LRF JRL
The Journal of Research on the Lepidoptera
Volume 43: 37-47
THE LEPIDOPTERA RESEARCH FOUNDATION, 21 December 2010
ISSN 0022-4324 (print)
ISSN 2156-5457 (online)

Evidence for the existence of three species in the genus *Archaeoattacus* (Lepidoptera: Saturniidae)

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Abstract. 27 specimens of the genus *Archaeoattacus* Watson [*in* Packard], 1914 were DNA barcoded. This resulted in three clearly different clusters: the first is a purely Himalayan group (i.e., nominotypical *Archaeoattacus edwardsii* (White, 1859)); the second is *Ar. staudingeri* (Rothschild, 1895) from Sundaland including the Malay Peninsula; the third comprises samples from all other parts of the continental range of the first species excluding the Himalaya, but also including the Malay Peninsula. For this population the name *Ar. malayanus* (Kurosawa & Kishida, 1984), **stat. n.** is available. The relationships between these three species as inferred from DNA barcode analysis were unexpected, with *Ar. staudingeri* being very close to *Ar. malayanus*, while *Ar. edwardsii* is more genetically distant in spite of the close similarity in morphology. Small, but evidently constant differences in male genitalia between the Himalayan *Ar. edwardsii* and the Indochinese *Ar. malayanus* support the distinction. The rooted mtDNA barcode tree, a distribution map, the types of the three species involved and several male genitalia are illustrated.

Key words: DNA barcoding, Oriental region, integrative taxonomy.

Introduction

The first two authors (W.A.N. & S.N.) were recently asked by Jeremy D. Holloway, London, about the status of several Sundanian species of Saturniidae for his new checklist of the Lepidoptera in this area. After preliminary analyses of the mtDNA COI barcode data we had gathered for the oriental genus *Archaeoattacus* Watson [*in* Packard], 1914, we observed genetic divergences suggesting the existence of three distinct species, thus contrasting with the current taxonomy of the genus recognizing only two species: *Ar. edwardsii* (White, 1859) and *Ar. staudingeri* (Rothschild, 1895) (see, e.g., Holloway, 1987: 112; Beck & Nässig, 2008: 160).

This result, which was not a total surprise to us since we had already seen similar patterns elsewhere (e.g., Naumann & Nässig, 2010), is further investigated in this work through an integrative approach combining molecular and morphological data.

History

The genus *Archaeoattacus* was described by J. H. Watson *in* Packard (1914: 265); its type species by original designation is *Attacus edwardsi* [*sic, recte edwardsii*] White (1859: 115) (Fig. 2), type locality "Dhargeeling" [= Darjiling, West Bengal, India].

A second species, *Attacus staudingeri* Rothschild, 1895(: 36) (Fig. 4), was already included into *Archaeoattacus* by Watson *in* Packard (1914: 265) and

*77th contribution to the knowledge of the Saturniidae. (76th contribution: Nässig, W. A., Kitching, I. J., Peigler, R. S., & Treadaway, C. G. (2010): The group of *Cricula elaezia*: Comments on synonyms and priority questions, with illustrations of barcode similarity trees, distribution maps, a revised checklist and a formerly unknown female (Lepidoptera: Saturniidae). Nachrichten des Entomologischen Vereins Apollo, Frankfurt am Main, N.F. 31 (3): 145-165.)
**20th contribution to the Saturniidae fauna of China. (19th contribution: Naumann, S., & Nässig, W. A. (2010): Two species in *Saturnia* (*Rinaca*) *zuleika* Hope, 1843 (Lepidoptera: Saturniidae). Nachrichten des Entomologischen Vereins Apollo, Frankfurt am Main, 31 (3): 127-143.)

Received: 26 October 2010
Accepted: 29 November 2010

later also by, e.g., Schüssler (1933: 22) and Bouvier (1936: 321-322). Its type locality is "NW Java" [probably correct: W Java, see below]. Seitz (1926: 502-503) introduced a misspelling ("‡*Archaeattacus*") without using it at the generic level and without making any clear distinction from species within the genus *Attacus*.

Watson *in* Packard (1914: 265) suggested to probably also include as third species in *Archaeoattacus* "a new smaller species, as yet undescribed, from Thibet, which M. Charles Oberthür has shown me in his collection." This species was described by Oberthür (1914: 56) as *Desgodinsia watsoni* [gen. et sp. n.], but because of homonymy of the generic name (see Fletcher & Nye, 1982: 50, 145), it was then for a long time included in the genus *Samia* Hübner, 1819 (for a review, see, e.g., Lemaire & Peigler, 1982). Much later Brechlin (2007) described a new genus, *Archaeosamia* Brechlin, 2007, for the species *watsoni*.

About 50 years after Seitz, Schüssler and Bouvier, treating *Archaeoattacus* as a subgenus within *Attacus*, Kurosawa & Kishida (1984: 132) described *Attacus* (*Archaeoattacus*) *edwardsii malayanus* (Fig. 3), a subspecies from the "Cameron Highlands, Malay Peninsula." Brosch *et al.* (1999: 39) formally synonymized this subspecies with *Ar. edwardsii*, because there did not appear to be constant and convincing differences from the broadly distributed non-Himalayan Asian mainland population in external and ♂ genitalia morphology. Peigler (1983 and especially 1989: 113) described some differences between the Malaysian and "Indian" specimens, but interpreted this as a clinal grade between "India" and Peninsular Malaysia along the Indochinese Peninsula.

This subspecies *malayanus* was also recorded from Borneo (Malaysia, Sarawak, near Miri) by Fukuda (2001: 90). However, this locality is doubtful (Peigler & Naumann, 2003: 32 stated categorically that this record is erroneous; U. & L. H. Paukstadt, 2006: 178-179 expressed doubt; but compare U. & L. H. Paukstadt, 2010: 163 where the authors mentioned "very few scattered records for Borneo"). There have been extensive collecting efforts in that area of Borneo, and to our knowledge this species was not found again. We think that it might have been either some mislabelled traders' material that probably came from West Malaysia or even Thailand or further North, or, alternatively, it might have been a recently introduced population. A natural immigration into Sarawak from the Malay Peninsula, for a species preferring mountainous environments (U. & L. H. Paukstadt, 2006: 178-179 classified the taxon explicitly as a "highland taxon"), is, however, unlikely.

Lampe (1984 [20. x.], 1985) was the first author to report the sympatric occurrence of *Ar. edwardsii* and *Ar. staudingeri* on the Malay Peninsula; the paper by Kurosawa & Kishida (1984 [xii.]) was published shortly after in the same year, and they evidently did not know *Ar. staudingeri* from the Peninsula at that time.

Results of the DNA barcode analysis: New evidence suggesting the existence of three distinct species

A total of 27 DNA barcodes were generated (see Decaëns & Rougerie, 2008 for details and references relative to the laboratory protocols used) and analysed, including 16 samples of *Ar. edwardsii sensu lato* and 11 samples of *Ar. staudingeri*. The sample distribution for the former species ranges from West Bengal (Himalayan India) to the Cameron Highlands (Peninsular Malaysia), thus encompassing the range of the typical *Ar. edwardsii* (described from West Bengal) and of the synonymized subspecies *malayanus* (described from the Cameron Highlands). The generation of DNA barcodes for samples from other regions (e.g. India: Nagaland; Laos; Vietnam) is still pending, but these are not expected to affect the results presented here.

We also included in our analysis a few specimens of the closely related genera *Samia* and *Archaeosamia* as outgroups. [*Archaeosamia* is generally included within *Samia* (see Peigler & Naumann, 2003), and *Samia*, in addition to *Attacus* Linnaeus, 1767 and *Coscinocera* Butler, 1879, is often considered to be closely related to *Archaeoattacus*.]

The dataset for all the samples used in our analyses is publicly accessible on Bold (The Barcode of Life Data Systems, see Ratnasingham & Hebert, 2007) within the following projects: SNPUB, SKPUB, RRPUB, MPPUB and SWNPR. Sequences have also been deposited in GenBank (see Table 1).

The preliminary analysis of sequence similarity using the analytical component of Bold (Neighbor Joining analysis based on K2P distances) revealed the existence of three distinct genetic clusters, and this pattern was confirmed by analysis of the sequences using the maximum parsimony (MP) and maximum likelihood (ML) phylogenetic reconstruction methods (results not shown), all three methods yielding the same general topology. Here we present the results of the Neighbor Joining (NJ) analysis run in MEGA4 (Tamura *et al.*, 2007) using K2P distances, with bootstrap support values calculated after 1000 replications.

Table 1. GenBank Accession numbers for the specimens used here.

Sample ID	Process ID	GenBank	Species	Deposition	Sequence Length	Sex	Country, Province/Island
BC SNB 1891	SASNB796-10	**HQ579828**	*Archaeoattacus edwardsii*	CSNB	658[0n]	♂	Bhutan
BC SNB 1892	SASNB797-10	**HQ579829**	*Archaeoattacus edwardsii*	CSNB	658[0n]	♂	Bhutan
BC SNB 1893	SASNB798-10	**HQ579830**	*Archaeoattacus edwardsii*	CSNB	658[0n]	♂	India, Arunachal Pradesh
B3220-wn-G02	SAWNA260-09	**GU703545**	*Archaeoattacus edwardsii*	SMFL	658[0n]	♂	India, West Bengal
BC-MNHN0032	SPMNP025-07	**HQ599803**	*Archaeoattacus malayanus*	MNHN	658[0n]	♂	China, Yunnan
BC-MNHN0033	SPMNP026-07	**HQ599804**	*Archaeoattacus malayanus*	MNHN	658[0n]	♂	China, Yunnan
BC-Roug1089	SATWA995-07	**HQ599806**	*Archaeoattacus malayanus*	CRRR	609[0n]	♀	China, Yunnan
BC-Roug1090	SATWA996-07	**HQ599805**	*Archaeoattacus malayanus*	CRRR	609[0n]	♂	China, Yunnan
BC-SK0202	SASKA202-07	**HQ599810**	*Archaeoattacus malayanus*	CSKK	474[0n]	♂	Malaysia, Pahang
BC-SK0203	SASKA203-07	**HQ599809**	*Archaeoattacus malayanus*	CSKK	658[0n]	♂	Malaysia, Pahang
BC-SK0207	SASKA207-07	**HQ599808**	*Archaeoattacus malayanus*	CSKK	658[0n]	♂	India, Meghalaya
BC SNB 1889	SASNB794-10	**HQ599807**	*Archaeoattacus malayanus*	CSNB	539[1n]	♂	Thailand, Ranong
BC SNB 1890	SASNB795-10	**HQ579827**	*Archaeoattacus malayanus*	CSNB	658[0n]	♂	Thailand, Chiangmai
B3220-wn-F12	SAWNA258-09	**GU703355**	*Archaeoattacus malayanus*	SMFL	658[0n]	♂	China, Yunnan
B3220-wn-G01	SAWNA259-09	**GU703352**	*Archaeoattacus malayanus*	SMFL	567[0n]	♂	Myanmar
BC-MNHN0031	SPMNP024-07	**HQ599802**	*Archaeoattacus malayanus*	MNHN	658[0n]	♂	China, Yunnan
BC-SK0204	SASKA204-01	**HQ599814**	*Archaeoattacus staudingeri*	CSKK	658[0n]	♂	Malaysia, Perak
BC-SK0205	SASKA205-07	**HQ599813**	*Archaeoattacus staudingeri*	CSKK	658[0n]	♂	Malaysia, Sabah (Borneo)
BC-SK0206	SASKA206-07	**HQ599812**	*Archaeoattacus staudingeri*	CSKK	658[0n]	♀	Malaysia, Perak
BC SNB 1884	SASNB789-10	**HQ579822**	*Archaeoattacus staudingeri*	CSNB	658[0n]	♀	Indonesia, Jawa Timur
BC SNB 1885	SASNB790-10	**HQ579823**	*Archaeoattacus staudingeri*	CSNB	564[0n]	♂	Indonesia, Jawa Timur
BC SNB 1886	SASNB791-10	**HQ579824**	*Archaeoattacus staudingeri*	CSNB	638[1n]	♂	Indonesia, Kalimantan Tengah
BC SNB 1887	SASNB792-10	**HQ579825**	*Archaeoattacus staudingeri*	CSNB	658[0n]	♂	Indonesia, Sumatera Barat
BC SNB 1888	SASNB793-10	**HQ579826**	*Archaeoattacus staudingeri*	CSNB	658[0n]	♀	Malaysia, Sabah (Borneo)
B3220-wn-F07	SAWNA253-09	**HQ599811**	*Archaeoattacus staudingeri*	SMFL	407[0n]	♂	Indonesia, Sumatra
B3220-wn-F09	SAWNA255-09	**GU703357**	*Archaeoattacus staudingeri*	SMFL	658[0n]	♂	Indonesia, Java
B3220-wn-F10	SAWNA256-09	**GU703354**	*Archaeoattacus staudingeri*	SMFL	658[0n]	♂	Malaysia, Sabah (Borneo)
B3220-wn-F04	SAWNA250-09	**GU703543**	*Samia cynthia*	SMFL	658[0n]	♂	Japan
B3220-wn-F05	SAWNA251-09	**GU703544**	*Samia cynthia*	SMFL	658[0n]	♂	Japan
B3220-wn-F06	SAWNA252-09	**GU703356**	*Samia cynthia*	SMFL	658[0n]	♀	Japan
BC-Roug1035	SATWB068-07	**HQ599815**	*Archaeosamia watsoni*	CRRR	634[0n]	♂	China, Fujian
BC SNB 1872	SASNB777-10	**HQ599816**	*Archaeosamia watsoni*	CSNB	658[0n]	♂	China, Guangdong
BC SNB 1876	SASNB781-10	**HQ579820**	*Archaeosamia watsoni*	CSNB	658[0n]	♂	China, Jiangxi

The three clusters within the genus are:
(1) a Himalayan group of *Archaeoattacus edwardsii* specimens;
(2) *Ar. staudingeri* from Sundaland including the Malay Peninsula (Lampe, 1984, 1985);
(3) a group of *Ar. edwardsii* samples from non-Himalayan continental Asia (China, Thailand), including the Malay Peninsula.

These three clades, as displayed in Fig. 1, are all well supported (bootstrap values of 100, 82 and 76 for the clusters (1), (2) and (3) described above, respectively). Clearly, *Ar. edwardsii* as currently defined (including all populations from the Himalaya, mainland Asia and the Malay Peninsula) does not form a cohesive genetic group with respect to DNA barcode data, and the genetic structure rather suggests the existence of three distinct lineages, with the lineage distributed in non-Himalayan mainland Asia and the Malay Peninsula

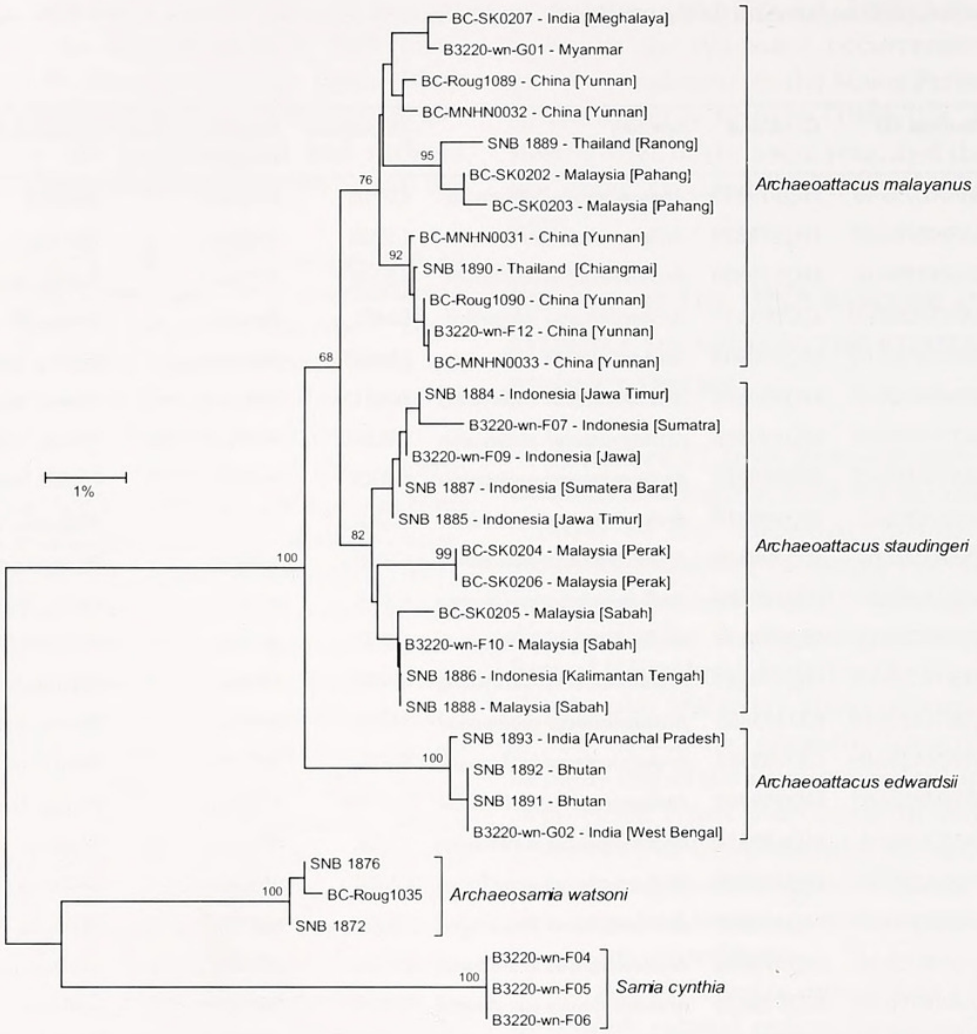


Figure 1. Neighbor Joining tree based on K2P distances for the 27 representatives of genus *Archaeoattacus* used in this study, plus 6 selected outgroups within the genera *Samia* and *Archaeosamia*. The tree was constructed using MEGA4, including all codon positions, with all ambiguous positions removed for each sequence pair. Bootstrap support values for the main genetic clusters are given above branches and were generated after 1000 replicates.

representing the currently synonymized taxon *malayanus*. Besides, the topology of the phylogenetic tree (as recovered from NJ, MP and ML analyses) suggests that malayanus is more closely related to *Ar. staudingeri* than to *Ar. edwardsii* (as also reflected by K2P distances: the smallest distance observed between *malayanus* and *staudingeri* is 1.4%, versus 3% between *malayanus* and the typical *edwardsii*).

This contradicts the original placement of *malayanus* as a subspecies of *edwardsii*, and suggests its validity as a distinct species given its occurrence in sympatry with *Ar. staudingeri* in the Malay Peninsula, a well-defined species from which it can easily be distinguished by clear differences in external morphology and small, but visible differences in ♂ genitalia. Whereas the external morphology of the moths suggested, in contrast, that *edwardsii* and *malayanus* are very closely related taxa, it is interesting to note that the unexpected pattern of relationships described above is consistent with the relationships and the distribution data reported for other groups of Saturniidae (e.g., *Saturnia* (*Rinaca*) *zuleika* Hope, 1843 and *S.* (*R.*) *lesoudieri* Le Moult, 1933, see Naumann & Nässig, 2010, but without the Sundaland component).

Further morphological evidence

We were unable to reliable distinguish the Himalayan *Ar. edwardsii* and the Indochinese *Ar. malayanus* in external imaginal morphology. However, there appear to be subtle consistent differences in ♂ genitalia morphology: The genitalia of *Ar. edwardsii* (GP WAN SMFL nos. 2127/10-2129/10; see Fig. 5) are

slightly larger, the valve apex is slightly more elongate and rounded; the phallus is slightly longer, with a slightly different shape, and its apical sclerotisation before the vesica is longer. These differences cannot easily be seen from photographs (scales are often slightly different among pictures), but when the genitalia are compared directly, they are easily visible. There is some variability in the ♂ genitalia of *Ar. malayanus* studied by us (GP WAN/SMFL no. 2130/10-2132/10; GP SNB 374/99-382/99, 394/99-395/99; Figs. 6-10), but all are smaller than *Ar. edwardsii*, and there is evidently no overlap with that species. There is almost no difference in ♂ genitalia between *Ar. malayanus* and *Ar. staudingeri* (see Fig. 11), an observation corroborating the relationships resulting from the analysis of barcode data.

The preimaginal instars of *Ar. edwardsii* from N. India (Himalaya) and of *Ar. staudingeri* from N. Sumatra were illustrated in colour by Lampe (2010: 260-261, pls. 254-255, legend p. 357) and, *Ar. staudingeri* from Borneo, by Häuser *et al.* (1996) and also (but with respect to Himalayan *Ar. edwardsii* or Assamese *Ar. malayanus*?) in several other publications. The differences in larval morphology between the Himalayan *Ar. edwardsii* and the Sundanese *Ar. staudingeri* are only minor but clear (compare the illustrations in Lampe, 2010). The preimaginal stages of the Indochinese population of *Ar. malayanus* have evidently not yet been described and illustrated in colour. Pinratana and Lampe (1990: pl. 1, fig. 1), show a larva of *Ar. edwardsii* from "N. India" (probably from the same source like in Lampe 2010?), but as the authors often do not provide exact locality data, this is not fully conclusive ("N. India" may be either the Himalayan *Ar. edwardsii* or the Assamese *Ar. malayanus*!) and requires further studies on basis of the updated taxonomy of the genus.

As a consequence of the congruent results of our molecular and morphological analyses, we propose to reinstate the previously synonymized taxon *malayanus* as a valid species within the genus *Archaeoattacus*. An updated checklist for the genus is provided below, including the geographical distribution of the three species as currently known to us.

It is interesting to note that in their later instars, the larvae of *Archaeoattacus*, as far as is known, present a unique characteristic that we consider a possible behavioural synapomorphy for the genus: they could all be considered "lumberjacks," chewing the twigs of their foodplants and letting them fall to the ground (e.g., Kuyten, 1962; Nässig, 1983; U. & L. H. Paukstadt, 1989; Häuser *et al.*, 1996). Also, the mature larvae produce a lot of silk and use it to fix many leaves, after cutting the petioles, to the twig near their cocoon, possibly to enhance its camouflage. Both traits may occasionally occur in species of the genus *Attacus*, but they have never been reported as regular behaviour there.

Abbreviations

Abbreviations of collections:

BMNH: The Natural History Museum, London (formerly British Museum (Natural History)), U.K.
CRRR: Collection Rodolphe Rougerie, Rouen, France.
CSKK: Collection Steve Kohll, Kayl, Luxembourg.
CSLL: Collection Swen Löffler, Lichtenstein/Sachsen, Germany.
CSNB: Collection Stefan Naumann, Berlin, Germany.
CWAN: Collection Wolfgang A. Nässig, now in SMFL.
MNHN: Muséum National d'Histoire Naturelle, Paris, France.
MZB: Museum Zoologicum Bogoriense, Cibinong, Bogor, West Java, Indonesia.
NSMT: National Science Museum, Natural History, Tokyo, Japan.
SMFL: Senckenberg-Museum, Frankfurt am Main, Lepidoptera collection, Germany.
ZMHU: Zoologisches Museum der Humboldt-Universität, Berlin, Germany.

Other abbreviations and conventions:

‡Invalid and unavailable name.
BC [no.] Barcode [with number].
GP [no.] Genitalia dissection [with number].

Annotated checklist of the genus *Archaeoattacus*

Distribution data are also illustrated on a map (see Map). The doubtful records for SW India from Cotes (1891) are not included.

Archaeoattacus edwardsii (White, 1859)

Attacus edwardsii White (1859: 115, pl. Annulosa lvii); type locality [India, West Bengal], [Darjiling]. Type (syntype) in BMNH [photo examined, Fig. 2].

Distribution: Himalaya (N. India, Nepal, Bhutan, China: Tibet).

Nepal: Allen (1993: 54, central & eastern hills up to 2500 m, Pokhara valley 350 m); Haruta (1992: 93, Godavari; 1994: 159, Khosi, Pheksinda).

India, West Bengal: Darjiling, Mangpu road, 1900 m, leg. W. Thomas, BC B3220-wn-G02, GP WAN/SMFL 2127-2129/10 (CWAN in SMFL). – Uttarakhand: Masuri (Mussoorie): Cotes (1891: 73). – Arunachal Pradesh (north of the Brahmaputra river, Himalaya): Along District, near Rapum, 2000-2100 m, 28.31589° N, 94.15221° E, leg. Bretschneider, BC 1893 SNB (CSNB). Near Rapum, 2000 m, 28.53176° N, 94.24941° E, leg. Bretschneider (CSNB, CSLL). Rapum, 1800 m, 28.31995° N, 94.15325° E, leg. Bretschneider (CSNB). [For Arunachal Pradesh, see also below under *Ar. malayanus*.]

China: South Central Tibet, Linzhi (29°38'44.84" N, 94°22'22.85" E): Zhang *et al.* (1986: col. pl. 6, fig. 55 ♂).

Bhutan: Mongar Dzongkhag, 5.5 km NNW Limithang, Yonkola, 1600 m, 27°18'31" N, 91°9'48" E, leg. P. Kautt & S. Naumann (CSNB). Thimphu Dzongkhag, Mo Chu valley, 16 km NW Punakha, 1500 m, 27°41'54" N, 89°46' 8" E, leg. P. Kautt & S. Naumann, BC 1891 & 1892 SNB (CSNB).

Ar. edwardsii ranges in the Himalaya from about 350 m to at least 2500 m (both extremes reported in

Nepal, Allen, 1993: 54).

♂♂ arrived in Bhutan at light between 20:00 and 23:30 h; specimens were observed flying in Nepal between vi. and viii., in West Bengal in late vi., in Bhutan in mid-vi., in Arunachal Pradesh in mid-vii.

Cotes (1891: 73) reported *Ar. edwardsii* also from Mysore (Karnataka) and the Western Ghats (cited by, e.g., Peigler, 1989: 113, but not listed by Arora & Gupta, 1979). However, we have never seen specimens from there and believe that this might be based on a misidentification. In case that there really is a population of an *Archaeoattacus* living in western and southwestern India, specimens should be barcoded to assess their identity.

Archaeoattacus malayanus (Kurosawa & Kishida, 1984), **stat. n.**

Attacus (*Archaeoattacus*) *edwardsii malayanus* Kurosawa & Kishida (1984: 132); type locality Peninsular Malaysia, Cameron Highlands. Holotype (by original designation) in NSMT, Japan [photo examined, Fig. 3].

Formally synonymized with *Ar. edwardsii* by Brosch *et al.* (1999: 39).

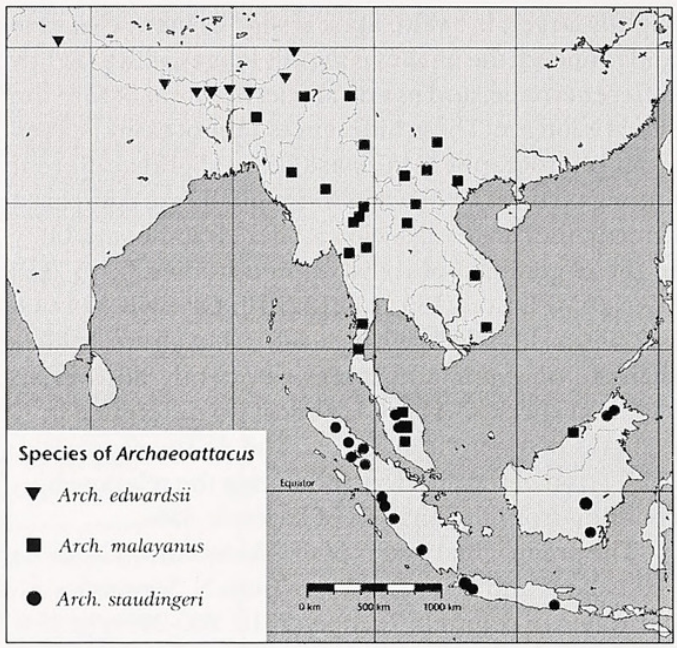
Distribution: India (Meghalaya; southern Arunachal Pradesh?, Nagaland?, no barcode results yet from these latter two); Myanmar, China, Thailand, Laos, Vietnam, Peninsular Malaysia; ?Borneo?.

India, Meghalaya: Khasi Hills, vic. Shillong, traders' material, GP WAN/SMFL no. 409/86, 2131/10-2132/10 (CWAN in SMFL). Khasi Hills, Shillong env., Mawphlang, 600-1000 m, GP 374, 375, 382/99 SNB, BC 1894 SNB (CSNB). Meghalaya, [Khasi Hills], BC SK 0207. — Arunachal Pradesh (south of the Brahmaputra river), Jairampur, [Changlang District, 20°21'5" N, 96°0'59" E; the city is at an elevation of around 880-900 m], from a photo by A. Vaidya (*in litt.* to I. J. Kitching, pers. comm.). [This specimen comes from a locality south of the Brahmaputra river valley and is most likely *Ar. malayanus*, but we have no specimens and barcode results from there.]

Myanmar, Kachin State: Nan Sa Bon, 25 km N Putao, 800 m, 27°23' N, 97°40' E, leg. S. Murzin & V. Siniaev (CSNB). Zi Yar Dam, 65 km NW Putao, 1250 m, 27°50' N, 97°1' E, GP 376/99 SNB, leg. S. Murzin & V. Siniaev (CSNB). Wa Sa Dam, 50 km NW Putao, 950 m, 27°39' N, 97°2' E, leg. S. Murzin & V. Siniaev (CSNB). Nan Thi, 50 km E Putao, 950 m, 27°31' N, 97°55' E, GP 377/99 SNB, leg. S. Murzin & V. Siniaev (CSNB). – Shan State: Shoe Pin (Shopping) Village, Utut Ni Pass, 1773 m (CSLL). Sekya Inn Village, Utut Ni Pass, ca. 10 km W Pindaya, 1712 m (CSLL). – Chin State: Mt. Victoria (Nat Ma Toung) Nationalpark, Chin Hills, Mindat City, Kall Nue, 1457 m (CSLL). – Kayin State: Dawna, NE Moulmein [Mawlamyine], ca. 1300 m, GP 378/99 SNB (CSNB, CSLL). – Tanintharyi Prov.: Tenasserim (CSLL) [no barcode yet available].

China, Yunnan: Zhu & Wang (1996). (NW), Dexin [Deying], Baimaxueshan, 4000 m [more reliable: 2500 m], leg. Ying *et al.*, BC B3220-wn-F12 (CSNB, CWAN in SMFL, CSLL). SW, Daxueshan, Yongde, 3500 m (CSLL). S, Xishuangbanna, 27 km NW Jinghong, vic. Beng Gang Ha Ni, 1800-2000 m (CSLL). – Guangxi: W. Guangxi, near E Yunnan borderline, Laogongshan, Xiling, 1800 m, leg. Li (CSNB).

Note: The altitudes given in the locality lists, especially for Chinese localities, refer mainly to the records of dealers, and we strongly suspect that altitudes given as, e.g. 4000 m or higher, for localities in Yunnan or Tibet, refer to the height of the mountain summit rather than to the real collecting locality somewhere on its slopes; serious data confirmed by European collectors range over lower altitudes (see also Naumann & Nässig, 2010: 56).



Map. Distribution data of the 3 species of the genus *Archaeoattacus* in SE Asia. Symbols may represent more than one locality in close proximity; not all places from the labels were located on maps. Symbols of type localities slightly enlarged. Localities with "?" mean either the locality does not appear to be part of natural distribution (*Ar. malayanus* in Borneo, Sarawak; Fukuda, 2001), or it has only been located approximately (Mt. Bayutawar, Kalimantan Selatan, CSNB), or the locality is based on a photograph only (*Ar. malayanus* in southern Arunachal Pradesh). Data compiled from literature, CWAN, SMFL, CSBN, CSLL and other sources. Map base from OMC, Martin Weinelt (www.aquarius.geomar.de/omc/, downloaded on 23. v. 2006; this address is no longer in existence), modified and localities added.

Thailand, Chiang Rai Prov.: Huai Khom (CSLL). – Chiangmai Prov.: Doi Phahompok, vic. Mae Ai, 2000 m, leg. T. Ihle, BC 1890 SNB (CSNB, CSLL). Vic. Chiangmai/Doi Inthanon, no details, trader's material (Pinratana & Lampe, 1990: 4, as "*Ar. edwardsii*"; CWAN [GP WAN/SMFL 2130/10] in SMFL, CSLL [1500 m]). Doi Inthanon, road km 37.4 ranger station, 1681 m (CSNB). Doi Suthep, 1400 m (CSLL). Doi Angkhang, 1400 m (CSLL). Maetaeng, GP 379/99 SNB (CSNB). – Tak Prov.: Doi Mussoe, 812 m (CSLL). – Ranong Prov.: Isthmus of Kra, Ranong TV Station, 500 m, BC 1889 SNB (CSNB, CSLL).

Laos: Brosch *et al.* (1999: 38); Central Laos, ca. 100 km E Louangphrabang (= Luangprabang), ca. 1400-1600 m (CWAN in SMFL). Phongsaly, Gnoi-ou (CSNB). – Louang Prabang Prov.: Phou Khoun, 1500 m (CSLL). – Vientiane Prov.: Ban Viang Kham, ca. 15 km S Phou Khoun, 950 m (CSLL). – Attapu Prov.: Dak Pok (CSLL).

Vietnam, [Hoang Lien Son/Lao Cai Prov.]: Mt. Fansipan area, Chapa vic., several localities, 1600-2400 m, GP 381 & 395/99 SNB (CSNB, CWAN in SMFL). Ta Phin, 1900 m (CSLL). – [Prov.] Plato Thai Nguyen: Mt. Ngoc Linh, 15°2' N, 107°59' E, 900-1400 m (CWAN in SMFL). – Lam Dong Prov.: Bhu Son, Lam Ha, 1320 m (CSLL).

Peninsular Malaysia: Genting Highlands, 1500 m (Lampe, 1984,

1985); Cameron Highlands (Kurosawa & Kishida, 1984); U. & L. H. Paukstadt (2004: 138-140; *Ar.* "*edwardsii*" is a "highland taxon"). Cameron Highlands, leg. H. F. Wong, GP 394/99 SNB (CSNB). Cameron Highlands, rd. Ringlet–Tanah Rata, Bharat tea estate, ca. 1800 m, GP 380/99 SNB, leg. S. Naumann (CSNB). Cameron Highlands, Tanah Rata, 1400-1500 m (CSLL). Cameron Highlands, Gunung Berinchang, 1700 m (CSLL). West, Fraser Hill (CSLL). – Perak Prov.: 83 km E Gerik, 920 m (CSLL).

?Borneo: Malaysia, Sarawak, Miri? Doubtful locality data (mislabelled traders' material or introduced population?) from Fukuda (2001: 90), see Peigler & Naumann (2003: 32), U. & L. H. Paukstadt (2006: 178-179; but also 2010: 163).

Ar. malayanus is ranging from ca. 500-2400 m.

Pinratana and Lampe (1990: 4) report specimens collected in Chiang Mai province, Thailand, in v.-viii. Specimens were found in Myanmar in iii. (Tenasserim), viii./ix. (other provinces), in Yunnan in v. and other months, in S Laos in iii., in Peninsular Malaysia in xii.-v. and ix. The tropical populations will probably be found at any time of the year, except during extended dry periods.

As there was never any distinction made between the Himalayan and extra-Himalayan populations of "*edwardsii*" prior to this work, and because both species are found in "North India" (i.e., *Ar. edwardsii* in the Himalaya only, *Ar. malayanus* in Meghalaya, probably southern Arunachal Pradesh and Nagaland), the literature concerning distribution, morphology and preimaginal stages (and other papers) is rather ambiguous with respect to the actual taxon treated therein. For example, the specimen from Myanmar figured by Peigler and Naumann (2003: fig. 89) as "*Archaeoattacus edwardsii*" surely is *Ar. malayanus*.

Archaeoattacus staudingeri (Rothschild, 1895)

Attacus staudingeri Rothschild (1895: 36); type locality "NW Java;" from label of lectotype: "Tjisolok, [18]92-93, G[e]relak" [6°57'0" S, 106°26'0" E, which in fact is W, but not really "NW" Java (close to the southern coast of W Java!)]. – Lectotype in ZMHU (designated by Nässig *et al.*, 1996: 25) [examined, Fig. 4].

Distribution: Sundaland (Sumatra, Peninsular Malaysia, Borneo, Java). – Peigler and Wang (1996: 59) suspected *Archaeoattacus staudingeri* to also live on the island of Bali, based on a picture on a T-shirt. However, this has not been subsequently confirmed (see Peigler & Naumann, 2003: 47), and we believe that the species does not inhabit Bali. From the eyespots shown on the T-shirt image, we suppose that a specimen or, more likely, a photograph of *Archaeoattacus edwardsii* or *Ar. malayanus* was the model for that (not quite naturalistic) depiction.

Indonesia, Java: West Java, Tjisolok, G[e]relak, Java occ. mer. [= NW Java], type locality (of the lectotype); Gn. Halimun National Park, 900-1000 m; Gn. Gedeh, 1000 m; Goalpara, 1500 m (all in MZB, see U. Paukstadt *et al.*, 2008: 229, 231). East Java, Malang, 1200 m, leg. U. & L. H. Paukstadt, BC 1884 & 1885 SNB (CSNB, CWAN in SMFL).

Indonesia, Sumatra: Aceh (= Nanggroe Aceh Darussalam), several localities (Nässig et al. 1996: 25-26; U. & L. H. Paukstadt 2009: 339). – Sumatera Utara, Sibolangit Plateau (van den Bergh 1915). Several localities not far from Lake Toba (e.g., Sindar Raya, 300 m; Naga Raja, 350 m; "Holzweg 3" near Prapat, 1150 m; "Sipirok III", 1300 m), leg. E. W. Diehl (Nässig *et al.*, 1996: 25-26). – Sumatera Barat, Bukittingi [formerly Fort de Kock] (van Eecke 1930). Padangpanjang, 775 m (Nässig *et al.*, 1996: 25-26). Padang, 800 m (SMFL). Mt. Singgalang, 1000 m, leg. S. Jakl (CSNB). Mt. Intan, Solok region, 900 m, (CSNB). Mt. Sanggul, Landai village, 1300 m, leg. S. Jakl (CSNB). 3 km NE Landai, 1200 m, leg. S. Jakl, BC 1887 SNB (CSNB). Mine Tambang, 6 km N Padangaro, 460 m (CSLL). Mt. Korinji (Kerinci), 3 km S Padangaro, 1000 m (CSLL). – Lampung, Pagar Alam, in MZB (Nässig *et al.*, 1996: 25-26, U. Paukstadt *et al.*, 2008: 231). Mt. Pesagi (CSLL).

Indonesia, Borneo, Kalimantan: Kalimantan Tengah, Gn. Payang, 400[-800] m, ca. 0.87742° S, 115.07975° E, BC 1886 (CSNB, CSLL). Kalimantan Selatan, Mt. Bayutawar, 400-800 m (CSNB). Mt. Meratus, 500-700 m (CSLL).

Malaysia, Borneo, Sabah: Mt. Kinabalu area: Taman Kinabalu Park Headquarters (1200-1500 m), Poring Hot Springs (600 m), Sayap (1000-1100 m) (Häuser *et al.*, 1996: 171) (CWAN in SMFL, CSLL). Mt. Trus Madi, 1100[-1600] m, GP 383/99 SNB, BC 1888 SNB (CSNB, CWAN in SMFL, CSLL). Mt. Marapok (CSNB).

Malaysia, Peninsula: Cameron Highlands, 900 m (Lampe, 1984, 1985; CSNB); U. and L. H. Paukstadt (2004: 140-141; *Ar. staudingeri* is a "typical lowland taxon"). – Perak: 30 km E Gerik, 420 m (CSLL).

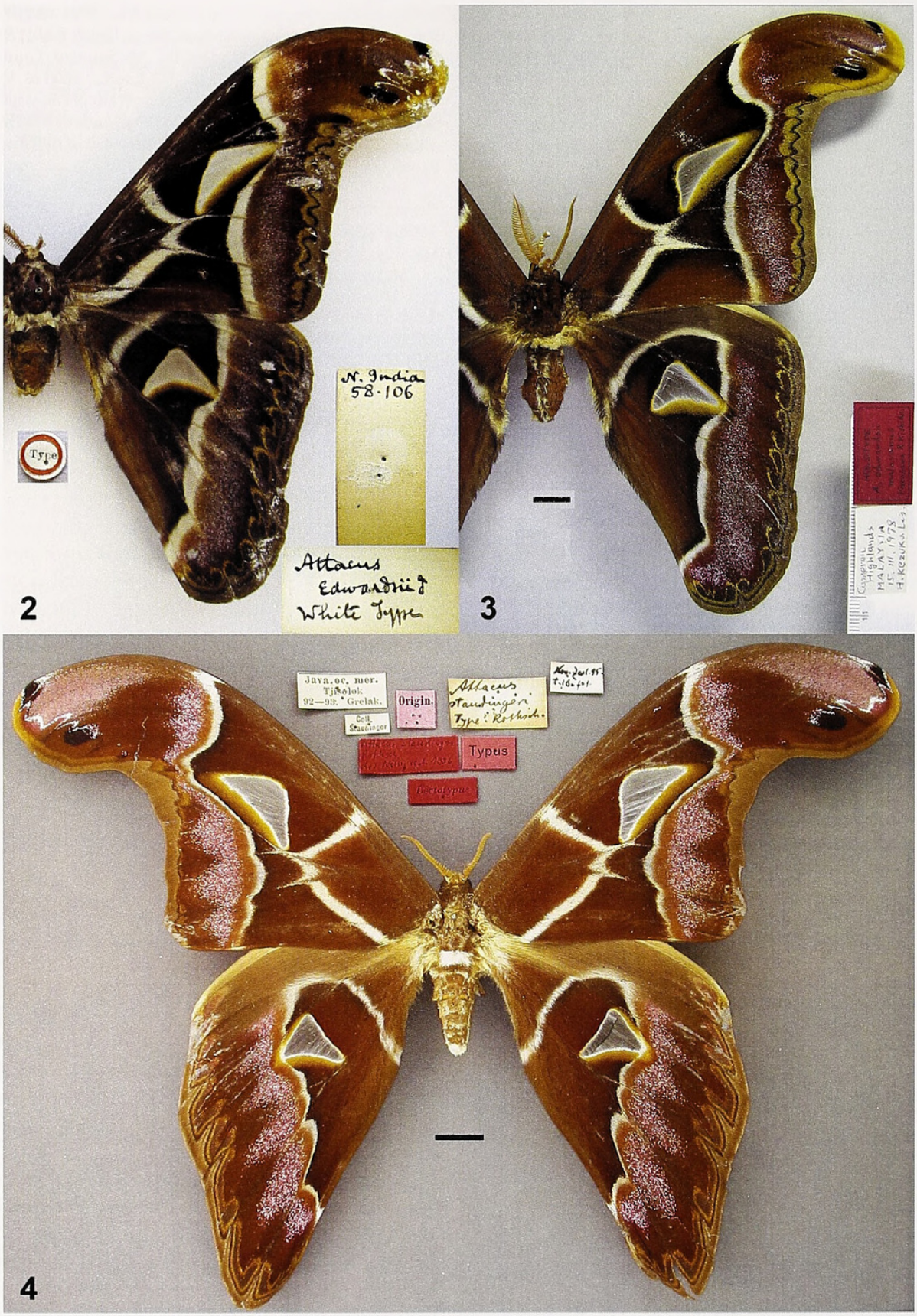
Ar. staudingeri ranges from about 300 to 1800 m elevation (both extremes observed on Sumatra: Nässig *et al.*, 1996: 25-26; U. & L. H. Paukstadt 2009: 339). Observations took place in iii. in Borneo, vi.-x. in Sumatra, ix. in Perak. The tropical populations will probably be found at any time of the year, except during extended dry periods.

Ar. staudingeri was never seriously doubted as being a distinct species; the differences in external imaginal (and larval) morphology are quite clear. Our results based on DNA barcodes, reporting that the species is genetically closer to *Ar. malayanus*, were then rather unexpected.

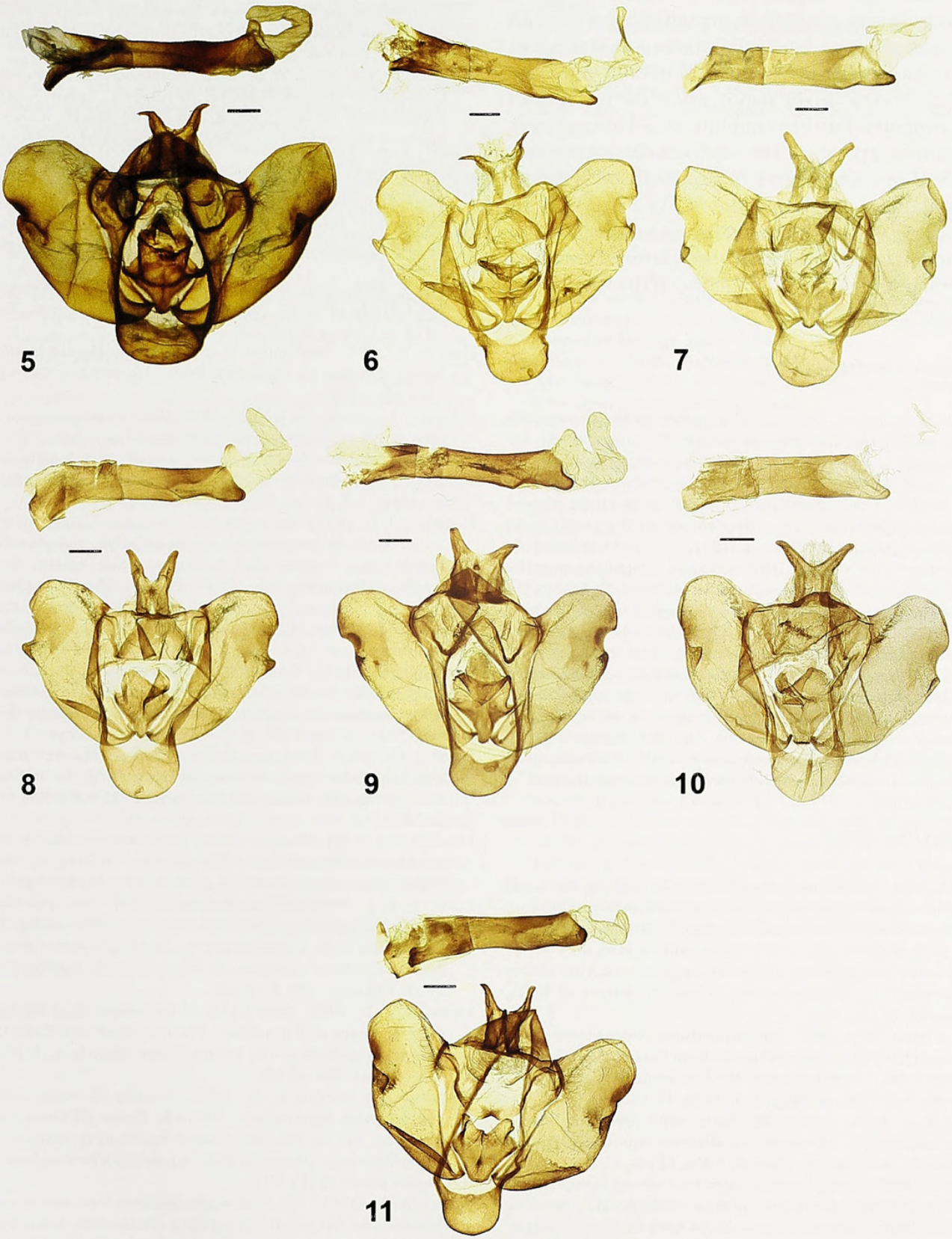
Discussion

Although not supported by the collecting data at the lowest altitudes (which are very similar in all three taxa), the general trait attributed to *Archaeoattacus edwardsii* (including *Ar. malayanus*) of preferring higher elevations and *Ar. staudingeri* preferring lower elevations (U. & L. H. Paukstadt, 2004: 140-141) is probably correct when considering all the data for the many specimens observed, and when considering the highest elevation records at which these taxa have been recorded.

Considering the variation of DNA barcode sequences within each of the three species now recognized within the genus *Archaeoattacus*, it is now interesting to observe a peculiar geographic structure shared by *Ar. malayanus* and *Ar. staudingeri*. The few samples sequenced from the Malay Peninsula (in the case of *Ar. malayanus*, including also the Isthmus of Kra, Thailand, Ranong prov.; we do not yet have barcode data for the specimen from Myanmar, Tenasserim) diverge significantly from those of other conspecific populations (up to 2% and 1.7% within *Ar. malayanus*



Figures 2-4. **2**. Syntype ♂ of *Attacus edwardsii* White, 1859, BMNH (photo © The Natural History Museum, London). **3**. Holotype ♂ of *Attacus* (*Archaeoattacus*) *edwardsii malayanus* Korosawa & Kishida, 1984, NSMT (photo V. Zolotuhin). **4**. Lectotype ♂ of *Attacus staudingeri* Rothschild, 1895, ZMHU (photo S. Naumann). Specimens not to the same scale; scale bars (where present) = 1 cm.



Figures 5-11. ♂ genitalia of *Archaeoattacus species*. **5**. *Ar. edwardsii*, India, West Bengal, Darjiling, GP 2127/10 WAN. **6**. *Ar. malayanus*, Peninsular Malaysia, GP 394/99 SNB. **7**. *Ar. malayanus*, Myanmar, Dawna, GP 378/99 SNB. 8. *Ar. malayanus*, N. Thailand, GP 379/99 SNB. **9**. *Ar. malayanus*, N. Vietnam, GP 381/99 SNB. **10**. *Ar. malayanus*, India, Meghalaya, Khasi Hills, GP 375/99 SNB. **11**. *Ar. staudingeri*, Borneo, Malaysia, Sabah, GP 383/99 SNB. Genitalia not exactly to the same scale; scale bars = 1 mm. Scans ex CSNB: U. Brosch. Phot. 5: W.A.N.

and *Ar. staudingeri*, respectively). There is no evidence that such divergence reflects an actual separation of lineages deserving a particular taxonomic status, but it is very interesting to observe that in both cases, the divergence occurs in the region where the two species live in sympatry. Further sampling would be necessary to confirm this pattern. The observed divergence may be caused by some degree of geographical isolation of populations inhabiting the Malay Peninsula, or alternatively we may be observing an interesting case of incipient speciation driven by reinforcing natural selection in the contact zone between the two species (Hoskin *et al.*, 2005).

Acknowledgements

Special thanks are due to staff members at the Biodiversity Institute of Ontario, University of Guelph, Ontario, Canada, for their assistance in the production of DNA barcodes. The molecular work was funded by NSERC and Genome Canada through a grant to Paul D. N. Hebert. Steve Kohll, Kayl (Luxembourg), kindly allowed us to use his sequence data from the Bold website for our analysis. Swen Löffler, Lichtenstein/Sachs., kindly provided a lot of data from his collection. Ulrich Brosch, Hille, scanned most of the genitalia (those from S.N.). Vadim Zolotuhin, Uljanovsk, kindly sent us the photo of the holotype of *Ar. malayanus* desposited in NSMT, which was not published in colour so far. Jeremy D. Holloway, London, while preparing his new checklist, pushed us to look for the barcode results for *Archaeoattacus* and thus induced the preparation of this paper. Ian J. Kitching, London, helped us with type material data and illustrations from BMNH and had a critical eye on the language of an earlier version of the manuscript. Thanks to Richard "Ric" S. Peigler and an anonymous reviewer for their critical comments on the submitted manuscript which helped us to improve the text.

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