An illustrated and annotated checklist of *Arhopala* Boisduval, 1832, taxa occurring in North Maluku and Maluku, Indonesia (Lepidoptera: Lycaenidae) — Part 6: The *hercules* species-group, with notes on some phenotypes from the New Guinea Region

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Abstract: This paper is the 6th in our series covering the species and subspecies of the lycaenid genus *Arhopala* Boisduval, 1832 that occur in the Indonesian provinces of North Maluku and Maluku and deals with the *hercules* species-group, *sensu* Evans (1957). Eight phenotypes comprising three species and six subspecies (two are polymorphic) are recognised as occurring there. The group ranges from North Maluku to the New Guinea Region. We analysed sequences from one mitochondrial and one nuclear locus to better understand patterns of genetic differentiation in relation to geography and morphology. The taxonomy of the Maluku representatives of the *hercules* species-group is discussed and revised, based on phenotypes, sympatry and DNA sequences. To come to our conclusions, it has been necessary to research some of the phenotypes present in the New Guinea Region. After the Maluku checklist, we provide notes and taxonomic suggestions for some taxa, respectively phenotypes found in the New Guinea region. One new species and one new subspecies are described from Aru: *Arhopala **fowlerorum*** Rawlins & Cassidy, **sp. n.** (holotype = HT male, NHMUK) and *Arhopala tyrannus **jheae*** Rawlins & Cassidy, **ssp. n.** (HT male, RMNH). Two forms are given new names, some new combinations are made, and an old combination revived. Some current synonyms are reversed, and one new synonym is proposed (see a taxonomic summary at the end). A map shows the full range of the *hercules* species-group taxa and includes all the islands and places discussed in the text. All taxa are illustrated in colour.

Keywords: Lepidoptera, Lycaenidae, Theclinae, *Arhopala*, *hercules* species-group, polymorphism, DNA barcodes, new taxa, Indonesia, North Maluku, Maluku.

Illustriertes und kommentiertes Verzeichnis der *Arhopala*-Arten (Lepidoptera: Lycaenidae, Theclinae), die in den Nordmolukken und Molukken (Indonesien) vorkommen — Teil 6: Die *hercules*-Artengruppe, mit Anmerkungen zu einigen Phänotypen aus der Neuguinea-Region

Zusammenfassung: Dies ist die sechste Publikation einer Serie über die Arten und Unterarten der Lycaenidengattung *Arhopala* Boisduval, 1832 aus den indonesischen Provinzen Nordmaluku und Maluku. Sie befaßt sich mit der Artengruppe von *hercules* (*sensu* Evans 1957). Acht identifizierbare Morphen („phenotypes“), die aus drei Arten und sechs Unterarten (davon zwei polymorph) bestehen, werden von dort identifiziert. Die *hercules*-Artengruppe kommt insgesamt von den Nordmolukken bis in die Region von Neuguinea vor. Wir analysierten DNA-Sequenzen von einem mitochondrialen (COI) und einem Kerngen (EF1a), um die Muster der genetischen Differenzierung im Zusammenspiel mit Geographie und Morphologie besser zu verstehen. Die Taxonomie der molukkischen Vertreter der *hercules*-Artengruppe wird auf der Basis von Morphologie, Sympatrie und DNA-basensequenzen diskutiert und revidiert. Es erwies sich als notwendig, einige der Morphen aus der neuguineanischen Region mit zu untersuchen, um das Artenspektrum zu verstehen. Nebst einer Checkliste aus der Molukkenregion geben wir zusätzlich Hinweise und taxonomische Vorschläge zu einigen der Taxa beziehungsweise Morphen („phenotypes“) aus der Neuguinea-Region. Vom Aru-Archipel werden eine neue Art (*Arhopala **fowlerorum*** **Rawlins & Cassidy, sp. n.;** Holotypus = HT Männchen in NHMUK) und eine neue Unterart (*Arhopala tyrannus **jheae*** **Rawlins & Cassidy, ssp. n.;** HT Männchen in RMNH) beschrieben. Zwei Formen bekommen neue infrasubspezifische Namen, einige neue Kombinationen werden aufgestellt und eine alte wird revidiert. Mehrere Synonyme werden revidiert, eine neue Synonymie wird aufgestellt (siehe eine taxonomische Zusammenfassung am Ende). Auf einer Karte werden die im Text behandelten Inseln und Lokalitäten illustriert von der Sulawesi- bis zur Neuguinea-Region. Alle Taxa werden farbig abgebildet.

Introduction

***Arhopala* Boisduval, 1832** (Lycaenidae, Theclinae, Arhopalini) is the 5th genus to be published in NEVA in this series on the lycaenid genera of the Indonesian provinces of North Maluku (Maluku Utara) and Maluku. As *Arhopala* is a large group, we have split the genus into sections for publication. Previous parts (Rawlins et al. 2018a, 2018b, 2018c, 2019a, 2019b) have covered an introduction to the genus and the *anthelus, theba, democritus, eumolphus, centaurus, fulla* and *thamyras* species-groups.

This is the 6th part of *Arhopala* and covers the *hercules* species-group, *sensu* Evans (1957). We recognise eight phenotypes comprising three species and six subspecies (two are polymorphic) as occurring in North Maluku and Maluku.

The taxonomy of the species-group is discussed and a new arrangement for the Maluku taxa is given, based on phenotypes, sympatry and DNA sequences. A table provides the data for all specimens sampled, along with GenBank accession numbers for all DNA sequences. A second table illustrates the pairwise differences between and within some phenotypes. Bayesian tree and Haplotype networks diagrams are provided.

To understand the Maluku *hercules* species-group taxonomy, it has been necessary to research some of the phenotypes present in the New Guinea region. After the Maluku checklist we provide notes and taxonomic suggestions for some taxa and phenotypes found in the New Guinea Region.

One new species and one new subspecies are described, two forms are given new names, some new combinations are made, and an old combination revived. Some current synonyms are reversed, and one new synonym is proposed.

For the biogeography of the region see Vane-Wright & Peggie (1994), Lohman et al. (2011: 209–216) and Rawlins et al. (2014: 5–8). For the purposes of this paper we make the following key points:

- We use the term Maluku to include both the Indonesian political provinces of North Maluku (= Maluku Utara) and Maluku.
- North Maluku province comprises: the Sula islands, the islands we term "northern Maluku" (see below), Obi and Gebe.
- Maluku province comprises: the islands we term "central Maluku" (see below), the Gorong, Watubela and Tayandu Island groups, the Banda Islands, the Kei Islands, the islands of Southwest Maluku (including Wetar), the Tanimbar Islands and the Aru Islands.
- We use the biogeographical term "northern Maluku" to mean the islands of Morotai, Halmahera, Ternate, Bacan, Kasiruta and Mandioli and some associated smaller islands.
- We use the biogeographical term "central Maluku" to mean the islands of Buru, Ambelau, Manipa, Kelang, Buano, Seram, Ambon, Haruku, Saparua, Nusa Laut, Geser and Seram Laut.

A Map shows these islands of Maluku and North Maluku, as well as the places and islands in the Sulawesi and New Guinea Regions that are discussed in the text. The Indonesian western half of the Island of New Guinea along with its associated offshore islands (previously variously known as Irian, Irian Jaya, West Irian, Irian Barat) now consists of two political provinces: West Papua and Papua. We use the term "New Guinea" in its geographical sense to mean the whole island including these two Indonesian Provinces along with the mainland part of the country of Papua New Guinea.

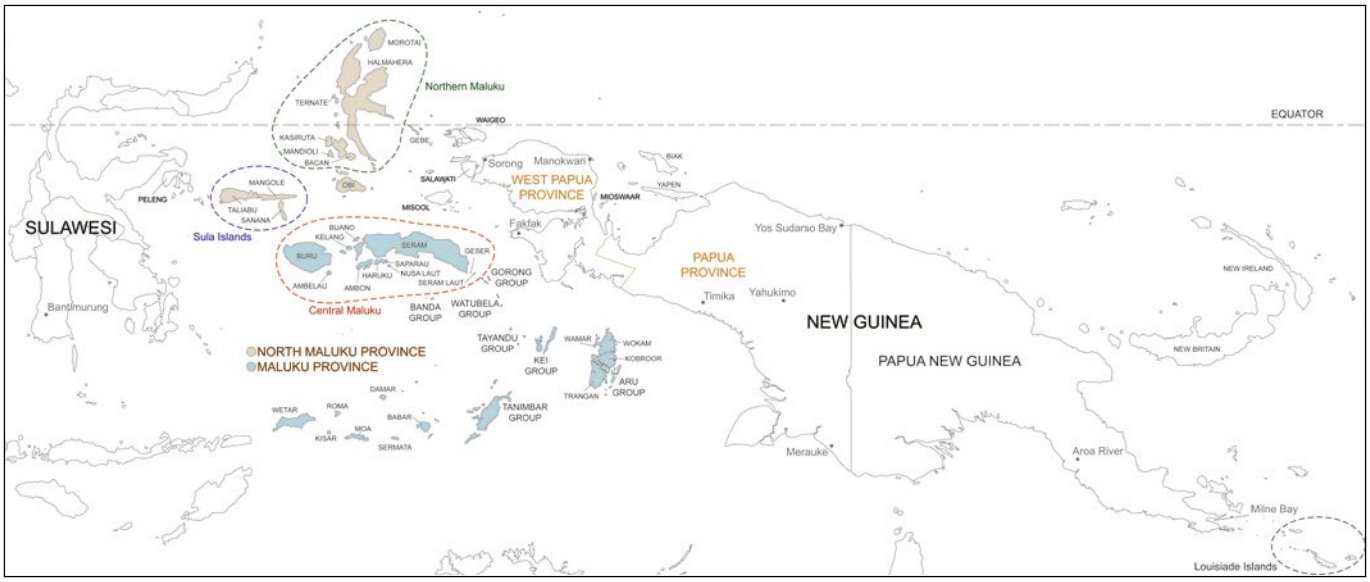
Both surfaces of both sexes of each taxon are illustrated in life-size. To reduce the number of plates needed, the specimens are illustrated "halved", showing the upperside on the left and the underside on the right. In most cases we have depicted the left half of the butterfly, but where the right side is in significantly better condition, we have shown this and flipped the image to allow easier comparison of similar taxa.

We have examined the collections of the Natural History Museum, London (NHMUK), and examined specimens and photographs from some other public and private collections.

We use "purple-blue" as general term for all the blue and purple hues of the uppersides of *Arhopala hercules* species-group specimens. In some cases, we will discuss the shade of purple-blue more specifically. We have found it difficult to accurately portray the exact hue of the purple-blue on the plate figures. When examining the specimens, the colours appear different depending on the lighting and angle of viewing. Thus, accurate comparison of taxa, based on this feature on the plates, is not wholly reliable.

Abbreviations used

AMNH	American Museum of Natural History, New York City, USA.
bp	DNA base pair(s).
CARR	Collection Andrew Rawlins, Rainham, Kent, UK.
coll.	collection.
comb. n.	combinatio nova = new combination.
CSSK	Collection Stefan Schröder, Köln, Germany.
f.	form.



Map: The islands of North Maluku and Maluku along with the Sulawesi and New Guinea Regions.

f. n.	new form.
fw(s)	forewing(s).
FwL	forewing length.
HT	holotype.
hw(s)	hindwing(s).
KSP	Koleksi Serangga Papua, Cenderawasih Universitas (UNCEN), Waena, Papua, Indonesia.
LT	lectotype.
MGCL	McGuire Center for Lepidoptera and Biodiversity, Gainesville, FL, USA.
NHMUK	The Natural History Museum, London, UK.
PD	postdiscal.
PT	paratype.
RMNH	Naturalis Biodiversity Center, Leiden, The Netherlands (formerly Rijksmuseum voor Natuurlijke Historie).
SMTD	Senckenberg Museum für Tierkunde, Dresden, Germany.
sp. n.	species nova.
ssp. n.	subspecies nova.
stat. rev.	status revivisco = status revived.
ST	syntype.
syn. n.	new synonym.
TL	Type locality (for phenotypes: the locality from which a phenotype is described; in this case this is not a category covered by the Code, ICZN 1999).
uns	underside(s).
ups	upperside(s).

Arhopala Boisduval, 1832

Type species: *phryxus* Boisduval, 1832 — designated by Scudder (1875: 120).

Taxonomic history of the *Arhopala hercules* species-group

In his revison of the *Amblypodia* group of Lycaenidae, Bethune-Baker (1903: 28) considered *tyrannus* Felder & Felder, 1865, *leo* Druce, 1894 and *herculina* Staudinger, 1888 as local varieties or forms of *Arhopala hercules* Hewitson, 1862.

Toxopeus (1930: 166) divided *Amblypodia hercules* into four species: *hercules, leo, herculina* and *tyrannus*. He listed a number of subspecies for each. This was essentially the same arrangement that Parsons (1998: 382) proposed (see below), except that Toxopeus considered *sophilus* Fruhstorfer, 1914 (from Obi) a subspecies of *tyrannus,* whereas Parsons raised *sophilus* to a full species. Toxopeus included *ate* Hewitson, 1863 as a subspecies of *tyrannus*. Subsequent authors treated *Arhopala ate* as an altogether different species.

Evans (1957: 100) included just two species in his *hercules* species-group — *hercules* and *ate*. He placed this species-group in the genus *Narathura* Moore, 1879, but this genus is now considered a synonym of *Arhopala,* as discussed in *Arhopala* part 1 (Rawlins et al. 2018a). Eliot (1972: 7) placed *A. ate* in the *cleander* subgroup of his *cleander* group. Parsons (1998: 383) included *A. ate* in the *cleander* subgroup of Evans' *democritus* species-group and we concur.

Evans (1957: 100) listed 10 subspecies of *hercules* (including two described in that treatise) and his distribution notes indicate that some taxa are sympatric. He justified this in his introduction (p. 86) by stating: "... in certain cases several subspecies appear to fly together, due perhaps to some ecological cause or to 'invasions' from other areas." We consider this unlikely and evidently so did Parsons (1998: 382), writing "Some of the taxa, in fact, fly together (as Evans pointed out: sic!) and so are distinct, reproductively isolated species." Parsons' revision postulated that the group comprised five species: *hercules, leo, herculina, tyrannus* and *sophilus*. This arrangement meant any sympatric taxa were now considered distinct species. He also noted that his arrangement was similar to that proposed by Toxopeus (1930: 162–168).

However, Schröder & Stradomsky (2016: 73) considered polymorphism the explanation for the sympatric occurrence of more than one phenotype. They tested this theory with analysis of mitochondrial and nuclear sequence DNA data from phenotypes identified as *herculina, leo, hercules, tyrannus* and Aru "*hercules*". They concluded that the DNA sequences of all specimens tested were very similar, indicating only one species was involved, and stated: "Because of the slight differences between *leo* and *herculina* it is most likely that both are not more different than varieties within the same subspecies." They added that the subspecific status of *tyrannus* remains speculative, noting its sympatric occurrence with *A. hercules stymphelus* Fruhstorfer, 1914 in Halmahera and Bacan. They tentatively assigned specimens from the Aru Islands (2 ♂♂ and 1 brown ups ♀) to *herculina* but noted that the sequences differed slightly from the mainland subspecies. Their paper, although helpful, did not fully resolve the situation, as they did not include *stymphelus, sophilus* or the Aru phenotype with purple-blue ups in the ♀.

For the purposes of this publication we aim to establish a credible working arrangement for the taxonomy of all phenotypes found in Maluku.

Distinguishing the *hercules* species-group phenotypes in Maluku

Several features distinguish the phenotypes:

Uppersides: All ♂♂ have similar shiny purple-blue uppersides, but the shade of purple-blue varies slightly between taxa. Some phenotypes have ♀♀ with brown uppersides, whilst in others the upperside is partly purple-blue. The width of the dark borders varies across the phenotypes with the purple-blue ♀ uppersides.

Undersides: Within phenotypes there is some variability in the underside markings, but generally they are consistent, at least in Maluku. The underside ground colour,

the colour, size and shape of the PD bands and the absence/presence/extent of turquoise tornal spots vary among phenotypes.

The phenotypes in Maluku with purple-blue ♀♀ are usually bigger, have narrower and straighter uns fw PD bands and the uns ground colour tends to be greener, rather than browner.

We recognise 8 phenotypes in Maluku.

- **Phenotypes 1–4** have ♀♀ with partially purple-blue ups.
- **Phenotypes 5–8** have ♀♀ with all brown ups.

Phenotype 1: *hercules* (Figs. 1–3). The largest of the phenotypes. Uns ground colour matt green, dramatically contrasting with the red-earthy-brown PD bands. Similar to *stymphelus* (Phenotype 2) but larger and ♀ upperside is a paler and more matt PURPLE-BLUE with very wide dark brown borders. Uns PD bands narrower, compared to specimen size, than in *stymphelus*. Fw apex more sharply angled than *stymphelus*. Well-developed uns hw turquoise-blue tornal spots, as *stymphelus, tyrannus* and *sophilus* phenotypes.

TL: Sulawesi. In Maluku recorded from Taliabu in the Sula Islands.

Phenotype 2: *stymphelus* (Figs. 10–15). Uns ground colour usually matt green (occasional specimens with mix of shades of green, brown and pink), dramatically contrasting with the red-earthy-brown broad PD bands. ♀ ups bright PURPLE-BLUE with very dark brown borders of variable width, but generally less broad than in *hercules*. Well-developed uns hw turquoise-blue tornal spots, as *hercules, tyrannus* and *sophilus* phenotypes.

TL: Bacan. Endemic to northern Maluku — recorded from Halmahera, Bacan, Ternate, Morotai, Mandioli, Kasiruta.

Note: In general, Morotai ♀♀ have much narrower ups dark borders, especially on the hindwing than ♀♀ from Bacan. Halmahera specimens are intermediate, but some individuals exhibit borders as narrow as typical Morotai ♀♀, whilst others are similar to typical Bacan ♀♀.

Phenotype 3: *leoesque* **f. n.** (Figs. 28–30). Uns ground colour dull, browny-green, with medium width reddish-earthy-brown PD bands. Uns fw PD bands usually straight. Usually with faint uns hw turquoise-blue tornal spots. ♀ ups PURPLE-BLUE with relatively narrow very dark brown borders.

We note here that this phenotype bears some resemblance to *leo* (TL: Humboldt Bay = Yos Sudarso Bay, New Guinea) treated by Toxopeus (1930: 167) and Parsons (1998: 383) as a full species — see also notes in the "Gebe" and "*Arhopala tyrannus herculina*" sections.

TL: Waigeo. In Maluku known only from 1 ♂ from Gebe.

Phenotype 4: *jheae* ssp. n. (Figs. 31–36). Uns ground colour light yellowish-grey with darker PD bands. Uns fw PD bands narrow and straight. No uns hw turquoise-blue tornal spots. ♀ ups PURPLE-BLUE with relatively narrow upperside hw dark brown borders. Fw termen slightly convex, unlike *fowlerorum* (Phenotype 8), also present on Aru.

TL: Aru. Endemic to Aru.

Phenotype 5: *tyrannus* (Figs. 4–9). Uns ground colour dark BROWN, with broad darker brown PD bands. Well-developed uns hw turquoise-blue tornal spots, as *stymphelus.* ♀ ups all BROWN.

TL: Halmahera. Endemic to northern Maluku — recorded from Halmahera, Bacan, Morotai, Kasiruta.

Phenotype 6: *sophilus* (Figs. 16–21). Similar to Phenotype 4 (*jheae* ssp. n.), but uns ground colour and PD bands lighter BROWN. Well-developed uns hw turquoise-blue tornal spots, as *hercules, stymphelus* and *tyrannus*. ♀ ups all BROWN.

TL: Obi. Endemic to Obi.

Phenotype 7: *herculina* (Figs. 22–27). Uns ground colour generally pale grey-brown, sometimes tinged with green or pink, with medium width reddish-earthy-brown PD bands. The uns fw PD band a bit variable but always irregular and not straight. In about one third of specimens (more in ♂♂) the uns PD band on hws (and occasionally also on fws) coalescing with cell end bars. No uns hw turquoise-blue tornal spots. ♀ ups lightish brown with creamy yellow suffusion in distal third to half of wings, especially fws.

TL: Waigeo. In Maluku known only from 4 ♂♂ from Gebe; uns typical *herculina*.

Phenotype 8: *fowlerorum* sp. n. (Figs. 37–42). Uns ground colour light to dark reddish-brown, with darker PD bands. Uns fw PD bands irregular and relatively broader than in Phenotype 3. Very faint or absent uns hw turquoise-blue tornal spots. ♀ ups uniformly BROWN.

TL: Aru. Endemic to Aru.

DNA sequencing and analysis

To help establish a credible taxonomy for these phenotypes, we sequenced two genetic markers from at least one specimen of each of the phenotypes noted above. However, we were not able to sequence specimens of *hercules* from Taliabu nor of *leoesque* or *herculina* from Gebe.

Materials and methods

We attempted to sequence a 1246 bp region of the cytochrome-c oxidase I (COI) mitochondrial gene and a 1066 bp region of the elongation factor 1a (EF1a) nuclear gene from multiple specimens in the *Arhopala hercules* species-group (Table 1). This was accomplished though PCR amplification using the primer pairs LCO1490/Butter-COI-R1 and Butter-COIb-F1/Butter-COIb-R2 for COI and the primer pairs ef44/ef51.1, ef46.1/ef52.6, and ef51.9/efrc-M4 for EF1a. Primer sequences, PCR

conditions, and sequencing information are provided in Braby et al. (2015). Alignment of each locus was trivial, as there were no indels, and performed with Sequencher 5.1 (equipment manufacturer: genecodes.com).

To infer relationships among focal taxa in the *hercules* species-group, we aligned our novel sequences with the previously published sequences of Schröder & Stradomsky (2016) and sequences of three *Arhopala* species outside the *hercules* species-group to serve as outgroups (Table 1). The COI sequences of Schröder & Stradomsky (2016) corresponded to the first 548 bp from the 5' end of the fragment that we sequenced. Their EF1a sequences were 434 bp in length and overlapped with the 5' end of the fragment that we amplified.

Trees for concatenated (COI + EF1a) and individual loci were inferred in a Bayesian framework using MrBayes 3.2 (Ronquist et al. 2012) on the CIPRES platform (www.phylo.org; Miller et al. 2010). Models of DNA substitution were first selected with the AICc optimality criterion in jModelTest 2.1.10 (Darriba et al. 2012) based on computation of likelihoods using 7 substitution schemes allowing estimation of Γ but not I. Parameter values for the substitution models were estimated from the data and allowed to vary independently between loci. Four Markov chains, three heated and one cold, were run simultaneously for 20 million generations. Trees were sampled every 1000 generations, and the first 25% of sampled trees were discarded as burn-in before calculating a consensus tree.

We inferred haplotype networks among COI and EF1a sequences (separately) with TCS 1.21 (Clement et al. 2000) using a 95% connection limit. To standardize comparisons among specimens, sequences of COI were trimmed to the 548 bp of overlap between all samples with sequence data in this region (28 samples) and sequences of EF1a were trimmed to the 406 bp of overlap between all samples with sequence data in this region (27 samples). Note that the COI fragment corresponds to the standard DNA barcoding fragment (Hebert et al. 2003). A preliminary phylogenetic tree (not shown) confirmed that the reduced COI dataset used for the haplotype reconstruction had sufficient variability to recover the relationships inferred with the larger datasets including COI: all four clades (described below) were recovered in the reduced dataset. To assess genetic differentiation among samples in the recovered clades, we calculated mean within-group and between-group uncorrected pairwise distances using Mega 7.0 (Kumar et al. 2016). Variance was calculated with 500 bootstrap replicates.

Results

We amplified and sequenced at least one locus from 23 specimens (Table 1). After combining our sequences with data from Schröder & Stradomsky (2016) and three other *Arhopala* species used as outgroups, jModeltest selected GTR+Γ as the best model for COI and TrNef as the best model for EF1a. Since this latter model cannot easily be implemented in MrBayes, we used the second most likely model, K80.

The phylogenetic tree inferred using both COI and EF1a (Diagram 1) recovers the *Arhopala hercules* species-group as monophyletic with four clades arising from a polytomy. Both specimens of *hercules* (Phenotype 1, from Peleng and Sulawesi) comprise a clade, all specimens of "Timika Phenotype A" (see below) comprise a clade, all specimens of *fowlerorum* (Phenotype 8) comprise a clade, and all remaining specimens form a weakly supported fourth clade. This last clade includes *stymphelus*, *leoesque, jheae, tyrannus, sophilus* and *herculina* (Phenotypes 2, 3, 4, 5, 6, 7) as well as *leontodamas* Toxopeus, 1930 (TL: Misool) and *droa* Evans, 1957 (from Timika). The tree inferred from only COI recovered the same four clades, each of which had branch support of 0.94 or higher. The tree inferred from EF1a was a bush — a polytomy with no bifurcations.

In the haplotype network of COI, individuals of Phenotype 1 (*hercules*) were genetically identical, as were individuals of Timika Phenotype A (Diagram 2). There were two haplotypes of Phenotype 8 (*fowlerorum*) that differed by 1 base pair (bp) from each other. Each of these phenotypes was at least 4 bp different from any other phenotype. The other phenotypes were not genetically distinctive and formed a cluster of related haplotypes separated by 1–3 bp. Note that since mtDNA (including COI) cannot recombine, the anastamoses apparent in the haplotype network result from inability of the analytical method we used to distinguish among equally probable relationships, and not from recombination between lineages.

There was little variability among EF1a sequences (Diagram 2). With two exceptions, all specimens sampled shared an identical EF1a sequence. One of five *fowlerorum* from Aru (ILL246) and one of two purple-blue ♀ *leoesque* from Waigeo (ILL241) had single, unique, base pair differences.

Uncorrected pairwise genetic distances among COI (DNA barcode) sequences were low (Table 2). Within-clade distances (± SE; on the diagonal) were all < 1%. The largest within-group genetic variability was among the larger "others" group, which excludes Phenotype 1 (*hercules*), Timika Phenotype A and Phenotype 8 (*fowlerorum*). Between-group variablility was higher, ranging between 1.018 ± 0.398% and 1.294 ± 0.427%.

Discussion

The most recent and currently accepted revision of the *hercules* species-group by Parsons (1998: 382–383) recognised five species: *hercules* (comprising 2 subspecies, the nominotypical and *stymphelus*), *tyrannus, sophilus, herculina* and *leo*. None of these species were monophyletic in any of our phylogenetic analyses (Diagrams 1 & 2). Moreover, only two of the eight phenotypes that we recognise in Maluku were monophyletic.

Arhopala hercules
Bantimurung, Sulawesi

P6 *A. tyrannus sophilus* AR-17-H016 Obi
P3 *A. tyrannus herculina* f. *leoesque* AR-17-H012 Waigeo
P3 *A. tyrannus herculina* f. *leoesque* DH-18-R052 Waigeo
P3 *A. tyrannus herculina* f. *leoesque* ILL244 Waigeo
A. tyrannus ILL243 Sorong
P7 *A. tyrannus herculina* f. *herculina* DH-18-R053 Waigeo
P7 *A. tyrannus herculina* f. *herculina* AR-17-H018 Waigeo
P2 *A. tyrannus tyrannus* f. *stymphelus* AR-17-H017 Bacan
P5 *A. tyrannus tyrannus* f. *tyrannus* ILL245 Halmahera
A. tyrannus ILL240 Sorong
P5 *A. tyrannus tyrannus* f. *tyrannus* AR-17-H009 Morotai
P2 *A. tyrannus tyrannus* f. *stymphelus* AR-17-H011 Morotai
P4 *A. tyrannus jheae* SS-17-A004 Aru
P4 *A. tyrannus jheae* SS-17-A003 Aru
A. tyrannus droa AR-17-H001 Timika
A. tyrannus droa AR-17-H002 Timika
A. tyrannus droa AR-17-H005 Timika
P4 *A. tyrannus jheae* AR-17-H006 Aru
P3 *A. tyrannus herculina* f. *leoesque* ILL241 Waigeo
A. tyrannus droa AR-17-H005 Timika
P5 *A. tyrannus tyrannus* f. *tyrannus* AR-17-H010 Halmahera
A. tyrannus leontodamas f. *leolike* AR-17-H013 Misool
P8 *A. fowlerorum* SS-17-A005 Aru
P8 *A. fowlerorum* ILL250 Aru
P8 *A. fowlerorum* SS-17-A001 Aru
P8 *A. fowlerorum* ILL251 Aru
P8 *A. fowlerorum* SS-17-A002 Aru
P8 *A. fowlerorum* ILL246 Aru
P1 *A. hercules* ILL247 Peleng
P1 *A. hercules* ILL242 Bantimurung
Arhopala sp. "Timika Phenotype A" AR-17-H003 Timika
Arhopala sp. "Timika Phenotype A" AR-17-H004 Timika
Arhopala sp. "Timika Phenotype A" DH-18-R051 Timika
Arhopala sp. "Timika Phenotype A" DH-18-R049 Timika
Arhopala major A25 Borneo
Arhopala amphimuta A10 Borneo
Arhopala zylda A15 Borneo

0.63
1
0.84
0.94
1
0.99
0.86
0.0040

Diagram 1: Bayesian concensus tree of *Arhopala hercules* species-group specimens from Wallacea and New Guinea based on COI and EF1a. Numbers above branches indicate Bayesian posterior probabilities. — Photo © Pingchung Lee and used with permission.

Meier et al. (2008) examined genetic variability among 5910 DNA barcodes from 1786 species in 738 lepidopteran genera and found that genetic variability within species averaged 0.7 ± 1.1% and that the smallest genetic difference between congeneric species averaged 1.9 ± 2.9%. The uncorrected pairwise differences of our COI barcode sequences between all *hercules* species-group samples ranged from 0–1.294%. This is within one standard deviation of the average within-species barcode variability observed in the Lepidoptera data of Meier et al. (2008), but less than the average smallest genetic divergence observed between congeners. Thus, the degree of variability observed in our dataset falls within a "grey area": it is within the previously observed overlap between inter- and intraspecific DNA barcode differences in Lepidoptera.

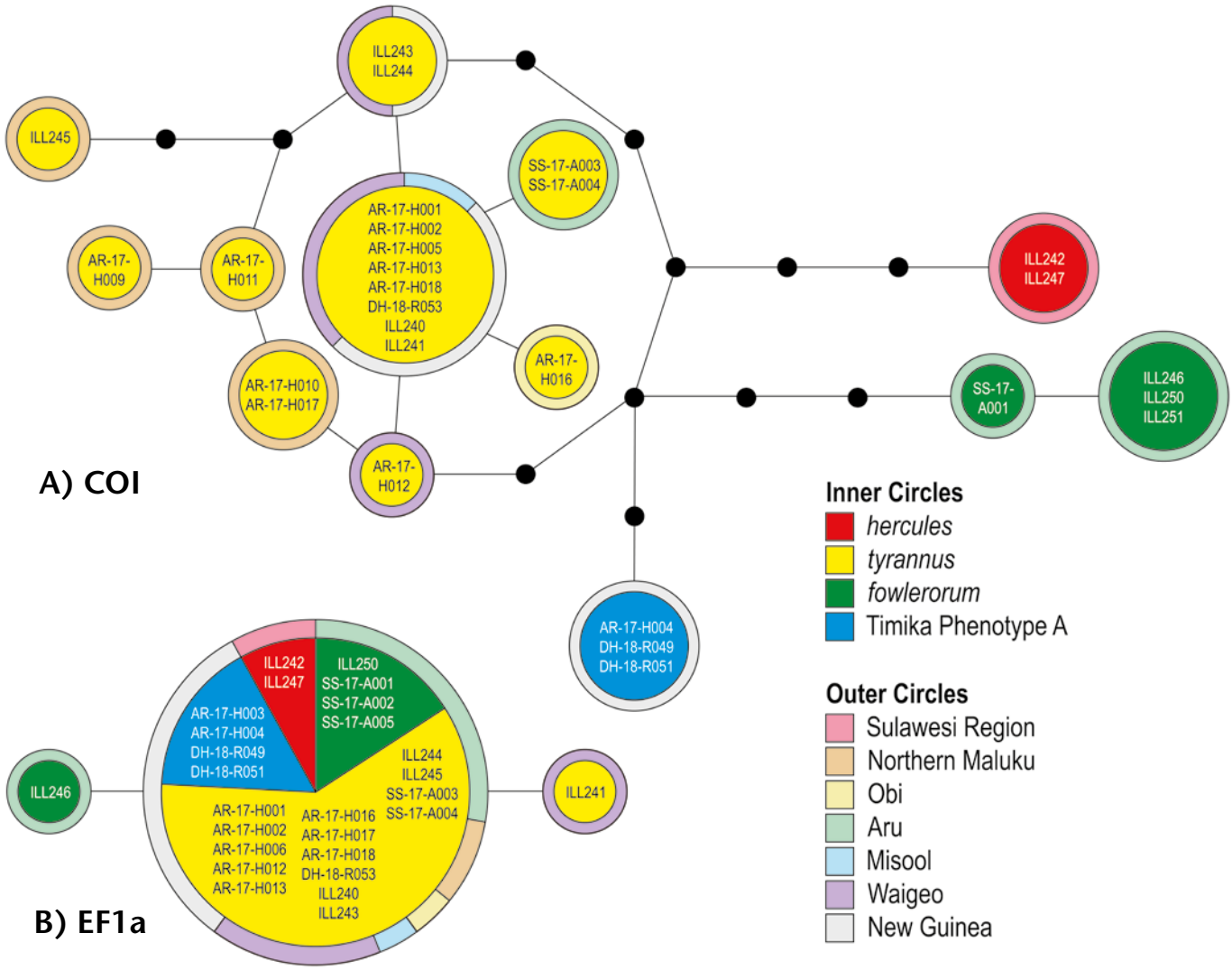


Diagram 2: Haplotype networks of COI and EF1a from *Arhopala hercules* species-group specimens sampled in Wallacea and New Guinea. Each circle represents a unique haplotype sequence shared by all of the listed samples; the size of circles is proportional to the number of samples sharing each sequence. Circles connected by a line are 1 bp different from each other. Small, black circles represent haplotypes not sampled in the current analysis. Colours in the inner pie chart of each circle indicate the proportional representation of each species sharing that haplotype. Colours in the outer circles indicate the proportional representation of locales from which the haplotype was sampled.

DNA sequence data including DNA barcodes can provide heuristic taxonomic information useful for identifying cryptic species (Bickford et al. 2007), for matching larvae with adults (Wells et al. 2001, Yeo et al. 2018), or for identifying phenotypically variable conspecifics wrongly considered different species (Wei et al. 2017). However, DNA sequences by themselves are an imperfect and occasionally error-prone source of data for delimiting and diagnosing species (DeSalle et al. 2005, Hickerson et al. 2006). Thus, this revision of the *Arhopala hercules* species complex from Maluku considers our genetic and phylogenetic results in conjunction with morphology (wing patterns, genitalia) and distribution information to arrive at taxonomic conclusions.

Species delimitation in the *Arhopala hercules* species-group

Our taxonomic decisions are guided by the biological species concept, which defines species as reproductively isolated groups of populations (Mayr 1940). We infer reproductive isolation between species by identifying characteristic phenotypic and/or genetic differences.

- We regard distinctive phenotypes found in different geographic areas with little or no genetic variation between them to be different subspecies, not different species.
- Morphologically distinctive phenotypes with little or no genetic variation between them that co-exist in the same geographic area (island) are regarded as different forms of the same subspecies.
- Morphologically distinctive phenotypes with distinctive genetic variation between them are regarded as different species, particularly when they coexist in the same area.

Thus, considerations of morphology (wing patterns, genitalia), genetic differentiation, and geography have guided our delimitation of taxa.

Sample codes (see Table 1) are used in parentheses where sequenced specimens are discussed in the text.

Table 1: Sample information of specimens of the **genus *Arhopala*** sequenced for this study. GenBank accession numbers for **COI** and **EF1a** are provided. The column **"♀"** lists the ups colour of female specimens, and **"Phen."** lists the phenotype number from the text.

Code	Species	Subspecies	Form	Phen.	♀ ups colour	Sex	Collection locality	Date	COI	EF1a
ILL246	*fowlerorum*			8		♂	Indonesia: Maluku, Aru (unspecified island)	I. 2010	KU189177	KU189188
ILL250	*fowlerorum*			8		♂	Indonesia: Maluku, Aru, Trangan Island	V. 2010	KU189179	KU189190
ILL251	*fowlerorum*			8	brown	♀	Indonesia: Maluku, Aru, Trangan Island	V. 2010	KU189180	–
SS-17-A001	*fowlerorum*			8		♂	Indonesia: Maluku, Aru, Trangan Island	2010	MK751171	MK751194
SS-17-A002	*fowlerorum*			8		♂	Indonesia: Maluku, Aru, Wamar Island, Dobo	XI. 2012	MK751172	MK751195
SS-17-A005	*fowlerorum*			8	brown	♀	Indonesia: Maluku, Aru, Wamar Island, Dobo	XI. 2012	MK751173	MK751196
ILL242	*hercules*			1	blue	♀	Indonesia: South Sulawesi, Bantimurung	IX. 2011	KU189173	KU189184
ILL247	*hercules*			1		♂	Indonesia: Central Sulawesi, Peleng Island	X. 2010	KU189178	KU189189
AR-17-H003	sp.			A		♂	Indonesia: Papua, Timika (New Guinea)	XI. 2016	MK751174	MK751197
AR-17-H004	sp.			A		♂	Indonesia: Papua, Timika (New Guinea)	XI. 2016	MK751175	MK751198
DH-18-R049	sp.			A		♂	Indonesia: Papua, Timika (New Guinea)	XI. 2017	MK751176	MK751199
DH-18-R051	sp.			A	brown	♀	Indonesia: Papua, Timika (New Guinea)	XI. 2017	MK751177	MK751200
AR-17-H001	*tyrannus*	*droa*			blue	♀	Indonesia: Papua, Timika (New Guinea)	I. 2016	MK751178	MK751201
AR-17-H002	*tyrannus*	*droa*				♂	Indonesia: Papua, Timika (New Guinea)	XI. 2016	MK751179	MK751202
AR-17-H005	*tyrannus*	*droa*				♂	Indonesia: Papua, Timika (New Guinea)	I. 2016	MK751180	MK751203
AR-17-H018	*tyrannus*	*herculina*	*herculina*	7	brown	♀	Indonesia: West Papua, Waigeo	III. 2014	MK751182	MK751205
DH-18-R053	*tyrannus*	*herculina*	*herculina*	7		♂	Indonesia: West Papua, Waigeo	XII. 2017	MK751184	MK751207
AR-17-H012	*tyrannus*	*herculina*	*leoesque*	3		♂	Indonesia: West Papua, Waigeo	VI. 2015	MK751181	MK751204
DH-18-R052	*tyrannus*	*herculina*	*leoesque*	3		♂	Indonesia: West Papua, Waigeo	XII. 2017	MK751183	MK751206
ILL241	*tyrannus*	*herculina*	*leoesque*	3	blue	♀	Indonesia: West Papua, Waigeo	X. 2009	KU189172	KU189183
ILL244	*tyrannus*	*herculina*	*leoesque*	3	blue	♀	Indonesia: West Papua, Waigeo	X. 2009	KU189175	KU189186
AR-17-H006	*tyrannus*	*jheae*		4		♂	Indonesia: Maluku, Aru (unspecified island)	IV. 2016	MK751185	MK751208
SS-17-A003	*tyrannus*	*jheae*		4		♂	Indonesia: Maluku, Aru, Wokum	VI. 2016	MK751186	MK751209
SS-17-A004	*tyrannus*	*jheae*		4	blue	♀	Indonesia: Maluku, Aru, Wokum	VI. 2016	MK751187	MK751210
AR-17-H013	*tyrannus*	*leontodamas*	*leolike*			♂	Indonesia: West Papua, Misool	II. 2017	MK751188	MK751211
AR-17-H016	*tyrannus*	*sophilus*		6		♂	Indonesia: North Maluku, Obi	I. 2013	MK751189	MK751212
ILL240	*tyrannus*	ssp.			brown	♀	Indonesia: West Papua, Sorong (New Guinea)	VIII. 2013	KU189171	KU189182
ILL243	*tyrannus*	ssp.			brown	♀	Indonesia: West Papua, nr. Sorong (New Guinea)	I. 2010	KU189174	KU189185
AR-17-H011	*tyrannus*	*tyrannus*	*stymphelus*	2		♂	Indonesia: North Maluku, Morotai	XI. 2016	MK751192	–
AR-17-H017	*tyrannus*	*tyrannus*	*stymphelus*	2		♂	Indonesia: North Maluku, Bacan	XII. 2005	MK751193	MK751215
AR-17-H009	*tyrannus*	*tyrannus*	*tyrannus*	5		♂	Indonesia: North Maluku, Morotai	III. 2016	MK751190	MK751213
AR-17-H010	*tyrannus*	*tyrannus*	*tyrannus*	5	brown	♀	Indonesia: North Maluku, Halmahera	II. 2016	MK751191	MK751214
ILL245	*tyrannus*	*tyrannus*	*tyrannus*	5		♂	Indonesia: North Maluku, Halmahera, Tobelo	X. 2009	KU189176	KU189187
A10	*amphimuta*						Malaysia: Sarawak, Lambir Hills (Borneo)		AB576375	AB576455
A25	*major*						Malaysia: Sarawak, Lambir Hills (Borneo)		AB576390	AB576470
A15	*zylda*						Malaysia: Sarawak, Lambir Hills (Borneo)		AB576380	AB576460

Sympatry and occurrence of phenotypes/taxa in Maluku

Within Maluku, sympatry of distinct *hercules* phenotypes occurs in northern Maluku, Gebe and Aru.

Taliabu, Sula Islands

Only one phenotype is recorded here — *hercules*. We have not sequenced any Taliabu specimens, but they are indistinguishable phenotypically from *hercules* from Sulawesi and Peleng. COI sequences from a Sulawesi (Bantimurung) ♀ (Sample code: ILL242) and a Peleng ♂ (ILL247) are identical to each other and, as noted above, form a clade separate from all other *hercules* species-group taxa. They differ by at least 6 bp from all other phenotypes. We treat the taxon found on Taliabu, Sulawesi and Peleng as ***Arhopala hercules***.

Northern Maluku

In northern Maluku the phenotypes *tyrannus* and *stymphelus* are sympatric. We have examined more than 40 specimens and the two phenotypes are stable, with no intermediate forms. In the COI haplotype network (Diagram 2) a *tyrannus* ♀ from Halmahera (AR-17-H010) and a *stymphelus* ♂ from Bacan (AR-17-H017 & Fig. 10) are identical and are 1 and 2 bp different, respectively, from a *stymphelus* ♂ (AR-17-H011) and a *tyrannus* ♂ (AR-17-H009) from Morotai.

The *tyrannus* ♀ ups is brown, whilst that of *stymphelus* is purple-blue. The wing shape in both phenotypes is similar. The uns of the two phenotypes are different colours but the pattern is the same. We consider them to be polymorphic forms of *tyrannus*. It is rare, but not unknown, for a butterfly to exhibit non-seasonal polymorphism in both sexes. For example, genetic evidence indicates that the syntopic species *Elymnias casiphone* Geyer, 1827 and *E. kamara* Moore, 1858 are the same species, with 2 ♂ and 2 ♀ forms (Wei et al. 2017).

We treat these phenotypes as ***A. tyrannus tyrannus* f. *tyrannus*** and ***A. tyrannus tyrannus* f. *stymphelus* comb. n.**

Below we discuss the records of *herculina* from Halmahera but note here that we consider the presence of *herculina* in northern Maluku as unconfirmed.

Obi

Only one phenotype is confirmed from Obi — *sophilus*. The records of *stymphelus* from Obi are considered erroneous, see note 3 under *Arhopala tyrannus tyrannus* f. *stymphelus*. Our phylogenetic analysis indicates that *sophilus* (AR-17-H016 & Fig. 16) falls within the large clade that includes *tyrannus* (Diagram 1). In the haplotype network, the *sophilus* COI sequence differs by only 2–3 bp from 4 *tyrannus*/*stymphelus* specimens (Diagram 2). As it is phenotypically distinct and geographically separated, we treat it as ***A. tyrannus sophilus* stat. rev.**

Gebe

Two phenotypes occur here. To correctly assign names to them we need to look at the situation in Waigeo in West Papua Province. Gebe lies about 70 km east of Halmahera and Waigeo is another 70 km further east.

There are two *hercules* species-group phenotypes present on Waigeo: *herculina* (Figs. 23, 26, 27) and *leoesque* (Figs. 29, 30). We briefly described these phenotypes above, but here we note the significant differences.

herculina: uns shades of grey-brown, sometimes with pink or green tinge, PD bands not straight and often conjoined to cell end bar (fws and/or hws). ♂ ups ♀ brown. Waigeo is the TL for *herculina*.

leoesque: generally bigger than *herculina*, uns browny-green, more green tinged than *herculina*, PD bands usually straight and rarely conjoined with cell end bar. ♂ ups purple-blue is slightly different shade to *herculina*. ♀ purple-blue. This phenotype differs slightly from the *leo* types (Figs. 64, 65) from Humboldt Bay (= Yos Sudarso Bay) in New Guinea. The uns of the *leo* types are a lighter and brighter green and have a narrower and straight fw PD band. Toxopeus (1930: 167) treated the *leoesque* phenotype on Waigeo as a distinct, un-named subspecies of *A. leo*.

The COI sequences from a brown *herculina* ♀ (AR-17-H018 & Fig. 23) and a purple-blue *leoesque* ♀ (ILL241), both from Waigeo, are identical. All other Waigeo specimens sequenced — 1 ♂ *herculina* (DH-18-RO53) and 2 ♂♂ & 1 ♀ *leoesque* (AR-17-H012 & Fig. 30, DH-18-RO52, ILL244) — are identical or fall within 1 bp of these two specimens. All fall in the same, polytomous clade as *tyrannus* and

Table 2: Average uncorrected pairwise differences at the COI barcoding locus between and within different phenotypes in the *Arhopala hercules* species complex. P = phenotype (see text); values are mean ± standard error. Within-group genetic variability is shown on the diagonal shaded in light grey.

	P1	PA	P8	Others
P1 = *hercules* (*n* = 2)	0.00000 (0.00000)			
PA = Timika Phenotype A (*n* = 3)	0.01095 (0.00402)	0.00000 (0.00000)		
P8 = *fowlerorum* (*n* = 4)	0.01141 (0.00423)	0.01049 (0.00408)	0.00091 (0.00088)	
Others (*n* = 19)	0.01287 (0.00437)	0.01018 (0.00389)	0.01294 (0.00427)	0.00290 (0.00112)

stymphelus (Diagram 1). Given their sympatry and lack of genetic differentiation, we consider the Waigeo *herculina* and *leoesque* phenotypes to be two forms of the same subspecies: ***A. tyrannus herculina* comb. n. f. *herculina*** and ***A. tyrannus herculina* comb. n. f. *leoesque* f. n.**

We have no sequence data from the *leo* types or any other specimens closely resembling them. Therefore, we are unable to confirm whether *leo* falls in the same clade as the Waigeo phenotypes, but we believe this is likely.

We have not seen any *hercules* species-group ♀♀ from Gebe, but the ♂♂ can be assigned morphologically to the same 2 phenotypes present on Waigeo. We have no DNA samples from the Gebe specimens (all are old specimens in the NHMUK), but we are confident the 2 phenotypes are polymorphs and consider them to be the same as those found on Waigeo — *A. tyrannus herculina* f. *herculina* and *A. tyrannus herculina* f. *leoesque.*

Evans (1957: 100) included the NHMUK Gebe specimens with *leontodamas* from Misool (see below), but we consider that the ♂♂ match the Waigeo phenotypes. Future examination of Gebe ♀♀ could change the taxonomy of Gebe *hercules* species-group phenotypes.

Aru

There has been confusion over the status of Aru *hercules* species-group taxa.

Evans (1957: 100) did not mention the presence of any Aru specimens in the NHMUK, but there is 1 ♂ placed with the long NHMUK *herculina* series from Waigeo. However, this specimen is not *herculina* — see below.

Parsons (1998: 382) included 1 MGCL ♂ from Aru with *herculina*. We have seen photographs of this specimen courtesy of Andy Warren. The data label states "Aru Islands, Dobo, 7. v. 1939, RG & CM Wind". It is typical of *fowlerorum* (Phenotype 8).

Parsons (1998: 382) considered that all *hercules* species-group taxa with "mauve" (purple-blue) upperside ♀♀ (along with their corresponding ♂♂) were either *Arhopala hercules* (Sulawesi & Maluku) or *Arhopala leo* (New Guinea Region). According to his arrangement, *jheae* ssp. n. (Phenotype 4) from Aru with purple-blue ♀♀ should be *A. leo.*

Schröder & Stradomsky (2016) analysed the COI and EF1a sequences of three *fowlerorum* (Phenotype 8) specimens from Aru — 1 ♂ (ILL250) and 1 brown ♀ (ILL251) from Trangan Island, and a further ♂ from an unspecified island in Aru (ILL246). These three specimens all had identical COI sequences. They stated: "Specimens from the Aru Islands are here tentatively assigned to *herculina* ... even though DNA data suggest that they slightly differ from the mainland subspecies. Females are completely brown and underside colour is variable; there are specimens with light green/mint green as well as pink undersides. They are lacking tornal green scales." They had not seen any Aru purple-blue ♀♀.

We have examined about 20 ♂♂ and 10 ♀♀ *hercules* species-group specimens from Aru (including some in CARR, CSSK). They can be readily divided into 2 phenotypes — *jheae* (Phenotype 4) and *fowlerorum* (Phenotype 8). Phenotype 4 has purple-blue ♀♀, is generally larger and has a more sharply angled fw apex. The uns ground colour is paler, generally a very pale yellowish-grey, with narrow and straight fw PD band. The ♂ upperside is a slightly darker, more purple and less shiny purple-blue than Phenotype 8. Phenotype 8 has brown ♀♀. The underside ground colour is generally medium brown, though somewhat variable, with fw PD band broader and irregular. These 2 phenotypes are only known from Aru and phylogenetic analysis shows they fall into separate clades.

All *jheae* (Phenotype 4) specimens analysed (a pair from Wokam Island [= Tanah Besar] [♂ SS-17-A003; purple-blue ♀ SS-17-A004] and 1 ♂ from an unspecified Aru island [AR-17-H006]) fall into the same clade as Waigeo *herculina* and *leoesque* phenotypes, *sophilus*, *stymphelus* and *tyrannus* specimens, as well as Timika *droa* (♂ AR-17-H002, purple-blue ♀ AR-17-H001). They differ by only 1–3 bp in COI. Below we describe this phenotype as ***Arhopala tyrannus jheae*** Rawlins & Cassidy, ssp. n.

We have sequenced three *fowlerorum* (Phenotype 8) specimens: 1 ♂ from Trangan Island (SS-17-A001) and a pair (♂ SS-17-A002; brown ♀ SS-17-A005) from Wamar Island. They fall in the same clade as the three Aru specimens analysed by Schröder & Stradomsky. These six *fowlerorum* specimens comprise one clade. COI sequences from four (SS-17-A001, ILL246, ILL 250, ILL 251) of the six were long enough to include the haplotype network (Diagram 2); they comprise two haplotypes that differ by 1 bp. The *fowlerorum* specimens differ from *jheae* specimens by 7–8 bp.

Phenotype 8 (*fowlerorum*) specimens differ morphologically from all other *hercules* species-group taxa and fall in a clade of their own. They are sympatric with Phenotype 4 (*jheae*), therefore *fowlerorum* and *jheae* must represent distinct species. We also note that most of the Aru Islands are separated by very narrow channels (50 m to

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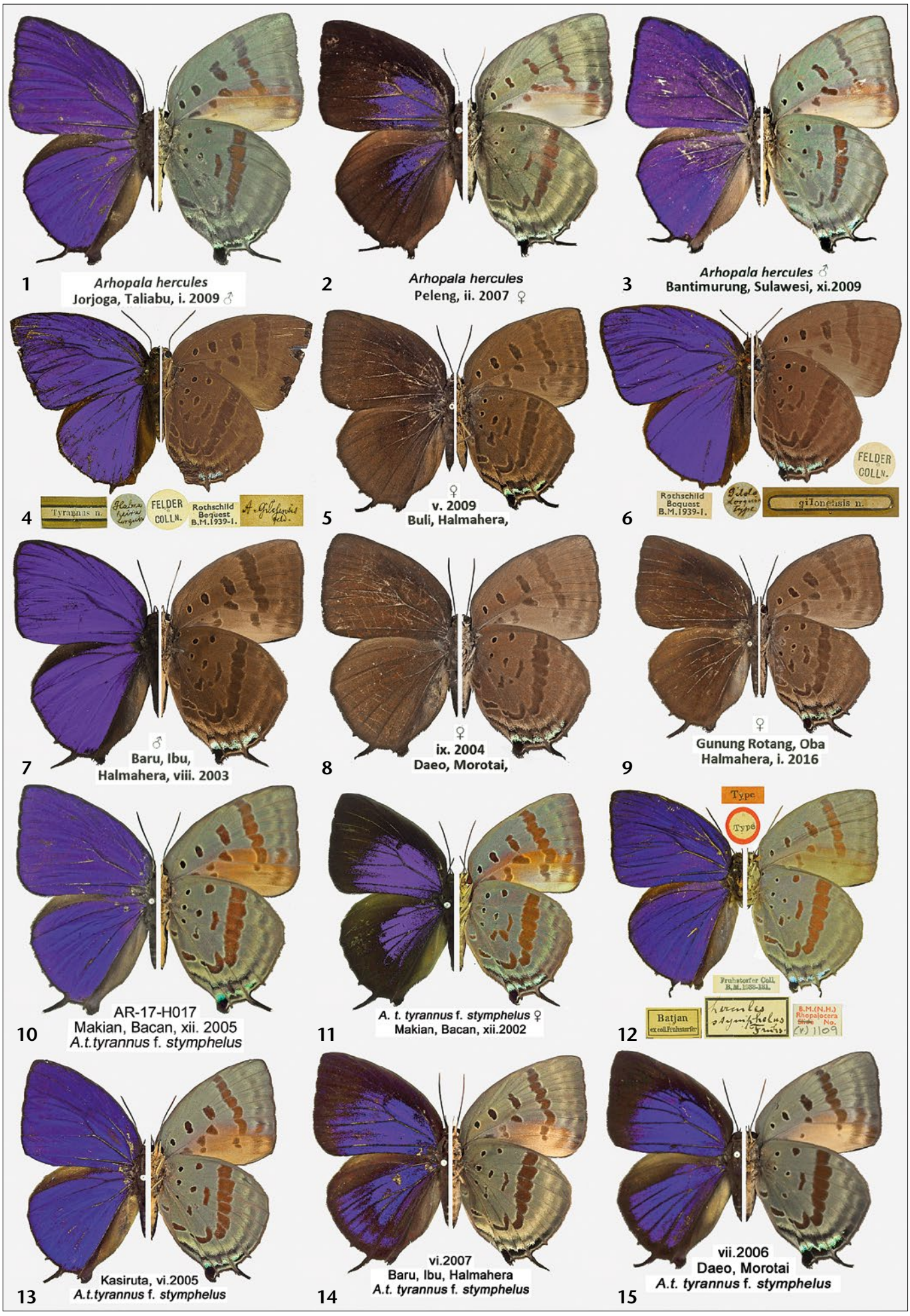
Figs. 1–15: *Arhopala hercules* species-group, Maluku. — **Figs. 1–3:** ***Arhopala hercules*. 1:** ♂, ups./uns., Taliabu (Jorjoga, I. 2009, CARR). **2:** ♀, ups./uns., Peleng (II. 2007, CARR). **3:** ♂, ups./uns., Sulawesi (Bantimurung, XI. 2009, CARR). — **Figs. 4–15**: Subspecies of ***Arhopala tyrannus***, ssp. ***tyrannus:*** **Figs. 4–9:** *A. tyrannus tyrannus* f. *tyrannus:* **4:** ♂, type, ups./uns., Halmahera (Halmaheira, Lorquin, Felder Colln., NHMUK). **5:** ♀, ups./uns., Halmahera (Buli, v. 2009, CARR). **6:** ♂, ups./uns., Halmahera (HT *gilolensis* = *tyrannus*, Gilolo, Lorquin type, Felder Colln., NHMUK). **7:** ♂, ups./uns., Halmahera (Baru, Ibu, VIII. 2003, CARR). **8:** ♀, ups./uns., Morotai (Daeo, IX. 2004, CARR). **9:** ♀, ups./uns., Halmahera (Gunung Rotang, Oba, I. 2016, CARR). – **Figs. 10–15:** *A. tyrannus tyrannus f. stymphelus:* **10:** ♂, ups./uns., Bacan (Makian, XII. 2005, AR-17-H017, CARR). **11:** ♀, ups./uns., Bacan (Makian, XII. 2002, CARR). **12:** ♂, type, ups./uns. Bacan (Batjan, ex coll. Fruhstorfer, B.M.(N.H.) Rhopalocera No. (v) 1109, NHMUK). **13:** ♂, ups./uns., Kasiruta (VI. 2005, CARR). **14:** ♀, ups./uns., Halmahera (Baru, Ibu, VI. 2007, CARR). **15:** ♀, ups./uns. Morotai (Daeo, VII. 2006, CARR). — For all plates: NHMUK specimen photographs are © Trustees of the Natural History Museum London, reproduced with permission.



1.5 km) and differentiation to subspecies within the Aru group is unknown. We describe Phenotype 8 as ***Arhopala fowlerorum*** Rawlins & Cassidy, sp. n.

It is possible that one or more New Guinea phenotypes represent subspecies of *A. fowlerorum* but that is beyond the scope of this paper.

Revised taxonomy of Maluku *hercules* species-group phenotypes/taxa

We consider the phenotypes of the *hercules* species-group found in Maluku represent 3 species: *hercules, tyrannus* and *fowlerorum* sp. n. We propose the following arrangement of taxa, with their ranges in Maluku:

- *A. hercules* – Taliabu – Phenotype 1.
- *A. tyrannus tyrannus* f. *tyrannus* – endemic to northern Maluku – Phenotype 5.
- *A. tyrannus tyrannus* f. *stymphelus* **comb. n.** – endemic to northern Maluku – Phenotype 2.
- *A. tyrannus sophilus* **stat. rev.** – endemic to Obi – Phenotype 6.
- *A. tyrannus jheae* **ssp. n.** – endemic to Aru – Phenotype 4.
- *A. tyrannus herculina* **comb. n.** – f. *herculina* – Gebe – Phenotype 7.
- *A. tyrannus herculina* **comb. n.** – f. *leoesque* **f. n.** – Gebe – Phenotype 3.
- *A. fowlerorum* **sp. n.** – endemic to Aru – Phenotype 8.

Annotated checklist of the *Arhopala "hercules* species-group" taxa of North Maluku and Maluku

Arhopala hercules (Hewitson, 1862)

(Fig. 1: ♂, Taliabu; Fig. 2: ♀, Peleng; Fig. 3: ♂, Sulawesi.)

Amblypodia hercules: Hewitson (1862: 3, pl. 8, figs. 92, 93); TL: Makassar, Sulawesi – see note 1.

Range: Sulawesi (NHMUK), Peleng, Taliabu in the Sula Islands (Tennent & Rawlins 2010).

Note 1: Hewitson noted "*Arhopala Hercules*, Boisd. MS." suggesting that Boisduval coined the name in an unpublished manuscript. Hewitson briefly described and illustrated the *hercules* ♂. He stated: "In the Collection of A. R. Wallace from Makassar and of Dr Boisduval from Java." Staudinger (1888: 280) noted that Boisduval's "Java" record seemed incorrect and Toxopeus (1930: 163) stated "ten onrechte ook uit Java vermeld", meaning mistakenly recorded from Java, and he is most likely referring to Hewitson's Boisduval record. We can safely conclude the species does not occur on Java. We do not know the whereabouts of any types.

Note 2: Evans (1957: 100) noted "♂ 35 mm. ♀ dull blue, borders 10 mm.; below green." This is the largest of the *hercules* species-group taxa.

Note 3: As noted earlier, COI barcode sequences from *hercules* from Bantimurung (Sulawesi) and Peleng are identical and form a separate clade from all other *hercules* species-group taxa. No Taliabu specimens were included in the genetic study. The 3 Taliabu ♂♂ examined are phenotypically indistinguishable from Sulawesi and Peleng specimens, however we note that these 3 have a slightly darker green uns than *most* Sulawesi and Peleng examples.

Note 4: The phenotype *stymphelus* from northern Maluku has been considered a subspecies of *hercules* by most authors, however, as discussed earlier and below, we consider *stymphelus* to be a form of nominotypical *tyrannus*. Thus, *hercules* is a monotypic species.

Arhopala tyrannus C. & R. Felder, 1865

Arhopala tyrannus: C. & R. Felder (1865: 225, pl. 29, figs. 1, 2); TL: Halmahera.

= *Arhopala gilolensis:* C. & R. Felder (1865: 225); TL: Gilolo, Halmahera.

Range: northern Maluku, Gebe, Obi, Aru, New Guinea Region including Waigeo, Misool, Sorong, Timika.

Note: Four subspecies occur in Maluku – *tyrannus* (with f. *tyrannus* & f. *stymphelus*), *sophilus*, *herculina* (with f. *herculina* & f. *leoesque*) and *jheae*. They are all geographically isolated from each other.

Arhopala tyrannus tyrannus C. & R. Felder, 1865

Range: endemic to northern Maluku.

Note: As discussed earlier, we consider the phenotypes *tyrannus* and *stymphelus* to represent 2 forms of *A. tyrannus tyrannus*.

Arhopala tyrannus tyrannus f. *tyrannus* C. & R. Felder, 1865

(Fig. 4: ♂ type, Halmahera; Fig. 5: ♀, Halmahera; Fig. 6: ♂, HT *gilolensis* = *tyrannus*, Halmahera; Fig. 7: ♂, Halmahera; Fig. 8: ♀, Morotai; Fig. 9: ♀, Halmahera.)

Arhopala tyrannus: C. & R. Felder (1865: 225, pl. 29, figs. 1, 2); TL: Halmahera – see note 1.

= *Arhopala gilolensis:* C. & R. Felder (1865: 225); TL: Gilolo, Halmahera – see note 2.

Synonym that we reject:

Arhopala tyrannus afranius: Fruhstorfer (1914: 156); TL: Aroa River, New Guinea – see note 3.

Range: form *tyrannus* is recorded from Halmahera, Bacan (NHMUK), Morotai, Kasiruta (Tennent & Rawlins 2010). A record from Buru is excluded – see note 4 –, and New Guinea is considered very unlikely – see note 3.

Note 1: The Felders described only the *tyrannus* ♂ in Latin, with a sentence at the end in German. They stated that *tyrannus* was similar to *hercules,* except for the underside. Their illustration of the ♂ clearly shows a brown uns, very different to the green uns of *hercules*.

There was no note of the number of specimens, but they wrote "Habitat: Halmaheira. (Lorquin.) Cll. F." indicating the specimen/s were collected by Lorquin on Halmahera and in their (Felder's) collection. P. J. M. Lorquin was a French entomologist who collected butterflies and beetles around the world. He was in Indonesia from 1860–1865.

Evans (1957: 100) treated *tyrannus* as a subspecies of *hercules* and stated only "♀ above and below dark brown". He noted that the ♂ "type" was in the NHMUK (Fig. 4).

Note 2: The Felders described *gilolensis* from Lorquin specimen/s from Gilolo in Halmahera, as the very next taxon after *tyrannus*, noting that the specimen/s was in their collection. Strangely, they stated that *gilolensis* was closely related to *A. silhetensis* Hewitson, 1862, even though it is clearly closer to *tyrannus*.

Toxopeus (1930) did not mention *gilolensis,* but Evans (1957: 100) synonymised it with *tyrannus* and noted that the ♂ "type" from Gilolo was in the NHMUK (Fig. 6). We have examined the *gilolensis* and *tyrannus* types and it is clear they represent the same taxon.

Note 3: Fruhstorfer (1914: 156), in German, described *afranius* as a subspecies of *tyrannus.* He described only the ♂ and compared it to the 6 *tyrannus* ♂♂ in his collection, noting that the

outline of the wings in *afranius* was noticeably more rounded and the hindwing tails broader and shorter. On the uns the spots in the forewing cell were brown instead of black and all bands and markings broader, in particular, the brown spot at the apex of the hindwing cell. He recorded the "Patria" as British New Guinea (= PNG), Aroa River, but did not indicate how many specimens he had examined.

Toxopeus (1930: 168) retained *afranius* as a subspecies of *tyrannus*. He noted 2 records: the first from British New Guinea (now PNG) – the Fruhstorfer "Aroa River" HT –, and the second from Dutch New Guinea (now Papua and West Papua, Indonesia) in "Mus. Leiden" (= RMNH). We have not examined this RMNH specimen, but consider it is unlikely to be nominotypical *tyrannus*.

Evans (1957: 100) listed *afranius* as a synonym of *tyrannus* and he noted that the *afranius* ♂ "type" was in the NHMUK (Fig. 75). This specimen is likely to be the HT and is superficially similar to the *tyrannus* ♂ type (Fig. 4) though there are some clear differences as Fruhstorfer pointed out.

Parsons (1998: 383) considered that the evidence for the occurrence of *tyrannus* in PNG was scant being based on only 1 NHMUK ♂ "supposedly from the Aroa River". He noted that this was partly corroborated by the record of *tyrannus* [i.e., *afranius*] given by Toxopeus (1930: 168) from "western Irian Jaya" (= West Papua). He was clearly not aware of any further records of *tyrannus* in PNG.

We consider that the NHMUK ♂ *afranius* type from Aroa River is not nominotypical *tyrannus* and exclude New Guinea from the range for *A. tyrannus tyrannus.*

Note 4: Evans (1957) listed 1 ♂ *tyrannus* from "Buru" in the NHMUK. His use of inverted commas indicated he doubted the location. We have examined this "Buru" *tyrannus* ♂ in the NHMUK. It bears the label "Mt. Mada, Buru, 3000 [feet], Sept[ember] [18]98 (Dumas)". Tennent & Rawlins (2010: 13) questioned the reliability of this label, and subsequently Rawlins & Cassidy (2016: 149) and Tennent (2016: 128) concluded that some of the specimens in the NHMUK with this label are not from Buru, but rather from Morotai. There are no other known specimens of any of the *hercules* species-group taxa known from Buru or anywhere else in central Maluku, so we confidently exclude Buru from the range for *tyrannus*.

We consider nominotypical *tyrannus* is restricted to northern Maluku.

Arhopala tyrannus tyrannus f. *stymphelus* Fruhstorfer, 1914, **comb. n.**

(Fig. 10: ♂, Bacan; Fig. 11: ♀, Bacan; Fig. 12: ♂ HT, Bacan; Fig. 13: ♂, Kasiruta; Fig. 14: ♀, Halmahera; Fig. 15: ♀, Morotai.)

Arhopala hercules stymphelus: Fruhstorfer (1914: 155); TL: Bacan – see note 1.

Range: form *stymphelus* is recorded from Halmahera, Bacan, Ternate (NHMUK), Morotai, Mandioli, Kasiruta (Tennent & Rawlins 2010) – see notes 3 & 4 below.

Note 1: Fruhstorfer described *stymphelus* in German from a pair from Bacan and 4 ♂♂ from Halmahera. He compared *stymphelus* to nominotypical *hercules* and noted *stymphelus*' smaller size, the darker greenish-grey and stronger red-brown bands of the underside, and the reduced hw blue tornal spots. He reported less extensive purple-blue areas (i.e. broader dark borders) on the ♀ ups. The ♂ type from Bacan is in the NHMUK (Fig. 12).

Note 2: Evans (1957: 100) also treated *stymphelus* as a subspecies of *hercules* and noted "♂ 30 to 33 mm. ♀ brighter purple-blue [than *hercules*], border 3–5 mm.; below green." This subspecies differs from nominotypical *hercules* by its smaller size and the different shade of purple-blue on the ♀ ups. The uns ground colour is consistently dark dull green. Only 2 of 55 specimens examined have this green suffused reddish-brown.

Note 3: Evans (1957: 100) noted 2 *stymphelus* ♂♂ from Obi in the NHMUK collections. We have examined these specimens and they both carry the same 2 labels stating "Obi, ex J. Waterstradt, 1904" and "Ex Oberthür Coll. Brit Mus. 19273". These labels are considered erroneous as discussed by Tennent & Rawlins (2012: 140), Rawlins et al. (2014: 13, 16, 29) and Rawlins & Cassidy (2016: 148). We consider that these specimens did not originate in Obi, but most likely came from Bacan. We have seen no further records from Obi and therefore exclude Obi from the range of *stymphelus*.

Note 4: Evans (1957: 100) noted 1 *stymphelus* ♂ from Misool in the NHMUK. We have examined this ♂ and confirm it is typical of *stymphelus*. It bears a label stating "Mysol" handwritten and below "Hewitson Coll. 79-69.3. *Amblypodia hercules*. Hew". We suspect this is a locality error and in the absence of further Misool records, we exclude Misool from the range for *stymphelus*.

Note 5: Schröder & Stradomsky (2016: 73) noted that *stymphelus* was also recorded from Yapen and Mioswaar. They illustrated 2 specimens from the KSP – a ♀ from Yapen (their fig. 3) and a ♂ from Mioswaar (their fig. 4 – note: their plate key mistakenly states ♀). Neither exhibit the typical and consistent uns markings found in northern Maluku *stymphelus*. In addition, the Yapen ♀ has much broader ups black borders even than Bacan specimens – see note 6. The specimen is typical of *A. hercules* from the Sulawesi Region. The Mioswaar ♂ is typical of *phalaereus* (Figs. 67–70) – see later. We consider these specimens are not *stymphelus* and exclude these islands from the range for *stymphelus*.

Note 6: In the ♀♀ the width of the black borders varies. In general, the borders are wider in Bacan than in Halmahera specimens and least wide in specimens from Morotai. Some Halmahera specimens have borders as wide as the narrower bordered Bacan ones, whilst others have borders as narrow as the widest bordered Morotai specimens. However, there is no overlap in this feature between Morotai and Bacan specimens.

Arhopala tyrannus sophilus Fruhstorfer, 1914, stat. rev.

(Fig. 16: ♂, Obi; Fig. 17: ♀, Obi; Fig. 18: ♂ type, Obi; Fig. 19: ♂, Obi; Fig. 20: ♀, Obi, Fig. 21: ♀ type, Obi.)

Arhopala tyrannus sophilus: Fruhstorfer (1914: 156); TL: Obi – see note 1.

Synonym that we reject:

Arhopala hercules obscurata: Ribbe (1926: 87); TL: West coast, New Guinea – see note 4.

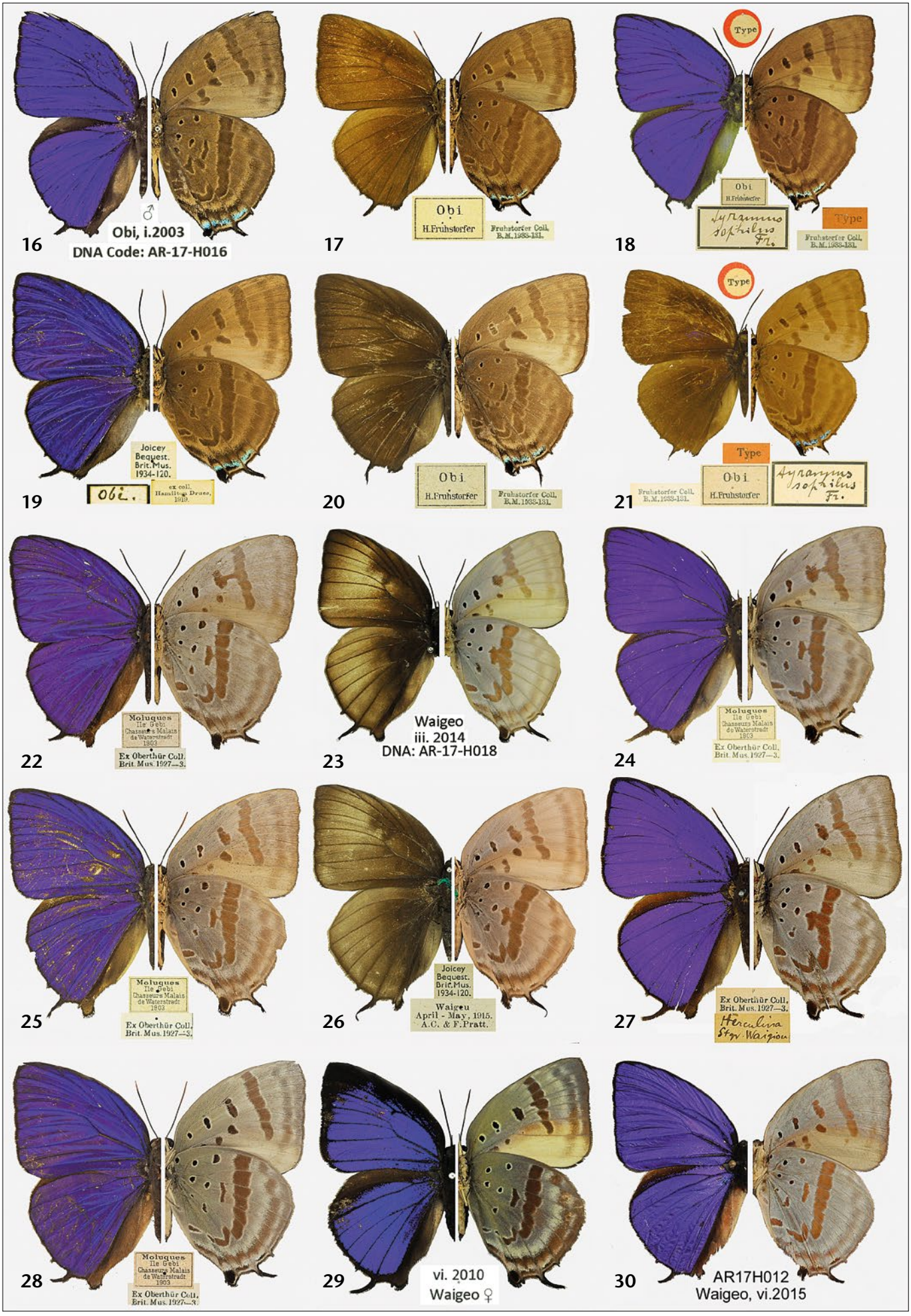
Range: endemic to Obi – but see notes 4 & 5.

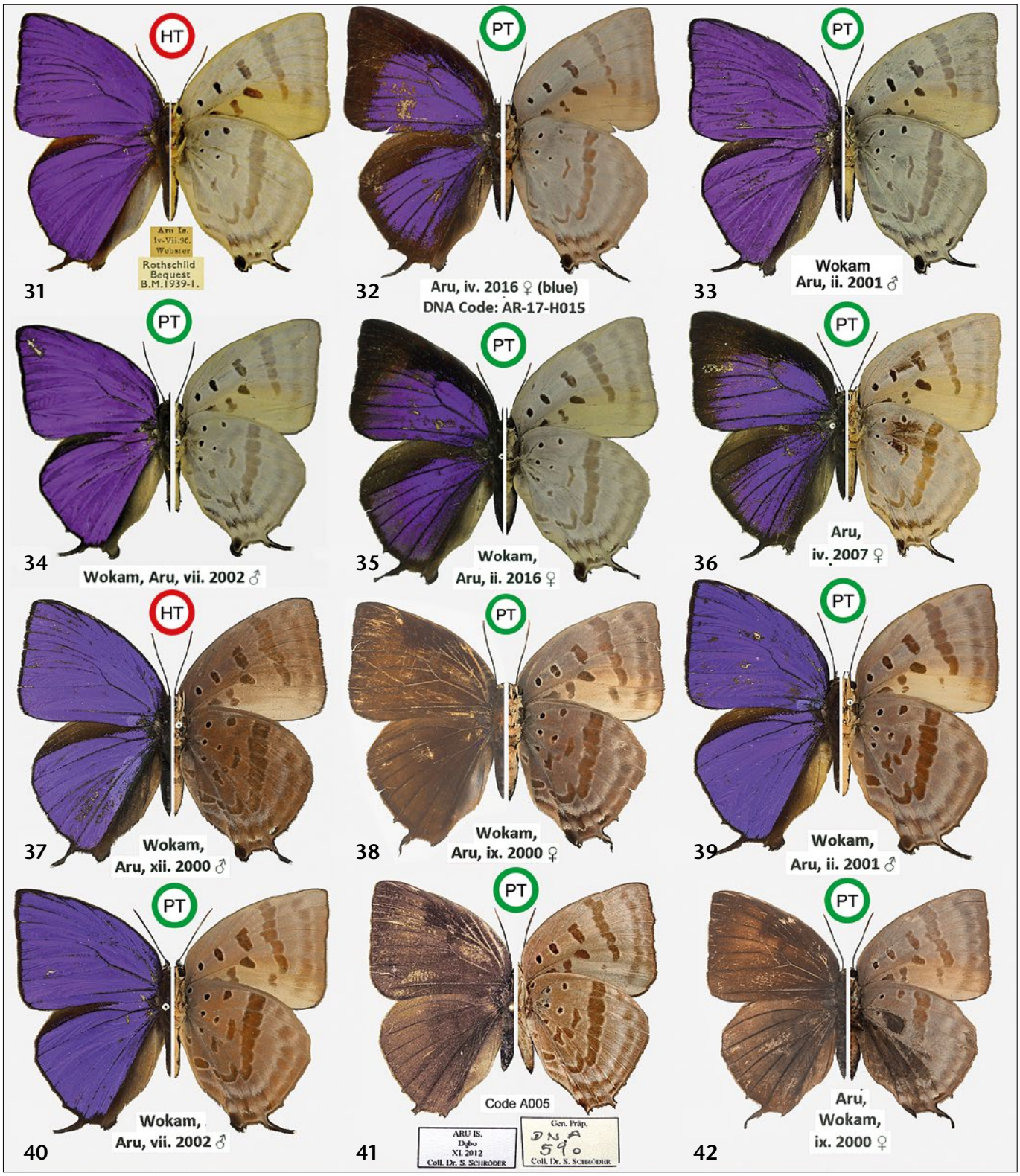
Note 1: Fruhstorfer described *sophilus* as a subspecies of *tyrannus* from 8 ♂♂ & 4 ♀♀ in his collection. He noted that the ♂ was much smaller and had a lighter grey-brown underside than *tyrannus* and that the ♀ ups was dark brown, sometimes with traces of blue in the discal area. Evans (1957: 100) reported that ♂ & ♀ types were in the NHMUK (Figs. 18, 21).

Note 2: Toxopeus (1930: 168) retained *sophilus* as a subspecies of *tyrannus* and stated that he had 2 ♂♂ in his collection. As he did with all *hercules* species-group taxa, Evans (1957: 100) treated *sophilus* as a subspecies of *hercules* and noted "♀ above, brown: below pale brown". Parsons (1998: 382) revised the status of *sophilus* to a full species.

Note 3: Phenotypically this taxon is broadly similar to nominotypical *tyrannus,* but as both Fruhstorfer and Evans noted, the *sophilus* underside ground colour is a lighter brown. The phylogenetic analysis indicates that *sophilus* falls within the large clade that includes *tyrannus* (Diagram 1). Its DNA barcode sequences differ by only 2–3 bp from 4 *tyrannus*/*stymphelus* specimens (Diagram 2), but it is phenotypically different and geographically separated, so we treat *sophilus* as a subspecies of *tyrannus*.

Note 4: Evans (1957: 100) listed *obscurata* Ribbe, 1926 from West New Guinea as a synonym of *sophilus* and recorded 4 ♂♂ and 4 ♀♀





Figs. 16–30: *hercules* species-group, Maluku. Subspecies of ***Arhopala tyrannus***. — **Figs. 16–21:** *A. tyrannus* ***sophilus:*** **16:** ♂, ups./uns., Obi (I. 2003, AR-17-H016, CARR). **17:** ♀, ups./uns., Obi (H. Fruhstorfer, NHMUK). **18:** ♂, type, ups./uns., Obi (H. Fruhstorfer, NHMUK). **19:** ♂, ups./uns., Obi (ex coll. Hamilton Druce, 1919, NHMUK). **20:** ♀, ups./uns., Obi (H. Fruhstorfer, NHMUK). **21:** ♀, type, ups./uns., Obi (H. Fruhstorfer, NHMUK). –**Figs. 22–30:** *A. tyrannus* ***herculina;*** **Figs. 22–27:** f. *herculina:* **22:** ♂, ups./uns., Gebe (Moluques, Ile Gebi, Chasseurs Malais de Waterstradt, 1903, NHMUK). **23:** ♀, ups./uns., Waigeo (III. 2004, AR-17-H018, CARR). **24:** ♂, ups./uns., Gebe (Moluques, Ile Gebi, Chasseurs Malais de Waterstradt, 1903, NHMUK). **25:** ♂, ups./uns., Gebe (Moluques, Ile Gebi, Chasseurs Malais de Waterstradt, 1903, NHMUK). **26:** ♀, ups./uns., Waigeo (Waigeu, April–May, 1915, A.C. & F. Pratt, NHMUK). **27:** ♂, ups./uns., Waigeo (Waigiou, NHMUK). – **Figs. 28–30:** *A. tyrannus herculina* **f. *leosque* f. n.: 28:** ♂, ups./uns., Gebe (Moluques, Ile Gebi, Chasseurs Malais de Waterstradt, 1903, NHMUK). **29:** ♀, ups./uns., Waigeo (VI. 2010, CARR). **30:** ♂, ups./uns., Waigeo (VI. 2015, AR17H012, CARR).

Figs. 31–42: *hercules* species-group, Maluku. — **Figs. 31–36:** Subspecies of ***Arhopala tyrannus:*** *A. tyrannus* ***jheae*** **ssp. n.: 31:** ♂, HT, ups./uns., Aru (Aru Is. IV.–VIII. [18]96, Webster, NHMUK). **32:** ♀, PT, ups./uns., Aru (IV. 2016, AR-17-H015, CARR). **33:** ♂, PT, ups./uns., Aru (Wokam, II. 2001, CARR). **34:** ♂, PT, ups./uns., Aru (Wokam, VII. 2002, CARR). **35:** ♀, PT, ups./uns., Aru (Wokam, II. 2016, CARR). **36:** ♀, PT, ups./uns., Aru (IV. 2007, CARR). — **Figs. 37–42:** ***Arhopala fowlerorum*** **sp. n.: 37:** ♂, HT, ups./uns., Aru (Wokam, XII. 2002, RMNH). **38:** ♀, PT, ups./uns., Aru (Wokam, IX. 2000, CARR). **39:** ♂, PT, ups./uns., Aru (Wokam, II. 2001, CARR). **40:** ♂, PT, ups./uns., Aru (Wokam, VII. 2002, CARR). **41:** ♀, PT, ups./uns., Aru (Dobo [Wamar], Code A005, Gen. Prep. 590, CSSK). **42:** ♀, PT, ups./uns., Aru (Wokam, IX. 2000, CARR).

in the NHMUK from "W. New Guinea." These specimens lack the turquoise-blue uns hw tornal spots that are well-developed in Obi *sophilus,* and also have narrower uns PD bands on both fws and hws, as well as a slightly yellower brown tinge to the uns ground colour. Thus, we consider them distinct from *sophilus*. Schröder & Stradomsky (2016: 77) placed *obscurata* as a synonym of *herculina* and designated a ♀ LT in the SMTD from Yapen (Fig. 66 — courtesy of SMTD website) — see note 2 under *Arhopala tyrannus herculina.* We exclude the *obscurata* records from West New Guinea in the range for *sophilus*.

Note 5: Evans (1957: 100) noted that there were 3 ♂♂ in the NHMUK labelled "Tenimber".

All 3 specimens bear the same 2 labels:

1. "Tenimber Is. South Yamdena. 20 m. N. of Saumlakki. June, July, Sept. 1918. W. J. C. Frost."
2. "Joicey Bequest. Brit. Mus. 1934-120."

These "Tanimbar" specimens do have the well-developed turquoise-blue uns hw tornal spots present in Obi *sophilus*, but they have broader and slightly stepped uns PD bands compared to the straighter edged bands in Obi *sophilus*. The "Tanimbar" specimens also exhibit increased contrast between the PD bands and the ground colour, and both are darker than in Obi *sophilus*.

We consider that they are not *sophilus*. We are not aware of any other records of any *hercules* group taxa from Tanimbar or Kei and we believe these specimens are mislabelled, most likely coming from the New Guinea Region. We exclude them from the Maluku checklist.

Note 6: Parsons (1998: 382) revised the status of *sophilus* to a full species. However, he did not consider that the species occurred in PNG and made no mention of *obscurata*.

Arhopala tyrannus herculina Staudinger, 1888, comb. n.

Arhopala hercules var. *herculina:* Staudinger (1888 (1): 280); TL: Waigeo — see note 1.

Synonyms that we reject:

Arhopala hercules obscurata: Ribbe (1926: 87); TL: west coast, New Guinea — see note 2.

Arhopala hercules phalaereus: Fruhstorfer (1914: 156); TL: Yapen — see note 3.

Amblypodia herculina leontodamas: Toxopeus (1930: 167); TL: Misool — see note 4.

Range: Gebe, Waigeo — see note 5 regarding Halmahera.

Note 1: Staudinger (1888), in German, described *herculina* as a variety of *hercules* from specimens from Waigeo sent by Dr. Platen. He stated that *herculina* was smaller than *hercules* and only slightly green-tinged at the base of the underside. He stated that 2 ♀♀ from Waigeo lacked this green completely and had no blue on the ups. He noted a 3rd ♀ from Waigeo was almost as blue as the ♂ on the ups, but with broad dark costal margin. This specimen doubtless corresponds to the phenotype considered to be *leo* by Evans (1957: 100) and Parsons (1998: 382). He also said that he had 2 specimens from purchased collections, of which the ♂ (from the Atkinson collection) should be from New Guinea and the ♀ from Halmahera. He noted that this ♀ only showed a little bit of green on the underside and formed a kind of transition to var. *herculina*. Unfortunately, he didn't specify whether it had brown or purple-blue ups. We suspect that this Halmahera ♀, if correctly labelled, was an atypical example of *stymphelus,* which was undescribed at that time.

Bethune-Baker (1903: 28–29, pl. 1, fig. 9) discussed "Var. *herculina* Stgr." and referred to 3 forms of the ♀ upperside. The 1st is all brown, the 2nd form brown but with whitish post discal area on the forewings, corresponding to Evans' description of the ♀ — see below. Bethune-Baker stated that the 3rd form was "Staudinger's blue female" and noted "the expanse of blue equalling that of *leo*". He opined that this form was in a transitional state with the underside pattern of individuals varying considerably. He further stated: "Staudinger described his variety from Waigeoe, but we have since received examples from Halmaheira."

Toxopeus (1930: 167) considered there were 5 subspecies of *A. herculina*. He restricted the nominotypical subspecies to Waigeo. The other 3 named subspecies — *phalaereus, leontodamas* and *obscurata* — are discussed below. He listed his 5th subspecies as "*A. h.* (*herculina*) subsp." from Halmahera and referenced Bethune-Baker (1903) — see note 5 below.

Evans (1957: 100) placed *herculina* as a subspecies of *hercules* and noted "♀ brown above, outer half yellowish. ♂ brighter blue than *leo.* Below, pale greenish to pinkish-grey or white: markings liable to much distortion." He noted 35 ♂♂ & 21 ♀♀ from Waigeo and 4 ♂♂ & 2 ♀♀ from Halmahera in the NHMUK — see note 5 below.

Parsons (1998: 382) revised the status of *herculina* to a full species and noted that *herculina* ♀♀ had brown uppersides. He considered *herculina* was a monotypic species, and as discussed in notes 3 & 4 below, he synonymised *leontodamas* and *phalaereus* with *herculina*. Thus, he gave the range for the species as Halmahera, Gebe, Waigeo, Misool, Yapen, Mioswaar, New Guinea and Aru. His Aru record was based on 1 ♂ in the MGCL, but this specimen is an example of *A. fowlerorum* sp. n. described below.

Parsons (1998: 382) noted "ST ♀ Waigiu (Dep?)." We have also been unable to locate any of the *herculina* STs. Some of Staudinger's specimens went to the NHMUK and some to the Museum für Naturkunde Berlin. Takanami (1989, 1992) did not include *herculina* in his papers on types in Berlin, so it is possible these STs were amongst the Berlin specimens lost in the 2nd World War.

Note 2: Ribbe (1926), in German, very briefly described *obscurata* from the west coast of New Guinea. He noted that there was no metallic colouring on the anal lobes and the ♀♀ were completely dark [i.e., ups all brown]. He also added, somewhat poetically, that the undersides looked as if they were poured over with milk!

Toxopeus (1930: 167) treated *obscurata* as a subspecies of *Amblypodia (hercules) herculina*, while Evans (1957: 100) listed it as a synonym of *sophilus*. Schröder & Stradomsky (2016: 77) rejected Evans' synonymy. They explained in detail their reasons, including: "*sophilus* differs strongly from *obscurata* in having a brown wing underside colour with very prominent tornal green scales". They considered that *obscurata* may be a synonym of *herculina* and designated a ♀ LT of *obscurata* in the SMTD (Fig. 66). The specimen bears a label stating: "A. B. Mayer, 1873, Ausus". Schröder & Stradomsky interpretated that as Ansus, an old name for Yapen, whereas Ribbe described *obscurata* from the west coast of New Guinea.

We agree that the *obscurata* LT ♀ is nothing like *sophilus,* but we also conclude it is not a synonym of *herculina*. It differs in two main ways from the *herculina* brown ♀ (f. *herculina*). The uns PD bands are much straighter in *obscurata* and the ups is uniformly dark brown, lacking the creamy yellow suffusion in the outer part of the wings present in Waigeo *herculina*.

We consider it likely that this LT does not truly represent Ribbe's syntype series, but the designation stands, and we propose that the *obscurata* LT ♀ is possibly synonymous with *phalaereus* — see below.

Three pairs from Kapaur (= Fak Fak, West Papua, on the west coast of New Guinea — 1 pair is illustrated in Figs. 71, 72) are placed as *obscurata* in the NHMUK, we assume by Evans. The ♀♀ also have brown ups, but with only very slight lightening in the outer areas of the wings. It is hard to be sure what exactly Ribbe meant by "the undersides were as if poured over with milk". In any case these Kapaur specimens also do not match *herculina* and we consider they represent a distinct taxon, geographically isolated from Waigeo *herculina*.

We do not speculate on the taxonomic status of the original STs of *obscurata,* without access to a definitive syntype.

Note 3: Fruhstorfer (1914: 156), in German, described only the ♂ of *phalaereus* (as a subspecies of *hercules*) from Doherty specimen/s from "Jobi" (= Yapen). He differentiated *phalaereus* from a series of 10 *Arhopala hercules herculina* from Waigeo and Misool in his collection, noting that the underside had a stronger greenish basal colour on the hindwing and a much broader red-brown PD band, especially on the hindwing. Toxopeus (1930: 167) listed *phalaereus* as a subspecies of *Amblypodia (hercules) herculina*. Evans (1957: 100) noted that the ♂ "type" was in the NHMUK (Fig. 67) and placed it as a valid subspecies of *hercules*. He stated "♀ above plain dark brown. Below dark to pale green." He recorded specimens in the NHMUK from Yapen, Mioswaar and W. New Guinea. Parsons (1998: 382) synonymised *phalaereus* with *herculina* and Schröder & Stradomsky (2016: 77) tentatively agreed. We have compared long series of *phalaereus* and Waigeo *herculina* in the NHMUK and find consistent differences. For example, the ups of all 20 *herculina* ♀♀ is a light brown changing to paler creamy yellow brown on the distal half of the wings, whereas that of *phalaereus* ♀♀ is a uniform and darker brown. The uns of *herculina* is generally a grey brown sometimes with tinge of green, whereas the *phalaereus* uns is consistently a relatively strong green. In more than one third of the 42 *herculina* specimens examined, the uns exhibits a coalescence between the cell end bar and the PD band on either or both fws and hws. This is present in the *phalaereus* type, but not in the other 50+ specimens examined. We therefore consider *phalaereus* is distinct from *herculina*.

Schröder & Stradomsky (2016: 77, fig. 14) and Parsons (1998: 382) regarded *phalaereus* as a synonym of *herculina*. Schröder & Stradomsky recorded that purple-blue ♀♀ also occur on Yapen and treated them as *herculina* f. *leo*. We think it likely that the purple-blue and brown ♀♀ phenotypes on Yapen represent polymorphic forms. But, as noted above we do not consider *phalaereus* synonymous with *herculina*.

Of the phenotypes examined, the uns of the *phalaereus* specimens most closely resemble "Timika Phenotype B" (see later), although the bands tend to be slightly narrower in *phalaereus*. The *phalaereus* ♂ ups is lighter, more purple and shinier than that of Timika Phenotype B, closely matching the ups of Timika Phenotype A and *droa* as well as Misool *leontodamas*. We have no DNA samples of *phalaereus* or "Timika Phenotype B" and so we refrain from speculating into which clade they fall.

Note 4: Toxopeus (1930: 167), in Dutch, described *leontodamas* as a subspecies of *Amblypodia* (*hercules*) *herculina* from 2 Waterstradt ♂♂ (type & paratype) received by Niepelt. He noted that the specimens came from Misool and were in his collection, now in the RMNH. Rob de Vos, the curator of Lepidoptera at the RMNH, kindly sent us photographs of 3 ♂♂ labelled as *leontodamas* types (Figs. 46–48). All three also bear scruffy pencil labels indicating they originated in Misool, but none has a Waterstradt legend label.

Rob de Vos (pers. comm. 2019) noted that Toxopeus often prelabelled "type" specimens prior to publication and in some cases these "type names" were never published. In this case, he may have had three specimens in mind to publish, but in the end only listed two. We consider the specimen with the label stating "TYPE Tox." to be the HT. There is no clue to distinguish which of the two specimens bearing the "PARATYPE Tox." labels is the true PT. On the basis that it is the better specimen, we elect the male shown in Fig. 47 as the PT and the specimen at Fig. 48 is considered not to be a PT.

Evans (1957: 100) listed *leontodamas* as a subspecies of *hercules*, reporting it as intermediate between *herculina* and *phalaereus*. He noted that the NHMUK had specimens from Misool and Gebe (5 ♂♂). Parsons (1998: 382) synonymised *leontodamas* with *herculina,* which he considered a full species. Schröder & Stradomsky made no comment on *leontodamas,* other than reporting Parsons' synonymy. As discussed earlier, we conclude that these Gebe specimens match Waigeo *herculina* — four represent f. *herculina,* and one is f. *leoesque*.

Unlike Parsons, we consider the ♂ types and the series of 14 ♂♂ and 2 ♀♀ of *leontodamas* from Misool in the NHMUK are consistently distinct from Waigeo *herculina*. For example, none have the uns hw PD band conjoined with the cell end bar, whereas about one third of *herculina* specimens from Waigeo exhibit this feature. The uns fw PD band is straighter in *leontodamas*. On the ♀ ups, the creamy white suffusion on the distal half of the wings present in Waigeo *herculina* is much reduced in Misool *leontodamas*. In the molecular phylogeny, 1 *leontodamas* ♂ from Misool (AR-17-H013 & Fig. 49) falls in the large clade with *tyrannus,* and therefore we give the combination ***A. tyrannus leontodamas* comb. n.**

Note 5: With regard to *herculina* records from Halmahera:

The Staudinger Halmahera ♀ and Bethune-Baker (see note 1 above) appear to be the original sources of subsequent records in the literature of the occurrence of *herculina* in Halmahera. There are also 4 ♂♂ and 2 ♀♀ in the NHMUK bearing Halmahera labels. The specimens bear the following labels:

- 1 ♂ has 2 labels: "Halmah. Plat." and "Ex coll. Bethune-Baker, B.M. 1927-360".
- 1 ♂ & 1 ♀ each have 2 labels "Halma. Plat." and "Ex coll. Bethune-Baker, B.M. 1927-360".
- 2 ♂♂ each have 2 labels: handwritten "Halmaheira" and "Ex coll. Bethune-Baker, B.M. 1927-360".
- 1 ♂ & 1 ♀ each have just 1 handwritten label "Halmaheira", but this is in same style as the 2 ♂♂ mentioned above which also bear ex coll. Bethune-Baker labels.

The labels indicate that at least 4 of these 6 specimens came from Bethune-Baker's collection and it seems likely that the other two were also ex coll. Bethune-Baker.

These specimens are typical of *herculina,* although we note that the PD bands on the uns are quite variable, but all lie within the range of variation found in *herculina* from Waigeo.

We consider these specimens do represent true *herculina*. However, we are unaware of any further records of *herculina* from Halmahera or anywhere else in northern Maluku, despite extensive collecting there in the last 25 years. We therefore have some doubts about the provenance of these "Halmahera" specimens and regard the occurrence of *herculina* on Halmahera as unconfirmed.

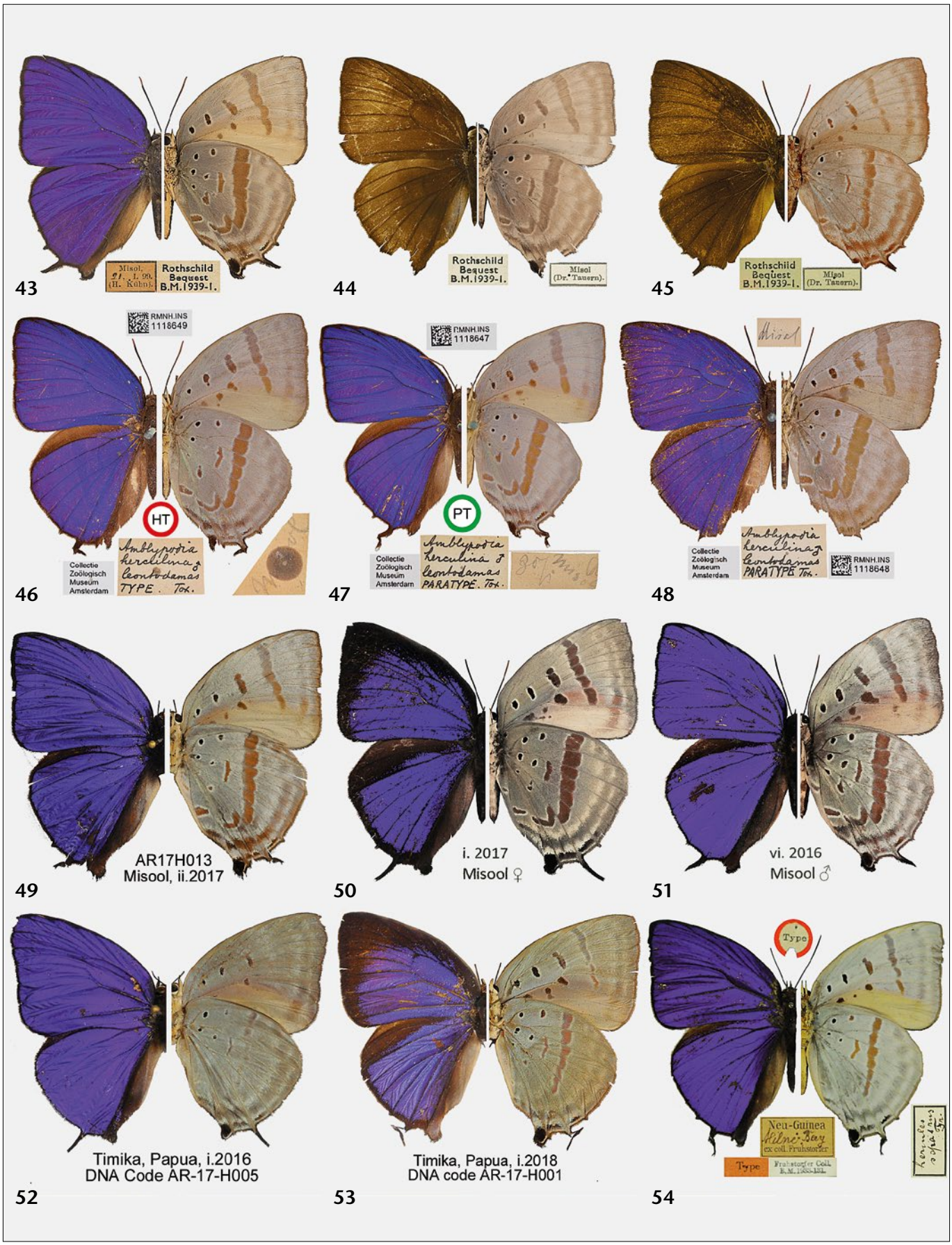
In summary on the identity of *herculina* and the two phenotypes found in Waigeo and Gebe:

Staudinger described *herculina* from Waigeo, initially noting that the uns was only slightly green-tinged at the base. He then described 2 different ♀ forms — 2 ♀♀ lacked this green completely and had no blue on the ups, whereas a 3rd ♀ had a blue ups with a broad, dark costal margin.

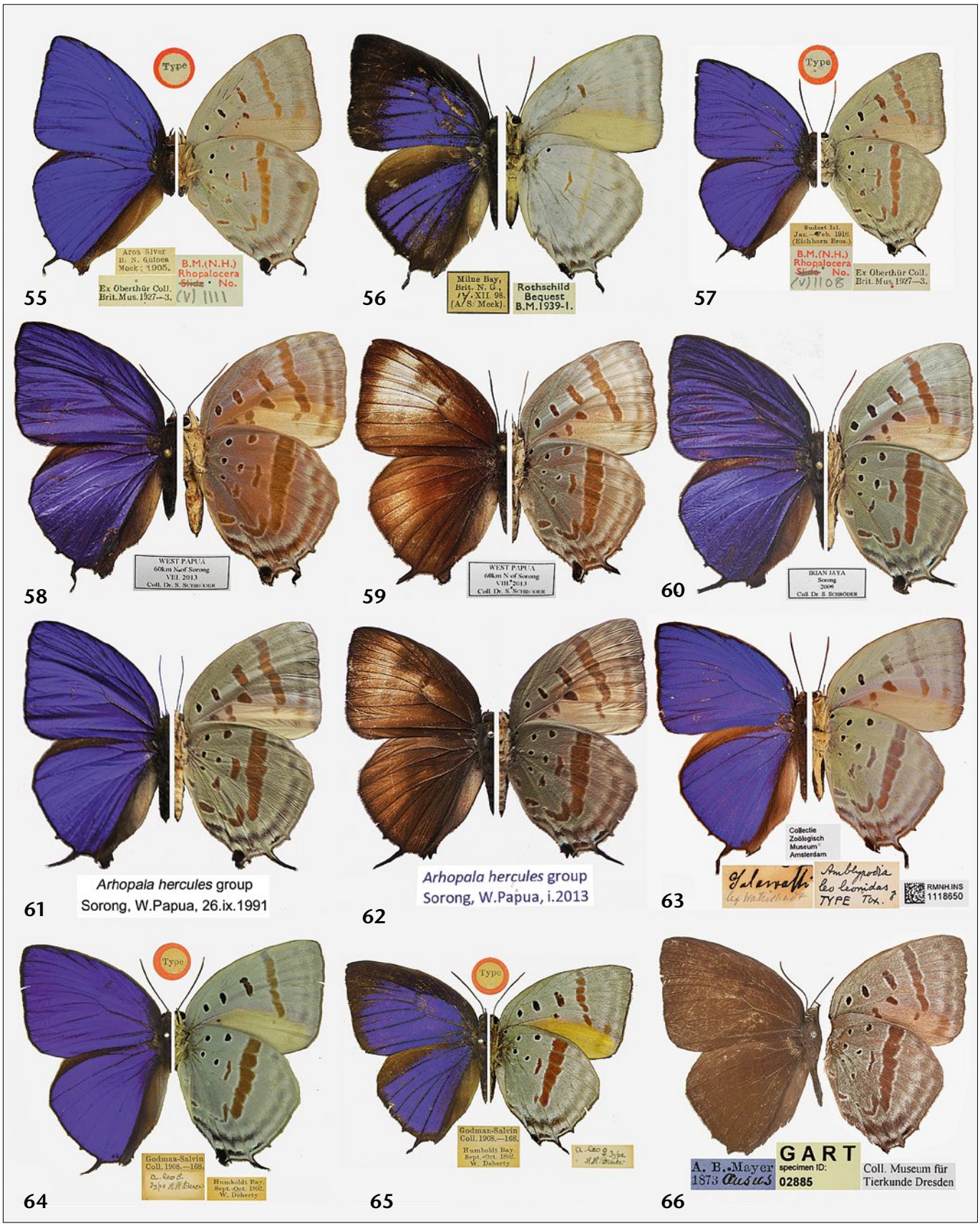
Bethune-Baker (1903: 28–29) pointed out that most authors accepted that the brown ♀ (our Phenotype 7) was typical of *herculina,* and both Evans (1957: 100) and Parsons (1998: 382) considered *herculina* ♀♀ to have brown ups (though Evans noted correctly that the outer half of the wings was yellowish).

Since then, the 2 phenotypes found on Waigeo (and now recognised on Gebe) — Phenotypes 7 (*herculina*) and 3 (*leoesque*) — have been treated as distinct species or subspecies. Phenotype 7 has been treated as "true" *herculina* (TL Waigeo) and Phenotype 3 has been associated with the New Guinea taxon *leo* (TL Humboldt Bay = Yos Sudarso Bay). Parsons (1998: 382) considered them to be full, monotypic species — *A. leo* and *A. herculina*. Despite their sympatry, Evans (1957: 100) treated them as *A. hercules leo* and *A. hercules herculina*. Toxopeus (1930: 167) treated Phenotype 7 as *A. herculina herculina* and Phenotype 3 as an un-named subspecies of *leo*.

Identical COI sequences in these 2 sympatric taxa suggest they are not different species. Moreover, they fall in the same clade as



Figs. 43–54: *hercules* species-group, New Guinea region. — Further subspecies of ***Arhopala tyrannus***. —**Figs. 43–48:** *A. tyrannus* ***leontodamas*** **f. *leontodamas*: 43:** ♂, ups./uns., Misool (Misol, 21. I. [18]99, H. KÜHN, NHMUK). **44:** ♀, ups./uns., Misool (Misol, Dr. TAUERN, NHMUK). **45:** ♀, ups./uns., Misool (Misol, Dr. TAUERN, NHMUK). **46:** ♂, HT, ups./uns., Misool (Misol, RMNH.INS 1118649, RMNH). **47:** ♂, PT, ups./uns., Misool (Misol, RMNH.INS 1118647, RMNH). **48:** ♂, ups./uns., Misool (Misol, RMNH.INS 1118648, RMNH). — **Figs. 49–51:** *A. tyrannus* ***leontodamas*** **f. *leolike* f. n.: 49:** ♂, ups./uns., Misool (II. 2017, AR17H013, CARR). **50:** ♀, ups./uns., Misool (I. 2017, CARR). **51:** ♂, ups./uns., Misool (VI. 2016, CARR). — **Figs. 52–54:** *A. tyrannus* ***droa*****: 52:** ♂, ups./uns., Papua (Timika, I. 2016, AR-17-H005, CARR). **53:** ♀, ups./uns., Papua (Timika, I. 2018, AR-17-H001, CARR). **54:** ♂, ups./uns., PNG ("*sopatrus*" = *droa*, Milne Bay, ex. coll. FRUHSTORFER, NHMUK).



Figs. 55–66: *hercules* species-group, New Guinea region. — Further subspecies of ***Arhopala tyrannus*** and **taxa of uncertain status.** — **Figs. 55–56:** *A. tyrannus* ***droa:*** **55:** ♂, HT, ups./uns., PNG (Aroa River, B.N.Guinea, 1905, Meek, B.M.(N.H.) Rhopalocera No. (v) 1111, NHMUK). **56:** ♀, ups./uns., PNG (Milne Bay, Brit.N.G. 12. xii. [18]98, A. S. Meek, NHMUK). — **Fig. 57:** *A. tyrannus* ***louisa:*** ♂, HT, ups./uns., Sudest Island (Jan.–Feb. 1916, Eichhorn Bros. B.M.(N.H.) Rhopalocera No. (v) 1108, NHMUK). — Taxa of uncertain status: **Figs. 58–62:** *A. tyrannus* ssp. ?*leonidas:* **58:** ♂, ups./uns., West Papua (60 km N. of Sorong, viii. 2013, CSSK). **59:** ♀, ups./uns., West Papua (60 km N. of Sorong, viii. 2013, CSSK). **60:** ♂, ups./uns., West Papua (Sorong, 2005, CSSK). **61:** ♂, ups./uns., West Papua (Sorong, 26. ix. 1991, CARR). **62:** ♀, ups./uns., West Papua (Sorong, i. 2013, CARR). – **Fig. 63:** *A.* ?*tyrannus leonidas*: ♂, HT, ups./uns., Salawati, West Papua (Salawatti, leg. Waterstradt, RMNH.INS 1118650, RMNH). — **Figs. 64–65:** *leo:* **64:** ♂, type, ups./uns., Papua (Humboldt Bay [Yos Sudarso Bay], Sept.–Oct. 1892, W. Doherty, NHMUK). **65:** ♀, type, ups./uns., Papua (Humboldt Bay [Yos Sudarso Bay], Sept.–Oct. 1892, W. Doherty, NHMUK). — **Fig. 66:** *phalaereus,* ♀, ups./uns., Yapen (LT *obscurata* = *phalaereus*, Ausus, 1873, A. B. Mayer, SMTD — Courtesy of website).

tyrannus. Thus, we treat Phenotype 7 as *A. tyrannus herculina* f. *herculina*. As Toxopeus, we recognise morphological differences between Phenotype 3 and *leo*. However, in recognition of the superficial similarity to *leo,* we name Phenotype 3 as *A. tyrannus herculina* f. *leoesque*.

Arhopala tyrannus herculina f. *herculina* Staudinger, 1888, **comb. n.**

(Fig. 22: ♂, Gebe; Fig. 23: ♀, Waigeo; Fig. 24: ♂, Gebe; Fig. 25: ♂, Gebe; Fig. 26: ♀, Waigeo; Fig. 27: ♂, Waigeo.)

Arhopala tyrannus herculina f. *leosque* **(f. n.)**

(Fig. 28: ♂, Gebe; Fig. 29: ♀, Waigeo; Fig. 30: ♂, Waigeo.)

We have previously discussed the appearance, taxonomic history and phylogenetic relationships of this phenotype.

Etymology: named to recognise the superficial morphological similarity and historical affiliation of this form with *leo*.

Arhopala tyrannus jheae Rawlins & Cassidy, ssp. n.

(Fig. 31: HT ♂, Aru; Fig. 32: PT ♀, Aru; Fig. 33: PT ♂, Aru; Fig. 34: PT ♂, Aru; Fig. 35: PT ♀, Aru; Fig. 36: PT ♀, Aru.)

Holotype ♂: Indonesia, Aru, iv.–vii. 1896 (NHMUK).

Paratypes (11 ♂♂, 4 ♀♀): 1 ♂, Gulila, Kobroor Island, Aru, iii. 1998; 1 ♂, Wokam Island, Aru, ii. 2001; 1 ♂, Wokam Island, Aru, vii. 2002; 1 ♂, Aru, iii. 2003; 1 ♂, 1 ♀, Aru, iv. 2007; 2 ♂♂, Aru, xii. 2008; 1 ♀, Wokam, Aru, ii. 2016; 1 ♀, Aru, iv. 2016 (all CARR). 3 ♂♂, 1 ♀, Tanah Besar (= Wokam), Aru, vi. 2016 (♀, DNA Code: SS-17-A004; 1 ♂, SS-17-A003) (CSSK). 1 ♂, Aru, iv. 2016 (AR-17-H006) (AMNH).

Etymology: named for Jhea, the first author's life partner.

Range: endemic to Aru (Wokam and Kobroor Islands).

Diagnosis and description

♂

(Figs. 31 [HT], 33, 34.)

FwL 29–32 mm (HT: 30 mm).

Upperside: ground colour shiny deep purple-blue with very narrow black borders, on the fws expanding slightly to 1 mm at the apex. Hw space 7 purple-blue at the base, otherwise very dark brown. Anal fold greyish-brown. A long white-tipped tail at vein 2 and a weak tooth at vein 3; tornal lobe conspicuously projecting.

Underside: ground colour light yellowish-grey, but yellower in fw spaces 1a–2. General pattern of markings typical for *hercules* species-group specimens. PD bands pale reddish-brown and relatively straight. Fw PD band straight, reaching from space 2 to space 9, slightly widening towards costa. The end-cell bar dislocated into 2 parts, reddish-brown; cell spots dark brown to black. Additional dark subbasal spots in space 1b; a dark basal spot in space 2. Hw PD band straight to vein 2, then dislocated basad. End-cell bar light reddish-brown; open V shape and well separated from PD band. Subbasal spots dark brown to black. Large black tornal spot in space 1a, with faint black spots in spaces 1b and 2. Some specimens, including HT, with a few faintly developed shiny turquoise-blue scales associated with the black tornal spots.

♀

(Figs. 32, 35, 36.)

FwL 30–33 mm.

Upperside: Ground colour deep purple-blue with wide very dark brown borders. Fw border 2.5 mm at tornus, widening to 9–10 mm at apex. Costal border 2.5 mm at base widening to apex. Hw spaces 1b to 5 purple-blue, space 6 purple-blue at the base, otherwise very dark brown. All veins very dark brown.

Underside: as male.

Note: Two *hercules* species-group phenotypes occur sympatrically on Aru. As described in more detail above, the phylogenetic results show that this phenotype falls in a clade with the phenotypes *tyrannus, stymphelus, sophilus* and *leo*. The other phenotype on Aru — described below as *A. fowlerorum* sp. n. — lies in a separate clade and the four specimens' COI barcode sequences differ by 7–8 bp from the sequences of the *jheae* specimens. The morphological differences between the 2 taxa have also been described earlier — see "Occurrence of taxa/phenotypes and sympatry in Maluku". Both phenotypes differ morphologically from all other *hercules* species-group taxa.

Arhopala fowlerorum Rawlins & Cassidy, sp. n.

(Fig. 37: HT ♂, Aru; Fig. 38: PT ♀, Aru; Fig. 39: PT ♂, Aru; Fig. 40: PT ♂, Aru; Fig. 41: PT ♀, Aru; Fig. 42: PT ♀, Aru.)

Holotype ♂: Indonesia, Aru, Wokam Island, xii. 2000 (RMNH).

Paratypes (21 ♂♂, 5 ♀♀): 1 ♂, 2 ♀♀, same data; 1 ♂, 1 ♀, Gulila, Kobroor Island, Aru, iii. 1998; 1 ♀, Wokam Island, Aru, ix. 2000; 1 ♂, Wokam Island, Aru, ii. 2001; 1 ♂, Wokam Island, Aru, vii. 2002; 1 ♂, Aru, iii. 2003; 1 ♂, Aru, ix. 2006; 1 ♂, Wokam Island, Aru, iii. 2015; 1 ♂, Aru, iv. 2016 (CARR). 7 ♂♂, Trangan Island, Aru, v. 2010; 3 ♂♂, 1 ♀, Dobo, Wamar Island, Aru, xi. 2012 (♀ SS-17-A005, 1 ♂ SS-17-A002) (CSSK). 1 ♂, Dobo, Wamar Island, Aru, 7. v. 1939, RG & CM Wind" (MGCL); 1 ♂, Trangan Island, Aru, v. 2010 (SS-17-A001); 1 ♂, Wokam Island, Aru, iii. 2015) (AMNH).

Etymology: named for Martin and Harriet Fowler, friends and role models of the first author.

Range: endemic to Aru (Wamar, Wokam, Kobroor & Trangan Islands).

Diagnosis and description

♂

(Figs. 37 [HT], 39, 40.)

FwL 28–31 mm (HT: 29 mm).

Upperside: ground colour shiny deep purple-blue (but a slightly lighter, bluer and shinier purple-blue than *jheae*) with very narrow black borders, on the fws expanding slightly to 1 mm at the apex. Hw space 7 purple-blue at the base, otherwise very dark brown. Anal fold greyish-brown. A long white-tipped tail at vein 2 and a weak tooth at vein 3; tornal lobe conspicuously projecting.

Underside: ground colour varies from light to dark reddish-brown (HT dark reddish-brown).

General pattern of markings typical for *hercules* species-group specimens. PD bands dark reddish-brown, always significantly darker than the ground colour. Fw PD band irregular, reaching from space 2 to space 9, and in some specimens, also a spot in space 1b shifted significantly inwards. The end-cell spot darker than PD band; cell spots dark brown to black. Additional dark subbasal spots

in space 1b; a dark basal spot in space 2. Hw PD band straight, from costa to vein 2, then dislocated basad. End-cell bar same colour as PD band. Subbasal spots dark brown to black. Large black tornal spot in space 1a, some specimens with faint dark marginal spots in spaces 1b and 2. Some specimens, including HT, with a few faintly developed shiny silver scales associated with these spots.

♀

(Figs. 38, 41, 42.)

FwL 27–29 mm.

Upperside: dark brown.

Underside: as male.

Note: See note under description of *A. tyrannus jheae.*

West Papua and Papua *hercules* species-group taxa — some notes and taxonomic suggestions

The situation in the New Guinea Region is more complicated with three (or possibly more) phenotypes occurring in at least one geographical location and increased intra-phenotype variability. This paper covers Maluku, but we make the following observations, which may be of use to future researchers studying this group in the New Guinea Region.

Waigeo

See the section on Gebe.

Misool

There are two phenotypes present on Misool. The first is *leontodamas* (Figs. 43–45) which has ♀♀ (Figs. 44, 45) with brown ups.

As discussed under *Arhopala tyrannus herculina,* Toxopeus (1930: 167) described *leontodamas* as a subspecies of *herculina* from ♂♂ from Misool, now in the RMNH (Figs. 46–48). The specimens match the ♂♂ in the NHMUK series from Misool.

Evans (1957: 100) maintained *leontodamas* as a distinct subspecies, but Parsons (1998: 382) synonymised it with *herculina*. We have compared the NHMUK series of specimens of *leontodamas* from Misool (14 ♂♂ & 2 brown ♀♀) and *herculina* from Waigeo (22 ♂♂ & 20 [all brown] ♀♀ — Evans noted 35 ♂♂ & 21 ♀♀, but some of the ♂♂ are the *leoesque* phenotype). We notice some consistent differences. For example, the uns PD band is usually irregular and often conjoined with the cell end bar in *herculina*, but never in *leontodamas*. The *leontodamas* ♀ upperside has a more uniform brown and lacks the distal creamy colouration on the outer parts of the wings present in *herculina*. We consider *leontodamas* is a distinct subspecies, endemic to Misool.

The second phenotype (Figs. 49–51) found in Misool has ♀♀ with purple-blue ups (Fig. 50). Toxopeus (1930: 167) treated this, and the similar phenotype found on Waigeo, as distinct un-named subspecies of *Arhopala leo*.

There are no *hercules* group purple-blue ♀♀ from Misool in the NHMUK. Parsons (1998: 383) did not include Misool in the range for *leo,* but had he seen purple-blue Misool ♀♀ he would undoubtedly have paced them as *A. leo*.

We have examined two purple-blue ♀♀ from Misool and consider them similar but not identical to Waigeo f. *leoesque* (see earlier). The ups in the Misool ♀♀ is more purple, less shiny, with wider black borders than Waigeo specimens.

The purple-blue Misool ♀♀ are larger and have a slightly more green-tinged uns, with more contrasting PD bands, than the Misool brown ♀♀.

It is less clear that the Misool ♂♂ fall into 2 distinct forms, corresponding with the ♀♀ forms.

The 14 ♂♂ in the NHMUK (e.g., Fig. 43) exhibit minor variation in uns ground colour (brownish with differing tinges of pink, grey or green). However, they all (along with the RMNH types) appear to conform to the uns of the brown ♀♀.

We have also examined ♂♂ from Misool (Figs. 49, 51) that are larger, have a slightly bluer ups and a more green-tinged uns, and we associate these with the purple-blue ♀♀.

We have DNA sequencing data from just one specimen from Misool — a "*leo*-like" phenotype ♂ (Fig. 49, AR-17-H013). This falls in the clade with *tyrannus, stymphelus* and both Waigeo phenotypes. Based on the situation in northern Maluku and Waigeo, the two Misool phenotypes are also likely to be forms of the same taxon.

We informally treat the two Misool phenotypes as ***Arhopala tyrannus leontodamas* comb. n. f. *leontodamas*** (with brown ♀) and ***Arhopala tyrannus leontodamas* comb. n. f. *leolike* f. n.** (with purple-blue ♀). We choose this name to reflect that this form, though broadly similar to both *leo* and f. *leoesque,* does have some distinguishing features.

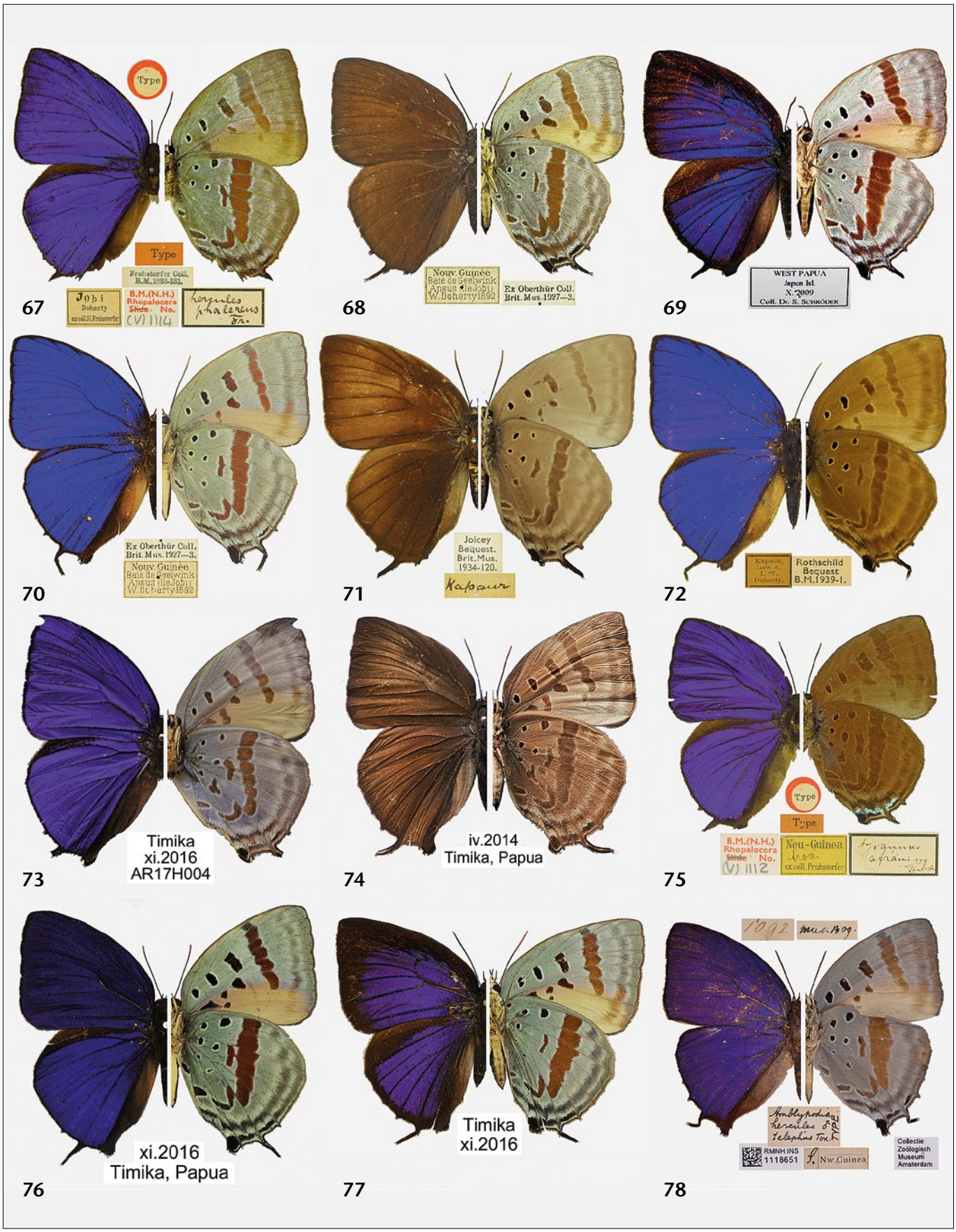
As mentioned earlier, Evans (1957: 100) included the NHMUK Gebe specimens with *leontodamas* from Misool, but we include them with *A. tyrannus herculina.*

Yapen

See notes 2 & 3 under *Arhopala tyrannus herculina*. In brief, the taxon *phalaereus* (Figs. 66–70, type Fig. 67) was described from Yapen. We consider it a valid taxon, but we have no DNA sequence data to determine its specific status. We consider the *obscurata* LT (Fig. 66) is likely a synonym of *phalaereus* – ***obscurata,* syn. n.**

Sorong and Salawati

All the specimens we have seen from Sorong (ca. 30) have uns with similar pattern of markings, but the ground colour and the colour of the bands varies (Figs. 58–62). Both brown and purple-blue (much less common — Hiromi



Figs. 67–78: *hercules* species-group, New Guinea region. — **Taxa of uncertain status.** — **Figs. 67–70:** *phalaereus:* **67:** ♂, type, ups./uns., Yapen (Jobi, Doherty, ex. coll. H. Fruhstorfer, Rhopalocera No. (v) 1114, NHMUK). **68:** ♀, ups./uns., Yapen (Baie de Geelwink, Ansus (Ile Jobi), 1892, W. Doherty, NHMUK). **69:** ♀, ups./uns., Yapen (Japen, x. 2009, CSSK). **70:** ♂, ups./uns., Yapen (Baie de Geelwink, Ansus (Ile Jobi), 1892, W. Doherty, NHMUK). — **Figs. 71–72:** Kapaur pair in NHMUK (see text): **71:** ♀, ups./uns., West Papua (Kapaur [Fak Fak], NHMUK). **72:** ♂, ups./uns., West Papua (Kapaur [Fak Fak], Low c., I. [18]97, Doherty, NHMUK). — **Figs. 73–74:** "Timika Phenotype A": **73:** ♂, ups./uns., Papua (Timika, xi. 2016, AR17H004, CARR). **74:** ♀, ups./uns., Papua (Timika, iv. 2014, CARR). — **Fig. 75:** *afranius:* ♂, ups./uns., type, New Guinea (Aroa [River], ex. coll. Fruhstorfer, B.M.(N.H.) Rhopalocera No. (v) 1112, NHMUK). — **Figs. 76–77:** "Timika Phenotype B": **76:** ♂, ups./uns., Papua (Timika, xi. 2016, CARR). **77:** ♀, ups./uns., Papua (Timika, xi. 2016, CARR). — **Fig. 78:** *telephus:* ♂, HT, ups./uns., New Guinea (Nw Guinea, Mus. Bog[or], RMNH.INS 1118651, RMNH).

Plate 7: *hercules* species-group ♀ phenotypes (undersides) from Timika (Papua).

Detani, pers. comm.) ♀♀ occur. Phylogenetic analysis of DNA sequences from 2 brown ♀♀ (ILL240 & ILL243) place this phenotype in the clade including *tyrannus,* both Waigeo phenotypes and Timika *droa* — see below.

Therefore the brown ♀ form (Figs. 59, 62) falls under *tyrannus*. It seems likely that the purple-blue ♀♀ represent a second form of the same taxon.

Toxopeus (1930: 167) described *leonidas* (as *Amblypodia (hercules) leo leonidas*) from a single ♂ from Salawati. We illustrate this specimen courtesy of Rob de Vos and the RMNH (Fig. 63). Evans (1957: 100) synonymised *leonidas* with *leo* and Parsons (1998: 383) followed Evans. The *leonidas* type is very similar to the *leo* ♂ type (Fig. 64) in the NHMUK. However, we have not been able to compare the shade of purple-blue on the ups and we have seen no further specimens from Salawati.

Salawati is a large, relatively flat island (highest point 931 m) at its closest less than 2 km off the coast, south of Sorong (see Map). As far as we know, there are no butterfly taxa endemic to Salawati. The Sorong ♂ in Fig. 60 appears similar to the *leonidas* type and they most likely represent the same taxon. Whether the Salawati *leonidas* type, both forms from Sorong, the *leo* types (Figs. 64, 65) and also *droa* and *loiusa* (see under Timika) all represent the same taxon, needs further research.

Timika

There are at least 3 distinct phenotypes present in Timika (Plate 7). Occasional specimens from Timika do not fall clearly into any of the 3 phenotypes.

The first phenotype (Figs. 52, 53) has a pale green uns with very thin or sometimes absent PD bands. Specimens closely match the HT of *droa* Evans, 1957 (TL: Aroa River; Fig. 55) and the series of *droa* from Milne Bay in the NHMUK. We have seen only purple-blue ♀♀. Parsons (1998: 383) synonymised *droa* and *louisa* (see below) with *leo* Druce, 1894. However, as Evans (1957: 100), we consider *droa* does merit status as a distinct subspecies – but see below. We also record *droa* from Yahukimo (2 ♂♂, v. 2009, CARR) and Asike, near Merauke (2 ♂♂, v. 2013, CARR), indicating this phenotype is widespread in New Guinea.

We have not been able to sequence any *droa* from Aroa River or Milne Bay, however the "Timika *droa*" phenotype (♂♂ AR-17-H002, AR-17-H005 & Fig. 52; ♀ AR-17-H001 & Fig. 53) lies in the clade including *tyrannus* and both Waigeo phenotypes. We therefore treat this phenotype as ***A. tyrannus droa* comb. n.**

We note that *louisa* Evans, 1957 (TL: Sudest = Tagula) is similar to *droa,* except smaller, and there are no *louisa* specimens with the minimal uns PD markings present in some *droa* from both Timika (Plate 7) and Milne Bay. The *louisa* HT is in the NHMUK (Fig. 57).

The *leo* ♂ & ♀ types are in the NHMUK (Figs. 64, 65). We note that *leo* is quite similar to *droa* and *louisa* but the uns PD bands are wider in *leo*.

The NHMUK has a series of 28 ♂♂ & 7 ♀♀ (all purple-blue) placed by Evans as *leo,* from various localities in New Guinea including Kapaur (= Fak Fak), Humboldt Bay (= Yos Sudarso Bay) and Dorey Bay (by Manokwari). There is considerable individual variation in the width of the bands. The width in the *leo* specimens with the narrowest bands (the *leo* types) is similar to that in the *droa* and *louisa* specimens with the widest bands. We have not been able to sequence DNA from *leo* and *louisa* but speculate that, like *droa,* they fall in the large clade with *tyrannus*. It maybe that these phenotypes represent a cline of closely related subspecies of *tyrannus* with *leo* occurring in north and west New Guinea, *droa* in the south and east and *louisa* restricted to some islands in the Louisiades.

We also note that the NHMUK contains a Fruhstorfer collection specimen, typical of *droa,* from Milne Bay. It bears a "Type" label and also a handwritten label stating "*hercules sopatrus* Fr." (Fig. 54). Talbot (1923: 83) listed the name in his paper on the Fruhstorfer types as *Arhopala hercules sopatrus,* ♂, from Milne Bay. We cannot find a formal description of the name and consider it may be a nomen nudum, but in any case, the specimen is a clear example of *droa*.

Two further phenotypes occur in Timika — we refer to them as "Timika Phenotype A" (Figs. 73, 74) and "Timika Phenotype B" (Figs. 76, 77). The first has uns ground colour varying through many shades of brown to a dull green, with medium wide PD bands and usually a curved or irregular hw PD band. This form is associated with brown ♀♀ (Fig. 74). Timika Phenotype B has a much brighter green uns ground colour, with broad, straight, markedly contrasting earthy-red PD bands. This form has a much less variable uns pattern and has purple-blue ♀♀ (Fig. 77). The ♂ ups is a much darker and matt purple-blue (Figs. 76).

Unfortunately, we did not sequence any Timika Phenotype B specimens, but Timika Phenotye A examples (brown ♀ DH-18-R051, ♂ AR-17-H004 & Fig. 73, ♂ DH-18-R049) fall in a clade of their own, quite separate from the clade with *tyrannus*, Waigeo and Timika *droa* specimens.

In the COI haplotype network, they differ by 6 bp from the Timika *droa* specimens. We consider that this Timika Phenotype A clade represents a species distinct from *A. hercules* (Sulawesi Region) and *A. tyrannus*.

It is possible that Timika Phenotype B represents a second form of Phenotype A or represents a third species in Timika.

We note here that *telephus* was described by Toxopeus (1930: 166) from 1 ♂ from south New Guinea. However the specimen bears a label stating "Nw Guinea". This HT is in the RMNH (Fig. 78, courtesy of RMNH) and is somewhat similar to Timika Phenotype B.

The New Guinea Region is extra-limital for this paper and genetic data from Timika Phenotype B and other *hercules*

species-group specimens from elsewhere in New Guinea are necessary to draw firm taxonomic conclusions, hence we do not assign names to these Timika phenotypes.

Summary and proposed taxonomy of some New Guinea *hercules* species-group phenotypes/taxa

The following new combinations are proposed:

- *A. tyrannus herculina* **comb. n.** (f. *herculina* & f. *leoesque* **f. n.**) — Waigeo, Gebe.
- *A. tyrannus leontodamas* **comb. n.** (f. *leontodamas* & f. *leolike* **f. n.**) — Misool.
- *A. tyrannus droa* **comb. n.** — south and east New Guinea (including Timika).
- The following suggestions need confirmation from further research and sequencing:
- *A. tyrannus leo* **comb. n.** (= *leonidas*) — Salawati, north and west New Guinea (including Sorong).
- *A. tyrannus louisa* **comb. n.** — Louisiade Islands (including Sudest = Tagula, Misima and Rossel).
- *A.* ?*tyrannus phalaereus* (= *obscurata*, **syn. n.**) — Yapen, Mioswaar, Ron.
- *A.* species (not *tyrannus*, *hercules* or *fowlerorum*) Timika Phenotype A — Timika.
- *A.* species Timika Phenotype B (? = *telephus*) — Timika. Possibly a 2nd form of Timika Phenotype A or a distinct species.

Summary of *hercules* species-group taxa found in Maluku

- *A. hercules.*
- *A. tyrannus tyrannus* f. *tyrannus.*
- *A. tyrannus tyrannus* f. *stymphelus* **comb. nov.**
- *A. tyrannus sophilus* **stat. rev.**
- *A. tyrannus jheae* **ssp. n.**
- *A. tyrannus herculina* **comb. nov.** – f. *herculina*
- *A. tyrannus herculina* **comb. nov.** – f. *leoesque* **f. nov**.
- *A. fowlerorum* **sp. n.**

(See end of Maluku section for distribution summary.)

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