Article

Sub-fossil Chironomidae (Diptera) from lake sediments in Central America: a preliminary inventory

LADISLAV HAMERLIK[1,2,5], FABIO LAURINDO DA SILVA[3,4] & MARTA WOJEWÓDKA[1]

[1]*Institute of Geological Sciences, Polish Academy of Sciences, Warsaw, Poland*

[2]*Department of Biology and Ecology, Matej Bel University, Banská Bystrica, Slovakia*

[3]*Laboratory of Systematic and Biogeography of Insecta, Department of Zoology, Institute of Biosciences, University of São Paulo, São Paulo, Brazil.*

[4]*Department of Natural History, NTNU University Museum, Norwegian University of Science and Technology, Trondheim, Norway.*

[5]*Corresponding author. E-mail: ladislav.hamerlik@gmail.com*

Abstract

The chironomid diversity of Central America is virtually underestimated and there is almost no knowledge on the chironomid remains accumulated in surface sediments of lakes. Thus, in the present study we provide information on the larval sub-fossil chironomid fauna from surface sediments in Central American lakes for the first time. Samples from 27 lakes analysed from Guatemala, El Salvador and Honduras yielded a total of 1,109 remains of four subfamilies. Fifty genera have been identified, containing at least 85 morphospecies. With 45 taxa, Chironominae were the most specious and also most abundant subfamily. Tanypodinae with 14 taxa dominated in about one third of the sites. Orthocladiinae were presented by 24 taxa, but were recorded in 9 sites, being dominant in only one site. Podonominae were collected only in one locality. Head capsules of *Heterotrissocladius* found in the high elevation lake Magdalena, Guatemala, represent a first record for the Neotropical region. Both relative abundance and species richness of Chironominae and Orthocladiinae showed significant relationship to elevation, while Tanypodinae were indifferent. Hopefully, the list of taxa provided by our study will be a base line for future limnological and paleolimnological investigations using chironomid remains in the region.

Key words: check list, non-biting midges, lakes sediments, Guatemala, El Salvador, Honduras

Introduction

Members of the non-biting midge family Chironomidae (Diptera) are true flies, with larvae inhabiting an enormous variety of aquatic ecosystems and usually dominating the benthic communities both in abundance and species richness (e.g. Cranston 1982; Ferrington 2008). The range of conditions under which chironomids are found is more extensive than that of any other family of aquatic insects. Even though most of the species are aquatic, some are semiterrestrial, living in moist habitats, or completely terrestrial. Moreover, Chironomidae is the only insect family that has colonized the marine benthos. The great species and habitat diversity combined with variable ecological requirements of species (Oliver 1971; Armitage *et al.* 1995) makes this family a valuable environmental indicator for aquatic ecosystems.

Chironomidae probably originated in the middle Triassic approximately 248–210 million years ago (Cranston *et al.* 2010) and comprises at least 10,000 species in more than 400 genera (Armitage *et al.* 1995; Sæther 2000), and roughly 6,200 of these are known to science (Ashe P. 2014, unpublished data). Nearly 900 species of Chironomidae are recognized from the Neotropical region (M. Spies, personal communication), of which 80% are assigned to one of the three subfamilies (out of the total eleven) Chironominae, Orthocladiinae and Tanypodinae (Spies *et al.* 2009). The remaining subfamilies are less species-rich, for example, Aphroteniinae, Buchonomyiinae, Chilenomyiinae, Prodiamesinae and Telmatogetoninae, have one or only few species within one or few genera.

Chironomid larvae, due to their chitinized head capsules, are preserved in lake sediments in good condition for a long period and their remains can be used for both limnological and paleolimnological studies. As lakes accumulate organic and inorganic remains constantly since their formation, their sediments represent a continuous environmental archive that contains information about the past of the lake and its environment. In addition, lake surface sediments accumulating in the deepest parts of the lake can also be important sources of recent distribution of species, since they contain remains of the contemporary biota from different parts of the lake (Frey 1976). While recent years have seen increased activity regarding Chironomidae in the region (e.g. Watson & Heyn 1992; Andersen & Pinho 2014; Andersen *et al.* 2015; Oliveira *et al.* 2013; Silva & Wiedenbrug 2015; Silva *et al.* 2014a, b; Siri *et al.* 2015; Trivinho-Strixino *et al.* 2013, 2015; Parise & Pinho 2016; Silva & Oliveira 2016; Epler 2017; Silva & Ferrington 2018), the knowledge of paleoenvironmental archives preserved in lake sediments particularly in Central America and the Caribbean region, remains fragmentary. Therefore, the present study provides information on the larval sub-fossil chironomid fauna from lake sediments in Central America for the first time. We hope that the obtained results will be helpful for limnologists and paleolimnologists working in the area and will encourage further studies in Central America.

Material and methods

Study area. Central America is a geologically young land bridge that connects North and South America and thus two main biogeographical realms, the Nearctic and the Neotropical regions. In the region, humid swamps and lowlands extend along both the west and east coasts, but four-fifths of Central America is either hilly or mountainous. Elevation steadily increases west of the Caribbean lowlands, until, toward the Pacific Coast, plateau highlands culminate in mountain ridges and some 40 volcanic cones, some of which attain elevations of more than 3,700 meters. It comprises of seven counties, in our study we focused on the three northern ones: Guatemala, Honduras and El Salvador. The subtropical ridge (high atmospheric pressure) from the northern Atlantic drives the climate of the region while the Intertropical Convergence Zone (ITCZ) and polar fronts of mid-latitude origin have a secondary impact (Taylor & Alfaro 2005). Due to the migration of the ITCZ there is a bimodal distribution of precipitation during the year with the rainfall season lasting from May until October (Hastenrath & Polzin 2013). Additionally, the microclimate of the area is strongly affected by topography (Karmalkar *et al.* 2011; Taylor & Alfaro 2005) resulting in significant elevational differences in precipitation and temperature. There are considerable annual and temporal variations ranging from <1000 mm in the lowlands to >2500 mm in the mountains (Taylor & Alfaro 2005). The mean annual temperature varies from 25–28°C at the Guatemalan lowlands, to 12–15°C in the highlands and mountain regions (Atlas Climatologico for 1928-2003, www.insivumeh.gob.gt).

Field sampling. Surface sediment samples were obtained and analysed from 27 lakes situated in three Central American countries: Guatemala (13 lakes), El Salvador (9) and Honduras (5) (Fig. 1, Tab. 1). Sediments were collected using an Ekman-Birge bottom sampler in autumn 2013. At each site, basic environmental parameters of waterbodies were measured and geographical coordinates were recorded by a handheld GPS. Physical and chemical parameters of lake water, such as temperature, pH, conductivity, dissolved oxygen and salinity, were measured with a multi-probe WTW 350i. Secchi-disk was used to estimate the water transparency and an echo-sounder to measure the maximum lake depth.

The lakes studied are scattered along a ~2800 m long altitudinal gradient (2 to 2863 m asl, Tab. 1) with an average elevation of 473 m. They varied considerably in area and depth with the largest lakes being Atitlán and Yojoa (125 and 79 km^2, respectively, Tab. 1), while the average size was about 22 km^2 and the area of some lakes was less than 0.10 km^2, such as Madre Vieja (0.10 km^2), Verde (0.10 km^2), Chiligatoro (0.04 km^2), El Rosario (0.02 km^2), Magdalena (0.01 km^2). Both shallow lakes (≤3 m depth, e.g. Comandador, El Muchacho, El Rosario, Grande, Magdalena, Jucutuma, Ticamaya, Jocotal, Los Negritos, Olomega) and deep lakes (>300 m, e.g. Lachuá, Atitlán and Chicabal) were included in the study. For summary of basic parameters of study lakes see tab. 1. For detailed description of environmental variables of the study sites in Guatemala, Salvador and Honduras see Wojewódka *et al.* (2016).

Chironomid analysis. For chironomid analysis, sub-samples consisting of ca 5 cm^3 sediment were used. The samples were deflocculated in warm 10% KOH for 20 min and rinsed on a 90 mm mesh sieve (Walker and

Paterson 1985). Chironomid head capsules were handpicked under a binocular microscope (40x power) and permanently mounted in Berlese mounting medium. Taxonomic identification was performed under a compound microscope at up to 400x magnification, with reference to Epler (2001), Prat (2011), Andersen *et al.* (2013), Brooks *et al.* (2007), Trivinho-Strixino (2014), Silva *et al.* (2018) and occasionally original descriptions. Morphotypes were frequently named after a described species that it resembled most. In case that it was possible to distinguish different morphotypes within a genus without giving it a specific name, we used type A, type B and so on. Voucher specimens are deposited in the Institute of Geological Sciences, Polish Academy of Sciences, Warsaw, Poland. Linear regression analysis was used to estimate the relationship of the relative abundance and taxonomic richness of different subfamilies along elevation. Pearson correlation was used to evaluate the significance of these relationships. Only relationships with $p < 0.05$ were considered significant.

TABLE 1. Basic parameters of the studied lakes (Wojewódka *et al.* 2016).

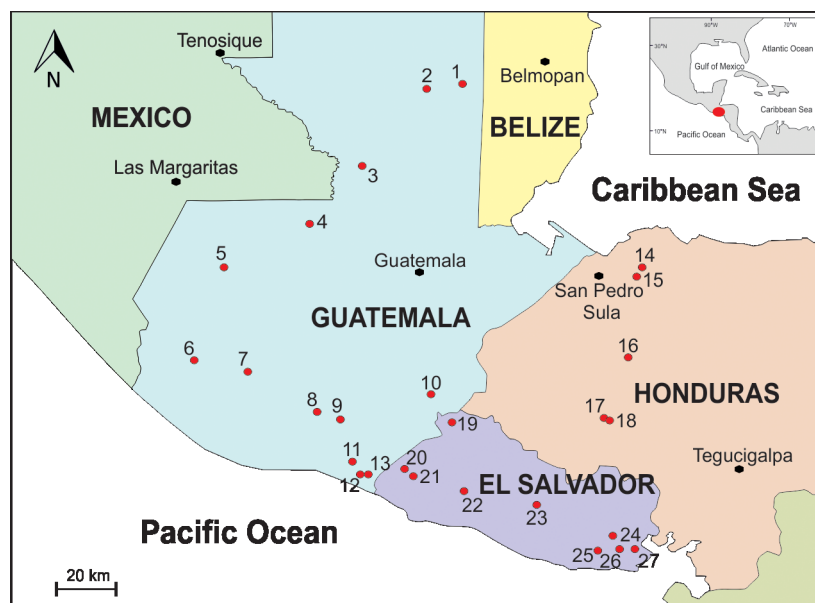| Lake ID	Lake name	Coordinates		Altitude (m a.s.l.)	Area (km²)	Depth (m)	Secchi depth (m)	pH	Conductivity (µS cm⁻¹)
		N	W						
Guatemala									
1	Sacnab	17.0583	89.3725	170	4.28	9	1.8	9.0	412
2	Salpetén	16.9815	89.6755	105	2.77	32	1.7	7.0	4520
3	Las Pozas	16.3432	90.1660	152	2.16	35	3.1	8.3	277
4	Lachuá	15.9321	90.6807	200	-	0.8	0.8	7.5	1020
5	Magdalena	15.5426	91.3956	2863	0.01	2.8	2.8	8.8	331
6	Chicabal	14.7875	91.6561	2726	0.21	330	1.6	9.0	12
7	Atitlán	14.6837	91.2239	1556	125	340	4.2	8.9	442
8	Calderas	14.4117	90.5913	1790	0.35	26	2.9	9.2	100
9	El Pino	14.3447	90.3941	1038	0.64	18	2.8	8.3	100
10	Ipala	14.5571	89.6394	1495	0.56	25	3.6	8.0	100
11	Comandador	13.9600	90.2544	20	0.65	1.7	0.5	7.4	251
12	El Muchacho	13.8892	90.1918	3	0.36	2	0.4	9.1	439
13	Grande	13.8903	90.1703	5	0.95	2	0.2	7.4	110
Honduras									
14	Ticamaya	15.5506	87.8897	17	2.91	2	0.8	7.2	100
15	Jucutuma	15.5123	87.9028	27	4.34	2	2	7.3	100
16	Yojoa	14.8606	87.9847	639	79.7	22	3.3	8.3	100
17	Chiligatoro	14.3756	88.1830	1925	0.04	5.5	0.9	7.4	100
18	Madre Vieja	14.3569	88.1376	1866	0.1	3.4	0.9	8.5	100
El Salvador									
19	Metapan	14.3094	89.4655	450	16	6	0.2	8.4	255
20	El Espino	13.9530	89.8652	689	0.99	5.5	0.4	8.5	85
21	Verde	13.8915	89.7872	1609	0.1	12	2.7	7.5	83
22	Chanmico	13.7786	89.3541	477	0.78	51	0.9	9.2	100
23	Apastepeque	13.6925	88.7448	509	0.38	47	6.1	8.6	100
24	Aramuaca	13.4294	88.1065	76	0.4	107	6.7	8.4	100
25	Jocotal	13.3371	88.2519	26	8.7	3	1.5	8.0	595
26	Olomega	13.3072	88.0551	66	25.2	2.5	0.9	7.7	105
27	Los Negritos	13.2831	87.9370	102	0.69	2	0.3	9.2	40

FIGURE 1. Distribution of the surveyed lakes in Central America. Number (ID) indicates given lakes: 1. Sacnab; 2. Salpetén; 3. Las Pozas; 4. Lachuá; 5. Magdalena; 6. Chicabal; 7. Atitlán; 8. Calderas; 9. El Pino; 10. Ipala; 11. Comandador; 12. El Muchacho; 13. Grande; 14. Ticamaya; 15. Jucutuma; 16. Yojoa; 17. Chiligatoro; 18. Madre Vieja; 19. Metapan; 20. El Espino; 21. Verde; 22. Chanmico; 23. Apastepeque; 24. Aramuaca; 25. Jocotal; 26. Olomega; 27. Los Negritos.

Results

In total, 1,109 remains of four subfamilies were collected (Table 2) and fifty genera have been identified, containing at least 83 species/morphotypes. At least two additional species were collected that could not be assigned to described genera and were identified as Pentaneurini type A and B. Chironominae (45 taxa) numerically dominated in about 70% of lakes and Tanypodinae (14) were prevalent in the rest of the sites. Orthocladiinae (24 taxa) were present in 9 sites, and dominated one site (Magdalena). Podonominae (1 taxon) were collected only in one locality (Magdalena).

Both relative abundance and species richness of Chironominae (p=0.007 and p=0.009, respectively) and Orthocladiinae (both p<0.001) showed significant relationship to elevation, while Tanypodinae were indifferent (Fig. 2). There was no correlation between total chironomid richness and elevation.

Discussion

Chironominae. The subfamily Chironominae is a dominant group in terms of described species in the tropical and subtropical lowlands, with the immature stages adapted to a wide array of freshwater habitats, in addition to brackish and marine waters (Ashe *et al.* 1987). Larvae of Chironominae exhibit a wide range of food sources, including aquatic plants, dead wood and leaves, organic-enriched sediments, among others (Silva & Farrell 2017). Numerous species, belonging to genera such as *Chironomus*, *Endotribelos*, *Goeldichironomus* and *Polypedilum*, contain haemoglobin which may contribute to their prevalence in the Neotropical Region, where oxygen concentrations are expected to be low (Silva & Farrell 2017). Chironominae is subdivided into three tribes: Chironomini, Pseudochironomini and Tanytarsini.

Chironomini was represented by at least 20 genera, comprising at least 33 species. *Goeldichironomus* was the most widespread and abundant genus. The genus has a wide distribution in lentic ecosystems, where larvae live both on littoral sandy sediments and in/on aquatic macrophytes. Larval *Goeldichironomus* favour floating and drifting vegetation of small standing water bodies. The genus has its main occurrence in the tropics and subtropics

of Central and South America. Several species are known from north and southeast Brazil. The second most frequent genus was *Chironomus*. This is a cosmopolitan genus with several hundred species. Numerous species of this genus are very abundant in heavily polluted standing or running waters, whereas some species commonly colonise small water bodies such as fountains (Hamerlik *et al.* 2011) or fish breeding tanks where they complete their life cycle in a few days (Correia *et al.* 2013). Spies & Reiss (1996) catalogued 19 species from the Neotropical Region. However, this number, obviously, represents outdated knowledge and significantly underestimates real diversity of *Chironomus* in the Neotropics, in view of several new species were described more recently (Correia & Trivinho-Strixino 2005, 2007; Correia *et al.* 2005, 2006, 2013). Other commonly encountered Chironominae were *Polypedilum*. This is one of the largest chironomid genera containing about 440 described species (Sæther *et al.* 2010). Larvae of *Polypedilum* occur virtually in all kinds of still and flowing waters. A few species are also found in extreme environments, such as bromeliad tanks (Epler *et al.* 2013) or small pools formed in shallow hollows on unshaded rocks in semi-arid regions of the African continent (Hinton 1951).

The tribe Pseudochironomini was represented by *Pseudochironomus* sp. and *Manoa* sp. *Pseudochironomus* includes non-biting midges whose larvae inhabit sandy or gravelly littoral sediments, primarily in meso- to oligotrophic lakes or in large, slow flowing rivers. The genus is Holarctic-Neotropical in distribution, with one or two species in the Palaearctic, about eleven species in the Nearctic and at least five species in the Neotropical region (Epler *et al.* 2013). *Manoa* was described from all stages from Amazonia, and a second adult species has been described from East Africa. Recently, the group was recorded from China (Qi *et al.* 2017) and Dominican Republic (Silva *et al.* 2015). In the Everglades, Florida, larvae of *M. pahayokeensis* Jacobsen and Perry are found in shallow waters subject to fluctuating water levels and seasonal drying (Jacobsen & Perry 2002). In addition to *Aedokritus*, *Megacentron* and *Riethia*, these genera have close relatives recorded from western Pacific/Australasia (Australia, New Zealand and New Caledonia), such expanded distribution seems to support Freeman's (1959, 1961) hypothesis that this tribe is an ancient Southern Hemisphere group (Silva & Farrell 2017).

Tanytarsini was represented by six taxa: *Cladotanytarsus*, *Micropsectra, Neozavrelia, Stempellina, Tanytarsus* gr. *ortoni* (a synonymous with the taxon "*Caladomyia*" in previous literature, Lin *et al.* 2017) and *Tanytarsus*. The latter was represented by five species, *Tanytarsus* types A–E. This genus is one of the most species rich genera of Chironomidae in the Neotropical region, and the immature stages occur in several different aquatic ecosystems (Trivinho-Strixino *et al.* 2015). The identification of adults of *Tanytarsus* is problematical due to the large interspecific variation in the genitalic morphology (Ekrem & Reiss 1999). In spite of this drawback, recent years have seen increased interest concerning the taxonomy of the group in the Neotropical region (Sanseverino & Trivinho-Strixino 2010; Sanseverino *et al.* 2010; Trivinho-Strixino e*t al*. 2015).

Orthocladiinae. Orthocladiinae is the second largest subfamily, with the greatest diversity of ecological requirements (Ashe & Cranston 1990). Several of the more primitive genera are aquatic, normally rheophilous, whilst numerous genera are lentic. Some orthoclads exhibit hygropetric behaviour in small standing waters, while several genera have developed semiterrestrial or fully terrestrial habits. Larvae of numerous species breed in brackish waters or are fully marine. There is no accepted division of Orthocladiinae into tribes (Silva & Farrell 2017). In our study, the subfamily was represented by 14 genera, comprising at least 25 species. *Cricotopus*, represented by seven morphotypes, was the most specious orthoclad. Despite its frequency, the group was sampled only at three localities: lakes Magdalena, Atitlán (Guatemala) and Yojoa (Honduras). The genus is one of the largest in the Orthocladiinae, comprising five subgenera, with worldwide distribution (Cranston *et al.* 1989). Larval *Cricotopus* inhabit a wide array of water bodies, from pristine streams and brooks to eutrophic ponds and brackish estuaries (Hirvenoja 1973; Boesel 1983). Several species are known to live associated with aquatic macrophytes and algae, while others may become so abundant in eutrophic waters that adult swarms may reach nuisance proportions (Spies 2000).

Another commonly found Orthocladiinae was *Psectrocladius*, represented by two morphotypes recorded from several localities in Guatemala and Honduras. The genus constitutes a large and ecologically diverse taxon containing over 100 species worldwide, predominantly distributed in the Northern Hemisphere. *Psectrocladius* is eurytopic with larvae that inhabit almost exclusively lentic systems, predominantly as periphyton inhabitants of shallow, standing or slow-flowing water bodies, ranging in size from small pools and cattle troughs to the largest lakes (Sæther & Langton 2011). Additionally, it is important to highlight the first register of the genus *Heterotrissocladius* in the Neotropical region (Hamerlik & Silva 2018). This genus, previously known only from the Holarctic, was recorded from the high elevation lake Magdalena in Guatemala in our study.

TABLE 2. Chironomid sub-fossils recorded in Central American lake sediments in 2013. For lake ID see Tab. 1, location of lakes is depicted in Fig. 1.Frequency expresses the percentage of occurrences of a specific taxon at all samples (lakes) analyzed.

Taxon	Frequency (%)	Locality (lake ID)
Chironominae		
Chironomini		
Apedilum sp.	19	1,3,7,9,25
Axarus sp.	4	16
Oukuriella type A	4	22
Oukuriella type B	19	10,15,16,23,25
Oukuriella type C	4	23
Cladopelma sp.	37	1,2,3,7,9,10,12,16,23,27
Chironomus anthracinus-type	44	1,4,6,7,9,12,14,15,16,17,25,26
Chironomus plumosus-type	33	1,6,7,9,14,18,21,22,24
Chironomus type C	15	11,19,21,22
Cryptochironomus sp.	15	1,8,10,23
Dicrotendipes notatus-type	7	4,7
Dicrotendipes nervosus-type A	7	16,23
Dicrotendipes nervosus-type B	30	1,3,7,8,11,22,23,25
Dicrotendipes nervosus-type C	7	9,2
Endochironomus albipennis-type	7	1,3
Endotribelos hesperium-type	15	7,16,17,21
Endotribelos albatum-type	4	6
Goeldichironomus pictus-type	59	1,2,3,8,11,13,14,15,16,17,19,22,23,25,26,27
Goeldichironomus neopictus-type	37	3,15,16,14,15,22,23,25,26,27
Goeldichironomus type A	11	11, 25, 26
Microtendipes pedellus-type	4	5
Lauterborniella agrayloides	11	1,18,21
Parachironomus varus-type	26	3,7,9,11,12,23,25
Paratendipes nudisquama-type	11	13,15,22
Pelomus psammophilus-type	4	1
Polypedilum type A	11	13,14,26
Polypedilum beckae-type	11	12,16,22
Polypedilum (*Tripodura*)-type	44	1,3,5,6,12,13,14,15,18,23,25,27
Xenochironomus sp.	7	7,23
Xestochironomus sp.	4	5
Zavreliella sp.	22	1,9,11,14,15,19
Pseudochironomini		
Pseudochironomus sp.	11	1,3,4
Manoa sp.	4	23
Tanytarsini		
Cladotanytarsus mancus-type	15	1,3,4,23
Micropsectra type A	4	5
Micropsectra type B	4	5
Micropsectra type C	7	16,23

TABLE 2. (Continued)

Taxon	Frequency (%)	Locality (lake ID)
Neozavrelia sp.	7	13,15
Stempellina sp.	4	1
Tanytarsus gr. *ortoni* type	4	3
Tanytarsus type A	11	2,7,10
Tanytarsus type B	15	1,16,17,23
Tanytarsus type C	15	4,16,22,23
Tanytarsus type D	7	15,18
Tanytarsus type E	19	2,4,10,16,17
Orthocladiinae		
Brillia sp.	4	5
Corynoneura lobata-type	4	5
Cricotopus cylindraceus-type	4	5
Cricotopus intersectus-type	4	5
Cricotopus sylvestris-type	4	7
Cricotopus type A	4	16
Cricotopus type B	4	16
Cricotopus type C	4	5
Cricotopus/Orthocladius sp.	4	5
Eukiefferiella claripennis-type	4	5
Eukiefferiella devonica-type	4	5
Eukiefferiella fittkaui-type	7	5,16
Heterotrissocladius marcidus-type	4	5
Metriocnemus eurynotus-type	4	5
Nanocladius sp.	4	16
Parakiefferiella bathophila-type	4	5
Paralimnophyes sp.	11	5,16,21
Parametriocnemus sp.	11	5,6,16
Psectrocladius psilopterus-type	7	5,17
Psectrocladius sordidellus-type	15	6,17,18,21
Rheocricotopus chalybeatus-type	4	5
Rheocricotopus effusus-type	4	5
Stictocladius multiserialis-type	4	23
Synorthocladius sp.	4	5
Thienemanniella lobopodema-type	4	10
Podonominae		
Parochlus sp.	4	5
Tanypodinae		
Ablabesmyia type A	63	1,3,4,7,8,9,10, 12,14,16,17,19,20,21,22,23,27
Ablabesmyia type B	7	2,17
Clinotanypus sp.	4	11
Coelotanypus concinnus-type	33	1,9,15,16,20,23,25,26,27
Fittkauimyia sp.	4	3

TABLE 2. (Continued)

Taxon	Frequency (%)	Locality (lake ID)
Labrundinia type Y	41	1,3,9,11,14,15,20,23,25,26,27
Labrundinia virescens type	52	3,4,7,9,11,13,14,15,16,18,19,20,24,27
Labrundinia paulae-type	7	16,23
Larsia sp.	15	13,16,18
Pentaneura sp.	7	15,17
Pentaneurini type A	11	11,13,15
Pentaneurini type B	4	5
Procladius sp.	44	1,3,5,6,7,8,10,16,17,18,21,23
Tanypus stellatus-type	22	11,12,19,20,26,27

Tanypodinae. Tanypodinae is the third most speciose subfamily in the Chironomidae, with species distributed widely across most of the globe, inhabiting numerous habits ranging from small streams and ponds to lakes and bays (Silva *et al.* 2011). The larvae of the majority of species are free-living and none are known to produce larval or pupal cases (Ashe *et al.* 1987). Normally considered as predators, some species of Tanypodinae feed on diatoms and detritus (Oliver 1971). Bitušík & Hamerlik (2014) found remains of testate amoebae, Cladocera and harpacticoid copepods in the gut content of tanypod larvae. The subfamily was represented by nine genera, comprising at least 14 species. *Labrundinia* was the most abundant and species rich, with at least three species. *Labrundinia* is a large group, mainly Neotropical, with immature stages occurring in a wide range of aquatic systems, from small streams and ponds to lakes and bays, where the larvae usually live associated with aquatic macrophytes or marginal vegetation in slow flowing streams or rivers (Silva & Fonseca-Gessner 2009; Silva *et al.* 2011, 2014c). Larval *Labrundinia* frequently have been reported as predators and have been recorded in several ecological studies (Trivinho-Strixino & Strixino 1993; Aburaya & Callil 2007; Maltchik *et al.* 2012). According to Silva *et al.* (2015), the genus may have had its initial diversification in warmer waters in the Neotropical region and that current presence in the Nearctic region and southern South America is due to subsequent dispersal.

With two species, *Ablabesmyia* was the second most specious and frequent tanypod. *Ablabesmyia* is one of the most characteristic and well-defined genera within the tribe Pentaneurini (Silva & Ekrem 2016). The genus is eurytopic and cosmopolitan with larvae inhabiting small and large standing and flowing waters from cold temperate to warm tropical climatic zones (Silva & Farrell 2017). Individual species may occupy quite varied habitats, and may include tolerant and sensitive species to acidity and humic content (Cranston & Epler 2013). The highest diversity of *Ablabesmyia* appears to be in the tropics and warm temperate zones.

Podonominae. Podonominae is a subfamily distributed worldwide with an amphitropical distribution. The group reaches its greatest diversity in the southern temperate belt, which comprises 84% of the podonomine's world fauna (Sæther & Andersen 2013). In our study, Podonominae was represented only by the genus *Parochlus*, recorded from Lake Magdalena in Guatemala. *Parochlus* is the most widespread and species-rich genus within Podonominae. Their immature stages live in cold springs and running waters. The genus is very diverse in the southern temperate zone, from sub- and true Antarctic, and in Australia, New Zealand and South America. According to Ashe & O'Connor (2009), *Parochlus* originated in the cooler waters of the high Andes and southern Neotropical latitudes. The presence of a single widespread species, *P. kiefferi*, in the Northern Hemisphere may be attributable to dispersal events from the Neotropical Region through the nearly continuous chain of mountains that extend from southern Chile to Arctic Canada (Ashe & O'Connor 2009). Therefore, it is expected that evidence of dispersal in *Parochlus* will be reflected as a series of close related species with older lineages found towards the south, with progressively younger lineages present further north, with *P. kiefferi* as the terminal species (Silva & Farrell 2017).

Diversity pattern along elevation. Taxa richness and proportion of some chironomid subfamilies changed significantly with altitude: Orthocladiinae increased, while Chironominae decreased considerably. Tanypodinae and total chironomid diversity did not respond significantly to altitude. These trends in both diversity and abundance of chironomids have been recorded previously for mountain lakes (Boggero *et al.*, 2006; Füreder *et al.*, 2006; Hamerlik & Bitušik, 2009) and alpine ponds (Hamerlik *et al.* 2017) and is attributed to overall temperature-
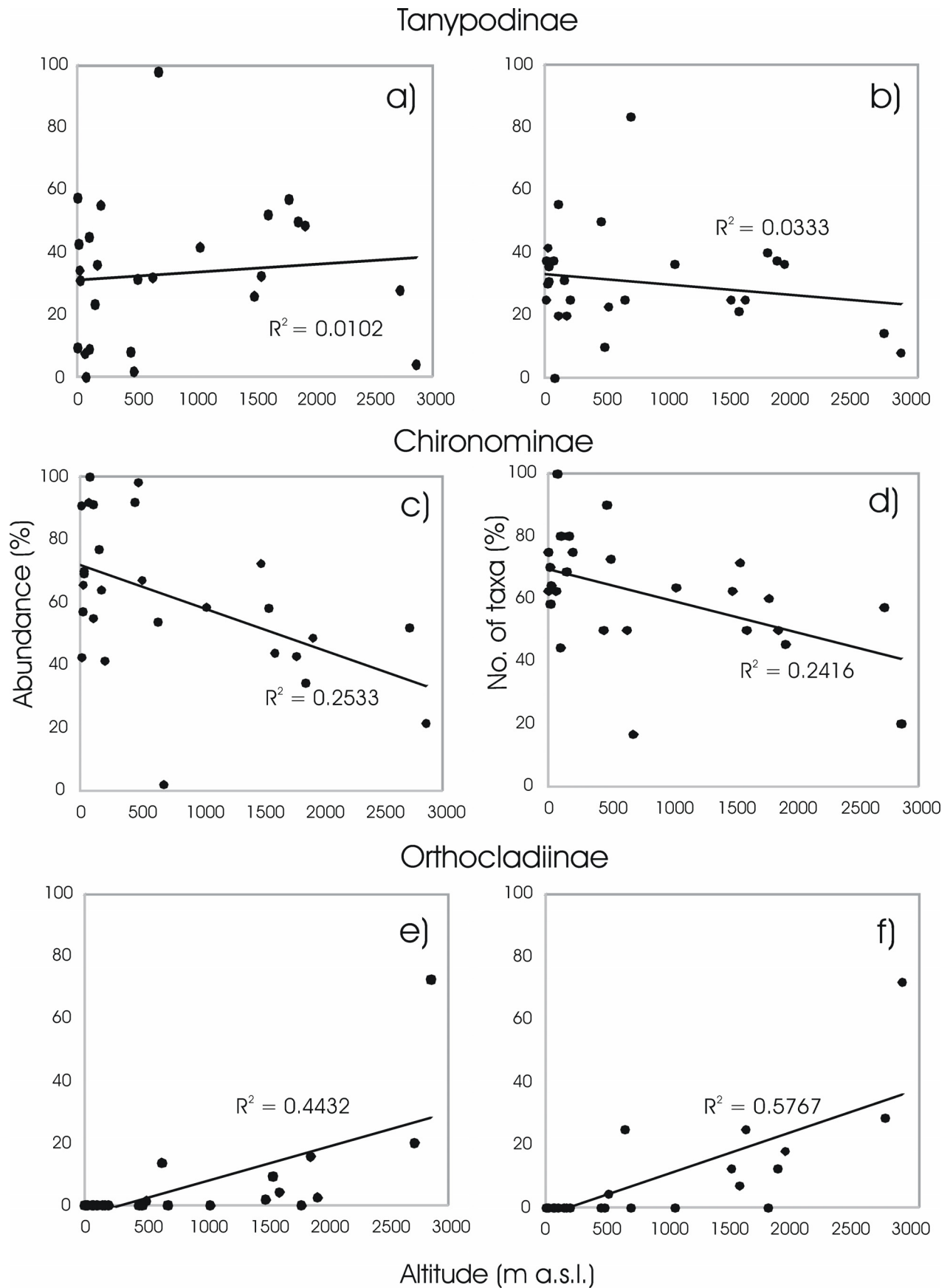
Tanypodinae

Chironominae

Orthocladiinae

FIGURE 2. Elevational distribution of the proportion of chironomid subfamilies Tanypodinae, Chironominae and Orthocladiinae on the total chironomid abundance (a, c, e) and taxonomic richness (b, d, f). P values are as follows a) *p*=0.61, b) *p*=0.36, c) *p*=0.007, d) *p*=0.009, e) *p*=0.0001, f) *p*=0.000004.

and oxygen preferences as well as feeding habits of the subfamilies. Orthoclads are frequently oxy-conformers not able to regulate oxygen uptake (Brodersen *et al*., 2004), and thus restricted to waters with high oxygen content, i.e. cold and oligotrophic high-altitude waterbodies. On the contrary, many Chironominae, especially from the tribe Chironomini, have physiological and behavioral adaptations to cope with warmer water and lower oxygen levels (Brundin, 1966) and thus usually dominate productive lowland waterbodies.

The weak response of the overall chironomid diversity to elevation is not surprising and has been recorded previously. First of all, chironomids apparently evolved in cool oxygen-rich mountain waterbodies (Brundin, 1966) and consequently many species developed special adaptations to cope with adverse climatic conditions (Füreder *et al*., 2006). Second, due to their weak competitive potential, chironomids can be easily outcompeted in milder environments that is characteristic for lower elevations (Armitage *et al*., 1995). More extreme abiotic conditions typical for higher elevation can result in reduced interspecific competition and favors well-adapted groups, such as chironomids.

Conclusion

Despite the generic richness recorded herein appears to be conceivably lower than the actual richness of chironomids in Central America, particularly considering the limited extension of the study, our results represent advance in documenting the diversity of the chironomid communities in Central America. Although our inventory documents relatively species-poor chironomid communities in the lakes of Central America, particularly when considered the Neotropics (see Silva & Farrell 2017), it is expected that by increasing the variety of sampling habitats and geographic area may reveal a greater diversity than currently detected. While recent years have seen increased activity concerning the chironomid fauna in the Neotropical region, the knowledge of the diversity and taxonomy as well as biogeography and phylogeny, especially in Central America, remains fragmentary. The present study contributes to the knowledge of sub-fossil Chironomidae from lake sediments in Central America and will hopefully motivate further studies in the Neotropical region.

Acknowledgements

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