

Taxonomy and ecology of two endemic freshwater crabs from western Jamaica with the description of a new *Sesarma* species (Brachyura: Grapsidae: Sesarminae)

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The type series of the Jamaican grapsid crab *Sesarma windsor* Türkay and Diesel, 1994, was re-examined and found to consist of two distinct forms. The holotype represented a form so far only recorded from a freshwater cave in western Jamaica. The other form inhabits burrows in the banks of mountain creeks in western Jamaica and is assigned to a new species, *Sesarma fossarum* sp. n. Both species are fully described and morphological differences partly interpreted as adaptations to the habitats where they occur. The new species and *S. bidentatum* Benedict, 1892, both from mountain creeks, closely resemble the cavernicolous *S. windsor* which suggests a fairly recent invasion of the cave habitat by the latter.

KEYWORDS: Taxonomy, ecology, radiation, Jamaica, freshwater, cave, Grapsidae, Sesarminae, *Sesarma*, new species.

Introduction

Jamaica is the only Caribbean island for which an endemic grapsid crab fauna has been reported. Seven species exclusively occur on this island, of which six belong to the subfamily Sesarminae and five to the genus *Sesarma* (Chace and Hobbs, 1969; Hartnoll 1964a, 1971; Türkay and Diesel, 1994). This unique level of endemism is the result of an adaptive radiation taking place on the island. One important evolutionary factor facilitating this adaptive radiation was probably the absence of freshwater crabs of the family Pseudothelphusidae (Potamoidea), common on most of the other Caribbean islands (Hartnoll, 1964a; Chace and Hobbs, 1969). Geological findings suggest that Jamaica was submerged until 20–25 million years ago and rose above sea level without a connection to any other land mass (Sykes *et al.*, 1982; Perfit and Williams, 1989). By then the Pseudothelphusidae were already well established in other freshwater habitats (Bott, 1970; Pretzmann, 1972) and seemingly unable to colonize Jamaica, thus allowing the exploitation of freshwater-related habitats by the otherwise mostly intertidal Grapsidae.

Hartnoll (1971) described the terrestrial *Sesarma cookei* from eastern Jamaica as an apparent ecological counterpart to the western *Sesarma jarvisi* Rathbun, 1914, it seems to be the last of a series of findings of new endemic Sesarminae for the island (Benedict,

1892; Rathbun, 1896, 1914). In recent years, however, intensive field studies on the reproductive ecology of the endemic Sesarinae (Diesel, 1989, 1992; Diesel and Schuh, 1993; Diesel and Horst, 1995) revealed that the freshwater crab *Sesarma bidentatum* Benedict, 1892 needed to be split into two distinct species: *S. bidentatum* in the east and *S. windsor* Türkay and Diesel, 1994 in the west of the island. Careful examination of more material by JR and CDS has now led to the conclusion that specimens from a cave in the Cockpit Country in Central West Jamaica (including the holotype of *S. windsor*) showed a number of characters that were consistently different from the non-cavernicolous specimens that had also been identified as *S. windsor*. Unfortunately the holotype of *Sesarma windsor* was most probably originally mislabelled, so that it was looked at as a large non-cavernicolous specimen by Türkay and Diesel (1994). In consequence the non-cavernicolous representatives of *S. windsor* are considered a new species, described in the following. In addition a redescription of *S. windsor* is given, so as to clarify the differences.

Type specimens have been deposited in the collections of the Senckenberg-Museum, Frankfurt a.M. (SMF), the National Museum of Natural History, Washington, D.C. (USNM), and the Museum für Naturkunde, Berlin (ZMB). Abbreviations and measurements: cb: carapace breadth, greatest breadth at posterior carapace; cl: carapace length, length from the medial front to posterior carapace end; bh: body height; iw: interorbital width, width of front at its proximal base; el: exorbital length, length from tip of exorbital tooth to notch anterior to anterolateral tooth. Maximal length of the merus of the walking legs was measured dorsally, while the total length (ischium-dactyl) of the 4th pereopod, and the palm length, were measured ventrally.

Systematic account

Sesarma windsor Türkay and Diesel, 1994

(Figs 1–3, 6–7)

Sesarma windsor Türkay and Diesel, 1994 (holotype only)

Not *Sesarma windsor*.—Diesel, 1992: 131—Diesel and Schuh, 1993: 15—Türkay and Diesel, 1994 (in part)—Anger, 1995—Schuh, 1995 [= *Sesarma fossarium* sp. n.]

Material examined

HOLOTYPE: ♂ (SMF 22331) uncertain locality and collection date; probably: Jamaica (Trelawny): Printed Circuit (cave system of Mouth River near Rock Spring; 18°18'N-77°34'W), from freshwater cave stream, 27 April 1993, leg. R. Diesel and G. Bäurle. Former labelling from Martha Brae River Head (as cited by Türkay and Diesel, 1994) turned out to be erroneous, since a comparison with the field notes revealed that no crab collected on that day reached the carapace width of this animal (23.95 versus 29.5 mm).

Other material. 1 ♂ and 1 ♀ (SMF 23271), Jamaica (Trelawny): Printed Circuit, from freshwater cave stream, 9 March 1995, leg. R. Diesel and C. D. Schubart; 2 ♂♂ and 2 ♀♀ (SMF 23272), same locality as SMF 23271, 23 April 1992, leg. R. Diesel and G. Bäurle; 1 ♂ (Coll. Diesel R-282), same locality as SMF 23271, 11 February 1993, leg. R. Diesel, C. D. Schubart and M. Schuh; 1 ♂ and 4 ♀♀ (Coll. Diesel R-257), same locality as SMF 23271, 15 April 1994, leg. R. Diesel and R. Schieke; 4 ♂♂ and 1 ♀ (Coll. Diesel R-317), same data as SMF 23271; 2 ♂♂ and 1 ♀ (Coll. Diesel R-327), same locality as SMF 23271, 3 April 1996, leg. R. Diesel, J. Reimer and C. D. Schubart.

Diagnosis. General body form flattened, body height < 0.5 × carapace breadth. Carapace comparatively broad and smooth; all regions well defined. Anterolateral borders

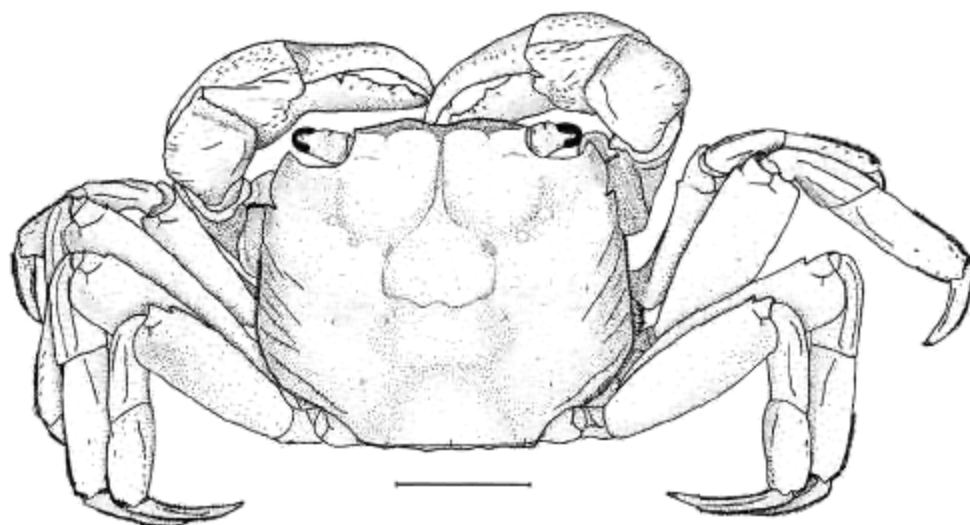


FIG. 1. *Sesarma windsor* Turkey and Diesel, 1994, male; Printed Circuit, Trelawny, Jamaica. Scale bar 1 cm.

with one tooth behind exorbital tooth. Exorbital tooth curved inward towards eye. Cornea partly reduced, resulting in narrowing of eye towards distal end. Line of granules on upper margin of chelipeds broken at least once; row of horny tipped tubercles on dactyl not reaching distal end. Walking legs long and slender: merus $> 2.5\times$ as long as broad. Pereiopod-4 $> 2\times$ as long as carapace length. Male gonopod slender, comparatively straight, terminal horny endpiece slightly deflexed. Female gonopore ventrally oriented; opercular membrane with a fold.

Description. Body form flattened ($bh/cb = 0.48 \pm 0.01$, $n = 24$). Carapace broader than long ($cl/cb = 0.86 \pm 0.01$, $n = 29$) widening posteriorly. Greatest breadth at posterior angles (except in three measured animals, where greatest breadth was found posterior to anterolateral tooth). Carapace regions clearly delimited, especially gastric ones. Carapace surface smooth, frontal and hepatic regions with short rows of coarse granules. Branchial regions with various oblique striae of different lengths fringed by setae. Otherwise no or very few setae on carapace (Fig. 1). Interorbital region subdivided into four frontal lobes. Median ones more bulged and broader than lateral ones. Lateral lobes often with continuous row of granules; median lobes with short and oblique row of granules (if any). Posterior frontal lobes reduced (in large animals a slight elevation still visible), instead a short row of granules usually present. Front relatively narrow ($iw/cb = 0.47 \pm 0.01$, $n = 29$). Frontal border granular with lateral margins subparallel (slightly divergent in large animals) and median indentation (Figs 1, 2A). Exorbital tooth broadly triangular; anterolateral margin anterior to deep notch curved and elongated ($el/cl = 0.17 \pm 0.01$, $n = 29$). Anterolateral tooth triangular and bent upwards, the tip thus pointing dorsofrontally (Fig. 2A, B). Posterior to tooth, a distinct bulge, where most frontal striae on gastric region meets anterolateral border, representing a second, now rudimentary anterolateral tooth. Posteriorly carapace slopes ventrally. In lateral view this sloping is visible in form of crease at top of bulges (Fig. 2B). Lateral carapace border ventrally fringed by row of long setae and parallel groove on pterygostomial plate. The setal row is interrupted several times by gaps subdividing it into 5 to 6 distinct groups (Fig. 2B); gaps tend to be at same height as anterolateral teeth and carapace striae. Lateral carapace border

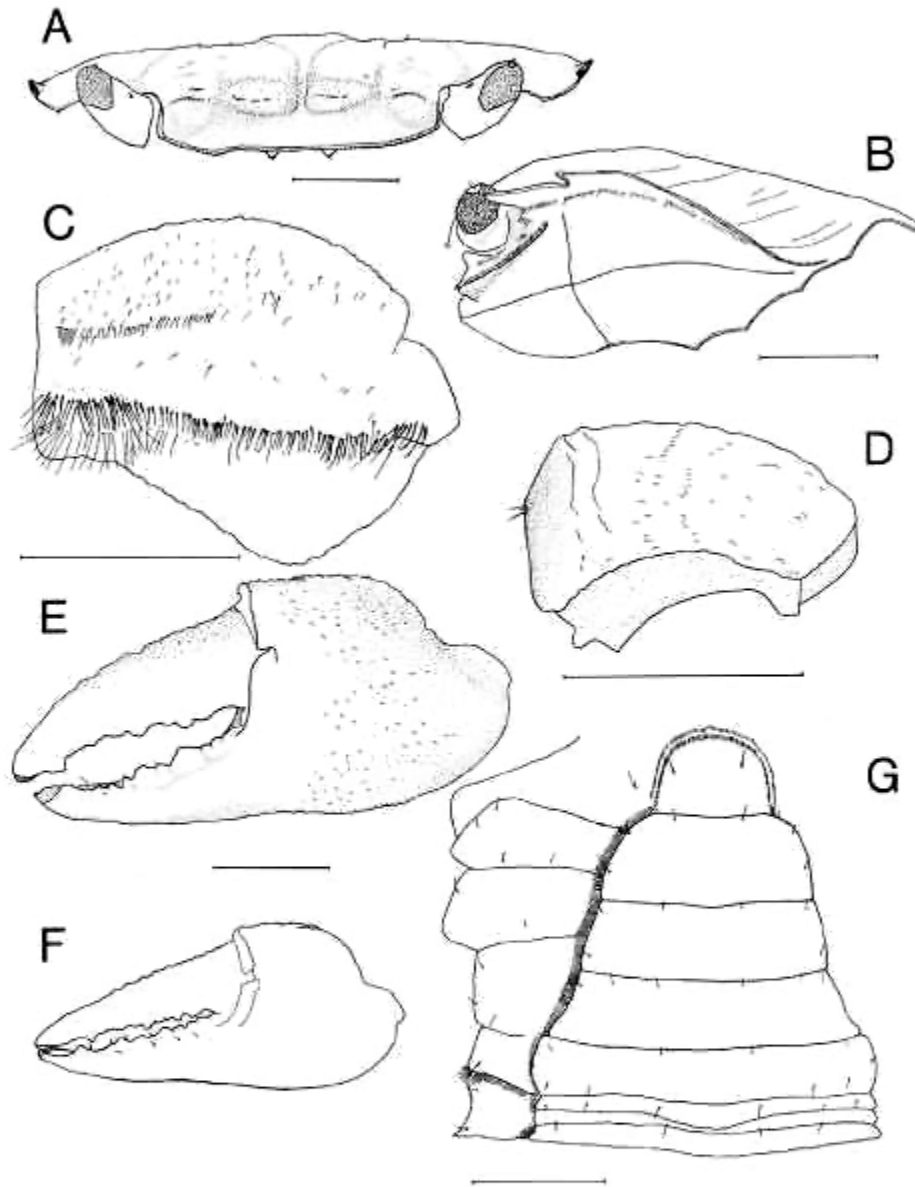


FIG. 2. *Sesarma windsor* Türkay and Diesel, 1994: (A) frontal view of carapace, (B) lateral view of carapace; (C) interior face of merus of left cheliped; (D) fronto-dorsal view of carpus of left cheliped; (E) outer face of left male chela; (F) outer face of left chela of similar sized female; (G) male pleon and sternites. All scale bars 0.5 cm.

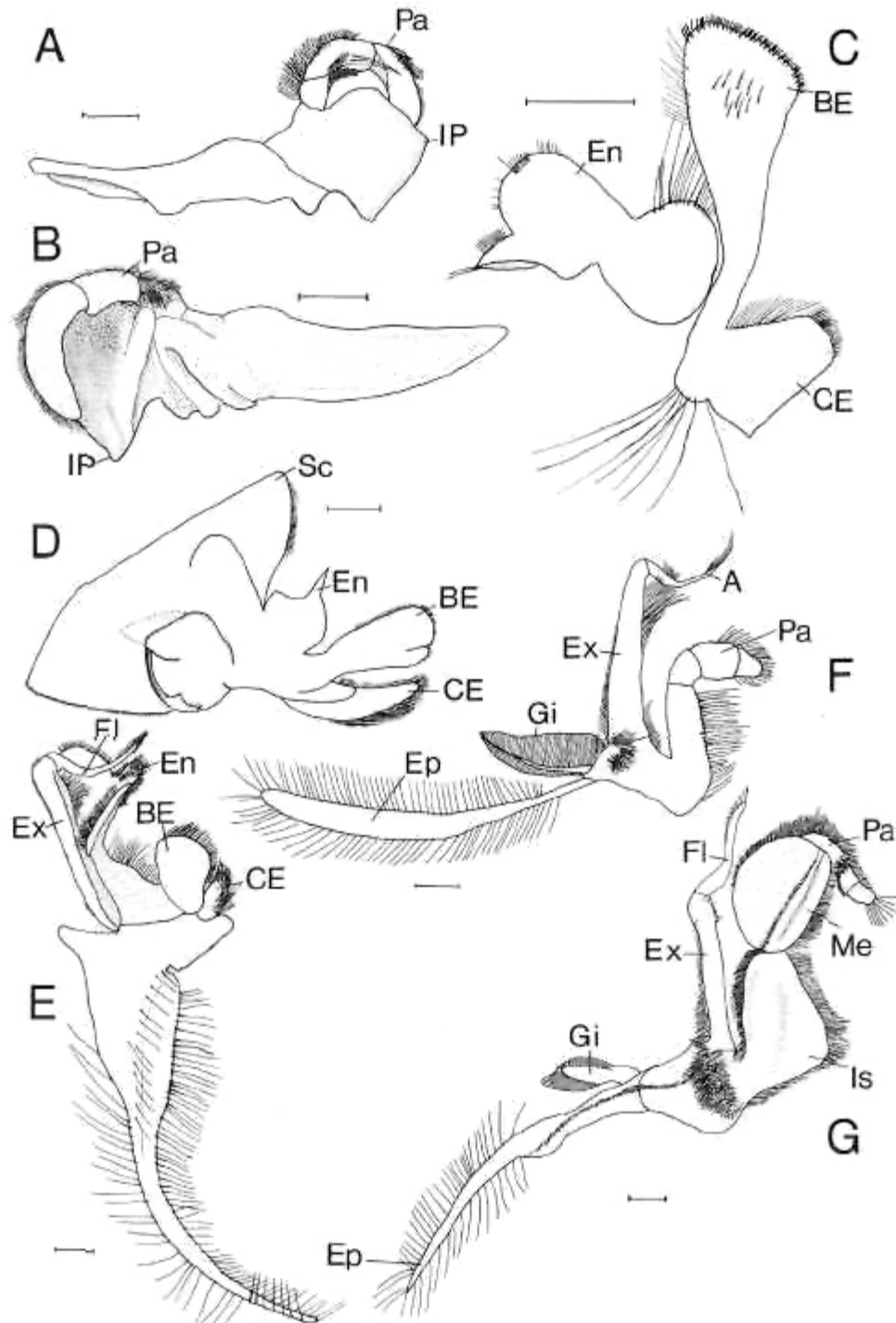
and parallel row of setae meet ventral carapace at height of third ambulatory leg without fusing, thus leaving small gap between them (Fig. 2B). Pterygostomian, subhepatic and subbranchial regions covered with dense and regular reticulation. Anterior triangular area, separated from remainder by grooves, is less densely reticulated. Epistome setose, with endostomial cristae along ventral border. Epistomial wings bent posteriorly at base, distal

end pointing anteriorly, in close connection with coxocerites of the 2nd antennae. Row of setae on epistomial wings almost horizontal, not connected with rest of partly reduced exterior row of setae of Verwey's groove. Interior row reduced to few reticulate setae (Fig. 7A). Infraorbital lobe distinct, suborbital border setose (Fig. 2B). Posterior border of orbit with few granules, parallel to front, not directed posterolaterally. Orbit with setae posterior to eye. Eyes show slight reduction: eyestalks gradually narrowing from basis to small cornea (Fig. 6A). Eyes with two sets of setae, one dorsofrontal in center of eyestalk, other in dorsal corneal gap.

Gap between third maxillipeds clearly exposes mandibles and palps of second maxillipeds. Mandibles with gnathal lobe (incisor process) and setose palp (3-jointed endopod) (Fig. 3A, B). First maxillae or maxillules small, with endopod and two endites, larger basal endite setose on aboral side and distally armed with small spines (Fig. 3C). Second maxillae with scaphognathite, a sharply tapering endopod and two endites (Fig. 3D). All three maxillipeds with long setose epipodite reaching into branchial chamber and an exopod with a distal setose flagellum. First maxillipeds in addition with setose heart-shaped endopod and two small endites with dense setal cover along interior margins (Fig. 3E). Second maxillipeds without endites but carrying podobranch and articulate palp (endopod) (Fig. 3F). Ischium and merus of third maxillipeds flattened and foliaceous. Ischium with longitudinal indentation. Merus with elevated, oblique hairy crest. Borders of both joints densely hairy. Setae on inner border of ischium longer, but cover less dense than on outer border. Setae on inner border of merus shorter towards distal end. Outer border of merus with few strong and dark spines. Distally setation denser continuing onto palp. The palp inserts distally at interior border of merus. Proximally insertion of a small podobranch and long epipodite. Exopod normally hidden behind endopod, outer margin with setae, diminishing distally. Short row of long setae on inner border, flagellum distally setose (Fig. 3G).

Chelipeds in adult animals homochelous, sexually dimorphic; those of females markedly smaller and weaker (Fig. 2E, F). Within animals, chelipeds are homochelous in both sexes. Merus triangular in cross section, all three borders with regularly spaced and similarly sized granules. Upper border with long setae on proximal half, subdistal projection and rounded distal tip. Inner face ventrally bulged, with two longitudinal rows of setae, lower one extending over full length, upper one only extending to proximal half. Dorsal to upper row an irregular field of short and stout setae (Fig. 2C). Ventral face triangular, smooth, and glabrous. Outer face with several rows of granules of varying length. Inner face of carpus with regular row of granules, proximally tuft of grooming setae in close connection with ventral setal row from inner face of merus. Mesial border angulate, with 1–3 coarse granules. Outer face with granular crests of different length (Fig. 2D). Palm approximately 0.5× as high as long (0.49 ± 0.01 in 11 adult ♀♀; 0.55 ± 0.02 in 17 adult ♂♂). Dorsal row of granules not continuous; sometimes broken only once at half its length, sometimes the granules are of irregular size and distance. Upper outer face often with 3–6 oblique lines of larger sized granules (Fig. 6B). Outer face completely covered with coarse granules. Inner face irregularly granulate, with a patch of larger granules in its center. Palm about 1.6× as long as dactylus (1.64 ± 0.05 in 11 adult ♀♀; 1.56 ± 0.06 in 17 adult ♂♂). Regular row of horny tipped tubercles on dorsal edge of dactylus from proximal to about 0.75 of length (Fig. 6B). Fingers in large animals slender and curved, resulting in an oval gap between the cutting edges (Fig. 2E); not so in small animals. Cutting edges with teeth along their whole length. Tips of fingers with horny edges. Tufts of setae parallel to teeth on inner side of fingers.

Percipods 2–5 moderately long; fourth longest, little > 2× carapace length



(2.05 ± 0.03 , $n = 17$). Merus of walking legs $> 2.5\times$ as long as broad (2. pereopod: 2.57 ± 0.15 ; 3. pereopod: 2.63 ± 0.13 ; 4. pereopod: 2.68 ± 0.14 ; 5. pereopod: 2.51 ± 0.16 ; $n = 25$). Upper border crested and with subdistal tooth. Posterior faces with transverse granular crests in pereopod 2–4. Anterior faces smooth and glabrous. Upper border of carpus with a granulated crest; posterior face with two longitudinal granular crests. Anterior face of pereopods 2–4 with one longitudinal crest (Fig. 6C), pereopod 5 smooth. Lower face with oblique crest of small granules. Propodus with slightly curved longitudinal crest on proximal half of anterior face as an extension of granules from carpus in pereopods 2–4 (Fig. 6C), not in pereopod 5. Similarly curved crest on posterior face of all pereopods. Lower face with distal black spines. Pubescence restricted to borders (not faces) of propodi (Fig. 6C); gradually decreasing from pereopod 2 to 5. Dorsal border of pereopod 2 almost completely covered with setae, while ventral border is only covered to 0.66 its length. Dorsal border of pereopod 5 covered to 0.33 its length, ventral border only with few black spines. Pereopods 3 and 4 with an intermediate pubescence. Dactyl slightly curved with six longitudinal rows of setae: dorsal, antero-dorsal, postero-dorsal, ventral, antero-ventral, postero-ventral. Distally dactyl horny-tipped and without setation (Fig. 6C).

Sternite III only pubescent at margin bordering sternite II and median close to anterior border, otherwise glabrous (Fig. 7B). Other sternites smooth and glabrous. Suture between male sternite VII and episternite VII does not reach margin of pleon; imaginary prolongation meeting border between abdominal segments 3 and 4 (Fig. 2G). In males third abdominal segment broadest; lateral borders convex. Fourth abdominal segment posteriorly broader than anteriorly; lateral borders concave. Fifth and sixth abdominal segments narrowing towards posterior border; lateral borders convex. Telson at base much narrower than base of last abdominal segment resulting in a broken contour at border between last segment and telson (Fig. 2G). Female abdomen broadly oval; telson about as long as broad. Male gonopods slender, slightly twisted. Horny apex slightly deflexed (Fig. 7D, E). Female sternum with deep indentation, resulting in strongly sloping gonopores and a ventral orientation of opercular membrane. Operculum with median slitlike fold (Fig. 7C).

Colour in life. *Sesarma windsor* has a dark yellow to orange ground colour with dotted brownish-red pigmentation, especially dense at the frontal and protogastric carapace regions.

Measurements. The following measurements refer to the largest males and females from the material studied respectively: carapace width: 31/25.7 mm; carapace length 26.9/22.1 mm; body height: 15.4/13 mm; frontal breadth: 14.9/12.2 mm.

Type locality. Holotype probably from Jamaica: Cornwall: Trelawny: Printed Circuit (cave system of Mouth River, close to Rock Spring; $18^{\circ}18'N-77^{\circ}34'W$), from freshwater cave stream. In March 1993 animals had been collected from there as well as from Windsor, allowing for possible confusion.

Distribution. *Sesarma windsor* is so far only known from its type locality.

Occurrence and habitat. Printed Circuit (locally also known as John Fordon Cave) is

FIG. 3. *Sesarma windsor* Türkay and Diesel, 1994; mouthparts: (A) right mandible; (B) right mandible (oral side); (C) 1. right maxilla or maxillule; (D) 2. right maxilla with scaphognathite; (E) 1. right maxilliped; (F) 2. right maxilliped; (G) 3. right maxilliped. All scale bars 0.1 cm. En: endopod, Ex: exopod, Ep: epipodite, BE: basal endite, CE: coxal endite, Gi: podobranch (gill), Fl: flagellum, Pa: palp, Me: merus, Is: ischium, Sc: scaphognathite, IP: incisor process.

an extended highly branched cave system with at least two subterranean streams contributing to the Mouth River (Peck, 1975; Fincham, 1977). *Sesarma windsor* inhabits the bed and banks of these subterranean streams. Thick layers of deposited sinter (calcium carbonate) on the carapace of large animals and comparative experiments on osmoregulation (Schubart and Diesel, unpublished) suggest extended periods of activity within the water. Only rarely were animals found in shallow burrows in the bank of the stream. In comparison to the sympatric *Sesarma verleyi* Rathbun, 1914, *S. windsor* seems to prefer areas with a higher degree of water movement like sinter pools and those sections of the cave which are closer to entrances.

Sesarma fossarum sp. n.
(Figs 4–7)

Material examined

HOLOTYPE: ♂ (SMF 23275), Jamaica (Trelawny): Head of Martha Brae River (18°21'N-77°39'W), from burrows in river banks, 22 July 1992, *leg.* G. Bäurle and M. Schuh.

PARATYPES: 1 ♂ and 1 ♀ (SMF 22332), Jamaica (Trelawny), same locality as holotype, 2 March 1993, *leg.* R. Diesel (also paratypes of *S. windsor* Türkay and Diesel, 1994); 1 ♀ (SMF 19571), 1 ♂ (SMF 19572), 1 ♂ (SMF 19573), same locality as holotype, 27 February 1987, *leg.* R. Diesel (also paratypes of *S. windsor* Türkay and Diesel, 1994); 1 ♂ (SMF 23273), same locality as holotype, 18 March 1993, *leg.* R. Diesel; 1 ♂ and 1 ♀ (SMF 23274), same locality as holotype, 15 March 1995, *leg.* R. Diesel and C. D. Schubart. 2 ♂♂ and 2 ♀♀ (USNM 282671), same data as SMF 23274; 2 ♂♂ and 2 ♀♀ (ZMB 27181), same data as SMF 23274; 2 ♂♂ (Coll. Diesel R-22, R-23), same locality as holotype, 10 March 1987, *leg.* R. Diesel; 2 ♂♂ (Coll. Diesel R-71), same locality as holotype, 3 July 1992; *leg.* M. Schuh; 3 ♂♂ and 2 ♀♀ (Coll. Diesel R-147), same locality as holotype, 2 March 1993, *leg.* R. Diesel; 9 ♂♂ and 2 ♀♀ (Coll. Diesel R-298), same

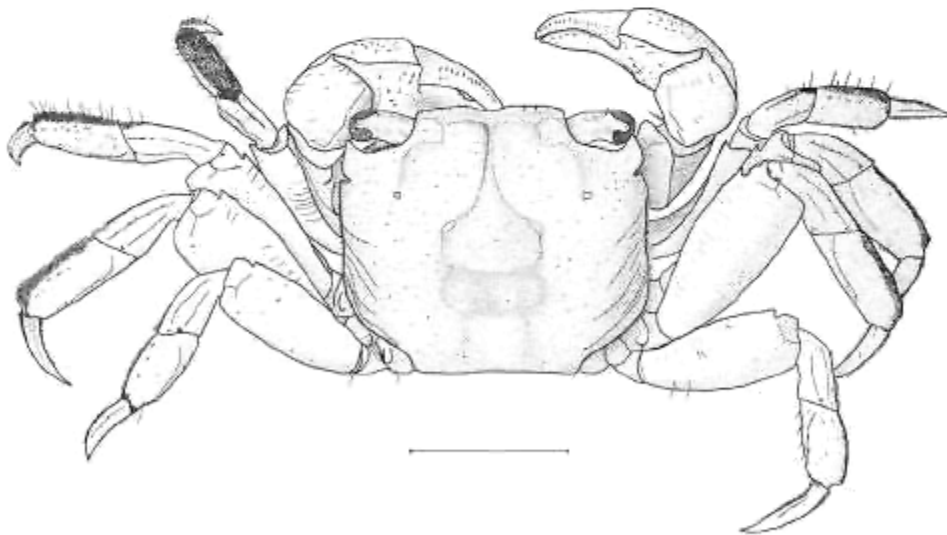


FIG. 4. *Sesarma fossarum* sp. n., male holotype (SMF 23275); Martha Brae River Head, Trelawny, Jamaica. Scale bar 1 cm.

locality as holotype, spring 1994, leg. R. Diesel and R. Schieke; 4 ♂♂ (Coll. Diesel R-329), same locality as holotype, under boulders in sinkhole, 22 March 1996, leg. C. D. Schubart and J. Reimer.

Etymology. The species was named after its typical habit of burrowing in the banks of freshwater streams: '*fossa, ae, f*' (Latin) = burrow, ditch. The genitive plural ending '= *arum*' is used in the sense of 'from the burrows'.

Diagnosis. General body form high, height > 0.5× carapace breadth. Carapace slightly broader than long, with small tufts of setae; all regions well defined. Anterolateral borders with one strong tooth behind short exorbital tooth. Posterior border of orbit directed postero-laterally. Upper margin of chelipeds with a continuous line of granules. Horny tipped tubercles on dactyl reaching to distal end. Male chelipeds large and strong. Merus of walking legs < 2.5× as long as broad. Pereiopod-4 > 2× as long as carapace. Male first pleopod comparatively broad and twisted; horny apex strongly deflexed. Female gonopore directed ventro-laterally because of shallow indentation in posterior sternum; mesio-frontal corner of operculum with a fold.

Description. Corresponds to the description of *S. windsor* by Türkay and Diesel (1994), with the following changes or additions.

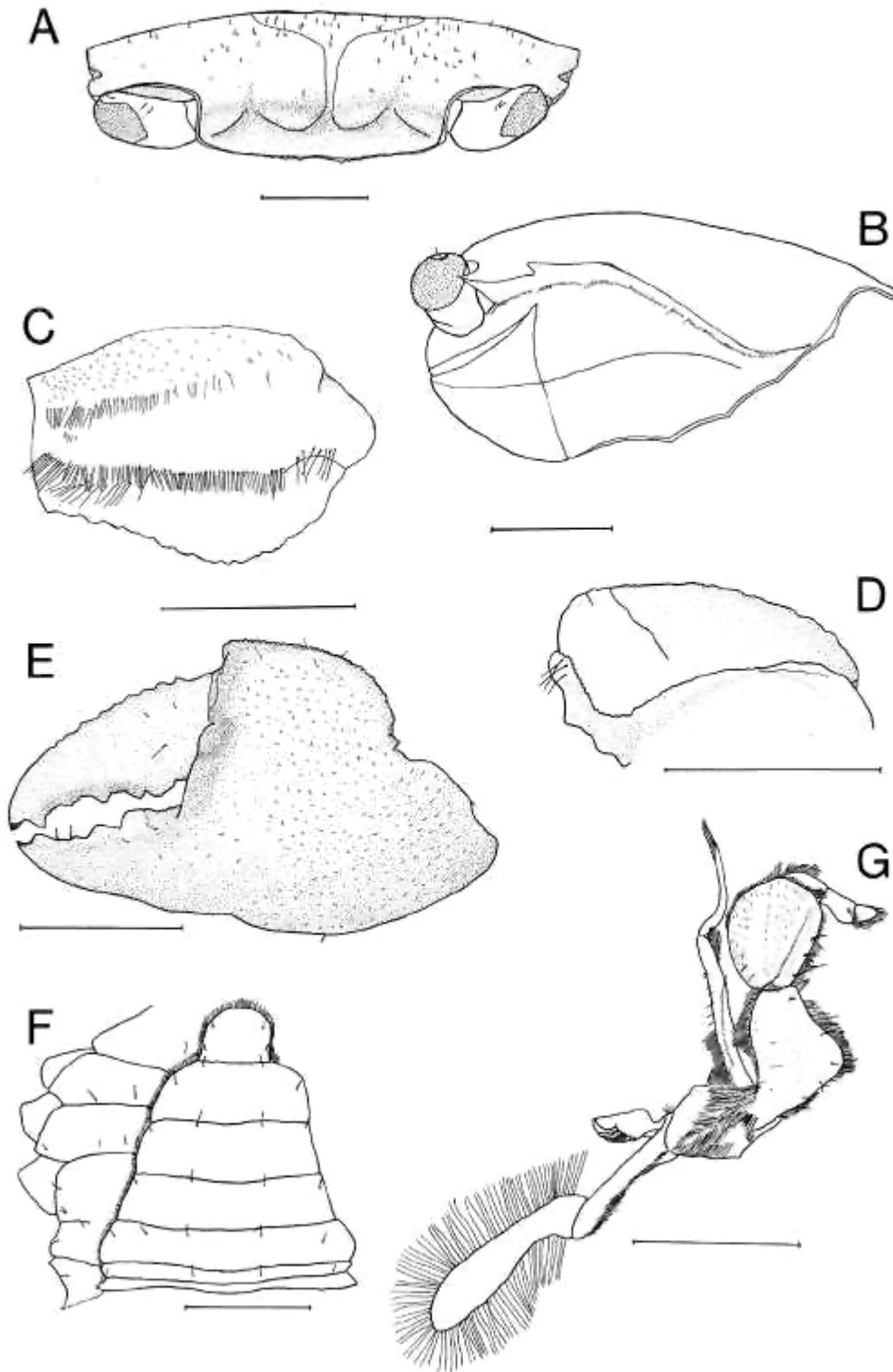
Morphometric relationships calculated to describe body- and carapace form of *S. fossarum* sp. n. are as follows: bh/cb = 0.52 ± 0.01 ; cl/cb = 0.87 ± 0.01 ; iw/cb = 0.49 ± 0.01 ; for all $n = 40$; el/cl = 0.16 ± 0.01 , $n = 38$. Carapace surface covered by tufts of small setae (Figs 4, 5A). Exorbital tooth broadly triangular and short, outer border not markedly rounded (Figs 4, 5B, 6D). Epistomial wings bent posteriorly at base, distal end pointing anteriorly. Interior row of setae from Verwey's groove mostly reduced, exterior row deflected (Fig. 7B).

Inner face of cheliped merus with two rows of setae (Fig. 5C). Inner face of carpus with a tuft of grooming setae (Fig. 5D). Upper border of palm always with continuous line of granules. Palm very strong; > 0.5× as high as long (0.52 ± 0.01 in 11 adult ♀♀; 0.61 ± 0.01 in 28 adult ♂♂) and about 1.6× as long as dactyl (1.67 ± 0.05 in 11 adult ♀♀; 1.57 ± 0.03 in 27 adult ♂♂). Fingers in adult males only moderately gaping. Dactyl with horny tipped tubercles reaching near to distal end (Fig. 5E).

Pereopods 2–5 moderately long, fourth < 2× as long as carapace (1.9 ± 0.05 , $n = 35$). Merus of walking legs < 2.5× as long as broad (2. pereopod: 2.4 ± 0.14 ; 3. pereopod: 2.45 ± 0.16 ; 4. pereopod: 2.43 ± 0.15 ; 5. pereopod: 2.39 ± 0.13 ; for all $n = 40$). Pubescence gradually decreasing from pereopods 2 to 5: present on anterior faces of propodi from pereopods 2 and 3, on upper borders of propodi of all walking legs, on more than half of lower borders of pereopods 2–3 (Fig. 6F) and less than half of pereopod 4. Pubescence on lower border of propodus of pereopod 5 only consists of few tufts and spines. Dactyl slightly curved with six longitudinal rows of setae: dorsal, antero-dorsal, postero-dorsal, ventral, antero-ventral, postero-ventral (Fig. 6F). Suture between male sternite VII and episternite VII does not reach margin of pleon, imaginary prolongation meets border between abdominal segments 3 and 4 (Fig. 5F). Male gonopods comparatively stout, slightly twisted; horny apex markedly deflexed (Fig. 7I,J). Female sternum with shallow indentation at posterior end, resulting in moderate sloping of gonopores and the opercular membrane pointing ventro-laterally (Fig. 7H).

Colour in life. *Sesarma fossarum* sp. n. has a dark orange to tan ground colour, the chelipeds are reddish cream.

Measurements. The following measurements refer to the largest males and females from the material studied respectively: carapace width: 26.2/24.2 mm; carapace length 23.1/21.2 mm; body height: 13.8/12.7 mm; frontal breadth: 12.8/12 mm.



Type locality. Jamaica: Cornwall: Trelawny: Sherwood Content District: Windsor: 'Cedar Grove' (Head of Martha Brae River; 18°21'N-77°39'W), 110 m altitude, from burrows above the water level in the bank of the Martha Brae River Head.

Distribution. So far only known from western Jamaica (map in Türkay and Diesel, 1994); all specimens taken for this description being from type locality.

Occurrence and habitat. The new species inhabits the upper reaches of streams and rivers. It constructs extensive burrow systems in the banks which descend below the water table. It is also found in moist beds of seasonally running streams, burrowing under stones or in the muddy banks. Specimens were also found up to 30 m inside the Windsor Great Cave, which they entered after a flooding. The burrows of *S. fossarum* sp. n. become regularly submerged for several weeks following the spring rainy season. Small individuals are usually found in the water, whereas large ones mostly stay in their burrows, leaving them mainly at night to forage along the banks above the waterline. This description is basically the one given for the occurrence and habitat of *S. windsor* by Türkay and Diesel (1994) and it corresponds to the preliminary notes on the habitat of *Sesarma* 'windsor' by Diesel (1992) and Diesel and Schuh (1993). The specimens mentioned by Türkay and Diesel (1994) from the cave stream Spring Garden Cave do not belong to *S. fossarum* sp. n. but to *S. windsor* as redescribed above.

Discussion

Sesarma fossarum sp. n. is closely related to *S. bidentatum* Benedict, 1892, and *S. windsor* Türkay and Diesel, 1984. While *S. bidentatum* is only known from eastern Jamaica, *S. windsor* and *S. fossarum* sp. n. occur in close geographic proximity in western Jamaica. The latter two species can be distinguished by the following characters:

- (1) Posterior border of orbit in *S. windsor* parallel to front, not directed posterolaterally as in *S. fossarum* sp. n. The exorbital tooth is strongly projected anteriorly and the outer margin is significantly longer than in *S. fossarum* sp. n. (Fig. 6A, D; Table 1).
- (2) Cornea partly reduced in *S. windsor* resulting in narrowing of the eye towards its distal end (Fig. 6A). In *S. fossarum* sp. n. the cornea is fully developed and broader than the stalk (Fig. 6D).
- (3) The granular crest on the dorsal border of the palm of the chelipeds in *S. windsor* is interrupted by gaps (Fig. 6B), often appearing like a series of parallel oblique crests rather than one continuous crest as in *S. fossarum* sp. n. (Fig. 6E). The cheliped dactyl bears a row of horny tipped tubercles not reaching farther than 0.75 of the proximal dactyl length in *S. windsor* (Fig. 6B), while tubercles extend near to the distal end in *S. fossarum* sp. n. (Fig. 6E). In these characteristics *S. windsor* resembles *S. bidentatum*.
- (4) In both species the base of the epistome wings are bent towards posterior, resulting in an interruption of the exterior row of setae of Verwey's groove. In *S. fossarum* sp. n. the exterior row of setae is deflexed while the interior row is reduced (Fig. 7A, F).
- (5) *S. windsor* is clearly less pubescent than *S. fossarum* sp. n. This can be best shown

FIG. 5. *Sesarma fossarum* sp. n.: (A) frontal view of carapace; (B) lateral view of carapace; (C) interior face of merus of left cheliped; (D) fronto-dorsal view of carpus of left cheliped; (E) outer face of left male chela; (F) male pleon and sternites; (G) 3. right maxilliped. All scale bars 0.5 cm.

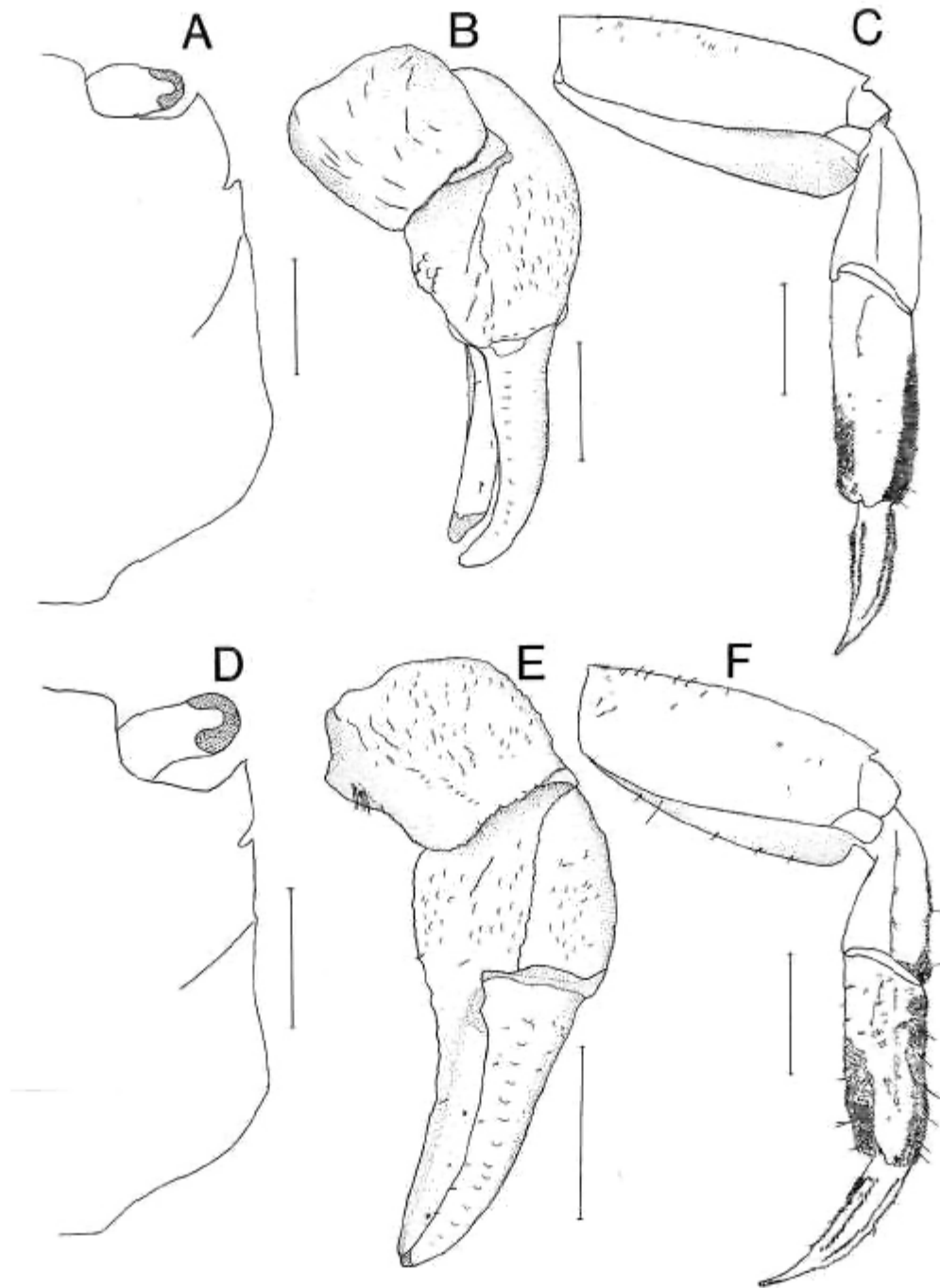


FIG. 6. Comparison of *Sesarma windsor* Türkay and Diesel, 1994 (A–C) with *Sesarma fossarum* sp. n. (D–F); (A–D) dorsal view of right carapace margin and eye, (B, E) dorsal view of left male chela (carpus, palm, and dactyl), (C, F) anterior side of 3. pereopod. All scale bars 0.5 cm.

Table 1. Comparison of morphometric relationships between adult *Sesarma windsor* and *Sesarma fossarum* sp. n. from western Jamaica. All samples were tested for normal distribution and compared by means of an unpaired two-tailed t-test. Values represent means, standard deviations, and sample size.

	<i>S. windsor</i>	<i>S. fossarum</i> sp. n.	$p \leq$
Carapace length/breadth	0.86 ± 0.01 (29)	0.87 ± 0.01 (40)	0.001
Body height/carapace breadth	0.48 ± 0.01 (24)	0.52 ± 0.01 (40)	0.001
Interorbital width/carapace breadth	0.47 ± 0.01 (29)	0.49 ± 0.01 (40)	0.001
Exorbital length/carapace length	0.17 ± 0.01 (29)	0.16 ± 0.01 (38)	0.001
4th pereopod length/carapace length	2.05 ± 0.03 (17)	1.9 ± 0.05 (35)	0.001
4th pereopod merus length/breadth	2.66 ± 0.14 (25)	2.43 ± 0.15 (40)	0.001
Male palm height/carapace length	0.45 ± 0.06 (16)	0.54 ± 0.02 (28)	0.001
Female palm height/carapace length	0.32 ± 0.01 (11)	0.36 ± 0.02 (11)	0.001
Male palm height/length	0.55 ± 0.02 (17)	0.61 ± 0.01 (28)	0.001
Female palm height/length	0.49 ± 0.01 (11)	0.52 ± 0.01 (11)	0.001

for the walking legs. In *S. fossarum* sp. n. the propodus of pereopods 2 and 3 is densely covered by setae on the anterior faces and along the entire dorsal border including the distal parts of the carpus. In *S. windsor* neither the anterior faces of the propodus nor the dorsal border of the carpus show similarly dense pubescence (Fig. 6C, F).

- (6) The anterior border of sternite III is angular and nearly glabrous in *S. windsor* (Fig. 7B), while it appears more gently rounded and more pubescent in *S. fossarum* sp. n. (Fig. 7G).
- (7) The female gonopores of *S. windsor* are sloping (because of the steep indentation in the sternum), resulting in a ventral orientation of the opercular membrane (Fig. 7C). In *S. fossarum* sp. n. the indentation in the sternum is more shallow posteriorly, the gonopores are less sloping and the opercular membrane is directed ventro-laterally (Fig. 7H).
- (8) The male gonopods are more slender, less twisted and with a horny apex less deflexed in *S. windsor* compared to *S. fossarum* sp. n. (Fig. 7D, E, I, J).
- (9) Adult females of *S. windsor* measured from 21.9 to 25.7 mm carapace width, adult males from 23 to 31 mm. *S. fossarum* sp. n. is conspicuously smaller, adult females measuring from 19.4 to 24.2 mm carapace width and males from 19.3 to 26.2 mm.
- (10) Differences in morphometry between the two species as shown in Table 1.

The etymology of *S. windsor* is derived from the geographical region 'Windsor', a depression in the heart of the Cockpit Country (Türkay and Diesel, 1994). The type series of Türkay and Diesel (1994) contained *S. windsor* and *S. fossarum* sp. n. both with Windsor as locality. Misled by the wrong label of the holotype they had to assume that this animal was also found in Windsor. The larger holotype was thus considered to be the adult form while the smaller paratypes would be younger stages. This is why their description of *S. windsor* in many points fits both species. After detecting the labelling mistake the two forms could now be separated not only in terms of morphology but also by their distinct geographical distribution. The present description is thus more precise. Unfortunately, however, remains the fact, that the name of one species is derived from a location where it does not occur.

Both of the described species occur in central West Jamaica, in the Cockpit Country, a

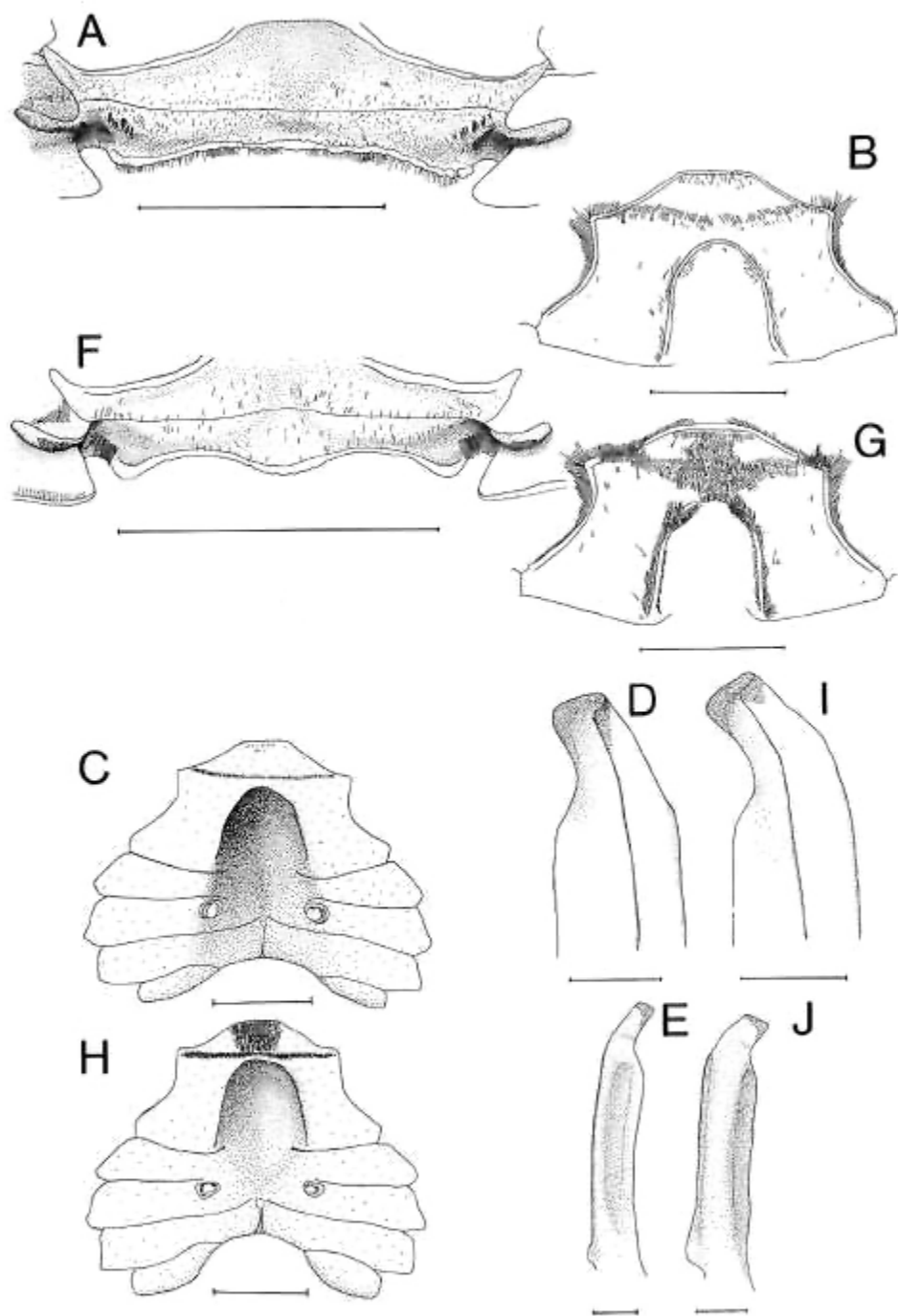


FIG. 7. Comparison of *Sesarma windsor* Türkay and Diesel, 1994 (A–E) with *Sesarma fossarum* sp. n. (F–J); (A, F) frontal view of epistome with Verwey's groove, (B, G) sternite III; (C, H) female sternum with gonopores; (D, I) left male gonopod, dorsal view, (E, J) left male gonopod, mesio-ventral view. All scale bars 0.5 cm.

landscape which is characterized by its thick limestone cover and the formation of karst cockpits. Limestone is a highly erosive rock due to the capacity of water to dissolve calcium carbonate. In consequence huge cave systems can be found all over western and central Jamaica and much of the precipitated water is carried down to the coastal plains via subterranean cave streams. This natural surrounding is important for understanding the biology of the two crabs described. Caves as the habitat of *S. windsor* are very common and in some parts of the country the most constant water source. On the other hand the comparatively soft limestone is indispensable for *S. fossarum* sp. n. in order to construct their burrows, which reach down to the water table and thus represent a retreat from predators and desiccation.

The direct comparison of the morphology of *S. fossarum* sp. n. and *S. windsor* revealed a certain number of differences which can partly be interpreted as adaptations to the habitats where the animals were encountered. The smaller eyes, the longer walking legs, and a lighter coloration (mostly yellow and orange) of *S. windsor* are probably adaptations to the cave habitat. *Sesarma verleyi* Rathbun, 1914, another endemic crab of Jamaica, lives exclusively in caves and is so far the only troglobitic grapsid crab reported from America (Hobbs *et al.*, 1977; Guinot, 1988). It is similarly but more strongly characterized by long limbs, reduced eyes, a pale coloration and a thin integument (Hartnoll, 1964a, b), all these being typical characteristics for cave crabs. This suggests a fairly recent invasion of the cave habitat by *S. windsor*. Further collecting is necessary to determine whether *S. windsor* occurs exclusively in caves and therefore should be regarded as the second grapsid troglobite for Jamaica and America or if it can also be found outside the cave habitat, making it a troglophile as postulated for *S. bidentatum* (Peck, 1992), which has been found in several Jamaican caves (Hartnoll, 1964a; Peck, 1992). In any case this species presents an interesting example of the commencement of adaptation to subterranean life.

Sesarma fossarum sp. n. on the other hand is characterized by a strong pubescence and short and broad walking legs. Both can be useful for a life in burrows. The hairs might be necessary to avoid adhesion of the sticky clay-like substratum and the short and broad legs will favour strength and mobility in a narrow habitat, which can turn out to be more important than velocity when moving over-ground. The conspicuous pubescence and the short and broad legs of *S. rectum* and *S. curacaoense*, two Caribbean congeners living in burrows in wet mangrove soil (Abele, 1992), give further evidence for this possible functional connection.

The biology of these crabs being closely tied to freshwater streams suggests that watersheds must present a serious biogeographic barrier for dispersal. This and the additional fact that the geological history of Jamaica is characterized by continuous changes in water level, repeatedly isolating parts of the island during the late Tertiary and the Pleistocene (Pregill and Olson, 1981), implies that speciation could have occurred frequently among closely related populations. The diversity of endemic Sesarminae on Jamaica seems to support this idea. The species *Metopaulias depressus*, *Sesarma jarvisi*, *S. cookei*, *S. verleyi*, *S. bidentatum*, *S. windsor*, and *S. fossarum* sp. n. constitute a monophyletic group (Reimer, Schubart and Diesel unpublished; Schubart, Diesel and Hedges, unpublished) and thus the outcome of an adaptive radiation taking place on the island. The strikingly different morphologies shown by the first four of the mentioned species are caused by adaptations to very specialized terrestrial or freshwater habitats: bromeliad leaf axils (Diesel 1989, 1992), snail shells (Diesel and Horst, 1995; Bärle and Diesel, unpublished), terrestrial burrow systems (Abele and Means, 1977) and freshwater caves (Hartnoll, 1964a, b). *Sesarma bidentatum*, *S. windsor* and *S. fossarum* are confined to freshwater streams. Their relative morphological similarity is probably due to similar

ecological demands or at least to longer evolutionary times in similar habitats. With continuing morphological and molecular studies on these similar looking freshwater species, we expect to distinguish several other species within a complex where until recently only one species had been recognized, and provide further insight into the mechanisms of speciation and evolution.

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References

- ABELE, L. G., 1992, A review of the grapsid crab genus *Sesarma* (Crustacea: Decapoda: Grapsidae) in America, with the description of a new genus, *Smithsonian Contributions to Zoology*, **527**, 1–60.
- ABELE, L. G. and MEANS, D. B., 1977, *Sesarma jarvisi* and *Sesarma cookei*, montane, terrestrial grapsid crabs in Jamaica (Decapoda), *Crustaceana*, **32**, 91–93.
- ANGER, K., 1995, The conquest of freshwater and land by marine crabs: adaptations in life-history patterns and larval bioenergetics, *Journal of Experimental Marine Biology and Ecology*, **193**, 119–145.
- BENEDICT, J. E., 1892, Decapod Crustacea of Kingston Harbour, *Johns Hopkins University Circular*, **11**, 77.
- BOTT, R., 1970, Betrachtungen über die Entwicklungsgeschichte und Verbreitung der Süßwasser-Krabben nach der Sammlung des Naturhistorischen Museums in Genf/Schweiz, *Revue Suisse de Zoologie*, **77**, 327–344.
- CHACE JR, F. A. and HOBBS JR, H. H., 1969, The freshwater and terrestrial decapod crustaceans of the West Indies with special reference to Dominica, *Bulletin of the United States National Museum*, **292**, 1–258.
- DIESEL, R., 1989, Parental care in an unusual environment: *Metopaulias depressus* (Decapoda: Grapsidae), a crab that lives in epiphytic bromeliads, *Animal Behaviour*, **38**, 561–575.
- DIESEL, R., 1992, Managing the offspring environment: brood care in the bromeliad crab, *Metopaulias depressus*, *Behavioral Ecology and Sociobiology*, **30**, 125–134.
- DIESEL, R. and HORST, D., 1995, Breeding in a snail shell: ecology and biology of the Jamaican montane crab *Sesarma jarvisi* (Decapoda: Grapsidae), *Journal of Crustacean Biology*, **15** (1), 179–195.
- DIESEL, R. and SCHUH, M., 1993, Maternal care in the bromeliad crab, *Metopaulias depressus* (Decapoda): maintaining oxygen, pH and calcium levels optimal for the larvae. *Behavioral Ecology and Sociobiology*, **32**, 11–15.
- FINCHAM, A. G., 1977, Jamaica underground, in G. Wadge and G. Draper (eds) *Special Publication of the Geological Society of Jamaica* (Kingston: Geological Society of Jamaica), 247 pp.
- GUINOT, D., 1988, Les crabes cavernicoles du monde, *Mémoires de Biospéologie*, **15**, 1–40.
- HARTNOLL, R. G., 1964a, The freshwater grapsid crabs of Jamaica, *Proceedings of the Linnean Society London*, **175**, 145–169.
- HARTNOLL, R. G., 1964b, Two cavernicolous decapods from Jamaica, *Crustaceana*, **7**, 78–79.
- HARTNOLL, R. G., 1971, *Sesarma cookei* sp. n., a grapsid crab from Jamaica (Decapoda, Brachyura), *Crustaceana*, **20**, 257–262.
- HOBBS JR, H. H., HOBBS III, H. H. and DANIEL, M. A., 1977, A review of the troglobitic decapod crustaceans of the Americas, *Smithsonian Contributions to Zoology*, **244**, 1–187.
- PECK, S. B., 1975, The invertebrate fauna of tropical American caves, part III: Jamaica, an introduction. *International Journal of Speleology*, **7**, 303–326.
- PECK, S. B., 1992, A synopsis of the invertebrate cave fauna of Jamaica, *NSS Bulletin*, **54**, 37–60.

- PERFIT, M. R. and WILLIAMS, E. E., 1989, Geological constraints and biological retrodictions in the evolution of the Caribbean Sea and its islands, in C. Woods (ed.), *Biogeography of the West Indies: Past, Present and Future* (Gainesville, Florida: Sandhill Crane Press), pp. 47–102.
- PREGILL, G. K. and OLSON, S.L., 1981, Zoogeography of West Indian vertebrates in relation to Pleistocene climatic cycles, *Annual Review of Ecology and Systematics*, **12**, 75–98.
- PRETZMANN, G., 1972, Grundlagen und Ergebnisse der Systematik der Pseudothelphusidae. *Zeitschrift für zoologische Systematik und Evolutionsforschung*, **11**, 196–218.
- RATHBUN, M. J., 1896, Description of a new genus and four new species of crabs from the West Indies. *Proceedings of the United States National Museum*, **19**, 141–144.
- RATHBUN, M. J., 1914, New genera and species of American brachyrhynchous crabs, *Proceedings of the United States National Museum*, **47**, 117–129.
- SCHUH, M., 1995, *Fortpflanzungsanpassungen bei der Besiedlung des Landes: vergleichende Untersuchungen zur Ökologie, Fortpflanzungsbiologie und Larvenphysiologie der semiterrestrischen Armases und Sesarma Jamaikas (Decapoda, Brachyura, Grapsidae)*, unpublished Ph.D. thesis, University of Bielefeld, Germany, 138 pp.
- SYKES, L. R., McCANN, W. R. and KAFKA, A. L., 1982, Motion of Caribbean plate during last 7 million years and implications for earlier Cenozoic movements, *Journal of Geophysical Research*, **87**, 10656–10676.
- TURKAY, M. and DIESEL, R., 1994, Description of a new species of *Sesarma* from Jamaica with notes on its occurrence and biology (Crustacea: Decapoda: Brachyura), *Senckenbergiana biologica*, **74** (1/2), 157–161.