

ALEXEY RESHCHIKOV

The world fauna of the genus *Lathrolestes*
(Hymenoptera, Ichneumonidae)



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LIST OF ORIGINAL PUBLICATIONS

- I Reshchikov A.V. 2010. Two new species of *Lathrolestes* Förster (Hymenoptera, Ichneumonidae) from Taiwan and Japan. *Tijdschrift voor Entomologie*, 153: 197–202.
- II Reshchikov A.V., Soper A., van Driesche R.G. 2010. Review and key to Nearctic *Lathrolestes* Förster (Hymenoptera: Ichneumonidae), with special reference to species attacking leaf mining tenthredinid sawflies in *Betula* Linnaeus (Betulaceae). *Zootaxa*, 2614: 1–17.
- III Reshchikov A.V. 2011. Three new species of *Lathrolestes* Förster (Hymenoptera, Ichneumonidae) from Nepal. *Zootaxa*, 2743: 49–55.
- IV Reshchikov A.V. 2011. *Lathrolestes* (Hymenoptera, Ichneumonidae) from Turkey with description of three new species and new synonymy. *Journal of the Entomological Research Society*, 13: 83–89.
- V Reshchikov A.V. 2011. Mexican species of *Lathrolestes* Förster (Hymenoptera: Ichneumonidae; Ctenopelmatinae), with descriptions of four new species and an identification key. *Tijdschrift voor Entomologie*, 154: 15–24.
- VI Reshchikov A.V. 2012. *Lathrolestes* (Hymenoptera, Ichneumonidae) from Central Asia, with a key to the species of the *tripunctor* species-group. *Zootaxa*, 3175: 24–44.
- VII Reshchikov A.V. 2012. Review and key to Russian Far East *Lathrolestes* (Hymenoptera, Ichneumonidae). *Zootaxa*, 3414: 1–32.
- VIII Reshchikov A.V., Veijalainen A., Sääksjärvi I.E. 2012. A new species of *Lathrolestes* (Hymenoptera, Ichneumonidae) from Ecuadorian Amazonia, with a key to the Neotropical species of the genus. *ZooKeys*, 251: 21–27.
- IX Reshchikov A.V. 2013. Two new species of *Lathrolestes* (Hymenoptera, Ichneumonidae) from Norway, northern Russia and Finland with a key to western Palaearctic species. *Zootaxa*, 3681: 059–072.
- X Reshchikov A.V. 2013. New species of *Lathrolestes* Förster (Hymenoptera: Ichneumonidae) from Côte d'Ivoire. *Biodiversity Data Journal*, 1: e1005. doi: 10.3897/BDJ.1.e1005.
- XI Reshchikov A.V. 2015. A new species of *Lathrolestes* Förster (Hymenoptera: Ichneumonidae) from Peruvian Amazonia. *Biodiversity Data Journal*, 3: e4327. doi: 10.3897/BDJ.3.e4327.

My personal contribution to the articles published in co-authorship referred to in this thesis (II, VIII) is the following: identification of the material, revision of the type materials, compiling identification keys, descriptions of new species, preparation of photos and drawings.

I. INTRODUCTION

Such a great and wonderful affluence, which is life on Earth, advanced over three billion years. In spite of about 300 years of taxonomy to describe this richness, major gaps still remain in our knowledge. The total global number of species is evaluated to be roughly 8.7 million species (Mora *et al.* 2011) whereas only about 1.9 million species have been described up to now (Chapman 2009). Insects probably constitute the largest share of unknown biota (Chapman 2009). One of the most species-rich ecological groups among insects are parasitoids (Gauld *et al.* 2002, Hamilton *et al.* 2010). These are insects whose larvae feed in or on other arthropods (usually insects), eventually causing the death of their hosts (Godfray 1994). The latter distinguishes them from parasites. The bulk of parasitoids belongs to Hymenoptera and Diptera. There are also a few species with parasitoid lifestyles among beetles (Coleoptera) and caddisflies (Trichoptera).

Ichneumonidae are the most species-rich family of hymenopteran parasitoids, and one of the largest insect families of all. The world fauna has been estimated to comprise between 60,000 and 100,000 species (Townes *et al.* 1965, Rasnitsyn 1969, Heinrich 1978), which means that the 24,281 described species probably only constitutes about 30% of their true diversity (Yu *et al.* 2012). The Ichneumonidae have a worldwide distribution, whereas their latitudinal diversity patterns are still a subject of some controversy. In particular, the classical view of decreasing species richness of Ichneumonidae towards the tropics (Owen & Owen 1974, Janzen 1981, Skillen *et al.* 2000) has recently been challenged and it has been argued that these large-scale patterns of Ichneumonidae may be artefacts owing to biases in sampling and species description (Santos & Quicke 2011, Veijalainen *et al.* 2012). Because of their lifestyle, ichneumonid wasps play an important role in terrestrial ecosystems, particularly in suppressing and regulating their host populations (Godfray 1994, Hochberg & Ives 2000). Ichneumonid wasps are also one of the most frequently used groups of parasitoids in biological control of insect pests (Heraty 2009). Nevertheless, their wider use in biological control programmes cannot be progressed without advances in systematics and ecology, host use in particular.

The Ctenopelmatinae is a species-rich subfamily of Ichneumonidae that includes mostly koinobiont endoparasitoids of sawfly larvae (Hymenoptera: Symphyta). The taxonomy of the subfamily is rather poorly known, and so is the taxonomy of the focal genus of this thesis – *Lathrolestes* FÖRSTER, 1869. It is a relatively large genus within the tribe Perilissini. Prior to this work, 59 species were known (Yu *et al.* 2012), of which 32 are Nearctic, 20 Palaearctic, one from the Afrotropical, four from the Neotropical, and two from the Oriental regions.

The aim of this work was to review the world fauna of the genus *Lathrolestes*. Since the genus has attracted little attention out of North America in the past, the primary component of this task was to describe the biodiversity

of the genus. Apart from describing new species and mapping their distribution records, I also produced identification keys for different regions. Even though compiling a complete key for the whole genus was not feasible within the time frame of this thesis, individuals from particular regions can now easily be identified using different keys for different regions. Another aim of my thesis was to revise previously described species and elucidate the taxonomy of the genus. Additionally, the results of my work revealed an extremely diverse ovipositor morphology in the genus as well as several new host records. Together with the revised taxonomy, these data help to understand evolutionary patterns in host use, morphological adaptations for using different host groups, and biogeographical patterns in this genus.

2. MORPHOLOGY

The genus *Lathrolestes* belongs to the subfamily Ctenopelmatinae, which could be distinguished from other subfamilies by the single character, presence of apical tooth of fore tibia, and the tribe Perilissini which differs from other tribes of the subfamily by the following character states: epicnemial carina is not reaching fore edge of the mesopleuron, notch between postscutellum and propodeum is V-shaped.



FIGURE 1. Variation in colouration and body size in the genus *Lathrolestes*: a) *L. fumipennis* RESHCHIKOV, 2012, b) *L. tripunctor* (THUNBERG, 1824), c) *L. laevipleuris* RESHCHIKOV, 2013, d) *L. norae* RESHCHIKOV, 2013, e) *L. buccinator* (HOLMGREN, 1857), f) *L. tolstoyi* RESHCHIKOV, 2012.

Adult *Lathrolestes* range in body length from 3 to 20 mm, and vary widely in colour (Fig. 1). The genus shows a well-defined sexual dimorphism in colouration: males frequently have considerably lighter colouration, e.g. in the form of a yellow face or a lighter lower part of the mesopleuron. Within the tribe Perilissini, the genus, together with the genus *Priopoda* HOLMGREN, 1856, can be recognized by the occipital carina not intercepting the hypostomal carina (Fig. 2b). *Lathrolestes* can be distinguished from the genus *Priopoda* 1) by the first tergite which – unlike in *Priopoda* – is not elongate, its length being less than twice as long as wide (Fig. 3a, b), and 2) by the absence of a notch in the hind margin of the male's last visible sternite (Fig. 3c, d) (Townes 1970). However, the latter has one exception, *L. fissus* RESHCHIKOV, 2010 (II) that has the last visible sternite with a notch.

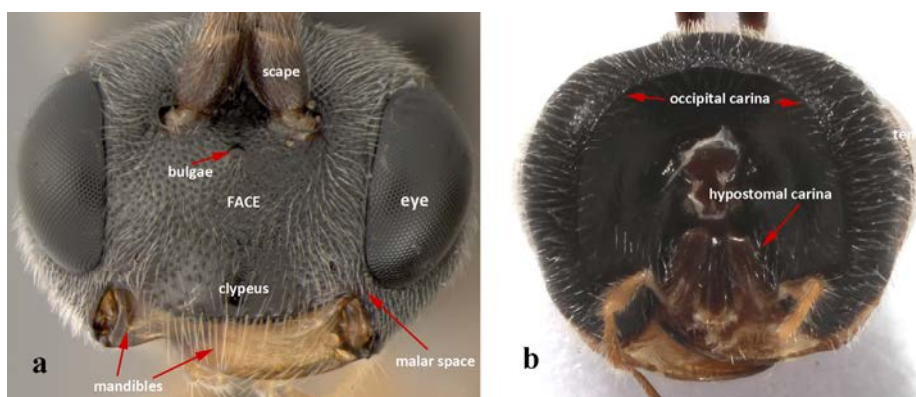


FIGURE 2. Head of *Lathrolestes*: a) anterior view, *L. buccinator*, b) posterior view, *L. orbitalis* (GRAVENHORST, 1829).

The **head** of *Lathrolestes* is orthognathous as in Ichneumonidae in general. The width of the malar space is widely used for identification of species (I–XI). Some species have a rather wide malar space, such as *L. luteolus* THOMSON 1883 (IX), whereas in some others, like *Lathrolestes peisseli* RESHCHIKOV 2011 (III), the malar space is narrow. Another diagnostic feature is whether the clypeus and face are separated by a deep groove, as in almost a third of *Lathrolestes* species, or by a shallow impression which in rare cases is hardly visible (Fig. 2a). Face can vary from flat to convex. The occipital carina provides a further diagnostic character: it is dorsally complete (Fig. 2b) in some species and interrupted in some others.

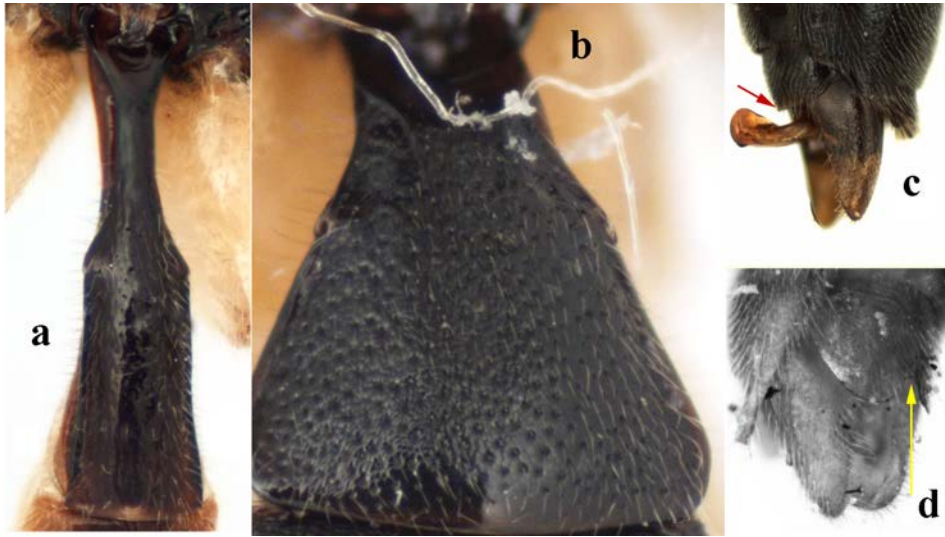


FIGURE 3. a) First metasomal tergite of *Priopoda impressa* RESHCHIKOV, 2012, b) first metasomal tergite of *Lathrolestes sparsus* RESHCHIKOV, 2012, c) last visible sternite of *Lathrolestes aitmatovi* RESHCHIKOV, 2012, d) last visible sternite of *Priopoda lisanevichi* RESHCHIKOV, 2012.

After Latreille's work (1821) no one doubts that the visible transition from the thorax to the abdomen, the so-called "wasp waist" in Apocrita, is actually formed by the second segment of the abdomen while the first abdominal segment (propodeum) is fused to the thorax and partially reduced. The **mesosoma** is therefore traditionally defined as consisting of five dorsal sclerites (Fig. 4): pronotum, mesoscutum, mesoscutellum, metanotum and propodeum (Snodgrass 1910, Matsuda 1970). In the systematics of *Lathrolestes*, the variously punctate surface of the mesopleuron is widely used for diagnosing species. The postpectal carina, a feature widely used in the systematics of Ichneumonidae, is usually absent in *Lathrolestes*, except for *L. peisseli* RESHCHIKOV 2011.

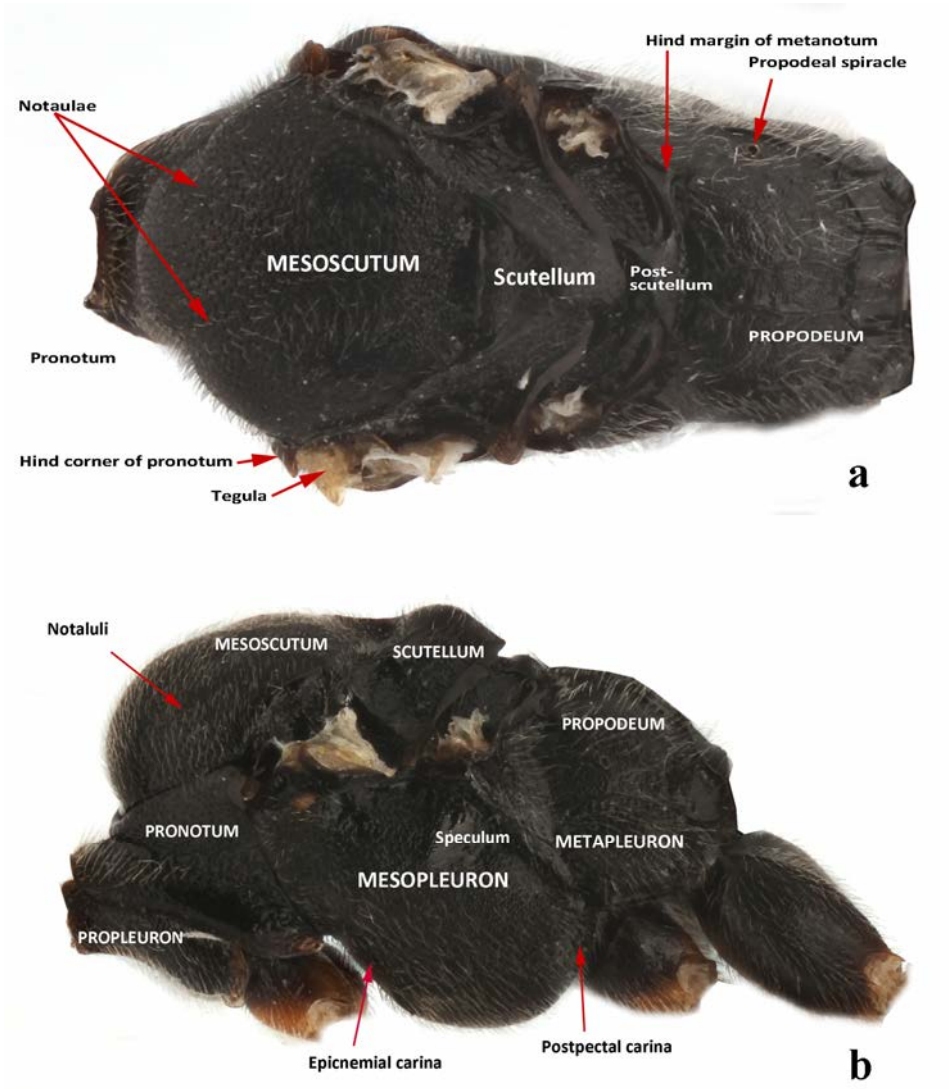


FIGURE 4. Mesosoma of *Lathrolestes*: a) lateral view, b) dorsal view.

Propodeum (Fig. 5) has a system of carinae that divides this segment into areas. A complete carination includes three pairs of longitudinal carinae (medial, lateral and pleural) and two transverse carinae (basal and apical). In *Lathrolestes*, this system of carinae may range from complete carination to reduced or completely absent carination. The high variation in this character allows it to be used in systematics of the genus. Propodeal carinae are completely absent in e.g. *L. verticalis* (BRISCHKE, 1871) and *L. ensator* (BRAUNS, 1898), whereas in *L. luteolator* (GRAVENHORST, 1829) they are complete.

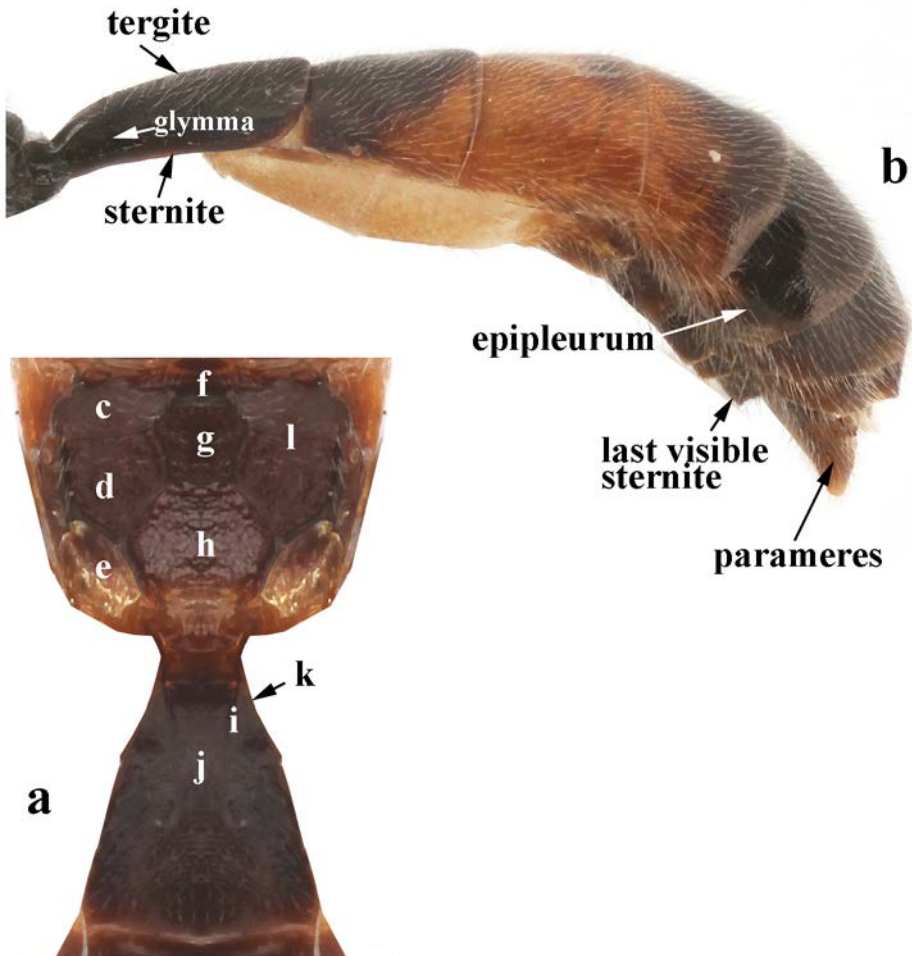


FIGURE 5. Propodeum and metasoma of *Lathrolestes*: a) propodeum and first metasomal tergite, b) metasoma, c) area externa, d) area dentipara, e) area postero-externa, f) area basalis, g) area superomedia, h) area petiolaris, i) dorsal carina, j) dorsal longitudinal groove, k) lateral carina, l) costula.

Wings of *Lathrolestes* also provide some important diagnostic characters (Fig. 6). Within the genus, the areolet (A in Fig. 6) can be petiolate or not. Another character showing between-species variation is the position of Rs+2r relative to the pterostigma. Some further diagnostic features can be found on the **legs**. For example, the fifth tarsomere of *L. unguularis* (THOMSON, 1883) and *L. zeugophorae* BARRON, 1994 is enlarged. Another feature of diagnostic importance is the structure of the tarsal claw (Fig. 7), that can be pectinate, simple or with a basal lobe. Members of the *tripuncator* species group have elongate claws with hair-like teeth (VI).

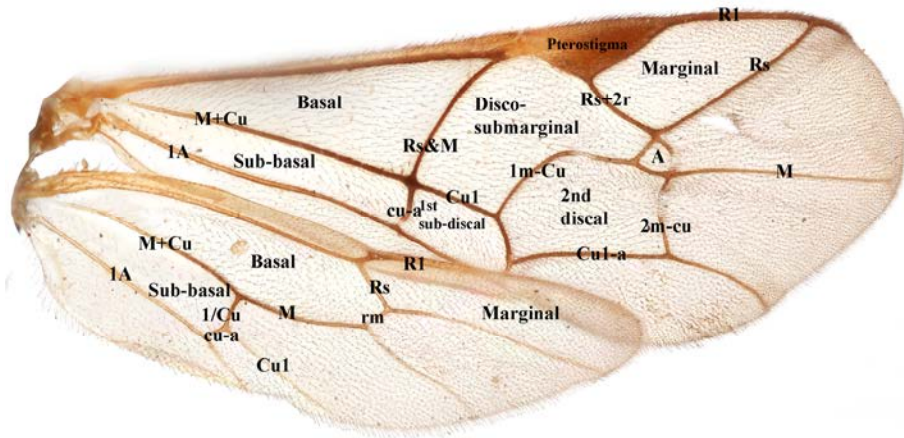


FIGURE 6. Nomenclature of wing cells and venation (Ross 1936), *Lathrolestes ensator*.

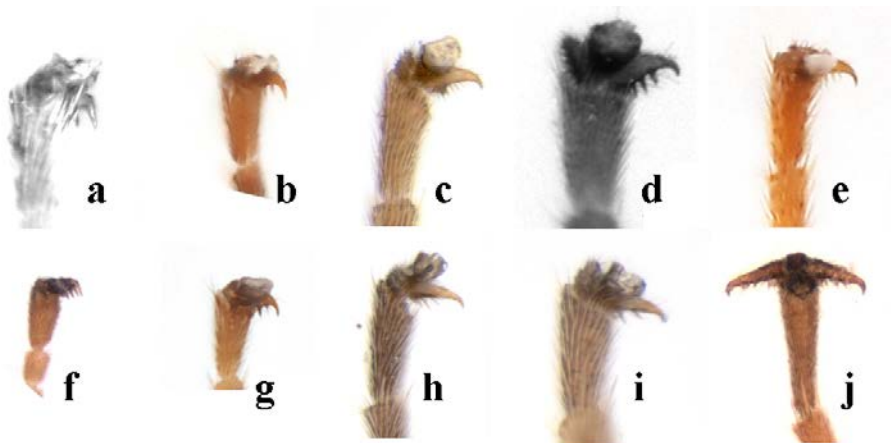


FIGURE 7. Variation in claws: a) *Lathrolestes bipunctatus* (BRIDGMAN, 1886), b) *L. clypeatus* (ZETTERSTEDT, 1838), c) *L. buccinator*, d) *L. ensator*, e) *L. luteolator*, f) *L. norrae*, g) *L. sp.*, h) *L. erythrocephalus* (GRAVENHORST, 1829), i) *L. orbitalis*, j) *L. kozlovi* RESHCHIKOV, 2012.

The **metasoma** refers to the abdomen, starting with the second abdominal segment (Snodgrass 1910), and it has many important characters (Fig. 5). In different species, the longitudinal dorsal and dorsomedial carinae of the first metasomal tergite can vary from well defined to reduced to varying degrees, to completely absent. The presence of the longitudinal depression between the longitudinal dorsal carinae is also of diagnostic value. The proportions of the first metasomal tergite vary markedly across species. Similarly, the second tergite of the metasoma can vary from almost square to elongate. The third and further tergites have no diagnostic characters, with the exception of the laterotergites not being separated from tergites in *L. kozlovi* RESHCHIKOV, 2012 and *L. aytmatovi* RESHCHIKOV, 2012. The shape of the last visible sternite edge is used for discriminating between males of the genera *Priopoda* and *Lathrolestes*. In males of *Priopoda* the edge is notched, while in *Lathrolestes*, with the exception of *L. fissus* RESHCHIKOV, 2010 (II), it is unnotched.

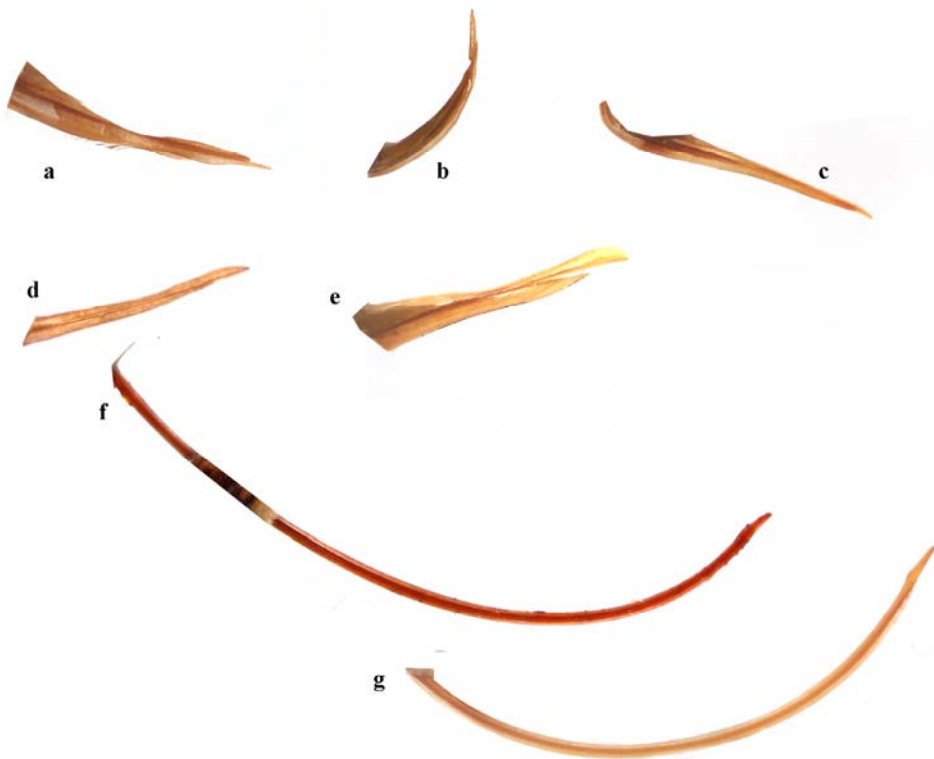


FIGURE 8. Types of ovipositor in *Lathrolestes*: a) with a shallow notch before apex, stout at base – *L. luteolator*, b) with a shallow notch before apex, curved upwards – *L. clypeatus*, c) stout in the basal half, with gradually narrowing apical half, without a shallow notch before apex – *L. bipunctatus*, d) thin, gradually narrowing towards apex – *L. luteolus*, e) swollen dorsally, without notch – *L. orbitalis*, f) and g) elongate, curved upwards, without a notch, with a nodus and apical teeth – *L. ensator* and *L. sp.*, respectively.

Members of the genus vary greatly in the shape of the **ovipositor** which therefore has a high diagnostic value for discriminating different species. The length of the ovipositor varies from a very short one in *L. occultor* AUBERT, 1984 to a rather elongate ovipositor in *L. ensator* (BRAUNS, 1898), in which it exceeds the length of metasoma. Surprisingly, this diversity of ovipositors has not been used in the systematics of *Lathrolestes* before my studies. To classify this variation, I distinguished a number of ovipositor types (Fig. 8).

Unlike in many other insect taxa, male genitalia are not widely used in the systematics of Ichneumonidae. However, in the case of *Lathrolestes*, Barron (1994) has distinguished several types of male genitalia (Fig. 9) and showed that, in some cases, they can be used for identifying species.

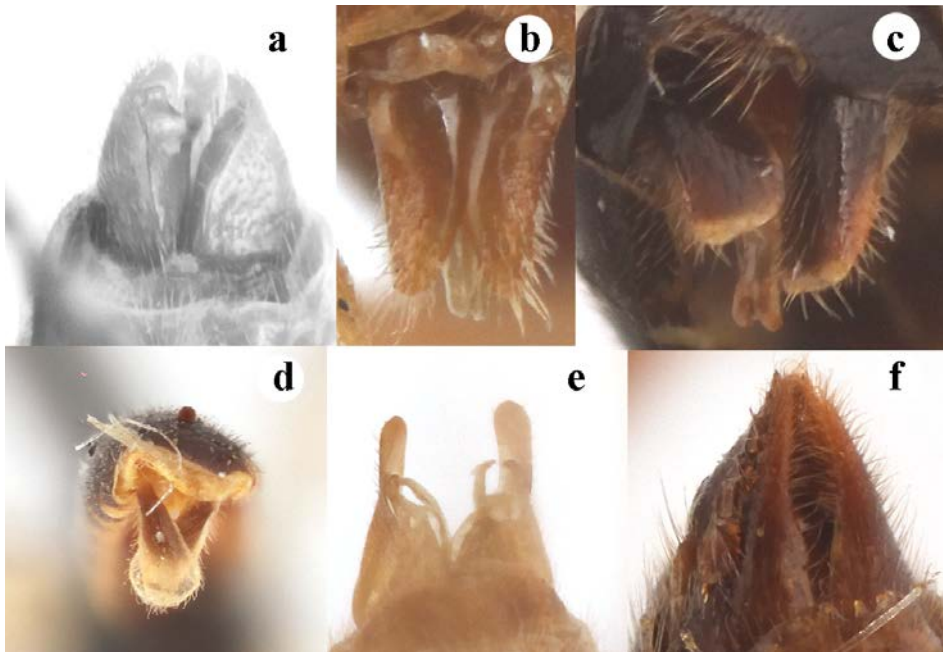


FIGURE 9. Types of male genitalia of *Lathrolestes*: a) *L. sp.*, b) *L. buccinator*, c) *L. caudatus*, d) *L. citreus*, e) *L. verticalis*, f) *L. tripunctor*.

3. ECOLOGY

The larvae of *Lathrolestes* species feed as koinobiont endoparasitoids, usually on leaf-mining sawfly larvae, most often those of the tribe Fenusini (Hymenoptera, Tenthredinidae). These sawflies feed on the foliage of deciduous trees or shrubs (Pschorn-Walcher & Altenhofer 1989), with the exception of *Metallus gei* (BRISCHKE, 1883), feeding on *Geum urbanum* LINNEAUS, 1753. A few species are also known to attack leaf-mining lepidopteran larvae of the family Eriocraniidae (*L. clypeatus* (ZETTERSTEDT, 1838) and *L. mnemonicae* (ROHWER, 1914) (Rohwer 1914, Heath 1961, Carlson 1979)) and leaf-mining beetle larvae of the family Megalopodidae (*L. zeugophorae* BARRON, 1994). The data on trophic interactions of the genus *Lathrolestes* are provided in Table 1 in Appendix.

Lathrolestes nigricollis has been successfully used against the birch leaf-miner, *Fenusa pusilla* (LEPELETIER, 1823) (Raske & Jones 1975, Guevremont & Quednau 1977, van Driesche *et al.* 1997, Langor *et al.* 2000, Casagrande *et al.* 2009), which was introduced from Europe to North America (Coulson 1992, Barron 1994, van Driesche *et al.* 1997) and where it has become an important pest (Fuester *et al.* 1984). The same species of *Lathrolestes* has also been successfully used to control another invasive birch pest, *Profenusa thomsoni* (Langor *et al.* 2000, Soper *et al.* 2015).

4. HISTORY OF RESEARCH

Despite the long research history (Table 2 in Appendix), there are still big gaps in our knowledge of the genus *Lathrolestes*. The genus was established by Förster (1869) but a number of species had already been previously described as belonging to other genera. For example, *L. luteolator* was originally described as belonging to *Mesoleptus*, *L. orbitalis*, *L. erythrocephalus* (GRAVENHORST, 1829), and one of the smallest species, *L. clypeatus* (ZETTERSTEDT, 1838) to *Tryphon*, and *L. buccinator*, *L. lucidulus*, *L. macropygus* and *L. pictilis* (HOLMGREN, 1857) to *Perilissus*. Carl Gustaf Thomson (1883) in his "Bidrag till kännedom om Skandinaviens Tryphoner" distinguished the tribe Perilissini as a separate group and described eight new species of *Lathrolestes*: *L. caudatus*, *L. constrictus*, *L. frontator*, *L. luteolus*, *L. nigricollis*, *L. pleuralis*, *L. unguularis*, *L. marginatus* (the latter is a junior synonym of *L. verticalis*).

A number of species have been described by American 19th century entomologists as well (Ashmead 1890, Davis 1897). After the enormous work on the higher-level taxonomy of Ichneumonidae by Henry Townes (Townes 1945, Townes & Townes 1951, Townes *et al.* 1961, Townes *et al.* 1965, Townes & Townes 1966, Townes 1970, Townes & Townes 1973), the Nearctic species of the genus *Lathrolestes* (Hymenoptera, Ichneumonidae) were revised by Barron (1994). As regards the other regions, Gauld *et al.* (1997) have described a further four species from the Neotropical region, and Uchida (1932, 1940) two species from the Oriental region. However, the Palaearctic members of the genus have not been reviewed before this study (IV, VI, VII, IX).

5. MATERIAL AND METHODS

Collecting and studied collections

One of the main parts of any study in systematics is the examination of type collections. This activity is most important in cases when the original descriptions and diagnoses are poor, and there is a lack of identification keys. The genus *Lathrolestes* was certainly one of these cases. For this review, I examined a rather high number of type specimens, both those of *Lathrolestes* as well as type specimens belonging to some other genera of Perilissini. This research was based on material from the following collections:

- AEI – American Entomological Institute, Gainesville, U.S.A.;
- ANSP – Academy of Natural Sciences of Philadelphia, U.S.A.;
- CNC – Canadian National Collections, Centre for Land and Biological Resources Research, Agriculture Ottawa, Canada;
- CRI – Crop Research Institute, Prague, Czech Republic;
- DABUH – University of Helsinki, Finland;
- EIHU – Entomological Institute, Hokkaido University, Sapporo, Japan;
- FEI – Finnish Environment Institute, Kuhmo, Finland;
- IZBE – Institute of Zoology and Botany, Tartu, Estonia;
- IZCR – Institute of Zoology, Palermo University, Palermo, Italy;
- KFD – Naturwissenschaftliche Sammlungen der Stadt Krefeld, Brempter Hof, Germany;
- KarRC – Karelian Research Centre of the Russian Academy of Sciences, Petrozavodsk, Russia;
- LEW – Laboratorium voor Entomologie, Landbouwhogeschool, Wageningen, The Netherlands;
- LS – Linnaean Society, London, England, UK;
- MAS – Mongolian Academy of Sciences, Entomology Collection, Ulaanbaatar, Mongolia;
- MZH – Finnish Museum of Natural History, Helsinki, Finland;
- MNHN – Muséum National d'Histore Naturelle, Paris, France;
- MRAC – Musée Royal de l'Afrique Centrale, (Congo Museum), Tervuren, Belgium;
- MUZM – Museo de Historia Natural de la Universidad Nacional Mayor de San Marcos, Lima, Peru;
- MZLS – Musée de Zoologie, Lausanne, Switzerland;
- MZLU – Zoologiska Institutionen, Lund, Sweden;
- MZVU – Museum of Zoology, Vilnius University, Lithuania;
- NCM – Norwich Castle Museum, Norwich, UK;
- HNHM – Hungarian Natural History Museum, Budapest, Hungary;
- NHM UiO – Natural History Museum, University of Oslo, Norway;
- NHRS – Naturhistoriska Riksmuseet, Stockholm, Sweden;

- NTNU – Norwegian University of Technical Science and Natural History, Trondheim, Norway;
- RMNH – Naturalis Biodiversity Centre, Leiden, Netherlands;
- SMF – Natur-Museum Senckenberg, Frankfurt, Germany;
- SPbU – Entomology Department, Saint Petersburg State University, Russia;
- TAMU – Texas A & M University, U.S.A.;
- USL – Zoological Museum Uppsala University, Uppsala, Sweden;
- USNM – U.S. National Museum of Natural History, Smithsonian Institute, U.S.A.;
- WDS – Bauer’s collection, Wendelstein, Germany;
- ZIN – Zoological Institute, Russian Academy of Science, Saint Petersburg, Russia;
- ZMHU – Zoologisches Museum, Humboldt Universität, Berlin, Germany;
- ZMUB – Zoological Museum, University of Bergen, Norway;
- ZMUM – Zoological Museum of Moscow University, Moscow, Russia;
- ZMUT – Zoological Museum University of Turku, Finland;
- ZSM – Zoologisches Staatsammlung, München, Germany.

The existing material was supplemented by collecting additional material in Norway, Finland, Russia, Ukraine and Mongolia. For this purpose, sweep nets, Malaise traps (Malaise 1937, Townes 1962) and yellow pan traps (Campbell *et al.* 2007, Frank & Dirrigl 2012) were used. All the material was preserved in ethanol. The revision of Nearctic species also involved insect rearings, revealing trophic interactions of some species (II).

Morphological analyses

Altogether about 2000 specimens were studied. External characters, including ovipositor structure, were studied using MBS-1, MBS-9, Olympus SZX16 and Leica MZ6 microscopes. Photographs were taken with Olympus E520, Q-Imaging and Canon 7D cameras, combined with the software packages Helicon Focus®, Automontage® and Zerene®, and Adobe Photoshop. Morphological terminology used in the thesis mostly follows that of Gauld (1997) and Eady (1968). The taxonomy follows the catalogue TaxaPad (Yu *et al.* 2012). The descriptions of all available type specimens were revised.

DNA sequences

Adults of *L. thomsoni*, *L. nigricollis* and *L. soperi* were subjected to DNA extraction (II) using the DNeasy kit as per the manufacturer’s instructions (Qiagen, Valencia, CA, USA). The barcode primers (Hebert *et al.* 2003) were used to amplify the mitochondrial cytochrome oxidase c subunit I (COI). Each

PCR reaction was carried out in 50 μ l reactions. PCRs contained 0.2 μ M of each primer, 0.2 mM of each dNTP, 2.5 mM MgCl₂, 2 U of Taq polymerase (Applied Biosystems, Carlsbad, CA), USA), 1x buffer supplied by the manufacturer (Qiagen) and 1 μ l genomic DNA. All reactions were carried out in an MJ Research Inc., a programmable thermocycler. An initial denaturation at 94°C for 1 min was followed by five cycles of 94°C for 1 min, 45°C for 1.5 min, and 72°C for 1.5 min; 35 cycles of 94°C for 1 min, 50°C for 1.5 min and 72°C for 1 min; 72°C for 5 min. PCR products were purified prior to sequencing using ExoSAP-IT (U.S. Biochemicals, Cleveland, OH) as per manufacturer's instructions. PCR products were sent to the Genomics Center at Yale University. Sequences were edited in Sequencher 4.2 (Gene Codes Corporation).

6. RESULTS AND DISCUSSION

As the main result of my thesis, I provide a taxonomic review of the world fauna of the genus *Lathrolestes*, which is based on an extensive survey of rather sparse specimens from most major world ichneumonid collections. The taxonomic studies conducted increased the known fauna of *Lathrolestes* by as much as 38%. The large proportion of previously undescribed species confirms the view that the share of insect species described is just the tip of the iceberg. The up-to-date species list of *Lathrolestes* totals now at least 103 (the holotype specimen of *Lathrolestes frontator* THOMSON, 1883 is lost and I could not study any material of this species) distinct species in the World fauna (I–XI). The following 40 species were described as new to science (see the full list of *Lathrolestes* species in the Appendix):

- | | |
|-------------------------------|-------------------------------|
| <i>L. acinaces</i> (IV) | <i>L. levaya</i> (VII) |
| <i>L. aitmatovi</i> (VI) | <i>L. lidae</i> (III) |
| <i>L. anularius</i> (VII) | <i>L. nigronitens</i> (VII) |
| <i>L. barroni</i> (II) | <i>L. nornae</i> (IX) |
| <i>L. cruentocaudus</i> (VII) | <i>L. obliquus</i> (VI) |
| <i>L. fascialis</i> (IV) | <i>L. palatynus</i> (VII) |
| <i>L. fiedleri</i> (XI) | <i>L. peisseli</i> (III) |
| <i>L. fissus</i> (II) | <i>L. pubescens</i> (VII) |
| <i>L. foveafacialis</i> (I) | <i>L. quetzalcoatlus</i> (V) |
| <i>L. fumipennis</i> (VII) | <i>L. roerichi</i> (III) |
| <i>L. gauldi</i> (VIII) | <i>L. ruficaudus</i> (VI) |
| <i>L. grahami</i> (VI) | <i>L. sachalinensis</i> (VII) |
| <i>L. hovdensis</i> (VI) | <i>L. soperi</i> (II) |
| <i>L. ivoriensis</i> (X) | <i>L. sparsus</i> (VII) |
| <i>L. kaspanyani</i> (VII) | <i>L. syringe</i> (II) |
| <i>L. kerzhneri</i> (VII) | <i>L. tepeyollotlis</i> (V) |
| <i>L. kozlovi</i> (VI) | <i>L. thomsoni</i> (II) |
| <i>L. kukulcanis</i> (V) | <i>L. tolstoyi</i> (VII) |
| <i>L. laevipleuris</i> (IX) | <i>L. xochiquetzalis</i> (V) |
| <i>L. langelandi</i> (I) | <i>L. zoticus</i> (IV) |

The very high number of new species leaves an assumption that many more species of this genus are still expected globally, especially from poorly studied tropical regions, but probably even from Europe as shown in IV and IX. In future studies, particular attention should be given to the Southeast Asian region, as this region is very species-rich in the major host groups of *Lathrolestes*. Moreover, recent sorting of Oriental material in two major ichneumonid collections (Naturalis, Leiden, Netherlands and Queen Sirikit Botanic Garden, Chiang Mai, Thailand) has revealed many morpho-species belonging to

Lathrolestes. Unfortunately, most of this material remained unavailable during the compilation of this thesis.

Besides the new species described, the following nomenclatural changes were proposed on the basis of taxonomic results of this work.

New synonyms:

L. nasoni DAVIS, 1897, a junior synonym of *L. caudatus* (THOMSON, 1883) (II)

L. citrofrontalis SCHMIEDEKNECHT, 1912, a junior synonym of *L. unguularis* (THOMSON, 1883) (IV)

Names resurrected from synonymy:

L. scutellatus (ASHMEAD, 1890) from synonymy with *L. luteolator* (GRAVENHORST, 1829) (II)

New combination:

L. erythrocephalus (GRAVENHORST, 1829) and *L. tripunctor* (THUNBERG, 1824) transferred to *Lathrolestes* from *Perilissus* (VI).

Lathrolestes can be distinguished by the combination of the occipital carina intercepting the hypostomal carina at the base of mandible and the hind wing with cu-a intercepted by Cu1 below the middle (Burks 1952, Townes 1970). Nevertheless, so far, diagnostic features of the genus *Lathrolestes* do not allow complete discrimination of this genus from the genera *Priopoda* HOLMGREN, 1856 and *Perilissus* FÖRSTER, 1855 (II). Various authors at various times have therefore treated some *Lathrolestes* species as belonging to these two genera. For example, Horstmann (2001) treated *L. erythrocephalus*, *L. buccinator* and *L. tripunctor* as belonging to *Perilissus*. In this thesis, these species are included in the genus *Lathrolestes*, as their occipital carina does not intercept the hypostomal carina before the base of the mandible, a characteristic feature of *Lathrolestes* (II). This thesis is the first step to solve this type of taxonomic problems. Future studies, preferably based on molecular data, must bring more clarity to genus-level taxonomy.

Within the genus, a number of distinct species groups have been distinguished for Nearctic species (Barron 1994, II): the *luteolator*, *nigricollis*, *breviremus*, *constrictus*, *truncatus*, *striatus*, and *bulbus* species groups. For Palearctic species, I found it premature to define species groups because of obvious blanks in our knowledge of real biodiversity. An exception was made for five new species, *L. obliquus*, *L. aitmatovi*, *L. kozlovi*, *L. hovdensis*, and *L. grahami*, which together with the previously known Palearctic species *L. buccinator* (HOLMGREN, 1857), *L. erythrocephalus* (GRAVENHORST, 1829), *L. orbitalis* (GRAVENHORST, 1829), and *L. tripunctor* (THUNBERG, 1824), were distinguished as the *tripunctor* species-group (VI). This group is easily

diagnosed by the swollen head, not narrowed behind the eyes, by elongate, parallel temples, by elongate claws with pectinate, hair-like teeth, and by the coarsely punctate face and mesopleuron. However, suggestions for species groups should primarily be based on phylogenetic analysis, not only interpretation of morphological features. Hopefully, with molecular data more readily becoming available, taxonomic progress at the within-genus level will be feasible. In this thesis, three species occurring in North America (**II**), *L. thomsoni*, *L. soperi* and *L. nigricollis*, were sequenced. The smaller DNA-based difference between *L. soperi* and *L. nigricollis* as compared to with *L. thomsoni*, matched the diagnosis of these species developed on morphological grounds.

Between-species variation in host use and respective differences in ovipositor structure displayed in my thesis may provide a further basis for distinguishing distinct species groups within *Lathrolestes*, or, perhaps, in the future, even for dividing *Lathrolestes* into different genera. Indeed, *Lathrolestes* displays a remarkably diverse host use for a single genus. As shown in Table 1 in Appendix, the hosts of the different species they attack range from free-living larvae (e.g. *Periclista*) to those concealed in the substrate (see below). Correspondingly, morphological analyses allowed me to recognize a remarkable diversity of ovipositor types within the genus (**II**) which is likely to reflect specialization for using different types of hosts on or within different substrates. For example, *L. ensator* is a parasitoid of a frugivorous sawfly, *Hoplocampa testudinea* (Nematinae, Hoplocampini) (Zapryanov 1985, Zijp & Blommers 1993, Babendreier 1996, Boeve 1996, Vincent *et al.* 2002, Zijp & Blommers 2002a, 2002b). This *Lathrolestes* species has an unusually elongate ovipositor which is curved upwards. This is likely an adaptation to parasitize host larvae within fruits. *L. caudatus*, attacking larvae of *Ardis brunniventris* (Blennocampinae, Blennocampini), a sawfly feeding within branches of dog rose (Evenhuis 1973, Hinz 1996), serves as another example of host specialization and a respective modification to the ovipositor structure. The ovipositor of this wasp is also elongate but has a nodus at its apex instead of a notch, a feature unusual for endoparasitoids. I suppose that such a modification of the ovipositor could be an adaptation for feeding in larvae within hard substrates, such as fruits and branches. Another species, *Lathrolestes luteolator*, attacks larvae of slug sawflies, *Caliroa* (Heterarthrinae, Caliroini) (Carl 1976). Attacking these sawflies requires narrow specialization since larvae of slug sawflies have specific defensive strategies (Boevé & Müller 2005). The ovipositor of this species of *Lathrolestes* is stout at the base and has a shallow notch. This ovipositor structure is probably an adaptation to prick through the cover of the sawfly's slime. This explanation is supported by the fact that most other *Caliroa* parasitoids have a similar ovipositor with a shallow notch (Kasparyan 1973, 1990), including *Hodostates* FÖRSTER, 1869 which differs from other Pionini with a typically slender needle-like ovipositor without a notch (Cameron & Wharton 2011).

Two species of *Lathrolestes*, *L. clypeatus* (ZETTERSTEDT, 1838) and *L. mnemonicae* (ROHWER, 1914) attack leaf-mining lepidopteran larvae of the family Eriocraniidae (Heath 1961, Rohwer 1914), possibly representing cases of shifts onto taxonomically different but ecologically similar groups of hosts. In the genus, such a shift has probably taken place twice: in the European *L. clypeatus*, and the American *L. mnemonicae*. Similar host shifts have also occurred in the subfamily Tryphoninae (Hymenoptera, Ichneumonidae), another ichneumonid group primarily attacking sawflies (Kasparyan & Tolkanitz 1999). Indeed, several species of the genus *Grypocentrus* RUTHE, 1855, mainly attacking leaf-mining sawflies, have also been reared from Eriocraniidae (Heath 1961, Jordan 1998). Similarities in ovipositor morphology between the two genera are likely to reflect adaptations for host use: in both *Lathrolestes* and *Grypocentrus*, species attacking eriocraniid leafminers have upcurved ovipositors. A similar adaptation to the same group of hosts has thus occurred within different subfamilies of Ichneumonidae.

The thesis also contributes to the knowledge of *Lathrolestes* ecology by new host records. Based on reared material, *Profenusa thomsoni* has been established as a host for two newly described species, *L. thomsoni* and *L. soperi* (II). This sawfly species has been mentioned as a host for *Lathrolestes* for the first time, although some other species of *Profenusa* are known as hosts for other *Lathrolestes* (see Table 1 in Appendix). The newly described species, *L. thomsoni*, mentioned above was successfully used as a biocontrol agent in Alaska (II, Soper *et al.* 2015). *Aprosthemina* sp. (Argidae, Sterictiphorinae) is the first host record (VI) for *L. erythrocephalus* (GRAVENHORST, 1829), as well as for *Lathrolestes* in general. However, another species of Argidae, *Sterictiphora geminata* (GMELIN, 1790) has previously been recorded as a host for *L. luteolator* (GRAVENHORST, 1829) (Aubert 2000).

Even though the data on *Lathrolestes* are still rather fragmentary, some biogeographical inferences can be made. Current knowledge of the biogeography of the genus suggests that the most species-rich region is the north temperate zone. Accordingly, 38 species are recorded from the Nearctic region (including two introduced Palearctic species and one Holarctic species), 49 species from the Palaearctic region, two from the Afrotropical region (X), ten from the northern part of the Neotropical region (VIII, IX, XI), and seven from the northern part of the Oriental region (I, III) (Fig. 10). *Lathrolestes* species are absent from the Australasian and Oceanic regions, with the exception of *L. luteolator* that has been introduced to New Zealand (Dumbleton 1936). The tropical fauna of the genus seems to have developed on the basis of invasions from the Holarctic along mountain ranges. In particular, in Neotropical and Oriental regions, *Lathrolestes* is known mostly from mountainous northern parts of the regions (I, III, VIII, IX), closely following the distribution patterns of their symphytan hosts (Malaise 1945). The present knowledge of latitudinal diversity trends of *Lathrolestes* is thus consistent with the classical understanding of general diversity patterns in Ichneumonidae, according to

which their diversity tends to decrease from temperate latitudes towards the tropics (Owen & Owen 1974, Janzen 1981, Skillen *et al.* 2000).

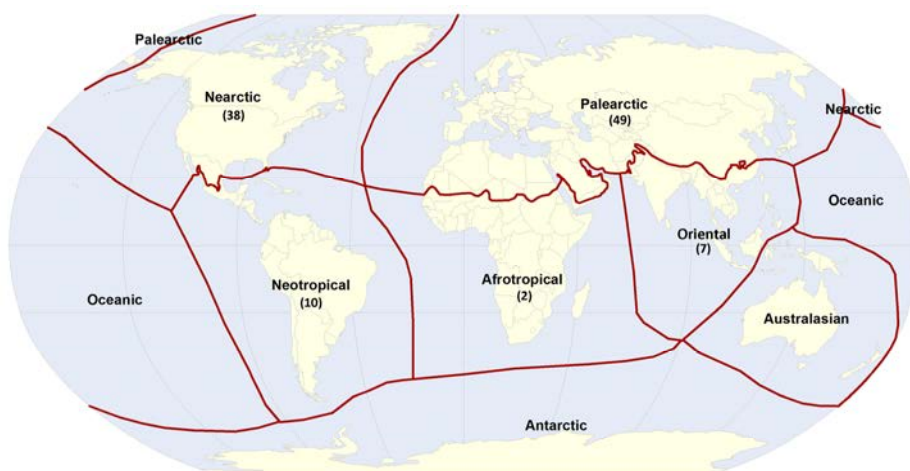


FIGURE 10. Distribution of the genus *Lathrolestes* in the world with numbers of known species given for each biogeographic region.

Recent studies (Santos and Quicke 2011, Veijalainen *et al.* 2012) have challenged this classical view by suggesting that the exceptional latitudinal diversity patterns of Ichneumonidae may be artefacts owing to biases in sampling and species description. However, an analysis of faunal composition of Ichneumonidae in Amazonia has shown that ichneumonid groups parasitizing on sawflies, such as Ctenopelmatinae and Tryphoninae, are indeed relatively species-poor in the tropics (Veijalainen *et al.* 2013). Low species diversity of these groups in the tropics has been suggested to be associated with low diversity of their major host groups (Kouki *et al.* 1994, Gauld 1997, Veijalainen *et al.* 2013, VII). Thus, in the case of *Lathrolestes*, the currently known latitudinal diversity trends may remain valid in the future as well. Nevertheless, although diversity of sawflies has been shown to be low for Afrotropics (Malaise 1945, Koch 2005), this is not necessarily the case in other tropical regions. In the Neotropical region, the diversity of Symphyta is not considered to be particularly low, but species are mostly associated with mountains with their cool climate (Malaise 1945). As mentioned above, this is also where most Neotropical *Lathrolestes* have been collected. By contrast, Southeast Asia is considered to be one of the biodiversity hotspots for Symphyta (Malaise 1945, Smith 1981, Wei & Niu 2009, Smith 2011). It is therefore plausible that the relatively low numbers of species attacking sawflies known from this tropical region is due to a lack of data.

The known distribution data suggest that most *Lathrolestes* species have rather limited distribution ranges. For example, there is just one Holarctic species, *L. caudatus*, that occurs both in the Palaearctic and Nearctic regions. In fact, before I synonymized *L. nasoni* with *L. caudatus* (II) no single species present in both the Palearctic and the Nearctic regions was known, with the exception of introduced species. Moreover, even truly trans-Palaearctic species are rare among *Lathrolestes*. Indeed, most species from the Palaearctic region have either European or East Palaearctic distribution ranges. In Tryphoninae, another group of ichneumonid wasps parasitizing sawflies, similar patterns of distribution have been shown for species of the genus *Monoblastus* HARTIG, 1837 (Kasparyan 1973). This genus mostly inhabits European broad-leaved forests and mixed coniferous forests of the Far East and the same types of forests in North America (Kasparyan 1973). Such distribution patterns are likely to reflect specialization to different hosts. Indeed, similarly to *Lathrolestes*, the main groups of sawflies known as their hosts show largely the same patterns of distribution, with a very low number of species occurring both in the Palaearctic and Nearctic regions (Taeger *et al.* 2010).

APPENDIX

All the species covered in this thesis are treated briefly below. Nomenclatural information (synonyms, type localities) is given only for the species for which information is absent in the papers (I–XI).

***Lathrolestes acinaces* RESHCHIKOV, 2011 (IV)**

Distribution. Western Palaearctic. Specimen studied from Turkey.

***Lathrolestes aitmatovi* RESHCHIKOV, 2012 (VI)**

Distribution. Eastern Palaearctic. Specimens studied from Kyrgyzstan.

***Lathrolestes albicinctus* (HABERMEHL, 1922)**

Perilissus albicinctus HABERMEHL, 1922: 353. Holotype ♀, ZSM [examined]. Type locality: Germany (Worms, Rhineland-Palatinate).

Distribution. Western Palaearctic. Specimens studied from Armenia.

***Lathrolestes anularius* RESHCHIKOV, 2012 (VII)**

Distribution. Eastern Palaearctic. Specimens studied from Russia (Primorsky Krai).

***Lathrolestes aquilus* BARRON, 1994**

Lathrolestes aquilus BARRON, 1994: 69. Holotype ♀, CNC [examined]. Type locality: USA (Echo Lake, Colorado).

Distribution. Nearctic. Specimens studied from USA (Colorado).

***Lathrolestes asperatus* BARRON, 1994**

Lathrolestes aquilus BARRON, 1994: 32. Holotype ♂, CNC [examined]. Type locality: Canada (Point Pelee, Ontario).

Distribution. Nearctic. Specimens studied from Canada (Ontario).

***Lathrolestes barroni* RESHCHIKOV, 2010 (II)**

Distribution. Nearctic. Specimens studied are from Canada (Quebec, Ontario).

***Lathrolestes bipunctatus* (BRIDGMAN, 1886)**

Grypocentrus bipunctatus BRIDGMAN, 1886: 358–359. Holotype ♀, NCM [examined]. Type locality: UK (Wimbledon, Surrey).

Distribution. Palaearctic. Specimens studied are from Norway, Russia (Murmansk Oblast, Sverdlovsk Oblast, Chita Oblast, Kamchatka Krai, Kunashir), and UK.

***Lathrolestes breviremus* BARRON, 1994**

Lathrolestes breviremus BARRON, 1994: 51. Holotype ♀, AEI [examined]. Type locality: USA (Parker Canyon, Arizona).

Distribution. Nearctic. Specimens studied from USA (Arizona).

***Lathrolestes buccinator* (HOLMGREN, 1857)**

Perilissus buccinator HOLMGREN, 1857: 122. Holotype ♀, NRM [examined]. Type locality: Sweden (Småland).

Perilissus vollenhoveni GRIBODO, 1880: 7. Holotype ♂, Museo Civico di Storia Naturale, Genoa, Italy [not examined]. Type locality: Italy (Nicotera, Calabria).
Distribution. Palaearctic. Specimens studied are from Armenia, Azerbaijan, Finland, France, Russia (Buryatia, Kamchatska Krai, Khabarovsk Krai, Krasnodarsk Krai, Krasnoyarsk Krai, Leningrad, Primorsky Krai, Sakhalin, Smolensk), Slovenia, Ukraine.

***Lathrolestes bulbus* BARRON, 1994**

Lathrolestes bulbus BARRON, 1994: 82. Holotype ♀, AEI [examined]. Type locality: USA (Corvallis, Oregon).

Distribution. Nearctic. Specimens studied from USA (Alaska, California, Nebraska, Nevada, Oregon).

***Lathrolestes bullatus* BARRON, 1994**

Lathrolestes bullatus BARRON, 1994: 65. Holotype ♀, AEI [examined]. Type locality: USA (Davis, California).

Distribution. Nearctic. Specimens studied from USA (California).

***Lathrolestes carinatus* BARRON, 1994**

Lathrolestes carinatus BARRON, 1994: 80. Holotype ♀, AEI [examined]. Type locality: USA (Potrero, California).

Distribution. Nearctic. Specimens studied from Canada (Alberta), USA (California).

***Lathrolestes caudatus* (THOMSON, 1883)**

Lathrolestes caudatus THOMSON, 1883: 917. Holotype ♀, lost, Type locality: Sweden, (Fogelsång, Skåne).

Lathrolestes nasoni DAVIS, 1897: 264. Holotype ♂, ANSP [examined]. Type locality: USA (Algonquin, Illinois).

Lathrolestes similis DAVIS, 1897: 265. Lectotype ♀, ANSP [examined]. Type locality: USA (Colorado).

Distribution. Holarctic. Specimens studied from Canada (Alberta, British Columbia, Ontario, Saskatchewan), Russia (Buryatia, Kamchatka, Khabarovsk Krai, Sakhalin), USA (Arizona, California, Colorado, Illinois, Minnesota, Montana).

***Lathrolestes citreus* (BRISCHKE, 1878)**

Perilissus citreus BRISCHKE, 1878: 75–76. Type lost. Type locality: Poland.

Distribution. Western Palaearctic. Specimens studied from Sweden.

***Lathrolestes clavipes* BARRON, 1994**

Lathrolestes clavipes BARRON, 1994: 44. Holotype ♀, CNC [examined]. Type locality: Canada (Hixon, British Columbia).

Distribution. Nearctic. Specimens studied from Canada (British Columbia), USA (Alaska, Oregon, Washington).

***Lathrolestes clypeatus* (ZETTERSTEDT, 1838)**

Tryphon clypeatus ZETTERSTEDT, 1838: 399. Holotype ♀, MZLU [examined]. Type locality: Sweden (Lapland).

Lathrolestes eriocraniae SEYRIG, 1928: 201. Holotype ♀, MNHN [not examined]. Type locality: France.

Distribution. Western Palaearctic. Specimens studied from Finland, Norway, Russia (Arkhangelskaya Oblast, Khabarovskiy Kray, Leningradskaya Oblast), Sweden.

***Lathrolestes cruenocaudus* RESHCHIKOV, 2012 (VII)**

Distribution. Eastern Palaearctic. Specimens studied from Russia (Primorskiy Kray).

***Lathrolestes constrictus* (PROVANCHER, 1882)**

Phygadeuon constrictus PROVANCHER, 1882: 336. Holotype ♂, Quebec [not examined].
Type locality: Canada (Quebec).

Lathrolestes rufigaster CUSHMAN, 1933: 13. Holotype ♀, USNM [examined]. Type locality: Canada (Grimsby, Ontario).

Distribution. Nearctic. Specimens studied from Canada (Ontario, Quebec), USA (Florida, Maine, North Carolina, Ohio, Virginia).

***Lathrolestes convexus* BARRON, 1994**

Lathrolestes convexus BARRON, 1994: 71. Holotype ♀, AEI [examined]. Type locality: USA (Ann Arbor, Michigan).

Distribution. Nearctic. Specimens studied from Canada (Ontario) and USA (Michigan, New York).

***Lathrolestes dentatus* BARRON, 1994**

Lathrolestes dentatus BARRON, 1994: 43. Holotype ♀, AEI [examined]. Type locality: USA (Corvallis, Oregon).

Distribution. Nearctic. Specimens studied from USA (California, Oregon).

***Lathrolestes ensator* (BRAUNS, 1898)**

Tryphonopsis ensator BRAUNS, 1898: 63. Holotype ♀, ZMHU [examined]. Type locality: Germany (Teschendorf, Mecklenburg-Vorpommern).

Lathrolestes dilatatus NORDENSTRÖM, 1905: 207. Holotype ♀, MZLU [examined]. Type locality: Sweden (Halland).

Distribution. Holarctic. Specimens studied from Byelorussia, Germany, Sweden.

***Lathrolestes erugatus* BARRON, 1994**

Lathrolestes erugatus BARRON, 1994: 34. Holotype ♀, AEI [examined]. Type locality: USA (Portal, Arizona).

Distribution. Nearctic. Specimens studied are from USA (Arizona, Texas).

***Lathrolestes erythrocephalus* (GRAVENHORST, 1829)**

Tryphon erythrocephalus GRAVENHORST, 1829: 220. Holotype ♀, lost, Type locality: Germany

Perilissus subcinctus horvathi KISS, 1926: 266. Holotype ♀, HNHM [examined]. Type locality: Hungary (Pápa, Veszprém).

Distribution. Western Palaearctic. Specimens studied from Czech Republic, Finland, Germany, Kazakhstan, Kyrgyzstan.

***Lathrolestes euryremus* BARRON, 1994**

Lathrolestes euryremus BARRON, 1994: 41. Holotype ♂, CNC [examined]. Type locality: Canada (Sable Island, Nova Scotia).

Distribution. Nearctic. Specimens studied from Canada (Nova Scotia).

***Lathrolestes fascialis* RESHCHIKOV, 2011 (IV)**

Distribution. Western Palaearctic. Specimens studied from Turkey.

***Lathrolestes fiedleri* RESHCHIKOV, 2011 (XI)**

Distribution. Neotropical. Specimen studied from Peru.

***Lathrolestes fissus* RESHCHIKOV, 2010 (II)**

Distribution. Nearctic. Specimens studied from USA (Florida, Georgia).

***Lathrolestes foveafacialis* RESHCHIKOV, 2010 (I)**

Distribution. Oriental Region. Specimens studied from China (Taiwan).

***Lathrolestes fumipennis* RESHCHIKOV, 2012 (VII)**

Distribution. Eastern Palaearctic. Specimens studied from Russia (Kunashir, Primorskiy Karay).

***Lathrolestes frontator* (THOMSON, 1883)**

Perilissus frontator THOMSON, 1883: 914. Holotype ♀, lost, Type locality: Sweden (Skåne).

Distribution. Western Palaearctic. Not examined.

***Lathrolestes gauldi* RESHCHIKOV et al 2012 (VIII)**

Distribution. Neotropical. Specimens studied from Ecuador.

***Lathrolestes gibbosus* BARRON, 1994**

Lathrolestes gibbosus BARRON, 1994: 63. Holotype ♀, CNC [examined]. Type locality: Canada (Old Chelsea, Quebec).

Distribution. Nearctic. Specimens studied are from Canada (Ontario, Quebec) and USA (North Carolina).

***Lathrolestes grahami* RESHCHIKOV, 2012 (VI)**

Distribution. Eastern Palaearctic. Specimens studied from China (Sichuan).

***Lathrolestes haroldi* GAULD, 1997**

Lathrolestes haroldi GAULD, 1997: 210. Holotype ♀, INBio [not examined]. Type locality: Costa Rica.

Distribution. Neotropical. Specimens studied from Costa Rica.

***Lathrolestes hovdensis* RESHCHIKOV, 2012 (VI)**

Distribution. Eastern Palaearctic. Specimen studied from Mongolia.

***Lathrolestes irenea* GAULD, 1997**

Lathrolestes irenea GAULD, 1997: 211. Holotype ♀, INBio [not examined]. Type locality: Costa Rica.

Distribution. Neotropical. Specimens studied from Costa Rica.

***Lathrolestes ivoriensis* RESHCHIKOV, 2013 (X)**

Distribution. Afrotropical. Specimens studied from Côte d'Ivoire.

***Lathrolestes jennyae* GAULD, 1997**

Lathrolestes jennyae GAULD, 1997: 213. Holotype ♀, BMNH [not examined]. Type locality: Costa Rica.

Distribution. Neotropical. Specimens studied from French Guiana (new record).

***Lathrolestes karenae* GAULD, 1997**

Lathrolestes jennyae GAULD, 1997: 214. Holotype ♀, BMNH [not examined]. Type locality: Costa Rica.

Distribution. Neotropical. Not studied.

***Lathrolestes kasparyani* RESHCHIKOV, 2012 (VII)**

Distribution. Eastern Palaearctic. Specimens studied from Russia (Amur Oblast).

***Lathrolestes kerzhneri* RESHCHIKOV, 2012 (VII)**

Distribution. Eastern Palaearctic. Specimens studied from Russia (Sakhalin).

***Lathrolestes kozlovi* RESHCHIKOV, 2012 (VI)**

Distribution. Eastern Palaearctic. Specimens studied from China (Inner Mongolia).

***Lathrolestes kukulcanis* RESHCHIKOV, 2011 (V)**

Distribution. Neotropical. Specimens studied from Mexico.

***Lathrolestes kulingensis* (UCHIDA, 1940)**

Prionopoda kulingensis UCHIDA, 1940: 124. Holotype ♀, UAMH [not examined]. Type locality: China (Kuling, Jiangxi).

Distribution. Oriental. Not studied.

***Lathrolestes laevipleuris* RESHCHIKOV, 2013 (IX)**

Distribution. Western Palaearctic. Specimens studied from Finland.

***Lathrolestes langelandi* RESHCHIKOV, 2010 (I)**

Distribution. Oriental. Specimens studied from China (Taiwan).

***Lathrolestes levaya* RESHCHIKOV, 2012 (VII)**

Distribution. Eastern Palaearctic. Specimens studied from Russia (Khabarovskiy Krai).

***Lathrolestes lidae* RESHCHIKOV, 2011 (III)**

Distribution. Oriental. Specimens studied from Nepal.

***Lathrolestes lucidulus* (HOLMGREN, 1857)**

Perilissus lucidulus HOLMGREN, 1857: 127. Lectotype ♀, NHRS [examined]. Type locality: Sweden (Anneberg, Småland).

Distribution. Western Palaearctic. Specimens studied from Russia (Chita Oblast, Khabarovskiy Krai, Ussuriyskiy Krai), Sweden.

***Lathrolestes luteolator* (GRAVENHORST, 1829)**

Mesoleptus luteolator GRAVENHORST, 1829: 42. Type lost. Type locality: Switzerland (Siegenshausen, Thurgau).

Tryphon gorskii RATZEBURG, 1852: 126–127. Type lost. Type locality: Lithuania (Vilnius).

Distribution. Palaearctic. Specimens studied from Norway, Russia (St Petersburg), South Korea (new record), Sweden.

***Lathrolestes luteolus* (THOMSON, 1883)**

Lathrolestes luteolus THOMSON, 1883: 917. Holotype ♂, MZLU [examined]. Type locality: Sweden (Lund, Skåne).

Distribution. Palaearctic. Specimens studied from Germany and Sweden.

***Lathrolestes macropygus* (HOLMGREN, 1857)**

Perilissus macropygus HOLMGREN, 1857: 126. Lectotype ♂, NHRS [examined]. Type locality: Sweden (Bohuslän), Norway (Dovre, Uppland).

Perilissus soleatus HOLMGREN, 1857: 126. Lectotype ♀, NHRS [examined]. Type locality: Sweden (Öland, Småland, Uppland, Dalarna).

Distribution. Palaearctic. Specimens studied from Germany, Russia (Chita Oblast, Kunashir, Leningrad Oblast, Primorsky Krai, Yakutia), Sweden.

***Lathrolestes meridionalis* (SMITH VAN BURGST, 1912)**

Ritzemabosia meridionalis SMITH VAN BURGST, 1912: 269. Holotype ♀, RMNH [examined]. Type locality: Tunisia.

Distribution. Western Palaearctic. Specimen studied from Tunisia.

***Lathrolestes messae* BARRON, 1994**

Lathrolestes messae BARRON, 1994: 60. Holotype ♀, CNC [examined]. Type locality: Canada (Barkers Point, New Brunswick).

Distribution. Nearctic. Specimens studied from Canada (New Brunswick).

***Lathrolestes minimus* TEUNISSEN, 1953**

Tryphonopsis ensator minimus TEUNISSEN, 1953: 17–18. Type [not examined]. Type locality: Netherlands (Leeuwarden, Friesland).

Distribution. Western Palaearctic. Not studied.

***Lathrolestes mnemonicae* (ROHWER, 1914)**

Sympherta mnemonicae ROHWER, 1914: 141–142. Holotype ♂, USNM [examined]. Type locality: USA (Falls Church, Virginia).

Polyoncus mentalis DAVIS, 1897: 306. Holotype ♀, ANSP [examined]. Type locality: USA (New Hampshire).

Distribution. Nearctic. Specimens studied from USA (New Hampshire, Virginia).

***Lathrolestes morator* AUBERT, 1984**

Lathrolestes morator AUBERT, 1984: 20. Holotype ♀, MZLS [examined]. Type locality: France (Fontainebleau, Île-de-France).

Distribution. Western Palaearctic. Specimens studied from France.

***Lathrolestes moravicus* (HABERMEHL, 1923)**

Perilissus moravicus HABERMEHL, 1923: 379. Holotype ♀, SMF [examined]. Type locality: Germany (Weiskirchen, Mähren).

Distribution. Western Palaearctic. Specimens studied from Russia (St Petersburg).

***Lathrolestes nigricollis* (THOMSON, 1883)**

Perilissus nigricollis THOMSON, 1883: 915–916. Holotype ♂, MZLU [examined]. Type locality: Sweden (Skåne).

Perilissus minutus BRIDGMAN, 1887: 370. Holotype ♀, NCM [examined]. Type locality: UK (Shiere)

Distribution. Holarctic. Specimens studied from Norway, Russia (Kuril islands, Saint Petersburg), Sweden, UK.

***Lathrolestes nigrifacies* (UCHIDA, 1932)**

Monoblastus nigrifacies UCHIDA, 1932: 216. Holotype ♂, DEI [examined]. Type locality: Taiwan (Taihorin).

Distribution. Eastern Palaearctic. Specimen studied from China (Taiwan).

***Lathrolestes nigronitens* RESHCHIKOV, 2012 (VII)**

Distribution. Eastern Palaearctic. Specimens studied from Russia (Jewish Autonomous Oblast, Primorskiy Krai, South Korea).

***Lathrolestes nornae* RESHCHIKOV, 2013 (IX)**

Distribution. Palaearctic. Specimens studied from Norway.

***Lathrolestes occultor* AUBERT, 1984**

Lathrolestes (Lathrolestodes) occultor AUBERT, 1984: 21. Holotype ♀, MZLS [examined]. Type locality: France (Fontainebleau, Île-de-France).

Distribution. Western Palaearctic. Specimens studied from France.

***Lathrolestes obliquus* RESHCHIKOV, 2012 (VI)**

Distribution. Eastern Palaearctic. Specimens studied from Kyrgyzstan, Uzbekistan, Tajikistan, Turkmenistan.

***Lathrolestes obscurellus* (DAVIS, 1897)**

Spanotecnus obscurellus DAVIS, 1897: 304. Holotype ♀, ANSP [examined]. Type locality: USA (Connecticut).

Distribution. Nearctic. Specimens studied from Canada (Ontario), USA (Connecticut, Florida, Oregon).

***Lathrolestes ochraceus* BARRON, 1994**

Lathrolestes ochraceus BARRON, 1994: 76. Holotype ♀, CNC [examined]. Type locality: USA (Forsyth, Georgia).

Distribution. Nearctic. Specimens studied from USA (Georgia, Illinois, Maryland, Ohio).

***Lathrolestes orbitalis* (GRAVENHORST, 1829)**

Tryphon orbitalis GRAVENHORST, 1829: 2554. Type lost. Type locality: Poland (Wrocław).

Perilissus bucculentus HOLMGREN, 1857: 123. Holotype ♀, NRM [examined]. Type locality: Sweden (Småland, Östergötland, Uppland, Dalarna, Lappland).

Distribution. Palaearctic. Specimens studied from Finland, Hungary, Norway, Russia (Dagestan, Irkutsk Oblast, Khabarovsk Krai, Krasnoyarsk Krai, Leningrad Oblast,

Moscow Oblast, Pskov Oblast, Primorsky Kray, Sakha Yakutia, Sverdlovsk Oblast, Tomsk Oblast, Yaroslavl Oblast), Sweden, UK, and Ukraine.

***Lathrolestes palatynus* RESHCHIKOV, 2012 (VII)**

Distribution. Eastern Palaearctic. Specimens studied from Russia (Jewish Autonomous Oblast).

***Lathrolestes peisseli* RESHCHIKOV, 2011 (III)**

Distribution. Oriental. Specimens studied from Nepal.

***Lathrolestes periclistae* BARRON, 1994**

Lathrolestes periclistae BARRON, 1994: 58. Holotype ♀, CNC [examined]. Type locality: Canada (Cap-Rouge, Quebec).

Distribution. Nearctic. Specimens studied from Canada (Quebec).

***Lathrolestes pictilis* (HOLMGREN, 1857)**

Perilissus pictilis HOLMGREN, 1857: 125. Lectotype ♀, NRM [examined]. Type locality: Sweden (Småland, Bohuslän, Uppland, Dalarna, (Tavelsjö) Västerbotten, Lappland).

Distribution. Palaearctic. Specimens studied from Russia (Buryatia, Chita Oblast, Khabarovsk Kray, Primorsky Kray, Sakha Yakutiya), Sweden.

***Lathrolestes pictus* CUSHMAN, 1933**

Lathrolestes pictus CUSHMAN, 1933: 11. Holotype ♀, CNC [examined]. Type locality: USA (Brookings, South Dakota).

Distribution. Nearctic. Specimens studied from Canada (Alberta), USA (Idaho, Oregon, South Dakota).

***Lathrolestes planus* BARRON, 1994**

Lathrolestes planus: BARRON, 1994: 49. Holotype ♀, AEI [examined]. Type locality: USA (Strawberry, California).

Distribution. Nearctic. Specimens studied from USA (California).

***Lathrolestes platynus* (DAVIS, 1897)**

Polyoncus platynus DAVIS, 1897: 306. Lectotype ♀, ANSP [examined]. Type locality: USA (Agricultural College, Michigan).

Distribution. Nearctic. Specimens studied from USA (Maine, Michigan).

***Lathrolestes pleuralis* (THOMSON, 1883)**

Lathrolestes pleuralis THOMSON, 1883: 916–917. Lectotype ♀, MZLU [examined]. Type locality: Sweden (Norrländ).

Distribution. Palaearctic. Specimens studied from Norway, Russia (Chita Oblast, Kamchatka, Khabarovsk Kray, Primorsky Kray, Sakha Yakutia), Sweden.

***Lathrolestes profenusae* BARRON, 1994**

Lathrolestes profenusae BARRON, 1994: 67. Holotype ♀, USNM [examined]. Type locality: USA (Lewiston, Maine).

Distribution. Nearctic. Specimens studied from USA (Maine, Ohio).

***Lathrolestes protenus* BARRON, 1994**

Lathrolestes protenus BARRON, 1994: 53. Holotype ♀, CNC [examined]. Type locality: USA (Highlands, North Carolina).

Distribution. Nearctic. Specimens studied from Canada (Ontario), USA (Alaska, Georgia, Maryland, Minnesota, North Carolina).

***Lathrolestes protrusus* BARRON, 1994**

Lathrolestes protrusus BARRON, 1994: 22. Holotype ♀, CNC [examined]. Type locality: USA (Laurel, Maryland).

Distribution. Nearctic. Specimens studied from Canada (Ontario), USA (California, Florida, Georgia, Maryland, New York, Oregon, Pennsylvania).

***Lathrolestes pubescens* RESHCHIKOV, 2012 (VII)**

Distribution. Eastern Palaearctic. Specimens studied from Russia (Khabarovskiy Krai).

***Lathrolestes quetzalcoatlus* RESHCHIKOV, 2011 (V)**

Distribution. Neotropical. Specimens studied from Mexico.

***Lathrolestes roerichi* RESHCHIKOV, 2011 (III)**

Distribution. Oriental. Specimen studied from Nepal.

***Lathrolestes ruficaudus* RESHCHIKOV, 2012 (VI)**

Distribution. Eastern Palaearctic. Specimen studied from Tajikistan.

***Lathrolestes ruwenzoricus* (BENOIT, 1955) (X)**

Distribution. Afrotropical. Specimen studied from Democratic Republic of Congo.

***Lathrolestes sachalinensis* RESHCHIKOV, 2012 (VII)**

Distribution. Eastern Palaearctic. Specimens studied from Russia (Sakhalin).

***Lathrolestes saliceti* (ROMAN, 1909)**

Lathrolestes saliceti ROMAN, 1909: 104. Lectotype ♂, NRM [examined]. Type locality: Sweden (Sarek, Lapland).

Distribution. Palaearctic. Specimens studied from Norway, Sweden.

***Lathrolestes scutellatus* (ASHMEAD, 1890)**

Prionopoda scutellata ASHMEAD, 1890: 441. Holotype ♀, USNM [examined]. Type locality: USA (Washington DC).

Homalomma caliroae ROHWER, 1915: 218–219. Holotype ♀, USNM [examined]. Type locality: USA (Falls Church, Virginia).

Homalomma eriocampoides ROHWER, 1915: 219. Holotype ♀, USNM [examined]. Type locality: USA (Falls Church, Virginia).

Distribution. Nearctic. Specimens studied from USA (District of Columbia, Virginia).

***Lathrolestes soperi* RESHCHIKOV, 2010 (II)**

Distribution. Nearctic. Specimens studied from USA (Alaska).

***Lathrolestes sparsus* RESHCHIKOV, 2012 (VII)**

Distribution. Eastern Palaearctic. Specimens studied from Russia (Jewish Autonomous Oblast, Kamchatka, Khabarovsk Krai, Primorsky Krai, Sakhalin).

***Lathrolestes striatus* BARRON, 1994**

Lathrolestes striatus BARRON, 1994: 78. Holotype ♀, AEI [examined]. Type locality: USA (Mount Rainier, Washington).

Distribution. Nearctic. Specimens studied from USA (Washington).

***Lathrolestes syringe* RESHCHIKOV, 2010 (II)**

Distribution. Nearctic. Specimens studied from USA (Georgia, South Carolina).

***Lathrolestes tepeyollotlis* RESHCHIKOV, 2011 (V)**

Distribution. Neotropical. Specimens studied from Mexico.

***Lathrolestes thomsoni* RESHCHIKOV, 2010 (II)**

Distribution. Nearctic. Specimens studied from Canada (Alberta, New Brunswick, Northwest Territories).

***Lathrolestes tolstoyi* RESHCHIKOV, 2012 (VII)**

Distribution. Eastern Palaearctic. Specimens studied from Russia (Primorskiy Krai).

***Lathrolestes tomostethi* (CUSHMAN, 1935)**

Perilissus tomostethi CUSHMAN, 1935: 558. Holotype ♀, USNM [examined]. Type locality: USA (Boston, Massachusetts).

Distribution. Nearctic. Specimens studied from Canada (Ontario), USA (Massachusetts, New York, Ohio).

***Lathrolestes tripunctor* (THUNBERG, 1824)**

Ichneumon tripunctor THUNBERG, 1824: 280. Holotype ♀, USL [examined]. Type locality: Sweden.

Ichneumon distichor THUNBERG, 1822: 272. Holotype ♂, USL [examined]. Type locality: Sweden.

Perilissus (Polyoncus) grandiceps THOMSON, 1883: 913. Holotype ♂, MZLU [examined]. Type locality: Sweden (Arrie, Skåne).

Perilissus longicornis BRISCHKE, 1871: 72. Type lost. Type locality: Poland.

Perilissus luteocephalus GIRAUD, 1872: 397–399. Lectotype ♀, MNHN [examined]. Type locality: France (Grenoble, Rhône-Alpes).

Perilissus singularis VOLLENHOVEN, 1878: 45. Lectotype ♂, RMNH [examined]. Type locality: Netherlands.

Distribution. Palaearctic. Specimens studied from Germany, Russia (Pskov Oblast), Sweden.

***Lathrolestes truncatus* (PROVANCHER, 1888)**

Mesochorus truncatus PROVANCHER, 1889: 333. Holotype ♀, Ste Foy University [not examined]. Type locality: Canada (Vancouver, British Columbia).

Spanotecnus iladus DAVIS, 1897: 303. Lectotype ♂, ANSP [examined]. Type locality: USA (New York).

Lathrolestes metalli CUSHMAN, 1933: 10. Holotype ♀, USNM [examined]. Type locality: Canada (Beamsville, Ontario).

Lathrolestes visscheri DE GANT, 1933: 5. Holotype ♀, USNM [examined]. Type locality: Canada (Ontario).

Distribution. Nearctic. Specimens studied from Canada (Ontario), USA (Alaska, California, Colorado, Georgia, Illinois, Kansas, Massachusetts, New York, North Carolina, Pennsylvania, Virginia, Washington).

***Lathrolestes unguularis* (THOMSON, 1883)**

Lathrolestes unguularis THOMSON, 1883: 918. Holotype ♂, MZLU [examined]. Type locality: Sweden (Pålsjö, Skåne).

Lathrolestes citrofrontalis SCHMIEDEKNECHT, 1912: type lost. Type locality: Germany

Distribution. Western Palaearctic. Specimens studied from Azerbaijan, Germany, Moldova, Sweden and Ukraine.

***Lathrolestes verticalis* (BRISCHKE, 1871)**

Perilissus verticalis BRISCHKE, 1871: 71. Type lost. Type locality: Poland.

Perilissus abdominalis BRISCHKE, 1878: 74. Type lost. Type locality: Poland.

Lathrolestes marginatus THOMSON, 1883: 917. Holotype ♂, MZLU [examined]. Type locality: Sweden (Lund, Skåne).

Distribution. Palaearctic. Specimens studied from Russia (Saint Petersburg) and Sweden.

***Lathrolestes xochiquetzalis* RESHCHIKOV, 2011 (V)**

Distribution. Neotropical. Specimens studied from Mexico.

***Lathrolestes zeugophorae* BARRON, 1994**

Lathrolestes zeugophorae BARRON, 1994: 29. Holotype ♀, CNC [examined]. Type locality: Canada (Banff, Alberta).

Distribution. Nearctic. Specimens studied from Canada (Alberta).

***Lathrolestes zoticus* RESHCHIKOV, 2011 (IV)**

Distribution. Western Palaearctic. Specimens studied from Turkey.

Table 1. Trophic interactions of the genus *Lathrolestes*.

<i>Lathrolestes</i> species	Host species	Host plant
<i>Lathrolestes bipunctatus</i> (BRIDGMAN, 1886)	Heterarthrinae, Fenusini: <i>Fenusa pusilla</i> (LEPELETIER, 1823) (Zirngiebl 1961) <i>Fenusa ulmi</i> (SUNDEVALL, 1847) (Hedwig, 1962)	<i>Betula pendula</i> (Lorenz & Kraus 1957) <i>Ulmus glabra</i> , <i>U. minor</i> (Liston 1993); <i>U. foliacea</i> (Scobiola-Palade 1974); <i>U. americana</i> , <i>U. elliptica</i> , <i>U. glabra</i> , <i>U. rubra</i> (Smith 1995)
<i>L. caudatus</i> (THOMSON, 1883)	Blennocampinae, Blennocampini: <i>Ardis brunniventris</i> (HARTIG, 1837) (Evenhuis 1973, Hinz 1996)	<i>Rosa rugosa</i> (Evenhuis 1973)
<i>L. citreus</i> (BRISCHKE, 1878)	Heterarthrinae, Fenusini: <i>Parna tenella</i> (KLUG, 1816) (Ozols 1961)	<i>Tilia cordata</i> (Kontuniemi 1960); <i>T. vulgaris</i> (Liston 1995)
<i>L. clypeatus</i> (ZETTERSTEDT, 1838)	Lepidoptera , Eriocraniidae: <i>Eriocrania salopiella</i> (STANTON, 1854), <i>E. sangii</i> (WOOD, 1891), <i>E. semipurpurella</i> (STEPHENS, 1835), <i>E. sparrmannella</i> (BOSC, 1791), <i>E. unimaculella</i> (ZETTERSTEDT, 1839) (Heath 1961)	<i>Betula</i> sp. (Kutenkova 1999)
<i>L. constrictus</i> (PROVANCHER, 1882)	Heterarthrinae, Fenusini: <i>Metallus rohweri</i> MACGILLIVRAY, 1909 (Barron 1994)	<i>Rubus</i> (Barron 1994)
<i>L. ensator</i> (BRAUNS, 1898)	Nematinae, Hoplocampini: <i>Hoplocampa testudinea</i> (KLUG, 1816) (Zapryanov 1985, Zijp & Blommers 1993, Babendreier 1996, Boeve 1996, Vincent <i>et al.</i> 2002, Zijp & Blommers 2002a, 2002b)	<i>Malus pumila</i> , <i>Malus sylvestris</i> (Zijp & Blommers 1993, Babendreier 1996, Boeve 1996, Vincent <i>et al.</i> 2002, Zijp & Blommers 2002a, 2002b)

<i>Lathrolestes</i> species	Host species	Host plant
<i>L. luteolator</i> (GRAVENHORST, 1829)	Heterarthrinae, Caliroini: <i>Caliroa annulipes</i> (KLUG, 1816) (Hinz 1961, Schönrogge 1991)	<i>Betula pendula</i> , <i>Fagus sylvatica</i> , <i>Quercus robur</i> , <i>Q. petraea</i> , <i>Q. cerris</i> , <i>Q. palustris</i> , <i>Q. rubra</i> , <i>Salix caprea</i> , <i>Tilia cordata</i> , <i>Vaccinium oxycoccus</i> (Schönrogge 1991); <i>Vaccinium vitis-idaea</i> (Verzhutskii 1981)
	<i>C. cerasi</i> (LINNEAUS, 1758) (Carl 1976)	<i>Cydonia oblonga</i> , <i>Mespilus germanica</i> , <i>Rubus</i> (Benson 1962); <i>Crataegus laevigata</i> (Chevin 1974); <i>Quercus robur</i> , <i>Q. petraea</i> , <i>Q. cerris</i> , <i>Q. palustris</i> , <i>Q. rubra</i> , <i>Rosa canina</i> , <i>Salix caprea</i> , (Schönrogge 1991); <i>Prunus avium</i> , <i>P. duclis</i> , <i>Pyrus</i> (Buczacki & Harris 1998)
	<i>C. cinxia</i> (KLUG, 1816) (Schönrogge 1991)	<i>Quercus robur</i> , <i>Q. petraea</i> , <i>Q. cerris</i> , <i>Q. palustris</i> , <i>Q. rubra</i> (Schönrogge 1991)
	Heterarthrinae, Heterarthrini: <i>Heterarthrus vagans</i> (FALLÉN, 1808) (Aubert 2000)	<i>Alnus</i> sp. (Benson 1952)
	Argidae, Sterictiphorinae: <i>Sterictiphora geminata</i> (GMELIN, 1790) (Aubert 2000)	<i>Rosa</i> sp. (Benson 1952)
<i>L. luteolus</i> (THOMSON, 1883)	Heterarthrinae, Fenusini: <i>Fenusia carpinifoliae</i> (LISTON, 1993) (Horstmann 2004)	<i>Ulmus carpinifolia</i> (Horstmann 2004)
<i>L. macropygus</i> (HOLMGREN, 1857)	Heterarthrinae, Fenusini: <i>Fenusia pusilla</i> (LEPELETIER, 1823) (Hedwig 1950)	<i>Betula pubescens</i> (Benson 1952)

<i>Lathrolestes</i> species	Host species	Host plant
	<i>Parna tenella</i> (KLUG, 1816) (Györfi 1947)	<i>Tilia cordata</i> , <i>T. platyphyllos</i> (Liston 1993)
	<i>Scolioneura betuleti</i> (KLUG, 1816) (Hedwig 1962)	<i>Betula pendula</i> (Hedwig 1962)
	Blennocampinae, Blennocampini: <i>Periclista albida</i> (KLUG, 1814) (Aubert 2000)	<i>Quercus petraea</i> , <i>Q. robur</i> (Lorenz & Kraus 1957)
<i>L. messae</i> BARRON, 1994	Heterarthrinae, Fenusini: <i>Messa populifoliella</i> (TOWNSEND, 1893) (Barron 1994)	<i>Populus</i> (Barron 1994)
<i>L. mnemonicae</i> (ROHWER, 1914)	Lepidoptera , Eriocraniidae: <i>Dyseriocrania auricyanea</i> (WALSINGHAM, 1882) (Rohwer 1914)	<i>Quercus</i> (Barron 1994)
	<i>D. griseocapitella</i> (WALSINGHAM, 1882) (Carlson 1979)	<i>Quercus</i> (Barron 1994)
<i>L. morator</i> AUBERT, 1984	Heterarthrinae, Fenusini: <i>Scolioneura betuleti</i> (KLUG, 1814) (Aubert 1984)	<i>Betula pendula</i> (Viramo 1969)
<i>L. nigricollis</i> (THOMSON, 1883)	Heterarthrinae, Fenusini: <i>Fenusa pusilla</i> (LEPELETIER, 1823) (Pschorn-Walcher & Altenhofer 1989)	<i>Betula populifolia</i> (Barron 1994)
<i>L. occultor</i> AUBERT, 1984	Heterarthrinae, Fenusini: <i>Messa nana</i> (KLUG, 1814) (Aubert 1984)	<i>Betula pendula</i> , <i>B. pubescens</i> (Kontuniemi 1960)
<i>L. periclistae</i> BARRON, 1994	Blennocampinae, Blennocampini: <i>Periclista albicollis</i> (NORTON, 1872) (Barron 1994)	<i>Quercus alba</i> , <i>Q. ilicifolia</i> , <i>Q. macrocarpa</i> , <i>Q. rubra</i> (Barron 1994)

<i>Lathrolestes</i> species	Host species	Host plant
<i>L. pictilis</i> (HOLMGREN, 1857)	Heterarthrinae, Fenusini: <i>Fenusa dohrnii</i> (TISCHBEIN, 1846) (Pschorn-Walcher & Altenhofer 1989); <i>F. pusilla</i> (LEPELETIER, 1823), <i>Profenusa</i> <i>pygmaea</i> (KLUG, 1814) (Aubert 2000)	<i>Alnus glutinosa</i> (Ozols 1959)
<i>L. platynus</i> (DAVIS, 1897)	Heterarthrinae, Fenusini: <i>Profenusa alumna</i> (MACGILLIVRAY, 1923) (Barron 1994)	<i>Quercus rubra</i> (Barron 1994)
<i>L. profenusae</i> BARRON, 1994	Heterarthrinae, Fenusini: <i>Profenusa sp.</i> (Barron 1994)	<i>Quercus rubra</i> (Barron 1994)
<i>L. soperi</i> RESHCHIKOV, 2010	Heterarthrinae, Fenusini: <i>Profenusa thomsoni</i> (KONOW, 1886) (Reshchikov <i>et al.</i> 2010)	<i>Betula pendula</i> , <i>B. papyrifera</i> (Reshchikov <i>et</i> <i>al.</i> 2010)
<i>L. thomsoni</i> RESHCHIKOV, 2010	Heterarthrinae, Fenusini: <i>Profenusa thomsoni</i> (KONOW, 1886) (Reshchikov <i>et al.</i> 2010)	<i>Betula pendula</i> , <i>B. papyrifera</i> (Reshchikov <i>et</i> <i>al.</i> 2010)
<i>L. tomostethi</i> (CUSHMAN, 1935)	Blennocampinae, Tomostethini: <i>Tomostethus multinctus</i> (ROHWER, 1909) (Barron 1994)	<i>Fraxinus americana</i> , <i>F. oregona</i> (Barron 1994)
<i>L. tripunctor</i> (THUNBERG, 1824)	Blennocampinae, Phymatocerini: <i>Rhadinoceraea micans</i> (KLUG, 1814) (Giraud 1872)	<i>Iris laevigatus</i> , <i>I. pseudacorus</i> , <i>I. spuria</i> , <i>Fraxinus excelsior</i> (Lorenz & Kraus 1957)
	Tomostethini: <i>Tomostethus nigrinus</i> (FABRICIUS, 1804) (Hinz 1961)	 <i>Fraxinus excelsior</i> (Lorenz & Kraus 1957)
<i>L. truncatus</i> (PROVANCHER, 1888)	Heterarthrinae, Fenusini: <i>Metalus rohweri</i> MACGILLIVRAY, 1909 (Barron 1994)	<i>Rubus</i> (Barron 1994)
	Blennocampinae, Blennocampini: <i>Periclista albicollis</i> (NORTON, 1872) (Barron 1994)	<i>Quercus rubra</i> (Barron 1994)

<i>Lathrolestes</i> species	Host species	Host plant
<i>L. unguularis</i> (THOMSON, 1883)	Heterarthrinae, Fenusini: <i>Fenusus pusilla</i> (LEPELETIER, 1823) (Pschorn-Walcher & Altenhofer 1989, Schönrogge & Altenhofer 1992)	<i>Betula pendula</i> , <i>Castanea sativa</i> (Lorenz & Kraus 1957)
	<i>Profenusus pygmaea</i> (KLUG, 1814) (Pschorn-Walcher & Altenhofer 1989, Schönrogge & Altenhofer 1992)	<i>Quercus robur</i> (Kontuniemi 1960)
<i>L. verticalis</i> (BRISCHKE, 1871)	Heterarthrinae, Fenusini: <i>Fenusus pusilla</i> (LEPELETIER, 1823) (Rudow 1919)	<i>Betula pendula</i> (Lorenz & Kraus 1957)
	<i>Metalus gei</i> (BRISCHKE, 1883) (Pschorn-Walcher & Altenhofer 1989)	<i>Geum urbanum</i> (Chevin 1980); <i>G. rivale</i> (Kontuniemi 1960)
	<i>M. pumilus</i> (KLUG, 1816) (Pschorn-Walcher & Altenhofer 1989)	<i>Rubus fruticosus</i> (Lorenz & Kraus 1957)
	<i>Scolioneura betuleti</i> (KLUG, 1816) (Aubert 2000)	<i>Betula pendula</i> (Viramo 1969)
	<i>Hoplocampa testudinea</i> (KLUG, 1816) (Jaworska 1992)	<i>Malus sylvestris</i> , <i>Pyrus communis</i> (Lorenz & Kraus 1957)
<i>L. zeugophorae</i> BARRON, 1994	Coleoptera , Megalopodidae: <i>Zeugophora sp.</i> (Barron 1994)	<i>Betula sp.</i> , <i>Populus tremula</i> (Bullock 1992, Cox 2007)

Table 2. Numbers of species of the genus *Lathrolestes* described by different authors.

Author and year of publication	No. of described species	Species valid at present
Thunberg 1824	2	1
Gravenhorst 1829	3	3
Zetterstedt 1838	1	1
Ratzeburg 1852	2	0
Holmgren 1857	6	4
Provancher 1882, 1889	2	2
Brischke 1878	5	2
van Vollenhoven 1878	1	0
Gribodo 1880	1	0
Thomson 1883	8	7
Bridgman 1886	2	1
Ashmead 1890, 1902	2	1
Davis 1897	9	2
Brauns 1898	1	1
Nordenström 1905	1	0
Schulz 1906	2	0
Roman 1909	1	1
Schmiedeknecht 1912	1	0
Smits van Burgst 1912	1	1
Rohwer 1915	3	1
Cushman 1933, 1935	4	3
Habermehl 1922, 1923	2	2
Kiss 1926	2	0
Seyrig 1928	1	0
Uchida 1932, 1940	2	2
DeGant 1933	1	0
Teunissen 1953	1	1
Benoit 1955	1	1
Hedwig 1958	1	0
Aubert 1984	2	2
Barron 1994	21	21
Gauld 1997	4	4
Total	95	64

SUMMARY IN ENGLISH

The total global number of species is evaluated to be roughly 8.7 million species whereas only about 1.9 million species have been described up to now. Insects probably constitute the largest share of unknown biota. Ichneumonidae, a family of hymenopteran parasitoids is one of the largest insect families of all, with the world fauna estimated to comprise between 60,000 and 100,000 species. Because of their lifestyle, ichneumonid wasps play an important role in terrestrial ecosystems, particularly in suppressing and regulating their host populations. They are also one of the most frequently used groups of parasitoids in biological control of insect pests.

The Ctenopelmatinae is a species-rich subfamily of Ichneumonidae that includes mostly endoparasitoids of sawfly larvae (Hymenoptera: Symphyta). The taxonomy of the subfamily is rather poorly known, and so is the taxonomy of the focal genus of this thesis – *Lathrolestes* FÖRSTER, 1869. Since the genus has attracted little attention out of North America in the past, the primary component of this thesis was to describe the biodiversity of the genus (I–XI). Apart from describing new species and mapping their distribution records, I also produced identification keys for different regions (I, II, V–IX). Another aim of this thesis was to revise previously described species and elucidate the taxonomy of the genus (I–XI). Moreover, evolutionary patterns in host use, morphological adaptations for using different host groups, and biogeographical patterns are outlined.

One of the main parts of any study in systematics is the examination of type collections. For this thesis, most of the type specimens of *Lathrolestes* species, as well as type specimens of species from some other genera of Ctenopelmatinae were examined. Besides examining the existing material in major world ichneumonid collections, additional material was collected in Norway, Finland, Russia, Ukraine and Mongolia. The revision of Nearctic species also involved insect rearings and revealing trophic interactions of some species.

As the main result of my thesis, I provide a taxonomic review of the world fauna of the genus *Lathrolestes* (I–XI). The taxonomic studies conducted increased the known fauna of *Lathrolestes* by 38%. The large proportion of previously undescribed species confirms the view that the share of insect species described is just the tip of the iceberg. Altogether, 40 species were described as new to science. The up-to-date list of *Lathrolestes* totals now 103 species in the World fauna. The very high number of new species leaves an assumption that many more species of this genus are still expected globally, especially from poorly studied tropical regions, but probably even from Europe. Besides the new species described, a number of nomenclatural changes are proposed (II, IV, VI).

Between-species variation in host use and respective differences in ovipositor structure displayed in my thesis may provide a basis for distinguishing distinct species groups within *Lathrolestes*, or, perhaps, in the future, even for

dividing *Lathrolestes* into different genera. In particular, different *Lathrolestes* species have a remarkably diverse host use for a single genus. As reviewed in the thesis, the hosts of the different species they attack range from free-living larvae to those concealed in the substrate. Correspondingly, morphological analyses allowed me to recognize a remarkable diversity of ovipositor types within the genus which is likely to reflect specialization for using different types of hosts on or within different substrates.

Current knowledge of the biogeography of the genus suggests that the most species-rich region is the north temperate zone. Accordingly, 38 species are recorded from the Nearctic region (including two introduced Palearctic species and one Holarctic species), 49 species from the Palaeartic region, two from the Afrotropical region (**X**), ten from the northern part of the Neotropical region (**VIII, IX, XI**), and seven from the northern part of the Oriental region (**I, III**). *Lathrolestes* species are absent from the Australasian and Oceanic regions, with the exception of *L. luteolator* that has been introduced to New Zealand. The present knowledge of latitudinal diversity trends of *Lathrolestes* is thus consistent with the classical understanding of general diversity patterns in Ichneumonidae, according to which their diversity tends to decrease from temperate latitudes towards the tropics. Also, the known distribution data suggest that most *Lathrolestes* species have rather limited distribution ranges. In fact, with the exception of introduced species, there is just one species present in both the Palearctic and the Nearctic regions. Moreover, even truly trans-Palaeartic species are rare among *Lathrolestes*: most species from the Palaeartic region have either European or East Palaeartic distribution ranges.

SUMMARY IN ESTONIAN

Perekonna *Lathrolestes* (Hymenoptera, Ichneumonidae) fauna maailmas

Maailmas on hinnanguliselt 8,7 miljonit liiki, kellest tänaseks on kirjeldatud vaid 1,9 miljonit. Putukad moodustavad arvatavasti suurima osa seni kirjeldamata elustikust. Üks liigirikkamaid putukasugukondi on kiletiivaliste (*Hymenoptera*) hulka kuuluvad parasiitse eluviisiga käguvamplased (*Ichneumonidae*). Oma eluviisi tõttu on käguvamplastel maismaaökosüsteemides oluline roll, eeskätt peremeesliikide (enamasti putukad) populatsioonide dünaamikat mõjutades. Käguvamplased on ka üks sagedamini kasutatavaid organisme kahjurputukate biotõrjes. Erinevatel hinnangutel võiks maailma olla 60000 kuni 100000 käguvamplase liiki, neist seni on kirjeldatud aga vaid veidi üle 24000.

Peamiselt lehevaablaste (*Hymenoptera*, *Symphyta*) vastsetel parasiteeriv alamsugukond *Ctenopelmatinae* on käguvamplaste hulgas üks liigirikkamaid. Alamsugukond tervikuna, nagu ka käesoleva doktoritöö keskmes olev perekond *Lathrolestes* FÖRSTER, 1869, on suhteliselt kesiselt uuritud. Doktoritöö esmaseks eesmärgiks oligi seetõttu perekonna liigilise koosseisu kirjeldamine (I–XI). Lisaks uute liikide kirjeldamisele ning leviku kaardistamisele, koostati töö käigus erinevatele piirkondadele liikide määramistabelid (I, II, V–IX). Samuti viidi läbi varem kirjeldatud liikide revisjon ning korrastati perekonna taksonoomiat (I–XI). Tähelepanu pöörati ka peremehekasutuse evolutsioonilistele mustritele, peremehekasutusega seotud morfoloogilistele kohastumustele ning perekonna biogeograafilistele mustritele.

Iga süstemaatika-alase töö üks keskseid osi on tüüpmaterjali uurimine. Käesoleva doktoritöö käigus uuriti enamiku perekonna *Lathrolestes* liikide tüüp-eksemplare, samuti mitmetesse lähedastesse perekondadesse kuuluvate liikide tüüp-eksemplare. Doktoritöö käigus töötati läbi olemasolev materjal enamikus suuremates käguvamplaste kollektsioonides üle maailma, lisamaterjali koguti mahukatel välitöödel Norras, Soomes, Venemaal, Ukrainas ja Mongoolias. Nearktiliste liikide revisjoni käigus selgitati ka mitmete liikide troofilisi interaktsioone (II).

Doktoritöö peamiseks tulemuseks on taksonoomiline ülevaade perekonna *Lathrolestes* liigilisest koosseisust maailmas (I–XI). Uute liikide kirjeldamise tulemusena suurenes perekonna teadaolevate liikide arv 38% võrra. Varem kirjeldamata liikide suur osakaal on taaskord kinnituseks arusaamale, et seni kirjeldatud liigid moodustavad putukate kogu liigirikkusest vaid “jäämäe nähtava osa”. Kokku kirjeldati doktoritöö käigus 40 teadusele uut liiki, mis viis maailmas teadaolevate *Lathrolestes*’e liikide koguarvu 103-ni. Suurt uute liikide osakaalu arvestades on usutav, et perekond täieneb uute kirjeldatud liikidega tulevikus veelgi, eriti suhteliselt kasinamalt uuritud troopiliste piirkondade arvel. Lisaks uute liikide kirjeldamisele pakuti töös välja mitmeid nomenklatuurseid muutusi (II, IV, VI).

Doktoritöö näitas perekonna piires suuri liikidevahelisi erinevusi peremehekasutuses. Nimelt parasiteerivad perekonna erinevad liigid väga erineva ökoloogiaga peremeesorganismidel, mis kajastub muneti ehituse morfoloogilistes kohastumustes. Morfoloogiliste tunnuste alusel eristati töös rida muneti tüüpe, mis on abiks liikide määramisel. Erinevused peremehekasutuses ning muneti morfoloogias võivad tulevastes uurimustes saada aluseks liigisiseste rühmade eristamisele ja võimalik, et ka perekonna *Lathrolestes* jagamisele erinevateks perekondadeks.

Praegused teadmised perekonna *Lathrolestes* biogeograafiast lubavad oletada, et perekond on kõige liigirikkamalt esindatud parasvöötmes. Saja kolmest liigist 38 on nearktilised (sh kaks Palearktisest introdutseeritud liiki ning üks holarktiline liik) ning 49 palearktilised. Afrotroopilisest regioonist on teada vaid 2 liiki (**X**), Neotroopilise regiooni põhjaosast 10 (**VIII, IX, XI**) ning Orientaalsest regioonist 7 (**I, III**). Austraalias ning Okeaanias perekonna esindajad puuduvad, erandiks on Uus-Meremaale introdutseeritud *L. luteolator*. Seega on perekonna liigilise mitmekesisuse laiuskraadiline jaotumus kooskõlas klassikalise arusaamaga käguvamplaste biogeograafilistest mustritest, mille kohaselt nende liigiline mitmekesisus on kõrgeim parasvöötmes ning kahaneb troopika suunas. *Lathrolestes*'e liikide levikuandmed lubavad oletada, et enamus liike on suhteliselt piiratud levilaga: jättes kõrvale introdutseeritud liigid, on vaid ühe liigi levila holarktiline. Niisamuti ei saa enamiku palearktiliste liikide puhul rääkida transpalearktilisest levikust: vaid üksikute liikide levila ulatub Euroopast Vaikse ookeanini.

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