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# Revision of the African geometrid genus *Zerenopsis* C. &. R. Felder – moths with peculiar life histories and mating behaviours (Geometridae: Ennominae: Diptychini)

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**Abstract:** The taxonomy of the African geometrid genus *Zerenopsis* C. &. R. Felder, 1874, placed in the subfamily Ennominae and tribe Diptychini (cycad moths), is revised. Based on a detailed comparison of morphological characters, *Diptychis* C. &. R. Felder, 1874 and *Paraptychodes* Warren, 1894 are placed as junior subjective synonyms of *Zerenopsis* C. &. R. Felder, 1874 (**syn. n**.). Consequently, five new species combinations (**comb. n.**) are proposed: *Zerenopsis geometrina* (C. &. R. Felder, 1874), *Zerenopsis meraca* (Prout, 1928), *Zerenopsis kedar* (Druce, 1896), *Zerenopsis tenuis* (Butler, 1878) and *Zerenopsis costimaculata* (Prout, 1913). Two new species are described: *Zerenopsis moi* Staude & Sihvonen (**sp. n.**) from Mozambique and *Zerenopsis flavimaculata* Staude & Sihvonen (**sp. n.**) from Malawi, raising the total number of species in the genus *Zerenopsis* from one to eight. The constituent species are diagnosable by morphological characters, particularly by facies and genetic COI data, whereas the male and female genitalia are rather uniform and less diagnostic. The life histories of *Z. lepida* (Walker, 1854), *Z. moi* and *Z. costimaculata* and the final-instar larvae of *Z. geometrina* and *Z. tenuis* are described. All known larvae are aposematic, feed on cycads during the early stages of their life cycle and accept other, unrelated plants in later instars. *Zerenopsis* adults are aposematic and diurnal. Lek behaviour is described for *Z. lepida*, *Z. tenuis* and *Z. moi*, and evidence is presented that it also occurs in other *Zerenopsis* species. This mating strategy is potentially unique among Geometridae. The androconial organs of the males are described and illustrated as forming a 'pheromone pocket' whose development is related to the lek behaviour. Information on habitat, distribution, conservation status and genetics is provided for the majority of the species. Diagnostic characters of the adults, including of the male and female genitalia where known, are described for all species.

**Key words:** Geometridae, Diptychini, *Zerenopsis*, lek behaviour, androconia, androconial organ, cycad, life history.

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## INTRODUCTION

The geometrid genera *Diptychis* C. & R. Felder, 1874, *Zerenopsis* C. & R. Felder, 1874 and *Paraptychodes* Warren, 1894 have traditionally been classified in the subfamily Oenochrominae on the basis of their hind-wing venation (e.g. Prout 1929–1935), but they were later placed in a subfamily Diptychinae (Staude 2001a), the cycad moths. This taxon was proposed by Janse (1933–1935) based on similarities in the male and female genital structures and details of the wing venation. Preliminary results of a current comprehensive study of their systematic position (Sihvonen, Mutanen & Staude in prep.) using extensive sets of molecular and morphological data indicate that this taxon is best placed as a tribe within Ennominae, and it is therefore treated here as such.

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The close morphological relationship of *Diptychis*, *Zerenopsis* and *Paraptychodes* has been recognised for a long time. Janse (1933–1935) noted it for the South-African genera *Diptychis* and *Zerenopsis* and Prout (1929–1935) for *Diptychis* and *Paraptychodes*. More recently Scoble (1999) classified *Paraptychodes* in Sterrhinae and *Diptychis* and *Zerenopsis* in Ennominae, but the genera were interspersed between other, non-African genera in a tentative arrangement of the phylogeny of geometrid genera, obscuring any close relationship between them. The association of *Paraptychodes* with Sterrhinae was refuted by Sihvonen & Kaila (2004) and Staude (2001a), the latter regarding it as a genus of Diptychini based on its tympanal organs, unique androconia and association with cycads. The larvae of *Diptychis*, *Zerenopsis* and *Paraptychodes* lack prolegs on segments A4–A5, as occur in the related genus *Callioratis* C. &. R.

Felder, 1874 (Staude 2001a), an unusual condition in Geometridae.

The Diptychini are closely associated with cycads (Staude 2001b), which constitute the primary larval host-plants of all species as known and span the native African genera *Encephalartos* and *Stangeria* as well as exotic genera such as *Cycas* and *Dioon*. Cycads are an ancient lineage of gymnosperms and generally toxic to most animals. The early-instar larvae of *Zerenopsis lepida* apparently are dependent on the cycad-specific toxin macrozamin (Donaldson & Boesenberg 1995), but in all Diptychini species of which the early-instar larvae are known, older larvae can switch to feed on a variety of other plant species (Staude 1994; 2001a). For instance, *Durbana setinata* Felder & Rogenhofer, 1875 uses the cycad *Stangeria eriopus* as its primary larval host-plant but flower heads of various herbaceous dicotyledonous angiosperms as secondary hosts (Staude 2001a). This strategy is thought to allow an expansion of the host-range in response to the dwindling of cycad populations. All Diptychini larvae and adults display aposematic or warning coloration, signalling their apparent poisonous properties to potential predators (Staude & Curle 1997).

Diptychini species may have one generation per year in temperate areas, two generations in subtropical areas and three or even more in tropical areas. Distribution ranges of cycad moths are closely associated with those of cycads, the moths only occurring in the vicinity of cycad colonies. However, there are many cycad populations in which the moths are absent, especially in drier areas. *Zerenopsis* species are known from the eastern side of Africa, from South Africa to Kenya.

Several species of Diptychini are of conservation concern because suitable habitats with sufficient cycad populations are becoming increasingly scarce. *Callioratis millari* Hampson, 1905 is probably South Africa's most endangered moth (Staude 2011), and *Callioratis grandis* Prout, 1922 in Malawi is critically endangered (Staude *et al.* 2011).

All Diptychini are diurnal, and in many species the adults show intricate lek mating behaviour, the males choosing specific lek sites from which they attract females (Staude 1996 2001a, Bayliss *et al.* 2009, Staude *et al.* 2011). Several species have distinctive male androconial organs, often on the hind-wing underside (Pls 2 & 3).

Before this article six genera comprising 15 described species were recognised in Diptychini (Staude 2001a, Staude *et al.* 2011). *Callioratis* was recently revised (Staude (2001), but the remaining genera and their species have not been subjected to a modern revision. The aim of this paper is to present the known information on the taxon and to subject it to a modern taxonomic revision.

## MATERIALS AND METHODS

Comparative morphological methods and COI sequence divergences were used to delimit the taxa and estimate their taxonomic status. We studied morphological characters of adults (including genitalia and wing venation) and immature stages (eggs, larvae and pupae), host-plant associations and behavioural traits, but not all these data sources were available for every taxon examined. All relevant type specimens known to us were examined.

For DNA analyses, one or two legs were removed from dried specimens and stored in an individual tube, most cases in absolute ethanol. DNA extraction, amplification and sequencing of the "barcode" region of the mitochondrial cytochrome c oxidase I (COI) gene region (658 base pairs) were carried out in the Canadian Centre for DNA Barcoding, Ontario, Canada, using standard high-throughput protocols (Ivanova et al. 2006, de Waard *et al.* 2008) as described by CCDB (2013). Sequence divergence within and between species was calculated using the Kimura 2-parameter model (Kimura 1980) and the neighbour-joining algorithm (Saitou & Nei 1987), as implemented in BOLD (http://www.boldsystems.org/). The Barcode Index Number (BIN) (Ratnasingham & Hebert 2007) was used to verify (sub)species identifications, since the clusters have been shown to be highly concordant with (sub)species when combined with morphological analysis (Ratnasingham & Hebert 2013).

Institutional abbreviations are as follows: ABRI = African Butterfly Research Institute, Nairobi, Kenya; BMNH = The Natural History Museum, London, United Kingdom; CTC = Curle Trust Collection, Johannesburg, South Africa; DMK = private collection of Douglas M. Kroon, Sasolburg, South Africa; HSS = private collection of Hermann S. Staude, Magaliesburg, South Africa; JB = private collection of Jonathan Ball, Cape Town, South Africa. MHNG = Muséum d'Histoire Naturelle, Geneva, Switzerland; OUM = Oxford University Museum of Natural History, Oxford, United Kingdom; SAM= South African Museum, Cape Town, South Africa; TMSA = Ditsong Museum of Natural History, Pretoria, South Africa (previously Transvaal Museum); VM = Virtual Museum of the University of Cape Town and The Lepidopterists' Society of Africa (http://vmus.adu.org.za/vm); ZSM = Zoologische Staatssammlung München, Munich, Germany.

Label data of types and dissected specimens are presented *verbatim* as they appear on the labels, a forward slash denoting separate lines and a semicolon separate labels, and additional information about specimens or labels is enclosed in square brackets. Data of other specimens are presented as captured in the database Lepidops 4.04ah (Coetzer & Coetzer 2009) and do not necessarily reflect label data *verbatim*. Data of countries, provinces and towns have been updated in most cases. Geo-references were either taken from specimen labels (very few cases) or generated from localities on the labels using resources such as Google Earth and Mapsource. Label data that were ambiguous or insufficient to allow an accuracy of at least a one-degree grid square were mostly omitted. The scale in the distribution map of the genus is one-degree grid squares (DGSs) and that of the species maps quarter-degree grid squares (QDGSs), except for Fig. 23, in

which the grids for records from ornamental gardens and parks containing cycads are slightly reduced to make overlaps visible. Distribution maps were generated using the database software Lepidops 4.04ah (Coetzer & Coetzer 2009).

The abdomens and genitalia were prepared for study using the method of Hardwick (1950). The aedeagus was photographed before and after eversion of the vesica, which is especially critical with valuable specimens, for instance types. The vesica was everted via the caecum, which was cut open with the aedeagus placed inside a hypodermic syringe (Sihvonen 2001). For study of the wing venation, the wings of one side of the body were removed from the specimens by gently pressing down or lifting up with fine forceps, then placed in a dish containing 99.5 % ethanol and the scales removed from both surfaces with fine brushes. The wings were then placed on a micro slide in a drop of ethanol, which was replaced by a drop of euparal, and they were finally covered with a cover slip. The preparations were left unstained.

Larvae and ova were collected by hand on cycad host-plants and transported in white, plastic 35 mm film canisters containing some piece of the host-plant. Single larvae were reared initially in 60 x 40 x 30 mm clear plastic containers and then in progressively larger ones as the larvae grew, initially on leaves of *Stangeria eriopus* or *Encephalartos villosus*, which were readily available. Many larvae were sleeved on leaves of potted *Encephalartos* plants. Containers were kept closed to maintain humidity (because of the dry climate where the laboratory was situated). Cleaning and airing was necessary every other day to prevent mould from forming in the containers. Larvae were reared in an unheated laboratory during summer but at approximately 20 °C when the ambient temperature dropped below 10 °C. Loose, compost-rich soil, sterilised in a microwave oven for 10 minutes, was provided for mature larvae as a pupation medium. Pupae were removed from the soil after three weeks and transferred to "ziplock" plastic bags hung up and breathed into twice weekly to provide some moisture. Some ova, larvae and pupae were preserved in a 70 % ethanol solution in sealed glass vials.

Moths and larvae were photographed using a Canon 7d reflex digital camera with a Tamron 60 mm macro lens, and a Canon MPE65 lens was used for photographing smaller objects such as androconia and ova. Image files were processed using the software program Adobe Photoshop, and the plates were arranged using Adobe Illustrator CS6.

Graphs of seasonal occurrence were prepared using the table function in Microsoft PowerPoint. Label data from specimens collected on a single visit to a locality were treated as a single occurrence event, even if spread over several days.

Descriptions of behaviour are based on observations conducted during the following field trips (supplemented by general observations over the past 20 years): ***Z. lepida*****:** 22–25 March 2012, Ngoye Forest Reserve, KwaZulu-Natal, South Africa; ***Z. moi*****:** 15–17 September 2000, Jay's Beach Lodge, Macaneta, Mozambique; ***Z. tenuis*****:** 03–06 January 2007, Manta Reef Lodge and Misali Island, Pemba Island, Tanzania; ***Z. costimaculata*****:** 20–22 July 2012, Jilore Forest Station, Arabuko Sokoke National Park, Kenya.

Description and illustrations of early stages are based on the following rearing experiments (rearing notes, further images and voucher specimens in HSS).
***Z. lepida*****:** *ex ovo* 04-iv-1994, rearing number 940404/1HSS, Krantzkloof Nature Reserve; *ex larva* 27-iv-1998, Ngoye Forest Reserve; *ex larva* 18-ii-2007, rearing number TZ13, farm Everon, Tzaneen; *ex ovo* 09-v-2011, rearing numbers Entu01–Entu05, Entumeni Nature Reserve; *ex larva* 17-ix-2012, rearing number 12HSS04, Krantzkloof Nature Reserve; *ex ovo* 29-ix-2012, rearing numbers 12HSS13–12HSS15, Macaneta, Mozambique.
***Z. geometrina*****:** *ex larva* 16-10-1996, rearing number 961016/1HSS, Krantzkloof Nature Reserve.
***Z. moi*****:** *ex ovo* 29-ix-2012, rearing numbers 12HSS16–12HSS18, Macaneta, Mozambique.
***Z. costimaculata*****:** *ex larva* 21-vii-2012, rearing numbers ARA1 and ARA2, Jilore Forest Station, Arabuko Sokoke National Park, Kenya.
***Z. tenuis*****:** *ex larva* 05-i-2007, Misali Island, off Pemba Island, Tanzania.

## RESULTS

### Systematics

***Zerenopsis*** C. & R. Felder, 1874

*Zerenopsis* C. & R. Felder, 1874, in Felder et al. (eds.) Reise öst. Fregatte Novara (Zool.) 2 (Abt. 2): pl. 100, fig. 19. Type species, by monotypy: *Zerenopsis leopardina* C. & R. Felder, 1874 [= Junior subjective synonym of *Zerenopsis lepida* (Walker, 1854)].
*Diptychis* C. & R. Felder, 1874, in Felder et al (eds.). Reise öst. Fregatte Novara (Zool.) 2 (Abt. 2): p. 100, fig. 20. Type species, by monotypy: *Diptychis geometrina* C. & R. Felder, 1874) **syn. n.**
*Paraptychodes* Warren, 1894, Novit. zool. 1: 379. Type species, by original designation: *Aletis tenuis* Butler, 1878 **syn. n.**
*Zerenopsis* Warren, 1894, Novit. zool. 1: 422. Type species, by original designation: *Zerenopsis leopardina* C. & R. Felder, 1874 [Junior homonym and junior objective synonym of *Zerenopsis* C. & R. Felder, 1874 (Fletcher 1979, Scoble 1999)].

### Diagnosis

Facies (Pl. 1) heterogeneous. Wingspan 28–55 mm. Colour variable, yellow to orange or white, often with variable black maculated pattern or large subapical spots on fore wings. Anal margin of hind wings in male with androconial organ, folded in all species except *Z. lepida* (Pls 2 & 3), hind tibiae with hair-pencil. Antennae in both sexes often clubbed (apex not expanded) or weakly filiform. Abdomen variably banded black and orange-yellow. Tympanal cavities large. 8th tergite in male slightly triangular, posterior margin narrower. Fore wings with vein $R_2$ fused or parallel to $R_3 + R_4$, forming areole. Hind wings with $M_2$ in female tubular, in male tubular or weakly tubular,

veins near anal margin ($CuA_2$, $A_2$) often reduced due to folding of anal margin. Male genitalia (Pls 4 & 5). Uncus prominent, sclerotised, acute. Socii small, setose. Gnathos arms narrow, fused ventromedially. Tegumen large, anterior margin and middorsal lines sclerotised. Juxta arms (labides) well-developed. Valves wide, ventromedially setose, ventral margin slightly concave or straight, apex wide, extension of costa acute. Saccus a narrow, sclerotised ring. Aedeagus rather straight, caecum present. Vesica simple, often a narrow tube, with several minute cornuti or cornuti absent. Differences between species minimal. Female genitalia (Pls 6 & 7). Papillae anales large, densely setose. Base of setae elongate, forming uneven, peg-shaped surface. Lamella postvaginalis small, elongated plate. Lamella antevaginalis prominent, sclerotised, ventromedial margin straight, elongate or invaginated. Posterior part of corpus bursae sclerotised, striate and often spinose. Corpus bursae large, roundish sac. Signum large, stellate. Differences between species minimal.

Immature stages. Ova smooth, ovoid in shape, not flattened. Larvae aposematic, with long secondary setae and well-developed chalazae. Well developed prolegs on A6 and A10 only, as typical for Geometridae (unlike in *Callioratis*, species of which have an additional pair of prolegs on A5). Pupae reddish-brown to dark-brown, cremaster with two or three pairs of (weakly) curved hooks.

**Diversity, distribution and ecology**

Eight species in wetter regions of eastern sub-Saharan Africa. Adults aposematic and diurnal, males with lek behaviour (where known). Larval host-plants (as known) cycads in early instars, various other plants in later instars.

**Genetics** (Fig. 1)

Analysis of the fragment (COI 5', >500 bp) of three specimens of *Z. lepida* (Ngoye, Krantzkloof, Mphaphuli), one of *Z. tenuis* (Pemba), one of *Z. geometrina* (Shongweni), one of *Z. kedar* (Pemba), one of *Z. costimaculata* (Arabuko) and two of *Z. moi* (Macaneta) revealed the following nearest-neighbour genetic distances (minimum pairwise distance, Kimura 2 parameter):

| | |
|---|---|
| *Z. lepida* - *Z. geometrina*: | 3.68 % |
| *Z. costimaculata* - *Z. tenuis*: | 5.37 % |
| *Z. kedar* - *Z. tenuis*: | 2.70 % |
| Z. *moi* - Z. *geometrina*: | 4.00 % |

Source: BOLD_database (http://www.barcodinglife.com/views/login.php; cf. Ratnasingham & Hebert (2007).

**Remarks**

Based on the comparative morphological analysis of adults and immatures stages, host-plant associations, behavioural characters and revision of all known and hitherto described taxa, we recognise only a single genus *Zerenopsis* C. & R. Felder, 1874, comprising eight species. As the original generic names of two of the described species, *Diptychis* C. & R. Felder, 1874 and *Zerenopsis* C. & R. Felder, 1874, were proposed in the same publication (Felder & Felder 1874), we apply the Principle of the First Reviser (Article 24.2.1, ICZN

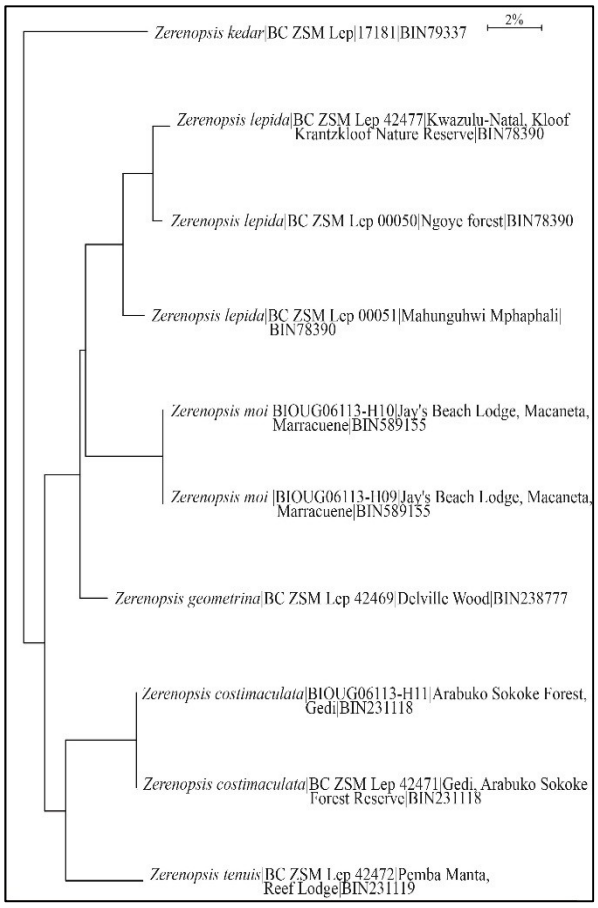


**Figure 1** – Neighbour joining tree (Kimura 2-parameter distance model for COI-5P marker) for African *Zerenopsis* specimens.

2012) and give *Zerenopsis* priority over *Diptychis*, because it is more extensively used in the literature. *Diptychis* and *Paraptychodes* Warren, 1894 are therefore treated as junior subjective synonyms of *Zerenopsis*, and consequently five new species combinations are effected. We also describe two new species in *Zerenopsis*.

The species of the genus *Zerenopsis* as redefined are rather different in facies (coloration and wing pattern), but in other morphological features, including the folding of the anal margin (androconial organ) in the hind wings of the males, the genitalia of both sexes and the characters of the larvae, the genus is very uniform. Furthermore, the COI sequence divergences found between the species (Fig. 1) are in concordance with the morphological findings.

**1. *Zerenopsis lepida*** (Walker, 1854)

*lepida* Walker, 1854, List Specimens lepid. Insects Colln Br. Mus. 2: 571, (*Deiopeia*). Holotype female (BMNH), [South Africa:] Port Natal.

*leopardina* C. & R. Felder, 1874, in Felder et al. (eds.) Reise öst. Fregatte Novara (Zool.) 2 (Abt. 2): Erklärung p. 10, pl. 100, fig. 19, (*Zerenopsis*). Holotype female (BMNH), [South Africa:] Natal. [Synonymy after Vári *et al*. (2002), here confirmed].

**Material examined**

**Types.** *Deiopeia lepida* Walker, 1854 holotype female (Pl. 1d iii–iv): [South Africa:] Port Natal; genitalia slide No. 17478 (BMNH) (genitalia and external characters examined). *Zerenopsis leopardina* C. & R. Felder,

1874 holotype female (Pl. 1d v): [South Africa:] Natal (BMNH) (examined externally).

**Dissected specimens.** Female genitalia: Prep. number 1925./ Pasi Sihvonen, SOUTH AFRICA, KwaZulu-Natal/ KwaDweshula, Ntimankulu forest/ 30°32'6.41S, 30°17'18.26E/28. Feb. 2010/ (leg. S. E. Woodhall); DNA sample/ No. 140/ Pasi Sihvonen; DNA sample/ 16660, Hermann Staude, South Africa (HSS) [Wings removed]. Male genitalia: Prep. number 1763./ Pasi Sihvonen and wings of the male: Prep. number 1805/ Pasi Sihvonen, both from the same specimen: South Africa, Natal,/ Pinetown, Krantzkloof/ Nature Reserve, 200m,/ 29°46'S/[on the label]30°49'E,/ H.S. Staude,/ 24-04-1998; South Africa/ Krantzloof/ Krantzkloof Nature Reserve/ 29°45'60.0 30°49'60.0/ 24.IV.1998 200m/ H.S. Staude/ HSS_D000.DB 13919; GEOMETRIDAE/ DIPTYCHINAE/ Zerenopsis/ lepida/ H.S. Staude - 19-02-2009/ HSS_D000.DB 13919; m/ DNA sample/ No. 129/ Pasi Sihvonen (HSS). Female genitalia: Prep. number 1764./ Pasi Sihvonen, South Africa, Kwazulu-/ Natal, Entumeni Nature/ Reserve, Grassland,/ 28°53'S/[on the label]31°23'E, 850m, 11-/ 04-1998,/ H.S. Staude; South Africa/ HSS_D000.DB 13921 (HSS). Female genitalia: Prep. number 1768./ Pasi Sihvonen, South Africa, Limpopo/ Province, Tzaneen, farm/ Evenron dry forest/, S23°50'48.5"/[on the label]E30°06'09.3",/ 780m, 18-02-2007/, H.S. Staude; HSS_D000.DB 10748/ GEOMETRIDAE/ DIPTYCHINAE/ Zerenopsis/ lepida/ H.S. Staude (HSS). Metathorax, female: Prep. number 1775./ Pasi Sihvonen, South Africa, Limpopo/ Province, Tzaneen, farm/ Evenron dry forest/, S23°50'48.5"/[on the label]E30°06'09.3",/ 780m, 18-02-2007/, H.S. Staude (HSS). Female genitalia: Prep. number 1824./Pasi Sihvonen, South Africa Northern/ Tvl. Mahunguhwi Mphaphuli/ cycad reserve 800 m/ 30.41E. 22.48S H.S. Staude/ 18.5.[19]94 emerged; ab larva collected 09-02-1994 on/ *Encephalartos transvenosus*/ Zamiaceae by R.G. Oberprieler/ 940219-1HSSRO (HSS).

**Other specimens. HSS:** *Natural habitats:* S32.408, E26.101, 1078m, 1983-11-05, Huntley Glen farm, Bedford, Eastern Cape, South Africa, E.L. Pringle; S28.95, E31.733, 270m, 1987-06-25, Ngoye forest, Eshowe, KwaZulu-Natal, South Africa, W.J. Staude; S27, E32.717, 50m, 1989-03-26, Manguzi forest, Manguzi, KwaZulu-Natal, South Africa, A.I. Curle; S31.616, E29.542, 1990-12-09, Port St. Johns, Eastern Cape, South Africa, W. Steele; S32.817, E28.017, 200m, 1993-01-22, Kwelera River, Gonubie, Eastern Cape, South Africa, emerged, R. Oberprieler; S23.817, E35.433, 50m, 1993-12-17, Praia do Tofo, Inhambane, Mozambique, R. Jeffery; S27, E32.717, 50m, 1993-05-31, Manguzi forest, Manguzi, KwaZulu-Natal, South Africa, S.E. Woodhall; S22.8, E30.683, 800m, 1994-05-19, Mphaphuli cycad reserve, Mahunguhwi, Limpopo, South Africa, R.G. Oberprieler; S29.767, E30.833, 200m, 1994-09-15, Kranzkloof Nature Reserve, Pinetown, KwaZulu-Natal, South Africa, H. S. Staude; S32.033, E29.1, 50m, 1995-12-11, Lulwaleni forest, Hole In The Wall, Eastern Cape, South Africa, H. S. Staude; S32.033, E29.150, 1995-12-10, Lulwaleni forest, Hole In The Wall, Eastern Cape, South Africa, H.S. Staude; S26.55, E31.967, 700m, 1996-03-09, Jilobi Forest, Siteki, Swaziland, H.S. Staude; S28.95, E31.733, 270m, 1998-04-26, Ngoye forest, Eshowe, KwaZulu-Natal, South Africa, H.S. Staude; S28.883, E31.383, 850m, 1998-04-11, Entumeni Nature Reserve, Entumeni, KwaZulu-Natal, South Africa, H.S. Staude; S28.95, E31.733, 270m, 1998-08-11, Ngoye forest, KwaZulu-Natal, South Africa, H.S. Staude; S29.767, E30.833, 200m, 1998-04-24, Krantzkloof Nature Reserve, Kloof, KwaZulu-Natal, South Africa, H.S. Staude; S28.883, E31.383, 750m, 1998-09-01, Entumeni Nature Reserve, Eshowe, KwaZulu-Natal, South Africa, S32.408, E26.101, 1078m, 1999-12-06, Huntley Glen farm, Bedford, Eastern Cape, South Africa, E.L. Pringle; S25.608, E30.7, 2000-11-15, Kaapsehoop, Mpumalanga, South Africa, I.A. Coetzer; S28.883, E31.383, 750m, 2000-04-10, Entumeni Nature Reserve, Entumeni, KwaZulu-Natal, South Africa, H.S. Staude; S33.033, E27.859, 50m, 2001-01-20, East London, Eastern Cape, South Africa, M. Helm; S27.567, E32.083, 650m, 2001-02-20, Ubombo forest, Ubombo, KwaZulu-Natal, South Africa, I.A. Coetzer; S27, E32.717, 50m, 2001-02-03, Manguzi forest, Manguzi, KwaZulu-Natal, South Africa, I.A. Coetzer; S29.767, E30.833, 450m, 2003-04-12, Krantzkloof Nature Reserve, Pinetown, KwaZulu-Natal, South Africa, H.S. Staude; S28.95, E31.733, 270m, 2003-08-30, Ngoye forest, Eshowe, KwaZulu-Natal, South Africa, H.S. Staude; S29.858, E30.733, 2004-02-14, Delville Wood, Shongweni, KwaZulu-Natal, South Africa, S.E. Woodhall; S29.611, E30.117, 2005-02-19, Shongweni, KwaZulu-Natal, South Africa, D. McDermott; S28.056, E32.089, 440m, 2007-04-30, Hilltop camp, Hluhluwe Game Reserve, KwaZulu-Natal, South Africa, H.S. Staude; S26.974, E32.421, 90m, 2008-04-29, Tembe Elephant Reserve, Kwangwanase, South Africa, S.E. Woodhall; S29.767, E30.835, 520m, 2009-05-03, Krantzkloof Nature Reserve, Kloof, KwaZulu-Natal, South Africa, H.S. Staude; S28.886, E31.377, 683m, 2011-05-09, Foz5 scarp forest, Entumeni Nature Reserve, KwaZulu-Natal, South Africa, H.S. Staude; S28.891, E31.457, 520m, 2012-04-15, Dlindza Forest, Eshowe, KwaZulu-Natal, South Africa, H.S. Staude; S25.717, E32.733, 30m, 2012-09-30, Jay's Beach Lodge, Macaneta, Marracuene, Mozambique, P.R. Ward; S25.717, E32.733, 30m, 2012-12-16 emerged, Jay's Beach Lodge, Macaneta, Marracuene, Mozambique, H.S. Staude. *Transformed habitats:* S23.847, E30.103, 780m, 2007-02-18, farm Evenron, Tzaneen, Limpopo, South Africa, H.S. Staude.**TMSA**: S31.667, E29.033, 600m, 1904-03-18, Transkei, Ngqeleni, [Eastern Cape],[South Africa]; S31.667,E29.033, 600m, 1904-01-21, Transkei, Ngqeleni, [Eastern Cape],[South Africa], S31.667, E29.033, 600m, 1907-09-08, Transkei, Ngqeleni, [Eastern Cape], [South Africa]; S31.667, E29.033, 600m, 1908-01-12, Transkei, Ngqeleni, [Eastern Cape], [South Africa]; S31.617, E29.533, 1908-03-17, Port St. John's, [Eastern Cape], [South Africa]; S31.617, E29.533, 1908-12-06, Port St. John's, [Eastern Cape], [South Africa]; S30.75, E30.25, 1911-11-02, Paddock, [KwaZulu-Natal], [South Africa]; S30.75, E30.25, 1914-11-22, Paddock, [KwaZulu-Natal], [South Africa]; S28.883, E31.467, 1914-11-13, Eshowe, [KwaZulu-Natal], [South Africa]; S28.883, E31.467, 1915-01-12, Eshowe, [KwaZulu-Natal], [South Africa], S29.867, E31, 1916-

08-22, Durban, [KwaZulu-Natal], [South Africa]; S29.867, E31, 1917-08-23, Durban,[KwaZulu-Natal], [South Africa], S29.867, E31, 1917-02-27, Durban, [KwaZulu-Natal],[South Africa]; S30.283, E30.75, 1918-04-01, Rietvlei, [KwaZulu-Natal], [South Africa]; S29.867, E31, 1919-03-31, Durban, [KwaZulu-Natal], [South Africa]; S29.867, E31, 1921-03-29, Durban, [KwaZulu-Natal], [South Africa]; S30.733, E30.467, 1925-04-20, Port Shepstone, [KwaZulu-Natal], [South Africa], S33.083, E27.817, 1925-10-14, East London, [Eastern Cape], [South Africa]; S30.283, E30.75, 1928-12-02, Scottburgh, [KwaZulu-Natal], [South Africa]; S31.6167, E29.533, 1936-04-05, Port St. John's, [Eastern Cape], [South Africa]; S28.883, E31.467, 1941-11-01, Eshowe, [KwaZulu-Natal], [South Africa]; S31.133, E29.65, 600m, 1946-06-01, Umzikaba river, Umzikaba, [Eastern Cape], [South Africa]; S29.85, E31.017, 1948-10-29, Cambridge, Durban, [KwaZulu-Natal], [South Africa]; S32.433, E28.65, 1950-09-02, Qora mouth, Quora, [Eastern Cape], [South Africa]; S29.867, E31, 1952-09-01, Durban,[KwaZulu-Natal], [South Africa]; S29.867, E31, 1954-01-03, Durban, [KwaZulu-Natal], [South Africa]; S29.867, E31, 1954-04-18, Durban, [KwaZulu-Natal], [South Africa]; S29.867, E31, 1954-02-18, Durban, [KwaZulu-Natal], [South Africa]; S29.867, E31, 1955-04-30, Durban,[KwaZulu-Natal], [South Africa]; S28.883, E31.467, 1955-12-01, Eshowe, [KwaZulu-Natal], [South Africa]; S32.233, E28.883, 1956-12-23, Transkei, Bashee River mouth, [Eastern Cape], [South Africa]; S29.783, E30.833, 1956-08-11, Kloof, [KwaZulu-Natal],[South Africa]; S29.867, E31, 1963-04-22, Durban, [KwaZulu-Natal], [South Africa]; S29.867, E31, 1963-04-01, Durban,[KwaZulu-Natal], [South Africa]; S33.033, E27.859, 1979-10-21, Beacon Bay, East London, [Eastern Cape], [South Africa]; S28.817, E32.1, 1979-10-03, Richard's Bay, [Kwazulu-Natal], [South Africa]; S32.233, E28.883, 1980-12-23, Transkei, The Haven, [Eastern Cape], [South Africa]; S31.617, E29.533, 1980-10-17, Port St. John's, [Eastern Cape], [South Africa]; S33.033, E27.859, 1984-12-12, Beacon Bay, East London, [Eastern Cape], [South Africa], S33.033, E27.859, 1984-11-25, Beacon Bay, East London,[Eastern Cape], [South Africa]; S32.183, E28.917, 1984-10-21, Cwebe forest, Cwebe, [Eastern Cape], [South Africa]; S32.283, E28.817, 1985-12-30, Dwesa Forest, [Eastern Cape], [South Africa]; S32.233, E28.883, 1986-01-26, Transkei, The Haven, [Eastern Cape], [South Africa]; S32.233, E28.883, 1988-03-27, Transkei, The Haven, [Eastern Cape], [South Africa]; S25.767, E28.2, 1988-02-22, Klapperkop, Pretoria, Gauteng, [South Africa]; S27.567, E32.067, 2001-02-12, Ubombo, KwaZulu-Natal, South Africa; S26.967, E32.717, 2001-02-12, Manguzi forest, Manguzi, KwaZulu-Natal, South Africa. **DMK:** S29.317, E30.233, 1990-11-22, Karkloof, KwaZulu-Natal, South Africa, S. Nevill; S29.4, E30.267, 1994-11-03, Karkloof falls, Karkloof, KwaZulu-Natal, South Africa, S. Nevill; S31.6, E29.517, 1993-09-03, Port St. Johns, Eastern Cape, South Africa, D.M. Kroon; S28.933, E29.2, 1460m, 1993-11-03, Cathedral Peak hotel, Winterton, KwaZulu-Natal, South Africa, N.V. Kroon; S31.05, E30.167, 1993-11-03, Umtamvuna, KwaZulu-Natal, South Africa S. Nevill, ; S29.483, E30.233, 1991-01-03, Howick, KwaZulu-Natal, South Africa, S. Nevill; S29.4, E30.267, 1993-11-25, Karkloof falls, Karkloof, KwaZulu-Natal, South Africa, S. Nevill ; S29.317, E30.233, 1991-03-03, Karkloof, KwaZulu-Natal, South Africa, S. Nevill ; S29.317, E30.233, 1991-11-14, Karkloof, KwaZulu-Natal, South Africa, S. Nevill; S25.783, E31.05, 1991-08-03, Barberton, Mpumalanga, South Africa, D.M. Kroon. **CTC:** S31.4, E29.683, 2001-05-04, Mboyti, Eastern Cape, South Africa; S32.543, E27.367, 2001-05-14, Stutterheim, Eastern Cape, South Africa: S33.033, E27.859, 2001-02-20, Buffalo Valley, East London, Eastern Cape,South Africa; S32.217, E28.867, 1999-01-03, 5km west of Bashee River, Butterworth, Eastern Cape, South Africa; S32.217, E28.867, 1998-07-29, 5km west of Bashee River, Butterworth, Eastern Cape, South Africa; S31.637, E29.546, 2001-04-18, Port St. Johns, Eastern Cape, South Africa; S28.839, E31.685, 2000-04-23, Ngoye forest, Eshowe, KwaZulu-Natal, South Africa; S25.6, E30.783, 2000-12-22, Kaapsehoop, Mpumalanga, South Africa; S30.999, E30.301, 2004-02-22, Munster, KwaZulu-Natal, South Africa; S28.918, E31.354, 2000-04-21, Sugar Estate, Entumeni, KwaZulu-Natal, South Africa; S26.999, E32.731, 2001-02-09, Manguzi, KwaZulu-Natal, South Africa; S26.999, E32.731, 1998-12-15, Manguzi, KwaZulu-Natal, South Africa; S27.469, E32.017, 2001-02, -16, Lebombo Mountains, Jozini, KwaZulu-Natal, South Africa; S30.7, E30.467, 2001-12-17, Umtentweni, KwaZulu-Natal, South Africa; S29.75, E30.833, 1970-01-25, Krantzkloof, KwaZulu-Natal, South Africa; S29.767, E30.75, 1967-02-04, Hillcrest, KwaZulu-Natal, South Africa; S28.9, E31.45, 1970-01-25, Eshowe, KwaZulu-Natal, South Africa.

**Photographic and observational records. HSS:** *Natural habitats*: S29.267, E29.5, 2000m, 1990-05, Giants Castle Reserve, Estcourt, KwaZulu-Natal, South Africa, M.C. Williams; S28.133, E32.533, 20m, 1999-11-14, Cape Vidal, St Lucia, KwaZulu-Natal, South Africa, H.S. Staude; S31.55, E29.5, 50m, 2004-12-18, Port St Johns, Eastern Cape, South Africa, H.S. Staude; S30.802, E30.276, 414m, 2005-04-06, Mbumbazi Nature Reserve, Paddock, KwaZulu-Natal, South Africa, H.S. Staude; S30.707, E30.270, 420m, 2005-04-06, Oribi Gorge Nature Reserve, Paddock, KwaZulu-Natal, South Africa, H.S. Staude; S28.441, E31.4014, 830m, 2006-04-27, Ophathe Game Reserve, Ulundi, KwaZulu-Natal, South Africa, H.S. Staude; S30.265, E30.608, 420m, 2010-10-16, Vernon Crookes NR, Scottburgh, KwaZulu-Natal, South Africa, W. Prinsloo; S25.798, E31.142, 1000m, 2010-03-21, Shiyalongoubo forest, Baberton, Mpumalanga, South Africa, P. Webb; S25.6, E30.767, 1600m, 2011-10-23, Kaapschehoop, Mpumalanga, South Africa, Cycad Society; S28.896, E31.453, 683m, 2011-04-03, Dlindsa Forest, Eshowe, KwaZulu-Natal, South Africa, H.S. Staude; S28.886, E31.377, 683m, 2011-05-09, Picnic site, Entumeni, KwaZulu-Natal, South Africa, H.S. Staude; S31.425, S29.717, 200, 2011-12-18, Mbotyi, Eastern Cape, South Africa, R.D. Stephen; S24.583, E30.8, Blyde River Canyon NR, Hoedspruit, Mpumalanga, South Africa, Cycad Society; S28.886, E31.377, 720m, 2012-03-23, Picnic site, Entumeni, KwaZulu-Natal, South Africa, H.S. Staude; S28.838,

E31.685, 445m, 2012-06-15, Ngoye Forest, Eshowe, KwaZulu-Natal, South Africa, H.S. Staude; S28.838, E31.685, 445m, 2012-04-14, Ngoye Forest, Eshowe, KwaZulu-Natal, South Africa, H.S. Staude. S28.838, E31.685, 445m, 2013-04-07, Ngoye Forest, Eshowe, KwaZulu-Natal, South Africa, H.S. Staude. *Transformed habitats*: 25.686, E28,163, 1320m, 1994-09-02, Pretoria North, Gauteng, South Africa, H.S. Staude; S29.556, 30.356, 830 m, 2001-10-20, Chase Valley, Pietermaritzburg, KwaZulu-Natal, South Africa, H.S. Staude; S33.65, E26.6, 2007-01-09, Bushmansriver, Kenton on Sea, Eastern Cape, South Africa, R. Butler; S33.3, E26.517, Grahamstown, Eastern Cape, South Africa, E.L. Pringle; S29.767, E30.75, 2007-11-16, Hillcrest, KwaZulu-Natal, South Africa, S.E. Woodhall; S29.829, E30.857, 430m, 2008-12-06, Winston Churchill Drive, Pinetown, KwaZulu-Natal, South Africa, G. Aiston; S33.517, E26.867, 2011-12-18, Kumbula Nursery, Bathurst, Eastern Cape, South Africa, L. Solomon; S25.667, E28.233, Montana, Pretoria, Gauteng, South Africa, Leonard.**VM records:** *Natural habitats*: S28.833, E31.733, 2008-05-04,Ongoye Forest, Mtunzini, KwaZulu-Natal, South Africa, L. & H. Heyns; S29.774, E30.832, 2009-12-28, Krantzkloof Nature Reserve, Pinetown, KwaZulu-Natal, South Africa, A. & I. Sharp; S28.8519, E31.853, 2009-7-4, Ongoye
Forest, Mtunzini, KwaZulu-Natal, South Africa, T. Strachan; S29.769, E30.723, 2010-12-27, Next to Alverstone tower, Hillcrest, KwaZulu-Natal, South Africa, P. Webb; S33.559, E26.848, 2012-02-22, Mansfield Game Reserve, Port Alfred, Eastern Cape, South Africa, A. & B. Kok. *Transformed habitats*: S29.6, E30.367, 2006-11-02-07, Taunton Road, Pietermaritzburg, KwaZulu-Natal, South Africa, K.L. Immelman; S29.541, E31.208, 2007-10-01, Balito, KwaZulu-Natal, South Africa, D. Cowie; S30.970, E30.269, 2008-03-03, Palm Beach, Munster, KwaZulu-Natal, South Africa, R.A. Dobson; S24.504, E30.836, 2008-11-17, flying around at top of trees, Hoedspruit, Limpopo, South Africa, P. Webb; S29.596, E30.348, 2009-11-19, 14 Villa Assumpta Place, Pietermaritzburg, KwaZulu-Natal, South Africa, B.R.G. Clulow; S30.301, E30.743, 2012-10-12, Scottburgh, KwaZulu-Natal, South Africa, P. Vos; S31.062, E30.245, 2013-1-19, San Lameer, Margate, KwaZulu-Natal, South Africa, M. Beneke. **iSpot records:** *Transformed habitats*: S30.301, E30.743, 2012-10-22, Scottburgh, KwaZulu-Natal, South Africa, Bushboy.

**Redescription** (Pls 1d, 8; Fig. 2) (diagnostic characters underlined)
Sexes similar but male smaller, wingspan ♂ 34–39 mm (AM = 36.5 mm, *n* = 19); ♀ 40–48 mm (AM = 43.2 mm, *n* = 27), male with variable black area along anal wing margins. Wings orange to yellow, decorated with black maculae of variable size. Number and extent of maculae variable between specimens, sometimes between opposite wings of the same specimen, occasionally few and small, normally round maculae, concentrated on medial and terminal areas and on fore-wing costa, in other specimens large and partly fused. Cilia black, orange or chequered orange-black. Hind wings similar, except basal area often

**Figure 2** – *Z. lepida* adult female, 13-iv-2013, Krantzkloof.

without black maculae; anal margin in male (Pls 2a, 3a) upturned but not folded over, base of upturned area with elongated, thickened scales (possibly androconia, or specialised pheromone-disseminating scales), on underside covered in black scales and long silvery or black setae. Wing underside similar to upperside. Frons and collar black or orange-black, tegulae also often orange-black. Antennae black, filiform in both sexes. Thorax black. Hind tibiae in male swollen, with prominent, black hair-pencil, bearing 2 + 2 minute spurs, in female with 2 + 2 large spurs. Abdomen banded orange-black, sometimes uniform black or orange. Tympanal organs large, meeting ventrally. Ansa broadened at both ends, with elongate projection at centre. Sternites and tergites 3–7 of both sexes undifferentiated. 8th tergite in male slightly triangular, posterior margin narrower. Male genitalia (Pl. 4d): uncus prominent, sclerotised, evenly tapering, weakly setose, apex acute; socii small, setose; gnathos arms narrow, fused ventromedially; tegumen large, anterior margin weakly sclerotised; juxta arms (labides) sclerotised, long, slightly bent subapically, narrow apex acute; juxta small plate; valves wide, ventromedially weakly setose, margins mostly bare, ventral margin slightly concave, apex wide, extension of costa narrow, acute; saccus a narrow, weakly sclerotised ring; aedeagus long, rather straight, caecum long; vesica straight, expanded tube, with numerous minute cornuti. Female genitalia (Pl. 6d): papillae anales large, membranous, densely setose; base of setae elongate, forming uneven, peg-shaped structure; apophyses posteriores long, narrow; apophyses anteriores short, stout, blunt, about 1/4 length of apophyses posteriores; lamella postvaginalis a round, sclerotised plate; lamella antevaginalis a prominent, wide plate, ventromedial margin straight; ductus bursae long, wide, sclerotised, posterior part short, sclerotised, striate and spinose; corpus bursae large, roundish, membranous sac; signum large, stellate.

**Immature stages**
**Ovum** (Fig. 3). Ovoid, bright yellow when laid, gradually darkening as larva develops inside, fully developed larva visible before hatching; shell translucent, surface finely sculptured with regular hexagonal dimples arranged in a circle at micropyle.

**Figure 3** – *Z. lepida* ova, one unfertilised, others with fully developed larva visible, 20-iii-2012, Ngoye.

**1st instar larvae** (Fig. 4). Full compliment of well developed white primary setae, on average longer than body diameter. Body deeply segmented (diameter smaller between segments), uniform yellow to creamy

**Figure 4** – *Z. lepida* first instar larvae, 22-iii-2012, Ngoye.

**Figure 5** – *Z. lepida* second instar larvae, 19-ix-2012, Krantzkloof.

**Figure 6** – *Z. lepida* third instar larvae, 30-ix-2012, Krantzkloof.

**Figure 7** – *Z. lepida* fourth instar larva, 21-iv-2012, Ngoye (northern KZN population).

on emergence, black maculae appearing around setal bases on all segments only after first feeding. Head black, true legs black, prolegs of body colour, anal plate brown, elongated black patch on pronotum separated from black head, well developed prolegs on A6 and A10 only.

**2nd instar larvae** (Fig. 5). As 1st instar but maculae around setal bases larger.

**3rd instar larvae** (Fig. 6). Ground colour uniform, generally deeper yellow to orange; brown secondary setae present, shorter than white primary setae.

**Figure 8 –** *Z. lepida* final instar larva, 27-x-2012, Krantzkloof (southern KZN population).

**Figure 9** – *Z. lepida* final instar larva, 10-viii-2011, Entumeni (northern KZN population).

**4th–6th instar larvae** (Figs 7–13). All three instars similar. Body no longer deeply segmented. Primary and secondary setae shorter than in 3rd instar, secondary setae shorter than primary setae. Ground colour and markings variable within and between populations. Short, variable, black, grey and white intersegmental lines present dorsoventrally in most specimens in southern populations, northern populations

(Mpumalanga and Limpopo provinces) with prominent black dorsoventral lines across anal segments as well as white rings around some or all black setal bases.

**Pupae** (Fig. 14). Reddish brown, AM = 19 x 8 mm (n = 20), with three pairs of cremastral hooks, splayed but merged at base of cremaster.

**Similar species**

In spite of its great variability in external appearance *Z. lepida* is quite a distinct species, somewhat similar to *Z. geometrina* but with all maculae well defined black, never grey. In its genitalia it is most similar to *Z. moi*, with which it is sympatric and which has the juxta arms (labides) long and straight (slightly bent in *Z. lepida*) and the margin of the lamella antevaginalis ventromedially invaginated (straight in *Z. lepida*). The ova and larvae of *Z. moi* are also similar to those of *Z. lepida*, except that in *Z. moi* the black pronotum is contiguous with the head in the early larval instars and the tufts of long white secondary setae (longer than primary setae) in the later instars are diagnostic.

**Figure 10** – *Z. lepida* final instar larva, 31-iii-2012, Ngoye (northern KZN population).

**Figure 11** – *Z. lepida* final instar larva, 02-xii-2012, Macaneta (Mozambique population).

**Figure 12** – *Z. lepida* final instar larva, 18-ii-2007, Tzaneen (Limpopo population).

**Figure 13** – *Z. lepida* final instar larva, Mphaphuli (Limpopo population) (photo R.G. Oberprieler).

**Figure 14** – *Z. lepida* pupae, 27-x-2012, Krantzkloof.

**Intraspecific variation** (Pl. 8, Figs. 7–13)

The various populations of *Z. lepida* show some genetic and phenotypic regional variation as well as phenotypic variation within populations (genetic variation within populations has not been studied). Isolated populations occur probably due to the largely scattered and isolated distribution of cycads across the range of *Z. lepida*.

*Phenotypic variation*: Adults of Eastern Cape (EC) populations (Pl. 8 m–n) generally have clearly defined large black maculae. Later-instar caterpillars are generally uniform orange with few black markings. Adults of populations in southern KwaZulu-Natal (KZN) (Pl. 8 k–l, o) often have merged black maculae, especially at the margins. Later-instar larvae generally have broken greyish longitudinal dorso-lateral bands between the segments (Figs 7–8). Adults (Pl. 8 g–j) and later-instar larvae (Figs 9–10) of populations in northern KZN, Swaziland and Mpumalanga are mostly similar to EC populations but generally with smaller black maculae. Adults of populations in Maputaland and Mozambique (Pl. 8 d–f) generally have much smaller maculae. Later-instar larvae have two broken dorso-lateral bands across all segments (Fig. 11). Adults of Limpopo populations (Pl. 8 a–c) are mostly similar to those of Swaziland and Mpumalanga populations, but later-instar larvae are distinctive with two well-defined black dorso-lateral bands and white rings around the setal bases (Figs 12–13).

Although many adults and later-instar larvae of the various populations can readily be regionally diagnosed, some individuals in each population show characters typical of other regions. This may possibly indicate that many seemingly isolated populations exchange genes with other populations on a limited basis. The female genitalia, however, of a specimen from the Mphaphuli population show no significant unique characters. DNA results of three specimens from different localities (Ngoye, Krantzkloof, Mphaphuli) revealed a maximum intraspecific distance of 2.49 % and an average of 1.85 % (see Fig. 1). This relatively large regional difference indicates that some

populations may have been separated for a long time, but DNA sequences from a larger sample of populations would be needed to investigate this possibility. The genetic differences correlate well with the habitus of the larvae, in that those of northern South African populations display distinct dorso-lateral lines, whereas these lines are absent in the coastal, southern populations of South Africa (see above). We have, however, not found any constant discontinuous differences in the external characters of the adults, including of the male and female genitalia. Given its wide distribution, *Z. lepida* would make a perfect subject for in-depth phenotypic and genetic studies to properly determine infraspecific variation. We therefore refrain from proposing any formal infraspecific names before such a study has been conducted.

**Genetics**

BIN: BOLD: AAH8390. The species is genetically heterogeneous, with a maximum variation of 2.7 % (*n* = 4, all from South Africa) and the single specimen from Limpopo Province with 2.2 % minimum pairwise distance from the three specimens from KwaZulu-Natal, which are genetically more similar to each other. The genetically nearest species are *Zerenopsis geometrina*, at 3.7 % distance, and *Z. moi* at 5.2 %.

**Life history and behaviour**

Donaldson & Boesenberg (1995) briefly described the life history of *Z. lepida* (as *Z. leopardina*), based on populations in the Eastern Cape Province, and included some information on behavioural aspects and larval phenology. This study is based on central and northern populations (Krantzkloof, Ngoye, Entumeni Nature Reserves, KwaZulu-Natal; Tzaneen, Limpopo; Macaneta, Mozambique).

**Ovum** (Figs 15–16): laid in randomly shaped clusters, AN = 114 (*n* = 5), usually on underside of young leaflets; eggs spaced well apart, equidistant from each other; larvae hatch after 6–12 days.

**Larvae, 1st instar** (Fig. 4): not consuming eggshell; after hatching congregating at tip of leaflet, gregarious, spinning loose web over feeding area, feeding by complete removal of green tissue within web, leaving veins and cuticle largely intact.

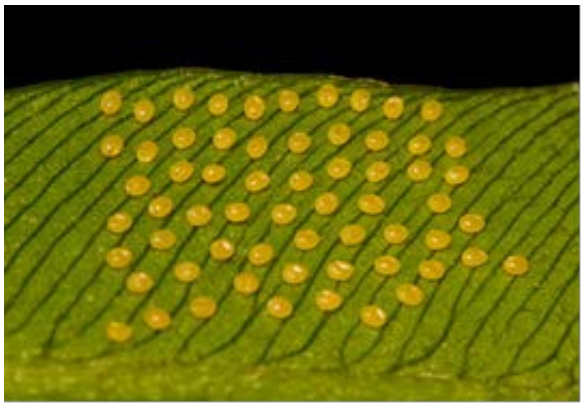

**Figure 15** – *Z. lepida* typical egg cluster, 22-iii-2012, Ngoye.

**Figure 16** – *Z. lepida* multiple egg clusters on one leaf, 24-iii-2012, Ngoye.

**Figure 17** – *Z. lepida* typical early instar larval damage on *S. eriopus*, 23-iii-2012, Ngoye.

**Larvae, 2nd instar** (Figs 5, 17): webbed feeding area no longer as dense, web progresses down to base of leaflet as green tisuse is consumed.

**Larvae, 3rd instar** (Fig. 6): no longer in web, now loosely gregarious, feeding on leaf edges; toward maturity mostly engaging in 'drop-down-and-disperse behaviour' (see below for explanation), remaining larvae no longer gregarious.

**Larvae, 4th to final instar** (Figs 7–13): usually 6 instars, sometimes 5; most feeding on secondary host-plants, often some distance away from nearest cycad; those remaining on cycad host normally feeding away from early-instar web, on edges of softer leaves or boring into stems and cones of cycad, hardened old leaves not consumed; final instar burrowing into loose soil under leaf litter, where constructing loose cocoon incorporating surrounding debris; final instar able to survive starvation for several weeks if palatable food unavailable (up to 6 weeks in laboratory); duration of larval stage under laboratory conditions (ample food available) on average 8 weeks in Spring/Summer (September–November) and 12 weeks in Autumn/Winter (April–July).

**Pupae:** rigid, not wriggling when disturbed; duration of pupal stage under laboratory conditions about 4 weeks but intermittent eclosions after up to 1 year recorded, even from same batch subjected to similar conditions.

**Figure 18** – *Z. lepida* mating pair, 15-vi-2012, Ngoye.

**Figure 19** – *Z. lepida* mating pair in captivity, 04-i-2013, reared from Macaneta.

**Imagines** (Figs 2, 18–19): diurnal, active from when it gets warmer in the morning till dusk, in sunny and cloudy, calm and windy weather if warm, but not when raining; not attracted to artificial light, visiting nectar sources.

**Drop-down-and-disperse behaviour:** In natural habitats, where ample surrounding plant cover with suitable secondary host-plants (see ecology) exists, most larvae drop from their cycad host during the third instar and disperse to feed on these secondary host-plants. This behaviour occurs *en masse*, with larvae all dropping off the cycad host within minutes and dispersing in all directions (as observed in Ngoye Forest on 22 March 2012). In transformed habitats, such as gardens, where such secondary plant cover does not exist, most larvae seem to remain on the cycad host, causing extensive damage.

**Oviposition:** primarily in morning; females flying from cycad to cycad, circling and hovering over plant and perching on leaflets, ovipositing only on some leaves, rejecting most and moving to next plant; tending to prefer very young leaves, often still unfolded; circling other plants structurally similar to host cycads but not ovipositing on these and eventually moving on; ovipositing on any young exposed cycad leaves of plants growing in a variety of habitats but avoiding ovipositing on cycads growing under closed canopy; readily laying eggs on leaves that already contain egg batches from other females (Fig. 16); males not interacting with ovipositing females. Males patrolling forest edges or flying high over cycad areas in morning when females are ovipositing.

**Figure 20** – *Z. lepida* host-plant *Stangeria eriopus* with lek tree in background, 23-iii-2012, Ngoye forest (for close-up of red circle see Fig. 21).

**Figure 21** – *Z. lepida* lek tree close-up with males fluttering and resting, 23-iii-2012, Ngoye.

**Lek behaviour** (Figs 20–21): occurring in afternoon on top of trees protruding from forest canopy not far from forest edge and near cycad colonies; freshly eclosed males flying high and straight to forest edge to find lek, where some perching males normally present; actively fluttering about, circling around chosen tree and engaging in aerial battles; actively pursuing visiting females.

**Remarks:** Latter behaviour differentiates behaviour from that of *Z. tenuis* and *Z. moi*. Actual mating behaviour immediately prior to copulation not observed. Mating pairs leave lek, female flying with hanging male to near cycads, remaining in copulation for some time (Fig. 18). Unaided copulation took place in captivity in closed containers by reared specimens (Fig. 19).

**Phenology** (Fig. 22)

The species is multivoltine and appears to breed continually throughout the year. Adults as well as ova and all larval stages can be found at all times of the year, but abundance varies. Records indicate two peak flight periods (Fig. 22), one in mid-summer and the other in autumn. Adults appear not to fly in winter in frost-prone colder areas of the Eastern Cape (E.L. Pringle pers. comm.), but they do occur in winter in northern KwaZulu-Natal.

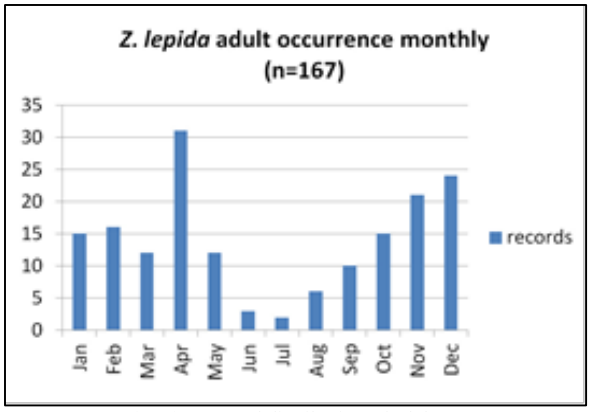


**Figure 22** – *Z. lepida* seasonal distribution of adults.

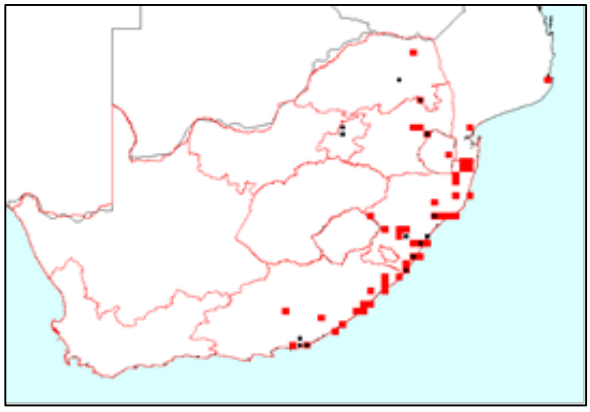

**Figure 23** – *Z. lepida* distribution map, red = records in natural habitats (QDGSs), black = records in transformed habitats (reduced from QDGS).

**Host-plants**

Donaldson & Boesenberg (1995) listed as primary host-plants 22 species of *Encephalartos* (Zamiaceae) belonging to various clades, three of *Cycas* (Cycadaceae) and *Stangeria eriopus* (Stangeriaceae). Here many additional species of these genera as well as the genus *Dioon* (Zamiaceae) are reported as primary host-plants in transformed habitats (Pretoria, Tzaneen, Durban, Pietermaritzburg) and *Encephalartos ferox* (Macaneta) and *E. hirsutus* (Limpopo Province) in natural habitats. As secondary host-plants Donaldson & Boesenberg (1995) listed *Carissa bispinosa*, *C. macrocarpa* (Apocynaceae), *Diospyros lycioides* (Ebenaceae), *Apodytes dimidiata* (unplaced in family) and *Maesa alnifolia* (Myrsinaceae). Later-instar larvae reported in this study were most frequently found on *Maesa lanceolata* and sporadically on flowers of various herbaceous plants in grassland and on *Diospyros whyteana* and *Carissa bispinosa* in forest (Ngoye, Entumeni, Hluhluwe-Umfolozi and Krantzkloof Nature Reserves). In the East London area later-instar larvae are most often found on cultivated *Sclerocarya birrea* (Anacardiaceae) (Q. Grobler pers. comm.). In captivity later-instar larvae eagerly accept *D. lycioides*.

**Habitat and distribution** (Fig. 23)

In the eastern parts of southern Africa, *Z. lepida* seems to be ubiquitous where cycads grow in sufficient numbers in frost-free, moist, natural and transformed habitats, below ~1000 m a.s.l. It appears to be absent from most drier habitats or cold habitats above ~1500 m a.s.l. even where cycads occur naturally. Repeated visits to such areas failed to reveal any evidence of the species' presence (Injasuthi; Monks Cowl; Queenstown–Stutterheim; Middelburg, Mpumalanga; Waterberg, Modjadji Cycad Reserve, Limpopo). Understanding the factors limiting the fundamental niche of this species is important given its well known pest status in horticulture (Giddy 1984, Goode 1989, Jones 1993, Fanfoni 2009). A comparison of the habitats at the recorded locations for *Z. lepida* with the habitats where cycads occur but where *Z. lepida* seems absent, using climatic data in Mucina & Rutherford (2006), suggests that *Z. lepida* is sensitive to severe winter frosts and dry conditions, limiting its fundamental niche. Sporadic outbreaks of *Z. lepida* in gardens in the Pretoria area have been reported (Waterkloof, October 1988, S.P. Norman; Pretoria North, 1994, H. Coetzee; Montana, 2012, Leonard), but as several years passed between outbreaks without any evidence of its occurrence in the interim, it appears that the species cannot survive the dry, cold winters of the Highveld (see also under range expansion below). However, it occurs naturally on the farm Huntley Glen near Bedford, Eastern Cape, a relatively dry area with heavy frosts (E.L. Pringle pers. comm.). This apparent exception may be due to suitable micro-habitats occurring in this area or may be due to intraspecific variation of the species, some southern populations being more tolerant of cold/dry conditions.

Giddy (1984) speculated that *Z. lepida* was historically restricted to the coastal Eastern Cape and KZN provinces and that the very recent anthropogenic translocation of cycads has resulted in the expansion of its range into other regions. Donaldson & Boesenberg (1995) found that all locality records from outside these two provinces available to them dated to after 1975 and thus came to the same conclusion as Giddy (1984). The phenotypic and genetic evidence presented here, however, suggests that at least the Mphaphuli population represents a part of the natural distribution range of the species. In Fig. 23 the records from natural and transformed habitats are differentiated. We found no evidence that any wild cycad population previously free from *Z. lepida* has recently been colonised by it. However, several colonisations have been recorded into transformed habitats, such as gardens and parks in which cycads have been extensively planted. Such gardens and parks in areas where *Z. lepida* occurs naturally nearby (e.g., Durban, East London, Grahamstown) are regularly utilised by *Z. lepida*, probably colonised from surrounding wild cycad populations. Records from gardens and parks in areas where no wild *Z. lepida* colonies occur nearby (e.g., Pretoria, Hoedspruit) are most probably due to anthropogenic translocation of cycads, which inadvertently introduced *Z. lepida*, as it seems unlikely that these areas were colonised from wild *Z. lepida* populations hundreds of kilometres away. A special case is the Tzaneen area, where *Z. lepida* is well established in gardens and at a cycad nursery. The Tzaneen larvae appear to be very similar to those of the population at Mphaphuli (see Figs 12–13). No evidence, however, of *Z. lepida* was found at the large well known cycad colony at Modjadji nearby. The Modjadji cycads, situated between Tzaneen and

Mphaphuli, grow in a very dry area, whereas the Tzaneen area is more humid and gardens are irrigated, probably creating a suitable habitat for *Z. lepida* to flourish (see Staude 2008).

**Figure 24** – *Charops* sp. (Ichneumonidae) reared from *Z. lepida* larva, Ngoye (photo M. Sommerer)

**Predators and parasitoids** (Fig. 24)

No larval mortality from pathogens was recorded during any rearing experiments. Parasitoids reared from wild-captured larvae appear to be less frequent than is usual for Geometridae. A single fly of the family Tachinidae was reared from a late-instar larva (captured on flowers at Krantzkloof in 1998). Sommerer (2014) however, found more than 50 % of 15 larvae (collected on *S. eriopus*, Ngoye, 2013) parasitised by one of two parasitoids, *Charops* sp. (Ichneumonidae: Campopleginae) and *Drino* sp. (Tachinidae). These larvae were collected at a time when most larvae in the brood had probably already pupated. It is the author's experience that larvae remaining on the host-plants after most others have pupated are generally parasitised, indicating that parasitoids may slow down the growth rate of larvae. No parasitoids were reared from wild-collected eggs or early-instar larvae reared to adults ($n$ > 142) from various localities (see materials and methods). No incident of any predator interaction with *Z. lepida* has been recorded.

**Defence strategies**

Adults and larvae display conspicuous orange and black aposematic signals (see Staude & Curle 1997). Larvae are obligatory feeders for the first three instars on cycad tissue containing the toxic MAM glycoside macrozamin (found in the tissue of all cycads) (Donaldson & Boesenberg 1995). These toxins were found to be sequestered by *Z. lepida* larvae under laboratory conditions and persisted into the adult stage even after later-instar larvae were switched to secondary host-plants not containing the toxins (J. Donaldson pers. comm.). This suggests that larvae as well as adults are protected by these sequestered toxins. The leisurely diurnal flight of the adults and the conspicuous larvae suggest that the aposematic coloration of *Z. lepida* serves as its primary defence strategy against predators. Apart from other Diptychini, a number of other species of Lepidoptera displaying similar aposematic signals and flight patterns were recorded to fly together with *Z. lepida*: *Pardopsis punctatissima*, *Telchinia rahira*, *Telchinia serena* (Nymphalidae: Heliconiinae); *Argina amanda* (Erebidae: Arctiinae); *Euproctis punctifera* (Erebidae: Lymantriinae); *Praezygaena myodes* (Zygaenidae).

**Conservation**

*Zerenopsis lepida* is a widespread species, common in its habitat and regarded as a horticultural pest. It therefore might seem to be of least conservation concern. This, however, is not the case. The unique genetic diversity of the various isolated wild populations (see under intraspecific variation above), which has as yet not been properly investigated, needs to be preserved and kept free of genetic contamination. The ongoing, large-scale removal of cycads from the wild, puts these isolated populations at risk of extinction. The *Z. lepida* population that existed with *Encephalartos hirsutus* (X. de Kock pers. comm.) has probably become extinct after the last specimens of this cycad species were removed from the wild. During a recent visit to the Mphaphuli Cycad Reserve no cycads or specimens of *Z. lepida* were seen (A. Coetzer pers. comm.). The ongoing illegal translocation of cycads all over South Africa inadvertently also translocates *Z. lepida*, putting isolated wild populations at risk of genetic contamination.

**2. *Zerenopsis geometrina* (C. & R. Felder, 1874) comb. n.**

*geometrina* C. & R. Felder, 1874, in Felder et al. (eds.) Reise öst. Fregatte Novara (Zool.) 2 (Abt. 2): Erklärung p. 4, pl. 100, fig. 20, (*Diptychis*). (Holo)type male (BMNH), [South Africa:] Natal. [*Diptychis geometrina* C. & R. Felder, 1874 is transferred from *Diptychis* C. & R. Felder, 1874 to *Zerenopsis* C. & R. Felder, 1874 (comb. nov.)].

**Material examined**

**Types.** *Diptychis geometrina* C. & R. Felder, 1874 holotype, male: [South Africa:] Natal (BMNH) (examined externally).

**Dissected specimens.** Male genitalia: Prep. number 1754./ Pasi Sihvonen, wings, male: Prep. number 1803./ Pasi Sihvonen, both from same specimen: S32.13, E28.52/ 300 m/ 5.5 km west of/ Mbashee River/ Mouth, E. Cape./ 3.i.1999./ A.I. Curle; South Africa/ The Haven/ West of Mbashee River/ S32.13, E28.52/ 03.01.1999 300m/ A.I. Curle/ HSS_d000.db 4112; GEOMETRIDAE/ DIPTYCHINAE/ Diptychis/ geometrina/ H.S. Staude 01-02-2005/ HSS_d000.db 4112; m/ DNA sample/ No. 127/ Pasi Sihvonen (HSS). Female genitalia: Prep. number 1755./ Pasi Sihvonen, S32.13, E28.52/ 300 m/ 8.0 km west of/ Mbashee River/ Mouth, E. Cape./ 29.xii.1998./ A.I. Curle.; South Africa/ The Haven/ West of Mbashee River/ S32.13, E28.52/ 29.xii.1998 300m/ A.I. Curle/ HSS_d000.db 4113; GEOMETRIDAE/ DIPTYCHINAE/ Diptychis/ geometrina/ H.S. Staude 01-02-2005/ HSS_d000.db 4113; f/ DNA sample/ No. 128/ Pasi Sihvonen (HSS). Female genitalia: Prep. number 1801./ Pasi Sihvonen = BMNH GEO 24787 [SOUTH AFRICA] Natal./ 1900-26.; Durban/ July 1900/ G.F. Leigh (coll. BMNH).

**Other specimens. BMNH:** S28.8, E31.880, 1911-05-16, Empangeni, [KwaZulu-Natal, South Africa]; S33.5167, E26.767, 1917-08-16, Grahamstown, [Eastern Cape, South Africa]; S29.88, E31.03, 1912-07-30, Bluff, Durban, [KwaZulu-Natal, South Africa]; S29.88, E31.03, 1911-08-01, Bluff, Durban, [KwaZulu-Natal, South Africa]; S29.85, E30.98, 1899-08-01, Durban, [KwaZulu-Natal, South Africa];

S30.8167, E30.233, 1909-06-05, Pondoland, [KwaZulu-Natal, South Africa]; S30.2, E30.783, 1917-08-16, Umkomaas, [KwaZulu-Natal, South Africa]; S29.883, E31.033, 1912-06-30, Bluff, Durban, [KwaZulu-Natal, South Africa]; S29.883, E31.033, 1912-07-14, Bluff, Durban, [KwaZulu-Natal, South Africa]; S29.883, E31.033, 1901-05-15, Bluff, Durban, [KwaZulu-Natal, South Africa]; S29.883, E31.033, 1900-07-15, Bluff, Durban, [KwaZulu-Natal, South Africa]; S30.2, E30.75, 1897-09-07, Umkomaas Mts, Umkomaas, [KwaZulu-Natal, South Africa]; S29.883, E31.033, 1912-06-15, Bluff, Durban, [KwaZulu-Natal, South Africa]. **TMSA:** S29.867, E31, 1900-08-09, Durban, [KwaZulu-Natal, South Africa]; S31.617, E29.533, 1953-07-27, Port St. John's, [Eastern Cape, South Africa]; S32.23, E28.88, 1982-01-24, Transkei, The Haven, [Eastern Cape, South Africa]; S32.23, E28.88, 1981-12-26, Transkei, The Haven, [Eastern Cape, South Africa]; S32.23, E28.88, 1982-09-18, Transkei, The Haven, [Eastern Cape, South Africa]; S32.23, E28.88, 1986-06-06, 10m, Transkei, The Haven, [Eastern Cape, South Africa], S32.23, E28.88, 1982-07-16, Transkei, The Haven, [Eastern Cape, South Africa]; S32.23, E28.88, 1982-08-10, Transkei, The Haven, [Eastern Cape, South Africa]; S32.23, E28.88, 1981-12-25, Transkei, The Haven, [Eastern Cape, South Africa]; S31.67, E29.033, 600m, 1908-08-24, Transkei, Ngqeleni, [Eastern Cape, South Africa]; S31.667, E29.033, 600m, 1908-08-08, Transkei, Ngqeleni, [Eastern Cape, South Africa]; S31.67, E29.03, 600m, 1907-09-30, Transkei, Ngqeleni, [Eastern Cape, South Africa]; S31.67, E29.033, 600m, 1907-10-06, Transkei, Ngqeleni, [Eastern Cape, South Africa]; S29.967, E30.933, 1900-08-09, Reunion, Durban, [KwaZulu-Natal, South Africa]; S29.867, E31, 1902-12-08, Durban, [KwaZulu-Natal, South Africa]; S29.867, E31, 1902-12-10, Durban, [KwaZulu-Natal, South Africa]; S30.28, E30.75, 1911-01-29, Scottburgh, [KwaZulu-Natal, South Africa]; S29.86, E31, 1956-09-03, Shongweni Dam, [KwaZulu-Natal, South Africa]; S25.67, E31.067, Noordkaap, [Mpumalanga, South Africa]. **HSS:** S32.217, E28.87, 300m, 1999-01-02, West of Mbashee River Mouth, The Haven, Eastern Cape, South Africa, A.I. Curle; S32.217, E28.87, 300m, 1999-01-03, West of Mbashee River Mouth, The Haven, Eastern Cape, South Africa, A.I. Curle; S30.38, E30.677, 100m, 2013-10-03, Umdoni Park, Pennington, KwaZulu-Natal, South Africa, J. Goossens; S32.236, E28.89, 1981-12-26, The Haven, Eastern Cape, South Africa, N.J. Duke; S29.86, E30.733, 2005-08-13, Delville Wood, Shongweni, KwaZulu-Natal, South Africa, S.E. Woodhall; S32.23, E28.87, 300m, 1998-12-29, West of Mbashee River Mouth, The Haven, Eastern Cape, South Africa, C. Ficq; S33, E27.75, 1997-12-09, Buffalo Pass, East London, Eastern Cape, South Africa, N.J. Duke; S30.28, E30.73, 1912-08-16, Scottburg, [KwaZulu-Natal, South Africa]; S33, E27.75, 1997-08-09, Buffalo Pass, East London, Eastern Cape, South Africa, N.J. Duke. **CTC:** S32.23, E28.89, 2004-12-27, Bashee River Mouth, Butterworth, Eastern Cape, South Africa, A.I. Curle; S32.23, E28.89, 1998-12-28, Bashee River Mouth, Butterworth, Eastern Cape, South Africa, C. Ficq.

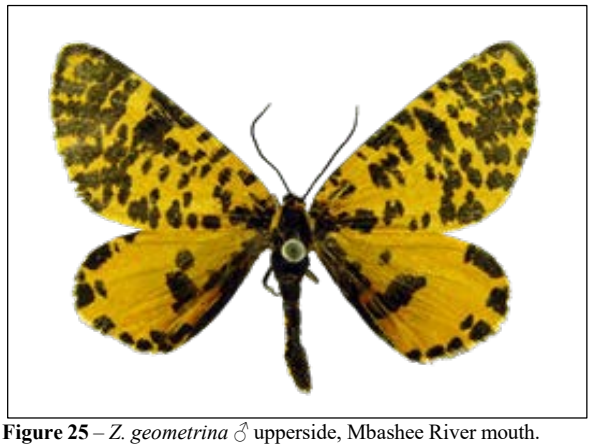

**Figure 25** – *Z. geometrina* ♂ upperside, Mbashee River mouth.

**Redescription** (Pl. 1a; Figs 25–26) (diagnostic characters underlined)

Sexes similar, wingspan ♂ 29–35 mm (AM = 32 mm, *n* = 8); ♀ 32–38 mm (AM = 35 mm, *n* = 9). Wings orange to pale yellow, decorated with blackish, elongated maculae. Number and extent of maculae variable between specimens, sometimes few and small, more often many small maculae partly fused; female often less decorated with blackish maculae. Fringes chequered pale yellow and blackish, sometimes

**Figure 26** – *Z. geometrina* ♀ upperside, Mbashee River mouth.

blackish if maculae prominent. Hind wings less decorated, maculae fewer and smaller, often prominent macula near end of cell; anal margin in male (Pl. 2a, 3b) on underside extended and folded over to form an elongated narrow pocket lined with silvery-white rounded thickened scales (possibly androconia) on both sides, with long silvery or black setae at base, small, grey, scaleless ribbed area at base of folded area. Wing underside similar to upperside except markings fainter. Frons and collar blackish or pale yellow-blackish, tegulae pale yellow, mixed with blackish. Antennae black, filiform in both sexes. Thorax orange. Hind tibiae in male swollen, with blackish hair pencil, bearing 2 + 2 minute spurs; in female with 2 + 2 minute spurs. Abdomen banded pale yellow-black. Tympanal organs large, meeting ventrally. Ansa broadened at both ends, with elongated projection at centre. Sternites and tergites 3–7 of both sexes undifferentiated. 8th tergite in male slightly triangular, posterior margin narrower. Male genitalia (Pl. 4a): uncus prominent, sclerotised, evenly tapering, weakly setose, apex acute; socii small, setose; gnathos arms narrow, fused ventromedially; tegumen large, anterior margin and

middorsal line sclerotised; juxta arms (labides) forked, long, curved, narrow, apex acute. Juxta small plate; valves wide, ventromedially weakly setose, margins mostly bare, ventral margin nearly straight, apex wide, extension of costa narrow, acute; saccus narrow, weakly sclerotised ring; aedeagus wide and short, rather straight, apex projected, caecum short, vesica straight, expanded, with small medial diverticulum, with several minute cornuti. Female genitalia (Pl. 6a): papillae anales large, membranous, densely setose; base of setae elongate, forming uneven, peg-shaped structure; apophyses posteriores long, narrow; apophyses anteriores short, stout, blunt-ending, about 1/2 length of apophyses posteriors; lamella postvaginalis a round, sclerotised plate; lamella antevaginalis a prominent, wide plate, ventromedial margin deeply invaginated; ductus bursae very short, membranous; posterior part of corpus bursae long, not expanded, sclerotised, striate and spinose, corpus bursae a large, elongated, membranous sac; signum large, shortly stellate.

**Immature stages**

**Final instar larva** (Fig. 27). Head black, distinct cream macula above mandibles; dorsal and lateral tufts of long white setae present, many longer than body diameter. Body not deeply segmented, ground colour white, four prominent black lines along length of body, yellow blotches around spiracle and dorsally on each segment. Well developed yellow and black prolegs on A6 and A10 only.

**Figure 27** – *Z. geometrina* final instar larva, 18-x-1996, Krantzkloof.

**Similar species**

*Zerenopsis geometrina* is most similar to *Z. meraca* but differs in the wings being shorter and broader, pale yellow to orange and normally more maculate (elongate and narrower, orange and less maculate in *Z. meraca*), the juxta arms (labides) long and the vesica with a small medial diverticulum and cornuti (juxta arms shorter, medial diverticulum and cornuti absent in *Z. meraca*), the lamella antevaginalis large, medially invaginated and ductus bursae not expanded (lamella antevaginalis small, weakly invaginated and ductus bursae expanded in *Z. meraca*).

**Genetics**

BIN: BOLD: AAX8777 (one specimen from South Africa examined). The genetically nearest species are *Z. lepida*, at 3.7 % distance, and *Z. moi*, at 4.0 %.

**Life history and behaviour**

The late Neville J. Duke (in Goode 1989; pers. comm.) observed an ovipositing female and found early-instar larvae only on *Stangeria eriopus* at The Haven but never succeeded in rearing larvae to adulthood. A final-instar larva was found by the first author on leaves of *Encephalartos villosus* growing in the shade (Fig. 28) at Krantzkloof Nature Reserve and reared to the adult stage on *E. villosus* and *Diospyros lycioides* (Ebenaceae)(rearing experiment 961016/1HSS). Males have been observed to fly high along forest edges and females low around *S. eriopus* plants, but no lek behaviour noted so far (A.I. Curle & S.E. Woodhall pers. comm.).

**Figure 28** – *Z. geometrina* host-plant *Encephalartos villosus,* 16-x-1996, Krantzkloof.

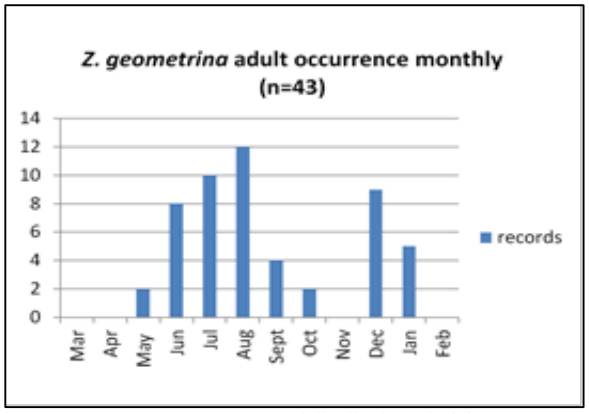


**Figure 29** – *Z. geometrina* seasonal distribution of adults.

**Phenology** (Fig. 29)

*Zerenopsis geometrina* appears to be bivoltine, with an extended winter and a short summer flight period, adult abundance peaking in December–January and July–August. The winter brood may occur from May to October, but this extended period is probably as a result of climatic fluctuations over the years (available data span more than one century). The longest recorded winter-brood flight period in one season is eight weeks (16 July–18 September 1982, at The Haven). The summer brood appears to be very short (only a few days recorded in any one season), with abundance much higher than in the winter brood (recorded data and N.J. Duke pers. comm.).

**Host-plants** (Fig. 28)

The early-instar larvae are gregarious on the cycad *Stangeria eriopus* (Stangeriaceae) (N.J. Duke in Goode 1989), and later-instar larvae have been found singly on *Encephalartos villosus* and on surrounding trees such as *Apodytes dimidiata* and *Mimusops obovata* (Duke & Duke 1998, Kroon 1999).

**Figure 30** – *Z. geometrina* distribution map (QDGSs).

**Habitat and distribution** (Fig. 30)
The species occurs along forest margins in and near coastal areas where the host-plant, *Stangeria eriopus,* grows, in the Eastern Cape and KwaZulu-Natal provinces of South Africa. There is one doubtful record from Noordkaap in the Mpumalanga province.

**Conservation**
*Zerenopsis geometrina* must be treated as Vulnerable (VU), as very few suitable habitats remain and these are threatened by indiscriminate removal of the primary host-plant, *Stangeria eriopus*, for the muti (medicine) trade and, in coastal areas, by housing development.

### 3. *Zerenopsis meraca* (Prout, 1928) **comb. n.**

*meraca* Prout, 1928, Bull. Soc. Lépidoptéres de Genéve 6 (1): 19, pl. 1, fig. 11, (*Diptychis*). Holotype female (MHNG), Mozambique méridional [south], 27 VIII 1902. [*Diptychis meraca* Prout, 1928 is transferred from *Diptychis* C. & R. Felder, 1874 to *Zerenopsis* C. & R. Felder, 1874 (comb. nov.)].

**Material examined**
**Types.** *Diptychis meraca* Prout, 1928 holotype, female: Mozambique méridional [south], 27 VIII 1902 (MHNG) (also genitalia examined [no slide number], illustrated in Plate 6b).
**Dissected specimens.** Male genitalia: Prep. number 1765./ Pasi Sihvonen, South Africa Natal Maputaland/ Mangusi forest reserve, 27°S, 32°43'E, 50m, December 1993/ N.K. Owen Johnston; South Africa/ Manguzi/ Mangusi/ 27.00.000S 32.43.000E / 18.xii.1993 50m/ Owen Johnston/ HSS_d000.db 4115; GEOMETRIDAE/ DIPTYCHINAE/ Diptychis/ meraca/ H S Staude, 01-02-2005/ HSS_d000.DB 4115; DNA sample/ No. 138/ Pasi Sihvonen (HSS). Female genitalia: Prep. number 1913./ Pasi Sihvonen, 27.02.518S 32.23.017E/ 87 M/ Tembe Elephant Park/ KwaZulu-Natal, RSA [Republic of South Africa]/ 28.iii.[20]01, N.K. Owen-Johnston/ Curle Collection (CCSA) (coll. CTC).
**Other specimens. HSS:** S26.98, E32.729, 80m, 1993-12-18, Manguzi Forest, Manguzi, KwaZulu-Natal, South Africa, N.K. Owen-Johnston. **CTC:** S27.035, E32.379, 86m, 2001-03-28, Tembe Elephant Park, Manguzi, KwaZulu-Natal, South Africa, N.K. Owen-Johnston. **TMSA:** S26.05, E32.55, 1938-12-10, Maputo, Mozambique, A.C. Daintree; S26.509, E31.957, 350m, 1994-03-13, Jilobi Forest, Siteki, Swaziland, N.J. Duke; S26.21, E32.005, 250m, 1997-12-02, Mlawula Nature Reserve, Simunye, Swaziland, N.J. Duke.

**Redescription** (Pl. 1b) (diagnostic characters underlined)
Wingspan 34–39 mm (*n* = 5). Wings elongate, orange, sparsely decorated with blackish, elongate maculae. Number and extent of maculae variable between specimens, normally few and small, occasionally maculae larger and partly fused. Fringes chequered orange and blackish, sometimes blackish if maculae prominent. Hind wings less decorated, maculae fewer and smaller; anal margin in male (Pl. 2c) on underside with long silvery setae at base, extended and folded over to form an elongated narrow greyish spoon-like pocket. Female less decorated with blackish maculae, hind wings without black except small discal spot (*n* = 2). Wing underside similar to upperside except markings fainter. Frons and collar blackish or orange-blackish, tegulae orange, mixed with blackish.
Antennae black, ventral setae white, filiform in both sexes. Thorax black. Hind tibiae in male swollen, with greyish hair-pencil, bearing 2 + 2 minute spurs, in female only with 2 + 2 minute spurs. Abdomen banded orange-black. Tympanal organs large, meeting ventrally. Ansa broadened at both ends, with elongated projection at centre. Sternites and tergites 3–7 of both sexes undifferentiated. 8th tergite in male slightly triangular, posterior margin narrower. Male genitalia (Pl. 4b): uncus prominent, sclerotised, evenly tapering, weakly setose, apex acute; socii small, setose; gnathos arms narrow, fused ventromedially; tegumen large, anterior margin and middorsal line sclerotised; juxta arms (labides) forked, short, curved, narrow, apex acute; juxta a rather large plate; valves wide, ventromedially weakly setose, margins mostly bare, ventral margin nearly straight, apex wide, extension of costa narrow, acute; saccus a narrow, weakly sclerotised ring; aedeagus wide and short, rather straight, apex projected, caecum short; vesica straight, expanded, without medial diverticulum, without cornuti. Female genitalia (Pl. 6b): papillae anales large, membranous, densely setose, base of setae elongate, forming uneven, peg-shaped structure; apophyses posteriores long, narrow; apophyses anteriores short, stout, blunt-ending, about 1/2 length of apophyses posteriores; lamella postvaginalis a round, sclerotised plate; lamella antevaginalis a narrow plate, ventromedial margin weakly invaginated; ductus bursae long, membranous, posterior part long, expanded, sclerotised, striate and spinose; corpus bursae a large, elongate, membranous sac; signum large, shortly stellate.

**Immature stages**
Unknown.

**Similar species**
*Zerenopsis meraca* is most similar *to Z. geometrina*, see there.

**Genetics**
No data available.

**Life history and behaviour**
Males were observed flying high along forest edges, and a female was found in the undergrowth (N.K. Owen-Johnston pers.comm.).

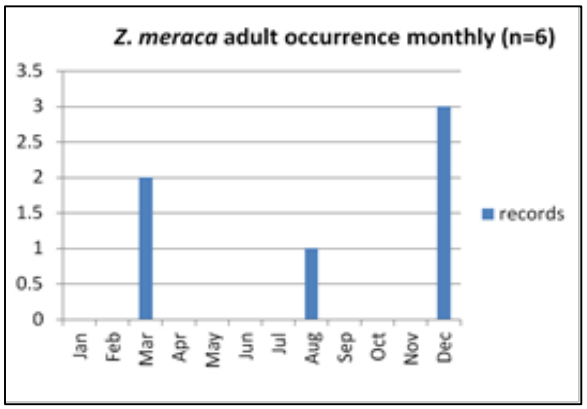


**Figure 31** – *Z. meraca* seasonal distribution of adults.

**Phenology** (Fig. 31)
The scant available data ($n$ = 6) suggest that the species is trivoltine, the adults flying in March, August and December.

**Figure 32** – *Z. meraca* distribution map (QDGSs).

**Habitat and distribution** (Fig. 32)
The species occurs in lowland forest habitats in Maputaland (northern KwaZulu-Natal, South Africa and southern Mozambique), adjacent areas in Swaziland.

**Host-plants**
The host-plants of *Z. meraca* are unknown. The cycad *Stangeria eriopus* occurs in the undergrowth of Maputaland forests from where it has been recorded, but no larvae have been found so far. This cycad species is most probably its primary host-plant.

**Conservation**
Data-deficient (DD).

**4. *Zerenopsis moi*** Staude & Sihvonen **spec. n.**
urn: lsid: zoobank.org: act: 131157DB-EC8C-469F-BE0C-282757CAF20C

**Material examined**
**Types.** Holotype, male: Mozambique, Marraquene,/ Jay's lodge, S25.43, E32.44,/ 30m, coastal dune scrub,/ 16-09-2000, H.S. Staude; Mozambique/ Marraquene/ Jay's Lodge/ 32.44.000E 25.43.000S/ 16.ix.2000 30 m/ H.S. Staude/ HSS_d000.db 4110; GEOMETRIDAE/ DIPTYCHINAE/ Paraptychodes/ moi/ H.S. Staude 01-02-2005/ HSS_d000.db 4110; DNA sample m/ No. 130/ Pasi Sihvonen; Male genitalia dissected: Prep. number 1702./ Pasi Sihvonen [blue rectangle label] HOLOTYPE/ *Zerenopsis/ moi*/ Staude & Sihvonen [red rectangle label] (TMSA).
Paratypes (57♂, 55♀): **TMSA:** 3♂, 3♀,; Mozambique, Marracuene,/ Macaneta, coastal dune/ scrub,/ 25°44'59,5"S/ 32°44'15,7"E,/ 30m, 11-21/12/2012 /emerged./ H.S. Staude; *ab ovo* (leg. P.R. Ward,/ 29-09-12) on/ *Encephalartos ferox*/ (Zamiaceae)/ Rearing Nos./12HSS16–12HSS18; GEOMETRIDAE/ DIPTYCHINAE/ *Zerenopsis moi*/ H.S. Staude / 14-05-2013/ HSS_D000.DB 19934; **HSS:** 1♀, same data as holotype except: Female genitalia dissected: Prep. number 1703./ Pasi Sihvonen [blue rectangle label; 3♂, 5♀, same data except no Prep. Number label; 6♂, 10♀,; Mozambique, Marracuene,/ Macaneta, coastal dune/ scrub,/ 25°44'59,5"S/ 32°44'15,7"E,/ 30m, 11-21/12/2012 /emerged./ H.S. Staude; *ab ovo* (leg. P.R.F. Ward,/ 29-09-12) on/ *Encephalartos ferox*/ (Zamiaceae)/ Rearing Nos./12HSS16–12HSS18; GEOMETRIDAE/ DIPTYCHINAE/ *Zerenopsis moi*/ H. S. Staude / 14-05-2013/ HSS_D000.DB 19934; 1♂, 3♀,; Moçambique/ TH Macaneta/ S 25°44.991'/ E 32°44.261'/ 29-Sep-2012/ P.R.F. Ward; GEOMETRIDAE/ DIPTYCHINAE/ *Zerenopsis moi*/ H.S. Staude / 14-05-2013/ HSS_D000.DB 19045; 3♂, 2♀,; Mozambique/ Marracuene/ 50km N. of Maputo/ 23–26 August 2001/ leg. A. Brinkman; Jays Beach Lodge/ 25.42.35S/ 32.45.19E; GEOMETRIDAE/ DIPTYCHINAE/ *Paraptychodes moi*/ H.S. Staude / 02-02-2008/ HSS_D000.DB 12049. **JB:** 1♂, 1♀,; Mozambique/ Marracuene/ 50km N. of Maputo/ 23–26 August 2001/ leg. A. Brinkman; Jays Beach Lodge/ 25.42.35S/ 32.45.19E; GEOMETRIDAE/ DIPTYCHINAE/ *Paraptychodes moi*/ H.S. Staude / 02-02-2008/ HSS_D000.DB 12049. **CTC:** 3♂, 4♀:; Macaneta – Mozambique/ 25.42.43S 32.45.04E/ 16\17\ix\2000/A.I. Curle; 3♂, 7♀, same data except 23.viii.2001; 12♂, 3♀, same data except 24.viii.2001; 12♂, same data except 25.viii.2001; 6♂, 13♀, same data except C.H. Ficq; 1♂, 1♀ same data except 23.xii.2001. **DMK:** 3♂, 2♀,; Macaneta – Mozambique/ 25.42.43S 32.45.04E/ 23.viii.2001/C.H. Ficq. All with yellow rectangular label reading 'PARATYPE/ *Zerenopsis/ moi*/ Staude & Sihvonen, 2014'.

**Description** (Pl. 1c; Figs 33–34) (diagnostic characters underlined)
Wingspan ♂ 34–39 mm (AM = 37 mm, $n$ = 17); ♀ 37–44 mm (AM = 40 mm, $n$ = 30). Male fore wings orange-yellow, apex and termen black, few small black dots near base; orange discal spots weakly expressed in fore wings only, lunular. Hind wings elongate, termen rather straight, apex angled; medial area narrowly orange, otherwise black; anal margin (Pls. 2 h–i, 3c; Fig. 33) on underside extremely extended, grey-silver, and folded over to cover about 2/3 of underside, making hind wing appear pointed (Fig. 33), pocket lined with white, silvery, elongate, rounded, thickened scales on both sides, elongate grey, scale-less ribbed area at base of folded area (androconial organ). Wing underside

**Figure 33** – *Z. moi* male showing folded hind wing to form 'pheromone pocket', 17-ix-2000, Macaneta.

**Figure 34** – *Z. moi* female, 17-ix-2000, Macaneta.

similar to upperside in fore wings; in hind wings basal part orange, costa black. Labial palpi short, apex black.Frons, head, collar, tegulae and thorax mixed orange and black. Hind tibiae swollen, with 2 + 2 spurs. Antennae clubbed, basal portion deeply invaginated in male. Abdomen irregularly striped orange and black. Female wings yellow. Fore-wing base with few small black dots, fore-wing apex, termen and hind-wing termen black. Hind-wing margin round. Wings below as above. Discal spots faint, orange, lunular, present in all wings. Proboscis developed. Labial palpi short, apex black. Frons, head, collar, tegula and thorax mixed yellow-orange and black. Hind tibiae not swollen, with 2 + 2 spurs. Antenna clubbed, basal portion not invaginated. Abdomen dorsally yellow-orange, ventrally irregularly striped, yellow-orange and black. Tympanal organs large in both sexes, round, well-separated. Ansa wide at base, constricted before wide apex. Abdominal segments 3–7 of both sexes sclerotised but undifferentiated. 8th tergite in male slightly triangular, posterior margin narrower. Male genitalia (Pl. 4c): uncus prominent, sclerotised, evenly tapering, weakly setose, apex acute; socii small, setose; gnathos arms narrow, fused ventromedially; tegumen large, anterior margin sclerotised; juxta arms (labides) sclerotised, long, straight, narrow, apex acute; juxta formed of two elongate, sclerotised plates; valves wide, medial area setose, margins mostly bare, ventral margin slightly concave, apex wide, extension of costa narrow, acute; saccus a narrow, weakly sclerotised ring; aedeagus long, slightly bent ventrally, caecum long; vesica a straight, expanded tube, with numerous minute cornuti. Female genitalia (Pl. 6c): papillae anales large, membranous, densely setose, base of setae elongated, forming uneven, peg-shaped structure; apophyses posteriores long, narrow; apophyses anteriores short, stout, blunt-ending, about 1/3 length of apophyses posteriores; lamella postvaginalis a round, sclerotised plate; lamella antevaginalis a prominent, wide plate, invaginated ventromedially; ductus bursae long, wide, sclerotised, posterior part elongate, sclerotised, striate and spinose; corpus bursae a large, roundish, membranous sac; signum large, stellate.

**Immature stages**

**Ovum** (Figs 35, 43). Ovoid in shape, bright yellow when laid, gradually darkening as larva develops inside, fully developed larva visible before hatching; shell translucent, surface smooth, finely sculptured with regular hexagonal dimples circularly arranged at micropyle.

**Figure 35** – *Z. moi* ova, 02-x-2012, Macaneta.

**1st instar larvae** (Figs 36, 43, 44). Full complement of well developed white primary setae, these on average longer than body diameter; body deeply segmented, large brownish black maculae around setal bases on all segments on emergence. Head black, thoracic legs black, prolegs of body colour, anal plate brown, pronotum merged with black head, well developed prolegs on A6 and A10 only.

**Figure 36** – *Z. moi* first-instar larval mass, 06-x-2012, Macaneta.

**2nd instar larvae** (Fig. 37). Like 1st instar but maculae around setal bases larger and black. Ground colour turning deeper orange during development.

**3rd instar larvae** (Fig. 38). Ground colour orange with reddish patches, brown secondary setae present, shorter

**Figure 37** – *Z. moi* second-instar larvae, 18-x-2012, Macaneta.

**Figure 38** – *Z. moi third*-instar larvae, 27-x-2012, Macaneta.

**Figure 39** – *Z. moi* fourth-instar larva, 03-xi-2012, Macaneta.

**Figure 40** – *Z. moi* fifth-instar larva, 03-xi-2012, Macaneta.

than white primary setae, the latter spiny; head dark brown.

**4th and 5th instar larvae** (Figs 39–40). Body no longer deeply segmented. Primary and secondary setae shorter than in 3rd instar, now mostly white, appearing in tufts, dorso-lateral ground colour more pronounced orange and red, yellow rings around some or all black setal bases, ventral ground colour whitish, head orange with reddish mottling.

**Figure 41** – *Z. moi* final instar larva, 16-xii-2012, Macaneta.

**Figure 42** – *Z. moi* pupa, 13-xi-2012, Macaneta.

**Final instar larvae** (Fig. 41). Like 5th instar, except for dorso-lateral ground colour almost uniformly deep red.
**Pupae** (Fig. 42). Dark brown, AM = 18 x 8 mm (*n* = 6), three pairs of cremastal hooks, splayed, merged at base of cremaster.

**Similar species**

There are no *Zerenopsis* species with a similar external appearance, but in its genitalia *Z. moi* is similar to *Z. lepida* except that its juxta arms are long and straight (slightly bent in *Z. lepida*) and the margin of its lamella antevaginalis is invaginated ventromedially (straight in *Z. lepida*). In its ova and larvae *Z. moi* is also similar to *Z. lepida*, but in the first three larval instars the elongate black patch on pronotum is merged with the head (separated by yellow ground colour in *Z. lepida*), and in the later instars the tufts of white secondary setae are longer than the primary setae and the ground colour is increasingly red.

**Genetics**

BIN: BOLD:ACG9155 (two specimens examined from Macaneta, both genetically identical). The genetically nearest species are Z. *geometrina*, at 4.0 % distance, and *Z. lepida*, at 5.2 %.

**Figure 43** – *Z. moi* larva emerging from egg, 06-x-2012, Macaneta.

**Figure 44** – *Z. moi* first-instar larvae blackening leaf tissue before consuming, 03-x-2012, Macaneta.

**Life history and behaviour**

**Ovum** (Fig. 43): laid in randomly shaped clusters on underside of young leaflet at base of leaf; eggs well apart, not touching each other; larvae hatch after 9 days.

**Larvae, 1st instar** (Figs 43–44): not consuming eggshell, after hatching congregating at base of leaf in a swirling mass, blackening leaf tissue before consuming it, not spinning web over feeding mass.

**Larvae, 2nd instar** (Fig. 37): gregarious, not blackening leaf tissue in a dense mass, feeding on one side of leaflet only, consuming leaflets at base of leaf first, working their way up.

**Larvae, 3rd instar** (Fig. 38): most moving to leaves of *Diospyros lycioides* provided in sleeve with cycad leaf, others not gregarious, feeding on leaf edges.

**Larvae, 4th–6 th instar** (Figs 39–41): most feeding on secondary host-plants as provided, some boring into main leaf stem of cycad host, hardened old cycad leaves not consumed; on maturity burrowing into loose sand provided, there constructing loose cocoon incorporating surrounding debris.

**Duration of larval stage**: under laboratory conditions (ample food available) 7 weeks in October–November.

**Pupae** (Fig. 42): rigid, not wriggling when disturbed; eclosing after 4–5 weeks (laboratory conditions).

**Imagines** (Figs 33–34): diurnal, not attracted to artificial light; active during good weather from morning until dusk, not flying during colder wet weather; females visiting nectar sources.

**Oviposition:** not recorded; egg batches found only on leaflets near base of leaf. Females were found primarily in valley areas between dunes where the host-plant *Encephalartos ferox* is most abundant, where males were not seen.

**Lek behaviour:** occurring from midday until afternoon; males not forming lek over particular tree but congregating on a high dune away from cycads, flying along the top; females visiting this 'dune lek' on occasion; but behaviour immediately prior to mating was not observed.

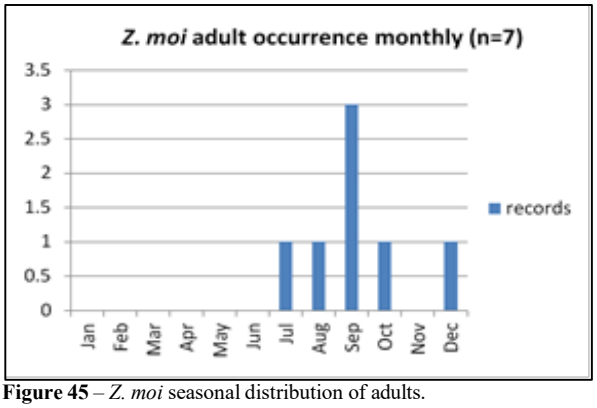


**Figure 45** – *Z. moi* seasonal distribution of adults.

**Phenology** (Fig. 45)

Adults as well as larvae were found at one locality during July, August, September, October and December, suggesting that the species is continually brooded with no specific flight period.

**Figure 46** – *Z. moi* host-plant *Encephalartos ferox* in the wild with typical feeding damage at base of leaves, 16-ix-2012, Macaneta.

**Host-plants** (Fig. 46)

Ova and larvae were found in the wild on *Encephalartos ferox*, a cycad that grows abundantly at the type locality. No later-instar larvae were found on other plants in the wild, but in captivity larvae from the third instar onward preferred *Diospyros lycioides* (Ebenaceae) to cycads.

**Figure 47** – *Z. moi* habitat, 18-ix-2000, Macaneta, Mozambique.

**Figure 48** – *Z. moi* distribution map (QDGSs).

**Habitat and distribution** (Figs 47, 48)
The species occurs in coastal dune thicket where its cycad host, *E. ferox*, is abundant. It is so far only known from the type locality and surroundings, where it can be very common at times. The host-plant occurs intermittently in similar dune habitat along the Mozambique coast north to the Zambezi river (P. Rousseau, pers. comm.), across a distance of over 1000 km, and thus it seems possible that more colonies of *Z. moi* will be found further north along the coast. *Encephalartos ferox* also occurs south of the type locality in Maputaland, northern KwaZulu-Natal. A visit to these stands of *E. ferox* revealed no evidence of *Z. moi*.

**Conservation**
Data-deficient (DD). Although adults can be abundant at their habitat, *Z. moi* is known only from its type locality. The recent increase in the local population in the area, in response to the increase in tourist lodges has resulted in the clearing of the surrounding thicket, which is of concern. Generally cycads are not removed and are found even within villages and lodges cleared of other bush. However, the possible effect of the destruction of suitable 'lek dunes' and of possible secondary host-plants on *Z. moi* is unknown. A search for more colonies of this species up the coast is recommended.

**Etymology**
The species is named after Moi Young, former wife of Gavin Young, who collected the first specimen on instruction by the first author who, after hearing that the Youngs were visiting the area to go fishing, had asked him to collect any orange moth he might come across in the vicinity of cycads. 'Moi' (spelled mooi) also means pretty in Afrikaans, and 'moi' is also a casual way to say hello in Finnish.

**5. *Zerenopsis kedar*** (Druce, 1896) **comb. n.**

*kedar* Druce, 1896, Ann. Mag. nat. Hist. (6) 17: 351, (*Aletis*). Holotype female (BMNH), East Africa [Tanzania]: Dar-es-Salaam. [*Aletis kedar* Druce, 1896 is transferred from *Paraptychodes* Warren, 1894 to *Zerenopsis* C. & R. Felder, 1874 (comb. nov.)].

**Material examined**
**Types.** *Aletis kedar* Druce, 1896 holotype female: East Africa [Tanzania]: Dar-es-Salaam (BMNH) (examined externally).
**Dissected specimens.** Female genitalia: Prep. number 1758./ Pasi Sihvonen, NGEZI FOREST/ N.W.PEMBA IS./ 18.5.2007/ SC ABRI Leg; Tanzania/ Pemba/ Ngezi forest/ 39°42'21.0 04°56'37.0/ 18.V.2007 0m/ SC ABRI Leg./ HSS_D000.DB 11990; GEOMETRIDAE/ DIPTYCHINAE/ Paraptychodes/ kedar/ H.S. Staude 31-01-2008/ HSS_D000.DB 11990; m/ DNA sample/ No. 133/ Pasi Sihvonen (HSS). Female genitalia: Prep. number 1759./ Pasi Sihvonen, Kenya coast, Kwale,/ 7-2000,/ S.C. Collins; Kwale 7-2000; Kenya/ Kwale/ 39.26.170E, 04.11.110S/ 15.VII.2000, 0m/ S.C. Collins / HSS_D000.db 8375; GEOMETRIDAE/ DIPTYCHINAE/ Paraptychodes/ kedar/ H.S. Staude - 01-08-2005/ Hss_d000.db 8375 (HSS).
**Other specimens. HSS:** S4.167, E39.45, 1950-04-15, Kwale, Kenya; S4.186, E39.44, 2000-07-15, Kwale, Coast, Kenya, S.C. Collins; S4.94, E39.706, 2007-05-18, Ngezi forest, Pemba, Tanzania, S.C. Collins; S4.217, E39.43, 1980-05-07, Shimba Hills, Kwale, Kenya, S.C. Collins; S4.217, E39.43, 1982-09, Shimba Hills, Kwale, Kenya, S.C. Collins.
**BMNH:** S4.05, E39.65, 1903-10-03, Wanga district, Mombasa, Kenya; S4.05, E39.65, 1937-12-15, Gazi, Mombasa, Kenya; S5.1, E38.63, 1950-05-15, Usambara Mountains, Amani, Tanzania; S5.1, E38.63, 1950-02-15, Usambara Mountains, Amani, Tanzania; S6.817, E39.3, 1963-11-22, Minaki, Dar es Salaam, Tanzania.
**CTC:** S4.24, E39.399, 2000-09-16, Shimba Hills National Park, Kenya, S.C. Collins.

**Figure 49** – *Z. kedar* female, upperside, Shimba Hills, Kenya.

**Redescription** (Pl. 1e; Fig. 49) (diagnostic characters underlined)
Only female known. Wingspan 43–44 mm ($n$ = 5). Wings usually dominated by white, blackish to grey markings often restricted to wing margins and blackish fore-wing transverse band, more extensive in one specimen examined (Pl. 1e). Fore-wing subapical spot white, enclosed by blackish area, also in costa. Occasionally a second, small white spot below the subapical one. Discal spots absent, fringes blackish. Hind wings white, with broad blackish marking along margins. Wing underside similar to upperside. Frons and collar yellow-orange, suffused with blackish. Antennae bipectinate, faintly white dorsally. Thorax blackish, mixed with white and yellow-orange. Hind tibiae with 2 + 2 spurs. Abdomen banded black and

yellow-orange. Tympanal organs large, meeting ventrally. Ansa weakly broadened at both ends, with elongated projection at centre. Sternites and tergites 3–8 undifferentiated. Female genitalia (Pl. 7a): papillae anales large, membranous, densely setose, base of setae elongate, forming uneven, peg-shaped structure; apophyses posteriores long, narrow; apophyses anteriores short, stout; lamella postvaginalis small, weakly sclerotised, concave plate; lamella antevaginalis a small sclerotised plate, weakly concave ventromedially; ductus bursae rather long, wide, membranous, posterior margin sclerotised, striate; corpus bursae a large, elongated sac; signum stellate, located ventrally, often with 11 long spikes.

**Immature stages**
Unknown.

**Similar species**
There are no species with similar external appearance.

**Genetics**
Short sequence of 384 bp available (without BIN). The genetically nearest species are *Z. tenuis*, at 2.7 % distance, and Z. *costimaculata*, at 4.6 % distance.

**Life history and behaviour**
Females have been observed flying low along forest edges (S.C. Collins, pers.comm.)

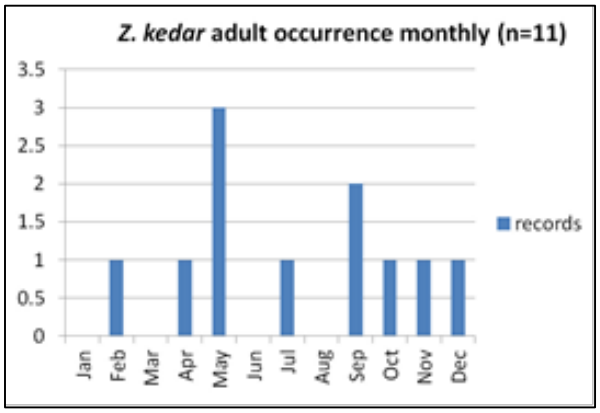


**Figure 50** – *Z. kedar* seasonal distribution of adults

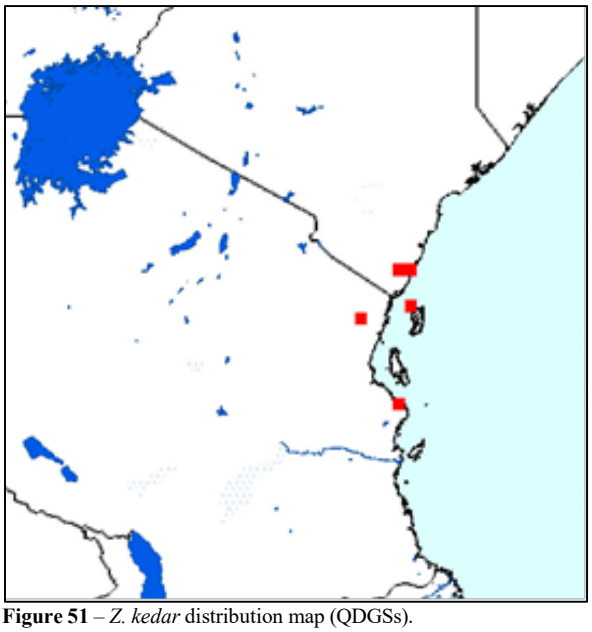

**Figure 51** – *Z. kedar* distribution map (QDGSs).

**Phenology** (Fig. 50)
The scant available data (of 11 specimens), spanning eight months, suggest that the species is continually brooded throughout the year.

**Host-plants**
Unknown.

**Habitat and distribution** (Fig. 51)
The species occurs in lowland forest habitats in southern Kenya and northern Tanzania, Pemba Island. Most records are from the Shimba Hills National Park.

**Conservation**
Data-deficient (DD). The species is only known from fewer than twenty specimens. Its occurrence in the Shimba Hills National Park affords it some protection.

### 6. *Zerenopsis tenuis* (Butler, 1878) **comb. n.**

*tenuis* Butler, 1878, Proc. zool. Soc. Lond. 1878 (2): 385, (*Aletis*). (Holo)type female (BMNH), Zanzibar [Tansania]: Dar-es-Salaam. [*Aletis tenuis* Butler, 1878 is transferred from *Paraptychodes* Warren, 1894 to *Zerenopsis* C. & R. Felder, 1874 (comb. nov.)].
*fulva* Hampson, 1891, Ann. Mag. nat. Hist. (6) 7: 183, (*Terina*). (Holo)type male (BMNH), [British] East Africa [Kenya]: Sabaki River district.
*perfulva* Prout, 1913, Novit. zool. 20: 395, (*Paraptychodes*). Holotype male (The Natural History Museum, London, UK), British East Africa [Kenya]: Witu.

**Material examined**
**Types.** *Aletis tenuis* Butler, 1878 (holo)type female: Zanzibar [Tansania]: Dar-es-Salaam (BMNH) (examined externally, abdomen in plastic tube). *Terina fulva* Hampson, 1891 (holo)type male: [British] East Africa [Kenya]: Sabaki River district (BMNH) (examined externally). *Paraptychodes perfulva* Prout, 1913 holotype male: British East Africa [Kenya]: Witu, 28.ii.1912 (S.A. Neave) (BMNH) (examined externally).
**Dissected specimens:** Female genitalia: Prep. number 1800./ Pasi Sihvonen = BMNH GEO 24786, [KENYA] Lamu,/ Br.[itish] E.[ast] A.[frica]; Rothschild/ Bequest/ B.M. 1939-1 (coll. BMNH).. Female genitalia: BMNH GEO 20606, Kurasini, nr./ Dar-es-Salaam,/ March 1907. [black margin]; Rothschild/ Bequest/ B.M. 1939-1 (coll. BMNH). Male genitalia: Prep. number 1700./ Pasi Sihvonen and wings of male: Prep. number 1804./ Pasi Sihvonen, both from the same specimen: Tanzania, Pemba Manta/ Reef Lodge,/ 04°53'26"S 39°40'47"E,/ coral rag forest,/ 03-01-2007, H.S. Staude; Tanzania/ Pemba/ Manta Reef Lodge/ 39°40'47.0 04°53'26.0/ 3.I.2007 0m/ H.S. Staude/ HSS_D000.DB 12027; GEOMETRIDAE/ DIPTYCHINAE/ Paraptychodes/ tenuis/ H.S. Staude 05-02-2008/ HSS-D000.DB 12027; DNA sample/ No. 132/ Pasi Sihvonen (HSS). Female genitalia: Prep. number 1701./ Pasi Sihvonen, Tanzania, Pemba Manta/ Reef Lodge,/ 04°53'26"S 39°40'47"E,/ coral rag forest,/ 03-01-2007, H.S. Staude; Tanzania/ Pemba/ Manta Reef Lodge/ 39°40'47.0 04°53'26.0/ 3.I.2007 0m/ H.S. Staude/ HSS_D000.DB 12027; GEOMETRIDAE/

DIPTYCHINAE/ Paraptychodes/ tenuis/ H.S. Staude 05-02-2008/ HSS_D000.DB 12027 (HSS).

**Other specimens. HSS:** S4.94, E39.70, 2007-05-18, Ngezi forest, Pemba, Tanzania, S.C. Collins; S4.24, E39.39, 2007-05-01, montane forest, Shimba Hills, Kenya, S.C. Collins. S3.33, E39.95, 50m, 2004-01-02, Arabuko Sokoke Forest Reserve, Gedi, Kenya, S.C. Collins; S3.33, E39.95, 50m, 2012-07-21, Arabuko Sokoke Forest Reserve, Gedi, Kenya, H.S. Staude; S3.36, E39.97, 1996-10-12, Gedi, Watamu, Kenya, S.C. Collins; S3.33, E39.95, 50m, 2004-01-02, Arabuko Sokoke Forest Reserve, Gedi, Kenya, S.C. Collins; S4.58, E38.35, 1998-12-03, Mkwaja, Kenya, S.C. Collins; S4.89, E39.68, 2007-01-03, Manta Reef Lodge, Pemba, Tanzania, H.S. Staude; S3.036, E40.138, 2000-08-08, Coral rag., Gongoni Coast, Kenya, S.C. Collins; S3.4, E39.88, 50m, 2005-12-29, Arabuko Sokoke Forest Reserve, Gedi, Kenya, S.C. Collins; S5.238, E39.61, 2007-01-05, Misali island, Pemba, Tanzania, H.S. Staude; S06.12, E39.31, 1990-09, Jozani forest, Zanzibar, Tanzania, S.C. Collins; 1998-04, Maloko, Kenya east coast, S.C. Collins. **BMNH:** S4.05, E39.65, 1923-01-23, Gazi, Mombasa, Kenya; S4.05, E39.65, 1922-12-15, Gazi, Mombasa, Kenya; S6.817, E39.3, 1963-11-22, Kurasini, Dar es Salaam, Tanzania; S6.82, E39.3, 1963-11-22, Dar es Salaam, Tanzania; S10.267, E40.05, 1897-05-01, Mikindani, Tanzania; S6.12, E39.25, 1885-01-01, Zanzibar, Tanzania. **CTC:** S4.24, E39.39, 2000-09-16, Shimba Hills National Park, Kenya, S.C. Collins; S3.23, 39.93, 2008-08-08;
Arabuko Sokoke National Park, Gedi, Kenya, S.C. Collins; S3.36, E39.97, 1997-10-19, Arabuko Sokoke National Park, Gedi, Kenya, S.C. Collins; S3.363, E39.97, 2005-12-30, Arabuko Sokoke National Park, Gedi, Kenya, S.C. Collins; S6.11, E39.3, 2000-07-14, Zanzibar, Tanzania, S.C. Collins.

**Redescription** (Pl. 1f; Fig. 52) (diagnostic characters underlined)

Sexes similar but male smaller, wingspan ♂ 28–34 mm (AM = 31 mm, *n* = 7); ♀ 33–45 mm (AM = 37 mm, *n* = 24). Wings yellow-orange. Fore wings with subapical spot, white in most specimens, occasionally yellow-orange, enclosed by blackish area, also on costa. Occasionally dark area in fore-wing apex faint, thus subapical spot barely visible. Discal spots absent, cilia concolorous with wings. Hind wings yellow-orange, faint blackish markings on apex; anal margin in male on underside (Pls. 2d, 3d) with long, whitish-orange setae at base, extended and folded over to form a half-elliptical pocket lined with long, cream-coloured, thickened scales (androconia) on both sides, long narrow grey, scale-less ribbed area at base of folded area. Wing underside similar to upperside. Frons and collar yellow-orange. Antennae black, faintly white ventrally, bipectinate in both sexes, pectinations longer in male. Thorax yellow-orange. Hind tibiae of both sexes with 2 + 2 spurs, in male with hair pencil. Abdomen banded black and yellow-orange. Tympanal organs rather large, not meeting ventrally. Ansa weakly broadened at both ends, with elongated projection at centre. Sternites and tergites 3–7 of both sexes undifferentiated. 8th tergite in male slightly triangular, posterior margin narrower. Male genitalia (pl. 5a): uncus prominent, sclerotised, evenly tapering, weakly setose, apex acute; socii small, setose; gnathos arms narrow, fused ventromedially; tegumen large, anterior margin sclerotised; juxta arms (labides) sclerotised, narrow, separate, apex weakly dentate; juxta small plate, valves wide, ventromedially weakly setose, ventral margin slightly concave, apex wide, extension of costa narrow, acute; saccus a narrow, sclerotised ring; aedeagus long, narrow, straight; vesica a narrow tube, slightly expanded at base, without sclerotisations. Female genitalia (Pl. 7b): papillae anales large, membranous, densely setose, base of setae elongate, forming uneven, peg-shaped structure; apophyses posteriores long, narrow; apophyses anteriores short, stout; lamella postvaginalis a small, weakly sclerotised, concave plate; lamella antevaginalis a small sclerotised plate, weakly concave ventromedially; ductus bursae rather long, wide, membranous; posterior margin of corpus bursae sclerotised, striate; corpus bursae a large, elongated sac; signum stellate, ventrally, often with 11 long spikes.

**Immature stages**

**Final instar larva** (Figs 53–54). Head black, dorsal area between eyes white. Dorsal and lateral tufts of long white setae, many longer than body diameter, on thoracic segments and A1 and A2 only, all other setae black, thick dense short black setae on A1–A5. Body not deeply segmented, ground colour white, prominent yellow lateral bands along length of body, black blotches around spiracles and dorsal setal bases on A1–A5. Well developed yellow prolegs on A6 and A10 only.

**Pupa** (Fig. 55). Pale reddish brown; cremastral hooks not splayed, merged at base of cremaster, number unknown.

**Figure 52** – *Z. tenuis* male, Pemba, February 2007, Tanzania.

**Figure 53** – *Z. tenuis* final instar larva, 06-i-2007, Pemba, Tanzania.

**Figure 54** – *Z. tenuis* final instar larva, Pemba,05-i-2007, Tanzania.

**Figure 55** – *Z. tenuis* pupa, Pemba, 12-i-2007, Tanzania.

**Similar species**

*Zerenopsis tenuis* is similar to *Z. costimaculata* and *Z. flavimaculata*, also being yellow-orange with a white or yellow-orange subapical spot on the fore wings, but the spot is enclosed in the costa, whereas it reaches the costa in *Z. costimaculata* and *Z. flavimaculata* and the spot margins are undulating in *Z. costimaculata* and rather smooth in *Z. flavimaculata*. The androconial organ, male genitalia and female genitalia show small diagnostic differences between these three species, as underlined in the descriptions and indicated on the relevant plates.

**Genetics**

BIN: BOLD: AAX1119 (one specimen from Tanzania). The genetically nearest species are *Z. kedar*, at 2.7 % distance, and *Z. costimaculata*, at 5.2 % distance.

**Life history and behaviour**

Males generally fly around specific (lek) trees and females fly low along the forest edge and in the forest undergrowth. Oviposition behaviour has not been observed.

**Lek behaviour** (Figs 56–57): males forming active leks (observed at three sites, Misali Island and Ngezi Forest, Pemba, Tanzania (January 2007), and Arabuko Sokoke Forest, Gedi, Kenya (July 2012); Ngezi Forest lek remaining active and at the same site for three consecutive days of observation); lek behaviour similar to that of *Z. lepida*: males choosing a tall tree protruding from the forest canopy, some continuously fluttering around it, many settling on it for long periods; occasionally some joining or leaving lek by flying up high and straight to and from lek; females visiting lek

**Figure 56** – *Z. tenuis* lek tree, 04-i-2007, Misali Island, Pemba, Tanzania.

**Figure 57** – *Z. tenuis* lek tree with fluttering males, 04-i-2007, Misali Island, Pemba, Tanzania.

in afternoon, their close presence invoking increased activity amongst fluttering males, but no competitive male/male interaction or males chasing passing females observed; females settling on lek tree and mating presumably taking place there (trees too tall for observation of actual behaviour immediately prior to mating); females flying low under lek tree invoking no response from the males above, and many females passing under tree without visiting lek.

**Phenology** (Fig. 58)

Available collecting data (21 records with dates) span nine months and indicate a peak of abundance in December–January, but these data may be biased due to more visits to the areas during the summer holiday period and may not necessarily reflect a natural

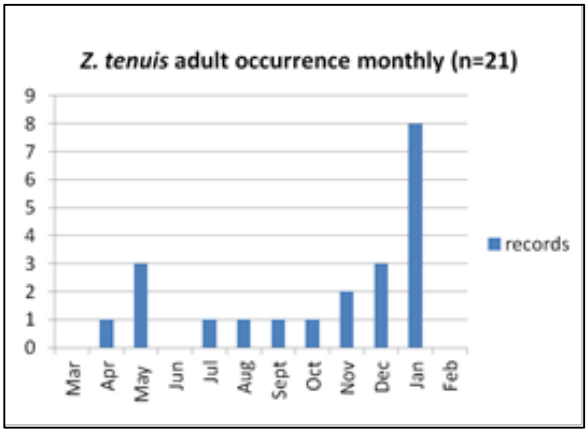


**Figure 58** – *Z. tenuis* seasonal distribution of adults.

increase in abundance at this time. It is most likely that the species is continually brooded and that adults may occur throughout the year.

**Host-plants**

A larva was taken on *Encephalartos hildebrandtii* at Jilore Forest Station near the Arabuko Sokoke National Park, Kenya, by S.C. Collins, and a final-instar larva was found on the trunk of a baobab tree (*Adansonia digitata*, Malvaceae) on Misali Island, Pemba, Tanzania, by the author (Staude 2008). This larva was feeding on *A. digitata* leaves and pupated soon after collection, constructing a loose cocoon incorporating frass and loose debris in the container. The adult emerged after 17 days. No cycads were found on the small island, despite an extensive search, certainly not below or in the vicinity of the lek tree or near the site where the larva was found. This observation suggests that an absolute dependence on cycads in the early instars, as demonstrated in *Z. lepida* (Donaldson & Boesenberg 1995), may not apply to *Z. tenuis* and that populations on offshore islands may be able to survive in areas no longer harbouring cycads. The distribution of the species, however, closely matches that of *E. hildebrandtii* (see Goode 1989 for cycad distribution), which includes Pemba island (Fig. 59).

**Figure 59** – *Z. tenuis* distribution map (QDGSs).

**Habitat and distribution** (Fig. 59)

The species occurs in coastal coral-rag forests and near coastal sand forests in Tanzania and Kenya, including the offshore islands.

**Conservation**

Although the species is widespread in coastal Kenya and Tanzania and locally common where it occurs, the alarming rate at which natural forest and cycads in particular are disappearing is of concern for the long-term survival of the species.

**7. *Zerenopsis costimaculata*** (Prout, 1913) **comb. n.**

*costimaculata* Prout, 1913, Novit. zool. 20: 395, (*Paraptychodes*). Holotype female (OUM), Nigeria (southern): Lagos district, Ndzooimi (see Remarks). [*Paraptychodes costimaculata* Prout, 1913 is transferred from *Paraptychodes* Warren, 1894 to *Zerenopsis* C. & R. Felder, 1874 (comb. nov.)].

**Material examined**

**Type.** See Remarks.

**Dissected specimens.** Male genitalia: Prep. number 1756./ Pasi Sihvonen, Kenya, Gedi, Arabuko Sokoke/ Forest Reserve, mixed sand/ forest, ~50m, 3°20'S/[on the label]39°57'E,/ ab larva *E. hildebrandtii*,/ Sept. 2002 R. Bennet; Kenya/ Gedi/ Arabuko Sokoke Forest/ 39.57.000E 03.20.000S/ 21.VII.2002 50 m/ H.S. Staude / HSS_d000.db 4111; GEOMETRIDAE/ DIPTYCHINAE/ Paraptychodes/ costimaculata/ H.S. Staude 01-02-2005/ HSS_d000.db 4111 (HSS). Female genitalia: Prep. number 1757./ Pasi Sihvonen, Kenya east coast, Malako,/ April-May 1998 ex. S.C. Collins; Kenya/ Malindi/ 39.51.400E 03.13.320S/ 11.IV.1998 0 m/ S.C. Collins/ HSS_d000.db 8376; GEOMETRIDAE/ DIPTYCHINAE/ Paraptychodes/ costimaculata/ H.S. Staude 01-08-2005/ HSS_d000.db 8376; f/ DNA sample/ No. 131/ Pasi Sihvonen (HSS).Female genitalia: Prep. number 1799./ Pasi Sihvonen = BMNH GEO 24785, KENYA/ Kilifi/ 13.VI.1944/ G.W. Jeffrey/ B.M. 1958-515; B.M. JEFFERI/ KILIFIF/ MOMBASA./ 13.6.[19]44 (coll. BMNH). Male genitalia: Prep. number 1979./ Pasi Sihvonen = BMNH GEO 24907, UGANDA/ 1927 29/ H.B. Moronel [handwritten, difficult to read, might be wrong]; Pres. By / Imp. Inst. Ent.,/ Brit. Mus./ 1930-577.; Paraptychodes/ costimaculata/ m Prout (coll. BMNH).

**Other specimens. HSS:** S3.33, E39.95, 50m, 2012-07-21, Arabuko Sokoke Forest Reserve, Gedi, Kenya, H.S. Staude; S3.33, E39.95, 50m, 2002-07-21, Arabuko Sokoke Forest Reserve, Gedi, Kenya, R. Bennet; S3.23, E39.86, 1998-04-11, Malindi, Kenya, S.C. Collins; S3.33, E39.95, 50m, 2008-08-04, Jilore Forest Station, Arabuko Sokoke Forest Reserve, Gedi, Kenya, S.C. Collins; S3.33, E39.95, 50m, 2004-01-04, Gedi Coast, Kenya, S.C. Collins; S3.33, E39.95, 50m, Jilore Forest Station, Arabuko Sokoke Forest Reserve, Gedi, Kenya, *ab larva* collected 21 July 2012 on *Encephalartos hildebrandtii* (Zamiaceae), emerged 18 to 22 December 2012, H.S. Staude. **BMNH:** S3.217, E40.1, 1891-10-30, Melindi, Kenya; S4.68, E39.15, 1923-06-15, 20 miles north, Moa, Tanga, Tanzania, W. Feather; S3.3, E39.95, 1921-01-30, Sokoke near coast, Gedi, Kenya, W.N. van Sommeren; S3.62, E39.85, 1944-06-13, Kilifi, Kenya, G.W. Jeffrey; 1927, Uganda, B. Morony. **CTC:** S3.33, E39.95, 2008-08-04, Arabuko Sokoke National Park, Gedi, Kenya, S.C. Collins; S4.24, E39.39, 2007-05-16, Shimba Hills National Park, Kenya, S.C. Collins; S4.24, E39.39, 2000-07-16, Shimba Hills National Park, Kenya, S.C. Collins.

**Redescription** (Pl. 1g; Figs 60–61) (diagnostic characters underlined)

Sexes similar, wingspan ♂ 40–49 mm (AM = 43 mm, *n* = 9); ♀ 44–55 mm (AM = 49 mm, *n* = 9). Wings yellow-orange; black spots variable, even between left and right wings. Fore wings with white subapical spot enclosed by blackish area but not in costa. Spot margins undulating. Occasional second white spot below

**Figure 60** – *Z. costimaculata* female, 21-vii-2012, Jilore Forest Station, Kenya.

**Figure 61** – *Z. costimaculata* adult female, Jilore Forest Station, Kenya.

subapical one. 1–3 small blackish dots in costa. Discal spots absent, cilia concolorous with wings. Hind wings yellow-orange, distinct blackish areas near margins; anal margin in male **(**Pls 2 f–g, 3 e–f**)** on underside with long, cream-coloured setae, extended and folded over to form a half-elliptical pocket lined with long, orange to cream-coloured, rounded and thickened scales (androconia) on both sides, broad outer margin of inside of pocket lined with black non-androconial scales (Pl. 2g), long narrow silvery-grey, scale-less ribbed area at base of folded area. Wing underside similar to upperside. Frons with ventral margin yellow-orange, otherwise blackish. Collar yellow-orange. Antennae black, weakly bipectinate in both sexes. Thorax-yellow-orange. Hind tibiae in both sexes with 2 + 2 minute spurs, in male with hair-pencil. Abdomen banded black and yellow-orange, with two lateral rows of black dots. Tympanal organs rather large, not meeting ventrally. Ansa weakly broadened at both ends, with elongate projection at centre. Sternites and tergites 3–7 of both sexes undifferentiated. 8th tergite in male slightly triangular, posterior margin narrower. Male genitalia (Pl. 5b): uncus prominent, sclerotised, evenly tapering, weakly setose, apex acute; socii small, setose; gnathos arms narrow, fused ventromedially; tegumen large, anterior margin sclerotised; juxta arms (labides) sclerotised, broad, separate, apex dentate; juxta a small plate; Valves broad, ventromedially densely setose, ventral margin slightly concave, apex wide, extension of costa wide, not acute; saccus a narrow, sclerotised ring; aedeagus long, narrow, caecum bent; vesica not everted, without sclerotisations. Female genitalia (Pl. 7c): papillae anales small, membranous, densely setose, base of setae elongate, forming uneven, peg-shaped structure; apophyses posteriores long, narrow; apophyses anteriores short, stout; lamella postvaginalis a small, weakly sclerotised, concave plate; lamella antevaginalis a large sclerotised plate, margin convex ventromedially; ductus bursae rather long, wide, membranous, posterior margin sclerotised, striate; corpus bursae large, laterally elongated sac; signum stellate, laterally, often with 11 long spikes.

**Immature stages**
**Ovum:** unknown.

**Figure 62** – *Z. costimaculata* first-/second instar larva, 25-vii-2012, Jilore.

**Figure 63** – *Z. costimaculata* second instar larva, 25-vii-2012, Jilore.

**Figure 64** – *Z. costimaculata* third instar larva tunnelling out leaf stem, 25-vii-2012, Jilore.

**1st–2nd instar larvae** (Figs 62–64): with a full complement of well-developed golden primary setae, on average shorter than body diameter; body translucent cream-coloured, deeply segmented, brownish-black maculae around setal bases on all segments, more prominent on A1–A5 with dorsal brown irroration in some specimens, head black, thoracic legs black, prolegs of body colour, anal plate black, elongate black patch on pronotum not merged with black head; well developed prolegs on A6 and A10 only.

**3rd instar larvae** (Fig. 65): ground colour yellow-orange, golden secondary setae present, mostly longer than the now brownish primary setae, these more spiny; head and anal plate deep orange; dorso-lateral area of A1–A5 black with setal bases swollen.

**Figure 65** – *Z. costimaculata* third instar larva, 25-vii-2012, Jilore.

**Figure 66** – *Z. costimaculata* fourth instar larva dorsal view, 25-viii-2012, Jilore.

**Figure 67** – *Z. costimaculata* fourth instar larva,08-ix-2012, Jilore.

**4th–5th instar larvae** (Figs 66–68): body appears still rather segmented; primary and secondary setae shorter than in 3rd instar, of equal length, more spiny, all setae deep orange, appearing in tufts and crinkled, making larvae appear scruffy; ground colour deep orange to reddish in some specimens, on A1–A5 almost completely obliterated by black; head orange with brownish mottling.

**Pupae** (Fig. 69): dark brown, AM = 20 x 8.5 mm (*n* = 15), only two pairs of cremastal hooks, one pair double the length of other, splayed, merged at base of cremaster.

**Figure 68** – *Z. costimaculata* fifth instar larva, 02-xii-2012, Jilore.

**Similar species**

*Zerenopsis costimaculata* is most similar to *Z. tenuis* and *Z. flavimaculata*. For adult differences see under *Z. tenuis*. Its later instar larvae are deep orange in ground colour (white in *Z. tenuis*) with an orange head (black in *Z. tenuis*). It occurs sympatrically with *Z. tenuis*, and the larvae of the two species may occur together.

**Genetics**

BIN: BOLD: AAX1118 (two specimens from Kenya, both genetically identical). The genetically nearest species is *Z. tenuis*, at 5.2 % distance.

**Life history and behaviour**

**1st–2nd instar larvae** (Figs 62–64): gregariously in web spun over new leaflets of freshly uncurled leaf, blackening leaf tissue before consumption, larger 2nd instar larvae tunnelling into stem of leaflet (Fig. 64).

**Figure 69** – *Z. costimaculata* second and third instar larvae gregariously consuming leaf petiole of host-plant *E. hildebrandtii*, in situ, 21-vii-2012, Jilore.

**Figure 70** – *Z. costimaculata* pupa, 24-xi-2012, Jilore.

**3rd instar larvae** (Figs 65, 69): gregarious, congregating *en masse* around main leaf stem, consuming outer layer, then tunnelling into leaf stem (Fig. 69) and completely hollowing out inside to leave only outer skin.
**4th–final instar larvae** (Figs 66–68): largely gregarious (only a few feeding singly on leaflet), most feeding on leaves by excavating one side and leaving outer cuticle intact or feeding on leaf stem removing outer surface; only few feeding on secondary host- plants (as provided in captivity); on maturity burrowing into loose sand and constructing loose cocoon incorporating surrounding debris; relatively slow growing (larval stage under laboratory conditions, sleeved with ample food available, lasting five months, July–November).
**Pupae** (Fig. 70): rigid, not wriggling when disturbed; under laboratory conditions adults eclose after 2–3 weeks.
**Imagines** (Figs 60–61): diurnal, active from morning until dusk, flying slowly like other aposematic species in area; females visiting nectar sources and flying from cycad to cycad, circling each plant before moving on, oviposition not observed.

**Mating behaviour:** not observed; no males observed during two full days of recording behaviour of females; females occasionally disappearing into canopy and likely visiting leks deep in the forest where observation from the ground is difficult; all males examined, except one in BMNH labelled 'Uganda' reared in captivity.

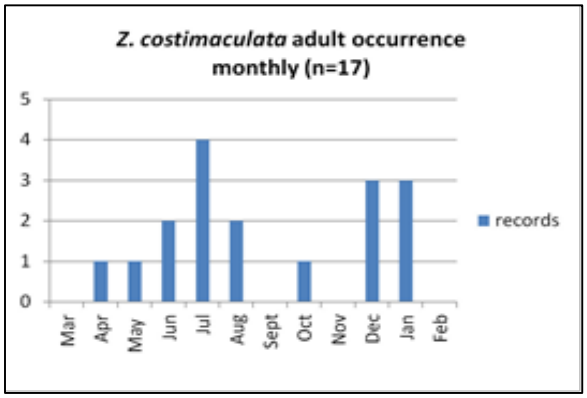

**Figure 71** – *Z. costimaculata* seasonal distribution of adults.

**Phenology** (Fig. 71)
The available records ($n = 17$) indicate that adults occur during eight months of the year. Early-instar larvae, later-instar larvae as well as adults were observed on the same day. Our rearing experiment suggests that one generation takes about six months to complete, and it thus appears that the species is bivoltine but that adult appearance is staggered, with most stages probably present at any time of the year.

**Host-plants** (Fig. 72)
Larvae were found in the wild on *Encephalartos hildebrandtii*, a cycad that grows widely on the East African coast. No later-instar larvae were found on other plants in the wild. In captivity some final-instar larvae fed on the leaves of *Diospyros lycioides* (Ebenaceae).


**Figure 72** – *Z. costimaculata* host-plant *E. hildebrandtii*, in situ, 22-vii-2012, Jilore.

**Habitat and distribution** (Fig. 73)
*Zerenopsis costimaculata* is much less widespread than *Z. tenuis*, only known to occur along the Kenyan and northern Tanzanian coasts. Searches for the species in inland colonies of *Encephalartos* in Kenya, however, revealed no sign of its presence. The record of a male in the BMNH labelled only 'Uganda' (its identity confirmed by dissection, slide PS1979/ BMNH GEO


**Figure 73** – *Z. costimaculata* distribution map (QDGSs).

24907) may be correct as a few colonies of *Encephalartos* occur in Uganda. The record of the holotype, from Nigeria, is most probably incorrect (see Remarks below).

**Conservation**
Data-deficient (DD). The species is known only from a few localities, and its presence has only been confirmed at the Arabuko and Shimba Hills localities in recent years. Natural vegetation with cycads at the Kilifi locality seems to have disappeared. Both the recently confirmed colonies occur in areas conserved in national parks, offering some protection.

**Remarks**
The holotype is apparently housed in the Oxford University Museum of Natural History, UK, but efforts by the current curator to locate the specimen have been unsuccessful. The type locality (Lagos district, Ndzooimi, in southern Nigeria) is very distant from all other known records, from the coastal areas of Kenya and Tanzania, and may be erroneous. Despite this, the identity of *Z. costimaculata* is not in doubt and we do not see it necessary to designate a neotype. The species is distinct in external appearance, and the BMNH has specimens identified by its author, L.B. Prout, and a female of that series (from Kenya: Sokoke) is illustrated in colour in Prout (1929–1935, plate 1h).

**8. *Zerenopsis flavimaculata* Staude & Sihvonen spec. n.**
urn: lsid: zoobank.org: act: C1BE6DF2-434F-4BC1-BB63-A85C29F902E1

**Material examined**
**Types.** Holotype, male: [MALAWI] 40.26./ Port Herald [Nsanje]/ Nr. Zambesi/ June 1926./ H. Barlow; Joicey/ Bequest. /Brit. Mus./ 1934-120; Male genitalia: Prep. number 1797./ Pasi Sihvonen = BMNH Geometridae/ genitalia slide/ No. 24783/ HOLOTYPE/ *Zerenopsis*/ *flavimaculata*/ Staude & Sihvonen, 2014 [red rectangle label] (BMNH). Paratype, female: [MALAWI] Limbe, Nyasa [=Nyasaland = Malawi],/ (H. Barlow).; Rothschild/ Bequest/ B.M. 1939-1; Female genitalia: Prep. number 1798./ Pasi Sihvonen = BMNH Geometridae/ genitalia slide/ No. 24784/ PARATYPE/ *Zerenopsis*/ *flavimaculata*/ Staude & Sihvonen, 2014 [yellow rectangle label] (BMNH).
**Other specimens:** Mozambique; Distant Coll./ 1911-383; Female genitalia: Prep. number 1796./ Pasi Sihvonen = BMNH Geometridae/ genitalia slide/ No. 24782 (BMNH) (not included in type series, see Remarks).

**Description** (Pl. 1h; Fig. 74) (diagnostic characters underlined)
Sexes similar, wingspan 37–41 mm. Wings yellow-orange. Fore wings with subapical spot yellow-orange, enclosed by blackish area but not in costa. Spot margins comparatively smooth. one to three small blackish dots along costa. Discal spots absent, cilia concolorous with wings. Hind wings yellow-orange, distinct blackish areas near margins; androconial organ of male (Pl. 2e) exteriorly similar to that of *Z. tenuis*, interior of pocket not examined. Wing underside similar to upperside.

**Figure 74** – *Z. flavimaculata* holotype male, Nsanje, Malawi, (BMNH).

Frons and collar yellow-orange. Antennae black, shortly bipectinate in both sexes. Thorax yellow-orange Hind tibiae in female with 2 + 2 spurs (the only known male missing hind legs, thus number of spurs and presence of hair-pencils unknown). Abdomen banded black and yellow-orange. Tympanal organs rather large, not meeting ventrally. Ansa weakly broadened at both ends, elongated projection at centre. Sternites and tergites 3–7 of both sexes undifferentiated. 8th tergite in male slightly triangular, posterior margin narrower. Male genitalia (Pl. 5c): uncus prominent, sclerotised, evenly tapering, weakly setose, apex acute; socii small, setose; gnathos arms narrow, fused ventromedially; tegumen large, anterior margin sclerotised; juxta arms (labides) sclerotised, narrow, separate, apex dentate; juxta forming a small plate; valves broad, ventromedially densely setose, ventral margin slightly concave, apex wide, extension of costa wide, acute; saccus a narrow, sclerotised ring; aedeagus long, narrow, caecum bent; vesica not everted, without sclerotisations. Female genitalia (Pl. 7d): papillae anales small, membranous, densely setose, base of setae elongate, forming uneven, peg-shaped structure; apophyses posteriores long, narrow; apophyses anteriores short, stout; lamella postvaginalis a small, weakly sclerotised, forming a concave plate; lamella antevaginalis a large sclerotized plate, margin concave ventromedially; ductus bursae rather long, wide, membranous, posterior margin sclerotised, striate; corpus bursae taking the form of a large, roundish sac; signum stellate, ventrally, often with 11 long spikes.

**Immature stages**
Unknown.

**Similar species**
*Z. flavimaculata* is similar to *Z. costimaculata* and *Z. tenuis*, also being yellow-orange with a white or yellow-orange subapical spot on the fore wings, but the spot is not enclosed in the costa, whereas it is enclosed in *Z. tenuis*; spot margins are rather smooth in *Z. flavimaculata* but undulating in *Z. costimaculata*. The androconial organ, male genitalia and female genitalia show small diagnostic differences between these three species, as underlined in the descriptions and indicated on the relevant plates.

**Phenology**
The holotype was collected in June, and the paratype bears no date on its label.

**Figure 75** – *Z. flavimaculata* distribution map (QDGSs).

**Host-plants**
Unknown.

**Habitat and distribution** (Fig. 75)
The species occurs in southern Malawi and probably Mozambique, but its distribution and habitat are poorly known. The holotype was taken in Port Herald [Nsanje] in southern Malawi, an area at about sea-level and with a subtropical climate, relatively dry and strongly seasonal. The warm-wet season extends from November to April, with a cool, dry winter season from May to August. The dominant vegetation is woodland savannah (mixed species). East of Nsanje, along the Shire River, the vegetation consists of perennially wet grasslands and swamps (Ndinde Marsh), whereas west of Nsanje the vegetation consists of open canopy woodland of hills and scarps, dominated by *Brachystegia* species (Panagos *et al.* 2011). During an expedition to the area undertaken to find *Z. flavimaculata* in June 2013, a colony of *Encephalartos gratus* was found ~80km south-east of Nsanje in adjacent Mozambique, but no evidence of the presence of cycad moths was found in it. There are no known localities harbouring cycads left near Limbe, the locality of the paratype (P. Rousseau, J. Bayliss pers. comm.), an area now almost completely transformed with few wild habitats remaining.

**Genetics**
No data available.

**Conservation**
Data-deficient (DD). Only known from the holotype male and paratype female.

**Etymology**
The specific epithet refers to the yellow subapical spot in the fore wings, from Latin adjective *flavus* (yellow) and noun *macula* (a spot).

**Remarks**
The three known specimens of this species are externally rather similar. However, one specimen labelled ' Mozambique., Distant Coll./ 1911-383' (last specimen on the right of Pl. 1h), differs slightly from the other two by having larger fore-wing yellow spots and the black area on hind-wing margin more undulating, almost as in *Z. costimaculata*, but its genitalia do not differ noticeably from those of the paratype. We prefer not to include this specimen in the type series of *Z. flavimaculata* due to these small external differences and because the female genitalia are very uniform in *Zerenopsis*, thus often not taxonomically informative between closely related species. Further, its exact locality is unknown and almost impossible to trace, Mozambique being a vast territory (801 590 km²). The rediscovery of this locality and the collecting of more specimens would elucidate whether this specimen is conspecific with the male and female from Malawi.

## DISCUSSION

**An expanded concept of *Zerenopsis***
The majority of Geometridae, approximately 18 000 of 23 000 species, have been described before 1940, prior to the time when the more revisionary and comparative, or modern, taxonomy arose (Gaston *et al*. 1995, Scoble *et al*. 1995). Consequently, many species were placed in genera and higher taxa that were not critically assessed and properly defined, partly because the judgement was based on external characters alone. The study of genitalia, which is one of the methods allowing more accurate taxonomical conclusions to be made, did not become a common practice until around the early 1940s. This is also the case with the genera *Diptychis*, *Zerenopsis* and *Paraptychodes*. The facies of the species as here revised are distinct and heterogeneous. Therefore it is understandable that the species were described in different genera, but their rather uniform genitalia demonstrate that they form a morphologically coherent group. In fact, in these moths the genitalia are so uniform that differences between the species are minute. External characters, including the facies, the hind-wing anal-margin androconial organs of the males and the hind-leg hair-pencils are in many instances more diagnostic for the species. This is an unusual trait in the Geometridae. Normally the genitalia provide further diagnostic differences, even more so, than features of the wings, legs and other structures.

The monophyly of *Zerenopsis* as here constituted is also supported by other morphological characters of adults and immatures stages, host-plant associations and behavioural traits, particularly in comparison with other genera of Diptychini.

This revision reduces the number of genera of Diptychini from six to four and increases the number of described species from 15 to 17: *Callioratis* (six described and one possibly undescribed), *Durbana* (one described), *Veniliodes* (two described and one possibly undescribed) and *Zerenopsis* (eight described). A revision of *Veniliodes* and *Durbana* is in preparation.

**Androconial organs and lek behaviour**
*Zerenopsis tenuis*, *Z. lepida* and *Z. moi* exhibit lek behaviour, and evidence suggests that this is also the case in other *Zerenopsis* species. Lek behaviour is also

recorded in the related Diptychini genus *Callioratis* (Staude 1996, Staude 2001a, Staude Bayliss & Sihvonen 2011), but apparently not elsewhere in Geometridae. Male aggregations prior to mating are also known elsewhere in the Lepidoptera, for instance in Hepialidae (e.g., *Hepialus humuli* (Linnaeus); Mallet 1984) and in Adelidae (swarming in several species of *Adela* Latreille and *Nemophora* Illiger & Hoffmannsegg; Heath & Pelham-Clinton 1983), hill topping in Papilionidae (Pinheiro 1990) and leks in Pieridae (DeVries 1980) and in Nymphalidae (Ross 1995).

Staude (1996) described a unique 'sex pheromone disseminating organ' in the Diptychini species *Callioratis abraxas* C. & R. Felder. This organ of the male is formed by the sealing off, in the resting position, of the fore-wing underside with the hind-wing upperside by means of specialised flattened scales situated on the wing margins. In the middle of the ensuing 'pocket' a patch of modified scales occurs on the fore-wing underside, presumed to be androconia. Similar modified scales, also presumed to be androconia, occur in all species of *Zerenopsis* of which the males are known. As in *C. abraxas*, they occur in special pockets, forming an 'androconial organ' in all species except *Z. lepida*, in which the androconia are not enclosed. In *Zerenopsis* spp. the pockets are formed by the tight backward folding of the inner hind-wing margin. As in *C. abraxas*, the edges of the pocket are smooth without setae to ensure the sealing of the pocket. The pocket increases the hind-wing surface of the male in all species except *Z. lepida*, and males with large pockets are likely able to store larger amounts of pheromones and thus have an advantage in attracting females.

No competitive interaction between males in the lek has been observed in *Zerenopsis tenuis* and *Z. moi*, but in *Z. lepida* leks males were observed to engage in competitive male interaction when females pass by. This difference in behaviour may be linked to the fact that *Z. lepida* males do not have androconial pockets.

It appears that there may be a link between the development of pocket-type androconial organs and lek formation in these moths. Although the androconial organs differ structurally between *Zerenopsis* and *Callioratis*, a parallel situation occurs in *C. abraxas* (Staude 1996) and *C. grandis* (Staude *et al*. 2011), where the development of pocket-type androconial organs and lek behaviour may be linked. In the Diptychini genera *Veniliodes* and *Durbana* as well as *Callioratis millari* no such pocket-type androconial organs occur, and their males also appear not to form leks or any form of communal aggregations.
Speculation about the possible reasons for these apparently connected developments falls outside the scope of this article. Further morphological and physiological investigations into the nature of these androconial organs and more detailed observations of the lek and mating behaviour are needed to elucidate the unusual mating systems of these fascinating moths.

The lek behaviour probably also explains the rarity or absence of males of *Zerenopsis* in museum collections. *Zerenopsis* males congregate at selected lek sites (often out of reach of collectors), whereas females move around more freely close to the ground and are more likely to be found by collectors. *Zerenopsis tenuis*, for example, is represented in the BMNH by more than 100 females and only one male (holotype of *perfulva* Prout, 1913, a junior subjective synonym of *tenuis* Butler, 1878). Potentially *Z. kedar* also exhibits lek behaviour, as so far all collected specimens are females.

## CONCLUSION

The species now included in the genus *Zerenopsis* form a uniform group from morphological, genetic, biological and ecological perspectives. Early-instar *Zerenopsis* caterpillars feed exclusively on cycads and appear to be dependent on them. This obligatory association restricts the distribution of these moths (several species being of conservation concern) and probably increasingly so as cycad populations dwindle across the African continent.

We hope that our study will encourage further studies in *Zerenopsis* and related Diptychini, potentially shedding light on the evolution of these moths and their truly peculiar life histories and mating strategies.

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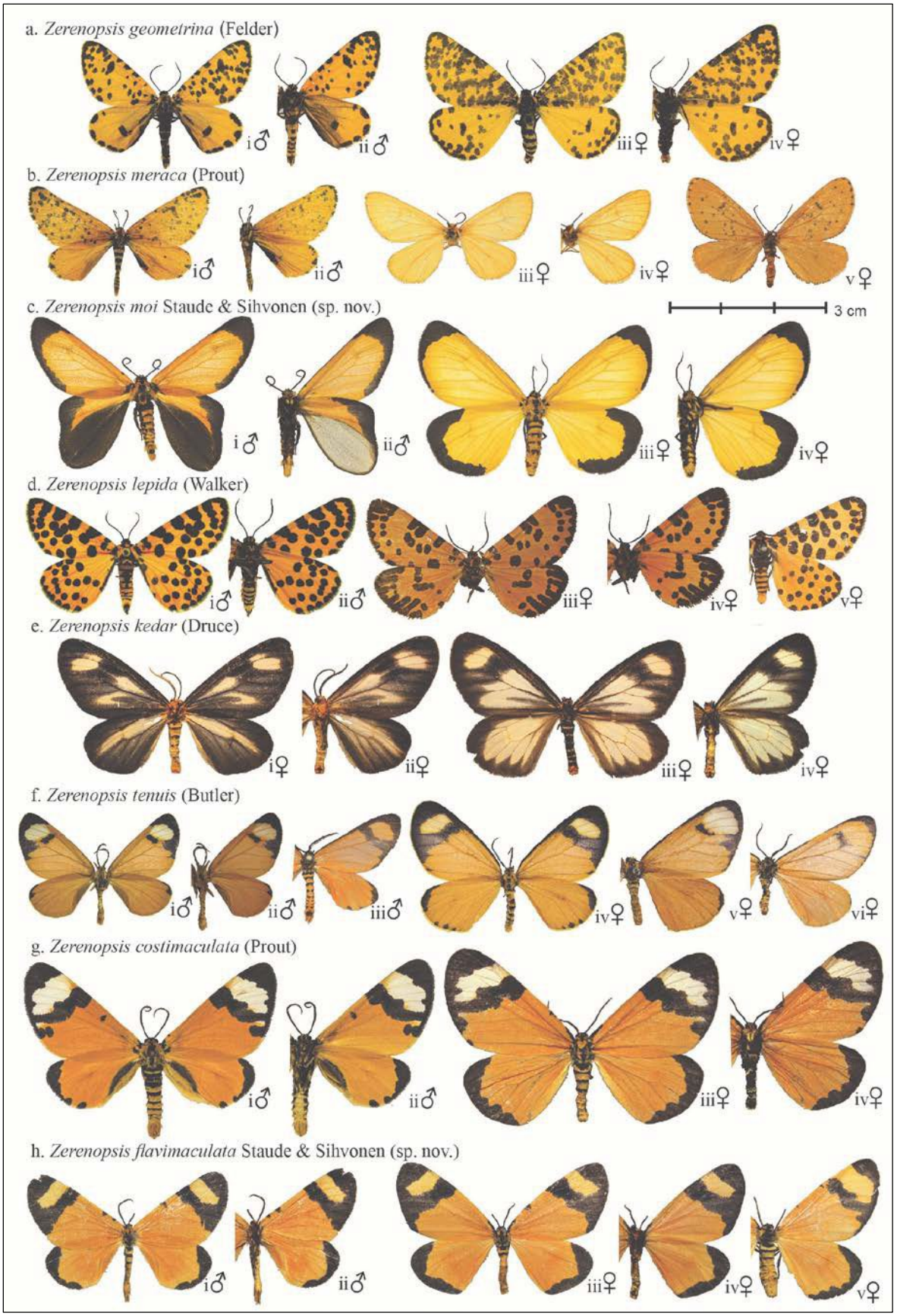


**PLATE 1**

Adults of *Zerenopsis*

**PLATE 1**

Adults of *Zerenopsis*

a. ***Z. geometrina*** (C. & R. Felder)
i male South Africa: The Haven, 26.xii.1981 (HSS).
ii male (underside), South Africa: The Haven, 26.xii.1981 (HSS).
iii female, South Africa: The Haven, 26.xii.1981 (HSS).
iv female (underside), South Africa: The Haven, 26.xii.1981 (HSS).

b. ***Z. meraca*** (Prout)
i male, South Africa: Natal, Maputaland, xii.1993 (HSS).
ii male (underside), South Africa: Natal, Maputaland, xii.1993 (HSS).
iii holotype, female, Mozambique: south (MHNG).
iv holotype, female (underside), Mozambique: south (MHNG).
v female, South Africa: Kwa-Zulu Natal, 28.iii.2001 (CTC).

c. ***Z. moi*** Staude & Sihvonen **sp. n.**
i paratype, male, Mozambique: Marraquene, coastal dune scrub, 16.ix.2000 (HSS).
ii paratype, male (underside), Mozambique: Marraquene, coastal dune scrub, 16.ix.2000 (HSS).
iii paratype, female, Mozambique: Marraquene, coastal dune scrub, 16.ix.2000 (HSS).
iv paratype, female (underside), Mozambique: Marraquene, coastal dune scrub, 16.ix.2000 (HSS).

d. ***Z. lepida*** (Walker)
i male, South Africa: KwaZulu-Natal, Eshowe, Ngoye Nature Reserve, 15.vi.2012 (HSS).
ii male (underside), South Africa: KwaZulu-Natal, Eshowe, Ngoye Nature Reserve, 15.vi.2012 (HSS).
iii holotype, female , South Africa: [Durban] Port Natal (without date) (BMNH).
iv holotype, female (underside), South Africa:[Durban] Port Natal (without date) (BMNH).
v female, South Africa (no other data) (BMNH), holotype of *Zereonopsis leopardina* Felder (junior subjective synonym of *Z. lepida*).

e. ***Z. kedar*** (Druce)
i female, Tanzania: Pemba, Ngezi forest, 18.v.2007 (HSS).
ii female (underside), Tanzania: Pemba, Ngezi forest, 18.v.2007 (HSS).
iii female, Kenya: Kwale, 15.vii.2000 (HSS).
iv female (underside), Kenya: Kwale, 15.vii.2000 (HSS).

f. ***Z. tenuis*** (Butler)
i male, Tanzania: Pemba, 3.i.2007 (HSS).
ii male (underside), Tanzania: Pemba, 3.i.2007 (HSS).
iii male, Kenya: Witu, 28.ii.1912 (BMNH), holotype of *Paraptychodes perfulva* Prout (junior subjective synonym of *Z. tenuis*).
iv female, Tanzania: Pemba Manta, 3.i.2007 (HSS).
v female, Africa, Pheiffer, (without date) (HSS).
vi female, Limbe (without date) (BMNH).

g. ***Z. costimaculata*** (Prout)
i male, Kenya: Gedi, Jilore forest station, , 16-xii.2012, reared (HSS).
ii male (underside), Kenya: Gedi, Jilore forest station, ,16.xii.2012, reared (HSS).
iii female, Kenya: Kilifi, 13.vi.1944 (BMNH).
iv female (underside), Kenya: Kilifi, 13.vi.1944 (BMNH).

h. ***Z. flavimaculata*** Staude & Sihvonen **sp. n.**
i holotype, male, Malawi: Port Herald, vi.1926 (BMNH).
ii holotype, male (underside), Malawi: Port Herald, vi.1926 (BMNH).
iii paratype, female, [Malawi:] Limbe (without date) (BMNH).
iv paratype, female (underside), [Malawi:] Limbe (without date) (BMNH).
v female, Mozambique (without date) (BMNH).


**PLATE 2**

Male androconial organs in *Zerenopsis*

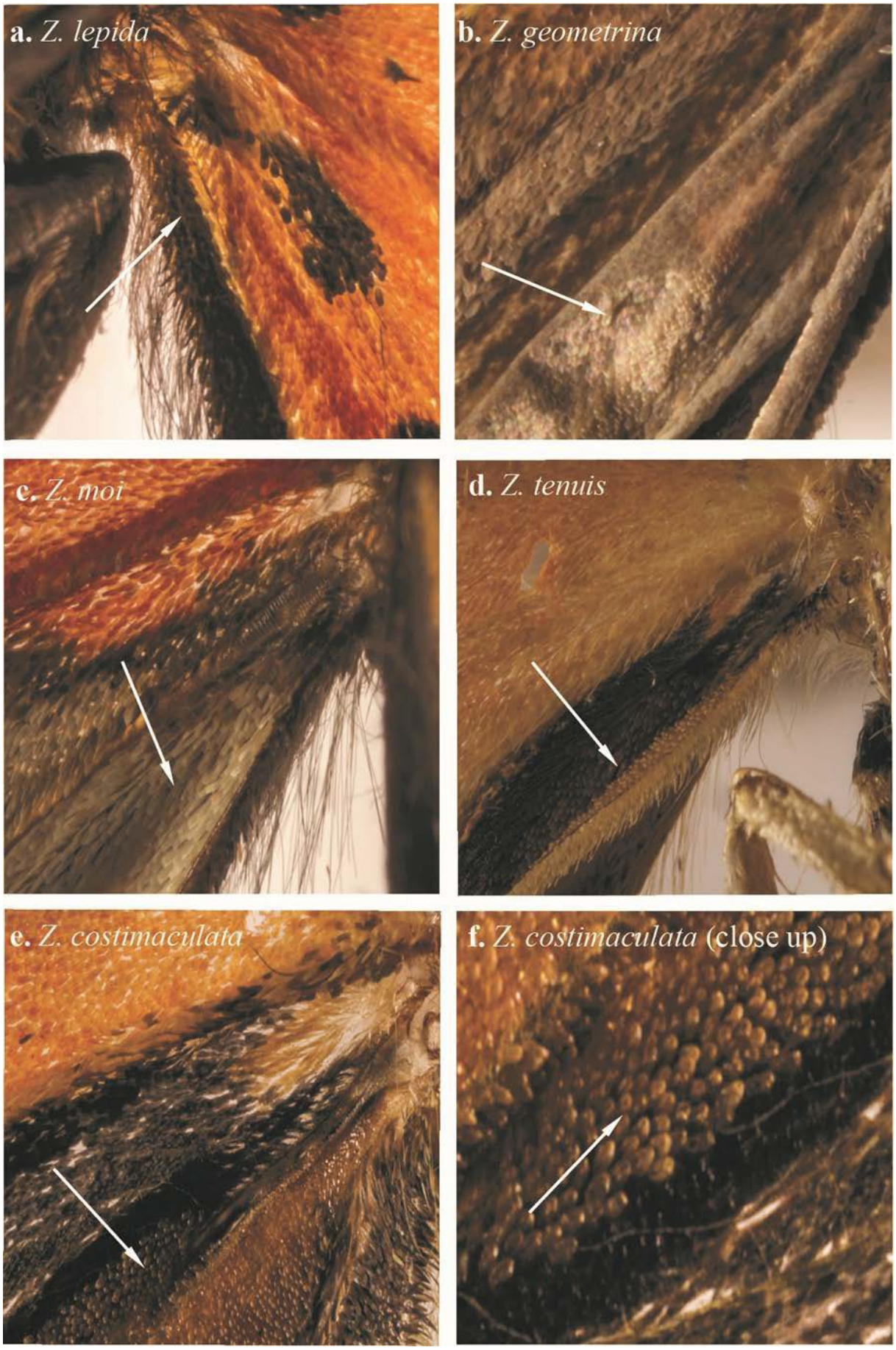


**PLATE 3**

Male androconia (scent disseminating scales) in *Zerenopsis*

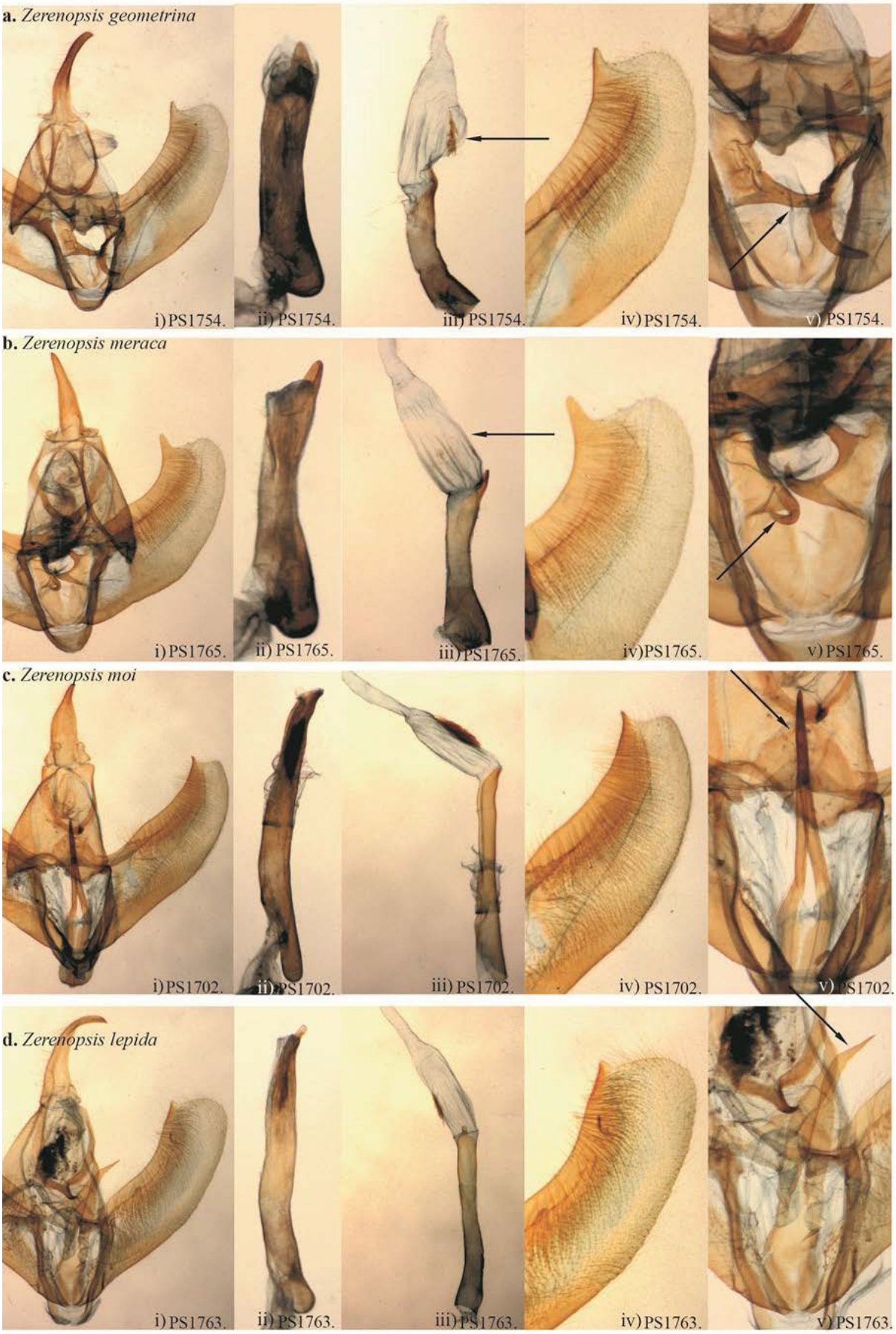
a. Zerenopsis geometrina
i) PS1754.
ii) PS1754.
iii) PS1754.
iv) PS1754.
v) PS1754.
b. Zerenopsis meraca
i) PS1765.
ii) PS1765.
iii) PS1765.
iv) PS1765.
v) PS1765.
c. Zerenopsis moi
i) PS1702.
ii) PS1702.
iii) PS1702.
iv) PS1702.
v) PS1702.
d. Zerenopsis lepida
i) PS1763.
ii) PS1763.
iii) PS1763.
iv) PS1763.
v) PS1763.

**PLATE 4**

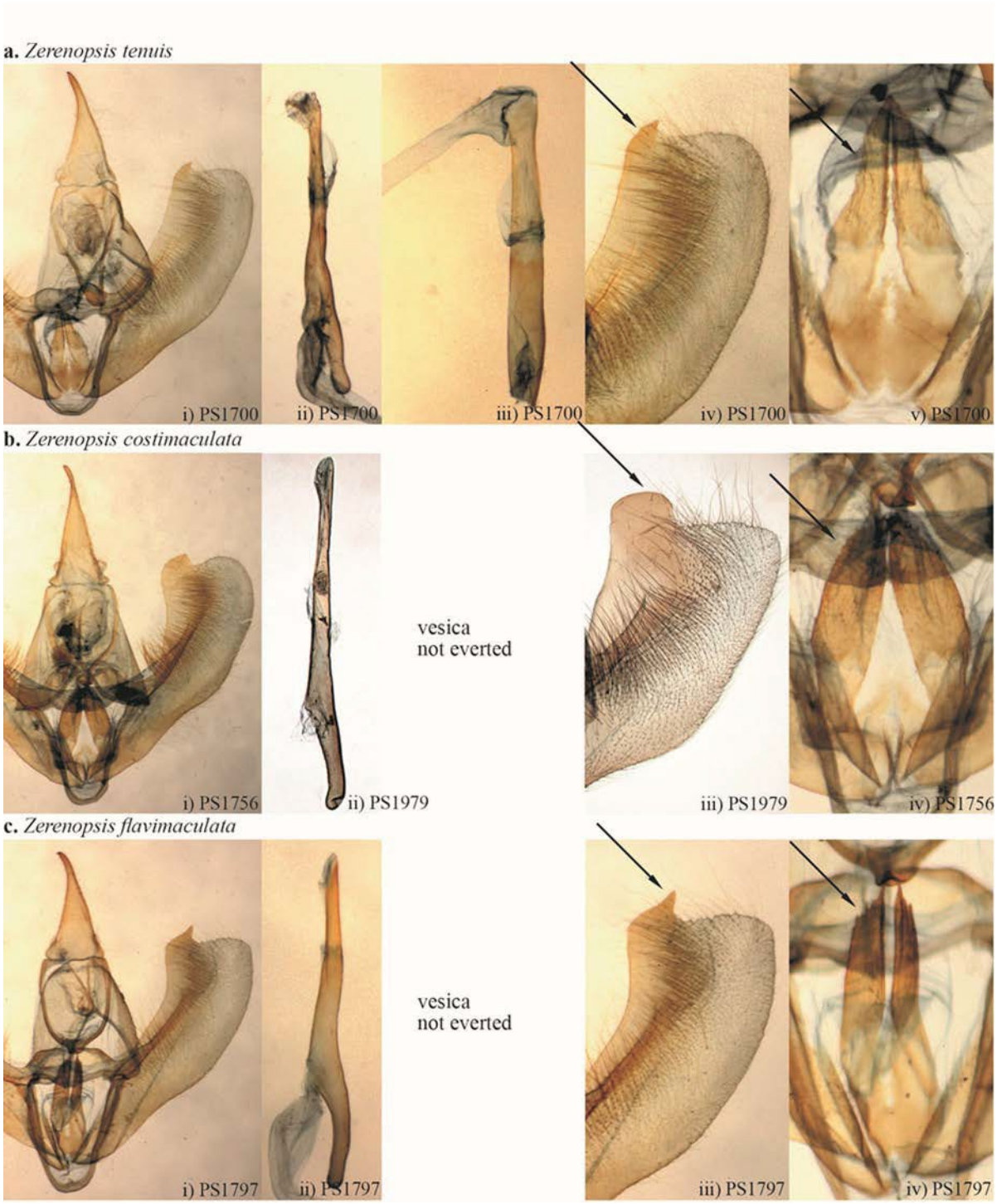
a. Zerenopsis tenuis
i) PS1700
ii) PS1700
iii) PS1700
iv) PS1700
v) PS1700
b. Zerenopsis costimaculata
i) PS1756
ii) PS1979
vesica
not everted
iii) PS1979
iv) PS1756
c. Zerenopsis flavimaculata
i) PS1797
ii) PS1797
vesica
not everted
iii) PS1797
iv) PS1797

**PLATE 5**

**PLATES 4 & 5**

Male genitalia in *Zerenopsis*

4a. ***Z. geometrina*** (C. & R. Felder)
i genitalia, South Africa: Eastern Cape, The Haven, 3.i.1999, slide PS1754 (HSS).
ii aedeagus, South Africa: Eastern Cape, The Haven, 3.i.1999, slide PS1754 (HSS).
iii vesica, South Africa: Eastern Cape, The Haven, 3.i.1999, slide PS1754 (HSS).
iv valva, South Africa: Eastern Cape, The Haven, 3.i.1999, slide PS1754 (HSS).
v juxta arms, South Africa: Eastern Cape, The Haven, 3.i.1999, slide PS1754 (HSS).

4b. ***Z. meraca*** (Prout)
i genitalia, South Africa: Natal, Maputaland, Mangusi forest reserve, December 1993, slide PS1765 (HSS).
ii aedeagus, South Africa: Natal, Maputaland, Mangusi forest reserve, December 1993, slide PS1765 (HSS).
iii vesica, South Africa: Natal, Maputaland, Mangusi forest reserve, December 1993, slide PS1765 (HSS).
iv valva, South Africa: Natal, Maputaland, Mangusi forest reserve, December 1993, slide PS1765 (HSS).
v juxta arms, South Africa: Natal, Maputaland, Mangusi forest reserve, December 1993, slide PS1765 (HSS).

4c. ***Z. moi*** Staude & Sihvonen **sp. n.**
i genitalia (holotype), Mozambique: Marraquene, 30m, coastal dune scrub, 16.ix.2000, slide PS1702 (TMSA).
ii aedeagus, (holotype), Mozambique: Marraquene, 30m, coastal dune scrub, 16.ix.2000, slide PS1702 (TMSA).
iii vesica, (holotype), Mozambique: Marraquene, 30m, coastal dune scrub, 16.ix.2000, slide PS1702 (TMSA).
iv valva, (holotype), Mozambique: Marraquene, 30m, coastal dune scrub, 16.ix.2000, slide PS1702 (TMSA).
v juxta arms, (holotype), Mozambique: Marraquene, 30m, coastal dune scrub, 16.ix.2000, slide PS1702 (TMSA).

4d. ***Z. lepida*** (Walker)
i genitalia, South Africa: Natal, Pinetown, Krantzkloof Nature Reserve, 200m, 24.iv.1998, slide PS1763 (HSS).
ii aedeagus, South Africa: Natal, Pinetown, Krantzkloof Nature Reserve, 200m, 24.iv.1998, slide PS1763 (HSS).
iii vesica, South Africa: Natal, Pinetown, Krantzkloof Nature Reserve, 200m, 24.iv.1998, slide PS1763 (HSS).
iv valva, South Africa: Natal, Pinetown, Krantzkloof Nature Reserve, 200m, 24.iv.1998, slide PS1763 (HSS).
v juxta arms, South Africa: Natal, Pinetown, Krantzkloof Nature Reserve, 200m, 24.iv.1998, slide PS1763 (HSS).

5a. ***Z. tenuis*** (Butler, 1878)
i genitalia, Tanzania: Pemba Manta Reef Lodge, coral rag forest, 03.i.2007, slide PS1700 (HSS).
ii aedeagus, Tanzania: Pemba Manta Reef Lodge, coral rag forest, 03.i.2007, slide PS1700 (HSS).
iii vesica, Tanzania: Pemba Manta Reef Lodge, coral rag forest, 03.i.2007, slide PS1700 (HSS).
iv valva, Tanzania: Pemba Manta Reef Lodge, coral rag forest, 03.i.2007, slide PS1700 (HSS).
v juxta arms, Tanzania: Pemba Manta Reef Lodge, coral rag forest, 03.i.2007, slide PS1700 (HSS).

5b. ***Z. costimaculata*** (Prout)
i genitalia, Kenya: Gedi, Arabuko Sokoke Forest Reserve, mixed sand forest, 50m, ex larva on *E. hildebrandtii*, Sept. 2002, slide PS1756 (HSS).
ii aedeagus, Uganda, 1927 (no other date), slide PS1979 (BMNH).
iii vesica not everted
iv valva, Uganda, 1927 (no other date), slide PS1979 (BMNH).
v juxta arms, Kenya: Gedi, Arabuko Sokoke Forest Reserve, mixed sand forest, 50m, ex larva on *E. hildebrandtii*, Sept. 2002, slide PS1756 (HSS).

5c. ***Z. flavimaculata*** Staude & Sihvonen **sp. n.**
i genitalia (holotype), Malawi: Port Herald [Nsanje], near Zambesi, June 1926, slide PS1797/BMNH Geometridae genitalia slide 24783 (BMNH).
ii aedeagus (holotype), Malawi: Port Herald [Nsanje], near Zambesi, June 1926, slide PS1797/BMNH Geometridae genitalia slide 24783 (BMNH).
iii vesica not everted
iv valva (holotype), Malawi: Port Herald [Nsanje], near Zambesi, June 1926, slide PS1797/BMNH Geometridae genitalia slide 24783 (BMNH).
v juxta arms (holotype), Malawi: Port Herald [Nsanje], near Zambesi, June 1926, slide PS1797/BMNH Geometridae genitalia slide 24783 (BMNH).

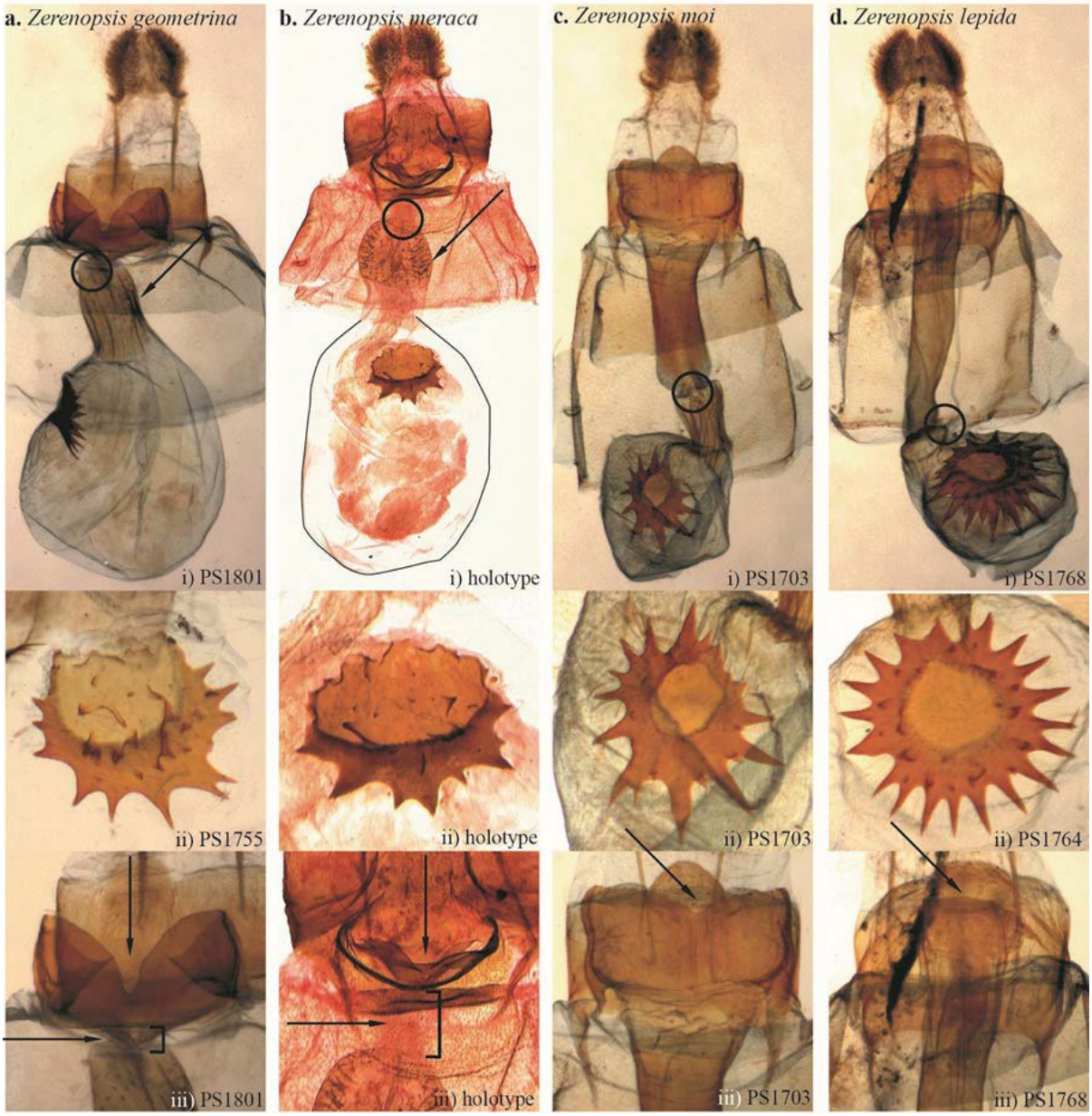
a. Zerenopsis geometrina
b. Zerenopsis meraca
c. Zerenopsis moi
d. Zerenopsis lepida
i) PS1801
i) holotype
i) PS1703
i) PS1768
ii) PS1755
ii) holotype
ii) PS1703
ii) PS1764
iii) PS1801
iii) holotype
iii) PS1703
iii) PS1768

**PLATE 6**

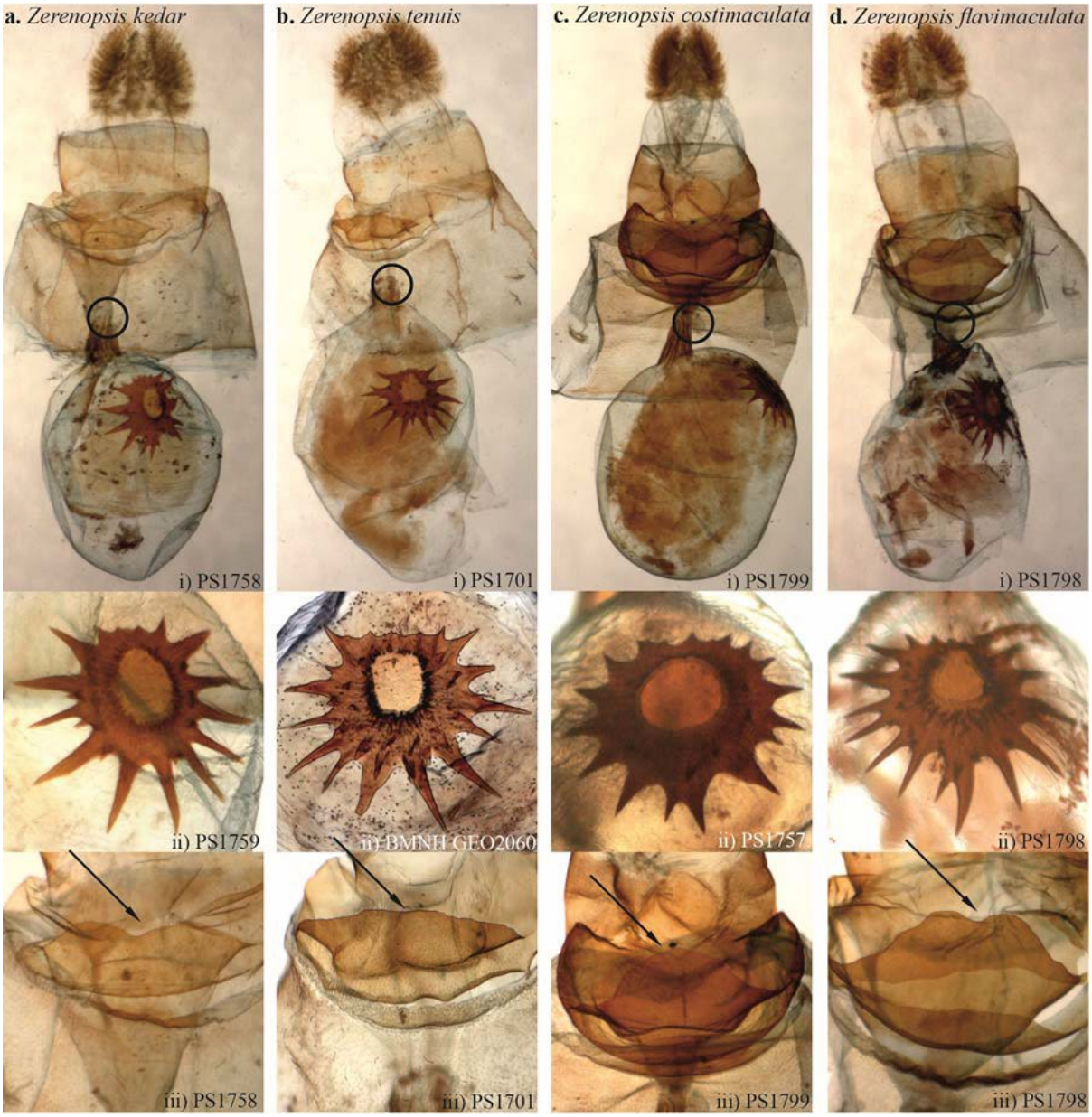
a. Zerenopsis kedar
b. Zerenopsis tenuis
c. Zerenopsis costimaculata
d. Zerenopsis flavimaculata
i) PS1758
i) PS1701
i) PS1799
i) PS1798
ii) PS1759
ii) BMNH GEO2060
ii) PS1757
ii) PS1798
iii) PS1758
iii) PS1701
iii) PS1799
iii) PS1798

**PLATE 7**

**PLATES 6 & 7**

Female genitalia in *Zerenopsis* (point of origin of ductus seminalis circled)

6a. ***Z. geometrina*** (C. & R. Felder)
i genitalia, South Africa: Natal, Durban, July 1900, slide PS1801/BMNH Geometridae genitalia slide 24787 (BMNH).
ii signum, South Africa: Eastern Cape, 8 km W of Mbashee River mouth, 29.xii.1998, slide PS1755 (HSS).
iii ostium bursae and adjacent structures, South Africa: Natal, Durban, July 1900, slide PS1801/BMNH Geometridae genitalia slide 24787 (BMNH).

6b. ***Z. meraca*** (Prout)
i genitalia (holotype), Mozambique: south (no date), no slide number (MHNG).
ii signum (holotype), Mozambique: south (no date), no slide number (MHNG).
iii ostium bursae and adjacent structures (holotype), Mozambique: south (no date), no slide number (MHNG).

6c. ***Z. moi*** Staude & Sihvonen **sp. n.**
i genitalia (paratype), Mozambique: Marraquene, Jay's Lodge, 30m, coastal dune scrub, 16.ix.2000, slide PS1703 (HSS).
ii signum (paratype), Mozambique: Marraquene, Jay's Lodge, 30m, coastal dune scrub, 16.ix.2000, slide PS1703 (HSS).
iii ostium bursae and adjacent structures (paratype), Mozambique: Marraquene, Jay's Lodge, 30m, coastal dune scrub, 16.ix.2000, slide PS1703 (HSS).

6d. ***Z. lepida*** (Walker)
i genitalia, South Africa: Limpopo Province, Tzaneen, 780m, 18.ii.2007, slide PS1768 (HSS).
ii signum, South Africa: KwaZulu-Natal, Entumeni Nature Reserve, Grassland, 850m, 11.iv.1998, slide PS1764 (HSS).
iii ostium bursae and adjacent structrures, South Africa: Limpopo Province, Tzaneen, 780m, 18.ii.2007, slide PS1768 (HSS).

7a. ***Z. kedar*** (Druce)
i genitalia, Tanzania: Pemba island, Ngezi forest, 18.vi.2007, slide PS1758 (HSS).
ii signum, Kenya: Kwale, July 2000, slide PS1759 (HSS).
iii ostium bursae and adjacent structures, Tanzania: Pemba island, Ngezi forest, 18.vi.2007, slide PS1758 (HSS).

7b. ***Z. tenuis*** (Butler)
i genitalia, Tanzania: Pemba Manta Reef Lodge, coral rag forest, 3.i.2007, slide PS1701 (HSS).
ii signum, Tanzania: Zanzibar, 1885 (no exact date), BMNH Geometridae genitalia slide 20607 (BMNH)
iii ostium bursae and adjacent structures, Tanzania: Pemba Manta Reef Lodge, coral rag forest, 3.i.2007, slide PS1701 (HSS).

7c. ***Z. costimaculata*** (Prout)
i genitalia, Kenya: Kilifi, 13.vi.1944, slide PS1799/BMNH Geometridae genitalia slide 24785 (BMNH).
ii signum, Kenya: Malindi, April-May 1998, slide PS1757 (HSS).
iii ostium bursae and adjacent structures, Kenya: Kilifi, 13.vi.1944, slide PS1799/BMNH Geometridae genitalia slide 24785 (BMNH).

7d. ***Z. flavimaculata*** Staude & Sihvonen **sp. n.**
i genitalia (paratype), Malawi: Limbe (no date), slide PS1798/BMNH Geometridae genitalia slide 24784 (BMNH).
ii signum (paratype), Malawi: Limbe (no date), slide PS1798/BMNH Geometridae genitalia slide 24784 (BMNH).
iii ostium bursae and adjacent structures (paratype), Malawi: Limbe (no date), slide PS1798/BMNH Geometridae genitalia slide 24784 (BMNH).

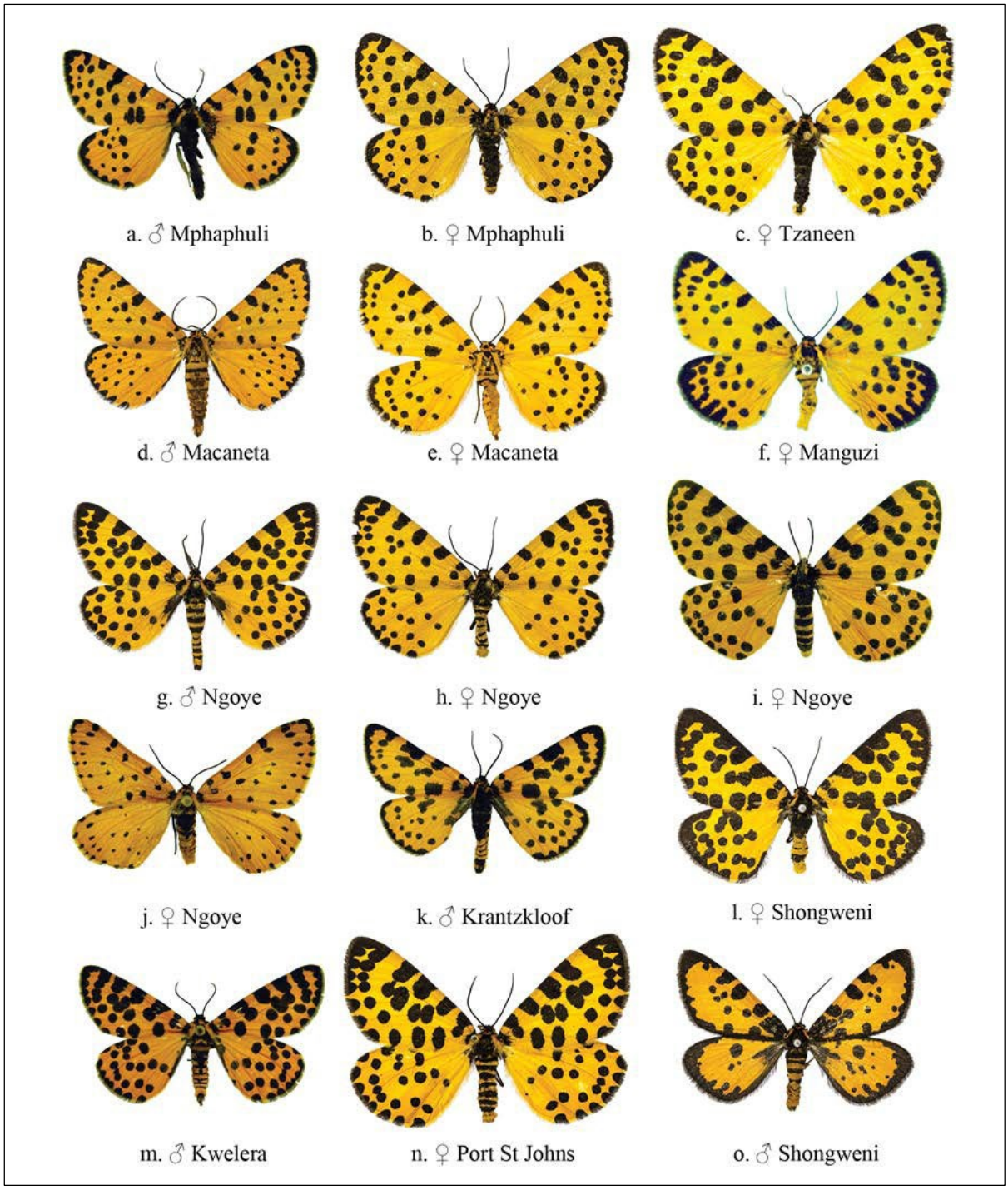


**PLATE 8**

*Zerenopsis lepida*, variation of adults (actual size) (all specimens in HSS)

a. male, South Africa: Limpopo, Mphaphuli Cycad Reserve, 1994-05-19
b. female, South Africa: Limpopo, Mphaphuli Cycad Reserve, 1994-05-19
c. female, South Africa: Limpopo, Tzaneen, farm Everon, 2007-02-18
d. male, Mozambique: Macaneta, 2012-12-26 emerged
e. female, Mozambique: Macaneta, 2012-12-29 emerged
f. female, South Africa: KwaZulu-Natal, Manguzi, 1989-03-26
g. male, South Africa, KwaZulu-Natal, Ngoye Forest Reserve, 2012-06-16
h. female, South Africa, KwaZulu-Natal, Ngoye Forest Reserve, 2012-03-22
i. female, South Africa, KwaZulu-Natal, Ngoye Forest Reserve, 1998-04-26
j. female, South Africa, KwaZulu-Natal, Ngoye Forest Reserve, 1998-04-28
k. male, South Africa, KwaZulu-Natal, Krantzkloof Nature Reserve, 1994-09-15
l. female, South Africa, KwaZulu-Natal, Shongweni, Delville Wood, 2004-02-14
m. male, South Africa, Eastern Cape, East London, Kwelera river, 1993-01-22
n. female, South Africa, Eastern Cape, Port St Johns, 2007-04-05
o. male, South Africa, KwaZulu-Natal, Shongweni, Delville Wood, 2004-02-14.