

*A redefinition of the morphology,  
range and relationship  
of Tropodiaptomus schubotzi  
(Van Douwe)  
(syn. Tropodiaptomus incognitus  
Dussart & Gras)  
and of Tropodiaptomus symoensi Einsle,  
with notes on Tropodiaptomus loveni  
(De Guerne & Richard)*

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SUMMARY

*The true identity of Tropodiaptomus schubotzi is established. Its range covers the Chari basin, including Lake Chad, where it has been extensively studied under the name Tropodiaptomus incognitus. In the oasis of Kufra in Libya, a relict population of Holocene age occurs which shows some amount of speciation, and is described as T. s. kufraensis n. ssp. Its nearest relative is T. symoensi which occupies the south-east of the Zaire basin. It is separated from T. loveni (De Guerne & Richard), known only from the lower Zaire basin, by the inundated forest zone of the middle Zaire. The relationship between these two Zairian species is rather distant although both belong to the same species-group, that of T. orientalis. T. schubotzi vicariates with T. kraepelini in the East. T. symoensi shows partial overlap with T. kraepelini in the south-east of the Zaire basin. Whether T. symoensi also overlaps or vicariates with other members of the T. loveni-T. kraepelini group, such as T. kissi and T. kieferi, is still uncertain.*

KEY WORDS : Crustacea — Copepoda — Calanoida — *Tropodiaptomus* — Africa — Biogeography.

RÉSUMÉ

UNE REDÉFINITION DE LA MORPHOLOGIE, DE L'AIRES DE RÉPARTITION ET DES RELATIONS ENTRE *Tropodiaptomus schubotzi* (VAN DOUWE) (SYN. *Tropodiaptomus incognitus* DUSSART & GRAS) ET *Tropodiaptomus symoensi* EINSLE, ET NOTES SUR *Tropodiaptomus loveni* (DE GUERNE & RICHARD)

*L'identité du Tropodiaptomus schubotzi est établie. Son aire de répartition comprend le bassin du Chari, y compris le Lac Tchad, où cette espèce a été étudiée en détail sous le nom de Tropodiaptomus incognitus. Une population relique se maintient dans l'oasis de Koufra en Libye. Elle date de l'holocène ancien et a atteint le niveau d'une sous-espèce. Dans le bassin du Zaïre l'espèce T. symoensi occupe au moins le sud-est de la région. Elle semble être le taxon le plus proche de T. schubotzi. Elle est séparée de T. loveni De Guerne & Richard, connu seulement du bas Zaïre, par la forêt inondée de la partie centrale du Zaïre. La relation entre ces deux espèces du Zaïre est plutôt éloignée, bien qu'elles appartiennent au même groupe d'espèces, celui de T. orientalis.*

*Le groupe du T. schubotzi est lui-même en vicariance avec le groupe du T. kraepelini vers l'est. Dans le sud-est du bassin du Zaïre, l'aire de répartition du T. symoensi et du T. kraepelini se recoupe partiellement. S'il existe aussi des recouvrements ou un vicariance avec d'autres membres du complexe T. schubotzi-symoensi, tel que le T. kissi et le T. kieferi, n'est pas encore prouvé.*

MOTS-CLÉS : Crustacé — Copépode — Calanoïde — *Tropodiaptomus* — Afrique — Biogéographie.

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## INTRODUCTION

Our knowledge of the systematics of the large African Calanoid genus *Tropodiaptomus* is constantly improving. A checklist is now available (DUSSART & DEFAYE 1983), the type-species of the genus, a non-African species, has been redescribed (DUSSART *et al.* 1984), and West-African (DUMONT *et al.* 1981) and Nile basin faunas (VERHEYE & DUMONT 1983) have been revised. Yet, the identity of a few species remains uncertain. The object of the present paper is to settle the status and redefine the range of some among these, originally described as *Diaptomus schubotzi* by VAN DOUWE (1914), *T. incognitus* (DUSSART & GRAS 1966), *Tropodiaptomus symoensi* (EINSELE 1971), and *Tropodiaptomus loveni* (DE GUERNE & RICHARD).

VAN DOUWE'S DESCRIPTION OF *Diaptomus schubotzi*

In a fairly detailed and well illustrated description VAN DOUWE attracts attention to the following features of this medium-sized (1.1-1.4 mm) species:

1. asymmetry of the female cephalosome and urosome (fig. 1);
2. asymmetry of the end-claws of the exopodites of  $P_5$  in the female: only one end-claw bears a blunt spine on its inner surface (fig. 2);
3. the endopodite of the female  $P_5$  is shorter than the basal segment of the exopodite. It has two long apical setae, of which the inner one is shortest. Their basis is lined with a row of spinules (fig. 2);
4. the first segment of the right exopodite of the male  $P_5$  has an apical external thorn-shaped expansion. The right endopodite is cylindrical, with a tuft of apical 'hairs' (fig. 3);
5. left  $P_5$  of the male: exopodite with thumb-shaped, 'ciliated' inner appendix, and finger-shaped apical appendix. Inner margin with denticulated, hyaline fringe (figs 4, 5);
6. antepenultimate segment of male prehensile antenna with long, curved appendix; segments 13 and 15 with a strong spine (figs 6, 7).

## RE-EXAMINATION OF TYPE MATERIAL

Some of the type material of VAN DOUWE is still in existence, and kept in the Museum of Berlin. No labeled slides exist, however, and therefore the type must be considered lost. Since *D. schubotzi* has only been found in one locality, a 'mare' at Fort Archambault, and the material submitted to us was labeled 'Altwasser bei Ft. Archambault', there

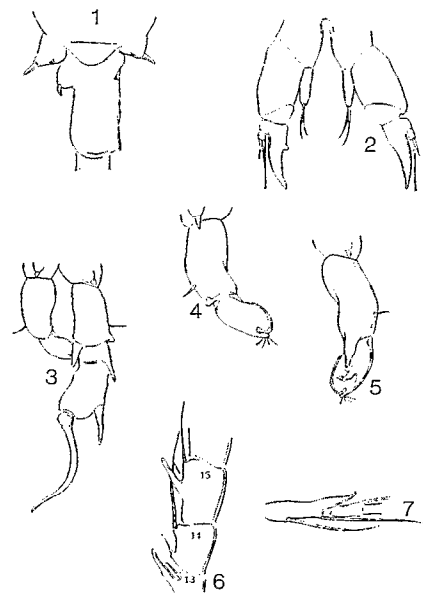


FIG. 1-7. — VAN DOUWE'S original illustrations of *Diaptomus schubotzi*. 1. female, end of cephalosome and top of urosome. 2. female  $P_5$ . 3. male  $P_5$ . 4-5. male, left  $P_5$ . 6. male prehensile antenna, segments 13-15. 7. male prehensile antenna, apex. *Diaptomus schubotzi*, illustrations originales de VAN DOUWE. 1. femelle, dernier segment thoracique et partie supérieure de l'urosome. 2.  $P_5$  de la femelle. 3.  $P_5$  du mâle. 4-5.  $P_5$  gauche du mâle. 6. mâle, segments 13-15 de l'antenne préhensile. 7. mâle, apex de l'antenne préhensile.

cannot be any doubt as to its nature. In the tube received, an adult male and female were found, besides copepodids. Both were dissected and mounted in glycerin. The male, labeled lectotype, and the female, labeled paralectotype have been redeposited in the Museum of Berlin.

**Male** (lectotype)

$P_5$  (fig. 8): in addition to the characters listed by VAN DOUWE, the basipodite 2 of the right  $P_5$  has 2 internal hyaline lamellae, and its external apical angle, distal to the insertion of the external seta, is swollen (I). Some distortion of the type specimen makes a detailed interpretation of the exopodite 1 rather difficult, but a long apical external spine is particularly prominent (1). It is flanked by a chitinous bud (2). On the inner apical angle (3) and the inner basal angle (4) additional but less visible chitinous swellings occur. The right endopodite is cylindrical, with two broadly triangular apical spines, and a row of short spinules.

The left  $P_5$  is as described by VAN DOUWE, but the apical finger of the exopodite is, of course, really



FIG. 8. *Tropodiaptomus schubotzi*, male lectotype, P5. *Tropodiaptomus schubotzi*, lectotype mâle, P5.

composed of two protuberances instead of one. The left endopodite is strongly tapering towards its apex, and set with a row of subapical spinules.

The male prehensile antenna (fig. 9) has a long, bluntly tipped appendix on segment 20, internal fleeces on segments 19, 18, and 17, and a complex articulation between segments 18 and 19, which involves a chitinous window (see arrow) near the tip of segment 18 (figs 9, 10). Spines occur on segments 10, 11, 13, and 15, but not on segment 16. The spine on segment 15 is strongly developed.

#### Female (paralectotype)

The asymmetry of the terminal segment of the cephalosome and of the first segment of the urosome is confirmed (fig. 11). The female P<sub>5</sub> (fig. 12) was quite well observed by VAN DOUWE. The hump on the inner surface on the end-claw of one of the two exopodites does not, however, stand in line with the internal row of spinules. The latter is rather short, and the spinules are small. The endopodite is long and thin, and with a characteristic notch on its internal surface close to its basal third.

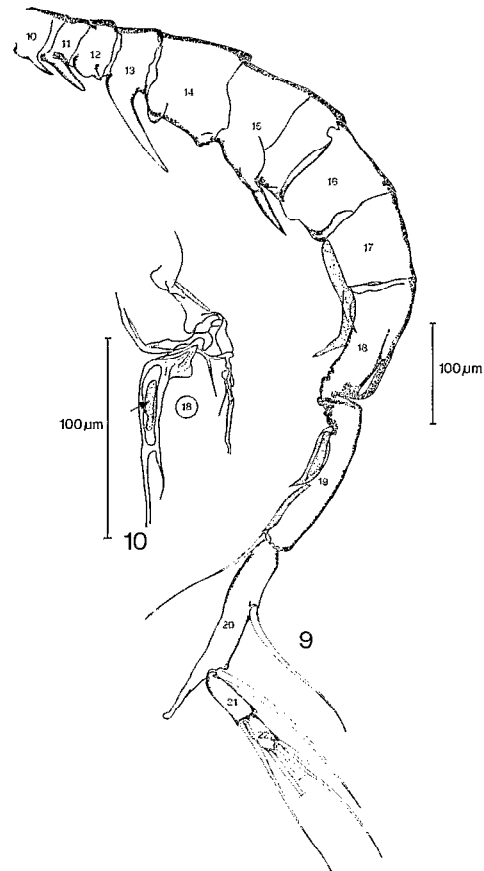


FIG. 9-10. — *Tropodiaptomus schubotzi*, male lectotype, prehensile antenna. *Tropodiaptomus schubotzi*, lectotype mâle, antenne préhensile.

#### THE POPULATION OF KUFRA OASIS: *T. schubotzi kufraensis* n. ssp.

Apart from the Nile, no *Tropodiaptomus* had to date been found in Africa north of the Sahel. It therefore came as a surprise to find *T. schubotzi* in Kufra oasis, south-east Libya (24°12' N., 23°18' E.), slightly north of the Tropic of Cancer. Specimens were found in plankton collections made here by the botanist A. Léonard on two separate occasions: 4 January 1965, and 8 October 1968. Both collections contained specimens. The first sample was taken in a small natron lake in the village of El Giof, at a site called Goudouie. The pond was fringed by *Phragmites*, *Ruppia maritima*, *Juncus maritimus*. The second came from a drinking-water well, rich in *Chara vulgaris* and diatoms (pers. comm. P. COMPÈRE, MEISE).

This outlying population must be considered as a relict of a former surface water connection between

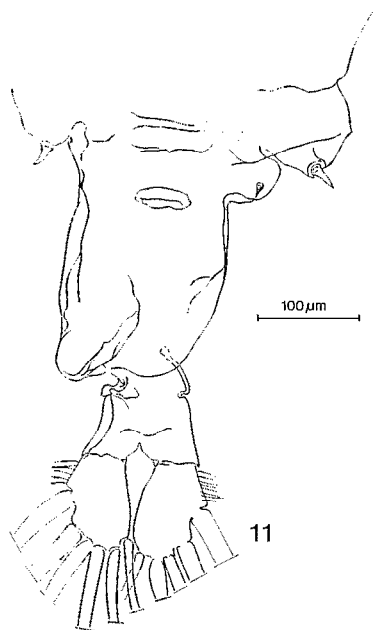


FIG. 11. — *Tropodiaptomus schubotzi*, female paralectotype, end of cephalosome and urosome. *Tropodiaptomus schubotzi*, paralectotype femelle, bout du céphalosome et urosome.



FIG. 12. — *Tropodiaptomus schubotzi*, female paralectotype, P5. *Tropodiaptomus schubotzi*, paralectotype femelle, P5.

Lake Chad and the waters of Kufra oasis. Most probably it dates back to the long humid interval (12,500-8,000 BP) that followed the Würm III deglaciation. The temporal isolation of this population appears considerable, and we therefore looked for signs of morphological divergence with stock populations. Although most specimens at our disposal were copepodids, and only a single adult female and male specimen were available, a series of distinctive characters were found. On the right  $P_5$  of the male, basipodite 2 has a single internal hyaline membrane, unlike the type, but rather like in *T. symoensi*. Chitin bud 4 on exopodite 1 occurs in a stand-alone position, not incorporated into the inner margin of the segment, and bears a pore on top (fig. 20). The apical segment of the exopodite has two hyaline lamellae, instead of one as in other populations (fig. 20). The antennal ornamentation was like in Chadian specimens figured by DUSSART & GRAS, i.e. the spine on segment 15 was greatly reduced in size (figs 23, 25).

The female is indistinguishable from Chadian specimens (e.g.  $P_5$ : fig. 19). While the Kufra population therefore adds to the overall variability of the species, there is as yet no reason to rank it higher than at the subspecies level. We name it *T. schubotzi kufraensis*, after its type locality. The male holotype and female allotype have been deposited in the British Museum, Natural History, London (Accession numbers: 1987.73 ; 1987.74).

A SYNONYM: *T. incognitus* Dussart & Gras

Because Fort Archambault (presently called Sarh) is situated in the inundation area of the Chari River which feeds Lake Chad, it was only natural to expect the presence of *T. schubotzi* in the latter lake. It appears indeed to live in the lake, from where it was erroneously described as a new species by DUSSART & GRAS in 1966. The figures offered by these authors (figs 13-17) illustrate some of the basic features of the species better than others: the asymmetry in the female habitus, the notch in the endopodite of  $P_5$ , the hump on one of the end-claws of the exopodite (called a 'spine') (but the asymmetry of the end-claws of the female  $P_5$  is not mentioned) are nicely figured, but the male  $P_5$  is superficially depicted, and segment 15 of the male prehensile antenna is figured with a small spine.

Examination of a series of animals from Lake Chad (leg. A. ILTIS, 24.03.1967) confirmed the asymmetry of the female  $P_5$  (fig. 18). The right  $P_5$  in the male was found to have two (I and II) chitinous thickenings along the anterior margin of the apical segment of the basipodite (II could also tentatively be identified on the lectotype: see fig. 8), and a

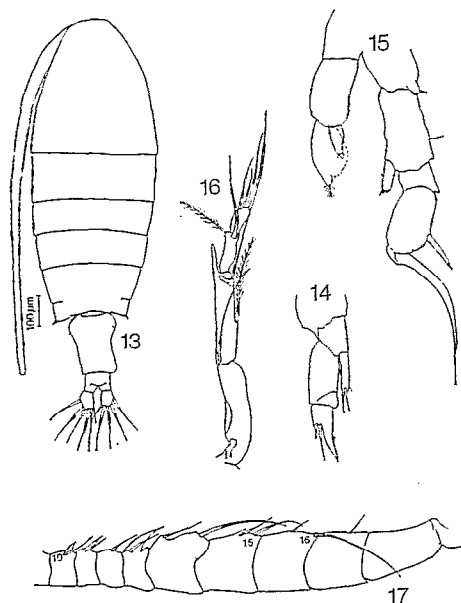


FIG. 13-17. — DUSSART & GRAS' illustrations of "*Tropodiptomus incognitus*". 13. female habitus. 14. female P<sub>5</sub>. 15. male P<sub>5</sub>. 16. male prehensile antenna, apical segments. 17. male prehensile antenna, middle segments. « *Tropodiptomus incognitus* », illustrations de DUSSART & GRAS. 13. femelle. 14. P<sub>5</sub> de la femelle. 15. P<sub>5</sub> du mâle. 16. mâle, segments apicaux de l'antenne préhensile. 17. mâle, partie centrale de l'antenne préhensile.

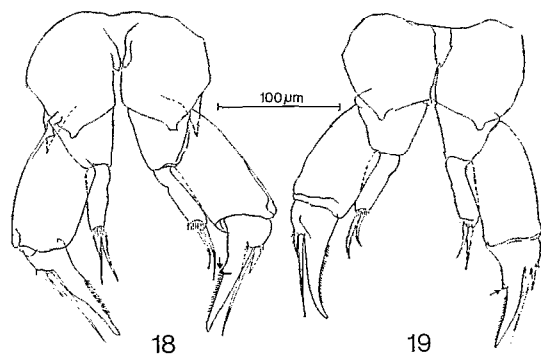


FIG. 18. — *Tropodiptomus schubotzi*, specimen from lake Chad, female P<sub>5</sub>. *Tropodiptomus schubotzi*, spécimen du lac Tchad, P<sub>5</sub> de la femelle.

FIG. 19. — *T. schubotzi kufraensis* n. ssp., specimen from Kufra oasis, female P<sub>5</sub>. *Tropodiptomus schubotzi kufraensis* n. ssp., spécimen de l'oasis de Koufra, P<sub>5</sub> de la femelle.

typical arrangement on the first segment of the exopodite: a strong external spine (1), and three chitinous knobs (2-4). The apical segment has an internal hyaline lamella, while a short hyaline fleece inserts between the apical and the lateral spine. The

endopodite is cylindrical, with two triangular apical spines and a row of spinules.

The spine on segment 15 of the male prehensile antenna varied between DUSSART & GRAS' original figure (fig. 17) and the type (figs 6, 9), over an average situation depicted in fig. 24.

#### A RELATED TAXON: *T. symoensi* Einsle

From lakes and swamps in the south-east of the Zaire catchment (Lakes Bangweolo and Moero), EINSLE (1971) described *T. symoensi* (figs 26-31). He illustrated the asymmetry of the female body (fig. 26). The male P<sub>5</sub> is figured from several angles (figs 28-31) and convincingly shows the chitinous thickenings I and II on the apical segment of the right basipodite, and three out of the four on the basal segment of the right exopodite. A hyaline lamella, of variable length, is figured on the inner surface of basipodite 2, right P<sub>5</sub> (figs 29, 31). Although these characters indicate a close relationship with *T. schubotzi*, a distinct difference is found on the inner basal angle of the basipodite 2 of the right P<sub>5</sub> (male), where a triangularly pointed expansion occurs (arrow on figs 29, 30).

We have re-examined some of EINSLE's material, and have no doubt whatsoever as to its specificity (at variance with the statement made in DUMONT & VERHEYE 1984) but also as to its extremely close relationship with *T. schubotzi*. The female body is less asymmetrical, but the end-claws of the female P<sub>5</sub> each bear a blunt spine, of unequal length (fig. 33). In the male, no spine is found on segment 15 of the prehensile antenna, but a small spine occurs on segment 16 instead (fig. 32). Significant diagnostic characters also occur in the right P<sub>5</sub> of the male. In addition to the outgrowth on the base of the basipodite, the external apical swelling (I) is more produced than in *T. schubotzi*, and supplemented by two chitinous buds (figs 35, 36). Swelling (II), likewise, is better developed than in *T. schubotzi*, but outgrowths 1, 2, and 3 on the right exopodite 1 are exactly as in that species. An important difference occurs in the shape of (4), which is spine-shaped, not rounded, and points internally. There even occurs a small swelling (5) in the base of exopodite 2, opposite the long spine (1) (figs 34-36). The right endopodite is shorter, more cylindrical, with a subapical tuft of spinules, but without the two larger, broad-based spines of *T. schubotzi* (figs 35-36).

These findings suggest that inter-basin crossing between the Zaire and the Chari valleys by a common ancestor took place, and was followed by allopatric speciation on either side of the divide. Because Lake Chad dried out during the late-Pleistocene arid phase that culminated around 18,000 BP, this basin-crossing most likely occurred during the long humid

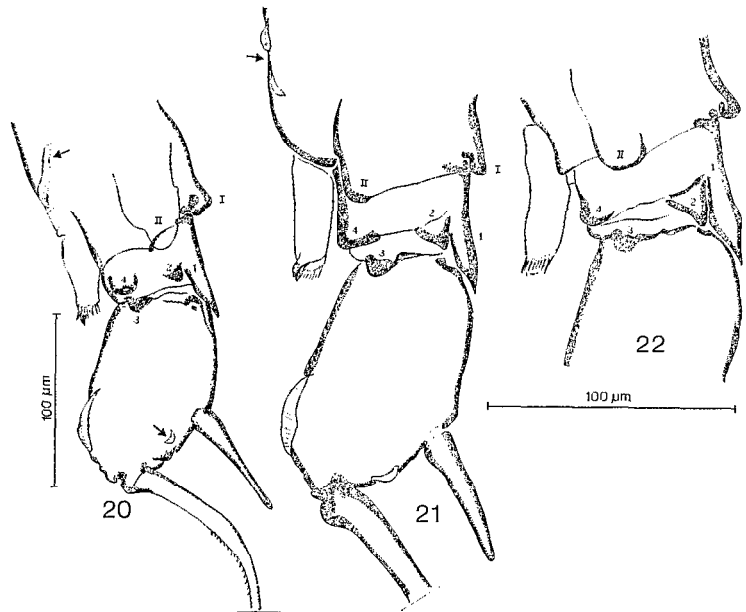


FIG. 20. — *T. schubotzi kufraensis*, specimen from Kufra oasis, male P5. *T. schubotzi kufraensis* n. ssp., spécimen de l'oasis de Koufra, P5 du mâle.

FIG. 21-22. — *T. schubotzi*, from lake Chad, male P5. *T. schubotzi*, spécimen du lac Tchad, P5 du mâle.

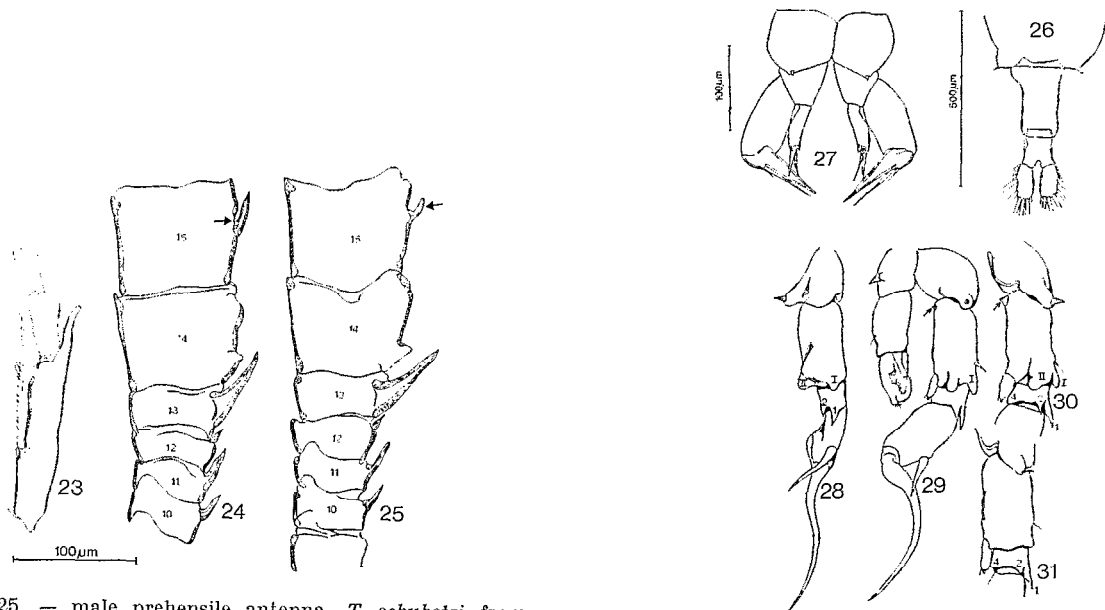


FIG. 23-25. — male prehensile antenna. *T. schubotzi*, from Lake Chad. 24. segments 10-15. *T. schubotzi kufraensis*, from Kufra oasis. 23. apical segments. 25. segments 10-15. *antenne préhensile du mâle. T. schubotzi, du lac Tchad. 24. segments 10-15. T. schubotzi kufraensis, de l'oasis de Koufra. 23. segments apicaux. 25. segments 10-15.*

FIG. 26-31. — EINSLE's illustrations of "*Tropodiatomus symoensi*". 26. female urosome. 27. female P5. 28-31. male P5, different views. « *Tropodiatomus symoensi* », illustrations d'EINSLE. 26. urosome de la femelle. 27. P5 de la femelle. 28-31. P5 du mâle, orientations différentes.

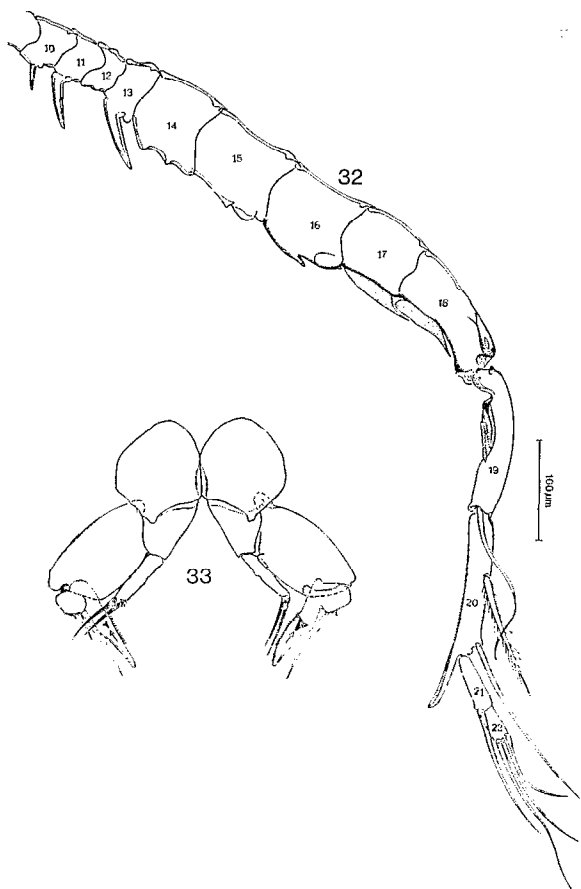


FIG. 32-33. — *T. symoensi*. 32. male prehensile antenna. 33. female P5. *Tropodiplomus symoensi*. 32. antenne préhensile du mâle. 33. P5 de la femelle.

interval that followed the Wurm III deglaciation (12,500-8,000 BP) (see also discussion).

It is of considerable interest to note that *T. symoensi* seems not to have expanded downstreams to the lower Zaire, perhaps because the humic and acidic inundated forest zone of the middle Zaire constitutes an effective barrier. However, in order to check this assertion, the only *Tropodiplomus* known to date from the lower Zaire, *T. loveni* (DE GUERNE & RICHARD), needed to be re-examined.

REDESCRIPTION OF *Tropodiplomus loveni* (De Guerne & Richard)

Originally described from Gabon (DE GUERNE & RICHARD 1890, 1891) and believed to be extending over most of the Zaire valley (TOLLINGER 1911), but in fact never found again after the original description. Illustrations of DE GUERNE & RICHARD 1891 (figs 37-39) show the female P<sub>5</sub>, the appendix on the

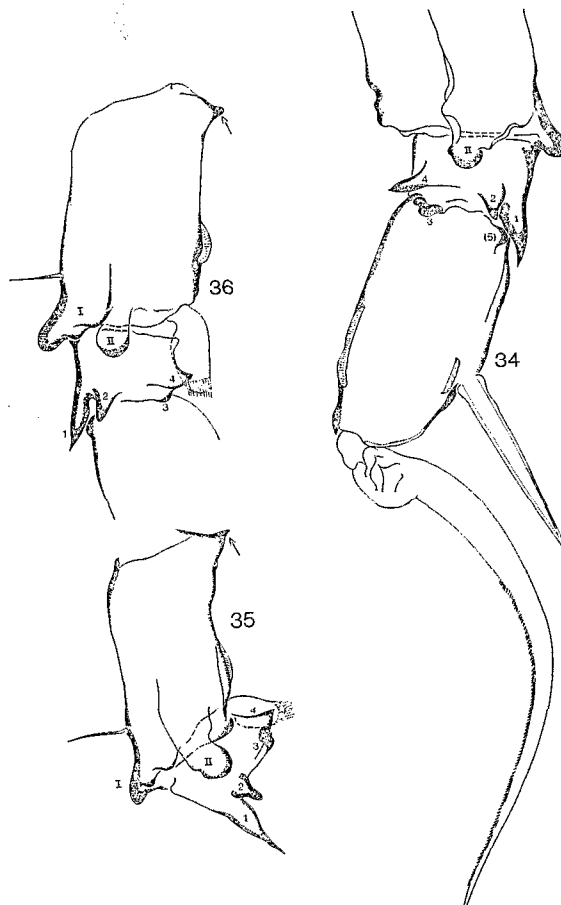


FIG. 34-36. — *T. symoensi*. 34. male right P5, with endopodite omitted. 35-36. male right P5, apical segment of basopodite, endopodite, and basal segment of exopodite. *Tropodiplomus symoensi*. 34. P5 droit du mâle sans endopodite. 35-36. P5 droit du mâle, segments apicaux du basopodite, endopodite, et segment basal de l'exopodite.

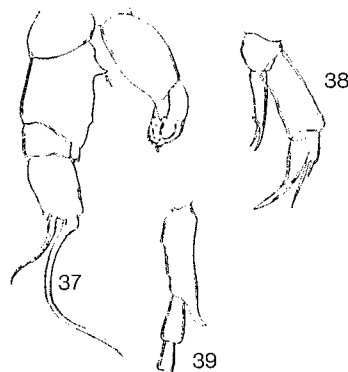


FIG. 37-39. — DE GUERNE & RICHARD's illustration of *Diaptomus loveni*. 37. male P5. 38. female P5. 39. male prehensile antenna, apical segments. *Diaptomus loveni*, illustrations de DE GUERNE & RICHARD. 37. P5 du mâle. 38. P5 de la femelle. 39. mâle, segments apicaux de l'antenne préhensile.

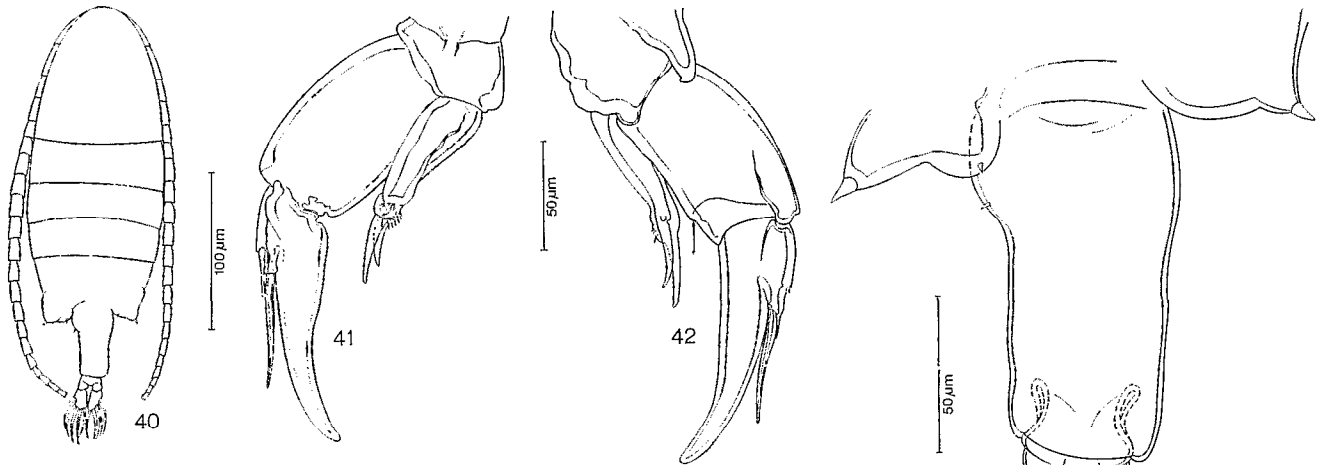
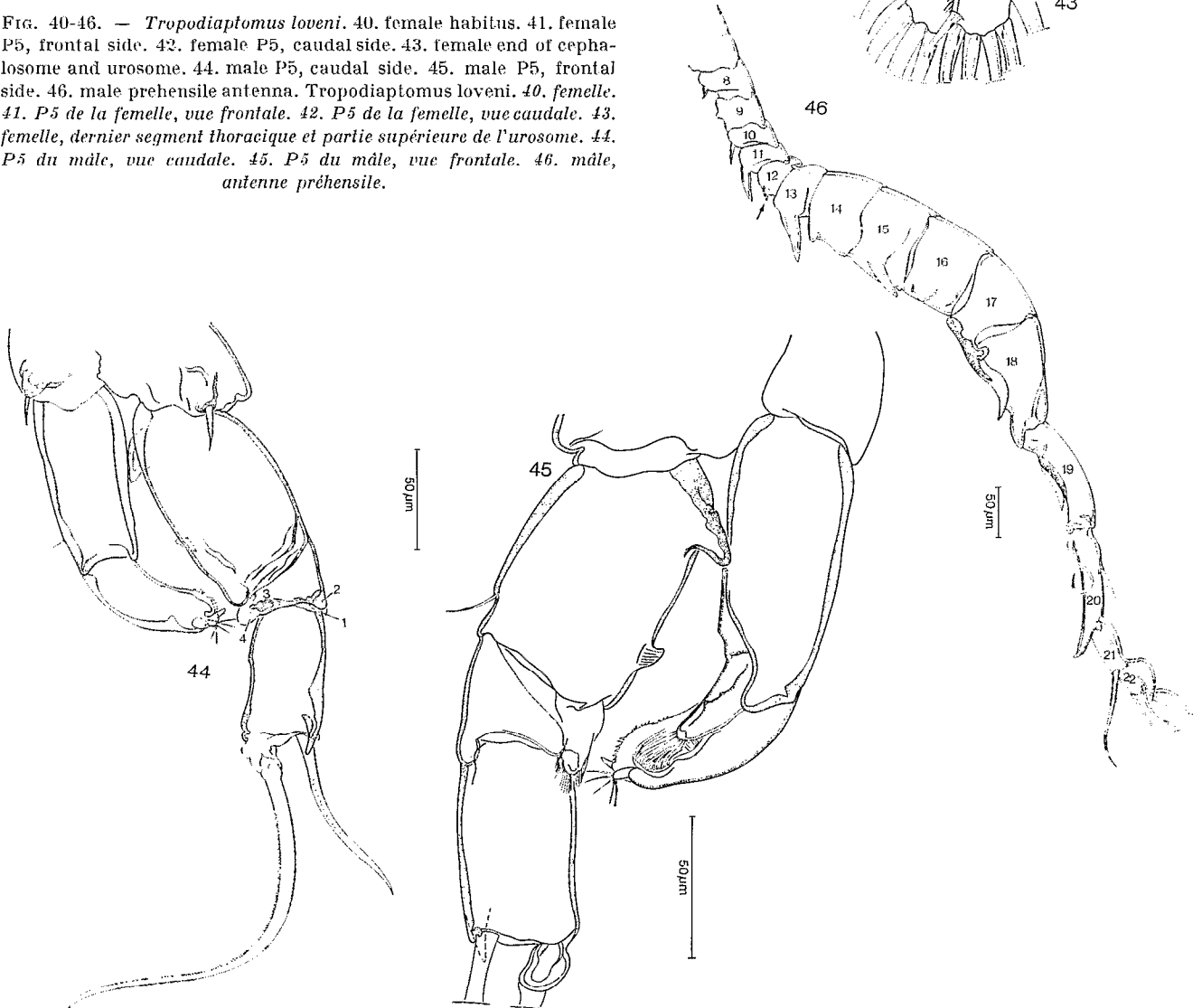


FIG. 40-46. — *Tropodiaptomus loveni*. 40. female habitus. 41. female P5, frontal side. 42. female P5, caudal side. 43. female end of cephalosome and urosome. 44. male P5, caudal side. 45. male P5, frontal side. 46. male prehensile antenna. *Tropodiaptomus loveni*. 40. femelle. 41. P5 de la femelle, vue frontale. 42. P5 de la femelle, vue caudale. 43. femelle, dernier segment thoracique et partie supérieure de l'urosome. 44. P5 du mâle, vue caudale. 45. P5 du mâle, vue frontale. 46. mâle, antenne préhensile.





antepenultimate segment of the male prehensile antenna and a prominent hook on the inner basal angle of the basipodite 2 of the male  $P_5$ . These characters were confirmed in a re-examination of the type material by DUSSART (1984). However, since the latter re-description failed to show certain details of structure now believed to be important, and no type specimens were indicated, we here describe the original material again.

The following material from Mayoumba, Congo, was examined: 1 male, which we subsequently labeled lectotype and 1 female, labeled paralectotype, now deposited in the British Museum, Natural History, London (Accession numbers : 1987.75; 1987.76); 1 male, 2 females and some seriously damaged specimens remained in the authors' collection, State University of Ghent.

#### Male (lectotype)

$P_5$  (figs 44-45): on the internal side the right basipodite bears a hyaline lamella and a basal, chitinous protuberance or hump. The basipodite shows no particular swollen apical angles. Outgrowths 1, 2, 3 and 4 on the right exopodite 1 less pronounced and more rounded than in *T. symoensi* (fig. 44). The exopodite 2 of the right  $P_5$  shows a pointed outgrowth, close to the implantation of the external end-claw which is strongly curved. The apices of the two claws of the right exopodite 2 are typically divergent. No hyaline lamella is visible. The right endopodite is cylindrical with an apical row of spinules. Left exopodite bearing 2 apical finger-shaped protuberances of which one is ciliated. Inner margin with denticulated fringe and central part of the exopodite bearing a 'comb' with long hairs and a central group of spinules, partly covered by the endopodite.

The antepenultimate segment of the male prehensile antenna bears and appendix of moderate length; spines occur on segments 8, 10, 11, 12, 13 and 15, but not on segments 9 and 16 (fig. 46).

#### Female (paralectotype)

Terminal segment of cephalosome and first segment of urosome asymmetrical (fig. 43).  $P_5$  (figs 41-42): symmetrical, endopodite bearing 2 apical spines, a subterminal and a terminal row of spinules. The end-claws on the exopodite appear to be devoid of an internal pecten. None of both claws show a blunt spine like in *T. symoensi*.

#### DISCUSSION (fig. 47)

*T. schubotzi* is the only African *Tropodiptomus* on which a considerable amount of ecological research has

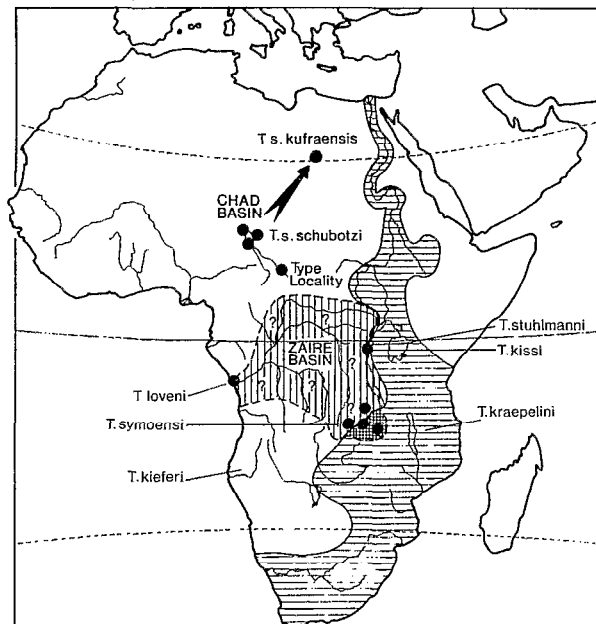


FIG. 47. — Ranges of *T. schubotzi*, *T. symoensi*, *T. loveni*, *T. kraepelini* (and related species), and occurrence of *T. kissi* and *T. kieferi* in Africa. Aire de répartition du *T. schubotzi*, *T. symoensi*, *T. loveni*, *T. kraepelini* (et espèces alliées), et citations de *T. kissi* et *T. kieferi* d'Afrique.

been performed. Data on biomass, development times and fertility (GRAS 1970, GRAS & SAINT-JEAN 1969, 1976, 1981a, 1981b), on its—mainly algal—dietary requirements (GRAS *et al.* 1971), and on its distribution pattern within Lake Chad (SAINT-JEAN 1983) are available. A synthesis can be found in CARMOUZE *et al.* 1983. It is a species with considerable plasticity in habitat choice, occurring in small pools as well as in sizeable lakes, and tolerant of rather wide fluctuations in salinity (e.g. within the zones of Lake Chad itself, but also between Lake Chad and the saline lakelet in Libya). *T. symoensi*, on the other hand, seems restricted to the less mineralized waters of the upper Zaire basin.

The geographic range of the *schubotzi-symoensi* species pair, as understood today, is shown in fig. 47. It might in fact well be a holocene newcomer in the geologically old Zaire basin. As argued earlier, it may have taken advantage of the great holocene pluvial to invade the upper Zaire coming from Lake Chad, the well-known pivot-point of aquatic faunas migrating east-west and north-south in subequatorial Africa (DUMONT & VERHEYE 1984). Because of competitive exclusion, it seems not to have succeeded in establishing itself in the Niger and Nile basins, but it managed to extend north as far as Kufra oasis.

It is remarkable that so few *Tropodiatomus* species have to date been found in the Zaire basin. Apart from *T. symoensi*, we know only to *T. loveni* to which it is only moderately related (at the species group-level).

This species-group to which the type-species of the genus, and *T. orientalis* Brady belongs, is the largest of the genus. Most if not all Asian taxa are part of it. Its characteristics are the female P<sub>5</sub> with endopodite adorned by two long, finely pointed spines, with one tuft of spinules at their foot. Male P<sub>5</sub>: right basopodite with an internal hump near its basal third; no peculiar outgrowth on its inner apical third; left P<sub>5</sub> with basopodite not notably wider than exopodite. Apex of exopodite spinulated and rounded; apical 'fingers' not strongly prominent.

To be included in this species-group is the African *T. kraepelini* complex which embraces such great-lakes endemics as *T. cunningtoni*, *T. stuhlmanni* and the ill-defined East-African *T. cf. orientalis*.

*T. symoensi* shows some amount of range overlap with *T. kraepelini* in the south-east of the Zaire basin. Possibly *T. schubotzi* vicariates with that same species (*T. kraepelini*) along the Nile-Chad divide. Moreover, there are at least two more species which belong to the same overall complex which may possibly vicariate or overlap with either *T. symoensi* or *T. loveni*, viz. *T. kissi* Dussart, from the Central Rift Valley and *T. kieferi* Marques, from Angola.

Since the morphology and ranges of the latter two species are not well worked out, details of their relationship with the *T. schubotzi-symoensi* complex must await further study.

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