

Skipper butterflies (Hesperioidae) and bar codes: how old are they, and how do the Aussie species fit in to the scheme of things? (Part one: the sub-family Trapezitinae and their ilk) – Andrew Atkins

Introduction

Formal, Latinized nomenclature (taxonomic description) of life forms has always been about unambiguous language communication. By expressing in any way possible, the similarity or difference between one or another species, or groups of organisms in a logical and comprehensive way, a formal order and ranking can be achieved. This systematic format can reveal the species' relationship (that is their connectivity) in structure, biology and evolution. But grouping and naming the biota may not always be entirely possible when there is a lack of fully researched information, or the number of species is large. Evolution can be a complex and mysterious three-dimensional (quantum?) process where the pathway of variation is marked by a multi-directional system of change and adaption.

Much of the world's biota is yet to be discovered, let alone formally named. Each species is a product of evolution – the change that the organism has undergone through time and as a result of geological or climatic events that occurred in the past, and of course, its in-born genetic diversity. Each taxon has its own history to be written: and somebody needs to do it.

Skipper butterflies (Hesperiidae) are a wonderful example of subtle but complex evolutionary change. Initially there seems to be a stasis of form and function throughout the 4-5000 or so described species (nearly a quarter of all butterflies) found throughout the world (except New Zealand or the polar regions). Many species seem (dare I say it!) a bit dull and unobtrusive, very quick, and devilishly hard to see. The 'father' of skipper systematics, W.H. Evans, said it all "*They are difficult to see and catch: difficult to kill and set: difficult to identify and classify. Few are of economic interest and most are small and drab. Nevertheless their serious study presents an endless number of baffling, though fascinating, problems to anyone gifted – or cursed – with an enquiring type of mind and with plenty of the patience and time needed for the purpose*". Few 'cursed' researchers would disagree with this observation, though there are some remarkably beautiful species to study, especially in the tropics. Many people who can recognise them (they are mostly hairy and fat-bodied and have hooked antennae) see skippers as moths, and they are not far from the truth.

If you have an enquiring mind and want to know all about these creatures, there is a ton of information yet to be uncovered about skippers, that is, their morphology, their distribution and origin, and how the adult and juvenile skippers interact with their habitats (life history): they are a somewhat 'under-done' group of butterflies! Just



where did they come from and how are all the various groups (genera and sub-families etc.) interconnected across the world?

Present systematic alignment describes the order Papilionidea (which includes all butterflies that contains seven families, one of which includes skipper butterflies (Hesperiidae)), which in turn is divided into seven subfamilies. In this study I deal mostly with the genera of the Australasian subfamily Trapezitinae and compare them, using the time-honored (!) morphological method, with relevant genera in the subfamilies Heteropterinae and Hesperinae which have a telltale distribution around the world.

Methodology

In this article (Part 1) I have focused my research on my favorite Australian group, the trapezitines (I call them 'Southern Deltas'), and include colour illustrations of link-groups of genera, and some black and white diagrams that include a family tree as I see it. This survey is mostly on comparative local and some continental genera (Appendix A). The methodology is traditional morphological (structural) components, utilizing adult and juvenile material as a comparative model to recent advanced molecular studies based in America.

A previous preliminary discussion paper on skippers, published as notes/summary of a talk given for the Entomological Society of Queensland in 2005 (*Atkins, *News Bulletin* 33[2]: 24-34), provided a generalised position on the phylogeny of these butterflies. This was in anticipation of a comprehensive combined molecular (DNA sequencing) and morphological study of the world's genera by Andy Warren *et al.*, published in 2008 and 2009.

The world of skippers

Essentially skippers (family Hesperiidae) can be sorted into two natural groups; the Pyrginae with larvae that feed on dicotyledon plants, and Hesperinae with larvae that feed on monocotyledon plants. The adults of the first group usually settle with wings spread apart, the second group mostly settle with wings upright or hind wings flatter like paper darts. For those readers who are unfamiliar with skippers, you always need to get close and look for those bent antennal clubs. You will often find them nectaring on flowers in sunny patches of your garden. These will belong to four subfamilies, two of which occur further afield into the northern hemisphere.

The Trapezitinae are something special, because it is the only subfamily of skippers restricted to Australasia. My research, lasting many years, indicates that it is a reasonably ancestral group of butterflies with possible links to South America via Gondwana. The New Guinea trapezitine genera are of special interest in this regard.

The Trapezitinae: a history

Waterhouse and Lyell (1932) established the subfamily Trapezitinae, characterized by "Forewings held erect when resting: often with a discal sexmark (dark, raised scales) above in male... Hindwing with vein 5 (M_2) absent... forewing with vein 5 (M_2) straight at base". The descriptions included 10 Australian genera and 51 species.



Plate 1



PLATE 1 (all Trapezitinae, except where marked (HESP) = Hesperinae, or (HET) = Heteropterinae.

(1) *Trapezites phigalia*, male upperside (VIC); (2) *T. phigalia*, female upperside (VIC); (3) *T. genevieveae*, male upperside (NSW); (4) *T. genevieveae* female upperside (NSW); (5) *Malaza carmides*, female upperside (Madagascar) (HESP?); (6) *T. phigalia*, female underside (VIC); (7) *T. waterhousei*, female underside (WA); (8) *T. genevieveae*, male underside (NSW); (9) *T. genevieveae*, female underside (NSW); (10) *Malaza carmides*, female underside (Madagascar) (HESP?); (11) *Prada rothschildi*, male upperside (PNG); (12) *P. rothschildi* female upperside (PNG); (13) *Rachelia extrusa*, male upperside (PNG); (14) *R. extrusa*, female upperside (PNG); (15) *Tiacellia tiacellia*, male upperside (PNG); (16) *Prada rothschildi*, male underside (PNG); (17) *P. rothschildi* female underside (PNG); (18) *Rachelia extrusa*, male underside (PNG); (19) *R. extrusa*, female underside (PNG); (20) *Tiacellia tiacellia*, male underside (PNG); (21) *Prada papua*, male upperside (PNG); (22) *P. papua*, female upperside (PNG); (23) *Heteropterus morpheus*, male underside (France) (HET); (24) *Pithauria marsena*, male upperside (Malasia) (HESP); (25) *Telicota ancilla*, male upperside (NSW); (26) *Prada papua*, male underside (PNG); (27) *P. papua*, female underside (PNG); (28) *Herimosa albovenata*, male underside (SA); (29) *Hesperilla mastersi*, female underside (NSW); (30) *Signeta peron**, male upperside (QLD)

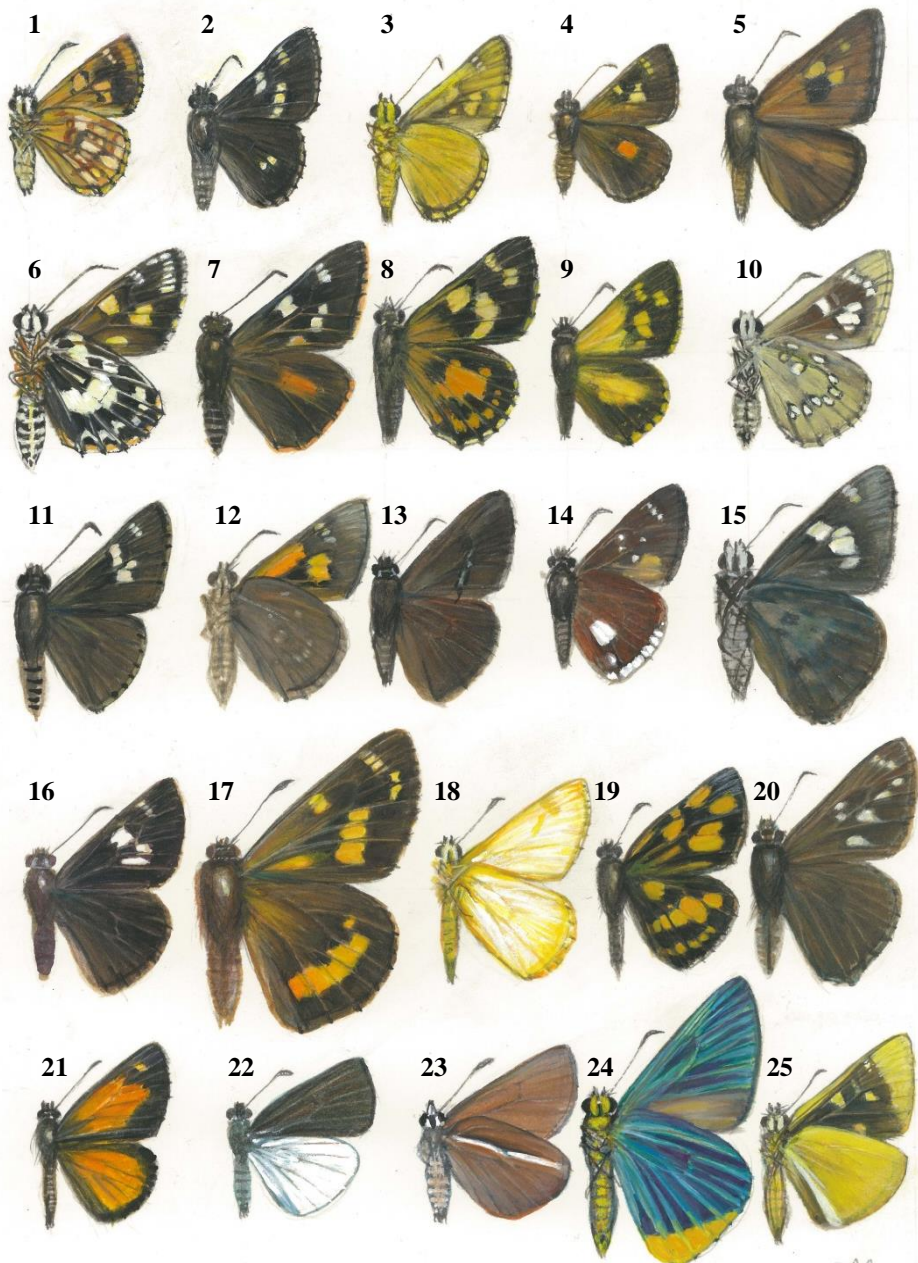
These were divided into two groups; **A.** male without sex brand – *Trapezites* Hübner, (1819), *Anisynta* Lower, 1911, *Oreisplanus* Waterhouse & Lyell, 1914 and *Mesodina* Meyrick, 1901; **B.** male with sex-brand (on forewing) – *Hesperilla* Hewitson, 1868, *Toxidina* Mabille, 1891, *Neohesperilla* Waterhouse & Lyell, 1914, *Motasingha* Watson, 1893, *Dispar* Waterhouse & Lyell, 1914 and *Signeta* Waterhouse & Lyell, 1914. Further modifications were made to this arrangement by the inclusion of two additional genera (both without sex brands), *Pasma* Waterhouse, 1932 and *Croitana* Waterhouse, 1932 in subsequent research. I also added the genera *Antipodia* (1984), *Proeidosa* (1973) and *Herimosa* (1994) to this subfamily. The discovery of the life history of several species also played an important role in the re-defining of some genera groups, which included the recognition of three distinctive larval forms within nine genera studied (Waterhouse, 1927). These genera groups are defined mostly by wing-vein alignment and male wing sexbrands, labial palpi, antennal clubs, leg spines and juvenile (egg, larva, pupa) differences. The majority of their larvae feed on grasses or sedges (like most of the linked genera included in this article), but two important genera feed on the Australian endemic *Lomandra* or *Patersonia* (Liliales).

Phylogeny

W. H. Evans in his important analysis of the world's Hesperidae held in the British Museum (Natural History) (1937-1952) had accepted the arrangement of the subfamily Trapezitinae “adopted by Australian authors”, probably referring particularly to Waterhouse (Evans, 1949), but in this work he also recognised a possible taxonomic relationship (hind-wing venation) of trapezitines to the New Guinea genus *Prada* Evans, 1949 (p. 31). This genus, together with the monotypic *Tiacellia* (described by Evans on p. 37), was placed within the *Prada* subgroup of the Platingia Group J. (1949, p.2). Evans in this work characterized the peculiar cell end of the hind-wing of the Australian group “... lower angle is upturned, the end cell is directed to the dorsum, instead of to the tornus or termen as usual and the medium vein has a branch to the origin of vein 4 (M_3), instead of to well above that point.



Plate 2



17 AA



PLATE 2 (all Trapezitinae, except where marked (HESP) = Hesperiiinae, or (HET) = Heteropterinae.

(1) *Anisynta monticolae*, female underside (VIC); (2) *Pasma tasmanica* male upperside (NSW); (3) *Neohesperilla xanthomera*, male underside (QLD); (4) *Dispar compacta*, female upperside (VIC); (5) *Signeta flammeata*, male upperside (NSW) (large specimen); (6) *Oreisplanus perornata*, female underside (VIC); (7) *Motasingha trimaculata*, female upperside (NSW); (8) *Antipodia chaostola*, female upperside (VIC); (9) *Croitana croites*, male upperside (WA); (10) *Proeidosa polysema*, female underside (QLD); (11) *Mesodina hayi*, male upperside (WA); (12) *M. aeluropis*, female underside (NSW); (13) *Toxidia melania*, male upperside (QLD); (14) *Felicena dirpha*, male underside (PNG); (15) *Hewitsoniella migonitis*, male upperside (PNG); (16) *Pedesta masuriensis*, male upperside (Himalayas) (HESP); (17) *Agathymus aryxna*, male upperside (USA) (HESP ‘Giant Skipper’); (18) *Argopteron aureipennis*, female underside (Nicaragua) (HET); (19) *Metisella midas*, male upperside (Kenya) (HET); (20) *Pelopidas agna*, female upperside (QLD) (HESP); (21) *Fulda corolla*, male upperside (Madagascar) (HET); (22) *Dalla semitargentea*, male upperside (Peru) (HET); (23) *Tsitana tulbagha*, female underside (South Africa) (HET); (24) *Pirdana hyela* female underside (Borneo) (HESP); (25) *Butleria fruticolens* female underside (Chile) (HET)

Vein 5 (M_2) is always well marked, at the termen central between veins 4 (M_3) and 6 (M_1), nearer to vein 6 (M_1) at its origin, where it is often decurved” (p. 19).

It is clear that both Waterhouse and Evans were somewhat at variance (or even contradictory) in the identification and morphological parameters of the Trapezitinae, although they agreed on its uniqueness. However, Parsons (1998) in his work with Papuan skippers doubted the validity of Trapezitinae, indicating the ‘diffuse’ nature of this subfamily with Hesperiiinae, illustrating variable states in the discocellulars (linking veinlets at the end of the cell) of the hind-wing in some New Guinea genera. Comparisons were made to *Toxidia inornatus* (Butler, 1883), *Rachelia extrusus* (C. Felder & R. Felder, (1867), *Tiacellia tiacellia* Evans, 1949, *Prada maria* Parsons, 1986, *Prada papua* (Evans, 1928) and *Prada rothschildi* (Evans, 1928).

The DNA (bar-coding) of skippers

In 2008 Andrew Warren *et al.* formulated a tentative systematic arrangement of the skipper butterflies based on the DNA of many (about 30%) of the genera found throughout the world. This momentous molecular study, which also included an updated review of morphological definition, confirmed the subfamily status of Hesperiiinae, Heteropterinae and Trapezitinae (the latter had received some ‘doubtful press’ in recent years!). The work included some species in several genera of the Australian subfamily. Since this work, a number of authors have contributed limited DNA studies on various other genera groups and families of butterflies circumscribed by the Papilionidae, Hedyliidae, and Hesperiiidae.

Warren has shown that aligning morphological data with that of molecular results can enhance the perceived phylogenetic arrangements of the Hesperiiidae, including a greater clarity in the placement and connectivity of genera groups. In the new phylogenetic arrangement, a more comprehensive hierarchic connectivity to continental faunas could be perceived. However the apparent evolutionary stasis and long evolutionary time frame achieved by skippers (a fifty million year old fossil



Plate 3

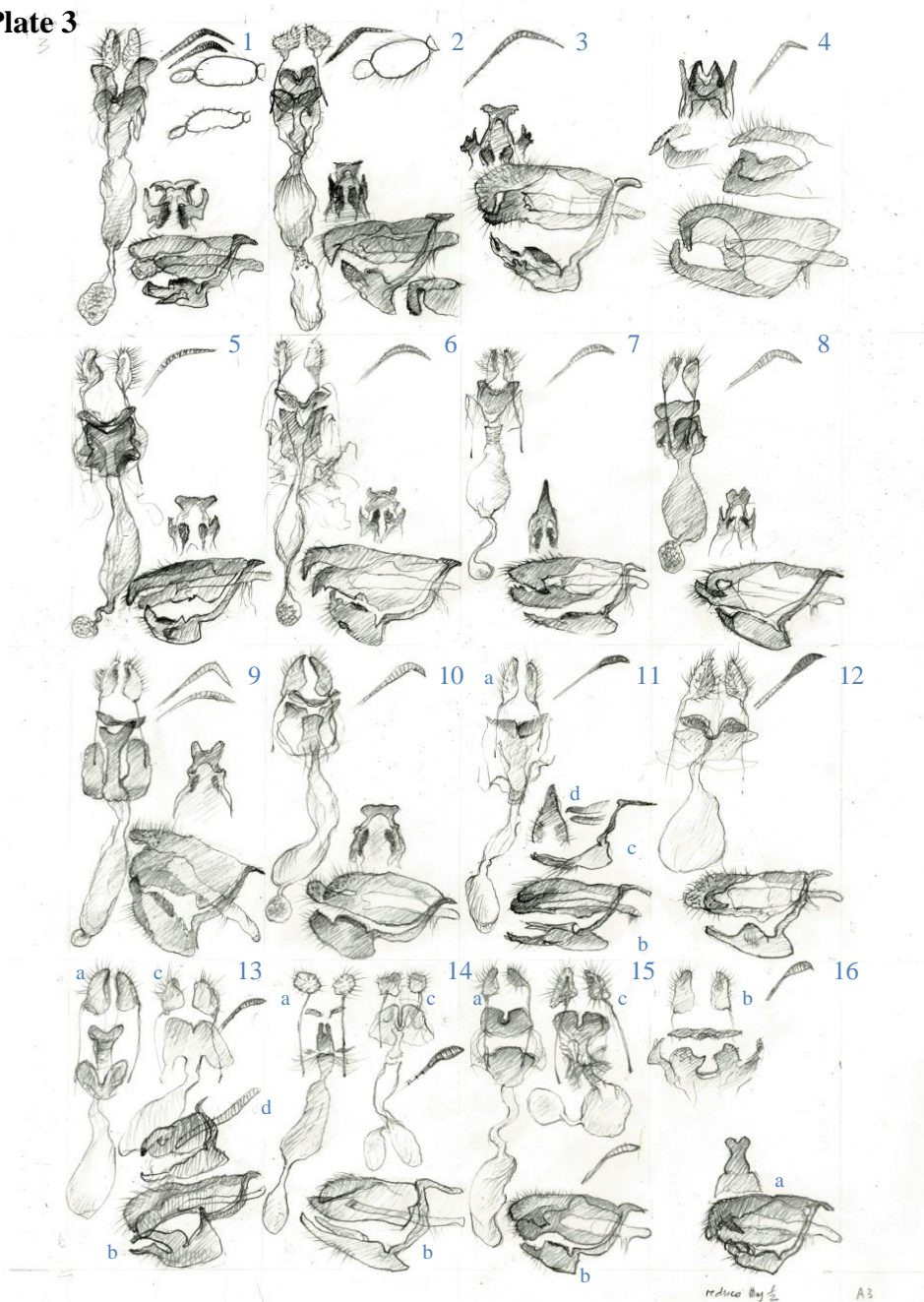


PLATE 3 (all Trapezitinae, except where marked (HESP) = Hesperinae, and (HET) = Heteropterinae. Anatomical features of skippers; mostly male and female genitalia (including uncus tip of male gnathos); also antennal club, and some labial palpi.

(1) *Trapezites symmomus* (Eungella, QLD) (also included smaller labial palpi and antennal club of *Trapezites sciron* from WA); (2) *Rachelia extrusa* (Cape York, QLD); (3) *Hewitsniella migonitis* (Sariba Is., PNG); (4) *Felicena dirpha* (right and left valvae tips, and below subspecies *F. d. nota*) (both PNG); (5) *Toxidia melania* (Nth. QLD); (6) *Signeta flammeata* (NSW); (7) *Dispar compacta* (VIC) (note narrow, pointed uncus-tip); (8) *Pasma tasmanica* (NSW); (9) *Neohesperilla crocea* (NT), uncus tip *N. xanthomera* (QLD); (10) *Anisynta sphenosema* (WA); (11) a. *Piruna pirus* (female) Nth Amer., b. *Dardarina aspila* (male), c. *Argopteron* sp. (male) (Chile) d. *Butleria soloi* (gnathos tip) (male) (Chile) (all HET); (12) *Tsitana tulbagha* (Sth. Africa) (HET); (13) a. *Fulda rhadama* (female), b. *F. coroller*, c. *Hovala amena* (female), d. *H. amena* (male) (all Madagascar and HET); (14) a. and b. *Metisella malgacha erina* c. *Hovala sacauus* (both Madagascar and HET); (15) a. and b. *Malaza carmides*, c. *Malaza fasturus* (female) (both Madagascar and HESP?); (16) a. *Agathymus aryxna* (male genit.) (Arizona, USA), b. *A. ricei* (USA) (both HESP)

skipper is reported, differing little from extant species), has provided little additional structural, distinguishing elements for comparative research. More fossils were needed!

Other Australian Groups

Euschemoninae, Coeliadinae, and the South American Eudaminae are the three basal subfamilies with morphologically constant structural characters that separate them from the other four subfamilies, or even from each other. In fact, at the subfamily level, each exhibits essentially a mosaic of collective character-sets and biological traits that differ in a quantitative arrangement rather than clear division. This includes genital morphology, which unfortunately shows variation and, enigmatically, a complexity that defies taxonomic solution. Nevertheless the adult and juvenile members of species in each subfamily clearly behave and ‘look’ reasonably different from each other. There are also some consistent structural features of each ancestral genera group (be they seemingly trivial) that can define an evolutionary pathway. From a biological perspective, the larvae of Coeliadinae and Eudaminae mostly feed on Legumes. The larva food plant of Euschemoninae is exclusively Monimiaceae. Clearly these three subfamilies show strong continental connectivity. Further detailed assessment of these dicot-feeding groups will be given in a future article.

Morphological connections – the missing links

The hierarchy of three subfamilies of mono-feeding skippers reached by Warren (2008) (Trapezitinae, Heteropterinae and Hesperinae) gave evidence of an important pathway to their evolution (Appendix B). It appears likely that these skippers split from the branch of dicot-feeding skippers somewhere near the pyginiid genera groups (*Pyrgus*, *Spialia*, *Gomalia* etc. and perhaps the Australian endemic *Nycterus*). The stout, robust genus *Trapezites* carried some morphological traits of these genera.



Plate 4

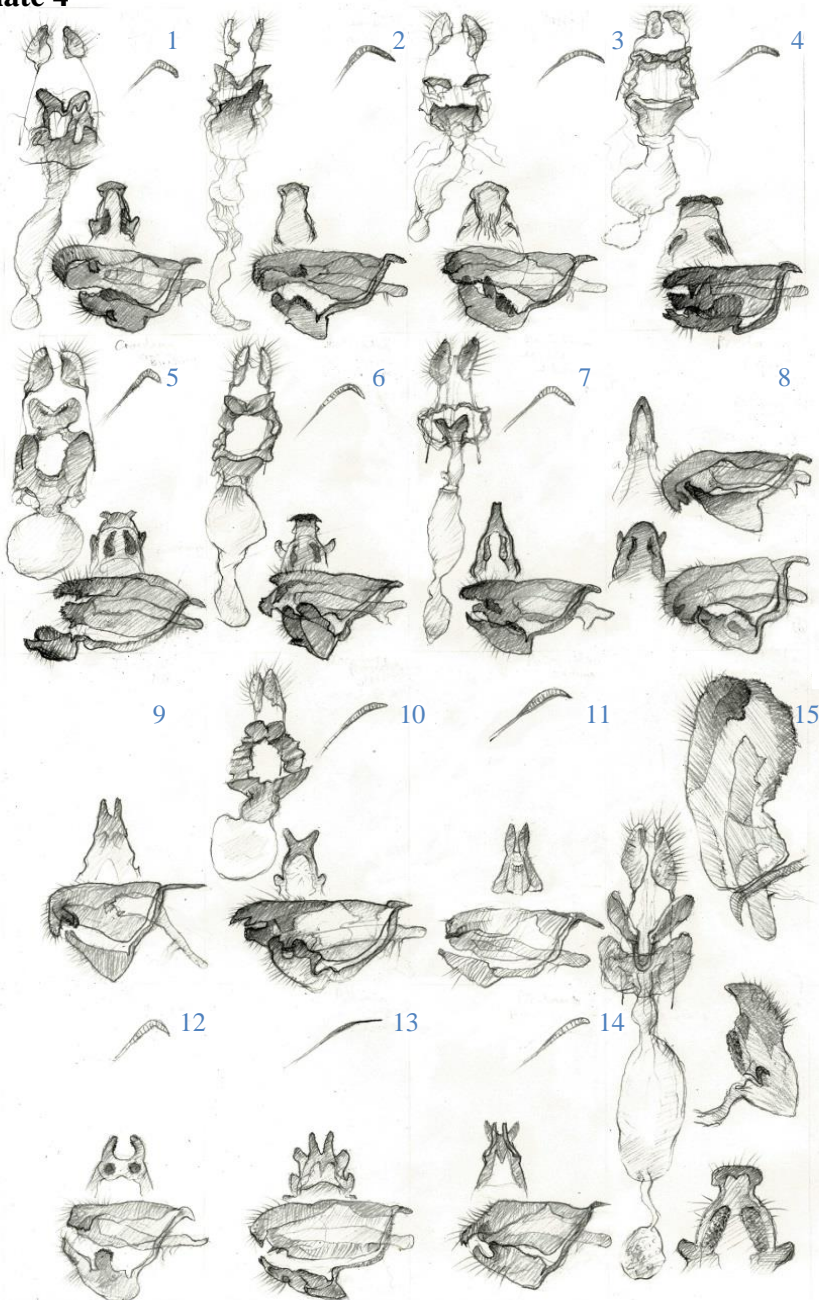


PLATE 4 (all Trapezitinae, except where marked (HESP) = Hesperinae, and (HET) = Heteropterinae. Anatomical features of skippers, mostly male and female genitalia (including detail of uncus); also antennal club.

(1) *Motasingha trimaculata* (NSW); (2) *Hesperilla mastersi* (VIC); (3) *Oreisplanus perornata* (VIC); (4) *Herimosa albovenata* (NSW); (5) *Croitana croites* (WA); (6) *Antipodia chaostola* (VIC); (7) *Mesodina aeluropis* (NSW); (8) a. *Prada papua*, b. *P. rothschildi* (both PNG); (9) *Tiacellia tiacellia* male genit. and uncus tip (PNG); (10) *Proeidosia polysema* (QLD); (11) *Pelopidas agna* (QLD) (HESP); (12) *Pedesta* sp. (Nepal) (HESP); (13) *Pithauria* sp. (Malaysia) (HESP); (14) *Pirdana hyela* (Borneo) (HESP); (15) *Trapezites atkinsi* (WA)

The morphological study (black and white plates 3, 4 and 5) reveals a tendency for species in the genera of trapezitines to become narrower and less robust in structure (adults, genitalia and juveniles). This may be as a result of a move to sedge and grass feeding (narrow leaf-shelters to hide in). This same structural change is seen in other continental groups of hesperiines of all three subfamilies. However their connectivity can clearly be seen in the male and female genitalia (within these subfamilies), which developed elongated, over-lapping valvae (ampulla and harpe)(eg *Anisynta*, *Butleria* and *Tsitana*), and the corpus bursae with accessory pouches (appendix) (seen in most trapezitines and *Butleria* and *Metisella*). The eggs of species in the three subfamilies have gone from heavily ribbed to fine, multiple faint ribs, and then finely to an almost smooth surface. There is also a general trend for the antennal clubs to be blunt and short and have broader, more rounded wings, especially genera groups that fly low in exposed, open habitats of cooler climates. Generally, species flying in rainforests have retained (speed-adapted) narrow and long fore-wings and have more startling wing patterns and colours (although there are many exceptions to this rule). Overall, along the family tree, there has been a general evolution of structures from complex to simple, accompanied in some genera by a loss or movement of wing-veins (especially illustrated in the black and white plates).

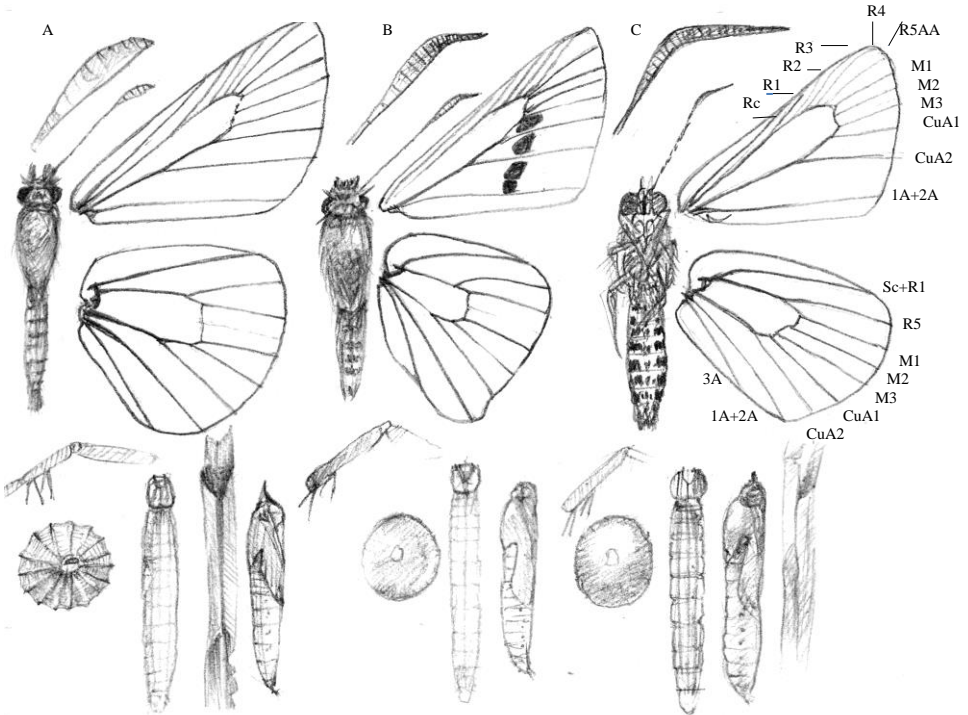
Conclusion

Compared to other families of Lepidoptera, Hesperidae (skippers) are poorly known, and yet they comprise more than a quarter (between 3,500 and 4,000 species) of all described butterflies. Following comparison with molecular research, a preliminary overview of the higher systematics of skippers is given (Appendix B). A preliminary ranking as a possible tribal relationship of the Trapezitinae is shown in Appendix C. A few additional structural and biological defining characters are included.

Although all Australian, African and South American genera studied yielded a scattering of species with very similar structural features (note the similarities of wing venation male and female genitalia, antennal club shape etc.), but these were not shared by all genera. Some structures were almost randomly shared, as if the genes operating these structures were held latent and expressed or re-expressed well after the genera had evolved from their original (ancestral) genera group forms.



Half-Plate 5a



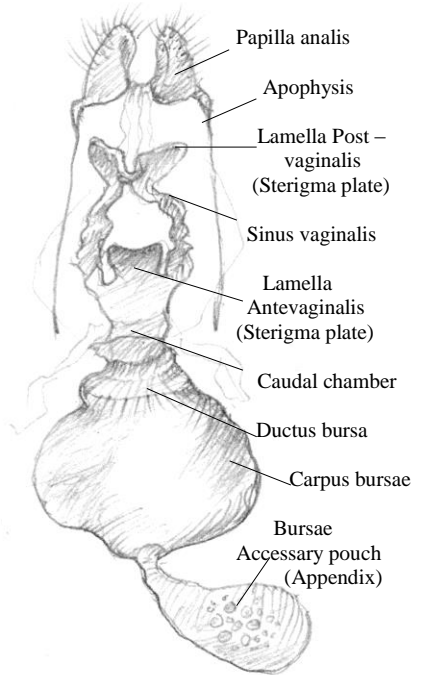
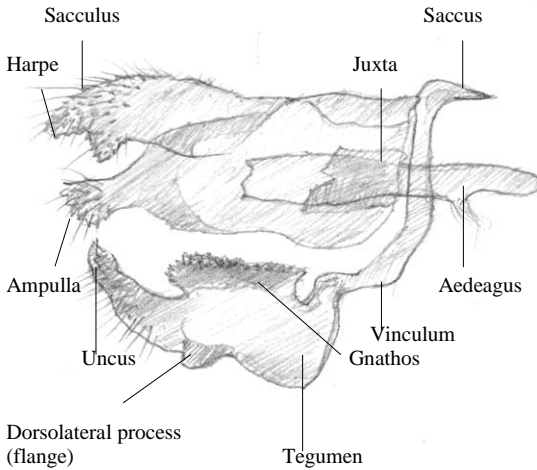
HALF-PLATE 5a. Wing venation, antennal club, hind leg spurs, egg, larva, larval shelter and pupa of male monocotyledon skippers (note downward sloping of veins M2, M3, CuA1 and CuA2 at cell in forewing and faint M2 of hindwing of fig. B which are noticeable variable trends in many species of hesperiines throughout the world). The three species illustrated have larva that all feed on grasses but have quite different eggs.

- A. *Butleria flavomaculata*, HETER. (Chile)
- B. *Telicota ancilla*, HESP. (Newcastle, NSW)
- C. *Oreisplanus munionga* TRAP. (Mt. Hotham, NSW)

The relationship of the Trapezitinae with Heteropterinae appears quite strong (molecular and morphological), all containing various ‘quantities’ of characters. These features include, bar-codes, long and slim build, blunt antennal clubs, complete venation and ribbed eggs, and in female genitalia, accessory pouches. The males have distinctive, overlapping valvae tips and elongate uncus. In at least one genus, several species had strongly ribbed eggs (especially in Trapezitinae). Most species in the genera of the Hesperinae have only fine ribs or more often smooth eggs. This latter character is important in the phylogenetic study of the monocot-feeding genera.



Half-Plate 5b



HALF-PLATE 5b Male and female genitalia of Trapezitinae (generalized).

A few genera of African Hesperinae feed on dicotyledons and also appear close to Trapezitinae (especially in juveniles) but I have not closely studied those groups. Little is known about the biology and life history of Madagascan genera (the heteropterines and so-called hesperiines (*Hovala*, *Malaza* etc). They are clearly of African stock, but older, and appear linked to Australasian trapezitines. (Did you spot the accessory pouches?)

The molecular data shows the position of the two subfamilies Trapezitinae and Heteropterinae in a phylogenetic ranking as the ancestral groups of all other monocot-feeders. Other genera groups appear to have evolved from them, presumably as separate continental entities following continental drift. They then have finally spread into the northern hemisphere, mixing in a vast complex of inter-connecting skipper fauna between the 'old world' and 'new world'. A scenario involving the timing and routes taken in the vicariance events of a putative Gondwanan skipper fauna is difficult to establish without further improved molecular studies based on more



species in more genera (and of course fossils). Thus the process in which the hesperiine fauna filtered into northern landmasses cannot clearly be defined, but island hopping is unlikely at least until the continents collided. Interesting too, is the exact relationship of the Yucca-burrowing megathymids (Giant Skippers) (Plate 2, fig. 17) from Central America. They are clearly hesperiines, but also have some structural affinities to the heteropterines and trapezitines (and like the genus *Trapezites*, they have robust larvae that also feed on Liliaceae This hypothetical scenario will undoubtedly also involve the pyrginid skipper subfamilies Euschemoninae, Coeliadinae, Eudaminae and Pyrginae, (my present research). All this needs further study.

The world distribution and subtle morphological connectivity of these groups form an interesting framework for more comparative bio-geographical, phylogenetic and improved molecular research. There is little doubt that skippers are a group of butterflies with a strong bi-centric distribution across the world. This indicates that they originated in Cretaceous Gondwana. The scenario parallels the distribution and evolution of songbirds (passerines) which DNA bar-coding research has strongly indicated an eastern Gondwana origin (Cracraft, 2001). There are many other examples of this distribution pattern of biota. Some researchers doubt that butterflies are old enough – that is to have a late Cretaceous origin. Time will tell!

Footnote

The classification of skippers is fraught with difficulties due to their morphological stasis, and it is unlikely that further morphological cladistic methods will clearly define the ‘natural’ genera and tribal groupings, or indeed to greatly improve the arrangement presented by Evans (1937-1955). Perhaps a multi-dimensional ‘Quantum’ gene analysis could be the answer to an unambiguous phylogeny of skippers?

My work was primarily based on morphological comparison of species in the extensive collections held by the Natural History Museum, London (1978-81). Since then some regional faunal studies (including cladistic) have altered or modified the classification. Many more species have been described and biological work has added further depth but, by and large, Evans’ morphological model has ‘held’ as it systematically dealt with a progressive ‘country-to-country’ faunal assessment: in other words he recognised the strong continental endemism of skippers.

Today, I am certain that those little Aussie battlers, the Trapezitinae, have taken a key role in the evolution of skippers, or at least have a pivotal place in the development and distribution of the monocot-feeders throughout the world. Am I jumping the gun? Well maybe, the signs (the pattern) are there, it just needs someone to follow this up.

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APPENDIX A

List of skipper genera studied in this document

TRAPEZITINAE (Australasian)

Hewitsoniella (PNG)

Rachelia

Trapezites

Tiacellia (PNG)

Prada (PNG)

Toxidia

Signeta

Pasma

Dispar

Felicena (PNG)

Neohesperilla

Anisynta

Motasingha

Oreisplanus

Hesperilla

Croitana

Herimosa

Proeidosa

Antipodia

HETEROPTERINAE (South and central America)

Dalla (Sth America)

Piruna (Mexico)

Argopteron (Chile)

Dardarina (Chile)

Butleria (Chile)

HETEROPTERINAE (Europe)

Heteropterus (France)

Carterocephalus (Scotland)

HETEROPTERINAE (Africa)

Metisella (South Africa)

Tsitana (South Africa)

Hovala (Madagascar)

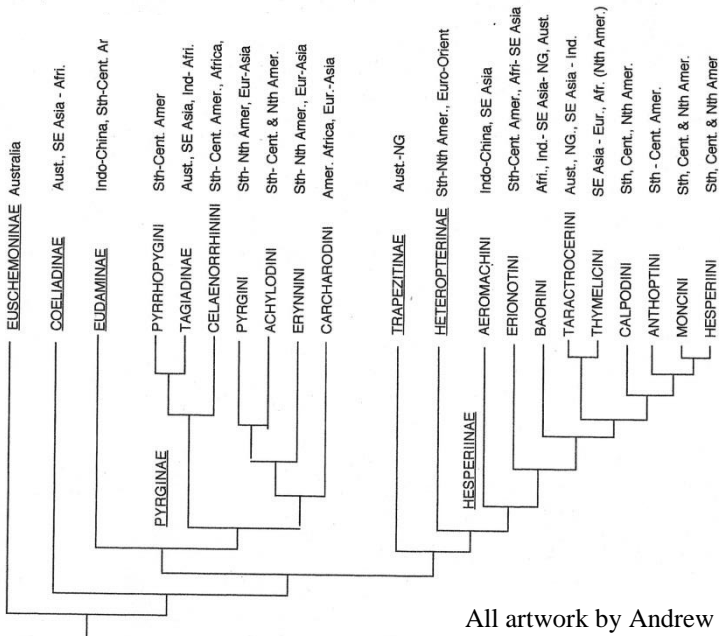
Piruna (North America)





Appendix B

Phylogeny of the subfamilies and tribes of the skippers (Hesperiidae)
of the World (including distribution), after Warren, *et al.* 2008



All artwork by Andrew Atkins

Appendix C

Proposed Phylogeny of the Trapezitinae (Atkins present research)

