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Checklist of the Fishes of the Kundelungu National Park (Upper Congo Basin, DR Congo): Species Diversity and Endemicity of a Poorly Known Ichthyofauna

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Abstract: The fish diversity of the Kundelungu National Park (KNP), one of the seven national parks of the Democratic Republic of the Congo, has never been thoroughly studied. This first checklist is presented based on a literature compilation and the study of historical (1939–1969) and recent collections (2012–2017). A total of 96 taxa are reported, including 64 native described species, one introduced species (*Poecilia reticulata*), 13 new species that await formal description and 18 possibly new species that require further investigation to verify their status. These taxa represent 39 genera and 17 families from the KNP including its Buffer Zone (BZ). Only six taxa, including five endemics, are known from the Core Zone on the Kundelungu Plateau (1300–1700 m alt.). At lower altitudes (800–1100 m), in the Annex Zone, 71 taxa, including 17 endemics, were found. Finally, 50 taxa, including 13 endemics and one introduced species, are known from its BZ. The fish fauna of the KNP is threatened by overfishing, destructive fishing practices, and habitat degradation due to mining pollution, and deforestation for agriculture on the river banks. The present study provides the much needed baseline data for the protection and conservation planning of this fish fauna, for which conservation suggestions are formulated.

Keywords: anthropogenic impacts; Endemism; Kundelungu Plateau; new species

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1. Introduction

The Kundelungu National Park (KNP) was created in 1970 to protect its abundant large mammal wildlife [1,2]. The park is located in the Haut Katanga Province, in the south-east of the Democratic Republic of the Congo (DR Congo). The protected area was extended from 2200 km^2 to 7600 km^2 in 1975, and now encompasses 2200 km^2 of Core Zone (CZ), located entirely on the Kundelungu Plateau (KP) and its immediate buttress region, and an Annex Zone (AZ) of 5400 km^2 covering most of the middle Lufira River Valley. These two zones correspond to the KNP *sensu stricto*; here referred to as KNP. However, the KNP is surrounded by a poorly defined Buffer Zone (BZ), which may extend at some places up to about 50 km beyond the outer limit of the two previous zones [1,2] (Figure 1). These

three distinct protection/conservation zones together are referred to as the KNP *sensu lato* (*s.l.*). Towards its north-western border, the KNP is connected to the Upemba National Park via the Lubudi-Sampwe hunting area [2], and together they form the Upemba-Kundelungu Complex [3].

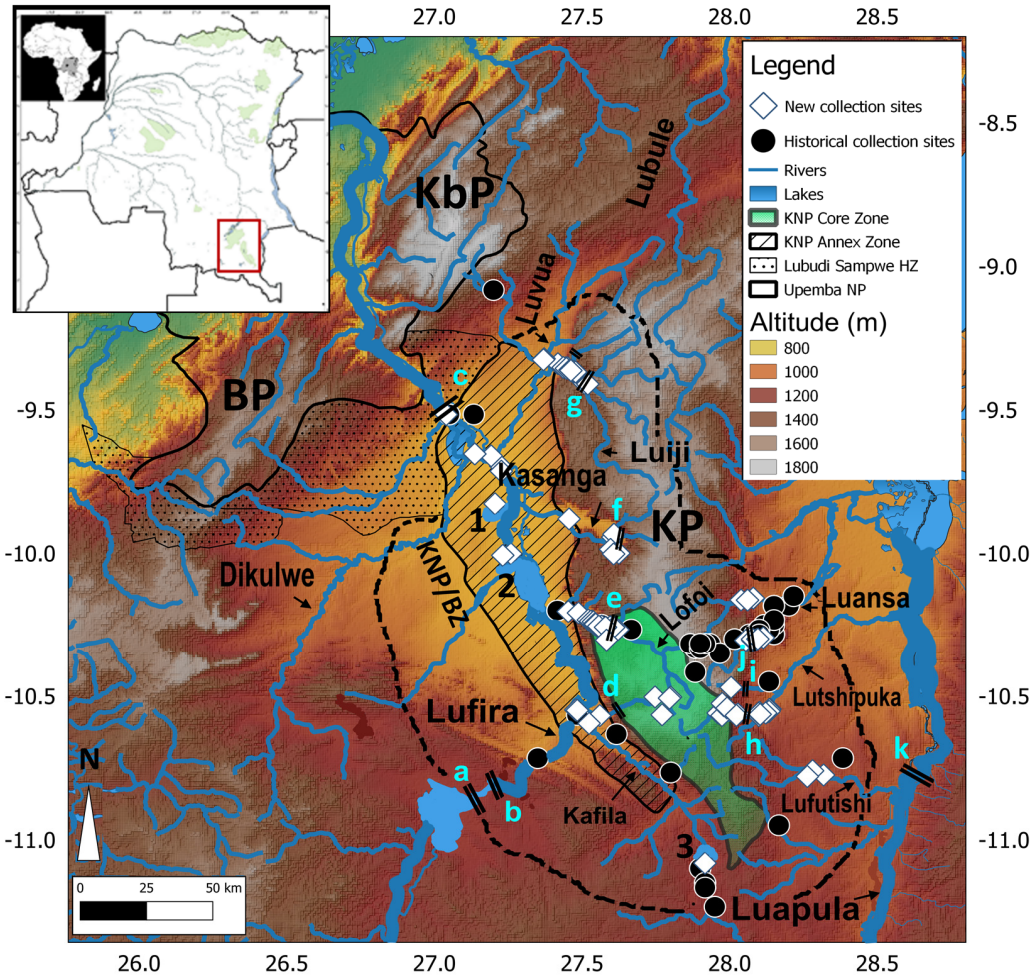

Figure 1. Map of the Kundelungu National Park (KNP, Haut Katanga, Democratic Republic of the Congo) and its surroundings: Falls are indicated by = and letters: (a) Mwadingusha, (b) Koni, (c) Kyubo, (d) Mwena, (e) Lofoi, (f) Kasanga, (g) Luiji, (h) Lutshipuka, (i) Masansa, (j) Luansa and (k) Mambilima. The three lakes sampled are (1) Bwaya, (2) Pungwe and (3) Lubanda. KP= Kundelungu Plateau (~1200 to 1700 m); KbP = Kibara Plateau (~1220 to 1850 m); BP = Biano Plateau (~1230 to 1630 m); CZ = Core Zone; AZ = Annex Zone and dashed line = Buffer Zone as defined in this study. See inserted legend for other details.

The Kundelungu Plateau (~9850 km^2) is the second largest of the five plateaux of the southern Congo Basin, after the Marungu Plateau [4,5]. However, the KNP covers only 2200 km^2, corresponding approximatively to one fifth of the KP total area, with the major part of it being mainly occupied by the cattle farm "Espoir", which was established in the 1940s [4]. The KP rises up to 1770 m above sea level [4,5] and is considered to be Katanga's water tower, containing several river sources. Some of these rivers drain east and are part of the Bangweulu-Mweru Ecoregion *sensu* Scott [6], while others drain west and are part of the middle Lufira (mLf) Basin [(upper Lualaba (uL) Ecoregion *sensu* Brown & Abell [7] ([4,5])] (Figure 1). A single river, the Lubule, drains the northern tip of the KP, running northwards parallel to Lake Moero and flowing into the Luvua River (not the one labelled in Figure 1) which is the outlet of Lake Moero [4]. All of the KP's rivers are intersected by one to four major falls, of which the Lofoi Falls (384 m) [8] is the highest in the Congo Basin.

The fish fauna of the uL Basin, i.e., the part of the Congo Basin from its source, through the Kamalondo Depression, up to its confluence with the Luvua River [7], has not been studied for quite some time. Most of the previous studies focussed mainly on the Kamalondo Depression [9–11], and the lower Lufira River, both situated in the Upemba National Park [9]. Studies on the Lufira River, a right bank affluent and one of the two major tributaries of the uL, focussed on its lower section [9], from the Kyubo Falls downstream to its confluence with the uL River in the Kamalondo Depression (Figure 1).

A few studies covered the upper Lufira Basin, mainly the man-made lakes of Mwadingusha and Koni, respectively from 1930 to 1934 and 1949 [12–14]. So far, the fish fauna of the middle Lufira Basin, in-between the Koni Dam upstream and the Kyubo Falls downstream (Figure 1), has not been well studied. Yet, it is an important river stretch that contains the AZ of the KNP and drains about 95% of the park. Some sporadic collecting efforts have been undertaken in the area, mainly between 1939 and 1969. The first collections made in the region were those by H.J. Bredo in 1939 [15]. Bredo's explorations were followed by other sporadic expeditions, the most important of which were: (i) the expeditions of the "Mission Piscicole du Katanga" between 1947 and 1949; (ii) the expedition of D.F.E. Thys van den Audenaerde in 1960 [16], and (iii) the expeditions of F. Malaisse between 1966 and 1969 [4]. Based on these collecting efforts, a total of 36 species were reported from the middle Lufira Basin. Due to the difficult access to the vast swampy region of the middle Lufira River Valley, the few fish collections made in the AZ of the KNP are mainly from areas near the major roads, i.e., the Minga-Sampwe Road, situated in-between the CZ and the AZ, and the Bunkeya-Kyubo Road, which is situated in the vicinity of the Kyubo Falls and forms the north-western limit of the AZ (Figure 1).

Although in the Bangweulu-Mweru Ecoregion, the main channel of the Luapula River and its tributaries in Zambia are relatively well explored [17–20], its affluents in the KNP, remain unexplored, with the exception of the Luansa River (Luanza *sensu* Malaisse [4]). Earlier ecologists, in particular Malaisse [4] and Balon & Stewart [21], were interested in the altitudinal gradient of two of the Luapula tributaries, the Luansa and the Luongo, and its influence on shaping fish distribution patterns. As a result, these rivers have been the only surveyed tributaries of the Luapula, until recently, despite the potential for existence of undescribed species, including narrow range endemics. The Luansa remained the only river of the KP for which its fish diversity was studied before our study. The expeditions of Malaisse (1976) [4] in the Luansa resulted in the identification of 18 species, of which only four are from the KP and the other 14 from lower areas in the plain of the Bangweulu-Mweru Ecoregion.

In this study, we present an overview of the species richness and distribution of the fishes of the KNP and its surroundings. After documenting the major threats to this fish fauna, suggestions for its protection and conservation are formulated.

2. Materials and Methods

2.1. Hydrography of the Study Area

The park is divided into two major ecoregions: the Bangweulu-Mweru, i.e., the middle and lower Luapula on the eastern flank of the KP and the upper Lualaba, exclusively the middle Lufira River on its western flank (Figure 1).

The Core Zone of the KNP covers the southern part of the KP (~1300–1700 m), a plateau that rose between 1300 and 1700 m, with steep buttresses of around 200 to 400 m high. It stretches out over the watershed of the two above mentioned ecoregions, and includes several headwater streams, some of them such as the Lofoi and Mwena rivers flowing westward into the middle Lufira Basin, and all belonging to the upper Lualaba Ecoregion [7]. Other headwater streams flowing eastwards, such as the Lufutishi in the middle Luapula Basin, or the Lutshipuka and its tributaries, the Masansa and Musipasi rivers flowing into the lower Luapula (Figure 1), all belonging to the Bangweulu-Mweru Ecoregion [6]. All these rivers, when flowing from the steep foothills of the KP, are intersected by one or more waterfalls.

The Annex Zone of the KNP covers the major part of the middle Lufira River (~800–1100 m), its vast swampy region, and associated marshes and lakes, such as Bwaya and Pungwe lakes. Most of the rivers of the KNP, including those of the CZ on the western slope of the KP are part of the middle Lufira Basin. The AZ covers the flood zone of the Kafila, Mwena, Lofoi, Kasanga, Luiji and Luvua rivers, all right bank tributaries of the mLf, and the Dikulwe, a left bank tributary of the mLf, the headwaters of which drain part of the south-eastern flank of the Biano Plateau and partially belong to the Upemba National Park.

The Buffer Zone covers up to 50 km adjacent to the AZ and the BZ [2]. It essentially covers, on the western side (WS) of the KP, the upper parts of the Kasanga, Luiji and Kafila rivers and the main channel of the middle Lufira River from the Koni Dam to its confluence with the Kafila. It also covers, on the eastern side of the KP, the middle parts of the Lufutishi, Lutshipuka and the upper and middle parts of the Luisé and its right bank tributary the Luansa.

2.2. Data Collection and Analyses

Data used for this checklist were taken from a variety of sources. These include: (i) a compilation of the information present in the scientific literature (e.g., [22–32]); (ii) collections maintained by the Royal Museum for Central Africa (RMCA); and (iii) dedicated surveys undertaken as part of the MbiSa-Congo I project (2012–2017). The occurrence of each species in the KNP and its surroundings was checked using the CLOFFA (Checklist of the freshwater fishes of Africa) [33–35], and the online species map tool in FishBase [36]. Specimens from historical collections of species that were not collected during our expeditions, or for which we assessed the identification as questionable, were reidentified.

The recent expeditions (2012–2017) were undertaken during the low-flow season (July–November) when the rivers were easily accessible. The sampled localities encompassed the entire CZ on the KP, the mLf, its tributaries and lakes in the AZ, and the rivers of the BZ (Figure 1).

A combination of fishing techniques was used, depending on habitats. They included monofilament gillnets, cast nets, dip nets, one or two ways fyke nets and angling. In a few instances rotenone was used for habitats such as rocky rapids that could not be efficiently sampled with more conventional methods (Figure A1 in Appendix A). Finally, some of the specimens were also bought from local subsistence fishers who use several fishing methods (Figure A2 in Appendix A).

At each locality, a subsample of the captured fishes, representing all the species collected at that site, was euthanised with Tricaine mesylate (MS−222) or clove oil. A representative number of specimens (up to five) was selected and photographed to capture the live colour pattern for each species. Fin clips were taken from the right hand pelvic and/or pectoral fin and stored in 95% alcohol for genetic studies. Voucher specimens were fixed in formalin (10%) in the field and afterwards transferred to 70% ethanol for long-term storage. All specimens from the recent surveys have been deposited into the fish collection at the RMCA. Reference collections have also been deposited at the "Unité de recherche en Biodiversité et Exploitation durable des Zones Humides" (BEZHU),/University of Lubumbashi, Lubumbashi and the "Centre de Surveillance de la Biodiversité", (CSB)/Kisangani, both in the Democratic Republic of the Congo.

Table A1 in Appendix B provides an overview of the fish diversity of the KNP subdivided into two major parts: (i) based on the major basins, i.e., the Lufira River (subdivided in the upper, middle and lower Lufira). The fish species diversity of the mLf was compared to that of the upper Lufira River [12–14], and the lower Lufira River [9,10]. Furthermore, the diversity of the Lufira and the KNP *s.l.* drained by the Luapula was compared to that of the whole Bangweulu-Mweru Ecoregion [9,20]; and of the Zambezian Headwaters Ecoregion [20,37]. (ii) Based on protection/conservation zones of the KNP which are the CZ, AZ (=KNP *sensu stricto*) and the BZ. However, in order to provide a more biogeographically meaningful discussion and to have well-defined protection/conservation hydrographic units, the boundaries of the three protection/conservation zones have been slightly modi-

fied. These modifications take into account the isolation of the upper parts of the rivers on the KP by their falls. Thus, the CZ encompasses only the parts of the rivers located on the KP above their major falls. For the same reasons, the AZ also includes the middle courses of rivers just downstream of these major falls on the western slope of the KP, even if some of these immediate buttress regions downstream of the falls are administratively recognised as part of the CZ. The BZ extends for approximately 30 km around the limits of the CZ and AZ, except at the northern end of the AZ, where the Lubudi Sampwe Hunting Zone, part of Upemba National Park, is directly adjacent to the AZ of the KNP (see the BZ delineation on Figure 1).

Identification certitudes were expressed by using the following open nomenclature qualifiers: sp., followed by a working name between simple quotation marks for specimens that do not correspond to any described species; cf., followed by a valid species name for specimens which differ somewhat from the corresponding species, but for which further investigation is needed, and 'complex' after the valid species name for a group of similar species characterised by unclear boundaries [38]. The term "taxa" was preferred to be used instead of "species" when referring to a number of taxonomic units composed of confirmed and unconfirmed species or only referring to the latter.

The validity of all species names and their spelling was verified in the "Catalog of Fishes" [39]. The family taxonomy follows Nelson et al. [40] and Fricke et al. [39]. The number of shared species and the Jaccard similarity index were used to compare the fish composition in the mLf with its neighbouring (sub)basins [20]. The Jaccard similarity index was calculated according to the formula $S = C/(N1 + N2 - C)$, with C, the number of shared species between the two basins, and N1 and N2, the total number of species for each of the two compared (sub)basins.

Institutional abbreviations: RMCA: the Royal Museum for Central Africa, Tervuren, Belgium.

Other abbreviations: ab: above falls; AZ: Annex Zone of the Kundelungu National Park; BZ: Buffer Zone of the KNP; CZ: Core Zone of the KNP; KNP: Kundelungu National Park; KP: Kundelungu Plateau; mLf: middle Lufira River; and *s.l.*: *sensu lato*.

3. Results

3.1. The Fish Diversity in the Kundelungu National Park (KNP) s.l.

The checklist for the KNP *s.l.* includes 64 described and valid native species, one introduced species (*Poecilia reticulata*), 13 new species that await formal description and 18 taxa that require further investigation regarding their status. These taxa represent 39 genera (one introduced), 17 families (one introduced) and 9 orders (Figure 2 and Table A1). These include 36 endemic taxa (12 described, 13 new and nine that require further investigations) which represent 9 families and 6 orders. Twenty-eight taxa are reported from the mLf Basin (upper Lualaba Ecoregion) on the western flank of the KP only, 15 taxa are reported from left bank tributaries of the lower and middle Luapula Basin (Bangweulu-Mweru Basin) on the eastern flank of the KP only and 49 species are shared between both basins. Cyprinidae [n = 17 taxa (18%), including three endemics], Cichlidae [n = 13 (14%), three endemics], and Kneriidae [n = 12 (13%), 11 endemics] are the three families that dominate the fish fauna of the park and represent about half of its fish diversity. They are followed by four families, which together account for about one third of the total species diversity, Amphiliidae [n = 9 species (9%), six endemics], Mochokidae [n = 8 (8%), five endemics], Clariidae [n = 6 (6%), no endemic]), and Mormyridae [n = 6 (6%), two endemics]. The remaining nine families are represented each by less than six species (Table A1).

Among the 95 native taxa, 48 were recorded from within the KNP *sensu stricto* (CZ and AZ), 21 in its BZ (including eight on the KP and 13 downstream of the KP) and 26 were shared between the KNP *sensu stricto* and the BZ. Firstly, the CZ, isolated by large falls bordering the KP, harbours only six native taxa: three endemic *Kneria* taxa (Kneriidae), one endemic *Amphilius* species, one endemic *Enteromius* species, and one widespread *Clarias* species (Table A1: CZ, Lfus & Ltus).

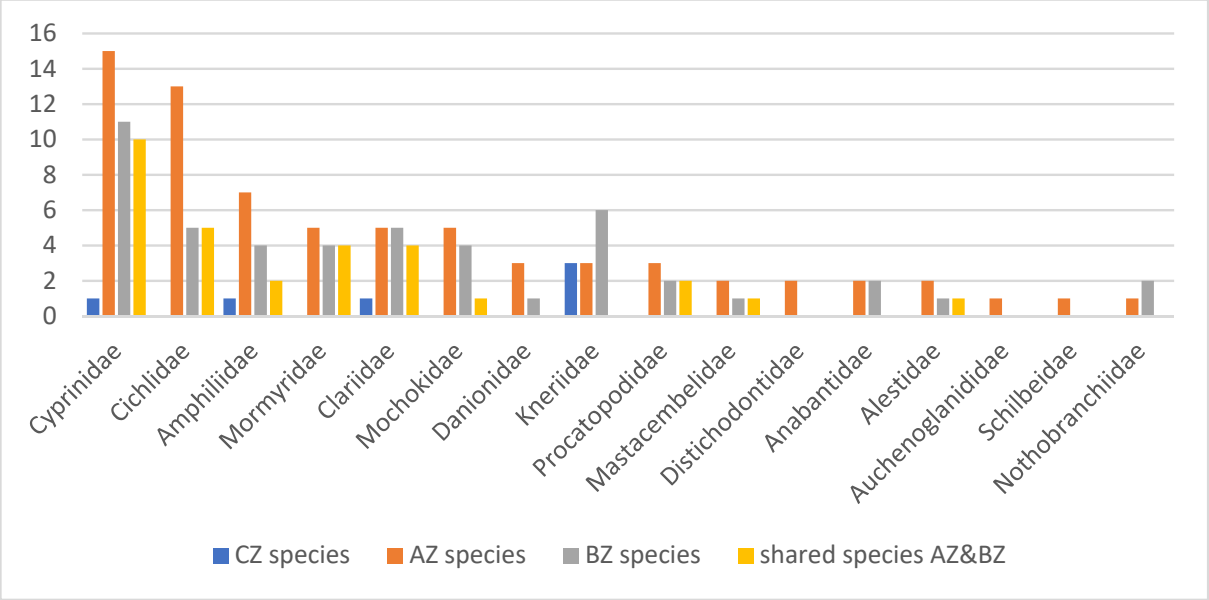

Figure 2. The native fish diversity per family and its distribution in the three conservation zones of the KNP. CZ, Core, AZ, Annex, and BZ, Buffer Zones.

Secondly, the AZ is richer in species harbouring 71 native taxa (17 endemics) distributed over 38 genera and 16 families. Two families, Cyprinidae (n = 15 species, 21%) and Cichlidae (n = 13, 18%) dominate its fish fauna in terms of species number. They are followed by Amphiliidae (n = 7, 10%), and Clariidae, Mormyridae, Mochokidae and Procatopodidae (n = 5 species each, 7%) (Table A1: AZ). The nine remaining families account for about 25% and are represented each by less than five taxa.

Finally, the BZ contains 49 native taxa distributed in over 29 genera and 14 families as well as one introduced species, *Poecilia reticulata*. Of this fauna, eight were collected on the KP and 41 below it. Of these species, 21 were collected in the BZ only among which 13 are endemic to it. The BZ is dominated by four families which account for about 60% of its fish fauna, i.e., Cyprinidae (n = 11 species), Kneriidae (n = 6), Cichlidae and Clariidae (n = 5 each) (Figure 2). The other ten families are represented each by less than four species (Table A1: mLf & BM columns).

3.2. Taxonomic Problems: Evidence for Hidden Species Diversity

During this study, numerous taxonomic problems were encountered. These problematic cases are discussed below.

3.2.1. Mormyridae

The Mormyridae is represented by species belonging to five genera in the study area. These fishes were only recorded from low altitude sections of the rivers (800–1100 m above sea level), and were absent from the KP on the high altitude reaches (1300–1700 m above sea level) (the differences in the altitude level represent the escarpments of the plateau). The genus *Cyphomyrus* Myers, 1960 is represented by two species, *C. discorhynchus* (Peters, 1852) and the endemic *C. lufirae* Mulelenu, Katemo Manda, Decru, Chocha Manda & Vreven, 2020. The other genera are represented by a single species each; *Marcusenius macrolepidotus* (Peters, 1852), *Petrocephalus catostoma* (Günther, 1866), *Pollimyrus stappersii* (Boulenger, 1915) and *Paramormyrops tavernei* (Poll, 1972). The populations for each of these species are allopatrically distributed as they were recorded on both sides of the plateau, except for *P. tavernei* which is only present in the middle Lufira Basin on the western side of the plateau. Interestingly, specimens from isolated populations of these species show some

notable variation in morphology and colouration pattern, which might point to geographic variation within the same species, or to the existence of undocumented species diversity.

3.2.2. Kneriidae

Although represented by only two genera, the family is the third most speciose in the KNP, with a total of 12 reported taxa, of which 10 belong to *Kneria* Steindachner, 1866 and two to *Parakneria* Poll, 1965. During our recent expeditions, *Kneria* was collected in almost all tributaries of the mLf and the Luapula on and below the KP. In contrast, *Parakneria* was only collected below the KP, and is more common in the mLf affluents, but extremely rare in the Luapula affluents.

During our field surveys in the KNP and its surroundings, 13 populations of *Kneria* were found. By their life colour pattern, none could be attributed to *K. wittei* Poll, 1944 nor to *K. stappersii* Boulenger, 1915 (Figure A3a–h) previously reported in the area. An ongoing integrative study using morphology and molecular (mtDNA: COI, CytB and ND2) data, revealed that these populations represent at least five new, with probably four additional putative species, and that both *K. wittei* and *K. stappersii* are restricted to their type basin outside the study area [for a more detailed argumentation see Supplementary materials (SM) Text SM: Kneriidae 1].

Two species of the genus *Parakneria* were previously known from the study area, *P. thysi* Poll, 1965 on the western and *P. malaissei* Poll, 1969 on the eastern side of the KP. Until now *P. thysi* (Figure A3m) was considered to be endemic to the rapids above the Kyubo Falls and to the stretch downstream of the Luvilombo Falls on the Luvilombo River [9,41]. Nevertheless, during our expeditions *P. thysi* was collected in five other tributaries of the mLf, i.e., the Dikulwe, Kafila, Mwena, Lofoi, and Luiji rivers. However, their conspecific status needs confirmation (for a more detailed argumentation see Text SM: Kneriidae 2).

Parakneria malaissei was originally described from the Luansa River, on the ES of the KP [42] in the vicinity of the KNP. According to Poll [42], the species occurs in the Luansa at an altitude between 1020 and 1050 m, which is below all the falls of the Luansa. However, Malaisse [4], who collected the types specimens, indicated this species occurs in the buttress zone of the KP between 1060 and 1310 m, which is in-between the first and third (the last one), most downstream falls on the Luansa. He named this zone as *Parakneria* zone due to their abundance in this zone. During our survey, sampling was done in the entire Luansa. Unfortunately, no specimens of *Parakneria* were found in the Luansa River, despite using various fishing techniques including the rotenone ichthyotoxin, which is often very effective in collecting these small-sized, fast swimming, and rheophilic species [43].

Two other fish species mentioned by Malaisse [4] from the same zone were indeed collected from this region, namely *Kneria* sp. 'luansaensis' (*K. wittei sensu* Malaisse [4]), and *Chiloglanis* sp. 'luansa-luisé' (*Chiloglanis* sp. *sensu* Malaisse [4] or *C. congicus* in the RMCA collection database). Malaisse [4] stated that those two species were less abundant than *P. malaissei* in this zone. In addition, the indigenous population of Kabiashia Village, the only village along the Luansa River, does not know *Parakneria*, what is curious given their otherwise accurate and extended knowledge of the fish fauna of the Luansa River, which is exemplified by the existence of vernacular names in the Bemba (Bantu) language for almost every species collected, even for small species such as *Zaireichtys brevis*. However, some rare specimens of *Parakneria* were collected from the Luisé River, of which the Luansa River is a right bank tributary, and from the Lutshipuka River (both lower Luapula Basin) (for a more detailed argumentation on their status see Text SM: Kneriidae 3). Nevertheless, *P. malaissei* seems to be either very rare or extinct in the Luansa River, or its report may be based on a doubtful location record. Indeed, Malaisse [4] might have confused *Parakneria* and *Kneria* as he sometimes mixed up both genera by giving them the same symbol and even referred to them jointly (see [4]: figure 37; [44]: figures 2.7.8). This point of view is further substantiated by the fact that the genus *Parakneria* was only described, and thus differentiated from the genus *Kneria*, by Poll in 1965 [41]. Therefore, Malaisse [4] may not have been aware of it during his fieldwork on the Luansa River from 1965 to 1968.

3.2.3. Cyprinidae

Cyprinidae is the most species-rich family in the Lufira Basin [9], the Luapula Basin [20], and the KNP. It also seems to be the family with the highest number of taxonomic problems in the KNP. The family is represented by three genera in the KNP *s.l.*, each containing some species with taxonomic uncertainties. Below, three problematic cases, currently under study are presented.

The first case concerns *Enteromius motebensis kamaiae* (David & Poll, 1937), a subspecies of *E. motebensis* (Steindachner, 1894) within the chubbyhead barb species complex [37,45]. The species of the chubbyhead barb species complex are characterised by the presence of a soft last unbranched dorsal fin ray, the usual lack of a distinct axial scale and a generally yellowish grey colouration with often a black spot at the base of the caudal fin [37,45]. These species are characteristic of cold water, high altitude streams [45]. *Enteromius m. kamaiae* was originally described as a subspecies, from the Kamaya River, a left bank tributary of the upper Lufira drainage [18]. Its taxonomic status has been unstable since. Without justification, the subspecies was elevated to species rank by Poll ([9]: table 1), and considered to be endemic to the upper Lualaba. Lévêque & Daget [46], however, synonymised it, without further justification, with *E. motebensis*, a view still held by some today [39,47]. This makes *E. motebensis* being composed of two distinct hydrographic populations, the first one currently only known from the headwater tributaries of the Marico, Crocodile and Steelpoort branches of the Limpopo River Basin in South Africa [37,45], identified in the past as *E. motebensis motebensis*, and the second one from the upper Lualaba River Basin, identified in the past as *E. m. kamaiae*, resulting in a disjunct distribution over a distance of about 2000 km.

On the KP, the *Enteromius* species of the chubbyhead barb species complex are common in all the sampled rivers on both flanks of the plateau. They are mostly limited to the head waters of these rivers, upstream of their major falls. Exceptionally, they also occur in the downstream vicinity of these falls, in the stretch of about five kilometres below the Luiji Falls (western side of the KP) and the Lutshipuka Falls (eastern side of the KP). Three new species, different from both *E. m. motebensis* and *E. m. kamaiae*, have been identified from the KP and its surroundings [48] (for a more detailed argumentation on their status see Text SM: Cyprinidae 1).

During our expeditions, *Labeobarbus* Rüppell, 1835 specimens were found in almost all the tributaries of the mLf, below their major falls, except for the Kasanga River. On the eastern side of the KP, *Labeobarbus* was collected only in the Luisé River and its right bank affluent, the Luansa (lower Luapula Basin), also below their major falls. All these fishes have a strongly ossified last unbranched dorsal fin ray and a yellowish-grey overall body colour, which, according to Banister [49], are the two key characters defining *L trachypterus* (Boulenger, 1915) and its junior synonym *L bredoi* Poll, 1948 (see [50] for discussion on this synonymy). However, based on the shape of the mouth, three mouth phenotypes were found: a *Labeobarbus*-mouth phenotype (rubber lips), a *Varicorhinus*-mouth phenotype (chiselmouth) and the last group with an intermediate-mouth phenotype [Figure A4e–g, and Vreven et al. [50], Vreven et al. [51] for a definition of the different mouth phenotypes] (for more details regarding these mouth phenotypes see Text SM: Cyprinidae 2). For now, all *Labeobarbus* specimens collected in the KNP *s.l.* with a rubber lip, chiselmouth and intermediate mouth phenotype are referred to as the *L. trachypterus* complex. This conclusion is based on the presence of a strongly ossified last unbranched dorsal fin ray, 28 to 32 lateral line scales (vs. 31 in *L. trachypterus*) and 12 circumpeduncular scales as in the description of *L. trachypterus* by Banister [49]. In addition, the overall yellowish-grey colour also corresponds to that of *L. trachypterus*.

Labeo rosae Steindachner, 1894, a southern African species [52], is reported from the mLf just downstream of Lake Koni based on two specimens (RMCA P-182678-679) [53]. Given some important morphometrics differences, however, the specimens of mLf are here referred to as *Labeo* cf. *rosae* (for a more detailed argumentation see Text SM: Cyprinidae 3). Although the scarcity of specimens in the historical collections may be due to the lack of intensive exploration of the mLf, their absence during recent collecting efforts might be due to their rareness or to their local extinction. Additionally, the possibility of this historical record representing a past, but not successful attempt of introduction of this species in the middle Lufira Basin as suggested by Van Steenberge et al. [53] is not to be excluded.

3.2.4. Danionidae

This family contains four species each in a different genus, *Chelaethiops* Boulenger, 1899, *Engraulicypris* Günther, 1894, *Neobola* Vinciguerra, 1895 and *Opsaridium* Peters, 1854, all living at low altitudes. However, only *Chelaethiops* case is detailed here. In fact, two species of the genus *Chelaethiops* are known from the upper Lualaba, *C. elongatus* Boulenger, 1899 originally described from Liranga Village, situated on the right bank of the middle Congo River just downstream of its confluence with the Ubangi River, and *C. congicus* (Nichols & Griscom, 1917) [54], originally described from Poko (Ubangi River, middle Congo). To date, both species are considered to be distributed throughout the Congo Basin [9,17,33], with *C. congicus* being reported from the Malagarasi Basin (Malagarasi-Moyowosi Ecoregion) [55] and the middle Lufira Basin [15,33] (upper Lualaba Ecoregion). Some specimens from the Kafila River, a right bank tributary of the upper part of the mLf, have originally been identified as *C. katangae* Poll, 1948, currently a junior synonym of *C. congicus* [23]. During our recent expeditions, specimens of *Chelaethiops* were collected in several affluents of the mLf, including the type locality of *C. katangae,* the Mwena River (for a more detailed argumentation see Text SM: Danionidae). An in-depth taxonomic study (morphology and genetics), however, is needed to solve the question of the validity of *C. katangae*.

3.2.5. Amphiliidae

In the KNP and its surroundings, this family is represented by three genera: *Amphilius* Günther, 1864, *Congoglanis* Ferraris, Vari & Skelton, 2011 and *Zaireichthys* Roberts, 1968. Only the genus *Amphilius* is present at both high (1300–1700 m), and low altitudes (800–1100 m). In contrast, the two other genera are only found at low altitudes on both sides of the plateau.

In comparison to the other two genera, the genus *Amphilius* is more species rich and abundant. The *Amphilius* specimens collected belong to two groups, i.e., the *A. uranoscopus* group found at both low and high altitudes on both sides of the KP and the *A. jacksonii* complex (AJC) found only at low altitudes on both sides of the KP.

Seven populations of the *A. uranoscopus* group were sampled in the KNP and its surroundings. A comparison of qualitative (life colouration and shape of the distal margin of the caudal fin) (Figure A5a–e), morphological and mtDNA data (COI, CytB and ND2) with those from taxa of the adjacent river basins, i.e., *A. cryptobullatus* Skelton, 1986 and *A. cubangoensis* (Pellegrin, 1936), or of those reported from the upper Lualaba and/or Luapula regions such as *A. kivuensis* Pellegrin, 1933, *A. grandis* Boulenger, 1905 and *A. uranoscopus* (Pfeffer, 1889), revealed the seven populations to belong to five new species for science [56] (for a more detailed argumentation see Text SM: Amphiliidae 1).

A recent revision of the *A. jacksonii* complex by Thomson et al. [32], in which morphological data were combined with the results of previous genetic research (Thomson, 2013) [57], split this species-group into six valid species. One of these, *A. frieli* Thomson & Page, 2015, is considered a widespread species known from the middle Luapula, upper Lualaba including the mLf, Chambeshi, and Lufubu rivers [32]. Specimens of *A. frieli* were collected in the rivers in the KNP and its surroundings, at low altitude downstream of the falls on both sides of the KP. The specimens of the Lofoi River (middle Lufira Basin) are

more similar to *A. frieli* than those of the Lutshipuka River (lower Luapula) (Figure A5f–g) (for a more detailed argumentation see Text SM: Amphiliidae 2). At this stage, however, we do not know if these differences are to be interpreted as intraspecific geographical variation or might point to a distinct species status for both populations studied. We noticed an overlap between various important diagnostic characters for several species of the AJC as provided by Thomson et al. ([32]: table 2). Thus, an additional study, including morphometric and genetics of all recently collected populations is needed to shed light on the taxonomic status of *A. frieli* of the KNP and its surroundings. Based on the distribution of most species of the AJC, and due to the wide distribution range attributed to *A. frieli* by Thomson et al. [32], it is not excluded that, *A. frieli*, throughout its distribution range, is composed of different allopatrically distributed cryptic species.

The genus *Zaireichthys* Roberts, 1968 includes the smallest African catfish species (<40 mm SL) [58,59]. Currently, one species; *Z. brevis* (Boulenger, 1915) has been identified for the KNP and its surroundings based on the RMCA collection database.

In the KNP *s.l.*, several populations of *Zaireichthys* were collected at low altitudes. Except for the population from the Luiji River, all populations correspond to what is defined as *Z. brevis* (*sensu* Roberts et al. [58]), based on their colour pattern and main counts. Due to its different colour pattern (Figure A5j); the population of the Luiji River is here identified as a new species for science (for a detailed argumentation see Text SM: Amphiliidae 3) and referred to as *Zaireichthys* sp. 'luiji'.

3.2.6. Mochokidae

The family is represented in the KNP *s.l.* by two genera, *Synodontis* Cuvier, 1816 and *Chiloglanis* Peters, 1868. The species *Euchilichthys royauxi* Boulenger, 1902, was described from the Oubangui River, the main right bank affluent of the middle Congo, at Banzyville (now Mobayi-Mbongo), and reported throughout the Congo Basin as far upstream as the Lufira Basin [9,60]. However, its identification from the mLf within the borders of the KNP seems to be an error (for more details see Text SM: Mochokidae 1). As such, it has not been retained as part of the KNP *s.l.* ichthyofauna.

The genus *Synodontis* contains three species among which two are endemic to the mLf in the Annex Zone, i.e., *S. lufirae* Poll, 1971 and the newly described *S. denticulatus* Ilunga, Abwe, Decru, Manda & Vreven, 2020 (for more details on its former identification see Text SM: Mochokidae 2).

Chiloglanis is the second most species rich of all African catfish genera just after *Synodontis* [59]. At the same time, it is morphologically the most diversified especially when considering the shape of the sucker disc and caudal fin; the latter being sexually dimorphic in some species [59]. Despite this diversity of forms, some species are difficult to distinguish from each other due to their similar colouration [59]. During our expeditions, *Chiloglanis* were collected on both sides of the plateau, in the middle sections of several affluents of the mLf and lower Luapula basins. For the KNP *s.l.*, *Chiloglanis* (5 species) is, after *Amphilius* (6 species) and *Clarias* (6 species), the most species rich of the catfish genera. To date, four species have been reported from KNP *s.l.*, i.e., *Chiloglanis congicus* Boulenger, 1920, *C. elisabethianus* Boulenger, 1915, *C. microps* Matthes, 1965 and *C. micropogon* Poll, 1952 [9], and at the RMCA collections database. However, based on the present study, only two valid species, *C. microps*, and *C. micropogon* are present, whereas the other two, *C. elisabethianus* and *C. congicus* do not exist in the area. The specimens attributed to these later two species represent two or three new species for science.

Chiloglanis congicus, was described from the Wagenia/Boyoma Rapids (middle Congo), based only on a single specimen [61]. The species was re-described by Poll [62] and its distribution extended to the Kinsuka/Kintambo Rapids (lower Congo). The species has also been identified from the Luansa (lower Luapula Basin) based on museum specimens collected in 1967. Additional specimens of *Chiloglanis* have been collected in the Luisé and its tributary the Luansa River during the present study. These specimens are similar to those of the Luansa River once identified as *C. congicus*. However, a comparison of

these specimens, referred here to as *Chiloglanis* sp. 'luansa-luisé' (Figure A6a–b′), with the holotype of *C. congicus* as well as two topotypic specimens from the Wagenia/Boyoma Rapids and three specimens from the Kinsuka/Kintambo Rapids show that *Chiloglanis* sp. 'luansa-luisé' morphologically clearly differs from both (for a detailed argument see Text SM: Mochokidae 3).

Chiloglanis elisabethianus has originally been described based on a holotype from the Lubumbashi River (middle Luapula Basin) [63]. Later, it has been reported from the upper Lualaba Ecoregion including the mLf and other tributaries of the Luapula ([9,20]; RMCA collections database. Several specimens similar to *C. elisabethianus* in colour pattern (Figure A6c–d′) and also possessing few mandibular teeth (6–9) arranged in one transverse row, were collected in Lufira and Luapula tributaries on both sides of the KP. A comparison of these specimens with the holotype and two topotypic specimens of *C. elisabethianus* shows that, despite their general similarity, the *Chiloglanis* specimens from the KNP *s.l.* cannot be unequivocally assigned to *C. elisabethianus*. Instead, those from the mLf are here identified as an undescribed species whereas those from the lower Luapula are identified as *C.* cf. *elisabethianus* pending an in depth study (for more details see Text SM: Mochokidae 4).

3.2.7. Auchenoglanididae

Within the KNP *s.l.* this family is only represented by the genus *Parauchenoglanis* Boulenger, 1911. These specimens seem to represent a currently unrecognised species, here referred to as *Parauchenoglanis* cf. *punctatus* (Boulenger, 1902) (for a detailed argumentation see Text SM: Auchenoglanididae). The species of the genus *Parauchenoglanis* were reviewed by Geerinckx et al. [29] who reduced the number of valid species from 18 to 9, among which six are from the Congo Basin and one from the Zambezi Basin [64]. However, no species has been reported from the Bangweulu-Mweru nor the upper Lualaba ecoregions by Geerinckx et al. [29], since, unfortunately, the historical collections from this area were not included in their study.

During our recent expeditions, *Parauchenoglanis* specimens were collected from several tributaries of the mLf.

At present, the specimens of the middle Lufira Basin are here referred to *P.* cf. *punctatus* due to their overall colour pattern similarity with that of the specimens of the *P. punctatus* species complex [64,65] (Figure A5i). However, a more elaborate study including a wider range of specimen sizes, from all-over the current distribution range of *P. punctatus*, will be necessary to establish the taxonomic status of the specimens of the mLf Basin.

3.2.8. Procatopodidae

Procatopodids are found in the plains on both sides of the plateau, i.e., in the AZ and BZ of the KNP, and comprise five species, all of them belonging to the southern African *Lacustricola* Myers, 1924 clade (*sensu* Bragança & Costa [66]; Bragança et al. [67]). Indeed, recently, the genus *Lacustricola* was found to be polyphyletic comprising two groups: the eastern Africa *Lacustricola*, which includes the type species *L. pumilus* (Boulenger, 1906), and the southern Africa *Lacustricola*, that are broadly distributed in the savannah environments of southern Africa and the upper section of the Congo Basin southern tributaries [66,67], and to which all species of the KNP *s.l.* belong.

In agreement with Bragança et al. [67] who recently evidenced the presence of hidden species diversity within the southern Africa *Lacustricola* clade, in the KNP two new species for science were found in the mLf: *Lacustricola* sp. 'lofoi' (Figure A7a), from the Lofoi and the Luvua rivers and *Lacustricola* sp. 'luiji' from the Luiji and Luvua rivers (for a detailed argumentation see Text SM: Procatopodidae).

The species *L. hutereaui* (Boulenger, 1913), first described from the Uele River (Oubangui River Basin), was considered to be a widespread species occurring from the Chad River Basin, in the north, to the Okavango, Zambezi rivers and Mozambique coastal river drainages, in the south. However, Bragança et al. [68] revealed that *L. hutereaui* represents a species complex and the species is probably restricted to the northern savannahs of

the Congo Basin, but there is no precise information on the species complex distribution and diversity in the Congo. In the KNP, a species belonging to the *L. hutereaui* complex, herein called *L.* cf. *hutereaui*, was recorded in the Lufira River and its right bank affluent the Kasanga (Figure A7e). *Lacustricola hutereaui* can easily be distinguished from other congeners, except *L. petnehazyi* (Nagy & Vreven, 2018), which was described for the upper Lufira Basin, by the presence of a conspicuous reticulate pattern on the margin of the flank scales and a barred caudal, anal and dorsal fins [69]. The taxonomic status of the different populations in the Congo Basin, including the KNP populations, will be reviewed in the future (Bragança, pers. data).

Specimens identified as *Lacustricola* cf. *johnstoni* (Figure A7c), were collected in the Kasanga River. This species could represent a new species, but this decision will need more comprehensive molecular and morphological studies. Bragança et al. [67] redescribed *L. johnstoni* (Günther, 1894), based on topotypic specimens from the Shire River, lower Zambezi, and presented a more inclusive haplotype analysis of *Lacustricola* taxa from southern Africa. The authors evidenced that in southern Africa and in the Congo, some specimens and populations that have been identified as *L. johnstoni* may well represent undescribed taxa. At the same time, it was well supported that *L. johnstoni sensu stricto* is a broadly distributed species occurring in the Zambezi, the Okavango and the Bangweulu system (Congo Basin). Therefore, the Kasanga River specimens are here referred to as *L.* cf. *johnstoni*, since they share with *L. johnstoni* the presence of two distinct dark bands on the medial portion of the male's anal fin, vertical bars on the male's caudal fin, an orange colouration on the female's anal, dorsal and caudal fins, and the bluish colouration on the male's flanks [67].

Finally, *L. moeruensis* (Boulenger, 1914) (Figure A7d), the type locality of which is Lake Moero in the Bangweulu-Mweru Basin, was found in the Kafila (KNP AZ, Lufira Basin) and Lutshipuka (KNP BZ, Luapula Basin) rivers. Despite sharing a similar colouration pattern with *L. johnstoni*, it can be distinguished from the latter by the presence of a comparatively shorter body and a more forward position of the dorsal fin, the first proximal radial of which is situated between the neural spines of vertebrae 13 and 14 (vs. 16 and 17 in *L. johnstoni*) [67].

3.2.9. Cichlidae

This family is the second most species rich of the KNP *s.l.*, only preceded by Cyprinidae. It is represented by 13 species known from the mLf, with 10 already previously reported from the KNP *s.l.*, including five endemics. Two of these endemics were already reported before, *Oreochromis salinicola* (Poll, 1948) from the BZ of the KNP [15] and *Orthochromis torrenticola* (Thys van den Audenaerde, 1963) from the AZ of the KNP [16]. The three remaining, instead, were collected for the first time during this study and are here preliminary named *Sargochromis* sp. 'lufira', *Coptodon/Tilapia* sp. 'pungwe' and *Pseudocrenillabrus* sp. 'lufira'.

Of the genus *Sargochromis* Regan, 1920, *S. mellandi* (Boulenger, 1905) is the only species known from the upper Lualaba and Bangweulu-Mweru. It was originally described from Lake Bangweulu, and has since been reported from throughout the Bangweulu-Mweru [17,70], and the upper Lualaba including the upper Lufira River [9,14,20]. During our recent expeditions, *Sargochromis* specimens were collected for the first time from the main channel of the mLf, its associated lakes and tributaries. These specimens were found to differ from all *Sargochromis* species currently known [70,71]; and referred to as *Sargochromis* sp. 'lufira' (Figure A8a) (for a more detailed argumentation see Text SM: Cichlidae 1).

The specimens of *Sargochromis* sp. 'lufira' from the lakes of the mLf differ somewhat from those of the rivers. The populations from the lakes are more slender, less blurry in terms of colour, and sometimes with fewer orange spots on the anal fin of the males. Comparison of the counts of these lake and river populations revealed no difference. Comparative analysis of the measurements, however, revealed a difference only at the anal fin base length, which is usually longer in the river populations, 18.3–20.2 (vs. usually

shorter, 16.3–18.9% L_S in the lake populations). Phenotypic plasticity (the ability of a single genotype to produce multiple phenotypes in response to variation in the environment) between river and lake populations is common in several cichlid fish species [72,73]. In one good studied case of *Astatotilapia burtoni* (Günther, 1894) the populations of the rivers are smaller than those from the lakes [74], which is the opposite of the *Sargochromis* of the mLf. However, cases exist for which the populations of the rivers are larger than those from the lakes. The cases of *Salariopsis fluviatilis* (Asso, 1801) (Freshwater blenny, Bleniidae) [75]; *Mastacembelus mastacembelus* (Banks & Solander, 1794) (Euphrates spiny eel, Mastacembeliidae) [76] and *Aphanius sophiae* (Heckel, 1847) (Persian Killifish, Aphaniidae) [77]. A thorough integrative study should be undertaken to clarify the status of these river vs. lake populations.

Three valid species of *Pseudocrenilabrus* Fowler, 1934 are currently known from the upper Lualaba and the Bangweulu-Mweru basins [35,78], *P. pyrrhocaudalis* Katongo, Seehausen & Snoeks, 2017, *P. nicholsi* (Pellegrin, 1928), and *P. philander* (Weber, 1897). The latter is a widespread species from the southern Kwazulu-Natal in South Africa northwards up to the southern Congo tributaries, including the KNP on both sides of the KP. However, *P. philander* has since long been recognised to represent a species complex [79,80].

During our recent expeditions, *Pseudocrenilabrus* specimens were collected in the mLf, all its tributaries and associated lakes and in the tributaries of the Bangweulu-Mweru. The specimens collected in the Bangweulu-Mweru tributaries are quite similar to what is currently referred to as *P. philander* in the upper Lualaba and Bangweulu-Mweru ecoregions (Figure A8i,j). Instead, for the mLf region another *Pseudocrenilabrus* taxon, here named *Pseudocrenilabrus* sp. 'lufira', has been collected (Figure A8g) (for a more detailed argumentation see Text SM: Cichlidae 2).

Finally, the tilapiinae cichlids of the KNP *s.l.* consist of representatives of three genera, i.e., *Coptodon* Gervais, 1853, *Oreochromis* Günther, 1889 and *Tilapia* Smith, 1840, each containing one or two valid species, respectively *Coptodon rendalli* (Boulenger, 1897), *Oreochromis mweruensis* Trewavas, 1983, *Tilapia sparrmanii* Smith, 1840 and *Tilapia ruweti* (Poll & Thys van den Audenaerde, 1965). Until 2013, *C. rendalli*, *T. sparrmanii* and *T. ruweti* were all placed in the same genus *Tilapia* [81,82]. Following a revision of the Haplotilapiinae; *T. rendalli* was transferred to the genus *Coptodon* [82]. Although they form two distinct phylogenetic clades, the morphological difference between *Coptodon* and *Tilapia* remains unclear. The only diagnostic feature is based on the shape of the vertical black bands on the sides of the body, which are Y-shaped close to the dorsal fin in *Coptodon* while they are straight in Tilapia (Schliewen, 2017, pers. comm) [83]. One tilapiinae specimen was collected from Lake Pungwe, one of the main lakes of the middle Lufira River. This specimen cannot be assigned to a particular genus without doubt. By its greyish colour, without apparent vertical black stripes, but with an orange band on its dorsal fin margin, it is similar to *O. mweruensis* (Figure A9b), a widespread species in the mLf [84]. However, the presence of a pharyngeal bone which is wider than long, with a toothed part longer than its non-toothed part, and with very strong bicuspid teeth underscores its similarity to *Coptodon/Tilapia*. The morphological difference between *Coptodon* and *Tilapia* is not clear cut, therefore without genetic analyses, we currently cannot correctly assign this specimen to one of these two genera. Nevertheless, this specimen, here named *Coptodon/Tilapia* sp. 'pungwe' (for a detailed argumentation see Text SM: Cichlidae 3), differs from both, all the *Coptodon* and all *Tilapia* species currently known from the KNP *s.l.* region.

4. Discussion

4.1. Contribution to Our Current Knowledge of the Fish Fauna Diversity of the Upper Lualaba and Bangweulu-Mweru Ecoregions

The present study is the first to provide a detailed inventory and a review of the distribution of the fish fauna of the KNP which is drained mainly by the mLf Basin. The occurrence of 36 species of the 47 previously reported from the mLf was confirmed, and 35 additional species are here reported for the first time. Among these additional species,

20 are new species, of which five *Kneria* and five *Amphilius* are to be described in coming papers. Two species, one Mochokidae and one Mormyridae, were described when this study was carried out [*Synodontis denticulatus* by Kasongo Ilunga et al. [85] and *Cyphomyrus lufirae* by Mukweze Mulelenu et al. [86], and five others are being described by other collaborators. Interestingly, all these new species are endemic to the KNP.

This study revealed that 11 species have wrongly been reported from the mLf. The specimens substantiating those reports either (i) belong to one of the new species for science, (ii) have been misidentified, or (iii) may have been mislabelled. With regard to the first category, specimens previously attributed to *Chiloglanis congicus*, *C. elisabethianus*, *Enteromius kamaiae*, *Kneria stappersii*, *K. wittei* and *Synodontis nebulosus*, are here identified, respectively as *Chiloglanis* sp. 'luansa-luisé-below falls ', *Chiloglanis* sp. 'lufira', *Enteromius* sp. 'kundelungu', *Kneria* sp. 'seegersi-lofoi-mwena-below falls ', *Kneria* sp. 'luansa-above falls', and *Synodontis denticulatus*. With regard to the second category, the specimens of *Brycinus imberi* and *B. macrolepidotus* turned out to be *B. lateralis*, a widespread species in the upper Lualaba, including the mLf [25] and specimens attributed to *Schilbe mystus* are *S. intermedius* as stipulated by De Vos [26] who stated that all Congo Basin identified *Schilbe mystus* are indeed *S. intermedius*, a widespread species in the mLf and the entire Congo Basin [26]. Finally, the last category corresponds to two species that have been reported to be present in the mLf, *Protopterus annectens* (Owen, 1839) and *Polypterus ornatipinnis* Boulenger, 1902 based on a single record of a single specimen each ([15], RMCA record). These species have not been found during our three years collection effort, not even in the rivers where the reported specimens supposedly were found. In addition, lungfishes are not known by the local fishermen from the mLf. The same is apparently true for *P. ornatipinnis*, known to be widely distributed throughout the Congo Basin including the lower Lufira River [87]. It therefore seems likely that a locality mislabelling has occurred during the cataloguing process. The intensive exploration of the mLf during this study now makes both the lower and middle Lufira basins the best explored sections of the Lufira Basin. The only part of the basin that remains less studied is that of the upper Lufira Basin. The exploration of the mLf has added ca. 33 species to the already very diverse fauna of the upper Congo, increasing the diversity of the upper Congo from about 301 [88] to about 334 species. Interestingly, this increase is almost entirely due to records of endemic species (28 taxa), which brings the number of upper Congo endemics from 45 [88] to 73, i.e., an increase of 62%. This confirms the upper Congo status as a hot spot for endemic species. In addition, certain rivers and their tributaries have only been partially or not at all explored. Considering the endemic character of the fauna of the Katanga Plateaux, which is linked to its geographic isolation, it is possible that the number of endemic species will increase with a more intense exploration of other tributaries and sub-tributaries of the mLf such as the upper part of the Luvua Basin (its tributaries flowing from the Kibara and Kundelungu plateaux), and the upper part of the Dikuluwe (flowing from the Biano Plateau).

From the Luapula Basin tributaries within the KNP *s.l.*, 35 species were previously recorded, mainly from the Luansa and Luisé rivers [4], and based on the RMCA collection database, from the Musipasi and Lufutishi rivers. The present study recognizes 44 taxa, 30 of which have previously been recorded, and 14 represent new records. Specimens of five of the previously reported species turned out to be new taxa. In addition, three new taxa were newly collected. All these new taxa are endemics, in addition to three endemics described from the area before this study.

The unconfirmed species either represent small-sized species from swampy areas, which we did not collect or are misidentified. Species such as *Enteromius haasianus* (David, 1936), maximum size of 3.2 cm SL, occurring in swamp and floodplain habitats [37], and *Ctenopoma multispine* Peters, 1844 and *Microctenopoma intermedium* (Pellegrin, 1920), reported from the Sange River in the Musipasi Floodplain, were not collected in this study probably because of the small mesh size nets (dip net) that caught some small fishes were not used in each sampling site or because the right habitat was not sampled. Sampling on the eastern side of the KP was limited to the upper and middle parts of rivers; hence swamps

and floodplains were not explored, except for the Lufutishi swamp. The records of four other species in the Luapula Basin tributaries were based on misidentifications. This is the case for specimens previously identified as *Amphilius uranoscopus*, *Enteromius kamaiae,* and *Kneria wittei*, which represent four new taxa, i.e., *Amphilius* sp. 'luansaensis', *Enteromius* sp. 'kundelungu', *Kneria* sp. 'luansa-ab' and *Kneria* sp. 'lutshipuka-below falls'. Furthermore, some specimens previously identified by Malaisse [4] as *Barbus oxycephalus* Boulenger, 1915 [a current junior synonym of *Labeobarbus stappersii* Boulenger, 1915, following Banister [49]] were re-identified as *L. trachypterus*.

This improvement in our knowledge of the fish species diversity and distribution for the area is not surprising, especially for a region with an exceptional habitat diversity and a fish fauna that has never been extensively studied. In African freshwaters, new species are discovered even in subbasins considered as among the best studied [89]. This is mainly due to misidentifications and the lack of further exploration of specific environments, such as small streams and swamps, or of certain fish groups due to the collecting methods and fish gear used [89]. This is the case, for instance, for the southern Africa region, which is considered as one of the best explored of Africa [37]. However, 32 new species [89] have been described since the publication of the second edition of the "Complete Guide to the Freshwater Fishes of Southern Africa" by Skelton [37], and many more are still to be described [90]. The same holds true for the Lualaba-Upemba-Lufira region where Poll [9] reported a total of 182 fish species, but for which Katemo Manda [88], after five years of extensive exploration, reports a total of about 235.

4.2. Ichthyobiogeography of the Rivers of the KNP s.l.

The KNP *s.l.* contains a high diversity of aquatic habitats, ranging from small, torrential, highland altitude streams on the KP (~1300–1700 m) with rapids, large falls on both flanks of the plateau, to rapids, pools, swampy areas, lakes and large rivers in the lowland areas of the park (~800–1100 m). Habitat diversity, flow speed and fragmentation by physical and/or related ecological barriers are known to be important factors driving fish diversity and endemicity [91–93]. With a total of 14 taxa belonging to four families, the rivers of the high-altitude zone in the CZ and BZ on the KP are species poor. This is probably due to the relatively cold temperature (15–20 °C, vs. 19.5–29.5 °C at lower altitudes [4]) and the isolation by large falls on both sides of the plateau, which form a barrier to fish dispersal. This relatively poor fish fauna contains 13 (86%) endemic taxa belonging to three fish families (Amphiliidae, Cyprinidae and Kneriidae). Five of these are found in the CZ, six in the BZ and two shared between both zones (Figure 3a; Table A2b,c). Seven of these endemics are restricted to a single subbasin of the plateau above the falls (Table A1). In some cases, two neighbouring basins each have a distinct species, with different phylogenetic affinities. This is for example the case of *Amphilius* sp. 'luansaensis' of the Luansa River which is more related to the *Amphilius* species of southern Africa, while *Amphilius* sp. 'muriellae-masansa-above and below falls', from the Masansa River, a neighbouring basin of the Luansa is closely related to other Luapula-Moero species [56]. This shows a different colonisation history between these two neighbouring basins, and possibly limited dispersal capacities for these species. In contrast, two species, *Enteromius* sp. 'kundelungu-ab' and *Kneria* sp. 'katwei-ab', are restricted to the KP above the falls, but distributed, respectively in four and three neighbouring subbasins above the falls. This is probably linked to the dispersal capacity of these species, which have already been recognized to have the ability to disperse on both sides of the plateau via its marshy areas [4].

In terms of dispersal capacities, three endemic species (*Amphilius* sp. 'murielae-masansa-above and below falls', *Amphilius* sp. 'luijiensis-above falls' and *Enteromius* sp. 'luiji') even if they do not disperse in nearby basins on the plateau, are found above and below the falls (above and below the plateau). In this case, the dispersal from up to downstream the falls is a more plausible hypothesis. However, the dispersal from down to upstream cannot be ruled out, in the Masansa River for example. Indeed, the southern part of the KP has a few rivers which descend the KP without being interrupted by large

waterfalls. This is the case of the Lufutishi, a basin close to that of Lutshipuka/Masansa which could have facilitated the colonisation by fish coming from downstream. However, to examine this hypothesis it will be necessary to explore the upper part of the Lufutishi, and also to better understand the dispersal pattern of the species composing the *Amphilius* cf. *cryptobullatus* complex, including *Amphilius* sp. 'murielae-masansa-above and below falls' by the use biogeographic tools such as haplotype networks.

The two remaining species, *Clarias dumerilli* and *C. theodorae*, are non-endemic air breathing and walking catfishes with a high dispersal capacity [24,59]. The former is the only species shared between all three zones, whereas the latter is shared between the AZ and the BZ (Figure 3a; Table A2b,c). Strangely, these two high dispersal species, are not found in all rivers of the KP. *Clarias dumerilli* even if present in all the three main basins explored from the western flank of the KP, was not collected in the two basins explored on the eastern flank [Lutshipuka, and its two tributaries (Masansa and Musipasi), and the Luansa rivers]. This makes this species, on the scale of the CZ, only known from Lofoi River on the western flank. On the eastern flank, *C. dumerilli* was only collected downstream from the falls (at the buttress of the plateau) in the Luansa River. Surprisingly, in the Luansa River above the falls, only *C. theodorae* was collected. It is not clear why these catfishes did not colonise all these nearby rivers, especially the Lutshipuka River, where not a single *Clarias* species is known from, while *Enteromius* sp. 'kundelungu' and *Kneria* sp. 'katwei' disperse in all the three basins.

The lowland sections of rivers on both sides of the plateau are more species rich, with 71 species reported from the mLf Basin in the AZ and 44 from the middle and lower Luapula tributaries in the BZ (Figure 3a; Table A2b,c). The AZ shares only one species with the CZ but shares nearly one third of its fish fauna with the BZ (Table A2b,c).

The relatively high endemicity level on the KP, but also on both sides of the KP in the lowland plains, may be the combined result of isolation by large waterfalls [92,93] and the geological stability of the plateau since its formation preventing subsequent river captures [94].

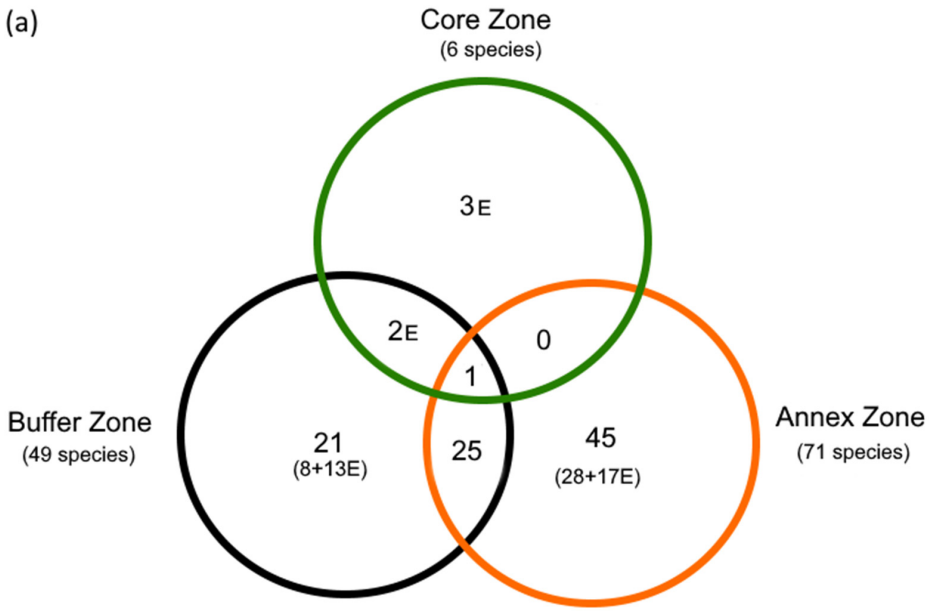

Figure 3. *Cont.*

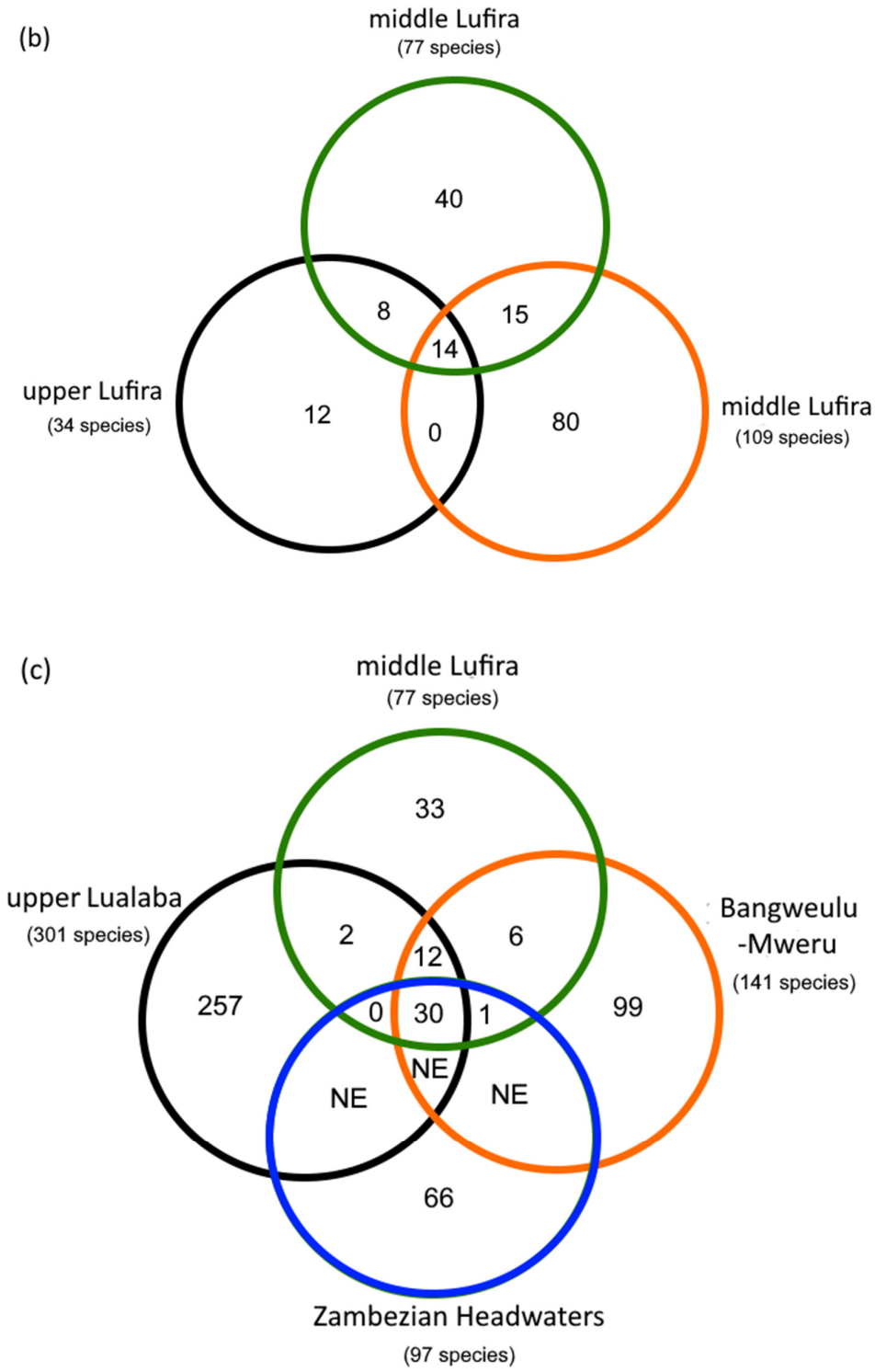

Figure 3. Venn diagrams showing the number of shared and non-shared species in (**a**) the three conservation zones of the KNP; (**b**) the three parts of the Lufira Basin; and (**c**) the upper Lualaba Ecoregion which include the middle Lufira Basin and its two nearby ecoregions. E, endemic species; and NE, not evaluated.

The mLf (77 species) was shown to be less species rich than the lower Lufira Basin (105 species, based on Poll [9] and Banister & Bailey [10]). This is probably due to its isolation from the lower Lufira River by the Kyubo Falls, which limits further upstream fish dispersal. As a result, the mLf only shares 37.7% (29 species) of its fish fauna with the lower Lufira Basin (J index 0.18) and 57.1% (44 species) with the entire upper Congo

Ecoregion (J index 0.13) (Table A2; Figure 3b,c). Surprisingly, the shared number of species between the mLf and the lower Lufira basins (lLf; 37.7%; J index 0.18) is slightly smaller than the number shared with the Zambezian Headwaters (ZH; 40.3%; 31 species, J index 0.22). It even shares more species with the Bangweulu-Mweru (63.6%; 49 species, J index 0.29) (Table A2; Figure 3b,c). The species shared between mLf on the one hand and the lower Lufira Basin and the upper Congo on the other, are widely distributed in Africa, such as *Clarias gariepinus, C. theodorae* [24]) and *Schilbe intermedius* [26], or widely distributed in the Congo Basin, such as *Distichodus maculatus* [9]. In contrast, the species shared between the mLf and the Bangweulu-Mweru and the Zambezian Headwaters are in most cases species common in some major southern African basins, including the Zambezi and the Okavango, and their natural distribution in the Congo Basin is limited to the High Africa part of the basin. These are, for instance, *Coptodon rendalli, Tilapia sparmanii* [95], *Serranochromis macrocephalus*, *S. robustus, S. thumbergi* (Cichlidae) [37], *Brycinus lateralis* (Alestiidae) [25], *Enteromius radiatus, E. unitaeniatus* (Cyprinidae) [37], *Clarias ngamensis,* and *C. stappersii* Boulenger, 1915 (Clariidae) [24]), which are all typically High Africa fishes *sensu* Roberts [96]. The shared fauna between mLf, Bangweulu-Mweru and Zambezi Headwaters is indicative of the paleo-connections between these basins. Indeed, both the paleo-Lufira and paleo-upper-Luapula were for a long time flowing south-eastward, and were connected to Zambezi River via the paleo-Chambeshi until at least the early Pleistocene (~1.8 Ma) [97]. These past connections facilitated the faunal exchanges between the mLf, the Luapula and the Zambezian Headwaters [20,94]. In addition, fish faunal exchanges between the Lufira Basin and the Zambezian Headwaters may still be possible due to the close proximity of the sources of the upper Lufira and the Kafue (upper Zambezi) rivers as reported by Bell-Cross [98] via inundated areas during heavy rainy seasons.

4.3. Protection/Conservation Issues

Currently, of the 94 native species reported from the KNP, only 60 are assessed in the IUCN Red List of Threatened Species (Table A1; Figure 4). Of the 34 described species that were not assessed, a few (*Chiloglanis micropogon* and *Clarias stappersii*) have not been evaluated for unknown reasons, while others (i.e., *Amphilius frieli* Thomson & Page, 2015, *Congoglanis sagitta* Ferraris, Vari & Skelton, 2011, *Cyphomyrus lufirae*, *Nothobranchius chochamandai* Nagy, 2014, *Nannocharax dageti* Jerep, Vari & Vreven, 2014, and *Synondontis denticulatus* were described after 2010 when the last IUCN assessment for the region was undertaken [99,100]. Among the evaluated species, 52 species (87% of the evaluated species, or 56% of the current total species diversity) are of least concern (LC), 3 vulnerable (VU), 4 data deficient (DD), and 1 critically endangered (CR) (Figure 4). Therefore, it appears that the overall conservation status of the fishes of the KNP is rather good. However, the status of these species is based on a global assessment, which is not necessarily the same as the local status [101]. The LC category concerns species with large distributions and abundant populations [101]. However, 37 species (40%) are endemic within the KNP *s.l.*; therefore, if all species are assessed, the actual proportion of the species of KNP fishes with a LC status will become smaller. Some species are still considered widely distributed, but this is not the case. As a result, their status will need to be re-evaluated. This is the case, for instance, for *E. eutaenia*, considered to be widespread in the Congo and southern Africa river basins, but which has shown to be composed of 17 mitochondrial lineages for some Congo Basin populations only [102]. *Kneria wittei* is also considered LC due to its supposed widespread distribution. However, a revision by Abwe [56] revealed that *K. wittei* is restricted to the Lukuga Basin, the left bank outlet of Lake Tanganyika, and that the Kundelungu Plateau populations represent a total of nine different new taxa. These results thus show that the IUCN database, which is very useful in assessing the degree of threats to species [103], needs to be updated for the fish species of the KNP *s.l.* based on the new taxonomic information available and taking also into account the numerous identified anthropogenic impacts.

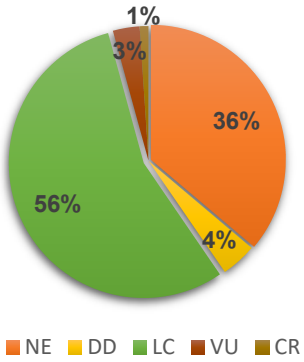

Figure 4. The conservation status of the KNP fishes (based on the actual fish diversity) according to the list of threatened species of the International Union for Nature Conservation (IUCN, 2019). NE: Not Evaluated, DD: Data Deficient, LC: Least Concern, VU: Vulnerable, and CR: Critically endangered.

The CZ is not inhabited and is relatively well controlled by the guards of the "Institut Congolais pour la Conservation de la Nature" due to the presence of their base camp on the plateau. Thus, its fish fauna is only slightly threatened by occasional subsistence fishing. In addition, artisanal mining prospection and exploitation considered as one of the principal threats to biodiversity in the KNP [2] has been observed along the Musipasi River (Abwe et al. 2014, pers. comm) [104] on the KP towards the northern border of the Core Zone of the KNP. Artisanal mining increases water turbidity, which threatens *Kneria* sp. 'musipasi-ab', usually living in clear water.

For the two other zones, i.e., the AZ and BZ, the situation is more complex. The AZ, with 71 reported taxa, is more species rich than the BZ with only 49 taxa (Table A1). More than half (40/71) of the AZ taxa, and even some families (Distichodontidae, Auchenoglanidae and Schilbeidae), were exclusively collected in this zone. Eighteen of the 49 taxa are found only in the BZ. Some families, such as Kneriidae and Nothobranchiidae do not have any shared taxa between these two zones. However, they have more endemic species in the BZ than in the AZ (respectively 6 vs. 5 and 2 vs. 1). These data show that protection/conservation efforts should be extended to the BZ, to enable the effective protection/conservation of other components of the KP fish fauna.

Unfortunately, fishing is considered as the principal source of income for the park to ensure its functioning [2] especially in the AZ. In fact, instead of the customary local traditional fishing that was once permitted in the AZ, intensive commercial artisanal fishing has developed in the lakes of the AZ, attracting even non-native fishermen and fish traders. Furthermore, as many people in the region depend heavily on fishing as their primary source of animal proteins and revenue, the pressure on the fish stocks is high. In addition, destructive fishing methods involving the use of ichthyotoxins, gill nets with small mesh sizes and even mosquito nets, and barriers with fykes are widely used. All these impacts create an uncertain future for the fish diversity of the KNP region. Deforestation of river banks for agriculture in the KNP may increase sediment loads in the rivers through erosion. Moreover, the reduction of the gallery forest vegetation has major ecological impacts, since it acts as a filter for sediment and various nutrients [105], constitutes an important exogenous source of food for fishes [106], and also acts as a water temperature regulator [105]. Pollution mainly originates in the upper Lufira Basin where mining effluents from industrial and artisanal mining activities are discharged into the tributaries of the Lufira River without any prior treatment [107,108].

In light of the above observations, the fishes of the KNP should deserve particular attention concerning their protection and sustainable management. In general, the fishes from the CZ are not much threatened. However, additional protection/conservation efforts should be directed to the AZ and BZ in particular by (i) allowing only sustainable subsistence fishing in the AZ as originally intended in the KNP's statutes [2], (ii) banning the wide-spread use of harmful fishing practices such as the use of ichthyotoxins, fish

barriers on rivers, etc., (iii) creation of no fishing lakes, (iv) regular monitoring to evaluate the fish stocks, and (v) prohibiting the water pollution by mining activities in the upper Lufira Basin as stipulated by the Democratic Republic of the Congo conservation law of 2014 (see Decree N°14/003 of 2014 related to nature conservation).

Our detailed checklist of the ichthyofauna of the KNP *s.l.* is a significant milestone in our knowledge and understanding of the fish diversity and distribution in the park, which has already been identified as a Key Biodiversity Area for freshwater conservation [109,110]. It is therefore expected that this checklist will underscore the key importance of the park as an aquatic freshwater protection/conservation area, and be used to guide fish preservation and conservation decisions by the managers of the "Institut Congolais pour la Conservation de la Nature" and other national and international actors involved in conservation efforts.

5. Conclusions

With 95 native taxa reported, the alpha taxonomic diversity of the fish fauna of the KNP is relatively high, represents about 1/10 of the fish species diversity of the Congo Basin and exhibits a quite exceptional rate of endemicity (40% of endemic taxa). Such a high rate of endemicity is probably the combined result of (i) the isolation of populations by large falls, (ii) the available habitat diversity (rapids, falls, ponds, streams and large rivers, lakes, large floodplains and temporary and/or permanent swamps), and (iii) the geological history of the large rivers on either side of the Kundelungu Plateau. In fact, the Lufira and the Luapula rivers, two major upper Congo River affluents, and two of the river basins draining the KNP, were until recently (~1.8 Mya) connected to the Zambezi River. These connections would explain at least part of the similarity between the fish faunas of the middle Lufira, Luapula and Zambezi rivers. The first shares more species with the Luapula, and almost the same number with the Zambezi, than with the lower Lufira Basin from which it is separated by the large Kyubo Falls.

This study represents the first baseline data on the fish diversity and its distribution in the KNP and can thus be used to guide the elaboration of protection, management, and sustainable use plans. It also documents threats to its fish and aquatic ecosystems. This makes it possible to carry out short-term targeted actions for the protection of certain species, especially the endemics of the park. The present documentation of the fish diversity followed the delimitation of the KNP and its, ill defined, Buffer Zone. Thus major parts of the north-eastern portion of the Kundelungu Plateau remained unexplored. Considering the high, single-basin, endemicity documented for the fish fauna of the plateau, continued inventory efforts of the fish diversity of the north-eastern flank of the Kundelungu Plateau are needed.

Supplementary Materials: The following supporting information can be downloaded at: https://www.mdpi.com/article/10.3390/d15020259/s1, Text SM: Details on the problematic taxonomic cases.

Author Contributions: Conceptualization, E.A. and E.J.W.M.N.V.; methodology, E.A. and E.J.W.M.N.V.; validation, E.J.W.M.N.V. and J.S.; formal analysis, E.A.; investigation and sampling, E.A., A.C.M., P.K.M., L.N.K., K.K., B.K.M., E.J.W.M.N.V., and C.M.M.; data curation, E.A. and E.J.W.M.N.V.; writing—original draft preparation, E.A. and E.J.W.M.N.V.; writing—review and editing, E.A., E.J.W.M.N.V., A.C.M., P.K.M., L.N.K., K.K., P.H.N.B., B.K.M., C.M.M. and M.K.I.K.; visualization, E.A.; supervision, E.J.W.M.N.V. and J.S.; project administration, E.A. and E.J.W.M.N.V.; funding acquisition, E.J.W.M.N.V. and J.S. All authors have read and agreed to the published version of the manuscript.

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Conflicts of Interest: The authors declare no conflict of interest. The funders had no role in the design of the study; in the collection, analyses, or interpretation of data; in the writing of the manuscript, or in the decision to publish the results.

Appendix A

Figure A1. Major fishing methods used, and some habitats sampled, during recent surveys (2012–2017): (**a**) gill net fishing in the Kasanga River; (**b**) placement of a double fyke net in the Luansa River; (**c**) dip net fishing in the Lutshipuka River; and (**d**) cast net fishing in the Lofoi River.

Figure A2. Illustration of some of the traditional fishing techniques as practiced by riparian communities in the KNP: (**a**) large scoop net, in the Dikulwe River; (**b**) fyke in Lake Bwaya; (**c**) dispersal of ichthyotoxin made from *Tephrosia vogelli* in the Lofoi River; (**d**) fences with fykes in the Lofoi River; (**e**) trap shelter in the Lofoi River; (**f**) cast net on Lake Bwaya; and (**g**) 'Matumpulo', i.e., gillnet fishing associated with the noise of oars, in Lake Bwaya.

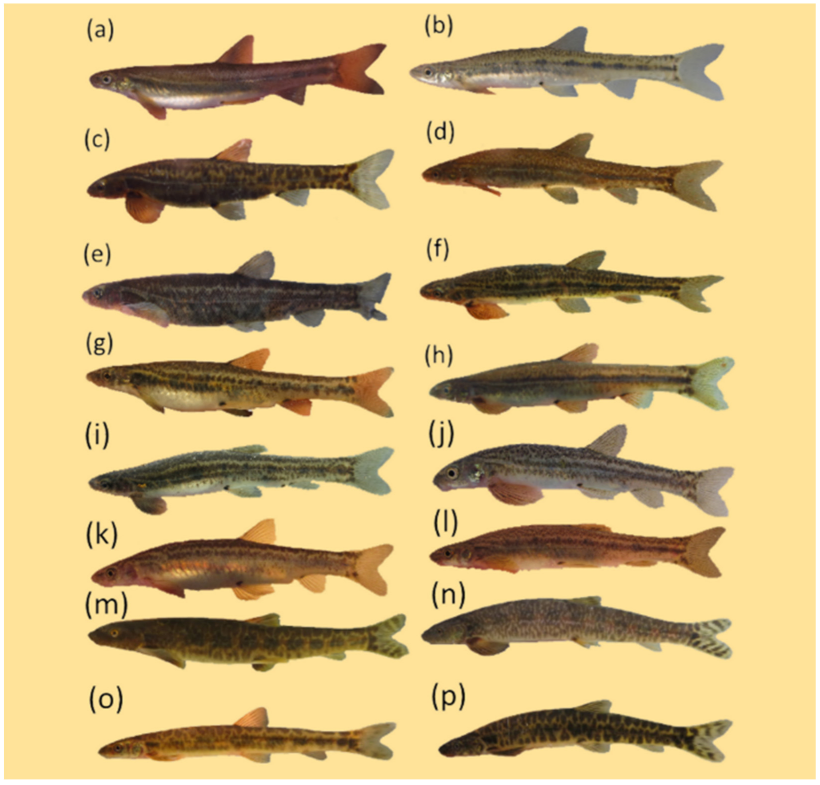

Figure A3. Life photographs of the females of the *Kneria* taxa as the holotype of *K. wittei* is a female, and unsexed specimens of the *Parakneria* species from the KNP and its surroundings. ab: above falls;

and bl: below falls. (**a**) Topotypic specimens of *Kneria wittei* from the Kamikuwa River, near Makala Village (Lukuga Basin); (**b**) *Kneria stappersii*, Kamatete River, right bank tributary of Lubumbashi River, type basin of the species; (**c**) *Kneria* sp. 'luansa-ab' of above the Luansa Falls, in the Luansa River; (**d**) *Kneria* sp. 'maxi' of below the Luansa Falls; (**e**) *Kneria* sp. 'katwei' of above the Lutshipuka Falls, in the Lutshipuka River; (**f**) *Kneria* sp. 'lutshipuka-bl', of below the Lutshipuka Falls; (**g**) *Kneria* sp. 'luijiensis' of above Luiji Falls in the Luiji River; (**h**) *Kneria* sp. 'restrictus' of below the Luiji Falls; (**i**) *Kneria* sp. 'kasangaensis' of above Kasanga Falls, in Kasanga Falls; (**j**) *Kneria* sp. 'musipasi-ab' of above Musipasi Falls, in Musipasi River; (**k**) *Kneria* sp. 'masansa-ab-uniform' of above Masansa Falls, in Masansa River; (**l**) *Kneria* sp. 'seegersii-lofoi-bl', of below the Lofoi Falls, in Lofoi River; (**m**) *Parakneria thysi* of the Kyubo rapids, above Kyubo Falls, its type locality; (**n**) *Parakneria* cf. *thysi* of the Lofoi River; (**o**) *Parakneria malaissei* complex, of the Luisé River; and (**p**) of the Lutshipuka River.

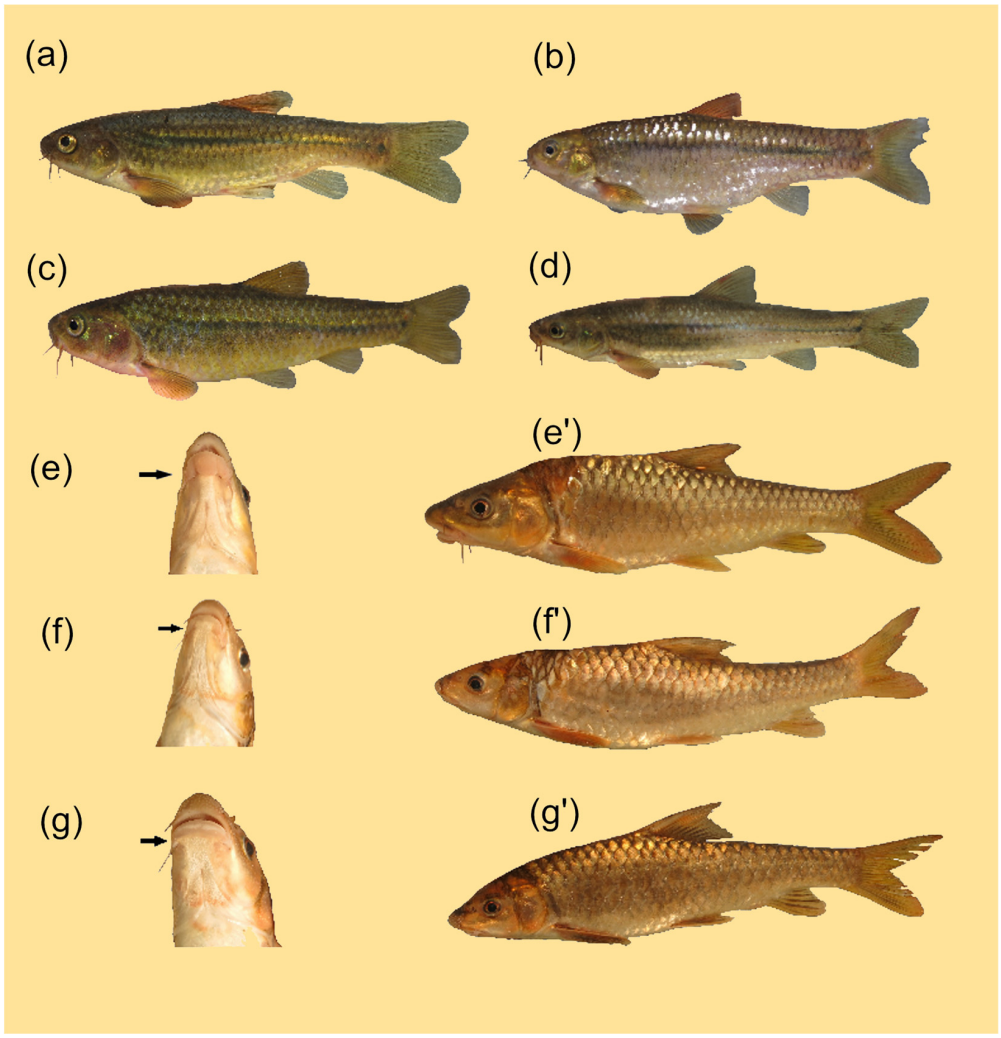

Figure A4. Life photographs pattern of representatives of the chubby head complex (*Enteromius* spp.) from the KNP and the ventral view of the head and lateral view of entire specimen of different mouth phenotype specimens of the *Labeobarbus trachypterus* complex from the Luiji River: (**a**) and (**b**) *Enteromius* sp. 'luiji' from the Luiji River, respectively from above (ab) and below (bl) its major falls; (**c**) *Enteromius* sp. 'kundelungu-ab' from the Lutshipuka River, above its major falls; and (**d**) *Enteromius* sp. 'lutshipuka-bl' from the Lutshipuka River, below its major falls; (**e**,**e′**) *Labeobarbus trachypterus* with rubberlips (*Lab.*-mouth); (**f**,**f′**) with intermediate mouth phenotype (intermediate-mouth); and (**g**,**g′**) *Labeobarbus* sp. 'varico-like′ with chiselmouth (*Var.*-mouth) phenotype specimen from the same location in the Luiji River, upstream of Sampwe Village. The arrows point to the lower jaw characteristics of the mouth phenotype.

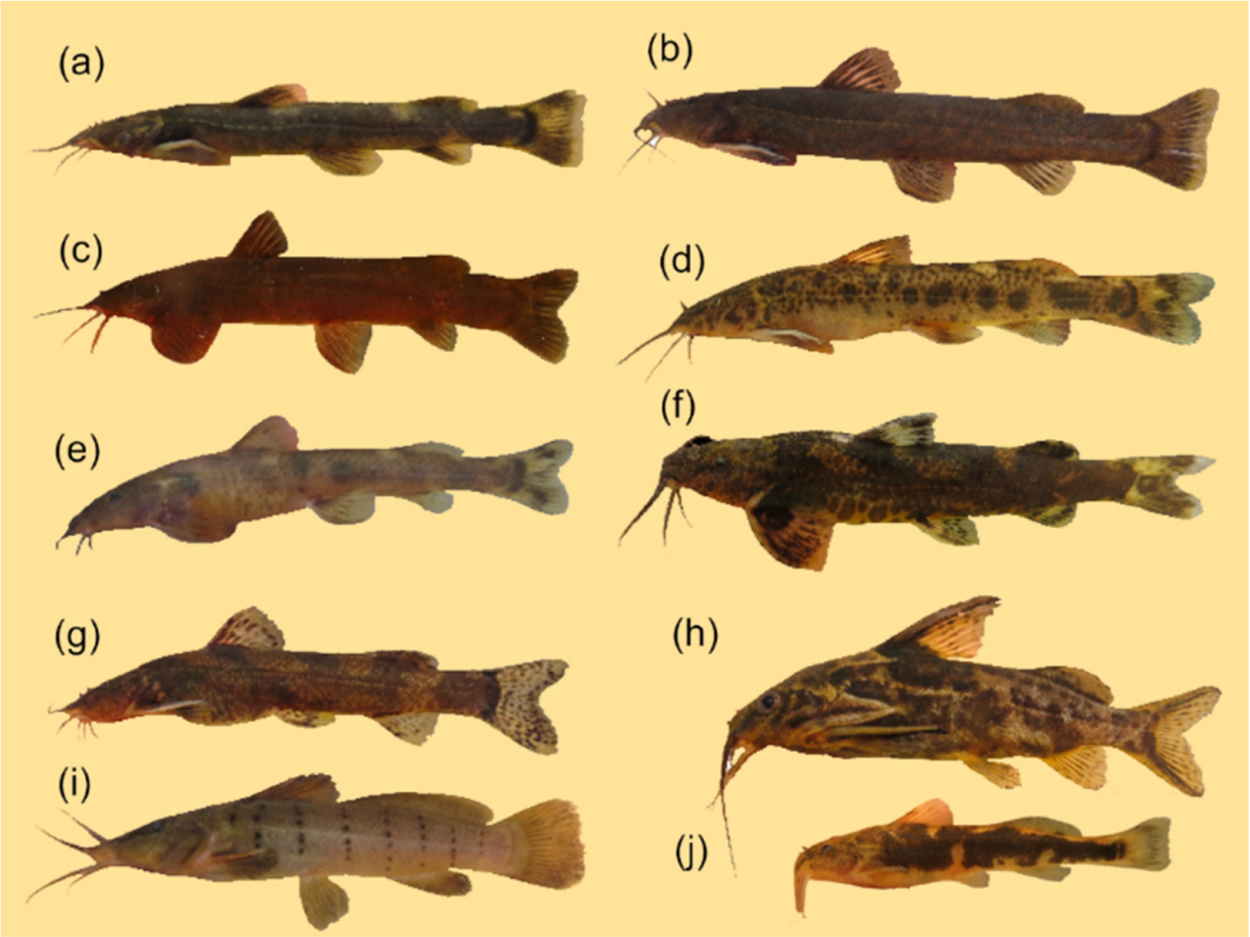

Figure A5. Life photographs of the putative new and new Siluriformes from the KNP *s.l.* ab, above falls and bl, below falls species. Details on the river system are only provided when not already evident in the cheironym (working name) given. (**a**) *Amphilius* sp. 'vandewallei-kyubo' from the Kyubo Rapids, above the Kyubo Falls; (**b**) *Amphilius* sp. 'murielae-masansa-ab/bl' from above the falls; (**c**) *Amphilius* sp. 'luansaensis-ab' from above the falls; (**d**) *Amphilius* sp. 'luijiensis-ab/bl' from above the falls; (**e**) *Amphilius* sp. 'elachymystax-luiji-bl-1' from below the falls; (**f**) *Amphilius frieli* from the Lutshipuka River, below the Falls; (**g**) *Amphilius frieli* from the Lofoi River, below the Falls (Middle Lufira Basin); (**h**) the holotype of *Synodontis denticulatus*, 80.3 mm SL; Lufira River, near its confluence with the Kafila River (Kienge Village); (**i**) *Parauchenoglanis* cf. *punctatus* from the Kafila River, a right bank tributary of the middle Lufira Basin in the AZ of the KNP; and (**j**) *Zaireichthys* sp. 'luiji' from the Luiji River.

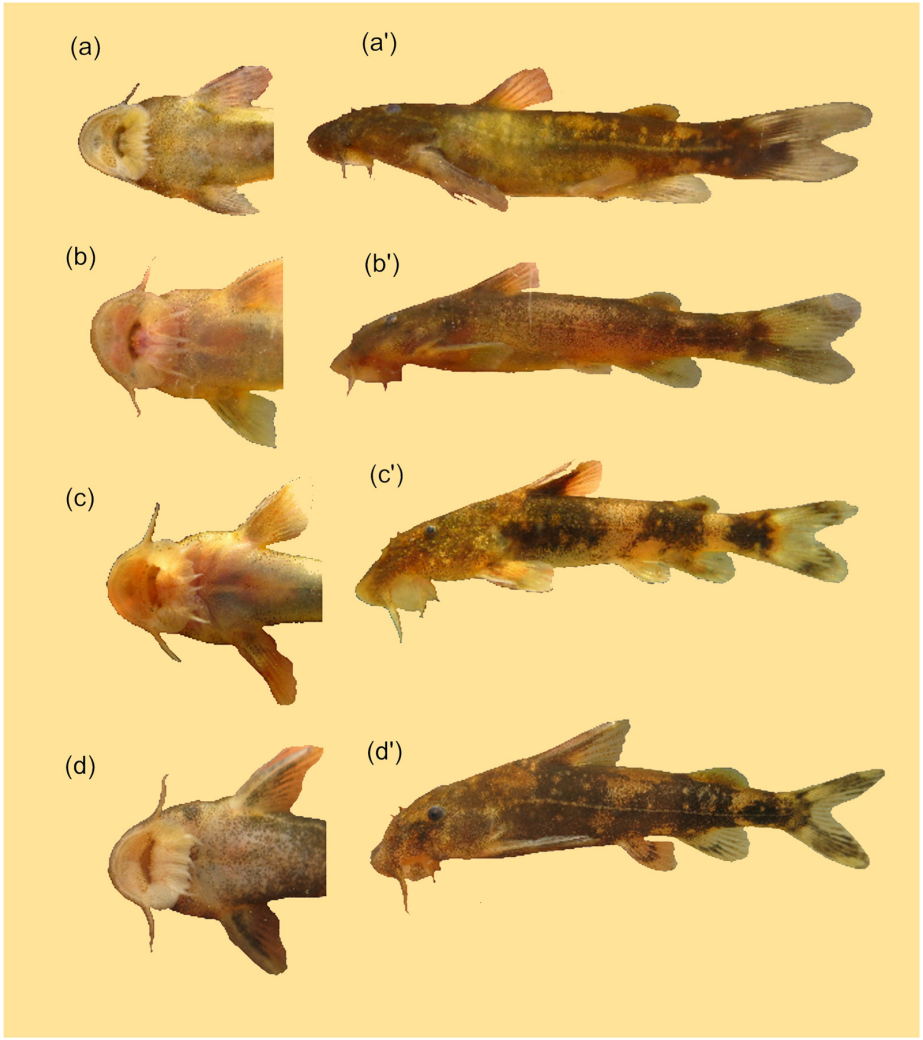

Figure A6. Life photographs of some *Chiloglanis* species from the KNP. (**a**,**a′**) *Chiloglanis* sp. 'luansa-luisé', male, from the Luansa River below the Luansa Falls; and (**b**,**b′**) female from Luisé River, below the Falls; note that this species and *Chiloglanis micropogon* are the only two *Chiloglanis* species from the KNP with a sexual dimorphic caudal fin; (**c**,**c′**) *Chiloglanis* sp. 'lufira' from the Luiji River below the falls; and (**d**,**d′**) *Chiloglanis* cf. *elisabethianus* from the Luansa River below the falls.

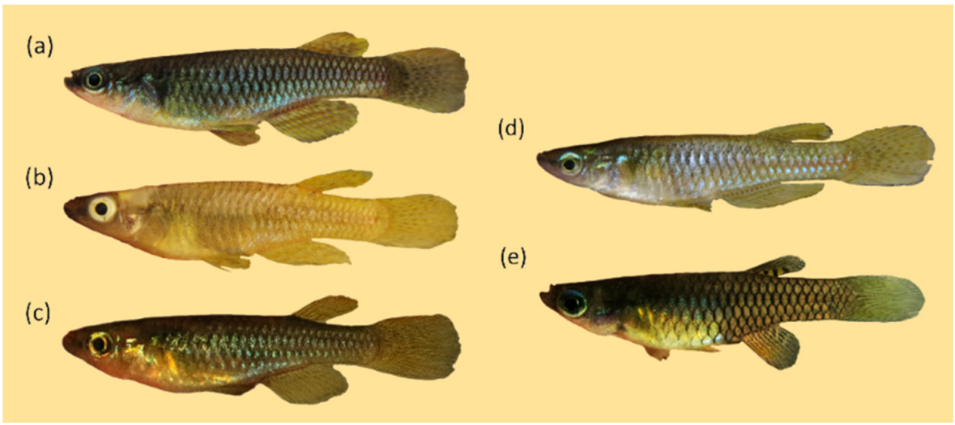

Figure A7. Life photographs of Procatopodidae from KNP. (**a**) *Lacustricola* sp. 'lofoi' from Lofoi River; (**b**) *Lacustricola* sp. 'luiji' from Luiji River; (**c**) *Lacustricola* cf. *johnstoni* (Günther, 1894) from the Kasanga River; (**d**) *Lacustricola moeruensis* (Boulenger, 1914) from the Lutshipuka River; and (**e**) *Lacustricola hutereaui* (Boulenger, 1913) from the Kasanga River.

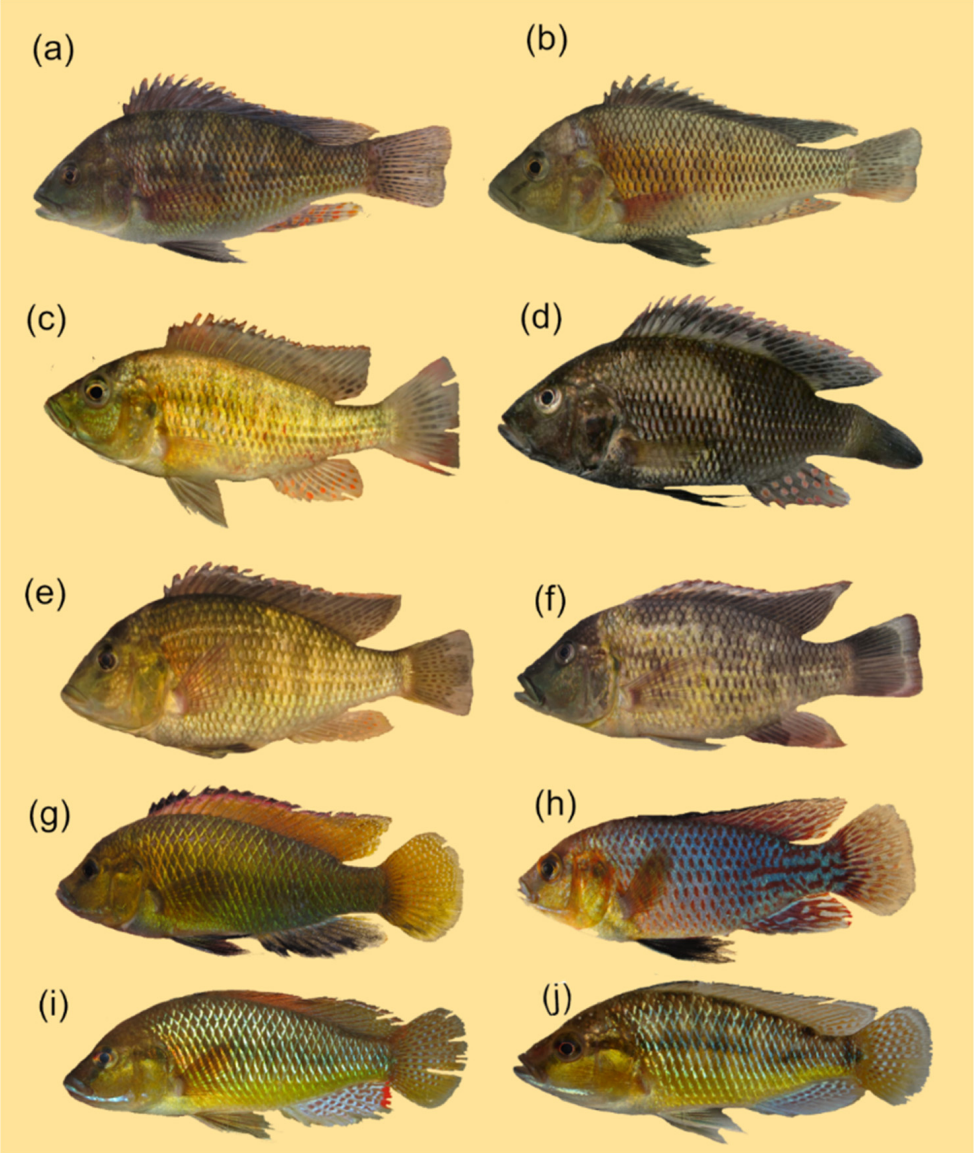

Figure A8. Life photographs of (**a**–**f**) the *Sargochromis mellandi* species complex and *Pseudocrenilabrus* spp. (**g**–**j**) from the upper Lualaba and Luapula Moero. (**a**) *Sargochromis* sp. 'lufira' from the Lofoi River, middle Lufira Basin; (**b**) *Sargochromis mellandi* from the upper Lufira River, upstream of the Panda River confluence; (**c**) *Sargochromis mellandi* from the Lake Nzilo, upper Lualaba River; (**d**) *Sargochromis mellandi* from the fish market of Samfya, Lake Bangweulu, upper Luapula Basin (photo by Cyprien Katongo; 2015); (**e**) *Sargochromis mellandi* from Lake Kipopo, middle Luapula Basin; (**f**) *Sargochromis mellandi* from the Luapula River at Kashobwe village, lower Luapula Basin; (**g**) *Pseudocrenilabrus* sp. 'lufira' from Lufira River, just above Kyubo Rapids, upper Lualaba Basin; (**h**) *Pseudocrenilabrus nicholsi*, from the Lualaba River, Kamalondo Depression, upper Lualaba Basin; (**i**) *Pseudocrenilabrus philander* from the Lutshipuka River, at bridge at Bowa Village, lower Luapula Basin and (**j**) *Pseudocrenilabrus philander philander*, male from Isokwe Island, Lake Moero, Luapula Basin ([78]: Figure 3).

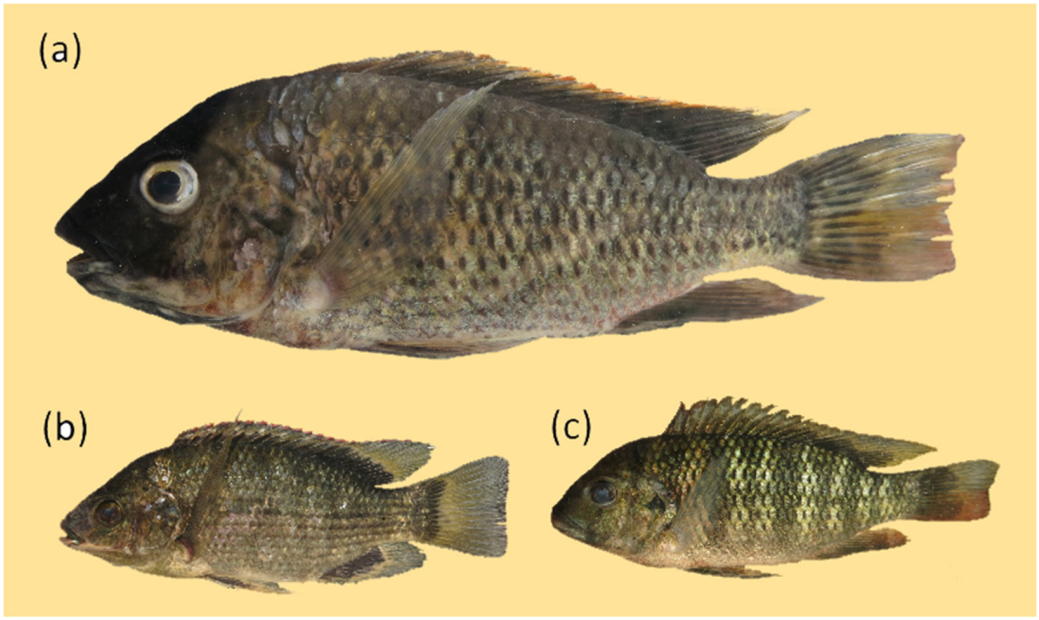

Figure A9. Life photographs of some Haplotilapiinae taxa of the middle Lufira Basin. (**a**) *Coptodon/Tilapia* sp. 'pungwe' from Lake Pungwe; (**b**) *Oreochromis mweruensis* from Lake Pungwe; and (**c**) *Coptodon rendalli* from Lake Lubanda.

Appendix B

Table A1. List of the fish species from the Kundelungu National Park (KNP) *s.l.*, and the middle Lufira Basin: according to (i) major basins, (ii) conservation zones and (iii) current IUCN status evaluation. Only species collected in and around the KNP, and shared between the middle Lufira and the Bangweulu-Mweru basins (from [20]) and the Zambezian Headwaters (ZH; from [37]) are listed. The subtotal includes the number of species from the KNP *s.l.*, while the total includes the species number known from the (sub)basins as a whole. The different (sub)basins are represented by the following abbreviations: BM: Bangweulu-Mweru; lLf: lower Lufira Basin; mLf: middle Lufira River Basin; uLf: upper Lufira River Basin; Lfus: Lofoi River upstream of the Lofoi Falls; Ltus: Lutshipuka River upstream of the Lutshipuka Falls; mLfb: middle Lufira River bed in the Annex Zone; Kfl: Kafila and Mwena rivers; Lfds: Lofoi River downstream of the Lofoi Falls; Ksds: Kasanga River downstream of the Kasanga Falls; Lv: Luvua River and its affluent the Luiji River downstream of the falls. The presence of a species is indicated by: (X): published data; (**+**): KNP 2012–2017 expeditions; (*): historic collection; (**ⁿ**): not in the KNP *sensu stricto*, i.e., the core and annex zones; (**ᴘ**): on the plateau above the falls; (**ᴘ′**): below the falls in the piedmont zone; (**E**): endemic species; and (**I**): introduced species. The IUCN redlist status details are as follows: LC: Least Concern; NT: Near Threatened; VU: Vulnerable; EN: Endangered; DD: Data deficient; and NE: Not Evaluated. The grey and dark grey highlight, respectively the middle Lufira and the Bangweulu-Mweru basins. Vernacular names: B, Bemba; K, Kisumbu; S, Sanga; and Sw, Swahili. bl: below falls, and ab: above falls.

	Major Basins					**Conservation Zones**									**IUCN**
	Lufira Basin			**BM**	**ZH ⁿ**	**Core Zone**		**Annex Zone**				**Buffer Zone**			
Species and Vernacular Names	**lLf ⁿ**	**mLf**	**uLf ⁿ**			**Lfus**	**Ltus**	**mLfb**	**Kfl**	**Lfds**	**Ksds**	**Lv**	**mLf**	**BM**	
Osteoglossiformes															
Mormyridae (6)															
Cyphomyrus discorhynchus (Peters, 1852)				+ *										+ *	LC
Cyphomyrus lufirae Mulelenu et al. (2020), Lububu (S)		XE + *						E +	E +			E +			
Marcusenius macrolepidotus (Peters, 1852), Lububu (S)	X +	+	X	X +	X			+		+	+			X +	LC
Paramormyrops tavernei (Poll, 1972), Sengi (S)		XE										XE +			LC
Petrocephalus catostoma (Günther, 1866), Bushimba drotea (B), Sengi (S)		+		+				+				+		+	LC
Pollimyrus stappersii (Boulenger, 1915)	X	+		X +							+ *			X +	LC
Gonorynchiformes															
Kneriidae (13)															
Kneria stappersii Boulenger, 1915				XE										+	LC
Kneria sp. 'katwei-ab', Mujingiri, Muringiri, Mulingili (S), Mwinjo (K)		E +				E + ᴘ	E + ᴘ								
Kneria sp. 'kasangaensis-ab', Mujingiri, Muringiri (S)		E +											E + ᴘ		
Kneria sp. 'luijiensis-ab', Mujingiri, Muringiri, Mulingili (S), Mwinjo (K)		E +											E + ᴘ		
Kneria sp. 'masansa-ab-uniform', Munjinjingiri (B)				E +			E + ᴘ								

Table A1. *Cont.*

Species and Vernacular Names	Major Basins					Conservation Zones									IUCN
	Lufira Basin			BM	ZH [n]	Core Zone		Annex Zone				Buffer Zone			
	lLf [n]	mLf	uLf [n]			Lfus	Ltus	mLfb	Kfl	Lfds	Ksds	Lv	mLf	BM	
Kneria sp. 'musipasi-ab', Munjinjingiri (B)				E +			E + [p]								
Kneria sp. 'luansa-ab', Munjinjingiri (B)				E +										E + * [p]	
Kneria sp. 'luansa-bl', Munjinjingiri (B)				E + *										E + *	
Kneria sp. 'seegersi-lofoi-mwena-bl', Mujingiri, Muringiri (S), Mwinjo (K)		E + *								E + *					
Kneria sp. 'restrictus-luiji-bl', Mujingiri, Muringiri, Mulingili (S), Mwinjo (K)		E +										E +			
Kneria sp. 'lutshipuka-bl', Munjinjingiri (B)				E +										E +	
Parakneria malaissei Poll, 1969 complex, Kipala matete (B)				XE +										XE +	DD
Parakneria thysi Poll, 1965 complex, Mujingiri, Muringiri, Kalumbu (S)		XE +						XE +	+	+		+			DD
Cypriniformes															
Cyprinidae (17)															
Enteromius afrovernayi (Nichols & Boulton, 1927)		+ *		X	X			+			+ *				LC
Enteromius eutaenia (Boulenger, 1904), Matule (B, S), Kipulumushi (S)	X	+ *		X +	X			+	+	+	+	+		X +	LC
Enteromius haasianus (David, 1936)	X +	X		X	X				X						LC
Enteromius kerstenii (Peters, 1868)		+		X	X			+	+	+	+				LC
Enteromius lineomaculatus (Boulenger, 1903), Kasepa (S)	X	+ *	X +	X +	X			+	+	+ *	+ *	+ *		+ *	LC
Enteromius multilineatus (Worthington, 1933)	X +	+ *		X	X			+			+ *				LC
Enteromius neefi (Greenwood, 1962), Kasepa (B)	X +	+		+						+				+ *	LC
Enteromius paludinosus (Peters, 1852), Mulumbwe (S), Lubwe (B) Kanfisha (B)	X +	+ *	X +	X +	X			+ *	+	+ *	+	+ *		X +	LC
Enteromius radiatus (Peters, 1853)		+ *		X +	X			+	+ *	+				+	LC
Enteromius trimaculatus (Peters, 1852), Kyaka (B,S) Malandala (B), Sese, Shamatonga (S)	X +	+ *		X +				+ *	+	+ *		+ *		X +	LC
Enteromius unitaeniatus (Günther, 1867), Pulumuji, Lwebe (S)		+ *		X	X			+	+	+		+ *			LC
Enteromius sp. 'kundelungu', Kalumbulwa (B), Mulumbwe, Kipulumushi (S)		XE +		XE +		E + [p]	E + [p]							XE +	
Enteromius sp. 'luiji', Mulumbwe, Kipulumushi (S)		E +										E +	+ [p & p']		
Enteromius sp. 'lutshipuka-bl', Kalumbulwa (B)				E +										E +	
Labeo cylindricus Peters, 1852, Kalongwe (B, S)	X +	+ *	X	X +	X			+ *	+	+		+		X +	LC

Table A1. *Cont.*

Species and Vernacular Names	Major Basins					Conservation Zones								IUCN
	Lufira Basin			BM	ZH [n]	Core Zone		Annex Zone				Buffer Zone		
	lLf [n]	mLf	uLf [n]			Lfus	Ltus	mLfb	Kfl	Lfds	Ksds	Lv	mLf	BM	
Labeo cf. *rosae* Steindachner, 1894		X *						X *				*			LC
Labeobarbus trachypterus (Boulenger, 1915) complex, Nkeni (K,S), Kaleya (B), Kachila (S)	X	X +		X +				+	X +	+		+		X +	LC
Danionidae (4)															
Chelaethiops congicus (Nichols & Griscom, 1917), Mulela hulu (S)	X +	X +							X +			+			LC
Engraulicypris brevianalis (Boulenger, 1908), Kisense (S)		+		X					+		+				LC
Neobola moeruensis (Boulenger, 1915)				XE +										+	LC
Opsaridium zambezense (Peeters, 1852), Mukelekele (S)		X +		X	X			+	+			+			LC
Characiformes															
Distichodontidae (2)															
Distichodus maculatus Boulenger, 1898, Kikwanya (S)	X	X +	X	X				+							LC
Nannocharax dageti Jerep, Vari & Vreven, 2014		+		X	X							+			NE
Alestidae (3)															
Brycinus lateralis (Boulenger, 1900), Mbelebembe (K) Pambia (S)	X +	X +	X +	X	X			X + *		+		+			LC
Brycinus peringueyi (Boulenger, 1923), Lutuntu (B)				XE +										+ *	LC
Micralestes humilis Boulenger, 1899, Mukelekele (B), Mbelebembe, Lupambia (S)	X	+		+				+	+	+		+		+	LC
Siluriformes															
Amphiliidae (9)															
Amphilius frieli Thomson & Page, 2015, Kilamba (S,K), Kilamba mabwe (B)		X + *		X +	X				X + *	+		+		X +	NE
Amphilius sp. 'murielae-mansansa-ab/bl', Kilamba-mabwe (B)				E +			E + p & p′							E + p & p′	
Amphilius sp. 'luansaensis-ab', Kilamba mabwe (B)				XE +										XE + p	
Amphilius sp. 'vandewallei-kyubo-ab', Kilamba (S,K)		E +						E +							
Amphilius sp. 'luijiensis-ab/bl-2′, Kilamba (S)		E +										E +	E + p & p′		
Amphilius sp. 'elachymystax-luiji-bl-1′, Kilamba (S)		E +										E +			
Congoglanis sagitta Ferraris, Vari & Skelton, 2011, Kamimbi (K, S)		+		X				+		+		+			NE
Zaireichthys brevis (Boulenger, 1915), Ngoyi wa Lulenda (K, S) Kanyensha (B)	X	+	X *	X +					+	+		+		X +	LC

Table A1. *Cont.*

Species and Vernacular Names	Major Basins					Conservation Zones									IUCN
	Lufira Basin			BM	ZH [n]	Core Zone		Annex Zone				Buffer Zone			
	lLf [n]	mLf	uLf [n]			Lfus	Ltus	mLfb	Kfl	Lfds	Ksds	Lv	mLf	BM	
Zaireichthys sp. 'luiji', Ngoyi wa Lulenda (K, S) Kanyensha (B)		E +										+			
Mochokidae (8)															
Chiloglanis cf. *elisabethianus* (Boulenger, 1915), Kaminye (S), Kinimba (B)		+		+ [n]										X +	VU
Chiloglanis micropogon Poll, 1952		+										+			NE
Chiloglanis microps Matthes, 1965	XE	XE +										XE +			LC
Chiloglanis sp. 'luansa-luisé'				E +										XE +	
Chiloglanis sp. 'lufira'		E +						+	+						
Synodontis lufirae Poll, 1971, Bongwe (S), Nkonkonko (K), Kakonkola (K, S)		XE +	X					XE +	X +	+	+	+			VU
Synodontis nigromaculatus Boulenger, 1905, Bongwe (B)				X +	X									+	LC
Synodontis denticulatus Ilunga et al., 2020, Bongwe (S), Nkonkonko (K), Kakonkola (K, S)		E +						E + *		+		+			NE
Auchenoglanididae (1)															
Parauchenoglanis cf. *punctatus* (Boulenger, 1902), Sokosoko (S)		+	X					+	+	+		+			LC
Clariidae (6)															
Clarias buthupogon Sauvage, 1879, Mulonge (B)				X +										X +	LC
Clarias dumerilii Steindachner, 1866, Kibobe (S, B)	X	+		+		+ p & p′				+	+	+	+	+	LC
Clarias gariepinus (Burchell, 1822), Hondehonde (B), Mulombe (S), Kabambale (Sw)	X	+	X	X +	X			+			+	+		X +	LC
Clarias ngamensis Castelnau, 1861, Mulombe, Mulombe kilundwe (S)	X	+	X	X	X			+	+		+				LC
Clarias stappersii Boulenger, 1915, Kineke (S, B)	X	+		X +	X					+	+	+		X +	NE
Clarias theodorae Weber, 1897, Mulemba, Musonfi (S) Mulonge (B)	X	+	X	X +	X			+	+	+	+			X +	LC
Schilbeidae (1)															
Schilbe intermedius Rüppell, 1832, Kandja (S)	X	X +	X	X	X			+	+	+	+	+			LC
Cyprinodontiformes															
Nothobranchiidae (3)															
Nothobranchius hassoni Valdesalici & Wildekamp, 2004		XE										XE			DD
Nothobranchius malaissei Wildekamp, 1978				XE +										XE	DD
Nothobranchius chochamandai Nagy, 2014				XE +										XE +	NE
Procatopodidae (5)															
Lacustricola moeruensis (Boulenger, 1914)		+		X +					+					+ *	LC

Table A1. *Cont.*

Species and Vernacular Names	Major Basins					Conservation Zones									IUCN
	Lufira Basin			BM	ZH [n]	Core Zone		Annex Zone					Buffer Zone		
	lLf [n]	mLf	uLf [n]			Lfus	Ltus	mLfb	Kfl	Lfds	Ksds	Lv	mLf	BM	
Lacustricola cf. *hutereaui* (Boulenger, 1913)		+		X	X			+			+				LC
Lacustricola cf. *johnstoni* (Günther, 1894), Tulumenso (K) Kisense, Kafunta (S)		+		+	X						+			+	LC
Lacustricola sp. 'lofoi'		E +								E +		+			
Lacustricola sp. 'luiji'		E +										E +			
Poeciliidae (1)															
Poecilia reticulata Peters, 1859		I											I		
Synbranchiformes															
Mastacembelidae (2)															
Mastacembelus frenatus Boulenger, 1901, Muntongwa (B), Mwanzaloka (S)		+ *	X	X + *						+		+		X + *	LC
Mastacembelus. sp. 'lufiraensis'	X	X						X							
Cichliformes															
Cichlidae (13)															
Coptodon rendalli (Boulenger, 1897), Kituku (S, B), Kakenge (S)	X	+ *	X	X +	X			+	+	+	+			+	LC
Coptodon/Tilapia sp. 'pungwe'		E +						E +							
Oreochromis mweruensis Trewavas, 1983, Pale (S)		X +	X	X +				X +	+		+			+	LC
Oreochromis salinicola (Poll, 1948)		XE											XE		VU
Orthochromis torrenticola (Thys van den Audenaerde, 1963), Lufindu (K, S)	X	XE +						XE +	+	+		+			LC
Pseudocrenilabrus philander (Weber, 1897), Bututulu, Kandongorio (S), Lufindu (K, S)	X	+ *	X	X +	X				+					+ *	LC
Pseudocrenilabrus sp. 'lufira', Bututulu, Kandongorio (S), Lufindu (K, S)		E +						E +	+	+	+	+			
Sargochromis sp. 'lufira', Marichongo, Musase, Likobo (S)		E +						E +	+	+		+			
Serranochromis robustus (Günther 1864), Makobo (S, B)		X +		X	X			+	+						CR
Serranochromis macrocephalus (Boulenger, 1899), Makobo (S, B)		+ *	X	X +				+	+	+		+		+ *	LC
Serranochromis thumbergi (Castelnau, 1861), Makobo (S, B)		+ *	X	X	X					+		+			LC
Tilapia ruweti (Poll & Thys van den Audenaerde, 1965)		+	X	X +	X			+						+	LC
Tilapia sparrmanii Smith, 1840, Kifinsa (S,B), Samba (B)	X	+ *	X	X +	X			+	+	+	+	+		+ *	LC
Anabantiformes															
Anabantidae (2)															
Ctenopoma multispine Peters, 1844, Nkomo (S)	X	+ *	X	X	X			+						*	LC
Microctenopoma intermedium (Pellegrin, 1920)		+		X	X						+			*	LC
Sub-total (KNP *s.l.* species)	29	77	22	64	31	3	5	43	34	34	23	45	6	45	
Total (all species of the sub-basin/zone)	109	77	34	141	97	6				71			49		

Table A2. Summary of the comparison of the fish species numbers of (**a**) the middle Lufira Basin (mLf), with neighbourhing basins; (**b**) the Core Zone (CZ) with the two other conservation zones, and (**c**) the Annex Zone (AZ), with the two other conservation zones of the KNP. N: Number of species, J: Jaccard similarity index, BZ: Buffer Zone, lLf: lower Lufira Basin, BM: Bangweulu-Mweru ecoregion, uC: upper Congo ecoregion, uLf: upper Lufira River Basin, and ZH: Zambezian Headwaters ecoregion.

(a)	**mLf**	**uLf**	**lLf**	**uC**	**BM**	**ZH**
N	77	34	109	301	141	97
Shared		22	29	44	49	31
Shared (%)		28.6	37.7	57.1	63.6	40.3
J		0.25	0.18	0.13	0.29	0.22
(b)	**CZ**	**AZ**	**BZ**			
N	6	71	49			
Shared		1	3			
Shared (%)		16.7	50.0			
J		0.013	0.058			
(c)	**AZ**	**BZ**	**CZ**			
N	71	49	6			
Shared		26	1			
Shared (%)		36.6	1.4			
J		0.277	0.013			

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