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Phylogeny and biogeography of the Platystictidae (Odonata)

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Citation

Tol, J. van. (2009, February 26). *Phylogeny and biogeography of the Platystictidae (Odonata)*. Retrieved from <https://hdl.handle.net/1887/13522>

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Note: To cite this publication please use the final published version (if applicable).

7. The Odonata of Sulawesi and adjacent islands.

Part 6. Revision of the genus *Drepanosticta* Laidlaw (Zygoptera: Platystictidae)

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Received July 31, 2006 / Revised and accepted August 27, 2006

Abstract

The genus *Drepanosticta* Laidlaw is revised for Sulawesi and adjacent islands. *D. ephippiata* Lieftinck is redescribed, and *D. bicolor* sp. n. (Buton Island), *D. hamulifera* sp. n. (Kabaena Island), *D. penicillata* sp. n. (central Sulawesi) and *D. watuwilensis* sp. n. (SE Sulawesi) are described as new to science. A key to the males is provided. Based on the structure of the posterior margin of the pronotum, *D. ephippiata* presumably represents a monophyletic clade with the *Drepanosticta lymetta* and *D. megametta* species-groups, including spp. from the mainland of New Guinea. This group is distributed from Mindanao (Philippines) eastward to the northern Moluccas, northern New Guinea and the Solomon Islands. The newly described species are morphologically quite diverse; they are presumably most closely related to species occurring SE of Sulawesi.

Introduction

The platystictid genus *Protosticta* Selys shows remarkable radiation in the Indonesian island of Sulawesi (Celebes) (van Tol, 2000), while only one

species of *Drepanosticta* Laidlaw is known from that area until now. The present paper revises the material of the genus *Drepanosticta* from Sulawesi, and the adjacent islands of Buton and Kabaena. No specimens are available from the islands of Saleyer, Sangihe, Talaud or the Sula islands. These islands are relatively poorly investigated, although one species of *Protosticta* is known from Sangihe (van Tol, 2000).

Drepanosticta ephippiata was described by Lieftinck (1937) from Tondano, not far from Manado in the northern arm of Sulawesi. Although it is confined to the northern arm and the central part of the island, and Pulau Peleng (Banggai archipelago), it still appears to be the most common and widespread species of *Drepanosticta* of Sulawesi. Four other species, newly described in the present paper, have more restricted ranges and are only known from the southern centre, the southeastern arm of Sulawesi, or the adjacent islands of Buton and Kabaena. These areas were mainly explored during the last twenty years during field work that started with Project Wallace (1985) in the northern peninsula, and continued in a series of expeditions organised by the National Museum of Natural History at Leiden, in co-operation with the

Previously published in: *Odonatologica* 36 [2007]: 171-189, figs. 1-35.

Indonesian universities of Makassar, Manado and Kendari, and the Indonesian Institute of Sciences (Jakarta and Bogor).

This paper is one of a series revising the Platystictidae of Southeast Asia (van Tol, 2000, 2005, in press), preparing a reconstruction of the phylogeny of this family. It is also a contribution to the revision of the Sulawesi odonate fauna.

Methods

Specimens were studied using stereomicroscopes (Leica MZ16A, Olympus). Illustrations were prepared using a camera lucida on the MZ16A. A Nikon D70S digital camera equipped with a 60 mm Micronikkor lens with bellows was used for the illustrations of the synthorax. Measurements are in millimetres, and were taken using a standard ruler (abdomen, wings), or an ocular ruler in a microscope (pterostigma, anal appendages). JvT numbers are preserved with the specimens studied, using a small label with the specimen, or written on the 5x3 inch label card in the envelope with the specimen. All specimens are preserved in the collection of papered specimens of the National Museum of Natural History (Leiden, The Netherlands), except if indicated otherwise.

Notes on phylogeny and biogeography

Affinities of Platystictidae of Sulawesi. – These paragraphs provide a preliminary analysis of the affinities of the Sulawesi Platystictidae, and hypothesize a scenario of their historical biogeography. Detailed studies of the phylogeny are in progress. The phylogenetic relationships and distribution patterns of the Sulawesi *Drepanosticta* species may contribute to understanding the historical relationships of the various parts of the island. This group of species does not show the radiation into a series of closely related taxa, as has been found in Sulawesi for the genus *Protosticta* (van Tol, 2000), or in the Philippines and the Moluccas for the genus *Drepanosticta* (van Tol, 2005, in press). The Sulawesi species here assigned to *Drepanosticta* are quite diverse in morphological characters. They presumably

have their closest affinities to species distributed east of Sulawesi. This is in contrast with the *Protosticta* species of Sulawesi, which have distinct western phylogenetic relationships.

D. ephippiata belongs to a clade with a distinct autapomorphy, a pair of processes on the hind margin of the pronotum, which otherwise occurs in the Philippines (Mindanao) (van Tol, 2005), the Moluccas (van Tol, in press), New Guinea (Lieftinck, 1932) and the Solomon Islands (van Tol, unpublished). Two presumably monophyletic groups within this clade were characterized by van Tol (2005), viz. the *D. lymetta* and the *D. megametta* group. Within this clade, the *D. megametta* group is well characterized by the flat processes. The other species can be divided into three groups, viz. the *D. lymetta* group s.s., an unnamed group confined to northern New Guinea, and the *D. ephippiata* group (*D. ephippiata* only), of which the relationships are presently not well understood. The Sulawesi *D. ephippiata* differs from the other species by the tapering, rather than widening, posterior processes of the posterior lobe of the pronotum.

The other species dealt with in the present paper are characterized by a simple hind margin of the posterior lobe of the pronotum, a distinct pale stripe over the metepisternum (Figs 31-35), and large dorso-ventrally compressed superior anal appendages. Species with such characters are also known from Flores, viz. *D. floresiana* Lieftinck, and Lombok, viz. *D. berlandi* Lieftinck (Lieftinck, 1939). The remarkably shaped superior anal appendage is a synapomorphy for the species of this group. The variation within the group of species of Sulawesi, however, is large and the phylogenetic relationships are subject to further analysis.

Notes on the historical biogeography. – Platystictidae are poorly dispersing, stenotopic odonates, and active 'island hopping' is not a plausible scenario. If the distribution of the present species or their ancestors is the result of dispersal with the islands rafting along the continental plates, the relationships of the Sulawesi platystictids would reflect the tectonic history of the region.



Figure 1. Distribution of *Drepanosticta* species in Sulawesi.
[Revised version].

The biogeography of Southeast Asia and the Pacific is still poorly understood, especially due to the complex geological history of the region, but also since well-founded phylogenetic reconstructions with estimates of the timing of splitting of lineages are virtually absent (Turner et al., 2001). The palaeohistory of Sulawesi is particularly complicated. The island consists of at least four palaeo-islands, which merged only between five and ten million years ago. Some of these palaeo-islands may have had a sub-aerial history for more than twenty million years, but others may have been submerged until they collided with other islands or continental fragments.

The genus *Protosticta* is widespread in the mainland of Southeast Asia and Borneo, and reaches its eastern limit in Sulawesi (van Tol, 2000). Species recently

described from the Philippines and assigned to *Protosticta* (van Tol, 2005) only share the loss of the Ab vein, a doubtful synapomorphy with the type species *Protosticta simplicinervis* (Selys) from Sulawesi. Anyhow, no platystictids with characters of *Protosticta* are known east of Wallacea. So, while *Protosticta* seems to represent a western element in the dragonfly fauna of Sulawesi, the *Drepanosticta* species of Sulawesi clearly belong to lineages with northern, eastern or southern ranges.

While the genus *Protosticta* is well represented in the southwestern arm of Sulawesi (van Tol, 2000), there are no records of *Drepanosticta* from that area. This is a clear indication of the poor dispersal power of the species in *Drepanosticta*. The southwestern part of the island already has approximately the same position to Borneo for about 45 million years (e.g., Wilson & Moss, 1999). Although it is still uncertain

whether this palaeo-island has ever been connected to Borneo, both areas have certainly been closer together during periods of lower levels of the oceans, e.g. during the last ice ages. Still, exchange between Borneo and Sulawesi of poorly dispersing biotas, such as Platystictidae, must have been difficult for the last 45 million years. Although the monophyly of all Sulawesi *Protosticta* has not been ascertained, the Bornean and Sulawesi species are certainly more closely related than those of Sulawesi and the mainland, or Sulawesi and the Philippines. If Borneo and Sulawesi have never been connected, this would include (at least) one *Protosticta* dispersal event between both islands. The absence of sister-group relationships between the *Drepanosticta* species of Borneo and Sulawesi, and the complete absence of *Drepanosticta* from the southwestern arm, suggests poor faunal exchange between both regions.

Drepanosticta ehippiata, here assigned to a clade

characterized by a pair of processes on the posterior margin of the pronotum, is widespread in the northern peninsula, and is also known from the Banggai archipelago and (doubtfully) from the region between Rantepao and Palopo. The distribution of the clade shows distinct congruence with island arcs that were formed during the Eocene, when the Australian plate moved northward and subducted under the Philippine plate, forming the Philippine Arc. At least during the Eocene (35 Ma) this island arc included from west to east peninsular north-eastern Sulawesi, Mindanao and parts of the Moluccas, including Halmahera (Hill & Hall, 2003). Along the eastern margin of the Philippine plate the north-south oriented (South) Caroline Arc was formed at the collision zone with the Greater Pacific Plate. These two island arcs came more or less in line in west-east orientation, due to back-arc spreading, during the Late Oligocene (25 Ma). The Caroline Arc collided from west to east to the Australian plate from the Late Miocene (10 Ma), a process continuing up to today. Due to clockwise turning of the Caroline plate, the position of certain islands changed rapidly. Halmahera, for instance, had a position east of and close to the Vogelkop peninsula during the Middle Miocene (15 Ma).

Biogeographical reconstructions indicate that the eastern Philippines are inhabited by several monophyletic groups, which seem to have moved, or have been moved, from the Papuan region in western direction. Several aquatic groups, including the Calicnemiinae (Platycnemididae) (Gassmann, 2005; van Tol & Gassmann, in press), show distributions including New Guinea and the Philippines, but excluding the Moluccas and Sulawesi. Polhemus (1995) and Polhemus & Polhemus (1998) hypothesized a pre-Eocene 'Inner Melanesian arc system' for such patterns. It is unusual that such distributions include the northern Moluccas and Sulawesi. However, the odonate genus *Diplacina* Brauer (Libellulidae) represents another monophyletic group with such a distribution pattern. *Diplacina* species are generally more dispersive. The sister-group of the Sulawesi species *Diplacina militaris* Ris occurs on Mindanao (*D. bolivari*), while *D. militaris* is represented in

Sulawesi with two parapatric subspecies (van Tol, 1987). One subspecies, *D. militaris dumogae* Van Tol is confined to the northern arm, while the nominal subspecies is distributed over the rest of Sulawesi.

The genus *Diplacina* is also found with many species in New Guinea, eastward into the d'Entrecasteaux and Bismarck Islands, and with several species in the Moluccas (Halmahera, Ambon).

Some, perhaps all, of the remaining species of Sulawesi *Drepanosticta* share unique characters with a group of species with southern and eastern distributions, including *D. berlandi* Lieftinck (Lombok) and *D. floresiana* Lieftinck (Flores), and even the Papuan species *D. auriculata* (Selys) (see Lieftinck, 1938: p. 81-82, Fig. 18). In Sulawesi, this group is at least represented by *D. penicillata* sp. n., but may also include some or all of the other new species described in the present paper. Sister-group relationships between Sulawesi and the Lesser Sunda Islands have previously been found for prasiine cicadas (Duffels, 1990) and butterflies (Holloway, 1990), but these relationships were mainly found for species confined to the drier zones of both areas. Species of such habitats usually have significantly higher dispersal power. Further range extension northward on Sulawesi may have been prevented by climatic conditions. However, such a scenario cannot easily be understood for the stenotopic and poorly dispersing *Drepanosticta* species of Sulawesi. Dispersal events from the Lesser Sunda Islands to Sulawesi (or visa versa) are thus less likely. The alternative hypothesis would include the arrival of the Sulawesi lineage on one or more of the island fragments forming Sulawesi. Unfortunately, there is little geological support for a sub-aerial history of the fragments now forming Central and Southeastern Sulawesi. Neither the position of Central Sulawesi close to NW Australia during the Eocene, nor the history of the southeastern peninsula, provide a palaeogeographical key to such relationships (see Hill & Hall, 2003).

In conclusion, the Sulawesi *Drepanosticta* fauna shows complex relationships to faunal elements of both northern and southern origin, but apparently not with Bornean elements. The results of ongoing phylogenetic

studies, based on analysis of both morphological and molecular characters, will provide the basis to test the hypothesis of the historical biogeography of this family in Sulawesi.

List of *Drepanosticta* species of Sulawesi

Drepanosticta Laidlaw, 1917

D. ehippiata Lieftinck, 1937

Distribution. – North and Central Sulawesi; Banggai archipelago.

D. bicolor sp. n.

Distribution. – Buton Island.

D. hamulifera sp. n.

Distribution. – Kabaena Island.

D. penicillata sp. n.

Distribution. – Central Sulawesi.

D. watuwilensis sp. n.

Distribution. – Southeastern Sulawesi.

Key to males of *Drepanosticta* species of Sulawesi and adjacent islands

1. Hind margin of pronotum with a pair of curved processes, approximately as long as median line of median lobe of pronotum (Figs 2-3)
 *D. ehippiata* Lieftinck
- Hind margin of pronotum straight, or lateral corners with a sharp edge, but without a pair of curved processes (e.g. Figs 8-9) 2
2. Synthorax black, except for a dirty yellow marking over posterior part of mesopleural suture, and a dirty yellow marking starting at hind margin of synthorax near interpleural suture, running anteriorly over metepisternum and metepimeron, continuing over ventrum *D. bicolor* sp. n.
- Synthorax brownish black with conspicuous pale yellow stripe over metepisternum; ventrum pale yellow 3
3. Inferior appendage in ventral view stout, width of terminal part about one-sixth total length of appendage (Fig. 29); setae of tip of inferior appendage not in a tuft . . . *D. watuwilensis* sp. n.

- Inferior appendage in ventral view slender, width of terminal part (perpendicular to body axis) about one-tenth total length of appendage (Figs 16, 23); tip of inferior with a tuft of brown setae. 4
- 4. Tip of inferior appendage with a sharp tooth directed dorso-axially (Fig. 16); transverse occipital carina with angulate lateral extremities. Distribution: Kabaena *D. hamulifera* sp. n.
- Tip of inferior appendage smoothly curved (Fig. 23); transverse occipital carina poorly developed; lateral extremities hardly visible. Distribution: Central Sulawesi. *D. penicillata* sp. n.

Systematic part

Drepanosticta ehippiata Lieftinck

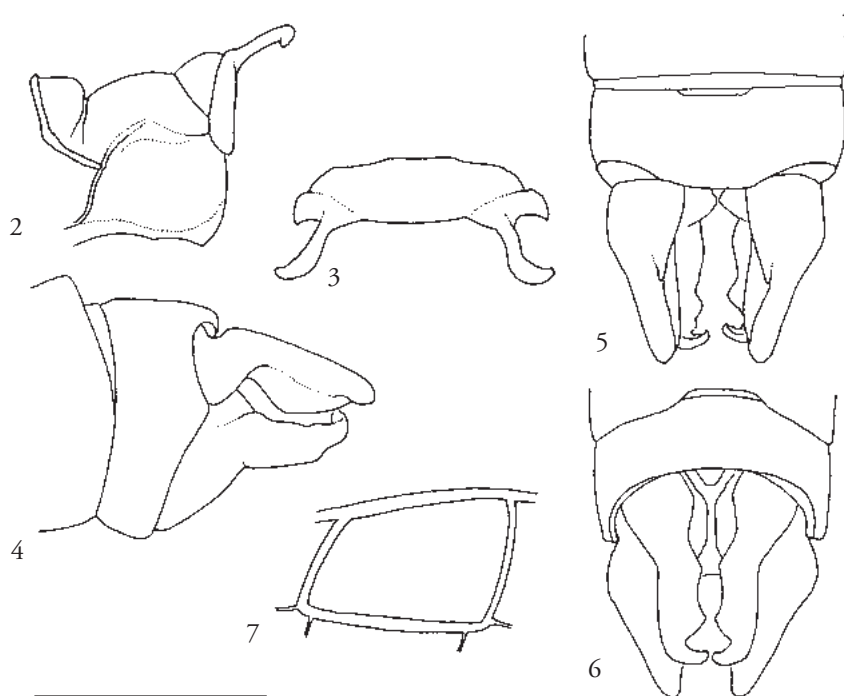
Figs 1-7, 31

Drepanosticta ehippiata Lieftinck, 1937: 72 [original description, relationships discussed]. – Lieftinck 1971: 86 [lectotype designated].

Material examined (31 specimens, including lectotype). – Northern Sulawesi: Tondano (type locality), 1935, 2 males; Manado, 19 May 1940, 1 male 1 female; Mapanget, 23 Jun 1940, 2 males; same site, 11 Aug 1940, 3 males 1 female; Pineleng, 14 Jul 1940, 2 males; Toli Toli, 6 Nov 1940, 1 female; same site, 5 Dec 1940, 6 males; Dampelas, 28 Nov 1940, 2 males 1 female; Airmadidi, 1 Dec 1940, 1 male; Kakaskasen [not found], 26 Dec 1940, 1 female; Dumoga-Bone National Park, 4 Jun 1985, 1 male 1 female. – Central Sulawesi: Tojambu (between Rantepao and Palopo), 29 Oct 1993, 1 male 1 female (purchased from insect dealer, locality uncertain). – Banggai Peninsula: Pulau Peleng, 31 Jul 1941, 2 males 1 female.

Description. – Small, brown species; distinguishable from other Sulawesi species by a pair of slender processes on posterior margin of posterior lobe of pronotum.

Male [JvT 11842, Celebes, Toli Toli]. – Head. Labium dirty ochreous, mandibles bluish white with anterior border brown, labrum bluish white, anterior one-fourth with brownish black border, gena dirty white, parts against the eye brownish black; anteclypeus bluish white; remaining part of head mat black with metallic lustre, underside of eyes shining black; occipital area with



Figures 2-7. *Drepanosticta ephippiata* Lieftinck, male. – 2, pronotum, left lateral view; 3, posterior lobe of pronotum, dorsal view; 4, anal appendages, left lateral view; 5, idem, dorsal view, 6, idem, ventral view; 7, pterostigma, right fore wing. Scale bar 1 mm.

transverse occipital carina distinct, lateral corners acute. Antenna with scapus and base of pedicellus creamish white, rest of pedicellus and flagellum pale brown. Thorax. – Pronotum (Figs 2-3) with anterior and central part of middle lobe brown, lateral sides of middle lobe and posterior lobe brownish black; anterior lobe simple, posterior lobe with two caudal processes, approximately 1.0-1.5 times the length of median line of posterior lobe, directed 60°, but with tip directed abaxially, distinctly swollen in some specimens, or somewhat wider than base in others. Synthorax (Fig. 31) dark brown, dorsal part mat, densely punctate, lower half of synthorax more shining; dirty yellow stripe over mesepimeron / metepisternum from just above stigma to hind margin, approximately five times as long as widest part just before distal end. Legs unicolorous yellow, but all femora with dirty-coloured rings against tibiae, distal one-fourth of hind tarsus dark; long setae (spines) on legs dark yellow, short setae of tibiae white.

Wings hyaline, reaching to halfway abdominal segment 6, venation brown; Px in fore wing 17, in hind wing 15; R4+5 arising at nodus; IR3 arising halfway first cell distal to subnodus; Arculus, especially in hind wing, distinctly distal to Ax2; Ab vein meeting Ac at hind margin of wing; number of cells between Arculus and place where CuP ends in hind margin of fore wing 8; of hind wing 10; CuP reaches hind margin of fore wing at level of Px4, in hind wing at level of Px6; pterostigma (Fig. 7) brown, quadrangular, costal side shorter than subcostal side; veins distal to pterostigma undivided.

Abdomen. – Slender; segment 1 brown, segment 2 brown with a pair of latero-anterior pale spots, segments 3-6 brownish black with basal pale rings against annulae, approximately one-fifth of each segment; segment 7 dark brown, basal one-third paler, segments 8-10 brownish black, without pale markings. Anal appendages (Figs 4-6) rather compact, yellow, superior appendage in dorsal view basally wide,

tapering caudally, with a dorsal tooth approximately one-third from tip, in lateral view from outside hollow; inferior appendage basally very wide, caudal part straight outside, innerside halfway with triangular tooth, leaving a concavity caudally, the tip turned sharply dorso-axially, no tuft of setae.

Female. – As the male, but posterior margin of posterior lobe of pronotum with rather short, triangular, erect projections; abdomen with segment 8 with small pale spot in latero-anterior corner, segment 9 brown, segment 10 and anal appendages pale; valve brown, somewhat extending beyond anal appendage.

Measurements (mm). – Male, abdomen including appendages 29, hind wing 20; female, abdomen 28, hind wing 21.

Variation. – Inferior appendages of specimens from Pulau Peleng (off Banggai peninsula) are more slender than in typical specimens from the northern arm of Sulawesi. They are assigned to *D. ephippiata* since no other diagnostic characters were found.

Distribution. – North and central Sulawesi (Fig. 1).

Drepanosticta bicolor spec. nov.

Figs 1, 8-13, 32

Material. – **Holotype** male [JvT 11867]. '1989 RMNH Expedition to Sulawesi / Indonesia. Northern Pulau Buton: / a few kms inland from Labuhan Tobelo: / Jismil camp along Sg Labuhan Tobelo. / Rivulet through hardly disturbed primary evergreen rain forest. Boulders covered / with calcareous deposit. 150 m asl. / 4°26'30"S 122°59'00"E. 18 Nov 1989; / sample 89JvT040. Leg. J. van Tol'.

Etymology. – *Bicolor*, for the two-coloured ventrum of the synthorax. An adjective.

Description. – A dark large *Drepanosticta*, with conspicuous black and ivory white ventrum; posterior margin of posterior lobe with sharp corners, but without a paired process.

Male [holotype, JvT 11867]. – Head. Labrum, mandibles and anteclypeus bluish white, anterior border of labrum brownish black, c. one-third the height of labrum medially, tapering towards corners; rest of

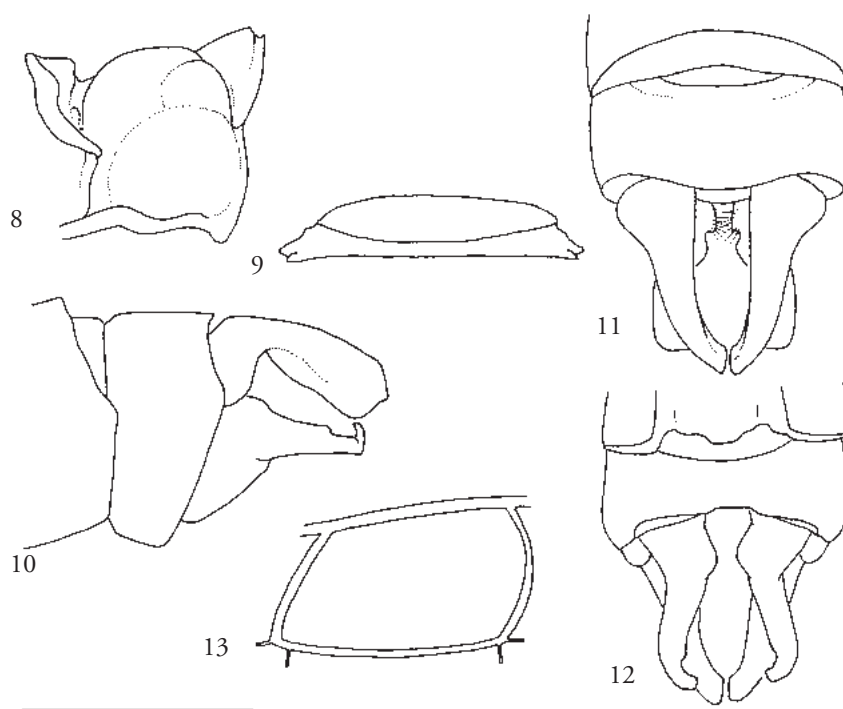
head black, shining on clypeus and against eyes, rest coriaceous; inconspicuous striae against eyes, transverse occipital carina poorly developed, hardly recognizable lateral extremities. Antenna with scapus brownish black, pedicellus dirty yellow, flagellum brown.

Thorax. Pronotum (Figs 8-9) dirty yellow, except for brown or brownish black anterior border of anterior lobe, central parts of paired convex structures of median lobe, and posterior lobe; anterior lobe with anterior margin erect, but not expanded; posterior lobe simple, hind margin straight, laterally turned c. 90° ventrad. Synthorax (Fig. 32) mat brownish black, except for dirty yellow posterior margin consisting of triangular marking in lower posterior corner of mesepisternum, a broadly triangular marking along posterior margin of metepisternum, and a larger pale marking on metepimeron, covering c. one-third of metepimeron, dorsally starting as continuation of marking on metepisternum, and obliquely towards ventral side, which continues ventrally over poststernum.

Legs with remarkable dirty yellow coxae, femora dirty yellow, with weak dark rings c. halfway, also dark rings against joints with tibiae; tibiae pale brown.

Wings hyaline, venation brown; Px in fore wing 17, in hind wing 17; R4+5 arising at or just proximal to nodus; IR3 arising c. halfway first cell distal to subnodus; Ab vein meeting Ac at or just before hind margin of wing (Y sessile or sub-sessile); number of cells between Arculus and place where CuP meets hind margin of fore wing 8, of hind wing 10; CuP reaching margin of hind wing at level of Px4 in fore wing, Px6 in hind wing; pterostigma (Fig. 13) brownish black, the central part brown; proximal side oblique, distal side convex; several veins posterior to pterostigma divided.

Abdomen. – Variegated; segments 3-7 brownish black, segments 8-10 and anal appendages mat black; pale marking dirty yellow as follows: segment 1 completely pale, segment 2 pale towards sternites; segment 3 with large triangular markings in ventro-anterior corners, and a pale ring of c. one-fifth the length of segment at c. one-fifth from hind margin, dorsally broken by dark line; segments 4-5 with pale rings at anterior margin



Figures 8-13. *Drepanosticta bicolor* sp. n., male. – 8, pronotum, left lateral view; 9, posterior lobe of pronotum, dorsal view; 10, anal appendages, left lateral view; 11, idem, dorsal view; 12, idem, ventral view; 13, pterostigma, right fore wing. Scale bar 1 mm.

and c. one-fifth from posterior border of segment, both c. one-fifth segment-length and dorsally broken by brown line; segment 6 only with anterior pale ring of one-fifth segment-length; segments 7-8 with large pale markings in ventro-anterior corners of tergite, c. one-third segment-length (marking on segment 8 much shorter since segment is much shorter); segments 9-10 concolorous black. Anal appendages (Fig. 10-12) with superiors in dorsal view slender, tapering towards top, distal two-thirds dorso-ventrally compressed, the distal part c. two times longer than high, to tip acute; inferiors with base stout, distal half narrow, straight, hardly tapering, the inferiors somewhat diverging, the tip turned axio-dorsad.

Female. – Unknown.

Measurements (mm). – Male, abdomen including appendages 37, hind wing 24.

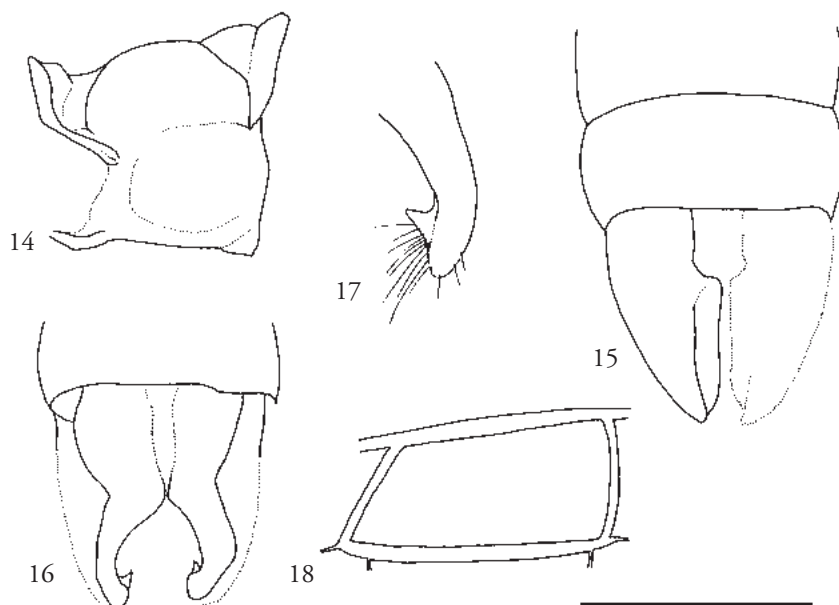
Remarks. – A rare species. Only one specimen was discovered during five days of field work; the only other platystictid on this site was *Protosticta geijskesi* Van Tol, a common and widespread lowland species in Sulawesi.

Distribution. – Buton Island (off southeastern Sulawesi) (Fig. 1).

Drepanosticta hamulifera sp. nov.

Figs 1, 14-18, 33

Material. – Holotype male [JvT 11872]: '1989 RMNH Expedition to Sulawesi / Pulau Kabaena (S of Sulawesi) 4 km S of Tengkeno. 5-8 Nov 1989 / Leg. R. de Jong / S8928R. – Cave camp. 300 m. Open / riverine forest along Sg. Lakambula' [hand-written label 6 Nov 1989]. – Paratypes: Same site, 2 males 2 females [JvT 11868-11871]. The paratypes in poor condition.



Figures 14-18. *Drepanosticta hamulifera* sp. n., male. – 14, pronotum, left lateral view (mirrored from a right lateral view illustration); 15, anal appendages, dorsal view; 16, idem, ventral view; 17, idem, detail of inferior appendage; 18, pterostigma, right fore wing. Scale bar 0.5 mm for fig. 17; 1 mm for all other figs.

Etymology. – *Hamulifer* (L.), hammer-carrying, for the shape of the superior appendage. An adjective.

Description. – Large *Drepanosticta*, hind margin of pronotum triangular, without conspicuous processes; synthorax and abdomen variegated due to conspicuous stripe over metepisternum and double pale markings on several abdominal segments; tip of inferior appendage with triangular tooth directed medio-anteriad, provided with tuft of setae; dorsum of distal half of abdominal segment 9, and segment 10, blue.

Male [holotype, JvT 11872]. – Head. [Labrum and anteclypeus damaged, but labrum bluish white with broad anterior brownish black border straight and not tapering towards corners], mandibles bluish white without dark anterior margin; rest of head black, shining against eyes, rest coriaceous, striate part against eyes posterior to antennae inconspicuous, very small pale spot lateral of lateral ocelli; transverse occipital carina well developed with angulate lateral extremities.

Antenna with scapus brown, pedicellus dirty yellow, flagellum brown.

Thorax. Pronotum (Fig. 14) dirty yellow, but posterior half of lateral lobes, and median portion of posterior lobe brown; anterior margin of anterior lobe semi-erect; lateral portion of posterior lobe semi-erect, no processes. Synthorax (Fig. 33) brownish black, especially posterior portion shining, rest semi-mat; wide greenish white stripe over metepisternum against interpleural suture, rather narrow anteriorly, running over metastigma, ending rounded well before posterior margin of metepisternum; metakatepisternum dark, but pale against metacoxa, metepimeron with pale marking in lower half, acute in anterior corner, widening posteriorly and covering full width of hind margin. Legs pale dirty yellow; femora with dark rings against joints with tibiae.

Wings hyaline, venation brown; Px in fore wing 16, in hind wing 14; R4+5 arising at nodus; IR3 arising halfway first cell distal to subnodus; Ab vein meeting

Ac just before hind margin of wing (Y sub-sessile); number of cells between Arculus and place where CuP meets hind margin of fore wing 9, of hind wing 10; CuP reaching hind margin of fore wing at level Px5, of hind wing at Px6; pterostigma (Fig. 18) pale brown; proximal side oblique, distal side convex; length subcostal side c. 2.2 times the height; few veins distal to pterostigma divided.

Abdomen pale brown, only posterior parts of segments 3-7 and segments 8-9 darker brown; pale dirty yellow markings as follows: segment 1 nearly fully dark yellow except for median part, segment 2 in antero-lateral two-thirds; segments 3-6 anterior one-sixth and crescent-shaped paired marking of one-fifth the segment length at one-sixth from posterior margin, but these markings diminishing in height from segment 3 to segment 6; segment 7 with pale ring in anterior one-fifth of segment, marking extending further posteriad against sternite; segment 8 with triangular marking in ventro-anterior corner; segment 9 with blue marking, covering approximately posterior half of segment, rounded anteriorly; segment 10 with bluish white dorsal marking. Anal appendages (Figs 15-17) pale, except for dark bases; superiors in dorsal view broad at base, gradually tapering towards top, distal three-quarters dorso-ventrally flattened, club-shaped, c. as long as high; inferiors in ventral view narrow, distal half clasper-like, distally rounded with a very short spine directed ventro-apicad, the rounded tip with dense brush of c. twenty long stout setae.

Female. – As the male, but smaller, and coloration probably more distinct (only teneral specimens available); last abdominal segments very short.

Measurements (mm). – Male: abdomen, including anal appendages, 46, hind wing 24; female: abdomen 37, hind wing 23.

Distribution. – Kabaena island (Fig. 1).

Drepanosticta penicillata sp. nov.

Figs 1, 19-24, 34

Material. – Holotype male. 'Indonesia. C Sulawesi / 40 km N of Wotu: just N of / Batas. Small stream nr bridge / road

Wotu-Tentena at km 4 / Disturbed primary forest; w= 2-4 m, / d=0.1-0.3 m, shade. Boulders. / 1200 m; 2°13'30"S 120°46'30"E / 24 Oct 1993; J. van Tol'. [JvT 1533]. – Paratypes: Same data, 1 male [JvT 1534]; C. Sulawesi, 30 km N of Wotu: Sg. Anoa, waterfall near bridge Wotu-Tentena, 650 m, 2°20'30"S 120°47'45"E, 23 Oct 1993, J. van Tol, 1 teneral female [JvT 1501].

Etymology. – *Penicillatus*, provided with a tuft of hairs, for the brush of hairs of the inferior appendages of the male. An adjective.

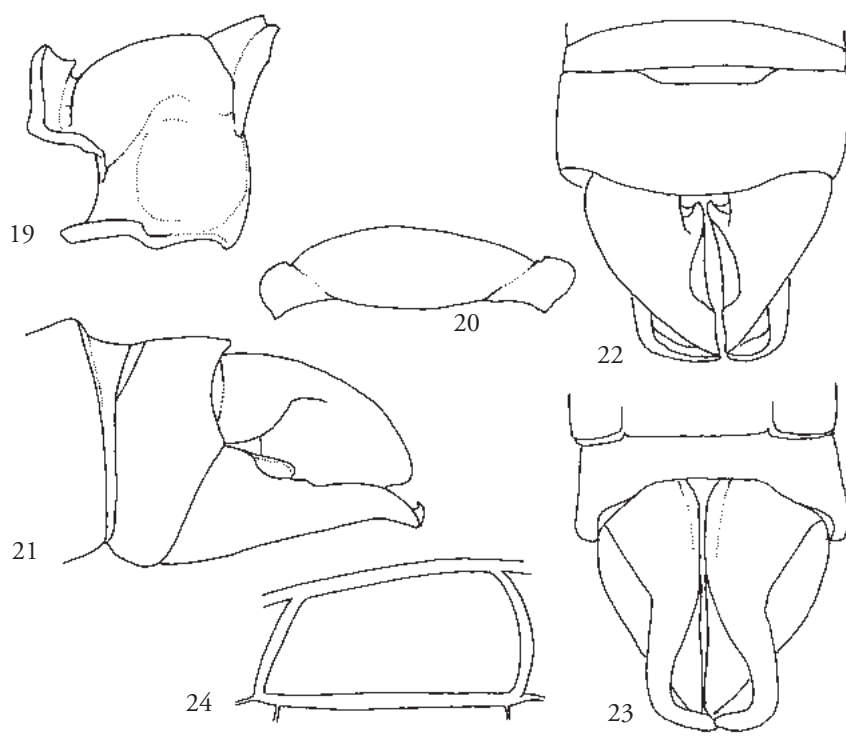
Description. – Large species; male with simple structure of prothorax and enormously developed superior appendage; synthorax with extensive pale markings; distal part of segment 9 and segment 10 pale, most probably blue or yellow.

Male [holotype male, JvT 1533]. – Head. Labium and maxillae pale yellow, mandibles bluish white without dark anterior border, labium white with anterior one-fourth brownish black, anteclypeus white, rest of head brownish black, especially vertex with purple shine; transverse occipital carina poorly developed, lateral extremities hardly visible.

Thorax. Pronotum (Figs 19-20) rather pale, with anterior lobe simple and completely yellow; middle lobe dirty white with small dark markings central on paired tubercle; lateral lobe pale white with a larger median dark marking; posterior lobe brownish black, but lateral corners somewhat paler, simple, median part flat, lateral corners somewhat erect, just expanding outside flat plane. Synthorax (Fig. 34) general coloration dark dorsally and lower parts yellow as follows: mesepisternum brownish black, mesokatepisternum brownish black except for centroposterior corner, mesepimeron yellow but area against mesopleural suture dark brown; metepi-sternum, metakatepisternum and metepimeron all yellow, but metapleural suture distinctly marked with brown stripe.

Legs with coxae all yellow, femora yellow with dark ring of one-fifth or one-sixth the femur length, approximately at same distance from tibia as width of ring; femora against tibiae also dark, tibiae brown, and tarsi pale brown.

Wings hyaline, venation brownish black; Px in fore



Figures 19-24. *Drepanosticta penicillata* sp. n., male. – 19, pronotum, left lateral view; 20, posterior lobe of pronotum, dorsal view; 21, anal appendages, left lateral view; 22, idem, dorsal view; 23, idem, ventral view; 24, pterostigma, right fore wing. Scale bar 1 mm.

wing 16, in hind wing 15; R4+5 arising at nodus, IR3 arising halfway first cell distal to subnodus; Arculus just distal to Ax2; Ab vein meeting Ac at hind margin of wing (Y-vein sessile); number of cells between Arculus and place where CuP meets hind margin of fore wing 8, of hind wing 9; CuP meeting hind margin of fore wing at level of Px4, of hind wing at level of Px5; pterostigma (Fig. 24) pale brown, the proximal corner acute, the distal side convex, c. 2.2 times wider than high; veins distal to pterostigma undivided. Abdomen. Segment 1 shining, dorsally with dark semicircle on otherwise yellow segment, segment 2 dorsally brown, anteriorly leaving approximately one-third of segment free, widening posteriorly to cover full segment width caudally, rest yellow; segments 3-7 brown, with yellow lateral spots anteriorly; segments

3-5 also with yellow lateral spots at c. three-quarters of segment-length; segment 8 dark brown, lateral sides anteriorly with yellow marking extending posteriorly to meet side margin just before segment border; segment 9 dark brown, posterior one-fifth with blue ring, not reaching the lateral corners; segment 10 dorsally yellow, and ventrally brown. Anal appendages (Figs 21-23) with superiors mat brownish black, enormously developed, inner margin curved sharply ventro-axiad, inner margin subterminally with small inward directed tubercle, lower portion very large with anterior border curved, and anteriorly nearly touching base in lateral view; inferiors pale yellow with inward directed tip brown, in ventral view slender, softly curved 90° outward; curved part slender, hardly tapering, the tip with dense tuft of short setae.

Female. – Characters hardly discernable; only female in poor condition (considered as conspecific based on extensive pale coloration of abdomen, and site at close distance from type locality).

Measurements (mm). – Male. Abdomen, including appendages, 42, hind wing 25.

Distribution. – Central Sulawesi (Fig. 1).

***Drepanosticta watuwilensis* sp. nov.**

Figs 1, 25-30, 35

Material. – Holotype male [JvT 11863]: '1989 RMNH Expedition to Sulawesi / Indonesia Sulawesi Tenggara: S of / Sanggona: Gunung Watuwila. Sungai / Lalonduwasi near Centipede camp. Small / shaded stream in very steep valley. / Clear running water of boulders. Small / pools. c. 3°49'S 121°40'E. c. 1050 m / asl. Sample 89]vT035. 2-4 Nov 1989 / Leg. J. van Tol' [with hand-written date 2 Nov 1989]. – Paratypes: same data, 2 males (JvT 11864-11865); Sulawesi Tenggara, S of Sanggona: Mokowu river near Mokowu camp, foot of Watuwila Mts, 150 m asl, 3°48'S 121°39'E. Rivulet with ponded areas, clear water, bottom with boulders, some sand. Largely shaded. 29-31 Oct 1989. J. van Tol [with hand-written date 29 Oct 1989], 1 male [JvT 11866].

Etymology. – *Watuwilensis*, for the type locality Gunung (= Mountain) Watuwila. An adjective.

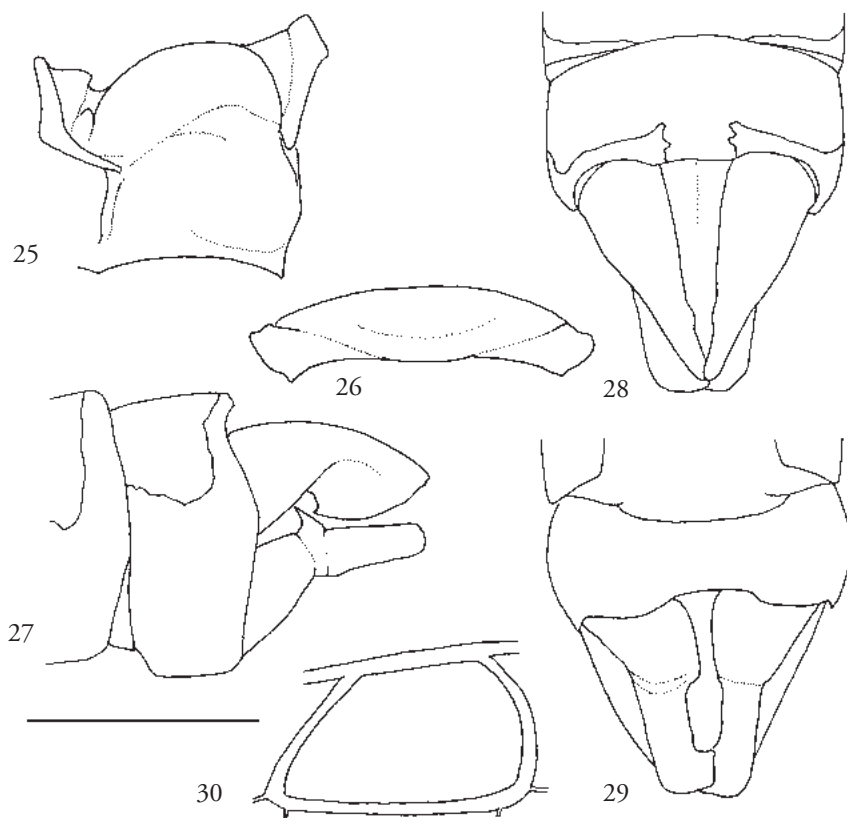
Description. – Relatively large species of *Drepanosticta*, with conspicuous pale stripes over metepisternum and metepimeron; pronotum simple; superior appendages distally dorso-ventrally compressed, enormously developed. Differs from similar *D. penicillata* sp. n. by the shape of pterostigma, more pronounced lateral extremities of postoccipital carina, and stouter inferior appendage, which lack a terminal tuft of setae.

Male [holotype, JvT 11863].– Head. Labrum, mandibles and anteclypeus bluish white, anterior one-fourth of labrum with brownish black stripe, tapering towards anterior corners; anterior border of mandibles not darker; rest of head black, clypeus, frons and parts of head against eyes shining, rest coriaceous with metallic lustre, fine longitudinal striae posterior to antennae; transverse occipital carina well developed,

lateral extremities angulate. Antenna with scapus black, pedicellus pale brown, flagellum brownish black, but paler against pedicellus.

Thorax. Pronotum (Figs 25-26) generally brownish black, but lateral corners of anterior lobe, and latero-anterior corner of median lobe dirty yellow; anterior lobe semi-erect, the anterior margin folded, more distinct in lateral corners; posterior lobe simple, without posterior processes, hind margin straight, laterally bent 135° ventrad. Synthorax (Fig. 35) brownish black with dirty yellow stripes over metepisternum, from anterior corner over metastigma gradually fading to brown toward posterior margin; metapleural suture with straight brown stripe, anteriorly continuing over dorsal half of metakatepisternum, the posterior part running more dorsad over suture; rest of metepimeron dirty yellow. Legs relatively dark, femora with superficial dark markings except for a pale ring near joints with tibiae, which are also dark.

Wings hyaline, venation brownish black; Px in fore wing 18, in hind wing 18; R4+5 arising at nodus; IR3 arising halfway first cell distal to subnodus; Ab vein meeting Ac near hind margin of wing (Y sub-sessile); number of cells between Arculus and place where CuP meets hind margin of hind wing 11; CuP reaching hind margin of wing at level of Px6 in fore wing, at level of Px7 in hind wing; number of cells between Arculus and place where CuP meets hind margin of fore wing 10, of hind wing 11; pterostigma (Fig. 30) brownish black, subcostal side c. 1.8 times wider than high, the proximal corner sharp, posterior margin irregularly convex, costal side ca half as long as subcostal side; many vein distal to pterostigma divided. Abdomen. Variegated due to double pale markings on many segments; base dark brown, with pale markings as follows: segment 1 with lateral yellow spots, sharply defined, dorsally half rounded; segment 2 somewhat paler in latero-anterior corners; segments 3-6 with two pairs of oval spots, one in latero-anterior corner, one at c. three-fifths the segment length, marking somewhat smaller on segment 6; segment 7 with pale marking in latero-anterior third; segment 8 as segment 7, but marking continues posteriorly along lateral



Figures 25-30. *Drepanosticta watuwilensis* sp. n., male. – 25, pronotum, left lateral view; 26, posterior lobe of pronotum, dorsal view; 27, anal appendages, left lateral view; 28, idem, dorsal view; 29, idem, ventral view; 30, pterostigma, right fore wing. Scale bar 1 mm.

margin of tergite; segment 9 with blue marking medio-posteriorly, lateral parts of tergite brownish black; segment 10 with blue dorsal marking. Anal appendages (Figs 27-29) somewhat shorter than segment 9, the inferiors somewhat longer than superiors; superior black, except for tip, in dorsal view base broad, strongly tapering, in lateral view club-shaped with broad and straight ventral margin; inferiors brownish black, the tips brown; base broad, distal half stout and parallel-sided at base, the tip turned 90° inward, blunt.

Female. – Unknown.

Measurements (mm). – Male, abdomen including appendages 44, hind wing 28.

Distribution. – Southeastern Sulawesi.

Remarks. – A relatively common platystictid on Gunung Watuwila above 1000 m, while only one specimen was found among 60 specimens of *Protosticta geijskesi* Van Tol along the foothill river at 150 m asl.

Acknowledgements

I am grateful for assistance and companionship during field work in Indonesia to our Indonesian colleagues and field guides, and to Mark Cooze, Dr. J.P. (Hans) and Greet Duffels, Stans Kofman, and Cor Lepelaar. Dr. Rienk de Jong and Jolanda Huisman successfully collected platystictids during their studies of butterflies and caddisflies. Lembaga Ilmu Pengetahuan Indonesia (director Mohamed Amir) issued permits for our fieldwork.



Figures 31-35. *Drepanosticta* Laidlaw of Sulawesi, head and thorax. – 31, *D. ephippiata* Lieftinck [JvT 11852]; 32, *D. bicolor* sp. n. [JvT 11687]; 33, *D. hamulifera* sp. n. [JvT 11782]; 34, *D. penicillata* sp. n. [JvT 1534]; 35, *D. watuwilensis* sp. n. [JvT 11864].

Dr. Matti Hämäläinen and Dr. J.P. Duffels kindly commented upon a draft of this paper, which greatly improved text and illustrations.

References

- Duffels, J.P., 1990. Biogeography of Sulawesi cicadas (Homoptera: Cicadoidea). p. 63-72. In: W.J. Knight & J.D. Holloway, *Insects and the rain forest of South East Asia (Wallace)*. The Royal Entomological Society of London.
- Gassmann, D., 2005. The phylogeny of Southeast Asian and Indo-Pacific Calicnemiinae (Odonata, Platycnemididae). – *Bonner zoologische Beiträge* 53 (2004): 37-80.
- Hill, K.C. & R. Hall, 2003. Mesozoic-Cenozoic evolution of Australia's New Guinea margin in a west Pacific context. p. 265-290. – In: R.R. Hillis & R.D. Müller (eds.), *Evolution and dynamics of the Australian plate*. – Geological Society of America, Special Paper 372.
- Holloway, J.D., 1990. Sulawesi biogeography – discussion and summing up. p. 95-102. – In: W.J. Knight & J.D. Holloway, *Insects and the rain forest of South East Asia (Wallace)*. The Royal Entomological Society of London.

- Lieftinck M.A., 1932. The dragonflies (Odonata) of New Guinea and neighbouring islands. Part I. Descriptions of new genera and species of the families Lestidae and Agrionidae. – *Nova Guinea* 15 (5): 485-602.
- Lieftinck, M.A., 1937. Descriptions and records of South-East Asiatic Odonata. – *Treubia* 16: 55-119.
- Lieftinck, M.A., 1938. The dragonflies (Odonata) of New Guinea and neighbouring islands. Part V. Descriptions of new and little known species of the families Libellaginidae, Megapodagrionidae, Agrionidae (sens. lat.), and Libellulidae (Genera *Rhinocypha*, *Argiolestes*, *Drepanosticta*, *Notoneura*, *Palaiargia*, *Papurgaria*, *Papuagrion*, *Teinobasis*, *Nannophlebia*, *Synthemis*, and *Anacordulia*). – *Nova Guinea (New Series)* 2: 47-128.
- Lieftinck, M.A. 1939. Sur quatre espèces nouvelles de Platystictidae de l'Inde orientale. – *Revue française d'Entomologie* 6: 144-154.
- Lieftinck, M.A., 1971. A catalogue of type-specimens of Odonata preserved in The Netherlands, with a supplementary list of the Odonata types described by Dutch scientists deposited in foreign institutional collections. – *Tijdschrift voor Entomologie* 114: 65-139.
- Polhemus, D.A., 1995. Two new species of *Rhagovelia* from the Philippines, with a discussion of zoogeographic relationships between the Philippines and New Guinea (Heteroptera: Veliidae). – *Journal of the New York Entomological Society* 103: 55-68.
- Polhemus, D.A. & J.T. Polhemus, 1998. Assembling New Guinea: 40 million years of island arc accretion as indicated by the distributions of aquatic Heteroptera (Insecta). p. 327-340. – In: R. Hall & J.D. Holloway (Eds), *Biogeography and geological evolution of SE Asia*. Backhuys Publishers, Leiden.
- Turner, H., P. Hovenkamp & P.C. van Welzen, 2001. Biogeography of Southeast Asia and the West Pacific. – *Journal of Biogeography* 28: 217-230.
- van Tol, J., 1987. The Odonata of Sulawesi and adjacent islands. Part 2. The genus *Diplacina* Brauer on Sulawesi. – *Zoölogische Mededelingen* 61: 160-176.
- van Tol, J., 2000. The Odonata of Sulawesi and adjacent islands. Part 5. The genus *Protosticta* Selys (Platystictidae). – *Tijdschrift voor Entomologie* 143: 221-266.
- van Tol, J., 2005. Revision of the Platystictidae of the Philippines (Odonata), excluding the *Drepanosticta halterata* group, with descriptions of twenty-one new species. – *Zoölogische Mededelingen* 79: 195-282.
- van Tol, J., in press. Revision of the Platystictidae of the Moluccas and Misool (Odonata). – *Deutsche Entomologische Zeitschrift* [Chapter 8 of this thesis].
- van Tol, J. & D. Gassmann, in press. Zoogeography of freshwater invertebrates of Southeast Asia, with special reference to Odonata. – In: W. Renema (Ed.), *Biogeography, time and place: Distributions, barriers and islands*. Springer Verlag, Dordrecht. [Chapter 2].
- Wilson, M.E.J. & S.J. Moss, 1999. Cenozoic palaeogeographic evolution of Sulawesi and Borneo. – *Palaeogeography, Palaeoclimatology, Palaeoecology* 145: 303-337.

