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A review of the afrotropical species of the genus *Graphium* (Lepidoptera: Rhopalocera: Papilionidae)

CAMPBELL R. SMITH & R.I. VANE-WRIGHT
Department of Entomology, The Natural History Museum, Cromwell Road, London SW7 5BD, U.K.

CONTENTS

> 'O! would the sons of men once think their eyes
> And reason given them but to study flies!
> See Nature in some partial narrow shape,
> And let the Author of the Whole escape:
> Learn but to trifle; or, who most observe,
> To wonder at their Maker, not to serve.'
>
> ALEXANDER POPE (1688–1744): THE DUNCIAD: BOOK IV (1742)

> 'Every established fact illuminates the world. True scholarship once aspired to add its modest light to that illumination. To clear a few cobwebs. No more.'
>
> Stated by ORMEROD GOODE, a character in A.S. BYATT's novel, THE BIOGRAPHER'S TALE (2000).

SYNOPSIS. The afrotropical species of the leptocircine genus *Graphium* are reviewed. We recognize 39 species. One of these, which we name *G. abri*, is described as new. Four further taxa are raised to specific rank: *G. biokoensis*, *G. schubotzi*, *G. olbrechtsi* (with subspecies *G. o. tongoni*) and *G. kigoma* (with synonym =*wranghami*). We regard *G. illyris* as a polytypic species comprising four subspecies, including *G. i. flavisparsus*. *G. auriger* and *G. poggianus* are treated as monotypic. Despite doubts, we treat *G. cyrnus* as bitypic. Diagnostic descriptions and illustrations of wing patterns are given for all species, together with descriptions of the male and, where known, female genitalia. Most of these are illustrated. Distribution maps are given for most taxa, and biogeographical analyses presented. The scant ecological (hostplant) and bionomic data are presented and discussed, together with discussions on mimicry and apparent sex ratios.

A cladistic analysis is given, together with an account of the characters used. The results of that analysis are neither well resolved nor robust, indicating that further characters from other sources would be helpful. The consensus trees suggest that many previously accepted species groups and phylogenetic interpretations may be questionable. The monophyly of an afrotropical subgenus *Graphium* (*Arisbe*) is called into question as Oriental species representing other subgenera are placed within it, suggesting that these subgenera need investigation.

INTRODUCTION

For the naturalist, according to Wallace (1865), '. . . it matters little to which group he especially devotes himself; all alike offer him endless materials for observation and research'. This, alone, justifies the study of the afrotropical papilionid butterflies. 'But,' he continues, 'for the purpose of investigating the phenomena of geographical distribution and of local or general variation, the several groups differ greatly in their value and importance'.

He goes on to recommend the butterflies as being particular suitable subjects for study as their wings, 'as Mr. Bates has well put it, "serve as a tablet on which Nature writes the story of the modifications of species".'

Aims and objectives

We began this study ten years ago, with the hope of establishing the species limits of African *Graphium* Scopoli, obtaining detailed knowledge of their individual distributions, and developing a robust understanding of their phylogenetic relationships. It was intended as a pilot study, to be followed by similar works on other groups of Leptocircini, and eventually all Papilioninae, to provide a global dataset for conservation evaluation (Forey *et al.*, 1994) in which the importance of phylogenetic diversity (Vane-Wright *et al.*, 1991; Williams *et al.*, 1991; Faith, 1994) as well as species richness and geographical distribution could be assessed.

Our success in achieving these goals has been limited. In particular, our cladistic analysis is far from robust, and raises more questions than it answers. However, our approach to conservation evaluation, established at the start of this project a decade ago, has been superseded by concerns about wider issues (e.g. Vane-Wright, 1996; Margules & Pressey, 2000; Williams & Araújo, 2000). Moreover, we have also come to realize that, with sufficient sampling and large enough groups, species richness alone is a good first-order surrogate for genetic diversity (Williams & Humphries, 1996), perhaps precluding any pressing need for cladistic analysis in biodiversity assessment: seemingly the impact of cladistic classification on the 'calculus of biodiversity' (Bininda-Emonds *et al.*, 2000) for the swallowtails would be small in relation to the costs involved and the time taken.

Nevertheless, if we are to rely on species richness as a measure of genetic diversity, and in particular on complementarity (Williams, 2001) as a basis for area selection, then species need to be meaningful units of comparison. The significance of what we will choose to call the same thing (identity), and that which we will not (non-identity), is thus heightened in the context of establishing conservation priorities. Cladistic analysis thus takes on new importance in relation to debates over the nature of species, and their very definition and recognition (Vane-Wright, 1992, 2001, in press, and references therein).

It turns out that many of the 39 afrotropical *Graphium* recognized here are very poorly-known and, despite our efforts, in many cases their limits as species are still problematic (e.g. cryptic species within the *G. policenes* complex; which taxa do and do not belong to *G. fulleri*, etc. – see relevant sections below). We are left, after 10 years of often fretful study, with a plethora of facts, some well established, some not, concerning the nomenclature, morphology, exo-phenotypic variation, and geographical distribution of African *Graphium*. Our epigraph from 'Ormerod Goode' talks of *established* facts: the tribulations we have suffered stem mainly from difficulties in assessing what is an established, or even 'establishable' fact in comparative biology. Our partial and insecure hypothesis of inter-relationships, based on cladistic analyses of observed morphological variations of the adult insects, is an outstanding example. It is perhaps ironic that, in the case of a group of butterflies blessed with the name *Graphium*, the evolutionary runes on these particular Batesian tablets seem so hard to read. We are left still Wondering what the Maker of these particular Flies had in Mind.

In the end, we have arrived at something more akin to a traditional taxonomic 'revision' than the diagnostic, prescriptive and sharply analytical work we originally envisaged. Naturally, we are disappointed not to have attained all our goals, and to be so far behind schedule – but, at the very least, we hope to have cleared a few cobwebs. Moreover, new horizons for the use of basic biodiversity 'facts' have come into view.

Of these, GloBIS is potentially the most significant. The Global Butterfly Information System (GloBIS) is a collaborative venture intended to create an international information system for open access world-wide to a vast store of information about butterflies, much of it never collated or available before. Funds are currently being sought to support GloBIS Phase I, a 3-year project to create a web-based fully synonymic catalogue for the estimated 100,000 different names that have so far been applied to butterflies. The first phase will also establish the basis of an interactive system for butterfly identification, provide a means to record and access information on distribution and biology, and begin to populate this interconnected network with extensive empirical data, literature references and digital images. For more information about GloBIS see www: ento.csiro.au/globis/, and Lamas *et al.* (in press).

Further goals

With respect to WORLDMAP (expected to be the main software for analysis of our distributional data), large strides have been made with gathering and analysing, for example, African biodiversity data (Williams *et al.*, 1999; Brooks *et al.*, 2001) and good progress with other regions (e.g. Latin America: Brooks *et al.*, 2000, and Europe: Williams *et al.*, 2000) is underway. However, much of this work (Lees *et al.*, 1999 for Madagascar is an exception) is focused on vertebrates and plants, and there is still a pressing need for good data about invertebrate groups for comparison (as we realized a decade ago at the start of this study). We also note the emergence of a wide range of data interpolation and extrapolation techniques for inferring species range and status, using environmental and other data to maximize our inevitably limited empirical knowledge of groups like insects. Once we have had feedback on the information and conclusions presented in this paper, we would hope to explore a program such as CLIMEX (Sutherst & Maywald, 1999) to develop 'probability of occurrence' maps for the species dealt with here.

In this context we here declare our intentions to create a complementary website for our swallowtail work, starting with additional information and images about afrotropical *Graphium*. We have already transmitted our primary results to Häuser (2001), for the GloBIS/GART web swallowtail check-list. In particular, we wish to encourage observers to submit high quality distributional data, validated by reference to this monograph and/or its associated website, to help fill in some of the many gaps in our knowledge of these striking and varied butterflies.

Some nomenclatural problems

The name *Graphium* was first introduced in 1777 by Giovanni Antonio Scopoli (1723–1788), professor of botany and chemistry at the University of Pavia, Italy, for a rather disparate group of about 57 species of the 'Papiliones' characterized by having the wings banded, but not tailed nor ocellate ['Alae fasciatae, non caudate, nec ocellatae' – thus excluding many species currently placed in the genus]. The name was largely ignored until Hemming (1933) selected *Papilio sarpedon* Linnaeus as its type species.

The first use of the generic name *Graphium* in a major work appears to be by Talbot (1939) in his account of the fauna of 'British India'. He included *Iphiclides* Hübner, currently afforded separate generic status, and *Meandrusa* Moore, treated by Miller (1987) as a genus in the Papilionini, as synonyms of *Graphium*. Since Talbot (1939) and the subsequent use of the name in the classification of Ford (1944*a*, *b*), *Graphium* has enjoyed almost universal acceptance. Talbot (1939) also introduced the tribal name Graphiini (see below).

Perhaps because of the belated acceptance of the name *Graphium*, a variety of ways of subdividing *Papilio* Linnaeus were employed. For example, Rothschild & Jordan (1906), Jordan (1907), and Jordan (1908) used the vernacular term 'kite swallowtails' for those species currently included in the Leptocircini (though Jordan, 1908, treated *Leptocircus* Swainson itself as a distinct genus).

It will be seen that some names in this paper, principally those described by Dufrane (1946), were introduced under the generic heading *Papilio* (*Cosmodesmus*). *Cosmodesmus* Haase (1892) was introduced as a subgeneric name for the Old and New World 'Segelfalter' in which he included most of the kite swallowtails, but excluded *Leptocircus*. Kirby (1896) restricted *Cosmodesmus* to just *Papilio protesilaus* Linnaeus 'and its allies' and Hemming (1964) cemented this restriction by designating *P. protesilaus* as type species, thereby condemning the genus to the status of a junior objective synonym of *Protesilaus* Swainson, 1832. The generic name was used as the basis of a tribal name Cosmodesmidi by Verity (1947 – see below).

Arisbe Hübner ([1819]) was established as a genus containing two species, *A. similis* Linnaeus, *sensu* Cramer (a misidentification of *Graphium leonidas* (Fabricius)) and *A. panope* Linnaeus, currently regarded as an infrasubspecific form of *Chilasa* (*Chilasa*) *clytia* Linnaeus (a widespread South Asian papilionine). Of these, Scudder (1875) selected the former as type species, with the identification corrected. Hemming (1965) applied to the ICZN to have Scudder's proposal accepted, and the ICZN (1967) concurred and duly listed *Arisbe* on the *Official List of Generic Names in Zoology* (ICZN, 1987) and designated *Papilio leonidas* as its type species, placing it on the *Official List of Specific Names in Zoology* (ICZN, 1987). See also Hemming (1967).

The name *Arisbe* is antedated by *Zelima* Fabricius (1807). This was published by Illiger in his *Magazin für Insektenkunde* as an extract from a supposedly forthcoming work of Fabricius, the *Systema Glossatorum*. Whether the latter was in fact published at the time is controversial: Griffin (1939) concluded that it was not; Comstock (1942) that it was; see also Brown (1987). A facsimile edition, edited by Bryk, was eventually published (Fabricius, 1938). Fabricius (1807) names only one of three included species, *Papilio pylades* Fabricius [here treated as a synonym of *G. angolanus baronis* Ungemach] which is thus the type species by monotypy (Hemming, 1967); Fabricius (1938) names the other two included species as *Z. leonidas* and *Z. orestes*, which Brown (1987) suspected as being 'a member of the *Papilio leonidas* Fabricius group in the broad sense . . .'.

However, *Zelima* Fabricius is a homonym of a Meigen dipteran name published in a pamphlet suppressed by the ICZN (1963). When suppressing Meigen's pamphlet, the ICZN also suppressed and placed on the *Official Index of Rejected and Invalid Generic Names in Zoology* (ICZN, 1987) a number of homonyms of Meigen names, including *Zelima* Fabricius.

A further generic name has been applied to the African species: *Ailus* Billberg (1820), which was apparently introduced as a replacement name for *Zelima* Fabricius, though Scudder (1875) did not know Billberg's reason, and Hemming (1967: 462–3) specifically stated it was not connected with the homonomy with Meigen's name. No species were listed with the name: Hemming (1967) uses *Papilio pylades* Fabricius [= *G. angolanus baronis* Ungemach] under the rules governing replacement names (Code, Article 67.8). Hemming (1967) accepted *Ailus* as a valid replacement name notwithstanding Walsingham & Durrant's (1902) opinion that the *Enumeratio* was simply a collection catalogue; that the new names within it should not be accepted as validly published; and endorsing '. . . Hummel's regret that any copy of it escaped the fire of 1822'.

Fortunately, *Arisbe* Hübner [1819] is available and is widely accepted as a senior subjective synonym and the valid subgeneric name for the afrotropical *Graphium*.

Graphiini, Lampropterini or Leptocircini?

A special problem has arisen over what name to apply to the tribe of 'kite' swallowtails including *Graphium* and its relatives, with Graphiini, Lampropterini and Leptocircini all being used by recent authors.

The genus-group name *Lamproptera* was introduced by G.R. Gray (1832) for the 'dragontail', *Papilio curius* Fabricius, 1787 (as '*Erycina* (*Lamproptera*) *curius* G.R. Gray'), on the legend to plate 102 of the Supplement on the Lepidoptera in Griffith's edition of Cuvier's *The Animal Kingdom*, but with no mention in the text and no description. According to the Code, Article 12.2.7, this constitutes an 'indication' and thus satisfies the requirements of Article 12 on availability. According to the Code, Article 56.2, it is not a junior homonym of *Lampropteryx* Stephens, 1831 [Lepidoptera: Geometridae].

Swainson (1832) gave a description of a new subgenus, *Urania* (*Leptocircus*) for the same species. He did not cite Gray's name and was not, evidently, proposing a replacement name for a homonym. He did, however, state, 'We are told the species has been 'made into a genus' by some continental methodist, but who, according to the disreputable and slovenly mode fast creeping *among us* [Swainson's emphasis], gives no definition. We have elsewhere expressed our reasons for rejecting all such names . . ., and we are thus pledged to do so upon every occasion.' As it is based on the same species, *Papilio curius* Fabricius, *Leptocircus* is a junior objective synonym of *Lamproptera* Gray. Notwithstanding the availability and validity of *Lamproptera* Gray, many subsequent authors followed Swainson. Among these, Kirby (1896) included *Lamproptera* Gray as a synonym of *Leptocircus* Swainson.

Kirby (1896) was also the first to apply a family-group name to the genus, describing the sub-family Leptocircinae solely for the genus *Leptocircus*.

Bryk (1929) recognized *Lamproptera* Gray as a valid genus, with *Leptocircus* Swainson as a junior synonym. At the same time he replaced the family-group name Leptocircinae Kirby with Lampropterinae (Bryk, 1929: 4, footnote; as synonyms of Papilionidae). However, the Code, Article 40.1, states that family-group names should not normally be replaced on the grounds of being based on a junior synonym, unless (Article 40.2) the name has been replaced before 1961 and this replacement '. . . *is in prevailing usage*' (our emphasis). Were such a replacement name to be accepted, the Code, Article 40.2.1, decrees that the replacement name 'retains its own author but takes its priority of the replaced name, of which it is deemed to be the *senior* synonym' (our emphasis). It recommends (Recommendation 40A) that it should be cited with the author and date of its replacement, and with the date of priority enclosed in parentheses. It would thus be cited as Lampropterinae Bryk 1929 (1896). As far as we are aware, Lampropterinae (as its tribal equivalent, Lampropterini) has only been used in major revisions or catalogues by Bridges (1988*a*,*b*), Ackery *et al.* (1995), and Holloway *et al.* (2001), whereas Leptocircinae or its equivalents has been widely used, including by Munroe (1961), Carcasson (1981), Hancock (1983), Ackery (1984, 1989), Igarashi (1984), Collins and Morris (1985), Scott (1986), DeVries (1987) and Eliot (1992). Thus Lampropterinae cannot be said to be in prevailing usage and should be rejected under that provision of the Code.

The name Graphiini was introduced by Talbot (1939) for the kite swallowtails of the world, including *Graphium* (*sensu lato*) and *Lamproptera* (but excluding *Teinopalpus* Hope, which he included in its own tribe), though nowhere does he state it to be 'new'. As such, it appears to be the first time that these two genera have been brought together below the family level. However, it is clearly junior to both Lampropterinae Bryk 1929, and Leptocircinae Kirby 1896. Despite this, the name Graphiini has been used by Ford (1944*a*, *b*), Miller (1987), Tyler *et al.* (1994), Pennington (1994) and Braby (2000). Should *Lamproptera* be excluded from the clade, which is unlikely given the work of Hancock (1983) and Miller (1987), Graphiini would be available as a tribal name. According to Miller (1987), Keith Brown, in a personal communication to Miller, intended to submit a recommendation to the ICZN that the name Graphiini be accepted rather than Leptocircini. To the best of our knowledge, no such proposal has been made. Neither name appears in the 'Official lists and indexes of names and works in zoology' (ICZN, 1987) or the supplement ([1991]), and we have found no reference to either name in volumes of the Bulletin of Zoological Nomenclature published since that date.

A further name has been applied to the group: Cosmodesmidi Verity (1947), based on the genus, *Cosmodesmus* Haase (see above) in its original, broad sense. This generic name is now regarded as a junior objective synonym of the neotropical genus *Protesilaus* Swainson. Cosmodesmidi Verity is a junior synonym of Leptocircinae, but could be revived should a name be needed for a clade composed e.g. solely of the neotropical Leptocircini.

Teinopalpidae Grote (1899) was introduced as a family name solely for the Asian genus *Teinopalpus* Hope. Though this has been included within the Leptocircini by some authors (e.g. Munroe, 1961; Hancock, 1983), we here follow Ehrlich (1958), Miller (1987) and later authors (e.g. Häuser, 2001; Vane-Wright, in press; Lamas *et al.*, in press) in treating it as a separate tribe, Teinopalpini, within the Papilioninae. Were the earlier classification accepted, Teinopalpini would anyway be junior to Leptocircini.

To summarize:

Lamproptera Gray, 1832, is an available and valid name for the genus including *Papilio curius* Fabricius.

Leptocircus Swainson, 1832, is an available name for the same genus, but invalid as it is a junior objective synonym. It was not established as a replacement name.

Leptocircinae Kirby, 1896, and its equivalents is available as a family-group name for *Lamproptera* together with any other genera considered to be part of the same monophyletic clade.

Lampropterinae Bryk, 1929, is an unnecessary replacement name for Leptocircinae, and has not been rendered valid by prevailing usage.

Graphiini Talbot, 1939, and Cosmodesmidi Verity, 1947, are junior subjective synonyms of Leptocircinae. Teinopalpini Grote, 1899, is external to the tribe.

Our conclusion is thus that the correct name for the tribe including *Graphium* and its relatives is Leptocircini Kirby, 1896.

HISTORY OF THE CLASSIFICATION OF AFROTROPICAL *GRAPHIUM*

Higher levels

Almost by definition, the first efforts to place *Graphium* and its relatives in a wider context within the Papilionidae did not take place until after the widespread acceptance of the generic name following Hemming's (1933) selection of a type species. Prior to that, as described above, the species were collectively identified within *Papilio* under the sobriquet 'kite swallowtails' or some equivalent (see, e.g. Rothschild & Jordan, 1906; Jordan, 1907; 1908; Aurivillius, 1899; 1910). Bryk (1930*b*) placed the afrotropical species (as *Papilio*) immediately following the afrotropical *Papilio* (in the modern sense); the Oriental species (subgenera *Pazala* Moore, *Pathysa* Reakirt, *Paranticopsis* Wood-Mason and de Nicéville, and *Graphium*) were placed (Bryk, 1930*a*) between Oriental *Papilio* and neotropical species now included in *Parides* Hübner.

That first attempt at a comprehensive analytic classification of the Papilionidae was by Ford (1944*b*), based largely on his studies of the chemistry of their pigments (Ford, 1944*a*). He divided the family into five tribes (Teinopalpini, Papilionini, 'Graphiini', Troidini and Cressidini) and described and figured an evolutionary scenario in which both the Papilionini and Graphiini were derived from a troidine ancestor. He postulated that the tribe Teinopalpini (consisting of just *Teinopalpus*) was derived from *Papilio* and that *Lamproptera* 'is the highest specialisation of the Graphiini'. Ford (1944*a*) included *Iphiclides podalirius* (Linnaeus) and American species now placed in *Eurytides* Hübner within *Graphium*; as well as *Meandrusa payeni* (Boisduval) (Papilionini according to Miller, 1987).

The next major contribution to the study of papilionid classification was by Munroe (1961). Munroe made significant changes to previous classifications of the Leptocircini. He separated the American species as the genus *Eurytides*; recognized *Iphiclides* as a good genus and erected the genus *Protographium* for the Australian species *leosthenes* Doubleday; and separated the species *payeni* and *sciron* Leech (=*gyas* Westwood) as belonging to the genus *Dabasa* Moore (=*Meandrusa*), though retained the latter within his Graphiini. He also included *Teinopalpus*.

More significantly for the present study, Munroe (1961) divided the remaining, Old World *Graphium* into three subgenera: *Pathysa*, *Arisbe* and *Graphium* and provided an evolutionary narrative of their relationships asserting that the most primitive were the Indo-Australian species of *G.* (*Graphium*), that the 'next stage of development . . .' were the African species, *G.* (*Arisbe*), and that the most specialized group was the remaining Indo-Australian species that he referred to *G.* (*Pathysa*). In this last subgenus, Munroe (1961) recognized three species groups: the mainly tailless *macareus* group, and the tailed *antiphates* and *eurous* groups that are now referred to the subgenera *Paranticopsis*, *Pathysa* and *Pazala*, respectively (see Häuser, 2001).

At the time Munroe was concentrating on the Papilionidae, Ehrlich (1958) produced a phylogeny and classification for all butterflies. Ehrlich and Munroe differed in their interpretations of some aspects of papilionid classification. Of particular significance to the present study is the position of *Teinopalpus*. Munroe (1961) included the genus within his Graphiini; Ehrlich (1958) treated it as a separate tribe within the Papilioninae, as had Talbot (1939) and Ford (1944*b*). Munroe & Ehrlich (1960) collaborated to attempt to resolve their differences. Over *Teinopalpus* they compromised by recognising two subtribes, the Teinopalpiti and Graphiiti (*recte* Teinopalpina and Leptocircina) within the tribe Graphiini. They also produced a branching diagram giving an 'Apparent sequence of separation of papilionid lines' where they illustrated an evolutionary scenario in which one genus could give rise to another genus or even a higher group. For example, in their figure the genus *Graphium* gives rise to the genus *Dabasa* [=*Meandrusa*] plus the entire Papilionini; and *Eurytides* apparently gives rise to a lineage including those three taxa and the genera *Protographium* and *Iphiclides*. We have attempted to re-interpret this as a cladogram, incorporating Munroe's (1961) classification of the subgenera of *Graphium*, as Fig. 1. It will be seen that when Munroe & Ehrlich's (1960) hypothesis is viewed in this way, the Leptocircini form a paraphyletic stem group leading to the Papilionini.

The next major revision of the Papilionidae was by Hancock (1983) in which he covered the family from the highest level down to that of the species group. His species group classification, as applied to the afrotropical *Graphium*, is discussed below. Here it is relevant to note that Hancock (1983) divided the genus into four subgenera, *Pazala*, *Pathysa* (including *Paranticopsis*), *Graphium*, and *Arisbe*, and that he included the afrotropical swordtailed species in *G.* (*Graphium*), and the non-swordtailed species in *G.* (*Arisbe*). Hancock (1983), like Munroe & Ehrlich (1960), subdivided the Leptocircini into two subtribes. His 'Teinopalpiti' included three genera, *Teinopalpus*, *Meandrusa* and *Iphiclides*. The remaining genera,

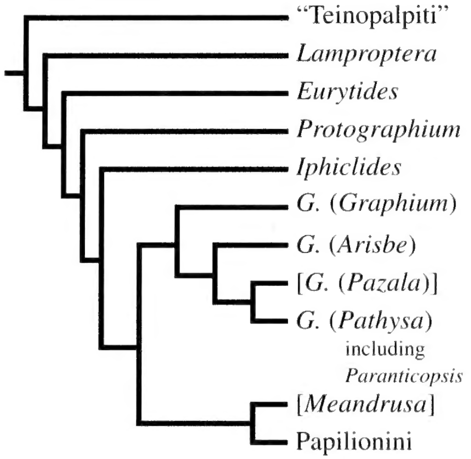


Fig. 1. Munroe & Ehrlich's (1960) interpretation of the phylogeny of the Leptocircini etc. Redrawn as a cladogram from their 'Apparent sequence of separation . . .'. The branching pattern of *Graphium* subgenera is interpreted from Munroe's (1961) account. See text.

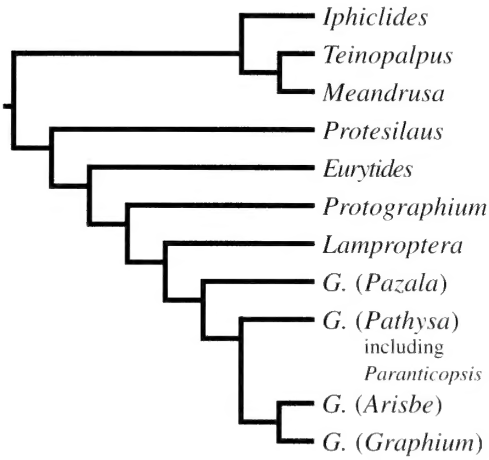


Fig. 2. Hancock's (1983) phylogeny of the Leptocircini. Hancock included the sword-tailed afrotropical species of *Graphium* in the subgenus (*Graphium*).

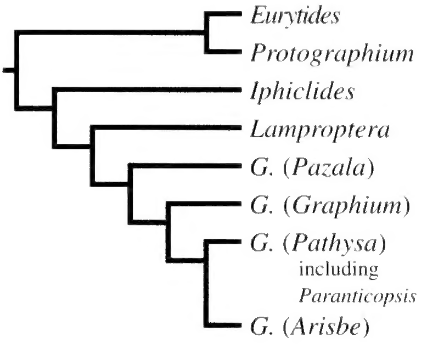


Fig. 3. Miller's (1987) phylogeny of the Leptocircini. Miller included *Protesilaus* as a subgenus of *Eurytides*.

Protesilaus, *Eurytides*, *Protographium*, *Lamproptera* and *Graphium* form Hancock's subtribe 'Leptocirciti'. Hancock's (1983) interpretation is illustrated here as Fig. 2.

Four years after Hancock's (1983) revision appeared, Miller (1987) published his phylogenetic study of the Papilioninae. Miller built on the work of his predecessors and added many of his own observations. He did not delve down to the level of the species or species group, and did not consider the other subfamilies other than as context. His was also the first study to employ computer based cladistic methodology using the principle of parsimony to generate cladograms. The principal difference from both Munroe (1961) and Hancock (1983) in the context of the present study is the exclusion of *Meandrusa* and *Teinopalpus* from the Leptocircini. Miller (1987) considered that the characters used to link *Teinopalpus* with the Leptocircini to be largely plesiomorphies, and placed it in a tribe of its own (the Teinoplapini) as sister to (Papilionini + Troidini). He placed *Meandrusa* as sister to *Papilio* within the Papilionini arguing that those characters that link it to the Leptocircini are homoplastic, whereas it shares the apomorphies of his (Papilionini + Troidini) clade, and with *Papilio*. Miller (1987) did have a basal dichotomy in the Leptocircini, giving a clade comprising the American *Eurytides* (including *Protesilaus* as a subgenus) and the Australian *Protographium leosthenes*. The other major clade included the Old World *Iphiclides*, *Lamproptera* and *Graphium*. Miller (1987) agreed with Hancock (1983) in placing *G.* (*Pazala*) as sister to the rest of *Graphium*, but differed in placing *G.* (*Graphium*) as sister to *G.* (*Pathysa*) and a monophyletic afrotropical *G.* (*Arisbe*). Miller's (1987) interpretation is illustrated as Fig. 3. For more insight into the earlier classifications, especially in relation to his own, see Miller (1987). See also Vane-Wright (in press).

Species level

The first comprehensive study of the afrotropical species (treated as part of *Papilio*) appears to have been by Aurivillius (1899; 1910). He placed them in six species groups, divided from the rest of *Papilio* as 'kite swallowtails' or 'segelfalter' in the later work, on the basis of their wing patterns. There is very little classificatory structure other than that two of the groups are subdivided in the later work, each into two.

Aurivillius' groups are:

The *ridleyanus* group, consisting of just that species.
The *pylades* [=*angolanus*] group of *endochus*, *pylades* [=*angolanus*] and *morania* (including *taboranus* as a subspecies).
The *tynderaeus* group of *cyrnus*, *tynderaeus* and *latreillianus*.
The *leonidas* group divided into: *leonidas* alone, and *levassori*, *philonoe* and the *adamastor* group (in our sense).
The *policenes* group. Again subdivided, with *antheus* and *evombar* forming one subgroup; *nigrescens* [=*policenoides*], *policenes* (with *liponesco* as a subspecies), *polistratus* (with *sisenna* as a separate species), *junodi*, *porthaon* and *colonna*.
The *kirbyi* group comprising *kirbyi* and *illyris*.

The next thorough investigation of the afrotropical swallowtail fauna was by Berger. His detailed work (1950) was on the fauna of the then Belgian Congo (now Democratic Republic of Congo) and in that work he did not apply a classification. However, he also published a systematic account (1951) in which he placed the 35 species known to him in 10 species groups based mainly on the male genitalia. His groups were:

'Groupe de *G. pylades* F.' [= *angolanus*], comprising: *endochus*, *taboranus*, *morania*, *pylades* [=*angolanus*] and incorporating, unlike Aurivillius (1910), *ridleyanus*.
'Groupe de *G. tynderaeus*' of *tynderaeus* and *latreillianus*, excluding *cyrnus*.
'Groupe de *G. ucalegon* HEW.' [our *adamastor*]. The tailless species, largely brown and cream, which are putative mimics of various specific or generalized *Amauris* models (see below). Berger (1951) subdivided the group into two subgroups, the first comprising: *hachei*, *auriger*, *ucalegon*, *simoni*, *fulleri*, *ucalegonides* [here regarded as a subspecies of *fulleri*], *almansor*, *odin* [= *schubotzi*], *olbrechtsi* and *aurivilliusi*; the second just *agamedes* and *adamastor*.
'Groupe de *G. leonidas* F.', including *leonidas* and *levassori* and incorporating *cyrnus*, but neither *philonoe*, nor the *adamastor* group.
'Groupe monospécifique de *G. philonoë* WARD'.
'Groupe de *G. illyris* HEW.', comprising: *illyris* and *kirbyi*, and also *gudenusi*, which was unknown to Aurivillius.
'Groupe de *G. policenes* CR.' including apart from *policenes*, *nigrescens* [=*policenoides*] and *liponesco* (as *boolae*), *junodi* and *polistratus*, but excluding *porthaon* and *colonna* as well as *antheus* and *evombar*.
'Groupe monospécifique de *G. colonna* WARD'.
'Groupe monospécifique de *G. porthaon* HEW.'.
'Groupe de *G. antheus* CR.', comprising *antheus* and *evombar*.

Hancock's (1983) phylogenetic analysis of the Papilionidae, discussed above, worked down to species group level. He continued to refine his understanding of the afrotropical species in a series of papers (e.g. 1985*a*, 1985*b*, 1986), culminating in a summary of his views at that time (Hancock, 1993). Here he reiterated his view that the afrotropical species of *Graphium* divide into two subgenera, *G.* (*Arisbe*) for the non-swordtailed species, with the swordtailed species placed in *G.* (*Graphium*), from which the Oriental species of that subgenus are derived. Hancock (1993) divided the species into 10 groups, very similar in content to those of Berger (1951). Hancock's groups were:

The *tynderaeus* group of *tynderaeus* and *latreillianus*, as in Berger (1951).
The *adamastor* group.
The *angolanus* group of *endochus*, *angolanus*, *ridleyanus* (Hancock, 1983 had this as a separate, monospecific group), *morania*, *schaffgotschi*, and *taboranus*.
G. philonoe as a monospecific group, as in Berger (1951).
The *leonidas* group of *cyrnus*, *levassori* and *leonidas*, as in Berger (1951).
All the above Hancock (1993) included in *G.* (*Arisbe*). The following five groups he placed in *G.* (*Graphium*):
G. colonna as a monospecific group, as in Berger (1951).
The *policenes* group of *policenes* and *junodi*, and *nigrescens* [=*policenoides*] and *polistratus*, as two pairs of sister species.
G. porthaon as a monospecific group, as in Berger (1951).
The *illyris* group of *illyris*, *kirbyi* and *gudenusi*, as in Berger (1951).
The *antheus* group of *antheus* and *evombar*, as in Berger (1951). It is from this group that the Oriental species are derived according to Hancock's (1993) figure 24.

Hancock's (1993) interpretation of the relationships of these species and groups are shown in Fig. 4.

To the above list of species level analyses should be added those of Saigusa *et al.* (1977, 1983) of the Oriental *G.* (*Graphium*). The significance of these to the present study is that, while the validity of the species groups they define within *G.* (*Graphium*) appear well founded, they apparently accepted (according to Miller, 1987) the monophyly of the subgenus without question and failed to report any synapomorphies for the subgenus. This may have a bearing on the interpretation of our results.

Our questions

In undertaking a cladistic analysis, it is important to keep in mind what questions are being asked. Without keeping this focus, it is easy to attempt too much, or to employ, for example, too many outgroups which cannot be scored properly for the characters under study. In the present work, given the difficulty we have had in getting clear and unequivocal 'characters' (see Cladistics section), we have limited ourselves largely to the following questions:

- Are the afrotropical *Graphium* monophyletic? In other words, is the subgenus *Arisbe* valid for the afrotropical species?
- Are the swordtailed afrotropical *Graphium* monophyletic?
- Are the non-swordtailed afrotropical *Graphium* monophyletic?
- Are Berger's (1951) and Hancock's (1993) species-groups monophyletic?
- Can we recognize any robust or informative relationships for each of Berger's (1951) 'groupe[s] monospécifique[s]': *colonna*, *porthaon* and *philonoe*, to other *Graphium*?
- Are the groupings and relationships described by Hancock (1983, 1993) valid?
- Can we recognize any well-founded higher groupings among the species-groups?

We have not sought to answer the following:

- Are the non-afrotropical subgenera of *Graphium* monophyletic?
- What are the cladistic relationships of the subgenera of *Graphium*?

Nor, clearly, are we in a position to present detailed (let alone robust) cladistic analyses to reveal relationships within the *adamastor*-group. The species of this group, although quite numerous, are very homogeneous in adult structure and colour pattern, and very little else is known about most of them.

MATERIALS AND METHODS

Studies were based on approximately 7300 afrotropical *Graphium* butterflies in the collections of The Natural History Museum, London and a further 2700 specimens from other collections, either on loan or seen during visits (see Abbreviations). Descriptions are based on typical (not necessarily type) examples, but all other specimens were examined to assess the amount and nature of the variability. All BMNH specimens were recorded on a specimen level database (Spec.Reg.) where each is given a unique record number that is added to the specimen. Recorded on the database are details of the collecting locality, which was used as the basis for the distribution mapping.

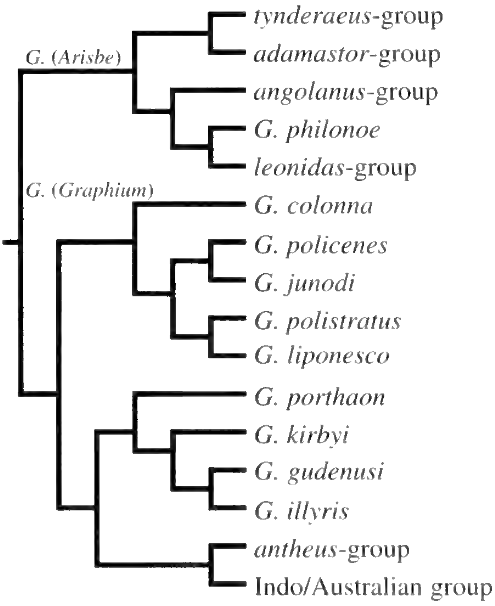


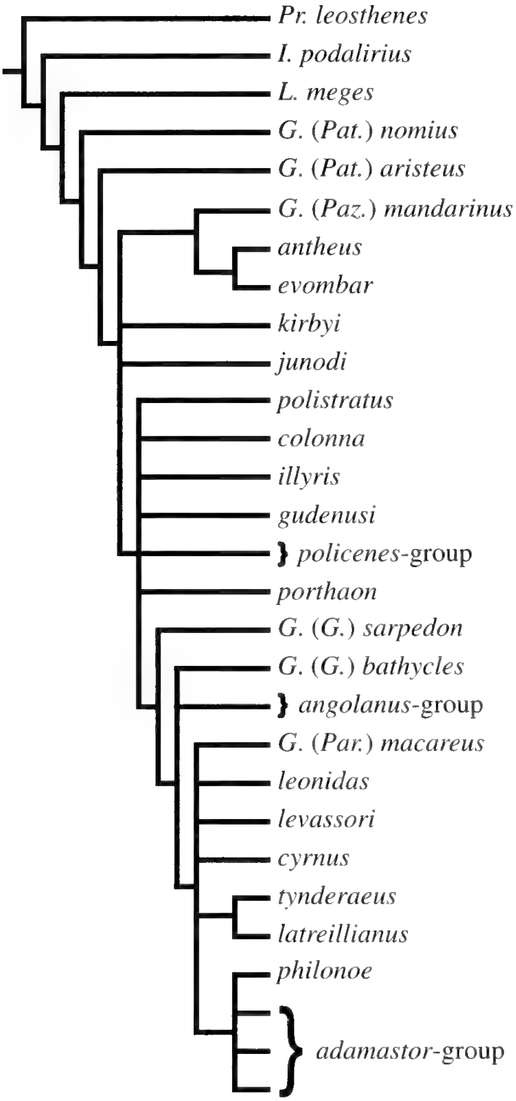
Fig. 4. Hancock's (1993) 'suggested phylogenetic relationships' of *Graphium (Graphium)* and *Graphium (Arisbe)*. Simplified and redrawn from Hancock (1993).

Nomenclature of wings and genitalia

In order to discuss the array of markings that form the colour pattern of these, and other, butterflies, the wing venation and the cells so defined are a valuable tool for navigation. Wing venation itself is useful in classification at higher levels. We largely follow the terminology used by Miller (1987) for the nomenclature of the veins and cells, as shown in Fig. 7. We have added the term 'posterior discocellular vein' to describe the vein that borders the discal cell posteriorly from its root to the root of vein M_3 of both the fore- and hindwings. This, we feel, avoids any confusion as to whether the vein is derived from the cubital or medial vein in ontogeny. It should be noted that Fig. 7 is taken from a specimen of *G. policenes*, but that the costal area of the forewing has been expanded in order to show the dispositions of the subcostal and radial veins more clearly.

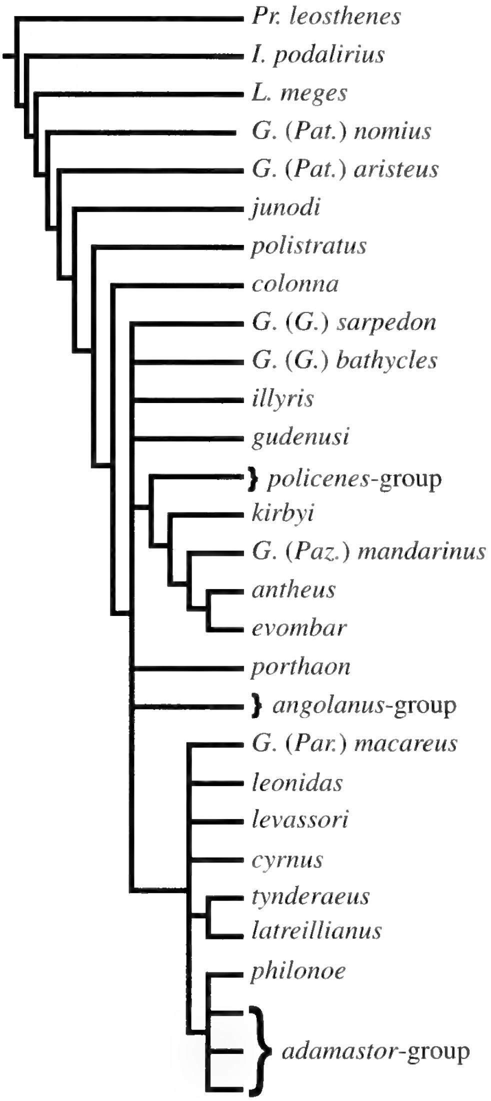
The terms we have used for the various pattern elements are shown in Figs 8 and 9.

The nomenclature of the male and female genitalia as employed in this study is illustrated in Figs 10 to 13. We have attempted to follow the nomenclature of Klots (1970) and Sibatani *et al.* (1954), with applications to the Papilionidae and particularly *Graphium* from van Son (1949 – notably for the females), Munroe (1961), Miller (1987), and Hancock (e.g. 1993). We have introduced names for structures that are particular to, or significant in, the afrotropical *Graphium*.



L = 176; CI = 33; RI = 68

Fig. 5. Cladogram of African *Graphium* and related taxa, derived from data matrix with multistate characters made inactive (see results p. 530).



L = 214; CI = 37; RI = 66

Fig. 6. Cladogram of African *Graphium* and related taxa, derived from data matrix with multistate characters made active and non-additive (unordered) (see results p. 530).

Thus, the extensions to the tip of the valve we have termed the dorsal and ventral terminal processes. The often finger-like and stoutly setose evagination from the dorsal part of the mesal face of the valve, called the dorsal process by Munroe (1961), we term the dorsal projection, to avoid confusion with other similarly located structures. Since the harpe in most afrotropical *Graphium* is subdivided into dorsal and ventral elements, we call these the dorsal harpe and ventral harpe, respectively, for brevity. These names are intended to aid observation and navigation. The homology of the structures across taxa should be inferences from cladistic analysis, not *a priori* assumptions suggested by existing nomenclature;

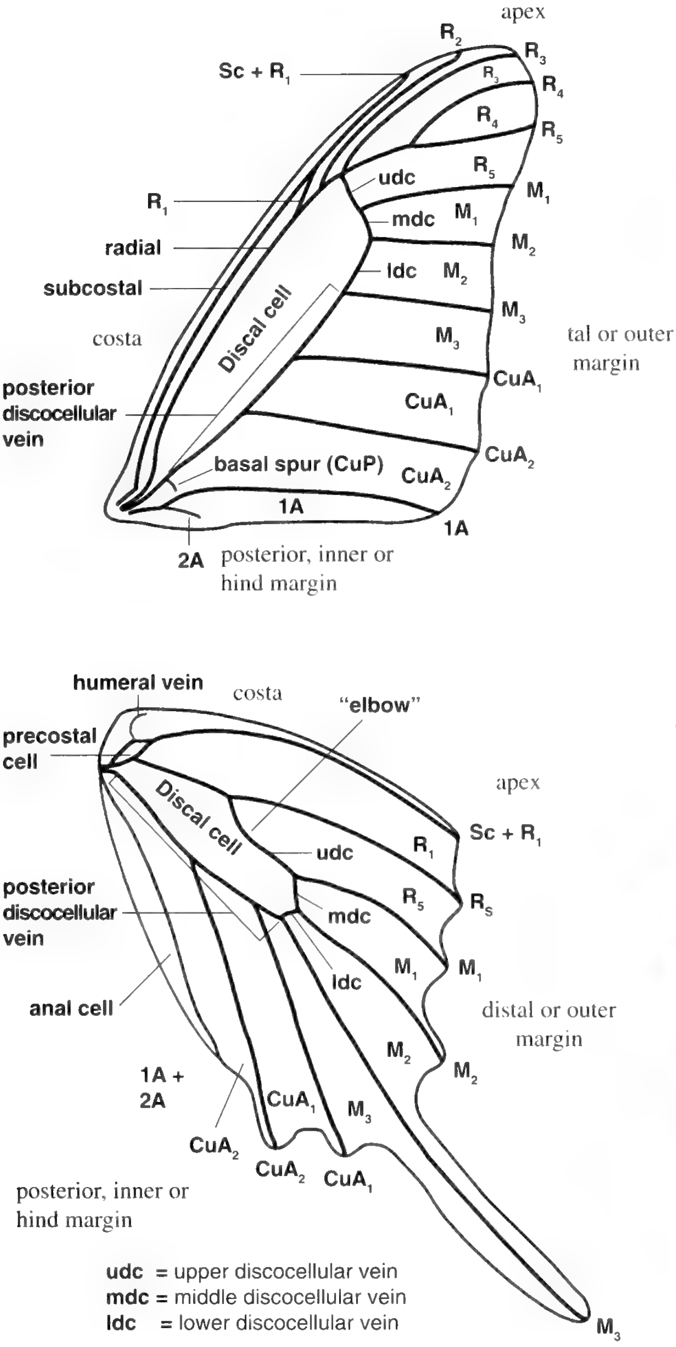


Fig. 7. Nomenclature of the veins and cells of the wings as used in this paper. Based on a specimen of *G. policenes*. The costal area of the forewing has been expanded in order to show the positions of the radial veins.

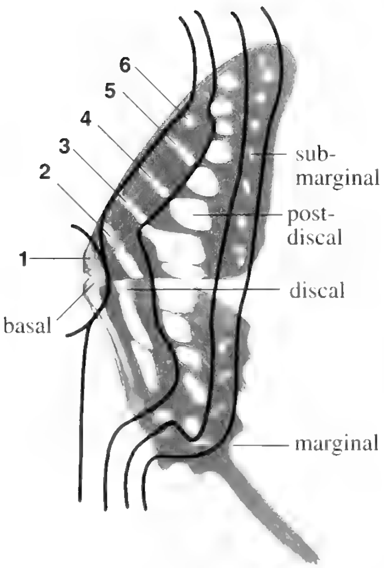


Fig. 8. Wing pattern element nomenclature used in this paper, with the numbering of the forewing discal cell bars used when discussing the swordtailed species.

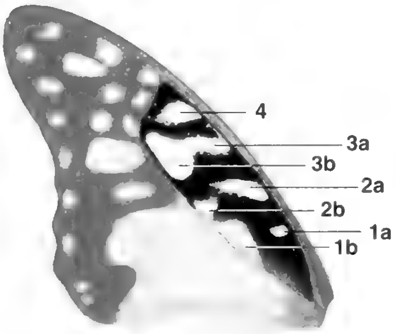


Fig. 9. Nomenclature of the forewing discal cell bars used in this paper for members of the *angolanus*-group. Illustrated from a specimen of *G. angolanus angolanus* ab. *lapydes* Suffert.

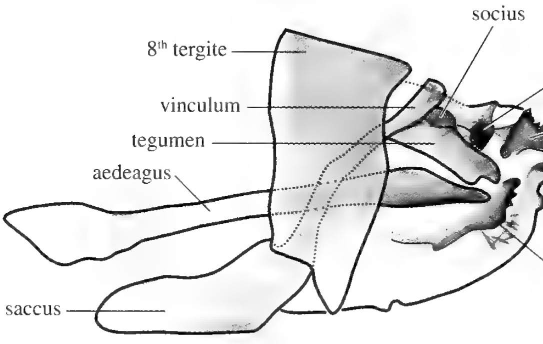


Fig. 10. Male genitalia of *Graphium policenoides* (ABRI specimen, left valve removed), showing the nomeclature used in this work.

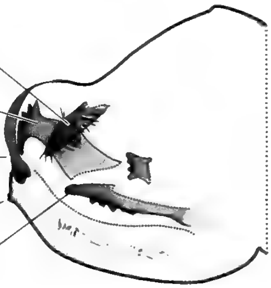


Fig. 11. Left valve of *Graphium ridleyanus* (BMNH Spec. Reg. No. 137439, vial No. 3161), showing the nomeclature used in this work.

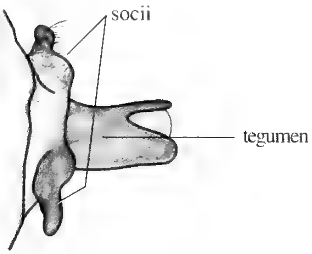


Fig. 12. Dorsal view of socii and tegumen of *Graphium kigoma* (ABRI specimen) to show 'prominent' socii.

this is especially true when comparing outgroup taxa.

The nature of the structures concerned and their variation across the taxa is discussed in the 'Characters used in the cladistic analysis' section, below.

Dissection and illustration methods

Genitalia were prepared by first removing the abdomen and soaking it overnight in a cold 10% (nominally) aqueous solution of KOH. After soaking, the preparation was neutralized and placed in water for dissection. Dissection was carried out under a Wild M8 stereo

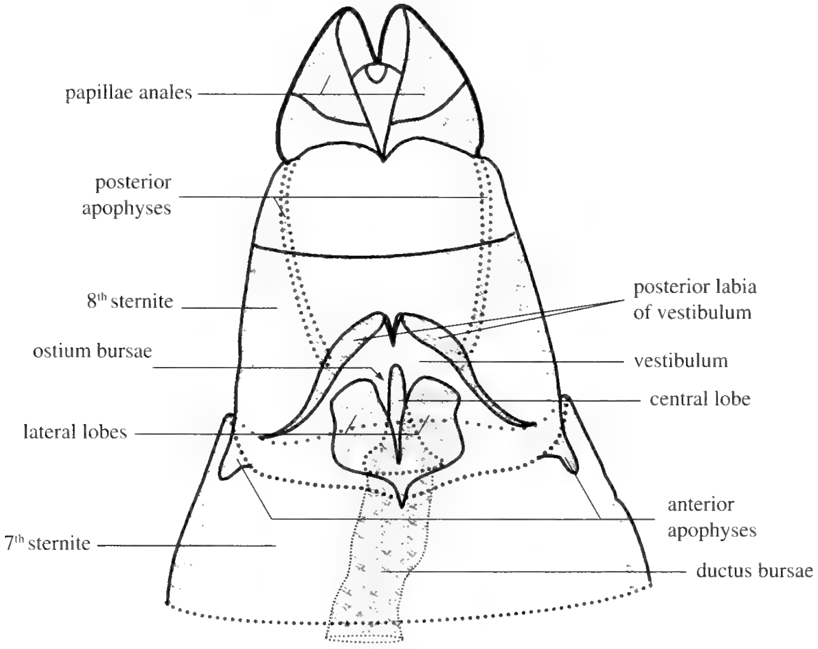


Fig. 13. Diagram of female genitalia typical of afrotropical *Graphium* to show nomenclature used in this work. Redrawn from van Son's (1949) figure 24 of *G. policenes*.

microscope. As far as possible scales and soft tissues were removed. For males, the genital capsule was removed by carefully tearing between the 7th and 8th abdominal segments with the aid of fine forceps. The left valve was removed in the same way. For females, the abdomen was pinned under water in a small petri dish partly filled with petroleum wax. The abdomen was cut between the tergites and sternites from the first to the 6th segment using fine surgical scissors, the dorsal portion peeled back and as much as possible of the soft tissue removed consistent with avoiding damage to the internal genital organs. The whole was then stained with Chlorazol black to aid distinguishing between the genital organs and other tissues (e.g. trachea). Successively more of the soft tissues were then removed and the distal segments opened to reveal the genital organs. In the case of both the males and females, the preparations and abdominal wall were dehydrated in successively more concentrated alcohol solutions, culminating in two changes of iso propyl alcohol (propan-2-ol). The preparations were stored in microvials in glycerol and are retrievable via the BMNH specimen registration system (Spec.Reg.). Where appropriate, both the Spec.Reg. and Rhopalocera vial numbers are given in the accompanying figures and text.

Images for illustration and examination were made using a video camera mounted on a stereo or compound microscope and employing Synoptics Ltd Auto-montage software. This eliminates the problem of very shallow depth of field in photomicroscopy by capturing a series of images of different layers through the object. The software selects the in-focus parts of each image and combines them into a compound montage in which the whole object is seen to be in focus. A further function of the software enables an anaglyph (red/cyan or red/green) stereoscopic image to be produced to better visualize the juxtaposition and relationships of these complex, three-dimensional objects.

The illustrations in this work were produced from the Auto-montage images using Adobe® Photoshop® software to emphasize the salient areas and de-emphasize the surrounding, less critical parts. This was mainly achieved using the 'dodge' and 'burn' tools to lighten and darken parts of the image as appropriate. Needless to say, no substantive changes were made to any image. The images were then compiled into plates that could be placed into Adobe® PageMaker® desktop publishing software.

Distributions and mapping techniques

The distribution maps shown in Figs 112 to 166, and in the biogeographic analyses of Figs 167 to 172 were generated from the biogeography and conservation analysis software, WORLDMAP (Williams, 1996). Raw locality data were recorded on specimen level databases (see above). Records from the literature were also recorded in this way. We intend to make the data, including the sources whether from specimens or the literature, available on the World Wide Web. Efforts were then made to find the exact co-ordinates of these localities in terms of longitude and latitude using a variety of published and on-line gazetteers. This was frustrated by finding duplicates of many names and by multiple spellings or formations of others. In other cases, it proved impossible to match old and often imprecise names with current interpretations. Nonetheless of some 4600 localities and their variant spellings, we were able to find credible longitude and latitude readings for nearly 3400. When the task of searching for localities was completed to the best of our ability and time would allow, the various databases were cross-queried and combined into a master in which every usable record of each taxon with its reliable longitude and latitude (converted to decimal, Geocode, form) was held. This was exported from the Paradox© database as an ASCII file that WORLDMAP was able to import directly.

Once in WORLDMAP it was possible to examine the distribution maps for each taxon to remove or edit any obvious errors or perverse records. A grid of standard 1° × 1° squares was used covering sub-Saharan Africa, and adjacent islands including Madagascar.

The distribution maps were generated by 'printing' them as 'encapsulated post script' files using an appropriate printer driver. The resulting files were edited as vector graphic files using CorelDRAW® software and compiled into the plates for placement into Adobe® PageMaker® files.

Depositories and Abbreviations

Institutions

BMNH	The Natural History Museum (formerly British Museum (Natural History)), London, U.K.
ABRI	African Butterfly Research Institute, Nairobi, Kenya (material loaned by Steve Collins)
AMSA	Australian Museum, Sydney, Australia
CMNH	Carnegie Museum of Natural History, Pittsburgh, U.S.A. (visited by I.J. Kitching courtesy of John Rawlins)
FIF	Forschungsinstitut Senckenberg, Frankfurt, Germany (visited by CRS courtesy of Dr Heinz Schröder (retired))
IRSN	Institut Royal des Sciences Naturelles, Brussels, Belgium (visited by CRS courtesy of M. Detry)
MRAC	Musée Royal de l'Afrique Centrale, Tervuren, Belgium (visited by CRS and material loaned courtesy of Ugo Dall'Asta)
MCSN	Museo Civico di Storia Naturale, Genoa, Italy
MNHN	Museum National d'Histoire Naturelle, Paris, France (visited by CRS courtesy of Jacques Pierre)
MNHU	Museum für Naturkunde der Humboldt-Universität,

	Berlin, Germany (visited by CRS and material loaned courtesy of Wolfram Mey)
NHRS	Naturhistoriska Riksmuseet, Stockholm, Sweden (information from Bert Gustafsson on types of *G. aurivilliusi*)
NMGM	National Museums and Galleries of Merseyside
NMK	National Museums of Kenya, Nairobi, Kenya
OXUM	Hope Entomological Collections, University Museum, Oxford, U.K. (visited by CRS and RIVW and material loaned courtesy of George McGavin)
SMNK	Staatliches Museum für Naturkunde, Karlsruhe, Germany (visited by CRS courtesy of Günther Ebert)
SMNS	Staatliches Museum für Naturkunde, Stuttgart, Germany (visited by CRS courtesy of Christoph Häuser)
ZSM	Zoologische Staatssammlung, München, Germany (visited by CRS courtesy of the late Dr Wolfgang Dierl)
ZMUH	Zoologische Museum, Universität von Hamburg, Hamburg, Germany
ZMUK	Zoological Museum, Københavens Universitet, Copenhagen, Denmark (visited by RIVW and material loaned courtesy of Dr Ole Karsholt)
ZISP	Zoological Institute, St-Petersburg, Russia (information on the Seba collection from A.L. Lvovsky)

Other abbreviations

CAR	Central African Republic
Spec.Reg.	BMNH Department of Entomology Specimen Register number. The Specimen Register is a specimen level database.
Code	International Code of Zoological Nomenclature. Fourth Edition (International Commission on Zoological Nomenclature, 1999).
ICZN	International Commission on Zoological Nomenclature.
HT, LT, PT, PLT, ST	Holo-, Lecto-, Para-, Paralecto-, Syn- type
ups	Upperside
uns	Underside

ACKNOWLEDGEMENTS We are grateful to those individuals listed above for allowing access to or loans from their institutions and for permission to use photographs of specimens in their care. Steve Collins in particular was a constant source of encouragement. In addition, we should like to thank Henk Bentje, Maurizio Bollini, John Boorman, David Hancock, Michel Libert, Rienk de Jong, Bernard Turlin, Eric Vingerhoet, and especially Torben Larsen for access to material, for information and for encouragement. We thank Colin Congdon for information on early stages and for the photographs reproduced here. Former colleague Julia Pope spent much time curating and databasing BMNH *Graphium* and finding obscure localities, and ably assisted CRS when he visited MRAC, IRSN and MNHN. Her role has been admirably taken over by Kim Goodger. Many thanks to both. Jack Gilbert, as volunteer and temporary member of BMNH staff, also helped with the difficult task of locating localities. We thank colleagues Brian Pitkin and Paul Williams for advice with the BMNH databasing system and WORLDMAP, respectively, and for developing techniques to link the two to produce the distribution maps, etc. Ian Kitching gave timely advice on cladistic coding and analytical techniques, but is in no way responsible for our lack of resolution. Ian also made an excellent job of reading the penultimate draft of the text. Thanks are also due to Janet Camp for transcribing Sevastopulo's manuscript accounts of early stages. Many of the photographs reproduced here were taken by the BMNH Photographic Unit, who also digitized them. Finally, we are immensely grateful to many colleagues – among whom Malcolm Scoble, Gaden Robinson and Phil Ackery should be singled out – for their encouragement and forbearance throughout this long project.

CLADISTICS

Coding and analytic methods

Complex morphological structures do not readily lend themselves to simple coding. The problem is to translate highly three-dimensional shapes we term 'organs' – formed by complex foldings and evaginations of the exoskeleton during ontogeny – into simple linguistic statements that can be further translated into numerical form, ideally as binary (0, 1) alternatives. Due to the often smooth transition from plain body wall into these shapes, these organs require delimiting (often by gestalt perception) before characters can be defined or prescribed. This represents a translation from Sir Karl Popper's 'World 1' of physical objects to his 'World 3' of 'objective contents of thought', specifically scientific thought (see, for example, essays in Popper, 1972). Thus a cladogram may be said to represent, not a branching diagram summarising the relationships of states of characters of organisms, but a branching diagram summarising the relationships of scientists' verbalized concepts of such characters. Other scientists may perceive and thus define and characterize the organs differently and it is necessary, therefore, to be as diligent in defining the characters and their states as possible. We have aspired to this ideal in the account that follows.

As far as possible we tried to use simple binary characters, preferably the presence *versus* the absence of a character or state (Pleijel, 1995). With some complex organs this required breaking down the overall character into a number of dependent characters which need not be mutually exclusive. This was done with the male terminal processes and dorsal projection (see below). In some cases, however, we were unable to define such dependent characters due to the variety and complexity of the organs concerned (such as the male dorsal and ventral harpes). In these cases we were forced to employ multistate characters to describe the organs. We are aware that there is still controversy as to how such characters should be analysed (Forey & Kitching, 2000, I.J.Kitching, pers. comm.), so have made our analyses both with and without this and the other two multistate characters. We are clear that ordering the character states – implying the steps required to get from any one state to another – indicates some relationship *a priori*, so have set these characters to be non-additive or unordered.

The data tables were managed using Winclada (BETA) ver. 0.9.9 (Nixon, 1999) and analysed using Nona (Goloboff, 1994). The resulting trees were then examined using Winclada. A variety of search parameters were used, principally a heuristic search with Nona set to find the maximum number of trees it could handle (20000). The number of replications was set to 200, 100 starting trees per replication, and the search strategy set as 'Multiple TBR + TBR (mult*max*)'. Ratchet (island hopping) was also tried and gave similar results.

Outgroup taxa

Choice of taxa to employ as outgroups was dictated primarily by the questions that we set ourselves to answer. In order to test the monophyly of the afrotropical species (as subgenus *Arisbe* within the context of the genus *Graphium*), we included members of the other nominal subgenera, *Pazala*, *Pathysa*, *Paranticopsis* and *Graphium s.s.*. We also included species from genera shown by previous studies (e.g. Hancock, 1983; Miller, 1987) to be basal to *Graphium* within the Leptocircini. This, we hoped, would provide a correct context for the relationships suggested by our analyses.

Characters used in the cladistic analysis

What follows is an account of the 63 numbered characters that we recognized. The data matrix is given below as Appendix I. We hope that our descriptions are, at the very least, sufficient to allow others to make and explore alternative codings, if they wish to do so. These include 11 characters taken from Miller (1987), referring to systems we have not examined in detail ourselves, and that relate mainly to higher level relationships within the Leptocircini. We have selected among these only characters that we consider well established and not obviously highly homoplastic. Our purpose in using these characters is to give some structure to the base of the cladogram.

1. Pupal shape: elongate = 0; squat = 1.

Miller (1987) cited Igarashi's (1979) figure of the pupa of *Protographium leosthenes*, which shows it to be squat in comparison with the elongate pupae of *Iphiclides*, *Lamproptera* and *Graphium*. According to Miller (1987), the pupa of *Eurytides marcellus* (now included in *Protographium*: Tyler *et al.*, 1994) is also blunt. Various other neotropical leptocircines now included in *Mimoides* Brown also possess squat pupae (Tyler *et al.*, 1994).

2. Papillae anales shape: rounded = 0; elongate = 1.

The papillae anales are paired, sclerotized structures surrounding the anus (Fig. 13). In most of the afrotropical species and all our outgroups they are smoothly rounded distally, giving a D-shaped outline. In the *adamastor*-group and *philonoe*, by contrast, the dorsal margin is expanded posteriorly to distort that regular curve.

3. Aedeagus shape: blunt = 0; pointed = 1.

Miller (1987) reported that the aedeagus of *Iphiclides*, *Lamproptera* and *Graphium* is drawn to a point distally (*G. (Pathysa) nomius* he considered an exception). By contrast, that in *Protographium leosthenes* is rounded and that of *Eurytides telesilaus* is also relatively blunt (Miller, 1987, fig.28).

4. Tegumen shape: broad = 0; narrowed = 1.

According to Miller (1987), the dorsolateral portion of the tegumen is broad and robust in most papilionids, including *Protographium* and *Eurytides*. In *Iphiclides*, *Lamproptera* and *Graphium*, the tegumen is dorsolaterally narrowed.

5. Pupa with dorsal horn: absent = 0; present = 1.

Miller (1987) observed, citing Igarashi (1979), that the pupae of *Lamproptera* and most *Graphium* are produced anteriorly into a horn, sometimes extending beyond the head.

6. Hindwing discal cell size: normal = 0; reduced = 1.

Miller (1987) cited Munroe (1961) in observing that the hindwing discal cell in *Lamproptera* is much reduced compared with that in other Papilionidae. Apparently autapomorphic.

7. Forewing R_5 origin: long-stalked with R_4 = 0; arising from R_{3+4} = 1.

Another autapomorphic character of *Lamproptera* for which Miller (1987) cited Munroe (1961). In most Leptocircini, forewing vein R_3 arises separately from the discal cell, with R_4 and R_5 long-stalked (see Fig. 7). In *Lamproptera*, R_3 and R_4 are long-stalked, with R_5 arising from their common stalk.

8. Forewing R_1: free = 0; fused with Sc = 1.

Miller (1987) observed that in two leptocircine groups, the *Eurytides dolicaon*-group and the genus *Graphium*, forewing vein R_1 fuses with the subcostal vein (Sc).

However, he pointed out that in the former, the vein is quite long, the anastomosis being well beyond the discal cell (see Miller, 1987: fig. 154), whereas in *Graphium* the vein is very short, the anastomosis being proximal to the tip of the discal cell (see Fig. 7). In other Leptocircines, the two veins do not anastomose.

9. Juxta: glabrous = 0; setose = 1.

Miller (1987) observed that the juxta is setose in *Graphium*. He pointed out that, while the juxta appears to be absent in *G.* (*Pathysa*) [*sensu lato*] the area of membrane at the appropriate position is 'covered with a dense mat of setae,' which he observed in no other Papilionidae.

10. Final larval instar thoracic segments and abdominal segment 10: plain = 0; tuberculate = 1.

The first instar larvae of *Lamproptera* and *Graphium* have long tubercles on the three thoracic segments and on abdominal segment 10. [Miller (1987) also claimed that, in addition, short, setose tubercles are found in final instar larvae in *Graphium* alone, but this requires confirmation.]

11. Horn-like signum: absent = 0; present = 1. (From Miller, 1987).

According to Miller (1987), who also cited Munroe (1961) and 'all subsequent researchers', the signum in *Graphium* other than *G.* (*Pazala*) occurs as a long, narrow, horn-like invagination into the bursa copulatrix.

12. Bundled androconial scales: absent = 0; present = 1. (From Miller, 1987).

Miller (1987) discussed various forms of deciduous scale in leptocircines. In particular, he identified and illustrated (as fig.101) a type unique to *Graphium* other than *G.* (*Pazala*). They occur in small packets or bundles, each of which arise from a single socket in the fold of the inner margin of the hindwing of the male. The filaments are deciduous and they are believed to act as PTPs – particles that help transfer pheromones to the female antennae during courtship (see Boppré, 1984). They have apparently been secondarily lost in *G. ridleyanus*.

WING-SHAPE, PATTERN AND SCALE CHARACTERS (13–28)

In preparing this work, as already discussed in general terms, we have encountered various difficulties of character description and coding. These have included unsolved problems regarding homology of the forewing discal cell-bars between the sword-tails, and the *angolanus*-, *adamastor*- and *leonidas*-groups, etc., difficulties that have been compounded by variability. Even a seemingly obvious character like hindwing tails (present *vs* absent) gives rise to problems, such as those presented by the existence of short tails *vs* crenulations of the hindwing margin. Inappropriate coding can easily lend unwitting support to paraphyletic groupings or worse, and we are by no means convinced that we have avoided such pitfalls, especially with regard to the many conditional or dependent characters listed below.

Wing-shape (13)

13. Hindwing vein M3 extended as tail: absent = 0; present = 1.

The 'swordtail' character that gives these butterflies their colloquial name, but which is far from universal. It consists of a long extension of hindwing vein M_3 with a broad extension of the surrounding membrane (Fig. 7). This feature is not present in the *adamastor*-group, *angolanus*-clade (though some taxa exhibit deeper scalloping of the wing margin, and even a short, pointed tail at M_3 in *angolanus baronis* itself), or *leonidas*-group, and some other species. In our suite of potential outgroup species it is present in *G.* (*Pathysa*) *aristeus*, *G.* (*Pathysa*) *nomius*, *G.* (*Pazala*) *mandarinus*, *Lamproptera meges*, *Iphiclides podalirius* and *Protographium leosthenes*; but not in *G.* (*Paranticopsis*) *macareus* or *G.* (*G.*) *sarpedon*.

Forewing discal cell transverse bars (characters 14–16)

14. Forewing discal cell transverse bars: absent = 0; present = 1.

Hancock (1993) drew a distinction between the angle of the bars which cross the forewing discal cell. In the swordtailed species, the bars are at right angles to the posterior discocellular vein, and at an obtuse angle to the line of veins M_2 to CuA_2 (see Fig. 8). The most basal bar is sometimes restricted so that it barely penetrates into the cell, but is present in the costal cell. In all the tail-less taxa, the bars – often represented by rows of spots or other marks – are more-or-less in line with veins M_2 to CuA_2 (see Fig. 9), and sometimes (as in *G. leonidas*) with elements nearly parallel to the posterior discocellular vein. It is thus very difficult to equate the bars in these taxa with any of the discal marking of the swordtailed species; it is equally difficult to homologize them between the non-tailed groups. For the non-tailed species we have therefore scored them as absent for the transverse bars (as narrowly defined) and as inapplicable (-) for the particular character states. Of our chosen outgroups, *Lamproptera meges* and *Iphiclides podalirius* have just four bars, *G.* (*Pathysa*) *aristeus* and *G.* (*Pathysa*) *nomius* have a fifth, and *G.* (*Pazala*) *mandarinus* has a sixth. We interpret *Lamproptera meges* as not being barred. Among the African swordtailed species, the bars can be seen faintly on the underside in *G. kirbyi*, but in *G. illyris* the bars have presumably been completely obfuscated or secondarily lost.

15. Transverse bar 5: absent = 0; present = 1. Apart from *G. illyris*, all African swordtailed *Graphium*, including *G. antheus* and *G. evombar*, have a fifth bar, as also seen in *G.* (*Pathysa*) species.

16. Transverse bar 6: absent = 0; present = 1. All African swordtailed *Graphium*, excluding *G. antheus* and *G. evombar*, and *G. illyris* possess a sixth, incomplete distal bar, usually represented by a mark at the radial vein (Fig. 8). *G.* (*Pazala*) *mandarinus* also has 6 bars, the sixth interrupted.

Hindwing underside rubral system (characters 17–24)

On the underside of the wing of swordtailed afrotropical *Graphium* is a series of red marks constituting what Schwanwitsch (1943) referred to as the rubra (stripe R^1). This system is most complete in *G. polistratus*, where a red element occurs in every cell (Fig. 177). However, the stripe is most striking in *G. policenes* and its close relatives (Figs 181–183), where it is generally broadest, but absent from cell M_1. Apart from the swordtailed species, rubral elements are found in members of the *angolanus*-group (where in most the colour is transposed to orange; the peculiar coloration of *G. ridleyanus* makes it difficult to score, as is also the case for the two members of the *tynderaeus*-group), and in some outgroup species. When any part of the system is present, it is always represented in cells CuA_1 and CuA_2, so scoring for its presence in these cells would be redundant. Since the system can be represented in any or all of the other cells of the hindwing, we score these separately. In some cases, a scattering of reddish scales is difficult to interpret as a clear indication of a rubral mark: these are scored as '?'. Taxa without any elements of the rubral system in evidence are scored as '-' separately for each element.

17. Hindwing underside rubral system: absent = 0; present (at least in part) = 1.
18. Rubral element in costal cell: absent = 0; present = 1.
19. Rubral element in cell R_1: absent = 0; present = 1.
20. Rubral element in cell R_5: absent = 0; present = 1.
21. Rubral element in discal cell: absent = 0; present = 1.
22. Rubral element in cell M_1: absent = 0; present = 1.
23. Rubral element in cell M_2: absent = 0; present = 1.
24. Rubral element in cell M_3: absent = 0; present = 1.

Basal markings of hindwing underside (characters 25, 26)

25. White tuft at base of hindwing underside: absent = 0; present = 1.
The bases of the underside hindwing of many non-swordtailed species possess a tuft of white scales on the subcostal and cubital veins where they merge proximal to the discal cell. The effect of the tuft is emphasized (to human eyes) by being surrounded by an area of black scales. This character is seen in all members of the *adamastor*-group and is also found in the *leonidas*-group and *G. philonoe*. Though other taxa may show similar features (e.g. some members of the *angolanus*-group have white scales, but not on the veins, nor set in a black milieu), they lack the combination of features that makes the character so striking.

26. Hindwing cell R_1 with black basal mark: absent = 0; present = 1.
Several members of the *adamastor*-group have a black spot, sometimes extended into a streak, near the base of hindwing cell R_1. In *G. auriger*, the whole basal area is dark, obscuring any mark, so the character is scored '?'. There is some homoplasy evident in the character as similar marks occur in other species, notably *G. tynderaeus*, *G. latreillianus* and *G. ridleyanus* (in this last case, possibly associated with mimicry of *Acraea*).

Scales (characters 27, 28)

In examining the wing patterns in an attempt to discover more characters, we observed that in some species the pale marks of the upper side are covered with normal sized, pigmented covering scales. In other species, the scales are reduced to just fine hairs, and the colour of the mark is thus that of the pigmented patch of the wing membrane. This type of scaling and pigmentation is also found in some Indo-Australian *Graphium* (Allyn *et al.*, 1982). In the african species there is sometimes a difference between the condition on the forewing and that on the hindwing. We have therefore been able to define two characters, both of which appear to be fairly homoplastic.

27. Upperside forewing pale spots with broad scales: absent = 0; present = 1.
28. Upperside hindwing pale spots with broad scales: absent = 0; present = 1.

GENITALIA (CHARACTERS 29–63)

The genitalia of Lepidoptera are often a rich source of characters independent of considerations such as mimicry (which can affect colour patterns very strongly), and *Graphium* is no exception. The nomenclature of the male and female genitalia as employed in this study is illustrated in Figs 10 to 13.

Male genitalia (characters 29–55)

Characters of the valve (characters 29–52)

Terminal processes (*characters 29–39*). The distal area of the valve of all afrotropical *Graphium* has two extensions, here termed the *dorsal* and *ventral terminal processes*. Of the outgroups, structures similar enough for us to have scored as present are exhibited by *G.* (*G.*) *sarpedon* (Fig. 67) and *G.* (*Pazala*) *mandarinus* (dorsal only – Fig. 68). Of the potential outgroup taxa, most lack what may be interpreted as a dorsal terminal process. In *G.* (*Graphium*) *sarpedon*, there is a rounded extension to the tip of the valve dorsally, separated by a deep notch from an area of serration along the valve edge. These appear to be homologous to the dorsal and ventral terminal processes, respectively. In *G.* (*Pazala*) *mandarinus* the postero-distal edge of the valve is serrate and produced ventrad into a tooth (notched at the tip).

The postero-ventral area of the valve of *Iphiclides podalirius* (Fig. 73) is extended to a point, and there is a notch on the ventral edge. It is possible that these are homologous with the two processes, modified allometrically, but we are doubtful enough to score them as '?'. Both of these scores are open to reinterpretation.

Dorsal terminal process (*characters 29–34*)

29. Dorsal terminal process: absent = 0; present = 1.

When present, this structure seems to conform to a few basic patterns, although it shows a wide variety of subtle variation among the species. It arises from the posterior edge of the valve, usually a little below the dorsal margin, often allowing the emergence of the dorsal harpe (*q.v.*) above it. The structure curves mesad and is often either toothlike in form itself, or is terminated by a small tooth. We have been able to extract four binary characters, for which those taxa that lack the process are scored as '-'

30. Dorsal terminal process gross shape: claw-like = 0; a mesad flange = 1.

The condition shown in *antheus* (Fig. 14) and *evombar* (Fig. 15) is radically different from the other afrotropical species, with a talon-like array of 3 or 4 very stout, claw-like teeth. In all the other afrotropical species there is a generally broader, unitary structure that curves mesad and terminates with at least one ventral tooth (apparently lacking in Asian *G.* (*G.*) *sarpedon*, Fig. 67). We believe the two structures are homologous as indicated by their position and by the way in which the teeth are directed mesad.

Those taxa with the talon-like teeth score '-' for the following four characters.

31. Dorsal terminal process with flange: tapering = 0; chisel-shaped = 1.

In most species, the process tapers to a ventral tooth, even if it is expanded dorsally proximally. In the *adamastor*-group (Figs 44–64), the process is relatively broadly based and quadrate. It curves mesad and terminates in a straight edge which is prolonged ventrally into a tooth. Although broad, it is not expanded dorsally to be contiguous with the dorsal valve rim; it curves around the vertical dorsal harpe. *G. philonoe* (Fig. 43) has a similar structure: curved mesad and fairly broad at the tip, but excavated dorsally to accommodate the elongate dorsal harpe. *G. porthaon* (Fig. 31) also seems to fall into this pattern. Though narrowed basally to accommodate the large dorsal harpe, it expands dorsally towards the tip to form a similar straight edge. The mesal/terminal edge is somewhat flattened. Our coding of these two species, especially *G. porthaon*, as similar to the *adamastor*-group is open to reinterpretation.

32. Dorsal terminal process with dorsal expansion: absent = 0; present = 1.

In the *angolanus*- (Figs 32–37) and *leonidas*- groups (Figs 38–40) and in *tynderaeus* (Fig. 41) and *latreillianus* (Fig. 42), the process is expanded dorsally, completely enclosing the dorsal harpe. The dorsal edge of the process is contiguous with the dorsal rim of the valve. The whole organ is curved mesad and there is a tooth ventrally at the tip.

33. Dorsal terminal process with basal tooth: absent = 0; present = 1.

In *G. policenes* (Fig 25, 27) and its very close relatives (*liponesco*, *biokoensis* and *policenoides* Figs 26, 28–30), in addition to the ventrad tooth at the tip of the process, there is a further, ventrad directed tooth arising from the base of this. In *liponesco*, this basal tooth is larger than the terminal tooth, whereas it is the smaller in the other three species. There is no such basal tooth in *polistratus* or *junodi*.

N.B. *G. kirbyi* (Fig. 16), *junodi* (Fig. 17), *polistratus* (Fig. 18), *colonna* (Fig. 19), *illyris* (Fig. 20–23) and *gudenusi* (Fig. 24), all score '1' for character 30, but '0' for characters 31–33, having just the simple process with a single, ventral terminal tooth.

34. Dorsal terminal process with serrations: absent = 0; present = 1.

In addition to the prominent teeth and other features described above, the terminal process may carry finer serrations. This appears to be a rather homoplastic feature, and it may also prove to exhibit intraspecific variation.

Ventral terminal process (characters 35–39)

35. Ventral terminal process: absent = 0; present = 1.

This structure, when present, comprises a simple, terminal extension to the valve edge in the form of a point or lobe, arising below the dorsal process, and is often serrate or denticulate. In several taxa it is more-or-less sessile, being represented by an area of serration along the valve edge. When clearly developed, various forms occur and we have been able to describe four binary characters, in which there is some homoplasy. Some combinations of these characters are possible, but the presence of some renders others impossible. We interpret the area of denticulation on the valve margin of *G.* (*Graphium*) *sarpedon* (Fig. 67) as homologous; the small notch on the ventral margin of the valve of *I. podalirius* (Fig. 73) may represent a similar structure, but we are less confident.

36. Ventral terminal process: sessile = 0; projecting = 1.

In the majority of species, the process clearly projects from the valve. In some species, however, it is only indicated by the presence of denticulation on the edge of the valve below the dorsal terminal process. Such taxa must be scored as '-' (inappropriate) for character states describing the nature of any projection. *G. policenes* appears to be polymorphic for the feature.

37. Ventral terminal process with denticulation: absent = 0; present = 1.

In the majority of species, the process is denticulate; in some species, such as *antheus* (Fig. 14) and *evombar* (Fig. 15) and in *G. almansor* (Figs 51, 52), the process is toothless. This state would appear to be a secondary loss. In several species, the presence of the otherwise sessile process is only revealed by the denticulation.

38. Ventral terminal process with point: absent = 0; present = 1.

In the majority of species with a projecting process, it is rounded or blunt. In several others, however, it comes to a point. The pattern of its occurrence suggests homoplasy.

39. Ventral terminal process with down-curve: absent = 0; present = 1.

In just three species, *almansor* (Figs 51, 52), *hachei* (Fig. 61) and *auriger* (Fig. 53) the process appears distinctly down-curved. In *hachei* and *auriger* it is blunt and denticulate. In *almansor* it is not denticulate but is sharply pointed, a form that appears to be autapomorphic for this polytypic species.

The dorsal projection (characters 40–46)

40. Dorsal projection: absent = 0; present = 1.

We use this term to refer to the prominent, more-or-less elongate extrusion from the inner valve wall at, or just below, its dorsal margin anterior to the dorsal harpe; it carries an array of stout setae (see Figs 10, 11). Munroe (1961), Miller (1987) and Hancock (1993) refer to it as the 'dorsal process'; we use the term dorsal projection to differentiate from the dorsal terminal process and the dorsal element of the harpe. It is found in similar form in all afrotropical *Graphium* except *G. antheus* (Fig. 14) and *G. evombar* (Fig. 15), where there is a setose hump posterior to the dorsal element of the cruciform harpe (*q.v.*), which we take to be the same organ, but in a sessile form (see below). Interpretation of our outgroups is in some cases problematic. It is clearly present in *G.* (*Paranticopsis*) (Fig. 65) and *G.* (*Pathysa*) (Figs 69, 70). In *G.* (*Pazala*) *mandarinus* (Fig. 68) there is a similarly placed structure of rather different form that we regard as probably homologous. In *G.* (*G.*) *sarpedon* (Fig. 67) there is a setose cylindrical projection in a similar position, but also a much less prominent structure somewhat anterior to this that also bears setae. *G.* (*G.*) *bathycles* (Fig. 66) has a less prominent, but setose, protuberance from the top of the valve, dorsal to the harpe. We score all of these as having the structure present as either erect or sessile. We have observed no similar organ in the extra-generic outgroups.

When present, and erect, we have been able to discern a variety of scoreable character states; when it is absent, these are scored as '-' (inappropriate).

41. Dorsal projection aspect: sessile = 0; erect = 1.

As mentioned, in *G. antheus* (Fig. 14) and *G. evombar* (Fig. 15) there is merely a hump with an array of stout setae. Some *G.* (*Pathysa*) (Fig. 70) and *G.* (*Paranticopsis*) *macareus* (Fig. 65) also have sessile 'projections', though in these taxa the setae are generally much stouter (see Munroe, 1961).

When sessile, the following characters must be scored as '-'(inappropriate).

42. Dorsal projection cross section: cylindrical = 0; compressed = 1.

In the *adamastor*-, *angolanus*-, and *leonidas*-groups, and in *latreillianus*, *tynderaeus*, and *philonoe* (Figs 32–64) – in other words, the non-swordtailed species – the projection is nearly circular in cross section throughout its length, though with much variation in size and orientation. For example, in *tynderaeus* (Fig. 41) it is very long and thin, whereas in *latreillianus* (Fig. 42) it is much shorter and stouter; *latreillianus* also exhibits a slight dorsal expansion distally. In both of these species, and in others, the projection is directed ventrad at its base before curving dorsad; in others it is almost horizontal, angled dorsad from the base, or even slightly ventrad. In some species it is angled posteriad, in others it is more or less normal to the valve wall, and in some, angled slightly anteriad. In the sword-tailed *G. porthaon* (Fig. 31) the projection is cylindrical distally, but arises from a very broad base. It is angled markedly ventrad basally before turning equally sharply dorsad about half way to end level with, or even a little above, the valve rim. We score this as cylindrical. In the remaining African swordtailed species with an erect projection (i.e. excluding *antheus* and *evombar*), the cross section is somewhat dorso-ventrally compressed basally, though sometimes with modifications described in the following three characters.

43. Dorsal projection base: broad = 0; narrow = 1.

In all of the swordtailed species (excluding *antheus* and *evombar*), members of the *angolanus*-group (apart from *endochus*, Fig. 33), and *philonoe* (Fig. 43) the projection tapers from a broad base. In the remainder, the diameter of the projection is much more constant, tapering only a little at the base.

44. Dorsal projection sides: tapering (triangular) = 0; parallel basally = 1.

In *junodi* (Fig. 17), *polistratus* (Fig. 18), and *colonna* (Fig. 19) the dorsal projection arises from a broad base and narrows continuously to the tip. In *polistratus* and *junodi*, it is nearly horizontal, dipping slightly distally; in *colonna*, however, it is sharply curved ventrad to wrap around the dorsal harpe and overlap the ventral harpe. In the remaining species, even those with a broad base, tapering is restricted to the basal area, with the distal portion more constant in size, or even expanded (see 46).

45. Dorsal projection twist: absent = 0; present = 1.

In *kirbyi* (Fig. 16), *junodi* (Fig. 17) and the *policenes*-group (Figs 25–30) the projection gives the distinct impression of being twisted distally, such that the antero-dorsal margin comes to lie much more ventrally. This is not shown in other species.

46. Dorsal projection distal expansion: absent = 0; present = 1.

Some species exhibit an expansion of the dorsal margin of the distal part of the projection. This could be give the appearance of a twist, but both can occur together, as in *kirbyi* (Fig. 16) and the *policenes*-group (Figs 25–30), yet in others such as *illyris* (Figs 20–23), *gudenusi* (Fig. 24), and also *latreillianus* (Fig. 42), the expansion is present without any twist. Other species lack either feature.

The Harpe (characters 47–51)

The harpe (sometimes referred to as the clasper, e.g. Miller, 1987) is a large and complex evagination from the mesal wall of the valve found in many Papilionidae, including all of our outgroup taxa.

47. Harpe: entire = 0; subdivided = 1.

In most afrotropical *Graphium*, and in some of our outgroup taxa, the harpe consists of two elements (Figs 10, 11). For convenience we name these the dorsal harpe, which projects from the wall near the dorsal edge, between the dorsal projection and the dorsal terminal process; and the ventral harpe, which is usually in the form of a flange along the inner wall of the valve, below the centre. The two are indicated as being part of the same structure by the presence in some taxa of a thickening of the valve wall linking them. This impression is reinforced by the form of the harpe in *antheus* and *evombar*, and in some outgroups, assuming the structures are homologous. In *antheus* (Fig. 14) and *evombar* (Fig. 15), the dorsal and ventral elements of the harpe are clearly connected by a free edge curving between them posteriorly. The ventral part is almost triangular in section and comes to a ventro-posteriorly directed point. There are a series of small serrations along the mesal edge. The dorsal element is more complex, being subdivided into a number of denticulate teeth. In *Protographium leosthenes* (Fig. 72) the structure is triangular, extending ventrad and posteriad from the dorsal margin. It appears to lack the dorsal element referred to in the following character, 48. *Iphiclides podalirius* (Fig. 73) and *Lamproptera meges* (Fig. 71) are more difficult to interpret, but we believe that they should also be considered to be 'entire', albeit in reduced form. *G.* (*Graphium*) *bathycles* (Fig. 66) has a harpe, but with the addition of a broad, serrate vertical extension from the edge connecting the dorsal and ventral elements, while *G.* (*Pazala*) *mandarinus* (Fig. 68) is scored with this state, though the lower element is divided into two parallel horizontal lamellae. *G.* (*Paranticopsis*) *macareus* (Fig. 65), *G.* (*Pathysa*) *aristeus* (Fig. 69) and *G.* (*Pathysa*) *nomius* (Fig. 70) have subdivided harpes, the latter with an additional triangular, serrate blade arising dorsal to the ventral harpe, which is directed somewhat ventrad. In fact, Miller (1987) used, 'Clasper composed of three parts' as a character helping to define the genus and claiming it to be typical of subgenera *Pazala*, *Pathysa*, and *Arisbe*. Our own studies have indicated that this tripartite arrangement is unusual in African species, being indicated only in *philonoe* (Fig. 43) and the *angolanus*-group where it seems to be of different origin (see character 51, state 5). *G.* (*Graphium*) *sarpedon* (Fig. 67) appears to have just the dorsal harpe. When the harpe is entire, the presence/absence and form of both the dorsal and ventral harpes must be scored as '-' (inappropriate).

The dorsal harpe (characters 48–49)

48. Dorsal harpe: absent = 0; present = 1.

The dorsal harpe is present in all the taxa in our analysis that have the harpe subdivided.

49. Dorsal harpe shape (multistate)

The organ is very varied in form in afrotropical *Graphium*, and some of these forms are quite complex. As a result, we have been unable to distinguish discrete, binary characters and so have been forced to adopt a single, multistate character.

The character states we have recognized are:

simple projection = 0;

Though in many ways dissimilar, both *G. kirbyi* (Fig. 16) and *G. colonna* (Fig. 19) have similar dorsal harpes in the form of a simple posteriorly (and slightly dorsally) directed spike, extending beyond the valve margin. In *G. colonna* it is cylindrical; in *G. kirbyi*, cylindrical basally, flattened and serrate at the tip.

simple hook = 1;

All members of the *adamastor*-group (Figs 44–64) have a simple, vertical hook that is more-or-less wrapped around posteriorly by a transom-like dorsal terminal process.

serrate, horizontal arc = 2;

In the *leonidas*-group (Figs 38–40) the dorsal harpe is quite short and horizontal. The posterior edge is laterally compressed and more-or-less arcuate (shallowly in *leonidas*, Fig. 38, strongly in *cyrnus*, Fig. 40) and deeply serrate. The dorsal terminal process is expanded and curves around the structure posteriorly so that it is entirely within the valve margin.

horizontal, laterally compressed, serrate = 3;

In the *angolanus*-clade (Figs 32–37), the harpe is horizontal. It is laterally compressed distally into a vertical plate the edge of which is serrate and it curves mesad. The dorsal terminal process is expanded around the harpe.

horizontal, cylindrical, bifid = 4;

More dubious as a homology, but the resemblance is suggestive. In *G. tynderaeus* (Fig. 41) the harpe is elongate and divided near the base into two branches, one posteriorly directed, the other more mesad, each with a pointed tip, but unadorned with serrae. That in *G. latreillianus* (Fig. 42) is much shorter and the posterior ramus is serrate dorsally. In *G. philonoe* (Fig. 43), the posterior ramus, slightly serrate dorsally near the tip, extends beyond the valve margin.

horizontal, acuminate, serrate = 5;

The dorsal harpe of the *policenes*-clade (Figs 25–30) is large, compressed, folded and serrate distally to resemble an exotic gable-end. The condition is not dissimilar to that in the *leonidas*-group, but there is no smooth curvature. The structure is large and projects beyond the valve margin.

with vertical and horizontal blades = 6;

G. junodi (Fig. 17) and *G. polistratus* (Fig. 18) share a similarly-shaped dorsal harpe having two laterally compressed 'blades': one nearly vertical (*junodi*) or angled (*polistratus*); the other projecting more nearly horizontally. The horizontal blade is broadly based along the basal part of the vertical; it has a ventrally directed hook at the tip in both species. The vertical blade is serrate along the mesal edge in both species. In *polistratus* the horizontal blade is serrate above; in *junodi* it is serrate below. This harpe may be seen as similar to the *policenes*-group, but with a part removed.

large, horizontal, compressed, serrate = 7;

G. illyris (Fig 20–23) also shows similarities to the *policenes*-clade. The dorsal harpe is large, horizontal, compressed and serrate distally. It is also slightly curved distally, but not acutely angled.

single compressed, obliquely angled = 8;

In *G. gudenusi* (Fig. 24) the dorsal harpe is a single, compressed, obliquely-angled blade, serrate distally and dorso-distally.

broad, compressed, spurred = 9;

G. porthaon (Fig. 31) has a broad, compressed blade with a long spur distally produced posteriorly well beyond the valve margin. The broad blade is serrate distally.

The ventral harpe (characters 50–51)

50. Ventral harpe: absent = 0; present = 1.

Among our outgroups that possess a subdivided harpe, *G. sarpedon* (Fig. 67) apparently lacks the ventral element. It is present in *G. (Pathysa) aristeus* (Fig. 69) and *G. (Pathysa) nomius* (Fig. 70) and in *G. (Paranticopsis) macareus* (Fig. 65), though in forms which do not appear to relate to those of the African species, so we have scored them as '-' (inappropriate) for the following character, as we have those species that lack the structure.

51. Ventral harpe shape (multistate):

In general, the structure forms a cylindrical or lamellar flange along the inner wall of the valve, normally projecting posteriorly from its root on the valve wall, so there is an 'external' (relative to the whole animal) or posterior edge as well as a mesal or anterior edge. As with the dorsal harpe, the variety and complexity of this organ has forced us to treat the character as an unordered multistate. Several of the states are autapomorphic.

a short vertical blade = 0;

In most species the root of the blade is more-or-less horizontal, even if the blade itself is angled. In both *G. junodi* (Fig. 17) and *G. polistratus* (Fig. 18), however, the root is largely in the vertical plane, so the major part of the blade is vertical with a narrow horizontal flange extending anteriad from the lower margin. In both species, the blade itself is short and subdivided into upper and lower lobes.

an elongate vertical blade = 1;

In *G. latreillianus* (Fig. 42) the blade is also vertically rooted, but elongate and concave like a gutter, curving mesad from base to tip.

cylindrical = 2;

In most species the blade is lamellate. In *G. tynderaeus* (Fig. 41), however, it is cylindrical (as is the dorsal harpe), elongate and divided into two rami distally.

a long, free, horizontal blade = 3;

In *G. philonoe* (Fig. 43) there is a long, free, horizontal blade, thickened basally, with a somewhat expanded, quadrate tip which is slightly serrate. There is also a small tooth-like element level with the anterior root of the ventral harpe, at the same horizontal level as the dorsal harpe. This does not appear to be homologous with the basal lamella of the *angolanus*-group as it is horizontal and is much more remote from the ventral harpe.

a posteriorly located, angled blade = 4;

The *policenes*-clade (Figs 25–30) also seems to hold together on characters of the ventral harpe. The blade is more-or-less normal to the valve wall, but at an angle to the horizontal, and ends level with – and close to – the small gap between the dorsal and ventral terminal processes. In *G. policenes* (Fig. 25), there are two broad 'teeth'; in *G. liponesco* (Fig. 26), these are themselves serrate; and in *G. policenoides* (Fig. 30), there are a few, deep serrations masking any subdivision.

with basal lamella = 5;

The members of the *angolanus*-clade (Figs 32–37) are united by the possession of a small serrate lamella at right angles to the valve wall and vertically aligned. In *G. endochus* (Fig. 33), this lamella is contiguous with the horizontal blade of the harpe. The small basal tooth in *philonoe* (Fig. 43) does not appear to be homologous. The horizontal blade is grossly or more finely serrate in all taxa and more-or-less explanate; in *G. angolanus* (Fig. 32) it is almost semicircular.

with palmate blade = 6;

In most afrotropical *Graphium*, the blade, though varying widely in size and shape, and in the presence and number of serrations, is more-or-less elongate. The members of the *leonidas*-group (Figs 38–40) have a distinctive palmate blade, broadening from a relatively narrow root before being subdivided into a number of stubby, rounded 'digits' (i.e. not acute serration).

a non-serrate, horizontal blade with vertical branch = 7;

The *adamastor*-group (Figs 44–64) share this pattern of a simple blade with a near-vertical blade arising from it basally. Within the group, the size of these two blades relative to each other and to the overall size of the valve varies (in *G. agamedes* (Fig. 45) the vertical blade is very small and in *G. abri* (Figs 49, 50) appears to have been lost altogether). In some taxa the ventral blade may be notched or subdivided apically, and there is some variation between individuals and even between different sides of the same individual.

a simple, elongate, serrate blade = 8;

In *G. kirbyi* (Fig. 16) and *G. illyris* (Fig. 20–23), the blade is elongate, more-or-less horizontally based and serrate along the margin. In *kirbyi*, the blade is long and narrow and terminates close to the dorsal terminal process. In *illyris*, it is widened level with the posterior end of its root into a broad triangle; the free posterior tip is level with the ventral terminal process. We score *G. colonna* here. Its blade is elongate, uniquely extending beyond the posterior margin of the valve dorsal to the dorsal terminal process and very close to the dorsal harpe. It is much less serrate than the other two, with just a large proximal tooth, but the overall appearance is not dissimilar to *G. kirbyi*.

a narrowly-based, triangular blade = 9.

In *G. gudenusi* (Fig. 24) and *G. porthaon* (Fig. 31) there is a very simple, horizontal, posteriorly-directed triangular blade. In *G. porthaon* it is non-serrate; in *G. gudenusi*, serrate. Whether the resemblance is anything other than homoplasy or plesiomorphy is dubious.

Other characters of male genitalia: (52–54)

52. Uncus: non-serrate = 0; serrate dorsally = 1.

G. antheus is apparently autapomorphic in having the uncus crowned with a serrate ridge; it is not present in *G. evombar*. The uncus of *Protographium leosthenes* is considerably longer than any of the other taxa in this study; *leosthenes* also has a pseuduncus (Miller, 1987).

53. Socii: sessile = 0; extended, prominent, free = 1.

Lateral to the uncus is a more or less prominent, usually setose ridge which we interpret as the socius (Klots, 1970). In all the non-swordtailed species, together with *porthaon*, this is extended as a prominent projection, as shown in Fig. 12. In the other swordtailed taxa the ridge itself is sometimes well-marked, but it does not extend into an elongate projection. *G.* (*Pazala*) *mandarinus* possesses paired, glabrous, horn-like projections, close to the uncus; they do not appear to be homologous.

54. Saccus: small = 0; large = 1.

We found that the saccus fell quite neatly into two size classes. *G. policenoides* (Fig. 10) exemplifies the larger size; a 'small' saccus would be about half of that. In practice, we found only *gudenusi* to be difficult to score. The distribution of character states appears somewhat homoplasious, with the *tynderaeus*-, *leonidas*-, *adamastor*-groups, together with *junodi* and *polistratus*, *illyris* and *kirbyi*, and all our outgroups having a small saccus. In all the *angolanus*-group, apart from *morania*, the *policenes*-group, *antheus* and *evombar*, *porthaon* and *colonna*, it was elongate.

Female genitalia (characters 55–63)

The female genitalia have been less exploited for characters than those of the male. This may in part be due to lack of available specimens, a factor that limited our own studies. However, we found that their study did reveal a number of useful features. A simplified diagram of the structures and the nomenclature we employ is shown as Fig. 13.

The vestibulum (55)

55. Cup-like vestibulum: absent = 0; present = 1.

The ostium bursae of afrotropical *Graphium* opens into a concavity termed the 'vestibulum' by van Son (1949), bounded posteriorly by folds (here termed 'labia': Fig. 13) formed from the sclerotized pleural region of the 8th segment (Miller, 1987). A very similar situation pertains in *G.* (*Pathysa*) *aristeus* (Fig. 107) and *nomius* (Fig. 108), *G.* (*Paranticopsis*) *macareus* (Fig.103) and *G.* (*G.*) *bathycles* (Fig. 104). *G.* (*G.*) *sarpedon* (Fig. 105) and *G.* (*Pazala*) *mandarinus* (Fig. 106) are both more difficult to interpret, having the depression bounded posteriorly by no more than a ridge, which may represent the reduction of the labia or be non-homologous. *Lamproptera meges* (Fig. 109) and *Iphiclides podalirius* (Fig. 110) apparently lack such a structure (as defined by posterior labia); in *Protographium leosthenes* (Fig. 111) there are paired posterior structures that may be homologous or merely analogous. Within the afrotropical species, we lack females of too many taxa to define subtler characters, though the similarity, for example, between the labia of *G. fulleri rileyi* (Fig. 99) and *G. kigoma* (Fig. 100) suggests that further study might be rewarding.

Ostium bursae (56)

The only character variable we have been able to identify for the ostium (which, after all, is merely an opening) is its position within the vestibulum.

56. Ostium bursae opening: posteriorly = 0; anteriorly = 1.

In most afrotropical *Graphium*, the ostium bursae opens anteriorly within the vestibulum, exceptions being *G. antheus* (Fig. 74), *G. evombar* (Fig. 75), *G. junodi* (Fig. 77), and *G. polistratus* (Fig. 78) and most members of the *angolanus*-clade (exceptions are *morania* and *schaffgotschi*; Figs 84–89). The situation is more variable with our outgroups, with the opening anterior in *G.* (*G.*) *bathycles* (Fig. 104) and *G.* (*G.*) *sarpedon* (Fig. 105); but posteriorly in *G.* (*Pathysa*) *aristeus* (Fig. 107) and *nomius* (Fig. 108), *G.* (*Paranticopsis*) *macareus* (Fig. 103), *G.* (*Pazala*) *mandarinus* (Fig. 106), *Lamproptera meges* (Fig. 109), *Iphiclides podalirius* (Fig. 110) and *Protographium leosthenes* (Fig. 111).

Ductus bursae (characters 57–59)

57. Ductus bursae: unsclerotized = 0; sclerotized = 1.

According to Miller (1987), in most Leptocircini (except *Lamproptera*) the ductus bursae is sclerotized at least from the ductus seminalis distad. If this is the case, it is only lightly sclerotized in the majority of afrotropical *Graphium*. However, in some species – the *angolanus*-clade (Figs 84–89), *polistratus* (Fig. 78), *colonna* (Fig. 79), *illyris* (Fig. 80), *gudenusi* (Fig. 81), *policenes* (Fig. 82), *porthaon* (Fig. 83), *leonidas* (Fig. 90) (but neither *levassori*, Fig. 91, nor *cyrnus*, Fig. 92), *philonoe* (Fig. 95), and *adamastor* (Fig. 96) (but no other members of that group we have examined) – sclerotization is noticeable. In the outgroups we have examined the condition is variable with the ductus well sclerotized in *G.* (*Graphium*) *bathycles* (Fig. 104) (but not *sarpedon*, Fig. 105), and *Iphiclides podalirius* (Fig. 110); not so in *G.* (*Pathysa*) *aristeus* (Fig. 107) and *nomius* (Fig. 108), *G.* (*Paranticopsis*) *macareus* (Fig. 103), or *Protographium leosthenes* (Fig. 111). The situation in *G.* (*Pazala*) *mandarinus* (Fig. 106) is less clear; we have scored it as '?' (not known).

58. Ductus bursae: straight = 0; kinked = 1.

The ductus bursae usually forms a simple tube connecting the bursa copulatrix to the ostium. In some taxa, however, it appears kinked or constricted just distal to the ductus seminalis. This occurs in several swordtailed species (but not *policenes*), the *angolanus*-clade (Figs 84–89), *leonidas* (but neither *levassori* nor *cyrnus*), *philonoe* and *adamastor* (but, again, no other members of that group that we have examined). In our outgroups, the condition is met with in *G.* (*Graphium*) *bathycles* and *Lamproptera meges*.

59. Ductus bursae: simple = 0; pocketed = 1.

The *angolanus*-clade (Figs 84–89) is also distinguished by having an expansion into a pocket of the sclerotized portion of the ductus just distal to the ductus seminalis. Curiously, this state is also found in *Lamproptera meges* (Fig. 109).

Central lobe (characters 60–61)

60. Central ostial lobe presence: absent = 0; present = 1.

Miller (1987) discusses three projections associated with the ostium bursae, a central lobe and two lateral lobes (see below). The central lobe appears to arise from the anterior margin of the ostium, so its position in the vestibulum varies with that of the ostium. It is present in all the afrotropical *Graphium* we have been able to examine, apart from the *angolanus*-clade (Figs 84–89). We regard similarly positioned structures seen in *G.* (*Graphium*) *bathycles* (Fig. 104) and *sarpedon*

(Fig. 105), and *G.* (*Pazala*) *mandarinus* (Fig. 106) as probably homologous; and one in *Iphiclides podalirius* (Fig. 110) more dubiously so. We found no such structures in *G.* (*Paranticopsis*) (Fig. 103) or *G.* (*Pathysa*) (Figs 107, 108), or in *Lamproptera meges* (Fig. 109) or *Protographium leosthenes* (Fig. 111).

61. Central lobe shape (multistate):

We have been able to distinguish six recognisable forms of the organ, but were unable to break this down into binary characters, so have had to resort to a multistate character. As with the dorsal and ventral harpe characters we see no way of determining the number of steps from one state to any other, so regard the character as unordered (non-additive).

very large, angled = 0;

In *G. antheus* (Fig. 74) and *G. evombar* (Fig. 75) the organ is very large and arises vertically before turning to produce a horizontal blade covering the ostium. The term blade may not be too fanciful: we found a part of an aedeagus – apparently broken or cut – in the ductus bursae of one female *G. antheus*. The aedeagus was not that of a *Graphium*! We cannot rule out a defensive function.

very large, not angled = 1;

In *G. junodi* (Fig. 77) and *G. polistratus* (Fig. 78) the organ is again very large, nearly occluding the vestibulum. Unlike *G. antheus* and *G. evombar*, however, it does arise from a vertical stalk. In both species, the lateral lobes are quite small.

long, narrow = 2;

In many other sword-tailed species (including *G. kirbyi*, Fig. 76, *G. gudenusi*, Fig. 81, *G. policenes*, Fig. 82, *G. porthaon*, Fig. 83) the process is narrow and relatively long, usually extending beyond the lateral lobes. *G. levassori* (Fig. 91) also has a long, narrow central lobe. In *G. leonidas* (Fig. 90), the lobe is relatively broad, but is parallel sided and exceeds the lateral lobes, so we have scored it with this state.

short, triangular = 3;

In *G. colonna* (Fig. 79) and *G. illyris* (Fig. 80), the central lobe is short, broad and triangular, not reaching the edge of the lateral lobes.

broad, bifid = 4;

In *G. tynderaeus* (Fig. 93), *G. latreillianus* (Fig. 94), and *G. philonoe* (Fig. 95) the organ is very broadly based and subdivided at the tip into two short branches.

large, broad, triangular =5.

In all of the *adamastor*-group examined (Figs 96–102), the central lobe is fairly large (often reaching to the tip of the lateral lobes, which are themselves quite large), broadly based and roughly triangular. There is some variation between species, particularly in the shape of the tip (some being indented, some truncate, etc.). The central lobe of *G. cyrnus* (Fig. 92) is similar (and scored here), though this is probably homoplasious.

Lateral ostial lobes (62)

62. Lateral ostial lobes: absent = 0; present = 1.

The lateral ostial lobes are paired growths emanating from the anterior wall of the vestibulum, as discussed by Miller (1987). They are present in all afrotropical *Graphium* except *antheus* (Fig. 74) and *evombar* (Fig. 75), where folds of the vestibulum wall may represent rudimentary homologues. They are clearly present in the *angolanus*-group, including *G. ridleyanus* (Fig. 89), *contra* Miller (1987). In afrotropical *Graphium* the lobes are setose and rugose, giving a fuzzy appearance, which Miller (1987) regarded as the single synapomorphy for his and Munroe's (1961) subgenus *Arisbe*, but we have seen similar fuzziness in other taxa; this is often very fine and makes scoring unreliable. SEM study might be revealing. Within those afrotropical *Graphium* that possess them, the size and shape of the lobes varies from small and lateral, not meeting mesally, to large and meeting or even overlapping, but there seems to be almost a continuum and we have not been able to characterize scoreable states within this variation. In our outgroups, presence of lateral lobes is very variable. They are seen as narrow, elongate structures in *G.* (*G.*) *bathycles* (Fig. 104), similar to those in *polistratus* (Fig. 78), but absent from, or rudimentary in, *G.* (*G.*) *sarpedon* (Fig. 105). They are small in *G.* (*Pathysa*) *aristeus* (Fig. 107), rudimentary (at most) in *G.* (*Pathysa*) *nomius* (Fig. 108), but large in *G.* (*Paranticopsis*) *macareus* (Fig. 103). In *Iphiclides podalirius* (Fig. 110) there is a sclerotized area extending anteriorly from the ostium as a flange with a free margin that may possibly be homologous, but they are clearly present in both *Lamproptera meges* (Fig. 109) and *Protographium leosthenes* (Fig. 111).

Anterior apophyses (63)

63. Anterior apophyses: absent = 0; present = 1.

In the majority of species, the folds of the eighth sternite that enclose the vestibulum are produced laterally in an anterior and slightly dorsal direction, to form paired apophyses (Fig. 13). According to Miller (1987) this character is present in all Leptocircini and most other papilionids. They are present in all afrotropical *Graphium* apart from *G. antheus* and *G. evombar*. Within the outgroups, they are found in *Protographium leosthenes*, *Iphiclides podalirius*, *Lamproptera meges*, *G.* (*G.*) *bathycles*; but not in *G.* (*Pazala*) *mandarinus*, *G.* (*G.*) *sarpedon*, *G.* (*Pathysa*) *macareus*. In the one specimen of *G.* (*Pathysa*) *nomius* so far examined there is a small apophysis present on the right side only.

Results of the cladistic analysis

General considerations

Regrettably, our data has proved inadequate to be able to recover a comprehensive and robust cladogram. What conclusions we may draw from the analyses must therefore be treated as tentative. Even so, we feel they give us sufficient information to comment on previous classifications. This serves to emphasize that more data are required (see Conclusions, below).

When we analysed our data set with all taxa and all characters active (multistate characters as non-additive or unordered), we obtained 12490 trees of length 189 steps (CI = 43; RI = 80), but a strict consensus reduced this virtually to a bush, with only the following groups recovered:

A clade composed of *tynderaeus* + *latreillianus*,
A clade with *G.* (*Pazala*) *mandarinus* the sister of *antheus* + *evombar*,
A clade comprising *policenes*, *liponesco*, *biokoensis* and *policenoides* as a polytomy,
A clade confirming the existence of an *angolanus*-group composed of *angolanus*, *endochus*, *morania*, *schaffgotschi*, *taboranus* and *ridleyanus*, with *morania* sister to the remainder.

To reduce greatly the number of possible trees, to speed up the analyses, and avoid difficulties arising from missing data (Strong & Lipscomb, 2000) and problematic optimisation, we subsequently excluded most species for which we lack data from females. This applied mostly to members of the otherwise well-defined *adamastor*-group, where we were unable to dissect females of *hachei*, *simoni*, *schubotzi*, *poggianus*, *abri*, *olbrechtsi* and *aurivilliusi*. We did include *G. policenoides*, as a check on the integrity of the *policenes* clade, for which females are only known with confidence for *policenes* itself. We also excluded all but three of the *angolanus*-group, retaining *angolanus*, *endochus* and *ridleyanus*.

Figs 5 and 6 show two strict consensus trees derived from our data set: one in which the three multistate characters (nos 49, 51, 61) were included in the analysis (as unordered or non-additive); the other in which the multistate characters were deactivated. We present both, as there is still some uncertainty as to the best way of handling multistates and their subsequent meaning in analysis (Forey & Kitching, 2000, I.J. Kitching, pers. comm.)

It will be seen that there is a fair degree of consistency between the two diagrams, some areas in which resolution is greater in one diagram, but not supported (albeit not contradicted) in the other, and a few conflicts.

Our initial questions

To deal with the questions asked above in turn:

We have not been able to recover a monophyletic clade including all afrotropical *Graphium* to the exclusion of all other taxa. Whenever they were included in the analyses, *G.* (*Graphium*) *sarpedon*, *G.* (*Graphium*) *bathycles*, *G.* (*Pazala*) *mandarinus*, *G.* (*Paranticopsis*) *macareus* all occurred within the structure. There does appear to be a clade consisting of the afrotropical *Graphium* together with those taxa to the exclusion of both *G.* (*Pathysa*) *aristeus* and *G.* (*Pathysa*) *nomius*. Though the inclusion of *G.* (*Graphium*), *G.* (*Pazala*) and *G.* (*Paranticopsis*) species may be the result of choice of characters, spurious coding, or insufficient taxon sampling, it certainly indicates that further examination of these taxa will be necessary to establish a robust overall classification of the genus. The inclusion of *G.* (*Paranticopsis*), but exclusion of *G.* (*Pathysa*) supports the separation of these two subgenera. The monophyly of the genus as a whole was well supported.

There does not appear to be solid support for a monophyletic clade for the swordtailed afrotropical *Graphium*. The only analysis in which we were able to 'force' such a clade was by excluding all non-*Graphium*, *G.* (*Pazala*), *G.* (*Paranticopsis*) and *G.* (*Pathysa*) and using *G.* (*Graphium*) *sarpedon* (which is tailless) as the outgroup. In other analyses a monophyletic group was indicated in some or even many of the possible most parsimonious trees, but examination showed the topology of these trees to be very variable and the consensus trees invariably collapsed them. Furthermore, whenever it was included in the analysis, *G.* (*Pazala*) *mandarinus* always emerged as sister to *antheus* + *evombar*. Analysis without *G.* (*Pazala*) *mandarinus* gives a similar result: many trees recovering a swordtailed clade, but others not doing so, and the strict consensus again collapsing these topologies. Our conclusion is that the swordtailed species form part of a paraphyletic stem-group assemblage.

Neither is there solid support for a monophyletic clade of afrotropical non-swordtailed species. With the multistate characters made inactive (Fig. 5) a clade is recovered comprising these species together with *G.* (*Graphium*) *bathycles* and *G.* (*Paranticopsis*) *macareus* and with *G.* (*Graphium*) *sarpedon* as its sister. The consensus tree when the multistates are included (Fig. 6) shows a clade comprising all the non-swordtailed taxa apart from the *angolanus*-clade, but with *G.* (*Paranticopsis*) *macareus* also included. The topology shown when the multistates are excluded (Fig. 5) is not contradicted in this analysis.

Berger's groups

Concerning Berger's (1951) groups:

1. 'Groupe de *G. pylades* F.' [= *angolanus*], compris-

ing: *endochus*, *taboranus*, *morania*, *angolanus*, *ridleyanus*, together with *schaffgotschi*. This group was recovered as a clade in all analyses and was robust enough to be represented by just three of the included species in many analyses (see above).

2. 'Groupe de *G. tynderaeus* comprising: *tynderaeus* and *latreillianus*. This clade was recovered in all analyses.
3. 'Groupe de *G. ucalegon* HEW.' [our *adamastor*], comprising: *hachei*, *auriger*, *ucalegon*, *simoni*, *fulleri*, *ucalegonides* [here regarded as a subspecies of *fulleri*], *almansor*, *odin* [= *schubotzi*], *olbrechtsi*, *aurivilliusi*, *agamedes* and *adamastor*, to which must be added *poggianus* and *abri*. These taxa always grouped together, but in our analyses *G. philonoe* was also included, despite its somewhat different appearance and genitalia. Further characters may clarify its status and thus the possible monophyly of an *adamastor* clade in which it would seem probable that *philonoe* would be included as sister to the clade.
4. 'Groupe de *G. leonidas* F.', comprising: *leonidas*, *cyrnus* and *levassori*. Perhaps surprisingly, given the overall similarity of their genitalia, a clade including this trio was not recovered. In the two consensus trees illustrated (Figs 5, 6), they form a polytomy with the *tynderaeus* clade, the *adamastor*-group + *philonoe*, and *G.* (*Paranticopsis*) *macareus*. In many of the source cladograms for the consensus, a paraphyletic topology is found where *leonidas* is sister to a polytomy of *cyrnus*, *levassori* and the *adamastor*/*philonoe*-group, but other topologies also occur. Perhaps character optimisation is a problem here and extra characters would give a robust result.
5. 'Groupe monospécifique de *G. philonoë* WARD'. As stated above, this species occurs as a polytomy with the *adamastor*-group. In many of the source trees, it pairs with *adamastor* itself, linked by having the ductus bursae partly sclerotized and 'kinked'. Features of the wing patterns suggest this may be a false result: *philonoe* must be a likely candidate as sister to the whole *adamastor*-group.
6. 'Groupe de *G. illyris* HEW.', comprising: *illyris*, *gudenusi*, *kirbyi*. We find no evidence of this grouping as a clade. In our view, the male genitalia are not as similar as Berger (1951) suggested (see Figs 16, 20–24), though the female genitalia of *kirbyi* (Fig. 76) and *gudenusi* (Fig. 81) are not dissimilar. Hancock (1993) also grouped this trio, characterising them by 'a reduction in the submarginal and discal pale areas of the forewing', though the former are somewhat variable in both *illyris* and *gudenusi* (and other species), and the latter are certainly not reduced in *gudenusi* or even *illyris* compared with species such as *colonna*, *polistratus* and *liponesco*.
7. 'Groupe de *G. policenes* CR.' Apart from *policenes*, *policenoides* (as *nigrescens*) and *liponesco* (as *boolae*), to which we would add *biokoensis*, Berger (1951) includes *junodi* and *polistratus*. As stated above, the first four of these species hold together very robustly. However, we do not see any evidence for including *junodi* and *polistratus* within this clade. There is some similarity in the dorsal harpe, though the dorsal terminal process, dorsal projection and ventral harpe are not very alike (cf. Figs 17, 18 with 25–30), and the female genitalia are markedly dissimilar (Figs 77, 78 cf. 82). The similarity of the male and female genitalia of *junodi* (Figs 17, 77) and *polistratus* (Figs 18, 78) suggests a close relationship between the two, but they do not group consistently as a clade in either analysis. When multistate characters are included (Fig. 6), a basal, paraphyletic relationship is suggested, but this is not recovered when those characters are ignored.
8. 'Groupe monospécifique de *G. colonna* WARD'. We found no close relationships for this species. When multistate characters are included in the analysis (Fig. 6), *colonna* appears to be part of the paraphyletic stem grouping, but this is not recovered when those characters are ignored. In addition to features of the male genitalia, the colour patterns of both larvae and adults appear to be highly autapomorphic.
9. 'Groupe monospécifique de *G. porthaon* HEW.'. Our analyses found no close relationships for this species.
10. 'Groupe de *G. antheus* CR.', comprising: *antheus*, *evombar*. Perhaps not surprisingly, given their highly characteristic dorsal terminal processes and even more extraordinary central ostial lobes, these species formed an unbreakable pair in all our analyses. Perhaps less predictably, all our analyses placed *G.* (*Pazala*) *mandarinus* as their sister. Some reassessment of the subgenera of *Graphium* and their relationships seems desirable. When multistate characters were included, this trio were placed with *kirbyi* and the *policenes*-group as successive sister clades; and this whole clade was positioned relatively high in the tree. With multistates de-activated, the trio were placed in polytomy with *kirbyi* and *junodi* in the stem leading to the remaining afrotropical species together with *G.* (*Graphium*) and *G.* (*Paranticopsis*) *macareus*. More characters are needed to resolve this conflict.

Hancock's phylogenetic scheme

Hancock (1993) followed Berger's (1951) groups, but his text and 'suggested phylogenetic relationship' diagram (see Fig. 4) gave additional structure. As far as we are aware, Hancock produced his phylogenetic scheme manually.

1. A basal dichotomy between the swordtailed species

(s.g. *Graphium*) and non-swordtailed species (s.g. *Arisbe*). The characters Hancock cited to justify this dichotomy are all related to the distinction between the swordtailed and non-swordtailed facies. Our own analyses yield a more pectinate structure, with the swordtailed species representing a stem grouping and the non-swordtailed species largely a crown group, with more or less resolution depending on whether the multistate characters are included.

2. A sister group relationship between the *tynderaeus*- and *adamastor*-groups. Our analyses do not recover such a structure, even if *philonoe* is included in the *adamastor*-group. Both our analyses suggest a polytomy between the species of the *leonidas* 'group', *G.* (*Par.*) *macareus*, and the *adamastor*-group + *philonoe*. As such, and with the proviso concerning *philonoe*, Hancock's (1993) scheme is not contradicted by our own.
3. A *leonidas* group. As stated above, such a group was not recovered by our analyses, but neither was it clearly refuted.
4. *G. philonoe* sister to *leonidas* group. This topology is contradicted in our analyses, where *philonoe* forms a polytomy with the members of the *adamastor*-group, or is even sister to *adamastor*.
5. *angolanus*-group sister to (*philonoe* + *leonidas* group). This is contradicted in our analyses, even if *philonoe* is ignored. Hancock (1993) apparently links them (though his diagram is not clear) by the apomorphy 'wing bases brick-red below'. This is true for the *angolanus*-group (dubiously so for *ridleyanus*), *cyrnus* and perhaps *G. levassori*, but does not apply to *philonoe* or *leonidas* where the colour is much more like Hancock's stated plesiomorphic 'red-brown or orange brown'. The distinction is in any case dubious and *tynderaeus* and *latreillianus* could be scored as brick red. In our analyses, the *angolanus*-group was placed either in polytomy with *G.* (*G.*) *bathycles* or in a wider polytomy including some swordtailed taxa and *G.* (*Graphium*), as the part of the stem to the remaining non-swordtailed species (plus *Paranticopsis*).
6. *angolanus* group + (*philonoe* + *leonidas* group) sister to (*tynderaeus* group + *adamastor* group). This is contradicted in our analyses, where the species of the *leonidas* 'group', the *tynderaeus* group and the *adamastor* group (with *philonoe*) form a polytomous crown, with the *angolanus* group in polytomy either with just *G.* (*G.*) *bathycles* or a wider grouping (see above) as the part of the stem.
7. A *policenes* group, including *junodi* and *polistratus* as well as *policenes* and '*nigrescens*' (as in Berger, 1951; see species account for Hancock's interpretation of this taxon). Our analyses do not recover such a clade. When multistate characters are not employed, a relationship of *polistratus* with a narrowly interpreted *policenes* group is not contradicted, although *junodi* is part of a stem polytomy relative to this. When multistate characters are included, both *junodi* and *polistratus* are in a paraphyletic stem grouping relative to the remaining afrotropical *Graphium*, etc. Hancock (1993) placed *junodi* as sister to *policenes*, with *polistratus* sister to '*nigrescens*', on the basis of the form of the 'dorsoapical process' (our dorsal terminal process). But these are quite distinctive in our narrowly interpreted *policenes* group (Figs 25–30), whilst those of *junodi* (Fig. 17) and *polistratus* (Fig. 18) are similar to each other. Other features of the male and female genitalia are also quite distinct (see above).
8. *colonna* sister to *policenes* group. Hancock (1993) linked *G. colonna* with his (and Berger's) broad *policenes* group on the basis of the ventral harpe being 'apically bifid' rather than entire. This depends on interpretation of the structures concerned. In *junodi* (Fig. 17) and *polistratus* (Fig. 18) they may be considered bifid, as they can in some *policenes* group (*sensu nobis*) (e.g. Figs 25, 29), though there is some variation in *policenes* itself, and that in *policenoides* (Fig. 30) might be considered 'quadrifid'. Alternatively, these taxa might be considered to have deeply or coarsely serrate ventral harpes, whereas those in *porthaon* to *illyris* are more finely serrate. It is hard to place *antheus* and *evombar* in this context, and *colonna*, too, seems to be very different.
9. A (*kirbyi* + (*gudenusi* + *illyris*)) clade. We do not recover an *illyris* group, sensu Hancock (1993) and Berger (1951) (see above). In our analyses the pairing *gudenusi* + *illyris* is not contradicted, but a linkage of these with *kirbyi* is contradicted whether multistate characters are included or not.
10. *porthaon* sister to (*kirbyi* + (*gudenusi* + *illyris*)). In our analyses, the position of *porthaon* is uncertain. A close relationship with *gudenusi* and/or *illyris* is not contradicted, but, given the above, one with *kirbyi* is contradicted.
11. *antheus* + *evombar* sister to oriental *G.* (*Graphium*). Hancock (1993) suggested that 'the ancestor of the *antheus* group appears to have spread to Southeast Asia to [g]ive rise to the Indo-Australian members of the subgenus *Graphium*.' Our analyses suggest no such scenario. Instead, a clade with *G.* (*Pazala*) *mandarinus* as the sister of *antheus* + *evombar* was recovered in all analyses. Hancock (1993) based his scheme on 'the placement of the red hindwing [rubral] spots and the structure of the male genitalia.' However, the pattern of 'loss' of rubral marks is quite complex in the afrotropical swordtailed species (see data matrix, Appendix 1, characters 17–24), and the occurrence of rubral marks is very variable in the oriental species of *G.* (*Graphium*). For example, the rubral system is conspicuous and ex-

tensive in *sarpedon*, *doson*, less so in *arycles*, *bathycles*, *agamemnon* and much reduced in *codrus* and *empedovana* (See Tsukada & Nishiyama, 1980). Moreover, the variety of male genitalia exhibited in oriental *G.* (*Graphium*) (Figs 66, 67, see also Saigusa *et al.*, 1977; Tsukada & Nishiyama, 1980) renders this claim dubious.

12. A clade of (*porthaon* (*kirbyi* + (*gudenusi* + *illyris*)) + (oriental *Graphium* (*antheus* + *evombar*). Hancock (1993) supported this by the reduction of the rubral marking, which we discuss immediately above and, by contrast with his (*colonna* (*policenes sensu lato*)), by the ventral harpe being entire, which we discuss under point 8, above. We did not recover this or any similar topology in our analyses.

Our findings

Our two consensus trees (Figs 5, 6) show constant features and differences, depending on whether the multistate characters are included or not. The constancies are at the base of the cladogram, and at its top. Both trees are pectinate, with the basal species and clades forming a typical stem group lineage. The base is similar to Miller (1987): *Protographium*, as the first taxon in the matrix, is placed at the root by the analytical software; *Iphiclides* becomes the sister to all the remaining taxa; then *Lamproptera*. From here it differs from Hancock (1983) and Miller (1987) in not placing *G.* (*Pazala*) as the sister group to the other *Graphium* subgenera. Nor is Munroe & Ehrlich's hypothesis of *G.* (*Graphium*) as sister to the other subgenera corroborated. Instead, the two species of *G.* (*Pathysa*) have been placed paraphyletically as a stem group to all the other *Graphium* species analysed. At the crown, both our analyses recover a polytomy comprising *G.* (*Paranticopsis*), *cyrnus*, *levassori* and *leonidas* separately, the *tynderaeus*-group, and the *adamastor*-group plus *philonoe*.

The differences between our two consensus trees are largely in resolution and in only a few cases represent conflict. One of these areas of conflict concerns the position of the (*mandarinus* + (*antheus* + *evombar*)) clade and its relationship with *G. kirbyi* and with the *policenes*-group.

When the multistate characters are de-activated (Fig. 5), this clade is placed in polytomy with *kirbyi* and *junodi* as basal to the rest of the afrotropical species (etc.). When the multistates are activated (Fig. 6), *kirbyi* is placed as sister to (*mandarinus* + (*antheus* + *evombar*)) (which is not contradicted by the alternative), but with the *policenes*-group placed as sister to these. This whole clade is part of a polytomy including *illyris*, *gudenusi* and *porthaon*, the two *G.* (*Graphium*) species, and the *angolanus*-group basal to the crown group of *G.* (*Paranticopsis*) to the *adamastor*-group.

A second area of conflict involves the relative positions of *G. colonna* and *G. polistratus*. When the multistate characters are active (Fig. 6), both species form part of a paraphyletic stem group, with *G. colonna* being placed as sister to most of the afrotropical species (etc.), *G. polistratus* as sister to *colonna* and the remainder, with *G. junodi* as sister to all *Graphium*, except *G.* (*Pathysa*). When the multistates are deactivated (Fig. 5), both species form part of the large polytomy of swordtailed species basal to the non-swordatiled afrotropical species, s.g. *Graphium* and s.g. *Paranticopsis*.

Of the non-conflicting differences, most noteworthy are the positions of the *angolanus*-group and two *G.* (*Graphium*) species. When multistates are active (Fig. 6), these taxa are each separately part of a large polytomy, already described, basal to the crown group. When the multistates are inactivated (Fig. 5), more resolution emerges, giving a clade comprising all the non-swordtailed species with *G.* (*G.*) *sarpedon* as the most basal, then a polytomy of *G.* (*G.*) *bathycles* plus the *angolanus*-group, then the crown group of *G.* (*Paranticopsis*) to the *adamastor*-group.

Overall, many, but not all of Berger's (1951) groups and 'groupes monospécifiques' have proved remarkably robust. On the other hand, Hancock's (1993) more ambitious hypotheses have proved extremely vulnerable in Popperian terms. Very few of his detailed phylogenetic interpretations are corroborated by our work. Finally, our own aspirations to produce a robust cladistic scheme have not been met. We remain of the opinion that lack of evidence (e.g. from early stages and DNA) rather than intrinsic uncertainty is the primary problem. Whether or not our own lack of insight into the characters we have used is a major contributory factor, will no doubt be decided by future studies.

INFORMATICS

Checklist

The *antheus*-clade
1. *antheus* (Cramer, [1779])
2. *evombar* (Boisduval, 1836)
    viossati Collins, 1997

3. *kirbyi* (Hewitson, 1872)
4. *junodi* (Trimen, 1893)
5. *polistratus* (Grose-Smith, 1889)
6. *colonna* (Ward, 1873)
7. *illyris* (Hewitson, 1872)
    flavisparsus (Fruhstorfer, 1903) **stat. rev.**
    girardeaui Guilbot & Plantrou, 1978
    hamatus (Joicey & Talbot, 1918
8. *gudenusi* (Rebel, 1911)

The *policenes*-clade
9. *policenes* (Cramer, [1775])
    telloi Hecq, 1999
10. *liponesco* (Suffert, 1904)
11. *biokoensis* Gauthier, 1984 **stat. n.**
12. *policenoides* (Holland, 1892)

13. *porthaon* (Hewitson, 1865)
    mackiei Collins & Larsen, 1991
    tanganyikae Kielland, 1978

The *angolanus*-clade
14. *angolanus* (Goeze, 1779)
    baronis (Ungemach, 1932)
15. *endochus* (Boisduval, 1836)
16. *morania* (Angas, 1849)
17. *taboranus* (Oberthür, 1886)
18. *schaffgotschi* (Niepelt, 1927)
19. *ridleyanus* (White, 1843)

The *leonidas*-group
20. *leonidas* (Fabricius, 1793)
    pelopidas (Oberthür, 1879)
    santamarthae (Joicey & Talbot, 1927)
    thomasius (Le Cerf, 1924)
21. *levassori* (Oberthür, 1886)
22. *cyrnus* (Boisduval, 1836)
    nuscyrus (Suffert, 1904)

The *tynderaeus* clade
23. *tynderaeus* (Fabricius, 1793)
24. *latreillianus* (Godart, [1819])
    theorini (Aurivillius, 1881)

25. *philonoe* (Ward, 1873)
    whalleyi (Talbot, 1929)

The *adamastor*-group
26. *adamastor* (Boisduval, 1836)
27. *agamedes* (Westwood, 1842*a*)
28. *schubotzi* (Schultze, 1913) **stat. rev.**
29. *olbrechtsi* Berger, 1950 **stat. rev.**
    tongoni Berger, 1969 **stat. rev.**
30. *abri* **sp. n.**
31. *almansor* (Honrath, 1884)
    birbiri (Ungemach, 1932)
    carchedonius (Karsch, 1895)
    escherichi (Gaede, 1915)
    uganda (Lathy, 1906)
32. *auriger* (Butler, 1876) **stat. rev.**
33. *fulleri* (Grose-Smith, 1883)
    boulleti (Le Cerf, 1912) **stat. rev.**
    rileyi Berger, 1950
    ucalegonides (Staudinger, 1884)
34. *poggianus* (Honrath, 1884)
35. *kigoma* Carcasson, 1964 **stat. n.**
36. *hachei* (Dewitz, 1881)
    moebii (Suffert, 1904)
37. *aurivilliusi* (Seeldrayers, 1896)
38. *ucalegon* (Hewitson, 1865)
    fontainei Berger, 1981
    schoutedeni Berger, 1950
39. *simoni* (Aurivillius, 1899)

Systematic and bionomic accounts of species

In the accounts that follow, the nomenclatures employed for the wing venation and patterning, and the male and female genitalia are shown in figs 7–13.

The species are treated, as far as is possible given the conflicts and inconsistencies between the two, in the order shown in our consensus trees (figs 5 & 6), from the base to the crown.

We continue to place all the afrotropical *Graphium* species in the nominal subgenus *Arisbe*, despite our analyses failing to give conclusive support for such a monophyletic clade. We do this for stability, following Miller (1987), Ackery *et al.* (1995) and others, but *contra* Hancock (1993), whose reconstruction has not been corroborated by other studies, including our own. This usage must be regarded as provisional pending further work on the other subgenera and the (eventual) production of a robust cladogram for the whole genus.

Some of the accounts are grouped into clades or groups, as in the checklist, each with a brief introduction. Those groupings termed clades are those which appear monophyletic in our analyses; those termed 'groups' have been treated as such by other workers, but were not recovered by us as monophyletic. They may represent paraphyletic grades.

The accounts follow a similar general order giving the synonymy with type localities and institutions; type evaluation information; the status of the taxon and how that may have changed with differing interpretations; a brief account on how the species may be distinguished from similar taxa; a description of the wing patterns, male and female genitalia, and early stages (where available or known); a brief description of the known distribution (countries enclosed in curly brackets are those in which a taxon may be inferred to occur, but for which there are no records); what information can be gleaned on host plants and bionomics; a statement on the conservation status, as recorded by Collins & Morris (1985); and a summary of the material studied.

For the scant accounts of the early stages, we give a brief description based on our own observations of preserved material and the distillation of illustrations and other published accounts. These accounts are then listed, followed by transcriptions of previously unpublished observations, where available, by the late Dimitri Sevastopulo, now deposited in the BMNH library.

For polytypic species the distribution of the descriptive accounts varies. In some cases a general description is given for the species as a whole, with the distinguishing features of each subspecies described in their separate accounts. In others, a detailed description is given for the nominotypical subspecies, with the distinguishing characters of the other subspecies given separately. In a few cases, detailed descriptions are given for each subspecies.

Identification

We present no artificial dichotomous key because we consider one is unlikely to be helpful. On the one hand, many species are instantly recognisable from the illustrations; on the other, many others, especially among the *adamastor* group, are both very similar and intraspecifically variable, requiring so many conditional or even contradictory statements that a key would be misleading. The easiest way to identify a butterfly is to compare it with a reliably identified specimen or with illustrations. We expect that readers will use the colour plates, supplemented by the 'similar species' or 'similar taxa' sections of the taxonomic accounts as their prime means of identification.

Genus *GRAPHIUM* Scopoli, 1777

Graphium Scopoli, 1777: 433. Type species by subsequent designation (Hemming, 1933): *Papilio sarpedon* Linnaeus, 1758. [Extralimital]

A presumptive clade of Papilionidae subfamily Papilioninae separable from other members of the tribe Leptocircini by three characters: male genitalia with juxta setose; female genitalia with a vestibulum ('cup-like process' of Saigusa *et al.*, 1977) bounded posteriorly by labia; and first instar larvae with paired setose tubercles on thoracic segments and anal segment. Other features listed by Miller (1987: 401–2) are homoplastic within the Papilionidae, or inconstant within *Graphium*, and even the three supposed autapomorphies listed here need confirmation.

DISTRIBUTION. Old World tropics and subtropics, with all species from the Afrotropical Region conventionally placed in subgenus *Arisbe*. The approximately 60 Indo-Australian Region species are currently divided among four other subgenera (*Pathysa*, *Paranticopsis*, *Pazala* and *Graphium* s.s.). Munroe (1961) indicates generic synonymy. The larvae generally feed on 'woody Ranales', including Annonaceae and Lauraceae (Ehrlich & Raven, 1965).

GRAPHIUM subgenus *ARISBE* Hübner [1819]

Arisbe Hübner [1819]: 89. Type species by subsequent designation (Scudder, 1875; ICZN, 1987): *Papilio leonidas* Fabricius, 1793.

Zelima Fabricius, 1807: 279. Type species by monotypy: *Papilio pylades* Fabricius, 1793. Name suppressed by ICZN (1963) for purposes of priority (but not homonymy; see Hemming, 1967).

Ailus Billberg, 1820: 81. Type species (replacement name for *Zelima* Fabricius): *Papilio pylades* Fabricius, 1793.

All *Graphium* known from the Afrotropical Region are placed here. We have been unable to recognize distinctive characters for this assemblage, but it remains possible that such features will be discovered in future (see 'Results of the cladistic analysis', above).

DISTRIBUTION. Afrotropical Region, including Madagascar and Comoro Islands, with 39 species currently recognized. Larvae mainly on Annonaceae.

1–2 The antheus clade

A pair of sister species, one widespread in Africa, the other from Madagascar and the Comoro Islands, recognized as a group by Berger (1951), Munroe (1961) and Hancock (1993), and corroborated by our analyses. They may be identified by the absence of bar or spot 6 in the forewing discal cell (see figs 173, 174) and by the presence of three bands, the distal two often fused or partly so, in the hindwing discal cell. The valves of the male genitalia are radically different from those in the remainder of the afrotropical species. The dorsal terminal process forms a talon-like array of stout claws, the dorsal projection is sessile and the harpe is a unified structure. The female genitalia are unlike their afrotropical congeners in lacking lateral ostial lobes, and in the unusual structure of the central ostial lobe; they also lack anterior apophyses.

Our analyses strongly link this pair with *G.* (*Pazala*) *mandarinus*. When multistate characters are disabled, this clade forms part of a polytomy (with *kirbyi* and *junodi*) basal to the clade including the remainder of the afrotropical species as well as species of *G.* (*Graphium*) and *G.* (*Paranticopsis*). When multistates are activated, this trio is placed as sister to *kirbyi*, with the *policenes* clade as sister to these four. This entire clade is placed higher in the consensus tree as part of a polytomy including other swordtailed species, species of *G.* (*Graphium*) and the *angolanus* clade, as basal to the 'crown group' (see above) of *G.* (*Paranticopsis*) *macareus*, the *leonidas* group and the *adamastor* group plus *philonoe*.

We treat the antheus clade here due to their radically different male and female genitalia, which seems to set the two species apart from the remainder of the afrotropical kite swallowtails.

1. ***Graphium* (*Arisbe*) *antheus*** (Cramer, [1779])

Large Striped Swordtail, (Figs 173, 239–241; map Fig. 112; genitalia Figs 14, 74)

We here treat *G. antheus* as a widespread, monotypic species, regarding the nominal taxon *nyassae* – treated by some authors as a subspecies – as infrasubspecific, for reasons elaborated below.

Papilio antheus Cramer, [1779]: 71, pl. 234, figs B,C. TYPE: [AFRICA]: 'Eiland *Amboina*' Cramer, [1779]: 71, (false locality). (Not seen.)
Papilio antheus Cramer; Gray, [1853]: 32; Aurivillius, 1899: 489.
Papilio (*Graphium*) *evombar* v. *antheus* Cramer; Bryk, 1930*b*: 568.
Papilio (*Graphium*) *antheus* [f. *antheus*] Cramer; van Son, 1949: 42; text figs 21, 22, 128; pls V (fig. 11), VI (fig. 11).
Graphium antheus antheus Cramer; Berger, 1950: 96, fig.96; Berger, 1981: 53, pl.19 fig. 2, 3 (♂♂); Kielland, 1990: 46.
Papilio (*Graphium*) *evombar antheus* (Cr.); Peters, 1952: 21.
Graphium (*Arisbe*) *antheus* Cramer; Munroe, 1961: 42; Ackery, Smith and Vane-Wright, 1995: 161.
Graphium antheus Cramer; D'Abrera, 1980: 48, 49 (figs); d'Abrera, 1997: 58, 59 (figs).
Graphium (*Graphium*) *antheus* Cramer; Hancock, 1983: 46; Hancock, 1993: 572.

SYNONYMS

[*Papilio agapenor* Fabricius; Boisduval, 1836: 255. Misidentification.]
Papilio antheus =*agapenor* Boisduval *nec* Fabricius; Gray, [1853]: 32; Aurivillius, 1899: 489.

Papilio nyassae Butler, 1877: 459. HOLOTYPE ♂: MALAWI: 'Lake Nyassa . . . [collected by] 'F. A. A. Simons . . . Type, B.M.' (Butler, 1877: 460). BMNH Spec.Reg. No. 136386.
Papilio antheus var. *nyassae* Butler; Aurivillius, 1899: 490.
Papilio evombar v. *nyassae* Butler; Bryk, 1930*b*: 569.
Papilio (*Graphium*) *antheus* f. *nyassae* Butler; van Son, 1949: 43.
Papilio (*Graphium*) *evombar nyassae* (B.); Peters, 1952: 21.
Graphium antheus nyassae Butler; Berger, 1981: 53, pl.19 figs 5 (♂), 6 (♀).
Graphium (*Arisbe*) *antheus* f. *nyassae* (Butler); Pennington, 1994: 306
Graphium (*Arisbe*) *antheus* =*nyassae* (Butler); Ackery *et al.*, 1995: 161.
Graphium antheus =*nyassae* (Butler); d'Abrera, 1997: 58.

Papilio lurlinus Butler, 1883: 106. LECTOTYPE ♂: KENYA: 'Victoria Nyanza' (Butler, 1883: 106) 'Rev. James Hannington' (Butler, 1883: 101). BMNH Spec.Reg. No. 136385 – **here designated**.
Papilio antheus var. (ab.?) *lurlinus* Butler; Aurivillius, 1899: 490.
Papilio antheus ab. (var.?) *lurlinus* Butler; Aurivillius, 1908: 25.

Papilio antheus evombaroides Eimer, 1889: 228, fig. V. HOLOTYPE ♂: GHANA: 'Goldküste' (Eimer, 1889: 228). Depository unknown (? Tübingen) (not seen).
Papilio antheus ab. *evombaroides* Eimer; Aurivillius, 1899: 490.

Papilio utuba Hampson, 1891: 182. LECTOTYPE ♀: KENYA: 'Sabaki River, East Africa' (Hampson, 1891: 179). BMNH Spec.Reg. No. 136387 – **here designated**.
Papilio antheus ab. *utuba* Hampson; Aurivillius, 1899: 490.

Papilio mercutius Grose Smith & Kirby, 1894: Papilio [33], pl.14 figs 1,2 (as *hollandi q.v.*). LECTOTYPE ♀: MOZAMBIQUE: 'Morakwen, Delagoa Bay (Rev. H. Junod) . . . November 10, 1892.' Grose-Smith & Kirby (1894: [33]). 'In the collection of Mr. H. Grose Smith' BMNH Spec.Reg. No. 136384 – designated Le Cerf (1924: 397).
Papilio antheus-nyassae f. indiv. *mercutius* Smith and Kirby; Le Cerf, 1924*a*: 397.

Papilio antheus latepictulus Strand, 1914*b*: 4. HOLOTYPE ♂: TANZANIA: 'D. O. Afrika: Kongoë, Kundusi 14. V. (Reuß)' (Strand, 1914*b*: 4). MNHU.
Papilio evombar ab. *latepictulus* Strand; Bryk, 1930*b*: 570.

UNAVAILABLE NAMES

Papilio antharis Godart, [1819]: 19, 52. [Unnecessary emendation].

Papilio hollandi Grose Smith & Kirby, 1894: Papilio pl.14 fig.1,2. [Invalid: a junior homonym of *Papilio hollandi* Edwards, 1892 (Papilionidae); the name was introduced on the plate, but objectively replaced by *mercutius* in the text.]

Papilio antheus ab. *scheffleri* Strand, 1909: 367. KENYA. MNHU. [infrasubspecific.]

Papilio antheus ab. *combinata* Strand, 1914*b*: 10. TANZANIA. MNHU. [infrasubspecific.]

Papilio antheus f. *micrevombaroides* Strand, 1914*b*: 10. TOGO. MNHU. [infrasubspecific.]

Papilio antheus ab. *misanus* Strand, 1914*b*: 10. TOGO. MNHU. [infrasubspecific.]

Papilio antheus ab. *Hoesemanni* Strand, 1914*b*: 10. TANZANIA. MNHU. [infrasubspecific.]

Papilio antheus ab. *rubrimacula* Strand, 1914*b*: 10.

TANZANIA. MNHU. [infrasubspecific.]

Papilio antheus ab. *comma* Strand, 1914*b*: 10. TANZANIA. MNHU. [infrasubspecific.]

Papilio (*Cosmodesmus*) *antheus antheus* ab. *mathieui* Dufrane, 1946: 120. DEMOCRATIC REPUBLIC OF CONGO. IRSN. [infrasubspecific.]

Papilio (*Cosmodesmus*) *antheus antheus* ab. *paradoxa* Dufrane, 1946: 120. DEMOCRATIC REPUBLIC OF CONGO. IRSN. [infrasubspecific.]

Graphium antheus f. *atrantheus* Basquin and Turlin, 1986: 1. CAR. ?MNHN (not seen). [infrasubspecific]

TYPE EVALUATIONS

Cramer [1779] did not state the collector when he described *Papilio antheus*, nor the collection in which he saw it and we have no knowledge of where the original specimens might be, if they survive. Fortunately, the illustrations may be attributed to current concepts of the taxon without controversy.

A specimen (BMNH Spec.Reg. No. 136241) from Boisduval's collection which reached BMNH via the Oberthür collection and the Levick bequest (BMNH Accession Register No. 1941–83) was labelled 'specimen typicum' of 'Var. agapenor' on two printed labels (presumably by Oberthür) and subsequently a round 'type' label was added by a BMNH curator. Needless to say, this has no status in nomenclature.

Butler (1877: 460), who stated that *P. nyassae* was one of the commonest butterflies of the Lake Nyassa district, did designate a type. The specimen labelled as 'type' in Butler's hand was purchased from F.A.A. Simons by the BMNH as accession number BMNH 1877–35. No further Simons specimens with this registration (i.e. paratypes) are to be found in BMNH, though several later reached BMNH via Godman and Salvin (BMNH 1917–2).

Butler (1883) described *Papilio lurlinus* from only the male, gave one wingspan and used the singular throughout, but nowhere definitely restricted his description to a single specimen and, although only a single specimen is almost certainly involved. That specimen, which reached the BMNH as part of a purchase from Rev. James Hannington registered as BMNH 1883–55, bears a label reading 'V. Nyanza/83–55' on one side, 'Papilio/lurlinus/type Butler' in Butler's hand on the other. In order to fix its status as the sole name bearing type, we here designate it as lectotype.

Papilio antheus evombaroides Eimer was described from a single male (Eimer, 1889: 228).

Hampson (1891) described only the female of *Papilio utuba*, gave one wingspan and used the singular throughout, and, although only a single specimen is almost certainly involved. The types of taxa described in the paper were, according to Hampson (1891: 179) 'presented to the Natural-History Museum'. The collection of 24 Lepidoptera from 'Sabaki River district of East Africa' 'Pres. by Keith Anstruther . . .' was registered as BMNH accession number 1890–118. The specimen of *Papilio utuba* bears a label reading 'Subaki [sic]/District./90–118/E. Africa/Papilio/Utuba' on one side; 'Papilio utuba/Hmpsn/type ♀' on the other. In order to fix its status as the sole name bearing type, we here designate it as lectotype.

Though Grose-Smith & Kirby (1894) were not explicit in their description of *Papilio mercutius*, almost certainly only one specimen was being referred to – only one size, provenance and collection date were given. Moreover, they stated it to be a male, but the specimen presumably concerned is a female. The specimen bears a label giving correct locality and date and a label reading 'Mercutius Grose Smith/Delagoa Bay. Type', and another reading just 'Type', both apparently in Grose Smith's hand. Le Cerf (1924: 397) described this specimen as 'Type H.T.', thus effectively selecting it as lectotype. The specimen is illustrated here as Fig. 239. Grose Smith's collection reached the BMNH as part of the Joicey Bequest, BMNH accessions register No. 1934–120. The taxon was illustrated by Grose-Smith & Kirby (1894) on Papilio pl.14 fig.1,2, as '*Papilio hollandi*' which they presumably realized was a junior homonym of *Papilio hollandi* Edwards, 1892 (Papilionidae) prior to publication.

In his description of *Papilio antheus latepictulus*, Strand (1914*b*: 4) specifically designates just one type specimen, which is to be found, clearly labelled, in MNHU.

TAXONOMIC STATUS

Papilio antheus Cramer ([1779)] was described as a species and has been accepted as such by most authors since. The treatment of the name as a variety of *evombar* by Bryk (1930) – and followed by Peters (1952) – is anomalous. Not only are the two clearly distinct, but the name *antheus* is senior by some 57 years.

Butler (1877) described *Papilio nyassae* as a good species and distinguished it from *G. antheus* by the reduction of the pattern elements, in particular by the wide separation of the transverse bands in the hindwing discal cell, and by the lack of a black and red rubral mark in this same cell on the underside. Subsequent authors have accepted its conspecificity with *G. antheus*, but many of these have accorded it subspecific status and applied the name to south-eastern populations. However, as pointed out by van Son (1949: 43), specimens with a prominent rubra in the hindwing are found in southern Africa, and there are specimens from Malawi in BMNH in which there is fusion between the hindwing discal cell bands. Moreover, *nyassae*-like specimens are far from rare in West Africa. For this reason, we prefer to treat *nyassae* as infrasubspecific and regard *G. antheus* as a widespread monotypic species which exhibits a great deal of variation, some of which shows (possibly clinal) changes in frequency across the continent. There is clearly considerable scope for further research into the genetics and population genetics of these systems using both conventional techniques (including crossbreeding) and molecular methods.

Butler (1883) described *Papilio lurlinus* as a good species, distinguishing it from *G. antheus* by 'the greater width of all the green markings on both surfaces' and features of the rubral pattern of the hindwing underside. All of these features fall easily within the range of variablilty of *G. antheus* (Cramer). Aurivillius (1899: 490) treated it as a 'var. (ab.?)' or 'ab. (var.?)' (Aurivillius, 1908: 25).

Papilio antheus evombaroides was established as a trinomen by Eimer (1889: 228) and presumably intended as a subspecies, despite being based on a single specimen. In it, the median and distal bands of the hindwing cell are extensively fused. However, this condition is found throughout much of the range of the species.

Hampson (1891: 182) described *Papilio utuba* as a good species, but this status has not been accepted by subsequent authors. It is the archetype for all those examples in which forewing discal cell bars 4 and 5 are connected along the posterior discocellular vein.

Although described as a good species, *Papilio mercutius* Grose-Smith & Kirby (1894: Papilio 33) has been accepted as infrasubspecific by all authors after Aurivillius (1899, 1908), who expressed doubts on its status in the latter work. As far as we are aware, no specimen other than the lectotype has been seen.

Strand (1914*b*) divided *G. antheus* into western and eastern subspecies, giving the name *latepictulus* to the latter. As far as we have been able to ascertain, no subsequent author has recognized *latepictulus* as a valid subspecies; those that divide *antheus* into subspecies seem (they are not always explicit) to give subspecific status only to *nyassae* (Butler).

Though described as a form, it is clear from the context, including the fact that it shares provenance with other variants of *G. antheus* named in the same paper, that *Papilio antheus* f. *micrevombaroides* Strand (1914*b*: 10) should be regarded as infrasubspecific.

SIMILAR SPECIES

Distinguished from most swordtailed afrotropical *Graphium*, apart from *G. evombar*, by the lack of a spot or mark in the forewing discal cell beyond bar 5. These two also have a large, elongate discal mark in hindwing cell M$_3$; in *G. policenoides* and occasionally in *G. junodi* there is a small, sometimes diffuse mark here. Compared to *G. evombar*, the forewing discal cell bars are much more sinuate in *G. antheus*.

DIAGNOSIS: PATTERN (FIG. 173)

Upperside dark brown with a pattern of green markings; both tend to fade.

Forewing discal cell with five transverse bars; bars 3 to 5 sinuate; no mark distal to bar 5. The bars are continued into the costal cell. Cell R$_3$ with an axillary discal spot (with adjacent spot in costal cell), post-discal and sub-marginal spots. Cell R$_4$ with just a submarginal spot. Cell R$_5$ with a basal spot (possibly representing a fusion of discal and post-discal elements) and a submarginal spot. Cells M$_1$ to M$_3$ with post-discal marks positioned basally along the posterior discocellular vein and reaching their respective anterior and posterior veins, and with submarginal spots. Cell CuA$_1$ with a post-discal mark which reaches both veins CuA$_1$ and CuA$_2$, and the posterior discocellular vein in the anterior half of the cell only; there is also a submarginal mark. In cell CuA$_2$ there are basal and discal marks contiguous with bars 1 and 2 of the discal cell; the post-discal mark is almost a parallelogram, reaching the veins 1A and CuA$_2$, but reaching the posterior discocellular vein only distally, where it is contiguous with discal cell bar 3; the submarginal mark is bifid. Cell 1A has basal, discal and post-discal marks contiguous with those in cell CuA$_2$.

Hindwing discal cell with a basal mark, a band linking the discal marks of cells R$_1$ and CuA$_1$, and a broader mark distally, the latter two sometimes partially or more extensively fused. In the costal cell there is a basal mark proximal to the precostal vein. In cell R$_1$ there is a transverse discal band, a broad, white post-discal mark and a variable, transverse submarginal mark. Cell R$_5$ has a basal discal/post-discal, and a transverse submarginal mark. Cell M$_1$ usually has a post-discal mark and a transverse submarginal mark. Cell M$_2$ has a small, basal post-discal and a submarginal mark; there is also a small, white marginal mark, but this is expressed more strongly as a white tip to the tail, which is an extension of vein M$_3$. In cell M$_3$ there is an elongate post-discal mark, and a lunulate submarginal mark; the white marginal mark is clear and extends some way along the tail; between this mark and the submarginal is an arc of narrow, pale, bluish scales. In cell CuA$_1$ there are discal, post-discal and narrow submarginal marks; between the discal and post-discal marks is a red mark or spot; there is a faint bluish arc between the submarginal mark and the margin, which has a marginal mark. Cell CuA$_2$ is largely white basally in males, but there is a small rubral mark and a clear marginal one.

The **underside** pattern largely reflects that of the upperside, though both the background and markings are generally paler. In the **forewing** discal cell, bars 3, 4 and 5 are dark edged, the distal edge of bar 3, proximal of bar 4 and distal of bar 5 being clearest. There are darker marks bordering many of the other pale areas, for example, the proximal margins of most submarginals. Expansion of such areas in cells CuA$_1$, CuA$_2$ and 1A means that the background appears darker here. There are also dark marks at the tips of the veins of both wings.

The **hindwing** is more complicated, partly made so by a rubral system less complete than in other species. In the anterior part of the discal cell, near the radial vein, there is a black spot between the central and distal bands; this is edged costally by a band of red scales. The discal pale mark is itself broken by an oblique band of background colour, 'isolating' the tip of the cell. In the costal cell, the areas between the basal, discal and post-discal marks are dark brown. There is a rubral element in cell R_1, consisting of a black mark traversed by red and pale bands, between the discal and post-discal marks. The post-discal mark of this cell and that in R_5 are edged with brown distally and there is a dark mark along the proximal edge of the submarginal mark, which is otherwise indistinct. Cell R_5 also has a dark mark proximal to the submarginal mark, slightly removed from it. In cell M_1 this dark mark also occurs, but is mainly confined to the posterior half of the cell; the area distal to the submarginal mark is also largely dark in the posterior half. In cell M_2 there is a dark oblique band proximal to the submarginal and the area distal to the submarginal is dark, with an arc of bluish scales near the submarginal. In cell M_3 there is a complex mark consisting of pale, bluish and dark bands between the post-discal stripe and the submarginal mark; distal to the latter is a dark area, also with a bluish arc. In cell CuA_1 there is a full rubral mark, consisting of a black mark traversed by red and pale bands, between the discal and post-discal marks; between the post-discal and submarginal marks are blue and brown bands, and the distal are is dark with a bluish arc. Cell CuA_2 has an extensive pale basal area, with a dark mark separating it from a discal mark; apart from a marginal mark by vein CuA_2, most of the rest of the cell is occupied by the rubral marking.

VARIATION

Graphium antheus is highly variable in the presence, extent and precise disposition of its pattern elements. Some particular variants are worth remarking.

Forewing discal cell with bars 4 and 5 linked by a linear mark at or close to the posterior discocellular vein (ab. *utuba* Hampson) (Fig. 239). The position and form of this link is variable on occassion it may be near the centre of the cell giving the appearance of a cross. In ab. *mercutius* Grose Smith and Kirby, bars 4 and 5 are completely fused into one broad bar and bars 2 and 3 are almost completely fused to give a broad bar with an included brown triangle (Fig. 240).

In ab. *utuba* Hampson, the discal and post-discal marks in forewing cell R_3 are fused.

Forewing cell R_4 with axillary post-discal mark.

The discal and post-discal marks in forewing cell R_5 are occasionally separate.

Forewing cell CuA_1 with submarginal mark reduced.

Forewing cell CuA_2 lacking submarginal mark.

The extent of fusion of the central and distal bands of the hindwing discal cell is quite variable, ranging from complete separation (at its extreme in *nyassae* Butler and ab. *scheffleri* Strand) to almost complete fusion (as in ab. *evombaroides* Eimer) (Fig. 241).

The submarginal mark of hindwing discal cell R_1 varies from being virtually as prominent as that in cell R_5 to absence.

Hindwing cell M_1 with post-discal mark highly reduced or even absent.

Hindwing cell CuA_1 with post-discal mark extending proximally around the rubral spot (along vein CuA_1), sometimes even fusing with the discal mark. Also, this cell may lack red pigment on the rubral spot.

DIAGNOSIS: ♂ GENITALIA (FIG. 14)

Dorsal projection sessile, with stout setae mainly on anterior to ventral surface. *Harpe* cruciform, the dorsal and ventral elements connected by a free edge posteriorly. *Dorsal harpe* bifid, with the cusps less splayed than in *evombar*, the anterior cusp with three denticles on the anterior edge; the posterior with one small denticle near the base on the dorsal edge. *Ventral harpe* tapering to a postero-ventral point, three denticles on the anterior edge. *Dorsal terminal process* a broad raised area with four very stout, claw-like teeth. *Ventral terminal process* narrow and tapering to a point. *Uncus* denticulate dorsally, bulbous basally, *socii* not prominent, setose. *Saccus* large. *Aedeagus* relatively short and stout; apparently not denticulate; slightly flared terminally.

DIAGNOSIS: ♀ GENITALIA (FIG. 74)

BMNH Spec.Reg. No. 137291; vial 4595: *ostium bursae* opening posteriorly; *ductus bursae* simple, not sclerotized, kinked or pocketed; *central lobe* large, horizontal and triangular, but arising from a vertical stem (see also van Son, 1949); *lateral ostial lobes* absent or rudimentary (there are diagonal flanges anterior to the *central lobe*, but they appear glabrous); *anterior apophyses* absent; *papillae anales* rounded.

EARLY STAGES

The mature larvae are generally olivaceous, greenish, or purplish velvety-brown, with mainly dark transverse stripes on the abdominal segments; the third thoracic segment, between the scoli, has a cream-coloured transverse band, contrasting strongly with the darker dorsum of the anterior thoracic segments; thoracic processes reduced to very low, blunt spines. Pupa green or brown, distinctive, cylindrical, with very short dorsal cephalic horn and short lateral cephalic points, thus appearing almost truncate anteriorly, with a longitudinal line or ridge running from cremaster to head that is ventrally reflexed posteriorly, so that in lateral view the ridge appears to start ventrally half way along the body, then sweep up to finish on the short dorsal cephalic horn.

Sevastopulo (MS) recorded the early stages of *G. antheus* thus:

[Egg]: Almost spherical, pale greenish, unsculptured. Laid

> singly on either surface of a leaf of the food-plant, usually near the edge. Hatched 14.i.64.
>
> First instar: Head black. Body black. Thoracic somites each with a large, black, branched, subdorsal scolus. Abdominal somites with a subdorsal series of branched black spines, that on the anal somite larger. Moulted 17.i.64.
>
> Second instar: Head dark brown. Body dark brown, 1st somite pale olive, anal somite white. The scoli on the thoracic somites brown tinged with olive, that on the anal somite white. The other spines obsolescent. Moulted 20.i.64.
>
> Third instar: Head brownish yellow. Body deep coffee brown, the 1st somite yellowish, 3rd with a transverse white dorsal line. Anal somite white. Thoracic somites each with a branched, yellowish, subdorsal scolus. Anal somite with a subdorsal white soclus pointing backwards. Legs, proleges, venter and sublateral area greenish. Moulted 23.i.64.
>
> Fourth instar: Similar. Moulted 26.i.64.
>
> Final instar: Head green. 1st somite olive, 2nd and 3rd blackish. Abdominal somites red-brown with two darker lines across the centre with a paler line between. Anal somite olive. The scoli on the thoracic somites reduced to short, blunt, black spines, a tranverse creamy band joining those on the 3rd somite. Scoli on anal somite reduced to short conical points. Sublateral area, legs, pro-legs and venter pale green. As the instar progressed the ground colour became more olive. Another larva had the ground colour dark green, a transverse purplish band on the 2nd and 3rd somites and the band joining the spines on the 3rd somite yellowish green. The double transverse lines on the abdominal somites purplish.
>
> Pupa suspended : Another pupa, formed on the side of a rusty tin, was purplish-brown with the wing-cases and thorax very slightly tinged with olive. The markings similar to the green form but the lines pinkish instead of yellowish white. The thoracic point shorter and blunter.
>
> Described from found larvae and one reared *ab ovo* from material found in the Marere Forest, pupated 6.ii.64 and a male emerged 17.ii.64
>
> [The description is accompanied by 13 black and white photographs.]

Van Son (1949: 44) reproduces notes from Gowan C. Clark. For most part Clark describes *antheus* early stages as similar to *policenes* (van Son, 1949 pl.XIV), but note the difference of first stage larval colour, according to van Son's footnote quoting Monteiro. However, the pupa (van Son, 1949: 231, fig. 128) appears to be significantly different. There is an excellent illustration of (*inter alia*) the first instar in Henning *et al.* (1997). Mrs Monteiro's drawing is deposited in BMNH (Monteiro, MS).

DISTRIBUTION (MAP Fig. 112)

Widely distributed in western, central and eastern Africa, whence it extends into South Africa. Countries confirmed include: Senegal, Guinea, {Guinea Bissau}, Sierra Leone, Liberia, Cote d'Ivoire, Ghana, Togo, Benin, Nigeria, Cameroon, Equatorial Guinea, Central African Republic, Gabon, Congo, Democratic Republic of Congo, Rwanda, Burundi, Angola, southern Sudan, Ethiopia, Uganda, Kenya, Tanzania (including Pemba), Malawi, Zambia, Zimbabwe, Mozambique, northern Botswana (Larsen, In prep.*b*), northern South Africa (Natal and Transvaal – van Son, 1949).

HOST PLANT RECORDS

Annonaceae:

Annona reticulata (extralimital in origin) (van Son, 1949: 44), (Henning *et al.*, 1997), (Kroon, 1999 – citing Pennington, 1994).

Annona senegalensis (Sevastopulo, MS), (Henning *et al.*, 1997), (Kroon, 1999 – citing Pennington, 1994).

Artabotrys monteiroae (van Son,1949: 44), (Henning *et al.*, 1997), (Kroon, 1999 – citing Pennington, 1994).

Artabotrys brachypetalus (Henning *et al.*, 1997).

Cleistochlamys kirkii (Henning *et al.*, 1997) (Kroon, 1999 – citing Henning *et al.*, 1997).

Hexalobus monopetalus (Henning *et al.*, 1997).

Monanthotaxis caffra (Kroon, 1999.

Monodora junodii (Kroon, 1999).

Uvaria caffra (van Son, 1949: 44), (Sevastopulo, MS – citing Pinhey), (Henning *et al.*, 1997), (Kroon, 1999 – citing Pennington, 1994).

Uvaria kirkii (Congdon, in litt. 1999, raised but not found on, for ?*antheus*).

Uvaria schweinfurthii (Monfort, 1987).

Uvaria welwitehii (Monfort, 1987).

Uvariodendron kirkii (Congdon, in litt. 1999, for ?*antheus*).

Apocynaceae:

Landolphia (Sevastopulo, MS – citing van Someren), (Larsen, In prep.*a*).

BIONOMICS

A monotypic species of lowland forests, wooded savannahs and coastal bush, its vertical range rarely extends above 1500 m (Larsen, 1996; Carcasson, 1960). However, Gifford (1965) says that it in Malawi it 'flies high into mountains'; for Tanzania, Kielland (1990) gives 0–1900 m. Larsen (In prep.*a*) notes that it can be found sparingly inside forests along rivers (and small streams: Birket-Smith, 1960), and quotes Condamin, who found that in Casamance it was often very common at the beginning of the rainy season. Larsen's own observations suggest that it may suddenly appear in numbers at various times of the year, partly explicable by its ability to diapause in the pupal stage for up to a year (Larsen, In prep.*b*). Hecq & Peeters (1992) record it from gallery forest, open forest and wooded savannahs in Central African Republic, but not from the most open habitats. Swanepoel (1953) noted its frequent occurrence in the dry bushveld of the Transvaal, and that westerly migrations were sporadic, apparently mainly occurring in years with good rainfall. Also regarding southern Africa, van Son (1949: 45) describes *antheus* as a butterfly of moderately open savannah, occasionally found on the edges of more densely forested localities, or in dry bushveld with Mopani and Baobab; it flies rapidly back and forth, attracted to flowers (e.g. acacias and *Grewia*; red and yellow flowers seem to be preferred according to Henning *et al.*, 1997), at which it will pause to nectar for a few moments before resuming flight. Larsen (In prep.*b*) describes the flight as 'fast and direct, usually several metres above the ground [with] amazing powers of twisting and turning', and Cooper (1973) describes it as very fast and evasive. As a result, Swanepoel (1953) considered that 'pursuit of this . . . exceedingly swift . . . swallowtail is definitely a waste of time'. According to Gifford (1965), in Malawi it flies up rivers in the morning, and down again in the afternoon, the main flight period being from Aug.–Jan., but it flies throughout the year in Cameroun (Darge, 1995); this may depend locally on season and life cycle. Van Son (1949) gives records for Jan., April, Aug., Oct., Nov., Dec.; Swanepoel (1953) describes the main flight in South Africa as August–April; Larsen (In prep.*b*) gives Dec.–Feb. as main flight period in Botswana, but also September. The butterflies are attracted by water (Larsen, In prep.*b*), damp sand (Gooch, 1880; Kielland, 1990), on which they settle on outstretched legs, wings fluttering, and mammal urine (Owen & Owen, 1972); these habits, combined with ready attraction to dead specimens placed on the ground (Cooper, 1973), offers the collector various easier means of capture (Swanepoel, 1953). According to Henning *et al.* (1997), *antheus* also patrol rocky slopes and woodland edges, typically flying 1–3 metres above the ground, but seem less territorial or aggressive compared with other swordtails. Females lay their eggs singly on the tips of young shoots of the hostplant; the eggs take about four days to eclosion; early instars are 'hole-feeders', and the larvae typically rest on a midrib; the leaf-like suspended pupal stage may last about a week, or emergence may be delayed for months, or even more than a year (Clark in van Son, 1949, Henning *et al.*, 1997).

CONSERVATION STATUS. 'Common and not in danger' (Collins and Morris, 1985: 60).

MATERIAL EXAMINED. 715 ♂♂; 63 ♀♀ in BMNH. 260 ♂♂; 13 ♀♀ from other collections.

2. *Graphium* (*Arisbe*) *evombar* (Boisduval, 1836)

Madagascan Striped Swordtail (Figs 174, 215; map Fig. 113; genitalia Figs 15, 75)

A close relative of *G. antheus*, 'replacing' it on Madagascar. Collins (1997, *in* d'Abrera, 1997) has recently described a further subspecies from Anjouan, Comoro Islands.

EARLY STAGES and LARVAL HOSTS. Apparently unknown, but hosts presumed by Paulian & Viette (1968) to be Annonaceae for *G. e. evombar*.

2a. *G.* (*Arisbe*) *evombar evombar* (Boisduval, 1836)

(Fig. 174; map Fig. 113; genitalia Figs 15, 75)

Papilio evombar Boisduval, 1836: 254. LECTOTYPE ♂: 'Madagascar' (Boisduval, 1836: 254–5). BMNH Spec.Reg. No. 135948. Designated Paulian & Viette (1968: 10). 4 PARALECTOTYPES ♂ and ♀: 'Madagascar' (Boisduval, 1836: 254–5) (not seen).

Papilio evombar Boisduval; Aurivillius, 1910: 25, p.8c; Bryk, 1930*b*: 567.

Papilio (*Graphium*) *evombar evombar* Boisduval; Peters, 1952: 21.

Graphium (*Arisbe*) *evombar* Boisduval; Munroe, 1961: 42; Paulian & Viette , 1968: 10; Ackery *et al.*, 1995: 162.

Graphium evombar Boisduval; D'Abrera, 1980: 48, 49 (figs).

Graphium (*Graphium*) *evombar* Boisduval, 1836; Hancock, 1983: 46; Collins and Morris, 1985: 61.

Graphium evombar evombar Boisduval; d'Abrera, 1997: 56, 57 (figs).

TYPE EVALUATIONS

Papilio evombar Boisduval (1836: 254) was described from 'cinq individus, mâles et femelles, pris à Madagascar par M. Goudot. – Coll. Boisd.'. The specimen selected by Paulian & Viette (1968: 10) as lectotype is from the Boisduval collection and reached the BMNH, via the Oberthür collection, as part of the Levick Bequest (BMNH accession No. 1941–83). It has (*inter alia*) an Oberthür 'Typicum/Specimen' label and a printed catalogue/drawer label also stating it to be a 'Specimen typicum'. There is, however, no proof of it having been collected by Goudot, so its true status is somewhat doubtful. The specimen was listed in a now defunct register of Rhopalocera types in the BMNH as No. 11882. We have seen no further specimens from Boisduval's collection, or apparently collected by Goudot.

TAXONOMIC STATUS

Papilio evombar Boisduval (1836: 254) was described as a species and has been accepted as such by most authors since, until the decription by Collins (1997, *in* d'Abrera, 1997) of a subspecies from the Comoro Islands. Bryk (1930: 567) treated *evombar* as the nominate subspecies of a bitypic species to include *G. antheus* (Cramer, [1779]).

SIMILAR SPECIES. Very similar to *G. antheus*, the specific differences are described below.

DIAGNOSIS: PATTERN (Fig. 174)

Like *G. antheus*, *G. evombar* may be distinguished from the rest of the striped, sword-tailed *Graphium* (that is, excluding *G. illyris*, and *G. kirbyi*) by the lack of a bar or mark 6 distally in the forewing discal cell. The extent of pale marking is generally greater than in

G. antheus – though both species are variable – and the markings themselves are generally paler, even allowing for fading of museum specimens. Specific points of difference include:

Forewing discal cell bars much less curved, with only bar five suggesting bisinuosity, and that not pronounced.

Discal and post-discal marks of forewing cell 1A almost completely fused, with at most a small brown mark between them along vein 1A. This condition is very rare in *G. antheus*.

The central and distal pale bands of the hindwing discal cell are usually (though not always) completely fused, a rare condition in *G. antheus*.

Underside patterns largely reflect those of the upperside, though the central and distal pale bands of the hindwing discal cell are separated by a band of the ground colour.

The rubral system, unlike other species apart from *antheus*, is confined to red spots with associated black marks in hindwing cells R_1, CuA_1 and CuA_2, with further black marking proximal to the submarginal marks of both wings, distal to the post discal marks of hindwing cells R_5 and M_1, and in the hindwing discal cell.

VARIATION

We have observed the following particular points within a general variability in the pattern elements:

Forewing discal cell with bars 4 and 5 connected along the median vein, as in the '*utuba*' variant in *G. antheus*. In the specimen in BMNH concerned (Spec.Reg. No. 136869) the marks in the costal cell are expanded to form a link between bars 3 and 4 and bar 5 and the discal spot of cell R_3.

Forewing cell R_4 usually lacks an axillary, post-discal spot, but is present in about one third of specimens.

The central and distal pale bands of the hindwing discal cell are generally completely fused, so the distal two-thirds or so of the cell is pale. In a few specimens, of both sexes, the two patches are separated by a dark line (on the underside, this separation is the norm, and the dark line can be seen from above); intermediates do occur.

The discal and post-discal bands of hindwing cell R_1 are often fused, but there is a range of states from this, via the presence of a few dark scales, to complete separation.

Roughly one half of specimens have a post-discal mark in hindwing cell M_1; sometimes this is very small.

The expression of the submarginal mark in hindwing cell M_3 varies from a clear crescent shape, with a scattering of pale scales distal to it, to merely a diffuse patch of such scales.

A crescent shaped post-discal spot is usually visible in hindwing cell CuA_1, though it may be highly reduced. The prominence of the rubral spot between it and the discal stripe – itself quite variable – also varies greatly.

On the underside, the extent of black scaling, for example proximal to the submarginal marks and between the middle and distal marks of the hindwing discal cell, is variable.

DIAGNOSIS: ♂ GENITALIA (Fig. 15)

Dorsal terminal process a broad raised area with four very stout, claw-like teeth. *Ventral terminal process* narrow and tapering to a point. *Dorsal projection* sessile, with stout setae mainly on anterior to ventral surface. *Harpe* cruciform, the dorsal and ventral elements connected by a free edge posteriorly. *Dorsal harpe* bifid, with the cusps more splayed than in *antheus*, the anterior cusp with denticulae on both edges, especially the anterior; the posterior cusp denticulate on the anterior edge (cf. *G. antheus*). *Ventral harpe* splayed ventrally into four teeth of which some are themselves denticulate edge (cf. *G. antheus*). *Uncus* denticulate dorsally, bulbous basally, *socii* not prominent, setose. *Saccus* large. *Aedeagus* relatively short and stout; slightly flared terminally; possibly with vesica finely denticulate.

DIAGNOSIS: ♀ GENITALIA (Fig. 75)

Very similar to *G. antheus*.

BMNH Spec.Reg. No. 135939; vial 5446: *ostium bursae* opening posteriorly; *ductus* elongate, simple, not sclerotized, kinked or constricted; *central lobe* large, horizontal and triangular, but arising from a vertical stem; *lateral ostial lobes* absent or rudimentary (there are diagonal flanges anterior to the *central lobe*, but they appear glabrous); *anterior apophyses* absent; *papillae anales* rounded.

EARLY STAGES. Unknown.

DISTRIBUTION (Map Fig. 113). Little detail appears to be available; widespread throughout Madagascar according to Collins and Morris (1985).

HOST PLANTS. Presumably Annonaceae.

BIONOMICS

Paulian & Viette (1968) considered it more common in the west, suggesting a preference for woodlands rather than dense forests. Records in Paulian & Viette are for Mar., Aug., Sept., Oct., Nov., Dec., with heights recorded at 500 and 1250 m.

CONSERVATION STATUS. 'Common and not threatened' (Collins and Morris, 1985).

MATERIAL EXAMINED. 48 ♂♂; 1♀ in BMNH; 28 ♂♂ 1 ♀ from other collections.

2b. *G. (Arisbe) evombar viossati* Collins, 1997

(Fig. 215; map Fig. 113)

Graphium evombar Boisduval; Turlin, 1994: 85 [Observation cited from Anjouan].

Graphium evombar viossati Collins, 1997, *in* d'Abrera, 1997: 56, 57 (fig.). HOLOTYPE ♂: COMORO ISLANDS: 'Fôret de Moya, S.E. Anjouan, Comoro Islands. Feb. 1991. 900m P. Walwanda in ABRI' (Collins, 1997, *in* d'Abrera, 1997) (not seen). PARATYPE ♂: 'Same data'. ABRI.

TYPE EVALUATION

Graphium evombar viossati Collins (1997) was described from the two specimens listed above, with type designations original. Collins (1997, *in* d'Abrera, 1997) stated that the taxon was known from 'few' individuals, including one or more females. Examination of more material is needed to assess critically the status of this taxon.

TAXONOMIC STATUS. *Graphium evombar viossati* Collins (1997) was established as a subspecies.

SIMILAR SPECIES. Like the nominate subspecies and *G. antheus*, *Graphium evombar viossati* Collins (1997) lacks any mark in the forewing discal cell distal to bar 5. Like the nominate subspecies, but unlike *G. antheus*, the bars in the forewing discal cell are straight. It may be distinguished from *Graphium e. evombar* by the following.

DIAGNOSIS: PATTERN (Fig. 215)

Green markings of upper surface reduced, but submarginal marks well developed (Collins, 1997, *in* d'Abrera, 1997). In detail: discal and post-discal spots in forewing cell 1A not completely fused (only joined at posterior margin of wing); discal and post-discal spots in hind-wing ups cell R_1 completely separate (rare or incomplete in the nominate race, though clear on uns); basal, discal and post-discal bands separated by dark lines (in the nominate race there is only 1 dark band in this cell, linking with vein CuA_2).

A female *Graphium e. evombar* in BMNH (Spec.Reg. No. 135939) from Camp Ambre in far north Madagascar also has the hindwing discal cell bands separated.

VARIATION. We have seen too few specimens to comment on this.

DIAGNOSIS: ♂ GENITALIA

Shows some features partly intermediate between *e. evombar* and *antheus*, and others (the dorsal terminal process) which are distinct from both.

Dorsal terminal process a broad raised area with only three stout, claw-like teeth; *ventral terminal process* narrow and tapering to a point; *dorsal projection* sessile, with stout setae mainly on anterior to ventral surface; *harpe* cruciform, the dorsal and ventral elements connected by a free edge posteriorly; *dorsal harpe* bifid, with the cusps more splayed than in *G. antheus*, the anterior cusp with denticulae on both edges; the posterior cusp denticulate terminally and anteriorly (cf. *G. antheus* and *G. e. evombar*); *ventral harpe* splayed ventrally but not subdivided into four teeth, but instead with general denticulation edge; *uncus* denticulate dorsally, bulbous basally; *socii* not prominent, setose; *saccus* large; *aedeagus* relatively short and stout; slightly flared terminally; possibly with vesica finely denticulate.

DIAGNOSIS: ♀ GENITALIA. None seen.

EARLY STAGES. Unknown.

DISTRIBUTION (Map Fig. 113). Known from the type locality. We have also seen a specimen from Lingoni, Anjouan, from ABRI, and Turlin (1994) recorded *evombar* having been observed at Pomoni, south-west Anjouan by M. Jean Redouly.

HOST PLANTS. Presumably Annonaceae.

BIONOMICS; CONSERVATION STATUS. Unknown.

MATERIAL EXAMINED. 1 ♂ from Anjouan on loan from ABRI.

3. *Graphium (Arisbe) kirbyi* (Hewitson, 1872)

Kirby's Swordtail, (Fig. 175; map Fig. 116; genitalia Figs 16, 76; early stages Figs 247, 248, 257, 258)

Berger (1950) and Hancock (1993) both placed *G. kirbyi* in a group with *G. illyris* and *G. gudenusi*, on the basis of the male genitalia and, in Hancock at least, the reduction of the colour pattern. Our figs of the male (figs 16, 20–23, 24, respectively) and female genitalia (76, 80, 81, respectively) do not in our opinion reveal a close relationship between *G. kirbyi* and the other species. In our analyses, when multistate characters are deactivated, *G. kirbyi* is placed in a polytomy with *G. junodi* and the (*mandarinus* + (*antheus* + *evombar*)) clade as basal to the remaining afrotropical species, etc. When the multistate characters are activated, *G. kirbyi* is placed higher up the cladogram, as sister to the (*mandarinus* + (*antheus* + *evombar*)) clade and with the *policenes* clade sister to these.

Papilio kirbyi Hewitson, 1872: 146. LECTOTYPE ♂: [EAST AFRICA]: 'Lagos' (Hewitson, 1872: 147). BMNH Spec.Reg. No. 220097 — **here designated**.

Papilio kirbyi Hewitson; Hewitson, 1873*a*: pl. Papilio. XIII. Fig. 42.

Papilio kirbyi kirbyi Hewitson; Aurivillius, 1910: 26, pl.8; Bryk, 1930*b*: 573.

Papilio (Graphium) kirbyi kirbyi (Hew.); Peters, 1952: 22.

Graphium kirbyi Hewitson; Carcasson, 1960: 31, pl.10 fig.3; D'Abrera, 1980: 46, 47 (fig.); Kielland, 1990: 47; Larsen, 1991: 117, pl.4 fig.22I; d'Abrera, 1997: 54, 55 (fig.).

Graphium (Arisbe) kirbyi (Hewitson); Munroe, 1961: 42; Ackery, Smith & Vane-Wright, 1995: 163.

Graphium (Graphium) kirbyi (Hewitson); Hancock, 1983: 46; Collins & Morris, 1985: 60.

SYNONYM

Papilio kirbyi var. *ottonis* Aurivillius, 1899: 492. TYPES: TANZANIA: 'Deutsch Ost-Afrika: Usambara.' 'Coll. Staudinger' (Aurivillius, 1899: 492). (Not seen.)

Papilio kirbyi ottonis Aurivillius; Aurivillius, 1910: 26, pl.8.

Papilio kirbyi v. *ottonis* Aurivillius; Bryk, 1930*b*: 573.

Papilio (*Graphium*) *kirbyi ottonis* Aurivillius; Peters, 1952: 22.

Graphium kirbyi f. *ottonis* Aurivillius; Carcasson, 1960: 31. (as syn. n.).

TYPE EVALUATIONS

Hewitson (1872) did not state his series length when describing *Papilio kirbyi*. In his catalogue of Hewitson's collection, Kirby (1879) lists only one specimen, from Lagos. That specimen is now in the BMNH, which it reached as part of the Hewitson bequest (BMNH Spec.Reg. 1879–69), and where it was labelled as 'Type H.T.' by a previous curator, which is why we designate it as lectotype. The butterfly itself, much damaged and repaired using wing parts of other species, nevertheless bears enough resemblance to the illustration in Hewitson (1873) to restrict the type series formally to that specimen.

Papilio kirbyi var. *ottonis* Aurivillius (1899) was described from an unstated number of specimens in Staudinger's collection. We have seen no specimens identified as *ottonis*, or with correct provenance.

TAXONOMIC STATUS

Papilio kirbyi was established by Hewitson (1872) as a species, giving Lagos as type locality. Specific rank has never been doubted, though the species was considered polytypic after the establishment of *Papilio k. ottonis* until its downgrading by Carcasson (1960).

Papilio kirbyi var. *ottonis* Aurivillius (1899) was established at subspecific rank (with a suggestion that it might be a separate species – 'species diversa?') partly, perhaps, because of the 'false locality' for the type of Hewitson's taxon. Carcasson (1960) reduced its rank to that of an infrasubspecific 'form', stating that 'it should be regarded as a varietal form, as it appears to fly with the nominate race'. Larsen (1991) pointed out that 'very fresh specimens [of *G. kirbyi*] have a greenish tinge to the discal band', the character used to define *ottonis*.

SIMILAR SPECIES

Very distinctive, with its dull brown wings crossed by a single, narrow band running from near the apex of the forewing to the middle of cell CuA_1 of the hindwing, with few – and faint – other marks. Only *G. illyris* shows a similar reduction of marking. In that species, however, the hindwing submarginal marks are enlarged, the hindwings are less narrowed, and the forewing band tends to curve towards the costal margin, rather than towards the apex.

DIAGNOSIS: PATTERN (Fig. 179)

Ground colour dull brown, slightly darker on the forewing distal to the post-discal marks, slightly paler distal to the line of the submarginal marks. Pale markings dull creamy white, but apparently showing a 'greenish tinge' in very fresh specimens (Larsen, 1991).

Forewing upperside discal cell with, at most, traces of 5 transverse bars, plus a distal spot. Cell R_3 variably with a post-discal spot distal to the root of vein R_4 and with a large, diffuse submarginal mark. Cells R_4 to 1A each with a narrow post-discal mark crossing the whole cell; veins R_4 to M_2 are dark, M_3 to 1A pale between the post-discal marks, giving the effect of a continuous band from the hind margin becoming punctuated anteriorly. Submarginal marks in these cells at most very faint, but their position is indicated by the ground colour becoming paler distally.

Forewing band continued across most of **hindwing** as the post-discal mark in cells R_1 and R_5, a transverse discal cell band and an elongate discal mark in cell CuA_1. Submarginal mark in cell R_1 usually faint, those in cells R_5 to M_2 clearer, those in cells M_3 to CuA_2 again fainter, but usually distinct. There is a variable number of pale scales and hairs distal to the discal cell mark, at the base of cell M_3 and around the discal mark in cell CuA_1, not just in females (*contra* d'Abrera, 1997), though it is generally clearer in that gender. There is also a variable amount of pale (bluish) scaling distal to the submarginal marks in cells R_5 to CuA_1. The tip of the tail is white, extending variably towards the base. Marginal marks are clear in cells M_3 to CuA_2, but not elsewhere.

The **underside** reflects the upperside with the following differences. **Forewing** discal cell marks are slightly more visible as narrow, sinuate bars. The area between the (position of the) post-discal mark and the submarginal in forewing cell R_3 is suffused with pale scales. The **hindwing** rubral system consists of red and brown bands crossing the costal and precostal cells proximal to the post-discal mark, a red band across the tip of the discal cell, a faint red patch in the axil of cell M_2, transverse bands in cells M_3 and CuA_1, and a soft-edged red spot in cell CuA_2. The submarginal marks are pale brown, and there is some bluish scaling between these and the margins; there is also blue scaling between the rubra and submarginal mark in cell CuA_1. The marginal marks in cells M_3 to CuA_2 are better developed.

VARIATION

Despite the simple pattern, some variation is evident. In particular, the size and appearance of the forewing submarginal marks varies between absence in most cells (especially posteriorly) and clear, if small, pale points. The hindwing submarginal marks are also variable in size, and that in cell R_1 may be absent. The extent of the scattering of pale scales around the wing band and distal to the submarginal marks varies between virtual absence to clear, if diffuse patches. Similar differences in the intensity of marking are seen on the underside.

Other differences we have noted include:

the post-discal mark in forewing cell R_3 varies from absence, to prescence as a small spot along vein R_4, to prescence as a band across the cell;

upperside hindwing cell CuA_2 sometimes with a small, but clear submarginal mark.

DIAGNOSIS: ♂ GENITALIA (Fig. 16)
Dorsal projection with base narrower than in the *policenes*-group, directed posteriad, angled slightly ventrad, twisted distally. *Dorsal harpe* a simple, cylindrical structure extending beyond the valve margin, flattened and serrate at the tip. *Ventral harpe* a simple, serrate, elongate blade, concave on its mesal edge, reaching close to the dorsal terminal process. *Dorsal terminal process* directed mesad, flattened in the horizontal plane at tip; tip serrate. *Ventral terminal process* broad-based, triangular, with coarse and fine serrations at tip. *Uncus* long, *socii* prominent, globular. *Saccus* short. *Aedeagus* short, with denticulate vesica.

DIAGNOSIS: ♀ GENITALIA (Fig. 76)
BMNH Spec.Reg. No. 220065; vial 3989: *ostium bursae* anterior; *ductus bursae* not extended nor well sclerotized nor kinked, constricted or pocketed; *central ostial lobe* long, thin, glabrous, pointed, extending well beyond laterals (much longer than in *G. illyris*); *lateral ostial lobes* broad, but not very long; *anterior apophyses* well developed; *papillae anales* rounded.

EARLY STAGES (FIGS 247, 248, 257, 258)
The mature larva has pale transverse stripes, and exceptionally long thoracic and anal processes (subequal in length to the width of the larval abdomen), those processes on the thoracic segments pale at base and at tips, but otherwise black. The pupa is dorso-ventrally somewhat compressed, with prominent lateral expansion just behind the thorax, and a pair of striking black or purplish spots on the dorsum of the third abdominal segment.

Photographs of egg, larvae and pupa sent by Colin Congdon in litt., 27.ix.1999, who notes that '*kirbyi* [larvae] live in deep shade, and pupate head down on the underside of a leaf.' Sevastopulo (MS) recorded the last two instars and pupa thus:

> Penultimate instar: Head yellowish. Body yellowish green with three transverse blackish lines on each somite. Subdorsal spines on the thoracic somites very long, black with the base yellow. Anal somite with a bifid spine, white in front, black behind. Legs, prolegs and venter green. Moulted 29.iv.68.
>
> Final instar: Similar to preceding but the black transverse lines replaced by bluish green. Osmeterium pouch with a black transverse line. The spines extremely long and tipped with white. When ready to pupate the markings fade.
>
> Pupa supported by a girdle and the cremaster. The venter flat and the whole pupa somewhat flattened, the outline from above being kite-shaped, except that the head is produced into a sharp point fronted to each eye. A small buff tubercle laterally on the pro-thorax. Meso-thorax produced above into the usual forward-pointed process. Colour green, abdominal somites with a subdorsal series of small, dark green dots. 3rd abdominal somite with two dark purplish spots dorsally. The thoracic horn marked frontally with chocolate. Two buff, slightly raised points on the edge of the wing case, presumably vestiges of the larval thoracic spines. 7th abdominal somite with a chocolate-brown, lateral spot.
>
> Described from a larva found at Jadini, which pupated 3.v.68, and a male emerged 3.vi.68.
>
> [The descriptions are accompanied by six black and white photographs.]

DISTRIBUTION (Map Fig. 116). Eastern Kenya and Tanzania only.

HOST PLANT RECORDS
Annonaceae:
Annona and *Uvaria* (Ackery *et al.*, 1995).
'unidentified annonaceous shrub' (Sevastopulo, MS).
Uvariodendron kirkii (Congdon, in litt. 1999, raised but not found on).

BIONOMICS
This distinct monotypic species is restricted to eastern districts of Kenya and Tanzania, where it is sometimes common in lowland coastal forests (rare in the Shimba Hills), also affecting coastal scrub and woodlands; inland, it occurs as far as Morogoro (Mathot, 1990; Ackery *et al.*, 1995; Larsen, 1996). Williams (1969) and Larsen (1996a; pers. comm., 1999) state that both sexes visit flowers, and the males often visit mud-puddles (notably on the Kenya coast); the flight is not so strong as the larger swordtails ('relatively weak and fluttering', according to Williams). Kielland (1990) gives a vertical range of 200–500 m., and notes that although 'females are very difficult to find', they should be looked for in the forest early in the day, when they are attracted to flowering bushes.

CONSERVATION STATUS. 'Local but sometimes common in coastal forests and not threatened' (Collins & Morris, 1985: 60).

MATERIAL EXAMINED. 49 ♂♂; 16 ♀♀ in BMNH. 10 ♂♂ from other collections.

4. *Graphium* (*Arisbe*) *junodi* (Trimen, 1893)

Mozambique, Scarce or Junod's Swordtail (Fig. 176; map Fig. 118; genitalia Figs 17, 77)

Placed in the *policenes* group by both Berger (1951) and Hancock (1993), with the latter regarding it as the sister species of *policenes* itself to the exclusion of '*nigrescens*' [=*policenoides*]. Our analyses do not recover such a relationship, placing it as part of a basal polytomy with *kirbyi* and the *antheus* clade when multistate characters are inactivated, or as part of a paraphyletic stem grouping with *polistratus* and *colonna* when they are active. Subjectively, both the male and female genitalia of *junodi* and *polistratus* are very similar, giving credence to that possibility, or suggesting an even closer relationship.

Papilio junodi Trimen, 1893: 138. LECTOTYPE ♀: MOZAMBIQUE: 'Morakwen, Delagoa Bay (*Rev. U. Junod*)'. (Trimen, 1893: 139). BMNH Spec.Reg. No. 149230. Designated Le Cerf (1924: 397). PARALECTOTYPES: 2 ♂♂, 1 ♀. Similar data. (Trimen, 1893: 139). (not seen). PARALECTOTYPE ♂: 'Hewitson Collection at the British Museum' [No locality]. (Trimen, 1893: 139). BMNH Spec.Reg. No. 220102.

Papilio junodi Trimen: Aurivillius, 1899: 491; Aurivillius, 1910: 26; Bryk, 1930*b*: 572.

Papilio (*Graphium*) *junodi* Trimen; van Son, 1949: 49; text fig. 25; pls V (fig. 13), VI (fig. 13); Peters, 1952: 22.

Graphium (*Arisbe*) *junodi* (Trimen); Munroe, 1961: 42; Pennington, 1994: 306, pl. 194; Ackery, Smith & Vane-Wright, 1995: 163.

Graphium junodi Trimen; D'Abrera, 1980: 48, 49 (figs); d'Abrera, 1997: 58, 59 (figs).

Graphium (*Graphium*) *junodi* (Trimen); Hancock, 1983: 46: Collins & Morris, 1985: 59.

TYPE EVALUATIONS

Papilio junodi Trimen was described 'from two males and two females' (Trimen, 1893: 139). One female example in BMNH (Spec.Reg. 149230) carries a large label in Trimen's hand with the following information: 'P. Junodi'; 'Rec[eive]^{d} 1–II–92', 'Decembre'; 'Morakwen'; 'flying in company of the others especially P. colonna'; and on the reverse: 'Delagoa Bay'. The specimen has been labelled as the 'Type' of *Papilio Junodi* in Le Cerf's hand, and has a Joicey collection label: 'Ex Trimen Coll./Cat. p. 380 No. 1'. Le Cerf (1924: 397) treated this as the 'Type (H.T.)' which constitutes the designation of that specimen as lectotype. The specimen reached the BMNH as part of the Joicey Bequest (BMNH accession No. 1934–120). According to Horn *et al.* (1990), Trimen's collection went to the Hill Museum, part or most of which subsequently reached BMNH as part of the Joicey Bequest (BMNH Accession Register No. 1934–120). Both Le Cerf (1924) and Gabriel (1932) list just one type specimen in the Hill Museum. We have not seen, and do not know the whereabouts of the other three specimens from which the description was made, which may have been sold or distributed separately following Joicey's death and before the bulk of the Hill Museum material reached the BMNH.

Trimen also refers to a 'small imperfect example, expanding only 3 in. 10 lin. [approx. 9.7 cm] in the Hewitson Collection at the British Museum'. This published wingspan lies above that given by Trimen for the male of the species: '3 in. 3–5½ lin.' (8.3–8.8 cm). However, Trimen's measurement would appear to be a misprint for 2 in. 10 lin. (7.2 cm), as the specimen concerned (BMNH Spec.Reg. No. 220102) measures 7.1 cm. The specimen has been labelled as paratype by an earlier curator and should be considered part of Trimen's type series, additional to the four specimens cited above.

TAXONOMIC STATUS. *Papilio junodi* Trimen was described as a full species and has been treated as such by all authors since. The taxon has not been divided into subspecies, and neither have any synonyms, nor infrasubspecific forms been described.

SIMILAR SPECIES

The pale markings of *G. junodi* make it superficially similar to *G. porthaon* from which it may be distinguished by the forewing discal cell bars being almost straight; the band consisting of forewing post-discal marks being more continuous; and the small size or absence of submarginal marks on the posterior part of the forewing and on the hindwing.

It may be distinguished from *G. polistratus* and *G. policenes* by its pale markings; generally more continuous forewing band; the absence of nacreous areas between the post-discal and submarginal marks of underside forewing cells R_5 to M_3; and the small size or absence of submarginal marks on the posterior part of the forewing and on the hindwing.

DIAGNOSIS: PATTERN (FIG. 176)

Upperside background colour dark brown; pale marks 'very light pale greenish-yellow' according to Van Son (1949 – see also Pennington, 1994: pl.194 fig.724i), but fading to cream. **Forewing** discal cell with five virtually straight bars and distal spot opposite cell R_5. Cell R_3 with small axillary discal spot, squarish or slightly rounded post-discal mark at root of vein R_4 and slightly diffuse submarginal mark. Cell R_4 usually just with submarginal mark. Cell R_5 with discal and post-discal marks fused. Cells M_1 to M_3 each with post-discal marks reaching the anterior and posterior veins of their respective cells and, in cells M_2 and M_3 the posterior discocellular vein; that in cell M_1 almost does so. The submarginal marks in these cells are smaller than those in cells R_3–R_5. Cell CuA_1 with post-discal mark reaching veins CuA_1 and CuA_2 and sometimes touching the posterior discocellular vein opposite discal cell bar 4; the submarginal mark small. Cell CuA_2 with a basal band, discal band contiguous with discal cell bar 2 and discal band of cell 1A; post-discal mark reaching veins CuA_2 and 1A, with an extension almost to the posterior discocellular vein anteriorly, opposite discal cell bar 3 (the shape of this mark is quite variable); usually there is a small submarginal mark confined to the anterior half of the cell. Cell 1A with basal, discal and post-discal bands, each contiguous with that in cell CuA_2.

Hindwing upperside discal cell with basal band and transverse band linking the discal mark in the costal cell and that in cell CuA_1. Costal cell (R_1) with basal, discal and post-discal marks; submarginal mark usually very faint. Cell R_5 with a transverse post-discal mark and, usually, a clear, transverse submarginal mark. Cell M_1 usually with a clear post-discal and a small submarginal mark confined to the anterior half of the cell. Cell M_2 sometimes with a post-discal mark and sometimes a small submarginal mark confined to the anterior half of the cell. Cell M_3 sometimes with an elongate, basal discal mark or scattering of white scales, occasionally with a small, distal post-discal mark and usually with a diffuse, crescent-shaped submarginal mark; there is sometimes a diffuse patch of pale scales distal to the submarginal mark. Cell CuA_1 with a large discal mark, extending about half the length of the cell; usually a small, somewhat diffuse post-discal mark, just proximal to a narrow, crescent-shaped and also diffuse submarginal mark. In females, there is a long discal mark in the cubital cell; in males this is obscured by particularly luxuriant androconial hairs. Marginal marks are prominent in cells M_3 to CuA_2, that in M_3 often almost joining the white tip of the tail.

The **underside** pattern reflects that of the upperside, but with the ground colour generally paler. On the **hindwing**, the rubral system is quite complete, with transverse red and associated bands in the precostal and costal (R_1) cells and cells R_5, M_2 (both basal) and M_3 to CuA_2 (between the discal and post-discal marks, where present); in the discal cell the bands are along the upper discocellular vein, opposite cell M_1. On the hindwing, also, there are darker patches on each side of the rubral marks, and distal to the post-discal marks in cells R_1 and R_5.

VARIATION

As implied above, the presence and extent of the discal, post-discal and submarginal marks of the hind wing show a great deal of variability. The post-discal mark in cell M_1 is present in all male specimens as a round spot, but may be reduced; it is present in 5 (of 8) females in BMNH. The post-discal mark in cell M_2 is less common, and usually smaller: only 1 female, but 11 males in BMNH have it. Only 1 male, but no females, has a clear post-discal mark in cell M_3; 2 further males have faint, diffuse areas of pale scales. 8 males and 2 females have a post-discal mark, usually as a diffuse patch of scales, in cell CuA_1. Most specimens have a few – sometimes very few – pale scales near the base of cell M_3. In all females, and a few males, a visible, if diffuse, elongate patch is visible and in a few specimens (male and female) this is condensed into a clear discal mark (See Pennington, 1994: pl.194 fig.724i). Submarginal marks may be clear in all cells from R_5 to CuA_1, though more usually those in cells M_1 and M_2 are reduced, faint or absent. Some specimens lack hindwing submarginals altogether. Submarginal marks are variable on the forewing, too: all specimens in BMNH have clear ones in cells R_3 to R_5; posterior to this, they are smaller, often fainter and sometimes, especially in females, absent.

DIAGNOSIS: ♂ GENITALIA (Fig. 17)

Dorsal projection broad based, nearly horizontal, narrowing to tip. *Dorsal harpe* with two laterally compressed blades: one nearly vertical, serrate along mesal edge; the other nearly horizontal, broadly based along basal part of vertical blade, serrate, with ventrally directed hook at tip. *Ventral harpe* a small blade in the vertical plane arising from a narrow base; deeply cleft into a dorsal and a ventral tooth; quadrate dorsally. *Dorsal terminal process* a simple tooth, directed mesad and slightly curved ventrad. *Ventral terminal process* sesile, serrate. *Uncus* elongate, *socii* prominent. *Saccus* short, rounded. *Aedeagus* short, with denticulate vesica.

DIAGNOSIS: ♀ GENITALIA (Fig. 77)

BMNH Spec.Reg. No. 149239; vial 3993: similar to *G. polistratus*: *ostium bursae* opening in posterior half of vestibulum; *ductus bursae* quite elongate, not sclerotized, without kink/constriction distal to *ductus seminalis* (unlike *G. polistratus*), not pocketed; *central ostial lobe* setose, extremely broad, covering most of posterior part of vestibulum, with a small central lip; *lateral ostial lobes* small, setose; *anterior apophyses* well marked; *papillae anales* rounded, with some long hook-like setae.

EARLY STAGES; HOST PLANTS. Unknown.

DISTRIBUTION (MAP Fig. 118)

Largely restricted to central and southern Mozambique, but also recorded from neighbouring parts of eastern Zimbabwe, where it appears to be particularly rare and may only have vagrant status (van Son, 1949; Cooper, 1973; Collins & Morris, 1985; Mathot, 1990; Ackery *et al.*, 1995). There is a specimen in BMNH labelled as being from Uganda (Mabiri Forest); and a specimen in MNHN labelled as being from Tanzania (Zanzibar), but these are extremely dubious.

BIONOMICS

An uncommon monotypic species found in lowland, mainly coastal forests (inland records are sporadic: Henning & Henning, 1992). According to Cooper (1973), *G. junodi* is found in dense rain forests, where it flies somewhat less rapidly and more directly than *G. antheus*, typically about 30–60 cm above the ground, and usually in shade. In Mozambique it is apparently on the wing throughout the year, but becomes scarce in the winter months (Cooper, *loc. cit.*). Williams (1969) states 'mainly from August to May', noting Dondo

Forest, near Beira, as a favoured locality. Henning & Henning (1992) give Jan.–April and July–Sept., and suggest that it may well be threatened by the continuing loss of its core lowland forest habitats.

CONSERVATION STATUS. 'Uncommon or scarce, but not known to be threatened' (Collins and Morris, 1985: 59).

MATERIAL EXAMINED. 14 ♂♂; 9 ♀♀ in BMNH; 4 ♂♂ from other collections.

5. *Graphium (Arisbe) polistratus* (Grose-Smith, 1889)

Dancing Swordtail (Fig. 177; map Fig. 117; genitalia Figs 18, 78)

Placed in the *policenes* group by both Berger (1951) and Hancock (1993), with the latter regarding it as the sister species of '*nigrescens*' [=*policenoides*] to the exclusion of *policenes* itself. Our analyses place it as part of the large polytomy basal to the tailless clade when multistate characters are inactive. When these characters are active, *polistratus* is placed in a paraphyletic stem grouping with *junodi* and *colonna*. Subjectively, both the male and female genitalia of *junodi* and *polistratus* are very similar, suggestive of a close relationship.

Papilio polistratus Grose-Smith, 1889: 121. HOLOTYPE ♀: KENYA: 'in the neighbourhood of Mombasa . . . captured by Mr. Last' (Grose-Smith, 1889). BMNH Spec.Reg. No. 141148.
Papilio polistratus Grose-Smith; Bryk, 1930*b*: 572.
Papilio (*Graphium*) *polistratus* Grose-Smith; van Son, 1949: 50; text fig. 26; pls V (fig. 14), VI (fig. 14).
Papilio (*Graphium*) *polistratus polistratus* (S.); Peters, 1952: 22.
Graphium polistratus Grose-Smith; D'Abrera, 1980: 46, 47 (fig. [as '*G. colonna* ♂ R' [*sic* – corrected in D'Abrera, 1982]]); Kielland, 1990: 48; d'Abrera, 1997: 56, 57 (fig.).
Graphium (*Graphium*) *polistratus* (Grose-Smith); Hancock, 1983: 46; Collins & Morris, 1985: 59.
Graphium (*Arisbe*) *polistratus* (Grose-Smith); Ackery, Smith & Vane-Wright, 1995: 165.

SYNONYMS

Papilio sisenna Mabille, 1890: 29. HOLOTYPE ♂: MOZAMBIQUE: 'côte de Mozambique'. BMNH Spec.Reg. No. 141165.
Papilio sisenna Mabille; Mabille & Vuillot, 1892: 62, pl.10 fig.4.
Papilio polistratus =*sisenna* Mabille; Le Cerf, 1924*a*: 398. [as syn. n.]
Papilio polistratus var. *sisenna* Mabille; Bryk, 1930*b*: 572.
Papilio (*Graphium*) *polistratus sisenna* (M.); Peters, 1952: 22.
Graphium (*Arisbe*) *sisenna* Mabille; Munroe, 1961: 42.
Graphium (*Arisbe*) *polistratus* =*sisenna* Mabille; Ackery, Smith & Vane-Wright, 1995: 165.

Papilio richelmanni Weymer, 1892: 98. HOLOTYPE ♀: TANZANIA: 'Tanga (Ostafrika) . . . Coll. Blass.' (Weymer, 1892: 99) (not seen).
Papilio polistratus ♀ab. *richelmanni* Weymer; Bryk, 1930*b*: 572.
Papilio (*Graphium*) *polistratus* ♀f. *richelmanni* Weymer; van Son, 1949: 51.
Papilio (*Graphium*) *polistratus sisenna* ♀ab. *richelmanni* (Weym.); Peters, 1952: 22.
Graphium (*Arisbe*) *polistratus* =*richelmanni* (Weymer); Ackery, Smith & Vane-Wright, 1995: 165.

TYPE EVALUATIONS

Though Grose-Smith (1889) used the singular throughout the description, gave one wingspan and even speculated that 'it is probably a hybrid', he did not state explicitly that he based his description of *Papilio polistratus* on a single specimen. However, his specimen, with the correct provenance, in BMNH is clearly labelled 'Type' in his own hand, and should be regarded as the holotype; this specimen was described as 'Type (H.T.)' by Le Cerf (1924: 398). It reached BMNH from Grose-Smith via the Joicey Bequest, BMNH Accession Register No. 1934–120. A second female specimen from Grose-Smith's collection was considered a paratype by Le Cerf (1924), but it must be excluded as being from the wrong locality (Kenya: Teita).

Papilio sisenna Mabille (1890) was described from a single male specimen from Mozambique, in a paper largely devoted to material collected by Alluaud in West Africa. A specimen in BMNH carries a blue determination label, apparently in Mabille's hand in which the '. . . senna' part of the species name is written over part of previous name ('Si . . . [indecipherable]); there is also an indecipherable locality. A further label, apparently in Le Cerf's hand states it to be 'Type/ex coll. Mabille' and there is also a printed Oberthür 'Typicum Specimen' label. The specimen, which consists of the wings and one antenna glued to card, reached the BMNH via Mabille's and Oberthür's collections as part of the Levick Bequest, BMNH Accession Register No. 1941–83.

Papilio richelmanni Weymer (1892: 98) was described from a single female in Blass's collection. The depository of that collection is not indicated by Horn *et al.* (1990).

TAXONOMIC STATUS

Papilio polistratus Grose-Smith (1889: 121) was established as a species, and has been accorded that status by all authors since, though Bryk (1930) and

Peters (1952) treated it as bitypic, with *sisenna* as a separate race.

Papilio sisenna Mabille (1890) was established as a species and treated as such by later authors including Aurivillius (1899; 1910). Le Cerf (1924: 398) recognized that it is the male of *Papilio polistratus* Grose-Smith and this has been accepted by most authors since.

Papilio richelmanni Weymer (1892: 98) was established as a species. Aurivillius (1899: 491) treated it as a variety of *Papilio polistratus* Grose-Smith. Le Cerf (1924: 398) recognized that it is a male-like female form of the latter, possessing clear post-discal marks in hindwing upperside cells M_1 to CuA_1 which are lacking in the holotype of *Papilio polistratus* Grose-Smith. This status has been accepted by subsequent authors.

SIMILAR SPECIES

Similar to the *G. policenes* group in having more-or-less straight bars in the forewing discal cell. The pale markings, especially the post-discal marks, are smaller than in *G. policenes*, more reminiscent of West African *G. liponesco*, but the hindwing post-discals are usually even further reduced. For example, that in hindwing cell R_5 is usually no more than a narrow, transverse band. Larsen (1991) recorded that, compared with *G. policenes*, the bands in *G. polistratus* are 'considerably less green in colour, and the underside is much darker', but these features will be more apparent in fresh specimens.

Most similar to *G. junodi*, from which it may be distinguished by the small size of the forewing postdiscal marks, which are isolated from each other, not forming a continuous band as they do in *G. junodi*. The latter also lacks the nacreous patches which connect the post-discal and submarginal marks on the forewing underside cells R_5 to M_3.

DIAGNOSIS: PATTERN (FIG. 177)

Forewing upperside discal cell with five narrow transverse bars and sometimes a distal spot near the posterior discocellular vein opposite cell R_5. Bars 3–5 are continued beyond the costal vein and each of these bars may be slightly sinuate. Cell R_3 always with an axillary discal spot (continued beyond vein R_3), a square post-discal spot level with the root of vein R_4 and a prominent submarginal spot. Cell R_4 has just a prominent submarginal mark, never a post-discal spot; cell R_5 has a basal post-discal mark and a prominent submarginal. In each of cells M_1 to CuA_1 there is a relatively small, rounded post-discal mark not touching the surrounding veins, these marks increasing in size from M_1 to CuA_1, but not forming a continuous band. The submarginal marks in these cells are narrow and elongate. In cell CuA_2 there is a basal and discal band contiguous with those in the discal cell (and cell 1A) and a square post-discal mark with a small antero-basal 'handle' (smaller than that in *G. policenes*) not usually reaching the posterior discocellular vein. This mark runs along vein 1A, but does not reach vein CuA_2. The submarginal mark in this cell is subdivided. Cell 1A has basal, discal and post discal marks, each contiguous with those in cell CuA_2.

The **hindwing** upperside discal cell has a basal band in its axil and one transverse band whose basal margin is in line with vein CuA_2: the band widens posteriorly. The costal cell has basal and discal bands, a post-discal spot and a transverse submarginal band. These marks are white, rather than green. The post-discal mark in cell R_5 is basal and the submarginal transverse and prominent; cell M_1 is similar, though the post-discal mark is smaller. In cell M_2 the post-discal mark is elongate, elliptical and centred about midway along the cell, and the submarginal mark is less prominent. In cell M_3 there is no discal mark and the post-discal is close to the submarginal mark, which is prominent and arcuate. Cell CuA_1 has an elongate discal mark in line with the transverse band of the discal cell; there is a small post discal spot and a fairly faint transverse submarginal mark. In each of cells M_2 to CuA_1 there is often a scattering bluish scales distal to the submarginal marks, most noticeably in cell M_3. The marginal marks of these cells are prominent, that in cell M_3 extending about half way along the tail, which has an elongate white tip. In cell CuA_2 there is a white basal mark (green fading to white in female, where it may be seen to continue into the anal cell) and a prominent marginal. There is a faint red tornal mark.

The **underside** pattern reflects that of the upperside in the usual manner: the ground and marking colours generally paler and the marks more diffuse. As in the members of the *policenes* group (but not in the more closely related *G. junodi*) there are paler marks linking the post-discal and submarginal marks in **forewing** cells R_5 to M_3, giving a nacreous appearance. The **underside** rubral system is narrower and less clear than in *G. policenes*. In particular, in *G. polistratus* the red band in the discal cell is sometimes reduced to a few scales; sometimes there are a few red scales in the axil of cell M_1. The scattering of bluish scales near the margins of cells M_2 to CuA_1 is more prominent on the underside. By contrast, the post-discal mark in cell CuA_1 is reduced, sometimes to a small dot.

VARIATION

LeCerf (1924) considered *G. polistratus* to exhibit two distinct female forms: the nominotypical form lacking the males' hindwing post-discal marks, and a male-like form (*richelmanni*). However, even the very few female specimens we have seen (4 in BMNH, 1 in ZSMC; we have not seen Weymer's type) shows the situation to be less clear-cut. One BMNH specimen (Spec.Reg. No. 141203) has small hindwing post-discal spots and thus appears to be intermediate. Moreover, two males from ?Kenya (BMNH Spec.Reg. Nos 141205 and 141206) have strongly reduced hindwing post-discal spots, very like the intermediate female.

In addition to the above, and to the normal variability in the size, shape and disposition of the various wing marks, we have observed the following individual variations:

forewing cell bars, while generally straight may be slightly curved or sinusoidal, particularly bars 3, 4 and 5; the distances between these bars are also variable;

distal spot on the forewing discal cell is variable in size, and often absent;

though usually narrow and linear, the submarginal marks in forewing cells M_2 to CuA_1 are sometimes more rounded;

submarginal marks in cell CuA_2 may be fused into a single lobe;

submarginal mark in the hindwing costal cell is variable, sometimes reduced to a fuzzy patch or even virtually absent;

the scattering of bluish scales near the margins of cells M_2 to CuA_1 is very variable, often being virtually absent;

the small post-discal mark in cell CuA_1 sometimes appears pink, due to the red scales of the rubra underneath (this is probably less noticeable in fresh specimens).

The expression of the rubral band of the hindwing underside is quite variable, especially that element in the discal cell, which is usually faint to virtually absent, but sometimes quite well marked. The size of the post-discal marks in posterior hindwing cells is particularly variable.

DIAGNOSIS: ♂ GENITALIA (Fig. 18)
Dorsal projection dorso-ventrally compressed, nearly horizontal, broad based, narrowing smoothly to tip; *dorsal harpe* with horizontal and angled blade-like branches, the horizontal broad-based, serrate above, with ventrad tooth ventrally at tip, the angled blade serrate along mesal edge; *ventral harpe*: a small blade in the vertical plane arising from a narrow base and deeply cleft into a dorsal and a ventral tooth, rather quadrate dorsally, with two small teeth on the dorsal angle; *dorsal terminal process* a mesad and ventrad curved tooth, finely serrate dorsally; *ventral terminal process* sessile, but serrate. *Uncus*: broad based; *socii* with prominent lateral lobes; *distal lobes*: tapering. *Saccus*: quite short, rather bulbous. *Aedeagus*: about as long as genitalia, slightly curved, vesica with a denticulate patch.

DIAGNOSIS: ♀ GENITALIA (Fig. 78)
BMNH Spec.Reg. No. 141147; vial 4704: similar to *G. junodi*; *vestibulum* broad with narrow posterior lip; *ostium bursae* opening in posterior half of vestibulum; *ductus bursae* somewhat sclerotized and kinked distal to the *ductus seminalis* (unlike *G. junodi*), but not pocketed; *central ostial lobe* setose, extremely broad, covering most of posterior part of vestibulum, with a small central lip; *lateral ostial lobes* narrow, well spaced basally, setose, longer than in *G. junodi*; *anterior apophyses* long; *papillae* D-shaped, with some long hook-like setae.

EARLY STAGES. Apparently unknown.

DISTRIBUTION (MAP Fig. 117)
Eastern Africa, from southern Somalia (Collins & Morris, 1985) to Mozambique (Delagoa Bay), inland to Malawi (van Son, 1949; Kielland, 1990; Ackery *et al.*, 1995; Larsen, 1996). Countries confirmed include Somalia, Kenya, Tanzania (including Zanzibar), Democratic Republic of Congo (not recorded by Berger, 1950, 1981), Malawi and Mozambique. There is a specimen in MRAC labelled as being from South Africa (Natal).

HOST PLANTS. Apparently unknown; according to Kielland (1990), the hosts are probably *Annona* and *Uvaria* (Annonaceae).

BIONOMICS
A monotypic species of closed, usually evergreen forests and heavy woodlands, also found in coastal areas and escarpments. Williams (1969), however, notes it as a species of open forest, woodland and coastal scrub. Gifford (1965) describes how in Malawi, where it can be found throughout the year, it also occurs in *Brachystegia* forest, flying in the deeply shaded understorey. Like *G. colonna*, the males often mud-puddle (Larsen, pers. comm., relates how he found the species in huge numbers on puddles at Kasane, northern Botswana), but the females remain within the forest and are rarely encountered (Larsen, 1996). Kielland (1990) notes it as 'flower loving', also readily attracted to moisture and dead decoys, and common in Tanzania from almost sea level to 900 m. (he also found it on top of Bondwa, 2140 m., in the Uluguru Mts). Van Son (1949) gives a record for January (Delagoa Bay); Williams (1969) gives Sept. to May for southern Africa. Swanepoel indicates that its behaviour is broadly similar to that of *G. antheus* and *G. policenes*.

CONSERVATION STATUS. 'Not particularly common, but no threats known' (Collins and Morris, 1985: 59).

MATERIAL EXAMINED. 63 ♂♂; 4 ♀♀ in BMNH; 16 ♂♂; 1 ♀ from other collections.

6. *Graphium (Arisbe) colonna* (Ward, 1873)

Black or Mamba Swordtail (Fig. 178; map Fig. 119; genitalia Figs 19, 79; early stages Figs 249, 250, 259, 260)

A species of very distinctive pattern, early stages and male genitalia that has been placed in a monospecific 'group' by both Berger (1951) and Hancock (1993). In our analyses it is placed as sister of all the afrotropical species (etc.) other than *junodi* and *polistratus* (multistate characters active), or as part of the polytomy basal to the tailless species (multistate characters inactive).

Papilio Colonna Ward, 1873: 151. LECTOTYPE: KENYA: 'Habitat, Ribé, East Africa' (Ward, 1873: 152). BMNH Spec.Reg. No. 136081 – **here designated**.

Papilio colonna Ward; Trimen, 1889: 209–11, pl.11 fig.5; Aurivillius, 1910: 26, pl.8.

Papilio collonna [*sic*] Ward; Bryk, 1930*b*: 573

Papilio (*Graphium*) *colonna* Ward; van Son, 1949: 53; text figs 29, 30; pls V (fig. 16), VI (fig. 16).

Papilio (*Graphium*) *colona* [*sic*] (W.); Peters, 1952: 22.

Graphium (*Arisbe*) *colonna* (Ward); Munroe, 1961: 42; Carcasson, 1981: 13 (fig.), 124; Pennington, 1994: 307, pl.195 figs 727i, ii; Ackery, Smith & Vane-Wright, 1995: 162.

Graphium colonna Ward; D'Abrera, 1980: 46, 47 (fig. [as '*G. gudenusi* ♂ V' [*sic* – corrected in D'Abrera, 1982]]); Keilland, 1990: 47; Larsen, 1991: 117, pl.4 fig.23I; d'Abrera, 1997: 56, 57 (fig.).

Graphium (*Graphium*) *colonna* (Ward); Hancock, 1983: 46; Collins & Morris, 1985: 60.

Synonyms

Papilio tragicus Butler, 1876: 56. LECTOTYPE ♂: [MOZAMBIQUE]: 'Zambesi' (Butler, 1876: 56). BMNH Spec.Reg. No. 136083 – **here designated**.

Papilio colonna = *tragicus* Butler; Trimen, 1889: 209. [as syn. n.]; Bryk, 1930*b*: 573.

Papilio colonna loncona Suffert, 1904: 107. LECTOTYPE ♀: TANZANIA: 'Mikindani . . . Deutsch-Ost-Africa' (Suffert, 1904: 107). BMNH Spec.Reg. No. 136082 – designated Le Cerf (1924: 398); PARALECTOTYPE(S): TANZANIA: 'Mikindani und Lindi, Deutsch-Ost-Africa' (Suffert, 1904: 107). number and gender unknown – none seen.

Papilio colonna ab. *loncona* Suffert; Aurivillius, 1910: 26 [as syn. n.]; Bryk, 1930*b*: 573.

Type evaluations

Ward (1873) gave no indication of series length when he described *Papilio colonna*. According to Horn *et al.*(1990), Ward's primary types were aquired by Oberthür. A specimen from Ward's collection, now in BMNH (via Oberthür and Levick collections, BMNH Spec.Reg. No. 136081), was labelled 'Type'. However, the only indication of locality that this specimen bears is a typewritten label from Levick's collection giving Zanzibar; this label also claims its type status. A further label on this specimen states 'Plate 13/ Upperside Fig. 1/Underside – 2' apparently in Ward's hand and referring to a plate in Ward's *African Lepidoptera* Part 3, which was never published. A copy of this in the Library of the Department of Entomology of BMNH has an uncoloured illustration very similar to the specimen concerned. We assume, therefore, that the Ward specimen in BMNH and labelled (by, presumably, Levick and later by a BMNH curator) as type, is indeed original Ward material. In order to confirm the status apparently accorded it by its label, we select this specimen as lectotype. The 'Zanzibar' locality we assume to be incorrect.

Butler (1876) gave no indication of series length when he described *Papilio tragicus*, but there is no suggestion of more than one specimen. The specimen here designated lectotype is labelled 'type' in Butler's hand. It reached BMNH via Godman & Salvin (BMNH accession 1917–2 – a batch of 3603 butterflies including 97 types). The locality in the description and on the specimen is just 'Zambesi'. We restrict the type locality to Mozambique on the grounds that *G. colonna* appears to be coastal, and not found in countries further up river (See Pennington, 1994).

Papilio colonna loncona was described by Suffert (1904) from several specimens in his own collection. A specimen from Mikindani in the Hill Museum was listed by Le Cerf (1924: 398) as 'Type (H.T.)', constituting selection as lectotype. It reached BMNH via the Joicey Bequest (BMNH accession 1934–20). No further Suffert material was seen by CRS in MNHU or elsewhere.

Taxonomic status

Papilio colonna Ward (1873) was established as a species, a status accepted by all authors since.

Papilio tragicus Butler (1876) was established as a species. It was placed in synonymy with *P. colonna* by Trimen (1889), a status accepted by all authors since.

Papilio colonna loncona Suffert (1904) was established as a subspecies distinguishable by lacking green stripes in hindwing cell CuA_1, a feature which is very variable in *G. colonna*. Aurivillius (1910) treated it as an aberration, as did Bryk (1930). We believe that the name has only been used infrasubspecifically since then.

Similar species

The reduction of post-discal marks on the forewing, the reduction and absence of discal and post-discal marks on the hindwing, and the presence (usually) of two red spots on the hindwing make *G. colonna* distinctive. The only possible confusion might be with certain aberrations of other sword-tailed species (e.g. *G. policenes* ab. *coussementi*) also lacking discal and post-discal marks.

Diagnosis: pattern (Fig. 178)

Upperside background colour dark chocolate brown with a pattern of blue/green marks, more vivid in fresh specimens. **Forewing** discal cell with 5 transverse bars, bar 2 being the widest, bar 5 sinuate; the bars continued into the costal area. A distal spot opposite cell R_5 represents bar 6. Cell R_3 with a small discal mark, quadrate post-discal mark level with root of vein R_4, and a transverse/linear submarginal mark. Cell R_4 usually with an axillary post-discal mark and a transverse/linear submarginal mark. Cell R_5 usually with fused discal and post-discal marks proximally, and a submarginal mark. Cells M_1 and M_2 each with a basal rhomboid or trapezoid post-discal mark set close to the posterior discocellular vein, and a transverse/linear submarginal mark. Cell M_3 with a linear post-discal mark, running diagonally distad from angle of the posterior discocellular vein and vein M_3 (but touching neither); the submarginal mark transverse/linear. Cell CuA_1 with post-discal mark linear, displaced distad and running distad posteriorly. Cell CuA_2 with narrow basal band; broader discal band continuous with discal cell bar 2; narrow, linear post-discal band running diagonally and slightly sinuously distad from angle of the posterior discocellular vein and vein CuA_2 (touching both); and transverse/linear submarginal mark almost continuous with post-discal mark of cell CuA_1. Cell 1A with narrow basal band; broader discal band continuous with that in cell CuA_2; and narrow post-discal mark in line with that in cell CuA_2.

Hindwing upperside discal cell with narrow basal band and a narrow band joining discal mark of cell R_1 to that of cell CuA_1 (where present). Cell R_1 with narrow basal mark; boader, mainly silvery discal mark; and narrow, transverse/linear submarginal mark. Cells R_5 and M_1 usually each with just a transverse, triangular submarginal mark, narrowing posteriad. Cells M_2 and M_3 with at most a very faint submarginal mark. Cell CuA_1 usually with a linear discal mark and a prominent red, transverse spot. Cell CuA_2 with a linear discal mark contiguous with the basal marks of the discal and costal cells; and usually a red spot. The tip of the tail on vein M_3 is white, sometimes extending more than halfway to the root on the hind margin, slightly less on the distal margin. Marginal marks clear in cells M_2 and CuA_1, but less so in other cells.

This pattern is mirrored on the **underside**, with a less dark ground colour, and less vivid marks. The rubral system is prominent with elements in the discal and all peripheral cells except M_1 and, usually, M_2 (less clear in cell M_3, but particularly prominent in cells CuA_1 and CuA_2); there is a dark brown mark distal to the rubra in each cell (these marks basal in cells M_1 and M_2). Faint submarginal marks are visible in cells M_2 to CuA_2.

VARIATION

There is variability in the extent, disposition and shape of the pale marks. Particular points we have noticed include:

in one BMNH specimen (Spec.Reg. No. 136260), forewing discal cell bars 2 and 3 are joined by a slightly diffuse pale band near the posterior discocellular vein;

forewing discal cell distal spot (bar 6) variable in size – sometimes reduced to a small spot;

discal and post-discal marks of forewing cell R_3 sometimes touch, occasionally almost fusing;

forewing cell R_4 post-discal spot varies considerably in size, and may be absent;

forewing cell R_5 occasionally with discal and post-discal marks partly free;

a few specimens have a small pale mark running along the cubital vein (slightly more frequent in Mozambique);

forewing cell 1A post-discal band is variable in size, and may be absent;

a few specimens show a small faint post-discal mark in hindwing cell R_5;

hindwing cell CuA_1 discal mark is very variable in length, and may be absent (as in f. *loncona* Suffert);

the red spot in hindwing cell CuA_2 may be reduced;

underside hindwing cell M_2 occasionally with axillary rubral mark.

DIAGNOSIS: ♂ GENITALIA (Fig. 19)

The only African species, apart from *G. antheus*, in which the dorsal and ventral elements of the harpe are clearly joined.

Dorsal projection broad based, narrowing to tip; sharply curved ventrally to wrap around dorsal harpe and overlap ventral harpe. *Dorsal harpe* pointed at tip, extending beyond valve margin dorsal to the dorsal terminal process. *Ventral harpe* with root extended to reach the root of the dorsal harpe; blade extending as a point beyond the valve margin, also dorsal to the dorsal terminal process (autapomorphy) and partly wrapped by the dorsal projection; a further point or tooth level with the ventral terminal process. *Dorsal terminal process* a mesally and ventrally directed chisel-like tooth. *Ventral terminal process* almost sessile, serrate. *Uncus* elongate; *socii* broad, but not prominent; *saccus* elongate. *Aedeagus* long, almost straight, apparently without denticulation.

DIAGNOSIS: ♀ GENITALIA (Fig. 79)

BMNH Spec.Reg. No. 136224; vial 3991: *vestibulum* transverse; *ostium bursae* opening anteriorly; *ductus bursae* sclerotized and elongate distally with kink/constriction distal to *ductus seminalis*, but not pocketed; *central ostial lobe* small, glabrous triangular, not reaching edge of laterals; *lateral ostial lobes* broad, but not very long, setose; *anterior apophyses* elongate; *papillae anales* rounded.

G. illyris is similar.

EARLY STAGES (Figs 249, 250, 259, 260)

The fourth larva has three green, saddle-markings, the one occupying the dorsum of abdominal segments 1–6 being the largest; above the lateral line, the remaining areas up to the green saddle marks are dark, and covered with granular, blunt points, as seen in alcohol preserved material (BMNH). In the final instar the brown areas are partly replaced by green, so that the saddles are less distinct from the rest of the body, to give a pattern of broken stripes and bands. Overall, the larva is very distinctive amongst the known species, somewhat reminiscent of that of a notodontid moth.

The bluish-green pupa is distinctive in shape, with the lateral longitudinal ridge running forward from the cremaster on each side curved around a smoothly bulbous expansion of the basal abdominal segments, and the anterior chisel-shaped, completely lacking a dorsal horn.

The larval and pupal stages are described by van Son (1949), based on the work of Mrs Monteiro (in Trimen, 1889). The mature larva, with its striking black markings, is referred to by Larsen (1996a) as 'magnificent'. Henning *et al.* (1997) and Colin Congdon (*in litt.*, 27.ix.1999) provide colour photographs. Sevastopulo (MS) recorded larvae of what is undoubtedly this species under the name '??*Papilio colona*', as follows:

> 1st instar – Head yellowish brown. Body blackish-olive, anal somite whitish. A double dorsal, a subdorsal and a lateral series of very small, setiferous scoli, the three thoracic subdorsal ones very much larger than the others. Moulted 29.iv.62.
>
> 2nd instar – Head olive-brown. Body dark coffee brown, 1st somite olive-yellow, an olive-yellow dorsal blotch on somites 6 to 8, straight across anteriorly and running into a point posteriorly. Subdorsal scoli on thoracic and anal somites large, the others reduced to bristles. Moulted 1.v.62.
>
> 3rd instar – Very similar. The contrast between the dark and pale areas greater. Subdorsal thoracic and anal scoli large and prominent, the others absent.
>
> Larvae found in Marere Forest. Died.
>
> 3rd instar – See previous description. Moulted 13.i.64.
>
> 4th instar – Similar to preceding. Osmeterium yellowish green. Moulted 20.i.64.
>
> Final instar – Head red-brown. Body black. 1st somite green dorsally with a subdorsal streak extending backwards onto the 2nd. A diamond-shaped dorsal green blotch from the posterior edge of the 4th somite to the 10th, the anterior edge fairly straight across, the posterior tapering to a blunt point. 11th and 12th somites also with a diamond-shaped dorsal green blotch, tinged slightly with red-brown. Thoracic somites each with a subdorsal yellowish scolus. Anal somite with divergent processes, yellow-brown above and blackish below. Venter, legs and prolegs reddish brown tinged with green.
>
> Described from a larva found in Marere Forest. Died.
>
> Osmeterium greenish yellow. Later in the instar the black of the lateral and sublateral areas turns a rich coffee brown. When preparing for pupation the green colour changes to a yellowish olive with a subdorsal olive stripe, slightly broader on the anterior edge of each somite and a double series of streaks laterally, the anterior above and the posterior below.
>
> [Sevastopulo's descriptions are accompanied by nine black and white photographs.]

DISTRIBUTION (Map Fig. 119)

An east African species, found from Somalia to Zululand. Countries confirmed include southern Sudan, southern Ethiopia, southern Somalia, Kenya, Uganda, Tanzania (including Pemba), Zambia, Malawi (apparently rare: Gifford, 1965), Mozambique and South Africa (Natal) (Ackery *et al.*, 1995).

HOST PLANT RECORDS

Annonaceae:

Annona sp. (Larsen, 1996).

A. monteiroae (Migdoll, 1988).

Artabotrys (possibly *A. monteiroae* or *A. brachypetalus*) (Larsen, 1996).

U. caffra (Henning *et al.*, 1997, as found in northern Kwa-Zulu).

Uvaria kirkii (Congdon, *in litt.* 1999, noting that although *colonna* was abundant at the time, larvae were not found on any other plant).

Uvaria sp. Larsen (1996a)

'unidentifed annonaceous shrub' (Sevastopulo, MS).

BIONOMICS

According to Larsen (1996a), this monotypic species primarily occurs in eastern coastal forests (and heavy woodland: Kielland, 1990), and other relatively low forests inland to Kulal, Meru and southern Ethiopia, various localities in Tanzania (Kielland, 1990) including Pemba, and evidently Malawi. Larsen (*op. cit.*) notes that males often mud puddle, and otherwise behave typically for the genus (including attraction to flowers, when the butterflies may fly low to the ground: Swanepoel, 1953). The more rarely encountered females can be seen at flowering shrubs in early morning (Williams, 1969). Swanepoel (1953) noted that nectaring may also be observed as late as 5 p.m., even along shaded and dark forest tracks. The flight is evidently fast and irregular, like other tailed *Graphium*, sometimes flitting high about trees and bushes, and hovering from time to time. The equally fast-flying females are rarely encountered. However, according to Henning *et al.* (1997), this species, although swift, does not fly 'as fast as its congeners unless aroused' (this impression is also given by Migdoll, 1988, who even says if is 'fairly slow flying . . . flying lazily along the edges of the forest'); Henning *et al.* also note that it seems less territorial than other species, but the butterflies will patrol around forest margins and dense bush, when they rarely fly much more than a metre above the ground (this fits with the description of Mrs Monteiro given in Trimen, 1889, 'she noticed that it seldom flew high, but kept about two feet from thr ground, pursuing a circular course in and about dense bush'). Kielland states that it occurs at altitudes from 0–600 m. For southern Africa van Son (1949) gives records from Jan.–May only, but Henning *et al.* (1997) give Nov. – Feb., with stragglers until April; Swanepoel (1953) described the flight period as end Sept. to April, and this is apparently repeated by Williams (1969), who also notes that it flies thoughout the year in more tropical areas, being most abundant during the rains; Migdoll (1988) gives stragglers in June and July for southern Africa. The larvae are distinctive (see above); the flanged pupae have weak girdles that often break, to leave the chrysalids suspended; the pupal stage lasts about two weeks (Henning *et al.*, 1997). See also Trimen (1889: 209–11), Monteiro (1891).

CONSERVATION STATUS. 'Not known to be threatened' (Collins & Morris, 1985: 60).

MATERIAL EXAMINED. 238 ♂♂; 47 ♀♀ in BMNH. 22 ♂♂; 6 ♀♀ from other collections.

7. *Graphium (Arisbe) illyris* (Hewitson, 1872)

Yellow- or Cream-banded Swordtail (Figs 179, 216–218; map Fig. 114, 115; genitalia Figs 20–23, 80)

A distinctive species comprising four subspecies from tropical West and central Africa and the island of Bioko.

Both Berger (1951) and Hancock (1993) included it in a group with *G. kirbyi* and *G. gudenusi*, on the basis of the male genitalia, though, in our opinion the resemblances are not marked and the female genitalia also differ. In our analyses, *G. illyris* is placed in a polytomy with other swordtailed species, including *G. gudenusi*, basal to the crown group. When multistate characters are active, this polytomy includes the *angolanus* group, etc.

The populations from the western (Sierra Leone to central Ghana), and eastern/southern (Nigeria to Democratic Republic of Congo) parts of the range can be divided into two subspecies. This was formalized by Guilbot and Plantrou (1978), who designated a neotype for *illyris* (believing Hewitson's type to be lost; it has now been found, see below) while restricting it to West African populations, and naming the central african race *girardeaui*, expressly excluding *G. i. hamatus* (Joicey & Talbot, 1918).

G. i. hamatus (Joicey & Talbot, 1918) was described from a single male specimen allegedly from Tanzania ('German East Africa'), though the species was not recorded there by Kielland (1990). It has similar, but not identical, genitalia to *i. illyris*, corroborating Guilbot and Plantrou's (1978) separation. Distinctive features of its wing pattern could represent a genuine racial difference, but may simply be individual variation. More material is needed to show either that this pattern can occur elsewhere in the species' range, or to confirm the presence of the species in Tanzania (with or without the *hamatus* pattern). Without further material, we therefore retain *hamatus* as a separate, if somewhat doubtful, subspecies, following the apparent intention of Guilbot and Plantrou (1978).

The Bioko population was described as a subspecies (*G. illyris flavisparsus* Fruhstorfer, 1903), but has been treated by recent authors (e.g. Canu, 1994; d'Abrera, 1997) as of specific rank, a change we regard as an unjustified example of grade inflation that would necessitate raising the status of the other subspecies (see below).

We give the pattern diagnosis for the species below, with subspecific differences covered under each of these. We have been able to examine the female genitalia of only the nominate race; this and the male genitalia are therefore described under *G. i. illyris*. The scant biological information is given at the species level.

SIMILAR SPECIES

G. kirbyi also has a simple upperside pattern, but in that species, the band on the forewing curves towards the apex of the wing; not the costa as it does in *G. illyris*. Details of this and other differences are described below.

DIAGNOSIS: PATTERN (Figs 179, 216–218)

Distinguished from almost all other sword-tailed afrotropical *Graphium* by its simple wing pattern. The ground colour of the **uppersides** of both wings is dark brown and there is a narrow yellow/cream band running from the inner to the costal margin of the **forewing**, just anterior to the tip of the discal cell. The band consists of the post-discal marks in cell 1A to M_1 and (probably) fused discal and post-discal marks R_3, largely proximal to the root of R_4, whereas in *G. kirbyi*, the band in cell R_3 is represented by a submarginal mark entirely and markedly distal to the root of R_4; only rarely in *G. illyris* is there a post-discal mark in cell R_4, unlike in *G. kirbyi*. The combined effect of this is that the band curves costally anteriorly in *G. illyris*, but apically in *G. kirbyi*. The discal cell usually lacks any marks; there are no basal or discal marks in cells CuA_1 or CuA_2. Submarginal marks are usually lacking (but see account for *G. i. illyris*, below).

The band is continued from the costal to the inner margin of the **hindwing**, consisting of the post-discal mark in cells R_1 and R_5, the distal band in the discal cell, and discal marks in the base of cell M_3 and in cells CuA_1 and CuA_2. There are more-or-less prominent, submarginal marks – bluish in *G. i. illyris*, *girardeaui* and *hamatus*, yellow in *G. i. flavisparsus* – and the marginal marks, too, are prominent, being pale in *G. i. illyris*, golden-yellow in *G. i. girardeaui*, *hamatus* and *flavisparsus* (in *G. kirbyi* the submarginals are much less prominent, and marginal marks are only faint). Apart from in cell R_5, where it forms part of the band, post-discal marks are absent, as are basal marks in the discal cell and costal cells and a discal mark in cell R_1. The tail on vein M_3 is white tipped. The hindwing is distinctly broader than in *G. kirbyi*.

This pattern is reflected on the **underside** with some complications, especially on the **hindwing**. The rubra is well marked. It consists of a narrow band crossing cell R_1 level with the root of vein R_5; accordingly, there is a very small red mark in the axil of cell R_5. The discal cell has a prominent red spot occupying most of the area distal to the pale band. There is, again, a very small red spot in the axil of cell M_2, and clear, but narrow, bands across cells M_3 and CuA_1, and a somewhat broader band across cell CuA_2. The submarginal spots are much less prominent than on the upper side, being pale brown. There is a small, pale post-discal spot near the base of cell M_1, and, between it and the sub-marginal mark, a scattering of bluish scales. There is a similar bluish dusting between the rubral and submarginal marks in cell CuA_1. Fainter bluish patches occur between the submarginal and marks of cells R_1 to M_2, and a few such scales may be seen in cells M_3 and CuA_1. The ground colour of the underside is paler brown than the upper, with the distal margin of the forewing paler still. On the hindwing there are darker areas between the various pale and rubral marks, especially distal to the main pale band.

Females – rare in collections – have a similar pattern to the males with similar inter-subspecific differences, though with less intense ground and marking colours.

VARIATION. See subspecies accounts.

DIAGNOSIS: ♂ GENITALIA (Figs 20–23)
The male genitalia described in some detail for *i. illyris*, below, with the differences shown by the other subspecies indicated in the appropriate sections.

DIAGNOSIS: ♀ GENITALIA (Fig. 80). See account for *G. i. illyris*.

EARLY STAGES; HOST PLANTS. Apparently unknown.

BIONOMICS
Four subspecies are recognized (*G. i. illyris, G. i. girardeaui, G. i. hamatus,* and *G. i. flavisparsus*), of which the last is a striking insular race. This beautiful west and central African rainforest butterfly is, according to Larsen (In prep.*a*), a seasonal, apparently lowland species, sometimes seen at water (he also gives a record from rotting fish); Larsen also notes (pers. comm., 1999) that it can often be found on mud, but in deeper forest than most *Arisbe*. Fontaine (1985: 114) states that in Congolese forests it prefers the borders of streams and rivers, and Darge (1995) indicates that subspecies *girardeaui* is mainly seen in the Mount Kala area of Cameroon along river banks, from Dec.–March, the female flying more slowly than the male. Although Collins & Morris (1985) considered it 'not uncommon', specimens are not plentiful in collections and Larsen implies that it can be quite scarce. Owen & Owen (1972) noted a single specimen seen from the North Gola Forest in Sierra Leone, which they considered to be its most westerly extension. Records for Jan., Mar., April, Oct., Dec. Canu (1994) describes *G. i. flavisparsus* from Bioko as rare, but nonetheless obtained about 20 specimens in 1984, captured during separate trips in January, April and October.

CONSERVATION STATUS. 'Not uncommon but not known to be threatened' (Collins and Morris, 1985: 60).

7a. *G. (A.) illyris illyris* (Hewitson, 1872)

Western Yellow- or Cream-banded Swordtail (Fig. 179; map Fig. 114; genitalia Figs 20, 80)

Papilio illyris Hewitson, 1873*a*: 232. LECTOTYPE ♂: GHANA: 'Gold Coast' (Hewitson, 1872: 233). BMNH Spec.Reg. No. 143454 – **here designated.**
Papilio illyris Hewitson, 1873*b*: [2], pl.13 figs 43, 44.
Papilio illyris Hewitson; Aurivillius, 1908: 26; Bryk, 1930*b*: 573.
Graphium illyris Hewitson; Berger, 1950: 91.
Papilio (Graphium) illyris illyris (Hew.); Peters, 1952: 22.
Graphium (Arisbe) illyris (Hewitson); Munroe, 1961: 42; D'Abrera, 1980: 46, 47 (fig.); Berger, 1981: 53, pl.17 figs 4, 8 (♂♂), pl. 18 fig. 1 (♀).
Graphium (Arisbe) illyris illyris (Hewitson); Guilbot & Plantrou, 1978: 69; Ackery, Smith & Vane-Wright, 1995: 163.
Graphium (Graphium) illyris (Hewitson); Hancock, 1983: 46; Collins & Morris, 1985: 60.
Graphium (Arisbe) illyris illyris (Hewitson); d'Abrera, 1997: 54, 55 (fig.).

UNAVAILABLE NAME
Papilio illyris f. *stictica* Le Cerf, 1924*a*: 399, pl.5, fig.52. GHANA.: '1 ♂, Gold Coast (Ghana), Koumassi, Friapere Forest, 1913 (BMNH)' (designated unnecessarily as neotype of *G. i. illyris* by Guilbot & Plantrou, 1978: 70). BMNH Spec.Reg. No. 143441. [infrasubspecific.]
Papilio illyris f. *stictica* Le Cerf, 1924; Bryk, 1930*b*: 573.
Graphium illyris illyris =*stictica* (Le Cerf); Guilbot & Plantrou, 1978: 68 (as syn. n.).

TYPE EVALUATIONS
Papilio illyris was described from an unstated number of specimens 'taken by Mr. Henry Rogers, on his way to St. Paulo de Loanda' (Hewitson, 1873*a*: 233). However, Hewitson described only the male, used the singular, and gave only a single size, so probably only one specimen was involved. According to Kirby (1879) there was one specimen of the taxon in Hewitson's collection at the time of its bequest to BMNH (BMNH accession No. 1879–69), which was believed lost, but which we have recently been able to locate. The specimen matches well with Hewitson's (1873*b*) figure. It previously had only a single printed label: 'Hewitson coll./79–69/Papilio' with 'Illyris' added by hand (possibly Kirby's). We designate that specimen as lectotype

in order to prevent confusion in the light of the following.

When Hewitson's type was presumed lost, Guilbot & Plantrou (1978) deemed it necessary to designate a neotype for the nominate, West African race, in order to clarify the status of the various subspecies. They chose the 'holotype' of Le Cerf's (1924) form *stictica*. They also designated other members of that type series as 'Paranéotypes' and a female from Ghana: Sunyami (BMNH Spec.Reg. No. 143439) as 'Néallotype', neither term recognized under the Code (ICZN, 1999). The specimen chosen as neotype by Guilbot & Plantrou (1978), being the prime exemplar of the form *stictica*, shows prominent submarginal spots on the forewing, a variable feature not seen in Hewitson's type. Under the Code (ICZN, 1999, Article 75.8), the neotype is now 'set aside' in favour of the newly designated lectotype.

TAXONOMIC STATUS

Papilio illyris was described by Hewitson (1872) as a species and has been regarded as the valid name for the taxon (now restricted to the West African subspecies) by all authors since then.

Papilio illyris f. *stictica* was described by Le Cerf (1924: 399) as a form pre-1960, but with the indication that other specimens from the same locality are not of this form, thus it should be considered infrasubspecific, despite the fact that on the legend to the plate, the taxon is styled '*P. illyris* Kirby [sic] f. (? an s.sp.) *stictica* nova'. It was described from 10 specimens – from an original 14 from the locality – in the Hill Museum, Witley, with a 'holotype' and nine 'paratypes' originally designated. Most, but not all of the contents of the Hill Musem reached the BMNH as the Joicey Bequest, BMNH accession No. 1934–120. Only six of the expected paratypes can be found in BMNH.

DIAGNOSIS: PATTERN (Fig. 179)

The differences in colour between the nominate subspecies and *G. i. girardeaui* are subtle and not totally reliable, but are enough – especially in combination – to distinguish them. These differences also separate *G. i. illyris* from *G. i. flavisparsus* and *G. i. hamatus*, both of which are more similar to *G. i. girardeaui*.

The pale band is generally slightly narrower in *G. i. illyris* and curves more markedly towards the costal margin anteriorly on the **forewing**. This is due to the spot in cell R_3 being smaller, not, or but barely reaching the root of vein R_4, whereas in *G. i. girardeaui* it generally reaches beyond the root by a millimetre or two. On the **hindwing**, the band appears to curve slightly away from the inner margin due to the discal mark being somewhat more narrowly based in cell CuA_1 compared to *G. i. girardeaui*, and being extended along vein CuA_2; the band also terminates in this cell, whereas in *G. i. girardeaui* , and *G. i. hamatus* it usually continues into cell CuA_2.

G. i. illyris often has a row of submarginal spots on the forewing, but this is by no means universal; as the spots range from distinct to obsolete. When distinct, they serve as a good identifier, as they are very unusual, and then only very faint, in *G. i. girardeaui*.

The hindwing of *G. i. illyris* appears narrower than that of *G. i. girardeaui*, which is somewhat expanded in the region of cell M_2, as shown in Fig. 217. Accordingly, the wing margin in *G. i. illyris* appears less scalloped in this region.

Guilbot and Plantrou (1978) pointed out that the submarginal marks of the hindwing, especially in cell CuA_1, are smaller in *G. i. girardeaui* but, as these are variable in both taxa, such differences can at best be regarded as variable.

The marginal marks of the hindwing in *G. i. illyris* are generally, though not always, paler than in *G. i. girardeaui*, in which they are deep gold.

VARIATION

The form *stictica* Le Cerf (1924) was named for individuals that exhibit submarginal spots in forewing cells R_3 to CuA_2, but this is a very variable feature ranging through degrees of faintness to absence and can vary between cells within a single wing. The submarginal spots on the hindwing are also somewhat variable, especially that in cell R_1 which may be present, faint or absent. The hindwing submarginal spots do not seem to covary with the forewing spots, either in size or clarity.

Marginal spots are sometimes visible on the forewing. Those on the hindwing are usually creamy white to pale yellow, but are occasionally darker, approaching the rich gold seen in the other subspecies.

The discal and post-discal marks which form the wing band vary in size between individuals, either in a co-ordinated way – so that the band can be broader or narrower – or by individual cells – so as to disrupt the regularity of the band. In particular, the spots of the anterior cells (R_3 to R_5) may be more-or-less contiguous or divided by the veins.

On the hindwing underside, the size and disposition of the rubral marks varies a little. For example, some individuals lack the brown spot at the centre of the red mark in the discal cell.

DIAGNOSIS: ♂ GENITALIA (Fig. 20)

Overall shape rather quadrate, with no dorsal, basal expansion. *Dorsal projection* dorso-ventrally compressed basally, but twisted to become laterally compressed distally and expanded dorsally, with a concavity on the posterior face; stout setae mainly on anterior face. *Dorsal harpe* horizontal, laterally compressed, broadening distally and recurved dorsally at tip; serrate distally. *Ventral harpe* broadly triangular, with broadest part level with distal origin; posterior angle a little expanded; mesal edge serrate. *Dorsal terminal process* tooth-like (faintly bifid at tip), directed sagittally. *Ventral terminal process* elongate, parallel sided, tooth-like and slightly serrate at the tip. *Uncus* long. *Socii* bulbous, setose. Saccus small. Aedeagus quite short, with some denticualtion on vesica.

DIAGNOSIS: ♀ GENITALIA (Fig. 80)
BMNH Spec.Reg. No. 149264; vial 3988: *ostium bursae* opening anteriorly; *ductus bursae* slightly elongate and sclerotized distally, with kink/constriction just distal of *ductus seminalis*; *central ostial lobe* small (not reaching end of laterals, much shorter than in *kirbyi*), triangular, glabrous spike; *lateral ostial lobes* large, very broadly based; *anterior apophyses* elongate; *papillae anales* rounded.

EARLY STAGES; HOST PLANTS. Unknown.

DISTRIBUTION (Map Fig. 114). Western Africa, recorded for Sierra Leone, Liberia, Ivory Coast, Ghana.

BIONOMICS, CONSERVATION STATUS. See species account.

MATERIAL EXAMINED. 29 ♂♂; 1 ♀ in BMNH. 4 ♂♂ from other collections.

7b. *G. (A.) illyris flavisparsus* (Fruhstorfer) stat. rev.

Bioko Yellow- or Cream-banded Swordtail (Fig. 216; map Fig. 115; genitalia Fig. 21)

Papilio illyris flavisparsus Fruhstorfer, 1903: 359. HOLOTYPE ♂: EQUATORIAL GUINEA: '. . . Fernando Po . . .' [Bioko] (Fruhstorfer, 1903: 359). Depository unknown (not seen).

Papilio illyris =flavisparsus Fruhstorfer; Bryk, 1930*b*: 573.

Graphium illyris flavisparsus Fruhstorfer; Guilbot & Plantrou, 1978: 68.

Graphium (Arisbe) illyris illyris =flavisparsus (Fruhstorfer); Ackery, Smith & Vane-Wright, 1995: 163.

Graphium flavisparsum [*sic*] Fruhstorfer; Canu, 1994: 313 (as stat. n.).

Graphium flavisparsus Fruhstorfer; D'Abrera, 1997: 54 (as stat. n.).

TYPE EVALUATIONS
Papilio illyris flavisparsus was described from '1 ♂ von Fernando Po . . .' (Fruhstorfer, 1903: 359). The author gave no indication of the whereabouts of the material, but it was presumably in his own collection or possibly Stettin (since the paper was in the *Stettiner Ent. Ztg*). There is no mention of the taxon in Martin's (1922) catalogue of Fruhstorfer's types.

TAXONOMIC STATUS
Papilio illyris flavisparsus was described by Fruhstorfer (1903: 359) as a subspecies and has been treated as such by most authors since. Recently, however, Canu (1994) and d'Abrera (1997) have treated the taxon as a full species. We think this is unjustified. The differences in wing pattern, though clear and consistent, are matters of size and position of a few marks which show individual variability throughout the genus. The genitalia are almost identical to those of *G. i. girardeaui*. In both pattern and genitalia, *flavisparsus* and *girardeaui* are more similar to each other than either is to *illyris*. Treating *flavisparsus* as a full species, therefore, would logically entail treating all three (and *hamatus*) as full species. We believe that *flavisparsus* demonstrates the generally accepted criteria of subspecies, namely a recognisable but similar phenotype coupled with allopatry, and so restore its status to that of a subspecies of *Graphium illyris*.

SIMILAR SUBSPECIES. *G. i. flavisparsus* is most similar in both pattern and male genitalia to the other central african subspecies, *G. i. girardeaui*.

DIAGNOSIS: PATTERN (Fig. 216)
The most striking difference between *G. i. flavisparsus* and *G. i. girardeaui* is the enlarged submarginal marks on the hindwing of the former, especially in cells M_2 and M_3. These are also yellow, without the bluish cast seen in the other subspecies. This brightness is reflected on the underside, where this region of the wing is also yellow, rather than the dull to dark brown seen in the other subspecies. Also on the hindwing, the marginal marks are considerably broader and more striking than in the other subspecies, with the same golden colour as in *girardeaui*.

The forewing pale band is even straighter in *G. i. flavisparsus* than in *G. i. girardeaui*. The mark in cell R_3 is almost entirely distal to the root of vein R_4 and probably represents just the post-discal mark. The mark in cell R_5 is smaller than is normal in the other subspecies, with the reduction on the proximal margin of the mark to give the effect of displacement from the cell base.

VARIATION
In some specimens there may be a small spot in the axil of forewing cell R_4. A small, but clear, submarginal dot may sometimes be seen in the angle between vein CuA_2 and the marginal mark in that cell. Canu (1994) states that marginal marks may be detected in cells M_2 to CuA_1 of the forewing in about half the specimens seen by him.

DIAGNOSIS: ♂ GENITALIA (Fig. 21)
Very similar to the nominate subspecies. The *dorsal harpe* is less obviously recurved, but with denticles on the mesal surface (more like *girardeaui*). The dorsal terminal process has some denticles on the external, ventral edge. The *ventral harpe* has some fine denticulation in addition to the coarser teeth.

DIAGNOSIS: ♀ GENITALIA. We have not been able to examine the female genitalia.

EARLY STAGES; HOST PLANTS; BIONOMICS; CONSERVATION STATUS. Unknown.

DISTRIBUTION (Map Fig. 115). Equatorial Guinea (Bioko).

MATERIAL EXAMINED. No specimens in BMNH. 2 ♂♂ from other collections (ABRI).

7c. *G. (A.) illyris girardeaui* Guilbot & Plantrou, 1978

Central African Yellow- or Cream-banded Swordtail (8 Fig. 217; map Fig. 115; genitalia Fig. 22)

Graphium illyris girardeaui Guilbot & Plantrou, 1978: 70. HOLOTYPE ♂: CENTRAL AFRICAN REPUBLIC: '1 ♂, Empire centrafricain, Bangui, II-1972 (*R. P. Godart*)' (Guilbot & Plantrou, 1978: 72.). 'coll. R. Guilbot' (Guilbot & Plantrou, 1978: 72.) – **not seen**. 10 PARATYPE ♂♂: CENTRAL AFRICAN REPUBLIC: '2 ♂, *id.*; 2 ♂, *id.*, III-1972 (*R. P. Godart*); 5 ♂, *id.*, 3-IV-1975' (Guilbot & Plantrou, 1978: 72.). CAMEROON: '1 ♂, Cameroun, Kala, 13-III-1975'. 'coll. R. Guilbot, J. Plantrou et MNHN' (Guilbot & Plantrou, 1978: 72.) – **not seen**. 1 PARATYPE ♀: CENTRAL AFRICAN REPUBLIC: '1 ♀, Empire centrafricain, Bangui, 9-IV-1975 (*R. P. Godart*)' (Guilbot & Plantrou, 1978: 72.). 'coll. J. Plantrou' (Guilbot & Plantrou, 1978: 72.) as 'allotype' – **not seen**.

Graphium (Arisbe) illyris girardeaui Guilbot & Plantrou; Ackery, Smith & Vane-Wright, 1995: 163.

Graphium (Arisbe) illyris girardeaui Guilbot & Plantrou; d'Abrera, 1997: 54.

UNAVAILABLE NAME

Papilio (Cosmodesmus) illyris ab. *addenda* Dufrane, 1946: 121. DEMOCRATIC REPUBLIC OF CONGO. IRSN. [infrasubspecific]

TYPE EVALUATIONS

Graphium illyris girardeaui Guilbot & Plantrou (1978) was described from the twelve specimens listed above, from among 30 ♂♂ and 3 ♀♀ studied by them, with type designations original.

TAXONOMIC STATUS

Graphium illyris girardeaui Guilbot & Plantrou (1978) was established explicitly for the central African (Nigeria to Democratic Republic of Congo) populations of the species. Guilbot & Plantrou (1978) excluded *G. i. hamatus* (Joicey & Talbot, 1918), described from a single specimen from Tanzania, which would otherwise be the senior name. In the absence of further data (see species' heading, above) we here follow Guilbot & Plantrou's (1978) arrangement.

SIMILAR SUBSPECIES. *G. i. girardeaui* is more similar phenotypically to subspecies *flavisparsus* and *hamatus* than any of these are to *G. i. illyris*.

DIAGNOSIS: PATTERN (Fig. 217)

The features which distinguish *G. i. girardeaui* from *G. i. illyris* are discussed in detail in the account for the latter subspecies. Briefly they are: pale wing band broader and less curved towards forewing costal margin; band continued into hindwing cell CuA_2; forewing submarginal marks, at most, extremely faint; hindwing expanded in the region of cell M_2, with wing margin more scalloped; marginal hindwing marks golden.

Compared with *G. i. flavisparsus*, *G. i. girardeaui* has smaller hindwing submarginal marks and these are bluish rather than yellow; submarginal areas of hindwing underside dull, not yellow; marginal marks of hindwing narrower; wing band slightly curved costally anteriorly in forewing.

G. i. girardeaui lacks the pale mark along the upper discocellular vein of the hindwing discal cell which distinguishes the only known specimen of *G. i. hamatus*.

VARIATION

As mentioned above, there is a certain amount of variability in the size and position of the elements which make up the main wing band and in the size of the hindwing submarginal marks.

In one specimen in BMNH there is a spot in forewing discal cell opposite cell R_5. A few specimens have a small spot in the axil of forewing cell R_4. Rarely, there are faint indications of submarginal marks on the forewing.

On the hindwing underside there is usually a small post-discal spot in cell R_5, though this is of variable size and is sometimes absent. Rarely, there is also a small post-discal spot in cell M_1.

As in the nominate subspecies there is some variability in the form of the hindwing underside rubral system. In particular, the brown mark distal to the red in the discal cell is of variable size and occasionally absent.

DIAGNOSIS: ♂ GENITALIA (Fig. 22)

Valve basically similar to the nominate race, with the following differences:

Dorsal harpe, narrower, with fewer serrations and so appearing less obviously curved in lateral view. *Ventral harpe* not serrate overall, but subdivided into a blade-like posterior process and a broad medial process, itself deeply bifid, the anterior part carrying a small toothlet near its tip on the anterior edge. *Ventral terminal process* shorter, broader, less tooth-like.

DIAGNOSIS: ♀ GENITALIA. We have been unable to examine the genitalia of any females of this subspecies.

EARLY STAGES; HOST PLANTS. Unknown.

DISTRIBUTION (Map fig. 115). Central Africa: Nigeria, Cameroon, Equatorial Guinea (Rio Muni), Gabon, Congo, Central African Republic, Democratic Republic of Congo.

BIONOMICS; CONSERVATION STATUS. See species account.

MATERIAL EXAMINED. 34 ♂♂ in BMNH. 50 ♂♂; 3 ♀♀ from other collections.

7d. *G. (A.) illyris hamatus* (Joicey & Talbot, 1918)

(Fig. 218; genitalia Fig. 23)

Papilio illyris hamatus Joicey & Talbot, 1918: 271. HOLOTYPE ♂: TANZANIA: 'German East Africa (British occupation), ex coll. Suffert, 1 ♂.' (Joicey & Talbot, 1918: 271). BMNH Spec.Reg. No. 143403.
Papilio illyris f. (? an s.-sp.) *hamatus* Joicey & Talbot; Le Cerf, 1924*a*: pl. 5 fig. 54 (and legend).
Papilio illyris v. *hamatus* Joicey & Talbot; Bryk, 1930*b*: 573.
Papilio (*Graphium*) *illyris hamatus* (J. & Ta.); Peters, 1952: 22.
Graphium illyris hamatus (Joicey & Talbot); Guilbot & Plantrou, 1978:
Graphium (*Arisbe*) *illyris illyris* =*hamatus* (Joicey & Talbot); Ackery, Smith & Vane-Wright, 1995: 163.

TYPE EVALUATIONS
Papilio illyris hamatus Joicey & Talbot, ([1918]: 271) was described from the single specimen from '. . . the collection of Joicey' (Joicey & Talbot, 1918: 271). The specimen concerned lacks a locality label, but does have a Hill Museum, round, red-bordered, 'Type/H.T.' label; a label stating 'ex coll. /Suffert./1912'; a handwritten label with just the number '51' or '57'; and with a handwritten determination label (possibly in Joicey's hand) giving the name and 'TYPE ♂ (H.T.)'. It reached the BMNH as part of the Joicey Bequest, BMNH accession No. 1934–140 and is identifiable as the specimen illustrated in Le Cerf (1924: pl. 5 fig. 54).

TAXONOMIC STATUS
Papilio illyris hamatus Joicey & Talbot, ([1918]: 271) was described as a subspecies. Guilbot & Plantrou (1978) reiterated that status and separated it from the Central African forest populations by establishing a new name (*girardeaui*) for them. The differences appear slight and, since only the single specimen is involved, may be the result of individual variation. Moreover, there are no other confirmed records of the species occuring in Tanzania, so this may be a false locality. However, the male genitalia are more similar to those of the West African subspecies than they are to the Central African one. Further material is certainly needed either to: a) demonstrate the presence of a population with this phenotype in Tanzania; b) demonstrate the presence of the *girardeaui* or *illyris* phenotypes in Tanzania; or c) demonstrate the occurrence of the *hamatus* phenotype elsewhere in the species' range. In the absence of such further material, we provisionally follow Guilbot & Plantrou (1978) in treating the two as distinct.

SIMILAR SUBSPECIES. *G. i. girardeaui*.

DIAGNOSIS: PATTERN (Fig. 218)
The main distinguishing character is in the hindwing discal cell. On the upper side, there is an extension of the yellow mark from its anterior, distal corner along the line of the upperdiscocellular vein to the midpoint of the lower discocellular. Here it meets a small post-discal mark at the base of cell M_2. On the underside, in the discal cell, there is a small white spot in the angle of the upper and lower discocellular veins. Around this proximally is a narrow brown band, around which, in turn, is the red band of the rubra. Again, there is a small white post-discal mark, itself with an intrusion of brown, at the base of cell M_2.

VARIATION. We know of only the type specimen.

DIAGNOSIS: ♂ GENITALIA (Fig. 23)
Generally more similar to *i. illyris* than to *i. girardeaui*, though with some features suggesting the latter.

Dorsal harpe clearly curved, but with serrations coarser than in *i. illyris*. Serrations on *ventral harpe* also coarser and with some gaps, suggesting a distinct posterior blade and broad, serrate, but not bifid, medial blade. *Dorsal terminal process* not denticulate, and not bifid at tip. *Ventral terminal process* broader than either, almost quadrate and clearly serrate at the tip.

DIAGNOSIS: ♀ GENITALIA. Female unknown.

EARLY STAGES; HOST PLANTS. Unknown.

DISTRIBUTION. Only known from the vague and dubious type locality.

BIONOMICS; CONSERVATION STATUS. See species account.

MATERIAL EXAMINED. The male holotype in BMNH only.

8. *Graphium (Arisbe) gudenusi* (Rebel, 1911)

Kigezi Swordtail (Figs 180, 242; map Fig. 127; genitalia Figs 24, 81)

Included in a group with *illyris* and *kirbyi* by both Berger (1951) and Hancock (1983) on the basis of a perceived resemblance of their male genitalia. In our opinion, this resemblance is not as close as those authors suggest. The male genitalia of *gudenusi* are, perhaps, more similar to those of *illyris* than *kirbyi*, but the female genitalia (not considered by Berger or Hancock) of *gudenusi* and *kirbyi* show the greater resemblance. In our analyses, *G. gudenusi* is placed in a polytomy with other swordtailed species, including *G. illyris*, basal to the crown group. When multistate characters are active, this polytomy includes the *angolanus* group, etc.

G. gudenusi is a rare, narrowly distributed, monotypic species found in forest areas of S.W. Uganda, and E. Zaire. The female was described from Burundi by Thiry (1993).

Papilio gudenusi Rebel, 1911: 409, pl. 13, figs 1,2. LECTOTYPE ♂: ZAIRE: 'Urwalde am Nordwestufer des Tanganika-Sees . . . 1900–2100m im Februar 1910'.(*loc. cit*: 410). NHMV [photographed K.F.M. Goodger] **here designated**; 4 PARALECTOTYPES ♂♂: ZAIRE: Same data. NHMV; 1 PARALECTOTYPE ♂: ZAIRE: Same data, BMNH Spec.Reg. No. 220034.

Papilio Gudenusi Rebel; Bryk, 1930*b*: 573.

Graphium gudenusi Rebel; Berger, 1950: 92–3, figs 91,92; D'Abrera, 1980: 46,47 (figs, as '*G. gudenusi* ♂ R' and '*G. polistratus* ♂ R' [*lapsus* for '*G. gudenusi* ♂ V' – corrected in D'Abrera, 1982]); Berger, 1981: 53, pl.18 fig. 4 (m); Thiry, 1993: 155, fig. (female described); d'Abrera, 1997: 54,55 (figs).

Papilio (Graphium) gudenusi (Rebel.); Peters, 1952: 22.

Graphium (Arisbe) gudenusi (Rebel); Munroe, 1961: 42; Ackery, Smith & Vane-Wright, 1995: 163.

Graphium (Graphium) gudenusi (Rebel); Hancock, 1983: 46; Collins & Morris, 1985: 60.

SYNONYM

Papilio Babaulti Le Cerf, [1932]: 275. HOLOTYPE ♂: ZAIRE: 'Type (H. T.) : 1 ♂, Kitembo, Congo belge oriental, région du lac Kivu, VIII-1931, ex Guy Babault'. (*loc. cit.*: 278). 'coll. Museum de Paris' (*ibidem*). MNHN.

Graphium gudenusi =*Babaulti* Le Cerf; Berger, 1950: 92. [as syn.]

TYPE EVALUATIONS

In his description of *Papilio gudenusi*, Rebel (1911: 410) states, 'Es liegen fünf . . . männliche Stücke vor'. Those 5 specimens are in NHMV, where our colleague K.F.M. Goodger observed and photographed them; they have identical locality and identification labels, the latter being in Rebel's hand with 'Type' written in red ink. The specimen selected as lectotype is that illustrated in the original description and readily identifiable by the position of the antennae and by an additional label reading 'Orig. Phot.' in the same hand. A further male specimen with identical locality and identification labels (including the word 'Type', which makes lectotype designation necessary) is in BMNH (Spec.Reg. No. 220034), which it reached via the W. Rothschild bequest (BMNH 1939–1). We regard this as a further paralectotype. It may be that Rebel sent this to Rothschild before finalising the text of his paper.

Papilio babaulti Le Cerf ([1932]) was described from the single male specimen, with type designation original; this specimen is readily identifiable in MNHN, where it was examined and photographed by CRS. It has correct locality label, a hand written identification label, apparently in Le Cerf's hand, including the phrase 'Type H.T.' and a red printed 'Type' label. A topotypical male, collected at Kitembo in July 1932 by Babault, is present in the BMNH (ex Rothschild collection).

TAXONOMIC STATUS

Papilio gudenusi Rebel (1911) was established as a species, a status accepted by all subsequent authors.

Papilio babaulti Le Cerf ([1932]) was established as a species. Examination of the holotype leaves no doubt that it is a synonym of *G. gudenusi*, and it was treated as such by Berger (1950), though we have not found a reference to the formal synonymy being established.

SIMILAR SPECIES

The distinctive obsolescence of the forewing discal cell bands mean that this species could be confused only with the very rare *G. policenoides*, from which it may be distinguished by the absence of post-discal marks of the hindwing.

DIAGNOSIS: PATTERN (Fig. 180)

Ground colour dark, nearly black, but appearing paler distal to the forewing submarginal marks (or their position) due to the scales (which are dark chocolate brown) being sparser and narrower. Pale markings almost lime green.

Upperside. **Forewing** discal cell with bars, especially the basal ones, almost obsolete; sinuate. Bar 5 more noticeable as a spot near the posterior discocellular vein, extending as a fine sinuous line costally. Bar 6 present, usually as a loop from the costal vein. Cell R$_3$ with a small discal mark, squarish post-discal mark, just distal to the root of R$_4$, and a small submarginal mark. Cell R$_4$ usually with just a faint submarginal mark. Cell R$_5$ with discal and post-discal marks usually fused to a greater or lesser degree and faint submarginal mark. Cells M$_1$ to M$_3$ each with a post-discal mark slightly concave on the distal face; the submarginal marks faint and becoming successively fainter posteriorly. Cell CuA$_1$ with a more-or-less rectangular post-discal mark reaching veins CuA$_1$ and CuA$_2$, but not the posterior discocellular vein; submarginal mark obsolete. Cell CuA$_2$ with basal and discal marks virtually undetectable, post-discal mark rectangular, reaching veins CuA$_2$ and 1A; submarginal mark obsolete. Cell 1A with just a post-discal mark, contiguous with that in cell CuA$_2$.

Hindwing upperside discal cell with a single broad band crossing the cell from the anterior discocellular vein from either side of the root of vein R$_5$ to the posterior discocellular vein opposite cell CuA$_1$; there is no sign of a basal band. Cell R$_1$ with just a white post-discal mark, contiguous with those of the forewing and hindwing discal cell and cell R$_5$. Cell R$_5$ with a basal discal mark and faint, linear/transverse submarginal mark. Cells M$_1$ and M$_2$ without post-discal marks, with linear/transverse submarginal marks; marginal marks faint. Cell M$_3$ usually without a post-discal mark, with a linear/transverse submarginal mark; marginal mark more pronounced. Cell CuA$_1$ with an elongate discal mark (possibly a fusion of discal and post-discal marks), a small submarginal mark and a marginal mark. Cell CuA$_2$ with just a marginal mark. The tail on vein M$_3$ narrows basally as well as towards the tip; the white mark at the tip is small.

The **underside** pattern, as usual, generally reflects that of the upperside, but the background is more complex. **Forewing** discal cell bars more prominent than on the upper side; bar 3 is edged with dark scales distally and bar 4 proximally; bar 6 surrounded by a nacreous area. A dark band runs just distal to the post-discal marks of the forewing, with paler patches mainly in cells R$_5$ to M$_3$ (but not nacreous as in *G. policenes*). The area distal to this band is paler, with even paler linear/transverse elements near the margin. On the **hindwing** the rubra consists of a band of elements crossing the costal cell and cell R$_1$, a band across the tip of the discal cell between the roots of R$_S$ and M$_3$/CuA$_1$, a mark in cell M$_3$, a very narrow, faint band across cell CuA$_1$, and a clearer element in CuA$_2$. There are sometimes small post-discal marks in cells M$_1$, M$_2$ and M$_3$ (see below), and indications of basal and discal marks in cell CuA$_2$. Between the post-discal areas and the submarginal marks of cells M$_1$ and M$_3$, and, more sparsely, in cell CuA$_1$, are patches of paler scales. Between the submarginal marks and the margins of cells M$_1$ to CuA$_1$ are patches of bluish scales. The marginal marks are clearer on the undersides, especially in cells M$_3$ to CuA$_2$.

Thiry (1993) described the female as being a little larger than the male, with some of the green marks of the forewing better developed and the submarginal marks of the forewing missing. These features are variable in the male, and it remains to be seen whether this is true for the female. Thiry (1993) reported that another female had been captured by Steve Collins in Rwanda, and we have examined the genitalia of yet another female, from Burundi kindly lent by Collins from ABRI (see below).

VARIATION

Among the series of 33 males in the BMNH is an aberrant specimen in which the spaces between forewing discal cell bars 3 and 4, and 5 and 6 are green suffused with a scattering of brown scales, to produce an effect of broad, but diffuse, green bands (Fig. 242). The specimen (BMNH Spec.Reg. No. 220027) is from Uganda: Impenetrable Forest, collected by Raymond Murphy, 26 December, 1972.

Other variants we have seen include:

forewing discal cell bar 6 in the form of a spot (usually it is a loop);

the expression of the forewing upperside submarginal marks is variable, with several specimens virtually lacking them in those cells posterior to cell R$_5$;

one specimen in BMNH (Spec.Reg. No. 220017) has a post-discal mark in forewing cell R$_4$;

the discal and post-discal marks in forewing cell R$_5$ are usually partly fused, but in some specimens they are free;

hindwing cell M$_3$ occasionally with a small, 1–2 mm lenticular green mark at the base, in angle of vein CuA$_1$ and the medial vein;

hindwing cells M$_2$ and M$_3$ sometimes have a scattering of pale scales between the submarginal marks and the margins;

the expression of post-discal marks in hindwing underside cells M$_1$ to M$_3$ is variable, with all specimens having a mark in M$_1$, some with one also in M$_2$, and a few with a mark in all three cells.

DIAGNOSIS: ♂ GENITALIA (Fig. 24)

Dorsal projection triangular with broad, horizontal base, twisted distally so tip is vertical; the tip is somewhat expanded, with setae on anterior face; *dorsal harpe* a single, compressed, obliquely-angled blade, serrate distally and dorso-distally; *ventral harpe* a triangular blade, serrate on its mesal/posterior edge, projecting posteriorly from the root; *dorsal terminal process* a simple, mesad and slightly ventrad directed tooth; *ventral terminal process* broad based, short, serrate, with a few serrations also between it and the dorsal terminal process.

Uncus elongate, with *socii* large and quadrate. *Saccus* short. *Aedeagus* short, almost straight, apparently without denticulation.

DIAGNOSIS: ♀ GENITALIA (Fig. 81)

Based on an ABRI Specimen from Ruguru, Burundi: *vestibulum* triangular; *ostium bursae* opening anteriorly; *ductus bursae* not elongate, but sclerotized distally, with kink/constriction distal to *ductus seminalis*, but not pocketed; *central ostial lobe* long, narrow, sclerotized, glabrous, slightly 'notched' at tip; *lateral ostial lobes* broad, but not very long, setose; *anterior apophyses* present; *papillae anales* rounded.

EARLY STAGES; HOST PLANTS. Apparently unknown.

DISTRIBUTION (Map Fig. 127). Limited to the areas of Lake Edward, Lac Kivu and northern Lake Tanganyika in extreme eastern Democratic Republic of Congo, including the Kigezi district of south-western Uganda, Rwanda and Burundi (Ackery *et al.*, 1995; Mathot, 1990; Collins & Morris, 1985).

BIONOMICS

This monotypic, very distinct, local, and generally scarce species occurs only in primary highland forest, from about 1000–2000 m. The female was unknown until recently (Thiry, 1993). Virtually nothing seems to have been recorded about its habits, although Williams (1969) states that males follow rivers and streams through the forests, settling occasionally on sand to drink. Raymond Murphy collected a long series of males from Kayonza Forest, Uganda, from August–December 1974, apparently with peak numbers in October.

CONSERVATION STATUS. 'Scarce and local, but not threatened at present . . . [but] human population pressure . . . is increasing and the species needs further study and monitoring' according to Collins and Morris (1985).

MATERIAL EXAMINED. 35 ♂♂ in BMNH; 18 ♂♂; 1 ♀ from other collections.

9–12 The policenes clade

We recognize four species within this well-defined clade of swordtailed butterflies found throughout the forested and some drier areas of sub-Saharan Africa.

Berger (1950) and Hancock (1993) both included *junodi* and *polistratus* (*q.v.*) in their respective *policenes* groups, on the basis of their male genitalia. However, the resemblance does not seem sufficient to warrant their inclusion, and the female genitalia are markedly different. In all our analyses, the four species we include were always recovered as a clade to the exclusion of *junodi* and *polistratus*. With multistate characters active the clade was placed as sister to a (*kirbyi* (*G.* (*Pazala*) *mandarinus* (*antheus* + *evombar*))) clade; with these characters inactive, were part of the polytomy of swordtailed species basal to the non-swordtailed afrotropical species, etc.

These four species may be recognized collectively by the presence of green markings (which fade with time and exposure to light) on a nearly black background above, and a similar, though paler and more complex pattern underneath, with a well developed rubral system on the hindwing underside. Unlike the superficially similar *G. antheus* and *G. porthaon* (and the distinctive *G. gudenusi*), the forewing discal-cell bars are more-or-less straight. *G. junodi* has reduced pale marks – and these cream-coloured – compared to the *policenes*-group. *G. polistratus* is very similar, even sharing the nacreous markings between the post-discal and submarginal marks of forewing underside cells R_5 to M_3. However, in that species the rubral system does not form such a continuous band as it does in the *policenes*-group, and the pattern of the hindwing discal area is different.

The male genitalia (especially the organs of the valve) are very similar among the members of the clade and very distinctive. They are described in detail for *G. policenes*, with the differences being emphasized in the accounts of the other species.

The taxonomy of the group has been the subject of considerable confusion, especially regarding the status of a number of named taxa from West and Central Africa, all characterized by reduced or obsolete transverse bars in the forewing discal-cell. Larsen (1994) largely resolved this, but our own researches have extended his findings to reveal that the species he referred to as *G. liponesco* in fact comprises two valid species, *G. liponesco* itself being restricted to West Africa from Guinea to Benin. A second species, to which the name *G. biokoensis* may be applied, is found from Cameroon to central Democratic Republic of Congo. That these taxa should be regarded as full species is indicated by the fact that each is sympatric with *G. policenes*, sometimes being found in mixed groups (Birket-Smith, 1960), and by consistent, if slight, differences in male genitalia.

The fourth member of the group is *G. policenoides*. This has the markings generally even more reduced than in *G. liponesco* and *G. biokoensis*, especially those in the forewing discal cell, which are almost obsolete. In contrast, this species has a prominent, elongate discal mark in hindwing upperside cell M_3. Its male genitalia are very similar to those of *G. biokoensis*.

Separation of *G. biokoensis* and *G. policenes* is not easy and may not be totally reliable. Further research, especially involving different data sources such as chemical analysis of pheromones and nucleic acid sequencing may refine the relationships hypothesized here.

A subspecies of *G. policenes*, *G. p. telloi*, has recently been described by Hecq (1999) from northern Central African Republic. We have not been able to examine the type material, though the illustrations suggest that the phenotype may lie within the normal range of this very variable species.

In the following species accounts, the 'diagnosis' sections for *G. p. policenes* provide a generalized description for the whole group, as well as specifically for *G. policenes*, with the differences shown by the other taxa being emphasized in the respective 'similar species' sections.

9. *Graphium* (*Arisbe*) *policenes* (Cramer [1775])

Small-striped, Speckled or Common Swordtail (Figs 181, 243, 244; map Fig. 123; genitalia Figs 25, 27, 82; early stages Figs 251, 252, 261, 262)

We here treat the species as bitypic, by including the very variable nominate subspecies and the recently described subspecies, *G. p. telloi* Hecq, though we have considerable reservations about the status of the latter.

9a. *Graphium (Arisbe) policenes policenes* (Cramer [1775])

Small-striped, Speckled or Common Swordtail (Fig. 181; map Fig. 123; genitalia Figs 25, 27, 82)

Papilio policenes Cramer, [1775], *in* Cramer, [1775–76]: 61, pl 37, figs A,B. [Africa]: 'Surinamen . . . Baron Rengers.' [not seen]

Papilio pompilius [Fabricius, 1787] = *policenes* Cramer; Fabricius, 1787: 8 [misidentification in part].

Papilio policenes Cramer; Gray, [1852]: 32; Bryk, 1930*b*: 571.

Papilio (*Graphium*) *policenes* [f. *policenes*] Cramer; van Son, 1949: 45; text-figs 23, 24; pls V (fig. 12), VI (fig. 12), XIV.

Graphium policenes policenes Cramer; Berger, 1950: 93, fig.93.

Papilio (*Graphium*) *policenes policenes* (Cr.); Peters, 1952: 22.

Graphium (*Arisbe*) *policenes* (Cramer); Munroe, 1961: 42.

Graphium policenes (Cramer); D'Abrera, 1980: 48, 49 (figs); Berger, 1981: 53, pl.18 figs 2 (♂), 5 (♀); Kielland, 1990: 48; Larsen, 1994: 150; d'Abrera, 1997: 56, 57 (fig.).

Graphium (*Graphium*) *policenes* (Cramer); Hancock, 1983: 46; Collins & Morris, 1985: 59.

Graphium (*Arisbe*) *policenes policenes* (Cramer); Ackery, Smith & Vane-Wright, 1995: 165.

SYNONYMS

Papilio agapenor Fabricius, 1793: 26. 'Habitat in Africa Mus. Dom. Drury' [not seen].

Papilio policenes = *agapenor* Fabricius; Gray, [1852]: 32.

Papilio scipio Palisot de Beauvoir, [1805]: 70, (Lep.) pl.2 fig.1. TYPE: ?♂: NIGERIA: 'les déserts derrière les royaumes d'Oware et de Galbar ou Kalabar' [not seen].

Papilio policenes = *scipio* Palisot de Beauvoir; Gray, [1852]: 32.

Papilio polixenus Godart, [1819]: 19, 52. An unnecessary emendation of *Papilio policenes* Cramer [1775].

Papilio policenes = *polixenus* Godart; Gray, [1853]: 32.

Papilio policenes var. *sudanicus* Schultze, 1916: 110. HOLOTYPE ♂: CAMEROON: 'Babungo im Grashochlande Kameruns' (*loc. cit.*). 'Ein ♂ coll. Schultze' (*loc. cit.*). SMNS Stuttgart.

Papilio policenes v. *sudanicus* Schultze; Bryk, 1930*b*: 572.

Graphium (*Arisbe*) *policenes policenes* =*sudanicus* Schultze; Ackery, Smith & Vane-Wright, 1995: 165.

Papilio policenes laurentia Le Cerf, 1924*a*: 398. HOLOTYPE ♂: SOUTH AFRICA: 'Type (H.T.): Un ♂, Natal, Durban, J. H. Bowdler [=Bowker], ex coll. R. Trimen (Cat. MSS., p. 377, No. 2)' (Le Cerf, 1924*a*: 398). BMNH Spec.Reg. No. 143588; PARATYPE ♀ : SOUTH AFRICA: 'Une ♀ , même origine (Cat. MSS., p. 377, No. 3)' (Le Cerf, 1924*a*: 398). BMNH Spec.Reg. No. 143587; PARATYPES: SOUTH AFRICA: '. . . une série d'exemplaires des deux sexes du Natal de la même collection.'. 2 ♀♀ in BMNH, Spec.Reg. Nos. 143586, 143589.

Papilio policenes v. *laurentia* Le Cerf; Bryk, 1930*b*: 571.

Papilio (*Graphium*) *policenes* f. *laurentia* Le Cerf; van Son, 1949: 46.

Graphium (*Arisbe*) *policenes policenes* =*laurentia* Le Cerf; Ackery, Smith & Vane-Wright, 1995: 165.

UNAVAILABLE NAMES

Papilio (*Cosmodesmus*) *policenes policenes* f. *guineensis* Dufrane, 1946: 121. GUINEA. IRSN [infrasubspecific].

Graphium policenes f. *coussementi* Berger, 1960: 71, 1 fig. DEMOCRATIC REPUBLIC OF CONGO. MRAC [infrasubspecific].

Graphium policenes f. *cousementi* Berger, 1981: 53. [Incorrect subsequent spelling of *coussementi* Berger, 1960.]

TYPE EVALUATIONS

Papilio policenes Cramer, [1775], was described from 'het Kabinet van den Hoog Welgeb. Heere Baron Rengers' (*loc. cit.*: 61). Cramer did not state the number of specimens, but used the singular in his description. Rienk de Jong of the Nationaal Natuurhistorisch Museum, Leiden, Netherlands, has informed us (pers. comm.) that Baron Rengers' collection was probably broken up and auctioned after his death. Although a few specimens have reached RMNH, the original *Papilio policenes* is not amongst them, and we must presume it lost. However, the taxon can be recognized readily from the figure.

Papilio agapenor Fabricius, (1793), was described from a specimen or specimens in Dru Drury's collection which was also broken up and sold at auction after his death. Part of it was bought by Alexander MacLeay and taken to Australia where it became part of the Australian Museum, Sydney, which McLeay established (See van Leeuwen, 1997). We do not know at present whether the type of *Papilio agapenor* survives there or elsewhere. Fortunately, the specimen was well illustrated by Jones, whose 'Icones' survive in OXUM.

In his description of *Papilio scipio* Palisot de Beauvoir, [1805], did not state the number of specimens. Palisot de Beauvoir's Nigerian collection was destroyed when the British overran the Owara trading station in 1791. However, the taxon can be readily recognized from the figure.

Papilio policenes var. *sudanicus* Schultze (1916) was described from a single male, though a specimen captured earlier was also referred to. The type specimen is readily identifiable in SMNS from the printed locality label and determination label in Schultze's hand, the latter bordered by red and black lines.

Papilio policenes laurentia Le Cerf (1924: 398) was described from the holotype and female paratype listed above, with designations original, and from an unstated number of further specimen of which two females can be positively identified in BMNH. The holotype and principal female paratype listed above, readily identifiable by their labelling, reached the BMNH as part of the Joicey bequest, BMNH accession No. 1934–120. The specific epithet was spelt '*aurentia*' by the author on the determination labels of the holotype and principal female paratype.

TAXONOMIC STATUS

Papilio policenes Cramer, [1775], was described as a species from Surinam, though the author stated that following two species, *P. castor* and *P. pollux* (both now in *Charaxes*), were also in Rengers' collection, and that both were from the Guinea coast. Cramer's plate 37 figs A & B clearly illustrates the african taxon as now understood.

Papilio agapenor Fabricius, (1793), was described as a species from Africa. Plate 51 of Jones' Icones clearly illustrates a butterfly referable to *G. policenes*.

Papilio scipio Palisot de Beauvoir, [1805], was described as a species which the author differentiated from *agapenor* Fabricius. The illustrations on pl. 2 (both labelled Fig. 1, not Figs 1 & 2, as stated in the text) are clearly identifiable as *G. policenes* as now understood.

Confusion over the type locality of *P. policenes* Cramer, [1775], may have led to the multiplicity of synonyms for the taxon. Fabricius was certainly familiar with Cramer's widely distributed work and included *policenes* Cramer in the synonymy of his *Papilio pompilius* (1787 – now considered a subspecies of *G.* (*Pathysa*) *antiphates* (Cramer)), but Palisot de Beauvoir was probably unable to refer to either of his predecessors' works. The error seems to have been recognized at quite an early date, but the full synonymy does not seem to have been finally resolved and laid out until the catalogue of Gray (1852).

Papilio policenes var. *sudanicus* Schultze (1916) was established as a variety pre-1960 with the indication of being a geographical variant and thus should be treated as an available name. It was established on the grounds that its green markings were more extensive. Whilst it is true that the specimen is well marked, similarly marked individuals are found elsewhere, alongside more 'normal' specimens: Dufrane (1946) named a very similar specimen from Guinea as an infrasubspecific form, *guineensis*. Schultze's name gives a misleading impression of its provenance. His earlier specimen (Schultze, 1916: 111) is from 'Mapéo im Atlantika-Gebirge (Mittel-Adamaua)', on the borders of Nigeria and Cameroon; Schultze's reference to 'Sudan' appears to refer here to the grassy highlands of northern Cameroon. Given the occurrence of this pattern throughout the species range, the status as subspecies is not tenable, and we therefore treat it as no more than infrasubspecific. See also *G. p. telloi* Hecq (below).

Papilio policenes laurentia Le Cerf (1924: 398) was described as a subspecies from eastern Africa from Tanzania southwards on the basis of paler green marks on the upper side and generally paler underside. However, van Son (1949) pointed out that such differences are due to fading, citing a series in the Transvaal Museum with 'brilliant green markings, and the ground colour of the underside . . . exactly the same as . . . specimens from Sierra Leone' (*loc. cit.*: 46). Van Son referred to *laurentia* as a form, drawing attention to the iridescent areas of the underside (see below) being more extensive, but stated that the typical form, though rare in East and South Africa, is sympatric. Van Son's (1949) plates 5, fig.12 and 6, fig.12 are stated to be of an 'intermediate form between f. *policenes* Cr. and f. *laurentia* Le Cerf'. Other authors (e.g. Pennington, 1994) have treated *laurentia* as a subspecies.

Papilio (*Cosmodesmus*) *policenes policenes* f. *guineensis* Dufrane (1946: 121) was established infrasubspecifically, though the author did speculate that it may repesent 'une race locale'. To the best of our knowledge, no subsequent authors have used the name at a higher level.

Graphium policenes f. *coussementi* Berger (1960: 71) was established as a form, but the author clearly intended it to be infrasubspecific (see Code Article 45.6.4., ICZN, 1999), as he was describing a specimen collected '. . . parmi des centaines de *G. policenes* typiques . . .'.

SIMILAR SPECIES

Very similar to *G. liponesco*, *G. biokoensis* and *G. policenoides*. Distinguished from all three by the broader markings, especially in the forewing discal cell. The red tornal spot on the hindwing is also much more prominent. *G. policenes* lacks the discal mark in hindwing upperside cell M_3 seen in *G. policenoides*, though a very few white scales may be seen at a point corresponding to the rubral mark of the underside. For the distinguishing featues of *G. p. telloi* see the subspecies account.

Also similar to the other sword-tailed *Graphium* species with more-or-less straight forewing discal cell bars: *G. polistratus* and *G. junodi*, though recognisable by its more prominent and complete hindwing underside rubral mark and hindwing upperside red tornal mark as well as the details of the disposition of the pale markings.

Diagnosis: pattern (Fig. 181)

Forewing upperside discal cell with 5 transverse bars (including the basal) and a distal spot by the costal vein, opposite cell R$_5$. In fresh specimens, the three basal bars are a brighter green than the rest, which are blue-green; in *G. liponesco*, all cellular bars are of the brighter colour (Larsen, 1994). The bars extend beyond the costal vein. Cell R$_3$ with a small, axillary discal mark, a square post-discal mark level with the root of vein R$_4$, and a small submarginal mark. Cell R$_4$ with a small marginal mark and sometimes a small post-discal mark. Cell R$_5$ with a square post-discal mark basal to the root of vein R$_4$. Cells M$_1$ to M$_3$ also have post-discal and submarginal marks, the latter somewhat elongate. In cell CuA$_1$, there is a basal mark contiguous with that in the discal cell and in cell CuA$_2$, and similarly bright green in fresh specimens; a discal mark forming a stripe with cell bar 2 and the discal mark in cell CuA$_2$, though blue-green in colour; the post-discal mark is extended into a 'handle' at its anterior/basal corner to form a continuous stripe with discal cell bar 3. The post-discal mark of cell CuA$_1$ is divided into small anterior and posterior spots. Cell CuA$_2$ also has basal and discal marks forming continuous stripes with those in cell CuA$_1$ and the discal cell; there is a post-discal, but no submarginal, mark.

On the **hindwing upperside**, the discal cell has a basal mark linking the basal mark of the costal cell with the discal mark of cell CuA$_2$. There is also a band linking the discal mark of the costal cell with that of CuA$_1$. The costal cell itself has basal, transverse discal, post-discal and, sometimes, submarginal marks; these are all paler than in other cells, with the post-discal white. Cells R$_5$ and M$_1$ both have squarish, basal post-discal marks and elongate submarginals. In cell M$_2$, the post-discal is slightly displaced from the base, elongate and rounded distally; the submarginal mark is again elongate and there is a scattering of pale scales between it and the margin, where there is a faint marginal mark. The tail has a small white tip. In cell M$_3$ there is no discal mark, unlike *G. policenoides*, though a very few white scales may be seen at a point corresponding to the rubral mark of the underside. The post discal mark begins roughly level with the distal margin of that in cell M$_2$; it is slightly longer than broad and is rounded distally. The submarginal mark crosses the whole cell and is often arcuate; there is a patch of pale scales more extensive than that in cell M$_2$ and the marginal mark is very clear and extends most of the length of the tail. Cell CuA$_1$ has an elongate discal mark continuing the stripe which runs through the discal cell from the costal margin. The post-discal mark is less long than it is broad; the submarginal is arcuate or sinuate and there are a few pale scales between it and the wing margin, which has a clear marginal mark. Cell CuA$_2$ has a discal mark at the base which fades into the anal fold/androconial apparatus. Near the distal end of the cell is a characteristic bright red tornal spot – in *G. liponesco*, *G. biokoensis* and *G. policenoides* usually only a diffuse scattering of red scales is seen.

The **underside** pattern, as is usual, reflects that of the upperside. Some features, however, help to distinguish *G. policenes* from other species. Extending distally from the post-discal marks of **forewing** cells R$_5$ to M$_3$ are patches of translucent white to pale orange scales which give a nacreous appearance. Such areas are also present around the forewing submarginal marks and in similar but more complex arrangements on the hindwing. Whilst most obvious in *G. policenes*, these nacreous patches are seen in all members of the *policenes*-group and to a lesser degree in *G. polistratus*, but not in any other species.

On the **hindwing**, the rubral system is better developed and more continuous in members of the *policenes*-group than in any other afrotropical *Graphium*. It comprises red lines crossing the hindwing costal cell and cell R$_1$ between the discal and post-discal marks. In cell R$_5$ the red line crosses the cell almost at the base, linking to a line which crosses the discal cell distally ending at the lower discocellular vein, opposite cell M$_2$. In cell M$_2$ itself, there is a prominent basal red spot. In cell M$_3$ the red band is slightly removed from the base of the cell. In cell CuA$_1$, the red line again crosses the cell between the discal and post-discal marks and is continued across cell CuA$_2$, but does not reach the inner margin.

Variation (Figs 243, 244)

The extent of the green wing markings varies between the very well marked condition seen in forms *sudanicus* Schultze and *guineensis* Dufrane and those approaching the condition seen in *G. liponesco* and *G. biokoensis*. In the latter case, *policenes* can usually be recognized by the extension the post-discal mark of forewing cell CuA$_2$ more-or-less reaching the posterior discocellular vein and the prominence of the hindwing upperside red tornal spot. More extensively marked individuals may be more common in the eastern and southern (drier) parts of the species' range, but both extremes may be met throughout.

More extreme reduction of the pattern of green marks is seen in melanic specimens such as f. *coussementi* Berger (pl.10 Fig. 243). In this striking animal, only the basal stripe, the four distal forewing cell bars and the submarginal marks remain. The thickness of the remaining forewing cell bars and the hindwing upperside red tornal spot confirm its specific identity. A very similar specimen from CAR is in ABRI. What appears to be an intermediate stage is shown by a further specimen from CAR in ABRI in which the discal and post-discal green marks are all 'fuzzy', being invaded by black scales (Fig. 243). At the other end of the spectrum, an increase in green marks over and above that of *sudanicus/guineensis* is exhibited by a specimen from Uganda in MRAC. In this, forewing cell bars 4 and 5 are virtually completely fused on the left side, slightly less so on the right. We have also seen specimens (in ZMUK) from the Jos Plateau in Nigeria with similarly extensive markings. On the **underside**, the extent and exact disposition of the nacreous areas is a little variable, with, for example, the form *laurentia* having these somewhat more extensive (van Son 1949: 46).

Other variants we have seen include:

forewing cell bars 4 and/or 5 slightly curved or kinked;

forewing distal mark varying between a solid, round spot to a thin U-shaped mark – in one South African specimen in BMNH it is virtually absent on the left wing, slightly larger on the right;

forewing cell R_3 without discal mark;

forewing cell R_4 with a small post-discal mark;

forewing cell CuA_2 with submarginal mark undivided, divided or with posterior half absent;

hindwing cell R_1 without submarginal mark.

DIAGNOSIS: ♂ GENITALIA (Figs 25, 27)

Valve: *dorsal projection* broad based and compressed, twisted distally into a vertical disc with stout setae in a tight antero-ventral cluster at the tip. *Dorsal harpe* large, horizontal and arcuate/reflexive in section; serrate distally. *Ventral harpe* with blade more-or-less normal to the valve wall, but at an angle to the horizontal, ending level with – and close to – the small gap between the dorsal and ventral terminal processes; divided into large basal and terminal teeth, and these sometimes subdivided to giving serrate appearance. *Dorsal terminal process* a mesad directed two branched structure, the dorsal branch elongate, the ventral a small, basal tooth; in *G. liponesco* these proportions are reversed (see below). *Ventral terminal process* generally small, triangular and denticulate.

DIAGNOSIS: ♀ GENITALIA (Fig. 82)

BMNH Spec.Reg. No. 149262; vial 3992: *ostium bursae* opening anteriorly; *ductus bursae* well sclerotized distally, but not noticeably kinked, constricted or pocketed; *central ostial lobe* long thin, setose, pointed extending well beyond laterals; *lateral ostial lobes* broad; *anterior apophyses* well developed; *papillae anales* rounded.

EARLY STAGES (Figs 251, 252, 261, 262)

The transverse stripes of the *policenes* larva are often highly contrasting and conspicuous, with the relatively long thoracic and anal processes smooth-looking from second instar onwards (they are in fact covered with short setae, but this is not readily apparent to the naked eye); thoracic segments 2 and 3 have conspicuous velvety-black transverse dorsal bands; notably, in the final instar, larvae may become almost entirely green, other than these two transverse black bands, but more often they are yellowish and retain the strongly contrasting dorsal transverse bands. The green pupa is somewhat flattened (cf *kirbyi*), with a very long dorsal horn, and the lateral expansion of the abdominal base more angular than *colonna*.

Van Son (1949) gave extensive descriptions from Gowan Clark, and also Trimen and Aurivillius. See also Trimen (1889), Haig (1936), Pinhey (1949: 148), Villiers (1957: figures of first and final instars and pupa), Carcasson (1981: final instar and pupa), Fontaine (1985: 80–81), Migdoll (1988: 138, showing larva, prepupa and pupa), and Henning *et al.* (1997). Sevastopulo (MS) noted that the descriptions of Aurivillius (1910: 25) and Trimen do not seem to correspond very well. Owen & Owen (1972) noted that the pupae show brown/green dimorphism. Sevastopulo (MS) recorded the two final instars and pupa as follows:

> 4th instar: Head olive-brown. Each somite with a black-edged white central band and a yellow band anteriorly and posteriorly, an intersegmental black line. These transverse bands merge into a greenish-white sublateral area. 1st to 3rd and 12th somites each with an outcurved subdorsal black spine. Legs blackish. Prolegs and venter greenish-white. Osmeterium greenish-white. Shape broadest across the 3rd somite, tapering towards the rear. Moulted 7.i.53.
>
> Final instar: At first very similar to preceding, except that the head is more olive and there are more or less broad, velvety black transverse dorsal stripes on the 2nd and 3rd somites. As the instar progresses, some larvae become an almost uniform green, except for the two transverse black bands, in others the markings become no more than dulled and faded. The sublateral and ventral whitish green area bounded above by a diffused smoky line edged above with yellow.
>
> Pupa green, slender, with a long flattened forward-pointing process from the thorax. The pupa fell during formation and was too deformed to describe in more detail, or to photograph.
>
> Described from larvae found at Entebbe, one of which pupated 15.i.53, the others dying. A male emerged 19.ii.53.
>
> [Sevastopulo's descriptions are accompanied by four black and white photographs.]

DISTRIBUTION (Map Fig. 123)

Found in forests practically anywhere in sub-saharan Africa (Larsen, 1996), but not in Comoros or Madagascar. Countries confirmed include: Mali, Guinea, Sierra Leone, Liberia, Ivory Coast, Ghana, Nigeria, Cameroon, Equatorial Guinea (inc. Bioko), Central African Republic, Gabon, Congo, Democratic Republic of Congo, Angola, Sudan, Uganda, Kenya, Tanzania, Malawi, Zambia, Mozambique, South Africa.

HOST PLANT RECORDS

Annonaceae:
cultivated *Annona* (Owen & Owen, 1972).
Artabotrys brachypetala (van Son, 1949, as possible additional host).

Artabotrys chrysophylla (van Son, 1949, as possible additional host).
Artabotrys monteiroae (Larsen, 1996).
Artabotrys sp. (Haig, 1936; Villiers, 1957; Sevastopulo, MS).
Polyalthia suaveolens (Fontaine, 1985).
Uvaria caffra (Haig, 1936; Larsen, 1996; Sevastopulo, MS).
Uvaria chamae (Haig, 1936).
Uvaria pulchra (Fontaine, 1985).
Apocynaceae:
Landolphia buchanani (Sevastopulo, MS).
Landolphia ugandensis (Sevastopulo, MS).
Landolphia sp. (Larsen, 1996).

BIONOMICS
This species is the most common and widely distributed of all the African swordtails, found in tropical areas 'throughout the year, in thick bush, woodland or forest' (Pinhey & Loe, 1977; see also Darge, 1995), although van Son (1949) gives only January–April for South Africa (but Trimen, 1889, specifies 4th Aug. 1865 for Durban, and Gooch, 1880, notes Nov. and Dec., while Migdoll, 1988, gives Sept.–April), and Gifford (1965) notes Aug.–Jan. for Malawi, where it apparently occurs in riverine forests at all elevations, including 'the driest valley watercourses'. Swanepoel (1953) considered that it did not occur in the dry bushveld where *G. antheus* is often found, preferring moister areas (such as coastal forests) where *antheus* is usually scarce. Hecq & Peeters (1992) record it only from gallery forest in the Sangba protected area in Central African Republic, and Fontaine (1985: 114) gives forest as its biotope in Democratic Republic of Congo. According to Kielland (1990), in Tanzania it occurs from about sea-level up to 2000 m.; although rarely encountered at such height, he considered it very common in riverine forests at low to medium elevation (Carcasson, 1960, says that it occurs in all forested areas in East Africa below 6000ft.). The flight is fast, erratic and often high, and Swanepoel describes its behaviour as very similar to that of *G. antheus* (although, if anything, it is apparently even more alert while nectaring), while Haig (1936) likens its 'zigzag flickering flight' to that of *Papilio phorcas*. Both sexes are attracted to flowers, about which they hover briefly with rapidly vibrating wings without settling, and water (including sweat), while the males sometimes occur on damp sand and mud (Gooch, 1880) in very large numbers; Larsen (In prep.*a*) also notes attraction to shrimp baits, and predation by agamid lizards. Males often patrol along the edges of suitable bush, and will chase intruders away. Females will interrupt their almost equally rapid flight to investigate potential hosts, using both antennae and feet to determine suitability. Eggs are laid singly on a suitable leaf. The larva is a mid-rib sitter and the five instars may be complete in 12 days. The leaf-like pupa is held upright against a stem by the girdle (Henning *et al.*, 1997) or fastened to a leaf midrib (Aurivillius 1910). Larsen (1996a) considers the life cycle sometimes unpredictable as the pupae may remain dormant for up to a year (see also Trimen's records in van Son, 1949), but may take as little as a week in ideal conditions (Henning *et al.*, 1997). The adults sometimes migrate in large numbers (Larsen, 1968).

CONSERVATION STATUS. 'Common . . . and not threatened' (Collins & Morris, 1985).

MATERIAL EXAMINED. 1050 ♂♂, 80 ♀♀ in BMNH; 300 ♂♂, 19 ♀♀ from other collections.

9b. *Graphium (Arisbe) policenes telloi* Hecq, 1999

Tello's Small-striped, Speckled or Common Swordtail

Graphium policenes telloi Hecq, 1999: 517–8, figs 3–4. HOLOTYPE ♂: CENTRAL AFRICAN REPUBLIC: 'Région Nord, P.N., Brendja 12.XII.1998, leg. J. Tello, MRAC, Tervuren.' [not seen]. 6 PARATYPE ♂♂: CENTRAL AFRICAN REPUBLIC: 'Mêmes données, dates échelonnées'; PARATYPE ♂: CENTRAL AFRICAN REPUBLIC: 'Sangba'. 'Coll. J. Hecq et MRAC.' [not seen].

TYPE EVALUATIONS. *Graphium policenes telloi* Hecq (1999) was described from the 8 specimens listed above.

TAXONOMIC STATUS
Graphium policenes telloi Hecq (1999) was established as a subspecies, based on perceived pattern differences described below.

G. policenes is variable in the extent of the wing markings, ranging from specimens very similar to *P. liponesco* and *P. biokoensis* to those with markings as extensive as those of the present taxon. In particular, the phenotypes *sudanicus* (Schultze, 1916) and *guineensis* (Dufrane, 1946) are similarly marked, as are some we have seen from the Jos Plaeau in Nigeria (in ZMUK, Copenhagen). It is possible that such extensive marking is associated with drier conditions, but it does seem to occur throughout the species' range. We therefore have reservations about the true status of *G. p. telloi*. More evidence is needed to confirm that an allopatric population exists or, conversely, that there is a continuity in the species' distribution and an alternative explanation for the difference in colour pattern (e.g. clinal change or a direct result of environmental, ontogenetic factors). Until more evidence is available we accept the *status quo*.

DIAGNOSIS: PATTERN
Hecq (1999) separated *G. p. telloi* from the nominate race on the basis of the wings being less falcate; with

the markings being larger and more contiguous; and these being light green rather than olive. In particular, he (*loc. cit.*) drew attention to the post-discal mark in forewing upperside cell CuA_1 being larger and consequently more contiguous with those in the neighbouring cells and less drawn out antero-costally; the band consisting of the hindwing discal cell band plus the post-discal mark of cell CuA_1 being more rectilinear, not separated by the intervening vein; the white post-discal mark of hindwing cell R_1 being whiter, more brilliant and much larger than in the nominate race; the black area distal to the post-discal mark of hindwing underside cell R_1 being reduced; the rubral system of the hindwing underside, being relatively narrower, with a higher proportion of red than in the nominate race.

DIAGNOSIS: ♂ GENITALIA. We have not been able to examine any. According to Hecq (1999) 'les genitalia ne sont pas suffisamment probants pour en tier des conclusions valables,'.

DIAGNOSIS: ♀ GENITALIA. Female apparently unknown.

DISTRIBUTION. Northern Central African Republic. Known from the type series only.

HOST PLANTS; BIONOMICS; CONSERVATION STATUS. Unknown.

MATERIAL EXAMINED. None.

10. *Graphium (Arisbe) liponesco* (Suffert, 1904)

Suffert's Narrow-Striped Swordtail (Fig. 182; map Fig. 124; genitalia Figs 26, 28)

Papilio policenes liponesco Suffert, 1904: 107. LECTOTYPE ♂: TOGO: 'Hinterland von Togo. Coll. Suffert' (Suffert, 1904: 107). BMNH Spec.Reg. No. 143016. – designated Le Cerf (1924: 398); 2 PARALECTOTYPE ♂♂: TOGO: Same data. 1 found. BMNH Spec.Reg. No. 142664.
Papilio policenes var. *liponesco* Suffert; Schultze, 1917*b*: 28.
Papilio policenes f. indiv. *liponesco* Suffert; Le Cerf, 1924*a*: 398.
Papilio policenes ab. *liponesco* Suffert; Bryk, 1930*b*: 571.
Papilio (*Graphium*) *policenes laurentia* ab. *liponesco* (Suff.); Peters, 1952: 22.
Graphium nigrescens liponesco Suffert; Hancock, 1986: 174.
Graphium liponesco Suffert; Larsen, 1994: 152 (partim); d'Abrera, 1997: 56, 57 (fig.) (partim).
Graphium (*Arisbe*) *policenoides liponesco* (Suffert); Ackery, Smith & Vane-Wright, 1995: 165 (partim).

SYNONYM

Papilio boolae Strand, 1909: 307. HOLOTYPE ♂: GUINEA: 'Ein ♂ von Boola' (Strand, 1909: 307), 'Herrn Leo Frobenius' (Strand, 1909: 307). 'Kgl. Zoologische Museum zu Berlin' (Strand, 1909: 307), MNHU.
Papilio boolae Strand; Bryk, 1930*b*: 570.
Graphium policenes =boolae Strand; Condamin and Roy, 1963: 415.
Graphium nigrescens liponesco =boolae Strand; Hancock, 1986: 174 (as syn. n.).
Graphium liponesco =boolae Strand; Larsen, 1994: 149.

TYPE EVALUATIONS

Papilio policenes liponesco Suffert (1904) was described from '3 männliche Exemplare'. One of these has a pink label in Suffert's hand giving the locality and stating it to be the 'Type'; it is evidently the specimen described by Le Cerf (1924: 398) as 'Type (H.T.)' which constitutes the selection of that specimen as lectotype. On the paralectotype found in BMNH, the determination and locality are also in Suffert's hand, but on a white label. Suffert's collection reached BMNH as part of the Joicey Bequest (BMNH Accession Register No. 1934–120).

Papilio boolae Strand (1909) was described from the single specimen, collected by Frobenius. The specimen concerned is readily identifiable in MNHU, having, *inter alia*, a determination label in Strand's hand, and an orange 'Type' label; CRS has added a further determination label.

TAXONOMIC STATUS

Papilio policenes liponesco Suffert (1904) was established as a subspecies. Birket-Smith (1960) misinterpreted it as *G. nigrescens* (Eimer) (now *G. policenoides*, q.v.), while treating specimens conforming to Eimer's taxon as an aberration ('*Papilio nigrescens* EIMER ab. *nigrescens* EIMER' [*sic*]). Hancock (1986) treated the taxon *liponesco* as a subspecies of *nigrescens*, but his interpretation of the latter followed that of Birket-Smith. Larsen (1994) examined these interpretations (and others) and recognized *Papilio policenes liponesco* Suffert as a full species occurring from Sierra Leone to Democratic Republic of Congo, though he speculated that the West African and equatorial populations may be separate subspecies. Our studies, especially of the male genitalia (see below), have shown it necessary to restrict the species to West Africa (Guinea to Benin), with the equatorial populations representing a separate species, *G. biokoensis* Gauthier (q.v.).

G. liponesco is sympatric with *G. policenes* and distinguishable on pattern and genital features.

Papilio boolae Strand (1909) was described as a species 'zwischen *nigrescens* Eim. und *policenes* Cr.'. Condamin and Roy (1963) treated it as a synonym of

G. policenes, Hancock (1986) synonymized it with his *G. nigrescens liponesco*, which Larsen (1994) raised to species rank. Examination of the holotype clearly shows it to be synonymous with *G. liponesco*, as restricted here to West Africa.

SIMILAR SPECIES
G. policenes; *G. biokoensis*; *G. policenoides*.

G. liponesco is distinguishable from *G. policenes* in being less boldly marked. In particular, the forewing bars are generally narrower and the post-discal marks of the forewing are smaller, appearing as a row of separate spots rather than a continuous band. The post-discal mark in forewing cell CuA_2 is almost square, with only a small projection at the anterior/costal corner, which is not contiguous with discal cell bar 3. On the hindwing, the red tornal spot, when visible at all, is represented only by a scattering of scales. The scattering of pale scales seen between the submarginal marks and the margin of hindwing cells M_2 to CuA_1 is lacking, or at least much less conspicuous.

Larsen (1994) noted that all the forewing cell bars, and the discal marks in cells CuA_2 and 1A are bottle green in fresh specimens of *G. liponesco*, whereas only the basal three discal cell marks and the basal marks of cells CuA_2 and 1A are this colour in *G. policenes*. Sadly, from an aesthetic as well as a heuristic point of view, the colours fade in older specimens. Larsen (1994) also drew attention to the fact (also mentioned by Birket-Smith, 1960) that the tail is relatively longer in *G. liponesco* and that the forewing is more falcate, both features more readily appreciated when comparing series of the two species.

G. liponesco is very similar to *G. biokoensis*. The shape of the dorsal terminal process of the male genital valve (see below) is the only reliable discriminator we have been able to find. *G. biokoensis* lacks the scattering of pale scales associated with the rubral mark in hindwing cell M_3 (see below).

G. liponesco may be distinguished from *G. policenoides* by its lack of an elongate discal mark in hindwing upperside cell M_3. There is usually a scattering of pale scales in this cell, as Larsen (1994) also noted, but they seem not to be associated with the discal mark, but rather with the rubral mark which occupies distal position and which can be seen through the wing from above with the aid of a lens. The bars of the forewing discal cell, though narrower than in *G. policenes*, are nevertheless well defined compared with *G. policenoides*, in which they are all but effaced. The submarginal marks of the posterior part of the forewing are better defined in *G. liponesco* than in *G. policenoides*, where they are represented by slight, diffuse pale marks.

DIAGNOSIS: PATTERN (Fig. 182). Similar to *G. policenes*, *G. biokoensis* and *G. policenoides*, with the differences noted above.

VARIATION
As usual, there is a general variation in the extent of the green markings. Particular variations include:
forewing cell R_3 with or without small discal spot;
hindwing cell M_3 sometimes with a scattering of pale scales in the position of a discal mark (see above);
hindwing cell CuA_2 sometimes with a small, red tornal spot.

DIAGNOSIS: ♂ GENITALIA (Figs 26, 28)
Follows the general *policenes*-group pattern. Unlike the remainder of the group, the dorsal terminal process has the lower, exterior branch much the larger with the upper, interior branch represented by a basal, serrate tooth. As in *G. biokoensis* and *G. policenoides*, the dorsal harpe is more finely serrate than in *G. policenes*.

DIAGNOSIS: ♀ GENITALIA. No reliably determined specimens available.

EARLY STAGES; HOST PLANTS; CONSERVATION STATUS. Apparently unknown.

DISTRIBUTION (Map Fig. 124). Found in western Africa, including Guinea, Sierra Leone, Ivory Coast, Ghana and Togo.

BIONOMICS
Generally a rare (but also much overlooked) monotypic species of moist evergreen and semi-deciduous forests (Emmel & Larsen, 1997; Larsen, In prep.*a*). According to Larsen (In prep.*a*) this rare butterfly usually appears smaller and flies more slowly than the abundant *G. policenes*, and is more restricted to primary forest habitats. Judging by the months noted by Larsen, it could be seasonal (Nov., Dec., Jan., Mar.). Larsen (1994) encountered *G. liponesco* in Ghana, where he caught males in the Kakum and Ankasa national parks. On all three occasions they were caught on damp sand or urine, in company with *G. policenes*. The different extent of the bottle-green of the forewings was immediately apparent. Note: Larsen (1994, In prep.*a*) included what we now recognize as a separate species (*G. biokoensis*) within his interpretation of *liponesco*; *G. biokoensis* occurs south-east of the 'Dahomey Gap', while true *liponesco* is so far only known to occur in countries to the west (Togo, Ghana, Ivory Coast, Guinea, Sierra Leone).

MATERIAL EXAMINED. 15 ♂♂ in BMNH; 6 ♂♂ from other collections.

11. *Graphium (Arisbe) biokoensis* Gauthier, 1984 stat. n.

Southern Narrow-Striped Swordtail (Fig. 183; map Fig. 126; genitalia Fig. 29)

Graphium policenes biokoensis Gauthier, 1984: 318, fig.5. HOLOTYPE ♂: EQUATORIAL GUINEA: 'Holotypus: ♂, Insel Bioko, 1. 1984 leg. J. G. CANU, in coll. A. GAUTHIER.' [not seen]. PARATYPE ♂♂ and ♀♀ (including 'Allotypus'): 'mit den gleichen Daten ... in coll. J. G. CANU, A. GAUTHIER, S. COLLINS, R. GUILBOT (Guyancourt).' [not seen].

Graphium liponesco Suffert; Larsen, 1994: 152 (partim); d'Abrera, 1997: 56, 57 (fig.) (partim).

Graphium liponesco = *biokoensis* Gauthier; Larsen, 1994: 152 (as syn. n.).

Graphium (*Arisbe*) *policenes biokoensis* Gauthier; Ackery, Smith & Vane-Wright, 1995: 165 (partim).

MISIDENTIFICATIONS

Papilo nigrescens Eimer, *sensu* Birket-Smith, 1960: 535. [Misidentification.]

Graphium nigrescens Eimer, *sensu* Berger, 1981: 53, pl.18 fig.6. [Misidentification.]

Graphium nigrescens nigrescens Eimer; Hancock, 1986: 174. [Misidentification.]

Graphium (*Graphium*) *nigrescens* =*biokoensis* Gauthier; Hancock, 1993: 568 (as syn. n.). [Misidentification.]

Graphium nigrescens Eimer, *sensu* Darge, 1994: 29, 30 fig. ♀. [Misidentification.]

UNAVAILABLE NAME

Papilo nigrescens ab. *intermedia* Birket-Smith, 1960: 540. Cameroon: 'river Nyong ... (Loc. 126)' [infrasubspecific].

Graphium liponesco f. *intermedia* Birket-Smith; Larsen, 1994: 152.

TYPE EVALUATIONS

Graphium policenes biokoensis Gauthier (1984) was described from the male selected as holotype, a female 'allotype' and an unstated number of paratypes of both sexes.

TAXONOMIC STATUS

Graphium policenes biokoensis Gauthier (1984) was described as a subspecies from the island of Bioko. Hancock (1993) synonymized it with what he interpreted as *G. nigrescens*. Larsen (1994) synonymized it with his interpretation of a widely distributed *G. liponesco*. The restriction of *G. liponesco* to West Africa leaves *biokoensis* as the oldest available name for the *policenes*-like butterflies with reduced markings from equatorial Africa. These show consistent, if slight, genital differences from *G. policenes* and are sympatric, so specific status is required.

Papilo nigrescens ab. *intermedia* Birket-Smith (1960) was described as an aberration of *nigrescens sensu* Birket-Smith (1960) on the basis of the specimen possessing 'a green spot on the root of ups. h.-w. space 3 [cell M_3] and with a more or less distinct red spot on the ups. h.-w. space 1c [the tornal spot]. According to Larsen (1994) the red spot of this specimen is 'almost imperceptible except under high magnification'. Larsen also reported green scaling in the base of hindwing cell M_3 and concluded that the proper placement of this aberration should be in *liponesco*.

SIMILAR SPECIES

G. liponesco; *G. policenes*; *G. policenoides*.

Very similar in wing pattern to *G. liponesco*, though lacking the patch of pale scales in hindwing upperside cell M_3 associated with the rubral mark. Clearly recognisable by the form of the male dorsal terminal process.

Differs from *G. policenoides* by lacking a clear discal stripe in hindwing upperside cell M_3 and by the forewing discal cell bars being clearly defined, if narrow.

Distinguishable from *G. policenes* by the reduction of the markings, especially of the forewing discal cell, though both species are variable. In most specimens the hindwing upperside tornal spot is faint. The male dorsal harpe (sometimes visible without dissection) is more finely serrate.

DIAGNOSIS: PATTERN (Fig. 183). Similar to *G. policenes*, *G. liponesco* and *G. policenoides*, with the differences noted above.

Darge (1994) described and illustrated the female (as *G. nigrescens*).

VARIATION. Shows some variation in the extent and size of the markings, including those of the forewing discal cell. Though normally faint, the hindwing upperside tornal spot is occasionally as clear as in *G. policenes*.

DIAGNOSIS: ♂ GENITALIA (Fig. 29)

Follows the general *policenes*-group pattern. Unlike *G. liponesco*, but like the remainder of the group, the dorsal terminal process has a large upper, interior branch, with the lower, exterior branch represented by a basal, serrate tooth. As in *G. liponesco* and *G. policenoides*, the dorsal harpe is more finely serrate than in *G. policenes*.

DIAGNOSIS: ♀ GENITALIA. No specimens available for dissection.

EARLY STAGES; HOST PLANTS; CONSERVATION STATUS. Unknown.

DISTRIBUTION (Map Fig. 126). Western-central Africa, including Nigeria, Cameroon, Equatorial Guinea (Bioko), Gabon, Congo, western Democratic Republic of Congo.

BIONOMICS

According to Darge (1994; as *G. nigrescens* Eimer), this species differs in behaviour from *G. policenes* and *G. antheus*, which occur in the same habitat, by 'un vol un peu different, moins saccadé et moins rapide.' He continues: 'Cette distinction, bien assimilée, permet à l'observateur attentif de 'cueillir' au sein d'une multitude d'exemplaires des deux espèces précitées, banales, l'unique exemplaire de *nigrescens* qui a pu s'y mêler.'

He also describes the adult female (as *nigrescens*) from a specimen collected in the Ototomo forest reserve, Cameroun, during January. Larsen (1994), who treated this butterfly as part of *G. liponesco*, considered it to be restricted to wetter forests (as is true *G. liponesco* to the west, and the broadly sympatric *G. policenoides*), and thus unlike the more widespread and presumably more adaptable *G. policenes*. Darge (1995, as *G. liponesco*) noted *biokoensis* as rare, and gave a single record for January from Mount Kala, Cameroon.

MATERIAL EXAMINED. 8 ♂♂ in BMNH. 9 ♂♂ from ZMUK.

12. *Graphium (Arisbe) policenoides* (Holland, 1892)

Dusky Swordtail (Fig. 184; map Fig. 125; genitalia Fig. 30)

Papilio policenoides Holland, 1892: 287. HOLOTYPE ♂: GABON: 'Talaguga, upon the Upper Ogové' (Holland, 1892: 287). 'Type in Collection Holland' (Holland, 1892: 287). CMNH (photographed I.J. Kitching). PARATYPE ♂: GABON: [?same data]. CMNH (photographed I.J. Kitching). [Senior subjective replacement name for *Papilio policenes nigrescens* Eimer (Larsen, 1994).]
Papilio policenoides Holland, 1893: 28, pl.1 fig.1.
Papilio nigrescens =*policenoides* Holland; Aurivillius, 1899: 490; Bryk, 1930*b*: 570.
Graphium nigrescens nigrescens =*policenoides* Holland; Hancock, 1986: 174.
Graphium policenoides Holland; Larsen, 1994: 151; d'Abrera, 1997: 56, 57 (fig.).
Graphium (*Arisbe*) *policenoides policenoides* Holland; Ackery, Smith & Vane-Wright, 1995: 165.

INVALID NAME

Papilio policenes nigrescens Eimer, 1889 : 223. HOLOTYPE ♂: CAMEROON: 'Kamerun . . . ein Falter – Männchen' (Eimer, 1889: 223). [not seen]. [Invalid; junior primary homonym of *Papilio philolaus nigrescens* Eimer, 1889 [Papilionidae].]
Papilio policenes Var. *nigrescens* Eimer; Aurivillius, 1891: 225.
Papilio nigrescens Eimer; Aurivillius, 1910: 25, pl.9 figs a,
Papilio nigrescens Eimer; Bryk, 1930*b*: 570.
Papilio (*Graphium*) *nigrescens* (Eimer); Peters, 1952: 22.
Papilo nigrescens ab. *nigrescens* Eimer; Birket-Smith, 1960: 540.
Graphium (*Arisbe*) *nigrescens* (Eimer); Munroe, 1961: 42.
Graphium nigrescens Eimer; D'Abrera, 1980: 48; Berger, 1981: 53, pl.18 fig. 6 (♂).
Graphium policenoides =*nigrescens* Eimer; Larsen, 1994: 151.
Graphium (*Arisbe*) *policenoides* = *nigrescens* Eimer; Ackery, Smith & Vane-Wright, 1995: 165.

TYPE EVALUATIONS

Papilio policenes nigrescens Eimer (1889) was described from a single individual among a group of *G. policenes* collected in Cameroon by 'Herrn Dr. Passavant' (Eimer, 1889: 223). According to Horn *et al.* (1990), Passavant's collection (principally of Diptera and Hymenoptera) is now in SMFD, Frankfurt. However, no likely specimen was seen there when briefly visited by one of us (CRS).

Papilio policenoides Holland (1892) was described from 'a large series of specimens', but one was originally selected as '[Holo]Type'. Holland's collection is now in the CMNH, Pittsburgh. Our colleague, I.J. Kitching was able to find and photograph the holotype and one further specimen (a paratype) in CMNH.

TAXONOMIC STATUS

Papilio policenes nigrescens Eimer (1889) was established as a subspecies. Since it was collected with a group of *G. policenes* (and presumably sympatric with them), this status does not accord with current interpretation of subspecies. Aurivillius (1891) treated it as a variety or subspecies of *policenes*, but later (Aurivillius 1899) elevated it to specific status, at the same time synonymising *Papilio policenoides*. Subsequent authors have interpreted the taxon variously as a recurrent aberration, subspecies or species. Larsen (1994) suggested that the pattern differences from both *G. policenes* and *G. liponesco* do not conform to a simple melanistic interpretation, nor does it occur in some areas where *G. policenes* (and other aberrations) are common. He also pointed out that all the specimens he saw were 'almost identical, with no transitional forms'. He concluded that Eimer's taxon is a good species, confined to 'very wet habitats' in the 'Cameroun/Gabon/Congo zone.' Our own studies support that conclusion. *Papilio policenes nigrescens* Eimer (1889: 223) is preoccupied by *Papilio* (now *Eurytides*) *philolaus nigrescens* Eimer (1889: 213).

Papilio policenoides Holland (1892) was established as a species. It was recognized as being synonymous with *P. nigrescens* Eimer by Aurivillius (1899). The name was first used as a subjective replacement name for *nigrescens* by Larsen (1994).

SIMILAR SPECIES

G. policenes, *G. liponesco*, *G. biokoensis*.

The reduction of the forewing discal cell bars seen in *G. liponesco* and *G. biokoensis* is more striking in *G. policenoides*. Bar 2 is very narrow (and continues as a narrow discal mark in cells CuA_2 and 1A), bars 3 and 4 are almost obsolete and bar 5 is clear only in the inner or medial half. The post-discal marks of the peripheral cells (R_3 to 1A) are generally smaller than in *G. policenes*, though less reduced than in *G. liponesco*;

the antero-costal corner of that in cell CuA_2 is less produced than in the other species. The submarginal marks of the forewing are smaller and fainter than in both *G. policenes* and *G. liponesco*, especially from cell M_2 backwards, where they are almost obsolete, being represented by no more than faint, diffuse, pale marks.

On the hind wing, the anterior submarginal marks, from cells R_1 to M_2 are reduced. The post-discal marks in these cells are somewhat smaller than in *G. policenes*, but larger than in *G. liponesco*. By contrast to this general reduction in wing marks, there is a charcteristic linear discal mark in cell M_3, not seen in *G. policenes* and, though there is sometimes a scattering of white scales in *G. liponesco*, this seems to have a different origin (see above). The mark in the discal cell gives the impression of being expanded along the cubital/medial vein to point towards the discal mark of cell M_3. As in *G. liponesco* and most *G. biokoensis*, the red tornal spot in cell CuA_2 is obsolete or very faint. Unlike *G. policenes*, there are no pale scales between the submarginal marks and the wing margins in cells M_2 to CuA_1. The marginal marks are less pronounced than in *G. policenes*.

The underside reflects the upperside, though the forewing discal cell bars and submarginal marks are more evident. On the hindwing the postdiscal mark of cell CuA_1 is virtually obsolete.

Larsen (1994) noted that the tail is proportioned as in *G. policenes*, not as relatively long as in *G. liponesco*. He also discussed the colour of the wing marks, which he noted to be 'less green', but wondered if this impression might have been the result of a paucity of fresh specimens. We have seen relatively few specimens, but some of these (e.g. the only one in the collections of BMNH, and one in MRAC) do show a brighter colour. For this reason, and a variety of others, more material would be welcome.

DIAGNOSIS: PATTERN (Fig. 184). Similar to *G. policenes*, *G. liponesco* and *G. biokoensis*, with the differences noted above.

VARIATION

According to Larsen (1994), 'all specimens seen are almost identical, . . . varying much less than the two other species [*G. policenes* and *G. liponesco*].' From the very few individuals which we have been able to compare in detail, we have observed the following:

there is some variation in the clarity of the forewing bars – a specimen in MRAC, photographed by CRS, shows these more clearly than other specimens. For example, bar 5 is complete.

The size of the discal mark in hindwing cell M_3 is somewhat variable. A specimen from Mayombe, Republic of Congo (coll. Jackson, now in ABRI) has this mark nearly twice as long as one from Banana, Republic of Congo (coll. Etienne, in MRAC).

In the Mayombe specimen, the hindwing discal cell band is wider along the medial/cubital vein, almost reaching the root of vein M_3.

The same specimen also shows the vestiges of a red tornal spot in hindwing cell CuA_2.

DIAGNOSIS: ♂ GENITALIA (Fig. 30)

Follows the general *policenes*-group pattern. Unlike *G. liponesco*, but like the remainder of the group, the dorsal terminal process has a large upper, interior branch, with the lower, exterior branch represented by a basal, serrate tooth. As in *G. liponesco* and *G. biokoensis*, the dorsal harpe is more finely serrate than in *G. policenes*.

DIAGNOSIS: ♀ GENITALIA. No specimens available for dissection.

EARLY STAGES; HOST PLANTS; CONSERVATION STATUS. Unknown.

DISTRIBUTION (Map Fig. 125). Western central Africa. Confirmed for Cameroon, Gabon, western Democratic Republic of Congo.

BIONOMICS

Apparently, this very poorly-known monotypic species only occurs in true rainforests. Berger (1981; as *G. nigrescens*) indicates that it very rare in Democratic Republic of Congo, and the female is unknown. According to Larsen (1994), this is a rare butterfly of the Cameroon-Gabon-Congo zone. Noting that few have been recorded from mud-puddles, he suggests that its scarcity might be related to occurrence in very wet habitats, or to synchrony of its flight period with rainy seasons, perhaps making it less dependent or likely to appear at mud puddles (primarily a dry season phenomenon). Larsen also notes that he has seen a total of 19 examples first hand or from photographs (more specimens than the present authors have seen), but he does not comment on their sex; so far as we are aware, the female is unknown (Darge's 1994 description of what he calls female *G. nigrescens* is a female of *G. biokoensis*.).

MATERIAL EXAMINED. 1 ♂ in BMNH. 12 ♂♂ from other collections.

13. *Graphium (Arisbe) porthaon* (Hewitson, 1865)

Coastal, Cream-striped, Dark or Pale-spotted Swordtail (Figs 191, 219; map Figs 120, 121; genitalia Figs 31, 83; early stages Figs 253, 254)

Both Berger (1951) and Hancock (1993) have treated *G. porthaon* as a monospecific group. In our analyses, it is placed in a polytomy with other swordtailed species basal to the crown group. When multistate characters are active, this polytomy includes the *angolanus* group, etc.

A species characterized by the wing markings being very pale, even in fresh specimens, and by the distal three forewing discal cell bars being strongly bisinuate.

The species occurs in Eastern Africa from coastal areas of Kenya to South Africa: Transvaal, with an isolated subspecies, *G. p. mackiei*, described from Meru Forest in Kenya and another, *G. p. tanganyikae* from the Kigoma district of western Tanzania. The diagnosis below is based on the nominate subspecies; the distinguishing characters – which are slight – of the other subspecies are given in the sections for those taxa. Biological information is also given in the species account, with some extra information in the accounts of each subspecies.

SIMILAR SPECIES

Most similar in general appearance to *G. polistratus*, less so to other sword-tailed *Graphium* including *G. antheus* and *evombar*, the *policenes*-group, *gudenusi*, *colonna* and *junodi*.

G. porthaon is distinguished from most other sword-tailed *Graphium* by the generally paler marking and by having the forewing discal cell bars 3–5 sinuate. In *G. polistratus*, these bars may be slightly curved, though rarely sinuate, and the cell spot distal to bar 5 is either absent or much smaller. In *G. antheus* the bars are also sinuate, but that species lacks a distal mark (as does *G. evombar*). *G. gudenusi* has sinuate bars, but they are almost obsolete. In the *policenes*-group, *colonna* and *junodi*, bars 3 & 4 are never more than slightly curved.

DIAGNOSIS: PATTERN (Figs 191, 219)

Upperside: Forewing discal cell with 5 transverse bars (including the basal) with bars 3–5 strongly sinuate. There is a prominent mark in the cell, distal to bar 5 and opposite cell R$_5$. The discal cell marks are produced beyond the anterior discocellular vein. Cell R$_3$ has a small, axillary discal spot, a prominent, squarish post-discal mark just distal to the root of vein R$_4$, and a prominent, squarish submarginal mark. In cell R$_4$ there is a small, axillary post-discal and a prominent, squarish submarginal mark. Cell R$_5$ has a discal mark which is sometimes fused to the larger post-discal mark, and prominent submarginal mark. In each of cells M$_1$ to M$_3$ there is a large post-discal mark and a prominent submarginal mark. The post-discals of these cell get progressively larger, and the submarginals more linear, posteriorly. Cell CuA$_1$ has transverse basal and discal bands, a squarish post-discal mark which reaches vein CuA$_2$ and nearly CuA$_1$, but not the posterior discocellular vein, and a subdivided submarginal mark. Cell CuA$_2$ has transverse basal and discal bands in line with those in cell CuA$_1$ and a larger post-discal mark, joined to that in CuA$_1$; there is no submarginal mark.

The **hindwing** discal cell has a basal band and another more distally, linking the discal mark of the costal cell with that of cell CuA$_1$. The band is narrow anteriorly, but broadens posteriorly, almost reaching the root of vein M$_3$. The costal cell has white basal, discal and post-discal bands and a linear, slightly crescentic submarginal mark. In cell R$_5$ there is a post-discal mark which is broad along vein R$_5$, but which does not quite reach the upper discocellular vein, instead curving parallel to it distally and narrowing to a blunt tip proximal to the root of vein M$_1$; there is a transverse, linear submarginal mark. Cells M$_1$ to M$_3$ usually each have a small post-discal mark situated progressively more distally within the cell, and a transverse, linear submarginal mark. Cell CuA$_1$ has an elongate discal mark which abuts the discal cell band, a small post-discal mark and a transverse, linear submarginal mark. The basal band is continued into cell CuA$_2$. Just distal to the submarginal mark and the margin of cells R$_1$ to CuA$_1$ is a pale patch consisting of scattered scales: creamy white in cells, R$_1$ to M$_1$; bluish in cells M$_2$ to CuA$_1$. There are distinct marginal marks in all cells, that in M$_3$ extending nearly half way along the tail, where it almost meets the extended white tip.

As usual, the **underside** pattern largely reflects that of the upperside, though the ground colour is a paler tan, becoming darker in the posterior cells (CuA$_1$ to CuA$_2$) of the **forewing**. The rubral system of the **hindwing** consists of a red band passing between the discal and post-discal marks of the costal cell and cell R$_1$, edged proximally with bluish scales in the latter. The ground colour here is a darker brown. In cell R$_5$ there is a faint red line, edged distally with brown, along the upper discocellular vein proximal to the post-discal mark. In the discal cell there is usually a small patch of bluish scales opposite cell M$_1$ and not reflected on the upperside, which may represent a relict rubral element. Cell M$_1$ itself normally has a red mark at its base. In cell M$_2$ there is a basal red mark and in M$_3$ a red arc, edged proximally with bluish scales, a little displaced from the cell base. In each of these cells a brown streak, along the cell's midline, connects the rubra to the post-discal spot. The pattern in cell CuA$_1$ is more complex, with the elongate discal mark surrounded by brown at its distal tip, then comes the red rubra, with its bluish proximal edge, which touches the small post-discal spot. This is more-or-less surrounded by a patch of bluish scales which extends to include the submarginal mark, though interrupted by an elliptical brown patch. Cell CuA$_2$ also has a blue edged rubral mark, adjoining that in cell CuA$_1$, with a brown mark distal to it. The pale patches between the submarginal marks and the margins seen in all cells are larger and brighter on the underside than their equivalents on the upperside, as are the marginal marks themselves.

VARIATION

There is, as usual, variation in the extent of the pale markings. For example, at one extreme, the forewing post-discal marks are more-or-less fused into a single band (e.g. in f. *vernayi*); at the other, these marks are reduced so that only those in cells CuA_1 and CuA_2 are touching (the lectotype of *porthaon* is like this).

Specific variations we have noted include:

the distal forewing discal cell mark varies between a small spot to a large solid spot which may be excised on its costal margin to form a crescent;

forewing cell R_4 with post-discal mark varying between vestigial and well marked;

forewing cell R_5 with discal and post-discal marks sometimes touching or partly or almost completely fused;

the post-discal marks of hindwing cells M_1–M_3 are very variable in size, with that in M_1 often absent and those in the other cells more rarely so (this is the prime characteristic of ssp. *tanganyikae* Kielland, but a series from Rabai, Kenya, includes a specimen (BMNH Spec.Reg. No. 141572) in which these marks are all absent, or very nearly so);

there is sometimes an area of scattered white scales towards the base of hindwing cell M_3, which sometimes becomes coherent enough to form a clear spot or even a streak (ab. *adjectus* Thurau);

the white or bluish scales distal to the submarginal marks of the hindwing are sometimes reduced almost to absence;

on the underside, the extent of the rubral elements in each cell is somewhat variable, for example, the element in cell R_5 may be stronger; that in M_1 reduced or absent; and that in the discal cell varies from absence to prescence of a bluish mark, to inclusion of a red spot

A more notable aberration is seen in a specimen from Kenya: Rabai (BMNH Spec.Reg. 141339). In this the left forewing discal cell bar 5 is particularly expanded and is joined to bar 4 by a pale mark close to the posterior discocellular vein.

DIAGNOSIS: ♂ GENITALIA (Fig. 31)

Although different in general appearance and the proportions of the organs, their relatively simple form shows some similarity with the *adamastor*-group.

Dorsal projection compressed basally and angled acutely downwards, turning dorsad by 90° about halfway along to project beyond the valve margin; the distal part more cylindrical. Unusually, the main concentration of setae is on the postero-ventral face. *Dorsal terminal process* projecting mesad; narrow basally to accommodate large dorsal harpe, expanding dorsad distally to form a straight edge similar to that seen in the *adamastor*-group; the mesal/terminal edge somewhat flattened. *Ventral terminal process* large, broad, long and finely serrate terminally. *Dorsal harpe* a broad, compressed hook produced dorso-posteriad well beyond valve margin; outer (postero-ventral) curve of the hook serrate and somewhat explanate; tip is finely serrate. *Ventral harpe* a simple, non-serrate, horizontal, triangular blade directed posteriad.

Uncus short, directed ventrad; *socii* prominent, with large projections. *Aedeagus* short, straight, with no sign of denticulation.

DIAGNOSIS: ♀ GENITALIA (Fig. 83)

BMNH Spec.Reg. No. 141581; vial 3990: *ostium bursae* opening anteriorly; *ductus bursae* elongate and sclerotized, with kink/constriction distal to *ductus seminalis*, but not pocketed; *central ostial lobe* long (exceeding lateral lobes) narrow, spatulate, slightly keeled ventrally; *lateral ostial lobes* broad, setose; *anterior apophyses* well marked; *papillae anales* rounded, with some long hook-like setae.

EARLY STAGES (Figs 253, 254)

The final instar larva is polymorphic, occurring in at least three forms: 'green', 'yellow' and 'black' (Henning *et al.*, 1997: 249). The black form gives clear indication of an underlying pattern of transverse stripes, and these are expressed with low contrast in the paler forms. The thorax may have more prominent transverse bands (dark in most cases, but possible pale in some 'black' or olivaceous individuals), but these bands are not expressed at all in some of the pale or green larvae. The thoracic processes of the mature larva are short. The pupa is also polymorphic, either brown finely speckled and streaked with black, bright green with brown marks, or overall greenish-gray with sepia marks, and rather leaf or bark-like, with a stout, blunt dorsal horn of moderate length, and perhaps slightly flattened in overall shape.

Van Son (1949) gives a partial account based on Monteiro (see Trimen, 1889), and Aurivillius (1910). Good illustrations are to be found in Henning *et al.* (1997). Photographs of egg and larva of '?*porthaon*' have been sent to us by Congdon (*in litt.*, 27.ix.1999), who also notes that development can be very rapid – this particular larva went from egg to final instar within 11 days, but then died. Sevastopulo (MS) recorded all stages as follows:

Egg: Small, spherical, pale yellow. Laid singly on the upper surface of a leaf of the food-plant. Hatched 13.i.64.

1st instar: Head black. Body blackish olive, anal somite white 1st somite with a subdorsal scolus, others with a subdorsal, bifid spine. A sublateral series of smaller, black spines; thoracic somites with an additional spine between the two series. Moulted 14.i.64.

2nd instar: Head yellowish olive. Body slate grey, transversely lined with darker. 1st somite yellowish olive, anal somite white. 1st somite with a subdorsal black spine, 2nd and 3rd with very small greenish subdorsal spines. Anal somite with a black subdorsal process. Moulted 16.i.64.

3rd instar: Similar.

Described from larvae reared from ova found in the Marere Forest, all of which died in the 3rd instar.

4th instar: Head brownish orange. Body greyish, each somite with a double, darker, transverse line. 1st and anal somite tinged with orange. 1st somite with a long, fine, outcurved, subdorsal, black spine. 2nd and 3rd with small, whitish, subdorsal spines. Anal somite with an outcurved, black spine. Venter, legs and prolegs whitish. Moulted 10.v.64.

Final (5th) instar: Head brownish orange. 1st somite yellowish with a transverse, black, dorsal line; 2nd and 3rd somites blackish brown with a yellowish grey transverse line posteriorly and anteriorly; anal somite yellow. Rest of the body yellowish-grey, each somite with a median, transverse whitish line edged on each side with a narrow blackish stripe, the intersegmental areas also blackish. The stripes end on the spiracular area, below which the body and venter are pale greenish grey. Thoracic somites each with a black subdorsal spine, anal somite with an outcurved yellow spine outlined with black. Spiracles white rimmed with brownish black. Legs and prolegs greenish.

Described from larvae found at Nyali, one of which pupated 16.v.64 and a female emerged 3.viii.64.

A larva found in Nyali in January 1965 had the head green. The body bright apple green with a yellow lateral line, below which the colour was slightly bluer. Osmeterium pouch with a transverse black line and with a blue-black spine at either end. 2nd and 3rd somites each with a blue-black, orange-based, short spine subdorsally. Anal processes green. Venter, legs and prolegs glaucous green. This larva formed a bright green pupa. The front and sides of the thoracic process marked with dark brown. The junction of the thorax and wing cases marked with pinkish brown. A lateral series of minute brown specks and a curved white subdorsal line from the base of the thoracic process to the cremaster, this line with a brown mark on it on the 4th abdominal somite.

Another larva had the head brown; the body green with a broad black transverse band on the 3rd somite, a narrower one on the 2nd and a black line on the 1st. 4th somite backwards with two smokey transverse lines enclosing one of bluer green on each somite.

Pupa suspended by the cremaster and a girdle. Color greenish grey, which is seen under a lens to be composed of green punctures on a whitish ground. A faint, slightly raised, white, subdorsal line on the abdominal somites, bearing a dark sepia mark on somites 3, 4 and 7. Prothorax with three sepia marks. Rather broad across the 3rd abdominal somite, thorax produced into a frontally directed process, head with two short pointed cones. Thoracic process tipped with sepia and with slight sepia markings along its edge. Another pupa had the ground colour mottled brownish grey, with markings similar to the green form. [Described from a larva found at Nyali which pupated on 16.v.64; a female emerged 3.viii.64.]

The larva found at Nyali in January 1965 with a green head (described above)

. . . formed a bright green pupa. The front and sides of the thoracic process marked with dark brown. The junction of the thorax and wing cases marked with pinkish brown. A lateral series of minute brown specks and a curved white subdorsal line from the base of the thoracic process to the cremaster, this line with a brown mark on it on the 4th abdominal somite.

Earlier, Sevastopulo (loc.cit.) described another pupa thus:

Pupa suspended by the cremaster and a girdle of dark brown silk. Colour brown, the dorsum heavily streaked and speckled with black, the venter paler and with the speckling arranged in more or less regular longitudinal lines. Shape with the head slightly bifid; thorax with a stout, blunt, forward-pointing process. Slightly constricted between head and pro-thorax, and again between meta-thorax and abdomen. Widely expanded across the tornus of the wing-cases, then tapering fairly sharply to the cremaster. Venter flattish. The shape is extremely difficult to describe in words and the pupa an extremely difficult one to photograph. Described from a pupa formed by a Jadini-caught larva 2.v.60, from which a male emerged 20.ix.60. [Sevastopulo's descriptions are accompanied by14 black and white photographs.]

HOST PLANT RECORDS

Annonaceae:
Annona sp. (Sevastopulo, MS; Ackery *et al.*, 1995)
Artabotrys monteiroae (Henning *et al.*, 1997)
Cleistochlamys kirkii (Henning *et al.*, 1997)
Friesodielsia obovata (Henning *et al.*, 1997)
Monodora junodii (Henning *et al.*, 1997)
Uvaria kirkii (Congdon, *in litt.*, 1999, for *?porthaon*)
Uvaria sp. (Sevastopulo, MS; Ackery *et al.*, 1995).

BIONOMICS

A butterfly of coastal forests (but not generally rainforest), riverine bush, woodland and dry savannah country in Kenya, with an isolated population at Meru (*p. mackiei*), it also occurs south to Lake Tanganyika, Botswana and Transvaal (van Son, 1949; Kielland, 1990; Larsen, 1996). In Tanzania Carcasson (1960) suggests that it occurs in well-wooded areas below 5000ft., but Kielland (*op. cit.*) indicates a maximum of 1900 m. In Malawi it flies up to 3500ft (Gifford, 1965), whereas in Kenya it is a species of the coastal forests. Berger (1950) gives a single record for eastern Democratic Republic of Congo, from Bukama, and Luna de Carvalho (1962) a single record from Angola (captured in September). For Malawi Gifford (1965) gives the flight period as July–Feb. In Natal the butterfly is on the wing during summer months, notably December and January (Henning *et al.*, 1997). Van Son (1949) includes records for April–June, June, July, Nov., Dec., while for Botswana Larsen (In prep.*b*) gives Dec.–Feb. and July. *G. porthaon* evidently flies all year in the tropical parts of its range (Williams, 1969).

This species is not uncommon according to Collins & Morris (1985), but generally uncommon according to Kielland (1990). Van Son describes how he observed *porthaon* flying back and forth among low xerophytic vegetation covering rocky hills in Zimbabwe, and found them difficult to capture due to their erratic flight and the uneven ground. However, by waiting at flowers of *Grewia* 'and other shrubs' to which they were attracted, he was able obtain specimens. Henning *et al.* (1997) state that the females fly more slowly, and both sexes are attracted to damp sand; they also note that the males patrol woodland and forest edges, mostly flying 2–3 metres above the ground. Kielland (1990) regarded *G. p. tanganyikae* to be local and quite rare, except at the beginning of the rains (October and November), when it can be more frequently encountered in the Mahale Mts, at about 800–1000 m. (west shore of Lake Tanganyika, Tanzania). Larsen (In prep.*b*) describes the flight (of *G. p. vernayi – sic*) as very similar to *G. antheus*, and records the butterflies avidly mudpuddling in company with *G. angolanus* and *G. leonidas*. Swanepoel (1953) also compares the behaviour of *porthaon* with *antheus*, including a tendency to migrate westwards in South Africa during years of good rainfall. Oviposition takes place on young tips, buds or flowers of the foodplant, the female curling her abdomen under a bract or leaf to lay her eggs singly. The first instar emerges after 3–4 days but (according to Henning *et al.*, 1997) does not eat its shell. The young larvae hide in bracts or along partly eaten shoots; later instars switch to resting on upper surface midribs, where they are hidden by other leaves. Fifth instar larvae are polymorphic, in dark, and green or yellow forms. The upright pupa is leaf or bark-like in appearance, and is attached to a stem of the foodplant.

CONSERVATION STATUS. 'Apparently not uncommon and no threat known' (Collins & Morris, 1985: 60), but see above.

13a. *G. (A.) porthaon porthaon* (Hewitson, 1865)

(Fig. 191; map Fig. 121; genitalia Figs 31, 83)

Papilio porthaon Hewitson, 1865: Pap pl 7, f 21,22. LECTOTYPE ♂: [MOZAMBIQUE]: 'Hab. Zambesi . . . In the Collection of W. C. Hewitson' (Hewitson, 1865) BMNH Spec.Reg. No. 141619 – **here designated**. 3 PARALECTOTYPE ♂♂: [MOZAMBIQUE]: same data. BMNH Spec.Reg. Nos. 141620, 141621, 141622.

Papilio porthaon Hewitson; Kirby, 1871: 559; Aurivillius, 1908: 26; Bryk, 1930*b*: 572.

Papilio (*Graphium*) *porthaon* Hewitson; van Son, 1949: 51; text figs 27, 28; pls V (fig. 15), VI (fig. 15); Peters, 1952: 22.

Graphium porthaon Hewitson; Berger, 1950: 96, fig.95; D'Abrera, 1980: 48, 49 (figs); Berger, 1981: 53, pl.19 fig. 1 (♂).

Graphium (*Arisbe*) *porthaon* (Hewitson); Munroe, 1961: 42.

Graphium (*Arisbe*) *porthaon porthaon* (Hewitson); Carcasson, 1981: 124; Pennington, 1994: 307, pl.195 fig.726a i, ii; Ackery, Smith & Vane-Wright, 1995: 165.

Graphium (*Graphium*) *porthaon* (Hewitson); Hancock, 1983: 46; Collins & Morris, 1985: 60.

Graphium porthaon porthaon Hewitson; Kielland, 1990: 48; d'Abrera, 1997: 58, 59 (fig. as *antheus*, but corrected on insert page).

Graphium porthaon [*porthaon*] Hewitson; Larsen, 1991: 119.

SYNONYM

Papilio porthaon vernayi van Son, 1936: 138, pl.2 fig.3. HOLOTYPE ♀: BOTSWANA: 'Kabulubula, Chobe River, 11–24. vii.30.' (van Son, 1936). TMSA – not seen.

Papilio (*Graphium*) *porthaon* f. *vernayi* van Son; van Son, 1949: 51 – (as stat. n.)

UNAVAILABLE NAME

Papilio porthaon ab. *adjectus* Thurau, 1903: 143. TANZANIA: 'Langenburg' (*ibidem*). ?MNHU – not seen. [infrasubspecific.]

TYPE EVALUATIONS

Hewitson (1865) was not explicit as to the number of specimens in his type series of *Papilio porthaon*, though he described only the male, gave one size and used the singular throughout the description. Kirby (1879) listed four specimens in his catalogue of Hewitson's collection at the time of its bequest to BMNH (Accession Register No.1879–69). These are in BMNH numbered 1– 4 in Kirby's hand. One of these, number 3, was labelled with a round BMNH or Hill Museum style 'Type HT' label by a previous curator. Since this most closely matches the Hewitson's (1865) figures 21 and 22, and in order to avoid future confusion, we select this specimen as lectotype.

Papilio porthaon vernayi van Son (1936) was described from a single female (van Son, 1949).

TAXONOMIC STATUS

Hewitson (1865) established *Papilio porthaon* at specific rank, and this has been accepted by all authors since.

Van Son (1936) established *Papilio porthaon vernayi* as a subspecies on the basis of a number of differences stemming from an increase in the extent of the pale marks, but established it on the single female example. However, he subsequently reported (van Son, 1949) that many typical specimens had been found at the same locality and concluded that his original specimen was an 'aberration'. The use of the abbreviation 'f.' in his revision is clearly intended to be taken as infrasubspecific. Subsequent authors have accepted this, though Pennington (1994) speculated that such well marked individuals might represent an extreme dry-season form.

DIAGNOSIS: PATTERN; DIAGNOSIS. ♂ GENITALIA; DIAGNOSIS. ♀ GENITALIA; EARLY STAGES; HOST PLANTS; BIONOMICS. See species account, above.

DISTRIBUTION (Map Fig. 121)

Mainly eastern Africa, but extending west to Angola and Democratic Republic of Congo. Countries confirmed include Kenya, Tanzania, Malawi, Zambia, Zimbabwe, Mozambique, Botswana, South Africa, Democratic Republic of Congo, Angola.

Berger (1981) records a single specimen from Democratic Republic of Congo: Bukama (Haut-Lomami) (in MRAC, seen by CRS).

CONSERVATION STATUS. No known threats according to Collins and Morris (1985: 60).

MATERIAL EXAMINED. 105 ♂♂; 33 ♀♀ in BMNH; 22 ♂♂; 6 ♀♀ from other collections.

13b. *G. (A.) porthaon mackiei* Collins & Larsen, 1991

Meru Cream-striped Swordtail (Fig. 219; map Fig. 120)

Graphium porthaon mackiei Collins & Larsen, 1991: 119 (cited as Larsen & Collins), 438, pl.4 fig.27i. HOLOTYPE ♂: KENYA: 'Meru Forest, xi. 1988 (S. C. Collins, leg.) . . . in the National Museum, Nairobi' (Collins & Larsen, 1991) NMKE. PARATYPES: 33 ♂♂, 8 ♀♀: '. . . from various years in coll. National Museum, Nairobi [NMKE], The Natural Histroy Museum, London [BMNH, 1 ♂, Spec.Reg. No.141573], T. B. Larsen, and S. C. Collins [ABRI].' (Collins & Larsen, 1991: 438–9).

Graphium (Arisbe) porthaon mackiei Collins & Larsen; Ackery, Smith & Vane-Wright, 1995: 166.

Graphium porthaon mackiei Collins & Larsen; d'Abrera, 1997: 58.

TYPE EVALUATION. *Graphium porthaon mackiei* Collins & Larsen (1991) was described from the 42 specimens listed above, with type designations original.

TAXONOMIC STATUS

Graphium porthaon mackiei Collins & Larsen (1991) was established as a subspecies on the grounds of its distinctive appearance, as detailed below, and its disjunct distribution. All members of the type series were collected in the months of November and December.

DIAGNOSIS: PATTERN (Fig. 219)

Collins & Larsen (1991) used the following criteria for establishing *G. (A.) porthaon mackiei*: '(1) the discal band of the forewings (and some of the hindwing markings) are considerably broader [than in *G. (A.) p. porthaon*], often twice as broad in space 1a [cell CuA_2]; (2) on the forewing the four large [post-discal] spots from space 1a to 3 [CuA_2 to M_3] are wholly fused; those in 2 and 3 [CuA_1 and M_3] are free in the nominate subspecies; (3) the ground colour of the bands is a much deeper and clearer cream.'.

G. porthaon is variable in the extent of the pale markings, and we have seen specimens of the nominate race with the forewing band of post-discal marks as extensive as those exhibited by *G. p. mackiei*. But in these specimens, the other markings also tend to be larger, whereas in *G. p. mackiei* other marks (e.g. forewing cell bars) are less pronounced.

The fact that all the specimens recorded by Collins & Larsen (1991) were captured in November and December raises the possibility that there may be a phenotypic, seasonal response.

DIAGNOSIS: ♂ GENITALIA

Almost identical to those of the nominotypical subspecies. In the only specimen we have seen, the dorsal terminal process is less upturned distally and the tips of the dorsal harpe and ventral terminal processes are slightly more coarsely serrate.

DISTRIBUTION (Map Fig. 120). Meru area of Kenya.

HOST PLANTS. Presumably Annonaceae, as listed for the species.

BIONOMICS. Larsen (1996) stated that there is a single annual brood, November–December.

CONSERVATION STATUS. Unknown.

MATERIAL EXAMINED. 1 ♂ in BMNH.

13c. *G. (A.) porthaon tanganyikae* Kielland, 1978

Kigoma Cream-striped Swordtail

Graphium (Arisbe) porthaon tanganyikae Kielland, 1978: 161, pl.6 figs 21–24. HOLOTYPE ♂: 'Kigoma, Kasoge, 12.x.1969, J. Kielland' (Kielland, 1978: 162); PARATYPE ♂: 'Kigoma, Kasoge, 12.x.1969, J. Kielland'; 'idem but November, 1969, J. Kielland'; 10 PARATYPE ♂♂: 'idem but Kefu, 12.iv. 1971'; PARATYPE ♀ ('Allotype'); 'idem but Kefu forest, 12.xi.1972' (all Kielland, 1978: 162). 'Holotype and allotype in the British Museum (Nat. Hist.), London, paratypes in J. Kielland collection.' (Kielland, 1978: 162). NONE SEEN (see below).

Graphium porthaon tanganyikae Kielland; D'Abrera, 1982: [?2].

Graphium porthaon tanganyikae Kielland; Kielland, 1990: 48, 265 pl.9; d'Abrera, 1997: 58.

Graphium (Arisbe) porthaon tanganyikae Kielland; Ackery, Smith & Vane-Wright, 1995: 166.

TYPE EVALUATION

Graphium (Arisbe) porthaon tanganyikae Kielland (1978) was described from the specimens listed above, with type designations original. Kielland intended the holotype and 'allotype' to be lodged in the BMNH, but by the time of his tragic death in 1995, this had not happened. Kielland's collection is now under the care of S.C. Collins who has informed us (pers. comm.) of his intention to carry out Kielland's wish when the specimens can be located.

TAXONOMIC STATUS

Graphium porthaon tanganyikae Kielland (1978) was established as a subspecies on the grounds of its distinctive appearance, as detailed below, and allopatric distribution. Without having seen either the type specimens themselves, or topotypic specimens we propose to maintain nomenclatural stability by not synonymising ssp. *tanganyikae* with ssp. *porthaon*. Clearly, more material from the Kigoma area would be helpful, as would any specimens found between there and the more coastal populations. Kigoma appears to be a minor area of endemism, so that differentiation of this population seems plausible.

DIAGNOSIS: PATTERN

Kielland (1978) distinguished ssp. *tanganyikae* from the nominate subspecies by '. . . reduced submarginal [post-discal] spots of the hind wing'. He noted that 'in one ♂ there are no spots or only a very faint dot in space 2 [cell CuA$_1$]; in another, 3 submarginal [post-discal] spots in 2, 3, 4 [cells CuA$_1$ to M$_2$]'. The expression of these post-discal marks in *G. porthaon* is variable; in BMNH there are specimens from coastal Kenya and Mozambique with similar reduction. Kielland (1978) also noted that 'the distance from the discal long spot in 2 [CuA$_1$] to the submarginal [post-discal] spot . . . is greater than the coastal races . . . [and] . . . forewing subbasal streak [the discal mark of cells CuA$_1$ and CuA$_2$] constantly narrow and . . . submarginal streaks . . . straight.' But these, too, are variable in *G. porthaon*, with specimens in BMNH with these features similar to those specimens illustrated by Kielland (1978, 1990). Other points mentioned by Kielland (1978) include a darker ground colour and the underside darker, with better developed black and red markings.

Thus the features used by Kielland (1978) to distinguish ssp. *tanganyikae* all seem to fall within the possible range of phenotypes shown by the nominate subspecies. It is possible that there is a clinal difference of the frequency of these characters from the western part of the species range to the coast.

DIAGNOSIS: GENITALIA. We have been unable to examine any specimens.

EARLY STAGES. Unknown.

DISTRIBUTION (Map Fig. 120). Kigoma district of Tanzania.

HOST PLANTS. Presumably Annonaceae, as listed for the species.

BIONOMICS. 'Found in glades and flying along footpaths of low level forest . . . (800–1000 m).' (Kielland, 1978: 162). See also species account.

CONSERVATION STATUS. Rare (Collins and Morris, 1985: 60).

MATERIAL EXAMINED. None – see above.

14–19 *The angolanus clade*

Included taxa: *G. a. angolanus*, *G. a. baronis*, *G. endochus*, *G. morania*, *G. taboranus*, *G. schaffgotschi*, *G. ridleyanus*.

A group recognized by Berger (1951) and Hancock (1993) of seven recognisable taxa in six species which our analyses never failed to recover (see above). They are united by features of the male genitalia, most notably a serrated, vertical basal lamella of the ventral harpe; the dorsal harpe in the form of a flattened club with serrate margins; the valve narrowing sharply posteriorly; the dorsal projection quite stout and directed somewhat posteriorly; the ventral terminal process small and serrate. The female genitalia are also characteristic in having the part of the ductus bursae distal to the ductus seminalis sclerotized and with a pocket-like expansion, and by the lack of a central ostial lobe in the vestibulum.

The wing pattern has an upper surface with white marks on a black background, a pattern largely mirrored on the underside where the background is chocolate or dun coloured, and some of the spots are silvery. The base of the forewing cell underside is brick red, and this colour extends into the basal area and anal margin of the hind wing (figs 185–190).

G. ridleyanus is an exception in having a (usually) brick red pattern on a brown background, with an array of black spots on the underside (see fig. 192, and below), normally considered to be associated with mimicry of *Acraea* (Nymphalidae) species. Uniquely within the genus, it has lost the bundled androconial scales of the inner margin of the hindwing of the males (see above).

Apart from *G. ridleyanus*, which is largely forest dwelling, most members of the group are associated with savanna on the outer edges of the main rainforest blocks of continental Africa. *G. endochus* inhabits forests in Madagascar.

When multistate characters are excluded from our analyses, the clade is placed in a polytomy with *G. (Graphium) bathycles* basal to the remainder of the non-swordtailed species. When multistates are activated, this structure is lost, and the clade forms part of a much more inclusive polytomy including, *inter alia*, many swordtailed species, but still basal to the remainder of the non-swordtailed species.

14. *Graphium (Arisbe) angolanus* (Goeze, 1779)

White Lady Swallowtail, or Savanna Swallowtail (Figs 185, 220; map Figs 128, 129; genitalia Figs 32, 84; early stages Figs 255, 263)

A widespread species of deciduous woodland and wooded savanna throughout much of tropical Africa. The species has long been regarded as bitypic, with a western/northern race formerly referred to as *G. a. pylades* (Fabricius) (a junior homonym) and an eastern/southern race (*G. a. angolanus* (Goeze)). *G. a. baronis* (Ungemach), described from Ethiopia in 1932 is here synonymized with *pylades* (Fabricius) and becomes available for use as a subjective replacement name, rendering an objective replacement name, *G. a. calabar* Hancock, 1985*a*, unnecessary. *G. a. howelli* Turlin & Lequeux, 1992, described from Pemba Island, Tanzania, is here synonymized with *G. a. angolanus*.

There appears to be some overlap in the ranges of the two taxa (notwithstanding some possible misidentifications and false localities), and the existence of a few intermediate phenotypes suggests the possibility of some gene flow between them. Whether the two taxa should be regarded as subspecies or full species may depend on further (e.g. molecular) study and, perhaps, which species concept is adopted. We here retain the generally accepted status.

We describe the species' pattern below, with brief comments on the differences between the subspecies, reflecting their overall similarity; those differences are described in more detail as part of the subspecies accounts.

SIMILAR SPECIES. *G. taboranus*, *G. schaffgotschi*, *G. morania*.

DIAGNOSIS: PATTERN (Figs 185, 220)
Distinguished from the three species listed above by the wider separation of the discal and post-discal spots on the hindwing undersides. The races may be separated by the patterns in the forewing upperside discal cell. To aid discussion of these features we have numbered the (potential) white patches, see Fig. 9.

Upperside ground colour dark brown with a pattern of white marks. **Forewing** discal cell with pattern of transverse bands. In *G. a. angolanus*, the proximal ones are confined usually to the costal part of the cell (though there is usually a scattering of white scales giving a greyish appearance); in *G. a. baronis*, there is usually a sinuous mark extending along the posterior discocellular vein connecting these bands. There is variation in these features in both subspecies, described in greater detail in the appropriate sections. Cell R_3 with a discal spot proximal to the root of vein R_4, a post-discal spot just distal to the root of vein R_4, and a submarginal mark. Cell R_4 with a post-discal and a submarginal mark. Cells R_5 and M_1 each with a discal spot, a post-discal spot approximately level with the root of vein R_4, and a submarginal mark. Cell M_2 with an elliptical mark that probably represents a fused discal and post-discal spot (especially in *G. a. angolanus*, where it is somewhat larger than in *G. a. baronis*), a submarginal mark and a narrow marginal mark. Cell M_3 in *G. a. angolanus* has a small, fuzzy-edged, elliptical post-discal mark; in *G. a. baronis*, the mark usually extends into the angle of vein CuA_1 and the posterior discocellular vein, extending along the latter as far as vein M_3. In both subspecies there is also a submarginal and a marginal mark. In cell CuA_1 the post-discal mark fills the basal two-thirds or so of the cell, and there is a submarginal and a marginal mark. The post-discal mark of cell CuA_2 extends similarly distally, but does not reach the very base of the cell, though here there is a scattering of white scales over the ground colour. There is a bifid submarginal mark and a faint marginal mark. The post-discal mark in cell 1A forms a continuous band with that in CuA_2, again not quite reaching the base.

The **hindwing** discal cell band is very broad, usually reaching beyond a line joining the roots of veins M_1 and CuA_1, sometimes reaching the end of the cell. The band does not quite reach the base of the cell, but here there is a scattering of white scales. This narrow, greyish area is contiguous with similar areas in the neighbouring cells and on the forewing, reflecting the brick red band of the underside. Cell R_1 has a broad band also with a greyish base. In *G. a. angolanus* there is often a small submarginal mark, apparently absent in *G. a. baronis*, and both subspecies have a small marginal mark. In cell R_5 there is a basal mark contiguous with those in the discal cell and cell R_1, a submarginal mark. Cell M_1 usually has just a submarginal and a marginal mark. Cells M_2 to CuA_1 each have a post-discal spot, a somewhat reflexed, chevron-shaped submarginal mark and a marginal mark. In addition, cell M_3 has a discal mark in the angle of the posterior discocellular vein and vein CuA_1, but not, or barely, reaching vein M_3. In cell CuA_1, this mark is larger, filling the basal area of the cell. Cell CuA_2 has a post-discal mark contiguous with this but in the anterior half of the cell only, posterior to this is a greyish area of scattered white scales overlaying the ground colour; distally there is usually a small to moderate orange tornal spot, small submarginal and marginal marks. Females are similar, though perhaps tending to be slightly less heavily marked and with a white anal cell (usually rolled and not easily seen in males).

The **underside** pattern is largely similar to the upper, but certain differences are striking. Over the anterior part of the forewing (roughly from vein M_2 forward) and on the hindwing, the ground colour is a pale chestnut brown. In **forewing** cell M_2 and posteriorly, as well as in the central part of the discal cell, it is dark brown. The basal half of the cell is brick red and this colour extends into the bases of the discal cell and cells R_1 and CuA_2 of the hindwing, where it is lined distally with a narrow dark brown stripe. There is also a narrow brown stripe along the distal margins of the white bands of **hindwing** underside cells R_1 and R_5, and just proximal to the distal margins of the discal marks in the discal cell and cells M_3 to CuA_2, giving a narrow white stripe just distal to the brown one. There are also brown marks on the proximal edges of the submarginal marks and, in cells M_2 to CuA_2, between these marks and the marginals. Some of the white markings are more extensive on the underside than on the upper. In particular, some of the forewing discal cell bands of *G. a. angolanus* may be extended to the posterior discocellular vein as a greyish or nacreous band of white scales on the darker background, and the post-discal spot of *G. a. angolanus* is surrounded by nacreous ring.

DIAGNOSIS: ♂ GENITALIA (Fig. 32)

Details are given below for *G. a. angolanus*, with the differences, which are slight, given for *G. a. baronis*.

In common with *G. endochus*, but unlike the rest of the group, the dorsal terminal process is not bifid, but it is very broad, apparently expanded dorsally and with a ventral hook, suggestive of a bipartite structure. Unlike *G. endochus*, the dorsal area is serrate. The ventral harpe is characteristic, being very short and broad (almost circular), and serrate on the mesal margin. The dorsal harpe is a long-stalked circular disc, slightly curved to follow the shape of the dorsal area of the dorsal terminal process, and serrate all round.

DIAGNOSIS: ♀ GENITALIA (Fig. 84)

Based on *G. a. angolanus*, BMNH Spec.Reg. No. 140358; vial 3985: *ostium bursae* opening posteriorly; *ductus bursae* well sclerotized distally kinked and with a marked pocket just distal to the *ductus seminalis* (see van Son, 1949); *central ostial lobe* absent; *lateral ostial lobes* setose, not well sclerotized (*contra* Miller, 1987); *anterior apophyses* present; *papillae anales* short, rounded.

EARLY STAGES (Figs 255, 263)

The larvae have a strong pattern of transverse stripes in the later instars (e.g. 4th), but in the final instar this pattern is much less contrasting, the larva being overall greenish in appearance (although the transverse stripes may still be evident, being bluish edged with brown). The lateral line is yellow and very conspicuous. The thoracic and anal processes are pilose except in the last instar, in which they are of moderate length (black on the thorax, yellowish on the anal segment) and are apparently smooth. The green or yellowish-green pupae have well-developed dorsal and lateral cephalic horns, with the abdomen somewhat flattened, and a number of dark or indigo spots and markings, including two conspicuous dots on the dorsum of abdominal segment 3.

There are sketches by Haig (1936), Seth-Smith (1938), and Villiers (1957); paintings and description by Coleridge (1916); see also Schultze (1917*b*), and van Son (1949). Photographs of egg, larvae and pupa have been sent to us by Colin Congdon (*in litt.*, 27.ix.1999). Written descriptions for all stages of both races found in Democratic Republic of Congo are given by Fontaine (1985: 77–79). Henning *et al.* (1997) figure early and late larvae and the pupa, and describe the life cycle: egg pure white when laid, changing to yellowish-brown with pink markings (if fertilized); the emergent larva eats the shell; at first only holes eaten in leaf lamina; the mature larva may occupy quite prominent branches in a tree, typically resting on the midrib of the upper surface of a leaf; larval development takes about two weeks; the green, upright, leaf-like pupal stage lasts from 12 days to to 2 years. Sevastopulo (MS) gave the following description of *G. angolanus baronis* early stages from Kenya:

> Egg: Typical papilionid ovum of a pale greenish-yellow. Laid singly on the upper surface of a leaf of the food-plant. Hatched 1.vi.60.
>
> 1st instar: Head black, bristly. Dorsum from 1st to 9th somite white, 10th somite backwards brownish-olive, with an interrupted black median line and a subdorsal and laterodorsal series of black spots. Rest of the body brownish-olive. First three somites each with a comparatively large subdorsal scolus. A series of paired black bristles on either side of the dorsal line and a similar subdorsal series from the 4th somite backwards. 12th somite with a pair of backward-pointing yellowish scoli. Shape rather swollen to junction of the 3rd and 4th somites, which are rather darker than the others, thereafter tapering. Moulted 3.vi.60.
>
> 2nd instar: Similar. Moulted 5.vi.60.
>
> 3rd instar: Head brownish-olive, the clypeus filled in with whitish. Dorsal area, white, each somite with a transverse median yellow band edged with black and with an intersegmental black line, 3rd and 4th somites dorsally suffused with blackish. A lateral black line bounding the white area, which encroaches onto the subdorsal area on the 10th and 11th somites. Lateral area, venter, legs and prolegs pale greenish. Scoli on the thoracic and 12th somites only, golden brown. Moulted 7.vi.60.
>
> 4th instar: Head brownish-olive, the clypeus filled in with whitish. Ground colour yellow, each somite with a transverse white band edged with black and with a black line intersegmentally. The stripe separating the lateral and subdorsal areas much narrower, olive. Lateral area olive with a pale green median line. Legs, prolegs and venter pale green. Osmeterium pouch with a black transverse line. Spiracles white rimmed with black. Scoli on the thoracic somites little more than spines. Moulted 10.vi.60.
>
> 5th (final) instar: Head green. Body green, each somite with a slightly bluer transverse stripe edged with brown. Osmeterium pouch with a black transverse line and with a second black line between the 1st and 2nd somites dorsally. A supra-spiracular whitish line bearing yellow dots, bounding the transversely striped area. Venter, legs and prolegs, also the lateral area pale green. Spiracles white rimmed with black. Osmeterium green, very reluctantly extruded. Thoracic somites each with a slender black subdorsal spine, 12th somite with the yellow scoli much reduced, little more than a pair of

stout spines. A fringe of short colourless setae bordering the vental area.

Pupa suspended by a girdle and the cremaster. The abdominal somites flattened ventrally, the line from the head to the first abdominal somite ventrally making an angle of about 30° with the horizontal. Head produced into two blunt cones. Thorax with a straight, forward-pointing, dorsal process extending beyond the front of the head. Colour rather yellow green, the anterior edge of the thoracic horn and a median line from the back of the head thereto dark brown. A dark brown quadrate spot above the wing-case on the posterior edge of the meso-thorax. A faint, slightly bluer, elliptical line running from the meta-thorax to the base of the cremaster bearing small dark brown marks, most pronounced on the 3rd and 4th abdominal somites. A series of minute indigo dots on the abdominal somites midway between the subdorsal line and the spiracles.

Described from larvae reared in Nyali from wild-found ova, one of which pupated 15.vi.60, and a male emerged 15.vi.60. Several pupae formed at the same time went into diapause, the imagines emerging at the end of August.

[Sevastopulo's descriptions are accompanied by 17 black and white photographs.]

GENERAL DISTRIBUTION (Map Figs 128, 129)

Found almost anywhere in western, northern tropical, central and eastern Africa, extending south into South Africa and perhaps northern Namibia, with possible distribution in northern Ethiopia, Eritrea and Somalia likewise uncertain. According to Turlin (1994), this species may recently have become established on Grande Comore, where he and others have made occasional captures within the last 20 years.

HOST PLANT RECORDS

Annonaceae:

Annona muricata (Villiers, 1957).

Annona senegalensis (Coleridge, 1916), (Schultze, 1917*b*), (Haig, 1936), (Seth-Smith, 1938), (Sevastopulo, MS), (Fontaine, 1985), (Henning *et al.*, 1997), (Congdon, in litt. 1999).

Annona squamosa (Sevastopulo, MS – noting a record from Le Pelley).

Hexalobus monopetalus (Kloppers & van Son, 1978).

Uvaria sp. (Ackery *et al.*, 1995), (Sevastopulo, MS – citing 'Van Someren typescript').

Apocynaceae:

Landolphia sp. (Ackery *et al.*, 1995), (Sevastopulo, MS – citing 'Van Someren typescript').

Malpighiaceae:

Sphedamnocarpus pruriens (according to Platt, as noted in van Son, 1949, and Pinhey).

BIONOMICS

In reading these notes, the possibility that *G. a. angolanus* and *G. a. baronis* represent marginally overlapping, parapatric sister-species should be borne in mind. According to Larsen (1996a), essentially 'a savannah and open woodland butterfly', in eastern and southern Africa it is found in savannas, gardens, and woodlands (van Son, 1949; Kielland, 1990; Gifford, 1965) and at forest margins, while in western Africa its habitats include 'open gardens and grassy places' (Owen & Owen, 1972), riverine forests, savannas, and savanna-forest margins (Owen, 1971: 12, 23). Although Haig (1936) states emphatically 'I have never seen it in forest', Hecq & Peeters (1992) also record it from a wide range of habitats in the Central African Republic, from gallery forest to open plains. The butterfly supposedly does not occur in extremely dry scrub (Ackery *et al.*, 1995) although, according to Seth-Smith (1938), it is at its most common in northern Ghana during the dry season. Apparently it does not fly much above 1500 m (Gifford, 1965), but Kielland (1990) gives its altitudinal range as 0–2200 m. The butterflies are attracted to puddles (Carpenter, 1915), and Larsen (In prep.*a*) quotes Schultze (1920) with respect to the high frequency of these butterflies drinking on wet sand, sometimes in groups of 50 or more; Larsen (In prep.*b*) recalls seeing hundreds at damp patches along the Chobe River in Botswana. Larsen also notes them nectaring at 'peacock flower' and forming a small communal roost at Accra, and how his father saw a vast migration near Abuja (Nigeria); Stoneham (1934) also comments on its strongly migratory behaviour. According to Gifford (1965), it flies throughout the year in Malawi, peaking during Sept.–June. In Rwanda, Monfort (1987) notes that it occurs from December to July, peaking in May-June. In the Democratic Republic of the Congo, Berger (1950) gives months iv, v, vi, viii, ix, xi and xii for 'vrai *pylades*' (subsp. *baronis*), which is restricted to the northern part of the country, and for subsp. *angolanus*, recorded mainly from the more southerly regions, he gives records for all months. Henning *et al.* (1997) note that in South Africa the butterfly flies 'throughout the warmer months' (cf. Kloppers & van Son, 1978), but Williams (1969) gives only April to September! In contrast again, for Botswana, where it is restricted to northern parts, Larsen (In prep. *b*) gives Dec.–April. Larsen describes the flight as restless, stopping only to water or feed from flowers, at which they hover in typical swallowtail fashion, and notes that they can be found hill-topping; in some contrast, Cooper (1973) suggests that the butterfly has a rapid but direct flight, and 'is fairly simple to catch by using a fast sweep of the net'. Swanepoel (1953) considered the flight to be 'fairly swift', but slower than *G. antheus*. Henning *et al.* (1997) describe the flight as 'low and fast . . . dodging . . . through the trees', and note that males establish territories when hilltopping, but are also territorial in flat areas, where 'they patrol [rapidly] back and forth' over a circuit of a kilometre or more in length. According to Henning *et al.* (1997), gravid females flutter into the interior of their tree hosts, to lay their eggs.

CONSERVATION STATUS. 'Common, often abundant and not threatened' (Collins and Morris, 1985: 56).

14a. *G. (A.) angolanus angolanus* (Goeze, 1779)

Angola White Lady Swallowtail (Fig. 185; map Fig. 129; genitalia Figs 32, 84)

Papilio angolanus Goeze, 1779: 87. TYPES: ANGOLA/SOUTH AFRICA: 'Promontorii B. S. et *Angolae* inquilinus'. Lost – see below.

Papilio angolanus [*angolanus*] Goeze, 1779; Kirby, 1877: 811.

Papilio pylades v. *angolanus* Goeze, 1779; Aurivillius, 1899: 481; Bryk, 1930*b*: 556.

Papilio pylades angolanus Goeze; Aurivillius, 1908: 21, pl. 7(b).

Papilio (*Graphium*) *pylades angolanus* Goeze; van Son, 1949: 33; text-figs 16, 17; Pls V (fig.6), VI (fig.6); Peters, 1952: 20.

Graphium pylades angolanus Goeze; Berger, 1950: 61, figs 61, 62.

Graphium angolanus angolanus Goeze; D'Abrera, 1980: 40, 41 (figs); Berger, 1981: 49, pl.12, figs 6 (♀), 7 (♂); Kielland, 1990: 46, 265 pl.9; d'Abrera, 1997: 48, 49 (figs).

Graphium (*Arisbe*) *angolanus* (Goeze); Hancock, 1983: 46.

Graphium (*A.*) *angolanus angolanus* (Goeze); Pennington, 1994: 305, pls 36, 193; Ackery, Smith & Vane-Wright, 1995: 160.

SYNONYMS

Papilio Corrineus Bertoloni, 1851: 173, pl. 1, figs 1–3. HOLOTYPE ♀: MOZAMBIQUE: 'Mozambico' (Bertoloni, 1851); 'Di questa nuova specie ho ricevuto un solo individuo' (Bertoloni, 1851: 174–5). 'Zool. Mus. Bologna' (Horn *et al.*, 1990) (not seen).

Papilio pylades var. *Corrineus* Bertoloni; Kirby, 1871: 562.

Papilio angolanus [*angolanus*] =*corrineus* Bertoloni; Kirby, 1877: 811.

Papilio corrineus Bertoloni; Trimen, 1889: 217.

Papilio pylades var. *angolanus* =*corrineus* Bertoloni; Bryk; 1930*b*: 557.

Papilio anthemenes Wallengren, 1857: 6. LECTOTYPE ♀: SOUTH AFRICA: 'Hab. in Caffraria. WAHLBERG' (Wallengren, 1857: 6). NRS **– here designated** (photocopy of insect and labels seen).

Papilio angolanus [*angolanus*] =*anthemenes* Wallengr[en]; Kirby, 1877: 811.

Papilio Corrineus =*anthemenes* Wallengr[en]; Trimen, 1889: 217.

Papilio pylades lapydes Suffert, 1904: 103. HOLOTYPE ♂: TANZANIA: 'Ein männliches Exemplar aus Kilossa, Deutsch-Ost-Africa.' (Suffert, 1904: 104). 'Coll. Suffert' (Suffert, 1904: 104) BMNH Spec.Reg. No. 139534.

Papilio pylades angolanus ab. *lapydes* Suffert; Aurivillius, 1908: 21.

Graphium angolanus howelli Turlin & Lequeux, 1992: 312, pl.1. HOLOTYPE ♂: TANZANIA: 'Ngezi forest, extrémité nord ouest de l'île Pemba, Tanzania, Juin 1988' (Turlin & Lequeux, 1992: 312). MNHN (Turlin & Lequeux, 1992: 312) (not seen). PARATYPES: 11 ♂ and 10 ♀ (including 'allotype'): same locality, but various dates ('allotype' is July 1990) (Turlin & Lequeux, 1992: 312). MNHN (including 'allotype') and colls Lequeux (Paris) and Turlin (Andrésy) (Turlin & Lequeux, 1992: 312). **Syn. n.**

UNAVAILABLE NAMES

Papilio pylades F. v. *angolanus* ab. *kitungulua* Strand, 1911: 294. TANZANIA. MNHU. [infrasubspecific]

Papilio pylades-angolanus ab. *hypochra* Boullet & Le Cerf, 1912: 246. CONGO REPUBLIC. MNHN. [infrasubspecific]

Papilio angolanus ab. *spoliatus* Schultze, 1913*b*: 50. DEMOCRATIC REPUBLIC OF CONGO. 'Mus. Hamburg' (not seen – presumed destroyed). [infrasubspecific]

Papilio (*Cosmodesmus*) *pylades angolanus* ab. *blariauxi* Dufrane: 118. DEMOCRATIC REPUBLIC OF CONGO. IRSN. [infrasubspecific]

Papilio (*Cosmodesmus*) *pylades angolanus* ab. *dawanti* Dufrane: 118. DEMOCRATIC REPUBLIC OF CONGO. IRSN. [infrasubspecific]

Papilio (*Cosmodesmus*) *pylades angolanus* ab. *deficiens* Dufrane, 1946: 118. DEMOCRATIC REPUBLIC OF CONGO. IRSN. [infrasubspecific]

Papilio (*Cosmodesmus*) *pylades angolanus* ab. *jottrandi* Dufrane, 1946: 118. DEMOCRATIC REPUBLIC OF CONGO. IRSN. [infrasubspecific]

Papilio (*Cosmodesmus*) *pylades angolanus* ab. *wansoni* Dufrane, 1946: 118. DEMOCRATIC REPUBLIC OF CONGO. IRSN. [infrasubspecific]

Papilio (*Cosmodesmus*) *pylades angolanus* ab. *addenda* Dufrane, 1946: 119. DEMOCRATIC REPUBLIC OF CONGO. IRSN. [infrasubspecific]

Graphium angolanus howelli f. *jozani* Turlin & Lequeux, 1992. TANZANIA. [infrasubspecific]

TYPE EVALUATIONS

In his description of *Papilio angolanus* Goeze (1779) was providing a name for a taxon described and figured, but not named by Seba (1765: [index:] 11, [main text:] 14, pl.9 figs 17–20). Seba illustrated the larva, pupa and the upper- and undersides of the adult. To judge from the figures, these are different individual specimens. According to Horn *et al.* (1990) Seba's collection is in the Zoological Museum, St Petersburg. We have been informed by Dr A. L. Lvovsky of the Zoological Institute, St Petersburg, that Seba's collection had been kept in the Kunstcamera in St Petersburg in the latter part of the 18th century. But, during reconstruction of the Kunstcamera to establish the Zoological Museum in 1832, the entomological part of Seba's collection was lost.

P. corrineus Bertoloni (1851) was described from a single individual, which appears from the figures to be a female. The taxon was described in a dissertation of the Istituto di Bologna and, according to Horn *et al.* (1990), Bertoloni's collection went to the 'Zool. Mus. Bologna'. We have so far been unable to examine the specimen.

Wallengren (1857) described only the female of *P. anthemenes* and gave one size, suggesting a single specimen, though not explicitly, and we therefore designate the specimen concerned as lectotype. Bert Gustafsson (pers. comm.) has sent images of the upper and undersides and labels. These give locality as 'Caffraria', show it to be from 'J. Wahlb[erg's]' collection; it is also labelled 'Type' and has a hand-written determination label, apparently in Wallengren's hand and so we designate that as lectotype to avoid future confusion. The specimen lacks post-discal spots in the forewing cell M_3 (see Variation, below).

P. lapydes was described from the single, clearly labelled specimen which reached the BMNH via the Joicey Bequest (BMNH 1934–120).

Graphium angolanus howelli Turlin & Lequeux, 1992, was described from the 22 specimens listed above, with type designations original.

TAXONOMIC STATUS

Papilio angolanus Goeze (1779) was established as a species. Kirby (1877) recognized its relationship with *P. pylades* Fabricius. This was followed by later authors, though several, following Aurivillius (1899), treated *pylades* as the nominate, with *angolanus*, despite its seniority, as a variety (later, subspecies) thereof.

Papilio corrineus Bertoloni (1851) and *Papilio anthemenes* Wallengren (1857) were both established as species. Kirby (1871) recognized *corrineus* as different from '*P. pylades*' by treating it as a variety. Later, Kirby (1877) synonymized both *corrineus* and *anthemenes* with *P. angolanus*, as a species distinct from '*P. pylades*'. Though some later workers (e.g. Trimen, 1889) continued to treat *P. corrineus* as a good species, most subsequent (and all recent) authors have recognized its synonymy with *angolanus*.

Suffert (1904) established *lapydes* as a subspecies of '*Papilio pylades*', but the opening of the description reads 'Die vorliegende Aberration stellt ein Übergangsstück von pylades Fabr. zu dessen var. angolanus, Goetze [sic] . . . ' (Suffert, 1904: 103) suggesting infra-subspecific status. It was treated as an aberration of *angolanus* Goeze by Aurivillius (1908) and of *pylades* Fabricius by Bryk (1930 – Bryk did not differentiate *pylades* Fabricius into subspecies). The specimen is heavily marked and, indeed, intermediate in appearance between typical *a. angolanus* and *a. baronis*, with forewing discal cell elements 1b and 2b both present and connected (as in *a. baronis*), but not reaching to within 2.4 mm of 3b (very rare in *a. baronis*). The post-discal mark in forewing cell M_3 is small and elliptical, but there is a small mark in the angle between the posterior discocellular vein and vein CuA_1 (a condition rarely seen in *a. baronis*). On the hindwing, there is a post-discal spot in cell M_1. Its identity with *a. angolanus* is confirmed by its provenance in southern Tanzania and by the small size of the rudimentary tail on hindwing vein M_3.

G. a. howelli Turlin & Lequeux (1992) from Pemba, falls easily within the range of variation exhibited by *G. a. angolanus*. In particular, of the distinguishing characters cited by Turlin & Lequeux (1992): the forewing shape is variable, including some examples with well marked concavity of the outer margin; the rudimentary tail on hindwing vein M_3 (etc.) are as in *G. a. angolanus*; submarginal marks of the forewing upperside are variable, with some well marked; the marks in forewing cells R_3 and R_4 are well within the range of variability of mainland examples; the post discal mark in forewing cell M_3 is sometimes present, its absence is by no means uncommon on the mainland; that in cell M_2 appears typical for *G. a. angolanus*; the extent of the hindwing post-discal marks is variable in Pemba and mainland examples – subdivision is by no means uncommon; the anal orange spot is often absent in mainland specimens. Similar variability is exhibited in the mainland and Pemba specimens for both the underside and female characters cited by Turlin & Lequeux (1992). We have no hesitation, therefore, in synonymising the two.

Specimens from Zanzibar show much of the variability seen in mainland populations, including all those variable traits used by Turlin & Lequeux (1992) to separate the form *jozani* (including some contrary to those they used to define *howelli*).

DIAGNOSIS: PATTERN (Fig. 185)

Usually readily distinguished from *G. a. baronis* by the absence of a sinusoidal white pattern in the forewing upperside discal cell along the posterior discocellular vein. The post discal white spot in forewing upperside cell M_3 is small, elliptical and isolated from the veins enclosing the cell; not extending into the postero-proximal corner of the cell. The rudimentary tail on hindwing vein M_3 is shorter than in *G. a. baronis*.

VARIATION

As in *G. a. baronis* there is a great deal of variation in the extent of the white marking as seen on the upper surface of the wings. A number of clear variants can be distinguished. These may occur in combination, are found throughout the subspecies range and not confined to a single sex. They include:

forewing discal cell spot 1a absent (ab. *wansoni* Dufrane);

forewing discal cell spot 1b present (inc. ab. *kitungulua*; ab. *addenda* Dufrane);

forewing discal cell spot 2b present (in ab. *blariauxi* Dufrane, but more prominent on underside; ab. *addenda* Dufrane);

forewing discal cell spots 1b and 2b joined;

forewing discal cell spots 2a and 3a joined;

forewing discal cell spots 2a and 2b joined to form band across cell (inc. ab. *kitungulua*);

forewing discal cell band 2 complete and expanded to fuse with 3;

black scales between forewing discal cell spots 3b and 4b (surrounded by white);

black scales invading between forewing discal cell spots 3b and 4b to give hook like appearance (ab. *deficiens* Dufrane, and particularly marked in ab. *jottrandi* Dufrane);

forewing discal cell spot 4a touching 3a+3b+4b;

discal and post discal spots in forewing cell M_2 partly free;

forewing cell R_5 with discal spot absent;

forewing cell M_1 with discal spot absent;

forewing cell M_2 with small spot in angle of veins M and M_2

forewing cell M_3 with post-discal spot absent (e.g. lectotype of *anthemenes* Wallengren; and ab. *dawanti* Dufrane; ab. *deficiens* Dufrane);

small white spot in forewing cell M_3 in angle of veins M and CuA_1;

hindwing discal cell with small white spot in apical area;

hindwing cell M_1 with post discal spot.

In some specimens the red on the undersides of the wings is lacking, leaving the ochraceous yellow of the background of most of the rest of the wing. Turlin & Lequeux (1992) suggest that this variant is under the control of a single gene. It has been named ab. *hypochra* by Boullet & Le Cerf (1912) and ab. *spoliatus* by Schultze (1913*b*).

DIAGNOSIS: ♂ GENITALIA (Fig. 32)

Valve: *dorsal projection*: long, directed somewhat posteriad and curving slightly ventrad, stout spines mainly on anterior edge; *dorsal terminal process*: broad, curved mesad, serrate terminally, the serrations becoming larger ventrally, with a serrate ventral hook; *ventral terminal process*: small, serrate; *dorsal harpe*: elongate and parallel sided basally, becoming nearly circular and serrate apically; *ventral harpe*: short, broad, serrate; *basal lamella*: broad with 6 or 7 serrations. *Uncus*: tapering distally; *soccii*: with prominent projections. *Aedeagus*: elongate, nearly straight, with no sign of denticulation. *Saccus*: elongate, narrow.

DIAGNOSIS: ♀ GENITALIA; EARLY STAGES; HOST PLANTS; BIONOMICS; CONSERVATION STATUS. See species account.

DISTRIBUTION (MAP FIG. 129)

The more southerly of the two subspecies.

Countries confirmed include (those in which both races occur indicated by *): Gabon, Congo*, Democratic Republic of Congo*, Rwanda, Burundi, Angola, Uganda*, Kenya*, Tanzania (inc. Pemba and Zanzibar), Malawi, Zambia, Zimbabwe, Mozambique, Namibia, Botswana, Swaziland, South Africa, Comoro Islands.

Records from Central African Republic may be less reliable.

Two specimens in BMNH labelled 'Lagos' are not, presumably, from Nigeria.

MATERIAL EXAMINED. 586 ♂♂; 195 ♀♀ in BMNH. 196 ♂♂; 60 ♀♀ from other collections.

14b. *G. (A.) angolanus baronis* (Ungemach, 1932)

Northern White Lady Swallowtail (Fig. 220; map Fig. 128)

Papilio pylades baronis Ungemach, 1932: 21, pl. 1 fig. 1. HOLOTYPE ♂: ETHIOPIA: 'Baro, 14 mai 25' (Ungemach, 1932: 21). 'Type dans ma collection' (Ungemach, 1932: 21). MNHN; PARATYPE ♂ : ETHIOPIA: 'Baro' (Ungemach, 1932: 21). MNHN; PARATYPES: 1 ♂, 1 ♀: ETHIOPIA: 'Didessa' (Ungemach, 1932: 21); 2 PARATYPE ♂♂: ETHIOPIA: 'Gambela' [10.v.1926] (all label data). MNHN. Senior (subjective) replacement name for *Papilio pylades* Fabricius, 1793, *nec* Stoll [1782] (preoccupied).

Papilio (Graphium) pylades baronis (Ung.); Peters, 1952: 20.

Graphium angolanus baronis Ungemach; D'Abrera, 1980: 40; d'Abrera, 1997: 48.

Graphium (Arisbe) angolanus baronis (Ungemach); Ackery, Smith & Vane-Wright, 1995: 161.

SYNONYMS

Graphium (Arisbe) angolanus calabar Hancock, 1985*a*: 97. (Unnecessary) objective replacement name for *Papilio pylades* Fabricius, 1793, *nec* Stoll [1782] (preoccupied.). **Syn. n.**

Graphium (Arisbe) angolanus calabar Hancock; Ackery, Smith & Vane-Wright, 1995: 161.

UNAVAILABLE NAMES

Papilio pylades Fabricius, 1793: 34. TYPE: 'Habitat in Africa Mus. Dom. Francillon' (Fabricius, 1793: 34) (not seen). A junior primary homonym of *Papilio pylades* Stoll [1782] (Lepidoptera: Castniidae). The oldest available (subjective) replacement name is *baronis* Ungemach, 1932. **Syn. n.**

Papilio pylades Fabricius; Kirby, 1871: 562.

Papilio angolanus var. *pylades* Fabricius; Kirby; 1877: 811.

Papilio pylades pylades F.; Aurivillius, 1908: 21, pl. 7(c); Peters, 1952: 20.

Papilio pylades [*pylades*] F.; Bryk, 1930*b*: 556.

Papilio (*Graphium*) *pylades* Fabricius; van Son, 1949: 33.

Graphium (*Arisbe*) *pylades* (Fabricius); Munroe, 1961: 42.

Graphium pylades pylades Fabricius; Berger, 1950: 60, fig.60.

Graphium angolanus pylades Fabricius; D'Abrera, 1980: 40, 41 (fig.); Berger, 1981: 49, pl.12 figs 4, 5; d'Abrera, 1997: 48, 49 (fig.).

Graphium (*Arisbe*) *angolanus* =*pylades* (Fabricius); Collins & Morris, 1985: 56.

Papilio (*Cosmodesmus*) *pylades pylades* ab. *houzeaui* Dufrane, 1946: 118. GUINEA. IRSN. [infrasubspecific]

Papilio (*Cosmodesmus*) *pylades pylades* ab. *houzeaui* '*minor*' Dufrane, 1946: 118. GUINEA. IRSN. [infrasubspecific]

TYPE EVALUATIONS

Fabricius (1793) described *Papilio pylades* from Francillon's collection, but without stating the number of specimens. According to Horn *et al.* (1990) Francillon's material went via J.C. Stevens to BMNH and OXUM, but we have found no Francillon specimens in either collection. Zimsen (1964) lists no material in Kiel.

Papilio pylades baronis Ungemach was described from Baro and Didessa, where Ungemach (1932) stated it to be common, but gave no series length; one of the Baro specimens was originally designated as 'Type'. The holotype, 4 male and 1 female paratypes, clearly labelled, are in MNHN.

Graphium (*Arisbe*) *angolanus calabar* Hancock, 1985*a*, was established as an objective replacement name for *Papilio pylades* Fabricius, 1793, with the same type specimen(s) (See Code Article 72.7 – ICZN, 1999).

TAXONOMIC STATUS

Papilio pylades Fabricius (1793) was established as a species and was treated as such until Kirby (1877) recognized its relationship with *P. angolanus*. This was followed by later authors, though several, following Aurivillius (1899), treated *pylades* as the nominate race, despite the seniority of *angolanus*.

As recorded by Hancock (1985), the name is a junior primary homonym (See Code Articles 23.4 and 53.3 – ICZN, 1999) of *Papilio* (now *Corybantes*) *pylades* Stoll [1782] (Lepidoptera: Castniidae) a large, distinctive moth from the Amazon region. *Graphium angolanus calabar* Hancock (1985) was proposed as an objective replacement name.

Papilio pylades baronis Ungemach (1932) was established as a subspecies intermediate between '*pylades* type et *angolanus*', in that the sinusoidal pattern lying along the posterior discocellular vein is reduced compared to typical '*pylades*', sometimes with a gap between it and band 3. However, as shown below, this feature is quite variable within the subspecies (and in *G. a angolanus* – see above). However, Ungemach's type specimens, and others we have seen from Ethiopia, are consistent in having the post-discal mark of forewing cell M_3 extending to the base of the cell in the angle of the posterior discocellular vein and vein CuA_1, and in having a pronounced rudimentary tail on hindwing vein M_3. These two features are characteristic of *G. a.* '*pylades*', which, when taken together with the sinusoidal forewing discal cell marking (albeit somewhat reduced), constitute convincing evidence that *G. a. baronis* (Ungemach, 1932) is synonymous with *G. a. pylades* (Fabricius, 1793). As such, it is the oldest available, subjective, replacement name (See Code Article 60.3 – ICZN, 1999).

SIMILAR SPECIES

The characteristic forewing upperside discal cell pattern should be sufficient to distinguish this taxon from the nominate race and other species such as *G. schaffgotschi*, *G. morania* and *G. taboranus*.

DIAGNOSIS: PATTERN (Fig. 220)

Generally readily distinguished by the presence in the forewing upper side discal cell of a sinusoidal pattern lying along the posterior discocellular vein. The pattern is the result of expansion and fusion of the various elements shown in fig. 9. The variation of these elements is considerable (see below).

Further characterized by the postdiscal mark of the forewing upperside cell M_3 which (usually) occupies the whole basal region of the cell (also see below).

In addition, the rudimentary tail on hindwing vein M_3 is slightly longer than in *G. a. angolanus*.

VARIATION

We have observed the following 15 discrete variations; there are probably more.

Forewing discal cell spot 1a missing;

Forewing discal cell spot 2a fused with 2b (ab. *houzeaui* Dufrane);

Forewing discal cell spot 3b not reaching 2b;

Black scales between forewing discal cell spots 3b and 4b;

Forewing discal cell spot 4a with a central black dot;

Forewing discal cell spot 3/4 made to look hook-like by dark scales between 3a and 4b;

Forewing cell M_1 with discal spot;

Forewing cell M_2 with white spot in angle of M vein with vein M_3;

Forewing cell M_2 with white spot in angle of M vein with vein M_2;

White post-discal spot of forewing cell M_2 extended to base of cell (may be partial);

White area of forewing cell M_3 reduced to a streak running from the angle of veins M and CuA_1 to middle of cell;

White streak running from the angle of vein CuA_1 and the posterior discocellular vein to middle of forewing cell M_3 clearly composed of a basal and post-discal element;

Basal and post-discal spots in forewing cell M_3 discrete;

Forewing cell M_3 with basal white patch missing;

Forewing cell M_3 with post-discal white patch missing.

Various of these may be found in combination, and most seem to occur at much the same frequency throughout the range, although statistical analysis would be needed to confirm this.

DIAGNOSIS: ♂ GENITALIA. Very similar to *G. a. angolanus*. The basal lamella of the harpe is somewhat smaller, with a large dorsal tooth and 3–5 smaller ventral ones.

DIAGNOSIS: ♀ GENITALIA. Very similar to *G. a. angolanus*. See species account.

EARLY STAGES; HOST PLANTS; BIONOMICS; CONSERVATION STATUS. See species account.

DISTRIBUTION (Map Fig. 128)
The more northerly of the two subspecies. Found in northern and western tropical Africa.

Countries confirmed include (those in which both races occur indicated by *): Mauritania, Senegal, Gambia, Mali, Guinea-Bissau, Guinea, Sierra Leone, Liberia, Ivory Coast, Burkina Faso, Niger, Ghana, Togo, Benin, Nigeria, Cameroon, Chad, São Tomé, [Gabon], Congo*, Central African Republic, northern Democratic Republic of Congo* (Berger, 1981), Sudan, Ethiopia, Uganda*, Kenya*, Tanzania*.

MATERIAL EXAMINED. 412 ♂♂; 83 ♀♀ in BMNH; 115 ♂♂; 16 ♀♀ from other collections.

15. *Graphium (Arisbe) endochus* (Boisduval, 1836)

Madagascan White Lady (Fig. 186; map Fig. 130; genitalia Figs 33, 85)

Papilio endochus Boisduval, 1836: 243–244. HOLOTYPE ♂: MADAGASCAR: 'trouvé à Madagascar par M Goudot. – Coll. Boisd.' (Boisduval, 1836: 244). BMNH – Spec.Reg. No. 135877.

Papilio endochus Boisduval, 1836; Bryk, 1930*b*: 555; D'Abrera, 1980: 38, 39 (figs).

Papilio endochus Boisduval; Aurivillius, 1908: 21, pl. 7(c).

Papilio (*Graphium*) *endochus* Boisduval.; Peters, 1952: 20.

Graphium (*Arisbe*) *endochus* Boisduval; Munroe, 1961: 42; Paulian & Viette, 1968: 22; Hancock, 1983: 46; Ackery, Smith & Vane-Wright, 1995: 162.

Graphium endochus Boisduval; d'Abrera, 1997: 46, 47 (figs).

TYPE EVALUATIONS
Papilio endochus Boisduval (1836) was described '. . . sur un individu mâle et unique . . . ' (Boisduval, 1836: 244). Paulian & Viette considered a specimen standing in the main collection of the BMNH to be the Holotype: 'Holotype: 1 ♂, « Madagascar » (*J. Goudot*) (coll. Boisduval < coll. Ch. Oberthür < coll. J. Levick < British Museum, N. H. ; type Rhopaloc. n° 11 847)' (Paulian & Viette 1968: 22). We here follow Paulian & Viette in accepting this specimen as Holotype; it is from Boisduval's collection and reached the BMNH via the Oberthür collection and the Levick Bequest (BMNH 1941–83). However, the specimen lacks any positive indication that it was collected by Goudot: there is no 'Goudot' label; the 'Typicum Specimen' label appears to be printed for Oberthür; the large hand written label (apparently in Oberthür's hand) has subsequent catalogue data as does the large printed label.

A further specimen (BMNH Spec.Reg. No. 135906) from the Levick Collection, ex Boisduval was labelled 'co-type'. It bears a label 'Ex typicalibus speciminibus'. It is labelled Madagascar but has neither precise provenance nor collector. It should not be considered part of the type-series.

TAXONOMIC STATUS. *Papilio endochus* Boisduval (1836) was established as a species. Its distinct appearance and geographical separation have never given cause to doubt that status.

SIMILAR SPECIES. None within afrotropical *Graphium*.

DIAGNOSIS: PATTERN (FIG. 186)
A striking black-and-white butterfly. Distinguished from other members of the *angolanus*-group by the simple pattern of the upperside which lacks submarginal marks and discal and post-discal spots in the apical areas of the forewings, with the exception of small discal and post-discal spots in some specimens (see below).

In the **forewing upperside** discal cell, all the white patches are joined along the posterior discocellular vein (patch 1a is usually absent). Spot 4a is small and usually completely subsumed in 3 + 4b (see below). Cell R_3 usually without marks. Cell R_4 often with a small post-discal spot. Cell R_5 without marks. Cell M_1 sometimes with a small spot close to the angle between the middle discocellular vein and vein M_2. Cells M_2 to CuA_1 with post-discal marks each crossing the cell width and of increasing length. Cell CuA_2 with post-discal mark longer still, but not reaching the base of the cell; though here there is a scattering of white scales over the ground colour, giving a grey appearance. Cell 1A with post-discal mark not quite reaching the cell base and nearly reaching the margin.

Discal cell of **hindwing upperside** with white band reaching tip of cell, but not quite to the base, though there is a scattering of white scales over the ground colour, giving a grey appearance. Cell R_1 with broad white band and grey base. Cell R_5 with fused discal and post-discal marks reaching beyond the root of vein M_1. Cells M_1 and M_2 with basal areas of white scales over the dark ground colour. Cells M_3 and CuA_1 with elongate discal marks. Cell CuA_2 with entire basal area to near the margin consisting of white scales over the ground colour, thus forming a continuous grey stripe running through the base of the hindwing and onto the base of the forewing. The marginal marks of the hindwing cells are prominent, exaggerating the effect of scalloping along the wing margin caused by the extension of the veins – especially M_3 – into rudimentary tails.

The **underside** is much more complex, with many of the spots which are absent from the upperside being present, sometimes as nacreous looking areas where white scales overlay the dark ground colour. This ground colour is largely dark brown, but with the basal third or so of the forewing discal cell and the very basal areas of the hindwing costal and discal cells brick red. In addition to bright white marks mirroring those of the upperside **forewing** discal cell and cells M_2 to 1A, cell R_3 has nacreous discal, post-discal and submarginal marks. Cell R_4 with post-discal and submarginal marks, the former with a white central spot (when present on the upperside) surrounded by a nacreous area. Cell R_5 with post-discal and submarginal marks. Cell M_1 with post-discal and submarginal marks. Cell M_2 with additional submarginal mark. Cell M_3 with small additional submarginal mark. Cell CuA_1 has a faint submarginal mark.

On the hindwing **underside**, in addition to those marks seen on the upperside, cells R_1 to M_2 have large nacreous submarginal marks, slightly concave distally. Cell M_1 also has a small basal red spot and small post-discal spot. Cell M_2 has a slightly larger basal red spot, with a white proximal margin, and a post-discal spot. In Cell M_3, the red spot is between the white discal mark and transverse post-discal mark; the submarginal mark is chevron-shaped, pointing proximad. Cell CuA_1 also has a red spot and chevron-shaped submarginal mark, but no post-discal mark. Cell CuA_2 is largely brown, with a red spot near the margin. The marginal marks are more extensive than on the upperside, especially those in cells R_1 to M_1.

VARIATION

A small post-discal spot is present in forewing upperside cell R_4 in about half of the specimens seen by us, including all females. Other spots that may occasionally occur include: cell R_3: discal (♀ only), post-discal; cell R_5: discal; cell M_1: discal; and there may be a spot in the costal margin just distal of the root of vein R_3.

The extent of white marking in the forewing discal cell is also variable. Spot 1a is occasionally present and, when it is, is usually fused with 1b. The extent of fusion between the distal spots (2 and 3+4) is variable and sometimes complete, to form a single, large, terminal rectangle. Occasionally, 4a is more-or-less separated from 3 + 4b.

The size and conspicuousness of the rubra of the upperside hindwing cubital cell of the female is quite variable.

There is also considerable variation in the presence, extent and fusion of the silvery spots of the underside fore- and hind-wings.

DIAGNOSIS: ♂ GENITALIA (Fig. 33)

Similar to *G. angolanus* in the form of the dorsal terminal process, which is not bifid, but with a ventral hook and somewhat expanded dorsal region surrounding the dorsal harpe. The dorsal harpe is similar to that in *G. angolanus*, though the disc is less circular and less serrate, especially dorsally. Most characteristic of the species is the form of the ventral harpe which is contiguous with the well-developed basal lamella. The whole structure is broad and serrate.

Valve: *dorsal projection*: long, directed somewhat posteriad and curving slightly ventrad, stout spines mainly on anterior edge; *dorsal terminal process*: curved mesad, serrate terminally, the serrations becoming larger ventrally, with a serrate ventral hook; *ventral terminal process*: angular, finely serrate ventrally; *dorsal harpe*: elongate and parallel sided basally, becoming nearly circular and slightly serrate apically; *ventral harpe*: broad and elongate, strongly serrate; *basal lamella*: contiguous with the ventral harpe, broad, strongly serrate. *Uncus*: tapering distally; *soccii*: prominent, with small projections. *Aedeagus*: elongate, nearly straight, with no sign of denticulation. *Saccus*: elongate, narrow.

DIAGNOSIS: ♀ GENITALIA (Fig. 85)

BMNH Spec.Reg. No. 135862; vial 5443: *vestibulum*: broad; *ostium bursae* opening posteriorly; *ductus bursae* enlarged and sclerotized distally, kinked and with pocket just distal to the *ductus seminalis*; *central ostial lobe* absent; *lateral ostial lobes* large, setose; *anterior apophysis* present; *papillae anales* rounded.

EARLY STAGES; HOST PLANTS. Unknown.

DISTRIBUTION (Map Fig. 130). Northern and eastern Madagascar.

BIONOMICS. According to Paulian & Viette (1968), this species occurs in wet rainforests. They record months of capture as Feb., Mar., Oct., Nov., Dec., at various altitudes up to 1640 m.

CONSERVATION STATUS. 'Apparently well distributed and not currently threatened, but it is a forest species and its status in a country which is being rapidly deforested should be carefully monitored' (Collins and Morris, 1985: 56).

MATERIAL EXAMINED. 64 ♂♂; 10 ♀♀ in BMNH; 34 ♂♂; 3 ♀♀ from other collections.

16. *Graphium (Arisbe) morania* (Angas, 1849)

Lesser, Scarce or Small White Lady, White Lady Swallowtail (Fig. 189; map Fig. 122; genitalia Figs 34, 86)

Papilio Morania Angas, 1849: 52, pl.30 fig.1. LECTOTYPE ♂: SOUTH AFRICA: 'Natal and the Zulu Country' (Angas, 1849: 52). BMNH Spec.Reg. No. 140774 – **here designated**.

Papilio pylades var. *morania* Ang[as]; Kirby, 1871: 562.

Papilio angolanus [*angolanus*] = *morania* Ang[as]; Kirby, 1877: 811.

Papilio morania morania Angas; Aurivillius, 1908: 22, pl. 7(b, c).

Papilio morania Angas; Bryk, 1930*b*: 557.

Papilio (*Graphium*) *morania* Angas; van Son, 1949: 37; text-figs 18, 19; pls V (fig. 7), VI (fig. 7).

Papilio (*Graphium*) *morania morania* (Angas); Peters, 1952: 20.

Graphium (*Arisbe*) *morania* (Angas); Munroe, 1961: 42; Hancock, 1983: 46; Pennington, 1994: 305, pls 37, 193; Ackery, Smith & Vane-Wright, 1995: 164.

Graphium morania Angas; D'Abrera, 1980: 40, 41 (figs); d'Abrera, 1997: 46, 47 (figs).

UNAVAILABLE NAMES

Graphium morania f. *vansoniana* Storace, 1953: 253. Storace was providing a name for a form informally described by Trimen (1889: 223) and illustrated by Van Son (1949: pl.12 fig.1). [infrasubspecific]

Graphium (*Arisbe*) *morania* var. *holoplaga* Grei, 1986: 11, figs (p.10, lower figures). SOUTH AFRICA: Transvaal, Boekenhout, Nylsvley. Coll. E. Grei (not seen). [infrasubspecific]

TYPE EVALUATION

Angas (1849) did not state the number of specimens in his type series when describing *Papilio Morania*; though only one is implied by the use of the singular throughout the description. Nor did he state where any specimens were deposited, though in his description on *Acraea nataliensis* on the same page he states, '. . . now in the collection of the British Museum, where I have placed it along with other rare examples from Natal' (Angas, 1849: 52). That donation was registered as BMNH Accession No. 1848–63 and includes a specimen of *morania* that must be regarded as original and is here selected as lectotype. It had previously been labelled as a syntype by one of us (RIVW).

The var. *holoplaga* was described from a single female, originally designated as holotype (Grei, 1986: 12).

TAXONOMIC STATUS

Papilio Morania Angas (1849) was established as a species, and accepted as such by most authors since, though some authors have regarded it as the nominate race of a bitypic species to include *G. schaffgotschi* (*q.v.*).

Although proposed as a form prior to 1961, it is clear that Storace (1953) considered *vansoniana* to be a transitional form and so it should be considered infrasubspecific. No types were designated.

SIMILAR SPECIES. *G. taboranus*, *G. schaffgotschi*. For distinguishing features, refer to the diagnoses and figures.

DIAGNOSIS: PATTERN (Fig. 189)

G. morania is distinguished from its relatives by the fusion of the two most distal white patches in the forewing upperside discal cell (spots 3 and 4).

Upperside. **Forewing**. Ground colour dark brown, with white markings. Discal cell with small spot (1a) near costal vein opposite vein CuA_2; transverse band (2a+b) opposite vein CuA_1 and large mark (3+4) in apex, slightly concave proximally. Cell R_3 with small discal spot; larger post-discal mark beyond root of vein R_4 and oblique, transverse submarginal mark. Cell R_4 with elongate post-discal mark and small submarginal mark. Cells R_5 and M_1 each with a small discal spot, larger post-discal mark and submarginal spot. Cell M_2 with large post-discal mark not quite reaching surrounding veins and small, transverse submarginal mark. Cell M_3 with small, elliptical, slightly fuzzy-edged post-discal mark, and small round submarginal mark. Cell CuA_1 with large post-discal mark reaching right into cell base, just reaching vein CuA_1 and contiguous with that in cell CuA_2, and small, transverse submarginal mark. Cell CuA_2 with large post-discal mark almost reaching cell base, contiguous with those in cells CuA_1 and 1A, and small, bifid submarginal mark. Cell 1A with post-discal mark almost reaching cell base, contiguous and co-extensive with that in cell CuA_2.

Hindwing discal cell with white band virtually reaching tip of cell, not quite reaching cell base. Cell R_1 with elongate band reaching near to cell base and contiguous and coextensive with marks in the discal cell and cell R_5, round submarginal mark, and marginal mark. Cell R_5 with post-discal mark reaching just beyond root of vein M_1, transverse submarginal mark, and marginal mark. Cell M_1 usually with small, post-discal spot, transverse, submarginal mark, and marginal mark. Cell M$_2$ with basal, slightly fuzzy, discal mark, usually a small, but clear post-discal spot, transverse, slightly angled submarginal mark, and marginal mark. Cell M$_2$ with more extensive basal discal mark, a small, but clear post-discal spot, transverse, distinctly angled submarginal mark, and marginal mark. Cell CuA$_2$ with extensive discal mark, transverse post-discal mark, chevron-shaped submarginal mark, and marginal mark. Cell CuA$_2$ with extensive discal mark, reaching to cell base, small orange tornal spot, very faint post-discal or submarginal mark, and marginal mark.

The **underside** pattern is largely similar to the upper, but there are differences in the ground colour. Over the anterior part of the forewing (roughly from vein M$_2$ forward) and on the hindwing, this is a pale chestnut brown. In **forewing** cell M$_2$ and posteriorly, as well as in the central part of the discal cell, it is dark brown. The basal half of the cell is brick red and this colour extends into the bases of the discal cell and cells R$_1$ and CuA$_2$ of the hindwing. In **hindwing** cells M$_1$ to CuA$_1$ there is a complex banding pattern between the discal marks (or cell base where there is no discal mark) and the post-discal marks, consisting of narrow dark, light and dark bands. The dark scales extend along the veins, so the light band is in the form of a transverse spot in each cell. In cells R$_1$ to CuA$_1$, the small area between the submarginal and marginal marks is dark brown. Cell CuA$_2$ fades from brick red at the base to pale chestnut; there is a paler tornal mark and a small post-discal or submarginal mark, surrounded by dark brown, and a marginal mark.

VARIATION

The overall variability in the amount of white is shown by: the size of forewing discal cell spot 1a, though it appears never to be completely absent; forewing discal cell spots 3+4 with scattering of black scales on costal edge (between 3a and 4a) or internally; discal cell spot 3b may occasionally be extended basally almost to contact 2b; spots (3+4) may completely fuse (var. *holoplaga* Grei – known only from the 'type'); forewing cell R$_3$ with discal spot occasionally almost absent; forewing cell M$_3$ variable, sometimes reaching vein CuA$_1$; hindwing cell M$_1$ (and, more rarely M$_2$) with post-discal spot missing. On the underside, the small pale spots between the discal and post-discal spots in cells M$_{2-}$CuA$_1$, which are usually orange-yellow, may be almost white. There is a single specimen of a remarkable variant in OXUM (Fig. 238). This lacks any trace of discal or post-discal marks on the forewing, except for somewhat diffuse mark in cell 1A, and a smaller mark in cell CuA$_2$. There are diffuse patches representing marks 2a and 3a near the costal vein in the forewing discal cell. On the hindwing, the discal cell and cells R$_1$, R$_5$, M$_3$, and CuA$_1$ have pale scales overlaying ground colour, giving a blue-grey appearance. Cell CuA$_2$ is largely white. This lack of marking is repeated on the underside, though without the grey coloration on the hindwing, the basal area of which is consequently brown.

DIAGNOSIS: ♂ GENITALIA (Fig. 34)

The male valve is similar to that in *schaffgotschi* and *taboranus*, but the elements of the bifid dorsal terminal process are shorter and broader and both are serrate. The ventral terminal process is better marked than in *schaffgotschi* and *taboranus*, consisting of a row of three teeth, themselves minutely serrate. The serrations of the dorsal harpe are better marked. The ventral harpe consists of a stout terminal tooth and a bifid one proximal to it, the outer edges of this are slightly serrate. The basal lamella is tricuspid: two lateral teeth (dorsal and ventral) with a bifid central one.

Valve: *dorsal projection*: long, directed somewhat posteriad and curving slightly ventrad, stout spines mainly on anterior edge; *dorsal terminal process*: curved mesad, bifid, each half serrate tapering to a sharp tooth; *ventral terminal process*: small, coarsely serrate; *dorsal harpe*: elongate and parallel sided basally, becoming broader and serrate apically; *ventral harpe*: tapering to a sharp point distally and with a large, bifid, serrate tooth proximally; *basal lamella*: broad, with three stout serrations, the central one slightly bifid. *Uncus*: tapering distally; *soccii*: well marked, with prominent projections. *Aedeagus*: elongate, nearly straight, with no sign of denticulation. *Saccus*: moderately elongate, narrow.

DIAGNOSIS: ♀ GENITALIA (Fig. 86)

BMNH Spec.Reg. No. 140725; vial 3984: *ostium bursae* opening anteriorly; *ductus bursae* enlarged and sclerotized distally, kinked and with pocket just distal to the *ductus seminalis*; *central lobe* absent; *lateral ostial lobes* large, setose; *anterior apophysis* present; *papillae anales* rounded.

EARLY STAGES

The final instar larvae do not have a pattern of conspicuous transverse stripes, but are instead almost unicolorous green (with yellow lateral stripe), or have lateral, dorso-lateral and dorsal longitudinal lines of discrete dots; like *angolanus*, the thoracic and anal process remain very spiny up to but not including the last instar; the dorsal and lateral cephalic processes of the green pupa are somewhat shorter and more acuminate than those of *angolanus*.

Migdoll (1988) describes the larva as 'beautifully decorated with bands of yellow and green'; van Son (1949) gives detailed notes based on G. Clark (pl. XII) and Trimen (1889). Henning *et al.* (1997) illustrate early and late instars, and the green, upright pupa, revealing a number of similarities to *G. angolanus*. The same authors give 4 days to hatching for the egg, and 15 days for the 5 larval instars to complete development. According to Trimen (quoted in van Son, 1949, and apparently Clark according to Henning *et al.*, 1997), pupal development lasts only 12–15 days in good conditions, but emergence may be delayed for one or even two years. The early stages of *G. morania* are also described by Monteiro (1891).

DISTRIBUTION (Map Fig. 122). South-eastern Africa. Countries confirmed include: Botswana, Zimbabwe, Mozambique, Swaziland, South Africa.

HOST PLANT RECORDS

Annonaceae:

Annona senegalensis (Pennington, 1994: 305), (Henning *et al.*, 1997).

Artabotrys brachypetalus (Pennington, 1994: 305), (Henning *et al.*, 1997).

Artabotrys monteiroae (Pennington, 1994: 305), (Henning *et al.*, 1997).

Hexalobus monopetalus (Pennington, 1994: 305), (Henning *et al.*, 1997).

Uvaria caffra (Pennington, 1994: 305), (Henning *et al.*, 1997).

Malpighiaceae:

Sphedamnocarpus pruriens (Larsen, In prep.*b* – suggested for Tswapong Hills, in Botswana).

BIONOMICS

A monotypic species found generally in woodland, savanna, dry bush and open country, Larsen (In prep.*b*) regards it as a species of drier habitats than *G. angolanus*, but otherwise very similar. For South Africa, van Son (1949) gives mainly October to March, but occasionally at any time; Williams (1969) states 'mainly from late August to early May'. The flight is apparently rapid, weaving, and often interrupted by visits to flowers (but in some contrast, Trimen, 1889, reports that at Durban in early 1867 'they flew low, and by no means rapidly, keeping about low trees and shrubs on the edge of the woods, sometimes settling on leaves, but very rarely on flowers'). For Botswana, Larsen (*op. cit.* and pers. comm.) records Jan., Feb. and Sept., and notes it to be frequent at damp spots, singly, but often in company with *G. antheus*; females are rarely encountered. Henning *et al.* (1997) note similar territorial behaviour to *G. angolanus*, and how the females lay single eggs on young leaves of their hosts. Kloppers & van Son (1978) suggest that, in the Kruger National Park, this species may be more abundant where *G. angolanus* is rare or absent; they record captures in Aug., Nov. and Dec. Migdoll (1988) comments that it is seldom seen in numbers, being a lone flier that tends to keep to the edges of woodland.

CONSERVATION STATUS. Collins & Morris (1985: 56) state that *G. morania* (including *G. schaffgotschi*) is not under threat.

MATERIAL EXAMINED. 53 ♂♂; 55 ♀♀ in BMNH. 17 ♂♂; 4 ♀♀ from other collections.

17. *Graphium (Arisbe) taboranus* (Oberthür, 1886)

Tabora Lady, Tabora Swallowtail (Figs 187, 188; map Fig. 132; genitalia Figs 35, 87)

Papilio Taboranus Oberthür, 1886: cxiv. HOLOTYPE ♀: TANZANIA: 'Tabora, dans l'Ounyanyambé, pendant les premiers mois de 1885' (Oberthür, 1886: cxv). BMNH Spec.Reg. No. 140620.

Papilio Taboranus Oberthür, 1888: 2, pl.1 fig.1.

Papilio morania taboranus Oberthür.; Aurivillius, 1908: 22, pl. 7(b).

Papilio morania var. *taboranus* Oberthür, 1886; Bryk, 1930*b*: 558.

Graphium taboranus [wet season f. *taboranus*] Oberthür; Berger, 1950: 58, fig. 57.

Papilio (*Graphium*) *morania taboranus* Oberthür; Peters, 1952: 20.

Graphium (*Arisbe*) *taboranus* Oberthür; Munroe, 1961: 42; Hancock, 1983: 46; Ackery, Smith & Vane-Wright, 1995: 166.

Graphium taboranus taboranus Oberthür; D'Abrera, 1980: 40, 41 (figs).

Graphium taboranus Oberthür; Berger, 1981: 49, pl.9 figs 4 (♂), 7 (♀); d'Abrera, 1997: 46, 47 (figs).

SYNONYM

Papilio nivinox Butler, [1894]: 667. LECTOTYPE ♂: ZAMBIA: 'Lake Mweru' (Butler, 1894: 667). BMNH Spec.Reg. No. 140619. – **here designated**; PARALECTOTYPE ♂: ZAMBIA: Same data. BMNH Spec.Reg. No. 140930.

Papilio nivinox Butler; Butler, 1895: 263, pl.16 fig.4; Butler, 1897: 851, 852.

Papilio morania var. *taboranus* =*nivinox* Butler, (attrib. 1893); Bryk, 1930*b*: 558.

TYPE EVALUATIONS

Oberthür (1886) did not give details of the original series for *Papilio taboranus*, but later (Oberthür, 1888: 2) states, 'Je ne possède que le seul exemplaire ayant servi de type à la description précitée'. The specimen reached the BMNH via the Levick Bequest (BMNH 1941–83). It has a red-printed 'Typicum/Specimen', a copy of the original description and a hand written label stating, 'a servi de modèle/à d'Apreval [the lithographer of Oberthür, 1888: pl.1], 1887' possibly in Oberthür's hand. This specimen was labelled with a round BMNH 'Type' label by an earlier curator. Oberthür subsequently obtained further specimens of the taxon.

Papilio nivinox (Butler, 1894: 667) was described from two specimens from Lake Mweru, collected by

Crawshay (Butler, 1894: 643); of these, the one with Butler's handwritten 'type' label is selected as lectotype to prevent confusion.

TAXONOMIC STATUS

Papilio taboranus Oberthür (1886) was established as a species and accepted as such by most subsequent authors, though Bryk (1930) treated it as a variety (subspecies) of *Papilio morania* Angas. Hancock (1985) separated *G. schaffgotschi* (Niepelt) (q.v.) as being neither a seasonal form, nor subspecies of *G. taboranus*.

Papilio nivinox (Butler, 1894: 667) was established as a species, but Butler (1897) subsequently speculated it might be the male of *Papilio taboranus* Oberthür and this, too, has been accepted by subsequent authors.

SIMILAR SPECIES

G. morania, G. schaffgotschi.

For distinguishing features, see below and figures.

DIAGNOSIS: PATTERN (Figs 187, 188)

Distinguished from other members of the *angolanus*-group by its darker appearance, especially in the female. In particular, the post-discal white patch in fore-wing cell CuA$_1$, though very variable in size, is reduced to an ellipse touching neither vein CuA$_1$, nor the posterior discocellular vein and only occasionally vein CuA$_2$; this appears to be autapomorphic. Unlike *G. morania*, the spot in the forewing discal cell opposite cell R$_5$ does not fuse with that opposite M$_2$ (though they may touch – see below).

In the hind-wing discal cell, the white patch rarely extends beyond the root of vein CuA$_2$ and the axillary white spot in cell M$_3$ is often missing.

Upperside. **Forewing**. Ground colour dark brown, with white markings. Discal cell with small spot (1a) near costal vein opposite vein CuA$_2$ sometimes present; transverse band opposite vein CuA$_1$ confined to costal half of cell (2a); band opposite cell M$_2$ complete (3a+b), extending proximad along posterior discocellular vein; Cell R$_3$ with small discal spot; larger post-discal mark beyond root of vein R$_4$ and small, oblique, transverse submarginal mark. Cell R$_4$ with elongate post-discal mark and small submarginal mark. Cell R$_5$ sometimes with small discal spot; usually with post-discal spot (these two spots vary independently); and submarginal spot. Cell M$_1$ usually with both a discal and post-discal spot and with a submarginal spot. Cell M$_2$ with large post-discal mark not quite reaching surrounding veins and small, transverse submarginal mark. Cell M$_3$ usually with small, elliptical, slightly fuzzy-edged post-discal mark, and small transverse submarginal mark. Cell CuA$_1$ with post-discal mark elliptical, not reaching surrounding veins; and a small submarginal mark. Cell CuA$_2$ with post-discal mark not reaching either the posterior discocellular vein nor vein CuA$_2$, and not reaching the base of the cell, but contiguous with that in cell 1A. There are few, if any white scales on the ground colour of the base of the cell, so there is no greyness seen in other species in the group. The submarginal mark of cell CuA$_2$ is bifid. Cell 1A with post-discal mark contiguous with that in cell CuA$_2$.

Hindwing discal cell with white band not reaching root of vein M$_1$ anteriorly and barely reaching root of vein CuA$_1$ posteriorly, not reaching cell base. Cell R$_1$ with transverse band not reaching to end of post-discal mark of cell R$_5$; a small submarginal and a marginal mark also present. Cell R$_5$ with post-discal mark reaching just beyond root of vein M$_1$, transverse submarginal mark, and marginal mark. Cells M$_1$ to CuA$_1$ each usually with a post-discal spot as well as a transverse submarginal and a marginal mark. In addition, cell CuA$_1$ also has a basal discal mark, reaching just beyond root of vein CuA$_1$. Cell CuA$_2$ has a scattering of silvery scales basally, a prominent, orange tornal spot and a marginal mark.

The **underside** pattern is largely similar to the upper, but there are differences in the ground colour. Unlike other members of the group, the **forewing** ground colour is dark, being only slightly lighter apically, with brick red in the basal third or so of the discal cell. The ground colour of the **hindwing** is largely bright chestnut, with dark brick red in the base of the costal and discal cell and cell CuA$_2$. There is an additional pale mark at the tip of the discal cell, opposite cell M$_1$. The post-discal spots of cells M$_1$ to CuA$_1$ are all somewhat larger than their upperside counterparts and with a dark proximal border. In cells M$_3$ and CuA$_1$, there is a transverse, dark bordered pale mark just proximal to the post-discal marks. In cell CuA$_2$, the tornal spot is prominent and there is a very small post-discal or submarginal mark. In Cells R$_1$ to CuA$_1$, the area between the submarginal and marginal marks is dark.

VARIATION (Fig. 188)

Females show a darker appearance than males, with the white patches even further reduced (Fig. 188). This is especially so of the post-discal marks of the forewing, each being elliptical and isolated from its neighbours, the hindwing discal cell band, which barely reaches the the root of vein R$_5$. The post-discal mark in hindwing cell R$_5$ is also reduced, not touching the surrounding veins.

There is considerable general variability. In the forewing discal cell, the spot (1a) opposite cell CuA$_1$ is rarely present, and then only as a small point (≤1 mm in diameter); the spot (4) opposite cell R$_5$ is variable in size, occasionally large enough to touch (but not fuse with) that opposite cell M$_2$ (3), sometimes very small or even – in the case of some females – missing. The post-discal spot of cell M$_3$, reduced, elliptical and variable (as in other taxa), may be absent altogether.

Other forewing spots, e.g. the discal and post-discal in cell R_5 may be reduced or missing.

In the hind wing, the post-discal spot in cell M_1 may be reduced or absent.

DIAGNOSIS: ♂ GENITALIA (Fig. 35)

G. taboranus is most similar to *G. schaffgotschi* in the possession of a strongly bifid dorsal terminal process which, unlike *G. morania*, is not serrate.

Valve: *dorsal projection*: long, directed somewhat posteriad and curving slightly ventrad, stout spines mainly on anterior edge; *dorsal terminal process*: curved mesad, bifid, each half tapering to a sharp tooth; *ventral terminal process*: small, serrate; *dorsal harpe*: elongate and parallel sided basally, becoming broader and nearly square and serrate apically; *ventral harpe*: broad with coarse serration, that at the posterior tip forming a sharp tooth; *basal lamella*: with three stout serrations. *Uncus*: tapering distally; *soccii*: well marked, with prominent projections. *Aedeagus*: elongate, nearly straight, with no sign of denticulation. *Saccus*: elongate, narrow.

DIAGNOSIS: ♀ GENITALIA (Fig. 87)

BMNH Spec.Reg. No. 140994; vial 3983: *ostium bursae* opening posteriorly; *ductus bursae* enlarged and sclerotized distally, kinked and with pocket just distal to the *ductus seminalis*; *central ostial lobe* absent; *lateral ostial lobes* large, setose; *anterior apophysis* present; *papillae anales* rounded.

EARLY STAGES. Apparently unknown.

DISTRIBUTION (Map Fig. 132)

Eastern equatorial Africa (Pinhey & Loe, 1977; Kielland, 1990):

Democratic Republic of Congo (Shaba), Angola, central, western and southern Tanzania, Malawi, Zambia, and Zimbabwe.

HOST PLANT RECORDS

Annonaceae:

Annona sp. (Kielland, 1990); (Ackery, Smith & Vane-Wright, 1995). It is not clear if this is an empirical record or an inference; if empirical, no record of the early stages is apparent.

BIONOMICS

A monotypic species of open savanna, bush, and *Brachystegia* woodland, in Tanzania it occurs between 1000–1600 m. (Kielland, 1990), and can be found in 'most months' (Pinhey & Loe, 1977), being 'most frequent during and after rainy seasons' (Williams, 1969). For Democratic Republic of Congo, Berger (1950) gives records only for Feb., Mar., May and Nov., but caution is needed because of the potential confusion with *G. schaffgotschi* (which Berger, and also Pinhey & Loe, regarded as merely a seasonal form). Kielland notes its behaviour and flight as like *G. angolanus*, 'but much less common'.

CONSERVATION STATUS. 'Not uncommon and not known to be threatened' (Collins and Morris, 1985: 56).

MATERIAL EXAMINED. 94 ♂♂; 18 ♀♀ in BMNH. 15♂♂; 5♀♀ from other collections.

18. *Graphium (Arisbe) schaffgotschi* (Niepelt, 1927)

Schaffgotsch's White Lady (Fig. 190; map Fig. 131; genitalia Figs 36, 88)

Papilio morania Schaffgotschi Niepelt, 1927: 53, fig.
HOLOTYPE ♂: NAMIBIA: 'Deutsch-Südw.-Afrika.' (Niepelt, 1927: 53). BMNH Spec.Reg. No. 140618.
2 PARATYPE ♂♂: NAMIBIA: 1 'Deutsch-Südw.-Afrika.' (Niepelt, 1927: 53). (not seen). 1 'Ovamboland' (Niepelt, 1927: 53). (not seen).

Papilio morania var. *Schafgotschi* [sic] Niepelt; Bryk, 1930*b*: 558.

Papilio (*Graphium*) *morania* f. *schaffgotschi* Niepelt; van Son, 1949: 37; Pennington, 1978: 178.

Graphium taboranus dry season f. *schafgotschi* [sic] Niepelt; Berger, 1950: 59, figs 58, 59; Berger, 1981: 49, pl.9, fig.5 (♂).

Papilio (*Graphium*) *morania schafgotschi* [sic] Niepelt; Peters, 1952: 20.

Graphium taboranus schaffgotschi Niepelt; D'Abrera, 1980: 40.

Graphium (*A.*) *taboranus schaffgotschi* Niepelt; Carcasson, 1981: 123.

Graphium (*Arisbe*) *schaffgotschi* Niepelt; Hancock, 1985*a*: 97 (as stat. rev.); Pennington, 1994: 305, pl.193; Ackery, Smith & Vane-Wright, 1995: 166.

Graphium schaffgotschi Niepelt; d'Abrera, 1997: 48, 49 (fig.).

TYPE EVALUATION

Papilio morania Schaffgotschi Niepelt (1927) was described from the three male specimens, with type designations original (Niepelt, 1927: 53). The holotype is clearly labelled and was part of a batch of Lepidoptera purchased from Niepelt (BMNH Accession Register No. 1928–151). We do not know where the paratypes are deposited.

TAXONOMIC STATUS

Papilio morania Schaffgotschi Niepelt (1927) was established as a subspecies. It has variously been regarded as a subspecies, variety or seasonal form of either *G. morania* or *G. taboranus*. However, Hancock (1985) pointed out that it occurs throughout the year and that its range overlaps with both *morania* and *taboranus*, and therefore accorded it specific status. This assessment was accepted in the second edition of Pennington (1994). The genitalia suggest a closer relationship with the *G. taboranus* (see below).

SIMILAR SPECIES
G. taboranus, *G. morania*

For distinguishing characters, see below and figures.

DIAGNOSIS: PATTERN (Fig. 190)
Very similar to *G. morania*, the description of which will suffice for *G. schaffgotschi*. Unlike *G. morania*, the two most distal spots in the forewing cell (3 and 4) are not fused, though in a few cases, they may touch for a short distance. Unlike *G. taboranus*, the post-discal spot of forewing cell CuA_1 reaches the posterior discocellular vein costally and vein CuA_2 posteriorly, at least in the male. In the female, this spot is elliptical and does not reach CuA_2, but the post discal mark in cell CuA_2 does reach that vein, unlike the condition in female *G. taboranus*.

VARIATION
Like the similar species, there is some variability in the extent of the white markings, but this is not very pronounced. In about one third of specimens there is a fourth mark (1a) in the forewing discal cell in the form of a point near the costal margin, opposite vein CuA_2. The post-discal mark in forewing upper side cell M_3 is variable in size, almost absent in some females; in the most marked specimens it is connected to vein CuA_1 by white scales. Upperside submarginals are variable in size, in some examples that in cell CuA_2 is divided. There is sometimes a post-discal spot in hindwing upperside cell M_1. The orange spot in hindwing upperside cubital cell is of variable size, virtually absent in some males.

DIAGNOSIS: ♂ GENITALIA (Fig. 36)
Very similar to *G. taboranus*, having a bifid, but not serrate, dorsal terminal process.

Valve: *dorsal projection*: long, directed somewhat posteriad and curving slightly ventrad, stout spines mainly on anterior edge; *dorsal terminal process*: broad, curved mesad, subdivided into two stout teeth, not serrate; *ventral terminal process*: small serrate; *dorsal harpe*: elongate and parallel sided basally, becoming nearly circular and serrate apically; *ventral harpe*: elongate and coarsely and unevenly serrate; *basal lamella*: narrow, with three small teeth, the central one longer. *Uncus*: tapering distally; *soccii*: with prominent projections. *Aedeagus*: elongate, nearly straight, with no sign of denticulation. *Saccus*: elongate, narrow.

DIAGNOSIS: ♀ GENITALIA (Fig. 88)
BMNH Spec.Reg. No. 140642; vial 3982: *ostium bursae* opening anteriorly; *ductus bursae* enlarged and sclerotized distally, kinked and with pocket just distal to the *ductus seminalis*; *central ostial lobe* absent; *lateral ostial lobes* large, setose; *anterior apophysis* present; *papillae anales* rounded.

EARLY STAGES. Apparently unknown.

DISTRIBUTION (Map Fig. 131)
Angola, southern Democratic Republic of Congo, and north west Zambia (Hancock, 1985*a*). Pennington (1994) states that 'some of the former 'Ovamboland' is now part of Angola' and questions the presence of *G. schaffgotschi* in 'southern Africa'. However, given the original type locality, its existence in the Grootfontein area of Namibia seems plausible.

HOST PLANTS. Not known, according to Pennington (1994), but presumably Annonaceae.

BIONOMICS
Judging by its distribution, this monotypic species must occur in dry scrub and savannah. Berger (1950) considered it as a dry season form of *G. taboranus*, and recorded it in southern Democratic Republic of Congo for April, May, June, July, Aug. and Dec., noting (Berger, 1981) that the dry season in southern Shaba is 'très longue', and that the females are very rare. According to (Hancock, 1985*a*) it has been recorded throughout the year except March and October.

CONSERVATION STATUS. Included as a subspecies of *G. taboranus* by Collins & Morris (1985: 56, but its elevated status noted on p. 124). Thus, not known to be under threat.

MATERIAL EXAMINED. 32 ♂♂; 14 ♀♀ in BMNH. 17 ♂♂; 2 ♀♀ from other collections.

19. *Graphium* (*Arisbe*) *ridleyanus* (White, 1843)

Ridley's or Red Graphium, Dwarf or Acraea Swallowtail (Fig. 192; map Fig. 133; genitalia Figs 37, 89)

Shown to be a member of the *angolanus* clade by its genitalia, this beautiful butterfly is striking both for its red coloration, believed to be mimetic of *Acraea* models (see below), and for the absence of deciduous androconial scales from the inner margin of the hindwing.

Papilio ridleyanus White, 1843: 262. LECTOTYPE ♂: DEMOCRATIC REPUBLIC OF CONGO/CONGO: 'ad oras fluminis Zaire Dom. Curror lexit.' (White, 1843: 262). 'Brit. Mus.' (White, 1843: 262) BMNH Spec.Reg. No. 136955 – **here designated**. PARALECTOTYPE ♀: DEMOCRATIC REPUBLIC OF CONGO/CONGO: Same data. BMNH Spec.Reg. No. 136956.

Papilio ridleyanus White; Aurivillius, 1908: 21, pl. 1(a); Bryk, 1930*b*: 554.

Papilio riddleyanus Bryk, 1928: 15. (incorrect subsequent spelling).

Graphium ridleyanus White; Berger, 1950: 63, figs 63, 64; D'Abrera, 1980: 40, 41 (figs); Berger, 1981: 49, pl.13 figs 3 (♂), 4 (♀); Kielland, 1990: 48; d'Abrera, 1997: 48, 49 (figs).

Papilio (*Graphium*) *ridleyanus* (White); Peters, 1952: 20.

Graphium (*Arisbe*) *ridleyanus* (White); Munroe, 1961:

42; Hancock, 1983: 46; Collins & Morris, 1985: 56; Ackery, Smith & Vane-Wright (1995): 166.

SYNONYM

Papilio ridleyanus njami Röber, 1928: 67. HOLOTYPE ♂: SUDAN: 'aus der Heimat der Njam-Njam' (Röber, 1928: 67). [SMTD?] (not seen).

Papilio ridleyanus njami Röber; Bryk, 1930*b*: 555.

Graphium (*Arisbe*) *ridleyanus* =*njami* Röber; Ackery, Smith & Vane-Wright (1995): 166. [as syn.]

UNAVAILABLE NAMES

Papilio ridleyanus ab. *infuscatus* Schultze, 1913*d*: 4–5. CAMEROON (not seen) [infrasubspecific].

Papilio ridleyanus f. *infuscatus* Schultze; Bryk, 1930*b*: 555.

Papilio ridleyanus var. *fumatus* Niepelt, 1915: 58. DEMOCRATIC REPUBLIC OF CONGO. BMNH Spec.Reg. No. 137437 [infrasubspecific].

Papilio ridleyanus f. *fumatus* Niepelt, 1915; Bryk, 1930*b*: 555.

Papilio ridleyanus var. *fumosus* Holland, 1920: 247. SUDAN. AMNH (not seen) [infrasubspecific].

Papilio ridleyanus =*fumosus* Holland; Bryk, 1930*b*: 555.

Papilio ridleyanus ab. *infuscatus* =*fumosus* Holland; Berger, 1950: 64.

Papilio ridleyanus f. indiv. ♀ *vitrea* Le Cerf, 1924*a*: 394. SUDAN. BMNH Spec.Reg. No. 137436 [infrasubspecific].

Papilio ridleyanus f. indiv. ♀ (? an s.-sp.) [sic] *rosa* Le Cerf, 1924*a*: 394. TANZANIA. BMNH Spec.Reg. No. 137435 [infrasubspecific].

Papilio ridleyanus ab. *semivitreus* Schultze, 1930: 176. CENTRAL AFRICAN REPUBLIC. (not seen) [infrasubspecific].

Papilio (*Cosmodesmus*) *ridleyanus* ab. *hecqueti* Dufrane, 1946: 118. DEMOCRATIC REPUBLIC OF CONGO. IRSN [infrasubspecific].

Papilio (*Cosmodesmus*) *ridleyanus* [f.] *minor* Dufrane, 1946: 118. DEMOCRATIC REPUBLIC OF CONGO. IRSN [infrasubspecific].

TYPE EVALUATIONS

Papilio ridleyanus White (1843) was described from both male and female specimens with textual indications of more than one male, possibly also more than one female. However, only a single male and single female (this smaller than the stated largest size of 'rather more than three inches and a half') with the correct provenance – 'Congo/A. Curror/[BMNH accessions register No. 18]43–56' – are at present to be found in BMNH. On both, the reverse side of this label is hand written, 'Papilio/Ridleyanus/(Type) White', apparently in White's hand. To avoid confusion, we select one of these – the male – as lectotype.

Papilio ridleyanus njami Röber (1928) was described from 'Das mir vorliegende ♂ dieser Art . . . ' – that is, a single individual. There is no information about the depository in the original description, but according to Horn *et al.* (1990), J.K.M. Röber was a lepidopterist employed by the city of Dresden. Matthias Nuss (pers. comm.) has informed us:

'There is one male in our collection labelled 'Africa Njam-Njam 1884'. The specimen came with the Staudinger & Bang-Haas ['Staudinger & Bang-Haas' are described in Horn as 'Insekten-Handlung in Dresden'] collection in our museum in 1961. It bears no determination label from Röber and no indication that it is the taxon *njami*. However, it fits the description given by Röber (reddish spots paler).'

TAXONOMIC STATUS

Papilio ridleyanus White (1843) was established as a species and treated as such by most authors since.

Papilio ridleyanus var. *fumatus* Niepelt (1915) was established as a variety, but it is clear from the description that an infrasubspecific taxon was intended: it was described from one individual amongst a number from the same locality. Although some subsequent authors (e.g. Bryk, 1930*b*) refer to the taxon as a form, there is no evidence that any of them were deliberately changing its status.

Papilio ridleyanus var. *fumosus* Holland (1920) was established as a variety, but based on individuals from the same localities as 'normal' specimens and thus should be considered infrasubspecific, notwithstanding Holland's use of the phrase '. . . I propose the subspecific name given above' in the description (Holland 1920: 248). Bryk (1930) treated the name as a synonym of *ridleyanus*. Berger (1950) treated it as a synonym of *G. ridleyanus* ab. *infuscatus* Schultze.

Papilio ridleyanus f. *rosa* Le Cerf (1924) was described as a 'f[orma]. indiv[indua].' and thus clearly infrasubspecific, although Le Cerf, lacking other specimens speculated that it might represent a subspecies. As far as we are aware, no author has given the name higher rank.

Papilio ridleyanus njami Röber (1928) was established as a subspecies, though the author uses the term 'Form' later in the description. It was treated as a variety (subspecies) by Bryk (1930). We can find no reference to the taxon until Ackery *et al.* (1995), who treated it as a synonym of *G. ridleyanus*. Given the variability of coloration of the species, we see no reason to dissent from that view.

SIMILAR SPECIES

Unmistakable for any other species of *Graphium*. Torben Larsen (*pers. comm.*) tells us that, in flight, it is disconcertingly similar to species of *Acraea*.

DIAGNOSIS: PATTERN (Fig. 192)

The pattern is a reduced version of that found in other members of the group, with a dark brown ground colour with an array of bright spots. Unlike related species, however, these are normally of a bright, brick-red colour. **Forewing upperside** with dark brown ground colour fading to translucency apically, costally and marginally. Discal cell crossed by darker bands level with cells M$_2$ and CuA$_1$, sometimes edged with yellowish scales. The only other spots are post-discal marks in cells M$_2$ to 1A. On the **hindwing** the red marks are expanded to leave a row of black dots between the post-discals and submarginals and a dark margin with no marginal marks. There are also black spots in the discal cell at the base, next to the upper discocellular vein distal to the root of vein R$_S$, and next to the lower discocellular vein, opposite cell M$_3$. Unusually within the afrotropical *Graphium* – and within the whole tribe (Miller, 1987) – the patch of androconial scales on the hind wing is absent and the anal cell does not wrap over cell CuA$_2$.

The **underside** pattern largely reflects that of the upperside, but the red coloration is paler, nearer salmon pink. On the **hindwing** there is an additional set of black spots basally in the precostal cell and cells R$_1$, M$_3$, CuA$_1$ and CuA$_2$, enhancing the *Acraea*-like impression.

VARIATION

There is a certain amount of variation in the pattern. For example, the proximal forewing discal cell bar may be edged proximally and/or distally with yellow (not present in *njami* Röber, 1928); the distal band may also be edged with yellow basally and, rarely, distally. There may also be small yellow marks peripheral to the forewing post-discal marks. The extent of the red marks is slighly variable with the post-discal in forewing cell CuA$_2$ being sometimes subdivided along the intervenosa. In ab. *hecqueti* Dufrane (1946), the post discal in forewing cell M$_2$ is reduced to a blackish ellipse. The size of the submarginal marks of the hindwing is somewhat variable, those in cells M$_3$ and CuA$_1$ occasionally absent.

More noticeable is the variability in colour. This ranges from very vivid (e.g. *rosa* Le Cerf, 1924), through smoky red (e.g. *fumatus* Niepelt, 1915; *infuscatus* Schultze, 1913*d*) and paler coloration (e.g. *njami* Röber, 1928) to lacking red altogether (e.g. *fumosus* Holland, 1920). In some, there are very few scales, so the whole wing surface is translucent (e.g. *vitrea* Le Cerf, 1924) or partially so (e.g. *semivitreus* Schultze, 1930).

This variation does not seem to have any geographical component.

DIAGNOSIS: ♂ GENITALIA (Fig. 37)

Linked to the *schaffgotschi/morania/taboranus* clade by the bifid structure of the dorsal terminal process, but this is broad, as in *angolanus*. The dorsal harpe is characteristic, being less circular than in its relatives and strongly serrate dorsally, resembling a cockscomb. The ventral harpe is quite broad and serrate, with a strong terminal tooth and several smaller ones anteriorly.

Valve: *dorsal projection*: long, directed somewhat posteriad and curving slightly ventrad, stout spines mainly on anterior edge; *dorsal terminal process*: curved mesad, finely serrate, bifid, each half tapering to a sharp tooth; *ventral terminal process*: small, not serrate; *dorsal harpe*: elongate and parallel sided basally, becoming broader apically, with a row of stout teeth dorsally ; *ventral harpe*: tapering to a sharp tooth apically with a row of teeth proimally; *basal lamella*: broad, with four stout teeth. *Uncus*: tapering distally; *soccii*: well marked, with prominent projections. *Aedeagus*: elongate, nearly straight, with no sign of denticulation. *Saccus*: elongate, narrow.

DIAGNOSIS: ♀ GENITALIA (Fig. 89)

BMNH Spec.Reg. No. 137028; vial 4697: *ostium bursae* opening posteriorly; *ductus bursae* enlarged and sclerotized distally, kinked and with pocket just distal to the *ductus seminalis*; *central ostial lobe* absent; *lateral ostial lobes* large, setose; *anterior apophysis* present; *papillae anales* rounded.

EARLY STAGES

Fontaine (1985: 79–80) gives a description of the early stages, but no illustrations, based on rearing the species at Isiro, Democratic Republic of Congo, in 1957. According to Fontaine (1985), the larva is comparable in general shape to *policenes* and *angolanus*. He describes the third instar as having a pair of subdorsal longitudinal stripes on each side (perhaps comparable to later instar *morania*?), but the final instar is almost entirely dull green except for a yellowish longitudinal lateral stripe (thoracic and anal processes are not mentioned in Fontaine's account, but we presume they are present; no record for first instar). The pupa is likened to that of *angolanus*, with a prominent dorsal cephalic horn.

His description is as follows:

> Deux *œufs* examinés le 23–6–57 : sphériques, blanchâtres et sans dessins.
>
> Une *chenille* au troisième stade, récoltée le 30–6 de la même année, sur *Popowia congoensis* Engl. et Diels (Annonaceae).
>
> Descrition: Trapue, renflée antérieurement comme celles des *Graphium angolanus* et *policenes*. Vert foncé, région latéro-stigmatale largement teintée de brun-noir. Deux bandes subdorsales longitudinales bien tranchées de même teinte, partant de derrière la tête et se rejoignant sur la ligne médiane au niveau du segment 10. En outre, sur chaque segment, une bande latérale toujours de même couleur, oblique de bas en haut et d'avant en arrière. Tête et pattes vert-foncé.
>
> Dernière mue le 2–7–57.
>
> Au stade adulte (le quatrième): Chenille entièrement vert-foncé, avec de chaque côté une ligne longitudinale stignatale jaune ; Osmatérium, jaunâtre. Chrysalidation le 9–7.

La *nymphe* est semblable comme forme à celle de *Graphium angolanus*, portant une longue apophyse thoracique médiane. Vert-clair, avec le bord interne des étuis teinté de jaune.

Ecl. Imago le 22–7–57: un mâle ab. *infuscatus*.

Durée du stade nymphal : 13 jours.

DISTRIBUTION (Map Fig. 133)
Central equatorial Africa. Countries confirmed include: Nigeria, Cameroon, Equatorial Guinea, São Tomé & Principe (São Tomé), Central African Republic, Gabon, Congo, Democratic Republic of Congo, Burundi, Angola, Sudan, Uganda, Tanzania, Zambia, Zimbabwe.

There is a specimen in MNHN labelled as being from Benin (Carnotville), and another from Chad (Fort Orchambault).

Records for 'Sierra Leone' (e.g. Berger, 1981; Mathot, 1990; Kielland, 1990) are all false according to Larsen (In prep.*a*).

HOST PLANT RECORDS
Annonaceae:
Popowia congoensis (Fontaine, 1985).

BIONOMICS
Mainly found in evergreen lowland forests and forest/savannah borders in western, central and eastern-central Africa, Fontaine (1985: 113, 118) indicates that it prefers river margins and water courses in forested areas, but also occurs in wooded savannahs and open forests. While Kielland (1990) also considered it a forest insect, he noted that it emerges into woodlands to feed from flowering trees and bushes; males are also attracted to mud and wet ground (e.g. Carpenter, 1915). Monfort (1987) records two males from a marshy, open area near Kigali (Rwanda). According to Kielland (1990), in Tanzania it occurs from 780–1200 m, and in most areas it apparently flies througout the year ('most of the year': Pinhey & Loe, 1977; Berger, 1950, includes records for all months in Democratic Republic of Congo), although Larsen (In prep.*a*) records only November for West Africa. Generally regarded as a good mimic of various *Acraea* species, *A. perenna* is probably the primary model (Birket-Smith, 1960), but *ridleyanus* is a variable butterfly (Berger, 1950, gives an extensive account of its variations in Democratic Republic of Congo), and its mimicry may be generalized, or even have an underlying polymorphism and involve a number of *Acraea* species (Larsen, In prep.*a*, suggests in addition to *A. perenna*, *A. zetes* and *A. pharsalus*, especially for darker females; Kielland suggests *A. egina* in Tanzania). Like many mimics, flight behaviour probably depends on situation. Thus Schultze (1917*b*) noted *ridleyanus* as a very strong flier, but Birket-Smith (1960), who observed them flying slowly together with *A. perenna* along riverbanks, considered that in both appearance and behaviour it was very difficult to separate them in nature, a view with which Larsen (In prep.*a*) concurs.

CONSERVATION STATUS. 'Rather widely distributed and not known to be threatened' (Collins and Morris, 1985: 56).

MATERIAL EXAMINED. 394 ♂♂; 25 ♀♀ in BMNH. 118 ♂♂; 7 ♀♀ from other collections.

20–22 The leonidas group

This group of three species, *leonidas*, *cyrnus* and *levassori*, was accepted by both Berger (1951) and Hancock (1993). Our analyses failed to recover it as a monophyletic clade, placing the species in a polytomy with the *tynderaeus* clade, the *adamastor/philonoe* clade and *G.* (*Pazala*) *macareus*, which together constitute what we refer to as the crown group. Of the three species, *G. leonidas* is widespread throughout most of subsaharan Africa, with subspecies on adjacent islands; *G. levassori* is confined to the Comoro Islands; and *G. cyrnus* is from Madagascar.

20. ***Graphium* (*Arisbe*) *leonidas*** (Fabricius, 1793)

Veined Swallowtail, Veined Swordtail, or Common Graphium (Figs 193, 221–223, 245, 246; map Fig. 137; genitalia Figs 38, 90; early stages Fig. 256)

Found throughout subsaharan Africa, with separate subspecies on the islands of São Tomé, Principe, and Pemba and Zanzibar.

SIMILAR SPECIES
Most similar to *G. cyrnus* and *G. philonoe*, but differences of both pattern and colour should allow little confusion.

We describe those elements of colour and pattern which distinguish *G. leonidas* immediately below. Due to their complexity and variability, we give details of pattern in the diagnosis section of the account of *G. l. leonidas*, with the diagnostic features of the other subspecies in the accounts of those taxa.

DIAGNOSIS: PATTERN (Figs 193, 221–223, 245, 246)
Upper surface of wings dark – almost black when fresh, but fading to dark brown – with an array of pale marks. These are greenish blue when fresh, but also fade, ultimately to cream. In *G. l. pelopidas* the marks of the hindwing are usually white even in fresh specimens. Those in hindwing cell R_1 are white in all populations. The marking pattern is variable at an individual level and further complicated by subspecific differences, some sexual dimorphism and by polymorphism.

Primarily distinguishable by colour: even when faded, the blue/green hue of the markings is detectable; in *G. cyrnus* they are bright yellow; in *G. philonoe*, white, even in fresh specimens. The clearest pattern differences are as follows. In both *G. cyrnus* and *G. philonoe* the main mark in the forewing discal cell is usually at least partly subdivided by the 'intervenosae'; this is not the case in *G. leonidas*. In both *G. cyrnus* and *G. philonoe* the post-discal spots in cells M_2 to CuA_1 of the forewing are subequal in size; in *G. leonidas* that in M_3 is clearly the largest, whereas that in CuA_1 is often very small or even absent. In both *G. cyrnus* and *G. philonoe* the post-discal spot in cell CuA_2 is extended basally to the origin of the cell; in *G. leonidas* it is an elliptical spot not reaching the surrounding veins. In *G. philonoe* the hindwing submarginal marks are subdivided; in *G. cyrnus* they are indented by the intervenosae; in *G. leonidas* they are almost entire (in some *G. l. pelopidas* they are sometimes reduced to small dots which may be subdivided). These features are largely reflected on the undersides. In addition, *G. cyrnus* has an array of black marks on the hindwing, detailed in the account of that species.

DIAGNOSIS: ♂ GENITALIA (Fig. 38)
Dorsal projection stout and very short. *Dorsal harpe* curved and serrate. *Ventral harpe* broad, with blade almost vertical, the tip and deeply serrate or palmate. *Dorsal terminal process* large, curved mesad, not explanate dorsally (unlike *G. levassori* and the *tynderaeus*-group); ventral tip acute, finely serrate on the dorsal and ventral edges. *Ventral terminal process* large and acute, finely serrate on both edges. *Uncus*, somewhat elongate *socii* prominent with prominent projections. *Saccus* very short, broad. *Aedeagus* short, stout, nearly straight, the tip extended and decurved, with no indication of denticulation.

DIAGNOSIS: ♀ GENITALIA (Fig. 90)
BMNH Spec.Reg. No. 137474; vial 4593; and 137979; vial 3986: *vestibulum* broad; *ostium bursae* opening anteriorly; *ductus bursae* slightly sclerotized distally and with a slight kink just distal to the ductus seminalis; *central ostial lobe* elongate, slightly tapering, rounded apically, setose; *lateral ostial lobes* setose, broad, rounded at tip; *anterior apophyses* long; *papillae anales* rounded, with many peg-like setae.

EARLY STAGES (Fig. 256)
The later instar larvae are greenish-white, tinged with buff, with striking dorsal and subdorsal brownish-white longitudinal stripes. Also outstanding is the pattern of oblique, slightly 'undulating' dorso-lateral stripes on the abdominal segments. The thoracic and caudal processes appear smooth the fourth and fifth instars, with the thoracic processes very highly reduced in the fifth. The yellowish-green pupa is distinctive in shape, evenly broadened to its mid-point when viewed from above, the ventral cephalic area rounded, without obvious horns, and the dorsal horn strongly recurved, almost normal to the long axis of the pupa; the two main longitudinal markings are pale.

Van Son (1949) gives descriptions based on Trimen (1889) and Gowan Clark, including pl. XIII. See also Haig (1936) and Carcasson (1981). Villiers (1957) and Henning *et al.* (1997) both give figures of first and final larval instars and the pupa (the latter as colour photographs). According to Henning *et al.* (1997), the egg hatches after four days; the larva rests on the upperside of the leaf, along the midrib; early instars are 'hole-feeders', but more mature larvae switch to leaf edges; the fifth and final instar lasts just under four weeks; the pupal girdle is fragile and may break, so that 'suspended' pupae may be encountered (Trimen, 1889). Sevastopulo (MS) gives the following description of instars 3–5 and the pupa:

> 3rd instar: Head pale green. Body pale green, minutely speckled with white. A branched white subdorsal scolus on each of the thoracic somites and a similar, backward-pointing scolus on the anal somite. Moulted 15.i.64.
>
> 4th instar: Head pale green. Body pale green, the dorsal area of the first five somites covered by an oval patch of olive suffusion with a double pale line running through the centre. 6th somite backwards with a series of oblique, lateral, olive lines. A slight olive suffusion laterally on the first four somites, continued backwards as a sublateral stripe. Scoli rather smaller than in the previous instar. Moulted 22.i.64.
>
> 5th instar: Head pale green. Body greenish-white, slightly buff-tinged. A green subdorsal stripe, broadest on the thoracic somites and containing a pale median line. A sublateral stripe, green on the thoracic somites and brownish thereafter, below which the body is a pale clear green. 5th to 11th somites each with a slightly undulate, darkish green, lateral line, extending sublaterally onto the somite before. Thoracic somites each with a small subdorsal tubercle replacing the scoli of the earlier instars. Anal somite with a pair of divergent white points. Legs, prolegs and venter pale clear green, similar to the sublateral area. The larval osmeterium, which is only rarely extruded, is a dull bluish purple.
>
> Described from larvae found in the Marere Forest and elsewhere, all of which died before pupating. Although none [was] bred through, the species has been identified positively from figures in Villiers . . . (1957).
>
> Pupa suspended by a girdle and the cremaster. Very similar in shape to *angolanus*. Head square across frontally (*angolanus* is slightly indented), thorax rising to a forward-pointing process. Colour leaf green, the thoracic process with a yellow line continued along the upper edge of the wing case and then sublaterally on the abdomen to the cremaster, the posterior portion purple brown in colour. A subdorsal line on the abdominal somites from the thoracic point to the cremaster, the two ends fairly close together but diverging in the centre, this line also yellow with the posterior portion purple brown. A series of fine, darker green, oblique lines between the subdorsal and sublateral lines.
>
> Described from a pupa [derived] from a larva found at Kwale (Shimba Hills), which pupated 12.iv.68, and a male emerged 24.iv.68.
>
> [Sevastopulo's descriptions are accompanied by 13 black and white photographs.]

DISTRIBUTION. See subspecies accounts.

HOST PLANT RECORDS

Annonaceae:

Annona chamae (Haig, 1936; Larsen MSb; Henning *et al.*, 1997).

Annona reticulata (Custard Apple – introduced) (Collins & Morris, 1985).

Annona senegalensis (Sevastopulo, MS – in captivity).

Annona squamosa (Sevastopulo, MS – in captivity).

Artabotrys cinerea (Haig, 1936; Larsen MSb; Henning *et al.*, 1997).

Enanthia chlorantha (Lees, 1989).

Friesodielsia (*Popowia*) *obovata* (Haig, 1936; Larsen MSb; Henning *et al.*, 1997).

Monanthotaxis caffra (Haig, 1936; Larsen MSb; Henning *et al.*, 1997).

Monanthotaxis fornicate (Congdon, *in litt.* 1999).

Popowia spp. inc. *caffra* (Sond.) (van Son, 1949: 42).

Popowia spp. (Villiers, 1957; Sevastopulo, MS).

Uvaria acuminata (Congdon, *in litt.* 1999).

Uvaria caffra (Haig, 1936; Larsen MSb; Henning *et al.*, 1997).

Uvaria kirkii (Congdon, *in litt.* 1999).

Uvaria sp. (Sevastopulo, MS).

Apocynaceae:

Landolphia sp. (Sevastopulo, MS).

BIONOMICS

On the mainland, *G. l. leonidas* is generally a common butterfly in forests (Fontaine, 1985: 114), wooded areas (e.g. *Brachystegia* formations), gallery forests (Hecq & Peeters, 1992; Fontaine, 1985: 116) and savannahs (Fontaine, 1985: 116), affecting a wide variety of habitats other than deserts and true rainforests (Larsen, 1996). The males area readily attracted to mud (often in numbers: Larsen, pers. comm.) and other sources of moisture (notably puddles: Carpenter, 1915; 'nitrogenous spots on river banks': Birket-Smith, 1960, or mammal urine: Owen & Owen, 1972). Both sexes can often be seen at flowering trees and bushes (e.g. *Lantana*: Trimen, 1889; Migdoll, 1988), and Owen & Owen (1972) indicate that it 'frequently enters gardens to feed from cultivated flowers'. In Tanzania it occurs from sea level to 2200 m. (Kielland, 1990); according to Gifford (1965), it flies up rivers in the morning and down in the afternoon. Larsen (1968) recorded a mixed migration in Nigeria that included *G. leonidas*; it lasted seven days (May 31st – June 6th 1967), with 15–20 individuals passing from west to east per hour when it was sunny (together with 20–30 *G. policenes*, five almost equally abundant species of Pieridae, and various 'followers'). In most tropical areas the Common Graphium can probably be seen 'throughout the year' (Pinhey & Loe, 1977, Williams, 1969). Congdon (*in litt.*, 1999) suggests, 'The wider choice of foodplants may help to explain the longer flying season of this butterfly.' Gifford (1965) gives Nov.–June as main flight period in Malawi. Larsen (In prep.*a*) gives records for west Africa for all months except Feb.; Berger, 1950, has records of all months for Democratic Republic of Congo. This seems true even for South Africa (van Son, 1949; Henning *et al.*, 1997), although in cooler areas it may only fly from Sept.–April (Williams, 1969). Larsen (In prep.*b*) records Dec.–May as the main flight period in Botswana, and also observes that it is sometimes migratory (Larsen, In prep.*a*). Individuals have been observed 'tree-topping' in groups (Larsen, In prep.*a*); males readily hill-top (Swanepoel, 1953), and often exhibit territorial behaviour (Kielland, 1990) – on hill tops and patrolling from perches along forest margins (Henning *et al.*, 1997), and perching on understorey trees within forests, from which vantage points they 'constantly drive off intruders' (Cordeiro, 1990).

Although the flight can be fast, erratic and weaving (Larsen, 1996; Henning *et al.*, 1997), in other circumstances it seems they fly 'briskly but not very swiftly' (Trimen, quoted in Swanepoel, 1953), and quite slowly when ovipositing (Larsen, In prep.*b*). Cooper (1973) describes the flight as comparatively weak and slow; Williams (1969) as 'sailing'. Kielland considered *G. leonidas* to be a good mimic of its putative model, *Tirumala petiverana* (Danainae), with which it flies in Tanzania; Sevastopulo (1973) suggested that the relationship may be Müllerian. Carpenter (1921), however, reports how he offered a specimen of *G. leonidas* to a monkey. After holding it for a long time, the monkey finally ate the butterfly without any sign of dislike. Cordeiro (1990) noted that, in addition to *T. petiverana*, *G. leonidas* is also very similar in appearance and behaviour to *Euxanthe wakefieldii* (Charaxinae), which often shares the same habitat. When settled, the Veined Graphium closes its wings (excellent photograph in Pinhey & Loe, 1977: 85; unusually for a papilionid it would seem, this is often done even when feeding at flowers: Henning *et al.*, 1997), thus heightening its resemblance to a danaid. In southern Africa, where f. 'brasidas' is common, mimicry for *Tirumala* (absent in South Africa) is replaced by mimicry for *Amauris*. A settled 'brasidas' can readily be mistaken for *A. echeria*, especially when resting at the end of a twig with its wings folded downwards, in typical danaid fashion (Trimen; see van Son, 1949: 40). Oviposition behaviour is described by Henning *et al.* (1997): a female approaches a suitable plant with fluttering wings, and legs extended. After leg contact is made, the plant is palpated with the antennal tips, as she locates the growing tips; one egg per young shoot or leaf is laid.

CONSERVATION STATUS. 'Not threatened' (Collins & Morris, 1985: 58).

20a. ***G. (A.) leonidas leonidas*** (Fabricius, 1793)

(Figs 193, 245, 246; map Fig. 137; genitalia Figs 38, 90; early stages Fig. 256)

Papilio Leonidas Jones, MS, pl.62, fig. 1.

Papilio Leonidas Fabricius, 1793: 35. TYPE: 'Habitat in Africa Mus. Dom. Drury' (Fabricius, 1793: 35). (not seen). Name placed on Official List of Specific Names in Zoology with Name Number 2007 (Opinion 823, ICZN, 1967: 218). ?AMSA. (not seen).

Papilio leonidas leonidas Fabricius; Aurivillius, 1908: 22.

Papilio leonidas [*leonidas*] Fabricius; Bryk, 1930*b*: 565.

Zelima leonidas Fabricius; Fabricius, 1938: 55.

Graphium leonidas f. *leonidas* Fabricius; van Son, 1949: 39; text-figs 20a–c; pls V (fig.8), VI (fig.8).

Papilio (*Graphium*) *leonidas leonidas* Fabricius; Peters, 1952: 20.

Graphium (*Arisbe*) *leonidas* Fabricius; Munroe 1961: 42; Hancock, 1983: 46; Collins & Morris, 1985: 58;

Graphium leonidas leonidas Fabricius; D'Abrera, 1980: 46, 47 (figs); Berger, 1981: 53, pl.17 figs 3 (♀), 7 (♂).

Graphium (*Arisbe*) *leonidas leonidas* Fabricius; Pennington, 1994: 305; Ackery, Smith & Vane-Wright, 1995: 163.

SYNONYMS

Papilio leonidas Variety *a*. Gray, [1853]: 7, pl.5 fig.3.

Papilio brasidas Felder & Felder, 1864: 307. LECTOTYPE ♂: SOUTH AFRICA: ['Zoolu' (Gray, [1853]: 7)]. BMNH Spec.Reg. No. 138110. **Here designated**.

Papilio leonidas =*brasidas* Felder; Kirby, 1871: 520.

Papilio leonidas var. *brasidas* Felder; Aurivillius, 1899: 487; Bryk, 1930*b*: 566.

Papilio leonidas brasidas Felder; Aurivillius, 1908 : 22.

Graphium leonidas f. *brasidas* Felder; van Son, 1949: 39; pls V, fig.9, VI, fig.9.

Graphium leonidas brasidas Felder; Peters, 1952: 20.

Graphium leonidas leonidas =*brasidas* Felder; D'Abrera, 1980: 46.

Graphium (*Arisbe*) *leonidas leonidas* f. *brasidas* Felder; Pennington, 1994: 305.

Graphium (*Arisbe*) *leonidas leonidas* =*brasidas* Felder and Felder; Ackery, Smith & Vane-Wright, 1995: 163.

Papilio leonidas onidale Suffert, 1904: 106. LECTOTYPE ♂: TANZANIA: 'Muanza am Südufer des Victoria-Nyanza' (Suffert, 1904: 107). BMNH. Spec.Reg. No. 138402 – designated Le Cerf (1924: 397); 1 PARALECTOTYPE ♂: Same provenance. BMNH. Spec.Reg. No. 138403.

Papilio leonidas ab. (?) *onidale* Suffert; Aurivillius, 1908 : 22.

Papilio leonidas [*leonidas*] ab. *onidale* Suffert; Bryk, 1930*b*: 566.

Graphium leonidas leonidas ab. *onidale* Suffert; Peters, 1952: 20.

Graphium (*Arisbe*) *leonidas leonidas* =*onidale* Suffert; Ackery, Smith & Vane-Wright, 1995: 163.

Papilio similis umanus Rothschild & Jordan, 1905: 191. HOLOTYPE ♂: SUDAN: 'between Dalba to the Uma River, Konta, 28. ii. 1901' (Rothschild & Jordan, 1905: 191). BMNH. Spec.Reg. No. 138401.

Papilio leonidas umanus Rothschild & Jordan; Aurivillius, 1908 : 22.

Papilio leonidas var. *umanus* Rothschild & Jordan; Bryk, 1930*b*: 567.

Graphium leonidas umanus Rothschild & Jordan; Peters, 1952: 21.

Graphium (*Arisbe*) *leonidas leonidas* =*umanus* Rothschild & Jordan; Ackery, Smith & Vane-Wright, 1995: 163.

UNAVAILABLE NAMES

Papilio similis [attributed to Linnaeus] Cramer, [1775], *in* Cramer, [1775–6]: 14. pl.9 figs B, C. [Misidentification].

Papilio leonidas [*leonidas*] var. *similis* Cramer; Bryk, 1930*b*: 565.

Papilio leonidas ab. (?var.) *interniplaga* Aurivillius, 1899: 487. TANZANIA. (not seen) [infrasubspecific]

Papilio leonidas ab. (?) *interniplaga* Auriv.; Aurivillius, 1908 : 22.

Papilio leonidas-leonidas f. ♀ *plagifera* Le Cerf, 1924*b*: 138. [?] SOUTH AFRICA. MNHN. [infrasubspecific]

Papilio leonidas brasidas f. indiv. ♀ *melusina* Le Cerf, 1924*a*: 397, pl.5 fig.48. SOUTH AFRICA. BMNH Spec.Reg. No. 138404. [infrasubspecific]

Papilio leonidas ab. *petiveranaides* Bryk, 1928: 15. UGANDA. ?NRS (not seen). [infrasubspecific]

Papilio (*Cosmodesmus*) *leonidas leonidas* ab. *obliterata* Dufrane, 1946: 119. DEMOCRATIC REPUBLIC OF CONGO. IRSN. [infrasubspecific]

Papilio (*Cosmodesmus*) *leonidas leonidas* [f.] *minor* Dufrane, 1946: 119. GUINEA. IRSN. [infrasubspecific]

Papilio (*Cosmodesmus*) *leonidas leonidas* ab. *subobliterata* Dufrane, 1946: 119. DEMOCRATIC REPUBLIC OF CONGO. IRSN. [infrasubspecific]

Papilio (*Cosmodesmus*) *leonidas leonidas* ab. *vreuricki* Dufrane, 1946: 119. DEMOCRATIC REPUBLIC OF CONGO. IRSN. [infrasubspecific]

Papilio (*Cosmodesmus*) *leonidas leonidas* ab. *mathieui* Dufrane, 1946: 119. DEMOCRATIC REPUBLIC OF CONGO. IRSN. [infrasubspecific]

Graphium leonidas leonidas ab. *vrydaghi* Berger, 1950: 91. DEMOCRATIC REPUBLIC OF CONGO. MRAC. [infrasubspecific]

Graphium leonidas leonidas ab. *leucosina* Berger,

1950: 91. DEMOCRATIC REPUBLIC OF CONGO. MRAC. [infrasubspecific]

Graphium leonidas leonidas ab. *djema* Berger, 1950: 91. CAR. MRAC. [infrasubspecific]

Graphium leonidas ab. *cyrnoides* Storace, 1953: 260. ZAMBIA/ZIMBABWE: 'Cascate Victoria'. MCSN (not seen). [infrasubspecific]

TYPE EVALUATIONS

Papilio Leonidas Fabricius (1793) was described from a specimen or specimens in Dru Drury's collection, which was broken up and sold at auction after his death. Part of it was bought by Alexander McLeay and taken to Australia where it became part of the Australian Museum, Sydney, which McLeay established (see van Leeuwen, 1997). We do not know at present whether the type of *Papilio Leonidas* survives there or elsewhere. Fortunately, the specimen was well illustrated by Jones, whose 'Icones' survive in OXUM; plate 62 shows a butterfly clearly recognisable as *G. leonidas*. Fabricius subsequently recorded the taxon in his *Systema Glossatorum* (published by Bryk in 1938) as *Zelima leonidas*, stating 'Habitat in Guinea Mus. Dom. Lund.'. Zimsen (1964) records three specimens, presumably these, in 'Kiel' (now in ZMC). For further information on the name *Papilio leonidas* see Hemming (1965; 1967: 59).

In their description of *Papilio brasidas*, Felder & Felder (1864: 307) were providing a name for *Papilio leonidas* Variety *a* Gray (1852: 7, pl.5, figs 3) and for the South African examples included by Trimen (1862: 22) and identified by him as 'G.R. Gray's 'Variety *a*'. Felder & Felder (1864) gave the localities as 'Africa austr. (Zulu, Port Natal)', referring to those stated by the earlier authors. Under the Code, Article 12.2.1 (ICZN, 1999), Felder & Felder's (1864) reference to Gray and Trimen constitutes an indication on which a valid name may be based. Gray based his description on more than one specimen – some variation is described. However, the figures are of an identifiable individual. Under the Code, Article 72.5.6 (ICZN, 1999) the specimen(s) concerned, not the illustration or description, should be regarded as the type(s); and according to Article 72.4.1 all such material should be so regarded. In the present case, all the material described by Gray and the South African material of Trimen thus constitute the syntypic series.

Gray (1852) was describing specimens presented to the BMNH by G.F. Angas (BMNH accession number [18]48–63) from 'S. Africa (Zoolu country (Zulu)'. We have been able to locate 2 specimens from this collection, 1 ♂ and 1 ♀. Since Gray decribed only the male, and since this is very similar to his illustration, we select that specimen, which has been registered as BMNH Spec.Reg. No. 138110, as lectotype for the nominal taxon *Papilio brasidas* Felder & Felder (1864).

In describing 'ab. (var.?)' *interniplaga* Aurivillius (1899) was providing a name for a taxon he considered Staudinger (1884) had misidentified as *G. leonidas pelopidas* Oberthür.

Papilio leonidas onidale (Suffert, 1904: 106) was described from: 'Ein männliches und ein weibliches Exemplar aus Muanza am Südufer des Victoria-Nyanza. Coll. Suffert.' (Suffert 1904: 107). These specimens are now in BMNH, ex Joicey Bequest (BMNH 1934–120). Le Cerf (1924: 397) selected the male as 'Type H.T.' and this specimen was so labelled. The female had an added BMNH round 'Type' label modified to read 'Para/Type/♀'. This has now been labelled as paralectotype.

Papilio similis umanus Rothschild & Jordan (1905: 191) was described from a single male. The specimen is clearly labelled, possibly in Jordan's hand. It reached the BMNH as part of the Rothschild Bequest (BMNH 1939–1).

TAXONOMIC STATUS

Papilio leonidas Fabricius (1793) was established as a species. This status has not been contested by authors, though the subsequent establishment of a series of subspecies has caused it to be regarded as the nominate race of a polytypic species.

Papilio brasidas Felder & Felder (1864) was described as a species, and it has since been treated variously as a full species (Trimen, 1889: 214), a subspecies or equivalent (Aurivillius 1899: 487 (etc.); Bryk, 1930*b*: 566) or as infrasubspecific (van Son, 1949: 39; D'Abrera, 1980: 46; Pennington, 1994: 305; Ackery *et al.*, 1995: 164). It is sympatric with *G. l. leonidas* over at least part of its range and there appears to be no seasonality involved (van Son. *loc.cit.*). Intermediates are also found. We therefore regard *Papilio brasidas* as infrasubspecific, possibly part of a regional polymorphism. Breeding experiments might confirm this.

Aurivillius (1899) described *interniplaga* as an 'ab. (var.?)'. No author since has used the name with clear subspecific rank.

Papilio leonidas onidale (Suffert, 1904: 106) was described as a subspecies. It was treated as an 'ab. (?)' by Aurivillius (1908) and as infrasubspecific by subsequent authors.

Papilio similis umanus Rothschild & Jordan, (1905: 191) was described as a subspecies and accepted as such by several subsequent authors. Carcasson (1981) did not include it as a valid taxon in his checklist, and Ackery *et al.* (1995), following Carcasson, treated it as a synonym of *G. l. leonidas*. Rothschild & Jordan (1905) differentiated it principally on the basis of a reduced pale band in the hindwing discal cell, reduced discal mark in hindwing cell R_1, and no discal mark in hindwing cell CuA_1. However, *G. l. leonidas* is, as detailed below, very variable in the expression of these features; all of the supposed distinguishing features of *umanus* occur elsewhere. Moreover, other Sudanese specimens (albeit from slightly further South) do not show these traits. We therefore regard *Papilio similis umanus* Rothschild & Jordan (1905) as synonymous with *G. l. leonidas*. Should further topotypic material exhibit the same combination of characters, that opinion may need to be revised.

DIAGNOSIS: PATTERN (Fig. 193)

Upperside: **Forewing** discal cell with three marks, the proximal obliquely angled from close to the radial vein to near the posterior discocellular vein opposite vein CuA_2; a more transverse mark opposite cell M_3, narrowing from the posterior discocellular towards the radial vein; and a semicircular spot opposite cell R_5, close to the radial vein. Cell R_3 has a post-discal spot originating level with the root of vein R_4 and a submarginal mark. Cell R_4 has a discal mark in the angle between veins R_4 and R_5 and a submarginal mark. In cell R_5 there is a small discal mark and a larger, somewhat elongate post-discal (possibly fused to the sub-marginal which is otherwise not evident). Cell M_1 usually has only a very small post-discal mark and a submarginal mark. Cells M_2 to CuA_2 each usually have a post-discal mark, the sizes of which vary according to subspecies, but those in cells M_2 and CuA_1 are smaller than the other two (that in CuA_1 often absent); that in cell M_3 forms a transverse band with the middle band in the discal cell. Cell 1A has no marking, unlike *G. l. pelopidas*. Cells M_1 to CuA_2 have prominent, entire submarginal marks (often greatly reduced in *G. l. pelopidas*).

The **hindwing** discal cell has a variable amount of pale marking, sometimes filling the whole cell, sometimes much less. Cell R_1 has a white post-discal mark. Cell R_5 has a prominent discal mark extending from the root of vein R_S. Cell CuA_1 also has a basal, discal mark. Cells M_2 to CuA_1 have more or less clear post-discal marks and all cells from R_1 to CuA_1 – and sometimes CuA_2 – have prominent, entire submarginal marks. Cell CuA_2 has an elongate discal mark and a small post-discal spot. Small marginal marks may be seen on the wing edges at the ends of the intervenosae.

The **undersides** are very similar, but with a paler ground colour. Some of the spots are extended by areas with pale scales but with the membrane dark, giving a somewhat nacreous appearance. Thus some spots which are very small on the upperside (e.g. in forewing cell CuA_1) may be more prominent underneath. The pale marks of the hindwing discal cell and adjacent marks are slightly orange, rather than blue. At the base of the hindwing is the black area with white scales on the subcostal and cubital veins, common to several taxa of the subgenus. In addition there is a crescent-shaped black area lying proximal to the humeral vein.

The **females** are similar, though generally with smaller pale marks, giving an overall darker impression. This is complicated by what appears to be a female sex-limited polymorphism in East Africa, where many specimens have the discal cell marking greatly reduced (sometimes virtually obsolete) and rendered fuzzy by scattering of the pale scales, and no (or very faint) discal marks in hindwing cells CuA_1 and CuA_2. This apparent polymorphism is additional to the unimodal polymorphism in Southern Africa between the normal and *brasidas* forms.

VARIATION (Figs 245, 246)

The form *brasidas* (Fig. 245) is characterized by a general reduction in the size and number of pale markings. In particular, the basal, oblique mark of the forewing discal cell is reduced to a small spot near the radial vein or, more often, absent. The main mark opposite cell M_3 is also reduced and interrupted by the intervenosae; at its most extreme it may be represented by just one small mark, either near the posterior discocellular vein (as in the 'holotype' of ab. *melusina* – Fig. 246) or near the radial vein. The post-discal mark in forewing cell M_2 is reduced to a small ellipse, or is absent. That in cell M_3 is also elliptical, not reaching the surrounding veins. This spot is never present in cell CuA_1 and is only small and elliptical in CuA_2, where the line of the intervenosa may be seen passing through it.

The post discal spots usually found in cells M_1 to CuA_2 of the hindwing are very reduced and commonly absent from most, if not all of these cells.

On both wings, the submarginal spots are reduced to small points, sometimes absent from some cells – especially of the forewing – or from all cells (ab. *melusina*).

The underside pattern reflects that of the upper side. The *brasidas* form occurs in Mozambique and South Africa, its frequency increasing southwards to become the more common form.

A further variant, more frequent and often more extreme in females, occurs in eastern Africa from Sudan to Malawi and westward into Congo. In it, the basal pale marking of the hindwing is reduced: the veins surrounding the discal cell are brown-scaled, and this suffuses into the pale marks of the discal cell itself and neigbouring cells R_1, R_5, CuA_1 and CuA_2. There is a range of expression ranging from the condition in the types of *onidale*, where the veins surrounding the cell are 'fuzzy' to cases where almost the entire discal cell as well as cell CuA_2 are suffused with brown. Cell CuA_1 often lacks a discal mark in these forms.

In *umanus* Rothschild & Jordan, the hindwing discal cell pale mark is particularly restricted, barely reaching the roots of veins R_S and CuA_2. The white discal patch in R_1 is not extended proximally.

In addition to the above, and to general variation in the size and shape of the pale marks, particular variations include:

Forewing discal cell with basal oblique mark extended to touch mark opposite cell M_3.

Forewing cell R_5 with discal spot absent.

Forewing cell M_1 with post-discal spot absent.

Forewing cell CuA_1 with post-discal spot very reduced or even absent.

Hindwing cell R_5 with a brown line in [post-]discal mark close to and parallel to medial vein.

Hindwing cell CuA_1 with post-discal mark touching discal. Ditto cell CuA_2.

Hindwing cell CuA_1 with post-discal mark absent from upperside.

DIAGNOSIS: ♂ AND ♀ GENITALIA (Figs 38, 90); EARLY STAGES (Fig. 256). See species account.

DISTRIBUTION (Map Fig. 137)
Widespread in western, central, eastern and south-eastern Africa; confirmed records include Senegal, Gambia, Mali, Guinea Bissau, Guinea, Sierra Leone, Liberia, Ivory Coast, Burkina Faso, Ghana, Togo, Benin, Nigeria, Cameroon, Chad, Equatorial Guinea (including Bioko), Central African Republic, Gabon, Congo, Democratic Republic of Congo, Rwanda, Burundi, Angola, Sudan, Ethiopia, Uganda, Kenya, Tanzania (not including Pemba and Zanzibar where it is replaced by *G. l. pelopidas*), Malawi, Zambia, Zimbabwe, Mozambique, Namibia, Botswana, Swaziland, and South Africa.

HOST PLANTS; BIONOMICS; CONSERVATION STATUS. See species account.

MATERIAL EXAMINED. 879 ♂♂, 216 ♀♀ in BMNH. 234 ♂♂, 35 ♀♀ from other collections.

20b. *G.* (*A.*) *leonidas pelopidas* (Oberthür, 1879)

Zanzibar Veined Swallowtail, Veined Swordtail, or Common Graphium (Fig. 221; map Fig. 137)

Papilio leonidas ? var. *Pelopidas* Oberthür, 1879: 55. HOLOTYPE ♂: TANZANIA: '1 ♂; Tchouacka (Zanguebar).' (Oberthür, 1879: 55). BMNH. Spec.Reg. No. 138398.

Papilio leonidas pelopidas Oberthür; Aurivillius, 1908: 22.

Papilio leonidas var. *pelopidas* Oberthür; Bryk, 1930*b*: 567.

Papilio (*Graphium*) *leonidas pelopidas* Oberthür; Peters, 1952: 21.

Graphium pelopidas Oberthür; D'Abrera, 1980: 44, 45 (fig.).

Graphium (*Arisbe*) *leonidas pelopidas* Oberthür; Carcasson, 1981: 124; Ackery, Smith & Vane-Wright, 1995: 164.

Graphium (*Arisbe*) *pelopidas* Oberthür: Collins & Morris, 1985: 58.

Graphium leonidas pelopidas Oberthür; Kielland, 1990: 47, 265; d'Abrera, 1997: 54, 55 (fig.).

SYNONYM

Graphium leonidas zanzibaricus Kielland, 1990: 47. HOLOTYPE ♂: TANZANIA: 'Zanzibar/[collected by] (E. Morland).' (label data). BMNH Spec.Reg. No. 138245.

Graphium (*Arisbe*) *leonidas pelopidas* =*zanzibaricus* Kielland; Ackery, Smith & Vane-Wright, 1995: 164, as syn. n..

Graphium leonidas pelopidas =*zanzibaricus* Kielland; d'Abrera, 1997: 54.

TYPE EVALUATIONS

Papilio leonidas ? var. *Pelopidas* was described by Oberthür (1879: 55) from a single individual. The specimen concerned, unambiguously identified by its labelling, reached the BMNH via the Levick Bequest (BMNH 1941–83).

In his description of *Graphium leonidas zanzibaricus* Kielland (1990: 47), was providing a name for a specimen illustrated by D'Abrera (1980: 45) as '*G. pelopidas* (Zanzibar pop.)'. Under the Code, Article 12.2.1 (ICZN, 1999), this constitutes a valid indication, and according to Article 72.5.6, the specimen concerned, not the illustration, should be regarded as the type. In this case, that specimen is readily identified by its general appearance, damage to its right antenna, its provenance, and by being labelled 'Photographed by/B. D'Abrera 77/78'. The specimen reached BMNH via the Rothschild Bequest (BMNH 1939–1).

TAXONOMIC STATUS

Papilio leonidas ? var. *Pelopidas* was established by Oberthür (1879: 55) before 1961 as a variety and should be treated as of subspecific rank under the Code, Article 45.6.4 (ICZN, 1999). The query in the original description refers to Oberthür's concern, as expressed in the text, that the taxon might warrant specific rank. Subsequent authors have generally treated it as subspecific.

Graphium leonidas zanzibaricus was described by Kielland (1990: 47) under the misapprehension that *G. l. pelopidas* was described from Pemba rather than Zanzibar, as pointed out by Ackery *et al.* (1995: 164) when synonymising the two. Comparison of the two holotypes confirms this synonymy, though that of *pelopidas* is slightly larger, and that of *zanzibaricus* lacks the distal oblique mark in the forewing upperside discal cell.

This begs the question as to whether the populations on the two islands are distinct. Kielland (1990) indicated that the Zanzibar population is 'somewhat intermediate between *leonidas* and [the Pemba population], with greatly reduced white submarginal markings of the h.[ind] w.[ings].' However, both populations show variation in these (and other) markings, with some Zanzibar specimens having considerably larger submarginal marks than some Pemba specimens. It would be very difficult to identify the island provenance of any given specimen from appearance alone. It thus seems unnecessary to establish a new taxon for the Pemba population.

Diagnosis: pattern (Fig. 221)
Differs from the nominate race in the expansion of some marks, and the reduction of others and by the hindwing marks being white, rather than bluish. These differences are believed to reflect mimicry of *Amauris niavius* rather than *Tirumala petiverana*.

The main forewing discal cell mark is broader than in the nominate race, being extended distally opposite part or most of cell M_2 (though it usually tapers close to the radial vein). The proximal, oblique mark in the forewing cell is usually reduced or absent. Post discal marks of forewing cells M_2 and M_3 expanded, that in cell M_2 usually reaching both the median vein and vein M_3; that in cell M_3 usually reaching veins M_2, M_3 and the medial vein. Forewing cell 1A usually with a post-discal mark (almost absent in the holotype!). The submarginal marks of both wings usually reduced to very small spots, or even absent in some cells. The post-discal spots of the hindwing are also usually reduced.

These differences are reflected on the underside.

Variation
Some specimens have a fully formed basal oblique mark in the forewing discal cell, as in the nominate subspecies. The size of the post-discal mark of forewing cell 1A is very variable: in some specimens it extends basally beyond vein 2A; in others it may be represented by a small patch (as in the holotype of *zanzibaricus*), an even smaller spot, or a few pale scales along the inner margin (as in the holotype of *pelopidas*).

Hindwing cell M_1 sometimes has a prominent post-discal spot, even when other post-discal and sub-marginal marks are strongly reduced or absent. This cell, and sometimes M_2 sometimes has a discal mark by their respective discocellular veins.

The general appearance of some specimens suggests that there might be some gene flow between the islands, especially Zanzibar, and the mainland.

Diagnosis: ♂ genitalia. Very similar to the nominate (more similar than *G. p. thomasius*). The *dorsal harpe* and *ventral harpe* are both slightly less explanate; *ventral terminal process* angled somewhat more ventrad.

Diagnosis: ♀ genitalia; early stages; host plants; bionomics. See species account.

Distribution (Map Fig. 137). Tanzania: The islands of Pemba and Zanzibar.

Material examined. 13 ♂♂, 7 ♀♀ in BMNH.

20c. *G. (A.) leonidas santamarthae* (Joicey & Talbot, 1927)

Principe Veined Swallowtail, Veined Swordtail, or Common Graphium (Fig. 222; map Fig. 137)

Papilio leonidas santa-marthae Joicey & Talbot, 1927: 12. HOLOTYPE ♂: SÃO TOMÉ & PRINCIPE: St. Principe, 2000ft (label data). BMNH Spec.Reg. no. 138400.
Papilio leonidas v. *santa-marthae* Joicey & Talbot; Bryk, 1930*b*: 567.
Papilio (Graphium) leonidas santa-marthae Joicey & Talbot; Peters, 1952: 20.
Graphium leonidas santamarthae Joicey & Talbot; D'Abrera, 1980: 46; d'Abrera, 1997: 54.
Graphium (Arisbe) leonidas santamarthae (Joicey & Talbot); Ackery, Smith & Vane-Wright, 1995: 164.

Type evaluations
Graphium leonidas santa-marthae Joicey & Talbot (1927) was described from '. . . one male.' '. . . collected by Mr. T. A. Barns during April and May, 1926, between 1500 and 2000 feet.' 'The types [of this and other taxa described] are now in the Hill Museum, Witley, Surrey' (Joicey & Talbot, 1927: 60). Much of the contents of the Hill Museum reached the BMNH as the Joicey Bequest, BMNH 1934–120, including the specimen described above.

Taxonomic status
Graphium leonidas santamarthae Joicey & Talbot (1927) was established as a subspecies from the island of Principe, and this status has been accepted by subsequent authors. We have only seen the holotype in which the pattern is very similar to *G. l. thomasius* from São Tomé, but it lacks the silvery wash characteristic of the latter subspecies. Given the relative isolation of the two islands from each other and from the mainland, subspecific status seems appropriate.

Similar subspecies. Upperside very similar to *G. l. thomasius*.

Diagnosis: pattern (Fig. 222)
It differs from the other races in the following: forewing discal cell with central mark larger, extending beyond the limits of cell M_3, very like *G. l. pelopidas*; forewing cell CuA_1 with well-marked, narrow, but elongate, post-discal mark; post-discal mark in hindwing cell CuA_1 not extended to fuse with discal; hindwing discal cell with dark tip with small pale mark.

In addition, the form of the post-discal mark is somewhat different, being broad near the base, before narrowing sharply basally to form a line along vein 1A.

Diagnosis: ♂ and ♀ genitalia; early stages; host plants; bionomics. See species account.

Distribution (Map Fig. 137). Only known from the island of Principe.

MATERIAL EXAMINED. The male holotype in BMNH only.

20d. ***G.* (*A.*) *leonidas thomasius*** (Le Cerf, 1924)

São Tomé Veined Swallowtail, Veined Swordtail, or Common Graphium (Fig. 223; map Fig. 137)

Papilio leonidas thomasius Le Cerf, 1924*b*: 137. HOLOTYPE ♀: SÃO TOMÉ & PRINCIPE: '. . . San Thome . . . ' (Le Cerf, 1924*b*: 138). MNHN.
Graphium leonidas thomasius Le Cerf; D'Abrera, 1980: 46, 47 (fig.).
Graphium (*Arisbe*) *leonidas thomasius* (Le Cerf); Ackery, Smith & Vane-Wright, 1995: 164.

LAPSUS
Graphium leonidas sanctithomae attrib. (Le Cerf); Pyrcz, 1992: 49.

TYPE EVALUATIONS
Papilio leonidas thomasius Le Cerf (1924) was described from 'Type : 1 ♀ , San Thome, Collection Muséum National de Paris.' The specimen concerned in MNHN is clearly labelled. A male specimen *ex* Hill Museum in BMNH (Spec.Reg. no. 137454) which was labelled as neallotype – probably by Le Cerf, who studied that collection – has no status in nomenclature.

TAXONOMIC STATUS
Described as a subspecies. Though very similar to *G. l. santamarthae*, which is known to us only from the holotype, the differences from that and from mainland specimens seem clear enough – and constant enough in the current taxon – to support that status.

DIAGNOSIS: PATTERN (Fig. 223)
The most striking difference shown by this race from all the others is a silvery 'wash' on the underside of the entire hindwing and apical and distal areas of the forewing, achieved by a covering of bluish-white scales.

Also differs from the nominate race in the following: post-discal mark of forewing cell CuA_2 extended along vein 1A towards base of wing; hindwing cells M_1 to CuA_1 with post-discal marks oblong, reaching (or almost so) the discocellular veins, that in CuA_1 thereby fusing with the discal mark. Like the nominate race, but unlike *G. l. pelopidas*, there is no marking in forewing cell 1A.

VARIATION
Only one specimen in BMNH has a post-discal mark in forewing cell CuA_1, and that very faint. In some females, the fusion between the hindwing cell CuA_1 discal and post-discal marks is not complete, giving a waisted appearance.

DIAGNOSIS: ♂ GENITALIA
Very similar to the nominate. The slight differences are:

Dorsal harpe slightly smaller, with fewer teeth (5 in the example examined, as compared with 7 in the nominate); *ventral harpe* with fewer 'fingers' (4 in the example examined, with the dorsal braoder than the rest, as compared with 6 in the nominate); *dorsal terminal process* slightly smaller than in the nominate, and with even finer denticulation; *ventral terminal process* broader based, but not as long.

DIAGNOSIS: ♀ GENITALIA. Not studied.

EARLY STAGES; HOST PLANTS. See species account.

DISTRIBUTION (Map Fig. 137). São Tomé and Principe: São Tomé.

BIONOMICS AND CONSERVATION STATUS
'The only species [of butterfly] apparently restricted to the dry primary vegetation is *Graphium leonidas sanctithomae* [*sic*]; therefore it should be considered as the most endangered butterfly species on the Sao Tomé island' (Pyrcz, 1991: 364).

MATERIAL EXAMINED. 4 ♂♂, 4 ♀♀ in BMNH. 1 ♂, 1 ♀ from other collections.

21. ***Graphium* (*Arisbe*) *levassori*** (Oberthür, 1890)

White Graphium (Fig. 194; map Fig. 140; genitalia Figs 39, 91)

Papilio Levassori Oberthür, 1890: 10, pl. 2, fig. 5. HOLOTYPE ♂: COMORO ISLANDS: Grande Comoro. 'Grande-Comore' (Oberthür, 1890: 10). BMNH – Spec.Reg. no. 136049.
Papilio Levassori Oberthür; Bryk, 1930*b*: 560.
Papilio (*Graphium*) *levassori* (Ob.); Peters, 1952: 21.
Graphium (*Arisbe*) *levassori* (Oberthür); Munroe, 1961: 42; Paulian & Viette, 1968: 19; Hancock, 1983: 46; Collins & Morris, 1985: 59, 222; Ackery, Smith & Vane-Wright, 1995: 164.
Graphium levassori Oberthür; D'Abrera, 1980: 44, 45 (fig.); d'Abrera, 1997: 52, 53 (fig.).

TYPE EVALUATIONS
Papilio Levassori Oberthür (1890) was described '. . . d'après us seul mâle . . . '. The specimen concerned, clearly labelled, reached the BMNH via the Levick Bequest (BMNH 1941–83). A female specimen *ex* Oberthür (Spec.Reg. no. 136050) which was given a BMNH 'type' label by an earlier curator is not part of the type series, having been collected by Humblot in 1894; it has now been labelled to this effect (by J.E. Pope, 1995). See also Paulian & Viette (1968: 19).

TAXONOMIC STATUS
Papilio Levassori Oberthür (1890) was established as a species, a status which, with its distinctive appearance and geographical isolation, has never been questioned.

SIMILAR SPECIES. Very distinctive. The only vaguely similar congener is *G. endochus*, from Madagascar.

Diagnosis: pattern (Fig. 194)

Upperside almost entirely creamy white, with narrow black borders along the costal and outer margins of the forewing and a slightly broader black outer margin of the hindwing. The forewing apex is also black. This pattern seems to be the result of expansion and fusion of the pale marks found in all relatives, as shown by the following details.

The **forewing** discal cell has a small suffusion of black scales opposite vein CuA_1. Forewing cell R_3 has a post-discal mark a little removed from the cell base and a small submarginal mark. In cell R_4 there is a post-discal mark in the cell base and a submarginal spot; veins R_3 to R_5 are black. Cell R_5 is white from the discocellular vein to near the margin. In cell M_1, however, a separate submarginal mark can be discerned, bounded proximally by a slightly diffuse arc of black scales. The remaining forewing cells are white with black margins; the veins are also white.

On the **hindwing**, submarginal marks can be discerned in cells R_1 and R_5. The black border is broader than on the forewing and appears wavy due both to it arcing proximad in each cell from M_2 to CuA_1, and to the presence of a marginal white mark in each cell.

This pattern is reflected on the **underside**, though the dark marking is much less intense. In addition, there is a brick red mark in the base of the **forewing** costal cell fading to the background colour distally. On the **hindwing** there is a black spot at the very base of the cells, surrounding the bases of the sub-costal, radial and cubital veins, and a pale orange shade surrounding the pre-costal vein.

Variation. Some slight variation in the extent of the dark areas.

Diagnosis: ♂ genitalia (Fig. 39)

Dorsal projection short and stout, though not expanded near tip, unlike *G. leonidas*. *Dorsal harpe* curved (though less markedly so than *G. leonidas*) with a few very stout teeth, some partly subdivided. *Ventral harpe* broad, the blade nearly vertical, the tip deeply serrate/palmate, with a complex pattern of teeth. *Dorsal terminal process* somewhat explanate dorsally, ventral tip acute and slightly serrate on dorsal and ventral edges. *Ventral terminal process* rounded, serrate and twisted so the anatomical mesal surface faces somewhat dorsad. *Uncus* shallow, *socii* prominent, with projections. *Saccus* short and broad. *Aedeagus* quite short and stout, slightly decurved, tapering distally; the tip extended and decurved.

Diagnosis: ♀ genitalia (Fig. 91)

BMNH Spec.Reg. No. 136050; vial 5444 -: *vestibulum* slightly bulbous; *ostium bursae* opening anteriorly; *ductus bursae* not sclerotized, kinked, constricted or pocketed; *central ostial lobe* elongate, narrow, laterally compressed, glabrous; *lateral ostial lobes* setose, broad, rounded at tip; *anterior apophyses* long; *papillae anales* rounded, with many peg-like setae.

Early stages. Apparently unknown.

Distribution (Map Fig. 140). Comoro Islands: Grande Comore only.

Host plants. The natural host(s) is apparently unknown. According to Collins & Morris (1985), *G. levassori* may now feed on cultivated Custard Apple, *Annona reticulata* (Annonaceae), but this appears to be speculation.

Bionomics

A rare endemic of Grande Comore, where it occurs in mid-montane forests (Collins & Morris, 1985), normally in the range of 500–1900 m. However, apparently seen occasionally at sea-level, so before destruction of the lower forests it may have occurred throughout the island. Viette (1980) records *levassori* on the wing at the beginning of heavy rains in April. Collins & Morris (1985) suggest that it may fly all year, but the great difficulty entomologists have had in locating this species could indicate a limited flight-period, perhaps Jan.–April. The idea that the butterfly has a short flight period is supported by Turlin (1994), who also notes that *G. levassori* exhibits strong convergence in pattern and colour with the Grande Comore endemic race of *Papilio dardanus* (*P. d. humbloti*), but is unsure if this could be a genuine case of mimicry.

Conservation status. Considered **Vulnerable** by Collins & Morris (1985: 59, 222).

Material examined. 4 ♂♂, 2 ♀♀ in BMNH. 2 ♂♂, 1 ♀ from other collections.

22. *Graphium (Arisbe) cyrnus* (Boisduval, 1836)

Madagascan Graphium (Figs 195, 224; map Figs 138, 139; genitalia Figs 40, 92)

This beautiful black and yellow butterfly is found throughout the island of Madagascar. We here follow Paulian & Viette (1968) in treating it as a pair of subspecies: one eastern (*G.* (*A.*) *c. cyrnus*); one western (*G.* (*A.*) *c. nuscyrus*), though with some doubts as to whether the differences observed are constant, reliable or of true taxonomic value.

Papilio cyrnus Boisduval (1836) was described simply from Madagascar, but the collector was given as Goudot. Paulian & Viette (1968) deduced that the specimens were caught during Goudot's second visit to the island and that the type locality should be restricted to the eastern coast of Madagascar, between Foulpointe (=Mahavelona, 17° 40' S 49° 30' E) and Tamatave (=Toamasina, 18° 10' S 49° 23' E).

Papilio cyrnus nuscyrus Suffert (1904) was described from a single individual from Mojange (=Majunga,

=Mahajanga, 15° 40' S 46° 20' E) on the North-West coast. Suffert (1904) distinguished it from the nominate race by its more extensive yellow markings. In particular, he noted that the post-discal marks in forewing bands M_3 to CuA_2 formed a single band contiguous with a small yellow post-discal mark in cell 1A. He also noted the main band in the forewing discal cell, opposite cell M_3, to be uninterrupted by 'intervenosae', and a small double mark in the proximal third of this cell. On the hindwing, Suffert (1904) noted a white apical mark in cell R_1, extending distad at the anterior and posterior tips (to form a chevron). On the forewing underside, he recorded a small double mark plus two separate marks in the basal third of the forewing cell, where he also noted that the reddish coloration reaches the posterior discocellular vein, unlike the nominate race, where it is confined to the costal half of the cell. All these features can be seen clearly in the holotype (Pl 8 fig. 224).

Paulian & Viette (1968) added that specimens are, on average, smaller than those of the nominate race, and that the colour of the markings is more vivid, though this latter point is hard to verify without comparing similarly aged specimens, preferably with a colorimeter.

In addition to the holotype, we have seen several specimens in MNHN and two in BMNH that closely fit this description. However, *G. cyrnus* shows considerable variation in the extent of its markings, and this is also true for those features described above and for those specimens identified as *G. c. nuscyrus*. For example, of three specimens in MNHN from Zombitsy, only one has a clear post-discal mark in forewing cell 1A; in only one (a different one) is the discal cell band undivided (and even here, the 'intervenosa' is visible within the band); and one specimen lacks marks at the base of the forewing discal cell and the apical mark in hindwing cell R_1. These features are also faint or lacking in several other specimens in MNHN identified as *G. c. nuscyrus*. Of the two specimens in BMNH most similar to the holotype of *G. c. nuscyrus*, one lacks marks in the base of the forewing cell, whose main band is interrupted, and the apical mark in hindwing cell is faint. Unfortunately neither of these specimens has a provenace more accurate than 'Madagascar'.

In addition, the diagnostic features listed by Suffert (1904) may occur singly or in combination in specimens from elsewhere within the island. For example, *G. c.* f. indiv. *adiecta* Storace (1953) has basal marks in the forewing discal cell, and *G. c.* f. indiv. *similis* Storace (1953) has the discal cell band complete. A specimen in BMNH (Spec.Reg. No. 136007) from Ambinanindrano, 50 km west of Mahanoro on the East coast, has basal marks in the forewing discal cell, the transverse band of that cell complete (on one wing) and prominent apical marks in hindwing cell R_1 (rare, but not unknown in other eastern specimens). Two specimens labelled as being from the Tananarive district (Spec.Reg. Nos 135970 and 135978) both have complete forewing discal cell bands, the former also has extensive marking in the basal area of that cell; the latter has distinct post-discal marks in forewing cell 1A.

Three specimens in BMNH (Spec.Reg. Nos 135949 to 135951) from Bejofo, one of the localities given for *nuscyrus* by Paulian & Viette (1968), while being quite extensively marked, are quite large, and lack basal marks in the forewing discal cell or post-discal marks in forewing cell 1A; furthermore in Nos 135949 and 135951, the forewing discal cell band is also interrupted; and, in 135951, the apical marks in hindwing cell R_1 are faint and subdivided. Indeed, were it not for their locality, it is doubtful if these specimens would have been separated from *c. cyrnus*. Moreover, many specimens in collections lack precise localities.

Overall, then, there seems room for doubt about the true status of *G. c. nuscyrus*. More specimens with accurate provenance are required: *cyrnus*-like material from *nuscyrus* localities (and *vice-versa*) would cast further doubt on its status. Live material would enable breeding experiments and could be used to test the possibility that environmental factors may affect pattern development. Fresh material would also permit DNA fingerprinting.

SIMILAR SPECIES

This species should not be confused with any other on Madagascar. In pattern, it is most similar to *G. leonidas*, but readily distinguished by its colour. It is similar in colour, and to an extent pattern, to *G. latreillianus* and *G. tynderaeus*, but details of both, as well as distribution, prevent misidentification.

DIAGNOSIS: PATTERN (Figs 195, 224)

See below for detailed description of *G. c. cyrnus*, and for distinguishing characters of *G. c. nuscyrus*.

VARIATION. See below.

DIAGNOSIS: GENITALIA (Fig. 40, 92)

See below. There is some variation in the size of some organs, e.g. the number of teeth on the dorsal and ventral harpe. This variation may be partially dependent on overall size.

EARLY STAGES; HOST PLANTS. Apparently unknown.

BIONOMICS

Little appears to have been recorded regarding the habits of this Madagascan endemic. Apparently it is widespread throughout most of the island, suggesting that it affects a range of habitats from savannah to woodland and forest. Paulian & Viette (1968) record specimens captured at heights from 640–1250 m., during Nov.–Mar.

CONSERVATION STATUS. 'Apparently common

throughout the island. Not known to be threatened' (Collins & Morris, 1985).

22a. *G. (A.) cyrnus cyrnus* (Boisduval, 1836)

Eastern Madagascan Graphium (Fig. 195; map Fig. 139; genitalia Figs 40, 92)

Papilio Cyrnus Boisduval, 1836: 239. LECTOTYPE ♂: MADAGASCAR: 'Pris à Madagascar par M. Goudot' (Boisduval, 1836: 240). BMNH Spec.Reg. No. 136044. Designated Paulian & Viette (1968: 15). PARALECTOTYPE ♂: same provenance. BMNH Spec.Reg. No. 136043. 2 PARALECTOTYPES: same provenance. MNHN (not seen).

Papilio cyrnus Boisduval, 1836; Bryk, 1930*b*: 558.

Papilio (*Graphium*) *cyrnus* Boisduval; Peters, 1952: 20.

Graphium (*Arisbe*) *cyrnus* Boisduval; Munroe, 1961: 42; Paulian & Viette, 1968: 15; Hancock, 1983: 46; Collins & Morris, 1985: 58; Ackery, Smith & Vane-Wright, 1995: 162.

Graphium cyrnus Boisduval; D'Abrera, 1980: 42, 43 (figs); d'Abrera, 1997: 50, 51 (figs).

UNAVAILABLE NAMES

Graphium cyrnus forma individuale *similis* Storace, 1953: 260. MADAGASCAR. ?MCSN (not seen) [infrasubspecific].

Graphium cyrnus forma individuale *adiecta* Storace, 1953: 260. MADAGASCAR. ?MCSN (not seen) [infrasubspecific].

TYPE EVALUATIONS

Papilio cyrnus Boisduval (1836) was described from '. . . quatre individus mâles et femelles. Pris à Madagascar par M. Goudot. – Coll. Boisd. et Coll. Lacordaire.' According to Horn *et al.* (1990), Boisduval's collection went to Oberthür and Lacordaire's to MNHN, whereas part of Goudot's collection went to MNHN, part to MNHU. Oberthür's collection reached BMNH via the Levick bequest (BMNH accession number1941–83). Paulian & Viette (1968) designated as lectotype a specimen from the Oberthür collection, *ex* Boisduval and carrying a rectangular label printed 'Typicum/ Specimen' in red and with a red border. It also has a typical Oberthür collection label including the phrase 'Specimina typica'. Unfortunately, there is no positive indication that it was collected by Goudot. A further male from the Oberthür collection, *ex* Boisduval in BMNH could be regarded as paralectotype.

TAXONOMIC STATUS

Papilio cyrnus Boisduval (1836) was established as a species. The status of *G. cyrnus* as a species has been accepted since; only whether it is mono- or bi-typic has been the subject of debate.

DIAGNOSIS: PATTERN (FIG. 195)

Upperside very dark brown with bright yellow markings. **Forewing** discal cell with transverse mark opposite cell M_3, usually interrupted by one or more intervenosae. A further round mark in cell opposite cell R_5, with a neighbouring white mark in the costal area [cell R_1]. Cell R_3 with discal, post-discal and submarginal marks. Cell R_4 with post-discal mark in the angle of R_4 and R_5, and a submarginal mark. Cell R_5 with a post-discal mark before origin of R_4, and a submarginal. Cell M_1 with post-discal mark, sometimes faint, and a submarginal. Cells M_2 to CuA_2 with post-discal and entire submarginal marks, both sets increasing in size posteriorly. The post-discals in cells M_2 to CuA_1 elliptical, not reaching surrounding veins; that in CuA_2 reaching veins CuA_2, 1A and the cubital vein, and extended to the cell base. The submarginal in CuA_2 slightly subdivided on the proximal margin. Cell 1A devoid of marking.

Mark in **hindwing** discal cell not reaching much beyond origins of veins R_5 and CuA_2, the remainder of the cell dark. Cell R_1 with a white post-discal mark and a faint, diffuse, divided submarginal. Cell R_5 with a relatively large post-discal mark, extending beyond that in the discal cell, and a submarginal mark. Cell M_1 usually without a post-discal mark, but with a submarginal. Cells M_2 to CuA_1 with quadrate submarginal marks and submarginals. The submarginal marks in cells M_1 to CuA_1 are partially subdivided by the intervenosae on their distal margins. The hindwing margins are scalloped between the veins, the effect heightened by the presence of small, white marginal marks.

The **underside** pattern reflects that of the upperside, but both the ground colour and markings are paler. The costal and distal margin of the forewing have a very narrow black border, as does the distal margin of the hindwing between the marginal marks.

The sub-costal and radial veins of the **hindwing**, and their immediate vicinty are usually pinkish-red, and this colour also occurs in the subcostal cell proximal to the precostal vein (distal to it is yellow) the basal area of cell R_1 as far as the post-discal mark, along the posterior margin of the wing, along the intervenosae of cells R_1 and R_5, and in the forewing in the costal half of the discal cell as far as the transverse mark, gradually fading towards the wing apex (it is still detectable on veins R_4 and R_5). Post-discal and submarginal marks are visible in hindwing cell CuA_2, as well as a discal mark in cell CuA_1.

The hindwing underside also has an array of black marks similar to that seen in *G. latreillianus*, but lacking in *G. leonidas*. In *G. cyrnus* the marks are proximal to the submarginal marks in each cell (between the submarginal and post-discal marks), proximal to the post-discal marks in cells M_1 to CuA_1, bordering the precostal vein proximally and in the distal part of the discal cell. This is additional to the mark at the base of the hindwing.

VARIATION

G. cyrnus is at least as variable as its congeners in the relative size of its markings and the presence and absence of some of them. The variability is discussed above in respect of subspecies separation.

Other variants include:

Distal mark of forewing discal cell with a dark mark, either on its costal edge or internally.

Forewing cell R_3 with discal and post-discal marks touching or even fused.

Forewing cell M_1 with small post-discal mark.

Forewing cell CuA_2 with submarginal mark subdivided by intervenosa.

Hindwing cell M_1 with post-discal mark.

Hindwing cell CuA_1 with discal mark.

Hindwing underside with black mark in discal cell small and divided into two.

Hindwing underside discal cell with small black mark opposite cell R_5.

Hindwing underside costal cell with small black and/or red mark just distal to precostal vein.

Hindwing underside cell R_1 with prominent black stripe in red area basal to post-discal mark.

Hindwing underside cell R_5 with a black mark proximal to, or surrounded by, post-discal mark.

DIAGNOSIS: ♂ GENITALIA (Fig. 40)

Dorsal projection short and stout, curved slightly dorsad and posteriad at tip. *Dorsal harpe* acutely recurved and strongly serrate, with 6 to 10 or more teeth. *Ventral harpe* broad, vertical and with 3 or 4 strong teeth. *Dorsal terminal process* expanded dorsally and curved mesad; the tip finely serrate on both edges. *Ventral terminal process* large, rounded and serrate and leading into an expanded ventral marginal area. *Uncus* rounded, *socii* with long projections. *Saccus* quite elongate. *Aedeagus* short, stout.

DIAGNOSIS: ♀ GENITALIA (Fig. 92)

BMNH Spec.Reg. No. 136014; vial 3987 -: *vestibulum* slightly bulbous (see *latreillianus* and *tynderaeus*); *ostium bursae* opening anteriorly; *ductus bursae* not sclerotized, kinked, constricted or pocketed; *central ostial lobe* long, broad, rounded-triangular setose; *lateral ostial lobes* setose, quite long, nearly quadrate, well-separated (quite narrow); *anterior apophyses* long; *papillae anales* rounded, with many peg-like setae.

EARLY STAGES; HOST PLANTS. Apparently unknown.

DISTRIBUTION (Map Fig. 139). Madagascar. If its subspecific status is recognized, confined to the eastern half.

BIONOMICS. See species account.

MATERIAL EXAMINED. 141 ♂♂, 16 ♀♀ in BMNH. 34 ♂♂, 1 ♀ from other collections.

22b. *G. (A.) cyrnus nuscyrus* (Suffert, 1904)

Western Madagascan Graphium (Fig. 224; map Fig. 138)

Papilio cyrnus nuscyrus Suffert, 1904: 104. HOLOTYPE ♂: MADAGASCAR: '. . . Mojange . . . '. MNHU 'Coll. kön. zool. Museum, Berlin.' (Suffert, 1904: 104).

Papilio cyrnus ab. *nuscyrus* Suffert; Aurivillius, 1908: 22; Bryk, 1930*b*: 558; Peters, 1952: 20.

Papilio cyrnus ab. (?) *nuscyrus* Suffert; Aurivillius, 1909: 331.

Graphium (Arisbe) cyrnus nuscyrus Suffert; Paulian & Viette, 1968: 18

Graphium (Arisbe) cyrnus =nuscyrus Suffert; Ackery, Smith & Vane-Wright, 1995: 162.

Graphium cyrnus =nuscyrus Suffert; d'Abrera, 1997: 50.

TYPE EVALUATIONS

Papilio cyrnus nuscyrus Suffert (1904) was described from 'Ein männliches Exemplar' in 'Coll. kön. zool. Museum, Berlin.' [MNHU] (Suffert, 1904), where it is clearly labelled. Those labels include an orange, printed 'Typus' label; Suffert's hand-written type determination label; a locality label giving the collection date of '6.12.91' and with 'A. Voeltzkow s.g.' apparently added later [the ink and possibly handwriting are different]; a printed collection number of 77684. CRS has added a handwritten determination label stating its holotype status.

TAXONOMIC STATUS

Papilio cyrnus nuscyrus Suffert (1904) was established as a subspecies. Aurivillius (1908, 1909) treated it as an aberration (1908), or possibly so (1909), though in the later work stated that he had not seen it. Bryk (1930) and Peters (1952) followed Aurivillius; Carcasson (1981) followed Peters and did not include it in his checklist; Ackery *et al.* (1995) followed Carcasson. By contrast, Paulian & Viette (1968) gave supporting evidence for its subspecific status. Here we follow them, but with the caveats listed above.

DIAGNOSIS: PATTERN (FIG. 224)

Apparently distinguished from the nominate race by:

small double basal mark usually present in forewing discal cell. These marks are more apparent on the underside;

transverse band of forewing discal cell not usually subdivided by intervenosae; in *G. c. cyrnus* f. *similis* Storace (1953), it is also undivided;

post-discal marks of forewing cells M_3, CuA_1 and CuA_2 expanded to form a band interrupted only by the veins;

forewing cell 1A usually with a green post-discal mark 3 mm long x 1·5 mm broad lying along the vein;

hindwing cell R_1 usually with a prominent white submarginal mark, deeply cleft distally (the expression of this feature is very variable: it is almost obsolete in some specimens);

forewing underside discal cell with brick red coloration sometimes extending across most of the cell width.

VARIATION. See above and in species introduction.

DIAGNOSIS: ♂ GENITALIA
Very similar to the nominate race. Of the two specimens in BMNH very similar to the holotype, one (Spec.Reg. No. 135975) has only 5 teeth on the dorsal harpe and 2 (one slightly bifid) on the ventral harpe; the other (Spec.Reg. No. 135974) has 10 on the dorsal harpe and 4 on the dorsal. A BMNH specimen from Bejofo (Spec.Reg. No. 135949) has 8 teeth on the dorsal harpe; 4 (3 slightly bifid) on the ventral.

DIAGNOSIS: ♀ GENITALIA. None seen.

EARLY STAGES; HOST PLANTS. Apparently unknown.

DISTRIBUTION (Map Fig. 138). Western Madagascar.

BIONOMICS; CONSERVATION STATUS. See species account.

MATERIAL EXAMINED. 2 ♂♂ (+3 very dubious) in BMNH. 19 ♂♂ (some dubious) from other collections.

23–24 *The tynderaeus clade*

Two species – the monotypic *G. tynderaeus* (Fabricius) and bitypic *G. latreillianus* (Godart) – with elongate forewings, tailless hindwings, striking upperside patterns of bright yellow or citrus markings on dark wings, and intricate underside patterns. The pair, both found in the lowland forests of West and Central Africa were recognized as a group by Berger (1951) and Hancock (1993), and form a robust monophyletic clade in our analyses. They are united by having the dorsal harpe of the male valve horizontal and deeply bifid – an apparent synapomorphy. The almost identical pattern of black marks on the underside may also link the two. The clade is part of the polytomy that forms the crown group in our analyses.

23. *Graphium (Arisbe) tynderaeus* (Fabricius, 1793)

Green Graphium, Green-spotted Graphium, or Green-spotted Swallowtail (Fig. 196; map Fig. 136; genitalia Figs 41, 93)

Papilio tynderaeus Jones, MS, pl. 57 fig.1

Papilio tynderaeus Fabricius, 1793: 35. TYPE: 'Habitat —— Mus. Dom. Drury' (Fabricius, 1793: 35). ?AMSA. (not seen).

Papilio tyndaraeus Fabricius; Godart, [1819]: 45. (incorrect subsequent spelling).

Papilio tynderaeus Fabricius; Aurivillius, 1899: 482; Aurivillius, 1908: 22, pl. 7(a); Bryk, 1930*b*: 558.

Papilio (Graphium) tynderaeus Fabricius; Peters, 1952: 20.

Graphium tynderaeus Fabricius; Berger, 1950: 66, figs 66, 67; D'Abrera, 1980: 40, 41 (figs); Berger, 1981: 49, pl.13 figs 5 (♀), 6 (♂); Kielland, 1990: 49; d'Abrera, 1997: 48, 49 (figs).

Graphium (Arisbe) tyndaraeus [*sic*] Fabricius; Munroe, 1961: 42. (incorrect subsequent spelling).

Graphium (Arisbe) tynderaeus Fabricius; Hancock, 1983: 46; Collins & Morris, 1985: 59; Ackery, Smith & Vane-Wright, 1995: 166.

SYNONYMS

Papilio nausinous Godart, [1819]: 17, 45. TYPE ♂: 'Afrique.' (Godart, [1819]: 45). [?] MNHN (not seen).

Papilio tynderaeus =nausinous Godart; Boisduval, 1836: 242; Bryk, 1930*b*: 559.

Graphium (Arisbe) tynderaeus =nausinous Godart; Ackery, Smith & Vane-Wright, 1995: 166.

Papilio tynderaeus var. *ochrea* Capronnier, 1889: cxix. HOLOTYPE ♂: ZAIRE: 'Lopori Strand, 13 fév. 1887. Cap. Martini' (Capronnier, 1889: cxix). IRSN (not seen).

Papilio tynderaeus 'ab. (artific.)' *ochrea* Capronnier; Aurivillius, 1899: 482.

Graphium (Arisbe) tynderaeus =ochrea Capronnier; Ackery, Smith & Vane-Wright, 1995: 166.

UNAVAILABLE NAMES

Papilio tynderaeus ab. *fraudatus* Gaede, 1916: 105. CAMEROON. MNHU. (not seen) [infrasubspecific].

Papilio tynderaeus ab. *incompleta* Dufrane, 1936: 42. ZAIRE. IRSN. [infrasubspecific.]

Graphium tynderaeus ab. *confluens* Berger, 1950: 67. ZAIRE. MRAC. [infrasubspecific.]

TYPE EVALUATIONS
Papilio tynderaeus Fabricius (1793) was described from a specimen or specimens in Dru Drury's collection, which was broken up and sold at auction after his death. Part of it was bought by Alexander McLeay and taken to Australia where it became part of the Australian Museum, Sydney, which McLeay established (See van Leeuwen, 1997). We do not know at present whether the type of *Papilio tynderaeus* survives there or elsewhere. Fortunately, the specimen was well illustrated by Jones, whose 'Icones' survive in OXUM; plate 57 shows a butterfly clearly recognisable as *G. tynderaeus*.

Godart, ([1819]: 45) gave no indication of series length in his description of *Papilio nausinous*. CRS did not find any type candidates during a visit to MNHN in 1997.

The text makes it clear that *Papilio tynderaeus* var.

ochrea Capronnier (1889) was described from a single individual, part of a donation to IRSN. CRS did not find any type candidates during a brief visit to IRSN in 1996.

TAXONOMIC STATUS

Papilio tynderaeus Fabricius (1793) was established as a species, a status accepted by authors subsequently.

Although Godart ([1819]) was aware of *P. tynderaeus* Fabricius – it is the next taxon discussed by him (with the name unnecessarily emended to '*tyndaraeus*') – he was unable sufficiently to identify it from Fabricius' (1793) description, as Boisduval (1836) discussed when synonymising the two.

It is not clear whether Capronnier (1889) intended *Papilio tynderaeus* var. *ochrea* to be subspecific or infrasubspecific in rank and so must be treated as the former under the Code (ICZN, 1999: Article 45.6.4). Aurivillius (1899) considered it to be an artificial aberration ('colore humore mutato!' – with colour changed by moisture). We can find no further mention of this nominal taxon until Ackery *et al.* (1995).

SIMILAR SPECIES. Most similar to *G. latreillianus* (Godart), but unlikely to be confused with it.

DIAGNOSIS: PATTERN (Fig. 196)

Distinguished from *G. latreillianus* by the shape of the hind wing margins, which are deeply scalloped between the veins in *G. tynderaeus*, more-or-less smoothly convex in *G. latreillianus*. The **forewings** are accuminate with a pronounced narrowing in the region of vein M$_1$. **Upperside** with ground colour dark-brown to almost black with prominent pale marks which are normally lemon yellow to lime green. In the forewing discal cell there are large marks (or clusters with various degrees of fusion – see below) opposite cells M$_2$ and M$_1$, and (usually) smaller spots opposite cells R$_5$ and vein CuA$_2$; in *G. latreillianus* there is just one group of marks, opposite cells M$_2$ and M$_3$.

In cell R$_3$ there is a small discal spot; a larger post-discal mark, distal to the root of vein R$_4$; and a subdivided submarginal mark. Cell R$_4$ has a post-discal and a subdivided submarginal mark. Cell R$_5$ has a large, roughly rhomboid, proximal mark (probably fused discal and post-discal marks); and a subdivided submarginal mark. Cell M$_1$ usually (see below) lacks a post-discal mark, but includes a subdivided submarginal mark. In cell M$_2$ the post-discal mark is nearly square; the submarginal mark subdivided. The post-discal mark in cell M$_3$ is roughly triangular, two sides being aligned with (but not touching) vein CuA$_1$ and the posterior discocellular vein; the elements of the subdivided submarginal mark are angled towards the midline proximally. The post-discal mark in cell CuA$_1$ is roughly elliptical; it touches vein CuA$_2$, but not vein CuA$_1$ nor the posterior discocellular vein; the elements of the subdivided submarginal mark are angled towards the midline proximally. In cell CuA$_2$, the post-discal mark is large and nearly rectangular, though concave distally; it does not quite reach the posterior discocellular vein, but does reach vein CuA$_2$ and is contiguous with that in cell 1A along vein 1A; there is neither basal nor discal band; and only the anterior element of the submarginal mark present. Cell 1A has just the post-discal mark, which is contiguous with that in cell CuA$_2$.

The **hindwing** discal cell band does not reach the root of vein R$_5$ anteriorly, and barely beyond the root of vein CuA$_2$ posteriorly. Cell R$_1$ has a transverse, white post-discal band and, at most, a very faint, subdivided submarginal mark. Cell R$_5$ lacks a post-discal mark; the submarginal mark is large and deeply indented distally (almost bifid), with the anterior element being the larger. Cells M$_1$ and M$_2$ both just have subdivided submarginal marks, the anterior element being the larger in each cell. Cells M$_3$ and CuA$_1$ each have larger marks, deeply indented distally, which are probably fused post-discal and submarginal marks. Cell CuA$_2$ has a discal band of lemon yellow overlaid with white scales in the posterior half of the cell in the males only.

The **underside** pattern largely reflects the pattern of the upperside, but the marks and ground colour are both paler, so the contrast is less marked. The ground colour is itself patchy, adding to the complexity of the pattern. On the **forewing**, in cells M$_2$ to 1A, from the bases of the cells to the line of the submarginal marks, it is quite dark, nearly as dark as the upper side. There are also dark marks just distal to the post-discal marks of cells R$_3$ to R$_5$; in the base of cell R$_4$ and between the intervenosae of cells R$_3$ and R$_4$. In the discal cell, the intervenosae are dark, as is the base of the cell and the area adjacent ot the posterior discocellular vein. The remainder of the ground colour is paler, almost mauve in hue. On the **hindwing**, the ground colour is mainly dark, with paler streaks extending proximad from the margins towards the submargianl marks. The pattern is further complicated bay an array of black spots. In the discal cell there is a small one basal to the pale band one distal to the band oppossite cell R$_5$ and another opposite cell M$_1$, this latter being crossed by a silvery, narrow, zigzag line or chevron. In the costal cell, there are also three spots: one basal to the precostal vein, one in the angle of the precostal vein and the third just proximal to the discal band. In cell R$_1$ there is a small spot just basal to the discal band, another just distal to it and a third between the latter and the submarginal area; the latter 2 are separated by a mauve transverse band. In cells R$_5$ to M$_2$ there are two spots, separated by a mauve band, proximal to the submarginal mark; these are more or less fused in cell M$_1$. In cell M$_3$ there is a spot proximal to the post-discal/submarginal mark. In cell CuA$_1$ there is a small mark, crossed by a narrow silvery line or chevron; a mauve mark distal to it; and a small gap before the post-discal/submarginal mark.

In cell CuA_2, there is a black spot proximal to the discal band, and two mauve marks distal to it.

The underside of the abdomen and sometimes the hairs of the anal wing margin are suffused with red.

VARIATION

The colour of the pale marks can vary between a matt yellow to a vivid lime green. In other specimens these marks may be orange to copper-coloured, as in var. *ochrea*, possibly due to the effect of chemicals.

There is considerable variation in the presence and fusion of the pale marks. Usually this is associated with the overall extent of the markings, but is occasionally contrary: a generally broadly marked specimen may lack a particular mark, and *vice versa*. Variants we have seen include:

the spot in the forewing discal cell opposite vein CuA_2 varies from absent (ab. *incompleta* Dufrane) to a band of partly fused spots reaching across most of the cell;

the forewing discal cell marking opposite cell M_3 may be partly subdivided by 'intervenosae';

the forewing discal cell marking opposite cell M_2 usually consists of a larger costal element and a smaller medial one, but these may fuse;

there is sometimes fusion between the costal parts of the forewing discal cell marks opposite cells M_2 and M_3; in ab. *confluens* Berger, these marks are almost completely fused;

a spot in the forewing discal cell opposite cell R_5 is usually present, but may be absent;

the discal mark in forewing cell R_3 is occasionally absent;

in one female in BMNH, the discal mark in forewing cell R_3 is present, but the post-discal is absent;

there is rarely a small post-discal mark in forewing cell M_1;

there may be some fusion between the subunits of the hindwing cell R_5 submarginal mark;

there is occasionally a small discal mark in hindwing cell CuA_1 in the angle of the cubital vein and vein CuA_2.

There appears to be no geographical pattern to this variation.

DIAGNOSIS: ♂ GENITALIA (FIG. 41)

Dorsal projection elongate, thin, angled ventrad basally, becoming horizontal distally, angled posteriad. *Dorsal harpe* elongate, horizontal, smooth, biramous, with both elements pointed; the exterior arm longer, curving mesad; the inner arm angled mesad. *Ventral harpe* long, broad, bifid, with both elements pointed, angled mesad and non-serrate. *Dorsal terminal process* curved mesad; dorsal edge convex, slightly denticulate; ventrally angle moderately acute; ventral edge denticulate. *Ventral terminal process* small, denticulate. *Uncus* curved ventrad dorsally. *Socii* with projections. *Saccus* quite long and deep. *Aedeagus* straight, no indication of denticulation.

Though linked with *G. latreillianus* by the possession of a horizontal, bifid dorsal harpe, many features readily distinguish the two. The overall shape of valve is much more elongate. The long, thin dorsal projection contrasts with that in *G. latreillianus* which is short and stout, though the orientation is similar. The dorsal harpe is also much longer than in *G. latreillianus*. The ventral harpe is deeply bifid – unlike *G. latreillianus*.

DIAGNOSIS: ♀ GENITALIA (FIG. 93)

BMNH Spec.Reg. No. 139223; vial 3981: similar to *G. latreillianus*: *vestibulum* somewhat bulbous; *ostium bursae* opening anteriorly; *ductus bursae* not sclerotized distally, and not noticeably kinked, constricted or pocketed; *central ostial lobe* very broadly based, bifid, clearly setose; *lateral ostial lobes* small, but quite broad and rugose, not well sclerotized, but with setae visible; *anterior apophyses* present; *papillae anales* slightly extended, but rounded.

The vestibulum of *latreillianus* and *tynderaeus* also seems very similar, projecting slightly from the body.

EARLY STAGES; HOST PLANTS. Apparently unknown.

DISTRIBUTION (Map Fig. 136)

Guinea, Sierra Leone, Liberia, Ivory Coast, Ghana, Togo, {Benin}, Nigeria, Cameroon, Equatorial Guinea (Rio Muni), Central African Republic, Gabon, Congo, Democratic Republic of Congo (Berger, 1981, notes all Democratic Republic of Congo except S. Lualaba and Haut-Shaba), Angola, Sudan, western Tanzania.

BIONOMICS

This distinctive and beautiful forest butterfly is monotypic. Larsen (In prep.*a*, quoting Schultze, 1917*b*) regards it as the fastest among all African Papilionidae. In some contrast, Birket-Smith (1960) says 'they are not very shy, but fly very steadily'! Relatively rare, this species is usually encountered as single individuals in dense lowland forest, gallery forests (Fontaine, 1985: 116), often along streams (e.g. Darge, 1995), sometimes at water on forest tracks or 'sucking moisture in sunshine at nitrogenous spots on the river banks' (Birket-Smith, 1960), or other places in the sun where they can feed from urine patches or mammal dung (Owen & Owen, 1972). However, it has been seen in secondary forest, and Kielland (1990) reports a specimen from the Kigoma District of Tanzania found 'in rather open, montane vegetation near a riverine forest', at 1450m, with another sighted in a 'vegetable garden' nearby. Larsen (*op. cit.*) gives records for all months except October and November. Berger (1950) lists many specimens from Democratic Republic of Congo, with records for all months; the females are rarely seen.

CONVERSATION STATUS. 'Widely distributed, not uncommon and no threats recognized' (Collins and Morris, 1985: 59).

MATERIAL EXAMINED. 228 ♂♂; 5 ♀♀ in BMNH. 183 ♂♂ from other collections.

24. *Graphium (Arisbe) latreillianus* (Godart, [1819])

Olive Graphium or Coppery Swallowtail (Figs 197, 225; map Figs 134, 135; genitalia Figs 42, 94)

A distinctive species of lowland forest from West and central Africa. There are two allopatric subspecies, *G. l. latreillianus* found west of Dahomey Gap from Sierra Leone to Benin; and *G. l. theorini* from the Niger Delta and Cameroon to western Uganda and south to Angola. They are sufficiently similar to allow a general description to be given below, with their differences pointed out in the subspecific accounts.

SIMILAR SPECIES

Distinctive, but most similar to *G. tynderaeus* (F.). It may be distinguished from the latter by the less acuminate forewings, less scallopped hindwings, and by details of pattern. The forewing post-discal spots are more elliptical than in *G. tynderaeus*, and submarginal marks (where present) are bifid, with the elements linear and parallel.

DIAGNOSIS: PATTERN (Figs 197, 225)

Upperside ground colour dark brown with matt yellow markings (very pale in females).

Forewings only slightly narrowed around vein M$_1$. Apart from an occasional small spot opposite cell R$_5$, the only marks in the forewing discal cell are gouped opposite cells M$_2$ and M$_3$ and consist of one or two longitudinal marks by the medial vein usually with smaller marks costally (the precise pattern depending on subspecies and individual variation, see below). Cell R$_3$ with axillary mark extending beyond root of vein R$_4$ (possibly a fused discal and post-discal mark). Cell R$_4$ with axillary post-discal mark. Cell R$_5$ with a quadrate mark near base of cell almost reaching, or just surpassing (*G. l. latreillianus*), or clearly surpassing (*G. l. theorini*) the root of vein R$_4$ and indented distally. Cell M$_1$ usually with a very small and faint post-discal mark. Cells M$_2$ and M$_3$ each with a quadrate post-discal mark, indented distally, more-or-less touching the posterior discocellular vein, but not, or barely reaching the veins anterior and posterior to it. The post-discal mark in cell CuA$_1$ is more elliptical, not touching vein CuA$_1$ and not, or barely reaching vein CuA$_2$ of the posterior discocellular vein. In cell CuA$_1$, the post-discal mark is again quadrate, but does not reach the posterior discocellular vein.

Unlike *G. tynderaeus* the **hindwing** margins are convex, not scalloped between vein M$_2$ and CuA$_2$.

The discal cell band is narrow, barely surpassing the roots of veins R$_5$ and CuA$_2$. Cell R$_1$ has a transverse post-discal band of white scales, which may 'spill' into the discal cell and the axillary area of cell R$_5$. Cells R$_5$ to CuA$_1$ each have paired elongate markings on either side of the intervenosa. These are presumably the submarginal marks, possibly fused with post-discal marks in cells M$_2$ and M$_3$. In cell CuA$_2$ there is a transverse discal band, contiguous with that in the discal cell, but extending further distally; in the anterior part of the cell it is yellowish, but becomes white posteriorly.

The **underside** reflects the pattern of the upperside, but the ground colour and markings are paler. In the **forewing** cells R$_3$ to CuA$_1$, and in the discal cell at the level of the transverse markings, there is a nacreous effect of reflective scales on the dark ground (less marked in *G. l. theorini*); the intervenosae are well marked. The wings are generally paler than in *G. tynderaeus*, giving much greater prominence on the **hindwings** to the array of black spots, the number and disposition of which is similar. In the discal cell there is one just basal to the cell band; a second just distal to it in the anterior part of the cell; and a third, larger one in the apex of the cell. This is longitudinally subdivided by a (pale) intervenosa, and is crossed transversely by a sinuate silvery line. The costal cell includes a spot just proximal to the precostal vein, a second in the angle of that vein, and a third just distal to the post-discal band. Cell R$_1$ also has three spots: one just distal to the post-discal band; one central within it; and one distal to it. Cells R$_5$ to CuA$_1$ each have two spots proximal to the submarginal (+post-discal) marks, in each case, the proximal spot being the larger. In cell CuA$_1$, this proximal spot is crossed by a transverse sinuate silvery line or chevron. Cell CuA$_2$ has a spot proximal to the cell band; another just distal to it, crossed transversely by a sinuate silvery line or chevron; and a small spot distal to that.

DIAGNOSIS: ♂ GENITALIA (Fig. 42)

Dorsal projection short, stout, angled ventrad basally, becoming horizontal distally, angled posteriad. *Dorsal harpe* horizontal, biramous, with both elements pointed; the exterior arm slightly longer, curving mesad, serrate dorsally; the inner arm angled mesad. *Ventral harpe* elongate, uniramous with blade almost vertical, slightly concave, curving mesad to a sharp tip. *Dorsal terminal process* curved mesad; dorsal edge strongly convex, slightly denticulate; ventrally angle serrate; ventral edge denticulate. *Ventral terminal process* small, serrate. *Uncus* rounded. *Socii* prominent, with prominent projections. *Saccus* short. *Aedeagus* short, slightly expanded dorsally near tip; tip extended.

Linked to *G. tynderaeus* by the possession of a horizontal, bifid dorsal harpe, but with many distinguishing features. The overall shape is much more quadrate, not elongated and tapering. The dorsal projection is short and thick, unlike *G. tynderaeus*. The dorsal harpe much shorter than in *G. tynderaeus*, and serrate on its upper edge. The ventral harpe is uniramous unlike *G. tynderaeus*.

DIAGNOSIS: ♀ GENITALIA (Fig. 94)
BMNH Spec.Reg. No. 140700; vial 3980 (*l. latreillianus*): similar to *G. tynderaeus*: *vestibulum* somewhat bulbous; *ostium bursae* opening anteriorly; *ductus bursae* not sclerotized distally, and not noticeably kinked, constricted or pocketed; *central ostial lobe* broad, bifid, sparsely and minutely setose; *lateral ostial lobes* small, broad, lightly sclerotized, setose; *anterior apophyses* present; *papillae anales* slightly extended, but rounded.

EARLY STAGES; HOST PLANTS. Apparently unknown.

DISTRIBUTION. See subspecies accounts.

BIONOMICS
The Olive Graphium occurs in two subspecies, *G. l. latreillianus* and *G. l. theorini*. This is another distinctive and rapid-flying species, found in primary and secondary lowland forests (Owen & Owen, 1972; Emmel & Larsen, 1997), although it apparently does sometimes occur in quite open country (Larsen MSa). Often thought to be quite rare, but may be as frequent as *G. tynderaeus*, and even quite common at wet spots, such as river banks or muddy puddles (Larsen, pers. comm., notes it as 'common at water, with Pieridae'). Owen & Owen (1972) record it at patches of urine beside streams, and that its behaviour is generally very similar to *G. tynderaeus* (cf. Darge, 1995). Larsen (In prep.*a*) has records for Jan., Mar., Apr., Aug., Oct., Nov. and Dec. For Democratic Republic of Congo, Berger (1950) gives records for all months except June.

CONSERVATION STATUS. 'Not threatened' (Collins and Morris, 1985: 59).

24a. *G. (A.) latreillanus latreillianus* (Godart, [1819])

West African Olive Graphium or Coppery Swallowtail (Fig. 197; map Fig. 135; genitalia Figs 42, 94)

Papilio latreillianus Godart, [1819]: 17, 44. TYPE ♂: [WEST AFRICA]: 'De l'Afrique.' (Godart, [1819]: 45). [?] MNHN (not seen).

Papilio latreillanus Godart; Aurivillius, 1881: 44; Capronnier, 1889: cxix. Incorrect subsequent spellings.

Papilio latreillianus latreillianus Godart; Aurivillius, 1908: 22, pl. 3(d).

Papilio latreillianus Godart; Bryk, 1930*b*: 559.

Papilio (Graphium) latreillianus latreillianus (Gt.); Peters, 1952: 20.

Graphium (Arisbe) latreillianus (Godart); Munroe, 1961: 42; Hancock, 1983: 46; Collins & Morris, 1985: 59.

Graphium latreillianus latreillianus Godart; D'Abrera, 1980: 40, 41 (fig.).

Graphium (Arisbe) latreillianus latreillianus (Godart); Ackery, Smith & Vane-Wright, 1995: 163.

SYNONYM

Papilio potamonianus Ehrmann, 1909: 86. HOLOTYPE ♂: [? LIBERIA] (Holland, 1927: 314): 'Upper Congo, W. Africa' (Ehrmann, 1909: 86). CMNH (Holland, 1927: 314) (photographed I.J. Kitching, xii 1998).

Papilio latreillanus [sic] =*potamonianus* Ehrmann; Holland, 1927: 314.

Papilio latreillianus [*latreillianus*] =*potamonianus* Ehrmann; Bryk, 1930*b*: 559.

Graphium (Arisbe) latreillianus theorini =*potamonianus* Ehrmann; Ackery, Smith & Vane-Wright, 1995: 163.

TYPE EVALUATIONS
Godart ([1819]: 45) gave no indication of series length in his description of *Papilio latreillianus*, but it is evident from the text that more than one (possibly several) specimens were involved. CRS was unable to locate material that could be part of the type series during a visit to MNHN in 1997.

Papilio potamonianus Ehrmann (1909) was described from single individual, which was bequeathed to the CMNH (Holland, 1927). Our colleague I.J. Kitching was able to find and photograph this specimen in CMNH. It is very elaborately labelled by Ehrmann and later curators.

TAXONOMIC STATUS
Papilio latreillianus Godart, ([1819]: 45) was established as a species. With the establishment of *P. l.* var. *theorini* Aurivillius (1881), this status became modified to be the nominate race of a bitypic species This status has been accepted by subsequent authors. Further efforts to locate type specimens could confirm the subspecific identity of the taxon, though there are indications in the text (e.g. the indication of the presence of submarginal marks on the fore- as well as the hindwing) that Godart was indeed describing the West African subspecies.

Papilio potamonianus Ehrmann (1909) was established as a species. Holland (1927) discussed its identity and provenance and concluded that the specimen was probably from Liberia and that 'the type fails to show the slightest difference from [*G. l. latreillianus*].' Inclusion of the taxon in synonymy with *G. l. theorini* by some subsequent authors (e.g. Ackery *et al.*, 1995) is probably the result of the false 'Upper Congo' locality.

DIAGNOSIS: PATTERN (Fig. 197)
Generally distinguishable from *G. l. theorini* by the

presence of submarginal marks on the forewing upperside and by the form of the marking in the **upperside forewing** discal cell. In *G. l. latreillianus* there are generally two, elongate marks along the posterior discocellular vein opposite cells M_2 and M_3, sometimes fused, sometimes separated by the intervenosa. Sometimes the more costal of these marks is subdivided into a proximal and a distal spot. Further small marks, with variable amounts of fusion, link to the costal vein both at the distal and proximal ends of the marking. In *G. l. theorini*, only the mark nearest the posterior discocellular vein is complete and is generally fused to a distal mark to give a hook-like shape, but with some variation (see below) (Fig. 225).

The post-discal markings of the forewing are generally larger than in *G. l. theorini*, and least in the posterior cells; in particular those in cells CuA_2 and 1A are contiguous. By contrast the marks in cells R_3 to R_5 are generally smaller than in *G. l. theorini*.

The **hindwing underside** background colour tends to show a greater degree of pink suffusion, viewed best when several specimens of both races are together.

VARIATION

The pattern and extent of markings in the forewing discal cell and elsewhere is, as indicated above, quite variable. The elongate mark closest to the medial vein is always entire, but of variable size. The next is usually entire and sometimes fused for part or all of its length to the first; it may be subdivided into proximal and distal elements. Next to this is sometimes a third linear mark, usually subdivided into proximal and distal elements. Next to the costal vein is usually a pair of marks, rarely fused into one linear mark. There is sometimes fusion between elements across the intervenosae. A small spot may be present near the apex of the cell opposite cell R_5. The forewing patterns can be asymmetric.

There is usually a post-discal spot of variable size in forewing cell R_4, but this may be virtually obsolete.

Forewing cell M_1 usually lacks a post-discal mark. However, occasionally there is a small mark posterior to the intervenosa and, more rarely, an even smaller mark anterior to it.

The submarginal marks of the forewing upperside are usually distinct, but may be very faint.

Hindwing cell CuA_1 may have a small mark in the angle of the posterior discocellular vein and vein CuA_1.

SEXUAL DIMORPHISM. We have seen just one female, from Ghana (MRAC), in which the wing markings are cream coloured and somewhat reduced, as in *G. l. theorini*.

DISTRIBUTION (Map Fig. 134). Recorded from Guinea, Sierra Leone, Liberia, Ivory Coast, Ghana, Togo, Benin.

BIONOMICS. See species account.

MATERIAL EXAMINED. 76 ♂♂ in BMNH. 17 ♂♂; 1 ♀ from other collections.

24b. *G. (A.) latreillianus theorini* (Aurivillius, 1881)

Central African Olive Graphium or Coppery Swallowtail (Fig. 225; map Fig. 135)

Papilio latreillanus [sic] var. *theorini* Aurivillius, 1881: 45. TYPE ♂: GABON: 'Gaboon-flodens mynning, mellan 0°,10' — 0°,30' N.L.' (Aurivillius, 1881: 38). NHRS (Aurivillius, 1899: 483) (not seen).

Papilio latreillianus theorini Aurivillius; Aurivillius, 1908: 22, pl. 3(d).

Papilio latreillianus v. *theorini* Aurivillius; Bryk, 1930*b*: 559.

Papilio (*Graphium*) *latreillianus theorini* (Aur.); Peters, 1952: 20.

Graphium latreillianus theorini Aurivillius; Berger, 1950: 68; D'Abrera, 1980: 40, 41 (fig.); Berger, 1981: 50, pl.14 figs 1 (♂), 5 (♀).

Graphium (*Arisbe*) *latreillianus theorini* (Aurivillius); Ackery, Smith & Vane-Wright, 1995: 163.

SYNONYM

Papilio aurivillianus Avinoff, 1926: 355, pl. 30, fig. 2. HOLOTYPE ♀: CAMEROON: '*Type:* a unique female, from Lolodorf, Cameroons, C. M. Acc. No. 4366, A. I. Good, *coll.*'. CMNH (Avinoff, 1926: 356) (not seen).

Papilio latreillianus v. *aurivillianus* Avinoff; Bryk, 1930*b*: 560.

Papilio latreillianus theorini =*aurivillianus* Avinoff; Ackery, Smith & Vane-Wright, 1995: 163.

UNAVAILABLE NAMES

Graphium latreillianus var. *theorini* ab. *infrapicta* Strand, 1914*a*: 159. CAMEROON. (not seen). [infrasubspecific.]

Graphium latreillianus theorini f. *xerophila* Berger, 1950: 69. ZAIRE. MRAC [seasonal form, infrasubspecific.]

Papilio latreillanus [sic] *theorini* ab. *lutea* Birket-Smith, 1960: 533. CAMEROON. ZMC (not seen). [infrasubspecific.]

TYPE EVALUATIONS

Aurivillius (1881) gives no series length in his description of *Papilio latreillianus* var. *theorini*; the type locality is taken from the introduction to the paper. The type depository is from Aurivillius (1899).

Papilio aurivillianus Avinoff (1926) was described from the single specimen, with type designation original.

TAXONOMIC STATUS

Papilio latreillianus var. *theorini* Aurivillius (1881) was described before 1961 and it is clear that the author recognized a geographical component to its status.

Under the Code, Article 45.6.4 (ICZN, 1999) it should be regarded as subspecific. It has been treated as such by subsequent authors.

Though described as a species, Avinoff (1926) stated that *P. aurivillianus* was collected together with 'a considerable series of males of *P. theorini*.' He argued that Aurivillius (1908) remarked that the sexes in the *tynderaeus*-group are alike; since *aurivillianus* shows some differences from the male *theorini*, he treated it as a good species. Though Avinoff was incredulous that his insect was the female of *latreillianus theorini*, the few females we have seen show the same differences of colour and pattern. The synonymy of *aurivillianus* with *theorini* need not be doubted.

DIAGNOSIS: PATTERN (Fig. 225)
Generally distinguishable from *G. l. latreillianus* by the absence of submarginal marks on the forewing upperside and by the form of the marking in the **upperside forewing** discal cell. In *G. l. theorini*, there is a single longitudinal mark along the posterior discocellular vein opposite cells M_2 and M_3, expanded costally at the distal end (by fusion with a smaller mark) to give a hook-like shape. Smaller marks, generally separated by 'intervenosae', bridge the gap to the costal vein. In *G. l. latreillianus* there are generally two, elongate, longitudinal marks sometimes fused, sometimes separated by the intervenosa, with a variable array of smaller marks between these and the costal vein.

The post-discal markings of the forewing are generally smaller than in *G. l. latreillianus*, at least in the posterior cells; in particular those in cells CuA_2 and 1A are separated by vein 1A. By contrast the marks in cells R_3 to R_5 are generally larger than in *G. l. latreillianus*.

The **underside hindwing** background colour shows less pinkish suffusion than in the nominate subspecies, but this is neither very reliable nor obvious in single specimens.

VARIATION
There is the usual variation in the extent of the pale markings and their disposition (ab. *infrapicta* Strand seems to represent the least marked). In the forewing upperside discal cell there is the characteristic hook-shaped longitudinal mark along the posterior discocellular vein opposite cells M_2 to M_3, with its distal expansion. At the distal end of this mark there is usually a row (sometimes only one, rarely none) of smaller marks across the cell to the costal vein; these may be fused, or partly so. The proximal end of the longitudinal mark may also be enlarged and there may be one, two or even three small marks across the cell; in the most heavily marked individuals there may be some fusion. In the least marked specimens, the longitudinal mark itself may be divided into two.

Though characterized partly by the lack of forewing submarginal marks, the occasional individual shows a slight trace of them.

Forewing cell M_1 usually lacks post-discal marks, but some specimens show a small spot anterior to the intervenosa, some a small spot posterior to the intervenosa, some both and these occasionally fused basally into a chevron.

On the hindwing, the submarginal marks in cell R_5, usually as prominent as in the other cells, are sometimes quite faint.

On the hindwing underside there is some variability in the size of the black spots. In particular, the central spot in cell R_1 varies between roughly the size of the others in that cell, to much smaller. The paired spots in cells M_1 to M_3 may touch or partially fuse.

Berger (1950) defined f. *xerophila* on the basis of the pale markings on the underside of the forewings (except those in cells CuA_2 and 1A) having a pinkish hue and the hindwing underside background being more uniform across the wing surface.

Birket-Smith (1960) states that the green marks of the upper side of the wings of ab. *lutea* is replaced by 'a brownish yellow'. This is often associated with exposure to light, but the author states his specimen to be recently emerged.

SEXUAL DIMORPHISM
In the female, the pale marks of the upperside are cream coloured. Their pattern is similar, but reduced, especially in the forewing discal cell where there is just a small mark along the posterior discocellular vein opposite cell M_2 and a further mark at an angle to this arising at its distal end; the two sometimes touch.

DISTRIBUTION (Map Fig. 135)
Recorded from Nigeria, Cameroon, Chad, Equatorial Guinea (Bioko), São Tomé & Principe (São Tomé), Central African Republic, Gabon, Congo, Democratic Republic of Congo, Angola and western Uganda (Ackery *et al.*, 1995; Larsen BWA-MS). In Democratic Republic of Congo, Berger (1981) indicates widespread except for Maï-Ndombe, Kwilu, Kwango and Haut-Shaba.

BIONOMICS. See species account.

MATERIAL EXAMINED. 141 ♂♂; 5 ♀♀ in BMNH. 157 ♂♂; 18 ♀♀ from other collections.

25. *Graphium (Arisbe) philonoe* (Ward, 1873)

White-Dappled Swallowtail or Eastern Graphium (Figs 198, 226; map figs 141, 142; genitalia Figs 43, 95; early stages Fig. 264)

Both Berger (1951) and Hancock (1993) regarded *G. philonoe* as belonging to a monospecific 'group.' Hancock (1993) placed it as sister to his *leonidas* group. Our own analyses failed to separate it from the *adamastor* group with which it forms part of the crown group in our cladograms. The form of the pattern, with a subdivided forewing discal cell band, is suggestive of a relationship, but the pattern more strikingly resembles those of *G. leonidas* or *G. angolanus*.

G. philonoe is a species of the forests and woodland of eastern Africa, with two recognized subspecies: the nominate from coastal Kenya south to Malawi and Mozambique; and *G. p. whalleyi* from southern Sudan, south-west Ethiopia and northern Uganda. In the following account, we give a general description for the species, with the distinguishing characters of the two subspecies in the appropriate sections. Biological information is also given at the species level.

SIMILAR SPECIES

With its upperside of dark brown with white markings, the overall impression of *G. philonoe* is similar to both *G. leonidas* and *G. angolanus*. However, the differences are sufficient that identification of this species should never be a problem. *G. philonoe* lacks the striking blue coloration of fresh *G. leonidas* specimens, associated with their mimicry of *Tirumala petiverana*, but the underside is very similar and begs the question as to whether *G. philonoe* closes its wings when settled, as does *G. leonidas* and its model (see section on mimicry, below). The upperside of *G. philonoe* is similar to that of *G. angolanus*, but the underside is very different.

The most obvious distinguishing feature of the species is the pattern of the forewing discal cell with its broad transverse band opposite cells M_2 and M_3, divided into three by the 'intervenosae'. On the hindwing, the submarginal spots of cells R_5 to CuA_1 are usually prominent (especially in subspecies *whalleyi*) and subdivided.

The underside pattern closely reflects the upperside.

DIAGNOSIS: PATTERN (Figs 198, 226)

Upperside ground colour dark brown with a pattern of white discal, post-discal and submarginal marks.

Forewing discal cell with a broad, white, transverse band opposite cells M_2 and M_3, narrowing towards the radial vein. This band is usually divided into three by intervenosae. Proximal to this band is a linear group of two or three small spots (the largest nearest the radial vein) forming a rudimentary, oblique band opposite cell CuA_1. Near the distal end of the discal cell there is usually a pair of spots opposite cell R_5. Forewing cell R_3 with prominent discal and submarginal marks and, sometimes, a post-discal mark. Cell R_4 with post-discal and submarginal marks. Cell R_5 with prominent post-discal mark level with root of vein R_4, and submarginal mark. Cell M_1 usually just with submarginal mark. Cells M_2 to CuA_1 with post-discal and submarginal marks, in M_2 and M_3 the post-discals are quadrate and come close to, but do not touch, the surrounding veins; that in CuA_1 is more elliptical and further distanced from the veins – especially the posterior discocellular. Cell CuA_2 has the post-discal mark extended to the base of the cell (presumably incorporating basal and discal marks), and usually a subdivided submarginal mark, faint in *G. p. philonoe*, well marked in *G. p. whalleyi*. Cell 1A either has a broad post-discal mark contiguous with that in cell CuA_2 (*G. p. philonoe*), or is unmarked (*G. p. whalleyi*).

The **hindwing** discal cell is normall clear white from almost the base to almost the tip. The costal cell is white from the precostal vein to the margin. Cell R_1 has a large discal/post-discal mark; a subdivided submarginal mark, fainter in *G. p. philonoe* than in *G. p. whalleyi*; and a marginal mark. Cell R_5 has a prominent axillary post-discal mark and a subdivided submarginal, the anterior part of which is much the more prominent. Cell M_1 usually has a clear post-discal mark and divided submarginal marks. Cell M_2 usually has just divided submarginal marks. Cell M_3 has an axillary discal mark and divided submarginals, as does cell CuA_1. Cell CuA_2 has fused discal and post-discal marks. Marginal marks may be present on the hindwing, especially in cells R_1, R_5 and CuA_1 and CuA_2; these are much more prominent in *G. p. whalleyi* than in *G. p. philonoe*.

The **underside** pattern reflects that of the upper side with the background colour somewhat paler. The wing bases, especially the hindwing, have a slight reddish hue. On the **hindwing** there is a black spot surrounding the humeral vein, the veins are generally bordered by dark scales, and there is a tuft of white scales at the bases of the subcostal and cubital veins.

DIAGNOSIS: ♂ GENITALIA (Fig. 43)

The most characteristic feature is the nearly horizontal, bifid dorsal harpe which projects beyond the valve margin. The small basal lamella suggests an affinity with the *angolanus* group. The details are given for each subspecies.

DIAGNOSIS: ♀ GENITALIA (Fig. 95)

BMNH Spec.Reg. No. 138415; vial 3977: *vestibulum* large, nearly circular; *ostium bursae* opening anteriorly; *ductus bursae* not extended, but sclerotized and with kink/constriction distal to *ductus seminalis*, not pocketed; *central ostial lobe* setose, short, broad, bifid; *lateral ostial lobes* setose, narrow and well separated; *anterior apophyses* present; *papillae anales* elongate dorsally, with particularly pronounced hook-like setae.

EARLY STAGES (Fig. 264)

The mature larva apparently lacks an obvious general pattern except a very conspicuous lateral white stripe running the entire length of the body, and a transverse yellow line on the third thoracic segment; coloration bright green, with the surface 'sprinkled with whitish specks'; the thoracic and cuadal processes are very conspicuous in the final instar, being whitish or largely so. The pupa is also quite distinctive, most similar to *leonidas*, but with the dorsal horn more forward pointing, the ventro-lateral cephalic points very weakly indicated, the whole pupa slightly flattened, and the lateral ridge running from the frontal horn to the cremaster whitish, contrasting with the overall green coloration.

Colour photographs of the egg, larvae and pupae of subsp. *philonoe* from Tanzania were sent to us by Colin Congdon (*in litt.*, 27.ix.1999). Congdon notes that 'the egg [which is spherical, unsculptured, and apparently pale green or translucent] is inserted into a tightly furled bud, and is completely invisible. We saw a female laying, and even so the egg could not be seen, and it was in fact difficult to unroll the bud without damaging the egg. Larvae were a good match for the foodplant, and we did not find them on anything else, even though the butterfly was plentiful.' Congdon's photographs and Sevastopulo's descriptions mostly correspond well, except that in the former the pupa is shown head-up; this may be because pupation takes place on a leaf, with the cremaster at the leaf base, so that if the weight of the pupa bends the leaf down, the pupa ends up in a head-down position (which appears to have been the case with Sevastopulo's Kwale specimen). Congdon's photograph of the first instar is indistinct, but it appears mostly blackish, while his picture of the mature larva differs from Sevastopulo's description in having the dorsum of the thorax, between the six spines, broadly chestnut-brown, becoming orange-brown anteriorly, adjacent to the head; the posterior yellowish line on the dorsum of the third abdominal segment is not evident.

Sevastopulo (MS) described the final instar and pupa of *G. philonoe philonoe* thus:

> [Final instar larva]: Head brownish, a vertical blackish line on each side of the clypeus and a transverse blackish line below the vertex. Body bright green, [as seen] under a lens sprinkled with whitish specks. A white dorso-lateral line. A transverse yellowish line posteriorly on 3rd somite. Thoracic somites each with a spine arising from the dorso-lateral line, so that on the 1st somite [is] orange, those on the 2nd and 3rd [are] colourless, the base orange with a black dot. Osmeterium pouch orange, [but] the larva refused to extrude its osmeterium, so the colour cannot be recorded. Shape broad in front, tapering from the 4th somite towards the rear, the anal somite produced into two whitish points. Legs, prolegs and venter green.
>
> Pupa supported by a girdle and the cremaster, head downwards. Green, a yellow lateral line running along the abdominal somites from the cremaster, along the upper edge of the wing case and onto the thoracic horn. A very fine yellow subordinal line on the abdominal somites with a reddish speck on the 3rd, this line is slightly out-curved and almost joins the cremaster. Traces of darker oblique lateral stripes between the subdorsal and lateral lines formed of darker green specks. Shape with the head only very slightly indented frontally, the thorax rising into a forward-directed, sharply pointed horn.
>
> Described from a full grown larva found at Kwale [Kenya] 20.xi.[19]66, pupated 23.xi.66, and a male emerged 2.xii.66.
>
> [Sevastopulo's descriptions are accompanied by seven black and white photographs.]

HOST PLANT RECORDS

Annonaceae:

Annona sp. (Ackery *et al.*, 1995; Sevastopulo, MS).
Uvaria acuminata (Congdon, *in litt.* 1999).
Uvaria sp. (Ackery *et al.*, 1995; Sevastopulo, MS; Kielland, 1990).

BIONOMICS

Of the two subspecies included, *G. p. philonoe* is generally found in lowland forests and woodlands. According to Larsen (1996a) this is 'a butterfly of the coastal forests . . . usually more common in open parts . . . and along the margins', while *G. p. whalleyi* occurs in gallery forests. Lamborn found subsp. *philonoe* in Malawi at about 500 m, in 'rather thin bush' (Gifford, 1965). Flight is less powerful than other *Graphium* (Williams, 1969, describes it as 'relatively weak'); males come to moisture (Kielland, 1990), while both sexes are strongly attracted to flowers, e.g. of *Maerua* (Larsen, 1996). S. Collins (quoted in Larsen, 1991: 237) evidently considers *G. p. whalleyi* to be a very good mimic of *Tirumala petiverana* (Doubleday) (Nymphalidae: Danainae). For Tanzania, Kielland (1990) records a specimen taken on the summit of Bondwa, at 2140 m. Williams (1969) states that it flies throughout the year.

CONSERVATION STATUS. 'Common in much of its range and not threatened' (Collins & Morris, 1985: 57).

25a. *G. (A.) philonoe philonoe* (Ward, 1873)

Southern White-Dappled Swallowtail or Eastern Graphium (Fig. 198; map Fig. 141; genitalia Figs 43, 95)

Papilio Philonoë Ward, 1873: 152. TYPE ♂: KENYA: 'Ribé.' (Ward,1873: 152). (not seen).
Papilio philonoë Ward; Bryk, 1930*b*: 565.
Papilio (Graphium) philonoë philonoë Ward; Peters, 1952: 21.
Graphium (Arisbe) philonoe (Ward); Munroe 1961: 42; Hancock, 1983: 46.
Graphium philonoe philonoe Ward; D'Abrera, 1980: 44, 45 (fig.); Kielland, 1990: 47.
Graphium (Arisbe) philonoe philonoe (Ward); Ackery, Smith & Vane-Wright, 1995: 164.

UNAVAILABLE NAME

Papilio philonoë f. *dulcinea* Stoneham, 1931: [1]. KENYA: 'Gede, Arubuka Forest' (Stoneham, 1931: [1]). NMK (not seen). [infrasubspecific.]

TYPE EVALUATIONS

Papilio Philonoë Ward (1873: 152) was described from material collected by Rev. T. Wakefield at Ribé, Kenya, with no indication of series length other than a single size. Horn *et al.* (1990) state that Ward's Rhopaloceran types went to Oberthür, the remainder to MNHN. Two *ex* Ward specimens in MNHN have been labelled as 'co-types', but their localities are given as 'Zanzibar', so should be excluded from the type series. A further 5 Ward specimen from Zanzibar are in BMNH, which they reached via the Oberthür collection and the Levick Bequest (BMNH accession no. 1941–83).

We have seen just one specimen labelled as from Ribé – BMNH Spec.Reg. No. 138575. This is from Hewitson's collection (BMNH accession no. 1869–79) and is listed in Kirby's (1879) catalogue, with the locality given in square brackets, indicating that it has been interpreted by Kirby from the published type locality.

TAXONOMIC STATUS

Papilio Philonoë Ward (1873: 152) was established as a species, a status accepted by subsequent authors. With the establishment of *P. p. whalleyi* Talbot (1929), this status became modified to become the nominate race of a bitypic species, and this has been accepted by subsequent authors.

Although described as a form pre-1961, and named in a trinomen, Stoneham (1931: [1]) indicated that he intended *dulcinea* to be infrasubspecific: he mentioned the occurrence of 'intergrades' between it and the 'typical' form.

DIAGNOSIS: PATTERN (Fig. 198)

The clearest distinction from *G. p. whalleyi* is the presence of a post-discal band in forewing cell 1A, thus forming a large white area in the basal part of the wings extending from forewing cell CuA_2 to the posterior margin of the hindwing.

The discal and post-discal marks of the fore- and hindwings are generally larger than in *G. p. whalleyi*. By contrast, the submarginal marks of the fore- and hindwings and the marginal marks of the hindwing are smaller and less prominent.

VARIATION

In addition to the usual variability of size and shape of the white marks, we have noted the following variants.

Basal mark of forewing discal cell with either two or three elements, or even, rarely, one.

The three elements of the central band of the forewing discal cell are usually clearly separated by the 'intervenosae', but there is a contiuous variation to almost complete fusion.

The distal mark in the forewing discal cell may occassionally be reduced to a single element or even be virtually absent.

Forewing cell R_3 with a post-discal mark.

Forewing cell R_4 lacking a post-discal mark.

Forewing cell M_1 with a post-discal mark.

Forewing cell CuA_1 with submarginal mark absent, or virtually so.

Hindwing cell M_1 with post-discal mark reduced or even absent.

Hindwing cell M_2 with a post-discal mark.

Hindwing cell CuA_2 with a submarginal mark.

Hindwing discal cell underside with faint, brown 'intervenosae'.

From the description (Stoneham, 1931: [1]) f. *dulcinea* would seem to have enlarged post-discal marks, probably in hindwing cells M_1 to M_3, but we have not seen examples.

DIAGNOSIS: ♂ GENITALIA (Fig. 43)

Dorsal projection quite stout, expanded distally, with stout setae confined to ventral face of tip. *Dorsal harpe* elongate, angled somewhat mesad and dorsad, extending beyond valve margin, with a mesad directed branch anterior to dorsal terminal process; tips of both branches broad (not acute) and denticulate. *Ventral harpe* broad, more-or-less parallel-sided (expanding slightly distally), angled somewhat mesad and dorsad, denticulate distally. There is also a small, horizontal *basal lamella*. *Dorsal terminal process* small, directed mesad, concave above to accommodate dorsal harpe, ventral angle not acute. *Ventral terminal process* small, denticulate. *Uncus* rounded. *Socii* prominent, but projections short. *Saccus* very short. *Aedeagus* quite short, slightly decurved basally, no denticulation.

DIAGNOSIS: ♀ GENITALIA; EARLY STAGES; HOST PLANTS; BIONOMICS; CONSERVATION STATUS. See species account.

DISTRIBUTION (Map Fig. 141). Coastal Kenya south to Malawi and Mozambique. Countries confirmed are Kenya, western Democratic Republic of Congo, Tanzania, Mozambique and Malawi.

MATERIAL EXAMINED. 123 ♂♂, 74 ♀♀ in BMNH. 53 ♀♀, 18 ♀♀ from other collections.

25b. *G. (A.) philonoe whalleyi* (Talbot)

Whalley's White-Dappled Swallowtail or Eastern Graphium (Fig. 226; map Fig. 142)

Papilio philonoe whalleyi Talbot, 1929: 72, pl.2 fig.3. HOLOTYPE ♂: SUDAN: '. . . Imatong Mountains . . . ' (Talbot, 1929: 72). BMNH Spec.Reg. No. 138585. PARATYPE ♂: SUDAN: 'Imatong Mountains and Opare Forest, 8,000 — 10,000 feet . . . collected by Captain R. C. R. Whalley' (Talbot, 1929: 72). BMNH Spec.Reg. No. 138586.

Papilio (*Graphium*) *philonoë whalleyi* (Ta.); Peters, 1952: 21.

Graphium philonoe whalleyi Talbot; D'Abrera, 1980: 44.

Graphium (*Arisbe*) *philonoe whalleyi* (Talbot); Ackery, Smith & Vane-Wright, 1995: 164.

TYPE EVALUATIONS

Papilio philonoe whalleyi was described by Talbot (1929: 72) from the two specimens listed above, with designations original. The holotype was clearly labelled as such in Talbot's hand and the paratype bore a BMNH style round paratype label. The specimens reached the BMNH as part of the Joicey bequest, BMNH accession number 1934–120.

TAXONOMIC STATUS

Papilio philonoe whalleyi Talbot (1929: 72) was described as a subspecies, a status not revised by subsequent authors, although Larsen (1991: 117) considered that it 'may well turn out to be a species in its own right.' Given the constant pattern difference, but only slight differences in the male genitalia, we see no reason to alter the status quo.

DIAGNOSIS: PATTERN (Fig. 226)

The most obvious distinguishing feature of this subspecies is the absence – or, at least, considerable reduction – of white marking in forewing cell 1A/2A.

In addition, there is a general reduction in the post-discal marks, but an expansion of the submarginal marks. In particular, the post discal marks of **forewing** cells M_2 to CuA_1 are each smaller than their counterparts in the nominate subspecies, further remote from their surrounding veins. By contrast the submarginal marks of the forewing are large and round, with that in cell CuA_2 subdivided by a fine line. On the **hindwing**, the submarginal marks are subdivided, but enlarged and elongate, giving the appearance of cloven-hoof prints. In addition, the marginal marks of the hindwing are more prominent, increasing the impression of scallopping of the wing margin.

VARIATION

The size, shape and proportions of the white marks are, as usual, variable. The following particular variants may be noted.

Forewing discal cell with basal mark may consist of two or three spots.

Post-discal mark of forewing discal cell R_3 may be absent, or almost so.

A very faint post-discal mark may rarely be seen in forewing cell M_1.

The post-discal spot in hindwing cell M_1 may be reduced or even absent.

A small post-discal spot may occassionally be seen in hindwing cell M_2.

The post-discal spot in hindwing cell M_3 may be reduced or even absent.

Brown 'intervenosae' are sometimes seen in the underside discal cell of the hindwing.

DIAGNOSIS: ♂ GENITALIA

Similar to the nominate subspecies, but each organ is more serrate.

Dorsal projection quite stout, curving dorsad and, at the tip, posteriad; expanded distally where it is slightly serrate, with stout setae confined to ventral face of tip. *Dorsal harpe* elongate, angled somewhat mesad and dorsad, extending beyond valve margin, with a mesad directed branch anterior to dorsal terminal process; tips of both branches broad (not acute) and denticulate, slightly more coarsely than in the nominate. *Ventral harpe* broad, more-or-less parallel-sided (expanding slightly distally), angled somewhat mesad and dorsad, denticulate distally. There is also a small, horizontal *basal lamella*. *Dorsal terminal process* small, directed mesad, concave above to accommodate dorsal harpe, ventral angle not acute. *Ventral terminal process* sessile, indicated by denticulation. *Uncus* rounded. *Socii* prominent, but projections short. *Saccus* very short. *Aedeagus* quite short, slightly decurved basally, no denticulation.

DIAGNOSIS: ♀ GENITALIA. None available for study. See species account.

EARLY STAGES; HOST PLANTS; BIONOMICS. See species account.

DISTRIBUTION (Map Fig. 142). Countries confirmed are southern Sudan, Ethiopia and Uganda.

MATERIAL EXAMINED. 10 ♂♂ in BMNH. 2 ♂♂ from other collections.

26–39 *The adamastor group*

A group of species recognized by both Berger (1951), who referred to it as the 'Groupe de *G. ucalegon* HEW.', and Hancock (1993). We prefer to follow Hancock (1993) in naming it after *G. adamastor* as this is the first named species in the group. In our analyses, whilst the group itself remained robust we have been unable to demonstrate it as being monophyletic, in that *G. philonoe* was always included as part of the polytomy. This clade forms part of the polytomous crown group.

The members of the group share a similar appearance of a dark ground colour (usually brown) with a pattern of pale marks (white, cream or yellow), but whose patterns are simpler than those seen in most sword-tailed and other afrotropical *Graphium*. They are said to be mimetic of particular or generalized *Amauris* and other models (see section on mimicry, below). They are linked by the presence of a tuft of white scales, usually surrounded by black, at the bases of the subcostal and/or cubital veins, just distal to their junction on the hindwing undersides (as also seen in *G. philonoe, G. cyrnus, G. levassori,* and *G. leonidas*). The undersides of the wing cells – especially the peripheral ones, but often also the discal cells – are marked by dark 'intervenosae', which often subdivide the pale spots. However, the most convincing feature uniting the group is the dorsal harpe of the male genital valve, which is in the form of a simple, upcurved hook.

The taxa show considerable variability, making the definition of subspecies and species limits problematic. This is compounded by the rarity (at least in collections) of many taxa and consequent lack of good biogeographical information: further specimens may blur the distinctions between the various subspecies – and even species – recognized here. Finding single, reliable characters for identification is often problematic; in the 'similar species' sections of the following accounts, we have often had to resort to a variety of variable characters, together with the figures. Even then, identification is made easier when there are series of specimens of the possible taxa for comparison.

The group appears to be confined to evergreen forests, apparently 'centred' on the Congo Basin. A few species occur to the west in West Africa and Gabon, while to the east the limit appears to be Uganda, western Kenya and western Tanzania, and Zambia to the south. Almost nothing seems to be known about them biologically, and the early stages have not been described in a single case. A basic biological 'shift' in this group may be to mimicry of *Amauris* (independent of the shift to *Tirumala* and *Amauris* mimicry in *G. leonidas*), but even this seems uncertain as several seem poor mimics, at least 'in the cabinet'. An unconfirmed host-plant record for *G. almansor* refers, tantalisingly, to the Anacardiaceae.

Berger (1951) subdivided the group into two: one consisting of ten species (*hachei*, *auriger*, *ucalegon*, *simoni*, *fulleri*, *ucalegonides* [here regarded as a subspecies of *fulleri*], *almansor*, *odin* [=*schubotzi*], *olbrechtsi* and *aurivilliusi*); the other of just two (*agamedes* and *adamastor*).

Hancock (1993) recognized just nine species, including *schubotzi*, *olbrechtsi* and *aurivilliusi* as subspecies of *auriger* (see also Hancock, 1985*a*); and *kigoma* as a subspecies of *poggianus*. He separated *almansor* and *poggianus* as a pair as sister to the remaining seven; *fulleri* as sister to the remaining six; then *auriger* + *hachei* as sister to two remaining pairs: *ucalegon* + *simoni* and *agamedes* + *adamastor*. In parenthetical notation this becomes:

((*almansor* + *poggianus*) (*fulleri* + ((*auriger* + *hachei*) ((*ucalegon* + *simoni*) (*agamedes* + *adamastor*)))))

We recognize 14 species in the group, including one apparently new to science.

We have not attempted a detailed analysis of the group due to the great intraspecific variability of the wing patterns, the contrasting comparative similarity of male genitalia, and the lack of females for study of many of the species.

However, some resemblances between certain taxa have influenced the order in which we have placed them. It must be emphasized, however, that these resemblances may well be plesiomorphic and thus give no real information on relationships at this level.

In one of these groups, the male genitalia are characterized by the dorsal terminal process being small and with the mesal edge at an angle to the vertical; the ventral terminal process prominent; and the ventral harpe small. Species showing these traits include *G. adamastor*, *agamedes*, *schubotzi*, *olbrechtsi*, *abri*, and possibly *almansor*. The second group has the dorsal terminal process relatively large, excavate ventrally and with the mesal edge more nearly vertical; and the ventral harpe relatively large and curved mesad. These features are seen in *G. auriger*, *fulleri*, *poggianus*, and *kigoma*, with possibly also *hachei*, and *aurivilliusi* (the genitalia of which we have only seen slide-mounted). In both *G. fulleri rileyi* and *kigoma* the posterior labia of the female vestibulum are deeply notched centrally, but this does not appear to be true in *G. auriger*, the only other species in this group of which we have been able to examine the female. Both *G. ucalegon* and *simoni* share the character of the presence of a scattering of pale scales in the distal part of the hindwing discal cell.

26. *Graphium* (*Arisbe*) *adamastor* (Boisduval, 1836)

Boisduval's Graphium (Fig. 199; map Fig. 158; genitalia Figs 44, 96)

As treated here, *Graphium adamastor* (Boisduval) is a monotypic West African species occurring from Sierra Leone to Cameroon, CAR, and northern Democratic Republic of Congo (Mongala & Bas-Uele – Berger, 1981). Through most of this range it is sympatric with the similar *G. agamedes*, and overlaps with *G. almansor carchedonius* in Togo, and with *G. almansor escherichi* in Cameroon and northern Democratic Republic of Congo.

Hancock (1985, unfortunately followed by Ackery *et al.*, 1995) erroneously included *G. almansor carchedonius* (Karsch, 1895) (*q.v.*) as a synonym, possibly due to misidentification. Hancock (1985: 101) combined *G. almansor wranghami* Kielland (1978) as a subspecies, but subsequently (1985: 126) transferred it to *G. poggianus* (Honrath, 1884) (*q.v.*).

Papilio adamastor Boisduval, 1836: 371. HOLOTYPE – ♂: 'Cote de Guinée' (Boisduval, 1836: 371). BMNH. Spec.Reg. No. 137632.

Papilio adamastor Boisduval; Kirby, 1871: 532; Aurivillius, 1899: 486; Aurivillius, 1908: 24.

Papilio adamastor [*adamastor*] Boisduval; Bryk, 1930*b*: 563.

Papilio (*Graphium*) *adamastor adamastor* (Boisd.); Peters, 1952: 21.

Graphium (*Arisbe*) *adamastor* (Boisduval); Munroe, 1961: 42; Hancock, 1983: 46; Collins & Morris, 1985: 57; Ackery, Smith & Vane-Wright, 1995: 160.

Graphium adamastor adamastor Boisduval; D'Abrera, 1980: 44, 45 (fig.).

Graphium adamastor Boisduval; Berger, 1981: 52, pl.16 fig. 4 (♂); d'Abrera, 1997: 52, 53 (fig.).

SYNONYMS

Graphium adamastor zongo Berger, 1950: 88, Fig.87. HOLOTYPE ♂: DEMOCRATIC REPUBLIC OF CONGO: 'Holotype : 1 ♂ Congo-Ubangi : Zongo-Mokoanghay (Lt TILKENS)' (Berger, 1950: 88). IRSN. 1 PARATYPE ♂: DEMOCRATIC REPUBLIC OF CONGO: '. . . 1 ♂ Congo-Ubangi : Zongo-Mokoanghay (Lt TILKENS)' (Berger, 1950: 88). MRAC. This specimen dissected as 'Tervuren Museum ♂ Genitalia Slide Nº Pa. 117'; dissection '15/749/2' on label in Berger's hand. 2 PARATYPE ♂♂: CAR: '. . . Chari-Chad: 1912 (ex coll. LE MOULT in Muséum de Paris) . . . ' (Berger, 1950: 88). MNHN - one seen. 1 PARATYPE ♂: '. . . sans localité (in Muséum de Paris)' (Berger, 1950: 88). MNHN (not seen).

Graphium adamastor f. *zongo* Berger; Berger, 1974: 75 (as stat. rev.); Berger, 1981: 53, pl.16 fig. 9 (♂ – PT).

Graphium adamastor zongo Berger; D'Abrera, 1980: 44; Hancock, 1985*a*: 101.

Graphium adamastor =zongo Berger; Ackery, Smith & Vane-Wright, 1995: 160; d'Abrera, 1997: 52.

Graphium adamastor dimbroko Berger, 1950: 89. HOLOTYPE ♂: SIERRA LEONE: 'Sierra Leone' (Berger, 1950: 89). MRAC; 1 PARATYPE ♂: IVORY COAST: 'Côte d'Ivoire: Dimbroko . . . ' (Berger, 1950: 89). MRAC; 1 PARATYPE ♂: IVORY COAST: '. . . sans localité précise . . . ' (Berger, 1950: 89). MRAC.

Graphium adamastor =dimbroko Berger; Berger, 1974: 75, (as syn. n.); Hancock, 1985*a*: 100; Ackery, Smith & Vane-Wright, 1995: 160.

TYPE EVALUATIONS

Papilio adamastor Boisduval (1836: 371) was described from '. . . un individu mâle, que nous devons à la générosité de M. Westermann.' A specimen from Boisduval's collection which reached the BMNH, via the Oberthür collection (as part of the Levick Bequest: BMNH accession no.1941–83), has generally been taken as the holotype. It has (*inter alia*) a printed Oberthür 'Typicum/Specimen' label and a printed catalogue/drawer label also stating it to be a 'Specimen typicum' and was furnished with a round, BMNH-style 'type' label. There is no proof that it was the specimen given to Boisduval by Westermann, but in the absence of any other candidate specimen it is reasonable to accept it as the holotype.

Graphium adamastor zongo Berger (1950: 88) was described from the five specimens listed above; type designations original.

Graphium adamastor dimbroko Berger (1950: 89) was described from the three specimens listed above; type designations original (Berger, 1950: 89).

TAXONOMIC STATUS

Papilio adamastor Boisduval (1836: 371) was established as a species and accepted as such by subsequent authors. Bryk (1930) included *schubotzi* and *odin* as varieties, whilst excluding the other taxa. Berger (1950) separated *odin* and *schubotzi* as a bitypic species. More recently, Hancock (1985 – see below) included *G. almansor carchedonius* (Karsch) as a synonym, based on a misidentification. Further details of these interpretations can be found in the sections on the taxa concerned.

Graphium adamastor zongo Berger (1950: 88) was established as a subspecies on the basis of, in particular, the presence of an oblique mark near the base of the forewing discal cell, upperside. Berger (1974: 75) noted that only some, but not all, specimens from Bangui, near the type locality, showed the character and consequently downgraded it. Although some authors (e.g. D'Abrera, 1980; Hancock, 1985*a*) have treated it as subspecific, the collections in BMNH confirm that, though not common, the variant exists throughout the species' range.

Graphium adamastor dimbroko Berger (1950: 89) was established as a subspecies, but the author himself (1975: 75) recognized that the species is very variable, and that *dimbroko* is well within that range. In fact, the defining characteristic of the taxon – the absence of a spot in the distal part of the forewing upperside discal cell – is also shown by the presumed holotype (see above) of *G. adamastor*.

SIMILAR SPECIES

In overall appearance, *G. adamastor* is, perhaps, most like *G. agamedes*, but the forewing discal cell band completely traverses the cell (this character also separates it from *G. aurivilliusi* and *G. olbrechtsi*), and the post-discal spot in forewing cell CuA_1 is reduced and generally displaced distally. Moreover, the spots near the apex of the forewing are more prominent, as are the submarginals. Some races of *G. almansor*, especially *G. a. carchedonius*, *G. a. escherichi* and *G. a. birbiri* are also similar, but they lack submarginal and post-discal marks in hindwing cells M_1 to CuA_1, a rare condition in *G. adamastor*. Also, their forewing apical areas are less translucent and the post-discal spot of forewing cell CuA_1 is often absent.

DIAGNOSIS: PATTERN (Fig. 199)

Upperside ground colour brown – fading to become somewhat translucent on the forewing apically and distally, due to a narrowing of the brown scales – with a pattern of white marks. **Forewing** discal cell crossed by a band opposite cell M_3, narrowing from the posterior discocellular to the radial vein and not interrupted by 'intervenosae'. Cell R_3 with a discal mark proximal to root of R_4; cell R_4 with subdivided submarginal mark. In cell R_5 there is a subdivided submarginal mark and a deeply forked mark level with the root of

R_4, but not reaching the upper discocellular vein; it is probably the post-discal mark. Cell M_1 is usually devoid of any marking. In cell M_2 there is an elongate post-discal mark, largely confined to the posterior half of the cell, but with a small anterior projection basally; the anterior element of the subdivided submarginal mark is mauch fainter than the posterior. The post-discal mark of cell M_3 is large, reaching veins M_3, CuA_1 and the posterior discocellular vein, and slightly notched distally. The submarginal mark is not subdivided, but there is a scattering of dark scales across it. The post-discal mark of cell CuA_2 is usually small and elliptical and displaced distally so that its distal margin is level with those in neighbouring cells; the submarginal mark is undivided. The post-discal mark of cell CuA_2 is elongate and has its proximal edge parallel to the posterior discocellular vein, in line with that of the post-discal of cell 1A; its distal edge is tapering and rounded and the submarginal mark is subdivided. The post-discal mark of cell 1A is elongate and tapering, with its proximal margin also parallel to the posterior discocellular vein.

The discal cell of the **hindwing** has a dark base and tip, the intervening area white. The slightly sinuate boundary between the white and distal areas is quite clear cut and is level with the root of vein CuA_1. Cell R_1 has a white post-discal mark aligned at its base with the base of the discal cell white mark and with the base of the post-discal mark in forewing cell 1A. The base of cell R_5 has a white mark that is quite deeply notched distally; there is a subdivided submarginal mark. In cell M_1 there is a clear elongate post-discal mark, but only in the anterior half of the cell. The submarginal mark is subdivided, with the anterior element significantly clearer. In each of cells M_2 to CuA_1 the post-discal marks are subdivided into lines either side of the midline and in line with the subdivided submarginals. In cell, CuA_1 there is in addition a discal mark occupying the base as far as the root of vein CuA_1. Cell CuA_2 has a white mark aligned with those of the neighbouring cells.

This pattern is reflected on the **underside**, with neither the ground colour nor the markings being so intense. On the **hindwing** the ground colour exhibits an orange cast, especially in the costal cell, where there is a small black spot along the distal curve of the humeral vein. The hindwing discal cell has two 'intervenosae' of orange and black scales. The hindwing peripheral cells and the apical cells (R_3 to M_2) of the forewing have prominent intervenosae.

VARIATION

G. adamastor has a high level of individual variability in the extent of its pale marking, and the description above only approximates the usual range. In general, different pattern elements vary in parallel: expansion of, say, the post-discal spot in forewing cell CuA_1 will be co-ordinated with expansion of the hindwing post-discals and submarginals. But this is not always the case, suggesting that the cause is not a single-locus genetic difference or a simple environmental factor.

Individual variants include the following:

Forewing discal cell with a mark opposite vein CuA_2, often in the form of an oblique line. Forewing discal cell with a distal spot opposite cell R_5, which may be very faint or very distinct. The holotype of *zongo* shows these well (see Berger, 1950: Fig.87); in *dimbroko* the latter is lacking and the basal stripe faint.

The submarginal marks in forewing cells are often faint, or even absent. By contrast, a small post-discal mark occasionally occurs in the angle of veins R_4 and R_5.

The post-discal mark in forewing cell R_5 may be completely divided and/or the tips may be extended distally to fuse with the submarginals. These, in turn, may be reduced or even absent.

Cell M_1 may show traces of a submarginal mark, usually subdivided, and, more rarely a (subdivided) post-discal mark; the submarginals and post-discals may even fuse.

The anterior part of the post-discal mark in cell M_2 is occasionally present as a line isolated from the rest of the mark, but sometimes fusing with the anterior submarginal element.

The form of the post-discal mark in cell M_3 may be more quadrate and less notched and it may touch the submarginal, which is sometimes subdivided.

The post-discal mark of cell CuA_1 is often extended towards the angle of the cubital and CuA_1 veins; sometimes it also touches or fuses with the submarginal.

On the **hindwings**, the most notable variation is in the post-discal marks of cells M_1 to CuA_1. At their most pronounced, these are fused proximally and may touch and almost fuse with the submarginal. In such cases a posterior post-discal element may be present in cell M_1. However, these marks may be very faint or even absent. The submarginals, too, are variable.

The extent of the white patch in cell CuA_2 is variable.

This variation is reflected on the underside where, in addition, the size and density of the black spot in the costal cell varies as does the intensity of the 'intervenosae' of the hindwing discal cell.

DIAGNOSIS: ♂ GENITALIA (Fig. 44)

Similar to *G. agamedes*, but characterized (usually) by the absence of a dorsal blade on the ventral harpe.

Dorsal projection set well below margin, slightly curved dorsad. *Dorsal harpe* hook-like, extending beyond margin. *Ventral harpe* usually without dorsal blade (in one of four specimens examined there is a moderate dorsal blade on the left valve only), the ventral blade not extending far across inner rim. *Dorsal terminal process* relatively small, with ventral angle prolonged into point. *Ventral terminal process* broad, elongate, inner margin curved to face somewhat dorsad, denticulate at tip. The inner *rim* is notably broad ventrally and posteriorly, with its associated group of stout setae near its inner edge, near the tip of the ventral blade of the ventral harpe. *Uncus* long, *socii* small but projecting. *Saccus* short. *Aedeagus* slightly curved, not denticulate.

DIAGNOSIS: ♀ GENITALIA (Fig. 96)
BMNH Spec.Reg. No. 138661; vial 3978: *ostium bursae* opening anteriorly; *ductus bursae* not elongate or sclerotized distally, but definitely kinked/constricted distal to the *ductus seminalis*; *central ostial lobe* glabrous, triangular, quite long (almost reaching tip of laterals); *lateral ostial lobes* setose, large, broad, triangular, not well sclerotized; *anterior apophyses* normal; *papillae* elongate dorsally.

EARLY STAGES. Apparently unknown.

DISTRIBUTION (Map Fig. 158)
Western and central Africa, including Mali, Guinea, Sierra Leone, Ivory Coast, Ghana, Togo, Benin, Nigeria, Cameroon, Central African Republic, Gabon, Congo, and northern Democratic Republic of Congo (Ubangi, Mongala) (Ackery *et al.*, 1995; Larsen, In prep.*a*).

HOST PLANT RECORDS. Annonaceae (Larsen, pers. comm.).

BIONOMICS
An inhabitant of transitional forest-savannah, where closed dry semi-deciduous forests meet the Guinea savannah in west Africa (Larsen BWA-MS), secondary forest (Owen & Owen, 1972), gallery forest (Hecq & Peeters, 1992), or savannah-forest mosaic, this species apparently never occurs in open savannahs or closed forest (Larsen, 1996b). According to Owen & Owen (1972) it is attracted by mammal urine and carrion. Larsen (Pers. Comm.), however, notes it as 'rare on sand', but he found females common at Boabeng-Fiema in Ghana, where the sex-ratio of *adamastor* seen on flowers at the edges of the forest was about 50: 50. Oviposition was also observed, low down on a plant of the family Annonaceae. A record for the butterfly in Ghana in June is given by Larsen (1996b).

CONSERVATION STATUS. 'Uncommon and local but not threatened' (Collins & Morris, 1985: 57 (including *almansor carchedonius*)).

MATERIAL EXAMINED. 73 ♂♂, 8 ♀♀ in BMNH. 35 ♂♂, 6 ♀♀ from other collections.

27. *Graphium* (*Arisbe*) *agamedes* (Westwood, 1842a)

Glassy Graphium (Fig. 200; map Fig. 159; genitalia Figs 45, 97)

As treated here, *Graphium agamedes* (Westwood) is a monotypic West African species occurring from Ghana to Cameroon, CAR, and northern Democratic Republic of Congo (Mongala & Bas-Uele). Through most of this range it is sympatric with the similar *G. adamastor*. *G. agamedes* overlaps with *G. almansor carchedonius* in Togo, and *G. almansor escherichi* in Cameroon and northern Democratic Republic of Congo.

Papilio agamedes Westwood, 1842*a*: 38. HOLOTYPE ♂: GHANA: 'Ashantee, tropical Africa . . . Mus. Hope.' (Westwood, 1842*a*: 38). OXUM type collection no. 3020.

Papilio agamedes Westwood; Westwood, [1842*b*]: 154, pl.37 fig.3; pl.39 fig.3.

Papilio agamedes Westwood; Kirby, 1871: 532; Aurivillius, 1908: 24; Bryk, 1930*b*: 563.

Papilio (*Graphium*) *agamedes agamedes* (Westwood); Peters, 1952: 21.

Graphium agamedes Westwood; Berger, 1950: 86, 87 (figs 85, 86); D'Abrera, 1980: 44, 45 (fig.); Berger, 1981: 52, pl.16 figs 8 (♂); d'Abrera, 1997: 52, 53 (fig.).

Graphium (*Arisbe*) *agamedes* (Westwood); Munroe, 1961: 42; Hancock, 1983: 46; Collins & Morris, 1985: 57; Ackery, Smith & Vane-Wright, 1995: 160.

SYNONYM

Papilio agamedes medesaga Suffert, 1904: 106. HOLOTYPE ♂: TOGO: '. . . Togo, Hinterland. Coll. Suffert' (Suffert, 1904: 106). BMNH. Spec.Reg. No. 137507.

Papilio agamedes ab. *medesaga* Suffert; Aurivillius, 1908: 24; Berger, 1950: 87.

Papilio agamedes f. *medesaga* Suffert; Bryk, 1930*b*: 564.

Graphium (*Arisbe*) *agamedes* =*medesaga* Suffert; Ackery, Smith & Vane-Wright, 1995: 160.

TYPE EVALUATIONS
In his description of *Papilio agamedes*, Westwood (1842*a*) gave no definitive indication of series length. However, Westwood ([1842*b*]: 154) made clear that he saw only a single specimen. The specimen concerned – the holotype – is in OXUM, clearly labelled and referred to in their index of types.

Papilio agamedes medesaga Suffert (1904: 106) was described from 'Ein männliches Exemplar . . .' (Suffert, 1904: 106). The specimen concerned, clearly labelled as such in Suffert's hand, reached the BMNH, via Rolle as part of the Joicey bequest (BMNH accession no. 1934–120) (Horn *et al.*, 1990).

TAXONOMIC STATUS
Papilio agamedes Westwood (1842*a*) was described as a species and has been accepted as such by most authors since. Bryk (1930) treated *G. aurivilliusi* (Seeldrayers) and *G. poggianus* (Honrath) as 'v[ar].s' of *P. agamedes*, and Peters (1952) followed this in treating them as subspecies.

Papilio agamedes medesaga Suffert (1904: 106), despite being based on a single specimen, was described as a subspecies on the presence of a spot near the apex of the forewing discal cell, subdivided submarginal and (post-) discal marks in forewing cell R_5, and larger and clearer post-discal and submarginal spots on the hindwing. These features are within the range of variability of *G. agamedes* (see below). Aurivillius (1908: 24) treated it as infrasubspecific and it has been accepted as such by authors since.

SIMILAR SPECIES

Most similar to *G. adamastor*, but the greater translucency and relative reduction of marking of the forewing, as well as the abbreviated discal cell band, should serve to separate them. The very rare *G. aurivilliusi* also shows similarities, but the diagnoses of the two should avoid confusion.

DIAGNOSIS: PATTERN (Fig. 200)

Upperside ground colour brown, with a pattern of white markings. The forewings become quite translucent distally, especially apically and distally to the post-discal marks of the outer margin. This is the result of narrowing the brown scales on the upperside and their almost complete absence, apart from along the veins and the midlines of the cells, on the underside. This translucency is more marked than in *G. adamastor*.

Forewing discal cell with a mark opposite cell M_3, narrowing costally and not usually reaching the radial vein. The triangular mark so formed is often interrupted by 'intervenosae'.

The pale marking is variable and, especially on the translucent areas, usually faint. This applies especially to the forewing submarginal marks and the discal/post-discals of the 'R' cells. Those marks usually visible include: Cell R_3 with an axial discal spot only. Cell R_4 usually unmarked. Cell R_5 variably marked with subdivided post-discal mark and sometimes with a subdivided submarginal mark. Cell M_1 is usually unmarked. As in *G. adamastor*, the post-discal mark of cell M_2 is largely confined to the posterior half of the cell (though less extended than in *G. adamastor*), with an extension along the posterior discocellular vein; there is usually no submarginal mark. The post-discal mark of cell M_3 is similar to that in *G. adamastor*, but not extended so far distally, so it does not reach the subdivided submarginal mark, which is itself very faint. The post-discal mark of cell CuA_1 is not reduced, unlike *G. adamastor*. The mark extends from the posterior discocellular vein (at least anteriorly), and reaches both veins CuA_1 and CuA_2 for most of its length; there is a faint submarginal mark. The proximal margin of the post-discal mark in cell CuA_2 is at an angle to the posterior discocellular vein, approaching the vein anteriorly, not parallel to it, as in *G. adamastor*. The submarginal mark in this cell is elongate, undivided, but faint. The proximal margin of the post-discal mark in cell 1A follows that of the mark in CuA_2, at the same angle to the cubital vein.

The **hindwing** is similar to that in *G. adamastor*. In the hindwing discal cell, the distal edge of the white mark is usually less regular, with the white extended along the middle and posterior discocellular veins. In cell R_1 there is a large post-discal mark, notched distally, and usually a subdivided submarginal mark. There is an axillary notched post-discal mark and subdivided submarginal mark in cell R_5, as in *G. adamastor*. Cell M_1 is also similar to that in *G. adamastor*, though the post-discal mark is usually less elongate and broader basally. Cells M_2 to CuA_1 have similar subdivided post-discal and submarginal marks; CuA_1 also has a basal discal mark, extending somewhat along the posterior discocellular, CuA_1 and CuA_2 veins. The white mark in cell CuA_2 extends further than in *G. adamastor*, reaching as far as the post-discal mark in cell CuA_1.

The upperside pattern is reflected on the **underside**, with the ground colour generally paler. On the hindwing this has an orange cast, as do the pale marks. The 'intervenosae' of the hindwing cell are composed entirely of dark scales; the posterior forks faintly distally.

VARIATION

The size and shape of the **forewing** discal cell mark is quite variable. At its smallest, it barely reaches half way across the cell; at its largest it may reach the radial vein. The shape is generally triangular, with the posterior discocellular vein as its base, but the interruptions by 'intervenosae' often breaks up the other two sides. A discal cell spot opposite cell R_5 – one of the characteristics of f. *medesaga* – occurs in about 20% of specimens. A subdivided submarginal mark occurs occasionally in forewing cell R_4. When it does occur, the post-discal mark in cell R_5 varies from a very faint single mark to a pair of well-marked lines, sometimes joined proximally; the presence and clarity of subdivided submarginals is also variable. Though usually unmarked, cell M_1 may have faint, subdivided submarginal marks, and such marks may be present in cell M_2. The post-discal mark in cell CuA_1, though visually linking those in neighbouring cells into a band, sometimes does not quite reach veins CuA_1 and CuA_2; in the few females in BMNH, it is elliptical, but is not 'offset' distally as is the case in *G. adamastor*. The submarginal marks in cells M_3 to CuA_2 vary from being absent to well marked, those in cells CuA_1 and CuA_2 may be subdivided or entire.

On the **hindwing**, the white marking of the discal cell varies in area to a limited extent, and its edge is variable in shape and complexity. The post-discal marks in cells M_1 to CuA_1 are variable in size, in the most strongly marked individuals (e.g. f. *medesaga*) the twin elements in each cell may be joined proximally. The submarginal marks in these cells are also variable.

On the underside, variable elements include the clarity of the cell midlines and the 'intervenosae' of the hindwing discal cell, and the size of the black mark in the angle of the hindwing precostal vein.

DIAGNOSIS: ♂ GENITALIA (Fig. 45)
Very similar to *G. adamastor*, the main difference being the presence of a small dorsal blade on the ventral harpe.

Dorsal projection elongate, cylindrical, slightly upcurving distally. *Dorsal harpe* hook-like, extending beyond margin. *Ventral harpe* with dorsal blade very small, directed mesad; the ventral blade not extending far across inner rim. *Dorsal terminal process* relatively small, with ventral angle prolonged into point. *Ventral terminal process* broad, elongate, inner margin curved to face somewhat dorsad, denticulate at tip. The inner *rim* is notably broad ventrally and posteriorly, with its associated group of stout setae near its inner edge, near the tip of the ventral blade of the ventral harpe. *Uncus* tapering; *socii* small but projecting. *Saccus* short. *Aedeagus* slightly curved, not denticulate.

DIAGNOSIS: ♀ GENITALIA (Fig. 97)
BMNH Spec.Reg. No. 138711; vial 3979: *ostium bursae* opening anteriorly; *ductus bursae* not elongate or sclerotized distally, but definitely kinked/constricted distal to the *ductus seminalis*; *central ostial lobe* glabrous, broad, truncate, almost reaching tip of laterals; *lateral ostial lobes* setose, long and broad, not well sclerotized; *anterior apophyses* normal; *papillae* elongate dorsally.

EARLY STAGES; HOST PLANTS. Apparently unknown.

DISTRIBUTION (Map Fig. 159)
Western and central Africa, with records for Guinea, ?Sierra Leone, Ivory Coast, Ghana (Volta Mts), Togo, Benin, Nigeria, Central African Republic, and northern Democratic Republic of Congo (Mongala, Uele) (Ackery *et al.*, 1995; Larsen, MSa; Berger, 1981), perhaps to border of Uganda (Emmel & Larsen, 1997). There is a specimen in MNHN labelled as being from Congo (near Brazzaville), and specimens in SMNS and ZSM purporting to be from Tanzania (without precise locality), though it is not listed in Kielland (1990) nor Congdon & Collins (1998).

BIONOMICS
A monotypic species of supposedly drier forests (Emmel & Larsen, 1997), *G. agamedes* apparently coexists with *G. almansor* and *G. adamastor* in the forest-savannah mosaics of the Volta Mountains, on the Ghana/Togo border (Larsen, 1996b). A specimen in NMGM was collected from the 'Odumase Swamp', Ashanti Province, Ghana. Williams (1969) considered it local and uncommon.

CONSERVATION STATUS. 'Local and uncommon but not regarded as threatened' (Collins & Morris, 1985: 57).

MATERIAL EXAMINED. 57 ♂♂, 4 ♀♀ in BMNH. 21 ♂♂ from other collections.

28. *Graphium* (*Arisbe*) *schubotzi* (Schultze, 1913) stat. rev.

Odin's Graphium (Fig. 201; map Fig. 166; genitalia Fig. 46)

Papilio [*agamedes*] var. *schubotzi* Schultze, 1913*a*: 73. LECTOTYPE ♂: DEMOCRATIC REPUBLIC OF CONGO: ['Duma (Ubangi-Distrikt), 16. IX.–19. X. [1910]' 'Dr. Schubotz'] **OR** ['Angu (Uelle-Distrikt) 1.–3. VI [1911]' 'Dr. Schubotz'] (Schultze, 1913*a*: 73). ZMUH (Schultze, 1917*a*: pl.25 fig.5 (legend)). [PRESUMED DESTROYED, 1943]; PARALECTOTYPE ♂: DEMOCRATIC REPUBLIC OF CONGO: 'Angu (Uelle-Distrikt) 1.–3. VI [1911]' 'Dr. Schubotz' (Schultze, 1913*a*: 73). SMNS; PARALECTOTYPE ♂: DEMOCRATIC REPUBLIC OF CONGO: 'Duma (Ubangi-Distrikt), 16. IX.– 19. X. [1910]' 'Dr. Schubotz' (Schultze, 1913*a*: 73). FIF; PARALECTOTYPE [?♂]): DEMOCRATIC REPUBLIC OF CONGO: [Duma] or [Angu] (Schultze, 1913*a*: 73). (Not traced). [Subjective replacement name for *Papilio odin* Strand, 1910 (preoccupied).]

Papilio adamastor v. *Schubotzi* Schultze; Schultze, 1917*a*: 535, pl.25 fig.5; Schultze, 1917*b*: 27; Bryk, 1930*b*: 563.

Papilio (*Graphium*) *almansor schubotzi* Schultze; Peters, 1952: 21.

Graphium odin schubotzi Schultze; Berger, 1950: 84, fig.81; Berger, 1974: 76; Berger, 1981: 51, pl.16 figs 5 (♂), 10 (♀ – 'NA').

Graphium odin schoubotzi [sic] Schultze; D'Abrera, 1980: 44.

Graphium auriger odin =*schubotzi* Schultze; Hancock, 1985*a*: 99 (as 'SYN. N.').

Graphium (*Arisbe*) *auriger schoubotzi* [sic] (Schultze); Ackery, Smith & Vane-Wright, 1995: 162; d'Abrera, 1997: 50.

SYNONYMS

Papilio odin Strand, 1910: 30,34. LECTOTYPE ♂: CAMEROON: 'von Herrn Oberleutnant F. Reuter an der Dume-Mündung in Kamerun' (Strand 1910: 29 – title). 'Kgl. zoologischen Museum' (Strand 1910: 29 – title) MNHU. [Invalid; junior primary honoym of *Papilio odin* Fabricius, 1793 (Riodinidae)].

Papilio adamastor v. *odin* Strand; Schultze, 1913*a*: 73; Schultze, 1917*a*: 535; Schultze, 1917*b*: 26, pl.16 fig.5; Bryk, 1930*b*: 563.

Graphium odin odin Strand; Berger, 1950: 83; D'Abrera, 1980: 44, 45 (fig.); Berger, 1981: 52, pl.17 fig. 2 (♂). 'Le specimen . . . [pl.17 fig. 2] . . . a un faciès voisin du vrai *odin*'.

Papilio (*Graphium*) *adamastor odin* (Str.); Peters, 1952: 21.

Graphium (*Arisbe*) *odin* (Strand); Munroe, 1961: 42; Hancock, 1983: 46.

Graphium auriger odin (Strand); Hancock, 1985*a*: 99 (as 'COMB. N.'); Collins & Morris, 1985: 57, 124.

Graphium (*Arisbe*) *auriger schoubotzi* [sic] =*odin* (Strand); Ackery, Smith & Vane-Wright, 1995: 162; d'Abrera, 1997: 50.

Graphium odin Eyeni Berger, 1950: 84. HOLOTYPE ♂: DEMOCRATIC REPUBLIC OF CONGO: 'Holotype: ♂, Bas Congo: Lemfu: 6–IV–30 (R. P. VAN EYEN) (Berger, 1950: 84). MRAC. fwl 39.2. 'Tervuren Museum ♂ Genitalia Slide N° Pa. 118.' **Syn. n.**

Graphium odin eyeni Berger; D'Abrera, 1980: 44.

Graphium odin schubotzi =*eyeni* Berger; Berger, 1981: 51 (as syn. n.).

Graphium auriger eyeni Berger; Hancock, 1985*a*: 100 (as 'COMB. N.').

Graphium (*Arisbe*) *auriger aurivilliusi* =*eyeni* Berger; Hancock, 1993: 568 (as syn. n.).

Graphium (*Arisbe*) *auriger eyeni* Berger; Ackery, Smith & Vane-Wright, 1995: 162; d'Abrera, 1997: 50.

TYPE EVALUATIONS

Schultze (1913*a*) described *Papilio* [*agamedes*] var. *schubotzi* from four specimens collected during Herzog Adolf-Friedrich zu Mecklenburg's second expedition to central Africa from the above two localities, but did not say how many were from each locality, nor did he specify a primary type. In his principal account of the Lepidoptera from that expedition, Schultze (1917*a*) illustrated the taxon with a specimen which he stated to be, '. . . dem Typus im Zool. Museum Hamburg', but did not identify its locality. Under the Code, Article 74.5 and 74.4 (ICZN, 1999), this constitutes the designation of that specimen as lectotype. The ZMUH was bombed in 1943 and, according to Horn *et al.* (1990), all the collections destroyed.

The paralectotype in SMNS has, in addition to a locality label and Schultze's determination label, a (?Schultze) collection number (182), and a hand written (probably Schultze's hand) determination/drawer label bordered in black and red. The paralectotype in FIF has, in addition to a locality label and Schultze's determination label, a (?Schultze) collection number (187), and a 'Senckenberg/Museum' label. The depository, locality and gender of Schultze's fourth specimen are not known to us.

Strand (1910) did not state his type series in his description of *Papilio odin*, and the provenance and depository above are taken from the title of the work. Schultze (1913*a*) stated that *odin* was described from one individual, thus restricting the type series to that one specimen as lectotype. A specimen in MNHU has, in addition to a locality label, an earlier Staudinger determination label (as '*Papilio* bei *ucalegon*') and Strand's determination label, an orange 'Type' label, confirming its identity as that lectotype.

Graphium odin Eyeni Berger (1950) was described from one specimen, with type designation original.

TAXONOMIC STATUS

Papilio [*agamedes*] var. *schubotzi* Schultze (1913*a*) was established as a vicariant variety within a group of taxa which Schultze (1913*a*) referred to as '*Papilio agamedes* Westw. und Verwandte', in which the author also included *odin*, *adamastor* and, tentatively, *aurivilliusi* (with *poggianus* as an especially light specimen of *adamastor*). In later works Schultze (1917*a*,*b*) applied the name *Papilio adamastor* var. *schubotzi*, perhaps recognising the seniority of Boisduval's species. Berger (1950) separated *odin* and *schubotzi* as a bitypic species. Berger (1981: 52, pl.17 fig.2) recorded and illustrated a specimen from Democratic Republic of Congo which he stated showed 'un faciès voisin de vrai *odin*.' Hancock (1985) synonymized the two, but placed them as a subspecies of *G. auriger*, which examination of the genitalia shows to be untenable. Our own studies have indicated that the characters used (e.g. by Berger, 1950) to differentiate *odin* and *schubotzi* show sufficient variability to undermine their separate taxonomic status. For example, the forewing discal cell mark of the lectotype of *odin* is large and triangular, as claimed to be characteristic of *schubotzi* (Berger, 1950). Berger (1950) further stated that the post-discal mark in the forewing cell M_2 of *odin* is absent or punctiform, but it is clearly present in the lectotype. We conclude, therefore, that *odin* and *schubotzi* are indeed synonymous, while perhaps showing some clinal variation in the frequency of some character states. Since the name *odin* is preoccupied, *Graphium schubotzi* should be used as a subjective replacement name for the monotypic species.

Strand (1910) established *Papilio odin* as a full species. Schultze (1913*a*, 1917*a*, 1917*b*) included it in a broad, polytypic interpretation of *P. agamedes*/*adamastor* and this was followed, at least in part, by later authors (e.g. Bryk, 1930*b*). Berger (1950) separated it as a bitypic species, with *P. adamastor schubotzi* Schultze (1913*a*). Hancock (1985) synonymized these two, but placed them as a subspecies of *G. auriger*. Subsequent authors have treated the taxon variously. Our own studies have confirmed the synonymy of *odin* and *schubotzi* and their independence from other species (see above). *Papilio odin* is the older name, but is pre-occupied by *P. odin* Fabricius (1793), itself a synonym of the oriental riodinid *Abisara echeria* (Stoll, [1790]). Despite the fact that confusion is very unlikely, *G. schubotzi* (Schultze) was treated as an available subjective replacement name by Ackery *et al.* (1995) and d'Abrera (1997).

Berger (1950) established *G. odin Eyeni* as a subspecies based on a single specimen. He differentiated it from *G. o. schubotzi* principally on the basis of the presence of a distal spot in the forewing discal cell and a somewhat narrower hindwing band. These features are variable in *G. schubotzi* and the former character is itself asymmetric in the holotype, being more prominent on the right wing. Berger (1981) himself synonymized it with *G. o. schubotzi*. Hancock (1985) included it as a subspecies of his broad *G. auriger*.

SIMILAR SPECIES

Generally rather undistinguished, but may be separated from other members of the clade by the following: lacks the clear submarginal marks shown by other members of the *adamastor* clade: *G. adamastor, agamedes, aurivilliusi, olbrechtsi* and *abri*. *G. schubotzi* is usually devoid of submarginal marks, with some specimens having very faint elements in some cells. Colour and its smaller size should distinguish it from other taxa with or without faint submarginals, such as *G. ucalegon, auriger, f. fulleri* and *f. ucalegonides*. *G. fulleri rileyi* is superficially very similar, but is generally somewhat larger, with less translucent forewings, the markings slightly yellower, and the black mark in hindwing underside cell R$_1$ is more concentrated into a basal spot or short streak. Unlike *G. ucalegon* and *simoni*, *schubotzi* does not have the distal part of the hindwing discal cell dusted with pale scales. Unlike *G. poggianus*, its forewing discal cell band does not cross the whole cell. *G. poggianus, G. k. kigoma* and *k. wranghami* also lack or have a highly reduced post-discal mark in forewing cell CuA$_1$.

The various subspecies of *G. almansor* generally lack a fully-formed post-discal mark in forewing upperside cell CuA$_1$, and/or the forewing discal band crosses the whole cell or is at least based on the radial vein.

DIAGNOSIS: PATTERN (Fig. 201)

Upperside dull brown becoming somewhat translucent peripherally, especially in the apical and distal areas of the forewing, with markings almost white. **Forewing** discal cell with roughly triangular mark opposite cell M$_3$, based along posterior discocellular vein and extending up to halfway across cell; sometimes interrupted by posterior intervenosa. Sometimes a small spot (often faint) opposite cell R$_5$. Cell R$_3$ with discal spot not reaching into angle of veins R$_3$ and R$_{4+5}$, but usually reaching root of R$_4$. Cell R$_4$ usually unmarked. Cell R$_5$ with post-discal mark deeply divided distally by intervenosa; usually no submarginal mark. Cell M$_1$ unmarked. Cell M$_2$ usually with a prominent post-discal mark largely confined to the area posterior to the intervenosa, with an anterior extension; no submarginal mark. Cell M$_3$ with post-discal mark usually reaching veins M$_3$ (or very nearly so), CuA$_1$ and the posterior discocellular vein, and usually well into the angles of these veins, rounded or slightly indented distally; no submarginal mark. Post-discal mark of cell CuA$_1$ variable in size, sometimes reaching all three surrounding veins, sometimes not, or barely, reaching any of them; no submarginal marks. Cell CuA$_2$ with submarginal mark not usually reaching posterior discocellular vein, sometimes either extensively or just reaching vein CuA$_2$, but always extensively reaching vein 1A, and extending almost to cell margin, often slightly indented basally by intervenosa; no submarginal mark. Cell 1A with post-discal mark.

Hindwing discal cell with pale mark reaching from near base usually reaching root of vein CuA$_1$ or nearly so, with a scattering of brown scales distally. Cell R$_1$ with post-discal mark indented distally by intervenosa; no submarginal marks. Cell R$_5$ with axillary mark usually indented distally; usually without submarginal mark. Cell M$_1$ without post-discal mark; the anterior element only of a subdivided submarginal mark sometimes present. Cell M$_2$ usually without a post-discal mark, but sometimes with a small spot slightly indented by the intervenosa; usually no submarginal mark, but sometimes the anterior element of a subdivided mark is present. Cell M$_3$ usually without post-discal mark, but sometimes with a subdivided mark comprising two small dots is present; usually no submarginal mark, but rarely either just the anterior or both elements of a subdivided mark is present. Cell CuA$_1$ with axillary discal mark present, sometimes extending to root of vein CuA$_1$; often indented distally and with a scattering of brown scales also distally; usually without a post-discal mark, but a small entire or subdivided mark sometimes present; usually no submarginal mark. Cell CuA$_2$ is white from base to near the margin (fused basal, discal and post-discal marks).

The **underside** pattern reflects that of the upperside, with the ground colour paler to reveal the intervenosae more clearly. On the hindwing there is a suffusion of orange which is especially noticeable in the pale marks. The hindwing discal cell shows two 'intervenosae', the posterior one sometimes reaching the tip of the cell near the root of vein M$_1$. In a few specimens there is the hint of a fork in this intervenosa. There is a prominent black spot in the angle of the hindwing humeral vein. Hindwing cell R$_1$ has a black basal streak more or less contiguous with the 'intervenosa' beyond the mark. The intensity of its expression is quite variable, ranging from a scattering of black scales to an almost solid line, but it is always clearly visible.

VARIATION

Some of the variation is detailed above, and there is the expected level of variation in the size of the markings. We have observed the following specific variants. Cell R$_4$ very occasionally shows very faint, subdivided submarginal mark (specimen in FIF). In the lectotype of *odin*, the post-discal mark of forewing cell R$_5$ is almost completely subdivided by the intervenosa; rarely, a faint, subdivided submarginal mark is present. Post-discal mark in cell M_2 variable, sometimes virtually absent, sometimes restricted to the area posterior to the intervenosa. The post-discal mark of cell M_3 shows some variation in size, sometimes not reaching vein M_3 and barely touching the other veins.

Hindwing cell R_5 sometimes has a faint, subdivided submarginal mark; in many of these specimens only the anterior element is at all clear. One specimen in MRAC shows a small, subdivided, but clear submarginal mark in cell CuA_1.

DIAGNOSIS: ♂ GENITALIA (Fig. 46)
Dorsal projection slightly curved dorsad. *Dorsal harpe* hook-like, extending beyond margin. *Ventral harpe* with short ventral blade barely reaching rim; dorsal blade somewhat larger, angled mesad. *Dorsal terminal process* relatively small, with ventral angle prolonged into point. *Ventral terminal process* broad, elongate, inner margin curved to face somewhat dorsad, denticulate at tip. The inner *rim* is notably broad ventrally and posteriorly, with its associated group of stout setae near its inner edge, near the tip of the ventral blade of the ventral harpe. *Uncus* rounded, *socii* prominent. *Saccus* short. *Aedeagus* slightly curved, not denticulate.

DIAGNOSIS: ♀ GENITALIA. No female specimen known to us.

EARLY STAGES; HOST PLANTS. Unknown.

DISTRIBUTION (Map Fig. 166). Records for Cameroon, Central African Republic, Congo, Democratic Republic of Congo.

BIONOMICS
Regarded here as monotypic, Darge (1995) notes this taxon (under the name *G. odin odin*) from Cameroon, flying mainly in November and December. Williams (1969) lists *G. odin* as a forest species, and claims that the sexes are alike. Berger (1950) gives records for Democratic Republic of Congo for January, June, September and October.

CONSERVATION STATUS. 'Not common but not threatened' (Collins & Morris, 1985: 57). Insufficiently known might be a better evaluation in the light of its revised specific status.

MATERIAL EXAMINED. 7 ♂♂ in BMNH. 24 ♂♂ from other collections.

29. *Graphium (Arisbe) olbrechtsi* Berger, 1950 stat. rev.

Olbrechts' Graphium (Figs 202, 227; map Figs 151, 153; genitalia Figs 47, 48)

Another rarely collected butterfly from the Congolese forests whose taxonomic status and relationships remain unclear, though apparently it is closely related to *G. schubotzi*. It was established by Berger (1950), who described a second subspecies, *tongoni*, in 1969. The two are linked by some weak characters including the lack of a basal, intervenosal, dark mark in hindwing underside cell R_1 and the presence of only one 'intervenosal' mark in the hindwing underside discal cell. The male genitalia are also very similar.

Hancock (1985) included *olbrechtsi* as a subspecies within his broadly-defined *G. auriger*, along with *tongoni*, *schubotzi* (as *odin*), and *eyeni*. This interpretation was followed by Collins & Morris (1985) and by Ackery, Smith & Vane-Wright (1995). Examination of the male genitalia of these taxa make such a view untenable. The valves of *G. olbrechtsi* (both subspecies), as well as *G. schubotzi*, are very similar to those of *G. agamedes*, with small ventral harpes and small, upward facing dorsal terminal processes. By contrast, the ventral harpe of *G. auriger* is large and distinctive, and its dorsal terminal process is larger and more nearly vertical. For further details, see the individual descriptions and figures.

The two subspecies are described separately.

EARLY STAGES; HOST PLANTS. Unknown.

BIONOMICS. Nothing appears to have been written about this species in nature. The original material was collected in February, August and November (Berger, 1950).

CONSERVATION STATUS. 'Uncommon and scarce . . . may deserve rare status. . . ' (Collins & Morris, 1985: 57).

29a. *G. (A.) olbrechtsi olbrechtsi* Berger, 1950 stat. rev.

(Fig. 202; map Fig. 151; genitalia Fig. 47)

Graphium Olbrechtsi Berger, 1950: 85, Fig. 82 (Holotype). HOLOTYPE ♂: DEMOCRATIC REPUBLIC OF CONGO: 'Holotype: 1 ♂, Sankuru: Mwene-Ditu: 21–VIII–35 (Ch. SEYDEL) (Berger, 1950: 85). MRAC. fwl 41.0 mm. 'Tervuren Museum ♂ Genitalia Slide N° Pa. 119.' (Genit prep. 4/43); 2 PARATYPE ♂♂: DEMOCRATIC REPUBLIC OF CONGO: 'Lualaba: Kafakumba: XII–30 (F. G. OVERLAET)' (Berger, 1950: 85). MRAC. '«Lomami River to Kinchu: 2–18–II–25» (Coll. JOICEY in British Museum).' (Berger, 1950: 85). BMNH Spec.Reg. No. 138834.

Graphium (Arisbe) olbrechtsi Berger; Munroe, 1961: 42; Hancock, 1983: 46.

Graphium olbrechtsi olbrechtsi Berger; D'Abrera, 1980: 44, 45 (fig.); Berger, 1981: 52, pl.17 fig. 1 (♂).

Graphium auriger olbrechtsi Berger; Hancock, 1985*a*: 100 (as 'comb. nov.'); d'Abrera, 1997: 50, 51 (fig.).

Graphium (Arisbe) auriger olbrechtsi Berger; Collins

& Morris, 1985: 57, 124; Ackery, Smith & Vane-Wright, 1995: 162.

TYPE EVALUATIONS

Graphium olbrechtsi Berger (1950) was described from the holotype and paratypes listed above, with type designations original. A further specimen from Sankuru: Mwene-Ditu in MRAC collected by Seydel (in MRAC) is excluded from the type series by date. Berger (1969) reported three topotypic male specimens in MRAC (of which we have seen two) in addition to the original type series. We have been able to recognize no further specimens in the collections we have been able to study.

TAXONOMIC STATUS

Graphium olbrechtsi Berger (1950) was established as a monotypic species. With the inclusion of *G. o. tongoni* Berger (1969) it is bitypic. Hancock (1985) included it in his broadly based, polytypic *G. auriger*, see above. Examination shows the male genitalia suggests a closer affinity with *G. agamedes*.

SIMILAR SPECIES

May be distinguished from the many similar species by the presence of just one intervenosal mark in the hindwing discal cell. Colour helps separate it from similarly marked species such as *G. agamedes* and *G. adamastor* (which has a reduced post-discal mark in forewing cell CuA$_1$, as does *G. poggianus kigoma*). The presence of hindwing post-discal marks (albeit sometimes faint) as well as the underside features distinguish it from *G. schubotzi*.

Distinguished from *G. o. tongoni* by its wing markings being pale cream rather than nearly white and by the forewing post-discal marks being less elongate. *G. o. olbrechtsi* has post-discal and submarginal marks in hindwing cells M$_1$ to CuA$_1$, which are absent (or virtually so) in *G. o. tongoni*.

DIAGNOSIS: PATTERN (Fig. 202)

Based on the holotype and Lomami River paratype.

Upperside ground colour brown, slightly translucent in the peripheral areas of the forewing, with marks pale yellowish cream. **Forewing** discal cell with mark opposite cell M$_3$ extending across about half of cell from posterior discocellular vein, interrupted by intervenosa; a further spot opposite cell R$_5$. Cell R$_3$ with discal mark reaching or just surpassing root of vein R$_4$; no submarginal mark. Cell R$_4$ with an elongate, slightly fuzzy post-discal mark; no submarginal mark. Cell R$_5$ with mark (probably fused discal and post-discal) indented distally by intervenosa; no submarginal mark. Cell M$_1$ with, at most (only seen in Lomami paratype) extremely small and faint post-discal mark subdivided by intervenosa; no submarginal mark. Cell M$_2$ with post-discal mark deeply indented by intervenosa, the posterior lobe somewhat larger than the anterior, especially in the holotype. In the holotype, very faint, subdivided submarginal marks can just be seen. Cell M$_3$ with a large post-discal mark, slightly concave distally, reaching the posterior discocellular vein and vein CuA$_1$, and almost, but not quite, vein M$_3$; the holotype shows a faint, fuzzy, subdivided submarginal mark, barely detectable in the Lomami paratype. Cell CuA$_1$ with post discal mark elongate, truncate distally, barely reaching the posterior discocellular vein or veins CuA$_1$ or CuA$_2$; holotype shows a faint, fuzzy, submarginal mark, barely detectable in the Lomami paratype. Post-discal mark of cell CuA$_2$ not reaching the posterior discocellular vein, barely reaching vein CuA$_2$, but running along vein 1A, indented proximally by intervenosa, convex distally; the submarginal mark represented by a hazy patch on the holotype. Cell 1A with post-discal mark convex proximally and distally.

Hindwing with pale mark filling most of discal cell extending almost to base and reaching beyond root of vein CuA$_1$, its edge slightly blurred and indented by intervenosa. Cell R$_1$ with discal/post-discal mark extending almost to base; faint, subdivided submarginal mark. In the holotype especially, the ground colour is paler in this cell, giving the appearance that the discal/post-discal mark is extended to include the submarginal. Cell R$_5$ with axillary post-discal mark almost reaching root of vein M$_1$, indented distally by intervenosa in the holotype; submarginal mark subdivided, the posterior element faint. Cell M$_1$ with post-discal spot faint in the holotype, clear in the Lomami paratype. Cell M$_2$ with post-discal spot clear in the Lomami paratype, smaller in the holotype. Cell M$_3$ with clear, subdivided post-discal mark in the Lomami paratype, in the holotype only the posterior element is clearly visible. Cells M$_1$ to M$_3$ all also have a faint, subdivided submarginal mark. Cell CuA$_1$ with axillary discal mark reaching vein CuA$_1$ or nearly so; clear post-discal spot; subdivided submarginal mark. Cell CuA$_2$ with silvery white mark extending to base and reaching level with the post-discal mark in cell CuA$_1$, then fading to margin.

The **underside** pattern reflects that of the upperside, but is paler, the veins particularly marked. Hindwing with small black spot in angle of humeral vein. Hindwing discal cell with only one visible intervenosal mark which branches distally in the holotype, but not in the Lomami paratype. There is no sign of a spot or line near the base of cell R$_1$.

VARIATION. See above.

DIAGNOSIS: ♂ GENITALIA (Fig. 47)

Based on the Lomami paratype. BMNH Spec.Reg. No. 138834. BMNH vial no. 4247.

Dorsal projection elongate, cylindrical, slightly upcurving distally. *Dorsal harpe* hook-like, extending beyond margin, carinate. *Ventral harpe* generally small, with dorsal blade the larger, directed mesad; ventral blade smaller, barely reaching rim, unlike the long, broad and curved blade of *G. auriger*. *Dorsal terminal process* small, with ventral angle prolonged into point, its face angled somewhat dorsad, as in *G. agamedes*. *Ventral terminal process* broad, length variable, inner margin curved to face somewhat dorsad, denticulate at tip, but not declivous as it is in *G. auriger*. Inner *rim* is notably broad ventrally and posteriorly, with its associated group of stout setae near its inner edge, near the tip of the ventral blade of the ventral harpe. *Uncus* quite narrow; *socii* prominent, with small projections. *Saccus* short. *Aedeagus* slightly curved, not denticulate.

DIAGNOSIS: ♀ GENITALIA. No females available for study.

EARLY STAGES; HOST PLANTS; BIONOMICS; CONSERVATION STATUS. See species account.

DISTRIBUTION (Map Fig. 151). Central and southern Democratic Republic of Congo. Known only from the type localites.

MATERIAL EXAMINED. 1 ♂ in BMNH. 4 ♂♂ from other collections.

29b. *G. (A.) olbrechtsi tongoni* Berger, 1969 stat. rev.

Maniema Graphium (Fig. 227; map Fig. 153; genitalia Fig. 48)

Graphium olbrechtsi tongoni Berger, 1969, 84. HOLOTYPE ♂: DEMOCRATIC REPUBLIC OF CONGO: 'Holotype ♂: Congo ex-belge: Maniema: Tongoni, 17.X.1955 (C. Alaerts) (Berger, 1969: 85). MRAC.; 1 PARATYPE ♂: DEMOCRATIC REPUBLIC OF CONGO: [Same data] (Berger, 1969: 85). MRAC; 1 PARATYPE ♂: 'Maniema, . . . entre Misisi et Kabambare, 16.X.1955 (C. Alaerts) (Berger, 1969: 85). MRAC.

Graphium olbrechtsi tongoni Berger; D'Abrera, 1980: 44; Berger, 1981: 52, pl.17 fig. 5 (♂ – HT).

Graphium auriger tongoni Berger; Hancock, 1985*a*: 100 (as 'comb. nov.'); d'Abrera, 1997: 50.

Graphium (*Arisbe*) *auriger tongoni* Berger; Ackery, Smith & Vane-Wright, 1995: 162.

TYPE EVALUATIONS

Graphium olbrechtsi tongoni Berger (1969) was described from the three specimens listed above, with type designations original.

TAXONOMIC STATUS

Graphium olbrechtsi tongoni Berger (1969) was established as a subspecies. Hancock (1985) transferred it into a more inclusive *G. auriger* along with *G. o. olbrechtsi*. In rejecting Hancock's hypothesis, we restore *tongoni* to its original status. The male genitalia, described below, corroborate this opinion.

SIMILAR TAXA

Berger (1969) distinguished *G. o. tongoni* from '*G. odin*' by having the post-discal marks of the forewing more clearly separated by well-marked veins, but this feature seems variable in the latter taxon (here regarded as synonymous with *G. schubotzi*). *G. o. tongoni* may, however, be distinguished from *G. schubotzi* by the lack of a basal dark streak in hindwing underside cell R_1 and by the presence of only a single 'intervenosal' mark in the hindwing underside discal cell, the latter character shared only with *G. o. olbrechtsi*.

Distinguished from *G. o. olbrechtsi* by its wing markings being nearly white rather than pale cream and by the forewing post-discal marks being more elongate. *G. o. olbrechtsi* has post-discal and submarginal marks in hindwing cells M_1 to CuA_1, which are absent (or virtually so) in *G. o. tongoni*.

DIAGNOSIS: PATTERN (Fig. 227)

Based largely on the holotype, photographed by CRS in MRAC and which is also illustrated in Berger (1981: pl.17 fig.5), and on a specimen on loan from ABRI.

Upperside ground colour brown, slightly translucent in the peripheral areas of the forewing, with marks more nearly white than in the nominate subspecies. **Forewing** without submarginal marks. Forewing discal cell with mark opposite cell M_3 extending from posterior discocellular vein about half way across cell subdivided by the posterior and, more clearly, by central 'intervenosae'; also a small apical spot opposite cell R_5. Cell R_3 with discal/post-discal mark not quite extending into angle of veins R_3 and R_{4+5}, but reaching root of R_4. Cell R_4 without marks. Cell R_5 with post-discal mark not reaching base of cell, indented by intervenosa, with the posterior lobe larger in the holotype, nearly equal in the ABRI specimen. Cell M_1 without marks. Cell M_2 with post-discal mark largely confined to posterior half, with just a small extension anteriorly, the mark reaching neither the posterior discocellular vein, nor veins M_2 nor M_3. Postdiscal mark of cell M_3 reaching posterior discocellular vein across most of its width, vein M_3 only basally and vein CuA_1 for a short stretch just distal of the base, slightly narrowing distally and shallowly indented by intervenosa. Post-discal mark of cell CuA_1 reaching posterior discocellular vein anteriorly, and reaching vein CuA_1, but not vein CuA_2, slightly tapering and truncate distally. Cell CuA_2 with post-discal mark broadly indented basally, not quite reaching posterior discocellular vein or vein CuA_2, but lying along vein 1A; truncate distally. Cell 1A with post-discal mark reaching vein 1A and inner margin.

Hindwing discal cell with pale mark extending to near base, but not reaching root of vein CuA_1 distally; distal margin slightly blurred. Cell R_1 with extensive discal/post-discal mark indented distally by intervenosa. Apart from the line of the intervenosa, cell R_1 is pale except at margin (from photographs it is hard to determine whether this is from the presence of pale scales or reduction of brown ones), this paleness subsuming faint, subdivided submarginal mark. Cell R_5 with axillary discal mark, indented distally by intervenosa; extremely faint, subdivided submarginal mark present. Cells M_1 to M_3 with, at most, barely detectable, subdivided post-discal marks. Cell CuA_1 with axillary discal mark barely reaching vein CuA_1; the rest of the cell, apart from the intervenosa, slightly pale. Cell CuA_2 with discal/post-discal mark occupying most of cell.

The **underside** pattern largely reflects that of the upperside. In addition, however, there appears to be a small discal mark in forewing cell R_5, though this may be an artefact caused by photographic flash. The hindwing discal cell has just one visible 'intervenosa' and that faint and confined to the distal part of the cell. No post-discal or submarginal marks are visible on the hindwing.

VARIATION

A worn specimen from Maniema, Democratic Republic of Congo, on loan from ABRI has the markings slightly more extensive than the holotype. The post-discal marks in forewing cells M_3 and CuA_1 reach the posterior discocellular vein across the whole cell width, and each runs along the veins anterior and posterior to them.

DIAGNOSIS: ♂ GENITALIA (Fig. 48)

Based on a specimen loaned from MRAC + specimen from Maniema, Democratic Republic of Congo (ABRI)

Very similar to *G. o. olbrechtsi*, and with the same differences from *G. auriger*. *Dorsal projection* elongate, cylindrical, slightly upcurving distally. *Dorsal harpe* hook-like, extending beyond margin, carinate. *Ventral harpe* with dorsal blade large, directed mesad; ventral blade small, barely reaching rim. *Dorsal terminal process* small, with ventral angle prolonged into point. *Ventral terminal process* broad, elongate, inner margin curved to face somewhat dorsad, denticulate at tip. Inner *rim* is notably broad ventrally and posteriorly, with its associated group of stout setae near its inner edge, near the tip of the ventral blade of the ventral harpe. *Uncus* quite narrow, *socii* prominent, with small projections. *Saccus* short. *Aedeagus* slightly curved, not denticulate.

DIAGNOSIS: ♀ GENITALIA. Female unknown.

EARLY STAGES; HOST PLANTS; BIONOMICS; CONSERVATION STATUS. See species account.

DISTRIBUTION (Map 153). Known only from the type localities. [N.B. including specimen in ABRI from Maniema]

MATERIAL EXAMINED. 3 ♂♂ in MRAC, 1 ♂ from ABRI.

30. *Graphium* (*Arisbe*) *abri* sp. n.

Collins' Graphium (Figs 203–205; map Fig. 160; genitalia Figs 49, 50)

Graphium (*Arisbe*) *abri* HOLOTYPE ♂: CENTRAL AFRICAN REPUBLIC: 'Zongo/RCA/xi · 85/S.C. COLLINS COLL' (Label data). ABRI. PARATYPE ♂: CENTRAL AFRICAN REPUBLIC: 'GRAPHIUM/♂/FORME/18 xii 82 RCA' (Label data). ABRI.

TAXONOMIC STATUS. Though described from just two individuals, we consider this taxon distinct enough to be regarded as a full species.

SIMILAR SPECIES. With its almost total lack of post-discal marks, *Graphium abri* is unlikely to be confused with any other taxon.

DIAGNOSIS: PATTERN (Figs 203–205)

Upperside ground colour dark brown, becoming somewhat translucent peripherally, especially in the apical and distal areas of the forewing. This is more noticeable on the holotype, where it affects even the hindwing, and is the result of narrowing of the scales. The pale marks are almost white. **Forewing** discal cell with a band comprized of small white marks separated by the intervenosae opposite cell M_3. In the holotype these marks are very faint and not seen in the space adjacent to the posterior discocelluar vein; they are clearer in the paratype, though that adjacent to the posterior discocelluar vein is faint and that by the radial vein small. There is also a mark near the apex of the discal cell, larger and clearer in the paratype than in the holotype. Cell R_3 with an axillary discal spot. In the holotype only there is a small submarginal mark posterior to the intervenosa. Cell R_4 with subdivided submarginal mark. Cell R_5 with small post-discal mark and subdivided submarginal mark, the posterior element being somewhat the larger. Cells M_1 and M_2 with subdivided submarginal marks, those in the paratype fainter than in the holotype. Cell M_3 with undivided (holotype) or subdivided submarginal marks. Cell CuA_1 with undivided submarginal mark. Cell CuA_2 with subdivided submarginal marks. Cell 1A unmarked.

Hindwing discal cell with a somewhat diffuse mark, subdivided by 'intervenosae' more clearly defined in the holotype. Cells R_1 to CuA_1 each with subdivided submarginal marks. In addition, cell R_1 has a diffuse discal mark, much larger and clearer in the paratype. Cells R_5 and CuA_1 have an axillary discal mark, in each case very small, faint and diffuse in the holotype. Cell

CuA_2 has an elongate basal/discal mark which is quite silvery.

The **underside** pattern reflects that of the upperside. The ground colour is paler and suffused with orange on the hindwing and the intervenosae better defined. The black mark with its central white tuft at the base of radial and cubital veins characteristic of the clade is well marked. There is a black spot in the angle of the humeral vein and a short linear intervenosal mark near the base of cell R_1.

DIAGNOSIS: ♂ GENITALIA (Figs 49, 50)
The lack of a dorsal blade on the ventral harpe, together with the broad rim strongly suggest close relationship with *G. adamastor* and *G. agamedes*.

Dorsal projection cylindrical, curved dorsad. *Dorsal harpe* hook-like, extending beyond margin. *Ventral harpe* without dorsal blade, the ventral blade small. *Dorsal terminal process* small, with ventral angle prolonged into point. *Ventral terminal process* broad, elongate, inner margin curved to face somewhat dorsad, denticulate at tip. The inner *rim* is notably broad ventrally and posteriorly, with its associated group of stout setae near its inner edge; *Uncus* tapering; *socii* small but prominent. *Saccus* short. *Aedeagus* short, slightly curved.

DIAGNOSIS: ♀ GENITALIA; EARLY STAGES; HOST PLANTS; CONSERVATION STATUS. Unknown.

DISTRIBUTION (Map Fig. 160). Known only from the types from CAR, the holotype being from Zongo on the Ubangi river, near Bangui.

BIONOMICS. We presume that this is another rare forest species, from the relatively low-lying Bangui district.

COMMENT. We name this small, dark and handsome butterfly after the African Butterfly Research Institute (ABRI) founded by Steve Collins, who loaned us the specimens. Again, more specimens and observations are needed to gain a better understanding of its nature, relationships, range and biology.

MATERIAL EXAMINED. The two male types from ABRI.

31. ***Graphium (Arisbe) almansor*** (Honrath, 1884)

Friar Graphium (Figs 206, 228–231; map Figs 161–165; genitalia Figs 51, 52, 98)

A well established polytypic species of *Amauris* mimics found as a series of subspecies throughout much of central tropical Africa from Togo to Tanzania, with populations or subspecies also found in southern Sudan (Yei District) and south-western Ethiopia. The subspecies are united by the form of their genitalia, especially the characteristic, hook-like ventral terminal process. Their wing patterns are quite diverse and are described separately, below. They are unusual in that, where the forewing discal cell band is incomplete, it fails to reach the posterior discocellular vein, rather than the radial vein, as is the case in other species.

EARLY STAGES. Despite the following (unconfirmed) host record, the early stages are unknown or unrecorded.

HOST PLANT RECORDS
Ackery *et al.* (1995) list *Pseudospondias* (Anacardiaceae), evidently based on the late Jan Kielland's (1990: 46) record for *P. microcarpa*. The status of this potentially very interesting record is uncertain, but clearly confirmation or refutation is required.

BIONOMICS
Forested areas, such as Kakamega (*C. a. uganda*), riverine forests in Mara and Nyanza (Larsen, 1996), gallery forests in the Central African Republic (*G. a. escherichi* [as *carchedonius*: Hecq & Peeters, 1992, who included a colour photograph of the butterfly resting on a leaf]), forests and heavy woodlands in W. Tanzania (Kielland, 1990), and wooded savannahs in Democratic Republic of Congo (Fontaine, 1985: 114). In West Africa, Larsen (1996b) describes this species, together with *G. adamastor*, as 'specifically adapted to the transition zone between forest and savannah', where it is never found in dense forest or open savannah, but only in the marginal areas of gallery or riverine forests, and savannah-forest mosaics. Thus in West Africa these species are exclusive to a narrow region where dry forest meets the Guinea savannah, in which they occur at rather low density (Larsen, 1996b). In the southern part of its range, *almansor* is recorded from heavy *Brachystegia* woodland. Larsen (pers. comm.) encountered *almansor* in huge numbers on damp sand in Volta and Obudu, but in general it is perhaps an uncommon and local species, apparently occurring throughout the year (Williams, 1969). Vertical range: up to 1500 m (Kielland, 1990; Ackery *et al.*, 1995). Temporal records: Jan., Dec. (Larsen, In prep.*a*).

CONSERVATION STATUS
The species is 'Not threatened' according to (Collins & Morris, 1985: 57), but the status of some of the more restricted subspecies, notably those in the North East, is worthy of further investigation.

31a. *G. (A.) **almansor almansor*** (Honrath, 1884)

Honrath's Friar Graphium (Fig. 206; map Fig. 165; genitalia Fig. 51)

Papilio almansor Honrath, 1884: 210, pl 7, f 9.

LECTOTYPE ♂: ? DEMOCRATIC REPUBLIC OF CONGO: '. . . von Guinea, der ersten Expedition des Dr. Pogge in's Innere Afrika . . .'. (Honrath, 1884: 210). MNHU –designated Berger (1950: 80).1
PARALECTOTYPE ♂: [FALSE LOCALITY]: '. . . Ashanti . . . ' (Honrath, 1884: 210). BMNH Spec.Reg. no. 138720.

Papilio almansor Honrath; Aurivillius, 1908: 24.

Papilio almansor [*almansor*] Honrath; Bryk, 1930*b*: 564.

Papilio (*Graphium*) *almansor almansor* (Honrath); Peters, 1952: 21.

Graphium (*Arisbe*) *almansor* (Honrath); Munroe, 1961: 42; Hancock, 1983: 46; Collins & Morris, 1985: 57.

Graphium almansor Honrath; D'Abrera, 1980: 44, 45 (fig.).

Graphium almansor almansor Honrath; Berger, 1950: 80, figs 75–8; Berger, 1981: 51, pl.16 figs 1 (♂), 6 (♀); Hancock, 1985*a*: 101; Kielland, 1990: 46, 326 fig.22; d'Abrera 1997: 52, 53 (fig.).

Graphium (*Arisbe*) *almansor almansor* (Honrath); Ackery, Smith & Vane-Wright, 1995: 160.

SYNONYMS

Graphium almansor kigoma 'dry season form' Kielland, 1978: 160; pl.4 figs 15, 16. [misidentification – see *G.* (*A.*) *kigoma* Carcasson.]

Graphium almansor almansor =*kigoma* dry season form *sensu* Kielland; Hancock, 1985*a*: 101; Kielland, 1990: 46.

Graphium almansor wranghami 'dry season form' Kielland, 1978: 160, pl.5 19, 20 ('dry season form'). PARATYPE ♂♂: TANZANIA: 4: 'Paratypes (d[ry]. s[eason]. f[orm].) Tanzania, Kigoma, Gombe Stream Nat. Park, December, 1972, J. Kielland.' (Kielland, 1978: 161). NMK, BMNH and coll. J. Kielland (Kielland, 1978: 161) – not seen. [misidentification – see *G.* (*A.*) *kigoma* =*wranghami* Kielland.]

Graphium almansor almansor =*wranghami* dry season form, Kielland; [Hancock, 1985*a*: 100].

UNAVAILABLE NAMES

Graphium almansor almansor f. *albescens* Berger, 1950: 81. DEMOCRATIC REPUBLIC OF CONGO. MRAC. [infrasubspecific]

Graphium almansor almansor f. *depuncta* Berger, 1950: 81. DEMOCRATIC REPUBLIC OF CONGO. MRAC. [infrasubspecific]

TYPE EVALUATIONS

Papilio almansor Honrath (1884) was described from 2 specimens: one sent to the author from 'Ashanti'; the other collected by Pogge in 'Guinea' (Honrath, 1884: 210). However, Horn *et al.* (1990) stated that Pogge made an expedition to 'Lualaba und dem Kassai-Land', southern Democratic Republic of Congo, in 1882, the specimens from which went to MNHU. Berger referred to the Guinea specimen as the 'type' and the 'Ashanti' specimen as 'paratype', thus restricting the type series.

The 'Guinea' specimen itself is readily identifiable in MNHU, matching closely Honrath's (1884) figure. It bears a locality label reading 'Guinea inter/Pogge', a determination label reading 'Almansor/Honrath *' and a further determination label also giving the reference. These labels appear to have been written by H. Dewitz, who was curator of the collection at the time (Horn *et al.*, 1990: 91, pl.8 fig.1). A further printed label gives a collection number of 21304. The specimen is illustrated here (Fig. 206).

According to Horn *et al.* (1990), Honrath's own collection went to the BMNH, via H.J. Adams (Adams Bequest BMNH Accession Register No. 1912–399). A specimen of *almansor* in BMNH from the Adams Bequest has a label reading 'Almansor mihi/Ashanti' and a small label with just the letter 'H' [? for Honrath]. This had been given a round BMNH 'Type' label by an earlier curator. We assume that this is Honrath's 'Ashanti' specimen and consider it the paralectotype. The taxon is found from Angola eastwards to Tanzania and is not known from Ashanti, Ghana.

For type evaluations of *Graphium almansor wranghami* dry season form, Kielland (1978), see account of *G. kigoma*.

TAXONOMIC STATUS

Papilio almansor Honrath (1884) was established as a monotypic species. Le Cerf (1924) incorporated *P. uganda* Lathy (q.v.) as an infrasubspecific form, but it was not until Bryk (1930) incorporated *P. uganda*, *P. carchedonius* Karsch, *P. escherichi* (and *P. graueri* Grünberg) as varieties (= subspecies), that its polytypic nature was recognized. That status has been accepted by subsequent authors.

Kielland (1978) described a 'dry season form' of *G. almansor kigoma* Carcasson (1964 – here included as *G. kigoma*). It is clear from the plate that this form was a misidentification of *G. a. almansor*, as subsequently recognized by Hancock (1985a) and accepted by Kielland (1990).

Graphium almansor wranghami Kielland (1978) was described in both wet and dry season forms. Hancock (1985*a*) recognized that the type series was mixed. He regarded the wet season form – represented by the holotype and five paratypes – as a genuine new taxon, which he subsequently (Hancock, 1985*b*) included as a subspecies of *G. poggianus* (we include it as a synonym of *G. kigoma*); the dry season form – including four paratypes – he recognized as another misidentification of *G. a. almansor*.

SIMILAR TAXA

Distinguished from other mimetic species of the clade by the forewing discal cell band extending from the radial vein towards – but not usually reaching – the posterior discocellular vein. The band is less extensive than in other subspecies, apart from *G. a. uganda*, in which the markings are much darker. The distal mark in the forewing discal cell, when present, is also useful.

DIAGNOSIS: PATTERN (Fig. 206)

Upperside ground colour dark brown with pale marks white. On the hindwing, areas of ground colour include orange-brown scales, giving a lighter and more blurred pattern.

Forewing discal cell with a transverse band opposite cell M$_3$ not usually reaching the posterior discocellular vein, but reaching the radial vein (or very nearly so). Usually a further mark distally in cell opposite cell R$_5$. Cell R$_3$ with a post-discal mark reaching just beyond root of vein R$_4$ and somewhat indented distally. Cell R$_4$ sometimes with a faint to clear mark in angle of veins R$_4$ and R$_5$; rarely with a very faint subdivided submarginal mark (sometimes represented by a few, scattered white scales). Cell R$_5$ with a large post-discal mark, deeply indented distally, or even completely subdivided, by the intervenosa; subdivided submarginal mark usually present, with the posterior element considerably the larger. Cell M$_1$ usually unmarked. Cell M$_2$ usually with a small to elongate post-discal mark confined to posterior half of cell. Cell M$_3$ with oblong post-discal mark not usually reaching the posterior discocellular vein, nor veins M$_3$ and CuA$_1$; a faint to clear, sometimes subdivided submarginal mark usually present. Cell CuA$_1$ usually with a small, distally placed post-discal spot present on midline of cell, and a faint to clear submarginal mark. Cell CuA$_2$ with post-discal mark not reaching vein CuA$_2$, and a faint to clear submarginal mark. Cell 1A with post-discal mark usually contiguous with that in cell CuA$_2$, the vein 1A sometimes clearly marked.

Hindwing discal cell with band usually reaching to the tip, sometimes with a small dark area – or scattering of brown scales – distal to the line between the roots of veins M$_1$ and CuA$_1$; the band also reaches to near the base of the cell. Cell R$_1$ with broad (discal + post-discal) band gradually fading to orange-brown distally and usually indented by intervenosa; a faint, bifid submarginal mark sometimes detectable. Cell R$_5$ with post-discal mark extending beyond root of vein M$_1$ and indented by intervenosa; faint to clear, bifid submarginal mark usually present. Cell M$_1$ with more-or-less extensive linear post-discal mark usually confined to anterior half of cell; usually a faint to clear submarginal mark present in anterior half of cell only. Cell M$_2$ sometimes with a pale mark at the base, along the lower discocellular vein and extending somewhat along veins M$_2$ and M$_3$; otherwise a scattering of white scales is usually present at the base of the cell; a faint, bifid submarginal mark usually present, often with a line of paler brown connecting it with the base of the cell, either side of the midline. Cell M$_3$ with a pale mark at the base, along the posterior discocellular vein and extending somewhat along veins M$_3$ and CuA$_1$ and usually with faint to clear, bifid submarginal mark connected to basal mark by pale brown lines. Cell CuA$_1$ similar. Cell CuA$_2$ with extensive mark of silvery scales reaching almost to base.

As usual, the **underside** pattern largely reflects that of the upperside, but with the ground colour paler, especially on the hindwing, and the intervenosae more obvious. Near the wing bases, especially of the hind wing, the ground colour becomes reddened. Some of the forewing spots have nacreous surrounding areas, but this is much less extensive or clear than in some other taxa (e.g. *G. fulleri*). There is a black mark in the angle of the humeral vein in hindwing costal cell, but no proximal black mark in cell R$_1$.

VARIATION

Much of the variability is indicated above. In particular, the submarginal marks, especially those of the hindwing upperside are variable in extent, visibility and even presence. Noteworthy variation includes:

Presence of an additional spot in forewing R$_4$ of (as in f. *albescens*).

Submarginal mark of forewing cell R$_5$ sometimes faint.

Cell M$_2$ post-discal mark sometimes absent.

Post-discal mark of hindwing cell M$_1$ occasionally extending into posterior half of cell proximally; in a few other examples the mark is subdivided into proximal and distal elements. The submarginal mark in cell M$_1$ may be absent.

Submarginals may be absent from hindwing cell M$_2$, but this is independent of the presence of a white mark in the base of the cell: in some specimens with a clear basal mark, there is no indication of a submarginal mark.

DIAGNOSIS: ♂ GENITALIA (Fig. 51)

Dorsal projection quite stout, slightly directed anteriad, slightly upcurved, cluster of stout setae at tip. *Dorsal harpe* quite broad, with dorsal extension short. *Ventral harpe* with broad ventral blade slightly curved mesad, pointed posteriorly (in the specimen examined (Spec.Reg. no. 138721), there is a pre-apical tooth on the dorsal, exterior margin on the right hand valve only); dorsal blade of similar length, pointed, curved somewhat mesad distally. *Dorsal terminal process* quite small, curved dorsally; a broad point ventrally. *Ventral terminal process* a narrow ventrad- and mesad-curved hook (in the specimen examined, the tip is bifid on the right hand valve only). *Rim* quite narrow. *Uncus* tapering, *socii* prominent, with prominent projections. *Saccus* small. *Aedeagus* quite short, curved near the base.

DIAGNOSIS: ♀ GENITALIA

BMNH Spec.Reg. No. 138740; vial 3269: *ostium bursae* opening anteriorly; *ductus bursae* not extended, sclerotized, kinked, constricted or pocketed distally; *central ostial lobe* broad, sclerotized, glabrous and indented at tip; *lateral ostial lobes* setose, long, broad, not well sclerotized; *anterior apophyses* present; *papillae* elongate dorsally.

EARLY STAGES; HOST PLANTS; BIONOMICS; CONSERVATION STATUS. See species account.

DISTRIBUTION (Map Fig. 165). Records from: Democratic Republic of Congo, Burundi, Angola, Uganda, Tanzania, Zambia, Malawi.

MATERIAL EXAMINED. 23 ♂♂, 4 ♀♀ in BMNH. 45 ♂♂, 4 ♀♀ from other collections.

31b. *G. (A.) almansor birbiri* Ungemach, 1932

Youbdo Friar Graphium (Fig. 228; map Fig. 162)

Papilio charcedonius [*sic*] *birbiri* Ungemach, 1932: 21. HOLOTYPE ♂: ETHIOPIA: '. . . Youbdo, en novembre 1926 . . .' (Ungemach, 1932: 21). MNHN; PARATYPE ♂: ETHIOPIA: same data. MNHN

Papilio (*Graphium*) *almansor birbiri* Ungemach; Peters, 1952: 21.

Graphium (*Arisbe*) *almansor birbiri* (Ungemach); Carcasson, 1981: 123; Ackery, Smith & Vane-Wright, 1995: 160.

Graphium almansor birbiri Ungemach; D'Abrera, 1980: 44; Hancock, 1985*a*: 102; d'Abrera, 1997: 52.

TYPE EVALUATIONS

Papilio charcedonius [*sic*] *birbiri* Ungemach (1932) was described from the two specimens listed above, with type designations original. The specimens concerned are in MNHN and are clearly labelled. A third Ungemach specimen in MNHN must be excluded from the type series.

TAXONOMIC STATUS

Papilio charcedonius [*sic*] *birbiri* Ungemach (1932) was established as a subspecies of *carchedonius*. By this time, this latter taxon had been itself included as a subspecies of *almansor* (Bryk, 1930*b*). Peters (1952) included *birbiri* as a subspecies of *almansor*, and this status has been accepted by subsequent authors. It is very similar to the West African *G. a. carchedonius* and the more south-westerly distributed *G. a. almansor*, but the slight differences shown in the few specimens we have seen, together with its disjunct distribution, suggest that subspecific status is justifiable.

SIMILAR TAXA

The forewing discal cell band in *G. a. birbiri* is generally larger than in *G. a. almansor*, though less so than *G. a. escherichi*. This band is generally broader than in *G. a. carchedonius*. There is no distal mark in the forewing discal cell, unlike *G. a. almansor*. The post-discal mark in forewing cell M_2 is generally smaller than that in *G. a. carchedonius*.

DIAGNOSIS: PATTERN (Fig. 228)

Upperside ground colour brown, with markings white. On the hindwing, the ground colour is a little paler, showing the intervenosae more clearly. The **Forewing** discal cell has a transverse band not reaching posterior discocellular vein (sometimes very nearly so); interrupted by anterior 'intervenosa' and with at least a line of brown scales marking the other 'intervenosae' (in the holotype these form a distinct, if fuzzy, dark patch in the centre of the band); no mark more distal in cell. Cell R_3 with post-discal mark not, or barely reaching root of vein R_4. Cell R_4 usually unmarked, though the holotype has a few white scales basally. Cell R_5 with a linear, bifid post-discal mark; in most examples, a very faint, bifid, submarginal mark can just be seen. Cell M_1 unmarked. Cell M_2 with a small post-discal mark, confined to posterior half of cell. Post-discal mark of cell M_3 sometimes reaching veins M_3, CuA_1 and the posterior discocellular vein (for part of cell width); submarginal mark faint or very faint, often bifid. Cell CuA_1 either lacking a post-discal mark (both of the types) or with a small distal mark on the midline. In one specimen in BMNH (Spec.Reg. No. 138822) there is a patch of mixed brown and white scales extending proximad from the post-discal mark. There is a small diffuse submarginal mark also in this cell. Cell CuA_2 with post-discal mark arcuate anteriorly, not reaching vein CuA_2; submarginal mark faint or very faint. Post-discal mark of cell 1A more-or-less contiguous with that of cell CuA_2.

Hindwing discal cell usually with band reaching tip, but with some brown scales at or near the tip. Usually no submarginal marks on hindwing, but one specimen in BMNH (Spec.Reg. No. 138822) shows very faint traces in cells R_5 and M_1. Cell R_1 with broad post-discal band deeply indented distally by intervenosa. Cell R_5 with discal mark normally extending beyond root of vein M_1; deeply indented distally by intervenosa. Cell M_1 with mark in angle of vein M_1 and middle discocellular vein rarely extending posterior to intervenosa. Cell M_2 with pale scales (sometimes very few) along lower discocellular vein, usually extending along veins M_2 and M_3. Cell M_3 with pale scales along posterior discocellular vein and extending along veins M_3 and CuA_1. Cell CuA_1 with pale scales along posterior discocellular vein and extending along veins CuA_1 and CuA_2. Cell CuA_2 with single white mark crossing cell from level with proximal edge of discal cell band to level with distal margin of marking in cell CuA_1.

The **underside** pattern reflects that of the upperside, but the ground colour is paler, becoming brick red towards the wing bases (especially of the hindwing), and the intervenosae consequently more marked. Hindwing with black spot in angle of humeral vein. In some specimens there is a linear black spot in cell R_1 on the midline, near the base.

VARIATION. See above.

DIAGNOSIS: ♂ GENITALIA

Dorsal projection quite stout, slightly directed anteriad, slightly upcurved, cluster of stout setae at tip. *Dorsal harpe* quite broad, dorsal extension quite short. *Ventral harpe* with broad ventral blade slightly curved mesad, pointed posteriorly; dorsal blade of similar length, pointed, curved somewhat mesad distally. *Dorsal terminal process* quite small, curved dorsally; a broad point ventrally. *Ventral terminal process* a narrow ventrad- and mesad-curved hook. *Rim* quite narrow. *Uncus* tapering, *socii* prominent, with prominent projections. *Saccus* small. *Aedeagus* quite short, curved near the base.

DIAGNOSIS: ♀ GENITALIA. No specimens available for examination.

EARLY STAGES; HOST PLANTS; BIONOMICS; CONSERVATION STATUS. See species account.

DISTRIBUTION (Map Fig. 162). South-western Ethiopia.

MATERIAL EXAMINED. 3 ♂♂ in BMNH. 3 ♂♂ in MNHN.

31c. *G.* (*A.*) *almansor carchedonius* (Karsch, 1895)

Togo Friar Graphium (Fig. 229; map Fig. 161; genitalia Fig. 52)

Papilio carchedonius Karsch, 1895: 285. LECTOTYPE ♂: TOGO: '. . . Hinterlande von Togo: Bismarckburg . . . 15. März bis 15. April 1891, ♂: Dr. R. Büttner; . . .' (Karsch, 1895: 286). MNHU, **here designated.** PARATYPE ♀: TOGO: same locality and collector, 'Jan. 1891' (Karsch, 1895: 286). MNHU. PARATYPE ♂: TOGO: same locality, '28. Dec. 1889, ♂, Hauptmann Eugen Kling' (Karsch, 1895: 286). MNHU. PARATYPE ♂♂: TOGO: Misahöhe (4. und 31. März 1894, 4. April 1893, 8. und 16. April 1894, Mai 1893, 18., 24. und 25. Oct., 1. Nov. und 7. und 9., Dec. 1893, nur ♂♂, Ernst Baumann . . .).' (Karsch, 1895: 286). MNHU.

Papilio carchedonius Karsch; Aurivillius, 1899: 486.

Papilio almansor v. *carchedonius* Karsch; Bryk, 1930*b*: 564.

Papilio (*Graphium*) *almansor carchedonius* Karsch; Peters, 1952: 21.

Graphium almansor carchedonius (Karsch); D'Abrera, 1980: 44, 45 (fig.); d'Abrera, 1997: 52, 53 (fig.) [as stat. rev.].

Graphium (*Arisbe*) *carchedonius* (Karsch); Hancock, 1983: 46.

Graphium (*Arisbe*) *adamastor* =*carchedonius* (Karsch); Hancock, 1985*a*: 100 (as syn. n.); Collins & Morris, 1985: 57; Ackery, Smith & Vane-Wright, 1995: 160.

Graphium (*Arisbe*) *almansor carchedonius* (Karsch); Larsen, in prep.

INCORRECT SUBSEQUENT SPELLING

Papilio charcedonius Karsch; Aurivillius, 1908 (German and French versions): 24, pl.9 row c. [misspelling]

UNAVAILABLE NAMES

Papilio (*Cosmodesmus*) *charcedonius* [sic] ab. *guineensis* Dufrane, 1946: 120. GUINEA. IRSN [Infrasubspecific].

Papilio (*Cosmodesmus*) *charcedonius* [*sic*] ab. *houzeaui* Dufrane, 1946: 120. GUINEA. IRSN [Infrasubspecific].

TYPE EVALUATIONS

Papilio carchedonius Karsch (1895) was described from the provenances listed above, but the author (an entomologist at MNHU from 1878–1921, according to Horn *et al.*, 1990) did not state exactly how many. There must have been at least 15, of which 5 were seen in MNHU by CRS. One of these is a male from Bismarckburg, collected by R. Büttner and bears *inter alia* a label apparently in Karsch's hand (See Horn *et al.*, 1990: pl.9 fig.60) reading, 'Papilio/carchedonius/ Karsch ∗'. The asterisk probably indicates that it was intended as the type and so we select this as lectotype.

A specimen in BMNH (Spec.Reg. No. 138829; ex Rothschild Bequest, BMNH Accession No. 1939–1) has a printed blue locality label reading 'Togo/ Bismarckburg/L.Conradt S.'; a rectangular, red, printed 'Type' label wih 'Co' and '♂' added by hand (both of these labels conforming to labels in MNHU); and a pencil written date label of '25/X. 93'. Despite the locality and type labels, this does not appear to be listed by Karsch (1895) and so should not be included in the type series. Neither should a specimen (Spec.Reg. No. 138831, ex Adams Bequest (BMNH 1912–399)) from Misahöhe, collected Baumann, 1893 (but without precise date), with 'Co'Type label as above and a determination label in Niepelt's hand.

TAXONOMIC STATUS

Papilio carchedonius Karsch (1895) was established as a species. Bryk (1930) was apparently the first to treat it as a variety (= subspecies) of *P. almansor*, though gave no argumentation. Hancock (1985) synonymized *carchedonius* with *G. adamastor* on the basis of features of the male genitalia. However, Hancock has subsequntly informed us (pers. comm.) that he did so on the basis of misidentified specimens. Certainly, our examination shows that *carchedonius* shares the characteristic hook-like ventral terminal process with other subspecies of *G. almansor* (see Fig. 52). D'Abrera (1997) restored *carchedonius* as a subspecies of *G. almansor*, and Larsen (In prep.*a* and *pers. comm.*) shares this opinion.

The incorrect subsequent spelling, *charcedonius*, was introduced by Aurivillius (1908) in the German and French versions, but not in that author's earlier works (e.g.1899) or in the English version. This spelling was followed by some later authors (e.g. Ungemach, 1932; Dufrane, 1946).

SIMILAR TAXA

Lacks the distal forewing discal cell mark of *G. a. almansor*, though the cell band is more complete, usually approaching the posterior discocellular vein. The hindwing discal cell band is more extensive, usually reaching the cell tip.

Except in well marked individuals (e.g. abs *guineensis* and *houzeaui*) the forewing discal cell band is narrower than *G. a. escherichi* and does not form such a conspicuous, contiguous band as neither the cell band nor the post-discal mark of cell M$_3$ reaches the posterior discocellular vein.

In *G. a. birbiri*, the forewing discal cell band is more quadrate – not conspicuously narrowing towards the costa.

Colour and the more extensive system of submarginal spots serves to differentiate *G. a. uganda*.

DIAGNOSIS: PATTERN (Fig. 229)

Overall colour and pattern similar to *G. a. almansor*.

Forewing discal cell with a transverse band opposite cell M$_3$ not usually reaching the posterior discocellular vein, but reaching the radial vein; narrowing costally; sometimes interrupted by the anterior 'intervenosa'. No mark in cell distal to this band. Cell R$_3$ with a post-discal mark reaching just beyond root of vein R$_4$ and somewhat indented distally. Cell R$_4$ usually with a faint and diffuse mark in angle of veins R$_4$ and R$_5$. Cell R$_5$ with a large subdivided post-discal mark contiguous with subdivided submarginal mark. Cell M$_1$ usually unmarked. Cell M$_2$ with post-discal mark largely confined to posterior half, but extending anteriad proximally, to a greater or lesser extent; no submarginal mark. Cell M$_3$ with post-discal mark not usually reaching any of the surrounding veins M$_3$, CuA$_1$ or the posterior discocellular vein; a faint to clear, usually bifid submarginal mark present. Cell CuA$_1$ usually without a post-discal mark; a faint to clear submarginal mark present. Cell CuA$_2$ with elongate post-discal mark, smoothly curved anteriorly, not reaching vein CuA$_2$; a faint to clear submarginal mark usually present. Cell 1A with post-discal mark contiguous with that in cell CuA$_2$.

Hindwing discal cell with band stretching from root of vein R$_1$ to tip, with at most a scattering of brown scales at tip. Cell R$_1$ with broad post-discal mark, usually becoming golden distally and indented by intervenosa. Cell R$_5$ with post-discal mark extending beyond root of vein M$_1$, indented distally. Cell M$_1$ with small faint to clear post-discal mark in angle of vein M$_1$ and middle discocellular vein, largely confined to anterior half of cell, but sometimes with a scattering of white scales posterior to intervenosa; faint to clear submarginal mark present in anterior half of cell. Cell M$_2$ with a white mark along lower discocellular vein, fading distally, but sometimes extending along veins M$_2$ and M$_3$; small, faint, bifid submarginal mark sometimes present. Cell M$_3$ with a basal white mark, extending along veins M$_3$ and CuA$_1$, fading distally; faint, bifid submarginal mark usually present. Basal white mark of cell CuA$_1$ occupying much of basal half of cell, but sometimes confined largely to margins; faint, bifid submarginal mark occasionally present. Cell CuA$_2$ with white mark extending from close to base to level with distal edge of white mark in cell CuA$_1$.

Underside pattern reflecting that of the upperside, but with the ground colour paler, especially on the hindwings. Sometimes a small, faint, somewhat nacreous post-discal mark visible distally and on the midline in forewing cell CuA$_1$, even when the equivalent mark is not present on the upperside. Black spot present in angle of hindwing humeral vein, but not basally in cell R$_1$. Hindwing discal cell 'intervenosae' pale orange, the posterior one sometimes appearing bifurcate distally.

VARIATION

In addition to the variability indicated above, the following particular variants may be noted.

In well-marked specimens, such as abs *guineensis* and *houzeaui*, the post-discal mark of forewing cell M$_3$ may reach the surrounding veins. In well-marked specimens a small post-discal mark may be present distally in cell CuA$_1$; in ab. *guineensis*, this extends towards the angle of the posterior discocellular vein and vein CuA$_1$ as a slightly fuzzy mark.

DIAGNOSIS: ♂ GENITALIA (Fig. 52)

Dorsal projection quite stout, slightly directed anteriad, slightly upcurved, cluster of stout setae at tip. *Dorsal harpe* broad, dorsal extension short. *Ventral harpe* with broad ventral blade slightly curved mesad, pointed posteriorly; dorsal blade of similar length, pointed, curved somewhat mesad distally (in the specimen examined (Spec.Reg. no. 138840), the blades on the right hand valve are both short). *Dorsal terminal process* quite small, curved dorsally; a broad point ventrally. *Ventral terminal process* a narrow ventrally and mesally curved hook. *Rim* quite narrow. *Uncus* tapering, *socii* prominent, with prominent projections. *Saccus* small. *Aedeagus* quite short, curved near the base.

DIAGNOSIS: ♀ GENITALIA. No specimens dissected.

EARLY STAGES; HOST PLANTS; BIONOMICS; CONSERVATION STATUS. See species account.

DISTRIBUTION (Map Fig. 161).

West Africa: according to Larsen (1996b) (Guinea to

Togo), where it is sympatric with *G. adamastor* and *G. agamedes*.

Berger (1950), gave a wider range, from Guinea to Central African Republic and neighbouring areas of Democratic Republic of Congo, but this appears to be the result of confounding the subspecies with *G. a. escherichi*, which he also included.

MATERIAL EXAMINED. 6 ♂♂ in BMNH. 10 ♂♂, 1 ♀ from other collections.

31d. *G. (A.) almansor escherichi* (Gaede, 1915)

Escherisch's Friar Graphium (Fig. 230; map Fig. 163)

Papilio escherichi Gaede, 1915: 71. HOLOTYPE ♂: CENTRAL AFRICAN REPUBLIC: 'Type: 1 ♂ 'Carnot, Neu-Kamerun XI. 13 . . .' (Gaede, 1915: 71). MNHU (not seen); 3 PARATYPE ♂♂: ?CENTRAL AFRICAN REPUBLIC: '. . . 3 ♂♂ von Carnot und Toro N. K., Sammler Forstmeister Escherisch' (Gaede, 1915: 71). MNHU (not seen).

Papilio carchedonius v. *escherichi* Gaede; Schultze, 1917*b*: 26, pl.16 fig.4.

Papilio almansor v. *escherichi* Gaede; Bryk, 1930*b*:

Papilio (*Graphium*) *almansor escherichi* Gaede; Peters, 1952: 21.

Graphium almansor escherichi Gaede; D'Abrera, 1980: 44; Berger, 1981: 51, pl.16 fig. 7 (♂); Hancock, 1985*a*: 102; d'Abrera, 1997: 52.

Graphium (*Arisbe*) *almansor escherichi* (Gaede); Ackery, Smith & Vane-Wright, 1995: 160.

SYNONYM

Graphium almansor snowi Gabriel, 1945: 151. HOLOTYPE ♂: SUDAN: 'B.M. Type No. Rh. 15072, S. Sudan, Dec., 1939, ♂' (Gabriel, 1945: 151). BMNH. Spec.Reg. no. 138824; 2 PARATYPE ♂♂: Same provenance, '. . . B.M. Type No. Rh. 15073–4 . . .' (Gabriel, 1945: 151). BMNH. Spec.Reg. nos 138825, 138826.

Graphium almansor escherichi = *snowi* Gabriel; Hancock, 1985*a*: 102 [as syn. n.].

Graphium (*Arisbe*) *almansor escherichi* = *snowi* Gabriel; Ackery, Smith & Vane-Wright, 1995: 160.

INCORRECT SUBSEQUENT SPELLING

Papilio (*Graphium*) *almansor mowi* Gabriel; Peters, 1952: 21.

TYPE EVALUATIONS

Papilio escherichi Gaede (1915) was described from the four specimens listed above, with holotype designation original. The description was in a paper titled 'Neue afrikanische Lepidoptera des Berliner Zoologischen Museums' [MNHU], but CRS did not find the types when he visited that institution.

Graphium almansor snowi Gabriel (1945) was described from the three specimens listed above, with type designations original. The specimens concerned are clearly labelled in BMNH.

TAXONOMIC STATUS

Papilio escherichi Gaede (1915) was established as a species. Schultze (1917*b*) treated it as a variety (= subspecies) of *P. carchedonius*; Bryk (1930) treated both as varieties of *P. almansor* and subsequent authors have included *escherichi* as a subspecies of the latter. Its different wing pattern, but similar genitalia support that status.

Graphium almansor snowi Gabriel (1945) was established as a subspecies, with the statement that it is 'readily distinguished from the other races of *almansor* by the large continuous discal band of the fore wing'. This feature is also characteristic of *G. a. escherichi*, of which Gabriel (1945) made no mention. Hancock (1985) stated it to be a synonym of *G. a. escherichi*, but without argumentation. Apart from the broad, continuous discal cell band, the holotype and one paratype of *snowi* show a scattering of pale scales in forewing cell CuA_1, also seen in *G. a. escherichi*, so we accept the synonymy.

SIMILAR TAXA

G. a. escherichi may be distinguished from other subspecies by the forewing discal band crossing the whole cell, being broadest along the posterior discocellular vein. It thus somewhat resembles *G. adamastor*, which has a post-discal spot distally on the midline of forewing cell CuA_1 and the hindwing discal cell band not reaching the cell tip; and *G. p. poggianus*, in which the hindwing discal cell band also does not reach the cell tip.

DIAGNOSIS: PATTERN (Fig. 230)

Upperside ground colour mid- to chocolate brown, with marks white.

Forewing discal cell with transverse band opposite cell M_3 crossing whole cell from posterior discocellular vein – where it is broadest, extending to midline of cell M_2 or nearly so – to the radial vein; sometimes interrupted by anterior 'intervenosa'. Cell R_3 with post-discal mark reaching or slightly surpassing root of vein R_4, often slightly diffuse distally and often indented distally. Cell R_4 usually with a sparse scattering of white scales proximally, sometimes forming a very faint post-discal spot. Cell R_5 with an elongate, bifid post-discal mark, the posterior element usually the broader and longer; sometimes a faint or very faint, bifid submarginal mark. Cell M_1 unmarked. Cell M_2 with post-discal mark largely confined to posterior half of cell, sometimes extending anterior to the intervenosa basally. Cell M_3 with quadrate post-discal mark reaching veins M_3, CuA_1, and the posterior discocellular vein, sometimes extending into angle of the latter two; sometimes a clear or faint, sometimes bifid submarginal mark present. Cell CuA_1 sometimes with a clear white mark present in angle of vein CuA$_1$ and the posterior discocellular vein, becoming diffuse postero-distally; in some specimens there is merely a scattering of pale scales here; and in others no visible mark. This is apparently not homologous with the post-discal mark as one specimen in BMNH also has a small post-discal mark more distally in the midline, on one wing connected with the proximal mark by a diffuse scattering of scales. A faint, sometimes diffuse, submarginal mark also usually present. Cell CuA$_2$ with post-discal mark arcuate anteriorly, not usually reaching vein CuA$_2$; diffuse, sometimes bifid submarginal mark usually present. Cell 1A with elongate post-discal mark contiguous with that in cell CuA$_2$.

Hindwing discal cell with band reaching tip of cell, sometimes with a few brown scales, or even a brown mark, near the tip. Cell R$_1$ with more-or-less extensive post-discal mark, indented distally. Cell R$_5$ with post-discal mark extending beyond root of vein to a variable extent; deeply indented by intervenosa; rarely a very small, very faint submarginal mark present. Cell M$_1$ with mark in angle of vein M$_1$ and middle discocellular vein rarely extending posterior to the intervenosa; occasionally a very faint post-discal mark present anterior to midline, and a faint submarginal mark; all three may be connected by a scattering of pale scales. Cell M$_2$ with pale scales along lower discocellular vein, usually extending along veins M$_2$ and M$_3$. Cell M$_3$ with pale scales along posterior discocellular vein and extending along veins M$_3$ and CuA$_1$. Cell CuA$_1$ with pale scales along posterior discocellular vein and extending along veins CuA$_1$ and CuA$_2$; in some cases, these coalesce, so the entire base of the cell is white, with a distal indentation. Cell CuA$_2$ with single white mark crossing cell from level with proximal edge of discal cell band to level with distal margin of marking in cell CuA$_1$.

The **underside** pattern reflects that of the upperside, but the ground colour is paler, becoming brick red towards the wing bases (especially of the hindwing), and the intervenosae consequently more marked.

Hindwing with black spot in angle of humeral vein. In some specimens there is a linear black spot in cell R$_1$ on the midline, near the base.

VARIATION. See above.

DIAGNOSIS: ♂ GENITALIA

Dorsal projection quite stout, slightly directed anteriad, slightly upcurved, cluster of stout setae at tip. *Dorsal harpe* broad, dorsal extension short. *Ventral harpe* with ventral blade broader than in the nominate race, slightly curved mesad, pointed posteriorly; dorsal blade slightly shorter, pointed, curved somewhat mesad distally (in BMNH Spec.Reg. no. 138827, there is a further, smaller blade or large tooth arising from the ventral, just posterior to the dorsal, but on the right valve only). *Dorsal terminal process* quite small, curved dorsally; a broad point ventrally. *Ventral terminal process* a narrow ventrad- and mesad-curved hook. *Rim* quite narrow. *Uncus* tapering, *socii* prominent, with prominent projections. *Saccus* small. *Aedeagus* quite short, curved near the base.

DIAGNOSIS: ♀ GENITALIA. No specimens available for examination.

EARLY STAGES; HOST PLANTS; BIONOMICS; CONSERVATION STATUS. See species account.

DISTRIBUTION (Map Fig. 163). From eastern Nigeria, Cameroon, Central African Republic, northern Democratic Republic of Congo to southern Sudan and Uganda, and possibly Congo.

MATERIAL EXAMINED. 7 ♂♂ in BMNH. 13 ♂♂ from other collections.

31e. *G. (A.) almansor uganda* (Lathy, 1906)

Uganda Friar Graphium (Fig. 231; map Fig. 164; genitalia Fig. 98)

Papilio uganda Lathy, 1906: 9, pl 2, f 11. LECTOTYPE ♂: UGANDA: '*Hab.* ENTEBBE, Uganda' (Lathy, 1906: 9). BMNH Spec.Reg. No. 138741 **here designated**; PARALECTOTYPE ♂♂: UGANDA: Same data. BMNH Spec.Reg. Nos. 138742, 138743.

Papilio almansor form *uganda* Lathy; Le Cerf, 1924*a*: 396 [as stat. n.].

Papilio almansor v. *uganda* Lathy; Bryk, 1930*b*: 564.

Papilio (*Graphium*) *almansor uganda* Lathy; Peters, 1952: 21.

Graphium almansor uganda (Lathy); D'Abrera, 1980: 44, 45 (fig.); Berger, 1981: 51, pl.16 figs 3 (♂); Hancock, 1985*a*: 102; Kielland, 1990: 46; d'Abrera, 1997: 52, 53 (fig.).

Graphium (*Arisbe*) *almansor uganda* (Lathy); Ackery, Smith & Vane-Wright, 1995: 160.

SYNONYM

Papilio graueri Grünberg, 1908: 58. HOLOTYPE ♂: UGANDA: 'Uganda, 1 ♂' (Grünberg, 1908: 60). (not seen).

Graphium almansor v. *graueri* Grünberg; Bryk, 1930*b*: 565

Papilio (*Graphium*) *almansor graueri* Grünberg; Peters, 1952: 21.

Graphium almansor uganda =*graueri* (Grünberg); Hancock, 1985*a*: 102 (as syn. [n.]).

Graphium (*Arisbe*) *almansor uganda* =*graueri* (Grünberg); Ackery, Smith & Vane-Wright, 1995: 160.

TYPE EVALUATIONS

In his description of *Papilio uganda*, Lathy (1906) gave no indication of series length, but gave a range of size and drew attention to one specimen having darker markings. He stated that the types of all the species decribed in the paper were in H. J. Adams' collection, which was bequeathed to BMNH as BMNH Accession Register No. 1912–399. A specimen from the Adams Bequest in BMNH has a determination label in Lathy's hand stating it to be 'Spec.[imen] typicum ♂', though the provenance, on a small printed label is given only as 'Uganda'. This was labelled as 'type' by an earlier curator and we legitimize that by selecting that specimen as lectotype. It is very similar to the specimen illustrated (by Horace Knight) in Lathy (1906). Two further specimens from the Adams Bequest, with provenance of Entebbe, should be regarded as paralectotypes. Further type material might be in the Royal Scottish Museum, Edinburgh, where the bulk of the Adams Bequest is now housed.

Papilio graueri Grünberg (1908) was described from a single male, but the author gave no information concerning the type depository. Horn *et al.* (1990) were unable to give any information on the whereabouts of his collection.

TAXONOMIC STATUS

Papilio uganda Lathy (1906) was established as a species and treated as such by subsequent authors. Le Cerf (1924) stated '. . . cette espèce n'est qu'une forme de *P. almansor* à laquelle elle est rattachée par toutes les transitions'. Bryk (1930) treated is as a variety (= subspecies) of *P. almansor*, a status which has been accepted by authors since. Its pattern is distinct from the other subspecies, but the form of the male genitalia firmly links it with them.

Papilio graueri Grünberg (1908) was established as a species. Bryk (1930) treated is as a variety (= subspecies) of *P. almansor*, and this was followed by Peters (1952). Carcasson (1981) did not include it in his checklist, but it appears to have been Hancock (1985) who first stated it to be a synonym of *G. almansor uganda*. This is clearly correct. Grünberg (1908) distinguished *graueri* from *uganda* by the presence of a black mark in hindwing underside cell R$_1$, but this is not uncommon in the latter. Coupled with its overall appearance, as shown in Grünberg's (1908) figure, and locality, separation is untenable.

SIMILAR TAXA

The relative reduction of the wing markings (contrasted with prominent hindwing submarginal marks) and their usually ochraceous colour on the posterior part of the forewing and entire hindwing, serve to distinguish *G. a. uganda* from the other subspecies, and from other mimetic species of the clade.

DIAGNOSIS: PATTERN (Fig. 231)

Considered by Poulton (1928) to be mimetic of *Amauris crawshayi oscarus* Thurau (Nymphalidae: Danainae). The putative '*echeria* mimicry complex' is discussed and illustrated by Vane-Wright & Boppré (1993). See also Discussion

Upperside ground colour mid- to chocolate brown. Wing markings white on anterior part of forewing (cell M$_3$ and anterior, together with the discal cell), usually cream to ochraceous on posterior part of forewing (cells CuA$_2$ and 1A) and entire hindwing. **Forewing** discal cell with a narrow band opposite cell M$_3$ not reaching the posterior discocelluar vein, not or barely surpassing the posterior 'intervenosa'; usually interrupted by the other 'intervenosae', especially the anterior. Cell R$_3$ with a generally small, but clear post-discal mark usually just surpassing root of vein R$_4$ and indented distally. Cell R$_4$ usually with small (sometimes very faint) post-discal mark in angle of veins R$_4$ and R$_5$; occasionally with faint, bifid submarginal mark. Cell R$_5$ with prominent, bifid post-discal mark in the form of paired streaks separated by the intervenosa; bifid submarginal mark usually also prominent, but sometimes faint. Cell M$_1$ often unmarked, but sometimes with (usually very faint) indications of post-discal and submarginal marks, especially anterior to intervenosa. Cell M$_2$ often unmarked, but sometimes with a small, linear (and sometimes faint) post-discal and/or submarginal mark in posterior half of cell. Cell M$_3$ with post-discal mark varying from a small, elliptical, linear feature (as in the lectotype) to a quadrate block, but never reaching the surrounding veins; submarginal mark small to prominent, sometimes bifid. Cell CuA$_1$ usually without post-discal mark; small and faint to prominent, sometimes bifid submarginal mark. Cell CuA$_2$ with small post-discal mark usually cream to ochraceous, not reaching vein CuA$_2$, usually reaching vein 1A; submarginal mark small and faint to large and prominent. Cell 1A with post-discal mark usually small, and usually reaching vein 1A.

Hindwing discal cell band variable in extent, sometimes reaching barely to root of vein CuA$_1$; sometimes more-or-less reaching cell tip, but even here with a scattering of brown scales. Peripheral cells of hindwing (cells R$_5$ to CuA$_1$ and sometimes cell R$_1$) generally with prominent, bifid submarginal marks, but these may be reduced – or even absent – in some or all cells. Cell R$_1$ with post-discal mark generally paler than in other hindwing cells, indented distally, sometimes fading into ground colour distally. Cell R$_5$ with post-discal mark not usually reaching root of vein M$_1$; indented distally. Cell M$_1$ usually without post-discal mark. Cell M$_2$ often with pale scales along the lower discocellular vein and vein M$_3$. Cell M$_3$ usually with pale scales along the posterior discocellular vein and veins M$_3$ and CuA$_1$; a few examples possess a clear, if faint, separate, bifid, post-discal mark. Cell CuA$_1$ usually with pale scales along the posterior discocellular vein and along veins CuA$_1$ and CuA$_2$. Cell CuA$_2$ with discal/post-discal band extending to end of androconial roll in males; in females, it does not cross the cell and reaches barely past the root of vein CuA$_2$.

The **underside** pattern reflects that of the upperside, but with the ground colour paler and the intervenosae consequently more prominent. The ground colour tends towards brick red at the wing bases, especially the hindwing. In **forewing** cell CuA_1 there is often a small post-discal mark of somewhat nacreous appearance, even when there is no corresponding mark on the upper side. On the **hindwing** there is a black mark in the angle of the humeral vein. In cell R_1 there is usually a patch of black scales near the base along the line of the intervenosa; in the majority of specimens, this is marked enough to form a coherent spot or streak (as described in *graueri*).

VARIATION

Within a distinctive overall 'gestalt', *G. a. uganda* shows a degree of variability in the colour, presence, size and exact disposition of markings unusual even in this clade. It is possible that there is a certain amount of gene flow with the nominate subspecies. Apart from the variation indicated above, the following may be noted.

In some specimens (including the lectotype) the hindwing markings may be pale cream; in a few they are almost white, as on the anterior part of the forewing.

The post-discal mark in forewing cell R_4 may be absent, as may the submarginal mark.

Forewing cell CuA_1 may have a small, elliptical, distal, post-discal mark (or even a scattering of white scales) along the midline.

One specimen in BMNH (Spec.Reg. No. 138775 – locality unknown) lacks any submarginal marks.

Hindwing cell M_1 sometimes has a faint post-discal mark in the base of the cell, usually confined to the anterior half.

DIAGNOSIS: ♂ GENITALIA

Dorsal projection quite stout, slightly directed anteriad, slightly upcurved, cluster of stout setae at tip. *Dorsal harpe* broad, dorsal extension short. *Ventral harpe* with ventral blade broader than in the nominate race slightly curved mesad, pointed posteriorly; dorsal blade slightly shorter, pointed, curved somewhat mesad distally; *Dorsal terminal process* quite small, curved dorsally; a broad point ventrally. *Ventral terminal process* a narrow ventrad- and mesad-curved hook. *Rim* quite narrow. *Uncus* tapering, *socii* prominent, with prominent projections. *Saccus* small. *Aedeagus* quite short, curved near the base.

DIAGNOSIS: ♀ GENITALIA (Fig. 98)

BMNH Spec.Reg. No. 138782; vial 3976: *ostium bursae* opening anteriorly; *ductus bursae* not extended, sclerotized, kinked, constricted or pocketed distally; *central ostial lobe* broad, sclerotized and truncate at tip; *lateral ostial lobes* setose, long, broad (almost touching), not well sclerotized; *anterior apophyses* present; *papillae anales* elongate dorsally.

EARLY STAGES; HOST PLANTS; BIONOMICS; CONSERVATION STATUS. See species account.

DISTRIBUTION (Map Fig. 164). Uganda, and neighbouring areas of western Kenya, north-western Tanzania and extreme eastern Democratic Republic of Congo (Rutshuru, Kivu: Berger,1981).

MATERIAL EXAMINED. 84 ♂♂, 5 ♀♀ in BMNH. 10 ♂♂ from other collections.

32. *Graphium (Arisbe) auriger* (Butler, 1876) stat. rev.

Gabon Graphium (Fig. 207; map Fig. 143; genitalia Figs 53, 101)

On the basis of its distinctive pattern and male genitalia, we here treat *Graphium (Arisbe) auriger* as a monobasic species.

Papilio auriger Butler, 1876: 57. LECTOTYPE ♂: GABON: 'Gaboon' (Butler, 1876: 57). BMNH Spec.Reg. No. 141675 – **here designated**. 2 PARALECTOTYPE ♂♂: GABON: same data. BMNH Spec.Reg. Nos 141676, 141677.

Papilio auriger Butler; Aurivillius, 1899: 485; Aurivillius, 1908: 23, pl.3b; Bryk, 1930*b*: 560.

Papilio (Graphium) auriger (B.); Peters, 1952: 21.

Graphium (Arisbe) auriger (Butler); Munroe, 1961: 42; Hancock, 1983: 46; Collins & Morris, 1985: 57.

Graphium auriger Butler; D'Abrera, 1980: 42, 43 (figs).

Graphium auriger auriger Butler; Hancock, 1985*a*: 99 [? As stat. n.]; d'Abrera, 1997: 50, 51 (figs).

Graphium (Arisbe) auriger auriger (Butler); Ackery, Smith & Vane-Wright, 1995: 161.

SYNONYM

Papilio harpagon Grose-Smith, 1890: 224. LECTOTYPE ♂: GABON: 'Gaboon' (Grose-Smith, 1890: 224). Designated Le Cerf (1924: 396). BMNH Spec.Reg. No. 141710; 2 PARALECTOTYPE ♂♂: GABON: same data. BMNH Spec.Reg. Nos 141711, 141712.

Papilio auriger =*harpagon* Grose-Smith; Druce, 1895: 333 [as syn. n.]; Aurivillius, 1899: 485.

Papilio auriger ab. *harpagon* Grose-Smith; Bryk, 1930*b*: 560.

Graphium auriger auriger =*harpagon* (Grose-Smith); Hancock, 1985*a*: 99.

Graphium (Arisbe) auriger auriger =*harpagon* (Grose-Smith); Ackery, Smith & Vane-Wright, 1995: 161.

TYPE EVALUATIONS

Butler (1876) described *P. auriger* in a paper 'Description of three new species of *Papilio* from the collection of Mr. Herbert Druce', but did not state the number of specimens in his type series. Three male specimens from 'Gaboon' from the Druce collection are in the BMNH, which they reached via the Godman and Salvin collection (BMNH 1918–4). All of these should be considered to belong to the type series. One bears a determination label stating it to be the 'Type', though this does not appear to be in Butler's hand (possibly Druce's). This has been considered the holotype and has been labelled with a BMNH round 'Type/H.T.' label by an earlier curator, and is the specimen selected here as lectotype to avoid further possible confusion. Butler (1876) gave the 'Expanse of wings' as '3 inches, 10 lines' (approx 9.8 cm). However, the wingspan (as set) of the largest of the presumed type series is only 8.45 cm – that of the lectotype 8.3 cm.

Grose-Smith (1890) did not state the original series length in his description of *Papilio harpagon*, but it must have been more than one as he states that there were specimens in his own and in Crowley's collections. A specimen in the BMNH from Grose-Smith's collection (via Joicey Bequest, BMNH 1934–120) bears a hand written 'Type' label and a determination label (possibly a drawer label) reading 'Harpagon Grose Smith/Gaboon Type'; both appear to be in Grose-Smith's hand. This was considered to be the holotype by Le Cerf (1924) and has been labelled with a BMNH round 'Type/H.T.' label by an earlier curator. Under the Code (ICZN, 1999), Article 74.6, Le Cerf's restriction constitutes the selection of a lectotype. Two specimens in BMNH from the Crowley Bequest (BMNH 1901–78) – one with labels stating it to be from 'Gaboon'; the other without provenance – are here considered paralectotypes.

TAXONOMIC STATUS

Papilio auriger Butler (1876) was established as a species.

Hancock (1985) regarded it as the nominate race of a polytypic species, in which he also included *schubotzi* Schultze (as a synonym of *odin* Strand), *eyeni* Berger, *tongoni* Berger and *olbrechtsi* Berger as subspecies. This usage was followed by Ackery *et al.* (1995) and d'Abrera (1997). Apart from the distinctive coloration and pattern of *auriger*, examination of the male genitalia shows this to be untenable. *G. schubotzi*, *eyeni*, *tongoni* and *olbrechtsi* all have very similar valves, with small dorsal and, especially, ventral harpes, small and oblique dorsal terminal processes and more-or-less horizontal ventral terminal processes. By contrast, *G. auriger* has a larger dorsal and, especially, ventral harpe (the latter quite characteristic), a larger, nearly vertical dorsal terminal process, and a ventrally directed ventral terminal process. Accordingly, we regard *G. auriger* as a monotypic species and treat *G. schubotzi* (with *odin* and *eyeni* as synonyms), and *G. olbrechtsi* (with *tongoni* as a subspecies) as distinct, species-level taxa.

Papilio harpagon Grose-Smith (1890) was established as a species. It was synonymized with *P. auriger* Butler (1876) by Druce (1895); a status accepted by subsequent authors (some treating it as a male aberration).

SIMILAR SPECIES

The generally darker background colour distinguishes *G. auriger* from most other members of the *adamastor* clade, including those taxa included as subspecies of *auriger* by Hancock (1985). The underside background is particularly dark; and a dark base to the hindwing, with a bright orange mark confined to the costal cell distal to the humeral vein appears characteristic. *G. ucalegon* may be similarly dark above, but its hindwing underside wing base is orange, with black spots.

DIAGNOSIS: PATTERN (Fig. 207)

Upperside background colour very dark brown (nearly black) slightly translucent on the apical/distal areas of the forewing due to narrowing of scales. Markings pale cream coloured. No submarginal marks present on either wing. **Forewing** discal cell with variably sized mark along posterior discocellular vein by cells M_2 to M_3 usually extending slightly beyond posterior intervenosa. Occassionally also a diffuse spot opposite cell R_5. Cell R_3 with axillary discal spot, sometimes becoming diffuse distally. Cell R_4 usually without marks. Cell R_5 with basal mark (probably fused discal and post-discal marks) extending slightly beyond root of vein R_4, divided distally by intervenosa. Cell M_1 usually without marks. Cell M_2 with post discal mark, usually confined mainly to posterior half, with an extension along posterior discocellular vein. Cell M_3 with post-discal mark filling most of basal half of cell, reaching posterior discocellular vein and veins M_3 and CuA_1 – all three veins being well marked by dark scales. Cell CuA_1 with post-discal mark spanning cell, reaching posterior discocellular vein in anterior half. Cell CuA_2 with no basal or discal marks; post-discal mark spanning cell, but not reaching posterior discocellular vein. Cell 1A with no basal or discal marks; post-discal mark spanning cell, in line with that in cell CuA_2.

Hindwing discal cell without basal band, the main band reaching or surpassing the root of vein CuA_1, with a scattering of pale scales in the area immediately distal to the band (not reaching the end of the cell). Costal cell without basal band, the one transverse band white. Cell R_5 white basally, to approximately level with discal cell band, but with brown indentations along the upper discocellular vein and vein R_5, and 'notched' distally by the intervenosa. Cells M_1 and M_2 without pale marks. Cell M_3 with white scaling just distal to posterior discocellular vein and for a short distance (≤ 3 mm) anterior to vein CuA_1. Cell CuA_1 with basal discal mark broadly indented distally by intervenosa. Cell CuA_2 with discal mark originating along posterior discocellular vein level with base of discal cell mark, terminating level with that in cell CuA_1.

The **underside** pattern reflects that of the upperside, though the colours of both background and pale marks are less intense. The intervenosae are more noticeable. In the **hindwing** discal cell there are two clear intervenosae: one projecting proximad from the line of vein M_1; the other in line with the intervenosa of cell M_1. The area of the costal cell proximal to the humeral vein (with small extensions beyond this vein and into the pre-costal cell) are vivid orange. There is a large, round, black mark (largely) just distal to the humeral vein, and a more elliptical one – less clear against the background – at the base of cell R_1. There is a small tuft of white scales on the base of the radial and cubital veins at their combined origin.

The **female** is very similar, but the apical/distal areas of the forewing are distinctly more translucent (see also Oremans, 1995: 600, fig.4).

VARIATION
Over and above the normal variability in the size and exact shape of the marking, we have observed the following variants:

Forewing discal cell band sometimes confined to area posterior to posterior intervenosa, more usually extending somewhat beyond (sometimes quite diffuse); forewing discal cell occasionally with a diffuse pale patch opposite cell R_5, sometimes forming a clear spot; forewing cell R_4 sometimes with an axillary post-discal mark, or a more diffuse area of pale scales; one specimen in BMNH (Spec.Reg. No. 141706) has a small post-discal spot anterior, and a much fainter mark posterior to the intervenosa in cell M_1, but this is asymmetrical, with the marks on the left wing being cleare than those on the right; the post-discal mark in cell M_2 sometimes projects distad anterior to the intervenosa; on the hindwing underside, the size and shape of the orange and black basal marks is quite variable; the posterior intervenosa of the hindwing discal cell may sometimes bifurcate distally.

DIAGNOSIS: ♂ GENITALIA (Fig. 53)
Dorsal projection cylindrical, based below valve rim, slightly upcurved distally. *Dorsal harpe* a simple hook, carinate on mesal face. *Ventral harpe* with horizontal blade considerably larger than vertical, ending at a point, almost reaching valve margin, broad and sometimes somewhat sinuate proximally; the dorsal blade angled posteriad and curved mesad. This feature distinguishes *G. auriger* from those taxa included as subspecies by Hancock (1985). Only *G. almansor* has a similarly well-developed ventral harpe. *Dorsal terminal process* relatively large (c.f. *G. schubotzi* and *olbrechtsi*), curved mesad, expanding dorsally and ventrally. *Ventral terminal process* rounded, directed somewhat ventrad, serrate. *Uncus* long, *socii* projecting laterally. *Saccus* short. *Aedeagus* long, curved, not denticulate.

DIAGNOSIS: ♀ GENITALIA (Fig. 101)
BMNH Spec.Reg. No. 141731; vial 5445: *vestibulum* transverse; *ostium bursae* opening anteriorly; *ductus bursae* not sclerotized, kinked/constricted or pocketed distally; *central ostial lobe* glabrous, broad, truncate, almost reaching tip of laterals, slightly indented at tip; *lateral ostial lobes* setose, long and broad, not well sclerotized; *anterior apophyses* normal; *papillae* elongate dorsally.

EARLY STAGES; HOST PLANTS. Unknown.

DISTRIBUTION (Map Fig. 143). Restricted to Equatorial Guinea, Gabon and Congo.

BIONOMICS
A monotypic, supposedly lowland forest species (Ackery *et al.*, 1995), about which little appears to have been recorded. Oremans (1995) encountered both sexes in the Mboko Forest, Lopé-Okanda reserve (Gabon), during September. G. Jones (specimen in NMGM, Liverpool Museum) found this species at Ivinga in December 1985, in 'tropical rain forest'.

CONSERVATION STATUS. 'Uncommon but not known to be threatened' (Collins & Morris, 1985: 57).

MATERIAL EXAMINED. 57 ♂♂; 1 ♀ in BMNH. 22 ♂♂ from other collections.

33. *Graphium (Arisbe) fulleri* (Grose-Smith, 1883)

Fuller's Graphium or Swallowtail (Figs 208, 232–234; map Figs 154–157; genitalia Fig 54–57, 99)

We here follow Hancock (1985) in treating *G. fulleri* as a polytypic species including *rileyi* and *ucalegonides* as subspecies. The genitalia are very similar and the various included taxa (apart from *G. f. boulleti* – about which see below) are largely allopatric.

Unlike Hancock, we revive *boulleti* Le Cerf to constitute a fourth subspecies of which various taxa described by Strand, Holland, Berger and Darge appear to be synonyms. We speculate that this 'taxon' may be a natural hybrid or transition between *fulleri fulleri* and *fulleri ucalegonides*, perhaps resulting from possible range expansion of the latter in recent times. Breeding experiments might elucidate this, should live insects of both sexes of both of these taxa be obtained (we have seen only males in collections). If hybrids unlike *G. f. boulleti* were to be produced, our hypothesis would be in doubt; were *boulleti*-like hybrids to result, but these infertile, the species-level status of the parental forms would need to be re-examined.

CONSERVATION STATUS
Collins & Morris (1985: 58, but see also p.124) treat *fulleri* and *ucalegonides* separately, but regarded both as not being threatened. They treated *G. weberi* (here included as a synonym of *G. f. boulleti*) as 'Insufficiently known'.

33a. ***G. (A.) fulleri fulleri*** (Grose-Smith, 1883)

Fuller's Graphium or Swallowtail (Fig. 208; map Fig. 156; genitalia Fig. 54)

Papilio Fulleri Grose-Smith, 1883: 234. LECTOTYPE ♂: CAMEROON: 'Camaroons [sic] (Fuller); in the collection of H. Grose Smith.' (Grose-Smith, 1883: 234). BMNH Spec.Reg. No. 138849. Designated Le Cerf (1924: 395); 3 PARALECTOTYPE ♂♂: CAMEROON: Same provenance (see below). BMNH Spec.Reg. Nos. 138846, 138850, 138853.

Papilio fulleri Grose-Smith; Aurivillius, 1908: 23; Schultze, 1917*b*: 26.

Papilio ucalegon v. *Fulleri* Grose-Smith; Bryk, 1930*b*: 562.

Graphium fulleri (Grose-Smith); Berger, 1950: 79; D'Abrera, 1980: 44, 45 (fig.).

Papilio (*Graphium*) *ucalegonides fulleri* (S.); Peters, 1952: 21.

Graphium (*Arisbe*) *fulleri* (Grose-Smith); Munroe, 1961: 42.

Graphium (*Arisbe*) *fulleri* (Grose-Smith); Hancock, 1983: 46; Collins & Morris, 1985: 58.

Graphium (*Arisbe*) *fulleri fulleri* (Grose-Smith); Hancock, 1985*a*: 98; Ackery, Smith & Vane-Wright, 1995: 162.

Graphium fulleri fulleri (Grose-Smith); d'Abrera, 1997: 50, 51 (fig.).

TYPE EVALUATIONS

Papilio Fulleri Grose-Smith (1883) was described from an unstated number of specimens in his own collection, collected by Fuller. Grose-Smith's collection was acquired by J.J. Joicey, and from it Le Cerf (1924) selected one specimen as 'Type (H.T.)', and listed three further paratypes. The lectotype, clearly labelled as type in Grose-Smith's hand, has had a round 'Type (H.T.)' label added by Le Cerf or subsequent curator. The three paralectotypes listed by Le Cerf have now been labelled as such. The material reached BMNH as part of the Joicey Bequest (BMNH 1934–120). A further Joicey Bequest specimen labelled 'Cameroon/ Fuller.' (BMNH Spec.Reg. Nos. 138854) is excluded from the type series as it was not, apparently, originally from Grose-Smith's collection.

TAXONOMIC STATUS

Papilio Fulleri Grose-Smith (1883) was established as a species. Bryk (1930) included it as a variety [=subspecies] of *P. ucalegon*. Peters (1952) included it as a subspecies of *P.* (*Graphium*) *ucalegonides* (despite it having the older name) alongside *boulleti* and *phrynon*, apparently for the first time. Hancock (1985) formally combined *fulleri*, *rileyi* and *ucalegonides* as subspecies of a polytypic species, with *fulleri* being the nominate race.

SIMILAR SPECIES

The colour combined with the prominent post-discal marks on the hindwing upperside should distinguish *G. f. fulleri* from most of its relatives. The features which separate it from *G. f. boulleti* are described in that section.

DIAGNOSIS: PATTERN (Fig. 208)

Upperside ground colour dark brown with markings yellow. **Forewing** discal cell usually without transverse mark opposite cell M_3 (see 'variation'), but with distinct, usually bifid distal mark opposite cell R_5. Cell R_3 with prominent mark not reaching axil, but extending beyond root of vein R_4, usually somewhat indented distally. Cell R_4 with post-discal mark usually prominent. Cell R_5 with post-discal mark and with submarginal mark absent, faint or distinct: when present it is bifid. Cell M_1 unmarked. Cell M_2 with post-discal mark usually more-or-less quadrate (slightly indented distally by internervosa) not reaching bordering veins; faint or small, bifid submarginal mark sometimes present. Post-discal mark of cell M_3 quadrate or somewhat rounded distally, more-or-less reaching posterior discocellular vein, but not veins M_3 or CuA_1; faint, undivided submarginal mark usually present. Cell CuA_1 with elliptical post-discal mark not reaching bordering veins; faint, undivided submarginal mark usually present. Cell CuA_2 with post discal mark quadrate to elliptical, often with proximal margin concave; not reaching vein CuA_2 or posterior discocellular vein, sometimes reaching vein 1A; faint, bifid submarginal mark sometimes present. Cell 1A with post-discal mark tapering distally, not reaching either vein 1A or the inner margin of the wing.

Hindwing. Discal cell band quite narrow, not reaching root of vein CuA_1. Post-discal mark in cell R_1 paler than the others, deeply, but narrowly indented distally by intervenosa. The mark has thin, hairlike scales over the membrane near the radial vein, with an increasing proportion of rounded, non-serrate scales nearer vein $Sc+R_1$ and distally (in the other subspecies, the entire mark is covered with such scales). Cell R_5 with axillary post-discal mark extending beyond line of discal cell band; faint to clear, albeit small, bifid submarginal mark. Cell M_1 with just a bifid submarginal mark, the anterior element much the larger, the posterior sometimes very faint. Cells M_2 and M_3 each with a clear, round to ovoid post-discal spot, sometimes slightly indented distally; and with bifid submarginal marks sometimes faint. Cell CuA_1 with small axillary discal mark, round to ovoid post-discal mark and faint, bifid submarginal mark. Cell CuA_2 with yellow discal and post-discal marks subsumed in the more extensive, paler region of androconial scales.

The **underside** pattern largely reflects that of the upperside, though the ground colour is somewhat paler and the intervenosae more prominent. The basal area of both wings becomes somewhat reddened, with the area anterior to the subcostal vein of the forewing, and the costal cell of the hindwing proximal to the precostal vein, being almost brick red. In addition, the post-discal mark of **forewing** cell CuA$_1$ is bordered by nacreous area, where white scales overlay the brown membrane; a similar area is sometimes present in the discal cell, corresponding to the position of a cell mark opposite cell M$_3$. On the **hindwing**, the basal black spot is particularly prominent; there is a black spot in the angle of the precostal vein and a black streak in cell R$_1$ becoming blurred distally, but almost connecting with the intervenosa.

VARIATION
There is the expected variability in the size, shape and prominence of the various marks, in particular the submarginal marks, as indicated above. In one specimen in BMNH (Spec.Reg. No. 138847), illustrated by d'Abrera (1980, 1997), there is a small linear mark in the forewing discal cell, opposite cell M$_3$.

DIAGNOSIS: ♂ GENITALIA (Fig. 54)
Dorsal projection quite stout, slightly directed anteriad, slightly upcurved, cluster of stout setae at tip. *Dorsal harpe* with a mesal carina. *Ventral harpe* with broad ventral blade, pointed posteriorly; dorsal blade of similar length, pointed, curved somewhat mesad distally. *Dorsal terminal process* of moderate size, ventral tip blunt. *Ventral terminal process* quite small, somewhat concave dorsally, convex and denticulate ventrally. *Rim* quite broad, a line of stout setae on its inner margin from ventral side of dorsal terminal process to ventral to dventral harpe. *Uncus* curved distally, *socii* prominent. *Saccus* short. *Aedeagus* short, curved ventrad, especially at base.

DIAGNOSIS: ♀ GENITALIA. No specimens available for dissection.

EARLY STAGES; HOST PLANTS; BIONOMICS. Apparently unknown.

DISTRIBUTION (Map Fig. 156). Apparently restricted to Cameroon, the paucity of records on our map reflecting the lack of precise provenances. Note: the spot seemingly in Nigeria represents in fact a specimen in BMNH (Spec.Reg. No. 138856) from Balika, N.W. Cameroon (9°00´ N 12°50´ E).

CONSERVATION STATUS. See species account.

MATERIAL EXAMINED. 14 ♂♂ in BMNH. 4 ♂♂ from other collections.

33b. *G.* (*A.*) *fulleri boulleti* (Le Cerf, 1912) stat. rev.

Boullet's Graphium or Swallowtail (Fig. 232; map Fig. 155; genitalia Fig. 55)

G. (*A.*) *fulleri boulleti* (Le Cerf, 1912) is the oldest name for a number of nominal taxa we believe to be synonyms.

Papilio Boulleti Le Cerf, 1912: 382–3. HOLOTYPE ♂: GABON: 'Type 1 ♂ . . . Congo français, chutes de Doumé (Ogooué) A. Marche (1881) in coll. Muséum de Paris' (Le Cerf, 1912: 383). MNHN.

Papilio ucalegon var. *boulleti* Le Cerf; Bryk, 1930*b*: 561.

Papilio (*Graphium*) *ucalegonides boulleti* Le Cerf; Peters, 1952: 21.

Graphium fulleri fulleri =*boulleti* (Le Cerf); Hancock, 1985*a*: 98 (as 'syn. nov.').

Graphium (*Arisbe*) *fulleri fulleri* =*boulleti* (Le Cerf); Ackery, Smith & Vane-Wright, 1995: 162.

SYNONYMS

Papilio Boulleti var. *transiens* Le Cerf, 1912: 383. HOLOTYPE ♂: GABON: 'Type : 1 ♂ . . . Congo français, rivière San Benito, Guiral (1885) in coll.Muséum de Paris' (Le Cerf, 1912: 383). MNHN.

Papilio ucalegon ♂ f. *transiens* Le Cerf; Bryk, 1930*b*: 562.

Papilio (*Graphium*) *ucalegonides boulleti* ♂ ab. *transiens* Le Cerf; Peters, 1952: 21.

Graphium fulleri fulleri =*transiens* (Le Cerf); Hancock, 1985*a*: 98 (as 'syn. nov.').

Graphium (*Arisbe*) *fulleri fulleri* =*transiens* (Le Cerf); Ackery, Smith & Vane-Wright, 1995: 162.

Papilio foersterius Strand, 1913*b*: 17. HOLOTYPE ♂: CAMEROON: 'Unikum von S. Kamerun, Nzimulana, 400–500 m, Ngoko Sanga (Foerster)' (Strand, 1913*b*: 17). MNHU.

Papilio Boulleti =*foersterius* Strand; Schultze, 1913*c*: 1 [as syn. n.].

Papilio ucalegon ♂ v. *foersterius* Strand; Bryk, 1930*b*: 562.

Papilio (*Graphium*) *ucalegonides boulleti* ♂ ab. *foersterius* Strand; Peters, 1952: 21.

Graphium fulleri fulleri =*foersterius* (Strand); Hancock, 1985*a*: 98 (as 'syn. nov.').

Graphium (*Arisbe*) *fulleri fulleri* =*foersterius* (Strand); Ackery, Smith & Vane-Wright, 1995: 162.

Papilio sanganus Strand, 1913*b*: 17. LECTOTYPE ♂: CAMEROON: ['S. Kamerun, Nzimulana, 400–500 m, Ngoko Sanga (Foerster).'] (Strand, 1913*b*: 17) – **here designated**. MNHU.

Papilio Boulleti = *sanganus* Strand; Schultze, 1913*c*: 1 [as syn. n.].

Papilio ucalegon ♂ v. *sanganus* Strand; Bryk, 1930*b*: 562.

Papilio (*Graphium*) *ucalegonides boulleti* ♂ ab. *sanganus* Strand; Peters, 1952: 21.

Graphium fulleri fulleri =*sanganus* (Strand); Hancock, 1985*a*: 98 (as 'syn. nov.').

Graphium (*Arisbe*) *fulleri fulleri* =*sanganus* (Strand); Ackery, Smith & Vane-Wright, 1995: 162.

Papilio sanganoides Strand, 1913*b*: 17. HOLOTYPE ♂: CAMEROON: ['S. Kamerun, Nzimulana, 400–500 m, Ngoko Sanga (Foerster).'] (Strand, 1913*b*:

17). MNHU. PARATYPE ♂: CAMEROON: ['S. Kamerun, Nzimulana, 400–500 m, Ngoko Sanga (Foerster).'] (Strand, 1913*b*: 17). MNHU.

Papilio Boulleti = *sanganoides* Strand; Schultze, 1913*c*: 1 [as syn. n.].

Papilio ucalegon ♂ v. *sanganoides* Strand; Bryk, 1930*b*: 562.

Papilio (*Graphium*) *ucalegonides boulleti* ♂ ab. *sanganoides* Strand; Peters, 1952: 21.

Graphium fulleri fulleri =sanganoides (Strand); Hancock, 1985*a*: 98 (as 'syn. nov.').

Graphium (*Arisbe*) *fulleri fulleri =sanganoides* (Strand); Ackery, Smith & Vane-Wright, 1995: 162.

Papilio Stetteni Strand, 1913*c*: 42. HOLOTYPE ♂: CAMEROON: 'Unikum von Süd-Kamerun, Molundu, „Mai-August, kleine Trockenzeit, aber mit Regen'. (Freiherr von Stetten).' (Strand, 1913*c*: 42). 'Type im Kgl. Zoolog. Museum Berlin' (Strand, 1913*c*: 43) MNHU (Photographed CRS, x.95).

Papilio Boulleti = Stetteni Strand; Schultze, 1913*c*: 1 [as syn. n.].

Papilio ucalegon v. *Stetteni* Strand; Bryk, 1930*b*: 562.

Papilio (*Graphium*) *ucalegon stetteni* Strand Peters, 1952: 21.

Graphium fulleri fulleri =stetteni (Strand); Hancock, 1985*a*: 98 (as 'syn. nov.').

Graphium (*Arisbe*) *fulleri fulleri =stetteni* (Strand): 140 [sic]; Ackery, Smith & Vane-Wright, 1995: 162.

Papilio weberi Holland, 1917: 14, pl. 4, fig. 1. HOLOTYPE ♂: CAMEROON: 'vicinity of Lolodorf, Cameroon' (Holland, 1917: 15). CMNH (Photograph examined). **Syn. n.**

Papilio weberi Holland; Bryk, 1930*b*: 563.

Papilio (*Graphium*) *weberi* Holland; Peters, 1952: 21.

Graphium weberi (Holland); D'Abrera, 1980: 42.

Graphium (*Arisbe*) *weberi* (Holland); Hancock, 1983: 46.

Graphium (*Arisbe*) *fulleri fulleri =weberi* (Holland); Hancock, 1985*a*: 97 (as 'syn. nov.'); Ackery, Smith & Vane-Wright, 1995: 162.

Graphium (*Arisbe*) *fulleri =weberi* (Holland); Collins & Morris, 1985: 58, 124, 220.

Graphium fulleri fulleri =weberi (Holland); d'Abrera, 1997: 50.

Graphium ucalegonides beloni Darge, 1995: 284, 286 figs 1, 2. HOLOTYPE ♂: CAMEROON: '1 ♂, Cameroun: Mount Kala, 900/1150m., 20 km. W. de Yaoundé, 15.III.1975 (Ph. Darge)' (Darge, 1995: 284, 286 figs 1, 2). Darge collection (Darge, 1995: 285). [not seen]. PARATYPE ♂: CAMEROON: '1 ♂, Cameroun: Ngat II, 28.II.1974 (Ph. Darge)' (Darge, 1995: 284). Darge collection (Darge, 1995: 285). [not seen]. PARATYPE ♂: CAMEROON: '1 ♂, id.: Meukonong, 700m., 19.III.1976 (Ph. Darge)' (Darge, 1995: 284). Darge collection (Darge, 1995: 285). [not seen]. PARATYPE ♂: CAMEROON: '1 ♂, id.: Ebodenkou, 20.X.1976 (Ph. Darge)' (Darge, 1995: 284). Darge collection (Darge, 1995: 285). [not seen]. PARATYPE ♂: CONGO: 'Congo (Ollombo, 6.II.1984)' (Darge, 1995: 284, 286 figs 3, 4). Darge collection (Darge, 1995: 285). [not seen]. **Syn. n.**

UNAVAILABLE NAMES

Papilio sanganoides ab. *divisimacula* Strand, 1913*b*: 18. CAMEROON: MNHU. [infrasubspecific]

Papilio Boulleti = divisimacula Strand; Schultze, 1913*c*: 1 [as syn. n.].

Papilio ucalegon ♂ f. *divisimacula* Strand; Bryk, 1930*b*: 562.

Papilio (*Graphium*) *ucalegonides boulleti* ♂ ab. *divisimacula* Strand; Peters, 1952: 21.

Graphium fulleri fulleri =divisimacula (Strand); Hancock, 1985*a*: 98 (as 'syn. nov.').

Graphium (*Arisbe*) *fulleri fulleri =divisimacula* (Strand); Ackery, Smith & Vane-Wright, 1995: 162.

Graphium ucalegonides ucalegonides f. *gabrieli* Berger, 1950: 78. CAMEROON: BMNH Spec.Reg. No. 143258. [infrasubspecific]

Graphium fulleri fulleri =gabrieli Berger; Hancock, 1985*a*: 98 (as 'syn. nov.').

Graphium (*Arisbe*) *fulleri fulleri =gabrieli* Berger; Ackery, Smith & Vane-Wright, 1995: 162.

TYPE EVALUATIONS

Papilio Boulleti and var. *transiens* Le Cerf (1912) were each described from single specimens, with type designation original. The specimens concerned are clearly labelled in MNHN, Paris.

Papilio foersterius and *P. stetteni* Strand (1913*c*) were each described from single specimens, which are clearly labelled in MNHU, Berlin.

Papilio sanganus Strand (1913*b*) was probably also described from a single specimen, though the author did not state this explicitly. The specimen concerned in MNHU, Berlin, has a 'Type' label as well as a determination label in Strand's hand and we here designate it as lectotype to avoid future confusion.

Papilio sanganoides Strand (1913*b*) was described from two individuals one of which was designated as 'Type' in the original description. That specimen is readily recognisable in MNHU, Berlin, by its pattern and is labelled 'Type'; the other specimen has this label modified to 'Co- Type'.

Papilio weberi Holland (1917) was described from the one specimen, stated as being in CMNH, with type designation original. The specimen concerned is clearly labelled in CMNH (Accession No. 4728), where it was photographed by our colleague I.J. Kitching.

Graphium ucalegonides beloni Darge (1995) was described from the five specimens listed above, with type designations original.

TAXONOMIC STATUS

Papilio boulleti Le Cerf (1912) was established as a species and treated as such by Schultze (1913*c*), but he subsequently (1917) synonymized it with *P. ucalegonides*. Bryk (1930) treated it as a variety (= subspecies) of *P. ucalegon*. Hancock (1985) synonymized it with *G. fulleri fulleri* which he regarded as the nominate subspecies of a polytypic species which included *G. f. rileyi* and *G. f. ucalegonides*.

Papilio foersterius, *P. sanganus*, *P. sanganoides* (all Strand, 1913*b*) and *P. stetteni* (Strand, 1913*c*) were all established as species, though even Strand (1913*b*) expressed some doubts as to their status. Schultze (1913*c*) synonymized them all with *P. boulleti*, characterising the taxon as being very variable. Strand (1913*d*) disagreed with this interpretation, characterising Schultze and himself as, respecitively, a 'lumper' and a 'splitter' (using the English terms). Schultze (1917*b*) subsumed all of them – including *P. boulleti* – in synonymy with *P. ucalegonides*. Bryk (1930) treated *P. stetteni* as a variety (= subspecies) and the other names as infrasubspecific within *P. ucalegon*, in which he also included as varieties *ucalegonides* Staudinger, *boulleti* Le Cerf and *fulleri* Grose-Smith. Hancock (1985) synonymized them with *G. fulleri fulleri*.

Papilio weberi Holland (1917) was established as a species. That status was accepted by authors until Hancock (1985) synonymized it with *G. f. fulleri*.

Graphium ucalegonides beloni Darge (1995) was established as a subspecies.

Our own examination of the types and/or photographs of all the above taxa, together with those of ab. *divisimacula* Strand (1913*b*) and f. *gabrieli* Berger (1950) as well as other specimens from Cameroon in ABRI, Nairobi, and in BMNH (including a specimen – Spec.Reg. No. 138848 – labelled as the holotype of '*Graphium fulleri* f. *pseudoucalegonides* B[er]ger ♂' by Berger, but apparently never published), lead us to believe that Schultze's (1913*c*, but not 1917) interpretation is substantially correct. Namely, that all these nominal taxa – including those described since 1913 – are separate from both *G. f. fulleri* and *G. f. ucalegonides*. Despite the high level of variability of wing pattern shown by the 18 specimens seen and/or illustrated, certain features are fairly constant (see also diagnosis).

The very high level of variability of a pattern somewhat intermediate between *G. f. fulleri* and *G. f. ucalegonides* – even in specimens from the same locality – leads us to speculate that this 'taxon' may possibly represent recurrent natural hybridisation or introgression between the two putative races.

SIMILAR TAXA

Ground colour and coloration of markings generally similar to those in *G. f. fulleri*, but distal mark of forewing discal cell usually absent (a small spot present in HT of *foersterius* and in 'pseudoucalegonides'), and there is sometimes a more-or-less extensive mark opposite cell M_3 (e.g. in *foersterius* HT, *sanganoides* LT, *divismacula*, illustrated PT of *beloni*, 'pseudoucalegonides', one Mt Kala specimen in ABRI). The post-discal mark in forewing cell M_2 is usually reduced, largely confined to the posterior half of the cell, or even absent; in *G. f. fulleri* it appears always to be fully formed. The post-discal mark in forewing cell CuA_1 is reduced *cf. fulleri*, sometimes being absent, or nearly so (e.g. *stetteni*, illustrated PT of *beloni*, *divisimacula*). On the hindwing upperside, the post-discal mark of cell R_1 is obscured by orange scales in a pattern which is 'smeared' distally to a variable extent, reminiscent of *G. f. ucalegonides*; in *G. f. fulleri* this mark is white and quite clear cut, albeit deeply indented by the intervenosa. The expression of post-discal marks in hindwing cells is variable, ranging from those in 'pseudoucalegonides' being almost as well developed as in *G. f. fulleri*, via small entire (deeply cleft in *foersterius*) or subdivided (e.g. *boulleti*, *stetteni*) marks, to complete absence (e.g. *sanganus*, *beloni*).

G. f. boulleti Le Cerf may be separated from *G. f. ucalegonides* by the following. Colour: whereas *G. f. boulleti* is a rich chocolate brown with yellow markings (like *G. f. fulleri*), *G. f. ucalegonides* is less intensely coloured, with markings dull, ochraceous yellow (this may be due to fading of the specimens we have seen, but specimens of *G. f. fulleri* of equal or greater age have retained their colour). Nearly all *G. f. ucalegonides* possess a clear, triangular mark in the forewing discal cell opposite cell M_3; only a few *boulleti* possess it (absence is a good indicator, presence not; see above). *G. f. ucalegonides* almost never exhibits post-discal marks in hindwing cells M_2 to CuA_1 (one specimen from Democratic Republic of Congo (Sankuru) in BMNH has a mark in M_3 and a very small one in CuA_1).

G. f. boulleti may be distinguished from *G. f. fulleri*, *G. f. ucalegonides* and *G. f. rileyi* – as well as from *ucalegon* and *simoni* – by the absence of a black intervenosal mark at the base of hindwing underside cell R_1, and from the latter two by the absence of pale powdering in the distal area of the hindwing discal cell.

DIAGNOSIS: PATTERN (Fig. 232)

Upperside ground colour chocolate brown with yellow markings.

Forewing discal cell usually devoid of marks, but sometimes a very small to quite large mark opposite cell M_3 present; occasionally a small mark opposite cell R_5. Cell R_3 with post-discal mark not reaching base of cell, extending a little beyond root of vein R_4. Cell R_4 sometimes with an axillary post-discal mark. Cell R_5 with post-discal mark not reaching base of cell, more or less indented distally by intervenosa; occasionally with a faint (*stetteni* HT, *weberi* HT), or extremely faint subdivided submarginal mark. Cell M_1 unmarked. Cell M_2 with variable post-discal mark, usually largely confined to posterior half of cell, occasionally absent; rarely with faint or extremely faint submarginal mark. Cell M_3 with post-discal mark occupying full width of cell and abutting medial vein and veins M_3 and CuA_1 at least basally, rounded or tapering distally; clear to very faint submarginal marks sometimes present. Cell CuA_1 with post-discal mark usually elliptical and not touching surrounding veins, occasionally occupying most of cell width, sometimes absent; submarginal mark usually absent, occasionally very faint (*weberi* HT). Cell CuA_2 with post-discal mark not reaching vein CuA_2, but lying along vein 1A, rounded or tapering distally; submarginal mark clear in *stetteni* HT, otherwise faint or absent. Cell 1A with post-discal mark more-or-less contiguous with that in CuA_2.

Hindwing discal cell band not reaching roots of veins M_1 or CuA_1 distally; edges clear. Cell R_1 with a diffuse, white, patch along radial vein which is 'smeared' into a diffuse orange mark extending a varying degree proximally and distally, as in *ucalegonides*, but not *fulleri* (see above). This patch consists of broad and rounded, white and orange or brown scales. Cell R_5 with an axillary post-discal mark usually bordered distally by a more-or-less extensive orange patch, as in cell R_1. Cell M_1 sometimes with a faint to very faint submarginal mark, confined to the anterior half of the cell. In *foersterius* only there is a small, but clear submarginal mark in the anterior half of the cell. Cells M_2 to CuA_1 show a variable pattern of post-discal marks as described above; expression of the submarginal marks is predictably variable. In addition, cell CuA_1 has a small discal mark usually confined to the angle of vein CuA_2 and the cubital vein, but extended along that vein as far as the root of CuA_1 as a narrow, slightly diffuse line in *sanganoides* and *divisimacula*. Cell CuA_2 with an elongate discal/post-discal mark consisting of white scales.

The **underside** largely mirrors the upper, but with ground colour and markings paler and intervenosae more prominent and with a reddish hue basally. As in *G. f. fulleri*, there is sometimes a nacreous rim around some **forewing** post-discal marks, especially that in cell CuA_1. Specimens lacking a forewing discal cell mark opposite cell M_3 sometimes have a nacreous patch here, too.

As mentioned above, there is no black mark near the base of **hindwing** cell R_1, a character which distinguishes this taxon not only from other subspecies, but also from both *G. ucalegon* and *G. simoni*.

VARIATION. See sections above.

DIAGNOSIS: ♂ GENITALIA (Fig. 55)
Very similar to the nominate subspecies.

Dorsal projection quite stout, slightly directed anteriad, slightly upcurved, cluster of stout setae at tip and anteriorly. *Dorsal harpe* with a mesal carina. *Ventral harpe* with broad ventral blade, pointed posteriorly; dorsal blade of similar length, pointed, curved somewhat mesad distally. *Dorsal terminal process* of moderate size, ventral tip blunt. *Ventral terminal process* quite small, somewhat concave dorsally, convex and denticulate ventrally. *Rim* quite broad, a line of stout setae on its inner margin from ventral side of dorsal terminal process to ventral to dventral harpe. *Uncus* curved distally, *socii* prominent. *Saccus* short. *Aedeagus* short, curved ventrad, especially at base.

DIAGNOSIS: ♀ GENITALIA. No specimens available for dissection.

EARLY STAGES; HOST PLANTS; BIONOMICS. Unknown.

DISTRIBUTION (Map Fig. 155).
Recorded localities: Cameroon, Equatorial Guinea, Gabon, Congo. There are specimens in MRAC ex van Riel labelled as from Democratic Republic of Congo (Ubangi-Abumombazi and Ubangi-Yakoma).

CONSERVATION STATUS. See species account.

MATERIAL EXAMINED
1 ♂ in BMNH ('*pseudoucalegonides*'). 17 ♂♂ from other collections including: *boulleti*: HT; *transiens*: HT; *foersterius*: HT; *sanganus*: HT; *sanganoides*: HT, PT; *stetteni*: HT; *divisimacula*: HT; *weberi*: HT (from photograph); *beloni*: 2 (as illustrations); *gabrieli*: HT; 5 specimens from ABRI. 3 ♂♂ labelled *ucalegonides* in FIF lack the spot in hindwing underside cell R_1 and are also probably *G. f. boulleti*.

33c. *G. (A.) fulleri rileyi* Berger, 1950

Riley's Graphium or Swallowtail (Fig. 233; map Fig. 154; genitalia Figs 56, 99)

Graphium ucalegonides Rileyi Berger, 1950: 78. HOLOTYPE ♂: GHANA: 'Holotype: 1 ♂ « West Africa, Gold Coast: Begoro; XI–1909 » (G. C. DUDGEON). – Coll. British Museum.' (Berger, 1950: 78). BMNH Spec.Reg. No. 143285; PARATYPE ♀: GHANA: 'Allotype: 1 ♀ « Accra, Gold Coast » (ex ROTHSCHILD).' (Berger, 1950: 78). BMNH Spec.Reg. No.143290; PARATYPE ♂♂: GHANA: 'tous in coll. British Museum': '1 ♂ « N. Ashanti: IV–06 » (G. C. DUDGEON)' (Berger, 1950: 78). BMNH Spec.Reg. No.143282; '1 ♂ « Ashanti: Prashu » (Crowley)' (Berger, 1950: 78). BMNH Spec.Reg. No.143263; '1 ♂ « Gold Coast: Jafo: march 1906 » (G. C. DUDGEON)' (Berger, 1950: 78). BMNH Spec.Reg. No.143284; '1 ♂ « N. Begoro: IV–06 » (G. C. DUDGEON)' (Berger, 1950: 78). BMNH Spec.Reg. No.143286; '2 ♂ ♂ « Friapere Forest, Coomassie: 1913 » (ex-coll. JOICEY)' (Berger, 1950: 78–9). BMNH Spec.Reg. No.138761, 143293; '1 ♂ « Gold Coast: Kumassie: 9–IV–13 » (J. D. G. SAUNDERS)' (Berger, 1950: 79). BMNH Spec.Reg. No.143292; '1 ♂ « Sungani [=Sunyani], Coomassie»' (Berger, 1950: 79). BMNH Spec.Reg. No.143291; IVORY COAST: '1 ♂ Côte d'Ivoire: Giguilo (Musée du Congo Belge)' (Berger, 1950: 79). MRAC.

Graphium ucalegonides rileyi Berger; D'Abrera, 1980: 42.

Graphium (Arisbe) fulleri rileyi Berger; Hancock, 1985*a*: 98 (as 'comb. nov.') ; Ackery, Smith & Vane-Wright, 1995: 162.

Graphium fulleri rileyi Berger; d'Abrera, 1997: 50.

TYPE EVALUATIONS

Graphium ucalegonides Rileyi Berger (1950) was described from the holotype and ten paratypes listed above, with type designations original (Berger, 1950: 78–9). The type specimens in BMNH reached that institution from various sources prior to Berger's description.

TAXONOMIC STATUS

Graphium ucalegonides Rileyi Berger (1950) was established as a subspecies. Hancock (1985) combined both *rileyi* and *ucalegonides* as subspecies of *G. fulleri*.

SIMILAR TAXA

Most similar to *G. f. ucalegonides*, from which it is best distinguished by colour, having somewhat darker ground colour and distinctively cream markings in contrast to those of *G. f. ucalegonides*. Colour also helps separate it from *G. f. fulleri* and *G. f. boulleti* (q.v.) and it also lacks the hindwing upperside post-discal marks of cells M$_2$ to CuA$_1$ of the former (and sometimes the latter). Does not have the 'powdering' of white scales seen in the hindwing upperside discal cells in members of the *ucalegon* clade, but posseses a dark mark near the base of hindwing underside cell R$_1$, which is not found in most of the remaining mimetic species (with the exception of the distinctive *G. auriger*).

DIAGNOSIS: PATTERN (Fig. 233)

Upperside ground colour very pale cream (paler than in *G. f. ucalegonides*). **Forewing** discal cell with roughly triangular mark based on posterior discocellular vein opposite cell M$_3$ usually reaching about half way across cell. Sometimes a small faint spot distally in cell, opposite cell R$_5$, and sometimes asymmetric. Cell R$_3$ with elongate post-discal mark not reaching base of cell, but extending beyond root of vein R$_4$, indented distally, with posterior fork the longer. Cell R$_4$ usually without post-discal mark, but a faint, fuzzy or even clear, large mark sometimes present. Cell R$_5$ with large post-discal mark extending beyond root of vein R$_4$, indented distally by intervenosa. Cell M$_1$ usually unmarked (but see below). Cell M$_2$ with post-discal mark laregly confined to posterior half of cell, usually with an anterior extension at the cell base which may extend distad to form a hook shape. Cell M$_3$ with a broad post-discal mark filling the base of the cell; sometimes a more-or-less faint, occasionally bifid submarginal mark almost touching the post-discal. Post-discal mark of cell CuA$_1$ variable, usually reaching veins CuA$_1$ and CuA$_2$, but only touching the posterior discocellular vein anteriorly, the mark not reaching into the angle of vein CuA$_2$ and the posterior discocellular vein; sometimes a faint submarginal mark almost touching the post-discal. Post-discal mark of cell CuA$_2$ never reaching the posterior discocellular vein; usually reaching vein CuA$_2$, but this is always clearly defined by brown scales; more-or-less contiguous with post-discal mark of cell 1A; occasionally with a very faint submarginal mark virtually contiguous with the post-discal. Cell 1A with post-discal co-extensive and contiguous with that in cell CuA$_2$.

Hindwing discal cell with broader band than *G. f. ucalegonides*, reaching nearer the base and usually to roots of veins M$_1$ and CuA$_1$ distally, or nearly so. Cell R$_1$ in both sexes with large, scaled, white post-discal mark, becoming more golden, and indented, distally. Cell R$_5$ with an axillary post-discal scaled mark (the scales somewhat narrower than in R$_1$) reaching or extending a little beyond the root of vein M$_1$; deeply indented distally. Cell M$_1$ sometimes with a faint to clear, linear post-discal mark in anterior half of cell at the base. Cell M$_2$ usually unmarked (but see below). Cell M$_3$ sometimes with a scattering of pale scales in angle of vein CuA$_1$ and posterior discocellular vein, but otherwise usually unmarked (but see below). Cell CuA$_1$ with discal mark in the form of a chevron, one arm of which runs along the posterior discocellular vein from its angle of the with vein CuA$_2$ towards the root of vein CuA$_1$; the other along vein CuA$_2$ to about the same extent. Cell CuA$_2$ with, in the male, a white scaled patch extending across the full width of the cell from near the base to somewhat beyond the level of the discal mark in cell CuA$_1$. In the female there is a partially scaled discal mark co-extensive with the discal cell band and discal mark of cell CuA$_1$. The anal cell, visible in the female, is largely white scaled, becoming golden brown distally.

The **underside** pattern largely reflects that of the upperside, with gound colour paler and intervenosae a little more prominent. The ground colour becomes somewhat reddened basally on the forewing, and distinctly orange on the hindwing. The 'intervenosae' of the **hindwing** discal cell are faint or even absent. There is a round black spot in the angle of the hindwing humeral vein, and an elongate, usually prominent black mark near the base of hindwing cell R$_1$, along the line of the intervenosa.

VARIATION

Apart from the variations described above, there is some variability in the size and shape of the markings, but less so than in some other taxa.

From a sample of two in BMNH, it would seem that females tend to be more extensively marked. One of the two (Spec.Reg. No. 143330) has a faint indication of a bisected submarginal mark in forewing cell R_5 and of a post discal mark in the anterior half of cell M_1, as well as bissected post-discal marks in hindwing cells M_2 and M_3, and faint submarginal marks in hindwing cells M_1 to M_3. Both females have distinct, if fuzzy, submarginal marks in forewing cells M_3 and CuA_1 and even indications of submarginal marks contiguous with the post-discal mark in forewing cell CuA_2.

DIAGNOSIS: ♂ GENITALIA (Fig. 56)
Dorsal projection quite stout, slightly directed anteriad, slightly upcurved, cluster of stout setae at tip. *Dorsal harpe* without a mesal carina (only one examined). *Ventral harpe* with broad ventral blade, pointed posteriorly; dorsal blade of similar length, pointed, curved somewhat mesad distally. *Dorsal terminal process* of moderate size, ventral tip blunt. *Ventral terminal process* quite small, somewhat concave dorsally, convex and denticulate ventrally. *Rim* quite broad, a line of stout setae on its inner margin from ventral side of dorsal terminal process to ventral to dventral harpe. *Uncus* curved distally, *socii* prominent. *Saccus* short. *Aedeagus* short, curved ventrad, especially at base.

DIAGNOSIS: ♀ GENITALIA (Fig. 99)
G. (*A.*) *fulleri rileyi* is the only subspecies for which a female was available for dissection. The indentation of the labia of the vestibulum make it very similar to *G.* (*A.*) *kigoma*.

BMNH Spec.Reg. No. 143330; vial 5281: *vestibulum* transverse, with labia deeply indented posteriorly on midline; *ostium bursae* opening anteriorly; *ductus bursae* elongate, not sclerotized, kinked/constricted or pocketed distally; *central ostial lobe* glabrous, broad, truncate, almost reaching tip of laterals; *lateral ostial lobes* setose, long and broad, not well sclerotized; *anterior apophyses* normal; *papillae* elongate dorsally.

EARLY STAGES; HOST PLANTS; BIONOMICS. Unknown.

DISTRIBUTION (Map 154). The West African representative of the species, with records from Ivory Coast and Ghana. Larsen (In prep.*a*) also records it from Burkina Faso and Togo.

CONSERVATION STATUS. Presumably not threatened.

MATERIAL EXAMINED. 17 ♂♂, 2 ♀♀ in BMNH. 4 ♂♂ from other collections.

33d. *G.* (*A.*) *fulleri ucalegonides* (Staudinger, 1884)

Staudinger's Graphium or Swallowtail (Fig. 234; map Fig. 157; genitalia Fig. 57)

Papilio ucalegonides Staudinger, 1884: 10, pl 6. LECTOTYPE ♂: ANGOLA/DEMOCRATIC REPUBLIC OF CONGO: 'Quango . . . Herrn Major von Mechow' (Staudinger, 1884). Designated Berger (1950). MNHU (not seen). 5 PARATYPE ♂♂: ANGOLA/DEMOCRATIC REPUBLIC OF CONGO: Same data. BMNH Spec.Reg. Nos 143274–8.

Papilio ucalegon ucalegonides Staudinger; Aurivillius, 1908.

Papilio ucalegon v. *ucalegonides* Staudinger; Bryk, 1930*b*: 561.

Graphium ucalegonides ucalegonides (Staudinger); Berger, 1950: 76, fig.73 [as stat. rev.] D'Abrera, 1980: 42, 43 (figs); Berger, 1981: 51, pl.15 figs 4 (♂), 8 (♀).

Papilio (*Graphium*) *ucalegonides ucalegonides* Staudinger; Peters, 1952: 21.

Graphium (*Arisbe*) *ucalegonides* (Staudinger); Munroe, 1961: 42; Hancock, 1983: 46.

Graphium fulleri ucalegonides (Staudinger); Hancock, 1985*a*: 99 (as 'comb. nov.'); d'Abrera, 1997: 50, 51 (fig.).

Graphium (*Arisbe*) *fulleri ucalegonides* (Staudinger); Collins & Morris, 1985: 58, 124; Ackery, Smith & Vane-Wright, 1995: 162.

SYNONYM

Papilio phrynon H(erbert). Druce, 1895: 332. LECTOTYPE ♂: DEMOCRATIC REPUBLIC OF CONGO: 'Upper Congo (*Mus. Druce*)' (Druce, 1895: 333) [Data label reads 'Matadi/Congo/Free/-State']. BMNH Spec.Reg. No. 143259 – designated Le Cerf (1924).

Papilio phrynon Druce; Aurivillius, 1908;

Papilio ucalegonides =*phrynon* Druce; Le Cerf, 1924*a*: 395 [as syn. n.].

Papilio ucalegon v. *phrynon* Druce; Bryk, 1930*b*: 562.

Papilio (*Graphium*) *ucalegonides phrynon* Druce; Peters, 1952: 21.

Graphium ucalegonides ucalegonides f. *phrynon* (Druce); Berger, 1950: 77, fig.74 (♂); Berger, 1981: 51, pl.11 fig. 6 (♂); pl.15 fig.7 (♀).

Graphium fulleri ucalegonides =*phrynon* (Druce); Hancock, 1985*a*: 99 (as 'syn. nov.').

Graphium (*Arisbe*) *fulleri ucalegonides* =*phrynon* (Druce); Ackery, Smith & Vane-Wright, 1995: 162.

UNAVAILABLE NAMES

Papilio (*Cosmodesmus*) *ucalegon ucalegonides* ab. *cuvelieri* Dufrane, 1946: 120. DEMOCRATIC REPUBLIC OF CONGO. IRSN. (not seen) [infrasubspecific].

Papilio (*Graphium*) *ucalegonides ucalegonides* ab. *cuvelieri* Dufrane; Peters, 1952: 21.

Graphium (*Arisbe*) *fulleri ucalegonides* =*cuvelieri* (Dufrane); Ackery, Smith & Vane-Wright, 1995: 162.

Graphium ucalegonides ucalegonides f. *addenda* Berger, 1950: 78. DEMOCRATIC REPUBLIC OF CONGO. MRAC. [infrasubspecific].

Graphium fulleri ucalegonides =*addenda* Dufrane; Hancock, 1985*a*: 99.

Graphium (*Arisbe*) *fulleri ucalegonides =addenda* Dufrane; Ackery, Smith & Vane-Wright, 1995: 163.

TYPE EVALUATIONS

Papilio ucalegonides Staudinger (1884) was described (somewhat tentatively; Staudinger wrote 'Should these differences . . . be constant, then one may consider this a good local form, and I coin for it the name Ucalegonides') from an unstated number of specimens collected by von Mechow at Quango and from another specimen from 'Innern Ostafrika'. Berger (1950) effectively designated a lectotype by stating 'Type: Ht Kwango, coll. STGR.' Staudinger's collection should be in MNHU (Horn *et al.*, 1990), though CRS did not see the specimen during a brief visit. There are, however, 5 specimens (of which Berger (1950) recorded two) from Kwango collected by von Mechow in BMNH, which we consider to be paralectotypes. They reached BMNH via the Oberthür bequest (BMNH accession register no. 1927–3; 4 specimens) and Adams bequest (BMNH accession register no. 1912–399; 1 specimen).

Druce (1895) did not designate a primary type nor state his series length explicitly in his description of *Papilio phrynon*. However, Le Cerf (1924) designated a 'Type (H.T.)' from the Hill Museum. He furnished the specimen with a round 'Type H.T' label. It also bears a determination label, apparently in Druce's hand, reading 'Papilio/phrynon/type Druce' and a locality label reading 'Matadi/Congo/Free/-State'. Since the original series length is unknown, we accept this as the lectotype. According to Horn *et al.* (1990), Druce's post-1880 collection was acquired by the Hill Museum, much of which was itself acquired by the BMNH as the Joicey Bequest, BMNH accession no. 1934–120.

TAXONOMIC STATUS

Papilio ucalegonides Staudinger (1884) was established as a species. Aurivillius (1908) treated it as a subspecies of *P. ucalegon* (having earlier (1899) included it as a species). This was followed by authors until Berger (1950) restored it to specific rank, with *G. u. rileyi* as a subspecies. Hancock (1985) placed it, together with *rileyi*, as a subspecies within *G. fulleri*.

Papilio phrynon Druce (1895) was established as a species. Aurivillius (1899; 1908) treated it as a species, but speculated that it might be synonymous with or an aberration of *P. ucalegonides*. Le Cerf (1924) synonymized it with the latter, which has been accepted by most subsequent authors, though Bryk (1930) treated it as a var. (= subspecies) of *P. ucalegon* and some other authors have treated in infrasubspecific to *ucalegonides*.

SIMILAR TAXA

Distinguished from the nominate race by colour and by the absence of hindwing upperside post-discal marks in cells M_2 to CuA_1. The features distinguishing it from *G. f. boulleti* are described in the section for that taxon. Similar in pattern to *G. f. rileyi*, though the hindwing discal cell band is generally narrower and the post-discal forewing cell CuA_1 is often much reduced compared with the latter. More reliable is colour: the ground colour is slightly paler; the marks distinctly brownish compared to *G. f. rileyi*, in which they are creamy. *G. f. ucalegonides* lacks the 'powdering' of pale scales in the dark park of the hindwing discal cell upperside which is a feature of the *ucalegon* clade, but posseses a dark mark near the base of hindwing underside cell R_1, which is not found in most of the remaining mimetic species (with the exception of the distinctive *G. auriger*).

DIAGNOSIS: PATTERN (Fig. 234)

Upperside ground colour mid- to dark brown (partly dependent on degree of fading) with pale brownish yellow markings. **Forewing** discal cell with a mark of variable size based on the posterior discocellular vein opposite cell M_3. Sometimes this does not reach the first 'intervenosa'; sometimes extends beyond the second; in a very few specimens it is missing (ab. *cuvelieri* Dufrane). Distal mark opposite cell R_5 usually absent, but sometimes present (f. *addenda* Berger). Cell R_3 with post-discal mark not reaching base of cell, but extending beyond root of vein R_4, sometimes fractionally; sometimes considerably, especially in the posterior half of cell. Cell R_4 sometimes without marking, but usually with an axillary post-discal mark which may be small and faint to large. Cell R_5 with a post-discal mark not reaching the cell base, notched distally by the intervenosa. Cell M_1 usually unmarked, but sometimes with a small, often linear mark in the anterior half. Cell M_2 usually with a small (sometimes very small) submarginal post-discal mark at base, largely confined to the posterior half. Post-discal mark in cell M_3 usually large, filling the basal half of the cell, quadrate, rounded or tapered distally; sometimes an extremely faint (occasionally clear) subdivided submarginal mark present. Post-discal mark of cell CuA_1 very variable: occasionally absent (as in LT of *phrynon*); sometimes a small, diffuse spot in the anterior half; sometimes quite large, reaching the posterior discocellular vein and veins CuA_1 and CuA_2, but with many intermediates; sometimes an extremely faint (occasionally clear) submarginal mark present. Post-discal mark in cell CuA_2 only very rarely reaching posterior discocellular vein, sometimes reaching vein CuA_2 and always reaching vein 1A; rounded or tapered distally; sometimes with an extremely faint (occasionally clear) subdivided submarginal mark. Cell 1A with a post-discal mark more-or-less contiguous with that in CuA_2.

Hindwing generally slightly paler than upperside, with clearer intervenosae. Discal cell band fairly narrow (the distal boundary generally running roughly from the 'elbow' of the upper discocellular vein to the root of vein CuA_2) and with clear cut boundaries. Cell

R_1 with an almost white, post-discal mark which gradually fades to golden brown distally, the whole composed of broad scales, somewhat rounded (not cuspid) at their tips. Cell R_5 with an axillary post-discal mark, also fading to golden brown distally to a greater or lesser extent. Cells M_1 to M_3 usually without marks (1 specimen in BMNH – Spec.Reg. No. 143349 – from Lulua-Sankuru, has a clear post-discal spot in cell M_3 almost subdivided by the intervenosa and a very small post-discal spot in cell CuA_1). Cell CuA_1 usually with a small discal mark in angle of vein CuA_2 and cubital vein. Cell CuA_2 with discal mark along cubital vein as far as root of vein CuA_2; pale scales associated with pheromone system sometimes not reaching vein CuA_2.

Underside paler than upperside, with intervenosae prominent, ground colour somewhat reddened towards the wing bases. Pattern largely mirroring that of the upperside with the following differences. **Forewing** discal cell mark and post-discal mark in cell CuA_1 with a nacreous surround. **Hindwing** discal cell with two clear 'intervenosae', the anterior meeting the medial vein at its elbow; the posterior reaching the discocellular vein just anterior to root of vein M_2. Costal cell with a black spot in angle of humeral vein. Cell R_1 with an more or less well clear, elongate, slightly fuzzy edged black mark near the base along the line of the intervenosa.

VARIATION

In addition to the variation detailed above, it should be noted that the extent of the golden brown area of the hindwing upperside is quite variable. Usually confined to cell R_1 and R_5, it sometimes is seen over most of the hindwing surface.

DIAGNOSIS: ♂ GENITALIA (Fig. 57)

Dorsal projection slightly longer than in *fulleri*, slightly directed anteriad, slightly upcurved, cluster of stout setae at tip and anteriorly. *Dorsal harpe* usually slightly carinate. *Ventral harpe* with broad ventral blade, pointed posteriorly (in one specimen, the tip is bifid); dorsal blade of similar length, pointed, curved somewhat mesad distally. *Dorsal terminal process* of moderate size, ventral tip blunt. *Ventral terminal process* quite small, somewhat concave dorsally, convex and denticulate ventrally. *Rim* quite broad, a line of stout setae on its inner margin from ventral side of dorsal terminal process to ventral to dventral harpe. *Uncus* curved distally, *socii* prominent. *Saccus* short. *Aedeagus* short, curved ventrad, especially at base.

DIAGNOSIS: ♀ GENITALIA. No specimens available for dissection.

EARLY STAGES; HOST PLANTS. Unknown.

DISTRIBUTION (Map Fig. 157)

Larsen (BWA) suggests old records from Nigeria are false, and that this taxon does not seem to occur west of Douala (see Darge, 1995).

Records from: Cameroon, Chad (Fort Orchambault, MNHN), Congo, Democratic Republic of Congo, ?Angola.

BIONOMICS. A forest butterfly (Fontaine, 1985: 114).

CONSERVATION STATUS. 'Not uncommon and not threatened' (Collins & Morris, 1985: 58).

MATERIAL EXAMINED. 92 ♂♂ in BMNH; 44 ♂♂ from other collections.

34. ***Graphium* (*Arisbe*) *poggianus*** (Honrath, 1884)

Pogge's Graphium (Fig. 209; map Fig. 150; genitalia Fig. 58)

We here follow Hancock (1985) in regarding *G. poggianus* as a good species, separate from *G. almansor*, etc. This very poorly known butterfly was until now considered to include three subspecies: the nominate, plus two from the Kigoma/Mpanda area of W. Tanzania. Examination of the genitalia, wing patterns and scales suggests that this is untenable, and that two separate species are involved.

Papilio poggianus Honrath, 1884: 210, pl.7 fig.10. HOLOTYPE ♂: ? DEMOCRATIC REPUBLIC OF CONGO: 'Guinea – ob an der Küste oder weit im Innern . . . nach einem ♂'. (Honrath, 1884: 210). MNHU 'Berl. entom. Museum.' (Honrath, 1884: 210).

Papilio poggianus Honrath; Aurivillius, 1908 : 24.

Papilio adamastor =poggianus Honrath; Schultze, 1913*a*. [as syn. n.]

Papilio agamedes poggianus Honrath; Bryk, 1930*b*: 564.

Papilio (*Graphium*) *agamedes poggianus* (Honrath); Peters, 1952: 21.

Graphium almansor almansor f. *poggianus* Honrath; Berger, 1950: 81, 82, fig.79 [as syn. n.]; Berger, 1981: 51, pl.16 fig. 2 (♂).

Graphium poggianus poggianus (Honrath); Hancock, 1985*a*: 101 (as 'stat. rev.'); d'Abrera, 1997: 52, 53 (fig. – holotype).

Graphium (*Arisbe*) *poggianus* (Honrath); Collins & Morris, 1985: 57.

Graphium (*Arisbe*) *poggianus poggianus* (Honrath); Ackery, Smith & Vane-Wright, 1995: 165.

TYPE EVALUATIONS

Papilio poggianus Honrath (1884) was described from a single specimen collected by Dr P. Pogge and seen by Honrath in the Berlin Entomological Museum, now MNHU. Honrath stated that the specimen was from 'Guinea'. However, Horn *et al.* (1990) stated that Pogge made an expedition to 'Lualaba und dem Kassai-

Land', southern Democratic Republic of Congo, in 1882, the specimens from which went to MNHU. Since the few specimens we have seen have all been from this part of Democratic Republic of Congo or from North-West Zambia, it is fairly certain that the holotype has that provenance.

The specimen itself is readily identifiable in MNHU, matching closely Honrath's (1884) figure. It bears a locality label reading 'Guinea inter/Pogge', a determination label reading 'Poggianus/Honrath *' and a further determination label also giving the reference. These labels appear to have been written by H. Dewitz, who was curator of the collection at the time (Horn *et al*., 1990: 91, pl.8 fig.1). A further printed label gives collection number 22881.

TAXONOMIC STATUS

Papilio poggianus Honrath (1884) was established as a species. Schultze (1913*a*) synonymized it with *G. adamastor*. Bryk (1930) included it as a variety (=subspecies) of *G. agamedes*. Berger (1950) argued that it is a form (infrasubspecific) of *G. almansor almansor*. Hancock (1985) restored *G. poggianus* to specific status largely on the basis of the male genitalia. Our own studies support this interpretation, with the male valve (we have examined the holotype) significantly different from *G. adamastor*, *G. agamedes* and *G. almansor*.

SIMILAR SPECIES

The form of the forewing discal cell band – crossing the cell uninterupted by intervenosae, tapering towards the radial vein, and concave posteriorly – is fairly characteristic for the species. *G. almansor escherichi* may have a similar pattern, but in that taxon, the intervenosae are apparent and the hindwing underside marks are decidedly pink proximally.

DIAGNOSIS: PATTERN (Fig. 209)

The few specimens we have seen show considerable variation; the holotype is particularly heavily marked.

Upperside ground colour dark chocolate brown somewhat paler on the hindwing, especially in the proximal areas of the peripheral cells (the holotype appears generally paler, but this is due to abrasion). Markings almost white.

Forewing discal cell with band crossing full width of cell (but not extending beyond radial vein) opposite cell M_3, more or less deeply convcave proximally (particularly in holotype). No spot in distal part of cell. Cell R_3 with post-discal mark usually reaching or just surpassing the root of vein R_4. Cell R_4 unmarked. Cell R_5 with post-discal mark indented distally to a greater or lesser extent, the posterior lobe being larger. Cell M_1 unmarked. Cell M_2 usually with a post-discal mark confined to the posterior half of the base of the cell. This mark may be quite extensive – as in the holotype – but it may be reduced, fuzzy, be represented by a small scattering of pale scales, or absent altogether. Post-discal mark of cell M_3 large, covering almost the full width of the cell basally, tapering somewhat distally; in some specimens there is the faint indication of a submarginal mark either almost touching or almost subsumed by the post-discal. Cell CuA_1 usually without a post-discal mark, but in the holotype and one other specimen there is a streak running from the angle of the posterior discocellular vein and vein CuA_1 towards the margin at the midline. In the holotype this streak is almost solid and reaches a slightly blurred submarginal mark; in the other (N.W. Zambia: Mwinilunga. ABRI) it is a fuzzy scattering of scales. A further specimen from Mwinilunga (ABRI) has a small, but clear spot on the midline of the cell, just proximal to a very faint submarginal mark, but on one side only. Extremely faint submarginal marks can be detected in a few other specimens. Cell CuA_2 with submarginal mark nowhere reaching either the posterior discocellular vein or vein CuA_2; usually contiguous with a blurred submarginal mark. Cell 1A with post-discal mark contiguous and almost coextensive with that in cell CuA_2.

Hindwing discal cell band very broad, from near base of cell, reaching root of vein M_1 anteriorly and beyond root of vein CuA_1 posteriorly, sometimes to root of M_3 or even beyond. Cell R_1 with large post-discal mark composed of rounded white scales, becoming golden distally, indented distally by intervenosa. Cell R_5 with axillary post-discal mark usually extending beyond root of vein M_1 and fading to gold anteriorly; indented distally. In the holotype there is a subdivided submarginal mark, the posterior portion quite clear; the anterior a scattering of white scales. Cell M_1 usually with a small, but prominent white post-discal streak near the cell base anterior to the intervenosa; occasionally also a very faint submarginal mark anterior to the intervenosa. The holotype has a clearly bifid submarginal mark and a small faint mark in the angle of vein M_1 and middle discocellular vein; a specimen from Ikelenge (Zambia, ABRI) lacks the post-discal streak (as does a specimen from Mwinilunga, Zambia, ABRI), but does have a diffuse anterior submarginal mark. Cell M_2 usually unmarked, but the holotype has an elongate, subdivided, somewhat diffuse submarginal mark in this cell and in cells M_3, and CuA_1. Cell M_3 with a basal mark, sometimes quite diffuse, along the medial vein and vein CuA_1. Cell CuA_1 has a basal mark in angle of vein CuA_2 and cubital vein extending as far as root of vein CuA_1 and sometimes a little way along this. Cell CuA_2 with a patch of silvery scales extending across the full width of cell and from almost the base to the distal end of the scent organ.

The **underside** pattern, as usual, largely reflects that of the upperside, with the ground colour paler and the intervenosae, in consequence, more prominent.

Forewing cell CuA_1 has an elliptical post discal mark of pale scales, giving a nacreous effect against the dark membrane, even where there is no such mark on the upper surface. Such nacreous areas surround the spots where they are present and provide a border to some other marks.

On the **hindwing**, there is a black spot in the costal cell just distal to the humeral vein, but no basal black spot in cell R_1. The discal cell has two intervenosae, usually not heavily marked, the anterior reaching the upper discocellular vein at the 'elbow'; the posterior reaching the middle discocellular vein anterior of the root of vein M_2.

VARIATION. See above.

DIAGNOSIS: ♂ GENITALIA (Fig. 58)
Based on dissections of the holotype (on loan from MNHU) and a specimen from ABRI.

Dorsal projection more-or-less normal to valve wall, but angled slightly dorsad. *Dorsal harpe* with mesal edge carinate and with transverse striae across vertical blade, which is sometimes somewhat sinuous. *Ventral harpe* with horizontal and dorsal blades almost equal in size (the vertical thus relatively large – this is an unusual feature within the clade – including *G. kigoma* – where the horizontal blade is generally significantly the larger); vertical blade angled posteriad and curved mesad; in the ABRI specimen studied the horizontal blade is deeply bifid. *Dorsal terminal process* smoothly curved dorsally, but ventral tip quite acute, connected to ventral terminal process by prominent ridge. *Ventral terminal process* smmothly curved dorsally, denticulate ventrally, facing somewhat dorsad. *Uncus* elongate, *socii* quite prominent, with prominent projections. *Saccus* small. *Aedeagus* elongate, slightly curved, non-denticulate.

DIAGNOSIS: ♀ GENITALIA. We have seen no females.

EARLY STAGES; HOST PLANTS; BIONOMICS. Unknown.

DISTRIBUTION (Map Fig. 150). Known only from the vague type locality (see above) and La Luvina in Democratic Republic of Congo (MRAC) and northern Zambia. Records for Angola seem to stem from Berger's (1950) assumption about the type locality.

CONSERVATION STATUS. 'Uncommon but no evidence of being threatened' (Collins & Morris, 1985: 57). With our restriction of the definition of the species, 'insufficiently known' might be more appropriate.

MATERIAL EXAMINED. 2 ♂♂ in BMNH. 4 ♂♂ from ABRI. HT ♂ from MNHU. 1 ♂ from MRAC.

35. *Graphium (Arisbe) kigoma* Carcasson, 1964 stat. n.

Kigoma Graphium (Fig. 210; map Fig. 152; genitalia Figs 59, 60 100)

Carcasson (1964) described *Graphium almansor kigoma* as a subspecies of *almansor* from the Kigoma district of western Tanzania, likening it in size to *poggianus*, which he regarded as an infrasubspecific form of *G. a. almansor*. However, the male valve of *kigoma* (and *poggianus*) lacks the hook-like ventral terminal process characteristic of *G. almansor*. Hancock (1985) raised *poggianus* to species level, with *kigoma* as a subspecies.

However, the male genitalia of *poggianus* and *kigoma* differ sufficiently for us to conclude that they are not conspecific. In particular, the dorsal blade of the ventral harpe of *kigoma* is smaller than the horizontal, unlike the situation in *poggianus* in which, unusually, it is at least as large.

We therefore here raise *kigoma* to full species status.

Kielland (1978) also described *Graphium almansor wranghami* as a subspecies of *almansor* from the Kigoma district, but from a mixed series including *G. a. almansor*. He later (1990) included both *wranghami* and *kigoma* as subspecies of *G. poggianus*, flying in adjacent parts of the Kigoma and Mpanda districts, giving the range of *kigoma* as 'From the Mahale Mts. in Kigoma, and Kampisa [near Katuma] in Mpanda to Malagarasi River, south of Kigoma town' while restricting that of *wranghami* to the Gombe Stream National Park, just to the north of Kigoma. In our view, based on the limited material to hand, the separation of these two supposed subspecies does not appear tenable. Though the extremes of the phenotypic differences look distinct, as shown in various published illustrations (Kielland, 1978: pl.4 figs 13, 14; pl.5 figs 17, 18; 1990: pl.9; though Carcasson's, 1964: 7, 8, illustrations of *kigoma* are similar to *wranghami*), there is considerable variability. Moreover, and crucially, we have seen a series of specimens from ABRI (collected by Collins and Kielland), from one locality in the Kigoma district, Kefu, two of which clearly conform to the '*kigoma*' phenotype (one is illustrated in Kielland, 1990: pl.9) and one to the '*wranghami*' phenotype (a fourth specimen, collected by Kielland and conforming to the '*wranghami*' pattern is labelled simply Kigoma district). When we assembled all of the material to hand, a continuum was seen in the various characters: extent of the forewing discal cell band and whether it is interrupted by the intervenosae; presence of submarginal marks in forewing cells M_3 to CuA_2 (absent or faint in '*kigoma*'; faint to clear in '*wranghami*'); post discal marks in hindwing cells M_2 to CuA_1 (almost absent to clear in '*kigoma*'; usually clear in '*wranghami*'); presence of submarginal marks in hindwing cells (absent or faint in '*kigoma*'; faint to clear in '*wranghami*'). In addition, the male valve of the one '*wranghami*' we have dissected conforms to the pattern shown by *kigoma*. We therefore conclude that *kigoma* and *wranghami* are, indeed, synonyms, with the former being the senior name.

Graphium almansor kigoma Carcasson, 1964: 66. HOLOTYPE ♂: TANZANIA: 'Makuyu, Kigoma, Tanganyika, I – 1962, K.U.A.P.E. [Kyoto University African Primate Expedition]' (Carcasson, 1964: 67). BMNH Spec.Reg. No. 149196; PARATYPE ♀ 'Allotype': Same locality 'V – 1962, K.U.A.P.E.' (Carcasson, 1964: 67). BMNH Spec.Reg. No. 149195; 8 PARATYPE ♂♂, 1 PARATYPE ♀: 'data as above . . . Kyoto Museum [not seen], Coryndon Museum (NMK) [not seen] and British Museum (Nat. Hist.)' (Carcasson, 1964: 67). BMNH ♂, Spec.Reg. No. 149197.

Graphium almansor kigoma Carcasson; D'Abrera, 1980: 44.

Graphium poggianus kigoma Carcasson; Hancock, 1985*a*: 101 (as 'comb. nov.').

Graphium (*Arisbe*) *poggianus kigoma* Carcasson; Kielland, 1990: 48, 265 pl.9; Ackery, Smith & Vane-Wright, 1995: 165; d'Abrera, 1997: 52.

SYNONYM

Graphium almansor wranghami Kielland, 1978: 160, pl.5 figs 17, 18 ('wet season form'), 19, 20 ('dry season form' – a misidentification of *G. a. almansor* (Honrath), q.v.). HOLOTYPE ♂: TANZANIA: 'Holotype (w[et]. s[eason]. f[orm].): Tanzania, Kigoma, Gombe Stream Nat. Park, December, 1972, J. Kielland.' (Kielland, 1978: 161). NMK (Kielland, 1978: 161) – not seen; PARATYPE ♂♂: TANZANIA: 5: 'Paratypes (w[et]. s[eason]. f[orm].): Same data and collector, 5 ♂.' (Kielland, 1978: 161). NMK, BMNH and coll. J. Kielland (Kielland, 1978: 161) – not seen.; 4: 'Paratypes (d[ry]. s[eason]. f[orm].): Same data, 4 ♂.' (Kielland, 1978: 161). NMK, BMNH and coll. J. Kielland (Kielland, 1978: 161) – not seen. **Syn. n.**

Graphium almansor wranghami Kielland; D'Abrera, 1982: [1].

Graphium adamastor wranghami Kielland; Hancock, 1985*a*: 101 (as 'comb. nov.').

Graphium poggianus wranghami Kielland; Hancock, 1985*b*: 126 (as 'comb. nov.'); d'Abrera, 1997: 52.

Graphium (*Arisbe*) *poggianus wranghami* Kielland; Kielland, 1990: 48, 265 pl.9; Ackery, Smith & Vane-Wright, 1995: 165.

TYPE EVALUATION

Graphium almansor kigoma Carcasson (1964) was described from the 11 specimens listed above. The holotype and 2 paratypes in BMNH were presented as (part of) BMNH Accession register No. 1964–320.

Graphium almansor wranghami Kielland (1978) was described from the holotype and nine paratypes listed above, with designations original. As discussed below, the four paratypes listed as representing the supposed dry season form have proved to be misidentifications of *G. almansor almansor* Honrath (q.v.). No specimens had reached BMNH by the time of Kielland's death in 1995.

TAXONOMIC STATUS

See also species introduction.

Graphium almansor kigoma Carcasson (1964) was established as a subspecies of *G. almansor*. Hancock (1985) concluded on the basis of pattern and male genitalia that it should be included as a subspecies of *G. poggianus* (Carcasson, 1964, treated *poggianus* as a form of *almansor*). Certainly, the forewing discal cell band and the male valve (e.g. the ventral terminal process) (see below) make inclusion within *G. almansor* untenable. We regard the differences in male genitalia sufficient to separate *kigoma* from *poggianus* and here accord it specific status.

In 1978, Kielland described and illustrated a 'dry season form' of *G. a. kigoma*, noting that it was 'similar to the nominate race [*G. a. almansor*]'. Hancock (1985) concluded that this was not the same taxon as *G. p. kigoma*, but was, in fact, *G. almansor*. Subsequently, Kielland (1990) included it as a synonym of *G. a. almansor* (*q.v.*).

Graphium almansor wranghami Kielland (1978) was established as a subspecies of *G. almansor*. Hancock (1985*a*) recognized that the type series was mixed, concluding that those described by Kielland (1978) as the dry season form were misidentifications of *G. almansor almansor* (Honrath), whilst those described as the wet season form (which included the holotype) were a genuine new taxon, which Hancock (1985*a*) included as a subspecies of *G. adamastor* (Boisduval). Hancock (1985*b*) later transferred it as a subspecies of *G. poggianus* (Honrath), based on the male genitalia. Kielland (1990) indicated his acceptance of this arrangement by including the dry season form in the synonymy of *G. a. almansor* and the wet season form as a subspecies of *G. poggianus* (Honrath). For reasons described above, we conclude that separation of *kigoma* and *wranghami* into subspecies is untenable, and here synonymize the two.

SIMILAR SPECIES

Distinguished from *G. poggianus* by the (usually) incomplete forewing discal cell band, which is often interrupted by the intervenosae; and by the presence in most specimens of post-discal marks in hindwing cells M_2 to CuA_1.

Superficially similar to *G. adamastor*, but that, too, has a complete discal cell band.

In *G. agamedes*, there is a large post-discal mark in forewing cell CuA_1, linking those in cells M_3 and CuA_2; and the marks in forewing cells R_3 to R_5 (especially the latter) are reduced or absent, with the whole apical/distal area much more translucent.

In the various subspecies of *G. almansor*, the forewing discal cell band is either complete or is based on the radial vein.

Unlike *G. adamastor*, *G. agamedes* and *G. almansor* and *G. poggianus*, *G. kigoma* posseses a basal, longitudinal black stripe in hindwing underside cell R$_1$.

Diagnosis: pattern (Fig. 210)

Upperside ground colour dull to dark brown, somewhat translucent on margins of forewing, markings pale cream to almost white.

Forewing discal cell with very variable, but generally triangular mark based on posterior discocellular vein opposite cell M$_3$, tapering towards the radial vein. At its most extensive (an ABRI specimen from Kefu, coll. Kielland, 1–[19]71), the base extends from opposite vein CuA$_1$ to the 'intervenosa' of cell M$_2$, and the mark virtually reaches the radial vein. In the holotype it extends across virtually the whole width of the cell, interrupted by the anterior 'intervenosa', but only slightly indented by the other 'intervenosae'; the element costal to the anterior 'intervenosa' slightly diffuse. At the other extreme (e.g. an ABRI specimen from Kefu, coll. Kielland, 1–[19]70), the mark comprises three somewhat diffuse patches, separated by the 'intervenosae' and becoming smaller costally. Other specimens, including the 'allotype' of *kigoma* and the female illustrated by Carcasson (1964: 65a, fig. 8) fall between these extremes. A few specimens have a distal mark in the discal cell opposite R$_5$, as reported by Carcasson (1964), though we have only seen this in the ABRI specimen from Kefu (coll. Kielland, 1–[19]71), mentioned above (but see also Kielland, 1978, pl.5 figs 17, 18). Cell R$_3$ with post-discal mark reaching root of vein R$_4$ or nearly so. Cell R$_4$ unmarked. Cell R$_5$ with post-discal mark indented distally, the posterior lobe the larger; subdivided submarginal mark usually present, sometimes contiguous with post-discal mark (as in the specimens figured in Carcasson, 1964). Cell M$_1$ unmarked. Cell M$_2$ sometimes with a small post-discal spot. When present, this is of varying size, usually small and triangular, but in the the ABRI specimen from Kefu (coll. Kielland, 1–[19]71), mentioned above it is linear, extending to equal that in M$_3$ and with a basal extension anteriad, beyond the intervenosa; in another ABRI specimen from Kefu (coll. Kielland, 1–[19]70), there is the element of a subdivided submarginal mark posterior to the intervenosa. Cell M$_3$ with a post-discal mark reaching the posterior discocellular vein and sometimes veins M$_3$ and CuA$_1$ and usually a clear to very faint subdivided submarginal mark. Cell CuA$_1$ usually without post-discal mark, but one male in BMNH (Spec.Reg. No. 149198) and the female figured in Carcasson (1964) show a small mark more-or-less level with the distal margins of those in the surrounding cells; in two Kefu specimens in ABRI, this is a larger linear feature along the mid-line of the cell; sometimes a faint to moderately clear submarginal mark. Post-discal mark of cell CuA$_2$ quite distal from posterior discocellular vein and not reaching vein CuA$_2$; submarginal mark absent to distinct and subdivided. Cell 1A with post-discal mark co-extensive with that in CuA$_2$.

Hindwing with discal cell band broad, but less extensive than in *G. poggianus*, not reaching the root of vein M$_1$ anteriorly barely to root of CuA$_1$ posteriorly, its distal margin variable in outline, sometimes extended along discocellular vein. Cell R$_1$ with broad post-discal band of rounded white scales, becoming golden brown distally and basally; indented by intervenosa. Cell R$_5$ with basal post-discal mark extending to root of vein M$_1$, or nearly so, tending to golden brown distally and indented by intervenosa, sometimes with very faint to clear, subdivided submarginal mark. Cell M$_1$ sometimes with a small, clear post-discal spot anterior to the intervenosa and sometimes with a faint and fuzzy to clear subdivided submarginal mark, the anterior element much the larger. The expression of the post-discal marks in cells M$_1$ to CuA$_1$ is variable, ranging from almost absent (e.g. holotype) to very clear (e.g. ABRI specimen from Kefu, coll. Kielland, 1–[19]70); where present, each is indented distally by intervenosa, sometimes completely divided (e.g. the female paratype, BMNH Spec.Reg. No. 149195). The submarginal marks in cells M$_1$ to CuA$_1$ absent to clear, subdivided. In addition there is an axillary mark in cell CuA$_1$ in the angle of posterior discocellular vein and vein CuA$_2$. In the males there is a large, scaled discal mark covering the full width of cell CuA$_2$; in the female paratype, this is smaller, largely non-scaled, but there are small scatterings of white scales representing post-discal and submarginal marks.

The **underside** pattern largely reflects that of the upperside, though the ground colour is paler and the intervenosae more prominent. The ground colour of the wing bases, especially the hindwing, is dark brick red. In **forewing** cell CuA$_1$ there is an elliptical, nacreous patch of silvery scales corresponding to the (usually absent) post-discal mark of the upperside. The **hindwing** discal cell has two undivided 'intervenosae' reaching the medial vein and the upper discocellular vein. There is a black spot in the crook of the humeral vein and an elliptical black mark near the base of cell R$_1$, which is slightly fuzzy distally and, occasionally, extends to link with the intervenosa.

Variation. See above.

Diagnosis: ♂ genitalia (Fig. 59, 60)

Dorsal projection quite stout, slightly upturned, directed slightly anteriad, with setae mainly on antero-distal face. *Dorsal harpe* with transverse carina, giving 'twisted' appearance; the tip of the left valve dorsal harpe of one specimen is bifid. *Ventral harpe* with broad horizontal blade curved somewhat mesad (in one specimen, this blade is fractionally truncate or even bifid at the tip), but not extending far across rim; vertical blade smaller (unlike in *G. poggianus*) angled posteriad and curved mesad. *Dorsal terminal process* rounded at dorsal tip; chisel shaped at ventral tip. *Ventral terminal process* smoothly curved dorsally, denticulate ventrally; somewhat twisted so lamella facing slightly dorsad. *Uncus* elongate, *socii* heavily ridged and prominent and with prominent projections. *Saccus* small. *Aedeagus* elongate, smoothly curved, non-denticulate.

Diagnosis: ♀ genitalia (Fig. 100)
Very similar to *G. (A.) fulleri rileyi*, in particular in that the labia of the vestibulum are deeply indented posteriorly at the midline.

BMNH Spec.Reg. No.149195 (PT); vial 5447: *vestibulum* rounded, with the labia deeply indented posteriorly mesally; *ostium bursae* opening anteriorly; *ductus bursae* not sclerotized, kinked/constricted or pocketed distally; *central ostial lobe* glabrous, broad, truncate, almost reaching tip of laterals; *lateral ostial lobes* setose, long and broad, not well sclerotized; *anterior apophyses* normal; *papillae* elongate dorsally.

Early stages; host plants; conservation status. Unknown.

Distribution (Map Fig. 152). The Kigoma and Mpanda districts of western Tanzania.

Bionomics. According to Kielland (1990, treating it as two subspecies), *G. kigoma* flies in the mixed forest remnants, mountains, hills and savannahs that border the eastern shore of Lake Tanganyika.

Material Examined. 3 ♂♂, 1 ♀ in BMNH. 4 ♂♂ from ABRI. 1 ♂ fro Tanzania: Kefu, coll. Kielland in MRAC. In addition, the various illustrations listed above.

36. *Graphium (Arisbe) hachei* (Dewitz, 1881)

Milky Graphium (Figs 211, 235; map Figs 144, 145; genitalia Fig. 61)

A species of forests in the Congo basin, distinctive in the simplicity of its pattern, having a single, very broad white stripe crossing the hindwing and posterior part of the forewing before seeming to curve into the forewing discal cell.

G. hachei is generally regarded as bitypic, with the nominate race occurring to the south and west (Gabon, Congo Republic, western Democratic Republic of Congo and northern Angola). *G. h. moebii* is more northern and eastern in distribution, occurring from Cameroon to northern and eastern parts of Democratic Republic of Congo. Though generally readily identifiable, some specimens – not always from the boundary zone – are somewhat intermediate in form (see 'variation' sections, below).

Similar species
No African *Graphium* precisely resemble *G. hachei*, with its simple and striking pattern.

Diagnosis: pattern (Fig. 211, pl. 9 Fig. 235)
Upperside ground colour brown with markings white. **Forewing**, distal to white mark (i.e. the distal part of discal cell, entirety of cells R_3 to M_1, distal parts of cells M_2 to CuA_2), translucent due to narrowing of scales, except along the veins.

Forewing discal cell with broad transverse band based on posterior discocellular vein between vein CuA_1 and M_2, not interupted by 'intervenosae', but not usually reaching radial vein. Cells R_3 to R_5 and usually M_1 without white marks. Cells M_2 to 1A with postdiscal marks across full width of cell, the extent and exact disposition varying with subspecies.

Hindwing with discal cell brown at base, the remainder white, or largely so, varying with subspecies and individual variation (all white in ssp. *hachei*; more variable in ssp. *moebii*).

Cell R_1 brown basally and marginally, the remainder white. Cells R_5 to CuA_2 white basally, the extent depending on subspecies and individual variation, but generally more extensive in ssp. *hachei* (see accounts for subspecies and their variation, below). Cell 1A with base brown, the remainder white.

Underside pattern similar. **Forewing** ground colour (in discal cell and bases of cells CuA_1 to 1A) slightly paler than upperside. **Hindwing** ground colour paler, with intervenosae more prominent; pale marks darker and less prominent. Hindwing discal cell with 2 clear 'intervenosae'. A black spot in angle of humeral vein. Bases of costal, precostal, discal and CuA_2 cells black, with a tuft of white scales at the base of the costal and cubital veins.

Variation
See accounts for subspecies. According to Williams (1969, see also Berger, 1981: pl.14 fig. 3) the sexes are alike.

Diagnosis: ♂ genitalia (Fig. 61). See accounts for individual subspecies.

Diagnosis: ♀ genitalia. No females available for study.

Early stages; host plants. Apparently unknown.

Bionomics
The Milky Graphium is an uncommon forest species (Williams, 1969; Fontaine, 1985: 114) of the greater Congo basin. For Zaïre, Berger (1950) gives records for all months. From Cameroon, Darge (1995) gives a record for March. Otherwise, little appears to have been recorded.

Conservation status. 'Uncommon, but not threatened' (Collins & Morris, 1985: 57–8).

36a. *G.* (*A.*) ***hachei hachei*** (Dewitz, 1881)

Dewitz's Milky Graphium (Fig. 211; map Figs 144; genitalia Fig. 61)

Papilio Hachei Dewitz, 1881: 286. LECTOTYPE ♂: ANGOLA: '. . . Herr Major v. Mechow von seiner Reiser nach Westafrika, (Quango) mitbrachte' (Dewitz, 1881: 286). MNHU (photographed CRS x.95) – **here designated**; 20 PARALECTOTYPE ♂♂ (Dewitz, 1882): ANGOLA: same data. MNHU (2 seen), BMNH (4 seen: Spec.Reg. Nos 138833, 141737–9), IRSN (1 – Berger, 1951).

Papilio Hachei Dewitz; Dewitz, 1882: 69–70, pl.3 fig.2.

Papilio hachei Dewitz; Aurivillius, 1908: 23.

Papilio hachei [*hachei*] Dewitz; Bryk, 1930*b*: 560.

Graphium hachei hachei Dewitz; Berger, 1951: 70; D'Abrera, 1980: 42, 43 (fig.); Berger, 1981: 50, pl.14 fig 6 (♂); d'Abrera, 1997: 50, 51 fig..

Papilio (*Graphium*) *hachei hachei* (D.); Peters, 1952: 21.

Graphium (*Arisbe*) *hachei* (Dewitz); Munroe, 1961: 42; Hancock, 1983: 46; Collins & Morris, 1985: 57.

Graphium (*Arisbe*) *hachei hachei* (Dewitz); Carcasson, 1981: 123; Ackery, Smith & Vane-Wright, 1995: 163.

TYPE EVALUATIONS

In his description of *Papilio hachei*, Dewitz (1881) did not state his series length, but in a more detailed redescription (Dewitz 1882), he stated that there were 21 male specimens, collected by von Mechow during a 'Reise von Malange nach dem Quango und deisen Fluss abwärts' from September to November, 1880. In the MNHU there are 3 specimens all labelled 'Hachei Dewitz */Quango/v. Mechow', apparently in Dewitz's hand. One of these also has a collection number (22541) and a larger determination label, with reference (probably a collection label) and this specimen, photographed by CRS, is the one here selected as lectotype. There are further specimens, collected by von Mechow from Quango, in BMNH (ex Oberthür Coll., BMNH 1927–3; and ex Oberthür Coll., via Levick Bequest, BMNH 1941–83) and in IRSN (Berger, 1951) which should be regarded as paralectotypes. (2 further specimens in BMNH (Spec.Reg. Nos 141734–5), ex Adams Bequest, BMNH 1912–39, are also from Quango, coll. Mechow, but are dated 1881). Hermann Dewitz was 'Kustos' for Lepidoptera and Hymenoptera at MNHU, according to Horn *et al.* (1990).

TAXONOMIC STATUS

Papilio hachei Dewitz (1881) was established as a species and accepted as such by authors since.

DIAGNOSIS: PATTERN (FIG. 211)

White areas generally more extensive than in ssp. *moebii*. In particular: post-discal mark in **upperside forewing** cell CuA$_1$ usually reaching posterior discocellular vein throughout cell width; post-discal mark in forewing cell CuA$_2$ usually reaching posterior discocellular vein in distal half of cell; post-discal mark in forewing cell CuA$_2$ usually reaching wing margin in posterior half of cell; distal part of **hindwing** discal cell entirely white, without dark scales; band of post-discal marks extending further beyond tip of hindwing discal cell (at least 2·5 mm, measured along vein M$_2$, often much greater). On the **underside**, the dark basal area of the hindwing is less extensive than in ssp. *moebii*.

VARIATION

Though generally more broadly marked than ssp. *moebii*, there is some variation. In one specimen in BMNH from Quango (von Mechow, 1881; Spec.Reg. No. 141735), there is a scattering of brown scales in forewing upperside cell CuA$_1$ along the posterior discocellular vein. In that specimen also, the post-discal mark in cell CuA$_2$ reaches the posterior discocellular vein only very close to vein CuA$_2$, and there is a scattering of brown scales in that area. Apart from these two anomalies, the specimen is a typically broad-banded *hachei*. The extent of the hindwing post-discal band beyond the discal is very variable, from the minimum 2·5 mm to 7·0 mm, measured along vein M$_2$.

DIAGNOSIS: ♂ GENITALIA (Fig. 61)

Dorsal projection cylindrical, based below valve rim, slightly upcurved distally. *Dorsal harpe* a simple hook, carinate on mesal face. *Ventral harpe* with broad ventral blade, bifid terminally; the dorsal blade is long and curved mesad. There may be asymmetry between the two valves: that on the left valve in the specimen examined is simple; that on the right bifid terminally. *Dorsal terminal process* curved mesad, expanding dorsally and ventrally, with mesal edge curved and inclined to about 45°. *Ventral terminal process* rounded, directed somewhat ventrad, serrate distally and ventrally. *Uncus* long, *socii* projecting laterally. *Saccus* very short. *Aedeagus* long, curved, not denticulate.

DIAGNOSIS: ♀ GENITALIA. No females available for study.

EARLY STAGES; HOST PLANTS; BIONOMICS; CONSERVATION STATUS. See species account for what little is known.

DISTRIBUTION (Map Fig. 144). Gabon, Congo Republic, western Democratic Republic of Congo and northern Angola.

MATERIAL EXAMINED. 9 ♂♂ in BMNH. 14 ♂♂ from other collections.

36b. *G.* (*A.*) ***hachei moebii*** (Suffert, 1904)

Suffert's Milky Graphium (Fig. 235; map Fig. 145)

Papilio möbii Suffert, 1904: 104. [An incorrect original spelling under the Code Article 32.5.2.1 (ICZN, 1999), which must be corrected to *moebii*]. HOLOTYPE ♂: DEMOCRATIC REPUBLIC OF CONGO: 'Ein männliches Exemplar aus Central-Africa, 6° s. Breite, 25–26° östl. Länge von Pogge erbeutet . . . Coll. kön. zool. Museum, Berlin' (Suffert, 1904: 105). MNHU – photographed CRS 26.x.95.

Papilio möbii Suffert; Aurivillius, 1908 : 23, pl.9c.

Papilio hachei f. *möbii* Suffert; Schultze, 1917*b*: 24; Bryk, 1930*b*: 560.

Papilio hachei-möbii Suffert; Le Cerf, 1924*a*: 395.

Graphium hachei moebii (Suffert); Berger, 1951: 70–2, figs 69–70 [as stat. rev.]; D'Abrera, 1980: 42, 43 (fig.); Berger, 1981: 50, pl.14 figs 2 (♂), 3 (♂); d'Abrera, 1997: 50, 51 (fig.).

Papilio (*Graphium*) *hachei hachei* f. *möbii* (Suffert); Peters, 1952: 21.

Graphium (*Arisbe*) *hachei moebii* (Suffert); Carcasson, 1981: 123; Ackery, Smith & Vane-Wright, 1995: 163.

SYNONYMS

Papilio hachei-möbii camerunicus Le Cerf, 1924*a*: 395. HOLOTYPE ♂: CAMEROON: 'Type (H.T.): Un ♂, Cameroon, Bitje, Ja River, wet season, ex G. L. Bates, coll. Hill Museum.' (Le Cerf, 1924*a*: 396). BMNH Spec.Reg. No. 141832. 3 PARATYPE ♂♂: CAMEROON: 'Trois ♂♂, même origine, Museum de Paris, et Hill Museum.' (Le Cerf, 1924*a*: 396). BMNH Spec.Reg. Nos 141833–5; MNHN (not seen).

Graphium hachei moebii =*camerunicus* (Suffert); Berger, 1951: 71 [as syn. n.].

Papilio (*Graphium*) *hachei camerunicus* (Suffert); Peters, 1952: 21.

Graphium hachei hachei =*camerunicus* (Suffert); Ackery, Smith & Vane-Wright, 1995: 163 [misidentification].

Papilio (*Cosmodesmus*) *martensi* Dufrane, 1946: 119. HOLOTYPE ♂: DEMOCRATIC REPUBLIC OF CONGO: 'Holotype: ♂, Equateur sans localité précise, Congo Belge . . . M. MARTENS' (Dufrane, 1946: 120). IRSN.

Graphium hachei moebii =*martensi* (Dufrane); Berger, 1951: 71 [as syn. n.]; Berger, 1974: 73.

Papilio (*Graphium*) *martensi* (Dufrane); Peters, 1952: 21.

Graphium hachei martensi (Dufrane); Berger, 1981: 50, pl.14 fig. 7 (♂) [misidentification].

Graphium (*Arisbe*) *hachei moebii* =*martensi* (Dufrane); Ackery, Smith & Vane-Wright, 1995: 163.

TYPE EVALUATIONS

Papilio möbii Suffert (1904) was described from the single specimen, which is in MNHU and bears the label: 'Centralafr. Pogge./6 S. B. 21–26° L. v. Green.[wich]' and a separate label with just the printed number 23038.

Papilio hachei-möbii camerunicus Le Cerf (1924) was described from the four specimens listed above with type designations original. Much of the contents of the Hill Museum reached the BMNH as the Joicey Bequest (BMNH accession no. 1934–120). No specimen in BMNH has Le Cerf's determination label, but one specimen includes all the provenance detail listed by Le Cerf (Bitje, Ja River, wet season, G.L. Bates), and we regard that as the holotype. Three further specimens are labelled as being from Bitje, Ja River, wet season, but without a collector's name; we treat these as paratypes (none was seen by CRS in MNHN). There are further specimens from Bitje, ex Hill Museum, in BMNH, but are not stated to be wet season specimens.

Papilio (*Cosmodesmus*) *martensi* Dufrane (1946) was described, apparently, from the one specimen, with type designation original.

TAXONOMIC STATUS

Papilio möbii Suffert (1904) was established as a species. Schultze (1917*b*) treated it as an infrasubspecific form; Le Cerf (1924) stated that *hachei* and *moebii* were 'formes d'une même espèce', and discussed transitional specimens. Berger (1951) raised *moebii* to subspecific status and synonymized both *camerunicus* and *martensi* with it (he later (1981) treated the latter as a subspecies). Apart from Peters' (1952) checklist, compiled from the literature, recent authors have accepted subspecific status for *moebii*.

Papilio hachei-möbii camerunicus Le Cerf (1924) was established as a subspecies. But the diagnostic characters in the description seem to be those usually applied to separate *G. h. moebii* from *G. h. hachei*. Since Le Cerf synonymized these at the same time, it seems likely that he confused the two. Berger (1951) synonymized *camerunicus* with *G. h. moebii*. Peters (1952) treated it as a subspecies (but also included *möbii* (*sic*) as a form of the nominate subspecies). Ackery, Smith & Vane-Wright (1995) included it as a synonym of *G. h. hachei*, but comparison of the types clearly shows this to be untenable. On distributional grounds also, *camerunicus* is part of the more widespread population which extends from Cameroon through CAR to northern and eastern Democratic Republic of Congo; with *G. h. hachei* being confined to western Democratic Republic of Congo and Angola.

Papilio (*Cosmodesmus*) *martensi* Dufrane (1946) was established as a species. It was synonymized with *G. hachei moebii* by Berger (1951) and treated as such by Berger (1974), but later used by him at subspecies level (Berger, 1981). However, that usage appears to be effectively a misidentification. The specimen illustrated (Berger, 1981: pl.14 fig.7) does not match the holotype of *martensi* (photographed by CRS in IRSN), which appears to be a perfectly normal *G. h. moebii*. Moreover, *P. martensi* was described from Democratic Republic of Congo: Equateur, which Berger (1981) included in the range of *G. h. moebii*, whilst restricting the range of *martensi* to Democratic Republic of Congo: Kivu. Accordingly we here follow Berger (1951, 1974) and later authors apart from Berger (1981) in treating *P. martensi* Dufrane as a synonym of *G. h. moebii* Suffert. Should the specimens from Kivu (as represented by Berger, 1981: pl.14 fig.7) prove to represent a separate taxon, it will require naming.

DIAGNOSIS: PATTERN (Fig. 235)
White areas generally less extensive than in ssp. *hachei*. In particular: **upperside forewing** cell CuA$_1$ usually with brown mark along posterior discocellular vein across most of cell width; post-discal mark in forewing cell CuA$_2$ not usually reaching posterior discocellular vein; post-discal mark in forewing cell CuA$_2$ not usually reaching wing margin; distal part of **hindwing** discal cell usually with at least a scattering of brown scales; band of post-discal marks not extending so far beyond tip of hindwing discal cell (at most 1·0 mm, measured along vein M$_2$, though sometimes with a scattering of white scales beyond this). On the **underside**, the dark basal area of the hindwing is more extensive than in ssp. *hachei*.

VARIATION
Forewing discal cell transverse mark occassionally reaches radial vein, sometimes as a faint patch beyond anterior 'intervenosa'.

Forewing cell M$_3$ sometimes has a small patch of brown scales in angle of posterior discocellular vein and vein M$_3$. The size of the brown patch at the base of forewing cell CuA$_1$ is variable, sometimes reduced to a narrow scattering of brown scales, sometimes absent (as in ssp. *hachei*). Post-discal mark in forewing cell CuA$_2$ occassionally reaching posterior discocellular vein close to root of vein CuA$_2$. In a few specimens from Kivu, the forewing appearance is similar to that in *G. h. hachei* – this seems to be the phenotype referred to as ssp. *martensi* by Berger (1981), but not Berger (1951, 1974) or Dufrane (1946).

Hindwing discal cell sometimes with a scattering of brown scales, or even a more coherent brown area, distally. The white area of the hindwing is variable in extent, but rarely extends more than a milimetre beyond tip of cell along vein M$_2$.

On the underside, the hindwing pale area is variable in extent and is often divided into a smaller more distinct core area surrounded by an area of mixed golden and white scales. This effect is usually visible from above.

In addition, Berger (1951) reported specimens in which the forewing discal cell mark is reduced and interrupted by 'intervenosae'; a specimen from Tshuapa: Eala in which the distal border of the forewing band is lobed; a female in which the forewing discal cell band is not only interrupted by 'intervenosae', but is narrowed into a series of spots and in which the hindwing black border is very broad and 'pénêtre de 2 mm. dans la cellule discoidale.'

DIAGNOSIS: ♂ GENITALIA
Very similar to *G. h. hachei*, but *ventral harpe* not asymmetrical, with dorsal blade simple on both valves (though Le Cerf (1924) reports some asymmetry in *camerunicus*, so this may be a variable feature). *Ventral terminal process* slightly smaller than in *G. h. hachei*.

DIAGNOSIS: ♀ GENITALIA. We have been unable to dissect any females.

EARLY STAGES; HOST PLANTS; BIONOMICS; CONSERVATION STATUS. See species account for what little is known.

DISTRIBUTION (Map Fig. 145). Cameroon to northern and eastern parts of Democratic Republic of Congo.

MATERIAL EXAMINED. 44 ♂♂ in BMNH. 46 ♂♂; 4 ♀♀ from other collections.

37. *Graphium (Arisbe) aurivilliusi*
(Seeldrayers, 1896)

Aurivillius' Graphium (Fig. 212; genitalia Fig. 62)

Papilio Aurivilliusi Seeldrayers, 1896: 499, fig. LECTOTYPE ♂: ?DEMOCRATIC REPUBLIC OF CONGO: 'Congo' (Seeldrayers, 1896: 501). MRAC. Designated Berger (1950: 86); PARALECTOTYPE ♂♂: same data. 1 MRAC – see below; 1 NHRS 'Reichs Museum Stockholm' (Seeldrayers, 1896: 501) (not seen).

Papilio aurivilliusi Seeldrayers; Aurivillius, 1908: 23.

Papilio agamedes v. *aurivilliusi* Seeldrayers; Bryk, 1930*b*: 564.

Papilio (*Graphium*) *agamedes aurivilliusi* Seeldrayer [sic]; Peters, 1952: 21.

Graphium aurivilliusi Seeldrayers; Berger, 1950: 85–86, figs 83–4 ('♂ Holotype'); D'Abrera, 1980: 44; Berger, 1981: 49, pl.17 fig. 6 (♂ – HT); d'Abrera, 1997: 52, 53 (fig. 'Holotype').

Graphium (*Arisbe*) *aurivilliusi* Seeldrayers; Munroe, 1961: 42; Hancock, 1983: 46; Collins & Morris, 1985: 57, 219; Ackery, Smith & Vane-Wright, 1995: 162.

Graphium (*Arisbe*) *auriger aurivilliusi* Seeldrayers; Hancock, 1993: 568 (as 'stat. nov.').

TYPE EVALUATIONS
Papilio Aurivilliusi Seeldrayers (1896: 499) was described from an unspecified number of males from among a batch of insects acquired by the author from 'Congo', but with no precise locality ('. . . je ne puisse indiquer avec précision, l'endroit où cet insecte, venant

de centre Africain, fut capturé.' Seeldrayers, 1896: 501). Seeldrayers (1896) dedicated the species to Aurivillius and lists the 'Reichs Museum Stockholm' and his own collection (now in MRAC) as the depositories. One of the specimens in MRAC has three separate labels stating it to be the 'Type' and was illustrated by Berger (1950: 86, figs 83, 84) as 'Holotype', which we accept as designation as lectotype. A further specimen in MRAC has two labels stating it to be the 'type' and is here considered as paralectotype. It was dissected as 'Genitalia prep. 5/43' which forms 'Tervuren Museum ♂ Genitalia Slide N° Pa. 120'. Dr B. Gustafsson has informed us (pers. comm.) of a specimen in NRHS, Stockholm, labelled 'Type offert à M le Professeur C Aurivillius par Emile Seeldrayers 1/11 1890' which should be considered a paralectotype.

TAXONOMIC STATUS

Papilio Aurivilliusi Seeldrayers (1896: 499) was established at specific rank and most authors have treated it as such. Bryk (1930, followed by Peters, 1952, and Bridges, 1988*b*) treated it as a variety (=subspecies) of [*G.*] *agamedes*, but Berger (1950) reasserted its distinct, specific status on morphological and anatomical grounds (presumably wing pattern and genitalia).

Hancock (1993) treated it as a subspecies of *G. auriger*, with *G. odin eyeni* Berger as a synonym. However, differences in pattern and genitalia (see below) clearly show that this is not the case. We follow Berger (1981) himself in considering *eyeni* to be a synonym of *G. schubotzi* (Schultze) (*q.v.*).

SIMILAR SPECIES

G. aurivilliusi, with its semitranslucent forewing margins and prominent post-discal marks in hindwing cells M_2 to CuA_1, is most similar to *G. agamedes*. *G. aurivilliusi* possesses prominent apical marks in the forewing discal cell, which is rare in *G. agamedes*. In addition, the hindwing post-discal marks of cells M_2 to CuA_1 are large and undivided; in *G. agamedes*, they are subdivided by the intervenosae. The main mark in the forewing discal cell, opposite cell M_3, is much more clearly subdivided by the 'intervenosae' than is the case in *G. agamedes*, to the extent of appearing as parallel, longitudinal stripes. These features should also distinguish *G. aurivilliusi* from other similar species such as *G. adamastor* and *G. olbrechtsi*.

DIAGNOSIS: PATTERN (Fig. 212)

Based on the Lectotype.

Upperside ground colour dark brown – becoming somewhat translucent on the forewing apically and distally due to a narrowing of the brown scales – with a pattern of almost white marks.

Forewing discal cell with mark opposite cell M_2 subdivided by 'intervenosae' to form a series of parallel longitudinal stripes, with size diminishing towards the costa, that nearest the costa (the 4th) faint. Apex of cell with a prominent mark bisected by an 'intervenosa'. Cell R_3 with axillary discal mark, extending distad posteriorly (possibly representing a fused post-discal mark); no submarginal mark. Cell R_4 with small post-discal mark slightly indented distally and small, faint, subdivided submarginal. Cell R_5 with discal mark slightly indented distally; submarginal mark small, faint, subdivided. Cell M_1 without marks. Cell M_2 with post-discal mark slightly indented distally by intervenosa, the posterior lobe slightly the larger; no submarginal mark. Cell M_3 with post-discal mark reaching discocellular vein and touching vein CuA_1, but not reaching vein M_3; convex distally; submarginal mark faint, subdivided. Cell CuA_1 with post-discal mark almost elliptical, reaching posterior discocellular vein anteriorly, but not quite touching either vein CuA_1 or CuA_2; submarginal extremely faint. Cell CuA_2 with large post-discal mark lying along vein 1A, but not reaching posterior discocellular vein, nor vein CuA_2; submarginal faint, undivided. Cell 1A with post-discal mark contiguous with that in cell CuA_2.

Hindwing discal cell largely occupied by a white mark, slightly indented apically, its margins well-defined. Apically to this mark is a small white spot. Cell R_1 with a single, elongate, white mark (possibly fused discal and post-discal), plus subdivided submarginal mark. Cell R_5 with post-discal mark in angle of veins R_5 and upper discocellular vein, slightly indented apically; submarginal mark subdivided, the anterior element being the larger. Cell M_1 with small post-discal spot and subdivided submarginal mark, the anterior element being the larger. Cells M_2 and M_3 with clear post-discal mark and subdivided submarginal marks, the elements subequal in size. Cell CuA_1 with discal mark in angle of veins CuA_1 and the posterior discocellular, a clear post-discal mark and subdivided submarginal mark. Cell CuA_2 with elongate white mark (fused discal and post-discal).

The **underside** reflects this pattern. The ground colour is paler on the **forewing** and slightly suffused with orange, especially basally in the discal cell; the intervenosae in this cell and others are more clearly defined. On the **hindwing**, the orange suffusion is greater and affects the pale marks too. The intervenosae are well defined. In the discal cell, the posterior 'intervenosa' branches apically to define the apical spot described above. There is a black spot in the angle of the humeral vein, but no basal black mark in cell R_1 (in fact, the pale mark continues almost to the base of this cell), unlike *G. schubotzi* (including *eyeni*).

VARIATION

The only other specimen we have been able to examine is the paralectotype in MRAC. Slightly more worn than the lectotype, it shows the following slight differences.

Forewing discal cell apical mark not subdivided. Forewing cell CuA_1 with post-discal mark not reaching posterior discocellular vein.

Hindwing discal cell with white patch larger, subsuming the apical spot described above. Discal and post-discal marks in hindwing cell CuA_1 fused.

DIAGNOSIS: ♂ GENITALIA (Fig. 62)
From MRAC slide Pa.120 (G/5/43) of the paralectotype. The specimen is distorted by slide mounting, so some features are difficult to interpret.

Dorsal projection distorted, but appears to be curved dorsad. *Dorsal harpe* hook-like, prominent. *Ventral harpe* dorsal blade apparently larger than ventral; the ventral blade quite small (c.f. *auriger*), bifid terminally. *Dorsal terminal process* distorted, but ventral angle appears to be pointed. *Ventral terminal process* rounded ventrally, denticulate. The *rim* appears to be broad, as in both *adamastor* and *agamedes*. *Uncus* quite short, *socii* prominent. *Saccus* small. *Aedeagus* broken, but showing slight curvature.

DIAGNOSIS: ♀ GENITALIA; EARLY STAGES; HOST PLANTS. Unknown.

DISTRIBUTION. Known only from the type series, with no locality more precise than 'Congo'.

BIONOMICS. Presumed to have been found in primary forest, it may have a very narrow, local distribution (Torben Larsen, pers. comm.).

CONSERVATION STATUS. 'Insufficiently known'. Collins & Morris (1985: 57, 219).

MATERIAL EXAMINED. The lectotype and paralectotype males in MRAC.

38. *Graphium* (*Arisbe*) *ucalegon* (Hewitson, 1865)

Creamy Graphium (Figs 213, 236, 237; map Figs 146 – 148; genitalia Figs 63, 102)

Papilio ucalegon was established by Hewtison (1865, *in* 1862–6) as a species. Staudinger (1884) added *ucalegonides* as a 'Lokalform' (subspecies). Aurivillius (1899) further added *simoni* as a new variety (*sensu* subspecies), raising *ucalegonides* to specific rank, which he later (1908) reversed. Berger (1950) raised both *ucalegonides* and *simoni* to specific status, but himself described a new subspecies, *G. ucalegon schoutedeni*, and a new infrasubspecific form, *fontainei*, which he later also raised to subspecific rank as *G. ucalegon fontainei* Berger (1981). It is this polytypic arrangement of *G. ucalegon*, excluding *G. ucalegonides* and *G. simoni*, which we follow here. However, the validity of separating *u. fontainei* from *u. schoutedeni* seems open to question.

EARLY STAGES; HOST PLANTS. Apparently unknown.

BIONOMICS
Regarded as a lowland evergreen rainforest species (Larsen, MSa; Fontaine, 1985: 114), Birket-Smith (1960) noted that males frequent sunny wet-spots on river banks, and shaded brooks within primary forest. For Mont Kala (Cameroun), Darge (1995) gives a single record for mid-March. Williams (1969) notes it as 'not uncommon in the Bwamba Forest', Uganda. Temporal records: Jan., Feb., Mar., Nov., Dec. (Larsen, MSa).

CONSERVATION STATUS. 'Not uncommon and not considered to be threatened' (Collins & Morris, 1985: 58).

38a. *G.* (*A.*) *ucalegon ucalegon* (Hewitson, 1865)

Hewitson's Creamy Graphium (Fig. 213; map Figs 146; genitalia Figs 63, 102)

Papilio ucalegon Hewitson, 1865: [3] pl.7, f ig.19. LECTOTYPE ♂: NIGERIA: 'Old Calabar' (Hewitson, 1865: [3]). BMNH Spec.Reg. No. 143096 – **here designated**. PARALECTOTYPE ♂: NIGERIA: same data. BMNH Spec.Reg. No. 143097; PARALECTOTYPE ♂: GABON: 'Gaboon'. BMNH Spec.Reg. No. 143130.

Papilio ucalegon ucalegon Hewitson; Aurivillius, 1908 : 23, pl.3 b; Bryk, 1930*b*: 560–1.

Papilio (*Graphium*) *ucalegon ucalegon* (Hew.); Peters, 1952: 21.

Graphium (*Arisbe*) *ucalegon* (Hewitson); Munroe, 1961: 42; Hancock, 1983: 46; Collins & Morris, 1985: 58.

Graphium ucalegon ucalegon Hewitson; D'Abrera, 1980: 42, 43 (fig.); Berger, 1981: 50, pl.15 fig. 1 (♂).

Graphium (*Arisbe*) *ucalegon ucalegon* (Hewitson); Ackery, Smith & Vane-Wright, 1995: 166.

SYNONYM

Papilio ucalegon legonuca Suffert, 1904: 106. HOLOTYPE ♂: CAMEROON: 'Ein männliches Exemplar aus Süd-Camerun. Coll. Suffert.' (Suffert, 1904: 106). BMNH. Spec.Reg. No. 143146.

Papilio ucalegon ucalegon ab. *legonuca* Suffert; Aurivillius, 1908 : 23 [as syn. n.]; Bryk, 1930*b*: 561.

Papilio ucalegon f. indiv. *legonuca* Suffert; Le Cerf, 1924*a*: 395, pl.5 fig.46.

Graphium ucalegon ab. *legonuca* Suffert; Berger, 1950: 74 (in ssp. *schoutedeni*).

Papilio (*Graphium*) *ucalegon* ab. *legonuca* Suffert; Peters, 1952: 21.

Graphium (*Arisbe*) *ucalegon ucalegon* =*legonuca* Suffert; Ackery, Smith & Vane-Wright, 1995: 166.

UNAVAILABLE NAMES

Papilio ucalegon ab. *superfluosa* Strand, 1912: 140. CAMEROON: 'Nlohe' (Strand, 1912). MNHU. [infrasubspecific].

Papilio ucalegon ab. *addenda* Strand, 1913*a*: 25. CAMEROON: 'Bibundi' (Strand, 1913*a*). MNHU. [infrasubspecific].

TYPE EVALUATIONS

Hewtison (1865, *in* 1862–6) gave no series length in his description of *Papilio ucalegon*. According to Kirby (1879) there were 4 specimens of *ucalegon* in Hewitson's collection at the time of its bequest to BMNH (BMNH accession no. 1879–69), from 'Calabar' and 'Gaboon'. We have been able to find 3 of these, individually numbered in Kirby's hand on labels printed at the time of the bequest: no. 2 from Gaboon; no.s 3 & 4 from Calabar. Of these, we select that labelled no. 4 as lectotype, being most similar to the illustration in the original description.

Papilio ucalegon legonuca Suffert (1904: 106) was described from a single specimen. It is readily identifiable as it is labelled 'Type' in Suffert's hand on his handwritten pink locality and determination labels. It can be identified as the specimen illustrated by Le Cerf (1924, I.5 fig.46) by the slight blemishes on the wings. Suffert's collection reached the BMNH via the Joicey bequest (BMNH 1934–120).

TAXONOMIC STATUS

We here follow Berger (1981) in treating *G. u. ucalegon* as one of three subspecies of a polytypic species (see above).

Papilio ucalegon legonuca Suffert (1904) was established as a subspecies which was distinguished from the nominate race by the lack of a white mark by the median vein in the anterior third of the discal cell. This is a variable feature in *ucalegon* and, in fact, Suffert's holotype is asymmetric: though the right forewing shows no mark, the left wing does have a small spot opposite cell M_3. Aurivillius (1908) treated it as an aberration, without formally synonymising it, and Le Cerf (1924) as a 'f. indiv.'; this status has been accepted by subsequent authors.

SIMILAR SPECIES

The scattering of pale scales distal to the band in the hindwing upperside discal cell links the species with *G. simoni* and distinguishes it from superficially similar taxa such as *G. fulleri ucalegonides*. *G. u. ucalegon* may be distinguished from *G. simoni* by having the wing markings more yellow; the forewing discal cell mark smaller, and the post-discal marks of the forewing and various marks on the hindwing smaller, forming a narrower band; and the black spot in hindwing underside cell R_5 almost circular. *G. u. schoutedeni* and *G. u. fontainei* both have paler wing marks.

DIAGNOSIS: PATTERN (Fig. 213)

Upperside. Ground colour dark brown, sometimes somewhat translucent distal to forewing post-discal marks due to narrowing of scales. Pale marks pale, almost buttermilk or citrous, yellow.

Forewing discal cell with pale mark opposite cell M_3 at most reaching first 'intervenosa', sometimes absent. Cell R_3 with an axillary (discal) mark largely confined to the area proximal to the root of vein R_4. Cell R_4 usually without a clear mark (see 'variation'), though often with a faint post-discal mark. Cell R_5 has a basal mark (fused discal and post-discal marks) more-or-less bissected distally by the intervenosa. Cell M_1 usually unmarked. Cell M_2 has a post-discal mark usually largely confined to the posterior half of the cell, though extending slightly further anteriad basally along the lower discocellular vein. The post-discal mark in cell M_3 usually reaches (or almost so) M_3 and CuA_1 and the posterior discocellular vein across most of the cell; it is usually slightly indented distally by the intervenosa. The post-discal mark of cell CuA_1 is somewhat variable in size, but usually reaches the posterior discocellular vein only near the root of CuA_1. Cell CuA_2 with no basal or discal marks; post-discal mark of variable size, usually contiguous with mark in cell 1A, but usually with a gap between it and that in cell CuA_1. Cell 1A without basal or discal marks, but with post-discal band usually contiguous with that in cell CuA_2. Usually no submarginal marks.

Hindwing. Discal cell with just one, relatively narrow transverse band usually extending little beyond the 'elbow' of the upper discocellular vein, if at all; its proximal edge usually fringed by a narrow area with a scattering of pale scales; the distal edge with a much broader area, sometimes filling remainder of cell. Cell R_1 without basal or discal bands; post-discal band white, indented by intervenosa distally and narrowly bordered by mottled areas proximally and distally; no submarginal mark. Cell R_5 with an axillary pale mark extending at most as far as root of vein M_1, incised distally by intervenosa and with faint mottling distally close to veins R_5 and M_1. Cells M_1 and M_2 have at most a faint scattering of pale cells proximally. In cell M_3 there is a more distinct mottled area proximally. Cell CuA_1 has a distinct discal mark in the axil of the posterior discocellular vein and vein CuA_2, with mottled areas the distal edge fading (due to fewer pale scales) along veins CuA_1 and CuA_2. Cell CuA_2 is largely pale in males; in females there is a distinct post-discal band which extends across the anal cell and is bordered proximally and distally by a mottling of pale scales. There are no submarginal marks on the hindwing.

Underside. Largely reflecting upperside pattern, though the ground colour is paler (dull brown on the forewing, brighter brown-orange on the hindwing), apart from the intervenosae, which are thus prominent. In the **forewing** discal cell there are three 'intervenosae' stretching most of the length of the cell, apart from the base; the posterior 'intervenosa' is branched approximately at the level of vein CuA_2, with the posterior branch reaching the posterior discocellular vein at approximately the level of vein CuA$_1$; due to the dark ground colour these 'intervenosae' are not very prominent. The marks in cells R$_5$ and M$_2$ have a white core much smaller than on the upperside, but with a pale orange fringe co-extensive with the upperside mark (where present, the post-discal mark of cell R$_4$ is represented just by such an orange mark). On the **hindwing**, the area proximal to the discal cell band and discal and post-discal bands of neighbouring cells is russet orange. There is is a prominent, round, black spot just distal to the humeral vein and another, slightly oblate, near the base of cell R$_1$. The very base of the wing – at the bases of the costal, precostal, discal and CuA$_2$ cells – is black, forming a prominent spot in the centre of which, on the bases of the radial and cubital veins, is a white tuft. Discal cell with two 'intervenosae', the posterior with a short branch distally. The proximal edge of the discal cell band is bordered pale orange. The intervenosae of the peripheral cells are dark and very prominent against the bright background.

VARIATION

Forewing cell R$_4$ usually lacks a clear post-discal mark, but there may be faint patch of pale scales either basally or slightly displaced from the base; sometimes there is a more coherent, if small mark (ab. *addenda*), or even a clear and elongate mark (ab. *superfluosa*). Cell M$_1$ occasionally has a small post-discal mark confined either to the anterior half of the cell, or to the posterior. Though usually largely confined to the posterior half of the cell, the post-discal mark of cell M$_2$ occasionally has an extension (sometimes free) anterior to the intervenosa. The post-discal mark in cell CuA$_1$ sometimes does not reach the posterior discocellular vein. Post-discal mark in cell CuA$_2$, though usually contiguous with mark in cell 1A, is sometimes separated from it by darkening of vein 1A; anteriorly, the mark sometimes reaches vein CuA$_2$ and contiguous with that in cell CuA$_1$, is sometimes separated from it by the vein being dark and/or the mark not reaching the vein. A few specimens show faint and diffuse (rarely slightly better defined) submarginal marks in some cells, especially R$_3$ to R$_5$ and M$_3$ to CuA$_2$.

The width of the band in the hindwing discal cell is variable, as are the sizes of the bordering mottled areas. These are usually narrow proximally, more extensive – sometimes filling the remainder of the cell – distally. Rarely, there is a post-discal mark in cell M$_1$; in the only such specimens seen by us, this is restricted to the area anterior to the intervenosa.

On the underside, there is some variation in the size and shape of the hindwing black spots. In addition, there is sometimes a scattering of black scales (sometimes forming a coherent, if fuzzy and elliptical spot) in cell CuA$_2$. Faint black marks are also sometimes seen in the discal cell between the proximal end of the anterior intervenosa and the anterior discocellular vein and, more rarely, between the two intervenosae. The length of the posterior branch of the posterior intervenosa is variable and may be virtually zero.

DIAGNOSIS: ♂ GENITALIA (Fig. 63)

Dorsal projection narrow, cylindrical, curving slightly dorsad and anteriad. *Dorsal harpe* a simple hook. *Ventral harpe* with horizontal blade curving mesad distally; vertical blade only slightly smaller, angled slightly posteriad and mesad, and curving further mesad. *Dorsal terminal process* directed strongly mesad; ventral angle more extended than dorsal, so mesal edge is at an angle of about 45° to the vertical in both the sagittal and transverse planes. *Ventral terminal process* small, rounded, serrate. *Uncus* moderate, *socii* very prominent. *Saccus* small. *Aedeagus* moderately long, slightly curved throughout length; no indication of denticulation.

DIAGNOSIS: ♀ GENITALIA (Fig. 102)

BMNH Spec.Reg. No. 143144; vial 4751: *vestibulum* transverse; *ostium bursae* opening anteriorly; *ductus bursae* elongate, not sclerotized, kinked/constricted or pocketed distally; *central ostial lobe* glabrous, broad, truncate, almost reaching tip of laterals; *lateral ostial lobes* setose, long and broad, not well sclerotized; *anterior apophyses* normal; *papillae* elongate dorsally.

EARLY STAGES; HOST PLANTS; BIONOMICS; CONSERVATION STATUS. See species account for the minimal amount known.

DISTRIBUTION (Map Fig. 146). Ivory Coast, Ghana, Nigeria, Cameroon, Equatorial Guinea, Congo, Gabon, western Democratic Republic of Congo, Angola.

MATERIAL EXAMINED. 121 ♂♂; 22 ♀♀ in BMNH. 58 ♂♂; 1 ♀ from other collections.

38b. *G. (A.) ucalegon fontainei* Berger, 1981

Fontaine's Creamy Graphium (Fig. 236; map Fig. 148)

Graphium ucalegon schoutedeni f. *fontainei* Berger, 1950: 74.

Graphium ucalegon fontainei Berger; Berger, 1981: 51, pl.15 fig. 5 (♂ – HT). HOLOTYPE ♂: DEMOCRATIC REPUBLIC OF CONGO: 'des environs de Lusambo. Coll. M. R. A. C.' (Berger, 1981). ['Sankuru: km. 43, route de Lusambo à Batempa: 19–VII–49 (Dr. M. FONTAINE)' (Berger, 1950: 74)]. MRAC.

Graphium (*Arisbe*) *ucalegon fontainei* Berger; Ackery, Smith & Vane-Wright, 1995: 166.

TYPE EVALUATIONS

Berger (1981) mentioned just a holotype, with details as above, when he established *Graphium ucalegon fontainei* at subspecific rank. The specimen is clearly labelled in MRAC, where it was photographed by CRS

(Fig. 236), and is clearly recognisable as the specimen illustrated by Berger (1981, pl.15 fig. 5). Details of its provenance were given by Berger (1951). Further specimens listed as paratypes by Berger (1950 – but not listed in 1981) have no status.

TAXONOMIC STATUS
Graphium ucalegon schoutedeni f. *fontainei* Berger (1950) was established infrasubspecifically as a (wet) seasonal form of a subspecies. The name was made available only when Berger (1981) raised it to subspecific rank.

Berger (1950) distinguished the form as having a wingspan smaller by 10–15 mm.; the pale bands and marks of the upperside 'nettement' smaller and narrower; and these being creamy yellow rather than ochraceous yellow. These features seem to us to be within the range of variation of *G. u. schoutedeni*, including specimens from western Uganda, an area well disjunct from the stated range of *fontainei*. For these reasons, we regard the status of *G. u. fontainei* as dubious, but lack sufficient evidence to formally synonymize it with *G. u. schoutedeni*.

It should be noted that the type locality is identical to that of one of the paratype localities given for *Graphium ucalegon schoutedeni* Berger (1950).

SIMILAR TAXA. Very similar, if not identical, to *G. u. schoutedeni*.

DIAGNOSIS: PATTERN (Fig. 236)
Apart from the features described above, Berger (1950) states that all the other characters are identical to those in *G. u. schoutedeni*. Distinguishable from *G. u. ucalegon* by the pale marks of the upper side being pale creamy white rather than citreous or buttermilk.

DIAGNOSIS: GENITALIA. We have been unable to dissect a male, and not seen a female.

EARLY STAGES; HOST PLANTS; BIONOMICS; CONSERVATION STATUS. See species account.

DISTRIBUTION (MAP 148)
According to Berger (1981), it is confined to the following southern areas within the Democratic Republic of Congo: southern Sankuru, Kabinda, Haut-Lomami and Lualaba.

MATERIAL EXAMINED. 10 ♂♂ in MRAC.

38c. *G. (A.) ucalegon schoutedeni* Berger, 1950

Schouteden's Creamy Graphium (Fig. 237; map Fig. 147)

Graphium ucalegon schoutedeni Berger, 1950: 73. TYPES: (See below).

Graphium ucalegon schoutedeni Berger; Berger, 1974: 74; D'Abrera, 1980: 42, 43 (fig.); Berger, 1981: 51, pl.14 figs 4 (♂ – HT), 8 (♀ – 'NA'); Kielland, 1990: 49.

Graphium (Arisbe) ucalegon schoutedeni Berger; Carcasson, 1981: 123; Ackery, Smith & Vane-Wright, 1995: 166.

TYPE SPECIMENS
HOLOTYPE ♂: DEMOCRATIC REPUBLIC OF CONGO: 'Holotype: 1 ♂; Uele: Bambesa: 17–IX–32 (J. VRIJDAGH)' (Berger, 1950: 73). MRAC. PARATYPE ♂♂ (all Berger, 1950: 73–4): DEMOCRATIC REPUBLIC OF CONGO: 'Congo Ubangi: Bomboma: V–35 (BALL). MRAC; 2 x 'Tshuapa: Flandria: 1926 (R. P. HULSTAERT). MRAC; 'Stanleyville: « Higher Lindi Tshoppo Watershed, S. of Makala*: 2.500 fts VIII–21 » (T. A. BARNS)'. BMNH Spec.Reg. No. 143224; ['Stanleyville'] '1 ♂ « Lualaba River* » (A. YALE MASSEY: 1906).' BMNH Spec.Reg. No. 143227; 'Kivu: 1 ♂, Costermansville*: 1939–40 (NOIROT)'. IRSN (not seen); 2 x 'Bas Congo: Léopoldville (SOHAL)'. MRAC; 'Sankuru: Km. 43, route Lusambo-Batempa: 16–VIII–49 et 27–IX–49 (Dr. M. FONTAINE)'. MRAC and coll. Fontaine (not seen). [N.B. The type locality of *G. u. fontainei*]; ['Sankuru'] '3 ♂♂, Bena-Bendi* : I–95 (CLOETENS)'. IRSN (not seen); ['Sankuru'] '1 ♂, La Kondue* (KONINGS)'. IRSN (not seen); ['Sankuru'] '1 ♂ « Lomami River to Wembo*: I–II–24 » (Major BRIGGS)'. BMNH Spec.Reg. No. 143228; UGANDA: '2 ♂♂ « Semliki Valley*, E. (British side), 2.300–2.800 fts, very dry Buafaba f., the edge of Congo forest »' ['(S. A. NEAVE)']. BMNH Spec.Reg. Nos. 143240, 143241; '1 ♂ «Southern Toro, Mbarara ft.*, Portal road: 3.800–4.200 fts, 22–24–X–11 » (S. A. NEAVE)'. BMNH Spec.Reg. No. 143233; '1 ♂ « Uganda: Bwamba*: IX–42 » (T. H. E. JACKSON)'. BMNH Spec.Reg. No. 143234.

In addition, Berger lists further paratypes which exhibit the character of the aberration *legonuca* Suffert:

DEMOCRATIC REPUBLIC OF CONGO: 'Stanleyville: 1 ♂ « Tshoppo [sic] Valley (South); 35 M. E. of Stanleyville: V–20 »' ['(T. A. BARNS)']. BMNH Spec.Reg. No. 143229; ['Stanleyville'] '1 ♂ « Lindi River, 20 M. above Bafwasende*; 2.300 fts: VII » (T. A. BARNS)'. BMNH Spec.Reg. No. 143230; 'Kivu: 1 ♂ « Mooghe to Lubutu and Walikale: 22–III–20–IV–24 » (Major BRIGGS)'. BMNH Spec.Reg.No. 143243; ['Kivu'] '1 ♂ « Oso River, Lowa Valley: 2.600 fts; VIII–21 (T. A. BARNS)'. BMNH Spec.Reg. No. 143231; 'Kwango: Kimbau: 1931 (Sœurs de l'Union du Sacré-Cœur)'. MRAC (not seen); 'Sankuru: 2 ♂♂, Bena Bendi*: I–95 (CLOETENS)'. IRSN (not seen); '1 ♂ « Congo Belge » (ex-coll. SEELDRAYERS[)]'. MRAC.

TYPE EVALUATIONS

Graphium ucalegon schoutedeni Berger (1950) was described from the holotype and 25 paratypes listed above, with type designations original. Depositories given in Berger (1950); asterisks indicate localities not represented (at the time of description) in MRAC (Berger 1950: 6). Berger (1981) designated a 'neallotype' (from Democratic Republic of Congo (Sankuru): Katokombe – in MRAC), which is not part of the type series.

TAXONOMIC STATUS

Graphium ucalegon schoutedeni Berger (1950) was established as a subspecies for specimens from Democratic Republic of Congo (apart from the extreme West) and Uganda. By establishing *G. u. fontainei*, Berger (1981) reduced the range to northern Democratic Republic of Congo and Uganda. This subspecific status (whether or not *G. u. fontainei* is subsumed within it) has been accepted by subsequent authors.

SIMILAR TAXA

Very similar in pattern to *G. u. ucalegon*; extremely similar in pattern and coloration to *G. u. fontainei*.

DIAGNOSIS: PATTERN (Fig. 237)

G. u. schoutedeni may be distinguished from *G. u. ucalegon* by a combination of the following characters:

Upperside pale markings creamy as opposed to citreous yellow.

Transverse band in hindwing discal cell generally narower than in the nominate subspecies.

The edges (especially the distal edges) of this band generally diffuse: in *G. u. ucalegon*, though there is a scattering of pale scales beyond the band edge, that edge is usually well defined; in *G. u. schoutedeni* it is much less so, often fading gradually.

The extent of the scattering of pale scales distal to the band is also usually greater, often occupying the remainder of the cell.

Hindwing cell CuA_1 lacks a clear discal mark subtending the angle of vein CuA_2 and the posterior discocellular vein: such a mark is usually prominent in *G. u. ucalegon*, but in *G. u. schoutedeni* there is usually just a pale line (slightly diffuse distally) bordering the base of the cell.

VARIATION

G. u. schoutedeni shows a similar level of variability to the nominate subspecies in terms of the presence, size and position of the pale marks. The *legonuca* 'form', lacking a mark in the forewing discal cell, is not uncommon. We have noticed no variants peculiar to this subspecies.

The variation shown by *G. u. schoutedeni* probably encompasses the phenotype described by Berger (1981) as *G. u. fontainei*.

DIAGNOSIS: ♂ GENITALIA

Similar to the nominate subspecies. The ventral terminal process appears more prominent, but this may be variable. In one specimen we have examined, the ventral harpe lacks a vertical blade on the left valve only.

DIAGNOSIS: ♀ GENITALIA. Not examined.

EARLY STAGES; HOST PLANTS; BIONOMICS; CONSERVATION STATUS. See species account.

DISTRIBUTION (Map Fig. 147). Northern and western Democratic Republic of Congo, western Uganda and north-western Tanzania. Probably also occurs in Rwanda.

MATERIAL EXAMINED. 11 ♂♂, 9 ♀♀ in BMNH. 19 ♂♂ from other collections.

39. *Graphium (Arisbe) simoni* (Aurivillius, 1899)

Simon's Graphium or Swallowtail (Fig. 214; map Fig. 149; genitalia Fig. 64)

Papilio ucalegon var. *Simoni* Aurivillius, 1899: 485. HOLOTYPE ♂: ANGOLA/DEMOCRATIC REPUBLIC OF CONGO: 'Congogebiet: Angola. — Von Lieutenant SIMON gefangen' (Aurivillius, 1899: 485). 'Mus. Bruxellense' (Aurivillius, 1899: 485) IRSN.

Papilio ucalegon var. *simoni* Aurivillius; Aurivillius, 1908: 23; Bryk, 1930*b*: 561.

Graphium simoni Aurivillius; Berger, 1950: 74 [as stat. n.]; Berger, 1974: 74 [description of female]; D'Abrera, 1980: 42, 43 (figs); Berger, 1981: 51, pl.15 figs 2,3 (♂), 6 (♀ – 'NA'); d'Abrera, 1997: 50, 51 (figs).

Papilio (*Graphium*) *ucalegon simoni* (Aur.); Peters, 1952: 21.

Graphium (*Arisbe*) *simoni* (Aurivillius); Munroe, 1961: 42; Hancock, 1983: 46; Collins & Morris, 1985: 58; Ackery, Smith & Vane-Wright, 1995: 166.

TYPE EVALUATIONS

In his description of *Papilio ucalegon* var. *Simoni*, Aurivillius (1899: 485) did not specify the number of specimens involved. Berger (1950: 75) effectively restricted the type series to the single specimen with correct provenance in IRSN, referring to it as the 'Type'. This is clearly labelled, including several determination labels stating it to be the type, one of which appears to be in Aurivillius' hand. Berger (1974) unnecessarily designated the one female in MRAC (from Democratic Republic of Congo: 'Yakoma (District du Congo Ubangi)') as 'néallotype'.

TAXONOMIC STATUS

Papilio ucalegon var. *Simoni* was established by Aurivillius (1899: 485) as a (pre-1961) variety. That subspecific status was accepted until Berger (1950) raised it to specific rank, which has been accepted by subsequent authors.

SIMILAR SPECIES

G. simoni can usually be distinguished from *G. ucalegon* by the following combination of characters. Pale markings nearly white; in *G. u. ucalegon* they are pale yellow; in *G. u. schoutedeni* and *G. u. fontainei* more creamy. Forewing discal cell mark larger, usually reaching beyond first intervenosa; in *G. ucalegon* the mark only very rarely extends beyond the first intervenosa and may be absent. The post-discal marks of the forewing and various marks on the hindwing are generally larger, forming a somewhat broader band (though this is best appreciated when specimens of both taxa are available for comparison). The mark in underside hindwing cell R_1 is often more elliptical than the typically almost circular mark in *G. ucalegon*.

DIAGNOSIS: PATTERN (Fig. 214)

Upperside ground colour brown, with pale marks nearly white. **Forewing** discal cell always with pale band opposite cell M_3, but this variable in extent, usually extending beyond first intervenosa, sometimes to radial vein, usually interrupted by 'intervenosae'. Cell R_3 with pale mark (fused discal + post-discal) extending almost from axil to root of vein R_4 or beyond. Cell R_4 sometimes with post-discal mark. Cell R_5 with a mark (fused discal + post-discal) extending from near base to beyond root of vein R_4. Cell M_1 devoid of pale marks. Cell M_2 with linear post-discal mark from lower discocellular vein along vein M_3, usually confined to posterior half of cell. Cell M_3 with post-discal mark spanning cell and reaching posterior discocellular vein across all or most of cell width, narrowing slightly to blunt tip distally. Cell CuA_1 with post-discal mark spannining cell width, sometimes reaching posterior discocellular vein anteriorly. Cell CuA_2 without basal or discal bands; post-discal mark spanning cell width, but not usually reaching posterior discocellular vein. Cell 1A without basal or discal bands; post-discal mark spanning cell width in line with that in cell CuA_2. There are no submarginal marks in any cell. **Hindwing** discal cell with no basal band. The main transverse band is bordered proximally and distally by areas with a scattering of white scales extending 1 or 2 mm proximad, filling the cell distally. Cell R_1 without basal or discal bands; the post-discal band pure white, with a scattering of white scales extending a few millimetres proximad and distad. Cell R_5 with an axillary pale mark extending as far as root of vein M_1, incised distally by intervenosa. Cells M_1 to M_3 each with a scattering of pale scales basally and extending a few millimetres along the respective anterior and posterior veins. Cell CuA_1 with a post-discal mark in angle of posterior discocellular vein and vein CuA_2 and extended along posterior discocellular vein and a few millimetres along vein CuA_1 and also a few millimetres along vein CuA_2. Cell CuA_2 with no basal mark, but an elongate mark across vein width from posterior discocellular vein (probably fused discal and post-discal marks. There are no submarginal marks in any cell. The **underside** pattern largely reflects that of the upperside, though the ground colour is paler, apart from the intervenosae, which are thus prominent. In the **forewing** discal cell there are three 'intervenosae' stretching most of the length of the cell, apart from the base; the posterior 'intervenosa' is branched approximately at the level of vein CuA_2, with the posterior branch reaching the posterior discocellular vein at approximately the level of vein CuA_1. The set of marks constituting the transeverse cell band are rendered somewhat more extensive by each individual mark being ringed by a grey area of mixed scales (in some places there is just the grey area where there is no spot above). The mark in cell R_5 has a white core much smaller than that on the upperside, but with a pale orange fringe co-extensive with the upperside mark (where present, the post-discal mark of cell R_4 is represented just by such an orange mark). Underside **hindwing** discal cell with two 'intervenosae', the posterior with a short branch distally. The area proximal to the post-discal mark of cell R_1 and the transverse mark of the discal cell vivid russet orange. A round black spot in angle of humeral vein; another (sometimes slightly elliptical) near base of cell R_1, a third at the base of the costal, precostal and discal cells and cell CuA_2, the latter surrounding a tuft of white scales in the axil of the discal cell and on the bases of the radial and cubital veins. There is also a somewhat fuzzy black mark in cell CuA_2 just proximal to the pale band.

The only female we have seen, from Democratic Republic of Congo: Yakoma, in MRAC (figured in Berger, 1981, pl.15 fig.6), fits well within this description and the variation below.

VARIATION

As indicated above, there is a considerable amount of variation in the extent and exact shape of the pale marks. We have noted the following particular examples. Forewing discal cell mark: at its smallest, this barely reaches the posterior 'intervenosa', though even in such cases a fuzzy patch may be seen beyond; at its most extensive the patch forms a coherent band almost reaching the radial vein; usually it falls between these extremes and is cut by the 'intervenosae'. Forewing cell R_4: a few specimens have a clear post-discal mark; in a few others there is a small fuzzy patch; in most there is no mark. Forewing cell CuA_1: in most specimens the proximal edge of the post-discal mark reaches the posterior discocellular vein only very close to the root of vein CuA_1, if at all; in some specimens, however, it does so up to 3 mm posterior to the vein root. Hindwing discal cell: the width of the band is very variable. Also, although in most specimens the entire distal area of the cell is suffused with white scales, in a few specimens there may be a small area or areas with few, if any, white scales. The extent of the pale areas in the bases of hindwing cells M_1 to CuA_1 is quite variable. In particular, the coherent discal mark in cell CuA_1 may be very small or extend across most of the cell along the posterior discocellular vein. On the underside, the form of the black spot in cell R_1 is variable in shape: normally quite round, but sometimes more elliptical or even elongate. The black mark in cell CuA_2 is also variable: normally a fuzzy patch, it is absent from some specimens.

DIAGNOSIS: ♂ GENITALIA (Fig. 64)
Dorsal projection relatively broad and slightly compressed basally; slightly upcurved distally. *Dorsal harpe* without carina. *Ventral harpe* with broad horizontal blade, hooked at tip; vertical blade slightly smaller, curved mesad, with pointed tip. *Dorsal terminal process* curved mesad, expanding more ventrally than dorsally, with mesal edge curved and inclined to about 60°. *Ventral terminal process* quite large, curved slightly mesad; tip rounded, slightly dentate posteroventrally. *Uncus* not long, *socii* projecting. *Saccus* short. *Aedeagus* long, slightly curved basally, not denticulate.

DIAGNOSIS: ♀ GENITALIA. None available for dissection.

EARLY STAGES; HOST PLANTS. Apparently unknown.

DISTRIBUTION (Map Fig. 149). Gabon, Congo, southern Central African Republic, western Democratic Republic of Congo. There is a specimen in BMNH labelled Nigeria: Calabar; and Williams (1969) included Cameroon.

BIONOMICS. Apparently monotypic, Berger (1981) notes that the female of this forest species is extremely rare. Berger (1950) included records for Jan., Feb., Apr., June, July, Aug., Sept., Oct.

CONSERVATION STATUS. 'Uncommon but not known to be threatened' (Collins & Morris, 1985: 58).

MATERIAL EXAMINED. 13 ♂♂ in BMNH. 24 ♂♂; 1 ♀ from other collections.

DISCUSSION

Biogeography, endemism and conservation evaluation

Afrotropical *Graphium* (*Arisbe*) exhibit a concentration of species richness around the Congo Basin (Central Africa), including Cameroon. Up to 13 species, one third of the total for the subgenus, are recorded from some 1° squares in this region (Fig. 167). Other areas of relatively high diversity occur to the east (Kenya, with up to 10 species from a single 1° cell) and west (Ghana, with up to 11 species per cell). Peripherally, to the north and south, and to a lesser extent in Madagascar, diversity is much lower. In many of these areas only *G. angolanus*, the most widespread of all African *Graphium*, has been recorded.

With respect to regional endemism for *Graphium* (*Arisbe*), Central Africa stands out, with *simoni*, *schubotzi*, *aurivilliusi*, *poggianus*, *biokoensis*, *gudenusi*, *olbrechtsi*, *hachei*, *abri*, *auriger*, *policenoides* and *ridleyanus* all more or less restricted to this area. However, a maximum of only 4 of these 12 species are known from single 1° squares. The most widespread of them is *G. ridleyanus*, responsible for most of the peripheral single-species records seen in Fig. 169. Only one species is strictly West African (*liponesco*), but two species (*adamastor* and *agamedes*) link West Africa with the western part of Central Africa, and no less than five have an essentially Central African + West African distribution (*ucalegon*, *fulleri*, *tynderaeus*, *latreillianus* and *illyris*), suggesting a strong faunal link between Central and West Africa.

Turning to East Africa, eight *Graphium* species are essentially restricted to this area (*colonna*, *polistratus*, *porthaon*, *philonoe*, *taboranus*, *kirbyi*, *junodi* and *kigoma*), indicative of a second major area of endemism. Southern Africa has two more or less endemic *Graphium* (*morania* and *schaffgotschi*) – both relatives of *G. angolanus*, one of five species that achieve more or less wide ranges within continental Africa (see below). Four species are restricted to the Malagassy subregion: *levassori* (Comoros), *evombar* (Madagascar + Comoros), and *cyrnus* and *endochus* (Madagascar). *G. angolanus* has also been recorded from the Comoros, but no other mainland species enters this zone. None of the Malagasy species occurs outside the sub-region.

The five wide-ranging species (*antheus*, *policenes*, *angolanus*, *leonidas* and *almansor*) are, given our still limited understanding of *Graphium* phylogenetics, highly dispersed in the sense of Williams *et al.* (1993). Each of these species represents a distinct major clade or group of *Graphium* (*Arisbe*), from base (*antheus*-clade) to crown (*almansor*, part of *adamastor*-group), with the *policenes*-clade, *angolanus*-clade and *leonidas*-group representing intermediate lineages (Figs 5, 6). Significantly, all of the Malagasy subregion endemics are closely related to three of these wide-ranging taxa: *G. evombar* is sister to *antheus*, *G. endochus* belongs to the *angolanus* clade, and *G. levassori* and *G. cyrnus* form a stem group with *leonidas*. This suggests the possibility that the Madagascan species originated by dispersal from the African mainland by progenitors of the highly eurytopic *antheus*, *angolanus* and *leonidas*. The most likely candidate for an alternative vicariant explanation would be (*antheus* + *evombar*), but it would seem extremely unlikely that this clade is anywhere near as old as the geological separation of Madagascar and Africa (in the order of 200 my). Indeed, many of the *Graphium* (*Arisbe*) species may be very young. The highly distinctive *G. levassori* occurs only on Grande Comore, considered by geologists to be little more than 100,000 years old (although the Comoros chain, including the northern tip of Madagascar, goes back some 10 million years: Emeric & Duncan, 1982). The evolution of the numerous splinter species of the *adamastor*-group in different parts of the Congo Basin may well be related to the formation of small savannah-islands, as the Congo rainforest has changed over the last one million years or so. Finally in this context, we note that neither the *policenes*-clade nor the *adamastor*-group are represented in the Malagasy subregion. *G. almansor* (*adamastor*-group) is the least extensive of the five widespread species, not occurring in far southern Africa. The absence of the *policenes* clade from Madagascar is perhaps more surprising.

Figure 170 is based on a WORLDMAP (Williams, 1996) 'near-minimum-set' analysis. Using the available data at 1° resolution, to include all afrotropical *Graphium* at least once requires eleven areas. Two of these (Central African Republic square for *G. abri* and Grande Comore for *G. levassori*) are irreplaceable (in the sense of Pressey *et al.*, 1993). The other nine (orange squares in Fig. 170) have a degree of flexibility (Pressey *et al.*, loc. cit.), 'cartooned' in Fig. 170 by the use of grey ellipses to show the general areas in which the main flexibility for each of these nine areas is focused. The importance of Central Africa is clear (six areas required), to which the addition of an endemic area for each of West Africa, East Africa, southern Africa, Comoros and Madagascar is necessary for complete representation. This pattern is also reflected, although not so clearly, in the map of smoothed mean range-size-rarity (Fig. 168).

If we overlay a map of unsmoothed mean range-size rarity with species richness (Fig 171), using Williams' two-colour technique (Williams & Gaston, 1998), we see a scattering of green, blue, white and black cells on the mainland, but with some concentration of blue cells in the Congo Basin. This suggests both a significant degree of under-recording (high heterogeneity) and the Central Africa area of endemism, the concentration of blue squares in this region indicating excess species richness above general expectation in relation to mean rage-size-rarity. The uniform green of the Comoros and Madagascar indicates the distinctness of these areas at species level (excess mean range-size rarity).

Finally, in Fig. 172, we have overlaid the species richness map for afrotropical *Graphium* (as in Fig 167) with a map of African bird species richness (using shared cells only; the bird data are those used in Williams *et al.* 1999). Although the butterfly data are clearly limited, it is apparent that the bird and butterfly species richness patterns are different. The butterflies show excess relative richness in West Africa and Congo Basin (blue), and relative poverty in East Africa generally, although there are some areas around Kenya, Uganda and Tanzania (white cells) that exhibit high relative diversity in both groups. This map fits our general belief that patterns of bird species richness in Africa do not reflect patterns of butterfly richness very well. However, for conservation evaluation generally, the degree to which patterns of complementarity are congruent is potentially far more significant, but we are not yet in a position to make such comparisons. All we can say here is that a network of areas within Central Africa is potentially very important for the survival of many species of afrotropical *Graphium*, but areas in the west, east, south, Comoros and Madagascar would also be needed to ensure complete representation.

Early stages

Only ten of the thirty-nine afrotropical *Graphium* species are known in their early stages. Various descriptions, notably the previously unpublished observations of Dimitri Sevastopulo, and references to published illustrations, are included above under the respective species. Original colour photographs of African *Graphium* early stages, kindly made available to us by Colin Congdon, are shown on Figs 247–264.

The life histories of several distinct species and groups (e.g. *illyris, gudenusi, latreillianus*) and the entire *adamastor*-group (unless *philonoe* is included) remain to be discovered. Even those that we do know, for the most part, are not described consistently or in detail, nor in most cases do we have the benefit of well-preserved study material. What we do have is a tantalising glimpse, enough to see that *Graphium* in particular, and the leptocircines more generally, have valuable early stage characters – with the potential to identify species and species groups, and help link them together.

The early stages of African *Graphium* probably all share the following characteristics: *Egg spherical, glossy, whitish or yellow* (Igarashi, 1984: 88). *Larva with paired osmeteria* (illustrated by Villiers, 1957: 10, for *angolanus*; an autapomorphy of Papilionidae). *Larvae without white saddle-mark on abdominal segments* (loss apomorphy of Leptocircini). *First instar larvae with branched or bifid setae on thoracic and abdominal segments* (confirmed for *antheus, policenes, porthaon, angolanus, morania* and *leonidas*, this unique feature of Leptocircini is shared with *Iphiclides* and *Protographium*: Igarashi, 1984; see also character 50 in Miller, 1987). *First instar larvae with long setose* *tubercles on thoracic segments 1–3 and abdominal segment 10*; confirmed for *antheus, colonna, policenes, porthaon, angolanus, morania* and *leonidas*, this feature is supposedly characteristic of *Graphium* + *Lamproptera* (Miller, 1987: 399, character 70; note that similar but smaller tubercles also occur on the other body segments in some species, but these are lost after first larval moult). *Larval thorax of later instars thickened or 'humped'* (Igarashi, 1984; apparent in all known African *Graphium*). *Pupa bullet-shaped, 'long'* (Igarashi, 1984: 88; plesiomorphic condition), not squat as in some other leptocircines, notably *Protographium* and *Eurytides* (Miller, 1987: 397; Tyler *et al.*, 1994). *Pupa with one or more lateral longitudinal ridges extending from cremaster to head* (Miller, 1987, character 51); supposedly an autapomorphy for Leptocircini, this character is variably manifest in the known African *Graphium*, and needs better definition based on examination of preserved material.

A number of early stage characters are variable across the 10 known species. Unfortunately, due to the general lack of preserved material, inconsistent descriptions, and the difficulty of assessing many characters from photographs and drawings, only six are recorded here (Table 1). Even for these the data are not complete, and the character definitions could undoubtedly be improved. Perhaps the most important suggestion is that the larvae and pupae, even of closely related species where these are known, are distinctive. Interestingly, we have formed the impression that this may prove to be more extreme in what we consider to be the basal, tailed species, and less so in what appear to be the tail-less crown-group. However, it is frustrating that we do not know enough to be able to assess whether or not the striking larval patterns of, for example, *colonna* (green-saddle) and *leonidas* (oblique lateral stripes), or the pupal forms of *antheus* (distinctive truncate anterior, without dorsal horn) (not illustrated) and *colonna* ('sinuate'), are autapomorphies, or represent potential synapomorphies linking these species to others for which we as yet know nothing of their early stages.

The relatively simple pupae of *philonoe* and *leonidas*, and also *angolanus* and *morania*, bear considerable resemblance to the pupae of the Oriental species *G. doson* and *G. sarpedon* (Igarashi, 1979: pl. 209, 205), and are not very different in general appearance to the pupa of *Lamproptera curius* (Igarashi *op cit.* pl. 218). In general form, both the larvae and pupae of *philonoe* look very similar to the corresponding stages of *G. macleayanum* (Parsons, 1999: pl. 112, figs 3028, 3029).

Table 1. Six larval and pupal characters that vary among the ten African *Graphium* species for which we have some knowledge of their early stages.

	1	2	3	4	5	6
antheus	S/L	0	T	S	1	0
kirbyi	VL	?	T	L	1	1
colonna	L	1	X	0	0	1
policenes	L	0	T	L	1	1
porthaon	S/L	?	T	M	1	1
angolanus	L	0	T	L	1	0
morania	S	0	D	L	1	0
ridleyanus	?	?	X	L	1?	0?
leonidas	S/L	0	O	L	0	0
philonoe	L	?	G	L	0	0

1. short (S), long (L) or very long (VL) tubercles on thoracic segments 1–3 and abdominal segment 10 in final instar larvae (S/L = short on thorax, long on anal segment) (good material of all larval stadia and more species would almost undoubtedly reveal many transformational changes affecting these tubercles);
2. some setae on 5th instar tubercles distinctly bifid at tip (1), or not (0) (confirmed only for *G. colonna*, but seems likely to occur in other species, as it involves retention of universal character found in first instar larvae);
3 mature larval pattern with transverse stripes (T), oblique stripes (O), 'dotted' (D), granular (G), or with some other pattern (X) (these differences as recorded here are not entirely reliable, as some degree of variation and even polymorphism is apparent, including unpatterned morphs in some cases);
4 pupa with dorsal horn long, often extending well beyond the head (L), short (S), intermediate (M), or absent (0) (Miller, 1987: character 69);
5 pupa with short latero-ventral head projections (1), or without, blunt (0);
6 pupa with distinct mid-length lateral projection or widening (1), or not (0).

Hostplant relationships

The great majority of food-plant records for the ten afrotropical *Graphium* for which early stages are known refer to the Annonaceae (soursop or custard-apple family), and members of this group appear to be the primary hosts. Use of Annonaceae is widespread in *Graphium* s.l. and other leptocircines, but other Papilionidae do not feed on them, nor do many other butterflies: examples include *Rapala* (Theclinae) and various nymphalines and charaxines.

Other recorded hosts for *Arisbe* include members of the Apocynaceae, Malpighiaceae, and possibly Anacardiaceae. These families are not considered to be closely related, and all require confirmation. The Anarcardiacae record (ex Jan Kielland) for a member of the poorly-known and largely mimetic *adamastor*-clade suggests the possibility of a hostplant shift connected with radiation of this crown group. However, our cladistic analyses suggest that *G. philonoe* also belongs to this clade, and this is known to be an Annonaceae-feeder.

The Annonaceae are considered to be a rather primitive group of flowering plants, usually associated with the Lauraceae, Hernandiaceae, Magnoliaceae and Winteraceae, and these 'woody Ranales' provide the major hosts for the Leptocircini. Minor host families include the Acanthaceae, Apocynaceae, Malvaceae, Monimiaceae, Myrtaceae, Rutaceae, Sapotaceae and Verbenaceae (Ehrlich & Raven, [1965]; Igarashi, 1979). The pantropical distribution of the Annonaceae, with up to 2000 species of trees, shrubs and lianes, divided among approximately 120 genera, closely matches the main distribution of the leptocircines. Where the butterflies extend into temperate areas where no Annonacaeae occur, they switch to other plant groups (e.g. *Iphiclides* on various Rosaceae). Berenbaum (1995) explores the hostplant chemistry probably responsible for the major patterns of hostplant use in the Papilionidae.

There is no convenient overview for the Annonaceae of the aftrotropics as a whole, but there are various regional floras. Le Thomas (1969) treats 29 genera in the flora of Gabon series, Verdcourt (1971) indicates 27 for East Africa, while Robson (1960) recognizes just 13 genera from the more southerly Flora Zambeziaca region. As most rearing of African *Graphium* has been done in Kenya and Tanzania, Verdcourt (1971) is perhaps most relevant. He accepts division of the family into two subequal subfamilies, with the Monodoroideae comprising two genera (including *Monodora*, known as a host for *G. antheus* and *G. porthaon*), and the much larger Annonoideae divided into six tribes. Of these tribes, four are represented by genera reported here as hostplants (Uvariae: *Uvaria*; Unoneae: *Uvariodendron, Artabotrys, Hexalobus, Polyalthia*; Mitrephoreae: *Friesodielsia, Cleistochlamys, Monanthotaxis*; and Annoneae: *Annona*). While this suggests that all regional African Annonaceae might be looked on as potential hosts for one or more *Graphium* species, the existing data should be treated with some caution, as there seem to be strong possibilities of misidentifications and/or confusing synonymy in the original citations (e.g., according to Verdcourt, 1971, the various species attributed in our lists to *Popowia* probably refer to *Monanthotaxis* or *Friesodielsia*). We have no host records for the three Madagascan *Graphium*; Cavaco & Keraudren (1958) recognized eleven genera of Annonaceae from the island, including *Uvaria, Hexalobus, Artabotrys, Polyalthia, Popowia* and *Annona* among those recorded as hosts in Africa. As in all areas of *Arisbe* biology, more records and better detail are urgently needed.

Mimicry in African *Graphium*

Faced with a selection of carefully chosen African *Graphium* species, such as *angolanus, ridleyanus, tynderaeus, leonidas, levassori, hachei, kirbyi* and *policenes*, it might be hard to imagine, judging from general appearance alone, that they could all belong to a single genus. Moreover, although our cladistic analyses have not given any confirmation, it is still possible that most or even all of the African species do form a monophyletic sub-group within *Graphium*, as Munroe (1961) supposed. Can we offer any explanation for this striking exo-phenotypic diversity in one relatively small group of butterflies?

Perhaps the most diverse African butterfly group, in terms of colour patterns, is the nymphalid genus *Pseudacraea* (illustrated in D'Abrera, 1980: 348–353). In this case the reason for diversity appears clear: most of the species are putative mimics of a whole range of models, notably various Acraeini and Danaini. The majority of Pseudacraeas mimic a single aposematic species but some, such as *P. eurytus*, are complex polymorphs that simulate numerous different models. Is mimicry likewise the explanation for great pattern diversity in African *Graphium*? The answer would appear to be 'only partly'.

Specific examples

Three African *Graphium* stand out as likely clear-cut examples of (presumed Batesian) mimicry. Most striking of all is *G. ridleyanus*, with its variable but typically bright red upperside pattern, strongly reminiscent of various *Acraea* species (such as *perenna, zetes, pharsalus, rogersi* and *egina*: all illustrated in d'Abrera, 1997). *G. ridleyanus* clearly belongs to the *G. angolanus* clade, and it is quite easy to imagine its evolution from an *angolanus*-like ancestor, in which the main cream coloured upperside pattern elements switched to orange-red. Such a change would be sufficient to create incipient mimicry on which natural selection could then act (Nicholson's two stage theory: Turner, 1984). A similar red colour is present on the underside of all other members of the *angolanus* clade, both distal and basal to the cream-coloured discal and post-discal elements that are red in *ridleyanus*. Whether or not these pigments are the same would be very interesting to investigate, including the question of their possible derivation from the metabolic pathway that creates the colour of the rubral elements (clearly present on the underside of *G. endochus*, the Madagascan representative of the *angolanus*-group; evidently switched to orange in other members of the clade).

Another African *Graphium* that seems undoubtedly mimetic is *G. leonidas*. This widespread species emulates, in different parts of its range and sometimes polymorphically, the patterns of two different Danaini: the 'blue-tigers' (*Tirumala petiverana*), and various *Amauris* species (the latter more in the southern and eastern parts of its range). Of particular interest is the habit of *leonidas*, when settled, of closing its wings, even when feeding at flowers. This is considered to increase resemblance to a danaid significantly, as many other mimetic swallowtails seem to 'give the game away' by continually fluttering their wings in such situations. It would be interesting to compare the means of blue colour production in this species and its model; almost certainly both employ bile pigments in the wing membranes to produce the striking, pale blue tiger-patterns.

The third species that is almost certainly mimetic is *G. almansor.* This species, a distinctive member of the *adamastor*-group, exhibits polytypic variation in mimicking various local *Amauris.* In particular, *A. almansor uganda* appears, to the human eye at least, to be a rather good mimic of the yellow, black and white *Amauris echeria* complex (Vane-Wright & Boppré, 1993: pl. 2, fig. 12). It is possible that the *adamastor* crown-group may include, in addition to *G. almansor*, several mimics of the black and white *Amauris niavius*, such as *G. philonoe* (Vane-Wright & Boppré, 1993: pl. 2, fig. 22), *G. poggianus*, *G. hachei* and even the mysterious *G. aurivilliusi.* However, some races of *almansor* approach the *niavius* pattern, but are perhaps rather more like *Amauris tartarea* and *A. dannfelti* (Vane-Wright & Boppré, 1993: pl. 2, figs 19, 20), and this is also true for several other *Graphium*, such *G. adamastor* and *G. agamedes.*

A fourth possible example of a mimetic taxon is *G. philonoe whalleyi*, which S. Collins (quoted in Larsen, 1991) considers to be an excellent mimic of the danaine, *Tirumala petiverana.*

Possible pre-adaptations for mimicry

Despite the rather cautious view expressed above, according to Hancock (1993), all of the tail-less species, 'with the exception of *G. tynderaeus* (Fabricius) . . . appear to be mimics of *Amauris* Hübner, *Bematistes* Hemming [= *Acraea*] or members of the *Princeps* [= *Papilio*] *zenobia* group.' While we would take issue with the last point (see below), it is certainly the case that many members of the *adamastor*-group could indeed be generalized mimics, looking somewhat like *Amauris*, but also with a strong hint of *Acraea*-like patterning (intervenosal radiating stripes and basal black spots of the hindwing undersides; orange-yellow coloration). If so, and if our consensus trees (Figs 5, 6) have any validity, it would be extremely interesting to make field observations on as many species as possible, with special reference to behaviour when settled. If *G. leonidas* is the stem species of a crown-group that includes the *adamstor*-group, *philonoe*, *cyrnus* and *levassori*, it is possible that none of these butterflies flaps its wings when at rest, and this could be an important pre-adaptation for mimicry.

Striking pattern simplification is seen in the Grand Comoro endemic *G. levassori*, to produce an all-cream coloured insect with just some darkening at the wing margins. This species occurs together with an endemic monomorphic race of *Papilio dardanus*, *P. d. humbloti*, in which both the males and females are all pale primrose-yellow with black borders. The *Graphium* is thus strongly reminiscent of a tail-less *humbloti* (Turlin, 1994). Although curious, mimicry seems an unlikely explanation of this case, and therefore observations on its behaviour at rest might be particularly revealing. Unfortunately this species has rarely been seen in nature, and is thought to be close to extinction. Observations on the curiously patterned (but in our view non-mimetic) *G. tynderaeus* and *G. latreillianus*, which appear to be part of the same polytomous complex (Fig, 5, 6), would also be very valuable in this context.

Another and more obvious pre-adaptation for mimicry of Danaini and Acraeini is the loss of the long hindwing 'swordtails'. If Figs 5, 6 are basically correct, then there has been a stepwise loss of hindwing tails in African *Graphium*, leading first to the short tails and crenulated hindwing margins of the *angolanus* and *tynderaeus* groups. This appears to have gone a stage further in *G. leonidas*, and to completion in the *adamastor*-group, in which the hindwing margin is virtually smooth and evenly rounded, like those of the various model species. If this is so, then the reduction of tails, possibly on emergence into a primarily open woodland or savannah habitat (proto-*angolanus*-group), could have been another key pre-adaptation for the evolution of mimicry in African *Graphium.*

Do some African *Graphium* mimic the *Papilio zenobia* group?

According to Hancock (1993), *G. latreillianus*, *G. illyris* and even some members of the *adamastor*-group are mimetic of members of the *Papilio zenobia* group, such as *P. gallienus* and *P. cypraeofila.* Such relatively 'simple' banded patterns are a recurrent feature among swallowtails, in all zoogeographic regions of the world. In our opinion, the type of pattern seen in *G. illyris* (and *G. kirbyi*) represents a generalized form of disruptive coloration, readily evolved and re-evolved from the swallowtail groundplan, and should not be regarded as mimetic – or at least not aposematic or pseudaposematic – without real evidence of a defensive, signal function.

Forest/savannah fluctuations and the evolution of mimicry

More generally, it can be speculated that speciation in this group, and opportunities for the evolution of mimicry, may be connected with the fluctuating dynamics of the savannah/forest system that appear to have affected much of the African biota. African *Graphium* seem fundamentally to be forest butterflies, but many occur in gallery forests, heavy woodlands and even a few in dry bushlands in addition to, or rather than wet evergreen rainforests. The 'white ladies' (*angolanus*-group) are particularly adaptable, and seem to flourish in very dry areas (although not in true deserts, nor in rainforests). This is especially interesting in relation to *G. ridleyanus*, the strikingly mimetic member of this species group which, unlike the 'white ladies', is restricted to the evergreen forests of the wider Congo basin. Given the apparently dramatic fluctuations that have affected the Congo, with many areas of savannah apparently isolated by advancing forests, it is conceivable that an open-country *G. angolanus*-like ancestor was trapped in a diminishing savannah surrounded on all sides by encroaching forest. Perhaps re-adaptation to forest life was triggered by or even dependent upon the evolution of mimicry.

The forests of the Congo Basin are striking for the number of large mammals, such as the bongo, which have most of their relatives living in open situations in other parts of Africa. If such a scenario of 'savannah entrapment' has any validity, it might have particular relevance to the seemingly explosive radiation of the exclusively forest-dwelling *adamastor*-group, perhaps from a *leonidas*-like ancestor. *G. leonidas* is the only African *Graphium* that is both mimetic and yet highly adaptable in its habitat requirements, being found in almost all situations other than true deserts and rainforests. As noted above, *leonidas* is mimetic, and it is plausible, as suggested by Hancock, that virtually all species of the *adamastor*-group are either specific or generalized mimics.

Possible changes to the underlying system of wing pattern homologies

In trying to reconstruct the phylogenetic relationships of the African *Graphium*, and in particular to address the question of their monophyly, our inability to make significant use of the variations in colour patterns has been a source of great frustration. This difficulty comes down to the seeming impossibility of making sense of the pattern elements, most notably, of members of the *adamastor*-group in relation to the complex pattern elements of the swordtails. This is so despite the seeming intermediate pattern systems of the *angolanus*- and *tynderaeus*- groups.

The patterns of the non-mimetic swordtails are relatively easy to interpret in terms of Schwanwitsch's (1943) general system for papilionid wing pattern homologies. A similar problem when dealing with mimetic species has long been recognized in the nymphalid genus *Heliconius*, an aposematic group widely involved in Müllerian mimicry. The wing patterns of most *Heliconius* are hard to relate to the Schwanwitsch/Suffert ground-plan for the Nymphalidae. In particular, Nijhout & Wray (1988) noted that 'one of the major difficulties in interpreting the homologies . . . is that in many species the patterns produced by many elements of the groundplan are fused into a continuous black field that can cover considerable areas of the forewing surface'.

Even so, based on the advanced knowledge of *Heliconius* wing-pattern genetics that is available, Nijhout (1991) was able to expound sophisticated systems involving at least 18 wing pattern genes in *H. erato* and no less than 22 in *H. melpomene*, necessary to derive the various patterns observed from a specialized *Heliconius* ground plan. Although the putatively mimetic African *Graphium* would seem to present the possibility of a parallel system in which large areas of the wing surfaces are just black or pale, of potential interest for comparison with *Heliconius*, currently there is absolutely no knowledge of their genetics whereby a start could be made. *Graphium leonidas* and *G. almansor* would appear to be the best, or perhaps only species that offer the natural pattern variations necessary to undertake such work.

Apparent sex ratios

The sex ratios of butterflies in collections are well known to show a strong bias to males. In some cases literally hundreds of males have been collected, but only a handful of females, or even none. Butterfly species known only from males far outnumber those known only from females. The explanation is not thought to lie in some major systematic deviation from a 1: 1 primary sex ratio at eclosion (either from eggs or pupae), but in the behaviour of the adult insects and their would-be human captors (Larsen, 1991: 22). Males often actively congregate in places where collectors can easily find and capture them (e.g. at flowers, fallen fruit, hill-tops; in the case of *Graphium*, particularly at damp sand or mud), whereas females are more elusive, perhaps flying less, or flying most of the time in dense forest or other vegetation in search of oviposition sites. With rare exceptions, where entire Lepidoptera 'families' are bred through (or sexed as larvae or pupae), a 1: 1 primary sex ratio is found. In the exceptional cases, there is a preponderance of females due to male-lethal or other unusual factors. Cases of primary sex ratio deviation in butterflies strongly in favour of males are, so far as we are aware, unknown.

In the course of this study, for all 39 species of afrotropical *Graphium*, we examined a total of 9978 specimens in collections, 8718 of which were males – giving a 'collections' sex ratio of seven males to one female (6.91: 1). All species were represented by at least two males, but for nine species we were unable to locate any female specimens at all. Three species were represented by over 1000 males (*policenes, angolanus* and *leonidas*); for these the collections sex ratios were, respectively, 13.6:1; 3.7:1; and 4.3:1. Thus, for *policenes* we can conclude that its females are probably even more 'secretive' or hard to find than the average *Graphium* (*Arisbe*), whereas the opposite appears true for *angolanus* and *leonidas*. Of the 15 further species for which we have been able to examine in excess of 100 male specimens, based on the average overall collections sex ratio, the numbers of females available deviate by more than twice the expected number in half (eight) of these cases. Of these, only one (as with *angolanus* and *leonidas*) has more females than expected (*philonoe*: 2.04 males per female); the other seven all show evidence (like *policenes*) of greater than average female rarity (*illyris, porthaon, ridleyanus, tynderaeus, almansor, fulleri* and *hachei*). Of these, *fulleri* shows the greatest deviation, with almost 100 males for each of the two females we located.

Even so, perhaps the most striking 'deviation' of all is seen in *G. morania* which, with a total sample of 129 specimens has an almost 1: 1 collections sex ratio (70 males: 59 females), suggestive that female *morania* either behave more like males, or their primary resources occur in much the same types of microhabitat. Investigation of these possibilities, in comparison with e.g. *policenes*, would offer an interesting project in comparative ecology. For the *angolanus* group as a whole, other than the mimetic *ridleyanus*, it is notable that for all five non-mimetic species the females are more readily collected than in most other species of the genus (the collections sex ratio for a total sample of just over 2000 of these five species is 3.5:1). So females in this group are collected at well over twice the average rate of females belonging to the other 34 species, perhaps suggestive of a phylogenetic component for this 'apparency'. However, seeming reversal in *ridleyanus* (512 males: 32 females) within the *angolanus*-group, a species which exhibits a shift to mimicry and forest habitat (from savanna), probably indicates that these phenomena, as generally supposed, are behavioural 'artefacts'. The observed deviations from a presumed 1: 1 primary sex ratio are evidently brought about by the interaction of basic differences in sexual activity and preferred habitats, and no doubt the general and local 'architecture' of those habitats.

CONCLUSIONS

We set out on this study hoping and expecting to produce a credible and robust cladogram of the afrotropical *Graphium*. In this, we have not succeeded. The level of recalcitrance in the butterflies proved greater than our competence as taxonomists. However, it is a strength of cladistics rather than a weakness that existing shibboleths, complacently adhered to, may be undermined. In this, we may claim some success. Our analysis has called into question the monophyly of the group. Neither have we corroborated Hancock's (1993) contention that afrotropical *Graphium* is neatly divided into a monophyletic non-swordtailed clade (*G.* (*Arisbe*)) and a swordtailed clade (*G.* (*Graphium*)) which gave rise to the oriental species. Some previously accepted internal groupings have likewise not been supported. All in all, our reconstruction is much less neat.

Munroe (1961) commented that Berger (1951) may have been led to emphasize the differences between the male genitalia, rather than recognising their overall similarity, by confining his study to the Afrotropical Region. It is possible that we are guilty of a similar parochialism, despite our best efforts.

It is our intention to undertake similar studies of the subgenera *Pathysa, Paranticopsis* and *Pazala*, and to re-examine the work of Saigusa *et al.* (1977, 1983) on subgenus *Graphium*, especially in the light of Miller's (1987) comments (see Introduction). Then we may be in a better position to assess the characters and character states of the afrotropical species and thereby be able to place them in a global context.

In the meanwhile much more information on the afrotropical species is required. Many species are known from only a few specimens and in some the females are not known (see above). It is very likely that further specimens will undermine the separate identity of some current taxa, and redefine the boundaries of others. The early stages of many species are unknown: knowledge of these would surely provide a wealth of data, and breeding experiments might prove valuable. The behaviour of many of these butterflies and their interrelationships with their environments are very poorly known and may provide useful characters. Our distribution maps of even the best-collected species are full of holes, while other species have been collected but once, and then without useful localities. Were we able to fill in some of these huge gaps in our knowledge, our *understanding* of the afrotropical kite swallowtails would be significantly enhanced. Perhaps the most important general result from this study is the realisation and demonstration that even the supposed 'flagship' swallowtail butterflies are in reality very poorly known.

There is still much to do in taxonomy, ontogeny, bionomics, ecology, faunistics and above all cladistics.

We intend to make much of the contents of this study available on the BMNH scientific website (http: // www.nhm.ac.uk/science/index.html), together with additional material including extra illustrations and searchable distributional and hostplant databases.

We very much wish to encourage students of these butterflies to submit their own records of localities, hostplants and other aspects of *Graphium* biology in order to make as much data as possible available to future workers. In this way the afrotropical kite swallowtails may become a little less poorly known and so make a more solid contribution to the study of '. . . the phenomena of geographical distribution . . .' and to '. . . illuminate . . . the world . . .' a little more brightly.

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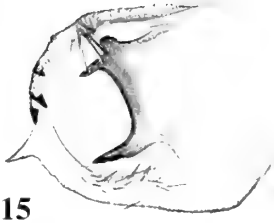
14

G. (*A.*) *antheus*
BMNH Spec.Reg. 136390
BMNH vial 3604



15

G. (*A.*) *e. evombar*
BMNH Spec.Reg. 135937
BMNH vial 3605

16

G. (*A.*) *kirbyi*
BMNH Spec.Reg. 220064
BMNH vial 3603

17

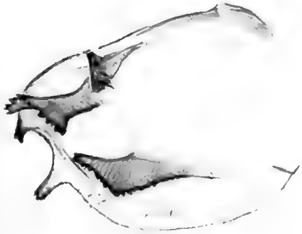
G. (*A.*) *junodi*
BMNH Spec.Reg. 149238
BMNH vial 3282

18

G. (*A.*) *polistratus*
BMNH Spec.Reg. 141191
BMNH vial 3844

19

G. (*A.*) *colonna*
BMNH Spec.Reg. 136216
BMNH vial 3600



20

G. (*A.*) *i. illyris*
BMNH Spec.Reg. 149265
BMNH vial 3602

21

G. (*A.*) *i. flavisparsus*
ABRI specimen

22

G. (*A.*) *i. girardeaui*
BMNH Spec.Reg. 143411
BMNH vial 4590
dorsal view; not to scale

Figs 14–22. Left valves of male *Graphium* (*Arisbe*). Scale ——— 1 mm.

23

G. (*A.*) *i. hamatus* **HT**
BMNH Spec.Reg. 143403
BMNH vial 4698
dorsal view; not to scale

24

G. (*A.*) *gudenusi*
BMNH Spec.Reg. 220031
BMNH vial 4257

25

G. (*A.*) *p. policenes*
BMNH Spec.Reg. 149263
BMNH vial 3159

26

G. (*A.*) *liponesco*
BMNH Spec.Reg. 143021
BMNH vial 4706

27

G. (*A.*) *policenes*
BMNH Spec.Reg.
142150
BMNH vial 4758

28

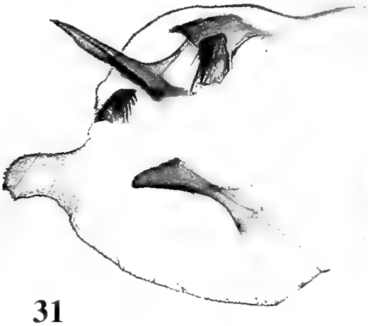
G. (*A.*) *liponesco*
BMNH Spec.Reg.
143017
BMNH vial 4705

29

G. (*A.*) *biokoensis*
BMNH Spec.Reg. 142660
BMNH vial 4754

30

G. (*A.*) *policenoides*
ABRI specimen



31

G. (*A.*) *p. porthaon*
BMNH Spec.Reg. 141594
BMNH vial 4721

32

G. (*A.*) *a. angolanus*
BMNH Spec.Reg. 140359
BMNH vial 3158

Figs 23–32. Left valves of male *Graphium* (*Arisbe*). Scale ———— 1 mm. Figs. 27 & 28 are posterior views to show dorsal terminal processes and dorsal harpes and are not to scale.

33

G. (*A.*) *endochus*
BMNH Spec.Reg. 135907
BMNH vial 3273

34

G. (*A.*) *morania*
BMNH Spec.Reg. 140724
BMNH vial 3275

35

G. (*A.*) *taboranus*
BMNH Spec.Reg. 140993
BMNH vial 3274

36

G. (*A.*) *schaffgotschi*
BMNH Spec.Reg. 140641
BMNH vial 3276

37

G. (*A.*) *ridleyanus*
BMNH Spec.Reg. 137439
BMNH vial 3161

38

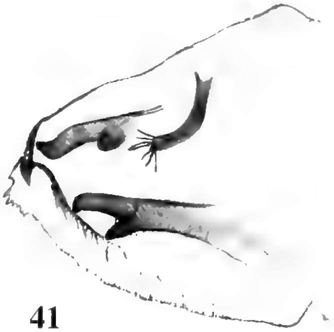
G. (*A.*) *l. leonidas*
BMNH Spec.Reg. 137980
BMNH vial 3164

39

G. (*A.*) *levassori*
BMNH Spec.Reg. 136047
BMNH vial 4253

40

G. (*A.*) *c. cyrnus*
BMNH Spec.Reg. 136013
BMNH vial 3278



41

G. (*A.*) *tynderaeus*
BMNH Spec.Reg. 139222
BMNH vial 3280

Figs 33–41. Left valves of male *Graphium* (*Arisbe*). Scale ———— 1 mm.

42

G. (*A.*) *l. latreillianus*
BMNH Spec.Reg. 140699
BMNH vial 3281

43

G. (*A.*) *p. philonoe*
BMNH Spec.Reg. 138476
BMNH vial 3277

44

G. (*A.*) *adamastor*
BMNH Spec.Reg. 138599
BMNH vial 3160

45

G. (*A.*) *agamedes*
BMNH Spec.Reg. 138710
BMNH vial 3267

46

G. (*A.*) *schubotzi*
BMNH Spec.Reg. 149268
BMNH vial 4234

47

G. (*A.*) *o. olbrechtsi*
BMNH Spec.Reg. 138834
BMNH vial 4247

48

G. (*A.*) *o. tongoni* **HT**
MRAC specimen

49

G. (*A.*) *abri* **HT**
ABRI specimen

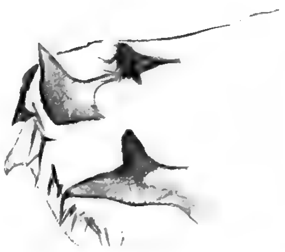
50

G. (*A.*) *abri* **PT**
ABRI specimen

Figs 42–50. Left valves of male *Graphium* (*Arisbe*). Scale 1 mm.

51

G. (A.) a. almansor
BMNH Spec.Reg. 138721
BMNH vial 4172



52

G. (A.) a. carchedonius
BMNH Spec.Reg. 138840
BMNH vial 3606

53

G. (A.) auriger
BMNH Spec.Reg. 149267
BMNH vial 3270

54

G. (A.) f. fulleri
BMNH Spec.Reg. 138858
BMNH vial 3271

55

G. (A.) f. boulleti
ABRI specimen

56

G. (A.) f. rileyi
BMNH Spec.Reg. 138761
BMNH vial 4244

57

G. (A.) f. ucalegonides
BMNH Spec.Reg. 136047
BMNH vial 4253

58

G. (A.) poggianus **HT**
MNHU specimen

59

G. (A.) kigoma **PT**
BMNH Spec.Reg. 149197
BMNH vial 4191

Figs 51–59. Left valves of male *Graphium* (*Arisbe*). Scale ——— 1 mm.

60

G. (*A.*) *kigoma* =*wranghami*
ABRI specimen

61

G. (*A.*) *h. hachei*
BMNH Spec.Reg. 138833
BMNH vial 4246

62

G. (*A.*) *aurivilliusi* **PLT**
MRAC specimen

63

G. (*A.*) *u. ucalegon*
BMNH Spec.Reg. 140641
BMNH vial 3276

64

G. (*A.*) *simoni*
BMNH Spec.Reg. 137439
BMNH vial 3161

65

G. (*Paranticopsis*) *macareus indicus*
BMNH Spec.Reg. 220130
BMNH vial 4694

66

G. (*Graphium*) *bathycles chiron*
BMNH Spec.Reg. 220134
BMNH vial 5453

67

G. (*Graphium*) *s. sarpedon*
BMNH Spec.Reg. 220117
BMNH vial 3608

Figs 60–67. Left valves of male *Graphium*. Scale ——— 1 mm.

68

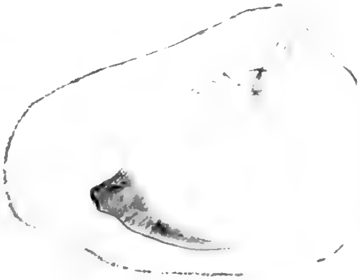
G. (*Pazala*) *m. mandarinus*
BMNH Spec.Reg. 220118
BMNH vial 3609

69

G. (*Pathysa*) *aristeus parmatus*
BMNH Spec.Reg. 220126
BMNH vial 4259

70

G. (*Pathysa*) *n nomius*
BMNH Spec.Reg. 220127
BMNH vial 4258



71

Lamproptera m. meges
BMNH Spec.Reg. 220136
BMNH vial 5455

72

Protographium leosthenes
BMNH Spec.Reg. 220124
BMNH vial 3612

73

Iphiclides p. podalirius
BMNH Spec.Reg. 220123
BMNH vial 3611

Figs 68–73. Left valves of male Leptocircini. Scale ——— 1 mm.

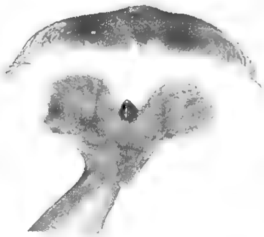
74 *G.* (*A.*) *antheus*
BMNH Spec.Reg. 137391
BMNH vial 3787

75 *G.* (*A.*) *e. evombar*
BMNH Spec.Reg. 135939
BMNH vial 5446

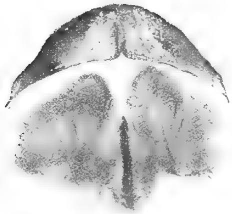
76 *G.* (*A.*) *kirbyi*
BMNH Spec.Reg. 220065
BMNH vial 3989

77 *G.* (*A.*) *junodi*
BMNH Spec.Reg. 149239
BMNH vial 3993

78 *G.* (*A.*) *polistratus*
BMNH Spec.Reg. 141147
BMNH vial 4704



79 *G.* (*A.*) *colonna*
BMNH Spec.Reg. 136224
BMNH vial 3991



80 *G.* (*A.*) *i. illyris*
BMNH Spec.Reg. 149264
BMNH vial 3988

81 *G.* (*A.*) *gudenusi*
ABRI specimen

82 *G.* (*A.*) *p. policenes*
BMNH Spec.Reg. 149262
BMNH vial 3992

Figs 74–82. Vestibula and associated organs of female *Graphium* (*Arisbe*) species. Scale ——— 1mm.

83

G. (A.) p. porthaon
BMNH Spec.Reg. 141581
BMNH vial 3990

84

G. (A.) a. angolanus
BMNH Spec.Reg. 140358
BMNH vial 3985

85

G. (A.) endochus
BMNH Spec.Reg. 135862
BMNH vial 5443

86

G. (A.) morania
BMNH Spec.Reg. 140725
BMNH vial 3984

87

G. (A.) taboranus
BMNH Spec.Reg. 140994
BMNH vial 3983

88

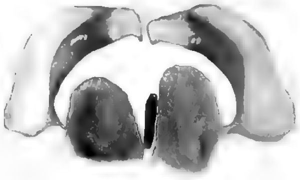
G. (A.) schaffgotschi
BMNH Spec.Reg. 140642
BMNH vial 3982

89

G. (A.) ridleyanus
BMNH Spec.Reg. 137028
BMNH vial 4697

90

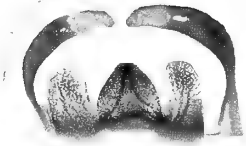
G. (A.) l. leonidas
BMNH Spec.Reg. 137474
BMNH vial 4593



91

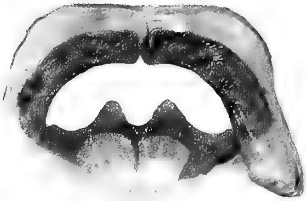
G. (A.) levassori
BMNH Spec.Reg. 136050
BMNH vial 5444

Figs 83–91. Vestibula and associated organs of female *Graphium* (*Arisbe*) species. Scale —— 1mm.



92

G. (*A.*) *c. cyrnus*
BMNH Spec.Reg. 136014
BMNH vial 3987



93

G. (*A.*) *tynderaeus*
BMNH Spec.Reg. 139223
BMNH vial 3968

94

G. (*A.*) *l. latreillianus*
BMNH Spec.Reg. 140700
BMNH vial 3980

95

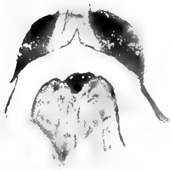
G. (*A.*) *p. philonoe*
BMNH Spec.Reg. 149239
BMNH vial 3977
N.B. Left lateral ostial lobe missing

96

G. (*A.*) *adamastor*
BMNH Spec.Reg. 138661
BMNH vial 3978

97

G. (*A.*) *agamedes*
BMNH Spec.Reg. 138711
BMNH vial 3979



98

G. (*A.*) *almansor uganda*
BMNH Spec.Reg. 138782
BMNH vial 3976

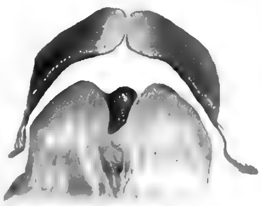
99

G. (*A.*) *fulleri rileyi*
BMNH Spec.Reg. 143330
BMNH vial 5281

100

G. (*A.*) *kigoma* **PT**
BMNH Spec.Reg. 149195
BMNH vial 5447

Figs 92–100. Vestibula and associated organs of female *Graphium* (*Arisbe*) species. Scale ▬ 1mm.



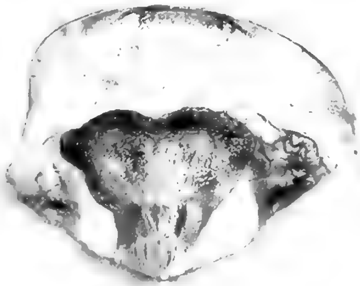
101 *G. (A.) auriger*
BMNH Spec.Reg. 141731
BMNH vial 5445

102 *G. (A.) u. ucalegon*
BMNH Spec.Reg. 143144
BMNH vial 4751

103 *G. (Paranticopsis) macareus indicus*
BMNH Spec.Reg. 220131
BMNH vial 4596

104

G. (G.) bathycles chiron
BMNH Spec.Reg. 220135
BMNH vial 5454



105

G. (G.) s. sarpedon
BMNH Spec.Reg. 220121
BMNH vial 5450

106 *G. (Pazala) m. mandarinus*
BMNH Spec.Reg. 220120
BMNH vial 5449

107 *G. (Pathysa) aristeus hermocrates*
BMNH Spec.Reg. 220125
BMNH vial 4700

108 *G. (Pathysa) n. nomius*
BMNH Spec.Reg. 220128
BMNH vial 4594

Figs 101–108. Vestibula and associated organs of female *Graphium* species. Scale — 1mm.

109

Lamproptera m. meges
BMNH Spec.Reg. 220137
BMNH vial 5456

111

Protographium leosthenes
BMNH Spec.Reg. 220139
BMNH vial 5458

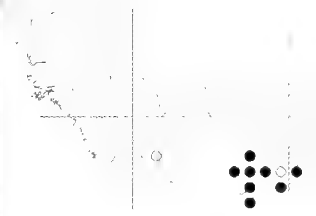
110

Iphiclides p. podalirius
BMNH Spec.Reg. 220138
BMNH vial 5457

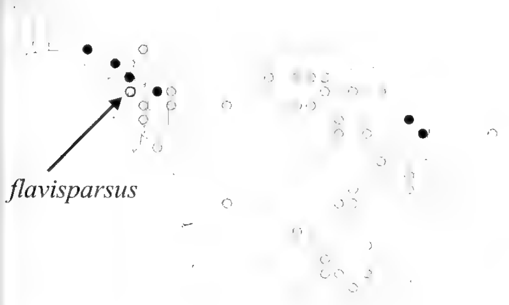
Figs 109–111. Female genitalia of some non-*Graphium* Leptocircini. Scale ▬ 1mm.

112 *G. antheus*

113 *G. evombar*



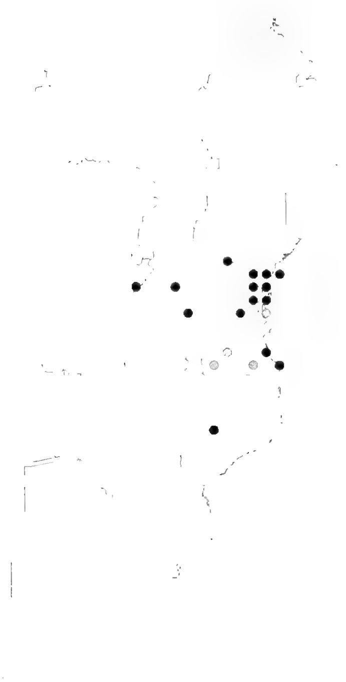
114 *G. i. illyris*



115 *G. illyris girardeaui* and *flavisparsus*

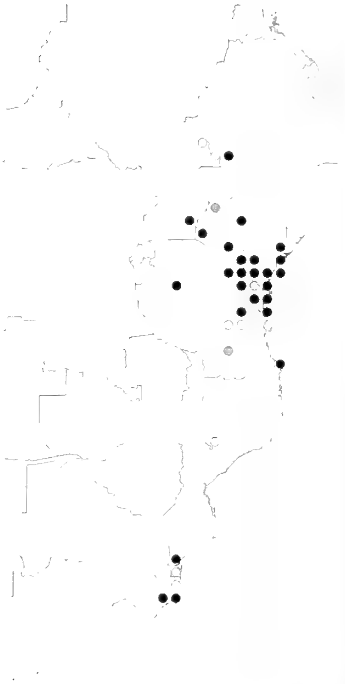
116 *G. kirbyi*

Figs 112–116. Distribution maps of afrotropical *Graphium*. *G. antheus* clade, and *G. kirbyi* and *G. illyris*. Solid circles: ● = BMNH records; shaded circles: ○ = other specimens seen; open circles: ○ = literature records.

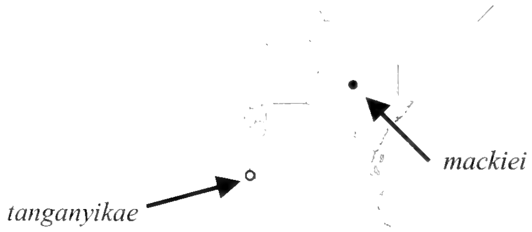


117 *G. polistratus*

118 *G. junodi*



119 *G. colonna*



120 *G. porthaon mackiei* and *G. p. tanganyikae*

121 *G. p. porthaon*

122 *G. morania*

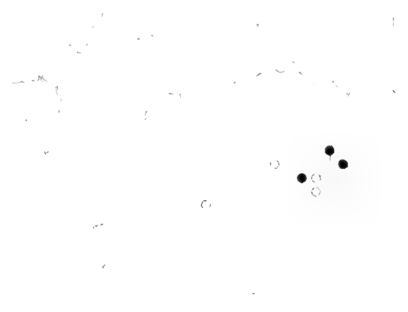
Figs 117–122. Distribution maps of afrotropical *Graphium*. Some swordtail species, and *G. morania*.
Solid circles: ● = BMNH records; shaded circles: ○ = other specimens seen; open circles: ○ = literature records.

123 *G. p. policenes*

124 *G. liponesco*

125 *G. policenoides*

126 *G. biokoensis*

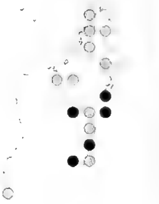


127 *G. gudenusi*

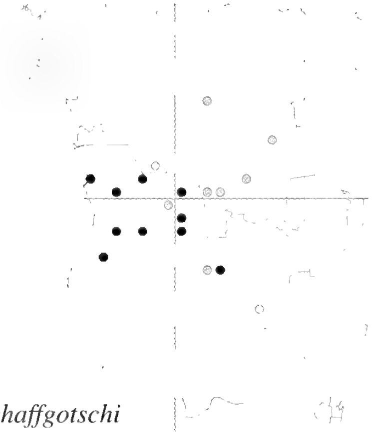
Figs 123–127. Distribution maps of afrotropical *Graphium*. *G. policenes* clade, and *G. gudenusi*.
Solid circles: ● = BMNH records; shaded circles: ○ = other specimens seen; open circles: ○ = literature records.

128 *G. angolanus baronis*

129 *G. a. angolanus*



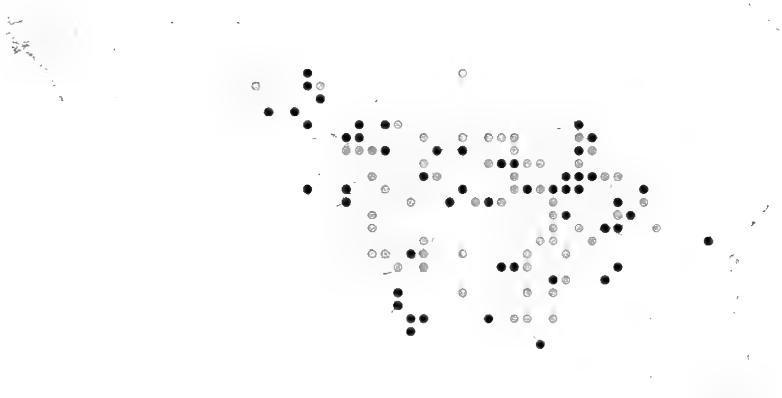
130 *G. endochus*



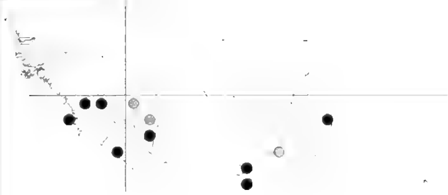
131 *G. schaffgotschi*

132 *G. taboranus*

Figs 128–132. Distribution maps of afrotropical *Graphium*. *G. angolanus* and relatives.
Solid circles: ● = BMNH records; shaded circles: ○ = other specimens seen; open circles: ○ = literature records.

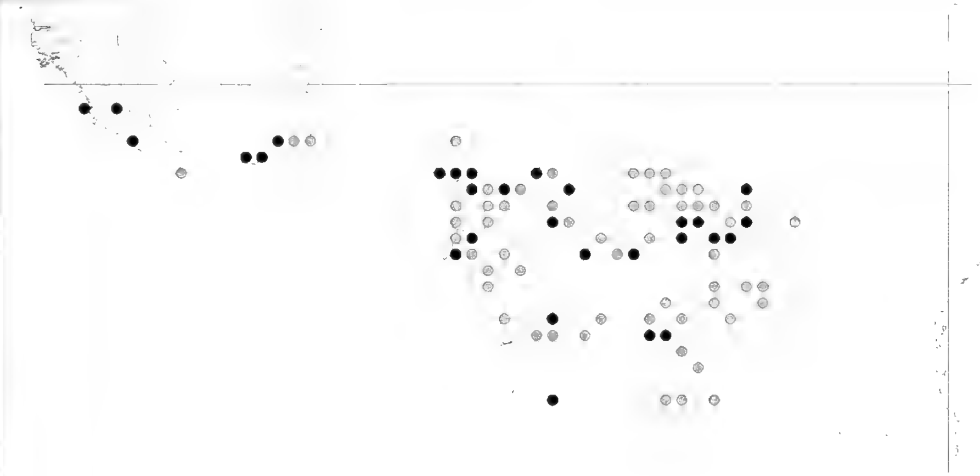


133 *G. ridleyanus*



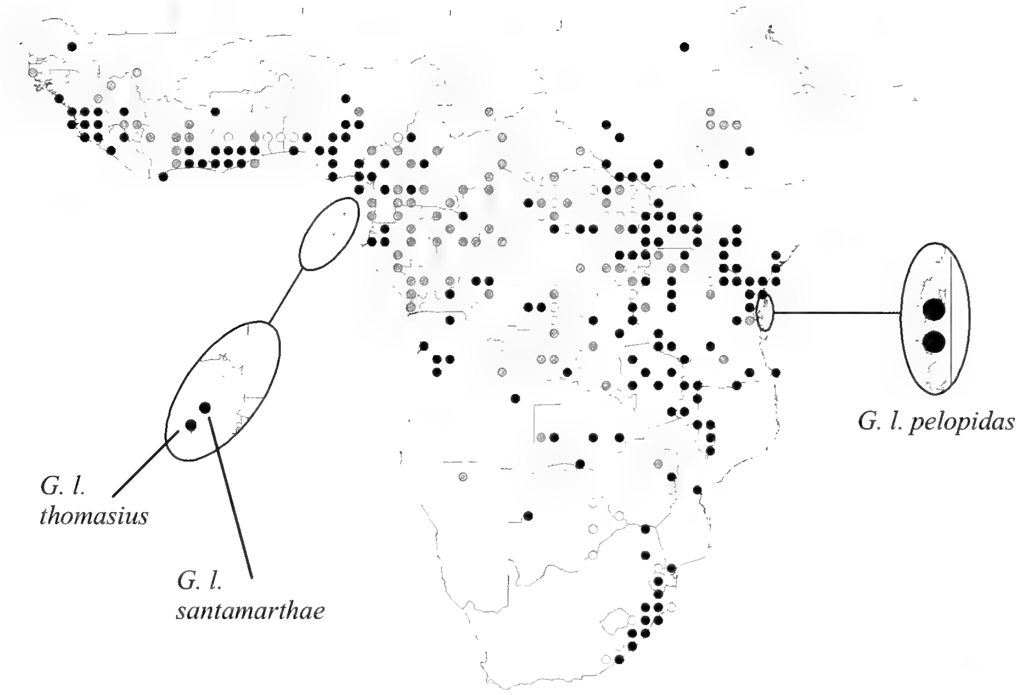
134 *G. l. latreillianus*

135 *G. latreillianus theorini*



136 *G. tynderaeus*

Figs 133–136. Distribution maps of afrotropical *Graphium*. *G. ridleyanus*, and *G. latreillianus* and *G. tynderaeus*. Solid circles: ● = BMNH records; shaded circles: ◍ = other specimens seen; open circles: ○ = literature records.



137 *G. leonidas*

138 *G. cyrnus nucyrus* **139** *G. c. cyrnus* **140** *G. levassori*

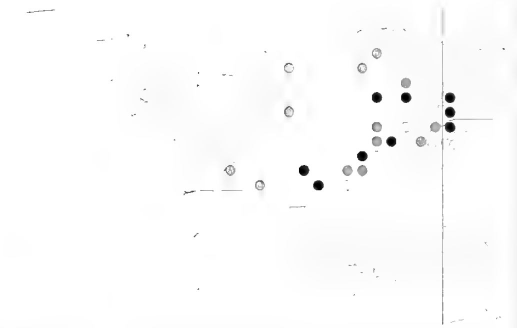
Figs 137 to 140. Distribution maps of afrotropical *Graphium*. *G. leonidas* group.
Solid circles: ● = BMNH records; shaded circles: ○ = other specimens seen; open circles: ○ = literature records.

141 *G. p. philonoe* **142** *G. philonoe whalleyi* **143** *G. auriger*

144 *G. h. hachei* **145** *G. hachei moebii*

Figs 141–145. Distribution maps of afrotropical *Graphium*. *G. philonoe*, *G. auriger* and *G. hachei*. Solid circles: ● = BMNH records; shaded circles: ○ = other specimens seen; open circles: ○ = literature records.

146 *G. u. ucalegon*

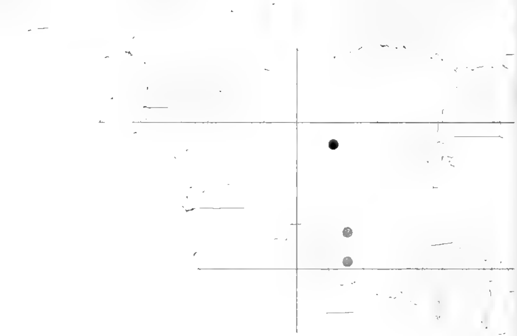


147 *G. ucalegon schoutedeni*

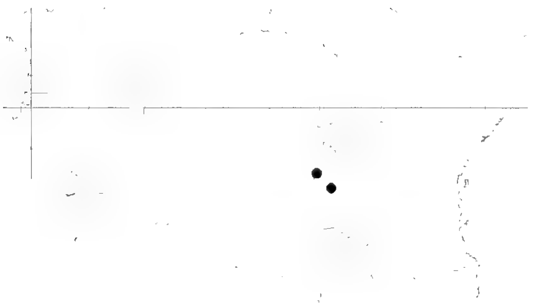
148 *G. ucalegon fontainei*

149 *G. simoni*

150 *G. poggianus*



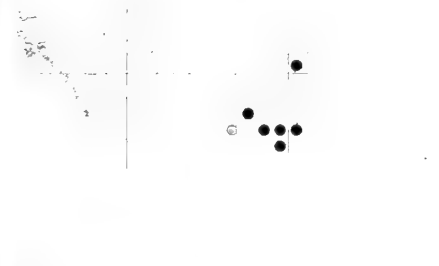
151 *G. o. olbrechtsi*



152 *G. kigoma*

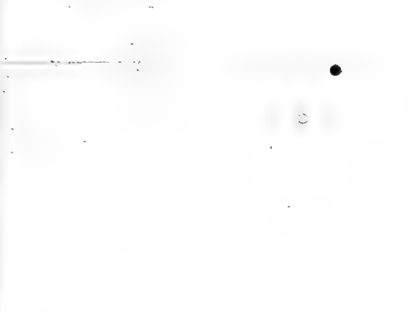
153 *G. olbrechtsi tongoni*

Figs 146–153. Distribution maps of afrotropical *Graphium*. *G. ucalegon* and other central African mimetic species. Solid circles: ● = BMNH records; shaded circles: ○ = other specimens seen; open circles: ○ = literature records.

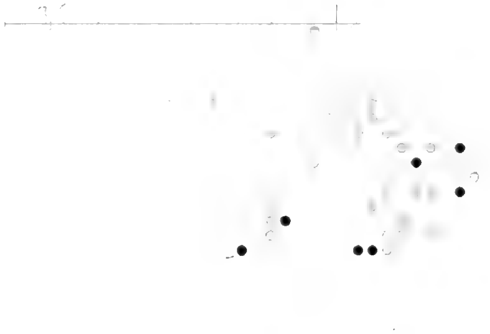


154 *G. fulleri rileyi*

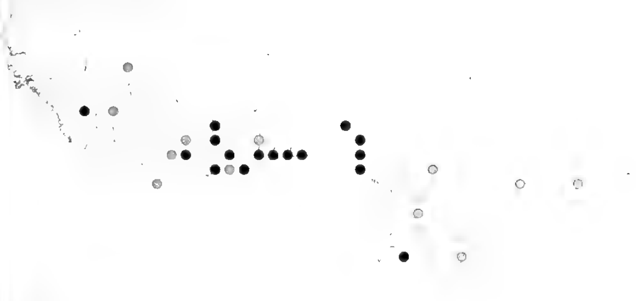
155 *G. fulleri boulleti*



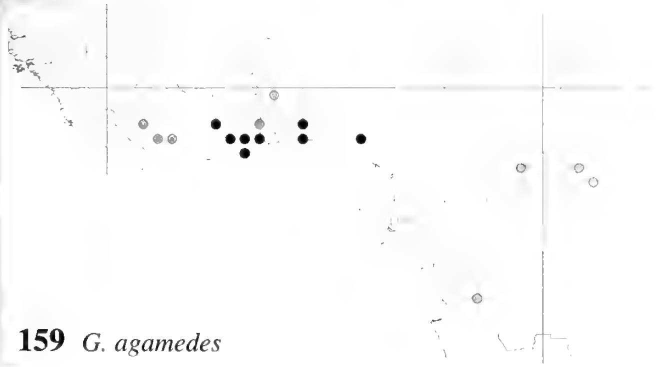
156 *G. f. fulleri*



157 *G. fulleri ucalegonides*



158 *G. adamastor*



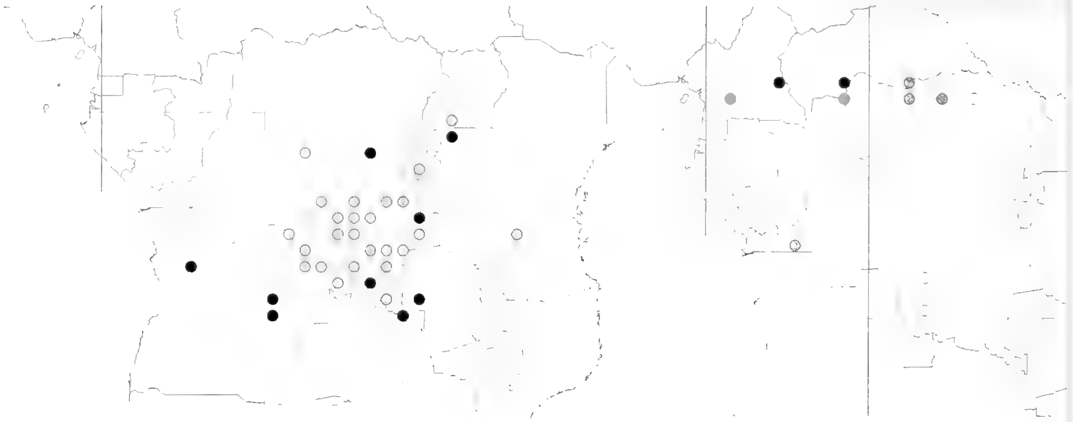
159 *G. agamedes*

160 *G. abri* **sp.n.**

Figs 154–160. Distribution maps of afrotropical *Graphium*. *G. fulleri* and other mimetic species. Solid circles: ● = BMNH records; shaded circles: O = other specimens seen; open circles: O = literature records.

161 *G. almansor carchedonius* **162** *G. almansor birbiri*

163 *G. almansor escherichi* **164** *G. almansor uganda*



165 *G. a. almansor* **166** *G. schubotzi*

Figs 161–166. Distribution maps of afrotropical *Graphium*. *G. almansor* and *G. schubotzi*.
Solid circles: ● = BMNH records; shaded circles: ○ = other specimens seen; open circles: ○ = literature records.

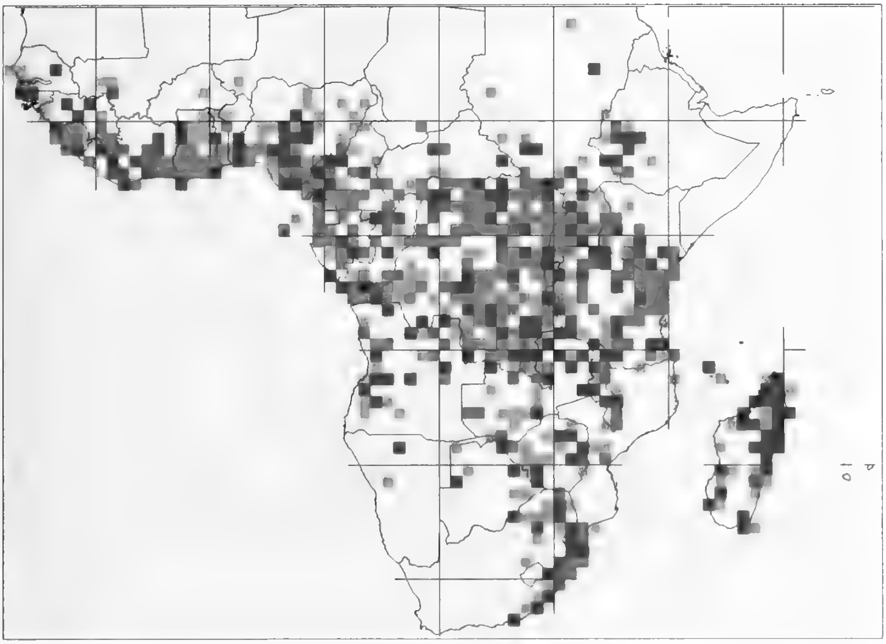


Fig. 167. Species richness map for African *Graphium*, based on databased specimen and literature records gathered during this study, displayed using WORLDMAP one degree grid (Williams, 1996). The 'hottest' squares (red) have records for 11 species, the coolest (blue) have only one. The map is built by integration of 39 separate maps for each species (note: no location is included for *G. aurivilliusi*, as its only provenance is unknown).

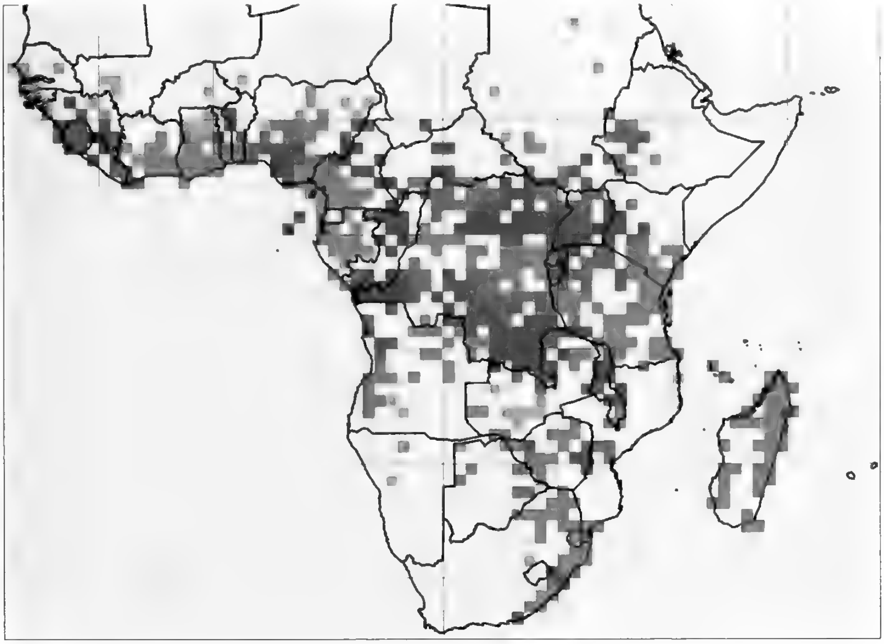


Fig. 168. Smoothed mean inverse range-size rarity map, derived from Fig. 167. Each species is given a value of one, divided equally across all squares that it occupies (species known from one square only, e.g. *G. abri*, score 1.0 in that square; a species recorded from 100 squares would score 0.01 in each of those squares), then all scores for each square are aggregated; next the value for each square is divided by the number of species recorded for that square; finally the scores have been smoothed (two rounds, 9-cell neighbourhood) using Williams' (1996) technique. Note suggestions of locally endemic faunas in West Africa (either side of Dahomey Gap), central, eastern and southern Africa, Comoros and Madagascar.

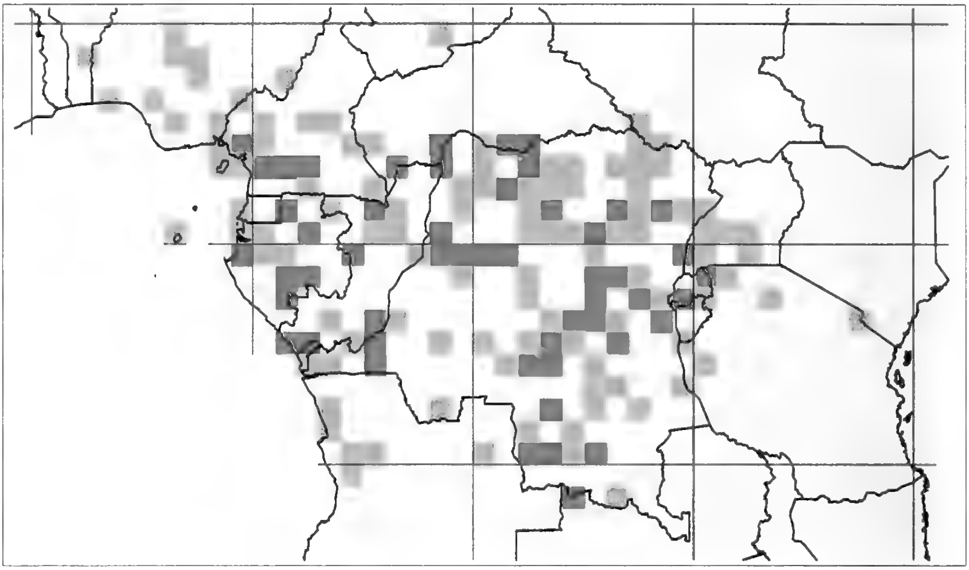


Fig. 169. Richness map for the subset of 12 *Graphium* species restricted to Central Africa (*simoni*, *schubotzi*, *aurivilliusi*, *poggianus*, *biokoensis*, *gudenusi*, *olbrechtsi*, *hachei*, *abri*, *auriger*, *policenoides* and *ridleyanus*). Most of the peripheral records for just one species refer to *G. ridleyanus*, some of which could be erroneous. The 'hottest' squares (red) have records for 4 species. The map is built by integration of the 12 separate maps for each species, although (as noted in Fig. 167) there is no precise location for *G. aurivilliusi*.

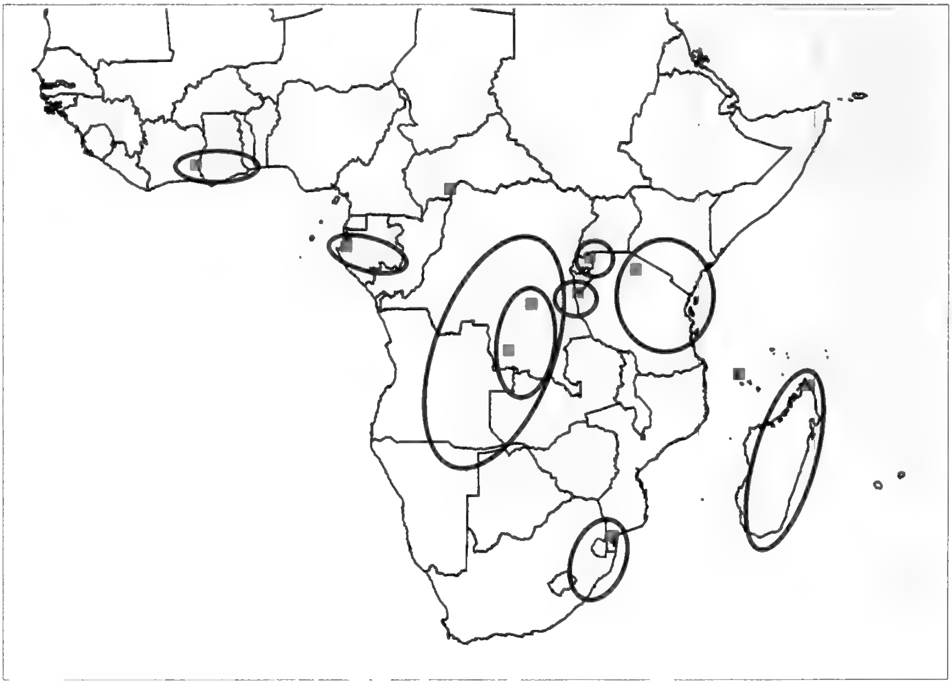


Fig. 170. The 'near-minimum-set' routine in WORLDMAP identifies a minimum of 11 areas to include all 38 mapped Afrotropical *Graphium* at least once (no precise information for *G. aurivilliusi*). Of these, two are irreplaceable (red squares for *G. abri* and *G. levassori*). The other 9 areas (orange squares as chosen by the computer program) all have some degree of flexibility; the 9 grey ellipses give an impression of where this flexibility is concentrated for each of these areas.

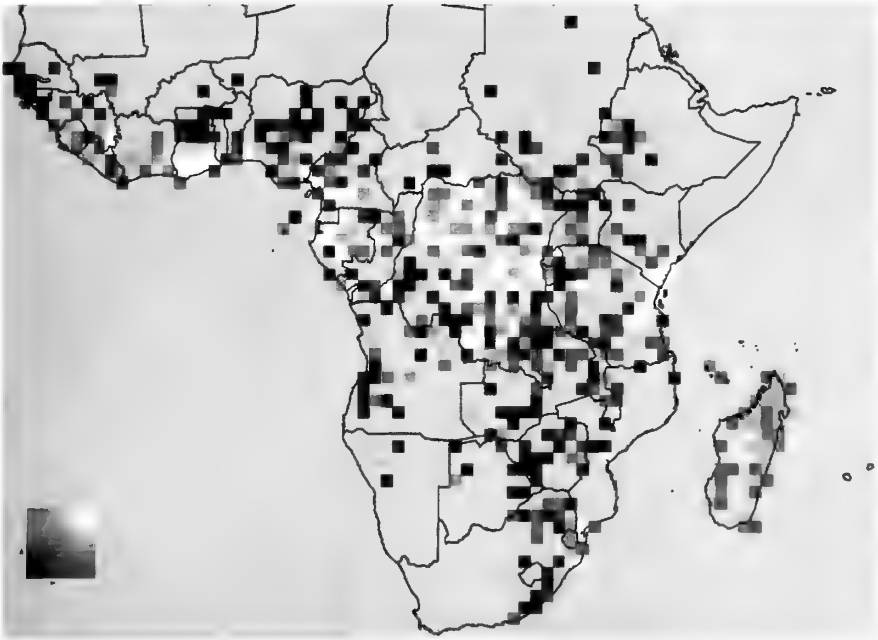


Fig. 171. Overlay of species richness (Fig 167) and mean range-size rarity (unsmoothed) using Williams two-colour technique (Williams, 1996). The scattering of green, blue, white and black cells on the mainland, but with some concentration of blue cells (excess species richness) in the Congo Basin suggests both under-recording and a 'faunal centre' (Central Africa: mainly the effect of the many *adamastor*-group species). The uniform green of the Comoros and Madagascar emphasises the distinctness of these *Graphium* faunas at species level.

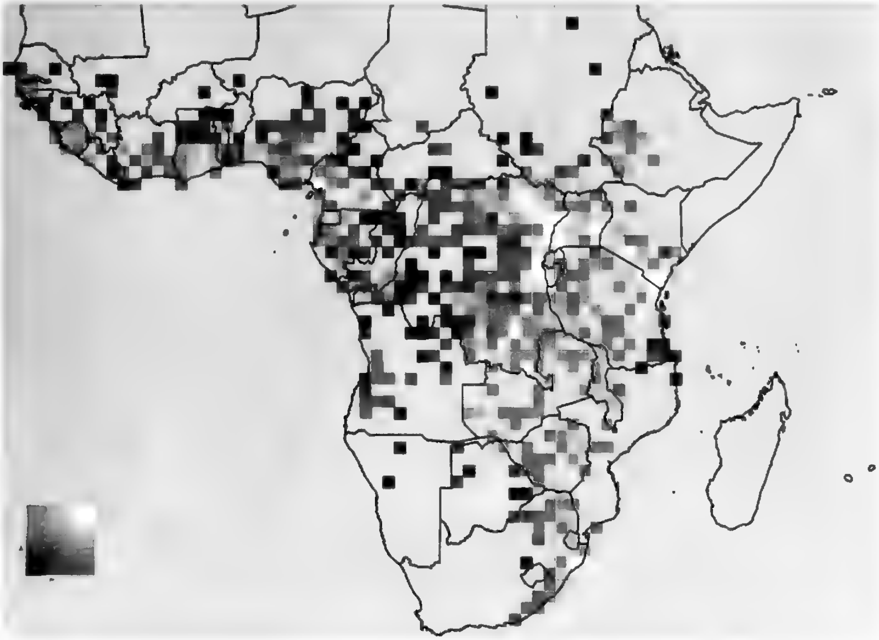
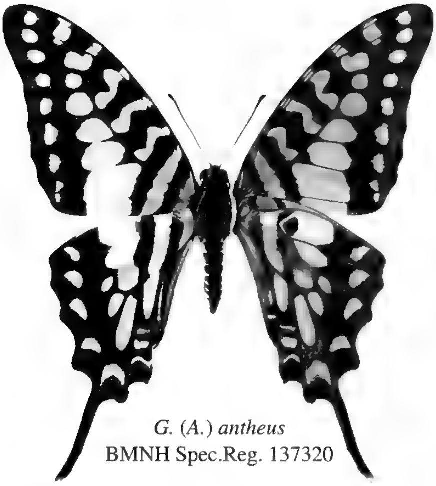


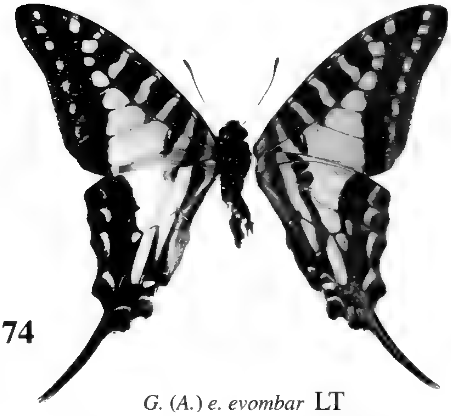
Fig. 172. Overlay of species richness (Fig. 167) for *Graphium* and African bird species richness (shared cells only; bird data as in Williams *et al.* 1999). Despite the limitations of the butterfly data, there is a strong suggestion that the bird and butterfly species richness patterns are not the same, with the butterflies showing excess relative richness in West Africa and the Congo Basin (blue), and relative poverty in East Africa generally – although there are some areas around Kenya, Uganda and Tanzania (white cells) that exhibit high relative diversity in both groups.

173



G. (A.) antheus
BMNH Spec.Reg. 137320

174

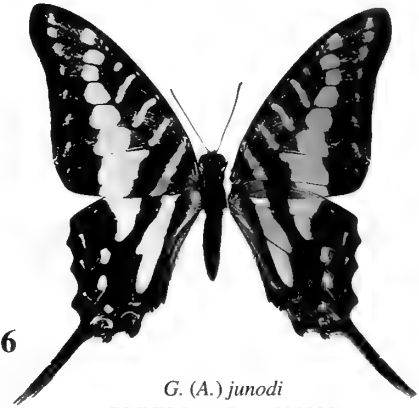


G. (A.) e. evombar LT
BMNH Spec.Reg.135948

175

G. (A.) kirbyi
BMNH Spec.Reg. 220074

176

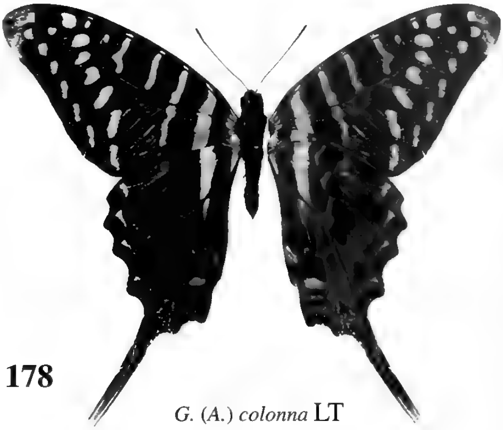


G. (A.) junodi
BMNH Spec.Reg. 220098

177

G. (A.) polistratus
BMNH Spec.Reg. 141200

178



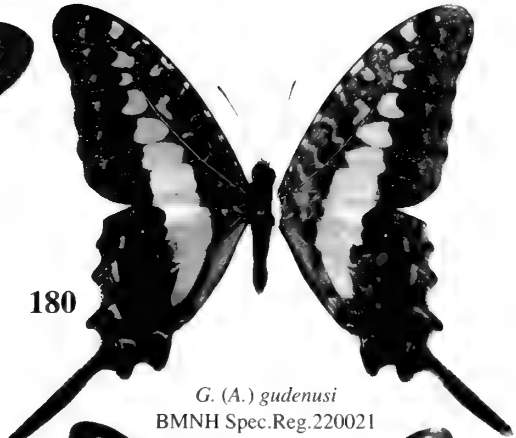
G. (A.) colonna LT
BMNH Spec.Reg.136081

Figs 173–178. Wing patterns of *Graphium* (*Arisbe*). Upperside of left wing and body to left; underside of left wing to right. Approx. 80% life size. Scale ▬ 1 cm.

179

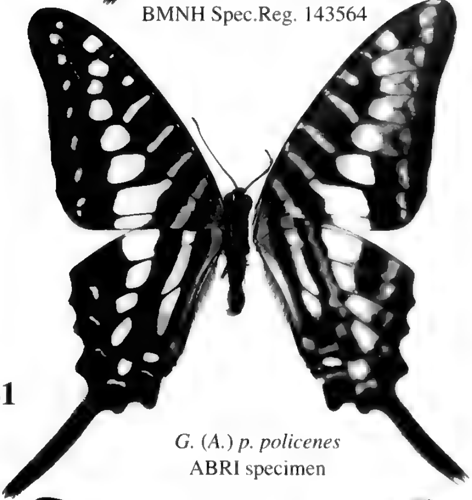
G. (*A.*) *i. illyris* LT
BMNH Spec.Reg. 143564

180



G. (*A.*) *gudenusi*
BMNH Spec.Reg.220021

181

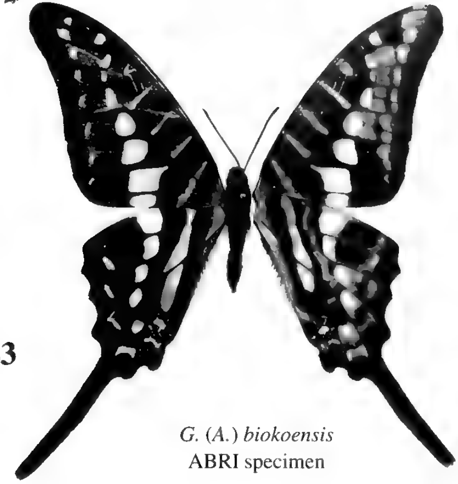


G. (*A.*) *p. policenes*
ABRI specimen

182

G. (*A.*) *liponesco* PLT
BMNH Spec.Reg. 142664

183

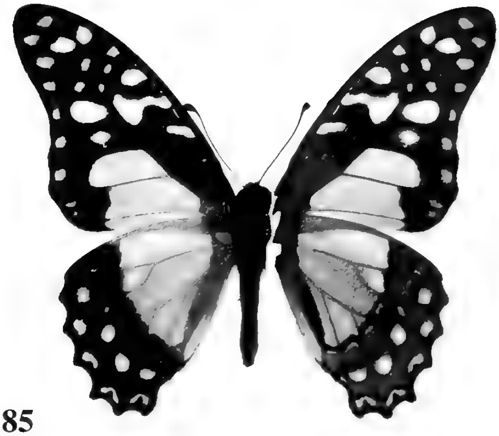


G. (*A.*) *biokoensis*
ABRI specimen

184

G. (*A.*) *policenoides*
MRAC specimen
Upperside only

Figs 179–184. Wing patterns of *Graphium* (*Arisbe*). Upperside of left wing and body to left; underside of left wing to right (except *G.* (*A.*) *policenoides*) . Approx. 80% life size. Scale ▬ 1 cm.

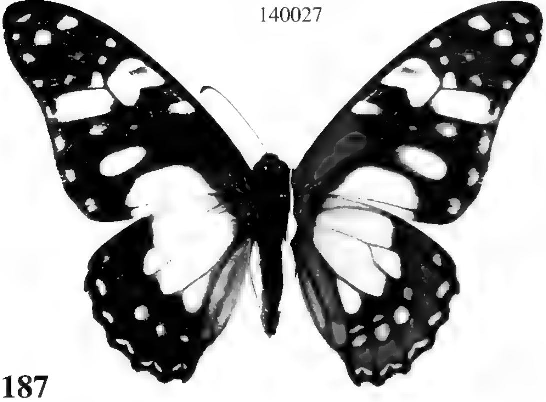


185

G. (*A.*) *a. angolanus*
BMNH Spec.Reg.
140027

186

G. (*A.*) *endochus* HT
BMNH Spec.Reg.135877



187

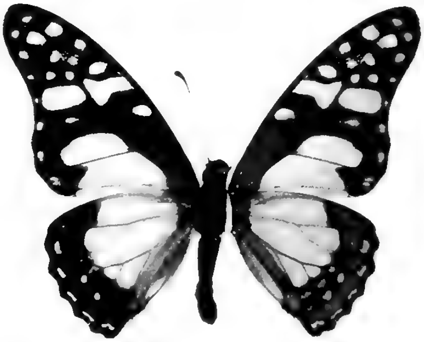
G. (*A.*) *taboranus* ♂
BMNH Spec.Reg. 140989

188

G. (*A.*) *taboranus* ♀ HT
BMNH Spec.Reg. 140620

189

G. (*A.*) *morania* HT
BMNH Spec.Reg. 140744



190

G. (*A.*) *schaffgotschi* LT
BMNH Spec.Reg.140618

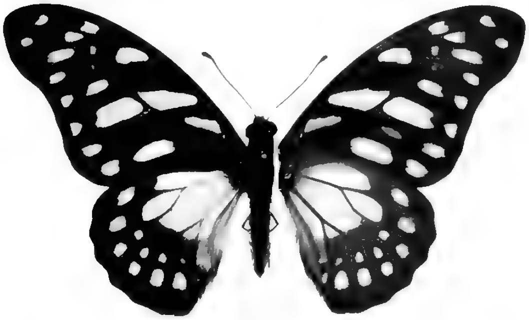
Figs 185–190. Wing patterns of *Graphium* (*Arisbe*). Upperside of left wing and body to left; underside of left wing to right. Approx. life size. Scale ▬ 1 cm.

191

G. (*A.*) *p. porthaon* LT
BMNH Spec.Reg. 141619

192

G. (*A.*) *ridleyanus* LT
BMNH Spec.Reg.136955

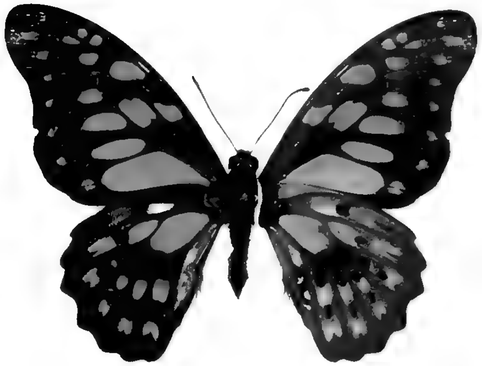


193

G. (*A.*) *l. leonidas*
BMNH Spec.Reg. 137667

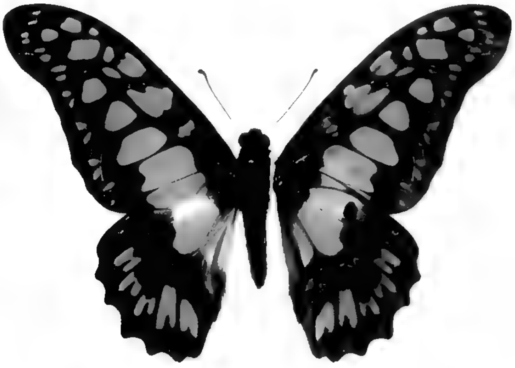
194

G. (*A.*) *levassori* HT
BMNH Spec.Reg. 136049



195

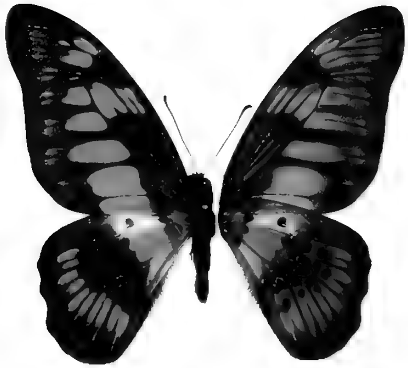
G. (*A.*) *c. cyrnus* LT
BMNH Spec.Reg. 136044



196

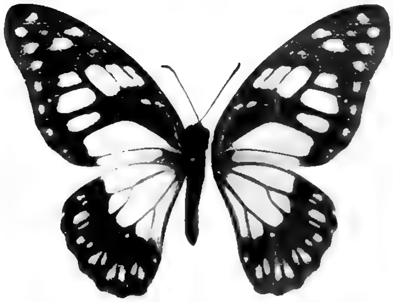
G. (*A.*) *tynderaeus*
BMNH Spec.Reg.
138912

Figs 191–196. Wing patterns of *Graphium* (*Arisbe*). Upperside of left wing and body to left; underside of left wing to right. Approx. 80% life size. Scale ▬ 1 cm.



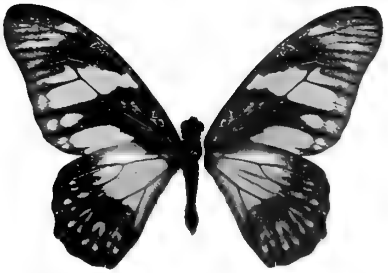
197

G. (A.) l. latreillianus
BMNH Spec.Reg. 140657



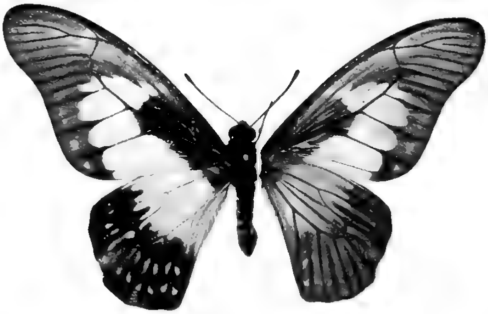
198

G. (A.) p. philonoe
BMNH Spec.Reg.
138437



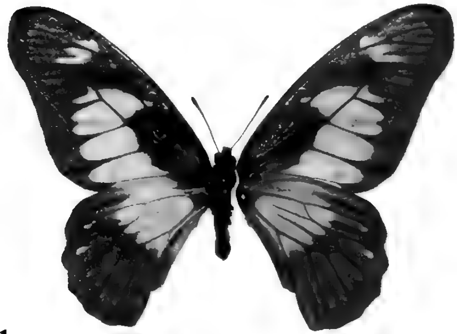
199

G. (A.) adamastor HT
BMNH Spec.Reg. 137632



200

G. (A.) agamedes HT
OXUM Specimen



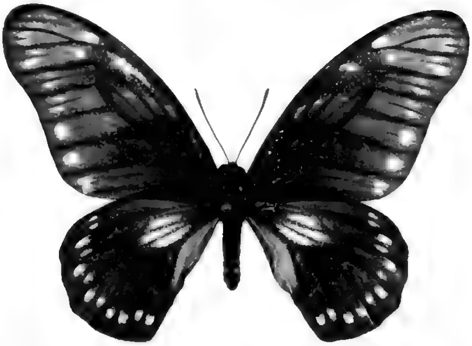
201

G. (A.) schubotzi PLT
SMNS Specimen

202

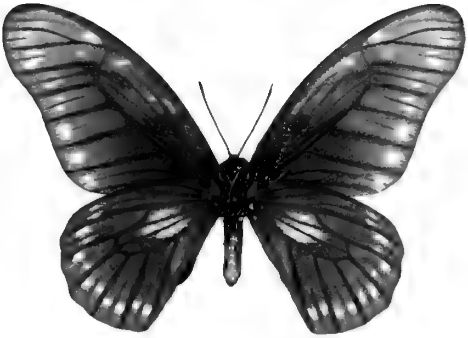
G. (A.) o. olbrechtsi HT
MRAC Specimen

Figs 197–202. Wing patterns of *Graphium* (*Arisbe*). Upperside of left wing and body to left; underside of left wing to right. Approx. 80% life size. Scale ▬ 1 cm.



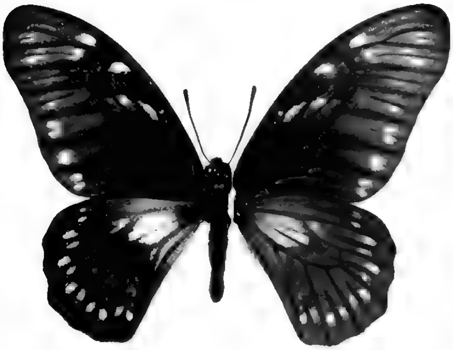
203

G. (*A.*) *abri* HT ups
ABRI Specimen. Actual size.



204

G. (*A.*) *abri* HT uns
ABRI Specimen. Actual size.



205

G. (*A.*) *abri* PT ups
ABRI Specimen. Actual size.

206

G. (*A.*) *a. almansor* LT
MNHU Specimen. Actual size.

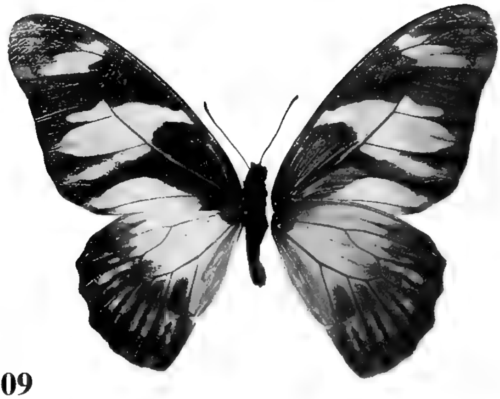
207

G. (*A.*) *auriger* LT
BMNH Spec.Reg. 141675

208

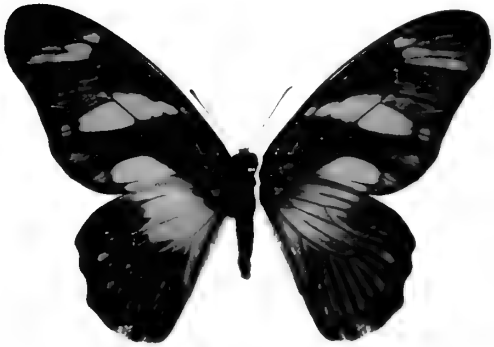
G. (*A.*) *f. fulleri*
BMNH Spec.Reg.138857

Figs 203–208. Wing patterns of *Graphium* (*Arisbe*). Upperside of left wing and body to left; underside of left wing to right. *G. abri* and *G. almansor* approx. life size: scale ▬ 1cm; *G. auriger* and *G. fulleri* approx. 80% life size. Scale ▬ 1 cm.



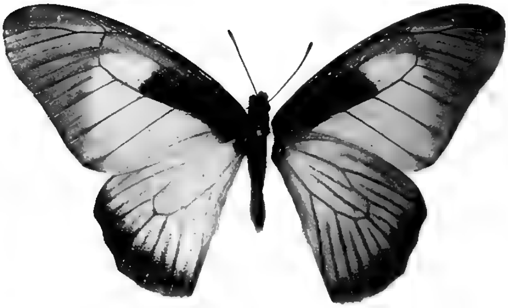
209

G. (A.) poggianus HT
MNHU Specimen



210

G. (A.) kigoma HT
BMNH Spec.Reg.
149196



211

G. (A.) h. hachei LT
MNHU Specimen

212

G. (A.) aurivilliusi LT
MRAC Specimen

213

G. (A.) u. uclaegon
BMNH Spec.Reg. 143181

214

G. (A.) simoni HT
IRSN Specimen

Figs 209–214. Wing patterns of *Graphium* (*Arisbe*). Upperside of left wing and body to left; underside of left wing to right. Approx. 80% life size. Scale ▬ 1 cm.

215

G. (*A.*) *evombar viossati* PT
ABRI Specimen

216

G. (*A.*) *illyris flavisparsus*
ABRI Specimen

217

G. (*A.*) *i. girardeaui*
BMNH Spec.Reg.
143422

218

G. (*A.*) *i. hamatus* HT
BMNH Spec.Reg.
143403

219

G. (*A.*) *porthaon mackiei*
BMNH Spec.Reg. 141573

220

G. (*A.*) *angolanus baronis*
HT
MNHN Specimen

221

G. (*A.*) *leonidas pelopidas* HT
BMNH Spec.Reg. 138398

222

G. (*A.*) *l. santamarthae*
HT
BMNH Spec.Reg. 138400

223

G. (*A.*) *l. thomasius* HT uns
MNHN Specimen

224

G. (*A.*) *cyrnus baronis* HT
MNHU Specimen

225

G. (*A.*) *latreillianus theorini*
HT
BMNH Spec.Reg. 141286

226

G. (*A.*) *philonoe whalleyi*
HT
BMNH Spec.Reg. 138565

Figs 215–226. Wing patterns of *Graphium* (*Arisbe*) subspecies. Unless stated, the right upperside is shown. Approx. 80% life size. Scale ▬ 1 cm.


227

G. (*A.*) *olbrechtsi tongoni* HT
MRAC Specimen


228

G. (*A.*) *almansor birbiri* HT
MNHN Specimen


229

G. (*A.*) *a. carchedonius* LT
MNHU Specimen


230

G. (*A.*) *a. escherichi*
BMNH Spec.Reg.
138827


231

G. (*A.*) *a. uganda* LT
BMNH Spec.Reg. 141573


232

G. (*A.*) *fulleri boulleti* HT
MNHN Specimen


233

G. (*A.*) *f. rileyi* HT
BMNH Spec.Reg. 143285


234

G. (*A.*) *f. ucalegonides*
BMNH Spec.Reg. 143324


235

G. (*A.*) *hachei moebii* HT
MNHU Specimen


236

G. (*A.*) *ucalegon fontainei*
HT
MRAC Specimen


237

G. (*A.*) *u. schoutedeni* HT
MRAC Specimen


238

G. (*A.*) *morania* aberration
OXUM Specimen

Figs 227–238. Wing patterns of *Graphium* (*Arisbe*) subspecies and one aberration. in each case, the right upperside is shown. Approx. 80% life size. Scale — 1 cm.

239

G. (*A.*) *antheus*
ab. *utuba*
BMNH Spec.Reg. 136785

240

G. (*A.*) *antheus*
ab. *mercutius* LT
BMNH Spec.Reg. 136384

241

G. (*A.*) *antheus*
ab. *evombaroides*
BMNH Spec.Reg.
141018

242

G. (*A.*) *gudenusi*
aberration
BMNH Spec.Reg. 220027

243

G. (*A.*) *policenes* ab.
coussementi "HT"
MRAC Specimen

244

G. (*A.*) *policenes*
aberration
ABRI Specimen

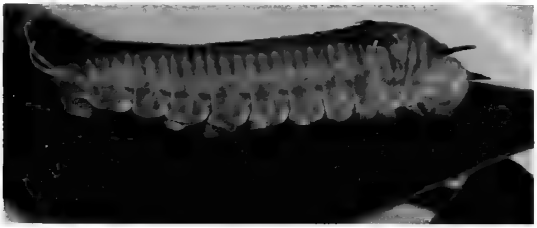
245

G. (*A.*) *leonidas*
f. *brasidas* LT
BMNH Spec.Reg. 138110

246

G. (*A.*) *leonidas*
ab. *melusina* "HT"
BMNH Spec.Reg. 138404

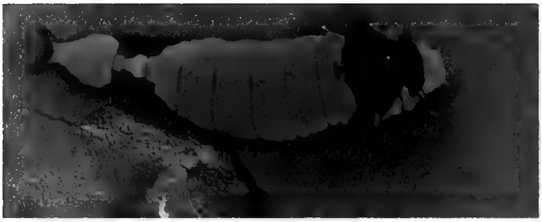
247 *G.* (*A.*) *kirbyi* final larval instar.
Dorsal view.



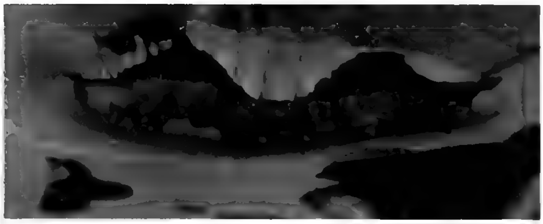
248 *G.* (*A.*) *kirbyi* final larval instar.
Lateral view.

Figs 239–246. Wing patterns of *Graphium* (*Arisbe*) aberrations. In each case, the right upperside is shown. Approx. 80% life size. Scale ▬ 1 cm.

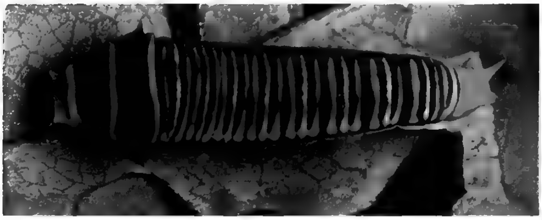
Figs 247, 248. Colin Congdon's photographs of *Graphium* (*Arisbe*) early stages. Not to scale.



249 *G.* (*A.*) *colonna* final larval instar.
Dorsal view.

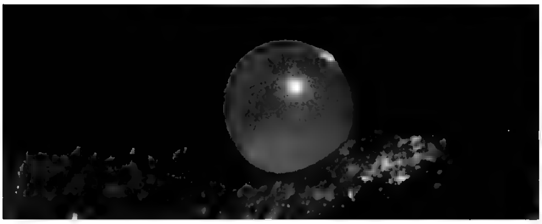


250 *G.* (*A.*) *colonna* final larval instar.
Lateral view.



251 *G.* (*A.*) *policenes* final larval instar.
Dorsal view.

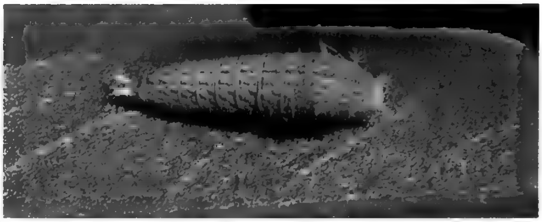
252 *G.* (*A.*) *policenes* final larval instar.
Lateral view.



253 Egg of butterfly tentatively identified as
G. (*A.*) *porthaon.*

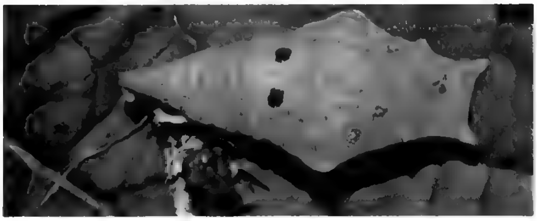
254 Final larval instar of butterfly tentatively
identified as *G.* (*A.*) *porthaon.*

255 *G.* (*A.*) *angolanus* final larval instar.
Lateral view.

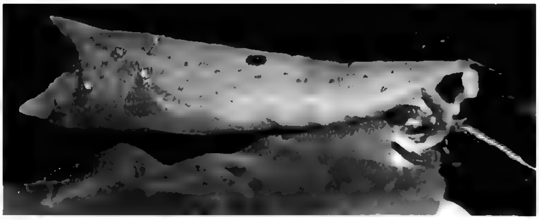


256 *G.* (*A.*) *leonidas* probable third larval instar.
Dorsal view.

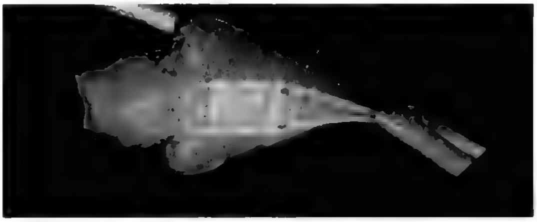
Figs 249–256. Early stages of *Graphium* (*Arisbe*). Larvae and egg photographed by Colin Congdon. Not to scale.



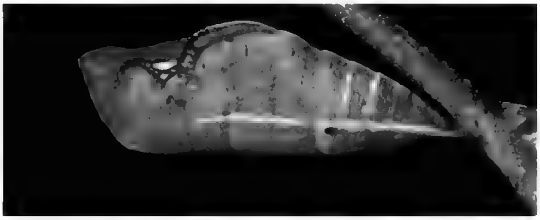
257 *G.* (*A.*) *kirbyi* pupa.
Dorsal view.



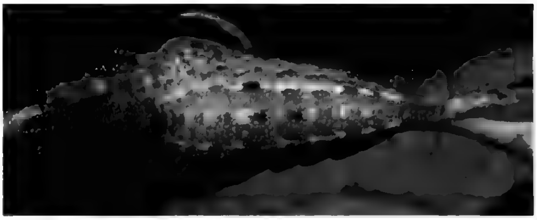
258 *G.* (*A.*) *kirbyi* pupa.
Lateral view.



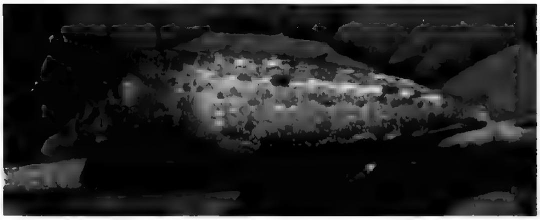
259 *G.* (*A.*) *colonna* pupa.
Dorsal view.



260 *G.* (*A.*) *colonna* pupa.
Lateral view.



261 *G.* (*A.*) *policenes* pupa.
Dorsal view.



262 *G.* (*A.*) *policenes* pupa.
Lateral view.

263 *G.* (*A.*) *angolanus* pupa.
Dorsal view.

264 *G.* (*A.*) *philonoe* pupa.
Lateral view.

Figs 257–264. Early stages of *Graphium* (*Arisbe*). Pupae photographed by Colin Congdon. Not to scale.

APPENDICES

Appendix 1. Amendments to Ackery, Smith & Vane-Wright (1995)

p. 160 *G. (A.) adamastor =carchedonius* Karsch. Here treated as a valid subspecies of *G. almansor*.

p. 160 *G. (A.) adamastor =guineensis* Dufrane and *houzeaui* Dufrane. Here treated as names infrasubspecific to *G. almansor carchedonius* Karsch.

p. 160 *G. (A.) angolanus angolanus =hypochroa* Boullet & Le Cerf. An incorrect subsequent spelling. Correctly *hypochra* Boullet & Le Cerf.

p. 161 *G. (A.) angolanus calabar* Hancock. Here regarded as a junior subjective synonym of *G. (A.) angolanus baronis* Ungemach.

p. 161 *G. (A.) angolanus calabar =pylades* Fabricius. Here treated as a synonym of *G. (A.) angolanus baronis* Ungemach.

p. 161 *G. (A.) angolanus calabar =houzeaui* Dufrane. Here treated as infrasubspecific to *G. (A.) angolanus baronis* Ungemach.

p. 161 *G. (A.) auriger eyeni* Berger. Here regarded as a junior subjective synonym of *G. (A.) schubotzi*.

p. 161 *G. (A.) auriger olbrechtsi* Berger. Here treated as a valid species.

p. 162 *G. (A.) auriger schoubotzi* Schultze. Here treated as a valid species. Also an incorrect subsequent spelling. Correctly *G. (A.) schubotzi* Schultze. Also 'Angu, Ubangi-Distrikt' correctly: 'Angu (Uelle-Distrikt)'.

p. 162 *G. (A.) auriger schoubotzi =odin* Strand. Here treated as a synonym of *G. (A.) schubotzi* Schultze.

p. 162 *G. (A.) auriger tongoni* Berger. Here treated as a valid subspecies of *G. (A.) olbrechtsi* Berger.

p. 162 *G. (A.) cyrnus nuscyrus* Suffert. Here treated as a valid subspecies.

p. 162 *G. (A.) fulleri =boulleti* Le Cerf. Here treated as a valid subspecies.

p. 162 *G. (A.) fulleri =foersterius* Strand; *=sanganus* Strand; *=sanganoides* Strand; *=stetteni* Strand; *=weberi* Holland. Here all regarded as junior subjective synonyms of *G. (A.) fulleri boulleti* Le Cerf.

p. 162 *G. (A.) fulleri =stetteni* Strand, 1913g: 140. Pagination incorrect. Correctly 42.

p. 162 *G. (A.) fulleri =transiens* Le Cerf; *=divismacula* Strand; *=gabrieli* Berger. Here all treated as infrasubspecific to *G. (A.) fulleri boulleti* Le Cerf.

p. 163 *G. (A.) illyris illyris =flavisparsus* Fruhstorfer. Here treated as a valid subspecies.

p. 163 *G. (A.) illyris illyris =hamatus* Joicey & Talbot. Here treated as a valid subspecies.

p. 163 *G. (A.) illyris illyris =addenda* Dufrane. Here treated as infrasubspecific to *G. (A.) illyris girardeaui* Guilbot & Plantrou.

p. 163 *G. (A.) latreillianus theorini =potamonianus* Ehrmann. Here treated as infrasubspecific to *G. (A.) latreillianus latreillianus* Godart.

p. 163 *G. (A.) latreillianus theorini =xerophila* Berger. Original combination incorrect. Correctly (as f. of *Graphium latreillianus theorini*).

p. 165 *G. (A.) poggianus poggianus* Honrath. Here treated as a monotypic species.

p. 165 *G. (A.) poggianus kigoma* Carcasson. Here treated as a valid species.

p. 165 *G. (A.) poggianus wranghami* Kielland. Originally described as a subspecies of *G. almansor* Honrath. Here treated as a junior subjective synonym of *G. (A.) kigoma* Carcasson.

p. 165 *G. (A.) policenes biokoensis* Gauthier. Here treated as a valid species.

p. 165 *G. (A.) policenoides policenoides* Holland. Here treated as a monotypic species.

p. 165 *G. (A.) policenoides policenoides =intermedia* Birket-Smith. Here treated as infrasubspecific to *G. (A.) biokoensis* Gauthier.

p. 165 *G. (A.) policenoides liponesco* Suffert. Here treated as a valid species.

p. 165 *G. (A.) policenoides liponesco =boolae* Strand. Here treated as a junior subjective synonym of *G. (A.) liponesco* Suffert.

Appendix 2. Data matrix employed in the analyses

For explanation of the characters and their interpretation, see text.

	1 5 10 15 20 25 30 35 40 45 50 55 60
Pr. leosthenes	10000000000011001?110?1100110-----0----0------0----000?00000-11
I. podalirius	00110000000011001111011?0011?-----?----0------0----0000-1001-?1
L. meges	00111110000010--0000000000?10-----0----0------0----000010110-11
Paz. mandarinus	00111001111011111010000000?11-----0----11-----0----000?0?001-00
Gr. sarpedon	00111001111100--1110111100001-----1----11-----11-0-000?10001-00
Gr. bathycles	00111001111100--1000111100000-----0----10-----0----000111101-11
Pat. aristeus	0011100111011110111110?100110-----0----11-----11-1-000100000-10
Pat. nomius	00111001110111101111111100110-----0----10-----11-1-000100000-0?
Par. macareus	00111001110100--0000000000000-----0----10-----11-1-000100000-10
antheus	001110011111111011101000000010----1101010-----0----101100001000
evombar	001110011111111011101000000110----1101010-----0----101100001000
illyris	00111001111110--11111011000011000111100101110111718000111101511
kirbyi	001110011111111111111001001111000111110111011111018000110001211
gudenusi	0011100111111111111011010000110001101--11101011181900?111101211
colonna	0011100111111111111110010000110001101--111000011018001111101311
polistratus	0011100111111111111111110000110001101--111000011610000101101111
junodi	0011100111111111111110110001110000101--111001011610000100001111
policenes	00111001111111111111101100001100111*1*0111011111514001111001211
liponesco	0?1110011111111111111011000011001111110111011111514001?????????
biokoensis	0?1110011111111111111011000011001111110111011111514001?????????
policenoides	0?1110011111111111111011000011001111110111011111514001?????????
porthaon	001110011111111111110011001111100011100110010011919011111101211
endochus	00111001111100--10000111001111010111110110110011315011101110-11
angolanus	00111001111100--10001001001111010111110110010011315011101110-11
schaffgotschi	00111001111100--1000?0010011110100101--110010011315011111110-11
morania	00111001111100--100001110011110101101--110010011315010111110-11
taboranus	00111001111100--100010010011110100101--110010011315011101110-11
ridleyanus	00111001111000--?-------0011110101101--110110011315011101110-11
tynderaeus	00111001111100--?-------0100110101101--110110011412010110001411
latreillianus	00111001111100--?-------0100110101101--110110111411010110001411
cyrnus	00111001111100--00000000100011010111100110110011216010110001511
levassori	00111001111100--00000000100111010111100110110011216010110001211
leonidas	00111001111100--00000000100011010111110110110011216010111101211
philonoe	01111001111100--000000001011111000101--110010011413010111101411
hachei	0?111001111100--00000000100111100011101110110011117010?????????
auriger	01111001111100--000000001?0011100011101110110011117010110001511
simoni	0?111001111100--00000000110111100011100110110011117010?????????
ucalegon	01111001111100--00000000110011100011100110110011117010110001511
fulleri	01111001111100--00000000110011100111100110110011117010110001511
olbrechtsi	0?111001111100--00000000100011100011100110110011117010?????????
schubotzi	0?111001111100--00000000110011100011100110110011117010?????????
aurivilliusi	0?111001111100--00000000100011100011100110110011117010?????????
poggianus	0?111001111100--0000000010?111100011100110110011117010?????????
kigoma	01111001111100--00000000110011100011100110110011117010110001511
agamedes	01111001111100--00000000100011100111100110110011117010110001511
abri	0?111001111100--000000001100111000111001101100111?010?????????
almansor	01111001111100--00000000101111100011011110110011117010110001511
adamastor	01111001111100--00000000100011100011100110110011117010111101511

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Synonyms and invalid names are in *italics*. Principal references are in **bold**.

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