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# Tropical African *Platycnemis* damselflies (Odonata: Platycnemididae) and the biogeographical significance of a new species from Pemba Island, Tanzania

**Abstract** The damselfly, *Platycnemis pembipes* sp. nov., is described from Pemba Island (Ngezi Forest, Tanzania) and its affinities with Guineo-Congolian and Malagasy congeners are examined. For this purpose the identity and distribution of Afrotropical *Platycnemis* is reviewed, especially the taxonomically confused continental species. The Pemba species is nearly identical to some species of the Malagasy radiation of *Platycnemis*, but distant from the Guineo-Congolian species that have tropical Asian affinities. It is argued that the species is a long-distance wind-borne arrival from Madagascar, which survived due to favourable climatic conditions on Pemba. Habitats on the mainland, only 50 km further, are or have been drier and therefore seem unsuitable. The new species, living proof of a remarkable colonisation event, is under immediate threat, confined to a single stream in an imperilled forest, over 1000 km from its nearest relatives. The holotype of the enigmatic *P. mauriciana*, not recorded on Mauritius after its description, cannot originate from the island as it pertains to the European *P. latipes*. Five species recalling the Asian genus *Copera* are known in the male sex from central and western Africa; all were confused to some degree with *P. congolensis* and a key is given. The lectotype of *P. congolensis* is designated and its identity is clarified. *Platycnemis flavipes* and *P. xanthopus* are junior synonyms of *P. nyansana*. Discovery of the *P. rufipes* female showed that *P. escherichi*, known only from the female holotype, is a junior synonym of it. The generic classification of *Platycnemis* and *Copera* is not resolved, but data and hypotheses that should aid future analysis are provided.

**Key words** damselflies, Zygoptera, *Platycnemis*, Africa, Pemba, biogeography, taxonomy, synonyms

## Introduction

A damselfly of the genus *Platycnemis* Burmeister, 1839 was recently discovered on Pemba Island, 50 km off the Tanzanian coast; separated by 1000 km of dry land and a similar distance of sea from its most proximal relatives in Uganda and the Comoros (Figs 1a, 2). Platycnemidine damselflies are represented by at least 35 species in Africa, Europe and Asia. Geographically four disjunct groups can be recognised: (1) six Western Palaearctic species, including the type species of *Platycnemis*; (2) at least five Guineo-Congolian species; (3) at least 10 species on Madagascar and associated islands, including the type species of *Proplatycnemis* Kennedy, 1920; (4) between 13 and 16 species in eastern Asia, including the type species of *Copera* Kirby, 1890 and *Pseudocopera* Fraser, 1922. Although highly

distinctive as a group (Fig. 1), platycnemidine taxonomy is unresolved. Most species are classified as *Platycnemis*, while part of the Oriental species have been placed in *Copera*, but this generic classification is poorly supported (Ris, 1915; Schmidt, 1951b; Martens, 1996; Hämäläinen, 2003). To understand the Pemba species' affinities and biogeography, the taxonomy, range and ecology of the Afrotropical *Platycnemis* (groups 2 and 3) must be reviewed (Tables 1–2, Fig. 2). In particular the taxonomy of the continental species is notoriously confused (Martens, 1996; Dijkstra, 2003). That of the insular species is quite well resolved (Schmidt, 1951b; Lieftinck, 1965), although their ecology is poorly known. Better knowledge of the group can only be obtained once the study of Madagascar's Odonata is intensified (Dijkstra & Clausnitzer, 2004). Besides the continental species we examined the enigmatic *P. mauriciana* of Mauritius. It is of particular interest because, like the Pemba species, it is highly isolated from its nearest

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**Figure 1** *Platycnemis* males. (a) *P. pembipes* sp. nov., Ngezi Forest, Pemba Island, 1 October 2001; (b) *P. nyansana*, Mpanga Forest, Uganda, 14 May 2003. Photographs by V. Clausnitzer (a) and K.-D.B. Dijkstra (b).

relatives. We do not attempt to resolve problems of the generic classification of *Platycnemis* and *Copera*, but provide data and hypotheses that should aid future analysis.

## Materials and methods

We reviewed relevant Afrotropical *Platycnemis* (type) material in the Natural History Museum, London (BMNH), Institut Royal des Sciences Naturelles de Belgique, Brussels (ISNB), Museo Civico di Storia Naturale “Giacomo Doria”,

Genova (MCSN), Muséum National d’Histoire Naturelle, Paris (MNHN), Musée Royal de l’Afrique Centrale, Tervuren (MRAC), Naturhistoriska Riksmuseet, Stockholm (NHRS), National Museums of Kenya, Nairobi (NMKE), Nationaal Natuurhistorisch Museum Naturalis, Leiden (RMNH), University of Michigan Museum of Zoology, Ann Arbor (UMMZ) and Museum für Naturkunde der Humboldt-Universität, Berlin (ZMHB). The Pemba species was compared with all continental African species and the insular *P. alatipes*, *P. hova*, *P. malgassicum*, *P. pseudalatipes* (all BMNH), *P. agrioides* and *P. aurantipes* (RMNH).

	Continental group	Insular group
Range (Fig. 2)	Uganda to The Gambia	Madagascar, Comoros and Pemba Island
Thorax	Often with distinct pale speckling, like spatter of bleach (Figs 3b–e)	Usually without pale speckling (Fig. 3a)
Dilations mid and hind tibiae	At most 2× as wide as shaft (Fig. 4b)	Up to 5× as wide as shaft (Fig. 4a)
Leg colour	Yellow to rufous, but never white and at most joints and tarsi darkened	Often white, but sometimes a reddish or bluish colour, can be extensively marked with black
Penis	Apex rounded; lateral branches absent (Fig. 6b)	Apex deeply incised; long lateral branches probably always present (Fig. 6a)
Cerci	Long, often with prominent internal branch (Figs 5b–f)	Short, with small (often poorly visible) branch (Fig. 5a)
/paraprocts	Two-thirds or more	Half or less
/segment 10	Equal or more	Equal or less

**Table 1** Comparison of Afrotropical *Platycnemis* groups.

Insular	
<i>agrioides</i> Ris, 1915	Mayotte, Comoros
<i>alatipes</i> (McLachlan, 1872)	Madagascar
<i>aurantipes</i> Lieftinck, 1965	Madagascar
<i>hova</i> Martin, 1908	Madagascar
<i>longiventris</i> Schmidt, 1951	Madagascar
<i>malgassica</i> Schmidt, 1951	Madagascar
<i>melana</i> * Aguesse, 1968	Nzwani, Comoros
<i>pembipes</i> sp. nov.	Pemba, Tanzania
<i>protostictoides</i> Fraser, 1953	Madagascar
<i>pseudalatipes</i> Schmidt, 1951	Madagascar
<i>sanguinipes</i> Schmidt, 1951	Madagascar
Continental	
<i>congolensis</i> Martin, 1908	Western Congo and Gabon
<i>guttifera</i> Fraser, 1950	Liberia to Nigeria, possibly Cameroon
<i>nyansana</i> Förster, 1916	Congo Basin to Uganda
<i>rufipes</i> (Selys, 1886)	Cameroon, possibly Gabon
<i>sikassoensis</i> (Martin, 1912)	Uganda to The Gambia

**Table 2** Distribution of continental and insular Afrotropical *Platycnemis* species.

\*corrected spelling

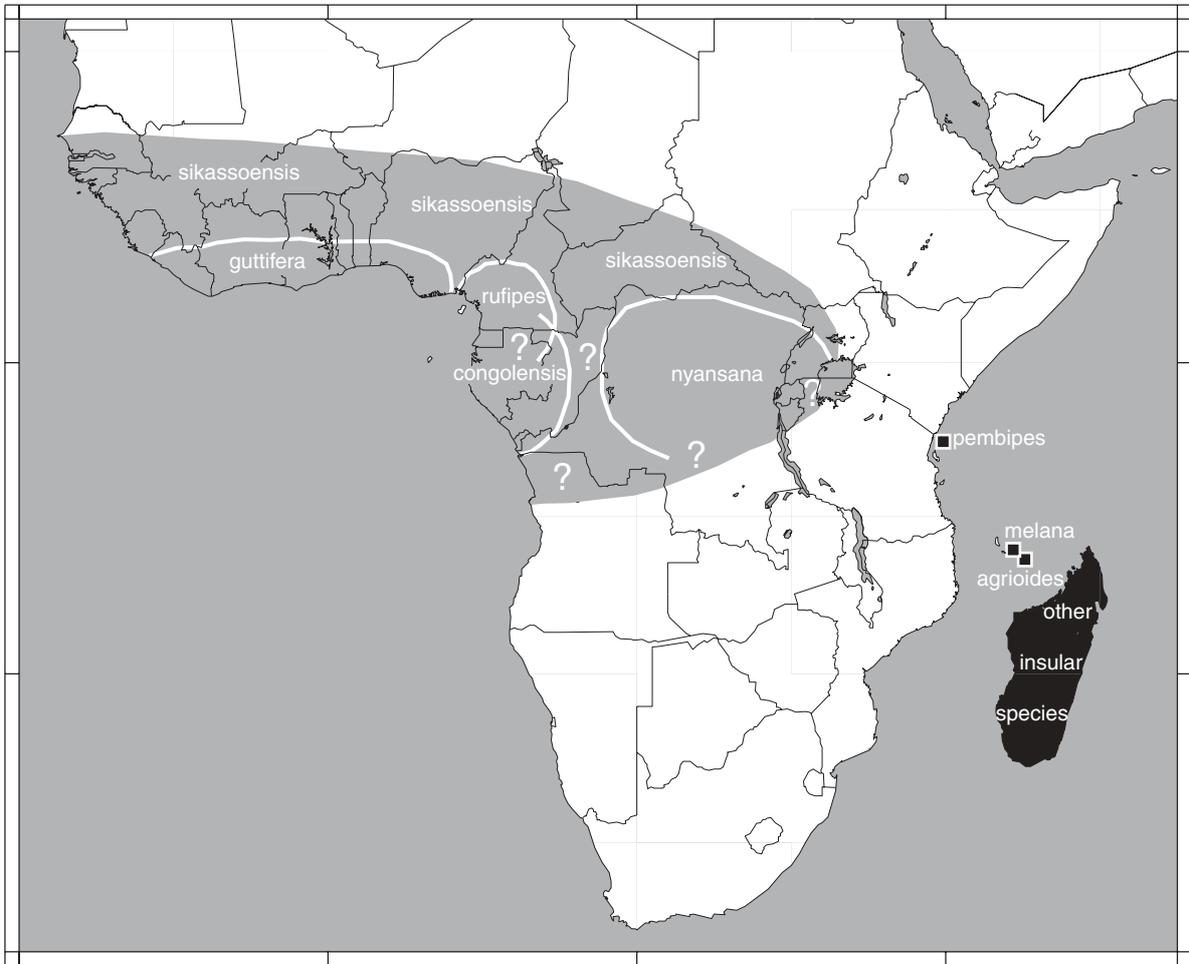
## Systematics

### Key to Afrotropical *Platycnemis* males

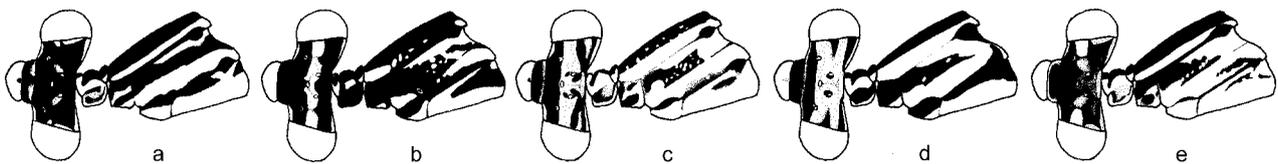
The differences between the continental and insular species are given in Table 1. The key below is only applicable for mature *Platycnemis* males west of the Mozambique Channel. The species are difficult to key as they demonstrate extreme colour change with age; the characters of colour and markings refer to fully mature specimens and are in-

cluded with some caution. A key to the Malagasy species is provided by Schmidt (1951b), with additions by Lieftinck (1965).

- 1 Dilations of mid and hind tibiae more than 3× as wide as shaft (Fig. 4a). Legs white. Cerci less than half length of paraprocts (Fig. 5a). Pemba Island, Tanzania ..... *pembipes* sp. nov. Dilations of mid and hind tibiae at most 2× as wide as shaft (Fig. 4b). Legs yellow to rufous. Cerci at least two-thirds length of paraprocts (Figs 5b–f). Uganda to The Gambia ..... 2
- 2 (1) Branches of cerci short, usually only visible in caudal view (Fig. 5f). Subapical pale ring of segments 3–7 reduced, abdomen appearing dark. Legs uniformly orange. Postclypeus with narrow pale border; synthorax usually with narrow complete antehumeral (pale) and humeral (black) stripes (Fig. 3e). Hindwing length 14–17 mm. Sunny rivers and streams ..... *sikassoensis* Branches of cerci long, usually well visible in lateral and dorsal view (Figs 5b–e). Segments 3–7 with pale basal and subapical rings (may be incomplete dorsally), giving abdomen annulated effect. Legs yellow to rufous, often darkened at joints ('ringed knees'). Postclypeus black at border; antehumeral stripe often broad and not bounded by humeral stripe, or mesepisternum largely dark (Figs 3b–d). Hindwing length 17–21 mm. Shaded forest pools, streams and rivers ..... 3
- 3 (2) Cerci distinctly shorter than paraprocts; branches of cerci diverge from and usually fall (just) short of cerci tips (Figs 5b, d). Mid- and hind tibiae distinctly widened. Legs yellow and darkened at joints ('ringed knees'). Synthorax with pale speckles and complete antehumeral stripe (Fig. 3c). Uganda to Gabon ..... 4
- 4 Cerci almost as long as paraprocts; branches of cerci lie close to and often surpass cerci tips (Figs 5c, e). Tibiae

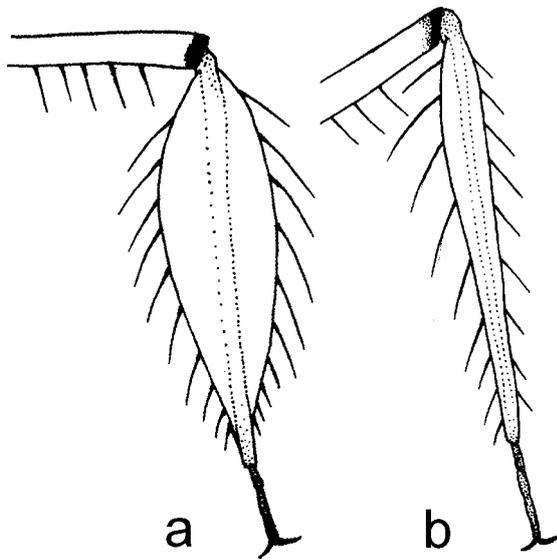


**Figure 2** Approximate distributions of Afrotropical *Platycnemis* species; insular (black) and continental (grey). Especially the general southern limits and contact zones of continental species are unclear; range of *P. sikassoensis* (at least partly) incorporates ranges of other continental species. See Table 2 for further details.



**Figure 3** *Platycnemis* mature male head in dorsal and thorax in lateral view. (a) *P. pembipes* sp. nov.; (b) *P. guttifera*; (c) *P. nyansana*; (d) *P. rufipes*; (e) *P. sikassoensis*. Individual variation is great; dark markings are strongly reduced in younger specimens. *P. congolensis* is similar to *P. nyansana*.

- not widened, or dilations are mere ridges. Legs uniformly rufous or yellow with darkened joints. Synthorax often either with only speckles or antehumeral stripe (Figs 3b, d). Liberia to Cameroon, possibly Gabon . . . . . 5
- 4 (3) Posterior border of pronotum drawn out into two slender vertical processes. Branches of cerci reach almost to tips of cerci. Western Congo and Gabon . . . *congolensis*  
 Pronotum without vertical processes. Branches of cerci fall well short of tips. Congo Basin to Uganda . . . . .  
 . . . . . *nyansana*
- 5 (3) Branches of cerci with expanded tips (Fig. 5e). Legs rufous. Synthorax with smooth-edged black and pale stripes, including complete antehumeral stripe, at most speckled with a dot or two (Fig. 3d). Cameroon, possibly Gabon . . . . . *rufipes*  
 Branches of cerci with slender pointed tips (Fig. 5c). Legs yellow with darkened joints. Synthorax with irregular speckled markings, antehumeral stripe often reduced to some pale speckles on an otherwise all black mesepisternum (Fig. 3b). Liberia to Nigeria . . . . *guttifera*



**Figure 4** *Platycnemis* male hind leg in lateral view. (a) *P. pembipes* sp. nov.; (b) *P. nyansana*.

***Platycnemis pembipes* sp. nov.**

Figs 1a, 3a, 4a, 5a, 6a, 7

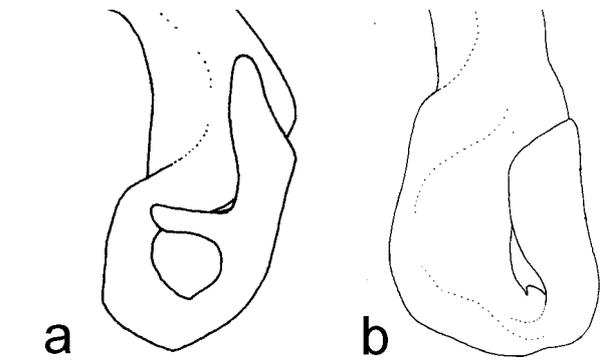
**Material examined**

Holotype ♂, paratypes (7 ♂, 2 ♀): Tanzania, Pemba Island, Ngezi Forest (04°56'16.6''S 39°42'38.6''E), 38 m a.s.l., 6–8 October 2001, leg. V. Clausnitzer. The holotype (RMNH INS 228162) and 7 paratypes (RMNH INS 228163 through 228169; 5♂, 2♀) are deposited in RMNH; 2 ♂ paratypes will be deposited in NMKE.

**Description**

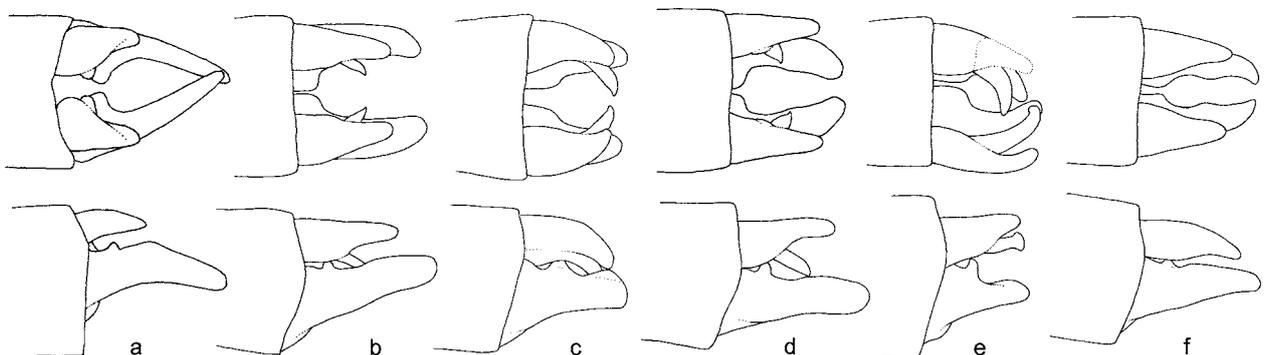
*Holotype male*

Black-and-white *Platycnemis* with strongly dilated white tibiae (Fig. 1a). Labium and genae whitish; labrum cream with a small blackish central spot at base; postclypeus black, narrowly pale at base; antennae black with second segment pale distally; dorsum of head black with restricted pale markings (tiny indistinct spot beside each lateral ocellus, narrow dot and line on eye border, long postocular streaks); underside largely white (Fig. 3a). Prothorax brownish black dorsally, with pale sublateral band and narrow lower border. Synthorax

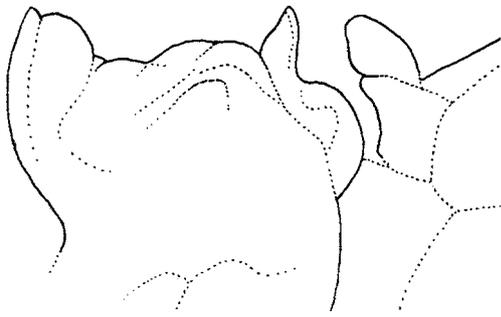


**Figure 6** *Platycnemis* male penis (genital ligula) in lateral view. (a) *P. pembipes* sp. nov.; (b) *P. nyansana*.

black dorsally down to interpleural suture, with complete creamy white antehumeral stripe less than one-fifth as wide as mesepisternum and as wide as humeral black stripe below it (Fig. 3a). Humeral stripe separates it from an equally wide pale stripe posterior of humeral suture, this posthumeral stripe interrupted along anterior two-fifths of suture but continued by pale stripe on mesokatepisternum. Synthorax sides and venter uniformly cream with a broad brownish black stripe on meta-pleural suture. Legs creamy white except for dark brown tarsi, blackish joints (especially femoral apices) and outer face of fore femora and tibiae; bristles brown. Fore tibiae with whitish expansions barely differentiated; mid and hind tibiae strongly expanded (about 3.5× as long as wide), all white (Fig. 4a). Abdomen brownish black; tergites 1 and 2 whitish ventrally, 3 to 6 with narrow pale ventral borders reduced apically but extended basally into narrow incomplete rings, giving abdomen an annulated impression; 7 to 9 dark; 9 with small apical white spot on each side; 10 entirely creamy white with apical rim narrowly and partially black. Appendages creamy white, cerci darkened ventrally, paraprocts black dorso-basally. Cerci roundly triangular, with black internal subbasal tooth, which is almost invisible without dissection. Paraprocts over twice as long as cerci and tergite 10, strongly curved in and down, with small dorsal subbasal knob (Fig. 5a). Penis (genital ligula) with deeply incised apex, making it strongly bilobed, and long and slender lateral branches (Fig. 6a). Wings clear; pterostigma blackish and about 1 cell long; its anterior and posterior borders equal in length, about 1.5× as long as distal and



**Figure 5** *Platycnemis* male appendages in dorsal (above) and lateral view (below). (a) *P. pembipes* sp. nov.; (b) *P. congolensis*; (c) *P. guttifera*; (d) *P. nyansana*; (e) *P. rufipes* (possible outline of damaged right cercus indicated); (f) *P. sikassoensis*.



**Figure 7** *Platycnemis pembipes* sp. nov. female pronotum in lateral view.

proximal borders. 15 postnodal veins in both fore wings. Measurements: abdomen (excluding appendages): 33.1 mm; hindwing: 18.5 mm; mid tibiae length  $\times$  width: 3.35  $\times$  0.95 mm; hind tibiae length  $\times$  width: 3.80  $\times$  1.12 mm.

#### *Paratype female*

Similar to holotype, but more faded, with dark markings reduced, indistinct and browner overall. Head pale brown overall with mere hints of darker markings, most clearly a dark line between eyes through bases of antennae. The hind lobe of the pronotum is slightly raised, forming a fairly low ridge that is shallowly incised at two points and therefore tripartite (Fig. 7). Pale brown synthorax with only dark brown dorsal half of mesepisterna and dark spot in humeral fossa distinct, latter extended into a very fine dark humeral stripe; a similar but weaker dark marking on metapleural suture. Legs evenly beige, very faintly darkened at femoral apices; tibiae not dilated. Tergites 1 and 2 pale brown, darker dorsally; 3 to 5 pale brown, apical sixth dark brown, slightly paler at base and basally of dark apical ring; 6 to 9 dark brown; apical border of 9 and entire tergite 10 dark cream. Ovipositor projects slightly beyond cerci. Pterostigma with pale brown centre, surrounded by a narrow cream border. 15 postnodal veins in fore wings. Measurements: abdomen: 32.0 mm; hindwing: 20.3 mm.

#### Variation

Paler, probably younger, males have all white cerci, facial markings more extensive and contrasting; dark thoracic markings reduced and slightly fragmented. 14–16 postnodal veins in fore wings.

#### Habitat, behaviour and accompanying species

Ngezi Forest is the only remaining large patch of tropical moist forest that once covered most of Pemba. It attained Forest Reserve status in 1959; today's gazetted area is about 1500 ha. The reserve is situated in the northwestern corner of the island and is bordered on most sides by the Indian Ocean, as well as by agricultural land. The climate is hot and humid with a mean annual rainfall of 1860 mm, with downpours almost every week of the year. Pemba has the highest rainfall in the coastal region, where the mean annual rainfall is below 1000 mm (Clarke, 2000). The monthly temperature variation of 3.8 °C is less than on the nearby mainland. The underlying bedrock is Pleistocene Azanian limestone. Most of the soils are alluvial sands; clayey soils are found in waterlogged areas by streams

and ponds. Ngezi is coastal swamp forest; a rare forest type in the coastal forest belt that is very distinct from other vegetation types (Clarke & Robertson, 2000): the dominant trees are often monocots and some parts are at least seasonally flooded. The small sluggish stream that supported *P. pembipes* is the only permanent one. It runs through the forest's centre towards mangroves in the north, bordered by a 30–50 m wide belt of riverine swamp forest dominated by *Barringtonia racemosa* and *Raphia farinifera*. The surrounding forest is defined as moist forest; dominated by the tree *Odyndea zimmermannii* (Beentje, 1990). No sunshine penetrates the dense canopy and the stream has cut a 1 m deep gully. The amount of light reaching the forest floor of moist coastal closed-canopy forest is only 0.2% of the sunlight (Moreau, 1935) and the stream's entrenchment increases its shadiness further.

Both sexes, including freshly emerged specimens, were found close to the stream. Males settled on twigs and leaves closely above or along it, facing the water. They approached females carefully, taking them into tandem position. Oviposition (seen only once) took place in tandem into dead plant material lying in the stream. The slight annual climatic variation on Pemba suggests the absence of seasonality, but more observations are needed to confirm this.

Ngezi Forest's odonates represent a typical coastal forest assemblage: *Teinobasis alluaudi* (Martin, 1896), *Gynacantha usambarica* Sjöstedt, 1909 and *Thermochoria jeanneli* Martin, 1915 were found in the flooded swamp forest, where they most likely reproduce, while *Tetrathemis polleni* (Selys, 1869) oviposited in puddles along the stream. Reproductively inactive *Aciagrion* cf. *zambiense* Pinhey, 1972 were found in the dense forest understorey. The *Aciagrion* may be a distinct East Coast species (own observations); more on *T. alluaudi* is provided in the discussion.

#### Etymology

The name, meaning 'Pemban foot', is consistent with names with the suffix *pes* that are prevalent in the genus.

#### *Platycnemis congolensis* Martin, 1908

Fig. 5b

*Platycnemis congolensis* Martin, 1908: 664 [lectotype ♂: Congo; MNHN (here designated)].

The identity of *P. congolensis* has long been unclear: records of that species appear to pertain to three to five species, although mostly the diagnosis by Schmidt (1951a) has been followed. MNHN possesses six and MCSN two specimens probably considered '*Platycnemis congolensis*' by Martin (1908, 1912), which are of diverse origin, specific identity, sex and completeness (Table 3). Three specimens have the indication 'type', although a primary type has not been designated. Only one of these is literally labelled 'Congo' and fortunately this is one of only four complete males. Because this is the only specimen with labels identifying it as a type of *P. congolensis* from the Congo, we designate it as the lectotype in order to end further confusion regarding the species' identity. It is not conspecific with Schmidt's species, differing in having the posterior border of the prothoracic hindlobe drawn

	Collection	Indicated locality	Labelled 'P. congolensis'	Labelled 'Type'	Damage	Identity
1♂	MNHN	'Congo'	yes	yes	none	<i>P. congolensis</i> LECTOTYPE
1♂	MNHN	'Congo'	yes	no	none	<i>P. congolensis</i>
2♀	MNHN	'Congo'	yes	no	none	unknown
1♂	MNHN	'Congo'	no	no	S8–10 absent	probably <i>P. nyansana</i>
1♂	MNHN	'Côte d'Ivoire'	yes	yes	S8–10 absent	probably <i>P. guttifera</i>
1♂	MNHN	'Sikasso' (Mali)	yes	yes	none	<i>P. sikassoensis</i>
1♂	MCSN	'F. Vaz'*	yes	no	none	<i>P. congolensis</i>
1♀	MCSN	'Guinée française'	yes	no	none	possibly <i>P. congolensis</i>

**Table 3** Details of 'Congolese' *Platycnemis* specimens labelled by René Martin in MNHN and MCSN.

\*Fernand-Vaz, present-day Omboué, on the Gabon coast south of Port-Gentil.

out into two slender vertical processes and the longer branch of the cerci. Schmidt's species is prevalent in Democratic Republic of Congo (DRC) and Uganda and should be called *P. nyansana* (see below). The distribution of *P. congolensis* is poorly known: The MCSN specimens are from coastal Gabon; NHRS possesses three of each sex from Mukimbungu in far western DRC on the Congo River just downstream of Luozi (Sjöstedt, 1917).

### *Platycnemis guttifera* Fraser, 1950

Figs 3b, 5c

*Platycnemis guttifera* Fraser, 1950: 615 [holotype ♂: Ziabli, Liberia; MNHN].

Described from Liberia and since reported from Côte d'Ivoire (Legrand, 1982; Legrand & Couturier, 1985), Ghana (O'Neill & Paulson, 2001), Liberia (Lempert, 1988) and Togo (T. Lieckweg, *pers. comm.*). BMNH possesses material from Nigeria, identified by R.M. Gambles as *P. rufipes*. Possibly ranges to Guinea and Cameroon, but no specified records have been published (Legrand & Couturier, 1985). Reported from deeply shaded calm and stagnant sections of larger streams and small rivers in rainforest (Legrand & Couturier, 1985; Lempert, 1988; Dijkstra & Lempert, 2003).

### *Platycnemis latipes* Rambur, 1842

*Platycnemis latipes* Rambur, 1842: 242 [type not designated: Montpellier, France; MNHN (not seen)].

*Platycnemis mauriciana* Selys, 1862: 34; nomen nudum (no description).

*Platycnemis mauriciana* Selys, 1863: 167 [holotype ♂: Ile Maurice; ISNB (seen)]; new synonymy.

*Platycnemis mauritiana* Selys, 1863 – Selys (1869: 24); misspelling.

The Odonata of Mauritius have been well studied, but *P. mauriciana* was not recorded after its description (Clausnitzer & Martens, 2004). A single male in Selys's collection labelled '(Ile de France)' and 'Platycn. mauriciana DS.' must represent the holotype, but lacks the terminal abdomen half, secondary genitalia, lower synthorax and three wings. Selys (1863, 1869)

already doubted the specimen's origin, regarding it a possible variety of the Western Palaearctic *P. latipes*. Fraser (1949) suggested that it could be close to a Malagasy species, possibly *P. hova*. Nonetheless the markings and broad tibiae clearly show that the male represents a Western Palaearctic species, either *P. latipes* or *P. dealbata*, which can best be separated by the appendages (lost in holotype). It is remarkable that Selys interpreted 'Ile de France' as Mauritius, as the island only bore that name officially from 1715 to 1810, while the part of France around Paris has been known by it since the late 14th century. The Ile de France region lies at the extreme northern limit of the recent range of *P. latipes* (Martens, 1996), of which we consider *P. mauriciana* a synonymy.

### *Platycnemis nyansana* Förster, 1916

Figs 1b, 3c, 4b, 5d, 6b

*Platycnemis nyansana* Förster, 1916: 25 [type ♂: Entebbe, Uganda; lost].

*Platycnemis flavipes* Navás, 1924: 12 [holotype ♂: Kibwezi, eastern Africa; MNHN (seen)]; new synonymy.

*Platycnemis xanthopus* Navás, 1924: 13 [holotype ♂: Kibwezi, eastern Africa; MNHN (seen)]; new synonymy.

*Platycnemis congolensis* nec Martin, 1908 – Schmidt (1951a: 223); Pinhey (1961: 19); Miller (1995: 4); Miller and Miller (2003: 121).

*P. nyansana* was described from Entebbe, but the type is not in UMMZ (where types from the same publication have been found) and thus appears to be lost (Garrison, von Ellenrieder & O'Brien, 2003). Two species occur in Uganda, including the Entebbe area. Fraser (1928) described *Copera subaequistyla*, a synonym of *P. sikassoensis* (see below), from Entebbe. Pinhey (1961) supposed that specimens from Kampala, Bwamba Forest (= Semliki NP) and nearby Congolese Mutwanga could pertain to *P. flavipes*, but listed them as *P. congolensis*. Indeed Navás's (1924) drawings of the *P. flavipes* appendages are similar to those by Schmidt (1951a) of so-called *P. congolensis* from Akula, Democratic Republic of Congo. Miller (1995) also reported *P. congolensis* from near Kampala. This second species differs from the *P. congolensis* lectotype in details of the male cerci and prothoracic hindlobe (see above) but matches the description of *P. nyansana*, being

larger than *P. sikassoensis* with darkened leg joints, double-ringed tergites 3 to 5 and shorter cerci.

Navás (1924) described *P. flavipes* and *P. xanthopus* from ‘Africa oriental inglesa: Kibwezi’. We only know of a place by that name halfway between Nairobi and Mombasa in the dry thornbush. This is an unlikely locality for the genus; moreover there are no other *Platycnemis* records from Kenya. The specimens could have come from Uganda and we do not regard *Platycnemis* as part of the Kenyan fauna. Contrary to Pinhey (1962), the holotypes of *P. flavipes* and *P. xanthopus* are not lost (Legrand & Lachaise, 1993). Their labels add no information about their origin, reading ‘B.E. Africa, Kibwezi’. The two are alike; differences described may follow from the *P. xanthopus* appendages being partly covered with glue. Both agree with *P. nyansana*, which is the oldest and thus valid name. *P. nyansana* favours stagnant pools in the deep shade of rainforest (Miller, 1995; Miller & Miller, 2003; own observations). Its range encompasses Uganda and most of the Congo Basin (Schmidt, 1951a; MRAC; own observations).

### ***Platycnemis rufipes* (Selys, 1886)**

Figs 3d, 5e

*Metacnemis rufipes* Selys, 1886: 139 [holotype ♂: Cameroon; BMNH (seen)].

*Allocnemis rufipes* (Selys, 1886) – Kirby (1890: 131).

*Platycnemis escherichi* Schmidt, 1951a: 224 [holotype ♀: Ekododo, Cameroon; ZMHB (seen)]; new synonymy.

*Platycnemis rufipes* (Selys, 1886) – Pinhey (1962: 110); Kimmins (1970: 181).

*Platycnemis congolensis* nec Martin, 1908 – Vick (1999: 246).

*Platycnemis camerunica* Fraser, in litteris [holotype ♂: Cameroon; BMNH (seen)]; nomen nudum.

The identity and generic affiliation of this species has been uncertain. Pinhey (1962) stated that ‘whilst this insect does not appear to be considered a true *Platycnemis* it does not seem to belong to *Allocnemis* nor perhaps to the related *Stenocnemis*. Gambles who has taken the species in Nigeria thinks it is a *Stenocnemis*.’ Kimmins (1970) added ‘currently placed (with doubt) in *Platycnemis*’. Neither author explained their doubts. The holotype perfectly matches *Platycnemis* by build, markings and appendages; moreover BMNH possesses conspecific material labelled as *Platycnemis camerunica* by Fraser (unpublished name).

*Platycnemis escherichi* is known only with certainty from the female holotype, which has two diagnostic spikes on the middle of the pronotum. Legrand (1975) reported males from NE Gabon, without diagnosing the male or explaining his identification. Considering the *P. escherichi* holotype’s origin and Schmidt’s (1951a) remark ‘*Allocnemis rufipes* Selys [...] hat uns nicht vorgelegen’ it stands to reason that both are conspecific. The *P. rufipes* holotype perfectly matches the markings illustrated by Schmidt (1951a), including the dark wedges beside the eyes and the wide tapering antehumeral stripe that are not seen in other species (Fig. 3d). Material from SW Cameroon published as *P. congolensis* by Vick (1999) includes both sexes; the males agree with *P. rufipes* and the females with *P. escherichi*, although ‘the size of the spikes is a little variable

and mostly a bit smaller than Schmidt’s drawing, but I do not think this significant’ (Vick, in litt.). Both sexes agree in markings and were collected in the same general area and once at the same site, substantiating the synonymy.

### ***Platycnemis sikassoensis* (Martin, 1912)**

Figs 3e, 5f

*Psilocnemis sikassoensis* Martin, 1912: 98 [holotype ♂: Sikasso, Mali; MNHN (seen)].

*Copera subaequistyla* Fraser, 1928: 127 [lectotype ♂: Entebbe, Uganda; BMNH (seen; designated by Kimmins, 1966: 214)]; junior synonym – Legrand (1982: 9).

? *Copera congolensis* (Martin, 1908) – Nielsen (1934: 180).

*Platycnemis subaequistyla* (Fraser, 1928) – Pinhey (1961: 19).

*Platycnemis sikassoensis* (Martin, 1912) – Pinhey (1962: 110).

Unlike its continental Afrotropical congeners, *P. sikassoensis* favours exposed habitats and is wide-ranging, inhabiting rather open flowing waters like large rivers and sunny streams, both in forest and savanna (Legrand & Couturier, 1985; Dijkstra & Lempert, 2003). The distribution of this small species incorporates the combined ranges of the larger ones, which appear to be allopatric and restricted to forest shade (Fig. 2). It has been recorded from Benin (Tchiboza & Dijkstra, 2004), Central African Republic (Pinhey, 1971), Côte d’Ivoire (Lindley, 1974; Legrand, 1982; Legrand & Couturier, 1985), Gambia (Gambles *et al.*, 1998), Ghana (Marshall & Gambles, 1977; O’Neill & Paulson, 2001), Guinea (Legrand & Girard, 1992; Legrand, 2003), Liberia (Lempert, 1988), Mali (Martin 1912; Dumont, 1977), Sierra Leone (Aguesse, 1968; Carfi & D’Andrea, 1994), Togo (T. Lieckweg, *pers. comm.*) and Uganda (Fraser, 1928; Pinhey, 1961). The species illustrated as *Copera congolensis* from Mobeka, Democratic Republic of Congo by Nielsen (1934) may also pertain to this species.

## **Discussion**

### **Relationships**

The two Afrotropical *Platycnemis* groups can be clearly separated by morphology and coloration (Table 1). The continental species are diagnosed and compared with *P. pembipes* in the key. The Pemba species perfectly fits the diagnosis of the insular group (Table 1) and is nearly identical to the Malagasy *P. aurantipes* and *P. hova*. The former is more colourful, with a more contrasting head pattern and orange-yellow legs. The male tibiae are shaped similarly, but are slightly narrower. Morphological differences are especially slight; the penises appear identical. The male cerci of *P. pembipes* are a bit more pointed; both species have a pale bulge on the inner border that lies more dorsal in *P. aurantipes*, making the internal profile more angular (dorsal view). The internal tooth of the cerci is well visible and pale with only a black tip in *P. aurantipes*, but entirely black and hard to see in *P. pembipes*. The female pronotal hindlobe of *P. aurantipes* is slightly broader and more deeply incised; the gap between the mesostigmal plate and mesepisternum is larger. *Platycnemis hova* also has more extensive and contrasting

pale facial markings; the penis apex is less deeply incised, the tibiae narrower and the appendages entirely white. The internal cercal tooth is black, but more prominent than in *P. pembipes*. Width and colour of the *P. pembipes* legs recall the Malagasy *P. alatipes* and *P. pseudalatipes*, whose body markings differ. *Platycnemis agrioides* and *Platycnemis melana* from the Comoros, geographically between *P. pembipes* and the Malagasy species (Fig. 2), are relatively dissimilar with their narrow tibiae and dark coloration.

The insular species are very uniform in their contrasting coloration and penis and appendage morphology (Schmidt, 1951b; Lieftinck, 1965), and are probably monophyletic. Similar traits are seen in Eurasian species, but not elsewhere in the Afrotropics. Several authors noted the similarity between the southern Asian *Copera* s.s. – as defined by Selys (1863) under the homonym *Psilocnemis* with type species *C. marginipes* (Rambur, 1842) designated by Kirby (1890) – and the Guineo-Congolian (continental) platycnemidines: Nielsen (1934) transferred *P. congolensis* to *Copera* and Schmidt (1951a) placed *P. nyansana* close to that genus by penis characters; at least *P. guttifera* and *P. sikassoensis* are similar in this regard (own observations). Fraser (1928, 1950) described *Copera subaequistyla*, now a synonym of *P. sikassoensis*, and *P. guttifera* emphasising their similarity to *C. marginipes* and *C. vittata* (Selys, 1863). Recently Donnelly (2002) listed the species as *Copera sikassoensis* for that reason, despite the status quo to place all African platycnemidines in *Platycnemis*. Indeed the two most common species in their respective continents, *P. sikassoensis* and *C. vittata*, are virtually identical except for differences in the male appendages and female pronotum.

Although it can be concluded that the Pemba species' nearest relatives are found in Madagascar and those of the continental species in tropical Asia, only worldwide phylogenetic research of the group can elucidate the exact relationships. The platycnemidine damselflies are probably a monophyletic group, but the prevailing separation into two genera almost undoubtedly makes *Platycnemis* paraphyletic. Of the four geographically disjunct platycnemidine groups, three are morphologically uniform and probably monophyletic. Only the large eastern Asian group is heterogeneous; besides species with Guineo-Congolian affinities (*Copera* s.s.), it includes species ranging into the Eastern Palaearctic that are more similar to the Western Palaearctic and Madagascar groups. Interesting in this regard is that Fraser (1962) illustrated a *Platycnemis* larva from Madagascar with frilled caudal lamellae. This is like those described for *C. marginipes* and *C. vittata* by Lieftinck (1940), while Western Palaearctic and Japanese *Copera* and *Platycnemis* (including the latter's type species) have unfrilled lamellae (Kawai, 1985; Martens, 1996). Discovery of the larva of African *Platycnemis* will help enlighten their position; it is assumed to have frilled lamellae. Another overlooked but possibly informative feature is eye-coloration, which is lost in preservation. Examined species with (assumed) frilled lamellae have a darker dorsum of the eye plus a distinct horizontal band below it, while unfrilled species only have a dark dorsal half (Eastern Palaearctic) or very faint markings altogether (Western Palaearctic).

## Biogeography

The forests of the eastern African coast and adjacent mountains are recognized as core areas of biodiversity and endemism in Africa (Kingdon, 1989; Fjeldså & Lovett, 1997; Burgess, 2000) and are listed as important conservation areas (Stuart *et al.*, 1990). This richness, especially of relict species, has been explained by the area's relative climate and habitat stability (Fjeldså *et al.*, 1997). Most island biota are similar to those on the mainland (Burgess, 2000). Pemba, however, is recognized for its great distinctiveness with a high degree of endemism despite its size (about 1000 km<sup>2</sup>) and proximity to the mainland (50 km, similar to the distance between Zanzibar and Tanzania). The moist forest of Ngezi, for instance, is peculiar in its floristic composition, combining tree species restricted to coastal East African forests, Madagascar links, eastern Indian species and Afromontane elements (Beentje, 1990). Despite the nearness of its mainland relatives, the owl *Otus pembaensis* is one of the most distinctive *Otus* species in and around the western Indian Ocean (Rasmussen *et al.*, 2001). The comparatively early separation from the mainland by faulting that produced the Pemba Channel, possibly 6–10 million years ago, may explain Pemba's unique position (Richmond, 1997; Clarke & Burgess, 2000). The Malagasy connection of *P. pembipes* has parallels in other Pemban taxa. The tree *Chrysaliducarpus pembanus* and palm *Dypsis pembanus* are endemics belonging to otherwise Madagascan genera (Beentje, 1990; Krain *et al.*, 1994). The tree genus *Typhonodorum* and the fruit bat *Pteropus voeltzkowi* also have their closest relatives in Madagascar (Beentje, 1990; Entwistle & Corp, 1997). Similarly, the latter's relative *Pteropus comorensis* inhabits Mafia off the Tanzanian coast and the Comoros, and is closely related to *Pteropus seychellensis* of the Seychelles. Other Pemban taxa show a stronger affinity to mainland Africa than to Madagascar: the milkweed genus *Secamone* has its greatest diversity in Madagascar (62 species) with only 16 species in continental Africa, but is represented on Pemba only by a mainland species (Goyder, 1991).

Keeping these affinities in mind, the questions arise (1) what the origin of *Platycnemis* on Pemba is and (2) why populations are absent from the mainland. The origin of *P. pembipes* is most likely from Madagascar by wind-aided dispersal across the Mozambique Channel. A strong monsoon follows the East African coast north(west-)wards from June to September (Richmond, 1997) and could carry damselflies over long distances. The American damselfly *Ischnura hastata* (Say, 1839) that has colonised the Azores and Galapagos Islands has been collected with nets fixed to aeroplanes at 300 m altitude (Cordero Rivera *et al.*, 2005). It is unlikely that *P. pembipes* is an ancient relict: Madagascar separated from the African mainland many millions of years earlier than Pemba, although it '... apparently slid south along the east African coast for most of the Cretaceous rather freely interchanging plant and animal taxa with the mainland at least until 90 Ma and perhaps intermittently thereafter' (Gentry, 1993). Such an ancient split would predict a much greater character divergence between species on Madagascar and Pemba, moreover *Platycnemis* species on the volcanic and relatively young

Comoros (at most 8 million years old) could also only reach these islands airborne. The Comoran species pair and *P. pembipes* both have close relatives on Madagascar, but are rather dissimilar to each other, suggesting the Comoros did not act as a stepping-stone between Madagascar and Pemba, but were colonised in a separate event.

The second question is more difficult to answer. Undiscovered populations may be present in unsampled coastal forests in Mozambique, southern Tanzania and Mafia Island. Alternatively insular species may have never reached the mainland or become extinct there. Considering the proximity of Pemba and the suspected mode of dispersal it is unlikely that *Platycnemis* never arrived on continental shores (see below). Subsequent extinction, on the other hand, seems probable. Tropical Africa has undergone marked climatic changes, for instance with a relatively wet period 12–10 000 years ago and a dry one in the few thousand preceding years (Hamilton, 1981). The impoverishment of the forest flora and fauna of Africa is due to extinctions during dry spells, glacial advances and the lack of refugia during the Pleistocene. Extinctions would have mainly hit the moist and hot lowland forests, i.e. cooling below the tolerance of tropical stenothermic species and altering their habitats. A number of plant taxa shared by the lowland forests of Madagascar and South America, for instance, are known as fossils but absent in mainland Africa today (Gentry, 1988, 1993). Examples of such random extinctions in the African rain forests are discussed by Colinvaux (1993) and Clausnitzer & Lindeboom (2002). Although the coastal forests of eastern Africa are considered relicts of a former pan-African tropical forest and are believed to have been more stable during cooler and drier periods than other African forests (Fjeldså *et al.*, 1997; Fjeldså & Lovett, 1997), small changes in temperature or humidity may have caused the extinction of forest species. The mainland coast is much drier than Pemba and is even drier now than in the past (Clarke, 2000): suitable habitats for *P. pembipes* or a related species may no longer be present.

The insular *Platycnemis* scenario has parallels in other Odonata, be it on a larger scale. The genera *Teinobasis* Kirby, 1890 and *Hemicordulia* Selys, 1870 have their greatest diversity in Australasia and the adjacent Pacific. They are poorly represented on the Asian mainland, but occur on several Indian Ocean islands, Madagascar and eastern Africa, with only a single species in each area occupied. This distribution and the restricted taxonomic differentiation of the scattered populations, suggest a recent wind-borne transoceanic colonisation. The damselfly *T. alluaudi* inhabits Madagascar, the Seychelles, coastal Kenya and Tanzania, Zanzibar and north Malawi, but populations are widely separated due to the scarcity of appropriate swamp forest habitat (Clausnitzer, 2003b). A complex of very similar *Hemicordulia* species inhabits Madagascar, the Seychelles and Mascarenes, and eastern Africa west to the Albertine Rift and south to KwaZulu-Natal, but records and habitat information are more fragmentary than in *Teinobasis* (K.-D.B. Dijkstra, unpublished). These cases show that the dispersal of Malagasy *Platycnemis* to the African coast is feasible, but restricted and probably reduced availability

of habitat may have precluded their survival in large parts of this region; perhaps conditions were only favourable on Pemba.

## Conservation

Owing to its distinctive fauna and flora, Pemba is recognised as a high priority site for conservation (Rodgers & Burgess, 2000); the Ngezi Forest is significant for biodiversity conservation on the regional and global level. Until recently Pemba was entirely covered with forest; clearing for cash crop plantations (cloves, cardamom) began in 1830 (Clarke & Karoma, 2000). Now just a few square kilometres of forest are left and endemic forest species are already thought to be extinct (Clarke *et al.*, 2000). This fate definitely awaits *P. pembipes*, living proof of a unique colonisation event, if the remaining forest on Pemba is not conserved. The species is one of several odonates that are almost certainly confined to a single stream and thus under imminent threat (IUCN, 2005). Others are *Amanipodagrion gilliesi* Pinhey, 1962 from the Usambaras on the nearby Tanzanian mainland (Clausnitzer, 2003a, 2004) and *Risiocnemis seidenschwarzi* Hämäläinen, 2000 from Cebu in the Philippines (Hämäläinen, 2004). *Platycnemis pembipes* has been submitted for inclusion in the global Red List as Critically Endangered.

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