Taxonomic studies of snapping shrimp of the *Alpheus* "Edwardsii" group from the Galápagos Islands (Decapoda: Caridea: Alpheidae)

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Abstract.—The taxonomy of three species of the Alpheus "Edwardsii" group from the Galápagos Islands is discussed. Diagnoses of A. bouvieri A. Milne-Edwards, 1878 and A. hebes Kim & Abele, 1988 are provided. Additional morphological characteristics of A. hebes are discussed. Examination of specimens revealed that A. galapagensis Sivertsen, 1933 is indistinguishable from A. canalis Kim & Abele, 1988. Alpheus galapagensis is redescribed and A. canalis is synonymized with it. Information on natural habitat and living color of these species is provided.

During field studies in 1998 at the Charles Darwin Research Station (CDRS), Isla Santa Cruz, Galápagos, one of us (MKW) collected specimens of *Alpheus* Fabricius, 1798 from the intertidal zone. The specimens represent four species. One of these shrimp was easily identifiable as *A. panamensis* Kingsley, 1878. The identity of the other three, however, were more difficult to establish. The specimens were compared with previously collected material and with descriptions in the literature. Diagnoses of these species are provided, along with new information on morphology, habitat, and living color.

One of the species could be identified as *A. galapagensis* Sivertsen, 1933 or *A. canalis* Kim & Abele, 1988. In 1925, Alf Wollebaek, Director of the Zoological Museum at Oslo, collected intertidal specimens at Isla Floreana (also called Isla Santa Maria or Charles Island), Galapágos. Sivertsen (1933) reported on these specimens, and designated two ovigerous females and one male as *Alpheus strenuus* Dana var. *galapagensis* Sivertsen, 1933. Subsequently, A. H. Banner & D. M. Banner (1966) and D. M. Banner & A. H. Banner (1982), in their discussions of *A. strenuus*, considered *A.*

galapagensis to be a distinct species. Kim & Abele (1988) were the first to use the species name A. galapagensis, yet did not examine any specimens, but based their opinions on Sivertsen's work. We compared our specimens from the Galápagos with the type material of A. galapagensis, paratypes of A. canalis, and additional specimens from western Mexico and the Galápagos. Alpheus galapagensis is redescribed using the paratype specimen, and A. canalis in synonymized with it.

Unless otherwise noted, specimens labeled as CDRS are in the collections of the Charles Darwin Research Station, Isla Santa Cruz, Galápagos. Catalogue numbers for CDRS specimens refer to a photographic catalogue of specimens compiled by Cleveland Hickman, Jr. of Washington and Lee University, Virginia, on behalf of the CDRS. Color data were derived from field notes and from photographs. Additional specimens were borrowed from the National Museum of Natural History, Smithsonian Institution Washington, D.C. (USNM), the Natural History Museum of Los Angeles County (LACM), the University of Southern California (USC), and the Zoological Museum at Oslo (ZMO). Carapace lengths (CL) are given in millimeters. Anatomical definitions follow Kim & Abele (1988).

Alpheus hebes Kim & Abele, 1988 Fig. 1

Alpheus hebes Kim & Abele, 1988:62, fig. 26.

Holotype.—1 male (CL 7.3) USNM 229919, Isla San Salvador, Galápagos, Velero III sta. 333–35, 11 Dec 1935.

Other material examined.-Galápagos: 1 Male (CL 4.1), intertidal rocky area in front of CDRS, S. side Isla Santa Cruz, CDRS 98-599, coll. M. K. Wicksten, 24 Aug 1998, mid-littoral, among rocks and sand; 1 male (CL 2.8), 1 female (CL 4.1), CDRS 98-AA, coll. M. K. Wicksten, 25 Aug 1998, mid-littoral, under rocks; 3 females (CL 2.5-4.5), CDRS 98-BB, coll. by M. K. Wicksten 24 Aug 1998; 1 male (CL 7.7), 1 ovig. female (CL 7.0), USNM 123877, Charles Island, Black Beach, coll. by W. L. Schmitt, 18 Jan 1934; 1 female (CL 2.5), ZMO F.89, Floreana, Post Office Bay, coll. by A. Wollebaek, 9 Jul 1925. Mexico: 11 males (CL 3.0-5.0), 12 females (CL 3.5-6.0), Magdalena Island, Tres Marias Islands, 9 May 1939, USC Field Party sta. 972-39 LACM.

Diagnosis.—Rostrum (Fig. 1A–C) very short, noncarinate, barely extending beyond ocular hoods, distal tip curved down. Ocular hoods separated from rostrum by very shallow rounded depression. Telson (Fig. 1E, F) with posterior margins rounded, armed with a pair of spines at each lateral end; lateralmost posterior telson spine curved upward in shape, not straight.

First segment of antennular peduncle (Fig. 1A–C) short; carina on ventral margin very shallow and broadly rounded (Fig. 1D). Second and third segments about equal in length to exposed part of first segment.

First percopods with merus lacking spine on distoventral margin. Major first percopod (Fig. 1G, H) with fingers arrayed with sparsely arranged tufts of setae; palm smooth, about 2.3 times long as high. Minor first pereopod (Fig. 1I) with fingers of chela as long as palm; fingers in male strongly balaeniceps on both inner and outer faces, not balaeniceps in female.

Second pereopod (Fig. 1J) with carpal articles with ratio 10:6:3:3:5.5. Chela about equal in length to proximal carpal article. Third and fourth pereopods (Fig. 1K, L) with movable spine on ischium. Fifth pereopod (Fig. 1M) with ischium without spine.

Color in life.—Chelae orange-brown, progressively darker towards bases of fingers, tips of fingers white. Much of body and legs light gray to green, dorsal area of carapace dark brown with U-shaped orange mark posterior to stomach. Orbital areas white, rostrum brown. Abdomen with transverse bars of dark gray-green to black alternating with light blue-gray bars, tail fan dark olive to black, becoming lighter and fading to white at posterior end, outer edge of uropods red. Red patches on bases of antennae, walking legs and ventrolateral parts of abdominal somites.

Habitat.—mid-littoral, under rocks on sand.

Size.—CL up to 11 mm.

Range.—Eastern Pacific from Baja California to Ecuador, Galapagos Islands.

Remarks.—This species is similar to A. bouvieri A. Milne-Edwards, 1878, but is distinguished by the shape of the rostrum (curved down rather than straight), and by the presence of movable spines on the ischia of the third and fourth pereopods. This species has a rostrum similar to that of A. chilensis Coutière, 1902 (in Lenz 1902), but can be distinguished by the lack of a spine on the distoventral margin of the merus of the first percopods. Kim & Abele (1988) depicted the minor chela in A. chilensis Holthuis (1952) as being weakly balaeniceps in males. However, the balaeniceps character is well developed in both A. chilensis and A. bouvieri. This species is also distinguishable from A. leviusculus Dana, 1852 by the shape of the rostrum, by the absence of spine on the merus of the first



Fig. 1. Alpheus hebes Kim & Abele, 1988. Male CDRS 98-599 (CL = 4.1 mm). A, carapace, lateral view (with third maxilliped); B, anterior region of same, dorsolateral view; C, same, dorsal view; D, carina below right first antennular segment; E, abdomen, lateral view; F, telson and uropods, dorsal view; G, left major first cheliped, inner face; H, same, outer face; I, right minor cheliped; J, left second pereopod; K, right third pereopod; L, right fourth pereopod; M, right fifth pereopod. Scale indicates 5 mm.

percopod, and by the degree of the balaeniceps condition in the minor chela.

Alpheus hebes can also be distinguished from the aforementioned species by the shape of the posterolateral spine on telson, which is curved dorsally rather than straight. This character was not included in the original description by Kim & Abele (1988), but was found to be present in the holotype of A. hebes and on all other specimens we have examined.

Examination of specimens used by Chace (1972:64) has confirmed their conspecificity with *A. hebes.* Chace referred to these specimens (USNM 123877) in his remarks on *A. bouvieri* and related species when he mentioned "another, possibly undescribed

species in the Galapagos Islands . . . a male and an ovigerous female without major chelipeds in the Smithsonian collections."

A small and badly damaged female specimen of A. hebes was discovered in the lot containing Sivertsen's types of Alpheus galapagensis. This specimen is not accounted for in the label, and consists of a cephalothorax, and a detached minor claw and abdomen. Evidently it had remained undetected until the present.

Alpheus bouvieri A. Milne-Edwards, 1878 Fig. 2

Alpheus Edwardsii.—Dana, 1852:542; 1855:11, pl. 34: fig. 2a-f.—Pocock, 1890:518 (in part). [Not Athanas Edwardsii Audouin, 1826]

- Alpheus Bouvieri A. Milne-Edwards, 1878: 231.—Coutière, 1898:131, fig. 1 (in part); 1899:15, fig. 291; 1905:907, pl. 85: fig. 44 (in part).
- Alpheus heterochaelis.—Kingsley, 1878: 194 (in part).—Rathbun, 1900a:152 (in part).—Luederwaldt, 1919:429 (in part). [Not Alpheus heterochaelis Say, 1818]
- Alpheus edwardsii.—Bate, 1888:542, pl. 97: fig. 1.
- Alpheus Edwardsii.—De Man, 1899:311 (in part).
- Alpheus bouvieri.—Rathbun, 1900b:312 (in part).—Sourie, 1954:253.—Forest & Guinot, 1958:9.—Ribeiro, 1964:5.— Crosnier & Forest, 1965:606; 1966:273, fig. 22a–j.—Uschakov, 1970:444.— Fausto-Filho & Furtado, 1970:286.— Chace, 1972:63.—Fausto-Filho, 1974:5; 1975:79.—Gore et al., 1978:225.—Christoffersen, 1979:303, figs. 2–5.—Kim & Abele, 1988:58, fig. 24.
- Alpheus bouvieri var. chilensis.—Schmitt, 1924a:162. [Not Alpheus bouvieri chilensis Coutière in Lenz, 1902].
- Crangon [Alpheus] Bouvieri.—Monod, 1933:462, fig. 1A–C.

Material examined.—Galápagos: 6 females (CL 3.0–5.5) intertidal rocky area in front of CDRS, S. side Isla Santa Cruz, CDRS 98-578, coll. M. K. Wicksten, 23 Aug 1998, midlittoral, among rocks and sand; 1 female (CL 5.5) USNM 57710, Eden Island, Williams Galápagos Expedition, 6 Apr 1923; 1 male (CL 6.0), 1 female (CL 6.0), USNM 110395, Clipperton Island, coll. C. R. Harrison, 10–15 Sep 1958. Mexico: 1 male (CL 3.7), 8 females (CL 3.0–5.5), Magdalena Island, Tres Marias Islands, 9 May 1939, USC Field Party station 972-39 LACM.

Diagnosis.—Rostrum (Fig. 2A–C) carinate, short, not reaching 0.5 length of first antennular segment, extending posteriorly about as far as eyestalks. Ocular hoods separated from rostrum by shallow rostro-orbital depressions.

First percopods with merus unarmed distoventrally. Major chela (Fig. 2E) thick; weakly setose. Minor chela sexually dimorphic, bearing balaeniceps-shaped setose crest on dactyl and accessory crest on opposable margin in males. Carpus of second percopods (Fig. 2F) with articles in ratio 10:4.3:3.3:3.0:4.3. Third (Fig. 2G), fourth, and fifth percopods without movable spine on ischium. Second pleopod of male with appendix masculina overreaching appendix interna. Telson (Fig. 2D) about 1.6 times as long as wide; uropodal exopod with transverse suture forming two conspicuous rounded lobes.

Color in life.—Chelae brown, progressively darker towards bases of fingers, tips of fingers white. Much of body light brown, legs pale. Abdomen with narrow transverse bars of medium brown alternating with pale brown areas, tail fan medium brown and gray, fading to pale brown at posterior end.

Remarks.-Alpheus bouvieri can be distinguished from similar species by the following combination of characters: straight tip of the rostrum, absence of a spine of the merus of the first pereopod, presence of a balaeniceps minor chela in the male, and absence of movable spines on the ischia of the third, fourth, and fifth pereopods. Alpheus bouvieri and A. hebes may be confused with each other due to similarities in major and minor chela shape, and transverse suture of the exopodal uropod. This species can be distinguished from A. hebes by the shape of the rostrum (straight rather than downcurved), and by the absence of movable spines on the ischia of the third and fourth pereopods.

Alpheus bouvieri has been treated as a subspecies of A. leviusculus by D.H. Banner & A.H. Banner (1982). However, justification of A. bouvieri as a distinct species was provided by Kim & Abele (1988).



Fig. 2. Alpheus bouvieri A. Milne-Edwards, 1878. Female CDRS 98-578 (CL = 4.8 mm). A, carapace, lateral view (with third maxilliped); B, anterior region of same, dorsolateral view; C, same, dorsal view; D, telson and uropods, dorsal view; E, right major cheliped, inner face; F, left second pereopod; G, left third pereopod. Scale indicates 5 mm.

Alpheus galapagensis Sivertsen, 1933 Fig. 3

- Alpheus strenuus var. galapagensis Sivertsen, 1933:3, pl. 1, figs. 1–5.
- Alpheus strenuus galapagensis.—A. H. Banner & D. M. Banner, 1966:184; D. M. Banner & A. H. Banner, 1982:228.
- Alpheus canalis Kim & Abele, 1988:72, fig. 30.
- Alpheus galapagensis.—Kim & Abele, 1988:102, fig. 43.

Paratypes.—2 ovigerous females (CL 14.5, 10.5), ZMO F.89, Isla Floreana, Post Office Bay, shore, Galapagos Islands, coll. A. Wollebaek, 25 September 1925.

Other material examined.—Galágapos: 1 ovigerous female (CL 7.6), Punta Espinosa, Isla Fernandina near Academy Bay, Isla Santa Cruz, coll. G. M. Wellington, 18 Sep 1974, LACM; 1 female (CL 3.4 mm), Academy Bay, near CDRS, CDRS 98-596, coll. M. K. Wicksten, 24 Aug 1998; 1 fe-

male (CL 3.9 mm), same locality, CDRS 98-598; 1 female (CL 6.8mm), same locality, 25 Aug 1998, CDRS 98-618; 1 female (CL 9.2 mm), same locality, sandy tide pool, 25 Aug 1998, CDRS 98-619; 1 female (CL 13.5), Punta Espinosa, Isla Fernandina near Academy Bay, Isla Santa Cruz, CDRS 99-42, coll. C. P. Hickman, 2 Jun 1999. Mexico: 1 male (CL 12.0), 1 ovigerous female (CL 13.0), 1 juvenile (CL 5.5), USNM 229925, San Francisco Island, Baja California, Velero III sta. 518-36, 25 Feb 1936 (paratypes of A. canalis); 10 males (CL 7.0-15.0), 5 females (CL 12.0-15.0), Guaymas Bay, Sonora, Velero III sta. 1041-40, 23 Jan 1940 LACM; 1 male (CL 12.5), Punta Chile, Mazatlán, Sinaloa, in tide pool, Texas A&M University Department of Biology teaching collection, coll. M. K. Wicksten, 8 Jan 1982.

Description of larger female paratype specimen.—Rostrum (Fig. 3A–C) acute, reaching 0.5 times length of exposed part of first article of antennular peduncle. Rostral carina narrowly rounded dorsally; extending posteriorly past eyes, joining carapace at broad angle when viewed from side. Ocular hoods separated from rostral carina by shallow rounded depressions.

Telson (Fig. 3E) about 1.6 times as long as wide, with 2 pairs of dorsal spines, and bearing longitudinal median depression on dorsal surface. Posterior margin rounded, armed with a pair of spines at each angle.

Antennular peduncle (Fig. 3A–D) with first segment short; shallow carina on ventral margin (Fig. 3D) subtriangular, with rounded apex (see *Remarks*). Second segment long, about 1.8 times length of exposed part of first segment and about 2.0 times length of third. Stylocerite (Fig. 3A– C) barely reaching end of first antennular segment.

Scaphocerite (Fig. 3A–C) about 2.8 times as long as broad. Distal spine reaching to end of or slightly exceeding third segment of antennular peduncle, much exceeding blade; blade reaching 0.5 times length of third segment. Carpocerite (Fig. 3A–C) barely longer than third segment of antennular peduncle. Basicerite with sharp spine.

Major first percopod (Fig. 3F, G) with movable finger regularly arched in profile except for very slight depression on upper margin near articulation, finger broadly rounded at tip; tip exceeding immovable finger. Both fingers with numerous tufts of setae. Palm about 2.35 times as long as high; superior transverse groove present, proximal shoulder vertical to groove. Superior outer palmar depression large and well-defined, extending to and encompassing oblique suture. Superior inner palmar depression extending proximally and fading toward middle of palm. Inner face of palm with deep longitudinal suture present near top margin at middle of palm; inferior transverse groove deep, slightly directed distally; proximal shoulder rounded and slanted distally. Inferior outer palmar depression narrow, obliquely inverse Vshaped. Inferior inner palmar depression broad. Inner face of palm with shallow longitudinal depression near inferior margin of palm. Merus about 1.8 times as long as wide, with spine on distoventral margin.

Minor first pereopod (Fig. 3H) with fingers of chela about as long as palm; setose distally. Setae pattern variable (fingers weakly balaeniceps in type specimens, but see *Remarks*). Palm with well-defined oblique suture.

Second percopod (Fig. 3I) with carpus subdivided into five articles decreasing in length (numbered from proximal end) 1, 2, 5, 3 = 4; articles with ratio approximately equal to 10:6:4:4:5. Finger tips with curved tufts of setae.

Third percopod (Fig. 3J) with merus about 1.6 times length of carpus; propodus about 1.1 times length of carpus, with 8 sets of spines present more or less in double rows; ischium with very small spine apressed and laying in a small rounded depression (see *Remarks*). Fourth percopod similar to third. Fifth percopod with propodus bearing dense combs of setae along distal 0.6 of length; ischium without spine.

Color in life (from field notes and photographs of CDRS specimens).—Upper surface distinctly dappled with faint grayish spots on pea-green to gray background, appearing dull green at distance. Lower surface white, tip of tail fan also white. Abdomen with faint grayish bands running length of lateral surfaces. Major chela darker, tips of fingers white. Minor chela green fading to white at tips of fingers. Walking legs blotched with gray and white. This color pattern is very similar to that observed in the field by MKW of the specimen from Mazatlan.

Habitat.—The specimens from Isla Santa Cruz were taken among tide pools in a lava flow. The area was exposed to strong surf at high tide. All were found in the mid and lower intertidal zone. Except for specimen CDRS 98-619, the specimens were collected under small rocks resting on sand amid small tide pools. Specimen CDRS 98-619 was found under a rock in a large sandy



Fig. 3. Alpheus galapagensis Sivertson, 1933. Female paratype ZMO F.89 (CL = 14.5 mm). A, carapace, lateral view (with third maxilliped); B, anterior region of same, dorsolateral view; C, same, dorsal view; D, carina below right first antennular segment; E, telson and uropods, dorsal view; F, right major cheliped, inner face; G, same, outer face; H, left minor cheliped; I, right second pereopod; J, right third pereopod. Scale indicates 5 mm.

tide pool between two predominately rocky areas.

Remarks.—Our specimens agree in general with the brief description given by Sivertsen (1933), and the subsequent comments by D. H. Banner & A. H. Banner (1982) and Kim & Abele (1988). The type material originally contained three specimens, one male and two females. We were informed, by Cathrine Vollelv at the Museum of Oslo, that the male specimen was lost.

In Sivertsen's (1933:3, pl. 1, figs. 1–5) illustrations, the minor chela is depicted as simple rather than balaeniceps-shaped, and the third pereopod is depicted as lacking a spine on the ischium. This was the basis by which previous authors recognized this as a distinct species, rather than a subspecies of *A. strenuus*. However, these specimens have a small movable spine on the ischium of the third pereopod. Furthermore, the minor claws in the type material have an incom-

plete balaeniceps condition, a rare feature in females of *Alpheus* and characteristic to only a few species, including *A. strenuus*. The minor chelae of the paratype specimens were detached and lacked a distoventral spine on the merus (Fig. 3H), which contrasts the presence of this spine on the major chelae of the paratype specimens (Fig. 3F, G). This, plus the presence of extra detached legs in the lot, casts some doubt as to whether these minor chelae correspond to the two female paratype specimens.

This species can be distinguished from A. *strenuus* Dana by the presence of a median longitudinal depression on the dorsal surface of the telson, a feature previously known from A. *nuttingi* (Schmitt 1924b). This species also differs from A. *strenuus* by the following proportions as provided by D. H. Banner & A. H. Banner (1982, for A. *strenuus strenuus*): the ratio of carpal segments of the second pereopod is 10:6:4:4:5 in the present species, versus 10:10:3:3:6 in

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A. strenuus; the second segment of the antennular peduncle of this species is longer in proportion than that of A. strenuus; and the antennal blade is much shorter in proportion to the antennal spine in A. galapagensis. Furthermore, the movable spine in the ischium of the third pereopod in A. strenuus is depicted by D. H. Banner & A. H. Banner (1982) as conspicuous, whereas it is very small in A. galapagensis.

Examination of other specimens revealed variability in setal pattern of the minor chelae. Most of the larger specimens (apart from paratypes) showed fingers as densely and evenly setose throughout the distal third of length. However, some of the specimens from Sonora, Mexico had the setae arranged as a row of tufts on both the fixed and movable fingers, a feature that approaches the condition of the paratypes.

The movable spines on the ischium of the third and fourth pereopods are minute and difficult to see. On the specimen illustrated, the tiny movable spine was present on the left third percopod but was undetectable on the right (the right third pereopod is illustrated with the spine as it is present on the left side). Additional disarticulated pereopods indicate that at least a third specimen was present in the type lot, probably the missing male. One large pereopod, possibly the third, conforms in every way the description above. Two smaller detached pereopods have a conspicuous spine on the ischium which does not match either the legs on the specimens or the other unattached legs, and may have belonged to another species.

Because of the agreement of morphological features, we consider *Alpheus canalis* Kim & Abele, 1988 to be a junior synonym of *Alpheus galapagensis* Sivertsen, 1933. Kim & Abele (1988), in their key to species of *Alpheus*, stated that *A. canalis* and *A. galapagensis* could be distinguished by the shape of the anterior margin between the base of the rostrum and middle of ocular hoods, and by the length of the distal spine of the scaphocerite. However, examination of additional specimens reveals complete intergradation of these features within populations, as well as for other antennal appendages, ventral carina on first antennular segment, major chelae, walking legs, body proportions, and telson.

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