Description of *Citharodactylus gagei* n. gen. *et* n. sp. (Monogenea: Gyrodactylidae) from the moon fish, *Citharinus citharus* (Geoffroy Saint-Hilaire), from Lake Turkana, Kenya

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Key words: ectoparasite; Africa; new species; new genus; parasite; viviparous.

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Abstract

A new genus and species of monogenean belonging to the Gyrodactylidae, *Citharodactylus gagei* n. gen. *et* n. sp. (Plathyhelminthes, Monogenea), is described from the gills of the moon fish, *Citharinus citharus* (Geoffroy Saint-Hilaire), a characiform fish collected from Lake Turkana in northern Kenya. The new viviparous genus can be readily distinguished from the six other gyrodactylid genera recorded from Africa and from the other viviparous genera within the Gyrodactylidae based on the morphology of the male copulatory organ (MCO), which consists of a muscular ovate organ with an opening onto the tegument through which the narrow tapered end of a sclerotised curved cone-shaped structure protrudes. The tegumental opening of the MCO is surrounded by a collar of short spines. Sequencing of the nuclear ribosomal DNA internal transcribed spacers 1 and 2, the 5.8S and the 18S rDNA genes and a comparison with the gyrodactylid species listed in GenBank confirmed the specimens are unique and do not match with any existing entry. When phylogenies for each genomic region were conducted (*i.e.* 0.064 gamma-corrected pairwise genetic distance based on a alignment of 1750 bp of the 1857 bp long 18S rDNA gene), the most similar match was that of *Afrogyrodactylus* sp. [= *A. girgifae* Přikrylová *et* Luus-Powell, 2014] from *Brycinus nurse* (Rüppell). The proposed name of the new parasite is *Citharodactylus* n. gen. which represents the seventh gyrodactylid genus to be found in Africa and, the 25th viviparous genus and the 32nd genus to be added to the Gyrodactylidae.

Introduction

Currently, there are six genera within the Gyrodactylidae described from African aquatic hosts, namely *Afrogyrodactylus* Paperna, 1968; *Diplogyrodactylus* Přikrylová, Matějusová, Musilová, Gelnar *et* Harris, 2009; *Gyrdicotylus* Vercammen-Grandjean, 1960; *Gyrodactylus* von Nordmann, 1832; *Macrogyrodactylus* Malmberg, 1957; and, *Mormyrogyrodactylus* Luus-Powell, Mashego *et* Khalil, 2003 (see von Nordmann 1832; Vercammen-Grandjean 1960; Paperna 1968; Luus-Powell et al. 2003; Přikrylová et al. 2009a). Of these, only *Gyrodactylus* is cosmopolitan, the remaining

genera are endemic to Africa. Of the African gyrodactylids, those belonging to *Gyrodactylus* are the most speciose with 33 species described to date (Table 1).

Characiformes are a highly diverse group of freshwater fish with nearly 2000 nominal species distributed globally; they represent a significant proportion of the freshwater fish fauna (Nelson 2006). The characiform fish fauna exhibits pronounced asymmetry in the distribution on the two sides of the Atlantic Ocean. The greatest diversity of characiforms is found in the Neotropics with 19 families and over 1700 species, while the African fauna is much poorer with only four families, *i.e.* the Alestidae, Citharinidae, Distichontidae and Hepsetidae, and 232 species (Nelson 2006; Van Der Laan et al. 2014). The Citharinidae is one of the less species-rich families in Africa with only eight species belonging to three genera. Citharinids, commonly known as lutefish, are distributed throughout much of tropical Africa, and constitute an important part of artisanal fishing catches (Weitzman and Vari 1998). Such is the case of the moon fish, *Citharinus citharus* (Geoffroy Saint-Hilaire), which is a commercially important species in several regions across Africa, where it represents a significant source of dietary protein for the local people (Ezenwaji and Ezenwaji 2009).

Although the number of fish monogeneans described from African hosts is increasing, only a few species are recorded from *C. citharus*. Of these, the accounts focus on two species, *i.e.* *Nanotrema citharini* Paperna, 1969 described from Ghanaian populations and, *Nanotrema niokoloensis* Musilová, Řehulková *et* Gelnar, 2011 (see Paperna 1969; Khalil and Polling 1997; Musilová et al. 2011) described from Senegal. In addition to these monogeneans, *C. citharus* is also a host to several myxozoans, *i.e*. to species of *Thelohanellus* Kudo, 1933 and *Myxobolus* Bütschi, 1882 (see Fomena et al. 2004, 2007), to the nematodes *Citharinella citharini* Khalil, 1967 and *Procamallanus leaviconchus* (Wedl, 1862) Baylis, 1923, to the paramphistome *Brevicaecum niloticum* McClelland, 1953, and to the acanthocephalan *Neoechinorhynchus africanus* Troncy, 1970 (see Khalil and Polling 1997).

The current study describes a new viviparous genus of gyrodactylid monogenean collected from the gills of *C. citharus* from Lake Turkana, Kenya, which was first reported as *Gyrodactylus* sp. 3 by Přikrylová et al. (2013) but never formally described. In the current study, both morphological and molecular analyses are applied to provide a formal description of the new species and the basis for erecting a new genus to accommodate it.

Materials and methods

Collection of host and parasite material

From two sampling trips made in September 2008 and September 2010, a total of 34 specimens of moon fish, *C. citharus* (mean total length 35.2 ± 5.9 cm; mean weight 608.3 ± 284.7 g), were collected from three sites on Lake Turkana, namely Kalokol (3°33' 29.1" N, 35° 54' 58.0" E; n = 8 specimens), Loiyangalani (2° 45' 43.18" N, 36° 41' 58.49" E; n = 12), and Todonyang (4° 27' 03.53" N, 35° 56' 37.08" E; n = 14). The fish were caught by local fishermen using seine nets and then immediately transported live to a mobile laboratory for screening for parasites. Fish were sacrified by severing the spinal cord just posterior to the cranium. Monogeneans removed from the gills were either prepared as whole mounts in ammonium picrate - glycerine (APG) (Malmberg 1970) or were fixed in absolute ethanol for subsequent molecular analyses. From the ethanol fixed specimens, their posterior attachment organs were excised using a scalpel blade and then subjected to proteolytic digestion as described in Paladini et al. (2009). The resultant hook preparations were arrested by adding a drop of APG and then by permanently sealing the edges with Pertex (Histolab Products AB, Gothenburg, Sweden) as applied in earlier studies (Rubio-Godoy et al. 2012). The corresponding anterior body portion of each excised gyrodactylid specimen was used for molecular characterisation. Prior to depositing the specimens in museum collections, the specimens in APG were transferred into Canada balsam following the procedure proposed by Ergens (1969).

101 ***Morphological analysis***

102 Morphometric analyses of the collected material were conducted at the Laboratory of Parasitology,
103 Department of Botany and Zoology, Masaryk University, Brno, Czech Republic and also at the
104 Aquatic Parasitology Laboratory, Institute of Aquaculture, University of Stirling, Stirling, United
105 Kingdom. The sclerotised elements within the posterior attachment organ were measured using 26
106 point-to-point morphometrics variables as described by Shinn et al. (2004) and Paladini et al.
107 (2011). A phase-contrast microscope Olympus BH2 fitted with a JVC KY-F30B 3CCD video
108 camera and KS300 (ver.3.0) (Carl Zeiss Vision GmbH, 1997) image analysis software were used to
109 obtain values for the analysed features. Images of the attachment apparatus and key anatomical
110 features were captured using a Zeiss AxioCam MRc digital camera mounted on top of an Olympus
111 BX51 compound microscope and using MRGrab 1.0.0.4 (Carl Zeiss Vision GmbH, 2001) software.

112 Drawings of the parasites were made under an Olympus BX51 microscope fitted with a
113 *camera lucida*. All measurements presented in the current study are expressed in micrometres,
114 unless otherwise stated, as the mean ± 1 standard deviation, followed by the range in parentheses.

115

116 ***Molecular analysis***

117 For molecular analysis, the ethanol fixative within each specimen tube was evaporated in a vacuum
118 centrifuge and then DNA from the parasite remaining in the tube was extracted using a DNeasy®
119 Blood & Tissue kit (Qiagen®) following the manufacturer's instructions. Amplification of the
120 internal transcribed spacer (ITS) region was conducted using primers ITS-1F (5'-
121 GTTTCCGTAGGTGAACCT-3') and ITS-2R (5'-TCCTCCGCTTAGTGATA-3') (Rokicka et al.
122 2007), while amplification of the 18S rDNA region was achieved by using a combination of the
123 primers SSU F (5'-GATCCTTCTGCAGGTTCACCTAC-3') and SSU R (5'-
124 AAGCTGGTTGATCCTGCCAGT-3') (Cunningham et al. 1995) with 18S F-INT (5'-
125 CTATTGGAGGGCAAGTCTGG-3') and 18S R-INT (5'-CCGAACATCTAAGGCATCA-3')
126 (Přikrylová et al. 2013), following the protocol detailed in Přikrylová et al. (2013). The sequencing

and phylogenetic analyses that were conducted for the for the current study are detailed within Přikrylová et al. (2013); the parasite material of interest in this altter study and re-evaluated here, is referred to as "*Gyrodactylus* sp. 3".

Results

Thirty-four wild moon fish were examined from the three sampling locations on Lake Turkana; only two fish (*i.e.* 5.8%) collected at Kalokol were infected with gill monogeneans (n = 22). The general morphology of the attachment apparatus and the presence of an embryo *in utero* indicated that the viviparous monogeneans belong to the Gyrodactylidae; however, the structure of the male copulatory organ (MCO) was unique among family members. Morphological and molecular descriptions of the parasite are provided below.

Class Monogenea Carus, 1863

Gyrodactylidae Cobbold, 1864

Citharodactylus n. gen. (Figs. 1 and 2; Table 2)

Body fusiform. Anterior end characterised by single pair of cephalic lobes, each bearing a spike sensillum and associated gland. Two excretory bladders present, in-line with the male copulatory organ (MCO). Eye spots absent. Pharynx spherical, consisting of a posterior and anterior bulb, the latter possessing two muscular rings surrounding a triangular mouth. Pharynx with eight short pharyngeal processes. Oesophagus branching into two simple, blind-ended intestinal crura that extend beyond the ovary. Viviparous, with up to two embryos *in utero*. MCO bulbous, ventrally positioned, close to the bifurcation of the intestinal crura. Central tube of MCO marked by three chambers of decreasing size, lying within a sclerotised, curved cone which tapers to a hollow tip which protrudes through an opening onto the tegument; the tegumental opening is surrounded by *ca.* 40 small, upwardly-facing, splinter-like spines. *Vesicula seminalis* located posterior to the

MCO. Vagina absent. Uterus positioned centrally, typically with at least an F1 embryo present. Single testis positioned posterior to the uterus; posterior to this is a single ovary. Opisthaptor delineated from the rest of the body, bearing a single pair of hamuli with a constriction between the shaft and point regions on each hamulus. Ventral bar simple, without antero-lateral processes and with a short, narrow, lingulate membrane. Dorsal bar thin, with prominent attachment points. Sixteen marginal hooks equally distributed around the periphery of the opisthaptor, each bearing a filament loop.

***Citharodactylus gagei* n. sp. (Figs 1 and 2; Table 2)**

Twenty-two specimens were used for the morphological study. Complete morphometric measurements of the body structures and opisthaptoral attachment structures are presented in Table 2. Body elongated, 616 (412–726) long, 90 (67–125) wide at the level of the uterus. Pharynx muscular bulb 33.8 (28.8–39.3) long and 30.8 (25.6–36.5) wide; anterior bulb of pharynx consisting of two thick muscular rings, with eight, short pharyngeal processes. Oesophagus short, branching into two intestinal caeca that pass down each side of the body and extend past the ovary. Excretory bladders present. MCO observed in 11 specimens; MCO bulb-shaped 23.5 (22.1–24.6) long × 20.1 (19.2–21.9) wide; positioned ventrally between the posterior pharyngeal bulb and the anterior part of the uterus; consisting of a principal conical spine originating from the centre of the bulb, surrounded by a series of *ca.* 40 small spines, 1–2 long and terminating as a tubular duct-like spine. There is a single testis; posterior to this is the ovary. Hamuli with long roots, 32.7 (28.1–35.1) long; with a thickened dorsal edge that tapers away from the dorsal bar attachment point to the apex of the root. Hamulus total length 66.8 (64.5–69.6); shaft 46.5 (43.4–49.1) long; point 26.3 (24.3–29.0) long and marked by a constriction between point and shaft regions. Ventral bar median portion thick, 6.5 (5.4–7.3) long, with no antero-lateral processes and with a narrow lingulate membrane, 6.7 (6.0–8.2) long. Dorsal bar simple, thin, 19.0 (14.7–23.8) long, with attachment points on hamuli, 8.9 (8.4–9.7) long. Sixteen marginal hooks of similar morphology, 30.7 (29.2–32.1) long.

Marginal hook sickle proper 5.1 (4.6–5.6) long, bearing filament loop approximately one sixth the length of the entire marginal hook structure. Sickle proper has: a narrow base with a flat underside; a narrow toe; a small additional curve on the inner face of the sickle between the base and shaft regions; a slightly forward projecting shaft region; a gracile sickle tip that projects slightly downwards and that terminates at a point beyond the limit of the toe; and, a narrow heel, that curves gently and extends approximately one third of the way up the length of the sickle proper.

Taxonomic summary

Type and only species: Citharodactylus gagei n. sp. (referred to as "*Gyrodactylus* sp. 3" *sensu* Přikrylová et al. 2013).

Type host: Moon fish *Citharinus citharus* (Geoffroy Saint-Hilaire) (Characiformes: Citharinidae), wild.

Site on the host: Gills.

Type locality: Lake Turkana, Kalokol, Ferguson's Gulf (3°33'33.56" N; 35°54'48.85" E).

Environmental conditions under which specimens were collected: Salinity and temperature, 2.5‰ and 27°C, respectively.

Type material: Holotype and three paratypes (acc. no. M-592) are deposited in the Helminthological Collection held at the Institute of Parasitology, Academy of Sciences of the Czech Republic, České Budějovice. A further two specimens (acc. nos. 2015.3.20.12-13) are deposited in the parasite collection of the Parasites and Vectors Section, The Natural History Museum (NHM), London, United Kingdom, and two additional specimens (acc. nos. M.T. 37789-90) are deposited in the parasite collection of the Royal Museum for Central Africa, Tervuren, Belgium.

Molecular sequence data: The 2536 bp ribosomal DNA sequence covering the 18S rDNA gene (1857 bp), ITS1 (295 bp), 5.8S gene (157 bp) and ITS2 (227 bp) is deposited in GenBank under accession numbers HF548669 (partial ITS region) and HF548670 (18S region).

General: Details of this species have been submitted to ZooBank (International Commission on Zoological Nomenclature (ICZN) 2012) with the Life Science Identifier (LSID) zoobank.org:pub: 7906DB59-27C5-4870-B961-261A4793AE74.

Etymology: The genus is named after the Latin name of the fish from which this parasite was recorded. The species is named after the local Turkana name of the host, *i.e.* "*gage*".

Differential diagnosis

Citharodactylus n. gen. can be differentiated from the other 25 viviparous genera within the Gyrodactylidae on the basis of the MCO (see Table 3). Species belonging to *Afrogyrodactylus* and *Diplogyrodactylus* possess elongated MCOs, however, neither are spined nor have outer spinous reinforcements (see Table 3). *Mormyrogyrodactylus* also has a muscular, tubular MCO bearing spines, however, the configuration of these are quite different to that of *C. gagei* n. sp. which possesses a sclerotised cone-shaped structure within the main MCO bulb. The hamuli of *C. gagei* n. sp. have a distinctive constriction at the junction between the point and shaft regions (Figs. 1a, 2c). This feature, however, is not restricted to the new genus described here; similar constrictions have been observed on the hamuli of *Afrogyrodactylus* sp. presented in Přikrylová and Luus-Powell (2014) and in Paperna´s drawings (1968), however, the hamuli of *Afrogyrodactylus* differ in that they have well-developed outer roots. Similar constrictions are seen on the hamuli of *Gyrodactylus nyongensis* Nack, Bilong Bilong *et* Euzet, 2005, but this species can be readily discriminated from *C. gagei* n. sp. by: the shape and arrangement of the MCO; by the larger size of the hamuli (64.5–69.6 for *C. gagei* n. sp. *vs* 150–166 for *G. nyongensis*); by a long, filamentous ventral bar membrane; and, by the morphology of their marginal hook sickles. *Gyrodactylus nyongensis* have short marginal hook shafts (Nack et al. 2005), which are, proportionally, about the half of the total length of the marginal hooks, whereas the specimens of *C. gagei* n. sp. have long shafts with marginal hook sickles that are only about 1/6 of the total length.

230 ***Molecular characterisation***

231 The PCR amplification of the two nuclear regions (ITS and 18S) from the three specimens of *C.*
232 *gagei* n. sp. resulted in identical sequence lengths of 679 (ITS1 + 5.8S + ITS2) and 1,857 bp (18S)
233 respectively. From the phylogenetic analyses that was conducted and detailed in Přikrylová et al.
234 (2013), *Afrogyrodactylus* sp. (= *A. girgifae* Přikrylová *et* Luus-Powell, 2014 collected from
235 *Brycinus nurse* (Rüppell)) emerged as a sister taxon to *Citharodactylus* n. gen. (*i.e. Gyrodactylus*
236 sp. 3 in Přikrylová et al. 2013). Here, the two genera differed by 112 bp (6%) across 1,860 bp used
237 for the alignment (0.064 gamma-corrected pairwise genetic distance under GTR + C + I model)
238 (Přikrylová et al. 2013). When the ITS sequences of both genera were aligned and compared using
239 MEGA6 (Tamura et al. 2013) they differed by 200 bp (28.5%) across the 701 bp alignment with
240 transitions and transversions included.

241

242 **Discussion**

243 *Citharodactylus gagei* n. gen. *et* n. sp. is a viviparous gyrodactylid with unique morphology,
244 supported by molecular analyses, and possesses a MCO that differs from the six other genera
245 described from Africa and from the other 31 genera within the Gyrodactylidae (Fig. 2e, Table 3).
246 The molecular analyses conducted by Přikrylová et al. (2013), which included species
247 representatives from ten gyrodactylid genera, confirmed the placement of *C. gagei* n. sp. (=
248 *Gyrodactylus* sp. 3 *sensu* Přikrylová et al. 2013) within the Gyrodactylidae as a sister taxon to the
249 genus *Afrogyrodactylus.*

250 Although the molecular analyses placed *Citharodactylus* n. gen. as a sister taxon to
251 *Afrogyrodactylus* the MCOs of both genera differ; those of *Afrogyrodactylus* species are typically
252 unarmed, elongated, muscular pouches, while that of *C. gagei* n. sp. has a sclerotised cone-shaped
253 structure housed within a muscular bulb, which is armed with a field of small spines around its
254 opening onto the tegument. Whether the MCO of *Citharodactylus* n. gen. also resembles that of

Gyreteroncus Euzet *et* Birgi, 1988, requires further investigation. Four species, three of which a name was ascribed to, were assigned to this genus by Euzet and Birgi (1988) in a conference abstract, however, these were never officially described and the genus is not valid and is considereda *nomen nudum*. The three "named" species in the abstract, *i.e. Gyreteroncus brienomyri* from *Brienomyrus niger* (Günther) and *G. caboti* and *G. chariensis* from *Marcusiensis cyprinoides* (L.), were said to possess an MCO "armed with numerous small spines". The fourth and unnamed species collected from *Polypterus senegalus* Cuvier, however, possesses an MCO without spines (see Fig. 3c in Přikrylová et al. 2009a). This observation was confirmed through the subsequent examination of *Gyreteroncus* sp. specimens collected from *P. senegalus* from Senegal. This species was subsequently transferred to a new genus erected by Přikrylová et al. (2009a) as *Diplogyrodactylus martini* Přikrylová, Matějusová, Musilová, Gelnar *et* Harris, 2009. The unpublished research notes linked to the conference abstract of Euzet and Birgi (1988) include sketches of the opisthaptoral armature of all four *Gyreteroncus* species, most notable are the marginal hooks which are of different sizes and sickle morphologies; this feature alone permits their ready discrimination from *C. gagei* n. sp.

A tubular armed MCO can be seen in egg-laying gyrodactylid genera, such as *Phanerothecium* Kritsky *et* Thatcher, 1977, and *Hyperopletes* Boeger, Kritsky *et* Belmont-Jégu, 1994 (see Kritsky and Thatcher 1977; Kritsky and Boeger 1991; Boeger et al. 1994; Bakke et al. 2007). In the other viviparous genera of Gyrodactylidae recorded from Africa, both tubular armed and non-armed MCOs can be found, such as in *Diplogyrodactylus* (see Přikrylová et al. 2009a), *Mormyrogyrodactylus* (see Luus-Powell et al. 2003) and in some undescribed *Gyrdicotylus* Vercammen-Grandjean, 1960 species (Prof. P.D. Harris, personal communication). Features of the MCO of each genera belonging to the Gyrodactylidae are summarised in Table 3.

The phylogenetic study of Přikrylová et al. (2013), based on two nuclear regions sequences, determined the relationship of *Citharodactylus* n. gen. (presented as *Gyrodactylus* sp. 3) to ten other genera within the Gyrodactylidae. Separate analyses of both ITS and 18S rDNA placed

281 *Citharodactylus* n. gen. as a sister taxon to *Afrogyrodactylus*. Both *Afrogyrodactylus* and
282 *Citharodactylus* n. gen. infect characiform fishes, specifically alestid and citharinid hosts,
283 respectively. The exact phylogenetic position of this cluster within the Gyrodactylidae, however,
284 would require a larger analysis with the inclusion of representatives from all taxa within the
285 Gyrodactylidae (see Table 3).

286 In the phylogenetic hypothesis, two of the African characiform families, the Citharinidae
287 and the Distichodontidae, form a sister group to all other characiforms (Ortí and Meyer 1997),
288 while the Alestide and the Hepsetidae appear to fit among the Neotropical families studied so far;
289 this is supported by morphological and molecular data (Ortí and Meyer 1997; Buckup 1998;
290 Calcagnotto et al. 2005). The study of Oliveira et al. (2011), however, proposes a more basal
291 position for these latter two families.

292 Apart for the pronounced asymmetry in the distribution of characiform fish fauna on both
293 sides of the Atlantic Ocean, there is also a disproportionate distribution of the African characiforms,
294 with *ca.* 95% of species belonging to the Alestidae and the Distichodontidae (*i.e.* 219 species),
295 while the remaining 13 species belong to the Citharinidae and to the Hepsetidae (Nelson 2006). As
296 characiform fish play an important role in African fisheries and ornamental communities, there is
297 much interest in researching their health status. Current knowledge regarding their parasite fauna,
298 however, is still limited with regards to their overall diversity on the continent.

299 Of the species within the Alestidae and Distichodontidae, the parasite fauna of 26 species
300 has been investigated; while only four belonging to the Citharinidae and Hepsetidae have been
301 studied (Khalil and Polling 1997). Alestid fish in Africa are parasitised by several monogenean
302 genera including a variety of oviparous (*e.g. Annulotrema* von Nordmann, 1832, *Characidotrema*
303 Paperna *et* Thurston, 1969 and *Afrocleidodiscus* Paperna, 1969) and viviparous (*e.g. Gyrodactylus*
304 von Nordmann, 1832 and *Afrogyrodactylus* Paperna, 1968) species (Paperna 1968; Paperna and
305 Thurston 1969; Thurston 1970; Ergens 1973a; Molnár and Mossalam 1985; Euzet and Birgi 1988).
306 The only monogenean genus that has been described from citharinids is *Nanotrema*, which includes

three species parasitising *C. citharus* (see Paperna 1969; Khalil and Polling 1997; Musilová et al. 2011). The current knowledge of parasites from characiform fish is still very limited, however, the description of another new viviparous gyrodactylid genus, such as *Citharodactylus* n. gen., suggests that parasite diversity on African fish is still highly unexplored.

Acknowledgements

The authors gratefully acknowledge the research grant from the Czech Science Foundation awarded to IP (project no. GBP505/12/G112), and The Royal Society research grant awarded to GP (project no. RG150640), which both partially supported the current study. The authors would also like to thank Professor Milan Gelnar (MU, Brno) for granting access to the facilities within Masaryk University enabling aspects of the morphological and molecular analyses to be conducted.

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Table 1. Genera and species belonging to the Gyrodactylidae (Monogenea) recorded from African hosts.

	Type-host	Type-locality	Reference
Afrogyrodactylus			
A. characinis	*Micralestes* sp.	Lake Volta, Ghana	Paperna 1968
A. girgifae	*Brycinus nurse*	Blue Nile, Sudan	Přikrylová and Luus-Powell 2014
A. kingi	*Micralestes acuditens*	Nwanedzi River, South Africa	Přikrylová and Luus-Powell 2014
Diplogyrodactylus			
D. martini	*Polypterus senegalus*	Mare Kountadala, Senegal	Prikrylová et al. 2009a
Gyrdicotylus			
G. galilaeus	*Xenopus laevis*	Lake Kivu, Dem. Republic of Congo	Vercammen-Grandjean 1960
Gyrodactylus			
G. aegypticus[1]	*Tilapia zillii*	Nile River, Egypt	El-Naggar and El-Tantawy 2003
G. alberti	*Clarias gariepinus*	Siba River into Lake Albert, Uganda	Paperna 1973
G. alekosi	*Clarias gariepinus*	Southern Mozambique	Přikrylová et al. 2012a
G. amphiliusi	*Amphilius atesuensis*	Lake Bosomtwi, Ghana	Paperna 1973
G. anabantii	*Ctenopoma muriei*	Swamp of south-east Kyoga, Uganda	Paperna 1973
G. camerunensis	*Clarias camerunensis*	Nyong Basin, Cameroon	Nack et al. 2005
G. cichlidarum	*Sarotherodon galilaeus*	Accra Plain and Akuse Lagoon, Ghana	Paperna 1968
G. clarii[2]	*Clarias gariepinus*	Siba River into Lake Albert, Uganda	Paperna 1973
G. ctenopomi	*Ctenopoma muriei*	unknown locality, Uganda	Paperna 1973
G. cyprinodonti	*Epiplatys* sp.[3]	Akuse Lagoon, Ghana	Paperna 1968
G. cytophagus	*Aplocheilichthys normani*	Akuse Lagoon, Adutor Lagoon, Ghana	Paperna 1968
G. ergensi	*Sarotherodon galilaeus*	Mare Simenti, Senegal	Přikrylová et al. 2009b
G. eyipayipi	*Syngnathus acus*	False Bay, South Africa	Vaughan et al. 2010
G. gelnari	*Clarias anguilaris*	Mare Simenti, Senegal	Přikrylová et al. 2012a
G. groschafti	*Clarias gariepinus*	Nile River, Egypt	Ergens 1973b
G. haplochromii	*Haplochromis elegans*	Lake George, Uganda	Paperna 1973
G. hildae	*Oreochromis niloticus*	Baro River, Ethiopia	García-Vásquez et al. 2011
G. ivindoensis	*Barbus holotaenia*	Mounianghi River, Gabon	Price and Gery 1968
G. kyogae	*Barbus prince*	East Lake Albert River System, Uganda	Paperna 1973
G. malalai	*Oreochromis niloticus*	Lake Turkana, Kenya	Přikrylová et al. 2012b
G. micralestis	*Micralestes* sp.[4]	Lake Volta, Ghana	Paperna 1968
G. nigritae	*Synodontis nigrita*	Niokolo Koba River, Senegal	Přikrylová et al. 2012a
G. nyanzae	*Oreochromis variabilis*	Lake Victoria, Uganda	Paperna 1973
G. nyongensis	*Clarias camerunensis*	Nyong Basin, Cameroon	Nack et al. 2005
G. rysavyi	*Clarias gariepinus*	Nile River, Egypt	Ergens 1973b
G. sturmbaueri	*Simochromis diagramma*	Lake Tanganyika, Zambia	Vanhove et al. 2011
G. synodonti	*Synodontis nigrita*	Niokolo Koba River, Senegal	Přikrylová et al. 2012a
G. thlapi	*Pseudocrenilabrus philander*	Okawango Delta, Botswana	Christison et al. 2005
G. thysi	*Simochromis diagramma*	Lake Tanganyika, Zambia	Vanhove et al. 2011
G. transvaalensis	*Clarias gariepinus*	Olifant and Elands Rivers, South Africa	Prudhoe and Hussey 1977
G. turkanaensis	*Clarias gariepinus*	Lake Turkana, Kenya	Přikrylová et al. 2012a
G. ulinganisus	*Oreochromis mossambicus*	Stellenbosch, South Africa	García-Vásquez et al. 2011

G. zimbae	*Simochromis diagramma*	Lake Tanganyika, Zambia	Vanhove et al. 2011
Macrogyrodactylus			
M. anabanti	*Ctenopoma murieri*	unknown locality, Uganda	Paperna 1973
M. clarii	*Clarias* sp.	Ethiopia	Gussev 1961
M. congolensis	*Clarias gariepinus*	Democratic Republic of Congo	Prudhoe 1957
M. ctenopomi	*Ctenopoma murieri*	Lake Albert system, Uganda	Paperna 1973
M. heterobranchii	*Heterobranchus logifilis*	River Agnéby, Ivory Cost	N'Douba and Lambert 1999
M. karibae	*Clarias gariepinus*	Lake Kariba, Zimbabwe	Douëllou and Chishawa 1995
M. latesi	*Lates niloticus*	Lake Volta, Ghana	Paperna 1969
M. polypteri	*Polypterus senegalus*	Gambia	Malmberg 1957
M. simentiensis	*Polypterus senegalus*	Mare Simenti, Senegal	Přikrylová and Gelnar 2008
Mormyrogyrodactylus			
M. gemini	*Marcusenius macrolepidotus*	Nwanedi-Luphephe Dams, South Africa	Luus-Powell et al. 2003

Footnotes: [1] *Nomen nudum* according to Harris et al. (2004); [2]Regarded as a junior synonym of *G. rysavyi* Ergens, 1973 in Paperna (1979); [3]This host is given as *Epiplatys fasciatus* in Paperna (1968), however, Fishbase (Froese and Pauly 2015) has no listing of this species as a valid species or as a synonym within its database. Fishbase, however, does list numerous species of which "*fasciatus*" forms part of the species root, therefore to avoid the propagation of misinformation, only the genus is referred to in the current study; [4]No further details are given in Paperna (1968, 1979).

Table 2. Morphological measurements (mean ± 1 standard deviation followed by the range in parentheses) of *Citharodactylus gagei* n. gen. *et* n. sp. from *Citharinus citharus* (Geoffroy Saint-Hilaire) collected from Lake Turkana, Kenya. Measurements are provided in micrometres and follow those detailed in Shinn et al. (2004) and Paladini et al. (2011).

Variable	***Citharodactylus gagei* n. gen. *et* n. sp. (n = 22)**
Total body length	616 ± 90.0 (412–726)
Total body width	90 ± 15.2 (67–125)
Total pharynx bulb length × width	33.8 ± 3.4 (28.8–39.3) × 30.8 ± 3.8 (25.6–36.5)
MCO bulb length × width	23.5 ± 0.8 (22.1–24.6) × 20.1 ± 0.9 (19.2–21.9)
Hamulus (H)	
H aperture	35.5 ± 0.9 (34.2–36.9)
H proximal shaft width	10.4 ± 1.2 (8.8–12.1)
H point length	26.3 ± 1.2 (24.3–29)
H distal shaft width	5.0 ± 0.3 (4.7–5.5)
H shaft length	46.5 ± 1.7 (43.4–49.1)
H inner curve length	5.7 ± 0.7 (5.1–6.7)
H aperture angle (°)	61.3 ± 0.7 (60.5–62.3)
H point curve angle (°)	24.3 ± 2.9 (21.1–27.7)
Inner H aperture angle (°)	70.0 ± 1.3 (68.2–71.4)
H root length	32.7 ± 1.6 (28.1–35.1)
H total length	66.8 ±1.3 (64.5–69.6)
Dorsal bar (DB)	
DB total length	19.0 ± 2.5 (14.7–23.8)
DB width	1.5 ± 0.3 (1.0–2.1)
DB attachment point length	8.9 ±0.6 (8.4–9.7)
Ventral bar (VB)	
VB total width	19.3 ± 1.0 (17.8–22.2)
VB total length	14.2 ± 2.1 (11.9–16.5)
VB process-to-mid length	2.2 ± 0.3 (1.9–2.7)
VB process length	n.a.
VB median length	6.5 ± 0.7 (5.4–7.3)
VB membrane length	6.7 ± 0.8 (6.0–8.2)
Marginal hook (MH)	
MH total length	30.7 ± 0.8 (29.2–32.1)
MH shaft length	25.2 ± 1.0 (22.5–26.5)
MH sickle length	5.1 ± 0.2 (4.6–5.6)
MH sickle proximal width	3.8 ± 0.2 (3.5–4.3)
MH toe length	2.2 ± 0.2 (1.9–2.2)
MH sickle distal width	3.4 ± 0.2 (3.0–3.8)
MH aperture	4.9 ± 0.3 (4.5–5.8)
MH instep/arch height	0.2 ± 0.1 (0.1-0.2)

Footnotes: n.a. = not available in that this species does not possess ventral bar processes.

Table 3. An annotated list of the 32 valid and 4 non-valid genera within the Gyrodactylidae Van Beneden *et* Hesse, 1863 providing brief details on the mode of reproduction, features regarding the male copulatory organ (MCO) and the armature of the attachment apparatus. Genera marked with an asterisk are found in Africa.

Genus	Validity	Mode of reproduction	MCO	MCO armature	Marginal hooks type	Hamulus roots	Accessory opisthaptoral sclerites present	Reference
Acanthoplacatus	Yes	Viviparous	Muscular non-eversible bulb	One apical spine + row of small spines	One	Single	No	Ernst et al. 2001
Accessorius	Yes	Viviparous	Bulbous	One apical spine + row of small spines	One	Single	Yes	Jara et al. 1991
Afrogyrodactylus	Yes	Viviparous	Muscular pouch	Spines absent	One	Inner and outer	No	Paperna 1968*
Aglaiogyrodactylus	Yes	Oviparous	Tubular copulatory organ sclerotised or not	Accessory piece comprised of one or more diverging branches associated with walls of copulatory sac	One	Inner and outer	No	Kritsky et al. 2007
Anacanthocotyle	Yes	Viviparous	Bulbous	One apical spine + row of small spines	One	No hamuli present	No	Kritsky and Fritts 1970
Archigyrodactylus	Yes	Viviparous	Bulbous	One apical spine + row of small spines	One	Inner and outer	Yes	Mizelle and Kritsky 1967
Citharodactylus n. gen.*	Yes	Viviparous	Muscular bulb with central sclerotised curved cone	Armed with numerous small spines	One	Single	No	present study
Diechodactylus	Yes	Viviparous	Bulbous	One apical spine + row of small spines	One	Single	Yes	Vianna et al. 2008
Diplogyrodactylus	Yes	Viviparous	Tubular	Spines absent	Two	Single	No	Přikrylová et al. 2009a*
Fundulotrema	Yes	Viviparous	Bulbous	One apical spine + row of small spines	One	Single	Yes	Kritsky and Thatcher 1977
Gyrdicotylus	Yes	Viviparous	Bulbous	Armed with a crown of 16-18 spines	One	Inner and outer	No	Vercammen-Grandjean 1960*

Gyreteroncus	Not valid	Viviparous	Not specified	Both armed (numerous small spines) and unarmed species	Three	Single	No	Euzet and Birgi 1988; Přikrylová et al. 2009a
Gyrodactyloides	Yes	Viviparous	Bulbous	One large apical spine and a row of smaller spines	One	Inner and outer	Yes	Bychowsky 1947
Gyrodactylus	Yes	Viviparous	Bulbous	One apical spine + row of small spines	Principally one	Single	No	von Nordmann 1832*
Hyperopletes	Yes	Oviparous	Pyriform	Two regions of numerous small rectangular spines	One	Inner and outer	No	Boeger et al. 1994
Ieredactylus	Yes	Viviparous	Bulbous	One large apical spine + row of smaller spines	Two	Single	Yes	Schelkle et al. 2011
Isancistrum	Yes	Viviparous	Bulbous	One apical spine + row of small spines	One	No hamuli present	No	de Beauchamp 1912
Laminiscus	Yes	Viviparous	Bulbous	One large apical spine + row of smaller spines	One	Inner and outer	Yes	Pálsson and Beverley-Burton 1983
Macrogyrodactylus	Yes	Viviparous	Bulbous	One apical spine + row of small spines	Two	Single	Yes	Malmberg 1957*
Metagyrodactylus	Yes	Viviparous	Eversible bulb	One apical spine + row of small spines	One?	Single	No	Yamaguti 1963
Micropolyclithrum	Question -able validity	Viviparous	Bulbous	Single spine	Not presented	Single	Yes	Skinner 1975
Mormyrogyrodactylus	Yes	Viviparous	Elongated muscular pouch	One long central spine + several spinelets	One	Single	Yes	Luus-Powell et al. 2003*
Neogyrodactylus Baugh, 1957 (syn. of *Metagyrodactylus*)	Not valid							Baugh 1957; Yamaguti 1963

Neogyrodactylus Prudhoe, 1957 (syn. of *Macrogyrodactylus*)	Not valid							Malmberg 1957; Prudhoe 1957
Nothogyrodactylus	Yes	Oviparous	Eversible cirrus	Accessory copulatory sclerites present	One	Single	No	Kritsky and Boeger 1991
Oogyrodactylus	Yes	Oviparous	Extrusible penis	Tip has ring of sclerotised tissue	One	Inner and outer	No	Harris 1983
Onychogyrodactylus	Yes	Oviparous	Variably coiled, eversible	Spine-like accessory sclerite	One	Inner and outer	No	Kritsky et al. 2007
Paragyrodactyloides Nunez, 1975 (syn. of *Gyrodactylus*)	Not valid							Nuñez 1975; Popazoglo and Boeger 2000
Paragyrodactylus	Valid	Viviparous	Bulbous	One apical spine + row of small spines	One	Single	Yes	Gvosdev and Martechov 1953
Paragyrodactylus Szidat, 1973 (syn. of *Gyrodactylus*)	Not valid							Szidat 1973; Popazoglo and Boeger 2000
Phanerothecioides	Yes	Oviparous	Variably coiled, eversible	Spines absent	One	Inner and outer	No	Kritsky et al. 2007
Phanerothecium	Yes	Oviparous	Eversible bulb which may be sclerotised	Numerous small spines	One	Inner and outer	No	Kritsky and Thatcher 1977
Polyclithrum	Yes	Viviparous	Bulbous	One apical spine + row of small spines	One	Inner and outer	Yes	Rogers 1967
Scleroductus	Yes	Viviparous	Bulbous	One large apical spine + row of smaller spines	One	Single	No	Jara and Cone 1989
Scutalatus	Yes	Viviparous	Bulbous	One apical spine + row of small spines	One	Single	Yes	Vianna et al. 2007

Swingleus	Yes	Viviparous	Bulbous	One apical spine + row of small spines	One	Single	Yes	Rogers 1969

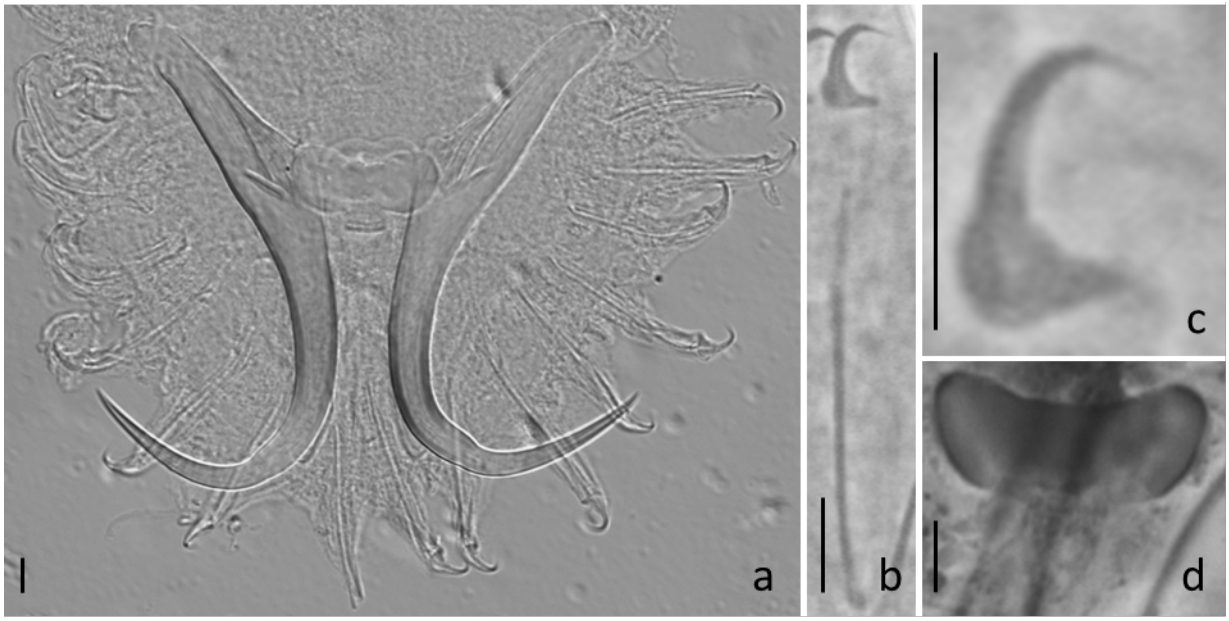

Fig. 1. Light micrographs of *Citharodactylus gagei* n. gen. *et* n. sp. from *Citharinus citharus* (Geoffroy Saint-Hilaire) collected from Lake Turkana, Kenya. a – opisthaptoral central hook complex showing the hamuli, the dorsal and the ventral bar (ventral view - with folded membrane); b – marginal hook; c– marginal hook sickle; d – ventral bar. Scale bars: a-c = 5 μm; d = 3 μm.

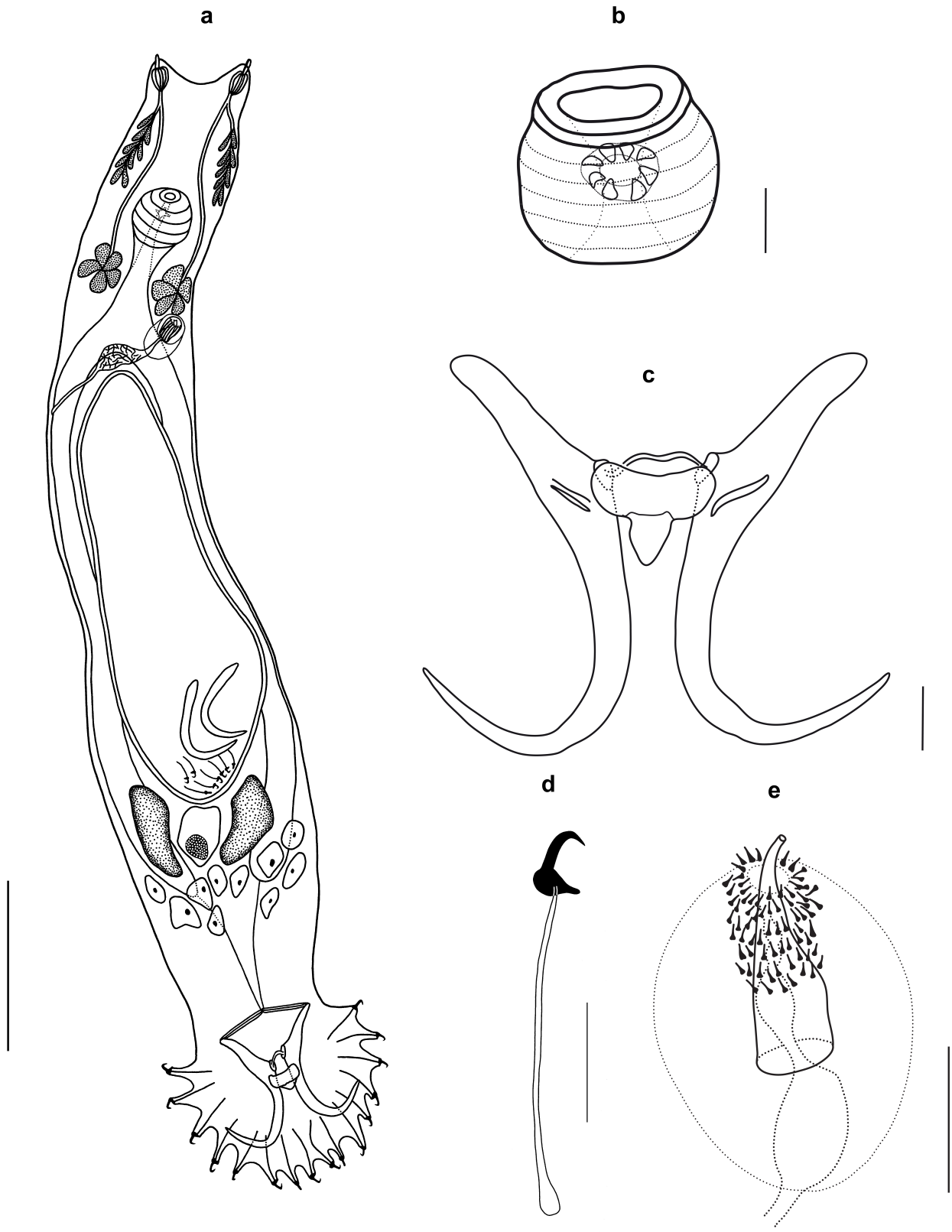

Fig. 2. Line drawings of *Citharodactylus gagei* n. gen. *et* n. sp. from from *Citharinus citharus* (Geoffroy Saint-Hilaire) collected from Lake Turkana, Kenya. a – composition of whole parasite; b – pharynx; c - opisthaptoral central hook complex; d – marginal hook; e - male copulatory organ. Scale bars: a = 50 μm; b-e = 10 μm.