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REVIEW ARTICLE

Trophic ecology of Plecoptera (Insecta): a review

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Abstract

We here review the current knowledge on the trophic ecology of stoneflies, an aquatic insect group of substantial ecological importance in lotic systems. We provide information on the feeding habits of nymphs and adults of the different families and highlight those studies that support particularly interesting findings. Regarding nymphs, we discuss the state of the art on aspects such as foraging strategies and behaviours, food acquisition mechanisms, the existence or absence of electivity for certain trophic resources, and enzymatic activity and its relationship with the assimilation efficiency of food. For adults, we highlight the differential importance of feeding among taxa. For both nymphs and adults, we report what is known about their role in aquatic and terrestrial food webs. Finally, we present some of the gaps on the trophic ecology of these insects and provide some research agendas that could be carried out to fill them.

Keywords: *Stoneflies, nymphs, adults, feeding habits, feeding behaviour*

Introduction

Feeding is one of the most important aspects of the biology of any animal. The trophic ecology of an animal group includes not only food habits but also aspects such as feeding strategies, food handling and roles within the food webs to which they belong (e.g. Gerking 1994). Unfortunately, information on this topic for some invertebrate groups is scattered and incomplete despite the diversity and ecological importance that those particular taxa may have.

Plecoptera (stoneflies) is a widely distributed insect order, including more than 3500 species, and a significant ecological component of running waters, particularly in unpolluted streams and rivers (Fochetti & Tierno de Figueroa 2008). Plecoptera is composed of two main groups: Arctoperlaria, including Systellognatha (six families) and Euholognatha (six families), and Antarctoperlaria (four families). Like some other aquatic insect

orders, stoneflies typically have aquatic (eggs and nymphs) and terrestrial (adults or imagoes) life stages. This fact has ecological implications from a trophic point of view in both environments and in the flow of matter and energy between them (e.g. Baxter et al. 2005).

Although the existence of data on the trophic ecology of Plecoptera is old, it was not until the beginning of the 20th century that the information that began to appear exceeded isolated observations and assumptions. Nevertheless, and despite the improvement on the topic in the last century, there are still many aspects that we do not know, and this is particularly remarkable in the case of adults.

In the present article, we review what is known about the trophic ecology of stoneflies, and we will also highlight some of the current gaps in the knowledge of this topic and, consequently, suggest future avenues of research.

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Nymphal feeding

The first data on the feeding of Plecoptera nymphs come from the early 19th century, from researchers such as Grau (1926) and Hynes (1941), although other authors also contributed observations, even earlier (see Brinck 1949, p. 154, for a review). Frison (1929) produced one of the first reviews of the studies carried out to date and provided new data on several species. Although much has been advanced in the knowledge of the trophic ecology of stonefly nymphs, there are still some gaps to face.

Plecoptera nymphs have a wide array of mechanisms to obtain their food, both behavioural and morphological. Thus, they are represented in almost all the functional feeding groups (FFGs) recognized by Merritt et al. (2017). Traditionally, within Arctoperlaria, Systellognatha nymphs have been classified as predators and those of Euholognatha as phytophagous–detritivorous, but exceptions are widespread in both cases. Some early authors suggested that the herbivorous feeding mode is the ancestral condition in Plecoptera (Chisholm 1962). Zwick (1980) separates Euholognatha and the vast majority of Antarctoperlaria, as detritivorous–phytophagous, from the predators Eustheniidae and Perloidea, with Chloroperlidae as omnivorous. Nonetheless, this author points out that this classification is an oversimplification and that feeding habits must be studied at the species level.

In Arctoperlaria, some differences in the mouthparts exist between Systellognatha and Euholognatha nymphs, such as the morphology of the mandibles or maxillae (Brinck 1949; Hynes 1976; Zwick 1980; Stewart & Stark 2002), but within these two groups, not many morphological differences are detected among species. An exception is the systellognathan Peltoperlidae and Pteronarcyidae, whose mouthparts are similar to those of the euholognathans due to adaptative convergence (Stewart 2009). Nonetheless, some taxa have developed particular characters of their mouthparts to improve their efficiency in obtaining certain resources. An example is represented by members of the genus *Brachyptera*, which have setae in the maxillae that are thought to function as brushes, improving the efficiency with which they scrape the algae attached to different types of substrates (Hynes 1941). In Antarctoperlaria, the gripopterygid *Notoperla archiplatae* (Illies, 1958) and the diamphipnoid *Diamphipnoa* also have a brush of stout bristles in the galea to feed on periphyton (Hynes 1976; Díaz Villanueva & Albariño 1999). Other species with hairs or sensilla in the mouthparts probably use them for gustation, such as the austroperlid *Klapopteryx kuscheli* Illies, 1960 (Albariño 2001) or several

taeniopterygids (Stewart & Stark 2002). Additionally, the labrum differs among Systellognatha and Euholognatha. In the first case, its morphology seems to favour the detaching of the prey and their transport backwards, while in the other case, it seems to assist in the collecting of the food, which is also helped by the action of the laciniae (Brinck 1949). Nonetheless, even species with typical phytophagous mouthparts may behave entirely as predators in later instars, as occurs in *Illiesoperla mayi* (Perkins, 1958) (Yule 1990), and in some other omnivore gripopterygids, which have mouthpart characteristics that resemble those of the carnivorous type (Sephton & Hynes 1983). Thus, morphological constraints do not seem to condition the feeding type of the nymphs, although they likely affect feeding efficiency.

The main structures that predator nymphs use to capture their prey are the mouthparts, particularly the laciniae, with which they grasp the prey, and the mandibles. Some authors suggest that the strong claws of the legs of some Systellognatha aid in catching prey (e.g. Monakov 2003). Many species swallow the prey almost entirely and do not chew them at all, the so-called engulfers (e.g. Jones 1949, 1950; Siegfried & Knight 1976; Allan 1982; Peckarsky 1982); thus, prey can be easily recognized after gut dissection or other methods of gut content analysis. Nonetheless, other authors point out opposite observations, i. e. that predators shred their prey (in Brinck 1949). In the foregut, predators have strong chitin teeth that may help to process the animal material (Zwick 1980; Kapoor 1997). The main prey captured and ingested by stonefly predators are Chironomidae, Baetidae (and other mayflies), Simuliidae and, sometimes, Trichoptera (even case-building larvae), but other organisms may also occasionally be part of their diet (e.g. Brinck 1949; Allan 1982; Allen & Tarter 1985; Peckarsky & Wilcox 1989; Sandberg & Stewart 2001; Bo et al. 2008). Curiously, experimental studies and observations under controlled conditions have shown that some prey are sometimes avoided, such as the predaceous dipterans referred to below, the mayflies *Ephemerella* or *Heptagenia* or the isopod *Asellus* (Molles & Pietruszka 1987; Peckarsky & Wilcox 1989; Tikkanen et al. 1997), probably due to defensive mechanisms or antipredator behaviours of these prey. Some of these strategies include swimming away from the predator (even entering the drift), crawling or staying in a freezing posture, and, particularly in *Ephemerella*, utilizing the scorpion posture (Peckarsky 1980,

1996; Fuller & Rand 1990; Wooster & Sih 1995). Molles and Pietruszka (1987) observed that the larvae of two predaceous dipterans produced aversive responses in *Hesperoperla pacifica* (Banks, 1900), while herbivorous Diptera of similar size and shape were consumed. This may support some of the predictions of the optimal foraging theory (Stephens & Krebs 1986), since the hazard of facing a dangerous prey probably does not overcome the reward of consuming it. Some of the predictions of this theory have also been supported by other studies in which stonefly predators show a preference for slow moving or sedentary prey in comparison to more mobile prey, even when the encounter rate with the latter is higher (Tikkanen et al. 1997).

Food selection occurs in several species, both in predators and phytophagous–detritivorous species (e.g. Hynes 1970; Shepard & Minshall 1984; Díaz Villanueva & Albariño 1999; Albariño 2001; Bo & Fenoglio 2005; López-Rodríguez et al. 2009c), albeit it has been more widely studied in predators. Some of the cases of the preference or electivity of prey by predators have been experimentally related to habitat complexity, for instance in trials where different levels of substrate complexity have been used (Peckarsky & Penton 1989; Turnbull & Barmuta 2002). Williams et al. (1993) demonstrated that under the same environmental conditions, the perlid predator *Dinocras cephalotes* (Curtis, 1827) had no preference between the two species of mayflies that were offered to it in a laboratory study. Nonetheless, predation efficiency decreased with increasing habitat complexity, at least in the interaction with one of the two preys. Some authors also suggest that the substratum not only provides shelter for preys but also affects the ease with which a predator senses or pursues prey by interfering with their antennae and agility (Fuller & Rand 1990). In other cases, body size seems to be the most important factor. In this respect, Sheldon (1969) found a strong correlation between the size of a stonefly predator and its mayfly prey. Supporting this, Allan and Flecker (1988) experimentally demonstrated that the body size of both prey and predator determines the interaction between some stoneflies and their prey. In this study, the researchers found that predators would obtain a greater reward from the consumption of smaller, more vulnerable prey (and from dipterans relative to mayflies), but the attacks did not seem to be biased towards the most profitable prey. In fact,

some authors have pointed out that certain predator stoneflies do not select prey on the basis of nutrient requirements (in terms of proteins and lipids) during their development (Duvall & Williams 2000). Other studies also support that prey vulnerability, together with fixed behavioural selection (such as the swimming motion of *Baetis* sp. nymphs, which act as a stimulus to attack in some Perlodidae predators; Peckarsky & Wilcox 1989), is a probable proximate cause of selective predation (Peckarsky & Penton 1989; Genito & Kerans 1999).

Together with size and vulnerability, hunger level influences prey selection (Allan et al. 1987; Williams 1987; Monakov 2003). In an experimental stream, Molles and Pietruszka (1987) demonstrated that hungry stonefly predators (*Hesperoperla pacifica*) had a wider prey spectrum than well-fed nymphs, which concentrated on intermediate-sized prey. The researchers explained their findings in light of the optimal foraging theory. Hunger levels are related to the loading time of the gut, but few studies have attempted to analyse gut loading time or clearance in Plecoptera (e.g. Henderson et al. 1990). For instance, Miyasaka and Gentai-Kato (2009a) found that the gut clearance time was similar among three species of perlids but that this time was greater in the winter (2 days) than in summer (1 day) in relation to temperature differences. In other aquatic insects, the loading time was determined to be 4 to 8 hours (Cummins 1973). This has implications in the case of predators, as it also conditions their functional response through the handling time (the time invested in detecting the prey, capturing it, swallowing it, etc.). Some authors pointed out that stonefly predators followed a type III functional response when exposed to baetid prey experimentally (Kratz 1996), although other studies (Elliott 2003) support a type II functional response (*sensu* Holling 1959). In an interesting set of experiments, Elliott (2003) found no change in the handling time of four species of predator stoneflies (perlids and perlodids) with prey density. Nonetheless, previous experiments showed differences in the handling time of the perlid *Acroneuria abnormis* (Newman, 1838) when preying on *Hydropsyche* (longer handling time) or *Baetis* (shorter; Genito & Kerans 1999).

In those nymphs that do not actively select trophic resources, much of the gut content reflects the availability of resources in the environment, suggesting that nymphs feed randomly on the most abundant trophic resources (Dudgeon 2000). This generalist trait has been widely accepted for these and many other aquatic insects (Cummins 1973) and may also

be responsible for some of the ontogenetic shifts in the diet of some species. Thus, ontogenetic shifts in the diet (metaphoetesis) of several species are a consequence of size limitation in the intake of trophic resources (for instance, some first-instar predators are not able to subdue certain prey because these prey are larger than them) but also of resource abundance during some moments of their developmental period. This behaviour is common in species inhabiting different regions (e.g. Winterbourn 1974; Fuller & Stewart 1977; Allan 1982; Fenoglio 2003; Bo & Fenoglio 2005; Miyasaka & Gentai-Kato 2009b; López-Rodríguez et al. 2009c). In fact, some studies have shown that the diet of different species of the same size is similar and that it differs between size classes of the same species (Allan 1982; Allan & Flecker 1988).

The absence of specialized mechanisms of food acquisition in most Plecoptera nymphs results in relatively common accidental ingestion of particular items. Accidental ingestion of animal remains by non-predator species is widespread among stoneflies (e.g. Brinck 1949; Cummins 1973; Díaz Villanueva & Albariño 1999; Albariño 2001; Kozáčková et al. 2009). Some authors suggest that the ingestion of such animal matter by nonpredatory insects is a way to adapt to a nutrient-deficient diet (Price et al. 2011). In rearing experiments, even dead nymphs have been found to be eaten by some individuals (Hynes 1941; Brinck 1949). Many nymphs simply collect the resources as they find them in their way. In fact, it is commonplace for some to swallow sand grains and other mineral particles when feeding (e.g. Brinck 1949; Brittain 1973; Derka et al. 2004; Zwick & Hohmann 2005; Kozáčková et al. 2009; Silveri et al. 2009; López-Rodríguez & Tierno de Figueroa 2012). Albeit accidental, some authors point out that mineral material could act as a gridding crop in some periphyton and detrital feeders (Cummins 1973). Exceptions have been found to this main generalist character, with some species behaving as specialists. One of them is *Notoperla archiplatae*, which tends to feed on diatoms but is not able to feed on coarse particulate organic matter (CPOM), even when this resource is experimentally manipulated to be the unique type of food available to nymphs (Albariño & Díaz Villanueva 2006).

The accidental ingestion of food items not belonging to the diet is also observed in predator nymphs, which sometimes show vegetal matter in their guts. In some cases, this matter may come from the gut of the prey eaten by the nymph (Brinck 1949; Dorvillé & Froehlich 2001), but several cases of typically predaceous species feeding on vegetal or detrital

matter have been reported (e.g. Berthélemy & Lahoud 1981). For instance, nymphs of several different species of *Isoperla* have been reported to feed on vegetal matter, algae and diatoms (Frison 1935; Brinck 1949; Hynes 1976; Stewart & Stark 2002; López-Rodríguez et al. 2009c).

Predators typically hunt by actively searching for prey, but some species, such as *Dimocras cephalotes*, behave like an ambush predator in dim light and a searching predator in darkness (Sjöström 1985). Elliott (2000) experimentally determined that *Dimocras cephalotes* and *Perla bipunctata* Pictet, 1833 behaved successfully as ambush predators at dusk and dawn, *Isoperla grammatica* (Poda, 1761) was a night searching predator, and *Perlodes microcephalus* (Pictet, 1833) was active during the day but below the substratum (and very active from dusk to dawn); thus, interspecific differences in the diel activity seem to be common among these organisms. Predaceous nymphs tend to accidentally find their prey in the same microhabitat that they occupy. In this process, the antennae seem to play an important role, mainly acting as tactile sensors (e.g. Brinck 1949; Peckarsky 1984). In some species, experimental studies have shown that predators can distinguish between the contact of the antennae with a conspecific and with a prey, and even among different prey species (Williams 1987). Some authors also point out that the eyes and the visual stimuli are relevant in prey hunting (e.g. Kühtreiber 1934), but some species are more active at night, when the sight sense is less effective (Elliott 2000). In an interesting experiment, Peckarsky and Wilcox (1989) proved that the perlodid *Kogotus modestus* (Banks, 1908) is able to discriminate and select prey using hydrodynamic cues associated with the swimming escape movement of the prey. Peckarsky (1982) also suggests that chemotactile mechanisms may be important in prey searching.

Feeding habits of Euholognatha

Nemouroidea is composed of five families, closely related to Scopuridae and together constituting the Euholognatha. The feeding of Notonemouridae has been studied in *Madenemura* nymphs from Madagascar, which feed on CPOM (including wood), fine particulate organic matter (FPOM), fungi, filamentous red algae and microorganisms (Benstead & Pringle 2004; Tierno de Figueroa et al. 2007), and in nymphs of *Afronemoura* from Cape (South Africa), which are shredders of CPOM (Palmer & O'Keeffe 1992). On the other hand,

South American Notonemouridae are classified as scrapers by Ramírez and Gutiérrez-Fonseca (2014), citing Domínguez and Fernández (2009). Nonetheless, more studies are needed to complete the study of the diet of these nymphs in this region. The remaining four families of Nemouroidea are widely known from a feeding point of view, and all the taxa studied up to now are phytophagous–detritivorous (Monakov 2003). Most Nemouridae are primarily detritivorous shredders and may also experience ontogenetic shifts in diet (e.g. Brittain 1973; Azzouz & Sánchez-Ortega 2000; López-Rodríguez et al. 2009a, 2010). In other species, FPOM is the main trophic resource they ingest; thus, they are considered collector–gatherers, even when diatoms or other algae are also found in the gut of these nymphs (e.g. López-Rodríguez et al. 2008; Kozáčková et al. 2009). Some other taxa feed on a mixture of both resources, thus acting as both shredders and collector–gatherers (e.g. Silveri et al. 2008b). Madsen (1974) also found that algae and CPOM were the main food items in the diet of *Amphinemura sulci-collis* (Stephens, 1836). A curious case is the species *Protonemura gevi* Tierno de Figueroa & López-Rodríguez, 2010, a cavernicolous stonefly of which only one population is known to date and that completes its entire life cycle in a cave (López-Rodríguez & Tierno de Figueroa 2012). This population is divided into two main groups of individuals, one at the entrance of the cave and one at the end, approximately 60 m away, and they differ in the main food components of their diet. Nymphs at the entrance are usually found on wood and feed mainly on CPOM, and nymphs at the end feed principally on detritus and, occasionally, on animal matter, as a possible response to the scarcity of food within the cave. Nonetheless, animal remains have been found in other non-cavernicolous nemourids (e.g. Kozáčková et al. 2009). Capniidae nymphs also show a quite variable diet, feeding mainly on detritus, diatoms, filamentous algae, fungi, mosses or pollen, and thus principally behaving as collector–gatherers or scrapers (e.g. Monakov 2003; Navarro-Martínez et al. 2007; López-Rodríguez et al. 2008, 2017; Bo et al. 2013; Boggero et al. 2014). Although some authors have catalogued Leuctridae as shredders (e.g. Lillehammer 1988), nymphs seem to be mostly detritivorous collector–gatherers or a combination of both FFGs (e.g. Tierno de Figueroa et al. 2003; López-Rodríguez et al. 2009b, 2012b; Murányi et al. 2012; Peralta-Maraver et al. 2012), but they can also incorporate other food items, such as diatoms (e.g. López-Rodríguez et al. 2009a). Thus, a relatively great variability in feeding habits also appears in this family.

Finally, Taeniopterygidae nymphs seem to be more phytophagous than detritivorous, although a wide trophic spectrum also exists in this case, since FPOM, diatoms, fungi, pollen, mosses, CPOM (e.g. Sephton & Hynes 1984; Azzouz & Sánchez-Ortega 2000; López-Rodríguez & Tierno de Figueroa 2006; Fenoglio et al. 2009a; Tierno de Figueroa et al. 2016; Quevedo-Ortiz et al. 2017) and animal remains have been found in their guts (e.g. Fenoglio et al. 2009a). They behave mainly as either collector–gatherers or scrapers, the latter mainly comprising nymphs of certain genera, such as *Brachyptera* (Hynes 1941; López-Rodríguez et al. 2009a).

To our knowledge, the only known study on the feeding behaviour of Scopuridae nymphs is that of Jin and Bae (2005), in which the species *Scopura scorea* Jin & Bae, 2005 was observed to feed on leaves from the riparian forest.

Feeding habits of Systellognatha (Perloidea and Pteronarcyioidea)

Some Systellognatha families have been more intensively studied than others from a feeding point of view. In general, Perloidea are considered mainly predators, but in many families and particular species, other food items form part of the nymphal diet, at least during some stage of their development. This is the case, for instance, of several species of Perlidae and Perlodidae, in which first instars (and, thus, small nymphs) are phytophagous–detritivorous (e.g. Brinck 1949; Berthélemy & Lahoud 1981; Azzouz & Sánchez-Ortega 2000; Ramírez & Gutiérrez-Fonseca 2014). In Perlodidae, nymphs of the genus *Isoperla* seem to be less predatory than other species (e.g. Hynes 1976; Feminella & Stewart 1986; Stewart & Stark 2002; López-Rodríguez et al. 2009c), and even when the nymphs act mainly as predators, their trophic spectrum is narrower than that of other coexisting perlodids (López-Rodríguez et al. 2012a). Other species from different genera of perlodids also show this feeding behaviour and include non-animal matter in their diets (e.g. Fenoglio et al. 2007a). The nymphal prey spectrum of this family is quite wide, including chironomids, baetids, heptageniids, hydropsychids and other trichopterans, blackflies, ceratopogonids, several families of stoneflies, and even odonates, which account for intraguild predation (e.g. Stewart & Stark 2002; Fenoglio et al. 2007a, 2009b; Fenoglio et al. 2010b; Silveri et al. 2008a; Tierno de Figueroa et al. 2016; López-Rodríguez et al. 2018b). A similar situation occurs in Perlidae nymphs, but, due to the slightly larger size of some species (e.g. *Perla*,

Dinocras), their effect on the prey populations may be greater than that of perlodids and tend to be frequently observed in higher levels of the food webs (e.g. Peralta-Maraver et al. 2017). Chironomidae and Baetidae seem to be some of the preferred prey of the nymphs with predaceous habits (although many others have also been pointed out), generally those of mid to final instars, and in most of the studied species, as in some other Perlodea, a trophic shift from primary to secondary consumers has been pointed out (e.g. Lucy et al. 1990; Dorvillé & Froehlich 2001; Tomanova et al. 2006; Fenoglio et al. 2007b; Bo et al. 2008; Tierno de Figueroa et al. 2015; Manko et al. 2016; Hurtado-Borrero et al. 2018; Tamaris-Turizo et al. 2018). Chloroperlidae, which are phylogenetically related to Perlodidae and Perlidae, are considered omnivorous (Zwick 1980). The items found in the gut of some of the studied species are FPOM and CPOM, unicellular organisms, but also other minor components, like chironomid larvae and Oligochaeta, are found in nymphs of intermediate to large size (e.g. Derka et al. 2004; Zwick & Hohmann 2005; Silveri et al. 2009; Rúa et al. 2011).

Regarding Pteronarcyioidea, most studies were carried out focusing on the family Pteronarcyidae. Near the beginning of the 20th century, Muttkowski and Smith (1929) pointed out that *Pteronarcys* fed on leaves. Since then, several other studies have contributed to the knowledge of this family in terms of several different aspects of the trophic ecology of its nymphs (e.g. McDiffett 1970; Nebeker 1971; Martin et al. 1981; Perry et al. 1987). Apart from detritus, the nymphs of some species also ingest filamentous green algae, diatoms and animal matter, such as mayfly nymphs or dipteran larvae (Richardson & Gaufin 1971; Fuller & Stewart 1977; Stewart & Stark 2002). Nymphs of Peltoperlidae, such as those of pteronarcyids, seem to be mainly shredders and thus skeletonize leaves (Wallace et al. 1970; Ruggles & Tarter 1991), but they sometimes ingest also diatoms and moss fragments (Elwood & Cushman 1975; Stewart & Stark 2002). To our knowledge, no specific studies exist on the feeding habits of Styloperlidae nymphs, although they are considered shredders of decayed tree leaves (DeWalt et al. 2018).

Feeding habits of Antarctoperlaria

Nymphs of *Antarctoperlaria* are also either predatory or phytophagous–detritivorous. A recent paper from Ramírez and Gutiérrez-Fonseca (2014)

classifies the four families of this suborder into FFGs according to the information in Domínguez and Fernández (2009). Based on this information, Austroperlidae are considered shredders; Diamphipnoidae are both scrapers (*Diamphipnoa* sp.) and shredders (*Diamphipnopsis* sp.); Eustheniidae are predators; and Gripopterygidae include scrapers, shredders and collector–gatherers. Few studies exist on the feeding habits of species from this suborder of Plecoptera, and most of them focus on the most diverse family of this suborder, the gripopterygids. Sephton and Hynes (1983) found that several species of this family feed on detritus, mixed with algae and higher plant tissues. The studies conducted by Froehlich (1969) and Froehlich and Oliveira (1997) show that different species of gripopterygids feed on CPOM (skeletonizing the tissues of leaves), mosses, algae and detritus. Díaz Villanueva and Albariño (1999) point out that periphyton (mainly diatoms) serves as the main trophic resource in the diet of *Notoperla archiplatae*. On the other hand, Tierno de Figueroa et al. (2006) found that two species of gripopterygids from Chile, namely *Antarctoperla michaelsoni* (Klapálek, 1904) and *Limnoperla jaffueli* (Navás, 1928), differed in nymphal feeding habits, with detritus serving as the main food item in the diet of the first, and diatoms serving as the main item in the diet of the second. Nonetheless, a previous study by Valdovinos (2001) in Chile suggested that the same two species acted in the processing of leaf litter as shredders, but no gut content analysis was carried out, and the function was assumed using the classification of FFGs by Merritt and Cummins (1996). Some species of *Illiesoperla* and *Eunotoperla* represent particular cases among members of this family because, contrary to other gripopterygids, they behave as predators (Sephton & Hynes 1983; Yule 1990). Their main prey are chironomids and mayflies, but they also feed on blackflies, stoneflies (in *Illiesoperla mayi*, including members of its own species; Yule 1990) and trichopterans. Analyses of the gut contents of austroperlids from Australia show that they feed on wood, shredding it, although they also incorporate other food items such as diatoms or detritus (Sephton & Hynes 1983). In South America, the species studied within this family also feed mainly on CPOM (Albariño 2001; Albariño & Díaz Villanueva 2006). On the other hand, the feeding habits of the family Diamphipnoidae are poorly investigated. A personal communication to Wantzen and Wagner (2006) by another researcher points out that large nymphs of this family are shredders, feeding even on wood. Nonetheless, as

mentioned before, they are considered either scrapers or shredders by some authors, depending on the species (Ramírez & Gutiérrez-Fonseca 2014). Finally, Eustheniidae are considered omnivores in Australia, and several species incorporate a substantial amount of animal matter into their diet, mainly chironomids and mayflies, as well as caseless tricopteran larvae (Winterbourn 1974; Devonport & Winterbourn 1976; Sephton & Hynes 1983; Turnbull & Barmuta 2002).

Trophic role of stonefly nymphs in ecosystems

Stream food webs are characterized by two different but interconnected carbon pathways, the detrital and the primary-producers pathways, although the former tends to be the most important (Wallace et al. 1997; Allan & Castillo 2007). In both pathways, we can find stoneflies at different trophic levels, and some taxa even simultaneously participate in the two pathways. Many Plecoptera nymphs are detritivorous or phytophagous during their entire development, thus belonging to the first trophic level. Other Plecoptera nymphs, as mentioned in previous paragraphs, are detritivorous or phytophagous only during their first instars, occupying the first trophic level, but shift to higher levels when they grow. Third, there are nymphs of certain species that, in a given period of their development, are both primary and secondary consumers; thus, they are truly omnivorous and belong to a trophic level slightly lower than that of the pure predators.

The resources on which the stonefly nymphs feed are important for their biomass production and thus for the biomass available for organisms in other trophic levels. This includes not only invertebrate and vertebrate predators but also decomposers and detritivores, which feed on the remains of these nymphs (such as exuviae). The effect of food quantity and, even more importantly, quality on the secondary production of these (and other) insects has been repeatedly studied. For instance, Yule (1986), comparing the diet and growth of six species of the gripopterygid *Dimotoperla*, found that those fed a high-quality diet were the fastest growing species and had larger sizes. López-Rodríguez et al. (2009c) pointed out that the secondary production of three species of perlodids inhabiting a temporary stream was a consequence of the differential contribution of each of the food items ingested by the nymphs. In a subtropical river, Benke et al. (2001) found that stonefly predators with a relatively high secondary production were consumed by other invertebrates, such as odonates or megalopterans, thus contributing importantly to their biomass and population. On the other hand,

Albariño and Balseiro (2011) suggested that the effect of deciduous plant species of low quality on the larval growth of an austroperlid species may have ecological implications for secondary production. Lieske and Zwick (2007) highlighted how the ingestion of biofilm causes faster growth than conditioned leaves under experimental conditions. This effect of food on the secondary production of nymphs is a consequence, finally, of assimilation efficiency and thus of the enzymatic pool they have to use to degrade and digest organic matter. The presence or absence of certain enzymes affects the spectrum of food on which nymphs can feed and the efficiency with which these insects digest these resources. There are a few studies that have assessed these biochemical aspects. One of these studies examined the digestive enzymes of two detritus-feeding pteronarcyid species and found that the proteolytic activity in the midgut of both species was high but that their digestive systems are not adapted to efficiently use the polysaccharides in the detritus (Martin et al. 1981). Another study analysed the activities of the main digestive enzymes in two species of perlodids inhabiting a temporary stream and with different food regimes, with one being more predaceous than the other (Tierno de Figueroa et al. 2011). The results showed that the species behaving mainly as predators had more activity of the enzymes related to the digestion of animal matter, such as protease, lipase and trypsin, than the more phytophagous species, which had higher amylase activity. Even in closely related species of large perlid predators, some differences have been reported in the enzymatic activities implicated in the digestion of food (López-Rodríguez et al. 2012c). These differences have been related to their trophic spectrum and the efficiency of assimilation of certain resources, and may be a factor determining their coexistence. In this respect, other physiological strategies may also play an important role (Sanz et al. 2014). On the other hand, environmental conditions, such as temperature or pH, also play an important role in the assimilation efficiencies and feeding of some nymphs (Nebeker 1971; Miyasaka & Gentai-Kato 2009a; Tixier et al. 2012), and this has consequences on growth (Sweeney et al. 1986).

The role of certain organisms in the assimilation efficiency of certain low-quality trophic resources by stoneflies (and by other macroinvertebrates in general) may be extraordinarily important, as occurs with microorganisms implicated in the decomposition of leaves fallen from the riparian vegetation. These organisms, mainly fungi and bacteria, could be viewed as keystone taxa in the sense of Paine (1995). Cummins (1973), Anderson and Cummins (1979) and Anderson and Sedell (1979) pointed out that the microbial organisms associated with several

different resources are the primary source of nutrition for aquatic insects and are important to process organic matter. Several authors have found that organic matter, particularly CPOM, becomes more attractive, palatable or assimilable to Plecoptera after microbial conditioning of leaves (Madsen 1974; Bengtsson 1984). For instance, *Pteronarcys proteus* Newman, 1838 seems to assimilate cellulose by means of acquired microbial enzymes obtained through the ingestion of microbially conditioned detritus (Sinsabaugh et al. 1985). This is probably widespread among other stonefly species, as many of them likely have weak cellulase activity in their guts, similar to many other aquatic insects (Monk 1976). In an interesting study, Reynolds et al. (1997) suggested that the nitrogen obtained by *Aphanicercia* species came from the microbial biofilm on the surface of leaves using stable isotopes.

Stonefly nymphs are also important in the processing and cycling of matter, as many of them are an important part of the detritivore coenosis, such as *Nemurella pictetii* (Klapálek, 1900) and *Leuctra nigra* (Olivier, 1811) in England (Henderson et al. 1990) or *Klapopteryx kuscheli* in the Andes (Albariño 2001). The latter was proven to process 88.75% of the CPOM placed in the experimental chamber in laboratory experiments. This suggests that this species is an important node in the transformation of CPOM into FPOM. Nonetheless, this species does not feed equally in leaves coming from different species of trees. In an additional *in situ* experiment with leaves from seven different species, Albariño and Balseiro (2011) demonstrated that this species was unable to consume tough leaves, and that among deciduous species, consumption was proportional to the C:N ratio (eating a higher quantity of high C:N ratio leaves). One of the most extensive studies carried out in a stonefly species (*Pteronarcys scotti* Ricker, 1952) is that of McDiffett (1970). This author measured respiration and egestion rates in the laboratory and growth rates in samples from the field using calorimetric determination. This allowed him to build a 17-month energy budget for an average nymph, which ingested approximately 13.4 kcal (approximately 3.2 g of dry matter). These results indicated a low assimilation and growth efficiency for the species studied but also suggested that a quantity of 5.2 g of leaves would be broken down by a nymph over a 14-month period. Further studies in other pteronarcyid species (*Pteronarcys proteus*) found that the assimilation was $119 \text{ kcal} \cdot \text{m}^{-2} \cdot \text{year}^{-1}$ and that the nymphs consumed between 41 and 64% of the litterfall in the study stream (Perry et al. 1987). Other estimates in particular environments, such as acid streams,

indicate a reduction of 10% in detritus consumption (Pretty et al. 2005). Some authors pointed out that the energy available for growth may be 34% and 41% in two different species of Plecoptera (in Zwick 1980). Within the detritivorous pathway, stoneflies may also participate in the decomposition process of dead animals, as suggested by Fenoglio et al. (2005) in an *in situ* experiment carried out with fish carcasses, although micro-consumers seem to have more importance in the process (Fenoglio et al. 2010a).

Those nymphs that behave mainly as predators are usually found in higher trophic levels in the macroinvertebrate food webs but they are also in mid to high trophic levels in freshwater food webs when including vertebrates. Thus, they may at least partially control populations of several other macroinvertebrates (chironomids, mayflies, blackflies) by direct consumption, although this would only have an important influence on the community structure if they are not generalists when feeding (Dudgeon 2000). Peckarsky (1982) compiled several studies that found a direct effect of stonefly predators on the prey populations of several macroinvertebrates, and Peckarsky (1991) confirmed these results experimentally. The effect of predators on prey populations also depends on abiotic regimes, and thus, benign hydraulic conditions for predators increase their impact (Peckarsky et al. 1990). As a consequence, trophic cascades may develop in lotic communities where stoneflies are in the highest trophic levels, as a consequence of the effect of some predators on their prey. An example is the study by Malmqvist (1993), in which both direct and indirect effects of a stonefly predator, namely *Diura nanseni* (Kempny, 1900), reduced leaf litter decomposition rates. Additionally, the consumption of predator nymphs by fish seems to cascade to lower trophic levels (Buria et al. 2010; Rodríguez-Lozano et al. 2016), although this pattern is not widespread (López-Rodríguez et al. 2018a). Additionally, stonefly predators may exert an indirect effect on the fitness of their prey. Peckarsky et al. (1993) assessed this effect on *Baetis bicaudatus* Illies, 1969 mayfly nymphs experimentally and found that the feeding rate was reduced in treatments with predator (Perlodidae) presence, probably as a consequence of a disruptive drift or swim response to predator encounters. Over the long term, prey living in the presence of predatory stoneflies caused *Baetis* nymphs to mature at smaller sizes. The presence of predators also conditions the particular microhabitat that potential prey exploit, but the effect may differ among species. In an experimental stream, Bo et al. (2010) tested this idea through a substratum selection experiment with two potential stonefly prey,

Amphinemura sulcicollis and *Brachyptera risi* Illies, 1969, and the predator *Perla marginata* (Panzer, 1799). These authors found that one of them changed its microhabitat preference when the predator was present, while the other remained in the habitat that the species frequented when the predator was absent.

Plecoptera are also part of the diet of some other macroinvertebrates. For instance, Townsend and Hildrew (1979) found that stoneflies, together with chironomids, were important in the diet of a trichopteran predator, namely *Plectrocnemia conspersa* (Curtis, 1834). Other studies have also found stonefly nymphs in the gut of predators, but they tend to be less frequent compared to other prey types (in Zwick 1980; Baekken 1981; Bo et al. 2011; Peralta-Maraver et al. 2017). Even those nymphs that are in the highest trophic levels of the macroinvertebrate food webs are frequently preyed upon by vertebrates, mainly fish. Several species of fish incorporate stoneflies into their diet, such as the brown trout (*Salmo trutta* Linnaeus, 1758), brook trout [*Salvelinus fontinalis* (Mitchill, 1814)], rainbow trout [*Oncorhynchus mykiss* (Walbaum, 1792)] and cutthroat trout [*Oncorhynchus clarki* (Richardson, 1836)], among others (e.g. Maitland 1966; Hubert & Rhodes 1989; Duffield & Nelson 1993, 1997, 1998; Montori et al. 2006; Fochetti et al. 2008). Even eels [*Anguilla rostrata* (Le Sueur, 1817)] have been found to incorporate perlids in their diet (Kopeck et al. 2019). Additionally, birds associated with aquatic environments, such as the grey wagtail (*Motacilla cinerea* Tunstall, 1771), white-throated dipper [*Cinclus cinclus* (Linnaeus, 1758)] and blue ducks [*Hymenolaimus malacorhynchos* (Gmelin, 1789)], incorporate stoneflies into their diet (Jost 1975; Veltman et al. 1995; Bougaham et al. 2014). Apart from the direct consumptive effects, stoneflies may suffer indirect effects of the presence of fish, as reported in the previous paragraph (Soluk & Collins 1988; Feltmate & Williams 1991). Moreover, other vertebrates may feed on stoneflies at times. For instance, Stewart et al. (2001) found a mature nymph of *Paracapnia augulata* Hanson, 1961 in the gut of the red-spotted newt [*Notophthalmus viridescens* (Rafinesque, 1820)] from North America, although this animal fed more frequently on adults.

Adult feeding

The trophic ecology of adult stoneflies is considerably less well known than that of the nymphs. This is partly due to the much longer life duration of the immature stages (where the growth of the animal is

concentrated) but also to the erroneous idea that adult stoneflies are relatively inactive. This last statement has been proven to be false, as pointed out by Zwick (1990) and Stewart (1994), who claimed that more scientific studies should address this issue due to its major ecological and evolutionary importance. In any case, many misconceptions about the feeding of these animals during their imaginal state (such as that most of them do not feed) have been maintained in the literature even more than 80 years after Frison (1935) highlighted the need to negate these erroneous ideas. Moreover, adult feeding data are currently available only for fewer than 150 species. Those data on trophic ecology are based on direct observations in nature or laboratory, gut content analyses, sometimes stable isotope analyses, or experiments, whereas for many other stoneflies, their imaginal feeding habits (or the absence of them) are assumed from extrapolations of what is known in other species.

The first information on Plecoptera adult feeding dates to more than a century ago, when authors such as Smith (1910) or Rousseau (1921) (in Frison 1929) stated that adult stoneflies do not feed. Nevertheless, some authors from the same time as Newcomer (1918) or Wu (1923) reported cases of adults feeding on vegetal matter; or even, two decades before, Kempny (1898, in Brinck 1949) suggested that adult Nemouridae are carnivorous. However, the most accepted idea was that stoneflies, like other aquatic insects with short adult lifespan (e.g. mayflies), do not ingest food when adults. Currently, it is known that stoneflies have an adult lifespan ranging from only a few days in some species that do not feed to some weeks in those that do feed (Hynes 1976), and that they perform some important activities during that stage of their life with consequent energetic costs (e.g. production of vibrational signals for mate encounter, aggregation behaviour, copulation, flight, dispersion, oviposition, etc.) (Stewart 1994).

The idea that adult stoneflies do not feed was partly supported by the assertion that the mouthparts are reduced at the imaginal stage (e.g. Mertens 1923; Schoenemund 1924, in Hynes 1942). Nevertheless, this is not true for all Plecoptera and, for instance, Burmeister (1839), almost a century before, had distinguished the genera *Nemoura* and *Perla* (reported as *Semblis*) according to the development of the mouthparts, which are respectively well developed or reduced. Kühtreiber (1934) pointed out that European Nemouroidea lack reduced mouthparts (even though he thought that they did not feed), and this is also true for the remaining

Euholognatha and Antarctoperlaria (Zwick 1980). Hynes (1976) pointed out that reduced mouthparts are present only in Systellognatha, although, like the remaining stonefly taxa, all of them drink water. However, as noted by Brinck (1949), while in large setipalpians (such as Perlidae and some genera of Perlodidae, mainly Perlodinae), mandibles are membranous rudiments, in the small ones, such as some Isoperlinae and especially in Chloroperlidae, despite having partially reduced mouthparts, mandibular teeth are sclerotized. On the other hand, K  threiber (1934, in Frison 1935) pointed out that the central part of the gut of adult stoneflies is reduced and, subsequently, it is not possible for them to feed. However, this is not true, at least for many species, because feeding has been demonstrated in a large number of taxa.

Frison (1935) highlighted a possible pattern of diurnal activity in adult stoneflies that are able to feed and nocturnal activity in those that are non-feeders. Nevertheless, this author also pointed out that many exceptions exist to this general pattern among the North American species that he had studied. Exceptions are common all around the world. For example, in southern Europe some Perlidae species of the genera *Dinocras* and *Perla*, in which adult feeding does not seem to be very important (Tierno de Figueroa & Fochetti 2001; R  a & Tierno de Figueroa 2013), can be active during the day.

Some authors have related the existence of adult feeding with the nymphal diet, considering that species with carnivorous nymphs (mainly Systellognatha) do not feed during the adult stage and that species with phytophagous–detritivorous nymphs (mainly Euholognatha and Antarctoperlaria) do feed in the adult phase (e.g. Lillehammer 1988). This does not seem to be true, at least in some cases. For example, many species of Chloroperlidae and small Perlodidae (Systellognatha), considered mainly predators when nymphs (e.g. Hynes 1976), actively feed when adults (e.g. Zwick 1990; Tierno de Figueroa & S  nchez-Ortega 1999; R  a & Tierno de Figueroa 2013).

Traditionally, it has been thought that Euholognatha stonefly feeding is important in females for the production of mature eggs, while in Systellognatha species, the eggs mature before adult emergence, and thus, the adults do not need to feed (Hynes 1942, 1976). However, this does not seem to be true in all Systellognatha species. For example, *Isoperla nevada* Aubert, 1952 (Perlodidae), which has mature eggs in the last nymphal stage, actively feeds during the adult

stage (Tierno de Figueroa & S  nchez-Ortega 1999; Tierno de Figueroa & Fochetti 2001). This also occurs in some Antarctoperlaria. For instance, *Stenoperla* species (Eustheniidae) from New Zealand mature a large quantity of eggs during their last nymphal stage, but they actively feed when adults (Winterbourn & Pohe 2017). Obviously, this does not mean that adult feeding in most stoneflies does not play an important role in the adult stage for egg maturation and/or other biological aspects, as demonstrated by some authors (e.g. Hynes 1942, 1974; Brinck 1949; Benedetto 1970; Rupprecht 1990; Zwick 1990; Winterbourn & Pohe 2017), a topic that will be addressed more in depth below.

A possible relationship between adult feeding, spermatogenesis and life-cycle duration has also been suggested (Fausto et al. 2002). The testes of two species of Perlidae (genera *Perla* and *Dinocras*), with a long life cycle (merovoltine) and in which adult feeding does not seem to be very important, contained only spermatozoa ready to enter the ducts. In contrast, in one species of *Siphonoperla* (Chloroperlidae) and one of *Isoperla* (small Perlodidae), with annual life cycles and adults that actively feed, different stages of spermatogenesis could be observed.

The existence of some adult Systellognathan species (particularly within Perlodidae) that feed and others that do not also indicates that feeding in adult stoneflies is not an exclusively phylogenetic character (Tierno de Figueroa & Fochetti 2001). In addition, apart from the different durations of the adult life (which will be addressed below), most adult activities seem to be common to the majority of Plecoptera taxa (mate searching behaviour, mating, dispersion, oviposition flight, etc.). However, more studies are necessary to elucidate differences between the groups. For example, it has been pointed out that Systellognatha disperse (migrate) at shorter distances than Euholognatha, and this fact was correlated with the idea that almost all the Systellognatha species do not feed as adults (Kuusela & Huusko 1996). Moreover, in this sense, differences in the activities performed by each sex, apart from those more evident, should receive more attention. For example, changes in habitat (spatial movement) seem to be more frequent in females (that must come back to the stream to oviposit) than in males (Petersen et al. 1999). In some cases, differences in adult activities between males and females could explain a different level of importance of feeding in the imaginal stage for each sex.

Although many of the previously mentioned aspects may influence the importance that feeding may have in the adult stage of the different taxa, both adult longevity (Hynes 1976) and, particularly, body size (Tierno de Figueroa & Fochetti 2001) seem to be the ones that best explain it. Unfortunately, data on the lifespan in adult stoneflies are limited. Nevertheless, those data (e.g. Khoo 1964; Hynes 1974; Elliott 1987, 1988a,b) seem to support, with some exceptions, that the taxa in which the adult life span is shorter are those in which feeding is not very important during the adult stage, such as *Dinocras* (Perlidae) or *Perlodes* (Perlodidae) (Tierno de Figueroa & Fochetti 2001; Rúa & Tierno de Figueroa 2013). On the other hand, feeding in adult stoneflies seems to depend to a large extent on the body size of the species, at least in Arctoperlaria. Thus, the larger species would have enough energy for adult life from the reserves accumulated during the nymphal stage, and thus would have no need to feed during the imaginal stage. Some authors (Zwick 1990; Beer-Stiller & Zwick 1995) have previously reported that most Systellognatha stoneflies accumulate biomass needed for reproduction during their nymphal stage. Moreover, most large-size Systellognatha tend to have long life cycles (2 or more years) (Hynes 1976; DeWalt et al. 2015). The smaller species would need to feed during the adult stage to obtain the energy required. Taking into account all the information on adult feeding that exists to date, it seems that a size of approximately 1.5 cm total length is the approximate limit above which an Arctoperlaria stonefly can develop a normal adult life without ingesting solid food (Tierno de Figueroa & Fochetti 2001) or by ingesting only a low quantity (Rúa & Tierno de Figueroa 2013).

Feeding habits of Euholognatha

Among Arctoperlaria, Nemouroidea feed during the adult stage, and they mainly ingest lichens and algae *sensu lato* (including also “blue-green algae” or Cyanoprokaryota), although their diet can be more diversified, as will be discussed below (e.g. Frison 1935; Hynes 1941, 1942; Brinck 1949; Rupperecht 1990; Tierno de Figueroa & Sánchez-Ortega 2000; Tierno de Figueroa & Fochetti 2001; Rúa et al. 2017). The importance of feeding in egg production and/or in increased longevity has been repeatedly pointed out in Nemouroidea (e.g. Hynes 1942; Brinck 1949; Harper & Hynes 1972; Elliott 1986; Rupperecht 1990; Zwick 1990). Hynes (1942) was the first to experimentally demonstrate that adults,

both males and females, of *Nemoura cinerea* (Retzius, 1783) (Nemouridae) live significantly longer when they feed. Individuals of *N. cinerea* that do not find food after their emergence die before they can mate and mature eggs. In some other species, such as *Capnia nigra* (Pictet, 1833) (Capniidae), mating can occur soon after emergence, and the absence of food is not a limiting factor for mating but is probably required for egg maturation (Hynes 1942). Later, Harper and Hynes (1972) demonstrated experimentally that feeding is also fundamental for egg maturation in *Allocapnia pygmaea* (Burmeister, 1839) (Capniidae), and they, as well as Harper (1973b), Zwick (1990) and other authors, concluded that Nemouridea must necessarily feed to produce eggs. For example, Elliott (1986) observed that the females of *Zwicknia bifrons* (Newman, 1838) (reported as *Capnia bifrons*) (Capniidae) laid fertilized eggs only if they had previously eaten algae and lichens.

Zwick (1990) quantified adult weight gain in *Leuctra prima* Kempny, 1899 (Leuctridae) in the terrestrial environment, and it was almost 50% in dry weight. Zwick (1990), and Beer-Stiller and Zwick (1995) showed weight gain in other species of *Leuctra* (Leuctridae) and in species of the genera *Protonemura* and *Nemoura* (Nemouridae) as evidence of adult feeding necessary to egg maturation and other functions, considering that weight gain occurs both in females and males. More recently, Macneale et al. (2002) reported that the *Leuctra ferruginea* (Walker, 1852) (Leuctridae) female increases in weight by 250% as a consequence of feeding in the terrestrial environment and that it must feed for egg maturation. They also reported that both males and females actively feed as adults (Macneale et al. 2002). Moreover, active metabolism of the ingested food has been demonstrated by means of the measurement of respired radioactive carbon dioxide in two Nemouroidea species, *Nemurella pictetii* (Nemouridae) and *Leuctra nigra* (Leuctridae) (Rupperecht 1990).

Regarding the food that nemouroidean stoneflies ingest, Frison (1929, 1935) pointed out that adults of the North American species that he had studied, belonging to the genera *Allocapnia* (Capniidae), *Taeniopteryx*, *Strophopteryx* (Taeniopterygidae), *Leuctra* (Leuctridae) and *Nemoura* (Nemouridae), are herbivorous and feed mainly on blue-green algae (Cyanoprokaryota). Previously, Newcomer (1918) had pointed out that some *Taenionema* species (reported as *Taeniopteryx*) could cause considerable damage to plants by feeding on buds and leaves, but Frison (1929) cast doubt on the generalizability of these facts (but see Schuh & Mote 1948). Harper

and Hynes (1972) reported that *Allocapnia pygmaea* (Capniidae) feeds actively on algae that cover bark and wood, and Harper (1973b) noted that *Nemoura arctica* Esben-Petersen, 1910 (reported as *Nemoura trispinosa* Claassen, 1923), *Amphinemura nigrita* (Provancher, 1876), *Prostoia completa* (Walker, 1852) (Nemouridae) and *Leuctra ferruginea* (Leuctridae), as well as other species of their respective families, feed on plants and debris.

In Great Britain, Hynes (1941) found that all the species of the families Taeniopterygidae (genera *Taeniopteryx* and *Brachyptera*), Nemouridae (genera *Amphinemura*, *Protonemura*, *Nemoura* and *Nemurella*), Capniidae (genus *Capnia*) and Leuctridae (genus *Leuctra*), both females and males, eat lichens and green algae as adults, both in nature and in the laboratory, but no buds as previously reported by Newcomer (1918). Brinck (1949) reported similar results for Swedish stoneflies. In nature, he found adults of Taeniopterygidae (genera *Taeniopteryx* and *Brachyptera*), Nemouridae (currently attributed to the genera *Amphinemura*, *Nemoura* and *Nemurella*), Capniidae (genus *Capnia*) and Leuctridae (genus *Leuctra*) feeding on lichens and algae, and some specimens of *Capnia nigra* and *Protonemura meyeri* (Pictet, 1841) (reported as *Nemoura meyeri*) feeding on decaying leaves. Brinck (1949) observed a few species of Nemouridae, Capniidae and Leuctridae feeding on leaves in the laboratory. Nemouroidea species feeding on leaves, and sometimes causing damage to ornamental plants, have also been reported by other authors (Wu 1923; Schuh & Mote 1948; Winkler 1964). In particular, Wu (1923) pointed out that young leaves are the food of *Soyedina vallicularia* (Wu 1923) (reported as *Nemoura vallicularia*).

However, few studies have investigated the composition of the gut contents by quantifying the different items ingested. Tierno de Figueroa and Sánchez-Ortega (2000), Tierno de Figueroa and Fochetti (2001), Luzón-Ortega and Tierno de Figueroa (2003) and Tierno de Figueroa et al. (2003) confirmed from such quantification (studied in 18 species of four families of Nemouroidea from southwestern Europe, i.e. Spain and Italy) that nutrition plays an important role in this superfamily, both in females and males, and that this process should be necessary for the activity of adults. They studied species of the genera *Brachyptera*, *Rhabdiopteryx* (Taeniopterygidae), *Amphinemura*, *Protonemura*, *Nemoura* (Nemouridae), *Capnia*, *Capnioneura* (Capniidae), *Leuctra* and *Tyrrhenoleuctra* (Leuctridae), and no differences in food quantity or composition were detected between sexes. The food composition varies among species, but the main components are lichens, Cyanoprokaryota

and fungi, whereas pollen is widely consumed by some spring or spring–summer species. In species that fly in other seasons, the presence of pollen is limited and probably is accidentally ingested while feeding on other resources or while drinking. Other items, such as CPOM (leaf pieces) and FPOM (detritus), were also detected in the gut contents analysed. López-Rodríguez and Tierno de Figueroa (2005) found that pollen and fungi (particularly spores) were the most abundant gut contents in *Nemoura lacustris* Pictet, 1865 (Nemouridae), and differences in gut composition were detected between the sexes. López-Rodríguez and Tierno de Figueroa (2012) only found detritus in the gut of the cavernicolous species *Protonemura gevi* (Nemouridae), probably related to the resource-poor environment which this species inhabits. More recently, Rúa et al. (2017) analysed the gut contents of 17 species belonging to the genera *Amphinemura*, *Protonemura* (Nemouridae), *Leuctra* (Leuctridae), and *Capnioneura* (Capniidae) from Spain. Although differences among species were detected, the main items consumed by the set of studied species were fungi followed by pollen, leaf, detritus and, at lower levels, lichens and animal matter. No significant differences between sexes were detected in the composition of gut contents. It is highly notable that *Protonemura globosa* Berthélemy & Whytton da Terra, 1980, whose flight period spans throughout the year, changes its diet in the different seasons, probably depending on the availability of different resources (Rúa et al. 2017). Something similar had been previously reported for *Amphinemura triangularis* (Ris, 1902) in Sierra Nevada (Spain), in which an increase in pollen content at the end of the flight period was detected (Tierno de Figueroa & Sánchez-Ortega 2000).

Data on adult feeding in Notonemouridae are limited. Hynes (1974) pointed out that four species of this family from Australia, *Austrocercia tasmanica* (Tillyard, 1924) (reported as *Spaniocerca tasmanica*), *Austrocercella tillyardi* (Kimmins, 1951) (reported as *Spaniocerca tillyardi*), *Notonemoura maculata* (Weir, 1967) (reported as *Varioperla maculata*) and a species reported as *Varioperla* sp. (currently *Neonemura* sp.), feed as adults and produce faeces in captivity. More recently, Winterbourn (2005) studied *Spaniocerca zelandica* Tillyard, 1923 and *Cristaperla fimbria* (Winterbourn, 1965) adult feeding in New Zealand and found that these species feed on fungi, pollen (predominantly from *Nothofagus*) and fine plant detritus, with a fragment of adult Diptera detected in the gut of a single male of *S. zelandica*.

Although, as previously mentioned, Kempny (1898, in Brinck 1949) suggested that adult Nemouridae are carnivorous, the ingestion of animal matter in Nemouroidea was first detected by Frison (1929), who observed an adult of *Taeniopteryx nivalis* Fitch, 1847 (Taeniopterygidae) acting as a cannibal in captivity and feeding upon a dead specimen of its cohort. Afterwards, Hynes (1974) observed the Notonemouridae *Notonemoura maculata* (reported as *Varioperla maculata*) from Australia feeding on dead corpses of its cohort. According to Saltveit (1977), the females of stoneflies can eat dead insects when food is scarce. Luzón-Ortega and Tierno de Figueroa (2003) observed some female *Nemoura fulviceps* Klapálek, 1902 (Nemouridae) in the laboratory eating parts of dead males (antennae, legs, wings, head) and defecating the rest of the cuticles in their subsequent excrements, and this behaviour was also detected in a male. They proposed that animal matter is probably a nutritional support for this species (as occurs also in phytophagous nymphs, as mentioned above). In fact, animal matter as a small part of the total gut contents has also been found in some species of Nemouridae (*Nemoura fulviceps* and *Protonemura globosa*), Leuctridae (*Leuctra aurimensis* Membiela, 1989, *Leuctra madritensis* Aubert, 1952 and *Leuctra maroccana* Aubert, 1956) and Notonemouridae (*Spaniocerca zelandica*) collected in nature, although the low proportion in which the animal matter was present could indicate that this food resource was accidentally ingested (Luzón-Ortega & Tierno de Figueroa 2003; Winterbourn 2005; Rúa et al. 2017). Nevertheless, Koshima and Hidaka (1981) reported adults of *Eocapnia nivalis* (Uéno, 1929) (Capniidae) on snow that were feeding on vegetal detritus but also on dead corpses of Collembola and Chironomidae. Finally, Madsen and Aagaard (2016), in a study on *Taeniopteryx nebulosa* (Linnaeus, 1758) (Taeniopterygidae) in Denmark, reported that adult feeding is on green algae and woody detritus, but they also found lichens and animal matter (rotifers and enchytraeid worms) in stonefly guts.

In addition to the Nemouroidea, Euholognatha also includes the family Scopuridae, with only eight species belonging to the genus *Scopura* from South Korea and Japan (DeWalt et al. 2018). Unfortunately, no data are available on the feeding habits of adults of this family.

Feeding habits of Systellognatha (Perloidea and Pteronarcyzoidea)

Traditionally, adult systellognathan stonefly species were assumed not to ingest food (e.g. Hynes 1942, 1976), although some data from the

literature partially contradict this affirmation. Claassen (1931, in Zwick 1980) pointed out that *Suvallia pallidula* (Newman, 1845) (Chloroperlidae) had been observed feeding on honeydew secreted by aphids. This fact was also pointed out later in other Chloroperlidae of the genus *Alloperla* (Hitchcock 1974, in Hynes 1976). Frison (1935), in his study on Illinois Plecoptera, pointed out that the adults of at least two species of *Isoperla* feed (those with more developed mouthparts; one of them is currently transferred to the genus *Chloroperla*, *Chloroperla minuta*). The remaining species studied by him that belong to the genera *Isoperla* (in part), *Hydroperla* (Perlodidae), *Perlinella* (reported as *Perlinella* and *Atoperla*), *Agnetina* (reported as *Neophasganophora*), *Perlesta*, *Acroneuria* and *Neoperla* (Perlidae) are non-feeders in the adult stage (Frison 1935). The fact that *Perlesta*, particularly *P. placida*, does not feed in the adult stage was confirmed by Snellen and Stewart (1979) by means of observations in nature and by gut dissections. Hynes (1941) found that all stonefly adults from Great Britain belonging to the currently accepted families Perlodidae, Perlidae and Chloroperlidae (including the current genera *Perlodes*, *Diura*, *Isogenus*, *Isoperla*, *Dinocras*, *Perla*, *Chloroperla*, *Siphonoperla* and *Xanthoperla*) do not feed. Brinck (1949), after studying the feeding of several stoneflies from Sweden, confirmed the statement of Hynes (1941) regarding non-adult feeding in those taxa. Nevertheless, this same author (Brinck 1949) found some gut content in a *Siphonoperla burmeisteri* (Pictet, 1841) individual (Chloroperlidae, reported as *Chloroperla burmeisteri*). Harper (1973a), in a study on setipalpiian Plecoptera from Canada, pointed out that *Isoperla transmarina* (Newman, 1838) (Perlodidae) and *Sweltsa onkos* (Ricker, 1936) (reported as *Alloperla onkos*) (Chloroperlidae) do not feed, even though females of the latter emerge with underdeveloped eggs. However, Zwick (1973) indicated that the pollen of coniferous plants is the usual food of the adults of some Chloroperlinae, and Rotheray and Liston (1985) observed an adult *Chloroperla tripunctata* (Scopoli, 1763) in nature that seemed to feed on the haemolymph of a Tenthredinidae species.

Subsequent studies demonstrated that some Systellognatha of the family Chloroperlidae [*Siphonoperla torrentium* (Pictet, 1841)] can metabolize food ingested in the adult stage (Rupprecht 1990) and gain weight during their adult life by feeding in the terrestrial environment (Zwick 1990). After

wards, Tierno de Figueroa and Sánchez-Ortega (1999) showed, from analyses of gut contents, that one species of the family Chloroperlidae (*Chloroperla nevada* Zwick, 1967) and two of small Perlodidae (*Isoperla grammatica* and *Isoperla nevada*) feed during the adult stage, and the proportion of the different dietary components changes over the flight period in relation to the availability of these resources. For example, both the presence and abundance of pollen of Pinaceae in the gut contents of *Chloroperla nevada* and *Isoperla nevada* were higher at the beginning of their flight period, being replaced by other types of pollen (fundamentally Poaceae) later coinciding with the relative abundance of these types of pollen in the environment. In addition to pollen, both sexes of the species studied also ingested leaf fragments and/or detritus as major components and fungi and algae *sensu lato* as minor components (Tierno de Figueroa & Sánchez-Ortega 1999). Another contemporary investigation in Perlodidae (Tierno de Figueroa et al. 1998) revealed that feeding also occurs during the adult stage in *Hemimelaena flaviventris* (Pictet, 1841) and that pollen, Cyanoprokaryota, lichens and vegetal fragments are the main resources ingested by this species. It is notable that females ingest more food than males in the species studied by Tierno de Figueroa et al. (1998) and Tierno de Figueroa and Sánchez-Ortega (1999), especially in the case of *Chloroperla nevada*. In addition, the mean quantity of the food ingested is lower in *Hemimelaena*, followed by *Isoperla* and *Chloroperla*, coinciding with a gradient of decrease in size.

In contrast with the results reported in the previous paragraph, Tierno de Figueroa and Sánchez-Ortega (1999) and Tierno de Figueroa and Fochetti (2001) found that adult solid feeding was unimportant in the species of Perlidae and Perlodidae of large size that they studied (including the genera *Perla* and *Dinocras* among the Perlidae and *Dictyogenus*, *Besdolus* and *Perlodes* among the Perlodidae). Only a limited quantity of gut contents (detritus, pollen or fungi) was found in a few specimens of these groups. From these findings, together with data from other previous studies, Tierno de Figueroa and Fochetti (2001) hypothesized that adults of large stoneflies do not need to ingest solid food and that the size from which adults do not need to actively feed is approximately 1.5 cm (see discussion on this topic above). This hypothesis has been confirmed by new data on some tropical Perlidae, *Anacroneuria* from Nicaragua (particularly *A. starki* Fenoglio & Morisi, 2002 and *A. talamanca* Stark, 1998) and *Neoperla* sp. from Gabon, which do not feed as adults (Fenoglio & Tierno de Figueroa 2003). As in the other studied large European Perloidea (Tierno de Figueroa & Sánchez-Ortega

1999; Tierno de Figueroa & Fochetti 2001), the vestigial nature of the adult mouthparts in these tropical Perlidae supports that the ingestion of solid food is not important in adult life (Fenoglio & Tierno de Figueroa 2003). The absence of specialized mouthparts and the scarcity (or even absence) of pollen in the guts (particularly of pollen of entomophilous plants) suggest that they do not feed on nectar (Tierno de Figueroa & Sánchez-Ortega 1999; Fenoglio & Tierno de Figueroa 2003).

Derka et al. (2004) studied the adult gut contents of *Isoptena serricornis* (Pictet, 1841) (Chloroperlidae) in Slovakia and found that the diet was fundamentally composed of pollen grains and, to a lesser extent, fungi, detritus and Cyanoprokaryota. They also found that males usually have a lower food content than females and attributed this to the greater reproductive effort of the females. This last fact was also pointed out by López-Rodríguez et al. (2007) when studying adult feeding habits of the Chloroperlidae *Siphonoperla torrentium* and *Xanthoperla apicalis* (Newman, 1836) from Slovakia, and it was statistically demonstrated in a *S. torrentium* population from Spain by Rúa and Tierno de Figueroa (2013). López-Rodríguez et al. (2007) found that pollen was the main ingested food for these species, together with detritus, leaf fragments and other resources, and that several individuals of both species had some animal remains (Arthropoda) in their gut that sometimes occupied a considerable percentage of the total content. As reported by Luzón-Ortega and Tierno de Figueroa (2003) in Nemouroidea, animal matter could also be an important nutritional complement in some Perloidea species. In fact, Rúa and Tierno de Figueroa (2013) found animal matter, together with pollen (as the main component), detritus and CPOM, in the gut of *Siphonoperla torrentium* from Spain as well. These data, together with those of López-Rodríguez et al. (2007) and other authors, show that predation and/or necrophagy are part of the active feeding habits of at least some Perloidea stoneflies in nature (as well as some Euholognatha and Antartoperlaria). Moreover, Rúa and Tierno de Figueroa (2013) also analysed the gut content of *Dinocras cephalotes* and *Marthamea selysii* (Pictet, 1841) (Perlidae) and found a low quantity of pollen followed by fungi, detritus and some animal matter in the former and a low quantity of fungi and pollen in the latter. The data obtained support the hypothesis that adult feeding is less important for large stoneflies than for the smaller ones, but although some of that food could be incidentally ingested while drinking, feeding habits in these large

Plecoptera could not be as negligible as previously hypothesized.

Regarding Pteronarcyioidea (families Pteronarcyidae, Peltoperlidae and Styloperlidae), information on adult feeding behaviour is extremely rare. Adults of Pteronarcyidae seem not to ingest food. According to Frison (1935), *Pteronarcys pictetii* Hagen, 1873 (reported as *Pteronarcys nobilis* Hagen, 1861) does not feed as an adult, and McDiffett (1970) pointed out that adults of *Pteronarcys scotti* do not feed and die a few days after emerging.

Feeding habits of Antarctoperlaria

Information on adult feeding in Antarctoperlaria is also limited, and no data exist for the nine species of the family Diamphipnoidae that are known (Vera Sánchez 2018).

A few studies have provided valuable knowledge on the adult feeding habits of Eustheniidae and Austroperlidae. Nebois (1959, in Hynes 1974) pointed out that *Thaumatoperla alpina* Burns & Neboiss, 1957 (Eustheniidae) chews leaves in captivity. Hynes (1974) reported that adults of all the families of Australian stoneflies, including Eustheniidae and Austroperlidae, feed and produce faeces. In particular, he observed *Cosmioperla australis* (Tillyard, 1921) (reported as *Stenoperla australis*), *Eusthenia venosa* (Tillyard, 1921) (reported as *Eustheniopsis venosa*), *Eusthenia* sp., *Thaumatoperla alpina*, *Thaumatoperla flaveola* Burns & Neboiss, 1957, *Thaumatoperla robusta* Tillyard, 1921 (Eustheniidae), *Austroheptura neboissi* Illies, 1969, *Austropentura victoria* Illies, 1969 and *Acruroperla atra* (Šámal, 1921) (Austroperlidae) ingesting food. In captivity, all these taxa except *Acruroperla atra* preferred rotten wood, and the fungus-infected wood is probably essential for egg production in most of these taxa. In fact, Hynes (1974) observed that *Austropentura victoria* only matures eggs when fed with this type of food. In nature, *Thaumatoperla flaveola* seems to feed on lichen, plant tissue, diatoms and possibly detritus, as Hynes (1974) deduced from examination of the faeces. All Eustheniidae and Austroperlidae studied feed frequently, except *Cosmioperla australis* (reported as *Stenoperla australis*), which eats very little and is the only taxon among those studied in Australia which emerges with fully developed eggs. Hynes (1974) highlighted that, in this sense, this genus resembles Perlodidae and Perlidae. Zwick (1981), based on these data from Hynes (1974), pointed out again that the adults of Australian

stoneflies seem to feed on plant material, except *Stenoperla* (Eustheniidae), which does not feed and emerges with fully developed eggs. It must be noted that *Stenoperla* is currently considered an endemic genus of New Zealand, while the former Australian *Stenoperla australis* Tillyard, 1921 was transferred to a different genus (*Cosmioperla*) (McLellan 1996). In fact, Winterbourn and Pohe (2017) showed, from gut content analyses, that *Stenoperla prasina* (Newman, 1845) and *Stenoperla maclellani* Zwick, 1979 (Eustheniidae) from New Zealand feed mainly on sooty mould fungi and, to a lesser extent, on plant tissue, pollen and the tree fern spores that they probably obtain by feeding on the trees. These authors pointed out that, as mature nymphs of these *Stenoperla* species have a great quantity of developed eggs, adult feeding provides energy mainly for mating and flight. No data on adult feeding are available for Eustheniidae and Austroperlidae from South America.

Feeding habits of adult Gripopterygidae have been studied in some species from South America, Australia and New Zealand. Froehlich (1969) pointed out that adults of Brazilian Gripopterygidae must feed to reach sexual maturity and that *Paragripopteryx* feed mainly on lichen. Benedetto (1970) found that *Paragripopteryx munoai* (Benedetto, 1969) (reported as *Jewettoperla munoai*) from Uruguay feeds on algae and fungi growing on wet stones and branches. This author also demonstrated that adults without food die within 50 hours, while adults that feed survive up to 20 days (females) or 13 days (males) (Benedetto 1970). Tierno de Figueroa et al. (2006) studied the gut contents of two species of Gripopterygidae from Chile, *Antarctoperla michaelsoni* and *Limnoperla jaffueli*, and found that the main component in the diet of both species was Pinaceae pollen, followed by detritus, fungi and other pollens. The ingested Pinaceae pollen belonged to the species *Pinus radiata* D. Don, 1836, an introduced tree in Chile, which means that *A. michaelsoni* and *L. jaffueli* have adapted to a new food resource.

Hynes (1974) reported that adults of 18 Australian Gripopterygidae of the genera *Leptoperla*, *Newmanoperla*, *Riekoperla*, *Neboissoperla*, *Trinotoperla*, *Illiesoperla*, *Dinotoperla* and *Eunotoperla* fed on the green algae and lichen from twigs in captivity and, in the case of *Dinotoperla serricauda* Kimmins, 1951, also on rotten wood. Moreover, some individuals of the species *Leptoperla kimminsi* McLellan, 1971, *Riekoperla williamsi* McLellan,

1971, *Riekoperla rugosa* (Kimmins, 1951) and *Dinotoperla serricauda* were observed scraping bark in nature. The study of faeces from individuals collected in the field showed that *Leptoperla cacuminis* Hynes 1974 ingests only vascular plant tissues (Hynes 1974).

According to Wisely (1953), *Holcoperla angularis* (Wisely 1953) (reported as *Apteryoperla angularis*) and *Apteryoperla monticola* Wisely 1953 (Gripopterygidae) from New Zealand feed on vegetal matter. Smith and Collier (2000) studied the diet of three other New Zealand species of this family, *Zelandobius furcillatus* Tillyard, 1923, *Zelandoperla decorata* Tillyard, 1923 and *Acroperla trivacuata* (Tillyard, 1923), and gut content analysis revealed that they feed mainly on fungi, pollen and detritus but also on vascular plant tissues, diatoms and invertebrates. Differences between species and sexes and in relation to the site where they were collected (riparian vegetation vs. channel rocks) were also detected. As noted in some Arctoperlaria species (e.g. Tierno de Figueroa et al. 1998; Tierno de Figueroa & Sánchez-Ortega 1999; Derka et al. 2004), *Zelandoperla decorata* and *Acroperla trivacuata* females had more food in their guts than the males, which probably indicates the great importance of adult feeding for females (Smith & Collier 2000). Laboratory feeding studies in *Zelandoperla decorata* demonstrated that longevity increases in individuals that are fed (Smith & Collier 2000), coinciding with that revealed in studies of other Arctoperlaria (Benedetto 1970) and Arctoperlaria (e.g. Hynes 1942; Brinck 1949; Harper & Hynes 1972). Among other studies in captivity, that of Collier and Scarsbrook (2000) is highly significant, since they reported that when *Zelandoperla decorata* is fed sugar solution and fungi, the females develop eggs, and both males and females gain weight (in Winterbourn & Pohe 2017).

Smith and Collier (2000), in their study on Gripopterygidae, found some incongruences between results obtained by means of gut content analyses and those from stable isotope analyses (coming from both the animals and the potential food resources), indicating that a combined investigation of the diet and the movements during the adult life is needed to resolve these issues. In fact, the use of particular riparian habitats conditioned by the existence of appropriate food sources must be an important and not yet well understood biological aspect in adult Plecoptera, males and females, throughout their adult life (Harper 1973b; Briers & Gee 2004).

Adult Plecoptera as a trophic resource and its role in the food webs

Some predators, such as birds – including dippers (*Cinclus* sp.) – small mammals, and amphibians, eat adult stoneflies (Zwick 1980 and references herein), and a list of potential predators would include a great diversity of riverine predators, both vertebrates and invertebrates, as well as some aquatic or semiaquatic organisms that can capture adult stoneflies during emergence. Here, we will cite only a few examples to illustrate this phenomenon. Harper and Magnin (1969) pointed out that *Isoperla frisoni* Illies, 1966 (Perlodidae) adults were preyed upon by birds but also by Cyprinidae when females lay the eggs. Stewart et al. (2001) found adults of six stonefly species belonging to the genera *Paracapnia* (Capniidae), *Taeniopteryx* (Taeniopterygidae), *Amphinemura* (Nemouridae) and *Leuctra* (Leuctridae) to be part of the diet of the red-spotted newt *Notophthalmus viridescens*. Adult Chloroperlidae have been observed to be preyed upon by *Hydrometra* (Hemiptera) when these stoneflies were emerging (Jaimez-Cuéllar pers. obs.). The importance of adult and nymph stoneflies as prey for trout, other salmonids and other game fish is also demonstrated by the rich specialized fly fishing bibliography; indeed, dozens of fly patterns have been created in this fishing modality during the years to imitate different Plecoptera species (e.g. Leiser & Boyle 1982).

Thus, Plecoptera are important as prey and primary or secondary consumers in aquatic food webs, while they act as mainly prey and primary consumers in terrestrial food webs. The adult stonefly transfer of carbon from freshwater to terrestrial ecosystems that occurs through predation on adult aquatic insects is particularly interesting (Collier et al. 2002). These authors carried out a study using stable isotopes of carbon and nitrogen to explore linkages between aquatic insect production and the nutrition of riparian spiders in New Zealand. They found that aquatic insects, including stoneflies, provide significant nutritional support, above 55%, for spiders. In the UK, Briers et al. (2005) carried out a study using stable isotopes and found that aquatic insects, mainly *Leuctra inermis* Kempny, 1899 (Leuctridae), emerging from the stream made up over 40% of the diet of spiders adjacent to the stream, but this percentage diminished sharply when the distance from the channel increased. In a review paper, Baxter et al. (2005) pointed out that aquatic insects

emerging from streams can contribute 25–100% of the energy or carbon of riparian consumers, such as birds, bats, lizards, salamanders, odonates, beetles and spiders.

Finally, in relation to the importance of Plecoptera in the human diet, it should be noted that Williams and Williams (2017) pointed out that adult and nymph stoneflies, according to their ecological and biological traits, are not good candidates for human entomophagy. Nevertheless, a few taxa have been recorded as edible (recompiled in Jongema 2017): *Pteronarcys californica* Newport, 1848 (as adults) and *Isoperla* sp. (without specifying whether adults or nymphs) from the Nearctic Region; *Kamimuria tibialis* (Pictet, 1841) (as nymphs), *Paragnetina tinctipennis* (McLachlan, 1875) (as nymphs), and Plecoptera gen. from Japan (Palearctic Region); *Nemoura* (as nymphs) from India (Oriental Region); and *Pteronarcys dorsata* (Say, 1823) (as nymphs), whose identity should be examined in more detail considering that it is a Nearctic species (not Oriental, as reported in the original paper).

Future challenges in the study of stonefly trophic ecology

After describing the existing information on the trophic ecology of Plecoptera, some topics still need to be treated more thoroughly (or even studied for the first time) to provide a more complete view, not only of the trophic ecology of this group but also of many other aspects of the biology of these insects. Thus, it is necessary to do the following research:

1. Increase the knowledge of species diets, particularly in certain families where data on trophic habits are very rare or non-existent. This is the case for Styloperlidae and Peltoperlidae within the Systellognatha, the Scopuridae within the Euholognatha, and Diamphipnoidae among the Antartoperlaria. Particularly interesting would be to study Gripopterygidae species from humid and cold mountains in South America and New Zealand that become semi-terrestrial in late instars, and Australasian Notonemouridae species that live hygropetrically and wander onto the land (in Hynes 1976), as well as to study the feeding habits of *Capnia lacustra* Jewett, 1965 aquatic adults from Lake Tahoe (USA) (Jewett 1963; Caires et al. 2016). It is also necessary to promote studies of this subject in the Neotropical, Afrotropical and Oriental regions, as well as in the eastern part of the Palearctic Region.
2. Describe the variability in feeding habits among congeneric species and populations of the same species as well as between sexes. In the latter case, and particularly for adults, compare the amount and type of food consumed by males and females within the same species and relate it to the different activities and functions carried out by each sex.
3. Study in adults, by means of comparative and experimental studies, how food availability influences feeding patterns. Additionally, it would be useful to perform new experiments in different taxa to evaluate the role of food in longevity, egg maturation and other biological aspects.
4. Conduct more studies aimed at thoroughly understanding the role of adults and nymphs in terrestrial and aquatic food webs. In particular, it would be interesting to more thoroughly understand the importance of riparian vegetation as a source of food for adult stoneflies and the influence of the management of this vegetation on this taxon, as reported by Briers and Gee (2004).
5. Carry out more studies on digestive enzymatic activity in nymphs and adults, and carry out more detailed studies on diet and nutrition. Particularly interesting would be to study the assimilation process of lignin and other compounds of species that feed on wood. As highlighted by Cohen (2004) in the preface of his book, insect diet is one of the most complex, misunderstood and underappreciated aspects of entomology. Unfortunately, this statement is especially true in some orders of insects, such as Plecoptera. It is also necessary to carry out new histological studies on the stonefly digestive system and, particularly, to describe the changes occurring in the passage from nymphs to adults. More microbiome-gut-related studies are also needed.
6. Perform research, as proposed by Stewart (1994), on behaviours related to adult trophic ecology, e.g. the existence of aggregation for feeding and feeding activity rhythms. Although considerably better known, more studies such as those of Peckarsky (1980, 1982, 1991, 1996) or Peckarsky and Penton (1989) are necessary to understand fundamental aspects of the trophic behaviour and ecology of the nymphs of several other species (food searching behaviours, predatory evasion behaviours, inter- and intraspecific competition, substrate selection, etc.).

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