A Cladistic Analysis of the Therini: 
A New Synonym of the Cidariini 
(Lepidoptera: Geometridae, Larentiinae) 

SEI-WOONG CHOI¹

ABSTRACT

To test the monophyly of the tribe Therini and resolve the relationship between Therini and Cidariini, 49 morphological characters of 38 species of Thera and related genera were analyzed cladistically. Five taxa from the Cidariini were chosen for outgroup comparisons. Monophyly of the Therini was not supported and the Therini newly synonymized with Cidariini. Five genera, Praethera Viidalepp, Thera Stephens, Pennithera Viidalepp, Heterothera Inoue, and Diathera Choi, are redefined monophyletically, and two new monotypic genera are proposed: Costicoma, n. gen. and Fascilunaria, n. gen. The combination Thera firmata (Hübner) is proposed. Relationships among the ingroup taxa are largely resolved: (Fascilunaria (Heterothera (Thera (Diathera, Pennithera)))). Synapomorphies and a diagnosis of each genus are given, and a key to the ingroup genera is provided.

INTRODUCTION

The geometrid subfamily Larentiinae is distributed worldwide and approximately 39 genera are shared among the Palearctic and Nearctic regions. Therini is a tribe of the Larentiinae and the type genus Thera Stephens occurs in the Holarctic region. Pierce (1914) placed Thera as a distinct group, Therinae, which is now referred to as a tribe (Holoway, 1997). Concurrently, Prout (1914) placed Thera as a subgenus within Cidaria, sensu lato, and subdivided the genus into two subgenera separated by the structure of the male antennae (shortly ciliated vs. bipectinate). Later, Prout (1941) upgraded Thera to the generic level.

Since the works of Pierce and Prout, several new genera and species within the Therini have been described, mainly from the

¹ Kalbfleisch Fellow, Division of Invertebrate Zoology, American Museum of Natural History.

Here I present a cladistic analysis of the Therini based on adult morphology. The analysis will focus on two things. First, a test of the monophyly of the Therini and an examination of relationships between Therini and Cidarini. Since my previous cladistic analysis (Choi, 1997), several papers have described additional members of the Cidarini (*Paradysstroma* Choi, 1998 and *Pseudodysstroma* Heydemann, 1961) and Therini (*Heterothera* and *Diathera*) (Choi, 1998a, 1998b, 1999) and confused our understanding of the phylogeny of these moths. Many synapomorphies for *Pennithera*, *Heterothera*, and *Thera* were found to be homoplastic, also occurring in *Paradysstroma* and *Pseudodysstroma*. For example, the presence of cucullus hairs and saccular processes in the male genitalia were synapomorphic for *Heterothera*, but these occur in *Pseudodysstroma* and *Diathera* as well. Similarly the corona-shaped processes at the distal part of the aedeagus, an autapomorphic character for *Thera*, is also observed in several species of *Heterothera* (see Choi, 1998a). Such homoplasy prompted the present analysis.

The second focal point is to understand the generic placement of *Thera exangulata* (Warren) and *T. cyphoschema* Prout. These taxa were included in the Therini by Prout (1938, 1941). Although I have described the genitalia and other aspects of morphology of these species (Choi, 1998a), the placement of these taxa remains uncertain.

Members of the Therini occur mainly in
Asia, except for *Thera*, which is Holarctic in distribution. Many of the Asian species are endemic to southwestern China, Taiwan, or northern India: four species of *Pennithera* and two species of *Heterothera* are endemic to Taiwan; six species of *Heterothera*, and all species of *Diathera* are endemic to southwestern China; and eight species of *Heterothera* are endemic to northern India. Thus, understanding of interrelationships of *Thera* and other Asian genera will provide the basis for future biogeographic studies.

**MATERIALS AND METHODS**

**TAXA AND CHARACTERS**

The ingroup comprised 38 species from the Holarctic and northern Oriental regions: 7 species of *Thera*, 1 *Praethera*, 8 *Pennithera*, 17 *Heterothera*, 3 *Diathera*, as well as "*Thera cyphoschema*" and "*T. exangulata*" (see appendix 1). In total, 49 characters from the genitalia and other morphological structures were used.

Adult specimens were obtained from the following museums and private collections: American Museum of Natural History, New York; Bulgarian Natural History Museum, Sofia; Hungarian Natural History Museum, Budapest; Institute of Botany and Zoology, Tartu; private collection of Katsumi Yazaki, Tokyo; The Natural History Museum, London; Zoologisches Forschungsinstitut und Museum Alexander Koenig, Bonn; Zoologisches National Museum, Helsinki; and Zoologische Staatssammlung München, Munich. Male and female genitalia were prepared by soaking the abdomen in cold 10% KOH for approximately 24 hours. Scales and tissues were removed, stained with Chlorazol Black, and mounted on slides in Euparal. Electron micrographs were taken with a Hitachi S4700 Field Emission Scanning Electron Microscope (FE-SEM). Morphological terms follow Forbes (1948) and Scoble (1992).

**CLADISTIC ANALYSIS**

The data matrix is provided in table 1. Five outgroups were used to root cladograms, all belonging to the tribe Cidariini: *Cidaria fulvata* (Forster), *Plemyria rubiginata* (Denis and Schiffermüller), *Dysstroma truncatum* (Hufnagel), *Paradysstroma corussarium* (Oberthür), and *Pseudodysstroma albovenosatum* (Heydemann). The choice of these outgroups was based on (1) a close relationship as shown by a previous cladistic analysis (*C. fulvata*, *P. rubiginata*, and *D. truncatum*; Choi, 1997) and (2) the fact that they share apomorphic characters with ingroup taxa for which ingroup relationships are ambiguous (*Paradysstroma corussarium* and *Pseudodysstroma albovenosatum*).

A parsimony-based computer program, NONA (Goloboff, 1993; Ver. 1.5; hold*hold/30mult*15), was used to find the most parsimonious trees. Multistate characters were treated as unordered during analyses.

**ACKNOWLEDGMENTS**

My sincere thanks to Jaan Viidalepp for providing material and translating his work (1980) into English and to David Grimaldi, Jim Miller, Fred Rindge, Toby Schuh (AMNH), Kauri Mikkola, and Malcolm Scoble for commenting on several versions of this manuscript and to Katsumi Yazaki (Tokyo), Kim Goodger (BMNH), Axel Hausmann (ZSM), and Dieter Stüning (ZFMK) for loaning material. Angela Klaus (AMNH) provided helpful assistance with scanning electron microscopy. I am very grateful to David Grimaldi, Michael Engel, Michael Pogue, and Jim Troubridge for reading the manuscript and offering appreciated criticism.

**RESULTS AND DISCUSSION**

**CHARACTER ANALYSIS**

Of the 49 characters, numbers 0–11 were from the head, thorax, and wing patterns; numbers 12–35 were from the male genitalia; and numbers 36–48 from the female genitalia.

**HEAD AND BODY** (figs. 2–23)

0. **Antennae of male**: (0) filiform; (1) pectinate. It is usual for species of moths in the Larentiinae to be diagnosed on the basis of bipectinate male antennae. Prout (1914) suggested that the groupings based on the antennal morphology of males or of both sexes do not always form natural taxa. However, even...
he classified *Thera* using this character, and his groupings were subsequently found to be polyphyletic (Viidalepp, 1980; Choi, 1997). *Thera* and *Praethera* have filiform antennae in both sexes, but *Pennithera* and *Heterothera* have bipectinate male antennae and filiform female antennae.

A study with the scanning electron microscope shows that there are four modifications of the male antennae; filiform with either short cilia (fig. 19) or long cilia (fig. 18), and pectinate with either short pectinations (fig. 21) or long pectinations (figs. 20, 22, 23). It was noted that the pectinations of some

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todontidae moths are shorter on one side (Miller, 1991). The difference in length is observed in an ingroup species, Heterothera firmata (fig. 20). Vidalepp (1980) and Inoue (1986a) illustrated the differences in pectination between these genera. The present results show that pectinations are quadripectinate, but differ in orientation, opposite (Heterothera firmata, H. taigana, H. serraria; figs. 20, 21, 23) or alternate (Pennithera comis; fig. 22). Different lengths of pectinations or cilia are common among the taxa examined and are difficult to code. Thus, I used two simple states, filiform versus pectinate.

1. Vertex: (0) black; (1) distinct with white scales. The vertex can be covered with either black or white scales. Several species

of *Heterothera* and *Pennithera* have white scales on the vertex [e.g., *Heterothera eclinosis* Choi, *H. yunannensis* Choi, *H. hoenei* Choi, *Pennithera abolla* (Inoue), *P. lugubris* Inoue, *P. subalpina* Inoue].

2. **Frons**: (0) covered with uniformly colored scales; (1) mixed white or ochreous and blackish scales. Most of the ingroup taxa have the frons covered with white/ochreous or blackish scales. Choi (1997) noted also that a rounded frons occurs in *Thera* and

*Heterothera*, and that this is an apomorph character of Cidarini.

3. **Foretarsal joints**: (0) indistinct in that scales covering them are same color as scales on rest of leg; (1) distinct with white scales. The tarsal joints of forelegs are usually distinct with white scales in *Thera*, *Praethera*, and *Diathera*, but are indistinct in several species of *Pennithera* [comis (Butler) and abolla (Inoue)] and *Heterothera* [serraria (Lienig), serrataria (Prout) and kurenzovi
Obscure tarsal joints are also observed in the outgroup taxa, except in *Cidaria fulvata* (which has white scales on the joints).

4. **Meso- and metathorax**: (0) middorsally white; (1) black.

5. **Metathorax**: (0) with white or yellow tufts; (1) with blackish tufts. Strong tufts occur on the dorsum of the metathorax, and this is often observed in some other taxa of the Larentiinae (Prout, 1914). It was noted that strong tufts occur on the metathorax in members of the Hydriomenini (Forbes, 1948) and Cidarini (Choi, 1997).

**WINGS** (figs. 2–17)

6. **Shape of antemedial line of forewing, from costa to dorsum**: (0) transverse, straight; (1) rounded or medially indented; (2) outwardly oblique.

7. **Forewing between basal and antemedial lines**: (0) unicolorous; (1) tinged with black scales.

8. **Basal part of forewing dorsally with a black dot**: (0) absent; (1) present, but dot small; (2) dot large. The pattern in the area between the basal and antemedial lines of the forewing varies in Therini. *Pennithera* is distinct by having a black dot on the dorsum. Some species of *Heterothera* [e.g., *quadrifulta* (Prout), *taigana* (Djakonov), *incerta* Inoue, and *consimilis* (Warren)] also have a small dot at the dorsum, but they differ from *Pennithera* in having a black band in the area between basal and antemedial lines (figs. 3, 4, 12, 13).

9. **Discal dot of forewing united with costal part of antemedial line**: (0) absent; (1) present. *Heterothera firmata* (Hübner), *H. etes* (Prout), and *Thera cyphoschema* have a long, thick discal dot united with the costal part of the antemedial line (fig. 10).
10. **Dorsum of central fascia:** (0) indistinct and uniform; (1) distinct with black scales.

11. **Dorsum of forewing:** (0) without a streak; (1) with a black horizontal streak.

There are three patterns of black dots in *Pennithera* and *Heterothera*: (1) a large round dot between the basal and antemedial line (e.g., *Pennithera lugubris* and *P. subcomis*) (figs. 12–13), (2) a long horizontal streak along the basal and central fascia (e.g., *Heterothera postalbida* (Wileman), *H. sororcula*).
Male Genitalia

12. Length of uncus compared to tegumen (figs. 24–28): (0) shorter; (1) longer. Three species of Diathera show a very long uncus compared to the length of tegumen and this long uncus is also observed in most species of Pennithera and Heterothera.

13. Length of tegumen compared to the total length of vinculum and saccus: (0) same; (1) longer; (2) shorter. Tegumen length is measured against the total length of the vinculum and saccus. This character divides Therini into three groupings: (Praethera), (Pennithera and Thera), and (Heterothera and Diathera). Praethera has a long tegumen, whereas Thera and Pennithera have a short tegumen. Diathera and Heterothera have nearly the same length between the tegumen and the total length of the vinculum and saccus.

14. Width of anterior end of tegumen compared to posterior end (= vinculum): (0) same or slightly shorter; (1) greatly shorter.

15. Shape of anterior end of tegumen (figs. 24–28): (0) slightly invaginated; (1) deeply invaginated.

16. Juxta with strongly sclerotized hairs (fig. 31): (0) absent; (1) present. A unique character of the juxta is observed in all species of Diathera, which is a structure covered with strongly sclerotized hairs.

17. Length of anellus lobe: (0) strongly extended from juxta, reaching more than half of uncus height; (1) slightly extended from juxta, rarely reaching bottom of uncus.

18. Shape of anellus lobes (figs. 29–36): (0) digitiform, without expanded body; (1) body expanded.

19. Anellus lobe: (0) unilobed; (1) bilobed.

20. Surface of anellus lobe: (0) smooth; (1) dentate.

21. Shape of anellus lobe: (0) digitiform; (1) rounded; (2) triangular; (3) flattened. The anellus lobes are lateral processes of the juxta that supports the ventral part of the aedeagus and are usually distinct in most groups of Cidarini (Choi, 1997). In Therini, the anellus lobes are distinctive in their length, sclerotization, and for the long apical hairs. The different shapes of the body of the lobes (e.g., triangular, cylindrical, or caplike) provide diagnostic features for the species of Heterothera, Diathera, and Pennithera (figs. 32, 35, 36): Pennithera possesses anellus lobes with a strongly expanded body; and Thera possesses digitiform lobes. But, the shapes of the lobes in Heterothera vary. In particular, the species from southwestern China have greatly modified anellus lobes that are bilobed with an expanded body, often with dentate surfaces: Heterothera yunnanensis, H. eclinosis, and Pennithera distintata (figs. 31, 33, 34).

22. Transtilla: (0) simple, membranous; (1) platelike, sclerotized; (2) thin, round, sclerotized. The transtilla, the dorsal part of the diaphragma, is usually simple and membranous in most ingroup taxa, whereas Thera shows a well-developed and sclerotized transtilla. Thera exangulata has a thin, round, sclerotized transtilla.

23. Shape of saccus (figs. 24–28): (0) flat or round and medially slightly projected; (1) medially invaginated; (2) medially strongly projected. The shape of saccus shows three states: (1) broad, flat, or round saccus (Praethera and Pennithera) (fig. 24), (2) medially invaginated or broad saccus (Heterothera and Diathera) (figs. 26, 28), and (3) medially strongly projected (Thera) (fig. 25). In Thera and Pennithera the saccus shows a sclerotized internal ring.

24. Costa of valva (figs. 37–44): (0) membranous; (1) sclerotized.

25. Shape of costa: (0) flat, not expanded; (1) basally expanded (fig. 40); (2) medially expanded (figs. 38, 41); (3) distally expanded.

26. Costa with a distal sclerotized process: (0) absent; (1) present. The costa, which is the dorsal part of the valva, is frequently modified and strongly sclerotized in Therini and this has been most frequently used by earlier authors (e.g., Viidalepp, 1980; Inoue, 1986a; Choi, 1997). In Thera, Pennithera, and Praethera, the costa has important diagnostic characters: Thera with a
slender costa with a medial triangular projection; in *Pennithera* it is basally greatly enlarged and distally sharply pointed; in *Diathera* the base is minutely toothed and medially greatly enlarged; in *Praethera* it is long, slender, and distally sharply pointed. However, in *Heterothera* the shape of the costa varies: with a medial, triangular process sim-
ilar to Thera (fig. 41), or basally or distally expanded (fig. 42). Choi (1997) noted that the absence of the distal costal process is pleiomorphic.

27. Ventral edge of sacculus: (0) invaginated (figs. 37–41, 44); (1) flat (figs. 42, 43).

28. Shape of dorsal edge of sacculus: (0) indistinct; (1) vertical (fig. 38); (2) straight and oblique (figs. 41, 42); (3) scalloped.

29. Process of sacculus: (0) absent; (1) clawlike or sharply pointed (figs. 38, 41, 42, 44); (2) stellate.

30. Number of saccular processes: (0) absent; (1) one; (2) two. The sacculus divides Therini into two groups based on whether it is sclerotized or membraneous. The former includes Thera and Heterothera, the latter Praethera, Diathera and Pennithera. The triangular and sclerotized sacculus diagnoses Heterothera. The sclerotized sacculus is usually coupled with projected processes on the distal part of sacculus, which are often called the “harpe” (Inoue, 1986a). In Heterothera, the process varies from simple and setose (e.g., tephroptilus) to clawlike [e.g., dentifasciata (Hampson)] and stellate (hoenei). Four species of Heterothera have two processes [postalbida, sororcula, undulata (Warren) and obscurata Choi; Choi, 1998a] (fig. 42). This character was also used in Viidalepp’s (1980) analysis (his #2).

31. Width of valva: (0) wider distally (figs. 39, 42); (1) even width (figs. 41, 43); (2) wider basally (fig. 40). The width of the valva diagnoses some members of Therini. In Praethera, Diathera, and Thera, the distal part of valva is wider, whereas in Pennithera the basal part is wider. In Heterothera, the valva is usually wider distally, except for three species (serraria, serrataria and kurentzovii) that have a basally wider valva.

**32. Distal part of the aedeagus:** (0) membranous, without spines; (1) scobinate (figs. 47, 49, 50); (2) with large spines (fig. 46). Therini has several derived character states on the distal part of the aedeagus. The distal spines in *Thera* have often been termed cornuti (e.g., Viidalepp, 1980; Choi, 1997), and this state may be a synapomorphy of *Thera* and *Heterothera* (Choi, 1998a). The scobination of the distal part of the aedeagus is morphologically part of the juxta. Because these two parts are fused, they are usually broken in genitalic preparations.

**33. Shape of the vesica:** (0) large, saclike (fig. 51); (1) tubular (fig. 45)

**34. Cornutus:** (0) absent; (1) large, spinular; (2) small setae; (3) mixed large and small spines.
35. **Cornuti:** (0) absent; (1) grouped into one patch; (2) grouped into several patches; (3) without grouping, scattered. Viidalepp (1980) divided the states of the cornuti into primary and secondary losses. For example, *Pennithera djakonovi* (Kurentzov) is coded as a primary loss because it lacks cornuti in the vesica. But most species of *Thera* are coded as secondary because they lack cornuti in the vesica while having spinal processes at the distal part of the aedeagus. Viidalepp also suggested that the presence of cornuti is a derived character in Therini.

The shape of the vesica is coded as tubular or large and saclike. For most ingroup taxa the vesica is tubular, whereas some outgroup taxa (*Dysstroma truncatum, Plenmyria rubiginata* and *Thera exangulata*) have a large, saclike vesica. Choi (1997) noted that several transformations occur in the vesica of *Heterothera*: several irregularly shaped diverticulae and many kinds of spinal processes and arrangements of the cornuti.

**Female Genitalia**

36. **Seventh sternite:** (0) simple, membranous; (1) with sclerotized processes; (2) scobinate. A densely scobinate seventh sternite diagnoses *Diathera*, while sclerotized processes diagnose *Pennithera*. In *Thera, Praethera*, and *Heterothera*, like outgroup taxa, the seventh sternite is simple and membranous.

37. **Lamella antevaginalis** (figs. 52–59): (0) membranous, without structures; (1) sclerotized with rounded structure; (2) sclerotized with two doughnutlike structures.

38. **Lamella antevaginalis with processes:** (0) absent; (1) minute spines; (2) large spines.

39. **Lamella postvaginalis:** (0) membranous; (1) sclerotized.

40. **Lamella postvaginalis with processes:** (0) absent; (1) large, barlike processes; (2) large, hornlike processes. Sterigmata (lamellae ante- and postvaginalis) occur around the ostium bursae and they are modified into various forms. Viidalepp (1980) noted that the well-developed sterigmata are plesiomorphic in this group. In *Heterothera*, these structures vary from simple (e.g., *consimilis*, *etes*, and *dentifasciata*) to spinelike (e.g., *postalbida, sororcula, and hoenei*) to large hornlike processes (e.g., *taigana*). In *Thera* there is no distinction between the lamella antevaginalis and the lamella postvaginalis, because the two structures are fused and semicircular (fig. 53).

41. **Length of ductus bursae compared to corpus bursae:** (0) shorter; (1) longer.

42. **Ductus bursae with a colliculum:** (0) present; (1) absent.

43. **Ductus bursae:** (0) membranous; (1) sclerotized; (2) with sclerites. The shape of the ductus bursae of *Heterothera* is variable. Unlike outgroup taxa, in which it is short and membranous with a colliculum, *Heterothera* and *Pennithera* have a sclerotized wall or sclerites in the ductus bursae. The shape of the ductus bursae in these taxa may be long, twisted, or basally greatly expanded. *Thera* and *Diathera* have a membranous ductus bursae, but lack a colliculum.

44. **Basal ductus bursae (anterior to antrum):** (0) simple, without modification; (1) funnel-shaped; (2) rounded and sclerotized. The basal part of the ductus bursae (anterior to the antrum) is usually simple and membranous. Two species (*Plenmyria rubiginata* and *Thera cyphoschema*) have a ductus bursae basally funnel shaped (fig. 58), but in several species of *Heterothera* (*serraria, serrataria* and *kurenzovi*) it is strongly sclerotized with a rounded opening.

45. **Distal ductus bursae:** (0) membranous; (1) flattened and sclerotized.

46. **Posterior corpus bursae:** (0) simple, membranous; (1) with sclerotized striations; (2) simple, sclerotized. The area between the ductus bursae and the corpus bursae is usually simple and membranous. But, several species of *Heterothera* (*serraria, serrataria*, and *kurenzovi*) have the corpus bursae strongly sclerotized.

47. **Signum:** (0) one-process; (1) several, placed in a patchlike band; (2) absent; (3) large, threadlike sclerite. Viidalepp (1980) indicated that the absence of a signum is a derived character of the Therini. In *Thera, Pennithera, Heterothera*, and *Diathera*, a signum is absent, whereas in *Praethera*, a minute nipple-shaped signum occurs (fig. 52). One species (*Thera exangulata*) shows a large, threadlike signum (fig. 59).

48. **Wall of the corpus bursae:** (0) sim-

ple, membraneous; (1) with wavelike striations; (2) with minute scobinations; (3) net-like and sclerotized. In Heterothera, the wall of the corpus bursae varies from simple (e.g., tephroptilus, sororcula, and quadrifula) to having wavelike striations (e.g., kurenzovi) to minutely scobinate (e.g., incerta, yunnanensis, and eclinosis) (figs. 55, 56). In Pennithera, the wall is usually membraneous and simple (fig. 57), but in Thera, Diathera, and Praethera wavelike striations are observed (figs. 52–54). Exceptionally,

Thera exangulata has a netlike, sclerotized wall (fig. 59).

CLADISTIC ANALYSIS

NONA produced 45 cladograms of length 256, consistency index = 0.30, and retention index = 0.66. The strict consensus cladogram is shown in figure 60. The successive weighting approach (Farris, 1969) for these 45 cladograms was applied by NONA and after two iterations one cladogram of weighted length 7819 was stabilized (table 2, fig. 61). The cladogram derived from the successive weighting provides better resolved ge-
C. interrelationships than the original cladograms: (Thera cyphoschema, (Heterothera, (Thera, (Diathera, Pennithera)))).

**Therini, a Synonym of Cidariini**

Both present analyses show that the tribe Therini is not monophyletic and both (figs. 60, 61) excluded *Praethera* from the ingroup taxa. Therefore, the results do not support the tribe Therini, and suggest that the Cidariini should be applied as the appropriate name for all ingroup taxa.

Both unweighted and successive weighting approaches support most ingroup taxa, *Praethera, Thera, Pennithera,* and *Diathera,* and the positions of two unplaced taxa, *T. exangulata* and *T. cyphoschema,* turned out to be part of a very basal member. Differences among the trees were a result of the placement of several taxa in *Heterothera,* *Heterothera* *firmata,* and the *serraria* group of *Heterothera* (*serraria,* *serrataria,* and *kurenzovi*). In the original cladograms, *H. firmata* was a basal taxon of *Pennithera* or formed an independent clade with the *serraria* group.

In his analysis for 16 species of *Thera* sensu Prout, Viidalepp (1980) divided this group into three genera and four subgenera (fig. 1), suggesting that Prout’s classification was unnatural. A cladistic analysis of the Cidariini resulted in some relationships different from Viidalepp’s hypothesis (Choi, 1997)—specifically that *Heterothera* was paraphyletic. Choi also indicated that the basal node of three genera, *Thera + Pennithera + Heterothera,* was supported by several synapomorphies. In the present analysis my preferred cladogram (fig. 61) resolves the generic relationships without *Praethera:* (*Fascilunaria, (Heterothera, (Thera, (Pennithera, Diathera))))*, and the basal clade is supported by three synapomorphies: male antennae bipectinate (character #0-1), antemedial line of forewing rounded or medially indented (#6-1), and signum absent (#47-2).

The present analysis confirms four previously known monophyletic taxa, which is partly consistent with the results of Choi (1997). However, the result indicates that *Praethera* is not closely related to *Thera,* and two new monotypic genera, *Fascilunaria* and *Costicoma,* and one combination, *Thera* *firmata* (Hübner), are suggested. Their formal classification is presented in appendix 1.
Fig. 60. Strict consensus cladogram derived from unweighted analysis using NONA. Abbreviations: C Cidaria, D Dysstroma, P Plemryia, Pe Pennithera, Pd Paradysstroma, Pr Praethera, Ps Pseudodysstroma, H Heterothera, T Thera, Di Diathera. Plus signs (+) indicate a taxon or node that produces the polytomy in the consensus cladogram; asterisks (*) indicate taxa that have ambiguous taxonomic positions.
Fig. 61. One cladogram derived from successive weighting approach using NONA. See fig. 60 for generic abbreviations and symbols. Each node number is indicated.
**TABLE 2**
Characters and Their Final Weights

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**SYSTEMATICS**

*Praethera* Viidalepp, 1980

**Type Species:** *Cidaria praefecta* Prout, 1914.

**Diagnosis:** Species of *Praethera* are characterized by the filiform male antennae, the subdorsally greatly shrunken central fascia with third cell half as wide as second, the male genitalia having a long tegumen, slender and sclerotized costa of valva upturned distally, membraneous saccus with a medially invaginated ventral edge and two bundles of cornuti on a tubular vesica, and the female genitalia having V-shaped, sclerotized lamella postvaginalis.

**Discussion:** In the present analysis, one species of *Praethera* is supported by seven autapomorphies: dorsum of the central fascia distinct with blackish scales (character #10-1), anellus lobe with expanded and flattened body (#18-1, #21-3), valva width wider distally (#31-0), cornuti large, spinular (#34-1), and lamella postvaginalis with a V-shaped sclerotization (#39-1).

Wing patterns of *Praethera*, especially the shape of the central fascia, place this group in Therini, but several genitalic characters differ from *Thera* and are closer to *Dysstroma truncatum*: long tegumen compared to vinculum and saccus, saccus membraneous, and presence of a colliculum and a signum.

Viidalepp (1980) demonstrated that *Praethera* is the sister group of *Heterothera*. He listed five apomorphic characters for *Praethera*: saccus massive and round; saccus membraneous; last tergite of female abdomen quadrilateral; ductus bursae modified; and both the collar of the bursa copulatrix and sterigma well-developed and strongly sclerotized. However, the present analysis shows that *Praethera* is placed as the sister taxon of *(Paradysstroma corussarium + Costicoma exangulata)*, not *Heterothera*. Two species of *Praethera* are known, *P. praefecta* (Prout, 1914) and *P. anomala* (Inoue, 1954), but the validity of the latter species is uncertain (Viidalepp, 1996). Both species occur in east Asia.

**Costicoma**, new genus

**Type Species:** *Perizoma exangulata* Warren, 1909.

**Diagnosis:** Species of *Costicoma* can be characterized by the forewing with blackish central fascia medially and dorsally greatly tapered, the valva with sclerotized costa and long hairs on the middle of costa, cornuti absent from vesica, and the female genitalia having the corpus bursae with a large, threadlike signum.

**Description:** Antenna filiform in both sexes. Frons mixed with ochreous and brownish scales. Labial palp short. Legs dark brownish, foreleg tarsal joints distinct with ochreous scales. Metathorax dorsum with blackish tufts. Forewing basally dark brown; basal line dentate, slanted; central fascia blackish, costally bulged; subterminal line whitish, scalloped; apical streak blackish. Hindwing whitish, basally tinged with blackish scales; postmedial line blackish. **Male genitalia.** Uncus long, basally tapering. Tegumen dome-shaped. Saccus rounded, medially expanded. Anellus lobe long, rod shaped, apically with long hairs. Transtilla thin, rounded, sclerotized. Valva slender; costa slender, distally with long hairs; saccus membraneous. Aedeagus cylindrical with large, sac-like vesica; cornutus absent. **Female genitalia.** Papillae anales simple. Anterior apophyses about ⅓ length of posterior apophy-
TABLE 3

Apomorphies in Cladogram Derived from Successive Weighting Approach Shown in Figure 61

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Discussion: There are four autapomorphies: uncus long (character #12-1); ventral edge of sacculus flat (#27-1); vesica large, saclike (#33-0), signum large, threadedlike (#47-3), and wall of corpus bursae with netlike sclerotizations (#48-3).

Costicoma exangulata is similar to Cidarria deleteria Hampson in the male genitalia having long hairs on the costa, but differs in the wing pattern and female genitalia (Choi, 1998a). Results here place C. exangulata as the sister taxon to P. corussarium, and the basal clade is supported by two apomorphic characters: blackish metathorax and thin, round transtilla. This taxon was included in the Therini (Prout, 1938), but is distinct from other species of Therini based on several apomorphic characters (Choi, 1998a): costa of valva strongly sclerotized with long hairs; large saclike vesica without a cornutus; os-
tium bursae broad; colliculum present; signum large, threadlike, and wall of corpus bursae with netlike sclerotization. Differences in wing pattern and genitalia separate *exangulata* from its sister genus *Paradysstroma*, suggesting a new genus, *Costicoma*. It is only known from northern India.

**Etymology:** The name refers to long hairs on the costa in the male genitalia, Costa (*Costa*) + Hairs (*Coma*).

*Fascilunaria*, new genus

**Type Species:** *Cidaria cyphoschema* Prout, 1926.

**Diagnosis:** Synapomorphies for *Fascilunaria* include bipectinate male antennae, the thin and crescent central fascia of the forewing with a discal dot united with costal part of the antemedial line, the male genitalia with a thick and short uncus, a saccular process, cornuti absent from vesica and the female genitalia with a simple sterigma, anterior to the antrum funnel shaped, a colliculum, and the large corpus bursae without a signum.

**Description:** *Antenna.* Male bipectinate with short pectination; female filiform. Frons white and ochreous scales. Labial palp long, about twice the eye diameter. Legs brownish, foreleg tarsal joints distinct with white scales. Metathorax dorsum with blackish tufts. Forewing grayish; basal line blackish, slanted; antemedial line blackish, medially strongly indented; postmedial line medially projected; central fascia thin. Hindwing white, with a black discal dot; postmedial line very weak. *Male genitalia.* Uncus short, thick. Tegumen dome shaped. Anellus lobe digitiform, medially and apically with hairs. Saccus rounded, medially projected. Valva weakly sclerotized; costa distally projected; sacculus with a process. Aedeagus slender, rod shaped, with a tubular vesica; cornutus absent. *Female genitalia.* Papillae anales simple. Anterior apophyses half of posterior apophyses in length. Sterigma simple, dorsally with thin, sclerotized stripes; antrum large, funnel shaped. Ductus bursae short, membranous, with a corpus bursae. Corpus bursae large, subspherical; signum absent.

**Discussion:** *Fascilunaria cyphoschema* has four apomorphies: discal dot united with the costal part of antemedial line (character #9-1), costa of the male valva with a distal expansion (#26-1), ductus bursae short (#41-0), and ductus bursae anterior to antrum funnel shaped (#44-1).

*F. cyphoschema* is similar to several members of *Heterothera* in the shape of the central fascia of the forewing as well as the anellus lobe and saccular process of the male genitalia. However, other aspects of the male and female genitalia of *F. cyphoschema* are different from those of *Heterothera*: uncus thick, short, and less sclerotized; cornutus absent; sterigma simple; anterior to antrum funnel shaped; membranous ductus bursae with a colliculum, and corpus bursae large. In the present analysis, the results demonstrate that *F. cyphoschema* forms a basal lineage of the clade comprising *Heterothera + Thera + Pennithera + Diathera* (fig. 61). This species is known from southwestern China, northern Vietnam and Burma (Choi, 1998a).

**Etymology:** The name refers to the shape of the central fascia of forewing, central fascia (*Fascia*) + crescent (*lunaria*).

*Thera* Stephens, 1831

**Type Species:** *Geometra variata* [Denis and Schiffermüller, 1775].

**Diagnosis:** Members of *Thera* have filiform male antennae; central fascia of the forewing thin and medially and dorsally narrowed; male genitalia with hook-shaped uncus, transtilla thin, platelike, saccus medially projected, costa of valva strongly sclerotized with medial and distal projections, saccus large, rounded, aedeagus slender with spinular processes distally; and female genitalia having lamella antevaginalis sclerotized, rounded; ductus bursae thin, long without a colliculum and the corpus bursae ovate without a signum.

**Discussion:** All species of *Thera* (except *firmata*) are united by four synapomorphies: male antenna filiform (character #0-0), saccus medially projected (#23-2), dorsal edge of saccus vertically sclerotized (#28-1), and lamella antevaginalis two doughnutlike structures without a seta (#37-2). The basal clade comprising *Thera* and *T. firmata* is
supported by one synapomorphy: transtilla large, platelike (#22-1).

Stephens (1831) proposed the genus Thera by separating it from Chesias Treitschke based on differences of the palpi, wing pattern and host plant (fir or juniper). Viidalepp (1980) defined the monophyly of Thera: sacculus tender and round; costa and sacculus of valva distinct; ductus bursae membraneous; and stergigma sclerotized. Choi (1997) redefined the monophyly of the genus using 11 synapomorphies and listed four uniquely derived characters: costa of valva with a medial projection; cucullus large; and cornuti on vesica fewer and arranged in a crown shape. About 12 species of Thera are known and they occur widely throughout the Holarctic region.

T. firmata has seven autapomorphies: vertex distinct with whitish scales (character #1-1), discal dot of forewing united to the costal part of antemedial line (#9-1), costa of valva with a distal expansion (#26-1), cornuti on vesica large and spinular and grouped into one-patch (#34-1, #35-1), and ductus bursae sclerotized (#43-1). Viidalepp (1980) moved it to Pennithera, on the basis of two apomorphies: indistinct sacculus and shortly bipectinate male antenna. However, Choi (1997) subsequently combined it with Heterothera, using three synapomorphies: apical streak of forewing absent, anelus lobe expanded, and sacculus flat and broad. In the present analysis, firmata is again associated with Thera.

Pennithera Viidalepp, 1980

**Type Species:** Larentia comis Butler, 1879.

**Diagnosis:** Members of Pennithera have male antennae bipectinate; forewing with a black dot at dorsum between basal and antemedial line, ante and postmedial lines strongly scalloped; tegumen short with narrow anterior end; costa of valva sclerotized with large basal and distal projections; aedeagus bent; vesica with several spinular cornuti; female seventh sternite sclerotized; stergigma simple; ductus bursae long, sclerotized without a colliculum; and corpus bursae small and ovate without a signum.

**Discussion:** Eight species of Pennithera are united by two synapomorphies: forewing between basal and antemedial lines tinged with black scales (#7-1) and ductus bursae sclerotized (#43-1). Viidalepp (1980) proposed the genus Pennithera and included three species, P. comis (Butler), P. djakonovi (Kurentzov) and P. firmata (Hübner), based on two apomorphies: sacculus massive and round, and last tergite of the female abdomen telescopic. Inoue (1982, 1986a) added five species, mainly from Taiwan: P. abolla (Inoue), P. subcomis (Inoue), P. lugubris Inoue, P. manifesta Inoue, and P. subalpina Inoue. Choi (1998a) combined one additional species Thera distractata Sterneck (1928).

Inoue (1986a, 1986b) noted that Pennithera is distinguished from Viidaleppia, a junior synonym of Heterothera, by quadripectinate male antennae with slender branches, costa of valva half-expanded basally, greatly invaginated medially and rounded distally; sacculus unsclerotized, cornuti few and thornlike; simple and unsclerotized lamellae ante- and postvaginalis, and slender ductus bursae. Choi (1997) listed six synapomorphies of Pennithera: male antenna with long pectinations; slender sacculus; female ninth abdominal segment long, nearly the same length as eighth tergite; long and sclerotized antrum; and twisted ductus bursae.

**Diathera** Choi, 1999

**Type Species:** Diathera fluctuata Choi, 1999.

**Diagnosis:** Members of Diathera have male antennae filiform; long uncus; juxta with short, strongly sclerotized hairs; costa of valva with minute dentate processes basally, greatly expanded medially; vesica without a cornutus; female eighth sternite scobinate; ductus bursae short, sclerotized, and the corpus bursae slender with scalloped processes on the wall.

**Discussion:** The three species of Diathera, all from southwestern China, are united by five synapomorphies: male antenna filiform (character #0-0), juxta with strongly sclero-
tized hairs (#16-1), medially invaginated sac-
cus (#23-1), valva wider distally (#31-0), and
female seventh sternite scobinate (#36-2).

The species of this genus are similar to
Pennithera externally, especially in the
strongly scalloped ante and postmedial lines
of the forewing. However, the structure of
the male antennae and the male and female
genitalia separate Diathera from Pennithera.

Heterothera Inoue, 1943

Type species: Cidaria postalbida Wile-
man, 1911. = Viidaleppia Inoue, 1982 [syn-
ononymized by Choi, 1997: 311]. Type species:
Cidaria quadrifulta Prout, 1938.

Diagnosis: Members of Heterothera are
variable in the male antennae, the shape of
central fascia of the forewing, and the geni-
talia. However, they generally show the fol-
lowing features: central fascia of the fore-
wing rather thick, outwardly oblique; tegu-
men same length as vinculum and saccus;
saccus medially invaginated; costa of valva
sclerotized with medial or distal expansion;
sacculus sclerotized with spinular process;
cucullus with long, dense hairs; aedeagus
long, cylindrical; vesica with several scatter-
ted, spinular cornuti; lamella ante- and
postvaginalis complicated with spinular or
patchlike structures; ductus bursae thick with
sclerites on the wall; and corpus bursae with-
out a signum.

Discussion: In the present analysis, one
synapomorphy, dorsal edge of sacculus scal-
loped (character #28-3), supports the group-
ing of 16 species of Heterothera. Inoue
(1943) proposed the genus Heterothera
based mainly on male genital characters: ab-
sence of uncus (this character was found to
be incorrect; see Choi, 1997); long anal tube;
saccus basally flat and broad; costa weakly
sclerotized, and sacculus well-developed. Vi-
idalepp (1980) noted that the broad, angulat-
ed saccus is the main derived character for
the genus. As noted above, Inoue (1982)
erected another genus, Viidaleppia. However,
Choi (1997) synonymized Viidaleppia under
Heterothera and listed seven synapomor-
phies: sacculus process (or harpe) small; cu-
cullus with hairs; saccus medially invaginat-
ed; cornuti scattered on vesica; lamella an-
tevaginalis with semicircular process; ductus
bursae relatively thick, and wall of ductus
bursae with sclerotized processes.

Key to Genera Examined Based on
Genitalia

1. Tegumen longer than total length of vinculum
and saccus; corpus bursae with a signum
Praethera (figs. 2, 21, 24, 29, 37, 45, 52)
— Tegumen shorter than total length of vinculum
and saccus; corpus bursae without a signum
................................................. 2

2. Sacculus sclerotized with a process; sterigma
of female genitalia developed with sclerites
................................................. 3
— Sacculus without a process; sterigma simple,
without modification ................. 5

3. Vesica without a cornutus; ductus bursae
membraneous ............................. 4
— Vesica with cornutus; ductus bursae sclerotized
Heterothera (figs. 3–7, 22, 23, 28, 35,
36, 41, 42, 50, 55, 56)

4. Uncus hooked; saccus strongly projected; aede-
agus with distal spinular processes; ste-
rigma with sclerotized processes ........
... Thera (figs. 8, 18, 25, 30, 38, 46, 53)
— Uncus short and thick; saccus rounded; aede-
agus distal part without spinular process; ste-
rigma simple, membraneous ...........
... Fascilunaria (figs. 17, 44, 48, 58)

5. Costa of male valva with long hairs; corpus
bursae with a long signum ............... 6
— Costa without long hairs; corpus bursae with-
out a signum ............................. 6

6. Costa of male valva with a large basal expan-
sion; vesica with cornuti; ductus bursae
sclerotizd . . . . Pennithera (figs. 11–14, 20,
27, 32, 33, 40, 47, 57)
— Costa with a large distal expansion; vesica
without cornuti; ductus bursae membraneous
. . . . Diathera (figs. 11, 26, 31, 39, 49, 54)

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APPENDIX 1

Formal Classification of Ingroup Taxa

Asterisks (*) indicate unexamined taxa.

**Costicoma** n. gen.
*exangulata* (Warren, 1909) n. comb.

**Praethera** Viidalepp, 1980
*anomala* (Inoue, 1954)
*praefecta* (Prout, 1914)

**Diathera** Choi, 1999
*brunneata* Choi, 1999
*fluctuata* Choi, 1999
*metacolorata* Choi, 1999

**Pennithera** Viidalepp, 1980
*abolla* (Inoue, 1943)
*comis* (Butler, 1879)
*distractata* (Sterneck, 1928)
*djakonovi* (Kurentzov, 1950)
*lugubris* Inoue, 1986
*manifesta* Inoue, 1986
*subalpina* Inoue, 1986
*subcomis* Inoue, 1978

**Fascilunaria** n. gen.
*cyphoschema* (Prout, 1926) n. comb.

**Thera** Stephens, 1829
*britannica* Turner, 1925
*cognata* (Thunberg, 1792)
*contractata* (Packard, 1873)
*cupressata* (Geyer, 1831)
*firmata* (Hübner, 1822) rev. comb.
*juniperata* (Linnaeus, 1758)
*latens* Barnes & McDunnough, 1917
*obeliscata* (Hübner, 1787)
*otsi* (Dyar, 1904)
*variata* (Denis & Schiffermüller, 1775)
*variolata* (Staudinger, 1899)
Heterothera Inoue, 1943
*consimilis (Warren, 1888)
*dentifasciata (Hampson, 1895)
*distinctata Choi, 1998
eclinosis Choi, 1998
etes (Prout, 1926)
hoenei Choi, 1998
incerta Inoue, 1986
karenzovi Choi, Viidalepp & Vasjurin, 1998
*mussooriensis Choi, 1998
*obscurata Choi, 1998
postalbida (Wileman, 1911)
quadrifulta (Prout, 1938)
serraria (Lienig, 1846)
serrataria (Prout, 1914)
sororcula (Bastelberger, 1909)
*stamineata Choi, 1998
taigana (Djakonov, 1926)
tephoptilus (Heydemann, 1961)
*triangulata Choi, 1998
undulata (Warren, 1888)
yunnanensis Choi 1998

APPENDIX 2
Reanalysis of Viidalepp’s Data Set

Here I present a reanalysis of the data presented by Viidalepp (1980). Fifteen characters appeared in the original diagram and most of them were binary, except for four characters (characters 4, 6, 7, 14) that he stated plesiomorphic, intermediate and apomorphic. I rescored these characters as multistate and treated them as additive in the analysis, because Viidalepp considered that the intermediate state was between the plesio- and apomorphy. Character number 15 was treated as inapplicable in the species of Thera and Heterothera because the male antennae of those species are filiform. The recoded data matrix was analyzed by Hennig86 using the implicit enumeration (ie*) using an all zero outgroup. This analysis resulted in 55 equally parsimonious trees with 33 steps, 57 consistency index, and 82 retention index. The strict consensus is shown in figure 1B.

Characters and Character States

1. Antenna of male pectinate (0), filiform (1).
2. Saccus processes simply pointed (0), bifid (1).
3. Uncus present (0), absent (1).
4. Saccus heavily sclerotized and broad, angulated platelike (0), massive and rounded (1), medially projected (2).
5. The last tergite of female abdomen with long apophyses and telescopic (0), with short apophyses and strongly sclerotized to limit the mobility of ovipositor (1).
6. The ductus and the collar of corpus bursae strongly sclerotized (0), intermediate (1), membraneous (2).
7. Sterigma well developed and sclerotized (0), intermediate (1), simple and slightly sclerotized (2).
8. Eighth sternite of female abdomen simple (0), fused to sterigma (1).
9. Costa indistinct and fused to other part of valva (0), distinct (1).
10. Saccus indistinct and fused to other part of valva (0), distinct (1).
11. Cornuti present in vesica (0), present in the dorsal part of aedeagus, corona-shaped (1).
12. Cornutus absent (0), present (1).
13. Uncus short (0), long (1).
14. Antenna of male pectinate (0), filiform with constricted or rounded ventral surfaces (1), filiform with cylindrical antennomeres (2).
15. Antennal pectination short (1), long (0).
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