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ORIGINAL PAPER

Aquatic invertebrate mandibles and sclerotized remains in Quaternary lake sediments

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Abstract Subfossil remains of aquatic invertebrates found in lacustrine sediments are useful paleoenvironmental indicators. Strongly scleroticized chitinous body parts from the exoskeleton or exuviae from invertebrates are often the most resistant to degradation during syn- and post-depositional processes. Invertebrate mandibles and body parts that superficially resemble mandibles, such as claw-like appendages and pygopodia, are frequently found in sieved Quaternary lacustrine, palustrine, and deltaic sediments. Guides, catalogs and atlases have been published that are well suited for the identification of subfossil remains for several invertebrate groups, such as chironomids, cladocerans, and ostracods, among others. However, aquatic invertebrate remains of several ecologically important invertebrate groups continue to be underused in paleoenvironmental studies, in part, because there are few visual keys or other documentation sources (e.g. descriptions, catalogs or atlases) that increase awareness and facilitate identification. Here we present sets of digital photomicrographs of pre-identified aquatic invertebrate specimens collected from streams, lakes and ponds that have been chemically cleared to preserve structures that are observed in subfossil remains in sieved sediment samples, commonly the > 100 µm size fractions. In addition, we present examples of these structures from Quaternary lake-sediment samples and cite the dispersed literature that demonstrate that these remains are preserved and remain identifiable in the fossil record. We document mandibles from several taxonomic groups that include Crustacea: Amphipoda, Isopoda, Ostracoda, and Notostraca; and Insecta orders: Coleoptera, Diptera, Ephemeroptera, Hemiptera, Odonata, Lepidoptera, Megaloptera, Plecoptera, and Trichoptera. The compilation of microphotographs also includes pygopodia and claw appendages of Plecoptera and Trichoptera, with additional images of other common invertebrate mouthpart and head remains. We describe several types of fossilizing structures that are, to our knowledge, not previously described in the paleoecological literature (e.g. mandibles of amphipods or plecopterans) but also show that some structures are considerably more variable

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than expected based on available descriptions, such as the mandibles of Ephemeroptera or Trichoptera, and that these can potentially be separated into different morphotypes useful for identification of subfossil material. We also discuss the potential of analyzing and interpreting the additional remains together with the remains of more commonly analyzed invertebrate groups (e.g. Chironomidae) to contribute to paleoenvironmental interpretations, which will allow assessments of functional groups (e.g. predators, shredders, grazers) or habitat types (e.g. littoral, profundal or lotic environments) that aquatic invertebrate remains originate from.

Keywords Arthropoda · Chitin · Crustacea · Hexapoda · Holocene · Insecta · Macroremains · Subfossils

Introduction

Chitinous remains from a wide range of aquatic and semi-aquatic invertebrate taxa accumulate in the sediments of depositional environments, such as lacustrine and palustrine ecosystems (Frey 1964; Lévesque et al. 1988; Smol et al. 2001a). Mandibles, larval head capsules, exoskeletal fragments, and many other remains of invertebrates are found when Quaternary sediments are sieved (Vandekerkhove et al. 2004; Rumes et al. 2005; Alekseev et al. 2007; Szeroczyñska and Sarmaja-Korjonen 2007; Morris et al. 2015). Chitinous remains persist for decades to hundreds of thousands of years in sediments (Verbruggen et al. 2010; Bolland et al. 2022) and may even fossilize over longer time spans under suitable depositional conditions (Gupta 2011; Bennike et al. 2023). Many invertebrate taxa tend to predominate in relatively narrow ranges of suitable environmental conditions and assemblage datasets of subfossil invertebrate remains are utilized as qualitative and quantitative paleoenvironmental indicators (Walker 1987; Clerk et al. 2000; Tóth et al. 2019; Płóciennik et al. 2020). Paleoecological assemblage data of sedimentary invertebrate remains therefore provide information on past invertebrate communities, variability through time, and inferred ecosystem changes (Smol et al. 2001b, 2021; Engels et al. 2008; Verbruggen et al. 2010; Plikk et al. 2019).

Many paleoenvironmental studies have made use of the chitinous remains of aquatic insect larvae (Uutala 1990; Walker 2001; Brooks et al. 2007; Luoto 2009; van Geel et al. 2020), cladocerans (Korhola et al. 2000; Pietrzak and Slusarczyk 2006), oribatid mites (Solhøy 2001; Hodgson and Convey 2005; Schatz and Behan-Pelletier 2008), and bryozoans (Crisman et al. 1986; Francis 1997, 2001; Courtney Mustaphi et al. 2016). For example, the distribution of subfossil chironomid assemblages in lacustrine sediments is closely related to water depth (Korhola et al. 2000), lake water nutrient or oxygen availability (Lotter et al. 1998; Quinlan and Smol 2001), climate conditions (Lotter et al. 1997; Heiri et al. 2007, 2011; Barley et al. 2006), and salinity (Verschuren 1997). Chironomid assemblages are therefore used for the reconstructions of lake-water level, deepwater oxygen, salinity or temperature variability through geologic time (Eggermont et al. 2006; Luoto and Salonen 2010). Similarly, subfossil cladoceran assemblages have been used to reconstruct lake-level changes (Korhola et al. 2000) and past trophic structures of aquatic food webs (Lamontagne and Schindler 1994; Jeppesen et al. 1996; Verschuren and Marnell 1997; Nevalainen et al. 2014). Many of these invertebrate groups have been identified to species, species group or genus level, allowing reconstructions of the taxonomic composition of the relevant invertebrate communities. However, identification of aquatic invertebrates to higher level taxonomic categories also provides valuable paleoecological information. For example, at the family level, Chaoboridae remains, particularly in comparison with the abundance of other benthic macroinvertebrate remains such as chironomid head capsules, provide valuable information on past changes of aquatic trophic conditions and particularly changes in deepwater oxygen concentrations in lakes (Lamontagne and Schindler 1994; Uutala and Smol 1996; Sweetman and Smol 2006; Luoto and Nevalainen 2009; Quinlan and Smol 2010; Tolonen et al. 2012). Ursenbacher et al. (2020) analyzed sediments from temperate European lakes and showed that the entire assemblage of chitinous invertebrate remains (> 100 µm) expressed as relative abundance data, and identified to the taxonomic levels of families to orders, similarly provided information on past lake-water-oxygen concentrations.

Invertebrate remains are described in identification keys and visual aid manuals for several taxa, such

as head capsules of chironomid larvae or exoskeletal fragments of cladocerans, which allow analysts to identify subfossil remains at taxonomic resolutions from (sub)species to family levels, morphological groups, or morphotypes (Brooks et al. 2007; Szeroczyñska and Sarmaja-Korjonen 2007; Korosi and Smol 2012a, 2012b; Chamutiová et al. 2020; Hamerlík et al. 2022). Remains of other ecologically-important taxa, such as mandibles and head parts of larval Trichoptera (caddisflies), have been described in dispersed literature (Frey 1964; Pitsch 1993; Greenwood et al. 2003; Brooks et al. 2007; Luoto 2009). Even with the proliferation of literature that documented chitinous remains found in the sediments of freshwater ecosystems, there remain uncertain attributions for many subfossil remains, a high degree of morphological variability within taxonomic units (phenotypic variation and instar morphologies), and uncertainties as to how the presence and quantification of invertebrate remains contributes to paleoenvironmental interpretations (Brooks et al. 2007).

Literature resources for the identification and analysis of the range of chitinous remains are relatively dispersed, highly specialized, and, in some cases, difficult to access. Privately-held collections and documentation have either limited accessibility, have not been peer-reviewed, or are unavailable to many researchers. In some cases, legacy collections are poorly archived or ultimately disposed of. The distribution of available resources impedes upon opportunities to optimize the use of invertebrate remains for paleoenvironmental interpretation. Here we provide an additional documentation of chitinous aquatic invertebrate mandibles and structures that superficially resemble mandibles, such as pygopodia and claw appendages, that are frequently observed in sieved lake-sediment samples used in paleoecological, paleoenvironmental and archaeological research. This study characterizes some of the variety of mandibles, mandible-like structures and other selected sclerotized remains of aquatic invertebrates that have received less attention in the paleoenvironmental literature. The photographs provide a compilation for paleolimnologists interested in the use of aquatic invertebrate remains to be consulted for identification and association of these remains with the modern taxonomies. The majority of specimens described in this compilation are based on specimens and structures derived from collections of the modern aquatic fauna, in contrast to other compilations intended for the identification of chitinous invertebrate structures that preserve as subfossils in lake sediments, such as descriptions of subfossil chironomid larvae head capsules (Brooks et al. 2007) or cladoceran exoskeleton structures (Szeroczynska and Sarmaja-Korjonen 2007). This ensures that the presented and described structures are from specimens that could be identified with the literature for modern specimens and are reliably associated with valid species, genus, subfamily and order names.

Descriptions focus on mandibles and mandible-like structures that have been cleared by chemical treatment to resemble fossil remains, from specimens that have been identified based on the modern aquatic invertebrate keys (Studemann et al. 1992; Waringer and Graf 2011; Lubini et al. 2012). The described remains can all be expected or have been observed (by the authors) to be present in samples prepared for chironomid analysis: sieved with a 100 µm mesh-size sieve and sorted under a stereomicroscope at 30–50 × magnification, with remains of interest mounted on microscope slides and examined at 100–400 × magnification. However, many can also be expected to occur in samples sieved with coarser mesh sizes, e.g. for plant macroremain analysis, or in samples prepared for examination of other fossil indicators under the microscope (e.g. slides for Cladocera or pollen analysis). The figures and descriptions presented here mainly originate from central Europe, but are relevant to a wide range of higher order aquatic invertebrate groups and habitats that may also be common in other biogeographic regions. They are intended to identify unknown mandible-like structures to such higher order categories (e.g. orders or families within the aquatic insects) and possibly different morphological subcategories (i.e. morphotypes) therein. However, the descriptions are not intended to provide identification to species, species-group or genus level, as the covered invertebrate groups have not been comprehensively analyzed to cover the full range of species and morphologies expected for central Europe. To increase the usefulness of this compilation we also include some additional fossil invertebrate structures, particularly from aquatic insect orders, that are commonly found together with mandibles and mandible-like structures in lake sediments and may confirm the presence of these taxa. Finally, we discuss some published

examples demonstrating how the inclusion of invertebrate remains identified to the taxonomic resolution used in this compilation (i.e. at the level of families to orders) supports the ecological interpretation of aquatic invertebrate records and how this compilation can be utilized for developing similar reconstructions, potentially at higher taxonomic resolution and based on ecologically-relevant morphotypes, in the future. This compilation serves analysts of lacustrine and palustrine sediments (Cook et al. 2011; Ursenbacher et al. 2020), fluvial deposits, paleolake sequences (Bolland et al. 2021), soils (Kienast et al. 2011), and archaeological deposits (Schelvis 1990; Law 2013; Tóth et al. 2019; Engels and Whitehouse 2023).

Materials and methods

Overview

The material used for photomicrography was prepared through two main approaches. The first approach prepared individual modern invertebrate specimens that have been pre-identified using available identification literature for these organism groups. Relevant structures were cleared of soft tissue by chemical treatment to artificially "fossilize". Body parts were mounted on microscope slides for examination under the compound microscope at 100–400 × magnification. The second approach used invertebrate remains sieved and sorted from lake sediments that were slide mounted, examined under the compound microscope, and identified based on paleoecological identification literature (Frey 1964; Brooks et al. 2007; Luoto 2009) or in comparison with our slide-mounted collections of pre-identified aquatic invertebrate remains. Attention and sampling effort was given to anatomical parts known a priori from experience to be found in Quaternary sediment records by the authors and for remains that have been misidentified in the literature or that are frequently encountered by analysts. Predominantly, the remains included mandibles, auxiliary mouth-part structures, and harder body parts such as claws and other appendage extremities. Digital photomicrographs were acquired of the remains and organized by taxonomic groups to document and aid invertebrate identification. We focus on chitinous structures and remains found to be abundant in the sieved sediment-size fractions > 100 µm, commonly used for chironomid (Walker and Paterson 1985; Walker 2001; Verschuren and Eggermont 2007) and plant remain analyses (Birks 2001; Beaudoin 2007; Hawthorne et al. 2018; Vachula 2019) of wet sediment-subsample volumes ranging from > 1 to 10s of cm^3 (Birks and Birks 1980).

Invertebrate specimens

Fieldwork sampling and rearing of aquatic invertebrates

We selected specimens from a collection of aquatic invertebrates stored in ethanol that had been identified to the species level and stored at Geoecology, Department of Environmental Sciences, University of Basel, Switzerland (Heiri and von Fumetti 2022). Selected specimens were primarily aquatic larval or adult life stages and included aquatic and semi-aquatic larvae. The specimens were collected from freshwater ecosystems in Switzerland and southern Germany during fieldwork (2003–2019). To expand this collection, seven additional ponds and lakes were sampled during September and October 2019 for arthropods and the sampling was done *ad hoc* spatially across several niches and substrates with a 500 µm mesh net. Individuals were aggregated into a site sample and 80% ethanol was added in the field for initial preservation. All individual specimens from each site were sorted and identified to the species level prior to chemical treatment, disarticulation of body parts, and mounted on microscope slides. Identification of specimens made use of descriptions from general identification guides for aquatic invertebrates such as Nilsson (1996), Stehr (1991), Merritt et al. (2008), and Rogers and Thorp (2019). Additional keys were used for Coleoptera (beetles) (Zahradník 1985; Amann et al. 1994), Megaloptera: Sialidae (alderflies) and Lepidoptera (caterpillars and butterflies) (Elliott 1977; Nagel 1989; Hölzel et al. 2001), Ephemeroptera (mayflies) (Studemann et al. 1992), Trichoptera (Waringer and Graf 2011), and Plecoptera (stoneflies) (Lubini et al. 2012).

The crustacean *Triops cancriformis* (Bosc, 1801) was reared from diapause eggs obtained from commercial sources in aquaria with 20–25 °C spring water, 12 h of daylight, aerator and food. The shed exuviae were sequentially collected and prepared for identification as described below.

Treatment and slide mounting of collected specimens

Preparation of modern specimens mounted on microscope slides improved the visibility and optical properties for digital photomicrographs (Porto et al. 2016; Silveira and Haro 2016; Taber 2019). To resemble subfossil remains, each specimen was treated with 10% potassium hydroxide (KOH) for 3–12 h at room temperature to improve the visibility of important structures (Hanley and Ashe 2003; Brooks et al. 2007; Porto et al. 2016). The duration of immersion time was dependent on the degree of sclerotization, body size and taxon of specimen processed, and the degree of transparency was monitored by eye throughout the work day. Generally, longer processing time was needed for adult Coleoptera and shorter durations for specimens with less sclerotized cuticles, such as Amphipoda. Immersion > 12 h was avoided to prevent deformation of soft tissue when mounted onto microscope slides. When necessary, the alkaline maceration was slowed overnight by refrigeration at 4 °C. After this treatment, KOH was replaced with water to stop the alkaline digestion process. The specimens were then sequentially dewatered in 80% and 100% ethanol for 5–10 min each immersion. The exoskeletons were dissected with a metal blade in a Petri dish with 100% ethanol under a stereomicroscope at 6–60 × magnification. Strongly sclerotized parts were disarticulated and positioned for visibility and photography and mounted with Euparal slide-mounting medium (optical qualities: density 0.99 g cm^{-3}, refractive index of 1.483 when liquid and 1.535 after solidification, manufactured by Carl Roth, Gilson 1906). The microscope slide collection is stored at Geoecology, University of Basel.

Subfossil invertebrate remains sorted from sediments

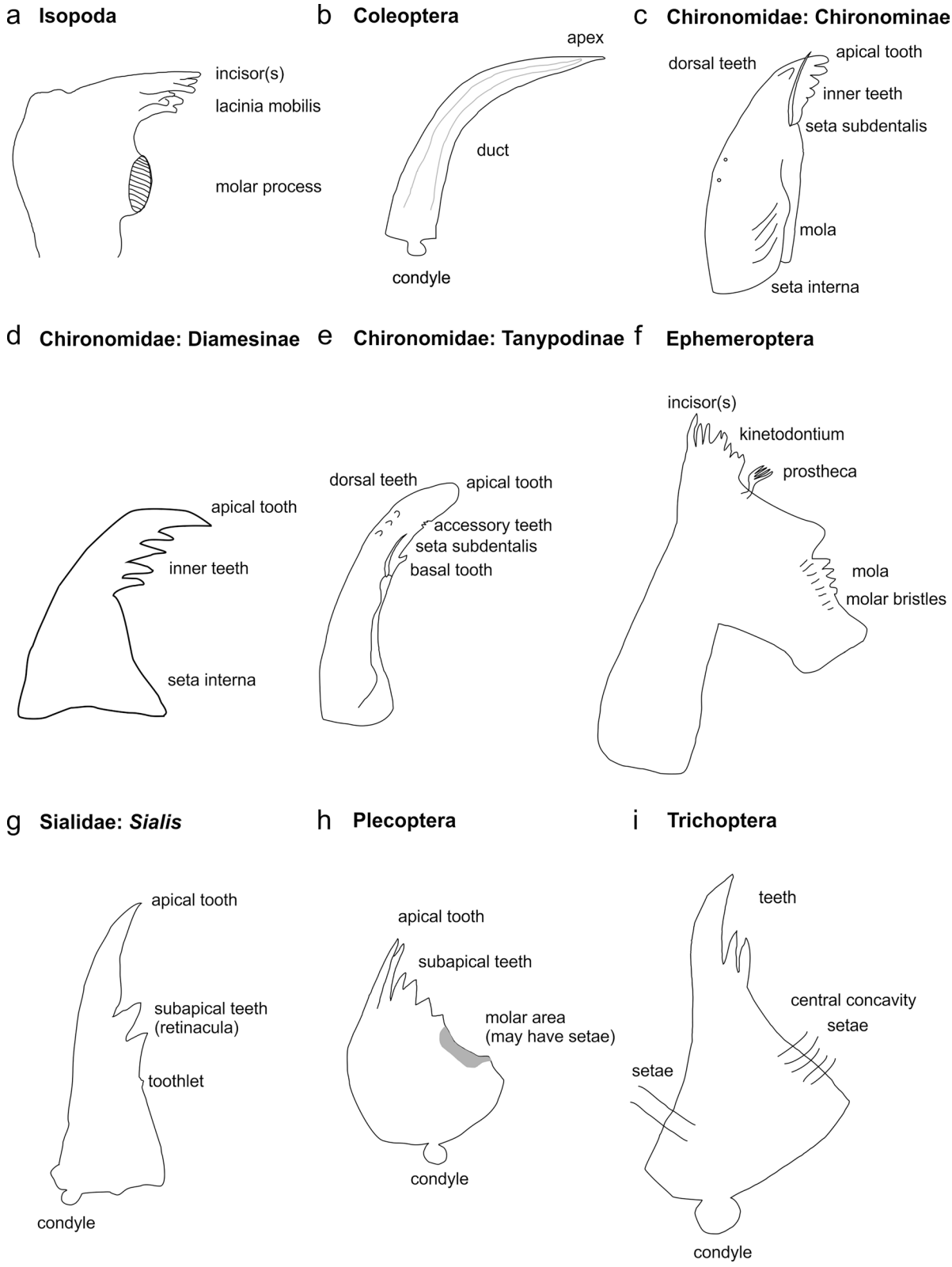
Some structures from previously prepared microscope slides of subfossil invertebrate remains from the collection at Geoecology, University of Basel, were also imaged. The slides were prepared throughout the course of previous research with taxonomic resolutions at the species level, morphotype group, or to the order. Identification of these remains relied on paleoecological identification literature (Frey 1964; Brooks et al. 2007; Luoto 2009), comparisons with descriptions in identification literature for modern aquatic invertebrates (Nilsson 1996; Merritt et al. 2008; Rogers and Thorp 2019) and comparisons of the remains with the collection of modern invertebrates hosted at Geoecology, University of Basel. Subsamples of wet or freeze-dried sediments were taken from lake-sediment cores and surface-sediment samples. These sediments had either been sieved without chemical deflocculation or were deflocculated at room temperature in 10% KOH for 2 h and then wet sieved with a 100 µm mesh. Chitinous invertebrate remains were manually picked with forceps at 30–40 × magnification, dehydrated at room temperature for ~24 h and mounted on slides with Euparal (Bigler et al. 2006; Heiri et al. 2011).

Digital photomicrography

A Leica DM 2500 LED compound optical microscope with a mounted digital camera (5 megapixels, Leica MC 170 HD) and Leica Application Suite software LAS EZ version 2.0.0 with 4, 10, 20, and 40 × objective lenses were used for image acquisition for slides obtained from the collection of modern invertebrate remains. Some images that required multiple focal depths were acquired with a Canon 90D EOS 35 mm camera and z-stack composite images processed with Adobe Photoshop software version 23.2.1. Representative scale bars used on digital images were calibrated with a calibration-micrometer slide. Bright field optics without a filter was used for images of darker sclerotized parts of some specimens. Phase-contrast microscopy was used for integuments and other structures of amphipods that contained residual amorphous or crystalline calcite.

Organisation and presentation

Editing of digital images to generate the photograph plates included vertical or horizontal flipping of some images, rotations, resizing, and masking of small empty areas with no alteration to the object imaged. Adobe Photoshop 2023 version 24.4.1 was used for color adjustments. The original unprocessed digital images are presented in a supplement for reference and printing on photograph paper. Digital photograph plates were assembled with CorelDraw 2018 version 20.1.0.708 software and arranged by taxonomic groups and include invertebrate mandibles from both the specimen collections and remains collected from sediments. The photographs have been organized


a Isopoda
incisor(s)
lacinia mobilis
molar process
b Coleoptera
apex
duct
condyle
c Chironomidae: Chironominae
dorsal teeth
apical tooth
inner teeth
seta subdentalis
mola
seta interna
d Chironomidae: Diamesinae
apical tooth
inner teeth
seta interna
e Chironomidae: Tanypodinae
dorsal teeth
apical tooth
accessory teeth
seta subdentalis
basal tooth
f Ephemeroptera
incisor(s)
kinetodontium
prostheca
mola
molar bristles
g Sialidae: Sialis
apical tooth
subapical teeth
(retinacula)
toothlet
condyle
h Plecoptera
apical tooth
subapical teeth
molar area
(may have setae)
condyle
i Trichoptera
teeth
central concavity
setae
setae
condyle

◂**Fig. 1** Stylized drawings of invertebrate mandibles that indicate some of the main anatomical features and the terminology used to describe different mandible types in this study. **a** Isopod mandible (after Karaman 1993; Mayer et al. 2009; Semsar-Kazerooni et al. 2016). **b** Aquatic Coleoptera larval mandible with internal duct and condyle joint at base. **c–e** Several examples of Chironomidae mandibles: **c** Chironominae: Tanytarsini mandible (after Saether 1980; Wiederholm 1983), **d** Diamesinae mandible (after Wiederholm 1983), **e** Tanypodinae mandible (after Saether 1980). **f** Sialidae: *Sialis* mandible (after Nilsson 1996; Archangelsky et al. 2017). **g** Ephemeroptera mandible (after Nilsson 1996; Kluge 2004; Bauernfeind and Soldán 2013; Kluge and Novikova 2016). **h** Plecoptera mandible (after Lillehammer 1988; Nilsson 1996). **i** Trichoptera mandible (stylized after Wallace et al. 2003; Edington and Hildrew 2005; Morse and Holzenthal 2008). The terms incisor, incisor process, incisors, and incisivi are used by different authors to refer to the teeth, or groups of teeth, that perform a cutting function in invertebrate mandibles. In this compilation we use incisors and incisivi interchangeably to refer to such teeth but try to follow the terminology used to describe the mandible morphology within individual invertebrate groups

partly to reflect systematics and balanced on each plate for pragmatic and aesthetic placement.

Results

A total of 168 photomicrographs were selected for presentation. The specimens belonged to 90 genera within 52 families of 11 orders. We present a total of 125 taxa from Crustacea: Amphipoda ($n=4$), Isopoda ($n=1$), Ostracoda (seed shrimps, $n=1$), and Notostraca (tadpole shrimps, $n=2$); as well as insect orders: Coleoptera ($n=13$), Diptera (true flies, $n=28$), Ephemeroptera ($n=20$), Hemiptera (true bugs, $n=8$), Odonata (dragonflies and damselflies, $n=3$), Lepidoptera ($n=1$), Megaloptera: Sialidae ($n=2$), Plecoptera ($n=8$), and Trichoptera ($n=34$). Several individual specimens were repeatedly used for photography to image multiple mandibles and other body parts, such as mouthparts or claws and leg appendages that exhibit a superficial similarity to mandibles.

Recognizing mandibles

Several sclerotized exoskeletal anatomical parts of invertebrates are found in sieved lake sediments that include mandibles and different claw or claw-like parts that superficially resemble mandibles. Here we describe some generalizations for the most common materials observed during microscopy and analysis of sieved remains and presented in this compilation (Coleoptera, Diptera, Ephemeroptera, Plecoptera, Trichoptera). The compilation has less generalizations for Crustacea, Hemiptera, Odonata, Lepidoptera, and Megaloptera, and instead the descriptions point the reader to more specialized literature. Analysts should be aware that anatomical nomenclature varies between taxa and within some taxonomic groups, and sometimes amongst the literature by different authors.

Typically, mandible morphology exhibited a more or less flat-ended posterior part at the base that is attached to the head and an anterior apex with a wide variety of teeth and subordinate teeth. The basic mandible for many taxa, particularly insects, consists of a flattened molar area towards the base of the mandible, for chewing and grinding food particles, and dentition, cusps and incisors, possibly together with sharp edges towards the apex, for piercing and cutting food or prey (Fig. 1; Krenn 2019). One or both of the joints (condyles) can be visible along the mandible base (posterior) in both modern and subfossil mandibles as a ball-socket structure for some taxa (Fig. 1) (e.g. Coleoptera, Lepidoptera: *Cataclysta*, Megaloptera: Sialidae, Ephemeroptera, Plecoptera, and some Diptera). The anterior part, or apex, commonly has specialized teeth dependent on the feeding ecology that are adapted to chew, scrape, crush or cut food and prepare for ingestion. Incisors and incisivi are generally the apical teeth for biting functionality. Ephemeroptera have a kinetodontium next to the incisors and a prostheca (Fig. 1), which can be disarticulated in subfossil material, and a broad mola region. Larval hemipterans and some coleopterans have piercing mouthparts for sucking, and some taxa have some adaptations modified for some chewing, such as Hemiptera: Corixidae (Savage 1990). Many of the studied taxa have more or less asymmetrical mandibles. In the mandibles of Ephemeroptera and Plecoptera, the molar part of the left and right mandible have a different morphology; in Trichoptera, asymmetry is readily visible in the presence or absence of molar setae. In many predator insect taxa, the molar area has been reduced (Krenn 2019).

Crustacea (Figs. 2–3)

Malacostraca: Isopoda (Figs. 2a, b)

Isopoda have relatively fragile exoskeletons and disarticulated and broken remains are found in fossil

records (Frey 1964). Many benthic isopods have mandibles adapted for scavenging, as is the case for *Asellus* (Fig. 2a,b), the main taxon found in central European freshwater habitats. Isopoda mandibles have a long mandible base and a broad mandibular palp at the anterior end (Fig. 2b). In our specimen the molar area is protruded, flattened and bigger than incisor and lacinia mobilis together. The incisivi are slightly curved overall and have thin, moderately pointed teeth (Fig. 2a). However, there is a high taxonomic diversity and range of feeding strategies within the group (Smith 2001) and the variability of Isopoda mandible remains in sediments has not been fully explored (Frey 1964).

*Malacostraca: Amphipoda (*Figs. 2c–e, g–i*)*

The amphipods include the gammarids, a group of crustaceans that can be abundant in littoral areas of lakes and within streams, while some taxa have more specialized habitats (Smith 2001; Wellborn et al. 2015; Alther et al. 2017). The mandible base of the three examined species, *Gammarus fossarum* (Koch, 1835), *G. lacustris* (Sars, 1863) and *Dikerogammarus villosus* (Sowinsky, 1894), is prominent and long, and at the anterior end there is a mandibular palp and a group of incisivi (cutting teeth) that may look blunt and rounded in dorsal view (Figs. 2c,d). In larger specimens the incisivi are pointed and more sclerotized (Figs. 2e,g–i). Beneath the incisivi, the lacinia mobilis is followed by a row of setae. The mandibles have a more or less prominent circular molar. Because of the lack of comparison to other amphipod groups, we did not attribute any morphotypes. We could not find a complete amphipod mandible in the subfossil collection, but disarticulated or incomplete incisivi are commonly found in lake sediments (Beer et al. 2007). This is most likely due to the fragile exoskeleton of amphipods. The incisivi are recognized by

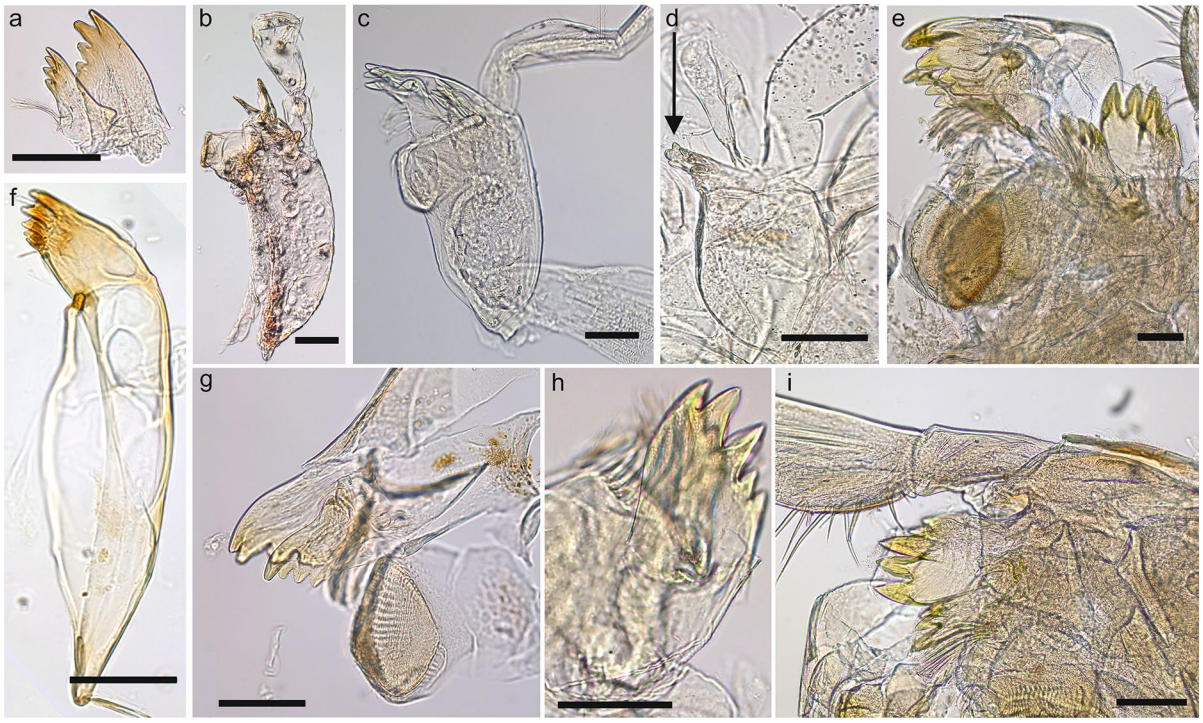


Fig. 2 Mandible and sclerotized mouthparts of several Crustacea taxa photographed from the prepared specimen collection. **a** Crustacea: Isopoda: *Asellus aquaticus* (Linnaeus, 1758), incisor. **b** *Asellus aquaticus*, mandible and fragment of palp. **c** Crustacea: Amphipoda: *Gammarus fossarum*, mandible. **d** *Gammarus lacustris*, mandible. **e** Crustacea: Amphipoda: *Dikerogammarus villosus*, incisors and molar. **f** Crustacea: Ostracoda, mandible. **g** *Gammarus* sp., mandible. **h** *Gammarus* sp., mandible. **i** *Dikerogammarus villosus*, palp (top left) and incisors (center left). The arrow in **d** indicates the location of the mandible in the photograph. Scale bar is 0.1 mm

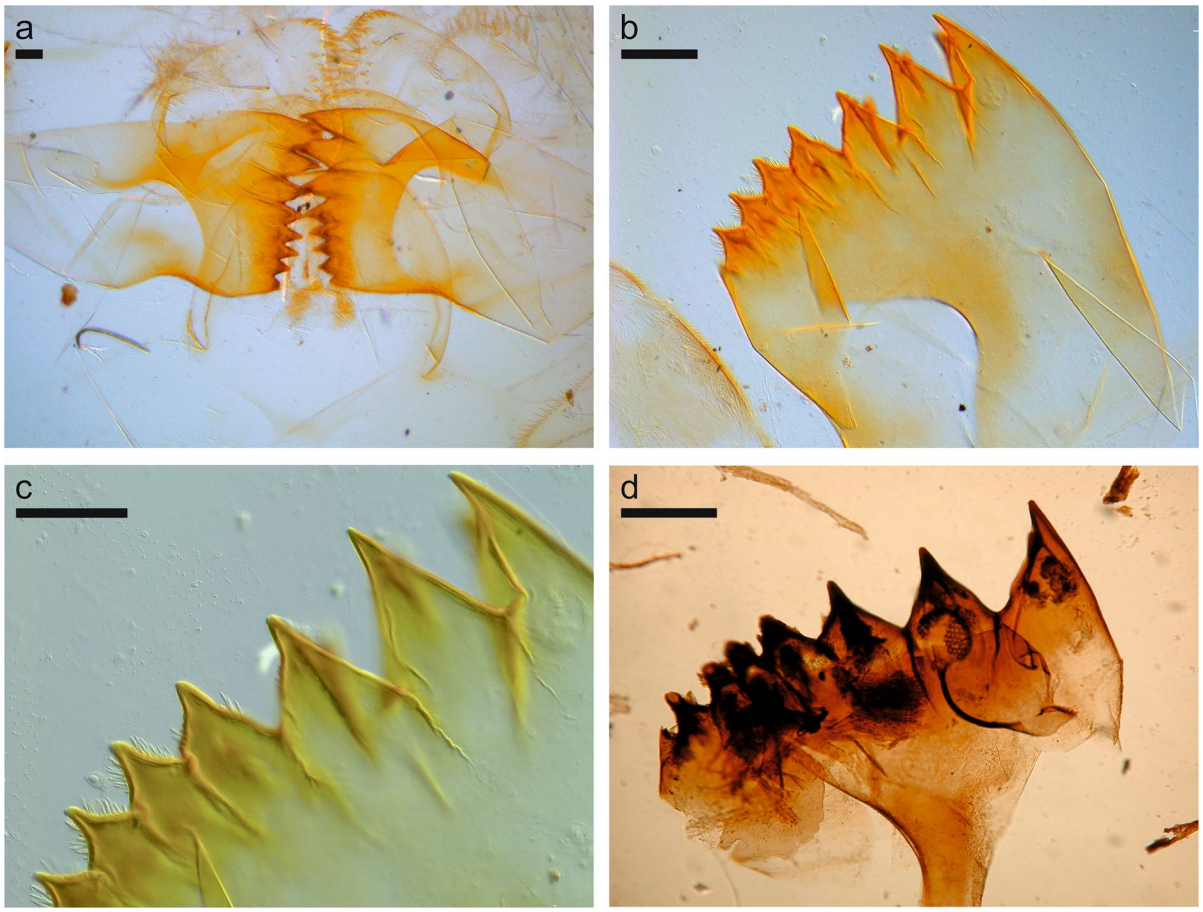


Fig. 3 Mandibles of Crustacea: Notostraca: Triopsidae. **a** both mandibles of an early exuvium of *Triops cancriformis* larva. **b** Single mandible from a larval exuvium of *T. cancriformis*. **c** Detail of *T. cancriformis* mandible at 200× magnification. **d** Single Triopsidae (*Triops* or *Lepidurus*) mandible fragment found in sieved late glacial aged lacustrine sediments. Images **a**–**c** are of exuvium shed from reared specimens. Scale bar is 0.1 mm

the slightly curved form and unserrated (plain) edges (Fig. 2c).

Oligostraca: Ostracoda (seed shrimps) (Fig. 2f)

Ostracods form carbonate carapaces with chitinous membranes and have chitinous exoskeletons (Kornicker 1979; Holmes 2001). Ostracods have an elongated mandibular corpus called a coxa with a large opening for soft tissue and a tapering pointed base (Fig. 2f; Smith et al. 2015). The mandibular palp has many setae at the apex. The endite at the apex of the mandible has six or seven small teeth in a row. The mandible seems to be among the most resistant of the chitinous Ostracoda subfossil remains observed in records and occasionally larger appendage remains connected to the mandibles can also be found. The analysis of chitinous remains in lake sediments complements interpretations of carbonate-shell remains, commonly applied to ostracod valves (Holmes 2001), notably in cases where post-depositional dissolution of sediment carbonates occurs and for ostracod taxa with higher proportions of chitinous complex within the carapaces (Kornicker 1979). Mandibles resembling the ostracod mandible presented here have occasionally been found by the authors in late Quaternary sediment samples (unpublished data).

Branchiopoda: Notostraca: Triopsidae (Fig. 3) (tadpole shrimps)

There are two extant genera of Triopsidae (*Lepidurus* and *Triops*) with most species living in temporary pools and ephemeral surface water (Longhurst 1955; Takahashi 1977; Brendonck 1996; Korhola and Rautio 2001), including anthropogenic wetlands (Grigarick et al. 1961; Brendonck et al. 2008). Morphologically similar fossils to extant taxa are found in deposits up to 170 million years ago (Suno-Uchi et al. 1997) and are characterized by a long telson and a single shield-shaped carapace on the dorsal side (Sars 1896; Smith 2001; Cáceres and Rogers 2015). Remains of naupliar and larval stages (Møller et al. 2003) and also the softer chitinous exoskeletal body parts of adults have yet to be reported in Quaternary sediment studies and perhaps only rarely preserve or are possibly unfamiliar to analysts. The mandibles of Notostraca grind while feeding (Fryer 1988; Richter 2004) and are sclerotized, particularly at the tooth apex, which makes them the most probable anatomical parts to be preserved and retained in sieved sediment samples. Subfossil mandibular remains of *Lepidurus arcticus* (Pallas 1793) and similar Notostracans have been observed in Quaternary deposits (Kirillova et al. 2016; Kotov et al. 2018; Zinovyev et al. 2019) and Triopsidae mandibles have been observed in late glacial lacustrine sediments in the Netherlands (authors' observations; Fig. 3d). The mouthparts of *Triops* consist of several appendages with a larger mandible, a first maxilla and smaller second maxilla, paragnath, the efferent duct of shell-gland, and thoracic appendage (Longhurst 1955; Hassan 2015). Morphological or morphometric differentiation between *Lepidurus* and *Triops*, as well as species, should be explored through additional detailed studies. As a paleoenvironmental indicator, *T. cancriformis* can indicate shallow open water with low ion concentrations, and loamy substrates with vegetation and organic detritus (Alonso 1985; Brendonck 1989) and few visual predators, such as fish, or limited predation pressures (Korhola and Rautio 2001; Waterkeyn et al. 2016).

Insecta (Figs. 4–15)

Coleoptera (beetles) (Fig. 4)

Adult Coleoptera remains are one of the most abundant groups in Quaternary sedimentary deposits (Elias 2001). In lacustrine and palustrine ecosystems, coleopteran remains are washed in from the catchment and are also autochthonously produced by aquatic larvae and adult life stages (Morris et al. 2015; Gurina et al. 2019). The remains of aquatic Coleoptera are useful for paleoenvironmental studies for supporting interpretations of oxygenation, near-shore environments (Scirtidae), or changing lotic influences (Ellis 1985, 1994; Wilson 1988; Smith 2000). Coleoptera, including the larvae, are a very diverse group of organisms with many generalist and specialized feeders, thus, a high diversity of morphotype remains are expected to be found in lake sediments. Larval mandibles connect to the head either approximate (mandible base near one another on the head) or not approximate (not near each other). Many of the aquatic larvae taxa have asymmetrical mandibles (Lawrence et al. 1999). This is an important consideration when enumerating Coleoptera mandible morphotypes from sediments that may include taxa with asymmetrical mandibles and thus multiple morphotypes for a single individual.

Many aquatic larvae mandibles of Coleoptera consist of long curved hooks with an internal hollow tube (Fig. 4a, b, e, f) with a conspicuous condyle at the mandible attachment point, including the larvae of epineuston water beetles of Gyrinidae: *Orectochilus villosus* (O.F. Müller, 1776) (Fig. 4a), *Agabus* (Fig. 4e), and diving beetles of Dytiscidae: *Nectoporus sanmarkii* (C.R. Sahlberg, 1826) (Fig. 4f; heterotypic synonym *Oreodytes sanmarkii*). The larval mandible of marsh beetles Scirtidae: *Elodes* have a shorter hook and a much broader base (Fig. 4d). The mandibles of the crawling water beetles of Haliplidae (Fig. 4c) also have a relatively shorter hook. Adult mandibles can be shorter and wider (Fig. 4h, i). Shorter and wider mandibles were also found in larvae of some Elmidae riffle beetles (Fig. 4g, j–m).

Diptera (true flies) (Figs. 5–7)

Several aquatic Diptera larvae remains have previously been investigated in detail, notably of the Chironomidae (Fig. 5; Frey 1964; Walker 1985; Brooks et al. 2007) and Chaoboridae (Fig. 6a; Frey 1964; Lamontagne and Schindler 1994; Uutala and Smol 1996; Sweetman and Smol 2006; Luoto and Nevalainen 2009; Quinlan and Smol 2010; Tolonen

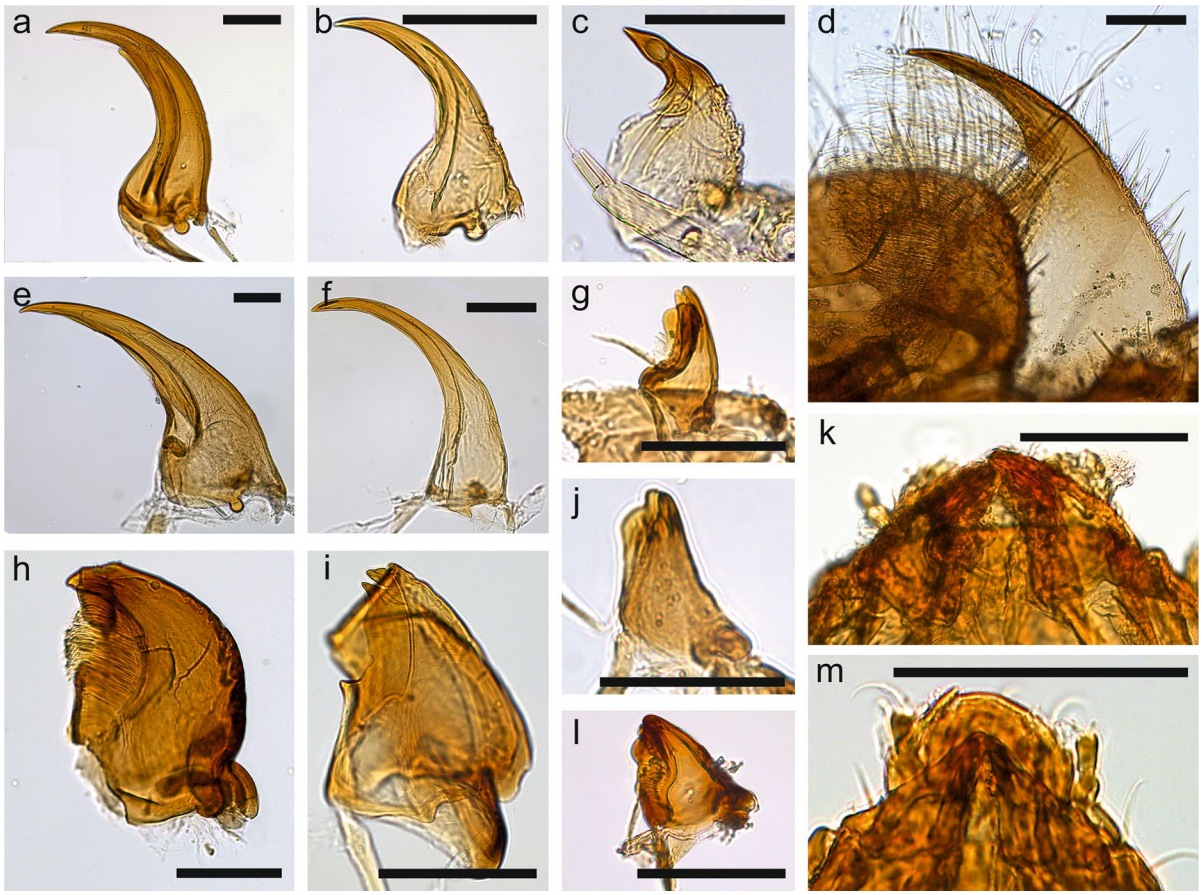
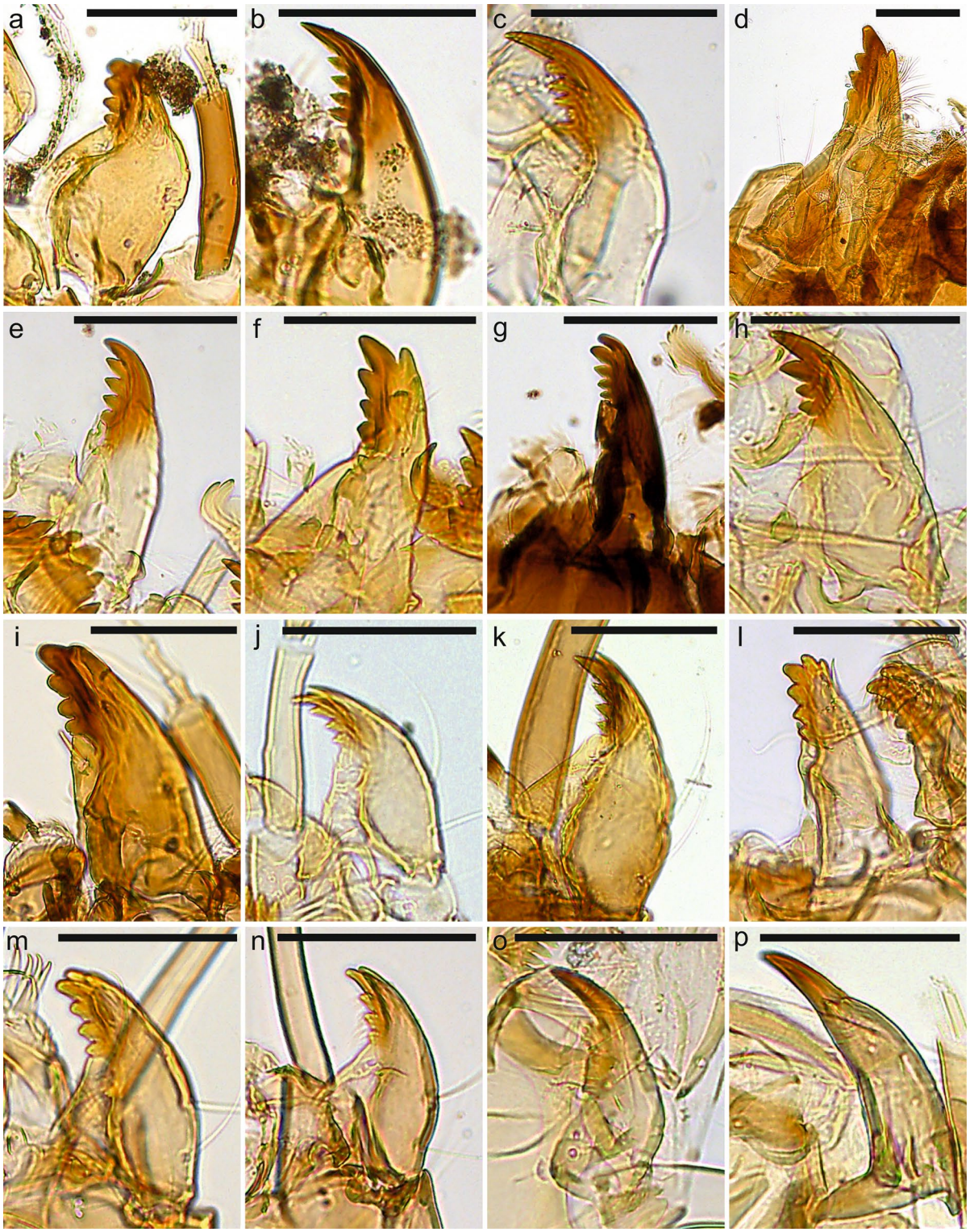


Fig. 4 Aquatic Coleoptera mandibles photographed from the prepared specimen collection. **a** Gyrinidae: *Orectochilus villosus*, larva. **b** unidentified Coleoptera, larva. **c** Haliplidae: *Haliplus* sp., larva. **d** Scirtidae: *Elodes* sp., larva. **e** Dytiscidae: cf. *Agabus* sp., larva. **f** Dytiscidae: *Nectoporus sanmarkii*, larva. **g** Elmidae: *Oulimnius tuberculatus* (Müller, 1806), larva. **h** Haliplidae adult. **i** Dytiscidae: *Hydroglyphus geminus* (Fabricius, 1792), adult. **j** Elmidae: *Esolus* sp., larva. **k** Elmidae: *Elmis* sp., larva. **l** Elmidae, larval exuvium. **m** Elmidae: *Limnius* sp., larva. All scale bars are 0.1 mm except **j** 0.05 mm

et al. 2012). Other remains of aquatic Diptera families have been presented (Frey 1964; Brooks et al. 2007) and analyzed in combination with other invertebrates and have produced detailed paleoenvironmental interpretations (Eggermont et al. 2008; Cook et al. 2011). These include Ceratopogonidae (Frey 1964), Simuliidae, and Thaumaleidae (Heiri and Lotter 2003; Brooks et al. 2007), Stratiomyidae (Rumes et al. 2005), and Tipulidae and Limoniidae (authors' observations; Figs. 6, 7). Chironomid, ceratopogonid, chaoborid, tipulid and psychodid mandibles are commonly observed in lake sediments (authors' personal observation; Figs. 6, 7), often associated with the larval head capsules (Fig. 7f) that include additional diagnostic features such as the mentum, hypostoma or head of the larva (Figs. 6h,l; Brooks et al. 2007). Analyses of dipteran larval remains often focus on head capsules rather than mandibles, although for some taxa, for example Chaoboridae and Simuliidae, mandibles are often observed and reported (Walker and Curry 1992; Rumes et al. 2005; Hamada et al. 2012) and identified to various levels of taxonomic resolution (Van Hoeve and Hendrikse 1998). Chironomid head capsules may be highly abundant in lake sediments (Porinchu and MacDonald 2003) and disarticulated mandibles from the larval head capsule may frequently be observed. Chironomid mandibles alone (Fig. 5), without the mentum, ventromental plates, and head capsule, may be morphologically identified to a lower taxonomic resolution (Cook et al.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◂**Fig. 5** Larval mandibles of aquatic Diptera: Chironomidae. **a** Chironominae: Tanytarsini: *Paratanytarsus austriacus*-type. **b** Diamesinae: *Pseudodiamesa*. **c** Orthocladiinae: *Psectrocladius sordidellus*-type. **d** Chironominae: Chironomini: *Glyptotendipes*. **e** Orthocladiinae: *Cricotopus*. **f** Chironominae: Chironomini: *Dicrotendipes notatus*-type. **g** Diamesinae: *Diamesa*. **h** Chironominae: Chironomini: *Endochironomus*. **i** Chironominae: Chironomini: *Microtendipes*. **j** Chironominae: Tanytarsini: *Cladotanytarsus mancus*-type. **k** Chironominae: Tanytarsini: *Micropsectra*. **l**, **m** Chironominae: Tanytarsini: *Tanytarsus lugens*-type. **n** Chironominae: Tanytarsini: *Tanytarsus mendax*-type. **o**, **p** Tanypodinae: *Procladius*. All scale bars are 0.1 mm

2011). However, for studies not focused on identifying the entire assemblage of invertebrate remains, this lower taxonomic resolution is useful for paleoenvironmental interpretations (Frey 1964; van Geel 2006; Ursenbacher et al. 2020), and fragmented chironomid mandibles have been reported as non-pollen palynomorphs on pollen slides (van Hoeve and Hendrikse 1998; McCarthy et al. 2021).

The order of Diptera has been divided into the two suborders Nematocera (Figs. 5a–p, 6a–i) and Brachycera (Figs. 6j–l; Hall and Gerhardt 2002; Courtney and Cranston 2015). Nematocera larvae have a developed or reduced head capsule with mandibles that often move in a horizontal plane (with some exceptions, e.g. in the Ceratopogonidae) as well as mandibles that lack an obvious condyle in the specimens we examined. In our samples we can distinguish mandibles of Chironomidae, which have an approximately triangular shape, and may have a prominent apical tooth (Fig. 1 and all morphotypes in Fig. 5) and inner teeth (Fig. 5a–n) or no obvious inner teeth and instead may have smaller accessory toothlets (Fig. 1; Figs. 5o,p). Other features include dorsal teeth that may be visible along the mandible and structures such as the setae interna (Fig. 1) and pecten mandibularis (Saether 1980; Wiederholm 1983; Courtney and Cranston 2015). These can be useful for confirmation of a chironomid mandible or assignment to more specific taxonomic ranks such as the subfamily, tribe, or genus. Some taxa have scythe-shaped mandibles instead of a triangular shape, and include *Procladius* (Fig. 5o, p; Mason 1973) and other Tanypodinae (Brooks et al. 2007). The pecten mandibularis is a group of setae that may be apparent near the ventral apex of the mandible (Wiederholm 1983).

Chaoboridae mandibles have a conspicuous and distinctive morphology, with three long and thin teeth and shorter subordinate teeth that differ in size, shape and position (Fig. 6a; Uutala 1990; Brooks et al. 2007). In our experience with sieved material, the *Chaoborus* mandibles are sometimes not intact and can be found fragmented to just a few sclerotized apical tooth tips that can easily be missed in a sample. Ceratopogonidae (Figs. 6b, c and 7a, b) have mandibles with comb-like teeth in *Dasyhelea*-type (Figs. 6b and 7a) and are rounded hooks with a rounded base in *Bezzia*-type (Figs. 6c and 7b). Simuliidae (Figs. 6d and 7d), Dixidae (Fig. 6e), Thaumaleidae (Fig. 6f), and Culicidae (Figs. 6g and 7g; Harbach 1977) have very similar mandibles with a bulbous base and rows and groups of distinct setae. Culicidae have serrated rake blades next to the apical tooth (Fig. 6g; Harbach 1977). Tipulidae (Figs. 6h and 7f) and Psychodidae (Figs. 6i and 7c) may also be semi-aquatic and the larvae have short, slender hypostoma with rows of blunt teeth.

Within the Brachycera (Fig. 6j–l), Sciomyzidae (Fig. 6j) for example, have strongly reduced head capsules and mandible-like mouthparts that usually move in a vertical plane (Barker et al. 2004). Empididae larvae are found in aquatic, semi-aquatic and terrestrial ecosystems and have been rarely investigated (Courtney and Merritt 2009; Fig. 6k). Stratiomyidae (Fig. 6l) have modified mouthparts that form a mandibular-maxillary apparatus. They have toothed rakes and serrated blades at the inner margin and groups of setae at the apical end of the apparatus. Brachycera remains and mandibles have rarely been reported from lake sediments and not observed by the authors. However, it is possible that the mandibles preserve well but are not recognized, and due to the small size may not be retained in the > 100 µm size fraction commonly examined for analyzing aquatic insect assemblages. Rumes et al. (2005) described Stratiomyidae and Ephydridae remains from African lake-sediment samples.

Ephemeroptera (mayflies) (Fig. 8)

Ephemeroptera are cosmopolitan and most larvae have an aquatic life stage and respond to ecosystem changes, climatic variability, and anthropogenic modifications, such as organic pollution, acidification, and deforestation effects (Elliott et al. 1988;


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◂**Fig. 6** Larval mandibles and other mouthparts of several families of Diptera. **a** Chaoboridae: *Chaoborus flavicans* (Meigen, 1830). **b** Ceratopogonidae: *Dasyhelea*-type. **c** Ceratopogonidae: *Bezzia*-type. **d** Simuliidae: *Simulium* sp. **e** Dixidae. **f** Thaumaleidae: *Thaumalea testacea* (Ruthe, 1831). **g** Culicidae. **h** Hypostoma of Tipulidae: *Tipula* sp. with hypostoma broken next to median tooth. **i** Psychodidae: *Jungiella* sp. **j** Larval Sciomyzidae mouth. **k** Larval head of Empididae: *Hemerodromia* sp. **l** Hypostoma of Stratiomyidae: *Stratiomys chamaeleon* (Linnaeus 1758). **a** was found in sieved sediments, **b–l** from prepared specimens. The arrow in **i** indicates the location of the mandible in the photograph. All scale bars are 0.1 mm

Barber-James et al. 2008). The mandible base of Ephemeroptera is elongated with a narrow posterior end, which gives these mandibles a readily recognizable overall morphology (Figs. 1 and 8; Studemann et al. 1992). Mandibles have well expressed incisivi generally organized as groups of teeth on one or two elongate processes (Walz and Burian 2008; Bauernfeind and Soldán 2013), with some inner teeth sometimes referred to as kinetodontium (Kluge 2004; Kaltenbach and Gattoliat 2021; Kaltenbach et al. 2021). An additional, shorter and more loosely attached appendage, the prostheca is often present at the interior to the kinetodontium (Kluge 2004; Walz and Burian 2008), but may be lost in subfossil mandibles. The molar region is protruded and flattened on the right mandible and often apparently curved and with one upper tooth on the left mandible. The molar region has a high degree of morphological variability between the taxa (Kluge 2015; Kluge and Novikova 2016) and is adapted to strain out water before food is swallowed (Sroka 2009). In our samples we found five recognizable types of ephemeropteran mandibles. In Baetidae-type the outer group of incisors and the kinetodontium is fused or partly fused and less visible (Fig. 8a–e). On slide-mounted mandibles, the incisor(s) and kinetodontium may be difficult to distinguish (Kluge and Novikova 2016). Some Baetidae (e.g. *Centropilum*) have a more distinct separation between the outer group of incisors and the kinetodontium and a slightly curved outer edge of the outer group of incisors but are otherwise very similar (Fig. 8h). In Caenidae-type, which included specimens of Caenidae, Ephemerellidae, Leptophlebiidae families, the two outer groups of incisors and the kinetodontium are separate processes, entirely separate or only touching at the base, with the outer edge of the outer group of incisors very straight (Fig. 8i–o). Ephemeridae-type was easily recognized by a tusk-like appendage typical for *Ephemera* sp. (Fig. 8p). Heptageniidae-type has an especially long mandibular base and long, serrated, "paddle shaped" outer process, separate from a smaller kinetodontium (Fig. 8q–t). Except for the serrations, separate incisors or teeth are not visible on the outer process. The genus *Rhithrogena* is included in Heptageniidae-type, but can be further distinguished by a very broad outer process and a short, stump-like kinetodontium (Fig. 8q). Since the outer process can be in a folded position, it can look narrower and the serrations can be hard to detect under the microscope. Ephemeroptera mandibles are commonly observed in Quaternary lake-sediment samples (Rumes et al. 2005; Brooks et al. 2007). Further study of Ephemeroptera mandibles will likely improve fossil mandible-morphotype groupings.

Hemiptera (true bugs) (Fig. 9)

Several hemipterans have aquatic or semi-aquatic life stages (Wetzel 2001) and adults of some taxa may make up a significant part of the community abundance and invertebrate biomass of the pleustonic habitats. Hemiptera have been found in many geological settings (Damgaard 2008; Hartung et al. 2016; Pêgas et al. 2018) and different types of sediments from the Late Pleistocene to present (Ratcliffe and Fagerstrom 1980; Miller 1983; Bennike 2000; Adams and Jenkins 2017). Many taxa are predatory in an intermediate level of the trophic system and some also feed on floating plants, algae and detritus. The feeding mouthparts of hemipterans do not have distinct mandibles, but in general have sucking mouthparts with a slender segmented beak for specialized feeding (Usinger 1956; Wang et al. 2020) and remains that include mouthparts (Figs. 9a–d, h), heads (Figs. 9e–g), and hemelytra preserve in sediments. The mouthparts of adult Corixidae have been slightly modified from strictly sucking mouthparts to allow for some chewing (Savage 1990). Several other body parts have been observed in sieved lacustrine sediment samples including clypeus, thorax and hemelytra from Corixidae and Heteroptera: Gerridae (Fig. 9h). Hemipteran remains can contribute a significant amount of identifiable chitinous remains in the sediments of some lakes (Rumes et al. 2005), although they are often not systematically enumerated and

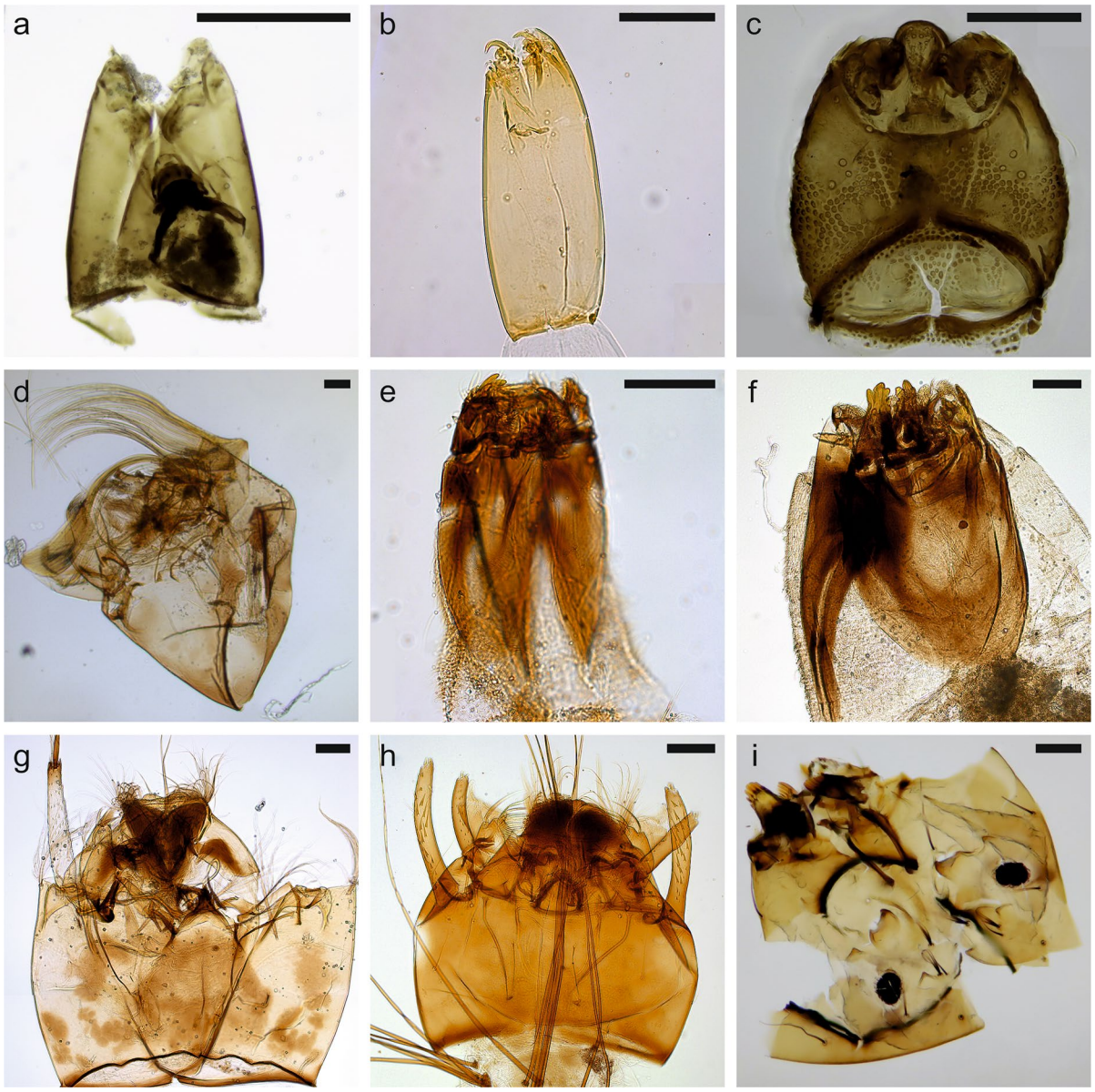

Fig. 7 Larval head capsules or mouth parts from several families of Diptera. **a** Ceratopogonidae: *Dasyhelea*-type, note the hypopharynx dislocated to the center-right side of the head capsule. **b** Ceratopogonidae: *Bezzia*-type. **c** Intact larval head capsule of Psychodidae: *Jungiella* sp. (z-stack composite of 31 images). **d** Simuliidae: *Simulium* sp. **e** Limoniidae larval head capsule. **f** Tipulidae: *Tipula* sp. **g** Larval Culicidae head (2-dimensional composite of 2 images). **h** Dixidae larval head capsule. **i** Thaumaleidae larval head capsule (z-stack composite of 16 images). **a–i** are from prepared specimens. Scale bar is 0.1 mm

reported in studies of aquatic insect assemblages (van Hoeve and Hendrikse 1998).

Odonata (dragonflies and damselflies) (Figs. 10a, b)

Odonata species predominantly have an aquatic larval life stage and the sclerotized mandibles preserve in lacustrine and palustrine sediments (Rumes et al.

2005), but similarly as with Hemiptera (Fig. 9), these mouthparts may not be recognized and are often not reported in studies examining other invertebrate remains. There is likely a high diversity of mouthpart remains from different taxa and instar stages that are understudied in paleoenvironmental studies. The larvae have several mouthparts used for predation that include mandibles, prementum, labrum and other features (DeWalt and Resh 2015). The mandibles shown in Fig. 10a–b have a robust base and are slightly elongated resulting in a somewhat triangular, pyramidal appearance. At the tip there is a row of incisivi that are broadly connected with each other at the base and may be serrated. A second crest parallel to the mandible teeth may be apparent that either has fully developed teeth (Fig. 10a) or is reduced to a crest with a sclerotized stump (Fig. 10b). Below the mandibles, the mouthparts of Odonata include a mask that is used for predation (see example in section on other invertebrate mouthpart and head capsule remains, below). The remains presented here offer a small sample of potential Odonata remains that could be found in sediments because the diversity of Odonata globally is very high and the aquatic larvae and nymphs grow through several instar stages with significant size increases.

Lepidoptera (caterpillars and butterflies) (Figs. 10c,d)

Less than 800 species of Lepidoptera (< 5% known taxa) are believed to exhibit an aquatic larval stage in lentic or lotic ecosystems (Mey and Speidel 2008; Zhang 2011; Luiza-Andrade et al. 2017). At least eight families have aquatic or semi-aquatic life stages, with few detailed studies (Hafele 1996; De-Freitas et al. 2019) and very few taxa have been investigated for remains in sediments and paleoenvironmental interpretations. Larvae of Crambidae: *Cataclysta lemnata* (Linnaeus 1758) are semi-aquatic and the remains accumulate in sediments with distributions across Asia, Europe and Africa (Agassiz 2012). The aquatic caterpillar feeds on several plants such as *Lemna*, *Spirodela* and *Azolla* (Nilsson 1996; Farahpour-Haghani et al. 2017). Adults use *Typha* and other emergent and pleustonic aquatic plants for copulation and egg laying (Pabis 2014).

The larval mandible of *Cataclysta lemnata* has a very short mandibular base and a broad apex that is either broadly equant rectangular or slightly trapezoidal in overall shape (Fig. 10c). Each mandible has five major teeth with distinct median ridges and a second row of three smaller teeth that can be found at the dorsal ridge that leads from the first dorsal tooth to the base of the mandible, occasionally in an arcing arrangement, giving the mandible a shovel-like shape (Fig. 10d). The outer margin shows two strong setae at the base. There is a bulbous condyle at the mandible attachment point to the head. Figure 10c shows the condyle at the base covered by the mandible chitin but partly visible in the deeper field of focus (*z*-axis of photomicrograph). In subfossil material the condyle may be more conspicuously exposed. Mandibles strongly resembling those of *Cataclysta lemnata* larvae have occasionally been observed in lake-sediment samples (authors' personal observation).

Other Lepidoptera remains of fully terrestrial species preserve in lake sediments, although not observed in the sieved samples presented here. Adult wing scales have a variety of morphologies (Montoro Girona et al. 2018; Milbury et al. 2019) and many are < 100 µm. For example, the > 53 µm sieve fraction has been investigated for wing scales preserved in Holocene sediments (Navarro et al. 2018a) and some Lepidoptera scales have been reported > 100 µm in the fossil record (Zhang et al. 2018). Several studies have shown that the wing scales of Lepidoptera taxa accumulate and preserve in Holocene and much older lacustrine sediments (Zhang et al. 2018). Wing scales of *Choristoneura fumiferana* (Clemens, 1865), *Lambdina fiscellaria* (Guenée, 1857), and *Malacosoma disstria* (Hübner, 1820) have been observed in lake sediments (Navarro et al. 2018b). The association between peak-accumulation rates of wing scales of *Choristoneura fumiferana* and periodic mass-emergence events has been shown for North American boreal forests during the Holocene (Montoro Girona et al. 2018).

Megaloptera: Sialidae (alderflies) (Figs. 10e, f)

All known Megaloptera have aquatic larval stages and remains of Sialidae have been reported in paleoenvironmental studies (Cover and Bogan 2015). Larval Sialidae are aquatic (Tachet et al. 2010) and generalist predators with mandibles that feature a long mandibular base and an overall slender and elongated form making a sharply pointed apical tooth, two or


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◂**Fig. 8** Ephemeroptera mandibles. **a** Baetidae: *Baetis rhodani* (Pictet, 1843), left mandible. **b** *Baetis rhodani*, right mandible. **c** Baetidae: *Cleon dipterum* (Linnaeus, 1761). **d** *Baetis* sp., note the dark band is caused by the edge of the glass coverslip. **e** *Baetis vernus* (Curtis, 1834). **f**, **g** Ephemeroptera. **h** Baetidae: *Centroptilum luteolum* (Müller, 1776). **i** Leptophlebiidae: *Paraleptophlebia* sp. **j** Leptophlebiidae: *Haprophlebia* sp. **k** Caenidae: *Caenis robusta* (Eaton, 1884). **l** Ephemerellidae: *Serratella ignita* (Poda, 1761). **m** *Caenis luctuosa* (Burmeister, 1839). **n** *Caenis* sp. **o** *Caenis horaria* (Linnaeus, 1758). **p** Ephemeridae: *Ephemera vulgata* (Linnaeus, 1758). **q** Heptageniidae: *Rhithrogena* sp. **r** Heptageniidae: *Ecdyonurus torrentis* (Kimmins, 1942). **s** Heptageniidae: *Electrogena lateralis* (Curtis, 1834). **t** Heptageniidae: *Heptagenia* sp. **a–f** and **h–t** were from prepared specimens, **g** from sieved sediments. Scale bars are 0.1 mm

three subapical teeth, and no distinct molar region (Nilsson 1996; Cover and Bogan 2015). Along the length of the mandible there are two subapical teeth (retinacula), and the distal tooth shows serration in well-preserved remains and a minute toothlet can be visible within the basal third (Fig. 1; Archangelsky et al. 2017). The mandibles are nearly symmetrical, not approximate, and have a clearly visible condyle (Fig. 1g; Archangelsky et al. 2017) at the attachment points to the head (Figs. 10e, f) although the condyle may be missing or obscured in subfossil material. The labrum and other parts of the head are also commonly found along with the mandibles (Fig. 10f) or disarticulated in the sediment subsamples. *Sialis* larval remains are common in lake-sediment samples and, due to their size and conspicuousness, have been reported in paleolimnological studies (van Hoeve and Hendrikse 1998; Brooks et al. 2007; Tóth et al. 2019; Ilyashuk et al. 2020; Bolland et al. 2021, 2022).

Plecoptera (stoneflies) (Fig. 11)

Plecoptera larvae are aquatic and many require high dissolved oxygen concentrations available in lotic environments (Wetzel 2001; Lubini et al. 2012; Tierno De Figueroa and López-Rodríguez 2019). The remains have only been reported from a few fossil and sediment studies (Frey 1964; Stötter 2015; Ursenbacher et al. 2020). Plecoptera mandibles generally function for biting or shredding detritus with later instars changing to become predatory in some taxa (Lillehammer 1988; Nilsson 1996; Wetzel 2001). The mandibles of Plecoptera have a short mandibular base and are relatively compact. The apical tooth or teeth and subapical teeth can have a plain edge or have visible serration and the molar area may or may not have setae (Lillehammer 1988; Zwick 2004; Teslenko and Zhiltzova 2006). The apical process of the mandible is dentate with varying number of teeth. The mandibles possess a molar area, either with a distinct mola with rows of short bristles or without distinct mola but rows of long setae (Lubini et al. 2012). Often a fully developed and preserved condyle joint is visible at the mandible base (Figs. 1h and 11a–h) but can sometimes be obscured by remaining chitin or appear missing in sedimentary material (Fig. 11h). The number of teeth and the form of the molar region is asymmetrical between the right and left mandibles (Figs. 11a, b) and should be noted and considered when identifying Plecoptera mandible fossils in a record and calculating derivations such as minimum counts of individuals.

In our samples we determined two morphotypes reflecting superfamily taxonomic levels. Nemouridae-type (Figs. 11a–c, e–g) are less than twice as long as their height and have an overall stout appearance. Mandibles show a distinct mola with short bristles, superficially comparable to Ephemeroptera mandibles (Fig. 8). Perlidae-type (Fig. 11d, h) have elongated mandibles that are longer than twice the height. The first tooth of the incisors is longer than the rest and appears prominent. The molar region is less pronounced and shows two rows of short and a row of long setae. The dorsal outer margin shows a hump, which leads to a very recognizable shape. Additional morphotype categorization is likely possible with further targeted research on taxonomic groups and biogeographies.

Trichoptera (caddisflies) (Fig. 12)

Trichoptera larvae and pupae are aquatic (Waringer and Graf 2011; Holzenthal et al. 2015) and the mandibles preserve well in sediments. Several other anatomical remains are readily identifiable (Pescador et al. 2004) that include other larval remains (Frey 1964; Williams 1988a, 1988b; Elias 2010; Vondrák et al. 2019), adult wings and the frontoclypeus (Elias 2001). Trichoptera tend to inhabit relatively shallow waters (Wiggins and Mackay 1978) although the remains have the potential to be transported to deep-water sediments of lakes (Frey 1964). Trichoptera assemblages are potentially useful for interpreting

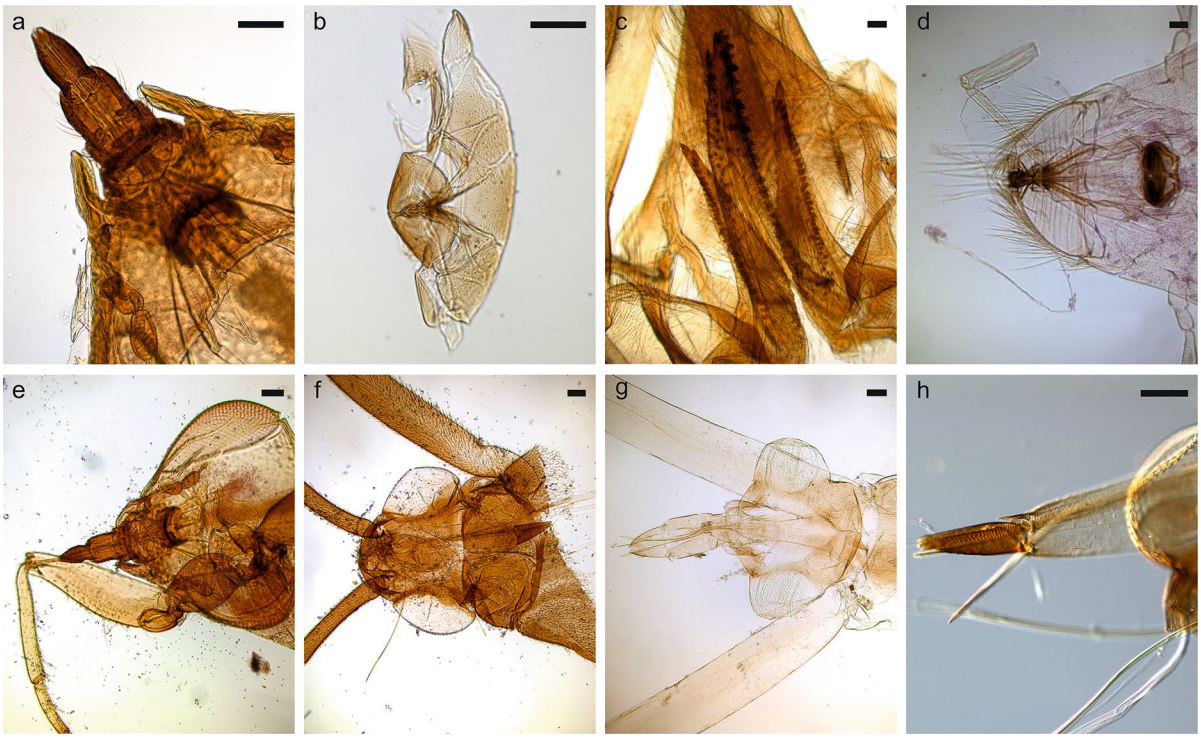


Fig. 9 Hemipteran heads and mouthparts. **a** Pleidae: *Plea minutissima* (Leach, 1817). **b** Corixidae: *Arctocorisa* sp. **c** Naucoridae: *Ilyocoris cimicoides* (Linnaeus, 1758). **d** Corixidae: *Corixa punctata* (Illiger, 1807). **e** Pleidae head. **f** Gerromorpha head, note that labium segments are pointing to the right of the image. **g** Nepidae: *Ranatra* sp. head. **h** Gerridae: *Gerris* sp. head. **a–h** were prepared specimens. Scale bars are 0.1 mm

taphonomic effects, autochthonous and allochthonous transport and deposition (Frey 1964), dissolved oxygen (Ursenbacher et al. 2020), and changing habitat types and diversity (Buczyńska et al. 2017).

Trichoptera mandibles are asymmetrical and in some taxa the overall shape of the mandible is similar yet there is a difference between each side for the arrangement of the grouped setae present in the central concavity (Wallace et al. 2003; Edington and Hildrew 2005; Morse and Holzenthal 2008). The mandibles are generally strongly sclerotized, more or less stout, and some exhibit an overall pyramidal shape (Fig. 12h, v, x,c1). A condyle may be visible at the mandibular base. There is high variability in mandible shapes, tooth morphometrics, and number of teeth, and mandibles may even lack large visible teeth. Manidible morphology reflects adaptions to different feeding strategies of scraping, grazing, or biting (Mackay and Wiggins 1979; Wiggins 1996). The degree that mandibles are sclerotinized reflects the taxonomy, function, and state of preservation (Fig. 12d and h) and may vary within an individual mandible from the apex of the teeth to the base (Fig. 12a, b1, d1). Mandibles of Polycentropodidae-type (Fig. 12l, n–p) are narrower than other Trichoptera mandibles, with the exception of the *Wormaldia*-type (family Philopotamidae; Fig. 12g1). Mandibles of the Polycentropodidae-type (Fig. 12l, n–p) may have a visible dorsal and ventral blade along the mesal margins and one striking tooth at the apex. The blades have a variable number of teeth. In the central concavity a small group of setae can be seen in some specimens, presumably only on the left mandible. They have two long setae at the outer margin. Furthermore, in *Plectrocnemia* the tooth at the apex may show serration on newly molted cuticles of larvae (Fig. 12l, o).

Wormaldia-type mandibles have a similar shape to the Polycentropodidae-type, however, *Wormaldia*-type only have one cutting edge and consists of specimens from two genera: *Wormaldia* and *Oecetis*. They

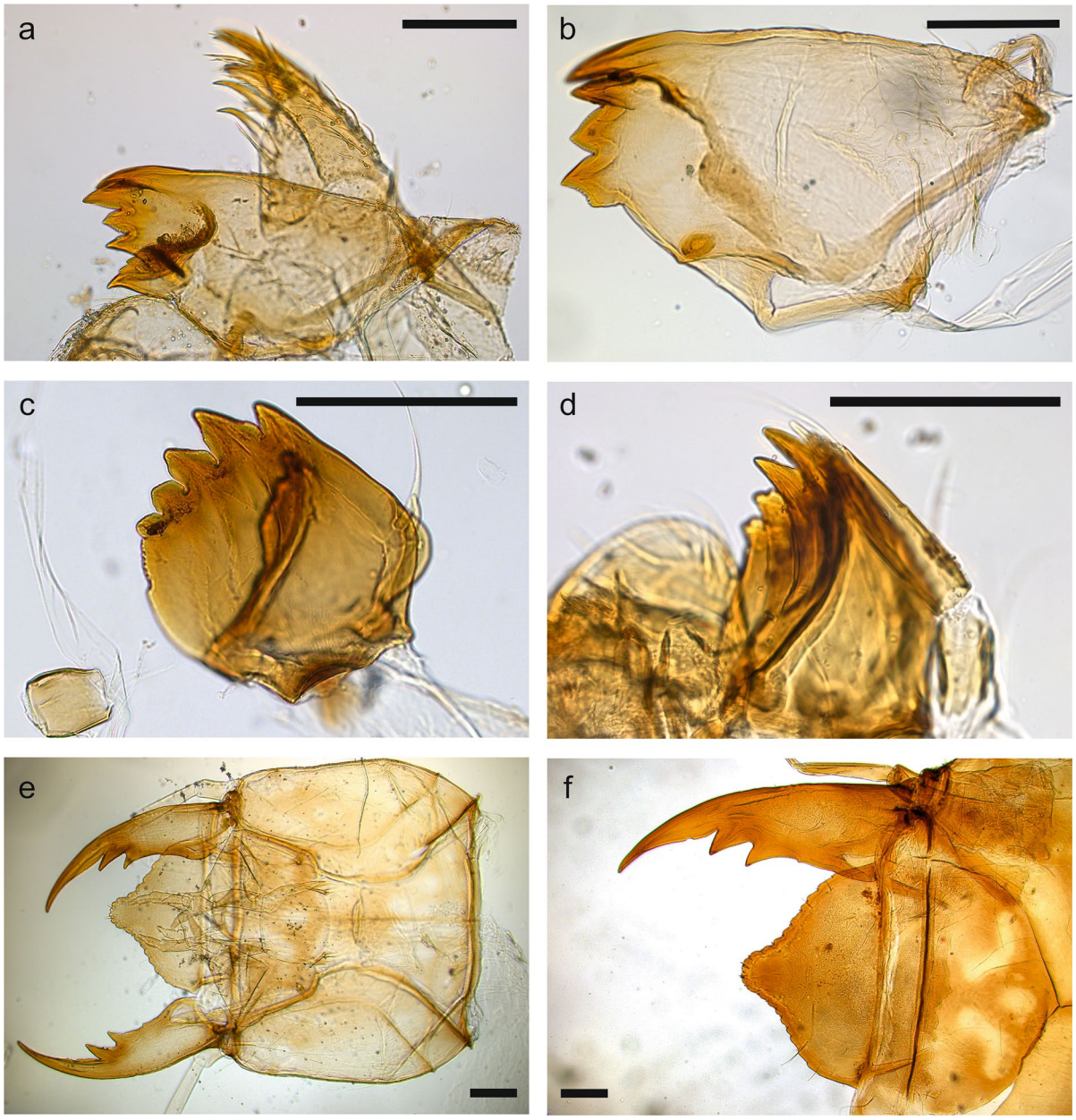


Fig. 10 Odanata (**a**, **b**), Lepidoptera (**c**, **d**), and Megaloptera (**e**, **f**) mandibles of taxa with (semi-)aquatic larvae or nymph life stages. **a** Cordulegastridae: *Cordulegaster bidentata* (Selys, 1843), mandible. **b** Coenagrionidae, mandible. **c**, **d** Crambidae: *Cataclysta lemnata*, mandible. **e** Sialidae: *Sialis lutaria*, mandible and labrum. **f** *Sialis* sp., mandible and labrum. **a**–**f** were from prepared specimens. Scale bars are 0.2 mm

have two long setae at the outer margin. The mandibles possess one sharp tooth at the apex, followed by a smaller tooth, as well as an additional tooth that has finely serrated mesal teeth on its margin. In addition, the inner margin of the mandibular base of *Wormaldia occipitalis* (Fig. 12g1) is convex with a small tooth before the margin changes to a concave form. This convex part is not present in mandibles of *Oecetis notata* (Fig. 12h1; Wallace et al. 2003).

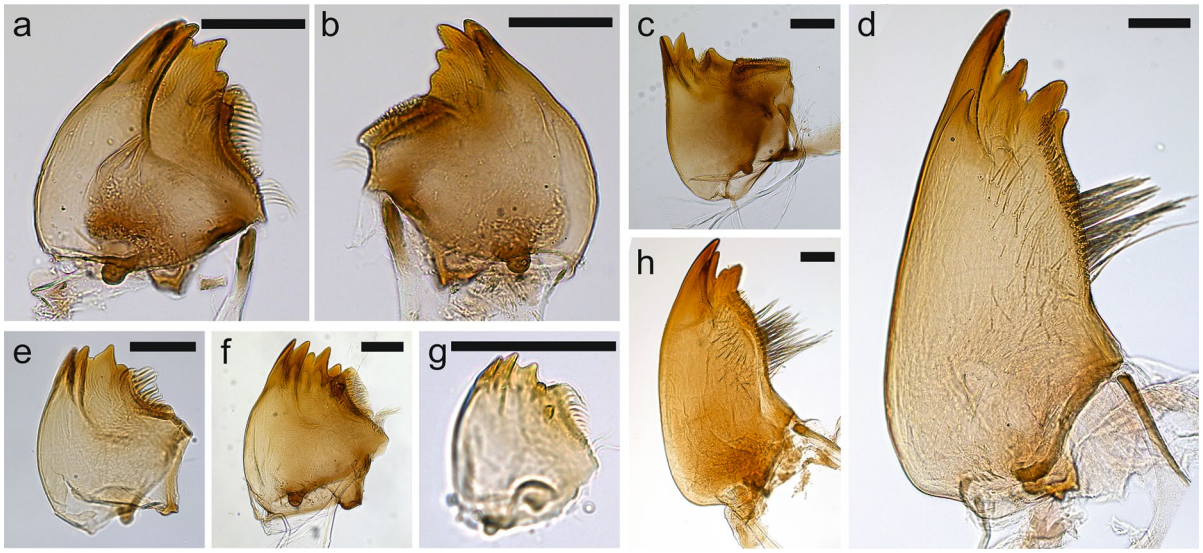


Fig. 11 Plecoptera mandibles from prepared specimens. **a** Nemouridae: *Nemurella pictetii* (Klapálek, 1900), left mandible. **b** *Nemurella pictetii*, right mandible. **c** Taeniopterygidae: *Brachyptera risi* (Morton, 1896). **d** Perlodidae: *Perlodes microcephalus* (Pictet, 1833). **e** Leuctridae: *Leuctra* sp. **f** Nemouridae: *Nemoura* sp. **g** Nemouridae: *Amphinemura* sp. **h** Perlodidae: *Perlodes jurassicus* (Aubert, 1946). Scale bars are 0.1 mm

Other mandibles with one cutting edge are the *Cheumatopsyche*-type (Fig. 12d1). They have a more or less triangular shape with a row of setae at the outer edge. The tooth at the apex is relatively blunt followed by three additional teeth below the apex, the middle of which is smaller than the others. Immediately behind the tooth at the apex there is a second smaller subapicodorsal tooth. At the molar region there is another blunt tooth, but with direction to the base of the mandible. Near this tooth a group of setae is present on the left mandible.

Lepidostomatidae/Limnephilidae-type consist of mandibles with a more pyramidal shape and a shovel-like central concavity. There are three to five pointed teeth toward the apex that are slightly bent inwards. These teeth sometimes have a different color than the mandibular base because of varying degrees of sclerotinization. In the central concavity there are either rows of long setae on both mandibles (*Potamophylax*, *Chaetopteryx*; Figs. 12a, h), a row of long setae on one and a row of few setae on the other mandible (*Lepidostoma*; Fig. 12b), a group of setae only on one side (*Crunoecia*; Fig. 12j) or two to four setae on both sides (*Limnephilus*; Figs. 12c, i). Almost all have two setae at the outer margin.

The *Agraylea*-type mandibles are structured for puncturing and are pyramidal with a sharp slope within the concave inner side and a clearly visible condyle on the inner side of the mandible base (Fig. 12c1).

Mandibles of *Rhyacophila* spp. have a very prominent pointed apex tooth with a smaller prominent tooth below it and were assigned to the Rhyacophilidae-type (Fig. 12q, r). Two long setae protrude from the outer margin. The mandibles are asymmetrical with one side having a stout basal tooth and the other having a straight cutting edge; but both lack brushes in the central concavity.

Several mandible morphotypes were not grouped into taxonomic types. The mandibles of two specimens (*Notidobia* and *Melampophylax*; Fig. 12s, u) do not show teeth and no differences in hue and some mounds are visible. *Notidobia* shows a blunt cutting edge (Fig. 12s) that is very strongly sclerotized and appears nearly opaque and dark colored. This is also the case in *Pseudopsilopteryx* (Fig. 12t), however, these mandibles show small teeth. Another group of Trichoptera mandibles are also nearly toothless and instead have a broad blade without a prominent apex for scraping and commonly have a difference in hue at the mandible base (Fig. 12v, w; Mackay and

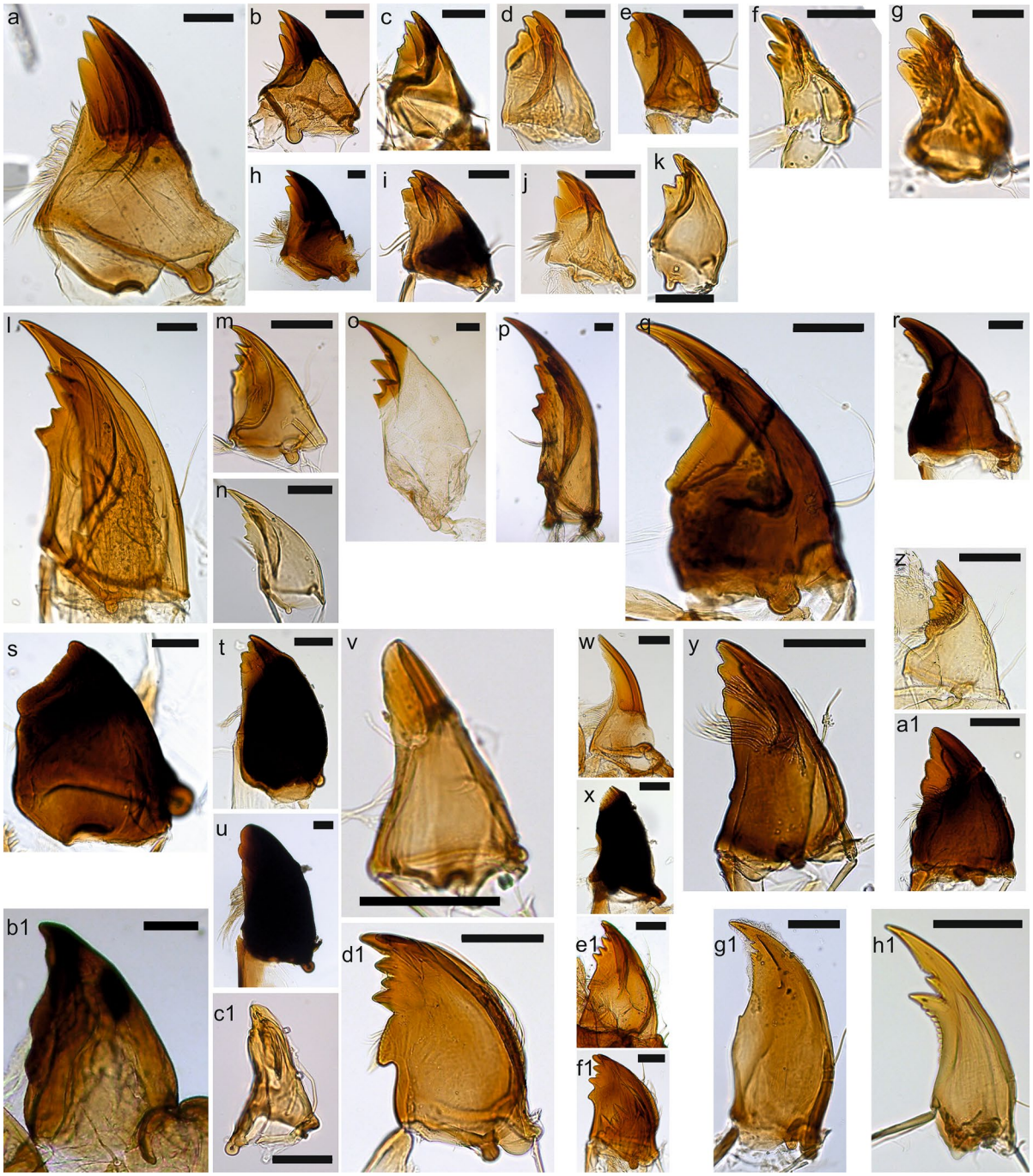
Wiggins 1979). Glossosomatidae (Fig. 12v) have few setae within the central concavity on both mandibles. *Drusus* (Fig. 12w) mandibles have rows of long setae on both mandibles. If the serration on the blade is preserved, both *Silo* (Fig. 12x) and *Tinodes* (Fig. 12z, a1) exhibit a serrated blade with no setae at the central cavity. Mandibles of *Oecetis* (Fig. 12h1) have previously been described by Rumes et al. (2005) and are characterized by a narrow apex tooth and two teeth below the apex, the larger, more basal of which is characterized by a distinct serrated outer edge. The morphological variety among the Trichoptera mandibles that remain ungrouped here suggest further subfossil types will likely be created with further research.

Scleroticized claw-like, hook-like, and other remains (Figs. 13, 14)

Many appendages and body structures that have a superficial semblance to mandibles preserve in Quaternary sedimentary deposits. Larger chitinous body parts have often been studied in detail, but finer remains are commonly unidentified and in some cases, several other body parts can resemble the remains of invertebrate mandibles. Generally, these include appendage and pseudopod structures such as tarsi, dactylus, and terminal claws; pygopodia; endopods; telsons; larval pseudopods, setae and bristles; and parts of some antennae. These are often collected during picking and mounting of invertebrate remains for microscope analysis but have only infrequently received significant focus or direct use in paleoenvironmental interpretations. Even remains identified to a relatively low taxonomic resolution provide ancillary paleoenvironmental information and the quality of preservation of chitinous remains is useful for interpreting the taphonomic processes of the stratigraphy. It may be worthwhile to record if a depositional unit is barren of other remains, such as chironomid head capsules. Figure 13 presents images of leg claws of several taxa of Plecoptera as examples of such structures, although it remains unclear whether subfossil leg claws are significantly different between species to allow a separation into distinct morphotypes. Figure 14 presents examples of some of the lower leg appendage claws and some pygopodia of Trichoptera taxa. Again, these may not be diagnostic for individual species and additionally the claws of different leg pairs may be different for the same individual. Particularly pygopodia can at first glance be misidentified as mandibles (e.g. Fig. 14b, d, f, h, j, l), but also the terminal claws of Trichoptera larvae (e.g. Fig. 14a, c, e, g, i, k) may superficially resemble mandibles, particularly of large specimens (Wallace et al. 2003; Edington and Hildrew 2005). Future studies of subfossil and reference material for these taxa may expand the range of claw and pygopodia types that can be identified from Quaternary lake sediments and would allow an assessment as to whether these can be consistently assigned to taxonomic groups or as body parts distinct from mandibles.

Other invertebrate mouthpart and head capsule remains

We also report a number of aquatic insect remains that are often found together with aquatic invertebrate mandibles and may confirm the identification of mandibular remains and are useful as paleoenvironmental indicators. The full assemblage of head capsule remains, mandibles, mandible-like remains (claws, tarsi and pygopodia), and other mouth parts provide evidence for paleoenvironmental conditions. Simuliid hypostomae (Adler et al. 2004; Craig and Porch 2013; Adler and Huang 2022) are commonly found in lake sediments together with simuliid mandibles (Fig. 6d) and invariably originate from running waters, similarly as Thaumaleidae larval head capsules (Figs. 6f, 7i). The head capsules of Limoniidae (Fig. 7e) or Tipulidae (Fig. 7f) can also commonly be found in lake sediments, often together with head capsules of Ceratopogonidae (Figs. 7a, b), or Psychodidae larvae (Fig. 7c), taxa that can colonize semi-aquatic ecosystems. Sciaridae head capsules, not shown here and described in Heiri and Lotter (2007), are often transported to lakes via streams and may therefore indicate transport by streams, even though the larvae of Sciaridae are terrestrial. The labrum of Ephemeroptera (Figs. 15a, b), Sialidae: *Sialis* (Fig. 15c), Trichoptera (Fig. 15d) or Plecoptera (not shown) may be isolated from lake-sediment samples and confirm the presence of these aquatic insect taxa. The labium, prementum, ligula, palps and movable hooks of Odonata larvae and nymph masks would also be diagnostic for this order, although it is unknown how well these remains preserve in sediments (Figs. 15g, h). Maxillae of the Plecoptera (Fig. 15f), Amphipoda: Gammaridae:



Gammarus (Fig. 15i), and many other taxa (e.g. Ephemeroptera) may also resemble mandibles and may potentially be mistaken for these structures.

Discussion

Laboratory processing of Quaternary lake-sediment subsamples for the analysis of chironomid head capsules (Hofmann 1986; Walker 2001; Porinchu and MacDonald 2003) or plant macroremains (Birks

◂**Fig. 12** Trichoptera mandibles photographed from prepared specimens. **a** Limnephilidae: *Potamophylax nigricornis* (Pictet, 1834). **b** Lepidostomatidae: *Lepidostoma hirtum* (Fabricius, 1775). **c** Limnephilidae: *Limnephilus* sp. **d** Sericostomatidae: *Sericostoma personatum/flavicorne*. **e** Leptoceridae: *Adicella reducta* (McLachlan, 1865). **f** Leptoceridae: *Setodes argentipunctellus* (McLachlan, 1877). **g** Beraeidae: *Beraeodes minutus* (Linnaeus, 1761). **h** Limnephilidae: *Chaetopteryx villosa/fusca*. **i** Limnephilidae: *Limnephilus* sp. **j** Lepidostomatidae: *Crunoecia irrorata* (Curtis, 1834). **k** Limnephilidae: *Anabolia* sp. **l** Polycentropodidae: *Plectrocnemia conspersa* (Curtis, 1834). **m** Leptoceridae: *Mystacides* cf. *longicornis* (Linnaeus, 1758). **n** Polycentropodidae: *Cyrnus trimaculatus* (Curtis, 1834). **o** Polycentropodidae: *Plectrocnemia geniculata* (McLachlan, 1871). **p** Polycentropodidae: *Polycentropus flavomaculatus* (Pictet, 1834). **q** *Rhyacophila tristis* (Pictet, 1834). **r** Rhyacophilidae: *Rhyacophila pubescens* (Pictet, 1834). **s** Sericostomatidae: *Notidobia ciliaris* (Linnaeus, 1761). **t** Limnephilidae: *Pseudopsilopteryx zimmeri* (McLachlan, 1876). **u** Limnephilidae: *Melampophylax mucoreus* (Hagen, 1861). **v** Glossosomatidae. **w** Limnephilidae: *Drusus annulatus* (Stephens, 1837). **x** Goeridae: *Silo nigricornis* (Pictet, 1834). **y** Psychomyiidae: *Psychomia pusilla* (Fabricius, 1781). **z** Psychomyiidae: *Tinodes maculicornis* (Pictet, 1834). **a1** *Tinodes dives* (Pictet, 1834). **b1** Odontoceridae: *Odontocerum albicorne* (Scopoli, 1763). **c1** Odontoceridae: *Agraylea sexmaculata* (Curtis, 1834). **d1** Hydropsychidae: *Cheumatopsyche lepida* (Pictet, 1834). **e1** Trichoptera. **f1** Hydropsychidae: *Hydropsyche siltalai* (Doehler, 1963). **g1** Philopotamidae: *Wormaldia occipitalis* (Pictet, 1834). **h1** Leptoceridae: *Oecetis notata* (Rambur, 1842). Scale bars are 0.1 mm, except for **c**, **d**, **g**, **i**, **j**, **k**, **n** and **c1** which were 0.05 mm

2001; Hawthorne et al. 2018) frequently uncovers a variety of invertebrate remains (Lévesque et al. 1988; Birks 2007). Mandible and mandible-like structures of aquatic invertebrates are particularly common and well preserved in lake sediments because of a combination of the high abundances of organisms, cuticle biochemistry and degree of sclerotization (Cohen 1987; Andersen 2010, 2012), and taphonomic processes of transport and deposition (Smol et al. 2001a; Gupta 2011). For many invertebrate groups, larval mandibles are not regularly the focus or consistently described in taxonomic literature. In cases where illustrations or photographs of mandibles are provided, the features that are clearly visible on subfossil material and potentially useful for identification are not necessarily shown. In both generalist and species-specific literature, the described mandible types for some diverse taxonomic groups, such as Trichoptera, Ephemeroptera or Plecoptera, may not be representative for the diversity of the entire group, or they may contain other mandible types that cannot be associated using existing identification aids. Mandibles of amphipods and structures from other key and often abundant organisms may only occasionally be recognized in sediments and have only been briefly mentioned throughout the paleoecological literature (Frey 1964; Beer et al. 2007) and detailed descriptions of these structures for paleoenvironmental researchers have not been published. As a consequence, a large number of chitinous invertebrate remains found in lake sediments, including many mandibles and mandible-like structures, cannot be confidently assigned to any aquatic invertebrate group with the currently available literature. Such unidentified remains are occasionally observed in high abundances but often unreported, leading to potential biases and missed opportunities for paleoenvironmental interpretations.

Descriptions and photographs of aquatic invertebrate mandibles presented in this article cover a wide range of higher order aquatic invertebrate taxa, ranging from the crustaceans to larvae of major aquatic insect orders. However, the vast majority of specimens were collected from central Europe and even for this study area only a fraction of the total aquatic invertebrate taxa that produce mandibles potentially preserving in lake sediments are covered. Nevertheless, our compilation significantly expands the diversity of mandible types that are described in keys or compilations intended for identifying fossil aquatic invertebrate remains and provides important new insights. First, for several taxa, mandibles are, to our knowledge, described for the first time in the paleoecological literature, enabling identification and tracing of aquatic invertebrate groups that are not routinely analyzed in studies of fossil aquatic invertebrate assemblages. For example, mandibles and larval remains of *Sialis* (Fig. 7e, f and labrum Fig. 15c) and chironomids are regularly reported, and have been illustrated in relatively early publications dealing with analysis of insect remains in lake sediments (Frey 1964; van Hoeve and Hendrikse 1998). However, some of the other remains that are reported here have not previously been described. For example, Beer et al. (2007) report amphipod mandibles in a sediment record from a lake in Kyrgyzstan, whereas we believe our description of *Gammarus* mandibles (Fig. 2) is the first description of this type of mandible in Quaternary paleoecological literature. Similarly, some mandible types have been found by the authors in sediment samples, such as the one of the aquatic Lepidoptera *Cataclysta*, but only the development of

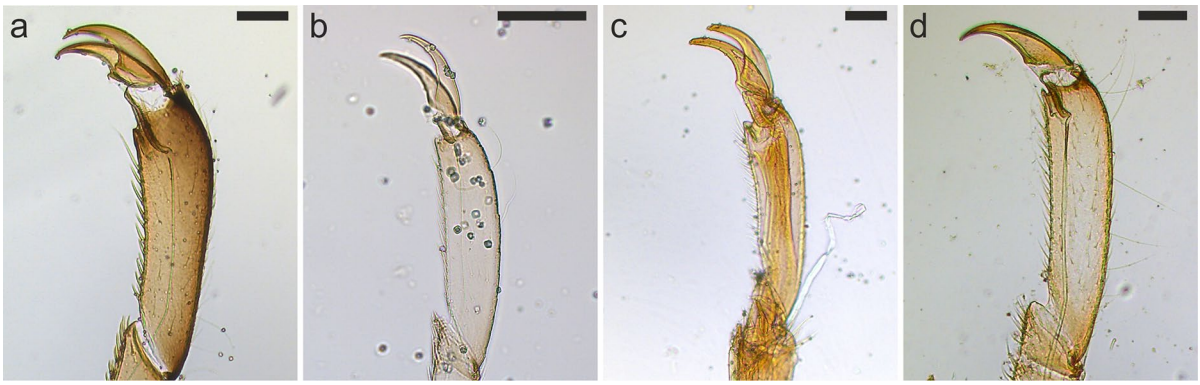


Fig. 13 Example legs and tarsal claws of Plecoptera. **a** Taeniopterygidae: *Brachyptera risi* leg. **b** Nemouridae: *Nemurella pictetii* leg. **c** Perlidae: *Perlodes jurassicus* leg. **d** Subfossil Plecoptera leg appendage. **a–d** from prepared specimens. Scale bars are 0.1 mm

this documentation of pre-identified specimens has allowed us to identify and associate this structure with a modern taxon name of a relatively cosmopolitan taxon. Finally, some mandible types, such as the mandibles of Plecoptera have not yet been illustrated in the paleoecological literature as far as we are aware, even though distinct morphotypes (in this case Perlidae-type, Nemouridae-type) seem to be apparent (Fig. 11).

Second, mandibles of several aquatic invertebrate groups have been described, also in publications addressing a paleoecological audience, but our compilation demonstrates that the morphological diversity of these structures is much higher than expected based on the available paleoecological descriptions. For example, Ephemeroptera mandibles described in Brooks et al. (2007), Rumes et al. (2005) and Luoto (2009) all belong to the same mandible type with an at least partly fused kinetodontium with the other incisor teeth, here named Baetidae-type (Fig. 8a–e). However, our compilation shows that at least several distinct mandible types can be separated within the Ephemeroptera larvae, which includes mandibles similar to the Baetidae-type but with kinetodontium separate from the other incisors (i.e. Caenidae-type and variants; Fig. 8i–o), mandible types with a broad tusk-like appendage characterizing *Ephemera* (Ephemeridae-type) or mandibles with a long serrated extension in place of the outer group of incisivi typical for Heptageniidae-type (Fig. 8q–t). It can be expected that further research will allow additional Ephemeroptera mandible types to be distinguished. Similarly, for Trichoptera two mandible types have previously been described in the paleoecological literature, including mandibles resembling the Polycentropodidae-type (Fig. 12l,n–p) by Luoto (2009) and Rumes et al. (2005) and the very similar mandibles of *Oecetis* and *Ecnomus* described by Rumes et al. (2005). However, our compilation shows that a wide range of additional mandible morphologies can be found within the Trichoptera, such as the strongly pyramidal shaped mandibles of Lepidostomatidae/Limnephilidae-type (Fig. 12a–c, h–j), that differ considerably from these described forms.

We expect that our compilation only covers a part of this variation, as we did not manage to cover the full range of Trichoptera larvae encountered across central Europe. It will therefore have to be determined whether fossil mandibles can be consistently identified to different Trichoptera taxa and subgroups of morphotypes based on the present compilation. However, several distinct groups seem apparent, including the Polycentropodidae-type with two inner cutting ridges (Fig. 12l, n–p), the previously described pyramidal Lepidostomatidae/Limnephilidae-type (Fig. 12a–c, h–j), and also the predatory mandibles of *Rhyacophila* (Fig. 12q, r) and *Oecetis* (Figs. 12h1). These types seem distinctive and recognizable and should be identifiable in the fossil record. Many of these mandibles were found by the authors in earlier research but could not be associated with any known taxa before this compilation. For the Odonata, one larval mandible type had been described from African lake sediments by Rumes et al. (2005). However, the

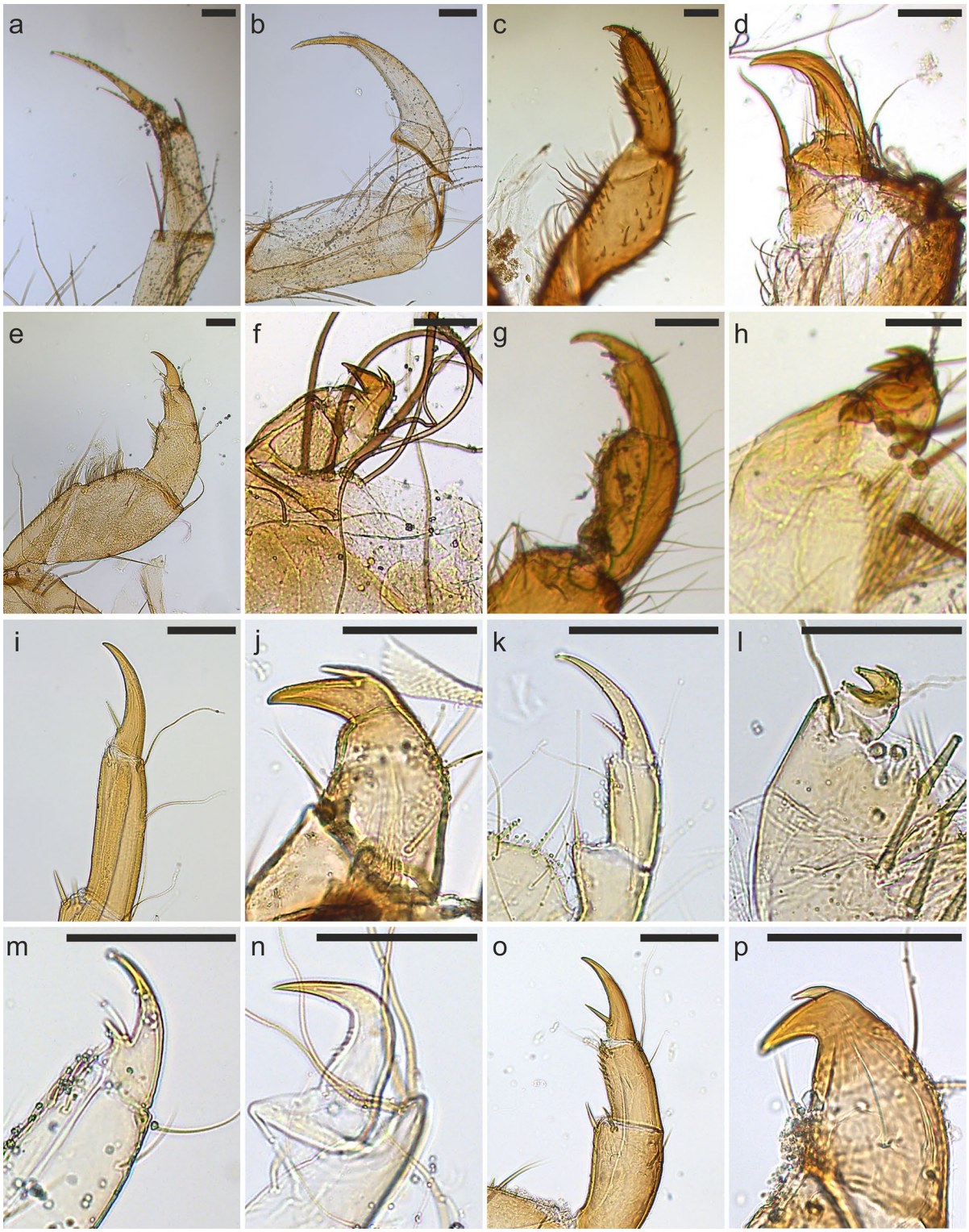
mandible types we describe here (Fig. 10a, b) differ considerably from this earlier description and indicate that also within the Odonata a considerable variety of mandible forms in Quaternary lake-sediment samples should be expected.

Applications to paleoenvironmental research

The descriptions of larval mandibles presented in this compilation facilitate and expand the identification of subfossil aquatic invertebrate mandible types preserved in Quaternary lake-sediment samples. The compilation supports researchers without access to modern reference collections to consistently identify and associate fossil mandibles with common aquatic invertebrates, in particular, the aquatic insect taxa (e.g. orders, families) that are often found amongst the remains in lake-sediment records. The high diversity of mandible types illustrated here, compared to earlier descriptions, ensure that previously undescribed mandible types within groups, such as Amphipoda, Isopoda, Trichoptera, Diptera, Plecoptera, Ephemeroptera, Odonata and aquatic Lepidoptera, will be recognized and classified consistently to these taxonomic groups. For several taxonomic groups, such as the Trichoptera, Ephemeroptera, Plecoptera and Diptera, a range of distinct morphotypes of mandibles seem apparent that can be identified in future studies. For Diptera, different mandible types have previously been described in the paleoecological literature and identified consistently in fossil records, for example: Chironomidae (McCarthy et al. 2021), Simuliidae (Currie and Walker 1992; Heiri 2004), and Chaoboridae (Uutala 1990; Lamontagne and Schindler 1994; Uutala et al. 1994). However, for Trichoptera, Ephemeroptera and Plecoptera, detailed taxonomic descriptions of different mandible types within these groups have, to our knowledge, not been published and used to classify mandible morphotypes observed in sediments.

Previous studies have introduced several chitinous remains, including mandibles of aquatic invertebrate groups, as paleoenvironmental indicators collected from surface-sediment samples or sediment cores (Frey 1964; Smol et al. 2001b; Luoto 2009). Additional insights are interpretable from sediment records when the chitinous remains presented here are combined with other remains (Adler and Courtney 2019), such as chironomid head capsules, Cladocera, Bryozoa, Oribatida, plant remains (Solhøy and Solhøy 2000; Verschuren et al. 2000; Courtney Mustaphi et al. 2021; Perret-dit-Gentil et al. in press) and other subfossils (Verschuren et al. 1999; Détriché et al. 2009). For example, the pattern of total chironomid head capsule abundance in combination with other aquatic invertebrate remains (including Trichoptera, Ephemeroptera and Chaoboridae mandibles) in surface sediments from Swiss lakes reflected bottom water oxygen concentrations at a threshold value of ~ 10% (Fig. 16a; Ursenbacher et al. 2020). The combination of chironomid assemblages based on head capsule identification and other aquatic invertebrate remains, including mandibles of Trichoptera and Ephemeroptera, was useful for examining cultural layers associated with archaeological lake-shore dwellings (Tóth et al. 2019), with Ephemeroptera characterizing lacustrine conditions before and after the deposition of the cultural layer, whereas these remains were not deposited during the existence of the lake-shore dwelling. This, together with major changes of the chironomid assemblage suggested a local eutrophication phase in near-shore environments. The invertebrate assemblage supported the interpretation that the cultural layers were deposited in situ into the sediments of Lake Zurich under lacustrine conditions and not on dry land (Fig. 16b). Both the chironomid assemblage and the other aquatic invertebrate remains from the infilled kettle-lake sediments at Slotseng, Denmark (Mortensen et al. 2011; Lemdahl et al. 2014), suggested an interval of shallowed lake water and possibly drier conditions during the late glacial (Fig. 16c). Relative abundances of indicator chironomid taxa and other invertebrate remains (e.g. *Chaoborus* mandibles) typical for fully lacustrine conditions decreased, whereas abundances increased of other chironomid taxa indicative of shallower water or even tolerant of semi-terrestrial conditions (e.g. *Limnophyes*). The presence of other semi-aquatic Diptera larvae, such as Limoniidae, as well as oribatid mites abundant in shallow-water, semi-terrestrial environments and soils, supported the interpretation of a short time interval of shallower and possibly even semi-terrestrial conditions at the transition from the Allerød to Younger Dryas (Fig. 16c).

These examples presented in Fig. 16 demonstrate the usefulness of identifying aquatic invertebrate and aquatic insect remains in Quaternary lake-sediment records, particularly in combination with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◂**Fig. 14** Example larvae claw appendages and pygopodia from prepared specimens of Trichoptera. **a** Polycentropodidae: *Plectrocnemia conspersa* tarsal leg claw and **b** pygopodium. **c** Hydropsychidae: *Hydropsyche siltalai* leg claw **d** pygopodium. **e** Lepidostomatidae: *Lepidostoma hirtum* leg claw and **f** pygopodium. **g** Leptoceridae: *Adicella reducta* leg claw and **h** pygopodium. **i** Limnephilidae: *Chaetopteryx villosa* leg claw and **j** pygopodium. **k** Leptoceridae: *Setodes argentipunctellus* leg claw and **l** pygopodium. **m** Psychomyiidae: *Tinodes maculicornis* leg claw and **n** pygopodium. **o** Limnephilidae: *Limnephilus* sp. leg claw and **p** pygopodium. Scale bars are 0.1 mm

identification of chironomid remains. The compilation and description of aquatic invertebrate mandibles presented in this study will allow a more reliable identification of major aquatic invertebrate groups such as Amphipoda, Ephemeroptera, Plecoptera, Trichoptera, Odonata and Coleoptera, also including mandible morphotypes not presently described in the paleoecological literature. As described above, within certain groups our compilation will also allow an identification of distinct morphotypes that will provide further (paleo-)ecological information in future assessments of fossil aquatic invertebrate assemblages in lake sediments. In this context it is interesting to note that several of the newly identified mandible types can be expected to provide information on past environmental conditions, trophic relationships and taphonomic processes. For example, Plecoptera and Ephemeroptera: Heptageniidae are usually restricted to running water environments (Moog 1995), and the mandible remains can therefore be used to indicate running water influence on fossil invertebrate assemblages. Similarly, the mandibles and head capsules of Simuliidae or Thaumaleidae have been used to indicate running water influence on fossil invertebrate assemblages (Currie and Walker 1992; Heiri and Lotter 2003; Heiri 2004). Rhyacophilidae as well as *Oecetis, Plectrocnemia,* and *Polycentropus* are predatory Trichoptera larvae (Moog 1995) and the description of these mandible types, similarly as those of the predatory Plecoptera: Perlodidae: *Perlodes* and the described Odonata and Coleoptera larvae, may help to more reliably separate predatory taxa in fossil aquatic insect assemblages. Similarly, the triangular mandible type characteristic of e.g. *Potamophylax*, *Limnophylus*, *Sericostoma*, *Pseudopsilopterix*, *Psychomyia* or *Melampophilax* often belong to shredders or grazers (Moog 1995) and may help to identify aquatic insect assemblages where these groups are particularly relevant.

As in the examples discussed above, the identification of these mandible types may be particularly useful combined with more detailed analyses of chironomid and other aquatic invertebrate remains such as Cladocera ephippia, Bryozoa sessoblasts and statoblasts, or Oribatida remains (not presented in this compilation). This will allow a detection and reconstruction of the contribution of remains, for example from deepwater taxa (such as profundal Diptera such as Chaoboridae and some Chironomidae, pelagic Cladocera; Figs. 5 and 6), littoral taxa (e.g. many shallow water Chironomidae and Cladocera taxa, Trichoptera, Ephemeroptera; Figs. 8, 12, 13, 14), semi-terrestrial taxa (e.g. some taxa of Chironomidae, Limoniidae, Psychodidae, Oribatida; Figs. 6 and 7) as well as lotic taxa (some Plecoptera, Simuliidae, Thaumaleidae, and lotic taxa within Chironomidae and Ephemeroptera; Figs. 6, 7, 11, 13 and 15) and thereby allow assemblage-wide inferences about past changes in habitats and environments based on aquatic invertebrate remains (Heiri 2004). Improved identification of mandible types facilitates the classification of functional groups (e.g. predators, shredders, grazers) within these assemblages, particularly for taxa with a wide range of feeding modes, such as e.g. Trichoptera larvae. This will potentially provide alternative approaches for the interpretation of aquatic ecosystem change based on aquatic invertebrate assemblages in lake sediments such as, e.g., reconstructions of the relevance of past functional groups (Luoto and Ojala 2018; Belle and Goedkoop 2021; Stivrins et al. 2021).

Conclusions

This compilation of chitinous remains observed in European lake sediments provides an additional tool for the analysis of subfossil invertebrate assemblages in late Quaternary and recent lake-sediment deposits (Ursenbacher et al. 2020; Bolland et al. 2021; Bennike et al. 2023). The descriptions include the dispersed taxonomic and paleoenvironmental literature on subfossil aquatic invertebrate remains in lake sediments. Many of the taxa presented have near cosmopolitan freshwater distributions and the compilation is therefore useful across many regions. However, specimens identified to species level mainly represent

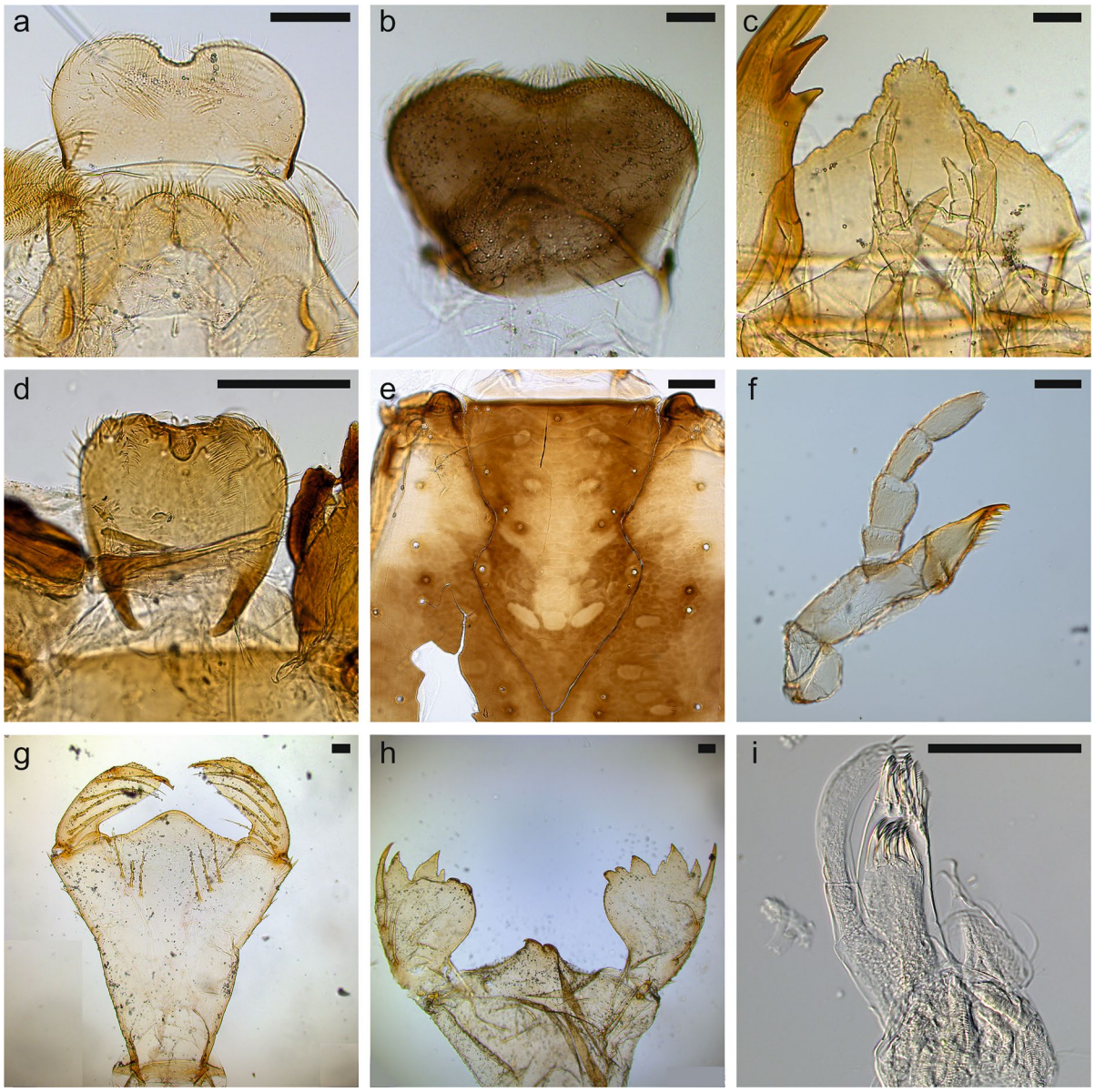

Fig. 15 Other aquatic invertebrate head and mouthpart remains from prepared specimens. **a** Labrum of Ephemeroptera: Leptophlebiidae: *Haprophlebia* sp. **b** Disarticulated labrum of Ephemeroptera: Ephemeridae: *Ephemera vulgata* (Linnaeus, 1758). **c** Labrum of Megaloptera: Sialidae: *Sialis lutaria* and part of one mandible at left. **d** Labrum of Trichoptera: Odontoceridae: *Odontocerum albicorne*. **e** Frontoclypeus and head chitin of Trichoptera: Rhyacophilidae: *Rhyacophila tristis* with sensory pits (round apertures), frontoclypeal suture outline, and coronal suture at bottom of image (Coppa et al. 2012; Friedrich et al. 2015). **f** Single maxilla and maxillary palp of Plecoptera: Nemouridae: *Nemoura* sp., note the mandible-like appearance and potential for confusion by analysts. **g** Odanata: Zygoptera mask showing prementum, labium, ligula, labial palps (with setae) and sclerotized movable hooks at the apex. **h** Odanata: Cordulegastridae: *Cordulegaster bidentata* mask showing part of the apical half of the prementum, ligula, large labial palps and movable hooks. **i** Maxilla of an Amphipoda: Gammaridae: *Gammarus fossarum* (Koch, 1836). Scale bar is 0.1 mm

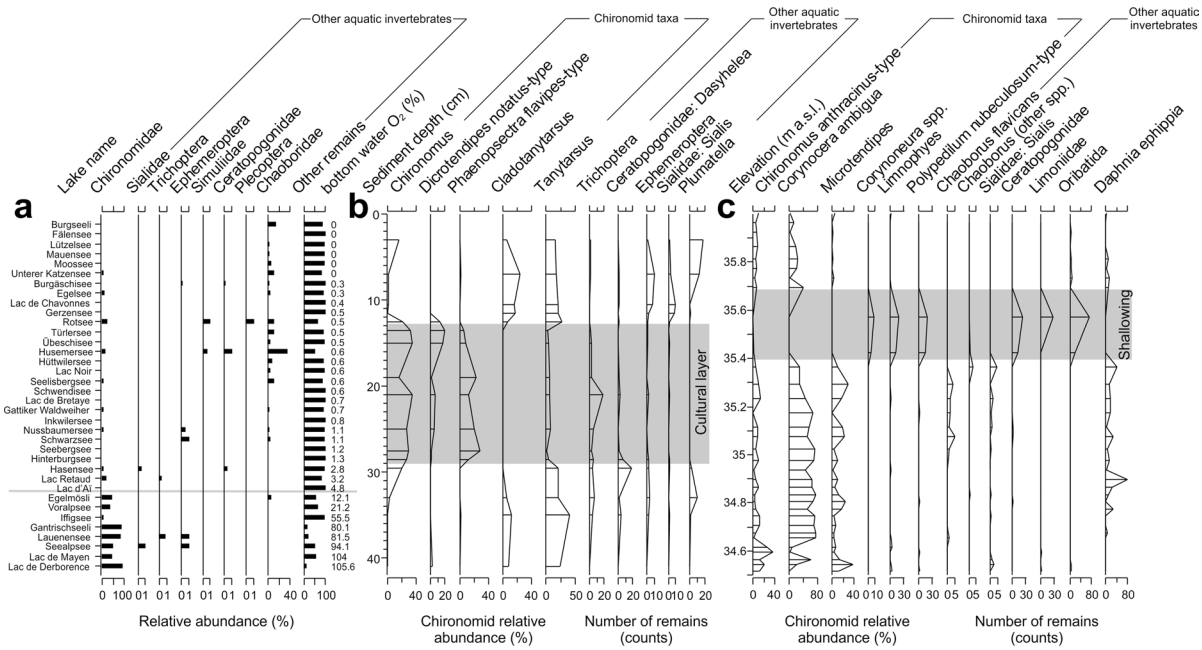

Fig. 16 Examples of aquatic invertebrate remains identified in lake-sediment studies from Europe. **a** Aquatic invertebrate assemblages in surface sediments from 36 lakes across Switzerland (Ursenbacher et al. 2020) compared with late summer bottom water oxygen concentration measurements. The sites are ordered according to bottom water oxygen concentration. The gray horizontal line shows the 10% bottom water-oxygen value that separates sites with high chironomid percentages from the remaining sites with low oxygen concentrations. **b** Aquatic invertebrate assemblages in sediment column 5060 obtained in a former Neolithic lake-side settlement at the site Zurich Opéra, Lake Zurich, Switzerland. The Neolithic cultural layer is indicated by the gray box (Tóth et al. 2019; Supplemental Fig. 1b). **c** Chironomid assemblages and counts of other aquatic invertebrate remains in sediments from the now infilled and terrestrialised former kettle lake at Slotseng, Denmark. The analyses support the interpretation of a late glacial shallowing of the lake in the section indicated by the gray box

the central European fauna, and future work will therefore be necessary to assess whether some of the newly presented mandible morphotypes are applicable to identifications outside of Europe or whether this classification needs to be modified and expanded to cover taxa from other biogeographic regions. Irrespective of these further developments, this compilation presents a first framework for the identification and morphotype assignment of aquatic invertebrate mandibles that goes significantly beyond previously presented classifications and describes mandibles and superficially similar structures from a large number of aquatic invertebrate species that were previously unrecognized, or only rarely identified, in palaeoecological studies.

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Declarations

Conflict of interest The authors declare to have no competing interests that might be perceived to influence the results and/or discussion reported in this paper.

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