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THE CAVERNICOLOUS FAUNA OF HAWAIIAN LAVA TUBES
8. Terrestrial Amphipoda (Talitridae), including a new genus and species with notes on its biology[1]

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Abstract: A remarkable blind troglobitic terrestrial amphipod, *Spelaeorchestia koloana,* n. g. and n. sp. is described from material collected in lava tubes and a limestone cave on the island of Kauai, Hawaiian Islands. It is allied to a diverse complex of surface species which are endemic to the Hawaiian Islands. Notes on its biology are included. Two tropicopolitan "tramp" species, *Talitroides alluaudi* Chevreux and *T. topitotum* Burt, are occasionally found in caves. This is the first record of these 2 introduced species in the Hawaiian Islands.

As part of a long-term IBP faunal inventory of caves, lava tubes, and underground caverns of the Hawaiian Islands (Howarth 1973), a number of interesting insects, arachnids, oniscoidean isopods and other terrestrial invertebrates were collected from a lava tube near Koloa, Kauai. Among the presumably troglobitic arthropods were specimens of a moderately large, blind, white amphipod crustacean. These animals were subsequently identified as a very distinctive new talitrid species, allied to *Parorchestia hawaiensis* (Dana) previously known from the Hawaiian Islands (Barnard 1955). Distinctive morphological features of this unique subterranean species justify its separate generic recognition, as recently instituted in other Indo-Pacific land amphipods (Bousfield 1971). The species is herewith described as *Spelaeorchestia koloana,* n. genus, n. sp. FIG. 1).

Family TALITRIDAE Bulycheva, 1957

Genus **SPELAEORCHESTIA** Bousfield & Howarth, **n. genus**

Diagnosis: Sexes closely similar, not conspicuously dimorphic; gnathopod 1 weakly subchelate, gnathopod 2 minutely chelate in both sexes. Maxilliped palp with terminal (4th) segment. Also distinguished by the following characters: Antenna 1, peduncular segment 3 longest, flagellum geniculate at segments 1 and 2; head shallow, buccal mass deep, prognathous; maxilliped palp, segments broader than wide; gnathopod 2, segment 2 linear, segment 3 longer than 4 (♀ and ♂); peraeopods, especially 6 and 7, very elongate, dactyls slender, attenuated; all pleopods very reduced, rami vestigial or lacking; uropods 1 and 2 with well developed prepeduncles, some terminal ramal spines elongate; telson, apex cleft; gills 2 and 6 elongate, lobate; brood plates vestigial or lacking in mature ♀.

Type-species: *S. koloana* Bousfield & Howarth, n. sp.

The morphotype of the new genus is one that might be predicted on the basis of remaining unrecognized combinations of gnathopod type in terrestrial amphipods. Thus animals with gnathopod 1 subchelate, and gnathopod 2 "mittenlike" in both sexes (at maturity) are technically generically distinct from all other recognized genera, but appear to have been derived from *Orchestia* or *Parorchestia* progenitors by neotenic loss (or failure to develop) of the

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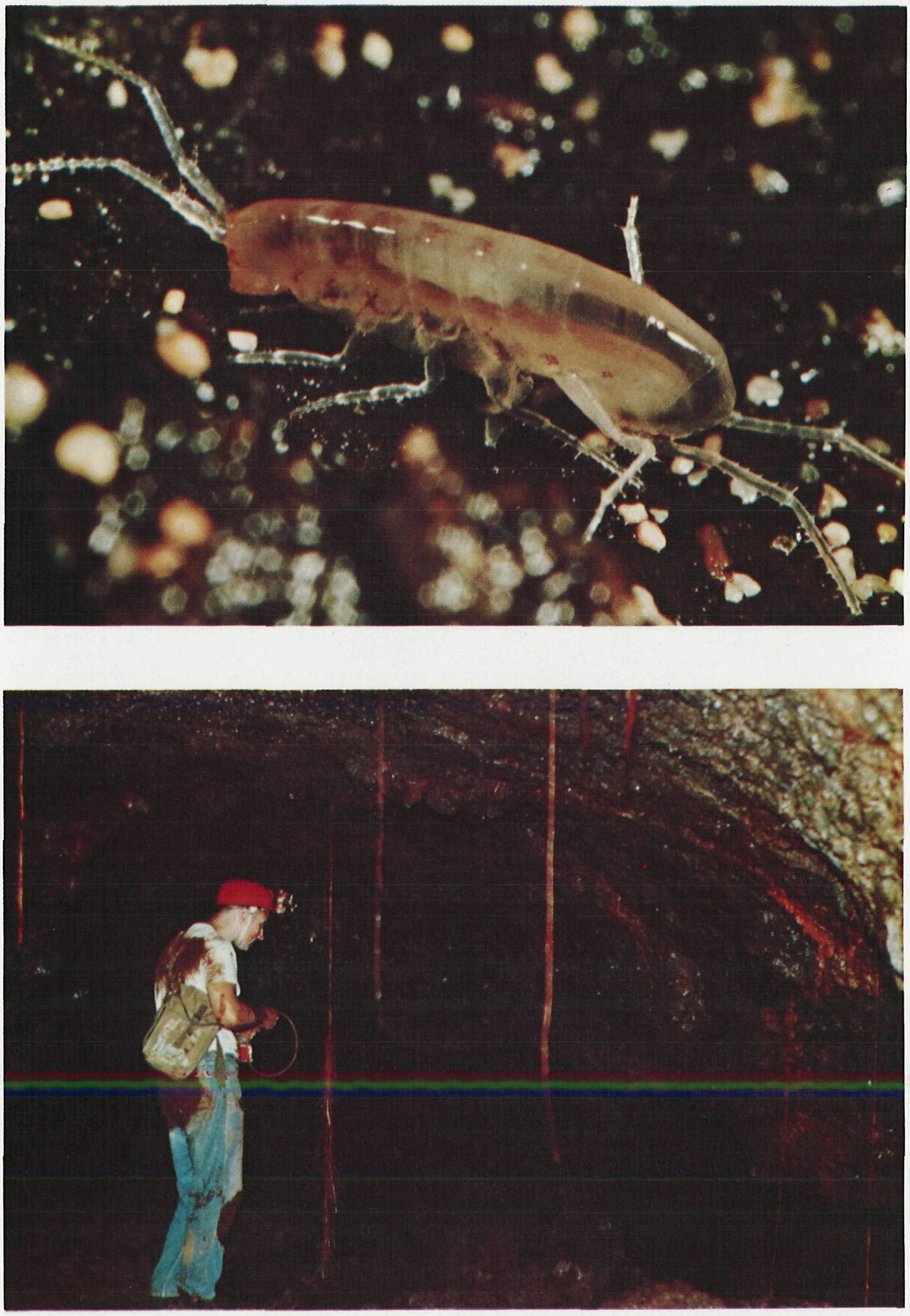

FIG. 1. Top: Living *Spelaeorchestia koloana,* n. genus, n. sp.; note hyaline integument and visible gut (Photo by W. P. Mull). Bottom: Type-locality; roots are probably of the tree *Pithecellobium dulce* (Photo by N. C. Howarth).

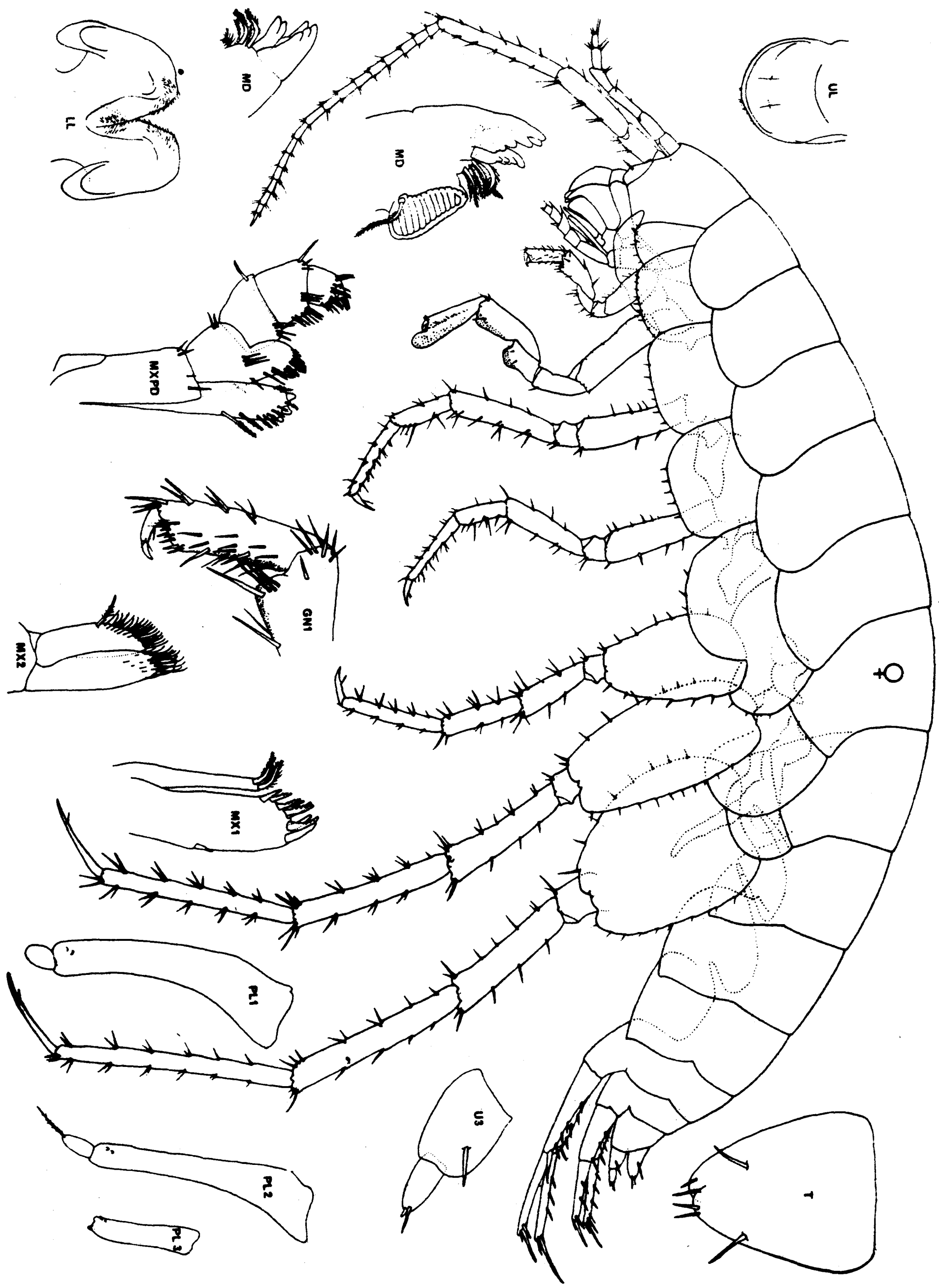

FIG. 2. *Spelaeorchestia koloana*, n. genus, n. sp., ♀ (holotype).

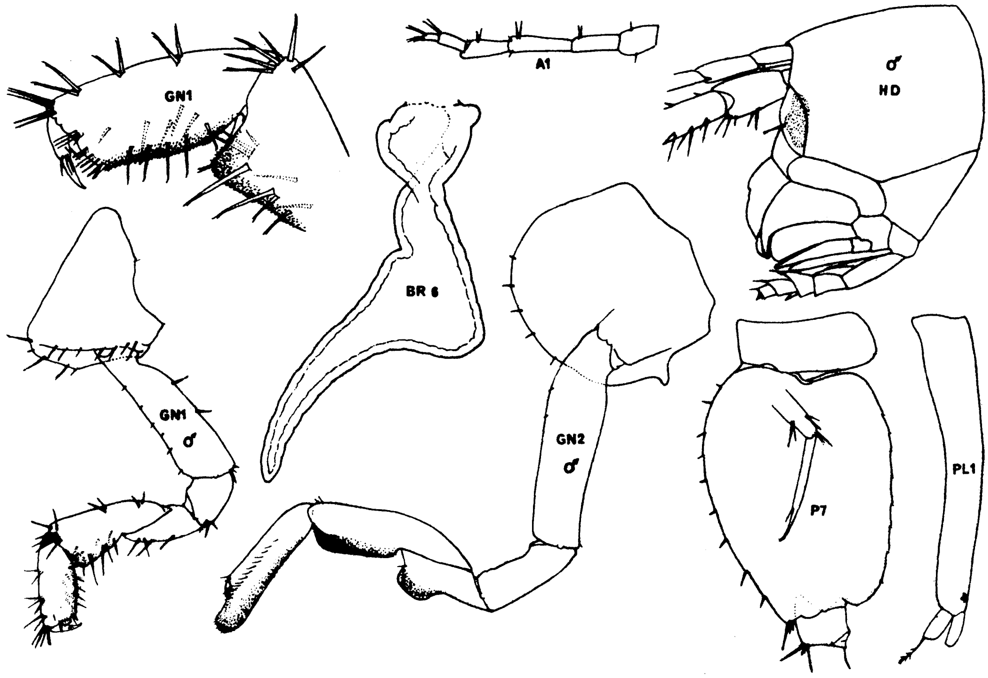

FIG. 3. *Spelaeorchestia koloana*, n. genus, n. sp., ♂.

powerfully subchelate condition in gnathopod 2 of the male. Hurley (1957) has already described new terrestrial species of *"Orchestia"* from New Zealand (e.g., *O. simularis, O. rubroannulata, O. improvisa)* showing various phases or stages of the present combination of gnathopod types in males and females. That author, however, declined to recognize these major distinctions at the generic level.

Spelaeorchestia koloana Bousfield & Howarth, **n. sp.** FIG. 1–3

Diagnosis: A blind, hyaline, slender-bodied, terrestrial amphipod with extremely elongate and richly spinose peraeopods and uropods, adapted for troglobitic existence.

♀. FIG. 2. Length, 10.0 mm. Adult (larviparous). Antenna 1, flagellum 3-segmented, apical segment with 2 groups of terminal setae: peduncular segment 1 (face) with 1 stout spine. Antenna 2 slender, elongate, flagellum 15 to 18-segmented, longer than peduncle. Eye facets and pigment lacking (small narrow elliptical eye "trace" faintly visible in some specimens). Mandible, left lacinia mobilis bidentate; 2 accessory blades stout, others slender. Maxilliped, inner plate apically with 2 stout and 1 small conical spine-teeth; palp segment 3 broader than long, terminal (4th) segment very small, with 2 unequal apical spines. Gnathopod 1 relatively small; segment 6 not longer than 5, elongate rectangular, palm distinct, convex, exceeded by closed dactyl. Gnathopod 2, segment 2 not expanded anteriorly, anterior margin with 5–6 widely spaced fine setae; segment 6 not longer than 5, distal pellucid lobe extending nearly 1/3 length of segment beyond minute dactyl. Peraeopod 4 nearly equal to 3, dactyl simple, not elongate. Peraeopod 5, coxal plate very broad, anterior lobe smoothly rounding below, slightly deeper than posterior lobe; basis relatively narrow, evenly shallow-convex behind. Peraeopod 6, coxal plate very deep behind, deeper than broad; basis elongate-ovate; segments 4–6 slender, progressively longer; dactyl very slender, length nearly equal to 1/2 segment 6. Peraeopod 7, basis broadly expanded, shallowly and evenly convex behind, more sharply convex in front; dactyl about 40% length of segment 6. Gill of peraeopod 2 extending anterad of coxal plate 1, may cover extreme lower proximal part of head; gill on peraeopod 5 bilobed, proximal lobe simple, directed medially. Gill on peraeopod 6 with narrow distal lobe attenuating anteroventrally. Brood plates reduced to minute lobes on P3–5, lacking on P2 in largest specimens. Abdominal side plates 1–3, posterior margins smooth, slightly sinuous, hind corners subacuminate. Pleopods 1 and 2 very reduced, subequal, single ramus (rarely 2 rami) reduced to a knob, optionally bearing an apical seta; pleopod 3 much shorter, stump-like, ramus reduced to a minute nubbin, or lacking. Uropod 1, peduncular margins spinose: outer ramus marginally smooth, inner with 3–4 marginal spines; apical spines elongate, longest attaining 1/2 length of ramus; inter-ramal spine equal to 1/3 length ramus. Uropod 2, rami subequal, both rami marginally spinose. Uropod 3, peduncle with 1 posterolateral spine; ramus shorter, with 2 unequal apical spines. Telson large, with single lateral and 2 apical spines on each side.

♂. (FIG. 3) Length, 7.5 mm. Grossly very similar to ♀. Head (in some specimens), antennal segment 1 with irregularly shaped or subelliptical subcuticular area (possibly antennal gland). Gnathopod 1, segment 2 with 2 stout posterior marginal spines; posterior "blister" weakly developed on segment 5, lacking on segment 4; segment 6 slightly shorter than segment 5; dactyl slightly exceeding spine at palmar angle. Gnathopod 2, segment 2 linear, anterior margin with a few proximal fine setae; segment 6 sublinear, slightly shorter than segment 5; segment 3 longer than 4. Peraeopod 7, basis less posteriorly expanded than in ♀ specimens examined. Gill on P6, narrow distal lobe curving anteroventrally, tip reaching segment 3 of peraeopod 7. Pleopods 1 and 2, peduncles longer and more slender than in ♀, extending below margins of epimeral plates; pleopods usually biramous, rami 1-segmented, outer ramus larger than inner, with single apical plumose seta. Uropod 1, inner ramus with 4–5 marginal spines.

Distinguished from ♀ by minute paired knob-like penis papillae on ventral surface of peraeon segment 7, between coxae of peraeopod 7; by the absence of brood plate rudiments; in gnathopod 1 by the relatively short, broad, posteriorly pilose segment 6 and tumescent and pilose posterior margin of segment 5; by the more elongate and more frequently biramous pleopods 1 and 2; and generally more spinose armature of uropod 1, inner ramus.

Distribution: Known only from caves near Koloa, Kauai.

Holotype ♀ (BISHOP S8506), length 10.0 mm, HAWAIIAN IS.: Kauai I., Koloa, Koloa Cave #2, 37 m, 11.VIII.1971, dark zone on floor, F. G. Howarth. Slide mount. Allotype ♂ (BISHOP S8507), length 8.5 mm, Koloa Cave #1, 37 m, 24.VI.1972, F. G. Howarth & W. C. Gagné. Slide

Paratypes, 10 ♀♀, 8 ♂♂, as follows: 1 ♀, 9.7 mm, 2 instar II, 4.4 mm, 1 instar I, 2.9 mm, same data as holotype; 1 ♀, 9.0 mm, 4 immature (imm.) ♀♀, 6.0–7.8 mm, 3 imm., 4.0–4.5 mm, in rotting wood; 1 ♀, 8.2 mm, F. G. & N. C. Howarth; 5 ♂♂, 7.0–8.8 mm, 2 ♀♀, 6.7, 8.4 mm, 1 imm., 5.2 mm, 20.I.1973, E. L. Bousfield & F. G. Howarth. 4 imm. ♀♀, 6.8–7.5 mm, 2 imm. ♂♂, 7.2 mm, 2 imm., 4.5–5.5 mm, 1 ♀, 9.0 mm, on tree root, all same data as allotype; 3 ♀♀, 7.0–9.6 mm, 3 ♂♂, 5.6–7.4 mm, upper section, 25.VI.1972. 1 ♀, 8.8 mm, 4 imm., 5.0–6.3 mm, Koloa Cave #3, 25 m, 24.VI.1972, F. G. Howarth & W. C. Gagné.

Other records: 1 ♂, 7.7 mm, 4 ♀♀ (2 ovigerous), 7–8 mm (diam. of eggs 0.5 mm), 5 imm., about 4.0 mm, Kauai I., Koloa, Limestone Quarry Cave, Passage D, 1–5 m, 5.VI.1973, F. G. Howarth & R. C. A. Rice; 3 imm. ♀♀, 6.5–7.2 mm, 3 imm., 5–6 mm, Passage D and E; 4 ♀♀, 7.5–8.2 mm, 5 imm. ♀♀, 6.5–7.0 mm, 8 imm., 3.0–5.5 mm, Passage F.

OTHER TERRESTRIAL AMPHIPODS FROM HAWAIIAN CAVES

Talitroides alluaudi Chevreux

Talitroides alluaudi Chevreux, 1901, Mem. Soc. Zool. France **14**: 389.

Distribution: Introduced to Hawaii by commerce. A nearly tropicopolitan species.

Cave records: 1 imm. ♀, HAWAIIAN IS.: Kauai I., Koloa, Koloa Cave #3, 25 m, 24.VI.1972, F. G. Howarth & W. C. Gagné. 17 specimens, mostly non-adult, Limestone Quarry Cave, Passages D, E, & F, 1–5 m, 5.VI.1973, F. G. Howarth & R. C. A. Rice. 7 specimens (mostly ♀), Knudsen Cave #1, 45 m, 23.VI.1972, F. G. Howarth & W. C. Gagné. 2 imm. ♀♀, Knudsen Cave #2, 45 m, 23.VI.1972, F. G. Howarth & W. C. Gagné. Ca 12 specimens, HAWAIIAN IS.: Oahu I.: Honolulu, Judd Street Cave, 30 m, 21.V.1972, F. G. & N. C. Howarth, F. D. Stone.

Talitroides topitotum Burt

Talitroides topitotum Burt, 1934, Spolia Zeylanica (Ceylon J. Sci., Section B) **18**(2): 181-91.

Distribution: Nearly cosmopolitan tramp species. Originally described from India, introduced to Hawaii by commerce where it is now the dominant leaf litter amphipod species.

Cave records: 2 imm. ♀♀, HAWAIIAN IS.: Kauai I., Koloa, Limestone Quarry Cave, 1–5 m, 21.VI.1972, dark zone, F. G. Howarth. 1 ovigerous ♀, 14 imm., 2 m, deep twilight, berlese debris, F. G. Howarth & W. C. Gagné. 6 specimens, HAWAIIAN IS.: Hawaii I., Honokaa, Hamakua Forest Reserve Caves, 600 m, 24.IV.1972, twilight zones, F. G. Howarth & J. Jacobi.

BIOLOGY OF SPELAEORCHESTIA KOLOANA

It is with some trepidation that we make these Kauai cave animals known, as their continued survival is tenuous. Over-collecting or disturbance of their habitat may send them to extinction. *S. koloana* should be considered rare and endangered. All its cave localities are in close juxtaposition to one another and isolated from any similar cave area. The major portion of Kauai is on the order of 5 to 7 million years old and spaces in basaltic lava have long since weathered away to deep soil. It is probable that the caves are a window to a much larger amphipod population existing in the cracks and vesicles in the Koloa lavas. *S. koloana* is, however, restricted to this relatively small area. The eyeless big-eyed hunting spider, *Adelocosa anops* Gertsch, is much more restricted (Gertsch 1973); the 2 species are among the most bizarre cave animals known in the world and are worthy of protection.

Description of caves

S. koloana is known from 4 caves all less than 50 m elevation within a small area on the southern coastal plain on the island of Kauai. Three of the caves are lava tubes within the same flow system and separated from each other by less than 200 m. The other is a limestone cave 7 km from the lava tubes. There are also several other lava tubes in the Koloa eruption series near Koloa, but most of these are short, dry remnant sections of once longer caves.

The caves are warm lowland caves. The temperature in the dark zone is relatively constant at 25°±1°C. There is no diurnal temperature cycle and probably only a minor annual fluctuation, but the data are too incomplete to reveal an annual cycle.

Lava tubes: The lava tubes were formed in a single flow of the Koloa volcanic series. The Koloa lavas are posterosional lavas; i.e., they commenced erupting 1.5 million years after the last flow of the building of the Kauai shield. The Koloa flows were not continuous but erupted off and on for about 1 million years. They cover about 1/2 the surface of eastern Kauai.

The ages of the lava tubes are unknown but they are not younger than late Pleistocene. The youngest Koloa flow, dated by potassium-argon determination, is 0.6 million years old (Macdonald & Abbott 1970). On the basis of the degree of preservation of the lava tubes, this date seems too old. They are, however, significantly older than the limestone cave, since the dunes in which the limestone cave formed rest on this flow.

The time of initial colonization of caves by the ancestor of *S. koloana* may be much earlier than the formation of these lava tubes. It is possible that the amphipod could have moved from older to younger caves during the Koloa series of eruptions, as is being done at the present time on the younger island of Hawaii by *Oliarus polyphemus* Fennah, *Lycosa howarthi* Gertsch and other cave animals (Howarth 1973).

The 3 lava tubes have a weathered clay soil on the floor. This soil has washed in through the entrances and cracks in the lava over the millennia. Occasionally, parts of the original lava floor are exposed. The lava of the wall is vesicular and fractured. Both the fractures and vesicles are partially filled with clay which confirms the great age.

Koloa Cave #1 is a relatively large lava tube with a large skylight entrance in midportion. A walkway passage leads downslope approximately 150 m and ends in a crawlway. The floor is composed of a thick layer of clay. The drying effect of the large entrance is noticable. However, during periods of rain or heavy irrigation of nearby sugarcane fields the seepage makes the end of the passage wet. The upslope section of the cave continues approximately 100m as a low crawlway. The small passage allows less evaporation and is wetter than the downslope section.

Koloa Cave #2 (FIG. 1) is the deepest and wettest lava tube known in the Koloa area. The cave trends downslope from the small entrance 150 m to a final muddy crawlway. The passage widens into small rooms separated by narrow low passages, so that evaporation from the entrance is minimal. Seepage is supplied by both rain and irrigation water. In both the downslope section of Koloa Cave #1 and in Koloa Cave #2, there are indications of stream activity in the clay floor.

Koloa Cave #3 is a short section of lava tube approximately 50 m long with a small entrance at each end. The passage is sinuous, which restricts air motion between the entrances and restricts the amount of evaporation. The population of amphipods in this cave appears tenuous.

Limestone cave: The limestone cave is a large elevated sea cave with subsequent erosion by a still-active, freshwater stream. It was formed in an extremely hard, calcareous sandstone hill. The hill is a well-cemented calcareous sand dune, probably formed during the Waipio Stand of the sea, which is undated but older than 120,000 years. The dune rests on and is thus younger than the Koloa lavas. The sea cave must have formed during the later higher stands of the sea, possibly the Waimanalo Stand at 7.6 meters above present level and dated at 120,000 years old (Ku et al. 1974). The entrance, which is at the bottom of a large sinkhole, opens into a large high room with numerous upper levels typical of erosion by the sea. A lower level stream passage cuts through the talus at the back of the room and the low solution passage continues approximately 40 m to a sump. The floor is composed of fine calcareous sand with piles of stream-deposited organic debris. In parts of the stream passage the substrate is a clayey mud.

Distribution in caves

The Hawaiian cave ecosystem can usually be divided into 4 zones (Howarth 1973). These are as follows: the entrance zone, where the surface and underground habitats meet each other; the twilight zone, where light progressively diminishes to zero; the transition zone, where light is nonexistent but the environmental effects from the entrance are still felt; and the true dark zone, where environmental conditions, especially the constantly saturated atmosphere, are stable. The size of the zones depends very greatly on the size and shape of the entrance and of the cave passages. When a cave has 2 entrances, the dark passage between is very often entirely transition zone because of the chimney effect between the 2 entrances. The specialized cave animals, troglobites, usually occur only in the true dark zone.

S. koloana is stenohygrobic and is restricted to damp or wet cave passages, where the relative humidity is higher than 95%. It is entirely absent from drier sections of the caves. The animal is probably able to disperse through cracks and anomalies in the lava within its range and retreat or advance as the moisture and food conditions allow. It has been absent from the downslope passage of Koloa Cave #1 on 2 occasions when that passage was dry and present there at other times when the floor was wetter. Even when the passage has been very wet in Koloa Cave #1, the amphipod distribution has been uneven; i.e., very common in a few areas and absent from large areas of the wet passage.

The amphipod has a wider distribution within Koloa Cave #2 and is also found in more caves than the spider *Adelocosa anops* Gertsch. Thus the amphipod possibly demonstrates a slightly wider humidity tolerance than its potential predator or it disperses more freely.

In the limestone cave the amphipod is most commonly encountered in the stream-deposited debris and on dead roots in the dark zone, but it also occurs in scattered sparse populations along the mud floor of the stream passage in the dark zone. An introduced amphipod, *Talitroides alluaudi* Chevr. was observed only on the debris in the cave.

Behavior

In the cave, *S. koloana* is usually found standing motionless or walking slowly on tree roots or on the floor. It is often found in numbers under rotting wood and in hollow roots and other places where food and the environment allow, but it is not gregarious.

When disturbed by touch, the animal will most often run slowly away rather than jump. If disturbed repeatedly or severely it will jump in typical amphipod fashion. However, the jump is not prodigious, usually within the range of 5–10 cm, and when the animal lands it will usually run slowly again.

It is strongly anemophobic. When disturbed by wind as from breath or aspirator the animal will often lie flat on the substrate and run away when the disturbance ceases. It may also jump or run when struck by a breeze.

S. koloana is very sensitive to the beam of an acetylene lamp. This is most likely because of sensitivity to the change in humidity but may also be a reaction to the slight rise in temperature. Usually the animal will run away from the lamp. No similar response is noticed to a flashlight beam. One animal, watched in the cave for 5 minutes, vibrated antenna 2 very rapidly or curled and performed cleaning motions on the 2nd antennae when the acetylene lamp was focused on it, but was not at all disturbed by flashlight. When a drop of water was placed near that animal, it drank eagerly both by mouth and by dipping its 2nd antennae in and cleaning them.

S. koloana is able to swim. Two individuals were purposely prodded into jumping into a pool of water on the cave floor and both swam rapidly and apparently naturally as do other terrestrial talitrids. They did, however, show considerable difficulty in breaking the surface tension to return to the land. One individual tried at several different locations along the edge of the pool to get leverage on the substrate to push itself out onto the shore. It swam freely between attempts.

Food

The food of *S. koloana* is composed of dead organic material, especially rotting tree roots and rotting wood. In Koloa Cave #2 the amphipods have been observed and collected around rotting sticks and branches on which they were apparently feeding in the dark zone, and on tree roots, (FIG. 1) probably the leguminous tree *Pithecellobium dulce.* They have also been observed scraping muddy areas of the floor with their mouthparts, but they may have been obtaining only moisture.

Two amphipods were collected at some unidentified frass, possibly feces of the cockroach *Periplaneta americana* which is common in the cave, but feeding was not ascertained.

In the limestone cave amphipods are found commonly in and around piles of rotting plant material washed in by the stream and also in the hollowed-out, rotting, large roots of a *Ficus* sp. where they were feeding primarily on the softer layer under the bark of the roots.

Laboratory rearing

Eight specimens were collected from the limestone cave and 6 from Koloa Cave #1 on 5

June 1973 and taken to Honolulu. The amphipods were kept in clear plastic sandwich boxes approximately 10 cm square and 3 cm high with a shallow layer of wet calcareous sand. They were first fed rotting plant material from the respective caves and this was replenished with bark of an endemic *Acacia koa* tree. Four large individuals were still living after 6 months. The amphipods fed extensively on the woody material and much of the bark had been consumed and reduced to frass (feces). The frass of the amphipods is a characteristic dark brown, soft, moist, grainy, soil-like material approximately 1.0 mm long by 0.3 mm in diameter. It is easily broken into an amorphous brown slime. Similar frass has been observed in the caves around and in rotting woody material. The frass of the exotic epigean species *Talitroides alluaudi,* as observed in Judd Street Cave on Oahu, was very similar except drier and firmer, but that cave is drier.

Mating and reproduction

Mating behavior remains unknown. Interestingly, the male lacks the large subchelate gnathopod 2, found in several other epigean talitrid genera, that are used to grasp the female during precopulatory "carrying" and amplexus. The vestigial brood plates in the female may reflect a decreased need for protection of the developing eggs because of lower frequency of disturbances and jumping activity and/or an adaptation to facilitate release of the very large newly hatched young.

Because the 2 sexes are grossly very similar, sex determination in the field is not possible and the sex ratio is unknown. However, nearly twice as many mature females as mature males have been collected (19 females to 10 males).

Biological associations

In Koloa Cave #2 the amphipod is preyed upon by the lycosid spider *Adelocosa anops* Gertsch. Most of the other biota in these caves, so far as is known, is introduced and composed of a number of soil, leaf litter, and scavenging arthropods such as cockroaches, termites, earwigs, isopods (Schultz 1973), spiders (Gertsch 1973), and Collembola (Bellinger & Christiansen 1974).

The roots now penetrating into the caves are all of recently introduced exotic plants, primarily weedy tree legumes, and in the limestone cave, a *Ficus* sp. What animals were once in these caves when native forest overlaid the area may never be known. Many cave species have probably become extinct with the advent of European contact and agriculture. These 2 highly specialized cave animals, one a general scavenger and the other a general predator, still survive.

Zoogeography

The finding of this remarkable new cave amphipod on Kauai is not entirely unexpected. According to Dalrymple et al. (1973), this island is the oldest of the existing high islands of Hawaii, minimally 5.6 million years old. A rich fauna of apparently largely endemic species of land amphipods is being disclosed in the IBP survey of the Hawaiian Islands, with greatest diversity in the oldest high islands. The precise mechanism of colonization of oceanic islands by terrestrial amphipods has not been established. However, these animals may have colonized, and diversified within the western leeward islands of the Hawaiian chain during the previous 80 (plus) million years, before erosion of these islands to sea level. A possible nearby source of specialized terrestrial amphipod immigrants to existing Hawaiian islands is thus envisaged. Further speculation on the origin and affinity of this fauna and the present troglobitic species awaits detailed analysis of the IBP survey material.

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