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Earliest occurrence of *Hydrocynus* (Characiformes, Alestidae) from Eocene continental deposits of Méridja Hamada (northwestern Sahara, Algeria)

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1 Earliest occurrence of *Hydrocynus* (Characiformes, Alestidae) from Eocene continental deposits
2 of Méridja Hamada, northwestern Sahara, Algeria

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19
20 **Abstract:** We here report the oldest remains (teeth) of the African tigerfish (*Hydrocynus*) from
21 the Oued Méridja and Garet Dermchane sections, Hamada of Méridja deposits, in southwestern
22 Algeria. The tigerfish, a large carnivorous fish today represented by several species in the
23 freshwaters of Africa, was previously found in upper middle to upper Eocene deposits in Egypt

and Libya. The remains described here are several million years older, being early to middle Eocene in age, and are associated with other fish elements including lungfish, polypterid, amiiform, possible cichlid, and *Alestes/Brycinus* material, along with several fish elements that cannot be associated with a specific taxon and some fragmentary amphibian bones. This represents the first description of a freshwater fish assemblage from the Eocene of Algeria, although a short list of fish taxa from Eocene Algerian deposits was previously reported. Furthermore, these new Algerian fossils allow us to assess the hypothesized existence of an east-west or west-east permanent hydrological connection between eastern and western parts of northern Africa. We suggest that the shared presence of tigerfish in the Eocene deposits of Algeria, Libya and Egypt does not necessarily indicate a permanent (i.e., non-seasonal) connection east-west or west-east among these areas. Rather, the observed faunal similarities could have been the result of seasonal flooding that caused the dispersal of *Hydrocynus* and associated taxa across coastal flood plains.

Key Words: *Hydrocynus*, Algeria, Eocene, Oued Méridja, Garet Dermchane

Résumé: Nous rapportons ici la découverte des plus anciennes dents fossiles représentant le poisson-tigre africain (*Hydrocynus*) dans les coupes de l'Oued Méridja et de Garet Dermchane, Hamada de Méridja, sud-ouest algérien. Le poisson-tigre, un grand poisson carnivore aujourd'hui représenté par plusieurs espèces dans les eaux douces africaines, avait déjà été découvert dans des sédiments datant de la fin de l'Éocène moyen-supérieur en Égypte et en Libye. Les fossiles que nous décrivons ici sont plus anciens de plusieurs millions d'années, datant de l'Éocène inférieur et moyen, et sont associés à d'autres fossiles de poissons, parmi

1 lesquels des fossiles de dipneuste, de polyptéride, d’amiiforme, de cichlide probable, et des
2 éléments ressemblants à *Alestes* et *Brycinus*, ainsi que des ossements de poissons ne pouvant pas
3 être identifiés de manière certaine et des fragments d’os d’amphibiens. Ceci représente la
4 première description d’une faune de poissons d’eau douce de l’Éocène provenant d’Algérie, bien
5 qu’une courte liste de poissons découverts dans des sédiments de l’Éocène algérien fut
6 précédemment publiée. En outre, ces nouveaux fossiles algériens nous permettent d’évaluer
7 l’hypothèse d’une connexion hydrologique permanente est-ouest ou ouest-est, à travers l’Afrique
8 du Nord. Nous suggérons que la présence de poissons-tigres dans l’Éocène de l’Algérie, de la
9 Libye et de l’Égypte n’indique pas nécessairement une connexion permanente (non saisonnière),
10 mais plutôt que les similarités observées entre ces faunes auraient pu être le résultat
11 d’inondations saisonnières permettant la dispersion d’*Hydrocynus* et de la faune associée.

12
13 Mots clés: *Hydrocynus*, Algérie, Éocène, Oued Méridja, Garet Dermchane

14
15 **Introduction**

16
17 The characiform fish genus *Hydrocynus* is endemic to Africa, where it is currently represented
18 by six extant species: *H. brevis* (Günther, 1864), *H. forskahlii* (Cuvier, 1819), *H. goliath*
19 (Boulenger, 1898), *H. somnorum* (Daget, 1954), *H. tanzaniae* Brewster, 1986, and *H. vittatus*
20 Castelnau, 1861. These fish range in size from the smallest species, *H. tanzaniae*, which has a
21 reported maximum size of 24.7 cm fork length, to the largest species, *H. goliath*, with a reported
22 maximum size of 133 cm fork length (Froese and Pauly 2015). The most widespread species, *H.*
23 *vittatus*, is found throughout Africa in all major river systems.

The fossil record of *Hydrocynus* is based predominantly on its distinctive, labiolingually compressed, conical teeth (as noted below); similar teeth are not found in any other living African freshwater fish, and so when such teeth are found in the fossil record they have been assigned to this genus. *Hydrocynus* has been reported from many Neogene deposits, predominantly in eastern Africa. Pliocene deposits with *Hydrocynus* remains are known from Lothagam, Ngorogo, Omo and Turkana in Kenya (Schwartz 1983; Stewart 2001, 2003a, 2003b), Malema in Malawi (Stewart and Murray 2013), Wadi Natrun in Egypt (Weiler 1926; Greenwood 1972), and the Lake Albert and Edward basins in Uganda (Van Neer 1994). Late Miocene or early Pliocene *Hydrocynus* teeth have been recovered from the Albertine rift in Uganda (Van Neer 1994) and from the Kossom Bougoudi, Kolle, and Koro Toro localities of Chad (Otero et al. 2009, 2010a, 2011), whereas more precisely dated late Miocene teeth are known from the Lake Albert Basin and Nkondo in Albertine Rift Valley of Uganda (Van Neer 1994), Toros-Menalla in Chad (Otero et al. 2010b), Nawata and Lothagam in Kenya (Stewart 1994, 2003a), and Manonga in Tanzania (Stewart 1997). Until recently, the late Miocene material was the oldest known.

The first Paleogene material of *Hydrocynus* reported was recovered from upper Eocene deposits of the BQ-2 locality, Fayum Depression, Egypt (Murray et al. 2010). This locality has been assigned to either the lowermost Jbel Qatrani Formation or the uppermost Birket Qarun Formation, but in either case, its age is estimated at 37 Ma on the basis of magnetostratigraphic and biostratigraphic data (Seiffert et al. 2003, 2005, 2008). More recently, *Hydrocynus* teeth were identified in the first Eocene freshwater fish assemblage described from Libya, in the middle to upper Eocene Dur At-Talah deposits, dated at 39–38 Ma on the basis of magnetostratigraphy and biostratigraphy (Otero et al. 2015). This is currently the earliest

1 reported occurrence of the genus, pre-dating the Egyptian material by one or two million years.
2 We here report newly collected *Hydrocynus* teeth from older deposits from a locality much
3 farther west, near the Algerian-Moroccan border.

4 This material was collected from newly discovered fossiliferous layers on the eastern and
5 western extremities of the Hamada of Méridja, west of Bechar, in southwestern Algeria (Fig. 1).
6 The deposits, located west of Oued Guir, are part of two sections (Fig. 2): the fluvio-lacustrine
7 Oued Méridja section, dated as late Paleocene–early Eocene (late Thanetian–early Ypresian),
8 approximately corresponding to 57–52 Ma, on the basis of the charophyte flora it contains
9 (Hammouda et al., submitted), and the fluvial Garet Dermchane section, which is less reliably
10 dated as middle–late Eocene on the basis of the gastropod fauna it contains (Adaci 2012), but
11 probably represents middle Eocene (Lutetian) deposits having been deposited before 41 Ma.
12 Additional support for the age of these deposits from the Hamada of Méridja is from a locality
13 on the southern edge of the hamada that was recently documented as early–middle Eocene in age
14 based on the fossil Boraginaceae nutlets and charophytes (56–41 Ma) it was found to contain
15 (Hammouda et al. 2015).

16 The present study represents the first detailed report of an Eocene freshwater fish assemblage
17 from Algeria, as well as the earliest report of *Hydrocynus*, represented by characteristic teeth
18 from both the Garet Dermchane and Oued Méridja sections. The new Algerian *Hydrocynus* and
19 the previously reported material from Libya (Otero et al. 2015) and Egypt (Murray et al. 2010)
20 document the broad geographic range of the genus in northern Africa during the Eocene.

21
22 **Geological setting**
23

1 A large proportion of the desert areas in the northwestern corner of the Algerian Sahara is
2 constituted by stony plateaus largely devoid of sand; these are known as “hamadas”. The
3 hamadas west of Bechar (Fig. 2) include the large Hamada of Guir that runs almost north-south
4 and is Neogene in age, as well as two other hamadas of Paleogene age, known as the Hamada of
5 Oum es Sbaa and the Hamada of Mériidja.

6 The Hamada of Oum es Sbaa stretches from Bechar to the eastern bank of Oued Guir. To the
7 east of the Mériidja locality, north of the Bechar–Kenadsa–Mériidja axis, outcrops of lacustrine
8 limestones contain the gastropod *Pseudoceratodes* (Clariond 1939); these deposits were
9 informally named “*Ceratodes* Hamada” and the limestones were assigned an early Eocene age
10 by Jodot (1953a). Near the village of Mériidja, an outcrop of these *Pseudoceratodes*-bearing
11 lacustrine limestones and underlying deposits was recently re-assigned to the latest Paleocene–
12 earliest Eocene by Hammouda et al. (submitted), on the basis of its diverse charophyte flora
13 (*Maedleriella cristellata*, *Maedleriella* sp., *Harrisichara leptocera*, *Peckichara disermas*, and
14 *Gyrogonia* sp.). These deposits are surmounted slightly disconformably by the detrital deposits of
15 the Hamada of Mériidja.

16 The Hamada of Mériidja covers an extensive area between Oued Guir east of Mériidja and the
17 Hamada of Boudenib in Morocco. It consists of two plateaus: the more easterly Mériidja plateau
18 and the westerly Dermchane plateau, the latter of which is the lateral equivalent of the Hamada
19 of Boudenib in Morocco. The continental deposits, rich in terrestrial gastropods identified as
20 *Clavator* at the time, were informally referred to as “*Clavator* Hamada” by Jodet (1953b), who
21 hypothesized an early Miocene (Aquitanian) age of deposition for them. Subsequently, a variety
22 of ages were suggested for these deposits, including Senonian (Menchikoff 1946; Lavocat 1954),
23 and Eo–Oligocene or Mio–Pliocene (Deleau 1952). The Hamada of Mériidja, as well as the

Hamada of Boudenib, has also been considered Oligocene in age (e.g., geological survey sheets “Hamada of Guir” [Choubert 1950] and “Morocco-West Algeria” [Anonymous 1952]).

Since those earlier works, these deposits have been assigned a middle to late Eocene age (see Truc et al. 1987; Truc 1988, 1989; El Youssi et al. 1989; El Youssi 1993) based on a revision of the gastropod fauna they were found to contain. However, more recent age estimates based on the association of a gastropod fauna (bulimes and helicids) with a sparse charophyte flora comprising *Nitellopsis (Tectochara) thaleri*, *Peckichara* sp., and *Raskyella* sp. collectively support a middle or late Eocene (Lutetian–Bartonian) age for these Hamada of Mériidja deposits (Adaci et al. 2005). At Garet Dermchane, indeterminate fish scales and bone fragments as well as internal molds of bulime gastropods indicate a middle to late Eocene age (Adaci 2012). Most recently, additional charophytes (*Peckichara disermas*, *Peckichara* sp., and *Harrisichara leptocera*) and one taxon of angiosperm seed (*Boraginocarpus algeriensis*) were collected from the southern edge of the Hamada of Mériidja and indicate an early to middle Eocene age of deposition (Hammouda et al. 2015).

Two sections represent the eastern and western extremities of the Hamada of Mériidja deposits: the Oued Mériidja section, representing part of the deposits referred to as the “*Ceratodes* Hamada” deposits by Jodot (1953a), and the Garet Dermchane section, representing the deposits Jodot (1953b) had referred to as the “*Clavator* Hamada” deposits. These two sections have yielded the fish material that we report here.

Oued Mériidja section (fluvio-lacustrine)

The fossiliferous locality in these fluvio-lacustrine deposits is situated on the left bank of the Oued Mériidja, about seventy kilometres west of Bechar, in an outcrop only preserving the upper

part of the “*Ceratodes* Hamada” deposits. The studied section is oriented southwest–northeast and its basic stratigraphy is depicted in Figure 3. The *Hydrocynus* teeth are essentially restricted to the lacustrine lower member, the base of which is constituted by reddish-brown micro-conglomerates approximately 0.5–1 metre thick at the outcrop. This lowermost layer is overlain by approximately six metres of gypseous marly clays containing abundant and relatively well-preserved *Hydrocynus* teeth and some other vertebrate remains. Above these clays are indurated whitish marls approximately 0.5 metre thick, followed by approximately 4.5 metre thick lacustrine stromatolithic and oncolithic limestones with *Pseudoceratodes*, capped by palustrine breccias. These lower units also contain internal moulds of terrestrial gastropods, microgastropods, and ostracods associated with a rich charophyte flora. Based on the abundant flora of charophytes (*Maedleriella cristellata*, *Maedleriella* sp., *Harrisichara leptocera*, *Peckichara disermas*, and *Gyrogonia* sp.), the age of these levels can be assigned to the late Palaeocene–early Eocene (late Thanetian–early Ypresian; Hammouda et al. submitted).

The lacustrine limestones in this sequence are slightly disconformably overlain by a high detrital mass (20–30 metres thick) that resulted from fluvial transport. This detrital layer is mainly composed of reddish-brown sandy-silty clays that are sometimes gypseous, above which are discontinuous sandy conglomerates, which are channelized in places. This member also contains a sparse assemblage of microgastropods and charophytes. The sequence ends with a calcitized sandy-carbonate layer approximately 1.5–2 metres thick; the surface of this layer forms the sub-tabular cover of the Méridja plateau.

Garet Dermchane section (fluvial)

1 The detrital Garet Dermchane section is composed of fluviially transported argillaceous, sandy,
2 and conglomeratic “*Clavator* Hamada” sediments, capped with resilient massive calcrete.
3 Several fossiliferous levels with vertebrate remains can be recognized, including one containing
4 *Hydrocynus* teeth (Fig. 4).

5 The studied section is oriented south-north, and located about 25 kilometres northwest of the
6 Oued Méridja section. The lower six metres of the exposure are composed of reddish-brown
7 sandy clays, which sometimes contain gypsum along with fine-grained yellowish and greenish
8 sandstones containing some charophyte gyrogonites. The fossiliferous levels are medium- to
9 coarse-grained, cross-stratified, and horizontally laminated beige sandstones and hard,
10 consolidated, sandy-argillaceous, micro-conglomerate layers, all of which intercalate with
11 reddish brown sandy clays over a thickness of approximately 15–20 metres. These layers contain
12 vertebrate remains associated with a sparse charophyte flora. The micro-conglomerate is the only
13 layer found to contain numerous well-preserved *Hydrocynus* teeth. It is probable that these levels
14 represent a depositional interval similar to that of the upper levels, and date to the middle–late
15 Eocene (probably Lutetian), but we cannot exclude the possibility of an older age of deposition
16 (early–middle Eocene).

17 The top 25 to 30 metres of this section are formed by double continuous, nodular, calcrete
18 slabs with sandy carbonate cement, with intercalated micro-conglomeratic and conglomeratic
19 levels of irregular thickness, with heterometric elements (centimetric to decimetric). This
20 member also contains internal moulds of terrestrial gastropods of middle to late Eocene age
21 (Adaci 2012). This Eocene gastropod fauna is also reported from the coeval and nearby Hamada
22 of Boudenib deposits in Morocco (El Youssi 1993).

Materials and methods

Several kilograms of sediments were collected from various levels in the Oued Mériidja and Garet Dermchane sections. The sediments with *Hydrocynus* teeth mainly correspond to the marly clays of Oued Mériidja and to the micro-conglomerate of Garet Dermchane. To extract the fossiliferous material, two to three kilograms of the indurated sediment sample from Garet Dermchane were soaked in a basin of 10% acetic acid for 48 to 72 hours. At least five kilograms of the unconsolidated sediment sample from Oued Mériidja were placed in 10 litres of water with 250 millilitres of hydrogen peroxide (110 vol) and 250 grams of sodium carbonate for 12 to 24 hours. Both samples were then carefully washed through a column of superimposed sieves (800 to 300 μm), and the resulting concentrate was dried and sorted under a binocular magnifying glass.

Photographs of the individual elements were taken under polarized light using a Nikon 1200C digital camera mounted on a Zeiss Discovery V8 stereo microscope. Multiple photographs (4-10, depending on the element) of slightly different focal points were taken for each fossil and focus stacked into a single image with greater depth of field using Adobe PhotoShop imaging software.

Systematic palaeontology

Order Characiformes Regan, 1911

Family Alestidae Hoedeman, 1951

Genus *Hydrocynus* Cuvier, 1816

Hydrocynus sp.

(Figs. 5A, B; 6)

MATERIAL: UALVP 56149–56161, 56165, 56166, 15 teeth from the Oued Méridja section (Figs. 5A, B), and UALVP 56169–56181, 56162, 56163, 15 teeth from the Garet Dermchane section (Fig. 6).

DESCRIPTION: Most of the teeth do not preserve the base, but in at least two (UALVP 56162, 56163) the base is partially preserved and shows striations (Fig. 6). The labiolingually compressed crowns have a slightly concave lingual side and slightly convex labial side; this causes the tip of the crown to curve somewhat lingually. The two lateral carinae, or cutting edges, of the crown end abruptly just above the base, resulting in a notch on either side of the tooth. All of these features in combination are diagnostic of *Hydrocynus* teeth (Otero et al. 2015).

The Eocene Algerian *Hydrocynus* teeth are small, ranging from 0.8 to 2.6 mm crown height. The base width to crown height ratio varies from 1:2 to 1:3.5, with the smaller teeth being proportionally broader than the larger teeth. Because some of the living species of *Hydrocynus* grow to over a metre, and thus the adults will have much larger teeth than the juveniles, we consider these differences in size and ratios to be within the variation that might be found in a single species. Size differences within the fossil tooth samples are likely based on age of the fish and whether the teeth represent unerupted replacement teeth, functional teeth, or naturally shed (old) teeth.

REMARKS: Labio-lingually compressed, conical teeth with mesial and distal carinae (or cutting edges) from Cenozoic freshwater deposits in Africa are generally assigned to the extant genus *Hydrocynus* (e.g., Stewart 2003a; Murray et al. 2010; Stewart and Murray 2013; Otero et al. 2015). Otero et al. (2015) considered the identification as *Hydrocynus* to be unambiguous if a

1 crenelated tooth base is preserved. However, the crenelated base is often missing from teeth that
2 are shed from the living fish and also in unerupted replacement teeth (Murray et al. 2010). Most
3 authors have not noted the presence of a crenelated base in their descriptions of fossil
4 *Hydrocynus* teeth, and when figures have been included in their papers those do not show the
5 crenelated base (e.g., Weiler 1926; Greenwood 1972; Van Neer 1994; Stewart 2001, 2003a,
6 2003b; Stewart and Murray 2013). We suspect the crenelated base is formed by the attachment
7 bone that is resorbed from shed teeth and not yet developed in replacement teeth, although this
8 needs to be confirmed in future studies. In the absence of a crenelated base, *Hydrocynus* teeth
9 can be confidently identified by their having a unicuspid, pointed crown that is strongly
10 compressed labio-lingually, with the labial face being gently convex and the lingual face being
11 gently concave, in addition to having a distinct notch in the enamel along either cutting edge at
12 the base of the crown (e.g., Otero et al. 2015). Few other African freshwater fishes are known to
13 have tall, large, conical teeth; such teeth are only found in the characiform *Hepsetus*, the channid
14 *Parachanna*, and the polypterid *Polypterus*. The teeth of these three genera are clearly unlike
15 those of *Hydrocynus*, in that all three are round in cross section rather than labio-lingually
16 compressed, and none has the cutting edge with a notch at the base of the crown that is found in
17 *Hydrocynus* (A.M.M., pers. observ., see also Roberts 1969, figs. 1, 16, 27; Clemen et al. 1998,
18 fig. 7; Murray et al. 2010, fig. 3A; Murray 2012, fig. 7; Otero et al. 2015, fig. 3K).

19 *Hydrocynus* teeth are highly distinctive at the generic level, but may not be diagnostic to
20 species level. Although different authors have suggested that the species of *Hydrocynus* may
21 (Weiler 1926) or may not (Greenwood 1972) be distinguished from one another based on tooth
22 morphology, most authors (e.g., Stewart 2003b; Murray et al. 2010; Otero et al. 2015) have not

designated fossil teeth to species, leaving them only as *Hydrocynus* sp. We follow that conservative convention here.

Associated ichthyofauna and other vertebrates

In both assemblages sampled from the Oued Méridja and Garet Dermchane sections, several other fish elements were recovered in association with the *Hydrocynus* teeth (Table 1). These include ganoid scales (Fig. 7A–C) from Garet Dermchane and teeth (Fig. 5C, D) from Oued Méridja, all identified as belonging to a polypterid (bichir). Ganoid scales are normally identified as belonging to polypterid fishes in African Cenozoic fossiliferous deposits (e.g., Murray et al. 2010; Otero et al. 2015), because the only other taxa that such scales might belong to, Lepisosteiformes and Semionotiformes, are unknown in post-Jurassic or post-Cretaceous (respectively) deposits in Africa (Murray et al. 2010). The teeth of polypterids are unique among African Cenozoic freshwater fishes. Tall conical teeth are found in polypterids as well as the characiforms *Hydrocynus* and *Hepsetus*, but polypterid teeth are distinct from those taxa by being round in cross section, having a much smaller cross-section diameter in relationship to crown height, and having the apical third to fifth of the tooth narrowing to a point.

A single, small cusped tooth from Garet Dermchane is identified as an *Alestes/Brycinus* alestid (Fig. 7D, E). Members of Alestidae may have unicuspid conical teeth, as found in *Hydrocynus*, or low molariform teeth with cusps or ridges, as found in the extinct genus *Sindacharax* and in the extant genera *Alestes* and *Brycinus*. *Sindacharax* teeth, as discussed by Stewart (2003b), generally are identified by having the cusps merged to form ridges; however, very small *Sindacharax* teeth may resemble the teeth of *Alestes* and *Brycinus* (Stewart 2003b).

Small and low cusped teeth from Cenozoic African deposits that lack ridges more closely resemble the teeth of the two extant genera and, thus, have been identified as *Alestes*-like or *Alestes/Brycinus* (e.g., Murray et al. 2010; Otero et al. 2015). Therefore, we identify the Garet Dermchane tooth as *Alestes/Brycinus*.

Two relatively blunt teeth, one from each section, are short, conical, and circular in cross-section, with a hollow shaft capped by a clearly defined hypermineralized tip (Figs. 5E; 7F, G). These correspond to the morphology of non-marginal teeth found in amiiform fishes, so we identify them as such. A small bony plate with two tooth sockets from Garet Dermchane (Fig. 7H, I) could also conceivably be an amiiform tooth plate, and may represent a fragment of a coronoid, dermopalatine, or prearticular. Small enameloid fragments from the same locality represent lungfish (Protopteridae) tooth plates (Fig. 7J).

There are also several elements that we leave unidentified. Although we are unable to identify the fish taxa these elements belong to, we report them here to aid in future comparisons among Eocene localities. These include a small plate with four round teeth ankylosed to it (Fig. 7K, L), which is not *Hyperopisus* (K. Stewart, personal communication, 2015) and it is unlikely to be *Egertonina* based on the figure of that fish in Otero et al. (2015, fig. 5). Two other teeth might belong to cichlid fishes or to some other unknown taxon (Fig. 7M–P). Three small, round, and flat teeth (Fig. 7Q–W) could conceivably belong to a tylochromine cichlid, but could just as easily belong to a non-cichlid fish.

In addition to the fishes, amphibians are represented in the Oued Mériidja and the Garet Dermchane sections by fragmentary, elongate bones (Fig. 7X). We identify these as being amphibian because the bones are small, hollow, have a relatively thick cortex, and lack trabeculae. Finally, a robust bulbous tooth (Fig. 7Y) is reminiscent of crocodilian material in its

overall form. However, it appears to have an outer translucent enameloid layer which is a fish-like feature that, to the best of our knowledge, does not occur in reptiles.

Hydrographic connections across Eocene Northern Africa

The distribution of *Hydrocynus* in three near-shore localities in northern Africa (Fig. 8) indicates that a freshwater connection existed at some point among these Eocene localities. Although the three localities are not precisely contemporaneous, they differ in age by only a few million years. The Egyptian locality is the youngest, representing an early Priabonian age corresponding to 37 Ma; the Libyan locality is of intermediate age, having been deposited during the late Bartonian, at 39–38 Ma; and the Algerian material described here is the oldest at early–middle Eocene, representing an Ypresian–Lutetian age roughly corresponding to 56–41 Ma. Otero et al. (2015) noted the high level of faunal similarity between the Dur At-Talah locality in Libya and the BQ-2 locality in the Fayum Depression in Egypt (Table 1). They suggested that the diversity of taxa in these ichthyofaunas indicated the presence of a freshwater system in northern Africa that attained a significant size, and included a variety of water bodies such as lakes, ponds, and streams. Otero et al. (2015) indicated the presence of a permanent hydrological system in their suggested scenario, which, although not explicitly stated by them, would suggest that this freshwater system connected basins between the east and west (i.e., Libya and Egypt). We expand upon this suggestion with a more explicit scenario in which the similarity in ichthyofaunas was caused by faunal exchanges among separate fluvial basins during seasonal flooding that provided temporary freshwater connections across the coastal flood plains.

The lateral migration of fishes over floodplains has been well documented. Many fishes, including larger characiforms, migrate through river systems to streams and lakes in the floodplains made accessible during high water intervals, both to spawn and also to take

1 advantage of more productive habitats (e.g., Daget 1958, Welcomme 1985, Fernandes 1997). It
2 is quite likely that *Hydrocynus* also made lateral migrations in the Eocene. In this way, there may
3 not have been a permanent freshwater connection among these areas, and the exchange of faunal
4 elements may have been limited to annual or even less frequent high water or flooding events.

5 In the Paleocene, there was a widespread marine transgression that covered most of northern
6 Africa and penetrated south through Egypt to reach Sudan (Tawadros 2001), leaving no habitat
7 in the area for freshwater fishes. The sea overall was retreating from northern Africa during the
8 Eocene, although with several episodes of transgression within that time (Tawadros 2001).

9 During the Cenozoic, tectonic activities in the central Mediterranean, much of it associated with
10 the rotation and northward movement of the African continent, were oriented along west–
11 northwest to east–southeast, and east–northeast to west–southwest axes (Tawadros 2012). In the
12 early Eocene, uplift of western Libya was occurring, and by the late Eocene, with further
13 regression of the sea to the north, areas of northern Africa became emergent, including the
14 western Sirte Basin and southern Cyrenica Shelf in Libya and Upper Egypt and the western Sinai
15 Peninsula (Tawadros 2001). The Atlas orogeny began in the middle Eocene, lifting the land in
16 the western part of northern Africa (Tawadros 2012). These uplifts and tectonic actions would
17 have resulted in roughly north–south fluvial systems, with highlands barricading west–east
18 connections.

19 The Lutetian (middle Eocene) was a time of rapid sea regression during which time northern
20 Africa had a tropical climate (Tawadros 2012). A tropical environment providing much
21 precipitation, combined with a retreating sea leaving coastal plains behind, would have resulted
22 in low gradient, seasonal flood plains in distal fluvial systems, where levees restricting
23 waterways tend to be smallest (Welcomme 1979). These seasonal flood plains would in turn

1 have allowed the dispersal of freshwater fishes across inter-watershed natural canals and into
2 neighbouring river basins. Additionally, the occurrence of stream capture events is increased in
3 tectonically active, low-lying flood plain settings, both as a direct result of tectonic stress and
4 following differential erosion (Lima and Ribeiro 2011), potentially further mixing faunas
5 between basins. We suggest that these are the probable mechanisms by which separate, roughly
6 north–south oriented basins developed ichthyofaunas similar to basins to the west or east.

7 Therefore, we suggest that the hydrological connection proposed between Egypt and Libya
8 extended much farther west, to the present day Algerian-Moroccan border, based on the faunal
9 similarities of all three fossiliferous freshwater localities. However, we also suggest that this
10 connection was not necessarily a permanent drainage feature connecting parts of northern Africa.
11 Rather, the tectonically active, low-lying flood plains that extended across much of northern
12 Africa at the time were likely prone to seasonal flooding and stream capture events, aiding the
13 dispersal of *Hydrocynus* and associated freshwater taxa across basins.

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Figure captions

Fig. 1. Location map of the studied sections of Oued Meridja and Garet Dermchane on the Hamada of Méridja in northwestern Sahara, Algeria.

Fig. 2. Geological map of the study region in northwestern Sahara, Algeria. Extracted from the geological map of northwest Africa at 1:2 000 000 scale, Morocco-West Algeria sheet (modified from Conrad 1969).

Fig. 3. Lithostratigraphic column and outcrop plates of the fluvio-lacustrine Oued Méridja section in northwestern Sahara, Algeria.

Fig. 4. Lithostratigraphic column and outcrop plates of fluvial Garet Dermchane section in northwestern Sahara, Algeria.

Fig. 5. Eocene fish teeth from the fluvio-lacustrine Oued Méridja section, Algeria. A, *Hydrocynus* UALVP 56165; B, *Hydrocynus* UALVP 56166; C, polypterid UALVP 56167; D, polypterid UALVP 56148; E, amiiform UALVP 56168 in labial (left) and undetermined side (right) views. Scale bars equal 0.5 mm.

Fig. 6. Eocene *Hydrocynus* teeth from the fluvial Garet Dermchane section, Algeria. A, B, UALVP 56162; C, D, UALVP 56163, in lingual (A, C); and undetermined side (B, D) views. Scale bars equal 1.0 mm.

Fig. 7. Eocene fish and other vertebrate remains from the fluvial Garet Dermchane section, Algeria. A–C, ganoid scale, UALVP 56183, belonging to a polypterid in external (A), internal (B), and undetermined side views (C); D, E, *Alestes/Brycinus* alestid tooth, UALVP 56186, in side (D), and occlusal (E) views; F, G, amiiform tooth, UALVP 56184, in lingual (F) and undetermined side (G) views. H, I, possible amiiform tooth plate, UALVP 56185, in occlusal (H), and undetermined side (I) views; J, fragment of a lungfish tooth plate, UALVP 56187, in occlusal view; K, L, bone with four rounded teeth, UALVP 56188, of an unidentified taxon in occlusal (K) and undetermined side (L) views; M–P, two possible cichlid teeth, UALVP 56190 (M, N) and UALVP 56189 (O, P) in undetermined side views (M, P), labial view (N), and lingual view (O); Q–S, unidentified tooth, UALVP 56164, in occlusal (Q), root (R), and undetermined side (S) views; T–U, unidentified tooth, UALVP 56191, in occlusal (T) and root (U) views; V, W, unidentified tooth, UALVP 56182, in root (V) and occlusal (W) views; X, fragment of an amphibian bone, UALVP 56192; Y, unidentified tooth, UALVP 56193, resembling a crocodile tooth but with a translucent enameloid external layer. Scale bars equal 1.0 mm.

Fig. 8. Palaeomap of the northern part of Africa during the middle Eocene showing relative locations of the three Eocene localities with *Hydrocynus* remains: 1, Oued Méridja and Garet Dermchane in northwestern Sahara, Algeria; 2, Dur At-Talah in southeastern Libya; and 3, BQ-2 in the Fayum region of northeastern Egypt. Political boundaries of modern North African countries are indicated for orientation only: A, Algeria; E, Egypt; L, Libya; M, Morocco. Map based on information from Smith et al. (1994, maps 7–8) and Tawadros (2001, fig. 37; 2012, fig.

- 1 20, 21), with modifications made to the shorelines in order to position the freshwater localities
- 2 on land.

Draft

Fig. 1. Location map of the studied sections of Oued Meridja and Garete Dermchane on the Hamada of Mériidja in northwestern Sahara, Algeria.
157x136mm (300 x 300 DPI)

Fig. 2. Geological map of the study region in northwestern Sahara, Algeria. Extracted from the geological map of northwest Africa at 1:2 000 000 scale, Morocco-West Algeria sheet (modified from Conrad 1969). 97x111mm (300 x 300 DPI)

Fig. 2. Geological map of the study region in northwestern Sahara, Algeria. Extracted from the geological map of northwest Africa at 1:2 000 000 scale, Morocco-West Algeria sheet (modified from Conrad 1969). 97x111mm (300 x 300 DPI)

Fig. 3. Lithostratigraphic column and outcrop plates of the fluvio-lacustrine Oued Méridja section in northwestern Sahara, Algeria.
108x135mm (300 x 300 DPI)

Fig. 4. Lithostratigraphic column and outcrop plates of fluvial Gareet Dermchane section in northwestern Sahara, Algeria.
137x219mm (300 x 300 DPI)

Fig. 5. Eocene fish teeth from the fluvio-lacustrine Oued Mériidja section, Algeria. A, *Hydrocynus* UALVP 56165; B, *Hydrocynus* UALVP 56166; C, polypterid UALVP 56167; D, polypterid UALVP 56148; E, amiiform UALVP 56168 in labial (left) and undetermined side (right) views. Scale bars equal 0.5 mm. 35x14mm (300 x 300 DPI)

Draft

Fig. 6. Eocene *Hydrocynus* teeth from the fluvial Garet Dermchane section, Algeria. A, B, UALVP 56162; C, D, UALVP 56163, in lingual (A, C); and undetermined side (B, D) views. Scale bars equal 1.0 mm.
69x56mm (300 x 300 DPI)

Fig. 7. Eocene fish and other vertebrate remains from the fluvial Garet Dermchane section, Algeria. A–C, ganoid scale, UALVP 56183, belonging to a polypterid in external (A), internal (B), and undetermined side (C) views; D, E, *Alestes/Brycinus* alestid tooth, UALVP 56186, in side (D), and occlusal (E) views; F, G, amiiform tooth, UALVP 56184, in lingual (F) and undetermined side (G) views. H, I, possible amiiform tooth plate, UALVP 56185, in occlusal (H), and undetermined side (I) views; J, fragment of a lungfish tooth plate, UALVP 56187 in occlusal view; K, L, bone with four rounded teeth, UALVP 56188, of an unidentified taxon in occlusal (K) and undetermined side (L) views; M–P, two possible cichlid teeth, UALVP 56190 (M,N) and UALVP 56189 (O, P) in undetermined side views (M, P), labial view (N), and lingual view (O); Q–S, unidentified tooth, UALVP 56164, in occlusal (Q), root (R), and undetermined side (S) views; T–U, unidentified tooth, UALVP 56191, in occlusal (T) and root (U) views; V, W, unidentified tooth, UALVP 56182, in root (V) and occlusal (W) views; X, fragment of an amphibian bone, UALVP 56192; Y, unidentified tooth, UALVP 56193, resembling a crocodile tooth but with a translucent enameloid external layer. Scale bars equal 1.0 mm.

123x84mm (300 x 300 DPI)

Fig. 8. Palaeomap of the northern part of Africa during the middle Eocene showing relative locations of the three Eocene localities with *Hydrocynus* remains: 1, Oued Méridja and Garet Dermchane in northwestern Sahara, Algeria; 2, Dur At-Talah in southeastern Libya; and 3, BQ-2 in the Fayum region of northeastern Egypt. Political boundaries of modern North African countries are indicated for orientation only: A, Algeria; E, Egypt; L, Libya; M, Morocco. Map based on information from Smith et al. (1994, maps 7–8) and Tawadros (2001, fig. 37; 2012, fig. 20, 21), with modifications made to the shorelines in order to position the freshwater localities on land.

78x33mm (300 x 300 DPI)

Table 1. Comparison of the osteichthyan taxa of the freshwater northern African Eocene localities of Oued Meridja and Garet Dermchane (this paper) and Glib Zegdou locality of Draa Hamada (Adaci et al. 2007), all in Algeria; Dur At-Talah in Libya (Otero et al. 2015); and Birket Qarun in Egypt (Murray et al. 2010). Taxa are listed here at the lowest taxonomic level at which they were reported.

Taxon/Locality	Algeria		Libya	Egypt
	O. Mériidja	G. Dermchane	Glib Zegdou	Dur At-Talah Birket Qarun
Sarcopterygii				
Dipnoi				
Lepidosireniformes				
Protopteridae		x	x	
<i>Protopterus</i>			x	x
Actinopterygii				
Cladistia				
Polypteriformes				
Polypteridae	x	x	x	
<i>Polypterus</i>			x	x
Neopterygii				
Holostei				
Amiiformes	x	x		
Teleostei		x	x	
Osteoglossiformes				
Gymnarchidae				
<i>Gymnarchus</i>			x	x
Elopiformes				
Phyllodontidae				
<i>Egertonia</i>			x	
Characiformes			x	x
Alestidae				
<i>Alestes/Brycinus</i>		x	x	x
<i>Hydrocynus</i>	x	x	x	x
Siluriformes			x	
? Clariidae			x	
Claroteidae			x	x
Mochokidae			x	x
Perciformes			x	x
Cichlidae			x	
Channiformes				
Channidae				
<i>Parachanna</i>			x	x