Resurrection of *Characidotrema* Paperna and Thurston, 1968 (Monogenea: Dactylogyridae) with Description of Two New Species from Togo, Africa

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The present study represents the first in a series dealing with selected dactylogyrid genera of African freshwater fishes. This series was initiated to develop the basis for eventual analysis of biogeographic relationships of the Ethiopian and Neotropical monogenean faunas. Similar studies on Neotropical Dactylogyridae are currently underway (see Kritsky and Thatcher, 1976, 1983; Kritsky et al., 1979, 1980, 1985, 1986a, b; Thatcher and Kritsky, 1983).

Materials and Methods

Fish hosts (5) were collected from the Mono River near Kolokopé, Togo, during November 1985. Gills were removed and placed in vials containing a 1:4,000 formalin solution; after about 1 hr, gills were agitated by vigorous shaking, and formalin concentration was increased to about 5% for preservation. Hosts were immediately preserved in 10% formalin after removal of the gills. Fish hosts and vials containing helminths were labeled and shipped to Idaho. Dactylogyrids were removed from vial sediments with the aid of a small probe and dissecting microscope and prepared for microscopy. Some specimens were mounted unstained in Gray and West’s medium for study of sclerotized structures; others were stained with Semichon’s carmalam or Gomori’s trichome and mounted in Harleco synthetic resin to determine features of the internal organ systems. Illustrations were prepared with the aid of a camera lucida or microprojector. Measurements, in micrometers, were made with a filar micrometer according to the procedures of Mizelle and Klucka (1953), except that cirrus length is an approximation by using a Minerva curvimeter on camera lucida drawings; average measurements are followed by ranges in parentheses.

In addition to the parasites collected from Togo, type and voucher specimens of all previously described species were examined as follows: *Characidotrema elongata* Paperna and Thurston, 1968 (MRAC 35.569, holotype, 2 paratypes); *C. brevipenis* Paperna, 1969 (MRAC 35.913, holotype, 3 paratypes); *Jainus brevipenis nzoiae* Paperna, 1979 (MRAC 35.713, holotype, 3 paratypes); *J. b. ruahae* Paperna, 1979 (MRAC 35.716, holotype, 2 paratypes, vouchers); *J. longipenis* Paperna, 1973 (MRAC 35.918, holotype, 2 presumed paratypes, 1 voucher); J. cf. *longipenis* of Paperna (1979) (MRAC 35.907, voucher); *C. nursei* Ergens, 1973 (CSAV M-282, holotype; MRAC 35.504, paratype); and *J. spinivaginus* Paperna, 1973 (MRAC 35.942, holotype). Acronyms are MRAC (Musee Royal de l’Afrique Centrale, Tervuren, Belgium) and CSAV (Institute of Parasitology, Czechoslovak Academy of Sciences, Prague). Type specimens of new species and vouchers of *C. brevipenis* Paperna, 1969, collected during the present study were deposited in the helminthological collections of the U.S. National Museum (USNM), the University of Nebraska State Museum (HWML), the Instituto Nacional de Pesquisas da Amazônia (INPA), and the Musee Royal de l’Afrique Centrale as indicated in the respective descriptions. Fish
hosts were deposited in the American Museum of Natural History (AMNH 57075).

Results

**Characidotrema** Paperna and Thurston, 1968

EMENDED DIAGNOSIS: Dactylogyridae, Ancyrocephalinae. Body robust, divisible into cephalic region, trunk, peduncle, haptor. Segments variably developed, smooth or with ciliated tufts. Usually 2 terminal cephalic lobes poorly developed; head organs present in cephalic lobes and adjacent cephalic zones; cephalic glands present. Eyes present, usually 2 pairs. Mouth subterminal, midventral; pharynx muscular, glandular; esophagus short; intestinal ceca (2) confluent posterior to testis, lacking diverticula. Gonads intercalary, partially overlapping; testis dorsal-posterior to ovary. Vas deferens looping left intestinal cecum; seminal vesicle a sigmoid dilation of vas deferens; copulatory complex comprising a tubular cirrus with variably developed base and accessory piece articulated to cirrus base; prostatic reservoir anteroventral to seminal vesicle. Oviduct short; uterus delicate; vagina dextral or dextroventral in anterior trunk; seminal receptacle immediately anterior to ovary. Genital pore midventral. Villariella well developed into 2 bilateral bands in trunk, confluent posterior to gonads. Peduncle short; haptor poorly developed, armed with dorsal and ventral pairs of anchors, dorsal and ventral bars, 7 pairs of hooks with ancyrocephaline distribution (Mizelle, 1936). Ventral anchor with diagonally truncate point, elongate deep and superficial root; dorsal anchor shaft slightly enlarged proximally. Ventral bar with 2 bilateral anterior arms and 1 posteromedial process. Hooks similar, with undilated shanks, poorly developed thumb. Parasites of gills of African characoid fishes of the genus *Alestes* (Alestidae).

**TYPE SPECIES, HOST, AND LOCALITY:** Characidotrema elongata Paperna and Thurston, 1968, from Alestes nurse (Rüppell), Jinja, Lake Victoria, Uganda; also reported from *A. leuciscus* Günther, Mawi River, Volta Lake, Ghana.

**OTHER SPECIES:** Characidotrema brevipes Paperna, 1969, from *A. nurse* and *A. baremose* (Joannis) (Ghana), from *A. cf. nurse* (Togo); *C. nursei* Ergens, 1973, from *A. nurse* (Egypt, Uganda) and *A. leuciscus* Günther (Ghana); *C. nzoiae* (Paperna, 1979) comb. n. from *A. jacksoni* Bou-lenger (Kenya); *C. ruahae* (Paperna, 1979) comb. n. from *A. imberi* Peters (Tanzania); *C. spinivaginis* (Paperna, 1973) comb. n. from *A. nurse* (Uganda); and *C. undifera* and *C. zelotes* spp. n., both from *A. cf. nurse* (Togo).

**Characidotrema elongata**

Paperna and Thurston, 1968 (Figs. 10–14)


**HOSTS AND LOCALITIES:** Alestes jacksoni Boulenger, Jinja, Lake Victoria, Uganda (type host and locality); *A. leuciscus* Günther, Mawi River and Volta Lake at the Black and White Volta confluence, Ghana (Paperna, 1969).

**SPECIMENS STUDIED:** MRAC 35,569 containing holotype and 2 paratypes.

**REMARKS:** The microscope slide containing the type specimens was invaded by bubbles which had filled with the dark ringing medium. As a result, the sclerotized structures of the holotype could not be observed. Thus, the figures and following observations are based on a paratype specimen present in slide ring "D".

Originally indicated by monotypy, *C. elongata* is the type species of the genus. It is characterized by possessing a short robust accessory piece which encircles the shaft of the cirrus with short terminal projections (Fig. 10). It closely resembles *C. nursei* from which it differs by lacking a well-developed distal flange on the cirral base. The presence of a posteromedial projection of the ventral bar (dorsal bar of Paperna and Thurston, 1968) could not be confirmed, although a suggestion of this structure is apparent in the paratype. Measurements of paratype "D" follow: cirrus 41; accessory piece 15; ventral anchor length 16, base width 10; dorsal anchor length 23, base width 8; ventral bar 12; dorsal bar 16.

Because of the poor condition of the slide, the vagina could not be observed in the paratype, but Paperna and Thurston (1968) indicate a sinistral vagina in the original diagnosis of Characidotrema. However, these authors mistakenly

Figures 1–9. Characidotrema brevipes Paperna, 1969. 1. Whole mount (ventral). 2. Vagina. 3. Hook. 4, 5. Copulatory complexes. 6. Ventral bar. 7. Dorsal bar. 8. Ventral anchor. 9. Dorsal anchor. All figures are based on specimens collected from Togo and are drawn to the same scale (30 µm) except Figure 1 (75 µm).
had the dorsoventral axis reversed as indicated in their description of the haptor of *C. elongata*. This suggests that the vagina actually opens on the right body margin in *C. elongata*, as it does in all other species of *Characidotrema* in which type material permitted verification.

Paperna and Thurston (1968) list *Alestes nurse* as the type host for this species. However, Paperna’s (1979) report of *C. elongata*, which is based on the type specimens, gives *A. jacksoni* as its host, and the slide containing the holotype and paratypes indicates the latter host. Greenwood (1959) has shown that the *Alestes* populations previously referred to *A. nurse* from Lake Victoria comprise the species *A. jacksoni*, while Géry (1977) suggests that *A. jacksoni* is a possible synonym of *A. imberi* (=*Brycinus imberi*). In either case, we consider the type host of *C. elongata* to be the *Alestes* species from Lake Victoria and its drainages assigned to *A. jacksoni* by Greenwood (1959).

*Characidotrema brevipes* Paperna, 1969
(Figs. 1–9, 15–19)

**SYNONYM:** *Jainus brevipes* (Paperna, 1969)


**HOSTS AND LOCALITIES:** *Alestes nurse* (Rüppell) (type host), Volta Lake at Kete Krachi, at Yeji (type locality), and at the Black and White Volta confluence, Ghana; *A. baremose* (Joannis), Volta Lake at Yeji, Ghana (Paperna, 1969); *A. cf. nurse*, Mono River, Kolokopé, Togo (new locality record).

**SPECIMENS STUDIED:** MRAC 35.913 containing holotype and 3 paratypes; 22 vouchers from Togo (USNM 79408; HWML 23555; INPA PA289-1,2; MRAC 37.112).

**REDESCRIPTION** (based on specimens from Togo): Body foliform, 317 (217–425) long; greatest width 91 (59–125) near midlength or in anterior half. Tegument smooth. Cephalic margin rounded or truncate, lobes poorly developed or absent; head organs, cephalic glands indistinct. Eyes equidistant, members of posterior pair larger than anterior pair; eye granules ovate to subspherical; accessory granules present in cephalic region and anterior trunk. Pharynx spherical, 19 (13–22) in diameter. Peduncle tapered posteriorly, broad; haptor subhemispherical, 27 (22–32) long, 32 (22–37) wide. Ventral anchor 19 (17–21) long, base 10–11 wide; dorsal anchor 26 (24–27) long, base 9 (8–10) wide. Bilateral arms of ventral bar delicate, posteromedial projection small; ventral bar 9–10 long. Dorsal bar 17 (16–19) long, simple, with tapered ends. Hook point delicate, thumb subtriangular; hook 17 (15–18) long; FH loop 0.5 shank length. Cirrus comprising curved shaft, ellipsoidal base with elongate distal projection; cirrus 39 (38–40) long; accessory piece 22 (20–24) long, variable, with slight terminal expansion. Testis subovate, 52 (49–56) × 30 (24–36); seminal vesicle with thick muscular wall proximally. Ovary subovate, 84 (45–144) × 25 (17–32); vagina at level of seminal vesicle, comprising a dumbbell-shaped tubular selerite; vitellaria composed of relatively large cellular masses extending from level of copulatory complex to peduncle.

**REMARKS:** Comparison of our specimens with the holotype of *C. brevipes* confirms that all are conspecific. Measurements of the sclerites of the holotype fall within ranges reported herein for specimens collected from Togo, while ranges reported by Paperna (1969, 1979) for the ventral and dorsal anchors and the ventral and dorsal bars of the species do not include the corresponding values of the holotype. Dimensions of the sclerites of the holotype follow (Paperna’s [1979] values are in parentheses): cirrus 38 (20–40); ventral anchor length 18 (30–40), base width 10 (none provided); dorsal anchor length 24 (35–40), base width 8 (none provided); ventral bar 13 (18); dorsal bar 16 (20).

*Characidotrema brevipes* is related to *C. nzoiae*
comb. n., C. undifera sp. n., and C. zeolotes sp. n. It differs from C. nzoiae by having a more elongate cirrus base, and from C. undifera and C. zeolotes by possessing a cirral shaft with a generally smooth curve.

Characidotrema nursei Ergens, 1973
(Figs. 20–32)


HOSTS AND LOCALITIES: Alstes nursei (Rüppell), Nile River, Cairo, Egypt (type host and locality); A. nurse, Lake Albert, Uganda (Paperna, 1973, 1979); A. leuciscus Günther, Volta Lake and Mawli River, Ghana (Paperna, 1979).

SPECIMENS STUDIED: ČSAV M-282, holotype; MRAC 35.504, paratype; MRAC 35.918, holotype, 2 paratypes, 1 voucher of Jainus longipenis Paperna, 1973; MRAC 35.907, voucher of Jainus cf. longipenis of Paperna (1979).

REMARKS: Independently and apparently without knowledge of the other, Ergens (1973) described Characidotrema nursei from Egypt and Paperna (1973) proposed Jainus longipenis from Uganda. Examination of the holotypes of each of these species confirms their conspecificity (compare Figs. 20–23, 24–28). Since Characidotrema nursei (30 March 1973) has priority over longipenis (29 September 1973), J. longipenis is considered a junior subjective synonym of C. nursei.

Ergens' (1973) description of the sclerites of this species is accurate and is the first to have depicted the nature of the point of the ventral anchor. Indeed, our examination of all previously described species in the genus and the 2 new species described herein indicates that the unique ventral anchor point could be sufficiently constant to be considered a generic character. The diagonally truncate or scoop-shaped point of the ventral anchor, therefore, has been incorporated as a diagnostic trait in the emended diagnosis. Measurements of the haptoral sclerites of the types of C. nursei and J. longipenis fall within the ranges provided by Ergens (1973) except for the total length of the cirrus (68–71, nobis).

Paperna (1979) reported Jainus cf. longipenis from Alstes leuciscus in Ghana. The specimen studied indicates that it is similar to C. nursei in morphology of haptoral and copulatory sclerites; it differs from C. nursei in being somewhat smaller (compare Figs. 20–23, 29–32). The tubular vagina, characteristic of C. nursei, is absent. Measurements of the voucher include: cirrus 50; dorsal anchor length 21, base width 8; ventral anchor length 16, base width 10; dorsal bar 14. Because of these differences, we provisionally include this specimen in C. nursei until the form is restudied from A. leuciscus.

Characidotrema nzoiae (Paperna, 1979) comb. n.
(Figs. 33–35)


HOST AND LOCALITY: Alstes jacksoni Bou-lenger, Nzoia River (Lake Victoria system), Kenya.

SPECIMENS STUDIED: MRAC 35.715 containing holotype and 3 paratypes.

REMARKS: The microscope slide containing the type specimens of this form was provided with 3 circular coverslips, each overlying 1 or 2 specimens of the species. The second (center) coverslip had a typed label partially overlying it which indicated the center specimen as the holotype. This specimen most closely conforms to the body shape of the species depicted in the wholemount figure (Plate XL) of Paperna (1979), except that the haptor is folded ventrally over the trunk, imparting a foreshortened specimen (not shown in the original drawing). All type specimens available for study were stained and mounted in resin, which precluded complete determination of the sclerotized parts. The ventral anchor of the holotype was not visible in a single microscopic plane, resulting in a foreshortened basal width (Fig. 35). The vagina opens on the right margin of the anterior trunk.

Although the copulatory complex shows some similarity to that of Characidotrema brevipenis, the size and shape of the base indicates that these specimens should be considered a separate species. Its closest relative is likely C. brevipenis as shown by the morphology of the cirral shaft, but the small cirral base is considered sufficiently different to warrant elevation of the form to separate specific status. This species is in need of redescriptions, which will depend on the collection of fresh material prepared to show internal anatomy and morphology of the haptoral and copulatory sclerites.
Figures 52–59. *Characidotrema undifera* sp. n. 52. Holotype (ventral). 53. Hook. 54, 55. Copulatory complexes. 56. Ventral bar. 57. Dorsal bar. 58. Ventral anchor. 59. Dorsal anchor. All figures are drawn to the 30-μm scale except Figure 52 (100 μm).
Characidotrema ruahae  
(Paperna, 1979) comb. n.  
(Figs. 36–40)  

**SYNONYM:** Jainus brevipenis ruahae Paperna, 1979.  

**HOST AND LOCALITY:** Alestes imberi Peters, Ruaha River, Tanzania.  

**SPECIMENS STUDIED:** MRAC 35.716 containing the holotype and 2 paratypes.  

**REMARKS:** This species is characterized by possessing a small cirrus with a base provided with 2 sclerotized flanges. The proximal flange is bent anteriorly, and the distal flange is elongate. Based on the morphology of the cirrus, this species is intermediate between _C. nursei_ and _C. brevipenis_ by having a coiled cirral shaft like that of _C. nursei_ and a cirral base with 2 well-developed flanges similar to those of _C. brevipenis_. The differences in the cirral base are considered sufficient to raise this form to specific rank, since cirral morphology is the most apparent morphological character distinguishing species in the genus. Measurements of the haptoral and copulatory sclerites of the holotype fall within the ranges provided by Paperna (1979); the vagina was not observed.

Characidotrema spinovaginus  
(Paperna, 1973) comb. n.  
(Figs. 41–45)  

**SYNONYM:** Jainus spinovaginus Paperna, 1973.  

**HOST AND LOCALITIES:** Alestes nursei (Rüppell), Lake Albert, Uganda (type) and Volta Lake, Ghana.  

**SPECIMEN STUDIED:** MRAC 35.942 containing the holotype.  

**REMARKS:** The spinous vaginal aperture depicted by Paperna (1973) distinguishes _C. spinovaginus_ from all other species in the genus. The species is most closely related to _C. nursei_ as shown by the comparative morphology of the copulatory complex. However, it can be separated further from _C. nursei_ by possessing longer anterior projections on each end of the ventral bar. Paperna did not present drawings of the haptoral sclerites which are presented here for the first time (Figs. 42–45); measurements of the holotype fall within ranges presented by Paperna (1973). Although visible, the position of the vagina could not be determined in the twisted holotype. The microscope slide containing the holotype had numerous specimens of _C. nursei_, which could easily be separated from _C. spinovaginus_ by the morphology of the vagina.

Characidotrema undifera sp. n.  
(Figs. 52–59)  

**HOST AND LOCALITY:** Alestes cf. nurse (Rüppell), Mono River, Kolokopé, Togo.  

**TYPE SPECIMENS:** Holotype, USNM 79404; paratypes, USNM 79405, HWML 23553, INPA PA291-1, 2, MRAC 37.111.  

**DESCRIPTION** (based on 18 specimens): Body spindle-shaped, 401 (303–499) long; greatest width 163 (140–238) near midlength. Cephalic region with 2 terminal, poorly developed cephalic lobes; head organs, cephalic glands indistinct. Eyes equidistant, anterior pair frequently dissociated; eye granules ovate; accessory granules present in cephalic region. Pharynx spherical, 34 (27–41) in diameter. Peduncle rapidly tapering posteriorly; haptor indistinct, appearing as simple extension of peduncle. Ventral anchor with robust basal projection; anchor 26 (23–29) long, base 13 (11–14) wide. Dorsal anchor 30 (28–31), base 10 (9–12) wide. Bilateral arms of ventral bar elongate, well developed; posteromedial projection short, indistinct; ventral bar 15–16 long. Dorsal bar rod-shaped, 15 (14–16) long. Hook delicate, with curved point, subtriangular thumb; hook 18 (14–20) long; FH loop 0.5 Shank length. Cirrus comprising a curved shaft with subterminal angular bend, large base with well-developed anterior and posterior flanges; cirrus 34 (33–35) long. Accessory piece 15 (13–18) long, curved, variable. Gonads subovate; testis 72 (53–85) × 38 (27–39); ovary 123 (75–150) × 39 (28–45). Vagina dextroventral, a delicate sclerotized tube with slight distal enlargement; vitellaria comprising large cellular masses extending in 2 bilateral zones from level of seminal vesicle to peduncle.  

**REMARKS:** _Characidotrema undifera_ most closely resembles _C. zelotes_ sp. n. in the general morphology of the copulatory complex. It differs from _C. zelotes_ by possessing (1) larger haptoral sclerites, (2) an obvious subterminal bend of the cirrus shaft, and (3) a larger body size. The specific name is from Latin (_undifera_ = wave bearer), and refers to the shape of the cirral shaft.

Characidotrema zelotes sp. n.  
(Figs. 46–51)  

**HOST AND LOCALITY:** Alestes cf. nurse (Rüppell), Mono River, Kolokopé, Togo.
Type specimens: Holotype, USNM 79406; paratypes, USNM 79407, HWML 23554, INPA PA290-1,2, MRAC 37.110.

Description (based on 15 specimens): Body foliiform, 216 (169-250) long; greatest width 111 (92-136) near midlength or in posterior half. Cephalic margin rounded or with 2 poorly developed terminal lobes; cephalic glands, head organs indistinct. Eyes equidistant, posterior pair larger; eye granules elongate ovate to subcircular; accessory granules occasionally present in cephalic area and anterior trunk. Pharynx spherical, 13-14 in diameter. Peduncle almost nonexistent; haptor an extension of peduncle or trunk. Ventral anchor 16 (13-18) long, base 9 (7-10) wide; dorsal anchor 22 (20-23), base 8 (7-9) wide. Bilateral arms of ventral bar delicate, postero-medial projection elongate; ventral bar 10 (9-11) long. Dorsal bar 15 (14-17) long, rod-shaped, with slightly tapered ends. Hook 15 (13-17) long, delicate, with fine point, indistinct thumb; FH loop 0.5 Shank length. Cirrus 28-29 long, comprising a tapered shaft in shape of interrogation point, enlarged base with large proximal and distal flanges. Accessory piece 13 (11-14) long, club-shaped, apparently articulated to cirrus base. Gonads overlapping, ovate to pyriform; testis 49 (45-53) x 33 (25-40); ovary 72 (64-79) x 34 (29-38). Seminal vesicle bulbous; prostatic reservoir with heavy wall. Vagina unsclerotized, a simple tube opening dextroventrally at level of seminal vesicle; vitellaria well developed, absent from cephalic and haptoral regions.

Remarks: The closest relative of this species is Characidotrema undifera sp. n., based on comparative morphology of the copulatory complex and haptoral sclerites. Features distinguishing these species are given in the remarks for C. undifera. The specific name is from Greek (zelotes, = an emulator) and refers to the similarity of this diminutive species with the larger C. undifera.

Discussion

Soon after its proposal, Characidotrema Paperna and Thurston, 1968, was placed in synonymy with the neotropical Jainus Mizelle, Kritsky, and Crane, 1968, by Paperna (1973). This synonymy is not without merit since members of both genera possess many similar and somewhat unique characteristics: (1) robust bodies with poorly developed peduncles and haptors; (2) modified ventral anchor-bar complexes; (3) overlapping gonads; (4) strongly developed vitellaria; and (5) both taxa are restricted as parasites of characid fishes. The synonymy has gone unchallenged in the literature, with Gussev (1976a, b, 1978) using Paperna’s (1973) proposal of congeneric Neotropical and Ethiopian species as evidence for an ancient evolutionary relationship between the monogenean faunas of the 2 biogeographical regions. Indeed, Gussev (1976b) points, in part, to Jainus (Characidotrema + Jainus sensu stricto) as evidence that monogenean distributions are better explained by mechanisms of continental drift than by the “landbridge” theories of Darlington (1957).

Our resurrection of Characidotrema does not challenge Gussev’s ideas on monogenean biogeography. At most, it suggests that vicariant speciation has occurred since the breakup of Gondwanaland with speciation events in this group of Monogenea progressing at a similar or slightly slower pace that that of their hosts. Characidotrema and Jainus will likely be shown to be sister groups that developed from a common ancestral group present in Gondwanaland prior to separation of the African and South American continents.

Our rationale for recognizing Characidotrema rests primarily on information obtained from the reexamination of the type specimens of previously described species. All of these species as well as the new species described herein possess a relatively uniform morphology of the haptoral sclerites, which is fundamentally different from that of Neotropical species of Jainus. Although the ventral anchor is highly modified in both genera, that of Characidotrema species possesses a diagonally truncate or scoop-shaped point and an anterior projection developed from the deep root of the base. In Jainus species, the ventral anchor point is never developed into a diminutive scoop, although it is frequently modified into a bladelike structure; modification of the ventral anchor base usually includes both the superficial and deep roots. Further, Neotropical Jainus species do not show the development of bilateral anterior projections of the ventral bar found in Characidotrema species, although some do exhibit anteromedial and/or postero-medial processes. The hooks of Characidotrema species lack a well-developed thumb and dilated shanks, while those of Jainus species possess a protruding thumb and shanks may be dilated. Features of the internal organ systems of species of both genera are strikingly similar, but the vagina of Jainus...
is always sinistral and that of Characidotrema species is dextral.

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