Subfossil Chironomidae (Diptera) in surface sediments of the sinkholes (cenotes) of the Yucatan Peninsula: Diversity and distribution

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ABSTRACT

Cenotes (sinkholes), formed by the dissolution of the carbonate rock, are the most common waterbodies on the Yucatan Peninsula. Despite their unique features and great amount in the region, our knowledge on the biota of cenotes remains fragmentary. Within the present study we analysed chironomid remains from surface sediment of ten cenotes situated in SE Mexico. In total, 20 taxa of 17 genera were recorded, and the total diversity was estimated to ~30 taxa. The most common taxa were *Polypedilum* (*Tripodura*) sp*., Tanytarsus ortoni*-type, *Fittkauimyia* sp., *Labrundinia* sp. and *Endotribelos* sp. There was a great variability in head capsule abundance among cenotes, ranging from 1 to 64 individuals per site with significantly higher number of remains recorded in open cenotes compared to the closed, cavern types. The results indicate that beside ecological features, such as low trophy, oxygen depletion, simplified habitat structure and fish predation, there are also taphonomical processes connected to the specific nature of cenotes that can hinder the accumulation of biological remains in the sediment. We conclude that due to poor sedimentation and preservation of remains, cenotes have limited potential for palaeolimnological studies.

Key words: Chironomids; head capsules; lakes; Mexico; Neotropical Region.

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INTRODUCTION

Due to its karstic nature, one of the unique feature of the Yucatan Peninsula is the almost complete absence of superficial waterbodies such as rivers and streams (Torres-Talamante *et al*., 2011). The most typical waterbodies of the region are sinkholes formed by the dissolution and collapse of limestone. In the Yucatan Peninsula (SE Mexico) these formations are called 'cenotes' (Torres-Talamante *et al*., 2011). Cenotes show a wide morphological variability from caves filled with ground water to open ones. Usually they have vertical walls and circular shape, with varying depth reaching tens of metres. Different cenote types can be distinguished based on the location, shape and size of the opening relative to the size of the waterbody area (Hall, 1977). Stable hydrological conditions together with low water-level fluctuation is a characteristic feature of cenotes (Sanchez *et al*., 2002). Most cenotes are oligotrophic to mesotrophic; only about 15% are eutrophic (Schmitter-Soto *et al.,* 2002). Despite their great amount on the Yucatan Peninsula (>7000;

Steinich and Marín, 1996), knowledge on the biota of cenotes is insufficient (Schmitter-Soto *et al*., 2002; Alcocer and Bernal-Brooks, 2010). To date, most attention was paid to crustaceans and zooplankton along with fish that show high endemism (Schmitter-Soto *et al.,* 2002 and references therein). Moreover, due to increased urbanization and tourism, they are becoming increasingly important for tourist activities but most of all, as sources of drinking water (Szeroczyńska and Zawisza, 2015). However, increasing human impact put the biota of cenotes under threat in the future.

Chironomids occur in a huge variety of aquatic ecosystems and are able to live within a range of conditions that exceed any other aquatic insect family. Their larvae often dominate the benthos of water bodies both in terms for abundance and diversity (Ferrington, 2008). Out of more than six thousand described species worldwide, about 900 are known from the Neotropical region (Spies *et al*., 2009). Even though an increased attention has been paid recently to the chironomid taxonomy in the Neotropical Region, our knowledge on the ecology of the species is still very poor. This is

particularly true for the fauna of some specific ecosystems, such as cenotes.

Within a bigger limnological investigation we analysed surface sediment samples from ten cenotes situated on the Yucatan Peninsula. The goal of the present paper is to bring new information on the distribution of chironomid taxa and structure of chironomid assemblages in cenotes and evaluate their potential for limnological and palaeolimnological studies.

METHODS

Study sites

Surface sediment samples were taken using an Ekman sediment grab from ten cenotes located in states Yucatan and Quinatana Roo, SE Mexico (Fig. 1). Eight cenotes were sampled in 2013, additional two (Xlacah, Yalahau, Fig. 2) in 2017. Prior to sediment sampling, basic physical and chemical characteristics, such as pH, temperature, conductivity salinity and oxygen content, were measured at every site using a WTW multi-probe. Water transparency was assessed with a Secchi-disc and maximum depth (if possible) with a portable sounder.

Due to small sample size and low number of sites, the environmental variables were not further used for statistical analysis. However, we believe that the environmental data could be valuable for the readers to get an impression about the nature of the cenotes, thus,

we include them as background data. From the six environmental variables measured (Tab. 1), Secchi-depth, oxygen concentration and conductivity showed considerable variations among the investigated sites. Secchi-depth varied between 2 and 15 m (7.6 m on average). Conductivity ranged from 70 to 2010 µS cm^{-1} (1210 µS cm^{-1} on average), but most of the cenotes (six) had conductivity higher than 1000 µS cm^{-1}. Water oxygen concentration was generally low (0.8-4.6 mg L^{-1}, 3.45 mg L^{-1} on average), however, except for one site it was higher than 3 mg L^{-1}. Small intra-site variability was found in water temperature (24.9-27.7˚C), pH (7.28-7.93) and salinity (0.03-0.07‰).

Chironomid analysis

For chironomid analysis, sub-samples consisting of ca. 5 g wet 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 Brooks *et al*. (2007) and Andersen *et al.* (2013). The taxon identified as *Caladomyia* based on Andersen *et al.* (2013) has been changed to *Tanytarsus ortoni*-type according to Lin et a. (2018) who suggested all *Caladomyia* being synonymized with *Tanytarsus* (precisely with *T. ortoni* group).
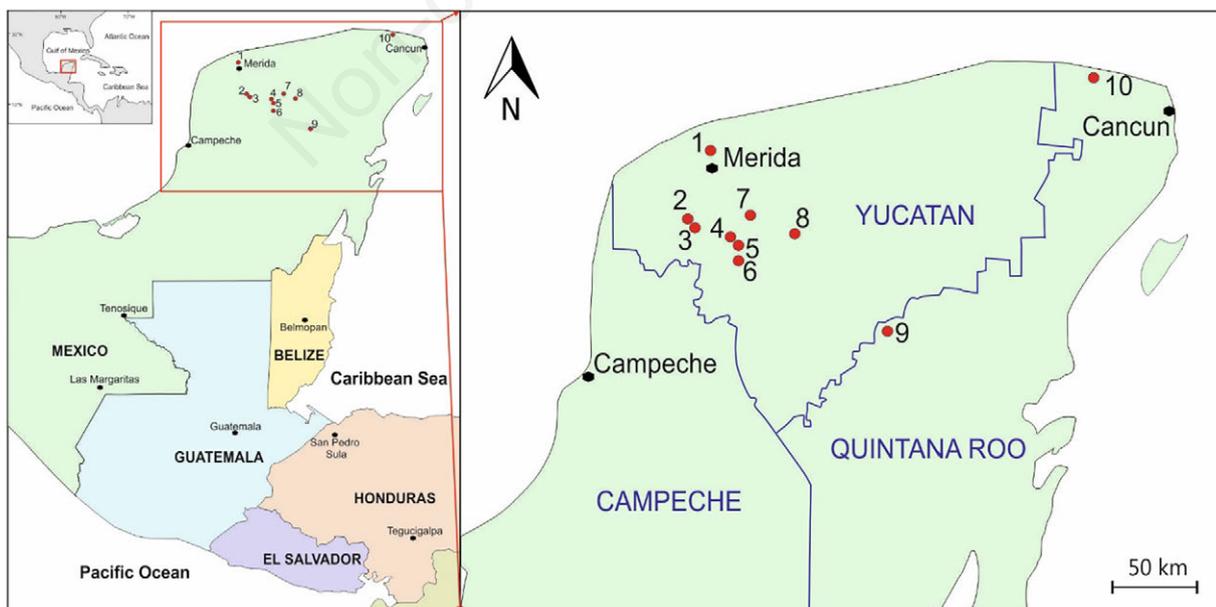

Fig. 1. Map of the study area showing the location of sampled cenotes. Numbers indicate the position of the cenotes: 1, Xlacah; 2, Dzonbacal; 3, Xbatún; 4, Chihuol; 5, Mucuyche; 6, Yumku; 7, Tekoh; 8, Oxolá; 9, Sacalaca; 10, Yalahau.

Statistical analysis

Chao-1 was calculated to assess the actual species richness at each site using the equation [Chao1 = S + F1 (F1 - 1) / (2 (F2 + 1)], where F1 is the number of singleton species and F2 the number of doubleton species. Sample rarefaction curve was fit using the Michaelis-Menten equation to estimate the total chironomid diversity of cenotes (Colwell and Coddington 1994).

Differences in diversity and abundance of subfossil chironomids in various types of cenotes were tested using t-test. For all analyses, PAST ver. 3.13 (Hammer *et al.*, 2001) was employed.

RESULTS

A total of 20 taxa belonging to three subfamilies, Chironominae (13 taxa), Tanypodinae (6 taxa) and Orthocladiinae (1 taxon) were recorded (Tab. 2). Average taxon richness per cenote was 4.9 and varied from 1 to 10 taxa. The assessed actual richness per site (Chao-1) ranged between 1 and 12, averaging 6.4 taxa. The total chironomid diversity of cenotes (using the actual method and taxonomic resolution) was estimated to less than 30 taxa. The number of head capsules varied greatly from 64 (cenote Mucuyche) to one individual (Tekoh, Chihuol) averaging 19 individuals per sample. With 10 taxa, cenote Xbatún contained the most diverse subfossil chironomid assemblage. Due to the paucity of the material (three samples containing only 1-2 remains) it is hard to assess the most frequent taxa, however, *Polypedilum* (*Tripodura*) sp*., Tanytarsus ortoni*-type, *Fittkauimyia* sp., *Labrundinia* sp. and *Endotribelos* sp., were present at least in 40% of the study sites.

Open type cenotes differed significantly from the closed ones (caverns) both in average number of
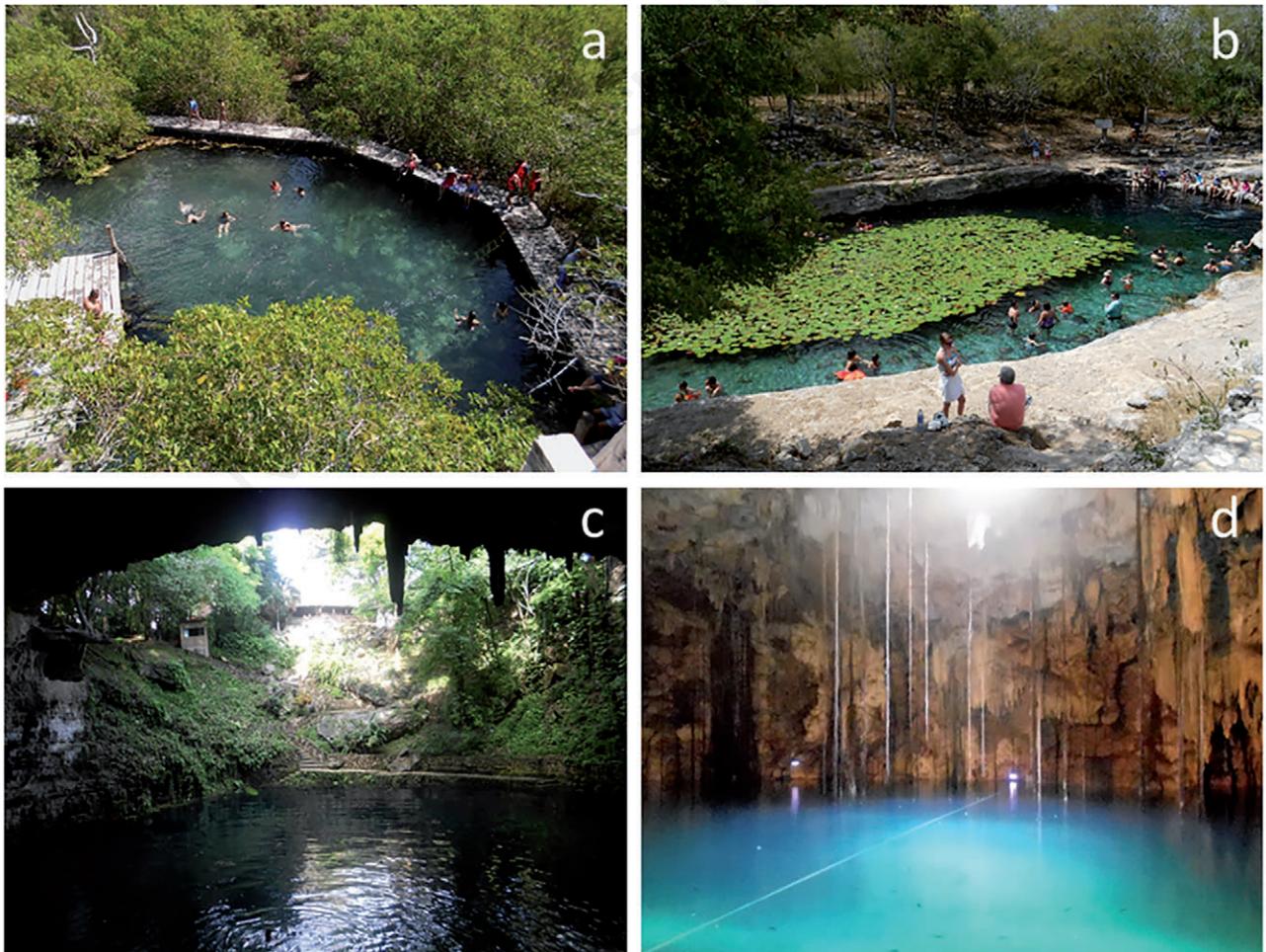

Fig. 2. View of two types of cenotes: open (a, b) and close cenotes (c, d). Yalahau (a) and Xlacah (b) have been sampled within the present study, while Zaci (c) and Samula (d) are illustrative pictures. Courtesy of Edyta Zawisza.

chironomid remains (32 in open *vs* 6 in closed cenotes, P=0.03), and in higher taxonomic richness (7.4 *vs* 2.4, P=0.002). Chironomini were common in both cenote types, while Tanypodinae and Tanytarsini tend to be more frequent in open cenotes, being recorded only in two and one closed type cenote, respectively.

DISCUSSION

In total, 20 taxa of 17 genera were recorded in the studied cenotes, and the total diversity was estimated (extrapolated) to less than 30 taxa. Vinogradova and Riss (2007) found as much as 84 taxa from 48 genera in 18 Yucatan lakes, however, 32 taxa were recorded as adults only. In a comprehensive check list of Mexican Chironomidae, Andersen *et al.* (2000) listed 61 species of 35 genera (and 25 extra genera with no species identified) from five subfamilies. Given that Spies and Reiss (1996) listed more than 700 species and 155 genera from the Neotropics, and Spies *et al.* (2009) 114 genera (including those with potential occurrence) from Central America, it is evident that the actual diversity of the region is dramatically underestimated.

The assemblage structure of cenotes was in good accordance with the taxonomic composition known from Mexico (Anderson *et al.*, 2000), showing the dominance of Chironominae followed by Tanypodinae. Orthocladiinae were rare, represented by few species only. Vinogradova and Riss (2007) compared the chironomid fauna of Yucatan water bodies with adjacent areas, such as Guatemala (Sublette and Sasa 1994), Colombia (Riss and Ospina 2000; Nazarova *et al.* 2004), central lowlands of Yucatan (Contreras-Ramos and Andersen 1999) and concluded that the chironomid fauna of the Yucatan lowland in general can be regarded as a Circum-Caribbean element.

There was a great variance in head capsule counts among cenotes, ranging from 64 to as few as 1-2 remains in three cenotes. We could argue that a relatively small amount of sediment was analysed and that could have caused the small head capsule counts. However, 5 g of material (and usually even as little as 1 g) is a standard amount of material used for palaeoecological investigation, since the sediment taken is analysed for multiple biotic and environmental proxies. Moreover, this standard amount of material allows easy comparison among cenotes but also with other palaeostudies. Nonetheless, the low number of remains is in accordance with the existing literature suggesting that the reason for that is the peculiar character of cenotes instead of the insufficient volume of material. For instance, Smirnov and Elías-Gutiérrez (2011) conducted an analysis of biotic remains in the surface sediments of 25 Yucatan waterbodies (15 of which were cenotes). They found very low numbers of chironomid head capsules and except for seven sites chironomids were not found at all. Vinogradova and Riss (2007) also witnessed low head capsule number in Yucatan lakes relative to temperate lakes and assumed it to be a result of synergic effect of several factors, such as the reduced durability of sediments, extremely high sedimentation rate in the lakes of the region, and disaggregation of remains due to disturbed sedimentation in shallow lakes.

In general, amount of chironomid remains and their diversity were significantly higher in open cenotes than in the closed, cavern types. Low diversity in closed cenotes is most likely an artefact of low abundance, sine the number of remains in these cenotes was strikingly low, not allowing estimation of actual taxonomical richness. At the same time, it is likely, that open cenotes are easier to colonize by insects and most likely represent a productive environment providing more food sources and

Tab. 1. Basic environmental variables of the studied cenotes.

ID	Name	Region	N	W	Altitude (m asl)	Depth* (m)	Secchi depth (m)	Temp. (°C)	O$_2$ (mg L^{-1})	pH	Cond. (µS cm^{-1})	Salinity (‰)	Cenote type
1	Xlacah	Y	21.0526	89.3552	9	40	-	-	-	-	-	-	O
2	Dzonbacal	Y	20.6697	89.7786	13	3	3	27.3	3.46	7.28	2010	0.09	C
3	Xbatún	Y	20.6737	89.7730	25	10	8	27.7	4.60	7.50	1790	0.08	O
4	Chihuol	Y	20.6350	89.6120	23	10	10	27.3	3.45	7.40	1400	0.06	C
5	Mucuyche	Y	20.6242	89.6065	17	18	15	27.5	3.68	7.38	1530	0.07	O
6	Yumku	Y	20.5781	89.6052	16	15	10	26.4	4.15	7.54	1060	0.04	C
7	Tekoh	Y	20.7301	89.4660	24	3	3	27.2	3.00	7.30	1030	0.04	C
8	Oxolá	Y	20.6782	89.2417	18	16	10	24.9	4.60	7.75	794	0.03	C
9	Sacalaca	QR	20.0667	88.5997	28	25	2	25.8	0.82	7.93	70	0.04	O
10	Yalahau	QR	21.2723	87.2421	0	2.5	-	-	-	-	-	-	O

Maximum sampled water depth and/or maximum water depth; Y, Yucatan; QR, Quintana Roo; O, open; C, cavern.

higher habitat diversity (e.g., due to the presence of macrophytes).

Previous studies pointed out low number and diversity of biotic remains in Yucatan waterbodies (Vinogradova and Riss, 2007; Smirnov and Elías-Gutiérrez, 2011). The potential reasons for that can be multiple: fish predation, low nutrient content, low oxygen content, habitat simplicity (absence of the littoral zone and macrophytes) and the connected (overflowing) character of cenotes.

Some authors consider fish predation as an important factor at least partly explaining low number of remains in cenotes (specially for Cladocera; Szeroczyńska and Zawisza, 2015), while others claimed that predatory pressure is not the real reason for the observed situation (Smirnov and Elías-Gutiérrez, 2011). Regarding chironomids, high fish density is usually connected to low head capsule concentrations and diversity (Langdon *et al.*, 2010). Only few fishes found in cenotes feed strictly on

planktonic cladocerans, and the majority attacks also microcrustacenas and insects (Cervantes-Martinez *et al.*, 2002; Smirnov and Elías-Gutiérrez, 2011), thus, an overpopulated fish stock could be one of the reasons for low chironomid abundance in cenotes. However, closed cenotes tend to be limited in fish or even fishless (Zawisza, personal observation), and thus, the low number of head capsules in them is most likely not connected to fish predation.

The oligotrophic character of most of the cenotes (Schmitter-Soto *et al.*, 2002) together with the absence of a littoral zone due to vertical walls, and in turn, the lack of submerged vegetation (Smirnov and Elías-Gutiérrez, 2011) can be also responsible for the low number and scarcity of remains. Cladocera usually reach higher abundances when submerged and floating plants are present what is often connected to higher trophic conditions. It applied for chironomid remains as well, since Vinogradova and Riss (2007) found higher

Tab. 2. List and relative abundances (%) of the recorded taxa. Frequency (%) is expressed as a percentage of localities with the occurrence of the taxon. Grey field denotes closed (cavern type) cenotes. Taxa with frequency >50% are in bold. Cenotes are ordered in decreasing taxon richness.

Taxa / Cenote	Xbatún	Mucuyche	Xlacah	Yalahau	Sacalaca	Dzonbacal	Yumku	Oxolá	Tekoh	Chihuol	Frequency (%)
Tanypodinae											
Ablabesmyia sp.	-	2	-	6	-	-	-	-	-	-	20
Coelotanypus sp.	2	2	-	-	-	-	-	-	-	-	20
Fittkauimyia sp.	2	20	4	-	36	23	-	-	-	-	**50**
Labrundinia sp.	12	5	11	-	9	-	8	-	-	-	**50**
Procladius sp.	-	8	-	-	-	-	-	-	-	-	10
Pentaneurini indet.	-	-	-	-	9	-	-	-	-	-	10
Orthocladiinae											
Smittia sp.	2	-	-	-	-	-	-	-	-	-	10
Chironominae											
Oukuriella sp.	-	-	75	-	-	-	-	-	-	-	10
Chironomus anthracinus-type	-	-	-	35	-	-	8	-	-	-	20
Chironomus plumosus-type	-	-	-	29	-	-	-	-	-	-	10
Cladopelma lateralis-type	5	8	-	-	18	-	-	-	-	-	30
Dicrotendipes nervosus-type	-	-	-	6	-	-	-	-	-	-	10
Endotribelos sp.	-	11	-	-	-	23	54	50	-	-	40
Paratendipes nudisquama-type	5	-	-	-	-	-	-	-	-	-	10
Polypedilum (*Asheum*) sp.	-	-	4	-	9	-	-	-	-	-	20
Polypedilum (Tripodura) sp.	5	23	4	-	-	38	31	-	100	100	**70**
Pseudochironomus sp.	2	-	-	6	-	-	-	-	-	-	20
Stenochironomus sp.	-	-	-	-	-	-	-	50	-	-	10
Tanytarsus ortoni-type	12	22	4	18	18	15	-	-	-	-	**60**
Tanytarsus type B	51	-	-	-	-	-	-	-	-	-	10
Chironominae (%)	80	64	86	94	45	77	92	100	100	100	
Chironomini (%)	16	42	82	71	27	62	92	100	100	100	
Tanytarsini (%)	64	22	4	23	18	15	-	-	-	-	
Tanypodinae (%)	17	36	14	6	55	23	-	-	-	-	
Orthocladiinae (%)	3	-	-	-	-	-	-	-	-	-	
Total abundance	41	64	28	17	11	13	13	2	1	1	
Number of taxa	10	9	6	6	6	4	4	2	1	1	
No. taxa estimated (Chao-1)	11.5	10	12	9	7	4	5	3	1	1	

abundance of chironomid remains in eutrophic lakes compared to oligotrophic ones, and trophic status was a factor driving chironomid communities in the region. The highest chironomid diversity was observed in cenote Xbatún (the only cenote of considerable abundance of Cladocera remains, Wojewódka, unpublished data), which is a popular tourist place and thus higher trophy can be expected. However, even though nutrient concentration was not measured in the cenotes, Secchi-depth (8 m, Tab. 1) detected in Xbatún does not indicate high pelagic production and does not corroborate the hypothesis of high trophic status.

Macrophytes provide available habitat for colonization and, in some cases, food source for some species, consequently they are important for structuring chironomid communities (Pinder, 1995 and citations therein). Larvae of several taxa, such as *Ablabesmyia*, *Labrundinia*, *Dicrotendipes* and some *Polypedilum* are associated with macrophytes (Brodersen *et al.*, 2001; Moller Pillot, 2009; Langdon *et al.*, 2010) and in our study these taxa are mainly linked to open cenotes, where development of macrophytes could be expected.

In general, there are two main cenote types. Lotic cenotes, with short residence time due to their interconnection with groundwater, have clear, well-oxygenated water and sandy-rocky bottom. The second type, lentic cenotes, is characterized by slow flow and turnover, and partially blocked connection with groundwater source. The water of these cenotes is usually turbid and due to thermal stratification, anoxic conditions can occur at the bottom (Schmitter-Soto *et al.*, 2002).

Low oxygen concentration can be a limiting factor for bottom dwelling organisms and could decrease chironomid diversity. However, larvae of some Chironominae, e.g., *Chironomus*, *Polypedilum* and *Endotribelos*, contain haemoglobin and thus can prosper in waters with hypoxic and anoxic conditions that can be a result of higher temperature and productivity of lowland lakes. Chironominae was the dominating subfamily and *Polypedilum* and *Endotribelos* were among the most common taxa in the investigated cenotes.

Except for the above factors reducing the richness of recent chironomid communities, there are features connected to the origin, hydromorphology and flow-through nature of the cenotes that can result in low number of remains. Unlike lakes, cenotes have irregular bottoms and are interconnected through subsurface basins and steams. This results in irregular sedimentation process and poor preservation of biotic remains. Thus, we hypothesise that the low number of remains and big variability among cenotes can be as much a result of taphonomical processes as of ecological adversity of the environment.

CONCLUSIONS

The taxonomic composition of the studied cenotes was in accordance with other studies from the region. There was a considerable variability in the number of head capsules per cenote and surface sediments of open cenotes contained significantly higher amount of remains compared to that of closed cenotes.

Our results indicate that the variability in abundance (and thus in diversity) of chironomid remains can be caused by the reduction of recent communities by low trophy, oxygen depletion and simplified habitat structure, or, in some cases, by fish predation. However, taphonomic processes, *i.e.* poor sedimentation and conservation of remains due to direct connection with groundwater and permanent water flow can also hinder the accumulation of remains in the sediments. Thus, we suggest that for limnological/ palaeolimnological studies, open lentic cenotes with higher trophic status should be chosen. This cenote type has higher potential to reflect environmental changes of the surrounding environment and can yield higher number of aquatic remains that is necessary for palaeoecological investigations.

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