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Two new sympatric species of *Eusarsiella* (Ostracoda: Myodocopida: Sarsiellidae) from the Florida Keys with a morphological phylogeny of Sarsiellinae

CELIA K. C. CHURCHILL^{1,2}, EMILY A. ELLIS¹, ALANNAH E. PIQUE¹ & TODD H. OAKLEY^{1,2,3}

¹Department of Ecology, Evolution, and Marine Biology, University of California, Santa Barbara ²Marine Science Institute, University of California, Santa Barbara ³Corresponding author. E-mail: oakley@lifesci.ucsb.edu

Abstract

We describe two new sympatric species of Sarsiellidae from coastal Florida, USA: *Eusarsiella bryanjuarezi* **sp. nov.** and *Eusarsiella eli* **sp. nov.** We also present a morphological character matrix and maximum likelihood phylogenetic analysis for Sarsiellinae based on original species descriptions, representing 139 sarsiellins (including *E. bryanjuarezi* and *E. eli*). While support values across the phylogeny are low, *E. bryanjuarezi* and *E. eli* form a sister group pair with 68 % bootstrap support. Our phylogeny also showed support for six other sympatric sister-species pairs, distributed across Sarsiellinae's range, which may be candidates for the study of speciation and niche differentiation. Similar to other analyses of myodocopids, our Sarsiellinae phylogeny recovered only three monophyletic genera: *Anscottiella, Cymbicopia*, and *Chelicopia*, indicating that characters used in taxonomy may often be homoplasious. Because of our finding of multiple polyphyletic genera, including the two most speciose genera in the subfamily (*Eusarsiella* and *Sarsiella*, the type genus) Sarsiellinae is a strong candidate for taxonomic revision.

Key words: systematics, taxonomy, ostracod, Sarsiellinae, Eusarsiella, morphological phylogeny

Introduction

Sarsiellidae Brady & Norman, 1896 (Ostracoda: Sarsielloidea) is a family of benthic marine ostracods known worldwide from subarctic to Antarctic latitudes, and intertidal to abyssal depths (Kornicker & Caraion 1980). Together with the families Philomedidae Müller, 1906 and Rutidermatidae Brady & Norman, 1896, Sarsiellidae is a member of the superfamily Sarsielloidea, which is particularly intriguing evolutionarily because it shows variation in genetically well-studied characters, especially lateral compound eyes (Rivera & Oakley 2009; Kornicker 1985). Although a nearly comprehensive morphological phylogeny was recently published (Karanovic 2012), molecular phylogenies including sarsiellids suffer from sparse species-level sampling (*e.g.*, a single species in Yamaguchi & Endo 2003; Oakley & Cunningham 2002; Tinn & Oakley 2008), and unlike many ostracod lineages with rich fossil records, there are no known sarsiellid fossils (Siveter *et al.* 2010). Therefore, current hypotheses of evolution within-Sarsiellidae, (e.g. that the genera *Spinacopia, Cymbicopia, Alphasarsiella*, and *Adelta* are plesiomorphic within Sarsiellinae; Karanovic 2012), depend solely on morphological characters.

Sarsiellidae includes two subfamilies: Sarsiellinae Brady & Norman, 1896 and Dantyinae Kornicker & Cohen, 1978. Sarsiellinae is considerably more diverse, including 14 genera (Kornicker 1991; 1995), whereas Dantyinae has only two (Kornicker & Thomassin 1998). The largest genus in Sarsiellinae is *Eusarsiella* Cohen & Kornicker, 1975 (79 species, see below), although its taxonomic status was questioned (Hall 1987). Here, we describe two new species of *Eusarsiella* from the Florida Keys, USA, which were collected at the same site off Long Key (Figure 1). Shallow-water myodocopins tend to exhibit high levels of endemism (Titterton & Whatley 1988) and low dispersal (Morin 1986), which could give them more opportunities for population subdivision (Palumbi 1994). However, the prevalence of sympatric species pairs in Sarsiellidae has not been investigated. We score

morphological characters based on a recent morphological cladistic study of Sarsiellinae (Karanovic 2012), present a new morphological phylogeny based on a revised and updated character list, and report the proportion of sympatry among supported sister species pairs.



FIGURE 1. Map of collecting sites in Florida, USA. The type locality for both species, off Long Key, Florida Keys, is indicated with a star. A second collecting locality for *Eusarsiella bryanjuarezi* in Indian River, Fort Pierce, Florida, is indicated with a circle. The length of the Florida Keys archipelago is indicated with a black dotted line. Scale bar = 100 km.

Material and methods

Sample collection. We collected ostracods *via* fine mesh aquarium hand nets from depths of 1–5 m under Florida Fish and Wildlife Conservation Commission Special Activity License #SAL-12-1381-SR (THO) and Florida Keys National Marine Sanctuary Research Permit #FKNMS-2012-105 (THO). Figure 1 shows collecting localities for both species described in this study. We washed collected sediment through 2 mm and 500 µm sieves, retaining the sediment between to sort under a dissecting microscope (0.67–4X magnification) for myodocopid ostracods. We initially identified ostracods by carapace morphology and compared specimens across sample sites. Voucher specimens were fixed and preserved in 95% ethanol. All type material is deposited at the Santa Barbara Museum of Natural History (SBMNH).

Morphological examination. For both *Eusarsiella* species described herein, we examined morphology using a dissecting microscope and a compound microscope. We examined carapaces in ethanol using depression slides (unmounted). We dissected the type specimens and mounted the limbs on slides in Hydro-Matrix® (Micro-Tech-Lab, Graz, Austria) to study anatomy.

Morphological character scoring. We initially scored traits of both new species based on a previously published list (Karanovic 2012), comprising 34 morphological characters of adult female sarsiellins, which are much more commonly collected than adult males. When we could not score two of the characters (2: Longitudinal ridges on the surface; 19: Endopod on L5: clearly separated from the basis; Karanovic 2012), we consulted original species descriptions for other sarsiellids included in Karanovic's analysis. We could not find any reference to these

characters in most descriptions, thus we excluded them from our analysis, leaving a total of 32 characters. Henceforth all character numbering refers to the current study. Upon noticing other discrepancies between the published character matrix (Karanovic 2012) and original species descriptions, we reviewed the entire matrix. We revised any inconsistent character states and characters themselves to reflect respective species descriptions. Our review led us to add the following additional states: Character 8, state 2—endopod of the A2 being trimeric; Character 18, Character 8, state 2—endopod of Limb 2 being trimeric; Character 18, state 3—three bristles on the exopod of the third limb; Character 19, state 3—endite of Limb 6 has three or more distal bristles; Character 23, state 2—no teeth or comb on Limb 7; Character 24, state 3—no opposite pairs of bell-bearing bristles distally on Limb 7.

139 sarsiellin species and two outgroups, the dantyins *Dantya tryx* and *Nealella monothrix*, are represented in our revised matrix. The revised data matrix is publicly available in MorphoBank (O'Leary & Kaufman 2012) Project 861: Morphological phylogeny of Sarsiellinae (Ostracoda: Myodocopida: Sarsiellidae). (http://www.morphobank.org)

We included all non-*Eusarsiella* and non-*Sarsiella* sarsiellins described from adult females. *Ancohenia robusta* (Brady, 1890), *Chelicopia obex* Kornicker, 1992, *Neomuelleriella mayottensis* Kornicker, 1992, and *Parasarsiella globulus* (Brady, 1887) are described only from males, and we therefore did not include them in our phylogenetic analysis. Hartmann described an adult female *Chelicopia rotunda* (Hartmann 1959) that Kornicker later determined was a juvenile male (Kornicker 1981b). The following species do not have detailed enough species descriptions to score adequately: *Chelicopia kornickeri* McKenzie, 1965, *Junctichela gracilis* (Scott, 1905), and *Junctichela similis* (Scott, 1905).

Revised character list

Abbreviations: LX, limb X

- 1 Rostrum: pronounced (0); absent or very small (1)
- 2 Anterior incisure on the shell: present (0); absent (1)
- 3 Fossae on the shell: rough (0); present but small (1); absent (2)
- 4 Caudal process on the shell: present and prominent (0); present but small (1); absent (2)
- 5 Posterior infold: with a row of prominent bristles starting from posterior part (0); only two prominent dorsal bristles present postero-dorsally, others much smaller and usually scattered (1)
- 6 L1: c-, f-, and g-bristles: normal (0); claw-like (1)
- 7 Number of bristles intero-distally on the fused third and fourth segments of L1: three (0), two (1); one (2)
- 8 Endopod on the L2: dimeric (0); monomeric (1); trimeric (2)
- 9 Second segment on the endopod L2: prominent and clearly divided (0); very short and almost fused with the previous one (1); absent (2)
- 10 Number of bristles on the first segment of endopod L2: three (0); two (1); one (2)
- 11 Apical bristle(s) on the endopod L2: present (0); absent (1)
- 12 Apical bristle(s) on the endopod L2: present and long (0); present and short (1); absent (2)
- 13 Number of apical bristles on the endopod L2: two (0); one (1); zero (2)
- 14 Number of bristles on the terminal segment of exopod L2: three (0); two (1)
- 15 Coxale endite on the L3: bifurcate, prominent and surrounded with spinous bristles (0), reduced to a single spine or absent (1)
- 16 Exopod on the L3: with a clear segment and apical bristle(s) (0); absent or only bristle left (1)
- 17 Endopodal segments of L3: at least one with more than two claws (0); all with one claw (1)
- 18 Number of bristles on the exopod L4: two (0); one (1); three (2)
- 19 Number of bristles on the endite of L6: two (0); one (1); three or more (2)
- 20 Number of distal bristles on the L6: more than fourteen (0); twelve or thirteen (1); eleven or fewer (2)
- 21 Distal end of the L7: with teeth at least on one side (0); without teeth (1)
- 22 Distal end of the L7 with: teeth on both sides (0); on one side only (1); on neither side (2)
- 23 L7, number of teeth on each comb: more than three (0); three or fewer (1); no teeth on comb (2)
- 24 Number of opposite pairs on the bell-bearing bristles distally on the L7: more than two (0); two (1); one (2); zero (3)

- 25 Number of claws on the furca: seven or more (0); six (1); five or fewer (2)
- 26 Number of claws fused with furcal lamellae: three (0); two (1); one (2)
- 27 Second claw on the furca: fused with lamellae (0); free (1)
- 28 Third claw on the furca: fused with lamellae (0); free (1)
- 29 Fourth claw on the furca: fused with lamellae (0); free (1)
- 30 Claws on the furca: gradually decreasing in length (0); one of the claws being shorter than its neighbors (1)
- 31 Bellonci organ: segmented (0); not segmented or segmentation not clear (1)
- 32 Lateral eye: present (0); absent (1)

Phylogenetics

Without a well-supported hypothesis of character evolution within Sarsiellidae we considered characters unordered, and since each character constitutes a separate evolutionary hypothesis we left them unweighted. We partitioned the morphological dataset by binary and multistate characters so that separate models of evolution (binary and MK, respectively) could be applied in RAxML v.7.2.8 (Stamatakis 2006). We conducted maximum likelihood analysis using the combined rapid bootstrap (500 replicates) and search for ML tree (100 searches) option (RaxML option "–f a"). *Alphasarsiella anax* Kornicker, 1995 and *Alphasarsiella altrix* Kornicker, 1995 only differ in one polymorphic state at Character 19 (*A. altrix* = 0, 1; *A. anax* = 0, 2), which is considered identical by RAxML (the current version does not allow polymorphic characters, so we converted all polymorphism to missing data "?"). Therefore, we only included one species (*A. altrix*) in the analysis; the resulting phylogenetic position would be the same for both *Alphasarsiella* species.

Systematics

Subclass Myodocopa Sars, 1866

Order Myodocopida Sars, 1866

Family Sarsiellidae Brady & Norman, 1896

Subfamily Sarsiellinae Brady & Norman, 1896

Genus Eusarsiella Cohen & Kornicker, 1975

Type species: Sarsiella tumida Scott, 1905 by subsequent designation in Cohen & Kornicker (1975).

Diagnosis. The most species-rich genus of the subfamily Sarsiellinae, with c-, f-, and g-bristles not claw-like on the first limb and the d-bristle present. These ostracods have an anterior incisure and the posterior infold bears a row of spinous bristles. In females, the seventh limb bears paired, terminal teeth. Each lamella of the furca with five claws; claw 1 fused to the lamella, claws 2–5 separated from lamella by suture. Claws decrease in length posteriorly along lamella. For a key to Sarsiellidae, see Kornicker (1986).

Composition. The genus includes 78 species—*Eusarsiella absens* (Kornicker, 1981); *E. africana* (Kornicker & Caraion, 1978); *E. alata* Poulsen, 1965; *E. antipex* Kornicker, 1995; *E. asciformis* (Hall, 1987); *E. athrix* Kornicker, 1986; *E. bakeri* Kornicker, 1986; *E. bedoyai* Baltanas, 1992; *E. bex* Kornicker, 1994; *E. capillaris* (Kornicker, 1958); *E. carinata* (Kornicker, 1958); *E. chessi* Kornicker, 1991; *E. childi* Kornicker, 1986; *E. claviformis* (Hall, 1987); *E. concentricostata* Hartmann, 1974; *E. cornuta* Poulsen, 1965; *E. costata* (Kornicker, 1958); *E. cresseyi* Kornicker, 1986; *E. culteri* Kornicker, 1986; *E. dentifera* Poulsen, 1965; *E. dispar* Kornicker, 1986; *E. disparilis* (Darby, 1965); *E. dominicana* Kornicker, 1986; *E. donabbotti* Cohen, 1989; *E. dornellasae* (Kornicker & Caraion, 1978); *E. edax* Kornicker, 1994; *E. elofsoni* Kornicker, 1986; *E. fallomagna* Kornicker, 1994; *E. falx* Kornicker, 1992; *E. fax* Kornicker, 11ffe & Harrison-Nelson, 2007; *E. gettlesoni* Kornicker, 1986; *E. gigacantha* (Kornicker, 1958); *E. gomoiui* (Kornicker & Caraion, 1978); *E. gomoiui* (Kornicker & Caraion, 1978); *E. iayx* Kornicker,

1994; E. janicea (Kornicker, 1976); E. longipenna Poulsen, 1965; E. lunata (Kornicker, 1975); E. magna Poulsen, 1965; E. maurae (Kornicker, 1977); E. microthrix (Chavtur, 1983); E. neapolis (Kornicker, 1974); E. nodimarginis (Darby, 1965); E. ocula (Kornicker & Caraion, 1978); E. ovalis Poulsen, 1965; E. ozotothrix (Kornicker & Bowen, 1976); E. paniculata Kornicker, 1986; E. phrix Kornicker, 1996; E. pilipollicis (Darby, 1965); E. pseudospinosa (Baker, 1977); E. punctata (Kornicker, 1958); E. radiicosta (Darby, 1965); E. reticulata (Hall, 1987); E. rudescui (Kornicker & Caraion, 1978); E. rugosa (Poulsen, 1965); E. ryanae Kornicker & Iliffe, 2000; E. saengeri Kornicker, 1996; E. spicata Poulsen, 1965; E. spinosa (Kornicker, 1995; E. spicata (Hall, 1987); E. spadix Kornicker, 1995; E. spicata Poulsen, 1965; E. spinosa (Kornicker & Wise, 1962); E. thominx Kornicker, 1987; E. truncana (Kornicker, 1958); E. tryx Kornicker, 1996; E. tubipora (Darby, 1965); E. tumida (Scott, 1905); E. uncus Kornicker, 1986; E. vema Kornicker, 1986; E. venazuelensis Kornicker, 1986; E. vernix Kornicker, 1996; E. uncus Kornicker, 1986; E. verna Kornicker, 1986; E. vernix Kornicker, 1996; E. uncus Kornicker, 1986; E. verna Kornicker, 1986; E. vernicker, 1996; E. vernicker, 1996; E. warneri Kornicker, 111ffe & Harrison-Nelson, 2002; E. zostericola (Cushman, 1906). For a current list of Eusarsiella species, see (Brandão et al. 2013).

Distribution. Cosmopolitan between the latitudes of about 63°N and 37°S. Known from depths of intertidal to 1120 m (Kornicker 1994).

Eusarsiella bryanjuarezi sp. nov.

Etymology. Named by the authors for Bryan Juarez, who provided critical assistance during the collection of these specimens.

Holotype: None designated.

Syntypes: SBMNH # 235521 two ovigerous females, "A" and "B" on five slides, and carapaces in ethanol. We chose to designate syntypes because given the low number of individuals available for morphological examination (2), we were not able to describe the species from a single individual. Type locality: (24.850002, -80.816925) off Long Key, Monroe County, Florida, USA. Collected by hand nets in algae, coarse sand, shells, 3–4 m depth. Collected by authors (CKCC, EAE, and THO).

Material examined. Syntypes (two ovigerous females).

Distribution. Known from the type locality and Indian River (a brackish lagoon, not a freshwater river), Fort Pierce, Florida, USA (27.462063, -80.312713).

Diagnosis. A *Eusarsiella* species, with a small, rounded caudal process and minute anterior incisure on the inner carapace margin. Shell ornamented with many fossae. The carapace of *E. bryanjuarezi* resembles both *E. dominicana* (known from the Dominican Republic) and *E. absens* (known from Bermuda). *E. bryanjuarezi* is nearly circular in lateral view, whereas both *E. dominicana* and *E. absens* are distinctly oval. The posterior margin of *E. bryanjuarezi* is flat in lateral view where that of *E. absens* is concave. *E. bryanjuarezi* and *E. absens* have different carapace sculptures: the former has a single rib extending from above the central adductor muscle attachments to the posterodorsal bulge, whereas the latter has an additional horizontal rib below the central adductor muscle attachments (see Kornicker 1986). *E. absens* in Kornicker 1986 (Figure 25) also has three to four weakly developed radiating ribs on the anterior portion of the carapace (Kornicker 1981a as *Sarsiella absens*), whereas *E. bryanjuarezi* has none. *E. bryanjuarezi* (1.03–1.05 mm) adult females are of a similar size to *E. dominicana* (1.08 mm) but *E. absens* (1.17–1.22 mm) are around 10 % larger (Kornicker 1986). Internal diagnostic features of the three species are as follows: On the first limb, the third and fourth fused podomeres have differing number of bristles. *E. bryanjuarezi* has a total of six bristles and one spine (see below), *E. dominicana* has a total of four bristles, and *E. absens* have four (Kornicker 1986). Finally, adult female *E. bryanjuarezi* have about 10 ommatidia while *E. dominicana* have four (Kornicker 1986) and *E. absens* have five (Kornicker 1981a).

Description of syntypes—Adult females. Carapace (Figure 2): Syntypes A and B. Length 1.05 mm, height 0.95 mm. Carapace oval but nearly circular in lateral view with flat posterior. Caudal process present, but highly reduced and round.

Ornamentation (Figure 2): Syntypes A and B. Carapace with many fossae; valve lined with bristles. One ridge present immediately medial to the valve margin, beginning dorsally above the caudal process and following the valve margin around to the ventral side of the caudal process.

Limb 1/Antennula (Figure 3A): Syntype A. First podomere bare. Second podomere with one dorsal bristle. Long third and short fourth podomeres fused; third podomere with one long dorsal bristle and one short ventral bristle; fourth podomere with one distal lateral spine, one short dorsal bristle and group of three ventral bristles: one short, one medium, and one long. Fifth podomere with long distal, ventral sensory bristle; sensory bristle of fifth podomere with minute proximal filaments and terminal spine. Short sixth podomere fused to fifth podomere with one short, medial, bare bristle. Seventh podomere: a-bristle half-length of b-bristle, bare; b-bristle half the length of c-bristle, bare; c-bristle long, with one proximal filament, one distal filament, and one terminal spine. Eighth podomere: d-bristle half-length of c-bristle, bare; e-bristle slightly longer than b-bristle, bare, appears open at tip; f-bristle long with terminal spine; g-bristle similar to f-bristle.





Limb 2/Antenna (Figure 3B): Syntype A. Protopodite with one lateral, stout, blunt bristle. Endopodite monomeric with one short proximal bristle and small terminal node bearing one minute bristle. Exopodite nonomeric. First podomere about length of podomeres 2–9, bare. Second podomere bearing one long distal ventral bristle with proximal ventral filaments and distal natatory setulae. Third podomere bearing one long distal ventral bristle with distal natatory setulae. Podomeres 4–6 decreasing slightly in length and width, each bearing one long distal ventral bristle resembling bristle of third podomere. Seventh and eighth podomeres each bearing one long distal ventral bristle with proximal filaments and distal natatory setulae. Ninth podomere with two terminal bristles; dorsal bristle short and bare, ventral bristle long with sparse proximal filaments and distal natatory setulae.

Limb 3/Mandibula (Figure 3C): Syntype A. Coxa with minute, dense stout spines along ventral margin and covering the medial ventral surface. Coxale endite reduced to a single spine. Posteroventral margin with two short, stout bristles and small clump of minute setulae dorsal to the shorter stout bristle. Large, flat spine covering medial coxale-basic joint. Basis with two distal ridges bearing one short stout bristle at the dorsal margin. Ventral margin with cluster of two or three bristles: one minute, two short and stout. Exopod absent. Endopod trimeric: First podomere with numerous spines on the medial surface, increasing in length distally; ventral margin with stout terminal claw. Second podomere with short dorsal bristle and stout terminal claw, slightly longer than terminal claw on first podomere. Third podomere with short dorsal bristle and ventral strout terminal claw, about twice as long as claw on first podomere.

Limb 4/Maxillula (Figure 3D): Syntype A. First endite with four bristles, two short, one long, one stout and medium length; dorsal fringe of short setulae. Coxa with dorsal process bearing one short bristle. Precoxa/coxa boundary difficult to discern. First endite with three bristles, two short and one long. Second and third endites bearing several bristles each. Exopod not observed. Endopod dimeric: first podomere with stout spinous and pectinate alpha and beta bristles. Second podomere with one small a-bristle, one small c-bristle, and five pectinate end bristles.



FIGURE 3. *Eusarsiella bryanjuarezi*, syntype, SBMNH #253221. Adult female. **A**, first limb, right side, lateral view, bristles labeled from podomere 5 to terminus; **B**, second limb, right side, lateral view, long bristles on podomeres 3–9 truncated (appearance is similar to bristle on podomere 2); **C**, third limb, left side, medial view; **D**, fourth limb, right side, medial view, **labels: ex**, exopodite, **II**; second endite, **III**, third endite, α , alpha bristle, β , beta bristle, **a**, a-bristle, **c**, c-bristle; **E**, fifth limb, right side, medial view; **I**, side, lateral view; **G**, seventh limb, terminal end, right side; **H**, furca, right lamella, lateral view; **I**, γ -sclerite. Scale bar = 100 μ m.

Limb 5 (Figure 3E): Syntype A. Epipodial appendage with about 27 pectinate bristles; single endite present and bare. Exopodite with five podomeres: first podomere with two bristles, one long with few minute, marginal filaments, one shorter and bare. Podomeres 2–5 fused. Second podomere with bristles bearing minute marginal filaments. The remaining podomeres have three bare bristles, though the distinction among joints is uncertain.

Limb 6 (Figure 3F): Syntype A. Single endite with one short, bare bristle. Terminal podomere projecting posteriorly with 10 or 11 bristles along the ventral margin. The most posterior of these bristles is the most hirsute. Some of the other bristles with terminal filaments and minute, marginal filaments. Bristles are followed by a space, and then two thick, long, and hirsute bristles.

Limb 7 (Figure 3G): Syntype B. Each limb with 10 bristles: six terminal (three on each side) and four proximal (two on each side). Each bristle bears four to seven bells; terminal bristles bear more bells than proximal. Distal third of the limb with medial and lateral ridges heading to the V-shaped opening of the terminus. Terminus with opposing combs, each with about six teeth distally on each margin.

Furca (Figure 3H): Syntype B. Each lamella with five claws; each claw curved with pointed tip. First claw is the longest and continuous with lamella; claws 2–5 are separated by a suture. First two claws have repeated rows of spines increasing in length distally along the posterior margin. Claws 3 and 4 have spines along the posterior margin. Claw 5 is short and bare.

Eyes: Lateral eyes with reddish pigment and about 10 ommatidia. Medial eye with very light brownish pigment.

 γ -sclerite (Figure 3I): Syntype B. Typical for the family.

Eggs: Syntypes SBMNH # 235521 with five and four embryos in the domicilia of syntypes A and B, respectively.

Eusarsiella eli sp. nov.

Etymology. Named by the authors for Elizabeth Ansier Oakley, who has provided critical assistance and support during numerous expeditions to collect myodocopids.

Holotype: SBMNH # 235522 one ovigerous female on five slides, and carapaces in ethanol. Type locality: (24.850002, -80.816925) off Long Key, Monroe County, Florida, USA. Collected by hand nets in algae, coarse sand, shells, 3–4 m depth. Collected by authors (CKCC, EAE, and THO).

Material examined. Holotype (adult female).

Distribution. Known only from the type locality.

Diagnosis. A *Eusarsiella* species, with a prominent, triangular caudal process and minute anterior incisure. Shell ornamented with many fossae and posterior processes bearing short bristles and one long bristle. Posterior processes decrease in size dorsally. Valve margin extremely hirsute. Short, anterior processes along the perimeter of the valve, bearing minute bristles. The carapace of *Eusarsiella eli* closely resembles the Caribbean *E. paniculata*, especially in the placement of processes and bristles ornamenting the carapace. The caudal process of *E. eli* is pointed postero-ventrally, whereas that of *E. paniculata* points posteriorly. The two species also differ in adult female size; *E. paniculata* (1.24–1.32 mm length and 0.95–1.03 mm height; Kornicker 1986) is relatively longer than *E. eli* (1.15 mm length and 1.11 mm height). Internal diagostic characters between the two species are as follows: The second podomere of the first limb is bare in *E. eli*, but bears a dorsal bristle in *E. paniculata*. Finally, the exopodite of the fourth limb has three bristles in *E. eli*, whereas *E. paniculata* has two.

Description of holotype—Adult female. Carapace (Figure 4): Length 1.15 mm, height 1.11 mm (holotype). Carapace slightly oval in lateral view with truncated postero-dorsal margin. Distinct caudal process pointing postero-ventrally.

Ornamentation (Figure 4): Prominent, triangular caudal process and distinct processes circling the valve. Processes along the valve margin hirsute, with two rows along the ventral margin. Carapace with shallow fossae concentrated in the center. Posterior processes, decreasing in size dorsally, each with numerous short bristles and one long bristle. Valve margin hirsute.

Limb 1/Antennula (Figure 5A): First and second podomeres bare. Long third and short fourth podomeres fused without a suture; third podomere bare; fourth podomere with one distal medium-length, ventral bristle and one longer, distal dorsal bristle. Fifth through eighth podomeres are fused. Fifth podomere with one large terminal bristle with one setula and one terminal spine. Sixth podomere bare. Seventh podomere bears the a-, b-, and c-

bristles, eighth podomere bears d-, e-, f-, and g-bristles. Bristles a through g are of typical length for genus; f-bristle has few, sparse setulae.



FIGURE 4. Eusarsiella eli, holotype, SMBNH #253222. Adult female. Photograph of carapace. Scale bar = 0.5 mm.

Limb 2/Antenna (Figure 5B): Protopodite bare. Endopodite monomeric with two short proximal bristles and one small terminal node bearing one minute apical bristle. Exopodite nonomeric. First podomere about the length of podomeres 2–9, bare. Second podomere bears one long distal bristle, with proximal ventral filaments and distal natatory setulae. Podomeres 3–8 follow the same fashion, though decreasing in length. Ninth podomere with two terminal bristles; dorsal bristle short and bare, ventral bristle long with sparse proximal filaments.

Limb 3/Mandibula (Figure 5C): Coxa with dense minute stout spines along ventral margin. Coxale endite reduced to single spine. Basis with one dorsal, distal, stout bristle at the dorsal margin. Two lateral, proximal, ventral bristles proximal to the dorsoventral margin. Ventral margin bears one minute bristle. Endopod trimeric: First podomere with numerous short, stout spines on the medial surface; ventral margin with stout terminal claw and short dorsal bristle. Second podomere with one ventral claw, slightly longer than the terminal claw on the first podomere. Third podomere with long terminal claw about twice the size of the terminal claw on the first podomere; one minute dorsal bristle and one larger ventral bristle.

Limb 4/Maxillula (Figure 5D): Precoxa bare. Coxa with dorsal process bearing a short, anterior bristle along the distal, antero-dorsal margin. First endite appears bare, but was not observed clearly. Second endite bears three very stout bristles. Third endite bears two distinct clusters of three bristles: posterior group with one short, one medium, and one longer, stout bristles with spines; anterior group has one stout bristle with spines and two medium bristles. Exopodite bears three medium-sized bristles. Endopod dimeric: first podomere with stout, spinous and pectinate alpha- and beta-bristles. Second podomere with two small a-bristles and five pectinate end bristles.

Limb 5 (Figure 5E): Epipodial appendage with 13 pectinate bristles; single endite present with one single bristle. Exopodite with five podomeres: first podomere with two bristles. Podomeres 2–5 are fused. Second podomere with three spinous bristles. The remaining podomeres have four bare bristles, though the distinction among joints is uncertain.

Limb 6 (Figure 5F): Single endite with one stout, short bristle. Terminal podomere with about 11 slender, hirsute bristles along the ventral margin. Short spines are followed by two hirsute, stout, posterior bristles.

Limb 7 (Figure 5G): Each limb with eight bristles: six terminal (three on each side) and two proximal (one on each side). Each bristle bears four to seven bells; terminal bristles bear more bells than proximal. Proximal bristles are located about 80 % down the full limb length. Terminus with opposing combs of about four teeth distally on each margin.



FIGURE 5. *Eusarsiella eli*, holotype, SBMNH #235522. Adult female. **A**, first limb, right side, medial view, bristles labeled from podomere 5 to terminus; **B**, second limb, right side, lateral view, long bristles on podomeres 3–9 truncated (appearance is similar to bristle on podomere 2); **C**, third limb, right lateral view; **D**, fourth limb, left lateral view, **labels**: **ex**, exopodite, **II**; second endite, **III**, third endite, **a**, alpha bristle, **β**, beta bristle, **a**, a-bristle; **E**, fifth limb, left medial view, long bristles on epipod truncated (appearance is similar to single hirsute bristle); **F**, sixth limb, right lateral view; **G**, seventh limb, right; **H**, furca, right lamella lateral view; **I**, γ -sclerite. Scale bar = 100 µm.

Furca (Figure 5H): Each lamella with five claws; each claw curved with pointed tip. Claw 1 is the longest and fused with lamella; claws 2–5 are separated by a suture. Claws are followed by several small spines.

Eyes: Lateral eyes with reddish pigment and about eight ommatidia, but was difficult to see. Medial eye with light amber pigment.

 γ -sclerite (Figure 5I): Typical for the family.

Eggs: Holotype SBMNH # 235522 with three embryos in the domicilium.

Results

Morphological character scoring

Our revised character matrix contains 441 character state changes from Karanovic's (2012) matrix, out of 4,448 total character states (excluding the two deleted characters in our analysis). Our matrix includes 141 species (139 sarsiellins + two dantyin outgroups) and 32 characters.



FIGURE 6. Morphological phylogeny from revised Sarsiellin character matrix (Part 1). The full phylogeny is presented on the left, with a dark gray box indicating the magnified upper part of the tree presented at right. Maximum likelihood bootstrap percentages greater than 30 shown above branches or next to nodes, space permitting. Monophyletic genera *Cymbicopia*, *Anscottiella*, and *Chelicopia* are indicated with gray boxes.



FIGURE 7. Morphological phylogeny from revised Sarsiellin character matrix (Part 2). The full phylogeny is presented on the left side, with a dark gray box indicating the magnified lower part of the tree presented at right. Maximum likelihood bootstrap percentages greater than 30 shown above branches or next to nodes, space permitting. Two new species of *Eusarsiella* described here are labeled with a black star. Subfamilies Sarsiellinae and Dantyinae (outgroup) are labeled.

Morphological phylogeny

Figures 6 and 7 show the maximum likelihood tree (phylogram and cladogram) and bootstrap support percentages from the phylogenetic analysis. Support levels are low throughout the tree, but a monophyletic Sarsiellinae is reasonably well supported (BS_{ML} = 84). Three monophyletic genera were recovered with moderate support: *Anscottiella* (BS_{ML} = 49), *Cymbicopia* (BS_{ML} = 47), and *Chelicopia* (BS_{ML} = 47), though the latter contains *Ancohenia hawaiiensis* (the only *Ancohenia* exemplar in our matrix). *Junctichela* is paraphyletic and contains two species of *Eurypylus* (*E. pulcher, E. chavturi*). The type genus of the family, *Sarsiella*, while polyphyletic, comprises only two clades: one of *S. spinulosa* and *S. nana* with moderate support (BS_{ML} = 49), and the other of all other *Sarsiella* species with lower support (BS_{ML} = 34). *Spinacopia* consists of two clades: one with very low support and containing the monotypic *Adelta theta*, and the other moderately supported (BS_{ML} = 53) and containing *Alphasarsiella altrix*. *A. theta* and *A. altrix* are the only representatives of their respective genera in the analysis. *Eusarsiella, Eurypylus*, *Metasarsiella*, and *Neomuelleriella* are all polyphyletic. *Parasarsiella* is represented only by *Parasarsiella poorei*, which is grouped sister to *Eusarsiella childi* with very low support.

Sympatry within Sarsiellinae

Our phylogeny shows six marginally supported sympatric sister pairs (Table 1). Each pair was collected from an identical collection locality. The pairs are as follows: Both new species from this study, *Eusarsiella bryanjuarezi* and *Eusarsiella eli*; *Sarsiella verae* Poulsen, 1965 and *Sarsiella longicornis* Poulsen, 1965; *Sarsiella spinulosa* Poulsen, 1965 and *Sarsiella nana* Poulsen, 1965; *Cymbicopia cervix* Kornicker, 1995 and *Cymbicopia climax* Kornicker, 1995; *Eusarsiella tryx* Kornicker, 1996 and *Eusarsiella phrix* Kornicker, 1996; *Eusarsiella dispar* Kornicker, 1986 and *Eusarsiella greyi* Kornicker, 1986.

Species pair	Support level	Locality	Reference
Eusarsiella bryanjuarezi, Eusarsiella eli	68	Florida Keys, Florida USA	this study
Sarsiella verae, Sarsiella longicornis	50	Trat, Thailand	Poulsen 1965
Sarsiella spinulosa, Sarsiella nana	64	Trat, Thailand	Poulsen 1965
Cymbicopia cervix, Cymbicopia climax	72	New South Wales, Australia	Kornicker 1995
Eusarsiella tryx, Eusarsiella phrix	35	Queensland, Australia	Kornicker 1996
Eusarsiella dispar, Eusarsiella greyi	44	Gulf of Mexico, off Texas, USA	Kornicker 1986

TABLE 1. Six supported sympatric species pairs recovered in the morphological phylogeny.

Discussion

We describe two new species from the same collection locality in Florida and show through phylogenetic analyses that the two species, along with five other sympatric pairs, are sister species. To our knowledge, this is the first publication to focus on sympatric sister species within Myodocopa, probably because most previous phylogenies investigated the relationships among genera and families, rather than species. Sympatric sister-species are interesting because close relatives are often assumed to share similar ecological roles. If so, sympatric sister pairs may be in direct competition. If not, one or both pairs may have evolved new ecological roles very recently. Documenting sympatric sister species sets the stage for future work into the ecological roles of those species that could disentangle these alternatives.

Previous ostracod morphological trees tend to be controversial due to homoplasy and uncertainties in character homologies (e.g., Syme & Oakley 2012), both of which may have affected the current analysis and led to low support values we observe. Still, the number of monophyletic genera recovered with moderate support (3) is the highest yet, to our knowledge, of any myodocopid morphological analysis.

Our morphological phylogeny sheds light on a few potential taxonomic problems. First, as in Karanovic's 2012 phylogeny, the small genus *Ancohenia* (two or three species, see methods section above; Kornicker 1976) is placed entirely within *Chelicopia*. However, our phylogeny only includes *Ancohenia hawaiiensis* because only males are known from *A. robusta*. Taxonomically, *Ancohenia* is delineated from *Chelicopia* by the nature of the f-and g- bristles on the first limb, *Ancohenia* with "claw-like" and *Chelicopia* with "normal" (Kornicker 1976). If a future analysis that includes *A. robusta* finds similar results to ours, *Ancohenia* could be collapsed into *Chelicopia*.

A more general challenge in sarsiellin taxonomy is the paucity of knowledge about intraspecific variation. This is exacerbated by extremely uneven collection of individuals by gender. Sampling sediment heavily favors collecting adult females over adult males, probably due to the high death rates of adult males, which leave the benthos (exposing themselves to predators) while seeking mates (Speiser *et al.* 2013). In our review of original species descriptions, we found that carapace-based characters are variable intraspecifically among sexes, which is somewhat concerning since this is often how species are identified. Moreover, many species are described from few individuals and thus intraspecific variation in carapace morphology and internal anatomy is generally unknown (but see Kornicker 1975 for examples of sarsiellid intraspecific variation). Unfortunately, the rarity of some species, including the two described here, makes the characterization of many individuals a challenge.

A third taxonomic challenge is the strong possibility that several sarsiellin genera are not monophyletic. Choice of characters was based on diagnostic keys to sarsiellin genera (Karanovic 2012), which in combination with our phylogeny calls into question the validity of the larger polyphyletic genera *Sarsiella*, *Spinacopia*, and

especially *Eusarsiella*, whose species are found distributed throughout the tree. Given these issues, and the generally low support of nodes in morphological analyses, discussions of hypothetical character polarity within Sarsiellinae (e.g. Karanovic 2012) will remain uncertain without a corroborating phylogenetic hypothesis, for example from molecular data.

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