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New *Caenis* species from Madagascar (Insecta: Ephemeroptera)

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Three new species of the genus *Caenis* Stephens 1835 from Madagascar are described: *Caenis nausicaae* sp. n., *Caenis gattolliati* sp. n. and *Caenis solida* sp. n. Variability and differing combination of characters in the *Caenis spinosa* group are described and discussed.

Keywords: *Caenis*, Madagascar, new species,. character variability, circle of races.

INTRODUCTION

In 1995 Malzacher described the first five *Caenis* species from Madagascar. Now the investigation of the whole material collected by the ORSTOM-team of Dr. Jean-Marc Elouard in the 1990s in nearly all regions of Madagascar allows the description of three new species. However, in two or three of these altogether 8 species the assignment to the genus *Caenis* is not sure.

The family Caenidae is represented in Madagascar by four genera, one of the subfamily Madecocercinae: *Madecocercus* Malzacher, 1995, and three of the subfamily Caeninae: *Caenis* Stephens, 1835, *Callistellina* Sun & McCafferty, 2008 and *Trichocaenis* Malzacher, 2009. The latter two are described on the base of larval stages only, and Sun & McCafferty conceded the possibility that the *Callistellina* larva could be the aquatic stage of one of the *Caenis* species for their part described only as imagines. Indeed the investigation of subimaginal genitalia in some larvae seems to confirm this (Malzacher 2009) (see discussion) and it could be the same case in *Trichocaenis*.

Closely related *Caenis* species, clearly distinguishable in their typical manifestation, often show different populations with intermediate character states and more or less differing combinations of characters e.g. the *Caenis pseudorivulorum* group and the *Caenis macrura* group in Europe (Malzacher 1986), the *Caenis argentina* group in South America (Malzacher 2001) and the *Caenis jinjana* group in Africa (Malzacher, in press). Those circumstances can also be observed in the *Caenis spinosa* group from Madagascar.

SYSTEMATIC ACCOUNT

Note: In *Material examined* the three toponyms of each sample mean: 1. name of the basin, 2. name of the river or stream, 3. name of the locality. All sex symbols apply to imaginal stages.

Caenis nausicaae sp. n.

Material examined. Madagascar: Holotype (micro-slide), P0253, Rianila, Rongaronga, Ambodifaho, 18:47:53 S, 49:04:50 E, 31.X.1994, 1 ♂. Paratypes:

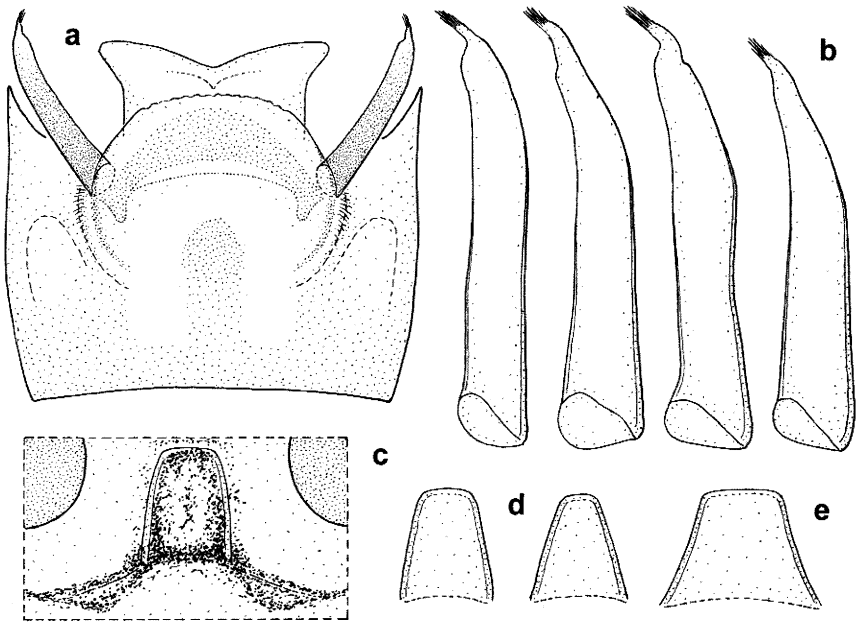

Fig. 1. *Caenis nausicaae* sp. n., ♂ (a–d), ♀ (e). — **a**: Sternite IX and genitalia. — **b**: Different shapes of forcipes. — **c**: Prosternum with sclerotized prosternal ridges and coxal hollows. — **d**: Prosternum, other shapes of sclerotized part. — e: Prosternum, sclerotized part, female.

P0253, Rianila, Rongaronga, Ambodifaho,18:47:53 S, 49:04:50 E, 31.X.1994, 19 ♂♂, 5 ♀♀. P0254, Rianila, Rianila, Antseranambe, 01.11.1994, 5 ♂♂, 1 ♀. P0124, Betsiboka, Kamoro, , 16:28:55 S, 47:10:06 E, 01.04.1993, 2 ♀♀. P0255, Rianila, Morongolo, Antanandava, 18:43:03 S, 49:06:53 E, 02.11.1994, 5 ♂♂. P0475, Tsiribihina, Mazy Aff. de Sakay, Sakay Babetville, 18:58:15 S, 46:29:00 E, 10.10.1995, 4 ♂♂. P0578, Betsiboka, Kamoro, Ambohimanatrika, 16:28:55 S, 47:10:06 E, P0646, Mananjary, Ivanana, Sandrakely, 21:06:27 S, 47:38:18 E, 09.11.1996, 70 ♂♂. Holotype and Paratypes are deposited in the Musée Cantonal de Zoologie, Lausanne, Switzerland, a few Paratypes in the authors collection.

Male imago

Measurements and colouration. Body length: 4.0–5.4 mm; wing length: 3.0–3.6 mm; length of fore leg: 2.0–2.8 mm. Ratio of fore femur : fore tibia = 0.73–0.81; ratio of fore tibia : fore tarsus = 1.38–1.51; ratio of fore leg : hind leg = 1.28–1.39; ratio of first segment of the fore tarsus : 2nd : 3rd : 4th : 5th = 1 : 2.0–2.5 : 1.3–1.8 : 1.0–1.7 : 0.9–1.4. Ratio of body length : length of cercus : length of terminal filum (about) = 1 : 2.5 : 3.3; ratio terminal filum : cercus = 1.5. Colouration of cuticle: Mesothorax yellowish brown; head, pro- and metathorax, coxae, trochanters, fore femora, pedicels and basal parts of the flagelli a little lighter. Abdomen white. Epidermal pigmentation of dorsal side like in Fig. 2a. On ventral side pigments are to be found on prosternal triangle (sides and base strongly coloured),

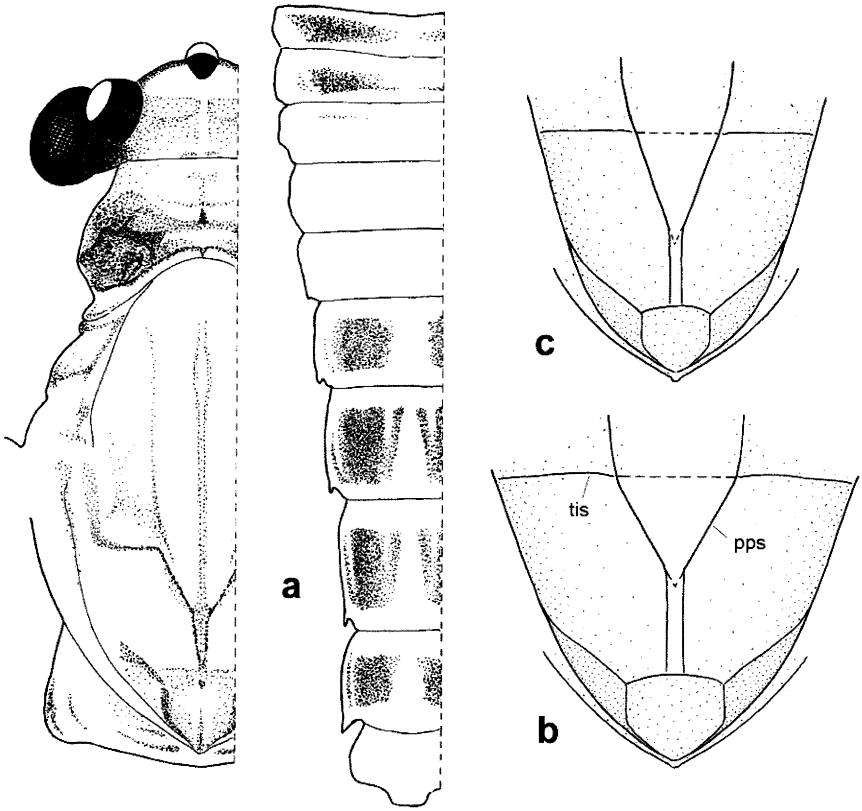

Fig. 2. *Caenis nausicaae* sp. n. (a–b), *Caenis namorona* (c). — **a**: ♂, Pattern of epidermal pigmentation, left half of body, dorsal view. — **b** and **c**: Mesonotum, posterior part. — pps = posterior parapsidal suture, tis = transverse interscutal suture.

sutures of mesosternum and around the coxal hollows. Fore legs are pigmented, too. — This species is characterized in the males by the interruption of the pigmentation on tergites 3–5.

Morphology. Head: base of antennal flagellum dilated. Dilated part 1.3 length of pedicel and about half as broad. Thorax. Sclerotized part of prosternum very broad in front; sometimes nearly rectangular, when posteriorly narrowed sides never concave rather straight or slightly convex (Fig. 1c). Metanotal triangle, formed by posterior parapsidal sutures (pps) and the line between the median ends of transverse interscutal sutures (tis) nearly equilateral (Fig. 2b). Abdomen: Lateral filaments of the abdominal segments short. No finger-like process on tergite II.

Genitalia and sternum IX as in Fig. 1a. Coloured part of the styliger sclerite crescent or sickle-shaped, apophyses short. Lateral sclerite narrow and strongly bowed. Forceps long, with an apical tuft of short and thin spines (Fig. 1b).

Female imago

Measurements and colouration. Body length: 6.6–7.6 mm; wing length: 4.2–4.5 mm.

The colouration is a little different from that of the males. The chitin of the mesonotum is dark brown. All abdominal tergites are evenly and strongly pigmented (tergites 3–5, too). Sclerotized part of prosternum broader than in the males, trapezoid with concave sides (Fig. 1d).

Eggs

Chorion nearly without a visible structure. Two flat epithemata with very small knobs. One long and narrow micropyle, hardly widened on its mouth, which lies on the equator.

Larva. Unknown.

Distribution. Seems to be scattered in the eastern part of Madagascar between the 16th and 22nd degree of latitude.

Etymology. Nausikaa is a Grecian legendary figure like Caenis. *Caenis nausicaae* however is dedicated to my first grand-child Nausikaa.

***Caenis gattolliati* sp. n.**

Material examined. Madagascar: Holotype (micro-slide): P0468, Tsiribihina, Kitsangy, Manalalondo, 19:15:15 S, 47:07:00 E, 04.10.1995, 1 ♂. Paratypes, P0468, Tsiribihina, Kitsangy, Manalalondo, 19:15:15 S, 47:07:00 E, 04.10.1995 3 ♂♂. Holotype and Paratypes are deposited in the Musée Cantonal de Zoologie, Lausanne, Switzerland.

Male imago

Measurements and colouration. Body length 4.2–4.8 mm; wing length 3.5–4.1 mm; foreleg 3.0–3.3 mm; ratio of forefemur : foretibia = 0.51–0.52; ratio of foretibia : foretarsus = 1.25–1,34; ratio of foreleg : hind leg = 1.64–1.65; ratio of first segment of foretarsus : 2nd : 3rd : 4th : 5th = 1 : 3.7 : 2.4–2.6 : 2.3–2.4 : 1.2–1.4. Colouration of cuticle: Meso and metathorax yellow, all other parts white. Epidermal pigmentation: Besides traces of greyish pigments on abdominal segments I and II no pigmentation recognizable. A very pale species.

Morphology. Head: broad and with small eyes. Seen from ventral distance between inner margins of eyes 2.7–3.0 times their width (Fig. 3d) (about 2.0 in *C. nausicaae* and other species of the *C. spinosa* group) (Fig. 3e). Base of antennal flagellum dilated. Dilated part 1.2 length of pedicel. Thorax: prosternal triangle narrow and pointed, sides concave, posterior third more or less convex (Fig. 3c). Metanotal triangle (see *C. nausicaae*) elongated isosceles. Abdomen: lateral filaments of abdominal segments VI–VIII of medium length (Fig. 3a). No finger-like process on tergite II.

Genitalia and sternum IX as in Fig. 3a. Penis lobes elongated, only slightly converging to the broadly rounded tips. Apophyses of styliger sclerite of medium length, more or less medially bent. Forceps medially more or less waisted with apical spines of medium length (Fig. 3b).

Female and larval stage: Unknown.

Distribution. Recorded only from the locus typicus: Mananalondo, river Kitsangy, about 100 km south-southwest from Antananarivo.

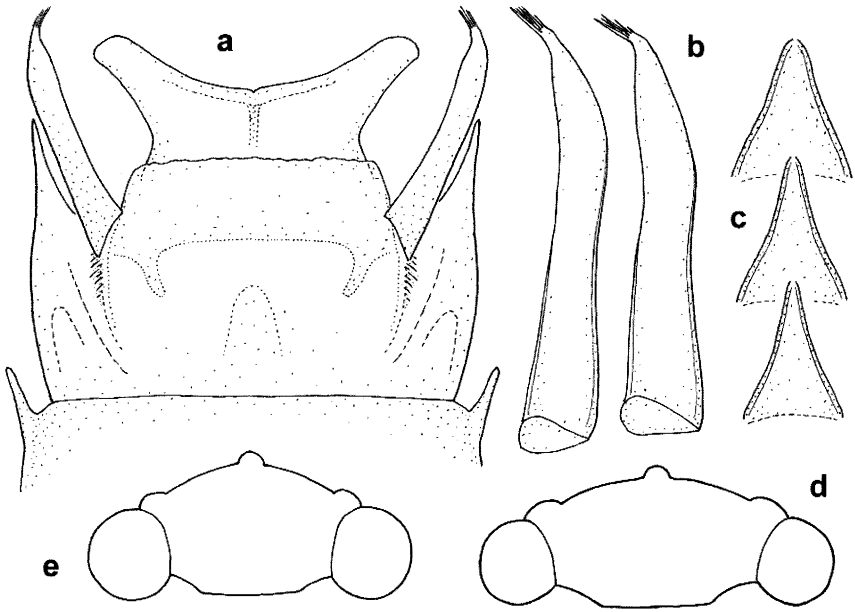

Fig. 3. *Caenis gattolliati* sp. n. (a–d), *Caenis nausicaae* (e), ♂. — **a**: Sternite IX and genitalia. — **b**: Different shapes of forcipes. — **c**: Prosternum, different shapes of sclerotized part. — **d** and **e**: Outline of head and eyes, ventral view.

Etymology. The epithet was given in honour of Dr. Jean-Luc Gattolliat, Lausanne, Switzerland, in recognition of his contributions to Malagasy Mayflies.

Caenis solida sp. n.

Material examined. Madagascar: Holotypue (micro-slide), P0646, Mananjary, Ivanana, Sandrakely, 21:06:27 S, 47:38:18 E 09.11.1996 1 ♂. Paratypes: P0646, Mananjary, Ivanana, Sandrakely, 21:06:27 S, 47:38:18 E 09.11.1996, 27 ♂♂. P0650, Mananuary, Vintanona, Andranomaitso, 21:20:37 S, 47:45:14 E, 12.11.1996, 2 ♂♂. Holotype and Paratypes are deposited in the Musée Cantonal de Zoologie, Lausanne, Switzerland, a few Paratypes in the authors collection.

Male imago

Measurements and colouration. Body length: 1.5–2.0 mm; wing length: 1.6–1.8 mm; length of fore leg: 1.2–1.4 mm. Ratio of fore femur : fore tibia = 0.60–0.66; ratio of fore tibia : fore tarsus = 1.06–1.17; ratio of fore leg : hind leg = 1.51–1.67; ratio of first segment of the fore tarsus : 2nd : 3rd : 4th : 5th = 1 : 3.4–3.9 : 1.7–1.9 : 1.4–1.7 : 1.3–1.6. Ratio of body length : length of cercus : length of terminal filament (about) = 1 : 3.2 : 4.7. Colouration of cuticle: thorax medium brown, ventral side a little lighter; other parts light yellowish brown. Epidermal pigmenta-

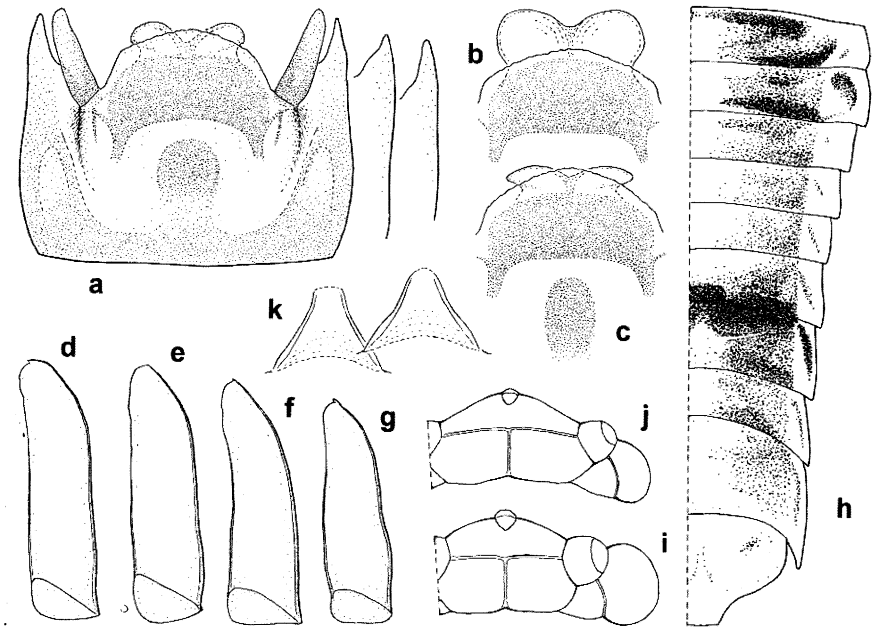

Fig. 4. *Caenis solida* sp. n. (a–h, j, k), *Caenis rutila* (i), ♂. — **a**: Sternite IX and genitalia, different shapes of posteriolateral spines. — **b** and **c**: Different shapes of penis, styliger sclerite and central sclerite (**c**). — **d–g**: Different shapes of forcipes. — **h**: Pattern of epidermal pigmentation, right half of abdomen, dorsal view. — **i** and **j**: Head, dorsal view, size of eyes. — **k**: Prosternum, different shapes of sclerotized part.

tion: head and pronotum brown, rather uniformly pigmented, the latter with paramedian and lateral dark spots and two sublateral lightenings. Mesonotal suture dark reddish-brown. Diffuse pigmentations in the hind part of mesonotum and, stronger, on margins of the scutellum. Transverse dark brown dashes or bands on metanotum. The abdominal tergites show a characteristic blackish brown pattern with intensifications on tergite 1, 2, 6 and 7 (Fig. 4h). All femora with subapical dashes. Fore tibiae and basal segments of caudal filaments diffusely pigmented.

Morphology. Body broad and stocky.

Head: broad and with smaller eyes (in comparison with the related *C. rutila* Malzacher, 1995) (Figs 4j and i). Base of antennal bristle slightly dilated. Thorax: prosternal triangle broad; tip rounded or more or less broadly blunt; sides behind the tip weakly concave (Fig. 4k). Length of mesonotum 7.5–8.5 length of median notal membrane. Abdomen: Lateral filaments of abdominal segments short or very short, often invisible.

Genitalia and sternum IX as in Fig. 4a. Penis with short and rounded lobes (Figs 4a and b) sometimes forming blunt tips when bent dorsally (Fig. 4c). Central sclerite large and circular or oval. Forceps as in Figs 4d–g, apically rounded, often with a tiny point at the end of the lateral margin.

Female and larval stage: Unknown.

Distribution. Only two records from Sandrakely, river Ivanana, about 100 km northeast from Fianarantsoa.

Etymology. The epithet *solida* refers to the stocky body-shape.

The *Caenis spinosa* group

The here newly defined *Caenis spinosa* group contains the species *Caenis spinosa* Malzacher, 1995, *Caenis namorona* Malzacher, 1995, *Caenis johannae* Malzacher, 1995, *Caenis nausicaae* and *Caenis gattolliati*. They can be distinguished from the other *Caenis* species of Madagascar by the following combination of characters: antennal flagellum basally dilated, dilated part as long or longer as the pedicel; forceps apically with a tuft of long spines, basally not contracted. Each species of the *Caenis spinosa* group can be distinguished from the other species of the group by the following combination of diagnostic characters:

Caenis spinosa: sclerotized part of prosternum triangular. Ratio fore femur : fore tibia 0.6–0.7. Abdominal filaments VI–VIII short to medium. Forceps of medium length, apical spines short. Penis lobes large and broadly triangular.

Caenis namorona: sclerotized part of prosternum trapezoid with concave sides. Fore tibia about as long as fore femur. Abdominal filaments VI–VIII very short. Forceps long and bowed, with long apical spines, their bases are forming an evenly curved line. Penis lobes long and isosceles triangular

Caenis johannae: sclerotized part of prosternum broadly triangular. Fore tibia about as long as or even a little shorter than fore femur. Abdominal filaments VI–VIII short. Forceps short and straight, with long apical spines. Penis lobes small triangular, sides of shaft diverging anteriorly.

Caenis nausicaae: sclerotized part of prosternum trapezoid with straight or convex sides. Ratio fore femur : fore tibia 0.7–0.8. Metanotal triangle nearly equilateral. Abdominal filaments VI–VIII short. Forceps straight, apical part more or less bent medially, apical spines short and thin. Penis lobes short triangular, sides of shaft nearly parallel. Styliger sclerite crescent- or sickle-shaped.

Caenis gattolliati: head broad, with small eyes. Sclerotized part of prosternum narrowly triangular. Fore tibia nearly twice as long as fore femur. Abdominal filaments VI–VIII medium to long. Forceps long, medially more or less waisted with apical spines of medium length. Penis lobes elongated, only slightly converging to the broadly rounded tips. Apophyses of styliger sclerite long and more or less bent medially.

In numerous populations, the here described shaping and combinations of features are given so that these specimens can be clearly assigned to one of the species. As common in the genus *Caenis*, characters are more or less variable, even within a population. In the great number of the remaining samples however nearly all sorts of other character combinations can be observed. Some examples for *Caenis namorona*, *Caenis spinosa* and different intermediate stages, all determined as «*Caenis spinosa* group», are shown in the diagrams 1–8. Each diagram shows the combination of character states of 8 different specimens from a sample. In the diagram 9 the character fluctuation of these 8 populations are shown for comparison.

The fields including the definite diagnostic characters of the two species *Caenis namorona* and *Caenis spinosa* are bordered by a thick line. The two numbers below in the diagrams 9 indicate how often these characters have been found in the 8 specimens examined. Diagrams 1 combined in 9. 1 and 2 combined in 9. 2 show cases of *Caenis spinosa*, diagram 8 (9. 8) of *Caenis namorona*. 7 (9. 7) is close to *Caenis namorona* whereas the diagrams 3 (9. 3) to 6 (9. 6) show intermediate stages with different combination of characters and different degrees of character fluctuation which can be extended over 5 or 6 states of a character as in 9.3 and 9.5.

DISCUSSION

Under those circumstances a description of further new species of the *Caenis spinosa* group based on imaginal morphological characters only seems not advisable. Nevertheless they could exist especially as populations of the *Caenis spinosa* group are accompanied by real *Caenis spinosa* in four cases and by real *Caenis namorona* in eight cases. This reveals that there are two populations with different genotypes or at least with differences in gene activity. Larval stages described in another paper (Malzacher 2009) show a number of clearly distinguishable forms with conspicuous diagnostic characters. Two of them could be assigned with reservation to the species *Caenis spinosa* and *Caenis johannae* but a third form was found together with a population of the *Caenis spinosa* group males at the same locality (P0476, Sakay Babetville). As no described *Caenis* species has been found there it is very likely that it concerns a new species with the preliminary name *Caenis trichocaenoides* (Malzacher 2009). For clarification these and other larvae should be reared.

The populations determined as *Caenis spinosa* group with their different character-state combinations show a rather random distribution in great parts of Madagascar. Therefore a group of subspecies linked by clines (a line of gradual change in character states across the geographic distribution) with two real species at the ends (circle of races) does not seem to be realized here, rather the above mentioned differently activated gene effects seem to be responsible for different coincidental character combinations. So the establishing of relationships by means of synapomorphies or cladistics is impossible under these circumstances.

As mentioned above *Caenis solida* is closely related to *Caenis rutila*. Malzacher (2009) supposes that *Caenis rutila* is identical with *Callistellina panda* because the subimaginal male genitalia of last instar larvae of the latter are very similar to those of *Caenis rutila*. So the *Caenis rutila* group seems to be identical with the genus *Callistellina* and *Caenis solida* therefore also a member of this genus. However, males should be reared from the larvae concerned before a renaming.

KEY TO THE MALES OF ALL MALAGASY *CAENIS* SPECIES

1 Base of the antennal bristle clearly dilated. Dilated part as long or longer than the pedicel **2**

— Base of the antennal bristle not or only slightly dilated. Dilated part doesn't reach the length of the pedicel **6**

2 Penis lobes elongated, only slightly converging to the broadly rounded tip. Head broad with small eyes (Fig. 4d) ..... ***C. gattolliati***
— Penis lobes more or less triangular. Eyes larger (Fig. 4e) **3**

3 Sclerotized ridges of prosternum forming a broadened more or less trapezoid structure, sometimes nearly rectangular (Figs 1c and d and Malzacher 1995, Fig. 3c), often strongly pigmented **4**
— Sclerotized ridges of prosternum forming a more or less triangular structure sometimes posteriorly broadly rounded **5**

4 Sides of prosternal trapezoid straight or slightly convex, sometimes nearly parallel, when posteriorly narrowed sides never concave (Fig. 1c). Metanotal triangle nearly equilateral (Fig. 2b). Hind margin of penis mostly straight, penis-lobes shortly triangular. Styliger sclerite crescent- or sickle-shaped (Fig. 1a). Forceps with short and thin apical spines (Fig. 1b). Abdominal tergites 3–5 (nearly) without pigments, strongly contrasting to the other tergites which shows large, darkbrown marks *) ..... ***C. nausicaae***
— Sides of prosternal trapezoid concave and posteriorly more diverging (Malzacher 1995, Fig. 3c). Metanotal triangle isosceles (Fig. 2c). Hind margin of penis incised, penis-lobes long (Malzacher 1995, Fig. 3a). Forceps with long apical spines, their bases are forming an evenly curved line (Malzacher 1995, Fig. 3b) ..... ***C. namorona***

5 Forceps straight with long apical spines, length of shaft 3.5–4 times length of spines (Malzacher 1995, Fig. 4b). Penis-lobes small. Head, abdominal tergites and sternite IX strongly pigmented (Malzacher 1995, Figs 7b and 4a) *). ... . ***C. johannae***
— Forceps more or less bowed, apical spines shorter, length of shaft 6–7 times length of spines (Malzacher 1995, Fig. 2d). Penis-lobes larger and broadly triangular ..... ***C. spinosa***

6 Forceps with an apical tuft of long spines, basally more or less broadened (Malzacher 1995, Fig. 5c). Abdomen without concentration of pigments on the tergites 6 and 7 ..... ***C. rugosa***
— Forceps apically with very short strong spines or without, basally not clearly broadened, often narrowed (Figs 4d–g and Malzacher 1995, Fig. 4b). Abdomen with a concentration of pigments on the 6th and the 7th tergite (Fig. 3h) *) **7**

7 Species of medium length, minimal length of body and wings: 2.5 mm. Eyes large and semi-spherical (Fig. 4i). Forceps elongated, apically more or less tapering and with 4–5 short spines (Malzacher 1995, Fig. 6c). Length of the mesonotum 5.3–6.3 length of the median notal membrane ..... ***C. rutila***
— Very small species, maximal length of body 2.0 mm and wings 1.8 mm. Eyes smaller and less domed (Fig. 4j). Forceps shorter, sides more or less parallel, without spines (Figs 4d–g). Length of the mesonotum 7.5–8.5 length of the median notal membrane ..... ***C. solida***

*) In all species there are populations with more or less reduced or even lacking pigmentation. Regard colour features therefore only additionally.

ACKNOWLEDGEMENTS

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Annex
Explanations see text

Diagram 1

1 a, b		nam			spin		
P0531	I	II	III	IV	V	VI	VII
ratio fore femur : tibia					—		
prosternal triangle shape					—		
abdom. filaments length				—			
forceps shape				—			
forceps length/width				—			
apical spines					—		
base of penis lobes						—	
penis lobes					—		
apophyses				—			

	nam			spin		
I	II	III	IV	V	VI	VII
			—			
		—				
			—			
				—		
			—			
				—		
					—	
				—		
			—			

1 c, d		nam			spin		
P0531	I	II	III	IV	V	VI	VII
ratio fore femur : tibia						—	
prosternal triangle shape					—		
abdom. filaments length					—		
forceps shape					—		
forceps length/width					—		
apical spines					—		
base of penis lobes					—		
penis lobes					—		
apophyses				—			

	nam			spin		
I	II	III	IV	V	VI	VII
					—	
				—		
				—		
				—		
				—		
				—		
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				—		
				—		

1 e, f		nam			spin		
P0531	I	II	III	IV	V	VI	VII
ratio fore femur : tibia					—		
prosternal triangle shape					—		
abdom. filaments length				—			
forceps shape					—		
forceps length/width				—			
apical spines					—		
base of penis lobes						—	
penis lobes					—		
apophyses				—			

	nam			spin		
I	II	III	IV	V	VI	VII
			—			
			—			
			—			
				—		
				—		
					—	
				—		
				—		
				—		

1 g, h		nam			spin		
P0531	I	II	III	IV	V	VI	VII
ratio fore femur : tibia						—	
prosternal triangle shape				—			
abdom. filaments length					—		
forceps shape					—		
forceps length/width					—		
apical spines					—		
base of penis lobes					—		
penis lobes					—		
apophyses					—		

	nam			spin		
I	II	III	IV	V	VI	VII
				—		
			—			
				—		
				—		
			—			
					—	
				—		
			—			
				—		

Diagram 2

2 a, b		nam			spin		
P0350	I	II	III	IV	V	VI	VII
ratio fore femur : tibia							▬
prosternal triangle shape					▬		
abdom. filaments length				▬			
forceps shape				▬			
forceps length/width					▬		
apical spines					▬		
base of penis lobes					▬		
penis lobes					▬		
apophyses					▬		

	nam			spin		
I	II	III	IV	V	VI	VII
					▬	
				▬		
		▬				
				▬		
				▬		
					▬	
			▬			
			▬			
			▬			

2 c, d		nam			spin		
P0350	I	II	III	IV	V	VI	VII
ratio fore femur : tibia						▬	
prosternal triangle shape						▬	
abdom. filaments length					▬		
forceps shape					▬		
forceps length/width				▬			
apical spines					▬		
base of penis lobes					▬		
penis lobes					▬		
apophyses					▬		

	nam			spin		
I	II	III	IV	V	VI	VII
						▬
				▬		
				▬		
			▬			
				▬		
				▬		
			▬			
			▬			
				▬		

2 e, f		nam			spin		
P0350	I	II	III	IV	V	VI	VII
ratio fore femur : tibia						▬	
prosternal triangle shape					▬		
abdom. filaments length					▬		
forceps shape				▬			
forceps length/width					▬		
apical spines				▬			
base of penis lobes					▬		
penis lobes					▬		
apophyses						▬	

	nam			spin		
I	II	III	IV	V	VI	VII
						▬
			▬			
			▬			
				▬		
				▬		
				▬		
					▬	
				▬		
				▬		

2 g, h		nam			spin		
P0350	I	II	III	IV	V	VI	VII
ratio fore femur : tibia						▬	
prosternal triangle shape				▬			
abdom. filaments length					▬		
forceps shape					▬		
forceps length/width					▬		
apical spines					▬		
base of penis lobes					▬		
penis lobes					▬		
apophyses						▬	

	nam			spin		
I	II	III	IV	V	VI	VII
				▬		
				▬		
			▬			
				▬		
				▬		
				▬		
				▬		
				▬		
				▬		

Diagram 3

3 a, b		nam			spin				nam			spin		
P0548	I	II	III	IV	V	VI	VII	I	II	III	IV	V	VI	VII
ratio fore femur : tibia		—										—		
prosternal triangle shape					—							—		
abdom. filaments length				—					—					
forceps shape			—									—		
forceps length/width			—								—			
apical spines				—										—
base of penis lobes				—								—		
penis lobes			—										—	
apophyses			—									—		

3 c, d		nam			spin				nam			spin		
P0548	I	II	III	IV	V	VI	VII	I	II	III	IV	V	VI	VII
ratio fore femur : tibia	—												—	
prosternal triangle shape					—					—				
abdom. filaments length			—									—		
forceps shape					—							—		
forceps length/width				—							—			
apical spines					—								—	
base of penis lobes			—									—		
penis lobes					—							—		
apophyses				—							—			

3 e, f		nam			spin				nam			spin		
P0548	I	II	III	IV	V	VI	VII	I	II	III	IV	V	VI	VII
ratio fore femur : tibia			—										—	
prosternal triangle shape						—							—	
abdom. filaments length			—							—				
forceps shape					—							—		
forceps length/width				—						—				
apical spines					—							—		
base of penis lobes					—								—	
penis lobes					—								—	
apophyses			—							—				

3 g, h		nam			spin				nam			spin		
P0548	I	II	III	IV	V	VI	VII	I	II	III	IV	V	VI	VII
ratio fore femur : tibia		—									—			
prosternal triangle shape						—				—				
abdom. filaments length			—						—					
forceps shape					—								—	
forceps length/width					—						—			
apical spines					—						—			
base of penis lobes			—						—					
penis lobes			—							—				
apophyses				—						—				

Diagram 4

4 a, b		nam			spin		
P0578	I	II	III	IV	V	VI	VII
ratio fore femur : tibia				▬			
prosternal triangle shape					▬		
abdom. filaments length			▬				
forceps shape			▬				
forceps length/width			▬				
apical spines		▬					
base of penis lobes			▬				
penis lobes			▬				
apophyses					▬		

	nam			spin		
I	II	III	IV	V	VI	VII
			▬			
				▬		
				▬		
	▬					
		▬				
				▬		
					▬	
					▬	
					▬	

4 c, d		nam			spin		
P0578	I	II	III	IV	V	VI	VII
ratio fore femur : tibia			▬				
prosternal triangle shape					▬		
abdom. filaments length			▬				
forceps shape	▬						
forceps length/width			▬				
apical spines		▬					
base of penis lobes		▬					
penis lobes			▬				
apophyses			▬				

	nam			spin		
I	II	III	IV	V	VI	VII
					▬	
				▬		
	▬					
▬						
	▬					
	▬					
	▬					
		▬				
			▬			

4 e, f		nam			spin		
P0578	I	II	III	IV	V	VI	VII
ratio fore femur : tibia			▬				
prosternal triangle shape					▬		
abdom. filaments length			▬				
forceps shape		▬					
forceps length/width		▬					
apical spines		▬					
base of penis lobes		▬					
penis lobes		▬					
apophyses		▬					

	nam			spin		
I	II	III	IV	V	VI	VII
			▬			
				▬		
				▬		
▬						
		▬				
					▬	
				▬		
					▬	
			▬			

4 g, h		nam			spin		
P0578	I	II	III	IV	V	VI	VII
ratio fore femur : tibia				▬			
prosternal triangle shape					▬		
abdom. filaments length					▬		
forceps shape			▬				
forceps length/width				▬			
apical spines						▬	
base of penis lobes				▬			
penis lobes			▬				
apophyses		▬					

	nam			spin		
I	II	III	IV	V	VI	VII
	▬					
				▬		
	▬					
		▬				
		▬				
		▬				
		▬				
			▬			
		▬				

Diagram 5

5 a, b		nam			spin		
P0663	I	II	III	IV	V	VI	VII
ratio fore femur : tibia						—	
prosternal triangle shape					—		
abdom. filaments length			—				
forceps shape			—				
forceps length/width				—			
apical spines			—				
base of penis lobes		—					
penis lobes		—					
apophyses		—					

	nam			spin		
I	II	III	IV	V	VI	VII
					—	
				—		
			—			
	—					
		—				
			—			
			—			
		—				
		—				

5 c, d		nam			spin		
P0663	I	II	III	IV	V	VI	VII
ratio fore femur : tibia						—	
prosternal triangle shape					—		
abdom. filaments length				—			
forceps shape			—				
forceps length/width			—				
apical spines			—				
base of penis lobes		—					
penis lobes				—			
apophyses			—				

	nam			spin		
I	II	III	IV	V	VI	VII
					—	
					—	
				—		
		—				
		—				
			—			
		—				
		—				
	—					

5 e, f		nam			spin		
P0663	I	II	III	IV	V	VI	VII
ratio fore femur : tibia						—	
prosternal triangle shape					—		
abdom. filaments length				—			
forceps shape					—		
forceps length/width				—			
apical spines			—				
base of penis lobes		—					
penis lobes		—					
apophyses	—						

	nam			spin		
I	II	III	IV	V	VI	VII
						—
				—		
			—			
				—		
	—					
	—					
		—				
		—				
	—					

5 g, h		nam			spin		
P0663	I	II	III	IV	V	VI	VII
ratio fore femur : tibia						—	
prosternal triangle shape						—	
abdom. filaments length				—			
forceps shape				—			
forceps length/width			—				
apical spines			—				
base of penis lobes		—					
penis lobes			—				
apophyses			—				

	nam			spin		
I	II	III	IV	V	VI	VII
						—
					—	
			—			
		—				
		—				
			—			
	—					
	—					
	—					

Diagram 6

6 a, b		nam			spin				nam			spin		
P0357	I	II	III	IV	V	VI	VII	I	II	III	IV	V	VI	VII
ratio fore femur : tibia				—								—		
prosternal triangle shape					—						—			
abdom. filaments length		—							—					
forceps shape		—								—				
forceps length/width		—								—				
apical spines			—						—					
base of penis lobes		—								—				
penis lobes		—								—				
apophyses			—							—				

6 c, d		nam			spin				nam			spin		
P0357	I	II	III	IV	V	VI	VII	I	II	III	IV	V	VI	VII
ratio fore femur : tibia				—								—		
prosternal triangle shape			—								—			
abdom. filaments length			—							—				
forceps shape		—								—				
forceps length/width			—							—				
apical spines			—						—					
base of penis lobes		—									—			
penis lobes			—								—			
apophyses			—								—			

6 e, f		nam			spin				nam			spin		
P0357	I	II	III	IV	V	VI	VII	I	II	III	IV	V	VI	VII
ratio fore femur : tibia				—							—			
prosternal triangle shape			—								—			
abdom. filaments length			—							—				
forceps shape			—							—				
forceps length/width				—							—			
apical spines			—						—					
base of penis lobes			—							—				
penis lobes			—						—					
apophyses				—					—					

6 g, h		nam			spin				nam			spin		
P0357	I	II	III	IV	V	VI	VII	I	II	III	IV	V	VI	VII
ratio fore femur : tibia				—								—		
prosternal triangle shape				—						—				
abdom. filaments length			—							—				
forceps shape		—									—			
forceps length/width		—								—				
apical spines		—								—				
base of penis lobes		—								—				
penis lobes			—							—				
apophyses		—									—			

Diagram 7

7 a, b		nam			spin				nam			spin		
P0248	I	II	III	IV	V	VI	VII	I	II	III	IV	V	VI	VII
ratio fore femur : tibia			—							—				
prosternal triangle shape		—							—					
abdom. filaments length			—						—					
forceps shape		—								—				
forceps length/width			—							—				
apical spines		—								—				
base of penis lobes			—							—				
penis lobes			—							—				
apophyses		—								—				

7 c, d		nam			spin				nam			spin		
P0248	I	II	III	IV	V	VI	VII	I	II	III	IV	V	VI	VII
ratio fore femur : tibia		—									—			
prosternal triangle shape		—									—			
abdom. filaments length		—							—					
forceps shape		—							—					
forceps length/width		—									—			
apical spines		—									—			
base of penis lobes			—							—				
penis lobes			—						—					
apophyses			—						—					

7 e, f		nam			spin				nam			spin		
P0248	I	II	III	IV	V	VI	VII	I	II	III	IV	V	VI	VII
ratio fore femur : tibia				—					—					
prosternal triangle shape		—							—					
abdom. filaments length		—						—						
forceps shape		—							—					
forceps length/width			—							—				
apical spines		—							—					
base of penis lobes				—					—					
penis lobes				—						—				
apophyses			—							—				

7 g, h		nam			spin				nam			spin		
P0248	I	II	III	IV	V	VI	VII	I	II	III	IV	V	VI	VII
ratio fore femur : tibia				—						—				
prosternal triangle shape		—							—					
abdom. filaments length		—							—					
forceps shape		—							—					
forceps length/width			—							—				
apical spines		—							—					
base of penis lobes		—							—					
penis lobes		—						—						
apophyses		—							—					

Diagram 8

8 a, b		nam			spin				nam			spin
P0835	I	II	III	IV	V	VI	VII	I	II	III	IV	V
ratio fore femur : tibia		—								—		
prosternal triangle shape		—							—			
abdom. filaments length		—							—			
forceps shape		—							—			
forceps length/width		—								—		
apical spines		—							—			
base of penis lobes		—							—			
penis lobes			—							—		
apophyses			—							—		

8 c, d		nam			spin				nam			spin
P0835	I	II	III	IV	V	VI	VII	I	II	III	IV	V
ratio fore femur : tibia		—								—		
prosternal triangle shape		—							—			
abdom. filaments length		—							—			
forceps shape		—								—		
forceps length/width			—							—		
apical spines			—							—		
base of penis lobes			—							—		
penis lobes		—							—			
apophyses			—						—			

8 e, f		nam			spin				nam			spin
P0835	I	II	III	IV	V	VI	VII	I	II	III	IV	V
ratio fore femur : tibia		—						—				
prosternal triangle shape		—							—			
abdom. filaments length		—							—			
forceps shape		—							—			
forceps length/width			—						—			
apical spines		—							—			
base of penis lobes			—						—			
penis lobes		—							—			
apophyses		—							—			

8 g, h		nam			spin				nam			spin
P0835	I	II	III	IV	V	VI	VII	I	II	III	IV	V
ratio fore femur : tibia		—									—	
prosternal triangle shape		—							—			
abdom. filaments length	—								—			
forceps shape		—								—		
forceps length/width		—								—		
apical spines		—							—			
base of penis lobes				—					—			
penis lobes			—							—		
apophyses			—							—		

Diagram 9

9. 1		nam			spin		
P0350	I	II	III	IV	V	VI	VII
ratio fore femur : tibia					1	4	3
prosternal triangle shape				2	5	1	
abdom. filaments length			1	3	4		
forceps shape				3	5		
forceps length/width				1	7		
apical spines				1	6	1	
base of penis lobes				2	5	1	
penis lobes				2	6		
apophyses				1	5	2	
		0			55		

9. 2		nam			spin		
P0531	I	II	III	IV	V	VI	VII
ratio fore femur : tibia				2	3	3	
prosternal triangle shape			1	3	4`		
abdom. filaments length				4	4		
forceps shape				1	7		
forceps length/width				4	4		
apical spines					6	2	
base of penis lobes					5	3	
penis lobes				1	7		
apophyses				5	3		
		1			53		

9. 3		nam			spin		
P0548	I	II	III	IV	V	VI	VII
ratio fore femur : tibia	1	2	1	1	1	2	
prosternal triangle shape			2		3	3	
abdom. filaments length		2	4	1	1		
forceps shape			1		6	1	
forceps length/width			2	5	1		
apical spines				2	4	1	1
base of penis lobes		1	2	1	3	1	
penis lobes			3		3	2	
apophyses			4	3	1		
		10			26		

9. 4		nam			spin		
P0663	I	II	III	IV	V	VI	VII
ratio fore femur : tibia						6	2
prosternal triangle shape					5	3	
abdom. filaments length			1	6	1		
forceps shape		1	4	1	2		
forceps length/width		1	5	2			
apical spines		1	4	3			
base of penis lobes		5	2	1			
penis lobes		3	4	1			
apophyses	1	4	3				
		20			20		

9. 5		nam			spin		
P0578	I	II	III	IV	V	VI	VII
ratio fore femur : tibia		1	2	4		1	
prosternal triangle shape					8		
abdom. filaments length		2	3		3		
forceps shape	3	2	3				
forceps length/width		3	4	1			
apical spines		4	1		1	2	
base of penis lobes		3	2	1	1	1	
penis lobes		1	4	1		2	
apophyses		2	2	2	1	1	
		23			17		

9. 6		nam			spin		
P0357	I	II	III	IV	V	VI	VII
ratio fore femur : tibia				5	3		
prosternal triangle shape			3	4	1		
abdom. filaments length		2	6				
forceps shape		3	4	1			
forceps length/width		2	4	2			
apical spines		4	4				
base of penis lobes		3	4	1			
penis lobes		2	5	1			
apophyses		2	6	3			
		25			5		

9. 7		nam			spin		
P0248	I	II	III	IV	V	VI	VII
ratio fore femur : tibia		2	3	3			
prosternal triangle shape		7		1			
abdom. filaments length	1	5	2				
forceps shape		7	1				
forceps length/width		1	6	1			
apical spines		6	1	1			
base of penis lobes		3	4	1			
penis lobes	1	2	4	1			
apophyses		4	4				
		41			0		

9. 8		nam			spin		
P0835	I	II	III	IV	V	VI	VII
ratio fore femur : tibia	1	4	2	1			
prosternal triangle shape		8					
abdom. filaments length	1	7					
forceps shape		6	2				
forceps length/width		3	5				
apical spines		6	2				
base of penis lobes		4	3	1			
penis lobes		4	4				
apophyses		3	5				
		48			0		

Table of character state variability in the *Caenis spinosa* group.

fore tibia length; ratio fore femur : fore tibia
1. 1.1 – 1.2 (or more)
2. 1.0
3. 0.9
4. 0.8
5. 0.7
6. 0.6
7. 0.5-0.4

prosternal triangle shape
1. apically broadly rounded and domed
2. apically broadly cut
3. narrower, apically cut or rounded
4. apically narrowly rounded
5. triangular, apically more or less pointed
6. sharply pointed

abdominal filaments length
1. very short, nearly invisible
2. very short
3. short
4. short-medium
5. medium

forceps shape
1. more or less straight
2. regularly bowed
3? more or less medially bent
4. more irregular and/or medially bent
5. weakly or only apically bowed
6. straight and with parallel sides

forceps length, width
2. very long, clearly surpassing penis
3. long, surpassing penis more or less
4. little shorter and broader
5. medium length, more or less broadened, particularly basally

forceps, apical spines
2. long, more or less bent, bases of spines forming a curved line
3. long, bases more or less irregularly arranged
4. shorter, bases irregularly arranged
5. medium length, base of tuft narrow
6. short
7. very short and thin

base of penis lobes
2. narrow
3. less broadened
4. more broadened
5. broad
6. very broad,

penis lobes
1. long and narrow
2. long isosceles triangular,
3. intermediate stage I
4. intermediate stage II
5. equilateral triangular
6. very short, or more or less inconspicuous

apophyses
1. long,
2. more or less narrow and a little shorter
3. shorter I, broader
4. shorter II,
5. short
6. very short or lacking