



# An illustrated guide of subfossil Chironomidae (Insecta: Diptera) from waterbodies of Central America and the Yucatan Peninsula

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**Abstract** We provide a photographic guide and taxonomic diagnosis of Chironomidae larval remains obtained from surface sediments and short cores of 92 waterbodies situated on the Yucatan Peninsula and in Central America, namely Mexico, Belize, Guatemala, El Salvador and Honduras. A total of 101 morphotypes belonging to 64 genera were identified. Chironominae was the most species-rich subfamily represented by 57 morphotypes of 34 genera. The most widespread and abundant genus was *Goeldichironomus* followed by *Chironomus* and *Polypedilum*. Orthoclaadiinae were represented by 26 morphotypes and 17 genera, with the most common one being *Cricotopus*. Remains of

this subfamily were recorded in only  $1/5$  of the surveyed lakes. Tanypodinae included 17 morphotypes belonging to 12 genera. *Labrundinia* along with *Ablabesmyia* and *Coelotanypus* were the most common genera. Subfamily Podonominae was represented by the genus *Parochlus*. We believe that our study includes most of the Chironomidae genera of Central America and will have broad applicability for both paleolimnologists and aquatic ecologists.

**Keywords** Subfossil chironomid larvae · Aquatic environments · Taxonomic diagnosis · Central America and Mexico

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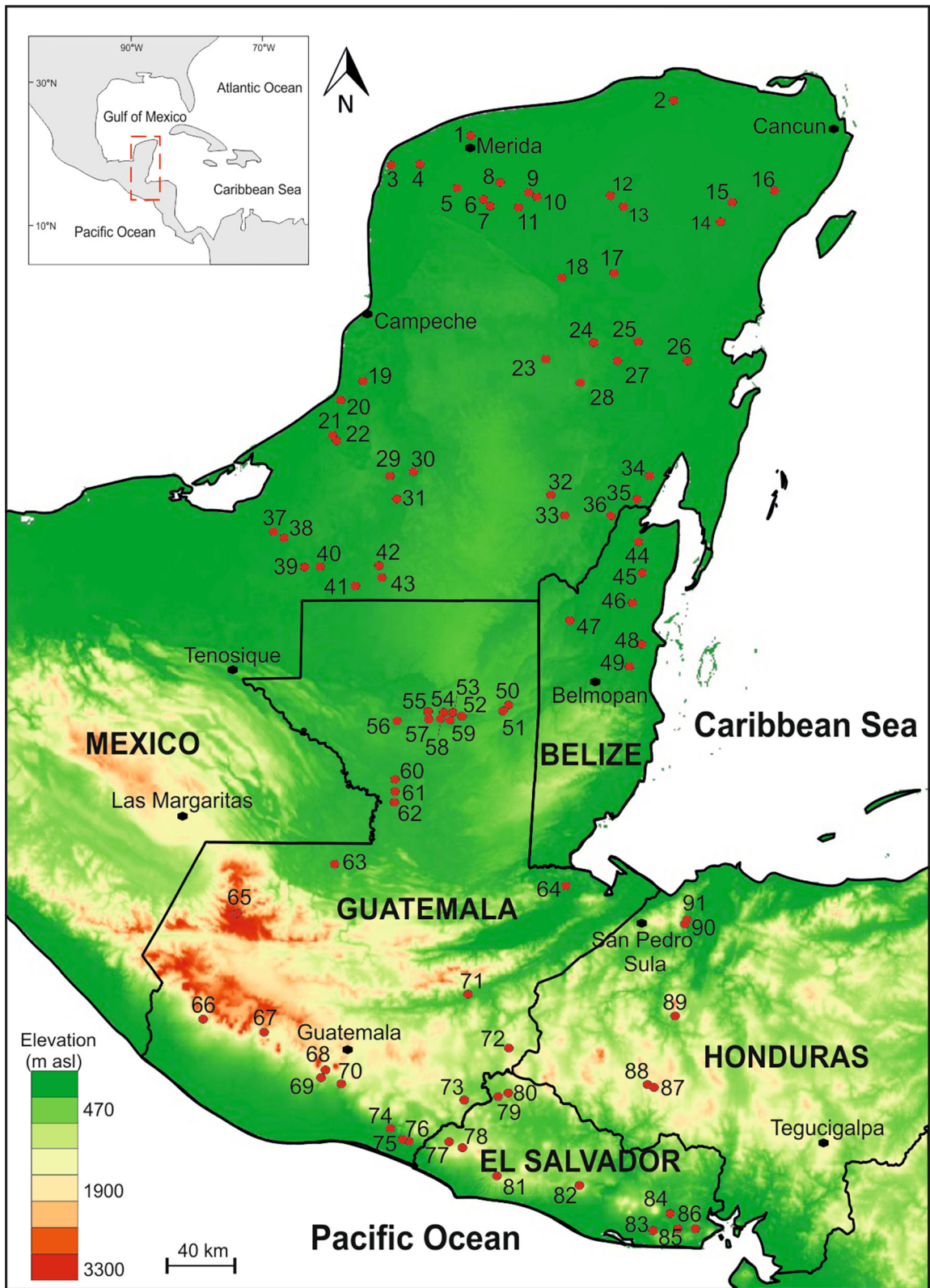
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## Introduction

Paleoecological records provide a valuable long-term perspective beyond the instrumental data on the dynamics of contemporary ecological systems. Paleoecology has become an important asset in conservation and management programs providing information about biodiversity conservation at different temporal and spatial scales related to biological invasions, wildfires, climate change and conservation management (Willis and Birks 2006). It provides information, which is absent in ecological studies: records of species assemblages spanning many generations intermingled with a changing environment. Willis and



◀ **Fig. 1** Map of the location of the surveyed lakes. **Mexico:** 1. Cenote Xlaka; 2. Loche; 3. Cenote Peten de Monos; 4. San Francisco Kana; 5. Cenote Chenha; 6. Chihuol; 7. Mucuyche; 8. Tekom; 9. Oxolá; 10. Yalahau; 11. Cenote Timul; 12. Cenote Yoknot; 13. Cenote Ya'ax'ëx; 14. Laguna Coba; 15. Punta; 16. Cenote Juarez; 17. Sacalaca; 18. San Miguel; 19. Jamulun Channel; 20. Rio Guerrero; 21. Chuina; 22. Xbacab; 23. Chacan Lara; 24. Ocom; 25. Kaná; 26. Chichancanab; 27. Corozo; 28. Nobec; 29. Silvituc; 30. Aguado Jobal; 31. Chan laguna; 32. Chacan Bata; 33. San Jose Aguilar; 34. Bacalar; 35. Milagros; 36. Sabanita; 37. Salto Grande; 38. Rio Candelaria; 39. Laguna del Cayucon; 40. Estado de México; 41. San Francisco Mateo; 42. Misteriosa; 43. Rio Cuba; **Belize:** 44. Progreso Lagoon; 45. Honey Camp B.; 46. Crooked Tree L.; 47. Gr. Pond Belize; 48. Almond Hill; 49. Belize; **Guatemala:** 50. Sacnab; 51. Yaxha; 52. Macancha; 53. Salpetén; 54. Peten Itza; 55. Perdida; 56. San Diego; 57. Sacpuy; 58. Quexil; 59. Rio Ixlu; 60. El Rosario; 61. Petebatun; 62. Laz Pozas; 63. Lachua; 64. El Golfete; 65. Magdalena; 66. Chicabal; 67. Atitlán; 68. Amatitlan; 69. Calderas; 70. El Pino; 71. Oquevix; 72. Ipala; 73. Atescatempa; 74. Comandador; 75. El Muchacho; 76. Grande; **El Salvador:** 77. El Espino; 78. Verde; 79. Guija; 80. Metapan; 81. Chanmico; 82. Apastepeque; 83. Jocotal; 84. Aramuaca; 85. Olomega; 86. Los Negritos; **Honduras:** 87. Madre Vieja; 88. Chiligatoro; 89. Yojoa; 90. Jucutuma; 91. Ticamaya

Birks (2006) discussed the considerable potential of synergy between neo-ecology and paleoecology, pointing to the need for better taxonomic resolution of the fossil remains to enhance the biological value of the fossil records.

The use of subfossil chironomids (Diptera: Chironomidae) as biological proxies of past environmental conditions is now a well-established approach (Walker 2001). The large species and habitat diversity in this family is presumably a result of its antiquity, relatively low vagility and evolutionary plasticity (Ferrington 2007), which makes them valuable indicators for recent ecological status of lentic and lotic aquatic ecosystems. Chironomids go through four larval stages, each leaving behind a molted head capsule that preserves in lake sediments through time. This capacity, together with their specific ecological preferences and narrow tolerances to environmental variables makes chironomids the most reliable aquatic group for reconstructing past climate and environmental conditions. The close relationship between chironomids and environmental variables, has allowed the development of chironomid-based quantitative models to reconstruct trophic status (Lotter et al. 1998; Langdon et al. 2006), oxygen level (Quinlan and Smol 2002), salinity (Henrichs et al. 2001; Eggermont et al.

2006), depth (Korhola et al. 2000; Engels et al. 2012), lake size and acidification (Mousavi 2002; Pegler et al. 2020), chlorophyll-a (Brodersen and Lindegaard 1999), and especially, air or water temperature (Eggermont and Heiri 2012). The performance and robustness of these models depend on many aspects, one of them is the taxonomic resolution. Therefore, an accurate identification of the subfossil remains is of key importance to ensure the quality of paleolimnological reconstructions, since even the most comprehensive study becomes meaningless if the subfossil material is misidentified (Cohen 2003). The most exhaustive identification key and catalogue of subfossil Chironomidae published to date is Brooks et al. (2007). While this guide is essential in the Palaearctic, it has only limited applicability in paleolimnology research in other biogeographical regions, e.g., in the Neotropics. Thus, as highly recommended by Larocque-Tobler (2014), it is important to provide illustrated guides that extend our knowledge on Chironomidae remains all over the world.

The Neotropical region hold a large number of indigenous taxa, such as *Coelotanypus*, *Djalmbatista*, *Fittkauimyia*, *Apedilum*, *Beardius*, *Endotribelos*, *Fissimentum*, *Goeldichironomus*, *Oukuriella*, *Pelomus* and *Xestochironomus*, however, this prevalence is difficult to evaluate at present as their fully geographic range is barely known. Nearly 900 species are recognized from the Neotropical Region of which 80% are assigned to one of the three subfamilies Chironominae, Orthoclaadiinae and Tanytopodinae (Spies et al. 2009). Studies on the taxonomic diversity of Chironomidae in the Neotropical region have witnessed increased activity regarding the family in recent years (Watson and Heyn 1992; Oliveira and Silva 2011; Andersen and Pinho 2014; Andersen et al. 2015; Silva et al. 2014, 2015; Siri and Donato 2015; Trivinho-Strixino et al. 2013, 2015; Parise and Pinho 2016; Silva and Oliveira 2016; Wiedenbrug and Silva 2016; Silva and Farrell 2017; Silva and Ferrington 2018; Pinho and Silva 2020; Shimabukuro et al. 2021). In the same fashion, paleolimnological investigations using chironomid remains in Mexico (Vinogradova and Riss 2007; Pérez et al. 2010, 2013; Hamerlík et al. 2018a) and Central America (Wu et al. 2015; 2017, 2019a, b; Hamerlík et al. 2018b) have lately undergone a resurgence of interest. Thus, there is a need for a taxonomic guide that will ultimately be helpful for a thorough analysis of the diversity and

distribution of the taxa encountered in the region. Here, we illustrate and provide taxonomic diagnosis for larval subfossil head capsules from the Family Chironomidae (Insecta: Diptera) from the Yucatan Peninsula (Mexico, Belize and Guatemala) and Central America (El Salvador and Honduras) aiming to increase the taxonomic and ecological knowledge of the northern Neotropical subfossil chironomids. As limnology is considered the study of aquatic systems including past, present and future projections we offer here a valuable tool not only for paleolimnological but also for limnological studies.

### Study area

Mexico and Central America represent a geologically young land bridge creating the Mesoamerican biocorridor that connects two biogeographical realms, the Nearctic and the Neotropical regions. This relatively small landmass, deeply influenced by the neighbouring oceans, gave rise to a variety of tectonic, lithological, climatic and ecological zones and in turn, to remarkable biodiversity in the region (Kalmalkar et al. 2011; Perez et al. 2011).

Surface-sediment samples were obtained from a total of 91 lakes across five countries: Mexico (41), Belize (6), Guatemala (30), El Salvador (9) and Honduras (5). In addition, short sediment cores were processed from lake Yojoa (Honduras) and Apastepeque (El Salvador) (Fig. 1). Most of the sampled lakes in Mexico, and some from Guatemala and Belize, lie in the Yucatan Peninsula. This region situated on a marine carbonate platform is of interest both to ecologists and paleoecologists due to its steep altitudinal ( $\sim 0\text{--}1560$  m a.s.l.) and precipitation ( $\sim 400\text{--}3200$  mm  $y^{-1}$ ) gradients increasing from the Northwest to the South (Pérez et al. 2011). The area is rich in aquatic ecosystems of different origins (tectonic, volcanic, karstic) with chemical characteristics mainly influenced by bedrock geology, climate, and saltwater intrusion at coastal sites (Pérez et al. 2011). On the other hand, lakes from Honduras, El Salvador and a few from Guatemala are located in quite different settings, characterized by humid swamps and lowlands along both the Pacific and Atlantic coasts, although a significant part of this part of Central America is mountainous.

A considerable part of the study area is located in a dry-tropical climate zone rich in aquatic ecosystems

with high aquatic biodiversity (Pérez et al. 2011). Additionally, the microclimate of the area is strongly affected by topography (Karmalkar et al. 2011; Taylor and Alfaro 2005) resulting in significant differences in precipitation and temperature. There are substantial annual and temporal rainfall variations ranging from  $< 1000$  mm in the lowlands to  $> 2500$  mm in the mountains (Taylor and Alfaro 2005). The mean annual temperature varies from  $25\text{--}28$  °C at the Guatemalan lowlands, to  $12\text{--}15$  °C in the highlands and mountain regions (Atlas Climatológico for 1928–2003).

### Material and methods

#### Fieldwork

Out of the 91 analyzed samples, 64 were obtained during summer/autumn of 2005–2006, 2008, 2013, and 2017 (Yucatan Peninsula) and 27 samples (El Salvador, Honduras and Guatemala) in autumn of 2013. A single sample was obtained from the deepest part of each lake, however, in case of big lakes, littoral samples were taken, too. The surveyed ecosystems included deep (10–340 m) and shallow ( $< 10$  m) lakes, “cenotes” (sinkholes), coastal lagoons, ponds, rivers and wetlands. Surface sediment samples were retrieved using an Ekman-Birge bottom sampler. At each site, standard environmental parameters were measured with a WTW 350i multiprobe and geographical coordinates were recorded by a handheld GPS. Maximum lake depth was measured using an echo-sounder (Table 1). For detailed description of environmental variables of the study sites in Guatemala, Salvador and Honduras see Wojewódka et al. (2016) and Hamerlík et al. (2018a); characteristics of some cenotes in Mexico are shown in Hamerlík et al. (2018b).

#### Chironomid analysis

Sub-samples consisting of approximately  $5\text{ cm}^3$  sediment were deflocculated in warm 10% KOH for 20 min and rinsed on a  $90\text{ }\mu\text{m}$  mesh sieve (Walker and Paterson 1985). Chironomid head capsules were handpicked under a binocular microscope ( $40\times$  power) and permanently mounted on slides in Berlese mounting medium. Taxonomic identification

**Table 1** List and basic variables of surveyed lakes. Lakes are ordered according to altitude within every country

Lake name/variable	Altitude m a.s.l	Coordinates		Temp °C	O <sub>2</sub> mg L <sup>-1</sup>	pH	Conductivity µS cm <sup>-1</sup>	Depth m
		N	W					
<b>Mexico</b>								
Bacalar	1	18.6650000	88.3908000	27.00	7.90	7.80	1221	16
Milagros	1	18.5115278	88.4266044	27.90	12.40	8.10	2720	4
Nobec	1	19.0157022	88.6795440	29.20	9.40	8.50	1231	0.5
Ocom	1	19.4246104	88.6412777	27.90	7.20	8.00	774	10
Yalahau	2	20.6570720	89.2170080	32.10	7.27	9.53	1930	12
Chichancanab	2	19.4677770	88.0555550	28.50	7.70	8.00	2060	14
Cenote Chenha	3	20.6897222	89.8762500	28.30	10.40	7.59	2520	2
San Francisco Kana	3	20.8561667	90.1179167	30.70	9.70	8.30	1751	0.5
Punta	3	20.6501667	87.6411666	26.80	7.20	8.00	754	20
Kaná	5	19.5008000	88.3954300	26.10	7.54	8.40	940	2.5
Rio Guerrero	5	19.2115556	90.7298889	26.40	3.60	7.71	2700	1
Cenote Xlaka	6	21.0910000	89.5981389	27.90	4.04	7.00	1452	45
Laguna Coba	7	20.4945000	87.7386667	28.90	8.70	8.50	1213	0.5
Cenote Timul	9	20.5941111	89.3565833	30.40	11.43	9.06	1465	0.5
Cenote Yoknot	13	20.7068333	88.7311111	25.20	5.30	7.40	949	45
Cenote Juarez	14	20.8026667	87.3399444	27.90	8.70	8.11	643	25
Corozo	16	19.2789000	88.5263600	30.20	2.63	8.25	413	1.3
Mucuyche	17	20.6242000	89.6064800	27.50	3.68	7.38	1530	18
Chuina	17	18.9614330	90.7127280	32.10	7.63	8.94	480	2.4
Oxolá	18	20.6782300	89.2416500	24.90	4.60	7.75	794	16
Xbacab	18	18.9398750	90.7201560	31.00	7.10	8.38	3060	4
Loche	20	21.4178611	88.1418889	32.00	14.40	9.44	4340	1
Chihuol	23	20.6350200	89.6120000	27.30	3.45	7.40	1400	10
Tekom	24	20.7300500	89.4660000	27.20	3.00	7.30	1030	3
Cenote Peten de Monos	25	20.8498889	90.3205000	26.60	1.40	6.90	3670	1.5
Cenote Ya'ax'ëx	27	20.6209444	88.4155556	26.40	10.60	8.02	793	47
Sacalaca	28	20.0666690	88.5997030	25.80	0.82	7.93	707	25
Salto Grande	30	18.1969560	91.1202170	30.40	4.94	7.50	1080	1
San Miguel	32	19.9346500	88.9983100	32.00	6.00	8.60	1700	0.1
Estado de México	34	18.0385000	90.8711470	29.00	3.10	7.20	1180	1.7
Sabanita	38	18.4008889	88.5723889	27.50	8.06	8.10	139.2	2.5
Rio Candelaria	44	18.1840000	91.0498889	26.90	1.90	7.71	1564	1.5
San Francisco Mateo	52	17.8988611	90.6563333	24.80	0.90	7.30	474	5
Misteriosa	53	18.0419110	90.4979530	30.80	7.73	8.30	1230	2.7
Chan laguna	67	18.4796390	90.2109170	30.70	9.20	9.76	148	2.4
Silvituc	69	18.6432220	90.2726940	30.00	6.40	8.68	205	3
Laguna del Cayucon	69	18.0428611	90.9758333	25.30	3.30	7.40	126.6	8
Aguado Jobal	74	18.6946389	90.1126111	31.70	10.85	8.30	241	0.5
Chacan Lara	90	19.1893889	89.1713889	27.20	6.01	7.50	173.6	3
Chacan Bata	91	18.4783611	89.0871944	26.30	2.20	6.90	145.5	0.5
San Jose Aguilar	107	18.3699444	89.0116111	26.50	4.83	7.78	488	3
Jamulun Channel	115	19.4661944	90.4958611	26.90	1.90	7.70	1564	1.5

**Table 1** continued

Lake name/variable	Altitude m a.s.l	Coordinates		Temp °C	O <sub>2</sub> mg L <sup>-1</sup>	pH	Conductivity μS cm <sup>-1</sup>	Depth m
		N	W					
<b>Belize</b>								
Almond Hill	1	17.4636111	88.3087770	27.50	6.40	7.10	1715	2
Honey Camp B	1	18.0153611	88.4389940	25.90	9.06	8.50	1481	8
Crooked Tree L	2	17.7785744	88.5270480	28.50	6.90	7.80	330	3.3
Progreso Lagoon	5	18.2178889	88.4153611	26.40	7.00	8.24	2040	3.2
Pond 1	33	17.3055500	88.4886077	27.40	7.50	8.00	244	1
Pond 2	77	17.6423356	88.9731322	28.20	5.80	7.30	192	1.5
<b>Guatemala</b>								
El Muchacho	3	13.8891806	90.1917722	30.00	5.90	9.10	439	2
El Gofete	4	15.6736944	88.9636944	27.20	6.40	7.65	191.5	7
Grande	5	13.8902750	90.1702833	27.00	3.70	7.43	110	2
Comandador	20	13.9600083	90.2543556	31.00	5.60	7.40	251	1.7
Perdida	75	17.0601944	90.0211583	28.80	9.80	8.80	232	4
Rio Cuba	80	17.9487222	90.4775278	24.90	7.30	7.80	2040	0.5
Salpetén	105	16.9814861	89.6754722	29.90	5.80	7.00	4520	10
Rio Ixlu	110	16.9742500	89.6866667	25.90	6.65	7.54	1025	1
Peten Itza	115	17.0059167	89.8539667	26.50	5.30	8.50	539	165
Petebatun	115	16.4195278	90.1802500	23.60	1.13	7.27	941	40
Quexil	120	16.9231000	89.8098611	32.30	4.53	8.50	204	25.5
Sacpuy	122	16.9756667	90.0145000	26.40	4.40	7.80	289	6
El Rosario	126	16.5255139	90.1600806	28.00	1.65	7.20	987	2
San Diego	134	16.9189722	90.4226667	25.40	1.02	7.30	189.2	8.1
Oquevix	148	15.0050556	89.7409444	31.40	6.87	7.70	238	10
Las Pozas	152	16.3431500	90.1660167	30.50	5.43	8.30	277	23.1
Macancha	165	16.9666667	89.6385777	26.80	4.95	8.05	850	80
Sacnab	170	17.0582611	89.3724667	33.70	6.14	9.02	412	9
Lachua	170	15.9183778	90.6731972	29.10	4.81	7.99	906	378
Yaxha	219	17.0185830	89.4075000	29.00	7.34	8.70	232	22
Guija	433	14.2480556	89.5472778	22.90	2.30	7.60	207	21.5
Atescatempa	587	14.2169722	89.6942222	27.30	6.70	7.95	283	2
El Pino	1038	14.3447139	90.3941361	29.30	2.00	8.27	100	6
Amatitlan	1200	14.4343611	90.5496111	20.60	2.59	8.07	642	23
Ipala	1495	14.5570556	89.6394472	22.70	2.77	8.01	100	25
Atitlán	1556	14.6836722	91.2239333	23.50	5.72	8.90	442	99
Calderas	1790	14.4117139	90.5913361	21.20	4.90	9.20	100.0	26
Chicabal	2726	14.7875278	91.6560500	19.70	5.41	9.00	12	10.3
Magdalena	2863	15.5425806	91.3956194	12.50	6.19	8.75	331	2.8
<b>El Salvador</b>								
Jocotal	26	13.3371333	88.2518583	32.00	3.00	8.00	595	3
Olomega	66	13.3072333	88.0550750	29.40	2.50	7.69	105	2.5
Aramuaca	76	13.4293889	88.1065111	33.10	4.12	8.40	100	107
Los Negritos	102	13.2830500	87.9369750	29.90	5.22	9.20	40	2
Metapan	450	14.3094361	89.4655333	30.10	3.10	8.40	255	6

**Table 1** continued

Lake name/variable	Altitude m a.s.l	Coordinates		Temp °C	O <sub>2</sub> mg L <sup>-1</sup>	pH	Conductivity μS cm <sup>-1</sup>	Depth m
		N	W					
Chanmico	477	13.7785722	89.3541222	29.60	3.36	9.22	100	51
Apastepeque	509	13.6924556	88.7448361	29.50	2.82	8.57	100	47
El Espino	689	13.9529667	89.8652139	30.40	6.60	8.50	85	5.5
Verde	1609	13.8914667	89.7871750	21.50	4.51	7.50	83	12
<b>Honduras</b>								
Ticamaya	17	15.5506056	87.8897278	32.00	1.56	7.24	100	2
Jucutuma	27	15.5122694	87.9027861	30.40	1.03	7.25	100	2
Yojoa	639	14.8606472	87.9846694	27.80	2.73	8.31	100	22
Madre Vieja	1866	14.3569222	88.1376222	20.60	2.72	8.45	100	3.4
Chiligatoro	1925	14.3756000	88.1829806	21.50	1.86	7.40	100	5.5

was performed under a compound microscope at up to 400 × magnification, with reference to Bitušík (2000), Epler (2001), Brooks et al. (2007), Prat et al. (2011), Cranston and Epler (2013), Epler et al. (2013), Andersen et al. (2013a, b), Sæther and Andersen (2013), Trivinho-Strixino (2014) Silva et al. (2018) and occasionally original descriptions. Diagnosis of genera followed Brooks et al. (2007), Cranston (2010), and Andresen et al. (2013a, b) unless stated otherwise. Voucher specimens (specimens collected in field surveys that are enough preserved to permit independent verification) are deposited in the department of Biology and Ecology, Faculty of Natural Sciences, Matej Bel University, Banska Bystrica, Slovakia and CENAC/APN, Bariloche, Argentina.

It is important to mention that in the case of chironomid subfossils, we are dealing with para-taxonomy (sorting of material to ‘species’ or rather morphotypes on the basis of external morphology) rather than taxonomy. Applicability of para-taxonomy is limited, but in some fields it can be the only way to get results about highly important scientific questions (Krell 2004). This is also the case of using subfossil chironomids in paleolimnology. After its burial in the sediment from the whole larval body, only the strongly sclerotized head capsule remains. In addition, during the taphonomic processes further structures vital for taxonomic identification are disconnected from the remains. Thus, paleo-chironomid researchers have to rely only on very limited morphological features to distinguish taxa (Larocque-Tobler 2014). It is

therefore very important to state that we are dealing with morphotypes and our identification is often putative and only further research will show the validity of some identifications. Regarding subfossil chironomid identifications, we generally use the mentum and ventromental plates, and in the case of Tanypodinae subfamily, the ligula, paraligula and the arrangement of dorsal and ventromental pores, as these features are usually well preserved in sediments. However, the use of other characters (antenna, mandible, premandible) is also possible, if they are present. In the case a subfossil remain lacks any identifiable part, it is considered as ‘unidentifiable’ and it can be proportionally allocated into similar morphotypes encountered in the sample.

In this article, the term “-type” after a species name means that the head capsule resembles the mentioned species. In some species-rich genera there may be several to tens of species represented by one type. In taxa with a broad distribution pattern we followed the terminology used in Brooks et al. (2007). For genera not present in the Palaearctic, new morphotypes were created, either using the name of species resembling the morphotype (e.g., *Endotribelos albatum*-type), or, when a good analogue was not found, after the lake’s name where the morphotype was sampled (e.g. *Goeldichironomus* type Olomega).

## Results

In total, 101 morphotypes belonging to 62 genera were recorded in the studied lakes. With 57 morphotypes and 33 genera, Chironominae was the most species-rich subfamily. Tribe Chironomini was represented by 42 morphotypes, followed by tribe Tanytarsini (12 morphotypes) and tribe Pseudochironomini (3 morphotypes). The most widespread and abundant genera were *Goeldichironomus*, *Chironomus* and *Polypedilum*. The most common Tanytarsini genus was *Tanytarsus*. Orthocladiinae were represented by 26 morphotypes belonging to 17 genera. Orthocladiinae were rare in the lake sediments and found only in one fifth of the surveyed lakes. One site, the high elevation lake Magdalena, Guatemala, harbored most of the morphotypes. Subfamily Tanypodinae was represented by 12 genera comprising 17 morphotypes. *Labrundinia*, *Ablabesmyia* and *Coelotanytus* were the most abundant and taxon-rich genera. Podonominae was represented only by the genus *Parochlus*, recorded in the high elevation lake Magdalena in Guatemala.

## Diagnosis of morphotypes

### Subfamily Chironominae

Larvae of Chironominae can be identified on the basis of the larval synapomorphy of the ventromental plate associated with silk extrusion. The Chironominae is a dominant group in the tropical and subtropical lowlands, with immature stages adapted to a wide range of freshwater habitats, including brackish and marine waters (Ashe et al. 1987).

### Tribe Chironomini

Characteristic features of the tribe are the following: antennae not placed on distinct pedestals, Lauterborn organs not situated on pedicels. Seta subdentalis located ventrally, on the opposite side of mandible from the seta interna. Ventromental plates variable in shape but usually well-developed and striated; this feature is secondarily reduced in the *Stenochironomus* complex (Cranston et al. 2012). For diagnostic characters of subfossil Chironomini see Fig. 2.

### *Apedilum* Townes (Fig. 3a)

**Morphology:** Mentum with pale bifid median tooth and 6 lateral teeth; 1st lateral tooth shorter and appressed to median teeth (in worn down menta hardly visible). Ventromental plates separated medially by width of a paired median mental tooth, curved and finely striated. Mandible with a slender apical tooth, 3 inner teeth, 1 dorsal and 1 surficial tooth. Premandible with 2 apical teeth and 1 small inner tooth. Antenna with 6 segments, Lauterborn organs alternate on apices of segments 2 and 3.

**Remarks:** *Apedilum* remains were common in lakes in Guatemala, but were also present in El Salvador (lake Jocotal). Subfossil remains occurred both in littoral and profundal areas of shallow to deep lakes along broad elevation gradients (26–1556 m a.s.l.). Water reaction was slightly alkaline (pH > 8) and conductivity varied between ~ 100 and ~ 1000  $\mu\text{S cm}^{-1}$ .

### *Axarus* Roback (Fig. 3b)

**Morphology:** Mentum with trifid median tooth, outer median teeth small; 6 pairs of lateral teeth, first tooth is the largest, following laterals slightly decreasing in size. Ventromental plates contact medially, very wide, nearly straight, with coarse striae restricted to a narrow transverse band. Mandible with slender apical tooth and 4 flattened inner teeth, however, in worn-down specimens the separation of teeth is rarely visible, dorsal tooth absent. Premandible with long, slender apical tooth and 4 shorter pointed inner teeth. Antenna with 5 segments, Lauterborn organs opposite.

**Remarks:** The combination of long, slender, medially contiguous ventromental plates and 4 flattened inner mandibular teeth distinguish the genus.

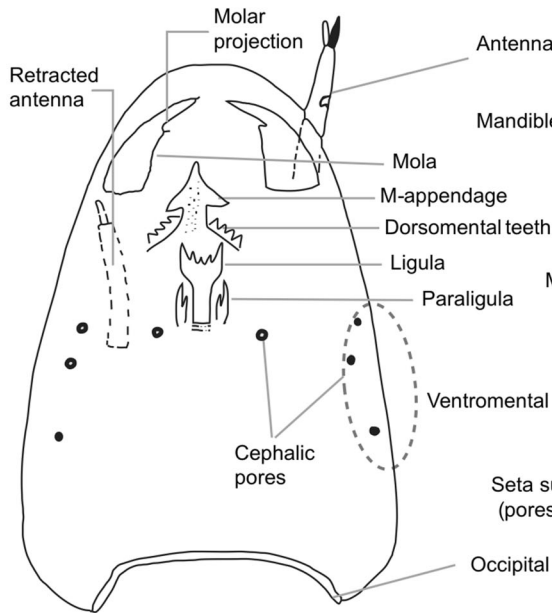
Remains were rare in the subfossil material, recorded only in the littoral sample of lake Yojoa, Honduras, situated at ~ 640 m a.s.l. with slightly alkaline water.

### *Chironomus* Meigen (Fig. 3c, e)

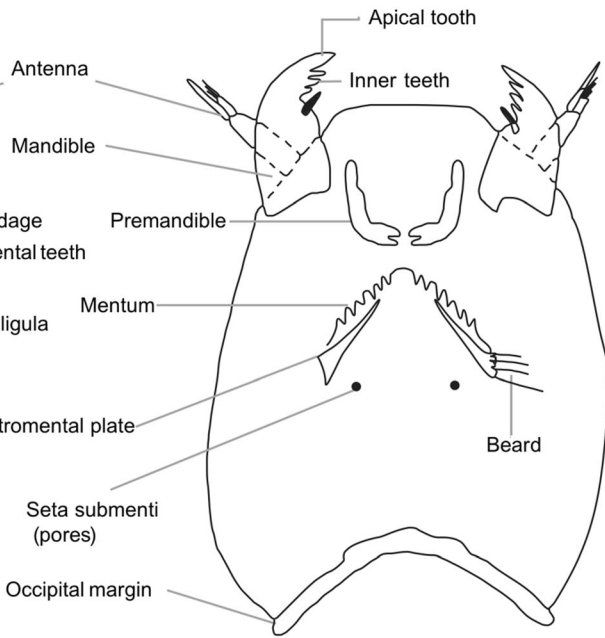
**Morphology:** Mentum with a characteristic pattern: trifid median tooth with outer teeth usually much smaller than median tooth (half or even less of the size of it); 6 pairs of lateral teeth, regularly decreasing in size, first lateral tooth long (usually the same size as



## Tanypodinae

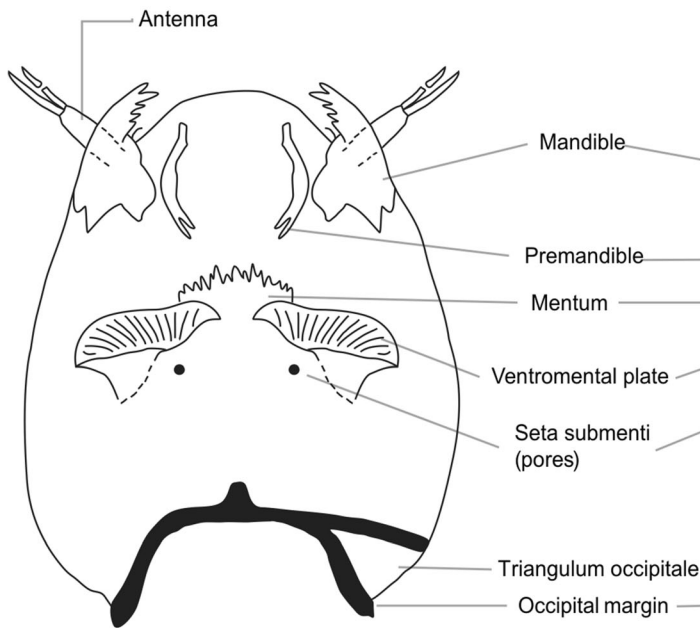


## Orthoclaadiinae

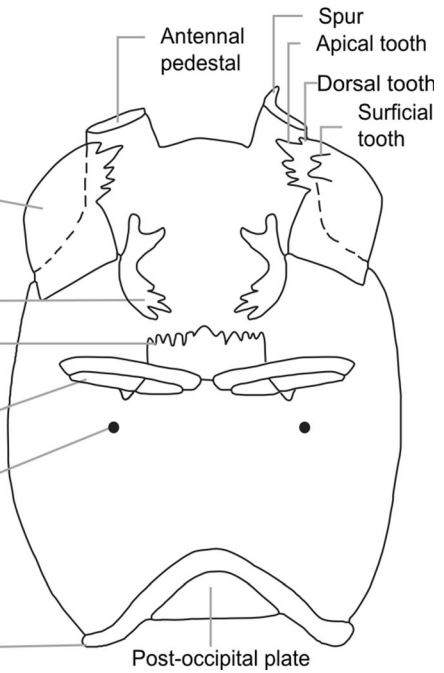


## Chironominae

### Tribe Chironomini



### Tribe Tanytarsini



◀ **Fig. 2** Larval head capsules showing diagnostic characters of subfamilies Tanypodinae, Orthocladiinae, and Chironominae tribes Chironomini and Tanytarsini

median tooth) and often partly fused with the shorter 2nd lateral; the size of the 4th lateral (which can vary in size from minute to equal to neighboring teeth) is an important character to distinguish morphotypes. Ventromental plates about as wide as mentum, striation most obvious at the base. Mandible usually with dark apical tooth, 2–3 inner teeth and a dorsal tooth. Premandible with 2 apical teeth, however, some Neotropical species may have 5 teeth. Antenna 5-segmented, Lauterborn organs opposite.

*Remarks:* One of the most species-rich genera with worldwide distribution comprising several hundred species with broad ecological preferences but primarily associated with soft sediments of nutrient-rich standing and flowing waters. Three morphotypes were distinguished in the Central American material.

*Chironomus plumosus*-type, lateral teeth of the mentum decreasing gradually, 4th lateral tooth longer than 5th, mandible with 3 inner teeth (Fig. 3c).

*Chironomus anthracinus*-type has mentum with the 4th lateral tooth short, 2 inner teeth on mandible (Fig. 3d).

In *Chironomus* type Salto Grande the 1st and 2nd lateral teeth are not fused, mandibles with 3 inner teeth and 1 dorsal tooth (Fig. 3e). This morphotype is not a typical member of the genus and was tentatively placed in it.

There was a great number of head capsules with a combination of characters of the *C. anthracinus*-type and *C. plumosus*-type. These remains can represent a gradient of natural intraspecific variability, but taking the huge number of *Chironomus* species into consideration, they may also be different species/types. Because of the problem with accurate identification of those types, we distinguish only the three basic morphotypes mentioned above. Description of new types requires complex research of the genus in the region.

*Chironomus* species show great ecological variability, which was reflected in the high frequency and broad distribution of remains across Central America. *C. anthracinus*-type and *C. plumosus*-type were common in all studied countries, *Chironomus* type Salto Grande was recorded only in the Salto Grande river,

Mexico. *Chironomus* larvae are typical bottom dwellers living in tubes on nutrient-rich substrata. They prefer stagnant waters of different size, but can also occur in slow flowing, organically polluted rivers, since they may tolerate very low oxygen content (Moller Pillot 2009). Due to hypoxia/anoxia tolerance of larvae, *Chironomus* remains will indicate warm, productive environments.

*Cladopelma* Kieffer (Fig. 3f)

*Morphology:* Mentum strongly arched, double median tooth (occasionally seems like medially notched median tooth), 7 pairs of lateral teeth. Three outermost teeth offset and clustered, with a characteristic pattern: 5th and 7th lateral are short and the 6th lateral is taller and broader. Ventromental plates broad, with fine striation, anterior margin often crenulated. Mandible without dorsal tooth, with apical tooth and 1–2 flat inner teeth. Premandible with 2 teeth. Antenna 5 segmented, Lauterborn organs absent.

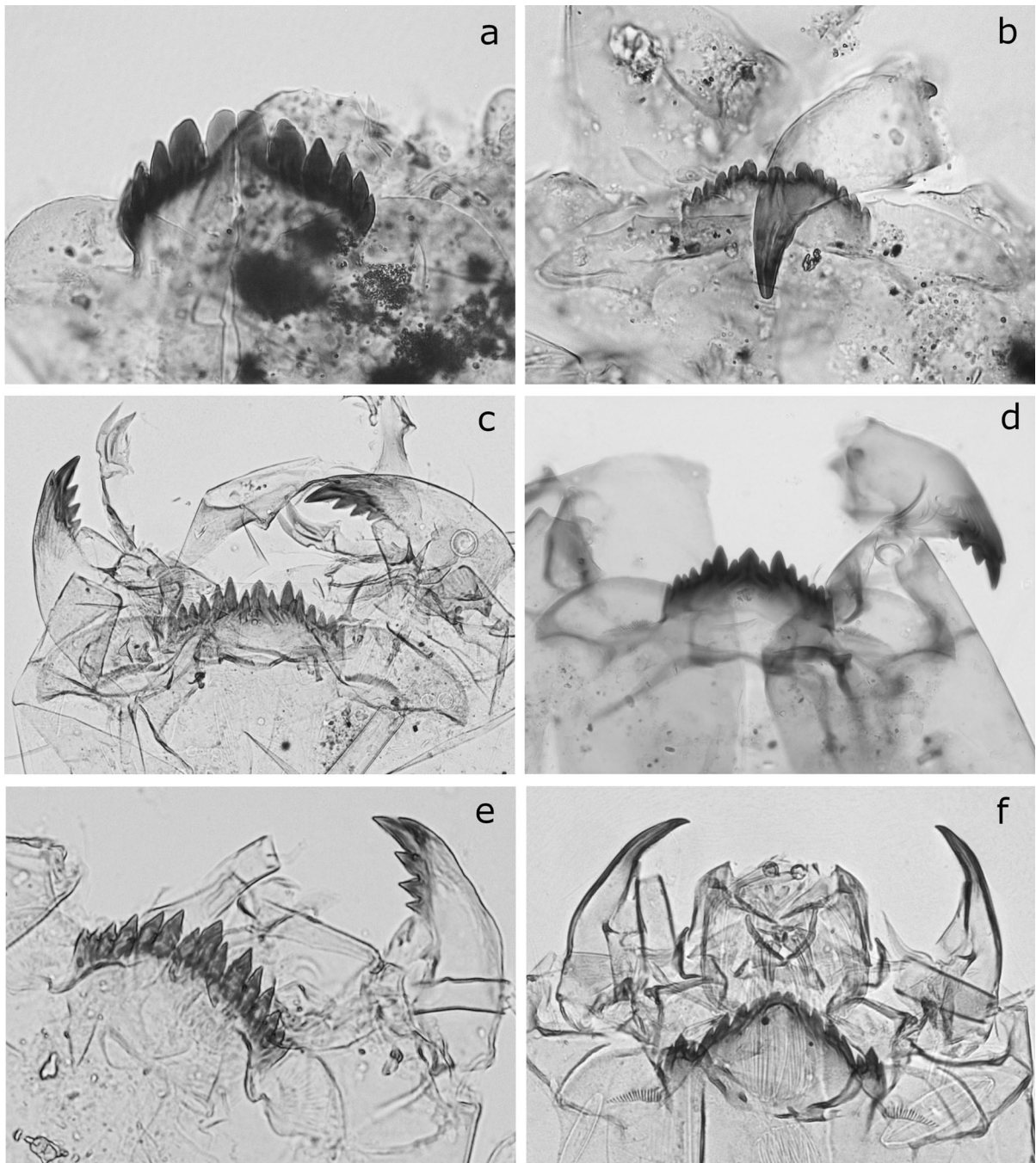
*Remarks:* The morphotype found in Central American lake sediments resembles that of *C. lateralis*-type (Brooks et al. 2007), but it has much broader median teeth and in generally, median area of the mentum.

Larval remains were common in surface sediments, recorded in every studied country, especially frequently in lakes of Mexico and Guatemala. Remains occurred in littoral and profundal samples of lakes along a broad range of size and elevation (3–1556 m a.s.l.), as well as long environmental gradient (pH 7.0–9.0; conductivity 40–4520  $\mu\text{S cm}^{-1}$ ).

*Cryptochironomus* Kieffer (Fig. 4a)

*Morphology:* Mentum concave with broad, domed pale median tooth and 6–7 pairs of dark lateral teeth; 1st lateral merged with median tooth; outermost lateral tooth notched apically. Ventromental plates very large, wider than mentum, with fine striation and smooth anterior margin. Mandible with long slender apical tooth and 2 pointy inner teeth, dorsal tooth absent. Premandible with 4–6 teeth declining in size from apex to base. Antenna 5-segmented, Lauterborn organs absent.

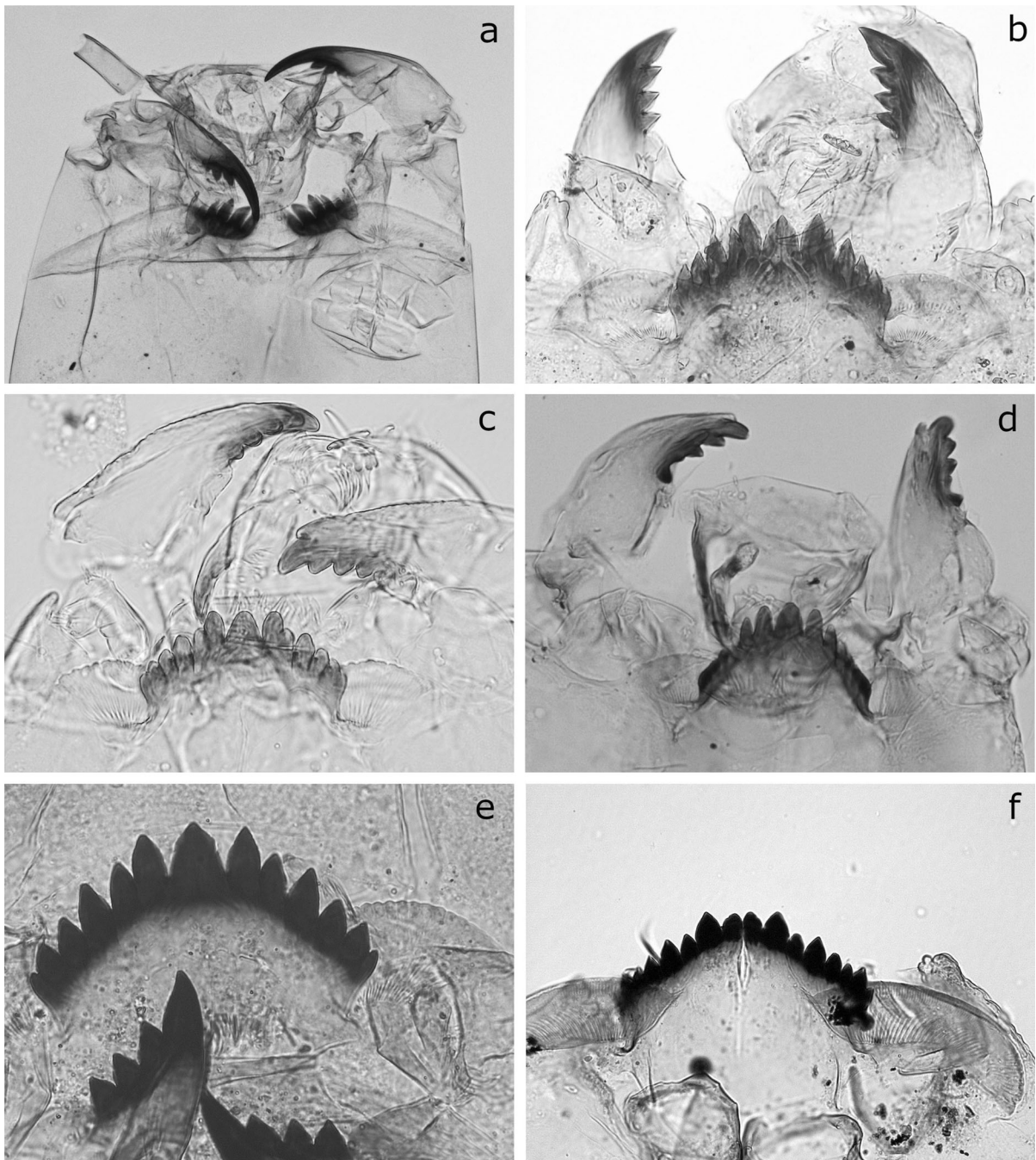
*Remarks:* This morphotype was relatively rare in the surface-sediments, only occurring in five lakes in Guatemala (Sacnab, Calderas, Peten Itza and Ipala), El



**Fig. 3** Subfossil remains of larval Chironominae from lakes of Central America and Mexico. Tribe Chironomini. a–*Apedilum* sp.; b–*Axarus* sp.; c–*Chironomus plumosus*-type; d–*Chironomus anthracinus*-type; e–*Chironomus* type Salto Grande; f–*Cladopelma* sp

Salvador (Apastepeque) and Belize. Remains were recorded from littoral and profundal samples of lakes significantly varying in size and depth located along an elevation gradient from sea level up to  $\sim 1800$  m.

Regarding conductivity, the lakes were in the lower end of the gradient (up to  $\sim 400 \mu\text{S cm}^{-1}$ ) and with slightly alkaline pH.



**Fig. 4** Subfossil remains of larval Chironominae from lakes of Central America and Mexico. Tribe Chironomini. a–*Cryptochironomus* sp.; b–*Dicotendipes notatus*-type; c–*Dicotendipes*

*Dicotendipes* Kieffer (Fig. 4b–e)

**Morphology:** Mentum with simple, robust median tooth that can be laterally notched, about the same

*nervosus*-type A; d–*Dicotendipes nervosus*-type B; e–*Dicotendipes nervosus*-type C; f–*Endochironomus albipennis*-type

height as 1st laterals; 5–6 lateral teeth, 1st lateral is the tallest, 2nd lateral is shorter and often partially merged with the 1st lateral, outermost laterals can be partly to completely fused to form a bulging lobe.

Ventromental plates narrow, visibly fan-shaped, completely striated, about half width of mentum; anterior margin smooth or crenate. Mandible with prominent apical tooth, pale dorsal tooth, 3 inner teeth; 1–2 small surficial teeth may be present, outer margin frequently crenulated. Premandible with bifid apical tooth and blunt basal tooth. Antenna 5-segmented, segment 4 is 4–6 × as long as broad; Lauterborn organs opposite. A useful character to distinguish the genus is the frontal apotome separated from the clypeus (except for 1 species), and there is a distinguishing antero-medial mark (oval to round or linear) on the frontal apotome; anterior margin of frontal apotome may be crenulated.

*Remarks:* Four morphotypes were distinguished.

*Dicrotendipes notatus*-type has smooth anterior margin of ventromental plates, 6 lateral teeth, 2nd lateral tooth fused with 1st. Mandible with 3 subequal inner teeth (Fig. 4b).

The following three types have anterior margins of ventromental plates crenulated. *Dicrotendipes nervosus*-type A has 6 lateral teeth, 2nd lateral reduced in size and fused with 1st lateral (Fig. 4c).

*Dicrotendipes nervosus*-type B (see *Dicrotendipes* sp. 1 in Trivinho-Strixino 2014), 1st and 2nd lateral teeth separate, teeth significantly decreasing in size laterally, outermost laterals are completely fused together forming a bulging lobe. Mandible with prominent apical tooth and 3 inner teeth, 3rd tooth minute; 1–2 surficial teeth; there is a dark lobe on the mola (Fig. 4d).

*Dicrotendipes nervosus*-type C has all 6 lateral teeth distinct, 1st and 2nd laterals separate, all mental teeth dark. Apical and inner teeth of mandible dark, 3 inner teeth of subequal size, surficial teeth absent (Fig. 4e).

In general, *Dicrotendipes* remains were common in lake sediments and occurred in all studied countries. *Dicrotendipes notatus*-type was rare and dominated in the littoral samples of a high elevation lake Atitlan, Guatemala (> 1500 m a.s.l.). *D. nervosus*-type B was the most frequently recorded morphotype of the genus occurring in ~ 25% of sites along a broad altitudinal gradient (up to ~ 1800 m a.s.l.).

*Endochironomus* Kieffer (Fig. 4f)

*Morphology:* Mentum of a characteristic pattern: distinct dorsomentum with 3–4 median teeth, the central ones shorter than outer pair; 6 pairs of lateral

teeth are delineated from median teeth by a distinct line linking the inner margin of ventromental plates to the bases of the outer median tooth. Ventromental plates elongate, outer margin strongly curved and rounded into a lobe; striae interrupted medially. Mandible with slender apical tooth and 3–4 inner teeth; dorsal tooth present, not extending beyond the outer margin, premandible with 3 teeth. Antenna 5-segmented, segments diminishing in size distally, Lauterborn organs opposite.

*Remarks:* In the Central American dataset only a morphotype with 4 median teeth, *Endochironomus albipennis*-type sensu Brooks et al. (2007), was identified. Head capsules of *Endochironomus* are rare in the Central American waterbodies (only recorded in 3 lakes in Guatemala), but relatively common in Mexico. It was associated with warm lakes (~ 30 °C) located in lower elevation (up to 170 m a.s.l.).

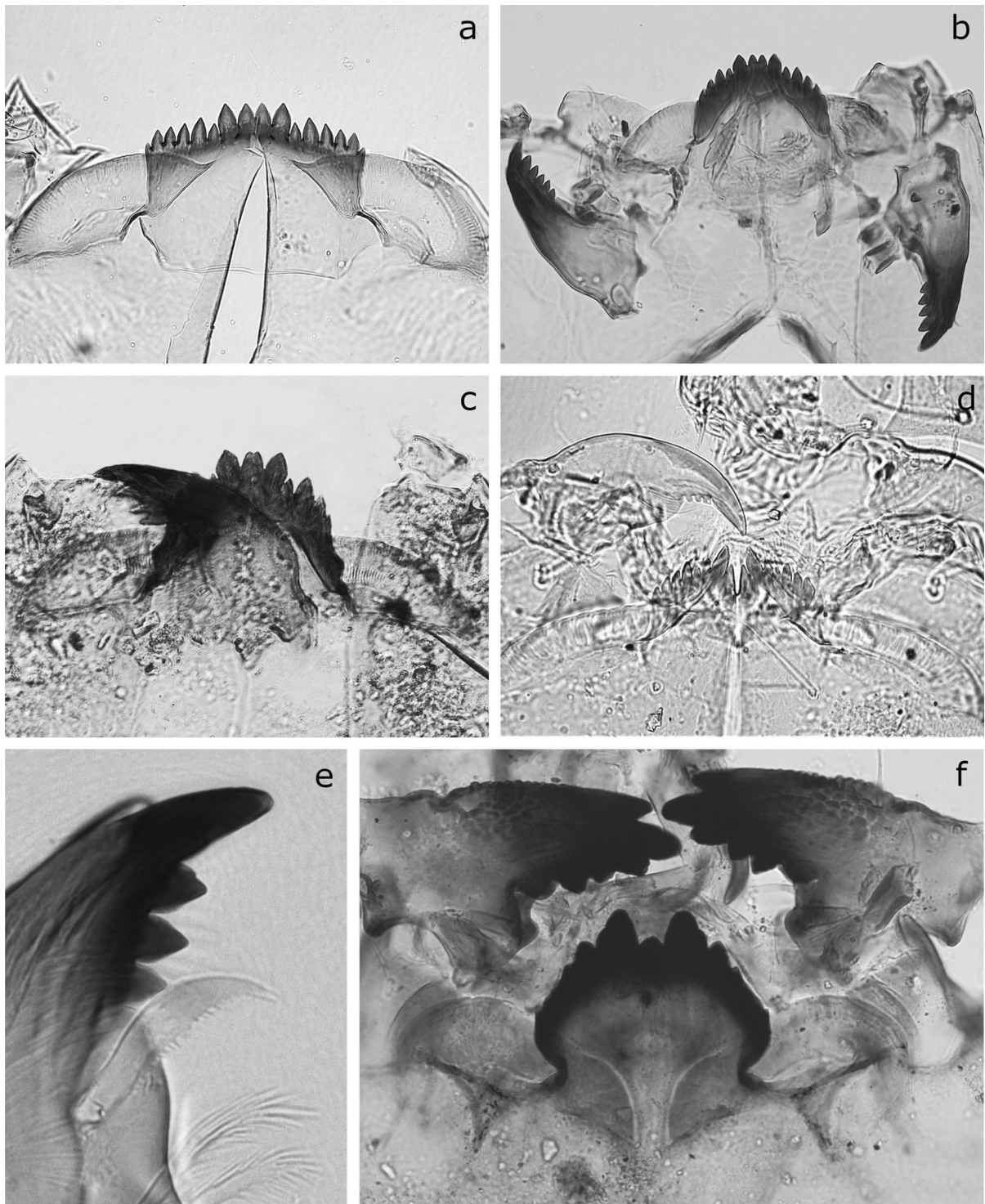
*Endotribelos* Grodhaus (Fig. 5a–c)

*Morphology:* Mentum with distinct dorsomentum bearing 3–4 median teeth, central tooth of those with 3 teeth sometimes notched; 6 pairs of lateral teeth are present with 1st much lower than median or 2nd; 6th lateral may be reduced or absent. When 4 median teeth are present, the 2 central teeth are subequal or smaller than the outer median teeth. Ventromental plates medially connected to bases of outer ventromental median teeth; relatively narrow and strongly curved; striae distinct and continuous. Mandible with strong apical tooth and 3–4 inner teeth; pale dorsal tooth present. In some species, there is a distinct gap between the mola (the inner margin of the mandibular base) and the inner mandibular tooth. Premandible with 2 long apical teeth and 1 blunt basal tooth. Antenna 5-segmented, Lauterborn organs minute, opposite.

*Remarks:* Three morphotypes were distinguished following Trivinho-Strixino (2014):

*Endotribelos albatum*-type (Roque and Trivinho-Strixino 2008) has a total of 16 teeth, 4 median teeth about the same size, higher than the lateral ones, 6 lateral teeth, the last one lower than the rest (Fig. 5a).

*Endotribelos grodhausi*-type has a total of 14 teeth, central medial teeth shorter and narrower than outer median teeth, mandibles with 4 (occasionally 5) inner teeth (Fig. 5b).



**Fig. 5** Subfossil remains of larval Chironominae from lakes of Central America and Mexico. Tribe Chironomini. a–*Endotribelos albatum*-type; b–*Endotribelos grodhausi*-type (the 5 inner teeth on the left mentum is probably a deformity); c–

*Endotribelos hesperium*-type; d–*Fissimentum dessicatum*-type; e–*Goeldichironomus amazonicus*-type: detail of mandible showing the characteristic comb-like seta subdentalis; f–*Goeldichironomus* type Olomega, mentum and mandibles

*Endotribelos hesperium*-type. Mentum is strongly arched, with odd number of teeth, 3 median teeth of subequal size, central tooth notched, higher than lateral ones, 5 lateral teeth, 1<sup>st</sup> lateral is small and pressed to the outer medial tooth; mandible with 3 equal inner teeth separated from dark mola by a large notch (Fig. 5c).

While *Endotribelos hesperium*-type has unique shape of mentum and is hard to confuse with other taxa, the two other types with 4 median mental teeth (*E. grodhausi*- and *E. albatum*-types) superficially resemble *Endochironomus* and can be distinguished from it by the shape of ventromental plates that is strongly curved and rounded into a lobe in *Endochironomus*. *Endotribelos albatum*-type is very similar to *Phaenopsectra* type A sensu Brooks et al. (2007) from which it can be perhaps distinguished by the outermost lateral tooth of mentum that is reduced in *E. albatum*-type, while normal size in *P.* type A. It is also extremely similar to *Phaenopsectra obediens* Epler (2001).

*Endotribelos* remains were rare; *E. albatum*-type was found only in a high elevation lake Chicabal, Guatemala at ~ 2700 m a.s.l. *E. grodhausi*-type was recorded in a cenote (sinkhole lake) in Mexico with high conductivity (> 1500  $\mu\text{S cm}^{-1}$ ). *E. hesperium*-type was the most common, found in 4 lakes located in Guatemala, El Salvador and Honduras.

*Fissimentum* Cranston and Nolte (Fig. 5d)

**Morphology:** Mentum with a deeply sunken pair of median teeth is unique and will easily distinguish *Fissimentum* from other genera. Ventromental plates elongate with smooth margin. Mandible with strong apical tooth and 3 small uniform inner teeth; dorsal tooth absent; seta subdentalis large, sinuous, extended up to apical tooth. Premandible bifid. Antenna 6-segmented, small to moderate Lauterborn organs alternate on 2nd and 3rd segments.

**Remarks:** Owing to the rheobiotic nature of larval *Fissimentum*, head capsules were rare in the subfossil material with one morphotype, *Fissimentum desiccatum*-type (Cranston and Nolte 1996) recognized.

The only site where *Fissimentum* head capsules were recorded was the Salto Grande river, Mexico. The remains were found in a soft sediment sample taken from a shallow depth (1 m) in the lowland section of the river (30 m a.s.l.) with

conductivity > 1500  $\mu\text{S cm}^{-1}$ ). Other records of the morphotypes exist from Lake Naha in the Lacandon forest, Chiapas, Mexico (Massaferro, unpublished data).

*Goeldichironomus* Fittkau (Figs. 5e, f, 6a–d)

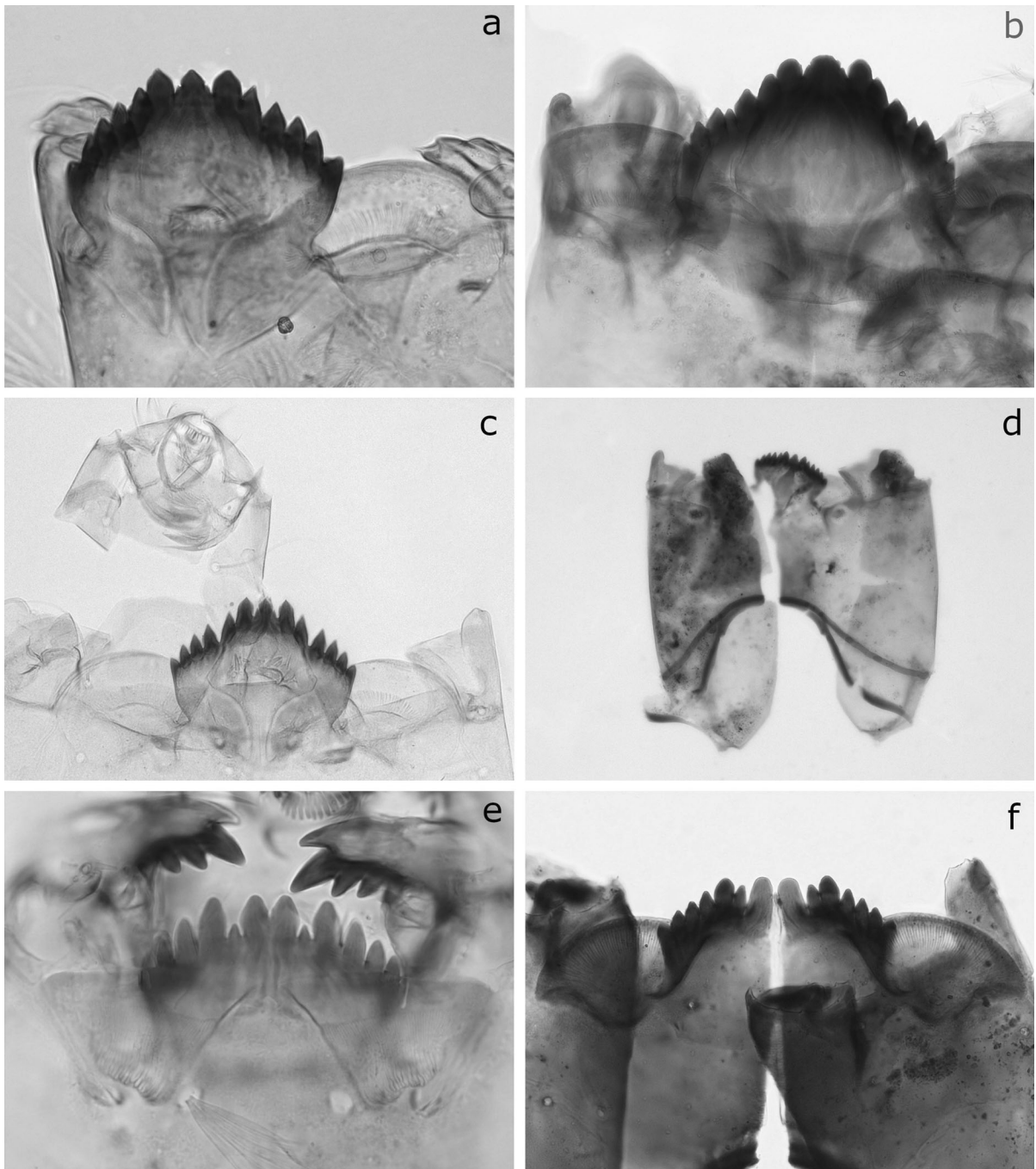
**Morphology:** Larvae of *Goeldichironomus* have unique features among the Chironomini tribe: mandible with a huge seta subdentalis that is toothed along its inner margin (Fig. 5e), heavily sclerotized ventral occipital margin with distinct triangulum occipitale (Fig. 6d), and ventromental plates of characteristic shape that are ventrally tilted, pointing downwards and almost touching medially. Mentum with a single laterally crenate median tooth (it may look trifid); number of lateral teeth may vary but usually with 6 pairs of laterals; 2nd lateral may be reduced and fused with 1st lateral, 4th lateral subequal or significantly lower than 3rd and 5th. Ventromental plates characteristic, wide, close medially, anterior margin smooth; striae continuous. Mandible with apical tooth followed by 3 inner teeth; pale dorsal tooth present; seta subdentalis remarkably large, comb-like with teeth on its inner margin. Premandible has 2–3 teeth. Antenna 5-segmented, segments are diminishing in size distally; Lauterborn organs opposite.

**Remarks:** *Goeldichironomus* is a species-rich and primarily tropical/subtropical genus with most of the species occurring in Central and South America. Four morphotypes were identified.

*Goeldichironomus* type Olomega has a unique combination of features that distinguish it from the other morphotypes of the genus: recessed small median tooth, 2nd lateral fused with the large 1st lateral, 4–6 lateral teeth reduced and merged. Mandibles with 4 inner teeth and 1 dorsal tooth, all dark, outer margin of mandibles with strong tubercles, mola extended as a large rounded lobe (Fig. 5f).

*Goeldichironomus amazonicus*-type has a total of 13 teeth, lateral teeth subequal, outermost lateral tooth large and pointing outwards (Fig. 6a).

*Goeldichironomus carus*-type has a total of 15 teeth, medium tooth broader than 1st lateral, notched laterally, 4th lateral minute, smaller than 3rd and 5th tooth, outermost lateral tooth minute (Fig. 6b). Larvae of this type with 4th lateral minute are identified as *G. pictus* group in Epler et al. (2013). However, *G. pictus* has more lateral teeth and because of the



**Fig. 6** Subfossil remains of larval Chironominae from lakes of Central America and Mexico. Tribe Chironomini. a–*Goeldichironomus amazonicus*-type; b–*Goeldichironomus carus*-type; c–

similarity of our morphotype and *G. carus* (Epler 2001), we named it after the latter one.

*Goeldichironomus holoprasinus*-type; d–head capsule of *Goeldichironomus* showing distinct triangulum occipitale; e–*Lauterborniella* sp.; f–*Microtendipes pedellus*-type

*Goeldichironomus holoprasinus*-type has a tall and narrow median tooth with a notch on each side, 1st lateral of the same height and width as median tooth;



2nd lateral teeth pressed towards 1st lateral creating a broad gap between the 2nd and 3rd laterals; outer 3rd to 6th lateral teeth pointing somehow outwards (Fig. 6c).

*Goeldichironomus* remains were frequent and abundant in surface sediments, often dominating in shallow and lowland lakes, occurring only rarely in high elevation lakes (only *Goeldichironomus amazonicus*-type in lake Chilligatoro situated at 1900 m a.s.l.). *Goeldichironomus amazonicus*-type and *G. carus*-type were recorded frequently in all studied countries; *G. amazonicus*-type over a wide range of ecosystem types such as rivers, ponds, lakes and cenotes. *Goeldichironomus* type Olomega was recorded in low elevation, warm and shallow lakes, in Guatemala and El Salvador, with depth up to 3 m, conductivity from 100 to 600  $\mu\text{S cm}^{-1}$ . *Goeldichironomus holoprasinus*-type occurred only in lake Jucutama, Honduras.

*Lauterborniella* Thienemann and Bause (Fig. 6e)

**Morphology:** Mentum uniformly brown, weakly pigmented, with a pair of rounded median teeth; 6 pairs of lateral teeth, 1st small, 2nd about as high as median teeth, outer laterals gradually decreasing in size. Ventromental plates wide, nearly triangular, with straight anterior margin, almost meeting medially, basal  $\frac{2}{3}$  striated, anterior  $\frac{1}{3}$  without striation; setae submenti large, plumose. Mandible with uniformly brown apical tooth and 2 inner teeth, very strong pale dorsal tooth present. Premandible with 3 teeth and 1 blunt basal tooth. Antenna 6-segmented; large Lauterborn organs alternate on 2nd and 3rd segment.

**Remarks:** The genus is monotypic with the only known species *L. agrayloides* (Kieffer).

*Lauterborniella* remains were recorded rarely and occurred both in lowland- and high elevation lakes.

*Microtendipes* Kieffer (Figs. 6f, 7a)

**Morphology:** Mentum with 3 median teeth, however, in case of *M. pedellus*-group the central tooth is minute and depressed, thus median tooth appears bifid, usually paler than lateral teeth, occasionally as dark as 6 lateral teeth, 1st and 2nd laterals fused, 1st is reduced. Ventromental plates strongly curved with continuous coarse striation; a line connecting the

upper inner margin of ventromental plates and the base of 2nd lateral tooth divides the mentum into central ventromentum and lateral dorsomentum. Mandible with short apical tooth and 3 inner teeth, pale dorsal tooth present. Premandible with 3 (*M. pedellus*-type) or 5 teeth (*M. rydalensis*-type). Antenna with 6-segmented, Lauterborn organs alternate on segments 2 and 3.

**Remarks:** Two morphotypes were distinguished (following Epler et al. 2013).

*Microtendipes pedellus*-type median teeth appearing bifid, but there is a vestigial tooth between them which is hardly visible. Median teeth usually pale, occasionally dark (Fig. 6f).

*Microtendipes rydalensis*-type pale and trifid median tooth, teeth are subequal, occasionally the central one slightly smaller (Fig. 7a).

Very rare in the surface samples, both types occurred exclusively in the high elevation lake Magdalena, Guatemala, situated at > 2800 m a.s.l. Indeed, this genus is known as a treeline indicator (Porinchi and Cwynar 2002).

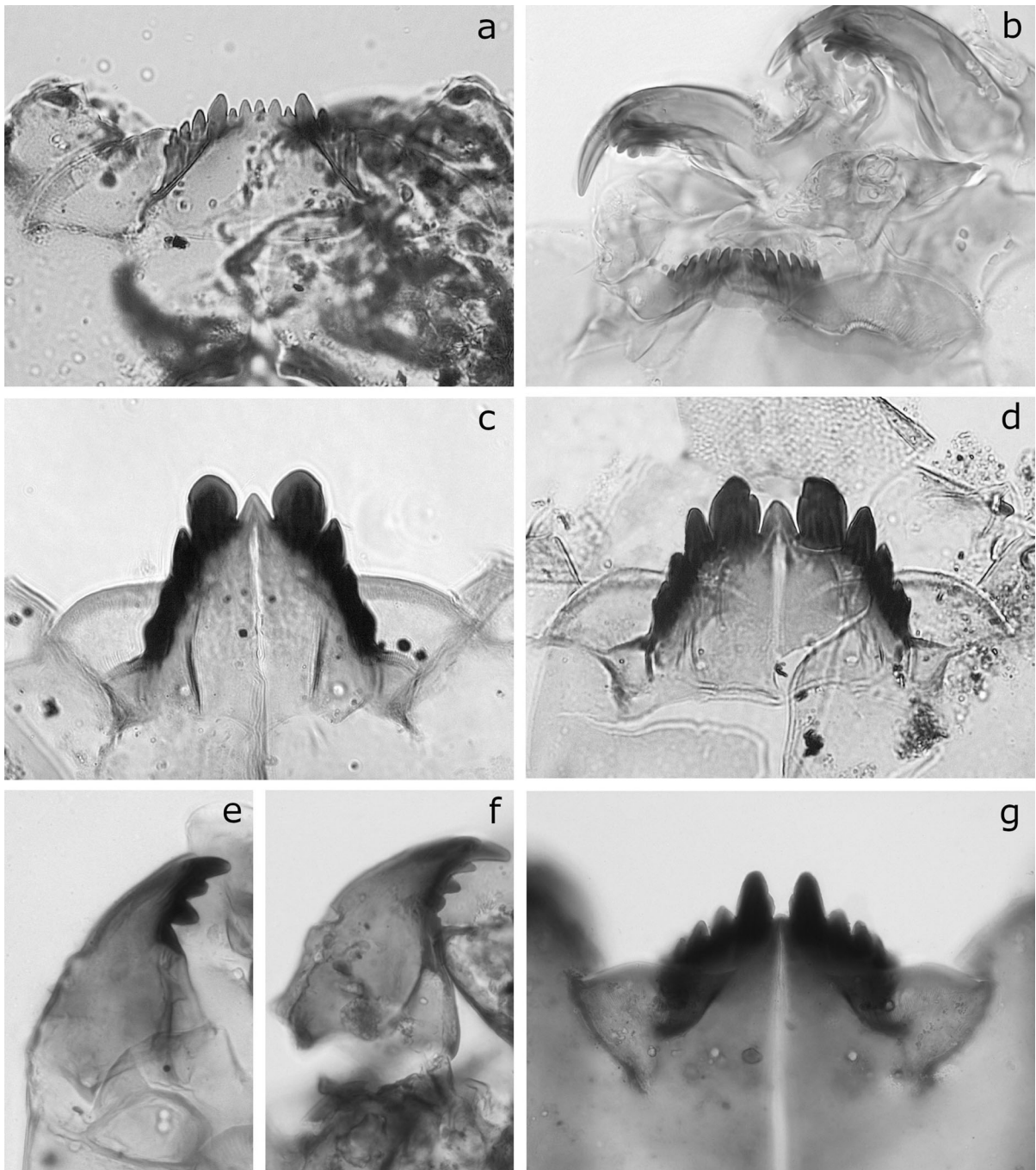
*Nilothauma* Kieffer (Fig. 7b)

**Morphology:** Mentum pale, rather horizontal, all teeth uniform in color, median tooth bifid, subequal or slightly shorter than 1st laterals, 6 lateral teeth evenly decreasing in size laterally. Ventromental plate slightly wider than mentum with only basal half striated.

Mandible of characteristic shape: with pale, long and slender apical tooth, up to 4 inner teeth on different focal plane, moderate dorsal tooth; all teeth pale or inner teeth slightly darker. Premandible with 3 teeth. Antenna 5-segmented, basal segment shorter than flagellum; Lauterborn organs not visible.

**Remarks:** The shape of the mentum and mandibles are unique for *Nilothauma* and it is not likely to confuse it with other genera. It is a species rich genus with worldwide distribution.

Subfossil remains were rare, only recorded in two relatively shallow, low altitude waterbodies (1 and 77 m a.s.l.), a pond in Belize (pH 7.3, conductivity 192  $\mu\text{S cm}^{-1}$ , depth 1.5 m) and in lake Ocom in Mexico (pH 8.0, conductivity 774  $\mu\text{S cm}^{-1}$ , depth 10 m).



**Fig. 7** Subfossil remains of larval Chironominae from lakes of Central America and Mexico. Tribe Chironomini. a–*rydalensis*-type; b–*Nilothauma* sp.; c–*Beardius* type Channico; d, e–

*Beardius* type Ipala: mentum d, mandible showing 2 inner teeth e; f, g–*Oukuriella pinhoi*-type: mandible showing 3 inner teeth f, mentum g

*Oukuriella* Epler / *Beardius* Reiss and Sublette (Fig. 7c–g)

Due to the extreme similarity of the two genera, we discuss them together

**Morphology:** Mentum with recessed simple or bifid median tooth, pale or dark; 5 pairs of lateral teeth, 1st lateral tooth much larger relative to the median, teeth declining in height laterally; ventromental plates short, curved and coarsely striated, medially separated by the distance between the first two lateral teeth. Mandible with short and dark apical tooth and 2 (*Beardius*) or 3 inner teeth (*Oukuriella*), dorsal tooth present. Premandible bifid. Antenna with 6-segmented, large Lauterborn organs alternately located at the apices of segments 2 and 3.

**Remarks:** In general, larval *Oukuriella* closely resemble *Beardius*, however, *Oukuriella* has 3 inner teeth on the mandible, while *Beardius* only 2. *Oukuriella* has 6-segmented antenna, while *Beardius* 5- to 7-segmented. Median mental tooth is always pale in *Beardius*, but can be both pale and dark in *Oukuriella*. Because antenna and mandibles are frequently missing in subfossil material, it may be problematic to distinguish these two genera from each other. However, the shape of the lateral end of dorsoventral plates seems reliable for distinguishing subfossil *Oukuriella* from *Beardius*. Plates of *Oukuriella* are pointing forward, while in *Beardius* they are pointing either laterally or backwards (L. Pinho, pers. comm., see also drawings in Trivinho-Strixino 2014).

**Morphotypes** of *Beardius* and *Oukuriella* were identified

*Beardius* type Chanmico has a small, pale, distinctly triangular median tooth and 4 lateral teeth (may be 5 with the outermost 2 teeth fused), 1st lateral dark, broad and round, the appearance of the whole mentum is arched; mandible with 2 inner teeth and a pale dorsal tooth (Fig. 7c).

*Beardius* type Ipala has a pale median tooth, 5 dark lateral teeth, mandible with 2 dark inner teeth and a large dorsal tooth (varying in size) (Fig. 7d, e).

*Oukuriella pinhoi*-type (Fusari et al. 2013) has unique features, such as small dark recessed median tooth, the same color as the 5 lateral teeth; mandible with 3 dark inner teeth, 1 dorsal tooth (Fig. 7f, g).

*Oukuriella pinhoi*-type and *Beardius* type Chanmico were rare, occurring in deep (47–51 m),

relatively high elevation lakes (~ 500 m a.s.l.) in El Salvador; *Oukuriella pinhoi*-type lake was recorded in lake Apastepeque; *Beardius* type Chanmico in the littoral sample from lake Chanmico. *Beardius* type Ipala was more common, its remains were recorded in various lake types from shallow to deep (2–47 m), along a broad altitudinal gradient from lowlands to 1500 m a.s.l., neutral to slightly alkaline pH (8.6) and with low oxygen content (1–3 mg L<sup>-1</sup>), but it was never very frequent or abundant.

*Parachironomus* Lenz (Fig. 8a, b)

**Morphology:** Mentum with a single median tooth (in some species notched medially); 7 lateral teeth, median tooth about twice as wide as 1st lateral, outermost tooth minute and depressed. Ventromental plates triangular with crenulated (scalloped) anterior margin. Mandible with long apical tooth and 2–3 inner teeth of various shapes, dorsal tooth absent. Pre-mandible with 2–4 teeth, no brush. Antenna with 5-segmented, small Lauterborn organs opposite.

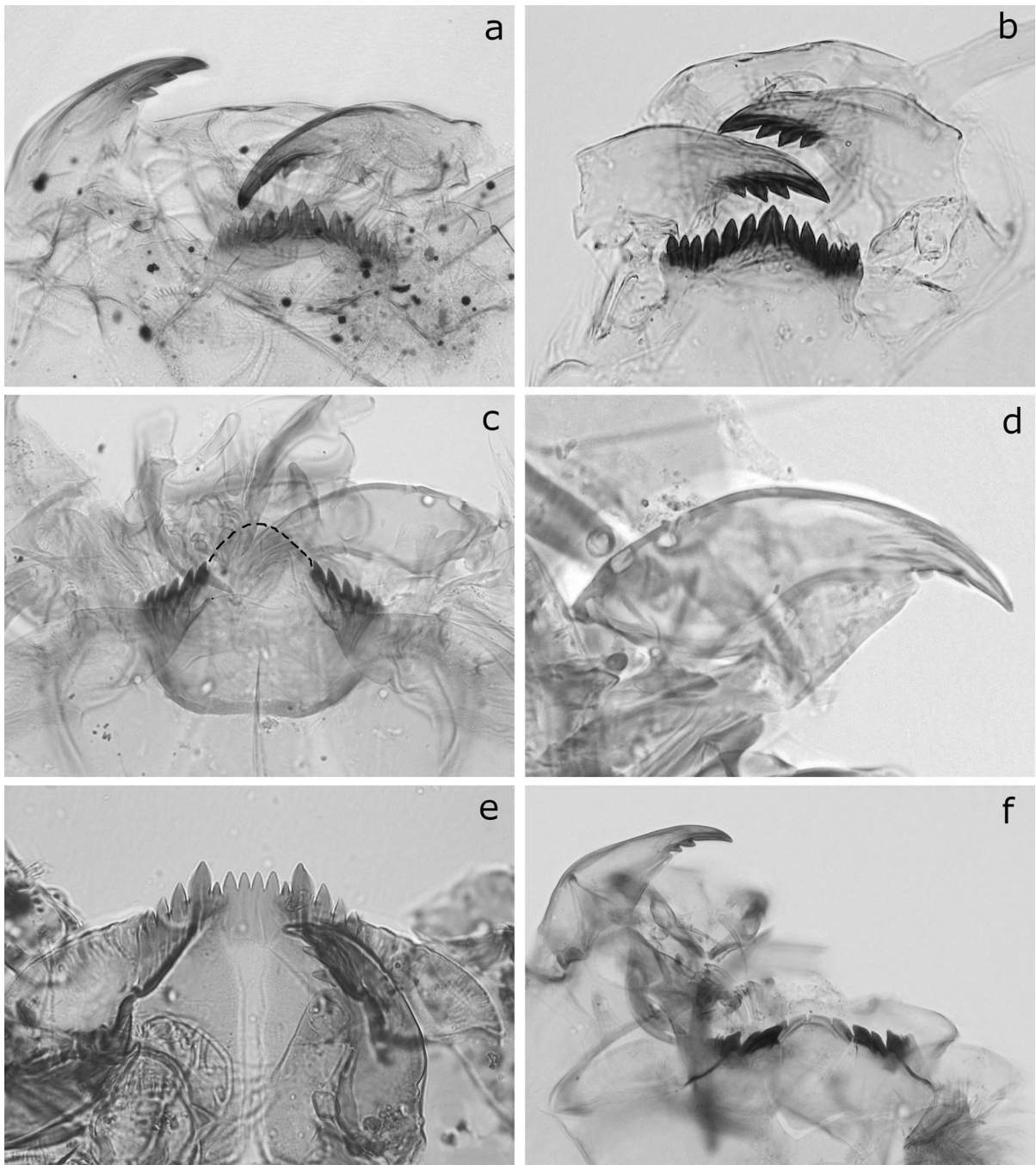
**Remarks:** Two morphotypes were distinguished. In *Parachironomus varus*-type (following Brooks et al. 2007) lateral teeth of mentum diminish in size gradually (points of teeth create an evenly decreasing slope) and there are 2 inner teeth on the mandible (Fig. 8a).

*Parachironomus longistilus*-type (following Trivinho-Strixino 2014) has a biconcave mentum with the lateral mental teeth creating a slightly concave curve on both sides of mentum with the 4th and 5th lateral teeth being lower than 3rd and 6th; mandible with 3 inner mandibular teeth (Fig. 8b). This type is referred to as *Parachironomus varus*-type B in Hamerlík and Silva (2021).

Larval *Parachironomus* remains were relatively frequent in lakes, ponds and cenotes along broad environmental gradients in all studied countries.

*Paralauterborniella* Lenz (Fig. 8c, d)

**Morphology:** Easily recognizable by the characteristic shape of mentum: simple, broadly domed and transparent median tooth clearly delineated from the dorsomentum with 6 dark lateral teeth evenly decreasing in size laterally (Fig. 8c). Ventromental plates widely separated medially, long, curved and coarsely striated. Mandible with slender apical tooth, dorsal



**Fig. 8** Subfossil remains of larval Chironominae from lakes of Central America and Mexico. Tribe Chironomini. a–*Parachironomus varus*-type; b–*Parachironomus longistilus*-type; c,d–*Paralauteborniella* sp.: mentum (c, dotted line indicates

tooth absent; according to the generic description (Epler et al. 2013) it has 3 distinct inner teeth, but the recorded specimen had only 2, a forward directing

anterior margin of the transparent median tooth), mandible d; e–*Paratendipes nudisquama*-type; f–*Pelomus psammophilus*-type

tapering tooth at the apical tooth and a blunt short one (Fig. 8d) resembling mandible of some species of the *Harnischia*-complex (e.g., *Paracladopelma*).

Premandible bifid. Antenna 6-segmented with alternate Lauterborn organs on apices of segments 2 and 3.

**Remarks:** *P. nigrohalteralis* (Malloch) is a species with broad distribution; in Central America it is known from Costa Rica and Nicaragua (Spies and Reiss 1996). As aforementioned, the recorded morphotype has obviously different mandibles and it is likely to represent another species.

The morphotype was very rare, only one head capsule was found in a shallow, low altitude lake Milagros, Mexico, with pH 8.10 and conductivity > 2700  $\mu\text{S cm}^{-1}$ .

#### *Paratendipes* Kieffer (Fig. 8e)

**Morphology:** Mentum with 4 uniform pale median teeth, 6 lateral teeth, 1st and 2nd lateral fused, 2nd lateral higher than median teeth; remaining lateral teeth decreasing gradually. Ventromental plates curved with coarse striation in the anterior half; ventromental plate delineation associated with the base of 2nd (in some species 1st) pair of lateral teeth. Mentum with an apical, 2 inner teeth and 1 dorsal tooth; pigmentation of mola may resemble 3rd inner tooth. Premandible with 2–3 teeth and a basal tooth. Antenna 6-segmented with alternate Lauterborn organs.

**Remarks:** The morphotype recorded in the studied material, *Paratendipes nudisquama*-type (following Pinder and Reiss 1983) was rare, occurring in few lakes in Guatemala, El Salvador and Honduras as well as some cenotes in Mexico. The remains were recorded in shallow lakes or in the littoral samples of deep lakes situated from 5 to 500 m a.s.l. with neutral to alkaline pH and conductivity from 100 to 4300  $\mu\text{S cm}^{-1}$ . Larval *Paratendipes* occur in both standing and flowing waters and prefer soft sediments and sandy bottoms (Epler 2001).

#### *Pelomus* Reiss (Fig. 8f)

**Morphology:** Mentum with 4 wide light median teeth creating a convex arc, followed by 3 pairs of darker teeth and several fine and short paler teeth; there is a big gap between 2nd and 3rd lateral teeth. Wide ventromental plates with coarse striation and smooth anterior margin. Mandible with long apical tooth and 2 inner teeth, dorsal tooth missing. Premandible with 2

large teeth and 1 small tooth. Antenna 6-segmented (Trivinho-Strixino and Strixino, 2008).

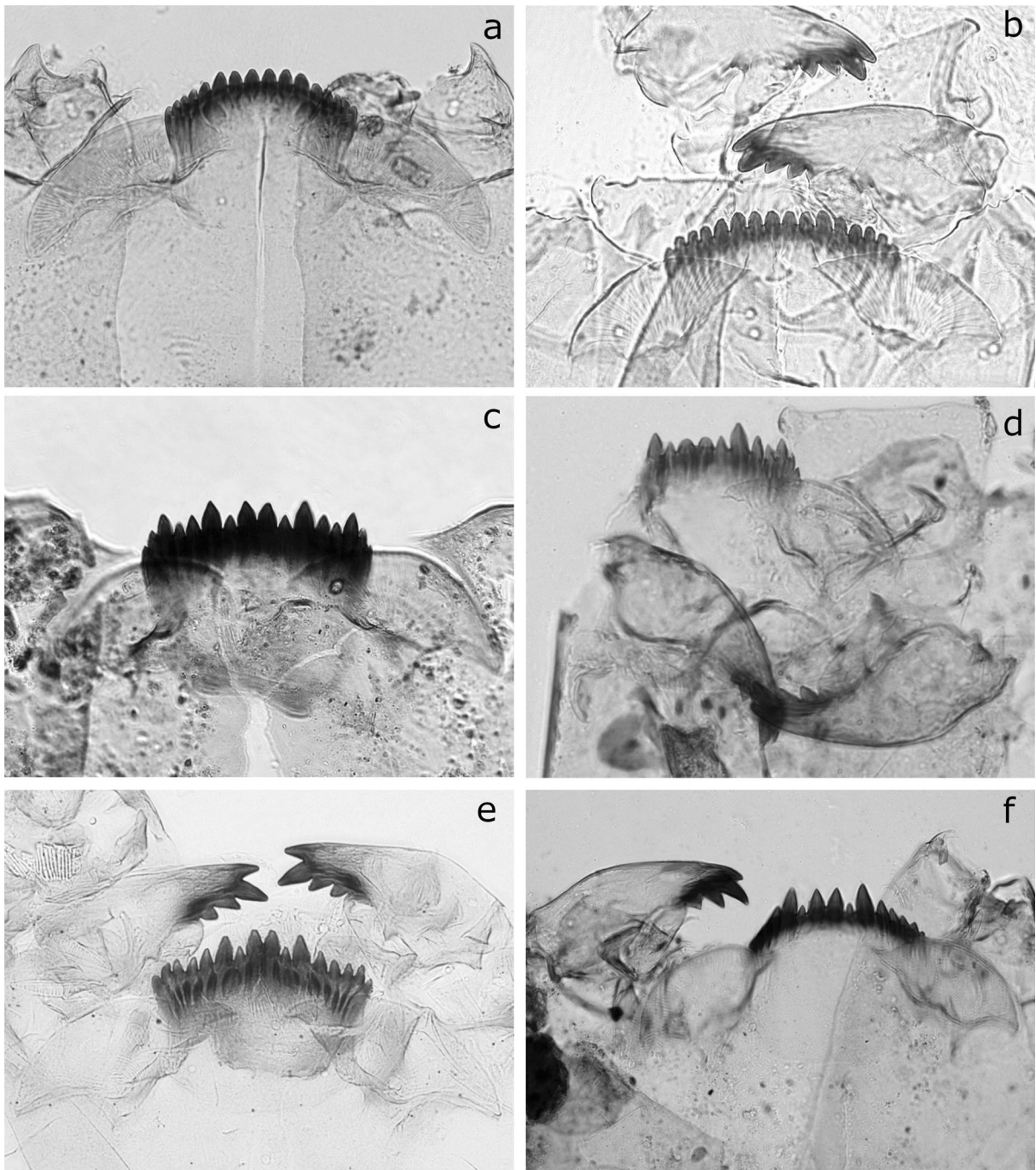
**Remarks:** The morphotype identified, *Pelomus psammophilus*-type (following Trivinho-Strixino and Strixino 2008), was recorded only in the shallow low altitude lake Sacnab, Guatemala.

#### *Polypedilum* Kieffer (Fig. 9a–f)

**Morphology:** Pattern of mental teeth varies, but always with double median tooth and 7 (occasionally 6) laterals; 1st lateral tooth may be minute (in this case 2nd lateral subequal to median teeth, Fig. 9c–f) or subequal to other teeth (in this case all mental teeth of similar size, Fig. 9a, b), outermost tooth short and recessed. Ventromental plates variable but broad and widely separated medially (by at least the width of median teeth); striae continuous. Mandible with all teeth dark, relatively short, apical tooth followed by 2–3 inner teeth, dorsal tooth usually present, occasionally absent. Premandible with 3 teeth (2 apical and 1 blunt basal tooth). Antenna with 5-segmented; Lauterborn organs opposite. Relative lengths of antennal segments 2–5 is an important identification character, e.g., segment 3 is minute in some species of the *Tripodura* subgenus.

**Remarks:** Species rich genus with worldwide distribution. Five morphotypes were identified following Epler (2001), Brooks et al. (2007) and Trivinho-Strixino (2014).

Two morphotypes have subequal mental teeth: *Polypedilum beckae*-type (most likely belonging to the *Asheum* subgenus, see Epler 2001) has ventromental plates slender and longer than width of mentum (*Asheum*-like), mandibles with 3 inner teeth, dorsal tooth absent (Fig. 9a). The morphotype resembles *Polypedilum sordens*-type (sensu Brooks et al. 2007) but can be distinguished from it by the subequal 6 median teeth (while in *P. sordens*-type the double median tooth is slightly taller than other teeth, and 1st lateral tooth is faintly shorter than median and 2nd lateral teeth (Brooks et al. 2007). Due to the elongate, lobed ventromental plates *P. beckae*-type could be confused with *Endochironomus*, which has either mentum with 3 median teeth or, if with 4 median teeth, they are distinctly longer than lateral teeth and/or 1st lateral tooth distinctly shorter than 2nd lateral tooth (Brooks et al. 2007).



**Fig. 9** Subfossil remains of larval Chironominae from lakes of Central America and Mexico. Tribe Chironomini. a–*Polypedilum beckae*-type (note the *Asheum*-like ventromental

*Polypedilum fallax*-type (see Trivinho-Strixino 2014) has shorter, fan-like ventromental plates and

plates); b–*Polypedilum fallax*-type; c,d–*Polypedilum* type A: normal mentum c, mentum with worn median teeth d; e–*Polypedilum tripodura*-type; f–*Polypedilum nubeculosum*-type

mandible with 2 inner teeth, dorsal tooth present (Fig. 9b).

Three morphotypes had typical “*Polypedilum*-like” menta, i.e. with extended median teeth, minute 1st lateral teeth and 2nd laterals subequal to median teeth in size (Fig. 9c–f) and mandibles with 2 inner teeth. Two morphotypes have very similar mentum with the 4<sup>th</sup> lateral tooth shorter than either of the two adjacent teeth, however, can be distinguished based on the arrangement of the outermost 3 lateral teeth: in *Polypedilum* type A (most likely *Polypedilum* subgenus, see *Polypedilum* sp. 2 and 6 in Trivinho-Strixino 2014) these teeth form a distinct cluster decreasing in size creating the appearance of a steep “slope” (Fig. 9c, d).

In *Polypedilum tripodura*-type the 6th (last) lateral tooth is only slightly lower than the penultimate one (Fig. 9e). Antenna of this type is characteristic for subgenus *Tripodura* with minute 3rd antennal segment.

*Polypedilum nubeculosum*-type differs from the previous two types in the arrangement of lateral teeth that are diminishing in size laterally with the 4th lateral tooth not being smaller than the 5th (Fig. 9f).

In general, *Polypedilum* remains were frequent in Central American lakes, occurring in every country and lake type (ponds, lakes, cenotes and rivers). *P. tripodura*-type was the most frequent occurring almost in half of the sites. *P. fallax*-type was the rarest morphotype, recorded only in shallow, low altitude lake Misteriosa, Mexico.

#### *Stenochironomus* Kieffer (Fig. 10a)

**Morphology:** Shape of head capsule very characteristic, dorsoventrally flattened, wedge-shaped. Mentum distinctive, concave, with 10–12 strongly pigmented teeth; 4 uniform median teeth and 3–4 pairs of elevated lateral teeth. Ventromental plate dramatically reduced forming a large weakly striated lobe. Mandible triangular with the proximal half black; apical tooth and 2 inner teeth present, dorsal tooth absent, instead, there is a ridge with 2 teeth (which is usually not visible in the subfossils). Premandible with 3 teeth. Antenna 5-segmented, Lauterborn organs minute, opposite on 2nd segment.

**Remarks:** Since *Stenochironomus* larvae mine both in living and dead leaves and wood (Epler 2001), head capsules of the genus were rare in lake sediments, only recorded in a few Guatemalan and Mexican lakes.

#### *Xenochironomus* Kieffer (Fig. 10b)

**Morphology:** Strongly pigmented mentum with a characteristic arrangement of teeth: recessed trifold median tooth with high, domed central part and 2 min outer teeth; 7 lateral teeth, 1st broad and tall, higher than median tooth, 2nd narrow and low, 3rd taller than 2nd, remainder decreasingly gradually. Ventromental plates broad and deep, separated by the width of the median teeth, striae fine and continuous. Mandible with a long apical tooth and 3 min inner teeth, dorsal tooth absent. Premandible lacking apparent teeth. Antenna 5-segmented. Lauterborn organs opposite.

**Remarks:** The shape of mentum of *Xenochironomus* is unique in Chironominae and unlikely to be confused with other genera (note though that larval mouth-parts are frequently worn).

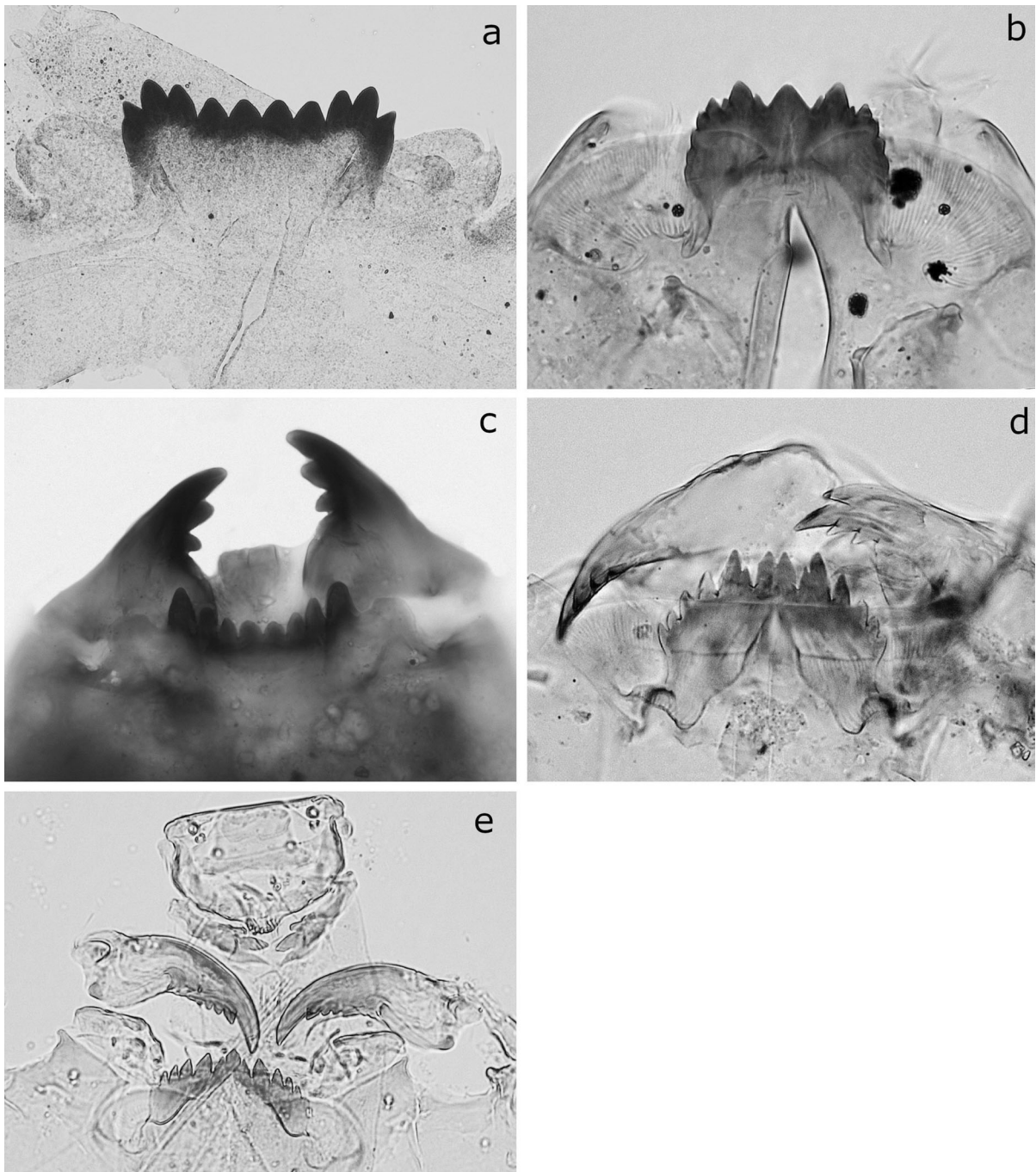
Perhaps due to the unique feeding habit of larvae (mining in freshwater sponges), remains were rare in Central American lakes, only recorded in 3 lakes in Guatemala, El Salvador and Mexico.

#### *Xestochironomus* Sublette and Wirth (Fig. 10c)

**Morphology:** Head capsule dorsoventrally flattened with a Y-shaped dorsal design. Mentum is strongly sclerotized, concave, with 8 teeth, most lateral teeth continuous with the edge of the ventromental plate. Ventromental plates vestigial without striation. Mandible robust, triangular apically, with 3–4 uncertainly distinct teeth. Apical tooth short, without dorsal tooth. Premandibular teeth with an uncertain number of teeth. Antenna with 5-segmented, Lauterborn organs absent.

**Remarks:** *Xestochironomus* has a unique shape of head and mentum and can be perhaps confused with *Stenochironomus* (and *Harrisius*, which is only known from Australia). *Xestochironomus* can be distinguished by 8 mental teeth (the other two genera have 10–12) and the squared off shape of head (relative to the more triangular head of the other two).

*Xestochironomus* is a species rich genus, only known from the New World (Andersen and Kristoffersen 1998). In Central America, remains were only recorded in high elevation lake Magdalena, Guatemala.



**Fig. 10** Subfossil remains of larval Chironominae from lakes of Central America and Mexico. Tribe Chironomini. a–*Stenochironomus* sp.; b–*Xenochironomus* sp.; c–*Xestochironomus* sp.; d–*Zavreliella* sp.; e–Chironomini indet

*Zavreliella* Kieffer (Fig. 10d)

**Morphology:** Mentum with double median teeth; 6 pairs of lateral teeth, 1st and 2nd partly fused together,

1st minute, 2nd about as tall as median teeth, remainder gradually decreasing in size. Ventromental plates nearly triangular, about as wide as mentum, almost touching medially, anterior margin smooth,



striae restricted to basal and lateral part. Mandibular teeth pale brown; apical tooth relatively short, 2 inner teeth and a strong dorsal tooth present. Premandible with 3 apical teeth and a single blunt basal tooth. Antenna 6-segmented, Lauterborn organs large, alternate on apex of 2nd and 3rd segments.

*Remarks:* The genus is very similar to *Lauterborniella* from which it can be distinguished by the 1st and 2nd lateral teeth of mentum which are distinctly separate in *Lauterborniella* (Plate 24), while partially fused in *Zavreliella*. In addition, setae submenti are branched in *Lauterborniella* but simple in *Zavreliella*.

*Zavreliella* was recorded in all studied countries except for Belize, however, the remains were not very frequent, occurring in 1–3 lakes per country. The morphotype was typically recorded in warm, shallow, low elevation lakes, however, exceptionally occurred also in a lake situated in > 1000 m a.s.l. (El Pino, Guatemala).

Chironomini indet. (Fig. 10e)

*Morphology:* Mentum with a trifold median tooth of triangular shape, outer teeth about half the size of the central tooth and partly fused with it; 5 pairs of lateral teeth, regularly decreasing in size, outermost minute. Ventromental plates shorter than mentum, curved, broadly separated medially; striae short, not reaching the anterior margin. Mandible with very long, curved apical tooth, 3 (4?) inner teeth diminishing in size towards the base, dorsal tooth absent; seta submentalis exceptionally long and slender, reaching apical tooth; seta interna probably absent; apical half of mandibles brownish, the same color as the mentum. Premandible with 2 apical teeth and 1 basal tooth. Antennae were missing in both recorded specimens.

*Remarks:* Due to the insufficient quality of the recorded head capsules, the generic placement of the morphotype within the tribe remains unclear. Some features, such as the absent dorsal tooth and pecten mandibularis on the mandible and relatively weakly sclerotized, pale mentum (Epler et al. 2013) indicate that it may be a member of the *Harnischia*-complex. This type is referred to as *Harnischia*-complex type A in Hamerlík and Silva (2021).

Very rare morphotype, only few specimens were found in a single site, the lowland river Salto Grande, Mexico.

Tribe Pseudochironomini

Characteristic features of the tribe are antenna not mounted on distinct pedestals, Lauterborn organs not placed on pedicels. Ventromental plates bar-like in near contact medially; seta submenti on the same side of mandible as seta interna (dorsal).

*Pseudochironomus* Malloch (Fig. 11a–d)

*Morphology:* Mentum with simple, broad, rounded median tooth, about as high as 1st laterals, 6 lateral teeth, 2nd laterals greatly reduced (in worn menta appears fused to the 1st laterals), remaining 4 laterals decreasing progressively. Ventromental plates “Tanytarsini-like”, slender and scarcely separated medially, with a characteristic stalk-like structure protruding below the plate. Mandible with pale apical tooth and 4 dark inner teeth, basal one blunt, dorsal tooth absent.

*Remarks:* Both major morphotypes distinguished by Epler (2001) were represented in the Central American material: type 1 with a mentum of linear shape bearing 13 teeth, here called *Pseudochironomus prasinatus*-type (Fig. 11a, b) and type 2 having a mentum with 11–13 teeth of more arcuate shape, with the last 1–2 teeth vestigial or fused, called *Pseudochironomus* type Las Pozas in the present paper (Fig. 11c, d).

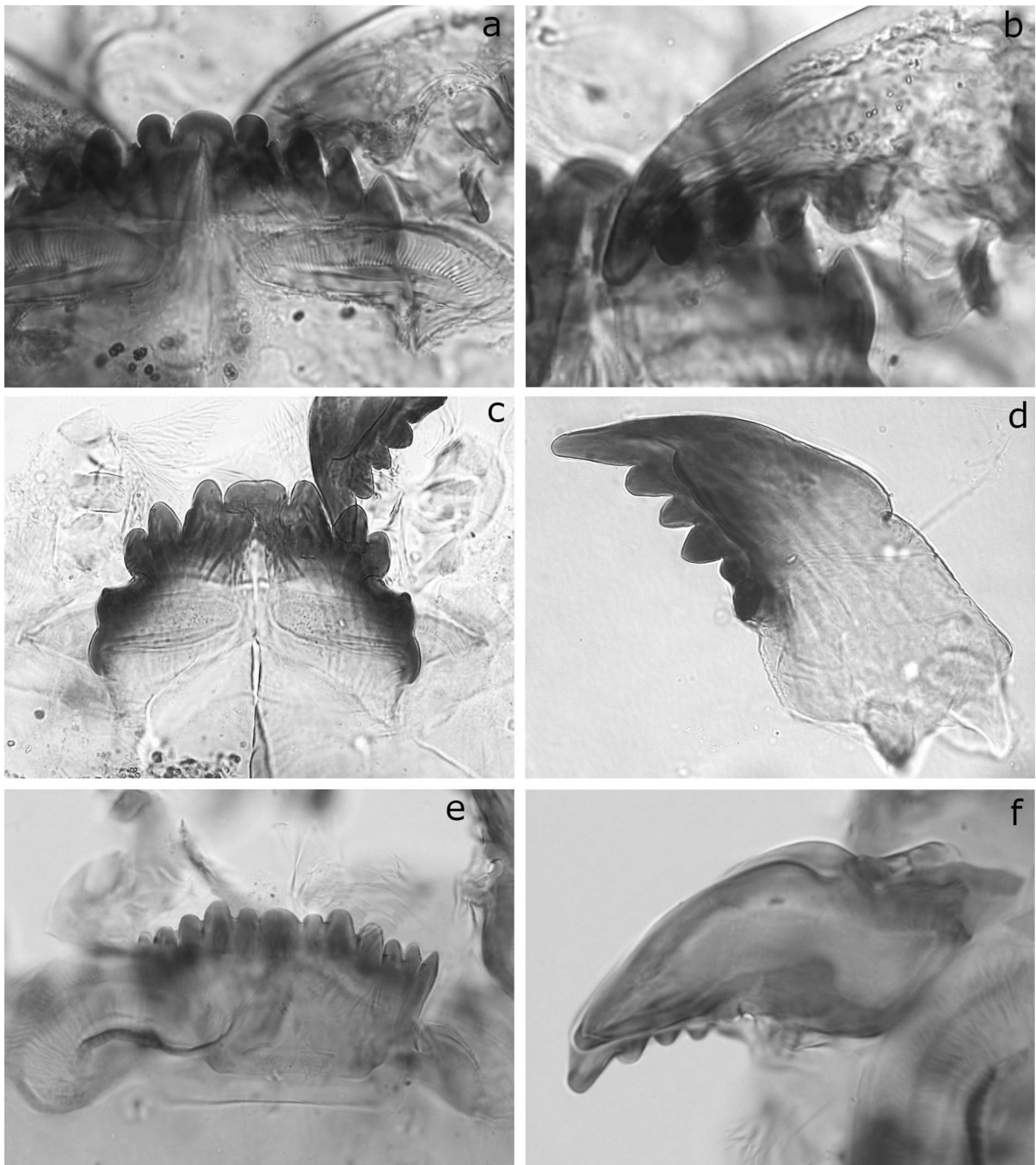
*Pseudochironomus* remains were rare; both types occurred occasionally in warm, low elevation lakes of different depth in Guatemala and Mexico and in lowland river Salto Grande, Mexico.

Pseudochironomini type A (Fig. 11e, f)

*Morphology:* Mentum has single median tooth and 6 laterals, 1st lateral reduced (Fig. 11e). Ventromental plates short and lobed, Tanytarsini-like, almost connecting medially, anterior margin strongly curved. Mandible with a pale apical tooth and 4 inner teeth, basal one broad, dorsal tooth absent (Fig. 11f).

*Remarks:* This morphotype most likely belongs to Pseudochironomini but its generic position is uncertain, it may belong to the genera *Pseudochironomus*, *Riethia* or *Manoa*.

Very rare, the only record is from the lowland river Salto Grande, Mexico.



**Fig. 11** Subfossil remains of larval Chironominae from lakes of Central America and Mexico. Tribe Pseudochironomini. a,b–*Pseudochironomus prasinatus*-type: mentum a, mandible b,

c,d–*Pseudochironomus* type Las Pozas: mentum c, mandible d, e,f–*Pseudochironomini* type A: mentum e, mandible f

#### Tribe Tanytarsini

Characteristic features of the tribe are antenna mounted on distinct elongated pedestal and well-

developed Lauterborn organs often situated on short to long pedicels. Ventromental plates generally wide and slender, almost touching each other medially, in few

genera narrow, separated medially by at least the width of the three median teeth. Figure 2 shows diagnostic characters of subfossils Tanytarsini.

#### *Cladotanytarsus* Kieffer (Fig. 12a–c)

**Morphology:** Mentum with broad median tooth often notched with outer teeth variable in size and degree of fusion, 5 pairs of lateral teeth, regularly decreasing in size or 2nd lateral much smaller than remainder laterals (in *C. mancus*-type, Fig. 12a). Ventromental plates slightly wider than mentum, very close medially. Post-occipital plate well developed. Mandible with dark apical tooth and 3 inner teeth, dorsal tooth pale. Premandible with 4 or 5 apical teeth. Antenna characteristic, with 2nd segment short, wedge-shaped, 3rd segment longer than 2nd; Lauterborn organs large, placed on short pedicels (Fig. 12b).

**Remarks:** The most characteristic feature of the genus is the distinctive antenna (see above). Some specimens lacking antennae can be distinguished from other Tanytarsini by the reduced 2nd lateral mental tooth (Fig. 12a), others by the unique shape of mentum bearing a compound median tooth and 4 pairs of lateral teeth (Fig. 12c).

Two morphotypes were identified: *Cladotanytarsus mancus*-type (Fig. 12a, b) and *Cladotanytarsus* type A (following Oliver et al. 1978). The distinctive feature of *Cladotanytarsus mancus*-type is the reduced 2nd pair of lateral teeth (shorter than 1st and 3rd lateral teeth).

*Cladotanytarsus* type A (Fig. 12c) corresponds to *Cladotanytarsus* sp. 3 of Oliver et al. (1978) and *Cladotanytarsus* sp. F of Epler (2014). The characteristic feature of this type is the very small first pair of lateral teeth of mentum that are close to the laterally notched median tooth, and as a consequence, the mentum seems to be composed of a compound median tooth and 4 pairs of separate lateral teeth (Cranston 2010). Since the antennae were missing in the head capsule, the generic placement of this larval remain is tentative.

Subfossil remains of *Cladotanytarsus mancus*-type were relatively frequent in lakes situated in lower elevations (below 500 m a.s.l.) of all countries but Honduras. One remain of *Cladotanytarsus* type A was found in the shallow, low elevation lake Milagros, Mexico.

#### *Paratanytarsus* Thienemann and Bause (Fig. 12d)

**Morphology:** Median tooth rounded or weakly notched laterally; with 5 pairs of lateral teeth, decreasing in size laterally; all median teeth uniformly dark. Ventromental plates close together medially, each plate slightly longer than width of mentum. Post-occipital arch is deeply incised, plate absent. Mandible with apical tooth and 2–3 inner teeth similar in color, dorsal tooth brown or yellowish. Premandible bifid. Antenna 5-segmented; placed on short pedestal without apical projection; Lauterborn organs small, sessile or placed on very short pedicels.

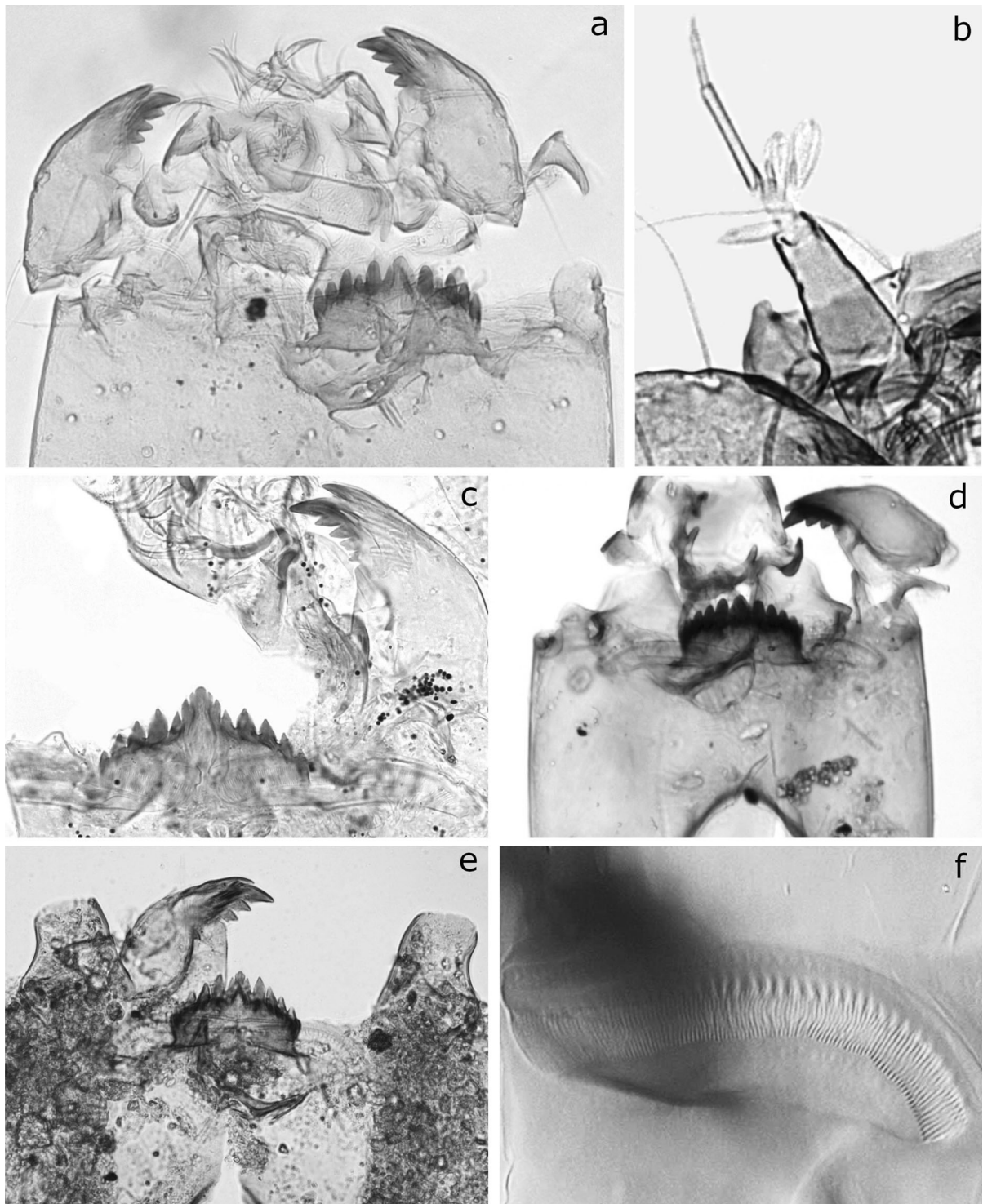
**Remarks:** Subfossil *Paratanytarsus* resembles *Micropsectra* and *Tanytarsus* but from both can be distinguished by the combination of the shape of post-occipital arch that is deeply incised and the short antennal pedestal. Moreover, while in *Paratanytarsus* the mentum is uniformly dark, in *Micropsectra* there is a pale area in the middle part of mentum. *Paratanytarsus* closely resembles *Neozavrelia* (especially those with 2 inner mandibular teeth) and can be distinguished by 5 pairs of well-developed lateral teeth of *Paratanytarsus* vs. 4 laterals of *Neozavrelia* (some *Neozavrelia* have 5 laterals as well, in which case 5<sup>th</sup> lateral tooth is minute). Moreover, *Neozavrelia* has not been recorded in the Neotropics so far, and larvae are cold-stenothermal and occur in high elevation waterbodies (Epler et al. 2013).

One morphotype was recorded, *P. penicillatus*-type which has mandible with 2 inner teeth (Brooks et al. 2007).

Relatively common in various lake types in Guatemala, Belize, Honduras and Mexico.

#### *Rheotanytarsus* Thienemann and Bause (Fig. 12e, f)

**Morphology:** Mentum with rounded or laterally notched median tooth and 5 pairs of gradually decreasing lateral teeth. Ventromental plates of characteristic shape, strongly curved in outer half and coarsely striated (Fig. 12f). Post-occipital plate weakly developed. Mandible with 2–3 inner teeth, dorsal tooth brown. Premandible bifid. Antenna 5-segmented on a short (about as long as broad) pedestal with triangular apical opening, spur absent, Lauterborn organs on short pedicels, not extending beyond antennal apex.



**Fig. 12** Subfossil remains of larval Chironominae from lakes of Central America and Mexico. Tribe Tanytarsini. a,b—*Cladotanytarsus mancus*-type: mentum and mandible a, antenna b; c—*Cladotanytarsus* type A; d—*Paratanytarsus penicillatus*-

type; e—*Rheotanytarsus* sp.; f—*Rheotanytarsus* sp.: detail of ventromental plate (note the distinct curve and strong striation; modified after Cranston 2010)

**Remarks:** *Rheotanytarsus* superficially resembles *Paratanytarsus*, but is characterized by the unique shape of ventromental plates that are strongly curved and conspicuously striated. The only type recognized, *Rheotanytarsus* sp., has laterally notched median tooth and 2 inner teeth on mandibles.

Larvae of *Rheotanytarsus* are rheobionts (associated with flowing waters), thus their remains are not common in lake sediments. Remains were very rare in Central America, too, recorded only in the lowland river Salto Grande, Mexico.

*Stempellina* Thienemann and Bause (Fig. 13a, b)

**Morphology:** Mentum with pale rounded or laterally slightly notched median tooth and 6 pairs of darker laterals, regularly decreasing in size (Fig. 13a). Ventromental plates fan-shaped, widely separated medially. Post-occipital plate weakly developed. Mandible with brown apical and 2 pointed inner teeth, dorsal tooth yellow. Premandible with 5 teeth. Antenna 5-segmented on prominent pedestal bearing a mesal palmate process (Fig. 13b), large Lauterborn organs placed on short pedestals.

**Remarks:** Head capsules of *Stempellina* can be easily separated from other Tanytarsini by the large, palmate expansion on the antennal pedestal. The morphotype that occurred in the paleo-material possessed about 12 prominent knob-like processes on dorsal surface of head, which is classified as *jo-hannseni*-type (following Cranston 2010).

Subfossils occurred occasionally in low elevation waterbodies of different depth in Guatemala and Mexico.

*Tanytarsus* van der Wulp (Figs. 13c–f, 14a–g)

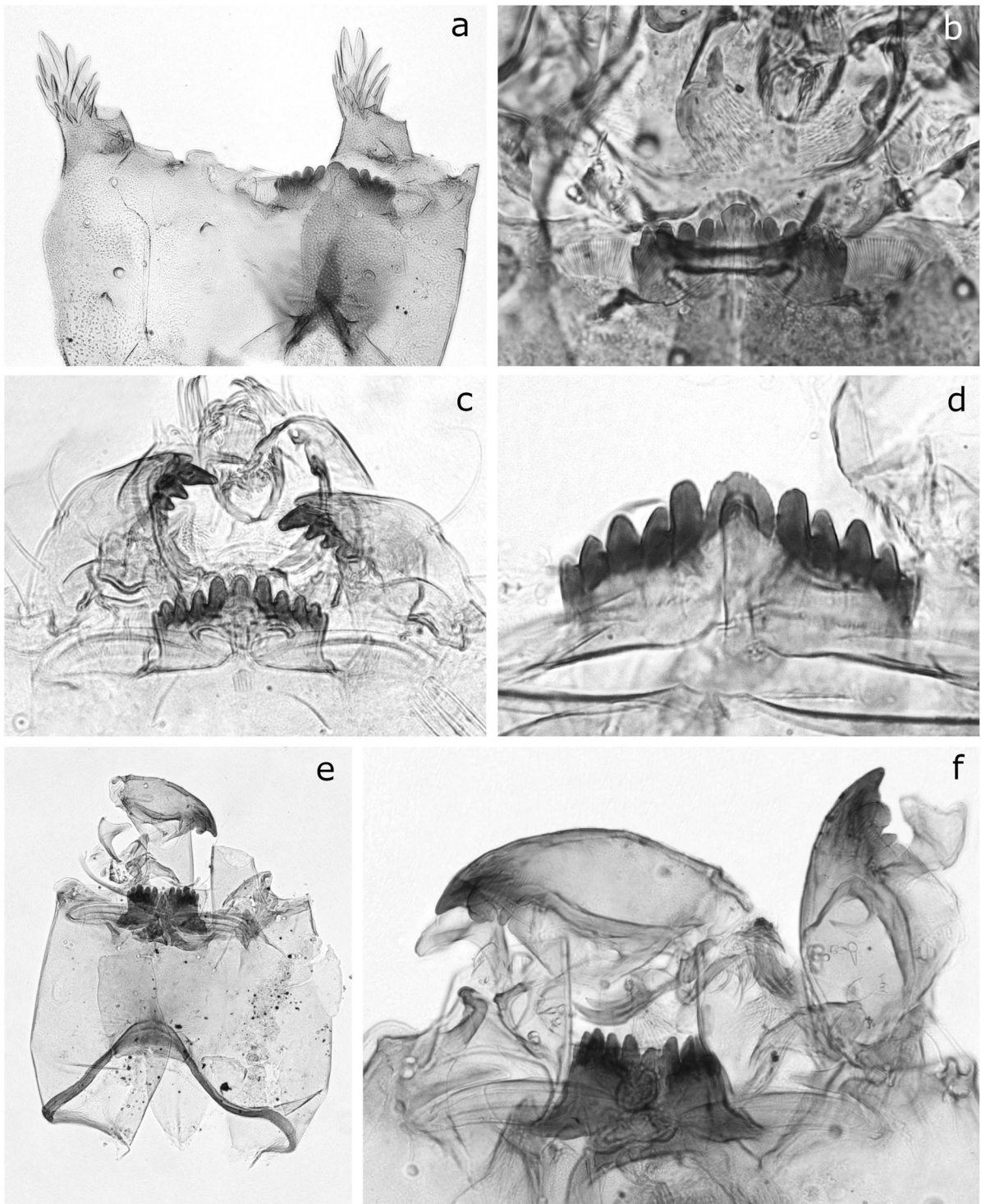
**Morphology:** Mentum with a single median tooth that can be rounded to laterally deeply notched, 5 pair of lateral teeth present. Ventromental plates close together medially, long and narrow, fine striated. Post-occipital plate present, well developed. Mandible with 2–3 inner teeth, 1–2 dorsal teeth and in some species/morphotypes 1–2 surficial teeth may be present additionally. Premandible with 3–5 teeth. Antenna with 5-segmented on tall pedestal usually without spur, however, in some species large spur may be present. Lauterborn organs on long stems that may be annulated in some Nearctic species.

**Remarks:** *Tanytarsus* most resembles *Micropsectra* and *Paratanytarsus*. These genera can be distinguished by premandibles bearing 2 apical teeth in *Paratanytarsus* and *Micropsectra*, while 3 or more teeth in *Tanytarsus*. In the absence of premandibles (usually the case in subfossils), *Tanytarsus* can be distinguished from *Paratanytarsus* by the length of antennal pedestals (short, i.e. as long as broad, in *Paratanytarsus*, and long, i.e. at least twice as long as broad in *Tanytarsus*). Moreover, *Paratanytarsus* is characterized by a deeply incised post-occipital arch with weakly developed or missing plate. *Micropsectra* can be distinguished from *Tanytarsus* by the shape of the spur on pedestal: in *Micropsectra* the spur is almost always present and is short and sharp, in *Tanytarsus* the spur is usually missing, or, if spur is present, then of different shape, mostly long, broad and rounded apically (Brooks et al. 2007).

Six morphotypes were distinguished in the subfossil material:

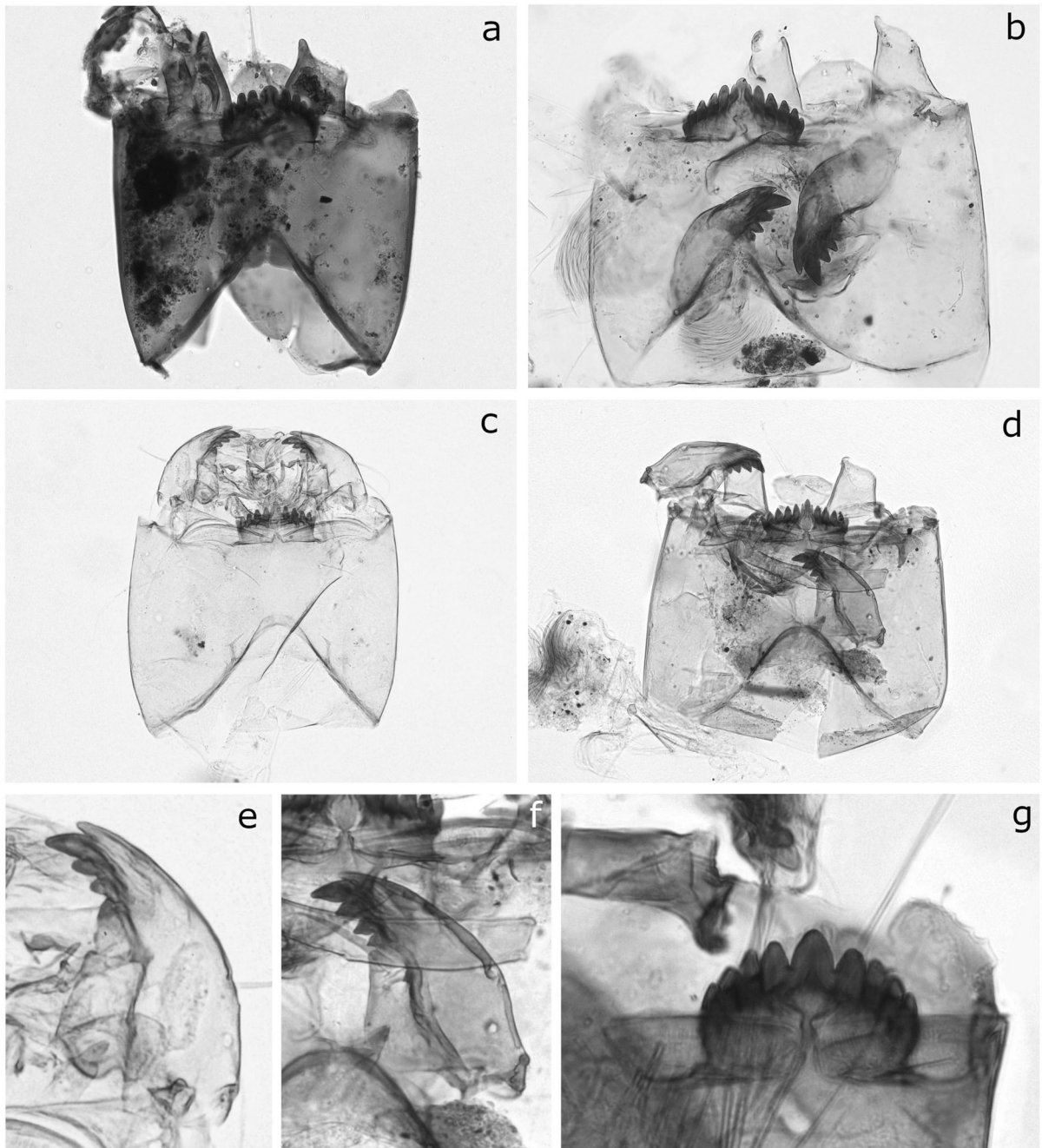
*Tanytarsus* type Yojoa (Fig. 13c, d) can be distinguished from other Tanytarsini by the single rounded median tooth with thickened margin around the whole tooth (appearing like a double rim). First lateral tooth almost as high as median tooth, rounded, 2nd to 5th laterals pointy, 2nd lateral short and frequently appressed to 1st lateral; 2 inner teeth and a dorsal tooth on mandibles, pedestal short and with a thorn bearing spines. Head capsules of some specimens with distinct reticulation. Post-occipital plate reduced or missing. These features (mandible with 2 inner teeth, and median tooth of mentum with thickened margin that runs completely around the tooth) also occur in two larval morphotypes, *Tanytarsus* sp. K and *T.* sp. R, described from Florida by Epler (2014).

*Tanytarsus norvegicus*-type (following Lin et al. 2018). A very distinct morphotype. Mentum with a characteristic shape, rounded median tooth recessed, paler than 5 lateral teeth, their size increasing from the 1st to 3rd, which is the tallest; from 3rd lateral teeth are laterally decreasing in size; outer lateral teeth compressed and partially superimposed on each other. Mandible with a strong apical tooth and a large surficial tooth partially obscuring inner teeth (their number is not obvious), dorsal tooth absent. Post-occipital plate present, no spur on antennal pedestal (Fig. 13e, f). This morphotype shows features that are shared with *Tanytarsus* and former *Corynocera* (placed to *Tanytarsus* recently as *T. norvegicus* group;



**Fig. 13** Subfossil remains of larval Chironominae from lakes of Central America and Mexico, Tribe Tanytarsini. a,b–*Stempelina* sp.: head capsule a, mentum b; c,d–*Tanytarsus* type Yojoa:

mentum and mandibles c, detail of mentum d, note the rounded median tooth with an inner chitinized arch); e,f–*Tanytarsus norvegicus*-type: head capsule e, mentum and mandibles f



**Fig. 14** Subfossil remains of larval Chironominae from lakes of Central America and Mexico. Tribe Tanytarsini. a–*Tanytarsus* type Magdalena; b–*Tanytarsus ortonii*-type; c,e–*Tanytarsus* type

A: head capsule c, mandible with 2 inner teeth e; d, f–*Tanytarsus* type B: head capsule d, mandible with 3 inner teeth f; g–Tanytarsini type A

Lin et al. 2018). Lin et al. (2018) hypothesize that the *T. norvegicus* species group originates in Laurasia which would explain its recent distribution in/near the Arctic and on the Qinghai-Tibet Plateau of the

northern hemisphere. However, the Central American records come from warm lowland lakes, and, thus, it is questionable whether this morphotype belongs in the *norvegicus* species group but because of their striking

resemblance, we placed it there tentatively. Epler (2014) described a morphotype from two lakes in Florida, *Tanytarsus* sp. beta, that has very similar features to our *T. norvegicus*-type.

*Tanytarsus* type Magdalena (Fig. 14a). The dark head capsule is distinctive for this morphotype; pedestals short, about as long or slightly longer than broad, bearing large, rounded spur. Mentum with median tooth and laterals rounded, dark; laterals slightly diminishing in size. Post-occipital arch narrow, plate present, slightly lighter than occipital margin. Due to the large rounded spur on the pedestal, this morphotype resembles some *Tanytarsus* types from Brooks et al. (2007), such as *Tanytarsus glabrescens*-type, *T. lactescens*-type and *T. pallidicornis*-type, but differs from all above mentioned by the strongly sclerotized, dark head capsule, short antennal pedestals and narrow post-occipital plate (usually characteristic for the *Micropsectra* genus). This type is referred to as *Micropsectra* type Magdalena in Hamerlík and Silva (2021).

*Tanytarsus ortoni*-type (Lin et al. 2018). Mandible with 2 inner teeth, distinct apically rounded spur on pedestals (varying in size) and premandible with 3 teeth. Post-occipital plate present but weakly developed (Fig. 14b). This type corresponds to the former genus *Caladomyia* that has recently been assigned to *Tanytarsus* (Lin et al. 2018).

*Tanytarsus* type A. Head pale, mentum with laterally notched median tooth paler than lateral teeth, broad pale post-occipital margin, plate with slightly concave to straight end, mandibles with 2 inner teeth, no spur on antennal pedestals (Fig. 14c, e).

*Tanytarsus* type B. Head capsule pale, dark and strongly concave post-occipital plate, mandibles with 3 inner teeth (Fig. 14d, f).

*Tanytarsus* remains were recorded in every country, but were not particularly frequent, except for *Tanytarsus ortoni*-type, which was common in lowland waterbodies in Mexico. Remains of *Tanytarsus* type Magdalena were rare in the study material, only recorded in high elevation lakes, such as Magdalena in Guatemala, Apastepeque, El Salvador and Yojoa in Honduras. *Tanytarsus norvegicus*-type was recorded in warm lowland lakes in Belize (Crooked Tree), Guatemala (Sacpuy) and a cenote in Mexico (Juarez). *Tanytarsus* type Yojoa was recorded from lakes in Guatemala and Honduras along a broad altitudinal

gradient from lowlands to high elevations (up to 2000 m a.s.l.).

*Tanytarsini* type A (Fig. 14g)

**Morphology:** Head capsule strongly sclerotized, brown. Mentum with rounded median tooth and 4 pairs of lateral teeth; median tooth longer and broader than 1st lateral, central triplet of teeth appear to be on a different focal plane; all median teeth uniformly dark. Ventromental plates close together medially, each plate slightly shorter than width of mentum. Post-occipital arch deeply incised, plate present but weakly developed. Premandible with 3 teeth. Mandible and antenna not present.

**Remarks:** The generic placement of the morphotype is uncertain, but the characteristic mentum with rounded median tooth and only 4 lateral teeth resemble that of *Neozavrelia*. Larvae of some *Neozavrelia* are considered cold-stenothermal and prefer high elevation waterbodies. The genus is, however, so far missing in the Neotropics (Epler et al. 2013).

One head capsule was recorded in the shallow, high elevation lake Chiligattoro, Honduras.

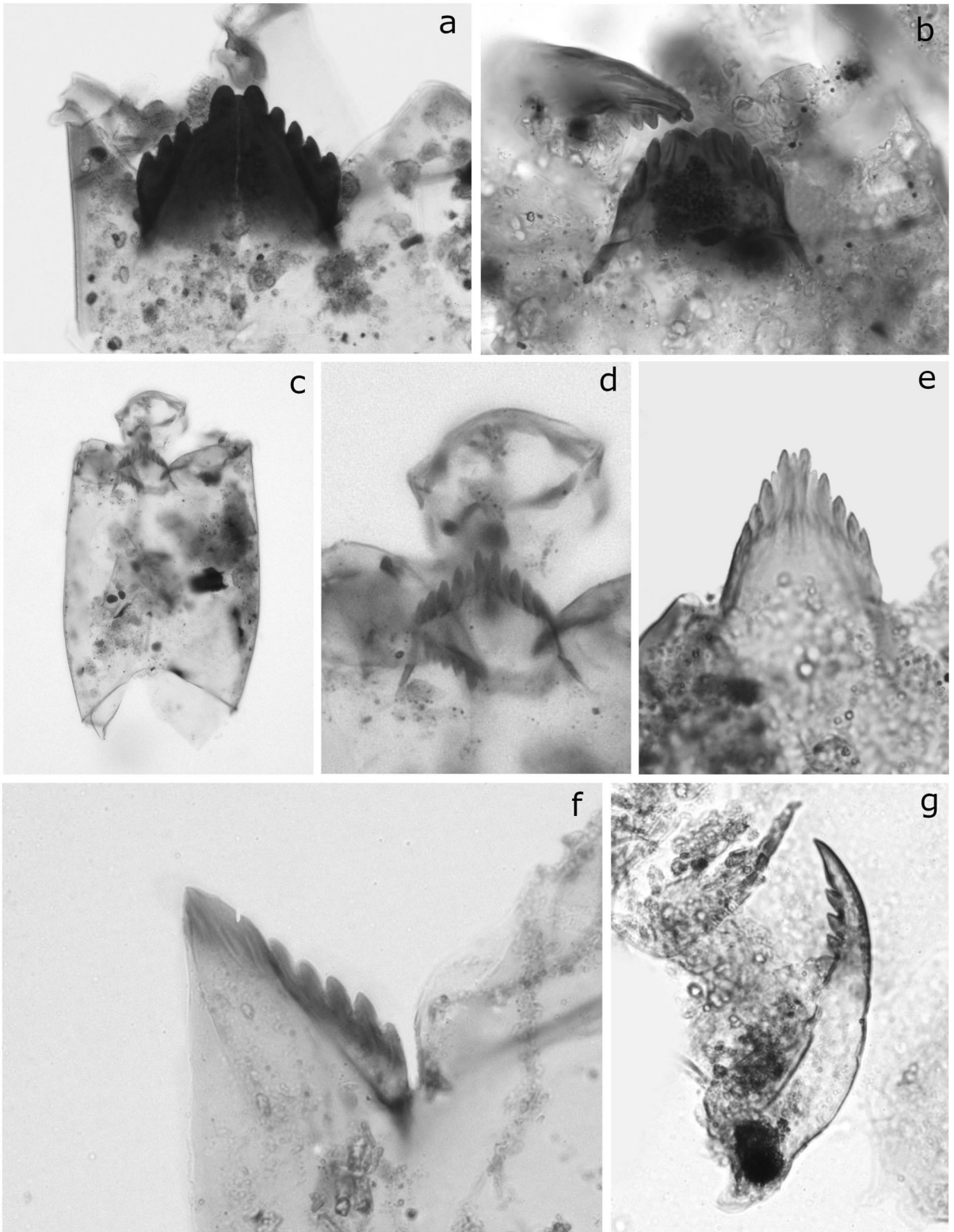
#### Subfamily Orthocladiinae

Larvae of Orthocladiinae show great morphological variability, however, can be separated from Chironominae by the eye-spots, which often are contiguous or, when separate with a dorsal eye-spot posterior to a ventral eye-spot (Andersen et al. 2013a, b). Another distinctive trait in the larval stage is the absence of striated ventromental plates, that are usually indistinct (perhaps with the exception of some *Nanocladius* species that can bear horizontal striae). There is no accepted division of Orthocladiinae into tribes. Figure 2 shows diagnostic characters of subfossils Orthocladiinae.

*Brillia* Kieffer (Fig. 15a)

**Morphology:** Mentum with a median complex consisting of a minute central tooth between bases of a pair of large median teeth; 5 pairs of lateral teeth, inner 3 lateral teeth of the same size and shape, 4th and 5th laterals smaller and appressed to each other (creating an appearance of one medially notched tooth). Seta submenti well below the mentum. Mandible with short





◀ **Fig. 15** Subfossil remains of Orthoclaadiinae larvae from lakes of northern Central America and the Yucatan Peninsula. a–*Brillia* sp.; b–*Bryophaenocladus/Gymnometriocnemus*; c–e–*Corynoneura* sp.: head capsule showing characteristic elongated shape c, menta d, e; f, g–*Cricotopus* type Magdalena: half of mentum f, mandible g

apical tooth and 4 inner teeth (4th one blunt not very visible). Premandible weakly bifid at apex. Antenna characteristic, with 4 segments; segment 2 divided into 2 parts.

*Remarks:* There are some taxonomic uncertainties in the *Brillia*-complex, thus the present head capsule can belong to one of the genera close related to *Brillia* with unknown immature stages, e.g. *Irisobrillia*, which has been recorded in the Neotropical region (Andersen and Mendes 2004) and in Central America (Spies and Reiss 1996; Watson and Heyn 1992).

*Brillia* head capsules were recorded in the high altitude lake Magdalena, Guatemala and cenote Bacalar, Mexico.

*Bryophaenocladus* Goetghebuer /  
*Gymnometriocnemus* Thienemann (Fig. 15b)

*Morphology:* Mentum with 2 (occasionally 1) broadly rounded median teeth and 4 pairs of lateral teeth. Ventromental plate heavily sclerotized but not extending beyond the lateral margin of flattened mentum; beard absent. Mandible with short apical tooth and 3 inner teeth. Premandible with 3 teeth. Antenna 5-segmented.

*Remarks:* Recent larvae of *Gymnometriocnemus* can be only distinguished from *Bryophaenocladus* by the faintly divided posterior parapods (*Bryophaenocladus* has parapods undivided). Since in the subfossil material the body is missing, subfossils of these two genera cannot be distinguished.

Only one head capsule was found in cenote Silvituc, Mexico. The rarity of this species rich genus with worldwide distribution in the Central American samples may be the consequence of a terrestrial/semiaquatic larval habits of the majority of species.

*Corynoneura* Winnertz (Fig. 15c–e)

*Morphology:* Head capsule very small, narrow and prolonged. Mentum strongly triangular in shape, with

2–3 median teeth, central tooth, if present, of various sizes from minute to subequal to outer median teeth; 5 pairs of lateral teeth. Mandible with short apical tooth, usually subequal or shorter than 1st inner teeth, 4 inner teeth present. Premandible broad with many (up to 12) very short teeth at the apex. Antenna characteristic, as long or longer than the head capsule, with 4 segments, 1st segment extremely long, 2nd and/or 3rd segment often dark.

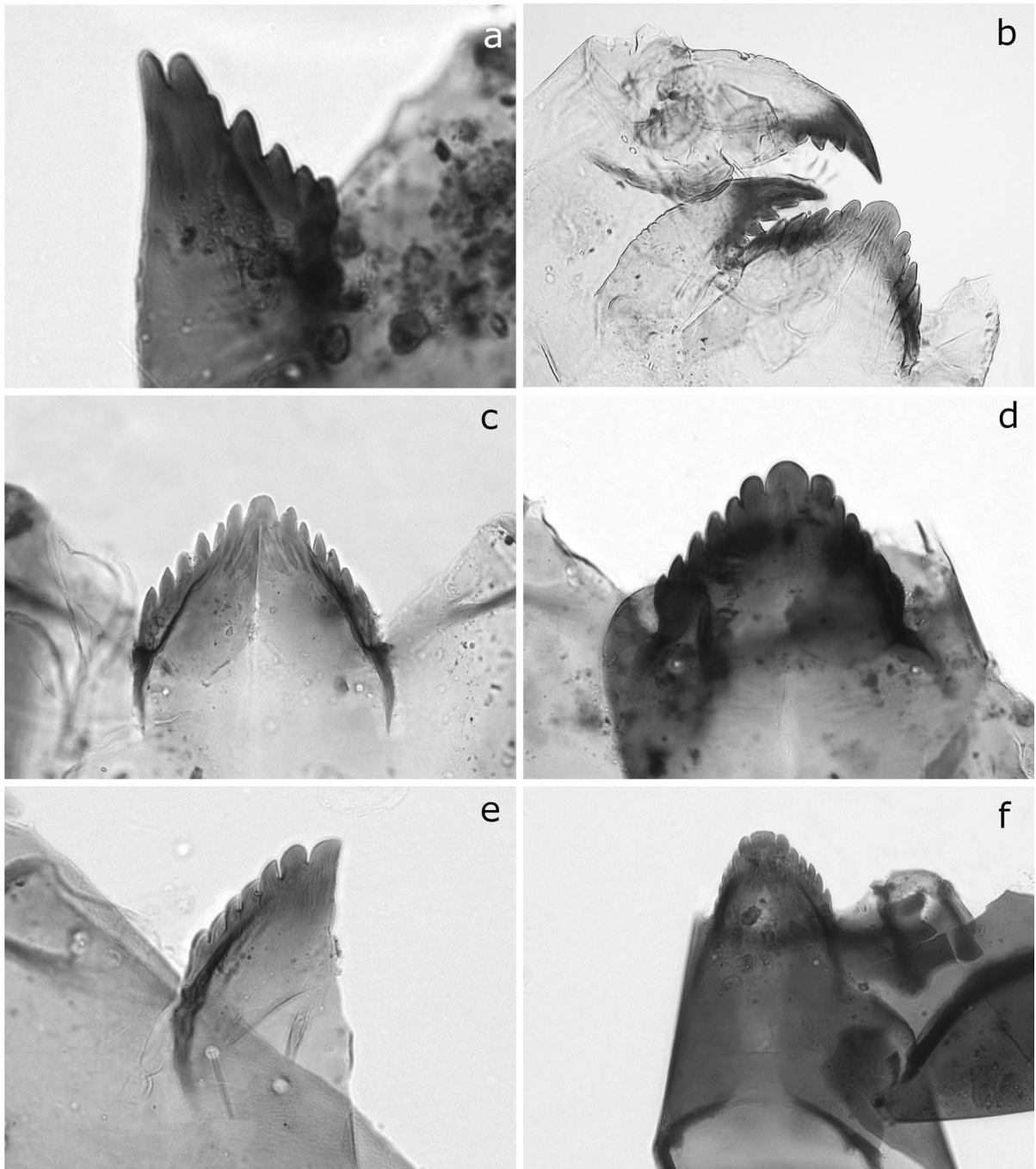
*Remarks:* *Corynoneura* resembles *Thienemanniella* and *Onconeura* both in size and shape of the head capsule, long antennae and shape of mentum. Antenna of *Corynoneura* is as long or longer than head, in *Thienemanniella* it is about  $\frac{1}{2}$  to  $\frac{3}{4}$  lengths of head, and in *Onconeura* antenna is about  $\frac{1}{3}$  of length of head (in addition *Corynoneura* has 4-segmented antenna, *Thienemanniella* and *Onconeura* 5-segmented). In case of missing antennae (typical for subfossil material), most *Corynoneura* species can be distinguished from the other two genera by presence of reticulation on head capsules, which does not occur in the other two genera. Moreover, *Corynoneura* heads are usually pale, while more obviously pigmented in *Thienemanniella*. Due to its small size, *Corynoneura* head capsules might be overlooked in the subfossil (and also recent) material.

One morphotype, *Corynoneura lobata*-type (sensu Brooks et al. 2007), was recorded in the Central American material. The typical feature of this morphotype is the strongly reduced 1st lateral teeth and minute central median tooth. Wrinkled sculpturing may be present on the head capsule, but reticulation is not obvious. In our material, larval head capsules did not possess sculpturing or reticulation. Moreover, the variety of shapes found for the menta (Fig. 15c–e) indicates that this morphotype includes multiple species.

Relatively frequent orthoclad, recorded in Guatemala (lakes Magdalena, Macancha, Sacpuy, El Gofete) and Mexico (lakes Chacan Bata and Rio Guerrero).

*Cricotopus* van der Wulp/*Orthocladus* van der Wulp (Figs. 15f, g, 16a–f)

Larvae of *Cricotopus* are extremely similar and often indistinguishable from *Orthocladus* both in the



**Fig. 16** Subfossil remains of Orthoclaadiinae larvae from lakes of northern Central America and the Yucatan Peninsula. a–*Cricotopus* type I; b–*Cricotopus* type Atitlan; c–*Cricotopus* type

A; d–*Cricotopus* type B; e–*Cricotopus* type D; f–*Orthoclaadius* (*Euorthoclaadius*) sp

recent- and subfossil stage, thus they are discussed together.

**Morphology:** Mentum with single median tooth of different size, usually with 6 pairs of lateral teeth (for the sake of completeness, few *Cricotopus* species have 5 or 7, *Orthocladius* 7–9 pairs of lateral teeth; these taxa were not recorded in the Central American material). Mandibles with a relatively short apical tooth and 3 inner teeth. Premandible with 1–2 apical teeth. Antenna usually with 5 segments (seldom with 4); reduced in some species.

**Remarks:** Both *Cricotopus* and *Orthocladius* have mentum with single median tooth and (usually) 6 lateral teeth, mandible with short apical tooth and 3 inner teeth. While in recent material the tuft of setae on the larval body in most *Cricotopus* species will distinguish *Cricotopus* from *Orthocladius*, this feature is absent in subfossil remains (due to lack of body). The following characters, in general, seem to be more typical for *Cricotopus* than *Orthocladius* (even though can be present in some *Orthocladius* as well): outer margin of mandible strongly crenulated, 2nd lateral tooth is smaller than 1st and/or reduced and fused to 1st lateral tooth, and outer four lateral teeth forming a distinct group. According to Brooks et al. (2007) lateral teeth of *Cricotopus* are usually more rounded and pointed apically and the median tooth is relatively narrow, while in general, *Orthocladius* have lateral teeth more rectangular and median tooth can be broad (> 3 times broader than 1st lateral).

As aforementioned, the two genera are extremely similar and thus our morphotypes are placed tentatively. Seven morphotypes were proposed, 6 *Cricotopus* and 1 *Orthocladius*. It is important to mention here that even though some *Cricotopus/Orthocladius* morphotypes have shown some similarity with the morphotypes identified in Brooks et al. (2007), due to the great differences in the species composition between the Neotropics and the Palaearctic and also the potential differences in the ecological requirements of the types (and thus their paleoecological interpretation) we preferred not to follow that key. However, if there is a similarity with the Palaearctic morphotypes, we always emphasize it in the comments. The correct assignment of these tentative morphotypes requires further research and comparison with recent Neotropical fauna.

*Cricotopus* type Magdalena. Broad pale median tooth, 6 lateral teeth, 1st lateral pale as median tooth, 5

outer lateral teeth darker; 1st lateral tooth separated from the median one with a narrow notch (Fig. 15f). Mandible with long slender apical tooth and 3 inner teeth (Fig. 15g). There is a similarity between *Cricotopus* type Magdalena and *C. bicinctus* (sensu Hirvenoja 1973) as well as *C. bicinctus*-type (sensu Brooks et al. 2007), especially when it comes to the color pattern of the mentum with the broad median tooth and 1st laterals being paler than remaining lateral teeth. However, in *C.* type Magdalena 1st laterals are separated from the median tooth by a weak notch while they are widely separated in *C. bicinctus*-type. Additionally, in *C. bicinctus*-type all lateral teeth are of the same size, while in *C.* type Magdalena the outermost lateral tooth is reduced.

*Cricotopus* type I. Head capsule brown, mentum strongly pigmented, uniformly colored; median tooth slightly taller and about 2 × as broad as 1st lateral tooth; 2nd lateral tooth minute and partly fused to 1st lateral (Fig. 16a). Similar to *Cricotopus intersectus*-type sensu Brooks et al. (2007), but the whole head capsule is dark. This morphotype also resembles larvae of both *Cricotopus sylvestris* group and *C. intersectus* group (sensu Hirvenoja 1973) but due to lack of diagnostic features, further identification is not possible.

*Cricotopus* type Atitlan. Median mental tooth rounded, considerably taller than 1st lateral tooth; 2nd lateral tooth small and partly fused with the 1st lateral tooth; median and first 2 lateral teeth pale, outer 4 lateral teeth darker. Premandible weakly bifid at apex. Outer margin of mandible strongly crenulated (Fig. 16b). The bifid premandible and shape of mentum suggest that the morphotype is likely to be a member of the *Cricotopus sylvestris* group sensu Hirvenoja (1973) and Andersen et al. (2013a, b), but the median tooth is considerably broader and shorter than in case of *Cricotopus sylvestris*-type (sensu Brooks et al. 2007).

*Cricotopus* type A. Mentum light brown; median tooth slightly taller and wider than 1st lateral; 2nd lateral tooth only slightly smaller than 1st and 3rd lateral teeth. All teeth are slender, taller than wide (Fig. 16c). This type superficially resembles *Orthocladius* type I and *O. trigonolabis*-type (sensu Brooks et al. 2007). However, in *Orthocladius* type I the median tooth is about the same width as 1st lateral tooth. In *O. trigonolabis*-type the apex of median tooth and 1st lateral tooth of mentum are at the same level.

Moreover, both types are cold stenothermic (*Orthocladius* type I has been recorded in Icelandic lakes) and thus very unlikely that *Cricotopus* type A from Central America corresponds to one of those types.

*Cricotopus* type B. Mentum strongly sclerotized, dark brown; median tooth domed, considerably taller than 1st lateral; 2nd lateral tooth smaller than 1st and 3rd lateral teeth (Fig. 16d). By the shape of mentum this type resembles larvae of *Cricotopus tremulus* group (sensu Hirvenoja 1973) and is likely to be a member of the group.

*Cricotopus* type D. Median tooth subequal to 1st lateral tooth; first lateral distinctively circular, broader in the middle than at the base (a typical feature of *Paratrichocladius*, currently a subgenus of *Cricotopus*, Cranston and Krosch 2015). Outer 5 laterals rectangular in shape, subequal with clearly apically flattened outline (Fig. 16e). In Hamerlík and Silva (2021) this morphotype was erroneously called *Cricotopus* type C, however, this name refers to a different morphotype described by Brooks et al. (2007)

*Orthocladius* (*Euorthocladius*) sp. Head capsule strongly pigmented, brown, the same color as mentum; median mental tooth with straight anterior margin, about 2 × as broad and about as high as 1st laterals; 1st lateral rounded, broader and taller than outer 5 lateral teeth of rectangular shape; mental extensions extended posteriorly beyond seta submenti; occipital margin dark brown (Fig. 16f).

*Cricotopus* were the most frequent and abundant orthoclad remains in Central American lake sediments and were found in Guatemala (lakes Atitlan, Magdalena, El Gofete), Honduras (lake Yojoa), Belize (Crooked Tree lake) and Mexico (Chacan Bata). Both *Cricotopus* and *Orthocladius* represent species rich genera with worldwide distribution, however, rarely reported from the Neotropics (Spies et al. 2009).

*Eukiefferiella* Thienemann (Fig. 17a–c)

**Morphology:** Head capsule usually dark and strongly pigmented with dark brown to black occipital margin. Mentum clearly striped (except for *E. devonica*-type with black mentum where it may be not visible) with 1–2 median and usually 5 (4 in *E. devonica*-type) pairs of narrow, pointy lateral teeth. Mandible with short apical tooth and 3–4 inner teeth; mola (inner margin of mandible) with up to 5 short spines. Premandible

broad with a single apical tooth. Antenna usually with 5 segments (occasionally with 4).

**Remarks:** The most characteristic feature distinguishing *Eukiefferiella* from other genera is the striped mentum and spines on the inner margin of mandible. Three morphotypes were distinguished according to Brooks et al. (2007) and Andersen et al. (2013a, b):

*Eukiefferiella claripennis*-type has mentum distinctly striated with bifid median tooth (separated with narrow notch), 5 lateral teeth (Fig. 17a).

*Eukiefferiella devonica*-type. Mentum with single broad median tooth and 4 lateral teeth; median tooth 2–3 times wider than 1st lateral. Mentum uniformly dark, strongly pigmented, striation not visible (Fig. 17b).

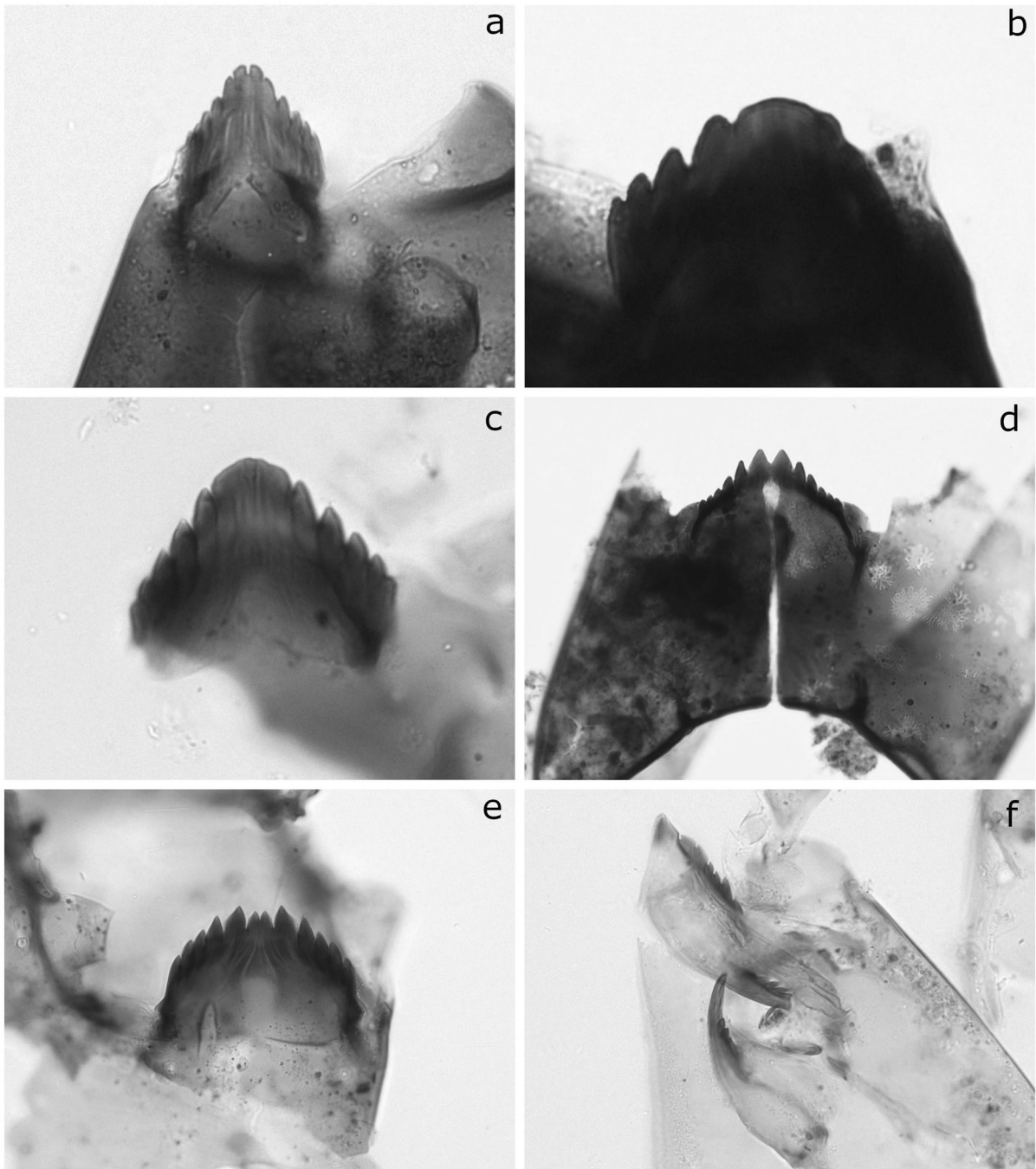
*Eukiefferiella gracei*-type. Mentum distinctly striped with single broad median tooth and 5 lateral teeth (Fig. 17c). This type is very similar to *E. fittkai*-type sensu Brooks et al. (2007) and also to *E. gracei* group sensu Andersen et al. (2013a, b). *E. fittkai* is a species with Palaearctic distribution (Spies and Sæther 2013) considered extremely oligo-stenothermal restricted to high altitude streams (Bitušík 2000), thus we prefer to name this type *E. gracei*-type (and distinguish it from a morphologically similar but ecologically most likely different *E. fittkai*-type).

All three morphotypes occurred in the high elevation lake Magdalena, Guatemala; *E. fittkai*-type was additionally recorded in the littoral samples of lake Yojoa, Honduras, situated in elevation > 600 m a.s.l.

*Heterotrissocladius* Spärck (Fig. 17d)

**Morphology:** Mentum usually with 2 median teeth (single only in extreme cold-stenothermic *H. maeeri*-type) and 5 pairs of lateral teeth; median teeth may be laterally notched (i.e. with accessory teeth). Ventromental plate distinct, extended beyond margin of flattened mentum. Mandible with a long, slender apical tooth and 3–4 inner teeth. Premandible with a single tooth. Antenna 7-segmented; 3rd segment much smaller than 4th; segment 7 hair-like, hardly visible. In some morphotypes (*H. marcidus*-type), submentum is darker than the rest of the head.

**Remarks:** From the similar genera with 2 median teeth and 5 pairs of lateral teeth (e.g. *Psectrocladius*), *Heterotrissocladius* can be distinguished by the strong bulbous ventromental plates extending beyond the



**Fig. 17** Subfossil remains of Orthoclaadiinae larvae from lakes of northern Central America and the Yucatan Peninsula. a–*Eukiefferiella claripennis*-type; b–*Eukiefferiella devonica*-type;

c–*Eukiefferiella gracei*-type; d–*Heterotrissocladus marcidus*-type; e–*Metriocnemus eurynotus*-type; f–*Nanocladus rectinervis*-type (note the extremely long ventromental plates)

lateral margin of the mentum and missing beard. In addition, the darker submentum, typical for *H. marcidus*-type, is also unique.

One morphotype was recorded in the cool, high elevation lake Magdalena, Guatemala. *Heterotrissocladus marcidus*-type is the first record from Central

America (Hamerlík and Silva 2018) and the second for the Neotropical region (Turcotte and Harper 1982). *Heterotrissocladus marcidus*-type is known to be the least thermally restricted morphotype of this cold-stenothermal genus associated with cold, nutrient-poor lakes (Sæther 1975).

*Metriocnemus* van der Wulp (Fig. 17e)

**Morphology:** Head capsule usually dark. Mentum with 1–2 median teeth (one species with 4) and 5–6 lateral teeth; generally, median teeth lower than first pairs of laterals. Mandible with short apical tooth and 4 (occasionally 5) inner teeth. Premandible with 2–4 apical teeth. Antenna 5-segmented, variable in size from normally developed to reduced.

**Remarks:** The double median tooth that is smaller than 1<sup>st</sup> lateral should be characteristic enough to separate the genus. The morphotype recorded, *Metriocnemus eurynotus*-type (Andersen et al. 2013a, b), has one pair of median teeth slightly smaller than 1st laterals, lateral teeth diminishing in size gradually; antenna 2 × as long as broad.

The morphotype was found in low elevation lake Magdalena, Guatemala.

*Nanocladius* Kieffer (Fig. 17f)

**Morphology:** Distinctive mentum with wide median area bearing 2 nipple-like median projections and 6 (occasionally 3 or 5 pairs) lateral teeth that are often very indistinct and may be fused. Exceptionally large ventromental plates extend beyond the lateral margin of the mentum, beard absent. Mandible with long slender apical tooth and 3 inner teeth. Premandible with simple or 3–5 very short apical teeth. Antenna 5-segmented; segment 5 hair-like.

**Remarks:** The characteristic shape of mentum with long ventromental plates extending well beyond the lateral margin of the mentum without beard will distinguish the genus from other orthoclads.

The recorded morphotype, *Nanocladius rectinervis*-type (following Brooks et al. 2007; Andersen et al. 2013a, b), was rare, only found in the littoral sample of lake Yojoa, Honduras. Even though the genus is generally characteristic for nutrient-rich waterbodies, larvae require relatively high oxygen content (Moller Pillot 2013). *Nanocladius rectinervis*-type is known to be thermophilic and linked to the

occurrence of macrophytes in the Palearctic (Brooks et al. 2007).

*Parakiefferiella* Thienemann (Fig. 18a)

**Morphology:** Mentum with 1 broad median tooth and 6 laterals. Ventromental plates characteristic, strongly developed, broad and protruding beyond the mentum laterally, rounded at apex. Mandible with a long slender apical tooth and 3 inner teeth. Premandible with a single or weakly bifid apical tooth. Antenna 6-segmented, but the last segment is hardly visible, vestigial.

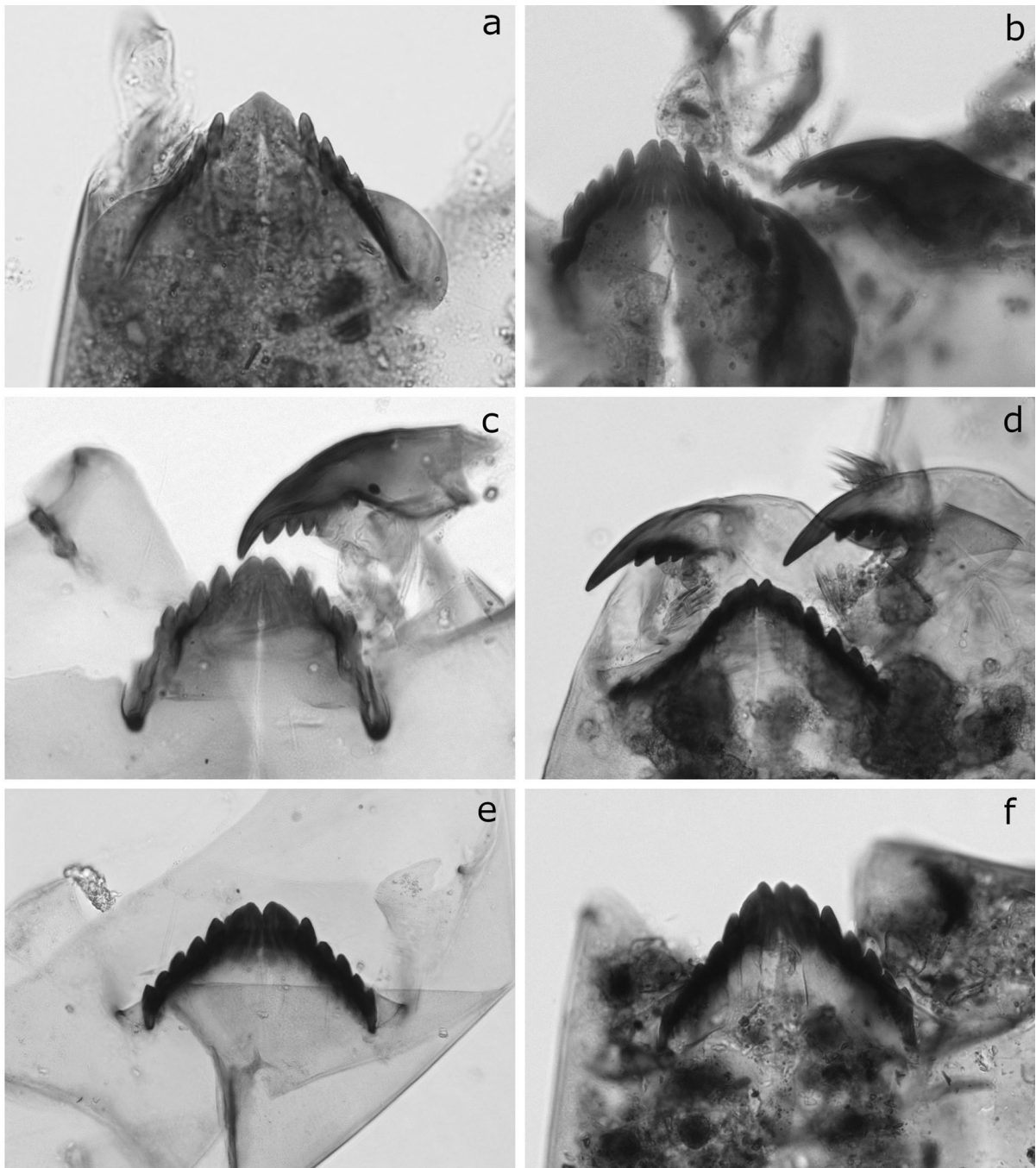
**Remarks:** Head capsules from Central American lakes resemble *Parakiefferiella bathophila*-type (Brooks et al. 2007 following Hofmann 1971), which has broad median and reduced 1st pair of lateral tooth, median and 1st laterals are pale, 2nd to 6th laterals dark. Worn down specimens of *P. bathophila*-type may have the median tooth rounded apically without an obvious separation of 1st lateral teeth. Our specimen, however, does not seem to be worn and in addition, *P. bathophila* does not occur in the Neotropics, thus we decided not to name our Central American type according to it.

The morphotype was found only in the cool, high elevation lake Magdalena, Guatemala.

*Paralimnophyes* Brundin / *Limnophyes* Eaton (Fig. 18b)

**Morphology:** Mentum with paired median teeth slightly higher than the 1st pair of the 5 lateral teeth that are decreasing in size gradually; mental teeth darkly pigmented, mentum frequently with pale stripes in the median region; a characteristic dark pigmented lobe projecting below the outermost lateral tooth. Mandible with short apical tooth and 3 (*Limnophyes*) or 4 (*Paralimnophyes*) inner teeth. Premandible with bifid apical tooth and 2 blunt inner teeth. Antenna relatively short (about ½ of length of mandible), with 5 segments; 4th segment longer than 3rd.

**Remarks:** The only way to distinguish *Paralimnophyes* from *Limnophyes* is the number of inner mandibular teeth (4 and 3, respectively). Subfossils without mandible are indistinguishable. Even though the records from Central American lakes had 4 inner teeth (when mandible was present) indicating



**Fig. 18** Subfossil remains of Orthoclaadiinae larvae from lakes of northern Central America and the Yucatan Peninsula. a–*Parakiefferiella* sp.; b–*Paralimnophyes/Limnophyes* (the 4 inner mandibular teeth indicate *Paralimnophyes*, but in

*Paralimnophyes*, the remains lacking mandibles could belong to both genera. *Paralimnophyes* has not been recorded from Central America, the closest record is

specimens lacking mandibles the two genera cannot be distinguished); c–*Parametriocnemus/Paraphaenocladus*; d–*Psectrocladius psilopterus*-type; e–*Psectrocladius sordidellus*-type; f–*Psectrocladius*, deformity (3 median mental teeth)

from Mexico (Alcocer et al. 1993). On the other hand, *Paralimnophyes* also closely resembles *Compterosmittia* (shape of mentum, 4 inner mandibular teeth)



and it is also indistinguishable from this genus in the subfossil material. Even though there are records of *Comptosmittia* from the Neotropics, due to the specific life-strategy of its larvae associated with pitcher plants, it is not likely to be present in lake sediments.

The morphotype was predominantly collected in high elevation lakes, such as Magdalena in Guatemala, Yojoa in Honduras and Laguna Verde in El Salvador, but also occurred in the low elevation lake El Gofete, Guatemala. Larval stages of most *Limnophyes* species are terrestrial or semiterrestrial with only few truly aquatic ones. Larval *Paralimnophyes* live in small lowland waterbodies and bogs at the water edge and among vegetation (Moller Pillot 2013).

*Parametriocnemus* Goetghebuer/  
*Paraphaenocladus* Thienemann (Fig. 18c)

**Morphology:** Mentum with 1–2 median teeth and 5 pairs of lateral teeth, 4th lateral tooth distinctly larger than 3rd and 5th laterals. Ventromental plate distinct, well developed, forming a lobe extending beyond outer mentum. Mandible with short apical tooth and 3 inner teeth. Premandible with 2–6 teeth (however, always 3 in *Paraphaenocladus*). Antenna 5-segmented.

**Remarks:** Without body, larval *Parametriocnemus* virtually cannot be distinguished from *Paraphaenocladus*. *Parametriocnemus* may be also confused with *Limnophyes*, which is, however, distinct by a pair of darkly pigmented lobe below outermost lateral tooth, subequal lateral teeth and weakly developed ventromental plates (Fig. 18b).

Recorded in cool, high elevation lakes Chicabal and Magdalena, Guatemala, as well as in lake Yojoa, Honduras. *Parametriocnemus* is primarily rheophilous, while larval *Paraphaenocladus* are predominantly terrestrial and semiterrestrial (Andersen et al. 2013b).

*Psectrocladius* Kieffer (Fig. 18d–f)

**Morphology:** Mentum with 1–2 median teeth of various shape and size, and 5 subequal laterals; if there is a single median tooth, then with low median or lateral projections, with triangular median point, trifold, or with pair of nipple-like median projections. Ventromental plate of characteristic triangular shape,

extending beyond outer tooth of mentum; short beard is present. Mandible with long apical tooth and 3 inner teeth. Premandible with single apical tooth.

**Remarks:** Two morphotypes were distinguished, both with bifid median tooth.

*Psectrocladius psilopterus*-type (Fig. 18d) resembles *P. sordidellus*-type in shape of mentum, but it has much broader median teeth (described by Cranston et al. 1983, as “single broad median tooth with median nipple-shaped projections”). However, in the subfossil material there is often a great amount of intermediate specimens, thus the two morphotypes are usually grouped together.

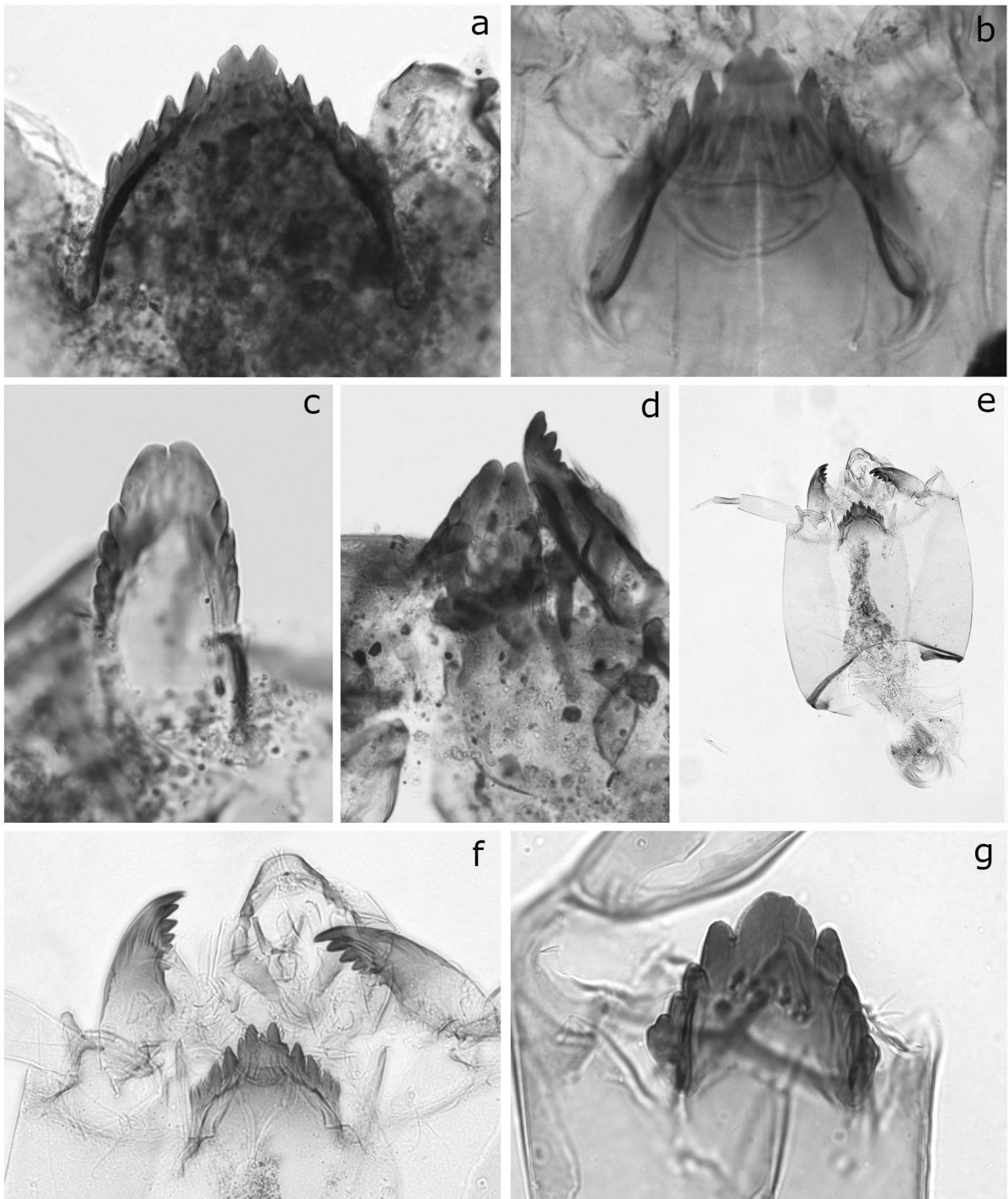
*Psectrocladius sordidellus*-type. Median teeth with a short median projection, lateral teeth subequal, pointy. Ventromental plates characteristically triangular, bearing short sparse beard (Fig. 18e). Specimens with buccal deformities seem to have trifid median tooth (Fig. 18f).

Together with *Cricotopus*, *Psectrocladius* is the most commonly found orthoclad in Central American lakes. Remains were characteristic for cooler high elevation lakes (above 1600 m a.s.l.), such as Chicabal, Magdalena (Guatemala), Laguna Verde (El Salvador), Chiligattoro and Madre Vieja (Honduras) but were also recorded in a big, low elevation lake Peten Itza. *Psectrocladius* is a large genus, larvae are limnionts, occupying all types of stagnant waters.

*Rheocricotopus* Thienemann and Harnisch  
(Fig. 19a, b)

**Morphology:** Mentum with paired median teeth and 5 lateral teeth; in some species/morphotypes there may be a minute accessory tooth between median and 1st lateral tooth. Ventromental plate broad, extending beyond the margin of outer mental tooth, apically truncate; beard long and dense. Mandible with short apical tooth and 3 inner teeth. Premandible with 1 apical tooth. Antenna 5-segmented.

**Remarks:** The strongly developed, bearded ventromental plates in combination with bifid mentum make *Rheocricotopus* unlikely to confuse with other Orthoclaadiinae. Morphotypes without accessory tooth may superficially resemble *Psectrocladius sordidellus*-type, which has smaller ventromental plates of distinctly triangular shape and only few short setae in the beard.



**Fig. 19** Subfossil remains of Orthoclaadiinae larvae from lakes of northern Central America and the Yucatan Peninsula. a–*Rheocricotopus fuscipes*-type; b–*Rheocricotopus effusus*-type; c,d–*Synorthoclaadius*; worn mentum c, normal mentum and

mandible d; e,f–*Thienemanniella* sp.: head capsule with antenna (e, note the ratio of the length of antenna to head), detail showing mentum and mandibles f; g–Orthoclaadiinae type A

Two morphotypes were distinguished (following Schmid 1993 in Brooks et al. 2007)

*Rheocricotopus fuscipes*-type has a small accessory tooth between the median and 1st lateral teeth (Fig. 19a). This morphotype is very similar to *R. chalybeatus*-type, listed in Brooks et al. (2007), but not present in the Central American material. The two types can be distinguished using the placement of seta submenti which is anterior to apex of ventromental plates in *R. fuscipes*-type while posterior to it in *R. chalybeatus*-type (Brooks et al. 2007).

*Rheocricotopus effusus*-type lacks accessory tooth next to the median tooth (Fig. 19b)

Both morphotypes occurred only in the cool, high elevation lake Magdalena, Guatemala. Larvae of the genus live in running waters but occasionally also in the littoral of cool, well-oxygenated lakes.

*Synorthocladus* Thienemann (Fig. 19c, d)

**Morphology:** Mentum strongly arched, triangular, with 2 long median teeth and 4 pairs of lateral teeth. Ventromental plate elongate; beard long, with branches radiating from a common area, this character is, however, frequently missing in subfossils. Mandible with short apical tooth and 3 inner teeth. Premandible with 1 apical tooth. Antenna 4-segmented; segment 2 usually apically broadened; segment 3 may be subdivided to 2 parts and antenna may appear 5-segmented.

**Remarks:** Larval *Synorthocladus* resembles *Parorthocladus*, which has 3 median teeth, while only 2 in *Synorthocladus*; moreover, *Parorthocladus* has not been recorded in the Neotropical region.

Remains were abundant in the cool, high elevation lake Magdalena, Guatemala, which was the only site where the morphotype occurred.

*Thienemanniella* Kieffer (Fig. 19e, f)

**Morphology:** Mentum with 2–3 median teeth and 5 pairs of lateral teeth. Mandible with apical tooth subequal to first of 4 inner teeth. Premandible with 1 apical tooth and distinct. Antenna at least  $\frac{1}{2}$  but no more than  $\frac{3}{4}$  length of head, with 5 segments; segment 3 unusually long; segments 4 and 5 small. Segment 3 is frequently darkened.

**Remarks:** *Thienemanniella* is similar to *Corynoneura* and *Onconeura* and can be distinguished from

them by the number of antennal segments (4 in *Corynoneura*) and the proportion of antenna to head: as long or longer than head in *Corynoneura*; about  $\frac{1}{3}$  in *Onconeura* and from half to  $\frac{3}{4}$  lengths of head in *Thienemanniella*. The morphotype found in the Central American lakes has a very long 3rd antennal segment, as long as the brown 2nd antennal segment (Fig. 19e), and the central median tooth in the mentum is shorter than  $\frac{1}{3}$  of the outer median tooth (Fig. 19f). It resembles *T. sp. B* (sensu Epler 2001), which may be a variant of *T. taurocapita* (Epler 2001).

Very rare morphotype, a single head capsule was found in the deep lake Ipala, Guatemala, situated at  $\sim 1500$  m a.s.l., and with slightly alkaline water (pH 8.01).

Orthoclaadiinae type A (Fig. 19g)

**Morphology:** Mentum of distinctive shape: with single domed median tooth and 4 pairs of lateral teeth, outermost lateral tooth medially notched. Ventromental plate small, beard absent. Antenna, mandible and premandible unknown.

**Remarks:** This morphotype resembles semi-terrestrial genera, such as *Mesosmittia* and *Bryophaenocladus*. Both are common in the Neotropics and are represented by multiple species (Spies et al. 2009).

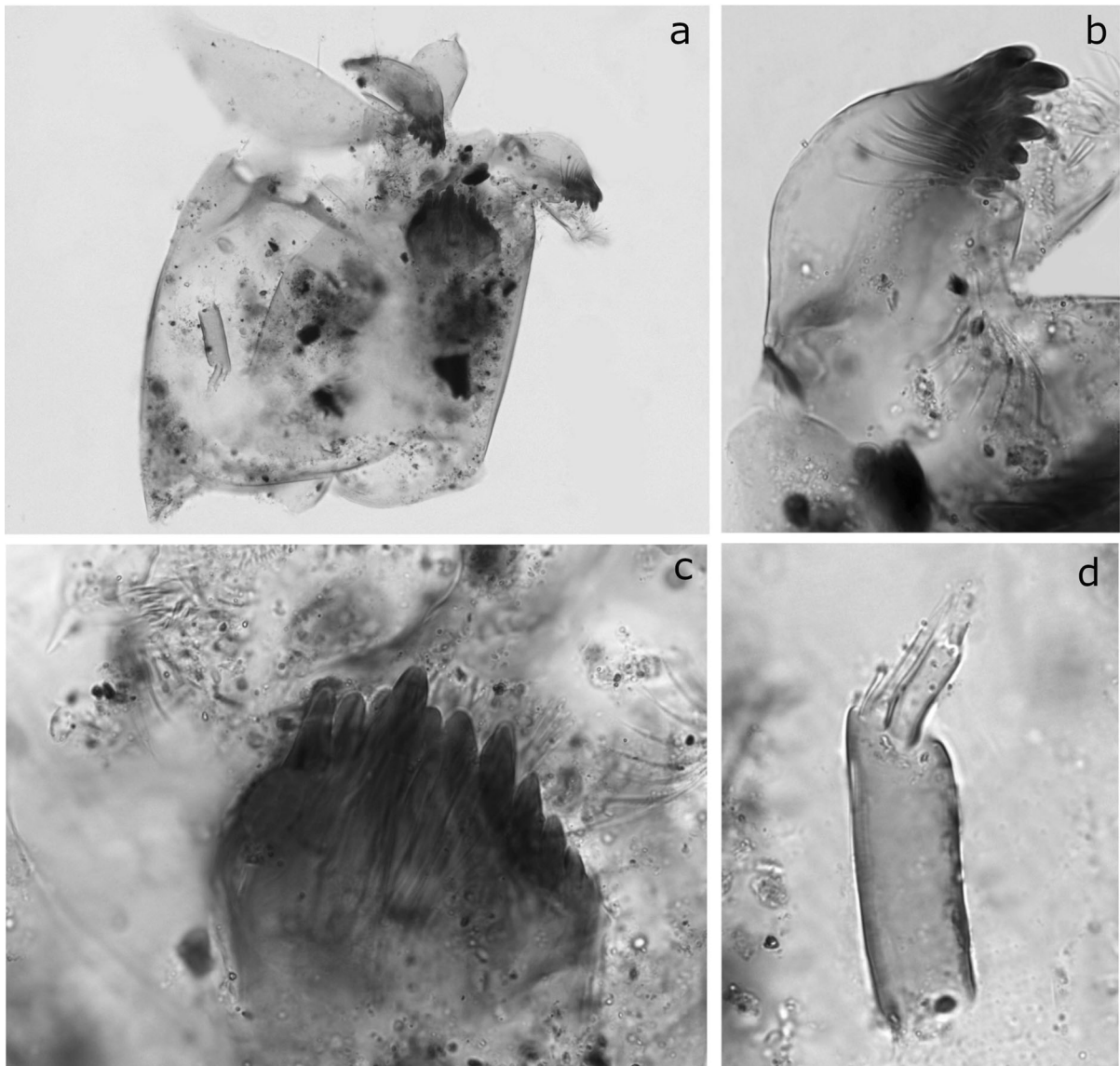
The only larval remain was found in the deep (47 m) lake Apastepeque, El Salvador, situated at  $\sim 500$  m a.s.l., with pH 8.57.

Subfamily Podonominae

Larval Podonominae are characteristic by distinctive labral sensillae, absence of premandibles and presence of weak ventromental plates. The mentum is also typical and consists of a single median tooth and 7–15 pairs of lateral teeth. Outer margin of mandible is strongly bent in the middle; 1 large apical, 1 small outer subapical and 4–9 inner teeth are present.

*Parochlus* Enderlein (Fig. 20a–d)

**Morphology:** Head capsule small to medium size, light brown. Mentum with 1 median tooth and 7 lateral teeth, the first two lateral teeth are shorter than the 3rd one; outer lateral teeth gradually diminishing in size. Mandibles with 5 teeth on the inner margin, (apical



**Fig. 20** Subfossil remains of larval Podonominae from lakes of Central America and the Yucatan Peninsula. a–d—*Parochlus* sp.: head capsule a, mandible b, mentum c, antenna d

and 2nd inner tooth are the largest, while the 1st one is minute) and 1 dorsal tooth. Premandible absent.

**Remarks:** The shape of mentum and mandible of *Parochlus* is unique and distinguish the genus from other chironomids.

Only two head capsules were found, both in the cool, high elevation lake Magdalena, Guatemala (~ 2800 m a.s.l.), which is in accordance with the ecology of the genus. Larvae inhabit various types of high elevation streams and springs; some species live

among mosses in cold small waterbodies located in high elevations (Brundin 1983).

#### Subfamily Tanypodinae

The typically predatory lifestyle in Tanypodinae is reflected in the larval mouth apparatus, which diverges from other Chironomidae in having a strong development of premental structures such as ligula and paraligulae (Cranston 1995). Moreover, the group is

easily recognisable by its retractile antennae, a feature that is unique in Chironomidae (Fig. 2). When it comes to subfossil material, however, most of the important diagnostic structures could be missing, which can hinder even generic identification. Therefore, the pattern of cephalic setation and sensory pores may be useful as distinctive characters for identification of the subfossil material. Larval cephalic setae in Tanypodinae and their importance in generic determinations have been studied by Kowalyk (1985), with subsequent corrections of Rieradevall and Brooks (2001), Brooks et al. (2007), and Cranston and Epler (2013). Figure 2 shows basic diagnostic characters of larval Tanypodinae.

*Ablabesmyia* Johannsen (Fig. 21a–c)

**Morphology:** Head capsule long, narrow, cephalic index (ratio of width / lengths of head) 0.60–0.65, pale yellow–brown with darker occipital margin with or without thorn-like projections on the ventral side (Fig. 21a). Maxillary palp basally subdivided in 2–6 segments (in our study 3 segments). Ligula with 5 teeth. Paraligulae bifid. Pecten hypopharyngis unequal-sized with 12–20 teeth (in 4th instar). Dorsomental teeth absent. Mandible with long apical tooth (3 × of the basal width), apical half dark brown to black; inner tooth large, blunt, mola (inner margin of mandible) expanded to large pointed tooth (in older literature called basal tooth, Wiederholm 1983).

**Remarks:** Larvae can be easily distinguished from other tanypodids by maxillary palp subdivided into 2–6 segments (note that *Paramerina*, currently a subgenus of *Zavrelimyia*, has also 2-segmented basal palp), however this trait is recurrent absent in the subfossil material. The two morphotypes identified in our study have the subdivision of basal segment of the maxillary palp into 3 segments (typical for the subgenus *Ablabesmyia*) and can be distinguished based on the shape of ligula.

*Ablabesmyia janta*-type (Fig. 21a, b) has apices of ligula teeth even or, if central tooth is smaller, inner teeth are subequal to or slightly exceed outer teeth (Epler 2001).

*Ablabesmyia monilis*-type (Fig. 21c) has a ligula with teeth increasing in size from the central tooth to outer teeth, so apices of ligula teeth form a clearly concave arc.

*Ablabesmyia* is one of the most species-rich Tanypodinae genera (Silva and Ekrem 2016) and it was one of the most common genera in the subfossil material, especially in lowland lakes of all studied countries.

*Clinotanypus* Kieffer (Fig. 21d)

**Morphology:** Head capsule long, conical; cephalic index about 0.7. Ligula with 5–7 teeth, tooth row deeply concave with very large outer teeth. Paraligulae simple with 4–5 short lateral teeth. Pecten hypopharyngis very long with a dense row of 20–35 teeth. Dorsomental teeth consist of 12–20 spinules in simple or laterally double row.

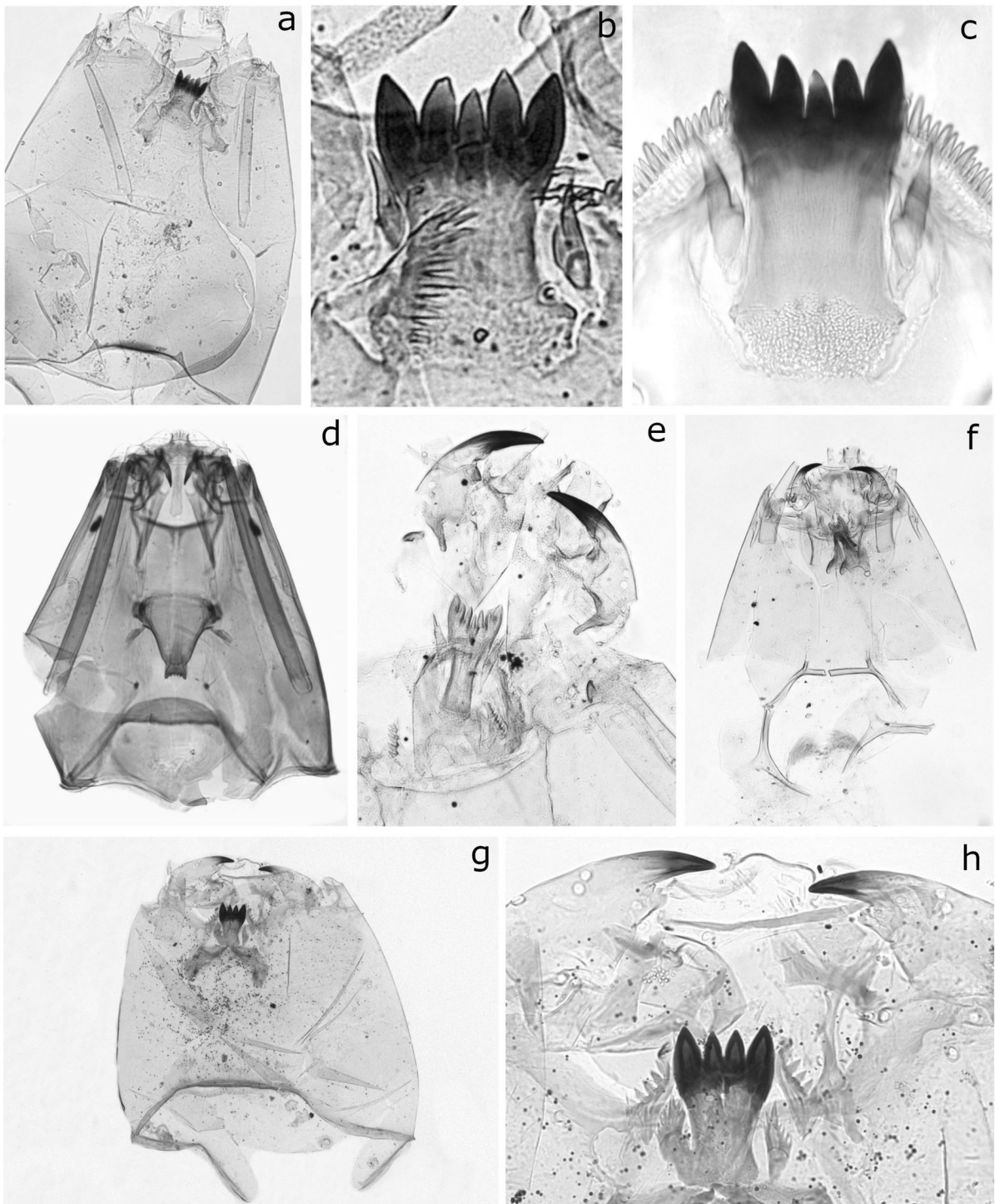
**Remarks:** Larvae of the closely related genera *Clinotanypus* and *Coelotanypus* belong to the tribe Clinotanypodini and can be distinguished from other tanypodids by dorsomental teeth arranged in longitudinal rows on the M appendage and ligula with 6–7 teeth (Silva and Ekrem 2016). *Clinotanypus* can be separated from *Coelotanypus* by the hooked mandible with a large inner tooth in contrast to the gently curved mandible with a broad, bluntly-rounded lamella of *Coelotanypus*.

Only one head capsule belonging to *Clinotanypus* was found in our material, in the shallow, low elevation lake Comandador, Guatemala.

*Coelotanypus* Kieffer (Fig. 21e, f)

**Morphology:** Head capsule prolonged (Fig. 21e); cephalic index about 0.7. Ligula with 7 teeth, tooth row concave, outer tooth larger than inner ones, apex of outermost inner tooth strongly curved outwards, pressed to outer tooth. Paraligulae strong and long with 2–3 spines on each side. Pecten hypopharyngis with a narrow row of 18–28 teeth. Dorsomentum with coarse granulation extending laterally over a loose row of 5–10 teeth.

**Remarks:** As mentioned above, *Coelotanypus* is closely related to *Clinotanypus* and can be separated from it based on the gently curved mandible with a broad, bluntly-rounded lamella (in *Coelotanypus*) in contrast to the strongly hooked mandible with a large inner tooth in *Clinotanypus* (Fig. 21f). Only one morphotype was recognized in the Central American material, and due to the 5 dorsomental teeth and similar ligula it was named as *concinus*-type



**Fig. 21** Subfossil remains of larval Tanypodinae from lakes of Central America and the Yucatan Peninsula. a,b–*Ablabesmyia janta*-type: head capsule (a, note the thorns on the post-occipital margin), ligula b; c–*Ablabesmyia monilis*-type; d–*Clinotanypus*

sp.: head capsule (photo from Bitušik and Hamerlík 2014); e,f–*Coelotanypus* sp.: detail of head capsule with ligula and mandibles e, head capsule f; g,h–*Djalmbatista* sp.: head capsule g, detail of labrum h

following Roback (1976). For more details on the taxonomy of Clinotanypodini see Roback (1976).

*Coelotanypus concinnus*-type was relatively abundant in the Central American subfossil material and was frequently recorded in all studied countries, usually in ponds, lakes and cenotes situated in lower elevations (up to 1000 m a.s.l.).

*Djalmabatista* Fittkau (Fig. 21g, h)

**Morphology:** Head capsule and occipital margin pale, rounded, cephalic index 0.85. Ligula with 4–5 teeth; in species with 5 teeth the median tooth is smaller than inner teeth. Apical half of teeth dark. Pecten hypopharyngis with 10–12 teeth. Paraligula short, multi-branched, very 3-dimensional. Dorsomentum with 7–8 teeth on each side. Mandible broadened basally, strongly curved apically; apical tooth 2 × as long as basal width; mola with creases, protruding as a large double tooth.

**Remarks:** *Djalmabatista* and *Procladius* Skuse belong to the tribe Procladiini, which can be distinguished by the round head capsule (Fig. 21g), well-developed dorsomenta tooth plates, mandible with large molar projection, ligula darkened over the distal half and pectinate paraligulae (Fig. 21h) (Silva and Ekrem 2016). These two genera can be separated from each other by the color of occipital margin (pale in *Djalmabatista*, dark in *Procladius*), mandible shape and the length of antennal blade (very long antennal blade exceeding flagellum in *Djalmabatista*, shorter than flagellum in *Procladius*). However, antennal blade is hyaline and usually missing in subfossil material. In our study, antennal blade was inconspicuous and the occipital margin varied from pale to dark. Even though some specimens had mandibles with large double teeth, we were not able to distinguish the two genera with certainty.

The morphotype with the ligula bearing 4 teeth was very rare, recorded only in a cenote Yalahau, Mexico (elevation 2 m a.s.l., pH 9.53, conductivity 1930  $\mu\text{S cm}^{-1}$ , depth 12 m).

*Djalmabatista* Fittkau /*Procladius* Skuse (Fig. 22a–c)

**Morphology:** Large, rounded head capsule, cephalic index 0.80–0.85. Mandible slender, uniformly curved with a dark apical tooth 3 × as long as basal width;

mola expanded to large broad, protruding tooth with a rounded apex. Ligula with 5 teeth, median tooth is the shortest, progressively growing towards the outer teeth; paraligulae multi-branched, pecten hypopharyngis with 10–15 teeth, second row of small teeth can be present. (Fig. 22a).

**Remarks:** *Procladius* can be separated from *Djalmabatista* by the dark occipital margin, mandible shape (Fig. 22b, c) and the length of antennal blade (which is shorter than flagellum in *Procladius* but significantly longer in *Djalmabatista*). In case that antenna is missing, *Djalmabatista* with 5-teeth ligula cannot be distinguished from *Procladius*. These some remains were common in lakes of all countries, covering virtually the whole surveyed gradient of altitude, depth (however, missing from the deepest lakes) and environmental variables.

*Fittkauimyia* Karunakaran (Fig. 22d, e)

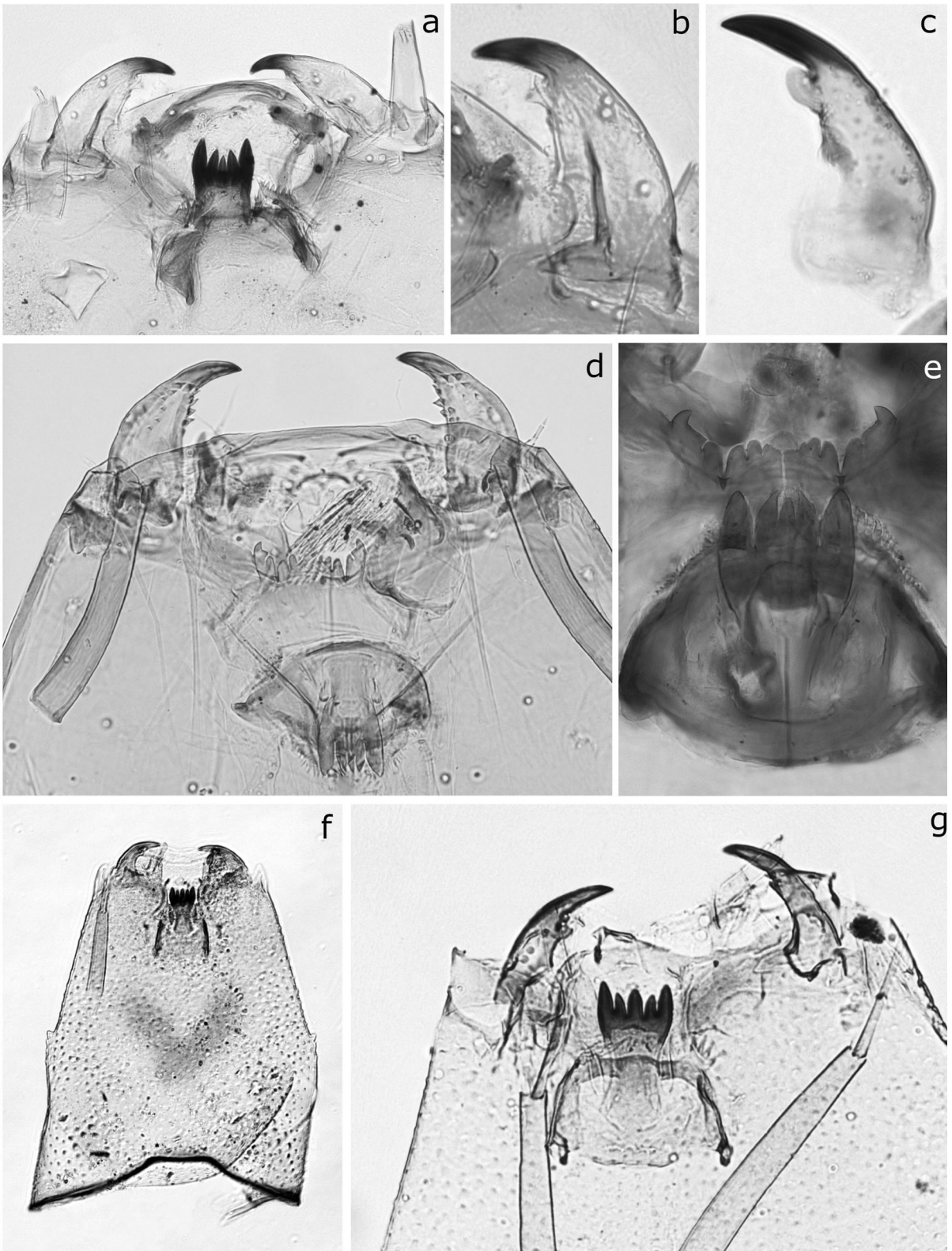
**Morphology:** Head capsule oval, medium-sized to large, cephalic index 0.64–0.75. Mandible with additional small dorsal and ventral teeth. Dorsomentum tripartite concave, continuous with lateral complex of structures, comprising an inwardly and an outwardly directed tooth. Ligula with curved inner lateral teeth.

**Remarks:** Genus *Fittkauimyia* belongs to the monotypic tribe Fittkauimyini and differ strongly from all other tanypods in the arrangement of the dorsomenta teeth and the shape of the mandible, ligula and dorsomentum (Silva and Ekrem 2016). Only one morphotype of *Fittkauimyia* was recorded in our study and was not assigned to any particular species/type.

Remains of the genus were only recorded in low elevation lakes (Las Pozas and Macancha in Guatemala) and cenotes (Tekom, Mucuyche and Sacalaca in Mexico) of various size and depth.

*Labrundinia* Fittkau (Figs. 22f, g, 23a–f)

**Morphology:** Head evenly coloured, sometimes with ventral maculation; surface may be smooth or covered with spinules, lateroventral and posteroventral spine groups present or absent (Silva et al. 2014). Ligula with 5 teeth, middle tooth usually longer than outer teeth; paraligulae bifid or multi-toothed; pecten hypopharyngis with 7 teeth of equal length (Silva et al. 2014).





◀ **Fig. 22** Subfossil remains of larval Tanypodinae from lakes of Central America and the Yucatan Peninsula. a–*Procladius/Djalmabatista* sp.: detail of labrum; b–*Procladius/Djalmabatista* sp.: mandible with *Djalmabatista*-like lobe on mola (double); c–*Procladius/Djalmabatista* sp.: mandible with *Procladius*-like lobe on mola (single rounded); d,e–*Fittkauimyia* sp.: head capsule d, ligula, dorsomental teeth and pecten hypopharyngis e; f,g– *Labrundinia* type Y: head capsule showing the Y-shape mark on the submentum f, detail of head capsule g

**Remarks:** Head capsules of *Labrundinia* and *Nilotanypus* are extremely similar in the shape of ligula and granulate basal area, but can be separated by a much smaller molar expansion in *Nilotanypus* than in *Labrundinia* (Figs. 22f, g, 23h). Moreover, most *Labrundinia* species possess a latero-ventral and/or caudoventral spine or group of spines. Species without spines are hardly to be distinguished from *Nilotanypus* subfossils.

Five types of *Labrundinia* were recorded in the surface sediments and they can be distinguished by the extent of the granulation of head capsule and features of the latero-ventral spines.

*Labrundinia* type Y has a head capsule fully granulated; in well chitinized specimens there is a distinct ventral darker Y-shaped area in the submental region (Fig. 22f, g). This type resembles *Labrundinia* sp. 12 described by Trivinho-Strixino (2014). Heads of the remaining four types are smooth, but differ in the shape of latero-ventral spines.

*Labrundinia paulae*-type (Fig. 23f) (sensu Silva et al. 2014) has one single, well developed spine on the lateral margin of the head capsule.

*Labrundinia virescens*-type has a group of several strong rounded latero-ventral spines of variable sizes, ligula with prominent median tooth, much longer than the lateral teeth (Fig. 23a, c).

*Labrundinia jasoni*-type has few weak latero-ventral spines (Fig. 23b, e) (Silva et al. 2014). This type was not present in surface sediments, occurring only in a short sediment core from lake Apastepeque.

Finally, *Labrundinia* type G can be recognized by its single small triangular lateroventral spine on the lateral margin of the head capsule (Fig. 23g).

*Labrundinia* is one of the most species-rich genus of the subfamily Tanypodinae. As can be seen from the foregoing, not only one feature will identify all

*Labrundinia* larvae. Therefore, larval *Labrundinia* should always be keyed with extra caution.

*Labrundinia* was the most common tanypod in Central American lakes. *Labrundinia* type Y and *L. virescens*-type were common in various waterbody types of all surveyed countries. *L. jasoni*-type was recorded only in lake Apastepeque, El Salvador; and *L. paulae*-type in lakes Apastepeque and Yojoa, Honduras, and Chan Laguna, Mexico.

*Nilotanypus* Kieffer (Fig. 23h)

**Morphology:** Head capsule narrow, yellow–brown; cephalic index about 0.45. Mandible weakly curved, apical ½ narrowed. Ligula with 5 teeth, twice as long as apical width. strongly narrowed in the middle. Area of muscle attachment occupying a triangular granulate region basally.

**Remarks:** In our study, *Nilotanypus* can be distinguished from the recognised *Labrundinia* types by its smooth head and lack of lateral spinose hump.

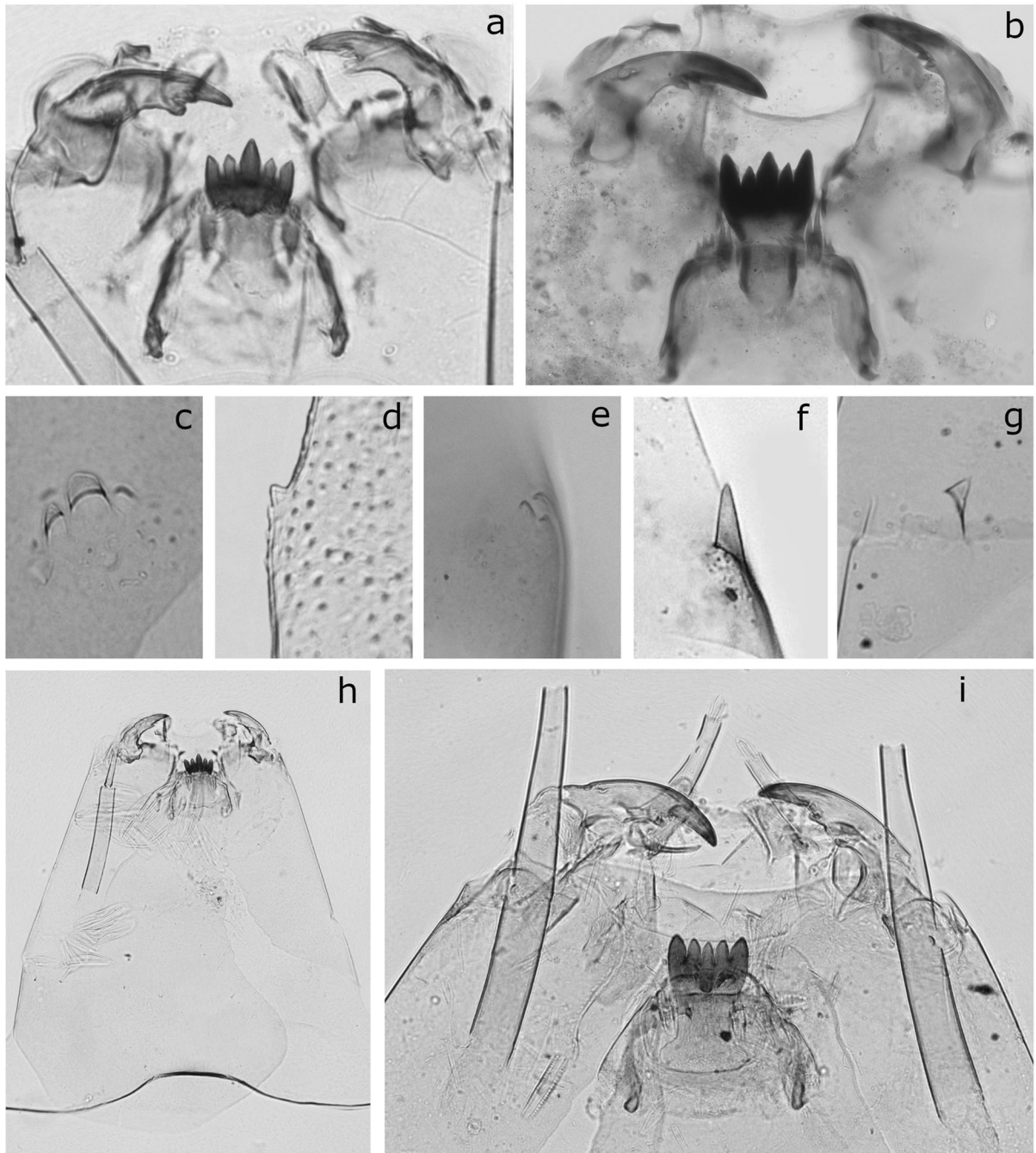
Larvae of *Nilotanypus* are rheobionts, favouring sandy substrates (Cranston and Epler 2013). Thus, subfossil head capsules are rare in lake sediments and most likely originate from the inlet. Herein, only one morphotype of *Nilotanypus* was found in the subfossil material of the deep, high elevation lake Atitlán, Guatemala.

*Larsia* Fittkau (Fig. 23i)

**Morphology:** Head capsule oval, narrow; cephalic index 0.6. Ligula with 5 teeth, tooth row concave to straight, middle section moderately narrowed; par-aligulae bifid; pecten hypopharyngis with about 17 subequal teeth; basal granulate area forms a narrow stripe. Mandible strongly curved, mola developed as a medium tooth, inner tooth well developed.

**Remarks:** Larval *Larsia* resemble *Natarsia*, in particular with regard to the appearance of ligula and the large molar tooth of the mandibula, however, *Larsia* has well developed inner mandibular tooth and *Natarsia* has a strongly sclerotized structure on both sides of the mentum.

Only one larval type of *Larsia* was identified in the material. This resembles the genus *Pentaneura* but can be distinguished from it by the broader ligula and concave tooth row.



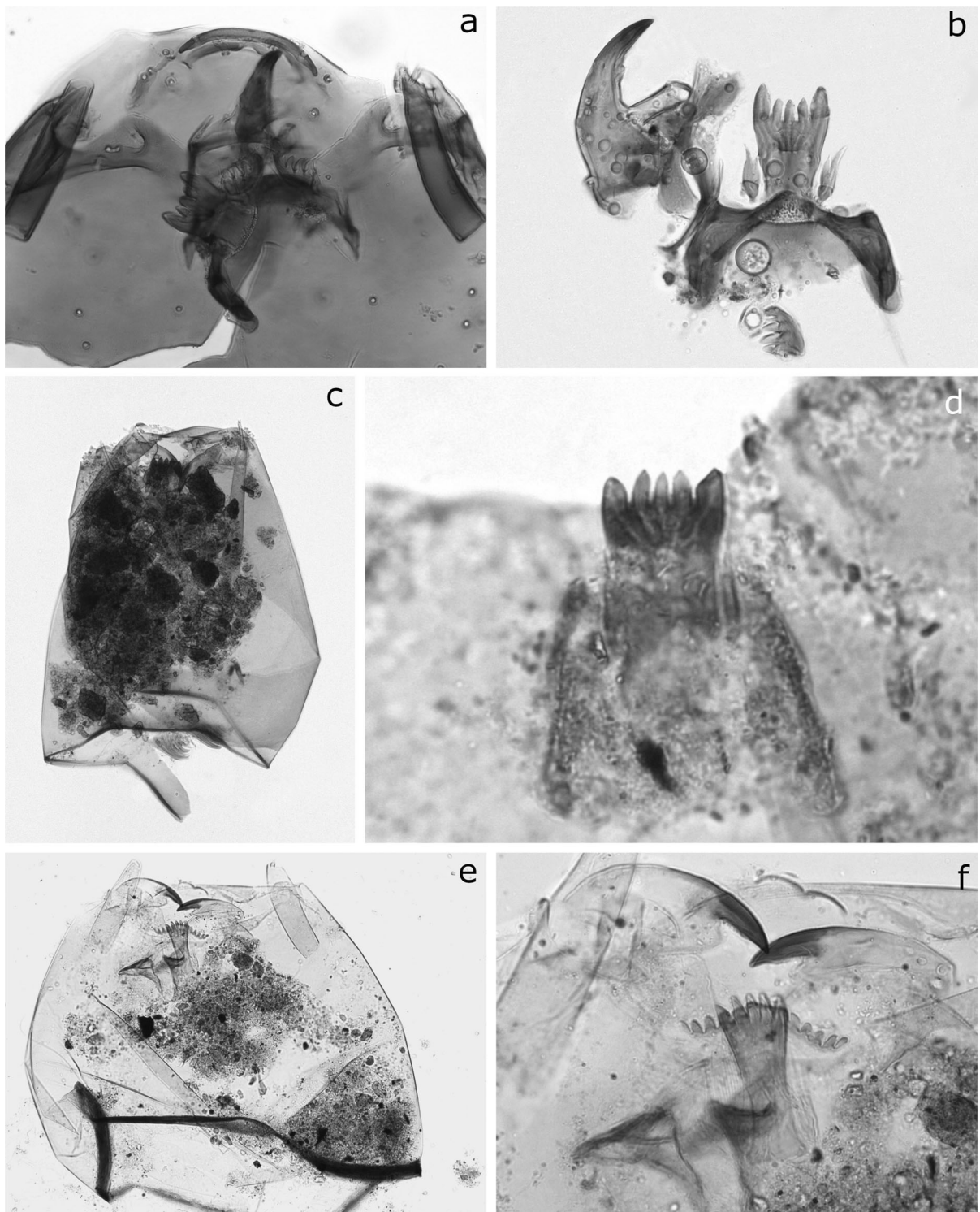
**Fig. 23** Subfossil remains of larval Tanypodinae from lakes of Central America and the Yucatan Peninsula. a–*Labrundinia virescens*-type; b–*Labrundinia jasoni*-type; c–g–dorsolateral

spurs of head capsules: *Labrundinia virescens*-type c, *Labrundinia* type Y d, *Labrundinia jasoni*-type e, *Labrundinia paulae*-type f, *Labrundinia* type G g; h–*Nilotanypus* sp.; i – *Larsia* sp

Rare morphotype, found in lakes of various elevation and depth, such as Jocotal, El Salvador; Yojoa and Madre Vieja, Honduras; Atescatempa, Guatemala; and Sabanita, Laguna Coba and Yalahau, Mexico.

Macropelopiini type A (Fig. 24a, b)

**Morphology:** Head capsule robust strongly pigmented, brown, cephalic index about 0.8. Ligula with 5 teeth,



**Fig. 24** Subfossil remains of larval Tanypodinae from lakes of Central America and the Yucatan Peninsula. a,b–Macropelopiini type A: detail of labrum with short antenna a, ligula,

paraligula, mandible, dorsosomental teeth b; c,d–*Pentaneura* sp.: head capsule c, ligula d; e,f–*Tanypus stellatus*-type: head capsule e, detail of labrum f

tooth row concave, middle and inner tooth subequal in size, outer tooth  $2 \times$  as long as middle tooth; inner tooth rather straight. Paraligula bifid, about half a length of ligula. Mentum with 4 (it could be 5, but 5th minute) dorsomental teeth on each side, inner tooth narrow pointy, middle and outer teeth broad and rounded. Mandible smoothly curved, apical tooth about  $2.5 \times$  longer than basal width, mola extending into apically-directed moderate point, small accessory tooth may be present, too. Antenna slightly longer than mandibula.

**Remarks:** Based on the appearance of the head capsule, this morphotype belongs to the Macropelopiini tribe. It resembles *Macropelopia*, but it has less dorsomental teeth (4–5 pairs). The specimen has very similar dorsomentum to *Apsectrotanypus* (bearing 5 teeth), but it does not have the vertical pale belt across the ventral part of the head, neither visible tentorial lines, which are characteristic features of *Apsectrotanypus*. Other options could be *Brundiniella* (but it has dorsomentum without the lobe extending to midline) or *Alotanypus* (but it has inner tooth of ligula is not pointing strongly outwards). Considering the aforementioned, the generic position of this morphotype remains unclear.

Very rare morphotype, found only in the shallow, low elevation lake Los Negritos (El Salvador) with low conductivity ( $40 \mu\text{S cm}^{-1}$ ).

*Pentaneura* Philippi (Fig. 24c, d)

**Morphology:** Head capsule narrow, elongate-oval; cephalic index 0.4–0.7 (Silva and Ferrington 2018). Mandible gradually curved and narrowed towards apex; inner tooth, large, apically directed, rounded, not projecting beyond margin of seta subdentalis (Silva and Ferrington 2018). Ligula with 5 teeth of almost equal size, tooth row straight or weakly concave; paraligula bifid, pecten hypopharyngis with 10–13 teeth, with several teeth of variable sizes and shapes.

**Remarks:** Only one *Pentaneura* morphotype was recorded in our study and was not assigned to any particular species/type.

Subfossil remains were rare, recorded in shallow lakes both in high elevations (lake Magdalena, Guatemala, lake Chiligatoro, Honduras) as well as situated in low elevation (Jucutama, Honduras).

*Tanypus* Meigen (Fig. 24e, f)

**Morphology:** Head capsule large, rounded, usually pale with dark occipital margin, cephalic index about 0.95. Mandible of unique shape, apical tooth about  $2 \times$  as its basal width, several small, subequal pointy accessory teeth present, mola bilobed apically. Ligula pale, slightly convex with 5 subequal teeth; paraligulae large and variable from bifid to multi-branched, pecten hypopharyngis strongly reduced. Dorsomental teeth present.

**Remarks:** One morphotype of *Tanypus* was recognized in the subfossil material examined and based on the shape of ligula, number of arms and shape of paraligulae was named as *Tanypus stellatus*-type. See Roback (1976) for more details on the morphology of *Tanypus stellatus*.

Remains of *T. stellatus*-type were recorded in shallow, low elevation ponds and lakes of El Salvador (Olomega, Metapan, El Espino, Los Negritos) and Guatemala (El Muchacho, Comandador), with relatively low conductivity ( $< 440 \mu\text{S cm}^{-1}$ ).

## Discussion

We describe and illustrated more than 100 chironomid morphotypes belonging to 4 subfamilies. More than half of the identified morphotypes belong to the subfamily Chironominae. Indeed, Chironominae is the largest chironomid subfamily in terms of described species in the Neotropics (Ashe et al. 1987). In the tribe Chironomini, *Goeldichironomus* was the most widespread and abundant genus, which is not surprising, since it is characteristic to the tropics and subtropics of Central and South America (Trivinho-Strixino and Strixino 2005). Larvae of this genus prefer littoral sandy substrate and floating and drifting vegetation of small standing waterbodies. The second most frequent genus was *Chironomus*, which is a large cosmopolitan genus comprising several hundred species. Numerous species of this taxon are very abundant in heavily polluted standing or running waters, whereas some species commonly colonize natural and artificial small waterbodies. Spies and Reiss (1996) catalogued 19 species from the Neotropical Region, however, this number represents outdated knowledge and significantly underestimates real diversity of *Chironomus* in the Neotropics, in view

of several new species described more recently (Correia and Trivinho-Strixino 2007; Correia et al. 2013; Trivinho-Strixino and Silva 2018). Three *Chironomus* morphotypes were distinguished, but there was a great variability in morphological features of the genus indicating considerably higher species richness. *Polypedilum* was also common with five recognized morphotypes. *Polypedilum* is one of the largest groups of the family containing about 440 described species (Sæther et al. 2010). Larvae occur virtually in all kinds of still and flowing waters; some species are associated with extreme habitats, such as bromeliad tanks (Epler et al. 2013) or small temporary rock pools in Africa (Hinton 1951).

The tribe Pseudochironomini was represented by two *Pseudochironomus* morphotypes and an unassociated morphotype. *Pseudochironomus* 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).

The tribe Tanytarsini was represented by a relatively low number of genera. The most common and diverse was *Tanytarsus*, with six distinct morphotypes. *Tanytarsus* is one of the most species-rich genera in the Neotropics, and immature stages show great ecological variability (Trivinho-Strixino et al. 2015).

The known faunistic (Ashe et al. 1987; Contreras-Ramos and Andersen 1999; Silva et al. 2015; Epler 2017; Watson and Heyn 1992) and paleolimnological studies in the region (Vinogradova and Riss 2007; Pérez et al. 2010, 2013; Wu et al. 2015) document the prevalence of Chironomini in Central American waterbodies with the dominance of Chironomini both in number of taxa and abundance. A slight deviation towards Orthocladiinae may occur in studies focusing on oligotrophic and lotic waterbodies (Epler 2017), but proportion of Chironomini on the taxonomic diversity is generally decreasing with elevation (Hamerlík et al. 2018a). Paleoecological studies also agree on the relatively low diversity of Tanytarsini, usually recording few genera, such as *Cladotanytarsus*, *Micropsectra*, *Paratanytarsus* and *Tanytarsus*, however, the number of morphotypes varies significantly according to the level of taxonomic resolution.

The richest environment for Orthocladiinae was the high elevation lake Magdalena, Guatemala, where as many as 18 morphotypes were documented. In addition, half of the recorded orthoclad taxa (13 morphotypes) were only recorded in lake Magdalena. With six taxa recorded, lake Yojoa, in Honduras, was the second most orthoclad-rich lake. In the remaining waterbodies, only one to three morphotypes were recorded. It is not surprising that lakes with the highest orthoclad diversity are located in high elevations (Magdalena, Chicabal, Atitlan, Ipala, Verde and Chiligattoro are situated between 1495 and 2863 m a.s.l., Yojoa at 639 m a.s.l.). The most common genera, *Cricotopus*, *Psectrocladius* and *Corynoneura*, were also present in lowland lakes in contrast to the majority of other orthoclads. *Cricotopus*, represented by six morphotypes, was the most species-rich genus recorded in all countries except for El Salvador. *Cricotopus* is one of the largest genera in the Orthocladiinae, comprising at least five subgenera, with worldwide distribution (Cranston et al. 1989). Larval *Cricotopus* inhabit an extremely wide range of waterbodies, from alpine and Arctic streams to eutrophic lakes and brackish estuaries (Hirvenoja 1973; Boesel 1983; Drayson et al. 2015). The genus *Psectrocladius* was represented by two morphotypes and sampled in every surveyed country. It is a large and ecologically diverse genus containing over 100 species worldwide, predominantly distributed in the Northern Hemisphere. Larvae of *Psectrocladius* inhabit exclusively lentic systems, predominantly feeding on periphyton in waterbodies ranging in size from small ponds to large lakes (Sæther and Langton 2011). Head capsules of *Corynoneura* occurred in lakes regardless of altitude, covering a broad altitudinal gradient. *Corynoneura* is a large genus with worldwide distribution. However, together with *Thienemanniella*, due to their small size it can be easily overlooked both in modern and subfossil material and hence real distribution and taxonomic richness of the genus is underestimated. The genus *Heterotrissocladius* was recorded for the first time in Central America (Hamerlík and Silva 2018a) from the high mountain lake Magdalena, Guatemala, located at 2863 m a.s.l. *Heterotrissocladius* is primarily a Holarctic genus with larvae occupying all kinds of standing waters from ponds to lakes as well as a broad variety of flowing waters Andersen et al. 2013a, b. Larvae of *H. marcidus*, which is probably the most

widespread species of the genus, are common inhabitants of alpine and subalpine lakes throughout Europe (Spies and Sæther 2013) and North America (Epler 2001).

In paleolimnological studies (Wu et al. 2017, 2019a,b; Pérez et al. 2010) and subfossil datasets (Vinogradova and Riss 2007; Pérez et al. 2013; Wu et al. 2015; Hamerlík et al. 2018b) from the region, Orthocladiinae represent a minor group limited to worldwide distributed genera such as *Psectrocladius*, *Cricotopus/Orthocladius*, *Limnophyes*, *Corynoneura/Thienemanniella* and *Eukiefferiella*. The situation is similar in faunistic studies dealing with modern material (Watson and Heyn 1992; Silva et al. 2015), however, Orthocladiinae may become the most species-rich group when surveys focus on high elevation areas (Hamerlík et al. 2018a) or lotic waterbodies (Epler 2017).

With five morphotypes, *Labrundinia* was the most abundant and species-rich genus in the Tanypodinae subfamily. The taxon is a large, predominantly Neotropical genus, 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 and Fonseca-Gessner 2009; Silva et al. 2011, 2014).

Previous studies from Central America are in accordance with our results when it comes to common genera, such as *Ablabesmyia*, *Coelotanypus*, *Labrundinia* and *Procladius*, however, they all bring records of genera not recorded in our survey. For instance, Silva et al. (2015) recorded *Monopelopia* and *Thienemannimyia* in Dominican Republic, Epler (2017) *Zavrelimyia (Paramerina)* and *Thienemannimyia* from Costa Rica, and Vinogradova and Riss (2007) reported *Natarsia* from the Yucatan Peninsula. The reasons for this discrepancy may be manifold. Some of the studies focused on lotic sites, i.e., springs, streams and rivers and thus recorded rheobiontic taxa that are not likely to occur in lakes and ponds. Indeed, Watson and Heyn (1992) combined sampling methods, such as kicking method and collecting pupal exuviae and adults, and identified as much as 15 Tanypodinae taxa, mostly in lotic waters of Costa Rica. In our study, we identified chironomid remains present in both surface-sediments and short cores. Likewise, using surface-sediment samples, Wu et al. (2015) identified eight Tanypodinae genera in 51 lakes in Costa Rica, while

Pérez et al. (2013) recorded 12 genera in 63 waterbodies located along a long geographical and ecological gradient from NW Yucatán Peninsula to southern Guatemala. Furthermore, in a sediment sequence taken from Petén Itza, Guatemala, Pérez et al. (2010) recorded seven genera. Three genera belonging to the tribe Macropelopiini (*Alotanypus*, *Apsectrotanypus* and *Macropelopia*) were common in the aforementioned paleo-studies, but they were not present in our survey. The reason for it can be that they were simply not present or were overlooked in our material or, more likely, these taxa were identified differently in our study, e.g. as Macropelopiini type A. All three morphotypes are very similar and can only be separated using the arrangement of dorsal and ventromental head pores that are sometimes barely detectable. Besides, as Spies et al. (2009) pointed out, Neotropical Macropelopiini is poorly known. Most Neotropical Macropelopiini species have been described from adult specimens only, and many do not match any recognized genus (Spies and Reiss 1996). Currently, two Macropelopiini genera can be recognized in Central America (Spies et al. 2009), but several undescribed species cannot be placed in existing genera.

Finally, the subfamily Podonominae was represented only by the genus *Parochlus*, recorded from Lake Magdalena in Guatemala. This genus is the most widespread and species-rich genus within Podonominae; immature stages live in cold springs and running waters, some occur among mosses in shallow tarns and other small waterbodies. The genus is very diverse in the southern temperate zone, from sub- and true Antarctic, and in Australia, New Zealand and South America. In Central America, the genus is limited to high elevation sites in Costa Rica, where unnamed species of the *P. araucanus* group was recorded (Watson and Heyn 1992; Epler 2017). Wu et al. (2019a) found *Parochlus* remains in a long sediment sequence covering the past ~ 8100 years taken from a high elevation lake in Costa Rica and its appearance is related to cold and low productivity conditions.

## Conclusions

This guide represents the first compilation of chironomid taxa from the Neotropics conveying mainly taxonomic, but also some ecological aspects of this

group of aquatic insects. Although this study is based only on characteristics of the larval head capsules, we believe this approach will help to improve the taxonomic and ecological knowledge of this group of insects, which is currently practically unknown in the region.

Even though there is an agreement between modern and subfossil fauna, there are still some inconsistencies in the taxonomic composition between paleo and modern specimens. Previous studies in the area highlight the need for regional illustrated guides and keys, so the results of paleo- and modern limnological studies can be compared and knowledge on the ecology can be finally linked to individual morphotypes. This applies even more for taxonomically poorly known areas, such as the Neotropical Region or its northern part, Central America.

We believe that our study includes most of the genera of the targeted area, and it can also be used for the northern Neotropics for both aquatic ecologists and paleolimnologists.

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