Phylogeny and biogeography of the genus *Taractrocera* Butler, 1870 (Lepidoptera: Hesperiidae), an example of Southeast Asian-Australian interchange

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Key words: Lepidoptera; Hesperiidae; *Taractrocera*; systematics; phylogeny; biogeography; Indo-australia.
The genus *Taractrocera* is distributed throughout the Oriental and Australian Regions. It contains 16 species, of which two, *T. fusca* and *T. trikora*, are described as new in this paper. All species are briefly characterized and the new species are described in full. The phylogeny of the genus is inferred, based on an analysis of morphological and genital characters, both of males and females. The biogeography of the genus is discussed in relation to the phylogeny. The genus has an Australian origin. After some diversification in Australia it dispersed into Asia, in or before the Miocene. It dispersed in the reverse direction, probably before the late-Miocene emergence of the Banda Arc and the Moluccas, 5-6 Mya. Three species are adapted to high altitude, one in the Himalayas and two in New Guinea. Apparently the adaptations occurred independently in the two areas. In New Guinea the high altitude species may have simply been carried up by the Pleistocene and recent uplift of the mountains. Possibly helped by the lowering of the sea-level several times during the Pleistocene, one Australian species colonized some of the Lesser Sunda Islands relatively recently.

Introduction

Fourteen species have been recognized in the genus *Taractrocera* Butler, 1870, with a combined distribution covering the whole of the Oriental Region (with a slight penetration into China) as well as the greater part of the Australian Region (Evans, 1949) (fig. 1). In this paper two new species are described from New Guinea.

Starting from the monophyly of the genus the distribution is remarkable in that the genus falls apart into two groups that hardly overlap, viz. a western (Oriental) one with nine species one of which just reaches Timor, and an eastern (Australian-Papuan) one with seven species of which also one species extends as far as Timor.

Since there is no evidence of a former land connection between continental Asia and Australia, at least one of the ancestors of the extant species must have crossed the water gap (unless the distribution dates back to Pangaean times, which is most unlikely as there is no indication that the butterflies, let alone the genus, are that old, and we, moreover, would expect many more similar distribution patterns in Hesperiidae; see also de Jong, 2003). Another remarkable feature is the absence of the genus from the Moluccas, suggesting that the connection between Australia and the Oriental Region was made through the Lesser Sunda Islands and not through New Guinea and the Moluccas. To place this distribution in a historical perspective phylogenetic analyses of the species of *Taractrocera*, and of this genus and its relatives were carried out.

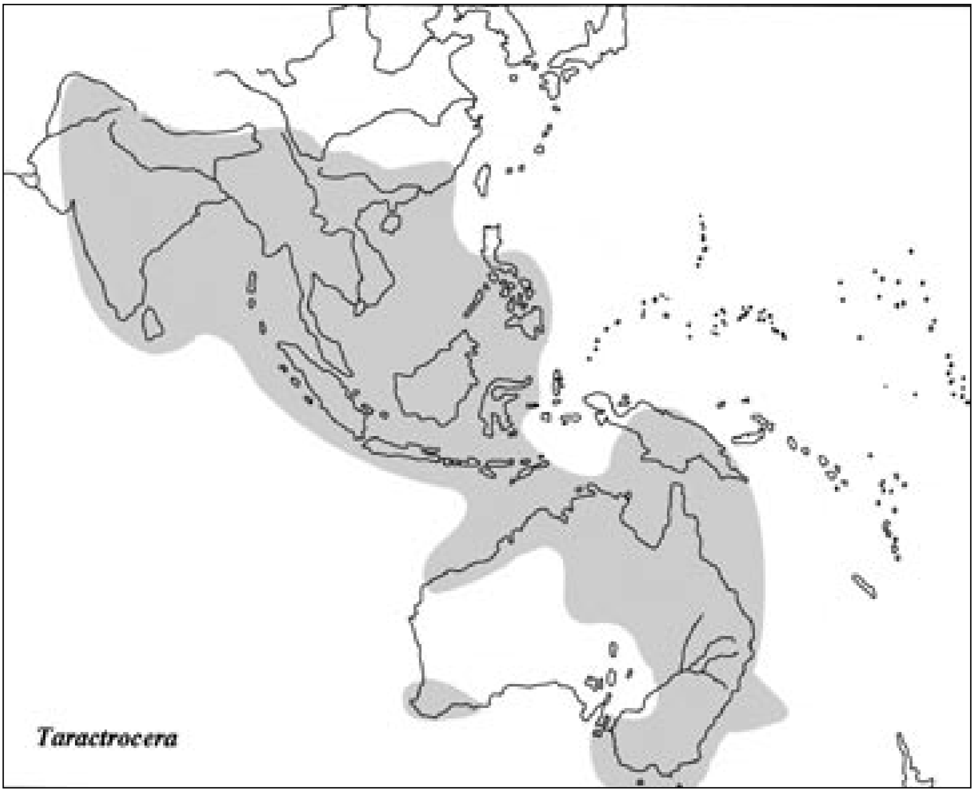


Fig. 1. Distribution of *Taractrocera*. The distribution includes Tasmania, just off the map.

The taxonomy and nomenclature of the genus as given by Evans (1949) are still valid, except for the corrections published by de Jong (1991), and the new species described below. For synonymy, see those papers. Since Evans (1949) is no more than a simplified key to the species, and descriptions and figures (except very schematic drawings of the male genitalia) are lacking, all species are described (including diagnostic features), and external characters as well as male and female genitalia are illustrated (often for the first time). Geographic variation has not been considered, but generally recognized subspecific taxa are listed.

Diagnosis, monophyly and relationship of the genus *Taractrocera*

The genus belongs to the hesperiine genera with tawny spots (in some species white or whitish). For *Taractrocera* and its (supposed) allies Evans (1949) created the *Taractrocera* group of genera, an Oriental-Australian assemblage of 14 genera and about 150 species. Two genera in the group, *Ocybadistes* and *Suniana*, share the characters ‘flattened antennal club’ and ‘3rd segment of palpi needle-like’ with *Taractrocera*. The three genera together are considered monophyletic. Voss (1952) placed these genera in the tribe ‘Taractroceridi’, together with the Oriental genus *Potanthus*, as well as some American genera placed by Evans (1955) in the *Hesperia* group, while some genera of Evans' *Taractrocera* group were placed in the tribe Hesperiidi by Voss. However, the diagnoses given by Voss for the two tribes are overlapping, and for the time being Evans' arrangement is to be preferred. *Taractrocera* can easily be distinguished from *Ocybadistes* and *Suniana* by the antennal club being hollowed and with rounded top (or at most a minute obtuse apiculus). This unique character seems to justify the hypothesis that the genus is monophyletic. In case of missing antennae, *Taractrocera* can be distinguished from *Suniana* by the male genitalia: in *Taractrocera* the uncus is entire, in *Suniana* it is deeply cleft. From *Ocybadistes*, *Taractrocera* males (except *T. papyria*) can be distinguished by the distally more or less indented valva.

Morphological characters

Wing venation and markings

Evans (1949) applied the still widely used British system of the naming of wing veins, numbering the veins from dorsum to costa from 1 to 12 in the forewing, and from 1 to 8 in the hindwing, and numbering each internervular space according to the number of the vein delimiting it posteriorly. In the Hesperiidae, where all species have 12 veins in the forewing and eight in the hindwing, it is a simple and useful system. Thus, in the present paper dealing with a single genus, in which the venation does not vary, it is most practical to apply this system, also because it considerably simplifies the naming of spots (see below). In a wider context, e.g. when studying the development of the venation in Hesperiidae or when comparing the venation in Hesperiidae to the venation in other butterfly families, where reduction and deletion of veins is common, it is inadequate, but this falls outside the scope of the present paper. For conversion to the system commonly used for Lepidoptera Table 1 will be helpfull. See also Scott (1990) and Ackery *et al*. (1999).

Although much work has been done on the homology of pattern elements in butterflies (e.g., Nijhout, 1991), the homology of at least part of the elements in Hesperiidae has not yet been studied. In Hesperiidae location of the spots is remarkably constant, and reference of the spots to the the number of the internervular spaces where they are located, is the most simple and straightforward method. Hence, I stick to the system applied earlier (e.g., de Jong, 1978), discerning a basal, a median and a submarginal spot in each internervular space, in addition to spots in the cell. Thus, "median spot 2" is the "median spot in space 2", or the "median spot in the space between the veins CuA2 and CuA1".

Note that various spots can be extended, reduced or absent. In *Taractrocera*, e.g., submarginal spots are absent from both forewing and hindwing, as are most (and in several species all) basal spots.

Table 1. Conversion table of two widely used systems of numbering of wing veins.

Forewing		Hindwing	
1	1A+2A	1a	3A
2	CuA2	1b	1A+2A
3	CuA1	2	CuA2
4	M3	3	CuA1
5	M2	4	M3
6	M1	5	M2
7	R5	6	M1
8	R4	7	Rs
9	R3	8	Sc+R
10	R2		
11	R1		
12	Sc		

Hence, unless otherwise stated, the spots mentioned in the species descriptions below are the median spots. In literature, median spots 6-8 are often called apical or subapical spots. Between veins 1 and 2 (1A+2A and CuA2) the lost CuP is often discernible in the division of the spots, which are then named 1b (posterior) and 1c (anterior), respectively. The indication 1a is reserved for the the space between the dorsum and vein 1.

Antennal club

Spoon-like; in dry material the disc may be more or less curved to the hollow side, making a comparison of length/width proportions between specimens and species difficult; apart from that, there is individual variation in the shape of the club; top rounded or, in some species, the ultimate segment pops up a little forming a very short apiculus; nudum 9-10 segments, brown or black. Evans (1949) placed much weight on the shape of the end of the antennal club. According to him the Oriental species have a rounded end, the Australian series a more or less triangular and shortly pointed end. The difference is, however, not visible in the material studied (figs 2-11).

Secondary sexual characters

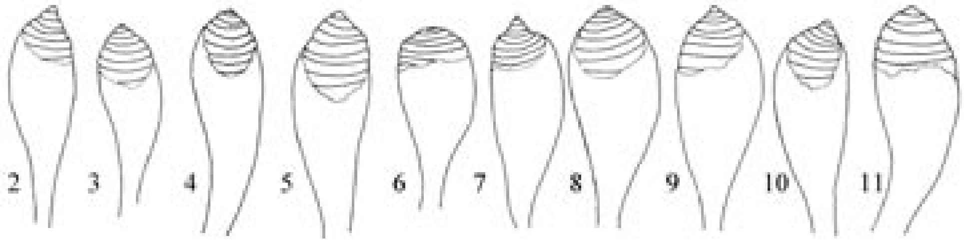
In most species secondary sexual characters are wanting. When patches of androconial scales occur, they take the form of a narrow or broader, continuous or broken stigma from vein 1 to vein 4 or 5, or obscure brands on either side of veins 1 to 4.

Male genitalia

Although strictly speaking not belonging to the genitalia, tergite VIII is modified in a way not found in the female: the distal edge varies from straight to (usually) more or less produced laterally, with in most species stiff, thorn-like hairs on the rim where it is produced. The actual genitalia are of a very simple build. The uncus is entire and varies a little in shape. It is broad where it joins the tegumen (line of fusion clearly visible), but suddenly narrows to the distal part, which is cylindrical to triangular or bottle-shaped in dorsal view. The valva is more or less indented apically, forming a rather narrow upper process and a broader lower process. The two processes are comparable with the costal process and the cucullus, respectively, in other Hesperiidae but not differentiated as usual. On the distal edge or on the inside of the lower process there is a row or group of short, straight to curved, tooth-like spines, usually directed inwards.

Female genitalia

Sinus vaginalis consisting of two bowl-like cavities on both sides of ostium, partly sclerotized; sclerotization imperceptibly passing into membranous area, which is more or less folded, with dense soft spines on the folds. Lamella antevaginalis present or absent; if present, varying from broad and short to narrow and long. Lamella postvaginalis always present, variously shaped and folded, smooth on ventral side (i.e. towards ostium; with one exception), smooth or spinulose on dorsal side. Ductus bursae and corpus bursae membranous, without special structures. Tergum VIII split into a left and a right sclerite, with well-developed apophyses anteriores; there is variation in the length of the apophyses anteriores and the shape of the sclerotization, but the variation in shape is difficult to define and the sclerotization is often vaguely outlined. Papillae anales as usual; there is variation in the length of the apophyses posteriores.



Figs 2-11. Antennal club of *Taractrocera* species. Boundary of scaling indicated by fine stippled line. 2, *T. ilia beta* (Papua New Guinea, Bulwa); 3, *T. dolon diomedes* (Australia, Northern Territory, Kakadu National Park); 4, *T. archias bavius* (Indonesia, Flores); 5, *T. flavoides* (China, Tsekou); 6, *T. ceramas ceramas* (India, Travancore); 7, *T. papyria papyria* (Australia, Tasmania); 8, *T. trikora* (paratype; for details of locality, etc., see text); 9, *T. fusca* (paratype; for details of locality, etc., see text); 10, *T. ardonia ardonia* (Indonesia, Sulawesi Selatan, Bantimurung); 11, *T. danna* (Nepal, Dolpa).

Ecology

The vernacular name for *Taractrocera* species is 'grass darts'. It indicates that, in general, the species are found in grassy places. These may be open, dry and hot roadsides, open dry woodland, more sheltered places with luxuriant vegetation, or subalpine grassland. The species occur from sea-level to about 4.000 m. Food plants are known for four species only (*T. archias*, *nigrolimbata*, *papyria* and *ina*), which all live on grasses, while one of these species (*papyria*) has also been found on *Carex* (Cyperaceae). Since *Taractrocera* belongs to the Hesperiinae, for which grasses are the main diet, it can be expected that the other *Taractrocera* species live on grasses as well.

The *Taractrocera* species

The characters of the species and their distribution are summarized in tables 2 and 3. If not stated otherwise, the distribution is based on material in The Natural History Museum, London (mainly published in Evans, 1949) and the National Museum of Natural History, Leiden.

The sequential order of the species is based on the preferred phylogenetic tree (see below, Phylogeny of *Taractrocera*).

Taractrocera anisomorpha (Lower, 1911)

External characters (figs 70, 86).— Spots on upper side orange-yellow. On upper side of forewing, spot in space 1bc largest spot of discal series, its outer edge parallel to termen, spots in spaces 6-8 closer to (or even touching) spots in spaces 4-5 than to cell spot; spot in space 2 not reaching cell spot. On upper side of hindwing, spots much wider than dark area between spots and termen in male, spots and dark area about equally wide in female; no spots in spaces 6 and 7 (as on underside). Underside of hindwing overlaid with yellow scales, more or less obscuring the spots.

Secondary sexual characters.— A broken, rather narrow stigma in spaces 1b, 1c, 2 and 3 (just crossing vein 4).

Male genitalia (figs 12, 27).— Latero-distal rim of tergite VIII weakly produced, rounded in ventral half, slightly reaching beyond dorso-distal edge; comb of stiff hairs occupying two thirds of lateral edge. In dorsal view, distal part of uncus elongate triangular, with pointed apex. Valva with upper process 1.6 times as long as wide, extending to about one third of lower process; lower process elongate-truncate; few spines, pointing inwards, on distal edge; indentation between upper and lower processes U-shaped.

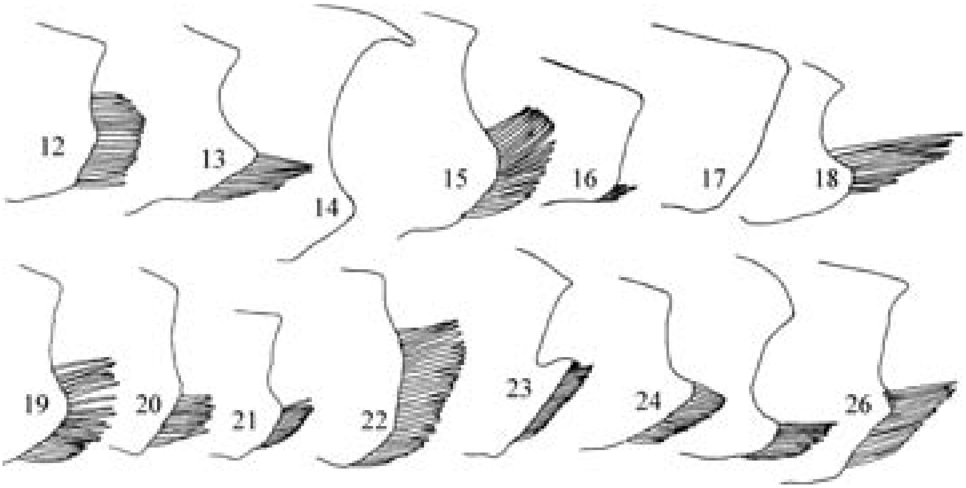
Female genitalia (fig. 44).— Antevaginal plate an elongate, gutter-like, smooth sclerite, reaching far beyond smooth, rectangular postvaginal plate, which is as long as wide, with a straight apical rim.

Distribution (fig. 58).— Northern half of Australia, in scattered localities from west to east, also in the centre (Alice Springs) (Braby, 2000); Timor and Wetar.

Geographic variation.— None.

Taractrocera ilia Waterhouse, 1932

External characters (figs 71, 87).— Spots on upper side orange-yellow. On upper side of forewing, spot in space 1bc oblique, upper part closer to termen than lower part; spots in spaces 6-8 midway between spots in spaces 4-5 and orange-yellow costal area, but spot in space 6 extending towards latter area; spot in space 2 separated from cell spot by almost its own width. Underside of hindwing weakly overlaid with yellow scales, spots well contrasting, no spot in space 6, but with spot in space 7.



Figs 12-26. Left lateral view of tergite 8 of males of *Taractrocera* species, 12, *T. anisomorpha* (Indonesia, Wetar); 13, *T. ilia beta* (Papua New Guinea, Bulwa); 14, *T. dolon diomedes* (Australia, Northern Territory, Kakadu National Park); 15, *T. ina* (Australia, Queensland); 16, *T. nigrolimbata nigrolimbata* (Indonesia, Java, Bogor); 17, *T. archias archias* (Indonesia, Java, Bogor); 18, *T. luzonensis dongala* (Indonesia, Sulawesi Tengah); 19, *T. flavoides* (China, Tsekou); 20, *T. tilda* (China, Ta-Tsien-Lou); 21, *T. ceramas ceramas* (India, Travancore); 22, *T. papyria papyria* (Australia, Sydney); 23, *T. trikora* (paratype; for details of locality, etc., see text); 24, *T. fusca* (paratype; for details of locality, etc., see text); 25, *T. ardonia ardonia* (Indonesia, Sulawesi Selatan, Mamasa); 26, *T. danna* (N India, Simla).

Secondary sexual characters.— A more or less zigzagging, discontinuous stigma in spaces 1b, 1c, 2 and 3-4.

Male genitalia (figs 13, 28).— Ventral two thirds of latero-distal rim of tergite VIII strongly triangularly produced; reaching well beyond dorso-distal edge; comb of stiff hairs only on ventral side of extension. In dorsal view, distal part of uncus bottle-shaped with cylindrical bottle-neck and truncate apex; a middorsal shallow ridge in apical half. Valva with upper process triangular, extending to middle of lower process; lower process elongate, 2.5 times as long as wide, rounded at distal end; spines on dorso-distal edge, not numerous, pointing upwards or a little distad; indentation between upper and lower processes widely U-shaped.

Female genitalia (fig. 46).— Antevaginal plate as in *T. anisomorpha*, a little more slender, apically more indented, and with a small, medial extension at 1/3 from apex. Postvaginal plate elongate, more than twice as long as wide, about 3/4 of length of antevaginal plate, apically rounded, dorsally spinulose.

Distribution (fig. 59).— In Australia only taken near Darwin and on the nearby Melville Island (Braby, 2000); in Papua New Guinea taken in the provinces Morobe, Madang, East Sepik and Western Highlands, from sea level to 2635 m, but the occurrence at higher elevations seems exceptional (Parsons, 1998). Judged from the number of specimens in collections the species is rarer in Australia than in New Guinea.

Geographic variation.— The species was described from Australia. The New Guinea populations have been separated as ssp. *beta* Evans, 1934.

Taractrocera dolon (Plötz, 1884)

External characters (figs 72, 88).— Spots on upper side orange-yellow. On upper side of forewing, spot in space 1bc oblique, upper part closer to termen than lower part; spots in spaces 6-8 closer to spots in spaces 4-5 than to orange-yellow costal area; spot in space 2 separated from cell spot by its own width. On underside of hindwing, no spot in space 7, but with spot in space 6; orange-yellow superscaling, more or less obscuring the spots.

Secondary sexual characters.— Obscure traces of brands above middle of vein 1 and on either side of veins 2, 3 and 4. In a male from near Darwin in The National Museum of Natural History, Leiden, the brands are practically invisible.

Male genitalia (figs 14, 29).— Dorso-distal rim of tergite VIII centrally produced; latero-distal rim triangularly produced in ventral half, not reaching beyond dorsal extension; no comb of stiff hairs. In dorsal view, distal part of uncus elongate triangular/conical, with bluntly pointed apex. Valva with upper process rounded, shorter than wide, extending to about one third of lower process; lower process truncate; spines in a straight row, pointing inwards, on distal edge; indentation between upper and lower processes V-shaped.

Female genitalia (fig. 45).— Antevaginal plate finger-like, slightly shorter than postvaginal plate, narrowing to rounded apex. Postvaginal plate dome-shaped, dorsally spinulose, but apical part smooth.

Distribution (fig. 60).— Australia, around Darwin and along the east coast; also recorded from Tagula in the Louisiade Archipelago (Braby, 2000).

Geographic variation.— Two subspecies are recognized, ssp. *dolon* from E

Australia and Louisiade Archipelago, and ssp. *diomedes* Waterhouse, 1933, from the area around Darwin.

Taractrocera ina Waterhouse, 1932

External characters (figs 73, 89).— Spots on upper side orange-yellow. On upper side of forewing, spot in space 1bc oblique, upper part closer to termen than lower part; spots in spaces 6-8 closer to spots in space 4-5 than to orange-yellow costal area; spot in space 2 separated from cell spot by its own width. Underside of hindwing with ochreous superscaling, veins finely outlined in black, spots yellow rather than orange, no spot in spaces 6 and 7.

Secondary sexual characters.— Absent.

Male genitalia (figs 15, 30).— Latero-distal rim of tergite VIII broadly rounded in ventral two-third, extending beyond dorso-distal edge; comb of stiff hairs occupying most of rounded extension. In dorsal view, distal part of uncus cylindrical in lower two thirds, narrowing to a pointed apex in upper one third. Valva with upper process finger-like, three times as long as wide, extending to three quarters of lower process, a few spines pointing downwards at ventral side of apex; lower process elongate, broad at base, but subequal to upper process in distal part; spines pointing upwards, along dorsal edge; indentation between upper and lower processes a wide U.

Female genitalia (fig. 47).— Antevaginal plate consisting of a smooth, narrow sclerotization ventrally of ostium. Postvaginal plate slightly longer than wide, apically slightly sinuate, dorsally spinulose.

Distribution (fig. 61).— Northern, central and eastern Australia in scattered localities, south to western New South Wales (but only a single male known from there; Braby 2000).

Geographic variation.— Evans (1949) distinguished two subspecies, but according to Common & Waterhouse (1981) the differences do not hold, and no geographic variation is mentioned by Braby (2000).

Taractrocera luzonensis (Staudinger, 1889)

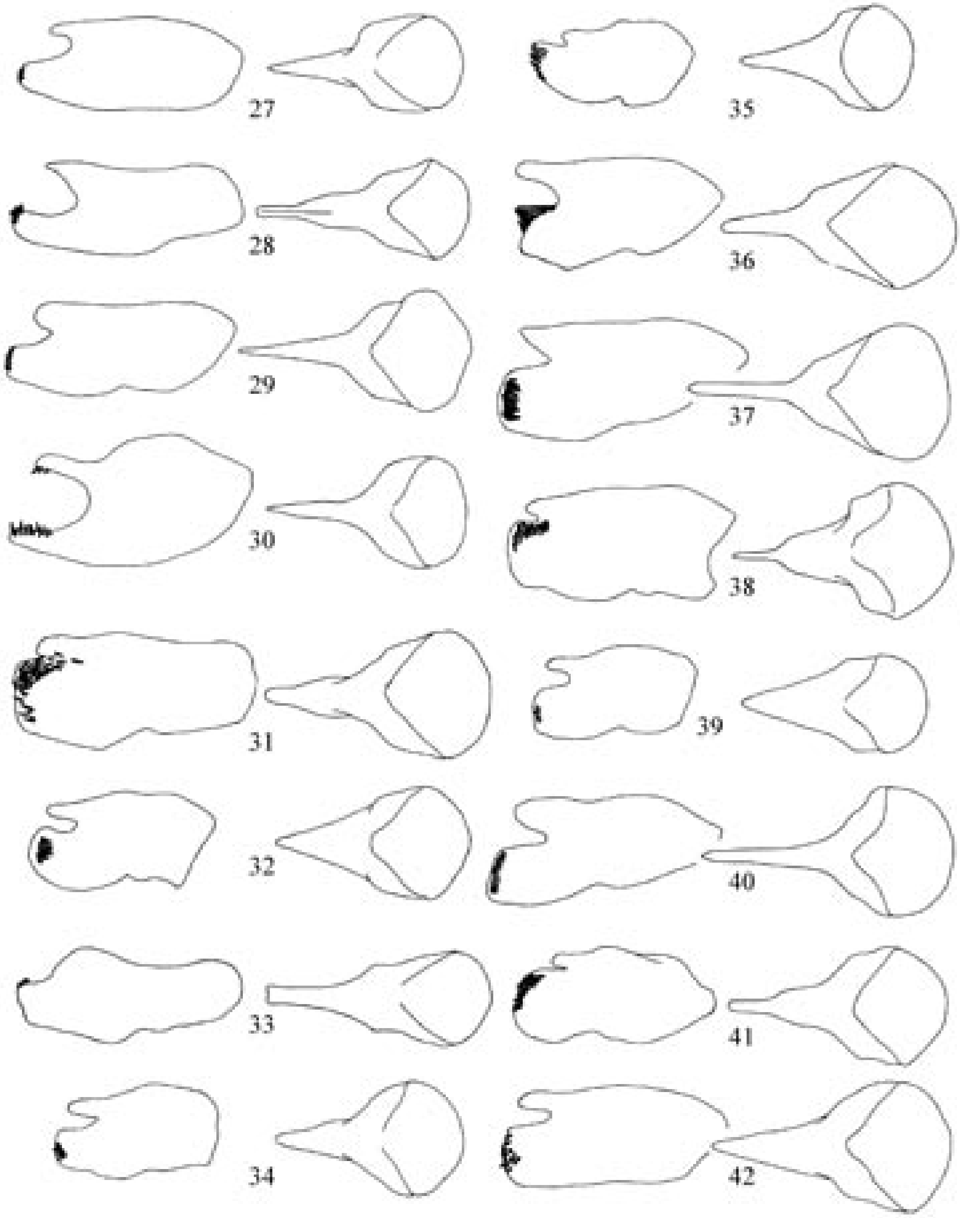
External characters (figs 74, 90).— Spots on upper side orange-yellow. On underside of hindwing (and usually on upper side as well), spot in space 7.

Secondary sexual characters.— Absent.

Male genitalia (figs 18, 37).— Ventral half of latero-distal rim of tergite VIII strongly produced, reaching well beyond dorso-distal rim; comb of stiff hairs longer than in any other species, occupying only upper part of extension. In dorsal view, distal part of uncus long, cylindrical, with pointed apex. Valva with upper process triangular, extending to middle of lower process; lower process rectangular with rounded corners; spines in a straight row, pointing inwards, near distal edge; indentation between upper and lower processes V-shaped.

Female genitalia (fig. 43).— Antevaginal plate rectangular, about 1.5 times as long as wide, in ventral view covering the equally sized postvaginal plate; latter with indented apical margin and smooth dorsal surface.

Distribution (fig. 64).— From SW Burma and N Thailand through Malaysia,



Figs 27-42. Male genitalia of *Taractrocera* species. Left, inside of left valva; right, dorsal view of tegumen and uncus. 27, *T. anisomorpha* (Indonesia, Wetar); 28, *T. ilia beta* (Papua New Guinea, Bulwa); 29, *T. dolon diomedes* (Australia, Northern Territory, Kakadu National Park); 30, *T. ina* (Australia, Queensland); 31, *T. tilda* (China, Ta-Tsien-Lou); 32, *T. ceramas ceramas* (India, Travancore); 33, *T. papyria papyria* (Australia, Sydney); 34, *T. trikora* (paratype; for details of locality, etc., see text); 35, *T. nigrolimbata nigrolimbata* (Indonesia, Java, Bogor); 36, *T. archias archias* (Indonesia, Java, Bogor); 37, *T. luzonensis dongala* (Indonesia, Sulawesi Tengah); 38, *T. flavoides* (China, Tsekou); 39, *T. fusca* (paratype; for details of locality, etc., see text); 40, *T. ardonia ardonia* (Indonesia, Sulawesi Selatan, Mamasa); 41, *T. maevius sagara* (India, Poona); 42, *T. danna* (N India, Simla).

Sumatra, Borneo, and the Philippines to Sulawesi and neighbouring islands. Common in many places in the Philippines and Sulawesi, but apparently rare elsewhere. In the National Museum of Natural History, Leiden, there is a specimen labeled as coming from "Tsingtau, Schandung, China or." (current names: Qingdao, Shandong). The abdomen is missing, but the hindwings have a spot in space 7 on upper and under side, characteristic of this species. In view of the further distribution of the species, this locality is unlikely, but not impossible.

Geographic variation.— Six subspecies are recognized, ssp. *luzonensis* in the Philippines (including Palawan), ssp. *zenia* Evans, 1934, in S Burma/S Thailand, ssp. *tissara* Fruhstorfer, 1910, in Sumatra and islands to the west, ssp. *stella* Evans, 1934, in Borneo and nearby islands, ssp. *dongola* in Sulawesi and Sula Archipelago, and ssp. *bessa* Evans, 1949, on islands to the south of Sulawesi (Salayar, Tukanbesi, Tanahjampea) and probably also in S Sulawesi.

Taractrocera archias (Felder, 1860)

External characters (figs 75, 91).— Spots on upper side orange-yellow. On upper side of forewing, spot in space 1bc oblique, upper part closer to termen than lower part; spots in spaces 6-8 closer (or even conjoined) to spots in space 4-5 than to orange-yellow costal area; spot in space 2 almost or actually reaching cell spot. On underside of hindwing, no spot in space 7.

Secondary sexual characters.— Absent.

Male genitalia (figs 17, 36).— Latero-distal rim of tergite VIII straight; no comb of stiff hairs. In dorsal view, distal part of uncus cylindrical, with broadly rounded apex. Valva with upper process elongate, thumb-like, 2.5 times as long as wide, extending almost as far as lower process; lower process triangular with rounded tip; long spines, pointing dorso-distad, on dorsal edge; indentation between upper and lower processes wide, rounded.

Female genitalia (fig. 49).— Short rectangular antevaginal plate, almost twice as wide as long. Postvaginal plate elongate-rectangular, more than twice as long as wide, with sinuate apical margin, dorsally spinulose, but apical part smooth.

Distribution (fig. 62).— Mainland SE Asia (Burma, Thailand, Vietnam, Malaysia), Java and Lesser Sunda Islands (east to Timor and Kisar).

Geographic variation.— Five subspecies are recognized, ssp. *archias* in Java, Bali and Banka, ssp. *samadha* Fruhstorfer, 1910, in N Burma, ssp. *quinta* Swinhoe, 1913, from

Figs 43-57. Female genitalia of *Taractrocera* species. Tergite 8 and papillae anales (and in part of the figures the bursa) omitted (except from fig. 43). Intersegmental membrane partly torn away to show sinus vaginalis better. 43, *T. luzonensis dongala* (Indonesia, Sulawesi Utara, Dumoga Bone National Park); 44, *T. anisomorpha* (locality unknown) (a, ventral view; b, lateral view with intersegmental membrane omitted to show the antevaginal plate, ap, and postvaginal plate, pp); 45, *T. dolon diomedes* (Australia, Northern Territory, Berry Springs); 46, *T. ilia beta* (Papua New Guinea, Bulwa); 47, *T. ina* (Australia, Queensland); 48, *T. archias archias* (Indonesia, Java, Kandergebergte); 49, *T. nigrolimbata nigrolimbata* (Indonesia, Java, Bogor); 50, *T. ceramas* (S India, Karwar); 51, *T. tilda* (China, Yunnan); 52, *T. papyria papyria* (Tasmania); 53, *T. fusca* (paratype; for details of locality, etc., see text); 54, *T. trikora* (paratype; for details of locality, etc., see text); 55, *T. ardonia ardonia* (Indonesia, Sulawesi Selatan, Bantimurung); 56, *T. maevius* sagara(India, Poona); 57, *T. danna* (N India, Simla).

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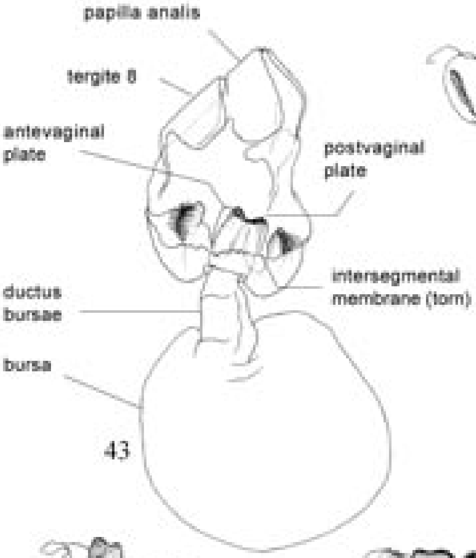

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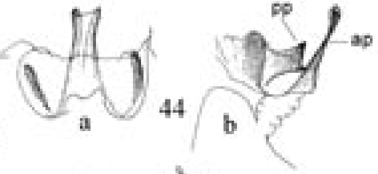

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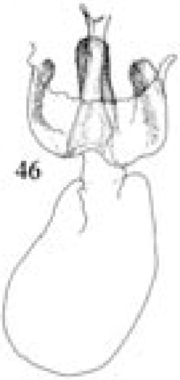

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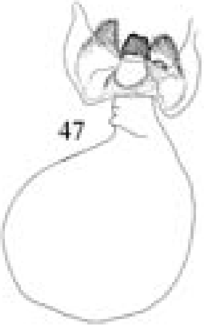

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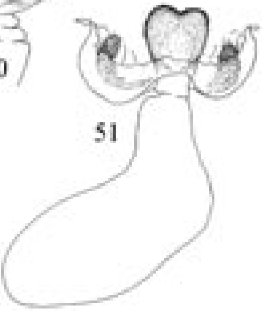

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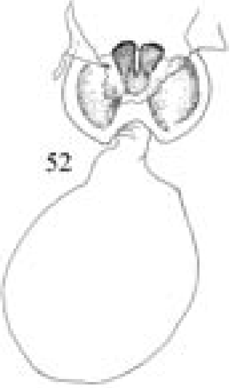

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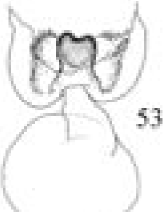

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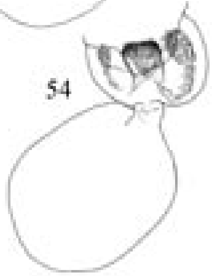

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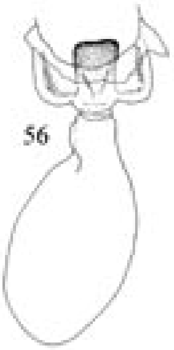

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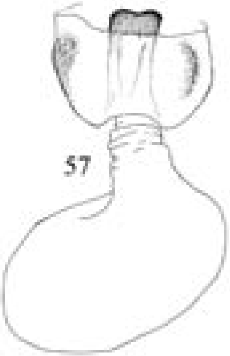

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Burma to Indochina and Malaya, and ssp. *kisaga* Frustorfer, 1910, and ssp. *bavius* Mabille, 1891, from the Lesser Sunda Islands.

Taractrocera nigrolimbata (Snellen, 1876)

External characters (figs 76, 92).— Spots on upper side orange-yellow. On upper side of forewing, spot in space 1bc parallel to termen; spots in spaces 6-8 always conjoined to spots in space 4-5; spot in space 2 almost or (usually) actually reaching cell spot, often broadly fusing with it. On underside of hindwing, no spot in space 7.

Secondary sexual characters.— Absent.

Male genitalia (figs 16, 35).— Latero-distal rim of tergite VIII straight; short comb of stiff hairs at ventro-distal corner. In dorsal view, distal part of uncus triangular, with rounded apex. Valva, upper process extending dorsad, not distad, distal edge vertical; lower process with almost straight, horizontal dorsal edge and evenly curved distal and ventral edge; spines pointing inwards or a bit distad, close to distal edge.

Female genitalia (fig. 49).— Broad, densely spinulose antevaginal plate, about five times as wide as long. Postvaginal plate more or less heart-shaped, dorsally spinulose, but apical part smooth.

Distribution (fig. 62).— Malaysia, Vietnam (Saigon), Sumatra, Java, Lesser Sunda Islands (east to Sumba), and S Sulawesi.

Geographic variation.— Two subspecies are recognized, ssp. *nigrolimbata* from Indochina to Java, and ssp. *talanta* (Plötz, 1885) from E Java, Lesser Sunda Islands and S Sulawesi.

Taractrocera flavoides Leech, 1894

External characters (figs 77, 93).— As *T. tilda*, but underside hindwing spots edged by small black spots, and tiny black dots on termen at the end of the veins.

Secondary sexual characters.— Absent.

Male genitalia (figs 19, 38).— Ventral half of latero-distal rim of tergite VIII roundedly produced, slightly reaching beyond dorso-distal edge; comb of stiff hairs moderately long, occupying half of lateral edge. In dorsal view, distal part of uncus strongly shouldered, apical part narrowly cylindrical and apex bluntly pointed. Valva with upper process slightly shorter than wide, extending almost to middle of lower process; lower process as in *T. tilda*, but more rounded; spines in dorso-distal area; indentation between upper and lower processes small, U-shaped.

Female genitalia (cf fig. 50).— Similar to *T. tilda*.

Distribution (fig. 65).— Restricted to the Chinese provinces of Sechuan (and neighbouring Thibet) and Yunnan.

Geographic variation.— None.

Taractrocera tilda Evans, 1934

External characters (figs 78, 94).— Spots on upper side orange-yellow. Upper side forewing, cell spots filling cell completely. Upper side hindwing, spot in space 4-5 slightly out of line, shifted towards termen, spot in space 6 conspicuous, as large as spot in space 3, cell spot conspicuous, comma-shaped. Underside hindwing, ground-colour strongly overlaid pale-ochreous, more or less obscuring the spots.

Secondary sexual characters.— Absent.

Male genitalia (figs 20, 31).— Ventral half of latero-distal rim of tergite VIII weakly and truncatedly produced, slightly reaching beyond dorso-distal edge; comb of stiff hairs moderately long, occupying one third of lateral edge. In dorsal view, distal part of uncus bottle-shaped, with broadly rounded apex. Valva with upper process hardly protruding, finely serrate; lower process large, truncate; dense row of spines near distal edge, curving basad in dorsal part; indentation between upper and lower processes very shallow.

Female genitalia (fig. 51).— Similar to *T. ceramas*, apical indentation a bit deeper.

Distribution (fig. 65).— Restricted to the Chinese provinces of Sechuan and Yunnan.

Geographic variation.— None.

Taractrocera ceramas (Hewitson, 1868)

External characters (figs 79, 95).— Spots on upper side orange-yellow. Extension of spots on forewing and hindwing variable. Upper side forewing, spots in spaces 4 and 5 widely detached from spot in space 3, closer to termen than to latter spot. Underside hindwing may be densely overlaid with ochreous scales, with which the spots hardly contrast, or with black spots and yellow veins.

Secondary sexual characters.— Absent.

Male genitalia (figs 21, 32).— Latero-distal rim of tergite VIII roundedly produced in lower half, slightly reaching beyond dorso-distal edge; comb of stiff hairs moderately long, occupying almost half of lateral edge. In dorsal view, distal part of uncus triangular, with rounded apex. Valva with upper process twice as long as wide, extending to two thirds of lower process; lower process semicircular, dorsal edge concave; spines in a short, more or less straight row, pointing inwards, at some distance from distal edge; indentation between upper and lower processes U-shaped.

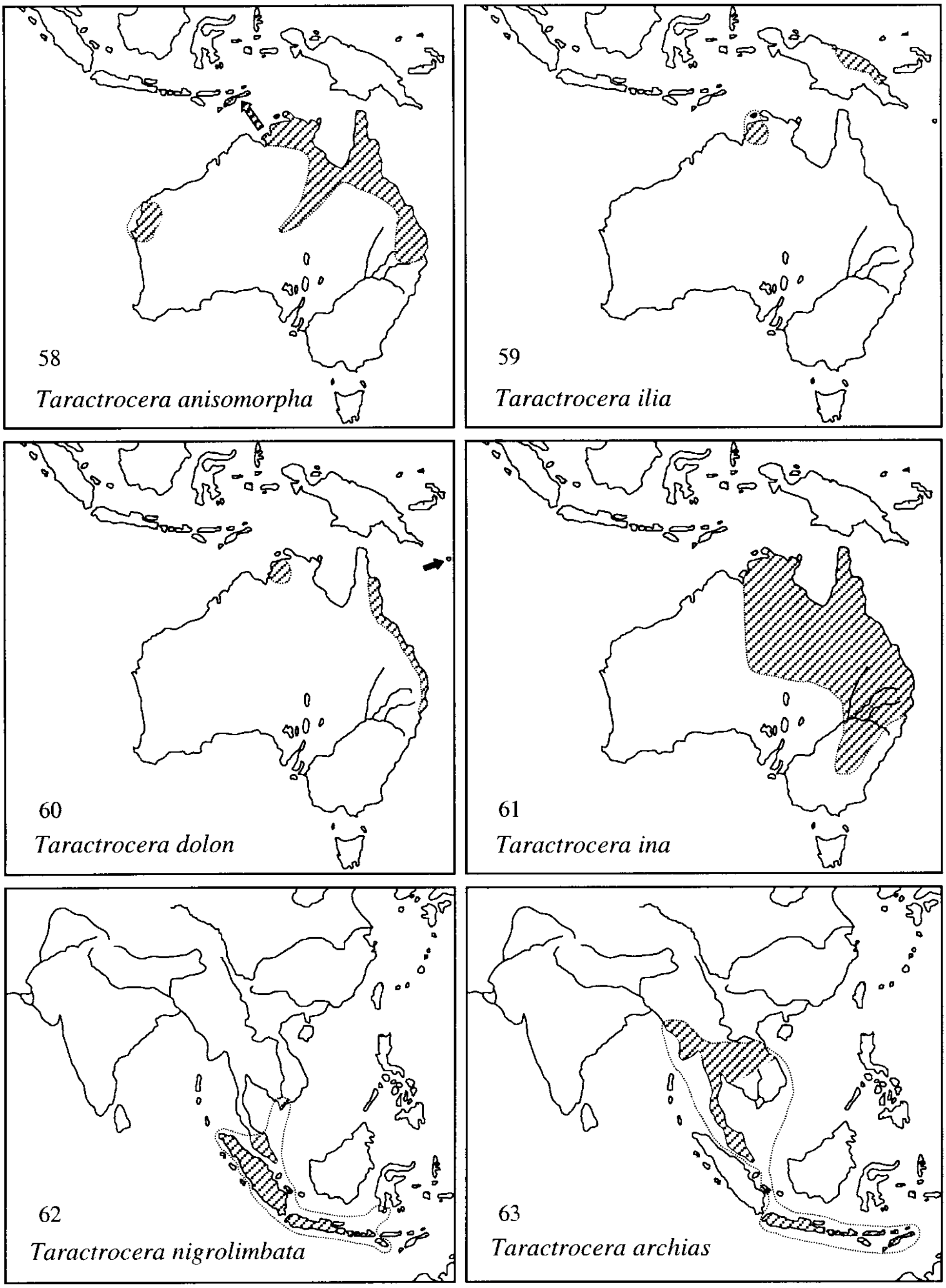
Female genitalia (fig. 50).— No antevaginal plate. Postvaginal plate in apical part wider than in basal part, apically sinuate by rounded angles and shallow indentation, dorsally spinulose.

Distribution (fig. 66).— S and W India, NE India and neighbouring Burma, S China. In India the species occurs from sea level to 1.100 m along grassy roads on jungle-covered slopes, and above 2.000 m where it avoids scrub and jungle and is very fond of the sunshine (Wynter-Blyth, 1957).

Geographic variation.— Six subspecies are recognized, viz. ssp. *ceramas*, ssp. *media* Evans, 1934, ssp. *nicevillei* Watson, 1893 and ssp. *oberthuri* Elwes & Edwards, 1897, from southern half of India, ssp. *atropunctata* Watson, 1896, from NE India/N Burma, and ssp. *thelma* Evans, 1934, from SE China.

Taractrocera papyria (Boisduval, 1832)

External characters (figs 80, 96).— Spots on upper side orange-yellow, a bit duller than in other species with orange-yellow spots. In the eastern part of its range easily



58 *Taractrocera anisomorpha*

59 *Taractrocera ilia*

60 *Taractrocera dolon*

61 *Taractrocera ina*

62 *Taractrocera nigrolimbata*

63 *Taractrocera archias*

Figs 58-63. Distribution of *Taractrocera* species.

distinguished from other *Taractrocera* species flying with it, and in fact from all other *Taractrocera* species except the next two, by the sharply outlined white spots on the underside of the hindwing. In SW Australia, where it is the only *Taractrocera* species, the spots are yellow and obscured by strong yellow superscaling.

Secondary sexual characters.— A linear continuous stigma from vein 1 to vein 5.

Male genitalia (figs 22, 33).— Latero-distal rim of tergite VIII slightly roundedly extended in ventral three quarters, hardly reaching beyond dorso-distal edge; comb of stiff hairs occupying entire edge of extension. In dorsal view, distal part of uncus shouldered, narrowing to a cylindrical structure with broad, shallowly indented apex. Valva without upper process, dorsal edge of valva only strongly bulging; lower process truncate; few small spines on dorsal edge, distal edge finely serrate.

Female genitalia (fig. 52).— No antevaginal plate. Postvaginal plate a deeply cleft, vaguely heart-shaped structure, dorsally spinulose.

Distribution (fig. 68).— Lord Howe Island; E, S and SW Australia; Tasmania (Braby, 2000). Evans (1949) also lists three specimens from NW Australia, but not recorded from there by Braby (2000).

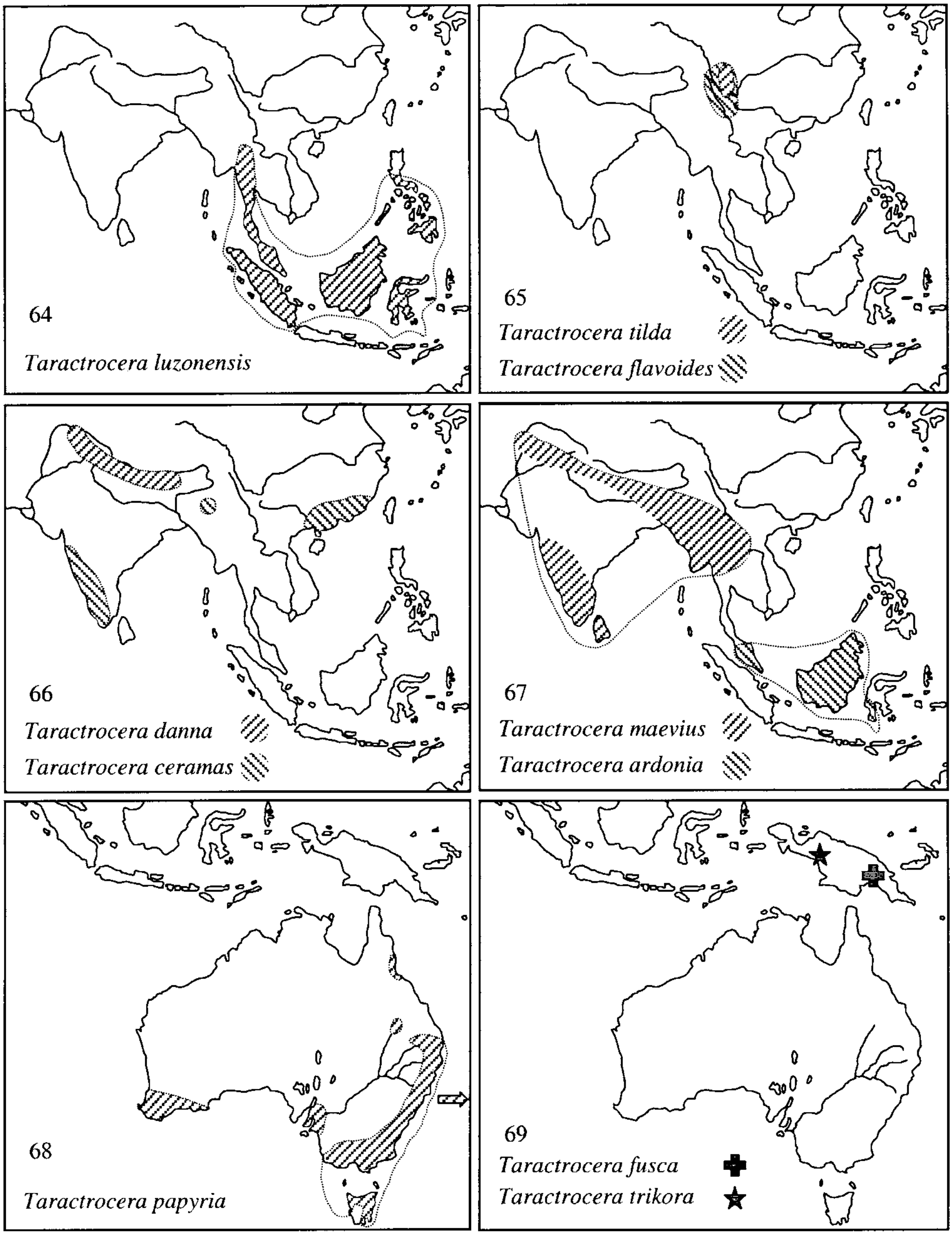
Geographic variation.— Two subspecies are recognized, ssp. *papyria* from Lord Howe Island, E and SE Australian and Tasmania, and ssp. *agraulia* (Hewitson, 1868) in SW Australia.

Taractrocera trikora spec. nov.

Material.— Holotype, ♂, "Neth.Ind.-American New Guinea Exp. 3250 m, Lake Habbema, 5.viii.1938, L.J. Toxopeus"; 27 ♂, 16 ♀, paratypes, as follows: same data as for holotype, but 29.vii (1 ♂, 1 ♀), 31.vii (1 ♂), 2.viii (1 ♂), 3.viii (1 ♂), 4.viii (2 ♂), 5.viii (4 ♂, 3 ♀), 6.viii (1 ♂), 8.viii (7 ♂, 1 ♀), 10.viii (3 ♂, 1 ♀), 11.viii (1 ♂, 2 ♀), 13.viii (2 ♂),19.viii (1 ♂, 3 ♀), 21.viii (1 ♀), 24.viii (1 ♂), 10.ix (1 ♀); "Neth.Ind.-American New Guinea Exp. 3800 m, Pass E side Wilhelminatop, 2.ix.1938, L.J. Toxopeus" (1 ♂); "Neth. Ind.-American New Guinea Exp. 3600 m, Valley E side Wilhelminatop, 3.ix.1938, L.J. Toxopeus" (2 ♀); idem, 7.ix (1 ♀). All types in National Museum of Natural History, Leiden, except two paratypes (1 ♂, 1 ♀) in each of the following institutes: Museum Zoologicum Bogoriense, Cibinong, Australian National Insect Collection, Canberra, and the Natural History Museum, London.

Antennal club.— Basal 3/5 of underside white or pale ochreous, apical 2/5 black.

Forewing (figs 81, 97).— Length ♂ 9.6-10.9 mm, ♀ 9.7-11.8 mm. Male and female similar. Upper side brown with more or less golden sheen and tawny to yellow spots; spots in spaces 1bc (may be absent), 2 and 3 more or less in a straight line, spots in spaces 4 and 5 more or less in continuation of these spots or slightly displaced outward, forming a narrow line pointing to outer margin just above end of vein 6; spot in space 6 narrow, just beyond end cell, continued into linear spot in space 7 which extends along vein 8 almost to apex, the spots in spaces 6 and 7 together forming a narrow line parallel to the line formed by the spots in spaces 4 and 5; narrow tawny line centrally in cell against cubitus, and more distad in cell usually a linear, more or less separate spot against radius; there may be some pale scales over the latter spot in spaces 9 and 10; fringes brownish, sometimes more or less tawny outwardly. Underside about as upper side; apical third more or less golden dusted, spots paler, more or less extended along veins, pale yellow or whitish in spaces 4-7; bluish white line along outer margin, inwardly bordered by narrow brown line.



Figs 64-69. Distribution of *Taractrocera* species.

Hindwing (figs 81, 97).— Upper side colours as on forewing; fringes tawny; spots in spaces 2-5 in a straight line almost reaching outer margin at end of vein 6; spot in space 6 linear, almost reaching outer margin at end of vein 7; vague linear spot in upper part, and often also in lower part of cell. Underside ground-colour dark brown, but largely overlaid by dense warm ochreous colouring from vein 2A to costa, narrowly bluish white along costa, and with narrow bluish white line along outer margin narrowly bordered by dark brown; spots as on upper side, but more extensive, also along veins, and pure white to pale cream-coloured, partly bordered by dark brown; also white streak along vein 2A.

Secondary sexual characters.— Male without brands or stigma.

Male genitalia (figs 23, 34).— Ventral half of latero-distal rim of tergite VIII slightly extended caudad, more strongly so in upper part where it points dorso-caudad , reaching well beyond dorso-distal edge of tergite; comb of stiff hairs occupying almost entire edge of extension. In dorsal view, distal part of uncus elongate-triangular, weakly shouldered, with broadly rounded apex. Valva, upper process twice as long as wide, with finely serrate dorsal edge, reaching to two thirds of lower process; lower process rounded-rectangular; few spines pointing inwards near distal edge.

Female genitalia (fig. 54).— No lamella antevaginalis. Lamella postvaginalis about as long as wide, slightly expanding towards apex; distal edge shallowly indented; dorsal and ventral sides covered with relatively long, soft spines. Ductus and corpus bursae membranous, without special structures. Apophyses posteriores about twice as long as papillae anales. Sclerites of tergum VIII more or less triangular, with base at caudal rim; apophyses anteriores 1.5 x as long as sclerite.

Etymology.— The species is named after Gunung Trikora, with 4750 m one of the highest mountain peaks in Irian Jaya. The mountain was formerly known as "Wilhelminatop". Lake Habbema, where most of the specimens of the type series were caught, is about 15 km north of the top of Gunung Trikora.

Distribution (fig. 69) and habitat.— Only known from the type locality. The habitat around Lake Habbema (water level at about 3225 m) was described by Toxopeus (1940) as "moorland, fens and sparse coniferous forest, furthermore the highest outposts of the high mountain moss forest." The few specimens caught higher up were collected in a swampy alpine vegetation. The collection period was at the end of the dry season.

Taractrocera fusca spec. nov.

Material.— Holotype, ♂, New Guinea, Western Highlands, Mt. Hagen Range, Murmur Pass, 8700 ft., 27.10-20.12.1961, W.W. Brandt; 4 ♂, 2 ♀, paratypes, same data as for holotype. Holotype and 3 ♂, 1 ♀ paratype in Australian National Insect Collection, Canberra; 1 ♂, 1 ♀ paratype in National Museum of Natural History, Leiden.

Antennal club.— Basal 3/5 of underside white or pale ochreous, apical 2/5 black.

Forewing (figs 82, 98).— Male, upper side, uniformly dark brown with slight ochreous dusting; underside dark brown, apical half with dense yellow superscaling, faint traces of spots and yellow linear lower cell spot. Female as male, but spots much better developed.

Hindwing (figs 82, 98).— Male, upper side as forewing, with faint traces of spots;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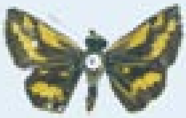
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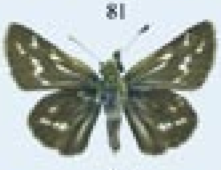
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underside warm yellow-brown, a clear-white stripe from base to termen in space 1c; narrow white spots in spaces 2-5, 7 and cell. Female as male but spots much better developed; on underside, spot in space 7 more or less extended along vein 6 to spot in space 5; black areas bordering the white spots, together with the warm yellow-brown ground-colour making the underside very attractive.

Secondary sexual characters.— Male without brands or stigma.

Male genitalia (figs 24, 39).— Ventral half of latero-distal rim of tergite VIII obtuse-triangularly extended caudad, more strongly so in upper part where it points dorso-caudad, reaching well beyond dorso-distal edge of tergite; comb of stiff hairs occupying entire edge of extension. In dorsal view, distal part of uncus triangular, with obtusely pointed apex. Valva, upper process twice as long as wide, with finely serrate dorsal edge, reaching to just beyond middle of lower process; lower process rounded-rectangular, shorter than wide, heavier than in *T. trikora*; few spines pointing inwards near distal edge.

Female genitalia (fig. 53).— No lamella antevaginalis. Lamella postvaginalis about as long as wide, slightly expanding towards apex; distal edge indented; dorsal side covered with relatively long, soft spines; ventral side smooth. Ductus and corpus bursae membranous, without special structures. Apophyses posteriores about 1.7 times as long as papillae anales. Sclerites of tergum VIII more or less rectangular, but narrowing ventrally; apophyses anteriores expanded near base, 1.7 x as long as sclerite.

Etymology.— The name relates to the dull brown colour of the upper side of the wings.

Distribution (fig. 69) and habitat.— Only known from the type locality. No information other than altitude: 8700 ft.

Taractrocera ardonia (Hewitson, 1868)

External characters (figs 83, 99).— Spots on upper side creamy/pale ochreous. Upper side forewing, cell spots overlapping, subequal or upper cell spot larger. Underside hindwing, veins darker than ground-colour between spots and termen.

Secondary sexual characters.— Absent.

Male genitalia (figs. 25, 40).— Latero-distal rim of tergite VIII with rounded process at ventral corner, reaching just beyond dorso-distal rim; comb of stiff hairs moderately

◀ Figs 70-101. Upper (70-85) and under side (86-101) of *Taractrocera* species, 1.23 x natural size. All specimens are males, and deposited in the National Museum of Natural History, Leiden. 70, 86, *T. anisomorpha* (Indonesia, Wetar, K. Schädler); 71, 87, *T. ilia beta* (Papua New Guinea, Bulwa, Febr. 1935, F.H. Taylor); 72, 88, *T. dolon diomedes*(Australia, Northern Territory, Kakado National Park, Nourlangie Creek, 30.iii.1991, R. de Jong); 73, 89, *T. ina* (Australia, Queensland, Mackay, 16 December 1934, V. Lindsay); 74, 90, *T. luzonensis luzonensis* (Philippines, Luzon, Mt. Makiling, 23.vi.1971. C.G. Treadaway); 75, 91, *T. archias archias* (Indonesia, Java, Bogor, Gn. Salak, 23.vii.1990, R. de Jong); 76, 92, *T. nigrolimbata nigrolimbata* (Indonesia, Java, Batavia, 1881; the same specimen was illustrated by Piepers, 1876: Pl. 7 fig. 5); 77, 93, *T. flavoides* (China, Tsekou, 1914, Père Ouvrard); 78, 94, *T. tilda* (China, Ta-Tsien-Lou, 1904, chasseurs du P. Déjean); 79, 95, *T. ceramas ceramas* (India, Travancore); 80, 96, *T. papyria papyria* (Australia, Sydney); 81, 97, *T. trikora* (paratype; for details of locality, etc., see text); 82, 98, *T. fusca* (paratype; for details of locality, etc., see text); 83, 99, *T. ardonia ardonia* (Indonesia, Sulawesi, Maros); 84, 100, *T. maevius maevius* (Sri Lanka, Colombo, 12.xii.1920); 85, 101, *T. danna* (N India, Simla).

long, occupying one fourth of lateral edge. In dorsal view, distal part of uncus long, cylindrical, with pointed apex. Valva with upper process large, rounded, as long as wide, extending to middle of lower process; lower process subrectangular, ventral edge convex; spines in a straight line, pointing inwards, near distal edge; indentation between upper and lower processes V-shaped with rounded base.

Female genitalia (fig. 55).— No antevaginal plate. Rectangular postvaginal plate, 1.5 times as long as wide, apically straight, dorsally spinulose, but apical part smooth., dorsally with two sharp longitudinal ridges, ventrally with a dull medial longitudinal ridge.

Distribution (fig. 67).— Malaysia, Borneo (Kalimantan, Sarawak, Brunei, Sabah), S Sulawesi (northernmost locality: Mamasa in W Toraja land). Evans (1949) also mentioned Sangihe ('Sangir') as locality, based on Plötz' '*?Telesto sangira*', but the apparent holotype of *?Telesto sangira* in the Zoologisches Museum der Bayerischen Staates, Munich, is from Bantimurung in S Sulawesi. In Sulawesi from sea level to at least 1.200 m.

Geographic variation.— Two subspecies are recognized, ssp. *ardonia* in Sulawesi and Salayar, and ssp. *sumatrensis* Evans, 1926, in Malay Peninsula and Borneo.

Taractrocera maevius (Fabricius, 1793)

External characters (figs 84, 100).— Spots on the upper side whitish to creamish/ pale ochreous. Upper side forewing, cell spots as in *T. danna*, but both smaller and not connected. Underside hindwing, veins paler than ground-colour.

Secondary sexual characters.— Absent.

Male genitalia (fig. 41).— Latero-distal rim of tergite VIII rather weakly produced at ventral corner, not reaching beyond dorso-distal rim; comb of stiff hairs moderately long, occupying one fourth of lateral edge. In dorsal view, distal part of uncus shouldered or bottle-shaped, with rounded apex. Valva with upper process slightly longer than wide, extending to about one third of lower process; lower process truncate-circular; spines in a slightly curved row near distal and dorso-distal edge, more or less pointing inwards; indentation between upper and lower processes narrow, almost a slit.

Female genitalia (fig. 56).— No antevaginal plate. Rectangular postvaginal plate, slightly longer than wide, apically almost straight, dorsally spinulose.

Distribution (fig. 67).— From Sri Lanka through India to N Pakistan, and through Nepal, NE India, Burma and N Thailand (Pinratana, 1985) to Laos (Motono & Negishi, 1989). In Nepal from below 1.500 ft to 9.000 ft (Smith, 1994).

Geographic variation.— Two subspecies are recognized, ssp. *maevius* in Sri Lanka, ssp. *sagara* (Moore, 1865) on the mainland.

Taractrocera danna (Moore, 1865)

External characters (figs 85, 101).— The white to creamy spots on the upper side readily distinguish this species from its congeners, except *T. maevius* and *T. ardonia*. Upper side forewing, lower cell spot connected to upper cell spot, larger than latter and extended towards the wing base. Underside hindwing veins concolourous with ground-colour.

Secondary sexual characters.— Absent.

Male genitalia (figs 26, 42).— Latero-distal rim of tergite VIII weakly produced just under middle, not reaching beyond dorso-distal rim; comb of stiff hairs moderately long, occupying almost half of lateral edge. In dorsal view, distal part of uncus elongate-triangular with rounded apex. Valva with upper process twice as long as wide, extending to about two thirds of lower process; lower process rectangular with rounded corners, slightly shorter than wide; spines pointing inwards, near distal edge; indentation between upper and lower processes deeply U-shaped.

Female genitalia (fig. 57).— No antevaginal plate. Elongate, rectangular postvaginal plate, more than twice as long as wide, apically shallowly indented, dorsally spinulose.

Distribution (fig. 66).— Restricted to the Himalayas, from Kashmir through Nepal, S. Thibet and Sikkim to Bhutan. In Nepal found between 4.500 ft and 13.000 ft (Smith, 1994).

Geographic variation.— None.

Phylogeny of the genus *Taractrocera*

The list of characters used for the phylogenetic analysis is given in table 2, and the accompanying characters matrix in table 3. The data were analyzed using three programs, viz., PAUP version 4B10 (Swofford, 2000), Hennig86 version 1.5 and PeeWee version 2.1. *Suniana sunias* (Felder, 1860) and *Ocybadistes walkeri* Heron, 1894, belonging to genera which are thought to form a monophyletic group with *Taractrocera*, were taken as outgroup. With all characters set to unordered, PAUP and Hennig86 yielded a single most parsimonious tree (fig. 102A) with length= 132, CI= 0.485 and RI= 0.575. With characters 2, 6, 32, 37, and 41 (characters for which ordering seems reasonable) set to ordered, PAUP and Hennig86 yielded three equally parsimonious trees with length= 137, CI= 0.467 and RI= 0.585. Among these trees, the tree with the best character fit, i.e. with the highest average character consistency index, viz., 0.5912 (see de Jong et al., 1996) is slightly different from the single tree found with all characters unordered (fig. 102B). PeeWee finds two trees in both cases (fig. 102C, D), i.e. with characters unordered, or with characters ordered as described above. The two trees with characters unordered have length= 133 and f= 267.1 (imported into PAUP, CI= 0.481 and RI= 0.569). The two trees with characters ordered are identical to the two trees with the characters unordered, but have length= 139 and f= 259.3 (imported into PAUP, CI= 0.460 and RI= 0.574). So altogether there are four trees which can be seen as so many hypotheses of the phylogeny of the genus. The nodes of the trees where the differences are found have been numbered in fig. 102, as follows:

1a *anisomorpha* at base; 1b *dolon+ilia* at base of genus;
2a *luzonensis+archias+nigrolimbata* monophyletic; 2b+2c paraphyletic;
3a *papyria* splits off before *ceramas*, *tilda* and *flavoides*; 3b thereafter;
4a *ceramas+tilda+flavoides* monophyletic; 4b paraphyletic.

The character support for the various clades was checked with the Trace Character Option of MacClade version 3.04. In table 4 the support is expressed in uniqueness of the character state in the genus, and its universality in the clade. Obviously, the best support is by those characters which have a unique state in all species of the clade. Since by the characters setting to ordered actually a new data matrix is created, the comparison is done separately for the trees with all characters unordered, and those with a

Table 2. Characters and characters states.

1 antennal club – 0 not hollowed; 1 hollowed

2 antennal club – 0 with ‘normal’ apiculus; 1 nudum triangular; 2 nudum semi-ellipsoid; 3 nudum semi-circular

3 nudum – 0 dark brown; 1 tawny; 2 black

4 palpi, hairs – 0 not concealing protruding 3rd segment; 1 long, concealing 3rd segment

5 wing markings upperside – 0 tawny; 1 white or whitish

6 upperside forewing, upper and lower cell spot – 0 filling most or all of cell; 1 forming single cell spot across cell, not filling cell; 2 separate; 3 only upper cell spot present; 4 no cell spots

7 upperside forewing, costa – 0 tawny from base to end cell; 1 brown from base to apex

8 upperside forewing, spot 1bc – 0 parallel to termen; 1 oblique, outer edge at vein 2 closer to termen than at vein 1; 2 reduced (only upper part present) or absent

9 upperside forewing, line through middle of spots 2 and 3 – 0 through apex or through costa close to apex; 1 through spots 6-8

10 upperside forewing, spots 4-5 – 0 midway betwenn termen and spot 3 or closer to latter; 1 widely detached, closer to termen than to spot 3

11 upperside forewing, spots 4-5 – 0 tending to be closer to the lower discal spots than to the apical spots; 1 always separate or farther from lower discal spots than from apical spots

12 upperside hindwing, cell spot – 0 well-defined; 1 weakly developed to absent

13 upperside hindwing, spots 4-5 – 0 in line with spots 1c-3; 1 out of line, closer to termen

14 upperside hindwing, spots 1c-5 – 0 more or less parallel to termen, with spot 5 only slightly closer to termen than to spot 1c or 2; 1 ob liaque, line through them ending on termen in space 6; 2 not in line

15 upperside or underside hindwing, discal band – 0 continued into space 7; 1 not continued into space 7

16 underside hindwing, colour of spots – 0 yellow; 1 white

17 underside hindwing, space 1c – 0 without white streak from base to termen; 1 with white streak from base to termen

18 underside hindwing, veins – 0 concolourous with ground; 1 paler than ground; 2 more or less darkened

19 underside forewing and hindwing – 0 no greyish white marginal line; 1 with fine greyish white marginal line

20 male, distal edge tergite 8 dorsally – 0 straight; 1 centrally extended

21 male, distal edge tergite 8 ventrolaterally – 0 straight; 1 with rounded extension; 2 with more or less triangular extension directed distally; 3 with dorsally directed extension

22 male, distal edge tergite 8 – 0 with ventrolateral spines; 1 smooth

23 male, upperside forewing – 0 no brand or stigma; 1 with brands or stigma

24 male genitalia, apex of uncus – 0 pointed; 1 rounded; 2 indented; 3 bipartite

25 male genitalia, in dorsal view, distal half of uncus with sides – 0 tapering to apex, sides straight (uncus more or less triangular); 1 tapering to uncus, sides wavy/sinusoid; 2 shouldered, from there parallel to apex

26 male genitalia, spines on valva – 0 absent; 1 present

27 male genitalia, spines on valva – 0 on distal edge of cucullus; 1 on dorsodistal edge of cucullus

28 male genitalia, costal process – 0 absent; 1 present

29 male genitalia, shape of costal process – 0 rounded; 1 triangular

30 male genitalia, costal process – 0 not reaching beyond middle of dorsal edge of cucullus; 1 well beyond middle of dorsal edge of cucullus

31 male genitalia, width of costal process at base – 0 <1/5 of total width of valva; 1 > ¼ of total width of valva

32 male genitalia, cucullus – 0 shorter than wide; 1 about as long as wide; 2 longer than wide

33 female genitalia, lamella antevaginalis – 0 absent; 1 present

34 female genitalia, lamella antevaginalis – 0 rectangular, longer than wide; 1 rectangular, wider than long; 2 elongate, finger-like

35 female genitalia, lamella postvaginalis – 0 absent; 1 present

36 female genitalia, lamella postvaginalis – 0 widt more or less parallel sides; 1 distally slightly expanded; 2 whole plate ovoid

37 female genitalia, lamella postvaginalis – 0 about as long as wide; 1 1-1.5 x as long as wide; 2 >2 x as long as wide

Table 2. Cont.

38 female genitalia, distal edge of lamella postvaginalis – 0 straight or slightly curved; 1 dome-shaped; 2 indented; 3 deeply cleft

39 female genitalia, dorsal side of lamella postvaginalis – 0 spinulose all over; 1 soft spines not reaching distal rim; 2 smooth

40 female genitalia, ventral side of lamella postvaginalis – 0 spinulose; 1 smooth

41 female genitalia, apophyses posteriores – 0 shorter than papillae anales; 1 1-1.5 x length of papillae anales; 2 > 1.5 x length of papillae anales

Table 3. Character matrix for *Taractrocera* and two outgroup taxa.

danna	1200121100	0101111111	2001010101	000-102201	2
maevius	1200121101	0101011100	1001111100	000-101001	2
ardonia	1100111200	0101010200	1000210101	110-101011	1
ceramas	1310031311	1112000000	1001010101	000-110201	2
tilda	1200000010	0002000000	1001111100	000-110201	2
flavoides	1100000010	0012000000	1000111100	000-110201	2
luzonensis	1210000100	0000000000	0100211111	1010101221	1
archias	1210000100	0100100000	0001211101	1011102211	1
nigrolimbata	1110000000	0100100000	0001010100	0011111211	1
dolon	1110000100	0000100000	2110010100	1212121111	2
ina	1100000100	0000100000	1000211101	0211100021	1
ansisomorpha	11?0000000	0000100000	1010010100	0212100021	1
ilia	1100000100	0000000000	2011111111	1212102101	1
papyria	1120000100	0101110010	10122110--	--0-110301	1
fusca	1121041200	0101111010	2001010101	010-110201	2
trikora	1121021100	0101011010	3001110101	110-110200	2
Ocyb. walkeri	0000000000	0000100000	001000-0--	--0-0-----	0
Sun. sunias	0020000000	0000000000	0013-0-0--	--0-100000	0

Table 4. Support for specified clades (see fig. 102) by character states

clade nr	supported by				
	char. nr	state	unique*	universal**	remarks
1a	30	1	-	-	4 reversals
	31	1	-	-	5 reversals
1b	-	-	-	-	
2a	37	1, 2	-	x	
2b	12	1	x	-	1 reversal
	24	1	-	-	2 reversals
2c	36	1	x	-	1 reversal
3a	3	2	x	-	1 reversal
	14	1	x	x	
	16	1	x	x	
	19	1	x	-	1 reversal
3b	-	-	-	-	
4a	9	1	x	x	
	13	1	x	-	1 reversal
	14	2	x	x	
4b	6	1, 2, 3, 4	x	x	
	7	1	x	x	

* relates to situation in *Taractrocera* only

** occurring in all species on the clade

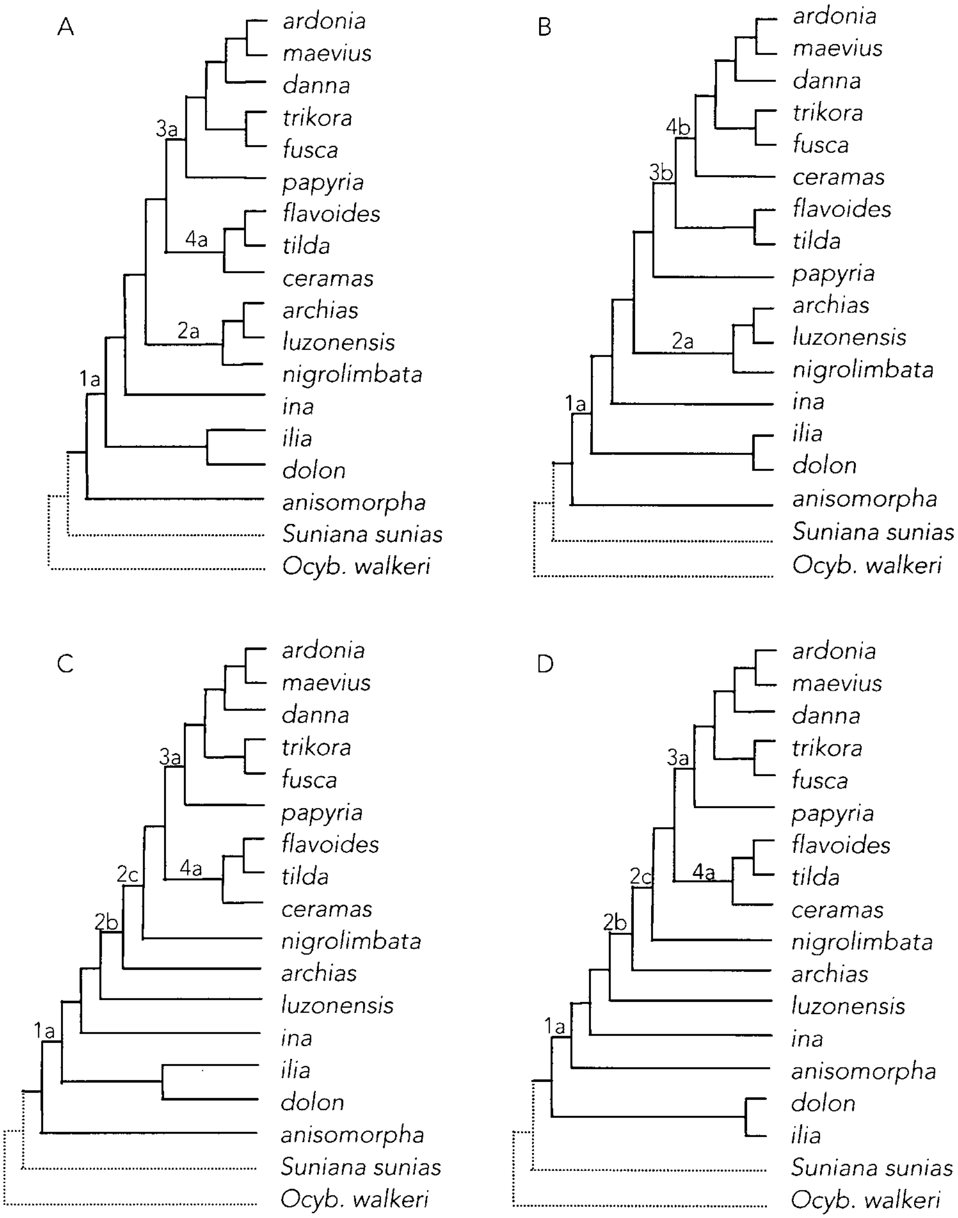

Fig. 102. Four most parsimonious trees for *Taractrocera* species and two outgroups. A, single most parsimonious tree generated by PAUP, with all characters set to unordered; B, preferred tree of three trees found by PAUP with a number of multistate characters set to ordered; C and D, the two trees found by PeeWee with characters either ordered or unordered. For further explanation, see text.

Table 5. Character support for the trees of fig. 102, based on table 3.

	unique	universal	unique & universal
unordered			
PAUP	7	5	4
PWE1	9	4	4
PWE2	9	4	4
ordered			
PAUP	2	3	2
PWE1	9	4	4
PWE2	9	4	4

number of characters ordered. Thus, tree A of fig. 102 is compared with trees C and D (all characters unordered), and tree B is compared with trees C and D (a number of characters ordered) (the PeeWee-trees, C and D, are topologically identical for characters either unordered or partly ordered).

The results are given in table 5. For unordered characters, both PeeWee trees turn out to be better supported than the PAUP tree, if we take uniqueness and universality as criteria. The difference is even stronger if we set some of the characters to ordered. This is not surprising, since the degree of homoplasy is the basis for calculation of character fit in PeeWee, while in PAUP (and Hennig86) the total number of changes on a tree, and not the number of changes per character on a particular tree, are taken as the criterion for tree selection. Intuitively a group is thought to be better supported the more characters it has of its own. For this reason I prefer the PeeWee trees. The two PeeWee trees differ in the position of *anisomorpha*, either at the base, or splitting off after *dolon+ilia*. The support for the two options can be read from table 4. The latter option is not supported by any single character. The former option is weakly supported by two characters, which, however, in the further evolution of the genus are reversed four and five times, respectively. Although this support is weak, it is more than nothing, and if a choice has to be made, the first PeeWee tree (= tree C) would be the preferable one. For the biogeographic considerations below, the difference is irrelevant.

Biogeography of the genus *Taractrocera*

Being distributed throughout the Oriental and Australian Regions, from Pakistan to Tasmania, with endemic species in both regions, *Taractrocera* is of interest in the study of the faunal interchange between the two regions. A first discussion of the biogeography of the genus in a wider context was given by de Jong (2001). The following aspects are discussed here: a) geographic origin of *Taractrocera*; b) dispersal from Australia to Asia; c) dispersal from Asia to Australia; d) adaptation to high altitude; e) distribution and ecology. In fig. 103 four area cladograms are given based on the trees in fig. 102. The areas have been chosen in the context of the faunal interchange between Asia and Australia. Thus, there is no sense, for instance, in presenting the Philippines as a separate area, and even the heterogeneous area "mainland Asia" is, for the present purpose, best treated as a single area.

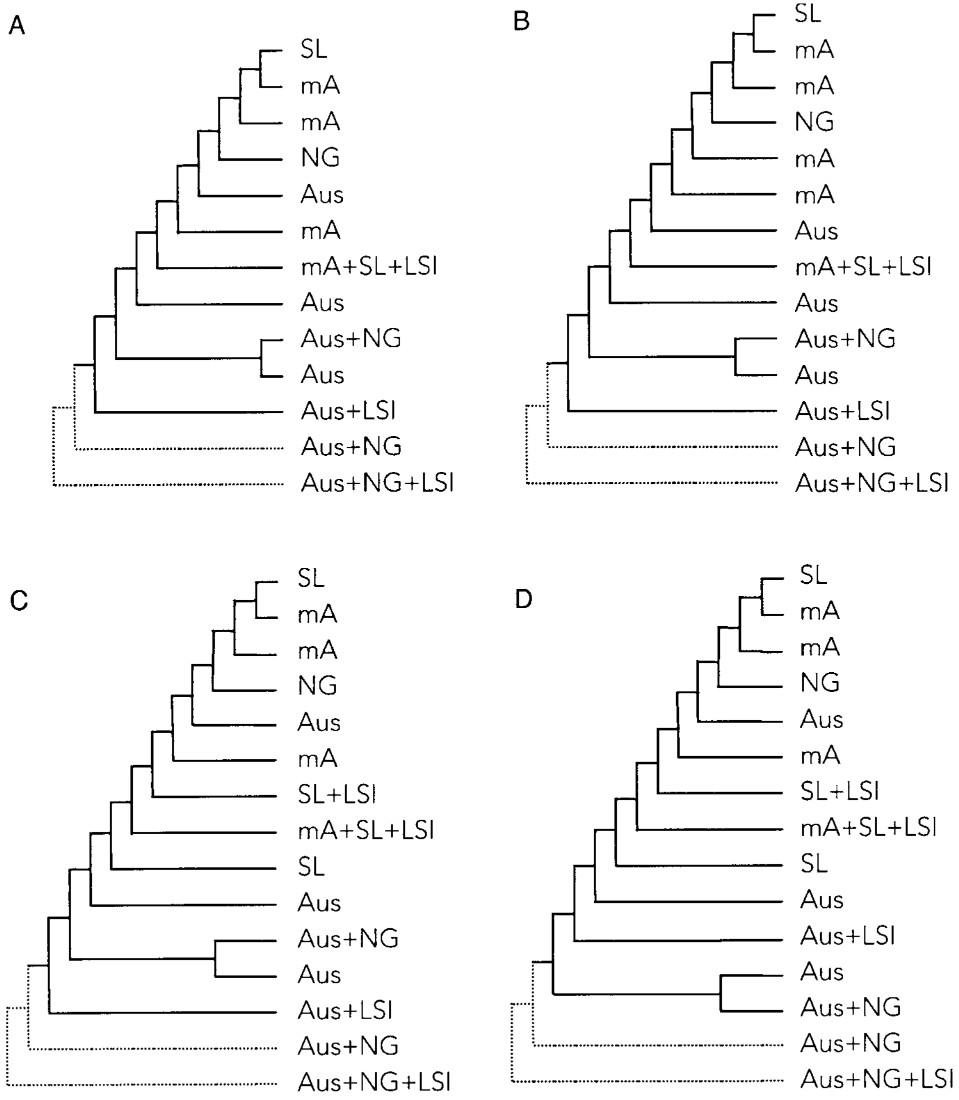

Fig. 103. Areacladograms based on the four phylogentic trees of fig. 102. Stippled lines: outgroup areas. Branches have been collapsed where the sister groups occupied the same general areas. Aus = Australia, LSI – Lesser Sunda Islands, mA = mainland Asia, NG = New Guinea, SL = Sundaland (plus Sulawesi).

Geographic origin of the genus *Taractrocera*

The area cladograms agree in an early differentiation of the genus in Australia. It does not imply that the genus is of Australian origin, but if the hypothesis of monophyly of *Taractrocera* + *Ocybadistes* + *Suniana* is correct (see above), this is an obvious conclusion (see also de Jong, 1990). In the absence of fossils and molecular data it is impossible to date the origin of *Taractrocera*. If monophyletic, the *Taractrocera* group of genera, with at present 14 genera and about 150 species, could either be a Gondwanan element, or an Asiatic element that somehow reached Australia. There is no proof of the occurrence of a sister group in another fragment of Gondwana, and consequently there is no proof of Gondwanan age (see also de Jong, 2003). Long distance dispersal from Asia to Australia in the early Tertiary seems unlikely because of sheer distance. According to Audley-Charles (1993: 16), "all islands of the Inner and Outer Banda Arc came into existence as islands during the late Miocene-Pliocene (...). Before the Miocene emergence there was no land occupying that part of the Earth known as the Banda Arc (...). The Banda Sea then extended all the way from the coast of Australia-New Guinea to Sulawesi." However, the 59 endemic Australian rodent species are considered the offspring of several waves of colonization from Asia (Keast, 1972; Lee et al., 1981). They first appear in the fossil record about 6-7 million years ago, but molecular evidence of extant species suggest that they may have entered Australia about 15 million years ago (Archer *et al.*, 1991, 1995). Bats have been present in Australia for a much longer time, and the majority, if not all bats had a Laurasian ancestry (Hall,1981; Godthelp et al., 1992), suggesting the presence of some kind of filter route. In view of the geographic position of Australia-New Guinea in the Miocene (see, e.g., Hall, 2002: figs 21-22), such a route would not have involved the present Banda Arc, if it would have existed at that time, but would have consisted of volcanoes and uplifted terranes that may have emerged and disappeared again since 20 Mya (Audley-Charles, 1987; Main, 1987) between New Guinea's Bird's Head and southeastern Sundaland (with which western Sulawesi was closely related). Thus, although the genus itself apparently originated in Australia, its ancestry may be Laurasian. This falls outside the scope of the present paper and has to await a phylogenetic study of the entire *Taractrocera* group of genera. Because of its present-day distribution, the evolving genus *Taractrocera* must have dispersed from Australia to Asia, and, as will be discussed below, there are reasons to suppose that the dispersal events took place in the Miocene before Australia (with New Guinea) reached its present position relative to Sundaland. It is, therefore, likely that the diversification of the *Taractrocera* group of genera preceded the collision of the Australian plate with the Asiatic plate.

Dispersal from Australia to Asia

At some stage the common ancestor of *T. ina* and its sister group invaded SE Asia. The dispersal event was followed by speciation in the Australian and Asiatic parts. The four area cladograms of fig. 103 agree in this respect. Again, the Miocene collision of the Australian plate with the Asiatic plate would have been the first realistic opportunity (i.e. if we refrain from invoking very long distance dispersal) for this dispersal event. There is some negative evidence that the dispersal of *Taractrocera* from Asia to Australia, which must have postdated the northward expansion if there is any truth in the reconstructed phylogeny, took place well before Australia-New Guinea reached its present position and before the Moluccas came into existence (see below, dispersal from Asia to Australia). This would place it not later than the late Miocene. We know nothing of differential speed of evolution. However, it seems unlikely that the diversification of the *Taractrocera* group of genera, leading to, among other things, the origin of the genus *Taractrocera*, the northward expansion of a subordinate group of *Taractrocera* and the southward expansion of an offshoot of this subordinate group, all took place in a short time span. This is an argument in favour of the idea that the diversification of the

Taractrocera group took place before the Australian plate collided with the Asiatic plate.

One of the extant Australian *Taractrocera* species, *T. anisomorpha*, also occurs in the eastern part of the Lesser Sunda Islands (Timor, Wetar). A similar pattern is found in the two genera with which *Taractrocera* forms a monophyletic group: *Ocybadistes walkeri* Heron, 1894 (Sumba to Tanimbar, New Guinea, Australia), *O. ardea* Bethune-Baker, 1906 (Wetar, New Guinea, Australia), and *Suniana lascivia* (Rosenstock, 1885) (Timor, Australia). The pattern recurs in other butterfly families as well, e.g., *Cressida cressida* (Fabricius, 1775) (Papilionidae) and *Candalides erinus* (Fabricius, 1775) (Lycaenidae). It is probably a widespread phenomenon. Van Steenis (1979) listed a number of plant species showing this pattern. Although lying on the Australian plate, Timor has never had a land connection with Australia: it emerged from the sea by uplift, about 5-6 Mya (Audley-Charles, 1993). Taxa occurring in Australia and Timor must have crossed the water gap. Apparently, this distribution pattern is not due to the history of Timor as part of the Australian plate, but to the fact that it is the first island to be reached when going from Australia to the northwest. In the Pleistocene the sea level repeatedly sunk 100 to 200 m, exposing large tracts of dry land. This would place Timor at a distance of no more than 80 km from Australia. The last severance of the land connection between Australia and New Guinea across the Torres Strait was only 6.500-8.000 years BP (Galloway & Kemp, 1981). It is uncertain whether the relative proximity of Timor was equally recent, but the fact that the Lesser Sunda Island representatives of the Australian species are not or only weakly differentiated from the Australian populations suggests a recent contact.

Dispersal from Asia to Australia

The four area cladograms differ with regard to details of the development in Asia and the subsequent spread to Australia and New Guinea. Area cladograms 103A, C and D agree in a relationship (Sundaland + mainland Asia (mainland Asia (Australia (New Guinea (mainland Asia (Sundaland, mainland Asia)))))). It suggests that at some time a Sundaland species became highly dispersive and extended its range over much of mainland Asia as well as into New Guinea and Australia. Thereafter it fell apart by vicariance into a number of species most of which speciated further in their respective general areas. In this scenario only a single dispersal event from Asia to Australia/New Guinea is needed. In area cladogram 103B two such dispersal events are needed. Thus, it is less parsimonious. Moreover, it suggests a direct relationship between mainland Asia and Australia, bypassing Sundaland. This seems a physical impossibility. For these reasons the scenario based on area cladograms 103A, C and D is preferred.

The expansion of the Asiatic species to the east was possibly helped by changing climatic conditions as part of the offshoot nowadays lives under temperate conditions or is at least tolerant of such conditions (see also below). For the dating and route of this expansion it may be meaningful that the clade concerned (*T. papyria* and its sister group) is absent from the Moluccas (as is the whole genus *Taractrocera*, except *T. luzonensis*, which occurs as far east as the Sula Archipelago, which administratively forms part of the Moluccas) and from the Lesser Sunda Islands. Extinction cannot be ruled out, but there are no indications to suggest that the clade ever had representatives in the

Moluccas or in the Lesser Sunda Islands. Moreover, the clade is also absent from North and East Sulawesi. Western Sulawesi (actually, the greater part of the province Sulawesi Selatan) has always been closely associated with Borneo (Hall, 1996, 1998, 2002; Moss & Wilson, 1998). It is uncertain when the eastern part, which separately came from the Australian plate, emerged. Audley-Charles (1987) depict it as still submerged in late Miocene. The northern arm derived from the east, as part of the island arcs on the collision zone of the Pacific and Australian plates. The restricted occurrence in Sulawesi and absence from the Moluccas and Lesser Sunda Islands could, thus, have a historical background and need not be the result of extinction. Obviously, if the expansion of this clade from Asia to Australia precedes the emergence of the present Banda Arc and the Moluccas (not later than 5-6 Mya; Audley-Charles, 1993), it pushes events in the evolution of *Taractrocera*, which must have occurred earlier if the phylogenetic reconstruction is correct, further back in time.

Adaptation to high altitude

Much has been written about origin and evolution of the mountain biotas of Indonesia and Australasia (e.g., Holloway, 1986; Smith, 1986a, 1986b;), including means and routes of dispersal from Asia to Australasia. In *Taractrocera* three species, *T. danna* (Himalayas), *T. fusca* and *T. trikora* (both New Guinea), are restricted to high altitudes. We do not need to postulate a special route for mountain species in this case. The three species do not form a monophyletic group and the adaptation to high altitudes could have evolved independently in the Himalayas and New Guinea. If we take the whole clade, of which the ancestor dispersed to Australasia, into consideration, we see, apart from the three high altitude species, one species, *T. papyria*, occurring from tropical Australia all the way down to Tasmania, where it reaches up to 600 m; one species, *T. maevius*, in mainland Asia, occurring from lowland to 2.700 m; and one species, *T. ardonia*, occurring in Sundaland from sea level to at least 1.200 m. Apparently this clade is rather tolerant of lower temperatures. Moreover, its sister group (*T. ceramas*, *T. tilda* and *T. flavoides*) shows the same characteristic. The Indian-Chinese *T. ceramas* occurs in two forms, one flying below 1.100 m, the other over 2.000 m. The other two species occur in the mountains of the Chinese provinces of Yunnan and Sechuan. With such a temperature tolerance it is not surprising to find high altitude species in New Guinea, of which the ancestor may have reached New Guinea at a time when the mountains were still almost non-existent. Much of New Guinea was still low-lying at the end of the Pliocene (Ollier, 1986). An uplift of 2260 m has been found for some parts of New Guinea in the last 120.000 years. *T. fusca* and *T. trikora* may have simply been carried up by the uplift of the mountains. Shortly before his untimely death Toxopeus (1950), the collector of *T. trikora*, attributed the paucity of butterflies of open habitats at high altitudes in New Guinea to the recent and fast uplift of the mountains, by which numerous species must have become extinct, while the few survivors who could adapt to cooler conditions became strongly isolated. Unfortunately this paper went largely unnoticed in biogeographical literature, as did his thesis (Toxopeus, 1930) on the species as a function of time and place, at the time a pioneering publication, but largely overlooked, since he never took the time to translate it into a more widespread language than Dutch (and few biogeographers take the trouble to expand their knowledge beyond their mother tongue).

Distribution and ecology

Phylogeny sets speciation events in a sequential order. In case of allopatric speciation (the "default setting" in the analyses) geographical events are, consequently, also set in a sequential order, which can be compared with the sequence of geological events. Often, and in the case of SE Asia usually, the focus is on the changing distribution of land and sea. For dispersing terrestrial organisms, however, the presence of land is not the only constraint in dispersal. Equally important are the availability of the correct habitat and, in case of phytophagous insects, the presence of the correct food plants. Seen in this light, the absence of *Taractrocera* from the Moluccas, the very restricted occurrence in New Guinea, and the presence of an Australian species in the Lesser Sunda Islands may have an ecological as well as a historical background. The adaptation to grassy places is advantageous in long distance dispersal, since this kind of habitat is more widespread than, e.g., mountain forest. Moreover, like many hesperiines, the *Taractrocera* species do not seem very dainty in their choice of grass species. The occurrence of only one of the five Australian species in New Guinea, in a few relatively dry spots only, indicates that rain forest is an almost insurmountable barrier for *Taractrocera*. Supposing that the habitat preference did not change drastically during the evolution of the genus, during the expansions of *Taractrocera* to the north and to the south a seasonally dry climate must have occurred in the area concerned. In this context it is relevant to note that in the Middle and Late Miocene a transition took place in Australia from widespread tropical forests to plant assemblages with an abundance of grasses (Crowley & North, 1991; White, 1996). The Miocene desiccation of Australia may have contributed to or even have caused the early radiation of the *Taractrocera* group of genera.

Discussion and conclusion

Examination of a single genus cannot reveal how far the inferred events were caused by general, external events affecting widely divergent groups of organisms, or by isolated events with internal causes (i.e. occurring only in the group under study). Although dispersal across inhabitable areas is the result of an internal cause, it is externally constrained by the available opportunities. In an expressive way, R.I. Vane-Wright (pers. comm.) compared it with the process of batik: although the dye is applied at random, it only sticks to the parts where the textile has not been waxed. The same pattern emerges, irrespective of the applied dye. The difference between jump dispersal and gradual dispersal (i.e. without jumping across inhabitable areas) is only a matter of degree. We can at best say that the more general a pattern is, the easier dispersal must have been. Therefore, if the inferred phylogeny of *Taractrocera* is correct and if our considerations about the biogeography are not biased by large-scale extinctions, it can be expected that similar patterns are found in other groups of organisms. So far, little work has been done in this area based on the phylogeny of the studied organisms. Available scenario's (e.g., Heatwole, 1987), although containing an important body of information, are rather superficial because they are not based on phylogenetic analyses or do not adequately take the complicated geological history into consideration. Fossils are also important in this context since they give a minimum age of the occurrence in an area. Based on a study of plant fossils, Truswell et al. (1987: 32) came to the conclusion that the fossil record "suggests that there was some measure of floristic interchange between Australia and regions to the north in the late Cretaceous and early Tertiary. There is limited evidence that dispersal occurred in both directions, with some Australian taxa crossing into Sundaland before the mid-Miocene collision." This agrees with the conclusion of the present study: if the dispersal of *Taractrocera* from Asia to Australasia indeed preceded the emergence of the Banda Arc and the Moluccas, the initial dispersal of *Taractrocera* from Australia to Asia could well have preceded the collision. Geological evidence for the presence of stepping stones or of northward-drifting fragments of Australian origin acting as Noah's ark in Mid-Tertiary is scant. However, in view of the rapid changes in the area in relatively recent times (Timor, for instance, was uplifted more than 3.000 m in the last 2 million years; Simandjuntak & Barber, 1996), it can be expected that traces of emergent land in mid-Tertiary have long since disappeared.

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