

# Global diversity of stoneflies (Plecoptera; Insecta) in freshwater

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**Abstract** Plecoptera, or stoneflies, is a small order of hemimetabolous insects: according to our data, more than 3,497 species have been described so far in the world. The total number of species has enormously increased in the last 30 years (2,000 species estimated in 1976) and, if the trend continues, then it will nearly double in the near future. The order is divided into the suborders Arctoperlaria and Antarctoperlaria, and includes 16 families: 12 arctoperlarian and 4 antarctoperlarian. The Arctoperlaria account for a total number of 3,179 species, and Antarctoperlaria, only 318 species. The total number of genera is 286. We give in this article the estimated number of species for each family. The fauna and diversity of stonefly in North America (650 species reported) and Europe (426 species) are best known. Nevertheless, in the last 25 years, a mean of 2.6 Plecoptera species per year were described in Europe. Stonefly-faunas of Australia (191 species, Tasmania included) and New

Zealand (104 species) are relatively well-known, while our knowledge of the Plecoptera of Central and South America (95 and 378 species respectively) is poor and still not representative of the real diversity. Africa has a reduced stonefly fauna (126 species). Asian stonefly diversity (approximately 1,527 species) is much greater than that of Europe or North America despite the fact that, except for Japan and Asiatic Russia that have been well studied, our knowledge of the remaining Asiatic areas is extremely poor. Even though our data indicate the Holarctic Region as the diversity hot-spot for the order, the analysis of the specific diversity divided by family suggests also an important role of tropical stoneflies.

**Keywords** Plecoptera · Distribution · Diversity · Zoogeographical regions

## Introduction

Plecoptera is a small order of hemimetabolous insects, commonly called stoneflies, with more than 3,497 described species (this article). Stoneflies are distributed over all continents except Antarctica, and constitute a significant ecological component of running water ecosystems. Their ecological requirements greatly limit the dispersal capacity of the nymphs and, because adults have reduced flight ability, stoneflies show a high percentage of

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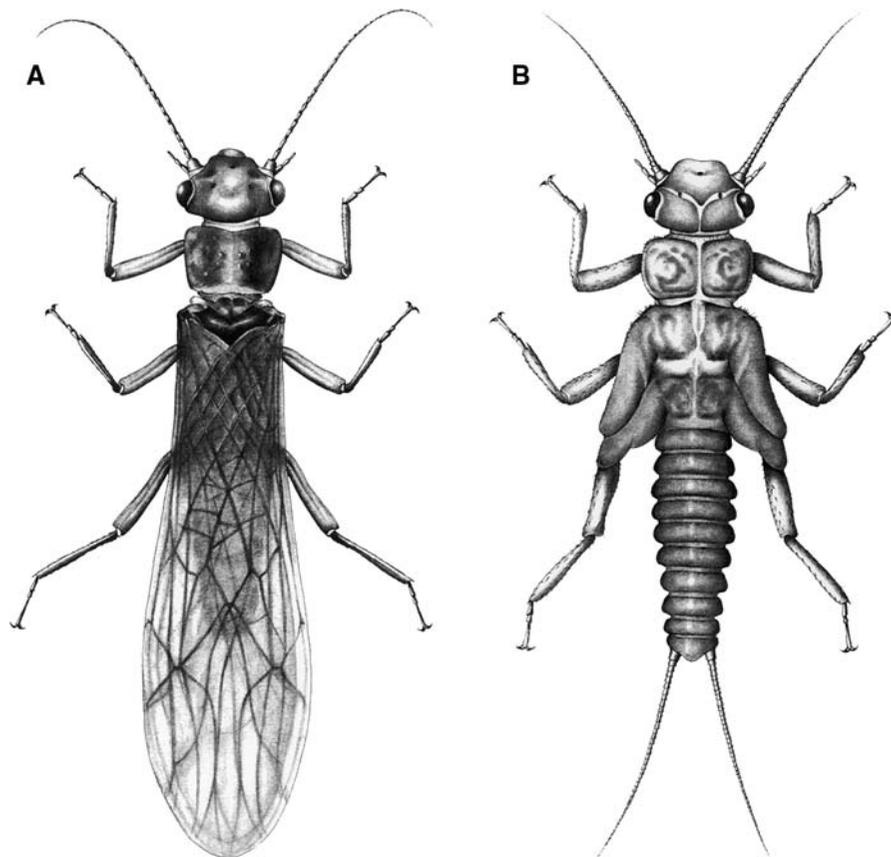
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endemism. Due to the growing pollution and alteration of water courses and to the high stenoecity of Plecoptera, numerous stonefly species are reduced to small isolated populations and many others have already gone extinct. Stoneflies are probably one of the most endangered groups of insects (Fochetti & Tierno de Figueroa, 2004).

Plecoptera can be easily recognized by several morphological characters: soft body, three segmented tarsi, elongate filiform antennae, mandibulated mouthparts, two compound eyes, two or three ocelli, two usually long cerci, 10-segmented abdomen with vestiges of the eleventh segment. Adults have two pair of membranous large wings (sometimes reduced or absent), and subequal fore and hind wings (hind wings slightly wider) that fold horizontally over and around abdomen when at rest (hence the name: *plecos* = folded; *pteros* = wings) (Fig. 1A). Nymphs are similar to adults (Fig. 1B), with a closed tracheal system with or without filamentous gills. When

present, gills are located on different parts of the body.

Plecoptera nymphs are aquatic and live mainly in cold, well-oxygenated running waters, although some species can also be found in lakes. Few species are adapted to terrestrial life in Sub-Antarctic areas: Hynes (1976) reported the tendency of southern hemisphere nymphs to leave the water. However, the increasing number of stoneflies described from the tropics and their high rate of endemism can modify the common belief that Plecoptera are cold-water specialists, and suggest instead that the true hot-spot for Plecoptera diversity are tropical areas (Zwick, pers. com.). The life cycle of stoneflies lasts for one or more years, but there are also bi- or tri-voltine species. Nymphal or egg diapause is not uncommon. The nymphs can moult up to 33 times before emerging. They feed on animal or vegetable matter as collectors, scrapers, shredders or predators.



**Fig. 1** A-Adult of *Nemoura*, and 1 B-Nymph of *Nemoura*

Adults are terrestrial or sub-aerial, with the exception of *Capnia lacustra* Jewett, whose adults have been collected only at a depth of 60–80 m in the Lake Tahoe (USA) (Jewett, 1963), and the adult females of *Zapada cinctipes* (Bank) that can remain under water for a long time (20–60 min) for ovipositing (Tozer, 1979). Adults lifespan is short, from a few days to weeks; they display complex behaviours related to mate searching (such as the use of intersexual vibrational communication in Arctoperlarian stoneflies) and oviposition (Stewart, 1994). The adult feeds on pollen, lichens, cyanobacteria, etc., although the adults of the largest species do not seem to feed (Tierno de Figueroa & Fochetti, 2001). Females produce 25–3,000 eggs, and lay their egg-clutches, or rarely each egg separately, on the water. Parthenogenesis and ovoviviparity have been also described for some species.

### Species diversity

According to our data, approximately 3,500 species of Plecoptera have been reported so far in the world (Tables 1, 2). They are divided as: North America 650 species (Stark & Baumann, 2005), Central America 95 species, South America 378 species (Heckman, 2003), Europe 426 species (Fochetti & Tierno de Figueroa, 2004), Africa 126 species (31 from Mediterranean Africa, with only 12 endemic species, 50 from tropical Africa, 33 from South Africa and 12 from Madagascar), Asia approximately 1,527 species [(about 784 from South-East Asia = 31 Taiwan, 32 Korea, 25 Philippines, 39 Borneo, 36 Indonesia, 17 Malaysia, 29 Thailand, 20 Vietnam, two Laos, three Myanmar, 28 Bhutan, two Bangladesh, 10 Sri Lanka, 112 India, 63 Nepal, 20 Pakistan, nine Afghanistan, 306 Japan, no species from Cambodia; Sivec & Yang 2001), China 350 (?) species (deduced from Yuzhou & Junhua, 2001, who report 231 species of Perlidae), West Asia about 114 species (two Syria, two Israel, 25 Iran, 15 Lebanon, 70 Asiatic Turkey), Asiatic Russia 279 species (179 Nemouroidea and about 100 Perloidea). Although a small number of species are shared by several countries, we consider the total sum as a good approximation], Australia 191 species (Michaelis & Yule, 1988), New Zealand 104 species (McLellan, 2006).

Very few species are shared among zoogeographical regions (mainly between Nearctic and Palaearctic and between Palaearctic and Oriental) or among continents, i.e. at borders between Africa and Europe or at the borders between Europe and Asia. Australia and New Zealand are obviously isolated; deserts or dry lands prevent stonefly migration from North to Central and South America, and from the Palaearctic to the Ethiopic Regions. Thus, the total number of described species should not be too far from the reported one.

In comparison to the papers by Hynes (1976) and Zwick (1980) who reported about 2,000 described stonefly species, the total number has enormously increased in the last 25 years and, if the trend continues then it will nearly double in the near future.

The fauna and diversity of stonefly in North America and Europe are best known. Nevertheless, new species have been described from these areas at a high rate: in the last 25 years, a mean of 2.6 Plecoptera species per year were described in Europe (Fochetti & Tierno de Figueroa, 2005). Stonefly-faunas of Australia (Tasmania included) and New Zealand are relatively well-known, while our knowledge of the Plecoptera of Central and South America is poor and still not representative of the real diversity.

Asian stonefly diversity is much greater than that of Europe or North America. This is true despite the fact that, except for Japan and Asiatic Russia that have been well studied, our knowledge of the remaining Asiatic areas is extremely poor. Our greatest lack of knowledge and the highest uncertainty regard Asiatic faunas occurs in the Oriental Region. For instance, according to Yuzhou & Junhua (2001) over 230 species of Perlidae, the most speciose family in the country, have so far been described from China. The identity of many of these species is questionable and cannot be checked because most of the types were lost or destroyed; nonetheless, intensive future research will certainly lead to the discovery of hundreds of new species in this country. In fact, a few intensive collecting trips to Taiwan almost doubled its stonefly-fauna (Sivec & Yang, 2001).

In Africa, a reduced number of species were collected, but we do not expect a great increase in Plecoptera diversity in the future. The results of recent studies on the systematics of the tropical tricky

**Table 1** Number of Plecoptera species in each family and each continent

	NAm	CAm	SAm	Eu	AF	AS <sup>a</sup>	NZ	AUS
Eustheniidae			2				4	15
Diamphipnoidae			5					
Austroperlidae			4				1	10
Gripopterygidae			73				70	134
Pteronarcyidae	10	1				2		
Peltoperlidae	22					24		
Styloperlidae						8		
Perlodidae	125	3		62	3	118		
Perlidae	82	71	277	18	55	546		
Chloroperlidae	95	2		19	1	89		
Scopuridae						8		
Taeniopterygidae	34			41	2	65		
Notonemouridae			17		43		29	32
Nemouridae	71	9		132	8	413		
Capniidae	156	8		21	4	126		
Leuctridae	55	1		133	10	128		
Total	650	95	378	426	126	1,527	104	191

<sup>a</sup> Asiatic Russia and China data have been arbitrarily subdivided (NAm = North America; CAm = Central American; SAm = South America; Eu = Europe; AF = Africa; AS = Asia; NZ = New Zealand; AUS = Australia)

**Table 2** Number of Plecoptera species in each family and each zoogeographical region

	PA <sup>a</sup>	NA	NT	AT	OL <sup>b</sup>	AU	World
Eustheniidae			2			19	21
Diamphipnoidae			5				5
Austroperlidae			4			11	15
Gripopterygidae			73			204	277
Pteronarcyidae	10	1					13
Peltoperlidae	22						46
Styloperlidae							8
Perlodidae	63	125	4				311
Perlidae	18	82	348	52			1,049
Chloroperlidae	20	95	2				206
Scopuridae							8
Taeniopterygidae	42	34					142
Notonemouridae			17	43		61	121
Nemouridae	136	71	9				633
Capniidae	21	156	8				315
Leuctridae	138	55	1				327
Total	438 <sup>a</sup>	650	474	95	350?	295	3,497

<sup>a</sup> Palaearctic Asia not included. PA: Palaearctic Region, NA: Nearctic Region, NT: Neotropical Region, AT: Afrotropical Region, OL: Oriental Region, AU: Australasian Region. <sup>b</sup> The distribution of Oriental Plecoptera cannot be unequivocally established

genus *Neoperla* might increase the species list and some new species could be described from Mediterranean countries (Morocco, Algeria, Tunisia), but the total stonefly diversity will not increase to the level of the other continents.

As we expected, the analysis of Plecoptera diversity and distribution shows their well-known ecological requirements as: they are absent from arid or semi-arid areas everywhere in the world. There are almost no records from West Australia, no records at all for Saudi Arabia, Yemen, Oman, Emirates, Kuwait and Iraq in Asia, and stonefly diversity in Africa is greatly limited by deserts and dry lands.

The order is divided into the suborders Arctoperlaria and Antarctoperlaria (see the phylogeny chapter below), and includes 16 families: 12 arctoperlarian and four antarctoperlarian. The Arctoperlaria account for a total number of 3,179 species, and Antarctoperlaria, only 318 species. They are listed in Table 2 with the estimated number of species for each family. The total number of genera is 286 (Table 3). Even though Table 1 is incomplete because it lacks details on the distribution of Chinese families and Far East Russia species, Perlidae is the most diverse family, with more than 1,000 described species. Since the last estimate (Zwick, 1980), the number of perlid species

almost doubled, due to the increase of faunistic research in Asia and, above all, to the improved knowledge of the systematics of the tropical genera *Neoperla* and *Anacroneuria*. The family Perlidae spreads over Holarctic, Oriental, Afrotropical and Neotropical Regions. The most diverse perlid areas are Asia, and Central and South America. Presently the Chinese perlid species represent about 25% of the world Perlidae, making China one of the most important areas of the world for perlid diversity (Yuzhou & Junhua, 2001). The Neotropical perlid fauna currently includes more than 350 species: *Anacroneuria* is the dominant and most diverse stonefly genus, (Stark, 2001) with almost 300 described species.

Perlodidae presently includes about 300 species, mainly in the Holarctic region. The most speciose perlodid genus, *Isoperla*, has a Holarctic distribution and has more than 100 species, a third of the total. A similar distribution is shown by the ancient genus *Arcynopteryx* [Aubert (1959) stated it is an Ercinic relict] and by the genus *Diura*. *A. compacta* (McLachlan) is distributed in North America and Europe, as well as *D. bicaudata* (Linnaeus) and *D. nanseni* (Kempny).

Chloroperlidae include more than 200 species mainly in the Holarctic region. The genera *Sweltsa* and *Alloperla* have a Nearctic and East Palaearctic distribution and includes almost 80 species. In Europe, only four genera and 19 species are present.

Taeniopterygidae is a family present in the Nearctic and Palaearctic Regions, with almost 150 species. The genus *Taeniopteryx* (20 species) is present in Europe and North America (even though the morphology of the nymphs slightly differs in the two continents), as well as the genus *Oemopteryx*. The genus *Doddsia* is shared by North America and Japan. The West Palaearctic genus *Brachyptera* includes more than 30 species.

Nemouridae was considered the most diverse family, with almost 400 described species (Zwick, 1980). The number currently is 633 species, but it is now the second most diverse family due to the enormous increase of Perlidae. The family has an Holarctic distribution with some genera reaching the Oriental Region; the genera *Amphinemura* (Holarctic; more than 100 species), *Nemoura* (Holarctic; 175 species) and *Protonemura* (Palaearctic; 135 species) account for 2/3 of the whole family. *Nemoura arctica* Esben-Petersen has a circum-arctic distribution.

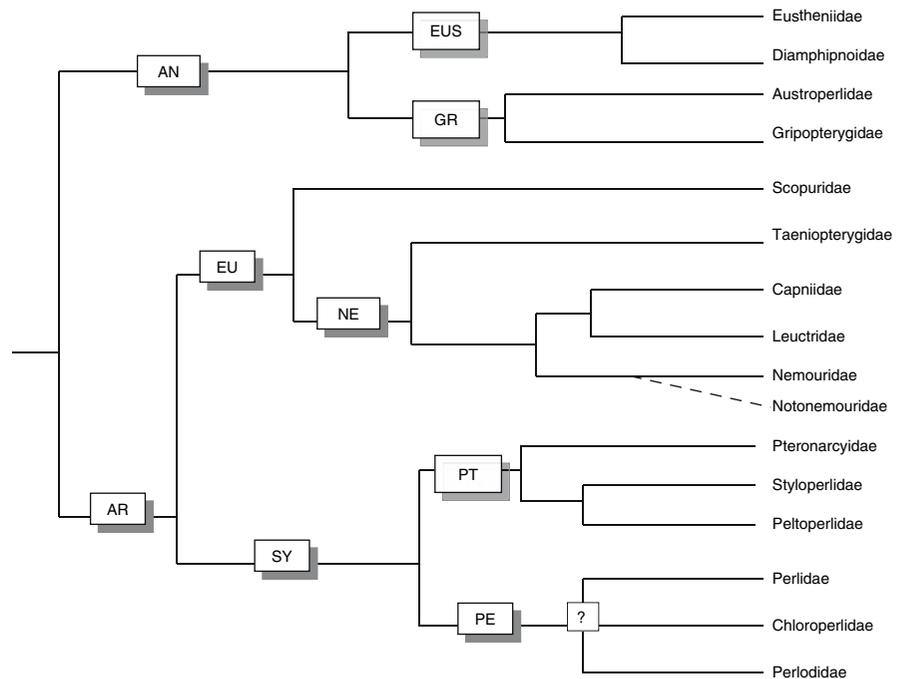
Capniidae and Leuctridae include a similar numbers of species, 311 and 321 respectively, both with mainly Holarctic distribution and a strict systematic affinity. The most diverse genera are the Holarctic *Capnia* (110 species), *Allocapnia* (Nearctic; 43 species), *Mesocapnia* (Nearctic and East Palaearctic, 19 species) among Capniidae, and *Leuctra* (Holarctic, reaching Northern India; 190 species) and *Rhopalopsola* (East Palaearctic and Oriental; 20 species) among Leuctridae. The genus *Megaleuctra* presently includes six North American and one North Korea species; it is also known the fossil record in North America and in Baltic amber.

Notonemouridae (121 species), is considered the sister taxon of Nemouridae (but see below), and thus is an Arctoperlarian family, but shows a disjunct South African (included Madagascar), South American and Australian (included New Zealand) distribution. The family may not be monophyletic (Zwick, 1990) and its biogeography is not fully understood yet. *Austrocercella* (15 species) is the most diverse genus.

Among the remaining Arctoperlaria, the small family (eight species) of wingless stoneflies Scopuridae is known only from Japan and Korea, and the family Pteronarcyidae (13 species) is present in North America and East Asia. Peltoperlidae has a disjunct North American and East Asian distribution (44 species). Styloperlidae a recently instituted family (eight species), erected from aberrant Peltoperlidae, is presently known only from China and Taiwan.

Among Antarctoperlaria, Gripopterygidae is the most diverse family, with 277 described species. It has a disjunct South American and Australian (included New Zealand) distribution, but no genera are shared between the two continents. *Dinotoperla* (33 species), *Leptoperla* (28 species), *Riekoperla* (26 species) are the most diverse Australian genera, *Zelandobius* (27 species) is the most diverse genus of New Zealand. The remaining Antarctoperlaria families are scarcely diversified: Diamphipnoidae (five species) is a small South American family, Eustheniidae includes two genera in South America (two species) one genus in New Zealand (four species) and three genera in Australia (15 species), while Austroperlidae includes 10 species in Australia (five genera), a single species, *Austroperla cyrene* Tylliard, in New Zealand, and four species (three genera) in South America.

**Fig. 2** Plecoptera phylogeny according to Zwick (2000). AN: Antartoperlaria; AR: Arctoperlaria; EUS: Eusthenioidea; GR: Griopterygoidea; EU: Euholognatha; NE: Nemouroidea; SY: Systellognatha; PT: Pteronarcyzoidea; PE: Perloidea. (redrawn from Zwick, 1990)



Among Antartoperlaria Eustheniidae are predators, as are Perloidea in the Northern hemisphere Arctoperlaria; Austroperlidae are shredders as are the Arctoperlaria Pteronarcyidae. Many Griopterygidae are scrapers, as are Brachypterainae in the Arctoperlaria fauna; other Griopterygidae genera are ecologically similar to genera and families of Nemouroidea.

### Phylogeny and historical processes

Stoneflies are Pterygota, Neoptera, Exopterygota insects. Although they are usually included among Polyneoptera (possibly they are the sister-group of the remaining Polyneoptera), the relationships of Plecoptera with other orders of this subdivision are poorly understood (Gullan & Cranston, 2005). Among Polyneoptera, Plecoptera can be identified by a combination of mostly primitive characters. Moreover, only a few derived characters support the Plecoptera monophyly (Zwick, 2000): in the adult, gonads form loops with the anterior ends medially fused; in the male, there is a complex arrangement of two superimposed seminal vesicles each of which forms an anterior loop; in the nymph, strong oblique

intersegmental ventrolongitudinal muscles are present that support laterally undulating swimming (this last character also occurs in Zygoptera). Two other probably derived characters have been reported for Plecoptera include the absence of an ovipositor (although it can secondarily appear in some taxa) and the existence of an accessory circulatory organ (cercus heart) in Perlidae and Perlodidae, that can be present in the other families as well.

The order includes 16 families whose relationships have been studied by several authors: we will follow the more recent and widely accepted classification by Zwick (2000) (Fig. 2), which recognizes two large groups: Antartoperlaria, present only in the Southern Hemisphere, and Arctoperlaria, distributed mostly in the Northern Hemisphere. The first taxon includes four families, the latter includes 12 families belonging to two subgroups (Systellognatha and Euholognatha) with six families each one.

The monophyly of Antartoperlaria is supported by morphological characters, while monophyly of Arctoperlaria is supported by ethological and morphological characters related to mate finding: the intersexual vibrational communication (drumming, tremulation, rubbing or combinations of them) and/or the existence of structures associated to it in the male

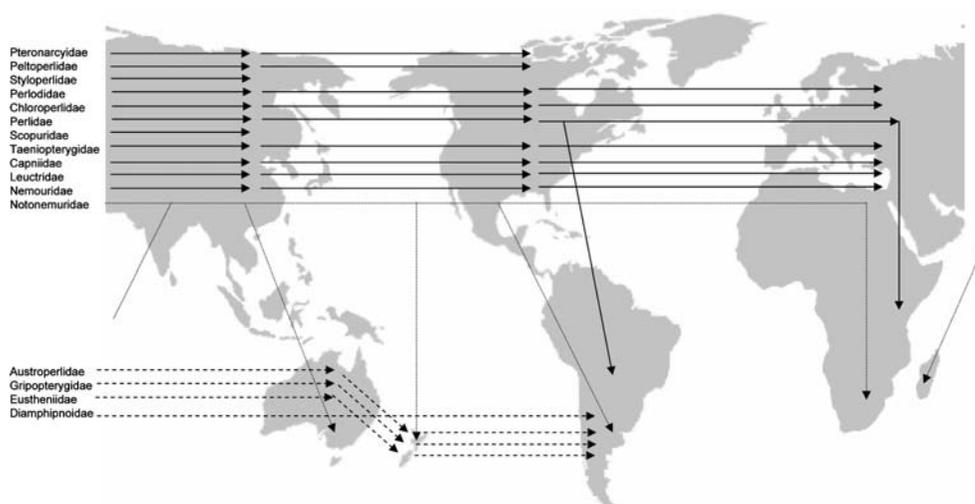
(lobes, hammers, etc.) that are widely present in all families of this group except Scopuridae, and absent in Arctoperlaria (Zwick, 2000). Among the existing families, only Notonemouridae seems to be a polyphyletic assemblage (McLellan, 2000).

According to Rohdendorf & Rasnitsyn (1980), recent stoneflies derived from Plecopteroidea from the Permian Period (including three orders: fossils Protoperlaria and Paraplecoptera, possibly not monophyletic, and Plecoptera). The oldest known Plecoptera fossils are from the early Permian Period, 258–263 m.y. ago (Sinitshenkova, 1997). According to this author, the origin and evolution of the group is linked to temperate areas; during the Mesozoic Period and the role of this group in lentic ecosystems was much more important than it has been afterwards.

According to Illies (1965), Banarescu (1990) and Zwick (1990, 2000) Arctoperlaria and Arctoperlaria originated as independent lines at the splitting of Pangea and the subsequent separation of Gondwanaland and Laurasia, at the end of Triassic Period (Fig. 3). Arctoperlaria possibly began their diversification before the continents separated, producing some sister-groups distributed in South America, Australia and New Zealand. The absence of Arctoperlaria from South Africa and India may be interpreted as a later extinction event. These lands became warmer and drier during their northward journey after separation from Antarctica and

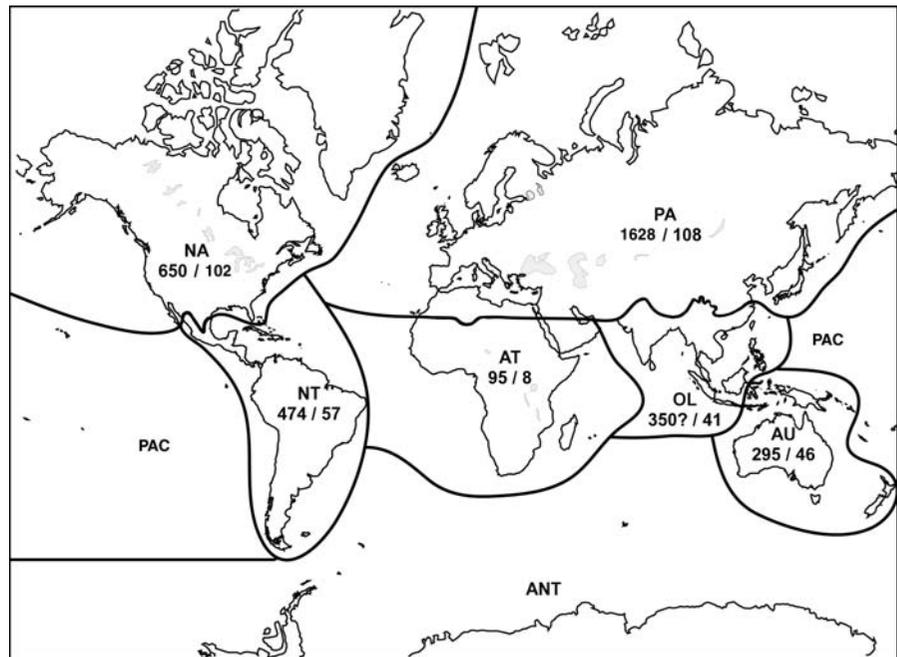
Australia. Before the isolation of Madagascar, Africa was for sure colonized by one family of Arctoperlaria, the Notonemouridae (Zwick, 1990).

The Arctoperlaria families mainly have a Holarctic distribution (with the exception of Notonemouridae which are exclusive of the Southern Hemisphere), with taxa (even species) in common between North America and East Asia. The European stonefly-fauna shares only a few genera with Asia and very few with North America. This may be due to Pleistocenic events, such as the temporal separation of Europe and Asia by the Turgai Strait, the extinctions that occurred in Europe (families Pteronarcyidae and Peltoperlidae) and the faunistic interchanges through the Bering Strait. The presence of arctoperlarian taxa in the Southern Hemisphere could be due to invasions from the Northern Hemisphere (Zwick, 1981). The distribution of the very distinct *Notonemoura* group excludes recent dispersal. It appears that the present distribution results from dispersal across Antarctica (Zwick, 1981, 1990). Nevertheless, Zwick (2000) reported two alternative hypotheses: extinction of Arctoperlaria in the Northern Hemisphere, and of Arctoperlaria in the Southern one. These hypotheses are based on the fact that, although stoneflies are an ancient insect order, their extant families may not necessarily be old, revealing recent and numerous speciation and extinction events, more than dispersive processes. Moreover, the scarce flight ability of these insects makes improbable long distance



**Fig. 3** Plecoptera families distribution; Arctoperlaria = continuous line; Arctoperlaria = dotted line (modified from Zwick, 1990)

**Fig. 4** Distribution of freshwater Plecoptera species and genera by zoogeographical region (species number/genus number). PA—Palaeartic; NA—Nearctic; NT—Neotropical; AT—Afrotropical; OL—Oriental; AU—Australasian; PAC—Pacific & Oceanic Islands, ANT: Antarctic



dispersal (Zwick, 2000). Also, according to Sinitshenkova (1997), the Northern and Southern faunas were isolated from the late Permian Period, when the Pangea still existed.

### Present distribution and main areas of endemism

The diversity for the various zoogeographical regions can be only roughly estimated; it should be approximately as follows: Nearctic 650 species, Palaeartic 1,628 species (it arbitrarily includes also Southern Chinese species) (Holarctic 2,278), Neotropical 474, Afrotropical (Ethiopic) 95 species, Oriental 350? species (Southern Chinese species not included), Australian 295 species (Table 3, Fig. 4). Even though these data indicate the Holarctic Region as the diversity hot-spot for the order, the analysis of the specific diversity divided by family suggests also an important role of tropical stoneflies (see below).

### The Afrotropical Region (Ethiopian)

As reported by Zwick (1998), although Africa (as well as India) was part of Gondwana, its plecopterafauna lacks members of the Gondwanian

Antarctoperlaria. As stated before, Anctartoperlaria must have been present in Gondwana before Africa (and India) split from it; climatic changes are thought to have caused their disappearance from these lands (Banareescu, 1990; Zwick, 2003). Only two Arctoperlaria families (Perlidae and Notonemouridae) are present today in the Afrotropical Region, and with a low specific diversity; one of them (Perlidae) is absent in Madagascar. Only the genus *Neoperla* Needham occurs throughout tropical Africa, including South Africa, with an uncertain number of species. They vary, according to the different authors, from only one [*Neoperla spio* (Newman)] to at least 50 (Zwick, 1998). The originally Oriental genus *Neoperla* reached Africa probably via the same route as the mammalian Ungulata during the Tertiary Period (Zwick, 1998). About 31 species of Notonemouridae, belonging to six genera (*Aphanicerca* Tillyard; *Aphanicerella* Tillyard; *Balinskycercella* Stevens & Picker; *Afronemura* Illies; *Aphaniceropsis* Barnard, and *Desmonemoura* Tillyard) besides two yet undescribed *Neoperla* species are present in South Africa (Villet, 2000). Only the endemic Notonemourid genus *Madenemura* Paulian, with the subgenera (considered as genera by some authors) *Madenemura* and *Tsaranemura* (Paulian, 1951), is present in Madagascar. Unfortunately, only the

**Table 3** Number of Plecoptera genera in each family and each zoogeographical region and total genera number

	PA	NA	NT	AT	OL	AU	World
Eustheniidae			2			3	5
Diamphipnoidae			2				2
Austroperlidae			3			6	9
Gripopterygidae			24			25	49
Pteronarcyidae	1	2	1				2
Peltoperlidae	4	6			4		11
Styloperlidae					2		2
Perlodidae	29	30	2		1		51
Perlidae	20	15	11	1	24		52
Chloroperlidae	14	12	2		2		17
Scopuridae	1						1
Taeniopterygidae	11	6					12
Notonemouridae			4	7 (8)		12	23
Nemouridae	8	12	2		6		21
Capniidae	13	10	3				17
Leuctridae	7	9	1		2		12
Total	108	102	57	8(9)	41	46	286

PA: Palaearctic, NA: Nearctic, NT: Neotropical, AT: Afrotropical, OL: Oriental, AU: Australasian

females of some species were described; the disappearance of holotypes and the lack of description of some material from collections make it difficult to estimate the total number of species living in Madagascar (Elouard, pers. com.). The totally endemic notonemourid fauna of Madagascar together with the absence of *Neoperla*, may be explained by the early isolation of Lemuria.

### The Oriental Region

Seven Arctoperlaria families are present in the Oriental Region, including 41 genera. The absence of Antarctoperlaria in India may be explained by the same reasons of its absence in Africa (see above). One family, Styloperlidae, composed of two genera and eight species endemic from Taiwan and South China, is endemic to this region. Peltoperlidae (with four Oriental genera) has a Nearctic-Asian distribution. The remaining families with Oriental representatives are also widely distributed in the Holarctic Region; only two of them are well-diversified in the Oriental Region: Perlidae (with 24 genera, 12 of which endemic from the Oriental Region) and Nemouridae (with six genera).

Perlodidae (one genus), Chloroperlidae (two genera) and Leuctridae (two genera) complete the list. Unfortunately, the poor and fragmentary knowledge of this region makes it difficult to estimate the real diversity and the exact number of Plecoptera species that must be much larger than what we know. In fact, the Chinese stonefly fauna is almost unknown and hundreds of species are probably still undescribed (Sivec & Yang, 2001). These authors estimate approximately 350 Plecoptera species in the countries forming the Oriental Region, Southern China excluded.

The Oriental stonefly fauna was colonized from close Palaearctic areas (Zwick, 1980), as suggested by the decrease in species numbers towards the south. The first penetration was by members of three families—Nemouridae, Peltoperlidae and Perlidae—that extended down into the rain forest of southeast Asia, thus having somewhat overcome the usual aversion of the order for warm climates.

### The Nearctic Region

The Nearctic Region includes 650 described species, distributed in 102 genera and nine families. Seven of

these families (Capniidae, Leuctridae, Nemouridae, Taeniopterygidae, Chloroperlidae, Perlidae, Perlodidae) and 10 genera (*Capnia*, *Leuctra*, *Amphinemura*, *Nemoura*, *Oemopteryx*, *Taeniopteryx*, *Agnatina*, *Iso-perla*, *Arcynopteryx*, *Diura*) also occur in the Palaearctic Region. There is a substantial division of eastern and western North America genera; only a few of them, in fact, transgress the barrier formed by the central prairies region and the Mississippi valley. Twelve of the western genera are shared with the Russian Far East or Japan, suggesting a recent invasion from the west. The genus *Anacroneuria* invaded from the south, bringing species into Central America, Texas and Arizona. This occurred after the formation of the Isthmus of Panama, during the Pliocene Period, about 4 millions years ago. Very few species have been able to disperse south into Central America, which has a mainly Neotropical stonefly-fauna.

According to Hynes (1988) North America has four groups of stoneflies with different origins:

- (1) The original eastern fauna that was present before the final break from Europe, a great many of which may have evolved initially in North America;
- (2) Invasions from the west, possibly over a long period, while the Cordillera was forming;
- (3) Invasion of one genus from the south after the formation of the isthmus;
- (4) Invasion by several species from the Bering Strait within the last few thousand years. These species may have survived the Pleistocene in the Alaskan refugium.

## The Neotropical Region

### Central America

The stonefly-fauna of Central America is poorly diversified. Deserts and dry areas prevent the immigration of the rich North American Plecoptera fauna: in fact less than 25 “Nearctic” species are known from Central America. They came during the Pleistocene Period, when stoneflies were able to cross the discontinuity between the southern Rocky Mountains and the Sierra Madre Occidental and disperse into northern, central and southern Mexico (Sargent et al.,

1991). On the other hand the “tropical” Plecoptera fauna is also scarce: only the genus *Anacroneuria* (Perlidae) has been able to colonize from the South, with a few scattered species across the countries (34 in Mexico, eight in Nicaragua, 12 in Costa Rica, 15 in Panama, two in Trinidad). However, much research is needed to get a reliable knowledge of Central America stonefly-fauna.

### South America

The stonefly fauna of South America is a complex mixture of arctoperlarian and antarctoperlarian species included in six families: Perlidae, Notonemouridae, Diamphinoidea, Eustheniidae, Austroperlidae, and Gripopterygidae (Tables 1, 2, 3). Among Antarctoperlaria, Eustheniidae (two species) is confined to southern South America, with two monospecific genera. The sister family, Diamphinoidea (five species), is found only in central Chile, with two genera. Austroperlidae (four species) also occurs only in Chile, with three genera. The family Gripopterygidae (73 species), the largest family of the suborder (24 genera, 10 of which are monospecific) is more widespread. Unlike the former families, the latter is also present in subtropical, but not in tropical, South America. Only two families of Arctoperlaria are found in this region, Perlidae and Notonemouridae. Perlidae is the most diverse family (277 species), including 11 genera: the very speciose genus *Anacroneuria*, restricted to Central America and the tropical South America, includes almost 220 species. *Kempnyia* (29 species) and *Macrogynoplax* (12 species) are diversified genera as well, while the remaining genera have few species. Finally, Notonemouridae (17 species), the only Plecoptera family with a Gondwanian distribution (not circumantarctic like the Antarctoperlaria), occurs in southern South America with four genera. However, it must be reminded that the monophyly of this family is still questioned (Zwick, 2000).

It must be noted that, considering the number of species, the true hot-spot of this area (that is almost coincident with the Neotropical Region), is the tropical belt. However, this is due to the presence of several speciose genera (especially the genus *Anacroneuria*). Considering generic diversity, the subtropical and temperate areas are more diversified, with many genera including few species.

## The Palaearctic Region

The Palaearctic Region which includes Europe, Northern Africa and a great part of Asia (except Southeast), includes ten families and more than 1,600 Plecoptera species.

Seven families (Perlidae, Perlodidae, Chloroperlidae, Taeniopterygidae, Nemouridae, Capniidae and Leuctridae), 35 genera and 426 species constitute the Plecoptera fauna of the European continent (Fochetti & Tierno de Figueroa, 2004). Thirty-seven percent of the European genera are monospecific, whereas the four more diversified ones (*Leuctra*, *Protonemura*, *Nemoura* and *Isoperla*) include approximately 70% of the European stonefly species. This fauna is relatively well known from a taxonomical and faunistic point of view. Nevertheless, new species continue to be described.

Although the European Plecoptera fauna is diverse, considerable extinctions probably occurred during Pleistocenic glaciations, because the most important European mountain chains are E–W oriented: when ice advanced southwards they hindered the movement of fauna to the South. Moreover, there have been limited relationships between European and Asian stonefly-faunas, as reported above. Thus, faunistic interchanges were only possible through Asia Minor and the mountain systems, whereas the Central European plains acted as a barrier, and only a few taxa could move across the Polar Circle (such as *Diura* Billberg or *Arcynopteryx* Klapálek) (Zwick, 1980).

High numbers of species exist in the Mediterranean peninsulas (particularly the Western ones) including many endemic species. This is due to the presence of mountain systems, which represent an optimal environment for stoneflies, and to the effect of glaciations, that favoured isolation and speciation processes. Also many species occur in Central Europe mountainous areas (Alpine or Carpathic) where cold streams are abundant. Nevertheless, the post-glacial invasion by widespread species has lowered the number of endemic species. On the contrary, Northern Europe has low species richness. Finally, no species or a few number of them are present in the Atlantic islands as a consequence of the low dispersion capacity of stoneflies.

Northern Africa Plecoptera are included in the same seven families present in Europe (Perlidae, Perlodidae, Chloroperlidae, Taeniopterygidae, Nemouridae, Capniidae and Leuctridae) and in the same

genera, with only one non-European genus: *Afrop-erlodes* Miron & Zwick. Some species are shared with Southern Europe or are very closely related. Currently 15 genera and about 31 species have been reported for this area (Sánchez-Ortega & Azzouz, 1998), approximately 1/3 of which are endemic. The similarity with Southern Europe and particularly with the Southern Iberian Peninsula may be explained by the existence in the past of a land bridge connecting the two areas. In fact, the Betic System (Spain) and the Rif Mountain (North West Africa) were separated only in the Lower Pliocene, when the Gibraltar Strait was formed (Sánchez-Ortega & Azzouz, 1998).

All Arctoperlaria families, except Notonemouridae and Styloperlidae, are present in Palaearctic Asia. The family Scopuridae is endemic from this region, and has a small distribution area and includes eight species belonging to the genus *Scopura* Uéno, which only occurs in Japan and Korea. Pteronarcyidae (only one genus with Asiatic species) and Peltoperlidae (four Palaearctic genera) have a Nearctic-Asian distribution. The remaining families show a wide Holarctic distribution and are well represented in the Asian part of the Palaearctic Region, some of them reaching the Oriental Region.

East Palaearctic (Asian) Plecoptera diversity is much greater than all the remaining continents, despite the poor and fragmentary knowledge of this area: the exact number of Asian Plecoptera species is difficult to estimate, but hundreds of new species will probably be described in the future. Japan with 306 species is an exception, because stoneflies from this country have been well studied, while the Chinese stonefly fauna is almost unknown (Sivec & Yang, 2001). Zhiltzova (1997, 2001) reported 350 species in the former USSR (also including the European part), and noted (1) a marked impoverishment of the fauna towards the North; (2) a high diversity of species in the Caucasus (3) a certain scarcity of Central Asia fauna, with a high degree of endemisms at the specific level concentrated in the Himalayan region; (4) a rather poor fauna in the East Siberian area, even though rich in genera number and endemic species, and (5) a very rich fauna in the South Russian Far East. Finally, the stonefly-fauna of South-West part of Asia is partly unknown; due to the general dry climate of the area, new species may be described in the future only from mountain systems.

From a zoogeographical point of view, the distribution of Pteronarcyidae, Peltoperlidae and several taxa within other families demonstrates that these evolved in the area that encompasses East and North Asia as well as North America, when the two continents were still joined together (Banarescu, 1990). The presence of the genus *Perlodes* Banks only in Europe and Japan, may be explained by its extinction in Siberia during the Ice Age (Banarescu, 1990).

### The Australian Region

Australia currently includes 191 species from 26 genera and four families. Gripopterygidae is shared with South America while Notonemouridae occurs in both South America and South Africa. All 191 Plecoptera species and 24 of the 26 Australian genera are endemic (Theischinger 1991). Tasmanian Plecoptera includes 47 species, 41 of which are endemic to the island. Plecoptera can be found throughout Australia, except the Northern Territory. Their distribution in Western and South Australia is restricted, due to the arid conditions. The genera *Cryptoperla*, *Tasmanoperla* (Austroperlidae), *Tasmanocerca* (Notonemouridae) and *Cardioperla* (Gripopterygidae) are limited to Tasmania. Many genera in all families are confined to mainland Australia. Only the family Gripopterygidae occurs in Western Australia.

New Zealand has 104 described species (McLellan, 2006), and the same four families as Australia. All genera are endemics to this island system, except *Notonemoura* and *Stenoperla*, that are shared with Australia, even though species of this genera are endemic in both countries. A considerable proportion of the entire stonefly-fauna is found in the high precipitation region of the Southern Alps and its subsidiary mountain ranges (McLellan, 2000), and endemisms are most numerous in South Island.

At least one species of *Neoperla* occurs in New Guinea, while no Plecoptera at all are present in New Caledonia.

The total Plecoptera species of the Australian Region is 295. This number is remarkably small if compared to the Holarctic and Oriental faunas, which are of entirely different composition, sharing no families with Australia (Zwick, 1981).

### Human related issues

Stoneflies represent a very important component of rivers and streams, both as biomass and as diversity of ecological roles, acting as primary or secondary consumers and as prey for other macroinvertebrates and fishes, including those of economic importance. From a scientific point of view, they have been used as biogeographical indicators and in evolutionary researches (for instance in the insect wings and respiratory proteins evolution). Their importance as human food is scarce, although some big species are included in the diet of some cultures. Stoneflies have been used for centuries in the sport of fly-fishing, and fishermen have a good general knowledge of them. Plecoptera are frequently employed as bioindicators of water quality: the highest values as indicators of good ecological and environmental quality are normally assigned to this group. Stoneflies do not cause economic damages to human crops although some damage to fruit trees and ornamental plants by adult Taeniopterygidae have been reported.

Unfortunately, water quality degradation and physical alteration of streams and rivers have caused a decrease in the number of Plecoptera species, particularly those inhabiting lowland rivers of industrialized countries (such as many Central European ones), or highly populated countries like the Asiatic ones. *Taeniopteryx araneoides* (Klapálek) and *Oemopteryx loewi* (Albarda), once common in large Central Europe rivers, are now extinct (Zwick, 2004). These are among the very few documented cases of extinction in insects. Many undescribed species, mainly from Asia, will probably go extinct before they are discovered (Sivec & Yang, 2001). Nevertheless, few Plecoptera species are included in the “official” lists of threatened species. Only one species, the chloroperlid *Alloperla roberti* Surdick endemic from Illinois (USA), is reported as extinct in the IUCN Red List of Threatened Species, (IUCN, 2004).

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## References

- Aubert, J., 1959. Plecoptera. *Insecta Helvetica* 1: 1–140.
- Banarescu, P. 1990. Zoogeography of Fresh Water. General Distribution and Dispersal of Freshwater Animal, Vol. 1. Aula-Verlag, Wiesbaden.
- Fochetti, R. & J. M. Tierno de Figueroa, 2004. Plecoptera. Fauna Europaea Web Service. <http://www.faunaeur.org> (Fauna Europaea project, ref. EVR1-CT-1999–2001).
- Fochetti, R. & J. M. Tierno de Figueroa, 2005. I Plecotteri europei: distribuzione e stato di conservazione. XX Congresso Italiano di Entomologia. Assisi 13–18.VI.2005.
- Gullan, P. J. & P. S. Cranston, 2005. *The Insects. An outline of Entomology*. 3rd ed. Blackwell Publishing Ltd, Oxford.
- Heckman, C. W., 2003. *Encyclopedia of South American Aquatic Insects: Plecoptera*. Kluwer Academic Publishers, Dordrecht.
- Hynes, H. B. N., 1976. Biology of Plecoptera. *Annual Review of Entomology* 21: 135–153.
- Hynes, H. B. N., 1988. Biogeography and origins of the North American stoneflies. *Memoires Entomological Society Canada* 144: 31–37.
- Illies, J., 1965. Phylogeny and zoogeography of the Plecoptera. *Annual Review of Entomology* 10: 117–140.
- IUCN, 2004. 2004 IUCN Red List of Threatened Species. <http://www.redlist.org>.
- Jewett, S. G., 1963. A stonefly aquatic in the adult stage. *Science* 139: 484–485.
- McLellan, I. D., 2000. A revision of *Cristaperla* (Plecoptera: Notonemouridae) and some comments on Notonemouridae and its generic groups. *New Zealand Journal of Zoology* 27: 233–244.
- McLellan, I. D. 2003. Endemism and biogeography of New Zealand Plecoptera (Insecta). *Illiesia* 2: 15–23. <http://www2.pms-lj.si/illiesia/papers.html>.
- Michaelis F. & C. M. Yule, 1988. Plecoptera. In Walton, D. W. & W. W. K. Houston (eds), *Ephemeroptera, Megaloptera, Odonata, Plecoptera, Trichoptera*. Zoological Catalogue of Australia, Vol. 6. Canberra, AGPS xi 315 pp (133–176), (Updated by Andrew A. Calder, CSIRO Entomology, Canberra, Australia, 2002).
- Paulian, R., 1951. Faunes des eaux douces de Madagascar I. Pléocoptères et Mégaloctères. *Mémoires Institut Scientifique Madagascar* 6: 53–62.
- Rohdendorf, B. B. & A. P. Rasnitsyn, 1980. [Historical Development of Insect Class]. *Trudy Paleontologicheskogo Instituta* 178: 1–267 (in Russian).
- Sánchez-Ortega, A. & M. Azzouz, 1998. Faunistique et phénologie des Pléocoptères (Insecta, Plecoptera) du Rif marocain (Afrique du nord). Relations avec les autres aires de la région méditerranéenne occidentale. *Mitteilungen der Schweizerischen Entomologischen Gesellschaft* 71: 449–461.
- Sargent, B. J., R. W. Baumann & B. C. Kondratieff, 1991. Zoogeographic affinities of the Nearctic stonefly fauna of Mexico. *Southwestern Naturalist* 36: 323–331.
- Shinitshenkova, N. D. 1997. Paleontology of stoneflies. In Landolt, P. & M. Sartori (eds), *Ephemeroptera and Plecoptera, Biology-Ecology-Systematics*. MTL Fribourg, 561–565.
- Sivec, I. & P. Yang, 2001. Stoneflies of Taiwan within the oriental stonefly fauna diversity. In Domínguez E. (ed.), *Trends in Research in Ephemeroptera and Plecoptera*. Kluwer Academic/Plenum Publishers, New York, 401–404.
- Stark B. P., 2001. A synopsis of the Neotropical Perlidae. In Domínguez E. (ed.), *Trends in Research in Ephemeroptera and Plecoptera*. Kluwer Academic/Plenum Publishers, New York, 405–422.
- Stark, B. P. & R. W. Baumann, 2005. North American Stonefly (Plecoptera) complete list. <http://www.mlbean.byu.edu/plecoptera/list.asp>.
- Stewart, K. W., 1994. Theoretical considerations of mate finding and other adult behaviors of Plecoptera. *Aquatic Insects* 16: 95–104.
- Theischinger G., 1991. Plecoptera (Stoneflies). In CSIRO (ed.), *The Insects of Australia. A textbook for students and research workers*. Vol. 1, 2nd ed. Melbourne University Press, Melbourne, 311–319.
- Tierno de Figueroa, J. M. & R. Fochetti, 2001. On the adult feeding of several European stoneflies (Plecoptera). *Entomological News* 112: 130–134.
- Tozer, W., 1979. Underwater behavioural thermoregulation in the adult stonefly, *Zapada cinctipes*. *Nature (London)* 281: 566–567.
- Villet, M. H. 2000. The stoneflies (Plecoptera) of South Africa. <http://www.ru.ac.za/academic/departments/zooento/Martin/plecoptera.html>.
- Yuzhou, D. & H. Junhua, 2001. Progress on taxonomic study of the family Perlidae from China. In Domínguez E. (ed.), *Trends in Research in Ephemeroptera and Plecoptera*. Kluwer Academic/Plenum Publishers, New York, 369–375.
- Zhiltzova, L. A., 1997. Zoogeographic features of the Euholognatha fauna (Plecoptera) of Russia and adjacent territories (within the limits of the former USSR). In Landolt, P. & M. Sartori (eds), *Ephemeroptera and Plecoptera: Biology-Ecology-Systematics*. MTL Fribourg, 186–192.
- Zhiltzova, L. A., 2001. Plecoptera fauna of Capniidae of Russia and adjacent territories (within the limits of the former USSR). In Domínguez E. (ed.), *Trends in Research in Ephemeroptera and Plecoptera*. Kluwer Academic/Plenum Publishers, New York, 423–429.
- Zwick, P. 1980. Plecoptera (Steinfliegen). In *Handbuch der Zoologie*, Walter de Gruyter, Berlin, 1–115.
- Zwick, P., 1981. Plecoptera. In: Keast A. (ed.) *Ecological Biogeography of Australia*, Vol. 2. The Hague, Junk, 1171–1182.
- Zwick, P., 1990. Transantarctic relationships in the Plecoptera. In Campbell I.C. (ed.), *Mayflies and Stoneflies, Life History and Biology*. Kluwer Academic Publishers, London, 141–148.
- Zwick, P. 1998. The African *Neoperla* (Plecoptera: Perlidae) revisited: towards an overdue revision. XIII International Symposium on Plecoptera, IX International Conference on Ephemeroptera. Tucumán (Argentina), 92.
- Zwick, P., 2000. Phylogenetic System and Zoogeography of the Plecoptera. *Annual Review of Entomology* 45: 709–746.
- Zwick, P., 2003. Biogeographical patterns. In Resh V. H. & R. T. Cardé, (eds), *Encyclopedia of Insects*. Academic Press, Elsevier Science, USA, 94–103.
- Zwick, P., 2004. Key to the West Palearctic genera of stoneflies (Plecoptera) in the larval stage. *Limnologica* 34: 315–348.