversity of spider crabs in the Western Atlantic from older to younger epochs (A–D). Genus names that were uncertain (aff., ?[genus], or “[genus]”) were not included. Geographic regions were defined as follows: Atlantic coast North America (here Maine to South Carolina); Gulf of Mexico (incl. Florida); Caribbean (Cuba to Panama to Barbados); Atlantic coast South America (here Argentina). The youngest epoch was arbitrarily chosen for genera that could be either from one epoch or the following. No records are known from the Paleocene and Oligocene.

Figure 3. Length/width ratio vs \log_2 width (mm) for extant *Maguimithrax spinosissimus* (Lamarck, 1818). Maximum length was determined without the rostral spines and width was measured without the anterolateral spines. Trend line is logarithmic. Data in Table S2.

Figure 4. Dorsal and ventral views of modern male specimens of *Maguimithrax spinosissimus* that differ in size. (A, B) UF 11447, Florida, USA; (C, D) UF 11388, Florida, USA (largest specimen). Note the difference in length/width ratios of the carapace. Scale bar width = 30 mm.

Figure 5. Length/width ratio vs \log_2 width (mm) for *Damithrax unguis* (Portell & Collins, 2004) from lower Miocene coral-associated limestones of Jamaica and modern *Damithrax hispidus* (Herbst, 1790) from Florida, USA, for comparison. Maximum length was determined without the rostral spines and width was measured without the anterolateral spines. Trend lines are logarithmic. Data in Table S2.

Figure 6. Growth series of dorsal carapaces of *Damithrax unguis* (Portell & Collins, 2004) from the lower Miocene coral-associated limestones of the Montpelier Formation in the Duncans Quarry, Jamaica. (A) = is RTV silicone rubber cast of external mold. (B–K) = internal molds. (A) UF 255051; (B) UF 113677; (C) UF 106768 (paratype); (D) UF 255053; (E) UF 112795; (F) UF 112783; (G) UF 112784; (H) UF 106697 (holotype); (I) UF 103954; (J, K) frontal and left-lateral views of UF 113677. Scale bar below (B) applies to (A–H). Scale bar width = 10.0 mm.

Figure 7. *Damithrax* cf. *D. pleuracanthus* from the late Pliocene–early Pleistocene of the MacAsphalt Shell Pit, Sarasota County, Florida, USA (UF 29057). (A) Dorsal view; (B) Ventral view; (C) Frontal view; (D) Right-lateral view; (E) Left-lateral view. Scale bar width = 10.0 mm.

Figure 8. Dorsal views of modern specimens and a single fossil specimen of *Damithrax* spp., all from Florida, USA. Upper row from left to right – modern *D. hispidus*: UF 12475, 11604, 1082,

1027 1086; Middle row – modern *D. pleuracanthus*: UF 3673, 9588 (largest specimen of lot), 7874,
1028 1052; lower row – fossil *Damithrax* cf. *D. pleuracanthus*: UF 29057. Scale bar width = 10.0 mm.

1029

1030 Figure 9. Posterior views of similar-sized, modern specimens and a single fossil specimen of
1031 *Damithrax* spp. (A) *D. hispidus*: UF 1082; (B) *D. pleuracanthus*: UF 7874; (C) *Damithrax* cf. *D.*
1032 *pleuracanthus*: UF 29057. For specimen sizes see Fig. 8.

1033

1034 Figure 10. Frontal views of similar-sized, modern specimens and a single fossil specimen of
1035 *Damithrax* spp. (A) *D. hispidus*: UF 1082; (B) *D. pleuracanthus*: UF 7874; (C) *Damithrax* cf. *D.*
1036 *pleuracanthus*: UF 29057. For specimen sizes see Fig. 8.

1037

1038 Figure 11. Type specimens of *Mithrax arawakum* sp. nov. from the lower Miocene coral-
1039 associated limestones of the Montpelier Formation in the Duncans Quarry, Jamaica. (A, D, E)
1040 Holotype, UF 112682, in dorsal, frontal, and left-lateral views, resp.; (B) Paratype, external
1041 mold, UF 112941; (C) Paratype, cast of external mold, UF 112941. Scale bar width = 10.0 mm.

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1043 Figure 12. The holotype of *Nemausa donovani* (Portell & Collins, 2004) from the lower Miocene
1044 coral-associated limestones of the Montpelier Formation in the Duncans Quarry, Jamaica (UF
1045 103958). (A) Dorsal view; (B) Frontal view; (C) Angled right-lateral view; (D) Upper view of
1046 rostrum and orbit; (E) Right-lateral view. Scale bar width = 5.0 mm for (A–C, E); 1.5 mm for
1047 (D).

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Figure 13. Length/width ratio vs \log_2 width (mm) for *Nemausa* spp. *Nemausa donovani* was not included because the total length could not be determined. Maximum length was determined without the rostral spines and width was measured without the anterolateral spines. Trend line is logarithmic. Data in Table S2.

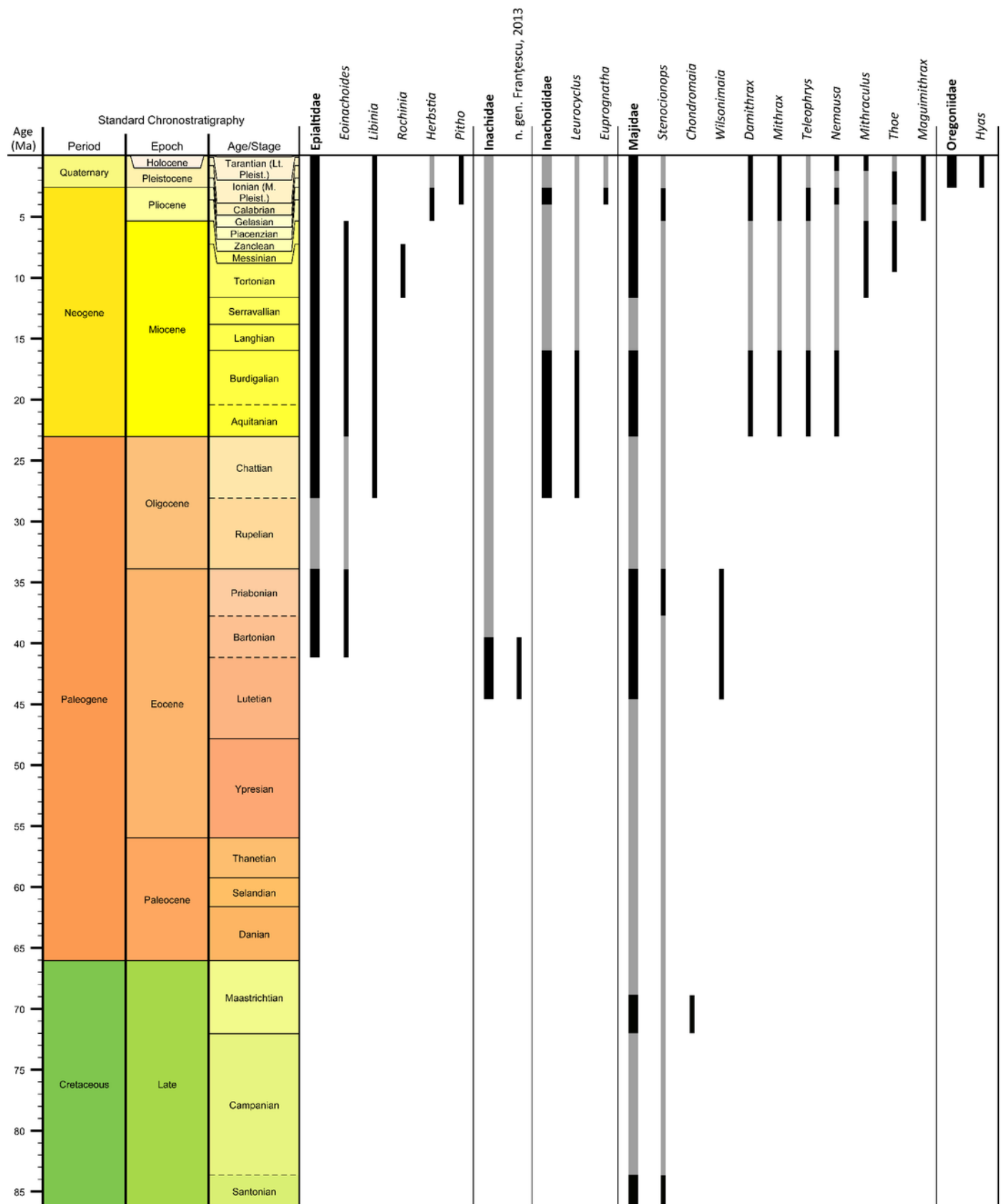
Figure 14. The holotype of *Nemausa miocenica* sp. nov. from the lower Miocene coral-associated limestones of the Montpelier Formation in the Duncans Quarry, Jamaica (UF 113651). (A) Dorsal view (internal mold); (B) Dorsal view (cast of external mold); (C) Frontal view; (D) Right-lateral view; (E) External mold; (F) Upper margin left orbit; (G) Cast showing bases of rostral horns and various orbital spines in more detail. Arrows in (G) indicate suborbital spines and broken outer orbital spine. Scale bar width = 20 mm for (A–E); 2.0 mm for (F); 10 mm for (G).

Figure 15. Growth series of dorsal carapaces of modern *Nemausa acuticornis* (Stimpson, 1871) from various localities of the Atlantic coast of Florida, USA. Note that specimens become relatively wider with age. (A) FSBC I-9758; (B) FSBC I-050561; (C) FSBC I-050562 (note the ‘unicorn’ rostrum instead of a double-horned rostrum); (D) FSBC I-050562; (E) FSBC I-050562; (F) FSBC I-050561; (G) FSBC I-050562; (H) FSBC I-050562. Scale bar width = 30 mm.

1

Stratigraphic ranges of families and genera of spider crabs (Majoidea) in the Western Atlantic.

Grey bars represent probable occurrences based on modern or bracketing fossil occurrences for that taxon. Chart arranged stratigraphically and by family. The Hymenosomatidae have no fossil record and the Priscinachidae are only known from Europe thus far. The ranges of families are derived from genera; genus names that were uncertain (aff., ?[genus], or “[genus]”) were not used. Timescale produced with TSCreator 6.4 (<http://www.tscreator.org>).

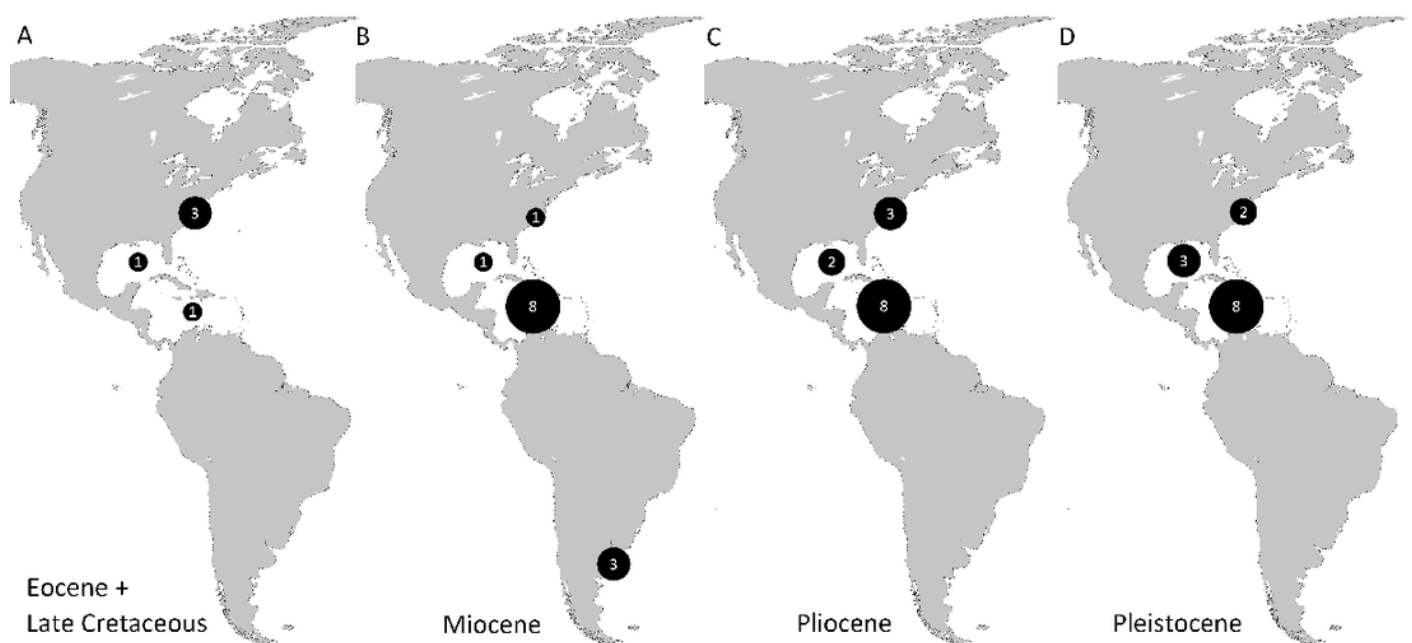


2

Genus-level diversity of spider crabs in the Western Atlantic from older to younger epochs (A-D).

Genus names that were uncertain (aff., ?[genus], or “[genus]”) were not included.

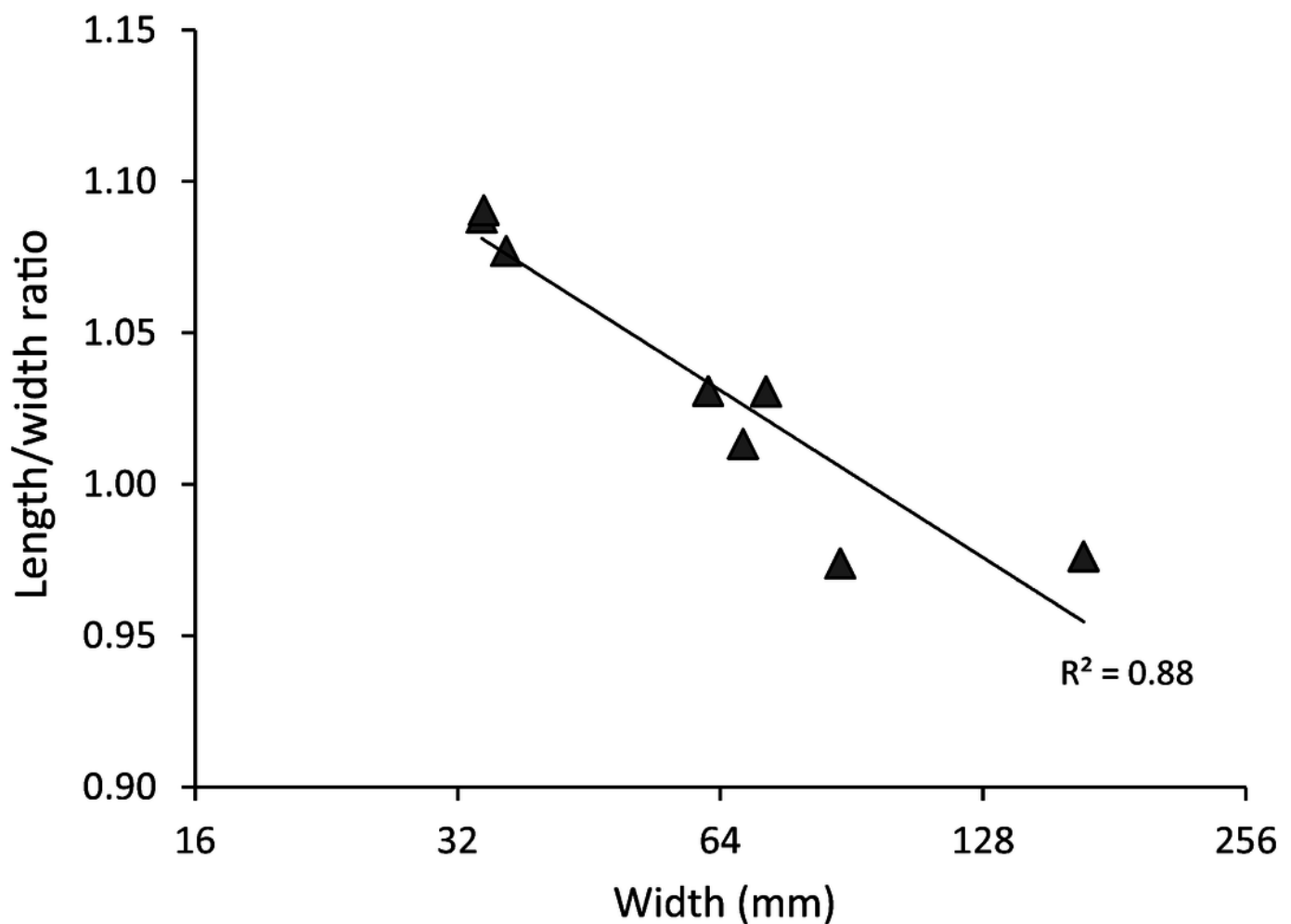
Geographic regions were defined as follows: Atlantic coast North America (here Maine to South Carolina); Gulf of Mexico (incl. Florida); Caribbean (Cuba to Panama to Barbados); Atlantic coast South America (here Argentina). The youngest epoch was arbitrarily chosen for genera that could be either from one epoch or the following. No records are known from the Paleocene and Oligocene.



3

Length/width ratio vs \log_2 width (mm) for extant *Maguimithrax spinosissimus* (Lamarck, 1818).

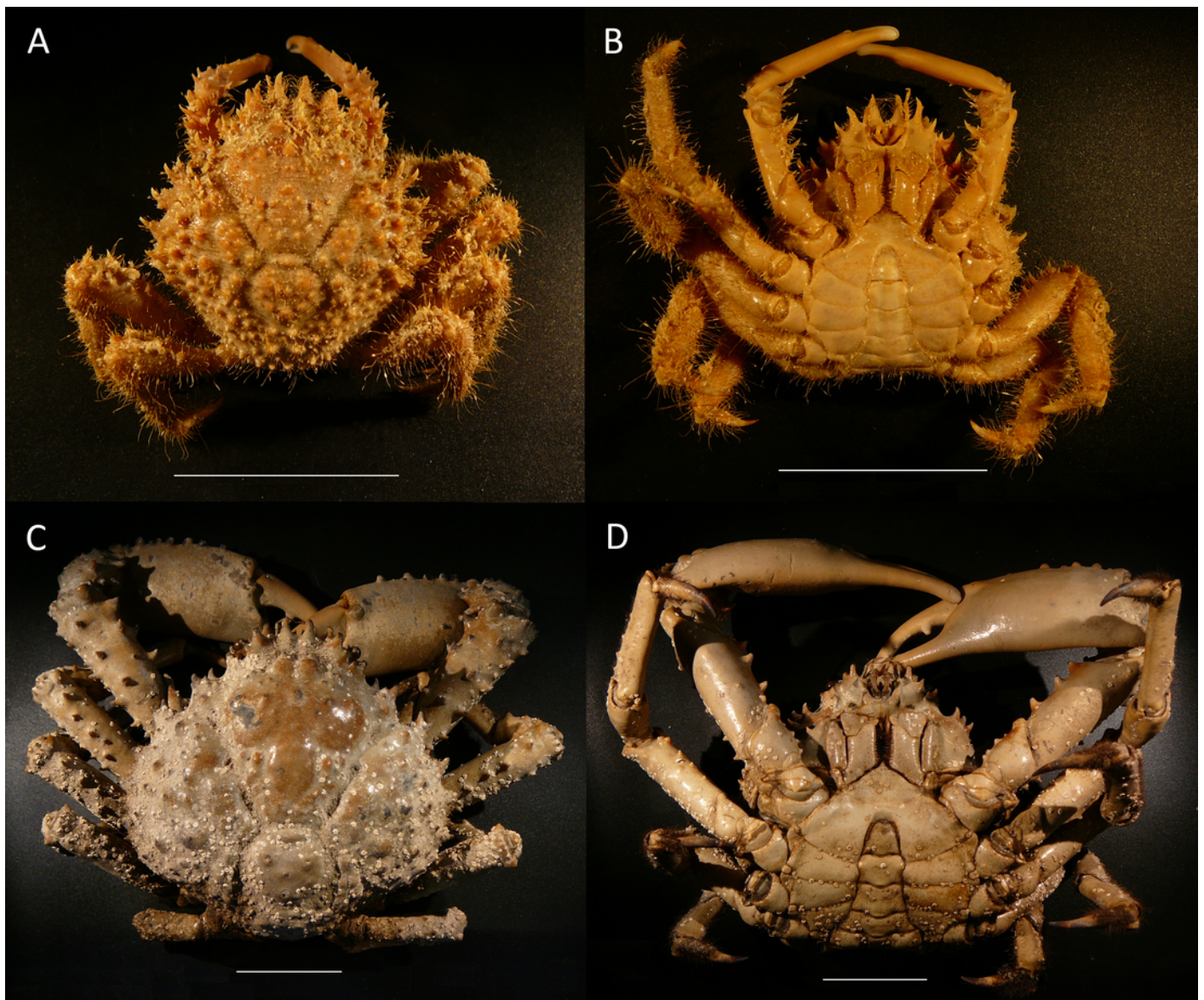
Maximum length was determined without the rostral spines and width was measured without the anterolateral spines. Trend line is logarithmic. Data in Table S2.



4

Dorsal and ventral views of modern male specimens of *Maguimithrax spinosissimus* that differ in size.

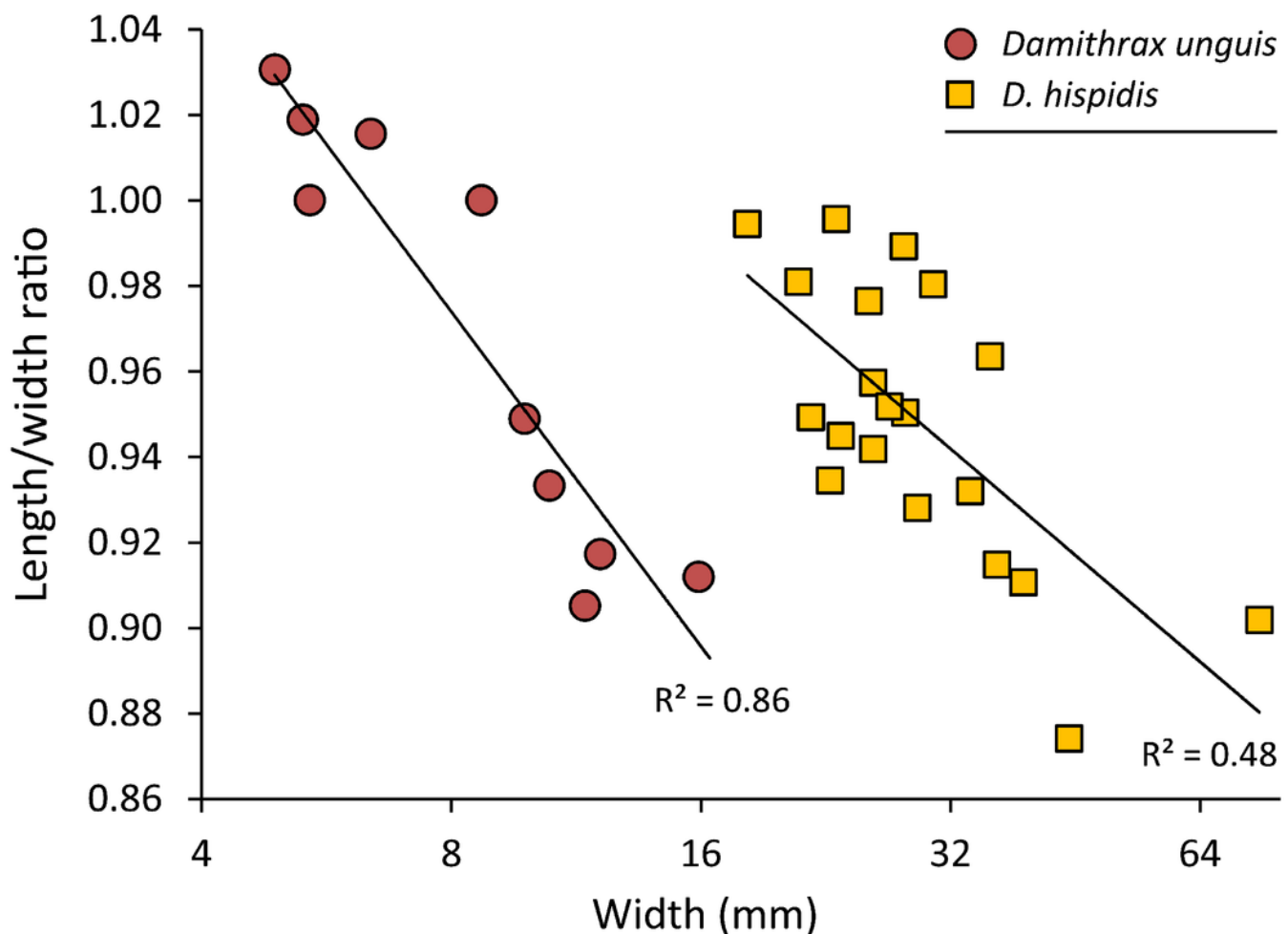
(A, B) UF 11447, Florida, USA; (C, D) UF 11388, Florida, USA (largest specimen). Note the difference in length/width ratios of the carapace. Scale bar width = 30 mm.



5

Length/width ratio vs \log_2 width (mm) for *Damithrax unguis* (Portell & Collins, 2004) from the lower Miocene of Jamaica vs modern *Damithrax hispidus* (Herbst, 1790) from Florida.

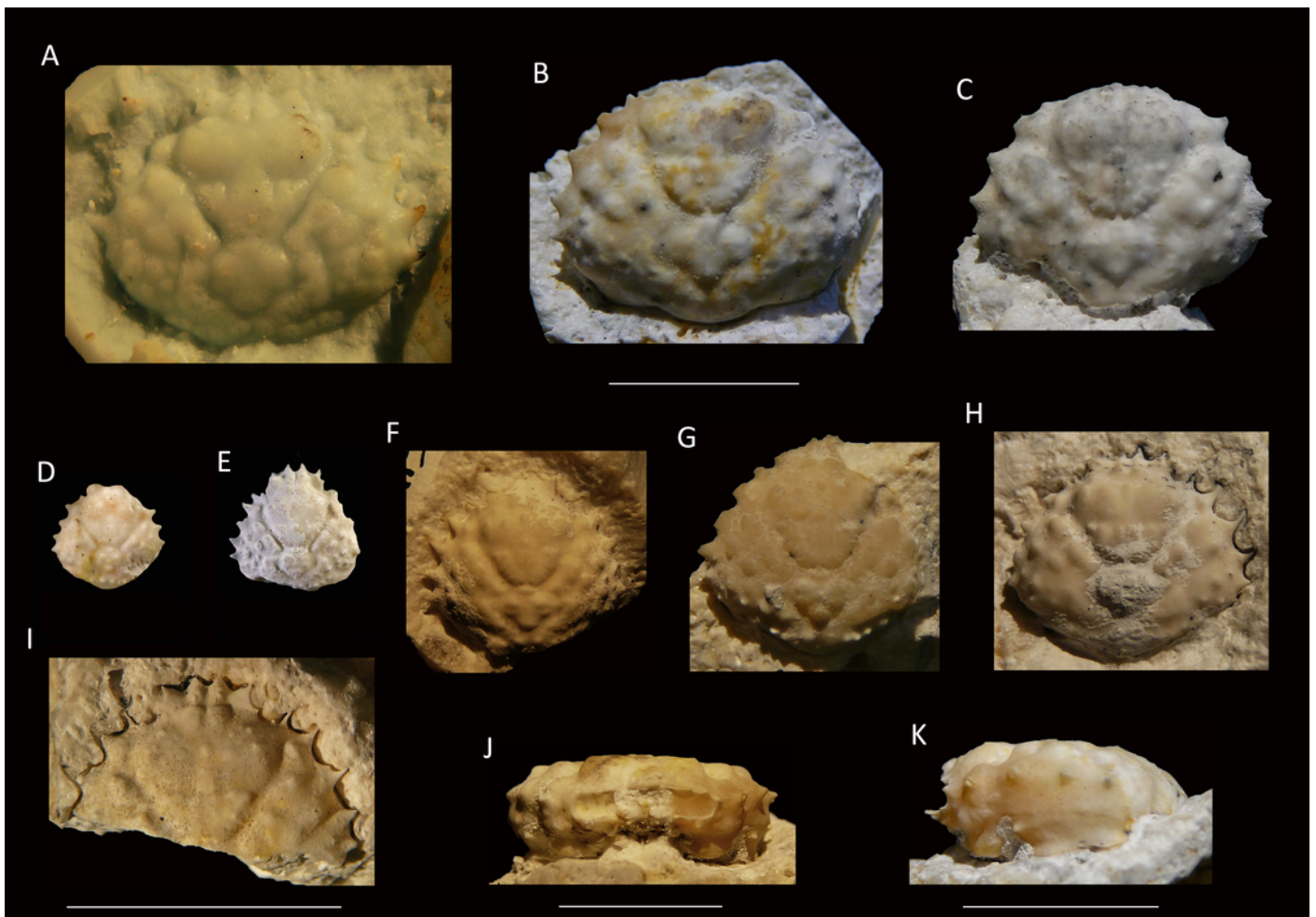
Maximum length was determined without the rostral spines and width was measured without the anterolateral spines. Trend lines are logarithmic. Data in Table S2.



6

Growth series of dorsal carapaces of *Damithrax unguis* (Portell & Collins, 2004) from the lower Miocene coral-associated limestones of the Montpelier Formation in the Duncans Quarry, Jamaica.

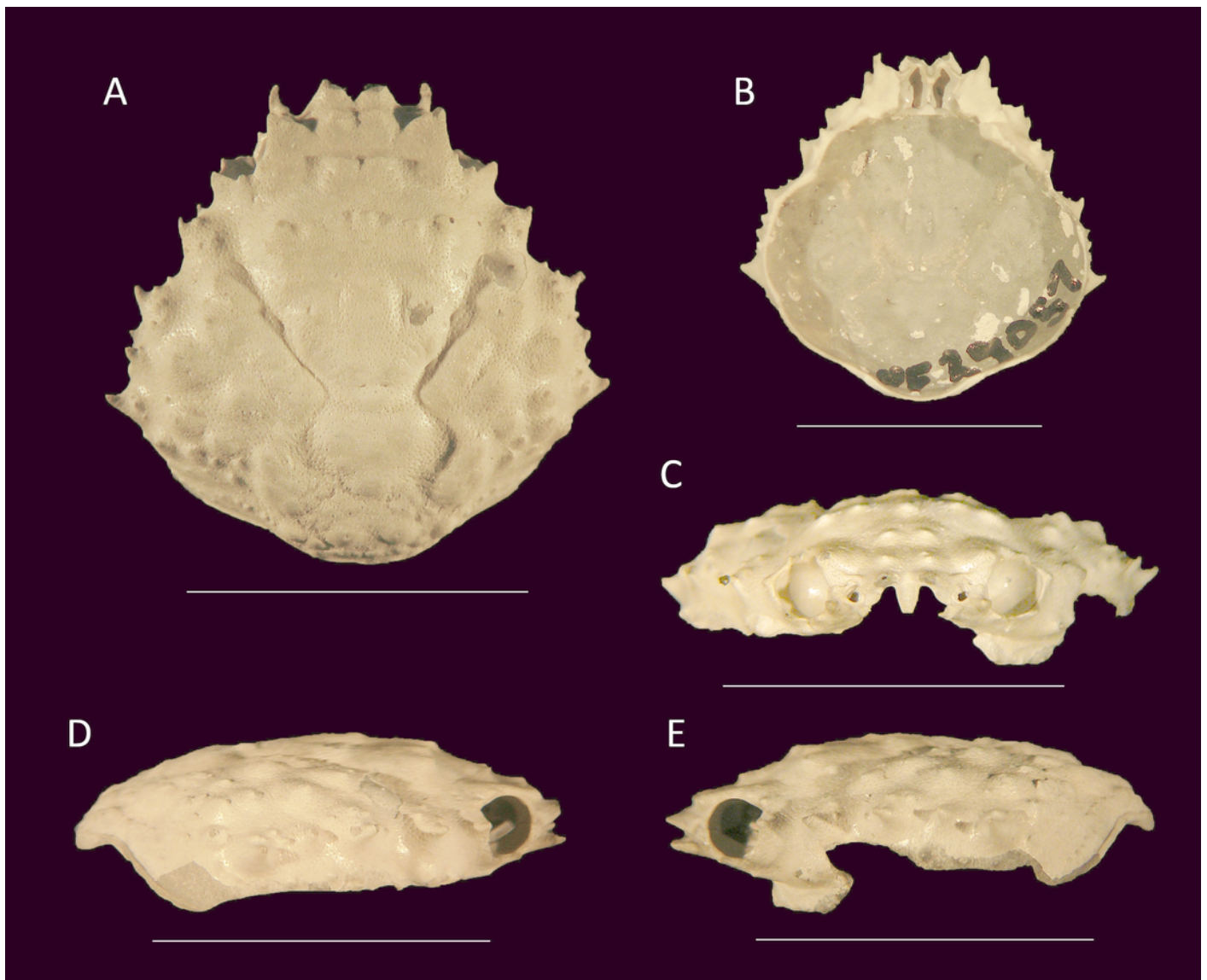
(A) = is RTV silicone rubber cast of external mold. (B-K) = internal molds. (A) UF 255051; (B) UF 113677; (C) UF 106768 (paratype); (D) UF 255053; (E) UF 112795; (F) UF 112783; (G) UF 112784; (H) UF 106697 (holotype); (I) UF 103954; (J, K) frontal and left-lateral views of UF 113677. Scale bar below (B) applies to (A–H). Scale bar width = 10.0 mm.



7

Damithrax cf. *D. pleuracanthus* from the late Pliocene–early Pleistocene of the MacAsphalt Shell Pit, Sarasota County, Florida, USA (UF 29057).

(A) Dorsal view; (B) Ventral view; (C) Frontal view; (D) Right-lateral view; (E) Left-lateral view.
Scale bar width = 10.0 mm.



8

Dorsal views of modern specimens and a single fossil specimen of *Damithrax* spp., all from Florida, USA.

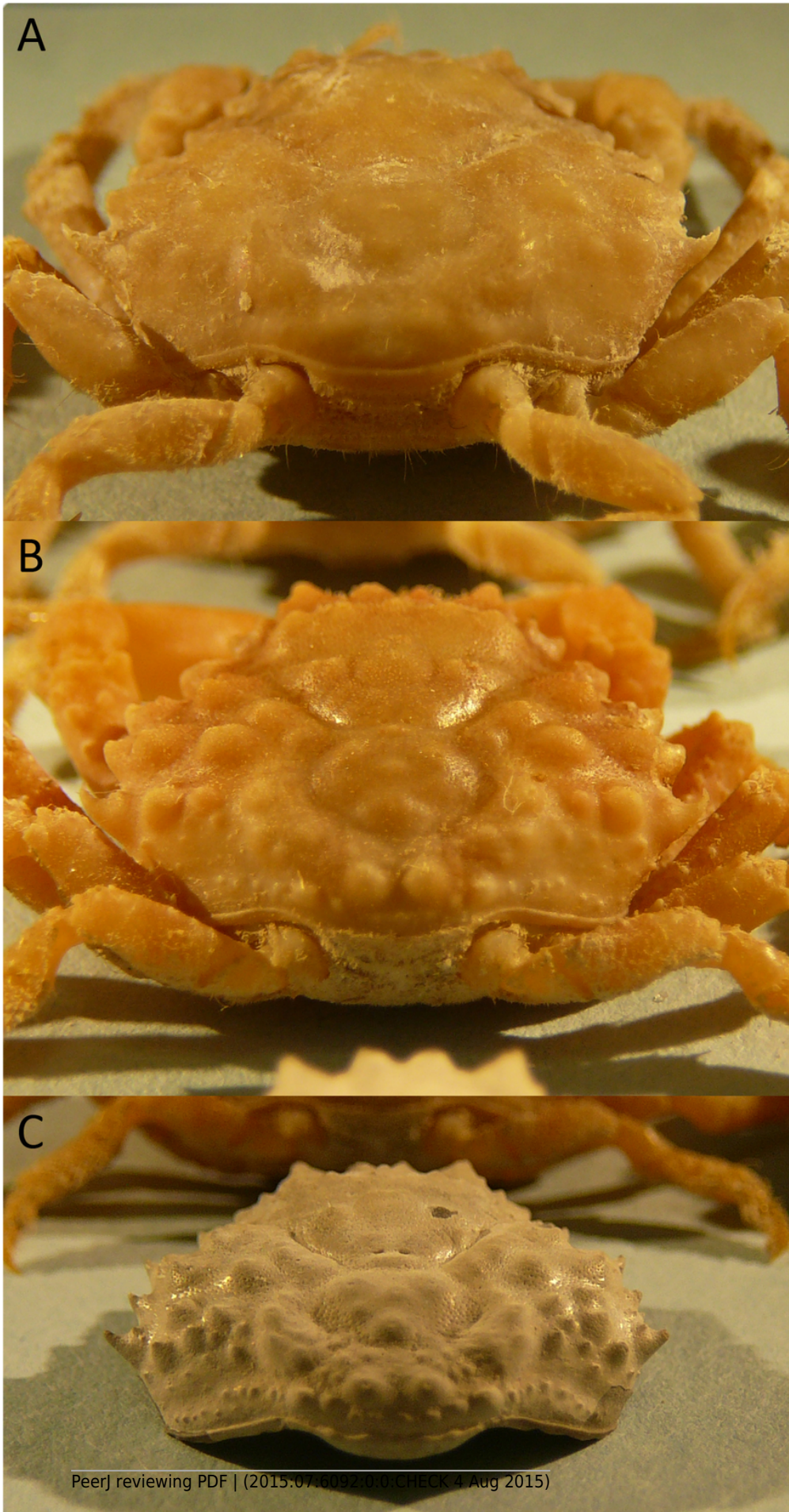
Upper row from left to right - modern *D. hispidus*: UF 12475, 11604, 1082, 1086; Middle row - modern *D. pleuracanthus*: UF 3673, 9588 (largest specimen of lot), 7874, 1052; lower row - fossil *Damithrax* cf. *D. pleuracanthus*: UF 29057. Scale bar width = 10.0 mm.



9

Posterior views of similar-sized, modern specimens and a single fossil specimen of *Damithrax* spp.

(A) *D. hispidus*: UF 1082; (B) *D. pleuracanthus*: UF 7874; (C) *Damithrax* cf. *D. pleuracanthus*: UF 29057. For specimen sizes see Fig. 8.



10

Frontal views of similar-sized, modern specimens and a single fossil specimen of *Damithrax* spp.

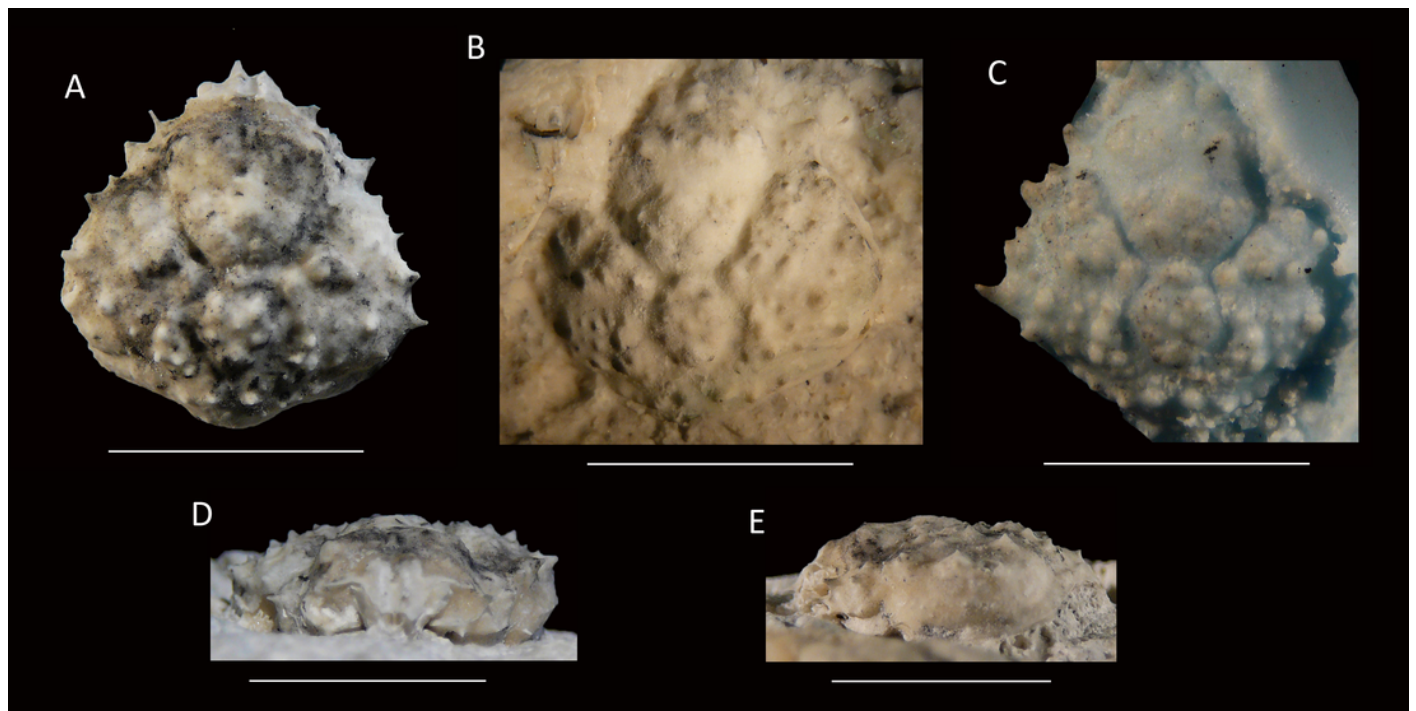
(A) *D. hispidus*: UF 1082; (B) *D. pleuracanthus*: UF 7874; (C) *Damithrax* cf. *D. pleuracanthus*: UF 29057. For specimen sizes see Fig. 8.



11

Type specimens of *Mithrax arawakum* sp. nov. from the lower Miocene coral-associated limestones of the Montpelier Formation in the Duncans Quarry, Jamaica.

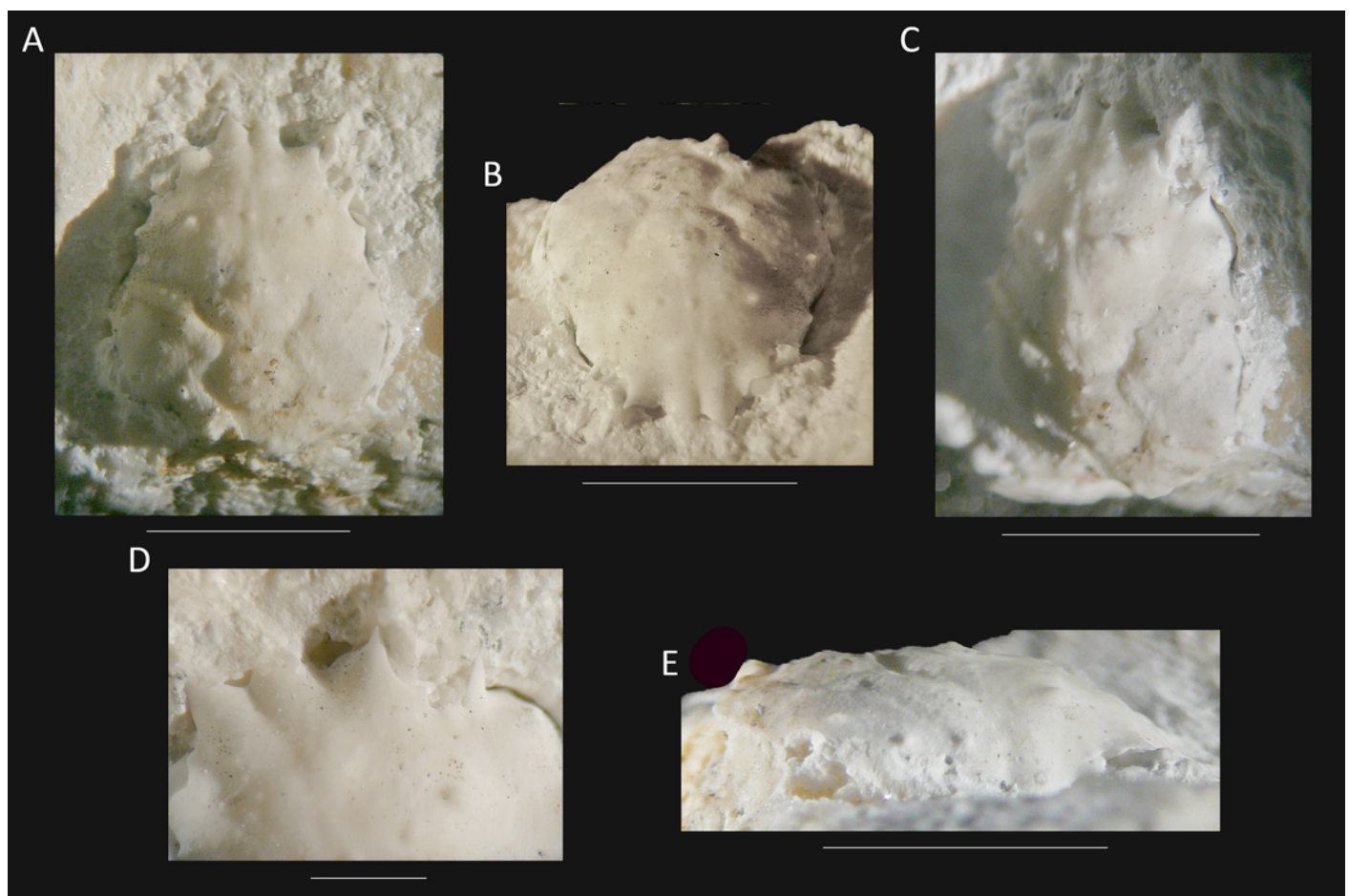
(A, D, E) Holotype, UF 112682, in dorsal, frontal, and left-lateral views, resp.; (B) Paratype, external mold, UF 112941; (C) Paratype, cast of external mold, UF 112941. Scale bar width = 10.0 mm.



12

The holotype of *Nemausa donovani* (Portell & Collins, 2004) from the lower Miocene coral-associated limestones of the Montpelier Formation in the Duncans Quarry, Jamaica (UF 103958).

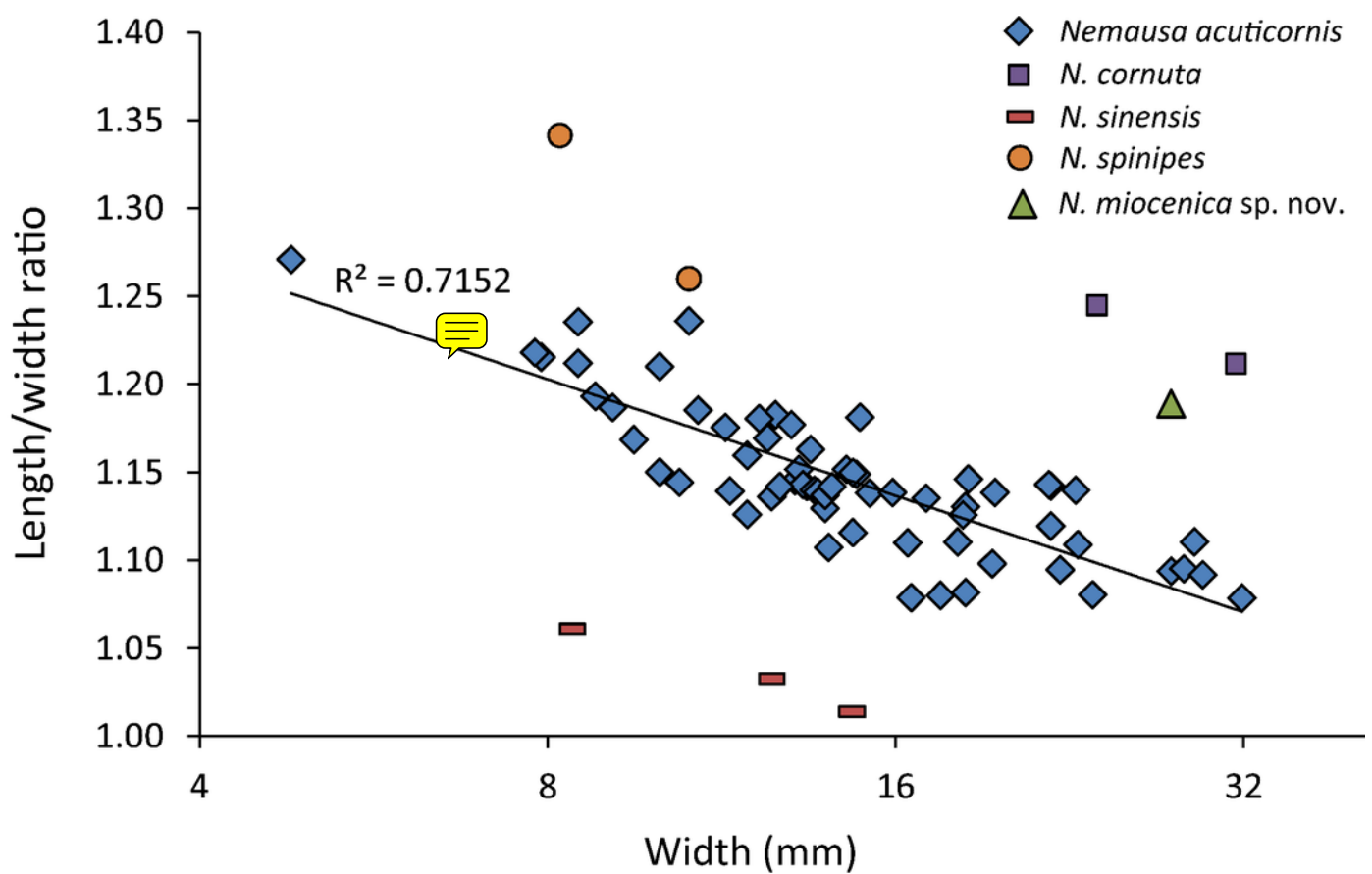
(A) Dorsal view; (B) Frontal view; (C) Angled right-lateral view; (D) Upper view of rostrum and orbit; (E) Right-lateral view. Scale bar width = 5.0 mm for (A-C, E); 1.5 mm for (D).



13

Length/width ratio vs \log_2 width (mm) for *Nemausa* spp.

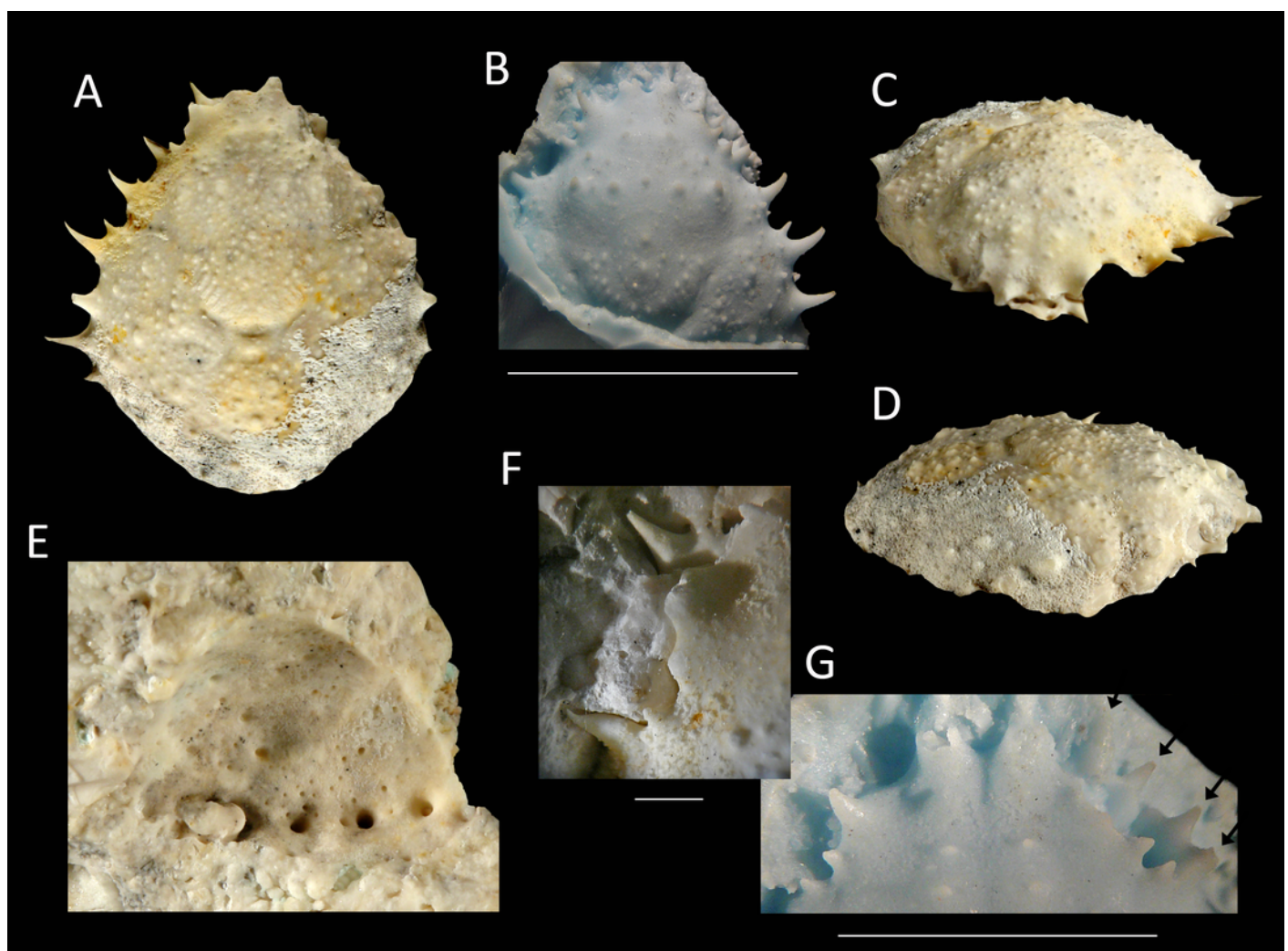
Nemausa donovani was not included because the total length could not be determined. Maximum length was determined without the rostral spines and width was measured without the anterolateral spines. Trend line is logarithmic. Data in Table S2.



14

The holotype of *Nemausa miocenica* sp. nov. from the lower Miocene coral-associated limestones of the Montpelier Formation in the Duncans Quarry, Jamaica (UF 113651).

(A) Dorsal view (internal mold); (B) Dorsal view (cast of external mold); (C) Frontal view; (D) Right-lateral view; (E) External mold; (F) Upper margin left orbit; (G) Cast showing bases of rostral horns and various orbital spines in more detail. Arrows in (G) indicate suborbital spines and broken outer orbital spine. Scale bar width = 20 mm for (A-E); 2.0 mm for (F); 10 mm for (G).



15

Growth series of dorsal carapaces of modern *Nemausa acuticornis* (Stimpson, 1871) from various localities of the Atlantic coast of Florida, USA.

Note that specimens become relatively wider with age. (A) FSBC I-9758; (B) FSBC I-050561; (C) FSBC I-050562 (note the 'unicorn' rostrum instead of a double-horned rostrum); (D) FSBC I-050562; (E) FSBC I-050562; (F) FSBC I-050561; (G) FSBC I-050562; (H) FSBC I-050562. Scale bar width = 30 mm.

