The life history and immature stages of *Spiramiopsis comma* HAMPSON, 1901 (Lepidoptera: Bombycoidea), with comments on its taxonomic position and on preimaginal characters of the Bombycoidea

by

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Abstract: A historical review is given of the taxonomic placements of the genus *Spiramiopsis* and of the previous records of the immature stages and larval foodplants of its sole species, *S. comma* HAMPSON. The only confirmed larval foodplants of the species are twining asclepiads of the genus *Secamone*. The entire life history and all immature stages of *S. comma* are described and illustrated, including the chaetotaxy of the first-instar larva. The larva and pupa of *S. comma* are compared with those of other bombycoid families having larvae with dorsal processes, viz. Brahmaeidae, Lemoniidae, Bombycidae, Saturniidae, Sphingidae and Mirinidae, to assess whether *S. comma* agrees with any of these in preimaginal characters and whether any such agreements are structurally identical. *Spiramiopsis* is placed in the latest phylogenetic classification system of the Bombycoidea (MINET 1994) according to its preimaginal characters, where it comes near the Lemoniidae and Brahmaeidae but is not traceable to any specific family. Its main preimaginal characters, viz. dorsal processes in the larva and metathoracic calli in the pupa, are discussed in more detail with reference to other bombycoid families, from which it is concluded that the former seems to be a groundplan condition in the Bombycoidea that can appear independently in most of its families, while the latter is an adaptive structure in mobile pupae to facilitate protrusion from the cocoon or the soil prior to eclosion of the adult. It is concluded that in its immature stages *Spiramiopsis* presents a unique combination of characters that does not occur in any other bombycoid group, and that many of these characters are primitive (plesiomorphic) so that *Spiramiopsis* appears to be close to the ancestral bombycoid form. In the light of the absence of any synapomorphic agreement in preimaginal characters between *Spiramiopsis* and Brahmaeidae, it is suggested that the agreement in alleged imaginal synapomorphies between these taxa needs to be reassessed, and that the exact distribution and phylogenetic significance of many bombycoid characters is in need of considerable further study.

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Die Entwicklung und Präimaginalstadien von *Spiramiopsis comma* HAMPSON, 1901 (Lepidoptera: Bombycoidea), mit Bemerkungen zu ihrer taxonomischen Stellung und zu Präimaginalmerkmalen der Bombycoidea

Zusammenfassung: *Spiramiopsis comma* HAMPSON ist ein taxonomisch und geografisch isoliertes Taxon der Bombycoidea, dessen Lebenslauf und Präimaginalstadien bislang nur sehr ungenügend bekannt waren. Diese werden hier zum ersten Male detailiert beschrieben und in Farbe abgebildet. Es wird eine historische Übersicht über die taxonomischen Stellungen der Gattung *Spiramiopsis* und über die bestehenden Angaben über die Präimaginalstadien und Futterpflanzen ihrer einzigen Art gegeben. Soweit bekannt, fressen die Raupen von *S. comma* nur an rankended Asclepiadaceen der Gattung *Secamone*. Der Lebenslauf und alle Präimaginalstadien von *S. comma* werden beschrieben und abgebildet, einschließlich der Chaetotaxie des ersten Larvalstadiums. Die Raupe und Puppe von *S. comma* werden mit denen anderer Bombycoidea verglichen, die ebenfalls larvale Dorsalfortsätze aufweisen, d. h. Brahmaeidae, Lemoniidae, Bombycidae, Saturniidae, Sphingidae und Mirinidae, um zu beurteilen, ob diese und andere Übereinstimmungen in Präimaginalmerkmalen ähnlich oder strukturell identisch sind. *Spiramiopsis* wird nach ihren Präimaginalmerkmalen in das neuste System der Bombycoidea (MINET 1994) gestellt, in dem sie nahe der Lemoniidae und Brahmaeidae zu stehen kommt aber nicht in irgendeine bestehende Familie fällt. Ihre Hauptpräimaginalmerkmale, die Dorsalfortsätze der Larve und die Metathorakalwülste der Puppe, werden eingehender und in Bezugnahme auf andere Familien der Bombycoidea besprochen, und hieraus ist ersichtlich, daß erstere als ein Grundplanmerkmal der Bombycoidea zu bewerten sind, das unabhängig in den meisten Familien auftreten kann, letztere dagegen als eine Anpassung bei Puppen, die vor dem Schlupf der Imago aus der Erde oder dem Kokon treten. *Spiramiopsis* stellt eine einzigartige Kombination von Präimaginalmerkmalen dar, die in keiner anderen Bombycoideagruppe vorkommt, und die meisten diese Merkmale sind primitiv (plesiomorph), so daß *Spiramiopsis* nahe der Stammform der Bombycoidea zu stehen scheint. Angesichts der Tatsache, daß *Spiramiopsis* keinerlei synapomorphe präimaginale Übereinstimmungen mit den Brahmaeidae zeigt, scheint die angegebene Übereinstimmung in Imaginalmerkmalen zwischen diesen beiden Taxa revisionsbedürftig, und die genaue Verbreitung und phylogenetische Bedeutung dieser wie auch anderer Merkmale der Bombycoidea bedarf eines eingehenderen Studiums, bevor sie als verläßliche Synapomorphien in Frage kommen. *Spiramiopsis* wird daher nicht in irgendeine bestehende Familie gestellt, sondern als *incertae sedis* in den Bombycoidea gelassen.

Introduction

Spiramiopsis comma HAMPSON, 1901 is an uncommon and taxonomically isolated moth from South Africa, whose affinities and taxonomic position have been contentious ever since its description. Although its final-instar larva and foodplant have been known for some time (though never properly studied), no further details of its life history have been published. We here report the first-ever documented rearing ab ovo of this unique moth species and describe and illustrate all its immature stages. We also compare its larva and pupa with those of other relevant bombycoid taxa and comment on its affinities and taxonomic position.

S. comma is only known to occur in south-eastern Africa, from the eastern Cape Province of South Africa through Transkei, Natal and Swaziland north along the escarpment of Transvaal, with a record from Beira in Mozambique as well. It seemingly only inhabits forests or dense bush but does not occur in drier savanna habitats, probably in alignment with the distribution of its foodplants, climbing asclepiads of the genus *Secamone*. *S. comma* occurs in thick coastal bush from the eastern Cape Province to southern Natal but in inland forests in northern Natal, in Swaziland it is found in thick bush and relict forests on the escarpment as well as in dry forests on the Lebombo mountains on the eastern border, and in Transvaal it has been recorded from moist montane forests along the Drakensberg escarpment. The collecting records of the moths indicate that it flies during the periods of September to November and again in January and February, implying two distinct generations per season. The moth is rarely collected in any numbers, usually taken at light as single male specimens, with females hardly ever coming to light (only about three light-collected females in all South African collections).

Historical review

The genus *Spiramiopsis* was erected by HAMPSON (1901) for a single new species, *S. comma* HAMPSON, 1901, described from one male specimen collected in 1883 along the Cowie River (probably at Port Alfred) in the eastern Cape Province, South Africa. The genus has remained monotypic ever since, no further species having been described or placed in it so far. HAMPSON (1901) placed his new genus together with *Lemonia* HÜBNER, [1820] 1816 and *Sabalia* WALKER, 1865 in a new family Sabaliidae (as Sabaliadæ) and recognized an affinity of this group of genera to the Brahmaeidae, but distinguished it from the latter by the absence of a proboscis.

Since then, *Spiramiopsis* has had a checkered history of taxonomic placement. AURIVILLIUS (1901) transferred it to Eupterotidae, a treatment followed by the influential publications of GAEDE (1927), MELL (1937) and PINHEY (1975). JORDAN (1923) included the genus in Brahmaeidae, a placement quoted by SEITZ (1927) but seemingly ignored afterwards (except MELL 1937) until very recently (SCOBLE 1992, MINET 1994). FORBES (1955) excluded *Spiramiopsis* from

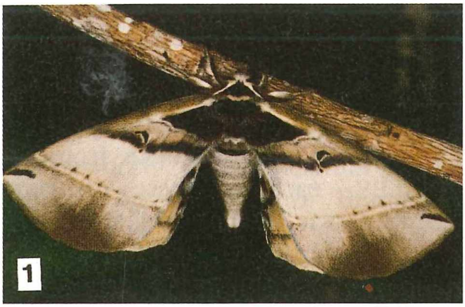
Eupterotidae again and placed it back in Lemoniidae (= Sabaliidae), followed by WATSON & WHALLEY (1975). FLETCHER & NYE (1982) transferred the genus from Brahmaeidae to Bombycidae on the basis of its larva and some (unspecified) external characters of the adult. Citing this treatment, HOLLOWAY (1987), however, was less committing and treated *Spiramiopsis* as of uncertain placement. VÁRI & KROON (1986) again placed *Spiramiopsis* in Brahmaeidae, stating as reason the similarity of its larva to that of the brahmaeid *Dactyloceras widenmanni* (KARSCH, 1895). However, the larva of *D. widenmanni* is as yet unknown, and the larval illustrations stuck into the *D. widenmanni* drawer in the Transvaal Museum, Pretoria, and used for the comparison are those of *Brahmaea ledereri* (ROGENHOFER, 1874), as copied from DE FREINA (1985, fig. 4a). Nonetheless, the comparison with a brahmaeid larva remains valid. Following VÁRI & KROON's (1986) deliberation, NÄSSIG & PAUKSTADT (1990) also included *Spiramiopsis* in Brahmaeidae. MINET (1994) finally studied *S. comma* in detail and supported the placement of *Spiramiopsis* in Brahmaeidae, identifying eight adult synapomorphies that define *Spiramiopsis, Dactyloceras* MELL, [1930] 1929, *Calliprogonos* MELL, 1937, and *Brahmaea* WALKER, 1855 (incl. *Brahmophthalma* MELL, [1930] 1929, *Acanthobrahmaea* SAUTER, 1967, and *Brachygnatha* ZHANG & YANG, 1993) together as a monophyletic group, viz. the family Brahmaeidae.

Published information about the larva of *S. comma* is only very scant and recent (WATSON & WHALLEY 1975, SCOBLE 1992, MINET 1994), although the larva has actually been known since the beginning of the century. Adult specimens of *S. comma* in the Transvaal Museum and in the Albany Museum, Grahamstown, reared by G. F. LEIGH in Durban in December 1907 indicate that he had found the larva of this species as early as that year, and similar specimens in the Natural History Museum, London, labelled "Durban, Jan. 1909, G. F. LEIGH" suggest that he may have reared it again the following year. LEIGH's fellow breeder of Lepidoptera in Durban in those days, Edgar L. CLARK, also reared *S. comma* from larvae in late 1908 and again in 1913, as evidenced by adult specimens in the Transvaal Museum labelled "17. I. 1909, e. larva" and "Bred 10/10/1913", respectively. The third and perhaps most prominent breeder of Lepidoptera in Durban in those days, Ernest E. PLATT, reared *S. comma* in Durban in November 1911, according to his unpublished breeding notes housed in the Transvaal Museum, and again in October/December 1917 and March/May 1918, judging from bred specimens dated 18/24. XII. 1917 and 5. V. 1918 as standing in the Albany Museum, to which PLATT had given his insect collection (JANSE 1969).

His notebooks and preserved larvae PLATT donated to the Transvaal Museum in Pretoria (JANSE 1969), but the blown larvae in this collection are not all PLATT's own but also originate from LEIGH, CLARK and H. W. BELL-MARLEY, each of these displaying a characteristic way of mounting their larvae. It appears that not all these larvae were labelled individually or properly so, as A. T. JANSE (of the Transvaal Museum) generally attached ink-written labels to the blown specimens, often in addition to the original label but sometimes his label being the only one. This is the case with the two blown larvae of *Spiramiopsis comma* in this collection, which only carry a label in JANSE's hand reading "Durban, *S. comma*". These two larvae are mounted in different ways, and from comparison with other, properly labelled larvae in the PLATT collection mounted in the same manner it seems that the larger one of these two larvae was reared and preserved by LEIGH, the smaller one by CLARK. It is on these two specimens that VÁRI & KROON's (1986) comparison and placement of *Spiramiopsis* in Brahmaeidae is based. PLATT himself apparently did not preserve any *Spiramiopsis* larvae, as also indicated in his breeding notes.

There are also three blown larvae of *S. comma* in the Natural History Museum, London, originally from the ROTHSCHILD collection in Tring (GOODGER, pers. comm.). These larvae are labelled "Durban, Natal, G. F. LEIGH" and could belong to the same series as the one in the Transvaal Museum, or come from an earlier or a later rearing. LEIGH had seemingly given one of his *S. comma* larvae to PLATT, while the others were presented to Lord ROTHSCHILD. It appears that the existence of these latter specimens in England was unknown to all the earlier authors who commented on the taxonomic position of *Spiramiopsis*.

After these early rearings of *S. comma,* its larva was apparently not seen again until December 1980, when Neville and Arthur DUKE found and photographed a fully grown caterpillar on *Clematis brachiata* near East London; these data have been recorded by NÄSSIG & PAUKSTADT (1990) and MINET (1994). However, the first complete rearing of *S. comma* reported here indicates that *Clematis* is not a foodplant for the species, and that the DUKE record must have been based on a fortuitous occurrence of the larva on this plant.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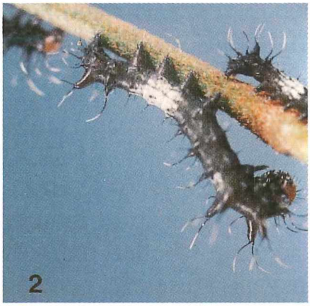
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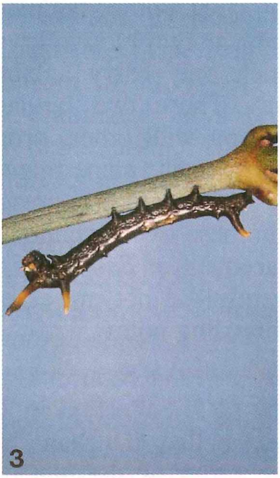
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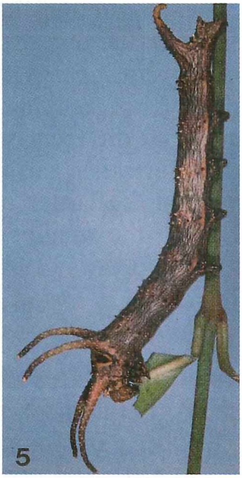
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Neither LEIGH, CLARK nor PLATT attached the name of the foodplant to any of their larval or reared adult specimens of *S. comma,* but in his impressive list of lepidopteran foodplants PLATT (1921) did publish a foodplant for this moth, namely *Secamone gerrardi* [sic!] (Asclepiadaceae). This information is also in PLATT's card index of larval foodplants, from which he prepared his published list and which is now housed in the Albany Museum (GESS, pers. comm.). PINHEY (1975), although citing PLATT's paper in his literature references, had apparently overlooked the entry of *Secamone* and *Spiramiopsis* as he credited this foodplant record to Arthur DUKE (East London, South Africa, formerly of Harare, Zimbabwe), who had given this record to PINHEY from PLATT's foodplant list, of which he had acquired a copy from PLATT himself even before it was published.

Larval foodplants

Only climbing asclepiads of the genus *Secamone* have been confirmed as foodplants of *Spiramiopsis comma.* PLATT (1921) recorded *S. gerrardii* HARV. ex BENTH. in Durban, while our larvae were fed on *S. alpini* SCHULTES. The record of *Clematis brachiata* THUNB. (Ranunculaceae) as on DUKE's 1980 photo (NÄSSIG & PAUKSTADT 1990, MINET 1994) proved to be accidental and false, as our larvae refused to feed on this plant. They also rejected other asclepiads in our feeding trials, namely *Asclepias fruticosa* L., *Araujia sericifera* BROT., *Pentarrhinum insipidum* E. MEY., *Brachystelma, Ceropegia* and various stapeliads, as well as *Cryptolepis oblongifolia* (MEISN.) SCHLTR. of the closely related Periplocoideae (or family Periplocaceae). Leaves of several Apocynaceae and even less closely related families were also offered to the larvae, with the same negative results. It thus seems that *Spiramiopsis comma* is host-specific to the asclepiad creeper *Secamone.* However, other climbing asclepiads still have to be tried in this regard, in particular other genera of the

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Colour plate:

Figs. 1–8: Life history of *Spiramiopsis comma* HAMPSON, as reared November/December 1993 in Mbabane, Swaziland. **Fig. 1:** Male imago in resting posture. **Fig. 2:** first larval instar. **Fig. 3:** second larval instar. **Fig. 4:** third larval instar. **Fig. 5:** fourth larval instar. **Fig. 6:** young fifth larval instar. **Fig. 7:** mature fifth larval instar. **Fig. 8:** metathoracic eyespots in fifth larval instar, dorsal view. [Photographs 1, 6 and 8 R. OBERPRIELER, 2–5 and 7 N. DUKE.]

Secamonoideae, and also species of *Ceropegia* and *Tylophora* as recorded as foodplants for *Dactyloceras* in central Africa by SCHULTZE (1914, 1931), if indeed these were correctly identified.

Secamone is a genus of 80 woody twiners or scrambling shrubs native to tropical and subtropical regions of the Old World, with 62 species occurring in Madagascar, 16 in continental Africa and 2 in south-east Asia (GOYDER 1992). It is placed together with seven allied genera in a subfamily Secamonoideae, which forms a link between the primitive Periplocoideae and the more advanced Asclepiadoideae. Of the five species of *Secamone* that occur within the distribution range of *Spiramiopsis comma,* all but *S. alpini* and *S. gerrardii* have very small and narrow leaves, which may make these species unsuitable as foodplants for *S. comma;* however, further studies and field observations are needed to assess the proper foodplant range of the moth.

Life history and behaviour

This description is based on a rearing ab ovo from a female collected on 26. X. 1993 inside a house in Mbabane, Swaziland. The female laid about 60 eggs in captivity, most of them during the night of 27. X. 1993.

1. Oviposition and hatching of the larvae

In captivity, the eggs were laid in small, loose clusters onto leaves and the walls of the container; in the wild they are presumably stuck singly or in small groups onto the leaves of the foodplant. The larvae started to hatch on the morning of 8. XI. 1994, from about 7:00 into the afternoon, sawing a large, horizontally crescentic emergence hole into the egg shell (fig. 9). They did not feed on the egg shell after emergence, but wandered off individually immediately after hatching.

2. Development and behaviour of the larvae

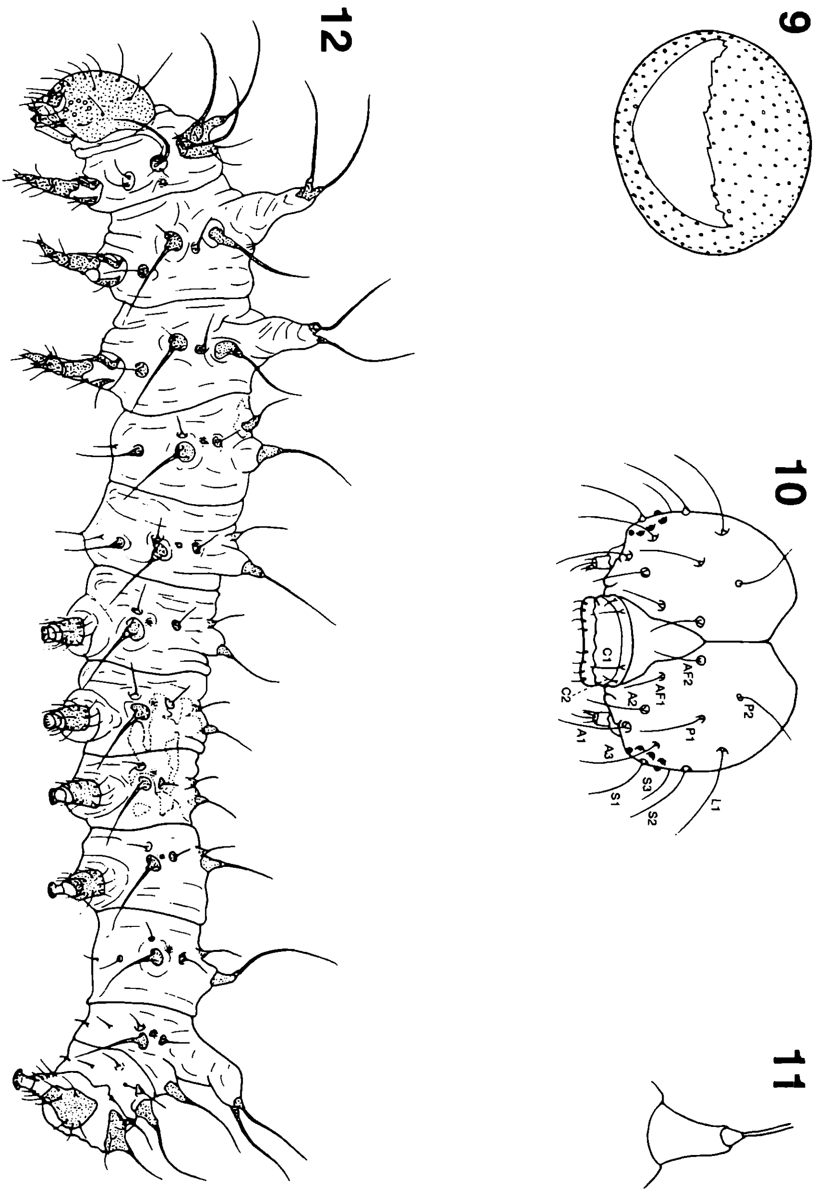
The first-instar larvae (fig. 2) are very distinctive in coloration, sporting a black body with white saddle and red head; however, the black colour fades to a dark leaden-gray as the larvae distend with feeding. They consistently refused to feed on leaves of *Clematis brachiata* as were offered to them, but immediately accepted those of *Secamone alpini,* a creeper growing in close proximity to where the female was caught. The larvae fed voraciously on these leaves, increasing their size threefold in 24 hours. When at rest, they lifted the front part of the body (up to the front prolegs) off the substrate and bent the head downwards onto the thoracic legs. After two full days, the larvae stopped feeding and prepared for the first moult.

The second instar (fig. 3) emerged one day after the first instar had stopped feeding, and consumed the shed skin before commencing to feed on leaves. It has lost all the setae of the previous instar but is equipped with two short, stout, fleshy processes dorsally on the meso- and the metathorax and a similar but single one on the eighth abdominal segment (A-8). Its colour is predominantly steel-gray but the dorsal processes partially orange. The larvae fed very rapidly and ate large quantities of leaf material in short periods, but remained inactive for lengthy periods with the front end of the body again raised at an angle. After three full days, they again stopped feeding and prepared to moult.

The third instar (fig. 4) again emerged a day after the second had stopped feeding and also consumed its shed skin. It is very similar to the previous one, but duller in appearance and with relatively longer dorsal processes. Feeding and resting was as before, and two days later the following moult commenced.

The fourth instar (fig. 5) also consumed its shed skin before feeding on leaves again. It is of the same colour as the third instar, but covered with small spinules that give it a cryptic, bark-like appearance. Its dorsal processes have become longer still and decline slightly forwards, and at the anterior base of each metathoracic process there is an orange-and-black eyespot. When the larva is at rest, these eyespots are concealed in a fold as the fleshy processes lean forwards, but when it walks or feeds the processes become erect, directing upwards and out sideways and exposing the colourful eyespots. In this stage, also, it became obvious that the larvae are soft-bodied and fragile, and the slightest pressure in trying to dislodge them from a twig results in rupturing the skin. After three-and-a-half days of feeding, the larvae positioned themselves head-downwards for the moult into the final instar.

The fifth instar (figs 6–8) is very similar to the fourth but even more cryptic and the dorsal processes longer and thinner. Feeding and resting is essentially as in the previous instars, except that the anal claspers are also usually lifted off the twig when the larva rests (fig. 7). Resting takes place with the head downwards or upwards and on the thicker stems of the foodplant, which have exactly the same colour and texture as the larva and on which it is therefore extremely well camouflaged (fig. 6). On mild disturbance, such as when the branch on which it sits is touched, the larva “freezes”, i.e. becomes completely motionless, but when it is more severely irritated, such as being poked or grabbed, it fully exposes its bright eyespots by erecting the flaccid thoracic processes (fig. 8) and by curling in the front part of its body, with which it may also carry out sideways, thrashing movements. No distress sounds of any nature were detected. For feeding, the caterpillar moves out from the stem onto the thinner tendrils and leaf petioles, but retreats back onto the thicker stems afterwards. Feeding was again rapid but only occurred in lengthy intervals, both during the day and at night, but in the wild the larva probably feeds predominantly at night. After seven days in the final instar, the larvae descended from their foodplants to select a spot for pupation.



Figs. 9–12: Immature stages of *Spiramiopsis comma* HAMPSON. **Fig. 9:** egg shell after hatching of larva, showing large emergence hole, dorso-lateral view. **Fig. 10:** head capsule, frontal view (for abbreviation of setae see text). **Fig. 11:** typical chalaza of first-instar larva, enlarged, lateral view. **Fig. 12:** first-instar larva, lateral view.

3. Pupation

To pupate, the larva crawls up to some solid object on the ground, such as a stone or dead branch, where it forms a slight, shallow scrape and then pulls dry leaves over itself, tying these together with a few silken strands to form a protective covering. Three days later the final moult to the pupa takes place. The shed larval skin usually remains stuck to the end of the cremaster, and the pupa becomes dark brownish-black in colour and has a rough texture.

4. General observations

The rapid growth of the larvae and the short duration of the larval stage are noteworthy. In only 21 days the larvae grew in size from 4 mm to about 65 mm. BILEK (1965) recorded a similarly short life cycle for *Brahmaea europaea* (19 days) and MELL (1930) an average of also 19 days (range 16–22) for *Brahmaea* in general. A larval stage lasting a month or longer in *Brahmaea,* as reported by DE FREINA (1985) and PAUKSTADT & PAUKSTADT (1986), is apparently always due to suboptimal breeding conditions, such as low temperatures and incorrect food (NÄSSIG, pers. comm.).

Another interesting phenomenon of the life history of *Spiramiopsis comma* concerns the ability of the feeding larvae to suppress the flow of sticky latex from the foodplant, which normally exudes readily and copiously from injured leaves. Sabotage of plant latex defences has been reported in several other lepidopteran larvae that feed on plants producing such a substance (COMPTON 1987, 1989), but no such behaviour has so far been observed in *S. comma,* and the exact mechanisms of how this species circumvents the latex of *Secamone* are not yet known. The latex is presumably not only a physical deterrent because of its viscosity and stickiness but also a chemical one, as *Secamone* is a member of the Asclepiadaceae, plants well known for containing highly toxic cardiac glycosides in their tissues. Nothing specific is known in this regard for *Secamone,* but preliminary tests have shown that leaf extracts of *Secamone* possess a strong ability to inhibit glutamate uptake into the insect epidermis (CAVENEY, pers. comm.), a mechanism that generally provides a powerful feeding deterrent for phytophagous insects. The conspicuous coloration of the first-instar larva of *S. comma* suggests that it may be aposematic, i.e. able to sequester some toxins from its foodplant, but in the later instars such unpalatability (if indeed present) is either lost or ineffective and the larva apparently better protected by a cryptic coloration.

5. Behaviour of the adult moth

Eclosion of the adult from the pupa takes place in the early evening (about 19:00–20:00). The male takes to the wing later the same night, while the female presumably remains stationary and releases her pheromone during the same time period, flying only the following night to lay her eggs, as most bombycoids do. During the day, the moths rest with their wings held flat and at an obtuse angle (120°–150°) to each other, the hindwings concealed under the forewings except for the inner (anal) margin, which is shortly rolled up (fig. 1). The abdomen is held straight but flexed downwards, in a manner seen also in several smerinthine Sphingidae.

Description of the immature stages

1. The egg (fig. 9)

Size: diameter 1.35 mm, height 0.75 mm. Perfectly circular in dorsal view, evenly dome-shaped with flat bottom in profile, of the "upright" type; evenly translucent white in colour; surface with numerous minute pores. Emergence hole of larva large and crescentic, spanning up to half the circumference of the egg.

2. The larva

First instar (figs 2, 12). Size: head capsule 0.75 mm wide, 0.69 mm long (high); body ca. 6.5 mm long when fully grown. Head hypognathous; dull orange, setae black with white tips; surface smooth. Body black turning gray later, with small white patch around D1 seta on first abdominal segment (A-1) and much larger, irregular white saddle on A-4 and A-5; primary setae black but the larger ones white in distal half; surface smooth but paired, stout, fleshy protuberances on mesothorax (T-2) and metathorax (T-3) and a single, middorsal one on A-8, larger setae situated on simple, elongate, sclerotized chalazae, no secondary setae present. Thoracic legs black, prolegs grayish with black sclerites; forecoxae fused mesally over entire length, prolegs with biordinal crochets arranged in a homoideous mesoseries.

Second instar (fig. 3). Size: head capsule 1.1 mm wide, 1.0 mm long; body ca. 15 mm long when fully grown; T-3 processes 2.4 mm long, T-2 processes slightly shorter, A-8 process 1.23 mm. Head orange-brown, setae shortened but on knob-like chalazae. Body grayish-brown, with faint, small, dark, longitudinal markings, white patches on A-1 and A-4/A-5 also much fainter and indistinct; primary setae reduced to very short, blunt stumps, chalazae also shortened; protuberances on T-2, T-3 and A-8 enlarged into straight, fleshy processes each with 2 very short setae at apex and with several short secondary setae on very short chalazae on surface, A-8 process bent shortly backwards at apex and orange-brown in distal half, thoracic processes straight throughout, orange-brown in distal half to two-thirds but with dark apex in T-2.

Third instar (fig. 4). Size: head capsule 1.9 mm wide, 1.8 mm long; body ca. 22 mm long when fully grown; T-3 processes 4.4 mm, A-8 process 2.8 mm. Coloration similar as in second instar but surface duller; small dark longitudinal markings on body more distinct, also present on head; short secondary setae on chalazae also sparsely on rest of body; dorsal processes even longer, A-8 process as in second instar but directed more caudad, thoracic ones slightly dark at base and at apex, orange-brown in middle, curving slightly cephalad, at anterior base of T-3 process a conspicuous dark patch.

Fourth instar (fig. 5). Size: head capsule 2.75 mm wide and long; body ca. 37 mm long when fully grown; T-3 processes 8 mm, A-8 process 4.5 mm. Dark body markings and secondary setae more prominent than in third instar; dorsal processes reclining even more but not bicoloured anymore, dark patch at anterior base of T-3 process surrounded by dark yellow; anal plate extended into short, blunt point projecting caudad, anal proleg triangular with obtuse posterior angle.

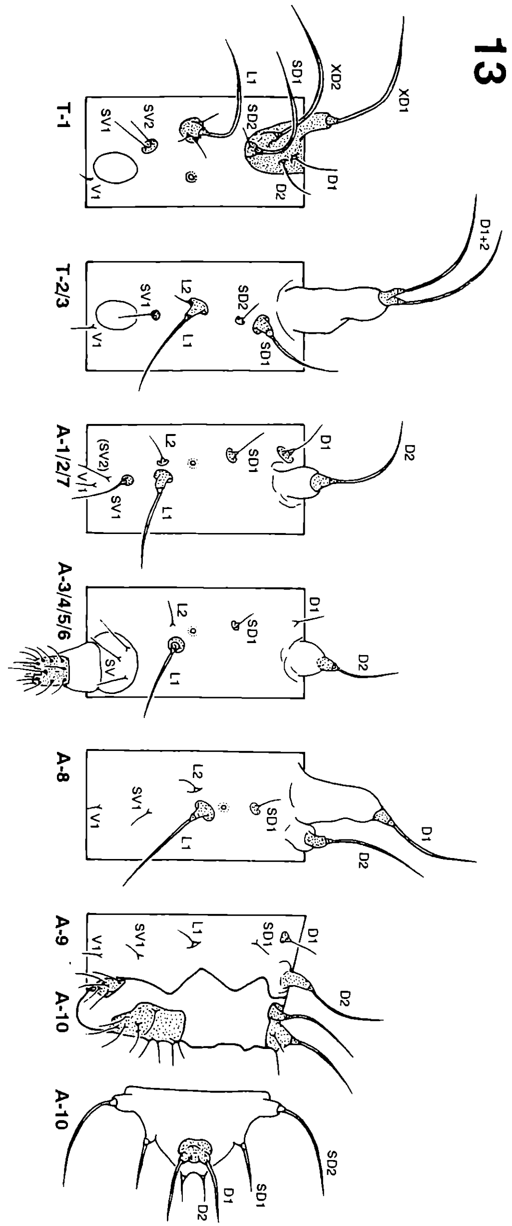
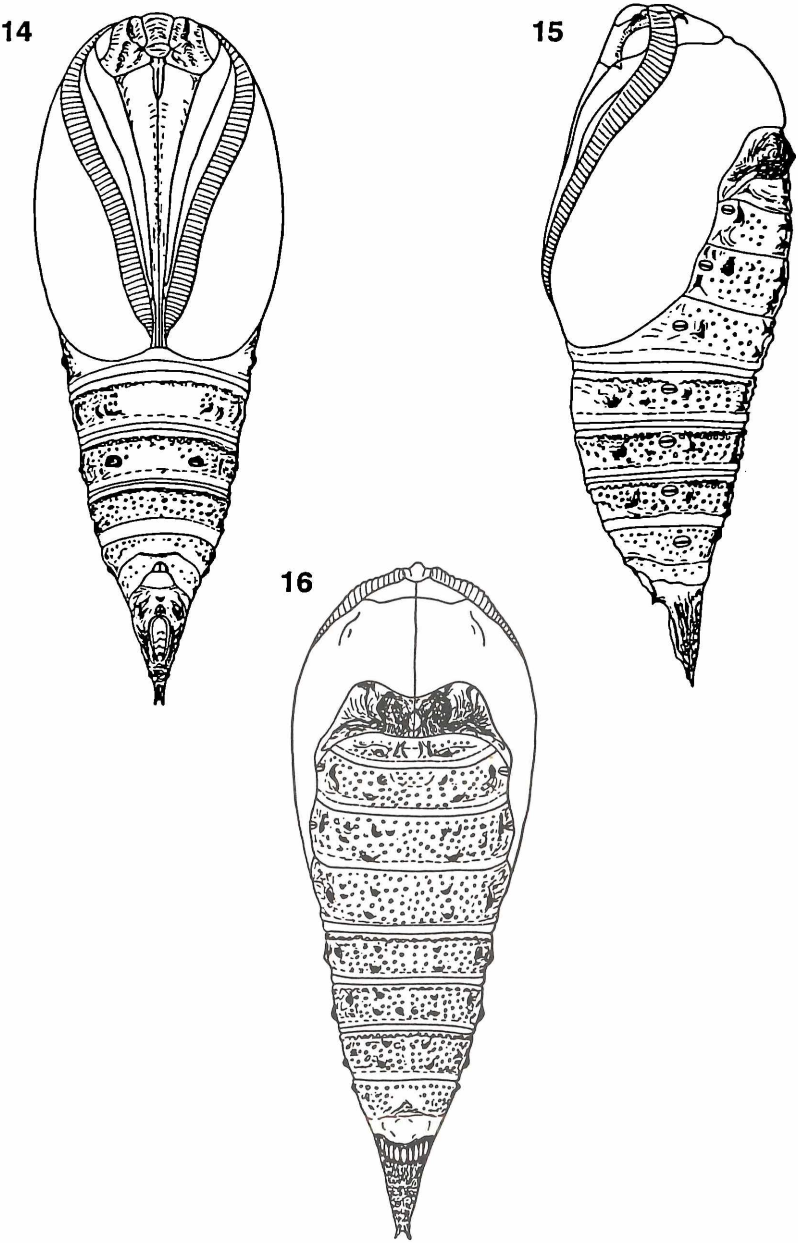


Fig. 13: Setal map of first-instar larva of *Spiramiopsis comma* HAMPSON (for abbreviation of setae see text).



Figs. 14–16: Pupa of *Spiramiopsis comma* HAMPSON. **Fig. 14:** ventral view. **Fig. 15:** lateral view. **Fig. 16:** dorsal view.

Fifth instar (figs 6–8). Size: head capsule 4.0 mm wide and long; body ca. 65 mm long when fully grown; T-3 processes 14 mm, A-8 process 8 mm. Mandibles without secondary hairs. Dark body markings and secondary setae on globular chalazae conspicuous, giving surface the appearance of rough bark; laterally just above prolegs a short longitudinal area without dark markings, forming an indistinct pale band from A-3 to A-8; thoracic processes directed anteriad and reclining, A-8 process with tip shortly curling back; dark black patch at anterior base of T-3 process on smooth, slightly raised, orange-yellow ground to form a conspicuous eyespot (fig. 8), hidden in cleft when T-3 process is reclined but exposed on disturbance; anal plate a short, prominent cone with short secondary setae.

3. Chaetotaxy of the first-instar larva

The nomenclature of the primary setae follows HINTON (1946, 1947), PEASE (1961) and STEHR (1987). The larger setae are situated on simple sclerotized protuberances, which may occur on even larger fleshy outgrowths of the body wall on the dorsum of the larva. These protuberances bear no secondary setae whatsoever and are termed chalazae (fig. 11), not scoli (1) (PEASE 1961, STEHR 1987, SCOBLE 1992). The exact positions, lengths and directions of the various primary setae are illustrated in figs. 10 and 13.

Head (fig. 10): P1 and P2 subequal, in a line parallel to adfrontal suture; AF1 and AF2 shorter but also subequal; A1, A2 and A3 also subequal, A3 slightly longer, A2 closer to adfrontal suture than A1, A3 in line with P1 and P2; L1 longest seta on head, nearly half head width, in line with AF1 and P1; S1 in centre of stemmatal arch, S2 and S3 posteriorly, in line with L1, S3 shorter than S1 and S2; SS2 and SS3 equal, SS1 much smaller; F seta absent; C1 twice as long as C2; labrum with 3 small outer setae and a minute mesal one. Antennal segment 2 with 2 setae, one twice as long as other; segment 3 with 2 minute apical setae.

Prothorax (T-1): Pronotal shield with 6 primary setae, 4 on anterior border (XD1, XD2, SD1, SD2) and 2 more posteriorly (D1, D2); XD1 and XD2 equal in length and

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(1) = Confusion surrounds the application of these two terms, at least in bombycoids. STEHR (1987) and SCOBLE (1992) defined chalaza as a conical protuberance bearing a single, apical seta, and scolus as any larger structure bearing multiple (primary and secondary) setae or branched spines. PEASE (1961), however, used the term scolus in a restricted sense only for multisetose protuberances in which the primary and secondary setae are indistinguishable from each other (as in Saturniinae) and chalaza for similar structures in which the primary setae are still identifiable (as in the New World saturniid subfamilies). These subfamilies thus have chalazae according to PEASE (1961) but scoli according to STEHR (1987). At least in Saturniidae, the difference between these two types of multisetose protuberances is an important and apparently taxonomically significant one (see also PEASE 1961, NÄSSIG 1989). In *Spiramiopsis*, also, those protuberances bearing more than one primary setae (e.g. the lateral setae on T-1) are chalazae only according to PEASE's (1961) definition but not to STEHR's (1987); it would be non-sensical to call such structures scoli but the others chalazae. On the other hand, the sharp, single spines of the final-instar larvae of Bunaeini (Saturniidae), which are clearly derived from typical scoli in the earlier instars, do not qualify for the term scolus under either PEASE's (1961) or STEHR's (1987) definition, but are appropriately termed "Stechdornscolus" by NÄSSIG (1989). Until the terminology of all these structures is fully clarified, it is imperative to clearly define the application of these terms whenever they are used in chaetotaxal studies, at least in bombycoids.

on prominent, separate chalazae; D1 above (dorso-mesally of) D2 and of equal length; SD1 (2) much stronger than SD2 and on prominent chalaza, SD2 very small and at base of this chalaza; 4 lateral setae (3), L1 as strong as XD1, XD2 and SD1, other 3 much shorter and on chalaza of L1, anterior and posterior ones subequal or anterior one slightly shorter, ventro-posterior one smallest, sometimes hardly visible; two subventrals, anterior one (SV2) shorter than posterior one (SV1); V1 minute.

Meso- and metathorax (T-2, T-3): D1 and D2 on prominent chalazae fused at their bases, carried on large fleshy process; SD1 (2) again much longer than SD2 but the latter on separate small chalaza; 2 lateral setae on same chalaza, L1 as on T-1, L2 anteriorly on chalaza, size as on T-1; one subventral (SV1); V1 very small.

Abdominal segments A-1, A-2, A-7: D1 anteriorly to antero-mesally of D2, not on chalaza, but D2 on prominent chalaza; SD1 similar to L1 (smaller than D1), SD2 absent; L1 and L2 in horizontal line, L1 posterior, large and on prominent chalaza, L2 anterior but much smaller (as SD1); SV1 as on T-1 but on A-1 and A-2 2x longer, on A-7 only half as long, on A-2 also a shorter SV2 beneath, as long as V1; V1 on A-1 and A-2 relatively strong (as long as L1) but on A-7 much smaller (as on A-8).

Abdominal segments A-3 to A-6: D1, D2 more or less as on A-1/A-2, but chalaza less prominent; SD1, L1 and L2 as on A-1/A-2; 3 subequal subventrals (SV) on outer proleg sclerite near dorsal border.

Abdominal segment A-8: D1 chalazae from both body sides fused at their bases, carried on large, fleshy, middorsal process, D2 on smaller chalaza latero-caudally of it; SD1, L1 and L2 as on A-1/A-2, but L1 a little longer; SV1 small, as on A-7; V1 very small.

Abdominal segment A-9: D1 small as on other abdominal segments except A-8, D2 on strong, elongate chalaza more dorso-mesally of D1, only half of its width at base apart from that of the other side but not fused; SD1 as on A-1/A-2; only one short lateral (L1) as long as L2 on other abdominal segments; SV1 as on A-7/A-8; V1 minute.

Abdominal segment A-10: Anal plate with 4 long setae in each half (D1, D2, SD1, SD2 according to Stehr 1987), outermost (SD2) and inner one (D1) on prominent chalazae, those of the D1 fused at base on meson; anal proleg with small, narrow outer sclerite with several setae, not in form of broad clasper.

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(2) = The identification of SD1 and SD2 is difficult and apparently not yet fully resolved. Hinton (1946) discussed this matter in detail and drew the following general conclusions as to the interpretation of these two setae: SD1 is invariably longer than SD2, SD1 is directly beneath SD2 on the thoracic segments, and SD2 is a minute seta on the abdominal segments and absent on A-9. In *Spiramiopsis comma,* however, the longer subdorsal seta (SD1 by that criterion) on all thoracic segments is situated above the shorter one. Since the larger subdorsal seta on the abdominal segments is universally regarded as SD1, and since such tactile setae generally maintain their length relation even if their position in respect to each other changes (see Hinton 1946), the larger subdorsal seta on the thoracic segments is here also regarded as SD1, although it is situated above the smaller one (here regarded as SD2).

(3) = Hinton (1946) regarded the lateral setal group as consisting of only three primary setae. In *S. comma* there are three similar, smaller setae in addition to the dominant one (L1), which are all to be considered as primary setae as secondary setae are not otherwise present in the first instar of this species.

4. The pupa (figs 14–16)

Length ca. 26 mm, width ca. 9 mm. Colour dark blackish-brown. Surface dull, matt, without any setae; on thorax and abdomen strongly sculptured with small, very shallow, circular to oval depressions with sharp borders and shiny inside, also with a dorsal, a subdorsal and a lateral row of small irregular calli, the dorsal row with 2 calli per segment, the others with only one. Epicranial suture absent; genae slightly raised and ridged; clypeo-labrum strongly rugose; labial palpi visible; proboscis fully exposed to between apices of wings, broad at base but gradually narrowing towards apex; forelegs and midlegs both broadly exposed nearly to apices of wings, forefemora not exposed; antennae long, stretching nearly to apex of wings but not touching on meson, segmentation indicated throughout length; hindtarsi exposed between apices of wings and proboscis. Wings not touching on meson, closest at apex where narrowly separated by proboscis and hindtarsi; hindwings completely concealed. Metathorax with a large, roundish, rugose callus on either side of meson; flanked on outside by prominent, pit-like furrow extending as a deep hole mesad into callus, hole not visible from above; on meson between calli a deep longitudinal depression.

Abdominal segments strongly tapering caudad, movable ones anteriorly with irregular, transverse, crenulate, callose ridge; apex long and pointed, strongly rugose, especially on dorsal surface, underside with 2 deep, longitudinal and parallel furrows and 2 anal processes just above, terminating in bifurcate cremaster.

Comparison of the immatures stages with those of other bombycoids having larvae with dorsal processes

1. Brahmaeidae

The larvae of *Brahmaea* s. l. and, to a lesser extent, *Dactyloceras* are similar to that of *Spiramiopsis comma* in that they also have fleshy, dorsal processes on thorax and abdomen. Also, *Spiramiopsis* has been placed in Brahmaeidae rather firmly on adult characters (MINET 1994), so that a comparison of its immature stages with those of other brahmaeid genera is the most compelling.

Dactyloceras is the only other African genus of Brahmaeidae, comprising about half a dozen species of which only one, *D. widenmanni* (KARSCH), occurs far enough south (Vumba Mountains, Zimbabwe) to possibly reach the distribution area of *S. comma*. The larvae of *Dactyloceras* are unfortunately only imperfectly known, only SCHULTZE (1914, 1931) providing descriptions and illustrations of the final-instar larvae of three species, viz. *D. lucina* (DRURY, 1782), *D. bramarbas* (KARSCH, 1895) and *D. ?tridentata* (CONTE, 1911), and of the pupa of the last species. These larvae agree with the final-instar caterpillar of *S. comma* in the following characters: T-2, T-3 and A-8 with fleshy dorsal processes that are generally flaccid but become turgid when the larva is disturbed; body marmorated with small, dark, longitudinal marks (except *D. ?tridentata*); anal prolegs raised off substrate in resting position; and feeding on climbing asclepiads. They differ, however, in the following features: A-1 to A-7 and A-9 with similar but slightly shorter dorsal processes; body sparsely covered with fine, soft, short hairs; A-8 process with numerous round yellow spots each with a short, black, central seta (except *D. ?tridentata*); A-3 prolegs raised off substrate when larva is disturbed, and head and legs tucked in between these. *D. ?tridentata* additionally differs in possessing similar fleshy dorsal processes on T-1 and laterally on all segments, and none of these *Dactyloceras* larvae have the conspicuous metathoracic eyespots of *S. comma*. The pupa of *D. ?tridentata* agrees with that of *S. comma* in the prominent metathoracic calli (although not entirely clear in figs. 1 b, c of SCHULTZE 1931: 141), in the anal processes above the cremaster, and in the pupation on the ground under leaves; it differs in the labial palpi being invisible, in the wings touching on the midline for a considerable distance, and in the non-tapering abdominal segments seemingly without transverse callose ridges. The agreement between the immatures of *S. comma* and *Dactyloceras* thus lies essentially in the fleshy dorsal processes (paired on T-2 and T-3 but single on A-8), the metathoracic calli of the pupa and in the larval foodplants. There are, however, several significant differences between the immatures of these two genera.

Brahmaea (incl. *Acanthobrahmaea, Brahmophthalma* and *Brachygnatha*) may be considered the Eurasian equivalent of *Dactyloceras;* it occurs from Italy in the West to China and Japan in the East and Java and Sulawesi in the South. The larvae of seven of its nine currently recognized species (NÄSSIG & PAUKSTADT 1990, ZHANG & YANG 1993) are known, but unfortunately still very incompletely described, particularly the first instars and their chaetotaxy. Of all the known *Brahmaea* larvae, that of *B. (Acanthobrahmaea) europaea* HARTIG, 1963 is most similar to the larva of *S. comma* in that it has fleshy dorsal processes of the same number, positions and development. The first-instar larva has paired, longish, setose dorsal processes on T-2 and T-3 and a similar but shorter and single tubercle middorsally on A-8; these processes become longer and thinner in the following instars but are reduced again in the final instar as the larva grows, to be completely lost (shed) just prior to pupation (BILEK 1965). The more or less uniform black colour of the first instar is gradually changed to a complex, broken, longitudinal pattern of black and yellowish-white in the final instar. The most important difference of this larva compared to *S. comma* is that it has proper, multisetose scoli (sensu STEHR 1987) in the early instars, seemingly four per segment, which are gradually reduced in the final instar until completely absent. The pupa has single, strong spines on the head and mesothorax, metathoracic calli, an anterior row of strong spines dorsally on the movable abdominal segments (A-5 to A-7), and a long and pointed cremaster (BILEK 1965, SAUTER 1967, 1987). Pupation also takes place on the ground under leaves. The natural foodplant appears unknown, but the species has been reared on *Ligustrum* (Oleaceae) in captivity.

In *Brahmaea* s. str., the first-instar larva is black with a reddish mid-dorsal band and the final instar also blackish in ground colour, albeit with various patterns of brown and white. In *B. ledereri* ROGENHOFER, 1973 the larva has a pair of long, fleshy, warty processes with coiled tips on T-2 and on T-3 and a similar but shorter single structure mid-dorsally on A-8, from the first to the fourth instar, while in the final instar these processes are reduced to short stubs (DE FREINA 1985). These processes are similar to those of *S. comma* in their number and positions, but differ in their curled tips and warty surface as well as in being already developed in the first instar. Another similarity seems to exist in the metathoracic colour pattern: in the fourth instar *B. ledereri* has a pair of conspicuous, velvety black patches with a brown centre dorsally on T-3 (DE FREINA 1985), which appear comparable to the metathoracic eyespots of *S. comma*. The pupa of *B. ledereri* again has strong, smooth metathoracic calli, also with a lateral groove running into these (MELL 1930, DE FREINA 1985), as well as a prominent median pit between these calli. However, the immature stages of *B. ledereri* differ from those of *S. comma* in the following features: eggs higher than wide and laid in large clusters; larvae on each side with a dorsal and a subdorsal row of setose scoli on abdominal segments (reduced in later instars); pupa without visible labial palpi, wings broadly touching on midline, movable abdominal segments not tapering and without callose ridges, and cremaster rudimentary. The larval foodplants are Oleaceae, mainly *Fraxinus* in the wild.

The larva of *Brahmaea tancrei* AUSTAUT 1896 differs in the first instar from that of *B. ledereri* in having the tips of its long processes not coiled – though coiling often occurs in the later instars (SUGI et al. 1987, PAUKSTADT & RAGUS 1990) – and in possessing an additional, shorter pair of similar processes dorsally on A-10, but is otherwise similar (4). These long processes carry numerous, stiff, short and blunt secondary setae. The shorter dorsal processes on the other segments bear from 3–5 stiff, blunt secondary setae in addition to the terminal primary one (are thus chalazae according to PEASE 1961 but scoli according to STEHR 1987, see above), and they arise from the D1 setae, with D2 a very small seta postero-laterally thereof (compare *Spiramiopsis*). Another row of similar structures occurs in a subdorsal position on all segments – *Spiramiopsis* has simple SD setae, often not even on chalazae. Laterally, *B. tancrei* has four small, subequal setae (mostly in a 1+3 configuration), not two with the posterior L1 strongly enlarged as in *Spiramiopsis,* and similar differences exist in the SV setae of these two taxa. Furthermore, *B. tancrei* differs from *S. comma* in a very different setal arrangement on the pronotal and the anal shield and in the structure of the crochets, which are uniordinal, heteroideous in *B. tancrei*. The pupa of *B. tancrei* again has no labial palpi, a shortened proboscis, wings broadly touching on the midline, smooth abdominal segments without any fortifications but small punctures, a short, knob-like cremaster, and two small, widely separated, shiny metathoracic calli with a short but deep, transverse, lateral groove. This groove, in fact, is the only preimaginal character by which *B. tancrei* and *S. comma* agree to some extent.

In *Brahmaea (Brahmophthalma),* the first-instar larva is yellowish-white with conspicuous black segmental bands, while the final instar is shiny bright yellow with black lateral markings and blackish legs. The first instar also has a pair of shorter dorsal processes on A-10 and rows of setose scoli on the other segments (PACKARD 1914, PEASE 1961 for *B. japonica* (BUTLER); PAUKSTADT & PAUKSTADT 1986, NÄSSIG & PAUKSTADT 1990 for *B. hearseyi* (WHITE)), varying from three such rows in *B. japonica* (PACKARD 1914, pl. 34, fig. 1a even illustrating a fourth, ventral row) to only a dorsal one in *B. hearseyi ardjoeno* KALIS, 1934 (NÄSSIG & PAUKSTADT 1990); presumably these are structurally the same as in *B. tancrei*. The final instar is completely smooth, without any traces of processes or scoli, and also has

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(4) = A similar larva was also described and illustrated by KOZLOV (1985 a) as *Brahmaea certhia* (FABRICIUS). However, this larva does not agree with the description of *B. certhia* as given by MELL (1930), who said it to have apically coiled dorsal processes like *B. ledereri* and no such processes on A-10; SUGI et al. (1987), however, did illustrate the larva of *Brahmaea certhia* as possessing such A-10 processes. Both the male genitalia illustrated by KOZLOV (1985 a) and the locality of his specimens also do not agree with those of B. certhia but with B. tancrei, as pointed out by PAUKSTADT & RAGUS (1990), who recognized KOZLOV's misidentification and regarded his illustrations as representing *B. tancrei*.

prominent thoracic eyespots. The egg is again round, milky white and finely punctate, but slightly flattened (wider than high). The pupa is similar to that of *Brahmaea* s. str., again without abdominal ridges, but has a stronger cremaster and matt metathoracic calli without lateral grooves but with lateral pits (MELL 1930). The larval foodplants are again Oleaceae, mainly *Ligustrum* in captivity. In their coloration and the development of the dorsal processes, the larvae of *Brahmophthalma* are even more dissimilar to those of *S. comma* than are the ones of *Brahmaea* s. str. (apparently more derived), and a detailed comparison of these with the immature stages of *S. comma* is therefore superfluous.

The immature stages of *Calliprogonos miraculosa* MELL, 1937 from China are as yet unrecorded, as are those of the newly described *Brachygnatha* (= *Brahmaea*) *diastemata* ZHANG & YANG, also from China, which are likely to be very similar to those of *B. tancrei*. Particularly those of *Calliprogonos* should be of considerable importance for the understanding of the phylogeny of the Brahmaeidae, as the genus is considered a primitive one (MELL 1937, SAUTER 1987).

The similarity between the immatures of *Spiramiopsis* and of other brahmaeids thus lies essentially in the flaccid dorsal processes of the larva and in the metathoracic calli of the pupa. However, this similarity is not an identical one, and there are numerous differences in the details of these structures. Also, both the larva and the pupa of *S. comma* differ substantially in other respects from the immature stages of typical brahmaeids, most importantly in the absence of scoli in the first-instar larva and in the presence of labial palpi and a fully exposed proboscis in the pupa. The only possibly significant agreement in preimaginal characters between these two taxa exists in the lateral grooves of the metathoracic calli; however, these are not quite identical, their development is not consistent in *Brahmaea* (see MELL 1930) and apparently also not in *Dactyloceras*, and similar structures also occur in *Lemonia* (NÄSSIG, pers. comm.), so that they cannot (at least not at this stage) be regarded as a synapomorphic agreement between the Brahmaeidae and *Spiramiopsis*.

2. Lemoniidae

Spiramiopsis has been associated with this family (as comprising the two genera *Lemonia* HÜBNER, [1820] 1816 and *Sabalia* WALKER, 1865) at its description (HAMPSON 1901) and again later (FORBES 1955), in both cases based exclusively on characters of the adult. Their immature stages have never been compared before. The larva of the Palaearctic *Lemonia* is densely hairy without elongated dorsal processes, although low scoli with long setae do occur in the first instar (see below). The larva of *Sabalia,* a genus comprising about half a dozen species occurring in eastern Africa as far south as Zimbabwe, is very poorly known, a description being available for only one of its species. FONTAINE (1975) described the first-instar larva of *S. tippelskirchi* KARSCH, 1898 as completely black with a pair of short, spiny dorsal processes on the first segment and sparse, short setae on the others, and the later instars as also black but with a yellow transverse band on each segment, each such band carrying a pair of dorsal ("subdorsal"), black, non-spiny processes, those on the first band being very long, flexible and "articulated" in the middle, and the second-last band (presumably A-8) carrying a single (middorsal) process slightly longer than those of the preceding segments. The position of the single dorsal process is somewhat confused in FONTAINE's description, as he states it to occur on the "second-last band" (i.e. A-8) in the second instar but on the "second-last" or "pre-anal segment" (i.e. A-9) in the third and fourth instars; it most probably occurs on A-8 as in other bombycoid larvae. Similarly, the long anterior pair of processes are described as occurring on the first or "post-cephalic" segment (i.e. T-1) in the first, third and fourth instar but on the "first transverse band" (probably T-2) in the second; since the first thoracic segment in bombycoid larvae is usually small and carries the pronotal shield but rarely any long processes, it seems that the long anterior dorsal processes of *S. tippelskirchi* are also borne on T-2 rather than on T-1. Indeed, from the prolegs visible in fig. 3 of FONTAINE's illustrations it appears that it is T-2 that carries the first yellow band and the long anterior processes, not T-1.

The eggs of *S. tippelskirchi* are large, spherical, (translucent) white and laid in a single-layered cluster of about 50 on the underside of a leaf, the larvae are highly gregarious in all instars and feed on *Euphorbia granti* (their conspicuous coloration thus probably aposematic), and the reddish-brown, wrinkled pupa rests in a simple cell under debris on the soil, without a cocoon (FONTAINE 1975). Unfortunately, no further details are available about the immature stages of *Sabalia*.

In its larva, *Spiramiopsis* is thus not strikingly similar to *Sabalia,* but its anterior larval dorsal processes are quite comparable to those of *S. tippelskirchi* in that they are also soft, fleshy and flexible to a large degree. The difference in coloration is probably due to the presumed aposematism of the *Sabalia* larva and thus not very significant, but the presence of shorter processes on the other segments sets the *Sabalia* larva apart from that of *Spiramiopsis;* in fact, this condition is much more similar to that found in the larvae of *Dactyloceras*. In its pupa, *Spiramiopsis* agrees with *Sabalia* in having a rough integument and a strong cremaster and in being formed in a simple cavity on the ground under debris, and possibly also in having metathoracic calli and exposed labial palpi, but a more detailed comparison of the pupae of these two taxa is unfortunately not possible due to a lack of information on the pupa of *Sabalia*.

3. Bombycidae

Spiramiopsis comma has been placed in this family by FLETCHER & NYE (1982) largely on the basis of its larva, without, however, giving any details of agreement in specific characters. The larva of typical Bombycidae (*Bombyx, Ocinara* (5)) is rather different from that of *S. comma*. In the first instar, the *Ocinara* larva has its primary setae on quite similar chalazae, but the arrangement and development of these is different: D1 is always stronger than D2 (opposite in *S. comma*), there are two equal L setae on all segments, and on A-9 D1 and D2 are on one fused chalaza. The A-8 process is, like in *S. comma,* formed by the fused chalazae of both D1, with D2 staying behind on a separate chalaza. In the later instars, all chalazae and nearly all primary setae are lost, but the body is sparsely covered with very fine secondary hairs, and the A-8 process is apically or anteapically invaginated and bears two minute terminal setae. Similar but paired processes may also occur dorsally on T-2, T-3 and A-2 to A-5 in true *Ocinara* and relatives (DIERL 1978), but are often reduced to absent, without any traces in any instar. In *Bombyx mori* (LINNAEUS, 1758) the first-instar larva has long primary and secondary setae situated on proper scoli, not on simple chalazae as in *Ocinara*. The pupa of *Bombyx* and *Ocinara* is also very different from that of *Spiramiopsis* (see MOSHER 1916: fig. 107 for *Bombyx; Ocinara* nearly identical) and of course encased in a silken cocoon.

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(5) = Referring to the African species of *Ocinara,* such as *O. ficicola* (WESTWOOD & ORMEROD, 1889), which differ in genitalic characters from true *Ocinara* as defined by DIERL (1978) and should go into a different genus, probably near *Penicillifera* DIERL, 1978 judging from the male genitalia.

Other bombycid groups (Phiditiinae, Prismostictinae etc., see MINET 1994) except Apatelodinae appear to more or less agree with this larval type, and neither these nor the hairy Apatelodinae can be regarded as close relatives of *Spiramiopsis comma* on larval characters. More similar is the larva of *Gastridiota adoxima* (TURNER, 1902), Bombycinae, which has comparable flaccid dorsal processes. The two anterior pairs of these processes, however, are not borne on T-2 and T-3 as in *S. comma,* but on A-1 and A-2, carrying the D1 setae of these segments at their tips (COMMON & EDWARDS 1991). In other details of the chaetotaxy of the first instar, in the short secondary hairs of the later instars, in the foodplant (*Ficus*) and in the type of cocoon, *Gastridiota* agrees quite well with typical bombycines, so that the similarity of its dorsal processes to those of *S. comma* is clearly due to convergence, over and above the difference in position of these structures.

Spiramiopsis thus displays little similarity in its immature stages to Bombycidae, other than in the simple chalazae of the first larval instar, and this agreement can hardly be construed as a synapomorphy to justify the placement of *Spiramiopsis* in Bombycidae.

4. Saturniidae

Dorsal thoracic and abdominal outgrowths comparable to those of *Spiramiopsis comma* also occur in several groups of Saturniidae. The processes most similar in this regard are found in the primitive Neotropical subfamily Arsenurinae, where particularly *Arsenura batesii arcaei* (DRUCE, 1886), as illustrated by BRENNER & LAMPE (1987), bears a striking resemblance to *S. comma* in its first and fourth instars, the first also being black with a white saddle and a red head and the fourth having very similar fleshy processes on thorax and abdomen. No detailed studies of arsenurine immature stages and larval chaetotaxy have yet been published, but the available, scattered information on their larvae has been comprehensively collated by PEIGLER (1993), allowing a certain degree of comparison to be made with the larva of *S. comma*. A good account of the immature stages of *Caio richardsoni* (DRUCE, 1890) was also recently published by WOLFE & PESCADOR (1994).

All known first-instar larvae of Arsenurinae have two large, apically bifid (bearing the two dorsal primary setae) dorsal processes on T-3, and similar structures may also occur on T-1 and/or T-2. The presence of such spikes on T-1 and/or T-2 is regarded as a plesiomorphic condition (PEIGLER 1993), since it also occurs in Ceratocampinae and

Hemileucinae; large, bifid subdorsal spikes on the thoracic segments are likewise interpreted as primitive. Such stiff, bifid spikes, however, do not occur in *S. comma* nor in brahmaeids and must be regarded as an independent development in Saturniidae. In the later instars of Arsenurinae, these dorsal spikes are invariably modified and reduced, and the flexible processes in the fourth instar of *Arsenura batesii arcaei* resembling those of *S. comma* are thus derived very differently and cannot reflect any close relationship. The similarity in coloration between the first instars of these two species is, likewise, only superficial, as their chaetotaxal arrangement and development is very different. A further difference between the first instars of these two taxa lies in the dorsal setae of A-9, *A. batesii arcaei* having a middorsal, fused spine as typical for the New World Saturniidae (see PEASE 1961), whereas in *S. comma* both D1 and D2 of A-9 are separate. However, the middorsal fusion of D2 on A-9 may not occur in all Arsenurinae, as indicated for *Caio richardsoni* by PACKARD (1914) and WOLFE & PESCADOR (1994) and for *Copiopteryx semiramis* (CRAMER, 1775) by TRAVASSOS (1946), and is also not present in *Aglia* OCHSENHEIMER, 1810 (Agliinae), whose larva is otherwise quite similar (and probably closely related) to that of the Arsenurinae. Information on the pupae of Arsenurinae is even scarcer than on their larvae. BRENNER & LAMPE (1987) described the pupa of *Arsenura batesii arcaei* as smooth without metathoracic calli or abdominal ridges, but small metathoracic calli do occur in *Caio championi* (DRUCE, 1886) (NÄSSIG, pers. comm) and in *C. richardsoni* (WOLFE & PESCADOR 1994); it remains to be seen which is the general condition and how much this character varies in the subfamily.

The larvae of Ceratocampinae do not have dorsal processes similar to those of *S. comma,* particularly not in the first instar. Their long, bifid dorsal spines are usually present on all thoracic segments as well as on A-8 (sometimes absent on T-1, or on T-1 and T-2) and are only comparable to those of Arsenurinae, Agliinae and Sphingidae. Details of the chaetotaxy of their first-instar larvae are given by PEASE (1961). Ceratocampine pupae do, however, have very prominent metathoracic calli and generally also strongly spinose abdominal ridges and a long, bifurcate cremaster, but these features also occur in several other groups of Saturniidae and in Brahmaeidae and have most probably been developed several times in the Bombycoidea (see discussion below).

Further chaetotaxal details by which *S. comma* differs from Saturniidae are as follows (partially after PEASE 1961): XD1 and XD1 on separate chalazae (fused in Saturniidae); T-1 with 4 lateral setae (2 in Saturniidae); T-2 and T-3 with 2 lateral setae (1 in Saturniidae); A-1 to A-7 with D1 smaller than D2 (opposite in Saturniidae) and L1 much smaller than L2 (equal or opposite in Saturniidae); A-9 with D2 on strong chalaza dorso-mesally of small D1 but not fused middorsally (fused in Ceratocampinae, Hemileucinae and Arsenurinae, in Saturniinae D2 much smaller than D1). *Spiramiopsis* therefore does not agree with Saturniidae in any significant preimaginal characters, and the similarity between its larva and that of certain Arsenurinae is clearly due to convergence.

5. Sphingidae

Although nearly all sphingid larvae have a prominent horn on A-8, only a few have similar thoracic processes. In the African *Lophostethus dumolinii* (ANGAS, [1849]), the first-instar larva already bears an impressive arsenal of huge, hard and hollow spines on all segments, and not only dorsally. On T-2 and T-3, D1 and D2 are placed on a large, apically bifid spike; on A-1 to A-7 D1 is on a similar but single spine, with D2 small and separate behind (opposite in *S. comma*); on A-8 D1 and seemingly also D2 from both sides are on an enormous, bifid spike; while A-9 is very narrow with a single small dorsal spine on each side. The larva also already has the characteristic triangular anal claspers and anal plate of sphingid caterpillars. This larva and its thoracic and abdominal spines are not at all comparable to those of *Spiramiopsis comma,* but much more similar to those of Arsenurinae and Ceratocampinae as discussed above. On chaetotaxal grounds, therefore, *L. dumolinii* must be regarded as a primitive (though specialized) member of the Sphingidae, and the possibility of a closer relationship to Arsenurinae and/or Ceratocampinae needs further investigation. Dorsal thoracic processes (often of quite different structure) also occur in certain other sphingid larvae, e.g. *Ceratomia amyntor* (GEYER, [1835]), where they have most probably evolved independently. Several sphingid pupae also have metathoracic calli, but seemingly always of a long, narrow, transverse form and not as pronounced as in Brahmaeidae and Saturniidae (see discussion below).

6. Mirinidae

Of the remaining bombycoid families sensu MINET (1994), only the monotypic Mirinidae display prominent, dorsal, thoracic larval processes (GERASIMOV 1937, KOZLOV 1985 b), but these are not flaccid and flexible but stiff and apically bifid. Also, in the chaetotaxy of its first-instar larva, in its pupa and in its cocoon (KOZLOV 1985 b) *Mirina christophi* (STAUDINGER, 1887) is very different from *Spiramiopsis comma*.

Discussion

Spiramiopsis comma thus possesses a mixture of preimaginal characters that agree with those of Brahmaeidae and of others that do not. Also, the main characters that agree with Brahmaeidae (fleshy dorsal processes in the larva and metathoracic calli in the pupa) occur in other bombycoid families, too, and it therefore has to be established how significant these and other relevant characters are in a phylogenetic sense. In a number of recent publications on the higher classification of the Lepidoptera, MINET (1986, 1991, 1994) has attempted to reclassify the Bombycoidea by means of synapomorphies that would support the delimitation and relationships of the major bombycoid lineages as monophyletic groups. Most of these synapomorphies are based on characters of the adult, but there are at least a few characters of the immature stages that provide a framework within which one can investigate the affinities of *Spiramiopsis*. We will here firstly attempt to place *S. comma* in the phylogenetic system of MINET (1994) on its preimaginal characters, and then discuss the phylogenetic value of some of these characters in order to assess the affinities and taxonomic position of *Spiramiopsis*.

1. Taxonomic placement of *S. comma* on preimaginal characters

The Bombycoidea s. lat. (BROCK 1971) or “bombycoid complex” (MINET 1994) share two synapomorphies based on the immature stages (after MINET 1991, 1994): larval prolegs with secondary setae, and pupa without distinct maxillary palpi. *Spiramiopsis comma* possesses both these characters and therefore belongs to this taxon alright. It also has the crochets of its larval prolegs arranged in a biordinal, homoideous mesoseries, a feature typical of bombycoids (STEHR 1987) although probably not a reliable synapomorphy.

Within the bombycoid complex, *S. comma* shares the preimaginal synapomorphies of the Bombycoidea s. str., viz. fused forecoxae in the final larval instar, and D1 setae of A-8 situated on a single, middorsal process (MINET 1991, 1994), but not those of the Lasiocampoidea, namely mandibles of mature larva with secondary setae, and prolegs with SV sclerite divided (but see 4. below), nor that of the Mimallonoidea.

MINET (1994) recognizes two major lineages within the Bombycoidea s. str., namely an "Ep-Sa" lineage (Eupterotidae, Bombycidae, Endromididae, Mirinidae, and Saturniidae) and a Carthaeidae + "L-S" (Lemoniidae, Brahmaeidae and Sphingidae) lineage. Of the two preimaginal synapomorphies of the "Ep-Sa" lineage, *S. comma* shares one (pupal forefemora concealed) but not the other (pupal proboscis shortened), having the plesiomorphic condition of the latter character in common with Carthaeidae and Sphingidae. Brahmaeidae, incidentally, also possess both these characters of the "Ep-Sa" lineage (see below). The "L-S" group is defined by MINET (1994) by only one preimaginal synapomorphy, namely the conspicuous sculpturing of the pupal metanotum. However, as detailed under 3. below, this character can hardly be construed as a synapomorphy as it also occurs in other bombycoid families and is related to pupal protrusion from the cocoon or the soil and thus adaptive and homoplasious. On preimaginal characters therefore, *Spiramiopsis* falls into the "L-S" group only by exclusion from others rather than by any clear, synapomorphic agreement in characters. Possibly such an agreement could exist in the presence of lateral segmental eyespots in the larva; these are present on all abdominal segments in *Carthaea* and sometimes in Sphingidae, but in the latter family often only on A-1 and/or A-2 or on T-3, in *Brahmaea* on T-2 and T-3 and in *Spiramiopsis* only on T-3 (though totally absent in the hairy *Lemonia* and in the presumably aposematic *Sabalia*).

Within the "L-S" group, MINET (1994) regards the Lemoniidae and Brahmaeidae as adelphotaxa (sister-groups) on the basis of three preimaginal synapomorphies: egg of the upright type, pupa with proboscis distinctly shortened, and pupal forefemora concealed. All three these synapomorphies are problematic. The "upright" type of eggs also occurs in other bombycoid families (MINET 1994) and in several other lepidopteran superfamilies and families, seemingly with no phylogenetic basis (SCOBLE 1992), and this character appears to be homoplasious also in Bombycoidea and is therefore of limited phylogenetic value. Its alleged synapomorphic occurrence in Lemoniidae and Brahmaeidae must remain suspect until its exact distribution among the Bombycoidea is known; however, *Spiramiopsis* does agree with Lemoniidae and Brahmaeidae in this character. The other two synapomorphies are exactly the same as in the "Ep-Sa" lineage above and perhaps indeed an independent acquisition in Lemoniidae and Brahmaeidae; however, this dual occurrence greatly compromises their cladistic value as synapomorphies in both groups. Also, the degree of exposure of the pupal proboscis seems to be related to the size of the wings of the adult in relation to its body, large and broad wings requiring a larger area on the pupal surface and obtaining this by meeting on the meson and at the expense of the proboscis and even other appendages. A gradual development of this feature is clearly visible in Sphingidae, and MELL (1930) described the same occurrence in Eupterotidae. This character is therefore of rather limited phylogenetic value. Exposed pupal forefemora occur widely only in Sphingidae, though not in all species and rudimentary in others, and this feature thus appears to be a peculiar plesiomorphy or redevelopment in this family rather than a groundplan condition of the Carthaeidae + "L-S" lineage. In any case, its absence in *Spiramiopsis* only excludes the genus from Sphingidae but does not indicate a close relationship to any other bombycoid family.

On family level within the Carthaeidae + "L-S" lineage, few preimaginal synapomorphies have been identified to assess the possible placement of *Spiramiopsis* in any of these families. The only possible preimaginal autapomorphy of the monotypic Carthaeidae so far indicated are the clubbed setae in the penultimate instar (COMMON 1966, 1990). *S. comma* does not have these, and its larva also differs significantly from that of *Carthaea saturnioides* WALKER, 1858 in not having proper scoli and, of course, in possessing paired T-2 and T-3 processes. Further chaetotaxal differences are indicated from COMMON's (1966) description, but the first-instar larva of *C. saturnioides* is not yet described and a precise comparison therefore impossible. The pupa of *C. saturnioides* agrees with that of *S. comma* in possessing a fully exposed proboscis and apparently also in the anteriorly pitted dorsum of the abdominal segments, but differs most conspicuously in the absence of labial palpi and metathoracic calli. Since the presence of an exposed proboscis in the pupa is clearly plesiomorphic and the abdominal pits likely to be adaptive (homoplasious), *Carthaea* and *Spiramiopsis* share no significant preimaginal characters and cannot be regarded as closely related; the absence of scoli in the larva and the presence of labial palpi in the pupa indicate *Spiramiopsis* to be more primitive than *Carthaea*.

The two genera of the family Lemoniidae, *Lemonia* and *Sabalia*, share four imaginal synapomorphies after MINET (1994) but as yet no preimaginal synapomorphies. The larva of *Lemonia* is densely hairy and has two rings of low scoli with long setae (i.e. two pairs of dorsal scoli) per segment in the first instar but no elongate dorsal thoracic processes and no middorsally fused scolus on A-8, and the pupa is smooth but thin-shelled with a strong, bifurcate cremaster, a pair of strong, laterally grooved metathoracic calli and exposed labial palpi (NÄSSIG, pers. comm). The larva thus bears no resemblance to that of *S. comma* whatsoever, but the pupa agrees notably in the exposed labial palpi and the metathoracic calli. The former character does not occur otherwise in the Bombycoidea s. str. but regularly in the Lasiocampoidea and must therefore be regarded as a plesiomorphy in the Bombycoidea, while the latter is adaptive (see 3. below) and thus a homoplasy in the Bombycoidea. However, the structural similarity between the metathoracic calli of *Lemonia* and *Brahmaea* (and to a lesser degree of *Spiramiopsis*) is possibly indeed synapomorphic and indicative of a close relationship between these taxa. The larva of *Sabalia* (FONTAINE 1975, see above) is much more similar to that of *Spiramiopsis* than is the one of *Lemonia,* but as yet no clear preimaginal synapomorphies are identifiable between these two genera, and a close relationship between them is as yet not indicated on preimaginal characters.

The Sphingidae are defined by two preimaginal autapomorphies after MINET (1994), viz. oblique lateral stripes on A-1 to A-7 in the larva, and hindwings not reaching A-4 in the pupa. Both these characters are not present in *Spiramiopsis,* and this genus is also so different from the Sphingidae in numerous other larval and pupal characters that any close relationship is very unlikely. The agreement between these two taxa in the dorsal larval processes and in the pupal metathoracic calli is discussed above and below.

For the Brahmaeidae, finally, MINET (1994) records no larval or pupal autapomorphies. As discussed above, the only preimaginal similarities between Brahmaeidae and *Spiramiopsis* are to be found in the fleshy larval processes and in the pupal metathoracic calli, but neither of these can be regarded as a synapomorphy to justify the inclusion of *Spiramiopsis* in Brahmaeidae (see above and 2. and 3. below).

In MINET's (1994) system of the Bombycoidea, therefore, *Spiramiopsis* is, on the characters of its immature stages, traceable to his second main lineage, the Carthaeidae + "L-S" group, but not further to any of the families. Its larva agrees with Bombycidae (tentatively in MINET's "Ep-Sa" lineage) in possessing simple chalazae and no secondary setae in the first instar, and its pupa with *Lemonia* in the exposed labial palpi; however, both these characters must be regarded as primitive (plesiomorphic), and *Spiramiopsis* does not show any synapomorphic preimaginal agreement with any bombycoid family as currently defined. The agreement in larval processes and pupal calli is discussed in more detail below.

2. Dorsal processes in bombycoid larvae

Elongated processes derived from the primary dorsal setae occur in the larvae of eight of the nine families of the Bombycoidea s. str. (sensu MINET 1994), being universally absent only in the Eupterotidae, although such processes may also be reduced to absent in some members of all the other families. In Bombycidae, Endromididae, Carthaeidae and Oxyteninae (a subfamily of Saturniidae according to MINET 1994) such processes are generally limited to a short "tail" on the eighth abdominal segment, originating from a middorsal fusion of the chalazae or scoli of the D1 setae (assumed for Oxyteninae, for which only general descriptions are available, e.g. JORDAN 1924, NENTWIG 1985, but no detailed chaetotaxal studies). This "tail" is soft and flexible in Bombycidae, Endromididae and Oxyteninae but more horn-like in Carthaeidae, and in Bombycidae similar but paired processes may occur on other segments as well (*Gastridiota, Ocinara*-group, see above).

In Brahmaeidae, fleshy processes occur not only middorsally on A-8, but also on other abdominal and on the thoracic segments; in *Brahmaea* as long, filamentous and paired structures on T-2, T-3 and sometimes on A-10, in *Dactyloceras* as shorter, stiffer tubercles on all segments and also laterally in addition to the paired dorsal processes. In *Brahmaea* these processes seemingly always arise from the D1 scoli (D1+D2 on the thorax), but detailed investigations of brahmaeid chaetotaxy are still outstanding. The setal arrangement of the first-instar larva of *Dactyloceras* is unknown but presumably similar to that of *Brahmaea*.

In *Sabalia* (Lemoniidae), fleshy processes occur again singly and middorsally on A-8 and in pairs dorsally on the other segments, particularly strongly elongated on T-2 (or T-1?); presumably these processes also arise from the D1 setae but chaetotaxal details are not available at present. In *Lemonia*, low dorsal scoli originating separately from the D1 and D2 setae occur in the first instar, but are completely reduced later.

In Saturniidae, elongated abdominal and thoracic processes occur most regularly and conspicuously in the subfamilies Arsenurinae, Agliinae, Ceratocampinae and Hemileucinae, but also in the saturniine tribes Attacini and Bunaeini. In the former four groups these processes are mostly very large, stiff, bifid structures bearing numerous secondary setae or spines, and soft, flexible processes only occur in very few species (e.g. *Arsenura batesii arcaei*), seemingly as a secondary development. In Attacini these processes (if elongated) are also soft and fleshy (e.g. *Attacus*), in Bunaeini they are always stiff and sharp but relatively short (e.g. *Bunaea*). In all these groups these processes again arise from the D1 chalazae or scoli (D1+D2 on the thorax), or SD1 and L1 if applicable, and A-8 also generally has a middorsal, fused D1 process (at least if elongated), which is larger than all other abdominal protuberances. The paired dorsal processes of T-2 and T-3 may also be enlarged considerably, but widely varying configurations of developments of the dorsal setae occur in this family.

In Sphingidae, the middorsal process of A-8 is a very dominant feature of the larva and often spectacularly long in the early instars, but reductions to varying degrees usually take place in the final instar. It is normally a single, unbranched and pointed horn directed obliquely backwards, but also originates from a middorsal fusion of the bases of the D1 setae. Thoracic and other abdominal processes are rare in Sphingidae, but conspicuously developed in a few species (e.g. *Lophostethus,* see above). These processes again arise from the D1 setae, or D1+D2 on the thorax.

Mirina (Mirinidae), finally, has long, setose dorsal and subdorsal spines on all segments except T-1 and A-10, seemingly arising from fused D1+D2 (or SD1+SD2) setae on all segments (KOZLOV 1985 b). A-8 again has a middorsally fused spine of greater length than those of the other abdominal segments, while the paired T-2 and T-3 processes are about as long as the entire larva and apically strongly bifid.

A few generalizations can be drawn from this review of larval processes in the Bombycoidea. Firstly, enlarged dorsal and subdorsal processes occur only in larvae that are not clothed in long secondary hairs; this is not only true among the families but also within, as woolly saturniid larvae also always have very small dorsal scoli. The absence of such enlarged processes in woolly larvae is likely to be secondary. Secondly, all non-woolly larvae have an enlarged, middorsal, fused process on the eighth abdominal segment, at least in the early instars but often reduced later; its absence in woolly larvae is again likely to be secondary (see also MINET 1994, and 4. below). Thirdly, similar but paired processes are mostly present on the second and/or third thoracic segments, always in company with the A-8 process but with or without similar, smaller structures on the other thoracic and abdominal segments. These thoracic processes always arise from a fusion of the bases of the D1 and D2 setae. Together, this seems to be the setal "groundplan" of bombycoid larvae, and various modifications of it have occurred in the different families and subfamilies, presumably mostly independently but sometimes resulting in rather similar developments. How taxonomically and phylogenetically significant such similarities are in the various cases remains to be studied; in particular, it has to be investigated whether they arise from comparable structures in the first larval instar. If not, they are almost certainly convergent developments reflecting the same groundplan but not synapomorphies indicating a close phylogenetic relationship.

In this context thus, the larva of *Spiramiopsis comma* reflects the typical groundplan of the non-woolly bombycoid larva, only modified by an inflation of the T-2, T-3 and A-8 processes and by a reduction of the secondary setae. The same modifications also occur, separately or jointly, in several other bombycoid families. Processes most similar to those of *S. comma* occur not in Brahmaeidae but in the fourth instar of the saturniid *Arsenura batesii arcaei* (see BRENNER & LAMPE 1987). In this species, however, these processes arise from structures in the first-instar larva that are very different from those of *S. comma* (see above), and they can thus hardly be interpreted as indicating a close relationship. Similarly, the long, filamentous outgrowths of *Brahmaea* arise from proper scoli sensu STEHR (1987) in the first larval instar and gradually decrease in length relative to the body size to the final instar, while those of *S. comma* arise from simple chalazae and gradually increase in length; a close relationship based on such processes different both in origin and in development is highly improbable. Indeed, simple chalazae as in *S. comma* occur in none of the "higher" bombycoid families but only in Bombycidae, which, in the mature larva and cocoon, are a more specialized family than *S. comma* and also display no synapomorphic development of the dorsal processes with *S. comma*. The dorsal larval processes of *S. comma* have, in fact, no comparable structures in all other bombycoids, as far as their larvae are known, and seem to represent a rather unique development that is similar to that of certain other bombycoid groups only because it is based on the same groundplan of setal configuration.

3. Callosities in bombycoid pupae

Metathoracic pupal calli have often been regarded as characteristic of the family Brahmaeidae (MELL 1930, SCHULTZE 1931, SAUTER 1987), but their exact structure and function has not been studied properly. In fact, such calli are not at all limited to the Brahmaeidae but also occur in *Lemonia* and several Sphingidae (see also MINET 1994), as well as in some Eupterotidae and in several groups of Saturniidae. A brief overview of these calli in especially Saturniidae is relevant in assessing the taxonomic and phylogenetic value of these structures in Brahmaeidae and in *Spiramiopsis*.

In Saturniidae, prominent pupal calli occur only in species that do not pupate in dense arboreal cocoons, but on or in the soil. Furthermore, in groups pupating in the soil, such calli are best developed in species that pupate at considerable depths, whereas those pupating just below the surface tend to have much smaller calli. In Attacini, the pupa is always very thin-shelled and has no callosities whatsoever; the adult escapes from the dense, arboreal cocoon by chemically softening the silk. In Saturniini, the pupa is generally somewhat more sclerotized and may have slight fortifications on the movable abdominal segments, but proper calli are absent and eclosion from the cocoon is as in Attacini.

The Ludiini also pupate in cocoons, but these are spun in natural cavities on the ground among detritus and are much weaker than those of Attacini and Saturniini. Eclosion from these cocoons is not by the emerging adult chemically softening the silk, but by the pupa protruding through the crumply and brittle anterior end of the cocoon, which is spun in a different fashion than the rest of the structure. In *Micragone* WALKER, 1855 and *Holocerina* PINHEY, 1956 this protrusion is facilitated by a large, rugose, single or divided prothoracic callus, while *Ludia* WALLENGREN, 1865 and *Holocerina* PINHEY, 1956 also have a pair of small, transverse, shiny calli on the metathorax. In addition, ludiine pupae have abdominal ridges that prevent the segments from telescoping when the pupa pushes forward, a spinulose surface and often a large cremaster with lateral spines, all structures that allow the pupa to push through the anterior end of the cocoon. In Hemileucinae, pupation also occurs among or beneath debris on the ground surface, in a more or less flimsy cocoon or (rarely) without cocoon (FERGUSON 1971), but the pupa has no special structures other than a rough integument and weak abdominal ridges to facilitate eclosion of the moth.

In Pseudapheliini, the pupae of genera that pupate in the soil (*Tagoropsis* FELDER, 1874, *Usta* WALLENGREN, 1863, *Urota* WESTWOOD, 1849) all have a pair of large, shiny calli on the meso- and on the metathorax, as well as strong, sometimes serrate ridges around the anterior end of the abdominal segments. By contrast, the pupae of those species that pupate simply on the ground under leaves (*Pseudaphelià* KIRBY, 1892, *Pselaphelia* AURIVILLIUS, 1904) have no such calli or ridges, but a long and pointed cremaster by which they move out from under the leaves prior to the adult eclosing.

The African Bunaeini have seemingly perfected pupation in the soil and developed a number of structures that allow the pupa to move to the soil surface from depths in excess of 100 mm. The pupal prothorax has a pair of hard, shovel-like calli directed anteriad, the meso- and metathorax each a pair of large, wrinkled calli, the abdominal segments strong but smooth anterior ridges, and the 10th abdominal segment a stout, pointed cremaster and prominent anal processes. In addition, the 7th abdominal segment displays an unusual (and probably synapomorphic) fortification in that its posterior edge is thickened and internally strengthened by a ring of short, radially arranged ridges, which allows this segment and the anterior portion of the pupa to rotate on the “tail” end (A-8 to A-10) anchored in the ground. During such rotating movements, the prothoracic calli loosen the soil ahead of the pupa and it can push through the ground, facilitated by the otherwise very smooth integument. Bunaeini that pupate in lesser depths of soil (e.g. *Heniocha* HÜBNER, [1819] 1816) again have considerably weaker calli than those that pupate very deeply, and *Eochroa trimenii* FELDER, 1874, which pupates on top of the soil in a few silken strands under leaves, has none of these structures at all but a short, rugose cremaster with a few hooked setae, much as in Saturniini and Hemileucinae.

In Ceratocampinae, which also pupate in the soil, *Eacles* HÜBNER, [1819] 1816 and *Citheronia* HÜBNER, [1819] 1816 have smooth pupae with large, flat metathoracic calli, while those of the other genera have sharp spines on the eyes and on the pro- and mesothorax, large transverse calli on the metathorax, transverse ridges with strong spines on the abdominal segments, a long, bifurcate cremaster, and a generally spinulose integument. These various spinosities are generally interpreted as devices assisting the pupa in moving to the soil surface prior to eclosion of the adult (FERGUSON 1971, LEMAIRE 1988), but no detailed studies have been published as to exactly how these structures are used and how the pupa moves. It seems more likely, however, that large spines and a rough integument are a hindrance rather than an aid for any object moving through dense soil, and that such body projections may be used to move on top of the ground rather than in the soil. This is supported by the fact that species pupating deep in the soil (e.g. Bunaeini) have a smooth integument, and by the observations of NÄSSIG & PAUKSTADT (1990) that the pupa of *Brahmaea europaea,* which has a similar cremaster and spines, uses these to crawl on the soil surface actively at night.

In other bombycoid groups that pupate in or on the soil, pupation is never very deep and the pupae therefore generally smooth and rarely with calli. Sphingid pupae are mostly smooth and slippery without any callosities, but weak, narrow, transverse metathoracic calli occur in some species and rings of small abdominal spines in others; BROCK (1990) has shown that these spines are indeed used by the pupa to partially protrude from the cocoon. In Sphinginae, the characteristic antespiracular furrows of the abdominal segments may also help the pupa in wriggling to the surface before eclosion. Apatelodinae pupate either in the soil or in cocoons (STEHR 1987); in soil-pupating forms the pupa is very compact and smooth and has a ring of peculiar, crenellate fortifications around the anterior margin of the abdominal segments (see also MOSHER 1916), but no metathoracic calli. Eupterotidae pupate mostly in loose, hairy cocoons on the soil or just below the surface, but also without cocoons on or in the ground; the pupae vary from very thin-shelled when in tough cocoons to hard-shelled when pupating in the soil and have cremasters and metathoracic calli of various developments, the latter sometimes very similar to those of Brahmaeidae (MELL 1930). *Lemonia* (Lemoniidae) also pupates in the ground without a cocoon and has a shiny pupa with a strong cremaster and metathoracic calli (the latter very similar to those of *Brahmaea*), while the wrinkled pupa of *Sabalia* rests on the ground under leaves and has a strong cremaster, possibly also metathoracic calli. *Carthaea* (Carthaeidae) has a hard, rugose pupa resting in a flimsy cocoon under debris on the soil surface but without special body projections other than a deeply pitted anterior margin of the abdominal segments and a strong cremaster (COMMON 1966, 1990); it is unknown whether this pupa protrudes from its cocoon before eclosion of the adult. *Endromis* OCHSENHEIMER, 1810 (Endromididae) pupates in a flimsy cocoon on the ground, from which the pupa protrudes by means of “cocoon-cutting” ridges on head and pronotum and dorsal abdominal spines (BROCK 1990), but it has no metathoracic calli.

In Bombycoidea therefore, metathoracic pupal calli, like other sclerotized pupal protuberances, are clearly adaptations of species pupating on or in the soil, with the function of assisting the pupa in protruding from the cocoon or in reaching the soil surface or some suitable place on it for the moth to eclose. BROCK (1990) has speculated whether this habit and associated structures represent the retention of an ancestral trait in Bombycoidea (a symplesiomorphy) or a secondary gain or "regain" acquired independently several times in this group (a convergence, or homoplasy); certainly neither the pupal protrusion *per se* nor the possession of any structure involved in this can be regarded as a synapomorphy defining any bombycoid group as a monophylum. Thus, the possession of pupal abdominal spines in *Brahmaea europaea* can hardly be regarded as an autapomorphy to define a genus (*Acanthobrahmaea* SAUTER, 1967) on in phylogenetic terms, it is either a retained bombycoid plesiomorphy or a functional adaptation evolved independently and parallel to that of the Ceratocampinae. Similarly, the simple presence of metathoracic calli in both *Spiramiopsis* and *Brahmaea* cannot be construed as a synapomorphy justifying the inclusion of *Spiramiopsis* in Brahmaeidae; this is only possible if their calli are shown to agree in some structural detail that is not present in the calli of other soil-pupating bombycoids.

It seems that such metathoracic pupal calli may be linked to the strong development of metathoracic processes in the groundplan of the bombycoid larva and may thus be part of the groundplan of the bombycoid pupa; possibly both were necessary to develop the soil-pupating habit in the first place, and the development of this latent feature in the pupa could then occur independently whenever the soil-pupating habit was evolved. Alternatively, the development of metathoracic and other callosities in the pupa may have taken place completely independently, i.e. without the feature being latent, or part of the bombycoid pupal groundplan. In either case, however, close relationships based on such pupal callosities can only be assumed if these protuberances agree in structural details, not merely in their presence; this may indeed be the case with *Lemonia* and Brahmaeidae but less likely with *Spiramiopsis*.

4. Hairiness and associated characters in bombycoid larvae

As mentioned under 2. above, the development of dorsal processes in bombycoid larvae, which is interpreted as a groundplan feature, appears to be secondarily suppressed in densely hairy (woolly) larvae, in which the secondary setae are very numerous (dense) and long. Such larvae occur in Eupterotidae, Apatelodinae, Lemoniidae and Saturniidae within the Bombycoidea s. str. (6), but also in Lasiocampidae and Anthelidae (i.e. the Lasiocampoidea). Besides their woolliness, the larvae of these groups also share certain other characters, which might either be more or less directly related to this condition (and thus independently evolved and of limited phylogenetic value), or perhaps indicative of a closer relationship than implied by the current classification of these groups.

The most characteristic feature of the naked bombycoid larva, the middorsal process of the eighth abdominal segment, is either not present or not developed in woolly bombycoid larvae. However, MINET (1994) still regards it as a synapomorphy for the Bombycoidea s. str., under the assumption that it is secondarily lost in all the groups with woolly larvae, as above. In the Saturniidae, which have both naked and woolly larvae, the Ludiini provide a credible scenario that the absence of this character in woolly larvae is indeed secondary and related to woolliness: a single, middorsal, fused but not enlarged scolus on A-8 is present in the less densely hairy larvae of *Holocerina, Micragone* and *Orthogonioptilum* KARSCH, 1893, a partially fused one in *Ludia*, and two separate, flat dorsal scoli in the more strongly woolly larvae of *Goodia* HOLLAND, 1893, *Vegetia* JORDAN, 1922 and *Decachorda* AURIVILLIUS, 1898 (the species so far investigated). If, then, the disappearance of this feature is secondary and linked to hairiness, one would also expect it to occur in the hairy Lasiocampidae and Anthelidae for the same reason (rather than being primarily absent in these families), in which case the presence of the fused A-8 process is not a synapomorphy for the Bombycoidea s. str. but probably only for the Lasiocampoidea + Bombycoidea. Indeed, several lasiocampid larvae (again the less hairy ones) also possess a middorsal, partially or completely fused A-8 protuberance, which may attain a considerable size in some species (e.g. *Rhinobombyx cuneata* AURIVILLIUS, 1879). MINET's (1994) assumption that a fused, middorsal A-8 process is primarily absent in the Lasiocampoidea rests largely on the larva of *Munychryia* WALKER, 1865 (Anthelidae), which is naked but still has widely separate D1 setae on A-8 (COMMON & MCFARLAND 1970). However, this larva is highly specialized to feed and conceal itself on thin, non-hairy

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(6) = The larva of *Xanthopan morganii* (WALKER, 1856) (Sphingidae) is also hairy, but only sparsely and shortly so and not really compareable to to the woolly larvae under discussion here.

Casuarina branchlets and is therefore most likely to have lost all its long setae secondarily (as noted by COMMON & MCFARLAND 1970) rather than representing a more primitive form that never possessed them primarily. It is therefore not convincing to assume separated D1 setae on A-8 as an anthelid groundplan condition from such an adapted larva alone; a fused A-8 process could just as easily be a groundplan condition in Anthelidae and Lasiocampidae as it is assumed to be in Eupterotidae, Apatelodinae and other bombycoid groups with woolly larvae. Much more difficult to expound, in fact, are the widely separated D1 setae on A-8 in the naked larva of *Salassa* (Saturniidae, Salassinae) (see NÄSSIG 1994), in which no reduction of a woolly condition is indicated and the assumption of a primary separation of these setae is therefore much more obvious than in *Munychryia*. By analogy to MINET's interpretation of this setal configuration in *Munychryia,* it would also be the groundplan condition of Saturniidae and thus of Bombycoidea, rather than that of the middorsally fused A-8 process. A similar problem is presented by *Cercophana vetusta* (WALKER) (Saturniidae: Cercophaninae), whose first-instar larva is only sparsely hairy and possesses separate D verrucae on both A-8 and A-9 (WOLFE & BALCÁZAR-LARA 1994): is this a secondary condition linked to the only very poorly developed hairyness of the larva, or does it represent the groundplan condition in Saturniidae? It is apparent that the exact distribution and phylogenetic significance of the character of the fused A-8 process in bombycoids is in need of further investigation before it can be regarded as a reliable synapomorphy.

The larvae of the Lasiocampoidea (Lasiocampidae and Anthelidae) have, according to MINET (1994), two further synapomorphies that may be related to hairiness in general, namely the presence of secondary setae on the mandibles of the mature larva, and the division of the SV sclerite of the ventral prolegs. Outside the Lasiocampoidea, i.e. in Bombycoidea s. str., hairy mandibles again occur only in groups that also have hairy larvae, namely in Apatelodinae and Eupterotidae, albeit not in *Lemonia* and hairy Saturniidae (Ludiini, some Saturniini). Similarly, a divided SV sclerite of the prolegs also occurs only in Apatelodinae and Eupterotidae other than in the Lasiocampoidea. It thus appears that either these two characters are related to hairiness in general and thus likely to develop in most hairy larvae, or that they represent a feature linking the Eupterotidae and Apatelodinae more closely to the Lasiocampoidea than MINET's (1991, 1994) system implies. The fact that some Apatelodinae (e.g. *Olceclostera* BUTLER, 1878) and some

Eupterotidae (e.g. *Trichophiala* AURIVILLIUS, 1879) in addition have free larval procoxae like Lasiocampoidea, thus not possessing the synapomorphy of fused ones of the Bombycoidea (MINET 1994), indeed suggests that a superfamily division between Lasiocampidae and Anthelidae on one side and Apatelodinae and Eupterotidae on the other may be too artificial and require the postulation of too many reversals. Truly independently evolved hairiness and the concomitant loss of the fused A-8 scolus apparently only occur in Saturniidae and in Lemoniidae; in Eupterotidae and Apatelodinae this condition and other, seemingly linked characters are presumably much older and probably related to those of the Lasiocampidae and Anthelidae. Again, further study is required before any of these features can be accepted as reliable synapomorphies; neither hairy mandibles nor divided SV sclerites nor fused/separate procoxae are constant in either Lasiocampidae or Eupterotidae.

Conclusions

Spiramiopsis does not fit into the family Brahmaeidae by any synapomorphic character of its immature stages. Firstly, only two such characters are vaguely similar, viz. the dorsal larval processes and the metathoracic pupal calli, and in both of these the similarity is only superficial but not based on any agreement in structural details. Secondly, *Spiramiopsis* is very different from Brahmaeidae in its first-instar larva and in its pupa, both of which appear considerably more primitive and share none of the more derived brahmaeid features (larval scoli, concealed pupal labial palpi and proboscis).

Although *Spiramiopsis* possesses some preimaginal features in common with other bombycoid families (simple larval chalazae with Bombycidae, pupal labial palpi with Lemoniidae, fully exposed pupal proboscis with Carthaeidae and Sphingidae), these common characters are all primitive (symplesiomorphic) and thus not indicative of any close relationship. Furthermore, they are not in common with any single bombycoid family but with several, thus presenting a mosaic of characters that are otherwise spread throughout the superfamily. *Spiramiopsis* displays a combination of preimaginal characters that is unique among the Bombycoidea.

By several of its preimaginal characters, *Spiramiopsis* is very primitive. Its first-instar larva has simple chalazae without any secondary setae, which are almost certainly more primitive than either the complex scoli of other naked bombycoid larvae or the densely setose verricules of woolly bombycoids and lasiocampoids. Its pupa has exposed labial palpi, in common only with *Lemonia* and with lasiocampoids and again a primitive feature that is not present in all the higher bombycoids. The pupa furthermore possesses a fully exposed proboscis, which is likewise considered a primitive condition and generally only present in *Carthaea* and (most) Sphingidae (also in the anthelid *Munychryia*). Its mode of pupation is also very generalistic, not nearly as specialized as in either soil- or cocoon-pupating forms, and although this same mode of pupation is likely to have occurred secondarily again in several of the latter forms, in *Spiramiopsis* it is most probably a primary condition. On the balance therefore, *Spiramiopsis* seems to combine more primitive preimaginal features than any other higher bombycoid taxon, suggesting, together with its isolated taxonomic position and geographical distribution, that it may be close to the ancestral bombycoid form.

The lack of any clear synapomorphic agreement in preimaginal characters of *Spiramiopsis* with any other bombycoid family suggests that *Spiramiopsis* should be placed in a family of its own. Such a treatment, however, is in contradiction to the eight synapomorphies of the adult that MINET (1994) identified as defining the family Brahmaeidae (including *Spiramiopsis*) as a monophylum. It therefore seems that these alleged synapomorphic agreements and their phylogenetic value need to be reassessed. On characters of the adult, there can be little doubt that *Spiramiopsis* belongs to the Lemoniidae + Brahmaeidae clade, but the imaginal characters of these two groups are also not yet fully studied. For example, the "tripectinate" antenna that SAUTER (1987) regarded as characteristic of *Brahmaea* also occurs very distinctly in *Sabalia* and in *Lemonia* (strongly developed in *L. balcanica* (HERRICH-SCHÄFFER, 1843), less so in *L. dumi* (LINNAEUS, 1761)), while in *Dactyloceras* and in *Spiramiopsis* there is ventrally between the antennal rami not quite such a long process as in the others but a setose small peg or low ridge quite comparable to this structure, probably a rudiment of it. The same "tripectinate" antenna also occurs in the South African *Xenosphingia jansei* JORDAN, 1920 (Sphingidae, if indeed this placement is correct) and, perhaps surprisingly, in the Australian Anthelidae and in phiditiine Bombycidae (see MINET 1994). Clearly this rather unique feature requires further investigation. Likewise, the absence of a proboscis, which MINET (1994) regards as an autapomorphy of the Lemoniidae, needs to be reassessed; a proboscis is also absent in *Spiramiopsis* (reduced to two small, curled lobes) and in *Dactyloceras widenmanni* but present in *D. lucina*! Nonetheless, Lemoniidae and Brahmaeidae are quite clearly closely related, as was indeed recognized long ago by KARSCH (1898, 1900) and HAMPSON (1901), the former even explicitly regarding *Lemonia dumi* as the "German representative of the Brahmaeidae" (KARSCH 1898). MINET (1994) supported this relationship rather strongly by six synapomorphies (the three preimaginal ones not reliable, see above). Perhaps, therefore, the concept of Brahmaeidae should be widened to include *Lemonia* and *Sabalia;* in that case *Spiramiopsis* would also belong to the same family. If, on the other hand, *Lemonia* and/or *Sabalia* are placed in their own families, the same could be argued for *Spiramiopsis,* especially on its preimaginal characters – its larva is just as different from that of Brahmaeidae as are those of the other two genera, and, among the larvae of these taxa, the greatest structural similarity probably exists between *Spiramiopsis* and *Sabalia*.

We thus conclude that the taxonomic position of *Spiramiopsis* is still not entirely clear and that it should be determined only from a careful study of all its relevant characters, both preimaginal and imaginal. Such a study would necessitate a similarly intensive investigation of *Brahmaea, Dactyloceras, Calliprogonos, Lemonia* and *Sabalia,* and probably also of *Xenosphingia* Jordan, 1920, in consideration of character states and evolutionary trends in the Bombycoidea as a whole.

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