

Revision of the *Bicyclus sciathis* species group (Lepidoptera: Nymphalidae) with descriptions of four new species and corrected distributional records

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Abstract. In this paper we present a thorough revision of the *sciathis* species group of the butterfly genus *Bicyclus* (Kirby). Type materials are discussed and in several cases lectotypes are assigned to specimens from original type series. Four new, and morphologically distinct, species are described (*B. elishiae* Brattström **sp.n.**, *B. heathi* Brattström **sp.n.**, *B. sigiussidorum* Brattström **sp.n.** and *B. subtilisuriae* Brattström **sp.n.**), along with a comprehensive molecular phylogeny that includes exemplar taxa of all currently recognized species. We also investigate the types of all previously synonymized taxa and in the process invalidate the name *B. ewondo* Libert. This was done after finding the previously missing holotype of *B. makomensis* (Strand), which clearly belongs to the same species and thereby gives the older name priority. The phylogeny showed that some distinctly different species were surprisingly closely related, suggesting a high rate of morphological evolution in parts of the *sciathis* group. The distributional records for the group are updated after investigating over 1700 specimens kept in a range of museum collections. Many species previously thought to be broadly sympatric were found to have much more restricted ranges, with the previous overestimations probably based on misidentified specimens. The higher level of allopatry now established will make identification of many morphologically similar species easier. The fact that species often have smaller ranges than previously known, meaning that the level of endemism for African butterflies is likely to be higher than current estimates, has important implications for conservation management. An identification key for males of all 13 currently recognized species in the species group is included.

This published work has been registered in ZooBank, <http://zoobank.org/urn:lsid:zoobank.org:pub:837A9D4C-779A-4497-8176-7151D409DFA5>.

Introduction

The genus *Bicyclus* (Kirby) (Lepidoptera: Nymphalidae) is a large genus of African butterflies. One of the species, *Bicyclus anynana* (Butler), has been the focus of hundreds of studies since it was introduced as a laboratory species in the mid-1980s. Today, although *B. anynana* is considered a model species for

studies of phenotypic plasticity, processes of life span and ageing, as well as the developmental genetics of butterfly wing patterns (Brakefield *et al.*, 2009), the rest of the more than 80 species in the genus remain relatively unknown. Identification of the often rather cryptic species has led to much confusion, and with a growing interest regarding the ecology of the other less well-studied species there is a need for a thorough revision of the whole genus. As part of a larger project studying evolutionary patterns across the whole subtribe Mycalesina (Reuter), we are now gradually revising all of *Bicyclus* and this paper is part of the taxonomic contributions from that work.

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The *sciathis* group was designated as a species group by Condamin (1973) when revising the genus *Bicyclus*. Before his early work on *Bicyclus* (Condamin, 1961), most species were placed in the genus *Mycalesis* (Hübner; see Hemming, 1937). To avoid confusion in the following text, we consistently use the name *Bicyclus* except when citing paragraphs of text from older literature, or when assigning lectotypes to original names. Condamin (1973) recognized the *sciathis* group by their shared tawny-brown underside patterns and male genitalia characters. He considered the *sciathis* group to have six members: *Bicyclus sciathis* (Hewitson), *B. procora* (Karsch), *B. analis* (Aurivillius), *B. hyperanthus* (Bethune-Baker), *B. uniformis* (Bethune-Baker) and *B. feae* (Aurivillius). Three further names were treated as junior synonyms after Condamin's (1973) revision: *Mycalesis benina* (Grünberg), *M. procora* var. *makomensis* (Strand) and *M. ribbei* (Neustetter). The number of junior synonyms is unusually low for any species group within the genus. This could partly be explained by the unusually low seasonal variation within the *sciathis* group. Historically the limited availability of material in museums led to many later synonymized descriptions in other *Bicyclus* species groups relating to seasonal morphs of previously described species. Another likely reason for the low number of synonyms is the general lack of material from this species group in older collections. All species in the group are predominantly found in wet, undisturbed rainforest habitats and, with the exception of *B. procora* and *B. uniformis*, they all tend to be quite rarely encountered in nature. Since Condamin's (1973) impressive monographic treatment of *Bicyclus*, three more species have been added as members of the species group: *B. amieti*, Libert, *B. ewondo*, Libert, and *B. ivindo*, Vande weghe.

During the re-curation of the extensive collections of *Bicyclus* kept at the African Butterfly Research Institute (ABRI) in Nairobi, Kenya, several specimens that did not fit into the existing classification were discovered. It also became clear that some of the species appeared to have narrower distributions than suggested by older records. This led to a further investigation of collections across several major European museums, including surveys of most of the available types, including all species considered as junior synonyms by Condamin (1973). Combining this with a robust molecular phylogeny, which includes exemplar taxa of all the currently recognized species, we can now present a thorough revision of the *sciathis* group in which we add four new morphologically distinct species. We also clear up biogeographic errors from the past, making our understanding of the species distributions clearer and better delineated. Some obvious tasks remain for future revisions; for example, the females of four species cannot be fully separated on morphological characters alone and three primary types (or type series) also still need to be located.

Material and methods

Acquisition of samples

Material was investigated across 13 museum collections (see Table 1) as well as from the private research collection of Oskar

Table 1. List of abbreviations for museum collections referred to in the text. The number of located and studied voucher specimens per collection is also indicated.

Acronym	Vouchers	Full name, city, country
ABRI	1309	African Butterfly Research Institute, Nairobi, Kenya
BMNH	157	Natural History Museum, London, United Kingdom
MNHB	5	Museum für Naturkunde, Humboldt-Universität, Berlin, Germany
MNHN	–	Muséum National d'Histoire Naturelle, Paris, France (not visited)
MRAC	170	Musée royal de l'Afrique central, Tervuren, Belgium
MCSNG	–	Museo Civico di Storia Naturale di Genova, Genoa, Italy (not visited)
NHMW	11	Naturalhistorische Museum, Vienna, Austria
NHRS	3	Swedish Museum of Natural History, Stockholm, Sweden
OUMNH	7	Oxford University Museum of Natural History, Oxford, United Kingdom
PCM	2	Powell-Cotton Museum, Quex Park, United Kingdom
SMNS	4	Stuttgart State Museum of Natural History, Stuttgart, Germany
UMZC	1	University Museum of Zoology, Cambridge, United Kingdom
ZFMK	7	Zoological Research Museum Alexander Koenig, Bonn, Germany

Brattström, Michel Libert, Robert Tropek and Robert Warren. We mainly focused on type material, but also recorded location data for all available specimens (not all supplementary material was investigated at all sites) to obtain an accurate estimate of the distributions of all species. This was done because we were confident that many old misidentifications had confused the current picture. If no records could be found to back up old observations, we wanted to have convincing arguments for discarding them. All investigated material is listed in Table S1. The original species descriptions were acquired through museum archives and libraries as well as from the Biodiversity Heritage Library (<http://www.biodiversitylibrary.org/>). We searched the visited museums for types using the list presented in Condamin (1973) and also searched for possible misplaced types at each collection. All pictured specimens [except *M. benina* (Figure S9L,J, File S1), the female paratype of *B. elishiae* sp.n. (Fig. 5B)] and the specimens belonging to a potential undescribed taxa (Fig. 9A,B), were photographed using a Nikon D300 and an AF-S Micro Nikkor 60 mm f/2.8G ED lens set at a fixed focus distance and with all exposure settings (including flash output) fully locked. Lighting was provided using a Metz Ring Flash 15 MS-1 (Metz mecatech GmbH, Zirndorf, Germany), and colours were balanced using a QP Card 201 (QP Card, Helsingborg, Sweden) together with the calibration software QPCOLORSOFT 501 v. 2.0.1 (QP Card, Helsingborg, Sweden). The RAW images were developed and edited using Adobe PHOTOSHOP CS4/CS5. The editing process involved removal of the background, and sharpening and aligning specimens. All operations were carried

Table 2. List of all samples included in the phylogenetic tree (Fig. 2). For samples provided by Antonia Monteiro, we sequenced additional genes using the original aliquots. For samples downloaded via BOLD, we used the barcodes provided.

Extract code	Voucher code	Species	Sample location	Data source	Types	Previous use of extract
KA723	KA-11-115	<i>B. amieti</i>	Mt Kupe, Cameroon	ABRI	–	–
KA724	KA-11-119	<i>B. amieti</i>	Mt Kupe, Cameroon	ABRI	–	–
KA1034	ABRI-14-031	<i>B. analis</i>	Nkolonyeng, Cameroon	ABRI	–	–
AM-98-R016	R016	<i>B. elishiae</i>	Dja, Cameroon	Antonia Monteiro	Paratype	Monteiro & Pierce (2001) as <i>B. sciathis</i>
GVWBA005-07	BC-GVW0005	<i>B. elishiae</i>	Oghoubi, Gabon	BOLD (Wande weghe)	Paratype	Vande weghe (2009) as <i>B. sciathis</i>
KA828	OB-ABRI-0046	<i>B. elishiae</i>	Ipassa, Gabon	ABRI	Holotype	–
KA305	KA01-5	<i>B. feae</i>	Moka, Bioko	Robert Warren	–	–
KA307	KA01-7	<i>B. feae</i>	Moka, Bioko	Robert Warren	–	–
KA722	KA-11-110	<i>B. feae</i>	Moka, Bioko	ABRI	–	–
KA1039	ABRI-14-797	<i>B. heathi</i>	Mamove, DRC	ABRI	Paratype	–
AM-97-W228	AM-97-W228	<i>B. hyperanthus</i>	Bwindi, Uganda	Antonia Monteiro	–	Monteiro & Pierce (2001)
KA726	KA-11-124	<i>B. ivindo</i>	Ipassa, Gabon	ABRI	–	–
KA851	OB-ABRI-0003	<i>B. ivindo</i>	Langoué, Gabon	ABRI	–	–
GVWBA010-07	BC-GVW0010	<i>B. makomensis</i>	Safala, Gabon	BOLD (Wande weghe)	–	Vande weghe (2009) as <i>B. ewondo</i>
KA965	KAP-ABRI-12-831	<i>B. makomensis</i>	Ndanga, Cameroon	ABRI	–	–
AM-97-V909	AM-97-V909	<i>B. procora</i>	Unknown, E DRC	Antonia Monteiro	–	Monteiro & Pierce (2001)
KA222	OB-IND-1030	<i>B. procora</i>	Bobiri, Ghana	Oskar Brattström	–	–
KA656	KA2-05	<i>B. procora</i>	Atewa Range, Ghana	Szabolcs Sáfián	–	–
KA224	OB-IND-0065	<i>B. sciathis</i>	Rhoko, Nigeria	Oskar Brattström	–	–
KA1028	OB-IND-1015	<i>B. sciathis</i>	Afi Mountains, Nigeria	Oskar Brattström	–	–
KA834	OB-ABRI-0069	<i>B. sigiussidroum</i>	Lolodorf, Cameroon	ABRI	Holotype	–
KA1032	ABRI-14-631	<i>B. sigiussidroum</i>	Lolodorf, Cameroon	ABRI	Paratype	–
KA3031	OB-ABRI-1034	<i>B. sigiussidroum</i>	Campo, Cameroon	ABRI	Paratype	–
KA3032	OB-ABRI-1037	<i>B. sigiussidroum</i>	Maan, Cameroon	ABRI	Paratype	–
KA3026	OB-ABRI-1003	<i>B. subtilisurae</i>	Kithokolo, DRC	ABRI	Paratype	–
AM-98-R004	AM-98-R004	<i>B. uniformis</i>	Dja, Cameroon	Antonia Monteiro	–	Monteiro & Pierce (2001)
KA654	KA2-03	<i>B. uniformis</i>	Atewa Range, Ghana	Szabolcs Sáfián	–	–
KA725	KA-11-120	<i>B. uniformis</i>	Mabira Forest, Uganda	ABRI	–	–
KA215	OB-IND-1226	<i>B. larseni</i> (outgroup)	Sapo NP, Liberia	Oskar Brattström	–	–
KA223	OB-IND-1016	<i>B. xeneas</i> (outgroup)	Afi Mountains, Nigeria	Oskar Brattström	–	–
KA740	OB-IND-1727	<i>B. nobilis</i> (outgroup)	Ologbo, Nigeria	Oskar Brattström	–	–

out using a standardized custom action set to ensure that images were comparable with regard to colour and size. The ventral images of all specimens have been mirror-imaged for easier comparison with the corresponding dorsal images. The copyright of all the voucher images belongs to the respective museums and their trustees.

Genitalia dissections

The abdominal tips of at least one male per species were dissected to inspect the genitalia characters. The abdominal tissues were first placed in individual glass vials containing about 500 µL of 10% KOH solution heated to just below boiling point. After 10 min the tissues were removed from the vials and placed in 70% ethanol solution. The genitalia were then cleaned from soft tissue under a stereomicroscope using a pair of micro forceps (Dumont #55, Dumont SA, Montignez, Switzerland). Images of the genitalia were taken using a Leica DFC495 digital camera coupled to a Leica M125 stereomicroscope. To improve the depth of field for the images, we used focus-stacking software provided with the microscope (Leica

Application Software version 3.8.0), and images were later cleaned up in Adobe PHOTOSHOP CS4/CS5, only neutralizing the background and balancing the contrast across samples. The structures themselves were not edited, except to remove dust, scales and streaks formed by chards of cover slides that were used to align some samples during photography. The genitalia were photographed whilst submerged in 70% ethanol and the angle can be slightly different between pictures (especially for the dorsal photographs), but all structural differences described in the text were verified by manually cross-comparing samples under the microscope from various angles.

Molecular phylogeny construction

A total of 28 specimens representing all previously described species in the *sciathis* group, as well as the four taxa being described as new species in this paper, were used as an in-group in this study (Table 2). Three additional taxa, *Bicyclus larseni* (Vande weghe), *B. nobilis* (Aurivillius) and *B. xeneas* (Hewitson), recovered as sister-group to the *sciathis* group in a recent phylogeny of the whole genus (Aduse-Poku *et al.*, 2015),

were used to root the tree. DNA sequences and, where possible, aliquots of extracts used in a previous *Bicyclus* phylogeny (Monteiro & Pierce, 2001) were obtained from the authors and used in the present study. Further genes were sequenced from some of the aliquots. A small set of barcode sequences were downloaded from the BOLD database, originating from specimens kept at ABRI, and used in a study focused on identifying female morphology of *B. sciathis* and *B. makomensis* (Vandeweghe, 2009). Additional samples were collected either by the first author during field expeditions between 2008 and 2014, or were obtained from colleagues active in field projects in Africa. The remaining samples were taken from the collections of ABRI. Genomic DNA was extracted from two legs per specimen using the Qiagen DNEasy extraction kit (Manchester, U.K.). A total of seven molecular markers; one mitochondria (cytochrome c oxidase subunit I, COI) and six nuclear (Ribosomal Protein S5, RpS5; Ribosomal Protein S2, RpS2; wingless, wgl; glyceraldehyde-3-phosphate dehydrogenase, GAPDH; Elongation factor 1-alpha, EF-1 α ; and Arginine Kinase, ArgKin) gene regions were amplified and sequenced for each of the exemplar taxa using primer pairs obtained from Wahlberg & Wheat (2008). Successful amplicons were cleaned with Exo-SAPIT (USB Corporation, Cleveland, OH, U.S.A.) and sent to Macrogen Services in Amsterdam, the Netherlands, for nucleotide sequencing. Resultant nucleotide sequences were aligned by eye using BIOEDIT (Ibis Biosciences, Carlsbad, CA, U.S.A., Hall, 1999).

The phylogenetic analyses were first carried out separately for each gene (producing gene trees) and later for all of the seven genes combined (but partitioned by gene) using maximum likelihood (ML) and Bayesian inference (BI) methods implemented in RAXML (Stamatakis, 2006) and BEAST (Drummond & Rambaut, 2007) programs, respectively. PARTITIONFINDER was used to select the best-fit models of gene partitioning schemes and nucleotide substitution models for each gene (Lanfear *et al.*, 2012).

Maximum likelihood phylogenetic inference analyses were implemented in RAXML-HPC2 v8.0.24, on the CIPRES Science Gateway v3.3 (Miller *et al.*, 2010), using the partition scheme from the PARTITIONFINDER analysis, under the GTRCAT model for the rapid bootstrapping phase, and GTRGAMMA for the final best-scoring ML tree. For bootstrapping, we performed 1000 ML pseudo-replicates analyses. Bootstrapping was performed under auto Majority Rule Criterion (autoMRE).

BEAST analyses were carried out using Markov chain Monte Carlo (MCMC) randomization using a birth–death process with an uncorrelated log-normal distribution model for lineage substitution rate variation. The MCMC chain was run for 10 million generations, with four independent runs. The resultant BEAST log files were viewed using the software TRACER v1.6 (Rambaut *et al.*, 2014) to inspect effective sample sizes of the parameters and points of convergence. With a 25% burn-in threshold, all post-burn-in trees from the four independent runs were combined using the software LOGCOMBINER v2.1.2 (Bouckaert *et al.*, 2014). TREEANNOTATOR v2.1.2 (Bouckaert *et al.*, 2014) was used to summarize information (i.e. nodal posterior probabilities, posterior estimates and highest posterior

density limits) from the individual post-burn-in trees onto a single maximum clade credibility (MCC) tree. The summarized information was visualized on the MCC tree using FIGTREE v1.4 (<http://beast.bio.ed.ac.uk/figtree>).

Collection of distributional data

Basic location data were recorded from the labels of all investigated material. Some of the older material had location descriptions too vague to be of much use, often including only country of origin or referring to a large geographic area. Such records were only used in cases where no better defined records were available from within the same broad area. We tried to locate the exact geographic position for all defined locations using a range of maps kept at the respective museums, notes from ABRI collectors, digital location databases provided by MRAC and Michel Libert, the Perry-Castañeda Library Map Collection (<http://www.lib.utexas.edu/maps/africa.html>) and also from basic web searches. The locations were later used to produce the distribution maps and are all presented in Table S1, to the closest possible degrees and minutes latitude/longitude. Locality names have been updated to their current names in those cases where old colonial names have been replaced in the post-independence era. We also searched all available literature and checklists for records of species within the group. To save space in Table S1 we have only included literature data for sites where no vouchers were available in museum collections and only where the source material was considered to be reliable.

Taxonomic nomenclature and considerations

All references to wing venation follow the system proposed by Wootton (1979). The vein and cell abbreviations used in the text are shown in Fig. 1A for reference. For species where no single formal type was originally designated, we have aimed to designate a lectotype amongst available syntypes. In cases where no type material has yet been located, we have not designated neotypes. Instead we have tried to present all data available in order to assist in future identification of suitable specimens for lectotype designations. The size of the holotypes of the species described in this paper were measured using the wing photos; this could be done because the same focus distance was used throughout all photography. But due to the fact that wings have often been set at a slight angle, measurements will undoubtedly contain small errors. Wing length is given as distance along the forewing measured from the base of the wing (where it attaches to the thorax) to the distal end of vein R5 (usually the longest possible distance).

Results

Type material and additional specimens

All available primary type specimens, including types of species treated as synonyms by Condamin (1973), were studied,

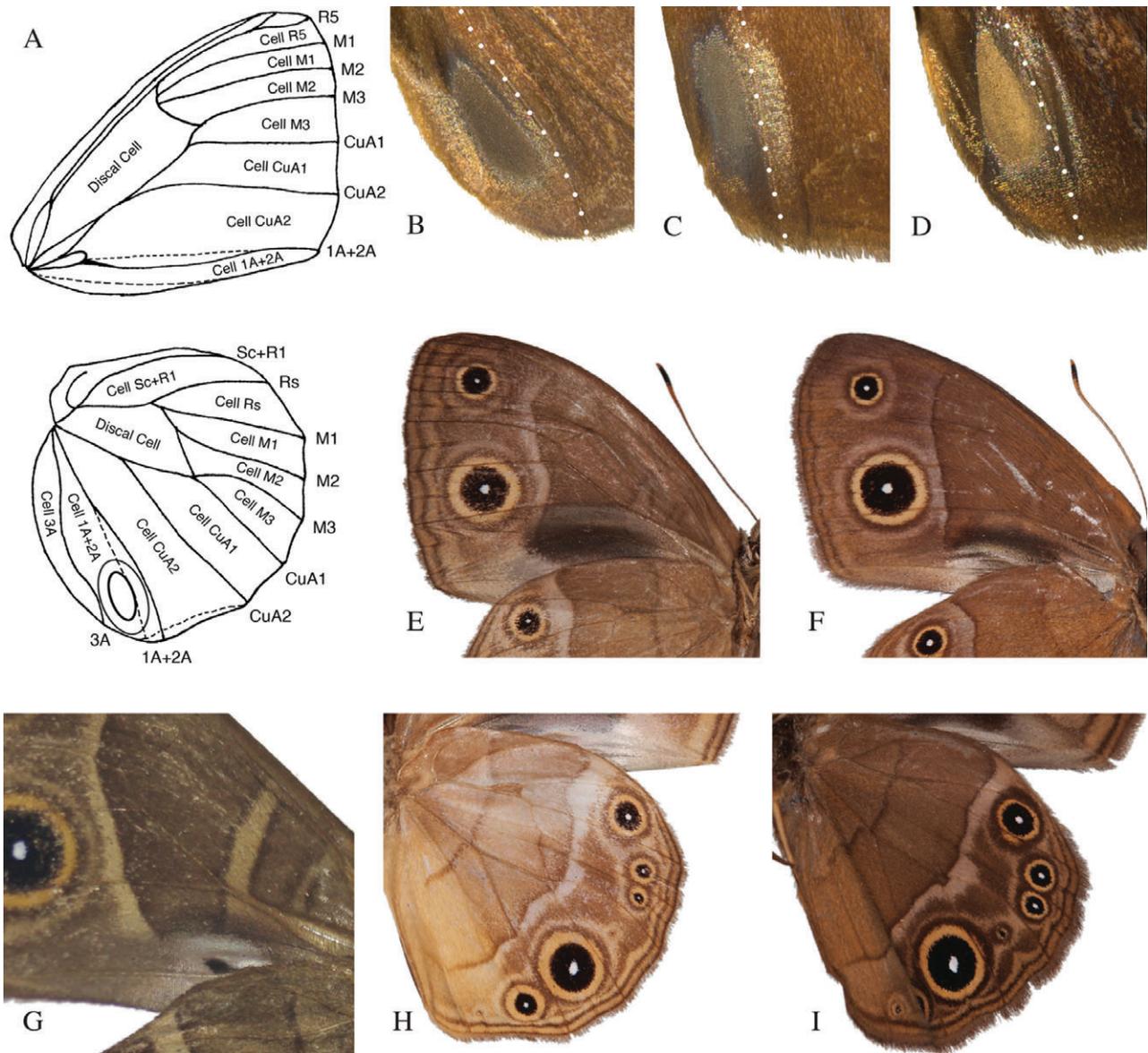


Fig. 1. Pattern of wing venation and androconial structures in the *Bicyclus sciathis* species group. (A) The venation pattern of *B. sciathis* with the names of cells (inside wing) and veins (outside wing margin) used throughout the text. The anal patch androconia present in the species related to *B. sciathis* is shown as two oval symbols. The schematic drawing is based on a male specimen collected in eastern Nigeria and shows the main morphological differences between *B. sciathis* and two closely related species (dashed lines) *B. elishiae* sp.n. and *B. sigiussidorum* sp.n. In the first species, vein 1A + 2A and CuA2 on the forewing are bent, while they run almost in parallel in the latter two species. (B) In *B. sciathis*, vein 1A + 2A on the hindwing bends outwards towards vein CuA2 so that most scales of the outer part of the anal patch androconia are not crossed by vein 1A + 2A (highlighted by white dots). The outer edge of the patch is not always well defined so some scales can still be present in cell CuA2. (C, D) In *B. elishiae* sp.n. (C) and *B. sigiussidorum* sp.n. (D), vein 1A + 2A (highlighted by white dots) crosses broadly over the outer part of the anal patch. The inner part of the patch stands out clearly from the outer scales and is raised above the wing surface as a small bulge. (E, F) In several species the basal part of cell CuA2 on the forewing underside has a dark shiny coloration. Species shown are *B. sciathis* (E) and *B. procora* (F). (G) For some species the size of the androconia on the ventral side of the forewing can have diagnostic value. The species shown is *B. amieti*. (H, I) Hindwing shape also has diagnostic value. In *B. elishiae* sp.n. the hindwing is almost circular (H) compared with the more typical shape found in *B. makomensis* (I). Also note the swelling of the wing veins at the point where vein Rs meets the hindwing discal cell; the size of this enlargement is important to separate *B. makomensis* from morphologically similar species.

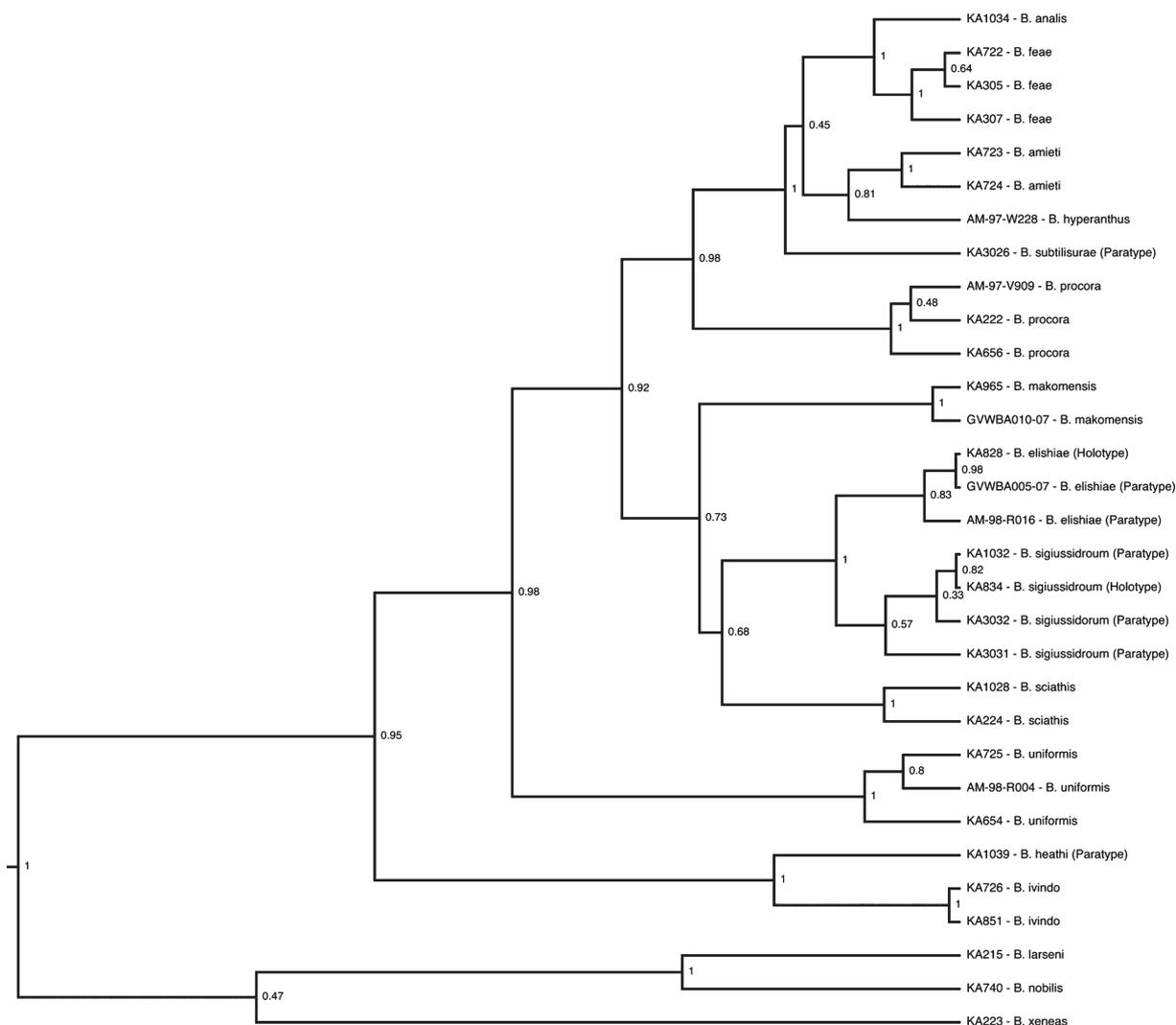


Fig. 2. Phylogenetic tree of the *Bicyclus sciathis* species group constructed from Bayesian analysis carried out in BEAST. Node labels show the posterior probability for each node. All the species are recovered as separate units. There is a surprisingly small genetic difference between the species in the top clade containing *B. amieti*, *B. analis*, *B. feae*, *B. hyperanthus* and *subtilisuræ* sp.n. All species in this clade are fully allopatric, but with quite large morphological differences, especially *B. feae*, which shows a markedly different arrangement of the androconial structures compared with the other species.

except for any of the types from the three following taxa. First, the type material of *B. feae* (deposited at MCSNG) was not investigated, but we did not find it necessary given how distinct the species is and material was readily available in other museums. Secondly and thirdly, the holotypes of *B. ewondo* and *B. amieti* (deposited at MNHN) were not investigated because they are morphologically quite distinct species and personal correspondence with the author of these two names (Michel Libert) verified our conclusions regarding the identity of those species. The locations of the primary types of two other taxa are currently not known. The holotype of *B. ivindo* could not be found, but we did investigate several specimens from the paratype series deposited at ABRI, one of which appears to be the allotype (more details can be found in File S1). The currently recognized

type of *B. uniformis* is almost certainly not the correct specimen and no obvious candidate for lectotype designation is available. Finally the type of *B. procora* remains missing despite much effort to locate it. In total we investigated 1737 specimens across all species of the group (Table S1); the samples with detailed collection data came from a total of 205 separate localities across the tropical forest zone of Africa, and a further 21 locations for which the exact position could not be found.

Phylogenetics

Representative samples of all species from the *sciathis* group were included in the final phylogenetic tree (Fig. 2). However,

we were not successful in sequencing all of the seven genes for all the exemplar taxa. The overall tree topologies emanating from both the ML and BI methods were largely congruent and generally well supported. The phylogeny from both methods confirmed the monophyly of the *sciathis* group. The taxa *B. heathi* and *B. ivindo* were recovered as sister to the rest of the *sciathis* group with high support (posterior probability, PP = 1; bootstrap support, BS = 100%). One of the two most common members of the group, *B. uniformis*, seems to have branched off next, after the split of *B. heathi* and *B. ivindo*. These two initial divergences within the group are estimated to have occurred at around 9.6 and 7.6 Ma (K. Aduse-Poku *et al.*, unpublished data).

The most important difference between the phylogenetic hypotheses produced by the two methods was the position of the *B. procora* in relation to the rest of the *sciathis* group. The ML tree topology suggested *B. procora* as sister to all *sciathis*-group species except for *B. heathi*, *B. ivindo* and *B. uniformis*. However, in the BI tree, *B. procora* is recovered as sister to a clade containing *B. amieti*, *B. analis*, *B. feae*, *B. hyperanthus* and *B. subtilisurae*. Overall, the systematic positions of most taxa within the *sciathis* group were established with appreciable confidence in the proposed phylogenies of the two methods. All species with multiple samples in the data matrix were retrieved as monophyletic in both methods, as would be expected of conspecifics.

Genitalia

We dissected a total of 34 males to investigate the genitalia for suitable identification characters. For the very rare species we could sometimes only investigate a single specimen, whilst two samples were dissected for the slightly more common species – especially if no obviously distinct characters were found in the first sample. For the common and widespread species, we investigated between three and five samples per species. The male genitalia of the species in the *sciathis* group are particularly characteristic and usually share two characters that set them apart from most other *Bicyclus*. In most species, the dorsal ridge of the valve tips are gradually turned inwards so that the edges of the valves end up more or less horizontal, pointing towards each other (e.g. Figs 3C, S4C; File S1). The subunci of most species are rather short, reaching just a little over half the length of the uncus. In most other species groups the subunci are markedly longer, often reaching at least two-thirds or more along the uncus. The base of the subunci is also flattened (e.g. Fig. 3C) in all species (except *B. uniformis*) (Fig. S5C; File S1), giving it a distinct shape found in no other *Bicyclus* species groups. A representative sample of the male genitalia for each species is included with the species plates. There is some individual variation in the degree of twist of the valve tips. Combined with the difficulties in aligning samples in a fully comparable way during photography, the appearance of the valves (especially in a lateral view) can appear to be more species-specific in the photographs on the plates than was actually found when looking at real samples under a microscope. The amount of material investigated is not substantial enough clearly to establish genital

characters useful for identification for all species, but in the cases where we have found a particular structure to have clear diagnostic value, this is noted in the species descriptions. Female genitalia were not investigated, but it could certainly be of interest for future studies. This would be particularly true for the four species closely related to *B. sciathis*, as the female morphology of this group is currently not very well understood (see the separate section in File S1). However, it is worth noting that Condamin (1973) did investigate the female genital morphology for all species known to him and claimed that in general they had little use. Judging from his images, this may be the case for the *sciathis* group.

Review of species

A full review of all previously described taxa (except for *B. makomensis*), notes on identification (complete with a key for male specimens) and detailed information on the updated geographic records can be found in File S1. All type designations and other taxonomic alternations for taxa treated in detail in File S1 are presented in Table 3. For a more detailed discussion about the arguments behind individual designations, please refer to the respective species sections in File S1. Distribution maps for all species are presented in Fig. 8A–D. The following section lists all details for one species, where the valid name has been changed, and the full descriptions of four new species.

Bicyclus makomensis (Strand) sp.rev.

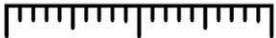
(Fig. 3A–D)

Mycalesis procora var. *makomensis*, Strand E. 1913. *Archiv für Naturgeschichte. Abteilung A*, 79(7), p. 144. (Type locality: Makomo, Equatorial Guinea).

= *Bicyclus ewondo*, Libert M. 1996. *Bulletin de la Société entomologique de France*, 101(2), 204–205. (Type locality: Ebogo, Cameroon). **syn.n.**

Type material. Condamin (1973) did not study the holotype of this species when he made his major revision of the genus. The same is true for several other types presumed to have been deposited at MNHB. Based on the original description, he made a decision to treat *Mycalesis procora* var. *makomensis* as a junior synonym of *B. procora* (Karsch). However, the holotype in question was rediscovered by Wolfram Mey (Curator of Lepidoptera, MNHB) in May 2013, and upon inspection it became clear, without any doubt, that Strand's type belongs to the same species later described by Libert (1996) as *B. ewondo*. Strand's (1913) original description focused the diagnosis on the ventral pattern, mainly the size and disposition of the eyespots. He stated that the dorsal surface was similar to the type material of *B. procora*. This is somewhat surprising as the androconial disposition is quite different between these two species, but it is not known how much importance was given, in general, to androconia as characters at that time. The types of *B. procora* have been impossible to locate despite a complete re-curation of all *Bicyclus* material at the MNHB made by the first author

Bicyclus makomensis (Strand)

20 mm 

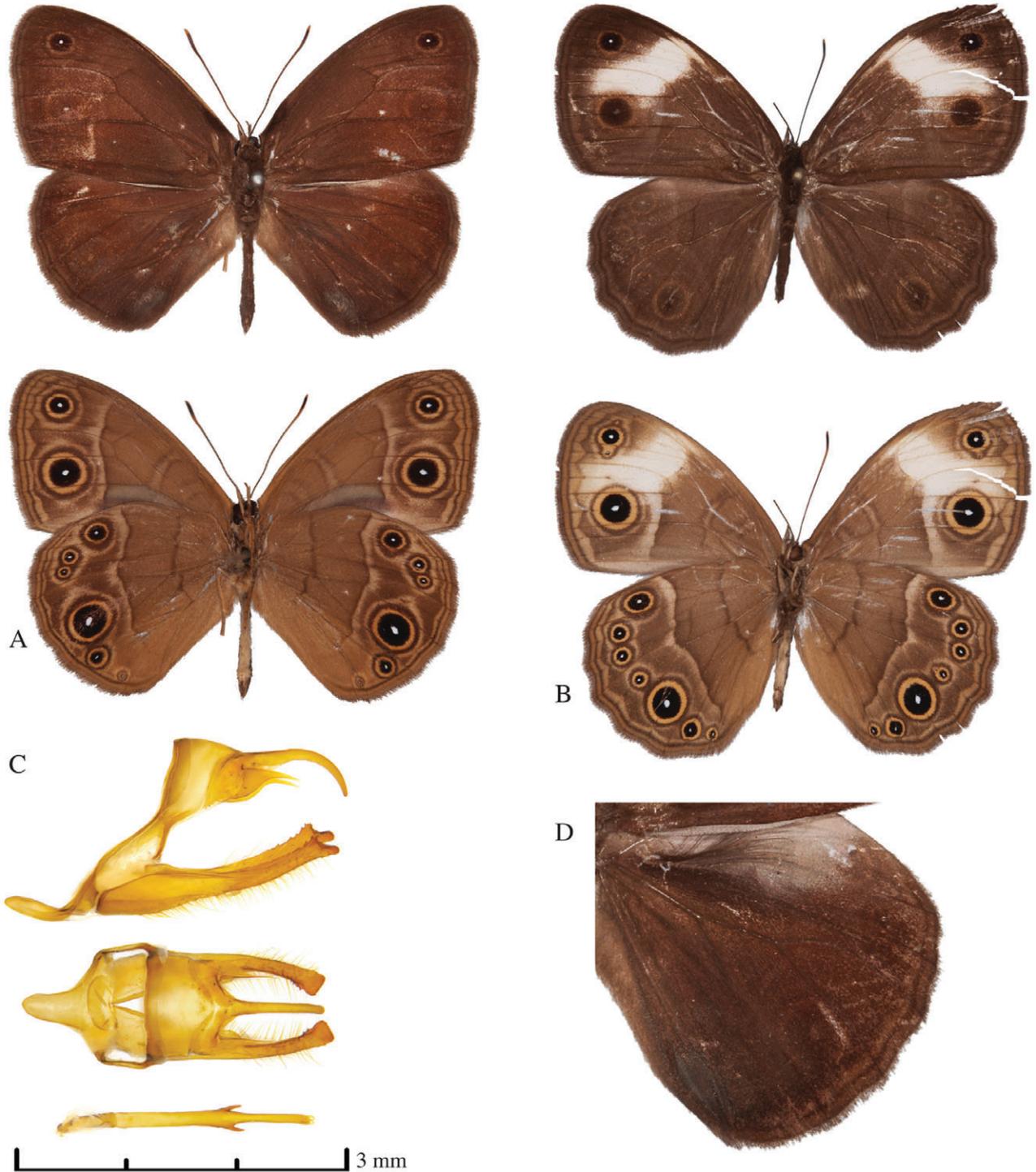


Fig. 3. *Bicyclus makomensis*. (A) Male holotype; (B) female (OB-ABRI-0108); (C) male genitalia (OB-ABRI-0101); (D) male hindwing androconia (OB-ABRI-0061).

Table 3. List of all new type status designations (listed in order of date of original description) and other taxonomic revisions made for previously described species where no nomenclature was changed during the current revision of the *sciathis* group. For details about individual designations, see File S1. Depository abbreviations are explained in Table 1.

Species name	Type status	Voucher code	Main label information	Depository	Figure	Comments
<i>Mycalexis sciathis</i>	Lectotype	BMNH(E)#1054533	Calabar, <i>M. sciathis</i> . Hew. Coll. 4	BMNH	Figure S9A, File S1	–
<i>Mycalexis sciathis</i>	Paralectotype	BMNH(E)#1054532	Cameroons, <i>M. sciathis</i> . Hew. Coll. 3	BMNH	Figure S9B, File S1	–
<i>Mycalexis analis</i>	Lectotype	NHRS-KAJO-0782	Hinterland, Jaunde-Stat., Zenker S.	NHRS	Figure S9H, File S1	–
<i>Mycalexis hyperanthus</i>	Lectotype	BMNH(E)#1377789	Makala, July 1906, Powell-Cotton	BMNH	Figure S9E, File S1	–
<i>Mycalexis hyperanthus</i>	Paralectotype	BMNH(E)#1054534	Makala, July 1906, Powell-Cotton	BMNH	Figure S9F, File S1	–
<i>Mycalexis hyperanthus</i>	Paralectotype	OB-POW-003	Between Makala and Beni	PCM	Figure S9G, File S1	–
<i>Mycalexis benina</i>	Holo/allotype	No codes used	Westl.v Ruwensori. NW Beni 1.08	MNHB	Figure S9I, File S1	Junior synonym of <i>Bicyclus uniformis</i> . Incorrectly treated by Condamin (1973) as junior synonym of <i>Bicyclus procora</i>
<i>Mycalexis uniformis</i>	None	BMNH(E)#1054537	Nairobi, June, F.J. Jackson	BMNH	Figure S9L, File S1	Specimen incorrectly placed as type
<i>Bicyclus ivindo</i>	Allotype	BC-GYW0015/KA-11-123	Ivindo NP, Langoué, Vande weghe	ABRI	Figure S8B, File S1	Were listed with MRAC as depository

in 2012 (see File S1). It is, however, still possible to rule out the possibility that the missing type belongs to the same species as the type of *B. makomensis*, because the type material of *B. procora* was collected in Togo and was described together with a large set of other species all originating from what we nowadays refer to as Togo. *B. procora* is the only member of the *sciathis* group that has ever been reported from Togo, and the only other species that could possibly be present, but overlooked, would be *B. uniformis*. Based on this we have therefore decided to consider *B. makomensis* as a valid name, of which *B. ewondo* should now instead be considered a junior synonym.

Separation from similar species. Males of this species can easily be confused with *B. sciathis*, *B. elishiae* and *B. sigius-sidorum*. The main difference between *B. makomensis* and the other three is the arrangement of the anal patch androconia on the dorsal hindwing. This patch in *B. makomensis* is rather vague (the patch is not obviously raised above the wing surface) and clearly crosses vein 1A + 2A (Fig. 3D), while in the other three the patches are very distinct and also fully (Fig. 1B), or almost fully (Fig. 1C, D), clear the vein. Another useful character is the hindwing shape, which is somewhat elongated and shaped like a typical *Bicyclus* wing (Fig. 1I), while the three similar species have almost circular hindwings (Fig. 1H). The black area in cell CuA2 on the ventral forewing is also less developed and hardly crosses further than the discal area (Fig. 3A). There is no discernible swelling of the base of vein Rs on the hindwing when seen from the ventral side (Fig. 1I), whilst in the other species there is a noticeable swelling (Fig. 1H) caused by a larger androconial pit on the dorsal surface of the hindwing (that is usually covered by the discal cell brush and therefore hard to spot from the dorsal side). Females of these four species are hard to separate and in many cases identification cannot be made on morphology alone (see separate section in File S1). In general, females of *B. makomensis* have a straighter outer margin to the ventral hindwing discal band (Fig. 3B). The male genitalia are very distinct with a pair of prominent lateral forward-facing spikes on the penis that are much better developed than in any other species in the whole *sciathis* group (Fig. 3C).

Distribution. The species is found widely across southern Cameroon (all verified locations are south of the Sanaga river), Equatorial Guinea (mainland) and most of Gabon (Fig. 8B). We have found no specimens from the Republic of Congo.

Bicyclus heathi Brattström, sp.n.

<http://zoobank.org/urn:lsid:zoobank.org:act:A750919F-5B2E-4E2C-9D1C-4EED4404B687>
(Fig. 4A–C)

Diagnosis. The male of this species shares the presence of an androconial brush in cell CuA2 on the hindwing with *B. ivindo*, *B. uniformis*, *B. feae* and *B. procora*. The latter two species are always of a smaller size, while the first two have a much more regular discal band on the ventral side (in both sexes). The wing morphology makes it look like a larger and darker version of

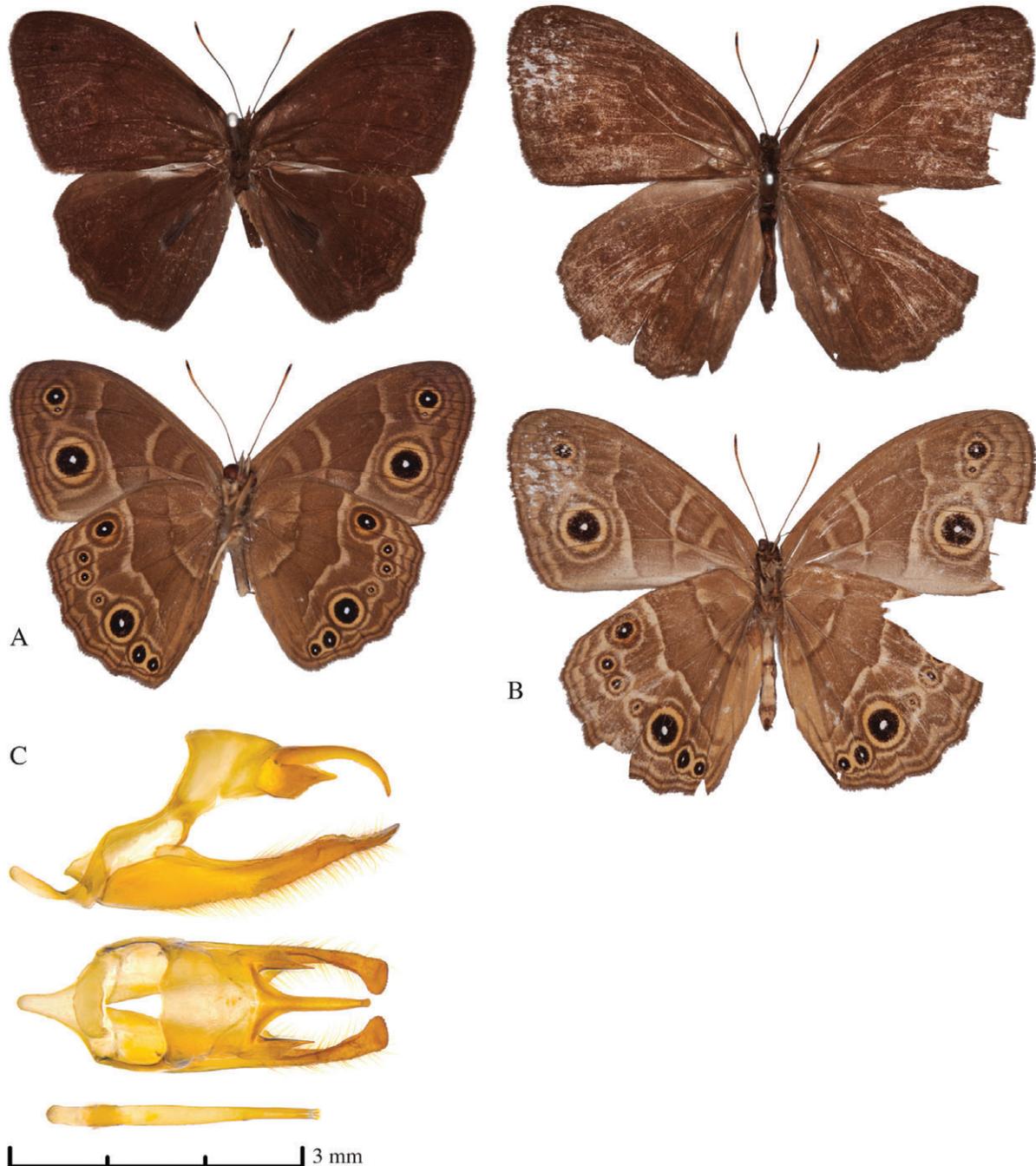
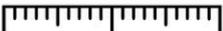
Bicyclus heathi Brattström, sp.n.20 mm 

Fig. 4. *Bicyclus heathi* sp.n. (A) Male holotype (ABRI-14-0001); (B) female allotype (OB-ABRI-0002); (C) male genitalia holotype (OB-IND-0001).

B. ivindo, but the margin of the male hindwing of *B. heathi* is more dentate than in *B. ivindo*.

Both sexes of *B. ivindo* tend to have a weaker scale cover on the dorsal wing surfaces, making the contrasting ventral pattern visible through the wings. *B. ivindo* has a well developed apical eyespot (with a white pupil) on the dorsal forewing, a character that is much less prominent in *B. heathi*. The forewing

is slightly more pointed than in *B. ivindo*, and this is more noticeable in the female. Both sexes have a darker patch in the ventral hindwing discal cell inside the discal band, a character not found in any similar species, but there is some variation amongst the known specimens of *B. heathi* in how well this patch is developed. The male genitalia are extremely distinct, making its status as a valid species absolutely clear. The two specimens

collected in 1978 were sampled for DNA, but no sequences of useful quality could be obtained. However, the paratype from Mamove (ABRI-14-797) was successfully sequenced and shows a rather large genetic difference compared with its sister species *B. ivindo* (3% divergence for the complete sequenced section of the COI gene).

Description. Holotype wing length: 27 mm. The dorsal wing surface is a dark, somewhat reddish, brown. No eyespots are present, except a small amount of lighter scales placed at the same position as the white pupil of the underside eyespot in cell CuA1 of the forewing. The spots on the ventral side can be faintly seen through the wings. The female is larger and the wing colour paler, with fewer reddish tones, than the male. The margin of the hindwing is neatly dentate and the cilia are of the same colour as the wings. In the male, the hindwings have two hairpencils on the dorsal surface, both covering patches of androconial scales. The upper hairpencil is dark brown and located in the discal wing cell and covers an androconial patch placed over the base of vein Rs. The lower brush is blackish-grey and placed basally in cell CuA2; its distal end covers a clearly visible patch of shiny blackish grey scales located in the basal part of vein CuA2.

The ventral side has a broad, fairly irregular discal band (slightly darker than the base colour) running across both wings with a lighter edge both distally and basally on the forewing. The inner edge is rather indistinctly marked on the hindwing, while the distal edge is well marked by a lighter edge. In most specimens, there is an additional darker area in the hindwing discal cell immediately inside the discal band, partly connecting to the band itself. The male genitalia are very distinct, with the subunci being almost flat and paddle-like (Fig. 4C); the relationship with the often distinct subunci in the *sciathis* group as a whole is clear, but this species has the most extreme deviation from the normally quite narrow *Bicyclus*-type subunci.

Distribution. With a low number of known specimens, the exact distribution is rather uncertain, but all known material originates from the Kivu region, suggesting it is limited to the medium altitude rainforest in north-eastern Democratic Republic of Congo (DRC) (Fig. 8D).

Etymology. The species is named in honour of Alan Heath, who collected the holotype and one paratype during a brief visit to the Irangi forest region in 1978.

Holotype. ♂, DEMOCRATIC REPUBLIC OF CONGO, 110 km NW Bukawu, Irangi forest, (01°50'S, 28°09'E), 12.iv.1978 (Alan Heath) (ABRI), specimen ID: OB-ABRI-0001.

Paratypes. DEMOCRATIC REPUBLIC OF CONGO, Kivu, Bucha (00°57'N, 29°14'E): 1♀, vi.1995 (ABRI), specimen ID: OB-ABRI-1002. DEMOCRATIC REPUBLIC OF CONGO, E Kivu, Mamove (00°49'N, 29°27'E): 1♀, ix.2012 (ABRI), specimen ID: ABRI-14-797. DEMOCRATIC REPUBLIC OF CONGO, Upper Maiko, Lubilinga Watershed, N. E.

Lubutu, 2800 ft. (00°40'S, 27°00'E): 1♀, viii.1921 (*T.A. Barns*) (BMNH), specimen ID: BMNH(E)1377790 [Depicted as female of *B. hyperanthus* in Condamin (1973, fig. 360)]. DEMOCRATIC REPUBLIC OF CONGO, 110 km NW Bukawu, Irangi forest (01°50'S, 28°09'E): 1♀, 12.iv.1978 (*Alan Heath*) (ABRI), specimen ID: OB-ABRI-0002. DEMOCRATIC REPUBLIC OF CONGO, Irangi (01°54'S, 28°27'E): 1♀, v.1990 (*ex. T. Bouyer*) (ABRI), specimen ID: OB-ABRI-1001.

Other investigated material. DEMOCRATIC REPUBLIC OF CONGO, Kivu, Irangi (01°54'S, 28°27'E): 1♂, no date (SMNS), specimen ID: SC-SMNS-0276. 1♀, no date (SMNS), specimen ID: SC-SMNS-0278. DEMOCRATIC REPUBLIC OF CONGO, Kivu, no detailed location: 1♀, 1971/72 (SMNS), specimen ID: SC-SMNS-0279. The three SMNS specimens have all been rather badly repaired in the past using pieces of wings from various other species of Satyrinae, including a European species!

***Bicyclus elishiae* Brattström, sp.n.**

<http://zoobank.org/urn:lsid:zoobank.org:act:ADB10737-4656-47A9-9F86-4E147D137A41>
(Fig. 5A–C)

Diagnosis. This species is closely related to *B. sciathis* and *B. sigiussidorum*. The males of these species have a pronounced, almost circular, hindwing shape, setting them apart from the otherwise somewhat similar species *B. makomensis*. All four species have a pronounced anal androconial patch (a character also shared with *B. analis*, *B. hyperanthus* and *B. subtilisurae*). The main three characters that, in combination, make *B. elishiae* stand out as a distinct taxon are: (i) the almost complete lack of androconial scales in cell CuA2 below vein CuA2 (a faint patch can be present) on the dorsal forewing (well developed in *B. sigiussidorum*); (ii) both veins 1A + 2A and CuA2 on the forewing are almost perfectly parallel along their full length (Fig. 1A) (clearly arched in *B. sciathis*); and (iii) the dark graphite grey colour of the anal patch of the hindwing (centre is lightly coloured in *B. sigiussidorum*). The male genitalia appear to be slightly different with rather straight valve types (except for the irregular dentation along all of its dorsal length) compared with *B. sigiussidorum*. However, the exact level of intraspecific variation in this species group has not been fully investigated because the material available for dissection is limited. Given the geographical distribution of this species, and the two closely related species *B. sciathis* and *B. sigiussidorum*, we treat them all as distinct species even if the genetic differences are quite small. The female paratypes are linked to the male holotype through the molecular phylogeny. At the moment females cannot be distinguished with certainty from any of the other white-banded species.

Description. Male. Holotype wing length: 23 mm. The dorsal wing surface is a warm brown with a hint of violet shine. There is a small, but well developed, apical eyespot on the forewing with

Bicyclus elishiae Brattström, sp.n.

20 mm 

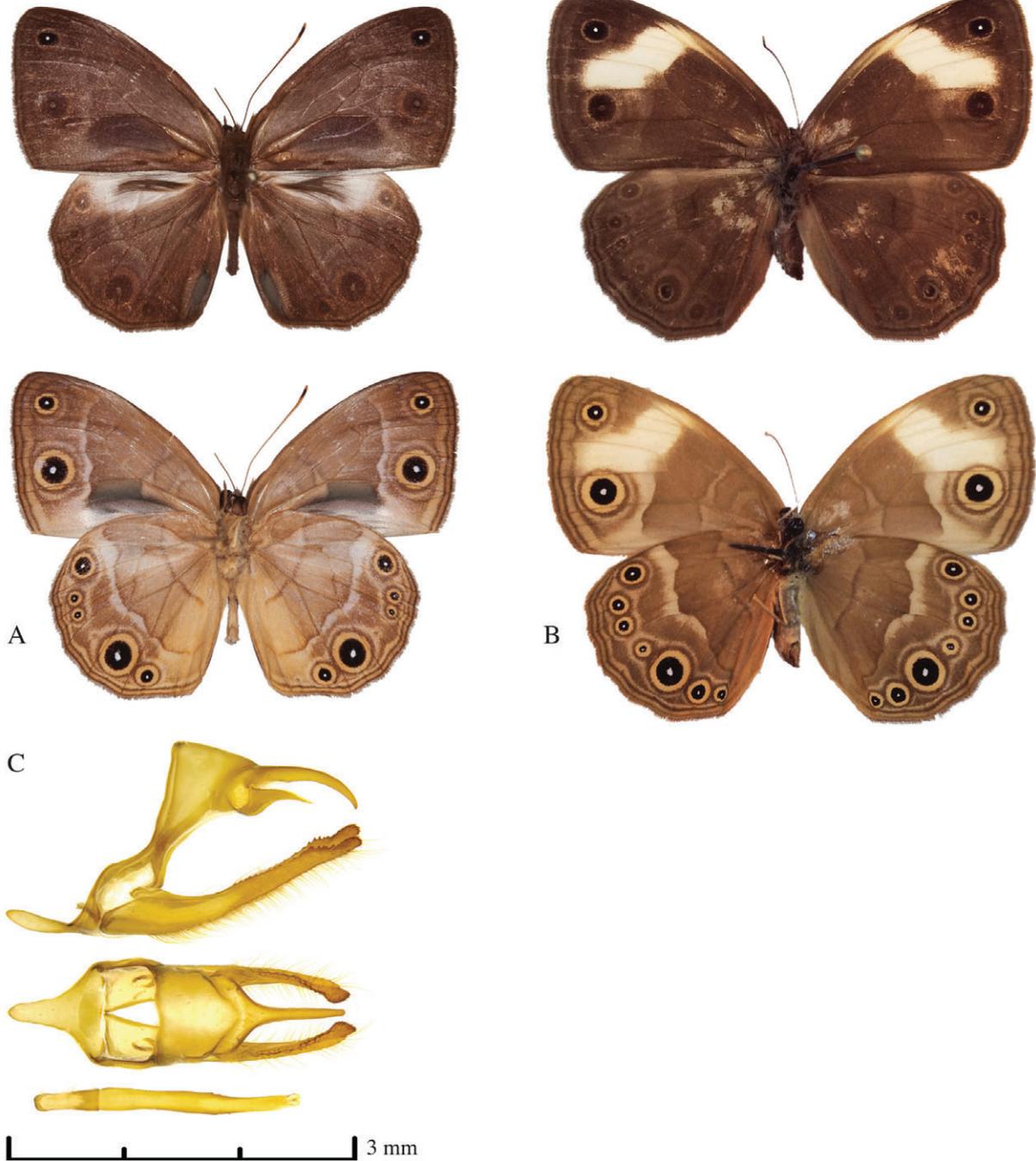


Fig. 5. *Bicyclus elishiae* sp.n. (A) Male holotype (OB-ABRI-0046); (B) female paratype (BCGVW0005); (C) male genitalia holotype (OB-ABRI-0046).

a narrow orange outline and just a few light scales marking the focus on the spot in cell CuA1. There is sometimes a faint patch of androconial scales in cell CuA2 below vein CuA2. There are no eyespots on the dorsal surface of the hindwing, but the base colour of both wings is quite thin so that several of the eyespots

on the ventral surface show through against a light background. The ventral ground colour is a much warmer, almost yellow, brown. The anal area of the hindwing is especially bright. There are two well developed eyespots on the forewing in cells CuA1 and M1. In the investigated specimens there are no additional

smaller spots between these, but variation with respect to such spots is not uncommon in *Bicyclus*. The hindwing eyespots are placed in a quite even line, but as a result of the size differences they look more irregular. The spot in cell CuA1 is always large and the spots in cell CuA2 (the most posterior one) and cell Rs are also well developed. The remaining spots are reduced and sometimes missing, especially the one in cell M3. The discal band running along both wings is irregular on the distal edge along its whole length. It is outlined with a line of fairly light scales, making it stand out well from the background colour. The dark shiny area in cells 1A + 2A and CuA2 of the forewing does not extend far under the eyespot in cell CuA1, barely reaching beyond the discal line. The hindwing tornal edge is not as rounded as in most *Bicyclus* and cell CuA2 is widened. This gives the hindwing an almost circular appearance (shared with *B. sciathis* and *B. sigiussidorum*). There are two androconia on the dorsal hindwing. The discal cell brush is dark brown and the hairs are attached along most of the posterior edge of the discal wing cell. The brush covers a quite large patch of pale yellow to brown scales located just where vein Rs meets the discal cell. This patch can be seen clearly as a swelling of the veins on the ventral side of the hindwing. The dorsal area around the discal wing cell androconia is very light, with a smooth transition back to the normal brown wing colour. There is also a well developed patch of dark, almost black, scales at the anal edge of the dorsal wing surface at the distal part of cell 1A + 2A. Vein 1A + 2A just clears the outer edge of these scales but crosses the scales immediately outside this patch. These scales are somewhat different in texture and colour than the normal brown base colour scales (Fig. 1C).

Female. The female is similar to *B. sciathis*, with a well developed white apical patch on both the dorsal and ventral forewing surfaces. At the moment, females of any of the species immediately around *B. elishiae* cannot always be told apart from the other white-banded species with absolute certainty. The three paratype females were assigned to the species based on their clustering in the phylogenetic analysis. More details are provided in a separate section in File S1, which discusses the females from this clade in greater detail.

Distribution. The species is only known from 13 recognized specimens, all from the same general area in Gabon, south-eastern Cameroon and south-western parts of the Republic of Congo (Fig. 8B). Given the lack of any large-scale systematic museum collections from parts of these regions, it is not possible to accurately estimate the eastern limit of the distribution. No specimens from the entire subgroup around *B. sciathis* have ever been reported from the DRC, so it probably only extends a little into the Republic of Congo. The species appears to be rare or localized throughout its distribution.

Etymology. The species is named in honour of Elishia Harji, the partner of the first author, as a sign of his appreciation for her understanding of his passion for butterfly taxonomy and the sometimes extensive travels it brings with it.

Holotype. ♂, GABON, Ivindo NP, Ipassa (0°27'N, 12°47'E), 17.xii.2004 (*Gaël Vande weghe*) (ABRI), specimen ID: OB-ABRI-0046/BC-GVW0002.

Paratypes. CAMEROON, Dja Reserve, (3°11'N, 12°49'E): 1♀, 13.ii.1998 (*Antonia Monteiro*) (will be placed at the Museum of Comparative Zoology, Harvard University) (included in Monteiro & Pierce (2001) as *B. sciathis*), specimen ID: R016. GABON, Ivindo NP, Koungou (0°20'N, 12°36'E): 1♀, 6.xii.2004 (*Gaël Vande weghe*) (ABRI), specimen ID: BC-GVW0004. GABON, Waka NP, Oghoubi (1°07'S, 11°08'E): 1♂, 4.xi.2005 (*Gaël Vande weghe*) (ABRI), specimen ID: KAP-ABRI-12-836. 1♂, 11.xi.2005 (*Gaël Vande weghe*) (ABRI), specimen ID: KAP-ABRI-12-837/BC-GVW0001. 1♀, 12.xi.2005 (*Gaël Vande Weghe*) (ABRI), specimen ID: KAP-ABRI-12-828/BC-GVW0005. 1♂, 24.iii.2007 (*Gaël Vande weghe*) (ABRI). REPUBLIC OF CONGO, Zanaga District, Loungou (2°30'S, 13°43'E): 1♂, 16.iv.2010 (*Gaël Vande weghe*) (ABRI), specimen ID: ABRI-14-635.

Other investigated material. CAMEROON, Mintom, (2°42'N, 13°17'E): 1♀, viii.2008 (*P.A.*) (ABRI), specimen ID: KA-11-073. CAMEROON, Moloundou, (2°03'N, 15°14'E): 1♀, vii.1991 (ABRI), specimen ID: ABRI-2015-00055. GABON, Ivindo NP, Langoué (0°12'S, 12°35'E): 1♂, 15.xi.2004 (*Gaël Vande Weghe*) (current voucher location unknown, studied via photo on BOLD system), specimen ID: BC-GVW0003.

***Bicyclus sigiussidorum* Brattström, sp.n.**

<http://zoobank.org/urn:lsid:zoobank.org:act:E3E6BD10-5B2E-49E4-8B2B-824B032646BD>

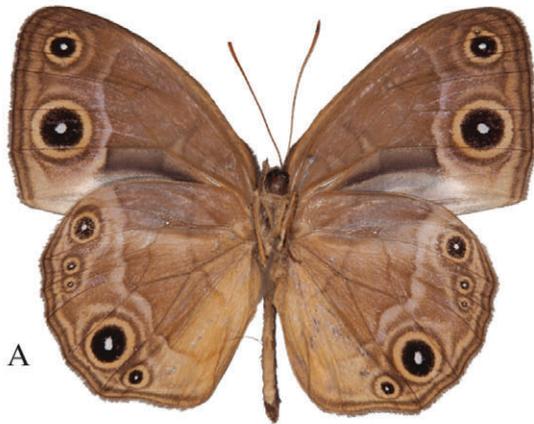
(Fig. 6A–C)

Diagnosis. This species is closely related to *B. sciathis* and *B. elishiae*, as it shares the same pronounced male wing shape (see diagnosis for previous species) and some androconial similarities. The main diagnostic difference that sets this species apart from the other similar-looking species is the lightly coloured central part of the hindwing anal androconia. In all other *Bicyclus* species that have an anal androconia, the patch is dark. The phylogeny and the well defined distributional pattern also support its status as a distinct taxon (see diagnosis for previous species). The female paratypes are linked to the male holotype through the molecular phylogeny. At the moment, females cannot be distinguished with certainty from any of the other white-banded species.

Description. Male. Holotype wing length: 23 mm. The dorsal wing surface is a rather pale brown with a violet shine more visible at specific angles. There is a small, but well developed, apical eyespot on the forewing with a narrow thin orange outline and just a few light scales marking the focus on the spot in cell CuA1. There are no eyespots on the dorsal surface of the hindwing but the base colour of both wings is quite thin, making many of the eyespots from the ventral surface shows through against a light

Bicyclus sigiussidorum Brattström, sp.n.

20 mm 



C



Fig. 6. *Bicyclus sigiussidorum* sp.n. (A) Male holotype (OB-ABRI-0069); (B) female paratype (OB-ABRI-1034); (C) male genitalia paratype (OB-ABRI-0045).

background. The ventral ground colour is a warmer, somewhat yellow, brown. The anal area of the hindwing is especially bright. There are two well developed eyespots on the forewing in cells CuA1 and M1. In the investigated specimens there are no additional smaller spots between these, but variation with respect to such spots is not uncommon in *Bicyclus*, and tiny yellow markings not forming proper eyespots can be seen in the available material. The hindwing eyespots are placed in a quite even line, but as a result of the size differences they look more irregular. The spot in cell CuA1 is always large and the spots in cell CuA2 (the most posterior one) and cell Rs are also well developed. The remaining spots are reduced and sometimes missing, especially the one in cell M3. The discal band running along both wings is highly irregular on its distal edge along its whole length. It is outlined with a fairly light line of light scales, making it stand out well from the background colour. The dark shiny area in cells 1A + 2A and CuA2 of the forewing does not extend far out under the eyespot in cell CuA1, just barely reaching beyond the discal line. There are two androconia on the hindwing. The discal cell brush is dark brown and the hairs are attached along most of the posterior edge of the discal cell. The brush covers a quite large patch of pale yellow to brown scales located just where vein Rs meets the discal cell. This patch can be seen as a swelling of the veins also on the ventral side of the hindwing. The dorsal area around the discal wing cell androconia is very light, with a smooth transition back to the normal brown wing colour. There is also a well developed oval patch of pale yellowish scales, centred in the middle of a patch of shiny grey scales at the anal edge of the dorsal wing surface at the distal part of cell 1A + 2A. Vein 1A + 2A clears the outer edge of this yellow area, but runs through the middle of the outer shiny scales. On the forewing there is a semi-circular-shaped patch of dark black scales with the rounded part pointing in the anterior direction. The base of this patch is placed dorsally just along the lower edge of vein CuA2 in line with the barely visible eyespot showing through from the underside. The patch extends downwards almost out to half the width of cell CuA2.

Female. The female looks similar to *B. sciathis* with a well developed white apical patch on both the dorsal and ventral forewing surfaces. Females of the species similar to *B. sigiusidorum* cannot be distinguished from the other white-banded species with certainty. The two paratype females were assigned to the species based on the clustering from the phylogenetic analysis. More details are provided in a separate section in File S1, which discusses the females from this clade in greater detail.

Distribution. The species is known from 12 identified specimens, with all records confined to the southern parts of Cameroon, north-western Gabon and a single specimen from mainland Equatorial Guinea (Fig. 8B).

Etymology. The species is named in honour of Ziggy Stardust, one of the many faces of David Bowie. The wing shape, along with the unique androconial scales below the eyespots, gives the species a rather 'glammy' appearance. The first author also fondly remembers David Bowie's early albums as regular

companions during evenings back at camp whilst working in the field. The Latin translation of the lyrics from Ziggy Stardust was retrieved from <http://everything2.com/title/Ziggy+Stardust> (accessed on 09 July 2015) and used when naming the species.

Holotype. ♂, CAMEROON, Mt Mille (Lolodorf) (3°17'N, 10°50'E), v.2011 (N.A.) (ABRI), specimen ID: OB-ABRI-0069.

Paratypes. CAMEROON, Dja Forest (3°09'N, 13°00'E): 1♂, iv.1997 (*S. Collins*) (ABRI), specimen ID: ABRI-14-633. CAMEROON, Lolodorf (3°17'N, 10°50'E): 1♂, ix.2010 (*P.A.*) (ABRI), specimen ID: KAP-ABRI-12-839. 1♂, iii.2012 (ABRI), specimen ID: ABRI-14-631. CAMEROON, Maan (2°22'N, 10°37'E): 1♂, vii.1999 (*S. Collins*) (ABRI), specimen ID: ABRI-14-632. 1♂, viii.2000 (*S. Collins*) (ABRI). 1♂, viii.2008 (*S. Collins*) (ABRI), specimen ID: OB-ABRI-0105. 1♀, i.2014 (ABRI), specimen ID: OB-ABRI-1037. CAMEROON, Campo (2°22'N, 9°50'E): 1♀, 9.iv.2013 (ABRI), specimen ID: OB-ABRI-1034. EQUATORIAL GUINEA, Balengue, Rio Muni (1°20'N, 9°30'E): 1♂, no date, (*F. Escalera*) (BMNH), specimen ID: BMNH(E) 1377784. GABON, Monts de Cristal NP, Mbei Tchimbelle Valley (0°42'N, 10°19'E): 2♂, iii.2007 (*P. Oremans*) (ABRI), specimen ID: ABRI-14-634 & OB-ABRI-0045.

***Bicyclus subtilisuræ* Brattström, sp.n.**

<http://zoobank.org/urn:lsid:zoobank.org:act:7D26F525-FA74-4E9B-95A6-8E87B7DCD7FD>
(Fig. 7A–C)

Diagnosis. The combination of the presence of a distinct black androconial patch on the forewing underside above vein 1A + 2A and the reduced dorsal eyespots sets *B. subtilisuræ* apart from similar species. The androconia and ventral eyespots are similar to *B. amieti*, but the dorsal eyespots are completely different and more similar to *B. hyperanthus*. *B. subtilisuræ* is also smaller and more lightly coloured than both of these species. The genitalia appear to be different from the related species, but as there is some individual variation within this species group and the material available for this species is limited, the exact patterns remain unknown.

Description. Holotype wing length: 23 mm. The dorsal wing surface has a uniform, rather dark brown ground colour in both sexes. The dorsal forewing has a small apical eyespot with a faint outer orange ring located in cell M1. In the males this spot can be all but completely reduced. In some specimens of both sexes there is a diffuse dark spot in cell CuA1, and depending on the light, the spot on the ventral side of cell CuA1 can be seen through the wings to the dorsal side. In some female specimens there is a tiny white pupil in the centre of this weakly developed spot. The ventral side has a pale brown, almost beige colour. The discal band is broad and outlined by a thin dark brown line on both sides. These lines are somewhat irregular, but run along the edges of the whole band across the length of both wings.

Bicyclus subtilisurae Brattström, sp.n.

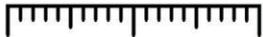
20 mm 



Fig. 7. *Bicyclus subtilisurae* sp.n. (A) Male holotype (OB-ABRI-0027); (B) female paratype (OB-ABRI-0030); (C) male genitalia paratype (OB-ABRI-0028).



Fig. 8. Distribution maps for the species in the *Bicyclus sciathis* species group. Records of different species from the same site have been slightly offset when presented in the same map so that all species symbols can be clearly seen. Multiple records close to each other have been collapsed to a single point. The complete distributional data are available in Table S1. (A) *B. uniformis* (open circles) and *B. procora* (filled circles). (B) *B. sciathis* (diamonds), *B. makomensis* (crosses), *B. sigiussidorum* sp.n. (circles) and *B. elishiae* sp.n. (squares); filled symbols represent male specimens, and open symbols represent females. (C) *B. amieti* (diamonds), *B. analis* (circles), *B. feae* (squares) and *B. ivindo* (crosses). (D) *B. hyperanthus* (circles), *B. heathi* sp.n. (diamonds) and *B. subtilisurae* sp.n. (crosses).

There is a less well-defined, but broader, pale band on the distal side of the outer line. On the basal side of the discal band is, at most, a slight lightening of the ground colour, but no clearly defined light band. The ventral forewing has two fully developed eyespots in cells CuA1 and M1, and there are sometimes small additional eyespots in the cells next to the spot in cell M1. On the ventral hindwing the lower spot in cell CuA2 is much reduced and often missing in the male. The upper spot in the same cell is displaced so that it sometimes touches the marginal line at the edge of the wing. The spot in cell M3 is reduced in size compared with the spots in cells M1 and M2 (especially in the male), a trait not shared by the similar-looking species *B. hyperanthus* and *B. analis* (but shared with *B. amieti*). Both sexes have the hindwing margin lightly but noticeably scalloped, especially well-pronounced in cell CuA2 in the male. The dorsal hindwing of the male has a small dark brown androconial brush in the hindwing discal cell located in a pale ivory-coloured area of the costal region that contains a small yellow androconial patch

located along the base of vein Rs. This patch is generally covered by the brush and therefore hard to detect in set specimens. The ventral forewing has a well developed androconial patch on the underside formed of black scales placed immediately above vein 1A + 2A in cell CuA2. This patch is much larger than in both *B. hyperanthus* and *B. analis*, in which this patch is so small it can be hard to see with the naked eye, but again this is similar to *B. amieti*, which has a well developed patch. The tornal area of the dorsal hindwing has a shiny dark graphite grey patch of androconial scales. The patch crosses over vein 1A + 2A and is somewhat angled so that its basal end is fully in cell 1A + 2A, while the distal end is located in both cells 1A + 2A and CuA2.

Distribution. All of the 23 known specimens are from a handful of locations in the Kivu region of DRC (Kasuo, Kithokolo, Maliva and Mt Hoyo) and one single location in north-western Tanzania (Minziro Forest) (Fig. 8D). *B. subtilisurae* occurs in sympatry with *B. hyperanthus* at most of the known locations in

DRC, but it appears to prefer higher altitudes, with all known locations being above at least 1000 m above sea level, thus limiting its range towards the west where *B. hyperanthus* extends further and is found down to around 400 m above sea level. The number of records of *B. subtilisurae* is low compared with the other members of the *sciathis* group collected in the same region, so it is likely to be both localized and rare.

Etymology. The valves of the male genitalia somewhat resemble a stylistic depiction of a woman's legs and feet, therefore the Latin name is formed from the feminine form of the words 'slender legs'.

Holotype. ♂, TANZANIA, Minziro Forest (1°03'S, 31°33'E), 23.vi.1991 (*Jan Kielland*) (ABRI), specimen ID: OB-ABRI-0027.

Paratypes. TANZANIA, Minziro Forest (1°03'S, 31°33'E): 1♀, 4.vii.1991 (*Jan Kielland*) (ABRI), specimen ID: ABRI-14-030. 1♂, i.1992 (*Jan Kielland*) (ABRI), specimen ID: ABRI-14-028. DEMOCRATIC REPUBLIC OF CONGO, Orientale, Mont Hoyo (1°13'N, 29°48'E): 1♂, ii.1996 (*P. Walwanda*) (ABRI), specimen ID: OB-ABRI-0028. DEMOCRATIC REPUBLIC OF CONGO, Kivu, Kithokolo-Lubero (0°10' S, 29°13'E): 1♀, i.2007 (ABRI), specimen ID: ABRI-14-029. 1♂, xi.2013 (ABRI), specimen ID: OB-ABRI-1003.

Other investigated material. TANZANIA, Minziro Forest (1°03'S, 31°33'E): 1♂, i.1991 (*Jan Kielland*) (ABRI). 1♀, 23.vi.1991 (*Jan Kielland*) (ABRI). 1♀, 27.vi.1991 (*Jan Kielland*) (ABRI). 1♀, 1992 (ABRI). 1♂, xii.1992 (ABRI). 1♂, iii.1994 (*I.B., P.N.*) (ABRI). 1♂, iv.1994 (*T.C., E.C., M.H.*) (ABRI). DEMOCRATIC REPUBLIC OF CONGO, Orientale, Mont Hoyo (1°13'N, 29°48'E): 2♂, ii.1996 (*P. Walwanda*) (ABRI). 2♂, v.1991 (ABRI), specimen ID: ABRI-14-026 (one specimen without code). 1♀, iv.1987 (ABRI). DEMOCRATIC REPUBLIC OF CONGO, Kivu, Kithokolo-Lubero (0°10'S, 29°13'E): 1♀, i.2007 (ABRI). 1♂, vi.2012 (ABRI). DEMOCRATIC REPUBLIC OF CONGO, Kivu, Maliva (0°10'N, 29°01'E): 2♀, ix.2012 (ABRI), specimen ID: OB-ABRI-1004 (one specimen without code). DEMOCRATIC REPUBLIC OF CONGO, Kivu, Kasuo, (00°14'S, 29°03'E): 1♂, vii.2013 (ABRI), specimen ID: ABRI-14-250.

Discussion

Potential additional taxon

Amongst the material provided by Michel Libert (photographs) there is a curious pair of specimens (Fig. 9A, B) related to *B. sigiussidorum* and *B. elishiae*. The male defies classification as it has characters from each of the two species: the dorsal forewing has a clear black androconial patch in the distal area of cell CuA2 (typical for *B. sigiussidorum*), while the

anal androconia on the hindwing is dark and vein 1A + 2A is not heavily bent inwards towards cell CuA2 (typical for *B. elishiae*). Further, the genitalia look somewhat different (Fig. 9C) with a less developed base of the subunci and with narrower valve tips. Finally, the discal cell brush is a light reddish tan, whereas all other similar species have a dark brown or black brush. The female specimen is very large and the discal band on the hindwing is heavily dented with a sharper angle than the other known specimens in the *sciathis* subgroup (the band has a similar shape in the male specimen as well). The specimens were collected from Bombe in Cameroon (4°26'N, 9°27'E), which is located well within an area where only *B. sciathis* would be expected for this subgroup (Bombe lies well north of Sanaga river, which is probably the absolute northernmost limit for *B. sigiussidorum*). As we only have access to a single pair, which are in a rather worn condition, we have not described this as a new species. But should more specimens be found with the same pattern, it should probably be considered a new taxon. Given the capture location, we find it unlikely that the odd phenotypes would be the result of a hybridization between any other species because they were collected well away from areas where more than one species in this subgroup is likely to be sympatric.

Evolutionary patterns

The phylogenetic tree recovered all currently described taxa as separate units, but also showed a remarkably small genetic difference for the species in the top clade (*B. amieti*, *B. analis*, *B. feae*, *B. hyperanthus* and *B. subtilisurae*) (Fig. 2). The species in this clade are morphologically rather distinct. Interestingly, most of them never occur in sympatry – only *B. hyperanthus* and *B. subtilisurae* have a small overlap. It is also possible that the two latter species occur in different habitats and altitudinal ranges at locations where both are found. The species in this clade that differs most in morphology is *B. feae*, which has a completely different set of androconia, with the loss of the anal patch (typical present in this clade) combined with the recurrence of a brush in cell CuA2 on the hindwing. This suggests that androconia can evolve very rapidly. Given that *B. feae* is endemic to Bioko, and is a rather recent split from *B. analis*, this rapid change might have been mediated through genetic drift in a small founding population. Another example of a similar gain/loss scenario involving the same androconia is *B. procora*, but in this case the evolutionary timescale for the change is much longer. The two widespread species *B. procora* and *B. uniformis* show very limited genetic variation, even with samples taken from the extreme ends of their range. The rate of androconial evolution in butterflies is a promising field for future research, and highly variable patterns are found even within *Bicyclus*. Comparing the *sciathis* group with another recently revised species group, the *ignobilis* group (Brattström *et al.*, 2015), substantial differences can be seen. Both groups are of a similar evolutionary age (Aduse-Poku *et al.*, 2015), occur in the same type of wet evergreen forest habitat and have similar distributional borders. However, the *ignobilis* group has only

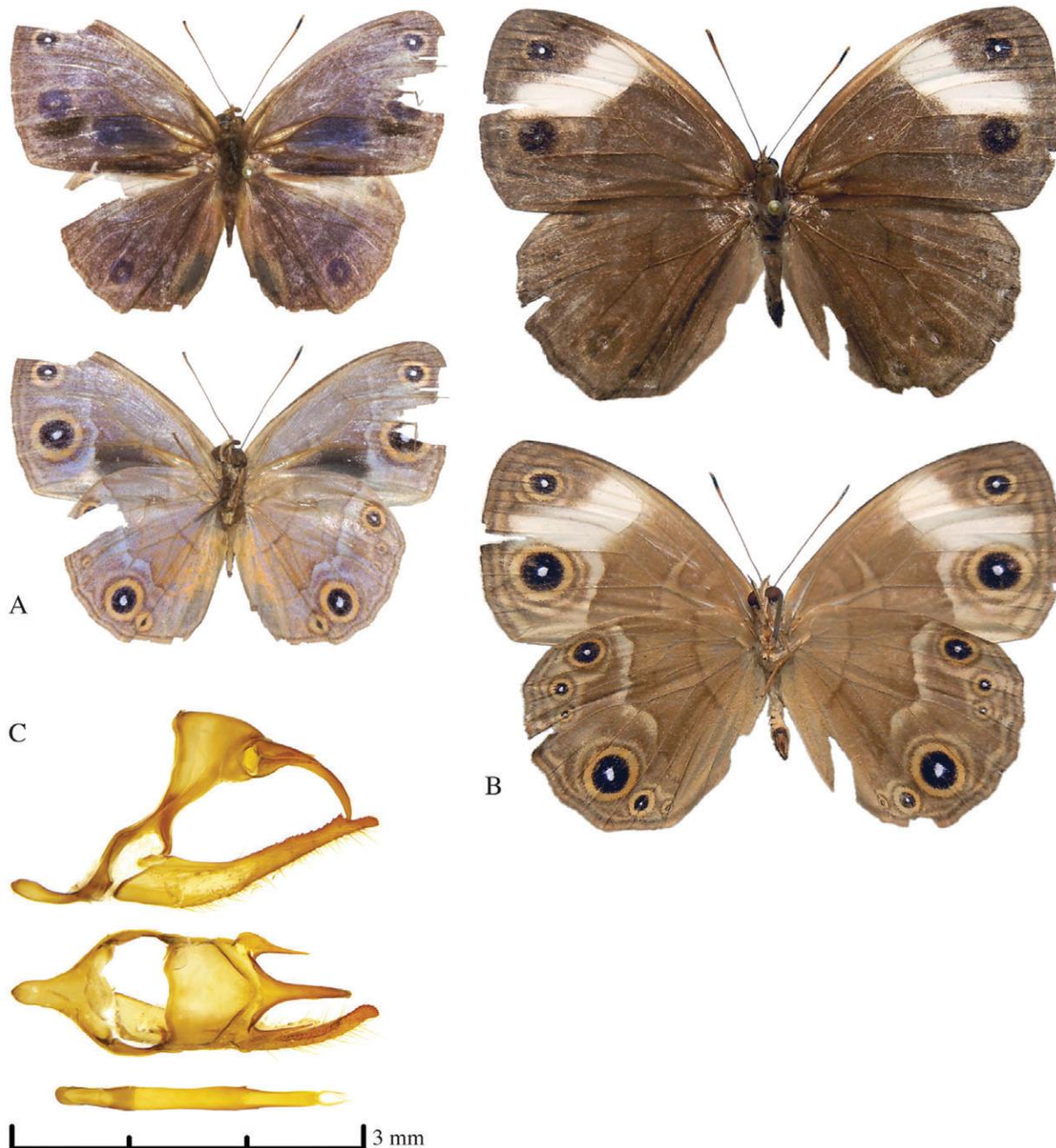
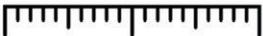
Bicyclus sp.20 mm 

Fig. 9. Unidentified and possibly new species closely related to *Bicyclus sigiussidorum*. As only a single pair is known, we have held back description of this taxon for the moment. If more, and morphologically consistent, material should appear from the same general area, the differences compared with the other species in this clade would probably justify its description as a new species. (A) Male collected in Bombe, Cameroon (*Michel Libert*); (B) female with the same collection data as the male; (C) genitalia from the male specimen. The left valve is missing from the specimen.

subtle androconial differences across species compared with the *sciathis* group. The *ignobilis* group also contains just six species, despite having undergone a similar revision. Systematic studies comparing the relative rate of evolution of sexual traits, and their

correlative patterns within larger groups of butterflies, could help our understanding of the relative importance of these traits and the role of sexual selection as a driver behind speciation processes.

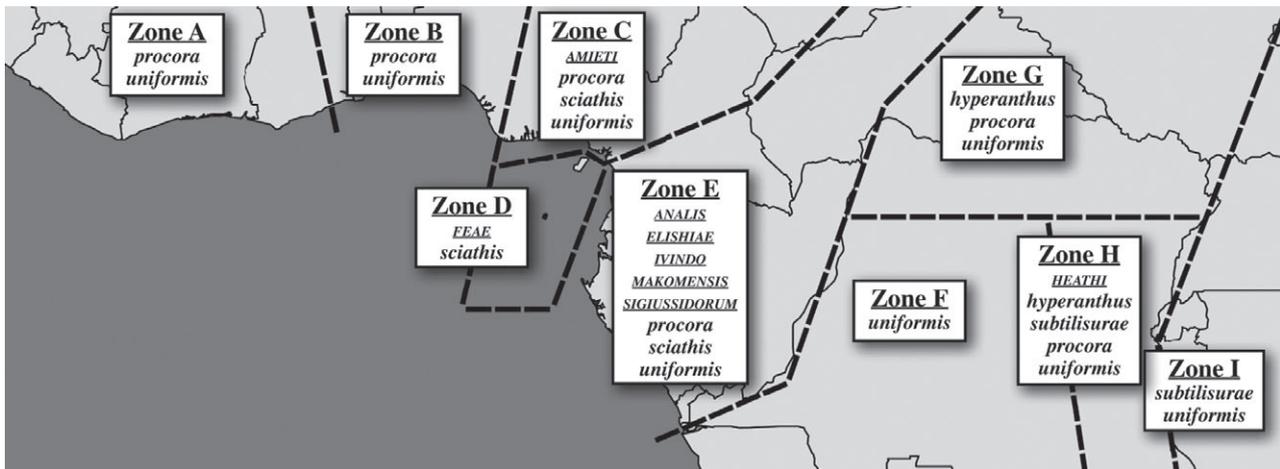


Fig. 10. Map showing nine biogeographic zones in tropical Africa of importance for *Bicyclus* distributions. The map is based on unpublished data investigating the distribution of all known *Bicyclus* taxa. The boxes show the species from the *sciathis* group present in each zone with the endemic species in underlined capital letters. In general the boundaries of these zones are formed by large rivers, islands separated from the mainland or dramatic changes in elevation (the borders shown in the figure are simplified).

Biogeographic implications

Our revised database of known collection locations for all species in the *sciathis* group paints a completely different picture from what was previously assumed. Many of the species in the group are notoriously difficult to separate and have therefore regularly been mixed up in museum collections and published checklists. This is particularly the case for females where androconial characters are absent. Condamin (1973) presented a picture of the group with a high degree of sympatry, possibly by repeating older records without being able to see voucher material. This meant that a higher number of similar species needed to be considered as possibilities when identifying any specimen. Torben B. Larsen (2005 and personal communication) suspected that many older West African records from the species group were due to misidentifications and that these false records had later been repeated without confirming them with any voucher material. Our investigation supports this supposition and clearly shows that most species in the group have much smaller ranges across the whole of the Afrotropical forest zone than previously estimated in the literature. In some cases, ranges have become smaller through splitting older species, but for frequently mixed-up species, such as *B. analis* and *B. hyperanthus*, confusion should now be avoidable, as they are never sympatric. There remain a few geographical regions where any specimen will still require a detailed investigation (Kivu region and western Uganda). But for areas like western Cameroon, where there is a total lack of sympatric distributions of morphologically similar species, identification is now relatively straightforward if the capture location is known. The fact that species in a group of African butterflies have smaller ranges than was previously thought, and that many species claimed to be widespread are in reality clusters of similar, but allopatric, species, is not unique to *Bicyclus*. For example, studies of Hesperiiidae (e.g. Libert, 2014; T.B. Larsen, personal communication) and Pieridae (e.g.

Mitter *et al.*, 2011) have found similar patterns. Studies such as these demonstrate the urgent need for a better systematic knowledge of African invertebrates, not least to enable better decision-making in conservation planning, as many groups are likely to show a higher degree of endemism than currently known.

As the total number of species in the *sciathis* group is quite low (and we have sequence data for just a few individuals per species), we did not make a full analysis of historic biogeographic patterns. However, some tentative hypotheses can still be suggested. These will have to be tested by future comparisons, including multiple *Bicyclus* species groups, and ideally be validated by comparing patterns across other groups of butterflies with similar habitat requirements and distributions. A general survey of distribution patterns of all known species of *Bicyclus* identified 11 main areas across sub-Saharan Africa (O. Brattström, unpublished data). Each individual taxon is generally found in more than one area, but the end of species distributions tends to follow roughly the outer borders of these identified zones. Two of the 11 zones have no species from the *sciathis* group (most likely due to these zones having no wet forest habitats), but the remaining nine areas that have at least one species present are shown in Fig. 10. In general the boundaries of these zones are formed by large rivers, islands separated from the mainland, or dramatic changes in elevation (the borders shown in Fig. 10 are simplified). The boundaries of these proposed zones are frequently shared by other butterfly groups (e.g. Carcasson, 1964; Larsen, 2005), as well as with other terrestrial animals (e.g. Schunke & Hutterer, 2004).

The origin for the *sciathis* group appears to have been the area in Cameroon, Gabon, Republic of Congo and DRC delimited by the Sanaga river in the north, the Congo River in the south and southeast, and the Ubangi River in the northeast (zone E). The subgroup made up of *B. amieti*, *B. analis*, *B. feae*, *B. hyperanthus* and *B. subtilisurae* contains a range of species occurring outside

zone E, but they have all separated from their common ancestor fairly recently, suggesting a general expansion of suitable habitat for the group a few million years ago. The current distributions in this subgroup are mostly without any known allopatry (*B. hyperanthus* and *B. subtilisurae* are possibly parapatric, but an altitudinal gradient appears to be at least partly separating them). This suggests they might have all evolved through drift occurring in isolated refugia after suitable habitat broke up into smaller fragments following an initial rapid expansion. For the subgroup around *B. sciathis*, all species have areas of sympatry in zone E, and there is no evidence that they have moved geographically in the same manner as the other subgroups. *B. heathi* (Zone H) and *B. ivindo* (Zone E) are geographically remarkably separated despite a close genetic relationship. The two widespread species in the group (*B. procora* and *B. uniformis*) show little genetic divergence between samples, even those originating from very distant sample locations. This suggests it is likely that both species recently expanded from a smaller core area.

There are suggestions in the literature that the Congo Basin was more or less fully submerged until the last few millions of years and that the river currently draining the basin to the west is a recent formation. This proposed lake in the Congo Basin would have been drained into the Indian Ocean prior to the formation of the East African highlands. This recent uplift led to a change in the flow direction and formation of the current Congo River (Stankiewicz & de Wit, 2006). This could explain why there is not a single endemic *Bicyclus* species (across all species groups) in the central Congo basin (Zone F), while a fairly high percentage of the species occurring in nearby regions are endemics to their respective areas (zone E, 17%; zone I, 27%) (O. Brattström, unpublished data). The *sciathis* group shows a high rate of endemism in zone E with five endemics amongst the eight species occurring in that area (Fig. 10). The historic presence of a massive lake in central Africa would also explain why an expansion eastwards did not happen until recently for the species in the *sciathis* group.

Supporting Information

Additional Supporting Information may be found in the online version of this article under the DOI reference: 10.1111/syen.12150

Table S1. Basic location data for all investigated specimens.

File S1. Revision of the *Bicyclus sciathis* species group (Lepidoptera: Nymphalidae) with descriptions of four new species and corrected distributional records.

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