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Hawaiian larval stomatopods: molecular and morphological diversity

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Abstract

Estimating stomatopod species diversity using morphology alone has long been difficult; though over 450 species have been described, new species are still being discovered regularly despite the cryptic behaviors of adults. However, the larvae of stomatopods are more easily obtained due to their pelagic habitat, and have been the focus of recent studies of diversity. Studies of morphological diversity describe both conserved and divergent traits in larval stomatopods, but generally cannot be linked to a particular species. Conversely, genetic studies of stomatopod larvae using DNA barcoding can be used to estimate species diversity, but are generally not linked to known species by analyses of morphological characters. Here we combine these two approaches, larval morphology and genetics, to estimate stomatopod species diversity in the Hawaiian Islands. Over 22 operational taxonomic units (OTUs) were identified genetically, corresponding to 20 characterized morphological types. Species from three major superfamilies of stomatopod were identified: Squilloidea (4 OTUs, 3 morphotypes), Gonodactyloidea (9, 8), and Lysiosquilloidea (6, 7). Among these, lysiosquilloids were more diverse based on larval morphotypes and OTUs as compared to previously documented Hawaiian species (3), while squilloids had a lower diversity of species represented by collected larvae as compared to the seven species previously documented. Two OTUs / morphotypes could not be identified to superfamily as their molecular and morphological features did not closely match any available information, suggesting they belong to poorly sampled superfamilies. The pseudosquillid, *Pseudosquillana richeri*, was discovered for the first time from Hawai'i. This study contributes an updated estimate for Hawaiian stomatopod diversity for a total of 24 documented species, provides references for identification of larval stomatopods across the three major superfamilies, and emphasizes the lack of knowledge of species diversity in more cryptic stomatopod superfamilies, such as Lysiosquilloidea.

Key words: genetics, DNA barcoding, identification, Pacific islands

Introduction

Larvae hold potential as an untapped resource for discovery of marine species diversity, especially for cryptic species. Stomatopods are a behaviorally cryptic group of crustaceans, currently consisting of over 450 species worldwide, with more species being discovered regularly (Ahyong 2001, 2002a; Manning 1995). While adult stomatopods are benthic and create burrows in hard structures (i.e., coral reefs) or soft substrates (e.g. mud or sand flats), larval stomatopods live in the water column and can be more easily collected than the adults. Because stomatopods generally have large clutches of eggs resulting in thousands of individuals hatching and hundreds making their way to the pelagic, larvae provide an increased opportunity to sample representative species diversity from a single wild catch, unlike catching adults that involves much more labor intensive and targeted sampling methods.

Despite this increased opportunity for sampling diversity, crustacean larval development remains largely a black box due to the difficulty in brooding and culturing crustacean larvae in laboratory settings. Three ecologically relevant phases have been used to describe stomatopod larvae: propelagic, pelagic, and juvenile or post-larval

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(Ahyong 2014). Few studies have been able to elucidate for individual species the number and timing of stages in each phase, which likely varies widely among species (Greenwood & Williams 1984; Hamano & Matuura 1987). Without knowledge and morphological description of each individual stage, morphological identification of wild-caught stomatopod larvae is impossible.

With the aid of DNA barcoding, which allows comparison of an individual's mitochondrial sequence against adult sequences published in genetic databases, estimates of stomatopod species diversity and insights to the larval cycle of these species are becoming increasingly possible (Barber & Boyce 2006; Cházaro-Olvera *et al.* 2018; Palero *et al.* 2016; Ueda *et al*. 2021; Wong *et al.* 2021). Though the morphology of larval stomatopods is dissimilar to that of adults, a wide array of larval morphological characters are found to correlate with adult-based taxonomic groups (Alikunhi 1967; Haug *et al.* 2016; Shanbhogue 1975). However, the genetic estimates of diversity provided from barcoding are rarely integrated with morphological diversity in larvae to provide species identifications, and even less so for identifying multiple stages in development.

In Hawai'i, the stomatopod diversity is relatively limited, with twenty documented species, two of which are endemic (Ahyong 2002a). For one of the more cryptic superfamilies of stomatopod, Lysiosquilloidea, there are at least five distinct larval morpho-groups in Hawai'i (Townsley 1953), while only three adult species have been identified from adults (Ahyong 2002a). This evidence suggests that the species diversity of Hawaiian stomatopods is higher than currently indicated for some groups.

Taking advantage of the bipartite life cycle of the stomatopod may help reduce the paucity of genetic information within this cryptic group while promoting morphological identification of larvae. The Hawaiian stomatopod fauna serves as a good proof of concept for the value of diversity estimation from larvae because of the geographic isolation and the relatively small number of well documented species. The guide presented here will aid future research in larval stomatopod biology and ecology by expanding on Barber & Boyce's (2006) larval barcoding approach. In brief: with the aid of DNA barcoding and morphological examination, approximate taxonomic identification for larval morpho-groups and species diversity of Hawaiian stomatopods was explored.

Methods

Specimen collections

Offshore pelagic stomatopod larvae were collected by the Pacific Islands Fisheries Science Center (PIFSC) of the National Oceanic and Atmospheric Administration (NOAA) on the Oscar Elton Sette Cruises: SE17-03 (April, 2017) in the waters of west O'ahu (LOPEC: Leeward O'ahu Pelagic Ecosystem Comparison), and SE16-06 (September, 2016) and SE17-04 (April, 2017) near the western coast of Hawai'i Island (hereafter "West Hawai'i"). Midwater trawls were conducted at 1.8 m (6 ft.), using an Isaacs-Kidd (IK) trawl (505 μm mesh) or with a 140 m^2 Stauffer modified pelagic Cobb trawl (graded mesh tapering down to 505 μm cod end). In either case, trawls were towed obliquely in either shallow (<200m) or deep sets (max 973m; Supplemental Table S1) All individuals were size sorted (>5mm) from bulk plankton samples and batch preserved in 95% ethanol.

Specimens from nearshore waters (0–100m offshore, 0–10m depth) were collected from southern Kāne'ohe Bay, O'ahu, Hawai'i, August 2016. Dive lights were used in shallow water after sunset to attract plankton, which were captured using aquaria fine-mesh hand nets. Stomatopods were live sorted from bulk plankton and preserved in 95% ethanol. Any post-larval stages of stomatopods caught were morphologically identified prior to barcoding. Several large stomatopod larvae (greater than 2 cm total length) washed up on the beach were collected from Kailua Beach Park at sunrise. Surviving individuals were kept alive until metamorphosis to post-larvae was complete and species could be identified morphologically (approximately 5 weeks, with total lengths of 50 mm). Molts of these post-larvae were preserved in 95% ethanol for DNA extraction.

To build a database of genetic sequences from identified individuals previously documented in Hawaiian waters (Ahyong 2002a; Townsley 1953), several adult stomatopods were collected from Hawai'i, USA and Queensland, Australia (Table 1) using hand nets and Yabby Pumps (model BP24, Alvey). Whole animals were preserved in 100% ethanol and single pleopods were used for DNA extraction.

TABLE 1. Adult specimens identified morphologically and molecularly barcoded to increase the diversity of species represented in COI databases.

Superfamily	Family	Morphological species ID	**Stage at Collection**	**Collection Location**	**NCBI A ccession Number**	**Museum ID**
Gonodactyloidea	Gonodactylidae	*Gonodactylellus* **n. sp.**	Adult	Kāne‘ohe, Hawai‘i, USA	OM638803	S19648
Gonodactyloidea	Gonodactylidae	*Gonodactylaceus falcatus*	Post-larvae	Wailupe, Hawai‘i, USA	OM638792	S19641
Gonodactyloidea	Odontodactylidae	*Odontodactylus brevirostris*	Adult	Waianae, Hawai‘i, USA	OM638829	S19661
Gonodactyloidea	Alainosquillidae	*Alainosquilla foresti*	Adult	Vanuatu	OM638802	AM P100675
Lysiosquilloidea	Nannosquillidae	*Pullosquilla* **n. sp.**	Adult	Kihei, Hawai‘i, USA	OM638812	S19652
Lysiosquilloidea	Nannosquillidae	*Pullosquilla litoralis*	Adult	Lizard Island Research Station, Queensland, Australia	OM638833	N/A
Lysiosquilloidea	Nannosquillidae	*Acanthosquilla derijardi*	Adult	Lizard Island Research Station, Queensland, Australia	OM638817	AM P105859
Squilloidea	Squillidae	*Oratosquilla fabricii*	Post-larvae	Kailua, Hawai‘i, USA	OM638777	S19670
Squilloidea	Squillidae	*Parvisquilla sinuosa*	Adult	Kāne‘ohe, Hawai‘i, USA	OM638790	S19668

Larval morphological descriptions

The literature contains a convoluted history of stomatopod larval-type naming schemes that varies based on locality (Townsley 1953), and is often focused on distinct morphological features due to the difficulty in identifying larvae to species. For this study we combined the most current terminology from the literature to form a three-level hierarchy for morphological descriptions: Level 1—larvae are divided by **type** based on body shape (i.e. Alima or Erichthus) (Ahyong 1997); Level 2—**subtypes** were defined and named within each larval type based on unique defensive features (i.e. Flying Saucer, Spiny Balloon, or Gnome-Hat; Haug *et al.* 2016); and Level 3—**morphotypes** were delineated within each subtype based on family or species level characteristics (i.e. SquAT A), with taxonomic associations verified by molecular methods.

The features of the two larval types were easily distinguishable—Alima-type larvae have long, thin, flattened, shield-like carapaces with eyes extending beyond the anterior edge attached to a bar-structure, while Erichthus-type larvae have truncated bodies with shorter, stalked eyes and the carapace tends to protectively encase the body (Fig. 1). Larvae collected at earlier developmental stages without maxillipeds or raptorial appendages that could not be easily categorized were classified as antizoeae (Ahyong *et al.* 2014; Haug *et al.* 2016). Subtypes were named for defensive features of the larval carapace, as the size and shape of the carapace was often the most noticeably modified structure. Alima-type larvae were all classified as a single ‘Shield’ subtype based on the small, squared carapace shape, while Erichthus-type larvae contained a larger diversity of carapace morphologies and therefore subtypes (see below). Subtypes within each type were further classified into morphotypes using the general size, shape, and spination of the carapace, maxilliped, telson, and uropods. Alima-type Shield subtype larvae were categorized as described by Feller *et al*. (2013), using carapace characters such as spinule number and carapace to total length ratios. Erichthus-type subtypes were categorized based on: (1) maxilliped, (2) telson, and (3) uropod features (e.g. general shape and spination), and (4) carapace characteristics (size, shape, and spinules on rostral

spines). Morphotype names were based on abbreviations of the superfamily or family of the larvae, and indicate the phylogenetic placement of each morphotype based on molecular barcoding data. Nomenclature for morphotypes is a three-letter family abbreviation, or two letter superfamily abbreviation, followed by larval type abbreviation (i.e. larvae in the family Squillidae Alima Type are SquAT, while the superfamily Lysiosquilloidea Erichthus Type are LyET). When superfamily could not be identified, morphotypes were labeled for the suborder Unipeltata: Erichthus-Type (UnET). The family, genus and species identifications of each morphotype were confirmed from molecular barcoding data when possible. All morphotypes within each subtype were then lettered alphabetically (A through C) following Barber & Boyce's (2006) nomenclature for different morphotypes within each family.

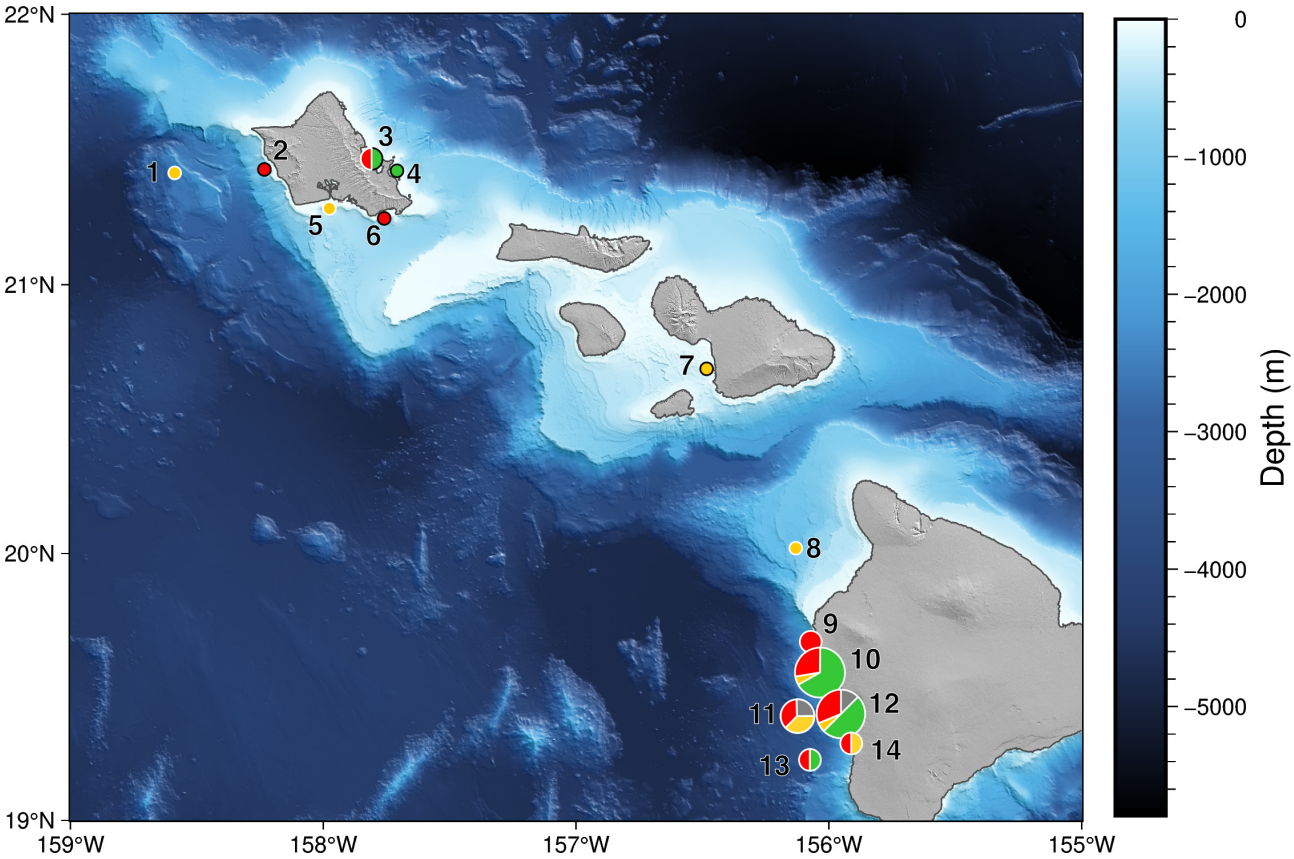

FIGURE 1. Sampling map of the lower main Hawaiian Islands with proportions of superfamilies collected from each site that were successfully barcoded. Ocean depth in meters is represented by a color gradient. Adults sampled from nearshore O'ahu and Maui are represented by a black outline, while larval tows from the Oscar Sette cruises are outlined in white. Colors of superfamily: gray—unknown, green—Squilloidea, yellow—Lysiosquilloidea, and red—Gonodactyloidea.

Photographic Documentation of Morphology

Representatives of each larval morphotype were photographed using a Canon (EOS600D) and FotoOptix phototube on an Olympus SZX12 dissection microscope. Photo stacks were generated by manually adjusting fine-tune focus on the microscope and taking between three and seven images per larva. Larvae larger than three cm were photographed using only the camera and a tripod. All specimens remained immersed in filtered 95% ethanol for the duration of photographing. Photos of larvae were stacked using Zerene Stacker software (Zerene Systems LLC, Richland, WA, USA). All specimens and photos have been deposited in the Bernice Pauahi Bishop Museum (HI, USA) to facilitate future research on the biology and morphology of stomatopod larvae; individual records can be found in Supplemental Information (Table S1).

Molecular Barcoding and Phylogenetic Analyses

For samples of both larvae and adults, DNA was extracted from the anterior most set of pleopods when available, moving posteriorly when specimens were damaged. For damaged larvae missing pleopods altogether, abdominal somites 1–3 were used for DNA extraction. Individuals smaller than 3 mm in total length were photographed and morphologically

characterized prior to whole body DNA extractions. Individual extractions were performed using DNEasy Blood and Tissue Kits (Qiagen, USA) according to the manufacturer's protocol and eluted into 100uL of milliQ water.

Approximately 700bp of the 5' end of the mitochondrial gene cytochrome c oxidase subunit I (COI) of larvae and adults were amplified using standard PCR conditions. Final concentrations of 400 nmol μL^{-1} LYS_COI primers (Forward: 5'-ACGCGACGATGATTATTYTCTAC-3' Reverse: 5'-GCTCGRGTRTCIACRTCYAT-3') were used initially, followed by LCOI-1490 5'GGTCAACAAATCATAAAGATATTG-3' with HCOI-2198 5'-TAAACTTCAGGGTGACCAAAAAATCA-3' for any animal where the COI region did not amplify. MyTaq™ Red Mix (Bioline, Swedesboro, NJ, USA) was used with 1.5uL DNA extract (at 3–25 ng/uL) in 25uL reactions for all PCR amplifications. Thermocycling profiles remained consistent, with an initial denaturation at 94°C for 2 minutes, followed by 50 cycles of 20s denaturation at 94°C, 10s annealing at 46°C, and 1 minute extension at 65°C, completed by a final extension of 7 minutes at 65°C.

After confirmation for size and presence of amplicons on a 0.8% agarose gel, 20uL of PCR products were purified using five units of Exonuclease I and 0.5 units of Shrimp Alkaline Phosphatase at 37°C for 30 minutes, then 80°C for 15 minutes. Cleaned products were submitted to Advanced Studies in Genomics, Proteomics and Bioinformatics (ASGPB) at the University of Hawai'i at Mānoa for sequencing with each primer (at 1.6 mM/uL of reaction). All sequences were cleaned and edited for base-calling errors using Geneious v.10.1.3 and *de novo* assembled to produce consensus sequences. Sequences generated as a part of this study were deposited to GenBank (Accession numbers are listed in Supplementary Table S1).

Individual sequences were aligned to a subset of published stomatopod COI sequences available from NCBI using the MAFFT algorithm (v7.309) as implemented in Geneious software to determine operational taxonomic units and, where possible, link larval sequences to adult species for identification. Operational taxonomic units (OTUs) were determined by percent similarity with a cutoff value of 95%, as in Palecanda *et al.* (2020). Species identification was made using a threshold cutoff of 97% similarity within the OTU against a reference adult voucher sequence (Barber & Boyce 2006). Maximum likelihood trees were constructed on Cyberinfrastructure for Phylogenetic research (CIPRES) servers; RAxML (Stamatakis *et al.* 2008) was implemented using the GTRGamma partition model with 1000 bootstrap replicates to generate newick tree files for visualization using FigTree software v.1.4.4 (Rambaut 2007).

Results

A total of 174 individual stomatopod larvae from Hawaiian waters were morphologically characterized and 63 were successfully sequenced. From these, species representing three superfamilies and seven families resulted in a total of 22 different OTUs that were molecularly identified from 20 distinct morphotypes (Table 2). From the 22 OTUs, 10 were identified to species based on comparisons with sequences from identified adults: one species was identified from Squilloidea—*Oratosquilla fabricii* (Holthuis, 1941); two from Lysiosquilloidea—*Lysiosquilla maculata* (Fabricius, 1793) and *Pullosquilla* **n. sp.**; and seven species from Gonodactyloidea - *Pseudosquilla ciliata* (Fabricius, 1787)*, Pseudosquillisma* sp.*, Pseudosquillana richeri* (Moosa, 1991)*, Gonodactylaceus falcatus* (Forskål, 1775)*, Gonodactylellus* n. sp.*, Echinosquilla guerinii* (White, 1861)*,* and *Odontodactylus brevirostris* (Miers, 1884). Two of these species (*Pullosquilla* **n. sp.** and *Pseudosquillana richeri*) have not previously been documented from Hawaiian waters as adults, though larval descriptions matching those of our *Pullosquilla* larvae were reported by Townsley (1953). Proportions of superfamilies per sampling site suggest that lysiosquilloid larvae tend to be more prevalent in the offshore pelagic trawl habitats, while squilloids are found closer to shore in these same trawls (Fig. 1). Gonodactyloid larvae are ubiquitous in habitats ranging from inshore shallow reefs (0–10 m) to deep offshore pelagic waters (0–570 m).

We combined the taxonomic links identified from barcoding with our morphological data to identify characters useful for larval identification in Hawaiian waters. Four major morphological features were helpful in identifying Hawaiian stomatopod larvae to superfamily quickly and consistently: size and shape of the carapace, eye position, telson shape, and maxilliped shape. It is important to note that staging of all morphotypes was not done, and size differences may be associated with stage differences. In general, however, all larvae examined here from offshore cruises looked to be late stage, as most were larger than 10 mm long and had fully developed raptorial appendages.

The following sections detail the characters used to distinguish among Alima-type and Erichthus-type larvae, as well as subtypes and morphotypes within each group.

TABLE 2. Identified larval types, subtypes, and morphotypes and associated molecular-based taxonomic identification. Percentages in parentheses after species identification are the lowest similarity to reference sequences. *Lysiosquilla maculata* erichthus Tank LysET C was not found in this study and is represented in parentheses.

Superfamily	Family	Genus/species	Larval Type	Larval Subtype	Morphotype Abbreviation	Number of larvae Barcoded
Gonodactyloidea	Gonodactylidae	*Gonodactylaceus falcatus* (95%)	Erichthus	Blow Dart	GonET—A	2
		Gonodactylellus **n. sp.** (98%)	Erichthus	Blow Dart	GonET—A	5
	Odontodactylidae	*Odontodactylus brevirostris* (100%)	Erichthus	Lance	OdoET—A, C	2, 1
		Odontodactylus sp.	Erichthus	Lance	OdoET—B, C	1, 3
	Protosquillidae	*Echinosquilla guerinii* (99%)	Erichthus	Gnome Hat	ProET—A	1
	Pseudosquillidae	*Pseudosquilla ciliata* (99%)	Erichthus	Torpedo	PseET—A	7
		Pseudosquillana richeri (98%)	Erichthus	Torpedo	PseET—B	1
		Pseudosquillisma sp. (98%)	Erichthus	Torpedo	PseET—C	1
		–	Erichthus	Torpedo	PseET—C	2
Squilloidea	Squillidae	*Busquilla* sp. (96%)	Alima	Shield	SquAT—A	7
		Oratosquillina fabricii (100%)	Alima	Shield	SquAT—A	7
		Alima sp. (*pacifica*-type) (96%)	Alima	Shield	SquAT—B	4
		–	Alima	Shield	SquAT—C	5
Lysiosquilloidea	Nannosquillidae	*Pullosquilla* **n. sp.** (99%)	antizoea, Erichthus	Rocket	NanET—A	1, 1
		–	Erichthus	Rocket	NanET—B	2
	Lysiosquillidae	–	Erichthus	Tank	LysET—A	1
		–	Erichthus	Tank	LysET—B	1
		Lysiosquilla maculata (99%)	antizoea, (Erichthus)	(Tank)	az, (LysET—C)	1, (0)
	Unknown	–	Erichthus	Flying Saucer	LyET—A	2
		–	Erichthus	Spiny Balloon	LyET—B	1
Unknown	–	–	Erichthus	Brawny	UnET—A	3
	–	–	Erichthus	Brawny	UnET—B	1

Alima-type larvae

Squilloidea

Alima-type larvae (Fig. 2A) are exclusive to the superfamily Squilloidea, which also contains the genus *Alima*. Currently the superfamily Squilloidea only contains the family Squillidae, and therefore one subtype is designated for this group. Adult squilloids are known to inhabit sandy or muddy-sand habitats from the intertidal zone to shelf and slope at depths, but are most common in subtidal shelf habitats. They typically build simple U-shaped burrows (Caldwell 1988). All larvae collected for this study were found in offshore pelagic habitats except for the last-stage larvae, which likely had returned inshore to the fine sand beach at Kailua to settle into juveniles.

Shield Subtype—Squillidae

Due to the flattened and thin shape of the carapace found in all Alima-type larvae, a single "Shield" subtype was designated, containing morphotypes SquAT A-C. Shield subtype larvae are very distinct from the larvae of other superfamilies in their telson structure, which has four or more intermediate denticles (Ahyong *et al.* 2014). Often accompanying the telson features are a squared, flattened carapace, and elongate eyestalks (Ahyong *et al.* 2014). The stalked eyes of SquAT larvae are mounted on a bar-like structure that resides at the most anterior point of the Shield. From our Hawaiian collections, we identified three morphotypes based mainly on differences in carapace spinule number and telson ratios (Table 3). Genetically, 4 OTUs of SquAT larvae were placed within the family Squillidae (Fig. 3).

Morphotype SquAT A—*Busquilla* sp. and *Oratosquilla fabricii*

A subsample of 73 SquAT A larvae were pulled from the bulk sample of the Alima-type larval specimens from West Hawai'i for identification (Fig. 4A; Table 3), of which 14 were barcoded successfully from inshore sites 10 and 12 in both shallow (0–190 m) and deep (0–570 m) trawls. SquAT A specimens are between 26 and 49 mm in length, have an inflated propodus of the raptorial claw, wider carapace, and more spinules than the other SquAT morphotypes (Table 3). This morphotype had an inconsistent number of carapace spinules (12–16), and genetically was identified as either *Busquilla* sp. (7 specimens, out 99% similarity) or *Oratosquilla fabricii* (7 specimens, OTU 99–100% similarity). Specimens of *Busquilla* from Hawai'i were 96% similar to the voucher sequence of *Busquilla plantei* Manning, 1978, which was a specimen from the Western Pacific (Porter *et al.* 2010). One more species, *Busquilla quadraticauda* (Fukuda, 1911), is also found in Hawai'i (Ahyong 2002a) and may share this larval morphotype. Because of the lower similarity of the *Busquilla* OTU to the reference sequence of *B. plantei*, it is possible that these individuals may be either *B. quadraticauda* or *B. plantei*. As such, the identity for this species could not be confirmed.

In general, the carapace spinules on *Busquilla* tended to be slightly more numerous and more pronounced than those of *O. fabricii*. This difference could also be due to differences in the relative stage of larval development. One last-stage SquAT A larva was collected from Kailua beach park (site 4, O'ahu), reared to adulthood, and then morphologically confirmed to be *O. fabricii*. This larva had less pronounced spinules with 12 anterior spinules on one side and 13 on the other based on a discarded last stage molt. While there is little information available for the larvae of either *Busquilla* or *O. fabricii*, multiple studies have been done to characterize larval stages of *Oratosquilla oratoria* (De Haan, 1844) (Hamano & Matsuura 1987; Kawamura *et al.* 1997; Kodama *et al.* 2009; Ohtomi *et al.* 2005, 2021). Last stage larvae of *O. oratoria* are smaller than the SquAT A morphotype described here (< 25.42 mm total length), with much less developed uropods and no information on carapace spinule counts (Hamano & Matsuura 1987). Thus it is difficult to draw any conclusions about developmental stage from previous literature. Additionally, post-larvae of *Busquilla* and *O. fabricii* are difficult to morphologically differentiate until they have reached a total length of at least 55 mm when the anterior bifurcation of the carapace is well developed (Ahyong 2002b). The shared larval morphology of these species warrants further study in Hawaiian larvae and post-larvae to yield a more thorough understanding of the radiation within this group.

Morphotype SquAT B—*Alima* sp.

A subsample of four, narrow, elongate, Shield larvae (35–46 mm total length) were identified and barcoded from both shallow (0–190 m) and deep (0–520 m) trawls at sites 10, 12 and 13 from West Hawai'i. One of the most pronounced morphological features of the SquAT B was the elongated carapace (length being more than twice

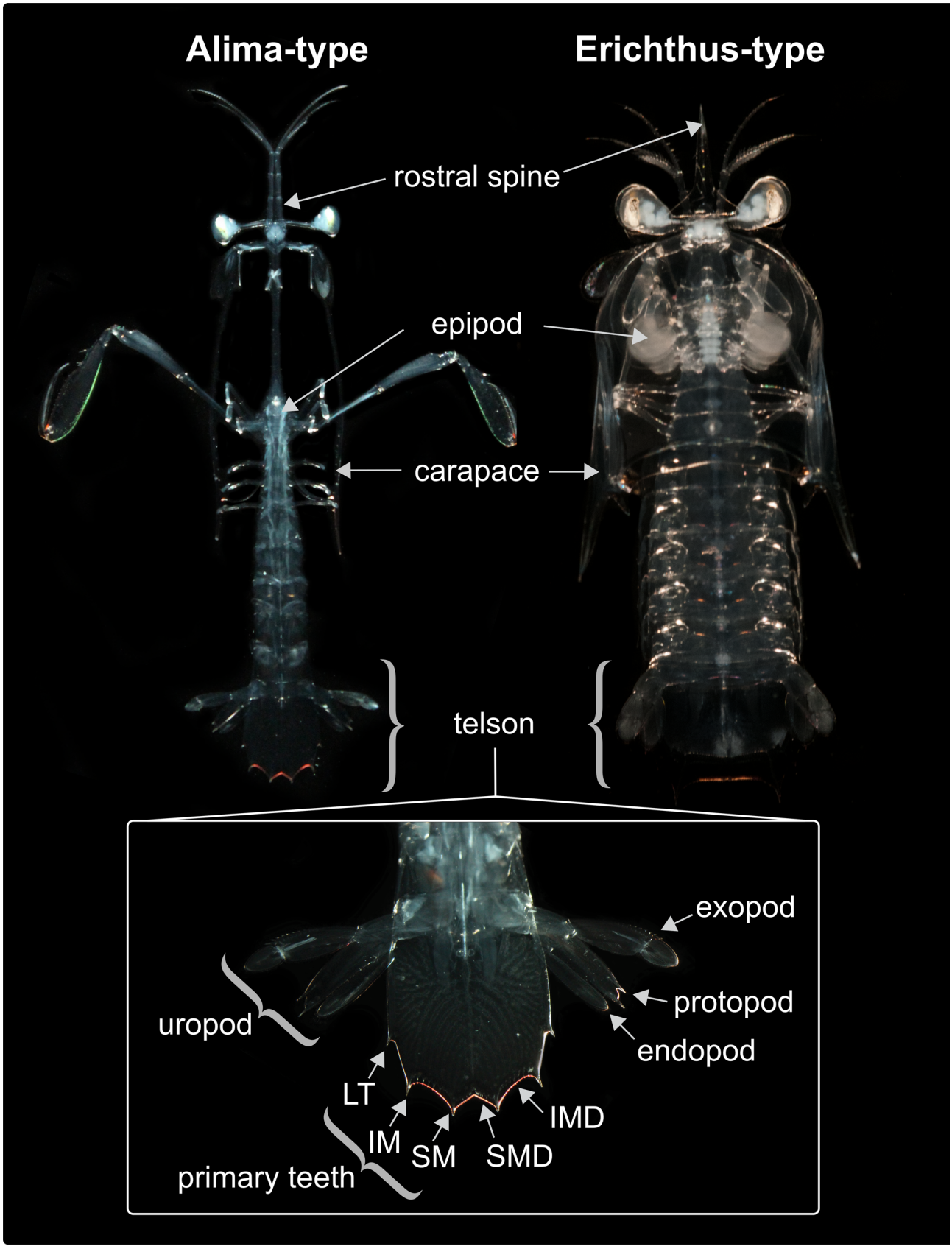

FIGURE 2. Terminology used in descriptive accounts for larval stomatopods. Enlarged telson details include lateral (LT), Intermediate (IM), and submedian (SM) primary teeth and denticles (IMD and SMD). Erichthus-type photo credit: Kate Feller & Megan Porter.

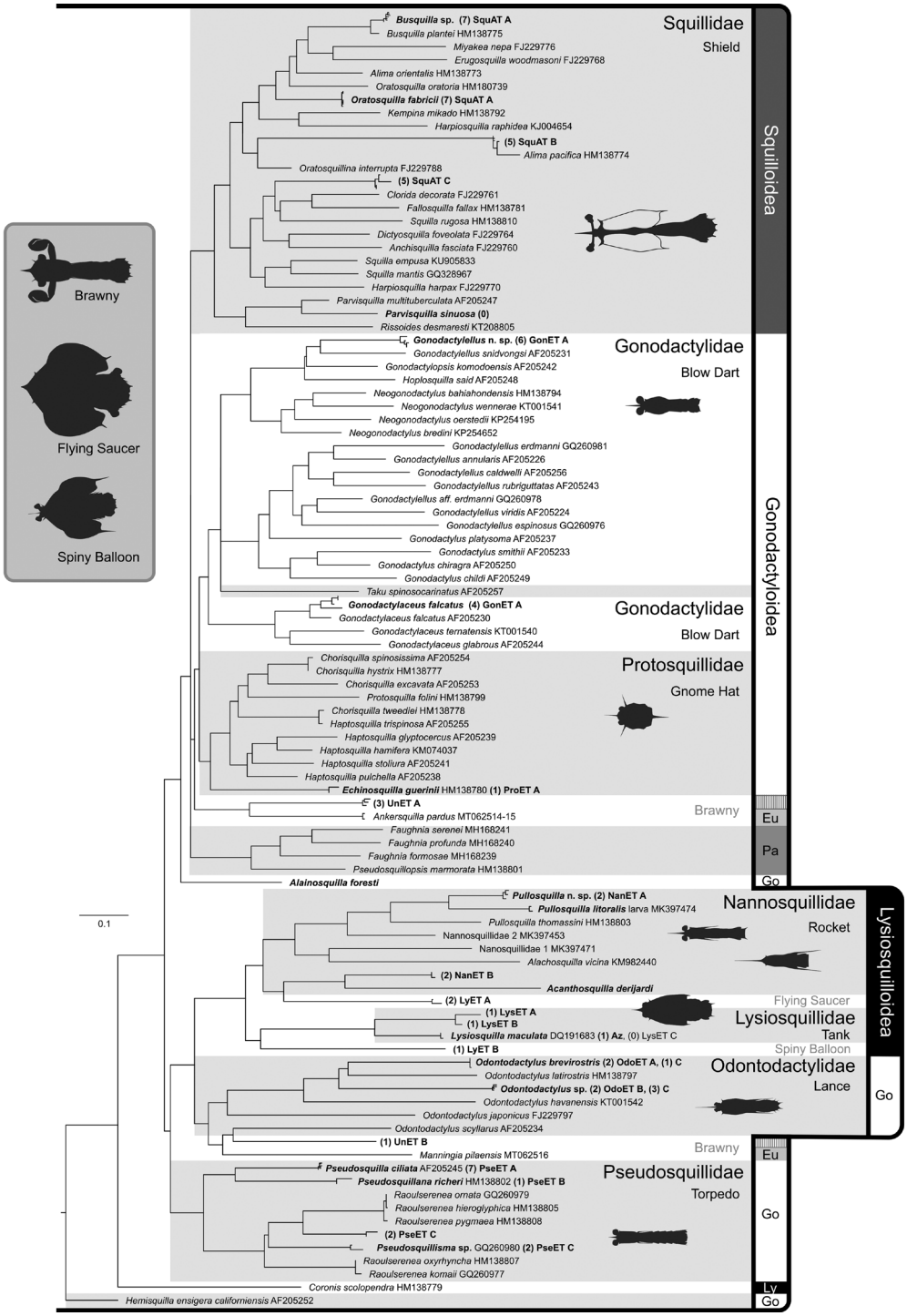

FIGURE 3. Maximum likelihood phylogeny of adult and larval stomatopod COI barcode sequences. Larval OTUs and associated morphotype-subtype designations include sequences from four Alima-type larvae OTUs (SquAT A, B, C—shield), 18 Erichthus-type OTUs (LyET A—flying saucer, LyET B—spiny balloon; ProET A—Gnome Hat; GonET A—Blow Dart; LysET A, B—Tank; NanET A, B—rocket; PseET A, B, C—Torpedo; OdoET A, B, C—Lance; UnET A, B—Brawny), and one Az (antizoea stage) OTU. Bold names indicate adult and larval specimens sequenced in this study; regular font used for publicly available sequences for species which were not identified from Hawaiian larvae. The number of larvae sequenced are in parentheses before OTU morphotype-subtype identities. Relevant family names are given for highlighted clades, superfamily names or abbreviations in the outer right column (Eu: Eurysquilloidea, Pa: Parasquilloidea, Go: Gonodactyloidea, Ly: Lysiosquilloidea), unknown superfamily represented by gray bars. Silhouettes of larval sub-types within the phylogeny are in black font (two rocket sub-type silhouettes are shown), grayed sub-types are shown in the inset. Note that brawny subtype-silhouette is the only one to include raptorial appendage depiction.

its width, Table 3), a characteristic not seen in other Hawaiian Shield larvae (Fig. 4B). SquAT B specimens also have a telson twice the length of the width (Table 3) with shortened uropods, features common in larvae from the genus *Alima* (Feller *et al*. 2013). Based on spinule count and body length to width ratios, the SquAT B larvae are morphologically similar to species of Group 1 *Alima*, consisting of *Alima pacifica* Ahyong, 2001 and *Alima neptuni* (Linnaeus, 1768) (Feller *et al.* 2013). The Hawaiian morphotype SquAT B was genetically similar (96% similar) to *A. pacifica* (Fig. 3)—a species that has not been recorded in Hawai‘i previously. The number of spinules on the margin of the carapace (13–14) does not match previous counts (12) for either the larger *A. pacifica* larvae (42.5 mm total length) nor the similarly sized *A. neptuni* larvae (41–43 mm total length) (Feller *et al*. 2013), indicating the Hawaiian larvae are unlikely to be either of these species. Additionally, *A. pacifica* is presently documented only from Australia and Indonesia in shallow reef flats (Ahyong 2001). The shallow water species, *A. neptuni* has been documented in the Hawaiian Islands (Ahyong 2002a; Townsley 1953) nearshore, but despite multiple nearshore collections searching for adult *Alima* specimens, none could be found for genetic comparison. Based on morphology not matching previous records from Group 1 *Alima* species (Feller *et al.* 2013; Manning 1962), SquAT B larvae may belong to the native *Alima maxima* Ahyong, 2002, the largest species of *Alima*, which is known from the Hawaiian Islands at depths between 95 and 188 m (Ahyong 2002a). Genetic similarity among the Hawaiian SquAT B was 99%, indicating that intraspecific variation is unlikely to span for the divergence observed with *A. pacifica*, providing further support that this larval type is unlikely to be *A. pacifica*.

Morphotype SquAT C—Squillidae

Five of the smallest Shield larvae (25-33 mm), were found in both shallow (0-190m) and deep (0-570m) trawls offshore at sites 10 and 12 of West Hawai‘i. This morphotype had the fewest carapace spinules (3 total) of the Shield larvae described here, resulting in a smoother looking carapace edge than the others (Fig. 4C, Table 3). Individuals of SquAT C were phylogenetically placed within the family Squillidae, and may be a species previously described from the Hawaiian Islands that has not yet been sequenced. Although this species clusters near *Squilla rugosa* Bigelow, 1893 in the COI phylogeny, the genetic similarity of this group to the voucher species of this clade range from 85–87%, which is not indicative of a good match (Lefébure *et al.* 2006). *Squilla* larvae have been identified previously based on the presence of epipods on five pairs of the maxillipeds (Morgan & Provenzano 1979). Although most larval specimens analyzed here were damaged, up to four epipods were seen. Alikunhi (1967) reported larvae with the same spinule number from both *Oratosquillina quinquedentata* (Brooks, 1886) and *Miyakella holoschista* (Kemp, 1911), but does not include a number of epipods present in larvae. As members of the SquAT C were the smallest, it may belong to either a diminutive squilloid, such as *Pontiosquilla mauiana* (Bigelow, 1931) (Manning 1995), a species originally described from Hawai‘i (Ahyong 2002a), or represent a species not previously described from Hawai‘i. Another diminutive squilloid, *Parvisquilla sinuosa* (Edmonson, 1921), is endemic to Hawai‘i (Ahyong 2002a). However, the post-larval specimen barcoded here was not similar (80–81%) to SquAT C sequences (Fig. 3), and in any case, species of *Parvisquilla* have only two epipods.

Erichthus-type Larvae

Six erichthus subtypes were identified to family: Tank (Lysiosquillidae), Rocket (Nannosquillidae), Blow Dart (Gonodactylidae), Gnome Hat (Protosquillidae), Torpedo (Pseudosquillidae), and Lance (Odontodactylidae). Two erichthus subtypes could be identified to the superfamily Lysiosquilloidea (Flying Saucer and Spiny Balloon), and one erichthus subtype could not be identified to superfamily (Brawny).

Lysiosquilloidea

Lysiosquilloid larvae could be separated from other erichthus-type larvae by the presence of sub-quadrate shaped maxillipeds, a distinguishing trait in adult lysiosquilloid stomatopods as well. Another obvious trait of the lysiosquilloid larvae was the deeper, and bulkier carapace than most other groups. In most subtypes (with the exception of the Rockets), the body of the animal could curl to fit snugly into the carapace, forming a defensive ball (Figure 5E). Only three lysiosquilloid species have been previously documented in the Hawaiian Islands: *Lysiosquilla maculata, Acanthosquilla multifasciata* (Wood-Mason, 1895)*,* and *Heterosquilloides insignis* (Kemp, 1911) (Ahyong 2002a). Based on barcoding, we identified six lysiosquilloid OTUs from Hawaiian waters, indicating a higher diversity than previously estimated. It is unlikely the higher diversity is a result of new colonization events, and more likely an absence of adult documentation due to the cryptic and burrowing nature of Lysiosquilloidea species (Caldwell 1988).

Because of the difficulty in collecting adult Lysiosquilloidea, there is little barcoding data available for species in this superfamily. Only two OTUs were identified to species: *L. maculata* and *Pullosquilla* **n. sp.** (Fig. 3).

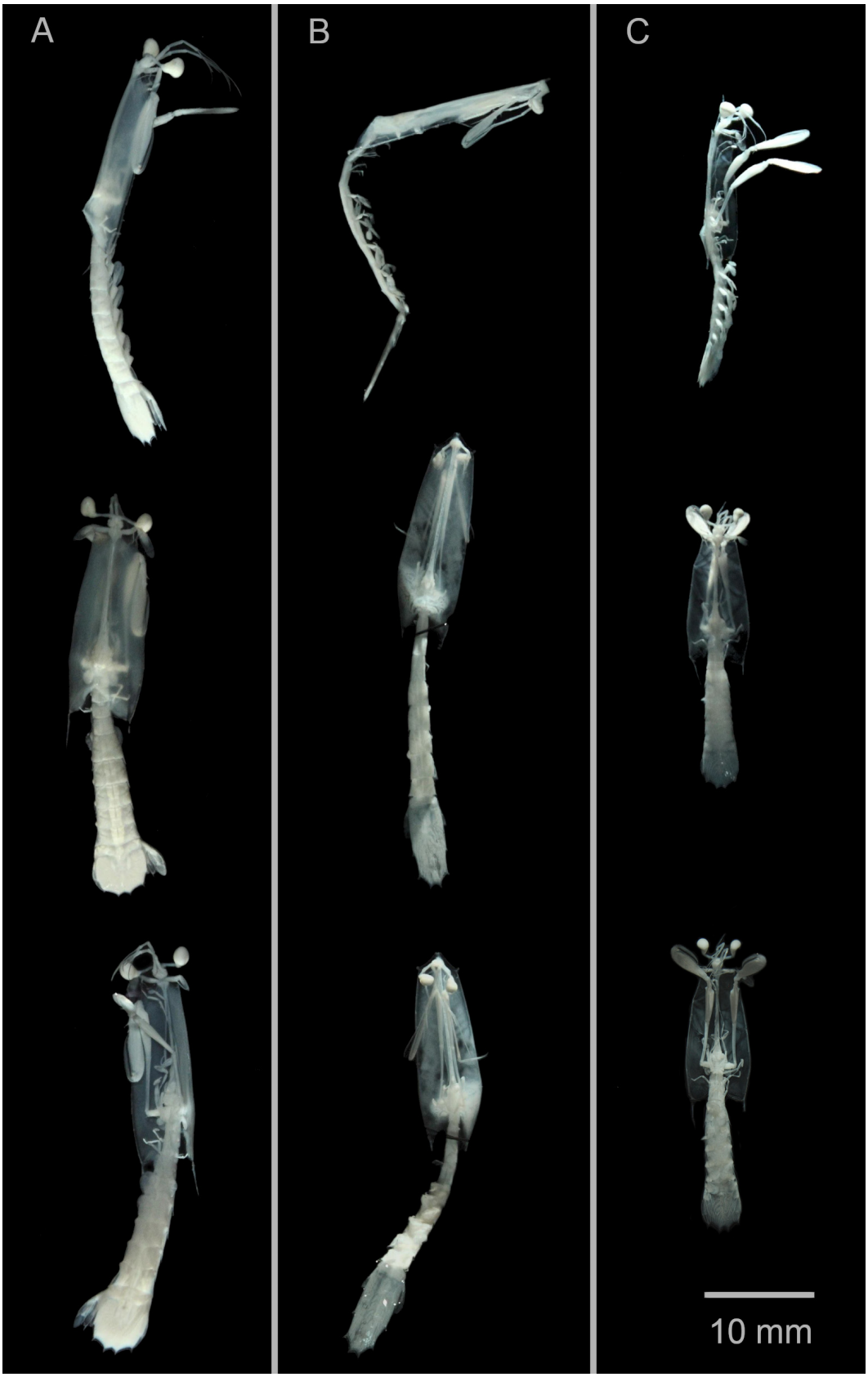

FIGURE 4. Morphotypes of **Shield type** larvae in the family Squillidae: SquAT A—*Busquilla* or *O. fabricii* (A), SquAT B—*Alima* pacifica-type (B), and SquAT C—Squillidae (C). Larval views are lateral (top row), dorsal (middle row) and ventral (bottom row) for all morphotypes. The 10 mm scale bar applies to all images.

The six molecular OTUs were sequenced from five distinct erichthus-type subtypes and two individual antizoea (not morphologically characterized here). Morphological differences observed among the lysiosquilloid larvae were primarily related to the carapace shape and length in comparison to the abdominal somites, and telson features (Table 4). Adults of this superfamily occur in intertidal to upper slope habitats where they burrow in sand and sandy-mud (Ahyong 2001). Adults may be found in simple sand and mud flats as well as in sandy habitats associated with reefs. Larvae were found similarly across a range of pelagic habitats, occurring both in nearshore shallow plankton tows (0–10 m), and in our deepest reef pelagic trawls (650–973 m). While the lowest number of individual lysiosquilloid larvae were found, the number of morphotypes were the second highest among the superfamilies (second only to the gonodactyloids).

Tank Subtype—Lysiosquillidae

Two morphotypes (LysET A, B) of the Tank subtype were collected offshore from West Hawai‘i. Often the carapace of these larvae was dorsally smooth and all around thickened compared to those of other Erichthus-type larvae. The telson of these larvae often did not have denticles between the non-movable primary intermediate (IM) and submedian (SM) teeth, but did have an extended separation between the SM teeth with multiple (typically 30 or more) pairs of SM denticles.

Morphotype LysET A—Lysiosquillidae

One smaller Tank morphotype, LysET A (18 mm, Fig. 5A, B) was collected in a shallow trawl at site 8 off West Hawai‘i. This morphotype has two posterolateral spines, the exterior spine being longer. The telson of this larva had one IM denticle, and 30 pairs of SM denticles. The sixth abdominal somite (AS6) has two flattened, fused teeth protruding centrally and directed posteriorly. The raptorial appendages of this larva are straight and slender in the propodus and dactyl segments, with no inflation. A blue color was observed in the telson of this specimen after storage in ethanol. Townsley (1953) also reported finding this larval morphotype from the Molokai Channel and identified it as a possible *Lysiosquilla* sp. The uropods of this individual reach past the lateral tooth of the telson, and a prominent spine is visible on the ventral side of the proximal uropodal plate. Additionally, in our specimen, the exopod had begun developing four prominent spines on the outer margin, while only one is present in the earlier description. The telson of the larva described by Townsley (1953) was also lacking the single IM denticle, and may represent a later stage of this morphotype. Genetically, this larva is sister to LysET B and both clustered together with *Lysiosquilla maculata*, supporting the morphological placement within the family Lysiosquillidae.

Morphotype LysET B—Lysiosquillidae

The large larvae of LysET B (approximately 30 mm, Fig. 5C–E) were the most frequently collected of the Tank subtype larvae from West Hawai‘i: 9 specimens of this morphotype were collected, of which only one could be barcoded from a deep trawl (0–580m) at site 12. These stunningly large larvae have also been previously reported from Molokai Channel, Hawai‘i (Townsley 1953). It was hypothesized to be a large species of *Lysiosquilla*, and here was closely grouped (85% similar) with *L. maculata*. These larvae have a broad telson with three primary teeth, 30 pairs of SM denticles and no IM denticles. Genetically, LysET A and B are the most similar, sharing an OTU, though their sequences diverge enough to indicate these are different species (95% similar), supporting the evidence of another undetermined Hawaiian lysiosquilloid species.

Morphotype LysET C—*Lysiosquilla maculata*

Lysiosquilla maculata was recorded from Hawai‘i as early as 1913 (Ahyong 2002a; Kemp 1913). Unfortunately, no Hawaiian *L. maculata* erichthus were found in this study, though the larvae have been described from Hawai‘i (Townsley 1953) and adults have been previously collected (Ahyong 2002a). Photos of *L. maculata* larvae taken from individuals collected from Lizard Island reefs, Queensland, Australia (Fig. 2) support the placement of these larvae into the Tank subtype because of the defensive carapace and sub-quadrate maxillipeds (not shown in photo). Additionally, the larvae of *L. maculata* have the pseudonym *Lysioerichthus duvaucellii* (Bigelow, 1931) and the description of this larva closely matches the common characteristics of other Tank subtype larvae found here (Brooks 1886; Shanbhogue 1975). A single antizoea of this species (Fig. 5N) was captured offshore of the southern coast of O‘ahu (site 5), which was similar (99%) to *L. maculata*, supporting their continued presence here. Adults of this species notably occur among the sandy flats of Kāne‘ohe Bay, O‘ahu (site 3), and a long-lived individual was reported to accept food from locals for several years.

TABLE 4. Morphological differences observed among Erichthus-type larvae with associated taxonomic identity assigned from molecular barcoding. Measured characters included: total length (mm) measured from rostral tip (when present) to telson tip; the intermediate denticles (IMD), submedian denticles on one side (SMD), and number of median (MD) carina present on the telson; spines and marginal teeth observed on the 6th abdominal somite (A6); general shape and features of the raptorial appendage (maxilliped 2). Dashes (—) indicate measurements could not be taken due to specimen damage or because records do not exist. Number of specimens observed for each morphotype are represented in parentheses after barcoding ID. For specimens where 0 larvae were observed, references were taken from Shanbhogue (1975).

Morphotype	Barcoding ID	TL (mm)	Maxilliped Shape	Number of Rostral Features		Number of Telson Features			A6 features		Raptorial appendage features	
				Spines	D	IMD	SMD	MD carina	Spines	Margin Teeth	Propodus	Dactyl
Lysiosquilloidea												
Tank—LysET A	*Lysiosquillidae* (1)	18	quadrate	0	0	1	30	0	0	2	straight	straight
Tank—LysET B	*Lysiosquillidae* (9)	30	quadrate	0	0	0	30	0	0	0	straight	straight
Tank—LysET C	*Lysiosquilla maculata* (0)	14.5	quadrate	1	–	2	35–39	–	2	0	straight	straight
Rocket—NanET A	*Pullosquilla* **n. sp.** (1)	9	quadrate	–	–	0	12	0	0	2	ovate	curved
Rocket—NanET B	*Acanthosquilla* sp. (3)	6–7	quadrate	0	9	2	8–9	0	0	0	ovate	curved
Flying Saucer—LyET A	— (2)	28–42	quadrate	0	0	3	40–50	0	0, 2	0, 2	ovate	curved
Spiny Balloon—LyET B	— (1)	16	quadrate	0	0	2	12	0	0	2	ovate	curved
Gonodactyloidea												
Blow Dart—GonET A	*Gonodactylaceus falcatus* (0)	2.5–2.9	–	–	–	–	13–21	0	2	0	ovate	curved
Blow Dart—GonET A	*Gonodactylellus* **n. sp.** (0)	5.6	–	–	–	–	–	–	–	–	–	–
Gnome Hat—ProET A	*Echinosquilla guerinii* (1)	13	ovate	3	0	2	–	0	0	0	ovate	curved
Torpedo—PseET A	*Pseudosquilla ciliata* (45)	21–24	ovate	1	0	2	15–20	0	0	2	straight	straight
Torpedo—PseET B	*Pseudosquillana richeri* (2)	14	ovate	0	6	2	8	0	0	2	straight	straight
Torpedo—PseET C	*Pseudosquillisma oculata*/ Pseudosquillidae (3)	24–34	ovate	2	1	2	18	1	0	2	straight	straight
Lance—OdoET A	*Odontodactylus brevirostris* (5)	16	ovate	0	5	2	25	1	0	2	straight	straight
Lance—OdoET B	*Odontodactylus* sp. (4)	23	ovate	0	4	2	14–15	0	0	2	straight	straight
Lance—OdoET C	*Odontodactylus* sp./ *Odontodactylus brevirostris* (10)	24–27	ovate	0	5	2	14–17	1	0	2, 4	straight	straight
Unknown												
Brawny—UnET A	– (4)	19–23	ovate	0	0	2	12–25	1	0	2	ovate	curved
Brawny—UnET B	– (1)	23	ovate	0	0	3	17	1	0	2	ovate	curved

Rocket Subtype—Nannosquillidae

Compared to the deep carapaces of Tank subtypes, the carapace of Rocket subtype larvae is shallower and narrower, giving the larvae a more streamlined appearance than the bulky Tank subtype (Fig. 5). The carapace of the Rocket larvae extends to different abdominal somites (AS), possibly depending on the genus of the larvae, and have remarkably long posterolateral spines (Fig. 5L, M). As the family name, Nannosquillidae, would suggest, these larvae are also much smaller than the lysiosquillid larvae, reaching maximum sizes of 10 mm among the collected specimens.

Morphotype NanET A—*Pullosquilla* n. sp.

One NanET A larva (9 mm) found offshore in a shallow trawl (0–160 m) near the coast West Hawai‘i (site 10) was barcoded. The distinctly shortened carapace (reaching only abdominal somite 3) of this morphotype distinguishes it from the other, more defensive looking morphotypes of Lysiosquilloidea (Fig. 5F, L). The telson of this larval stage had 3 primary teeth, 1 large IM denticle and 12 pairs of SM denticles. Genetically, these larvae are a species of *Pullosquilla* Manning, 1978*,* incorrectly referred to as *Coronida* Brooks, 1886, by Townsley (1953), for specimens from the Ala Wai canal in Honolulu, Hawai‘i. One *Pullosquilla* post-larva was collected from Maui (site 7) and reared to an adult, and genetic sequence from this specimen distinguish this species from its Australian relatives *Pullosquilla litoralis* (Michel & Manning, 1971) (88% similarity) and *Pullosquilla thomassini* Manning, 1978 (85% similarity). Adults were also found in Kāne‘ohe Bay, Hawai‘i and were collected for morphological comparison. Adults of this species are translucent white with white chromophores and orange coloration can be observed through the translucent cuticle from the ripe ovaries of adult females, much like *P. litoralis* (Ahyong 2001). It is likely that this is an undescribed species of *Pullosquilla* since no adults have been previously reported from Hawai‘i, and telson features of the Hawaiian species do not match either *P. litoralis* or *P. thomassini*. One antizoea (Fig. 5N) was also collected from nearshore O‘ahu, which barcodes to the Hawaiian *Pullosquilla* sequences. All three *Pullosquilla* sequences are 98–99% similar to each other, suggesting this species exists on at least three Hawaiian Islands (Maui, O‘ahu, and Hawai‘i).

TABLE 3. Morphological differences in larval carapace and telson characters among morphotypes of Squillidae Alima-Type (SquAT) larvae, with associated taxonomic identity assigned from molecular barcoding.

	SquAT A	**SquAT A**	**SquAT B**	**SquAT C**
Barcoding ID	*Busquilla* sp.	*Oratosquilla fabricii*	*Alima* sp.	Squillidae
Total length (mm)	30–49	26–48	35–46	25–33
Carapace length (mm)	20–22	18–22	22–23	15–16
Carapace width (mm)	6–10	8–10	6–7	4–6
Telson height (mm)	5–8	5–6	8	4
Telson width (mm)	3–5	4–5	3	4
Carapace anterior margin spinules	12–16	10–13	9	1
Carapace posterior margin spinules	4–5	5–6	4–5	2
Telson IM denticles	8–10	6–8	12	8
Number of larvae measured	73		4	5

Morphotype NanET B—*Acanthosquilla*

Three NanET B larvae between 6–7 mm total length were collected from deep trawls (0–550 m) from sites 11 and 14 off West Hawai‘i, of which two could be barcoded. These larvae appear very compact compared to other lysiosquilloid larvae: the carapace of these larvae is quite long, often extending beyond the 6th abdominal segment, and tightly tucked around the body of the animal with greatly elongate rostral and posterolateral spines (Fig. 5G, M). This is a feature shared by species of *Acanthosquilla* in the Red Sea (Gurney 1946; Shanbhogue 1975). Unlike other lysiosquilloid larvae thus far, markedly fewer telson SM denticle pairs (8–9) were observed with three primary teeth and two IM denticles. A median carina on the telson and single spine on the propodus of the raptorial claw on the larger individual could indicate a stage difference. The dactylus of both specimens have a slightly inflated heel and no spination. A blue coloration was also observed on the dorsal surface of the telson of both specimens

after preservation in ethanol. Previously, NanET B was recorded as coroniderichthus; expected to be in the genus *Coronida* by Townsley (1953). The family Lysiosquillidae has since undergone major revisions introducing the families Nannosquillidae and Coronididae (Manning 1980). Morphology of larvae attributed to the family Coronididae from India suggest large triangular carapaces would be present in larvae of *Coronida* (Shanbhogue 1975), which does not match the specimens seen here; though identification of larval coronidids remains to be confirmed. Additionally, few species of Coronididae are present in the Pacific (Ahyong 2001). Instead, this could be the larvae of the nannosquillid, *Acanthosquilla multifasciata*, which occurs in Hawai'i (Ahyong 2002a). The observed larval morphology closely matches descriptions of *Acanthosquilla* larvae in the Arabian Sea, although previous reports of *A. multifasciata* larvae found 4 ventral rostral spinules (Shanbhogue 1975), while the Hawaiian specimens had 9; therefore only genus level identification was made here. These larvae do not cluster closely with any identified adult genetic sequences, though they do cluster distantly with *Acanthosquilla derijardi* Manning, 1970 (82% similar), supporting this as a member of Nannosquillidae.

Flying Saucer Subtype—Lysiosquilloidea

The flying saucer larval subtype, coined initially by Haug *et al*. (2016) from Gideon's larva 2, is characterized by a flattened, wide carapace, extending well beyond the margins of the abdomen (Fig. 5H, I). The wide wing-like structures on the carapace fold ventrally inward to form nearly closed pockets on the lateral edges of the animal. It is important to note that the initial description of the flying saucer larvae was based on Australian species with ovate maxillipeds, while the larvae described here had sub-quadrate maxillipeds, suggesting either the superfamily Erythrosquilloidea or Lysiosquilloidea. Because the COI sequence of this morphotype was nested within the superfamily Lysiosquilloidea (Fig. 3), it is suggested to be a member of this group, rather than Erythrosquilloidea, which is predicted to be sister to Lysiosquilloidea (Van Der Wal *et al.* 2017).

Morphotype LyET A

Two relatively large (28 and 42 mm) individuals were collected: one during the day in a deep (650–973 m) trawl off the west coast of O'ahu (site 1) and the other from a shallow (0–177 m) night trawl (site 11) off the coast of West Hawai'i. The telson of these larvae had 3 primary teeth, with 3 IM denticles, and over 40 pairs of SM denticles. One individual (42 mm) had two prominent, dorsally pointed spines on AS6, while the other (28 mm) had two flattened marginal teeth instead. The raptorial appendages of these larvae have wide, ovate propodi with scimitar shaped dactyls. The larger individual had very inflated propodus and dactyl compared to the smaller individual, which could suggest these differences are developmental. Genetically these larvae were nearly identical (98%), so it is likely that they represent two different developmental stages of the same species. No evidence of the flying saucer morphotype has been documented from the Hawaiian Islands previously, which may indicate this is either a new introduction or a rare undescribed species. The original descriptions of flying saucer larvae predicted this morphotype to be in the family Tetrasquillidae (Haug *et al.* 2016). It is possible that these are larvae of *Heterosquilloides insignis*, which are found in deep water habitats (380–435 m) (Ahyong 2001) or *Tetrasquilla mccullochae* (Schmitt, 1940), which is recorded from French Polynesia; neither has characterized larval morphologies. However, a lack of genetic information and previous descriptions of this morphotype make it impossible to offer an identity for this larval morphotype beyond the level of superfamily.

Spiny Balloon Subtype—Lysiosquilloidea

The Spiny Balloon morphotype was initially described by Haug *et al.* (2016) from a single specimen of 18 mm in length with sub-quadrate propodi, indicating this to be a lysiosquilloid or erythrosquilloid.

Morphotype LyET B

A single individual of LyET B (16 mm) was found in a shallow trawl (0–177 m) at site 11 off the West coast of Hawai'i. The posterolateral spines are similar in length to the rostral spine, and extend only to the tip of the telson. The telson has three primary teeth with 2 IM denticles, and 12 pairs of SM denticles. The carapace of this larva is cordiform, with a tip formed anteriorly and slightly inflated ventrolateral pockets (Fig. 5J, K). The rostral and posterolateral spines of this specimen were damaged, and complete length could not be determined. Genetically this species clusters weakly within Lysiosquilloidea, near Lysiosquillidae (Fig. 3). A flattened uropodal basiopodal spine on Gideon's Larva 1 suggested that the larva was a member of Tetrasquillidae (Haug *et al.* 2016), but the

uropods of this larva were not developed enough to see this spine. Without more genetic representation of other lysiosquilloid families, including Tetrasquillidae and Coronididae, it is not possible to determine the family of this larval morphotype.

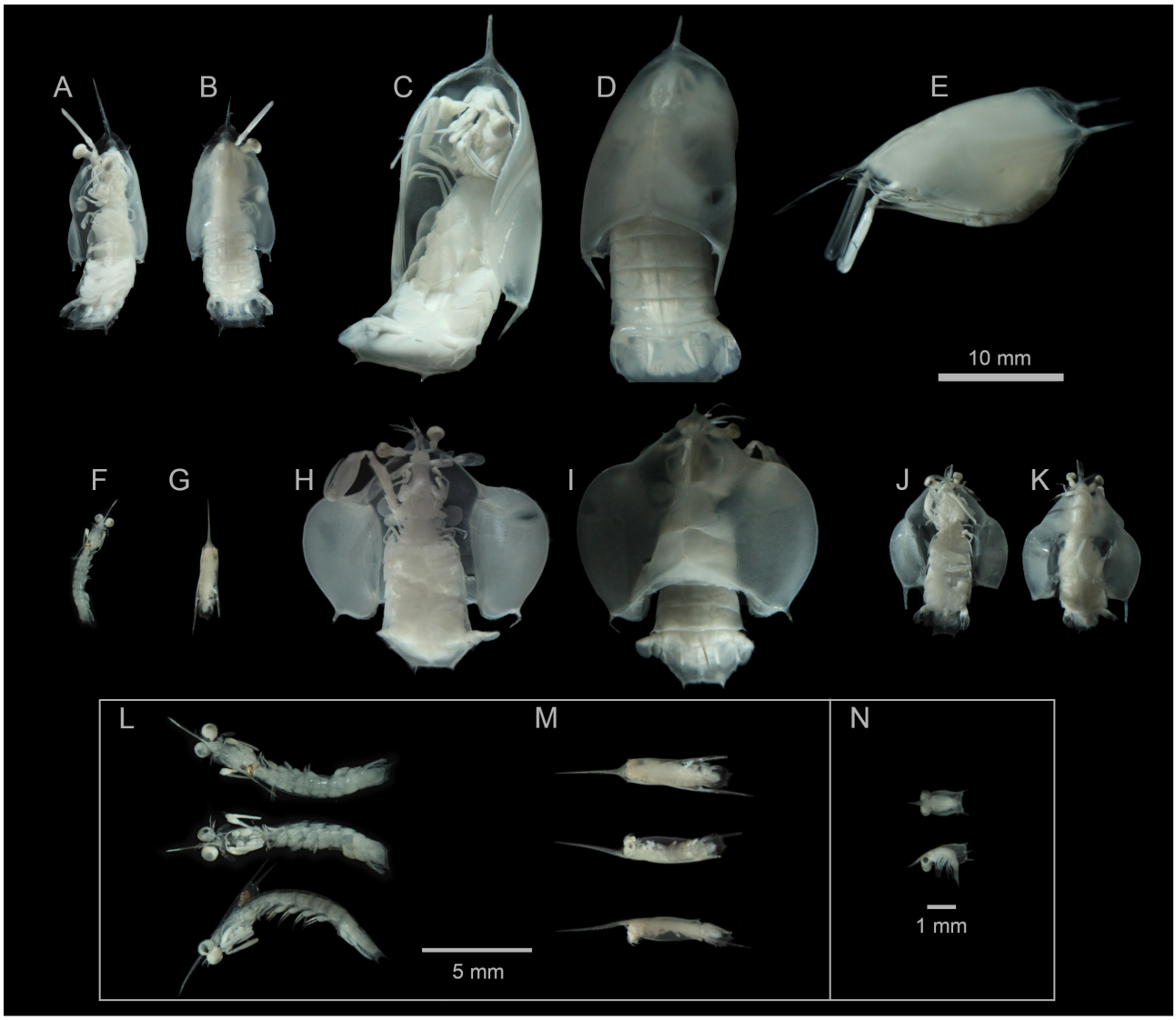

FIGURE 5. Lysiosquilloidea erichthus-type larval subtype and morphotype morphology. **Tank types**: LysET A—Lysiosquillidae ventral (A) and dorsal (B) views; LysET B—Lysiosquillidae ventral (C), dorsal (D), and lateral defensive posture (E) views. **Rocket types**: NanET A—*Pullosquilla* n. sp dorsal view (F); NanET B—Nannosquillidae dorsal view (G). **Flying Saucer type**: LyET A—ventral (H) and dorsal (I) views. **Spiny balloon type**: LyET B—ventral (J) and dorsal (K) views. Close up of Rocket types: NanET A (L) and NanET B (M): dorsal (top), ventral (middle), and lateral (bottom) views. Scale bar of 10 mm applies to images A-K. Scale bar of 5mm applies to images L and M only. Antizoea larva of *Lysiosquilla maculata* with 1 mm scale bar; dorsal (top) and ventral (bottom) views (N).

Gonodactyloidea

Four subtypes were found in the superfamily of Gonodactyloidea, in order of smallest to largest total length: Blow Dart, Gnome Hat, Torpedo, and Lance. Of these, Blow Dart subtypes were consistently the smallest (<5 mm) and individuals were all collected from nearshore O‘ahu habitats; Gnome Hat subtypes could be identified by their distinctive triangular shape, as named by Haug *et al.* (2016); Torpedo subtypes could be identified by a prominent accessory rostral spine (with the exception of the single *Pseudosquillana* larvae, with a broken rostral spine); and Lance subtypes could be quickly distinguished by their long telson spines. In total, nine genetic groups were identified from eight morphotypes with seven genetically identified to the species level, one to genus, and one to

family. The adult habitats of the gonodactyloids tend to be rocky bottom or coral substrate from shallow intertidal flats to deeper reef habitats (Ahyong 2001). The larvae of this group were equally ubiquitous in our sampling, appearing in all pelagic habitats sampled, though not in nearly as many numbers as the squilloids.

Blow Dart Subtype—Gonodactylidae

The Blow Dart subtype has, perhaps, some of the best described erichthus-type larvae with eight instars being described for *Neogonodactylus oerstedii* (Hansen, 1895) (Provenzano & Manning 1978) and *Neogonodactylus bredini* (Manning, 1969) in Morgan & Goy 1987). This larval subtype develops walking legs at the final pelagic stage, which can be seen as elongating buds in earlier stages. The propodi of maxillipeds 3–5 are ovate, the raptorial appendage has an ovate propodus and the dactyl is scimitar shaped (Table 4). In general, Blow Dart subtypes spend their fourth and fifth stages in the pelagic, and some comparisons of stage V (second pelagic stages) larvae have been done (Provenzano & Manning 1978). In Hawai‘i, two species in Gonodactylidae have been documented: *Gonodactylaceus falcatus* and *Gonodactylellus snidvongsi* (Naiyanetr, 1987) (Ahyong 2002a). While the fifth stage has been described in *Gonodactylaceus falcatus* (Shanbhogue 1975), not much is known of the *Gonodactylellus* larvae that are found in the same habitats (as reported here). *Gonodactylellus snidvongsi* itself, is now known to represent a species complex (Ahyong & Erdman 2007; Ahyong 2016), and what has been reported from Hawai‘i under that name (as well as *Gonodactylus hendersoni* Manning, 1967) represents an undescribed species currently under study, introduced from the Indo-Malaysian Pacific; we refer to it here as *Gonodactylellus* **n. sp.** (see below). Based on the morphology of the adults collected for this study, the larvae presented here are likely to be *Gonodactylellus* **n. sp.**

Morphotype GonET A—*Gonodactylaceus falcatus* and *Gonodactylellus* n. sp.

All GonET A larval traits reported here are from ten specimens collected hand nets or light traps in shallow (0–2 m) habitats of Kāne‘ohe Bay, O‘ahu (site 3) and live sorted. Because of this, any morphological differences were observed while the animals were alive, rather than after preservation as with the other larval-types. These small larvae molt into slightly larger (up to 10 mm) post-larvae with different colored eyeshine: those of *Gonodactylaceus falcatus* are green-gold (adult retina) and black (larval retina), while those of *Gonodactylellus* n. sp. have burgundy-gold (adult retina) and white (larval retina) eyeshine. When collecting larvae during the same lunar cycle, *Gonodactylellus* n. sp. are relatively larger (approximately 5 mm) with a full-body green hue while those of *G. falcatus* are smaller (approximately 3–4 mm) with a brown hue in life. Based on size, the *G. falcatus* larvae collected were likely at stage III or IV (Shanbhogue 1978). It is unknown what stage the *Gonodactylellus* larvae were, as a full developmental cycle including all larval stages has not been described. It is known that the largest specimens of *G. falcatus* at stage V can reach approximately 4.5 mm, which could be used as a distinguishing trait to differentiate from the larger (6 mm) *Gonodactylellus* larvae (Fig. 6A). Closer morphological examination would be needed to identify larvae smaller than 4.5 mm, as it is unknown what the minimum size of the *Gonodactylellus* larvae can be, and not enough individuals were captured in this study to make that distinction. Genetically, these two species are very distinct, with *G. falcatus* (OTU 98% similarity) clustering with other *Gonodactylaceus* species and *Gonodactylellus* clustering near *G. snidvongsi* (85% similarity) (Fig. 3). There is evidence suggesting *Gonodactylellus* is a polyphyletic genus (Barber & Boyce 2006; Ahyong 2022). The Hawaiian *Gonodactylellus* sp. and *Gonodactylellus snivongsi* were both deeply divergent from the other species of *Gonodactylellus*, which would further support polyphyly of this genus. The presence of *Gonodactylellus* has long been a topic of confusion in Hawai‘i. *Gonodactylellus* **n. sp.** in Hawai‘i has been variously misidentified as *Gonodactylellus demanii* (Henderson, 1983), *G. hendersoni,* and *G. snidvongsi* (Manning 1967; Ahyong 2002a). *Gonodactylellus* **n. sp.** is a member of the *molyneux*-group in *Gonodactylellus* (Ahyong 2001), which is phylogenetically nearest to the genera *Hoplosquilla* Holthuis, 1964 and *Gonodactylopsis* Manning, 1969 (Ahyong & Erdmann 2007; Ahyong 2022). *Gonodactylaceus falcatus* has been present in Hawai‘i since its introduction from the Philippines or South China Seas via concrete barges (Manning & Reaka 1981) and continues to be seen regularly in shallow reef habitats around Hawai‘i. The adults of *Gonodactylellus* **n. sp.** Have been found in the same rubble substrate as juvenile *G. falcatus*. It is unlikely these two species compete heavily for space as adults, since the *Gonodactylellus* are much smaller in size (17 mm) and burrow within the rubble, while the *G. falcatus* (to 60 mm) are more often found in burrows under the same rubble (adults have been seen at sites 3 and were collected from site 6 for this study). Ecological studies would need to be done to look into the interactions of these two species to make any conclusive remarks. It is possible that earlier stages of this morphotype are present from the pelagic trawls; however they would have been excluded from this study based on our size sorting (>5mm).

Gnome Hat Subtype—Protosquillidae

The Gnome Hat subtype is in the family Protosquillidae, and have previously been described with specimens like "Morphotype 4: gnome-hat larvae" (Haug *et al.* 2016). The carapace is squared or trapezoidal in dorsal view, with prominent spines present on each corner. These larvae are well suited for defensive postures as the telson tucks completely into the carapace for protection (Haug & Haug 2014) making body observations difficult after preservation. Proterichthus larvae of *Chorisquilla tuberculata* (Borradaile, 1907) are currently the only other species of this larval subtype described (Michel & Manning 1972).

Morphotype ProET A—*Echinosquilla guerinii*

A single Gnome Hat larvae (13 mm) was found in a shallow trawl (0–160 m) at site 10 off West Hawai'i. The carapace of this animal expands around the body, has slight depressions on the lateral sides, and prominent spines can be seen on each corner of the inflated carapace as well as the most dorsal point (Fig. 6B). The maxillipeds of these larvae are ovate. The telson has two IM denticles, and numerous (more than 30 pairs) SM denticles, unlike the Gnome Hat larvae described by Haug *et al*. (2016), which only has 20 pairs of SM denticles and one IM denticle. The 6th abdominal somite was not ornamented with spines or marginal teeth. Barcode sequences from this morphotype matched *Echinosquilla guerinii* (99% similar), a protosquillid previously documented in Hawai'i with a uniquely spiny telson known to inhabit rocky substrate at depths of 12–25 m (Ahyong 2001, 2002a). Adults of this species tend to inhabit deeper reef burrows and have been found in Western O'ahu up to 24 m in depth (site 2, personal observation).

Torpedo Subtype—Pseudosquillidae

These larvae can be quickly identified by their long slender appearance, shortened carapace (not reaching past the thoracic somites), and short carapace spines. This larval subtype has ovate maxillipeds and a terminally articulated uropodal exopod as in the family Pseudosquillidae. The Torpedo larvae collected in this study were divided into three morphotypes, separated by a paddle telson shape (as in PseET A, *Pseudosquilla ciliata*), dorsally recurved accessory rostral spine (as in PseET C) or a small late stage larvae (less than one centimeter, as in PseET B, *Pseudosquillana richeri*, Fig. 6B). Adults of this family inhabit coral reefs and associated seagrass beds from intertidal to 86 m depth, often under boulders or rubble rather than in crevices (Ahyong 2001) The larvae of *P. ciliata* and *P. richeri* were found exclusively in shallow trawls (0–212 m) at sites 9 and 12, while morphotype PseET C was present in both shallow and deep (0–500 m) trawls from sites 9, 10 and 12.

Morphotype PseET A—*Pseudosquilla ciliata*

The larvae of *Pseudosquilla ciliata* are the best known pseudosquillids, once being described as *Pseuderichthus communis* (Hansen, 1985) (Shanbhogue 1975; Townsley 1953). Forty-five PseET A larvae were found off the coast of West Hawai'i ranging between 21 mm and 24 mm total length (TL), seven of which were barcoded. The carapace of these slender larvae tucks closely around the body, but do not fold inward as in the larvae of Lysiosquilloidea, and do not extend past the last (eighth) thoracic somite (Fig. 6C). The telson has 2 IM denticles, and 20 pairs of SM denticles, with no lateral lobe. Often a red iridescence was observed in the margin between the SM teeth of preserved specimens. The raptorial appendages of this larval stomatopod are remarkably narrow in comparison to previous morphotypes, with both the dactyl and the propodus being relatively straight. All larvae identified here genetically matched sequences from *P. ciliata* (99–100% similarity, Fig. 3). *Pseudosquilla ciliata* has been observed in Hawai'i since early stomatopod explorations in 1886, and was reportedly displaced by invading *G. falcatus* in shallow reef habitats (Kinzie 1968). *Pseudosquilla ciliata* can still be found in burrows of fine muddy substrate or in areas with high algal growth in Hawaiian shallow reef habitats.

Morphotype PseET B—*Pseudosquillana richeri*

The smallest of the Torpedo subtype is PseET B (14 mm, Fig. 6B). Two larvae of this morphotype were found off the West Coast of Hawai'i, only one of which could be barcoded. The rostral spine of these specimens was broken, and could not be observed. The telson of this larva had three primary teeth, two IM denticles, and eight pairs of SM denticles. While no specific literature could be found with larvae similar in morphology to this individual, it is clear from the narrow carapace, thin raptorial appendage, and general body shape that it belongs to the Torpedo subtype. This larva barcoded to *Pseudosquillana richeri* (98% similarity, Fig. 3), a species that has not previously been

recorded in the Hawaiian Islands (Ahyong 2002a). *Pseudosquillana richeri* is widely distributed from the Red Sea to Australia, and throughout Oceania and French Polynesia (Poupin *et al.* 2019), therefore it is not surprising that this species is present in Hawai‘i. During the 2018 summer surveys of adult stomatopods from Kāne‘ohe Bay, two adult *P. richeri* were personally observed, indicating this species has successfully colonized Hawaiian waters.

Morphotype PseET C—*Pseudosquillisma* sp. or Pseudosquillidae

Three larvae (24–34 mm) were found off the coast of West Hawai‘i and barcoded, each having a distinct, dorsally recurved rostral accessory spine and one rostral denticle (Fig. 6D). The telson has 2 IM denticles, 18 pairs of SM denticles separated by a central bifurcation, and a pronounced median carina on the dorsal surface. Otherwise, this morphotype was very similar in form to that of PseET A, with a slender build and long body. In the literature, pseudosquillid larvae are rare and often not described. Often post-larval descriptions of species of *Raoulserenea* Manning, 1995 and *Pseudosquillisma oculata* (Brullé, 1837) were reported together, as morphologically these two genera are very similar. One reported difference at this stage is *Raoulserenea* having postero-lateral spines on AS4–5 instead of AS5 only in *P. oculata* (Ahyong 2002a). Posterolateral spines on AS4 were not observed on any of the specimens here. Species within the genera *Raoulserenea* and *Pseudosquillisma* can be identified as adults by the number of dorsolateral carinae on the telson, which have yet to develop in larvae and post-larvae, making this larval morphotype difficult to distinguish. Early stages of a pseudosquillid larvae, thought to belong to *P. oculata*, were previously named *Pseuderichthus distinguendus* (Hansen, 1895). *Pseudosquillisma oculata* has been attributed a near cosmopolitan distribution, but it represents a species complex, with true *P. oculata* only in the Atlantic Ocean (Ahyong 2014). Nevertheless, the species of the complex are all very similar as adults, so it is likely that larvae will also be similar. The description of larvae under the name *P. oculata* from the Arabian Sea (Shanbhogue 1975), which would correspond to *Pseudosquillisma tweediei* Ahyong, 2014, closely matches the morphology of the larvae seen here. Genetically, these notes on morphology are supported as one larva could be identified as the Indo-Pacific *P.* ‘*oculata*’ (98% similarity) while two individuals clustered outside *Raoulserenea* (86–88% similarity). While *Pseudosquillisma* has been reported from Hawai‘i, thus far, there have been no instances of *Raoulserenea* species documented from Hawai‘i.

Lance Subtype—Odontodactylidae

As observed by Townsley (1953) and Michel (1970) the Erichthus-type larvae of the genus *Odontodactylus* Bigelow, 1983 can be quickly distinguished from other Erichthus-type larvae by the long, curved primary teeth of the telson. The Lance subtype have been reported to have very slender raptorial appendages, like the Torpedo subtype, but lack the pectination along the upper margin of the propodus and the dactylus is slightly inflated at the base (Townsley 1953). While previous observations did not have direct evidence to support these features being unique to the genus *Odontodactylus* (i.e., lack of figures), the genetic and morphological data collected here support that these are unifying features of Lance subtype larvae. At least two developmental larval stages were collected from two species of *Odontodactylus*. Because the number of developmental stages of Odontodactylus is not known, the staging could not be identified here. Predicted earlier stages of the two species (OdoET A and OdoET B) are distinguishable morphologically and genetically, but the predicted later stage (OdoET C) did not have any morphological differences that could be identified here. Subsequently, individuals from the later stage were either *Odontodactylus brevirostris* or a different species of *Odontodactylus*. Three species of *Odontodactylus* have been described from Hawai‘i: *O. brevirostris*, *Odontodactylus hawaiiensis* Manning, 1967, and *Odontodactylus hansenii* (Pocock, 1893) (Ahyong 2002a). As adults, these three species are very similar, being distinguished primarily by the number of raptorial teeth and features of the telson carinae (Manning 1967). These features have yet to develop in the larvae, which may contribute to the lack of distinction in later stage larvae. Adults of *O. brevirostris* were collected from a field of coralline algal clusters that had been used to build rubble burrows between 24–27 m depth in May 2016 from western O‘ahu (site 2). Occasionally, adults were also found hunting on a reef shelf at shallower depths (12–18 m) but we were unable to collect any of these individuals while diving with hand nets. All *Odontodactylus* larvae were found both in shallow (0–160 m) and deep (0–570 m) trawls at sites 10–14.

Morphotype OdoET A—*Odontodactylus brevirostris*

Five Lance subtypes, OdoET A (23-25mm), were collected from West Hawai‘i (Fig. 6E) of which two from deep (0-550 m) night trawls could be barcoded. The rostral spine of this morphotype has five denticles, while the telson

has 3 margin teeth, two IM denticles, and 25 pairs of SM denticles. This morphotype has a distinct median carina on the dorsal surface of the telson, and two teeth on the margin of the AS6. A description of larvae similar to these is presented by Townsley (1953), though the size range in the larvae found previously may indicate that multiple species were present in his sampling. A similar sized larva was examined from the Marquesas that was identified as *O. brevirostris* (Ahyong 2002b). Genetically, these larvae clustered closely with sequences from an *O. brevirostris* adult from O‘ahu, Hawai‘i (99–100% similar, Fig. 3) and are thereby identified as such. *Odontodactylus* are widespread throughout the Pacific and have been observed in Hawai‘i as early as the 1870s on the H.M.S Challenger at depths greater than 100 m (Brooks 1886).

Morphotype OdoET B—*Odontodactylus* sp.

Four smaller Lances (16 mm TL) of OdoET B were found off the coast of West Hawai‘i, although only one from a deep (0-550 m) night trawl was barcoded. This morphotype looks nearly identical to OdoET A except for having four rostral denticles (rather than 5), 14–15 pairs of SM teeth, and lack of a median carina on the telson. The small size of this Lance subtype larva could indicate either a developmental difference from OdoET A, or a distinct larval group. Michel (1970) recorded a 16 mm *O. brevirostris*-like larval group, which were later established as belonging to either *O. hansenii* or *Odontodactylus havanensis* (Bigelow, 1893) (Ahyong 2001). Of those suggested species, only *O. hansenii* have been recorded in Hawai‘i. During larval stages, *O. hansenii* are more developed at smaller sizes than *O. brevirostris* and become well developed post-larvae at 25 mm, while *O. brevirostris* are not well developed until about 30 mm (Ahyong 2001). *Odontodactylus hawaiiensis* also has ‘smaller’ post-larvae (26 mm), and by inference smaller late larvae, which would place it in the same size groups as *O. hansenii*. This larva was genetically distinct from *O. brevirostris* (83% similar), forming a separate sister clade (Fig. 3). This morphotype is hypothesized to belong to one of either species previously found in Hawai‘i—*O. hawaiiensis* or *O. hansenii,* neither of which has COI data available (Ahyong 2002a).

Morphotype OdoET C—*O. brevirostris* or *Odontodactylus* sp.

Ten larvae of this morphotype, ranging in size from 24–27mm TL, were collected from West Hawai‘i, of which five from deep (0-550 m) night trawls were barcoded successfully. It appears that both early stages (OdoET A and B) molt into OdoET C, and previous morphological differences disappear, resulting in mixed genetic results. It is also possible that larval morphotypes of these two species are difficult to distinguish at all stages, as OdoET A may be a later stage than the OdoET B captured were. All specimens had five rostral denticles, 2 IM denticles, 17 pairs of SM denticles, and a median carinae. The raptorial appendages of these specimens were slender and straight, lacking pectination. Literature suggests larvae may be distinguished by size (for *O. brevirostris* and *O. hansenii*) (Ahyong 2001), but that was not the case here for individuals smaller than 25 mm. The largest and smallest individuals that were sequenced clustered with OdoET B (Fig. 3), which would have developed into post-larvae by 25 mm if it were *O. hansenii* (Ahyong 2001). Consequently, the *Odontodactylus* larvae for OdoET B and OdoET C may represent *O. hawaiiensis*, as no other species of *Odontodactylus* have been found in Hawai‘i, though this could not be confirmed in this study.

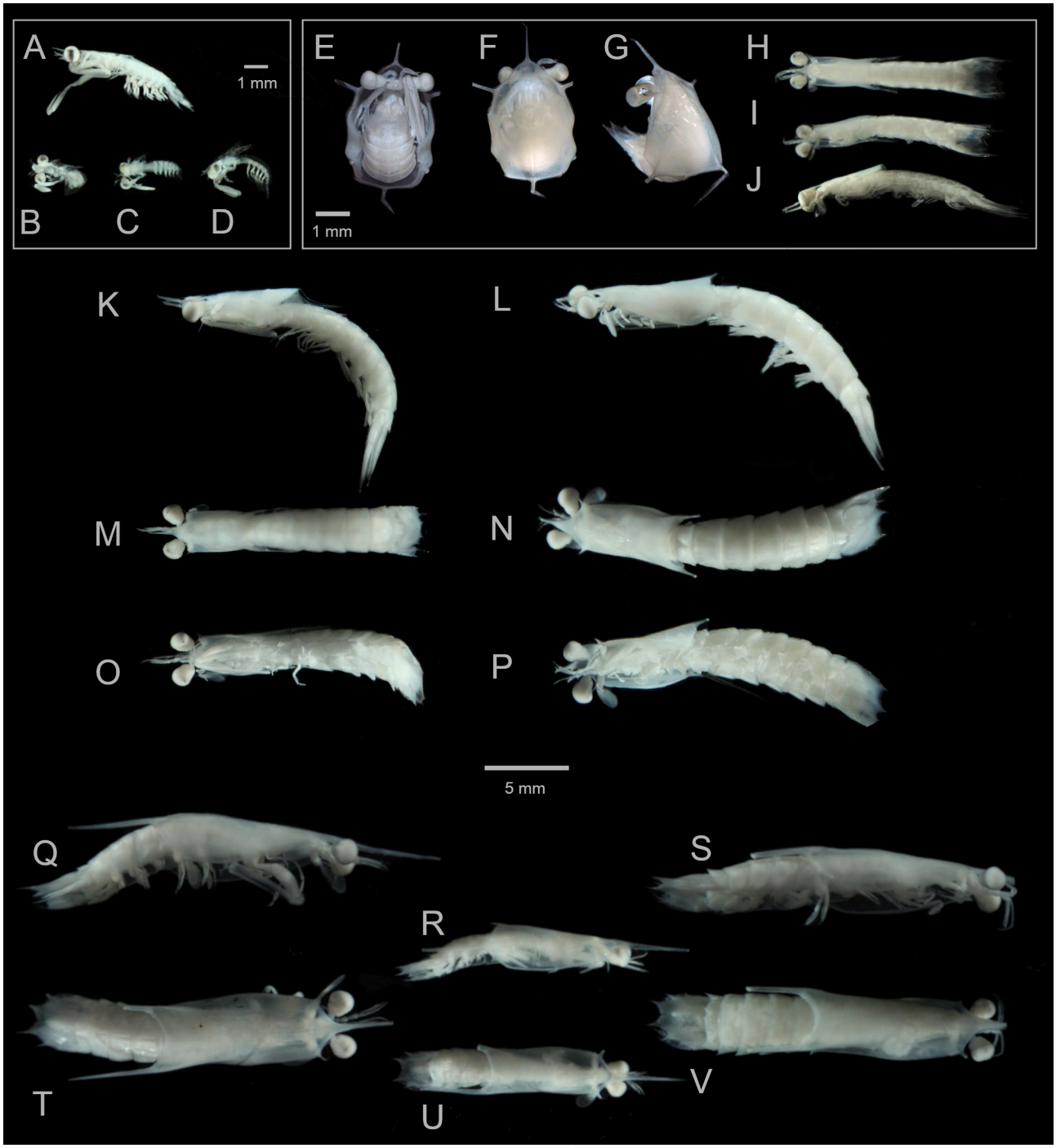

FIGURE 6. Gonodactyloidea erichthus-type larval subtypes and morphotypes. **Blow Dart type**: GonET A—Gonodactylidae; *Gonodactylellus* **n. sp.** lateral view (A) and *Gonodactylaceus falcatus* ventral (B), dorsal (C), and lateral view (D). **Gnome Hat type:** ProET A—Protosquillidae; *E. guerini* ventral (E), dorsal (F), and lateral view (G). **Torpedo type**: Pseudosquillidae; PseET B—*P. richeri* dorsal (H), ventral (I), and lateral views(J); PseET A—*P. ciliata* (K, M, O) and PseET C - *P. oculata* or unknown pseudosquillid (L, N, P) lateral, dorsal, ventral views respectively. **Lance type:** Odontodactylidae; OdoET A—*O. brevirostris* (Q, T) OdoET B—*Odontodactylus* sp. (R, U) and OdoET C—*O. brevirostris and Odontodactylus sp*. Lateral and dorsal views. Scale bar 5 mm applies to images K-V.

Unknown Superfamilies

Two larval morphotypes were collected that we could not morphologically or molecularly place within a superfamily. Both morphotypes were relatively large (>20 mm), and at first glance could be mistaken for post-larvae based on their shortened carapace and well developed telson, pleopods, pereiopods, and maxillipeds. These larvae have quite enlarged raptorial propodi, in comparison to other erichthus-type larvae (with the exception of the flying saucer type), and was named the 'Brawny' subtype. Likely these morphotypes belong to one of three superfamilies which are known from deep water (>100 m) habitats, as few molecular sequences are represented from any of these superfamilies. The larvae were found only from offshore trawls, despite their late stage appearance and relatively large size.

Brawny Subtype—Unipeltata

Morphotype UnET A—Eurysquilloidea or Parasquilloidea

Four individuals (19–23 mm) were collected from West Hawai'i in both shallow (0–177 m) and deep (0–550 m) trawls from sites 11 and 12; of these four, three were barcoded. All individuals had one well defined median carina on their telson, as well as two teeth on the margin of the sixth abdominal somite (Fig. 7A, C, E). The maxillipeds 3–4 of this morphotype are ovate, suggesting Gonodactyloidea, Parasquilloidea, Eurysquilloidea, or Bathysquilloidea (Ahyong 2001). The telson has three primary teeth, 2 IM teeth, two primary spines on the uropodal protopod, and a subcylindrical body suggesting a gonodactyloid, or possibly eurysquilloid (Ahyong 2001; Manning & Camp 1993). The only gonodactyloid family without published COI sequences that may cluster with this group is Alainosquillidae (Ahyong & Harling 2000); however, this larva did not cluster with the representative *Alainosquilla foresti* Moosa, 1991 sequence included here (83% similarity). Genetically, this group clusters distantly with the eurysquillid, *Ankersquilla pardus* Ahyong, Porter & Caldwell, 2020 (Fig. 3). No larval morphology of eurysquillids has been documented, though the telson features and uropod of the larvae are similar to the characters of adult *A. pardus* (Ahyong *et al*., 2020). Late larval *Bathysquilla* Manning, 1963 already have the characteristically differentiated primary telson teeth and long raptorial claw, unlike the conventional layout of this post-larva, so it is unlikely to be a bathysquilloid. Potentially, it could be a parasquilloid, but none are known from the central Pacific and the uropod does not match. The published parasquilloid COI sequences also do not cluster closely with those of the Hawaiian specimens, increasing the likelihood that this morphotype belongs to Eurysquilloidea, which contains a single family, Eurysquillidae.

Morphotype UnET B—Bathysquilloidea or Eurysquilloidea

One individual (23 mm) found off the West coast of Hawai'i, in a deep (0–550 m) trawl at site 11, had an enlarged raptorial claw propodus and dorsally compressed body (Figure 7B, D, F). The uropodal protopod had two spines, the exopod was not yet articulated, and a prominent median carina was present on the telson surface. A movable spine was already present on the raptorial propodus, and fine pectinations were developing on the inner margin of the propodus. The ovate maxillipeds 3–4 and compressed body suggest taxonomic placement within the Eurysquilloidea or Bathysquilloidea (Ahyong 2001). Genetically, this species clustered between Odontodactylidae and a eurysquillid species: *Manningia pilaensis* (de Man, 1888), but was distinct from either group. Phylogenetically, Bathysquilloidea were expected to cluster within Gonodactyloidea, near Pseudosquillidae, while Eurysquilloidea were expected to cluster nearer Squilloidea and Parasquilloidea (Van Der Wal *et al.* 2017), but the proximity of *Manningia* in this region indicates more data is needed to discount Eurysquilloidea. The COI barcodes used in this study resulted in separation of the eurysquillid species available, as well as a split of the Odontodactylidae and Pseudosquillidae from other gonodactyloids, making inference from phylogenetics currently impossible. The genetic similarity of this larva to either *Odontodactylus scyllarus* (Linnaeus, 1758) or *M. pilaensis* was low (80%), which, by process of elimination, may suggest support for this larva being a bathysquilloid. Morphologically, one representative larva of Bathysquilloidea (*Bathysquilla crassispinosa* (Fukuda, 1909)) has been described from South Africa; however, the described specimen did not have a dorsally compressed body, and each abdominal somite was ornamented with a median spine on the posterior margin (Manning 1991), which is very different from the specimen presented here. The morphological difference might also suggest this larva as some type of eurysquilloid, though

Indosquillidae, within the superfamily Bathysquillidae, is known to have dorsal compression as an adult which may be observed in the larvae as well. As in the described bathysquilloid larva, the uropodal exopod is not yet articulated, though the characteristic primary telson teeth are not developed at this stage like we would have expected for this superfamily. Adults of *Bathysquilla microps* (Manning, 1961) have been found in Hawai‘i (Ahyong 2002a), while no eurysquilloids have been found. However, both these superfamilies are known to be even more secretive than other stomatopod taxa, as they inhabit deep water habitats and are seldom found alive. These conditions currently preclude determination of the superfamily placement of this larva.

FIGURE 7. Erichthus-type larvae of unknown superfamily designated as from Suborder Unipeltata (UnEt). **Brawny types:** UnET A (left) and UnET B (right), lateral (A, B), dorsal (C, D), and ventral (E, F) views. Scale of 10 mm applies to all images.

Discussion

In this study we combined molecular barcoding and morphological descriptions in order to create a means of identification for larval stomatopods from Hawaiian and other Pacific Island waters. Diagnostic morphological traits allow for characterization of larvae to species, and can be used to identify multiple stages within the genus *Odontodactylus*. As a first glance at Hawaiian species diversity, 20 morphotypes were established from 10 larval subtypes, with 22 OTUs identified from genetic barcoding. The 20 adult species previously documented from Hawai‘i include: one Bathysquilloidea, nine Gonodactyloidea, three Lysiosquilloidea, and seven species of Squilloidea (Ahyong 2002a). The larvae collected here, however, represent a different level of diversity among the superfamilies, which may be a result of sampling methods or could be due to species-specific reproductive seasonality. Using morphology and molecular data we identified zero Bathysquilloidea, nine Gonodactyloidea, seven Lysiosquilloidea, and only four species of Squilloidea, as well as two species that we were unable to place within a superfamily. Of the species expected to be in Hawai‘i, *Pseudosquillana richeri* was newly recorded. Many more larval forms likely exist in the Hawaiian Islands that have yet to be documented, especially in the case of the squilloids. Most notably, the larvae of the family Squillidae were numerous, but lacked the species diversity described based on adult populations (four OTUs here, as compared to seven known species). Supporting this notion, adults of the endemic species *Parvisquilla sinuosa* were found, but no larval morphotypes were collected,

possibly indicating a sampling bias against squilloid type larva, nearshore light trapping may offer more diversity for this, typically, shallow water group. Additionally, although there have been some major efforts to collect adult stomatopods from the Hawaiian Islands, it is clear from the diversity of larvae described in this study that there are still more species yet to be discovered, especially in the superfamily Lysiosquilloidea. In general, the morphology of larval characteristics remains understudied, and more detailed work and ground-truthed sequences are needed to match larvae and adults. Identification diagnostics of larval morphology could serve a wide range of biodiversity and ecological studies by expanding our ability to identify diversity of species whose adults have gone previously undetected.

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