

The life history of *Pseudantheraea discrepans* (BUTLER, 1878), with an ecological comparison with *P. imperator* ROUGEOT, 1962 (Lepidoptera: Saturniidae, Saturniinae, Urotini)

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Abstract: The biology of the small African saturniid genus *Pseudantheraea* WEYMER, 1892 is described and illustrated, presenting the first full account of its immature stages and life history. Based on a rearing of *P. discrepans* from Cameroon on *Salix* (Salicaceae) in Germany, this species has a slow larval development, fully gregarious larvae until prepupal dispersal and a green, spiny pupa suspended in a flimsy cocoon among low foliage. The egg of *P. imperator* is more than twice the size of that of its sister-species, and its neonate larva is also larger. The distribution, ecology and ethology of the two species are compared, showing that they have different ecological preferences and appear to be locally fully allopatric in Cameroon. The taxonomy and nomenclature of the two species is updated.

Die Biologie von *Pseudantheraea discrepans* (BUTLER, 1878) und ein ökologischer Vergleich mit *P. imperator* ROUGEOT, 1962 (Lepidoptera: Saturniidae, Saturniinae, Urotini)

Zusammenfassung: Das vorhandene Wissen über die kleine afrikanische Gattung *Pseudantheraea* WEYMER, 1892 wird zusammengetragen. Nach einem kurzen Überblick über die Erforschungsgeschichte werden die Präimaginalstadien von *P. discrepans* aus Kamerun beschrieben und farblich abgebildet, basierend auf einer Zucht in Deutschland. *P. discrepans* hat bis zum Präpuppenstadium, in dem die Raupen sich einzeln, eine ausgeprägt gesellige Lebensweise. Die Raupen entwickeln sich langsam, und die Puppe hängt mit dem Kremaster fixiert in einem sehr löchrigen Kokon im Unterwuchs. Sie ist grün, hat eine sehr dicke Kutikula mit Dornen darauf und hängt oft völlig frei im Laubwerk der Büsche. Einige Beobachtungen über die Eier und die L₁- Raupe von *P. imperator* werden beigelegt. Die Eier von *P. imperator* sind über zweimal so groß wie die ihrer Schwesterart. Aspekte der Verbreitung, Ökologie und Ethologie der beiden Arten werden dargestellt und, soweit möglich, verglichen. Obwohl beide Arten einander habituell sehr ähnlich sind, haben sie gut unterschiedene ökologische Präferenzen und scheinen in Westafrika völlig allopatrisch zu leben, zumindest nach den Studien des Erstautors in Kamerun. Die Männchen von *P. imperator* fliegen signifikant später in der Nacht als die von *P. discrepans*. Eine Aktualisierung des Katalogs mit kritischer Checkliste der beiden zur Zeit anerkannten Arten und ihrer Synonyme beschließt die Arbeit.

***Pseudantheraea discrepans* (BUTLER, 1878): Notes sur l'éco-éthologie, la zoogéographie, les premiers stades et l'élevage, et comparaison avec *P. imperator* ROUGEOT, 1962 (Lepidoptera: Saturniidae, Saturniinae, Urotini)**

Resumé: La biologie du petit genre de Saturniidae africain *Pseudantheraea* WEYMER, 1892 est décrite et illustrée par la première description des stades préimaginaux et du cycle biologique, sur la base d'un élevage de *P. discrepans*

effectué en Allemagne sur *Salix* (Salicaceae). Cette espèce a un développement larvaire lent, des chenilles complètement grégaires jusqu'au stade prépupal et une chrysalide verte, fortement épineuse, suspendue dans un cocon très lâche fixé dans le feuillage. Les oeufs de *P. imperator* ont au moins le double de la taille de celle de son espèce soeur, ainsi qu'une chenille néonate plus grosse. La distribution géographique, l'écologie et l'éthologie des deux espèces sont comparées, ce qui met en évidence des préférences écologiques différentes et une allopatrie totale au Cameroun. La taxonomie et la nomenclature des deux espèces sont mises à jour.

Introduction

Pseudantheraea discrepans (BUTLER, 1878), the type-species of the genus *Pseudantheraea* WEYMER, 1892, is a member of the somehow enigmatic tribe Urotini (formerly Pseudapheliini, see OBERPRIELER 1997) within the Saturniinae, of unclear affinities both to Bunaeini and to Saturniini. Within the Urotini, *Pseudantheraea* belongs to a possibly monophyletic group of genera comprising also *Maltagorea* BOUYER, 1993, *Tagoropsis* C. & R. FELDER, 1874 and *Sinobirma* BRYK, 1944 and perhaps *Pseudaphelia* KIRBY, 1892 and *Pselaphelia* AURIVILLIUS, 1904 (for definitions and supposed phylogeny, see NÄSSIG & OBERPRIELER 1994, OBERPRIELER 1997: 148–149). M. R. COOPER (2002) alleged the former four genera to be a “compact monophyletic group” and formalised a “tribe Tagoropsini” for them, moving *Pseudaphelia*, *Pselaphelia* and other genera into a “tribe Eudaemoniini” and leaving only *Urota* WESTWOOD, 1849 and *Usta* WALLENGREN, 1863 in Urotini, but as this concept is not based on any solid phylogenetic argumentation, we do not follow it here.

The Urotini in the wider sense (OBERPRIELER 1997) remain a poorly defined group, currently held together only by the character of the bipectinate male antenna. While this character is most likely an apomorphy (a reduction of the quadripectinate antenna that characterises Saturniidae in general, which can be seen in details of the antennal morphology; OBERPRIELER 1997), such a modification also occurs in other saturniids and can at present not be regarded as a synapomorphy for the Urotini. A full discussion of this issue and other potentially apomorphic characters for the tribe was provided by OBERPRIELER (1997: 148–149). The phylogenetic relationships of *Pseudantheraea* are equally unresolved. BOUYER (1993) regarded it as the sister taxon of *Maltagorea*, but the recognition of *Sinobirma* as a member of Urotini (Näs-

¹ 65th contribution to the knowledge of the Saturniidae.

SIG & OBERPRIELER 1994) and the consideration of a larger set of characters (including those of the immature stages, OBERPRIELER 1997) suggest other possibilities. Details of its life history as described here also indicate a possible close relationship with *Tagoropsis*.

The preimaginal stages of *Pseudantheraea* have never been fully described and illustrated. PREUSS (1890) – cited with incorrect date and journal title by BOUVIER (1927, 1936) and ROUGEOT (1949) – published a few anecdotal observations on unidentified “brown larvae with black spines” turning into “green spiny pupae” (probably correctly interpreted as *P. discrepans* by BOUVIER 1928, 1936), and ROUGEOT (1949) briefly described the preimaginal stages and later (1962) provided a poor-quality black-and-white photograph of the mature larva. SEYDEL (1939: fig. 16) furnished a nondescript photograph of the eggs. The peculiar arboreal pupa was mentioned and depicted a number of times earlier (e.g., HOLLAND 1892: pl. 5, AURIVILLIUS 1905, GARDINER 1982: pl. xx) but never described in detail.

We here describe and illustrate the larva and pupa of *P. discrepans* in greater detail for the first time, based on a rearing by the second author in Germany from eggs laid by a ♀ collected in Cameroon by the first author. The ecology and imaginal behaviour of *P. discrepans* as based on field observations in Cameroon are also discussed and contrasted with those of the rarer *P. imperator* ROUGEOT, 1962.

Rearing report

1. *Pseudantheraea discrepans*

(by Rudolf E. J. LAMPE & Wolfgang A. NÄSSIG)

Eggs laid between 16. and 18. June 1993 by a ♀ collected at Nkoevone, Cameroon, on 15. June 1993 and airmailed to Germany hatched there starting on 16. July, i.e., one month after oviposition. This incubation time is comparatively long for non-diapausing saturniid eggs and may have been caused by either the airmail transport or the dry rearing conditions in Germany. However, a similarly long incubation time occurs in the bunaeine *Cirina forda* (WESTWOOD, 1849) in southern Africa (OBERPRIELER 1995), and COOPER & COOPER (2002) report nearly as long an incubation time (20–23 days) also for *Tagoropsis flavinata* (WALKER, 1865) in South Africa.

The first larval instar commenced on 16. July 1993, the second (i.e., the first moult) on 28. July, the third on 6. August, the fourth on 15. August, the fifth on 23. August, the sixth on 31. August and the seventh on 10. September. The first larvae initiated prepupal behaviour (liquid defaecation) on 22. September, rested for two days and then started spinning a flimsy cocoon. The first pupa appeared on 2. October 1993, concluding about 10 weeks of larval development.

This is a fairly long larval development within Saturniinae, although African species tend to show such comparatively slow development at least under laboratory

conditions. However, it does not reach the duration of, e.g., *Saturnia pinratanai* LAMPE, 1989 (compare LAMPE & NÄSSIG 1994), which took about 17 weeks in captivity to complete its larval development of also 7 instars.

The *P. discrepans* larvae were reared inhouse in open containers on cut twigs of the foodplant in water, at summer temperatures of about 23–25 °C. The only substitute foodplants accepted were *Salix caprea* and other willows (Salicaceae).

Larval mortality was high in first instar, more than half the caterpillars (7 of 13) not reaching the first moult. The cause for this high mortality is not clear; it may have been the dehydrating conditions. Possibly the small number of larvae may also have been a factor; KLOK & CHOWN (1999) showed that gregarious young larvae of a saturniid moth have better survival chances in larger aggregations. The *P. discrepans* larvae were gregarious in all instars and fed synchronously, so that a lack of intensive, steady tactile contact due to their small numbers may have exerted further stress on them. The larvae were not sprayed with water because of the fear of promoting bacterial infections. In total, 6 pupae were obtained, 5 of them ♀♀.

Larval behaviour was characterized by an intensively gregarious habit in all instars. Feeding and resting were nearly always carried out synchronously and in tactile contact. Another unexpected observation was that the larvae always left their feeding site in the late afternoon (around 17 h Central European Summer Time) for approximately one hour and congregated at the neck of the bottle in which the branches were kept.

Tagoropsis flavinata displays exactly the same behaviour: highly gregarious in all instars, moving to new feeding sites in procession and together retreating to the base of the stem in the late afternoon, from where they may emerge again at night to feed (OBERPRIELER, pers. comm.). COOPER & COOPER (2002) record the larvae as feeding mainly at night, but in OBERPRIELER's rearings they also did so during the day (their aposematic coloration would be ineffective at night).

A number of explanations can be offered for this behaviour:

- Regular wandering to a separate resting place on the tree trunk.
- Regular changing of the feeding site (i.e., crawling to other twigs of the foodplant) to avoid becoming a permanent, localized food resource for small (vertebrate) predators; gregarious caterpillars often have a “all or none” chance for survival. (This is unlikely at least for *T. flavinata*, as the larvae are highly aposematic and feed quite openly in the bushes; OBERPRIELER, pers. comm.)
- Regular changing of the feeding site to avoid a chemical reaction of the foodplant due to permanent feeding on one twig. (This is the most plausible explanation for this behaviour in *T. flavinata*, whose food-

plant [*Allophylus*, Sapindaceae] contains cyanolipids [characteristic of Sapindaceae] and strongly liberates hydrogen cyanide [HCN] from crushed leaves. Especially the voraciously feeding larger larvae may be periodically deterred from feeding by high concentrations of HCN released from the leaves they damage. It is likely that also the aposematic coloration and the gregarious behaviour of *Tagoropsis* larvae are adaptations related to the chemistry of their hosts. A similar situation may occur in *P. discrepans* on its natural hosts, *Uapaca* [Euphorbiaceae] and *Poga* [Rhizophoraceae] [ROUGEOT 1962, PINHEY 1972]; OBERPRIELER, pers. comm.)

- Avoiding a specific predator or parasitoid hunting for larvae at that time.

Prepupal behaviour: The larvae stopped feeding and expelled liquid faeces. About two days later they turned dark and began spinning a few silken strands to form a flimsy cocoon, a process that took about two further days. The prepupa anchored itself to this cocoon by its cremaster and remained motionless for some days before eventually pupating, and extending the time from liquid faecation to actual pupation to about 10 days. The exuvia of the last larval skin was not pushed together towards the back but remained at nearly its normal length (as occurs also in some Bunaeini pupating in the soil) and usually fell out of the open-meshed cocoon (Fig. 11). (In comparison, the *T. flavinata* pupa pushes the larval skin right back; it pupates shallowly in the soil but does not form a proper pupal chamber; OBERPRIELER, pers. comm.)

Cocoons were usually spun in horizontal orientation, so that the pupa initially lay horizontal as well, but its front part would easily slip free from the cocoon, and the silken strands generally became loose from some of the supporting leaves so that the pupa then hung down freely with only its cremaster firmly anchored in the silken strands of the base of the cocoon (see also SCHULTZE 1914: 151).

Description of the immature stages

Eggs (Fig. 1): Comparatively small for a saturniid of that body size (ca. 1.5 mm in length and 1 mm in diameter), ovoid, slightly flattened, pure greenish white. As usual for a gregarious species, the eggs are laid in clusters. Due to collecting circumstances, the ova were deposited as irregular clusters within a plastic bag.

L₁ (Fig. 2): Relatively small, ca. 5–6 mm long before feeding. Head reddish, prothoracic shield dark brown, body blackish but paler after feeding; some variability. Scoli small, unobvious, like body colour, hairs white.

L₂ (Fig. 3): Similar to L₁.

L₃ (Fig. 4): Head and prothoracic shield reddish brown, body colour blackish. Hairs differentiated into stiff, black bristles (especially on thoracic segments [T1–3] and 1st abdominal segment [A1]) and soft, white hairs. Scoli

paler brownish, slightly elongate but in shape still similar to the usual “asterisk-like warts” (“Sternwarzen”) type of most Saturniinae (NÄSSIG 1989).

L₄ (Fig. 5): Head reddish, body ground colour nearly black. Scoli on T1–3 and A1 blackish, elsewhere paler brown; more elongate but still more or less of the “asterisk-like wart” (“Sternwarzen”) type.

L₅ (Fig. 6): Body colour changed to brown, spiracles black. Scoli further elongated; apical (primary) seta stouter, harder and stiffer.

L₆ (Fig. 7): Body colour reddish brown. Dorsal scoli of T2–3 and A1 black (thereby conspicuous), the others concolorous with body. Spiracles black. Scoli much more elongate, approaching the spine-like type (“Stechdornscolus”, NÄSSIG 1989). DEML & DETTNER (2002) use the term “thorn scolus”, or formally “*scolus pungentispinosus*”. Soft hairs in white, bristles in colour of scoli.

It is noteworthy that at least the dorsal scoli of the larvae start as a more or less average saturniine scolus in L₁, then become longer and develop into a scolus type which is somewhat transitional between the normal scoli (“asterisk-like warts” or “Sternwarzen”-like) of many Saturniini and the typical spines of most Bunaeini (compare NÄSSIG 1989, OBERPRIELER & NÄSSIG 1994). In L₅, the bristle at the tip of the scolus becomes a prolongation of the scolus and is very stiff and pointed. Only the presence of several additional, much softer, long hairs on the lateral scoli and shorter hairs/bristles on the dorsal scoli differentiates the scoli of the L₆ of *Pseudantheraea* from the typical spines of many Bunaeini (compare tables 5 & 6 in OBERPRIELER & NÄSSIG 1994). Dorsally, the last instar (L₇) of *Ps. discrepans* has nearly true spine-like scoli of the Bunaeini type, because the additional hairs on the scoli become further reduced in the last moult (see Figs.).

L₇ (Fig. 8): Colouration as before. Dorsal scoli now functionally full spines. Anal plate extremely broad, rounded and strongly sclerotized, with a thick outer rim. Dorsal and subdorsal prothoracic scoli reduced and integrated into the strong prothoracic shield, with soft white hairs. Spiracles round, black.

In all instars the dorsal abdominal scoli on all abdominal segments remain separate on the mid-dorsal line.

Prepupa (Figs. 9/10): Before the final liquid defaecation, the larvae reached about 120 mm in length but were comparatively slim, only about 15 mm in diameter (without scoli). The cocoon was very flimsy, only consisting of a few, but very strong, silken strands holding together a few leaves, and a relatively large mat at the base, where the barbed bristles of the pupal cremaster hook in. The larval exuvia remained at full length and usually fell down to the ground (Fig. 11).

Pupa (Figs. 12/13): Ground colour green, with black pattern, spines and cremaster. Strong spines dorsally on the prothorax, at the wing base, next to the mouthparts (possibly the mandibles?), on a rim encircling the abdominal



Colour Plates 1 & 2: *Pseudantheraea discrepans*. Cameroon. Fig. 1: ova. Fig. 1: L₁. Fig. 3: L₂. Fig. 4: L₃. Fig. 5: L₄. Fig. 6: L₅. Fig. 7: L₆. Fig. 8: L₇. Figs. 9, 10: Praepupa spinning flimsy cocoon and shortly before pupation moult in cocoon. Fig. 11: Fresh pupa with larval skin. Fig. 12: Pupa in very flimsy cocoon. Caused by wind and movements of the food plant, the pupa may easily fall out of these few silken strands and then will hang freely in the plant, head down, held by the cremaster hooks in a silk bolster. Fig. 13: Pupa out of cocoon; see silk in cremastral hooks. Figs. 14, 15: Imagines, Fig. 14 ♂, Fig. 15 ♀. — Photographs: R.E.J.L.



segments not covered by the wing sheaths, and on the large cremaster. Cremaster with a strong, nearly round structure at the apex carrying many barbed hooks to attach the pupa in the silk. Cuticle very hard and thick. Abdominal segments actively flexible.

The pupae turned darker before the imagines hatched.

Eclosion of the imagines

The pupae were kept freely in a room at about 20–24 °C and 50–60 % relative humidity, and consequently sprayed with water daily. In late January 1994, one of the pupae turned olive-brownish, and after about 5 days a crippled ♀ hatched. To avoid further losses, the pupae were then kept in a big plastic box with an airtight cover, sprayed daily and placed beneath a heater; thus ensuring high humidity (ca. 90–100 %) and temperatures of around 28 °C during the day and 21 °C at night to simulate the hot rainy season of West Africa. This is in agreement with SCHULTZE's (1914: 151) observations and was obviously the correct treatment as four healthy ♀♀ hatched between 17. II. and 11. III. 1994 (3 around 21.30 h, 1 at 19.30 h Central European Time, in most cases shortly after the regular evening spraying) and fully expanded their wings. The ♀♀ stayed calm during their first night, waiting for ♂♂, and were preserved the next morning. Eventually a single ♂ hatched on 31. III., after 22.00 h. The ♂ pupa's development was comparatively slow; first, slight colour changes were observed on 21. III. and the final darkening with an extension of the pupal abdomen took place three days before hatching. It is possible that this delay was influenced by a full moon four days before the hatching date.

2. *Pseudantheraea imperator*

(by Thierry BOUYER)

Preimaginal information

Eggs: 21 eggs were deposited in a row between 23. and 25. December 1992 by a ♀ taken at light in a littoral rain forest in Cameroon and kept in a plastic bag. They were round (ca. 2.8 mm in length and 2.7 mm in diameter), white in colour but covered with a brownish secretion. The larvae hatched on 18./19. January 1993, giving an incubation time of 26–27 days under nearly natural environmental conditions. This is again a long period in comparison with other African rainforest Saturniidae but quite similar to those of *P. discrepans*. No foodplant offered was accepted by these larvae in Cameroon.

L₁: Ground colour bordeaux (= dark red), head orange. Otherwise similar to *P. discrepans*, but larger.

Distribution, biology and behaviour

(by Thierry BOUYER)

Pseudantheraea is a forest-inhabiting genus in West and Central Africa comprising two species, *P. discrepans* and *P. imperator*. *P. discrepans* has a large distribution range,

from the Ivory Coast to Uganda in the north and from Angola to the Democratic Republic of Congo (= Zaïre) in the south, covering the whole West and Central African forest block. The range of *P. imperator* is more restricted, stretching from southern Nigeria to Uganda and from Angola to northwestern Zambia and covering only the centre of the African forest zone. On a regional scale, the distribution area of *P. discrepans* totally overlaps the range of *P. imperator*, but on a local scale the two species appear to be allopatric, no cases of them having been collected syntopically being known to the authors. The data used here stem from 125 collecting nights over two years in Central, South and West Cameroon at 10 localities. Neither in a single collecting night nor at a single site were both species collected together. All localities where *P. discrepans* was found (5 for 92 ♂♂ and 24 ♀♀) can be characterized as moist, dense semi-deciduous forest ("domaine de la forêt dense humide semi-décidue") or high-altitude forest, while the localities of *P. imperator* (4 for 25 ♂♂ and 2 ♀♀) are all situated in moist, dense evergreen coastal lowland forest ("forêt dense humide sempervirente littorale de basse altitude"; floristical categories after LETOUZEY 1968). It thus appears that these two species inhabit biotopes and habitats sufficiently different to be considered totally paratopic.

A more detailed study on a continental scale would be required to assess whether there is any overlap of ecological niches and geographical ranges of these two species. In Cameroon, their correlation with different forest types is well marked, but this might be different on a continental scale. Different forest types can be mixed locally, and limits between different forest categories are not always clear. Further collecting records may perhaps also change this picture, but the data available (from the author's own collecting as well as from material examined in collections) are sufficient to indicate a tendency. Hostplant data can probably also be useful in this regard. For example, populations of *P. imperator* in Angola and Zambia do not inhabit the same forest type as those in Cameroon, because the "forêt dense humide sempervirente littorale de basse altitude" is limited to the Guinea Gulf.

The larvae of *P. discrepans* are gregarious and also polyphagous (ROUGEOT 1962). Like with other gregarious species, many adults can be collected in one night at light. The great number of relatively small ova deposited in a single cluster is another typical sign of gregarious larval lifestyle. When fully grown, the larvae descend from their host trees and spin their cocoons in the understorey vegetation at approximately human eye level or higher. Several dozen pupae can often be found within a small area. The larvae are sometimes eaten by local people in tropical Africa, just like those of many other African Saturniidae (MALAISSE & LOGNAY 2003).

Much less is known about the biology and ecology of *P. imperator*. Specimens are much rarer at light and never numerous in one night. The following observations may

provide some clues about the life habits of this species:

- The eggs are significantly larger than those of *P. discrepans*, perhaps indicating a lesser degree of larval gregariousness.
- The abundance of imagines arriving at light is more similar to that of species with solitary larvae.
- The pupa has never been found so far, which may indicate a significant difference in pupation behaviour, such as pupation occurring at a different height, perhaps in the canopy or on the ground, under leaf litter, etc.

The sum of these differences indicates that the two species, in spite of their close resemblance in external habitus, are very distinct in their biology and behaviour and probably adapted to rather different ecological niches.

During two years of research in Cameroon, the arrival times at light of *Pseudantheraea* were recorded on the specimen labels as a number in parentheses after the collecting date. Each such number represents the full hour following it, with numbers 6 to 12 referring to 18:00 h and 0:00 h and numbers 1 to 5 to 1:00 h and 5:00 h. As the light was usually switched on around 18:30 h, this first period was only about half an hour long (BOUYER 1994).

From these data it is evident that ♂♂ of *P. discrepans* ($n_{\text{♂♂}} = 92$) arrived throughout the night but with a clear peak in the hour after 22:00 h and at a lower level until before 2:00 h (Fig. 16). At any one site in any one night, ♂♂ of *P. discrepans* usually arrived in quite a narrow time window; the combined arrival time curve (Fig. 16) is “flattened” due to the different conditions of various nights and sites. Collecting data for the ♀♀ are much fewer ($n_{\text{♀♀}} = 24$) but show that arrival is also spread throughout the night, but with a weak peak after 19:00 h. The difference in arrival times between ♂♂ and ♀♀ of *P. discrepans* was analysed by means of the non-parametric KOLMOGOROV-SMIRNOV test and proved statistically significant ($D = 0.4221$, $p < 0.005$).

The total number of *P. imperator* collected is much smaller ($n_{\text{♂♂}} = 19$, $n_{\text{♀♀}} = 2$; Fig. 17) and the resulting curve therefore less informative; however, the difference in arrival times between ♂♂ of *P. discrepans* and ♂♂ of *P. imperator* (the latter arriving much later, after midnight) was also highly significant ($D = 0.4937$, $p < 0.001$). The 2 ♀♀ of *P. imperator* arrived early, but this number is too small for reliable statistical analysis.

Generally, the arrival at light of saturniid ♀♀ in humid forest biotopes starts at dusk and rarely continues after midnight; *P. discrepans* is one of the few species in which

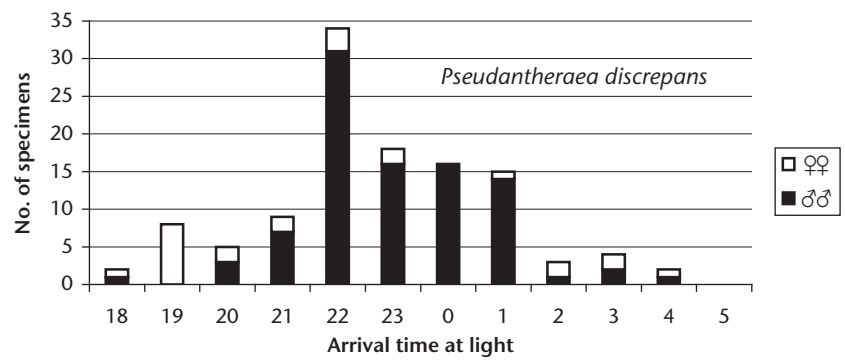


Fig. 16: Arrival times at light of *Pseudantheraea discrepans* (♂♂ and ♀♀) at different localities in Cameroon; data collected by the first author, $n = 92$ ♂♂, 24 ♀♀.

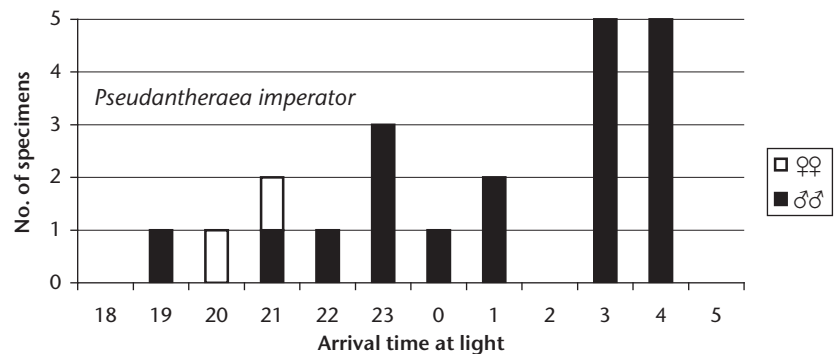


Fig. 17: Arrival times at light of *Pseudantheraea imperator* (♂♂ and ♀♀) at different localities in Cameroon; data collected by the first author, $n = 19$ ♂♂, 2 ♀♀.

♀♀ are regularly also found after midnight (33 % of the ♀♀). As ♀♀ are usually more sedentary and prefer to remain in the area where the larval foodplants grow, they generally arrive at light much less frequently, while the ♂♂ are more active, because they have to search for the ♀♀. Numbers of ♂♂ at light, therefore, on average reflect the actual flight activity more closely than those of ♀♀ (but see also the discussion of flight periods in African Saturniidae by OBERPRIELER 1995: 9).

This analysis of arrival times at light in *Pseudantheraea* illustrates the value of recording these times in detail (at least in one-hour intervals), especially for sister-taxa. Similar results were obtained with two other saturniid genera, *Orthogonioptilum* KARSCH, 1893 (BOUYER 1994) and *Aurivillius* PACKARD, 1902 (BOUYER 1999a), and also with Sphingidae (BOUYER, in preparation).

However, the recording of arrival times at light has certain limitations:

- ♀♀ tend to be more localized close to the larval foodplants and are weaker fliers than the ♂♂. This affects their abundance at lights, in that only the few individuals in the immediate surroundings of the light are attracted to it. When moving the light to a different place later at night, often a new peak of ♀♀ attracted is noticed.
- Specimens (especially ♂♂) arriving late at light do not necessarily reflect a late activity period. They can be specimens that arrived earlier but settled down unnoticed in the vicinity of the light and only later, perhaps

on being disturbed by other insects or larger animals, approach the light.

- Some specimens arriving late are badly worn and damaged, which probably reflects a behavioural distortion caused by high individual age rather than a natural activity pattern. This factor can sometimes be important, e.g. the case of a ♀ of *Aurivillius jolyanorum* BOUYER, 1999 (BOUYER 1999a). In statistic analyses, such extreme records should be excluded.

Ideally, the effect on activity patterns of external factors such as cloud coverage, moon and star light intensity, temperature, humidity, elevation, local ecological factors, etc., should be measured and corrected for in such activity analyses.

Discussion

(by Wolfgang A. NÄSSIG & Thierry BOUYER)

Pupation in African Saturniidae takes place either in a cocoon in the vegetation or on tree trunks, under stones, etc. (tribes Saturniini, Micragonini) or in the litter or soil in pupal cells (tribe Bunaeni) (see, e.g., NÄSSIG & OBERPRIELER 1994). Those Urotini of which the pupation behaviour is known also prefer pupation close to or in the soil, except for *Pseudantheraea discrepans*: *Pselaphelia* and *Pseudaphelia* pupate free under leaf litter on the ground, *Tagoropsis* and *Urota* shallowly in the soil but not in proper cells, and *Usta* a little deeper in the soil in small cavities (OBERPRIELER 1995, 1997, COOPER & COOPER 2002). *Eochroa* – a primitive member of Bunaeni, placed in its own tribe by COOPER (2002) – also spins a flimsy cocoon among vegetation at the base of its foodplant (OBERPRIELER 1995, 1997).

The pupation mode of *P. discrepans*, of a freely suspended green pupa in an flimsy arboreal cocoon in low vegetation, is unique in the family (as far as known). However, unusual types of pupation also occur on other continents (i.e., in unrelated groups of Saturniidae), usually in isolated species. In the Neotropical region, *Neorcarnegia basirei* (SCHAUS, 1892), a monotypic and rather aberrant genus of the subfamily Ceratocampinae, spins a one-sided, “tent-like” cocoon against a hard substrate such as a rock close to the ground, but the pupa is quite similar to those of other Ceratocampinae pupating in the soil (DRECHSEL & LAMPE 1996). In Australia, *Opodiphthera excavus* LANE, 1995, of the Saturniini, is unique in its genus in spinning a sand-covered, relatively weak cocoon in the upper layer of the soil (4–5 cm deep) under litter, while all other *Opodiphthera* (SENSU LATO) species for which the pupation mode is known pupate in hard silken cocoons between leaves, on tree barks, etc. (LANE 1995). And a flimsy cocoon in the vegetation close to the soil is spun by *Eochroa* (OBERPRIELER 1995).

Pupation in the soil may be an adaptation to dry climates or to frequent bushfires, as it occurs mainly in species inhabiting dry bush or savanna-type environments. In general, cocoon spinning in Saturniidae most probably

represents a plesiomorphic trait in the family, and flimsy cocoons, especially on or near the ground, as in these four species, may signify intermediate steps of multiple, independent evolutionary shifts from cocoon to pupation in the soil.

Review of the nomenclature of *Pseudantheraea*

(by Wolfgang A. NÄSSIG & Thierry BOUYER)

Although only two species are generally accepted within the genus today, several additional taxa have been described, and there is considerable confusion in older as well as current literature (e.g., MALAISSE & LOGNAY 2003 still regard *discrepans* and *arnobia* as distinct species). We here present a short updated review of the nomenclature of the genus (see FLETCHER & NYE 1982, BOUYER 1999b: 43, pl. 4, top).

Abbreviation:

‡ = Name not available (either infrasubspecific or based on misinterpretation, misspelling or other error).

Pseudantheraea WEYMER, 1892

Stettiner Entomologische Zeitung 53: 109

Type-species: *Pseudantheraea daphne* WEYMER, 1892, Stettiner Entomologische Zeitung 53: 110, by monotypy. [Ghana]: Goldküste, Addah. – The name *daphne* is a junior subjective synonym of *Copaxa discrepans* BUTLER, 1878, Annals and Magazine of Natural History (5) 2: 461.

= *Cremastochrysalis* KARSCH, 1893 [“1892”], Berliner Entomologische Zeitschrift 37: 499. – *Cremastochrysalis* is a junior synonym of *Pseudantheraea* WEYMER, 1892.

Type-species: *Saturnia arnobia* WESTWOOD, 1881, Proceedings of the Zoological Society of London 1881: 142, pl. 12 (Annulosa), fig. 2, by original designation. [Nigeria], Calabar. – The name *arnobia* is a junior subjective synonym of *Copaxa discrepans* BUTLER, 1878 (already proposed by KARSCH 1893: 500).

=‡ *Pseudoantheraea* [sic]: SONTHONNAX (1901: 51) and possibly other [earlier?] publication[s] by the same author (see note below under *P. arenosa*). – Incorrect subsequent spelling of *Pseudantheraea* WEYMER, 1892.

=‡ *Crematochrysalis* [sic]: PAGENSTECHE (1909: 433). – Incorrect subsequent spelling of *Cremastochrysalis* KARSCH, 1893.

(We list only a few, common incorrect subsequent spellings but have not specifically scanned the literature for other spelling errors, which neither have any nomenclatural validity nor any scientific value.)

The genus currently includes two valid species:

1. *Pseudantheraea discrepans* (BUTLER, 1878)

Copaxa discrepans BUTLER, 1878, Annals and Magazine of Natural History (5) 2: 461. – Type material in BMNH, London (potential syntype seen [T.B.]). – Type locality: [Nigeria], Old Calabar.

= *Saturnia arnobia* WESTWOOD, 1881, Proceedings of the Zoological Society of London 1881: 142, pl. 12 (Annulosa), fig. 2. – Type(s) not examined (possibly in Oxford? Not located). – Type locality: [Nigeria], Calabar.

Note: This taxon is erroneously listed as “*arnobia* WESTWOOD, 1849 [sic!], Proc. zool. Soc. Lond.: 142 [sic!]” by GAEDE (1927: 345) and PINHEY (1972: 52). Although most Lepidoptera publications by J. O. WESTWOOD (* 1805, † 1893; see HORN *et al.* 1990) were printed in the 1840ies

and 1850ies (which probably caused this mistake), there is at least this one late saturniid work by him published in 1881. [SCHÜSSLER (1933: 230), for example, provided a correct date and citation.]

- = *Pseudantheraea daphne* WEYMER, 1892, Stettiner Entomologische Zeitung 53: 110. – 2 syntypes (♂ and ♀) in ZMHU, Berlin (located by S. NAUMANN [pers. comm.]; ♂ seen [T.B.]). – Type locality: [Ghana]: Goldküste, Addah.

=‡ *Antheraea arenosa* “MAASSEN IN LITT.”: SONTTHONNAX (1901: 51) and possibly other [earlier?] publication[s] by the same author, see note. This name (evidently an unpublished IN LITTERIS name of MAASSEN) was not made available by SONTTHONNAX, because he listed it in synonymy with *Pseudoantheraea* [sic!] *arnobia* (WESTWOOD, 1881) (ICZN 1999: Art. 11.6). – Locality: “Gabon, Cameroun”.

Note: SONTTHONNAX (1901, in the “Essai de classification ...”), is probably not the earliest publication of this article with more or less identical contents. This series of publications was made available to a larger readership only within the collection “Essai de classification ...” (and a facsimile reprint edition of this series in the 1970ies). However, these “Essais” are only extracts of earlier prints of the same papers (in most cases identically word-by-word) in other series published by the “Laboratoire d’Études de la Soie” in Lyon, France. Unfortunately these earlier series are not available in most (including French) libraries, and therefore we were not able to clarify the question of the valid earliest publication date of this name here. – These dating and priority questions are to be solved in a forthcoming publication by BROSCHE, NAUMANN & CLARY (in preparation) specifically dealing with the obscure publication series of the “Laboratoire d’Études de la Soie” in Lyon (BROSCHE, NAUMANN, pers. comm.).

- = *Bunaea arenosa* PACKARD, 1914 (as “*Bunaea arenosa* STAUDINGER”), Monograph of the bombycine moths of North America [edited by COCKERELL], Part III: 43). – No type material existing (no specimen referred to in the description, see below). – Type locality: “Cameroons”.

Notes: The use of this name by PACKARD (1914: 43) was multiply incorrect and confused (see below), but he in fact was the first author to validate the name *arenosa* in the sense of the Code, because he published the name together with a description (however, as no specimens were cited, no types are in existence!). – U. BROSCHE (IN LITT.) refers to Articles 11.6.1 and 50.7 of ICZN (1999) and argues that PACKARD validated a name formerly listed in synonymy, in which case the authorship of the taxon is that of the first publication in synonymy (i.e., *Bunaea arenosa* ([SONTHONNAX, 1901]); but see note above). However, Art. 11.6.1 explicitly states that: “if ... a name published as a junior synonym had been treated before 1961 as an available name **and either adopted as the name of a taxon or treated as a senior homonym**, it is made available thereby ...” [bold print ours]. The name “*Antheraea arenosa* MAASSEN IN LITT.”, listed by SONTTHONNAX in synonymy, was treated as an available name but neither adopted as the name of a taxon nor as a senior homonym by him or any subsequent author. Further, PACKARD’s description of “*Bunaea arenosa* STAUDINGER” (not MAASSEN!) does not refer to either MAASSEN or SONTTHONNAX and was clearly not intended as a validation of MAASSEN’s or SONTTHONNAX’ taxon. In our opinion (and in reconfirmation of the established interpretation, see, e.g., SCHÜSSLER 1933: 231, 1934: 685), an interpretation following Art. 11.6.1 and 50.7 of the Code does not apply here. The facts that PACKARD attributed the authorship to STAUDINGER (not MAASSEN), regarded the species as “not

a *Bunaea*” and listed *Cremastochrysallis arnobia* (with “ab. *discrepans*” [sic!]) as a separate species in a different genus ten pages later indicate that he was unaware of SONTTHONNAX’ earlier publication of the name *arenosa*. – On the monochrome plate CXIII, PACKARD (1914) then illustrated a ♂ of “*Cremastochrysallis arenosa*” [sic!], further compounding the confusion pertaining to the two treatments in the text. There is no reference to this plate in the text of either taxon, and it appears that PACKARD obtained and added it later but was prevented from adapting the text by his sudden death. COCKERELL (the posthumous editor of PACKARD’s unfinished monograph) added the statement: “*C. arenosa* MAASSEN IN LITT.”, was published by SONTTHONNAX as a synonym of *C. arnobia* (WESTWOOD). Mr. J. H. WATSON considers it as a distinct species” in the legend of this plate. – Some later authors, such as GAEDE (1927: 334) and PINHEY (1972: 52), referred the authorship of *arenosa* to “MAASS[EN]” [without date], but this is evidently only an IN LITTERIS reference and not a valid authorship. – Fortunately, irrespective of its correct authorship *arenosa* is a junior subjective synonym of *discrepans* and does not threaten the validity and nomenclature of the species.

- =‡ “*Antheraea sciron*” SENSU SEITZ (1928, Großschmetterlinge der Erde vol. 10: plate 56A a, centre top [and the descriptive part in the text on p. 513, which is evidently based on this illustration]), NEC WESTWOOD, 1881. – Misidentification of the specimen illustrated; the text (except the description) correctly deals with WESTWOOD’s Papuan taxon *sciron* (an *Opodiphthera* [SENSU LATO] species, tribe Saturniini, compare NÄSSIG & LEMAIRE 2002: 98). (The illustration also depicts a ♀, not a ♂ as stated in the legend; this mistake was corrected by SEITZ 1933: 909 in the final corrigenda of vol. 10.) The identification error is seemingly based on an interchanging of the numbers 2 and 3 in the legend of WESTWOOD’s plate (1881: pl. XII) by either the artist of SEITZ’s (1928) plates or by SEITZ himself; WESTWOOD’s (1881) text, illustration, and legend are, however, correct. NIEPELT (1934: 114) already noted this mistake, referring to the specimen illustrated by SEITZ (1928) as “*Antheraea arnobia* WESTW[OOD]”, and this confusion of an Australian-Papuan and an African species is thus fortunately confined to SEITZ (1928).

‡*Pseudantheraea discrepans* f. *pulverulenta* DUFRANE, 1953 (infrasubspecific, individual aberration). – Locality: Kamituga, Kivu (Belgian Congo = Zaïre, = Democratic Republic of Congo).

‡*Pseudantheraea discrepans* f. *extrema* DUFRANE, 1953 (infrasubspecific, individual aberration). – Locality: Kamituga, Kivu (Belgian Congo = Zaïre, = Democratic Republic of Congo).

2. *Pseudantheraea imperator* ROUGEOT, 1962

Pseudantheraea imperator ROUGEOT, 1962: Les Lépidoptères de l’Afrique noire occidentale, Fasc. 4, Attacidés (= Saturniidés). – Institut Français d’Afrique noire: Initiations Africaines, Dakar, xiv: 75. – Holotype ♂ (by original designation) in Musée national d’Histoire naturelle, Paris (examined [T.B.]). – Type locality: Gabon, [Mouila].

Acknowledgements

Thanks are due to Ulrich BROSCHE, Hille, Germany, Stefan NAUMANN, Berlin, Germany, and especially Rolf G. OBERPRIELER, Canberra, Australia, for their support with bibliography and information, various critical comments on earlier manuscript versions and intense discussions over

the years. Konrad FIEDLER, Bayreuth, Germany, kindly provided the statistical analysis. For the permission to examine and to take photographs of potential type specimens, the senior author thanks David CARTER (BMNH, London), Wolfram MEY (ZMHU, Berlin), and Jacques PIERRE (MNHN, Paris).

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