Aquatic invertebrates of epiphytic tank bromeliads on the island of Trinidad, W.I.: an illustrated checklist

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ABSTRACT
Tank bromeliads are common epiphytes throughout the Neotropics. Their leaf rosettes store rainwater and debris, creating detrital-based aquatic ecosystems with a rich fauna. In this paper, we provide the first illustrated checklist of the aquatic bromeliad invertebrates of Trinidad, based on a sample of ~150 plants from the Northern Range. Using a combination of morphological identification and DNA barcoding, we found 48 different invertebrates, distributed across 21 families from four classes, with many rare species. We also include the complete dataset associated with this species guide, in the hope of supporting future research aimed to resolve important biogeographical and ecological questions around this system.

Key words: phytotelmata; bromeliads; aquatic invertebrates; checklist; biogeography

INTRODUCTION

Bromeliads (Poales: Bromeliaceae Juss.) represent a speciose group of approximately 3,400 herbaceous plants, with a distribution spanning from northern Argentina to southern Florida, USA, and from the summits of the Andes to the Amazonian lowlands (Givnish *et al.* 2014, Zizka *et al.* 2020). The family includes a diversity of growth forms, including epiphytic tank bromeliads, which show unique features, such as their interlocking leaves which form a rosette that is able to capture rainwater and falling debris from vegetal and animal sources (Benzing 2000). These plants usually do not use their roots to extract nutrients, except at very young stages or under very dry circumstances (Leroy *et al.* 2019, Takahashi *et al.* 2022), or for the so-called 'ant gardens' (Leroy *et al.* 2012). Instead, they primarily use their roots to secure a footing on a diversity of surfaces, from trees to rocks. Epiphytic tank bromeliads typically live from a few months to a few years, and can reach very high densities of several thousand individuals (Jocque *et al.* 2010) and impound up to 50,000 L of water per hectare (Williams 2006). Therefore, epiphytic tank bromeliads represent a widespread lentic environment in tropical and subtropical forests, and provide environments that are occupied by specific communities of organisms, including those of conservation interest (Ladino *et al.* 2019).

Although bromeliads may be best known for harbouring habitat specialist species of amphibian, such as the dwarf marsupial frog *Flectonotus fitzgeraldi* Parker 1934 (Smith *et al.* 2021), they also harbour diverse invertebrate communities. These invertebrates represent a range of specialisation to the bromeliad habitat, with some species being obligate specialists (e.g., Young 1981, Dupont *et al.* 2023), while others use the habitat more opportunistically (Benzing 2000). Nonetheless, these invertebrate communities are surprisingly diverse, with 852 taxa identified in over 10 countries (Céréghino *et al.* 2018). These taxa encompass a diversity of taxonomic and functional groups, principally revolving around the processing of leaf litter decomposing in the rosette (Cummins *et al.* 2005, Leroy *et al.* 2017, Céréghino *et al.* 2018, Dézerald *et al.* 2018). Even if algae can reach measurable densities within bromeliads, autochthonous production derived from these organisms remains minor (Brouard *et al.* 2011, Farjalla *et al.* 2016), in particular due to strong competition with bromeliads for nutrients (Rogy and Srivastava 2023). Because of the broad geographic distribution of tank bromeliads, and the simple yet diverse food webs they harbour in their phytotelmata, these plants have been a strong model system to develop and test ecological theory (Srivastava *et al.* 2004).

Despite Trinidad and Tobago being a country with well-documented biodiversity and the site of much field research, we could only find one account of a complete census of these communities, a census that was conducted on just a few bromeliads more than a century ago (Scott 1912). More precisely, research on bromeliads in Trinidad and Tobago tends to focus on the plants themselves (e.g., Broadway and Smith 1933, Males *et al.* 2023), on terrestrial insects that use the plants as food sources (González and Cock 2004), or on endangered endemic species associated with the plants, such the golden tree frog *P. auratus* (Torresdal *et al.* 2017) or the piping-guan *Pipile pipile* Jacquin 1784 (Hayes *et al.* 2009). There are a few accounts of bromeliad-harboured invertebrates in the country, but these primarily concern specific groups such as mosquitoes Culicidae (Downs and Pittendrigh 1946, Aitken 1967), copelatine dytiscids (Balke *et al.* 2008), *Copestylum* syrphids (Rotheray *et al.* 2007) or *Phaenostoma* hydrophilids (Clarkson *et al.* 2014). Given the unique biogeography of Trinidad and Tobago and its rich bromeliad fauna of more than 50 species (Baksh-Comeau *et al.* 2016), the country is likely to be the home of a unique bromeliad fauna, allowing researchers to improve our understanding of ecological systems in general. In this paper, we provide an illustrated checklist of bromeliad-inhabiting aquatic invertebrates. We have made the data from the survey openly accessible on an online repository, and hope it will be of use to future researchers choosing to work on this system.

MATERIAL and METHODS

Sampling locations

In September and October 2022, we collected live bromeliads from six different sites across the north of the island of Trinidad, Trinidad & Tobago (Fig. 1): Arima Valley (UTM 20P 687093E, 1182499N elevation: 282m a.s.l.), Brasso Seco (690372E, 1189043N 137m a.s.l.), La Laja (687899E, 1184151N 588m a.s.l), Las Lapas (684477E, 1186610N 601m a.s.l.), Marianne River (685482E, 1190444N, 39m a.s.l.), and Morne Bleu (685447E, 1186370N 631m a.s.l .).

Moreover, on specific occasions, we opportunistically collected bromeliads that had recently fallen from nearby trees, thus still holding a portion of their phytotelma, from five different locations along roads: F1 (686783E, 1184829N, 304m a.s.l.), F2 (686028E, 1185718N, 390m a.s.l.), F3-F5 (684822E, 1186366N, 571m a.s.l.), F6 (685668E, 1186870N, 511m a.s.l.), and F7 (686615E, 1184949N, 383 m a.s.l.).

Sampling protocol

At each site, we followed the same sampling protocol. First, we identified the focal bromeliad to the genus level, and carefully removed it from its support tree to avoid damaging the root system. During this procedure, we placed a large plastic container under the plant to collect any water that could fall from the bromeliad rosette. We then turned the plant upside-down to pour any leftover water it contained into the same container, measured the resulting water volume as a proxy of the realised size of the aquatic habitat, and brought the plant back to the William Beebe Tropical Research Station (Simla). Once at the field station, we carefully washed each leaf well of the bromeliad with a water hose, using pincers to extract large detritus or detritus that adhered to the wall of the bromeliad wells. After thoroughly washing the bromeliad, we measured the maximum amount of water it could contain, as well as the height of the central well and the width of the plant with its longest leaves extended, all representing proxies for the maximum size of the bromeliad habitat. We carefully inspected the collected water and detritus to extract any live invertebrate that we found, and separated water from detritus through a series of three mesh sieves (2 mm, 1 mm and 0.53 mm), each representing a resource for different functional groups of aquatic invertebrates (respectively loose, coarse and fine detritus). In short, in addition to the bromeliad communities, we collected different variables related to the size of the habitat, and the basal resources available to the invertebrate communities. At the end of the sampling protocol, we replanted all collected bromeliads near the station, in accordance with guidance from the Forestry Division (Trinidad).

Identification of specimens

We separated collected insects into morphospecies and preserved one to ten individuals of each, depending on natural abundances, in 95% ethanol for later identification through DNA barcoding. Using our expertise of bromeliad communities and field observations, we excluded organisms that were using bromeliads as freshwater refugia more than a permanent habitat, such as the common planarian *Dolichoplana striata* Moseley 1877 (Tricladida, Geoplanidae) and the invasive nemertean *Geonemertes pelaensis* Semper 1863 (Hoplonemertea, Prosorochmidae). We also attempted to raise, when possible, larvae to adult stages, in order to obtain information on the morphospecies throughout its life cycle.

In addition to morphological identification, we were able to extract DNA from 46 individuals belonging to 32 morphospecies, and photographed all individuals before processing. We performed DNA extraction using the DNeasy Blood & Tissue Kit (Qiagen, Venlo, the Netherlands). To amplify the barcoding region of the COI, we used the universal primers LCO-1490 (5'-GGTCAACAAATCATAAAGATATTGG-3') and HCO-2198 (5'- TAAACTTCAGGGTGACCAAAAAATCA -3'), which targets a 758 bp sequence, or RON (5'-GGATCACCTGATATAGCATTCCC-3') and NANCY (5'-CCCGGTAAAATTAAAATATAAACTTC-3'), targeting a 439 bp segment, as an alternative when the former pair failed. We set the thermocycler to 94˚C for 3 minutes for initial denaturation, followed by 35 amplification cycles (denaturation at 94˚C for 30 sec, annealing at 50˚C for 30 sec, and elongation at 72˚C for 45 sec), and a final elongation period of 72˚C for 10 min. Finally, we visualised the PCR products through gel electrophoresis and sent them to Psomagen (Rockville, MD, USA) for Sanger sequencing.

RESULTS & DISCUSSION

We found 48 different bromeliad-inhabiting invertebrates from approximately 150 bromeliads over six different sites in the Northern Range (Table 1, Figure 1). These spanned 4 classes of invertebrates: Clitellata, Turbellaria, Crustacea and Hexapoda. Based on prior knowledge of the morphology of the bromeliad fauna from nine different countries, spanning Puerto Rico to Argentina, combined with DNA barcoding, we were able to identify three species to the species level, seven to the genus level, eight to the subfamily level, twenty to the family level and ten to the order or class level. Even though our sampling was restricted to a few sites in Trinidad's Northern Range, the invertebrate fauna of Trinidadian bromeliads revealed interesting patterns.

Several species that we collected are of scientific interest, informing for example biogeography, biodiversity and public health. First, we found that the COI sequence of our morphospecies Crassiclitellata *sp. 1* (Fig. 2b) matched with another bromeliad-associated species that has only previously been reported from the island of Martinique, while the COI

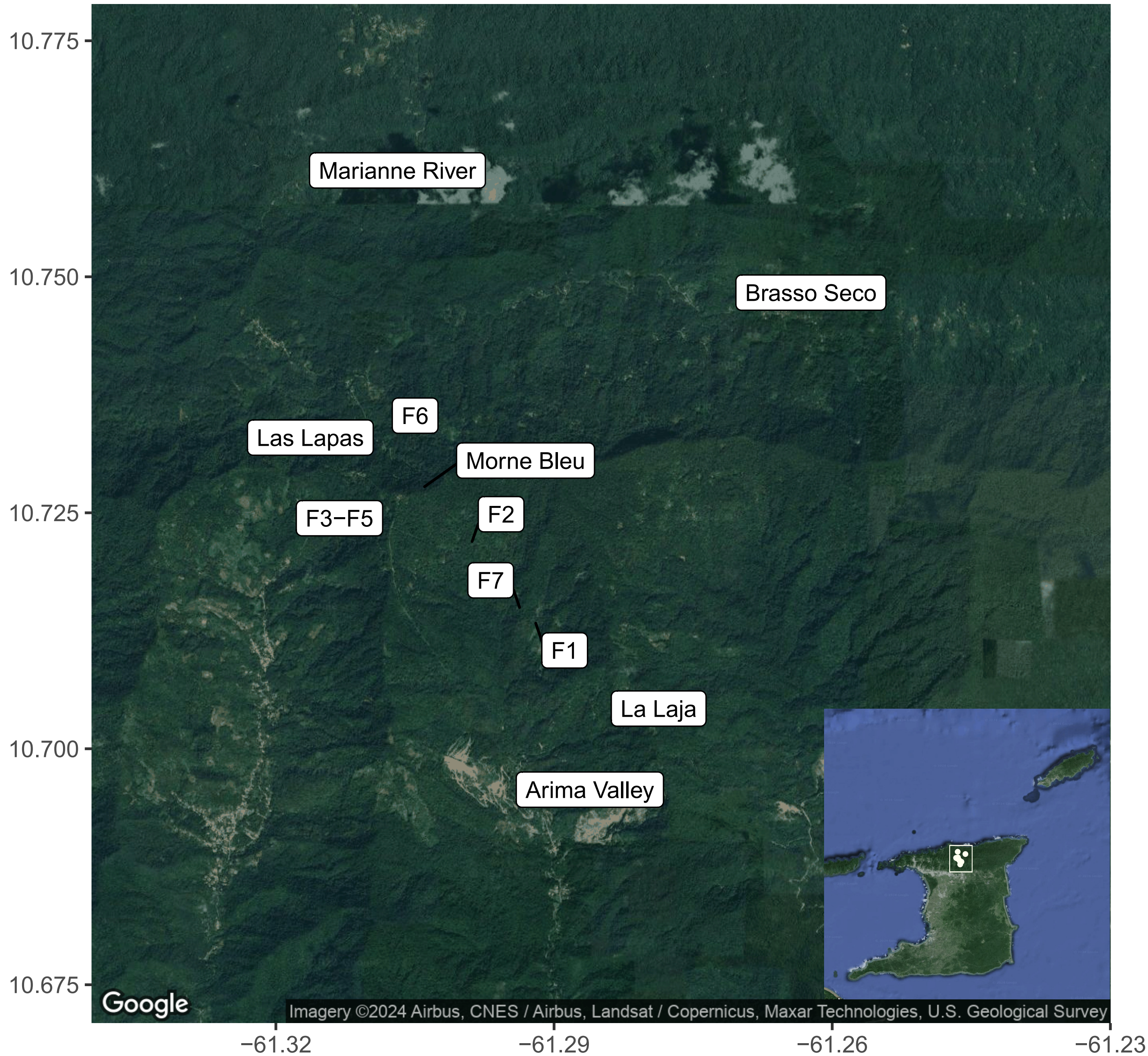

Fig. 1. Map of sites within the island of Trinidad. Sites starting with "F" represent opportunistic collection of recently fallen bromeliads on roadsides, while the other sites underwent more systematic sampling.

Table 1. Summary of collected species and morphospecies in classes (a) Clitellata and (b) Turbellaria, and subphyla (c) Crustacea, and (d) Hexapoda. Specimen ID =if applicable, identifier of the amplified sequence of specimens belonging to the species/morphospecies in the BOLD system (Ratnasingham and Hebert 2007). Empty rows mean that the morphospecies was only identified to the class level.

A.

Order	Family	Subfamily	Genus	Species(naming authority)	Specimen ID
				sp. 1	
Crassiclitellata				*sp. 1*	BIBAR-T004 T005
	Acanthodrilidae		*Dichogaster*	*andina* (Cognetti1904)	BIBAR-T009
Haplotaxida	Enchytraeidae			*sp. 1*	BIBAR-T003

B.

Order	Family	Subfamily	Genus	Species (naming authority)	Specimen ID
Tricladida				sp. 1	
				sp. 2	
				sp. 3	

C.

Class	Order	Family	Subfamily	Genus	Species	Specimen ID
Copepoda					sp. 1	
Ostracoda	Podocopa				sp. 1	

D

Order	Family	Subfamily	Genus	Species(naming authority)	Specimen ID
Coleoptera	Curculionidae			sp. 1	BIBAR-T034
	Dytiscidae			sp. 1	BIBAR-T026-T030
			Desmopachria	sp. 1	
	Elateridae		*Pyrophorus*	sp. 1	BIBAR-T035
	Hydrophilidae			sp. 1	BIBAR-T036
				sp. 2	BIBAR-T033
				sp. 3	BIBAR-T037
	Scirtidae			sp. 1	BIBAR-T024
Diptera	Schizophora			sp. 1	BIBAR-T043
	Cecidomyiidae			sp. 1	BIBAR-T092
Ceratopogoninae	Ceratopogonidae			sp. 1	BIBAR-T047 T048
				sp. 2	BIBAR-T044 T046
				sp. 3	BIBAR-T050 T051
	Forcipomyiinae			sp. 1	BIBAR-T078 T079
				sp. 2	
				sp. 3	
				sp. 4	
Chironomidae	Chironominae			*Polypedilum* sp. 1	BIBAR-T053 T054
				sp. 2	BIBAR-T057
		Tanypodinae		sp. 1	
Corethrellidae				sp. 1	BIBAR-T063 T064

Table 1. Continued. Summary of collected species and morphospecies in classes (a) Clitellata and (b) Turbellaria, and subphyla (c) Crustacea, and (d) Hexapoda.

D

Order	Family	Subfamily	Genus	Species(naming authority)	Specimen ID
Culicinae	Culicidae	Anophelinae	*Anopheles*	*homunculus* (Komp 1937)	BIBAR-T073
			Culiseta	sp. 1	BIBAR-T067
			Wyeomyia	sp. 1	
			Toxorhynchites	*haemorrhoidalis* (Fabricius 1787)	BIBAR-T074 T076
	Dolichopodidae			sp. 1	BIBAR-T042
	Drosophilidae			sp. 1	BIBAR-T102
				sp. 2	BIBAR-T103
	Lauxaniidae			sp. 1	BIBAR-T100
	Limoniidae			sp. 1	BIBAR-T089
	Psychodidae			sp. 1	
				sp. 2	BIBAR-T083
	Stratomyiidae			sp. 1	BIBAR-T084
				sp. 2	
				sp. 3	BIBAR-T085
	Syrphidae		*Copestylum*	sp. 1	
			Quichuana	sp. 1	BIBAR-T087
	Tabanidae		*Stibasoma*	*fulvohirtum* (Wiedemann 1828)	BIBAR-T095
Odonata	Suborder Anisoptera			sp. 1	BIBAR-T019
	Coenagrionidae			sp. 1	BIBAR-T020

sequence of another Clitellata morphospecies matched with *Dichogaster andina* Cognetti 1904, a widespread peregrine species thought to be invasive in the region (Dupont *et al.* 2023). Second, we found one specimen of *Desmopachria* (Fig. 3d, Coleoptera: Dytiscidae), of which only one species has previously been found in Jamaican bromeliads (Young 1981), while another, undescribed specimen of the genus has been collected in a bromeliad from southern Brazil (Albertoni *et al.* 2016). Third, we found specimens of the malaria vector *Anopheles homunculus* Komp 1937 (Fig. 5a) in three of our six sites. Although this species displayed relatively low densities compared to other mosquito species (12/179 mosquito individuals overall, in eight bromeliads), further research should examine which factors determine the abundance of this vector, in particular relating to natural predators such as larval *Toxorynchites haemorrhoidalis* Fabricius 1787 (Fig. 5d) and odonate nymphs (Fig. 3j-l). Despite our attempts to raise larvae to from larval stages to adulthood, we were only able to do so successfully for a handful of specimens (Fig. 6).

Our survey was restricted to six sites in a narrow part of the Northern Range, yet the communities of these different sites varied widely. For example, top predators like odonates and dytiscids were not present at the Marianne River site, and co-occurred at Brasso Seco, La Laja and Las Lapas. While these predators usually displace each other at site and bromeliad levels (Atwood *et al.* 2014, Amundrud and Srivastava 2020), we found one instance of a bromeliad in Brasso Seco where the two predators co-occurred in the same bromeliad. Moreover, the relative abundances of the detritivore functional groups (*sensu* Cummins *et al.* 2005) shifted considerably across our sites. This difference is almost akin to those seen across countries (e.g. Trzcinski *et al.* 2016, Srivastava *et al.* 2023), with some Trinidadian sites being more similar to Caribbean communities like Puerto Rico, and others to continental communities such as French Guiana or Costa Rica. This substantial variation in a restricted geographical extent warrants further research on its drivers, and the expansion of surveys to other areas of the country. We hope that the dataset associated with this illustrated checklist will support this research effort, and will spark interest in using bromeliads as model ecosystems to answer important questions in biogeography and ecology (Srivastava *et al.* 2004).

Tank bromeliads, being aquatic ecosystems in a forest matrix, are ecologically equivalent to island or patch habitats. As such, dispersal plays an important role, revealing intricate patterns of speciation for species with within-bromeliad reproduction and dispersal relying on phoresy, such as ostracods (Little and Hebert 1996, Lopez *et al.* 1999).

Moreover, the system has been used as a model system to develop the new field of trophic metacommunities (Guzman *et al.* 2018, Guzman *et al.* 2019), and the new concept of the multidimensional stoichiometric niche (González *et al.* 2017). In terms of functional traits (McGill *et al.* 2006), bromeliads have helped researchers to fill important knowledge gaps around constraints surrounding the functional trait space (Céréghino *et al.* 2018) and trait-based assembly patterns (Srivastava *et al.* 2023) of ecological communities. Moreover, bromeliad communities have also been used to study the effects of climate change, particularly around altered precipitation patterns (Trzcinski *et al.* 2016, Romero *et al.* 2020, Srivastava *et al.* 2020) and increased temperatures (Antiqueira *et al.* 2018). Therefore, bromeliads represent an ideal system to advance ecological research and better understand the future impacts of climate change.

In conclusion, epiphytic tank bromeliads of the island of Trinidad harbour a diverse invertebrate community. Our survey only covered a relatively small area of the island, which suggests that extending sampling efforts to other regions may uncover considerable additional diversity. We hope that the illustrated checklist presented here and

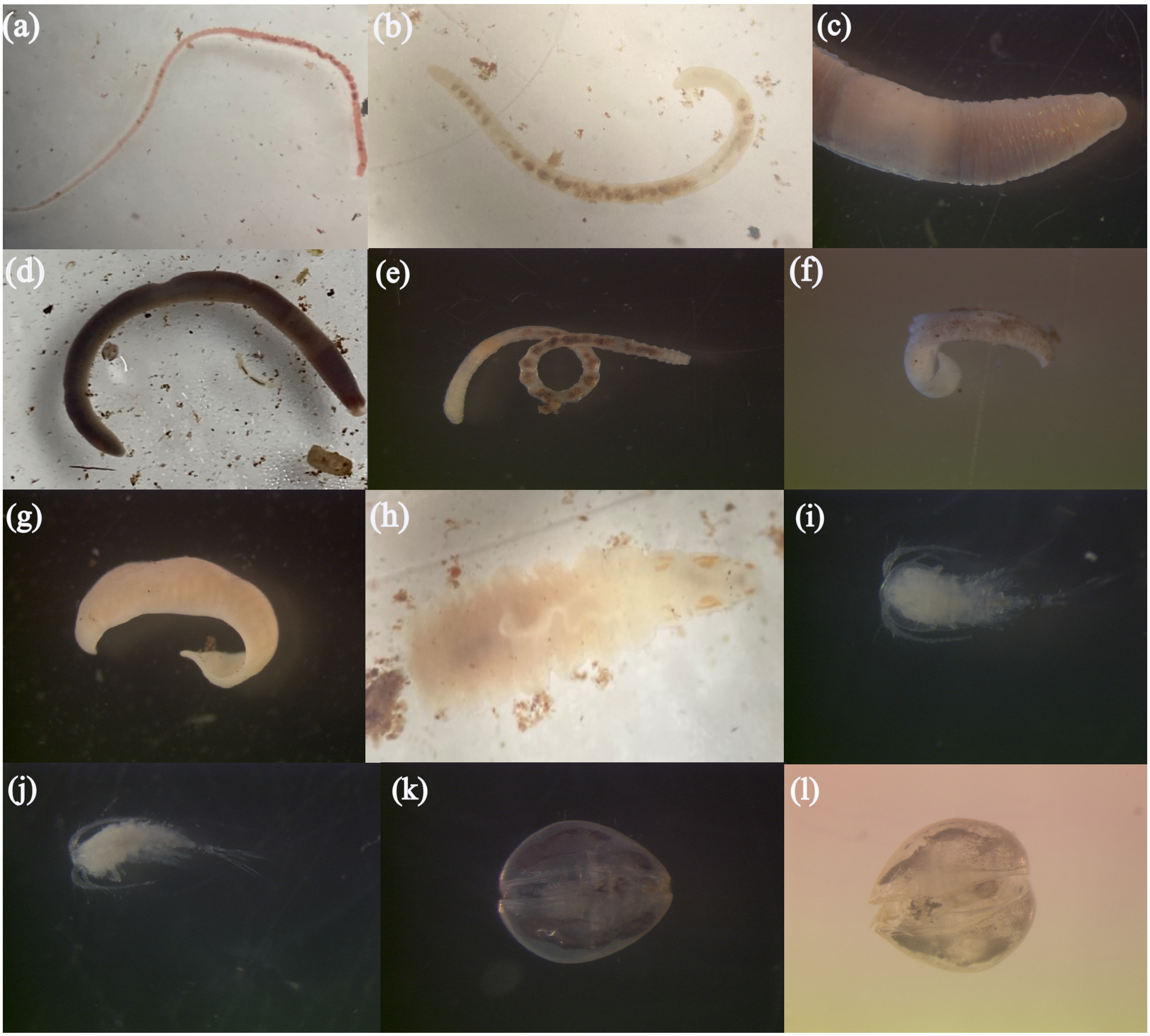

Fig. 2. Pictures of species and morphospecies in classes Clitellata and Turbellaria, and subphylum Crustacea. Class Clitellata: **(a)** Clitellata *sp. 1*, **(b)** Crassiclitellata *sp. 1*, **(c)** and **(d)** *Dichogaster andina* (Cognetti 1904), **(e)** Enchytraeidae *sp. 1*, **(f)** Tricladidae *sp. 1*, **(g)** Tricladidae *sp. 2*, **(h)** Tricladidae *sp. 3*, **(i)** and **(j)** Copepoda *sp. 1*, and **(k)** and **(l)** Podocopa *sp. 1*.

the associated data will assist further research on the biogeography of bromeliads, and on the main questions challenging the field of ecology today.

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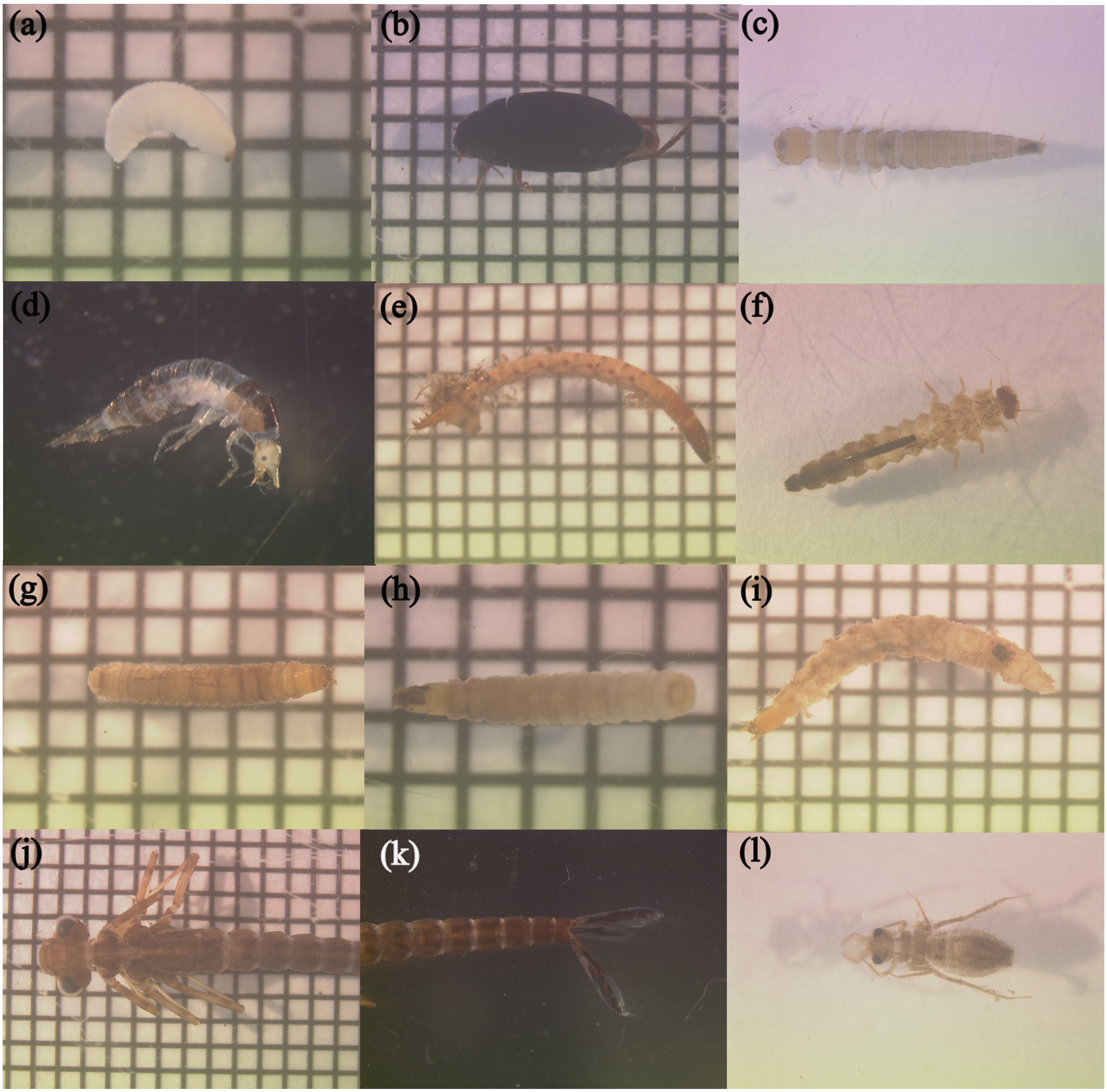

Fig. 3. Pictures of morphospecies in subphylum Hexapoda, orders Coleoptera and Odonata. Order Coleoptera: **(a)** Curculionidae sp. 1, Dytiscidae sp. 1 (**b**) adult and (**c**) larva, **(d)** *Desmopachria* sp. 1, **(e)** *Pyrophorus* sp. 1, **(f)** Scirtidae sp. 1, Hydrophilidae **(g)** sp. 1, **(h)** sp. 2 and **(i)** sp. 3. Order Odonata: **(j)** and **(k)** Coenagrionidae sp. 1, and **(l)** Anisoptera sp. 1. On pictures with gridlines, each grid represents 1x1mm.

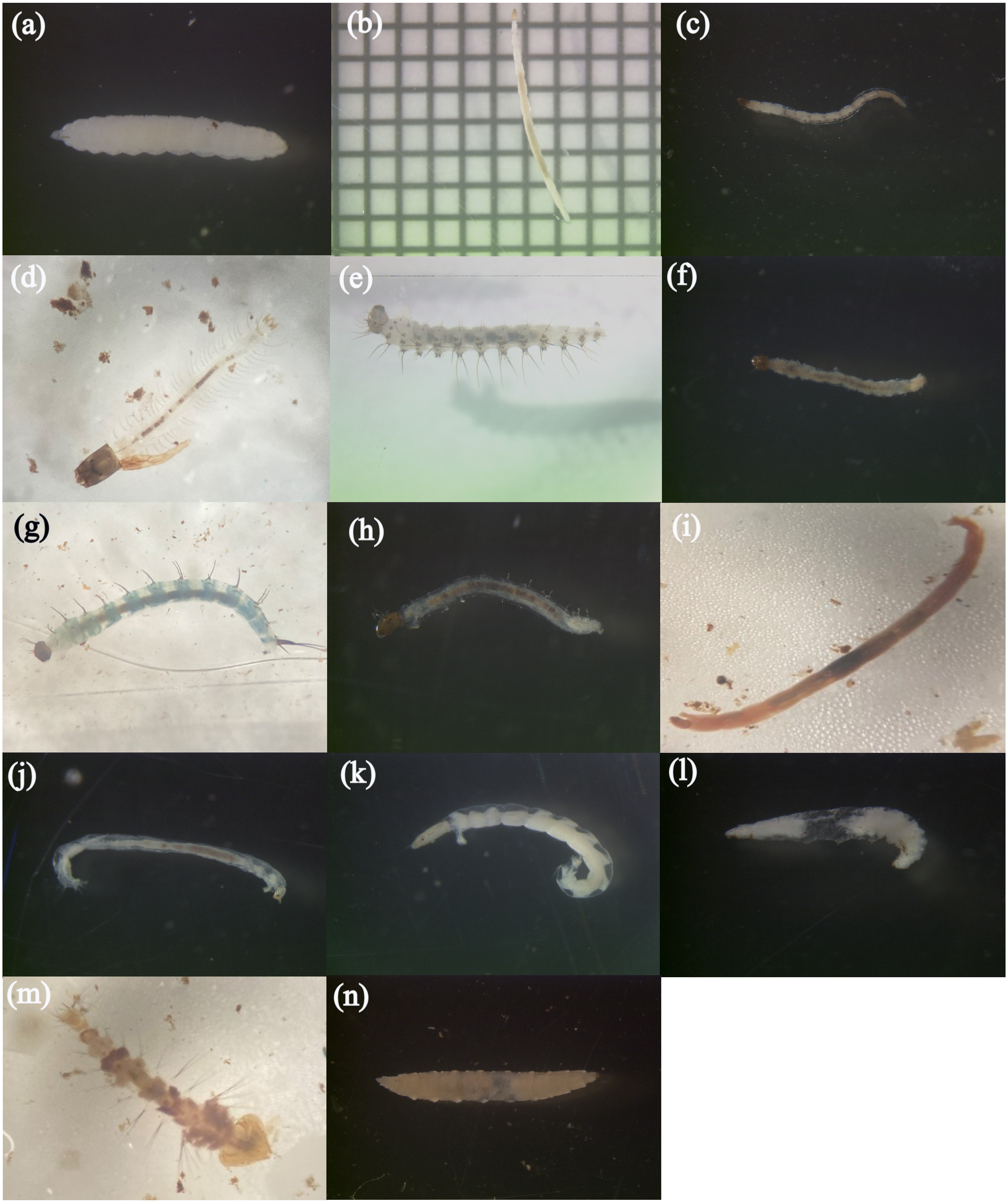

Fig. 4. Pictures of species and morphospecies in subphylum Hexapoda, order Diptera. (a) Cecidomyiidae sp. 1, Ceratopogoninae **(b)** sp 1., **(c)** sp. 2 and **(d)** sp. 3, Forcipomyiinae **(e)** sp. 1, **(f)** sp. 2, **(g)** sp. 3 and **(h)** sp. 4, **(i)** *Polypedilum* sp. 1, **(j)** *Polypedilum* sp. 2, **(k)** Tanypodinae sp. 1, **(l)** Schizophora sp. 1, **(m)** Corethrellidae sp. 1, and **(n)** *Stibasoma fulvohirtum* (Wiedemann, 1828). On pictures with gridlines, each grid represents 1x1mm.

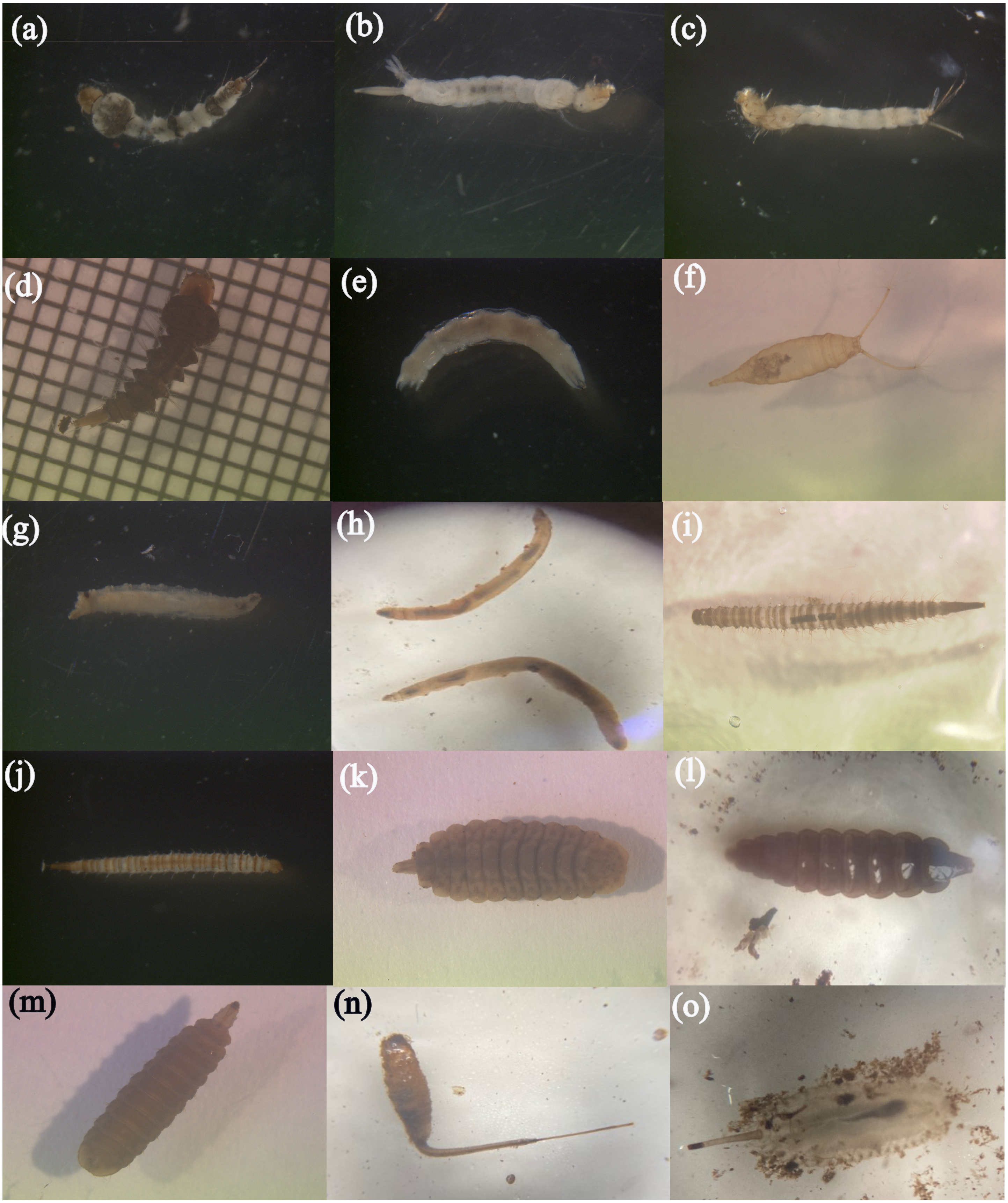

Fig. 5. Pictures of species and morphospecies in subphylum Hexapoda, order Diptera. (a) Anopheles homunculus (Komp 1937), (b) Culiseta sp. 1, (c) Wyeomyia sp. 1, (d) Toxorhynchites haemorroidalis (Fabricius 1787), (e) Dolichopodidae sp. 1, Drosophilidae (f) sp. 1 and (g) sp. 2, (h) Limoniidae sp. 1, Psychodidae sp. 1 (i) and (j) sp. 2, Stratomyiidae (k) sp.1, (l) sp. 2 and (m) sp. 3, (n) Quichuana sp. 1, and (o) Copestylum sp. 1. On pictures with gridlines, each grid represents 1x1mm.

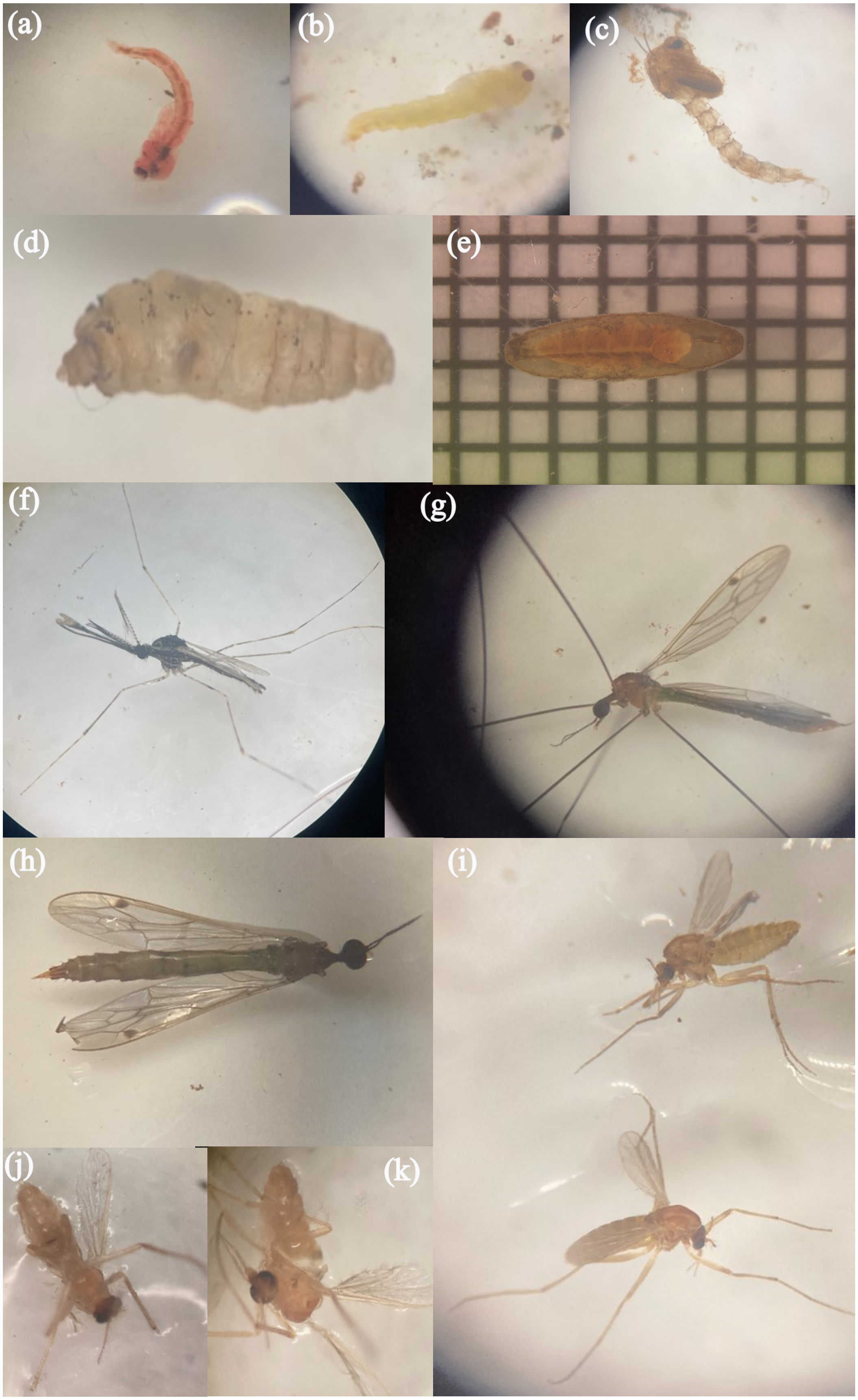

Fig. 6. Pictures of pupae and terrestrial adults of species and morphospecies. Pupae of Polypedilum (a) sp. 1 and (b) sp. 2, (c) Tanypodinae sp.1, (d) Psychodidae sp. 1, and (e) Lauxaniidae sp. 1. Terrestrial adults of (f) *Anopheles homunculus* (Komp 1937), (g) and (h) Limoniidae sp. 1, (i) *Polypedilum* sp. 2, and (j) and (k) Tanypodinae sp. 1. On pictures with gridlines, each grid represents 1x1mm.

Open data statement

All data from the survey of the six sites, including additional pictures for all species and morphospecies, is on https://knb.ecoinformatics.org/view/doi%3A10.5063%2FF11J9874 and all code is available on https://github.com/pierrerogy/trinidad_species_checklist. Finally, species barcodes are available on BOLD (Ratnasingham and Hebert 2007): dx.doi.org/10.5883/DS-BIBART.

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