

Süßwasserfauna von Mitteleuropa  
Freshwater Fauna of Central Europe

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von Mitteleuropa  
Bd. 21/26  
Empididae



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## General part

The Diptera family Empididae comprises three subfamilies; Empidinae, Hemerodromiinae and Clinocerinae (Sinclair and Cumming 2006) with some genera and species-groups of uncertain affinities considered *incertae sedis* as discussed in the following section. The family is important in biodiversity research as a biological indicator of certain biotopes (Plant 2014; Ivković and Plant 2015; Plant et al. 2017), as well as in evolutionary and behavioural research (Svensson and Petersson 1992; Cumming 1994; Funk and Tallamy 2000) and provides valuable models of sexual selection theory (LeBas et al. 2003; Gwynne 2008; Wheeler et al. 2012). The subfamilies Hemerodromiinae and Clinocerinae are widely known as ‘aquatic dance flies’ and they are amongst the most important predacious Diptera in lotic habitats (Wagner 1997a, Sinclair 2008). Both subfamilies are widely distributed all over the world except Antarctica. The subfamily Hemerodromiinae consists of two tribes (Hemerodromiini and Chelipodini) with more than 500 species and 18 genera (Plant 2011a, 2011b, 2011c, 2020). The subfamily Clinocerinae comprises 17 genera with more than 460 species (Sinclair and Cumming 2006; Sinclair 2008; Saigusa and Sinclair 2022).

In Europe there are 52 species of Hemerodromiinae belonging to 4 genera and 201 species of Clinocerinae belonging to 9 genera (Yang et al. 2007; Wagner and Gerecke 2008; Raffone 2011; Ivković et al. 2012a, 2014, 2017; Kustov and Zhrebilo 2014, 2015; Sinclair and Shamshev 2014; Palaczyk et al. 2015; Wagner et al. 2022). In Central Europe, there are 36 species of Hemerodromiinae and 92 species of Clinocerinae.

## Higher Phylogeny and Systematics of Empidoidea

The Empidoidea superfamily is here taken to include the families Hybotidae, Dolichopodidae, Atelestidae and Brachystomatidae as well as Empididae. The superfamily is situated phylogenetically between the lower and higher Diptera (Sinclair and Cumming 2006) but familial relationships within it have been subject to controversy. Chvála (1983) proposed a five-family system for the Empidoidea (Atelestidae, Microphoridae, Dolichopodidae, Hybotidae and Empididae) but since then a better resolution of the phylogeny has been developed, for example with the morphological studies of Wiegmann et al. (1993), Cumming et al. (1995), Yang (2004) and Sinclair and Cumming (2006). The most recent morphological evaluation of the Empidoidea by Sinclair and Cumming (2006) proposed five monophyletic families Atelestidae, Hybotidae, Dolichopodidae, Empididae and Brachystomatidae while analyses by Moulton and Wiegmann (2007) suggested that Chvála’s (1983) family system is still valid with the exception of the family Microphoridae which they included in Dolichopodidae. Finally, Pape et al. (2011) recognized eight families (Atelestidae, Brachystomatidae, Dolichopodidae, Empididae, Homalocnemiidae, Hybotidae, the “*Iteaphila*-group” and Oreogetonidae). Divergence times for Empididae (primarily subfamily Empidinae) were estimated to the late Jurassic or early Cretaceous (Chvála 1983; Grimaldi and Cumming 1999).

Chvála (1983) placed Empidinae, Brachystomatinae, Hemerodromiinae, Clinocerinae and Oreogethoninae in Empididae *sensu stricto*, while Sinclair and Cumming (2006) considered that Empididae should contain only the subfamilies Empidinae, Hemerodromiinae and Clinocerinae with five genera in the *Ragas*-group, *Brochella* Melander, *Philetus* Melander and three genera in the *Hesperempis*-group remaining *incertae sedis* in Empididae. Phylogenies based on nucleotide sequence data were constructed by Moulton and Wiegmann (2004, 2007) and Wahlberg and Johanson (2018). Confirmation of the monophyly of the Empidoidea already established by the morphological studies of Chvála (1983) and Sinclair and Cumming (2006) has been provided by nucleotide sequence data of Moulton and Wiegmann (2007). Wahlberg and Johanson (2018) established a new family within Empidoidea, Ragadidae, and removed the family status of Brachystomatidae.



At this time, Empididae comprise three subfamilies: Empidinae, Clinocerinae and a third subfamily classified as Brachystomatinae (*sensu* Wahlberg and Johanson 2018) or Hemerodromiinae (*sensu* Sinclair and Cumming 2006). In this book the well-known classification by Sinclair and Cumming (2006) is followed.

## Hemerodromiinae

### Included genera

Two tribes of Hemerodromiinae are recognised here, Hemerodromiini and Chelipodini (see following section on **Phylogeny and the fossil record**).

Hemerodromiini: included genera are. – *Antipodromia* Plant; *Chelifera* Melander; *Cladodromia* Bezzi; *Colabris* Melander; *Doliodromia* Collin; *Hemerodromia* Meigen; *Metachela* Coquillett and *Neoplasta* Coquillett. *Sematopoda* Collin and *Xanthodromia* Saigusa that were originally assigned to Hemerodromiinae but are now placed tentatively in Brachystomatidae (Sinclair and Cumming 2006). Only *Chelifera*, *Hemerodromia* and *Metachela* are known from Europe.

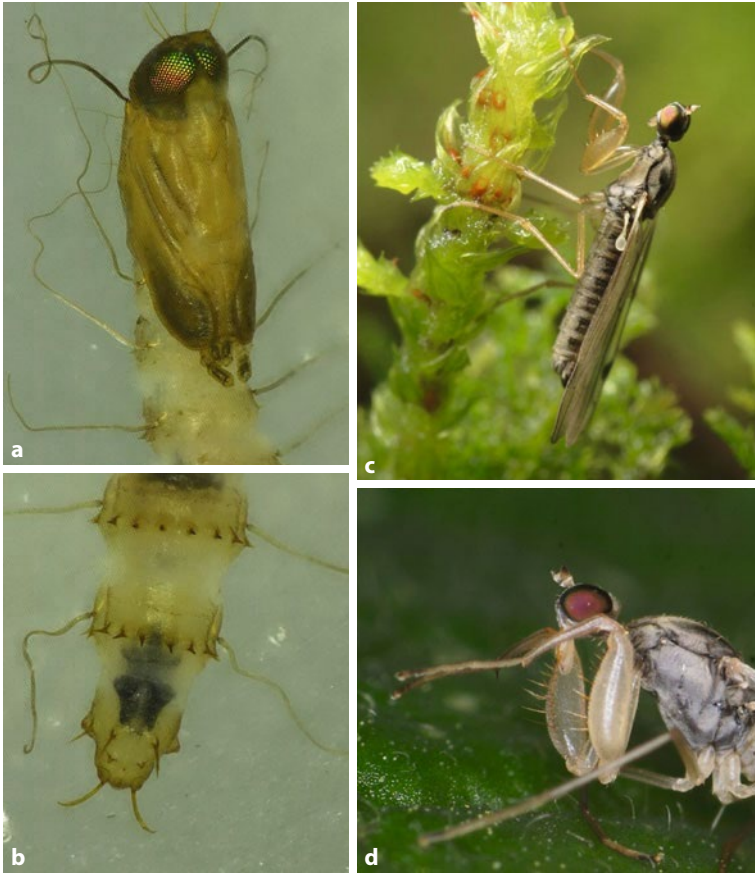
Chelipodini: included genera are. – *Achelipoda* Yang, Zhang and Zhang; *Afrodromia* Smith; *Anaclostectedon* Plant; *Chelipoda* Macquart; *Chelipodozus* Collin; *Drymodromia* Becker; *Monodromia* Collin; and *Sororsenexa* Plant.

Only *Chelipoda* is known from Europe, *Phyllodromia* is treated as subgenus (Plant 2007).

### Morphology

**Eggs.** Elongated; length 0.3–0.5 mm in *Chelifera* and 0.4–0.5 mm in *Neoplasta*; width approximately 0.1 mm (Wagner 1997a, Harkrider 2011). Females of *Neoplasta parahebes* MacDonald & Turner may produce from 60 to 90 eggs (Harkrider 2011).

**Larvae.** Small, whitish and vermiform, head capsule incomplete hemicephalic with retractile sclerites; the prolegs (abdominal ambulatory processes of larvae unlike segmented true legs) are well developed. Length of final instar of *Hemerodromia* spp. 4.0–4.3 mm; *Chelifera* spp. from Europe 6.0–6.7 mm (Ivković *personal observation*). Larvae of some *Metachela* have been measured at 5.5 mm and of some *Neoplasta* 4.5 mm (MacDonald and Harkrider 1999). The size of the newly hatched larvae of *Neoplasta parahebes* ranges from 600 to 800 µm, while the last of the three larval instars is around 4 mm in length (Harkrider 2011). However, the number of larval stages is unknown for other hemerodromiine genera. Brocher (1909) described *Chelifera preclatoria* (Fallén) larvae. Pomeisl (1953) gave a short description and figures of the anal segments of *Hemerodromia unilineata* Zetterstedt and *Chelifera flavella* Zetterstedt. Vaillant (1964) provided descriptions of larvae of *Hemerodromia unilineata* (Zetterstedt), *Chelifera stigmatica* (Schiner) and *Chelifera trapezina* (Zetterstedt). Dumbleton (1966) described a larva he thought to be of *Chelifera tantula* Collin from the New Zealand Sub Antarctic but based on Dumbleton's Fig. 3, Plant (2011a) considered it to have been incorrectly assigned to *Chelifera*. Larvae of *Chelifera*, *Hemerodromia*, *Metachela* and *Neoplasta* all have 7 proleg-s, but there are generically important differences in the anal segment (Figs 1–3). *Hemerodromia* has prominent divided apical lobes bearing setae, while *Chelifera*, *Metachela* and *Neoplasta* lack apical lobes (Vaillant 1964; Niesiołowski 1992a; Bremmer et al. 2009). Keys to some genera of aquatic Hemerodromiinae are provided by Brindle (1973), Niesiołowski (1992a) and Wagner (1997a) while Brammer et al. (2009) provide a good key for differentiation of larvae and pupae for the aquatic genera of Nearctic Hemerodromiinae that is also useful for European genera of aquatic Hemerodromiinae. So far as is known, only species of *Chelipoda* have larvae that do not occur under the water surface; the larva of *Chelipoda (Phyllodromia) melanocephala* (Fabricius) has been described by Tréhen (1969); it lacks prolegs and is 2.37–3.20 mm in length.



**Plate 1** *Hemerodromia unilineata* - oblique view of pharate adult in pupal skin (a) apical end of pupa with pharate adult (b); *Chelifera precatorea*: adult (c), front part of body with raptorial fore legs (d). (Photos: a, b Wagner; c, d Plant)

**Pupae.** The pupae of aquatic Hemerodromiini in the genera *Hemerodromia*, *Chelifera*, *Metachela* and *Neoplasta* are uniquely characterised by the presence of extremely long spiracular processes (Plate 1, Figs 4–6). These are apparently used for anchoring the pupa to the substrate of lotic and lentic habitats as well as for respiration (Wagner 1997a). The pupae of *Neoplasta*, *Metachela*, *Hemerodromia* and *Chelifera* are easily distinguished by the pattern of hooks and setae of the tergites and a good key exists for these aquatic genera (Brammer et al. 2009). The pupae of the non-aquatic Chelipodini remain unknown.

**Imagines.** Diagnosis. Small to medium sized flies from 1.0 to 5.5 mm (mostly 2.5 to 5.0 mm). Highly distinctive possessing raptorial forelegs with coxa very elongate and femur swollen bearing at least one row of strong setae ventrally. Forelegs separated from mid legs by much more than the distance between mid and hind legs (Plates 1, 2).

**Head.** Subovate or more usually distinctly posteroventrally compressed, ground colour usually dark but sometimes yellowish. Eyes reniform with anterior ommatidia enlarged, closely approximated or narrowly separated on face. Antenna with postpedicel short pointed conical, apical stylus shorter (*Hemerodromiini*) or longer (*Chelipodini*).



**Plate 2** Adults of: *Chelifera stigmatica* (a); *C. precatória* (b); *Chelipoda vocatoria* (c); *Chelifera stigmatica* (d). (Photos: Plant)

**Thorax.** Elongate. In lateral view scutum rather evenly arched but prescutellar area sometimes distinctly flattened and fused katepisternum + anepisternum distinctly arched along ventral margins. Scutum and laterotergite with setae well developed (Chelipodini) or scutal setae small and laterotergite bare (Hemerodromiini).

**Wing.** Elongate, axillary angle weakly developed. Vein C circumambient (except *Sororsenexa*) with only fine setulae along anterior margin but usually with distinct bristle near base. In European genera, cell dm present (but fused with bm in *Hemerodromia* and *Metachela*, lacking in *Phyllostromia* in which crossvein dm-cu absent) and cup present (absent in *Hemerodromia*); fork  $M_{1+2}$  and  $R_{4+5}$  present (Hemerodromiini) or absent (Chelipodini). Stigma present or absent but membrane otherwise unmarked, translucent clear or faintly tinted yellowish or greyish.

**Legs.** Front legs distinctly raptorial; with coxa very elongate (as long or longer than distance between its point of insertion on thorax and point of insertion of hind coxa) and femur inflated bearing distinct rows of setae and minute denticles ventrally. Mid and hind legs slender with short coxae and lacking raptorial modifications.

**Abdomen.** Usually with sternites less sclerotized than tergites. In European genera terminalia large with epandrium and hypandrium fused and keel-shaped, strongly reflexed anteriorly, clasping cerci not prominent (Chelipodini) or terminalia smaller with epandrium and hypandrium separate, extending posteriorly or only weakly reflexed anteriorly with well-developed clasping cerci dorsally (Hemerodromiini).

### Phylogeny and the fossil record

The phylogeny of Hemerodromiinae based on nucleotide sequence data suggests that this subfamily is most closely related to and a sister-group to Empidinae (Collins and Wiegmann 2002; Moulton and Wiegmann 2007) as established previously by the morphological analyses of Chvála (1983) and Sinclair and Cumming (2006). A detailed morphological cladistic study of Hemerodromiinae was

reported by Plant (2011a) who confirmed that the subfamily is monophyletic and a sister group to Empidinae from which it may have diverged by the late Jurassic or early Cretaceous, around 140 Mya. Few fossil Hemerodromiinae have been described and are all from Late Eocene or Oligocene Baltic amber (Plant et al. 2011a). Monophyly of the two tribes (Hemerodromiini and Chelipodini) was not proven, although the tribal concepts have been applied successfully in the Northern Hemisphere and in some parts of Southern Hemisphere, with the exception of some Neotropical and Australasian forms (Plant 2011a). Chelipodini radiated into two speciose sister groups, the ‘widespread *Chelipoda*-like group’ and the ‘Austral *Chelipoda*-like group’. A sister-group relationship between the widespread group and the Austral group (which subsequently radiated to include modern ‘Gondwanan’ forms) may indicate an early differentiation of the two groups, pre-dating later Gondwanan fragmentation (Plant 2011a). The phylogeny of Hemerodromiini has been less well studied and certain forms with some characteristics of Chelipodini (e.g. *Chelipodozus* Collin) were weakly resolved in this subfamily (Plant 2011a).

## Biogeography

The tribe Chelipodini (*sensu* Plant 2011a) is present in all biogeographical realms except the Afrotropical. *Sorosenexa* is confined to Australia; it is probably the most ‘plesiomorphic chelipodine genus’ (Plant 2011b) in a sister-group relationship with all other Chelipodini (Plant 2011a, 2011b). *Anaclastotedon* is undoubtedly one of the more plesiomorphic Chelipodini (Plant 2010) and in a cladistic analysis Plant (2011a) retrieved it as ‘basal’ group subtending the widespread and Austral Chelipodini clades. *Anaclastotedon* is currently found in Australia and eastern Asia and likely had a southern temperate origin with later extension northwards into Asia during the Tertiary. The widespread *Chelipoda*-like group has a worldwide distribution, including New Zealand and Australia while the Austral *Chelipoda*-like group has much narrower distribution, confined to New Zealand, New Caledonia, Lord Howe Island and Vanuatu (Plant 2011a). *Monodromia* is endemic to New Zealand. The systematic relationship of *Phyllodromia* to *Chelipoda* remains unclear but is undoubtedly very close in the case of Northern Hemisphere forms (MacDonald 1993; Plant 2011a) which have been described from the Holarctic and are known to be present in the Oriental (Plant 2015). Although *Phyllodromia* is present in New Zealand (Plant 2005) antipodean forms may be incorrectly generically assigned as they were recovered within the Austral group of *Chelipoda* in the cladistic analysis of Plant (2011a). *Afrodromia* and *Drymodromia* that were traditionally regarded as Chelipodini and are restricted to the Afrotropical are currently thought to be ‘basal’ to the entire Hemerodromiinae (Plant 2011a).

*Chelipodozus*, which is only doubtfully included in Hemerodromiini (Plant 2011a) is known with certainty only from southern South America although forms perhaps referable to it are also present in Australia. In South America it has clear Andean affinities (*sensu* Morrone 2006) with loci of endemism mostly within Chile (Plant 2008).

The tribe Hemerodromiini is present in all biogeographical realms except Antarctica (Plant 2011a). *Hemerodromia* is considered to be of recent northern origin with greatest diversity in the Northern Hemisphere, but it is also speciose in southern Africa and the mountains of the African Eastern Arc (Plant 2011a) and there are numerous undescribed species from Southeast Asia hinting at an undisclosed centre of diversity in the region (Plant 2011a, 2020). *Hemerodromia* is present in the Amazon Basin in Brazil (Câmara et al. 2014, 2015) and there are at least 80 undescribed species present in tropical and subtropical regions of the Neotropics (J.T. Câmara *pers.com.*) although the genus is apparently absent from Chile and southern Argentina. The genus *Neoplasta* is restricted to Nearctic and Neotropical realms. *Neoplasta inturbida* Collin from New Zealand is probably a species of *Cladodromia* and there are some described species of *Neoplasta* from Chile and many undescribed *Neoplasta*-like Australasian forms that probably require reassignment to *Cladodromia* or putative new genera. *Metachela* is also restricted to the Nearctic and Neotropical realms with the exception of one species, *Metachela nigriventris* (Loew) which occurs in Central Europe (Yang et al. 2007). *Chelifera* is globally distributed excepting the Afrotropical Realm, with the greatest diversity in the Holarctic. Whereas at temperate latitudes *Chelifera* has been found to occur across a wide elevation

range, in tropical regions it is more or less restricted to high mountains and may have dispersed into the Oriental tropics along montane ‘corridors’ of cool, moist forest uplifted by Himalayan orogenesis (Plant et al. 2012). *Antipodromia* is endemic to New Zealand (Plant 2011c) as is *Doliodromia* (Collin 1928) while *Colabris* is confined to the Meso-American Neotropics (Yang et al. 2007). Species of *Cladodromia* have been described from South America and New Zealand and undescribed species are present in Australia. However, the systematic relationships between forms of ‘*Cladodromia*’ found in different parts of the world, and with ‘*Neoplasta*’ have not been investigated and the relationships between Southern Hemisphere forms of *Cladodromia*-like taxa remains unclear.

## Biology and Ecology

The biology of the immature stages of Chelipodini is little known. Adults of most genera are associated with shaded terrestrial habitats on moist soils although *Monodromia* and *Sororsenexa* have been found in dry forest biotopes. *Chelipoda vocatoria* (Fallén) and *Phyllodromia melanocephala* (Fabricius) have been caught in emergence traps placed over soil or decomposing wood (Delettre et al. 1998) and it is assumed that immature stages of all Chelipodini are essentially terrestrial or at most, semi-aquatic, favouring damp or waterlogged edaphic conditions. Tréhen (1969) has described the larva of *P. melanocephala* extracted from soil but found no obvious morphological adaptations for life in aquatic habitats. The larvae of Chelipodini are assumed to be predators of other soil organisms.

So far as is known, the immature stages of Hemerodromiini are entirely aquatic. Females of *Neoplasta* may deposit eggs in various substrates, such as branches submerged in the water, usually in small clusters (Harkrider 2011). Females of *Chelifera* spp. were found depositing eggs in moss mats that are constantly washed by water (Ivković *personal observation*). Larvae can be found in a wide variety of substrata, e.g. gravel, macrophytes, moss-carpets, bark of rooting wood of still or fast flowing streams and rivers (Wagner and Gathmann 1996; Harkrider 2011; Ivković et al. 2007, 2012b) and some species can also be found along the shoreline of lakes (Prziborov and Shamshev 2006; Ivković et al. 2010). They can be also found in sand and silt, but in low densities (Wagner and Gathmann 1996; Ivković et al. 2007, 2012b). *Hemerodromia* larvae mostly prefer moss or stony substrate and they have been taken in emergence traps placed over such substrates (Ivković et al. 2007, 2012b). Positive correlation was established between number of emerging specimens of Hemerodromiinae and water velocity (Harper 1980; Ivković et al. 2012b). Adults are usually found in the riparian vegetation close to the water where larvae occur. Niesiołowski (1992) gives a schematic description of preferences of different Hemerodromiinae genera for various types of habitats along water courses, but this needs to be treated with caution as it refers only to Poland and the habitat associations may not be sustained over a wider geographical area.

Larvae and adults of *Neoplasta* have been reported feeding on chironomids (Harkrider 2000a, 2011) and larvae have been found in pupal cases of Trichoptera (Knutson and Flint 1971). Peterson (1960) reported that adult *Neoplasta scapularis* (Loew) “probed at larvae of *Simulium piperi* Dyar and Shannon”. Harkrider (2011) even recorded feeding of male *Neoplasta scapularis* on a *Neoplasta parahebes* male. Peterson (1960) also reported feeding of adult *Metachela collusor* Melander on adult Simuliidae. Feeding of adult *Chelifera siveci* Wagner was observed on adult Psychodidae in riparian vegetation in Alipaša’s springs, Montenegro (Ivković *personal observation*). Several females of *Chelifera trapezina* were repeatedly observed feeding on a single large prey item (Mycetophilidae) but males were never observed feeding in groups. Larvae of *Hemerodromia sequyi* Vaillant were found feeding on *Simulium* larvae (Vaillant 1953a), and Hamada (1993) showed an association between *Hemerodromia* larvae and *Simulium perflavum* Roubaud larvae. The abundance of Hemerodromiinae larvae (*Hemerodromia*) is correlated with the abundance of available prey, mainly Chironomidae and Simuliidae larvae (Harper 1980; Ivković et al. 2007). Positive correlations between number of *Hemerodromia unilineata* individuals and Chironomidae and Simuliidae specimens have been found from several sites and microhabitats in different studies performed in Croatia (Ivković et al. 2012b). A similar relationship was established for *Chelifera siveci* but only with abundance of Chironomidae (Ivković et al. 2013b).

Phenology studies have revealed that, for different species (or even within a species) there can be one or two, and in some cases multiple generations per year depending on the species and the geographical region where the species occurs or even different positions along the water course (Harper 1980; Masteller and Buzby 1993; Wagner and Gathmann 1996; Harkrider 2000b; Ivković et al. 2007, 2012b). During an investigation of daily emergence patterns, Ivković et al. (2013c) established that *Hemerodromia unilineata* emerges during the daytime and that increasing water temperature positively stimulates emergence. Emergence only commenced when a threshold water temperature of 16 °C was reached and increased rapidly at higher temperatures. Sex ratio varies depending on the species and the generation and a sex ratio of 1:1 has only rarely been recorded. Usually, the number of males of *Chelifera trapezina* (34–46%) and *Chelifera diversicauda* Collin (29–36%) are somewhat lower than the number of females. Extreme differences in sex ratio among different years were observed for *Chelifera pyrenaica* Vaillant (16–41%) and *Chelifera siveci* (20–60%) (Wagner and Gathmann 1996; Ivković et al. 2013b). For *Neoplasta parahebes* and *Chelifera loveti* Melander the sex ratio is close to 1:1 and in case of *Neoplasta scapularis* and *Metachela albipes* (Walker) males predominate (Harkrider 2000a). Size differences between the sexes in *Chelifera* are obvious and females are always larger than males (Wagner and Gathmann 1996; Ivković *personal observation*).

Zonation along the river watercourse has been established on various occasions for Hemerodromiinae. Where different species occur in different habitats, some species have a stronger preference for headwater streams or upper parts of a river (e.g. *Chelifera precabunda*, *Chelifera precatorea*, *Chelifera siveci*) while others may be more frequent in lower parts of a rivers (e.g. *Hemerodromia* spp.) (Harper 1980; Ivković et al. 2007, 2012b). The biggest influence on Hemerodromiinae assemblages along longitudinal gradients of rivers and streams is mean (or maximum) yearly water temperature (Ivković et al. 2007, 2012b) and the biggest influence in changes in abundance and community structure during the years is probably due to changes in water discharge but even more than that changes through time that takes communities to develop (Wagner and Gathmann 1996). At least some aquatic Empididae appear to be cold tolerant and may even actively migrate towards habitats that will freeze with the onset of winter (Oswood et al. 1991). Hemerodromiinae occur across a wide range of elevations although Chelipodini diversity is low in relatively arid lowland tropical forests experiencing seasonal drought (Plant et al. 2012).

Joost (1980b) reported usage of front legs of the males of *Hemerodromia illiesi* Joost, 1980 and other Hemerodromiinae (some *Chelifera*) not just for catching prey but also for wrestling with other males, “as when they meet, they move their bodies, swinging like wrestlers, then they try to heave up the opponent, using the front legs, and throw him into the air. In this way they seem to maintain the best mating places”. On the other hand, males of Neotropical *Neoplasta* seem to guard the undersides of leaves and they chase away any other males that land but no “wrestling” was observed (Plant *personal observation*). Mating behaviour is not recorded for any species in Hemerodromiinae. Mermithid nematode parasites (Nematoda: Mermithidae) have been observed parasitizing different species of genus *Neoplasta* (e.g. *Neoplasta parahebes*, *N. scapularis*), and they were also observed parasitizing *Chelifera loveti* Melander and two species of *Metachela* (*Metachela albipes* (Walker), *M. collisor* (Melander)) (Harkrider 2010).

## Clinocerinae

### Included genera

*Afroclinocera* Sinclair; *Asioclinocera* Saigusa & Sinclair; *Asymphyloptera* Collin; *Bergenstammia* Mik; *Clinocera* Meigen; *Clinocerella* Engel; *Dolichocephala* Macquart; *Hypenella* Collin; *Kowarzia* Mik; *Oreothalia* Melander; *Phaeobalia* Mik; *Proagomyia* Collin; *Proclinopyga* Melander; *Rhyacodromia* Saigusa; *Roederiodes* Coquillett; *Trichoclinocera* Collin and *Wiedemannia* Zetterstedt.

Only *Bergenstammia*, *Clinocera*, *Clinocerella*, *Dolichocephala*, *Kowarzia*, *Phaeobalia* and *Wiedemannia* are known from Central Europe with *Trichoclinocera* known from North Europe and *Roederiodes* from South Europe.



## Morphology

**Eggs.** Elongated, in *Roederiodes wirthi* Chillcott, length from 0.3–0.45 mm and 0.12–0.16 mm in width (Sinclair and Harkrider 2004). Each female of *R. wirthi* may produce from only a few to more than 60 eggs which are typically scattered over the surface of the oviposition site, either individually or in groups of two or three, lightly attached to the surface (Sinclair and Harkrider 2004). The sizes of the eggs of other species of Clinocerinae are unknown.

**Larvae.** Apneustic, whitish, medium sized and vermiform with eight pairs of well-developed prolegs or in *Dolichocephala*, with creeping welts (Wagner 1997a; Sinclair and Harkrider 2004; Plate 3). Larvae of *Wiedemannia ouedorum* Vaillant were described by Vaillant (1951a) as 7.0 mm long and 0.8 mm wide. Mature larvae of *Trichoclinocera* are 4.5–6.0 mm in length (Sinclair 1994). Vaillant (1952, 1953b) described larvae that can be found in the hygropetric habitats such as *Clinocera nigra* Meigen, *Clinocera stagnalis* (Haliday), *Kowarzia barbatula* (Mik), *Kowarzia bipunctata* (Haliday) and *Dolichocephala ocellata* (Costa). Dumbleton (1966) gave a description of *Clinocera* larvae, most likely *Clinocera gressitti* Smith, which was 4.5–5.5 mm long. Pomeisl (1953) described the anal segments of several Clinocerinae (*Wiedemannia lamellata* (Loew), *Clinocera appendiculata* (Zetterstedt) and *Clinocera stagnalis* (Haliday)). Brindle (1964, 1973) provided a detailed description of *Clinocera stagnalis*, which is 5.0–6.0 mm when fully grown, and provided some additional details for other Clinocerinae occurring in Britain (e.g. *Wiedemannia bistigma* (Curtis), *Wiedemannia lota* Walker). Niesiolowski (1992) described several Clinocerinae larvae (e.g. *Clinocera appendiculata* (Zetterstedt), *Wiedemannia zetterstedti* (Fallén)). There are three larval instars found in *Roederiodes wirthi* and the final instar is 4 mm long; a complete description was provided by Sinclair and Harkrider 2004. The larvae of *Roederiodes junctus* Coquillet was described by Needham and Betten (1901).

**Pupae.** (Plate 3) Prothorax bearing respiratory organ (Sinclair and Harkrider 2004). The pupae of Clinocerinae from North America can be distinguished at generic level (Sinclair and Harkrider 2004), but no such key exists for the European genera. Pupae of *Wiedemannia ouedorum*, *Clinocera nigra*, *Clinocera stagnalis*, *Kowarzia barbatula*, *Kowarzia bipunctata* and *Dolichocephala ocellata* were described by Vaillant (1951a, 1951b, 1952). Dumbleton (1966) gave a description of what was probably *Clinocera gressitti* pupae, which was 6.0 mm in length. Brindle (1969) provided a description of *Wiedemannia rhynchops* (Nowicki) pupae. Niesiolowski (1992) described several different Clinocerinae pupae (e.g. *Clinocera wesmaeli* (Macquart), *Wiedemannia fallaciosa* (Loew)). Pupae of *Trichoclinocera* spp. were collected from rocky substrate and described by Sinclair (1994). Although not observed, adult eclosion in *Trichoclinocera* is hypothesized to involve spines and caudal hooks that hold the pupa fast to benthic mosses and algae, allowing the teneral adult to pull itself free and float up to the surface (Sinclair 1994). This mechanism might also apply with *Clinocera* and *Wiedemannia*. Pupae of *Roederiodes wirthi* were described by Sinclair and Harkrider (2004) and were 4.3–4.4 mm long.

Currently, descriptions of both the larvae and the pupae are of limited use as the immatures of most species remain undescribed. Descriptions are, however, useful for genus level identifications, although caution is required as certain genera remain little studied.

**Imagines.** Diagnosis. Medium sized flies 3.0–6.0 mm (*Asymphyloptera* 1.0–1.5 mm). The wings are narrow (anal lobe not developed, forming an obtuse angle), CuA<sub>2</sub> recurved with apex of cell cup, labellum sucker-like, empodium pulvilliform, and stout, erect, costal setae.

**Head.** Eyes dichoptic, widely separated below antennae, densely pubescent (bare in *Proclinopyga*, some *Proagomyia*). Face iridescent or with blue pruinescence; sides of face nearly parallel. Pair of divergent ocellar setae. Antennae with first flagellomere globular to strongly tapered; arista biarticulated with second flagellomere short, third flagellomere filiform. Unpaired, thinly sclerotized, anterior ventrocervical sclerites present or consisting of darkly pigmented membrane. Mouthparts with long, slender apodeme arising from dorsal margin of labrum (except *Asymphyloptera*, *Proagomyia*); labrum broadly triangular in frontal view (except *Roederiodes* and *Asymphyloptera*); lacinia