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Ulenberg, S.A.

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Phylogeny of the *Yponomeuta* species (Lepidoptera, Yponomeutidae) and the history of their host plant associations

Sandrine A. Ulenberg

This study presents the results of cladistic analyses of the morphology of 1) the subfamilies of the Yponomeutidae, 2) the genera of the Yponomeutinae, and 3) the species of *Yponomeuta* Latreille, 1796. The sequential steps in the evolution of the host plant associations, the presumed key factor in the processes of speciation within *Yponomeuta*, as extrapolated from the cladograms are discussed. The hypothesis that the present-day host plant associations evolved from an ancestral relation with Celastraceae through speciation in allopatry mostly on *Euonymus* is supported by the underlying study. The biogeographical patterns suggest speciation through dispersion from Australia, the Oriental region, Africa to western Europe. Sandrine A. Ulenberg, Zoological Museum, University of Amsterdam, Plantage Middenlaan 64, 1018 DH Amsterdam, The Netherlands. s.a.ulenberg@uva.nl

Introduction

The study of speciation mechanisms as a means to gain a better understanding of the origins of biological diversity has always been a key area in biological research. Recently, the role of ecological specialisation has received considerable attention. Good theoretical (Dieckmann & Doebeli 1999; Doebeli & Dieckmann 2000; Janz & Nylin 2008; Percy *et al.* 2004; Via 2001) as well as empirical progress is being made, in particular in our understanding of the evolution of insect–plant relations and speciation in phytophagous insects (Kölsch & Pedersen 2008; Via 2002; Via & Hawthorne 2002).

One of the model systems developed for this purpose is the genus *Yponomeuta* Latreille, 1796 and its host relations. Since the 1970s many multidisciplinary studies have been dedicated to the associations between *Yponomeuta* species and their host plants. The main objectives of studying this model were to obtain insights into the evolution of the host relations, and the speciation processes that have led to the present-day associations (Bakker *et al.* 2008; Hora & Roessingh 1999; Menken 1996; Menken *et al.* 1992; Menken & Roessingh 1998; Raijmann & Menken 2000). According to Menken & Roessingh

(1998) “These studies were based on the working hypothesis that the present-day host plant associations evolved from an ancestral relation with Celastraceae through speciation in allopatry mostly on *Euonymus* and through host shifts in sympatry or allopatry to mainly Rosaceae, following the scenario of host race formation (Bush 1975)”. In the present paper the validity of this working hypothesis is tested by analysing the most probable sequence of the evolutionary changes in the host plant associations of *Yponomeuta* based on their species phylogeny.

Yponomeuta’s distribution and host plant associations

The species of the genus *Yponomeuta* are phytophagous and have a wide, mainly palaearctic, distribution. The genus is represented in all major eco regions except South America and Antarctica. Host-associations are known for 39 of the 76 species. Of the 39 *Yponomeuta* species with a known host-association, 32 are mono- or oligophagous within one genus of trees or shrubs. Of those 32, 27 species feed on Celastraceae genera, of which 22 exclusively feed on species of the genus *Euonymus*. The *Yponomeuta* species that do not use Celastraceae as their host plant

feed on Crassulaceae, Rosaceae, Rhamnaceae, or Salicaceae (see Gershenson & Ulenberg 1998).

Classification of the Yponomeutidae

The systematic position of the (sub)families within the superfamily Yponomeutoidea was open to discussion until recently and differently treated by systematists, according to the historical review in Gershenson & Ulenberg's (1998) book on the Yponomeutinae.

No general consensus exists regarding the ranks of the higher taxa in Yponomeutidae. Some authors (Kyrki 1990; Moriuti 1977) lowered the position of what was formerly regarded as a well-defined family, the Yponomeutidae, to the level of subfamily. Kyrki (1984) discussed the different classifications of earlier authors and in his paper published in 1990 tentatively reclassified the Holarctic Yponomeutoidea, its families and subfamilies based on what he regarded as apomorphies. Kyrki's reclassification was followed by Scoble (1992) and Dugdale *et al.* (1998) in their treatment of the Yponomeutoidea. Heppner (1998), in his general classification of Lepidoptera, summarized the characters defining Yponomeutidae. However, though he recognized three subfamilies (viz. Yponomeutinae, Saridoscelinae and Cedestinae), he did not treat these in detail. Neither of them published on the phylogeny of the groups within the Yponomeutidae.

Material and Methods

The subfamilies of the Yponomeutidae and the genera of the Yponomeutinae were analysed cladistically to determine the sister group of *Yponomeuta* and the history of the host plant associations within the Yponomeutinae leading to those in *Yponomeuta*.

The subfamilies of the Yponomeutidae

The relationship between the subfamilies of the Yponomeutidae has been investigated largely based on the characters given by Kyrki (1990). One character state was changed, viz., the number of segments of the maxillary palp in the Yponomeutinae. Kyrki gives the number as four. According to the observations of Gershenson & Ulenberg (1998) the number of segments in this subfamily is less than four, as they did not count the protuberance of the stipes as basal maxillary segment (see also Moriuti 1977; Dugdale *et al.* 1998). Heppner (1998: 51) mentioned 1–2 for the family Yponomeutidae (Yponomeutinae, Saridoscelinae, Cedestinae).

For a description of the characters and the matrix, see Table 1.

In the analysis an all-zero outgroup, with zero as

plesiomorphic state, was incorporated based on Kyrki's opinion on plesio- and apomorphies of the subfamilies. This hypothetical ancestor is chosen as outgroup because the group most related to the Yponomeutidae is unknown. In this and the following analyses, PAUP* 4.0b10 (Swofford 2003) was used, all characters were unordered and of equal weight. An exhaustive search was made for the most parsimonious tree.

The genera of the Yponomeutinae

The phylogenetic relationships of the yponomeutine genera was examined utilizing a maximum parsimony analysis of the type species of the genera in the subfamily. The search was heuristic.

The characters of the type species were taken from the literature, viz., Diakonoff (1967), Friesse (1960), Gates Clarke (1965), Gershenson (1974, 1990), Gershenson & Ulenberg (1998), Huemer & Tarmann (1991), Koster (1990), Koster & Schreurs (1992), Moriuti (1971, 1977) and Zagulajev (1990). Most of the characters were checked on collection material. Of four genera no specimens of the type species could be studied, viz., *Epinomeuta truncatipennella* Rebel, 1936 (fossil), *Opsiclina leucomorpha* (Lower, 1900), *Paradoxus osyridellus* Millière, 1869, *Parahyponomeuta egregiellus* (Duponchel, [1839]).

As the literature did not give sufficient insight in their characters, neither of other species classified in these four genera, they were not incorporated in the analysis.

Saridoscelis sphenias Meyrick, 1894, the type species of the only genus classified in the Saridoscelinae, the Yponomeutinae's presumed sister group, served as outgroup.

For a description of the characters and the matrix, see Table 2a and 2b.

A heuristic search for the most parsimonious tree was performed with PAUP* 4.0b10 (Swofford 2003), all characters were unordered and of equal weight. Starting trees were obtained via stepwise addition with random sequence. The number of replicates was one million. The branch-swapping algorithm was tree-bisection-reconnection (TBR).

The species of *Yponomeuta*

The phylogeny of the *Yponomeuta* species treated in Gershenson & Ulenberg (1998) was investigated, viz., the *Yponomeuta* species of the world exclusive of the Americas. One of the six Nearctic *Yponomeuta* species, *Y. multipunctellus* Clemens, has been incorporated in the cladistic analyses. The other five species have been left out because of the author's insufficient insight in the American fauna.

Fig. 1A-C. *Yponomeuta malinellus*. – A, head; B, fore wing; C, hind wing. **D-E.** *Yponomeuta padellus* (L.) D, male genitalia; E, female genitalia. **F.** *Yponomeuta morbillosus* Zel., bursa copulatrix.

Eumonopyta unicornis Moriuti, 1977 (male), *Prioteina melanaster* (Meyrick, 1907) and *Teinoptila interruptella* Sauber, 1902 served as outgroups.

The following species have not been incorporated in the analyses because no specimens could be investigated and thus no characters checked. The five not investigated American species are among them:

Yponomeuta

atomocellus Dyar, 1902 (American)

africanus Stainton, 1862

? *alienellus* Walker, 1863

athyris Meyrick, 1928

? *chalcocomus* Meyrick, 1938

euonymella Chambers, 1872 (nec Linnaeus, 1758) (American)

effetus Meyrick, 1924

enneacentrus Meyrick, 1925

favillaceus Meyrick, 1923

grossipunctellus Guenée, 1879

leucothorax Meyrick, 1913 (American)

liberalis Meyrick, 1913

madagascariensis Gershenson, 2003

martinellus Walker, 1863 (American)

occyporus Meyrick, 1932

semialbus Meyrick 1913 (American)

stenodoxus Meyrick, 1931

For a description of the characters and the matrix see Table 3a and 3b. *Yponomeuta*'s apomorphies — the characters 9, 26, 34, 41, 52 and 61 of Table 2a and 2b, the shape of the forewings; a spined, rectangular gnathos; a quadrate shaped uncus; the shape of the saccus; the number of cornuti — were incorporated in the analyses to support the genus' monophyly.

A

B

C

Fig. 2. *Yponomeuta multipunctellus*. – A, habitus male, Trailhead vic Cosby, 35°45.2'N 83°12.4'W, Tennessee, USA, 22.vi.2001, 700 m, D. & M. Davis (ZMAN); B, male genitalia with aedeagus, ventral view, Trailhead vic Cosby, 35°45.2'N 83°12.4'W, Tennessee, USA, 22.vi.2001, 700 m, D. & M. Davis (RV 1027, ZMAN); C, female genitalia, lateral view, Sugarland Visit Ctr., 35°37'N 83°28'W, Tennessee, USA, 24.vi.2001, 1000 m, D. & M. Davis (RV 1028, ZMAN).

Illustrations of the characters are given in Figure 1 and can be found in Gershenson & Ulenberg (1998). As their study does not treat the characters of the American species *Y. multipunctellus*, they are depicted here (see Fig. 2).

A heuristic search was done with PAUP* 4.0b10 (Swofford 2003) for the most parsimonious trees, all characters were unordered and of equal weight. Starting trees were obtained via stepwise addition with simple addition sequence. The total number of rearrangements tried was 459544184. The branch-swapping algorithm was TBR.

Results

The phylogeny of the subfamilies of the Yponomeutidae

PAUP* found six most parsimonious trees of length 20. The 50% Majority-rule consensus of the six trees is shown in Fig. 3.

The Yponomeutinae and the Saridoscelinae came out of the analysis as each other's most closely related groups. Both subfamilies have scales and spines on the abdominal tergites (ch. 4), a basal scape on the aedeagus (ch. 6) and a bulged ventral margin of the mandible in the larvae (ch. 10).

The phylogeny of the genera of the Yponomeutinae

PAUP* found 91 most parsimonious trees of length 341. The 50% Majority-rule consensus of the 91 trees is shown in Fig. 4.

The monophyly of the Yponomeutinae is supported by equally sclerotized 7th and 8th tergites (ch 76, state 2) in all genera.

In Table 4 the host plant associations of the genera of the Yponomeutinae are listed. The host plant association of *Zelleria rorida* Philpott and *Z. sphenota* Meyrick with Viscaceae mentioned by Gershenson and Ulenberg (1998) should be *Loranthus* (Loranthaceae) (J. Dugdale, pers. comm.). The association of *Zelleria hepariella* Stt. with *Artemisia vulgaris* L. (Asteraceae) mentioned in Gershenson & Ulenberg (1998) probably is wrong (P. Huemer, pers. comm.). The host plant associations have not been incorporated in the PAUP* analyses. Their supposed changes through time are inferred by simply plotting manually the host plants on the cladogram (Fig. 4).

By doing so one may conclude that four of the five host plant families of *Yponomeuta* were exploited early in the evolution of the Yponomeutinae, before the appearance of *Yponomeuta*. These are the plant families Celastraceae, Crassulaceae, Rhamnaceae

Fig. 3. Majority rule consensus tree of six trees of the subfamilies of the Yponomeutidae using PAUP 4.0b10, for the parsimony settings see text, for the characters see Table 1. Numbers on the branches are frequencies of the clades in the set of most parsimonious trees.

and Rosaceae. The association of *Yponomeuta* with Salicaceae is not known to occur in the other genera within the subfamily.

The following host plant families are only known to be exploited by the listed genera. Whether these associations are apomorphies cannot be concluded as long as not all plant associations of the Yponomeutinae are known. They are given here to inspire future scientists to work on the host plants of this group of moths.

- Fagaceae and Hamamelidaceae for *Thecobathra*
- Empetraceae for *Paraswammerdamia*
- Grossulariaceae for *Euhypnomoeutoides*
- Salicaceae for *Yponomeuta*
- Rubiaceae for *Ptiloteina*
- Coriariaceae and Saxifragaceae for *Kessleria*
- Caprifoliaceae, Epacridaceae, Loranthaceae, Myrtaceae, and Oleaceae for *Zelleria*
- Ericaceae for *Cedestis*, but *Parahypnomoeuta* species, not treated here, also feed on this family (see Gershenson & Ulenberg 1998)
- Santalaceae for *Paradoxus* (not treated here, see Gershenson & Ulenberg (1998))

The phylogeny of the species of *Yponomeuta*

PAUP* retained 5373 trees of length 160. The 50 % Majority-rule consensus tree is given in Fig. 5.

By manually plotting the host plants over the cladogram the following picture arises. The host plant associations (Table 5, the host plant associations were not incorporated in the analyses) show a shift from the Celastraceae to other plant families in the clade from *Y. orientalis* to *Y. evonymellus*, viz., to Rosaceae in *Y. orientalis*, *Y. mahalebells*, *Y. padellus*, *Y. meridionalis*, *Y. malinellus* and *Y. evonymellus*, to Salicaceae in *Y. albonigratus*, *Y. gigas* and *Y. rorrellus*, to

Fig. 4. Majority rule consensus tree of 91 trees of the genera of the Yponomeutinae using PAUP 4.0b10, for the parsimony settings see text, for the characters see Table 2a and 2b. Numbers on the branches are frequencies of the clades in the set of most parsimonious trees. Also indicated are the host plant families (see Table 4).

Crassulaceae in *Y. sedellus*, to Rhamnaceae in *Y. rhamnellus* (Fig. 5). Due to the unresolved dichotomies among the species *Y. orientalis* to *Y. evonymellus* this phylogenetic study does not resolve the question whether the association of *Y. refrigeratus* and *Y. cagnagellus* with Celastraceae is a reversal or simply the preservation of the old host plant choice. Different species of *Euonymus* are exploited by *Yponomeuta*. Most of these *Euonymus* species serve as host plant for more than one *Yponomeuta* species. *Euonymus sieboldianus* e.g. is exploited by seven *Yponomeuta* species, viz., *Y. mayumivorellus*, *Y. menkeni*, *Y. osakae*, *Y. polystictus*, *Y. polystigmellus*, *Y. spodocrossus* and *Y. tokyonellus*. These seven species are all distributed in Japan, three also occur in China and one also in Russia. The same holds for other *Euonymus* species and the *Yponomeuta*'s feeding on them (see Table 5). That means that presumably many *Yponomeuta* species occur in sympatry with each other.

The distribution pattern as shown by the cladogram (Fig. 5, Table 5) shows a basal split between a clade (*Y. horologus* to *Y. multipunctellus*), distributed over Africa, Australia, the New Hebrides, China, Russia, North America and a clade (*Y. leucophaeus* to *Y. evonymellus*) distributed from Java, Africa, Japan, China, India, Nepal, Central Asia, the Middle East, Russia, Armenia, Ukraine, Anatolia, the Caucasus to Europe, inclusive of the Canary Islands. *Yponomeuta gigas*, from the Canary Islands, is placed among the Eurasian species and not among African species, which should be its place from a biogeographic view (see Fig. 3 in Cox 2001). The butterflies of the Canary Islands, however, are predominantly Palearctic (Higgins 1975: 7; R. de Jong pers. comm.), the same holds apparently for *Yponomeuta*.

Fig. 5. Majority rule consensus tree of 5373 trees of the species of *Yponomeuta* using PAUP 4.0b10, for the parsimony settings see text, for the characters see Table 3a and 3b. Numbers on the branches are frequencies of the clades in the set of most parsimonious trees. Also indicated are the host plant families and the distribution (A = African, Au = Australian, E = Eurasian, N = North American, O = Oriental, Z = New Zealand).

Discussion

Cladistic analysis of the *Yponomeuta* species was hampered by the low number of morphological characters. This is not surprising, *Yponomeuta* has many sibling species. On top of that the characters prove to express insufficient phylogenetic information resulting in a high number of homoplasies and subsequently in thousands of trees. Therefore, the results of the cladistic analysis had to be summarized in a 50% Majority Rule Consensus Tree. The conclusions based on these trees can therefore only be tentative. A molecular phylogeny of a part of the species treated here has been constructed which solves some of the polytomies (Turner *et al.* in prep.).

The cladograms of 1) the subfamilies of the Yponomeutidae, 2) the genera of the Yponomeutinae, and 3) the species of *Yponomeuta* indicate that the association of *Yponomeuta* with Celastraceae originated early within the Yponomeutidae. The Yponomeutinae's closest relative, the Saridoscelinae, feed on Celastraceae. Within the Yponomeutinae the basal genera feed on different plant families, among which Crassulaceae, Rhamnaceae and Rosaceae that are also exploited by *Yponomeuta*. The host shifts to Salicaceae are concentrated in *Yponomeuta*. It is striking that the host shifts in *Yponomeuta* from Celastraceae to other plant families occur high up in the cladogram, in the clade – found in all computed trees – from *Y. orientalis* to *Y. evonymellus* (Fig. 5). Once it had happened, host shifts were repeated. It may be that the first host shift somehow facilitated subsequent shifts. The nature of such changes is as yet still unclear; it might involve the sensory system, either in the perception or in the processing of phytochemical cues related to host acceptance (Hora & Roessingh 1999; Menken & Roessingh 1998; Roessingh *et al.* 2000), but could also involve changes in digestive and detoxification systems (Kooi 1990). The hypothesised reversal in *Y. cagnagellus* to Celastraceae is confirmed by *cagnagellus* sensitivity to the plant compound benzaldehyde. Benzaldehyde is common in Rosaceae and absent in Celastraceae. Rosaceae – feeders are sensitive to this compound, while Celastraceae – feeders are insensitive. *Yponomeuta cagnagellus*'s sensitivity for benzaldehyde while feeding on Celastraceae supports a former association with Rosaceae (Roessingh *et al.* 2007).

The hypothesis that the present-day host plant associations evolved from an ancestral relation with Celastraceae through speciation mostly on *Euonymus* species is supported by the present study. Whether speciation of the *Yponomeuta* species feeding on different plant species and families occurred in

sympatry rather than in allopatry cannot be inferred from the cladograms. Most of these species, though, are sympatric and closely related, clustered in the same clade (Fig. 5). This sympatry can be secondary. Speciation can have followed the way suggested by Janz & Nylin (2008) in their paper on oscillation of host plant range and speciation: a specialist expands its host, may or may not expand its geographical distribution, gets adapted to the local circumstances, speciates and specialises. This scenario covers sympatric as well as allopatric speciation.

Many of the different *Yponomeuta* species feeding on the same host plant are distributed in the same area and are presumably sympatric as well. Also these species could have evolved in allopatry, perhaps even on different host plants and have become secondary sympatric, shifting host plant to the present one.

Yponomeuta's ancestor was, most probably, widely distributed over the world. *Yponomeuta*'s sister groups are widely distributed over different continents. *Teinoptila* is found in Australia, New Guinea, Indonesia, the Philippines, Thailand, India, Japan, China and Africa. *Eumonopyta* occur in Japan, *Ptiloteina* in the Philippines, India, Sri Lanka and Africa.

The distribution of *Yponomeuta* shows an early radiation from the regions its sister groups occur, i.e. Africa, Australia, south east Asia, the east Palaearctic, China, the east Palaearctic to Europe. Lepidoptera are considered of Early Jurassic origin (Kozlov *et al.* 2002), when all southern continents plus North America formed a single continent (Metcalf 1998). *Yponomeuta*'s distribution, however, does not suggest speciation through vicariance starting in the Early Jurassic. This corroborates the findings of de Jong and van Achterberg (2007) that 'the evidence for the impact of the fragmentation of Pangea and Gondwana on the global distribution of butterflies ... is considered to be weak' (see also Yoder & Nowak 2006).

Speciation through host plant shift can be inferred from this study, viz., from Celastraceae, starting with shifts within *Euonymus* (see Table 5 and Fig. 5), to species of other plant families. The age of the Celastraceae and that of the Yponomeutoidea as currently estimated support this conclusion. Both groups are considered to be of the same age. The Celastraceae are 42 million years old according to Davies *et al.* (2004), and *Epinomeuta* Rebel, the only known yponomeutoid fossil, found in the Baltic amber fauna inhabiting rich forests, is estimated to have lived 35 – 40 million years ago (Kusnetsov 1941; Poinar 1992).

Whether the *Yponomeuta* and the *Euonymus* species cospeciated is a question beyond the scope of this paper. Detailed dating of the species of both genera is required to answer this question (Percy *et al.* 2004). The species feeding on Crassulaceae, Rosaceae, Rhamnaceae, or Salicaceae did certainly not evolve through cospeciation with their hosts. The plant species exploited in these families are not closely related which leads to the conclusion that the *Yponomeuta* species evolved through sequential speciation on these plants.

Yponomeuta is an example of a group of moths that radiated over the world, expanded its host plant association and shows that an originally specialized host plant range is not an evolutionary dead-end (Kölsch & Pedersen 2008). The study by Bakker *et al.* (2008) revealed no host plant fidelity in the adults of *Y. padellus* and *Y. cagnagellus* in their choice of a mating place, a good start for host plant shift!

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References

- Bakker, A.C., P. Roessingh & S.B.J. Menken, 2008. Sympatric speciation in *Yponomeuta*: no evidence for host plant fidelity. – *Entomologia Experimentalis et Applicata* 128: 240–247.
- Bush, G.L., 1975. Sympatric speciation in phytophagous parasitic insects. *Evolutionary Strategies of Parasitic Insects and Mites* (ed. by P.W. Price). – New York, Plenum, pp. 187–206.
- Cox, C.B., 2001. The biogeographic regions reconsidered. – *Journal of Biogeography* 28: 511–523.
- Davies, T.J., T.G. Barraclough, M.W. Chase, P.S. Soltis, D.E. Soltis, V. Savolainen & P.R. Crane, 2004. Darwin's abominable mystery: Insights from a supertree of the Angiosperms. – *Proceedings of the National Academy of Sciences of the United States of America* 101(7): 1904–1909.
- Diakonoff, A., 1967. *Microlepidoptera of the Philippine Islands*. – United States National Museum Bulletin 257: 1–484.
- Dieckmann, U., & M. Doebeli, 1999. On the origin of species by sympatric speciation. – *Nature* 400: 354–357.
- Doebeli, M. & U. Dieckmann, 2000. Evolutionary branching and sympatric speciation caused by different types of ecological interactions. – *The American Naturalist* 156: S77–S101.
- Dugdale, J.S., N.P. Kristensen, G.S. Robinson & M.J. Scoble, 1998. The Yponomeutoidea. – In: Kristensen, N.P. (ed.): *Lepidoptera, Moths and Butterflies 1: Evolution, Systematics, and Biogeography*. *Handbuch der Zoologie IV Arthropoda: Insecta*: 119–130. Walter de Gruyter, Berlin, New York.
- Friese, G., 1960. Revision der paläarktischen Yponomeutidae unter besonderer Berücksichtigung der Genitalien. – *Beiträge zur Entomologie* 10(1/2): 1–131.
- Gates Clarke, J.F., 1965. Catalogue of the type specimens of Microlepidoptera in the British Museum (Natural History) described by Edward Meyrick, Vol. V. – *Trustees of the British Museum (Natural History), London*, pp. 1–581.
- Gershenson, Z.S., 1974. [Small Ermine Moths: Yponomeutidae]. – *Fauna Ukraini* 15(6): 1–132. (in Ukrainian)
- Gershenson, Z.S., 1990. Fam. Yponomeutidae. Keys to the insects of the European part of the USSR 4, *Lepidoptera* 2 (ed. by G.S. Medvedev). – Brill, Leiden, pp. 436–455.
- Gershenson, Z.S. & S.A. Ulenberg, 1998. The Yponomeutinae (Lepidoptera) of the World exclusive of the Americas. – *Verhandelingen van de Koninklijke Nederlandse Akademie van Wetenschappen, afdeling Natuurkunde*, 2de reeks 99: 1–202.
- Heppner, J.B., 1998. Classification of Lepidoptera, Part 1. – Introduction. *Holarctic Lepidoptera* 5, supplement 1: i–iv, 1–148, index 1–6.
- Higgins, L.G., 1975. The classification of European Butterflies. – Collins, London, 320 pp.
- Hora, K.H. & P. Roessingh, 1999. Oviposition in *Yponomeuta cagnagellus*: the importance of contact cues for host plant acceptance. – *Physiological Entomology* 24: 109–120.
- Huemer, P. & G. Tarmann, 1991. Westpaläarktische Gespinstmotten der Gattung *Kessleria* Nowicki: Taxonomie, Ökologie, Verbreitung (Lepidoptera, Yponomeutidae). – *Mitteilungen der Münchener Entomologischen Gesellschaft* 81: 5–110, Abb. 248.
- Janz, N. & S. Nylin, 2008. The oscillation hypothesis of host-plant range and speciation. – In: K.J. Tilmon (ed.), *Speciation, and Radiation: the Evolutionary Biology of Herbivorous Insects*: 203–215. – University of California Press, Berkeley, California.
- Jong, R. de & C. van Achterberg, 2007. Global disjunctions and flying insects. – In: Renema, W. (ed.): *Biogeography, Time, and Place: Distributions, Barriers, and Islands*: 4–44. Springer.
- Kölsch, G. & B.V. Pedersen, 2008. Molecular phylogeny

- of reed beetles (Col., Chrysomelidae, Donaciinae): the signature of ecological specialization and geographical isolation. – *Molecular Phylogenetics and Evolution* 48: 936–952.
- Kooi, R.E., 1990. Host-plant selection and larval food-acceptance by small ermine moths. – University of Leiden, Studies in *Yponomeuta* 9: 1–151.
- Koster, J.C., 1990. Het geslacht *Ocnerostoma* in Nederland (Lepidoptera: Yponomeutidae). – *Entomologische Berichten*, Amsterdam 50: 149–153.
- Koster, J.C. & A. Schreurs, 1992. *Zelleria hepariella*, nieuw voor de Nederlandse fauna (Lepidoptera: Yponomeutidae). – *Entomologische Berichten*, Amsterdam 52: 117–119.
- Kozlov, M.V., V.D. Ivanov & A.P. Rasnitsyn, 2002. Order Lepidoptera Linné, 1758. The Butterflies and Moths. In: Rasnitsyn, A.P. & D.L.J. Quicke (eds.): *History of Insects*: 220–227. – Kluwer Academic Publishers
- Kusnetsov, N.Ya., 1941. [Lepidoptera of the amber fauna]. – Academy of Sciences, Moscow-Leningrad, 136 pp. (In Russian)
- Kyrki, J., 1984. The Yponomeutoidea: a reassessment of the superfamily and its suprageneric groups (Lepidoptera). – *Entomologica Scandinavica* 15: 71–84.
- Kyrki, J., 1990. Tentative reclassification of holarctic Yponomeutoidea (Lepidoptera). – *Nota Lepidopterologica* 13(1): 28–42.
- Menken, S.B.J., 1996. Pattern and process in the evolution of insect-plant associations: *Yponomeuta* as an example. – *Entomologia Experimentalis et Applicata* 80: 297–305.
- Menken, S.B.J. & P. Roessingh, 1998. Evolution of insect – plant associations: sensory perception and receptor modifications direct food specialization and host shifts in phytophagous insects. – In: Howard, D., & S.H. Berlocher (eds.): *Endless Forms: Species and Speciation*: 145–156. Oxford University Press.
- Menken, S.B.J., W.M. Herrebout & J.T. Wiebes, 1992. Small ermine moths (*Yponomeuta*): their host relations and evolution. – *Annual Review of Entomology* 37: 41–66.
- Metcalf, I., 1998. Palaeozoic and Mesozoic geological evolution of the SE Asian region: multidisciplinary constraints and implications for biogeography. *Biogeography and geological Evolution of SE Asia* (ed. by R. Hall and J.D. Holloway). – Backhuys Publishers, Leiden, The Netherlands, pp. 25–41.
- Moriuti, S., 1971. Two new genera and a new species of the Indian Yponomeutidae (Lepidoptera). – *Kontyû* 39(3): 251–255.
- Moriuti, S., 1977. Fauna Japonica, Yponomeutidae s. lat. (Insecta: Lepidoptera). – Tokyo, pp. i–vi, 1–327, 95 plates, 583 Figs.
- Percy, D.M., R.D.M. Page & Q.C.B. Cronk, 2004. Plant-insect interactions: double-dating associated insect and plant lineages reveals asynchronous radiations. – *Systematic Biology* 53(1): 120–127.
- Poinar, G.O. Jr., 1992. *Life in Amber*. – Stanford University Press, 368 pp.
- Raijmann, L.E.L. & S.B.J. Menken, 2000. Temporal variation in the genetic structure of host-associated populations of the small ermine moth *Yponomeuta padellus* (Lepidoptera, Yponomeutidae). – *Biological Journal of the Linnean Society* 70: 555–570.
- Roessingh, P., K.H. Hora, S. Ying Fung, A. Peltenburg & S.B.J. Menken, 2000. Host acceptance behaviour of the small ermine moth *Yponomeuta cagnagellus*: larvae and adults use different stimuli. – *Chemoecology* 10: 041–047.
- Roessingh, P., Sen Xu & Menken, S.B.J., 2007. Olfactory receptors on the maxillary palps of small ermine moth larvae: Evolutionary history of benzaldehyde sensitivity. – *Journal of Comparative Physiology* 193: 635–647.
- Scoble, M.S., 1992. The Lepidoptera. – Natural History Museum Publications, Oxford University Press, pp. i–ix, 1–404.
- Swofford, D.L., 2003. PAUP*. Phylogenetic analysis using parsimony (*and other methods). Version 4. – Sinauer Associates, Sunderland, Massachusetts.
- Turner, H., N. Lieshout, W. van Ginkel & S.B.J. Menken, in prep. Molecular phylogeny of the small ermine moth genus *Yponomeuta* (Lepidoptera, Yponomeutidae) in the Palaearctic – evolutionary and biogeographical implications.
- Via, S., 2001. Sympatric speciation in animals: the ugly duckling grows up. – *Trends in Ecology & Evolution* 16: 381–390.
- Via, S., 2002. The ecological genetics of speciation. – *American Naturalist* 159: S1–S7.
- Via, S. & D.J. Hawthorne, 2002. The genetic architecture of ecological specialization: correlated gene effects on host use and habitat choice in Pea Aphids. – *American Naturalist* 159: S76–S88.
- Yoder, A.D. & M.D. Nowak, 2006. Has vicariance or dispersal been the predominant biogeographic force in Madagascar? Only time will tell. – *Annual Review of Ecology, Evolution and Systematics* 37: 405–431.
- Zagulajev, A.K., 1990. Fam. Plutellidae. In: Medvedev, G.S. (ed.): *Keys to the insects of the European part of the USSR* 4, Lepidoptera 2: 473–522. – Leiden.

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Table 1. Characters and data matrix of the subfamilies of the Yponomeutidae (0 is the presumed plesiomorphic state, 1 the apomorphy (Kyrki 1990)).**Characters**

01. Adult head: antennal scape: with pecten (0), without pecten (1)
02. Adult head: maxillary palp: 4 segments (0), less than 4 segments (1)
03. Adult thorax: pterostigma from Sc: to R2 or R3 (0), to R1 (1)
04. Adult abdomen: tergites: with normal scales (0), with scales and spines (specialized scales) (1)
05. Adult abdomen: 8th abd. sternite: sclerotized as the 7th (0), more strongly sclerotized than the 7th (1)
06. Male genitalia: aedeagus: without basal scape (0), with basal scape (1)
07. Male genitalia: teguminal processes: unscaled (0), with specialized scales (1)
08. Larva head : cranial seta P1: below Af2-P2 line (0), on line with or higher than Af2-P2 (1)
09. Larva head: cranial seta V1: short (0), long (1)
10. Larva head: ventral margin of mandible: evenly arched (0), bulged (1)
11. Larva head: antennal segments 3 + 4: shorter than segments 1 + 2 (0), longer than segments 1 + 2 (1)
12. Larva abdomen: crochets: uniserial (0), bi- or multiserial (1)
13. Larva feeding: exophagous, often in web (0), endophagous (1)

Data matrix

taxon/character	1	2	3	4	5	6	7	8	9	10	11	12	13
Ancestor	0	0	0	0	0	0	0	0	0	0	0	0	0
Scythropiinae	0	0	0	0	1	0	0	0	1	0	0	1	0
Saridoscelinae	0	0	1	1	1	1	1	0	1	1	1	1	0
Yponomeutinae	0	1	1	1	0	1	0	0	1	1	1	1	0
Attevininae	1	1	1	0	1	0	0	1	0	0	1	1	0
Praydinae	1	1	1	0	1	0	0	1	0	0	0	1	1
Argyresthiinae	0	1	1	0	1	0	1	0	0	0	0	0	1

Table 2a. Characters of the genera of the Yponomeutinae.

01. Adult: resting position: of the *Argyresthia*-type, with head down, body in an angle of 45° to the substrate (see Fig 8.1K in Dugdale et al. 1998) (1), other type (2)
02. Adult head: crown: with dots (1), without dots (2)
03. Adult head: scales appressed on crown (1), scales not appressed on crown (2)
04. Adult head: proboscis: vestigial (1), developed (2)
05. Adult head: maxillary palpus: 1-segmented (1), 3-segmented (2)
06. Adult head: labial palpus: 2nd segment broadened (1), 2nd segment not broadened (2)
07. Adult thorax: with large patagia covering tegulae (see Fig 164–166 in Moriuti 1977) (1), with small patagia not covering tegulae (2)
08. Adult thorax: forewing shape: elongate (1), elongate-ovate (2), lanceolate (3)
09. Adult thorax: forewings: length < 3.5 times width (1), length > 3.5 times width (2)
10. Adult thorax: forewing: M3 + Cu1 fused (1), M3 + Cu1 separated (2)
11. Adult thorax: forewing: A1+2 basal fork abbreviated (1), A1+2 basal fork not abbreviated (2), A1+2 without basal fork (3)
12. Adult thorax: forewing: R2 and R1 fused, R4 and R5 stalked, M1 and M2 fused (1), all veins separated (2)
13. Adult thorax: forewing: R1 strongly bent at base (1), R1 straight (2)
14. Adult thorax: forewing : with oblique termen (1), termen not oblique (2)
15. Adult thorax: forewing: with accessory cell (1), without accessory cell (2)
16. Adult thorax: forewing with transverse banded pattern (1), without (2)
17. Adult thorax: forewing monochrome (1), not monochrome (2)
18. Adult thorax: forewing with distinct dots (1), without (2)
19. Adult thorax: hindwing shape: lanceolate (1), elongate (2), elongate-ovate (3), ovate-lanceolate (4)
20. Adult thorax: hindwing: Cu1 and Cu2 stalked (1), Cu1 and Cu2 separated (2)
21. Adult thorax: hindwing: Sc and R1 entirely fused (1), Sc and R1 not entirely fused (2)
22. Adult thorax: hindwing: M3 and Cu1 short-stalked (1), M3 and Cu1 widely remoted (2), M3 and Cu1 fused (3)
23. Male genitalia: gnathos: wider than high (1), as wide as high (2)
24. Male genitalia: gnathos: well developed (1), obsolete (2)
25. Male genitalia: gnathos: dilated anteriorly (1), not dilated anteriorly (2)
26. Male genitalia: gnathos: densely spined (1), without spines (2)
27. Male genitalia: gnathos: with granules (1), without granules (2)
28. Male genitalia: gnathos: arms long (1), arms rudimentary (2), arms short (3), without arms (4)
29. Male genitalia: gnathos: with ventral plate (1), without ventral plate (2)
30. Male genitalia: gnathos: ventral plate fused with membrane of tuba analis (1), ventral plate not fused with membrane of tuba analis (2)
31. Male genitalia: gnathos: ventral plate large (1), ventral plate small (2)
32. Male genitalia: gnathos: ventral plate membranous (1), ventral plate not membranous (2)
33. Male genitalia: gnathos: ventral plate with paired processes (1), ventral plate without paired processes (2)
34. Male genitalia: gnathos: ventral plate tongue-shaped (1), ventral plate half circular (2), ventral plate spatulate (3), ventral plate rectangular (4), ventral plate triangular (5), ventral plate cylindrical (6)
35. Male genitalia: socii: pointed apically (1), not pointed apically (2)
36. Male genitalia: socii: with 1 tooth (1), with 2 teeth (2), with 3–4 teeth (3), without teeth (4)
37. Male genitalia: socii: with one or more lateral spines (1), without lateral spines (2)
38. Male genitalia: socii: covered with dense long hairs (1), without such hairs (2)
39. Male genitalia: socii: slender (1), as membranous lobes (2), differently shaped (3)
40. Male genitalia: uncus: large (1), small (2), rudimentary (3)
41. Male genitalia: uncus: rectangular (1), half circular (2), triangular (3), quadrate (4), quadrate with 2 processes (5), rudimentary (6)
42. Male genitalia: tegumen: with broad caudal margins (1), with narrow caudal margins (2), with extremely narrow caudal margins (3)
43. Male genitalia: valva: broad (1), narrow (2)

44. Male genitalia: valva: apex hook-shaped (1), apex rounded (2)
45. Male genitalia: valva: outer margin convex (1), outer margin with deep concavations (2), outer margin slightly concaved (3), outer margin differently shaped (4)
46. Male genitalia: valva: without cucullus + sacculus (1), with weakly differentiated cucullus + sacculus (2), with well differentiated cucullus + sacculus (3)
47. Male genitalia: valva: densely covered with hairs (1), not densely covered with hairs (2)
48. Male genitalia: valva: dorsally densely clothed with thick hairs (1), dorsally not densely clothed with thick hairs (2)
49. Male genitalia: transtilla: present (1), absent (2)
50. Male genitalia: saccus: bulbous anteriorly (1), not of such shape (2)
51. Male genitalia: saccus: shorter than valva (1), longer than valva (2)
52. Male genitalia: saccus: slender (1), saccus broad not set from vinculum (2), saccus U-shaped not set from vinculum (3), saccus stout (4)
53. Male genitalia: sacculus: undefined (1), weakly defined (2), well defined (3)
54. Male genitalia: sacculus: spined (1), not spined (2)
55. Male genitalia: sacculus: with apical spine (1), without apical spine (2)
56. Male genitalia: sacculus: finger-like (1), not finger-like (2)
57. Male genitalia: sacculus: long (1), short (2)
58. Male genitalia: sacculus: large (1), sacculus small (2)
59. Male genitalia: sacculus: broad (1), sacculus narrow (2)
60. Male genitalia: vinculum: small (1), vinculum large (2)
61. Male genitalia: vesica with: 1 cornutus (1), 2 cornuti (2), 4 cornuti (3), without cornuti (4)
62. Male genitalia: vesica with: 2 rows of spines (1), cluster of spines (2), without spines (3)
63. Male genitalia: aedeagus: nearly length of valva (1), as long as or longer than valva (2), 1 ½ times longer than valva (3), 1 ⅔ times longer than valva (4), 2 times longer than valva (5), 2–3 times longer than valva (6)
64. Male genitalia: aedeagus: slender (1), stout (2)
65. Male genitalia: basal scape of aedeagus: long (1), short (2)
66. Male genitalia: aedeagus: with one or more rows of teeth in outer wall (carina) (1), without teeth in outer wall (carina) (2)
67. Female genitalia: antrum: broad (1), narrow (2)
68. Female genitalia: antrum: sclerotized (1), not sclerotized (2)
69. Female genitalia: antrum: short (1), long (2)
70. Female genitalia: apophyses: short (1), long (2)
71. Female genitalia: apophyses anteriores: ventral branch well defined (1), ventral branch not well defined (2)
72. Female genitalia: apophyses anteriores: much shorter than apophyses posteriores (1), not much shorter than apophyses posteriores (2)
73. Female genitalia: apophyses posteriores: branched (1), not branched (2)
74. Female genitalia: signum present (1), signum not present (2)
75. Female genitalia: signum: small (1), large (2)
76. Female genitalia: papillae analis: membranous folds between papillae analis denticulated (1), membranous folds between papillae analis not denticulated (2)
77. Female genitalia: ductus bursae: membranous (1), sclerotized (2)
78. Female genitalia: ductus bursae: denticulated (1), not denticulated (2)
79. Female genitalia: ductus bursae: long (1), short (2)
80. Female genitalia: lamella postvaginalis: with pair of lobes (1), without pair of lobes (2)
81. Female genitalia: ovipositor: short (1), long (2)
82. Male abdomen: coremata: present (1), absent (2)
83. Adult abdomen: sclerotization of 8th abdominal tergite more strongly sclerotized than 7th (1), 7th and 8th tergite equally sclerotized (2)

Table 2b. Data matrix of the genera of the Yponomeutinae.

Taxon/character	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
<i>Saridoscelis sphebias</i> Meyrick, 1894	2	2	2	2	2	2	2	2	1	2	2	2	2	1	2
<i>Banghaasia ildefonsella</i> Friese, 1960	2	2	?	1	1	?	?	1	2	1	?	2	?	?	?
<i>Cedestis farinatella</i> (Duponchel, 1838)	2	2	2	1	2	2	?	3	2	1	3	2	2	2	2
<i>Euhypnomeuta stannellus</i> (Thunberg, 1788)	2	2	2	2	1	2	?	2	1	2	3	2	2	1	2
<i>Euhypnomeutoides albithoracellus</i> Gaj, 1954	2	2	2	2	2	2	2	1	2	2	1	2	2	1	1
<i>Eumonopyta unicornis</i> Moriuti, 1977	2	2	2	2	?	2	2	2	2	2	1	2	2	1	2
<i>Kessleria zimmermanni</i> Nowicki, 1864	2	2	2	2	1	2	2	3	2	2	1	2	2	2	2
<i>Klausius minor</i> Moriuti, 1977	2	2	2	2	?	2	2	1	2	2	1	2	2	1	2
<i>Lamprosthia lucella</i> Moriuti, 1977	2	2	1	2	?	2	2	2	2	1	1	2	2	1	2
<i>Metanomeuta fulvicrinis</i> Meyrick, 1935	2	2	2	2	?	2	2	1	2	1	1	2	2	1	2
<i>Niphonympha dealbatella</i> (Zeller, 1847)	2	2	2	2	2	2	2	2	1	2	2	2	1	1	2
<i>Ocnerostoma piniariellum</i> Zeller, 1847	2	2	2	1	1	2	2	3	1	1	1	1	2	2	2
<i>Oreocostoma bicornigerum</i> Moriuti, 1971	2	2	2	1	1	2	2	3	2	1	1	1	2	2	2
<i>Paraswammerdamia lapponica</i> (Petersen, 1932)	2	2	2	2	1	2	2	2	1	1	1	2	2	1	2
<i>Pseudoswammerdamia combinella</i> (Hübner, 1786)	2	2	2	2	1	2	2	3	2	1	3	2	2	2	2
<i>Piloteina melanaster</i> (Meyrick, 1907)	2	2	1	2	1	2	2	2	2	2	3	2	2	1	1
<i>Swammerdamia pyrella</i> (de Villers, 1789)	2	2	2	2	1	2	2	2	1	1	1	2	2	1	2
<i>Teinoptila interruptella</i> Sauber, 1902	2	1	1	2	1	2	2	2	2	2	1	2	2	1	1
<i>Thecobathra acropercna</i> Meyrick, 1922	2	2	2	2	2	2	1	2	1	2	2	2	1	1	2
<i>Xyrosaris dryopa</i> Meyrick, 1907	1	2	2	2	1	1	2	3	2	2	1	2	2	2	2
<i>Yponomeuta evonymellus</i> (Linnaeus, 1758)	2	2	2	2	1	2	2	2	1	2	1	2	2	1	1
<i>Zelleria hepariella</i> Stainton, 1849	1	2	2	2	1	2	2	3	2	2	1	2	2	2	2

Table 2b continued. Data matrix of the genera of the Yponomeutinae.

Taxon/character	43	44	45	46	47	48	49	50	51	52	53	54	55	56	57
<i>Saridoscelis sphebias</i> Meyrick, 1894	2	2	3	2	2	2	2	1	2	1	3	2	2	2	2
<i>Banghaasia ildefonsella</i> Friese, 1960	2	2	4	1	2	2	2	2	1	1	1	1	2	?	?
<i>Cedestis farinatella</i> (Duponchel, 1838)	2	2	4	1	2	2	2	2	1	1	2	1	2	?	?
<i>Euhypnomeuta stannellus</i> (Thunberg, 1788)	2	2	4	2	2	2	2	2	2	1	3	2	2	2	2
<i>Euhypnomeutoides albithoracellus</i> Gaj, 1954	2	1	4	2	2	2	1	2	1	4	3	1	2	2	2
<i>Eumonopyta unicornis</i> Moriuti, 1977	1	2	1	2	1	2	1	1	1	4	3	1	2	2	2
<i>Kessleria zimmermanni</i> Nowicki, 1864	2	2	4	2	2	2	2	2	1	1	3	1	2	2	2
<i>Klausius minor</i> Moriuti, 1977	1	2	2	1	2	2	2	2	1	3	1	2	2	?	?
<i>Lamprosthia lucella</i> Moriuti, 1977	1	2	1	2	1	2	2	1	1	4	3	1	2	2	2
<i>Metanomeuta fulvicrinis</i> Meyrick, 1935	1	2	4	2	2	2	1	2	2	1	2	1	1	2	1
<i>Niphonympha dealbatella</i> (Zeller, 1847)	1	2	1	2	2	2	2	2	2	2	2	2	2	2	2
<i>Ocnerostoma piniariellum</i> Zeller, 1847	2	2	1	1	1	2	2	2	1	1	2	1	2	2	2
<i>Oreocostoma bicornigerum</i> Moriuti, 1971	2	2	4	2	2	2	2	1	1	1	3	1	2	2	2
<i>Paraswammerdamia lapponica</i> (Petersen, 1932)	2	2	3	3	2	2	2	2	2	2	3	2	2	2	2
<i>Pseudoswammerdamia combinella</i> (Hübner, 1786)	2	1	3	3	2	2	2	2	2	4	3	2	2	2	1
<i>Piloteina melanaster</i> (Meyrick, 1907)	1	2	4	2	1	2	2	2	1	4	3	2	2	1	1
<i>Swammerdamia pyrella</i> (de Villers, 1789)	2	2	1	2	2	2	2	2	1	1	2	1	2	2	2
<i>Teinoptila interruptella</i> Sauber, 1902	1	2	1	2	1	1	1	1	1	4	3	1	2	2	1
<i>Thecobathra acropercna</i> Meyrick, 1922	1	2	1	2	1	2	2	1	2	3	2	2	2	2	2
<i>Xyrosaris dryopa</i> Meyrick, 1907	1	2	1	3	1	2	1	1	1	1	1	2	2	?	?
<i>Yponomeuta evonymellus</i> (Linnaeus, 1758)	1	2	1	2	1	2	1	1	1	1	3	1	2	1	1
<i>Zelleria hepariella</i> Stainton, 1849	1	2	1	2	2	2	1	2	1	1	3	1	1	2	2

16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42
1	2	2	3	2	1	2	2	1	2	2	2	2	2	?	?	?	?	?	1	4	2	1	3	1	5	1
2	2	2	2	?	?	3	1	1	2	1	2	1	1	2	1	2	2	1	1	1	2	2	3	2	1	2
1	2	2	1	2	1	3	2	1	2	2	2	1	1	2	2	1	2	1	1	1	2	2	3	2	1	2
2	1	2	3	2	1	3	2	1	2	2	2	1	1	2	2	2	2	2	2	3	2	2	3	2	1	2
2	2	2	4	2	1	3	2	2	2	2	2	4	1	2	2	2	2	3	1	1	2	2	1	2	1	1
2	2	1	3	2	1	3	2	1	2	2	2	3	1	2	2	2	1	2	1	1	2	2	1	2	2	1
2	2	2	1	2	1	3	1	1	2	1	2	3	1	2	1	2	2	1	1	1	2	2	1	1	1	1
2	2	2	3	1	1	3	2	2	2	2	2	4	2	?	?	?	?	?	2	4	2	2	1	3	6	3
2	2	2	3	2	1	3	2	1	2	2	2	3	1	2	2	1	2	2	1	1	2	2	1	1	1	2
2	2	2	3	2	1	3	1	1	2	2	1	1	1	2	1	2	2	1	1	4	2	2	3	1	1	2
2	2	2	3	2	1	1	2	1	2	2	2	2	1	1	2	2	2	2	2	4	2	1	3	3	6	2
2	1	2	1	1	1	3	2	2	2	2	2	1	1	2	1	1	2	1	1	4	2	2	1	2	1	2
2	1	2	1	2	1	3	2	1	2	2	2	1	1	2	1	1	2	1	1	1	2	2	3	1	1	2
2	2	2	3	2	1	3	2	1	2	1	2	1	1	2	2	2	2	4	1	1	1	2	1	1	1	2
2	2	1	2	2	1	3	2	1	1	2	2	1	1	2	2	2	2	4	1	1	2	2	1	2	1	1
2	2	1	3	2	2	3	1	1	2	2	2	1	1	2	2	2	2	2	1	2	2	2	2	2	1	2
2	2	2	3	2	1	3	1	1	2	2	1	1	1	2	1	2	2	4	1	1	2	2	1	2	1	1
2	2	2	3	2	1	3	2	1	2	2	2	1	1	2	1	2	1	2	1	2	2	2	1	2	1	2
2	2	2	3	2	1	2	2	1	1	2	2	1	1	1	2	2	2	5	1	1	2	2	1	2	3	2
2	2	2	1	2	2	3	1	1	2	1	2	4	1	2	2	2	2	5	2	4	1	2	2	1	5	2
2	2	1	3	2	2	3	2	1	2	1	2	3	1	2	1	2	1	4	1	1	2	2	1	2	4	2
2	2	2	1	2	1	3	2	1	2	1	2	4	1	2	1	2	2	6	1	1	2	2	1	1	1	1

58	59	60	61	62	63	64	65	66	67	68	69	70	71	72	73	74	75	76	77	78	79	80	81	82	83
1	1	1	4	2	4	1	2	1	2	1	1	1	2	2	2	1	2	2	2	2	2	1	1	1	1
?	?	1	2	3	2	2	2	2	2	2	2	2	1	2	2	2	?	2	1	2	?	1	2	2	2
?	?	1	1	3	6	1	2	2	2	2	2	1	1	2	2	1	2	2	2	2	1	1	1	2	2
2	2	1	4	3	3	2	2	1	1	1	1	1	2	2	2	2	2	2	2	2	1	1	1	2	2
1	1	2	4	3	4	2	2	1	2	2	1	2	2	2	2	2	?	2	2	2	1	1	2	2	2
2	2	2	1	3	1	2	2	2	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	2	2
2	1	1	3	3	5	2	2	2	1	1	1	2	1	2	2	2	?	2	2	2	1	1	2	1	2
?	?	2	4	1	4	1	2	2	2	1	2	1	1	1	1	1	1	1	1	1	1	2	1	2	2
1	1	2	4	1	4	1	2	2	2	1	1	2	2	2	2	1	1	2	1	1	1	1	1	1	2
2	2	?	4	2	4	1	1	1	1	1	1	2	1	2	2	2	?	2	2	2	2	1	2	2	2
2	2	2	2	3	2	2	2	2	1	1	2	2	1	2	2	2	?	2	2	2	2	2	2	1	2
2	1	1	4	2	6	1	1	2	2	2	1	1	1	1	2	2	?	2	2	2	2	1	1	1	2
2	1	1	2	3	3	1	2	2	2	1	1	2	1	1	2	2	?	2	1	1	1	1	1	2	2
2	2	2	4	3	4	2	2	1	2	2	1	2	1	2	2	1	2	2	1	1	2	1	1	1	2
1	1	2	4	3	4	2	2	1	1	1	2	2	2	2	2	1	2	2	2	2	2	1	1	2	2
1	2	1	4	1	6	1	2	2	1	1	2	2	1	2	1	2	2	2	2	2	1	1	2	2	2
1	1	2	1	2	3	2	2	1	1	1	1	2	2	2	2	1	2	2	2	1	2	1	2	1	2
1	1	1	4	1	6	1	2	2	1	1	2	2	1	1	2	1	2	1	2	1	1	1	2	1	2
2	2	1	4	2	5	2	2	1	1	1	2	2	1	2	2	1	2	2	2	2	2	1	2	2	2
?	?	1	4	2	2	1	2	2	2	1	1	1	2	1	2	2	?	1	2	1	1	1	1	2	2
2	2	1	3	3	3	1	2	2	1	1	2	2	1	2	2	2	?	1	1	1	2	1	1	1	2
2	2	1	4	1	3	1	2	2	2	1	2	2	1	2	2	2	?	2	2	1	1	1	1	1	2

Table 3a. Characters of the *Yponomeuta* species. The numbers behind the slash refer to the numbers in Table 2a.

01. Adult head: with 2 dots (1), with 4 dots (2), without dots (3)
02. Adult thorax: forewing: dots large (1), dots small of various size (2)
03. Adult thorax: forewing: with dark spots or suffusions (irrespective of dots) (1), without dark spots or suffusions (irrespective of dots) (2)
04. Adult thorax: forewing: with dots (1), without dots (2)
05. Adult thorax: forewing: dots arranged in 3 rows (1), dots arranged in 4 rows (2), dots arranged in 5 or more rows (3), dots not arranged in rows (4)
06. Adult thorax: forewing: ground colour white or greyish-white (1), ground colour not white or greyish-white (2)
07. Male genitalia: aedeagus: shorter than or nearly as long as valva (1), aedeagus longer than valva (2)
08. Male genitalia: aedeagus length : valva length: <1.5 : 1 (1), >1.5 : 1 (2)
09. Male genitalia: valva: with valvula (1), without valvula (2)
10. Male genitalia: valva: with cucullus (1), without cucullus (2)
11. Male genitalia: valva: of bean-like shape (1), of pear-like shape (2), of other shape (3)
12. Male genitalia: socius: of lobe-like shape (1), of finger-like shape (2)
13. Male genitalia: socius: with one claw (1), with two claws (2), without claws (3)
14. Male genitalia: saccus length : valva length: 1 : <2 (1), 1 : 2–3 (2), 1 : >3 (3)
15. Male genitalia: sacculus: equal or shorter than saccus (1), longer than saccus (2)
16. Male genitalia: aedeagus length: 1 : <2.5 (1), 1 : 2.5 – 4 (2), 1 : >5 (3)
17. Male genitalia: aedeagus length: 1 : <4 (1), 1 : >4 (2)
18. Female genitalia: signum: present (1), absent (2)
19. Female genitalia: signum: weakly spined (1), strongly spined (2)
20. Female genitalia: membranous folds between papillae analis: without denticles (1), denticulated (2)
21. Female genitalia: apophyses anteriores: nearly equal to apophyses posteriores (1), shorter than apophyses posteriores (2), longer than apophyses posteriores (3)
22. Female genitalia: membranous folds between papillae analis: elongated (1), not elongated (2)
23. Female genitalia: lobes of vaginal plate: arched (1), not arched (2)
24. Female genitalia: membranous folds between papillae analis: with sclerotized plate (1), without sclerotized plate (2)
25. Female genitalia: intersegmental sclerite between papillae analis: present (1), not present (2)
26. Female genitalia: papillae analis length : apophyses anteriores length: 1 : <2 (1), 1 : >2 (2)
27. Female genitalia: dorsal branch of apophyses anteriores equal or shorter than common stem (1), dorsal branch of apophyses anteriores longer than common stem (2)
28. Female genitalia: ventral branch of apophyses anteriores archely fused (1), not as such (2)
29. Female genitalia: apophyses posteriores length : common stem of apophyses anteriores length = <2 : 1 (1), >2 : 1 (2)
- 30/09. Adult thorax: forewings: length < 3.5 times width (1), length > 3.5 times width (2)
- 31/26. Male genitalia: gnathos: densely spined (1), without spines (2)
- 32/34. Male genitalia: gnathos: ventral plate tongue-shaped (1), ventral plate half circular (2), ventral plate spatulate (3), ventral plate rectangular (4), ventral plate triangular (5), ventral plate cylindrical (6)
- 33/41. Male genitalia: uncus: rectangular (1), half circular (2), triangular (3), quadrate (4), quadrate with 2 processes (5), rudimentary (6)
- 34/52. Male genitalia: saccus: slender (1), saccus broad not set from vinculum (2), saccus U-shaped not set from vinculum (3), saccus stout (4)
- 35/61. Male genitalia: vesica with: 1 cornutus (1), 2 cornuti (2), 4 cornuti (3), without cornuti (4)

Table 3b. Data matrix of the *Yponomeuta* species.

taxon/character	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
<i>E. unicornis</i> Moriuti, 1977 (♂)	3	2	1	1	3	2	1	1	2	2	1	2	1	3	2	2	1	?
<i>P. melanaster</i> (Meyrick, 1907)	3	2	2	1	1	2	2	2	2	2	3	1	2	1	2	1	1	1
<i>T. interruptella</i> Sauber, 1902	1	?	1	2	?	2	2	2	2	2	3	2	2	3	2	3	2	1
<i>Y. albognigratus</i> Gershenson, 1972	3	2	2	1	1	1	2	1	2	2	1	2	1	2	1	2	1	2
<i>Y. anaticus</i> Stringer, 1930	3	2	2	1	2	2	1	1	2	2	1	2	2	2	2	2	1	2
<i>Y. bipunctellus</i> Matsumura, 1931	3	2	1	1	3	2	2	1	2	2	2	2	2	1	2	2	1	2
<i>Y. cagnagellus</i> (Hübner, [1813])	3	2	2	1	1	1	2	1	2	2	1	2	1	1	1	2	1	2
<i>Y. catharotis</i> Meyrick, 1935	3	2	2	1	1	1	1	1	2	2	1	2	1	2	2	1	1	2
<i>Y. cinafactus</i> Meyrick, 1935	3	2	2	1	2	2	2	1	2	2	1	2	2	2	2	2	1	2
<i>Y. difflluellus</i> Heinemann, 1870 (♂)	3	2	2	1	4	1	2	1	2	2	1	2	1	1	1	1	?	?
<i>Y. eurinellus</i> Zagulajev, 1969	1	2	1	1	3	2	1	1	2	2	1	2	2	2	1	1	1	2
<i>Y. evonymellus</i> (Linnaeus, 1758)	3	2	2	1	3	1	2	1	2	2	1	2	1	1	1	1	2	1
<i>Y. falkovitsi</i> Gershenson & Ulenberg, 1998 (♀)	3	2	2	1	2	2	?	?	?	?	?	?	?	?	?	?	?	2
<i>Y. fumigatus</i> Zeller, 1852	2	2	2	1	1	2	2	2	2	1	3	1	3	1	1	3	2	1
<i>Y. gigas</i> Rebel, 1892	3	2	2	1	1	2	2	1	2	2	1	2	1	2	1	2	1	2
<i>Y. griseatus</i> Moriuti, 1977	3	2	1	1	2	2	2	1	2	2	1	2	2	1	1	2	1	2
<i>Y. griseomaculatus</i> Gershenson, 1969 (♀)	3	2	1	1	3	2	?	?	?	?	?	?	?	?	?	?	?	2
<i>Y. hemileucus</i> Meyrick, 1932	3	2	2	1	1	2	2	2	2	1	3	1	3	1	1	3	2	1
<i>Y. borologus</i> Meyrick, 1935 (♂)	3	2	2	1	1	1	2	2	1	2	3	2	2	1	1	1	1	?
<i>Y. internellus</i> Walker, 1863	3	2	2	1	2	1	2	2	2	3	3	2	1	3	2	?	?	1
<i>Y. irrorellus</i> (Hübner, 1796)	3	2	1	1	1	1	2	1	2	2	1	2	1	1	1	2	1	2
<i>Y. javanellus</i> Gershenson & Ulenberg, 1998 (♀)	3	2	2	1	3	1	?	?	?	?	?	?	?	?	?	?	?	2
<i>Y. kanaellus</i> Matsumura, 1931	3	2	2	1	1	1	2	1	2	2	1	2	1	1	2	2	1	2
<i>Y. kostjuki</i> Gershenson, 1985 (♀)	3	2	2	1	2	2	?	?	?	?	?	?	?	?	?	?	?	2
<i>Y. leucophaeus</i> Gershenson & Ulenberg (♀)	2	2	2	1	1	2	?	?	?	?	?	?	?	?	?	?	?	2
<i>Y. mahalebells</i> Guenée, 1845	3	2	2	1	1	1	2	1	2	2	1	2	1	1	1	1	2	2
<i>Y. malinellus</i> Zeller, 1838	3	2	2	1	1	1	2	1	2	2	1	2	1	1	1	2	1	2
<i>Y. mayumivorellus</i> Matsumura, 1931	3	2	2	1	2	2	2	1	2	2	1	2	2	1	2	2	1	2
<i>Y. meguronis</i> Matsumura, 1931	3	2	2	1	3	2	2	1	2	2	1	2	2	1	2	2	1	2
<i>Y. menkeni</i> Gershenson & Ulenberg (♂)	3	2	2	1	3	1	1	1	2	2	1	2	1	1	1	1	1	?
<i>Y. meraculus</i> Bradley, 1962	3	?	2	2	?	1	1	1	2	2	3	2	2	3	2	2	1	1
<i>Y. meridionalis</i> Gershenson, 1972	3	2	2	1	1	1	2	1	2	2	1	2	1	1	1	2	1	2
<i>Y. minipunctatus</i> Gershenson & Ulenberg (♂)	3	2	2	1	3	1	1	1	2	2	1	2	1	2	1	2	1	?
<i>Y. mintemius</i> (Povel, 1985) (♂)	2	2	2	1	1	2	2	2	2	1	3	2	2	2	1	2	2	?
<i>Y. minuellus</i> Walker, 1863	3	2	2	1	3	1	2	1	2	2	1	2	1	1	1	2	1	2
<i>Y. montanatus</i> Moriuti, 1977 (♀)	3	2	2	1	3	2	?	?	?	?	?	?	?	?	?	?	?	2
<i>Y. morbillosus</i> Zeller, 1877	?	2	1	1	?	2	2	2	2	2	3	2	1	1	1	2	1	1
<i>Y. multipunctellus</i> Clemens, 1860	3	2	2	1	2	1	2	2	2	2	1	2	1	2	2	2	2	2
<i>Y. myriosemus</i> Turner, 1898	3	2	2	1	1	1	2	2	2	2	1	2	2	2	2	3	2	?
<i>Y. orientalis</i> Zagulajev, 1969	3	2	2	1	2	1	2	1	2	2	1	2	1	2	1	2	1	2
<i>Y. osakae</i> Moriuti, 1977 (♂)	3	2	2	1	2	2	2	1	2	2	1	2	2	2	1	2	1	?
<i>Y. padellus</i> (Linnaeus, 1758)	3	2	2	1	1	1	2	1	2	2	1	2	1	1	1	2	1	2
<i>Y. paradoxus</i> Gershenson, 1979 (♀)	3	2	2	1	1	1	?	?	?	?	?	?	?	?	?	?	?	2
<i>Y. parvipunctus</i> Gershenson & Ulenberg, 1998 (♀)	3	2	2	1	2	2	?	?	?	?	?	?	?	?	?	?	?	1
<i>Y. pauciflore</i> Efremov, 1969	3	2	2	1	3	1	2	1	2	2	1	?	1	1	2	2	1	2
<i>Y. paurodes</i> Meyrick, 1907	3	2	2	1	1	1	2	2	2	2	3	2	1	3	2	3	1	1
<i>Y. plumbellus</i> (Denis & Schiffermüller, 1775)	3	2	1	1	2	1	2	1	2	2	2	2	1	2	2	2	1	2
<i>Y. polystictus</i> Butler, 1879	3	2	2	1	3	1	2	1	2	2	1	2	1	1	1	2	1	2
<i>Y. polystigmellus</i> C. et R. Felder, 1862	3	2	2	1	3	1	2	1	2	2	1	2	1	1	1	2	1	2
<i>Y. pseudostrigillatus</i> Gershenson & Ulenberg, 1998	3	1	2	1	3	1	2	2	1	2	3	2	1	1	1	2	1	1
<i>Y. pustulellus</i> Walker, 1863	1	1	2	1	2	1	2	2	2	2	3	2	1	3	2	3	1	1
<i>Y. refrigeratus</i> Meyrick, 1931	3	2	2	1	3	1	2	1	2	2	1	2	1	2	2	2	1	2
<i>Y. rhannellus</i> Gershenson, 1974 (♂)	3	2	2	1	1	1	2	1	2	2	1	2	1	1	1	2	1	?
<i>Y. rorrellus</i> (Hübner, 1796)	3	2	2	1	1	1	2	1	2	2	1	2	1	2	1	2	1	2
<i>Y. sedellus</i> Treitschke, 1832	3	2	2	1	1	2	2	1	2	2	1	2	2	2	2	2	1	2
<i>Y. sistrophorus</i> Meyrick, 1909 (♀)	2	2	2	1	1	2	?	?	?	?	?	?	?	?	?	?	?	1
<i>Y. sociatus</i> Moriuti, 1972	3	2	2	1	3	1	2	1	2	2	1	2	1	1	1	2	1	2
<i>Y. spodocrossus</i> Meyrick, 1935	3	2	2	1	2	1	2	1	2	2	1	2	1	1	1	2	1	2
<i>Y. strigillatus</i> Zeller, 1852	3	1	2	1	3	1	2	2	2	2	3	1	1	2	2	2	1	1
<i>Y. subplumbellus</i> Walsingham, 1881	3	2	2	1	1	2	2	2	2	2	2	2	1	2	2	3	2	1
<i>Y. tokyonellus</i> Matsumura, 1931	3	2	2	1	3	1	2	1	2	2	1	2	1	1	1	2	1	2
<i>Y. yanagawanus</i> Matsumura, 1931	3	2	1	1	2	2	2	1	2	2	1	2	2	2	1	2	1	2
<i>Y. zagulajevi</i> Gershenson, 1977 (♀)	3	2	2	1	1	1	?	?	?	?	?	?	?	?	?	?	?	2

Table 3b continued. Data matrix of the *Yponomeuta* species.

taxon/character	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35
<i>E. unicornis</i> Moriuti, 1977 (♂)	?	?	?	?	?	?	?	?	?	?	?	2	2	2	2	4	1
<i>P. melanaster</i> (Meyrick, 1907)	2	1	2	2	1	2	1	1	1	2	2	2	2	2	1	4	4
<i>T. interruptella</i> Sauber, 1902	2	1	2	2	1	2	1	1	?	2	?	2	2	2	1	4	4
<i>Y. albonigratus</i> Gershenson, 1972	?	2	1	2	1	2	1	1	1	2	1	1	1	4	4	1	3
<i>Y. anatolicus</i> Stringer, 1930	?	1	3	1	1	2	2	2	1	2	2	1	1	4	4	1	3
<i>Y. bipunctellus</i> Matsumura, 1931	?	1	1	2	1	2	2	2	1	2	2	1	1	4	4	1	3
<i>Y. cagnagellus</i> (Hübner, [1813])	?	2	2	2	1	2	1	1	1	2	2	1	1	4	4	1	3
<i>Y. catharotis</i> Meyrick, 1935	?	2	1	1	1	2	2	1	1	2	1	1	1	4	4	1	3
<i>Y. cinefactus</i> Meyrick, 1935	?	1	1	2	1	2	2	1	2	2	1	1	1	4	4	1	3
<i>Y. diffuellus</i> Heinemann, 1870 (♂)	?	?	?	?	?	?	?	?	?	?	?	1	1	4	4	1	3
<i>Y. eurinellus</i> Zagulajev, 1969	?	1	1	2	1	2	2	1	1	2	1	1	1	4	4	1	3
<i>Y. evonymellus</i> (Linnaeus, 1758)	?	2	2	2	1	2	1	1	2	2	2	1	1	4	4	1	3
<i>Y. falkovitschi</i> Gershenson & Ulenberg, 1998 (♀)	?	1	3	2	1	2	1	2	1	2	1	1	?	?	?	?	?
<i>Y. fumigatus</i> Zeller, 1852	2	1	3	2	1	2	2	1	2	2	1	1	1	4	4	1	3
<i>Y. gigas</i> Rebel, 1892	?	2	1	2	1	2	1	1	1	2	2	1	1	4	4	1	3
<i>Y. griseatus</i> Moriuti, 1977	?	1	1	2	1	2	2	2	1	2	2	1	1	4	4	1	3
<i>Y. griseomaculatus</i> Gershenson, 1969 (♀)	?	1	1	2	1	2	1	1	1	2	1	1	?	?	?	?	?
<i>Y. hemileucus</i> Meyrick, 1932	2	1	3	2	1	2	2	1	2	2	1	1	1	4	4	1	3
<i>Y. horologus</i> Meyrick, 1935 (♂)	?	?	?	?	?	?	?	?	?	?	?	1	1	4	4	1	3
<i>Y. internellus</i> Walker, 1863	1	2	1	2	1	2	2	1	1	2	1	1	1	4	4	1	3
<i>Y. irrorellus</i> (Hübner, 1796)	?	2	1	2	1	2	1	2	1	2	1	1	1	4	4	1	3
<i>Y. javanellus</i> Gershenson & Ulenberg, 1998 (♀)	?	1	1	1	1	2	2	2	2	2	2	1	?	?	?	?	?
<i>Y. kanaellus</i> Matsumura, 1931	?	1	3	1	1	2	2	2	2	2	2	1	1	4	4	1	3
<i>Y. kostjuki</i> Gershenson, 1985 (♀)	?	1	3	2	1	2	2	2	1	2	2	1	?	?	?	?	?
<i>Y. leucophaeus</i> Gershenson & Ulenberg (♀)	?	1	1	2	1	2	2	2	1	2	1	1	?	?	?	?	?
<i>Y. mahalebells</i> Guenée, 1845	?	2	2	2	1	2	1	1	1	2	2	1	1	4	4	1	3
<i>Y. malinellus</i> Zeller, 1838	?	2	2	2	1	2	1	1	2	2	2	1	1	4	4	1	3
<i>Y. mayumivorellus</i> Matsumura, 1931	?	1	1	2	1	2	2	1	1	2	1	1	1	4	4	1	3
<i>Y. meguronis</i> Matsumura, 1931	?	1	2	1	1	2	2	1	2	2	2	1	1	4	4	1	3
<i>Y. menkeni</i> Gershenson & Ulenberg (♂)	?	?	?	?	?	?	?	?	?	?	?	1	1	4	4	1	3
<i>Y. meraculus</i> Bradley, 1962	2	1	1	2	1	2	2	1	2	2	2	1	1	4	4	1	3
<i>Y. meridionalis</i> Gershenson, 1972	?	2	1	2	1	2	1	1	2	2	2	1	1	4	4	1	3
<i>Y. minipunctatus</i> Gershenson & Ulenberg (♂)	?	?	?	?	?	?	?	?	?	?	?	1	1	4	4	1	3
<i>Y. mintennus</i> (Povel, 1985) (♂)	?	?	?	?	?	?	?	?	?	?	?	1	1	4	4	1	3
<i>Y. minuellus</i> Walker, 1863	?	1	1	2	1	2	2	1	2	2	2	1	1	4	4	1	3
<i>Y. montanatus</i> Moriuti, 1977 (♀)	?	1	1	2	1	2	2	1	1	2	2	1	?	?	?	?	?
<i>Y. morbillus</i> Zeller, 1877	1	1	3	2	2	2	1	1	1	2	1	1	1	4	4	1	3
<i>Y. multipunctellus</i> Clemens, 1860	?	2	2	2	?	2	2	1	1	2	2	1	1	4	4	1	3
<i>Y. myriosemus</i> Turner, 1898	?	?	?	?	?	?	?	?	?	?	?	1	1	4	4	1	3
<i>Y. orientalis</i> Zagulajev, 1969	?	2	1	2	1	2	1	1	1	2	1	1	1	4	4	1	3
<i>Y. osakae</i> Moriuti, 1977 (♂)	?	?	?	?	?	?	?	?	?	?	?	1	1	4	4	1	3
<i>Y. padellus</i> (Linnaeus, 1758)	?	2	2	2	1	2	1	1	2	2	2	1	1	4	4	1	3
<i>Y. paradoxus</i> Gershenson, 1979 (♀)	?	2	1	2	1	2	1	1	1	2	1	1	?	?	?	?	?
<i>Y. parvipunctus</i> Gershenson & Ulenberg, 1998 (♀)	2	1	1	2	1	1	2	1	1	1	1	1	?	?	?	?	?
<i>Y. pauciflore</i> Efremov, 1969	?	1	1	2	1	2	2	2	1	2	2	1	1	4	4	1	3
<i>Y. pauroides</i> Meyrick, 1907	1	1	3	2	1	2	2	1	2	2	2	1	1	4	4	1	3
<i>Y. plumbellus</i> (Denis & Schiffermüller, 1775)	?	1	2	2	1	2	2	2	2	2	2	1	1	4	4	1	3
<i>Y. polystictus</i> Butler, 1879	?	1	1	2	1	2	2	1	2	2	2	1	1	4	4	1	3
<i>Y. polystigmellus</i> C. et R. Felder, 1862	?	1	1	2	1	2	2	1	1	2	2	1	1	4	4	1	3
<i>Y. pseudostrigillatus</i> Gershenson & Ulenberg, 1998	1	1	1	2	2	2	2	2	1	1	2	1	1	4	4	1	3
<i>Y. pustulellus</i> Walker, 1863	1	2	1	2	1	2	2	1	1	2	1	1	1	4	4	1	3
<i>Y. refrigeratus</i> Meyrick, 1931	?	2	1	2	1	2	1	1	1	2	1	1	1	4	4	1	3
<i>Y. rhamnellus</i> Gershenson, 1974 (♂)	?	?	?	?	?	?	?	?	?	?	?	1	1	4	4	1	3
<i>Y. rorrellus</i> (Hübner, 1796)	?	2	2	2	1	2	1	1	1	2	2	1	1	4	4	1	3
<i>Y. sedellus</i> Treitschke, 1832	?	2	1	2	1	2	1	1	1	2	1	1	1	4	4	1	3
<i>Y. sistrophorus</i> Meyrick, 1909 (♀)	1	?	?	?	?	?	?	?	?	?	?	1	?	?	?	?	?
<i>Y. sociatus</i> Moriuti, 1972	?	1	1	2	1	2	2	1	2	2	2	1	1	4	4	1	3
<i>Y. spodocrossus</i> Meyrick, 1935	?	1	1	1	1	2	2	1	1	2	2	1	1	4	4	1	3
<i>Y. strigillatus</i> Zeller, 1852	1	1	2	2	1	1	2	2	2	2	2	1	1	4	4	1	3
<i>Y. subplumbellus</i> Walsingham, 1881	1	1	1	2	1	2	2	2	1	2	2	1	1	4	4	1	3
<i>Y. tokyonellus</i> Matsumura, 1931	?	1	3	2	1	1	2	2	1	2	2	1	1	4	4	1	3
<i>Y. yanagawanus</i> Matsumura, 1931	?	1	1	2	1	2	2	2	1	2	2	1	1	4	4	1	3
<i>Y. zagulajevi</i> Gershenson, 1977 (♀)	?	1	2	2	1	2	2	2	1	2	2	1	?	?	?	?	?

Table 4. Host plant associations of the genera of the Yponomeutinae.

<i>Saridoscelis</i>	Celastraceae
<i>Banghaasia</i>	Unknown
<i>Cedestis</i>	Ericaceae and Pinaceae
<i>Euhypnomeuta</i>	Crassulaceae
<i>Euhypnomeutoides</i>	Celastraceae and Grossulariaceae
<i>Eumonopyta</i>	Unknown
<i>Kessleria</i>	Coriariaceae and Saxifragaceae
<i>Klausius</i>	Unknown
<i>Lampresthia</i>	Unknown
<i>Metanomeuta</i>	Unknown
<i>Niphonympha</i>	Unknown
<i>Ocnerostoma</i>	Pinaceae
<i>Orencostoma</i>	Unknown
<i>Paraswammerdamia</i>	Betulaceae, Empetraceae and Rosaceae
<i>Pseudoswammerdamia</i>	Rosaceae
<i>Ptiloteina</i>	Rubiaceae
<i>Swammerdamia</i>	Betulaceae, Crassulaceae, and Rosaceae
<i>Teinoptila</i>	Celastraceae
<i>Thecobathra</i>	Fagaceae and Hamamelidaceae
<i>Xyrosaris</i>	Celastraceae
<i>Yponomeuta</i>	Celastraceae, Crassulaceae, Rhamnaceae, Rosaceae and Salicaceae
<i>Zelleria</i>	Caprifoliaceae, Celastraceae, Epacridaceae, Loranthaceae, Myrtaceae, Rhamnaceae, and Oleaceae

Table 5. Host plant associations and distribution of 60 species of *Yponomeuta* Latreille, *Eumonopyta unicornis* Moriuti, *Priloteina melanaster* (Meyrick), and *Teinoptila interruptella* Sauber.

Host plants: Rubiaceae (1), Celastraceae (2), Salicaceae (3), Rosaceae (4), Rhamnaceae (5), Crassulaceae (6)

Distribution: West Palaearctic (1), East Palaearctic (2), Japan (3), Trans Palaearctic (4), Africa (5), Australia (6), South East Asia (7), North America (8)

Distribution according to biogeographic regions (Cox 2001): Eurasian (1), African (2), Oriental (3), Australian (4), New Zealand (5), North American (6)

moth species	Host plants	Distribution	Biogeographic region
<i>E. unicornis</i>	?	3: Japan	1 Eurasian
<i>P. melanaster</i>	1 Rubiaceae (<i>Plectronia wightii</i>)	7: India, Philippines, Sri Lanka (other <i>Priloteina</i> sp. 5: Africa)	3 Oriental (other <i>Priloteina</i> sp.: 2 African)
<i>T. interruptella</i>	? (other <i>Teinoptila</i> spp: 2 Celastraceae: <i>Euonymus japonicus</i>)	6, 7: Australia, New Guinea, Philippines, Tukangbesi Islands (other <i>Teinoptila</i> spp. 3, 5, 7: Africa, China, India, Japan, Java, Thailand)	3, 4 Oriental & Australian (other <i>Teinoptila</i> spp.: 1 Eurasian, 2 African, 3 Oriental)
<i>Y. albonigratus</i>	3 Salicaceae (<i>Salix oxycarpa</i>)	2: Kirgizia, Tadzjikistan, Uzbekistan	1 Eurasian
<i>Y. anatolicus</i>	2 Celastraceae (<i>E. sp.</i>)	2: Russia, 3: Japan	1 Eurasian
<i>Y. bipunctellus</i>	2 Celastraceae (<i>E. fortunei</i>)	3: Japan	1 Eurasian
<i>Y. cagnagellus</i>	2 Celastraceae (<i>E. europaeus</i> , <i>E. verrucosus</i>)	1: Caucasus, Europe	1 Eurasian
<i>Y. catharotis</i>	2 Celastraceae (<i>E. alatus</i>)	2: China, Russia	1 Eurasian
<i>Y. cinefactus</i>	2 Celastraceae (<i>E. sp.</i>)	2: China, Russia	1 Eurasian
<i>Y. diffluellus</i>	?	2: Poland, Russia	1 Eurasian
<i>Y. eurinellus</i>	2 Celastraceae <i>E. macropterus</i> , <i>E. oxyphyllus</i>)	2: China, Russia, 3: Japan	1 Eurasian
<i>Y. evonymellus</i>	4 Rosaceae (<i>Prunus asiatica</i> , <i>P. cerasus</i> , <i>P. domestica</i> , <i>P. padus</i> , <i>Sorbus aucuparia</i>)	4: Trans Palaearctic	1 Eurasian
<i>Y. falkovitshi</i>	?	2: Russia	1 Eurasian
<i>Y. fumigatus</i>	?	5: Congo, Kenya, South Africa	2 African
<i>Y. gigas</i>	3 Salicaceae (<i>Populus alba</i> , <i>Salix canariensis</i>)	5: Canary Islands	2 African
<i>Y. griseatus</i>	2 Celastraceae (<i>E. sp.</i>)	3: Japan	1 Eurasian
<i>Y. griseomaculatus</i>	?	2: Russia	1 Eurasian
<i>Y. hemileucus</i>	?	5: Uganda, Zaire	2 African
<i>Y. horologus</i>	?	5: Congo	2 African
<i>Y. internellus</i>	2 Celastraceae (<i>Cassine australis</i>)	6: Australia	4 Australian
<i>Y. irrorellus</i>	2 Celastraceae (<i>E. europaeus</i> , <i>E. verrucosus</i>)	1: Caucasus, Europe	1 Eurasian
<i>Y. javanellus</i>	?	7: East Java	3 Oriental
<i>Y. kanaiellus</i>	2 Celastraceae (<i>E. alatus</i>)	3: Japan	1 Eurasian
<i>Y. kostjuki</i>	?	2: Russia	1 Eurasian
<i>Y. leucophaeus</i>	?	7: East Java	3 Oriental
<i>Y. mahalebells</i>	4 Rosaceae (<i>Prunus mahaleb</i> , <i>P. avium</i> , <i>P. cerasus</i> , <i>P. spinosa</i>)	1: Europe	1 Eurasian
<i>Y. malinellus</i>	4 Rosaceae (<i>Malus praecox</i> , <i>M. sylvestris</i>)	1: Caucasus, Europe	1 Eurasian
<i>Y. mayumivorellus</i>	2 Celastraceae (<i>E. fortunei</i> , <i>E. sieboldianus</i>)	3: Japan	1 Eurasian
<i>Y. meguronis</i>	2 Celastraceae (<i>E. fortunei</i> , <i>E. japonicus</i>)	3: Japan	1 Eurasian
<i>Y. menkeni</i>	2 Celastraceae (<i>E. alatus</i> , <i>E. sieboldianus</i>)	3: Japan	1 Eurasian

moth species	Host plants	Distribution	Biogeographic region
<i>Y. meraculus</i>	?	6: New Hebrides	5 New Zealand
<i>Y. meridionalis</i>	4 Rosaceae (<i>Crataegus korokowii</i> , <i>C. songarica</i> , <i>C. turkestanica</i>)	2: Tadzhikistan	1 Eurasian
<i>Y. minipunctatus</i>	?	7: India	3 Oriental
<i>Y. mintennus</i>	2 Celastraceae (<i>E. japonicus</i>)	7: Java	3 Oriental
<i>Y. minuellus</i>	?	7: India, Nepal	3 Oriental
<i>Y. montanatus</i>	2 Celastraceae (<i>E. oxyphyllus</i>)	3: Japan	1 Eurasian
<i>Y. morbillosus</i>	?	5: Kenya, Zanzibar	2 African
<i>Y. multipunctellus</i>	2 Celastraceae	8 North America	6 North American
<i>Y. myriosemus</i>	?	6: Australia	4 Australian
<i>Y. orientalis</i>	4 Rosaceae (<i>M. halliana</i> , <i>M. micromalus</i> , <i>M. pallasiana</i> , <i>M. pumila</i> , <i>M. sieboldii</i>)	2: Russia, 3: Japan	1 Eurasian
<i>Y. osakae</i>	2 Celastraceae (<i>E. sieboldianus</i>)	3: Japan	1 Eurasian
<i>Y. padellus</i>	4 Rosaceae (spp. of <i>Amelanchier</i> , <i>Cotoneaster</i> , <i>Malus</i> , <i>Prunus</i> , <i>Sorbus</i>)	1: Caucasus, Europe, Middle East)	1 Eurasian
<i>Y. paradoxus</i>	?	2: Armenia	1 Eurasian
<i>Y. parvipunctus</i>	?	5: Zaire	2 African
<i>Y. pauciflore</i>	2 Celastraceae (<i>E. pauciflorus</i>)	2: Russia	1 Eurasian
<i>Y. paurodes</i>	2 Celastraceae (<i>Cassine australis</i> , <i>Elaeodendron</i> sp.)	6: Australia	4 Australian
<i>Y. plumbellus</i>	2 Celastraceae (<i>E. europaeus</i> , <i>E. verrucosus</i>)	1: Anatolia, Caucasus, Europe	1 Eurasian
<i>Y. polystictus</i>	2 Celastraceae (<i>E. maackii</i> , <i>E. oxyphyllus</i> , <i>E. sieboldianus</i>)	2: China, Russia, 3: Japan	1 Eurasian
<i>Y. polystigmellus</i>	2 Celastraceae (<i>E. alatus</i> , <i>E. sieboldianus</i>)	2: China, Russia, 3: Japan	1 Eurasian
<i>Y. pseudostrigillatus</i>	?	5: Cameroon, Congo	2 African
<i>Y. pustulellus</i>	2 Celastraceae (<i>Cassine australis</i> , <i>Elaeodendron</i> sp.)	6: Australia	4 Australian
<i>Y. refrigeratus</i>	2 Celastraceae (<i>E. maackii</i>)	2: Russia, 3: Japan	1 Eurasian
<i>Y. rhamnellus</i>	5 Rhamnaceae (<i>Rhamnus catharticus</i>)	2: Ukraine	1 Eurasian
<i>Y. rorrellus</i>	3 Salicaceae (<i>Salix</i> spp.)	1: Caucasus, Europe	1 Eurasian
<i>Y. sedellus</i>	6 Crassulaceae <i>Hylotelephium</i> <i>taqueti</i> , <i>Sedum</i> spp.)	4: Trans Palaearctic	1 Eurasian
<i>Y. sistrophorus</i>	?	5: South Africa	2 African
<i>Y. sociatus</i>	2 Celastraceae (<i>Celastrus orbiculatus</i> , <i>E. macropterus</i>)	3: Japan	1 Eurasian
<i>Y. spodocrossus</i>	2 Celastraceae (<i>E. macropterus</i> , <i>E. sieboldianus</i>)	3: Japan	1 Eurasian
<i>Y. strigillatus</i>	?	5: Burundi, Cameroon, Ghana, Kenya, South Africa	2 African
<i>Y. subplumbellus</i>	?	5: South Africa, Zimbabwe	2 African
<i>Y. tokyonellus</i>	2 Celastraceae (<i>E. sieboldianus</i>)	2: China, 3: Japan	1 Eurasian
<i>Y. yanagawanus</i>	2 Celastraceae (<i>E. alatus</i> , <i>E. japonicus</i> , <i>E. sp.</i>)	3: Japan	1 Eurasian
<i>Y. zagulajevi</i>	2 Celastraceae (<i>E. alatus</i>)	2: China, Russia	1 Eurasian