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RESEARCH ARTICLE

Trait evolution of the male genitalia in the speciose genus *Caenis*, with emphasis on forcipes structure (Insecta: Ephemeroptera: Caenidae)

Peter Malzacher

Abstract

The trait evolution of different forceps types within the species-rich genus *Caenis* Stephens, 1835 and their worldwide distribution are partly interpreted as a result of reproductive isolation due to continental drift, thus reflecting possible phylogenetic relationships. Consequently, a hypothetical subdivision of the genus is suggested.

Keywords: *Caenis*, continental drift, forceps, male genitalia, phylogeny, species groups.

Zusammenfassung

Die Merkmalsevolution der verschiedenen Forceps-Typen innerhalb der Großgattung *Caenis* Stephens, 1835 und ihre weltweite Verbreitung werden als Ergebnis reproduktiver Isolation durch Kontinentaldrift interpretiert, die mögliche phylogenetische Verwandtschaft widerspiegelt. Dementsprechend wird eine hypothetische Unterteilung der Gattung vorschlagen.

Introduction

In the first half and in the middle of the 20th century, efforts were made to separate species groups from the genus *Caenis* and establish these as separate genera, namely *Caenodes* Ulmer, 1924, *Austrocaenis* Barnard, 1932, and *Caenomedea* Thew, 1960, as summarized by Thew (1960). At that time, only about 40 species of *Caenis* were known, whereas about 160 are recognized today. In the original publications, diagnostic characters, particularly the shape of the genitalia and forcipes, were often insufficiently described or even erroneous. Hence, they cannot fulfil the demands of modern taxonomy and phylogenetics (cf. Malzacher 1993: 414).

Within the suborder Pannota, only the genus *Neoephemera* McDunnough, 1925 shows forcipes with four segments. Within Ephemerelloidea, a reduction to three or two-segmented forcipes can be observed (McCafferty & Wang 2000). A similar tendency in reduction of forceps segments can be found independently within Caenoidea (Caenotergaliae sensu Kluge 2000). It is regarded as an apomorphic character in the *Potamanthellus* lineage of Neoephemeridae by Bae & McCafferty (1998). The forcipes decrease both in length and in number of segments from four in *Neoephemera* to three or two in different species of *Potamanthellus* Lestage, 1930. Edmunds (1975) supposed for Caenidae a *Potamanthellus*-like ancestor. If so, the reductive tendency would have continued in the evolution of Caenidae, finally leading to one-segmented forcipes, which is a striking apomorphic character of the entire family. These forcipes, as well as the reduced ones in *Potamanthellus*, have lost the main function of fixing the female abdomen in position during copula, which is the case in all other families of Ephemeroptera (Malzacher 1991; Malzacher & Staniczek 2006). Unfortunately, there are no direct observations and investigations on the copulatory mode of Caenidae, so any assumption would be merely speculative. However, a probable functional change of these structures led to an explosive development of new forms in Caenidae (Malzacher 1991), the discovery of which is still ongoing (e.g., Malzacher & Staniczek 2006; Malzacher 2013; Malzacher & Sangpradub 2021). For the genus *Caenis*, the presently known traits and their phylogenetic interpretability are summarized and discussed in this contribution.

Material and methods

Forcipes of the herein mentioned species were either redrawn from original descriptions and other publications (Malzacher 1986, 1990, 1991, 1993, 2001, 2010, 2011, 2013, 2015, 2018, 2021; Da Silva 1993; Malzacher & Staniczek 2006, 2018; Pescador & Richard 2006; Molineri 2009; Lima et al. 2016 Malzacher & Barber-James 2021; Malzacher & Sangpradub 2021; Molineri 2009; Molineri et al. or drawn from specimens in 75% EtOH out of coll. Malzacher (deposited at State Museum of Natural History Stuttgart, Germany). Holotypes were embedded in Euparal as whole mounts. Specimens were investigated under a Wild M3 stereo microscope and a Leitz Laborlux microscope, and drawn with a Zeiss Camera Lucida attached to the latter.

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Paleogeographic maps were generated in R (version 4.2.0) (R Core Team 2022). Data was pulled from Macrostrat.org and converted to shape maps via the R package velociraptr (Zaffos 2019).

Different forceps shapes in species of *Caenis* and their geographical distribution

The genus *Caenis* is present in all biogeographic realms except for Australia, New Zealand, and Iceland.

The forcipes of the genus *Caenis* show four main types of apices (Malzacher 1991), three of which with different subtypes.

Type 1 forcipes (Figs. 1, 5)

Forceps apically more or less broadly rounded, sometimes irregularly, with small bumps, tiny sclerotized tips, or spines.

Type 1a. The simplest forms are short and broadly rounded forcipes combined with weakly structured, nearly unsclerotized genitalia. They can be found in West Africa in *Caenis elouardi* Malzacher, 1990 (Fig. 1d–f), *Caenis wegeneriana* Malzacher, 2021 (Fig. 1a–c), and *Caenis vermifera* Malzacher, 2011 (Fig. 1g), and in Eastern South America [*Caenis reissi* group, e.g., *Caenis sigillata* Malzacher, 1986 (Fig. 1j) and *Caenis reissi* Malzacher, 1986 (Fig. 1k)].

Type 1b. More evolved, more or less elongated and coloured forcipes, often with the above-mentioned inconspicuous apical structures, can be found in the whole of South and Central America, e.g., in the *Caenis pflugfelderi* group: *Caenis pflugfelderi* Malzacher, 1990 (Fig. 1m), *Caenis panamensis* Malzacher, 2001 (Fig. 1o), and in the *Caenis argentina* group: *Caenis ludicra* Navas, 1920 (Fig. 1l), *Caenis gonseri* Malzacher, 2001 (Fig. 1n). The most elongated and developed forms are present in Cuba, in *Caenis cubensis* Malzacher, 2001 (Fig. 1p–q). Few species with apically rounded forcipes are also present in the Oriental Realm: *Caenis obtusostilata* Malzacher, 2021 (Fig. 1h), *Caenis ranauensis* Malzacher, 2015 (Fig. 1i), and *Caenis martensi* Malzacher, 2018 (like Fig. 1h) (see "Biogeographic and phylogenetic considerations").

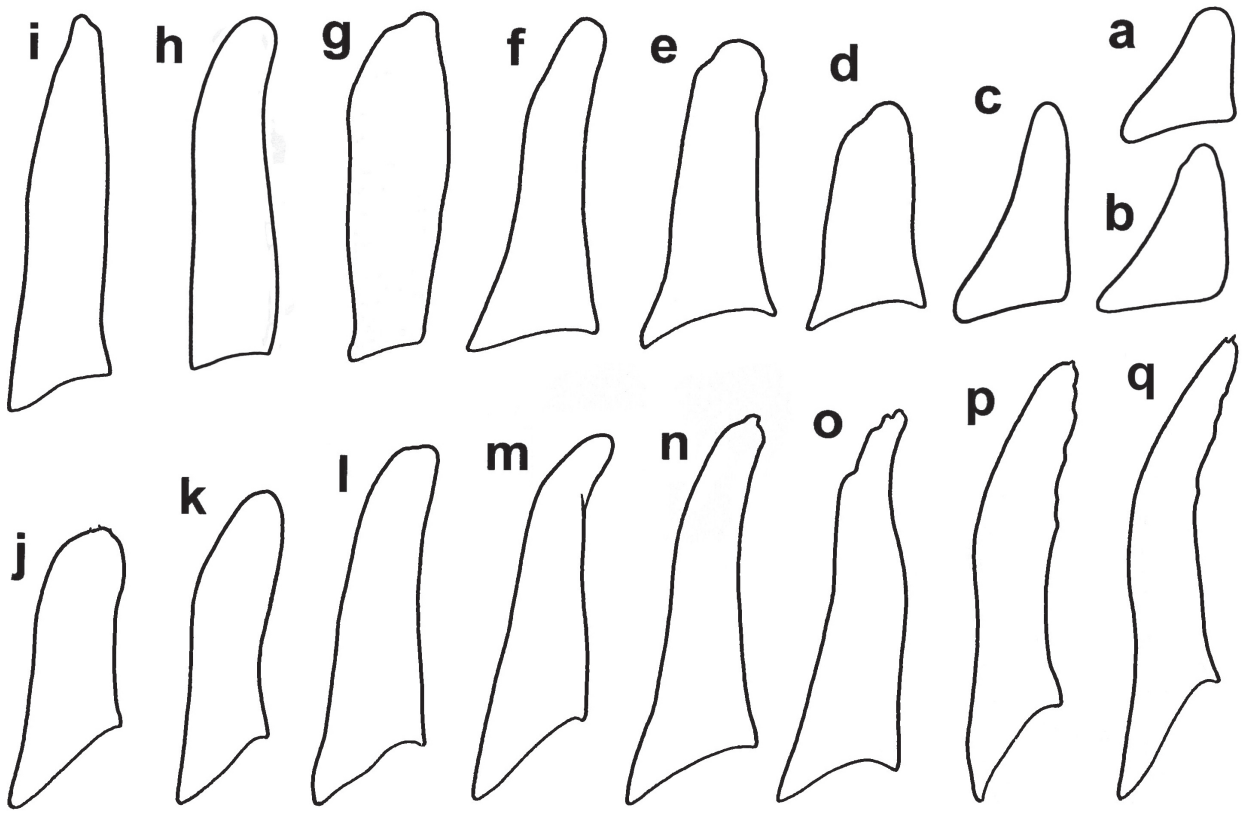

Fig. 1. Forceps type 1, apically rounded. **a–c**. *Caenis wegeneriana*, different shapes. **d–f**. *Caenis elouardi*, different shapes. **g**.*Caenis vermifera*. **h**. *Caenis obtusostilata*. **i**. *Caenis ranauensis*. **j**. *Caenis sigillata*. **k**. *Caenis reissi*. **l**. *Caenis ludicra*. **m**. *Caenis pflugfelderi*. **n**. *Caenis gonseri*. **o**. *Caenis panamensis*. **p–q**. *Caenis cubensis*, different shapes.

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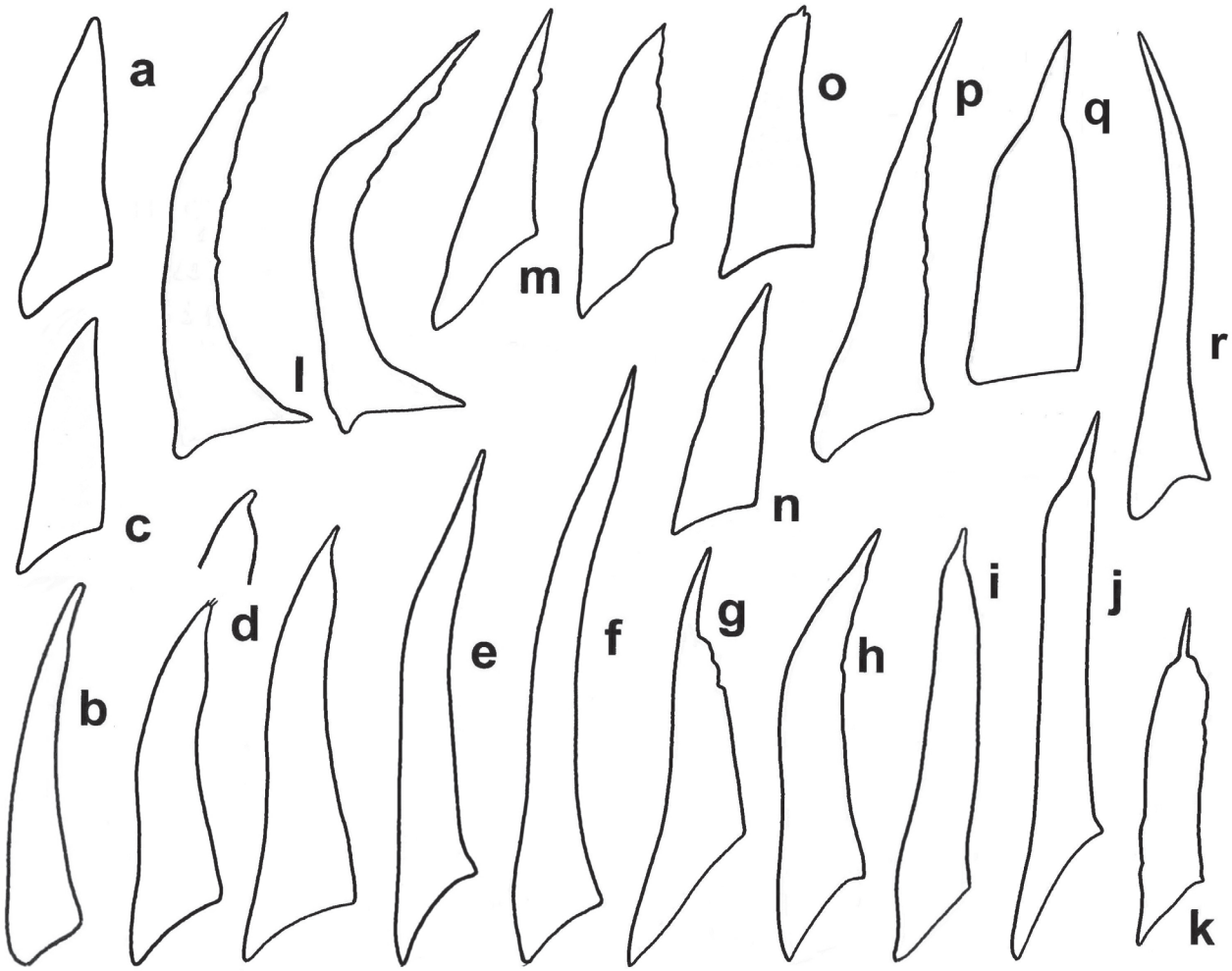

Fig. 2. Forcipes of intermediate stage between type1 and type 2 (a, b); forceps type 2a, with strongly sclerotized, pointed tips (c-r). **a**. *Caenis eglinensis*. **b**. *Caenis cuniana*. **c**. *Caenis punctata*. **d**. *Caenis* sp. (*diminuta* group), three different shapes. **e**. *Caenis amica*. **f**. *Caenis latipennis*. **g**. *Caenis burmeisteri*. **h**. *Caenis pseudamica*. **i**. *Caenis teipunensis*. **j**. *Caenis fittkaui*. **k**. *Caenis candelata*. **l**. *Caenis rivulorum*, different shapes. **m**. *Caenis robusta*, different shapes. **n**. *Caenis strugaensis*. **o**. *Caenis wui*. **p**. *Caenis horaria*. **q**. *Caenis ludovici*. **r**. *Caenis fregatula*.

Type 2 forcipes
(Figs. 2c–r, 6)

Forcipes with strongly sclerotized, mostly long and pointed tips, more or less aligned to the longitudinal axis.

Transitionary stages between types 1 and 2, with long tips more or less apically rounded, are found in *Caenis eglinensis* Pescador, 2006 (Fig. 2a) from Florida and *Caenis cuniana* Froehlich, 1969 (Fig. 2b) from Amazonia.

Type 2a (Figs. 2c–r, 6). The typical type 2a species, with acute sclerotized tips, are widely distributed in South and Central America: forcipes with straight tips, more or less converging evenly to the tip as in *Caenis pseudamica* Malzacher, 1990 (Fig. 2h), with medially stepped tips in *Caenis burmeisteri* Malzacher, 1990 (Fig. 2g) and forcipes more or less abruptly narrowed between shaft and tip in the *Caenis fittkaui* group: *Caenis teipunensis* Molineri, 2011 (Fig. 2i), *Caenis fittkaui* Malzacher, 1986 (Fig. 2j), and *Caenis candelata* Malzacher, 1986 (Fig. 2k). In North America, type 2a forcipes are found in the *Caenis diminuta* group (Provonsha 1990), e.g., *Caenis* sp. with short, often slightly blunt tips (Fig. 2d), and in *Caenis amica* Hagen, 1861 (Fig. 2e) and *Caenis latipennis* Banks, 1907 (Fig. 2f), both with more or less evenly converging tips. Similar forcipes tips are also predominant in the Palearctic Realm in species of the *Caenis horaria* lineage: *Caenis rivulorum* Eaton, 1884 (Fig. 2l), *C. horaria* (Linnaeus, 1758) (Fig. 2p), and shortened forms like in *Caenis robusta* Eaton, 1884 (Fig. 2m), *Caenis strugaensis* Ikonomov, 1961 (Fig. 2n), and *Caenis wui* Malzacher, 2016

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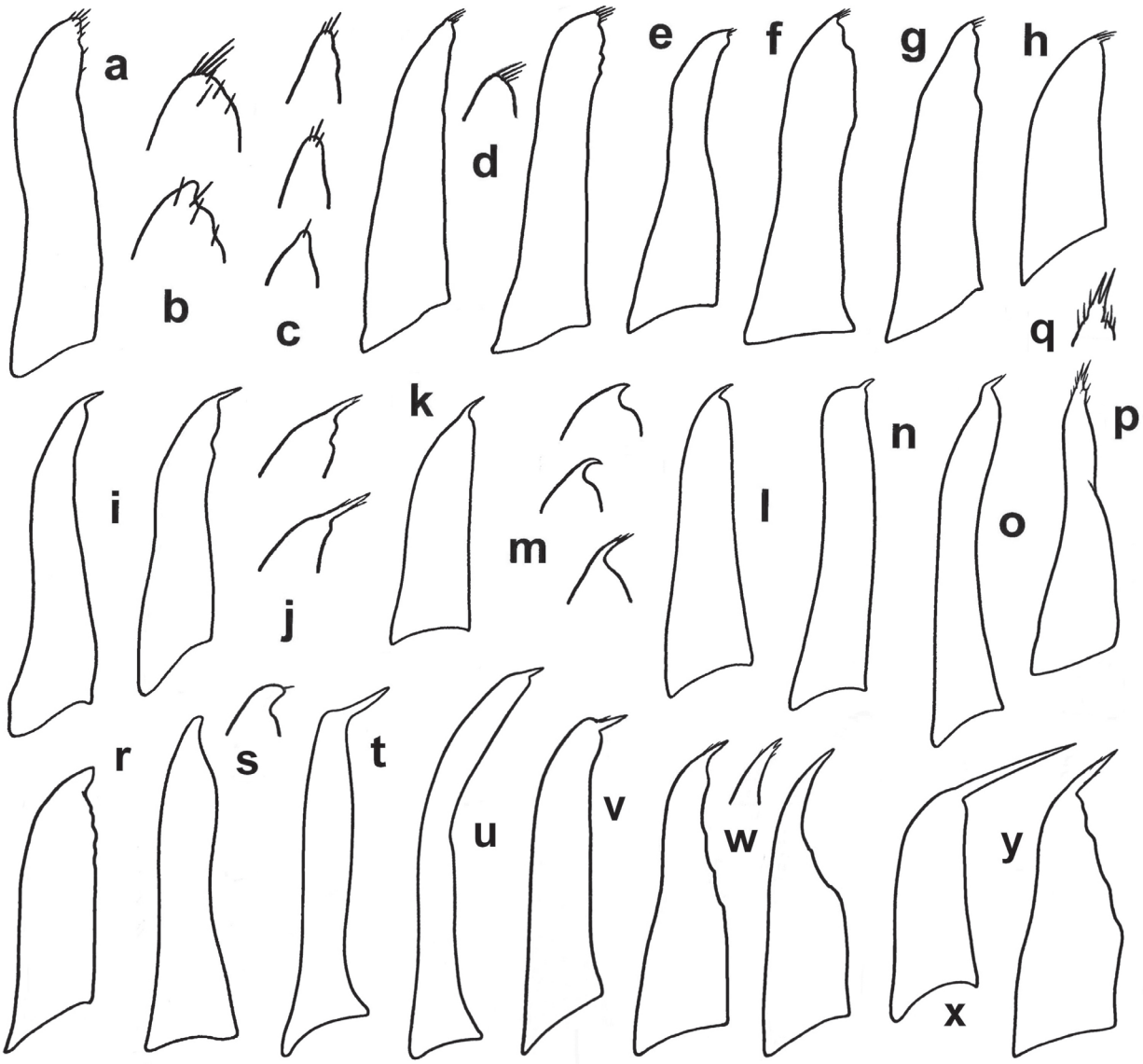

Fig. 3. Forceps type 3a, with a number of small bristles extending beyond apex (a–h); forceps type 3b, with an apical spine of stuck bristles (i–o); forcipes of intermediate evolutionary stages (p–v); forceps type 2b, with strongly sclerotized tips (w–y). **a**. *Caenis anceps*. **b**. *Caenis anceps*, different shapes of tip at higher magnification. **c**. *Caenis hilaris*, different shapes of tip. **d**. *Caenis beskidensis*, different shapes and tip at higher magnification. **e**. *Caenis pseudorivulorum*. **f**. *Caenis lactea*. **g**. *Caenis picea*. **h**. *Caenis karenae*. **i**. *Caenis pusilla*, different shapes. **j**. *Caenis pusilla*, different shapes of tip at higher magnification. **k**. *Caenis gephyria*. **l**. *Caenis nigropunctatula*. **m**. *Caenis nigropunctatula*, different shapes of tip at higher magnification. **n**. *Caenis abdita*. **o**. *Caenis bidigitata*. **p**. *Caenis valentinae*. **q**. *Caenis valentinae*, tip at higher magnification. **r**. *Caenis ghibana*. **s**. *Caenis afrocaenoides*, with different shapes of tip. **t**. *Caenis angolensis.* **u**. *Caenis filappendices*. **v**. *Caenis nigricola*. **w**. *Caenis basuto*, different shapes. **x**. *Caenis guttata*. **y**. *Caenis maratha.*

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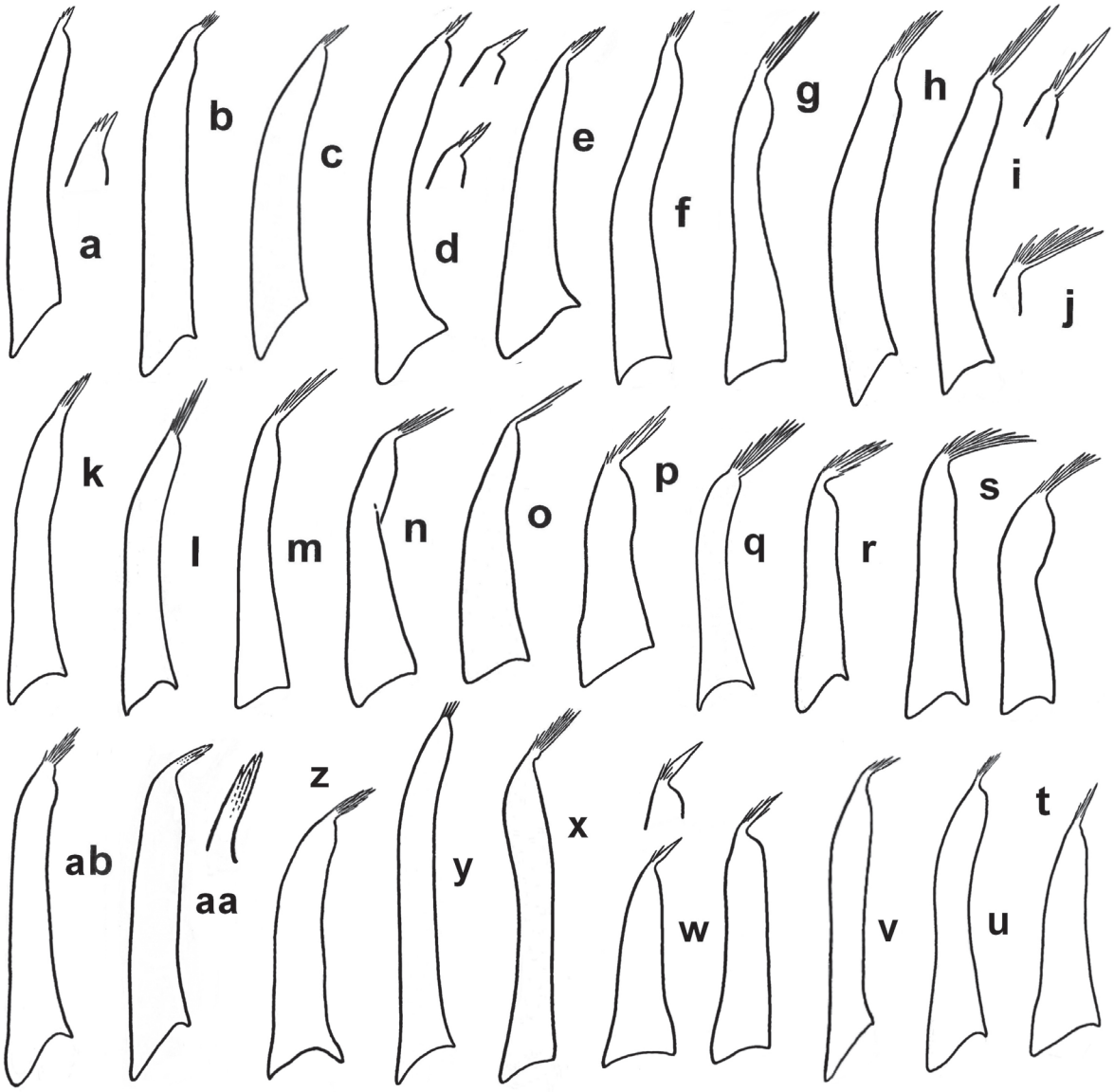

Fig. 4. Forceps type 4, with terminal tuft of spines. **a**. *Caenis corbeti*, with tip in higher magnification. **b**. *Caenis nausicaae*. **c**. *Caenis albicans*. **d**. *Caenis gilliesi*, with tips at higher magnification. **e**. *Caenis octulusa*. **f**. *Caenis pallida*. **g**. *Caenis gretathunbergae*. **h**. *Caenis namorona*. **i**. *Caenis cibaria cibaria*, with two different shapes of tip. **j**. *Caenis cibaria kunda*, forceps tip. **k**. *Caenis occulta*. **l**. *Caenis grafi*. **m**. *Caenis jinjana*. **n**. *Caenis jinjanoides*. **o**. *Caenis pugiata*. **p**. *Caenis douglasi*. **q**. *Caenis armata*. **r**. *Caenis noctivaga*. **s**. *Caenis kivuensis*. **t**. *Caenis liebenauae*. **u**. *Caenis alicae*. **v**. *Caenis antelucana*. **w**. *Caenis ulmeriana*. **x**. *Caenis unidigitata*. **y**. *Caenis longiforcipata*. **z**. *Caenis macrura*. **aa**. *Caenis hoggariensis*. **ab**. *Caenis luctuosa*.

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Fig. 5. Distribution of *Caenis* species with forceps type 1.

(Fig. 2o). Two further species that seem to possess this forceps type can be found in the Oriental Realm: *Caenis ludovici* Malzacher, 2021 (Fig. 2q) and *Caenis fregatula* Malzacher, 2013 (Fig. 2r). *Caenis horaria* was recently recorded from Ethiopia (Malzacher 2021).

Type 2b (Figs. 3w–y, 6). Besides the presence of this type in the Holarctic and Oriental realms and South America, few species in Africa also show more or less elongated, pointed, and sclerotized forceps tips (*Caenis edwardsi* group, e.g., *Caenis basuto* Demoulin, 1970, Fig. 3w), but they are clearly bent medially and often provided with few short bristles. A very similar shape can be found in Western India (*Caenis maratha* Malzacher, 2015, Fig. 3y) and, with a very long, lanceolate tip, in Thailand (*Caenis guttata* Malzacher, 2015; Fig. 3x).

Type 3 forcipes
(Figs. 3a–o, 7)

Forceps apically with a number of small trichomes extending beyond apex. These bristles are more or less bent medially (contrary to Type 2a).

Type 3a. The bristles are more or less concentrated in a dense group and about as long as, or only slightly longer than, the trichoma covering the general surface of the forceps. This type is represented in North America by a couple of species of the *Caenis hilaris* group (Provonsha 1990), e.g., *Caenis anceps* Traver, 1935 (Figs. 3a, b) and *Caenis hilaris* Say, 1939 (Fig. 3c). Here, variation in the number, density, and degree of extension of the bristles beyond the apex occurs even within the same species (Fig. 3a–c). Forcipes with dense groups of bristles forming a small apical tuft occur mainly in the Palearctic Realm, in *Caenis beskidensis* Sowa, 1973 (Fig. 3d), *C. pseudorivulorum* Keffermüller, 1960 (Fig. 3e), and *Caenis lactea* (Burmeister, 1839) (Fig. 3f); in the Oriental Realm, this group is represented by *Caenis picea* Kimmins, 1947 (Fig. 3g) and *Caenis karenae* Malzacher, 2021 (Fig. 3h).

Type 3b. Here, the apical bristles are condensed to such an extent that they form a single, short spine. This subtype is represented in the West Palearctic Realm by *Caenis pusilla* Navas, 1913 (Figs 3i, j) and in the East Palearctic Realm by a couple of species, e.g., *Caenis jungi* Braasch, 1980 and *Caenis kopetdagi* Kluge, 1985 (both very similar to the short form of *Caenis pusilla*, Fig. 3i, left). Oriental species with this forceps type are *Caenis gephyria* Malzacher, 2015 (Fig. 3k), *Caenis nigropunctatula* Malzacher, 2015 (Fig. 3l, m), *Caenis abdita* Malzacher, 2015 (Fig. 3n), and *Caenis bidigitata* Malzacher, 2015 (Fig. 3o).

Type 3 seems not to be present in the Afrotropical Realm or South America.

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Type 4 forcipes
(Figs. 4, 8)

Forcipes with a terminal tuft of long spines, clearly longer and in most cases clearly thicker than the remaining trichomes covering the surface. The length of the tufts and width of the spines differ widely in different species. The angle between the shaft and the tuft also varies, sometimes even in the same species.

Out of 67 species with type 4 forcipes, 47 are recorded from the Afrotropical Realm, among them *Caenis corbeti* Malzacher, 1990 (Fig. 4a), *Caenis nausicaae* Malzacher, 2010 (Fig. 4b), *Caenis albicans* Malzacher, 2020 (Fig. 4c), *Caenis gilliesi* Malzacher, 1990 (Fig. 4d), *Caenis octulusa* Malzacher, 2012 (Fig. 4e), *Caenis pallida* Malzacher, 1990 (Fig. 4f), *Caenis gretathunbergae* Malzacher, 2021 (Fig. 4g), *Caenis namorona* Malzacher, 1995 (Fig. 4h), *Caenis cibaria cibaria* Eaton, 1879 (Fig. 4i), *Caenis cibaria kunda* Malzacher, 1993 (Fig. 4j), *Caenis occulta* Malzacher, 1990 (Fig. 4k), *Caenis grafi* Malzacher, 2021 (Fig. 4l), *Caenis jinjana* Kimmins, 1956 (Fig. 4m), *Caenis jinjanoides* Malzacher, 2011 (Fig. 4n), *Caenis pugiata* Malzacher, 2014 (Fig. 4o), *Caenis douglasi* Malzacher, 1993 (Fig. 4p), *Caenis armata* Malzacher, 2021 (Fig. 4q), *Caenis noctivaga* Malzacher, 1990 (Fig. 4r), *Caenis kivuensis* Demoulin, 1956 (Fig. 4s), *Caenis liebenauae* Malzacher, 1990 (Fig. 4t), *Caenis alicae* Malzacher, 1990 (Fig. 4u), and *Caenis antelucana* Malzacher, 1990 (Fig. 4v). All these species underline the dazzling array of shapes in forceps type 4. In the Palearctic Realm, eight species are known within the *Caenis macrura* and *Caenis luctuosa* groups; figured here are *Caenis macrura* Stephens, 1835 (Fig. 4z), *Caenis hoggariensis* Grandi, 1951 (Fig. 4aa), and *Caenis luctuosa* (Burmeister, 1839) (Fig. 4ab). In the Oriental Realm, 7 species belong to this group, among them *Caenis ulmeriana* Malzacher, 2015 (Fig. 4w), *Caenis unidigitata* Malzacher, 2013 (Fig. 4x), and *Caenis longiforcipata* Malzacher, 2020 (Fig. 4y). Four species are recorded from the Australasian Realm, whereas type 4 is absent from both the Nearctic and Neotropical realms.

Unassigned species

A few species cannot be definitely assigned to one of the four forceps types (Fig. 3p–v). *Caenis valentinae* Grandi, 1951 (Fig. 3p, q), from Italy, is morphologically close to type 3 species, but its forceps is armed with two strong spines and a few short bristles (Fig. 3q).

Five species from Africa, namely *Caenis ghibana* Malzacher, 1990 (Fig. 3r), *Caenis afrocaenoides* Malzacher, 2021 (Fig. 3s), *Caenis angolensis* Malzacher, 2021 (Fig. 3t), *Caenis filappendices* Malzacher, 2021

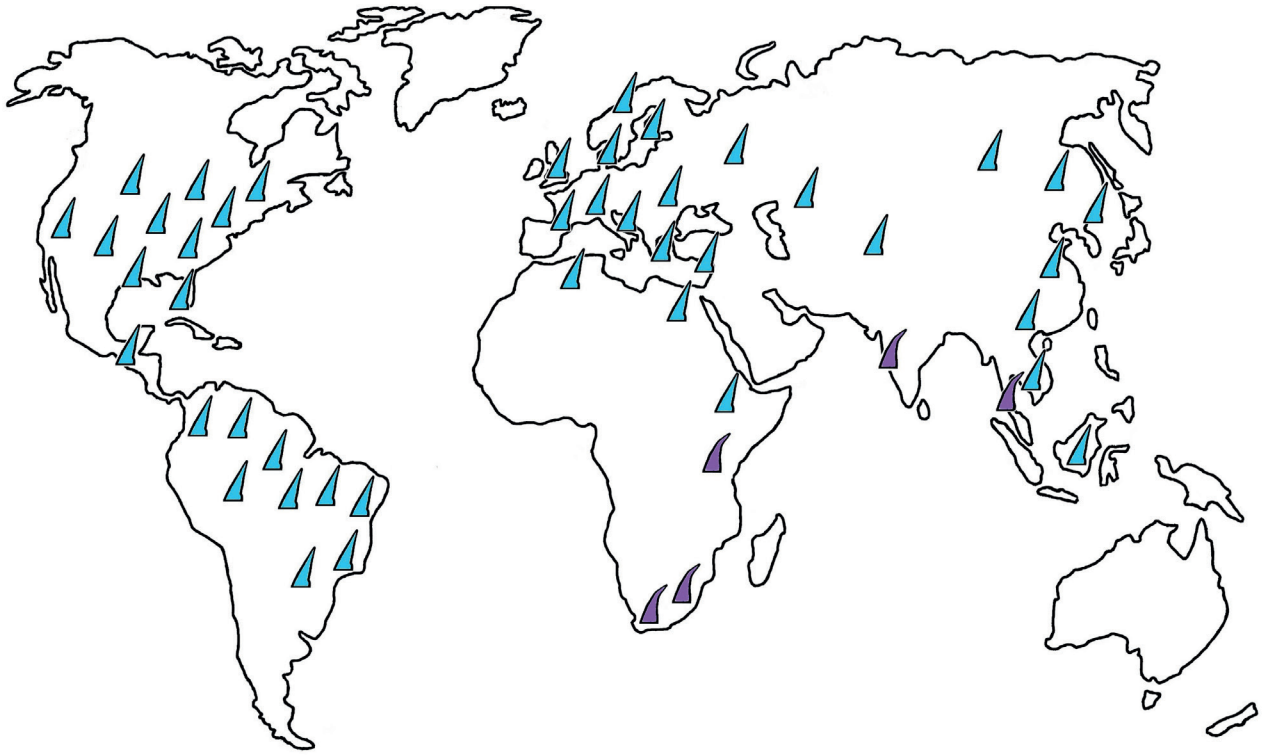

Fig. 6. Distribution of *Caenis* species with forceps type 2; blue: type 2a, violet: type 2b.

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Fig. 7. Distribution of *Caenis* species with forceps type 3; orange: type 3a with short bristles apically, brown: type 3b with an apical spine of stuck bristles.

(Fig. 3u), and *Caenis nigricola* Malzacher, 2011 (Fig. 3v), seem to represent intermediate stages between types 1a and 4.

Evolution and dispersal of the genus *Caenis* deduced from the extant distributions of different forceps types

Forceps type 1 as a starting point in Caenis *forceps evolution*

Regarding the forcipes in Caenoidea, there is an evolutionary tendency toward a reduction in length and number of segments. The most strongly reduced forms, combined with weakly sclerotized and little structured genitalia, could have been the initial stages of evolution within Caenidae, as seen within *Caenis* with type 1 forcipes in Africa (Fig. 1a–d) and South America (Fig. 1j–k). The probable distribution of the first *Caenis* species in Gondwana is shown in Fig. 9. About 150 million years ago, Gondwana was still undivided. The flow direction of the ancient Amazon River to the west (Grabert 1991) supported a drift of aquatic insects in this direction, which also resulted in an extended distribution of primitive *Caenis* forms in the area later to become South America. A further development in South America led to a variety of species with different shapes of forcipes (e.g., *C. ludicra*, *C. pflugfelderi*, *C. gonseri*, *C. panamensis*, *C. cubensis*; Fig. 1l–q). In Africa, however, primitive forms remained only in the western and southwestern parts of the continent.

After the separation of Gondwana, a spread back to Africa of more highly evolved South American forms with rounded forcipes became impossible. As a consequence, forceps types 2 and 3, which evolved in the New World out of forms with apically rounded forcipes, cannot be found in the Afrotropical Realm (except *C. horaria*—see below).

The evolution of forceps type 2

The forcipes in the New World became longer and their tips became more and more pointy (Fig. 1m–q), at first still more or less rounded apically (Fig. 2a, b). Further development led to long and sclerotized tips (Fig. 2d–k). Figure 11 shows such a possible development starting from apically rounded forcipes (in Figs. 11–13, the forcipes of extant species are used to illustrate this development). From a shape like that in *C. gonseri* (rounded tip with a small bump), the evolutionary development could have proceeded to intermediate stages with forcipes converging evenly to a more

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or less rounded tip (*C. eglinensis*, *C. cuniana*), and forcipes like in *C. cuniana* could have developed into ones with acute, sclerotized tips (*C. pseudamica*). From here, one branch led via shapes like those in *C. teipunensis* and *Caenis amacayacu* Lima, 2016 to more or less abruptly narrowed tips (*C. fittkaui*, *C. candelata*), whereas another branch led to species with medially stepped tips (*Caenis tarapoto* Molineri, 2009; *C. burmeisteri*). Because of its elongated forceps base, *C. burmeisteri* could represent an initial stage for the highly differentiated forcipes in *Brasilocaenis* Puthz, 1975 (see Malzacher 1990 and below). On the other hand, *Caenis elidioi* Lima, 2016, with forcipes closely fitting to the styliger sclerite, could also represent an antecedent stage to *Brasilocaenis* (Lima et al. 2016). Lima et al. (2019) recently included *C. elidioi* in *Brasilocaenis* and confirmed the monophyly of this genus.

Forcipes with long and rounded tips shaped like in *C. eglinensis* may have given rise to another lineage (Fig. 12) with short variable tips, as in an undetermined North American species of *Caenis* (Fig. 2d) similar to *Caenis diminuta* Walker, 1853. This line finally leads to the other North American species of the *Caenis diminuta* group (Provonsha 1990), e.g., *C. amica* and *C. latipennis*, with long, strongly sclerotized, acute tips.

When Laurasia was still undivided 80 million years ago, in the Upper Cretaceous (Fig. 10), species with type 2 forcipes may have spread eastwards to the area that would later become the Palearctic Realm (*C. horaria*, *C. rivulorum*, *C. robusta*), eventually reaching the future Oriental Realm (*C. fregatula*, *C. ludovici*). Only in the recent past, the West Palearctic *C. horaria* may have invaded Ethiopia via the Nile valley, from populations north of the Sahara desert.

All type 2 species so far mentioned represent type 2a. Type 2b, found in the *Caenis edwardsi* group (*Caenis edwardsi* Kimmins, 1939, *C. basuto*, and *Caenis subota* Malzacher, 2012), developed independently in Africa and could have branched off from species with a forceps shape like in *C. ghibana* (see Fig. 13). The type 2b group probably reached the Oriental Realm by drifting on the Indian tectonic plate, and is today represented by *C. maratha* in India.

The evolution of forceps type 3

Type 3 is not present in the Neotropical Realm. It obviously originated in the Nearctic, where type 3a (Fig. 7, orange) is found in a couple of species (*Caenis hilaris*

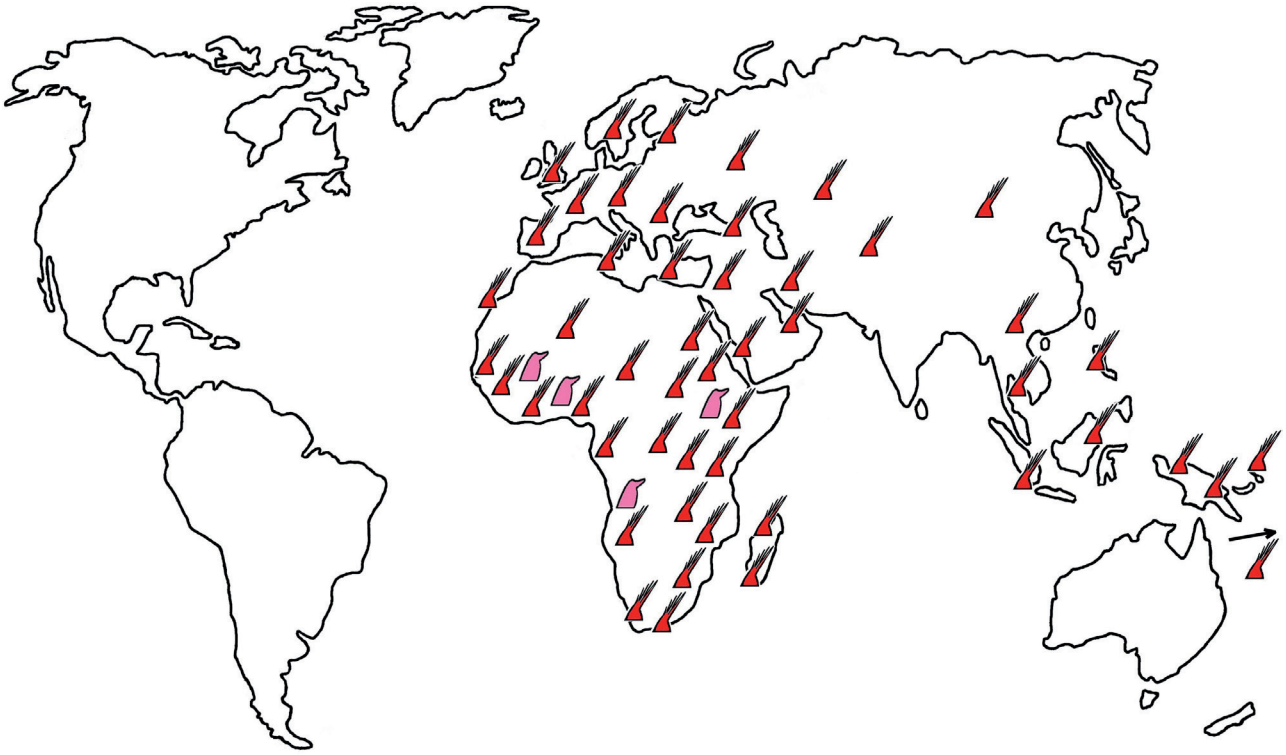

Fig. 8. Distribution of *Caenis* species with forceps type 4; red: fully developed type 4, pink: intermediate evolutionary stages. Arrow points to record on Fiji Islands, about 2,500 km east of Australia.

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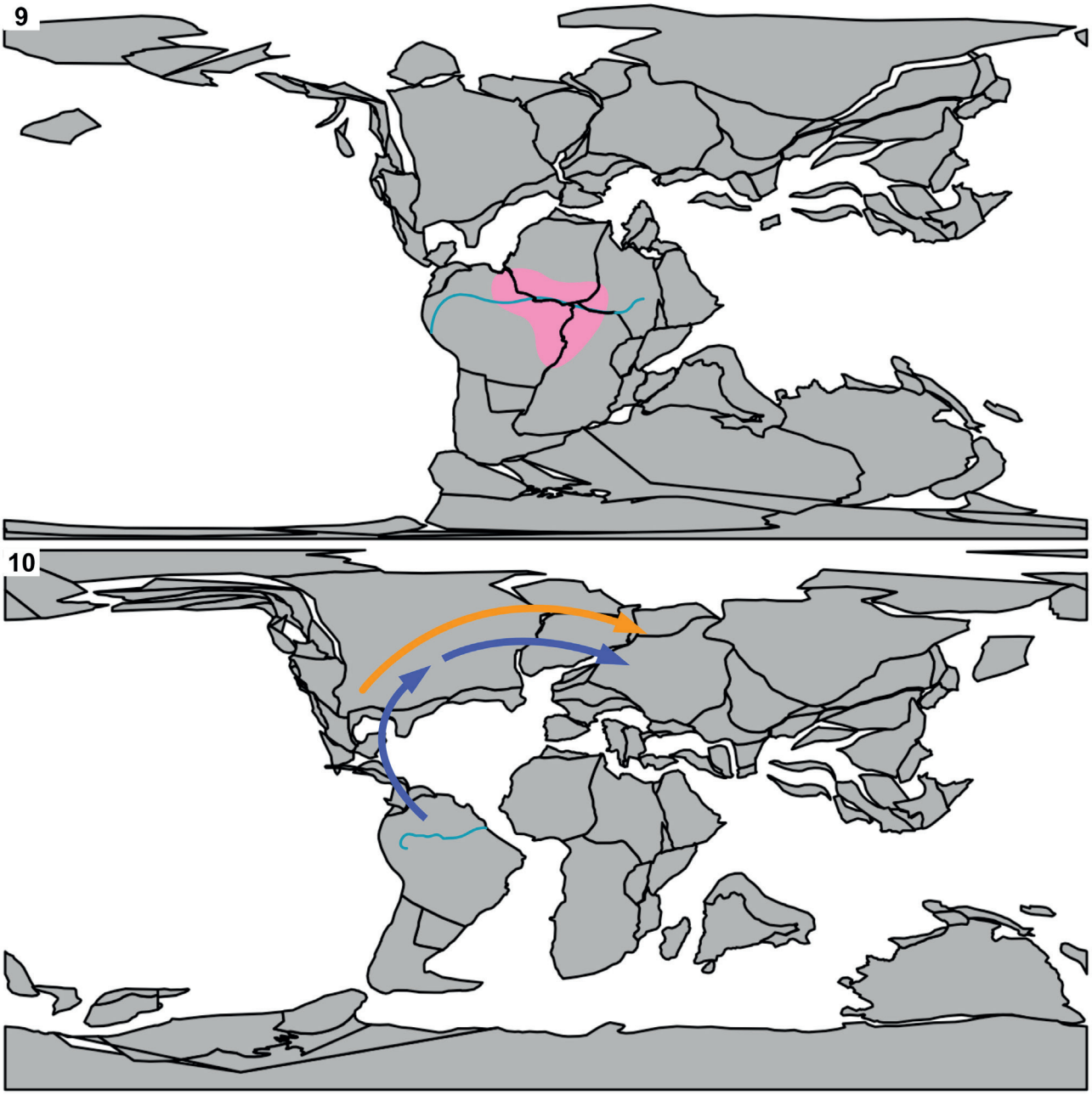

Figs. 9–10. Arrangement of continental plates (generated in R). – **9**. Upper Jurassic, about 150 million years ago; ancient Amazonas indicated in blue; pink shows assumed area of Gondwanan origin of the genus *Caenis*. **10**. Upper Cretaceous, about 80 million years ago (note changed course of Amazonas compared to Fig. 9); blue arrows show assumed dispersal of species with forceps type 2; orange arrow indicates assumed dispersal of species with forceps type 3a.

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group; PROVONSHA 1990). A shape like that in *C. cubensis* could represent the initial stage for the development of forcipes like those in *C. hilaris*, *Caenis tardata* McDunnough, 1931 and *C. anceps* (Fig. 11, top). A high variability, even within single populations, can be found in *C. anceps* (Fig. 3a, b) and *C. hilaris* (Fig. 3c).

Type 3 also spread eastward to the Palearctic Realm, where it is found in species like *C. beskidensis*, *C. pseudorivulorum*, and *C. lactea*, finally reaching the Oriental Realm with an Indian species, *C. picea*, which is closely related to *C. lactea*, and *C. karenae* from Thailand.

Type 3b forcipes with small spines of stuck bristles (Fig. 7, brown) seem to have developed in the Palearctic Realm with a wide distribution in the East Palearctic (*C. pusilla* group, *C. pusilla*) and with numerous species in the Oriental Realm, e.g., *C. gephyria*, *C. nigropunctatula*, and *C. abdita*.

The evolution of forceps type 4

As there are no species with tufted forcipes recorded from the New World, it is obvious that type 4 originated in Africa after its separation from South America. As aforementioned, there are 47 species with type 4 forcipes present in Africa and Madagascar, 9 in the Palearctic, 7 in the Oriental Realm, and 4 in the Australasian Realm (New Guinea, Bismarck Archipelago, Fiji).

Figure 13 shows a possible evolution of this group. A forceps shape like that of *C. ghibana* may have given rise to a first branch leading via *C. nigricola* to *C. gilliesi*, the base of the TA lineage (with tufted forcipes and a dilated base of the antennal flagellum), with a further African species, *C. cibaria*. With five species, among them *C. unidigitata*, the lineage is more speciose in the Oriental Realm.

A forceps shape like that in *Caenis kungu* Eaton, 1879 could be the origin of two further lineages. One led to species with an apical **t**uft of spines on the forcipes and triangular **p**enis lobes, but without a dilated base of the antennal flagellum (TP lineage). This lineage, with about eight Afrotropical species, such as *Caenis rugosa* Malzacher, 1995 and *C. kivuensis*, also invaded the Palearctic Realm with five species (*Caenis macrura* group), the Oriental Realm with one (*C. longiforcipata*), and the Australasian

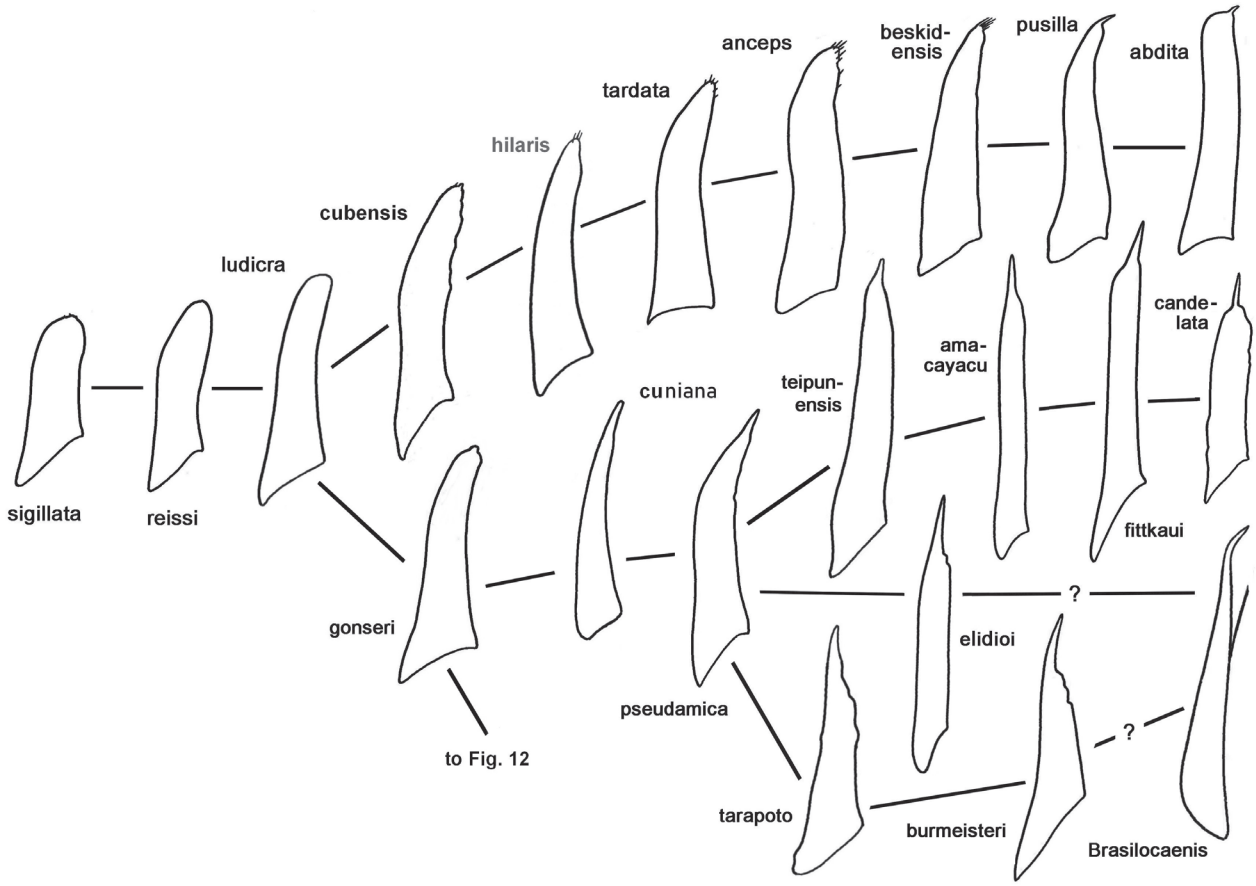

Fig. 11. Evolutionary development of forceps type 3 (upper branch) in the Nearctic, Palearctic, and Oriental realms and forceps type 2a (lower branches) in the Neotropical Realm.

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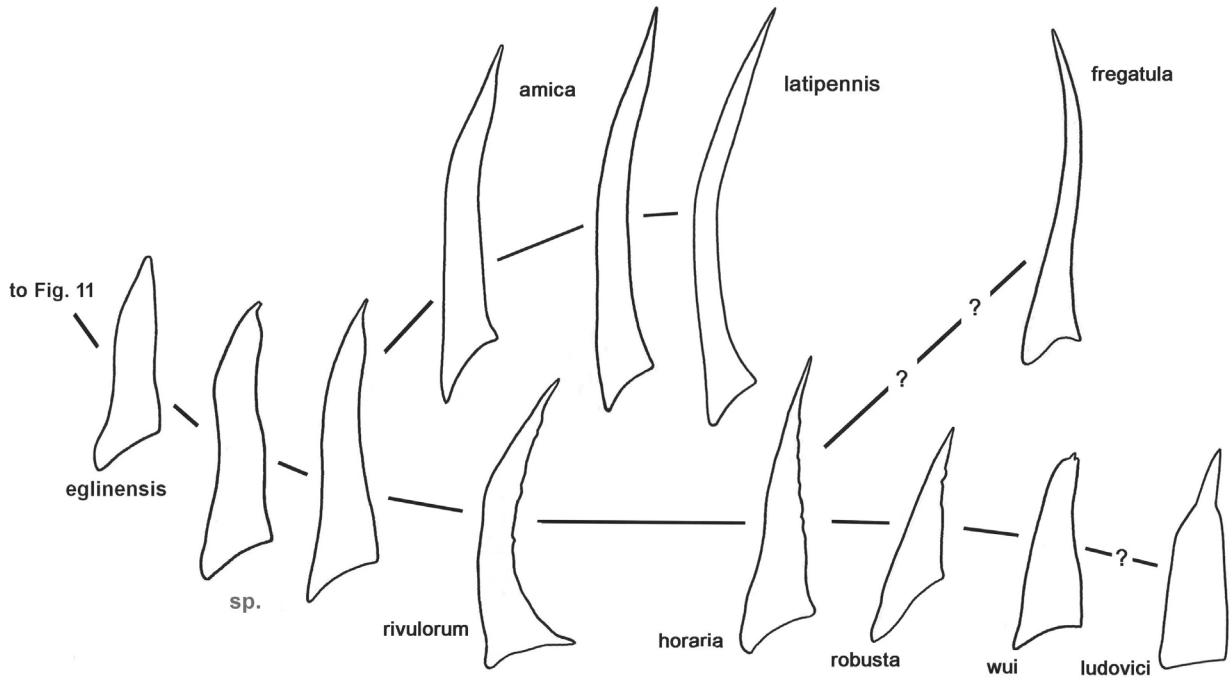

Fig. 12. Evolutionary development of forceps type 2a in the Nearctic, Palearctic, and Oriental realms.

Realm with four: *Caenis novaeguineae* Bruggen, 1957, *Caenis insularis* Demoulin, 1969, *C.* sp. from Fiji, and *Caenis marawakensis* Malzacher, 2018 (Australasian species not shown in Fig. 13; see below). The second lineage contains the large group of TPA species (see Malzacher 2011). In this group, the **t**ufted forcipes occur together with triangular **p**enis lobes and **a**ntennae with a dilated flagellum base. Forty such species are known: 36 Afrotropical (e.g., *C. jinjana*, *C. brevipes*, *C. armata*, and *C. gretathunbergae*), three Palearctic (*C. luctuosa*, *C. hoggariensis*, and *Caenis antoniae* Malzacher, 1992), and a single Oriental species (*Caenis annulata* Navas, 1923). Several of these TPA species additionally show long, more or less broadly rounded and bent apophyses on the styliger sclerite, combined with moderate or long lateral filaments on the abdominal segments (TPA+). Besides one species from Palestine (*C. antoniae*), they are all recorded from Africa (*Caenis scotti* group, e.g., *C. occulta*). There are, however, a number of intermediate stages for these two characters.

In the basal sector of the tree in Fig. 13, between *C. vermifera* and *C. gilliesi*, there are few branches whose derivation is somewhat ambiguous. Among them is the species group with apical tufts on the forcipes only (T lineage, without triangular penis lobes and dilated base of antennal flagellum). It contains the African species *C. cincta* and the Oriental species *C. ulmeriana*. Concerning the morphology of the genitalia, *C. filappendices* also closely resembles *C. gilliesi*, but the dilation of the antennal flagellum is only slightly developed in the latter. *Caenis angolensis* is also related to these forms, but its precise derivation is uncertain.

An early branch-off from a stage between *C. vermifera* and *C. ghibana* shows a lineage that may have led to the genus *Afrocaenis* Gillies, 1982 via *C. afrocaenoides*.

Biogeographic and phylogenetic considerations

The present distribution of *Caenis* species with primitive, short, rounded forceps in South America and West Africa clearly points to a Gondwanan origin of the genus *Caenis* in the Upper Jurassic or even earlier, before the split between Africa and South America (see Fig. 9). Somewhat surprising is the presence of three species with apically rounded forcipes in the Oriental Realm (Fig. 5) (Malzacher 2018; Malzacher & Sangpradub 2021). An explanation could be that during pluvial periods, when the Sahara and other deserts along the northern turning circle were green and abundant in water, an eastward spread of these species from West Africa to the Oriental Realm could have been possible. In arid periods, populations of these species would have vanished again in the desert areas.

Within the TPA lineage, the larvae of 13 species are known so far. Eleven of them show a combination of

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three characters: labial palps with very short third segment (ratio of length of second to third segment 2.0–3.0), hind margin of sternum IX with a deep indentation, and cuticle with shield- or funnel-shaped microtrichia. In the remaining two West Palearctic species, *C. luctuosa* and *C. hoggariensis*, shield- or funnel-shaped microtrichia are lacking. These two species could represent their own group within the TPA lineage, also because they are geographically separated from the remaining TPA species. There are additional larvae from Africa that also show these three characters, but they cannot be assigned to any of the described species. In any case, these characters can be considered synapomorphic for all TPA species except *C. luctuosa* and *C. hoggariensis*.

Besides *C. marawakensis* from New Guinea (Malzacher & Staniczek 2018), there are three further species with type 4 forcipes recorded from the Australasian Realm, more precisely from the Southwest Pacific Basin: *Caenis* sp. from Fiji (Flowers 1990), *C. insularis* from the Bismarck Archipelago (Demoulin 1969, as *Caenomedea insularis*), and *C. novaeguineae* from New Guinea (van Bruggen 1954, as *Tasmanocoenis novaeguineae*) (for a discussion of these synonymies, see Malzacher & Staniczek 2018). Although their descriptions are more or less fragmentary or insufficient, forcipes with an apical tuft of spines were drawn by these authors in the respective figures of each of these species. It is thus most noteworthy that type 4 in its eastward expansion extended beyond the biogeographic border of the Wallace Line (see also Malzacher & Staniczek 2018). A comparable transgression of species with forceps types 2 and 3 cannot be observed to date.

A prime example of spatial separation of populations resulting in new taxa is provided by continental drift (Wegener 1915). In the case of *Caenis*, the split of Gondwana presumably led to the development of different lineages, represented by forcipes types 2 and 3 on the one hand and type 4 on the other, which might justify the splitting of the speciose genus *Caenis* into different genera. In this case, species with type 4 forceps, with an apical tuft of spines, would keep the name *Caenis*, because the type species *C. macrura* belongs to this group. A definite splitting of genera, however, may not be feasible at this time, due to the following four considerations:

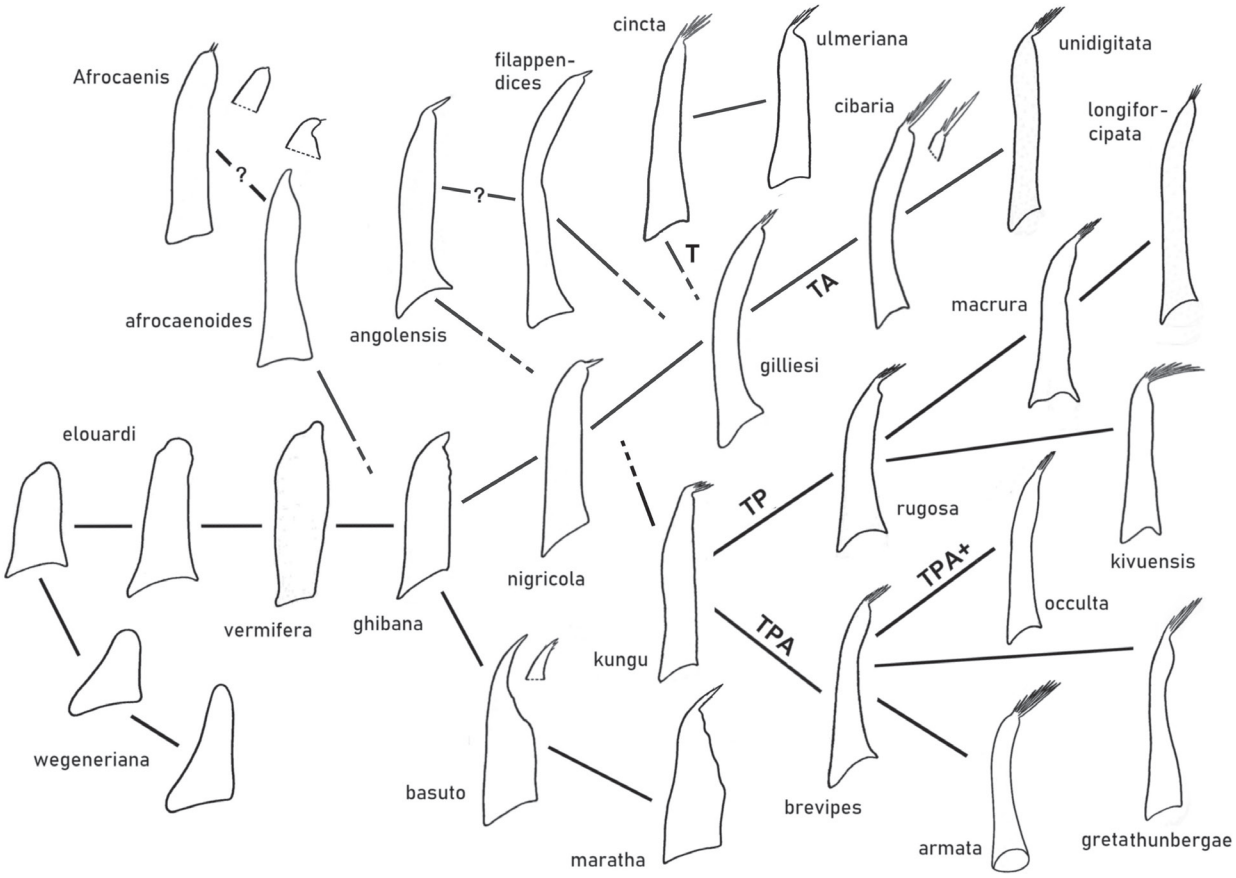

Fig. 13. Evolutionary development of forceps type 4 in the Afrotropical, Palearctic, and Oriental realms.

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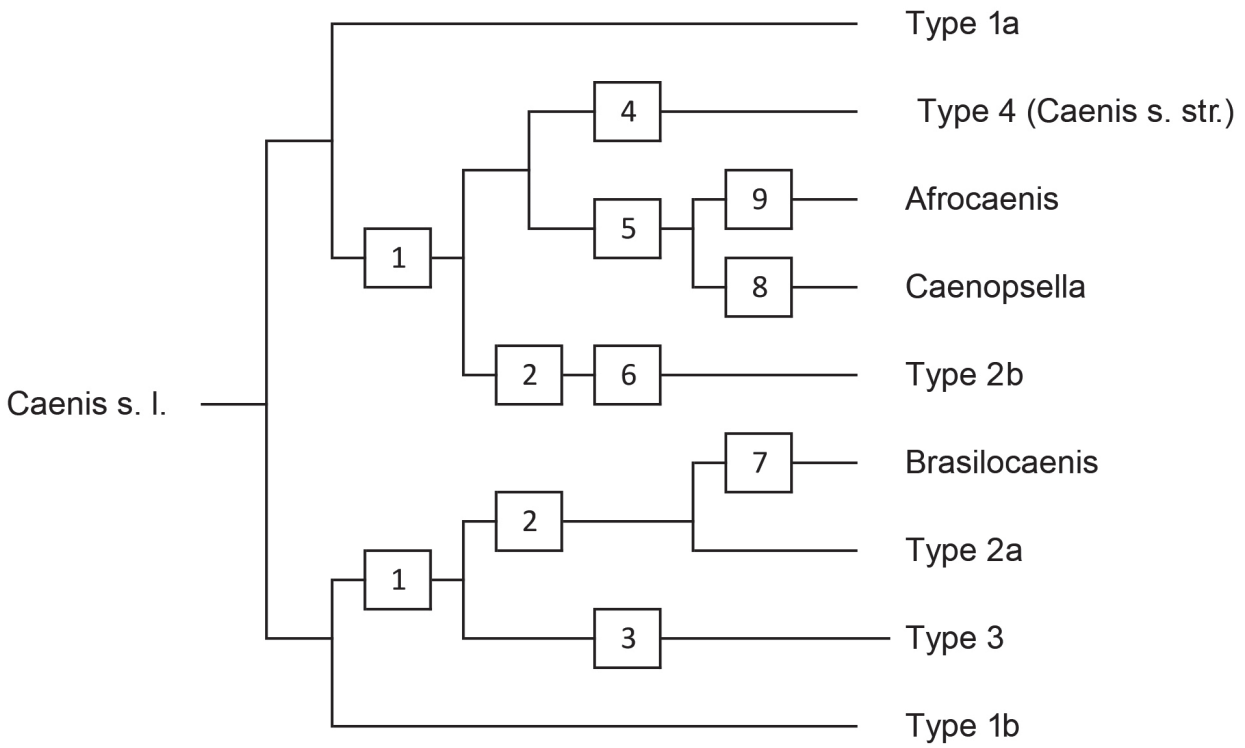

Fig. 14. Hypothetical grouping of the species-rich genus *Caenis* and related genera

(1) There are transitional stages that are not clearly assignable to one of the different types.

(2) In the adults, except for the genitalia, the shape of the antennal base, and the shape of the tarsomeres there are almost no morphological characters available for phylogenetic analyses.

(3) Larval characters are of limited use, as for nearly half of all the described species only the imagines are known (more than three quarters in the Afrotropical Realm).

(4) The few characters available are non-unique, e.g., the supposed apomorphies of the TPA species (very long forcipes with a tuft of long and strong spines and deeply indented hind margin of larval sternite IX) can also be found in *Kalimaenis* Malzacher, 2013, a genus of Clypeocaenini from Borneo. The remaining genera of this tribe, however, are plesiomorphic in having short and apically rounded forcipes or forcipes with inconspicuous apical structures. A deeply indented hind margin of larval sternite IX appears randomly in one species with type 1 forceps (*C. tenella* from South America) and another one with type 3 forceps (*C. bajaensis* from Central and North America). Likewise, Provonsha (1990) was not able to assign *C. bajaensis* to one of the two North American lineages.

These limitations in both lack of characters and obvious homoplasies have been a hindrance to splitting the genus *Caenis*. However, the underlying geographical patterns in the different structures of the forcipes may be useful as a first step toward an improved taxonomy of the genus (for a hypothetical grouping, see Fig. 14; for characters, see Table 1). It is hoped that the application of molecular methods and the morphological descriptions of larval stages will lead to a better understanding of the evolution and phylogeny of Caenidae.

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