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ERKI ÕUNAP

Systematic studies on the subfamily Sterrhinae (Lepidoptera: Geometridae)

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LIST OF ORIGINAL PUBLICATIONS

This dissertation is a summary of the listed articles, which are referred to by the respective Roman numerals:

I Õunap, E., Viidalepp, J. & Saarma, U. 2005. Phylogenetic evaluation of the taxonomic status of *Timandra griseata* and *T. comae* (Lepidoptera: Geometridae: Sterrhinae). *European Journal of Entomology* **102:** 607–615.

II Õunap, E., Viidalepp, J. & Saarma, U. 2008. Systematic position of Lythriini revised: transferred from Larentiinae to Sterrhinae (Lepidoptera, Geometridae). *Zoologica Scripta* **37:** 405–413.

III Õunap, E., Mironov, V. & Viidalepp, J. 2009. Molecular phylogeny of the genus *Lythria* and description of the male genitalia of *L. venustata* (Lepidoptera: Geometridae: Sterrhinae) *European Journal of Entomology* **106:** 643–650.

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My personal contribution to the articles referred to in this thesis is as follows:

Ref. **I** – collection and identification of material, laboratory procedures, responsible for writing the article.

Ref. **II** – collection and identification of material, laboratory procedures, phylogenetic analysis, responsible for writing the article.

Ref. **III** – collection and identification of material, laboratory procedures, microphotographing, phylogenetic analysis, responsible for writing the article.

1. INTRODUCTION

The family Geometridae has been recognized as a natural unit long before the origin of taxonomy as a science. The 'looping' or 'earth-measuring' movement of geometrid larvae, which results from the incomplete set of the abdominal prolegs (Minet & Scoble, 1999), had already been mentioned by Linnaeus (1758). Since that time, systematics as a discipline has undergone immense development and research on Geometridae has not been an exception: more than 21 000 species are known today (Scoble, 1999; Hausmann, 2001), making Geometridae the second largest family of Lepidoptera after Noctuidae (Heppner, 1998; Kitching & Rawlins, 1999). During the two and a half centuries that have passed since the publication of the tenth edition of Linnaeus's Systema Naturae (1758), many naturalists and professional researchers have tried to create a 'natural' system of Geometridae that reflects the true evolutionary relationships between the taxa. Therefore it is not surprising that discussion about 'natural' and 'unnatural' groupings of taxa are frequent in earlier literature (e. g. Meyrick, 1892; Prout, 1912–16). The sources of information used to improve the system, however, have been different during the history of geometridology. In the 18th and 19th century, researchers mostly relied on wing pattern and shape, which, however, may exhibit significant plasticity, resulting in similar external appearance of taxa that do not share common evolutionary history. Therefore, older literature often contains mysterious misplacements of taxa that seem incomprehensible in the light of modern knowledge (for just one example, see the composition of the genus *Aspilates* Treitschke, 1827 in Duponchel, 1830).

In the late 19th and early 20th century, studies on wing venation and genitalia became common in lepidopterology which resulted also in groundbreaking studies in geometrids by Meyrick (1982), Petersen (1904) and Pierce (1914). The use of this completely new evidence led to a more stable system of Geometridae, as most of the subfamilies recognized in the early 20th century are still considered valid having similar species composition (for comparison, see Prout, 1912–16; Müller, 1996; Holloway, 1997).

The traditional, morphologically established system of Geometridae currently comprises nine valid subfamilies: Ennominae, Larentiinae, Sterrhinae, Geometrinae, Desmobathrinae, Oenochrominae, Archiearinae, Orthostixinae and Alsophilinae (Holloway, 1997; Hausmann 2001). Quite surprisingly, though respective analytical methods have been available for more than half a century (Moritz & Hillis, 1996), no studies have been published that address the phylogenetic relationships between the subfamilies of Geometridae on the basis of morpho-cladistic analysis. Even the most recent comprehensive handbooks (e. g. Holloway, 1997; Minet & Scoble, 1999; Hausmann, 2001) still consider the monophyly of several subfamilies questionable and phylogenetic relationships between them tentative.

Recent advances in molecular systematics (e. g. Abraham *et al.*, 2001; Young 2006; Yamamoto & Sota 2007; Wahlberg *et al.*, 2010), have repeatedly

shown that at least the four largest subfamilies, Larentiinae, Ennominae, Sterrhinae and Geometridae are monophyletic entities. On the other hand, all these works indicate that the traditionally recognised small Palaearctic subfamily Alsophilinae is in fact an apomorphic subdivision of the subfamily Ennominae. Moreover, Young (2006) has shown that the Tasmanian Archiearinae do not group together with the Palaearctic archiearins, but cluster within Ennominae. However, the phylogenetic relationships between subfamilies also conflict between the aforementioned molecular phylogenetic studies (for details, see below).

At a narrower, within-subfamily scale, the global situation is far more complicated. On the one hand, numerous excellent morphology-based revisions are available that address systematic problems from global point of view in selected tribes (e. g. Choi, 1997; Scoble & Krüger, 2002; Pitkin *et al.*, 2007) or deal with some taxonomic groups thoroughly within one biogeographic region (e. g. Pitkin, 1996, 2002; Choi, 2002, 2004). On the other hand, most of the tribes and genera are still awaiting critical taxonomic examination. The revision by Sihvonen & Kaila (2004) is the only study to date that has addressed taxonomic problems at the subfamily level by sampling material from all biogeographic regions. Moreover, there still are no molecular phylogenetic studies that have comprised all or even reasonable proportion of traditionally recognized tribes or genera from one or several large subfamilies.

On a species-group level, the situation differs remarkably between the geographic regions. Species composition is reasonably well known in some parts of the world, especially in the western Palaearctic: new species are only rarely described from that region (but see Hausmann, 2004; Huemer & Hausmann, 2009). On the other hand, regions with the most diverse fauna still seem to be quite poorly studied and new thoroughly conducted revisions regularly lead to the discovery of a number of new taxa (e. g. Holloway, 1993, 1996, 1997; Hausmann, 2003; Pitkin, 2005). Intrageneric phylogenetic relationships in Geometridae are also largely unknown, though at least one relatively comprehensive treatment (Canfield *et al.*, 2008) is available. As a conclusion, it is evident that there still are numerous problems awaiting examination in systematics of Geometridae, ranging from species-group to family-group level.

In the present thesis, I will concentrate on several systematic problems in the subfamily Sterrhinae. Article **I** was conducted to solve ambiguous status of the two European *Timandra* Duponchel, 1829 species, while the articles **II** and **III** focus on the systematic placement and intrageneric phylogeny of the genus *Lythria* Hübner, 1823, respectively. In addition to these already published studies, this thesis also reports original results contributing to the knowledge of phylogenetic relationships in the subfamily Sterrhinae as a whole. A detailed overview of the questions addressed is given in the next chapter.

2. OVERVIEW OF THE PROBLEMS

2.1. The Timandra *griseata*/ *T. comae* question

The European 'blood-vein' loopers have traditionally been regarded as one species. Nevertheless, there has been a lot of confusion regarding the generic placement and correct spelling of the name of this species. Several names have been used by different authors, but the following three combinations have been used most often: *Calothysanis amata* (Linnaeus, 1758) (e. g. Meyrick, 1892; Prout, 1934–39), *Calothysanis amataria* (Linnaeus, 1761) (e. g. Nordström, 1943; Kaisila, 1954) and *Timandra amata* (Linnaeus, 1758) (e. g. Staudinger & Rebel, 1901; Prout, 1912–16). Due to extensive variation in the appearance of the 'blood-veins', a number of intraspecific taxa have been described: Prout (1912–16) listed altogether eight varieties within what he regarded as *Timandra amata*. A few decades later, he (Prout, 1934–39) listed three further varieties of *Calothysanis amata*, noting that *griseata* Petersen, 1902 and *comae* Schmidt, 1931 may rather be designated the rank of a subspecies of *amata* and a separate species, respectively. In this work (Prout, 1934–39) he also treated the eastern Palaearctic *comptaria* Walker, earlier (Prout, 1912–16) thought to be a form of *amata*, as a separate species: *Calothysanis comptaria* (Walker, 1861).

Subsequently, Nordström (1943) tried to resolve the confusion stemming from the inconsistent usage of names *amata* Linnaeus, 1758 and *amataria* Linnaeus, 1761. He revealed that *Phalaena amata* Linnaeus, 1758 was in fact a junior synonym of *Phalaena punctaria* Linnaeus, 1758, and that the name *amataria* was a subsequent emendation of *amata*. However, the moths Linnaeus had at hand when describing *amataria* were not the same species he earlier had believed to be *amata*. The name *amataria* was nevertheless to be considered as a junior synonym of *amata*. Therefore, the European 'blood-vein' appeared to be without a valid name. Nordström (1943) also found that all older species-group names previously used for the same species were unavailable due to various reasons and that the oldest available name for this taxon was *griseata* Petersen, 1902, originally described as an Estonian subspecies of *amata*. Though Nordström (1943) was well aware that the Code for Zoological Nomenclature would recommend abandoning *amataria*, he still preferred to keep this old name and used a combination *Calothysanis amataria* (L.) 1761 (*griseata* Peters. 1902). He also found that there were some morphological differences between the individuals of *C. amataria* from northern and southern Europe and described the southern specimens as *C. amataria brykaria* Nordström, 1943, regarding the northern taxon as the nominate subspecies.

A few decades later, Fletcher (1979) pointed out that the Nordström's way of retaining the name *amataria* for the European 'blood-vein' was incorrect. He nevertheless agreed with Nordström (1943) that the oldest available name for this species was *griseata*. In the same monograph, Fletcher (1979) noted that the type-species of the genus *Calothysanis* Hübner, 1823 was *Geometra imitaria* Hübner, 1799, which in fact belongs to the genus *Scopula* Schrank,

1802. The name *Calothysanis* is therefore a junior synonym of *Scopula* and thus unavailable for the genus comprising the 'blood-veins'. The oldest available name for this genus appears to be *Timandra*, which has been most frequently used in recent publications (e. g. Inoue *et al.*, 1982; Müller, 1996; De Prins, 1998; Redondo & Gastón, 1999; Hausmann, 2004), though few authors such as Koch (1984) and Viidalepp & Remm (1996) have still used *Calothysanis*.

Recently, Kaila & Albrecht (1994) showed that morphological differences between the northern and southern subspecies of *Timandra griseata* Petersen, 1902 are sufficient to regard them as separate species. As they found that the taxa *comae* Schmidt, 1931 and *brykaria* Nordström, 1943 are conspecific, they used the older name *comae* for the southern species. In addition, they also emended the name from *comae* to *comai* (for details, see Kaila & Albrecht, 1994 and Kullberg *et al.*, 2002), resulting in the combination *Timandra comai* Schmidt, 1931. According to the study by Kaila & Albrecht (1994), the differences between *T. griseata* and *T. comai* are the following: ground colour of the wings is whitish in *T. griseata*, yellowish in *T. comai*, grey suffusion is dense, almost covering the ground colour in *T. griseata* and less conspicuous in *T. comai*. The wingspan of *T. griseata* appeared to be on average larger than that of *T. comai*, the ciliae of wings are hardly reddish in *T. griseata* but bright pink in *T. comai* (Kaila & Albrecht, 1994; Kaila *et al.*, 1999). Forewing discal spot is weak in *T. griseata* but usually distinct in *T. comai*. The male genitalia of *T. griseata* and *T. comai* appeared to be indistinguishable (Kaila & Albrecht, 1994) but the position of the appendix bursae in females was found to be different in *T. griseata* and *T. comai*. In addition to the morphological differences, both the distribution and phenology of *T. griseata* and *T. comai* were also found to be different (for details, see Kaila & Albrecht, 1994, 1995).

As *T. griseata* and *T. comai* appeared to be extremely closely related and literally indistinguishable in some cases, the lepidopterist community in Europe quite sceptically welcomed the treatment by Kaila & Albrecht (1994, 1995); for details, see Hausmann (1997). A few years later, Sihvonen (2001) examined this question by everting vesicae of males – a technique that had not been used by Kaila & Albrecht (1994). He found that there are undoubtedly some loosely species-specific differences between the shape and angle of the lateral diverticulum of the everted vesicae of *T. griseata* and *T. comai* (Sihvonen, 2001). Moreover, these differences appeared to be anatomically compatible with the differences in female genitalia reported by Kaila & Albrecht (1994). Therefore, Sihvonen (2001) found that it is justified to treat *T. griseata* and *T. comai* as separate species.

In his major monograph covering all European sterrhines, Hausmann (2004) treated *T. griseata* and *T. comae* [he found the emendation from *comae* to *comai* by Kaila & Albrecht (1994) to be unjustified] as separate species. However, he also noted that the validity of species rank of *T. comae* was still controversial though some tentative evidence from mtDNA-based analyses (Miller *et al*., 2001, Trusch *et al*., 2002) seemed to support the species rank of *T. griseata* and

T. comae (Hausmann, 2004). Therefore, some further investigation was necessary to solve the '*Timandra griseata/ T. comae* question'.

As the morphological treatments by both Kaila & Albrecht (1994) and Sihvonen (2001) had been conducted thoroughly, no significant progress was expected from further morphological examination. Instead, new evidence either favouring or rejecting the concept of two closely related species was expected from a molecular phylogenetic study, as mtDNA sequences had repeatedly proven useful in solving systematic questions concerning closely related taxa (e. g. Sperling *et al.*, 1999; Kruse & Sperling, 2001; Wiens & Penkrot, 2002). Article **I** in the present dissertation is an original phylogeny-based attempt to clarify the status of *T. griseata* and *T. comae*, analysing genetic variation at two mitochondrial protein-coding genes.

2.2. The systematic position of Lythriini

Although the genus *Lythria* has been well known to lepidopterists, its placement in Geometridae has puzzled taxonomists for about a century. This small group comprises few diurnal species that are similar to the extent that no attempts have been made to split this genus. Moreover, as the external appearance of *Lythria* species is so strikingly different from all other geometrid taxa, this genus has consistently been treated as an entity of its own with no close relatives (e. g. Staudinger & Rebel, 1901; Prout, 1912–16, 1934–39; Müller, 1996; Viidalepp, 1996). This point of view has even more been emphasized since Herbulot (1962), who raised a monobasic tribe Lythriini for the genus *Lythria*. The only remarkable exception of the treatment described above is the approach by Leraut (1997) who united Lythriini and Cataclysmiini into one tribe using the name Lythriini.

The situation becomes more complicated when the exact placement of the genus *Lythria* in the family Geometridae is considered. Meyrick (1892), whose work laid the basis of modern subdivision of Geometridae into subfamilies, placed *Lythria* into family Hydriomenidae, which is now considered to be equivalent to Larentiinae. All subsequent major treatments of Geometridae have followed this treatment (e. g. Staudinger & Rebel, 1901; Spuler, 1903–10; Prout, 1912–16; Herbulot, 1962; Müller, 1996; Viidalepp, 1996; Scoble, 1999), with the exception of Pierce (1914), who put *Lythria* into his Cosymbiinae, which is currently considered to be equivalent to the 'Timandrini lineage' from Sterrhinae (Sihvonen & Kaila, 2004). However, several authors have only recently pointed to morphological characters that may link *Lythria* with some sterrhine taxa: both Sihvonen & Kaila (2004) and Hausmann (2004) have noted that close affinities can be found between Lythriini and Rhodometrini from Sterrhinae. Thus, an intriguing problem has emerged as to whether Lythriini cluster together with Larentiinae or Sterrhinae.

Recent molecular phylogenetic approaches have shown subfamilies Sterrhinae and Larentiinae as clearly distinct monophyletic entities (Abraham *et al.*,

2001; Young, 2006; Yamamoto & Sota, 2007), though their exact placement within the Geometridae has been resolved differently. Specifically, Abraham *et al.* (2001) and Young (2006) proposed Larentiinae as a sister group to the rest of Geometridae, while Yamamoto & Sota (2007) found that Larentiinae and Sterrhinae are closely related groups in a separate monophyletic lineage which is sister to other Geometrid subfamilies. Nevertheless, the taxon sampling on a tribe level has been far from extensive and majority of the sterrhine and larentiine tribes have not been included into these earlier studies.

Article **II** in the present dissertation is an original study addressed to solve the ambiguities related to the systematic position of Lythriini. For that purpose, two mitochondrial and three nuclear gene fragments were sequenced from representatives of all Palaearctic sterrhine tribes, five larentiine tribes and three Lythriini species. Moreover, several morphological characters earlier thought to be synapomorphic for Sterrhinae and Larentiinae were critically assessed and their systematic utility discussed.

2.3. The phylogeny of the genus *Lythria* and the elaborated genital morphology of *L. venustata*

As discussed above, the genus *Lythria* is morphologically a distinct group which has been recognised as such since its description in 1823. Until early 20th century, systematists disputed whether there are one or two widespread species in Europe: e. g. Hofmann (1894), Staudinger & Rebel (1901) and Spuler (1903–10) interpreted the whole complex as a single species, *L. purpuraria* (Linnaeus, 1758), while others, e. g. Borkhausen (1794), Laspeyrés (1803) and Duponchel (1830), treated this group as two closely related species currently known as *L. purpuraria* and *L. cruentaria* (Hufnagel, 1767). This question was finally solved by Prout (1912–16) and Zerny (1916) who found significant differences between the male genitalia of *L. purpuraria* and *L. cruentaria*.

The second intrageneric problem in genus *Lythria* was the status of *L. sanguinaria* (Duponchel, 1842). As this taxon externally clearly differs from both *L. purpuraria* and *L. cruentaria*, it was treated as separate species in earlier works (e. g. Hofmann, 1894; Staudinger & Rebel, 1901; Spuler, 1903–10). However, both Prout (1912–16) and Zerny (1916) noted that the male genitalia of *L. sanguinaria* were extremely similar to those of *L. cruentaria* and therefore treated the former as a subspecies of the latter. This point of view was subsequently followed by several authors, including Herbulot (1962), Müller (1996) Leraut (1997) and Scoble (1999). Only recently, Viidalepp (in press) showed that both male and female genitalia of *L. sanguinaria* and *L. cruentaria* exhibit consistent, though small differences and therefore raised the former to the species rank again. This point of view was implicitly supported by our earlier study (**II**), as the genetic differences between *L. sanguinaria* and *L. cruentaria* were found to be almost as substantial as those between *L. cruentaria* and *L. purpuraria*. However, the aforementioned study (**II**) was still controversial

with respect to the exact phylogenetic position of *L. sanguinaria*: instead of the grouping (*L. purpuraria* (*L. sanguinaria*, *L. cruentaria*)) which was expected on the basis of both external and genital morphology, an unexpected topology (*L. cruentaria* (*L. sanguinaria*, *L. purpuraria*)) was recovered.

The third intrageneric question in *Lythria* is the phylogenetic placement of *L. plumularia* (Freyer, 1831) and *L. venustata* Staudinger, 1882. Both Staudinger (1882) and Prout (1912–16) regarded these species as possible sister taxa due to their external similarity but the genital morphology of these species remained unknown until very recently (Vasilenko, 2009). Moreover, as only the holotype of *L. venustata* was known until 2006, it has been impossible to extract DNA from this remarkably rare species, and constructing the complete molecular phylogeny of the genus *Lythria* was therefore not feasible. Article **III** in the present dissertation is an attempt to construct the complete molecular phylogeny of the genus *Lythria*, covering all known species and using analysis of one mitochondrial and two nuclear genes. In addition to the previous, we were able to illustrate the *L. venustata* adults for the first time and elaborate the male genital morphology of this species.

2.4. The phylogeny of the subfamily Sterrhinae

The subfamily Sterrhinae, which comprises more than 2800 described species worldwide, is one of the four main subfamilies of Geometridae (Scoble, 1999; Hausmann, 2004). According to the modern view, Sterrhinae has been divided into eight tribes and more than a hundred genera (Holloway, 1997; Heppner, 2003; Sihvonen & Kaila, 2004; **II**). The phylogenetic relationships between the subtaxa of Sterrhinae, however, are still largely unknown and, as repeatedly emphasized, require further phylogenetic treatment (e. g. Hausmann, 2004; Sihvonen & Kaila, 2004). In the following sections I will give a short overview of the few most important studies that have had major influence on systematics and phylogeny of Sterrhinae. In section 4.4 I will discuss the validity of these earlier opinions in the light of the most recent data.

The foundation of the currently recognised system of Geometridae was laid with the work of Meyrick (1892). Based on wing venation, he divided the European fauna of geometrid moths into six families. One of these was Sterrhidae, which is currently recognised as equivalent to Sterrhinae. Though Meyrick (1892) briefly discussed the possible relationships between the genera in his Sterrhidae [e.g. suggesting close relationships between *Leucophthalmia* Hübner, 1823 (=*Cyclophora* Hübner, 1822) and *Calothysanis* (=*Timandra*), as well as between *Leptomeris* Hübner, 1825 (=*Scopula*), *Cinglis* Guenée, 1858 and *Problepsis* Lederer, 1853], his presumptions remained rather tentative.

Two decades later, Pierce (1914) treated the present-day Sterrhinae on the basis of genital morphology as three different groups: Ptychopodinae (which is referable as Sterrhini), Acidaliinae (equivalent to Scopulini) and Cosymbiinae (which included genera from Rhodometrini, Timandrini, Cosymbiini, Lythriini

and *Parascotia* Hübner, 1825; the latter has subsequently been moved to Noctuidae). Pierce (1914) considered the presence or absence of gnathos as the key element in subdividing the family Geometridae into two groups, Gnathoi and Agnathoi, and split Sterrhinae between these groups: Ptychopodinae was placed into Gnathoi, but Acidaliinae and Cosymbiinae into Agnathoi. Thus, it is obvious that Pierce (1914) did not regard Sterrhinae as a monophyletic entity.

Prout (1912–16) united the Sterrhinae again, using the name Acidaliinae. He divided this subfamily into three groups: *Cyllopoda*-group (which is exclusively Neotropic and therefore was not treated in detail in this monograph), *Acidalia*-group [comprising *Acidalia* Bruand, 1846 (=*Scopula*) and several other genera, most notably it included also *Anisephyra* Warren, 1896, *Ptochophyle* Warren, 1896 (=*Chrysocraspeda* Swinhoe, 1893) and *Timandra*] and *Cosymbia*-group [which comprised only *Cosymbia* Hübner, 1823 (=*Cyclophora*) and *Cinglis*]. In addition to splitting Palaearctic fauna between *Acidalia*- and *Cosymbia*-groups, he also briefly discussed the possible phylogenetic relationships between the genera, relying mostly on the number of areoles in the forewings and on the number of spurs on hindtibiae of the moths. However, in contrast to Pierce (1914) and according to Meyrick (1892), Prout (1912–16) treated *Rhodometra* Meyrick, 1892 as a member of Larentiinae.

In further treatments of African (Prout, 1929–35), Neotropical (Prout, 1935–38) and Indoaustralian (Prout, 1920–41) geometrids, Prout mentioned few further subtaxa of Sterrhinae: the *Rhodostrophia*-group comprising *Rhodostrophia* Hübner, 1823 as the central taxon and a number of smaller genera he believed to be closely associated with it (Prout, 1920–41); the '*Calothysanis* (=*Timandra*)-stem' with few genera associated with *Calothysanis* (Prout, 1920–41); and the *Asellodes*-group comprising only the Neotropic *Proutoscia* Schaus, 1912 and *Asellodes* Guenée, 1858 (=*Pseudasellodes* Warren, 1904) (Prout, 1935–38). In all these monographs, Prout gave detailed morphological descriptions of the genera and briefly discussed their possible phylogenetic relationships. As an important reconsideration, Prout (1929–35) moved *Rhodometra* back to Sterrhinae. In conflict with the modern understanding (Holloway, 1996, 1997; Sihvonen & Kaila, 2004), Prout (1929–35) treated the brightly coloured diurnal *Aletis* Hübner, 1820 and *Cartaletis* Warren, 1894 as oenochromine taxa, though he was aware of similarities in genitalia of these genera and Sterrhinae.

In his supplement to the geometrid fauna of the Palaearctic region, Prout (1934–39) mentioned that Sterrhinae were much less homogenous and harder to delimit than had earlier been thought. On the one hand, he found that the boundaries between the tribes were clear but on the other he noted that there are several larentiine taxa (especially in the *Asthena*-group, which is referable as Asthenini – see Xue & Scoble, 2002) that share some characters with sterrhines and could therefore even be considered as a separate subfamily. The latter point of view, however, has not been followed by subsequent authors. Prout (1934–39) also noted that though there was no new system of Sterrhinae, the results of an undergoing study by Sterneck (1941) had to be taken into account. Compared to his first treatment of the Palaearctic fauna (Prout, 1912–16), however,

he did introduce only very few changes: *Cosymbia* was placed close to *Calothysanis*, *Pylargosceles* Prout, 1930 was moved close to *Rhodostrophia* and *Cinglis* was transferred from *Cosymbia*-group to *Scopula*-group. In conclusion, Prout (1934–39) proposed five tribes: Rhodostrophiicae (=Rhodostrophiini), Cosymbiicae (=Cosymbiini), Cyllopodicae (=Cyllopodini), Scopulicae (=Scopulini) and Sterrhicae (=Sterrhini) and also mentioned that in addition to these there are some peculiar forms or intermediate links such as the enigmatic *Asellodes* (=*Pseudasellodes*) and *Rhodometra* or sterrhine-like asthenins. This classification was in slight conflict with that of Sterneck (1941), who did separate Calothysanicae form Cosymbicae, but Prout (1934–39) found this division poorly justified.

Sterneck (1941) laid a steady basis on the current tribal classification of Sterrhinae. He divided the subfamily into three main lineages relying mostly on characters of the male genitalia found in Palaearctic taxa. The most diverse of those comprised Sterrhicae (=Sterrhini), Cosymbicae (=Cosymbiini) and Calothysanicae (=Timandrini), while Scopulicae (=Scopulini) and Rhodostrophicae (=Rhodostrophiini) were kept separately as two other main lineages. However, the exact phylogenetic relationships between the tribes were left unresolved. Similar treatment (i. e. keeping Cosymbiini and Timandrini as separate tribes), was used a few years later by Forbes (1948) in his treatment of North American Geometridae.

Herbulot (1962) tried to solve the problems with closely related *Rhodometra* and *Casilda* Agenjo, 1952, that did not fit easily with either Sterrhinae nor Larentiinae, by placing them into a separate subfamily Rhodometrinae. Though this treatment was initially followed by Viidalepp (1976), it was later abandoned (Müller, 1996; Viidalepp, 1996; Holloway, 1997). Herbulot's (1962) system of Sterrhinae, however, was identical to that of Sterneck (1941), as he also regarded Cyclophorini (=Cosymbiini) and Calothysanini (=Timandrini) as separate tribes and the order of tribes (Sterrhini, Cyclophorini, Calothysanini, Scopulini, Rhodostrophiini).

In contrast to earlier authors, Hausmann (1993) treated Cyclophorini (=Cosymbiini), Calothysanini (=Timandrini) and Rhodometrini as closely related groups, not as placed to different ends of the system of Sterrhinae. He found that Calothysanini should be placed between Cyclophorini and Rhodometrini, as had already been suggested by Viidalepp (1976). Hausmann (1993) also noted that Rhodostrophiini, which share few anatomical similarities with Cyclophorini, Calothysanini and Rhodometrini, could be placed as preceding those in the system of Sterrhinae.

Nakamura (1994), who studied the pupal morphology of Japanese sterrhines, however, still treated *Timandra* and *Cyclophora* as members of the same tribe, Cosymbiini, as had earlier been done [e. g. by Prout (1934–39)]. As he described Cosymbiini as the only tribe that 'strikingly differ from the others in various characteristics', Nakamura (1994) intelligibly treated this tribe as a sister to the rest of Japanese Sterrhinae (i. e. Sterrhini, Scopulini and Rhodostrophiini). Considering the phylogenetic relationships between these three

tribes, Nakamura (1994) found that Sterrhini was a sister to the Scopulini+Rhodostrophiini clade. Another recent study on the pupal morphology of Sterrhinae (Patočka & Turčáni, 1994) did not include the phylogenetic component within it; their key to the identification of genera together with the accompanying figures, however, indicates substantial morphological similarities between the pupae of *Timandra*, *Rhodometra* and, most interestingly, *Lythria*. These findings are consistent with the rearrangements of tribes earlier suggested by Hausmann (1993) and even support the classification of Pierce (1914, see above).

Holloway (1997) put the results of his revision of the Bornean geometrids into a broader systematic context. He specified the diagnoses of the genera and tribes found on Borneo and introduced several genus-group rearrangements to Sterrhinae (e. g. regarding *Anisodes* Guenée, 1858 as a synonym of *Cyclophora*, but keeping majority of Bornean species earlier treated as belonging to *Anisodes* in separate genera *Perixera* Meyrick, 1886 and *Mesotrophe* Hampson, 1893). In addition to the genus and species level revision, Holloway (1997) also gave the tentative phylogeny of Geometridae, treating Sterrhinae and Larentiinae as sister groups. The subfamily Sterrhinae was divided into two lineages, one of which comprised Timandrini+Rhodometrini+Cosymbiini and the other Rhodostrophiini+Cyllopodini+Scopulini+Sterrhini. The exact phylogenetic relationships between the tribes of the first lineage were left unresolved, while Sterrhini was believed to be sister to the (Scopulini (Cyllopodini, Rhodostrophiini)) assemblage in the other lineage.

Holloway *et al.* (2001) stated that sterrhines are not strongly defined as a whole, though their component tribes are – a finding consistent with Prout (1934–39). Their subdivision of Sterrhinae into tribes and list of key features of each tribe as well as proposed sister-group relationships between the tribes were consistent with Holloway (1997).

Sihvonen & Kaila (2004) subsequently conducted a major morpho-cladistic analysis revising the tribal classification of Sterrhinae in general and delimiting the tribe Scopulini in particular. On the one hand, their analysis demonstrated that the relatively few characters that were in earlier literature thought to be critical in delimiting the tribes within Sterrhinae are not sufficient to resolve the phylogeny of the subfamily on a global scale. On the other hand, an extensive morphological examination of adults and preimaginal stages allowed Sihvonen & Kaila (2004) to compile a data matrix comprising a total of 95 different characters for 54 sterrhine taxa plus five outgroup species. Analysis of this expanded matrix concluded with a well-resolved phylogenetic tree where all previously defined tribes were supported by several characters. The tribal relationships within the subfamily according to Sihvonen and Kaila (2004) are the following: Sterrhinae is subdivided into two main lineages, informally named as ‘Scopulini lineage’ and ‘Timandrini lineage’. The ‘Scopulini lineage’ comprises tribes Rhodostrophiini, Cyllopodini, Sterrhini and Scopulini and the ‘Timandrini lineage’ tribes Cosymbiini, Timandrini and Rhodometrini, respectively. Though Sihvonen & Kaila (2004) repeatedly stressed the possible short-

comings and disputable points of their analysis (e. g. taxon sampling strongly biased towards Scopulini; uncertain position of genera *Craspediopsis* Warren, 1895, *Trygodes* Guenée, 1858, *Semaeopus* Herrich-Schäffer, 1855, *Haemalea* Hübner, 1823, *Leptostales* Möschler, 1890, *Crypsityla* Warren, 1900 and *Pseudasellodes*; and, placement of the larentiine outgroup within the 'Timandrini lineage'), their results can still be regarded as the most comprehensive hypothesis concerning the phylogeny of the subfamily Sterrhinae.

In his treatment of the European fauna, Hausmann (2004) generally agreed with the findings of Sihvonen & Kaila (2004), as he also supported dividing the subfamily into 'Scopulini lineage' and 'Timandrini lineage'. However, contrarily to Sihvonen & Kaila (2004), Hausmann (2004) treated *Holarctias* Prout, 1913 as a separate genus and downgraded the monotypic *Apostates* Warren, 1897 to a synonym of *Rhodostrophia*. Moreover, Hausmann (2004) did not adopt the results of the exhaustive morpho-cladistic examination of the tribe Scopulini (Sihvonen, 2005), already available when he was compiling his monograph. In the aforementioned study, Sihvonen (2005) analysed more than 140 morphological and ecological characters from all known Scopulini genera, covering the full geographic range and morphological variation of the tribe. As a result of the phylogenetic analysis, he suggested broadening the concept of the mega-diverse genus *Scopula* and downgrading the majority of the known genera to synonyms of this. In addition to these revolutionary rearrangements, Sihvonen (2005) showed that the tribe Scopulini is divided into two lineages, comprising genera *Isoplenodia* Prout, 1932, *Dithalama* Meyrick, 1888, *Zythos* Fletcher, 1979 and *Somatina* Guenée, 1858 on the one hand, and *Lipomelia* Warren, 1893, *Problepsis* and *Scopula* on the other. He also specified the concepts of these smaller genera and listed all known species of the tribe. To date, none of the other sterrhine tribes have been studied as comprehensively from the morpho-cladistic point of view as was Scopulini by Sihvonen (2005).

Even if molecular systematics has rapidly expanded during the last two decades and molecular component has become a common element of systematic research (Caterino *et al.*, 2000; Mallet & Willmott, 2003; Viidalepp *et al.*, 2007), Geometridae in general and Sterrhinae in particular have remained relatively little studied from this point of view. To the best of my knowledge, only few molecular systematic studies are available that have included Sterrhinae. The earliest of those, an article by Abraham *et al.* (2001) was addressed as testing the credibility of existing morphological hypotheses over the systematics of subfamilies of Geometridae. Though some of the results (e. g. paraphyly of Ennominae in addition to the unexpected placement of Archiearinae and Alsophilinae) by Abraham *et al*. (2001) contradicted the earlier expectations of the systematics of Geometridae, they resolved their five-species Sterrhinae sample as a well-supported monophyletic clade, which was sister to all other geometrid subfamilies except Larentiinae. Few years later, Young (2006) composed a major study to resolve the phylogenetic relationships between the Tasmanian Ennominae on the basis of both molecular and morphological data. Due to the exhaustive taxon sampling she was able to

address questions of the phylogeny of Geometridae on a larger scale. One of her several side results was a confirmation to the position Sterrhinae as sister to the rest of Geometridae except Larentiinae (Young, 2006), which had earlier been recovered by Abraham *et al.* (2001).

Though the phylogenetic position of Larentiinae and Sterrhinae was concordant between Abraham *et al.* (2001) and Young (2006), it was soon questioned. Yamamoto & Sota (2007) showed a contradicting phylogeny where Larentiinae and Sterrhinae were resolved as a well-supported monophyletic clade sister to the rest of Geometridae. Moreover, their taxon sampling was considerably more extensive than that of Abraham *et al.* (2001) and Young (2006), as they had sampled four sterrhine taxa from four tribes and 13 larentiine taxa from six tribes. The respective numbers were five sterrhines from two tribes and five larentiines from three tribes in Abraham *et al.* (2001) and two sterrhines from two tribes and five larentiines from five tribes in Young (2006). Due to more exhaustive taxon sampling, the study by Yamamoto & Sota (2007) was the first one that truly shed light on the molecular phylogeny of Sterrhinae. The topology of their Sterrhinae clade agrees with Sihvonen & Kaila (2004) when the presence of 'Timandrini lineage' and 'Scopulini lineage' is considered but the subdivisions of the latter were in conflict with Sihvonen & Kaila (2004). Specifically, in Yamamoto & Sota (2007), *Pylargosceles* (Rhodostrophiini) tended to group together with *Problepsis* (Scopulini) while *Scopula* (Scopulini) appeared as sister taxon to them, but a position of *Pylargosceles* as sister to *Problepsis*+*Scopula* grouping was expected considering the classification by Prout (1920–41) and Sihvonen & Kaila (2004).

The first molecular phylogenetic study that examined the phylogenetic relationships between most of the currently recognised sterrhine tribes was article **II**. Though the focus of that study was to critically evaluate the systematic position of the enigmatic tribe Lythriini, the taxon sampling strategy simultaneously allowed testing the hypotheses of Sihvonen & Kaila (2004) in a slightly broader sense. The division of Sterrhinae into the 'Scopulini lineage' and 'Timandrini lineage', suggested by Sihvonen & Kaila (2004), was confirmed in article **II** and the grouping of tribes within these lineages was also found to be concordant with the results of Sihvonen & Kaila (2004).

The most recent advances in understanding the position of Geometridae and its subgroupings in the phylogenetic tree of Lepidoptera can be found in the articles by Regier *et al.* (2009) and Wahlberg *et al.* (2010). Both studies resolved Sterrhinae and Larentiinae as closely related taxa, sisters to the rest of Geometridae as had been shown by Yamamoto & Sota (2007), thus contradicting the results by Abraham *et al.* (2001) and Young (2006), who had revealed Larentiinae as a single monophyletic subfamily sister to the rest of Geometridae, including Sterrhinae. However, in contrast to all earlier molecular works, Regier *et al.* (2009) found Sterrhinae paraphyletic, but it must be pointed out that the bootstrap support indices favouring this topology were below 50. Therefore I conclude that the present knowledge allow us to treat Sterrhinae as a monophyletic subfamily. The known phylogenetic relationships within sub-

family Sterrhinae are, however, still to be considered as preliminary, requiring further molecular treatment, as the taxon sampling at genus level has been far from comprehensive in all available molecular phylogenetic studies (see also Hausmann, 2004; Sihvonen & Kaila, 2004; **II**).

The section 4.4 of the current study is an attempt to improve the known molecular phylogeny of the subfamily Sterrhinae. For that purpose, I concatenated molecular data that were used in articles **II–III** and as many additional unpublished original molecular data from as different sterrhine taxa as possible. In total, 43 sterrhine species belonging to 14 genera were studied by using sequences of two mitochondrial and four nuclear gene fragments.

3. MATERIAL AND METHODS

3.1. Material sampling and identification

Both dry pinned moths from several public and private collections and fresh material were used for this study. The fresh moths were collected either by daytime netting or by attracting them to artificial light at night. The abdomens of fresh moths were stored in 96% ethanol at –20ºC prior to the extraction of genomic DNA. Thoraces with head, legs and wings were pinned and kept as vouchers in the collection of Institute of Agricultural and Environmental Sciences (IZBE).

The *Timandra* specimens for article **I** were identified according to the morphological criteria given by Kaila & Albrecht (1994, 1995) and using the material loaned for reference from Finnish Museum of Natural History (FMNH), as well as expert advice from Dr. Lauri Kaila (FMNH). Material used in the articles **II** and **III** was identified using handbooks by Hausmann (2004), Koch (1984), Prout (1912–16, 1935–38), Viidalepp & Remm (1996) and collection of IZBE for reference.

In addition to papers **I-III**, a wider phylogenetic analysis of Sterrhinae was performed on the basis of 43 sterrhine species belonging to 14 genera and seven tribes together with two outgroup taxa from subfamily Larentiinae (Table 1). This is essentially an extension of articles **II** and **III** (see also chapter 4.4). As the geographic and taxonomic coverage for this study was wider than that of the earlier publications, additional sources (Holloway, 1997; McGuffin, 1967; Prout, 1920–41) were used for identification of moths.

Table 1. Information on the taxa used in the wider phylogenetic analysis of Sterrhinae (section 4.4). Collecting site (AUS, Australia; CAN, Canada; ESP, Spain; EST, Estonia; FG, French Guiana; ITA, Italy; JPN, Japan; KAZ, Kazakhstan; PER, Peru; SUI, Switzerland; USA, United States of America) and date, collector's name and depository of the voucher are indicated. Tribal assignment of sterrhine genera follows Sihvonen & Kaila (2004) and article **II**.

Species	Collecting locality	Date	Collector	Depository
subfamily Larentiinae				
Phibalapteryx virgata (Hufnagel, 1767)	EST, Harjumaa, Haavakannu	10.06.2006	E. Õunap	coll. IZBE
Trichopteryx carpinata (Borkhausen, 1794)	EST, Saaremaa, Viidumäe Nature reserve, Audaku	05.05.2001	E. Õunap	coll. IZBE
subfamily Sterrhinae				
tribe Cosymbiini				
Cyclophora albipunctata (Hufnagel, 1767)	EST, Põlvamaa, Piusa railway station	25.07.2006	E. Õunap	coll. IZBE
Cyclophora nebuligera (Butler, 1881)	PER, prov. Amazonas, Rio Huallaga quedebras	18.–22.10.2004	J. Viidalepp	coll. IZBE
Cyclophora nodigera (Butler, 1881)	PER, prov. Amazonas, Rio Huallaga quedebras	18.–22.10.2004	J. Viidalepp	coll. IZBE
Cyclophora pendularia (Clerck, 1759)	EST, Põlvamaa, Kiidjärve	02.07.2004	E. Õunap	coll. IZBE
Cyclophora pendulinaria (Guenée, 1858)	CAN, NS, Truro, Bible Hill	14.08.2000	V. Soon	coll. IZBE
Cyclophora punctaria (Linnaeus, 1758)	EST, Saaremaa, Viidumäe Nature reserve, Audaku	14.06.2001	E. Õunap	coll. IZBE
Pleuroprucha insulsaria (Guenée, 1858)	CAN, NS, Truro, Bible Hill	17.07.2000	V. Soon	coll. IZBE
Pleuroprucha rudimentaria (Guenée, 1858)	PER, Rio Maranon, Balsas E pampa, 1220m	07.10.2004	J. Viidalepp	coll. IZBE

Table 1. (continued)

Species	Collecting locality	Date	Collector	Depository
tribe Lythriini				
Lythria cruentaria (Hufnagel, 1767)	EST, Harjumaa, Põhja-Kõrvemaa Landscape reserve, Jussi heath	29.06.2004	E. Õunap	coll. IZBE
Lythria plumularia (Freyer, 1831)	SUI, Graubünden Albula-Pass 1800 m. TF	20.06.2005	R. Baumberger	coll. N. Pöll
Lythria purpuraria (Linnaeus, 1758)	ESP, Barcelona 50 km N, Sant Pere de Vilamajor	21.08.1999	T. Tammaru	coll. T. Tammaru
Lythria sanguinaria (Duponchel, 1842)	ESP, (MA) Tres Cantos 740 m	15.05.2006	G. King	lost in mail
Lythria venustata Staudinger, 1882	KAZ, W Kazakhstan, Atirau reg., Karabatan env.	01.05.2006	R. Kadyrbekov	coll. ZISP
tribe Rhodometrini				
Rhodometra sacraria (Linnaeus, 1767)	EST, Pärnumaa, centre of Nigula Nature Reserve	23.08.2000	M. Kruus	coll. IZBE
tribe Rhodostrophiini				
Pylargosceles steganioides (Butler, 1878)	JPN, Yoshida, Sakyo, Kyoto	unknown	unknown	coll. KUHE
Rhodostrophia calabra (Petagna, 1786)	ITA, Basilicata mer. Vallo Noce Trecchina, 320 m	03.06.1996	A. Hausmann	coll. IZBE
Rhodostrophia vibicaria (Clerck, 1759)	EST, Põlvamaa, Piusa sand pit	18.07.2004	E. Õunap	coll. IZBE
Tricentra albiguttata (Warren, 1906)	FG, Belizon	04.01.2003	V. Soon	coll. IZBE
Tricentra brunneomarginata Warren, 1906	FG, Belizon	04.01.2003	V. Soon	coll. IZBE

Table 1. (continued)

Species	Collecting locality	Date	Collector	Depository
tribe Scopulini				
Antitrygodes divisaria (Walker, 1861)	AUS, QLD, Mossman 10 km N	27.03.2002	J. Viidalepp	coll. IZBE
Problepsis ocellata (Frivaldszky, 1845)	unknown	unknown	unknown	coll. ZSM
Problepsis sancta Meyrick, 1888	AUS, QLD, Benarkin NP	19.03.2002	J. Viidalepp	coll. IZBE
Pseudasellodes fenestraria (Guenée, 1858)	FG, Camp Caiman	06.11.2002	V. Soon	coll. IZBE
Scopula caricaria (Reutti, 1853)	EST, Põlvamaa, Verhulitsa	21.07.2004	E. Õunap	coll. IZBE
Scopula corrivalaria (Kretschmar, 1862)	EST, Põlvamaa, Verhulitsa	21.07.2004	E. Õunap	coll. IZBE
Scopula decorata (Denis & Schiffermüller, 1775)	EST, Saaremaa, Mändjala	13.07.2004	E. Õunap	coll. IZBE
Scopula floslactata (Haworth, 1809)	EST, Saaremaa, Viidumäe Nature reserve, Audaku	14.06.2001	E. Õunap	coll. IZBE
Scopula immorata (Linnaeus, 1758)	EST, Tartumaa, Ülenurme	16.06.2004	I. Taal	coll. IZBE
Scopula immutata (Linnaeus, 1758)	EST, Saaremaa, Viidumäe Nature reserve, Audaku	30.06.2001	E. Õunap	coll. IZBE
Scopula nemoraria (Hübner, 1799)	EST, Tartumaa, Täsvere	25.06.2004	E. Õunap	coll. IZBE
Scopula ornata (Scopoli, 1763)	EST, Saaremaa, Mõntu gravel pit	14.07.2004	E. Õunap	coll. IZBE
Scopula rubraria (Doubleday, 1843)	AUS, SA, Adelaide	09.04.2002	J. Viidalepp	coll. IZBE

Table 1. (continued)

Species	Collecting locality	Date	Collector	Depository
tribe Sterrhini				
Idaea aversata (Linnaeus, 1758)	EST, Harjumaa, Paldiski	21.07.2006	E. Õunap	coll. IZBE
Idaea humiliata (Hufnagel, 1767)	EST, Saaremaa, Viidumäe Nature reserve, Audaku	01.07.2001	E. Õunap	coll. IZBE
Idaea muricata (Hufnagel, 1767)	EST, Põlvamaa, Verhulitsa	21.07.2004	E. Õunap	coll. IZBE
Idaea pallidata (Denis & Schiffermüller, 1775)	EST, Põlvamaa, Piusa railway station	23.06.2004	E. Õunap	coll. IZBE
Idaea serpentata (Hufnagel, 1767)	EST, Põlvamaa, Veski	26.06.2004	E. Õunap	coll. IZBE
Idaea straminata (Borkhausen, 1794)	EST, Saaremaa, Viidumäe Nature reserve, Audaku	01.07.2001	E. Õunap	coll. IZBE
Idaea sylvestraria (Hübner, 1799)	EST, Saaremaa, Kogula	16.07.2004	E. Õunap	coll. IZBE
tribe Timandrini				
Haematopis grataria (Fabricius, 1798)	USA, MD, Beltsville, suburb	15.09.1999	T. Tammaru	coll. T. Tammaru
Timandra comae Schmidt, 1931	EST, Tartumaa, Tatra valley near Kambja	11.09.2003	E. Õunap	coll. IZBE
Timandra dichela (Prout, 1935)	JPN, Yoshida, Sakyo, Kyoto	unknown	unknown	coll. KUHE
Timandra griseata Petersen, 1902	EST, Tartumaa, Tatra valley near Kambja	02.07.2003	E. Õunap	coll. IZBE

3.2. Sequencing of mitochondrial and nuclear gene fragments

The genomic DNA was extracted using High Pure PCR Template Preparation Kit (Roche Diagnostics GmbH, Mannheim, Germany). Most often the two to three anterior segments of abdomen were crushed and used for the extraction, keeping the posterior part of the abdomen with genitalia intact at –20ºC as voucher and backup of the genetic material. However, for a few specimens used in studies **II** and **III**, two to three legs were used, or, alternatively, the whole abdomen was used for extraction in a way that kept genitalia intact (see Knölke *et al.*, 2005). The extraction was carried out following the manufacturer's instructions, with the exception that the first incubation step was 55ºC for up to 12 hours rather than 1 hour.

In total, sequences of two mitochondrial and three nuclear gene fragments were used for phylogenetic analysis in articles **I–III**. Of the mitochondrial genes, cytochrome oxidase subunit 1 (*COI*) was used in articles **I**, **II** and **III** while NADH dehydrogenase subunit 1 (*ND1*) was included into analysis in articles **I** and **II**. The nuclear genes for elongation factor 1 alpha (*EF-1α*) and wingless (*wgl*) were used in articles **II** and **III** while 28S rRNA expansion segment D2 (*28S D2*) was used only in article **II**. Primers used for PCR and sequencing were either taken from earlier publications (Caterino & Sperling, 1999; Belshaw & Quicke, 1997; Brower & DeSalle, 1998; Monteiro & Pierce, 2001; Viidalepp *et al*., 2007) or were newly developed and first published in articles **I** and **II**. Reaction conditions for PCR, shrimp alkaline phosphatase and exonuclease I treatment and cycle sequencing reaction, carried out on T1 Thermocycler (Biometra, Göttingen, Germany), can be found in Materials and Methods of articles **I–III** at the end of this dissertation. The sequences were resolved on ABI 377 automated sequencer (Applied Biosystems, Forster City, USA).

Two mitochondrial (*COI*, *ND1*) and four nuclear [*EF-1α*, *wgl*, 28S rRNA expansion segment D1 (*28S D1*) and *28S D2*] gene fragments were used for the broader phylogenetic analysis of Sterrhinae (chapter 4.4). Both PCR and cycle sequencing reaction conditions are presented in Table 2. The sequences were resolved on ABI 377 automated sequencer.

Table 2. Primers and annealing temperature for PCR and cycle sequencing (CS) used in wider phylogenetic analysis of Sterrhinae (section 4.4). *COI* and *ND1* were in some occasions amplified as four or three partially overlapping sections.

Primer	Primer sequence	Gene region	Direction	PCR	CS	Source
Cov-1f	5'-TCG CTT ATT ATT CAG CCA TTT TAT T-3'	COI, 5' half	Forward	50°C	47°C	**II**
Cov-1r	5'CTG CAC CAT TTT CTA CAA TTC TTC T-3'	COI, 1st section	Reverse	50°C	50°C	**II**
Ron	5'-GGA TCA CCT GAT ATA GCA TTC CC-3'	COI, 2nd section	Forward	49°C	53°C	Caterino & Sperling, 1999
Nan	5'-CCC GGT AAA ATT AAA ATA TAA ACT TC-3'	COI, 5' half	Reverse	49–50°C	47°C	**I**
V1	5'-ATA TTA TTA ACW GAT CGA AAY TTA AAT AC-3'	COI, 3' half	Forward	45–50°C	47°C	**II**
V2	5'-TGA AAA TGA GCT ACW ACA TAA TAA GTA TCA-3'	COI, 3rd section	Reverse	50°C	45°C	**II**
4f2	5'-ATT AAA ATT TTT AGT TGA TTA GC-3'	COI, 4th section	Forward	50°C	45°C	**II**
4r2	5'-CTT TAT AAA TGG GGT TTA AAT C-3'	COI, 3' half	Reverse	45–50°C	47°C	**II**
Ndf1	5'-TAA GCA TTT GTT TTG AA-3'	ND1, 1st section	Forward	31–44°C	38–45°C	This study
Ndr1	5'-TTT MTG TTG AYT TTC TTC-3'	ND1, 1st section	Reverse	31–44°C	44°C	This study
LepND1r	5'-TTT DTG TTG ADT WTC WTC-3'	ND1, 1st section	Reverse	35–43°C	38–45°C	This study
LepND2f	5'-AYT CTC TTT CAC CTT CAG CA-3'	ND1, 2nd section	Forward	48°C	45°C	**II**
LepND2r	5'-TTT AGG TTA TAT TCA RRT TCG-3'	ND1, 2nd section	Reverse	48°C	45°C	**II**
Ndf3	5'-TTA GTA AAT AAT TTA ATA GCA TC-3'	ND1, 3rd section	Forward	37°C	37°C	**II**
Ndr3	5'-AGG TTG GTT TCT ATC T-3'	ND1, 3rd section	Reverse	37°C	37°C	**II**
D1F	5'-GGG GAG GAA AAG AAA CTA AC-3'	28S D1	Forward	58°C	47°C	Abraham *et al.*, 2001
D1R	5'-CAA CTT TCC CTT ACG GTA CT-3'	28S D1	Reverse	58°C	47°C	Abraham *et al.*, 2001
D2F	5'-AGA GAG AGT TCA AGA GTA CGT G-3'	28S D2	Forward	58°C	55°C	Belshaw & Quicke, 1997
D2R	5'-TTG GTC CGT GTT TCA AGA CGG G-3'	28S D2	Reverse	58°C	55°C	Belshaw & Quicke, 1997
LepWG1	5'-GAR TGY AAR TGY CAY GGY ATG TCT GG-3'	Wingless	Forward	58°C	55°C	Brower & DeSalle, 1998
LepWG3	5'-ACT YCG CAR CAC CAR TGG AAT GTR CA-3'	Wingless	Reverse	58°C	55°C	Brower & DeSalle, 1998
ef44	5'-GCY GAR CGY CAR CGT GGT ATY AC-3'	EF-1α	Forward	58°C	58°C	Monteiro & Pierce, 2001
efrcM4	5'-ACA GCV ACK GTY TGY CTC ATR TC-3'	EF-1α	Reverse	58°C	58°C	Monteiro & Pierce, 2001

Table 2. (continued)

Primer	Primer sequence	Gene region	Direction	PCR	CS	Source
Cho2	5'-CTA CGT CAC CAT CAT CGA-3'	EF-1α, 5' half	Forward	58°C	57°C	Viidalepp *et al.*, 2007
LepEF-1f	5'-AAR TAC TAT GTC ACN ATC ATY GA-3'	EF-1α, 5' half	Forward	55°C	55°C	**II**
Verdi4	5'-CAC CAG TCT CCA CAC GGC C-3'	EF-1α, 5' half	Reverse	58°C	57°C	Viidalepp *et al.*, 2007
LepEF-1r	5'-ACA CCA GTT TCN ACW CKG CC-3'	EF-1α, 5' half	Reverse	55°C	55°C	**II**
EF51.9	5'-CAR GAC GTA TAC AAA ATC GG-3'	EF-1α, 3' half	Forward	58°C	57°C	Monteiro & Pierce, 2001
LepEF-2f	5'-CCC ACA GAC AAG SCY CTV CGT-3'	EF-1α, 3' half	Forward	61°C	55°C	**II**
Niina2	5'-CCT GGA AGG ACT CCA CRC ACA G-3'	EF-1α, 3' half	Reverse	58–61°C	57°C	Viidalepp *et al.*, 2007

3.3. Phylogenetic analysis

Consensus sequences were created with the program CONSED (Gordon *et al.*, 1998) using sequence data from both DNA strands. Sequences were double-checked by eye and aligned with CLUSTALW (Thompson *et al.*, 1994), using BIOEDIT (Hall, 1999) as a sequence editor. In addition to the original data, few sequences downloaded from Genbank were also included into the phylogenetic analysis in articles **II** and **III**.

In all articles, combined datasets comprising data from two (**I**), three (**III**) or five (**II**) separate gene regions were used. The homogeneities between different gene sequences were calculated using the partition homogeneity test in PAUP* 4.0b10 (Swofford, 1998). In articles **I** and **III**, this test revealed no significant incongruence between the selected gene regions and the respective data matrices were subsequently analysed as single entities. However, in article **II** significant incongruence was detected between different genes and the data were therefore partitioned according to the respective genes prior to the phylogenetic analysis. Optimal substitution models for complete datasets in articles **I** and **III** and for each gene region in article **II** were calculated using MODELTEST 3.06 (Posada & Crandall 1998). Phylogenetic analyses were conducted using the following software: MRBAYES 3.1 (Ronquist & Huelsenbeck 2003) for Bayesian phylogenetic inference in articles **I**, **II** and **III**; MEGA 2.1 (Kumar *et al.*, 2001) for neighbour-joining (NJ) in article **I**; PAUP*4.0b10 for maximum parsimony (MP), NJ and maximum likelihood (ML) in article **III**; RAXML-VI-HPC (Stamatakis, 2006) for ML in article **II**; BEAST 1.4.6. (Drummond and Rambaut, 2007) for additional Bayesian phylogenetic inference in article **II**. Reduced median joining network in article **I** was calculated with NETW 4106 (Bandelt et al., 1999). The exact details of the phylogenetic analysis can be found in the reprints of the respective papers in the end of the present dissertation. The results of phylogenetic analyses were visualised with TREEVIEW 1.6.6 (Page 1996) or FIGTREE v1.1.2, the latter being a supplementary software to BEAST.

The list of sequence data used in the broader phylogenetic analysis of Sterrhinae (chapter 4.4) is presented in Table 3. All studied gene fragments were aligned with CLUSTALW using default settings. Alignment of mitochondrial and nuclear protein-coding genes was straightforward and a few indels followed the same taxon-specific patterns, which were revealed already in papers **II** and **III**. The alignment of expansion segments D1 and D2 of 28S rRNA, however, resulted with several indels in data matrix. As noted e. g. by Lutzoni *et al.* (2000) and Yamamoto & Sota (2007), the imprudent use of data with indels may violate positional homology and lead to artefacts. To avoid this threat, all positions with indels were removed from 28S sequences prior to the phylogenetic analysis. The length of successfully sequenced fragments of D1 varied from 293–296 bp and the length of aligned data matrix was 297 bp. Four positions with indels were excluded from data matrix resulting in a 293 bp indel-free matrix. The alignment of D2 was more complicated, as the length of

successfully sequenced fragments varied from 415–443 bp and the length of aligned data matrix was 472 bp. Of those positions 93 contained indels and were removed, resulting in a 379 bp indel-free data matrix. As D1 and D2 are different regions of the same rRNA gene and therefore share a similar evolutionary history, the indel-free data matrices were concatenated and treated as single 672 bp entity in phylogenetic analysis.

Partition-homogeneity test, carried out in PAUP*4.0b10, revealed significant incongruencies between the different genes and the data matrix was therefore partitioned according to the genes. MODELTEST 3.06 was used to calculate the optimal substitution model for each of the five partitions following Akaike Information Criterion.

Bayesian phylogenetic analysis was performed using MRBAYES 3.1 and the GTR+Γ+I model selected by MODELTEST was fitted to each of the five partitions. Four simultaneous Markov chains (one cold and three heated) were run for ten million generations with trees sampled every 1000 generations. Likelihood values were inspected and the first 2500 sampled trees were discarded as 'burn-in'. To estimate posterior probabilities of recovered branches, a 50% majority rule was applied. Phylograms were created as average-branch-length consensus trees and visualised with TREEVIEW 1.6.6.

The partitioned ML tree was constructed with RAXML-VI-HPC. As the GTR+Γ+I model is not implemented in RAXML-VI-HPC, a separate GTR+Γ model was fitted for each partition in search for the best known likelihood tree. Initially, 200 random MP trees were generated and used as starting points for maximum likelihood analysis, resulting in 200 scored ML trees. Thereafter, non-parametric bootstrapping was performed with 1000 replicates. Finally, the information from the 1000 bootstrapped topologies was drawn on the single best-scoring ML tree from the initial run and results were visualized with TREEVIEW 1.6.6.

Table 3. GenBank accession numbers for the sequences used in the wider phylogenetic analysis (section 4.4). Authorships of the sequences downloaded from GenBank are indicated as follows: #article **II** from the current dissertation; ¤article **III** from the current dissertation; *Abraham *et al.*, 2001; †Knölke *et al.*, 2005; ‡Snäll et al., 2007; ±Yamamoto & Sota, 2007. Sequence accession numbers in *italics* indicate that less than 75% of the full sequence length was available.

Species	**COI**	**ND1**	**EF-1α**	**wgl**	**28S D1**	**28S D2**
Phibalapteryx virgata	EU443352#	unpublished	EU443290#	EU443311#	unpublished	EU443371#
Trichopteryx carpinata	EU443349#	unpublished	EU443287#	EU443308#	unpublished	EU443368#
Cyclophora albipunctata	EU443360#	unpublished	EU443297#	–	unpublished	EU443376#
Cyclophora nebuligera	unpublished	unpublished	–	unpublished	unpublished	unpublished
Cyclophora nodigera	unpublished	unpublished	unpublished	unpublished	unpublished	unpublished
Cyclophora pendularia	unpublished	unpublished	unpublished	–	unpublished	unpublished
Cyclophora pendulinaria	unpublished	–	–	–	unpublished	–
Cyclophora punctaria	EU443361#	unpublished	EU443298#	EU443318#	unpublished	EU443377#
Pleuroprucha insulsaria	unpublished	unpublished	–	–	unpublished	–
Pleuroprucha rudimentaria	unpublished	unpublished	unpublished	–	unpublished	unpublished
Lythria cruentaria	EU443365#	unpublished	EU443302#	EU443322#	unpublished	EU443381#
Lythria plumularia	GQ857123¤	–	GQ857125¤	GQ857127¤	–	–
Lythria purpuraria	EU443367#	–	EU443304#	EU443324#	unpublished	EU443383#
Lythria sanguinaria	EU443366#	unpublished	EU443303#	EU443323#	unpublished	EU443382#
Lythria venustata	GQ857124¤	–	GQ857126¤	GQ857128¤	–	–
Rhodometra sacraria	AJ870398†	unpublished	EU443305#	EU443325#	unpublished	EU443384#
Pylargosceles steganioides	*AB265361*±	–	AB265510±	–	AB265583±	–
Rhodostrophia calabra	EU443355#	*EU443334#*	EU443293#	EU443314#	unpublished	EU443374#
Rhodostrophia vibicaria	EU443354#	unpublished	EU443292#	EU443313#	unpublished	EU443373#
Tricentra albiguttata	unpublished	unpublished	–	–	unpublished	unpublished
Tricentra brunneomarginata	unpublished	unpublished	–	unpublished	unpublished	unpublished
Antitrygodes divisaria	unpublished	unpublished	*unpublished*	–	unpublished	–
Problepsis ocellata	AJ870401†	–	–	–	–	–

Table 3. (continued)

Species	COI	ND1	EF-1α	wgl	28S D1	28S D2
Problepsis sancta	unpublished	*unpublished*	unpublished	unpublished	unpublished	–
Pseudasellodes fenestraria	unpublished	unpublished	unpublished	–	unpublished	unpublished
Scopula caricaria	unpublished	unpublished	unpublished	–	unpublished	unpublished
Scopula corrivalaria	unpublished	unpublished	–	–	unpublished	unpublished
Scopula decorata	EU443359#	*EU443338*#	EU443296#	EU443317#	unpublished	EU443375#
Scopula floslactata	unpublished	unpublished	unpublished	unpublished	unpublished	unpublished
Scopula immorata	unpublished	unpublished	unpublished	unpublished	unpublished	unpublished
Scopula immutata	unpublished	unpublished	unpublished	unpublished	unpublished	unpublished
Scopula nemoraria	unpublished	unpublished	unpublished	–	unpublished	unpublished
Scopula ornata	EU443358#	unpublished	EU443295#	EU443316#	AF178887*	AF178911*
Scopula rubraria	unpublished	unpublished	–	–	unpublished	–
Idaea aversata	EU443357#	unpublished	EU443294#	EU443315#	AF178890*	AF178914*
Idaea humiliata	unpublished	unpublished	unpublished	unpublished	–	unpublished
Idaea muricata	unpublished	unpublished	unpublished	unpublished	unpublished	unpublished
Idaea pallidata	unpublished	unpublished	unpublished	unpublished	unpublished	unpublished
Idaea serpentata	unpublished	unpublished	unpublished	unpublished	unpublished	unpublished
Idaea straminata	EU443356#	unpublished	AY948507‡	AY948534‡	AF178889*	AF178913*
Idaea sylvestraria	unpublished	unpublished	unpublished	unpublished	unpublished	unpublished
Haematopis grataria	EU443364#	*unpublished*	EU443301#	EU443321#	unpublished	EU443380#
Timandra comae	EU443363#	unpublished	EU443300#	EU443320#	unpublished	EU443379#
Timandra dichela	*AB265359*±	–	AB265508±	–	AB265581±	–
Timandra griseata	EU443362#	unpublished	EU443299#	EU443319#	unpublished	EU443378#

4. RESULTS AND DISCUSSION

4.1. The Timandra *griseata*/ *T. comae* question

Sequencing the mitochondrial *COI* and *ND1* genes resulted in obtaining 392-bp and 398-bp fragments, respectively. The total length of the combined data matrix was 790 bp, with no insertions or deletions found. Sequencing these two gene fragments was successful for all 43 *Timandra* specimens analysed in article **I**. Both NJ and Bayesian phylogenetic analysis divided the sampled *Timandra* individuals into two well-supported clades (article **I**, Fig. 3). One of those clades comprised primarily *T. comae* (27 *T. comae* and one *T. griseata*), whereas the other included mostly *T. griseata* (15 *T. griseata* and one *T. comae*). The minimum spanning network (article **I**, Fig. 2) also separated the studied individuals into two distinct clusters, which were separated by 10 mutations. These clusters were also almost entirely comprised of conspecific specimens. Since the specimens were divided between the two main subdivisions of the phylogenetic trees according to their morphological differences, not randomly or according to the geographic position of their respective collecting sites, we concluded that *T. griseata* and *T. comae* are likely to be two distinct species, as had been suggested earlier on the basis of morphological analysis by Kaila and Albrecht (1994) and Sihvonen (2001).

However, the position of one *T. griseata* and one *T. comae* specimen, collected at Nigula Nature Reserve, SW Estonia in 1990 and at Põõsaspea Cape, NW Estonia in 2001, respectively (article **I**, Table 1) did pose a question about monophyly of these species. Both *COI* and *ND1* sequences of these specimens were identical to commonest haplotypes of the 'wrong' species (article **I**, Table 2, Fig. 2). Phylogenetic analyses therefore inevitably positioned those specimens into the 'wrong' clades (article **I**, Figs. 2 and 3). To exclude the possibilities of misidentification, contamination, sequencing error etc, the morphological characters of these two specimens were critically re-examined and the whole laboratory procedure from DNA extraction to sequencing was repeated, which verified the results and pointed to incomplete lineage sorting in *Timandra griseata/ T. comae* assemblage.

Following the Mayr's (1963) biological species concept, it is generally assumed that species must be monophyletic entities (Harrison, 1998). However, as shown by Pamilo & Nei (1988) and summarized by Wahlberg *et al.* (2003) and Funk & Omland (2003), both polyphyly and paraphyly may arise during the speciation process. Complete lineage sorting may or may not have occurred during speciation and it cannot be assumed as an ineluctable event (Wahlberg *et al.*, 2003). Moreover, several empirical studies have recently shown that the incomplete lineage sorting in animals may be more common than thought earlier (Sota & Vogler, 2001; Wahlberg *et al.*, 2003, Peters *et al.*, 2007; Zakharov *et al.*, 2009)

Incomplete lineage sorting can be a result of two different evolutionary processes: it may reflect the genetic polymorphism of the ancestral population

(e. g. Baker *et al.*, 2003; Wahlberg *et al.*, 2003; Koblmüller *et al.*, 2010) or it may occur because of recent or ancient introgressive hybridisation between the two extant species (e. g. van Herwerden *et al.*, 2006; McDevitt *et al.*, 2009; Zakharov *et al.*, 2009). Distinguishing between those two processes is difficult, as both produce similar topologies in gene trees (Peters *et al.*, 2007; Eckert & Carstens, 2008; Koblmüller *et al.*, 2010). Solving this kind of dilemma requires rigorous testing of alternative hypotheses, as explained in Knowles (2004) and Peters *et al.* (2007). Due to the lack of information available, we did not perform any tests to reveal the nature of the two 'wrongly' placed *Timandra* specimens. Instead, we critically analysed the available information and concluded that recent hybridisation is the most likely scenario for *Timandra griseata/ T. comae* assemblage compared to retaining ancestral polymorphism.

The intraspecific genetic structure of *T. griseata* and *T. comae* is completely different (highly divergent, indicating ancient radiation in *T. griseata*; but showing limited divergence, pointing to recent radiation in *T. comae*) and the closest haplotypes of these taxa are separated from each other by at least 10 substitutions (article **I**, Fig. 2). The mtDNA haplotype of the 'wrongly' placed *T. comae* specimen from Cape Põõsaspea, NW Estonia, is identical to the commonest haplotype of *T. griseata*, which belongs to the haplogroup genetically most distant from the haplotypes of *T. comae* (article **I**, Figs. 2 and 3). If there was some radiation of ancient *Timandra* mtDNA haplotypes incongruent with the radiation of taxa, it is highly unlikely that the subsequent independent evolution of these haplotypes resulted in exactly the same nucleotide sequence in some of the contemporary *T. griseata* specimens and the *T. comae* specimen from NW Estonia. Similarly, one *T. griseata* specimen collected in Nigula Nature Reserve in SW Estonia had an mtDNA haplotype identical to the main haplotype of *T. comae* and we concluded that this particular individual was also of hybrid origin, rather than carrying 'wrong' phenotype because of incongruence between gene tree and species tree.

Moreover, detailed look into the phenology of *T. griseata* and *T. comae* supports the hybridisation hypothesis. These species are protandric (i. e. males appear earlier than females) like most insects with discrete generations (e. g. Carvalho *et al.*, 1998). The flight periods of the two *Timandra* species differ, but overlap partially in Finland (Kaila & Albrecht, 1994) and we found that similar pattern is valid also in Estonia (article **I**, Fig. 4). During summer, there are two periods when hybridisation between *T. griseata* and *T. comae* is possible. The first generation of *T. comae* is on the wing from late May to the end of June, while the flight period of the first generation of *T. griseata* starts in late June and lasts until the second half of July. Therefore, for a short period in late June adults of both genders of *T. comae* are present, but only male *T. griseata* individuals have hatched. As no *T. griseata* females are yet available, these males may occasionally mate with *T. comae* females. The flight period of the second generation of *T. comae* starts in late July when the flight period of *T. griseata* have not ended yet, which means that there is another short period of time when both genders of *T. griseata* adults are present in the nature

but only male *T. comae* specimens are on the wing. Thus, male *T. comae* individuals may occasionally mate with *T. griseata* females. Similar hybridisation pattern has been shown to be true in some closely related sphingids with partially overlapping flight periods (Pittaway, 1993) and we see no reason why this kind of mechanism could not exist in Geometrids, unless there is a strong reproductive isolation barrier between species. To date, there is no evidence for such barrier between *T. griseata* and *T. comae*. However, it must be pointed out that it is not likely that there are many receptive females available at the end of the flight period of the species. The probability for hybridisation between *T. griseata* and *T. comae* is therefore low, which may explain why only few *Timandra* specimens of hybrid origin were found. Moreover, the habitat preference of *T. griseata* and *T. comae* differs also, as the former prefers more humid habitats and thus occurs only sparsely in Estonia, which further reduces the probability of hybridisation between these species.

It is interesting to note that though *T. griseata* and *T. comae* are currently sympatric in southern Fennoscandia, northern part of the Baltic countries and northwestern part of European Russia (Kaila & Albrecht, 1994; Kaila *et al.*, 1999; Savenkov & Šulcs, 2004; Mironov *et al.*, 2008), they used to be allopatric earlier. Kaisila (1954) showed that the earliest Finnish specimen of *T. comae* (as *Calothysanis amataria brykaria* in his paper) had been collected in 1920 while all older specimens turned out to be *T. griseata* (*C. a. amataria*). Our investigation of Estonian insect collections resulted in similar finding, as the earliest Estonian *T. comae* specimen had been collected in 1943 and all older *Timandra* specimens were *T. griseata*. These observations indicate that the *T. griseata* and *T. comae* became sympatric as recently as in early 20th century. Since the sympatry of *T. griseata* and *T. comae* is so recent, it is possible that even if the hybridisation between these taxa is disadvantageous, no effective hybridisation barriers have yet been evolved.

4.2. The systematic position of Lythriini

Sequencing of mitochondrial and nuclear gene fragments was completely successful for 20 out of 22 taxa sampled in this study. Only sequencing a portion of *ND1* from *L. purpuraria* and fragment of *wgl* from *Cyclophora albipunctata* (Hufnagel, 1767) failed and the respective positions were therefore coded as missing for phylogenetic analysis. Alignment of the partial sequences of *ND1* and *EF-1α* was straightforward, no indels were recovered and the lengths of the successfully sequenced fragments were 596 bp and 883 bp, respectively. The full sequence of COI was 1536 bp for most of the studied species, but only 1533 bp for both *T. griseata* and *T. comae*, as there was an 8-bp AAAAATAT insertion between the COI positions 1531 and 1532 in these species, which resulted in formation of a TAA stop codon in positions 1531–1533. The partial sequence of *wgl* also contained length variation, as all five larentiine taxa had a specific 6-bp GGTGCA or AGTCCA insertion, which was

missing in all other studied taxa, including the three *Lythria* species. Aligning the partial sequence of *28S D2* was the most complicated, as the length of the successfully sequenced gene fragment varied from 412 to 449 bp and the length of the aligned data matrix was 477 characters. This matrix contained indels in 105 positions, and these positions were removed from the data matrix for reasons described above. The final length of the indel-free *28S D2* data matrix was 372 characters. The total length of the combined molecular data matrix was 3784 bp.

Bayesian and ML analysis resulted in a well-resolved phylogenetic tree of identical topology (article **II**, Fig. 1). The two geometrid subfamilies sampled in this study, Larentiinae and Sterrhinae, were resolved as two reciprocally monophyletic entities with good statistical support by both methods of phylogenetic analysis in almost all nodes (article **II**, Fig. 1). These results are concordant with the earlier molecular phylogenetic studies that have resolved Sterrhinae and Larentiinae as distinct monophyletic entities (Abraham *et al.*, 2001; Young, 2006; Yamamoto & Sota, 2007). The possible paraphyly of Sterrhinae, shown by Sihvonen & Kaila (2004) is therefore to be regarded as an artefact, suspected also by these authors themselves.

The article **II** did not contribute to the discussion concerning the position of Larentiinae and Sterrhinae in the wider phylogeny of Geometridae, as no other subfamilies were sampled. Similarly, as only five out of a total of 18 larentiine tribes (Heppner, 2003) were sampled, no significant contribution to understanding the phylogeny of this subfamily was made. However, this limited analysis still revealed Trichopterygini as sister to the rest of Larentiinae (article **II**, Fig. 1), which supported the earlier view by Holloway (1997) and Yamamoto & Sota (2007).

The phylogenetic analysis divided the subfamily Sterrhinae into two main lineages. The 'Scopulini lineage' comprised the tribes Rhodostrophiini, Scopulini and Sterrhini and the 'Timandrini lineage' the tribes Cosymbiini, Timandrini, Rhodometrini and Lythriini, respectively (article **II**, Fig. 1). These results are highly concordant with those by Sihvonen & Kaila (2004), as their 'Scopulini lineage' comprised Rhodostrophiini, Cyllopodini, Scopulini and Sterrhini together with two uncertain groupings of few Oriental and Neotropic genera; and their 'Timandrini lineage' contained Cosymbiini, Timandrini and Rhodometrini, respectively.

As noted above, phylogenetic relationships within the 'Scopulini lineage' were highly concordant between Sihvonen & Kaila (2004) and article **II**. Specifically, Sihvonen & Kaila (2004) had revealed that Rhodostrophiini was sister to other three tribes in 'Scopulini lineage', with Cyllopodini in turn being sister to Scopulini+Sterrhini clade. Rhodostrophiini was placed as sister to Scopulini+Sterrhini clade in article **II** and as Cyllopodini had not been sampled in this study, there were no discrepancies regarding the phylogenetic relationships within 'Scopulini lineage' between article **II** and Sihvonen & Kaila (2004). These findings are in conflict with Holloway (1997) and Abraham *et al.* (2001), who had provisionally suggested that Sterrhini was sister to other tribes

in ‘Scopulini lineage’, with Scopulini in turn appearing as sister to Cyllopodini+ Rhodostrophiini clade. However, it must be pointed out that bootstrap support for the ‘Scopulini lineage’ was quite low, only 56, in ML analysis, though Bayesian posterior probability was almost maximum (article **II**, Fig. 1). Moreover, careful examination of the data matrix from the article by Sihvonen & Kaila (2004) revealed that there is also a lack of strictly synapomorphic morphological characters unique to the ‘Scopulini lineage’. Only the placement of sensilla on the ventral surface of male flagellomeres seems to support the monophyly of the ‘Scopulini lineage’, as they appear as arranged regularly in this group but are missing or arranged randomly in the ‘Timandrini lineage’. Therefore I still see a slight possibility that the monophyly and tribal composition of ‘Scopulini lineage’ may appear questionable when further molecular phylogenetic analysis with more comprehensive taxon sampling is performed.

The tribal groupings within the ‘Timandrini lineage’ were also highly concordant between article **II** and Sihvonen & Kaila (2004). Cosymbiini was revealed as sister to Timandrini+Rhodometrini clade by Sihvonen & Kaila (2004). Cosymbiini was also found to be sister to other three tribes in article **II**, with Timandrini in turn being sister to Rhodometrini+Lythriini clade (article **II**, Fig. 1). As Sihvonen & Kaila (2004) did not include Lythriini into their morpho-cladistic analysis, there is no conflict between their paper and article **II**. Statistical support to the ‘Timandrini lineage’ and its subclades was high in both Bayesian and ML analysis (article **II**, Fig. 1). As Lythriini was placed deep inside the ‘Timandrini lineage’, we conclude that this tribe unequivocally belongs to Sterrhinae, as proposed by Pierce (1914) nearly 100 years ago, and not to Larentiinae as suggested by all subsequent authors including Sihvonen & Kaila (2004) and Hausmann (2004).

This conflict between the traditional classification and molecular data needed further clarification. For this purpose, several critical morphological characters of Lythriini, Sterrhinae and Larentiinae were examined. These results also supported assigning Lythriini to Sterrhinae instead of Larentiinae. The most important character used to distinguish between Sterrhinae and Larentiinae is the length of the fusion of subcostal vein and costal margin of the hindwing discal cell. It is long in Larentiinae and most often short, sometimes reduced to connection in only one point in Sterrhinae (Meyrick, 1892; Prout, 1912–16; Common, 1990; Hausmann, 2001; Sihvonen & Kaila, 2004). The fusion between the subcostal vein and costal margin of the hindwing discal cell is long in Lythriini and this tribe has therefore been assigned with Larentiinae since Meyrick (1892). However, the detailed revision of literature reveals that this type of fusion has been recorded in several sterrhines as well: Prout (1929–35), Sihvonen & Kaila (2004) and Hausmann (2004) have shown it to be characteristic to Rhodometrini; Prout (1929–35; 1920–41) described it in several African and Indoaustralian *Sterrha* Hübner, 1825 (=*Idaea* Treitschke, 1825) species etc. Therefore the hindwing venation of Lythriini can not be interpreted as linking this tribe with Larentiinae instead of Sterrhinae, as it may indicate close affinities with either of those two subfamilies.

Another important character that usually allows one to easily distinguish between Larentiinae and Sterrhinae is the presence or absence of the first discocellular vein (DC_1) on the forewing. In Sterrhinae, veins R_1-R_5 branch from the costal margin of the discal cell before its apex and are therefore separated from vein M_1. The distalmost slice of the costal margin of the discal cell that is positioned between the origin of R_1-R_5 and origin of M_1, has been interpreted as the first discocellular vein (DC_1) (Forbes, 1948). This vein is most often absent in Larentiinae, as veins R_2-R_5 or R_3-R_5 are stalked or connate with M_1. As DC_1 is present in Lythriini, it could be interpreted as supporting the close relationships between Lythriini and Sterrhinae. Unfortunately, DC_1 is also present in the pantropic larentiine genus *Eois* Hübner, 1818 (Prout, 1929–35), thus invalidating the use of the presence or absence of this vein as linking Lythriini with either Sterrhinae or Larentiinae.

In addition to pointing out that wing venation alone does not allow to classify genera as unequivocally belonging to Larentiinae or Sterrhinae, we found that there are at least three important synapomorphies that link Lythriini with Sterrhinae instead of Larentiinae. First, transverse lines on the forewings are singular in Sterrhinae (Sihvonen & Kaila, 2004) and Lythriini, while multiple transverse lines grouped into bands are common in Larentiinae (Holloway, 1997). Second, a short oblique line from exactly the forewing apex to the submarginal wavy line ('streak' sensu Sihvonen & Kaila, 2004) is found in many larentiines, but is lacking in Sterrhinae and Lythriini. Third, the shape of ansa in tympanal structures has been diagnosed as apically dilated in Larentiinae and Sterrhinae (Holloway, 1997). There seems, however, to exist a qualitative difference: the ansa is distinctly T- or axe-shaped in Larentiinae and less dilated, triangular both in Sterrhinae and Lythriini.

In addition to the characters discussed above, linking Lythriini and Sterrhinae in general, we also found four morphological and ecological characters that support the placement of Lythriini as sister to Rhodometrinae in the 'Timandrini lineage'. Of those, feeding on Polygonaceae in the larval stage is shared by Timandrini, Rhodometrini and Lythriini. There are only few oligophagous lepidopterans associated with Polygonaceae (Seppänen, 1970) and this trait may thus be a putative synapomorphy for these groups. Forewing post-medial fascia scaled reddish is a condition shared by Lythriini and Rhodometrini, but occurs also in some taxa belonging to Timandrini and Rhodostrophiini. However, in all other above mentioned taxa there is also at least one reddish fascia on the hindwing, but both Lythriini and Rhodometrini (excl. *Ochodontia* Lederer, 1853) have no reddish fasciae in their hindwings. Lythriini and Rhodometrini (excl. *Ochodontia*) also share the presence of small, membranous socii at the base of the uncus. Though socii can be found also in Timandrini and Scopulini, they are differently shaped in these tribes. The presence of dark discal spots on all wings has been listed as a sterrhine synapomorphy by Covell (1983) and the pale centering of those spots has been subsequently emphasized as characteristic to the subfamily by Holloway

(1997). Missing hindwing discal spots is therefore another characteristic unique to the Lythriini+Rhodometrini assemblage.

The results of the morphological examination therefore support placing Lythriini to Sterrhinae as sister group to Rhodometrini, as was first suggested by Pierce (1914) nearly 100 years ago. However, though the genus-level relationships within Sterrhinae are well supported by both morphological and molecular data, an unexpected grouping was found regarding the intrageneric phylogenetic relationships within *Lythria*. Specifically, *L. cruentaria* was found to be sister to *L. sanguinaria*+*L. purpuraria* clade (article **II**, Fig. 1), but both external and genital morphology indicated that *L. sanguinaria* and *L. cruentaria* are sister taxa with *L. purpuraria* being more distant (Viidalepp, in press). As *L. sanguinaria*+*L. purpuraria* clade was located on a tip of a very short branch with relatively low statistical support on the phylogenetic tree (article **II**, Fig. 2), we concluded that relationships between *Lythria* species were not unequivocally resolved. This conclusion was later confirmed in article **III**, which addressed the intrageneric phylogeny of *Lythria* and therefore was built up on a different taxon sampling strategy.

4.3. The phylogeny of the genus *Lythria* and elaborated genital morphology of *L. venustata*

Sequencing mitochondrial and nuclear gene fragments was completely successful for all eight taxa included in article **III**. Alignment of the partial sequences of *EF-1α* and *wgl* was straightforward, no indels were recovered and the lengths of the successfully sequenced fragments were 883 bp and 383 bp, respectively. The length of the full sequence of the *COI* differed between the two *Timandra* species and the rest of the taxa as described in the previous section, being 1533 and 1536 bp, respectively. The total length of the combined molecular data matrix was 2810 bp.

All methods of phylogenetic analysis yielded an identical well-resolved tree, which exhibited maximal or near-maximal indices of support for all nodes (article **III**, Fig. 3). *Rhodometra sacraria* (Linnaeus, 1767) was found to be sister to the genus *Lythria*, with the eastern Palaearctic *L. venustata* in turn appearing as sister to the remaining four *Lythria* species. Two groupings of closely related taxa were found: *L. cruentaria* appeared as sister to *L. sanguinaria*, whereas *L. purpuraria* was placed as sister to *L. plumularia* (article **III**, Fig. 3). This topology supports the results of article **II**, which resolved Rhodometrini as sister to Lythriini. An additional morphological examination was performed and a few more morphological conditions that link Lythriini with 'Timandrini lineage' in general and support its position as sister to Rhodometrini in particular were found in addition to those reported in article **II**. First, Lythriini have no sensilla on the ventral surface of the male flagellomere, which is a condition characteristic to the 'Timandrini lineage' (Sihvonen & Kaila, 2004). Second, both Lythriini and Rhodometrini have naked uncus and

the arms of transtilla do not meet dorsally in neither of these tribes. These two synapomorphies were reported as characteristic to Rhodometrini by Sihvonen & Kaila (2004). Third, the following common conditions may also be extrapolated as supporting the close relationships between Lythriini and Rhodometrini: large vinculum (resembling that of Scopulini; see Sihvonen & Kaila, 2004), weak tegumen, weak juxta, absence of saccus and presence of a pair of pad-like socii on the base of uncus in *Casilda* and *Lythria*.

The examination of the male genitalia of all *Lythria* species supported the intrageneric phylogeny revealed on the basis of molecular data. *L. purpuraria* and *L. plumularia* which form one clade of sister taxa share the presence of two cornuti on the vesica, the presence of a pair of long posterio-lateral extensions on the tegumen and a short, sack-like valvula attached to the roughly triangular valva (article **III**, Figs. 4–5). The valvula is approximately as long as it is broad in these two species. The members of the second clade of sister taxa, *L. cruentaria* and *L. sanguinaria*, share short, roughly rectangular valvae with long membranous valvulae, short posterio-lateral extensions on the tegumen and the presence of one cornutus on vesica (article **III**, Figs. 6–7). The valvula is approximately four times longer than it is broad in these taxa, and it is clearly more slender in *L. sanguinaria* than in *L. cruentaria*. *L. venustata*, which was positioned as sister to the other *Lythria* species, has clearly different genitalia, as its valvae are distally bipartite, the valvulae are absent and the remnants of the socii are missing. The posterio-lateral extensions of the tegumen, which are characteristic to *Lythria*, are visible, but much shorter in *L. venustata* (article **III**, Fig. 8). The shape of the aedeagus of *L. venustata* resembles the slim aedeagi of the *L. cruentaria*+*L. sanguinaria* clade and it also has only one cornutus on the vesica. The rounded shape and massive sclerotization of the vinculum gives the genital armature of *L. venustata* a distinctive appearance. In contrast to all other *Lythria* species, *L. venustata* has a well developed juxta.

The results of molecular phylogenetic analysis and morphological examination in article **III** are therefore in accordance to each other. These results, however reject the earlier hypotheses about the close relationships between *L. venustata* and *L. plumularia* suggested by Staudinger (1882), Prout (1912–16) and Vasilenko (2009). The similar ochreous-yellow ground colouration of these two taxa in contrast to the greenish yellow ground colouration of the remaining three species apparently is not a synapomorphy, but is to be regarded either as plesiomorphic or homoplasic condition. Similarly, awkward intrageneric relationships found in article **II** (see above) could be rejected.

Our examination revealed that the recent description of the male genitalia of *L. venustata* (Vasilenko, 2009) is partially misleading. He described the male genitalia of *L. venustata* as having long finger-like socii on the posterior edge of the tegumen. These 'socii' are actually the projections of the sacculi. This misinterpretation apparently has happened because Vasilenko (2009) did not spread the tough and strongly sclerotized valvae. Furthermore, in Vasilenko's (2009) interpretation *L. venustata* also lacks an uncus and the most distal part of the genitalic capsule is instead the anellus. As this structure apparently is

positioned distal to vinculum and tegumen instead of starting from fultura inferior (article **III**, Fig. 8A), we interpret it as a weakly sclerotized uncus.

Considering the phylogenetic position of *L. venustata* and the extent of its morphological differences with other *Lythria* species, it may be appropriate to move *L. venustata* into a separate genus, as was already suggested by Vasilenko (2009). However, as female *L. venustata* and its genital morphology is yet to be described, we preferred not to take this step, but to highlight this as a point for consideration in the future studies.

4.4. The phylogeny of the subfamily Sterrhinae

Contrary to the analyses the articles **I-III** are based on, the sequencing was less successful in the study presented in this section. COI was the only gene that was at least partially sequenced for all 45 taxa included into the analysis (Table 3). The number of taxa with respective sequences of gene fragments missing are the following: seven for *ND1*, eight for *EF-1α*, fifteen for *wgl*, four for *28S D1* and ten for *28S D2* (Table 3). *Problepsis ocellata* (Frivaldszky, 1845) was the only species that was represented only by a single gene fragment (full sequence of *COI*) in the combined data matrix; the number of successfully sequenced gene fragments was at least three for all other species included into the analysis (Table 3). Alignment of the partial sequences of *ND1* and *EF-1α* was straightforward, no indels were recovered and the lengths of the successfully sequenced fragments were 918 bp and 932 bp, respectively. The length of the full sequence of the *COI* differed between the two *Timandra* species and the rest of the taxa as described in chapter 4.2, being 1533 and 1536 bp, respectively. Similarly, the length of the partial sequence of the wgl differed between the two larentiine outgroup taxa and the studied sterrhines as described in chapter 4.2, being 400 and 394 bp, respectively. The length of the indel-free concatenated *28S* data matrix was 672 bp. Details of the sequencing and aligning of this gene region and removal of the indels are described in Material and Methods. The total length of the combined data matrix was 4466 bp.

Bayesian analysis resulted in a well-resolved phylogenetic tree with reasonable statistical support to most of the nodes (Fig. 1). The ML analysis, however, was less successful, as several nodes were either unresolved or poorly supported (Fig. 2). The main topologies of the Bayesian and ML trees, however, are similar and therefore I believe that several generalizations are possible. The discordancies between Bayesian and ML analysis will be discussed in detail below.

Both methods of phylogenetic analysis recovered Sterrhinae as a monophyletic entity split into two lineages (Figs. 1–2). The tribal composition of these lineages is consistent with Holloway (1997), Sihvonen and Kaila (2004) and article **II**. Specifically, the 'Scopulini lineage' comprises tribes Rhodostrophiini, Scopulini and Sterrhini and the 'Timandrini lineage' consists of tribes Cosymbiini, Timandrini, Rhodometrini and Lythriini, respectively (Figs.

1–2). The phylogenetic relationships within these lineages were concordant with Sihvonen & Kaila (2004) and article **II**, as Rhodostrophiini appeared as sister to Scopulini+Sterrhini clade in 'Scopulini lineage' and Cosymbiini was resolved as sister to the rest of 'Timandrini lineage', with Timandrini in turn being sister to Rhodometrini+Lythriini assemblage (Figs. 1–2). The systematic position of Cyllopodini, which was placed at the different position in the 'Scopulini lineage' by Sihvonen & Kaila (2004) and Holloway (1997) unfortunately cannot be verified in this study due to the lack of material. The intratribal phylogenetic relationships of the other tribes, however, will be discussed separately in the following sections.

Rhodostrophiini, comprising 22 genera and more than 200 species worldwide together with genera of uncertain association (Scoble, 1999; Sihvonen & Kaila, 2004), was represented in current analysis by five species (Table 1). In addition to the two species from the type genus, *Rhodostrophia*, I also sampled two *Tricentra* Warren, 1900 species and the only species from the monotypic *Pylargosceles*. Both Bayesian and ML analysis have resolved Rhodostrophiini identically [i. e. *Tricentra* as well supported sister to similarly well supported *Rhodostrophia*+*Pylargosceles* clade (Figs. 1–2)]. As Neotropic *Tricentra* and primarily Palaearctic *Rhodostrophia* were resolved as a well-supported monophyletic clade, I find it likely that even with increased number of genera and species Rhodostrophiini will still be resolved as monophyletic or 'natural' group. Nevertheless, it is interesting to note that the genus *Rhodostrophia* itself has been found paraphyletic, as *R. vibicaria* (Clerck, 1759) has been grouped together with *Pylargosceles steganioides* (Butler, 1878), whereas *R. calabra* (Petagna, 1787) has been placed as sister to them. In case future studies reveal there is true paraphyly, reconsideration of the generic placement of *P. steganioides* will be required. However, the current phylogenetic placement of *Pylargosceles* may also have been caused by insufficient taxon sampling, as genera morphologically closest to *Pylargosceles*, i. e. *Symmacra* Warren, 1896, *Metallaxis* Prout, 1932 etc. (Prout, 1920–41) were not sampled in the current study.

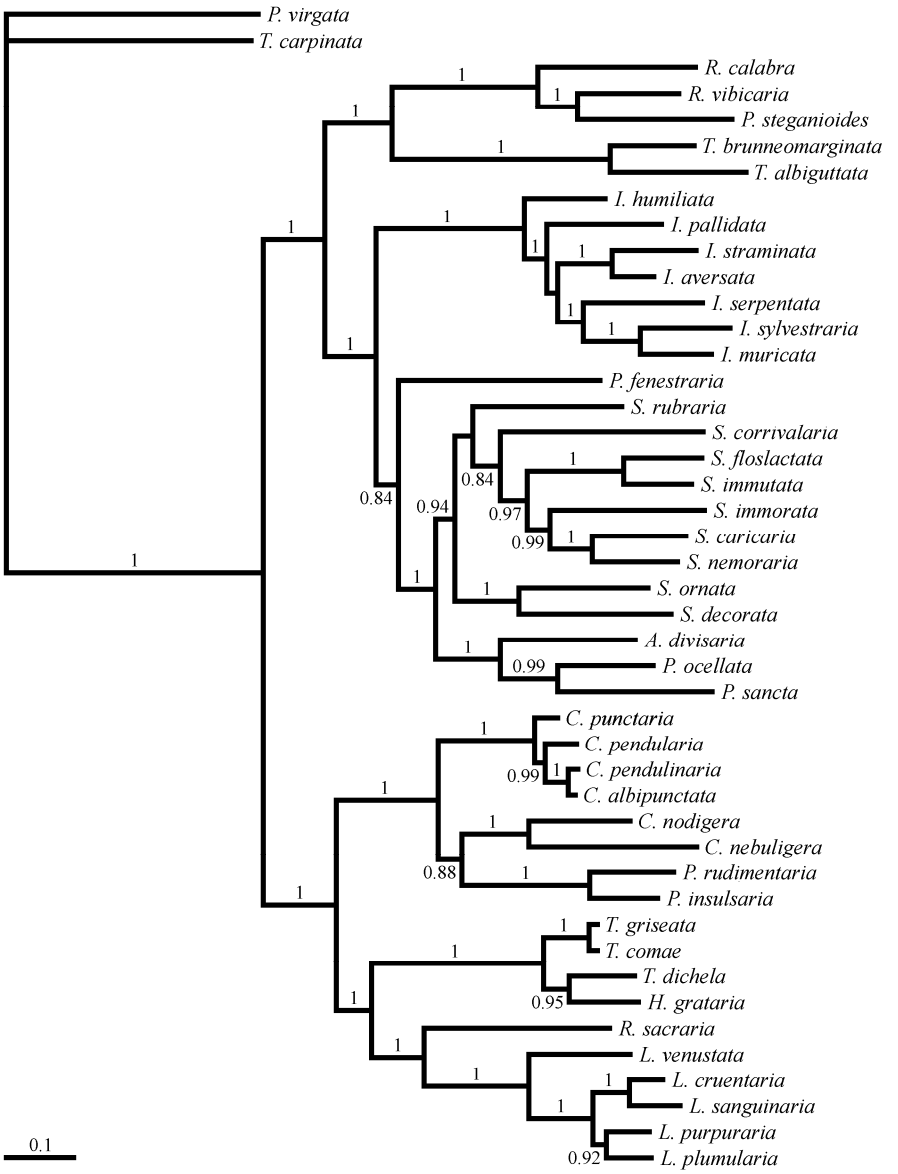

Fig. 1. Bayesian phylogenetic tree (five partitions, GTR+I+Γ model for each partition) of Sterrhinae, based on a 4466-bp combined sequence of *COI*, *ND1*, *EF-1α*, *wgl* and *28S*. Bayesian posterior probabilities are given above or below the branches. Posterior probabilities inferior to 0.80 are not presented.

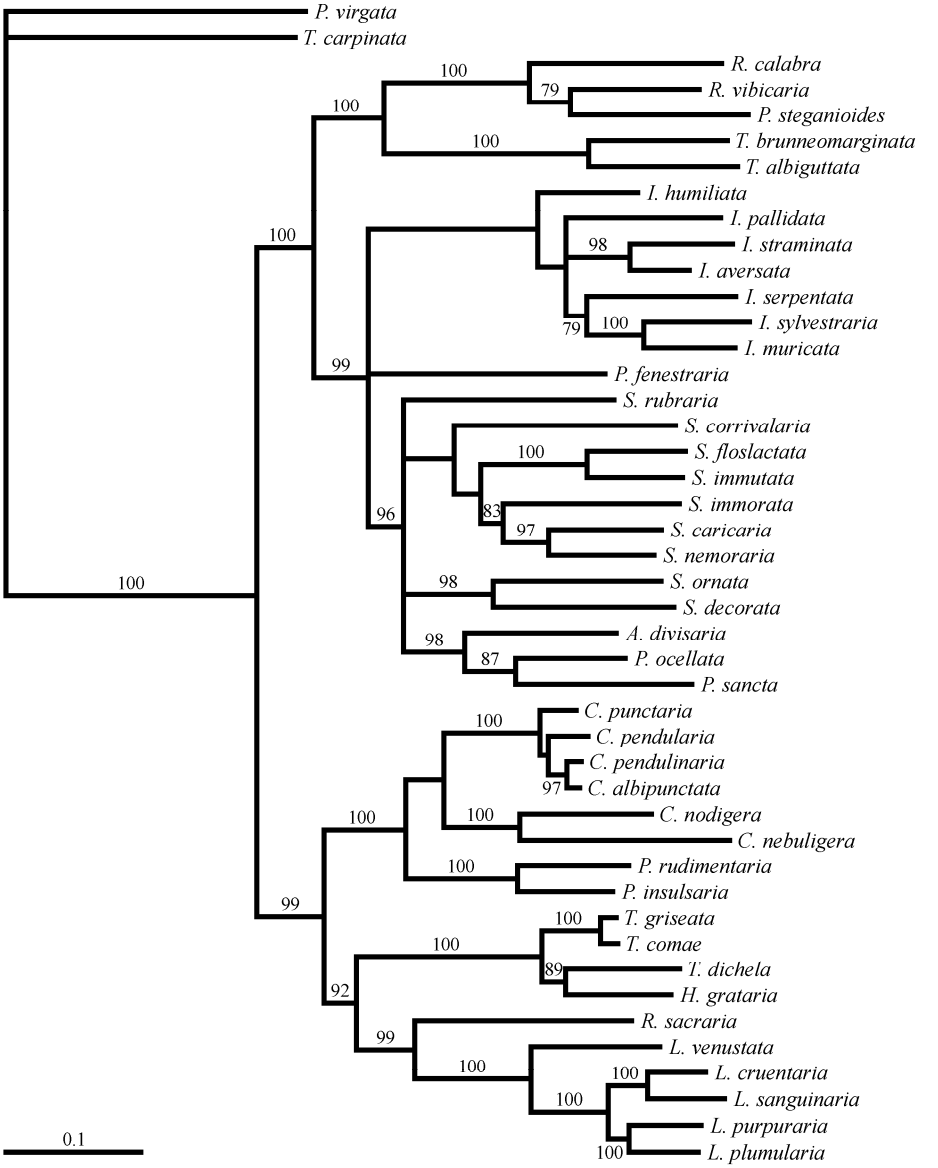

Fig. 2. Maximum likelihood phylogenetic tree (five partitions, GTR+Γ model for each partition) of Sterrhinae, based on a 4466-bp combined sequence of *COI*, *ND1*, *EF-1α*, *wgl* and *28S*. Bootstrap supports are given above or below the branches. Bootstrap supports inferior to 70 are not presented, branches with supports lower than 50 are collapsed.

Sterrhini is the second largest tribe in Sterrhinae, comprising 25 genera and more than 850 species worldwide together with genera of uncertain association (Scoble, 1999; Sihvonen & Kaila, 2004). This group was quite poorly represented in the current analysis, as only seven European species belonging to the most diverse genus *Idaea* were studied (Table 1). As the Sterrhini sample was so limited, it is not surprising that this tribe was resolved as very well supported monophyletic entity by both methods in phylogenetic analysis (Figs. 1–2). The intrageneric phylogeny was also similar by both Bayesian and ML approach, though the latter did not resolve one node (Figs. 1–2). However, it must be noted that the intrageneric phylogenetic relationships are in conflict with groupings suggested by Sterneck (1941) and Hausmann (2004) mainly on the basis of genital morphology. *I. humiliata* (Hufnagel, 1767), which was the only representative of *inquinata*-group in my analysis, was placed as sister to the rest of sampled *Idaea* species. The *subsericeata*-group, represented by *I. pallidata* (Denis & Schiffermüller, 1775) and *I. sylvestraria* (Hübner, 1799), was paraphyletic as well as *aureolaria*-group, represented by *I. serpentata* (Hufnagel, 1767) and *I. muricata* (Hufnagel, 1767). Only *aversata*-group, represented by *I. aversata* (Linnaeus, 1758) and *I. straminata* (Borkhausen, 1794), appeared monophyletic (Figs. 1–2). These results may indicate that these subgroupings of *Idaea*, being established by Sterneck (1941) according to the length of aedeagus and number of cornuti on vesica are not always correct, as noted by Sterneck himself and Hausmann (2004). However, it is interesting to note that from the three species groups noted above only the *aversata*-group has been mentioned as 'natural' by Hausmann (2004) whereas the *aureolaria*-group has been noted to be heterogeneous and the description of morphological variation in *subsericeata*-group also indicates significant diversity. Therefore it is possible that further molecular systematic treatment with more comprehensive taxon sampling will subdivide the genus *Idaea* into species-groups that differ from those currently considered valid by Hausmann (2004). Further treatment with extended data matrix on genus level is absolutely necessary to test the monophyly of Sterrhini (see also Sihvonen & Kaila, 2004).

Scopulini is by far the largest tribe of Sterrhinae, comprising about 1000 species worldwide together with genera of uncertain association (Scoble, 1999; Sihvonen & Kaila, 2004). The number of genera, however, is a point for discussion. The traditional treatment (Prout, 1912–16, 1929–35, 1935–38, 1920–41; Holloway, 1997; Scoble, 1999; Sihvonen & Kaila, 2004) divided Scopulini into as many as 31 genera when taxa tentatively associated with this tribe were also considered. Contrasting to this point of view, Sihvonen (2005) conducted a major morpho-cladistic examination of Scopulini and his analysis showed the mega-diverse genus *Scopula* as paraphyletic, comprising many taxa earlier treated as belonging to smaller separate genera. For example, *Aletis*, *Cartaletis* and *Antitrygodes* Warren, 1895, whose external morphology does not resemble the usually inconspicuous look of most of *Scopula* species, were resolved as clades between the several species of *Scopula* and other smaller genera (e. g. *Glossotrophia* Prout, 1913, *Stigma* Alphéraky, 1883, *Scopuloides*

Hausmann, 1993) traditionally considered as more closely related to it (Sihvonen, 2005). To avoid paraphyly in *Scopula* on the one hand and not to create a multitude of new genera (which would have been necessary, if all older genera retained their status) on the other, Sihvonen (2005) synonymized several traditionally recognised genera under the widened concept of *Scopula*. The number of genera in Scopulini was thus reduced to seven, but it must be kept in mind that the six genera that were only tentatively assigned to Scopulini by Sihvonen & Kaila (2004) were not studied in this analysis. In any case, the total number of Scopulini genera is less than 15 considering the results of Sihvonen & Kaila (2004) and Sihvonen (2005). Hausmann (2004) refused to adopt the widened concept of *Scopula* and kept European genera (e. g. *Oar* Prout, 1913, *Cinglis*, *Holarctias* and *Glossotrophia*) treated as synonyms to it by Sihvonen (2005) still as separate entities according to the traditional classification (Prout, 1912–16; Sterneck, 1941; Holloway, 1997). However, he noted that the widened concept of *Scopula* may be justified if further examinations of additional datasets together with inclusion of additional species worldwide support the findings of Sihvonen (2005). In the present thesis I prefer to follow the treatment of Hausmann (2004), as this way it is more convenient to link my results with the traditional system of Scopulini and place them into a broader context. Whether the revolutionary rearrangements by Sihvonen (2005) are correct, is to be investigated in further molecular phylogenetic studies.

In total, 13 Scopulini species belonging to four genera were included in the analysis (Table 1). Of those, *Pseudasellodes* has only tentatively been assigned to Scopulini earlier (Sihvonen & Kaila, 2004) but the remaining three genera, *Scopula*, *Antitrygodes* and *Problepsis*, have been found to fit within this tribe unambiguously (Holloway, 1997; Hausmann, 2004; Sihvonen, 2005). The Bayesian analysis resulted in placing *Pseudasellodes* as sister to the rest of Scopulini, with *Scopula* in turn being sister to *Antitrygodes*+*Problepsis* clade (Fig. 1). These results point that it may be appropriate to consider *Pseudasellodes* as unequivocally belonging to Scopulini. As was the case with *Idaea* (see above), the groupings within *Scopula* were not fully concordant with those expected on the basis of morphological examination. On the one hand, *S. ornata* (Scopoli, 1763) and *S. decorata* (Denis & Schiffermüller, 1775), belonging to supposedly monophyletic *ornata*-group in subgenus *Scopula* Schrank, 1802 (Hausmann, 2004) were indeed resolved as well-supported clade sister to the rest of *Scopula* (Fig. 1). On the other hand, the heterogeneous *immorata*-group also from subgenus *Scopula* (Hausmann, 2004), which was represented by *S. corrivalaria* (Kretschmar, 1862), *S. immorata* (Linnaeus, 1758), *S. caricaria* (Reutti, 1853) and *S. nemoraria* (Hübner, 1799) in this analysis was paraphyletic, as a clade comprising *S. floslactata* (Haworth, 1809) and *S. immutata* (Linnaeus, 1758) (belonging to *ternata*-group and *incanata*-group from subgenus *Calothysanis* Hübner, 1823 sensu Hausmann, 2004, respectively) was placed inside the *immorata*-group (Fig. 1). The Australian *S. rubraria* (Doubleday, 1843), which contrasting to European *Scopula* species has finely dentate antennae with exceptionally dense hairbrushes, was grouped within the genus

Scopula as sister to the rest of the sampled species except *ornata*-group (Fig. 1). Close relationships between *Antitrygodes* and *Problepsis* (Fig. 1) were expected already by Prout (1929–35, 1920–14), as he found these genera sharing several important characters. This finding, however, is in conflict with the modern revision by Sihvonen (2005), who treated *Antitrygodes* as synonym of *Scopula*, but *Problepsis* as belonging to its sister clade. My current knowledge does not allow a decision as to which treatment is more appropriate, reinstating *Antitrygodes* as valid genus or widening the concept of *Scopula* so that it also includes *Problepsis* and possibly *Lipomelia* (see Sihvonen, 2005). More comprehensive sampling of Scopulini genera is required to solve this question.

The ML analysis, however, was less successful considering the phylogenetic relationships within Scopulini, as the whole Sterrhini+Scopulini+*Pseudasellodes* complex was not fully resolved (Fig. 2). According to this analysis, *Pseudasellodes* cannot be linked to neither Sterrhini nor Scopulini with confidence, thus pointing that the treatment by Sihvonen & Kaila (2004), who only tentatively assigned this genus with Scopulini, may be correct. It must be kept in mind that *Asellodes* (=*Pseudasellodes*) was treated as a 'mystic' separate or intermediate group already by Prout (1934–39, 1935–38) and its position away from both Sterrhini and Scopulini may thus also be justified. I think that expanding the data matrix by including at least one additional species of *Pseudasellodes* may be sufficient to solve ambiguities regarding to the phylogenetic position of this genus, as both my own experience and literature data (Hedtke *et al.*, 2006) suggest that breaking down the long branches by adding taxa closely related to those located in tip of the long branch significantly helps to increase the accuracy and reliability of the phylogenetic analysis. Phylogenetic relationships within the *Scopula+Antitrygodes+Problepsis* assemblage were also not fully resolved in ML analysis, as a polytomy was discovered in the respective node (Fig. 2). The phylogenetic relationships within the European *Scopula* species except *ornata*-group, however, were resolved identically to the Bayesian approach, though with low support to some nodes (Figs. 1–2). In conclusion, the conflict between the results of Bayesian and ML analysis suggests that more comprehensive taxon sampling and perhaps expanding the list of genetic markers (which is advisable practice to overcome the problems with poorly resolved phylogenies – see e. g. Rokas *et al.*, 2003; Mallarino *et al.*, 2005; Wahlberg & Wheat, 2008) is required to solve the remaining questions in the genus level systematics of Scopulini.

The tribe Cosymbiini, which is sister to all other tribes in 'Timandrini lineage', comprises 16 genera and more than 500 species worldwide, including taxa of uncertain association (Scoble, 1999; Sihvonen & Kaila, 2004). This tribe was included into my analysis as eight species from genera *Cyclophora* and *Pleuroprucha* Möschler, 1890 (Table 1). Cosymbiini were resolved as well-supported monophyletic entity by both methods of phylogenetic analysis (Figs. 1–2). Phylogenetic relationships within the tribe, however, were resolved differently. ML analysis showed *Pleuroprucha* and *Cyclophora* as distinct clades, though bootstrap support to *Cyclophora* was low (Fig. 2). Neotropic

C. nodigera (Butler, 1881) and *C. nebuligera* (Butler, 1881) appeared as sisters to the clade comprising three species from Palaearctic region and Nearctic *C. pendulinaria* (Guenée, 1858). This kind of intrageneric divergence was quite expected, as according to the traditional classification (Prout, 1935–38) *C. nebuligera* and *C. nodigera* had for long been treated as belonging to genus *Anisodes*, which only recently (Holloway, 1997) was synonymized with *Cyclophora*. In contrast to the results from ML analysis, *Cyclophora* was resolved as paraphyletic in Bayesian phylogenetic inference, though the posterior probability value was not high (0,86). *C. nodigera* and *C. nebuligera* were grouped together with the two *Pleuroprucha* species, forming clade sister to the Palaearctic and Nearctic *Cyclophora* species (Fig. 1). This result together with the low support to *Cyclophora* in ML analysis (Fig. 2) indicates that Holloway's treatment to subordinate all species from old *Anisodes* that did not fit with *Perixera*, *Mesotropha* nor *Zeugma* Walker, 1863 (=*Dizuga* Warren, 1896) under *Cyclophora* requires further examination. More comprehensive taxon sampling in Cosymbiini in general and in *Cyclophora* and related genera in particular is essential before any conclusive results can be drawn regarding to the monophyly of Holloway's *Cyclophora* and its phylogenetic relationships with the sister genera.

Timandrini is one of the four small tribes in Sterrhinae, as it comprises only 4 genera and 45 species worldwide (Scoble, 1999; Sihvonen & Kaila, 2004). In my analysis this tribe was represented by three species from its type genus, *Timandra*, and the only species from the monotypic *Haematopis* Hübner, 1823 (Table 1). Both ML and Bayesian analysis resolved Timandrini as a well supported monophyletic clade (Figs. 1–2). Interestingly, both methods of phylogenetic analysis resolved *Timandra* as paraphyletic, placing *T. dichela* (Prout, 1935) as sister to *H. grataria* and not into the same clade with *T. griseata* and *T. comae* (Figs. 1–2). Considering the external and genitalic morphology of *H. grataria* (Fabricius, 1798) and *T. dichela* this result is likely to be an artefact of the analysis, probably caused by insufficient amount of successfully sampled markers in *T. dichela* (Table 3). Further examination is therefore needed and expanded taxon sampling on the one hand together with more complete data matrix on the other should solve the ambiguities in my current results.

Rhodometrini and Lythriini are the two smallest tribes in Sterrhinae, comprising three genera with 17 species and one genus with five species, respectively (Sihvonen & Kaila, 2004; article **III**). In article **III** we used *R. sacraria* from Rhodometrini and all five *Lythria* species from Lythriini and unfortunately I could not further expand the list of sampled taxa. Therefore, no new information was obtained in the current analysis compared to the results of article **III**. Sampling more species from *Rhodometra*, as well as at least a few species from its sister genus, *Casilda*, is essential to improve the molecular phylogeny of Rhodometrini. This tribe currently also comprises the enigmatic *Ochodontia* (Viidalepp, 1996; Hausmann, 2004), which has earlier been subordinated to Larentiinae (e. g. Meyrick, 1892; Prout, 1912–16) but also

shares several morphological characters with Timandrini (Sihvonen & Kaila, 2004). Whether the current systematic position of *Ochodontia* is correct or not, should be examined in a separate study.

In conclusion, I consider that material presented in this section further proves that tribal phylogeny of Sterrhinae, first suggested by Sihvonen & Kaila (2004) and subsequently confirmed in article **II**, is probably correct. Phylogenetic relationships within the tribes, however, still need thorough molecular systematic treatment and expanded taxon sampling at the genus level is the key element to obtain additional valuable information of phylogeny of Sterrhinae. Another potentially useful source of additional information, simultaneous analysis of morphological and molecular data, should also be considered in further systematic research of Sterrhinae. This kind of treatment has proven useful in phylogenetic studies of Rhopalocera (Wahlberg *et al.*, 2005) and occasionally it has been used in research of other Geometridae (Viidalepp *et al.*, 2007; Wahlberg *et al.*, 2010), but no combined analyses of Sterrhinae are hitherto available.

SUMMARY

This thesis is focused on solving selected systematic problems in subfamily Sterrhinae (Lepidoptera: Geometridae), which comprises more than a hundred genera and over 2800 described species worldwide. Despite numerous efforts to unravel the taxonomy of Geometridae in general and Sterrhinae in particular, it still remains largely unresolved. Whereas studies based on 'traditional' morphological methods have significantly contributed towards that goal, many taxonomic issues clearly require more advanced approaches such as those provided by the molecular phylogenetic analysis. In total, four different taxonomic problems were studied using molecular phylogenetic treatment and the summary of the results is presented in the next four sections.

European 'blood-vein' loopers from genus *Timandra* were recently shown to be two distinct, but morphologically very similar species. This point of view, however, was quite sceptically received in the European lepidopterist community, as differences between the respective species, *Timandra griseata* and *T. comae*, were sometimes found to be too obscure to justify the formal separation of the taxa. Molecular phylogenetic analysis in article **I** divided *Timandra* individuals into two well-supported clades according to their morphological identity. Therefore I find that *T. griseata* and *T. comae* can be regarded as two distinct species. Few specimens in the 'wrong' clade are most likely of hybrid origin, but frequent hybridisation between *T. griseata* and *T. comae* is unlikely due to their different phenology and habitat preference.

Palaearctic tribe Lythriini is a small group of diurnal geometrid moths which comprises only a single genus *Lythria* with five species. This group is morphologically peculiar, as it shares several characters with subfamilies Larentiinae and Sterrhinae, thus obscuring the boundaries between them. Historically, *Lythria* has almost without exceptions been grouped within Larentiinae, and only recently few authors have again pointed out its morphological similarities with some genera from Sterrhinae. Molecular phylogenetic analysis in article **II** demonstrated that Lythriini undoubtedly belong to Sterrhinae, being a sister to Rhodometrini. This position was also supported by several morphological conditions. Two of the most important characters usually used to discriminate between Sterrhinae and Larentiinae, details of the venation of the hindwing and forewing, were shown to be plesiomorphic and thus unsuitable for further use as arguments to unite lower-rank taxa into either of those diverse subfamilies. Analysis in article **II** also supported some recent morphology-based expectations about the phylogeny of Sterrhinae. Specifically, the studied tribes were split into two lineages as follows: Rhodometrini, Sterrhini and Scopulini form the 'Scopulini lineage', whereas Cosymbiini, Timandrini, Rhodometrini and Lythriini constitute the 'Timandrini lineage'.

Lythria venustata is an extremely rare Eastern Palaearctic species, which hitherto has been recorded only from Kazakhstan. Its genital morphology was poorly known and as no fresh material was available until the most recent time, even theoretically there was no possibility to recover the systematic position of

this species by using molecular treatment. In article **III** these shortcomings were treated, as full molecular phylogeny of genus *Lythria* was constructed and morphology of the male genitalia of all *Lythria* species was examined. *L. venustata* was found to be a sister to four remaining *Lythria* species, which were split into two groupings: *L. purpuraria*+*L. plumularia* clade and *L. cruentaria*+*L. sanguinaria* clade. This phylogeny was also supported by genital morphology. Moreover, few aspects of the genitalia of *L. venustata* appeared as intermediate between other *Lythria* species and *Rhodometra*, a type genus of Rhodometrini. Since Rhodometrini has been resolved as sister to Lythriini in article **II**, the similarities between *Rhodometra* and *L. venustata* may be interpreted as a further support to the position of the latter as sister to other *Lythria* species.

In addition to article **II** where some of the taxonomic problems of Sterrhinae as a whole were addressed, this thesis also presents an attempt to resolve the molecular phylogeny of Sterrhinae on a broader scale by including an expanded set of sterrhine taxa to the molecular phylogenetic analysis. The results clearly confirm an earlier hypothesis of two lineages in Sterrhinae by joining Rhodostrophiini, Sterrhini and Scopulini into the 'Scopulini lineage' and Cosymbiini, Timandrini, Rhodometrini and Lythriini into the 'Timandrini lineage'. Moreover, the tribal groupings within these lineages were also concordant with earlier findings: Rhodostrophiini was resolved as sister to Scopulini+Sterrhini assemblage in 'Scopulini lineage' and Cosymbiini appeared to be sister to the remaining three tribes in 'Timandrini lineage'. Of those three, Timandrini was found to be sister to Rhodometrini+Lythriini clade. Some discordancies pointing to the need of further research were, however, also discovered.

SUMMARY IN ESTONIAN

Süstemaatika-alaseid uurimusi alamsugukonnast kuluvaksiklased (Lepidoptera: Geometridae: Sterrhinae)

Käesolevas väitekirjas keskenduti valitud süstemaatika-alaste probleemide lahendamisele kuluvaksiklaste (Sterrhinae) alamsugukonnas (Lepidoptera: Geometridae). Sellesse kosmopoliitse levikuga liblikarühma kuulub rohkem kui 100 perekonda ja üle 2800 kirjeldatud liigi. Kuigi klassikaliste morfoloogiliste meetoditega oli kuluvaksiklaste taksonoomia vallas tehtud olulisi edusamme, oli selgelt vaja kasutada kaasaegsemaid meetodeid, et jõuda mitmete oluliste, kuid seni vastuseta fülogeneetiliste probleemide lahenduseni. Järgnevais lõikudes tutvustan nelja molekulaarse süstemaatika meetodite abil lahendatud probleemi.

Hiljuti näidati, et Euroopa oblikavaksikud perekonnast *Timandra* kuuluvad kahte eraldiseisvasse, kuid morfoloogiliselt väga sarnasesse liiki. Sellesse käsitlusse suhtuti euroopa liblikauurijate poolt võrdlemisi skeptiliselt, kuna nende kahe liigi, põhja-oblikavaksiku (*Timandra griseata*) ja hariliku oblikavaksiku (*T. comae*) vahelisi erinevusi peeti mõnikord liiga ebaselgeteks, et õigustada kahe liigi eristamist. Molekulaarsetel tunnustel põhinev fülogeneetiline analüüs artiklis **I** jagas oblikavaksikud kaheks statistiliselt tugevasti toetatud klaadiks vastavalt nende kuulumisele „morfoloogilistesse liikidesse“. Seetõttu ma järeldan, et *T. griseata* ja *T. comae* on tõepoolest kaks eraldiseisvat liiki. Üksikud isendid „vales” klaadis on suure tõenäosusega hübriidid, kuid *T. griseata* ja *T. comae* vaheline sage hübridiseerumine on vähetõenäoline nende liikide erineva fenoloogia ja elupaigaeelistuse tõttu.

Palearktilise levikuga triibus punavaksikud (Lythriini) on väike rühm päevase eluviisiga vaksiklasi, kuhu kuulub vaid perekond *Lythria* (punavaksik) viie liigiga. Morfoloogilisest vaatepunktist on see rühm tähelepanuväärne, kuna ühendab tunnuseid kirivaksiklaste (Larentiinae) ja kuluvaksiklaste alamsugukondadest, ähmastades sellega nendevahelist piiri. Ajalooliselt on punavaksikuid peaaegu eranditult liigitatud kirivaksiklaste hulka ning alles viimastel aastatel on mõned autorid rõhutanud nende ja teatud kuluvaksiklaste perekondade vahelisi sarnasusi. Molekulaarsetel tunnustel põhinev fülogeneetiline analüüs artiklis **II** näitas, et punavaksiklased kuuluvad kahtlemata kuluvaksiklaste hulka, olles kõrbevaksikute (Rhodometrini) sõsarrühmaks. Seda järeldust toetavad ka mitmed morfoloogilised tunnused. Kaks peamist tunnust, mida on tavaliselt kasutatud kiri- ja kuluvaksiklaste eristamiseks, nimelt ees- ja tagatiiva soonestus, osutusid plesiomorfseteks ning seetõttu ei sobi need edaspidi argumendiks madalama süstemaatilise taseme rühmade liigitamisel ühte neist kahest liigirikkast alamsugukonnast. Lisaks eelnevale toetas fülogeneetiline analüüs artiklis **II** teatud määral ka hiljutisi morfoloogiapõhisele kladistikale tuginevaid oletusi kuluvaksiklaste fülogeneesi kohta. Täpsemalt jagunesid uuritud triibused kaheks liiniks, millest „Scopulini liini” kuuluvad triibused

Rhodometrini, Sterrhini ja Scopulini ning „Timandrini liin" koosneb triibustest Cosymbiini, Timandrini, Rhodometrini ja Lythriini.

Lythria venustata on äärmiselt haruldane idapalearktilise levikuga liik, mida on seni leitud vaid Kasahstanist. Selle liblika genitaalide morfoloogia kohta oli vähe teada ning kuna kuni kõige viimase ajani polnud kusagilt võtta värsket materjali, polnud *L. venustata* süstemaatilise asukoha kindlakstegemine molekulaarsete meetodite abil isegi teoreetiliselt võimalik. Artiklis **III** käsitleti neid kitsaskohti terve perekonna *Lythria* fülogeneesipuu molekulaarsete tunnuste abil väljaselgitamise ning kõigi liikide isaste liblikate genitaalide uurimise teel. Leiti, et *L. venustata* on sõsarrühmaks neljale ülejäänud *Lythria* liigile, mis omakorda jagunesid kaheks lähedaste liikide grupiks: *L. purpuraria+L. plumularia* klaadiks ja *L. cruentaria+L. sanguinaria* klaadiks. Niisugust fülogeneesipuud toetas ka liblikate genitaalide morfoloogia. Lisaks eelnevale selgus, et mõnede tunnuste osas on *L. venustata* genitaalid üleminekuvormiks teiste *Lythria* liikide ning perekond *Rhodometra* (triibuse Rhodometrini tüüpperekond) vahel. Kuna artiklis **II** näidati, et Rhodometrini on Lythriini sõsarrühm, võib *Rhodometra* ja *L. venustata* vahelist sarnasust tõlgendada kui täiendavat argumenti, mis õigustab viimase paiknemist ülejäänud *Lythria* liikide sõsarrühmana.

Nagu ülalpool märgitud, toetasid artikli **II** tulemused kõige kaasaegsemaid morfoloogiapõhiseid hüpoteese kuluvaksiklaste fülogeneesi kohta. Kuna mainitud artiklis ei olnud aga kavas molekulaarsete tunnuste abil lahendada kuluvaksiklaste fülogeneesi laiemas mastaabis, siis uuriti vaid väikest arvu taksoneid. Käesolevas dissertatsioonis esitan lisaks publitseeritud tulemustele ka laiendatud valimi põhjal koostatud kuluvaksiklaste mastaapsema fülogeneesipuu. Tulemuste usaldusväärsuse hindamiseks kasutasin nii suurima tõepära kui Bayesi analüüsimeetodeid. Analüüside tulemused toetavad üheselt varasemaid hüpoteese, mille kohaselt Rhodostrophiini, Sterrhini ja Scopulini moodustavad ühe kahest evolutsiooniliselt liinist („Scopulini liin") ning Cosymbiini, Timandrini, Rhodometrini ja Lythriini teise, nn. „Timandrini liini". Triibustevahelised suhted nendes liinides on samuti identsed varem leitutega. Täpsemalt asetus Rhodostrophiini Scopulini+Sterrhini klaadi sõsarrühmaks „Scopulini liinis" ning Cosymbiini leiti olevat ülejäänud kolme triibuse sõsarrühm „Timandrini liinis". Neist kolmest on Timandrini omakorda Rhodometrini+Lythriini klaadi sõsarrühmaks. Siiski leiti ka mõned edasise uurimistöö vajalikkusele osutavad ebakõlad.

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