Taxonomy, phylogeny and zoogeography of the hexaploid Torini of the Middle East and North Africa

Dissertation

zur Erlangung des Doktorgrades

der Naturwissenschaften

vorgelegt beim Fachbereich Biowissenschaften

der Johann Wolfgang Goethe-Universität

in Frankfurt am Main

von

Kai Borkenhagen

aus Kiel

Frankfurt am Main 2017

(D30)

Vom Fachbereich Biowissenschaften
der Johann Wolfgang Goethe-Universität als Dissertation angenommen.

Dekanin:	Prof. Dr. Meike Piepenbring
Gutachter:	Prof. Dr. Sven Klimpel
	Prof. Dr. Bruno Streit

Datum der Disputation: 03.11.2017

Table of Contents

Abstract

Fishes of the tribe Torini Karaman, 1971 (Teleostei: Cyprinidae) are a diverse group of primary freshwater fishes, distributed in Africa, the Middle East, and Indomalaya. They are an important component of the native freshwater-fish fauna of the Middle East and North Africa, and occur in most large river systems of the Levant, Arabia, Mesopotamia, southern Iran, and Morocco. They belong to the subfamily Cyprininae, are characterised by being tetraploid or hexaploid, having large scales, and a smooth and ossified last unbranched ray in the dorsal fin. As primary freshwater fishes they are not able to tolerate marine conditions and depend on direct freshwater connections for their dispersal. This makes them an ideal model for zoogeographic studies.

Prior to this study, the diversity of the Torini species in the Middle East and North Africa was not well understood. The validity of several genera and species was unclear, and the generic assignment of several species changed frequently.

In this PhD project the taxonomy, phylogeny, and zoogeography of the Torini of the Middle East and North Africa were investigated with morphological, as well as molecular methods. More than 1550 fish specimens were examined morphologically. Some of the specimens, including the types of most nominal species, were already available from museum collections. The remaining specimens were collected during expeditions to Ethiopia, Iran, Jordan, Morocco and Syria. Tissue samples were collected for molecular genetic analyses. The mitochondrial genes for cytochrome *b*, NADH dehydrogenase subunit 4 and the tRNAs for serine and histidine were sequenced from more than 120 specimens, representing 20 species of Torini and two small, diploid African barbs (Cyprinidae, tribe Smiliogastrini). Molecular data were analysed with Bayesian inference and other methods.

The analyses confirmed that the hexaploid Torini of Africa and the Middle East form a monophyletic group. In the Middle East and North Africa the Torini are represented by the genera *Arabibarbus*, *Carasobarbus*, *Mesopotamichthys*, and *Pterocapoeta*. These genera are each morphologically diagnosable, monophyletic, and genetically distinct. The species '*Labeobarbus*' *reinii* cannot be assigned to any of these genera, because it is morphologically dissimilar and genetically clearly separated from each of them. A generic name for this species is presently not available and until the description of a new genus it is preliminarily assigned to the genus '*Labeobarbus*'.

Out of the 28 species-group taxa described from the Middle East and North Africa until now, 15 are valid: *Arabibarbus arabicus*, *A. grypus*, *A. hadhrami*, *Carasobarbus apoensis*, *C. canis*, *C. chantrei*, *C. exulatus*, *C. fritschii*, *C. harterti*, *C. kosswigi*, *C. luteus*, *C. sublimus*, *Mesopotamichthys sharpeyi*, *Pterocapoeta maroccana,* and '*Labeobarbus*' *reinii*.

The phylogenetic relationships between the Middle Eastern and North African Torini are well resolved, based on the analysis of mitochondrial DNA sequences from nearly all relevant species.

The interspecific and intraspecific morphological and genetic diversity is shaped by the zoogeographic history. Conclusions can be drawn about the events that shaped the evolution of this group. The Torini originated in the Indomalayan biogeographical realm and colonised the Middle East and Africa during the Miocene via the *Gomphotherium* landbridge. The Indomalayan Torini are tetraploid, whereas those of the Middle East and Africa are hexaploid. Molecular phylogenetic analyses showed that the hexaploid Torini cluster within the tetraploid Torini. This makes the tetraploid Torini a paraphyletic group with respect to the hexaploid Torini. Morocco was colonised in two independent waves. The first came from sub-Saharan Africa and is represented by *Pterocapoeta maroccana*. The second originated in the Middle East and gave rise to *C. fritschii*, *C. harterti*, and probably '*L.*' *reinii*. The Tigris-Euphrates system is the largest freshwater system in the Middle East. Its central position between the Orontes River and Jordan River in the West, the Iranian tributaries to the Persian Gulf in the East, and the Arabian Peninsula in the South made it an important crossroad for the colonisation of the Middle East by Torini and other freshwater biota. During the Miocene the predecessors of the Jordan and Orontes rivers were connected to the Tigris-Euphrates system. The Jordan River was separated from the Euphrates before the Orontes. Arabia was colonised in two waves. The first (*A. arabicus*, *A. hadhrami*, *C. exulatus*) dates to the Pliocene, whereas the second (*C. apoensis*) ended as recently as the late Pleistocene or early Holocene.

Kurzfassung

Die Fische des Tribus Torini Karaman, 1971 (Teleostei: Cyprinidae) sind eine artenreiche Gruppe primärer Süßwasserfische, die in Afrika, dem Vorderen Orient und im südöstlichen Asien (Orientalis) vorkommen. Im Vorderen Orient und Nordafrika sind sie eine bedeutsame Komponente der heimischen Süßwasserfischfauna. Sie kommen in allen größeren Gewässersystemen der Levante, der Arabischen Halbinsel, Mesopotamiens, Südirans und Marokkos vor. Torini sind tetraploid oder hexaploid, haben große Schuppen und einen glatten, verknöcherten letzten unverzweigten Strahl in der Rückenflosse und gehören zur Unterfamilie Cyprininae. Als primäre Süßwasserorganismen vertragen sie kein Salzwasser und ihre Verbreitung hängt von direkten Süßwasserverbindungen ab. Daher eignen sie sich hervorragend als Modell für zoogeographische Studien.

Bis zu der hier vorgelegten Arbeit war die Gültigkeit vieler vorderorientalischer und nordafrikanischer Arten der Torini unklar und ihre Gattungszugehörigkeit wechselte oft.

Im Rahmen dieser Doktorarbeit wurde die Taxonomie, Phylogenie und Zoogeographie der Torini des Vorderen Orients und Nordafrikas mit morphologischen und molekulargenetischen Methoden untersucht. Dazu wurden mehr als 1550 Fische bearbeitet, darunter auch die Typusexemplare der meisten nominellen Arten. Ein Teil des untersuchten Materials war in Museumssammlungen vorhanden, der andere Teil wurde im Laufe von Expeditionen nach Äthiopien, in den Iran, nach Jordanien, Marokko und Syrien gesammelt. Es wurden Gewebeproben genommen und die mitochondrialen Gene für Cytochrom *b*, NADH Dehydrogenase Untereinheit 4 und die tRNAs für Serin und Histidin sequenziert. Die mehr als 120 Gewebeproben umfassen 20 Arten der Torini und zwei kleine, diploide afrikanische Barbenarten (Cyprinidae, Tribus Smiliogastrini). Die Sequenzdaten wurden mit der bayesschen Methode und anderen phylogenetischen Methoden analysiert.

Die Analysen haben bestätigt, dass die hexaploiden Torini Afrikas und des Vorderen Orients eine monophyletische Gruppe bilden. Im Vorderen Orient und Nordafrika kommen die Gattungen *Arabibarbus*, *Carasobarbus*, *Mesopotamichthys* und *Pterocapoeta* vor. Diese Gattungen sind anhand morphologischer Merkmale diagnostizierbar. Sie unterscheiden sich genetisch deutlich voneinander und bilden jeweils monophyletische Gruppen. Die Art '*Labeobarbus*' *reinii* kann keiner derzeit beschriebenen Gattung zugeordnet werden, da sie sich morphologisch und genetisch deutlich von diesen

unterscheidet. Bis zur Beschreibung einer neuen Gattung wird die Art vorläufig unter dem Gattungsnamen '*Labeobarbus*' geführt.

Von den 28 bisher aus dem Vorderen Orient und Nordafrika beschriebenen Arten und Unterarten sind 15 gültig: *Arabibarbus arabicus*, *A. grypus*, *A. hadhrami*, *Carasobarbus apoensis*, *C. canis*, *C. chantrei*, *C. exulatus*, *C. fritschii*, *C. harterti*, *C. kosswigi*, *C. luteus*, *C. sublimus*, *Mesopotamichthys sharpeyi*, *Pterocapoeta maroccana* und '*Labeobarbus*' *reinii*.

Durch die Analyse der mitochondrialen DNS-Sequenzdaten und die Abdeckung fast aller relevanten Arten im Datensatz konnten die Verwandtschaftsverhältnisse der vorderorientalischen und nordafrikanischen Torini weitgehend geklärt werden.

Die zwischenartliche und innerartliche morphologische und genetische Diversität wurde durch die zoogeographische Entwicklung geprägt und ermöglicht daher Rückschlüsse auf die Evolution dieser Artengruppe. Die Torini stammen aus der Orientalis und haben den Vorderen Orient und Afrika im Miozän besiedelt. Die Ausbreitung erfolgte über die *Gomphotherium*-Landbrücke. Die Torini aus Indien, China und Südostasien sind tetraploid und die vorderorientalischen und afrikanischen Torini sind hexaploid. Molekulargenetische Analysen zufolge entstammen die hexaploiden Torini den tetraploiden Torini. Die tetraploiden Arten bilden also eine paraphyletische Gruppe in Hinblick auf die hexaploiden Arten. Marokko wurde zweimal unabhängig besiedelt. Die erste Besiedlung erfolgte von südlich der Sahara. *Pterocapoeta maroccana* ist ein Relikt dieses Ereignisses. Die zweite Besiedlung erfolgte vom Vorderen Orient aus. Auf sie gehen *C. fritschii*, *C. harterti* und '*L.*' *reinii* zurück.

Das Euphrat-Tigris-System ist der größte Süßwasserkörper im Vorderen Orient. Es liegt zwischen dem Orontes und dem Jordan im Westen, den iranischen Zuflüssen zum Persischen Golf im Osten und der Arabischen Halbinsel im Süden. Diese zentrale Position machte es zu einer wichtigen Drehscheibe für die Besiedlung des Vorderen Orients durch Torini und andere Süßwasserorganismen. Im Miozän waren die Vorläufer des Orontes und des Jordan mit dem Euphrat verbunden. Der Jordan verlor seine Verbindung zum Euphrat vor dem Orontes. Die Arabische Halbinsel wurde in zwei Einwanderungswellen besiedelt. Die erste erfolgte im Pliozän und umfasste die Vorfahren von *A. arabicus*, *A. hadhrami* und *C. exulatus*. Die zweite endete erst im späten Pleistozän oder zu Beginn des Holozäns. Auf diese Besiedlungswelle geht *C. apoensis* zurück.

Zusammenfassung

Die Fische des Tribus Torini Karaman, 1971 (Teleostei: Cyprinidae) sind, mit über 200 gültigen Arten, eine vielgestaltige Gruppe primärer Süßwasserfische, die in Afrika, dem Vorderen Orient und im südöstlichen Asien (Orientalis) vorkommen (Krupp 1985b, Yang et al. 2015, Coad 2016, Vreven et al. 2016). In ihrem Verbreitungsgebiet sind sie ein bedeutsamer Teil der heimischen Süßwasserfischfauna. Sie kommen in allen größeren Gewässersystemen der Levante, der Arabischen Halbinsel, Mesopotamiens, Südirans und Marokkos vor (Heckel 1843, Boulenger 1909, Boulenger 1911, Pellegrin 1921, Banister und Clarke 1977, Krupp 1983a, Krupp 1985b, Borkenhagen und Krupp 2013, Borkenhagen 2014, Coad 2016). Torini weisen einen evolutionär tetraploiden oder hexaploiden (2n ≈ 100 oder 2n ≈ 150) Chromosomensatz auf (Arai 2011, Berrebi et al. 2014, Yang et al. 2015). Sie haben große Schuppen, und der letzte unverzweigte Strahl ihrer Rückenflosse ist mehr oder weniger stark verknöchert und glatt. Sie gehören zur Unterfamilie Cyprininae (Yang et al. 2015). Als primäre Süßwasserorganismen sind sie nicht in der Lage in Salzwasser zu überleben. Damit sind sie für ihre Ausbreitung auf direkte Verbindungen zwischen Süßwasserkörpern angewiesen. Ihre Verbreitung spiegelt die historische Entwicklung ihres Lebensraumes wider und daher eignen sie sich hervorragend als Modell für zoogeographische Studien (Kinzelbach 1987, Krupp 1987, Heller 2007, Saitoh et al. 2011).

Bis zu der hier vorgelegten Arbeit war die Gültigkeit vieler nomineller Arten der Torini des Vorderen Orients und Nordafrikas unklar, und die Gattungszugehörigkeit einiger Arten wechselte oft (Borkenhagen und Krupp 2013, Borkenhagen 2014). Das machte die taxonomische Revision dieser Gruppe erforderlich. Eine korrekte taxonomische Zuordnung ist die Grundlage für weitere Forschung sowie die Voraussetzung für die Entwicklung von Management- und Artenschutzkonzepten.

Im Rahmen dieser Dissertation wurde die Taxonomie, Phylogenie und Zoogeographie der Torini des Vorderen Orients und Nordafrikas mit morphologischen und molekulargenetischen Methoden untersucht. Dazu wurden mehr als 1550 Fische bearbeitet, darunter auch die Typusexemplare der meisten nominellen Arten. Das untersuchte Material war teilweise in Museumssammlungen vorhanden und wurde teilweise im Laufe von Expeditionen nach Äthiopien, in den Iran, nach Jordanien, Marokko und Syrien gesammelt. Darüber hinaus wurden Gewebeproben genommen und die mitochondrialen Gene für Cytochrome *b*, NADH Dehydrogenase Untereinheit 4 und die tRNAs für Serin und Histidin sequenziert.

Die mehr als 120 Gewebeproben umfassen 14 Arten der Torini aus dem Vorderen Orient und Nordafrika, drei Arten aus Afrika südlich der Sahara, drei Arten aus Südasien, sowie zwei kleine, diploide afrikanische Barbenarten (Cyprinidae, Tribus Smiliogastrini). Die Sequenzdaten wurden sowohl mit phylogenetischen (bayessche Methode und Maximum-Parsimonie-Methode) als auch mit populationsgenetischen Methoden (Haplotypennetzwerk-Analyse) untersucht.

Die hexaploiden Torini Afrikas und des Vorderen Orients bilden eine monophyletische Gruppe (Borkenhagen 2014, Yang et al. 2015, Borkenhagen 2017). Im Vorderen Orient und Nordafrika sind sie durch die Gattungen *Arabibarbus*, *Carasobarbus*, *Mesopotamichthys* und *Pterocapoeta* vertreten. Diese Gattungen sind anhand morphologischer Merkmale diagnostizierbar, unterscheiden sich genetisch deutlich voneinander und bilden jeweils monophyletische Gruppen (Karaman 1971, Ekmekçi und Banarescu 1998, Borkenhagen 2014, Yang et al. 2015, Borkenhagen 2017).

Die Gattung *Arabibarbus* Borkenhagen, 2014 zeichnet sich durch mittlere bis große Körpergröße, einen verknöcherten, glatten Hauptstrahl in der Rückenflosse, normalerweise acht verzweigte Flossenstrahlen in der Dorsalis und fünf verzweigte Flossenstrahlen in der Analis aus; die Schuppen sind groß und schildförmig und weisen zahlreiche parallele Radien auf; in der Seitenlinie befinden sich 29 bis 44 Schuppen; die Schlundzähne haben an ihrer Spitze einen Haken, und die Schlundzahnformel ist 2.3.5-5.3.2; es sind zwei Bartelpaare vorhanden (Borkenhagen 2017). Die Arten der Gattung sind hexaploid (Arai 2011, Berrebi et al 2014, Borkenhagen 2014, Yang et al 2015, Borkenhagen 2017). *Arabibarbus hadhrami* ist die Typusart der Gattung (Borkenhagen 2017).

Die Gattung *Carasobarbus* Karaman, 1971 umfasst mittelgroße Arten mit einem glatten, verknöcherten Hauptstrahl in der Rückenflosse; typischerweise enthält die Dorsalis neun oder zehn und die Analis sechs verzweigte Flossenstrahlen; die großen Schuppen sind schildförmig und weisen zahlreiche parallele Radien auf; es befinden sich 25 bis 39 Schuppen entlang der Seitenlinie; die Schlundzähne sind hakenförmig, und die Schlundzahnformel ist 2.3.5-5.3.2 oder 2.3.4-4.3.2 (Ekmekçi und Banarescu 1998, Borkenhagen und Krupp 2013). Die Arten der Gattung *Carasobarbus* sind hexaploid (Arai 2011, Berrebi et al 2014, Yang et al 2015). Innerhalb der Gattung lassen sich anhand morphologischer Merkmale zwei Untergruppen voneinander abgrenzen (Borkenhagen und Krupp 2013). *Carasobarbus fritschii* und *C. harterti* haben vier Schlundzähne in der mittleren Zahnreihe, während alle anderen Arten der Gattung fünf haben. Die zweite Gruppe umfasst *C. kosswigi* und *C. sublimus* und zeichnet sich durch eine spatelförmige Unterlippe aus. Bei *Pseudotor* Karaman, 1971 und *Kosswigobarbus* Karaman, 1971 handelt es sich um Synonyme von *Carasobarbus* (Borkenhagen und Krupp 2013).

Mesopotamichthys Karaman, 1971 ist eine monospezifische Gattung und zeichnet sich durch das Fehlen von Barteln aus; die Schlundzähne sind löffel- bis schaufelförmig und ihre Formel lautet 2.3.5-5.3.2; die Lippen sind gut entwickelt und fleischig; die Orbitalknochen sind breit, und das Lacrimale ist kurz und breit; die Dorsalis hat acht verzweigte Flossenstrahlen; der Hauptstrahl ist mäßig verknöchert und glatt; die Analis hat fünf verzweigte Flossenstrahlen; das Peritoneum ist schwarz, und die Schuppen weisen viele parallele oder konvergente Radien auf (Karaman 1971). *Mesopotamichthys* ist hexaploid (Borkenhagen 2014; Borkenhagen 2017).

Die Gattung *Pterocapoeta* Günther, 1902 ist nach derzeitiger Auffassung monospezifisch (Eschmeyer 2015). Entlang der Seitenlinie liegen ungefähr 45 mittelgroße Schuppen; die Dorsalis hat mehr als neun verzweigte Flossenstrahlen und ihr Hauptstrahl ist nur schwach verknöchert; der Ansatz der Rückenflosse liegt vor dem Ansatz der Bauchflossen; die Schnauze ist stumpf, abgerundet und trägt ein unterständiges, bogenförmiges Maul; die Unterlippe ist mit einer flexiblen Hornscheide bedeckt; normalerweise besitzen Vertreter dieser Gattung ein Paar kurzer Barteln, doch bei einigen Individuen ist es nur rudimentär entwickelt oder fehlt gänzlich; die Schlundzahnformel ist 2.3.4-4.3.2 (Günther 1902). Einige Arten aus Afrika südlich der Sahara stehen dieser Gattung nahe (Tsigenopoulos et al. 2010, Yang et al. 2015), und eine Revision erscheint notwendig.

'*Labeobarbus*' *reinii* (Günther, 1874) bildet eine isolierte Linie innerhalb der hexaploiden Torini (Tsigenopoulos et al. 2010, Berrebi et al. 2014, Yang et al. 2015). Da sich die Art sowohl morphologisch als auch genetisch von allen bisher beschriebenen Gattungen unterscheidet, wird sie vorläufig in die Gattung '*Labeobarbus*' gestellt. Sollte sich die isolierte Position dieser Art in weiteren Studien bestätigen, so ist die Beschreibung einer neuen Gattung gerechtfertigt.

Von den 28 bisher aus dem Vorderen Orient und Nordafrika beschriebenen Arten und Unterarten sind 15 gültig.

Arabibarbus arabicus (Trewavas, 1941) hat 29 bis 38 Schuppen entlang der Seitenlinie, einen langen, hohen, keilförmigen Kopf und einen kräftigen, seitlich abgeflachten Körper; die Dorsalis ist hoch, und ihr Hauptstrahl ist stark verknöchert; die Brust- und Bauchflossen sind kurz; die Art kommt in den Wadis im Südwesten der Arabischen Halbinsel vor; sie bewohnt dort sowohl Gewässer, die ins Rote Meer münden, als auch Gewässer, die ins Landesinnere fließen und dort in der Wüste versickern (Trewavas 1941, Banister und Clarke 1977, Krupp 1983a, Borkenhagen 2014).

Arabibarbus grypus (Heckel, 1843) hat 33 bis 44 Schuppen entlang der Seitenlinie, einen runden, kurzen Kopf und einen zylindrischen Körper; der Hauptstrahl der Dorsalis ist nur schwach verknöchert; die Rückenflosse, sowie die Brust- und Bauchflossen sind vergleichsweise kurz; die Art kommt im Euphrat-Tigris-System und in den Flüssen im südlichen Iran vor; außerdem gibt es wenige Nachweise aus dem Orontes (Heckel 1843, Kähsbauer 1963, Krupp 1985b, Coad 1996, Borkenhagen 2014, Coad 2016).

Arabibarbus hadhrami Borkenhagen, 2014 hat 29 bis 32 Schuppen entlang der Seitenlinie, einen langen, hohen und keilförmigen Kopf, sowie einen schlanken, seitlich abgeflachten Körper; die Dorsalis ist hoch und ihr Hauptstrahl ist stark verknöchert; die Brust- und Bauchflossen sind lang; die Art kommt im Bereich des Wadi Hadhramaut / Wadi al-Masila und seiner Nebenflüsse vor (Borkenhagen 2014).

Carasobarbus apoensis (Banister und Clarke, 1977) hat ein Paar Barteln, 10 verzweigte Strahlen in der Dorsalis, 27 bis 32 Schuppen entlang der Seitenlinie und 12 Schuppen um den Schwanzstiel; der Hauptstrahl der Dorsalis ist kürzer als der Kopf; die Art lebt in den Hedschas-Bergen in Saudi-Arabien und besiedelt dort Wadis, die ins Rote Meer münden, genauso wie Wadis, die ins Innenland entwässern (Banister und Clarke 1977, Krupp 1983a, Borkenhagen und Krupp 2013). *Carasobarbus apoensis* ist eng mit *C. luteus* verwandt (Borkenhagen 2017).

Carasobarbus canis (Valenciennes in Cuvier und Valenciennes, 1842) hat zwei Paar Barteln, 29 bis 35 Schuppen entlang der Seitenlinie und 12 Schuppen um den Schwanzstiel; der Hauptstrahl der Dorsalis ist kürzer als der Kopf; die Art ist im gesamten Jordan-System verbreitet und kommt in Bächen, Flüssen und Seen vor; außerdem gibt es Nachweise aus den beiden mediterranen Küstenflüssen Na'aman und Yarqon (Cuvier und Valenciennes 1842, Krupp 1985b, Krupp und Schneider 1989, Ekmekçi und Banarescu 1998, Goren und Ortal 1999, Borkenhagen und Krupp 2013). Die Population in der Oase Azraq ist von Menschen ausgesetzt worden (Krupp und Schneider 1989) und heute vermutlich wieder erloschen (Hamidan 2004).

Carasobarbus chantrei (Sauvage, 1882) hat zwei Paar Barteln, 31 bis 38 Schuppen in der Seitenlinie und normalerweise 14 oder 16 Schuppen um den Schwanzstiel; der Hauptstrahl der Rückenflosse ist so lang wie der Kopf oder kürzer; die Art kommt in den Fließgewässern und Seen des Orontes-Systems vor; außerdem sind Exemplare aus dem Küstenfluss Nahr Marqiyah bekannt (Sauvage 1882, Krupp 1985a, Krupp 1985b, Krupp und Schneider 1989, Borkenhagen und Krupp 2013). Aus dem Ceyhan Nehri liegen keine Belegexemplare vor, und Nachweise aus dem Nahr Quwayq und dem Euphrat-Tigris-System sind zweifelhaft (Krupp 1985a, Krupp 1985b, Borkenhagen und Krupp 2013).

Carasobarbus exulatus (Banister und Clarke, 1977) hat zwei Paar Barteln, 26 bis 32 Schuppen entlang der Seitenlinie, 12 Schuppen um den Schwanzstiel und neun verzweigte Strahlen in der Dorsalis; der Hauptstrahl der Dorsalis ist so lang wie der Kopf oder länger; die Art besiedelt die Gewässer des Wadi Hadramaut / Wadi al-Masilah Systems und dessen pleistozäne Zuflüsse (Banister und Clarke 1977, Krupp 1983a, Borkenhagen und Krupp 2013). Das Wadi Maran ist der westlichste Ort, an dem diese Art nachgewiesen wurde (Borkenhagen und Krupp 2013). Meldungen liegen auch aus dem Marib-Stausee (Al-Safadi 1995) und dem Wadi Hajr (Attaala and Rubaia 2005) vor.

Carasobarbus fritschii (Günther, 1874) hat zwei Paar Barteln, 30 bis 39 Schuppen in der Seitenlinie und 14 bis 20 Schuppen um den Schwanzstiel; die Dorsalis ist normalerweise kürzer als die Afterflosse, und mehr als 15 % ihres Hauptstrahls sind biegsam; das dorsale Profil des Kopfes ist konvex (Günther 1874a, Pellegrin 1921, Borkenhagen und Krupp 2013). *Carasobarbus fritschii* ist in Marokko weit verbreitet und kommt sowohl in Flüssen vor, die ins Mittelmeer münden (Oued Moulouya), als auch in Flüssen, die in den Atlantik fließen (Oued al-Maleh, Oued Bou Regreg, Oued Igrounzar / Oued Ksob, Oued Iqem, Oued Oum er Rbia, Oued Sebou, Oued Tennsift); es gibt einen Nachweis aus dem Oued Kiss in Algerien (Günther 1874a, Pellegrin 1921, Karaman 1971, Borkenhagen und Krupp 2013).

Carasobarbus harterti (Günther, 1901) hat zwei Paar lange Barteln, 31 bis 38 Schuppen entlang der Seitenlinie und 13 bis 17 Schuppen um den Schwanzstiel; die Dorsalis ist länger als die Analis, und weniger als 15 % ihres Hauptstrahls sind biegsam; das dorsale Kopfprofil ist gerade (Günther 1901, Pellegrin 1921, Borkenhagen und Krupp 2013). Die Art kommt in den Unterläufen von Oued Oum er Rbia und Oued Tennsift in Marokko vor (Günther 1901, Pellegrin 1921, Karaman 1971, Borkenhagen und Krupp 2013).

Carasobarbus kosswigi (Ladiges, 1960) hat zwei Paar Barteln, 32 bis 38 Schuppen in der

Seitenlinie und 14 bis 16 Schuppen um den Schwanzstiel; der Hauptstrahl der Dorsalis ist deutlich länger als der Kopf; der schmale Mund hat eine spatelförmige Unterlippe mit einem Mittellobus (Ladiges 1960, Coad 1982, Borkenhagen und Krupp 2013). Die Art lebt in den Flüssen und Bächen des Euphrat-Tigris-Systems (Ladiges 1960, Coad 1982, Krupp und Schneider 2008, Borkenhagen und Krupp 2013) und ist in Hinsicht auf *C. sublimus* paraphyletisch (Borkenhagen et al. 2011, Borkenhagen 2017).

Carasobarbus luteus (Heckel, 1843) hat zwei Paar Barteln, 25 bis 33 Schuppen entlang der Seitenlinie und normalerweise 12 Schuppen um den Schwanzstiel; der Hauptstrahl der Dorsalis ist ungefähr so lang wie der Kopf oder etwas kürzer (Heckel 1943, Borkenhagen und Krupp 2013, Coad 2016). Die Art kommt im Euphrat-Tigris-System und den Flüssen entlang der südlichen Küste Irans, wie Mand, Helleh, Kol und Naband vor; außerdem besiedelt sie das abflusslose Becken des Maharloo-Sees (Heckel 1843, Ekmekçi und Banarescu 1998, Krupp und Schneider 2008, Borkenhagen und Krupp 2013, Coad 2016). *Carasobarbus luteus* ist eng mit *C. apoensis* verwandt (Borkenhagen 2017). Im Naband existiert eine atypische Population (Borkenhagen und Krupp 2013). Die Population im Fluss Queiq ist erloschen (Borkenhagen und Krupp 2013). Nachweise aus dem Orontes und aus Damaskus sind zweifelhaft (Borkenhagen und Krupp 2013).

Carasobarbus sublimus (Coad und Najafpour, 1997) hat zwei Paar Barteln, 27 bis 29 Schuppen in der Seitenlinie und 12 Schuppen um den Schwanzstiel; der Hauptstrahl der Dorsalis ist ungefähr so lang wie der Kopf; der Mund ist schmal, und die spatelförmige Unterlippe weist einen Mittellobus auf (Coad und Najafpour 1997, Borkenhagen und Krupp 2013). Die Art kommt im A'la und Fahliyan in Südostiran vor; außerdem gibt es einen möglichen Nachweis aus dem Kashgan (Coad und Najafpour 1997, Esmaeili et al. 2006, Borkenhagen und Krupp 2013, Coad 2016).

Mesopotamichthys sharpeyi (Günther, 1874) hat keine Barteln, 29 bis 37 Schuppen entlang der Seitenlinie und eine Rückenflosse mit vier unverzweigten und sieben bis neun verzweigten Flossenstrahlen; die Analis hat drei unverzweigte und fünf verzweigte Flossenstrahlen; die Schnauze ist rund und stumpf; auf dem ersten Kiemenbogen befinden sich 13 bis 19 Kiemenreusendornen (Günther 1874a, Coad 2016). Die Art kommt im unteren Bereich des Euphrat-Tigris-Systems, sowie im Zohreh und Karkheh in Iran vor (Günther 1874b, Kähsbauer 1963, Karaman 1971, Ekmekçi und Banarescu 1998, Freyhof 2014, Coad 2016).

Pterocapoeta maroccana Günther, 1902 hat normalerweise ein Paar kurzer Barteln, 43 bis

47 Schuppen entlang der Seitenlinie, vier unverzweigte und 9 bis 11 verzweigte Flossenstrahlen in der Dorsalis; die Analis hat drei unverzweigte und fünf verzweigte Flossenstrahlen; das Maul ist unterständig, und der Unterkiefer trägt eine scharfe Hornkante (Günther 1902, Karaman 1971, Pellegrin 1921). Die Art kommt im Oued Oum er Rbia und im Oued Talmest in Marokko vor; auch aus dem System des Oued al-Maleh liegen Meldungen vor (Günther 1902, Karaman 1971, Pellegrin 1921, Werner 1931).

'*Labeobarbus*' *reinii* (Günther, 1874) hat zwei Paar lange Barteln und 25 bis 32 Schuppen entlang der Seitenlinie; die Dorsalis hat drei bis vier unverzweigte und acht oder neun verzweigte Flossenstrahlen; die Analis hat drei unverzweigte und fünf verzweigte Flossenstrahlen; das Maul ist leicht unterständig, hat gut entwickelte, fleischige Lippen, und der Unterkiefer trägt einen kleinen Mittellobus (Günther 1874a, Pellegrin 1921, Karaman 1971). Die Art ist in Marokko endemisch und scheint heutzutage auf den Unterlauf des Oued Tennsift beschränkt zu sein (Crivelli 2006). Es existieren jedoch auch Belege für ein historisches Vorkommen im Oued Oum er Rbia (Günther 1902, Pellegrin 1921).

Durch die Analyse der mitochondrialen DNS-Sequenzdaten und die umfangreiche Abdeckung von Arten im Datensatz konnten die Verwandtschaftsverhältnisse der mittelöstlichen und nordafrikanischen Torini weitgehend geklärt werden.

Die zwischenartliche und innerartliche morphologische und genetische Diversität wurde durch die zoogeographische Entwicklung geprägt und ermöglicht daher Rückschlüsse auf die Evolution dieser Artengruppe (Borkenhagen 2017). Die Torini stammen aus der orientalischen Region und haben den Vorderen Orient und Afrika im Miozän besiedelt (Wang et al. 2013, Borkenhagen 2017). Die Ausbreitung erfolgte über die *Gomphotherium*-Landbrücke (Borkenhagen 2017). Auch Welse der Familie Clariide und Karpfenfische der Gattung *Labeo* haben diese Route genutzt (Agnese und Teugels 2005, Tang et al. 2009). Die ältesten fossilen Karpfenfische der Arabischen Halbinsel stammen aus dem Burdigalium (20,5 bis 16 Ma vor unserer Zeit; Otero 2001, Otero und Gayet 2001).

Die Torini der Orientalis (*Hypselobarbus*, *Lepidopygopsis*, *Naziritor*, *Neolissochilus, Osteochilichthys* und *Tor*) sind tetraploid, und die vorderorientalischen und afrikanischen Torini (*Arabibarbus*, *Carasobarbus*, *Mesopotamichthys*, *Pterocapoeta*, *Labeobarbus*, *Acapoeta* und *Sanagia*) sind hexaploid (Tsigenopoulos et al. 2010, Arai 2011, Berrebi et al. 2014, Borkenhagen 2014, Yang et al. 2015, Borkenhagen 2017). Die Hexaploidie hat sich möglicherweise durch die Hybridisierung zwischen einer tetraploiden Torini-Art und einem

Vertreter der Gattung *Cyprinion* entwickelt (Yang et al. 2015). Da aus der Orientalis keine hexaploiden Arten bekannt sind, hat dieses Ereignis vermutlich während der Ausbreitung der Torini nach Westen stattgefunden (Borkenhagen 2017). Im Gegensatz zu den hexaploiden Torini sind die tetraploiden Torini eine paraphyletische Gruppe, da die tetraploiden Arten der Gattungen *Neolissochilus* und *Tor* näher mit den hexaploiden Torini verwandt sind, als mit den tetraploiden Arten der Gattung *Hypselobarbus* (Borkenhagen 2017).

Die Aufspaltung zwischen *Pterocapoeta*, den afrikanischen Torini und den vorderorientalischen Torini ist in der phylogenetischen Analyse nicht aufgelöst (Borkenhagen 2017). Im Miozän war die Süßwasserfischfauna des Maghreb von typisch afrikanischen Vertretern wie *Lates* und *Polypterus* geprägt (Otero und Gayet 2001, Stewart 2001). Dagegen sind die meisten Arten der rezenten Süßwasserfischfauna dieser Region europäischen oder vorderorientalischen Ursprungs (Otero und Gayet 2001, Stewart 2001). Die meisten afrikanischen Arten verschwanden im Pliozän oder Pleistozän (Otero and Gayet 2001, Stewart 2001). *Pterocapoeta maroccana* ist ein Relikt dieser frühen Fauna, die aus Gewässern südlich der Sahara stammte (Borkenhagen 2017).

Die Aufspaltung der Gattungen *Arabibarbus*, *Carasobarbus* und *Mesopotamichthys* ist nicht aufgelöst (Borkenhagen 2017). Sie fand vermutlich im späten Miozän oder Pliozän statt (Tsigenopoulos et al. 2010, Borkenhagen 2014, Borkenhagen 2017).

Eine zweite Besiedlung des Maghreb erfolgte vom Vorderen Orient aus entlang der südlichen Küste des Mittelmeeres (Borkenhagen 2017). Sie fand während der Lago-Mare-Phase (5,50–5,33 Ma vor unserer Zeit) der Messinischen Salinitätskrise statt, als das Mittelmeer vom Atlantik abgeschnitten war und sich in den tiefen Becken große Süßwasserseen befanden. Der Wasserspiegel lag mehr als 1000 m unter dem heutigen Niveau (Krijgsman et al. 1999). Auf diese Besiedlungswelle gehen *C. fritschii*, *C. harterti* und '*L.*' *reinii* zurück (Borkenhagen 2017). Zur selben Zeit erreichten vermutlich auch die Vertreter der Gattung *Luciobarbus* Marokko.

Die Abspaltung von *C. kosswigi* und *C. sublimus* von den anderen vorderorientalischen *Carasobarbus*-Arten kann keinem bestimmten paläogeographischen Ereignis zugeordnet werden (Borkenhagen 2017).

Durch seine zentrale Lage zwischen Jordan und Orontes im Westen, den iranischen Zuflüssen zum Persischen Golf im Osten und der Arabischen Halbinsel im Süden stellte das Euphrat-Tigris-System eine wichtige Drehscheibe für die Besiedlung des Vorderen Orients mit Torini dar (Borkenhagen 2017). Im Miozän waren die Vorläufer von Jordan und Orontes mit dem Euphrat verbunden (Krupp 1985b, Heller 2017). Der Jordan verlor seine Verbindung zum Euphrat im Pliozän (Krupp 1985b). Dadurch wurde die Stammeslinie *C. canis* von der Stammeslinie von *C. apoensis*, *C. chantrei*, *C. exulatus* und *C. luteus* getrennt (Borkenhagen 2017). Im Pliozän wurde die Arabische Halbinsel von den Vorläufern der Arten *A. arabicus*, *A. hadhrami* und *C. exulatus* besiedelt (Borkenhagen 2014, Borkenhagen 2017). Historische Flusssysteme, wie z. B. Wadi al-Batin und Wadi ar-Rimah, stellen mögliche Verbindungen dar (Beineke 2006, Borkenhagen 2014, Borkenhagen 2017).

Als der Orontes seine Verbindung zum Euphrat verlor, wurden die Vorläufer von *C. chantrei* von *C. apoensis* und *C. luteus* isoliert (Borkenhagen 2017). Seitdem hat es keine Verbindung zwischen Jordan und Orontes mehr gegeben (Krupp 1985b, Kinzelbach 1987, Por 1989, Chorowicz et al. 2005, Heller 2007).

Bei *C. luteus* finden sich zwei sehr unterschiedliche Linien mitochondrialer Haplotypen (Borkenhagen et al. 2011, Borkenhagen 2017). Der Grund dafür könnte historischer Polymorphismus sein.

Die genetische Distanz zwischen *C. apoensis* und *C. luteus* ist gering (Borkenhagen 2017). Dies deutet auf eine relativ kurze Isolationszeit hin. Während der humiden Klimaphasen des Pleistozäns und möglicherweise sogar bis ins Holozän stellten Wadi al-Batin und Wadi ar-Rimah eine mögliche Verbindung zwischen dem Euphrat-Tigris-System und den Gewässern der Arabischen Halbinsel dar (Al-Sulaimi and Pitty 1995, Beinecke 2006, Berger et al. 2012, Engel et al. 2012, Drake et al. 2013, Rosenberg et al. 2013, Borkenhagen 2014, Borkenhagen 2017). Über diese Verbindung könnten die Vorfahren von *C. apoensis* die Gewässer des Hedschas-Gebirges erreicht haben.

Introduction

In my thesis I examine the taxonomy, phylogeny, and zoogeography of the hexaploid Torini of the Middle East and North Africa. The first step is a taxonomic revision of the relevant genera and species with morphological methods. Building on that, the geographic distribution and information on ecology and conservation status are compiled. The phylogenetic relationships of the species are analysed by molecular phylogenetic methods. The resulting phylogenetic hypothesis is discussed with reference to the paleogeographic development of the area of occurrence, in order to draw conclusions on the colonisation history and events that shaped the evolution of Torini.

The study organisms

With more than 200 valid species (Eschmeyer 2015), the tribe Torini Karaman, 1971 (family Cyprinidae) is a diverse group of primary freshwater fishes, distributed over Africa, the Middle East, and Indomalaya (Krupp 1985b, Yang et al. 2015, Coad 2016, Vreven et al. 2016). They belong to the subfamily Cyprininae (Yang et al. 2015) and are characterised by being tetraploid or hexaploid (Arai 2011, Berrebi et al. 2014, Yang et al. 2015), having large scales, and a smooth and ossified last unbranched ray in the dorsal fin. In the Middle East and North Africa, where they are represented by the genera *Arabibarbus* Borkenhagen, 2014, *Carasobarbus* Karaman, 1971, *Mesopotamichthys* Karaman, 1971, and *Pterocapoeta* Günther, 1902, as well as the species '*Labeobarbus*' *reinii* Günther, 1874, they are an important component of the autochthonous freshwater fish fauna, and occur in most large river systems of the Levant, Arabia, Mesopotamia, Iran, and Morocco (Heckel 1843, Boulenger 1909, Boulenger 1911, Pellegrin 1921, Banister and Clarke 1977, Krupp 1983a, Krupp 1985b, Borkenhagen and Krupp 2013, Borkenhagen 2014, Coad 2016).

The scientific description of Middle Eastern and North African Torini began in the middle of the 19th century. Prominent ichthyologists of that time, like Achille Valenciennes and Johann Jakob Heckel, were the first to describe species from the Jordan and Mesopotamia (Cuvier and Valenciennes 1842, Heckel 1843, Borkenhagen and Krupp 2013). At the end of the 19th and the beginning of the 20th century Albert Günther and George Albert Boulenger studied the freshwater fishes of Morocco (Günther 1874a, Boulenger 1902, Borkenhagen and Krupp 2013). Although freshwater fish from Arabia were known since the middle of the 19th century, the first Arabian species of Torini was described as recently as the middle of the 20th century (Trewavas 1941). Three of the four Arabian species of Torini were described less than 40 years ago (Banister and Clarke 1977, Borkenhagen 2014).

Prior to this study the validity of many nominal species of Torini from the Middle East and North Africa was unclear and their generic assignment changed frequently. Many species were listed in the genus *Barbus* sensu lato. *Barbus* s. l. was a “monstrous aggregation” (Myers 1960) that contained more than 800 phylogenetically unrelated species from Africa, Asia and Europe, and was in urgent need of revision (Berrebi et al. 1996). For phylogenetic purposes morphological characters turned out to be largely inconclusive in this group of fishes, due to high intraspecific variability, low interspecific variability, and a high amount of homoplasy (Berrebi et al. 1996). Despite Karaman's (1971) efforts no acceptable generic concept for Middle Eastern Torini existed until recently. With the onset of molecular methods the situation improved considerably and now reasonable hypotheses of evolutionary relationships exist for many taxa, formerly subsumed in *Barbus* s. l. (Durand et al. 2002, Tsigenopoulos et al. 2003, Tsigenopoulos et al. 2010, Levin et al. 2012, Berrebi et al. 2014, Casal-Lopez et al. 2015, Doadrio et al. 2016). The Middle Eastern Torini however still proved to be problematic, due to the scantiness of material and the difficulties to obtain fresh tissues for molecular analysis. Karaman (1971) recognised the Torini as a group of closely related species. Banister and Clarke (1977) and Krupp (1983a, 1985b) proposed the existence of a monophyletic group of species, clearly distinct from all other Torini in the Middle East and North Africa. This group was later formally revised and classified as *Carasobarbus*, based on morphological examination (Ekmekçi and Banarescu 1998). The results were eventually confirmed and extended by molecular genetic studies, based on the mitochondrial cytochrome *b* marker (Durand et al. 2002, Tsigenopoulos et al. 2010). These studies still suffered from an incomplete taxon sampling of Middle Eastern and North African species and failed to draw convincing nomenclatorial consequences.

The present study considerably extended the sample size of morphologically examined specimens (Borkenhagen and Krupp 2013, Borkenhagen 2014) and also the taxon sampling for molecular phylogenetic analysis (Borkenhagen et al. 2011, Borkenhagen 2014, Borkenhagen 2017). It significantly improved the understanding of species diversity and phylogenetic relationships within the Torini of the Middle East and North Africa and a reasonable generic concept was proposed (Borkenhagen and Krupp 2013, Borkenhagen 2014, Borkenhagen 2017).

The study area

Situated between Europe, Asia, and Africa, the Middle East is the only transition zone between three zoogeographic realms in the world (Krupp 1983b, Krupp et al. 2009). It lies between the Palaearctic, Indomalayan, and Ethiopian realm. In the past it was an important pathway for terrestrial and limnetic animals, but with the onset of hyperarid conditions it also acts as a barrier for their dispersal.

Up to the Oligocene, Africa and Eurasia were divided by the Tethys Sea. About 19 Ma ago, in the early Miocene, the African continent collided with Eurasia and the *Gomphotherium* landbridge was formed (Harzhauser et al. 2007). This facilitated the exchange of terrestrial and limnetic organisms between these continents. After an initial humid phase, conditions became more arid in the upper Miocene, and the hitherto continuous freshwater habitats became more and more isolated from each other (Krupp and Schneider 1988). This fragmentation led to a high degree of endemism in freshwater organisms (Krupp and Schneider 1988). Since the onset of large scale desertification in the upper Miocene, the Middle East turned into an in-crossable barrier to freshwater fishes (Krupp and Schneider 1988).

Nowadays most of the Middle East and North Africa is characterised by a depauperate freshwater fish fauna. The Arabian Peninsula for example, is almost as large as India, but hosts only 17 species of primary freshwater fishes (Krupp 1983a, Borkenhagen 2014), whereas more than 930 species are known from India (Krupp 1983a, Bagra et al. 2009). Other parts of the Middle East, such as Mesopotamia or Iran, have more diverse species inventories (Coad 1996, Abdoli 2000, Jouladeh-Roudbar et al. 2015, Coad 2016).

With an area of 879790 km^2, the Tigris-Euphrates river basin is the largest freshwater system in the Middle East (Coad 1996, FAO 2009b). From a zoogeographic perspective it forms a continuous unit (Banister 1980). Tigris and Euphrates both arise in the Turkish high plateau and flow for more than 2600 km, before they discharge into the Persian Gulf (Rzóska and Talling 1980). The Euphrates River arises in the Anatolian highlands (FAO 2009b). After entering Syria, it receives (or received) its largest tributaries, the Queiq and the Nahr al-Khabur (FAO 2009b). The Tigris River flows east of the Euphrates. Tigris and Euphrates arise as fast flowing highland streams, turn to large, slow flowing rivers, which meander through the Mesopotamian desert plains, and join to form the Shatt al-Arab. The Shatt al-Arab is joined by the Karun in a delta, which is characterised by swamps and marshland (Rzóska and Talling 1980, FAO 2009b). This leads to high habitat diversity with different ecological conditions and an ichthyofauna (52 species in 23 genera and 7 families) that compares to the Indus and the Nile in terms of generic diversity (Coad 1996).

The Orontes (or Nahr al-Asi) drains an area of 24660 km^2 in the northern Levant (FAO 2009b). Its source lies in the Lebanese mountains (FAO 2009a). The whole river is characterised by a constant change of fast and slow flowing stretches (Krupp 1985b, FAO 2009a). The Karasu Çayı and the Afrin Nehri, its biggest tributaries, join the Orontes through Lake Amik and the Kücük Asi (Krupp 1985b, FAO 2009a). Lake Amik was drained in the 1950's (Krupp 1985b). The Orontes reaches the Mediterranean Sea near Samandağ (FAO 2009a).

The Orontes, in its present form, is of Pleistocene origin (Krupp 1985b). The Proto-Orontes drained eastward, and was connected to the Queiq and the Euphrates (Krupp 1985b).

The Jordan River flows through the central part of the Dead Sea Transform fault system. Its river basin covers 18500 km^2 (FAO 2009c). Its headwaters arise in the Hermon Mountain range (FAO 2009c). It collects many small tributaries from the Galilee Mountains, the Golan Heights, as well as the Judean and Samarian Hills (Goren and Ortal 1999). After the confluence of its headwaters, the Jordan flows south and crosses the Hula Valley (FAO 2009c), and then joins Lake Tiberias (FAO 2009c), with about 170 km^2 the largest freshwater lake in the Middle East (Goren and Ortal 1999). After leaving Lake Tiberias, the Jordan receives its biggest tributary, the Nahr al-Yarmuk (FAO 2009c), and eventually reaches the Dead Sea (Krupp and Schneider 1989), a highly saline closed lake (Rzóska and Talling 1980). The Jordan River features a great variety of different ecosystems (FAO 2009c) and a unique ichthyofauna (at least 26 species; Krupp and Schneider 1989, Goren and Ortal 1999).

During the Miocene the Jordan and the Euphrates were connected through the Palmyra Basin and Damascus Basin (Krupp 1985b, Por 1989, Heller 2007). The Jordan Valley started to form at the turn of Miocene to Pliocene, about 5.3 Ma ago (Krupp and Schneider 1989), and the connection between Jordan and Euphrates broke in the Pliocene (Krupp 1985b). At this stage the Jordan flowed from South to North and drained into the

Mediterranean Sea. At the beginning of the Pleistocene, the Jordan Valley deepened and became an internal drainage basin, which flowed from North to South (Krupp and Schneider 1989). Since the Pliocene no direct connection existed between the Jordan and the Orontes (Heller 2007).

The Arabian Peninsula is characterised by an arid climate, and freshwater ecosystems are fragmented and rare. Wadis, temporary streams, are the predominant form of freshwater habitat (Krupp 1983a). Most wadis are permanent only in their upper course and not one wadi reaches the sea throughout the whole year (Banister and Clarke 1977, Krupp 1983a). These hyperarid conditions are a relatively recent phenomenon (Banister and Clarke 1977, Krupp 1983a). Up to 17000 years ago, rivers and freshwater lakes existed in the centre of the Arabian Peninsula (Krupp 1983a). The last remnants of these, the Layla Lakes, dried up during the 1990s (Krupp et al. 1990, Kempe and Dirks 2008, Jennings 2010). The Hejaz Mountains in the west, the highlands and coastal plains around Sana’a in the southwest, and the Hadramaut area in the south are the only places on the Arabian Peninsula where Torini occur (Trewavas 1941, Banister and Clarke 1977, Krupp 1983a, Borkenhagen and Krupp 2013, Borkenhagen 2014).

During the Pliocene and Pleistocene several large rivers existed on the Arabian Peninsula (Beineke 2006). For example the Wadi al-Batin and Wadi ar-Rimah originated on the flanks of the Hejaz Mountains and drained into the Persian Gulf (Beineke 2006). Water flow continued until the late Pleistocene (Al-Sulaimi and Pitty 1995, Drake et al. 2013) or possibly even the early Holocene (Berger et al. 2012, Engel et al. 2012, Borkenhagen 2017).

Due to their small size, fragmentation, and delicate ecological balance, all freshwater habitats in Arabia face negative impacts by human water use (Freyhof et al. 2015).

The rivers of southern Iran drain to the Persian Gulf (e.g. Zohreh, Mand, Helleh, Kol, Naband) or form isolated inland basins (Lake Parishan, Lake Maharloo; Coad 1995). All of these were connected to the Tigris-Euphrates river system at times of low sea level, such as the last glaciation (Banister and Clarke 1977, Krupp 1983a, Wolfart 1987, Borkenhagen et al. 2011).

In the north and west, Morocco has a well-developed system of rivers. These rivers drain the Atlas and the Rif Mountain ranges. In addition to some smaller ones, the largest river draining into the Mediterranean Sea is the Oued Moulouya. The major rivers draining to the Atlantic Ocean are the Oued Sebou, the Oued Bou Regreg, the Oued Oum er Rbia, the Oued Tennsift, and the Oued Ksob / Oued Igrounzar. The Oued Sous and Oued Draa, as well as the wadis draining into the Sahara Desert are not inhabited by Torini.

At the end of the Miocene the Mediterranean Sea became isolated from the Atlantic Ocean and, as a consequence, the water level dropped more than 1000 m (Krijgsman et al. 1999). During the Lago Mare phase (5.50–5.33 Ma bp) large freshwater lakes existed in the Mediterranean basin (Krijgsman et al. 1999). All rivers draining into the Mediterranean Sea extended their course accordingly, and several of them came into contact with each other. This allowed the migration of freshwater organisms along the shores of the Mediterranean Sea (Tsigenopoulos et al. 2003).

Taxonomy

Taxonomy, and in particular the rule set that governs its practise (e.g. ICZN, ICBN), provides a framework for describing and classifying biodiversity, and allows precise communication about organisms. As such, taxonomy is the prerequisite for almost all other areas of biological research, as well as monitoring, conservation and management of biodiversity. A taxonomical system that reflects the evolutionary relationships of taxa is the most efficient way of organising information on morphological, ecological, behavioural, physiological, and other properties of organisms.

To be of practical use, a generic concept has to (1) be based on monophyletic groups that reflect the evolutionary history and phylogenetic relationships of the species, (2) be morphologically (or ecologically or biogeographically) distinct and diagnosable, and (3) be reasonably compact in the number of species it contains (Gill et al. 2005, Talavera et al. 2013). The stability of the taxonomic system and the age of lineages have been proposed as additional criteria for generic classifications, but uncertainties of age estimates and different evolutionary ages between higher level taxa make the latter criterion difficult to apply in practise (Talavera et al. 2013, Collard and Wood 2015).

The problem of species concepts is as old as the practise of taxonomy, and up to now a great number of species concepts have been proposed (Mayden 1999, Mayden 2002, De Queiroz 2007, Hendry 2009). None of these concepts met universal acceptance (Hendry 2009). Apart from several exceptions, speciation is usually a gradual process (De Queiroz

2007, Hendry 2009). Defining an objective and universally applicable threshold is thus impossible. For this reason there is usually a grey zone, in which different species concepts can lead to different conclusions (De Queiroz 2007). Numeric and quantitative methods promise objectivity, but fail to address the gradual nature of speciation processes. The *Biological Species Concept* and the *Evolutionary Species Concept* are the most popular of these concepts (Mayden 1999, Hendry 2009). The *Biological Species Concept*, however, is difficult to apply to allopatric populations (Hendry 2009) and the *Evolutionary Species Concept* is not intended as an operational concept, but rather as a theoretical framework (Mayden 1999). A practical solution to this dilemma is the separation of species conceptualisation and species delimitation (Mayden 1999, De Queiroz 2007). Species delimitation is the everyday concern of taxonomists and demands operational criteria, against which evidence from data can be judged (Mayden 1999, De Queiroz 2007). Morphological analysis (supplemented by molecular genetic data, where necessary) is the most widely used practical approach for discovering, delimitating, and describing species.

Molecular phylogenetics

Molecular genetic analyses are a cheap and efficient method for reconstructing phylogenies, when morphological characters are ambiguous and homologies are difficult to establish. Molecular phylogenetics relies on the comparison of molecular characters and computerised data analysis to infer evolutionary relationships (Knoop and Müller 2009). Early methods were based on various techniques like protein electrophoresis or DNA-DNA hybridisation. Modern methods focus on DNA or protein sequences (Knoop and Müller 2009). In the beginning, methods for phylogenetic reconstruction relied on parsimony or on distance matrices, while today most programs implement likelihood based approaches, which rely on nucleotide substitution models (Knoop and Müller 2009). Bayesian inference and maximum likelihood methods differ in some statistical assumptions, but, given enough data, both methods usually yield similar parameter estimates and recover similar topologies (Knoop and Müller 2009). Heuristic search algorithms facilitate the search for good trees in the amount of all possible trees (Knoop and Müller 2009).

Genetic markers should be chosen carefully, to be adequate for the question at hand (Knoop and Müller 2009). Mitochondrial DNA has certain shortcomings in the context of phylogenetic reconstructions (Yang et al. 2012). Mitochondrial markers are linked and have to be considered as coming from one locus (Yang et al. 2012). Due to their rapid evolution, they are not suitable for the resolution of deep nodes (Yang et al. 2012). However, the problem of establishing homology of paralog genes in nuclear markers is not easy to overcome in polyploid species (Saitoh et al. 2011, Yang et al. 2012, Pasco-Viel et al. 2014, Yang et al. 2015). For phylogenetic analyses of closely related species and zoogeographic reconstructions mitochondrial markers are useful, because they evolve fast enough to provide resolution for young speciation events and are a reliable indicator for past connections between populations.

Cytochrome *b* is a widely used marker in molecular phylogenetic analyses (Zardoya and Meyer 1996, Briolay et al. 1998, Durand et al. 2002, Miya et al. 2006, Tsigenopoulos et al. 2010, Yang et al. 2015). This leads to a high number of cytochrome *b* sequences available for comparison, though this marker might not be suitable for distantly related lineages (Miya et al. 2006). ND4 has high power in resolving phylogenetic relationships within Cypriniformes (Miya et al. 2006). Both ND4 and cytochrome *b* showed good performance in resolving tetrapod relationships (Zardoya and Meyer 1996). This is the reason for choosing these markers in the molecular phylogenetic studies presented here.

Zoogeography

Primary freshwater organisms depend on freshwater connections for their dispersal, because they cannot tolerate saline conditions. For this reason their present-day distribution and phylogenetic relationships reflect the paleogeographic development of freshwater habitats within their geographic range. Cyprinids are primary freshwater fishes that are widespread in the Middle East and North Africa, where they inhabit every major freshwater body. This makes them ideal models for biogeographic studies (Kinzelbach 1987, Krupp 1987, Heller 2007, Saitoh et al. 2011).

Knowing the zoogeographic history of a species, helps to identify and understand important events that shaped its evolution. Until the present study not much was known about the zoogeographic history of the Torini from the Middle East and North Africa. Speculations were mainly based on similarity in habitus (Trewavas 1941, Banister 1973, Banister and Clarke 1977, Krupp 1983a). The phylogenetic reconstructions presented here are the first that allow reliable zoogeographic conclusions (Borkenhagen et al. 2011, Borkenhagen 2014, Borkenhagen 2017).

Data sources and sample collection

For the present study morphological and molecular genetic data were combined. For morphological analyses more than 1550 specimens of Torini from the Middle East were examined, and additional specimens from Africa and Indomalaya were also taken into account (Borkenhagen and Krupp 2013, Borkenhagen 2014). A large part of the specimens were collected during field expeditions to Ethiopia, Iran, Jordan, Morocco, and Syria between 2005 and 2011. These are now part of the fish collection of the Senckenberg Research Institute and Museum of Nature, Frankfurt am Main. The rest of the material was already part of the Senckenberg Museum collection, studied during visits at the Natural History Museum, London, the Naturhistorisches Museum Wien, the Musée Royal de l'Afrique Centrale, Tervuren, the Muséum National d'Histoire naturelle, Paris, and the Zoologisches Museum Hamburg, or loaned from other museum collections (Borkenhagen and Krupp 2013, Borkenhagen 2014).

During the field research tissue samples were collected for molecular genetic analyses. The mitochondrial genes for cytochrome *b* (CYTB), NADH dehydrogenase subunit 4 (ND4) and the tRNAs for serine (tRNA-Ser) as well as histidine (tRNA-His) were sequenced for more than 120 specimens, representing 20 species of Torini and two species of Smiliogastrini (Borkenhagen et al. 2011, Borkenhagen 2014, Borkenhagen 2017). Sequences from NCBI GenBank (https://www.ncbi.nlm.nih.gov/genbank/) were used to complement the genetic datasets.

The studies presented here considerably extend the taxon sampling for molecular genetic analyses and complement the material for morphological examination (Borkenhagen et al. 2011, Borkenhagen and Krupp 2013, Borkenhagen 2014, Borkenhagen 2017).

Aims and components of the study

As described above, prior to the present analyses a consistent generic concept was missing and the validity of several nominal species was unclear. The morphological and genetic variability within and among species was not understood, and the factors that shaped this variability were unknown. Information on biology, habitat, and conservation status of the species was scattered in the literature. The phylogenetic relationships between species, their zoogeographic history, and the factors that shaped the evolution of

Middle Eastern and North African Torini remained unknown. This prompted the following aims of the study:

1. To define monophyletic genera, based on diagnosable characters.
2. To gather data on all nominal species of Torini in the Middle East in order to assess their validity, give a detailed re-description of all species, based on a sample of specimens large enough to evaluate the intraspecific morphological variability, and map their distribution, based on records confirmed by voucher specimens.
3. To summarise information on biology, habitat and conservation status of each species, and to discuss the taxonomic history of each species.
4. To assess the interspecific and intraspecific genetic variability and to correlate it to habitat characteristic, paleogeographic development, and evolutionary history.
5. To reconstruct the phylogenetic relationship of the Middle Eastern and North African species, in order to evaluate the present taxonomic status from a phylogenetic point of view.
6. To correlate their present day distribution and their phylogenetic relationships with their zoogeographic history and the paleogeographic evolution of the Middle East and North Africa, in order to draw conclusions on the factors that shaped their evolution.

Borkenhagen et al. 2011: Molecular systematics of *Carasobarbus* from Iran

In this study my colleagues and I investigated the interspecific and intraspecific diversity of partial cytochrome *b* sequences of *Carasobarbus* species from Iran and adjacent areas. We applied phylogenetic methods (Bayesian inference, maximum parsimony analysis) as well as methods of population genetics (haplotype network analysis). This study was the first one that included DNA sequence data for *C. sublimus*. It was also the first study to include samples for *C. luteus* and *C. kosswigi* from several different river systems in Iran and Syria. We found very different patterns of genetic diversity in these three species and proposed causal explanations for these patterns, based on ecological observations and the paleogeographic development of the region.

This study contributes to aims number 4, 5, and 6.

Borkenhagen and Krupp 2013: Taxonomic revision of the genus *Carasobarbus*

In this study Dr Krupp and I revised the genus *Carasobarbus*, based on morphological data of more than 1300 specimens. We presented an updated and extended definition of the genus, described all *Carasobarbus* species in detail, and proposed a key for their identification. We collected the available information on distribution, ecological preferences, and conservation status for each species, and summarised their taxonomic history. We found nine *Carasobarbus* species to be valid. This study was the first one to include sufficient material from different river systems, to assess intraspecific morphological variation within and between geographical populations.

This study contributes to aims number 1, 2, and 3.

Borkenhagen 2014: A new genus and species of cyprinid from the Arabian Peninsula

In this study I described a new species of Torini from the Arabian Peninsula. In addition, I re-described two closely related species from Arabia and Mesopotamia. I proposed a new genus for these three species, and analysed their phylogenetic affinities and zoogeographic history, based on phylogenetic analysis of complete cytochrome *b* sequences. This study was the first one to include DNA sequences of *A. arabicus*, *A. hadhrami* and *M. sharpeyi*. It was the first study to recognise the close phylogenetic relationships between the species of *Arabibarbus* and to reconstruct the zoogeographic relationships of Arabian Torini, based on molecular phylogenetic methods.

This study contributes to aims number 1, 2, 5, and 6.

Borkenhagen 2017: Molecular phylogeny of Torini from the Middle East and North Africa

In this study I investigated the phylogeny of the Torini from the Middle East and North Africa, based on the mitochondrial markers cytochrome *b*, ND4 and the tRNAs for histidine and serine. I discussed the taxonomy and evolutionary history of the Torini in light of the results of the phylogenetic analysis. This study presented the first phylogenetic analysis of Middle Eastern and North African Torini with a nearly complete taxon sampling and based on multiple mitochondrial markers. It is the first study that resolves most of the phylogenetic relationship of the Middle Eastern and North African Torini. It confirms the phylogenetic position of these species within all Torini. Important historical events were identified that had major implications for the evolution of the Torini.

This study contributes to aims 1, 4, 5, and 6.

Discussion

The diversity of the Torini from the Middle East and North Africa was investigated at the genus level, species level, and intraspecific level with morphological (Borkenhagen and Krupp 2013, Borkenhagen 2014), and molecular methods (Borkenhagen et al. 2011, Borkenhagen 2014, Borkenhagen 2017). Of the 28 nominal species of Torini from the Middle East and North Africa, 15 were found to be valid (Table 1, Borkenhagen and Krupp 2013, Borkenhagen 2014, Borkenhagen 2017). For this study type material of most nominal species from the Middle East and North Africa (25 of 28) was examined. Additional material from museum collections and freshly collected material was used to establish the geographical distribution of each species and to assess the intraspecific morphological variability (Borkenhagen and Krupp 2013, Borkenhagen 2014). Because interspecific morphological differences were minor and a phylogenetic interpretation of morphological characters was not feasible in many cases (Berrebi et al. 1996, Borkenhagen and Krupp 2013, Vreven et al. 2016), more than 120 mitochondrial DNA sequences, representing 14 species of Torini from the Middle East and North Africa, three species of Torini from sub-Saharan Africa, and three species of Torini from Indomalaya, were collected and analysed. In addition, two sequences of small, diploid African barbs (Cyprinidae, tribe Smiliogastrini) were included in the analyses. Sequences from NCBI GenBank were used to complement the dataset. Information on biology, habitat, and conservation status of the species was compiled from the literature. The paleogeographic development of the area was correlated with the phylogenetic relationships of the species, in order to draw conclusions on the factors that shaped the evolution of the Middle Eastern and North African Torini.

This approach yielded new information on the taxonomy, geographical ranges, phylogenetic relationships, and zoogeographic history of the Torini of the Middle East and North Africa. The validity of all nominal taxa was investigated and assessed, based on a consistent species concept and uniform criteria for species delimitation. A generic concept for all species from the Middle East and North Africa was developed, based on monophyletic groups that are morphologically diagnosable. The phylogenetic relationships of the species were mostly well resolved, based on the analysis of mitochondrial DNA markers. Based on the discussion of the paleogeographic development of the region, several important events and key factors that shaped the evolution of the Torini, were identified.

The following discussion summarises the results and conclusions of Borkenhagen et al. (2011), Borkenhagen and Krupp (2013), Borkenhagen (2014) and Borkenhagen (2017), and puts them into perspective with the state of knowledge prior to these studies and other important advances in the taxonomy, phylogeny, and zoogeography of Torini. Gaps in the present state of knowledge are identified and possible future research questions are pointed out.

Table 1: List of species group taxa of Middle Eastern and North African Torini. The left column lists the original name used in the scientific description; the right column lists the present status of each nominal taxon.

original taxon name	**valid taxon name**
Arabibarbus hadhrami Borkenhagen, 2014	*Arabibarbus hadhrami* Borkenhagen, 2014
Barbus apoensis Banister and Clarke, 1977	*Carasobarbus apoensis* (Banister and Clarke, 1977)
Barbus arabicus Trewavas, 1941	*Arabibarbus arabicus* (Trewavas, 1941)
Barbus beddomii Günther, 1868	Carasobarbus canis (Valenciennes in Cuvier and Valenciennes, 1842)
Barbus canis Valenciennes in Cuvier and Valenciennes, 1842	Carasobarbus canis (Valenciennes in Cuvier and Valenciennes, 1842)
Barbus continii Vinciguerra, 1926	*Carasobarbus canis* X *Luciobarbus longiceps*
Barbus exulatus Banister and Clarke, 1977	*Carasobarbus exulatus* (Banister and Clarke, 1977)
Barbus faoensis Günther, 1896	*Mesopotamichthys sharpeyi* (Günther, 1874)
Barbus fritschii Günther, 1874	*Carasobarbus fritschii* (Günther, 1874)
Barbus grypus Heckel, 1843	*Arabibarbus grypus* (Heckel, 1843)
Barbus harterti Günther, 1901	*Carasobarbus harterti* (Günther, 1901)
Barbus parieschanica Wossughi et al., 1983	*Carasobarbus luteus* (Heckel, 1843)
Barbus paytonii Boulenger, 1911	*Carasobarbus fritschii* (Günther, 1874)
Barbus reinii Günther, 1874	'*Labeobarbus*' *reinii* (Günther, 1874)
Barbus riggenbachi Günther, 1902	*Carasobarbus fritschii* (Günther, 1874)
Barbus rothschildi Günther, 1901	*Carasobarbus fritschii* (Günther, 1874)
Barbus sharpeyi Günther, 1874	*Mesopotamichthys sharpeyi* (Günther, 1874)
Barbus sublimus Coad and Najafpour, 1997	*Carasobarbus sublimus* (Coad and Najafpour, 1997)
Barynotus verhoeffi Battalgil, 1942	*Carasobarbus chantrei* (Sauvage, 1882)
Capoeta atlantica Boulenger, 1902	*Carasobarbus fritschii* (Günther, 1874)
Capoeta waldoi Boulenger, 1902	*Carasobarbus fritschii* (Günther, 1874)
Cyclocheilichthys kosswigi Ladiges, 1960	*Carasobarbus kosswigi* (Ladiges, 1960)
Labeobarbus chantrei Sauvage, 1882	*Carasobarbus chantrei* (Sauvage, 1882)
Labeobarbus kotschyi Heckel, 1843	*Arabibarbus grypus* (Heckel, 1843)
Pterocapoeta maroccana Günther, 1902	*Pterocapoeta maroccana* Günther, 1902
Systomus albus Heckel, 1843	*Carasobarbus luteus* (Heckel, 1843)
Systomus albus var. *alpina* Heckel, 1843	*Carasobarbus luteus* (Heckel, 1843)
Systomus luteus Heckel, 1843	*Carasobarbus luteus* (Heckel, 1843)

The tribe Torini Karaman, 1971

The classification of families and subfamilies within the order Cyprinoidea was subject to frequent changes (Nelson 2006, Saitoh et al. 2006, Mayden et al. 2008, Mayden et al. 2009, Yang and Mayden 2010, Yang et al. 2010, Yang et al. 2012, Yang et al. 2015). The tribes Barbini, Schizopygopsini, Schizothoracini, Spinibarbini, Acrossocheilini, Cyprinini, Poropuntiini, Smiliogastrini, Torini, Labeonini, and Probarbini belong to the subfamily Cyprininae (Yang et al. 2015). Karaman (1971) was the first to define the tribe Torini for the genera *Tor* Gray, 1834 (type genus), *Pseudotor* Karaman, 1971, *Carasobarbus*, *Mesopotamichthys*, *Varicorhinus* Rüppell, 1835, and *Kosswigobarbus* Karaman, 1971. His definition of Torini also included the genera *Garra* Hamilton, 1822, *Typhlogarra* Trewavas, 1955, *Hemigarra* Karaman, 1971, *Hemigrammocapoeta* Pellegrin, 1927, *Labeo* Cuvier, 1816, and *Tylognathoides* Tortonese, 1938, which are only distantly related to the Torini and are nowadays considered Labeonini (Stiassny and Getahun 2007, Yang et al. 2015).

As defined here, Torini include the Indomalayan genera *Hypselobarbus* Bleeker, 1860, *Osteochilichthys* Hora, 1942, *Lepidopygopsis* Raj, 1941, *Naziritor* Mirza and Javed, 1985, *Neolissochilus* Rainboth, 1985, and *Tor*, the African genera *Labeobarbus* Rüppell, 1835 (including *Varicorhinus)*, *Acapoeta* Cockerell, 1910, and *Sanagia* Holly, 1926, as well as the Middle Eastern genera *Arabibarbus*, *Carasobarbus*, *Mesopotamichthys*, *Pterocapoeta,* and '*Labeobarbus*' (Yang et al. 2015, Vreven et al. 2016, Borkenhagen 2017). Torini are a monophyletic group (Yang et al. 2015, Borkenhagen 2017), characterised by large scales and a smooth, (more or less) ossified last unbranched dorsal-fin ray (Borkenhagen 2017).

Indomalaya

The representatives of the genera *Neolissochilus* Rainboth, 1985 and *Tor* Gray, 1834 are frequently called mahseers (Laskar et al. 2013, Hoàng et al. 2015). They are evolutionary tetraploid (Arai 2011, Yang et al. 2015). The main distinguishing characters between the genera are the possession of a fleshy lobe on the lower lip and a high number of gill rakers on the lower limb of the first gill arch in *Tor*, and the absence of a fleshy lobe and a low number of gill rakers in *Neolissochilus* (Rainboth 1985, Laskar et al. 2013, Hoàng et al. 2015). Mahseers occur in Afghanistan, Pakistan, India, Southeast Asia, the Malayan Peninsula, China, and on the Indonesian islands Borneo, Java, and Sumatra (Roberts 1999, Laskar et al. 2013, Khaironizam et al. 2015).

The genus *Hypselobarbus* Bleeker, 1860 is characterised by the possession of one or two pairs of barbels, long, branched gill rakers, a strongly convex distal margin of the anal fin in adult specimens with branched anal-fin rays two to four considerably longer than the first branched ray (Knight et al. 2013). *Hypselobarbus* species are evolutionary tetraploid

(Arai 2011). The genus is endemic to India, and the Western Ghats of India is the main area of its distribution (Arunachalam et al. 2012). Despite a recent molecular (Arunachalam et al. 2012) and morphological (Knight et al. 2013) revision, *Hypselobarbus* is paraphyletic in its present form (Yang et al. 2015). The validity of the genus was under debate (Arunachalam et al. 2012, Knight et al. 2013, Arunachalam et al. 2014, Khare et al. 2014) until the designation of a neotype for *Barbus mussullah* Sykes, 1839 (Knight et al. 2014). The number of species in this genus is still growing (Arunachalam et al. 2016a, Arunachalam et al. 2016b, Arunachalam et al. 2016c). The *Hypselobarbus* species analysed in Yang et al. (2015) are genetically clearly distinct from *Tor*.

The genus *Naziritor* Mirza and Javed, 1985 from India and Pakistan belongs to the Torini (Khare et al. 2014, Yang et al. 2015). The phylogenetic position of this genus is not clear, because the type species (*Tor zhobensis* Mirza, 1967) has not yet been included in molecular studies, yet.

Osteochilichthys Hora, 1942 is characterised by a lower jaw with a sharp trenchant edge, a slightly papillated or smooth lower lip that is adnate to the lower jaw but not covering the cutting edge, upper lip fimbriated or entire, adnate to upper jaw, a rostral fold that overhangs the median part of the upper lip in adults, snout covered with tubercles, last unbranched ray of dorsal fin not ossified and not serrated, and 10 to 11 branched dorsal-fin rays (Pethiyagoda and Kottelat 1994). This genus encompasses four species (Eschmeyer 2015), all of which occur in India.

With a sheath of enlarged scales covering the belly and the base of the anal fin, a serrated last unbranched dorsal-fin ray, and a lateral line that is distinctly curved in the caudal region (Dahanukar et al. 2013), the monospecific genus *Lepidopygopsis* Raj, 1941 is morphologically very distinct from other Torini. It resembles schizothoracines (Cyprinidae, tribe Schizothoracini). Two molecular phylogenetic studies included it in Torini, based on the same set of sequences (Dahanukar et al. 2013, Yang et al. 2015). This remarkable result warrants reappraisal with independent data (Borkenhagen 2017).

Sub-Saharan Africa

Hexaploid Torini are widespread in sub-Saharan Africa and occur in all major river systems (Vreven et al. 2016). Of about 275 nominal species, about 125 are currently considered valid (Vreven et al. 2016). The genera *Labeobarbus* Rüppell, 1835 and *Varicorhinus* Rüppell, 1835 were originally differentiated by the thickness of the lips and the presence/absence of cartilaginous tubercles on the snout (Rüppell 1835). Starting with Boulenger (1909), most authors used the presence of a sharp horny sheath on the lower jaw, to define the genus *Varicorhinus*, but the usefulness of this character is dubious (Tweddle and Skelton 1998, Levin 2012, Vreven et al. 2016). Together *Labeobarbus* and *Varicorhinus* form a monophyletic group (Tsigenopoulos et al. 2010, Yang et al. 2015), but they are not reciprocally monophyletic, and *Varicorhinus* should be considered a synonym of *Labeobarbus* (Tsigenopoulos et al. 2010, Berrebi et al. 2014, Vreven et al. 2016). The monospecific genera *Sanagia* Holly, 1936 and *Acapoeta* Cockerell, 1910 belong to Torini (Yang et al. 2015, Vreven et al. 2016). *Sanagia* and *Acapoeta* might compromise the monophyly of *Labeobarbus* (Yang et al. 2015).

Generic concept for the Middle Eastern and North African Torini

The generic concept for the Middle Eastern Torini suggested below is based on the criteria monophyly, morphological diagnosability, and reasonable compactness. The proposed genera fulfil these criteria, because all of them are monophyletic groups that can be diagnosed by a combination of morphological characters. They encompass one to nine species each.

Arabibarbus Borkenhagen, 2014

Arabibarbus is characterised by medium to large body size, modally eight branched dorsal and modally five branched anal fin rays, large shield-shaped scales with numerous parallel radii, a lateral line with 29 to 44 scales, pharyngeal teeth that are hooked at their tips, their count being 2.3.5-5.3.2, and the possession of two pairs of barbels (Borkenhagen 2014). *Arabibarbus hadhrami* Borkenhagen, 2014 is the type species of this genus. Molecular genetic analyses demonstrate that *Arabibarbus* is a monophyletic group (Borkenhagen 2014, Borkenhagen 2017). Based on their phylogenetic position, species of this genus are most probably hexaploid (Tsigenopoulos et al. 2010, Berrebi et al. 2014, Borkenhagen 2014, Yang et al. 2015, Borkenhagen 2017).

Species of this genus were placed in the genera *Barbus* Daudin, 1805, *Labeobarbus*, and *Tor* by former authors (Borkenhagen 2014). However, these generic names are not available for this group of species, because their type species (*Cyprinus barbus* Linnaeus, 1758, *Labeobarbus nedgia* Rüppell, 1835, and *Tor hamiltonii* Gray, 1834 respectively) are not closely related to *Arabibarbus* (Borkenhagen 2014). *Arabibarbus arabicus* (Trewavas, 1941), *A. grypus* (Heckel, 1843) and *A. hadhrami* Borkenhagen, 2014 differ from the species of the genus *Carasobarbus*, by having five instead of six branched rays in the anal fin and modally eight instead of modally nine to 10 branched rays in the dorsal fin (Borkenhagen and Krupp 2013, Borkenhagen 2014). *Mesopotamichthys* has no barbels, whereas *Arabibarbus* has two pairs (Karaman 1971, Borkenhagen 2014). *Pterocapoeta* Günther, 1902 has more than nine branched rays in the dorsal fin and lips without horny sheaths (Günther 1902). Phylogenetic analyses show a clear distinction between the genera *Arabibarbus*, *Carasobarbus*, *Mesopotamichthys*, and *Pterocapoeta* (Borkenhagen 2014, Borkenhagen 2017). This justified the description of a new genus (Borkenhagen 2014).

Carasobarbus Karaman, 1971

Carasobarbus Karaman, 1971 is diagnosed by medium body size, 9 or 10 branched dorsal-fin rays, six branched anal-fin rays, large shield-shaped scales with numerous parallel radii, lateral line with 25 to 39 scales, hooked pharyngeal teeth numbering 2.3.5-5.3.2 or 2.3.4-4.3.2, and one or two pairs of barbels (Borkenhagen and Krupp 2013). Species of *Carasobarbus* are evolutionary hexaploid (Tsigenopoulos et al. 2010, Arai 2011, Berrebi et al. 2014, Yang et al. 2015, Borkenhagen 2017).

The monophyly of *Carasobarbus* was indicated in several molecular phylogenetic studies (Tsigenopoulos et al. 2010, Borkenhagen 2014, Yang et al. 2015), and confirmed by a molecular study with a complete taxon sampling (Borkenhagen 2017). The possession of six branched rays in the anal fin and more than eight branched rays in the dorsal fin are synapomorph characters of *Carasobarbus* (Borkenhagen and Krupp 2013).

Over the time at least 14 different generic names (*Barbellion* Whitley, 1931; *Barbus; Barynotus* Günther, 1868; *Capoeta* Valenciennes, 1842; *Carasobarbus; Cyclocheilichthys* Bleeker, 1859; *Kosswigobarbus; Labeobarbus; Luciobarbus* Heckel, 1843; *Pseudotor; Puntius* Hamilton, 1822; *Systomus* McClelland, 1838; *Tor* and *Varicorhinus*) were applied to members of *Carasobarbus* (Borkenhagen and Krupp 2013). Most of these names have to be rejected, because their type species are unrelated to *Carasobarbus* species (Durand et al. 2002, Tsigenopoulos et al. 2010, Yang et al. 2015, Borkenhagen 2017) or because they do not share the diagnostic characters of the genus (Borkenhagen and Krupp 2013). Until the revision of the genus (Borkenhagen and Krupp 2013), *Carasobarbus*, *Kosswigobarbus,* and *Pseudotor* were available. Borkenhagen and Krupp (2013) found them to be subjective synonyms and, acting as first reviser, selected *Carasobarbus* to have priority, in accordance with article 24.2 of the International Code for Zoological Nomenclature (ICZN 1999). Thus *Carasobarbus* is the valid name for this genus.

Within *Carasobarbus* two monophyletic subgroups can be identified, based on synapomorph characters. *Carasobarbus fritschii* (Günther, 1874) and *C. harterti* (Günther, 1901) share the possession of pharyngeal bones with four teeth in the medial row, while all other *Carasobarbus* species have five teeth in the medial row (Borkenhagen and Krupp 2013). This group is congruent with *Pseudotor*. C*arasobarbus kosswigi* (Ladiges, 1960) and *C. sublimus* (Coad and Najafpour, 1997) have a spatulate lower jaw and a lower lip with a median lobe (Borkenhagen and Krupp 2013). Both characters are unique to these two species and not found in any congeners or other Middle Eastern Torini (Borkenhagen and Krupp 2013). These two species are congruent with *Kosswigobarbus*. Molecular phylogenetic analysis supports the monophyly of both groups (Borkenhagen 2017). Accepting *Pseudotor* and *Kosswigobarbus* as valid genera would render *Carasobarbus* paraphyletic, according to several phylogenetic hypotheses, based on mitochondrial cytochrome *b* (Tsigenopoulos et al. 2010, Borkenhagen 2014, Yang et al. 2015), whereas the most recent phylogenetic reconstruction, based on a larger set of mitochondrial markers, does not speak against it (Borkenhagen 2017). Nevertheless I recommend leaving *Pseudotor* and *Kosswigobarbus* in the synonymy of *Carasobarbus*, in order to avoid a proliferation of small and insufficiently distinguished genera.

Mesopotamichthys Karaman, 1971

The genus *Mesopotamichthys* is monospecific. Its type species is *Barbus sharpeyi* Günther, 1874. It is characterised by not having barbels, pharyngeal teeth (2.3.5-5.3.2) intermediate between spoon-shaped and shovel-shaped, developed and fleshy lips, broad orbital bones, short Lacrimale, sensory canals on head similar to those of *Tor*, dorsal fin with eight branched rays, last unbranched ray moderately ossified, anal fin with five branched rays, relatively large scales with numerous parallel or convergent radii, and a black peritoneum (Karaman 1971). This combination of characters is not found in any other genus of Torini in the Middle East and North Africa (Karaman 1971, Ekmekçi and Banarescu 1998, Borkenhagen and Krupp 2013, Borkenhagen 2014, Borkenhagen 2017). *Mesopotamichthys* is genetically distinct from *Arabibarbus*, *Carasobarbus*, *Pterocapoeta*, and '*L.*' *reinii* (Borkenhagen 2014, Borkenhagen 2017). Based on its phylogenetic position, the genus *Mesopotamichthys* is most likely hexaploid (Borkenhagen 2014, Borkenhagen 2017).

Pterocapoeta Günther, 1902

The genus *Pterocapoeta* is characterised by scales of moderate size (about 45 in the lateral line), a dorsal fin with a weakly ossified ray, more than nine branched rays in the dorsal fin, dorsal fin commencing in front of the pelvic fins, a broad and obtusely rounded snout, an inferior, traverse and slightly arched mouth, smooth lips, lower lip with a flexible horny sheath, lack of lower labial fold and symphysal tubercles, one pair of short barbels that are rudimentary or even completely absent in some specimens, no enlarged anal scales, and pharyngeal teeth numbering 2.3.4-4.3.2 (Günther 1902). This combination of characters is not found in any other genus of Torini in the Middle East and North Africa (Karaman 1971, Ekmekçi and Banarescu 1998, Borkenhagen and Krupp 2013, Borkenhagen 2014, Borkenhagen 2017). *Pterocapoeta* is genetically clearly distinct from the other Middle Eastern and North African Torini, based on analyses of the mitochondrial DNA markers (Tsigenopoulos et al. 2010, Berrebi et al. 2014, Yang et al. 2015, Borkenhagen 2014, Borkenhagen 2017). Based on its phylogenetic position, the genus *Pterocapoeta* is most likely hexaploid (Tsigenopoulos et al. 2010, Berrebi et al. 2014, Borkenhagen 2014, Borkenhagen 2017). At present, the genus is restricted to one species from North Africa (Eschmeyer 2015). Two cytochrome *b* sequences indicate that *Labeobarbus bynni occidentalis* (Boulenger, 1911), GenBank no. AF180870 and *Labeobarbus habereri* (Steindachner, 1912), AF180869 from sub-Saharan Africa are closely related to *P. maroccana* Günther, 1902 (Tsigenopoulos et al. 2010, Yang et al. 2015). The sequence AF180870 does not cluster with other *Labeobarbus bynni* (Forsskål, 1775) sequences and its identity is doubtful (Tsigenopoulos et al. 2010). A revision of *Pterocapoeta* cannot be limited to North African species, but has to consider species from sub-Saharan Africa, as well.

'*Labeobarbus*' *reinii* (Günther, 1874)

‘*Labeobarbus*’ *reinii* forms an isolated lineage within the Middle-Eastern lineage of Torini (Tsigenopoulos et al. 2010, Berrebi et al. 2014, Yang et al. 2015, Borkenhagen 2017). Should this result be corroborated by further studies, the description of a new genus will be justified. I preliminarily use the genus '*Labeobarbus*', because no generic name is currently available for this species (Yang et al. 2015).

Middle Eastern and North African species of Torini

The main criterion for recognizing the species listed below was morphological dissimilarity. The null hypothesis “two populations belong to the same species” was only rejected when there was sufficient evidence. Slight differences between allopatric populations were only considered significant, when these differences were consistently observed in a sufficiently large sample of specimens. Molecular genetic characters were used to verify these decisions.

***Arabibarbus arabicus* (Trewavas, 1941)**

Arabibarbus arabicus has 29 to 38 scales in the lateral line, the wedge-shaped head is long (24.3–30.8 % SL) and high (13.9–17.0 % SL), the body is strong and laterally flattened, the dorsal fin is high (22.9–35.5 % SL) and well ossified, the pectoral fins (18.0–22.2 % SL) and pelvic fins (14.9–18.6 % SL) are short (Trewavas 1941, Banister and Clarke 1977, Krupp 1983a, Borkenhagen 2014).

The type locality of *Arabibarbus arabicus* is the Wadi Kharid, 20 miles north-east of Sana’a, the capital of Yemen (Trewavas 1941). It was originally described in the genus *Barbus* (Trewavas 1941). Karaman (1971) placed the species in the genus *Tor*. *Cyprinus arabicus* Valenciennes (ex Ehrenberg) in Cuvier and Valenciennes, 1842 is not a homonym to *A. arabicus*, because it refers to a species of *Garra* (Borkenhagen 2014).

Arabibarbus arabicus inhabits the south-western Arabian Peninsula (Yemen and Saudi Arabia), where it occurs in wadis draining inland, as well as wadis draining to the Red Sea (Trewavas 1941, Banister and Clarke 1977, Krupp 1983a, Borkenhagen 2014).

Arabibarbus grypus (Heckel, 1843)

Arabibarbus grypus has 33 to 44 scales in the lateral line, the round head is shorter (19.9–25.4 % SL) and lower (12.6–16.0 % SL) than in its congeners, the body is cylindrical, the dorsal fin is short (17.8–24.2 % SL) and only weakly ossified, the pectoral fins (16.0–19.3 % SL) and pelvic fins (14.3–17.5 % SL) are shorter than in *A. hadhrami* (Heckel 1843, Borkenhagen 2014, Coad 2016).

The type locality of *Arabibarbus grypus* is the Tigris at Mosul (Heckel 1843). *Arabibarbus grypus* was originally described as *Barbus grypus*. Karaman (1971) transferred the species to the genus *Tor*. The majority of other authors did not accept this proposal (e.g. Krupp 1985b, Coad 1995, Abdoli 2000, Krupp and Schneider 2008, Tsigenopoulos et al. 2010; but Coad 2016 adopts the generic name *Tor* for this species). *Labeobarbus kotschyi* Heckel, 1843, described from the Tigris at Mosul, is a junior synonym (Krupp 1985b, Coad 1991, Coad 1995, Coad 1996, Borkenhagen 2014, Jouladeh-Roudbar et al. 2015, Coad 2016).

Arabibarbus grypus occurs in the Tigris-Euphrates basin and in the rivers of southern Iran (Heckel 1843, Kähsbauer 1963, Krupp 1985b, Coad 1996, Borkenhagen 2014, Coad 2016). There are a few doubtful records of this species from the Orontes (Krupp 1985b).

Arabibarbus hadhrami Borkenhagen, 2014

Arabibarbus hadhrami has 29 to 32 scales in the lateral line, the wedge-shaped head is longer (27.8–32.5 % SL) and higher (15.5–18.4 % SL) than in its congeners, the body is slender and laterally flattened, the dorsal fin is high (26.5–32.4 % SL) and well ossified, the pectoral fins (19.9–23.9 % SL) and pelvic fins (16.8–19.9 % SL) are longer than in its congeners (Borkenhagen 2014).

Its type locality is the Wadi Mara, a tributary to Wadi Dawan, but it also occurs in several other places in the Wadi Hadramaut / Wadi al-Masila drainage basin (Borkenhagen 2014).

Carasobarbus apoensis (Banister and Clarke, 1977)

Carasobarbus apoensis is characterised by having one pair of barbels, usually 10 branched rays in the dorsal fin, 27 to 32 scales in the lateral line, usually 12 scales around the least circumference of the caudal peduncle, and a last unbranched ray of the dorsal fin that is shorter than the head (Banister and Clarke 1977, Krupp 1983a, Borkenhagen and Krupp 2013).

The type specimens of *Carasobarbus apoensis* were collected at Khamis Mushait, Wadi Turabah and Wadi Adamah (Banister and Clarke 1977). It was originally described as a member of the genus *Barbus*. Later it was transferred to the genus *Carasobarbus* (Ekmekçi and Banarescu 1998). An unidentified species of *Barbus* was reported from several localities in the Hejaz Mountains, where it occurs together with *C. apoensis* (Alkahem and Behnke 1983). The specimens were tentatively considered to be atypical *C. apoensis* (Alkahem and Behnke 1983). Examination of the available museum material did not substantiate any hints for an undescribed species of Torini (Borkenhagen and Krupp 2013).

Carasobarbus apoensis and *C. luteus* (Heckel, 1843) are closely related to each other (Borkenhagen 2017).

Carasobarbus apoensis occurs in the Hejaz Mountains in Saudi Arabia, where it inhabits wadis draining towards the Red Sea (e.g. Wadi Hadiyah, Wadi Haqqaq, Wadi Ilyab), as well as wadis draining inland (e.g. Wadi Turabah, Wadi Adamah, Wadi Buwah; Banister and Clarke 1977, Krupp 1983a, Alkahem and Behnke 1983, Borkenhagen and Krupp 2013).

Carasobarbus canis (Valenciennes in Cuvier and Valenciennes, 1842)

Carasobarbus canis is characterised by two pairs of barbels, 29 to 35 scales in the lateral line, usually 12 scales around the least circumference of the caudal peduncle, and a last unbranched ray of the dorsal fin that is shorter than the head (Cuvier and Valenciennes 1842, Krupp 1985b, Krupp and Schneider 1989, Ekmekçi and Banarescu 1998, Borkenhagen and Krupp 2013).

The type locality of C*arasobarbus canis* is the Jordan River, and it was classified as a member of the genus *Barbus* in the original description (Cuvier and Valenciennes 1842). Later authors assigned it to *Luciobarbus* (Heckel 1843), or *Labeobarbus* (Günther 1864). Only four years later Günther (1868) transferred it back to *Barbus.* Karaman (1971) and

Banarescu (1977) placed it in *Tor.* Later it was again placed in *Barbus* (Banister and Clarke 1977, Krupp 1983a), until a revision of Middle Eastern Torini placed it in *Carasobarbus* (Ekmekçi and Banarescu 1998). MNHN 0000-1413 is the lectotype of this taxon (Krupp and Schneider 1989). *Barbus beddomii* Günther, 1868, described from Lake Tiberias, is a junior synonym of *C. canis* (Berg 1949, Karaman 1971, Krupp and Schneider 1989, Borkenhagen and Krupp 2013).

Carasobarbus canis occurs in the Jordan River system, where it inhabits rivers, streams and lakes (Cuvier and Valenciennes 1842, Krupp 1985b, Krupp and Schneider 1989, Ekmekçi and Banarescu 1998, Goren and Ortal 1999, Borkenhagen and Krupp 2013). Records from the coastal rivers Na'aman and Yarqon are also confirmed by voucher specimens (Krupp and Schneider 1989, Borkenhagen and Krupp 2013). The population in Azraq Oasis was introduced by humans (Krupp and Schneider 1989) and is probably extinct (Hamidan 2004).

Carasobarbus chantrei (Sauvage, 1882)

Carasobarbus chantrei is characterised by two pairs of barbels, 31 to 38 scales in the lateral line, usually 14 to 16 scales around the least circumference of the caudal peduncle, and a last unbranched dorsal-fin ray that is equal to or shorter than the head (Sauvage 1882, Krupp 1985a, Krupp 1985b, Borkenhagen and Krupp 2013).

The type specimens of *Carasobarbus chantrei* were originally collected at the Amik Gölü and the Orontes River at Hama (Sauvage 1882). The species was placed in the genus *Labeobarbus* by Sauvage (1882). Only two years later the same author transferred it to the genus *Barbus* (Sauvage 1884). *Barynotus verhoeffi* Battalgil, 1942 was described from Amik Gölü, Turkey (Battalgil 1942). This species was erroneously synonymised with *C. canis* (Ladiges 1960). *Carasobarbus chantrei* was synonymised with *C. canis* and thus transferred to the genus *Tor* (Karaman 1971). *Barynotus verhoeffi* was transferred to the genus *Barbellion* (Fowler 1976). *Carasobarbus chantrei* was re-described as a valid species and provisionally placed into the genus *Barbus* sensu lato (Krupp 1985a). The type series was found to be inhomogeneous (MNHN B-2889 are *Arabibarbus grypus*) and thus MNHN A-3866 was designated as lectotype of *C. chantrei* (Krupp 1985a). This fixed the type locality to Amik Gölü. MNHN B-2889 is not listed as types for *C. chantrei* in the 'Catalog of Fishes' (Eschmeyer 2015).The species was transferred to the genus

Carasobarbus (Ekmekçi and Banarescu 1998).

Carasobarbus chantrei occurs in the rivers, streams and lakes of the Orontes river system (Sauvage 1882, Krupp 1985b, Krupp and Schneider 1989, Borkenhagen and Krupp 2013). It was also recorded from the Nahr Marqiyah, a coastal river in Syria, which drains into the Mediterranean Sea, but this occurrence might be the result of translocation (Borkenhagen and Krupp 2013). A record from the Ceyhan Nehri (Krupp 1985b) is not confirmed by voucher specimens. Few records from the Queiq and the Tigris-Euphrates system exist, but all of these are dubious (Krupp 1985a, Krupp 1985b, Borkenhagen and Krupp 2013).

Carasobarbus exulatus (Banister and Clarke, 1977)

Carasobarbus exulatus is characterised by a dorsal fin with nine branched rays in most specimens, last unbranched ray of dorsal fin as long as or longer than head, two pairs of barbels, 26 to 32 scales in the lateral line, and usually 12 scales around the least circumference of the caudal peduncle (Banister and Clarke 1977, Krupp 1983a, Borkenhagen and Krupp 2013).

Carasobarbus exulatus was originally described from the Wadi Hadramaut and Wadi Maran in Yemen (Banister and Clarke 1977). The species was first placed in the genus *Barbus* (Banister and Clarke 1977) and later transferred to *Carasobarbus* (Ekmekçi and Banarescu 1998).

Carasobarbus exulatus occurs in the Wadi Hadramaut / Wadi al-Masila drainage system in Yemen and its Pleistocene tributaries (Banister and Clarke 1977, Krupp 1983a, Borkenhagen and Krupp 2013). A record from Wadi Maran is the westernmost locality of this species (Borkenhagen and Krupp 2013). The species is also reported from Lake Ma’rib (Al-Safadi 1995) and Wadi Hajr (Attaala and Rubaia 2005).

Carasobarbus fritschii (Günther, 1874)

Carasobarbus fritschii is characterised by two pairs of barbels, 30 to 39 scales in the lateral line and 14 to 20 scales around the least circumference of the caudal peduncle, the dorsal fin is usually shorter than the anal fin and more than 15 % of its last unbranched ray are flexible, the dorsal profile of the head is convex (Günther 1874a, Pellegrin 1921, Borkenhagen and Krupp 2013).

The type locality of *Carasobarbus fritschii* is the Oued Ksob near Essaouira in the Oued Igrounzar drainage (Günther 1874a, Borkenhagen and Krupp 2013). The species was classified as a member of the genus *Barbus* in the original description (Günther 1874a). In the next four decades five further species were described from Morocco, but turned out to be junior synonyms of *C. fritschii*: *Barbus rothschildi* Günther, 1901 from Oued Oum er Rbia; *B. riggenbachi* Günther, 1902 from Oued Oum er Rbia and Oued Talmest; *Capoeta atlantica* Boulenger, 1902 and *C. waldoi* Boulenger, 1902 from Oued Nfis; and *B. paytonii* Boulenger, 1911 from Oued Oum er Rbia (Pellegrin 1939, Karaman 1971, Berrebi 1981, Lévêque and Daget 1984, Borkenhagen and Krupp 2013). The large number of junior synonyms can be explained, because these species descriptions were based on slight differences in the shape of the mouth and lower jaw, or the degree of ossification of the dorsal-fin rays, in combination with small sample sizes (Borkenhagen and Krupp 2013). The examination of a large number of specimens revealed that these characters are highly variable within the populations of *C. fritschii* (Borkenhagen and Krupp 2013).

Carasobarbus fritschii or its junior synonyms have been placed in several different genera, such as *Barbus* (Pellegrin 1919, Berrebi 1981, Azeroual et al. 2000, Machordom and Doadrio 2001, Leggatt and Iwama 2003, Colli et al. 2009), *Capoeta* (Boulenger 1902), *Labeobarbus* (Boulenger 1919, Pellegrin 1921, Pellegrin 1939, Doadrio 1994, Tsigenopoulos et al. 2010, Berrebi et al. 2014, Vreven et al. 2016), *Pseudotor* (Karaman 1971), *Varicorhinus* (Fowler 1976), or the provisional genus '*Barbus*' (Borkenhagen et al. 2011). *Carasobarbus fritschii* was transferred to the genus *Carasobarbus*, based on the possession of a smooth last unbranched dorsal-fin ray, modally nine branched dorsal-fin rays, six branched rays in the anal fin, and shield-shaped scales with numerous parallel radii (Borkenhagen and Krupp 2013). Molecular phylogenetic analyses (Durand et al. 2002, Tsigenopoulos et al. 2010, Borkenhagen 2014, Borkenhagen 2017) support the close relationship to other *Carasobarbus* species.

Fishes of the lots SMF 636 and SMF 952 were considered to be types for *C. fritschii*, but, based on their collection history, it was concluded that they are not part of the type series (Borkenhagen and Krupp 2013).

Carasobarbus fritschii is widespread in Morocco. It occurs in the Oued Moulouya system, which drains into the Mediterranean Sea, as well as in the Oued al-Maleh, the Oued Bou Regreg, the Oued Igrounzar / Oued Ksob, the Oued Iqem, the Oued Oum er Rbia, the

Oued Sebou, the Oued Tennsift and their tributaries, which drain into the Atlantic Ocean (Günther 1874a, Pellegrin 1921, Karaman 1971, Borkenhagen and Krupp 2013). There is one record from the Oued Kiss in Algeria (Borkenhagen and Krupp 2013).

Carasobarbus harterti (Günther, 1901)

Carasobarbus harterti is characterised by two pairs of long barbels, 31 to 38 scales in the lateral line and 13 to 17 scales around the least circumference of the caudal peduncle, a dorsal fin that is longer than anal fin, less than 15 % of the length of the last unbranched ray in the dorsal fin are flexible, and a straight dorsal profile of the head (Günther 1901, Pellegrin 1921, Borkenhagen and Krupp 2013).

The type locality of *Carasobarbus harterti* is the Oued Oum er Rbia (Günther 1901). It was originally placed in the genus *Barbus* (Günther 1901). The generic names *Barbus* subgenus *Labeobarbus* (Boulenger 1919, Pellegrin 1921) or *Barbus* (Pellegrin 1919, Pellegrin 1939) were used by later authors. *Carasobarbus harterti* was synonymised with *Carasobarbus fritschii*, but regarded as a valid subspecies (Karaman 1971). Karaman (1971) synonymised *B. rothschildi*, *B. riggenbachi* and *B. paytonii* with this subspecies and placed it in the newly erected genus *Pseudotor*.

Karaman's proposal did not meet broad acceptance and most authors continued using *Barbus* (Fowler 1976, El Gharbi et al. 1993, Azeroual et al. 2000, Leggatt and Iwama 2003, Colli et al. 2009, Borkenhagen et al. 2011) or proposed using *Labeobarbus* (Doadrio 1994, Tsigenopoulos et al. 2010, Berrebi et al. 2014). The species was transferred to the genus *Carasobarbus*, based on the possession of a smooth last unbranched dorsal-fin ray, nine branched dorsal-fin rays, six branched rays in the anal fin, and shield-shaped scales with numerous parallel radii (Borkenhagen and Krupp 2013). Molecular phylogenetic analyses (Durand et al. 2002, Tsigenopoulos et al. 2010, Borkenhagen 2014, Yang et al. 2015, Borkenhagen 2017) confirm the close relationship to other *Carasobarbus* species and support this decision.

Carasobarbus harterti occurs in the lower course of the Oued Oum er Rbia and Oued Tennsift in Morocco (Günther 1901, Pellegrin 1921, Karaman 1971, Borkenhagen and Krupp 2013).

Carasobarbus kosswigi (Ladiges, 1960)

Carasobarbus kosswigi is characterised by two pairs of barbels, 32 to 38 scales in the lateral line, usually 14 to 16 scales around the least circumference of the caudal peduncle, a last unbranched dorsal-fin ray that is markedly longer than the head, a narrow mouth, and a spatulate lower lip with a median lobe (Ladiges 1960, Coad 1982, Borkenhagen and Krupp 2013).

The type locality of *Carasobarbus kosswigi* is the Batman Çayı. The species was originally placed in the genus *Cyclocheilichthys* (Ladiges 1960). Karaman (1971) erected the new genus *Kosswigobarbus* for this species. In a detailed re-description of this species it was assigned to the genus *Barbus* (Coad 1982). Ekmekçi and Banarescu (1998) re-validated *Kosswigobarbus. Kosswigobarbus* was sometimes used as a subgenus of *Barbus* (Tsigenopoulos et al. 2010). Recently *C. kosswigi* was placed in *Carasobarbus*, based on molecular (Borkenhagen et al. 2011, Borkenhagen 2017) and morphological characters (Borkenhagen and Krupp 2013).

According to molecular phylogenetic analyses, *Carasobarbus kosswigi* is closely related to the other species of *Carasobarbus* and forms a monophyletic cluster with them (Durand et al. 2002, Tsigenopoulos et al. 2010, Borkenhagen et al. 2011, Borkenhagen 2014, Yang et al. 2015, Borkenhagen 2017). One of the specimens analysed is more closely related to *C. sublimus* than to other *C. kosswigi* sequences, which makes *C. kosswigi* paraphyletic with respect to *C. sublimus* (Borkenhagen et al. 2011, Borkenhagen 2017). This might be attributed to incomplete lineage sorting (Borkenhagen et al. 2011), because *C. kosswigi* is adapted to fast-flowing sections of rivers (Krupp and Schneider 2008), which are typically restricted to headwaters and separated by long stretches of slow current, which leads to a fragmentation of populations and a low degree of genetic connectivity between them. Paraphyly of mitochondrial markers on the species level is a taxonomically widespread and common phenomenon in animals (Funk and Omland 2003).

Carasobarbus kosswigi occurs in the rivers of the Tigris-Euphrates system (Ladiges 1960, Coad 1982, Krupp and Schneider 2008, Borkenhagen and Krupp 2013).

Carasobarbus luteus (Heckel, 1843)

Carasobarbus luteus is characterised by one pair of barbels, 25 to 33 scales in the lateral line, typically 12 scales around the least circumference of the caudal peduncle, and a last unbranched ray of the dorsal fin that is about as long as the head or slightly shorter (Heckel 1943, Borkenhagen and Krupp 2013, Coad 2016).

Carasobarbus luteus was described as *Systomus luteus*, based on a series of syntypes from the Orontes and the Tigris (Heckel 1843). According to the museum labels, all but one of the type specimens are either from the Tigris or from the Queiq. Heckel might have confused the Orontes with the Queiq (Borkenhagen and Krupp 2013). The remaining type specimen (NMW 10827) is labelled “Damascus”. The Damascus basin is an endorheic inland basin, separated from the Euphrates by hundreds of kilometres of desert land. The specimen might be mislabelled and cannot be assigned to any of the drainage systems, where *C. luteus* occurs (Borkenhagen and Krupp 2013).

The designation of NMW 54253:2 as lectotype established the Tigris at Mosul as the type locality (Borkenhagen and Krupp 2013). The type locality of *Systomus albus* Heckel, 1843, a junior synonym described in the same publication (Heckel 1843), is affected by the same ambiguity (Borkenhagen and Krupp 2013). *Systomus albus alpina* Heckel, 1847 was described from Lake Parishan (Heckel 1847). *Systomus albus* and *S. albus* var. *alpina* are synonyms of *C. luteus* (Günther 1868, Ladiges 1960, Karaman 1971, Ekmekçi and Banarescu 1998, Borkenhagen and Krupp 2013). *Carasobarbus luteus* was assigned to the genus *Barbus* (Günther 1868). Sauvage (1882, 1884) listed *C. luteus* and *C. albus* as valid species and assigned them to the genus *Barynotus*. Misra (1947) assigned *C. luteus* to *Barbus* subgenus *Puntius*. Ladiges (1960) used the name *Barynotus albus* for both species. According to the ICZN, Günther (1868) has to be considered the first revising author and his choice of *luteus* has priority over Ladiges' choice of *albus*. Eventually the genus *Carasobarbus* was erected for this species (Karaman 1971). Some authors accepted the new taxonomic position (e.g. Wossughi 1978, Bianco and Banarescu 1982, Ahmed et al. 1984, Naama and Muhsen 1986), whereas others retained the genus *Barbus* (Banister and Clarke 1977, Krupp 1985a, Krupp 1985b, Coad 1995, Coad 1996), until the revision by Ekmekçi and Banarescu (1998). Fowler (1976) placed *C. luteus* in the genus *Barbellion*. *Barbus parieschanica* Wossughi, Khoshzahmat and Etemadfar, 1983, another junior synonym, was described from Lake Parishan (Wossughi et al. 1983). In the description the species name is also spelled *B. parschanica*, but Coad (1995), as the first revising author, fixed *B. parieschanica* as the correct spelling.

An atypical population of *C. luteus* exists in the Naband River, but more material is necessary to evaluate its status (Borkenhagen and Krupp 2013). Despite slight morphological differences between the populations of *C. luteus* from Mesopotamia and Iran (Borkenhagen and Krupp 2013), they belong to the same species (Borkenhagen et al. 2011, Borkenhagen and Krupp 2013).

The genetic distance between *Carasobarbus luteus* and *C. apoensis* is comparatively small (Borkenhagen 2017). For the dataset used in Borkenhagen (2017), the between group mean p-distance for *C. apoensis* and *C. luteus* is 0.7 %, whereas the between group mean p-distance for all other *Carasobarbus* species is 2.5–9.6 % (Borkenhagen unpublished).

Carasobarbus luteus has the largest range of all *Carasobarbus* species. It occurs in the Tigris-Euphrates system and in the rivers along the southern coast of Iran, such as the Mand, the Helleh, the Kol, the Naband, as well as the Lake Maharloo (Heckel 1843, Ekmekçi and Banarescu 1998, Krupp and Schneider 2008, Borkenhagen and Krupp 2013, Coad 2016). The population in the Queiq is probably extinct as a consequence of drought (Borkenhagen and Krupp 2013). Records from the Orontes and from Damascus are dubious (Borkenhagen and Krupp 2013).

Carasobarbus sublimus (Coad and Najafpour, 1997)

Carasobarbus sublimus is characterised by two pairs of barbels, 27 to 29 scales in the lateral line, 12 scales around the least circumference of the caudal peduncle, a last unbranched dorsal-fin ray that is about as long as the head, a narrow mouth with a spatulate lower jaw, and median lobe on lower lip (Coad and Najafpour 1997, Borkenhagen and Krupp 2013).

The type locality is the A'la River at Pol-e Tighen in Iran (Coad and Najafpour 1997). *Carasobarbus sublimus* was described in the genus *Barbus* and the authors hypothesised a close relationship to *C. apoensis*, *C. canis*, *C. chantrei*, *C. exulatus*, *C. kosswigi*, and *C. luteus* in the original description (Coad and Najafpour 1997). Some authors use the genus *Kosswigobarbus* for this species (Esmaeili et al. 2010, Coad 2016). *Carasobarbus sublimus* was transferred to *Carasobarbus*, based on morphological characters and close genetic relationship (Borkenhagen et al. 2011, Borkenhagen and Krupp 2013).

Carasobarbus sublimus occurs in the A'la River and the Fahliyan River in south-western

Iran (Coad and Najafpour 1997, Esmaeili et al. 2006, Borkenhagen and Krupp 2013, Coad 2016). The presence of *C. kosswigi* in the Kashkan River is uncertain, because locality data for CMNFI 79-0277 is questionable (Borkenhagen and Krupp 2013). Though it is unlikely that *C. kosswigi* and *C. sublimus* occur sympatrically, for the time being it is a possible record of *C. sublimus* from the Kashkan River (Borkenhagen and Krupp 2013).

Mesopotamichthys sharpeyi (Günther, 1874)

Mesopotamichthys sharpeyi is characterised by a lack of barbels, 29 to 37 scales in the lateral line, a dorsal fin with four unbranched and seven to nine, usually eight, branched rays, an anal fin with two or three unbranched and usually five branched rays, a round and obtuse snout, 13 to 19 gill rakers on the first gill arch, and a pharyngeal teeth count of 2.3.5-5.3.2 (Günther 1874a, Coad 2016).

The type locality of *Mesopotamichthys sharpeyi* is the Tigris River near Baghdad (Günther 1874b).

This species was originally described in the genus *Barbus* (Günther 1874b). Karaman (1971) created the monospecific genus *Mesopotamichthys* for this species. *Barbus faoensis* was described from Fao at the Persian Gulf (Günther 1896). It is a junior synonym of *Mesopotamichthys sharpeyi* (Karaman 1971, Ekmekçi and Banarescu 1998, Coad 2016).

Mesopotamichthys sharpeyi occurs in the lower reaches of the Tigris-Euphrates system, as well as the Zohreh River and Karkheh River in Iran (Günther 1874b, Kähsbauer 1963, Karaman 1971, Ekmekçi and Banarescu 1998, Freyhof 2014, Coad 2016).

Pterocapoeta maroccana Günther, 1902

Pterocapoeta maroccana is characterised by usually having one pair of short barbels, 43 to 47 scales in the lateral line, four unbranched and nine to 11 branched rays in the dorsal fin, three unbranched and five branched rays in the anal fin, a mouth that is inferior and has a sharp horny edge on the lower jaw (Günther 1902, Pellegrin 1921, Karaman 1971).

The type localities of *Pterocapoeta maroccana* are the Oued Oum er Rbia and the Oued

Talmest in Morocco (Günther 1902). The species was sometimes classified as *Varicorhinus* (Lévêque and Daget 1984, Azeroual et al. 2000, Tsigenopoulos et al. 2010) or *Labeobarbus* (Berrebi et al. 2014, Vreven et al. 2016). *Pterocapoeta* is morphologically and genetically clearly different from all other Torini (Günther 1902, Borkenhagen 2017).

Pterocapoeta maroccana is endemic to Morocco and occurs in the drainage systems of the Oued Oum er Rbia (BMNH 1902.7.28.37-39,) and the Oued Tennsift (NMW 19541, NMW 19544 SMF 33351). The species was also recorded from the “Oued bou-Aceila” (=Oued Bou Asseïla), a tributary to the Oued al-Maleh (Werner 1931).

'*Labeobarbus*' *reinii* (Günther, 1874)

'Labeobarbus' reinii is characterised by usually having two pairs of long barbels, 25 to 32 scales in the lateral line, three or four unbranched and eight or nine branched rays in the dorsal fin, three unbranched and five branched rays in the anal fin, a mouth that is subterminal to inferior and has well developed, fleshy lips and a small median lobe on the lower lip (Günther 1874a, Pellegrin 1921, Karaman 1971).

The type locality of this species is the Oued Tennsift in Morocco (Günther 1874a). Today its range seems to be restricted to the lower reaches of the Oued Tennsift in Morocco (Crivelli 2006), but historical records from the Oued Oum er Rbia exist (Günther 1902, Pellegrin 1921) and are confirmed by voucher specimens (MNHN 1912-94–96, MNHN 1927-98).

Phylogenetic relationships of the Torini

Members of the tribe Torini are cyprinid fishes (family Cyprinidae) and belong to the subfamily Cyprininae (Yang et al. 2015). Within the Cyprininae the Torini are sister to a clade encompassing all other tribes, except Labeonini and Probarbini (Clade A sensu Yang et al. 2015). Similar phylogenetic relationships were recovered in Borkenhagen (2017).

Within the Torini, the tetraploid Indomalayan species (genera *Hypselobarbus*, *Lepidopygopsis*, *Naziritor*, *Neolissochilus, Osteochilichthys* and *Tor*) are paraphyletic with respect to the hexaploid Middle Eastern and African species (Yang et al. 2015, Borkenhagen 2017). The hexaploid species from the Middle East and Africa form a well-supported monophyletic group (Tsigenopoulos et al. 2010, Yang et al. 2015, Borkenhagen 2017). The phylogenetic analyses in Yang et al. (2015) and Borkenhagen (2017) are both based on mitochondrial markers. Yang et al. (2015) has a more extensive taxon sampling of Cyprininae and includes more species of Torini from Indomalaya and sub-Saharan Africa, whereas Borkenhagen (2017) focusses on the Middle Eastern and North African Torini. Most of the differences between these two studies concern weakly supported branches: Yang et al. (2015) did not resolve the relationships between the hexaploid Torini, *Neolissochilus* and *Tor*, whereas Borkenhagen (2017) found strong support for a sister group relationship between *Neolissochilus* and *Tor*. *Mesopotamichthys* clusters within *Carasobarbus* in Yang et al. (2015), whereas it is clearly distinct from *Carasobarbus* (high support) and sister group to *Arabibarbus* (moderate support) in Borkenhagen (2017). According to Borkenhagen (2014) *Arabibarbus* and *Carasobarbus* are sister groups and *Mesopotamichthys* is the sister group to both of them. Support for this is only moderate. The relationship between *Arabibarbus*, *Carasobarbus* and *Mesopotamichthys* remains unresolved (Borkenhagen 2014, Yang et al. 2015, Borkenhagen 2017).

Paleogeography and evolution of the Torini of the Middle East and North Africa

Cyprinids evolved in Asia (Saitoh et al. 2011). Torini originated in the Indomalayan realm and colonised Africa via the Middle East (Wang et al. 2013, Borkenhagen 2017). This can be deduced from the fact that the African and Middle Eastern Torini (hexaploid) cluster within the (tetraploid) Indomalayan Torini (Yang et al. 2015, Borkenhagen 2017). By application of the parsimony principle a colonisation from Indomalaya to Africa is more likely than a colonisation in the other direction, because this would imply the extinction of all tetraploid lineages of Torini in Africa and the Middle East.

Closing of the Tethys Sea (Wolfart 1987) and the formation of the *Gomphotherium* landbridge in the Miocene, about 19 Ma ago (Rögl 1999, Harzhauser et al. 2007) facilitated the westward expansion of the Torini from the Indomalayan realm to the Middle East and Africa (Borkenhagen 2017). The last landbridge across the Red Sea disappeared 12 to 6 Ma ago (Rögl 1999, Fernandes et al. 2006) and restricted the connection between Africa and Asia to the Sinai Peninsula. A molecular clock study based on cytochrome *b* data estimates the origin of the hexaploid Torini at 9.9 Ma before present (Wang et al.

2013), but no confidence interval is given, and this result should be interpreted with caution. Several other freshwater organisms used similar pathways and demonstrate that dispersal along this route was possible. About 18 to 15 Ma ago, airbreathing catfish (Clariidae) colonised Africa from Asia (Agnese and Teugels 2005). Cyprinids of the genus *Labeo* spread along the same route (Tang et al. 2009). According to a molecular clock estimate, based on cytochrome *b* sequences, this happened 20.5 to 14.8 Ma ago (Tang et al. 2009). Considering the usual confidence intervals of such estimates, this timeframe is in good agreement with a colonisation via the *Gomphotherium* landbridge. Tiger frogs (*Hoplobatrachus* Peters, 1863) spread from Asia to Africa via Arabia in the Miocene (Kosuch et al. 2001). Smiliogastrin cyprinids ("*Puntius*") migrated from Asia to Baluchistan and southern Arabia and reached Africa in the region of Somalia (Karaman 1971). Cyprinid fossils found on the Arabian plate and dated to the Burdigalian (20.5 to 16 Ma ago; Otero 2001, Otero and Gayet 2001) support a colonisation route from Asia via Arabia to Africa. The alternative hypothesis of a very early (125 Ma, with a confidence interval of 65–167 Ma) split between the African and Asian Torini and a possible Gondwana origin of Torini (Dahanukar et al. 2013) has to be rejected for several reasons: First, it does not explain the absence of Torini from Madagascar and Australia. Second, the molecular clock was calibrated with only one calibration point. This calibration point lies far outside the group of interest. It was derived from another molecular clock analysis (Saitoh et al. 2011), and was in itself probably already an overestimation (Saitoh et al. 2011). Third, the effect of saturation and its influence on molecular dating was completely ignored. In combination, these factors probably lead to a considerable overestimation of divergence times. More realistic molecular clock approaches for Torini (Tsigenopoulos et al. 2010) and Labeonini (Tang et al. 2009) date the separation of Asian and African cyprinids to the Miocene and are compatible with the colonisation of Africa from Asia via the *Gomphotherium* landbridge. Wang et al. (2013) proposed a younger age of 9.94 Ma ago for the hexaploid Torini, based on a molecular clock of cytochrome *b* sequences. It cannot be assessed, whether this dating hypothesis is in conflict with the hypotheses mentioned above, because no confidence interval was reported.

The Torini of Africa and the Middle East are hexaploid, whereas the Indomalayan Torini are tetraploid (Tsigenopoulos et al. 2010, Arai 2011, Berrebi et al. 2014, Borkenhagen 2017). Hexaploidy can arise by hybridisation between a tetraploid and a diploid ancestor (Oellermann and Skelton 1990), and it is likely that the hexaploid Torini resulted from hybridisation between tetraploid Torini and diploid *Cyprinion*-like cyprinids (Yang et al.

2015). Because no hexaploid Torini are known from Indomalaya, this hybridisation probably occurred during the westward range extension of the Torini (Yang et al. 2015, Borkenhagen 2017).

The divergence between *Pterocapoeta*, the African hexaploids and the Middle Eastern hexaploids is unresolved (Borkenhagen 2017). The Miocene freshwater fish fauna of the Maghreb includes *Lates* Cuvier, 1828, *Polypterus* Lacepède, 1803 and *Clarias* Scopoli, 1777 and can be considered typically African, whereas the modern fish fauna of the Maghreb is influenced by Europe and the Middle East (Otero and Gayet 2001, Stewart 2001). During Plio-/Pleistocene times most of the typically African fish fauna disappeared from the Maghreb region (Otero and Gayet 2001). *Pterocapoeta* possibly is a relic of the Miocene African fauna (Borkenhagen 2017).

The split between *Arabibarbus*, *Carasobarbus* and *Mesopotamichthys* is not resolved (Borkenhagen 2017). It probably happened during the late Miocene or Pliocene (Tsigenopoulos et al. 2010, Borkenhagen 2014, Borkenhagen 2017).

During the Lago Mare phase (5.5 to 5.33 Ma ago; Krijgsman et al. 1999) of the Messinian salinity crisis Morocco was colonised by Torini for a second time, when *Carasobarbus* species (and probably the ancestor of ‘*L.*’ *reinii*) spread from the Middle East along the southern edge of the Mediterranean Sea (Borkenhagen 2017). A similar route was suggested for *Luciobarbus* (Tsigenopoulos et al. 2003).

Carasobarbus kosswigi and *C. sublimus* have a mouth with a spatulate lower lip and are adapted to strong currents (Borkenhagen and Krupp 2013). The split between these species and the other species of the eastern group of *Carasobarbus* cannot be correlated to any particular palaeographic event.

The connection between Jordan and Euphrates broke in the Pliocene (Krupp 1985b) and isolated the ancestors of *C. canis* from the ancestors of *C. apoensis*, *C. chantrei*, *C. exulatus*, and *C. luteus* (Borkenhagen 2017).

During the Pliocene the Arabian Peninsula was colonised by the ancestors of *A. arabicus*, *A. hadhrami* and *C. exulatus*, which came from the Tigris-Euphrates system (Borkenhagen 2014, Borkenhagen 2017). Historical river systems, for example the Wadi al-Batin and Wadi ar-Rimah, are possible pathways (Beineke 2006, Borkenhagen 2014, Borkenhagen 2017).

Until the outbreak of the north Syrian basaltic lava (e.g. Homs basalt: 6.5 to 2 Ma ago; Chorowicz et al. 2005), the Orontes was connected to the Euphrates (Krupp 1985b, Kinzelbach 1987, Por 1989, Heller 2007). This separated the ancestors of *C. chantrei* from the ancestors of *C. apoensis* and *C. luteus* (Borkenhagen 2017).

Carasobarbus luteus has two divergent genetic lineages (Borkenhagen et al. 2011, Borkenhagen 2017). One is spread over its entire range, and the other seems to be restricted to the Nahr al-Khabur in Syria, where both lineages occur sympatrically (Borkenhagen et al. 2011, Borkenhagen 2017). It might be a case of retained ancient polymorphism (Borkenhagen et al. 2011, Borkenhagen 2017).

Because the genetic distance between *C. luteus* and *C. apoensis* is minor, the separation between them probably occurred recently, compared to other species of *Carasobarbus* (Borkenhagen 2017). The climate was much more humid in the Arabian Peninsula during several periods of the Pleistocene (Rosenberg et al. 2013). The most recent of these periods occurred 163 ka, 54 ka and 40 ka before present (Drake et al. 2013). Because the Wadi al-Batin incised through the Dibdibba formation during the time of low sea level during the last glacial (Al-Sulaimi and Pitty 1995), we may assume water flow during this time. In the Holocene Arabia experienced further humid periods (Berger et al. 2012, Engel et al. 2012) and connections between the Tigris-Euphrates system and the Hejaz Mountains in Saudi Arabia might have existed even then (Borkenhagen 2017). The migration route between the Hejaz Mountains and the Tigris-Euphrates system disappeared, when the Wadi al-Batin and Wadi ar-Rimah ceased to flow.

Methods

For this study a combination of morphological and molecular methods has been used. Both approaches complement each other and provide information on different aspects. Only a combination of both methods can provide a comprehensive picture.

Morphological methods are useful for the delimitation of species, and assessment of interspecific and intraspecific morphological variation. In addition they can be used to propose generic concepts, based on characters, which facilitate identification of specimens. In contrast to molecular genetic analysis, morphological examination can be performed on historical collections (museum collections), including type specimens. This usually leads to a wealth of available material from different localities and examination of type specimens is often the only way to resolve taxonomic problems. Museum collections help to map the exact range of a species, based on voucher specimens. However, in closely related species it is often impossible to infer phylogenetic relationships from morphological characters, due to homoplasy and other problems.

Molecular genetic methods usually rely on freshly collected samples, because DNA extraction from historical, formaldehyde-fixed museum specimens (including most types) is not possible. The validity of molecular genetic analyses depends on proper (usually morphological) species identification. On the other hand, a well resolved molecular phylogenetic hypothesis can be useful for a critical reappraisal of morphological species delimitation. In addition, it can be used to test the monophyly of taxonomic groups and to evaluate generic concepts. The phylogenetic hypothesis forms the backbone for zoogeographic considerations and the interpretation of the evolutionary history.

The usefulness of a molecular genetic dataset depends on several factors, such as the accuracy of species identification, the extent of taxon sampling, the amount of phylogenetic signal in the dataset, and the validity of the analytical approach.

The taxonomic revision of Middle Eastern and North African Torini (Borkenhagen and Krupp 2013, Borkenhagen 2014) provides a reliable taxonomic framework for the molecular phylogenetic analyses presented here. The taxon sampling of relevant species from the Middle East and North Africa is nearly complete (Borkenhagen 2017).

The use of nuclear markers for polyploid species is problematic, because each gene exists in several paralog copies and it is difficult to establish homology (Saitoh et al. 2011, Yang et al. 2012, Pasco-Viel et al. 2014, Yang et al. 2015). For this reason mitochondrial markers were used in Borkenhagen et al. (2011), Borkenhagen (2014), and Borkenhagen (2017). Mitochondrial markers evolve rapidly and are suitable for resolving phylogenetic relationships between closely related taxa. Because saturation is a potential problem that can hamper the reliable reconstruction of phylogenetic relationships (Knoop and Müller 2009, Lemey et al. 2009), the dataset was checked for effects of saturation. The whole dataset shows only a minor degree of saturation (Figure 1). Within the Torini saturation is even lower (Figure 2). The hexaploid Torini do not show signs of saturation (Figure 3).

Bayesian inference and maximum likelihood approaches are generally accepted methods for molecular phylogenetic analyses (Knoop and Müller 2009, Lemey et al. 2009). Both methods provide congruent results, if the quality of the dataset is sufficient (Knoop and Müller 2009, Lemey et al. 2009). The dataset used in Borkenhagen (2017) complies with these requirements, and the resulting hypotheses can be regarded with confidence.

Molecular clocks rely heavily on assumptions, which are rarely fulfilled in real world datasets, and the resulting estimates of divergence time should be interpreted with great caution (Knoop and Müller 2009, Lemey et al. 2009). High quality calibration points are necessary to make meaningful inferences from molecular clock analyses (Knoop and Müller 2009, Lemey et al. 2009). In the case of hexaploid Torini, molecular clock based hypotheses have been published before (Tsigenopoulos et al. 2010). Molecular clock analysis of the dataset presented here (Borkenhagen 2017) does not reveal significant new insights, due to uncertainties in calibration and large confidence intervals (Borkenhagen unpublished).

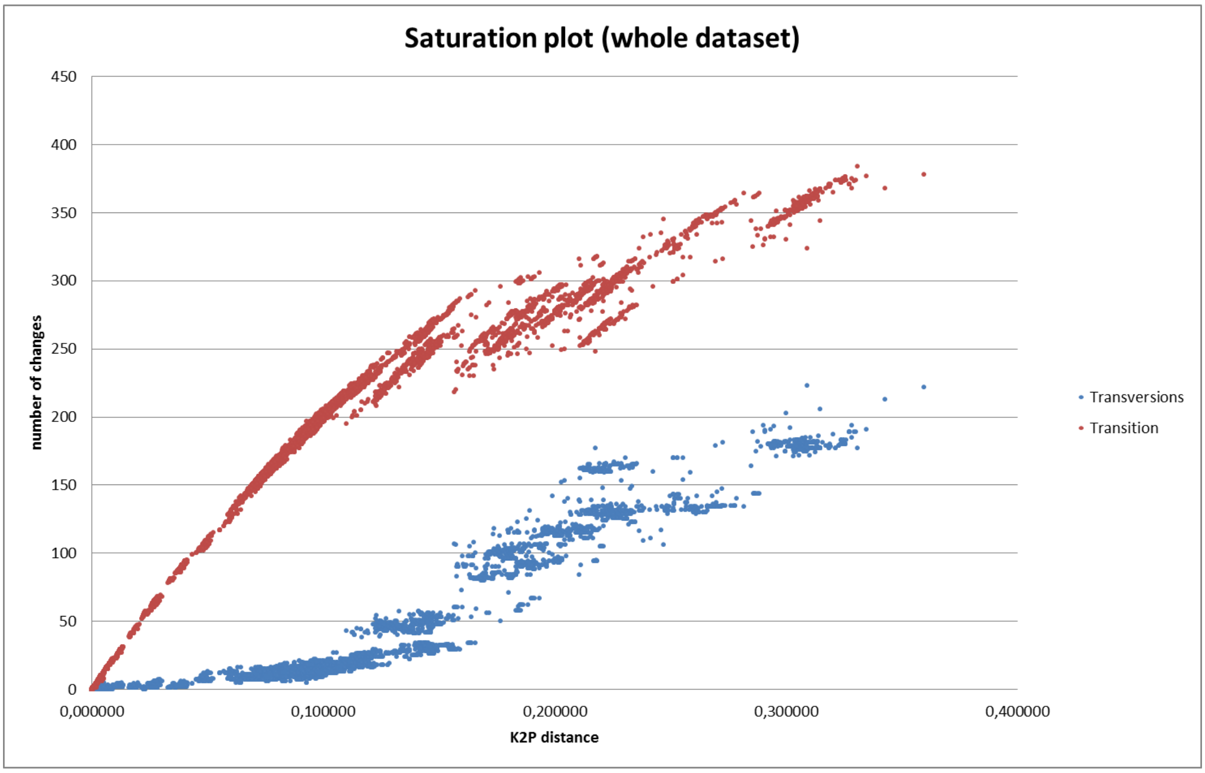

Figure 1: Pairwise plot of number of transitions and number of transversions over Kimura 2 Parameter distance for the whole dataset in Borkenhagen (2017). In right part of the graph the relation between the number of mutations and the K2P distance starts to deviate from a linear correlation. This indicates some saturation in the dataset.

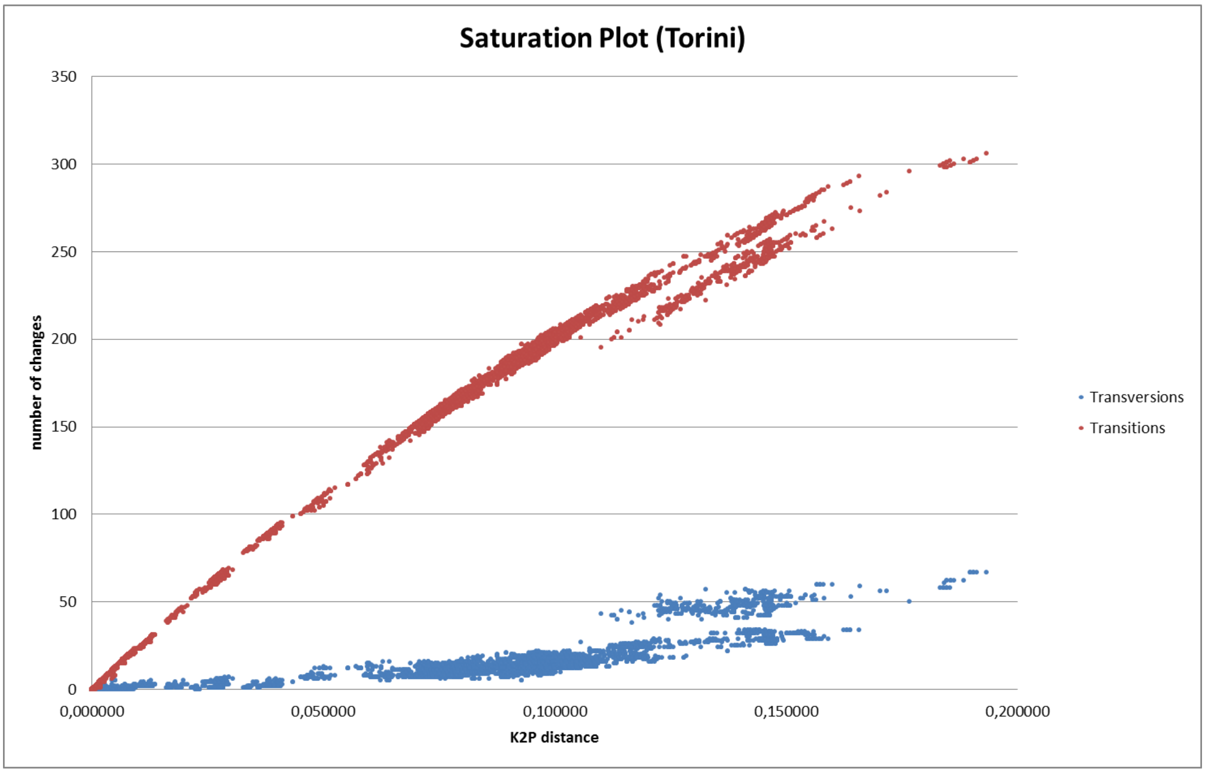

Figure 2: Pairwise plot of number of transitions and number of transversions over Kimura 2 Parameter distance for all species of Torini in Borkenhagen (2017). The relation between the number of mutations and the K2P distance deviates only slightly from a linear correlation. This indicates only weak effects of saturation.

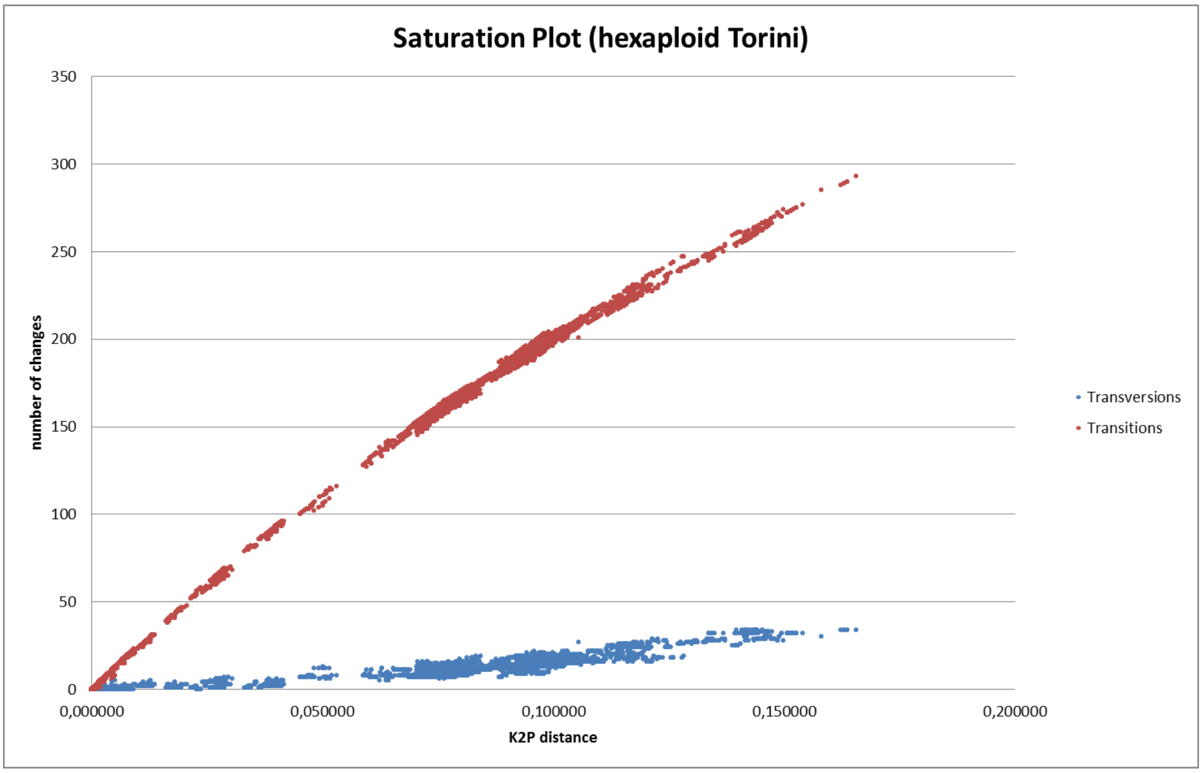

Figure 3: Pairwise plot of number of transitions and number of transversions over Kimura 2 Parameter distance for all species of hexaploid Torini in Borkenhagen (2017). The relation between the number of mutations and the K2P distance is almost linear. The dataset is not impacted by saturation.

Conclusions

The hexaploid Torini of Africa and the Middle East form a monophyletic group. In the Middle East they are represented by the genera *Arabibarbus*, *Carasobarbus*, *Mesopotamichthys*, and *Pterocapoeta*. These genera are each monophyletic, morphologically diagnosable, and genetically distinct from each other. A generic name for the species '*Labeobarbus*' *reinii* is not available. Of the 28 species group taxa described until now, 15 are valid: *Arabibarbus arabicus*, *A. grypus*, *A. hadhrami*, *C. apoensis*, *C. canis*, *C. chantrei*, *C. exulatus*, *C. fritschii*, *C. harterti*, *C. kosswigi*, *C. luteus*, *C. sublimus*, *Mesopotamichthys sharpeyi*, *Pterocapoeta maroccana,* and '*Labeobarbus*' *reinii*.

The phylogenetic relationships between the Middle Eastern and North African Torini are generally well resolved, based on the analysis of mitochondrial DNA sequences and an extensive taxon sampling. Only minor cases of ambiguity remain.

The interspecific and intraspecific morphological and genetic diversity is shaped by the zoogeographic history. Conclusions can be drawn about the events that shaped the evolution of this group. The Torini originated in Asia or India and colonised the Middle East and North Africa in the Miocene via the Arabian Peninsula (*Gomphotherium* landbridge). The Asian Torini are tetraploid, whereas those of the Middle East and Africa are hexaploid. The tetraploid Torini are paraphyletic in respect to the hexaploid Torini. Morocco was colonised in two independent waves. The first came from sub-Saharan Africa and is represented by *P. maroccana*. The second came from the Middle East and gave rise to *C. fritschii*, *C. harterti*, and probably '*L.*' *reinii*. The Tigris-Euphrates system is an important crossroad for the evolution of the Torini in the Middle East. The Jordan River was separated from the Euphrates before the Orontes. Arabia was colonised in two waves. The first (*A. arabicus*, *A. hadhrami*, *C. exulatus*) dates to the Pliocene, whereas the second (*C. apoensis*) happened as recently as the late Pleistocene or early Holocene.

References

Abdoli A (2000) The inland water wishes of Iran [in Farsi]. Iranian Museum of Nature and Wildlife, Tehran.

Agnese J-F, Teugels GG (2005) Insight into the phylogeny of African Clariidae (Teleostei, Siluriformes): Implications for their body shape evolution, biogeography, and taxonomy. Molecular Phylogenetics and Evolution 36(3):546–553. doi: 10.1016/j.ympev.2005.03.028

Ahmed HA, Al-Hammar MA, Al-Adhub AHY (1984) The reproductive biology of *Carasobarbus luteus* (Pisces, Cyprinidae) in Al-Hammar Marsh, Iraq. Cybium 8(4):69–80.

Alkahem AF, Behnke RJ (1983) Freshwater fishes of Saudi Arabia. Fauna of Saudi Arabia 5:545–567.

Al-Safadi MM (1995) A pilot study of lake Ma'rib, Yemen. Hydrobiologia 315(3):203–209.

Al-Sulaimi JS, Pitty AF (1995) Origin and depositional model of Wadi Al-Batin and its associated alluvial fan, Saudi Arabia and Kuwait. Sedimentary Geology 97:203–229.

Arai R (2011) Fish karyotypes: A check list. Springer, Tokyo.

Arunachalam M, Chinnaraja S, Chandran A, Mayden RL (2014) On the identities of *Cyprinus* (=*Hypselobarbus*) *curmuca* Hamilton, *Barbus* (=*Hypselobarbus*) *kolus* Sykes, and *Hypselobarbus kurali* Menon and Rema Devi (Cypriniformes: Cyprinidae), with descriptions of three new species of *Hypselobarbus* from peninsular India. Species 11(31):72–94.

Arunachalam M, Chinnaraja S, Mayden RL (2016a) Description of a new species of *Hypselobarbus* from Kerala region of Western Ghats, peninsular India (Cypriniformes: Cyprinidae). Iranian Journal of Ichthyology 3(2):73–81.

Arunachalam M, Chinnaraja S, Mayden RL (2016b) New species of *Hypselobarbus* (Cyprinidae: Cypriniformes) from Cauvery River Basin, South India. International Journal of Pure and Applied Zoology 4(1):99–106.

Arunachalam M, Chinnaraja S, Mayden RL (2016c) Remarkable rediscovery of *Barbus* (=*Hypselobarbus*) *mussullah* (Sykes) after 175 years of hiatus and description of a new species of *Hypselobarbus* Bleeker from peninsular India (Cyprinidae: Cypriniformes). FishTaxa 1(1):1–13. doi: 10.7508/jft.2016.01.001

Arunachalam M, Raja M, Muralidharan M, Mayden RL (2012) Phylogenetic relationships of species of *Hypselobarbus* (Cypriniformes: Cyprinidae): An enigmatic clade endemic to aquatic systems of India. Zootaxa 3499:63–73

Attaala AM, Rubaia BS (2005) First record of the eel *Anguilla bengalensis* from Arabia with notes on freshwater fishes from Hadramout, Yemen. Zoology in the Middle East 34:35–44. doi: 10.1080/09397140.2005.10638080

Azeroual A, Crivelli AJ, Yahyaoui A, Dakki M (2000) L'ichtyofaune des eaux continentals du Maroc. Cybium 23(3):17–22.

Bagra K, Kadu K, Nebeshwar-Sharma K, Laskar BA, Sarkar UK, Das DN (2009) Ichthyological survey and review of the checklist of fish fauna of Arunachal Pradesh, India. Check List 5(2):330–350.

Banarescu P (1977) Position zoogéographique de l'ichthyofaune d'eau douces d'Asie occidentale. Cybium 2:35–55.

Banister KE (1973) A revision of the large *Barbus* (Pisces, Cyprinidae) of East and Central Africa. Studies on African Cyprinidae Part II. Bulletin of the British Museum (Natural History) Zoology 26(1) 1–148.

Banister KE (1980) The fishes of the Tigris and Euphrates rivers. In: Rzóska J, Talling JF (eds) Euphrates and Tigris, Mesopotamian Ecology and Destiny. Monographiae biologicae, vol. 38. Junk, The Hague, pp 95–106.

References

Banister KE, Clarke MA (1977) The freshwater fishes of the Arabian Peninsula. Journal of Oman Studies (Special Report):111–154.

Beineke J (2006) Spät-Quartäre Paläogeographie der Arabischen Halbinsel. Dissertation. Universität Paderborn, Paderborn.

Berg LS (1949) Presnovodnye ryby Irana i sopredel'nykh stran [Freshwater fishes of Iran and adjacent countries]. Trudy Zoologicheskogo Instituta Akademii Nauk SSSR 8:783–858.

Berger J-F, Bravard J-P, Purdue L, Benoist A, Mouton M, Braemer F (2012) Rivers of the Hadramawt watershed (Yemen) during the Holocene: Clues of late functioning. Quaternary International 266:142–161. doi: 10.1016/j.quaint.2011.10.037

Berrebi P (1981) Contribution a l'etude du sous-genre *Labeobarbus*. Bulletin de l'Institut Scientifique, Rabat 5:59–72.

Berrebi P, Chenuil A, Kotlík P, Machordom A, Tsigenopoulos CS (2014) Disentangling the evolutionary history of the genus *Barbus sensu lato*, a twenty years adventure. In: Alves MJ, Cartaxana A, Correia AM, Lopes LF (eds) Professor Carlos Almaça (1934–2010): Estado da Arte em Áreas Cientícas que Desenvolveu. Museu Nacional de História Natural e da Ciência, Lisboa, pp 29–55.

Berrebi P, Kottelat M, Skelton P, Ráb P (1996) Systematics of *Barbus*: State of the art and heuristic comments. Folia Zoologica 45(Suppl.1):5–12.

Bianco PG, Banarescu P (1982) A contribution to the knowledge of the Cyprinidae of Iran (Pisces, Cypriniformes). Cybium 6(2):75–96.

Borkenhagen K (2014) A new genus and species of cyprinid fish (Actinopterygii, Cyprinidae) from the Arabian Peninsula, and its phylogenetic and zoogeographic affinities. Environmental Biology of Fishes 97(10):1179–1195. doi: 10.1007/s10641-014-0315-y

Borkenhagen K (2017) Molecular phylogeny of the tribe Torini Karaman, 1971 (Actinopterygii: Cypriniformes) from the Middle East and North Africa. Zootaxa 4236(2):291–301. doi: 10.11646/zootaxa.4236.2.4

Borkenhagen K, Esmaeili HR, Mohsenzadeh S, Shahryari F, Gholamifard A (2011) The molecular systematics of the *Carasobarbus* species from Iran and adjacent areas, with comments on *Carasobarbus albus* (Heckel, 1843). Environmental Biology of Fishes 91(3):327–335. doi: 10.1007/s10641-011-9787-1

Borkenhagen K, Krupp F (2013) Taxonomic revision of the genus *Carasobarbus* Karaman, 1971 (Actinopterygii, Cyprinidae). Zookeys 339:1–53. doi: 10.3897/zookeys.339.4903

Boulenger GA (1902) Description of Two new Cyprinid Fishes from Morocco. Annals and Magazine of Natural History (Series 7) 9(50):124–125.

Boulenger GA (1909) Catalogue of the fresh-water fishes of Africa in the British Museum (Natural History), vol. 1. Taylor & Francis, London.

Boulenger GA (1911) Catalogue of the fresh-water fishes of Africa in the British Museum (Natural History). Taylor and Francis. London, i-xii + 1-529.

Boulenger GA (1919) La distribution en Afrique des Barbeaux du sous-genre *Labeobarbus*. Comptes Rendus Hebdomadaires des Seances de l'Academie des Sciences 169:1016–1018.

Briolay J, Galtier N, Brito RM, Bouvet Y (1998) Molecular phylogeny of Cyprinidae inferred from cytochrome b DNA sequences. Molecular Phylogenetics and Evolution 9(1): 100–108. doi:10.1006/mpev.1997.0441

Casal-Lopez M, Perea S, Yahyaoui A, Doadrio I (2015) Taxonomic review of the genus *Luciobarbus* Heckel, 1843 (Actinopterygii, Cyprinidae) from northwestern Morocco with the description of three new species. Graellsia 71(2):e027. doi: 10.3989/graellsia.2015.v71.135

Chorowicz J, Dhont D, Ammar O, Rukieh M, Bilal A (2005) Tectonics of the Pliocene Homs basalts (Syria) and implications for the Dead Sea Fault Zone activity. Journal of the Geological Society 162:259–271.

Coad BW (1982) A re-description and generic re-assignment of *Kosswigobarbus kosswigi* (Ladiges, 1960), a cyprinid fish from Turkey and Iran. Mitteilungen aus dem Hamburgischen Zoologischen Museum und Institut 79:263–265.

Coad BW (1991) Fishes of the Tigris-Euphrates Basin. A Critical Checklist. Syllogeus 68:1–49.

Coad BW (1995) Freshwater fishes of Iran. Acta Scientiarum Naturalium, Brno 29(1):1–64.

Coad BW (1996) Zoogeography of the fishes of the Tigris-Euphrates Basin. Zoology in the Middle East 13:51–70.

Coad BW (2016) Freshwater fishes of Iran. www.briancoad.com/Species%20Accounts/Contents%20new.htm. Accessed 15 September 2016.

Coad BW, Najafpour N (1997) *Barbus sublimus*, a new species of cyprinid fish from Khuzestan Province, Iran. Ichthyological Exploration of Freshwaters 7(3):273–278.

Collard M, Wood B (2015) Defining the genus *Homo*. In: Henke W, Tattersall I (Eds) Handbook of paleoanthropology. Springer, New York, 2107–2144.

Colli L, Paglianti A, Berti R, Gandolfi G, Tagliavini J (2009) Molecular phylogeny of the blind cavefish *Phreatichthys andruzzii* and *Garra barreimiae* within the family Cyprinidae. Environmental Biology of Fishes 84(1):95–107.

Crivelli AJ (2006) *Barbus reinii*. In: IUCN (ed) IUCN Red List of Threatened Species, 2011 edn.

Cuvier G, Valenciennes A (1842) Histoire naturelle des poissons, vol. 16.

Dahanukar N, Philip S, Krishnakumar K, Ali A, Raghavan R (2013) The phylogenetic position of *Lepidopygopsis typus* (Teleostei: Cyprinidae), a monotypic freshwater fish endemic to the Western Ghats of India. Zootaxa 3700(1):113. doi: 10.11646/zootaxa.3700.1.4

De Queiroz K (2007) Species concepts and species delimitation. Systematic Biology 56(6):879–886. doi: 10.1080/10635150701701083

Doadrio I (1994) Freshwater fish fauna of North Africa and its biogeography. Annales du Musee Royal de l'Afrique Centrale Zoologie 275:21–34.

Doadrio I, Casal-López M, Perea S, Yahyaoui A (2016) Taxonomy of rheophilic *Luciobarbus* Heckel, 1842 (Actinopterygii, Cyprinidae) from Morocco with the description of two new species. Graellsia 72(1):e039. doi: 10.3989/graellsia.2016.v72.153

Drake NA, Breeze P, Parker A (2013) Palaeoclimate in the Saharan and Arabian Deserts during the Middle Palaeolithic and the potential for hominin dispersals. Quaternary International 300:48–61. doi: 10.1016/j.quaint.2012.12.018

Durand JD, Tsigenopoulos CS, Ünlü E, Berrebi P (2002) Phylogeny and biogeography of the family Cyprinidae in the Middle East inferred from cytochrome *b* DNA - Evolutionary significance of this region. Molecular Phylogenetics and Evolution 22(1):91–100. doi: 10.1006/mpev.2001.1040

Ekmekçi FG, Banarescu P (1998) A revision of the generic position of *Barynotus* (*Systomus*) *verhoeffi*, and the validity of the genera *Carasobarbus*, *Kosswigobarbus* and *Mesopotamichthys* (Pisces, Cyprinidae). Folia Zoologica 47(Suppl. 1):87–96.

El Gharbi S, Lambert A, Berrebi P (1993) Le genre *Barbus* (sous-genres *Barbus* et *Labeobarbus*) au Maroc. Génétique et parasitologie. Cahiers d’éthologie 13(2):223–226.

Engel M, Brückner H, Pint A, Wellbrock K, Ginau A, Voss P, Grottker M, Klasen N, Frenzel P (2012) The early Holocene humid period in NW Saudi Arabia – Sediments, microfossils and palaeo-hydrological modelling. Quaternary International 266:131–141. doi: 10.1016/j.quaint.2011.04.028

Eschmeyer WN (2015) Catalog of Fishes: Genera, Species, References. Electronic version. research.calacademy.org/research/ichthyology/catalog/fishcatmain.asp. Accessed 1 March 2015.

Esmaeili HR, Coad BW, Gholamifard A, Nazari N, Teimori A (2010) Annotated checklist of the freshwater fishes of Iran. Zoosystematica Rossica 19(2):361–386.

Esmaeili HR, Teimory A, Gholami Z, Hosseinie F (2006) Range extension of *Barbus sublimus* Coad and Najafpour, 1997 (Actinopterygii: Cyprinidae) and its sympatric species in Southwest of Iran. Iranian Journal of Animal Biosystematics 2(1):19-14.

FAO (2009a) Asi-Orontes Basin. AQUASTAT website. Food and Agriculture Organization of the United Nations (FAO). www.fao.org/nr/water/aquastat/basins/asi-orontes/index.stm. Accessed 17 September 2016.

FAO (2009b) Euphrates-Tigris Basin. AQUASTAT website. Food and Agriculture Organization of the United Nations (FAO). www.fao.org/nr/water/aquastat/basins/euphrates-tigris/index.stm. Accessed 17 September 2016.

FAO (2009c) Jordan Basin. AQUASTAT website. Food and Agriculture Organization of the United Nations (FAO). www.fao.org/nr/water/aquastat/basins/jordan/index.stm. Accessed 17 September 2016.

Fernandes CA, Rohling EJ, Siddall M (2006) Absence of post-Miocene Red Sea land bridges: biogeographic implications. Journal of Biogeography 33(6):961–966. doi: 10.1111/j.1365-2699.2006.01478.x

Fowler HW (1976) A Catalog of World Fishes (XXV). Quarterly Journal of the Taiwan Museum 29(3&4):277–396.

Freyhof J (2014) *Mesopotamichthys sharpeyi*. In: IUCN (ed) IUCN Red List of Threatened Species.

Freyhof J, Hamidan NA, Feulner GR, Harrison I (2015) Chapter 3. The status and distribution of freshwater fishes of the Arabian Peninsula. In: García N, Harrison I, Cox N, Tognelli MF (eds) The status and distribution of freshwater biodiversity in the Arabian Peninsula. International Union for Conservation of Nature, pp 16–29.

Funk DJ, Omland KE (2003) Species-level paraphyly and polyphyly: Frequency, causes, and consequences, with insights from animal mitochondrial DNA. Annual Review of Ecology, Evolution, and Systematics 34(1):397–423.

Gill FB, Slikas B, Sheldon FH (2005) Phylogeny of titmice (Paridae): II. Species relationships based on sequences of the mitochondrial cytochrome-*b* gene. The Auk 122 (1): 121–143. doi: 10.1642/0004-8038(2005)122[0121:POTPIS]2.0.CO;2

Goren M, Ortal R (1999) Biogeography, diversity and conservation of the inland water fish communities in Israel. Biological Conservation 89(1):1–9.

Günther A (1868) Catalogue of the fishes in the British Museum. Catalogue of the Physostomi, containing the families Heteropygii, Cyprinidae, Gonorhynchidae, Hyodontidae, Osteoglossidae, Clupeidae, Chirocentridae, Alepocephalidae, Notopteridae, Halosauridae, in the collection of the British Museum, vol. 7.

Günther A (1874a) Notice of some new species of fishes from Morocco. Annals and Magazine of Natural History 13(75):230–232.

Günther A (1874b) A contribution to the fauna of the river Tigris. Annals and Magazine of Natural History (Series 4) 14(79):36–38.

Günther A (1896) Descriptions of two new species of fishes (*Mastacembelus* and *Barbus*). Annals and Magazine of Natural History (Series 6) 17(101):397.

Günther A (1901) Second notice of new species of fishes from Morocco. Novitates Zoologicae. A Journal of Zoology in Connection with the Tring Museum 8:367–368.

Günther A (1902) Third notice of new species of fishes from Morocco. Novitates Zoologicae. A Journal of Zoology in Connection with the Tring Museum 9:446–448.

Hamidan N (2004) The freshwater fish fauna of Jordan. Denisia 14:385–394.

Harzhauser M, Kroh A, Mandic O, Piller WE, Göhlich U, Reuter M, Berning B (2007) Biogeographic responses to geodynamics: A key study all around the Oligo–Miocene Tethyan Seaway. Zoologischer Anzeiger - A Journal of Comparative Zoology 246(4):241–256. doi: 10.1016/j.jcz.2007.05.001

Heckel JJ (1843) Ichthyologie. In: Russegger J von (ed) Reisen in Griechenland, Unteregypten, im nördlichen Syrien und südöstlichen Kleinasien: mit besonderer Rücksicht auf die naturwissenschaftlichen Verhältnisse der betreffenden Länder, unternommen in dem Jahre 1836, 1(2), Stuttgart.

Heckel JJ (1847) Die Fische Persiens, gesammelt von Thoedor Kotschy. In: Russegger J von (ed) Reisen in Europa, Asien und Africa: unternommen in den Jahren 1835 bis 1841, 2(3).

Heller J (2007) A historic biogeography of the aquatic fauna of the Levant. Biological Journal of the Linnean Society 92:625–639. doi: 10.1111/j.1095-8312.2007.00850.x

Hendry AP (2009) Evolutionary biology: Speciation. Nature 458: 162–164. doi: 10.1038/458162a

Hoàng HĐ, Phạm HM, Durand JD, Trần NT, Phan PĐ (2015) Mahseers genera *Tor* and *Neolissochilus* (Teleostei: Cyprinidae) from southern Vietnam. Zootaxa 4006(3):551–568. doi: 10.11646/zootaxa.4006.3.8

ICZN (1999) International code of zoological nomenclature, 4th edn. International Trust for Zoological Nomenclature c/o Natural History Museum, London.

Jennings MC (2010) Atlas of the breeding birds of Arabia. Fauna of Saudi Arabia 25:1–751.

Jouladeh-Roudbar A, Vatandoust S, Eagderi S, Jafari-Kenari S, Mousavi-Sabet H (2015) Freshwater fishes of Iran; an updated checklist. AACL BIOFLUX 8(6):855–909.

Kähsbauer P (1963) Zur Kenntnis der Ichthyofauna von Iran. Annalen des Naturhistorischen Museums in Wien 66: 317–355.

Karaman MS (1971) Süßwasserfische der Türkei. 8. Teil. Mitteilungen aus dem Hamburgischen Zoologischen Museum und Institut 67:175–254.

Kempe S, Dirks H (2008) Layla Lakes, Saudi Arabia: The world-wide largest lacustrine gypsum tufas. Acta Carsologica 37 (1):7–14.

Khaironizam MZ, Akaria-Ismail M, Armbruster JW (2015) Cyprinid fishes of the genus *Neolissochilus* in Peninsular Malaysia. Zootaxa 3962(1):139–157. doi: 10.11646/zootaxa.3962.1.7

Khare P, Mohindra V, Barman AS, Singh RK, Lal KK (2014) Molecular evidence to reconcile taxonomic instability in mahseer species (Pisces: Cyprinidae) of India. Organisms Diversity & Evolution 14 (3):307–326. doi:10.1007/s13127-014-0172-8

Kinzelbach R (1987) Faunal history of some sreshwater invertebrates of the Northern Levant (Mollusca, Crustacea). Beihefte zum Tübinger Atlas des Vorderen Orients A 28:41–61.

Knight JDM, Rai A, D'souza RKP (2014) A further note on the identity of *Barbus mussullah* Sykes (Teleostei: Cyprinidae). Zootaxa 3821:280–284. doi: 10.11646/zootaxa.3821.2.8

Knight JDM, Rai A, D'souza, RKP (2013) On the identities of *Barbus mussullah* Sykes and *Cyprinus curmuca* Hamilton with notes on the status of *Gobio canarensis* Jerdon (Teleostei: Cyprinidae). Zootaxa 3750(1–5):201–215. doi: 10.11646/zootaxa.3750.3.1

Knoop V, Müller K (2009) Gene und Stammbäume. Ein Handbuch zur molekularen Phylogenetik, 2nd edn. Spektrum, Heidelberg.

Kosuch J, Vences M, Dubois A, Ohler A, Böhme W (2001) Out of Asia: Mitochondrial DNA evidence for an oriental origin of tiger frogs, genus *Hoplobatrachus*. Molecular Phylogenetics and Evolution 21(3):398–407. doi: 10.1006/mpev.2001.1034

Krijgsman W, Hilgen FJ, Raffi I, Sierro FJ, Wilson DS (1999) Chronology, causes and progression of the Messinian salinity crisis. Nature 400(6745):652–655. doi:10.1038/23231

Krupp F (1983a) Freshwater fishes of Saudi Arabia and adjacent regions of the Arabian Peninsula. Fauna of Saudi Arabia 5:568–636.

Krupp F (1983b) Recent changes in the distribution of Syrian freshwater fishes. Roczniki Nauk Rolniczych Seria H Rybactwo 100(3):79–88.

Krupp F (1985a) *Barbus chantrei* (Sauvage 1882), a valid species of cyprinid fish from the northern Levant. Results of the travels of R. Kinzelbach to the countries of the Middle East, No. 72. Senckenbergiana Biologica 66(1/3):17–25.

Krupp F (1985b) Systematik und Zoogeographie der Süßwasserfische des levantinischen Grabenbruchsystems und der Ostküste des Mittelmeeres. Dissertation. Johannes Guttenberg - Universität, Mainz.

Krupp F (1987) Freshwater ichthyogeography of the Levant. Beihefte zum Tübinger Atlas des Vorderen Orients A 28:229–237.

Krupp F, Khalaf M, Malek M, Streit B, Al-Jumaily M (2009) The Middle Eastern Biodiversity Network: Generating and sharing knowledge for ecosystem management and conservation. Zookeys 31:3–15. doi: 10.3897/zookeys.31.371

Krupp F, Schneider W (1988) Die Süßwasserfauna des Vorderen Orients. Anpassungen und Besiedlungsgeschichte einer Zoogeographischen Übergangszone. Natur und Museum 118(7):193–213.

Krupp F, Schneider W (1989) The fishes of the Jordan River drainage basin and Azraq Oasis. Fauna of Saudi Arabia 10:347–416.

Krupp F, Schneider W (2008) Die Fischfauna des Nahr al-Ḫābūr, Nordost-Syrien. Umwelt und Subsistenz der assyrischen Stadt Dūr-Katlimmu am unteren Khabur. Berichte der Ausgrabung von Tall Šēḫ Ḥamad / Dūr-Katlimmu 8.

Krupp F, Schneider W, Nader IA, Khushaim O (1990) Zoological survey in Saudi Arabia, spring 1990. Fauna of Saudi Arabia 11: 3–9.

Ladiges W (1960) Süsswasserfische der Türkei. I. Teil Cyprinidae. Mitteilungen aus dem Hamburgischen Zoologischen Museum und Institut 58:105–150.

Laskar BA, Bhattacharjee MJ, Dhar B, Mahadani P, Kundu S, Ghosh SK, Laudet V (2013) The species dilemma of Northeast Indian mahseer (Actinopterygii: Cyprinidae): DNA barcoding in clarifying the riddle. PLoS ONE 8(1):e53704. doi: 10.1371/journal.pone.0053704

Leggatt RA, Iwama GK (2003) Occurrence of polyploidy in the fishes. Reviews in Fish Biology and Fisheries 13(3):237–246. doi: 10.1023/B:RFBF.0000033049.00668.fe

Lemey P, Salemi M, Vandamme A-M (eds) (2009) The phylogenetic handbook. A practical approach to phylogenetic analysis and hypothesis testing, 2nd edn. Cambridge University Press, Cambridge, UK, New York.

Lévêque C, Daget J (1984) Cyprinidae. In: Daget J, Gosse J-P, Thys van den Audenaerde DFE (eds) Check-list of the freshwater fishes of Africa. CLOFFA, vol. 1. ORSTOM, Paris, pp 217–342.

Levin BA (2012) New data on morphology of the African scraping feeder *Varicorhinus beso* (Osteichthyes: Cyprinidae) with the special reference to specialized traits. Journal of Ichthyology 52(11):908–923. doi: 10.1134/S0032945212110069

Levin BA, Freyhof J, Lajbner Z, Perea S, Abdoli A, Gaffaroğlu M, Özuluğ M, Rubenyan HR, Salnikov VB, Doadrio I (2012) Phylogenetic relationships of the algae scraping cyprinid genus *Capoeta* (Teleostei: Cyprinidae). Molecular Phylogenetics and Evolution 62(1):542–549. doi: 10.1016/j.ympev.2011.09.004

Machordom A, Doadrio I (2001) Evolutionary history and speciation modes in the cyprinid genus *Barbus*. Proceedings of the Royal Society of London Series B - Biological Sciences 268(1473):1297–1306.

Mayden RL (1999) Consilience and a hierarchy of species concepts: Advances toward closure on the species puzzle. Journal of Nematology 31(2):95–116.

Mayden RL (2002) On biological species, species concepts and individuation in the natural world. Fish and Fisheries 3(3):171–196. doi: 10.1046/j.1467-2979.2002.00086.x

Mayden RL, Chen WJ, Bart HL, Doosey MH, Simons AM, Tang KL, Wood RM, Agnew MK, Yang L, Hirt MV, Clements MD, Saitoh K, Sado T, Miya M, Nishida M (2009) Reconstructing the phylogenetic relationships of the earth's most diverse clade of freshwater fishes-order Cypriniformes (Actinopterygii: Ostariophysi): A case study using multiple nuclear loci and the mitochondrial genome. Molecular Phylogenetics and Evolution 51(3):500–514. doi: 10.1016/j.ympev.2008.12.015

Mayden RL, Tang KL, Wood RM, Chen W-J, Agnew MK, Conway KW, Yang L, Simons AM, Bart HL, Harris PM, Li J, Wang X, Saitoh K, He S, Liu H, Chen Y, Nishida M, Miya M (2008) Inferring the Tree of Life of the order Cypriniformes, the earth's most diverse clade of freshwater fishes: Implications of varied taxon and character sampling. Journal of Systematics and Evolution 46(3):424–438. doi: 10.3724/SP.J.1002.2008.08062

Misra KS (1947) On a second collection of fish from Iraq. Records of the Indian Museum 45:115–127.

Miya M, Saitoh K, Wood R, Nishida M, Mayden RL (2006) New primers for amplifying and sequencing the mitochondrial ND4/ND5 gene region of the Cypriniformes (Actinopterygii: Ostariophysi). Ichthyological Research 53(1):75–81. doi: 10.1007/s10228-005-0303-5

Myers S (1960) Preface to any future classification of the cyprinid fishes of the genus *Barbus*. Stanford Ichthyological Bulletin 7:212–215.

Naama AK, Muhsen KA (1986) Feeding periodicites of the mugilid *Liza abu* (Heckel) and cyprinid *Carasobarbus luteus* (Heckel) from Al-Hammar marsh, Southern Iraq. Indian Journal of Fisheries 33(3):347–350.

Nelson JS (2006) Fishes of the world, 4th edn. John Wiley, Hoboken N.J.

Oellermann LK, Skelton PH (1990) Hexaploidy in yellowfish species (*Barbus*, Pisces, Cyprinidae) from southern Africa. Journal of Fish Biology 37(1):105–115. doi: 10.1111/j.1095-8649.1990.tb05932.x

Otero O (2001) The oldest-known cyprinid fish of the Afro-Arabic Plate, and its paleobiogeographical implications. Journal of Vertebrate Paleontology 21(2):386–388. doi: 10.1671/0272-4634(2001)021[0386:TOKCFO]2.0.CO;2

Otero O, Gayet M (2001) Palaeoichthyofaunas from the Lower Oligocene and Miocene of the Arabian Plate: palaeoecological and palaeobiogeographical implications. Paleogeography Palaeoclimatology Palaeoecology 165(1-2):141–169. doi: 10.1016/S0031-0182(00)00158-9

Pasco-Viel E, Yang L, Veran M, Balter V, Mayden RL, Laudet V, Viriot L (2014) Stability versus diversity of the dentition during evolutionary radiation in cyprinine fish. Proceedings of the Royal Society B: Biological Sciences 281(1780):20132688. doi: 10.1098/rspb.2013.2688

Pellegrin JM (1919) Sur la faune ichthyologique des eaux douces du Maroc. Comptes rendus hebdomadaires des séances de l'Académie des sciences 169:809–811.

Pellegrin J (1921) Les poissons des eaux douces de l’Afrique du Nord française Maroc (Algérie, Tunisie, Sahara). Mémoires de la Société des Sciences Naturelles du Maroc 1(2).

Pellegrin J (1939) Les barbeaux de l'Afrique du nord Française: description d'une espèce nouvelle. Bulletin de la Société des sciences naturelles du Maroc 19:1–10.

Pethiyagoda R, Kottelat M (1994) Three new species of fishes of the genera *Osteochilichthys* (Cyprinidae), *Travancoria* (Balitoridae) and *Horabagrus* (Bagridae) from Chalakudy River, Kerala, India. Journal of South Asian Natural History 1(1):97–116.

Por FD (1989) The legacy of Tethys. An aquatic biogeography of the Levant. Monographiae biologicae, vol. 63. Kluwer, Dordrecht.

Rainboth WJ (1985) *Neolissochilus*, a new genus of South Asian cyprinid fishes. Beaufortia 35(3):25–35.

Roberts TR (1999) Fishes of the cyprinid genus *Tor* in the Nam Theun watershed (Mekong Basin) of Laos, with description of a new species. Raffles Bulletin of Zoology 47(1):225–236.

Rögl F (1999) Mediterranean and Paratethys. Facts and hypotheses of an Oligocene to Miocene paleogeography (short overview). Geologica Carpathica 50(4):339–349.

Rosenberg TM, Preusser F, Risberg J, Plikk A, Kadi KA, Matter A, Fleitmann D (2013) Middle and late Pleistocene humid periods recorded in palaeolake deposits of the Nafud desert, Saudi Arabia. Quaternary Science Reviews 70:109–123. doi: 10.1016/j.quascirev.2013.03.017

Rüppell E (1835) Neuer Nachtrag von Beschreibungen und Abbildungen neuer Fische, im Nil entdeckt. Museum Senckenbergianum 2(1):1–28.

Rzóska J, Talling JF (eds) (1980) Euphrates and Tigris, Mesopotamian Ecology and Destiny. Monographiae biologicae, vol. 38. Junk, The Hague.

Saitoh K, Sado T, Doosey MH, Bart HL, Inoue JG, Nishida M, Mayden RL, Miya M (2011) Evidence from mitochondrial genomics supports the lower Mesozoic of South Asia as the time and place of basal divergence of cypriniform fishes (Actinopterygii: Ostariophysi). Zoological Journal of the Linnean Society 161(3):633–662. doi: 10.1111/j.1096-3642.2010.00651.x

Saitoh K, Sado T, Mayden RL, Hanzawa N, Nakamura K, Nishida M, Miya M (2006) Mitogenomic evolution and interrelationships of the Cypriniformes (Actinopterygii: Ostariophysi): the first evidence toward resolution of higher-level relationships of the world's largest freshwater fish clade based on 59 whole mitogenome sequences. Journal of Molecular Evolution 63(6):826–841. doi: 10.1007/s00239-005-0293-y

Sauvage HE (1882) Catalogue des poissons recueillis par M. E. Chantre pendant son voyage en Syrie, Haute-Mésopotamie, Kurdistan et Caucase. Bulletin de la Société philomathique de Paris 6:163–168.

Sauvage HE (1884) Notice sur la faune ichthyologique d' l'oust de l'Asie et plus particulièrement sur les poissons recueillis par M. Chantre pendant son voyage dans cette région. Nouvelles Archives du Muséum d’Histoire Naturelle, Paris (Ser. 2) 7:1–41.

Stewart KM (2001) The freshwater fish of Neogene Africa (Miocene-Pleistocene): systematics and biogeography. Fish and Fisheries 2(3):177–230. doi: 10.1046/j.1467-2960.2001.00052.x

Stiassny MLJ, Getahun A (2007) An overview of labeonin relationships and the phylogenetic placement of the Afro-Asian genus *Garra* Hamilton, 1922 (Teleostei : Cyprinidae), with the description of five new species of *Garra* from Ethiopia, and a key to all African species. Zoological Journal of the Linnean Society 150(1):41–83. doi: 10.1111/j.1096-3642.2007.00281.x

Talavera G, Lukhtanov VA, Pierce NE, Vila R (2013) Establishing criteria for higher-level classification using molecular data: the systematics of *Polyommatus* blue butterflies (Lepidoptera, Lycaenidae). Cladistics 29(2) 166–192. doi:10.1111/j.1096-0031.2012.00421.x

Tang Q, Getahun A, Liu H (2009) Multiple in-to-Africa dispersals of labeonin fishes (Teleostei: Cyprinidae) revealed by molecular phylogenetic analysis. Hydrobiologia 632(1):261–271. doi: 10.1007/s10750-009-9848-z

Trewavas E (1941) 3. Freshwater fishes. British Museum (Natural History) expedition to southwest Arabia 1937–8 1(3):7–15.

Tsigenopoulos CS, Durand JD, Ünlü E, Berrebi P (2003) Rapid radiation of the Mediterranean *Luciobarbus* species (Cyprinidae) after the Messinian salinity crisis of the Mediterranean Sea, inferred from mitochondrial phylogenetic analysis. Biological Journal of the Linnean Society 80(2):207–222. doi: 10.1046/j.1095-8312.2003.00237.x

Tsigenopoulos CS, Kasapidis P, Berrebi P (2010) Phylogenetic relationships of hexaploid large-sized barbs (genus *Labeobarbus*, Cyprinidae) based on mtDNA data. Molecular Phylogenetics and Evolution 56(2):851–856. doi: 10.1016/j.ympev.2010.02.006

Tweddle D, Skelton PH (1998) Two new species of *Varicorhinus* (Teleostei: Cyprinidae) from the Ruo River, Malawi, Africa, with a review of other southern African *Varicorhinus* species. Ichthyological Exploration of Freshwaters 8(4):369–384.

Vreven EJWMN, Musschoot T, Snoeks J, Schliewen UK (2016) The African hexaploid Torini (Cypriniformes: Cyprinidae): review of a tumultuous history. Zoological Journal of the Linnean Society 177(2):231–305. doi: 10.1111/zoj.12366

Wang J, Wu X, Chen Z, Yue Z, Ma W, Chen S, Xiao H, Murphy RW, Zhang Y, Zan R, Luo J (2013) Molecular phylogeny of European and African *Barbus* and their West Asian relatives in the Cyprininae (Teleostei: Cypriniformes) and orogenesis of the Qinghai-Tibetan Plateau. Chinese Science Bulletin 58(31):3738–3746. doi: 10.1007/s11434-013-5878-z

Werner F (1931) Ergebnisse einer zoologischen Forschungsreise nach Marokko. II. Fische. Sitzungsberichte der Kaiserlichen Akademie der Wissenschaften. Mathematisch-Naturwissenschaftliche Classe 140:261–270.

Wolfart R (1987) Late cretaceous through quaternary palaeogeographic evolution of the Middle East. Beihefte zum Tübinger Atlas des Vorderen Orients A 28:9–22.

Wossughi G (1978) Beitrag zur Systematik und Zoogeographie der Cyprinidae (Pisces: Teleostei) des Mittleren Ostens, unter besonderer Berücksichtigung des Irans. Dissertation. Universität Hamburg, Hamburg.

Wossughi GH, Khoshzahmat A, Etemadfar A (1983) Recognition of fresh-water fishes in the area between Noorabad of Mamasany, Kazeron and Dashtestan. Journal of Veterinary Faculty, University of Tehran 38(2–4):21–44.

Yang L, Hirt MV, Sado T, Arunachalam M, Manickam R, Tang KL, Simons AM, Wu H-h, Mayden RL, Miya M (2012) Phylogenetic placements of the barbin genera *Discherodontus*, *Chagunius*, and *Hypselobarbus* in the subfamily Cyprininae (Teleostei: Cypriniformes) and their relationships with other barbins. Zootaxa 3586:26–40.

Yang L, Mayden RL (2010) Phylogenetic relationships, subdivision, and biogeography of the cyprinid tribe Labeonini (*sensu* Rainboth, 1991) (Teleostei: Cypriniformes), with comments on the implications of lips and associated structures in the labeonin classification. Molecular Phylogenetics and Evolution 54(1):254–265. doi: 10.1016/j.ympev.2009.09.027

Yang L, Mayden RL, Sado T, He S, Saitoh K, Miya M (2010) Molecular phylogeny of the fishes traditionally referred to Cyprinini *sensu stricto* (Teleostei: Cypriniformes). Zoologica Scripta 39(6):527–550. doi: 10.1111/j.1463-6409.2010.00443.x

Yang L, Sado T, Vincent Hirt M, Pasco-Viel E, Arunachalam M, Li J, Wang X, Freyhof J, Saitoh K, Simons AM, Miya M, He S, Mayden RL (2015) Phylogeny and polyploidy: resolving the classification of cyprinine fishes (Teleostei: Cypriniformes). Molecular Phylogenetics and Evolution 85:97–116. doi: 10.1016/j.ympev.2015.01.014

Zardoya R, Meyer A (1996) Phylogenetic performance of mitochondrial protein-coding genes in resolving relationships among vertebrates. Molecular Biology and Evolution 13(7):933–942.

Erklärung zu den Autorenanteilen

an der Publikation: **The molecular systematics of the *Carasobarbus* species from Iran and adjacent areas, with comments on *Carasobarbus albus* (Heckel, 1843)**

Status: publiziert
Name der Zeitschrift: Environmental Biology of Fishes
Beteiligte Autoren: Kai Borkenhagen (KB)
Hamid Reza Esmaeili (HE)
Sasan Mohsenzadeh (SM)
Fatemeh Shahryari (FS)
Ali Golamifard (AG)

Was hat der Promovierende bzw. was haben die Koautoren beigetragen?
(1) zu Entwicklung und Planung
Promovierender: 50 %
Co-Autor HE: 20 %
Co-Autor SM: 10 %
Co-Autor FS: 10 %
Co-Autor AG: 10 %

(2) zur Durchführung der einzelnen Untersuchungen und Experimente
Promovierender: 50 % KB war an der Feldarbeit und an den Laborexperimenten beteiligt.
Co-Autor HE: 25 % HE war an der Feldarbeit und an den Laborexperimenten beteiligt.
Co-Autor FS: 25 % FS war an der Feldarbeit und an den Laborexperimenten beteiligt.

(3) zur Erstellung der Datensammlung und Abbildungen
Promovierender: 50 % KB war an der Datensammlung beteiligt und hat alle im Manuskript verwendeten Abbildungen erstellt.
Co-Autor HE: 20 % HE war an der Datensammlung beteiligt.
Co-Autor FS: 15 % FS war an der Datensammlung beteiligt.
Co-Autor AG: 15 % AG war an der Datensammlung beteiligt.

(4) zur Analyse und Interpretation der Daten
Promovierender: 60 % KB hat alle Daten analysiert und war wesentlich an der Interpretation der Ergebnisse beteiligt.
Co-Autor HE: 20 % HE war an der Interpretation der Ergebnisse beteiligt.
Co-Autor FS: 20 % FS war an der Interpretation der Ergebnisse beteiligt.

(5) zum Verfassen des Manuskripts
Promovierender: 50 %
Co-Autor HE: 20 %
Co-Autor SM: 10 %
Co-Autor FS: 10 %
Co-Autor AG: 10 %

Unterschrift Promovend: ____________________________ Datum/Ort: ___________________

Zustimmende Bestätigungen der oben genannten Angaben

Unterschrift Betreuer: _______________________________ Datum/Ort: __________________

Environ Biol Fish
DOI 10.1007/s10641-011-9787-1

The molecular systematics of the *Carasobarbus* species from Iran and adjacent areas, with comments on *Carasobarbus albus* (Heckel, 1843)

Kai Borkenhagen · Hamid Reza Esmaeili ·
Sasan Mohsenzadeh · Fatemeh Shahryari ·
Ali Gholamifard

Received: 21 July 2010 / Accepted: 14 March 2011
© Springer Science+Business Media B.V. 2011

Abstract The diversity of cytochrome *b* sequences of *Carasobarbus* species from Iran and adjacent areas was investigated. Two divergent haplotype groups were found for *C. luteus*. The first one is widespread and congruent with the biogeographical hypothesis of a recent isolation among the various populations as a consequence of rising sea levels following the last Pleistocene glaciation. The second one is restricted to the Khabur River in Syria. The possibility that one of these groups corresponds to *C. albus* is discussed, but we conclude that it is more likely that *C. luteus* is a single species that retained two divergent mitochondrial lineages. The mitochondrial sequence diversity found for *C. kosswigi* and *C. sublimus* is high, possibly due to small population size and consequent genetic drift. *Carasobarbus kosswigi* is paraphyletic with respect to *C. sublimus*, indicating a recent speciation event of these taxa.

Keywords Cyprinidae · *Carasobarbus luteus* · Mitochondrial introgression · Biogeography · Cytochrome b · Middle East

---

K. Borkenhagen (✉)
Senckenberg Research Institute and Museum of Nature,
Frankfurt, Germany
e-mail: kborkenhagen@senckenberg.de

H. R. Esmaeili · S. Mohsenzadeh · F. Shahryari ·
A. Gholamifard
Department of Biology, College of Sciences,
Shiraz University,
Shiraz, Iran

Introduction

Cyprinid fishes (Cyprinidae) are the major element of the Eurasian temperate freshwater fish fauna with respect to abundance and species diversity (about 220 genera and 2420 species worldwide; Nelson 2006). This complex group is characterised by considerable morphological variability, which reflects the high diversity of their habitats and ecological traits. In a recently updated list of freshwater fishes of Iran, 15 species of the *Barbus* s.l. group are listed (Coad 2010). Three of these belong to the genus *Carasobarbus* Karaman, 1971, namely *C. luteus*, *C. kosswigi* and *C. sublimus*. This genus is characterised by moderate body size, a smooth last unbranched dorsal-fin ray, nine to ten (usually ten) branched dorsal-fin rays, six branched anal-fin rays and large scales with numerous parallel radii (Krupp 1985; Borkenhagen 2005).

Carasobarbus luteus (Heckel, 1843), which is called *himri* in Iran, is widely distributed in the rivers Tigris and Euphrates and adjacent drainage basins. In Iran, it is found in the Tigris River Basin including the Hawr Al Azim Marsh, the Persian Gulf Basin including the Helleh, Dalaki, Shapur, Mond and Dasht-e Palang rivers and Lake Famur (Parishan), the Lake Maharlu Basin and the Hormozgan Basin. It has been extirpated in the Quweiq in northern Syria. A few records from the Orontes in western Syria exist, but its presence there is doubtful (Wossughi 1978; Bianco and Bănărescu 1982; Krupp 1985; Borkenhagen

Published online: 14 April 2011

2005; Coad 2010). Different populations vary in morphometric characters and colouration. Two other species and one subspecies were described, reflecting this variation, but were later considered synonyms. These are *Systomus albus* Heckel, 1843 from Orontes and Tigris, *Systomus albus alpina* Heckel, 1846 from the Qarah Agaj and Lake Parishan and *Barbus parieschanica* Wossughi, Khozahmat & Etemadfar, 1982 from a river near Lake Parishan.

Carasobarbus kosswigi (Ladiges, 1960) occurs across the Tigris-Euphrates System in Iraq, Syria and Turkey. In Iran it inhabits the rivers Dez and Karkheh and their tributaries (Abdoli 2000; Coad 2010). A closely related species, *C. sublimus* (Coad & Najafpour, 1997) was described from the A'la River in Khuzestan (Tigris Basin) and subsequently reported from the Persian Gulf Basin (Esmaeili et al. 2006).

The aim of this study was to assess genetic variation among *Carasobarbus* species and populations in Iran and adjacent countries. Our objective was to compare the degree of genetic variation of widespread vs. geographically restricted species, and to explore potential relationships between ecological conditions, such as range size, and genetic diversity within evolutionary lineages. We were also interested in how morphological and genetic variation within *C. luteus* compare, and evaluated the status of *C. luteus* relative to current synonymies.

Materials and methods

Specimens used in this study were collected from 20 localities including the Tigris-Euphrates System and the southern basins of Iran (Lake Famur and Qarah Agaj River in the Gulf Basin, springs of Maharlu Basin and springs of Hormuz Basin in southern Fars Province) (Fig. 1) using electric fishing gear, cast nets and hook and line. Tissue samples were fixed in 96% ethanol. Voucher specimens are held in the Collections of the Biology Department, Shiraz University, Iran (CBSU) and the Senckenberg Research Institute and Museum of Nature, Frankfurt, Germany (SMF). Additional acronyms refer to the Institute of Hydrobiology, Chinese Academy of Sciences, Wuhan, China (IHBCAS), the National Museum of Natural History Madrid, Spain (MNCN), the Natural History Museum Vienna, Austria (NMW) and the Zoological Museum of Tel-Aviv University, Israel (Tel-AvivZM). All specimens included in the molecular analysis are listed in Table 1. For taxonomic comparison the types of *Systomus albus* (NMW 53674-7 (4), NMW 53680 (1), NMW 91400 (1), SMF 812 (1)), *Systomus albus alpina* (NMW 53678 (5), NMW 53679 (2), NMW 53681 (2), NMW 53682 (2)) and *Systomus luteus* (NMW 10827 (1), NMW 54247 (2), NMW 54248 (1), NMW 54249 (1), NMW 54250 (2) NMW 54253 (2), NMW 54254 (3), NMW 54255 (2), NMW 80043 (2), SMF 6784 (1)) were studied.

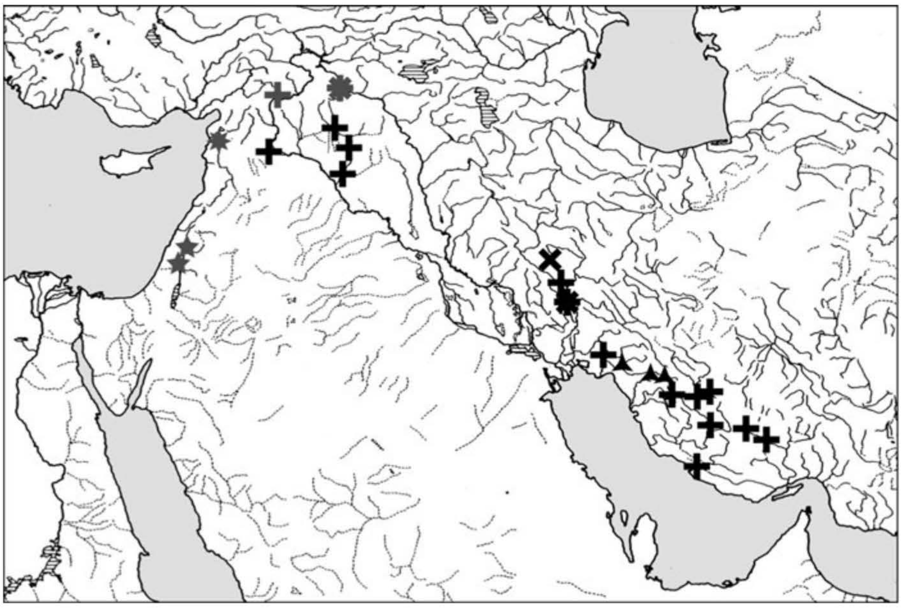

Fig. 1 Map of collection sites of *C. canis* (★), *C. chantrei* (✸), *C. kosswigi* (✖), *C. luteus* (✚) and *C. sublimus* (▲). Black symbols indicate samples from this study, grey symbols indicate localities of sequences from GenBank. The cross with four bars is the result of superposition of the two types of normal crosses

Table 1 Material used in this study. Coordinates in brackets where inferred from locality names

GenBank No.	Collection No	Species	Locality	Coordinates	Collector	Date	Author	Remark
AF145944	–	*Carasobarbus luteus*	Tigris R.–Diyarbakir, Turkey and Euphrates R.–Adiyaman, Turkey	[37°54′39″N 40°14′12″E; 37°45′ 50″N 38°16′40″E]	–	–	Durand et al. 2002	
AF145945	–	*'Barbus' grypus*	Tigris R.–Diyarbakir, Turkey and Euphrates R.–Adiyaman, Turkey	[37°54′39″N 40°14′12″E; 37°45′ 50″N 38°16′40″E]	–	–	Durand et al. 2002	
AF145947	–	*Carasobarbus canis*	Tiberias Lake, Israel	[32°48′41″N 35°36′16″E]	–	–	Durand et al. 2002	
AF180852	–	*Carasobarbus chantrei*	Orontes R.–Antakya, Turkey	[36°12'0″N 36°9′0″E]	–	–	Durand et al. 2002	
AF180853	–	*Carasobarbus kosswigi*	Tigris R.–Diyarbakir, Turkey	[37°54′39″N 40°14′12″E]	–	–	Durand et al. 2002	
AF180854	–	*'Barbus' paytonii*	Oum Erbia River, Morocco	[32°48′N 6°50′W]	–	–	Durand et al. 2002	
AF180855	–	*'Barbus' harterti*	Sebou River, Morocco	[34°04′N 5°33′W]	–	–	Tsigenopoulos et al. 2010	
AF180856	–	*'Barbus' fritschii*	Sebou River, Morocco	[34°04′N 5°33′W]	–	–	Tsigenopoulos et al. 2010	
AF287457	MNCN 92A	*Varicorhinus maroccanus*	Oum Erbia, El Borj, Morocco	[32°48′N 6°50′W]	–	–	Machordom & Doadrio 2001	
AF288486	Tel-AvivZM P11367	*Carasobarbus canis*	David River, Bet Shean, Israel	[32°30′N 35°30′E]	–		Machordom and Doadrio 2001	
AY463516	IHBCAS uncatalogued	*Neolissochilus heterostomus*	Irrawaddy River Drainage, Tengchong, Yunnan Province, China	[25°01′N 98°29′E]	–	–	He et al. 2004	
FN821720	CBSU M125	*Carasobarbus luteus*	Bream bridge, Noor Abad, Fahlian River, Zohreh River System, Gulf Basin, Iran	30°19′24.2″N 51°14′32.5″E	H. R. Esmaeili	5 Oct 2008	this study	
FN821721	CBSU M129	*Carasobarbus luteus*	Khuzestan, Abbaran Village, Maroon River, Jarahi, Tigris-Euphrates System, Iran	30°40′59.82″N 49°49′15.00″E	H. Zareian	12 Sep 2008	this study	
FN821722	SMF 32889	*Carasobarbus luteus*	Balarud River, Khuzestan, Tigris-Euphrates System, Iran	32°35′19″N 48°17′11″E	N. Alwan, K. Borkenhagen	3 Mar 2008	this study	
FN821723	CBSU M127	*Carasobarbus luteus*	Faryab village, Mohr, Lamerd, Fars, Mehran River, Hormuz Basin, Iran	27°29′24.38″N 52°56′16.56″E	A. Gholamifard	01 Jan 2008	this study	
FN821724	CBSU M126	*Carasobarbus luteus*	Near Zali village, Kazeron, Parishan lake, Gulf Basin, Iran	29°31′41.2″N 51°46′25.0″E	A. Gholamhosseini	10 Jan 2008	this study	
FN821725	CBSU M128	*Carasobarbus luteus*	Simakan warm water spring, Qarah Agaj River, Mond River System, Gulf Basin, Iran	28°36′31.62″N 53°08′46.62″E	A. Gholamifard	10 Jan 2008	this study	
FN821726	CBSU M131	*Carasobarbus luteus*	Kaftarak, Shiraz, Maharlu lake, Maharlu Basin, Iran	29°33′21.0″N, 52°44′22.6″E	A. Gholamhosseini	18 Nov 2008	this study	
FN821727	SMF 30823	*Carasobarbus sublimus*	Kheir Abad River, Gulf Basin, Iran	30°31′38.9″N 50°24′44.9″E	K. Borkenhagen	6 Nov 2006	this study	
FN821728	SMF 30834	*Carasobarbus sublimus*	Kheir Abad River, Gulf Basin, Iran	30°31′38.9″N 50°24′44.9″E	K. Borkenhagen	6 Nov 2006	this study	
FN821729	SMF 30835	*Carasobarbus sublimus*	Kheir Abad River, Gulf Basin, Iran	30°31′38.9″N 50°24′44.9″E	K. Borkenhagen	6 Nov 2006	this study	
FN821730	SMF 31014	*Carasobarbus luteus*	Spring Golabii, 35 km north from Darab, Hormuz Basin, Iran	28°47.255′N 54°22.321′E	J. Freyhof	2007	this study	finclip only

Table 1 (continued)

GenBank No.	Collection No	Species	Locality	Coordinates	Collector	Date	Author	Remark
FN821731	SMF 31017	*Carasobarbus luteus*	Spring Pirbanoo about 10 km south of Shiraz, Maharlu Basin, Iran	29°31.135′N 52°27.933′E	J. Freyhof	2007	this study	finclip only
FN821732	SMF 31308	*Carasobarbus luteus*	al Jaboul, Tigris-Euphrates System, Syria	36°03′35.6″N 37°33′0.7″E	N. Hamidan	23 Jun 2008	this study	
FN821733	SMF 31315	*Carasobarbus luteus*	Nahr al Khabur at Ghawat, Tigris-Euphrates System, Syria	35°28′50.9″N 40°39′54.2″E	N. Alwan, K. Borkenhagen, F. Wicker	28 Oct 2008	this study	
FN821734	SMF 31316	*Carasobarbus luteus*	Nahr al Khabur at Al Shaddadah, Tigris-Euphrates System, Syria	36°03′46.4″N 40°44′29.6″E	N. Alwan, K. Borkenhagen, F. Wicker	28 Oct 2008	this study	
FN821735	SMF 31317	*Carasobarbus luteus*	Nahr al Khabur at Tall Tamer, Tigris-Euphrates System, Syria	36°39′07.1″N 40°21′51.3″E	N. Alwan, K. Borkenhagen, F. Wicker	29 Oct 2008	this study	
FN821736	SMF 31319	*Carasobarbus sublimus*	Rud-e Fahliyan, Gulf Basin, Iran	30°11′08.6″N 51°31′14.8″E	N. Alwan, K. Borkenhagen	29 Feb 2008	this study	
FN821737	SMF 31320	*Carasobarbus sublimus*	Rud-e Fahliyan, Gulf Basin, Iran	30°11′08.6″N 51°31′14.8″E	N. Alwan, K. Borkenhagen	29 Feb 2008	this study	
FN821738	SMF 31321	*Carasobarbus sublimus*	Tang-e Sheeb River, Gulf Basin, Iran	30°19′20.6″N 51°14′32.1″E	N. Alwan, K. Borkenhagen	29 Feb 2008	this study	
FN821739	SMF 31322	*Carasobarbus luteus*	Dez River, Tigris-Euphrates System, Iran	32°23′13.5″N 48°23′48.2″E	N. Alwan, K. Borkenhagen	2 Mar 2008	this study	
FN821740	SMF 31323	*Carasobarbus kosswigi*	Dez River, Tigris-Euphrates System, Iran	32°23′13.5″N 48°23′48.2″E	N. Alwan, K. Borkenhagen	2 Mar 2008	this study	
FN821741	SMF 31325	*Carasobarbus kosswigi*	Karkheh River near Pol-e Dokhtar, Tigris-Euphrates System, Iran	33°09′36.1″N 47°43′11.7″E	N. Alwan, K. Borkenhagen	3 Mar 2008	this study	
FN821742	SMF 32610	*Carasobarbus luteus*	Shoor River, Qalatoyed, Darab, Kol River System, Hormuz Basin, Iran	28°10′20.1″N, 55°14′57.1″E	H. R. Esmaeili	27 May 2009	this study	finclip only
FN821743	SMF 32611	*Carasobarbus luteus*	Shoor River, Qalatoyed, Darab, Kol River System, Hormuz Basin, Iran	28°10′20.1″N, 55°14′57.1″E	H. R. Esmaeili	27 May 2009	this study	finclip only
FN821744	SMF 32612	*Carasobarbus luteus*	Shoor River, Qalatoyed, Darab, Kol River System, Hormuz Basin, Iran	28°10′20.1″N, 55°14′57.1″E	H. R. Esmaeili	27 May 2009	this study	finclip only

Nomenclature of drainage basins follows Abdoli (2000) and Coad (2005). The Tigris Basin is considered to be part of the Tigris-Euphrates System (TES).

DNA extraction, amplification and sequencing

DNA extraction was performed according to the protocol given in Durand et al. (2002) or by phenol chloroform extraction. Part of the cytochrome *b* gene was amplified with the primers H15891 (5′ GTTTGATCCCGTTTCGTGTA 3′) and L15267 (5′ AATGACTTGAAGAACCACCGT 3′) (Briolay et al. 1998). The PCR protocol encompassed an initial denaturation at 94°C for 5 min, 35 cycles at 94°C (1 min), 50°C (1 min), 72°C (1 min), and final extension at 72°C (10 min). PCR products were purified and then sequenced on an ABI 3730 machine.

Phylogenetic analysis

Additional *Carasobarbus* sequences obtained from NCBI GenBank were included in the present analysis (Table 1). The closely related species '*Barbus*' *fritschii* Günther, 1874, '*Barbus*' *grypus* Heckel, 1843, '*Barbus*' *harterti* Günther, 1901, '*Barbus*' *paytonii* Günther, 1901, *Varicorhinus maroccanus* (Günther, 1902) and *Neolissochilus heterostomus* (Chen & Yang, 1999) were used as outgroup taxa (Machordom and Doadrio 2001; Tsigenopoulos et al. 2010). *Neolissochilus heterostomus* was also used to root the tree.

The alignment and sequence statistics were performed with MEGA 4.0.2 (Tamura et al. 2007). Maximum parsimony analysis with heuristic search (TBR), 1000 bootstrap replicates and 15 random addition searches per replicate (nreps = 15 addseq = random) was performed with PAUP*4.0b10 (Swofford 2003). For the Bayesian analysis the GTR substitution model with invariable sites and gamma distribution (nst = 6, rates = invgamma) was proposed by AIC in MrModeltest 2.2 (Nylander 2004). MrBayes 3.1.2 (Ronquist and Huelsenbeck 2003) was run for 10000000 generations in two independent runs, one tree was sampled each 1000 generations and the first 2000000 generations of each run were discarded as burnin (samplefreq = 1000, nchains = 4, savebrlens = yes, nruns = 2, burnin = 2001). This resulted in a total of 16000 trees sampled. Effective sample size was checked with Tracer (Rambaut and Drummond 2007) and found to be higher than 800 for all parameters. A haplotype network was generated with TCS 1.21 (Clement et al. 2000).

Results

Part of the cytochrome *b* gene sequence of 36 individual specimens was examined and yielded an unambiguous and gap-free alignment of 524 base-pairs. Among 524 nucleotide sites 403 were constant, 121 were variable, and 78 were parsimony informative. These sequences were composed of low G content (mean 15.2%) and almost equal A, C, and T contents (mean: 28.1%, 26.9%, and 29.8% respectively). A + T content was higher (57.9%) than G + C content (42.1%). Maximum parsimony and Bayesian inference yielded the same overall tree topology. Figure 2 shows the condensed cladogram combined from both methods. Only clades with bootstrap support or posterior probability higher than 50% are displayed. Figure 3 shows the haplotype network for *Carasobarbus canis* (Valenciennes, 1842), *Carasobarbus chantrei* (Sauvage, 1882) and *C. luteus*.

Among the 18 sequences of *C. luteus*, five different haplotypes were found. The most common haplotype, '*C. luteus* HT1' was recovered 11 times (AF145944, CBSU M125, CBSU M129 + 131, SMF 31017, SMF 31308, SMF 31316, SMF 32610-32612, SMF 32889) in specimens collected from the Tigris-Euphrates System, the Persian Gulf Basin, the Maharlu Basin and the Hormuz Basin. The haplotype '*C. luteus* HT2' was recovered three times (CBSU M126-128) in the Hormuz Basin and the Persian Gulf Basin. The haplotype '*C. luteus* HT3' was recovered in two specimens (SMF 31315 and SMF 31317) from the Khabur River in Syria. Two other sequences (SMF 31014 and SMF 31322) represent unique haplotypes. The six sequences of *C. sublimus* yielded four different haplotypes with sequences SMF 30823 and SMF 31320 as well as SMF 30834 and SMF 31321 having the same haplotype. All other sequences included in this study represent unique haplotypes.

The results show that *C. luteus* is composed of two divergent groups: One contains fish from the Tigris-Euphrates System and the basins of southern Iran (group 1: 'C. *luteus* HT1', 'C. *luteus* HT2', SMF 31322 and SMF 31014), while the other contains two specimens

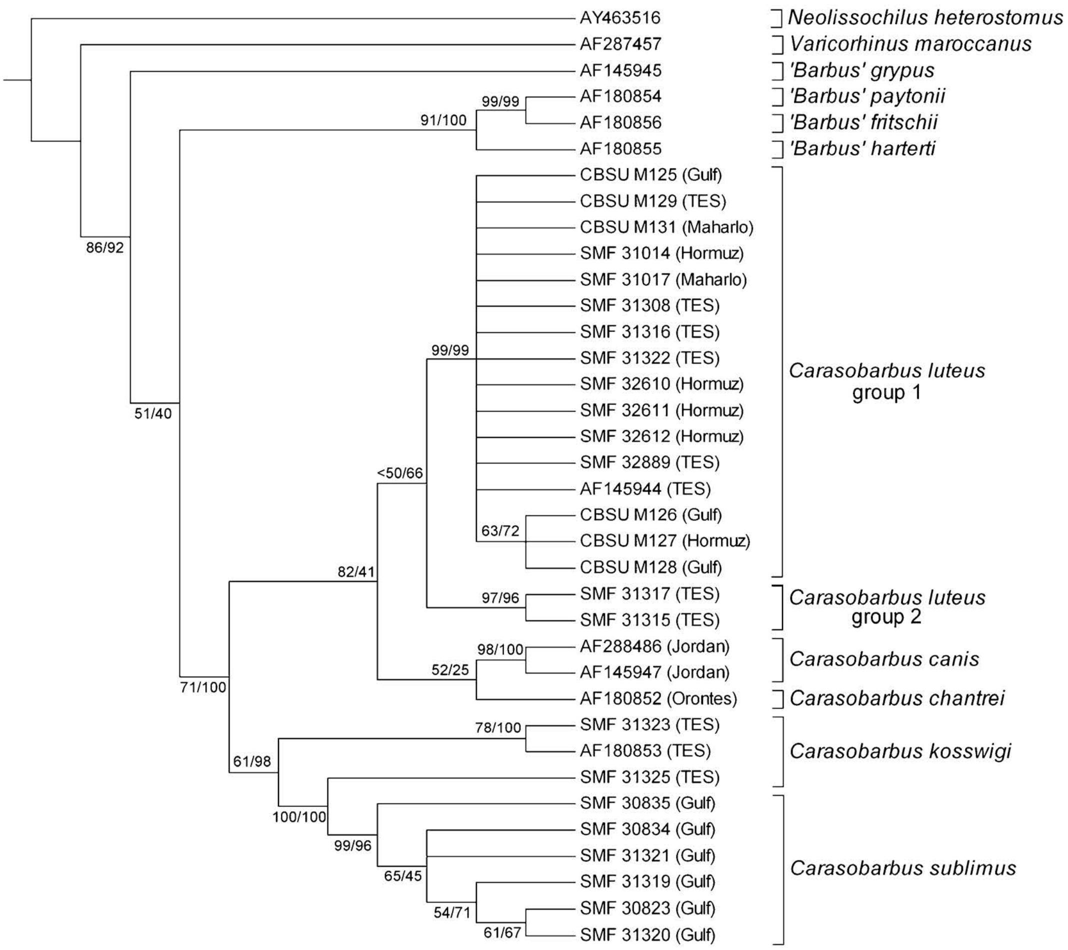

Fig. 2 Cladogram of *C. luteus* and related taxa obtained from cytochrome *b* sequences with maximum parsimony and Bayesian inference method. Tree condensed to support values higher than 50%. First value is the bootstrap support of the MP analysis, second value is the posterior probability of the Bayesian analysis

from the Khabur river (group 2: 'C. *luteus* HT3'). The genetic distance between the two groups is roughly similar to the distances among either of these groups and the species *C. canis* and *C. chantrei* (Fig. 3, Table 2).

According to our phylogenetic hypothesis *C. kosswigi* is paraphyletic with respect to *C. sublimus*. The mean number of nucleotide differences between the three *C. kosswigi*-sequences is strikingly high (29.7 nucleotides), compared to the other groups (0 to 1.5 nucleotides).

Discussion

Base composition in the sequences is similar to that of previously reported fish cytochrome *b* sequences (Cantatore et al. 1994; Briolay et al. 1998; Tang et al. 2006), including low G content and almost equal A, C, and T contents.

There is strong genetic divergence between *C. luteus* group 1 and group 2, comparable to the genetic distance between *C. canis* and *C. chantrei.* These two groups might correspond to the two species described by Heckel from the TES (*C. luteus* and *C. albus*). According to the original description, *C. albus* resembles *C. luteus* but differs in having a blunter head with a thicker, slightly protruding nose. The eye diameter is smaller than in *C. luteus* (6 times in head length vs. 5.5 times), the mouth is less slanted and the dorsal fin is shorter and has a longer base. The angle of the shoulder girdle above the pectoral fins is smaller, the body is more stout and the colouration is

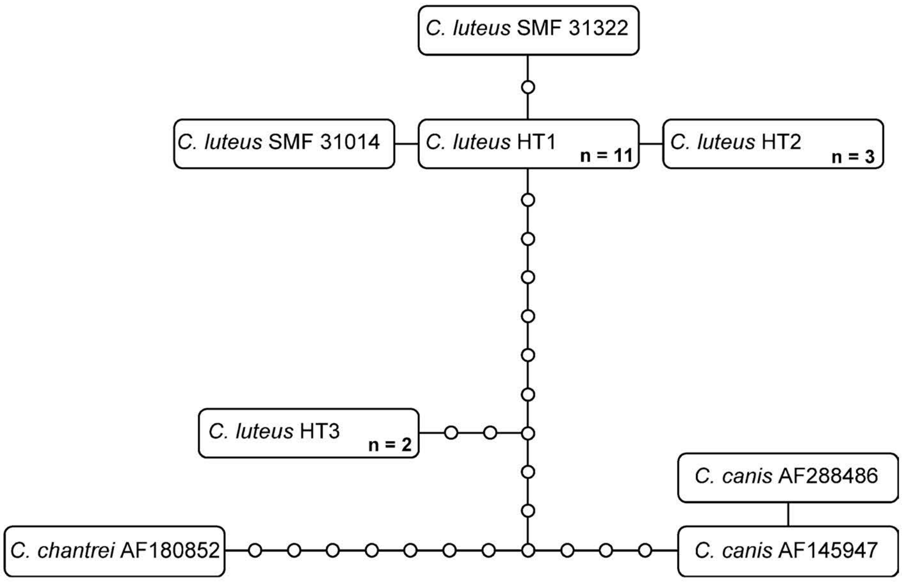

Fig. 3 Haplotype Network of *C. luteus*, *C. canis* and *C. chantrei* showing the high evolutionary distance between two specimens from the Khabur river (*C. luteus* HT3) and the other populations

lighter (Heckel 1843). We were not able to unambiguously identify our fish according to these characters. In the four specimens collected in Syria (SMF 31308 and SMF 31315-31317) we found the following distribution of characters: SMF 31308 agrees well with *C. albus* in having a blunt, round nose, a rather short dorsal fin with comparably long base and a small eye. Its eye diameter is about 5% of its standard length (vs. 7% to 10% in the other three specimens) but is larger than stated in the original description (4.6 times in head length). However the eye diameter of the other three specimens is only 3.0 to 3.7 times in head length. The angle of the shoulder girdle is rather large, which agrees more with the description of *C. luteus*. In the other three specimens it is rather small. SMF 31315-31317 agree better with *C. luteus* in head shape, dorsal fin shape and eye size. However the angle above the pectoral fin is rather small. Furthermore, the morphology of the specimens does not agree with their genetic grouping: SMF 31308 and SMF 31316 belong to group 1 and SMF 31315 and SMF 31317 belong to group 2, while SMF 31316 is morphologically more similar to SMF 31315 and SMF 31317 than to SMF 31308. This problem is further confounded by allometric growth. Comparison of the types of *C. albus*, *C. albus alpina* and *C. luteus* did not reveal any meaningful difference between these taxa and it was not possible to assign SMF 31308 and SMF 31315-31317 to any of them. A more likely alternative to the presence of two

Table 2 Mean genetic distance between groups expressed as number of different nucleotides

	C. canis	*C. chantrei*	*C. kosswigi*	*C. luteus* I	*C. luteus* II	*C. sublimus*	*B. fritschii*	*B. harterti*	*B. paytonii*	*B. grypus*	*V. maroccanus*
C. chantrei	12										
C. kosswigi	31	30									
C. luteus I	15	13	29								
C. luteus II	11	13	29	10							
C. sublimus	40	39	30	35	38						
B. fritschii	34	32	37	31	33	41					
B. harterti	28	28	37	27	25	41	16				
B. paytonii	32	30	35	29	31	39	2	16			
B. grypus	27	25	36	26	24	40	22	24	20		
V. maroccanus	43	38	47	41	41	53	41	43	41	35	
N. heterostomus	44	42	48	43	41	60	41	41	41	37	41

separate species would be the existence of two highly divergent mitochondrial lineages in a single species. This could be either due to retained polymorphism as for example seen in some lepidopterans (Dasmahapatra et al. 2010) or to introgression from another species, as observed in a population of *Misgurnus anguillicaudatus* (Cantor, 1842) from a stream in Imaizumi, Miyagi, Japan (Šlechtová et al. 2008). In this population, which is autochthonous and probably not influenced by artificial stocking (Jörg Bohlen, pers. comm. 19 May 2010), two mitochondrial lineages show stable coexistence: One is similar to other *Misgurnus* mitochondrial lineages, while the other resembles those of *Cobitis* s.l. and was probably transferred to *M. anguillicaudatus* by mitochondrial introgression (Šlechtová et al. 2008). A possible donor species of either of the two *C. luteus* mitochondrial lineages could not be identified. Although it might be undiscovered or extinct, we consider it to be more likely that *C. luteus* is a single species with two divergent mitochondrial lineages especially because *C. luteus* is widespread and abundant in the TES, which could correspond to a large effective population size. Since mitochondrial DNA is not useful for detecting hybridisation and the sequencing of homologous nuclear markers is problematic in polyploid species, the use of AFLP markers seems to be a promising approach for further studies of this issue (Dasmahapatra et al. 2010).

Specimens belonging to *C. luteus* group 1 were found across the area sampled, while group 2 was restricted to the Khabur River in the present study. Haplotype *'C. luteus* HT1' was the most common one and occurred in the most western sampling site (al Jaboul, Syria) as well as the most eastern one (Shoor River, Iran). This indicates that isolation between the different basins is very recent. During the last Pleistocene glaciation, which had its maximum about 30000 years before present and ended about 10000 years ago, the sea level was about 100 m lower than today and the shallow Persian Gulf was dry (Wolfart 1987). During this phase the Shatt al-Arab extended south-east to the Sea of Oman and thus connected the rivers of the Persian Gulf coast to the Tigris-Euphrates System. *Carasobarbus luteus* is a generalistic species with broad niches, tolerating large changes in the environment and thus colonises a wide variety of habitats. It occurs in small streams as well as the lowland parts of big rivers and probably formed a continuous panmictic population until the sea level rose again at the end of the last glaciation. The Quweiq was a tributary to the TES until very recently (Krupp 1987) and thus was probably also part of this continuum.

The paraphyly of *C. kosswigi* with respect to *C. sublimus* is probably due to incomplete lineage sorting and indicates a recent speciation event, however due to the comparably small number of basepairs analysed, our phylogenetic hypothesis should not be overstated. The number of nucleotide differences between the individuals of *C. kosswigi* is surprisingly high. This can, to some extent, be explained by its rare occurrence and small populations, which are likely susceptible to genetic drift and founder effects. It seems unlikely that the *Carasobarbus* samples SMF 31323 and SMF 31325 represent different species, because no morphological differences are apparent between the two specimens. Another factor that might add to the heterogeneity of *C. kosswigi* and *C. sublimus* sequences is the ecological niche these species occupy. Both species live in small rivers and mountain streams and are much less likely to migrate through the lowland parts of rivers than *C. luteus*, resulting in a much lower likelihood of gene flow among populations. Further investigations with larger sample sizes could yield interesting insights into population dynamics and migration patterns of *C. kosswigi* and *C. sublimus*, however the samples necessary for such a study are difficult to obtain, due to their low abundance and remote habitats.

Acknowledgement We are grateful to J. Freyhof, A. Gholamhosseini, N. Hamidan and H. Zareian for supplying specimens, finclips and tissue samples. We thank Friedhelm Krupp, Masoumeh Malek and Alireza Sari for help with organising KB's fieldwork in Iran. Friedhelm Krupp offered valuable comments on the manuscript. The study was supported by the Biodiversity and Climate Research Centre (BiK-F), Frankfurt, which is part of research funding programme "LOEWE". KBs fieldwork was funded by the German Academic Exchange Service (DAAD), in the framework of the project "Establishment of a Middle Eastern Biodiversity Network". We are also thankful to Shiraz University for financial support.

References

Abdoli A (2000) The inland water fishes of Iran. Iranian Museum of Nature and Wildlife, Tehran

Bianco PG, Bănărescu P (1982) A contribution to the knowledge of the Cyprinidae of Iran (Pisces, Cypriniformes). Cybium 6:75–96

Borkenhagen K (2005) Systematik und Zoogeographie der “großschuppigen Barben” des Vorderen Orients. Christian-Albrechts-Universität, Kiel

Briolay J, Galtier N, Brito RM, Bouvet Y (1998) Molecular phylogeny of Cyprinidae inferred from cytochrome *b* DNA sequences. Mol Phylogenet Evol 9:100–108

Cantatore P, Roberti M, Pesole G, Ludovico A, Milella F, Gadaleta MN, Saccone C (1994) Evolutionary analysis of cytochrome b sequences in some perciformes: evidence for a slower rate of evolution than in mammals. J Mol Evol 39(6):589–597

Clement M, Posada D, Crandall K (2000) TCS: a computer program to estimate gene genealogies. Mol Ecol 9 (10):1657–1660

Coad BW (2005) Endemicity in the freshwater fishes of Iran. Iranian Journal of Animal Biosystematics 1(1):1–13

Coad BW (2010) *Barbus*. In: Freshwater fishes of Iran. http://www.briancoad.com/Species%20Accounts/Barbus.htm. Accessed 15 Jul 2010

Dasmahapatra KK, Elias M, Hill RI, Hoffman JI (2010) Mitochondrial DNA barcoding detects some species that are real, and some that are not. Molecular Ecology Resources 10(2):264–273

Durand JD, Tsigenopoulos CS, Ünlü E, Berrebi P (2002) Phylogeny and biogeography of the family Cyprinidae in the Middle East inferred from cytochrome *b* DNA—evolutionary significance of this region. Mol Phylogenet Evol 22:91–100

Esmaeili HR, Teimory A, Hosseini F, Gholami Z (2006) Range extension report for *Barbus sublimus* Coad and Najafpoor, 1997 (Actinopterygii: Cyprinidae) along with its sympatric species in southwest Iran. Iranian Journal of Animal Biosystematics 2(1):19–24

He D, Chen Y, Chen Y, & Chen Z (2004) Molecular phylogeny of the specialized schizothoracine fishes (Teleostei: Cyprinidae), with their implications for the uplift of the Qinghai-Tibetan Plateau. Chinese Science Bulletin, 49(1):39–48

Heckel JJ (1843) Ichthyologie [von Syrien]. In: von Russegger J (ed) Reisen in Europa, Asien und Africa, mit besonderer Rücksicht auf die naturwissenschaftlichen Verhältnisse der betreffenden Länder unternommen in den Jahren 1835 bis 1841. E. Schweizerbart’sche Verlagshandlung, Stuttgart, pp 990–1099

Krupp F (1985) Systematik und Zoogeographie der Süßwasserfische des levantinischen Grabenbruchsystems und der Ostküste des Mittelmeeres. Johannes Gutenberg Universität, Mainz

Krupp F (1987) Freshwater ichthyogeography of the levant. Beihefte zum Tübinger Atlas des Vorderen Orients 28:229–237

Machordom A, Doadrio I (2001) Evolutionary history and speciation modes in the cyprinid genus *Barbus*. P Roy Soc Lond B Bio 268:1297–1306

Nelson JS (2006) Fishes of the world, 4th edn. Wiley, Hoboken

Nylander JAA (2004) MrModeltest v2. Program distributed by the author. Evolutionary Biology Centre, Uppsala University

Rambaut A, Drummond AJ (2007) Tracer v1.4, Available from http://beast.bio.ed.ac.uk/Tracer

Ronquist F, Huelsenbeck JP (2003) MRBAYES 3: Bayesian phylogenetic inference under mixed models. Bioinformatics 19:1572–1574

Šlechtová V, Bohlen J, Perdices A (2008) Molecular phylogeny of the freshwater fish family Cobitidae (Cypriniformes: Teleostei): delimitation of genera, mitochondrial introgression and evolution of sexual dimorphism. Mol Phylogenet Evol 47:812–831

Swofford DL (2003) PAUP*. Phylogenetic analysis using parsimony (*and other methods). Version 4. Sinauer Associates, Sunderland, Massachusetts

Tamura K, Dudley J, Nei M, Kumar S (2007) MEGA4: Molecular Evolutionary Genetics Analysis (MEGA) software version 4.0. Mol Biol Evol 24:1596–1599

Tang Q, Liu H, Mayden R, Xiong B (2006) Comparison of evolutionary rates in the mitochondrial DNA cytochrome *b* gene and control region and their implications for phylogeny of the cobitoidea (Teleostei: Cypriniformes). Mol Phylogenet Evol 39:347–357

Tsigenopoulos CS, Kasapidis P, Berrebi P (2010) Phylogenetic relationships of hexaploid large-sized barbs (genus *Labeobarbus*, Cyprinidae) based on mtDNA data. Mol Phylogenet Evol 56:851–856

Wolfart R (1987) Late Cretaceous through Quaternary palaeogeographic evolution of the Middle East. Beihefte zum Tübinger Atlas des Vorderen Orients 28:9–22

Wossughi G (1978) Beitrag zur Systematik und Zoogeographie der Cyprinidae (Pisces, Teleostei) des Mittleren Ostens, unter besonderer Berücksichtigung des Irans. Universität Hamburg, Hamburg

Erklärung zu den Autorenanteilen

an der Publikation: **Taxonomic revision of the genus *Carasobarbus* Karaman, 1971 (Actinopterygii, Cyprinidae)**

Status: publiziert
Name der Zeitschrift: Zootaxa
Beteiligte Autoren: Kai Borkenhagen (KB)
Friedhelm Krupp (FK)

Was hat der Promovierende bzw. was haben die Koautoren beigetragen?
(1) zu Entwicklung und Planung

Promovierender: 50 %
Co-Autor FK: 50 %

(2) zur Durchführung der einzelnen Untersuchungen und Experimente

Promovierender: 100 % KB hat alle Belegexemplare untersucht.

(3) zur Erstellung der Datensammlung und Abbildungen

Promovierender: 100 % KB hat alle Daten zusammengetragen und alle Abbildungen erstellt. Sofern nicht anders angegeben wurden alle Fotos von KB und FK gemacht.

(4) zur Analyse und Interpretation der Daten

Promovierender: 100 % KB hat alle Daten analysiert und interpretiert.

(5) zum Verfassen des Manuskripts

Promovierender: 75 %
Co-Autor FK: 25 %

Unterschrift Promovend: ____________________________ Datum/Ort: __________________

Zustimmende Bestätigungen der oben genannten Angaben

Unterschrift Betreuer: ______________________________ Datum/Ort: __________________

ZooKeys 339: 1–53 (2013)
doi: 10.3897/zookeys.339.4903
www.zookeys.org

RESEARCH ARTICLE

A peer-reviewed open-access journal
ZooKeys
Launched to accelerate biodiversity research

Taxonomic revision of the genus *Carasobarbus* Karaman, 1971 (Actinopterygii, Cyprinidae)

Kai Borkenhagen[1,2], Friedhelm Krupp[1,3]

1 *Senckenberg Research Institute and Museum of Nature, Senckenberganlage 25, 60325 Frankfurt am Main, Germany* **2** *Research and Technology Centre (FTZ), University of Kiel, Hafentörn 1, D-25761 Büsum, Germany* **3** *Qatar Museums Authority, P.O. Box 2777, Doha, Qatar*

Corresponding author: *Kai Borkenhagen* (kai.borkenhagen@ftz-west.uni-kiel.de)

Academic editor: *N. Bogutskaya* | Received 22 February 2013 | Accepted 12 September 2013 | Published 3 October 2013

Citation: Borkenhagen K, Krupp F (2013) Taxonomic revision of the genus *Carasobarbus* Karaman, 1971 (Actinopterygii, Cyprinidae). ZooKeys 339: 1–53. doi: 10.3897/zookeys.339.4903

Abstract

Representatives of the fish genus *Carasobarbus* Karaman, 1971 (Actinopterygii: Cyprinidae) from the Middle East and North Africa were previously placed in 14 different genus-group taxa (*Barbellion*, *Barbus*, *Barynotus*, *Capoeta*, *Carasobarbus*, *Cyclocheilichthys*, *Kosswigobarbus*, *Labeobarbus*, *Luciobarbus*, *Pseudotor*, *Puntius*, *Systomus*, *Tor* and *Varicorhinus*). The generic assignment of several species changed frequently, necessitating a re-evaluation of their taxonomic status. In this study, the genus *Carasobarbus* is revised based on comparative morphological examinations of about 1300 preserved specimens from collections of several museums and freshly collected material. The species *Carasobarbus apoensis*, *C. canis*, *C. chantrei*, *C. exulatus*, *C. fritschii*, *C. harterti*, *C. kosswigi*, *C. luteus* and *C. sublimus* form a monophyletic group that shares the following combination of characters: medium-sized barbels with a smooth last unbranched dorsal-fin ray, nine or 10 branched dorsal-fin rays and six branched anal fin-rays; scales large, shield-shaped, with many parallel radii; the lateral line containing 25 to 39 scales; the pharyngeal teeth hooked, 2.3.5-5.3.2 or 2.3.4-4.3.2; one or two pairs of barbels. The species are described in detail, their taxonomic status is re-evaluated and an identification key is provided. A lectotype of *Systomus luteus* Heckel, 1843 is designated. *Carasobarbus* Karaman, 1971, *Kosswigobarbus* Karaman, 1971, and *Pseudotor* Karaman, 1971 are subjective synonyms, and acting as First Reviser we gave precedence to the name *Carasobarbus*.

Keywords

Cyprinidae, SW Asia, NW Africa, taxonomy

Copyright *Kai Borkenhagen, Friedhelm Krupp.* This is an open access article distributed under the terms of the Creative Commons Attribution License 3.0 (CC-BY), which permits unrestricted use, distribution, and reproduction in any medium, provided the original author and source are credited.

Introduction

The species of the cyprinid genus *Carasobarbus* Karaman, 1971 are distributed across SW Asia and NW Africa. They occur in all major river systems of the Levant, Mesopotamia, southern Iran, the western and south-western Arabian Peninsula and in northern Morocco. *Carasobarbus* species are an important element of the ichthyofaunas of these areas.

Research about the Mesopotamian and Levantine representatives of *Carasobarbus* began as early as the middle of the 19th century. Important ichthyologists of that era, such as A. Valenciennes and J. J. Heckel, were the first to study these fish. One of the most prominent biological collections from the Middle East of this time was made by T. Kotschy from 1836 to 1840. It is stored at the Museum of Natural History of Vienna and encompasses the type specimens of many zoological and botanical taxa (Kähsbauer 1963). The Moroccan ichthyofauna was described towards the end of the 19th century and the start of the 20th century by A. Günther and G. A. Boulenger. An expedition lead by C. du Gast in 1912 was one of the first systematic sampling efforts in this area (Pellegrin 1912). The Arabian representatives were reported only about 35 years ago by K. E. Banister and M. A. Clarke. In 1971, M.S. Karaman established the monotypic genus *Carasobarbus* for *Systomus luteus* Heckel, 1843 characterised by a laterally compressed and high-backed body, a narrow and high head, a single pair of barbels, pharyngeal bones with three rows of spoon-shaped teeth, a pharyngeal teeth count 2.3.5-5.3.2, a subterminal to terminal mouth, weakly developed lips that run along the jaws as a thin band, no median lobe on the lower lip, infraorbital bones of normal size, a short and broad first infraorbital (lacrimal) bone that is shorter than the eye diameter, a dorsal fin that is moderately long and has 10 branched rays, the origin of the dorsal fin being above the ventral fins, the last unbranched ray of the dorsal fin being well ossified and smooth, the anal fin with six branched rays, and large scales with numerous parallel radii. We revised and expanded Karaman's (1971) diagnosis of the genus that now contains the nine following species: *Carasobarbus apoensis* (Banister et Clarke, 1977), *C. canis* (Valenciennes in Cuvier and Valenciennes 1842), *C. chantrei* (Sauvage, 1882), *C. exulatus* (Banister & Clarke, 1977), *C. fritschii* (Günther, 1874), *C. harterti* (Günther, 1901), *C. kosswigi* (Ladiges, 1960), *C. luteus* (Heckel, 1843), and *C. sublimus* (Coad & Najafpour, 1997). Members of this genus were listed in 14 different genera and subgenera in the past: *Barbellion* Whitley, 1931, *Barbus* Cuvier, 1816, *Barynotus* Günther, 1868, *Capoeta* Valenciennes in Cuvier and Valenciennes 1842, *Carasobarbus* Karaman, 1971, *Cyclocheilichthys* Bleeker, 1859, *Kosswigobarbus* Karaman, 1971, *Labeobarbus* Rüppell, 1835, *Luciobarbus* Heckel, 1843, *Pseudotor* Karaman, 1971, *Puntius* Hamilton, 1822, *Systomus* McClelland, 1839, *Tor* Gray, 1834, and *Varicorhinus* Rüppell, 1835.

The objectives of the current study are to (1) define a monophyletic genus that is based on synapomorphic characters, (2) provide a conclusive diagnosis of the genus *Carasobarbus*, (3) give a detailed re-description of all species based on a sample of specimens large enough to show the intraspecific variability, (4) map the range of each species based on records confirmed by voucher specimens, (5) summarise information on biology, habitat and conservation status of each species, (6) discuss the taxonomic history and current status of each species, (7) provide an identification key. This will form a baseline for a molecular phylogenetic and zoogeographic analysis of *Carasobarbus* and related genera that is currently in preparation and will be published separately by the first author.

Methods

Abbreviations for ichthyological collections follow Sabaj-Pérez (2010) and Fricke and Eschmeyer (2013).

Nomenclature of geographic names follows the spelling recommended by the "United States Board on Geographic Names" (http://geonames.usgs.gov/), even though the transcriptions/transliterations of these toponyms are sometimes inconsistent. Wādī or Oued refer to a temporary stream. Nahr, Naẖal, Nehri, Rūdkhāneh or Rūd refer to a permanent river or stream. Buḩayratt, Göl or Daryācheh refer to a lake. ʻAyn or Aïn refer to a spring. Geographical coordinates in parentheses are original coordinates, given by a publication, the collector or a collection database. Coordinates determined ex post are marked by brackets. Most of these are from the National Geospatial-Intelligence Agency gazetteer (http://geonames.nga.mil/ggmagaz/) and as a consequence, do not refer to the actual site of collection, but to the geographic feature itself. For some of the well known waterbodies and cities the conventional name is used: Euphrates (Nahr al Furāt / Fırat Nehri), Jordan River (HaYarden / Nahr al Urdan), Lake Homs (Buḩayratt Qaṭṭīnah), Lake Tiberias (Yam Kinneret / Buḩhayratt Ṭabarīyā), Orontes (Nahr al ʻĀşī / Asi Nehri), Tigris (Dicle Nehri / Nahr Dijlah), Aleppo (Ḩalab), Damascus (Dimashq), Mosul (Al Mawşil).

Twenty morphometric measurements were taken from specimens straightened whenever necessary; severely damaged and bent specimens were not used. There are some differences in the way of taking measurements (e.g. Hubbs and Lagler 1958 vs. Banister and Clarke 1977, Krupp 1983a). In this study, seven measurements were done over projections to the body axis. They are as follows: total length (the distance between projections of the tip of the snout and the posterior margin of the longest lobe of the caudal fin, with the caudal fin spread to its natural maximum), standard length (SL) (the distance between projections of the tip of the snout and the end of the hypural plate), preanal length (the distance between projections of the tip of the snout and the origin of the anal fin), predorsal length (the distance between projections of the tip of the snout and the origin of the dorsal fin), preventral length (the distance between projections of the tip of the snout and the origin of the ventral fin), head length (HL) (the distance between projections of the tip of the snout and the posterior margin of the bony opercle), and length of the caudal peduncle (the distance between projections of the insertion of the anal-fin base and the end of the hypural plate). The other measurements were done point-to-point: body depth (BD) as the maximum depth of the body (without dorsal fin) taken orthogonal to body axis; depth (minimum) of the caudal peduncle as the smallest depth of the caudal peduncle; length of the dorsal and anal fins as length of the last unbranched ray in the dorsal and anal fins, respectively; lengths of the pectoral and ventral fins as the distance from the fin base to the tip of the pectoral and ventral fins, respectively; length of the dorsal-fin base and the anal-fin base as a distance

Table 1. Comparison of morphometric characters of specimens between 50 mm SL and 150 mm SL. All measurements expressed as percentage of SL.

		total length	**preanal length**	**predorsal length**	**preventral length**	**head length**	**caudal peduncle length**	**body depth**	**caudal peduncle depth**	**dorsal fin length**	**pectoral fin length**	**ventral fin length**	**anal fin length**	**dorsal-fin base length**	**anal-fin base length**	**anterior barbel length**	**posterior barbel length**	**eye diameter**	**mouth width**	**interorbital distance**
C. *apoensis*	max	130.5	81.0	55.8	57.9	31.2	18.1	32.6	12.3	24.5	22.6	20.0	21.3	19.4	10.8	0.0	6.6	8.1	9.0	10.5
	min	121.0	76.3	48.5	51.3	26.5	11.8	25.4	10.2	16.7	18.1	16.9	16.8	15.1	7.2	0.0	2.4	5.5	5.7	8.1
	med	126.0	78.8	53.1	53.9	28.8	14.2	29.1	11.1	21.1	20.2	18.1	18.8	17.3	8.8	0.0	4.8	6.3	7.4	9.5
	n	41	43	44	44	44	44	44	44	42	44	44	43	44	44	0	44	44	44	44
C. *canis*	max	132.6	82.1	56.4	58.0	32.4	17.2	31.2	12.6	30.7	24.4	21.9	22.3	20.5	10.1	3.9	6.3	9.0	8.8	9.6
	min	121.2	75.0	47.8	50.9	26.2	12.5	26.7	9.9	18.0	18.4	16.1	14.9	16.8	7.0	0.7	2.3	5.4	6.2	7.1
	med	126.3	78.4	51.6	54.3	29.1	14.8	28.9	11.9	21.5	20.5	18.0	18.7	18.6	8.6	2.3	4.8	6.6	7.1	8.6
	n	54	56	56	56	56	56	56	56	46	56	56	56	56	56	52	55	56	54	56
C. *chantrei*	max	134.8	82.3	53.9	55.3	30.0	17.1	35.8	14.0	27.5	24.4	21.8	23.8	21.2	10.2	2.5	4.7	8.9	8.1	10.3
	min	121.9	72.8	47.7	50.6	22.2	11.7	26.4	11.0	18.8	17.6	16.4	16.3	17.2	7.0	0.5	2.2	5.0	5.8	7.7
	med	129.7	77.9	50.6	53.0	26.1	14.5	30.8	12.6	24.6	21.7	19.8	20.4	19.2	8.8	1.1	3.4	6.9	6.9	9.2
	n	81	84	84	84	84	84	84	84	76	82	84	83	84	84	68	84	84	81	84
C. *exulatus*	max	134.8	82.3	53.9	55.3	30.0	17.1	35.8	14.0	27.5	24.4	21.8	23.8	21.2	10.2	2.5	4.7	8.9	8.1	10.3
	min	121.9	72.8	47.7	50.6	22.2	11.7	26.4	11.0	18.8	17.6	16.4	16.3	17.2	7.0	0.5	2.2	5.0	5.8	7.7
	med	129.7	77.9	50.6	53.0	26.1	14.5	30.8	12.6	24.6	21.7	19.8	20.4	19.2	8.8	1.1	3.4	6.9	6.9	9.2
	n	81	84	84	84	84	84	84	84	76	82	84	83	84	84	68	84	84	81	84
C. *fritschii*	max	137.5	82.9	53.7	55.3	26.8	18.8	34.3	13.6	28.0	25.2	23.8	31.3	20.6	11.9	5.6	8.3	8.8	9.8	10.7
	min	121.1	73.6	44.9	47.0	18.8	10.7	24.8	10.6	19.6	19.3	15.8	18.1	15.0	6.6	1.4	2.8	4.7	5.4	6.3
	med	129.8	77.1	49.3	50.7	23.0	15.0	29.2	11.9	23.6	22.2	20.5	22.4	17.4	9.1	3.1	4.7	6.6	7.1	9.1
	n	229	243	244	243	244	244	244	243	196	244	244	242	243	243	242	244	244	244	244
C. *harterti*	max	140.9	78.0	53.7	55.8	27.5	18.4	31.6	13.3	31.8	25.5	24.8	24.1	19.0	10.3	9.1	9.6	9.5	7.1	9.6
	min	122.6	70.9	46.5	48.5	21.2	12.3	26.8	11.8	25.8	21.5	20.4	18.9	16.5	8.4	4.5	5.5	5.9	5.2	7.4
	med	131.8	75.0	49.8	51.1	24.4	16.0	29.2	12.8	28.9	23.5	22.8	21.1	18.0	9.3	6.6	7.8	7.4	6.2	8.4
	n	19	24	24	24	24	24	24	24	11	24	23	23	24	24	24	24	24	24	24
C. *kosswigi*	max	133.9	79.7	53.4	51.9	25.3	16.0	32.8	12.9	35.5	23.8	21.8	26.4	21.8	11.1	5.5	7.4	8.1	5.9	8.5
	min	127.1	75.4	47.0	48.7	22.8	11.9	26.2	10.4	26.1	20.1	19.1	20.0	18.1	8.8	2.8	3.6	4.8	3.7	7.3
	med	130.4	77.7	49.7	50.8	24.5	14.5	31.1	11.9	28.8	22.1	20.8	22.6	19.9	10.0	4.3	5.1	5.9	4.6	7.9
	n	14	15	15	15	15	15	15	15	14	15	15	15	15	15	15	15	15	15	15
C. *luteus*	max	134.1	84.0	56.3	57.9	33.1	15.8	40.1	14.3	31.9	24.6	22.7	23.7	22.6	10.7	3.2	7.1	10.1	10.7	11.3
	min	120.4	74.7	47.3	48.6	21.7	8.6	26.2	11.0	17.6	17.9	16.8	15.8	14.9	6.6	0.6	2.8	0.0	5.1	7.4
	med	127.5	79.1	52.2	53.4	27.3	13.2	33.6	12.8	24.9	21.4	19.8	19.9	19.2	9.0	1.7	4.4	7.2	7.1	9.6
	n	257	264	268	265	267	266	268	268	241	267	268	266	267	267	41	266	265	233	268
C. *sublimus*	max	137.9	81.4	57.0	56.8	30.1	14.8	33.4	13.8	29.9	25.5	23.8	28.4	22.1	11.5	7.0	9.7	10.0	7.6	9.0
	min	131.9	76.5	49.1	49.6	25.2	10.3	27.9	11.8	19.7	22.9	21.0	21.9	19.4	8.7	4.1	5.1	5.6	3.6	6.8
	med	134.4	77.9	52.5	54.2	27.7	13.0	30.6	12.8	28.3	24.3	22.2	23.9	20.7	10.2	5.4	8.0	8.9	6.4	8.4
	n	16	18	18	18	18	18	18	18	14	18	18	18	18	18	18	18	18	18	18

between the origin and the insertion of the fin; length of the anterior and posterior barbels as distance from the barbel base to the tip of the barbel when straightened; horizontal diameter of the eye as a distance between the anterior and the posterior bony margins of the eye cavity; width of the mouth as a distance between the two posterior ends of the lower jaw; interorbital distance as a distance between the upper margins of the eye cavities across the head. For comparison between species, all measurements are expressed as percentage of SL. To attenuate effects of allometric growth, only specimens in the size range between 50 mm SL and 150 mm SL were used for the box-plots and the data given in Table 1.

In addition, seven meristic characters were analysed. The last branched anal- and dorsal-fin rays were counted as one when lying directly adjacent to each other without an interspace. Scales in the lateral line were counted from the first scale with a pore to the last scale on the caudal peduncle (some authors only count to the end of the hypural plate). Scales above the lateral line were counted between the origin of the dorsal fin and the lateral line; the lateral line was not included and a scale on the mid-line of the back was counted as 0.5. Scales below the lateral line were counted between origin of the anal fin to the lateral line; the lateral line was not included and a scale on the mid-line of the belly was counted as 0.5. Scales around the least circumference of the caudal peduncle were counted as one circle of scales around the least circumference of the caudal peduncle. Number of pairs of barbels was counted as two when anterior and posterior pairs are present, counted as one if only posterior pair is present and counted as 1.5 if posterior pair and one single anterior barbel is present.

For counting the number of pharyngeal teeth, the pharyngeal bones were extracted in a subsample of specimens and the pharyngeal teeth counted sometimes only on one side. Lost teeth were counted when the point of insertion was clearly visible. Scales were extracted in the anterior part of the body, above the lateral line.

We did not differentiate between male and female specimens because sex determination was not possible without dissection.

Results

Genus *Carasobarbus* Karaman, 1971

http://species-id.net/wiki/Carasobarbus

Carasobarbus Karaman 1971: 230; type species: *Systomus luteus* Heckel, 1843, by original designation, also by monotypy.

Kosswigobarbus Karaman 1971: 239; type species: *Cyclocheilichthys kosswigi* Ladiges, 1960, by original designation, also by monotypy.

Pseudotor Karaman 1971: 229; type species: *Barbus fritschii* Günther, 1874, by original designation.

Diagnosis. Medium-sized cyprinids with an ossified, smooth last unbranched dorsal-fin ray; 9 or 10 branched dorsal-fin rays and 6 branched anal-fin rays; large, shield-shaped scales with numerous parallel radii; the lateral line with 25 to 39 scales; the pharyngeal teeth hooked at their tips, their count being 2.3.5-5.3.2 or 2.3.4-4.3.2; 1 or 2 pairs of barbels present.

Carasobarbus species are evolutionarily hexaploid (Machordom and Doadrio 2001, Gorshkova et al. 2002, Leggatt and Iwama 2003, Tsigenopoulos et al. 2010).

Remarks and discussion. '*Barbus*' *grypus*, *Mesopotamichthys sharpeyi* and '*Barbus*' *reinii* from the Middle East have five branched rays in the anal fin. The hexaploid species from Africa (*Labeobarbus* and *Varicorhinus*), which are the sister group to *Carasobarbus* and the other species from the Middle East (Tsigenopoulos et al. 2010, KB unpublished), have five branched rays in the anal fin. The Asian species (*Tor* and *Neolissochilus*) are sister group to the species from Africa and the Middle East (Tsigenopoulos et al. 2010, KB unpublished) and have five branched rays in the anal fin. By application of the parsimony principle the possession of six branched anal-fin rays is a synapomorphy of the genus *Carasobarbus*. The possession of nine to 10 branched rays in the dorsal fin is synapomorphic for *Carasobarbus*, because the closely related Middle-Eastern species '*Barbus*' *grypus*, *Mesopotamichthys sharpeyi* and '*Barbus*' *reinii* as well as many African hexaploids have the plesiomorphic state of eight branched rays in the dorsal fin. However, in some African species the number of branched dorsal-fin rays is increased convergently. These two synapomorphies establish *Carasobarbus* as a monophyletic group. Analyses of the mitochondrial cytochrome *b* gene confirm the monophyly of this genus (Durand et al. 2002, Tsigenopoulos et al. 2010, KB unpublished data). Colli et al. (2009) found *Carasobarbus* to be monophyletic in their maximum likelihood analysis but not in their neighbour joining analysis. '*Barbus*' *grypus* Heckel, 1843 is the sister taxon of the genus *Carasobarbus* (Tsigenopoulos et al. 2010).

Out of the generic names *Barbellion*, *Barbus, Barynotus*, *Capoeta*, *Carasobarbus*, *Cyclocheilichthys*, *Kosswigobarbus*, *Labeobarbus*, *Luciobarbus*, *Pseudotor*, *Puntius*, *Systomus*, *Tor,* and *Varicorhinus* that were used for this taxon – or its parts – by previous authors, only *Carasobarbus*, *Kosswigobarbus* and *Pseudotor* are available for the genus in question. All other generic names have not been considered, because their type species are not closely related to the species under discussion here (Durand et al. 2002, Tsigenopoulos et al. 2010, KB unpublished data) or do not share the characters mentioned above. *Carasobarbus*, *Kosswigobarbus* and *Pseudotor* are subjective synonyms. They all were established in the same publication (Karaman 1971) and thus none of them has priority. We, acting as First Reviser, select *Carasobarbus* to have priority in accordance with article 24.2 of the International Code for Zoological Nomenclature (ICZN 2012). Thus *Carasobarbus* is the valid name for this genus.

Within the genus, several species share characters that are potentially synapomorph and elucidate sister group relations. *Carasobarbus fritschii* and *C. harterti* both have pharyngeal bones with four teeth in the medial row. This character is probably synapomorph, because all other congeners have five teeth in the medial row. This group corresponds to *Pseudotor*. *Carasobarbus kosswigi* and *C. sublimus* share the possession of a spatulate lower jaw and a median lobe on the lower lip. The spatulate lower jaw is synapomorph, because no congener and no other closely related species shares this character. The close phylogenetic relationship between *C. kosswigi* and *C. sublimus* is confirmed by genetic analysis (Borkenhagen et al. 2011). These two species correspond to *Kosswigobarbus*.

Carasobarbus apoensis (Banister & Clarke, 1977)

http://species-id.net/wiki/Carasobarbus_apoensis

Barbus apoensis Banister and Clarke 1977: 113.

Material. Type material. Holotype of *Barbus apoensis*: BMNH 1976.4.7:166, Saudi Arabia, permanent stream near Khamīs Mushayt (N18°17', E42°34'), F. Tippler, 12 Dec 1968.

Paratypes of *Barbus apoensis*: BMNH 1976.4.7:167-171, 5, same data as holotype. - BMNH 1976.4.7:172-175, 4, Saudi Arabia, upper Wādī Turabah near Aţ Ţā'if (N22°56', E40°54'), G. Popov. - BMNH 1971.2.11:1-2, 2, Saudi Arabia, intermittent watercourse in Wādī Adamah (N19°53', E41°57'), J. P. Mandaville, 27 Oct 1969.

Non-type material. Endorheic darinages. BMNH 1980.7.1:15, 1, Saudi Arabia, Wādī Habayaba between Aţ Ţā'if and Ash Shafā [N21°11', E 40°24'], A. Farag, 1980. - SMF 30167, 3; SMF 30170, 10 Saudi Arabia, Wādī Būwah (N20°45', E41°8'), F. Krupp and W. Schneider, 21 Mar 1990. - SMF 30169, 6; SMF 33147, 4, Saudi Arabia, Wādī Būwah (N20°44', E41°7'), F. Krupp and W. Schneider, 21 Mar 1990. - SMF 30168, 6; SMF 30171, 9, Saudi Arabia, Wādī Turabah (N20°32', E41°17'), F. Krupp and W. Schneider, 20 Mar 1990.

Streams draining towards the Red Sea. CMNFI 87-0135, 1; CMNFI 87-0137, 4, Saudi Arabia, Wādī Hadīyah (N25°34', E38°41'). - SMF 33149, 1, Saudi Arabia, Wādī Ḩaqqaq (N22°49', E39°22'), W. Büttiker, 5/6 May 1983. - SMF 33148, 2, Saudi Arabia, Wādī 'Ilyab (N20°5', E40°54'), H. Felemban and J. Gasparetti, 28 Oct 1983. - SMF 33539, 3, Saudi Arabia, Wādī 'Ilyab (N20°7', E40°57), W. Büttiker, 10–11 Nov 1983.

Unknown drainage system. SMF 33146, 4, Saudi Arabia, Al Ḩijāz, W. Büttiker.

Diagnosis. One pair of barbels, usually 10 branched rays in the dorsal fin, 27 to 32 scales in the lateral line, usually 12 scales around the least circumference of the caudal peduncle, last unbranched ray of dorsal fin shorter than head.

Description. The body depth is comparatively low and a nuchal hump is present in adults but not developed in juveniles. The height of the caudal peduncle is relatively low (Table 1). The dorsal and ventral fins are usually positioned behind the middle of the body. The head is elongate with a straight or slightly concave dorsal profile. The ventral profile of the head is slightly convex. (Figs 1, 2). The head length is about equal to the body depth. The mouth is broad and terminal or slightly sub-terminal with one pair of barbels (Fig. 3, Table 2). Only one out of 65 specimens had two pairs of barbels and in one specimen a single anterior barbel was present. The eyes are in the anterior half of the head and slightly protuberant. The morphometric characters are summarised in Table 1.

Figure 1. *Carasobarbus apoensis*, holotype (BMNH 1976.4.7:166) from a permanent stream near Khamīs Mushayt, © The Natural History Museum, London.

Figure 2. *Carasobarbus apoensis*, live specimen from Wādī Turabah.

The dorsal fin and its base are rather short. It usually has four unbranched and 10 branched rays (Table 3). The last unbranched ray is considerably shorter than the head (Fig. 4), weakly ossified, and its distal part is flexible. The anal fin has three unbranched and six branched rays (Table 4). Pectoral and ventral fins are relatively short (Table 1).

Carasobarbus apoensis has 27 to 32 scales in the lateral line (Table 5), usually 4.5 scales above the lateral line (Table 6), 3.5 or 4.5 scales below the lateral line (Table 7) and 12 scales around the least circumference of the caudal peduncle (Table 8). The scales are shown in Fig. 5.

The pharyngeal teeth count is 2.3.5- in 12 specimens, -5.3.2 in two specimens and 1.3.5- in one specimen. The pharyngeal teeth are hooked at their tips (Fig. 6).

Live colouration is golden with olive fins. The upper side is darker than the belly (Fig. 2). In ethanol-preserved specimens the upper side is dark, the belly yellow and the fins are grey or yellow (Fig. 1). Juveniles have a dark lateral spot on the caudal peduncle.

The maximum length observed in the material examined is 288 mm SL.

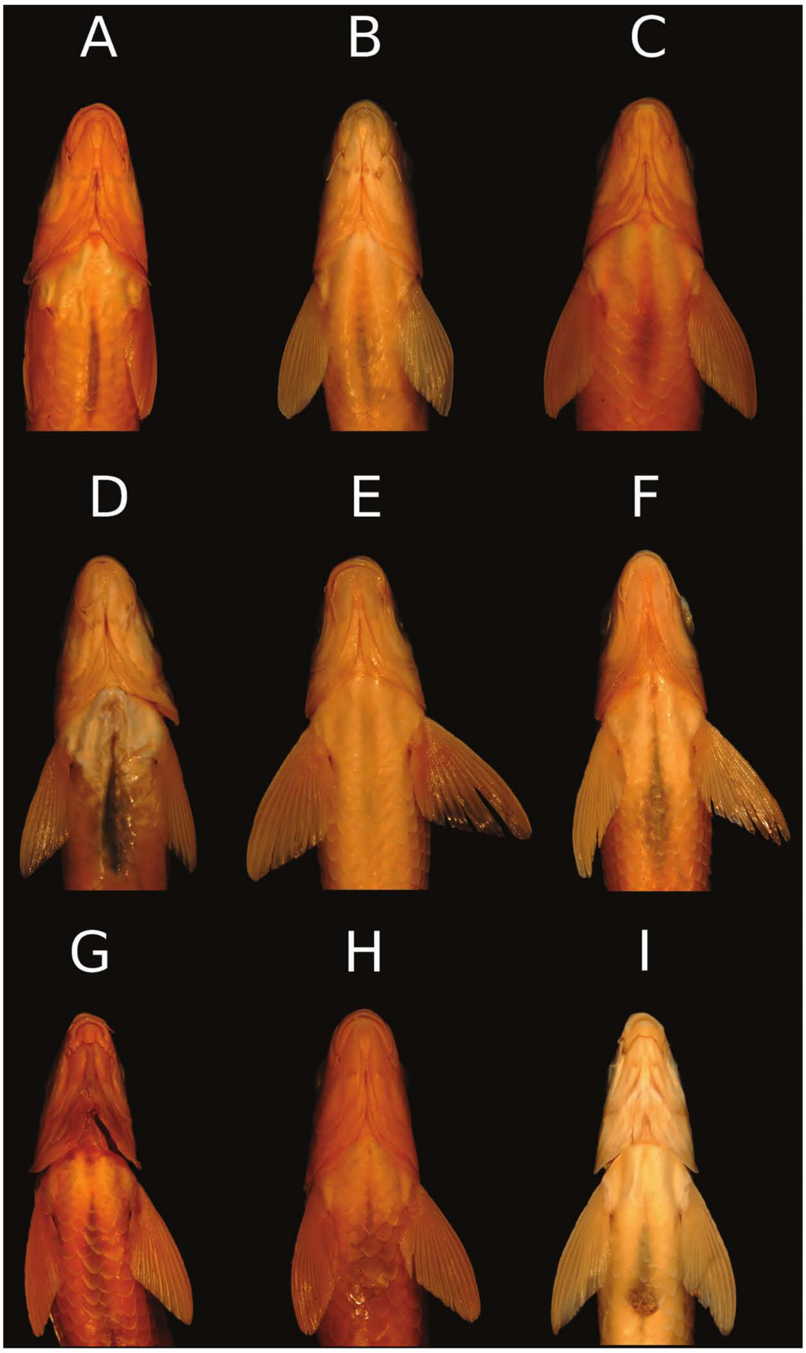

Figure 3. Ventral view of the head and chest. **A** *C. apoensis* (SMF 30167, 108.6 mm SL) **B** *C. canis* (SMF 33135, 108.3 mm SL) **C** *C. chantrei* (SMF 33133, 122.9 mm SL) **D** *C. exulatus* (SMF 33109, 103.7 mm SL) **E** *C. fritschii* (SMF 33446, 89.6 mm SL) **F** *C. harterti* (SMF 33368, 93.6 mm SL) **G** *C. kosswigi* (SMF 30173, 107.1 mm SL) **H** *C. luteus* (SMF 30176, 120.7 mm SL) **I** *C. sublimus* (SMF 33118, 80.2 mm SL), pictures resized to facilitate comparison.

Table 2. Number of pairs of barbels.

	n	1	1,5	2
C. apoensis	65	63	1	1
C. canis	89	4	1	84
C. chantrei	157	5	6	146
C. exulatus	83			83
C. fritschii	299	2		297
C. harterti	30			30
C. kosswigi	23			23
C. luteus	421	365	9	47
Naband population	10			10
C. sublimus	18			18

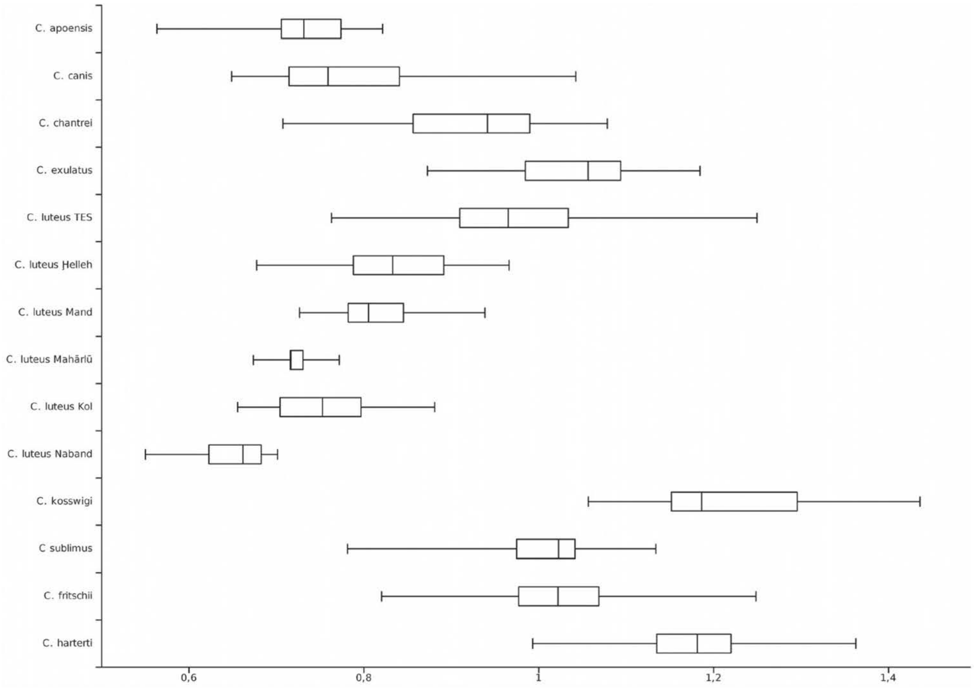

Figure 4. Last unbranched dorsal-fin ray length / head length; TES = Tigris-Euphrates system.

Carasobarbus apoensis differs from all congeners, except *C. luteus*, by having one rather than two pairs of barbels. For a comparison with *C. luteus* populations see below.

Distribution. *Carasobarbus apoensis* occurs in the Al Ḩijāz mountain range in wadis draining either inland or towards the Red Sea (Fig. 7). It is endemic to Saudi Arabia.

Habitats and biology. This species inhabits the upper courses of wadis, which are characterised by strong seasonal fluctuations in water levels, temperature and other physiochemical parameters.

Table 3. Number of branched dorsal-fin rays.

	n	**7**	**8**	**9**	**10**	**11**
C. apoensis	66			2	63	1
C. canis	90			5	85	
C. chantrei	196			21	164	11
C. exulatus	110		8	99	3	
C. fritschii	297	1	23	268	5	
C. harterti	30			30		
C. kosswigi	23			3	20	
C. luteus	441		1	23	411	6
Naband population	10			1	9	
C. sublimus	18			2	16	

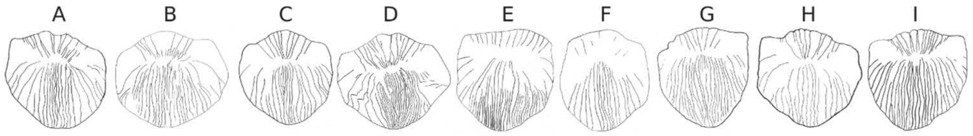

Figure 5. Striation pattern of scales taken from anteriour part of the boby above lateral line. **A** *C. apoensis* **B** *C. canis* **C** *C. chantrei* **D** *C. exulatus* **E** *C. fritschii* **F** *C. harterti* **G** *C. kosswigi* **H** *C. luteus* **I** *C. sublimus*.

Conservation status. *Carasobarbus apoensis* is rated Least Concern and still occurs in large numbers, but abstraction of large specimens by recreational fishing, water abstraction and habitat loss might become problematic for this species (BCEAW 2002).

Remarks and discussion. *Carasobarbus apoensis* was originally described from Khamīs Mushayt, Wādī Turabah and Wādī Adamah as a member of the genus *Barbus* (Banister and Clarke 1977). It was later transferred to the genus *Carasobarbus* (Ekmekçi and Banarescu 1998). Alkahem and Behnke (1983) reported an unknown *Barbus* and tentatively considered these specimens to be atypical *C. apoensis*. We did not find any evidence of an undescribed *Carasobarbus* species that occurs sympatrically with *C. apoensis*, thus we agree with their conclusion.

Carasobarbus apoensis is very closely related to *C. luteus* (KB unpublished data).

Carasobarbus canis (Valenciennes in Cuvier and Valenciennes 1842)

http://species-id.net/wiki/Carasobarbus_canis

Barbus canis Valenciennes in Cuvier and Valenciennes 1842: 186.
Barbus beddomii Günther 1868: 110.

Material. Type material. Lectotype of *Barbus canis*: MNHN 0000-1413, 1, Jordan River [N31°46', E35°33'], Bové, 1833 (designated by Krupp and Schneider 1989).

Paralectotype of *Barbus canis*: MNHN 0000-3944, 1, same data as lectotype.

Table 4. Number of branched anal-fin rays.

	n	5	6	7
C. apoensis	65		65	
C. canis	90	2	88	
C. chantrei	197	3	194	
C. exulatus	109	3	106	
C. fritschii	296	3	293	
C. harterti	30		29	1
C. kosswigi	23		23	
C. luteus	439	3	435	1
Naband population	10		10	
C. sublimus	18		18	

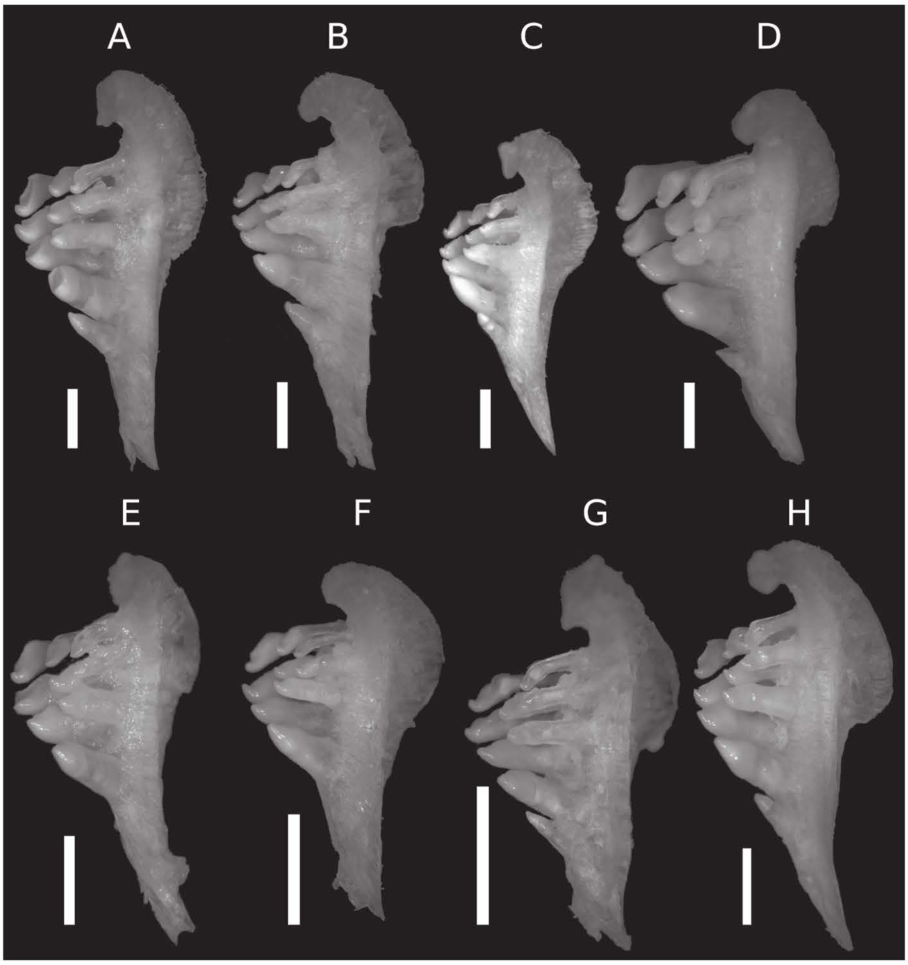

Figure 6. Pharyngeal bone. **A** *C. apoensis* (SMF 30168, 190.1 mm SL) **B** *C. canis* (SMF 30175, 168.7 mm SL) **C** *C. chantrei* (SMF 33133, 165.9 mm SL) **D** *C. exulatus* (SMF 33107, 170.1 mm SL) **E** *C. fritschii* (SMF 33405, 147.2 mm SL) **F** *C. harterti* (SMF 33396, 105.9 mm SL) **G** *C. kosswigi* (SMF 30174, 141.5 mm SL) **H** *C. luteus* (SMF 30179, 143.4 mm SL). Scale bar = 3 mm.

Holotype of *Barbus beddomii*: BMNH 1863.11.3:5, 1, Lake Tiberias [N32°48', E35°35'], T. W. Beddome.

Non-type material. Jordan River Drainage. SMF 14075, 2, Lake Tiberias (N32°48', E35°35'), M. Goren, 15 Mar 1968. - SMF 33134, 16, Syria, Nahr al Yarmūk near Jallayn (N32°44'21", E35°58'56"), N. Alwan et al., 16 Oct 2008. - SMF 24464, 1, Jordan, Nahr al Yarmūk near Maqārin (N32°43', E35°53'), F. Krupp and W. Schneider, 23 Sep 1985. - SMF 30175, 11, Syria, Lake Muzayrīb [N32°42'40", E36°1'39"], F. Krupp and W. Schneider, 12 Apr 1989. - SMF 33135, 17, Jordan, Wadi al-ʻArab near the dam (N32°37'6", E35°37'46"), N. Alwan et al., 25 Oct 2008. - SMF 17123, 16, Wādī al Yābis (N32°24', E35°36'), F. Krupp and W. Schneider, 23 Jul 1980. - ZMH H 2343, 3, Jordan, Wādī Kufrinjah (N32°16'25", E35°33'42"). - SMF 24344, 3; SMF 24345, 17, Jordan, Nahr az Zarqā’ (N32°12', E35°50'), F. Krupp and W. Schneider, 22 Jul 1980. - SMF 24339, 3, Jordan, Nahr az Zarqā’ (N32°10', E35°37'), F. Krupp and W. Schneider, 21 Jul 1980. - SMF 24340, 1, Jordan, Nahr az Zarqā’ near Sadd al Malik Talal (N32°10', E35°49'), F. Krupp and W. Schneider, 22 Jul 1980. - SMF 24331, 7; SMF 24346, 3, Jordan, Nahr al Yarmūk channel (N32°08', E35°36'), F. Krupp and W. Schneider, 21 Jul 1980. - NMW 53961, 1, Jordan River [N31°46', E35°33'], Cenoni, Dec 1898.

Azraq Oasis. BMNH 1956.2.24:15-16, 2; BMNH 1965.11.24:2, 1, Jordan, wetland near Azraq ash Shīshān [N31°50', E36°49'].

Coastal rivers of the Mediterranean Sea. BMNH 1949.9.16:124, 1, Israel, Naẖal Naʻaman [N32°54'42", E35°4'50"]. - NMW 22367, 1, Israel, Naẖal Naʻaman [N32°54'42", E35°4'50"], H. Steinitz, 21 Oct 1955. - SMF 9229, 1, Israel, Naẖal Yarqon [N32°6'7", E34°46'32"].

Diagnosis. Two pairs of barbels, 29 to 35 scales in the lateral line and usually 12 scales around the least circumference of the caudal peduncle, last unbranched ray of dorsal fin shorter than head.

Description. The body is low. A nuchal hump is present in adults but absent in juveniles. The largest body depth is at the origin of the dorsal fin. The head is long, rather low and fairly narrow with straight dorsal and convex ventral profile (Figs 8, 9). The head length approximately equals the body depth. The mouth is terminal or slightly subterminal. Two pairs of barbels are present (Table 2). The lips are smooth and thin (Fig. 3). The eyes are at the end of the anterior half of the head. The morphometric characters are summarised in Table 1.

Pectoral, ventral, dorsal and anal fins are comparatively short (Table 1). The dorsal fin usually has four unbranched and 10 branched rays (Table 3). The last unbranched ray is ossified and its distal part is flexible. It is usually markedly shorter than the head (Fig. 4). The anal fin usually has three unbranched and six branched fin rays (Table 4).

There are 29 to 35 scales in the lateral line (Table 5), usually 4.5 or 5.5 scales above the lateral line (Table 6), usually 4.5 scales below the lateral line (Table 7) and usually 12 scales around the least circumference of the caudal peduncle (Table 8). The scales are shown in Fig. 5.

Table 5. Lateral line scale count.

	n	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39
C. apoensis	60			1	9	15	20	14	1							
C. canis	74					1	3	16	19	12	13	10				
C. chantrei	168							5	11	31	48	36	29	7	1	
C. exulatus	79		1	3	17	18	24	13	3							
C. fritschii	264						1	12	21	39	75	58	36	15	4	3
C. harterti	24							1		5	9	4	4		1	
C. kosswigi	19								1	7	2	3	5		1	
C. luteus	390	11	52	79	120	84	29	9	5	1						
Naband population	8				1	3	3	1								
C. sublimus	11			4	3	4										

The pharyngeal teeth count is 2.3.5-5.3.2 in 23 specimens, 2.3.3-5.3.2 in one specimen, 2.3.5- in one specimen and -5.3.2 in one specimen. The pharyngeal teeth are hooked at their tips (Fig. 6).

Live specimens are silvery to bronze coloured. The posterior third of the body and the fins are distinctly yellow in many specimens (Fig. 9). Ethanol-preserved specimens are brownish yellow and the back is only slightly darker than the rest of the body (Fig. 8). The fins are brownish yellow. Juveniles have a dark lateral spot on the caudal peduncle.

Carasobarbus canis differs from *C. apoensis* and *C. luteus* in having two pairs of barbels vs. one, from *C. kosswigi* and *C. sublimus* in having a crescent-shaped lower lip without median lobe vs. a spatulate lower lip with median lobe, from *C. exulatus* in modally having 10 branched dorsal-fin rays vs. nine and from *C. chantrei*, *C. fritschii* and *C. harterti* in modally having 10 scales around the least circumference of the caudal peduncle vs. 14 or 16.

Distribution. *Carasobarbus canis* occurs in the Jordan River system (Fig. 7). There are only few records from coastal rivers of the Mediterranean Sea (Naẖal Na‘aman and Naẖal Yarqon). A recent treatment of the inland water fish communities of Israel does not report *C. canis* from coastal rivers (Goren and Ortal 1999). The population in the Azraq Oasis was introduced by humans (Krupp and Schneider 1989). Since the year 2000 this species was not found in Azraq (Hamidan 2004) and the population may have disappeared due to drought. Records from the Tigris-Euphrates system (Banister 1980) are based on misidentifications.

Habitats and biology. *Carasobarbus canis* inhabits a wide range of rivers, lakes and ponds (Goren 1974) with clean as well as polluted water (Mir 1990). Adults reach a length of about 40 cm (max. 66 cm) and are of economic importance locally (annual catch in Israel 1970-85 about 50 t, Fishelson et al. 1996). It feeds on fish, aquatic invertebrates, algae and detritus (Ben-Tuvia 1978, Spataru and Gophen 1985, Krupp and Schneider 1989). The relative proportion of fish in the diet increases with body length and small cyprinids of the genus *Mirogrex* are their most important prey (Spataru and Gophen 1985). The spawning grounds are (among others) at the shore of Lake Tiberias where the spawn-

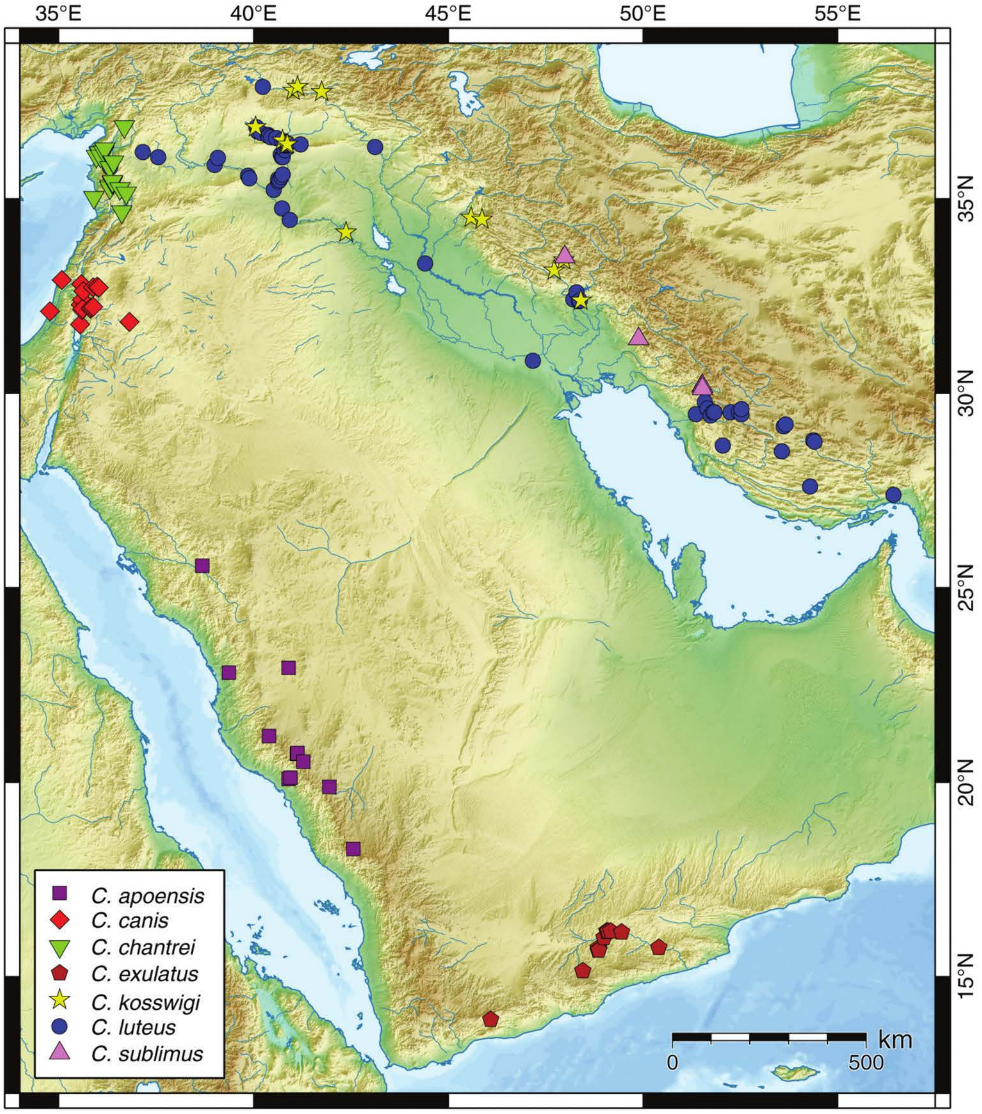

Figure 7. Map of the distribution of *C. apoensis*, *C. canis*, *C. chantrei*, *C. exulatus*, *C. kosswigi*, *C. luteus*, and *C. sublimus*.

ing occurs in shallow water over hard bottom in December and January, one month after the start of the rainy season (Fishelson et al. 1996). The sticky eggs attach to the substrate. Winter spawning is seen as evidence for an origin in cooler areas (Fishelson et al. 1996).

Conservation status. Catches in Lake Tiberias are declining (Fishelson et al. 1996). The species is rated Least Concern by the IUCN (Crivelli 2006a). The population in Lake Tiberias does not face serious threats; the riverine populations are declining and threatened by pollution, water extraction, drought and fragmentation due to damming (Crivelli 2006a).

Table 6. Number of scales above the lateral line.

	n	3,5	4	4,5	5	5,5	6	6,5	7
C. apoensis	60		2	45	7	6			
C. canis	82			48	11	20	3		
C. chantrei	171			4	1	147	6	13	
C. exulatus	79		3	70	5	1			
C. fritschii	276			15		226		35	
C. harterti	28					4		24	
C. kosswigi	21					8	5	7	1
C. luteus	389	6	2	315	19	46	1		
Naband population	8			8					
C. sublimus	17			16		1			

Figure 8. *Carasobarbus canis*, lectotype (MNHN 1413) from Jordan River.

Figure 9. *Carasobarbus canis*, live specimen from Wadi al-'Arab.

Remarks and discussion. *Carasobarbus canis* was described from the Jordan River as a member of the genus *Barbus* (Cuvier and Valenciennes 1842). Later it was assigned to *Luciobarbus* (Heckel 1843), and *Labeobarbus* (Günther 1864). Subsequently it was transfered back to *Barbus* (Günther 1868) and then placed in *Tor* (Karaman 1971, Banarescu 1977), *Barbus* (Banister and Clarke 1977, Krupp 1983a), *Carasobar-*

Table 7. Number of scales below the lateral line.

	n	3	3,5	4	4,5	5	5,5	6	6,5
C. apoensis	57		14		41		2		
C. canis	80		2	3	65	1	9		
C. chantrei	173			1	84	3	84	1	
C. exulatus	79		24	1	51	3			
C. fritschii	286		7	3	151	5	117	1	2
C. harterti	29		1		10		18		
C. kosswigi	23				4	3	15		1
C. luteus	384	2	125	16	231	9	1		
Naband population	8				8				
C. sublimus	17		1		13	1	2		

bus (Ekmekçi and Banarescu 1998) and *Barbus* subgenus *Carasobarbus* (Tsigenopoulos et al. 2010). MNHN 0000-1413 was designated as lectotype (Krupp and Schneider 1989). *Barbus beddomii* is considered to be a junior synonym of *C. canis* (Berg 1949, Karaman 1971, Krupp and Schneider 1989).

Carasobarbus chantrei (Sauvage, 1882)

http://species-id.net/wiki/Carasobarbus_chantrei

Labeobarbus chantrei Sauvage 1882: 165.
Barynotus verhoeffi Battalgil 1942: 292.

Material. Type material. Lectotype of *Labeobarbus chantrei*: MNHN A-3866, Turkey, Amik Gölü [N36°12'24", E36°9'26"], H. Chantre, 1881 (designated by Krupp 1985a).

Paralectotypes of *Labeobarbus chantrei*: MNHN A-3937, 1, same data as lectotype. - MNHN A-3938, 2; MNHN A-3939, 3; MNHN A-3940, 1, Syria, Ḩamāh [N35°9'0", E36°43'59"], H. Chantre, 1881.

Non-type material. Orontes River drainage. MNHN B-2977, 1, Syria, Orontes, A. Gruvel, 1829. - BMNH 1934.1.25:4, 1, Syria, Orontes. - FSJF 2311, 11, Turkey, Karasu Çayı below dam of Tahtaköprü Barajı (N36°51'7", E36°41'10"), M. Özulug and J. Freyhof, 7 Nov 2007. - SMF 17115, 8, Turkey, Orontes, 8 km E of Hatay (N36°17', E36°11'), J. Winkler and B. Koster, 20 Sep 1982. - CMNFI 88-0019, 1, Turkey, 8 km southwest of Hatay (N36°11', E36°3'). - SMF 17110, 4, Turkey, tributary to Orontes (N36°11', E36°3'), F. Krupp, 23 Aug 1978. - SMF 17122, 2, Turkey, 2 km southeast of Samandağı (N36°6', E35°58'), F. Krupp, 23 Aug 1978. - FSJF uncatalogued, 16, Turkey, at Sinanlı (N36°5'51", E36°4'43"), M. Özulug and J. Freyhof, 8 Nov 2007. - SMF 33130, 40, Syria, near Mashra'a el Būz (N35°57'3", E36°23'45"), N. Alwan et al., 8 Oct 2008. - SMF 33131, 58, Syria, ʻAyn az Zarqa (N35°56'40", E36°24'9"), N. Alwan et al., 8 Oct 2008. - SMF 17107, 1, Syria, Jisr ash Shughūr (N35°48', E36°19'), F. Krupp, 20 Aug 1980. - SMF 17109, 2, Syria, main bridge at

Table 8. Number of scales around the least circumference of the caudal peduncle.

	n	10	11	12	13	14	15	16	17	18	19	20
C. apoensis	60			58	2							
C. canis	85			80	1	4						
C. chantrei	168			4	7	110	27	20				
C. exulatus	87	1	6	80								
C. fritschii	253					3	12	212	26	23		1
C. harterti	28				2	4	3	18	1			
C. kosswigi	21			1	2	10	3	5				
C. luteus	408	3	2	399	4							
Naband population	9			8	1							
C. sublimus	17			17								

Jisr ash Shughūr (N35°48', E36°19'), F. Krupp, 19 Aug 1978. - CMNFI 88-0018, 4, Syria, ʻAyn Zaqa (N35°27', E36°23'). - SMF 17114, 1; SMF 17121, 7, Syria, ʻAyn Zaqa (N35°27', E36°23'), F. Krupp, 25–27 Mar 1979. - BMNH 1968.12.13:188-190, 3, Syria, spring lake at Qalʻat al Maḍīq [N35°25', E36°23']. - SMF 17120, 7, Syria, aquaculture pond near Qalʻat al Maḍīq (N35°25', E36°23'), F. Krupp, 8 Aug 1978. - SMF 33132, 5, Syria, stream at Qalʻat al Jarras (N35°19'49", E36°18'38"), N. Alwan et al., 12 Oct 2008. - SMF 17111, 6, Syria, ʻAšārna (N35°17', E36°19'), F. Krupp, 11 Aug 1978. - SMF 17117, 5, Syria, near Shayzar (N35°16', E36°34'), F. Krupp, 27 Mar 1979. - SMF 24349, 3, Syria, Shayzar (N35°16', E36°34'), F. Krupp and W. Schneider, 17 Aug 1980. - SMF 17118, 1, Syria, 200 m below western outlet of Lake Homs (N34°40', E36°37'), F. Krupp and W. Schneider, 3 Aug 1978. - SMF 17119, 5, Syria, western outlet of Lake Homs (N34°40', E36°37'), F. Krupp and W. Schneider, 3 Aug 1978. - SMF 33133, 24, Syria, Lake Homs at Qaṭṭīnah (N34°39'43", E36°37'6"), N. Alwan et al., 13 Oct 2008.

Mediterranean coastal rivers. SMF 31669, 1; SMF 31670, 1, Syria, Nahr Marqīyah (N35°1'50", E35°54'18"), N. Alwan et al., 10 Oct 2008.

Tigris-Euphrates system. SMF 12966, 1, Turkey, Balıklıgöl at Şanlıurfa [N37°8'52", E38°47'4"], L. Lortet, 1884.

Diagnosis. Two pairs of barbels, 31 to 38 scales in the lateral line and usually 14 to 16 scales around the least circumference of the caudal peduncle, last unbranched dorsal-fin ray equal to or shorter than head.

Description. The body is comparatively high-backed and laterally compressed in mid-sized specimens but low-backed and almost cylindrical in large specimens. In large specimens a pronounced nuchal hump is present, in smaller specimens it is only weakly developed or absent. The maximum body depth is at the origin of the dorsal fin. The head is short and blunt with a convex ventral profile and a slightly convex to straight dorsal profile (Figs 10, 11). The mouth is terminal or slightly sub-terminal with two pairs of short barbels (Table 2).The body depth is usually greater than the head length (Fig. 12).The eyes are slightly protuberant and lie at the end of the anterior half of the head. The morphometric characters are summarised in Table 1.

Figure 10. *Carasobarbus chantrei*, paralectotype (MNHN A-3939) from Orontes at Ḩamāh.

Figure 11. *Carasobarbus chantrei*, live specimen from Buḩayratt Qaţţīnah.

The dorsal fin usually has four unbranched and nine to 11 branched rays (Table 3). The last unbranched ray is ossified but not very thick and flexible in its distal part. It is usually shorter than the head (Fig. 4). The anal fin usually has three unbranched and five or six branched rays (Table 4).

There are 31 to 38 scales in the lateral line (Table 5), 4.5 to 6.5 scales above the lateral line (Table 6), four to six scales below the lateral line (Table 7) and 12 to 16 scales around the least circumference of the caudal peduncle (Table 8). The scales are shown in Fig. 5.

The pharyngeal teeth count is 2.3.5-5.3.2 in two specimens, 2.3.5- in 11 specimens, -5.3.2 in two specimens and 1.3.5- in one specimen. The pharyngeal teeth are hooked at their tips (Fig. 6).

Small live specimens are silvery; larger specimens are silvery or bronze coloured and sometimes have yellow pectoral and ventral fins (Fig. 11). Small ethanol-preserved specimens are silvery with a somewhat darker back and a salmon pink hue. Juveniles have a dark lateral spot on the caudal peduncle. Ethanol-preserved adults are yellow-brown and the back is only slightly darker than the rest of the body (Fig. 10).

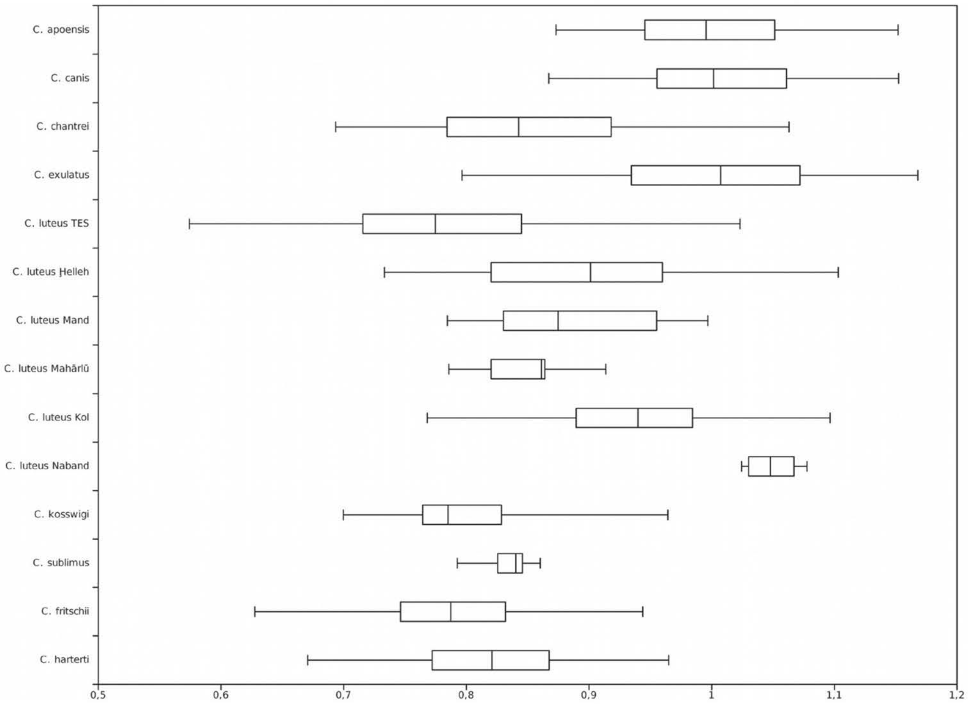

Figure 12. Head length / body depth; TES = Tigris-Euphrates system.

The maximum length observed in the material examined is 385 mm SL.

Carasobarbus chantrei differs from *C. apoensis*, *C. canis*, *C. exulatus*, *C. luteus* and *C. sublimus* in having 31 to 38 scales in the lateral line vs. 27 to 32, 29 to 35, 26 to 32, 25 to 33 and 27 to 29 respectively and modally 14 scales around the least circumference of the caudal peduncle vs. 12. It differs from *C. kosswigi* and *C. sublimus* in having a crescent-shaped lower lip without median lobe vs. a spatulate lower lip with median lobe and from *C. exulatus*, *C. fritschii* and *C. harterti* in modally having 10 branched dorsal-fin rays vs. nine.

Distribution. *Carasobarbus chantrei* occurs in the Orontes river drainage system (Fig. 7). Two juvenile specimens where collected in Nahr Marqīyah, a coastal river in Syria. This species had never before been reported from this location (Krupp 1985a) and it has most likely been introduced by humans. Two potential records from Nahr Quwayq (MNHN A-3861, MGHN 3554) are discussed in Krupp (1985a, c). Locality data for MHNL 3554 are ambiguous (Krupp 1985a). The locality for MNHN A-3861 is given as "Syria, Aleppo" in Krupp (1985a) and considered to be from Nahr Quwayq. The collection database of the MNHN gives "Origine: Syrie, localité: Alep, Milieu: Continent, Bassin hydrologique: Asi, Cours d'eau: Asi" as locality. As these data are contradictory, it is likely that the specimens do not come from the Nahr Quwayq, but from the Orontes (=Asi) and *C. chantrei* does probably not occur in the Nahr Quwayq. A record from the Ceyhan Nehri (Krupp 1985c) is not backed by specimens. Records from the

Tigris-Euphrates basin are misidentified *C. luteus* (Krupp 1985a, Krupp and Schneider 1991) and the specimen from Balıklıgöl at Şanlıurfa in Turkey (SMF 12966) is probably mislabelled or was introduced there (Krupp 1985a). It is not included in the map.

Habitats and biology. *Carasobarbus chantrei* occurs in a wide range of habitats stretching from stagnant waters of lakes to rapidly flowing river courses.

Conservation status. *Carasobarbus chantrei* is utilised as food fish locally but is increasingly replaced by carp (Krupp 1985a). During a field survey in Syria in 2008, the species was still abundant in parts of the Orontes. However, large stretches of this river, especially in the Al Ghāb area, suffer heavily from water abstraction and pollution by sewage and domestic waste and are devoid of fish. The species is rated "Endangered B1ab(ii,iii)" by the IUCN (Crivelli 2006b). The main threat is habitat degradation due to water extraction, pollution and drought (Crivelli 2006b).

Remarks and discussion. *Carasobarbus chantrei* was described from the Orontes and placed in *Labeobarbus* by Sauvage (1882). He transferred it to *Barbus* two years later (Sauvage 1884). In 1942 *Barynotus verhoeffi* was described from Amik Gölü, Turkey (Battalgil 1942). Ladiges (1960) erroneously synonymised *B. verhoeffi* with *C. canis*. Karaman (1971) synonymised *C. chantrei* with *C. canis* and thus transferred it to the genus *Tor* (sensu Karaman 1971). Fowler (1976) transferred *Barynotus verhoeffi* to the genus *Barbellion*. In 1985 Krupp redescribed *C. chantrei* as a valid species and provisionally placed it into the genus *Barbus* sensu lato. He found the type series to be inhomogeneous (MNHN B-2889 are *'Barbus' grypus*) and designated MNHN A-3866 as lectotype of *C. chantrei* (Krupp 1985a). The 'Catalog of Fishes' does not list MNHN B-2889 as types for *C. chantrei* (Eschmeyer 2011). Ekmekçi and Banarescu (1998) transferred the species to the genus *Carasobarbus*. Tsigenopoulos et al. (2010) used *Barbus* subgenus *Carasobarbus*.

Carasobarbus exulatus (Banister & Clarke, 1977)

http://species-id.net/wiki/Carasobarbus_exulatus

Barbus exulatus Banister and Clarke 1977: 116.

Material. Type material. Holotype of *Barbus exulatus*: BMNH 1976.4.7:299, Yemen, Wādī Ḩaḑramawt at Qasam (N16°10', E49°4'), W. A. King-Webster.

Paratypes of *Barbus exulatus*: BMNH 1976.4.7:308, 1; BMNH 1976.4.7:300-307, 8, same data as holotype. - BMNH 1976.4.7:328-329, 2; BMNH 1976.4.7:330-331, 2, Yemen, Wādī 'Idim/Wādī Ḩaḑramawt at Ghuraf (N16°0', E49°0'), W. A. King-Webster. - BMNH 1976.4.7:309, 1; BMNH 1976.4.7:310-318, 9; BMNH 1976.4.7:319-327, 9, Yemen, Wādī Ḩaḑramawt at Ghayl 'Umar (N15°44', E48°51'), W. A. King-Webster. - BMNH 1976.4.7:332-333 probably Wādī Marrān in Wādī Aḩwar system [N13°53'51", E46°05'14"], G. Popov, 2 Aug 1962.

Non-type material. Wādī Ḩaḑramawt/al Masīlah drainage. BMNH 1976.5.17:9-10, 2, Yemen, Wādī al Khūn (N16°10', E49°10'). - SMF 33108, 10, Yemen, Wādī al

Khūn (N16°9'51", E49°6'2"), F. Krupp et al., 3 Jun 2005. - SMF 33109, 17, Yemen, Wādī al Khūn (N16°9'45", E49°4'46"), F. Krupp et al., 3 Jun 2005. - SMF 33110, 14, Yemen, Wādī al Masīlah near Fughmah (N16°8'36", E49°27'7"), F. Krupp et al., 4 Jun 2005. - SMF 33111, 1, Yemen, Wādī al Masīlah at al Hind (N15°44'53", E50°24'32"), F. Krupp et al., 5 Jun 2005. - SMF 33106, 8, Yemen, Wādī ‘Idim at Ghayl ‘Umar near Arḍ ar Raydah (N15°40'51", E48°51'59"), F. Krupp et al., 2 Jun 2005. - SMF 33107, 11, Yemen, Wādī ‘Idim near Ghayl ‘Umar (N15°40'10", E48°51'4"), F. Krupp et al., 2 Jun 2005. -SMF 33105, 13, Yemen, Wādī Mara in Wādī Daw‘an system (N15°8'36", E48°26'58"), F. Krupp et al., 31 May 2005.

Diagnosis. Dorsal fin with 9 branched rays in most specimens; last unbranched ray of dorsal fin as long as or longer than head; 2 pairs of barbels; 26 to 32 scales in the lateral line and usually 12 scales around the least circumference of the caudal peduncle.

Description. The body is not particularly high backed and the maximum body depth is at the origin of the dorsal fin or slightly in front of it (Fig. 13). A nuchal hump is present in adult specimens (Fig. 14) but absent in juveniles (Fig. 15). The caudal peduncle is slender. The head profile is convex ventrally and straight dorsally. The body depth is about the same as the head length (Fig. 12). In specimens below 100 mm SL, the head is rather narrow, in larger specimens it becomes wider. The mouth is subterminal and comparatively narrow. Two pairs of barbels are present (Table 2), the posterior one is rather long. The eyes are at the end of the anterior half of the head and slightly protuberant. The morphometric characters are summarised in Table 1.

The dorsal fin is long and usually has four unbranched and eight to 10 branched rays (Table 3). The last unbranched ray is strongly ossified and only the tip is flexible. Its length is about the same as the head length (Fig. 4). The anal fin is long, usually has three unbranched and five or six branched rays (Table 4).

There are 26 to 32 scales in the lateral line (Table 5), 4 to 5.5 scales above the lateral line (Table 6), 3.5 to five scales below the lateral line (Table 7) and 10 to 12 scales around the least circumference of the caudal peduncle (Table 8). The scales are shown in Fig. 5.

The pharyngeal teeth count is 2.3.5-5.3.2 in one specimen, 2.3.5- in 16 specimens, -5.3.2 in one specimen and 2.3.4- in one specimen. The pharyngeal teeth are hooked at their tips (Fig. 6).

In live specimens and freshly preserved specimens the back and the sides are grey to golden, the belly is yellowish white and the fins are sometimes golden to orange (Fig. 15). Preserved specimens have a dark back and a lighter belly, the fins are whitish or greyish. Juveniles have a dark spot on the sides of the caudal peduncle.

The maximum length observed in the material available is 288 mm SL.

Carasobarbus exulatus differs from all congeners, except *C. fritschii* and *C. harterti* in modally having nine instead of 10 branched dorsal-fin rays. It differs from *C. fritschii* and *C. harterti* in modally having 12 scales around the least circumference of the caudal peduncle vs. 16 and in having 26 to 32 scales the lateral line vs. 30 to 39 and 31 to 38 respectively.

Figure 13. *Carasobarbus exulatus*, holotype (BMNH 1976.4.7:299) from Wādī Ḥaḍramawt at Qasam, © The Natural History Museum, London, photo P. Hurst.

Figure 14. Adult *Carasobarbus exulatus*, live specimen from Wādī al Khūn.

Figure 15. Juvenile *Carasobarbus exulatus*, live specimen from Wādī al Khūn.

Distribution. This species is endemic to Yemen and occurs in Wādī Ḩaḑramawt / Wādī al Masīlah and its pleistocene tributaries (Banister and Clarke 1977, Krupp 1983a, Fig. 7). It is also known from Sadd Ma'rib (Al-Safadi 1995), a dam lake at N15°23'46", E45°14'37" and Wādī Ḩajr (N14°02'42", E48°40'27"), where they are "found throughout the whole year and are distributed all over the stream" (Attaala and Rubaia 2005).

Locality data for BMNH 1976.4.7:332-333 is given as "Wadi Maran, E. Yemen" (Banister and Clarke 1977), which is most likely Wādī Marrān [N13°53'51", E46°05'14"], representing the westernmost record of this species that is backed by specimens.

Habitats and biology. The biology of this species is mostly unknown.

Conservation status. During a field expedition in 2005 one of the authors saw large, continuous water bodies in the Wādī Ḩaḑramawt / Wādī al Masīlah area. The species is rated as "Endangered B1a, b; B2a, b" and water extraction is identified as the main threat (BCEAW 2002).

Discussion. *Carasobarbus exulatus* was described from Wādī Ḩaḑramawt and Wādī Maran in Yemen and placed in *Barbus* (Banister and Clarke 1977). Later it was transferred to *Carasobarbus* (Ekmekçi and Banarescu 1998).

Carasobarbus fritschii **(Günther, 1874) comb. n.**

http://species-id.net/wiki/Carasobarbus_fritschii

Barbus fritschii Günther 1874: 231.
Barbus rothschildi Günther 1901: 368.
Barbus riggenbachi Günther 1902: 447.
Capoeta atlantica Boulenger 1902: 124.
Capoeta waldoi Boulenger 1902: 124.
Barbus paytonii Boulenger 1911: 82.

Material. Type material. Syntypes of *Barbus fritschii*: BMNH 1874.1.30:27-31, 5, Morocco, Oued Ksob in Oued Igrounzar drainage [N31°28'59", W9°46'3"], K. v. Fritsch and J. Rein, 1872.

Syntypes of *Barbus paytonii*: BMNH 1903.10.29:17-20, 7, Morocco, Oued Oum er Rbia [N33°19'40", W8°20'2"], F. W. Riggenbach.

Syntypes *Barbus riggenbachi*: BMNH 1902.7.28:20-21, 2, Morocco, Oued Oum er Rbia [N33°19'40", W8°20'2"], F. W. Riggenbach. - BMNH 1902.7.28:19, 1, Morocco, Oued Talmest [N31°52'15", W9°18'31"], F. W. Riggenbach.

Syntypes *Barbus rothschildi*: BMNH 1901.7.26:6-7, 2, Morocco, Oued Oum er Rbia [N33°19'40", W8°20'2"], E. Hartert.

Syntypes of *Capoeta atlantica*: BMNH 1902.1.4:18-19, 2, Morocco, Oued Nfis at Trigadir-el-hor (Tagadirt n'Bour?) [N31°9'21", W8°6'2"], E. G. B. Meade-Waldo.

Syntypes of *Capoeta waldoi*: BMNH 1902.1.4:16-17, 2, Morocco, Oued Nfis at Trigadir-el-hor (Tagadirt n'Bour?) [N31°9'21", W8°6'2"], E. G. B. Meade-Waldo.

Non-type material. Oued al Maleh drainage. SMF 33412, 5; SMF 33510, 1; SMF 33511, 1; SMF 33512, 1, Morocco, Oued al Maleh above the dam (N33°33'53", W7°22'3"), K. Borkenhagen and J. Freyhof, 19 Apr 2011. - MNHN 1919-0365, 1; MNHN 1919-0366, 1, Morocco, Oued Bou Asseïla near Chaouia [N33°19'34", W7°16'46"], H. Millet, 1919.

Oued Bou Regreg drainage. MNHN 1939-0124, 1, Morocco, Oued Akrech [N33°56'7", W6°47'41"], J. M. Pérès, 1939. - SMF 33411, 10; SMF 33503, 1; SMF 33504, 1; SMF 33505, 1, Morocco, Oued Korifla above the dam lake (N33°44'0", W6°43'43"), K. Borkenhagen and J. Freyhof, 18 Apr 2011.

Oued Igrounzar drainage. BMNH 1889.7.19:9, 1, Morocco, near Essaouira [N31°30'45", W9°46'12"], C. Payton. - SMF 636, 4; SMF 952, 6, Morocco, Oued Ksob [N31°28'59", W9°46'3"], K. v. Fritsch and J. Rein, 1872. - SMF 33405, 19; SMF 33446, 1; SMF 33450, 1; SMF 33451, 1, Morocco, Oued Ksob near Essaouira (N31°28'0", W9°45'32"), A. Azeroual et al., 11 Apr 2011. - SMF 33388, 1; SMF 33389, 1; SMF 33390, 1; SMF 33404, 20, Oued Igrounzar between Ounara and El Ghazouane (N31°27'21", W9°41'4"), A. Azeroual et al., 10 Apr 2011. - SMF 33406, 2, Oued Igrounzar near El Khemis des Meskala (N31°21'31", W9°24'20"), A. Azeroual et al., 11 Apr 2011.

Oued Iqem drainage. SMF 33509, 1, Morocco, Oued Iqem near Skhirat (N33°53'22", W6°59'56"), K. Borkenhagen and J. Freyhof, 19 Apr 2011.

Oued Kiss drainge. MNHN 1924-0174, 1, Algeria, Oued Kiss at Marsa Ben Mehid (N35°4'59", W2°10'1"), C. A. Alluaud, 1924.

Oued Moulouya drainage. SMF 33407, 8; SMF 33408, 4; SMF 33479, 1; SMF 33481, 1; SMF 33484, 1, Morocco, Oued Za near Guefaït (N34°13'36", W2°23'34"), K. Borkenhagen and J. Freyhof, 15 Apr 2011. - MNHN 1926-0070, 1, Morocco, Oued Melloulou near Guercif [N34°13'32", W3°21'13"], P. M. Pallary, 1926. - NMW 19533, 1, Morocco, Ras el Aïn near Aïn Beni Mathar (=Berguent) [N34°0'41", W2°1'47"], F. Werner. - NMW 19532, 1, Morocco, Oued Za [N32°57'0", W5°12'0"], F. Werner.

Oued Oum er Rbia drainage. BMNH 1902.7.28:22-26, 5, Morocco, Oued Oum er Rbia [N33°19'40", W8°20'2"], F. Riggenbach. - BMNH 1903.7.1:8, 2, Morocco, El Jadida [N33°15'18", W8°30'22"], F. Riggenbach. - MNHN 1927-0099, 1; MNHN 1927-0100, 1; MNHN 1989-0535, 1, Morocco, Oued Oum er Rbia near Khenifra [N32°56'21", W5°40'7"], A. Gruvel and R. Dollfus, 1927. - MNHN 1928-0054, 1; MNHN 1928-0055, 1, Morocco, Oued Oum er Rbia near Khenifra [N32°56'21", W5°40'7"], P. Pallary, 1928. - SMF 33513, 1; SMF 33514, 1; SMF 33515, 1, Morocco, Oued Oum er Rbia near Boulaouane (N32°51'33", W8°2'41"), K. Borkenhagen and J. Freyhof, 20 Apr 2011. - SMF 33344, 1; SMF 33345, 1; SMF 33346, 1; SMF 33394, 12, Morocco, Oued Srou at bridge between Tighassaline and Khenifra (N32°49'51", W5°36'36"), A. Azeroual et al., 7 Apr 2011. - SMF 33360, 1; SMF 33361, 1; SMF 33362, 1; SMF 33395, 17, Morocco, Oued Derra near Oulad Yaïch (N32°26'23", W6°19'24"), A. Azeroual et al., 9 Apr 2011. - SMF 33363, 1; SMF 33364, 1; SMF 33365, 1; SMF 33397, 22, Morocco, Oued Oum er Rbia (N32°18'53", W6°54'33"), A. Azeroual et al., 9 Apr 2011.

Oued Sebou drainage. SMF 33410, 9; SMF 33494, 1; SMF 33495, 1; SMF 33496, 1, Morocco, Oued Ouergha between Sidi Qacem and Ouazzane (N34°27'52", W5°30'39"), K. Borkenhagen and J. Freyhof, 17 Apr 2011. - MNHN 1939-0125, 1; MNHN 1939-0126, 1; MNHN 1939-0127, 1, Morocco, El Gharb [N34°25', W6°20'], J. M. Pérès, 1939. - MNHN 1939-0122, 2; MNHN 1939-0123, 2; MNHN 1939-0145, 1, Morocco, Oued Sebou [N34°15'53", W6°41'5"], J. M. Pérès, 1939. - SMF 33409, 15; SMF 33489, 1; SMF 33491, 1; SMF 33493, 1, Morocco, Oued Lahdar near Taza (N34°14'35", W4°3'55"), K. Borkenhagen and J. Freyhof, 16 Apr 2011. - MNHN 1924-0191, 3, Morocco, Oued Beth near Dar Bel Hamri [N34°11'14", W5°57'54"], C. A. Alluaud, 1924. - MNHN 1920-0061, 1; MNHN 1920-0062, 1, Morocco, Oued Bou Hellou [N34°9'19", W4°25'33"], P. M. Pallary, 1920. - MNHN 1922-0065, 1, Morocco, Moulay Yacoub [N34°5'17", W5°10'54"], C. A. Alluaud, 1922. - MNHN 1920-0202, 1, Morocco, Faraoun near Volubilis [N34°4'25", W5°33'25"], C. A. Alluaud, 1920. - MNHN 1939-0128, 1; MNHN 1939-0129, 1, El Mabbabat [?], J. M. Pérès, 1939.

Oued Tennsift drainage. BMNH 1904.11.28:60, 1; BMNH 1905.11.28:60-63 and BMNH 1904.11.28:57-58, 6, Morocco, Oued Chichaoua [N31°43'48", W8°49'48"], F. Riggenbach. - MNHN 1919-0379, 1; MNHN 1919-0380, 1; MNHN 1919-0381, 1; MNHN 1919-0382, 1, Morocco, Oued Nfis near Dar Goundafi [N31°43'41", W8°21'1"], P. M. Pallary, 1919. - MNHN 1988-1146, 4, Morocco, Oued Nfis [N31°43'41", W8°21'1"], Goubier, VI.1988. - MNHN 1922-0066, 1; MNHN 1922-0067, 1; MNHN 1922-0068, 1, Morocco, Oued Chichaoua near Chichaoua [N31°32'37", W8°45'46"], C. A. Alluaud, 1922. - SMF 33371, 1; SMF 33372, 1; SMF 33373, 1; SMF 33374, 1; SMF 33398, 3, Morocco, Oued Nfis near Tameslouht (N31°27'2", W8°8'22"), A. Azeroual et al., 10 Apr 2011. - SMF 33378, 1; SMF 33379, 1; SMF 33380, 1; SMF 33399, 14; SMF 33403, 22, Morocco, Oued Nfis near Ouirgane (N31°13'24", W8°6'50"), A. Azeroual et al., 10 Apr 2011. - MNHN 1925-0371, 1, Morocco, Oued Nfis near Ouirgane [N31°10'40", W8°4'24"], J. Pellegrin, 1925.

Diagnosis. Two pairs of barbels, 30 to 39 scales in the lateral line and 14 to 20 scales around the least circumference of the caudal peduncle; dorsal fin usually shorter than anal fin and more than 15 % of its last unbranched ray flexible, dorsal profile of the head convex.

Description. The body is of moderate height and sometimes has a small nuchal hump in larger specimens. The head is round with a convex dorsal profile and convex or straight ventral profile (Figs 16, 17). The head length is shorter than the body depth (Fig. 12), the mouth is inferior with two pairs of barbels (Table 2). The lower lip is crescent shaped and sometimes weakly keratinised. The eyes are in the anterior half of the head. The morphometric characters are summarised in Table 1.

The dorsal fin is short and weakly ossified and more than 15 % of the length of its last unbranched ray is flexible. Its last unbranched ray is about as long as the head (Fig. 4). It usually has four unbranched and seven to 10 branched rays (Table 3). The anal fin usually has three unbranched and five or six branched rays (Table 4). Its length is rather variable in adult specimens. It reaches the base of the caudal fin in some specimens.

Figure 16. *Carasobarbus fritschii*, syntype (BMNH 1874.1.30:27-31) from Oued Ksob, © The Natural History Museum, London.

Figure 17. *Carasobarbus fritschii*, from Oued Ksob.

Carasobarbus fritschii has 30 to 39 scales in the lateral line (Table 5), usually 5.5 scales above the lateral line (Table 6), usually 4.5 or 5.5 scales below the lateral line (Table 7), and 14 to 20 scales around the least circumference of the caudal peduncle (Table 8). The scales are shown in Fig. 5.

The pharyngeal teeth count is 2.3.4-4.3.2 in two specimens, 2.3.4- in one specimen and -4.3.2 in eight specimens. Pharyngeal teeth are hooked at their tips (Fig. 6).

Live specimens are silvery and usually have a dark longitudinal band above the lateral line. Fins are hyaline to slightly orange (Fig. 17). Ethanol-preserved specimens are yellow-brown, the back is usually distinctly darker than the belly and flanks.

The maximum length observed in the material available is 180 mm SL.

Carasobarbus fritschii differs from all congeners except *C. exulatus* and *C. harterti* in having nine instead of 10 branched dorsal-fin rays. It differs from *C. exulatus* in having 30 to 39 scales in the lateral line vs. 26 to 32 and modally 16 scales around the least circumference of the caudal peduncle vs. 12. It differs from *C. harterti* in having a convex dorsal head profile and a last unbranched dorsal-fin ray that is weakly ossified and flexible for more than 15 % of its length vs. a straight dorsal head profile and a strongly ossified last unbranched dorsal-fin ray that is flexible in less than 15 % of its length.

Distribution. *Carasobarbus fritschii* is widespread and abundant in Northern and Central Morocco (Fig. 18). It occurs in the Oued al Maleh, Oued Bou Regreg, Oued Igrounzar, Oued Moulouya, Oued Oum er Rbia, Oued Sebou and Oued Tennsift drainage systems, and in numerous small coastal rivers. Most records are from Morocco, but one specimen is from the Oued Kiss in Algeria.

Habitats and biology. *Carasobarbus fritschii* occurs in a wide range of running water courses and dam lakes.

Conservation status. *Carasobarbus fritschii* is a hardy species and occurs in near-natural as well as heavily modified habitats. It is tolerant against pollution, damming and the presence of several exotic species (KB pers. obs.). The IUCN rates *C. fritschii* as "Least Concern" and *Barbus paytonii* (which is treated as a junior synonym in this study) as "Vulnerable B2ab(iii)" (Crivelli 2006c, Crivelli 2006e). According to the latter assessment the population in the lower Oued Oum er Rbia is adversely affected by agricultural pollution (Crivelli 2006e).

Discussion. *Carasobarbus fritschii* was described from the Oued Ksob as a member of the genus *Barbus* (Günther 1874). The same author described *Barbus rothschildi* from the Oued Oum er Rbia (Günther 1901). It is a junior synonym of *C. fritschii*. One year later Günther (1902) described *Barbus riggenbachii* from Oued Oum er Rbia and Oued Talmest. It is a junior synonym of *C. fritschii*. In the same year *Capoeta atlantica* and *Capoeta waldoi* were described from Oued Nfis (Boulenger 1902). These two species were placed into *Capoeta*, based on the keratinised lower lip that occurs in some specimens of *C. fritschii*. Both are junior synonyms of *C. fritschii*. *Barbus paytonii* was described from Oued Oum er Rbia (Boulenger 1911). It is a junior synonym of *C. fritschii*. In the same publication Boulenger transferred *C. waldoi* to the genus *Barbus*. The junior synonyms listed above were described, based on slight differences in mouth and lower lip shape or the degree of ossification of dorsal-fin rays. Sample sizes were usually very small. The examination of a large number of specimens revealed high variability and a continuous distribution of these characters. Boulenger (1919) transferred all species to the genus *Barbus* subgenus *Labeobarbus*, based on the possession of scales with parallel radii and an unserrated last unbranched dorsal-fin ray. Pellegrin (1919) listed the species in the genus *Barbus* but later (Pellegrin 1921, 1939) accepted the subgenus *Labeobarbus*. Pellegrin (1939) synonymised B. *riggenbachi* with *B. rothschildi* and did not list *C. atlantica*. Karaman (1971) created the genus *Pseudotor* and synonymised *C. atlantica* and *C. waldoi* with *Pseudotor fritschii fritschii*. Fowler (1976) accepted all previously described species and transferred *C. atlantica* and *C. waldoi* to the genus *Varicorhinus*. Berrebi (1981) used the genus *Barbus* subgenus *Labeobarbus* and found no relevant differences between *B. fritschii* and *B. paytonii* in his morphometric and biochemical analysis. El Gharbi et al. (1993) highlighted the African distribution of the subgenus *Labeobarbus*. Doadrio (1994) and Tsigenopoulos et al. (2010) used *Labeobarbus*. Subsequent authors used the genus *Barbus* (Azeroual et al.

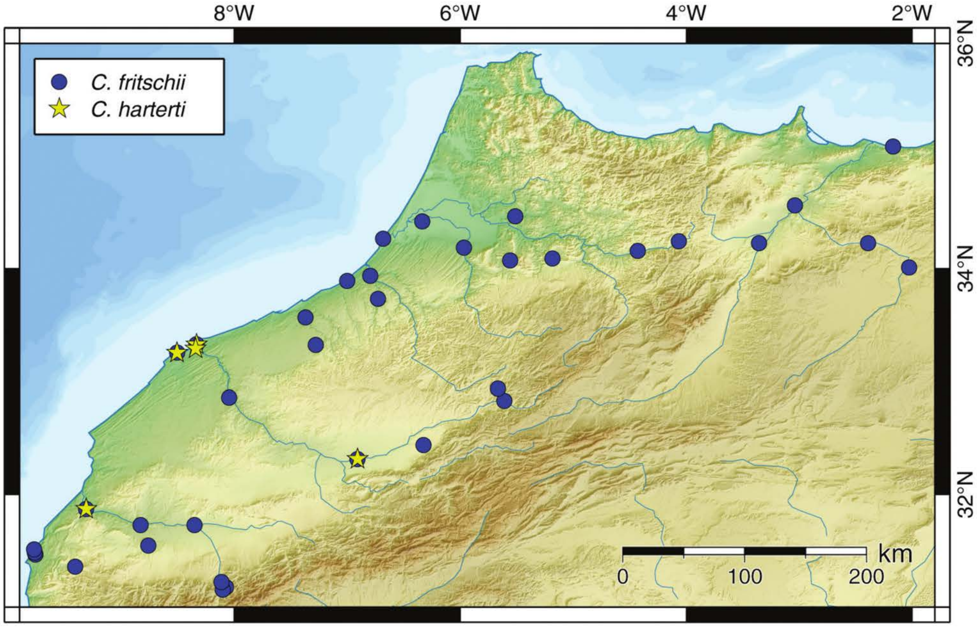

Figure 18. Map of the distribution of *C. fritschii* and *C. harterti*.

2000, Machordom and Doadrio 2001, Leggatt and Iwama 2003, Colli et al. 2009) or the provisional genus '*Barbus*' (Borkenhagen et al. 2011). We transfer this species to the genus *Carasobarbus*, based on the possession of a smooth last unbranched dorsal-fin ray, modally nine branched dorsal-fin rays, six branched rays in the anal fin and shield-shaped scales with numerous parallel radii. Analysis of molecular genetic characters (Durand et al. 2002, Tsigenopoulos et al. 2010, KB unpublished data) support this decision.

The name of this species is frequently misspelled "*Barbus fritschi*".

The 'Catalog of Fishes' lists SMF 636 and SMF 952 as types for *C. fritschii* (Eschmeyer 2011). Both lots where collected by K. v. Fritsch and J. Rein in Oued Ksob in 1872, together with the types of '*Barbus*' *reinii* Günther, 1874, *Luciobarbus nasus* (Günther, 1874) and the syntypes of *C. fritschii*. SMF 636 contains seven specimens: one *Luciobarbus nasus*, one *Luciobarbus ksibi (*Boulenger, 1905), one '*Barbus*' *reinii* and four *C. fritschii*. SMF 952 contains eight specimens: two '*Barbus*' *reinii* and six *C. fritschii*. In the original description Günther (1874) did not state the number of type specimens on which he based the description of *C. fritschii*, but in the same paper he described *Luciobarbus nasus* (as *Barbus nasus*), based on two specimens and '*Barbus*' *reinii*, based on three specimens. It is likely that Günther never saw the lots SMF 636 and SMF 952, because all syntypes of *Luciobarbus nasus* and '*Barbus*' *reinii* are in the BMNH. The collectors, K. v. Fritsch and J. Rein probably deposited these samples immediately in the SMF and we conclude that SMF 636 and SMF 952 are not part of the type series of *C. fritschii*.

Carasobarbus harterti (Günther, 1901), comb. n.

http://species-id.net/wiki/Carasobarbus_harterti

Barbus harterti Günther 1901: 367.

Material. Type material. Syntypes: BMNH 1901.7.26:4-5, 2, Morocco, Oued Oum er Rbia [N33°19'40", W8°20'2"], E. Hartert.

Non-type material. Oued Oum er Rbia drainage. BMNH 1902.7.28:27-33, 7; BMNH 1903.10.29:11-15, 8, Morocco, Oued Oum er Rbia [N33°19'40", W8°20'2"], F. Riggenbach. - BMNH 1903.7.1:5-7, 3, Morocco, Oued Oum er Rbia near El Jadida [N33°15'18", W8°30'22"], F. Riggenbach. - MNHN 1912-0089, 1; MNHN 1912-0090, 1; MNHN 1912-0091, 1; MNHN 1912-0092, 1; MNHN 1912-0093, 1, Morocco, Oued Oum er Rbia near Azemmour [N33°17'22", W8°20'33"], C. du Gast, 1912. - SMF 33366, 1; SMF 33368, 1; SMF 33370, 1, Morocco, Oued Oum er Rbia (N32°18'53", W6°54'33"), A. Azeroual et al., 9 Apr 2011.

Oued Tennsift drainage. BMNH 1902.7.28:34, 1, Morocco, Oued Talmest [N31°52'15", W9°18'31"], F. Riggenbach.

Diagnosis. Two pairs of long barbels; 31 to 38 scales in the lateral line and 13 to 17 scales around the least circumference of the caudal peduncle; dorsal fin longer than anal fin and less than 15 % of the length of its last unbranched ray is flexible, dorsal profile of the head straight.

Description. The body is of moderate height and without a nuchal hump. The head is triangular with almost straight dorsal and ventral profile (Figs 19, 20). The head length is shorter than the body depth (Fig. 12). The mouth is subterminal with two pairs of long barbels (Table 2). The eyes are in the anterior half of the head and relatively big. The morphometric characters are summarised in Table 1.

The dorsal fin is long and strongly ossified and less than 15 % of the length of its last unbranched ray is flexible. Its last unbranched ray is as long as or longer than the head (Fig. 4). It usually has four unbranched and nine branched rays (Table 3). The anal fin usually has three unbranched and six or seven branched rays (Table 4). It does not reach the caudal fin origin.

Carasobarbus harterti has 31 to 38 scales in the lateral line (Table 5), usually 5.5 or 6.5 scales above the lateral line (Table 6), 4.5 to 6.5 scales below the lateral line (Table 7) and 13 to 17 scales around the least circumference of the caudal peduncle (Table 8). The scales are shown in Fig. 5.

The pharyngeal teeth count is -4.3.2 in four specimens examined. The pharyngeal teeth are hooked at their tips (Fig. 6).

Live specimens are silvery with an olive tinge and orange fins (Fig. 20). Ethanol-preserved specimens are yellow-brown, the back is darker than the belly and flanks.

The maximum length observed in the material examined is 250 mm SL.

Carasobarbus harterti differs from all congeners except *C. exulatus* and *C. fritschii* in having nine rather than 10 branched dorsal-fin rays. It differs from *C. exulatus* in having 31 to 38 scales in the lateral line vs 26 to 32 and modally 16 scales around the

Figure 19. *Carasobarbus harterti*, syntype (BMNH 1901.7.26:4-5) from Oued Oum er Rbia, © The Natural History Museum, London.

Figure 20. *Carasobarbus harterti*, live specimen from Oued Oum er Rbia.

least circumference of the caudal peduncle vs. 12. It differs from *C. fritschii* in having a straight dorsal head profile and a last unbranched dorsal-fin ray that is strongly ossified and flexible for less than 15 % of its length vs. a convex dorsal head profile and a last unbranched dorsal-fin ray that is weakly ossified and flexible for more than 15 % of its length.

Distribution. *Carasobarbus harterti* occurs in the rivers of the Oued Oum er Rbia and Tennsift drainage systems in Morocco (Fig. 18).

Habitats and biology. *Carasobarbus harterti* is less common than *C. fritschii* and inhabits only the lower and middle course of big rivers.

Conservation status. The IUCN rates this species as "Vulnerable A2ace" (Crivelli 2006d). The population has declined more than 30 % in the time from 1996 to 2006 due to urban, agricultural and industrial pollution (Crivelli 2006d).

Discussion. *Carasobarbus harterti* was described from Oued Oum er Rbia as *Barbus harterti* (Günther 1901). Some authors placed this species in the genus *Barbus* subgenus *Labeobarbus* (Boulenger 1919, Pellegrin 1921) while others continued using the genus *Barbus* (Pellegrin 1919, 1939). Karaman (1971) synonymised it with *C. fritschii*, but regarded it as a distinct subspecies. He incorrectly synonymised *B. rothschildi*, *B. riggenbachi* and *B. paytonii* with this subspecies and placed it in his newly erected genus *Pseudotor*. Subsequent authors did not accept Karaman's proposal and continued using *Barbus* (Fowler 1976, El Gharbi et al. 1993, Azeroual et al. 2000, Leggatt and Iwama 2003, Colli et al. 2009, Borkenhagen et al. 2011) or proposed using *Labeobarbus* (Doadrio 1994, Tsigenopoulos et al. 2010). We transfer this species to the genus *Carasobarbus*, based on the possession of a smooth last unbranched dorsal-fin ray, nine branched dorsal-fin rays, six branched rays in the anal fin and shield-shaped scales with numerous parallel radii. Analysis of molecular genetic characters (Durand et al. 2002, Tsigenopoulos et al. 2010, KB unpublished data) support this decision.

***Carasobarbus kosswigi* (Ladiges, 1960)**

http://species-id.net/wiki/Carasobarbus_kosswigi

Cyclocheilichthys kosswigi Ladiges 1960: 135.

Material. Type material. Holotype of *Cyclocheilichthys kosswigi*: ZMH H 1148, Turkey, Batman Çayı [N37°47'16", E41°0'51"], C. Kosswig, IV.1939.

Non-type material. Tigris-Euphrates system. NMW 90369, 1, Turkey, Batman Çayı near Baschkaja [N37°53'15", E41°7'56"], V. Pietschmann, 15 Jul 1914. - NMW 90805, 1, Turkey, Gökçesu Çayı (N37°45', E41°45'), 26 Sep 1985. - ZMH 9548, 2, Turkey, Ceylanpınar [N36°50'50", E40°3'0"]. - SMF 33119, 1, Syria, Nahr al Khābūr at Al Ḩasakah [N36°30'9", E40°44'52"], F. Krupp. - SMF 30172, 1, Syria, Nahr al Khābūr near Tall Budayrī (N36°24', E40°52'), F. Krupp, 2–4 Nov 1986. - SMF 30173, 1, Syria, Nahr al Khābūr near Nahāb (N36°23', E40°50'), F. Krupp, 23–27 May 1989. - SMF 30174, 1, Syria, Nahr al Khābūr near Nahāb (N36°23', E40°50'), F. Krupp, 28 Sep–8 Oct 1988. - CMNFI 79-0290, 2, Iran, Qaşr-e Shīrīn (N34°31', E45°35'). - CMNFI 79-0289, 1, Iran, 25–30 km from Qaşr-e Shīrīn (N34°28', E45°52'). - BMNH 1974.2.22:1292-1296, 4; BMNH 1974.2.22:1281, 1, Iraq, Euphrates at Ḩadīthah [N34°8'23", E42°22'41"], 19 Oct 1953. - CMNFI 79-0275, 1, Iran, Rūdkhāneh-ye Kashgān, 2 km from Maʻmūlān (N33°25', E47°58'). - SMF 33129, 3, Iran, Rūdkhāneh-ye Karkheh at Pol-e Dokhtar (N33°9'36", E47°43'12"), N. Alwan et al., 3 Mar 2008. - ZM-CBSU 4153, 1; ZM-CBSU 4154, 1, Iran, Rūdkhāneh-ye Dez at Dezfūl [N32°22'57", E48°24'7"], F. Bossaghzadeh, 8 Jun 2005.

Diagnosis. Two pairs of barbels; 32 to 38 scales in the lateral line, usually 14 to 16 scales around the least circumference of the caudal peduncle; last unbranched dorsal-fin ray markedly longer than head; mouth narrow, lower lip spatulate and median lobe present.

Description. Body moderately high, laterally compressed and without a nuchal hump. The greatest body depth is at the point of the origin of the dorsal fin. The ventral profile of the head is straight, its dorsal profile has a slight to pronounced hump

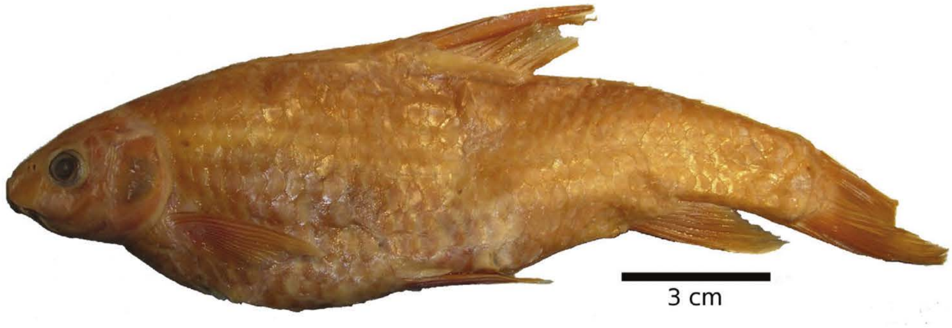

Figure 21. *Carasobarbus kosswigi*, holotype (ZMH 1148) from Batman Çayı.

Figure 22. *Carasobarbus kosswigi*, live specimen from Rūdkhāneh-ye Karkheh.

near the nostrils (Figs 21, 22). The head is short and narrow. The mouth is inferior. The maximum body depth is bigger than the head length (Fig. 12). The lips are comparatively thick and the lower jaw is narrow with a sharp horny sheath and a median lobe. The two pairs of barbels (Table 2) are stout and the anterior pair is quite long. The eyes are rather high in the middle of the head and rather small. The morphometric characters are summarised in Table 1.

The dorsal fin is long and usually has four unbranched and nine or 10 branched rays (Table 3). The last unbranched ray is long and well ossified; only the tip is flexible. It is considerably longer than the head (Fig. 4). The anal fin usually has three unbranched rays and six branched rays (Table 4). Its base is long. The bases of the dorsal and anal fin have a sheath of scales.

There are 32 to 38 scales in the lateral line (Table 5), 5.5 to seven scales above the lateral line (Table 6), 4.5 to 6.5 scales below the lateral line (Table 7) and (12) 14 to 16 scales around the least circumference of the caudal peduncle (Table 8). The scales are shown in Fig. 5.

The pharyngeal teeth count is 2.3.5-5.3.2 in seven specimens, 2.3.5- in one specimen and -4.3.2 in one specimen. The pharyngeal teeth are hooked at their tips (Fig. 6).

Live specimens are silvery. The back is darker than the belly, which is almost white (Fig. 22). Fixed specimens are yellow-brown and some have a darker back.

Carasobarbus kosswigi differs from all congeners, except *C. sublimus*, by having a spatulate lower jaw with a median lobe on the lower lip vs. a crescent-shaped lower jaw and a lower lip without median lobe. It differs from *C. sublimus* by having 32 to 38 scales in the lateral line vs. 27 to 29 and modally 14 scales around the least circumference of the caudal peduncle vs. 12 and by having a longer and more ossified last unbranched ray in the dorsal fin.

Distribution. *Carasobarbus kosswigi* occurs in the Euphrates-Tigris system (Fig. 7).

Habitats and biology. *Carasobarbus kosswigi* is rare, inhabits fast-flowing reaches of rivers and feeds on small animals (Krupp and Schneider 2008). The maximum length is about 150 mm SL and this species has no economic importance (Krupp and Schneider 2008).

Conservation status. Little information is available, but because this species is dependent on fast-flowing water, it is probably impacted by the construction of dams.

Discussion. *Carasobarbus kosswigi* was described from the Batman Çayı and placed in the genus *Cyclocheilichthys* (Ladiges 1960). Karaman erected the new genus *Kosswigobarbus* for this species (Karaman 1971). Coad gave a detailed re-description of this species and transferred it to the genus *Barbus* (Coad 1982). *Kosswigobarbus* was revalidated (Ekmekçi and Banarescu 1998) and sometimes used as a subgenus of *Barbus* (Tsigenopoulos et al. 2010). Later the species was placed in *Carasobarbus* (Borkenhagen et al. 2011).

Carasobarbus kosswigi is paraphyletic with respect to *C. sublimus* (Borkenhagen et al. 2011).

Carasobarbus luteus (Heckel, 1843)

http://species-id.net/wiki/Carasobarbus_luteus

Systomus luteus Heckel 1843: 1161.
Systomus albus Heckel 1843: 1163.
Systomus albus var. *alpina* Heckel 1847: 257.
Barbus parieschanica Wossughi et al. 1983: 34.

Material. Type material. Nahr Quwayq basin. Paralectotypes of *Systomus luteus*: NMW 54248, 1; NMW 54250:1-2, 2; NMW 54254:1-3, 3; SMF 6784, 1, Syria, Nahr Quwayq near Aleppo [N36°12'10", E37°9'31"], T. Kotschy, 17 May 1842.

Syntypes of *Systomus albus*: NMW 53674-53677, 4; NMW 53680, 1; SMF 812, 1, Syria, Nahr Quwayq near Aleppo [N36°12'10", E37°9'31"], T. Kotschy, 18 May 1842.

Rūd-e Mand basin. Syntypes of *Systomus albus alpina*: NMW 53678, 5; NMW 53679:1-2, 2; NMW 53681:1-2, 2, Iran, Rūdkhāneh-ye Qarah Āghāj near Shīrāz [N29°31'3", E52°15'0"], 2 Jan 1844.

Rūdkhāneh-ye Ḩelleh basin. Syntypes of *Systomus albus alpina*: NMW 53682:1-2, 2, Iran, Daryācheh-ye Parīshān [N29°31'7", E51°47'47"].

Tigris-Euphrates system. Lectotype of *Systomus luteus* (by present designation): NMW 54253:2, Iraq, Tigris near Mosul [N36°20'6", E43°7'8"], T Kotschy, 10 Apr 1843.

Paralectotypes of *Systomus luteus*: NMW 54247:1-2, 2; NMW 54249, 1; NMW 54253:1, 1; NMW 54255:1-2, 2; NMW 80043, 2 same data as lectotype.

Syntype of *Systomus albus*: NMW 91400, 1, Iraq, Tigris near Mosul [N36°20'6", E43°7'8"], 11 Apr 1843.

Unknown drainage system. Paralectotype of *Systomus luteus*: NMW 10827, 1, Syria, "Damascus", T. Kotschy, 1837.

Non-type material. Daryācheh-ye Mahārlū basin. CMNFI 79-0047, 1, Iran, source of Ab-e Paravan marshes 19.9 km from Shīrāz University [N29°36', E52°32']. - FSJF 2232, 2, Iran, Pirbano spring about 10 km south of Shīrāz (N29°31'8", E52°27'56"), A. Abdoli and J. Freyhof, 21 Apr 2007. - ZM-CBSU 3439, 1; ZM-CBSU 3449, 1; ZM-CBSU uncatalogued, 1, Iran, Pol-e Berenji, southwest of Shīrāz [N29°27'30", E52°32'0"], H. R. Esmaeili et al. - CMNFI 79-0347, 1, Iran, Solţānābād marshes near Pol-e Berenji (N29°27'30", E52°32'0").

Orontes basin. MNHN 1977-0255, 1, Syria, Orontes, Gruvel, 1929, only one of two specimen examined. - MNHN 1977-0257, 1, Syria, Orontes, Gruvel, 1930. - SMF 24341, 1, Syria, Orontes at Jisr ash Shughūr (N35°48', E36°19'), F. Krupp, 21 Mar 1979 (aberrant specimen).

Rūd-e Mand basin. CMNFI 79-0206, 1, Iran, Qanat 41 km from Estahbān on road to Kharāmeh (N29°12', E53°40'). - CMNFI 79-0160, 1, Iran, cement pool near spring along road to Neyrīz (N29°9', E53°37'). - ZM-CBSU 4934-4942, 9, Iran, Dareh Daarveshan between Rudbal and Simakan (N28°39'10", E52°2'27"), H. R. Esmaeili et al. - ZM-CBSU 101-103, 3; ZM-CBSU 110, 1; ZM-CBSU uncatalogued, 1, Iran, Rūdkhāneh-ye Sīmakān near Jahrom [N28°30'0", E53°33'38"], H. R. Esmaeili et al.

Rūdkhāneh-ye Ḩelleh basin. CMNFI 79-0026, 1, Iran, Rūdkhāneh-ye Shāhpūr near Shahr-e Tārīkhī-ye Neyshābūr (N29°47', E51°35'). - ZM-CBSU 5180-5190, 10; ZM-CBSU 5192, 1, Iran, Kāzerūn, Sarab Dokhtar [N29°37'10", E51°39'15"], H. R. Esmaeili et al. - ZM-CBSU 6508-6517, 10; ZM-CBSU 6574, 1; ZM-CBSU 6602-6607, 6; ZM-CBSU 6610, 1; ZM-CBSU 6614+6615+6617-6619, 5; ZM-CBSU uncatalogued, 12, Iran, Daryācheh-ye Parīshān [N29°31'7", E51°47'47"], H. R. Esmaeili et al. - CMNFI 79-0240, 2; CMNFI 79-0304, 3, Iran, Daryācheh-ye Parīshān (N29°31', E51°50'). - CMNFI 79-0125, 1, Iran, Rūdkhāneh-ye Dālakī near Dālakī (N29°28', E51°21'). - ZM-CBSU 2650-2651, 2; ZM-CBSU 2654-2655, 2, Iran, spring at Palangī Dādīn, near Kāzerūn, Rūdkhāneh-ye Dālakī [N29°25'20", E51°43'54"], H. R. Esmaeili et al.

Rūdkhāneh-ye Kol basin. ZM-CBSU 3219-3229, 11; ZM-CBSU 3252-3260, 9, Iran, Golabi spring north of Dārāb [N28°47'15", E54°22'19"], H. R. Esmaeili et al. - FSJF 2253, 6, Iran, Golabi spring 35 km north of Dārāb (N28°47'15", E54°22'19"), A. Abdoli and J. Freyhof, 21 Apr 2007. - CMNFI 79-0155, 1, Iran, spring at Gavanoo, east of Ḩasanābād [N28°47', E54°22']. - CMNFI 79-0154, 2, Iran, Korsia village on Dārāb-Fasā road (N28°45'30", E54°24'0"). - ZM-CBSU 5622-5626, 5, Iran, Tang-e Khūr near Lār [N27°36', E54°17'], H. R. Esmaeili et al.

Rūdkhāneh-ye Naband basin. CMNFI 79-0187, 10, Iran, stream and pools at Sarkhūn, Rūdkhāneh-ye Sarzeh (N27°23'30", E56°26'0").

Tigris-Euphrates system. SMF 30208, 1, Turkey, Tigris at Diyarbakır (N37°53', E40°14’), R. Kinzelbach, 1982. - SMF 30176, 11, Syria, Nahr al Khābūr at Ra’s al ‘Ayn (N36°51', E40°4'), F. Krupp, 24–26 May 1989. - SMF 30186, 12, Syria, ‘Ayn Sālūba and ‘Ayn Hamza near Ra’s al ‘Ayn (N36°51', E40°4'), F. Krupp, 3 Oct 1988. - SMF 30200, 2, Syria, ‘Ayn Sālūba at Ra’s al ‘Ayn (N36°51', E40°4'), F. Krupp, 3 Oct 1988. - SMF 30190, 7, Syria, Nahr al Khābūr 2 km East of Tall Junaydīyah (N36°44', E40°6'), F. Krupp, 26 May 1989. - SMF 30197, 2, Syria, Nahr al Khābūr 2 km East of Tall Junaydīyah (N36°44', E40°6'), F. Krupp, 5 Oct 1988. - SMF 30179, 3, Syria, Nahr al Khābūr at Tall ʿAtaš (N36°42', E40°11'), F. Krupp, 26 May 1989. - SMF 30188, 3, Syria, Nahr al Khābūr at Tall ʿAtaš (N36°42', E40°11'), F. Krupp, 6 Oct 1988. - SMF 31317, 1; SMF 33139, 7, Syria, Nahr al Khābūr at Tall Tamr (N36°39'7", E40°21'51"), N. Alwan et al., 29 Oct 2008. - SMF 30199, 1, Syria, Nahr al Khābūr at Tall Naşrī (N36°37', E40°23'), F. Krupp, 6–7 Oct 1988. - SMF 30178, 1; SMF 30202, 10, Syria, Nahr al Khābūr near Tall Bāz (N36°35', E40°27'), F. Krupp, 7 Oct 1988. - SMF 30184, 1; SMF 30193, 3, Syria, Nahr al Khābūr at Tall Bāz (N36°35', E40°27'), F. Krupp, 26 May 1989. - SMF 30181, 1; SMF 30192, 3, Syria, Nahr al Khābūr at Tall Umm al Māʿaz (N36°34', E40°35'), F. Krupp, 27 May 1989. - SMF 30183, 3, Syria, Nahr al Khābūr at Umm al-Māʿaz (N36°34', E40°35'), F. Krupp, 7 Oct 1988. - SMF 30182, 2, Syria, Nahr al Khābūr at Al Ḩasakah (N36°30', E40°44'), F. Krupp, 27 May 1989. - SMF 30195, 1, Syria, Nahr al Khābūr at Al Ḩasakah (N36°30', E40°44'), F. Krupp, 7 Oct 1988. - SMF 30185, 1; SMF 30213, 6, Syria, Nahr al Khābūr and Wādī Furātī at Tall Tayyiǧ (N36°26', E40°52'), F. Krupp, 8 Oct 1988. - SMF 30189, 4, Syria, Nahr al Khābūr at Baḩrat Khātūnīyah (N36°24', E41°13'), F. Krupp, 23–24 May 1989. - SMF 30214, 5, Syria, Nahr al Khābūr at Tall Budayrī (N36°24', E40°49'), F. Krupp, 26 Sep–8 Oct 1988. - SMF 30206, 7, Syria, Nahr al Khābūr at Tall Budayrī (N36°24', E40°52'), F. Krupp, 2–4 Nov 1986. - SMF 30177, 3, Syria, Nahr al Khābūr at Nahāb (N36°23', E40°50'), F. Krupp, 28 Sep–8 Oct 1988. - SMF 30201, 23, Syria, Nahr al Khābūr at ‘Ayn Ṭābān (N36°22', E40°50'), F. Krupp, 28 Sep 1988. - SMF 30191, 2, Syria, Nahr al Khābūr at mouth of Wādī ar Raml (N36°15', E40°48'), F. Krupp, 8 Oct 1988. - SMF 30196, 1, Syria, Nahr al Khābūr at Umm Rukaybah (N36°8', E40°42'), F. Krupp, 8 Oct 1988. - SMF 30194, 3, Syria, Nahr al Khābūr at Ash Shaddādah (N36°4', E40°44'), F. Krupp, 9 Oct 1988. - SMF 31316, 1; SMF 33138, 2, Syria, Nahr al Khābūr at Ash Shaddādah (N36°3'46", E40°44'30"), N. Alwan et al., 28 Oct 2008. - SMF 33152, 6, Syria, Jisr Shānīn (N36°3'4", E39°5'10"), F. Krupp and W. Schneider, 19 Aug 1980. - SMF 31308, 1, Syria, Mamlaḫat al Jabbūl (N36°3'36", E37°33'1"), N. Hamidan, 23 Jun 2008. - SMF 28707, 18, Syria, Euphrates down stream Buḫayratt al Asad (N35°51'48", E39°0'34"), R. Beck, Jun 1998. - SMF 30198, 2, Syria, Nahr al Khābūr at Tall ash Shaykh Ḩamad (N35°37', E40°45'), F. Krupp, 21 Sep–14 Oct 1988. - SMF 30204, 1; SMF 30205, 4, Syria, Nahr al Khābūr at Tall ash Shaykh Ḩamad

(N35°37', E40°45'), F. Krupp, 20 Oct–9 Nov 1986. - SMF 33140, 1; SMF 33141, 37, Syria, Euphrates at Harmūshīyah (N35°35'52", E39°51'25"), N. Alwan et al., 31 Oct 2008. - SMF 30203, 2, Syria, Nahr al Khābūr 8 km South of Tall ash Shaykh Ḩamad (N35°33', E40°43'), F. Krupp, 24 Oct 1986. - SMF 28737, 5, Syria, Euphrates between Ḩalabīyah-Zalābīyah and Dayr az Zawr, R. Beck, Jun 1998. - SMF 28630, 3, Syria, Euphrates upstream Dayr az Zawr (N35°31', E39°54'), R. Beck, 23 May 1998. - SMF 28674, 41, Syria, Euphrates upstream Dayr az Zawr [N35°31', E39°54'], R. Beck, 30 May 1998. - SMF 33153, 1, Syria, Nahr al Khābūr at Aş Şuwar (N35°30', E40°38'), F. Krupp, 15 Mar 1979. - SMF 31315, 1; SMF 33137, 1, Syria, Nahr al Khābūr at Ghawat (N35°28'51", E40°39'54"), N. Alwan et al., 28 Oct 2008. - SMF 30187, 2, Syria, Nahr al Khābūr near Ḩarījīyah (N35°27', E40°38'), F. Krupp, 10 Oct 1988. - SMF 30180, 5, Syria, Nahr al Khābūr at Mashikh (N35°14', E40°31'), F. Krupp, 10 Oct 1988. - SMF 28663, 6, Syria, Euphrates at Qalʻat aş Şāliḩīyah (Dura Europos) [N34°45'0", E40°43'30"], R. Beck, 28 May 1998. - SMF 28758, 2, Syria, Euphrates at Abū Kamāl at mouth of Wādī Ratqah [N34°26'45", E40°56'0"], R. Beck, 9 Jul 1998. - NMW 93019:1-2, 2, Iraq, Tigris at Baghdād [N33°20'26", E44°24'3"], V. Pietschmann, Aug 1910. - SMF 33127, 4, Iran, Rūdkhāneh-ye Bālārūd (N32°35'19", E48°17'11"), N. Alwan et al., 3 Mar 2008. - BMNH 1980.8.28:6, 1, Iran, Rūdkhāneh-ye Dez at Dezfūl [N32°25', E48°13']. - SMF 33125, 1, Iran, Rūdkhāneh-ye Dez at Dezfūl (N32°22'40", E48°22'58"), N. Alwan et al., 2 Mar 2008. - SMF 33121, 5, Iran, Rūdkhāneh-ye Dez at Dezfūl (N32°21'49", E48°21'28"), K. Borkenhagen et al., 3 Nov 2006. - SMF 17303, 1, Iraq, Hawr al Ḩammār (N30°50', E47°10'), L. A. J. Al-Hassan, 1986. - SMF 30211, 1, Iraq, ʻAyn Zālah 50 km west of Mosul, Z. Rahemo, 1990.

Unknown drainage system. SMF 33120, 2, Syria, fish market in Damascus (reported to be from Buḩayratt Ar Rastan [N34°56', E36°44'] in Orontes drainage), F. Krupp. - CMNFI 79-0687, 4, Iran, Shīrāz bazar (probably from Rūd-e Mand basin or Daryācheh-ye Mahārlū basin).

The lectotype (NMW 54253:2) is a specimen of 211 mm SL, collected in the Tigris near Mosul on 10 Apr 1843 by T. Kotschy (Fig. 23). It has four unbranched and 10 branched rays in the dorsal fin, three unbranched and six branched rays in the anal fin, 27 scales in the lateral line and one pair of barbels. A bigger specimen (216 mm SL) from the same lot (NMW 54253:1) was not selected as lectotype, because it is atypical in having 11 branched rays in the dorsal fin and two pairs of barbels. The designation of a lectotype became necessary to fix the type locality of *S. luteus* (see Discussion).

Diagnosis. One pair of barbels; 25 to 33 scales in the lateral line, and typically 12 scales around the least circumference of the caudal peduncle; last unbranched ray of the dorsal fin about as long as the head or slightly shorter.

Description. Specimens from Rūdkhāneh-ye Naband basin were excluded from this species description (see below).

The dorsal profile is convex up to the origin of the dorsal fin and a nuchal hump is present in specimens longer than about 100 mm SL. This species has a high back and caudal peduncle (Figs 23, 24). The ventral profile of the head is convex, its dorsal pro-

Figure 23. *Carasobarbus luteus*, lectotype (NMW 54253:2) from Tigris near Mosul, © Naturhistorisches Museum Wien, photo E. Lavergne.

Figure 24. *Carasobarbus luteus*, live specimen from Nahr al Khābūr.

file is almost straight to convex and has a hump near the nostrils in juvenile specimens. The mouth is sub-terminal. The barbels are short and stout. The maximum body depth is usually greater than the head length (Fig. 12). Usually one pair of barbels is present, but about 10 % of the specimens have two pairs of barbels (Table 2). The eyes are at the back of the anterior half of the head. They are big and slightly protuberant. The morphometric characters are summarised in Table 1.

The dorsal fin usually has four unbranched and eight to 11 branched rays (Table 3). In specimens from the Tigris-Euphrates drainage system the last unbranched ray of the dorsal fin is strong with only the tip being flexible and it is about as long as the head. It is shorter and less ossified in Iranian populations (Fig. 4). The anal fin usually has three unbranched rays and five to seven branched rays (Table 4).

There are 25 to 33 scales in the lateral line (Table 5), 3.5 to 6 scales above the lateral line (Table 6), 3 to 5.5 scales below the lateral line (Table 7) and 10 to 13 scales around the least circumference of the caudal peduncle (Table 8). The scales are shown in Fig. 5.

The pharyngeal teeth count is 2.3.5-5.3.2 in 26 specimens, 2.3.4-5.3.2 in two specimens, 2.3.5-4.3.2 in one specimen, 2.3.5-5.3.3 in one specimen, 1.3.5-5.3.2 in one specimen, 2.3.5- in one specimen and 2.3.4- in one specimen. The pharyngeal teeth are hooked at their tips (Fig. 6).

Live specimens are silvery to olive and sometimes have yellowish fins (Fig. 24). Ethanol-preserved specimens are light yellowish brown to grey. In most cases the back is darker than the rest of the body. Some of the lighter coloured specimens have a salmon hue, others are silvery. The fins are yellowish brown to grey. Juveniles have a dark spot on the sides of the caudal peduncle.

Carasobarbus luteus from Ḩelleh, Kol, Mahārlū and Mand populations: The last unbranched ray of the dorsal fin is shorter and less well ossified. It is pronouncedly shorter than the head (Fig. 4). The mouth is wider and the body is not as high-backed as in specimens from the Tigris-Euphrates system (Fig. 12).

Carasobarbus luteus from Rūdkhāneh-ye Naband basin: In this population all specimens examined had two pairs of barbels (Table 2). The anterior pair is longer than in specimens from Tigris-Euphrates system with two pairs. The last unbranched ray in the dorsal fin is considerably shorter than the head (Fig. 4) and comparatively weak. Compared with specimens from Tigris-Euphrates system, the dorsal and ventral fins tend to be slightly further away from the head. The head is longer and the body not as high backed as in specimens from Tigris-Euphrates system (Fig. 12). The general body shape (Fig. 25) resembles that of *C. apoensis* and *C. canis*. Some of the gill rakers are y-shaped in the largest specimen examined.

Carasobarbus luteus, except the population from Rūdkhāneh-ye Naband, differs from all congeners, except *C. apoensis*, in having one instead of two pairs of barbels. It differs from *C. apoensis*, *C. canis*, *C. chantrei*, *C. fritschii*, *C. harterti* and *C. kosswigi* in modally having 28 scales in the lateral line vs. 30, 32, 34, 34, 34 and 33 respectively. It differs from *C. kosswigi* and *C. sublimus* in having a crescent-shaped lower lip without median lobe vs. a spatulate lower lip with median lobe and from *C. exulatus*, *C. fritschii* and *C. harterti* in modally having 10 rather than nine branched dorsal-fin rays. All populations, except the one from Rūdkhāneh-ye Naband differ from *C. apoensis* in having a shorter head and a higher back. The population from Rūdkhāneh-ye Naband is very similar to *C. apoensis* in body shape, but differs in having two as compared to one pair of barbels.

Distribution. *Carasobarbus luteus* has a much greater range than any of its congeners and its distribution area is fragmented, resulting in several isolated populations. It is widespread all over the Tigris-Euphrates drainage system, and occurs in the rivers of south-western Iran (Fig. 7). The Nahr al Quwayq population, from one of the sites of the type locality, is probably extirpated due to drought and pollution (Krupp 1980, Krupp 1983b). There are only few, mostly older, records from the Orontes (Krupp 1985c, Krupp 1987). During recent fieldwork *C. luteus* was not found there. Because *C. chantrei* is still widespread and abundant in many parts of the Orontes, it is unlikely

Figure 25. *Carasobarbus luteus*, specimen (CMNFI 79-0187) from Rūdkhāneh-ye Sarzeh.

that *C. luteus* disappeared due to habitat degradation. It might have been driven out by competition with *C. chantre*i or records were based on misidentifications or mislabelled specimens. One specimen (NMW 10827) is reported from Damascus. Because *C. luteus* does not occur in the Damascus basin and it is highly unlikely that it ever occurred there, the origin of this specimen is unclear.

Habitats and biology. *Carasobarbus luteus* is mainly herbivorous. It feeds on algae, aquatic plants, detritus and small invertebrates, the main feeding period is at noon, but food is also taken at night (Naama and Muhsen 1986). The intestine is long (Ali 1986). The maximum size is 38 cm total length and 750 g, but normally they are smaller than 35 cm and weight less than 500 g (Ahmed 1982). They reach maturity at the age of one or two years and at a size of about 14 cm; the spawning period is June and July in the Tigris-Euphrates system, the eggs are spawned among reeds, roots or other aquatic vegetation and fecundity is high (Al Hazzaa and Hussein 2003a).

This species can tolerate saline waters to some degree (Al-Hassan and Muhsin 1986, Mohamed et al. 1993) and is of commercial importance due to its size and abundance (Ahmed 1982, Barak and Mohamed 1983, Krupp and Schneider 2008).

There are attempts on aquaculture of this species. The stickiness of the eggs can be lowered by several chemical treatments for this purpose (Al Hazzaa and Hussein 2003b). During spawning males get reddish brown in the anterior part of the body and greenish at the caudal peduncle while females are less colourful (Al Hazzaa and Hussein 2003a). Males can produce series of sharp clicking noises which do not seem to be associated with aggressive behaviour (Al Hazzaa and Hussein 2003a).

Larvae hatch at 64 degree-days in well oxygenated water and the eyes are still without pigments at this stage. The development is similar to that of other cyprinids (Al Hazzaa and Hussein 2003a). Ahmed et al. (1984) studied the reproductive biology of *C. luteus*.

Conservation status. *Carasobarbus luteus* is widespread and abundant in the Tigris-Euphrates system. Peripheral populations, like those in smaller Iranian rivers and the Nahr al Quwayq in Syria are more threatened or have already been extirpated (see above).

Discussion. *Carasobarbus luteus* was described as *Systomus luteus* by Heckel (1843). Heckel (1843) listed Orontes, Tigris, Aleppo and Mosul as type localities. As all but one of the type specimens are either from the Tigris-Euphrates system or from the Nahr al Quwayq and Aleppo is located on the Nahr al Quwayq and not on the Orontes, Heckel may have confused these two rivers. One of the type specimens (NMW 10827) is from “Damascus” and can not be attributed to any of the relevant drainage systems. By designating NMW 54253:2 as lectotype we fix the Tigris near Mosul as type locality for *S. luteus*. The same confusion exists for the type localities of *Systomus albus*, which was also described from Tigris and Orontes in the same publication. A few years later *Systomus albus* var. *alpina* was described from the Daryācheh-ye Parīshān (Heckel 1847). These three taxa where later synomymised and placed in the genus *Barbus* (Günther 1868). Sauvage (1882, 1884) accepted *C. luteus* and *C. albus* as valid species and transferred them to the genus *Barynotus*. Later, both species where synonymised again and transferred to the genus *Barbus*, subgenus *Puntius* (Misra 1947) or the genus *Puntius* (Menon 1956). Ladiges (1960) synonymised both species under the name *Barynotus albus*. Because Günther (1868) had previously selected *luteus* as the valid species name, he is to be considered the first revising author and Ladiges’ action is not valid. Kähsbauer (1963) lists the species under two different generic names: *Barbus* (as *B. luteus*) and *Systomus* (as *S. albus* var. *alpina*). Karaman (1971) erected the new genus *Carasobarbus* for this species. This met mixed acceptance. While some authors accepted the new taxonomic position (e.g. Wossughi 1978, Bianco and Banarescu 1982, Ahmed et al. 1984, Naama and Muhsen 1986), others did not embrace it (e.g. Banister and Clarke 1977, Krupp 1985a, c, Coad 1995, Coad 1996) until the revision by Ekmekçi and Banarescu (1998). Fowler (1976) placed *C. luteus* in the genus *Barbellion*. Tsigenopoulos et al. (2010) used *Barbus* subgenus *Carasobarbus. Barbus parieschanica* was described from Daryācheh-ye Parīshān (Wossughi et al. 1983). In the same publication the species name is also spelled *B. parschanica*, but *B. parieschanica* is probably the intended spelling (Coad 1995). Coad (1995) as the first revising author fixed *B. parieschanica* as the correct original spelling. *Barbus parieschanica* is a synonym of *C. luteus*. The ‘Catalog of Fishes’ lists RMNH 2463 as possible syntype of *S. luteus* and RMNH 2464 of *S. albus* var. *alpina* (Eschmeyer 2011). We did not examine these specimens.

We do not think that the population at Rūdkhāneh-ye Naband should be elevated to specific rank, because the number of specimens available is too low. We provisionally consider it an atypical population of *C. luteus* that might have been affected by bottleneck effects and accelerated morphological change, due to the restricted size and extreme conditions (high salinity and temperature) of its habitat. It would be very interesting to collect more samples for morphological studies and molecular sequence analysis.

In spite of some morphometric differences, *C. luteus* populations of Tigris-Euphrates system and Iran belong to the same species (Borkenhagen et al. 2011); specimens from Rūdkhāneh-ye Naband were not included in that study.

Carasobarbus luteus and *C. apoensis* are closely related to each other (KB, unpublished data) and *C. apoensis* might be the ecologically specialised sister species of *C. luteus*, that is adapted to the environmental conditions of the wadi ecosystems of the Al Ḩijāz mountains.

Carasobarbus sublimus (Coad & Najafpour, 1997)

http://species-id.net/wiki/Carasobarbus_sublimus

Barbus sublimus Coad and Najafpour 1997: 274.

Material. Type material. Holotype of *Barbus sublimus*: CMNFI 1995-0009, Iran, Rūdkhāneh-ye A'lā near Pol-e Tīghen (N31°23'30", E49°53'0"), B. W. Coad et al., 20 Sep 1995, not examined.

Paratypes of *Barbus sublimus*: CMNFI 95-0009a, 1, same data as holotype. - CMNFI 95-0010, 1, same data as holotype, not examined. - CMNFI 95-0011, 3, Iran, Rūdkhāneh-ye A'lā near Pol-e Tīghen (N31°23'30", E49°53'0"), G. Eskanderi, Dec 1994, only one specimen examined.

Non-type material. Rūdkhāneh-ye Kashgān. CMNFI 79-0277, 1, Iran, Rūdkhāneh-ye Kashgān at Harpul Kashkow, 50 km from Khorramābād (N33°30'0", E47°59'30"), K. Evans and H. Assadi, 5 Jul 1977.

Rūdkhāneh-ye Zohreh drainage. ZM-CBSU 5781-5786, 6, Iran, Rūdkhāneh-ye Fahlīān at Nūrābād [N30°6'51", E51°31'18"], H. R. Esmaeili et al. - SMF 33117, 3, Iran, Rūdkhāneh-ye Fahlīān (N30°11'10", E51°31'14"), K. Borkenhagen et al., 29 Nov 2007. - SMF 33118, 6, Iran, Rūdkhāneh-ye Fahlīān (N30°11'9", E51°31'15"), N. Alwan et al., 29 Feb 2008.

Diagnosis. Two pairs of barbels; 27 to 29 scales in the lateral line, 12 scales around the least circumference of the caudal peduncle; last unbranched dorsal-fin ray about as long as the head; mouth narrow, lower jaw spatulate and median lobe present on lower lip.

Description. A nuchal hump is not developed. The maximum body depth is at the anterior end of the dorsal fin base. The ventral profile of the head is almost straight; the dorsal profile is convex and evenly curved (Figs 26, 27). The maximum body depth is greater than the head length (Fig. 12). The mouth is inferior, narrow, the lips are thick and the lower jaw is spatulate with a horny sheath and a median lobe on the lower lip. The two pairs of barbels (Table 2) are well developed. The eyes are at the posterior end of the anterior half of the head. Some morphometric characters are summarised in Table 1.

The dorsal fin usually has four unbranched and nine or 10 branched rays (Table 3). The last unbranched ray of the dorsal fin is weakly ossified and about as long as the head (Fig. 4). The anal fin usually has three unbranched and six branched rays (Table 4) and its base is surrounded by a sheath of scales. Pectoral, ventral and anal fins are longer than in all other *Carasobarbus* species (Table 1).

There are 27 to 29 scales in the lateral line (Table 5), 4.5 or 5.5 scales above the lateral line (Table 6), 3.5 to 5.5 scales below the lateral line (Table 7) and 12 scales around the least circumference of the caudal peduncle (Table 8). The scales are shown in Fig. 5.

The pharyngeal teeth count is 2.3.4-5.3.2, 2.3.4-5.3.1 or 3.3.4-4.3.3 (Coad and Najafpour 1997). The pharyngeal bones available were too small for photography but are very similar to those of *C. kosswigi* (Fig. 6).

Live specimens from Rūdkhāneh-ye Fahlīān are silvery with hyaline fins (Fig. 27). Live specimens from Rūdkhāneh-ye A'lā are silvery with a slightly darker back, the

Figure 26. *Carasobarbus sublimus*, paratype (CMNFI 95-0011) from Rūdkhāneh-ye A'lā, photo S. Tränkner.

Figure 27. *Carasobarbus sublimus*, live specimen from Rūdkhāneh-ye Fahlīān.

scales have dark pigments on their hind margin; pectoral, ventral and anal fins have a yellow to orange hue, which is most obvious with fins folded back; dorsal and caudal fins are grey or hyaline (Coad and Najafpour 1997). Ethanol-preserved specimens are yellowish brown with a somewhat darker back and juveniles have a dark spot on the sides of the caudal peduncle.

Carasobarbus sublimus differs from all congeners, except *C. kosswigi*, by having a spatulate lower jaw with a median lobe on the lower lip vs. a crescent shaped lower jaw and a lower lip without median lobe. It differs from *C. kosswigi* by having 27 to 29 scales in the lateral line vs. 32 to 38 and modally 12 scales around the least circumference of the caudal peduncle vs. 14 and by having a shorter and less ossified unbranched last dorsal-fin ray.

Distribution. This species is known from Rūdkhāneh-ye A'lā, Rūdkhāneh-ye Fahlīān and possibly Rūdkhāneh-ye Kashgān (see discussion) in south-western Iran (Fig. 7).

Habitats and biology. *Carasobarbus sublimus* is adapted to streams with fast currents with water flowing over hard substrate (Coad and Najafpour 1997). The biggest specimen known has a SL of 115 mm (Coad and Najafpour 1997).

Conservation status. Little is known about the conservation status of *C. sublimus*, but because this species is dependent on fast-flowing water, it is probably impacted by the construction of dams.

Discussion. *Carasobarbus sublimus* was described in the genus *Barbus* and aligned with *C. apoensis*, *C. canis*, *C. chantrei*, *C. exulatus*, *C. kosswigi* and *C. luteus* in the original description (Coad and Najafpour 1997). Coad recommends the use of the genus *Kosswigobarbus* for this species (Coad 2011). It was transferred to *Carasobarbus*, based on morphological characters and close genetic relationship (Borkenhagen et al. 2011).

Locality data for CMNFI 79-0277 is not beyond doubt, because this lot was mentioned as *C. kosswigi* in the original description of *C. sublimus* (Coad and Najafpour 1997). According to morphometric and meristic characters (scales in lateral line, above lateral line and around the least circumference of the caudal peduncle; length of dorsal, pectoral, ventral and anal fin) this specimen is within the range of *C. sublimus* and outside the range of *C. kosswigi*. It might be an aberrant specimen or it might have been accidentally swaped with CMNFI 1995-0010 (a specimen of similar size from the same locality as the types of *C. sublimus*). We had no opportunity to examine CMNFI 1995-0010. Though we think it is unlikely that *C. kosswigi* and *C. sublimus* occur sympatrically, for the time being we consider it to be a possible record of *C. sublimus* from the Rūdkhāneh-ye Kashgān.

Hybrids

Two putative intergeneric hybrids of *C. canis* with other cyprinids are known, one with *Capoeta damascina* (Valenciennes in Cuvier and Valenciennes 1842) and one with *Luciobarbus longiceps* (Valenciennes in Cuvier and Valenciennes 1842).

Carasobarbus canis × *Capoeta damascina*

The hybrids are intermediate in many morphometric and meristic characters (Mir et al. 1988). The head resembles that of *Capoeta damascina*, the mouth is more inferior than in *C. canis* and the lips are thicker. The scales are larger than in *Capoeta damascina* and smaller than in *C. canis* (Mir et al. 1988, Fig. 28). Oogonia and spermatogonia coexist in the gonads of both sexes and the development of the gametes is disturbed, thus the hybrids are sterile (Fishelson et al. 1996).

Carasobarbus canis × *Luciobarbus longiceps*

These hybrids are intermediate in many morphometric and meristic characters (Krupp 1985b, Fig. 29). The lateral line scale count matches that of *C. canis*. Heterologous

Figure 28. *Carasobarbus canis* x *Capoeta damascina*, aquarium photograph of SMF 17184, originally from Nahr az Zarqā'.

Figure 29. Holotype of *Barbus continii* = *Carasobarbus canis* x *Barbus longiceps* preserved specimen (SL=165 mm), Lake Tiberias (MCSN 22300).

cells are present in the gonads of this hybrid but the gametes mature normally (Fishelson et al. 1996). This hybrid was described as *Barbus continii* Vinciguerra, 1926 from a single specimen (Krupp 1985b).

Key to the *Carasobarbus* species

1 Branched dorsal-fin rays 9, Yemen and NW Africa **2**
– Branched dorsal fin rays 10 .... **4**
2 Scales around least circumference of the caudal peduncle 10–12, Yemen .... ***C. exulatus***
– Scales around least circumference of the caudal peduncle 13–20, Morocco **3**
3 Dorsal profile of head convex, more than 15 % of the last unbranched dorsal-fin ray flexible .... ***C. fritschii***
– Dorsal profile of head straight, less than 15 % of the last unbranched dorsal-fin ray flexible .... ***C. harterti***
4 Lower jaw spatulate and lower lip with a median lobe **5**
– Lower jaw u-shaped or crescent shaped and lower lip without median lobe..... **6**

5 Scales around the least circumference of the caudal peduncle 12, 27–29 scales in the lateral line, head about as long as dorsal fin...................... ***C. sublimus***

– Scales around the least circumference of the caudal peduncle 12–16, 32–38 scales in the lateral line, dorsal fin longer than the head .... ***C. kosswigi***

6 Modally 14 (12–16) scales around the least circumference of the caudal peduncle.. ***C. chantrei***

– Modally 12 (10–14) scales around the least circumference of the caudal peduncle **7**

7 Usually two pairs of barbels, Jordan River and adjacent waterbodies .... ***C. canis***

– Usually one pair of barbels, Mesopotamia, southern Iran and Arabia.......... **8**

8 Head about as long as body depth, dorsal fin markedly shorter than head, modally 30 scales in the lateral line, Western Arabian Peninsula........ ***C. apoensis***

– Head shorter than body depth, dorsal fin about as long as head (except in Iranian populations), modally 28 scales in lateral line, Mesopotamia and southern Iran.. ***C. luteus***

Authors contribution

KB and FK developed the concept for this study and conducted field research independent of each other. KB collected, analysed and interpreted the data presented in this study and prepared the manuscript. FK reviewed the manuscript.

Acknowledgements

We are grateful to James Maclaine, Oliver Crimmen, Patrick Campbell (BMNH); Hamid Reza Esmaeili (ZM-CBSU); Guy Duhamel, Romain Causse, Patrice Pruvost, Claude Ferrara, Zora Gabsi (MNHN); Ernst Mikschi, Helmut Wellendorf, Christa Prenner, Matthias Reithofer (NMW) and Horst Wilkens (ZMH) for making the collections under their care available for study and to Jörg Freyhof for providing additional specimens.

Phil Hurst, Edouard Lavergne and Sven Tränkner contributed specimen photos. Nina Bogutskaya and Florian Wicker offered valuable comments on the manuscript. Eva Feltkamp prepared the maps.

We thank Nisreen Alwan, Zuhair Amr, Abdelhamid Azeroual, Mehrgan Ebrahimi, Hamid Reza Esmaeili, Jörg Freyhof, Christiane Frosch, Mehdi Ghanbari-Fardi, Zeinab Gholami, Abbas Kazemi, Masoumeh Malek, Majid Moradmand, Hossein Parsa, Sobhan Rahimi, Hassan Rahimian, Bettina Reichenbacher, Hassan Salehi, Alireza Sari, Adwan Shehab, Wolfgang Schneider, Azad Teimori, Florian Wicker and Uwe Zajonz for help with organising and participating in fieldwork in Iran, Jordan, Morocco, Saudi Arabia, Syria and Yemen.

Part of the fieldwork was funded by the German Academic Exchange Service (DAAD), in the framework of the project "Establishment of a Middle Eastern Biodiversity Network”. Field work in Yemen was supported by the Coastal Zone Management Pilot Project of the Environment Protection Authority Yemen and the World Bank and received financial support from grant TF 023492 of the Global Environment Facility. Field research in Saudi Arabia and Yemen was funded by the Saudi Wildlife Authority (SWA, formerly National Commission for Wildlife Conservation and Development, NCWCD) and King Abdulaziz City for Science and Technology (KACST), Riyadh, Saudi Arabia.

This research received support from the SYNTHESYS Project, which is financed by European Community Research Infrastructure Action under the FP6 “Structuring the European Research Area” Programme (grants AT-2427 and FR-3580).

The FAZIT Foundation funded two research visits to the BMNH.

The study was supported by the Biodiversity and Climate Research Centre (BiK-F), Frankfurt, which is part of research funding programme “LOEWE”.

References

Ahmed HA (1982) Crowth [sic] of the cyprinid fish, *Barbus luteus* (Heckel) in Tharthar Reservoir, Iraq. Bulletin of Basrah Natural History Museum 5: 3–15.

Ahmed HA, Al-Hammar MA, Al-Adhub AHY (1984) The reproductive biology of *Carasobarbus luteus* (Pisces, Cyprinidae) in Al-Hammar Marsh, Iraq. Cybium 8 (4): 69–80.

Al Hazzaa R, Hussein A (2003a) Initial observations in himri (*Barbus luteus*, Heckel) propagation. Turkish Journal of Fisheries and Aquatic Sciences 3: 41–45.

Al Hazzaa R, Hussein A (2003b) Stickiness elimination of himri barbel (*Barbus lutes*, Heckel) eggs. Turkish Journal of Fisheries and Aquatic Sciences 3: 47–50.

Al-Hassan LAJ, Muhsin KA (1986) The presence of *Barbus luteus* and *Heteropneustes fossilis* in the Khor al Zubair, in the North-West of the Arabian Gulf. Zoology in the Middle East 1: 116–119. doi: 10.1080/09397140.1986.10637531

Ali AM (1986) Morphometric characteristics of the khimri, *Barbus luteus* (Cyprinidae), from Tartar Reservoir and the Tigris River (Iraq). Journal of Ichthyology 25 (5): 168–171.

Alkahem AF, Behnke RJ (1983) Freshwater fishes of Saudi Arabia. Fauna of Saudi Arabia 5: 545–567.

Al-Safadi MM (1995) A pilot study of lake Ma’rib, Yemen. Hydrobiologia 315 (3): 203–209. doi: 10.1007/BF00051950

Attaala AM, Rubaia BS (2005) First record of the eel *Anguilla bengalensis* from Arabia with notes on freshwater fishes from Hadramout, Yemen. Zoology in the Middle East 34: 35–44. doi: 10.1080/09397140.2005.10638080

Azeroual A, Crivelli AJ, Yahyaoui A, Dakki M (2000) L’ichtyofaune des eaux continentals du Maroc. Cybium 23 (3): 17–22.

Banarescu P (1977) Position zoogéographique de l’ichthyofaune d’eau douces d’Asie occidentale. Cybium 2: 35–55.

Banister KE (1980) The fishes of the Tigris and Euphrates rivers. In: Rzóska J, Talling JF (Eds) Euphrates and Tigris, Mesopotamien Ecology and Destiny. Junk, The Hague, 95–106. doi: 10.1007/978-94-009-9171-2_9

Banister KE, Clarke MA (1977) The freshwater fishes of the Arabian Peninsula. Journal of Oman Studies (Special Report): 111–154.

Barak NAA, Mohamed AM (1983) Biological study of the cyprinid fish, *Barbus luteus* (Heckel) in Garma Marshes. Journal of Biological Sciences. Research Baghdad 14(2): 53–70.

Battalgil F (1942) Türkiye tatlısu balıkları hakkında. Contribution à la connaissance des poissons des eaux douces de la Turquie. Revue de la Faculté des Sciences de l'Université d'Instanbul, Série B: Sciences Naturelles 7(4): 287–306.

Ben-Tuvia A (1978) Fishes. In: Serruya C (Ed) Lake Kinneret, 407–430.

Berg LS (1949) Presnovodnye ryby Irana i sopredel'nykh stran [Freshwater fishes of Iran and adjacent countries]. Trudy Zoologicheskogo Instituta Akademii Nauk SSSR 8: 783–858.

Berrebi P (1981) Contribution a l'etude du sous-genre *Labeobarbus*. Bulletin de l'Institut Scientifique, Rabat 5: 59–72.

Bianco PG, Banarescu P (1982) A contribution to the knowledge of the Cyprinidae of Iran (Pisces, Cypriniformes). Cybium 6(2): 75–96.

Bleeker P (1859) Negende bijdrage tot de kennis der vischfauna van Banka. Natuurkundig Tijdschrift voor Nederlandsch Indië 18: 359–378.

Borkenhagen K, Esmaeili HR, Mohsenzadeh S, Shahryari FGA (2011) The molecular systematics of the *Carasobarbus* species from Iran and adjacent areas, with comments on *Carasobarbus albus* (Heckel, 1843). Environmental Biology of Fishes 91(3): 327–335. doi: 10.1007/s10641-011-9787-1

Boulenger GA (1902) Description of two new cyprinid fishes from Morocco. Annals and Magazine of Natural History (Series 7) 9(50): 124–125.

Boulenger GA (1905) Another new *Barbus* from Morocco. Novitates Zoologicae. A Journal of Zoology in Connection with the Tring Museum 12: 505.

Boulenger GA (1911) Catalogue of the fresh-water fishes of Africa in the British Museum (Natural History). London.

Boulenger GA (1919) La distribution en Afrique des Barbeaux du sous-genre *Labeobarbus*. Comptes Rendus Hebdomadaires des Seances de l'Academie des Sciences 169: 1016–1018.

BCEAW (2002) Conservation Assessment and Management Plan (CAMP) for the Threatened Fauna of Arabia's Mountain Habitat. Final Report. The Breeding Centre for Endangered Arabian Wildlife, Sharjah; UAE.

Coad BW (1982) A re-description and generic re-assignment of *Kosswigobarbus kosswigi* (Ladiges, 1960), a cyprinid fish from Turkey and Iran. Mitteilungen aus dem Hamburgischen Zoologischen Museum und Institut 79: 263–265.

Coad BW (1995) Freshwater fishes of Iran. Acta Scientiarum Naturalium, Brno 29(1): 1–64.

Coad BW (1996) Zoogeography of the fishes of the Tigris-Euphrates Basin. Zoology in the Middle East 13: 51–70. doi: 10.1080/09397140.1996.10637706

Coad BW (2011) Freshwater Fishes of Iran. http://www.briancoad.com

Coad BW, Najafpour N (1997) *Barbus sublimus*, a new species of cyprinid fish from Khuzestan Province, Iran. Ichthyological Exploration of Freshwaters 7(3): 273–278.

Colli L, Paglianti A, Berti R, Gandolfi G, Tagliavini J (2009) Molecular phylogeny of the blind cavefish *Phreatichthys andruzzii* and *Garra barreimiae* within the family Cyprinidae. Environmental Biology of Fishes 84(1): 95–107. doi: 10.1007/s10641-008-9393-z

Crivelli AJ (2006a) *Barbus canis*. In: IUCN (2012) IUCN Red List of Threatened Species. Version 2012.2. http://www.iucnredlist.org

Crivelli AJ (2006b) *Barbus chantrei*. In: IUCN (2012) IUCN Red List of Threatened Species. Version 2012.2. http://www.iucnredlist.org

Crivelli AJ (2006c) *Barbus fritschii*. In: IUCN (2012) IUCN Red List of Threatened Species. Version 2012.2. http://www.iucnredlist.org

Crivelli AJ (2006d) *Barbus harterti*. In: IUCN (2012) IUCN Red List of Threatened Species. Version 2012.2. http://www.iucnredlist.org

Crivelli AJ (2006e) *Barbus paytonii*. In: IUCN (2012) IUCN Red List of Threatened Species. Version 2012.2. http://www.iucnredlist.org

Cuvier G, Cloquet H (1816) Le règne animal distribué d'après son organisation pour servir de base à l'histoire naturelle des animaux et d'introduction à l'anatomie comparée. Les reptiles, les poissons, les mollusques et les annélides, 532 pp.

Cuvier G, Valenciennes A (1842) Histoire naturelle des poissons. Volume 16, 472 pp.

Doadrio I (1994) Freshwater fish fauna of North Africa and its biogeography. Annales du Musee royale de l'Afrique Centrale, Zoologie 275: 21–34.

Durand JD, Tsigenopoulos CS, Ünlü E, Berrebi P (2002) Phylogeny and biogeography of the family Cyprinidae in the Middle East inferred from cytochrome *b* DNA - Evolutionary significance of this region. Molecular Phylogenetics and Evolution 22(1): 91–100. doi: 10.1006/mpev.2001.1040

Ekmekçi FG, Banarescu P (1998) A revision of the generic position of *Barynotus* (*Systomus*) *verhoeffi*, and the validity of the genera *Carasobarbus*, *Kosswigobarbus* and *Mesopotamichthys* (Pisces, Cyprinidae). Folia Zoologica 47 (Suppl. 1): 87–96.

El Gharbi S, Lambert A, Berrebi P (1993) Le genre *Barbus* (sous-genres *Barbus* et *Labeobarbus*) au Maroc. Génétique et parasitologie. Cahiers d'éthologie 13(2): 223–226.

Eschmeyer WN (Ed) (2011) Catalog of Fishes. California Academy of Sciences. Electronic version http://research.calacademy.org/research/ichthyology/catalog/fishcatmain.asp [14 July 2011]

Fishelson L, Goren M, Vuren J van, Manelis R (1996) Some aspects of the reproductive biology of *Barbus* spp., *Capoeta damascina* and their hybrids (Cyprinidae, Teleostei) in Israel. Hydrobiologia 317 (1): 79–88. doi: 10.1007/BF00013728

Fowler HW (1976) A Catalog of World Fishes (XXV). Quarterly Journal of the Taiwan Museum 29 (3&4): 277–396.

Fricke R, Eschmeyer WN (2013) Guide to Fish Collections. California Academy of Sciences. Electronic version. http://research.calacademy.org/research/ichthyology/catalog/collections.asp [accessed 15 May 2013]

Goren M (1974) The freshwater fishes of Israel. Israel Journal of Zoology 23: 67–118.

Goren M, Ortal R (1999) Biogeography, diversity and conservation of the inland water fish communities in Israel. Biological Conservation 89 (1): 1–9. doi: 10.1016/S0006-3207(98)00127-X

Gorshkova G, Gorshkov S, Golani D (2002) Karyotypes of *Barbus canis* and *Capoeta damascina* (Pisces, Cyprinidae) from the Middle East. Italian Journal of Zoology 69(3): 191–194. doi: 10.1080/11250000209356459

Gray JE (1830-35) Illustrations of Indian zoology; chiefly selected from the collection of Major-General Hardwicke, F.R.S. 20 parts in 2 vols.

Günther A (1864) Report on a collection of reptiles and fishes from Palestine. Proceedings of the Zoological Society of London 1864.

Günther A (1868) Catalogue of the fishes in the British Museum. Catalogue of the Physostomi, containing the families Heteropygii, Cyprinidae, Gonorhynchidae, Hyodontidae, Osteoglossidae, Clupeidae, Chirocentridae, Alepocephalidae, Notopteridae, Halosauridae, in the collection of the British Museum.

Günther A (1874) Notice of some new species of fishes from Morocco. Annals and Magazine of Natural History 13(75): 230–232. doi: 10.1080/00222937408680848

Günther A (1901) Second notice of new species of fishes from Morocco. Novitates Zoologicae. A Journal of Zoology in Connection with the Tring Museum 8: 367–368.

Günther A (1902) Third notice of new species of fishes from Morocco. Novitates Zoologicae. A Journal of Zoology in Connection with the Tring Museum 9: 446–448.

Hamidan N (2004) The freshwater fish fauna of Jordan. Denisia 14: 385–394.

Hamilton F (1822) An account of the fishes found in the river Ganges and its branches. Printed for A. Constable and company [etc., etc.]. Edinburgh, 426 pp.

Heckel JJ (1843) Ichthyologie. In: Russegger J von (Ed) Reisen in Griechenland, Unteregypten, im nördlichen Syrien und südöstlichen Kleinasien mit besonderer Rücksicht auf die naturwissenschaftlichen Verhältnisse der betreffenden Länder, unternommen in dem Jahre 1836, Stuttgart.

Heckel JJ (1847) Die Fische Persiens, gesammelt von Theodor Kotschy. In: Russegger J von (Ed) Reisen in Europa, Asien und Africa unternommen in den Jahren 1835 bis 1841.

Hubbs CL, Lagler KF (1958) Fishes of the Great Lakes Region. The University of Michigan Press. Ann Arbor, 213 pp.

ICZN (2012) International Commission on Zoological Nomenclature. Fourth Edition. The International Trust for Zoological Nomenclature. http://www.nhm.ac.uk/hosted-sites/iczn/code/

Kähsbauer (1963) Zur Kenntnis der Ichthyofauna von Iran. Annalen des Naturhistorischen Museums in Wien 66: 317–355.

Karaman MS (1971) Süßwasserfische der Türkei. 8. Teil: Revision der Barben Europas, Vorderasiens und Nordafrikas. Mitteilungen aus dem Hamburgischen Zoologischen Museum und Institut 67: 175–254.

Krupp F (1980) Die Verbreitung syrischer Süßwasserfische unter dem Einfluß des Menschen. Natur und Museum 110 (6): 157–164.

Krupp F (1983a) Freshwater fishes of Saudi Arabia and adjacent regions of the Arabian Peninsula. Fauna of Saudi Arabia 5: 568–636.

Krupp F (1983b) Recent changes in the distribution of Syrian freshwater fishes. Roczniki Nauk Rolniczych HT 100 (3): 79–88.

Krupp F (1985a) *Barbus chantrei* (Sauvage 1882), a valid species of cyprinid fish from the northern Levant. Senckenbergiana Biologica 66 (1/3): 17–25.

Krupp F (1985b) *Barbus continii* Vinciguerra 1926, a possible natural hybrid of *Barbus canis* and *Barbus longiceps* (Pisces: Osteichthyes: Cyprinidae). Senckenbergiana Biologica 66 (1/3): 9–15.

Krupp F (1985c) Systematik und Zoogeographie der Süßwasserfische des levantinischen Grabenbruchsystems und der Ostküste des Mittelmeeres. PhD thesis, University of Mainz, Mainz, Germany, VII+215+169 pp.

Krupp F (1987) Freshwater ichthyography of the Levant. In: Krupp F, Schneider W, Kinzelbach R (Eds) Proceedings of the Symposium on the Fauna and Zoogeography of the Middle East, Mainz 1985. Beihefte zum Tübinger Atlas des Vorderen Orients, Wiesbaden, A 28: 229–237.

Krupp F, Schneider W (1989) The fishes of the Jordan River drainage basin and Azraq Oasis. Fauna of Saudi Arabia 10: 347–416.

Krupp F, Schneider W (1991) Bestandserfassung der rezenten Fauna im Bereich des Nahr al-Ḫābūr. In: Kühne H (Ed) Die rezente Umwelt von Tall Šēḫ Ḥamad und Daten zur Umweltrekonstruktion der assyrischen Stadt Dūr-Katlimmu 1, Berlin, 69-85.

Krupp F, Schneider W (2008) Die Fischfauna des Nahr al-Ḫābūr, Nordost-Syrien. In: Kühne H (Ed) Umwelt und Subsistenz der assyrischen Stadt Dūr-Katlimmu am unteren Ḫābūr 8, Harrassowitz-Verlag, Wiesbaden, 41–51.

Ladiges W (1960) Süsswasserfische der Türkei. I. Teil Cyprinidae. Mitteilungen aus dem Hamburgischen Zoologischen Museum und Institut 58: 105–150.

Leggatt RA, Iwama GK (2003) Occurrence of polyploidy in the fishes. Reviews in Fish Biology and Fisheries 13(3): 237–246. doi: 10.1023/B:RFBF.0000033049.00668.fe

Machordom A, Doadrio I (2001) Evolutionary history and speciation modes in the cyprinid genus *Barbus*. Proceedings of the Royal Society of London Series B - Biological Sciences 268(1473): 1297–1306. doi: 10.1098/rspb.2001.1654

McClelland J (1839) Indian Cyprinidae. Asiatic Researches 19(2): 217–471.

Menon MAS (1956) On a third collection of fish from Iraq. Records of the Indian Museum 54: 139–157.

Mir S (1990) Taxonomical studies and the geographical distribution of freshwater fishes of Jordan. Bangladesh Journal of Zoology 18(2): 157–175.

Mir S, Al-Absy A, Krupp F (1988) A new natural intergeneric cyprinid hybrid from the Jordan River drainage, with a key to the large cyprinids of the southern Levant. Journal of Fish Biology 32(6): 931–936. doi: 10.1111/j.1095-8649.1988.tb05436.x

Misra KS (1947) On a second collection of fish from Iraq. Records of the Indian Museum 45: 115–127.

Mohamed ARM, Al-Hassan LAJ, Ali TS (1993) The presence of a cyprinid fish, *Barbus luteus* in marine waters of Iraq. Arquivos do Museu Bocage, Nova Serie 2(25): 415–416.

Naama AK, Muhsen KA (1986) Feeding periodicites of the mugilid *Liza abu* (Heckel) and Cyprinid *Carasobarbus luteus* (Heckel) from Al-Hammar Marsh, Southern Iraq. Indian Journal of Fisheries 33(3): 347–350.

Pellegrin J (1912) Reptiles, Batraciens et Poissons du Maroc (mission de Mme Camille du Gast). Bulletin de la Société Zoologique de France 37: 255–262.

Pellegrin J (1921) Les poissons des eaux douces de l'Afrique du Nord française Maroc: Algérie, Tunisie, Sahara. Mémoires de la Société des Sciences Naturelles du Maroc 1 (2).

Pellegrin J (1939) Les barbeaux de l'Afrique du nord Française: description d'une espèce nouvelle. Bulletin de la Société des sciences naturelles du Maroc 19: 1–10.

Pellegrin JM (1919) Sur la faune ichthyologique des eaux douces du Maroc. Comptes rendus hebdomadaires des séances de l'Académie des sciences 169: 809–811.

Rüppell E (1835) Neuer Nachtrag von Beschreibungen und Abbildungen neuer Fische, im Nil entdeckt. Museum Senckenbergianum 2(1): 1–28.

Sabaj-Pérez M (2010) Standard Symbolic Codes for Institutional Resource Collections in Herpetology and Ichthyology. http://www.asih.org/files/Coll_Abbr_v2.0_SabajPerez_8Nov2010.pdf

Sauvage HE (1882) Catalogue des poissons recueillis par M. E. Chantre pendant son voyage en Syrie, Haute-Mésopotamie, Kurdistan et Caucase. Bulletin de la Société philomathique de Paris 6: 163–168.

Sauvage HE (1884) Notice sur la faune ichthyologique de l'oust de l'Asie et plus particulièrement sur les poissons recueillis par M. Chantre pendant son voyage dans cette région. Nouvelles Archives du Muséum d'Histoire Naturelle, Paris (Ser. 2) 7: 1–41.

Spataru P, Gophen M (1985) Food composition of the barbel *Tor canis* (Cyprinidae) and its role in the Lake Kinneret ecosystem. Environmental Biology of Fishes 14(4): 295–301. doi: 10.1007/BF00002634

Tsigenopoulos CS, Kasapidis P, Berrebi P (2010) Phylogenetic relationships of hexaploid large-sized barbs (genus *Labeobarbus*, Cyprinidae) based on mtDNA data. Molecular Phylogenetics and Evolution 56(2): 851–856. doi: 10.1016/j.ympev.2010.02.006

Vinciguerra D (1926) Sopra una collezione di pesci della Palestina. Annali del Museo Civico di Storia Naturale Giacomo Doria 52: 210–226.

Whitley GP (1931) New names for Australian fishes. Australian Zoologist 6(4): 310–334.

Wossughi G (1978) Beitrag zur Systematik und Zoogeographie der Cyprinidae (Pisces: Teleostei) des Mittleren Ostens, unter besonderer Berücksichtigung des Irans. PhD thesis, University of Hamburg, Hamburg, Germany, 89 pp.

Wossughi GH, Khoshzahmat A, Etemadfar A (1983) Recognition of fresh-water fishes in the area between Noorabad of Mamasany, Kazeron and Dashtestan. Journal of Veterinary Faculty, University of Tehran 38(2-4): 21–44.

Appendix

Table of localities for all lots examined. (doi: 10.3897/zookeys.339.4903.app) File format: OpenDocument spreadsheet (ods).

Explanation note: Table of localities for all specimens examined as a spreadsheet to make them more easily available for use in biodiversity databases and geospatial investigations.

Copyright notice: This dataset is made available under the Open Database License (http://opendatacommons.org/licenses/odbl/1.0/). The Open Database License (ODbL) is a license agreement intended to allow users to freely share, modify, and use this Dataset while maintaining this same freedom for others, provided that the original source and author(s) are credited.

Citation: Borkenhagen K, Krupp F (2013) Taxonomic revision of the genus *Carasobarbus* Karaman, 1971 (Actinopterygii, Cyprinidae). ZooKeys 339: 1–53. doi: 10.3897/zookeys.339.4903 Table of localities for all lots examined. doi: 10.3897/zookeys.339.5903.app

Erklärung zu den Autorenanteilen

an der Publikation:	**A new genus and species of cyprinid fish (Actinopterygii,Cyprinidae) from the Arabian Peninsula, and its phylogenetic and zoogeographic affinities**
Status:	publiziert
Name der Zeitschrift:	Environmental Biology of Fishes
Beteiligte Autoren:	Kai Borkenhagen

Was hat der Promovierende bzw. was haben die Koautoren beigetragen?
(1) zu Entwicklung und Planung
Promovierender: 100 %

(2) zur Durchführung der einzelnen Untersuchungen und Experimente
Promovierender: 100 % KB hat alle Belegexemplare untersucht und die Laborarbeiten zur DNS-Sequenzierung durchgeführt.

(3) zur Erstellung der Datensammlung und Abbildungen
Promovierender: 100 % KB hat alle Daten zusammengetragen und alle Abbildungen außer der Verbreitungskarte und dem Habitatfoto erstellt.

(4) zur Analyse und Interpretation der Daten
Promovierender: 100 % KB hat alle morphologischen Daten und die DNS-Sequenzdaten analysiert und alle Ergebnisse interpretiert.

(5) zum Verfassen des Manuskripts
Promovierender: 100 %

Unterschrift Promovend: ____________________________ Datum/Ort: ___________________

Zustimmende Bestätigungen der oben genannten Angaben

Unterschrift Betreuer: _______________________________ Datum/Ort: __________________

Environ Biol Fish
DOI 10.1007/s10641-014-0315-y

A new genus and species of cyprinid fish (Actinopterygii, Cyprinidae) from the Arabian Peninsula, and its phylogenetic and zoogeographic affinities

Kai Borkenhagen

Received: 27 November 2013 / Accepted: 9 July 2014
© Springer Science+Business Media Dordrecht 2014

Abstract *Arabibarbus hadhrami*, a new species of cyprinid fish from the Hadhramaut Province of Yemen, is described. It has modally 30 scales (29–32) in the lateral line, the wedge-shaped head is longer (27.8–32.5 % SL) and higher (15.5–18.4 % SL) than in its congeners. The body is slender and laterally flattened. The dorsal fin is high (26.5–32.4 % SL) and well ossified. The pectoral fins (19.9–23.9 % SL) and pelvic fins (16.8–19.8 % SL) are longer than in its congeners. Two closely related species, *Arabibarbus arabicus* and *Arabibarbus grypus* are re-described and compared to the new species. Based on morphological and molecular characters the new genus *Arabibarbus* is erected for these three species. It is characterised by medium to large body size, an ossified, smooth principal dorsal fin ray, eight branched dorsal and five branched anal fin rays, large shield-shaped scales with numerous parallel radii, a lateral line with 29 to 44 scales, pharyngeal teeth that are hooked at their tips, their count being 2.3.5–5.3.2 and the possession of two pairs of barbels. *Arabibarbus hadhrami* is the type species of the new genus. The phylogenetic position of the new genus is analysed, based on the mitochondrial cytochrome *b* gene. It is the sister taxon to the genus *Carasobarbus* Karaman, 1971 and closely related to *Mesopotamichthys* Karaman, 1971, *Pterocapoeta* Günther, 1902 and '*Barbus*' *reinii* Günther, 1874. *Arabibarbus* probably colonised the Arabian Peninsula about 4 Ma ago, coming from the Tigris-Euphrates drainage in the East via Wādī ar Rimah/Wādī al Bāṭin.

Keywords Cyprinidae · Barbinae · Southern Arabia · *Arabibarbus hadhrami* · Cytochrome *b*

Introduction

Because of its arid climate the Arabian Peninsula has a depauperate freshwater-fish fauna. All primary freshwater fishes belong to the family Cyprinidae. The first scientific report on a freshwater fish from the Arabian Peninsula is the description of *Cyprinus arabicus* Valenciennes (ex Ehrenberg) in Cuvier & Valenciennes, 1842. The identity of this species remains unclear, since Valencienne's description is rather brief and the drawing it was based on is not traceable. Banister and Clarke (1977) and Krupp (1983) reviewed the Arabian freshwater fish fauna and described the majority of known species. Krupp (1983) listed 14 species, including the two secondary freshwater fish species *Aphanius dispar* (Rüppell 1829) and *A. sirhani* Villwock et al. 1983. Since then four additional species, *Acanthobrama hadiyahensis* Coad, Alkahem and Behnke, 1983, *Garra dunsirei* Banister, 1987, *G. lautior* Banister, 1987 and *G. smarti* Krupp and Budd, 2009, and a new subspecies, *G. barreimiae gallagheri* Krupp, 1988, were described.

K. Borkenhagen
Senckenberg Research Institute and Museum of Nature,
Senckenberganlage 25, 60325 Frankfurt am Main, Germany

K. Borkenhagen (✉)
Research and Technology Centre (FTZ), University of Kiel,
Hafentörn 1, 25761 Büsum, Germany
e-mail: kai.borkenhagen@ftz-west.uni-kiel.de

Published online: 04 August 2014

Together with the new species reported here, 17 species of primary freshwater fishes are known from the Arabian Peninsula.

The purpose of this paper is to describe a new species of cyprinid fish from the Wadi Hadhramaut/Wadi al Masila drainage basin in Yemen, and to explore its phylogenetic position and zoogeographic origin. Because it is most closely related to *Arabibarbus arabicus* (Trewavas 1941) and *Arabibarbus grypus* (Heckel 1843), I provide detailed species accounts for these two species. The new genus *Arabibarbus* is erected to contain all three species.

Materials and methods

Material and morphological analysis

The material used for the morphological analysis is listed in each species account. For comparison of morphometric characters only well preserved specimens of more than 100 mm standard length (SL) were included, in order to minimise errors of measurement and effects of allometric growth.

Morphometric measurements were taken from specimens straightened whenever necessary; severely damaged and bent specimens were not used. In this study, nine measurements were taken over projections to the body axis. Total length (distance between projections of the tip of the snout and the posterior margin of the longest lobe of the caudal fin, with the caudal fin spread to its natural maximum), standard length (SL) (distance between projections of the tip of the snout and the end of the hypural plate), preanal length (distance between projections of the tip of the snout and the origin of the anal fin), predorsal length (distance between projections of the tip of the snout and the origin of the dorsal fin), prepelvic length (distance between projections of the tip of the snout and the origin of the pelvic fin), head length (distance between projections of the tip of the snout and the posterior margin of the bony opercle), length of the caudal peduncle (distance between projections of the insertion of the anal-fin base and the end of the hypural plate), pre-orbital length (distance from the tip of the snout to the anterior margin of the orbit), mouth length (distance from the tip of the snout to the junction of maxilla and mandible). All other measurements were point-to-point: Head height (taken orthogonal to the body axis at the posterior margin of the skull), body depth (maximum depth of the body (without dorsal fin) taken orthogonal to body axis), depth (minimum) of the caudal peduncle (smallest depth of the caudal peduncle), height of the dorsal and anal fins (length of the last unbranched ray in the dorsal and anal fins, respectively), ossified dorsal fin length (distance from the base of the last unbranched dorsal fin ray to the point where the ray becomes flexible), lengths of the pectoral and pelvic fins (distance from the fin base to the tip of the pectoral and ventral fins, respectively), length of the dorsal-fin base and the anal-fin base (distance between the origin and the insertion of the fin), length of the anterior and posterior barbels (distance from the barbel base to the tip of the barbel when straightened), horizontal diameter of the eye (distance between the anterior and the posterior bony margins of the eye cavity), width of the mouth (distance between the left and right junction of maxilla and mandible), interorbital distance (distance between the upper margins of the eye cavities across the head), and axillary scale length (distance from the base of the pelvic fin to the tip of the axillary scale). For comparison between species, all measurements are expressed as percentage of SL.

In addition, several meristic characters were analysed. The last branched anal- and dorsal-fin rays were counted as one when lying directly adjacent to each other without an interspace. Scales in the lateral line were counted from the first scale with a pore to the last scale on the caudal peduncle (some authors only count to the end of the hypural plate). Scales above the lateral line were counted between the origin of the dorsal fin and the lateral line; the lateral line was not included and a scale on the mid-line of the back was counted as 0.5. Scales below the lateral line were counted from the origin of the anal fin to the lateral line; the lateral line was not included and a scale on the mid-line of the belly was counted as 0.5. Scales around the least circumference of the caudal peduncle were counted as one circle of scales around the least circumference of the caudal peduncle.

For counting the number of pharyngeal teeth, the pharyngeal bones were extracted in a subsample of specimens and the pharyngeal teeth counted, sometimes only on one side. Lost teeth were counted when the point of insertion was clearly visible. Scales were extracted in the anterior part of the body, above the lateral line.

I did not differentiate between male and female specimens, because sex determination is not possible without dissection, which was avoided to prevent damage to the specimens.

Museum acronyms are from Fricke and Eschmeyer (2013): the Natural History Museum, London, UK (BMNH), the Collection of the Biology Department, Shiraz University, Iran (ZM-CBSU), the Institute of Hydrobiology, Chinese Academy of Sciences, Wuhan, China (IHBCAS), the National Museum of Natural History Madrid, Spain (MNCN), the National Museum of Natural History, Paris, France (MNHN), the Natural History Museum Vienna, Austria (NMW), the Senckenberg Research Institute and Museum of Nature, Frankfurt, Germany (SMF) and the Zoological Museum of Tel Aviv University, Israel (TAU).

The spelling of geographic names follows the "United States Board on Geographic Names" (http://geonames.usgs.gov/). Wadi (wādī) refers to a temporary stream. Nahr, Nehri, Rūdkhāneh or Rūd refer to a permanent river or stream. 'Ayn refers to a spring. Geographical coordinates in parentheses are original coordinates, given by a publication, the collector or a collection database. Coordinates determined ex post are marked by brackets. Most of these are from the National Geospatial-Intelligence Agency gazetteer (http://geonames.nga.mil/ggmagaz/) and, as a consequence, do not refer to the actual site of collection, but to the geographic feature itself. For some of the better known waterbodies and cities the conventional name is used: Euphrates (Nahr al Furāt/Fırat Nehri), Orontes (Nahr al 'Āşī/Asi Nehri), Tigris (Nahr Dijlah/Dicle Nehri), Wadi Hadhramaut (Wādī a Ḩaḑramawt), Wadi al Masila (Wādī al Masīlah), Mosul (Al Mawşil), Sana'a (Şan'ā').

For species of *Barbus* s.l., that cannot be assigned to an existing genus, the provisional taxon '*Barbus*' is used (Berrebi et al. 1996).

DNA extraction, amplification and sequencing

The material used in the phylogenetic analysis is listed in Table 1. DNA extraction was performed with the DNeasy Blood & Tissue Kit (QIAGEN), according to the manufacturer's instructions for ethanol-fixed tissue samples. The mitochondrial cytochrome *b* gene was amplified with the primers H15891 (5′ GTT TGA TCC CGT TTC GTG TA 3′) and L15267 (5′ AAT GAC TTG AAG AAC CAC CGT 3′) as well as H16461 (5′ CTT CGG ATT ACA AGA CC 3′) and L15803 (5′ TGA GGG GGA TTT TCA GTA GA 3′) (Briolay et al. 1998; Tsigenopoulos et al. 2002). The PCR protocol encompassed an initial cycle at 94 °C for 2 min, 50 °C for 1 min and 71 °C for 1 min, 35 cycles at 94 °C (20 s), 50 °C (30 s), 71 °C (40 s), and final extension at 71 °C (1 min). PCR products were purified and then sequenced from both ends with the same primers with a standard cycle sequencing chemistry, Bigdye 3.1 (Applied Biosystems) according to the manufacturer's instructions. Sequences were assembled in SeqMan (Lasergene).

Phylogenetic analysis

Additional sequences obtained from NCBI GenBank were included in the present analysis (Table 1). Seven African hexaploid barbel species of the genera *Labeobarbus* Rüppell, 1835 and *Varicorhinus* Rüppell, 1835 were used as outgroup, because analysis of the mitochondrial cytochrome *b* gene (Tsigenopoulos et al. 2010) and morphological characters (e.g. a smooth last unbranched dorsal-fin ray and large shield-shaped scales with numerous parallel radii) indicate, that these species are phylogenetically close to the large-scaled barbels from the Middle East. *Neolissochilus heterostomus* Chen and Yang in Chen, Yang and Chen, 1999 was used to root the tree.

The alignment and sequence statistics were performed with MEGA 5.05 (Tamura et al. 2011). For the Bayesian analysis the HKY substitution model with invariable sites and gamma distribution (nst=2, rates=invgamma) was proposed by AIC in MrModeltest 2.2 (Nylander 2004). MrBayes 3.1.2 (Ronquist and Huelsenbeck 2003) was run for 4,500,000 generations in two independent runs. One tree was sampled each 1,000 generations and the first 1,500,000 generations of each run were discarded as burnin (samplefreq=1000, nchains=4, savebrlens=yes, nruns=2, burnin=1501), after which the average deviation of split frequencies decreased to values below 0.007769. This resulted in a total of 6,000 trees sampled. Effective sample size was checked with Tracer (Rambaut and Drummond 2009) and found to be between 1996 and 5960 for all parameters.

A rough estimate of divergence time was obtained by dividing the between group mean number of nucleotide differences by a divergence rate of 1.05 % per Ma (used by Tsigenopoulos et al. 2010 for cytochrome *b* of hexaploid large-sized barbs).

Table 1 Material used for the phylogenetic analysis. Sources without date refer to di*rect submissions to NCBI GenBank*

GenBank	Coll. No	Species	Locality	Coordinates	Source
KF876021	SMF 30740	*Arabibarbus arabicus*	Wādī Zabīd, Yemen	14°4′21″N 43°39′1″E	this study
KF876022	SMF 30742	*Arabibarbus arabicus*	Wādī Zabīd, Yemen	14°4′21″N 43°39′1″E	this study
KF876023	SMF 30764	*Arabibarbus hadhrami*	Wādī Mara, Yemen	15°8′36″N 48°26′57″E	this study
KF876024	SMF 30771	*Arabibarbus hadhrami*	Wādī Mara, Yemen	15°8′36″N 48°26′57″E	this study
KF876025	SMF 30827	*Arabibarbus grypus*	Rūd-e Mand, Iran	28°26′16″'N 51°30′10″'E	this study
KF876029	SMF 31324	*Arabibarbus grypus*	Rūdkhāneh-ye Bālārūd, Iran	32°35′19″'N 48°17′11″'E	this study
KF876027	SMF 30837	*Arabibarbus grypus*	Rūdkhāneh-ye Kheyrābād, Iran	30°31′39″'N 50°24′45″'E	this study
KF876028	SMF 31318	*Arabibarbus grypus*	fish market in Dayr az Zawr, Syria	35°20′N 40°08′E	this study
KF876026	SMF 30836	*Arabibarbus grypus*	Rūdkhāneh-ye Kheyrābād, Iran	30°31′39″'N 50°24′45″'E	this study
KF876031	SMF 34904	*Mesopotamichthys sharpeyi*	fish market, Baghdād, Iraq	[33°20′N 44°24′E]	this study
KF876032	SMF 34905	*Mesopotamichthys sharpeyi*	fish market, Baghdād, Iraq	[33°20′N 44°24′E]	this study
KF876033	SMF 34906	*Mesopotamichthys sharpeyi*	fish market, Baghdād, Iraq	[33°20′N 44°24′E]	this study
KF876030	SMF 33350	*Pterocapoeta maroccana*	Oued Srou, between Tighassaline and Khenifra, Morocco	32°49′51″N 5°36′36″W	this study
AF287457		*Pterocapoeta maroccana*	Oued Oum er Rbia, El Borj, Morocco	[33°01′08″N 5°37′55″W]	Machordom & Doadrio (2001)
AF145945		*Arabibarbus grypus*	Dicle Nehri, Diyarbakır, Turkey and Fırat Nehri,Adıyaman, Turkey	[37°54′39″N 40°14′12″E; 37°45′50″N 38°16′40″E]	Durand et al. (2002)
AF288486	TAU P113-67	*Carasobarbus canis*	Na al Dawid, Bet She'an, Israel	[32°30′N 35°30′E]	Machordom & Doadrio (2001)
AF145947		*Carasobarbus canis*	Yam Kinneret, Israel	[32°48′41″N 35°36′16″E]	Durand et al. (2002)
AF180853		*Carasobarbus kosswigi*	Dicle Nehri, Diyarbakır, Turkey	[37°54′39″N 40°14′12″E]	Durand et al. (2002)
AF180852		*Carasobarbus chantrei*	Asi Nehri, Hatay, Turkey	[36°12′N 36°9′E]	Durand et al. (2002)
AF145944		*Carasobarbus luteus*	Dicle Nehri, Diyarbakır, Turkey and Fırat Nehri,Adıyaman, Turkey	[37°54′39″N 40°14′12″E; 37°45′50″N 38°16′40″E]	Durand et al. (2002)
AF180855		*Carasobarbus harterti*	Oued Sebou, Morocco	[34°04′N 5°33′W]	Tsigenopoulos,C.S., Naran,D. and Berrebi,P.
AF287430	MNCN 103 M	*Carasobarbus fritschii*	Oued Ksob, Essaouira, Morocco	[31°28′59″N 9°46′03″W]	Machordom & Doadrio (2001)
AF180854		*Carasobarbus fritschii*	Morocco		Durand et al. (2002)
AF287429	MNCN 16A	*Carasobarbus fritschii*	Oued Zamrine, Khouribga, Morocco	[32°52′52″N 6°54′23″W]	Machordom & Doadrio (2001)
AF180856		*Carasobarbus fritschii*	Oued Sebou, Morocco	[34°04′N 5°33′W]	Tsigenopoulos,C.S., Naran,D. and Berrebi,P.
AF145946		*'Barbus' reinii*	Oued Tennsift, Morocco	[32°01′56″N 9°20′39″W]	Durand et al. (2002)

Table 1 (continued)

GenBank	Coll. No	Species	Locality	Coordinates	Source
AF287444	MNCN 87 M	*'Barbus' reinii*	Oued Ksob, Essaouira, Morocco	[31°28′59″N 9°46′03″W]	Machordom & Doadrio (2001)
AF180862		*Varicorhinus beso*	T'ana Hāyk', Ethiopia	[12°00′N 37°20′E]	Durand et al. (2002)
AF180864		*Varicorhinus wurtzi*	Rokel River, Sierra Leone	[8°33′N 12°48′W]	Durand et al. (2002)
AF180877		*Labeobarbus polylepis*	Komati Rivier, South Africa	[25°51′29″S 32°43′48″E]	Tsigenopoulos,C.S., Naran,D. and Berrebi,P.
AF180830		*Labeobarbus marequensis*	Tzaneen Lake, South Africa	[23°48′S 30°10′E]	Tsigenopoulos et al. (2002)
AF180828		*Labeobarbus ethiopicus*	T'ana Hāyk', Ethiopia	[12°00′N 37°20′E]	Tsigenopoulos et al. (2002)
AF112406		*Labeobarbus intermedius*	T'ana Hāyk', Ethiopia	[12°00′N 37°20′E]	Tsigenopoulos & Berrebi (2000)
AF287420		*Labeobarbus bynni*	Nahr an Nīl, Egypt	[30°10′N 31°06′E]	Machordom & Doadrio (2001)
AY463516	IHBCAS ——	*Neolissochilus heterostomus*	Ayeyarwady River Drainage, Tengchong, Yunnan Province, China	[25°01′N 98°29′E]	He et al. (2004)

Results

Arabibarbus gen. nov

Type species: *Arabibarbus hadhrami* sp. nov.

Diagnosis

Arabibarbus is characterised by medium to large body size, an ossified, smooth principal dorsal fin ray, modally eight branched dorsal and modally five branched anal fin rays, large shield-shaped scales with numerous parallel radii, a lateral line with 29 to 44 scales, pharyngeal teeth that are hooked at their tips, their count being 2.3.5–5.3.2 and the possession of two pairs of barbels.

Taxonomic affinities

The genus *Arabibarbus* differs from *Carasobarbus* in modally having eight branched dorsal-fin rays (vs. 9–10), modally five branched anal fin rays (vs. six) and usually a lower body depth (18.2–25.8 % SL in *Arabibarbus* vs. 24.8–40.1 % SL in *Carasobarbus*, see Borkenhagen and Krupp 2013). It differs from *Mesopotamichthys* in having two well-developed pairs of barbels (vs. no barbels). It differs from *Pterocapoeta* Günther, 1902 in having eight branched dorsal-fin rays (vs. more than nine) and lips without horny sheaths (vs. lips with a horny sheath).

The genus *Arabibarbus* constitutes a monophyletic group in the cytochrome *b* phylogram. It is genetically distinct from the Moroccan species *'Barbus' reinii*, the African genera *Labeobarbus* and *Varicorhinus* and the Asian genera *Tor* Gray, 1834 and *Neolissochilus* Rainboth, 1985. The ploidy level of all *Arabibarbus* species is unknown, but due to their close relationship to *Carasobarbus* and the African hexaploids they are expected to be evolutionary hexaploids.

The name *Arabibarbus* is an allusion to the geographic range of the new genus.

Arabibarbus hadhrami sp. nov. (Figs. 1–4)

Material

Holotype: SMF 34837, Wādī Mara, tributary to Wādī Daw'an, Wadi Hadhramaut/Wadi al Masila system, Yemen (15°08′36″N 48°26′58″E), F. Krupp et al., 31 May 2005.

Paratypes: BMNH 1976.4.7:187–195, 9, Wadi Hadhramaut at Qasam, Yemen (16°10′N 49°4′E), W.A.

Fig. 1 Habitus. **a**: *Arabibarbus hadhrami* holotype (SMF 34837, 129 mm SL). **b**: *Arabibarbus arabicus* (SMF 33116, 235 mm SL). **c**: *Arabibarbus grypus* (SMF 30241, 175 mm SL). Specimens resized to facilitate comparison, scale bar=3 cm

King-Webster. - BMNH 1976.5.17:8, 1, Wadi Hadhramaut, Yemen [16°0′N 49°0′E], R.B. Serjeant. - BMNH 1976.4.7:185, 1, Wadi Hadhramaut at Ghuraf, Yemen (16°0′N 49°0′E), W.A. King-Webster. - BMNH 1976.4.7:176–184, 9; BMNH 1976.4.7:186, 1, Wadi Hadhramaut at Ghayl ‘Umar, Yemen (15°44′N 48°51′E), W.A. King-Webster. - SMF 33113, 11, Wādī ‘Idim at Ghayl ‘Umar near Ar ar Raydah, Yemen (15°40′51″N 48°51′59″E), F. Krupp et al., 2 Jun 2005. - SMF 33114, 2, Wādī ‘Idim near Ghayl ‘Umar, Yemen (15°40′10″N 48°51′04″E), F. Krupp et al., 2 Jun 2005. - SMF 30764, 1; SMF 30771, 1; SMF 33112, 15, same data as holotype.

Diagnosis

Arabibarbus hadhrami has modally 30 scales (29–32) in the lateral line, the wedge-shaped head is longer (27.8–32.5 % SL) and higher (15.5–18.4 % SL) than in its congeners. The body is slender and laterally flattened. The dorsal fin is high (26.5–32.4 % SL) and well ossified. The pectoral fins (19.9–23.9 % SL) and pelvic fins (16.8–19.9 % SL) are longer than in its congeners. It occurs in the Wadi Hadhramaut/Wadi al Masila drainage basin.

Description

The body is slender and laterally flattened, a nuchal hump is absent or small (Fig. 1). The head is wedge-shaped and elongate with a straight or slightly convex dorsal profile and a slightly convex or almost straight ventral profile. The head length is greater than the body depth. The mouth is sub-terminal with two pairs of well-developed barbels, which are usually longer than the eye diameter. A median lobe is present on the lower lip (Fig. 2). In some specimens the lips are fleshy. The eyes are lateral in the anterior half of the head and slightly protuberant. The morphometric characters are summarised in Table 2.

The dorsal fin is high and has four (n=52 specimens) unbranched and seven (n=7), eight (n=42) or nine (n=2) branched rays. The last unbranched ray is about as long as the head, well ossified and only the tip is flexible. The anal fin has three (n=52) unbranched and five (n=52) branched rays. Pectoral and pelvic fins are relatively long (Table 2).

Arabibarbus hadhrami has 29 to 32 scales in the lateral line (Table 3), 3.5 (n=4) or 4.5 (n=38) scales above the lateral line, 3.5 (n=4) or 4.5 (n=39) scales below the lateral line and 12 (n=43) scales around the caudal peduncle. The scales are shield-shaped and have numerous parallel radii (Fig. 3).

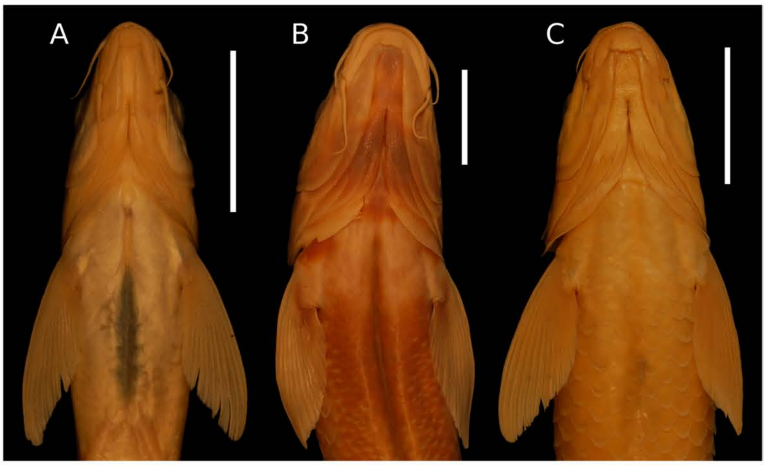

Fig. 2 Head and chest in ventral view. **a**: *Arabibarbus hadhrami* holotype (SMF 34837, 129 mm SL). **b**: *Arabibarbus arabicus* (SMF 33116, 235 mm SL). **c**: *Arabibarbus grypus* (SMF 30241, 175 mm SL). Photos resized to facilitate comparison, scale bar=3 cm

The pharyngeal teeth count is −5.3.2 (n=5). The pharyngeal teeth are hooked at the tip (Fig. 4). There are 11 (n=2) or 12 (n=3) gill rakers on the lower limb and four (n=5) gill rakers on the upper limb of the first gill arch.

Table 2 Comparison of morphometric characters of specimens with more than 100 mm SL. All characters in percent of SL

	Arabibarbus hadhrami					*Arabibarbus arabicus*				*Arabibarbus grypus*			
	Min	Max	Median	Holotype	n	Min	Max	Median	n	Min	Max	Median	n
SL in mm	102.2	205.0	119.7	128.9	17	104.4	253.0	131.2	18	117.8	315.0	197.0	26
total length	126.8	132.8	129.0	132.1	12	120.6	130.9	128.5	18	118.8	128.5	123.8	24
preanal lenght	74.8	79.1	77.4	76.6	17	73.5	79.4	76.4	18	74.1	79.4	77.4	26
predorsal length	49.4	54.2	53.1	51.9	17	46.8	52.7	49.1	18	45.8	52.7	48.0	26
prepelvic length	51.0	56.7	54.4	52.8	17	49.8	57.1	52.2	18	47.7	52.8	50.7	26
head length	27.8	32.5	31.1	28.6	15	24.3	30.8	26.2	18	19.9	25.4	22.5	26
head height	15.5	18.4	16.6	16.2	17	13.9	17.0	15.5	18	12.6	16.0	14.6	26
caudal peduncle length	13.2	18.3	15.9	15.7	17	12.6	18.4	15.2	18	13.9	16.9	15.3	26
body depth	20.6	25.1	22.6	24.1	17	20.8	25.8	23.8	18	18.2	23.3	21.7	26
caudal peduncle depth	8.7	10.7	9.9	10.0	17	9.1	10.8	9.7	18	9.1	10.6	9.8	26
pectoral-fin length	19.9	23.9	21.5	23.0	17	18.0	22.2	20.3	18	16.0	19.3	18.3	26
pelvic-fin length	16.8	19.8	18.1	18.7	17	14.9	18.6	17.0	18	14.3	17.5	15.9	26
dorsal-fin height	26.5	32.4	30.7	31.8	7	22.9	35.5	27.0	15	17.8	24.2	20.7	25
ossified dorsal-fin height	22.9	28.9	25.8	28.9	17	20.0	32.4	25.9	18	13.7	19.1	16.7	25
anal-fin height	17.9	22.3	20.8	21.0	17	17.1	21.7	19.6	18	15.1	18.1	17.0	26
anal-fin-base length	6.9	9.0	8.0	8.4	17	6.5	8.9	7.5	18	6.5	7.8	7.2	26
dorsal-fin-base length	12.5	15.4	14.3	15.2	17	13.1	16.6	15.1	18	11.6	14.7	12.9	26
anterior-barbel length	7.0	9.0	8.2	9.0	6	7.5	11.4	8.5	11	3.3	5.9	4.7	26
posterior-barbel length	6.8	9.4	8.5	9.0	17	8.3	12.3	9.8	18	4.4	6.3	5.5	25
pre-orbital length	8.1	11.9	10.2	8.6	15	6.7	11.7	8.5	18	5.2	8.9	6.5	26
eye diameter	5.0	7.5	6.3	6.8	17	4.8	6.9	5.3	18	3.6	6.6	4.9	26
mouth width	6.2	8.8	7.0	6.3	15	5.2	8.5	7.2	18	5.6	8.7	6.8	26
mouth length	6.1	9.6	7.5	7.6	15	5.3	9.7	6.6	16	4.2	5.8	5.0	24
interorbital width	6.9	9.0	7.3	7.3	17	6.4	8.6	7.3	18	7.9	9.2	8.5	26
axillary-scale length	4.7	5.8	5.3	5.6	17	3.5	5.0	4.7	18	5.2	7.3	6.0	26

Table 3 Number of scales in the lateral line

	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	n
A. hadhrami	7	14	13	8													42
A. arabicus	1	1	2	10	29	20	14	2		1							80
A. grypus					2		1	2	11	11	15	10	4			1	57

Colouration

Fixed specimens are golden to brown, the dorsum has an orange hue and is darker than the side of the abdomen and the venter. The chromatophores are more concentrated at the margins of the scales, resulting in a diffuse reticulate colour pattern.

Description of the holotype

The holotype (SMF 34837) is an adult specimen of 128.9 mm SL. It has four unbranched and eight branched rays in the dorsal fin, three unbranched and five branched rays in the anal fin, 32 scales in the lateral line and 12 scales around the caudal peduncle. It has two pairs of barbels. Its head length is 28.6 % SL, its head height is 16.2 % SL, its predorsal length is 51.9 % SL its pectoral fin length 23.0 % SL its pelvic fin length 18.7 % SL and its preorbital length is 8.6 % SL.

Habitat and distribution

Arabibarbus hadhrami occurs in the Wadi Hadhramaut/ Wadi al Masila drainage basin (Fig. 5) and is endemic to Yemen. Its habitat (Fig. 6) is characterised by high seasonal fluctuations in discharge. During the dry season, many sections of the wadis cease to flow and break up into series of isolated pools, connected by subterranean streams.

During the collection of part of the type specimens in May and June 2005, large waterbodies were present in the Wadi Hadhramaut/Wadi al Masila system and Wadi al Masila, the lower course of Wadi Hadhramaut, was a continuous stream flowing at low to medium speed. It was about 130 km long, up to 20 m wide and up to 8 m deep. The water disappeared underground a few kilometres before reaching the Indian Ocean (F. Krupp, pers. comm.).

Other species present at the time of collection in 2005 were *Carasobarbus exulatus* (Banister and Clarke 1977), *Cyprinion acinaces* Banister & Clarke, 1977, *Garra lautior* Banister, 1987, *G. mamshuqa* Krupp, 1983 and possibly *G. tibanica* Trewavas, 1941.

Etymology

The name of the new species is derived from its native range, the Hadhramaut Province in Yemen and was chosen in honour of the people who live there and call themselves "Hadhrami".

Arabibarbus arabicus (Trewavas, 1941)

Barbus arabicus Trewavas, 1941
Tor arabicus, - Karaman 1971

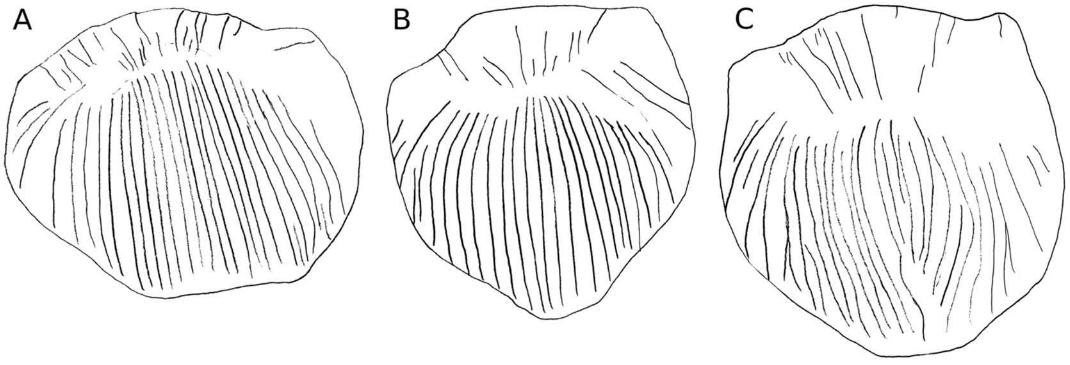

Fig. 3 Scale striation pattern. **a**: *Arabibarbus hadhrami*. **b**: *Arabibarbus arabicus*. **c**: *Arabibarbus grypus*. Scales taken form the anterior region of the body, above the lateral line. Resized to facilitate comparison

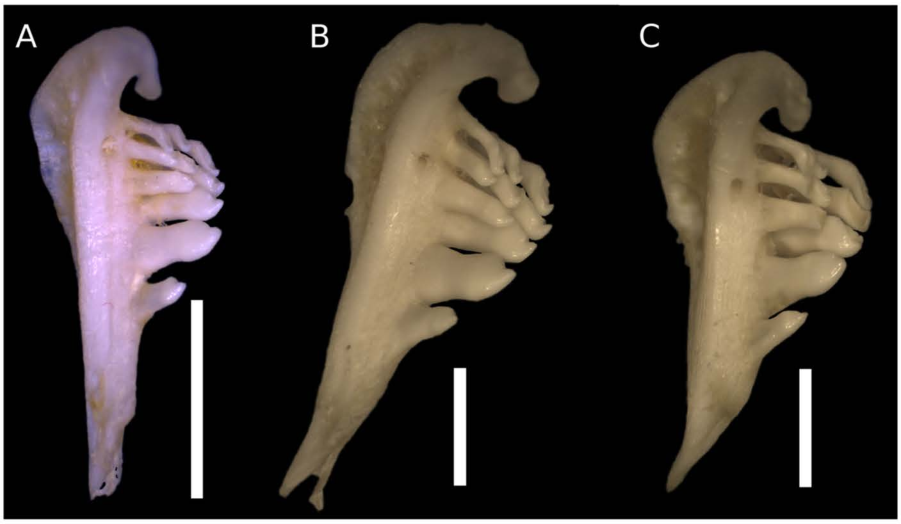

Fig. 4 Pharyngeal bones. **a**: *Arabibarbus hadhrami* (SMF 33112, 120 mm SL). **b**: *Arabibarbus arabicus* (SMF 33116, 235 mm SL). **c**: *Arabibarbus grypus* (SMF 28759, 227 mm SL). Photos resized to facilitate comparison, scale bar=5 mm

Barbus arabicus, - Banister and Clarke 1977
Barbus arabicus, - Krupp 1983

Material

Holotype (by monotypy): BMNH 1940.2.15:1, 1, Wādī al Khārid 20 miles Northeast of Sana'a, puchased on the fish market of Sana'a, dried specimen stored in ethanol, Yemen [15°40′N 44°28′E), P. W. R. Petrie.

Additional material: BMNH 1976.4.7:196–197, 2, Wādī ash Sharqīyah near Ṣa'dah, tributary to Wādī al Jawf, Yemen [16°41′59″N 43°58′12″E], G. Popov, 25 Jul 1962. - BMNH 1976.4.7:201–272, 72, Wādī Mawr near Az Zuhrah, Yemen [15°43′26″N 42°59′45″E], I. G. Dunn, 26 Dec 1973. - SMF 33155, 6, Wādī Mawr at the dam, Yemen (15°39′51″N 43°13′39″E), F. Krupp et al., 2 Apr 2004. - BMNH 1976.4.7:335, 1, Wādī Ẓahr 15 km northwest of Sana'a, Yemen [15°27′19″N 44°8′ 50″E], I. G. Dunn. - BMNH 1976.4.7:273–283, 11, Wādī al 'Ayn 120 km form Al Ḩudaydah on road to Sana'a, Yemen [15°26′43″N 43°41′36″E], I. G. Dunn, 21 Dec 1973. - BMNH 1976.4.7:284–298, 15, Wādī Surdūd 80 km from Al Ḩudaydah on Al Ḩudaydah to Sana'a road, Yemen [15°10′N 43°30′E], I. G. Dunn. - SMF 33116, 21, Wādī Shallāl tributary to Wādī Surdūd near Khamīs Banī Sa'd, Yemen (15°08′20″N 43°36′33″E), F. Krupp et al., 11 Apr 2004. - BMNH 1976.4.7:198–200, 3, Wādī Sihām near Al Ḩudaydah, Yemen [14°41′N 42°59′11″E], G. Popov, 16 Sep 1962. - SMF 30740, 1; SMF 30742, 1; SMF 33115, 27, Wādī Zabīd near Qaryat az̧ Z̧uhrah, Yemen (14°04′21″N 43°39′01″E), F. Krupp et al., 10 Apr 2004. - BMNH 1977.10.4:7, 1, on road from Al Ḩudaydah to Sana'a, Yemen, C. Hubbs, Oct 1977.

Diagnosis

Arabibarbus arabicus has modally 33 scales (29–38) in the lateral line, the wedge-shaped head is longer (24.3–30.8 % SL) and higher (13.9–17.0 % SL) than in *A. grypus*. The body is strong and laterally flattened. The dorsal fin is high (22.9–35.5 % SL) and well ossified. The pectoral fins (18.0–22.2 % SL) and pelvic fins (14.9–18.6 % SL) are shorter than in *A. hadhrami*. It occurs in the wadis of the south-western Arabian Peninsula.

Description

The body is strong, slender and laterally flattened, a nuchal hump is absent or very small (Fig. 1). The head is wedge-shaped and elongate with a straight dorsal profile and straight or slightly convex ventral profile. The head length is greater than the body depth. The mouth is broad and subterminal with two pairs of well-developed barbels, which are considerably longer than the eye diameter and a small median lobe on the lower lip (Fig. 2). The eyes are lateral in the anterior half

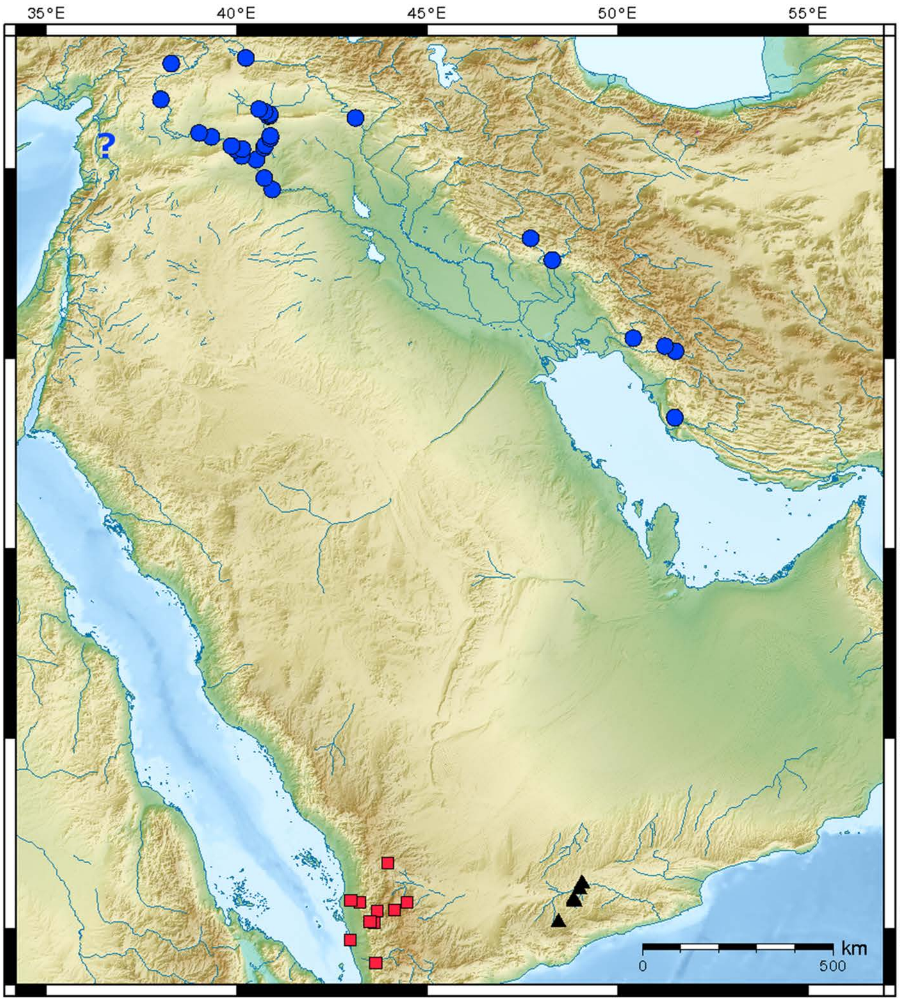

Fig. 5 Map of the Arabian Peninsula with the geographic distribution of *Arabibarbus arabicus* (■), *Arabibarbus grypus* (●) and *Arabibarbus hadhrami* (▲)

of the head and slightly protuberant. The morphometric characters are summarised in Table 2.

The dorsal fin is high and has three (n=1) or four (n=97) unbranched and seven (n=1), eight (n=98) or nine (n=1) branched rays. The last unbranched ray is longer than the head, well ossified and only the tip is flexible. The anal fin has three (n=98) unbranched and five (n=98) or six (n=1) branched rays.

Arabibarbus arabicus has 29 to 38 scales in the lateral line (Table 3), 4.5 (n=61) or 5.5 (n=6) scales above the lateral line, 3.5 (n=1), 4.5 (n=53) or 5.5 (n=7) scales below the lateral line and 12 (n=69) scales around the caudal peduncle. The scales are shield-shaped and have numerous parallel radii (Fig. 3).

The pharyngeal teeth count is −5.3.2 (n=5). The pharyngeal teeth are hooked at the tip (Fig. 4). There are 11 (n=1), 12 (n=3) or 13 (n=1) gill rakers on the lower limb and three (n=1), four (n=2) or five (n=2) gill rakers on the upper limb of the first gill arch.

Colouration

Specimens preserved in ethanol have a dark brown dorsum. Flanks and belly are yellow-brown.

Habitat and distribution

Arabibarbus arabicus occurs in the wadis of the south-western Arabian Peninsula (Fig. 5; Krupp 1983). The abiotic characters of the habitat are similar to those of the habitat of *Arabibarbus hadhrami.*

Fig. 6 Habitat of *Arabibarbus hadhrami* in Wādī Daw‘an, photo F. Krupp, 31 May 2005

Garra sahilia sahilia Krupp, 1983, *G. sahilia gharbia* Krupp, 1983, *Garra tibanica* Trewavas, 1941, *Cyprinion acinaces acinaces* Banister and Clarke, 1977 and *Aphanius dispar* occur sympatrically with *A. arabicus* (Krupp 1983).

Arabibarbus grypus (Heckel 1843)

Barbus grypus Heckel, 1843
Labeobarbus kotschyi Heckel, 1843
Tor grypus, - Karaman, 1971
Barbus grypus, - Krupp 1985
Tor grypus, - Coad 2013

Material

Syntypes of *Barbus grypus* Heckel, 1843: NMW 54160, NMW 54161 and NMW 91023, 4, Iraq, Tigris at Mosul [36°20′6″N 43°7′8″E], T. Kotschy, 3 Apr 1843. - SMF 2613, 1, same data as other syntypes, dry specimen.

Syntypes of *Labeobarbus kotschyi* Heckel, 1843: NMW 49729 and NMW 91022, 2, Iraq, Tigris at Mosul [36°20′6″N 43°7′8″E], T. Kotschy, 9 Apr 1843.

Additional material: NMW 90484, 1, Syria, Euphrates at Jarābulus [36°49′10″N 38°0′40″E], V. Pietschmann, 20 May 1914. - SMF 30244, 1, Syria, Nahr al Khābūr at Tall Umm al-Māʿaz (36°34′N 40°35′E), F. Krupp, 27 May 1989. - SMF 34003, 1, Syria, Nahr al Khābūr near Al Ḩasakah (36°30′N 40°44′ E), F. Krupp, 7 Oct 1988. - SMF 30241, 1; SMF 33540, 1; SMF 33542, 3, Syria, Nahr al Khābūr and Wādī Furātī at Tall Tayyiğ (36°26′N 40°52′E), F. Krupp, 8 Oct 1988. - SMF 30247, 1, Syria, Nahr al Khābūr near Tall Budayrī (36°24′N 40°52′E), F. Krupp, 2–4 Nov 1986. - SMF 30245, 1, Syria, Nahr al Khābūr near Nahāb (36°23′N 40°50′E), F. Krupp, 23–27 May 1989. - SMF 34005, 1, Syria, Euphrates near bridge of Ar Raqqah [35°56′3″N 39°0′39″E]. - SMF 30279, 1, Syria, Nahr al Khābūr near ‘Alwah [35°51′51″N 40°53′ 4″E], F. Krupp, 9 Oct 1988. - SMF 28731, 11, Syria, Euphrates, Ar Raqqah to Ḩalabīyah/Zalābīyah [35°50′N 39°20′E], R. Beck, 13 Jun−14 Jun 1998. - SMF 33543, 1, Syria, Nahr al Khābūr near Dashīshah (35°48′N 40°53′E), F. Krupp, 9 Oct 1988. - SMF 33541, 1; SMF 34007, 2, Syria, Nahr al Khābūr near Tall ash Shaykh Ḩamad (35°37′N 40°45′E), F. Krupp, 21 Sep−14 Oct 1988. - SMF 34004, Syria, 1, Euphrates at Harmūshīyah (35°35′52″N 39°51′25″E), N. Alwan et al., 31 Oct 2008. - SMF 30246, 1, Syria, Nahr al Khābūr 8 km south of Tall ash Shaykh Ḩamad (35°33′N 40°43′E), F. Krupp, 24 Oct 1986. - SMF 28680, 1, Syria, Euphrates upstream of Dayr az Zawr [35°31′N 40°9′0″E], R. Beck, 31 May 1998. - SMF 28748, 1, Syria, Euphrates, between Ḩalabīyah/Zalābīyah and Dayr az Zawr [35°30′N 39°59′E], R. Beck, 15 Jun−16 Jun 1998. - SMF 28631, 2, Syria, Euphrates at Dayr az Zawr [35°20′N 40°8′E], R. Beck, 23 May 1998. - SMF 31318, 1, Syria, Euphrates, fish market in Dayr az Zawr [35°20′N 40°08′E], N. Alwan et al., 28 Oct 2008. - SMF 34006, 1, Syria, Nahr al Khābūr near Mašiẖ (35°14′N 40°31′E), F. Krupp, 10 Oct 1988. - MNHN 2002–1539, 1, Syria, Nahr al Khābūr [35°7′37″N 40°25′38″E], Ali, 6 Aug 1998. - SMF 28650, 1, Syria, Euphrates at Qal‘at aş

Ṣāliḥīyah (Dura Europos) [34°45′0″N 40°43′30″E], R. Beck, 28 May 1998. - SMF 28759, 3, Syria, Euphrates, Abū Kamāl at mouth of Wādī Ratqah [34°26′45″N 40°56′0″E], R. Beck, 9 Jul 1998. - SMF 33128, 5, Iran, Rūdkhāneh-ye Karkheh near Pol-e Dokhtar (33°9′36″N 47°43′12″E), N. Alwan et al., 3 Mar 2008. - SMF 33126, 5, Iran, Rūdkhāneh-ye Bālārūd (32°35′19″N 48°17′11″E), N. Alwan et al., 3 Mar 2008. - SMF 33124, 4, Iran, Rūdkhāneh-ye Shīb (30°19′21″N 51°14′32″E), N. Alwan et al., 29 Feb 2008. - SMF 33123, 1, Iran, Rūdkhāneh-ye Fahlīān (30°11′9″N 51°31′15″E), N. Alwan et al., 29 Feb 2008. - SMF 33122, 12, Iran, Rūd-e Mand between Khvormūj and Kākī (28°26′16″N 51°30′10″E), K. Borkenhagen et al., 7 Nov 2006. - CBSU 4499, 1, Iran.

Diagnosis

Arabibarbus grypus has modally 39 scales (33–44) in the lateral line. The round head is shorter (19.9–25.4 % SL) and lower (12.6–16.0 % SL) than in its congeners. The body is cylindrical. The dorsal fin is short (17.8–24.2 % SL) and only weakly ossified. The pectoral fins (16.0–19.3 % SL) and pelvic fins (14.3–17.5 % SL) are shorter than in *A. hadhrami*. It occurs in the Tigris-Euphrates basin, in the rivers of southern Iran and possibly the in the Orontes.

Description

The body is slender and laterally flattened in small juveniles. It is strong and cylindrical in larger specimens. A nuchal hump is absent (Fig. 1). The head is short and round with a convex dorsal profile and a straight to slightly convex ventral profile. The head length is greater than the body depth. The mouth is sub-terminal with two pairs of barbels, which are about as long as the eye diameter. A median lobe is present on the lower lip (Fig. 2). It is small in some specimens but well developed in others. The lips are inconspicuous in most specimens, but can be thick and fleshy in some. The eyes are lateral in the anterior half of the head and slightly protuberant. The morphometric characters are summarised in Table 2.

The dorsal fin is short and has three (n=4) or four (n=68) unbranched and seven (n=3), eight (n=69) or nine (n=3) branched rays. The last unbranched ray is about as long as the head, weakly ossified and the distal part is flexible. The anal fin has three (n=71) or four (n=1) unbranched and four (n=2), five (n=71) or six (n=1) branched rays.

Arabibarbus grypus has 33 to 44 scales in the lateral line (Table 3), 4.5 (n=54) or 5.5 (n=2) scales above the lateral line, 3.5 (n=2), 4.5 (n=50), five (n=1) or 5.5 (n=1) scales below the lateral line and 11 (n=1) or 12 (n=54) scales around the caudal peduncle. The scales are shield-shaped and have numerous parallel radii (Fig. 3).

The pharyngeal teeth count is −5.3.2 (n=9) and 2.3.5.–5.3.2 (n=2). The pharyngeal teeth are hooked at the tip (Fig. 4). There are 13 (n=2) 14 (n=6) or 15 (n=3) gill rakers on the lower limb and three (n=1), four (n=7) or five (n=3) gill rakers on the upper limb of the first gill arch.

Colouration

Live specimens are light grey to bronze and white ventrally. The back is darker than the flanks. The caudal fin is slightly orange in many specimens. Fixed specimens are yellow to brown, the dorsal area is darker than the flanks and the belly.

Habitat and distribution

Arabibarbus grypus occurs in the Tigris-Euphrates basin (Fig. 5) and in the rivers of southern Iran (Abdoli 2000; Coad 2013). Two records with a total of four specimens from the Orontes are documented in Krupp (1985) but were not examined in this study. This species inhabits small to large rivers and can attain sizes of up to 2 m and a mass of 100 kg (Krupp and Schneider 2008). For other fish species occurring sympatrically with *A. grypus* see Coad (1995), Krupp and Schneider (2008) and Coad (2013).

Comparison of the species

Arabibarbus hadhrami differs from *A. arabicus* and *A. grypus* by having modally 30 scales in the lateral line vs. 33 and 39 respectively (see Table 3 for ranges). Its head tends to be longer and higher, its predorsal length tends to be greater, its paired fins tend to be longer and its preorbital length tends to be greater than in *A. arabicus* and *A. grypus* (Fig. 7). There is no geographical overlap between the species and their extents

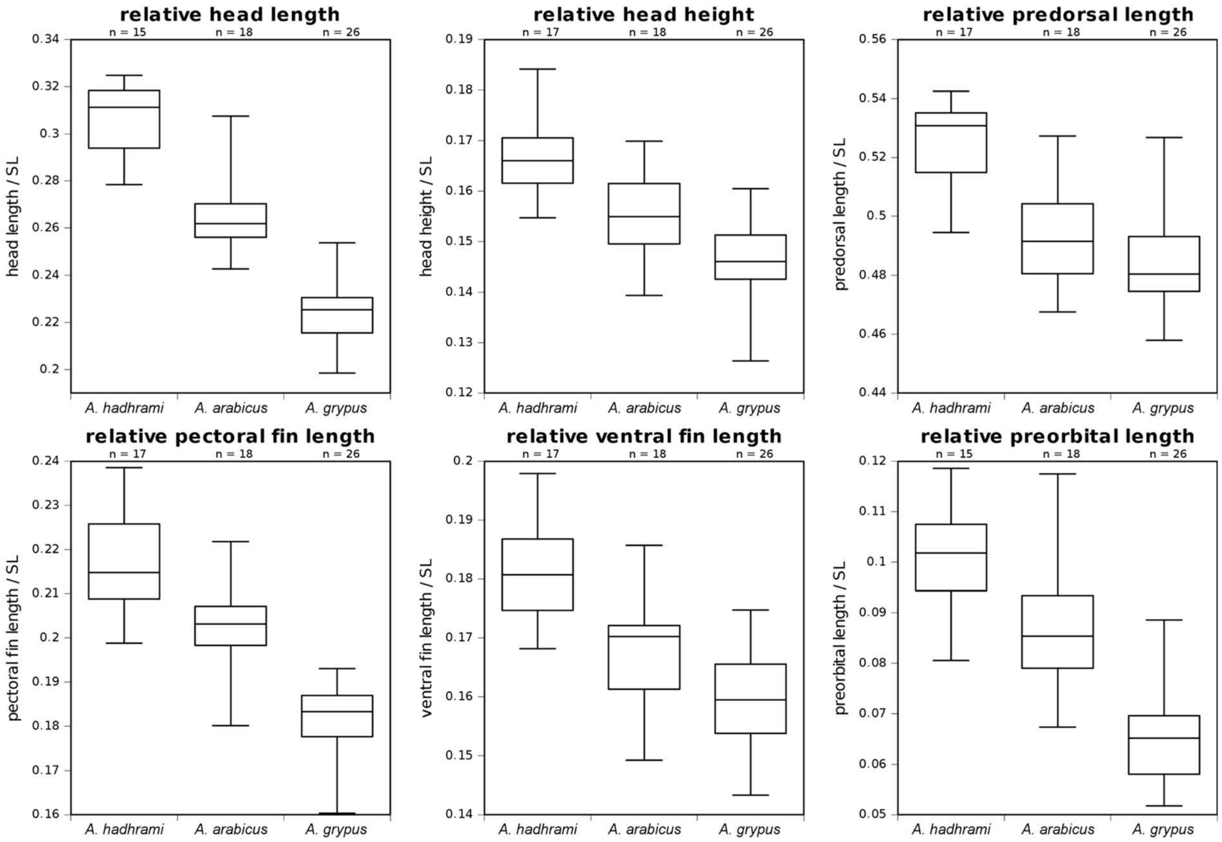

Fig. 7 Comparison of six morphometric characters. Only specimens of more than 100 mm SL were taken into account. Whiskers indicate maximum and minimum. The box indicates the first and third quartile. The bar in the middle of the box indicates the median

of occurrence are separated by vast stretches of arid land (Fig. 5).

Phylogenetic analysis

The phylogram (Fig. 8) is rooted with *Neolissochilus heterostomus*, an Asian species. The rest of the species are divided into two major clades, one is composed of species from Subsaharan Africa and the Nile, the other encompasses the Middle Eastern and North African taxa. *Arabibarbus hadhrami* forms a well-supported clade together with *A. arabicus* and *A. grypus*. Within this clade all three species form well-supported subclades, their interrelationships, however, are not well resolved. Together they are the sister group of the genus *Carasobarbus*. *Mesopotamichthys* is sister to *Arabibarbus* and *Carasobarbus*, whereas '*Barbus*' *reinii* is sister to these three genera. *Pterocapoeta maroccana* Günther, 1902 is the sister group to all other Middle Eastern and North African species. However, the phylogenetic relationships between *Arabibarbus*, *Carasobarbus*, *Mesopotamichthys*, *Pterocapoeta* and '*B*'. *reinii* receive only weak support (posterior probability of 66 % to 48 %) and should not be overinterpreted.

The between-group mean distance, based on 1141 base pairs of the cytochrome *b* gene, for *A. hadhrami* and *A. arabicus* is 52.00 nucleotides (4.557 %), for *A. hadhrami* and *A. grypus* 50.17 nucleotides (4.397 %) and for *A. arabicus* and *A. grypus* 42.83 nucleotides (3.754 %). With the divergence rate of 1.05 % per Ma, as used in Tsigenopoulos et al. (2010) for a very similar set of cyprinid fish, this leads to an estimated age of roughly 4 Ma (4.34 – 3.57 Ma) for the radiation of this group. The mean number of nucleotide differences between *Arabibarbus* and *Carasobarbus* is 77.71 (75.70 without *C. kosswigi*, a species with a long branch in the phylogram, that indicates an accelerated nucleotide

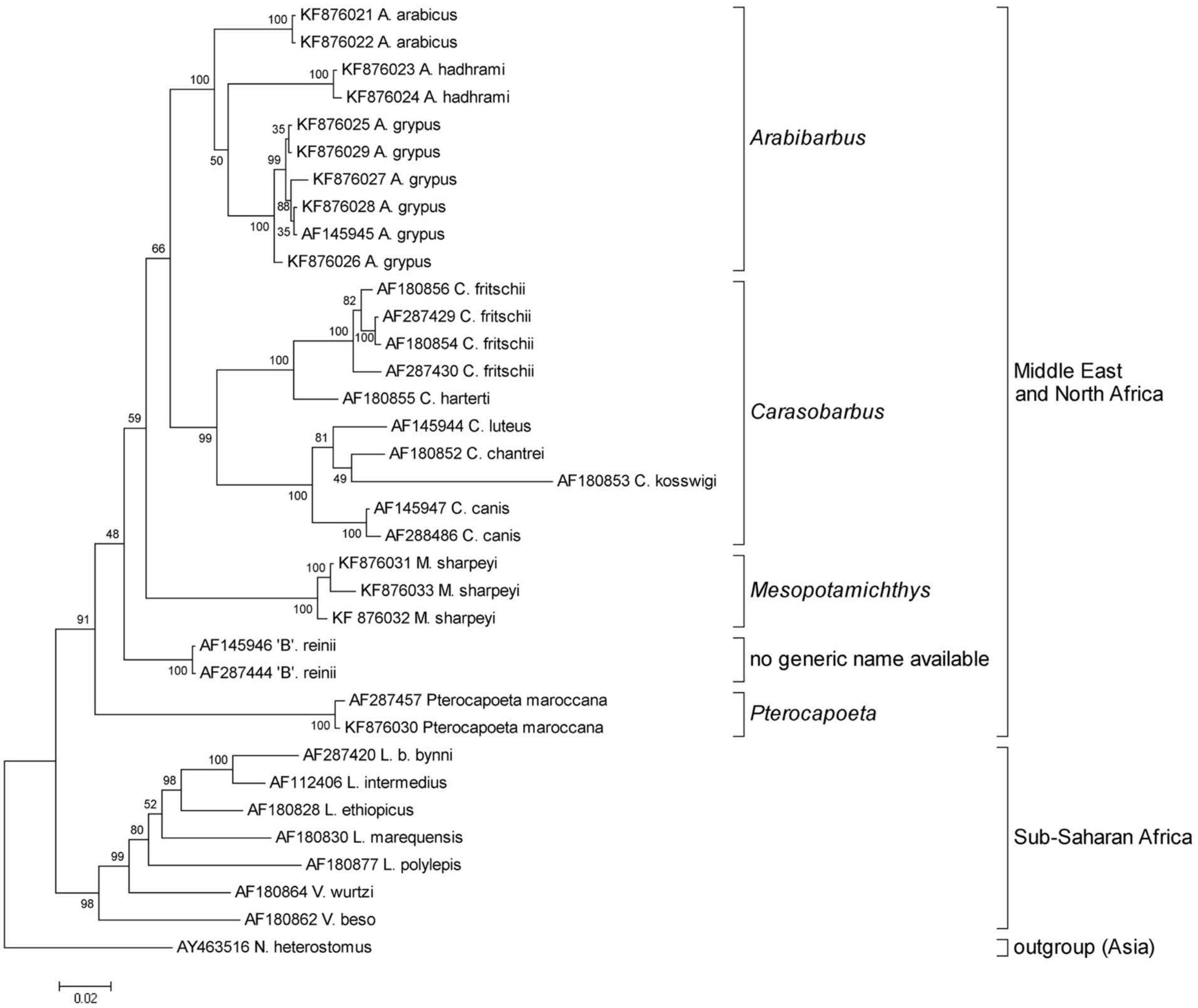

Fig. 8 Phylogram based on Bayesian inference from mitochondrial cytochrome *b* sequences. Numbers on nodes indicate the posterior probability in percent. NCBI GenBank accession numbers for all sequences are given in front of each species name. Scale bar indicates the number of expected nucleotide changes per site

substitution rate, which might negatively affect the precision of the divergence time estimate). This is equivalent to 6.811 % (6.635 % without *C. kosswigi*) and a divergence time of roughly 6.5 Ma (6.3 Ma without *C. kosswigi*).

Discussion

Taxonomic considerations

Arabibarbus arabicus was described from the vicinity of Sana'a, the capital of Yemen. *Cyprinus arabicus* Valenciennes (ex Ehrenberg) in Cuvier & Valenciennes, 1842 is a possible homonym to *A. arabicus*. The original description does not give a type locality, but Palacky (1895) gives "Gomfuda" (=Al Qunfudhah, Saudi Arabia, 19° 07′ 35″N 41° 04′ 44″E) as the place where this species was found. *Cyprinus arabicus* was described as having a small mouth, short head, very short barbels and a colourful spot behind the upper edge of the operculum (Cuvier and Valenciennes 1842). It is very likely, that *C. arabicus* is a species of *Garra* Hamilton, 1822. This name is not in conflict with the name *A. arabicus*.

Arabibarbus grypus was described from the Tigris at Mosul (Heckel 1843). This species was placed in the genus *Tor* by Karaman (1971). This met poor acceptance (e.g. Krupp 1985; Coad 1995; Abdoli 2000; Krupp and Schneider 2008; Tsigenopoulos et al. 2010; but see Coad 2013 for an exception).

Arabibarbus arabicus, *A. grypus* and *A. hadhrami* form a well-supported monophyletic group (Fig. 8). Members of this group were placed in the genera *Barbus*, *Labeobarbus* and *Tor* by former authors. None of these generic names is available for the group, because their type species [*Cyprinus barbus* Linnaeus, 1758, *Labeobarbus nedgia* Rüppell, 1835 and *Tor hamiltonii* Gray, 1834 respectively] are not closely related to *Arabibarbus*. *Arabibarbus arabicus*, *A. grypus* and *A. hadhrami* do not possess the synapomorphic characters of *Carasobarbus*, six branched rays in the anal fin and nine to 10 brached rays in the dorsal fin (Borkenhagen and Krupp 2013). They differ from *Mesopotamichthys* in having two pairs of barbels instead of no barbels (Karaman 1971). They differ from *Pterocapoeta* by having eight branched dorsal-fin rays as compared to more than nine and lips without horny sheaths (Günther 1902). In addition the phylogenetic analysis does not support grouping *Arabibarbus arabicus*, *A. grypus* and *A. hadhrami* with *Mesopotamichthys* or *Pterocapoeta*. Thus the description of a new genus became necessary.

The validity of the monospecific genera *Mesopotamichthys* and *Pterocapoeta* is supported by my phylogenetic analysis.

Phylogenetic analysis

The tree topology recovered in this study (Fig. 8) is essentially compatible with that recovered by Tsigenopoulos et al. (2010). Only two incompatibilities exist: The first is the position of *Labeobarbus marequensis*, which is sister to *Labeobarbus polylepis* according to their results and sister to the East African species of *Labeobarbus* according to my results. The second is the placement of *Carasobarbus chantrei*. Tsigenopoulos et al. (2010) found it to be sister to *C. kosswigi* while in this study it is sister to *C. luteus*. Both nodes in question received only weak to moderate support in both studies and neither is of any relevance for the phylogenetic placement of *A. hadhrami*.

Biogeographic interpretation

It is possible to infer the biogeographic history of a species by analysing its phylogenetic position as well as its and its relative's present day distribution. Trewavas (1941) hypothesised a close relationship of *A. arabicus* to *Carasobarbus canis* form the Jordan River system. Karaman (1971) and Banister and Clarke (1977) hypothesised a close relationship of *Arabibarbus arabicus* to the East African large barbels. Krupp (1983) follows their opinion and suggests a colonisation over the Red Sea from the West. In contrast, the results of my molecular phylogenetic analysis show that *A. arabicus* and *A. hadhrami* are closely related to *A. grypus*. This implies that the south-western part of Arabia was not colonised from the West, but more likely form the Tigris-Euphrates drainage system in the East. The radiation of the existent species of *Arabibarbus* happened in the Pliocene. The Wādī ar Rimah/Wādī al Bāṭin system connected the Tigris-Euphrates system to the wadis of the al Ḩijāz mountain range during the Pliocene and the Pleistocene (Beineke 2006) and is a possible pathway.

Acknowledgments I am grateful to James Maclaine, Oliver Crimmen, Patrick Campbell (BMNH); Hamid Reza Esmaeili (CBSU); Guy Duhamel, Romain Causse, Patrice Pruvost, Claude Ferrara, Zora Gabsi (MNHN); Ernst Mikschi, Helmut Wellendorf, Christa Prenner, Matthias Reithofer (NMW) and Hort Zetzsche (SMF) for making the collections under their care available for study. I thank Hamid Reza Esmaeili, Friedhelm Krupp, Masoumeh Malek, Alireza Sari and Adwan Shehab for help with organising fieldwork in Iran and Syria and Nisreen Alwan, Mehrgan Ebrahimi, Hamid Reza Esmaeili, Christiane Frosch, Mehdi Ghanbari-Fardi, Zeinab Gholami, Abbas Kazemi, Masoumeh Malek, Majid Moradmand, Hossein Parsa, Sobhan Rahimi, Hassan Rahimian, Bettina Reichenbacher, Hassan Salehi, Azad Teimori and Florian Wicker for their help and company during fieldwork. Amer Al-Shamma'a collected, Nashat Hamidan shipped and Florian Wicker sequenced the samples of *M. sharpeyi*. Heike Kappes and Barbara Herte helped with the laboratory experiments. Tilman Alpermann, Jörg Freyhof, Friedhelm Krupp and Florian Wicker offered valuable comments on the manuscript and Eva Feltkamp prepared the maps.

Fieldwork in Iran and Syria was funded by the German Academic Exchange Service (DAAD), in the framework of the project "Establishment of a Middle Eastern Biodiversity Network". This research received support from the SYNTHESYS Project, which is financed by European Community Research Infrastructure Action under the FP6 "Structuring the European Research Area" Programme (grants AT-2427 and FR-3580). The FAZIT foundation funded research at the BMNH. The study was supported by the Biodiversity and Climate Research Centre (BiK-F), Frankfurt, which is part of research funding programme "LOEWE".

References

Abdoli A (2000) The Inland Water Fishes of Iran [in Farsi]. Iranian Museum of Nature and Wildlife, Tehran

Banister KE (1987) Two new species of *Garra* (Teleostei-Cyprinidae) from the Arabian peninsula. Bull Br Mus Nat Hist Zool 52(1):59–70

Banister KE, Clarke MA (1977) The Freshwater Fishes of the Arabian Peninsula. J Oman Stud (Spec Rep):111–154

Beineke J (2006) Spät-Quartäre Paläogeographie der Arabischen Halbinsel. Universität Paderborn, Paderborn, 201 pp

Berrebi P, Kottelat M, Skelton P, Ráb P (1996) Systematics of *Barbus*: State of the art and heuristic comments. Folia Zool 45(1):5–12

Borkenhagen K, Krupp F (2013) Taxonomic revision of the genus Carasobarbus Karaman, 1971 (Actinopterygii, Cyprinidae). ZooKeys 339:1–53

Briolay J, Galtier N, Brito RM, Bouvet Y (1998) Molecular phylogeny of Cyprinidae inferred from cytochrome b DNA sequences. Mol Phylogenet Evol 9(1):100–108. doi:10.1006/mpev.1997.0441

Chen X, Yang J, Chen Y (1999) A review of the cyprinoid fish genus *Barbodes* Bleeker, 1859, from Yunnan, China, with descriptions of two new species. Zool Stud 38(1):82–88

Coad BW (1995) Freshwater fishes of Iran. Acta Scientiarum Naturalium, Brno 29(1):1–64

Coad BW (2013) Freshwater Fishes of Iran. http://www.briancoad.com/Species%20Accounts/Contents%20new.htm. Accessed 3 August 2013

Coad BW, Alkahem HF, Behnke RJ (1983) *Acanthobrama hadiyahensis*, a new species of cyprinid fish from Saudi Arabia. Natl Mus Nat Sci, Publ Nat Sci 2:1–5

Cuvier G, Valenciennes A (1842) Histoire naturelle des poissons, vol. 16, Paris

Durand JD, Tsigenopoulos CS, Ünlü E, Berrebi P (2002) Phylogeny and Biogeography of the Family Cyprinidae in the Middle East Inferred from Cytochrome *b* DNA - Evolutionary Significance of this region. Mol Phylogenet Evol 22(1):91–100

Fricke R, Eschmeyer WN (2013) Guide to Fish Collections. California Academy of Sciences. Electronic version. http://research.calacademy.org/research/ichthyology/catalog/collections.asp [accessed 15 May 2013]

Gray JE (1834) Illustrations of Indian zoology; chiefly selected from the collection of Major-General Hardwicke, F.R.S. 20 parts in 2 vols

Günther A (1874) Notice of some new species of fishes from Morocco. An Mag Nat Hist 13(75):230–232

Günther A (1902) Third notice of new species of fishes from Morocco. Novitates Zoologicae J Zool Connect Tring Mus 9:446–448

Hamilton F (1822) An account of the fishes found in the river Ganges and its branches. Printed for A. Constable and company [etc., etc.], Edinburgh

He D, Chen Y, Chen Y, Chen Z (2004) Molecular phylogeny of the specialized schizothoracine fishes (Teleostei: Cyprinidae), with their implications for the uplift of the Qinghai-Tibetan Plateau. Chinese Sci Bull 49(1):39–48

Heckel JJ (1843) Ichthyologie. In: Russegger J von (ed) Reisen in Griechenland, Unteregypten, im nördlichen Syrien und südöstlichen Kleinasien: mit besonderer Rücksicht auf die naturwissenschaftlichen Verhältnisse der betreffenden Länder, unternommen in dem Jahre 1836, 1 (2), Stuttgart

Karaman MS (1971) Süßwasserfische der Türkei. 8. Teil. Mitt Hamb Zool Mus Inst 67:175–254

Krupp F (1983) Freshwater fishes of Saudi Arabia and adjacent regions of the Arabian Peninsula. Fauna Saudi Arab 5:568–636

Krupp F (1985) Systematik und Zoogeographie der Süßwasserfische des levantinischen Grabenbruchsystems und der Ostküste des Mittelmeeres, Doctoral Thesis, Johannes Guttenberg - Universität, Mainz, VII+215+169 pp

Krupp F (1988) Freshwatwer Fishes of the Wadi Batha Drainage. J Oman Stud (Spec Rep) 3:401–404

Krupp F, Budd K (2009) A new species of the genus *Garra* (Teleostei: Cyprinidae) from Oman. Aqua Int J Ichthyol 15(2):117–120

Krupp F, Schneider W (2008) Die Fischfauna des Nahr al-Ḫābūr, Nordost-Syrien. In: Kühne H (ed) Umwelt und Subsistenz der assyrischen Stadt Dūr-Katlimmu am unteren Ḫābūr 8. Harrassowitz-Verlag, Wiesbaden, pp 41–51

Linnaeus C (1758) Systema naturae per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis, vol. 1, 10th edn., Holmiae

Machordom A, Doadrio I (2001) Evolutionary history and speciation modes in the cyprinid genus *Barbus*. P Roy Soc Lond B Bio 268(1473):1297–1306

Nylander JAA (2004) MrModeltest v2. Program distributed by the author. Uppsala University, Evolutionary Biology Centre

Palacky J (1895) Die Verbreitung der Fische. Selbstverlag

Rainboth WJ (1985) *Neolissochilus*, a new genus of South Asian cyprinid fishes. Beaufortia 35(3):25–35

Rambaut A, Drummond AJ (2009) Tracer v1.5, Available from http://beast.bio.ed.ac.uk/Tracer

Ronquist F, Huelsenbeck JP (2003) MrBayes 3: Bayesian phylogenetic inference under mixed models. Bioinformatics 19(12):1572–1574. doi:10.1093/bioinformatics/btg180

Rüppell E (1829) Atlas zu der Reise im nördlichen Afrika. Fische des Rothen Meers, vol. 2. Heinrich Ludwig Brönner, Frankfurt am Main

Rüppell E (1835) Neuer Nachtrag von Beschreibungen und Abbildungen neuer Fische, im Nil entdeckt. Mus Senckenberg 2(1):1–28

Tamura K, Peterson D, Peterson N, Stecher G, Nei M, Kumar S (2011) MEGA5: Molecular evolutionary genetics analysis using maximum likelihood, evolutionary distance, and maximum parsimony methods. Mol Biol Evol 28(10):2731–2739. doi:10.1093/molbev/msr121

Trewavas E (1941) 3. Freshwater fishes. British Museum (Natural History) expedition to southwest Arabia 1937–8 1 (3):7–15

Tsigenopoulos CS, Berrebi P (2000) Molecular phylogeny of north mediterranean freshwater barbs (genus *Barbus*: Cyprinidae) inferred from cytochrome b sequences: biogeographic and systematic implications. Mol Phylogenet Evol 14(2):165–179. doi:10.1006/mpev.1999.0702

Tsigenopoulos CS, Kasapidis P, Berrebi P (2010) Phylogenetic relationships of hexaploid large-sized barbs (genus *Labeobarbus*, Cyprinidae) based on mtDNA data. Mol

Phylogenet Evol 56(2):851–856. doi:10.1016/j.ympev.2010.02.006

Tsigenopoulos CS, Ráb P, Naran D, Berrebi P (2002) Multiple origins of polyploidy in the phylogeny of southern African barbs (Cyprinidae) as inferred from mtDNA markers. Heredity 88(6):466–473

Villwock W, Scholl A, Krupp F (1983) Zur Taxonomie, Verbreitung und Speziation des Formenkreises *Aphanius dispar* (Rüppell, 1828) und Beschreibung von *Aphanius sirhani* n. sp. (Pisces: Cyprinodontidae). Mitt Hamb Zool Mus Inst 80:251–277

Erklärung zu den Autorenanteilen

an der Publikation:	**Molecular phylogeny of the tribe Torini Karaman, 1971 (Actinopterygii: Cypriniformes) from the Middle East and North Africa**
Status:	publiziert
Name der Zeitschrift:	Zootaxa
Beteiligte Autoren:	Kai Borkenhagen

Was hat der Promovierende bzw. was haben die Koautoren beigetragen?
(1) zu Entwicklung und Planung
Promovierender: 100 %

(2) zur Durchführung der einzelnen Untersuchungen und Experimente
Promovierender: 100 % KB hat alle Laborarbeiten zur DNS-Sequenzierung durchgeführt.

(3) zur Erstellung der Datensammlung und Abbildungen
Promovierender: 100 % KB hat alle Daten zusammengetragen und alle Abbildungen erstellt.

(4) zur Analyse und Interpretation der Daten
Promovierender: 100 % KB hat alle Daten analysiert und die Ergebnisse der Analysen interpretiert.

(5) zum Verfassen des Manuskripts
Promovierender: 100 %

Unterschrift Promovend: ____________________________ Datum/Ort: __________________

Zustimmende Bestätigungen der oben genannten Angaben

Unterschrift Betreuer: ______________________________ Datum/Ort: __________________

Zootaxa 4236 (2): 291–301
http://www.mapress.com/j/zt/

Copyright © 2017 Magnolia Press

Article

ISSN 1175-5326 (print edition)
ZOOTAXA
ISSN 1175-5334 (online edition)

https://doi.org/10.11646/zootaxa.4236.2.4
http://zoobank.org/urn:lsid:zoobank.org:pub:30698E58-7526-487C-ACC2-BF7ABB48A29F

Molecular phylogeny of the tribe Torini Karaman, 1971 (Actinopterygii: Cypriniformes) from the Middle East and North Africa

KAI BORKENHAGEN[1,2,3]

[1]*Senckenberg Research Institute and Museum of Nature, Senckenberganlage 25, 60325 Frankfurt am Main, Germany*
[2]*Research and Technology Centre (FTZ), University of Kiel, Hafentörn 1, 25761 Büsum, Germany.*
E-mail: kai.borkenhagen@ftz-west.uni-kiel.de
[3]*Johann Wolfgang Goethe-Universität Frankfurt am Main, Fachbereich Biowissenschaften, 60438 Frankfurt, Germany*

Abstract

Freshwater fishes of the cyprinid tribe Torini are widespread in Africa the Middle East and Indomalaya. The relationships of Middle-Eastern Torini are analysed based on mitochondrial markers (Cyt b, ND4) of the majority of relevant species. I present a larely well resolved phylogeny, which confirms the validity of the morphologically defined genera *Arabibarbus*, *Carasobarbus*, *Mesopotamichthys* and *Pterocapoeta*. The Torini originated in Indomalaya and colonised Africa via the Middle East. Morocco was colonised two times independently, first from sub-Saharan Africa and secondly along the southern margin of the Mediterranean Sea. The Tigris–Euphrates system is an important crossroad for the colonisation of the Jordan River, the Orontes River and the watercourses of the Arabian Peninsula by freshwater fishes. The Jordan lost its connection to the Euphrates earlier than the Orontes. The Arabian Peninsula was colonised from the Tigris–Euphrates system in at least two independent events.

Key words: Cyprinidae, Cyprininae, Arabia, Levant, Mesopotamia, Maghreb

Introduction

The exchange of terrestrial and limnetic organisms between Africa and Eurasia began, when the *Gomphotherium* landbridge was formed during the early Miocene, about 19 Ma ago (Harzhauser *et al.* 2007). This event facilitated the colonisation of the Arabian Peninsula and Africa by cyprinids coming from Eurasia (Couvering 1977, Cavender 1991, Otero 2001, Tang *et al.* 2009).

Members of the tribe Torini Karaman, 1971 are tetraploid or hexaploid (Arai 2011, Berrebi *et al.* 2014) cyprinids (family Cyprinidae) with large scales and a smooth and ossified last unbranched dorsal-fin ray. They belong to the subfamily Cyprininae (Yang *et al.* 2015) and are widespread in Africa, the Middle East and the Indomalayan biogeographic realm. In the Middle East and North Africa, they are represented by the genera *Arabibarbus*, *Carasobarbus*, *Mesopotamichthys* and *Pterocapoeta* and the hitherto unclassified species '*Labeobarbus*' *reinii* (Günther, 1874). Together with the genera *Labeobarbus* (including *Varicorhinus*) from sub-Saharan Africa these genera form a monophyletic group, which is characterised by having 2n≈150 chromosomes and thus being evolutionary hexaploid (Tsigenopoulos *et al.* 2010, Borkenhagen 2014). The evolutionary tetraploid (2n≈100) Indomalayan genera *Neolissochilus*, *Tor*, *Hypselobarbus*, *Naziritor*, *Osteochilichthys* and *Lepidopygopsis* are their closest relatives (Yang *et al.* 2015). The hexaploid lineage of Torini is possibly the result of a hybridisation between tetraploid Torini and diploid (2n≈50) *Cyprinion*-like ancestors that probably took place during the colonisation of the Middle East and Africa (Yang *et al.* 2015).

This study is based on a nearly complete taxon sampling of Middle Eastern and Northern African Torini. *Arabibarbus arabicus* (Trewavas, 1941) and '*Labeobarbus*' *reinii* are the only relevant species missing from the dataset, because no fresh material was available for sequencing. Many species are represented by several sequences from different localities, in order to account for geographic diversity and intraspecific variability. The objectives of the study are to (1) reconstruct the phylogenetic relationship of the Middle Eastern species, (2) evaluate the present

Accepted by J. Freyhof: 5 Jan. 2017; published: 23 Feb. 2017

taxonomic status from a phylogenetic point of view and (3) to draw conclusions on the factors that governed the evolution of Torini.

Material and methods

DNA extraction, amplification and sequencing. The material used in the phylogenetic analysis is listed in the supplementary material S1. DNA extraction was performed with the DNeasy Blood & Tissue Kit (QIAGEN), according to the manufacturer's instructions for ethanol-fixed tissue samples. The mitochondrial cytochrome *b* gene was amplified with the primers H15891 (5′ GTT TGA TCC CGT TTC GTG TA 3′) and L15267 (5′ AAT GAC TTG AAG AAC CAC CGT 3′) as well as H16461 (5′ CTT CGG ATT ACA AGA CC 3′) and L15803 (5′ TGA GGG GGA TTT TCA GTA GA 3′) (Briolay *et al.* 1998, Tsigenopoulos *et al.* 2002). The mitochondrial ND4 gene and the tRNAs for histidine and serine were amplified with the primers H11618 (5′ TGG CTK ACK GAK GAG TAK GC 3′) and L10681 (5′ GCK TTT TCT GCK TGT GAR GC 3′) as well as H12296 (5′ CAA GAG TTT TTG GTT CCT AAG 3′) and L11427 (5′ CCW AAG GCS CAT GTW GAR GC 3′) (Miya *et al.* 2006). In cases where these primers proved ineffective, the internal primers were modified. For cytochrome *b* 5′ RTT TGA TCC TGT TTC GTG GA 3′ was used instead of H15891 and 5′ TGR GGR GGA TTT TCA GTA GA 3′ was used instead of L15803. For ND4 5′ TGR CTY ACA GAT GAR TAR GC 3′ was used instead of H11618 and 5′ CCA AAA GCR CAY GTA GAR GC 3′ was used instead of L11427. The PCR protocol encompassed an initial cycle at 94 °C for 2 min, 50 °C for 1 min and 71 °C for 1 min, 35 cycles at 94 °C (20 s), 50 °C (30 s), 71 °C (40 s), and final extension at 71 °C (1 min). PCR products were purified and then sequenced from both ends with the same primers with a standard cycle sequencing chemistry, Bigdye 3.1 (Applied Biosystems) according to the manufacturer's instructions. Sequences were assembled in SeqMan (Lasergene).

Phylogenetic analysis. The dataset for the phylogenetic analysis consists of the partial gene for the mitochondrially encoded NADH dehydrogenase subunit 4 (ND4, 1370 bp), the tRNA for histidine and part of the tRNA for serine (tRNAs, 134 bp) and the complete mitochondrial gene for cytochrome *b* (Cyt *b*, 1267 bp). The dataset encompasses original sequences for 118 taxa and sequences for 23 additional taxa from NCBI GenBank (supplementary material S1). The distantly related cyprinid species *Alburnus alburnus* (Linnaeus, 1758) was used to root the tree.

The alignment and sequence statistics were performed with MEGA version 6 (Tamura *et al.* 2013).

Two independent phylogenetic analyses were performed: 1) on the unpartitioned alignment and 2) on an alignment split into three partitions (ND4, tRNAs and Cyt *b*), with independent nucleotide substitution model and unique parameters for each partition. The reason for these two approaches was to safeguard against potential problems with overparametrisation in the partitioned dataset.

For the Bayesian analysis a suitable nucleotid substitution model was proposed by AIC and AICc in jModelTest 2.1.10 (Guindon & Gascuel 2003, Darriba *et al.* 2012; Table 1). MrBayes 3.1.2 (Ronquist & Huelsenbeck 2003) was run for 7500000 generations in two independent runs. One tree was sampled each 1000 generations and the first 1001 trees of each run were discarded as burnin (supplementary material S2). This resulted in a total of 13000 trees sampled. Effective sample size for each model parameter was checked with Tracer version 1.5 (Rambaut & Drummond 2009).

TABLE 1. Nucleotide substitution models proposed for the different datasets/partitions by AIC and AICc in jModelTest 2.1.10 and settings used for the analysis in MrBayes 3.1.2.

Dataset	Unpartitioned	ND4	Cyt b	tRNAs
proposed model	GTR+I+G	GTR+I+G	GTR+I+G	GTR+G
MrBayes parameters	nst = 6 rates = invgamma	nst = 6 rates = invgamma	nst = 6 rates = invgamma	nst = 6 rates = gamma

Results

The 141 sequences yielded an alignment of 2771 basepairs and contained insertions and deletions in several sequences (Table 2).

Tree topologies and posterior probabilities derived from the partitioned and unpartitioned datasets were virtually identical (supplementary material S3-6). The analysis of the unpartitioned alignment encompassed 14 parameters and the effective sample size was between 367 and 5346 for all parameters. The analysis of the partitioned alignment encompassed 40 parameters and the effective sample size was between 271 and 13000 for all parameters. In all analyses the two parallel runs showed good convergence and the resulting trees were pooled and analysed together. Due to the similar outcomes of both analyses, only the result of the partitioned dataset (Figure 1) is described and discussed in the following.

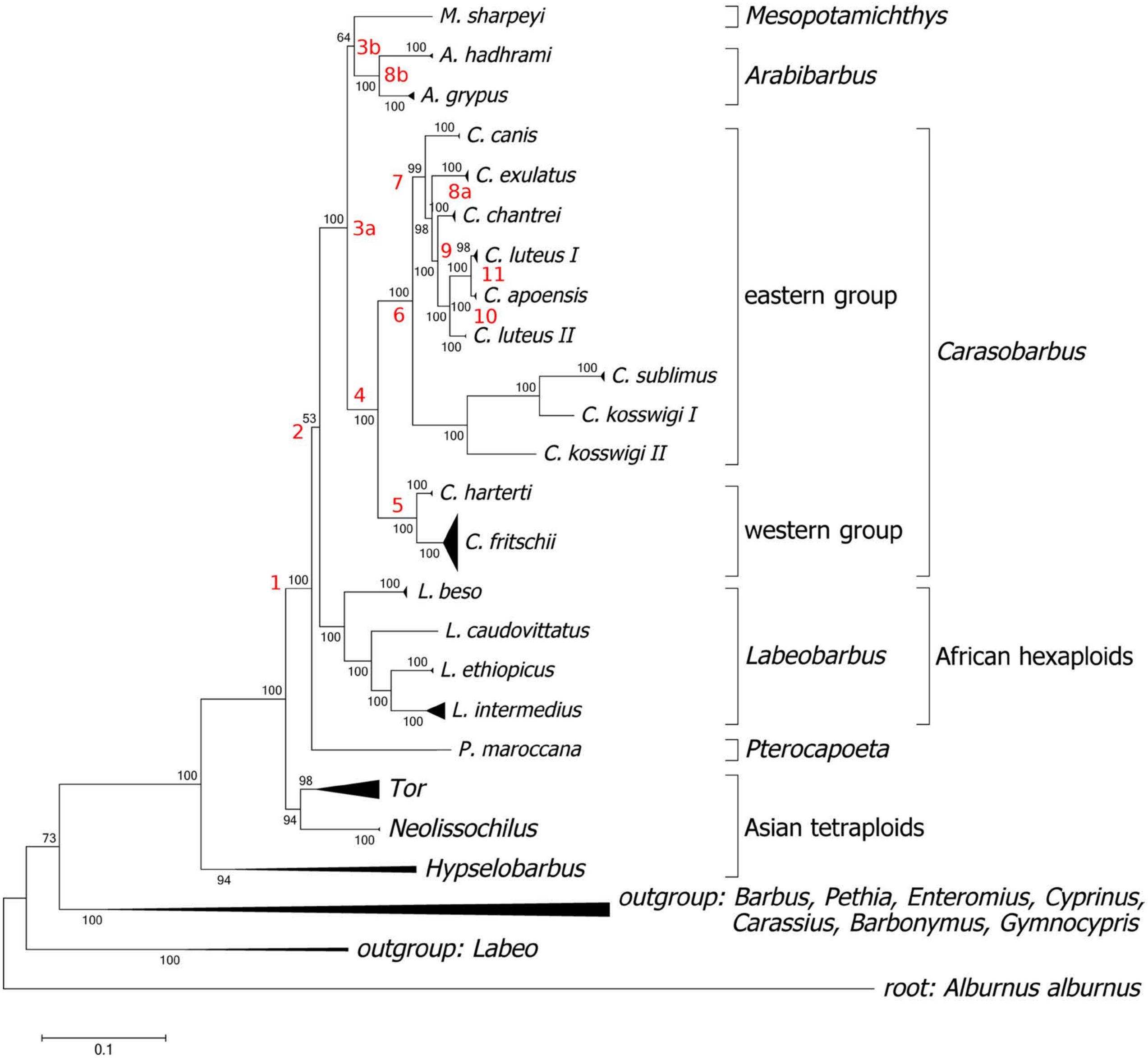

FIGURE 1. Maximum likelihood phylogram based on a set of mitochondrial markers and derived by Bayesian inference. Support values (posterior probability in percent) are shown beside each node. Monophyletic clades of several sequences were collapsed in order to achieve a clearer arrangement of taxa.

The genus *Hypselobarbus* is the sister taxon to all other Torini in the phylogram (Figure 1). The tetraploid Indomalayan genera *Neolissochilus* and *Tor* are sister to each other and together form the sister group to the hexaploid Torini from Africa and the Middle East. Within the hexaploid Torini the split between *Pterocapoeta maroccana* and all other species is unresolved. The African genus *Labeobarbus* is the sister group to the Middle Eastern genera *Arabibarbus*, *Carasobarbus* and *Mesopotamichthys*. Within the Middle Eastern species the relationship between *Mesopotamichthys*, *Arabibarbus* and *Carasobarbus* is not resolved. Within *Carasobarbus* the western species *C. fritschii* (Günther, 1874) and *C. harterti* (Günther, 1901) are sister to each other and together form the sister group to the eastern species *C. apoensis* (Banister & Clarke, 1977), *C. canis* (Valenciennes in Cuvier & Valenciennes, 1842), *C. chantrei* (Sauvage, 1882), *C. exulatus* (Banister & Clarke, 1977), *C. kosswigi* (Ladiges, 1960), *C. luteus* (Heckel, 1843) and *C. sublimus* (Coad & Najafpour, 1997). *Carasobarbus sublimus* clusters within *C. kosswigi*. *Carasobarbus kosswigi* and *C. sublimus* are sister to the rest of the eastern species. *Carasobarbus canis* from the Jordan River is sister to *C. apoensis*, *C. chantrei*, *C. exulatus* and *C. luteus*. *Carasobarbus exulatus* from the Arabian Peninsula is sister to *C. apoensis*, *C. chantrei* and *C. luteus*. *Carasobarbus chantrei* from the Orontes River is sister to *C. apoensis* and *C. luteus*. *Carasobarbus apoensis* from the Arabian Peninsula clusters between two divergent lineages of *C. luteus*. One atypical specimen of *C. exulatus* (SMF 30784) clusters with *A. hadhrami* Borkenhagen, 2014.

TABLE 2. Details of gene mutations found in the sequence alignment.

Species name	GenBank No.	Type of mutation	Gene	Alignment pos.
A. alburnus	AB239593	insertion	tRNA histidine	1371
C. sublimus	KU575125	insertion	tRNA serine	1452
C. sublimus	KU575126	insertion	tRNA serine	1452
C. sublimus	KU575127	insertion	tRNA serine	1452
C. sublimus	KU575128	insertion	tRNA serine	1452
C. sublimus	KU575129	insertion	tRNA serine	1452
C. sublimus	KU575130	insertion	tRNA serine	1452
P. ticto	AB238969	deletion	tRNA serine	1483
T. putitora	KC914620	deletion	Cyt *b*	1534
T. putitora	KC914620	insertion	Cyt *b*	1550
T. tambroides	JX444718	insertion	Cyt *b*	2390 to 2502
E. trimaculatus	AB239600	insertion	Cyt *b*	2752 to 2763

Discussion

In this study the most complete molecular phylogeny of Torini from the Middle East and North Africa to date is presented. It includes representatives of all four genera and 13 of 15 species of the presently known members of Torini from this region. The majority of branches of the mtDNA based Bayesian tree were well resolved. The effect of partitioning the dataset on tree topology and posterior probabilities was negligible (supplementary material S3-6). This indicates that there was no effect of overparametrisation on the phylogenetic analysis.

Mitochondrial DNA (mtDNA) has certain shortcomings in reconstructing species trees (Yang *et al.* 2012). However, in the case of polyploid species it is very difficult to establish homology of sequences for nuclear DNA, due to the paralogs of each gene (Saitoh *et al.* 2011, Pasco-Viel *et al.* 2014, Yang *et al.* 2012, Yang *et al.* 2015). To avoid this issue, the present study was based on mtDNA.

The resultant phylogeny is discussed in relation to previously published nuclear and mitochondrial gene phylogenies and the current taxonomic status of this group.

Comparison to previously published phylogenies. A phylogram of African and Middle-Eastern hexaploid Torini, based on cytochrome *b*, and with a less complete taxon sampling of species from the Middle East, but more extensive samples of African species (Tsigenopoulos *et al.* 2010), agrees with the phylogram presented here in the general topology of the Indomalayan, Middle-Eastern and African species. The topology within *Carasobarbus* is also similar, but differs in the placement of *C. kosswigi*, which was sister to *C. chantrei* in their analysis.

A cladogram, based on a short fragment of cytochrome *b*and with a less extensive taxon sampling than in the present study (Borkenhagen et al. 2011), yielded essentially the same topology as presented here, but differs in the placement of *C. chantrei*, which is sister to *C. canis* in that analysis. However support values for that branch are very low.

An analysis of cytochrome *b* sequences of several Middle-Eastern Torini (Borkenhagen 2014) differs from the phylogram of the present study in the placement of *Mesopotamichthys*, *Pterocapoeta* and *C. kosswigi*. All nodes in question received only weak statistical support in the study of Borkenhagen (2014).

Recently two phylogenetic hypotheses were presented (Yang *et al.* 2015). One is based on the nuclear marker RAG1 with a limited taxon sampling. The other encompasses a more extensive set of taxa and is based on an alignment of several mitochondrial markers with data gaps for several markers in many species. Cytochrome *b* forms the backbone of this alignment. The topology derived from the RAG1 dataset agrees with the one presented here in the placement of all mutually covered genera (*Labeobarbus* (including *Varicorhinus*), *Carasobarbus*, *Tor*, *Neolissochilus* and *Hypselobarbus*). The topology based on the mitochondrial dataset differs from the one based on RAG1 and the one presented here: *Tor* and *Neolissochilus* are not resolved as sister groups and *Mesopotamichthys* clusters within *Carasobarbus*. The nodes in question received only weak to moderate support, but it is still surprising, because one would expect the two mitochondrial datasets to yield more similar results then a mitochondrial and a nuclear dataset. The good agreement between the RAG1 topology and the topology presented here lends additional credibility to these hypotheses.

Systematic classification and taxonomic considerations. The classification of families and subfamilies in the order Cyprinoidea is not well established and was subject to frequent changes in the past (e.g. Nelson 2006, Saitoh *et al.* 2006, Stiassny & Getahun 2007, Mayden *et al.* 2008, Mayden *et al.* 2009, Yang *et al.* 2010, Yang *et al.* 2012, Yang *et al.* 2015). I follow Yang *et al.* (2015) in regarding Barbini, Schizopygopsini, Schizothoracini, Spinibarbini, Acrossocheilini, Cyprinini, Poropuntiini, Smiliogastrini, Torini, Labeonini and Probarbini as belonging to the subfamily Cyprininae.

The genera *Arabibarbus*, *Carasobarbus*, *Hypselobarbus*, *Labeobarbus* (including *Varicorhinus*), *Mesopotamichthys*, *Neolissochilus*, and *Pterocapoeta* (together with the genera *Osteochilichthys*, *Naziritor* and the species ‘*Labeobarbus*’ *reinii*, which were not included in the present study) form a well-supported monophyletic group (= tribe Torini; Yang *et al.* 2015), characterised by comparatively large scales and a smooth, ossified last unbranched dorsal-fin ray.

Within the Torini, hexaploid species of the Middle East and Africa form a monophyletic group, whereas the tetraploid species from Indomalaya do not (Figure 1; Yang *et al.* 2015).

Some authors proposed to lump all hexaploid Torini in *Labeobarbus* (Tsigenopoulos *et al.* 2010, Berrebi *et al.* 2014, Vreven *et al.* 2016), while others opposed this notion (Borkenhagen et al. 2011, Borkenhagen & Krupp 2013, Borkenhagen 2014, Coad 2015).

Vreven *et al.* (2016) expressed their concern, that accepting the validity of *Arabibarbus*, *Carasobarbus*, *Mesopotamichthys* and *Pterocapoeta* would render *Labeobarbus* paraphyletic. They cite the trees presented in Tsigenopoulos *et al.* (2010) and Berrebi *et al.* (2014) as evidence. From these trees and Yang *et al.* (2015) as well as my tree (Figure 1) it is evident that this is not the case. It merely necessitates a re-evaluation of the status of ‘*Labeobarbus’ habereri* (Steindachner, 1912), ‘*L.’ bynni occidentalis* (Boulenger, 1911), and ‘*L.*’ *reinii*. All other African *Labeobarbus* (including *Varicorhinus*) species form a well-supported monophyletic group (Yang *et al.* 2015). Interestingly, Vreven *et al.* (2016) retain the African genera *Acapoeta* and *Sanagia*, though these two genera are likely to compromise the monophyly of *Labeobarbus*.

The clades in the phylogram (Figure 1) are compatible with the genera *Arabibarbus*, *Carasobarbus*, *Mesopotamichthys*, *Labeobarbus*, *Tor*, *Neolissochilus* and *Hypselobarbus*.

Middle East and North Africa: *Arabibarbus* Borkenhagen, 2014 is diagnosed by medium to large body size, an ossified, smooth last unbranched dorsal-fin ray, modally eight branched dorsal-fin rays, modally five branched anal-fin rays, large, shield-shaped scales with numerous parallel radii, a lateral line with 29 to 44 scales, hooked pharyngeal teeth, numbering 2.3.5-5.3.2 and the possession of two pairs of barbels (Borkenhagen 2014). The genus occurs in Arabia, Mesopotamia and the Iranian tributaries to the Persian Gulf. *Arabibarbus* is represented by two species in the present study and its monophyly is supported by 100 % posterior probability. In Borkenhagen (2014) all three species of *Arabibarbus* where included in an analysis based on cytochrome *b* and the genus received a support level of 100 % posterior probability. Vreven *et al.* (2016) suggested that *Arabibarbus* might be tetraploid. However, it is much more likely that *Arabibarbus* is hexaploid (Tsigenopoulos *et al.* 2010, Berrebi *et al.* 2014).

Carasobarbus Karaman, 1971 is diagnosed by medium body size, ossified, smooth last unbranched dorsal-fin ray, nine or 10 branched dorsal-fin rays, six branched anal-fin rays, large shield-shaped scales with numerous parallel radii, lateral line with 25 to 39 scales, hooked pharyngeal teeth numbering 2.3.5-5.3.2 or 2.3.4-4.3.2 and one or two pairs of barbels (Borkenhagen & Krupp 2013). The genus occurs in the Maghreb, the Levant, Arabia, Mesopotamia and southern Iran (Borkenhagen & Krupp 2013) and is hexaploid (Arai 2011). All species of *Carasobarbus* are represented in the present study and the genus received a support level of 100 % posterior probability. The insertion of 1 bp, detected within the tRNA for serine (position 1452) in *C. sublimus* is possibly a synapomorph character of this species. The specimen SMF 30784 is morphologically intermediate between *A. hadhrami* and *C. exulatus*. It is a possible hybrid between these two species.

The monospecific genus *Mesopotamichthys* Karaman, 1971 is characterised by not having barbels, pharyngeal teeth (2.3.5-5.3.2) intermediate between spoon-shaped and shovel-shaped, developed and fleshy lips, broad orbital bones, short lacrimale, sensory canals on head similar to those of *Tor*, dorsal fin with 8 branched rays, last unbranched ray moderately ossified and smooth, anal fin with 5 branched rays, relatively large scales with numerous parallel or convergent radii and a black peritoneum (Karaman 1971). Its generic distinctness is supported by the phylogram presented here.

'*Labeobarbus*' *reinii* is not represented in the present analysis, because only a cytochrome *b* sequence is available. Tsigenopoulos *et al.* (2010), Berrebi *et al.* (2014), and Yang *et al.* (2015) indicate that '*L.*' *reinii* forms an isolated lineage within the Middle-Eastern lineage of Torini. Should this result be corroborated by further studies, the description of a new genus will be justified.

The genus *Pterocapoeta* Günther, 1902 is presently restricted to one North-African species, *P. maroccana* Günther, 1902 (Eschmeyer 2015). Two cytochrome *b* based studies indicate that '*Labeobarbus*' *bynni occidentalis* (GenBank no. AF180870) and '*Labeobarbus*' *habereri* (AF180869) from sub-saharan Africa are closely related to *P. maroccana* (Tsigenopoulos *et al.* 2010, Yang *et al.* 2015). Although statistical support for this group is low in both studies, a revision of these species may possibly lead to their inclusion in the genus *Pterocapoeta*. The identity of the sequence AF180870 needs verification, because it does not cluster with the other *L. bynni* sequences analysed in Tsigenopoulos *et al.* (2010).

Sub-Saharan Africa: There are about 275 nominal species of Torini in Africa, about 125 of which are currently considered valid (Vreven *et al.* 2016). The genera *Labeobarbus* Rüppell, 1835 and *Varicorhinus* Rüpell, 1835 where originally described, based on differences in the anatomy of the lips and snout (lips thick and fleshy in *Labeobarbus*, lips thin and round snout with cartilaginous tubercles in *Varicorhinus*). Later the sharp horny sheath on the lower jaw became an important character of *Varicorhinus* (Boulenger 1909), but this character is not universally applicable (Tweddle and Skelton 1998, Levin 2012, Vreven *et al.* 2016). These two genera together form a monophyletic lineage within the hexaploid Torini, but are not reciprocally monophyletic (Tsigenopoulos *et al.* 2010, Yang *et al.* 2015). Based on an analysis of the mitochondrial control region Levin *et al.* (2013) suggested that *Varicorhinus* is a monospecific genus. According to Tsigenopoulos *et al.* (2010), Berrebi *et al.* (2014) and Vreven *et al.* (2016), *Varicorhinus* is a synonym of *Labeobarbus*. The monospecific genera *Sanagia* Holly, 1936 and *Acapoeta* Cockerell, 1910 are also members of Torini and probably part of the *Labeobarbus* lineage (Yang *et al.* 2015, Vreven *et al.* 2016). For a detailed review of the African Torini see Vreven *et al.* (2016). A molecular phylogenetic analysis of *Labeobarbus* was presented by Beshera *et al.* (2016).

Indomalaya: Fishes of the genera *Neolissochilus* Rainboth, 1985 and *Tor* Gray, 1834 are referred to as mahseers (Laskar *et al.* 2013, Hoàng *et al.* 2015). *Tor* and *Neolissochilus* are tetraploid (Arai 2011). *Tor* is characterised by a fleshy lobe on the lower lip and higher number of gill rakers on the lower limb of the first gill arch, whereas *Neolissochilus* is characterised by a lower lip generally missing a median lobe and a lower number of gill rakers on the lower limb of the first gill arch (Rainboth 1985, Laskar *et al.* 2013, Hoàng *et al.* 2015). They occur in mountain streams from Afghanistan, Pakistan and India to Southeast Asia up to the Malayan Peninsula and the Indonesian islands Borneo, Java and Sumatra in the south and up to China in the north (Roberts 1999, Laskar *et al.* 2013, Khaironizam *et al.* 2015).

Species of the genus *Hypselobarbus* Bleeker, 1860 are tetraploid (Arai 2011). The genus is characterised by one or two pairs of barbels, long, branched gill rakers, a strongly convex distal margin of the anal fin in adult specimens with branched anal-fin rays 2–4 considerably longer than the first branched ray (Knight *et al.* 2013). *Hypselobarbus* are endemic to the rivers of peninsular India, with the Western Ghats being the core area of their distribution (Arunachalam *et al.* 2012). They are potamodromous and omnivorous, usually attain a size of 25 – 100 cm. They are fished and reared in aquaculture for human consumption (Arunachalam *et al.* 2012). Recently, a molecular (Arunachalam *et al.* 2012) and a morphological revision (Knight *et al.* 2013) of the genus were presented. *Barbodes carnaticus* (Jerdon, 1849) might be a member of *Hypselobarbus* (Arunachalam *et al.* 2012). The description of more *Hypselobarbus* species in the future is likely (Arunachalam *et al.* 2012). Knight *et al.* (2013) treat *Hypselobarbus* as a valid genus and *Gonoproktopterus* as a synonym, whereas Khare *et al.* (2014) treat *H. mussullah* (Sykes, 1839), the type species of *Hypselobarbus*, as a member of the genus *Tor*. There was confusion regarding the validity of the genus *Hypselobarbus* and the number of species it contains (Arunachalam *et al.* 2014, Khare *et al.* 2014, Knight *et al.* 2014), but the issue was settled by the designation of a neotype for *Barbus mussullah* (Knight *et al*. 2014). The species of *Hypselobarbus* analysed here form a well-supported monophyletic group and are genetically clearly distinct from *Tor* (Figure 1).

Naziritor Mirza & Javed, 1985 is part of the Torini (Khare *et al.* 2014, Yang *et al.* 2015).

Osteochilichthys Hora, 1942 is a genus currently represented by four species from southern India (Eschmeyer 2015) and characterised by a lower jaw with a sharp trenchant edge, a slightly papillated or smooth lower lip that is adnate to the lower jaw but not covering the cutting edge, upper lip fimbriated or entire, adnate to upper jaw, a rostral fold that overhangs the median part of the upper lip in adults, snout covered with tubercles, last unbranched ray of dorsal fin not ossified and not serrated and 10 to 11 branched dorsal-fin rays (Pethiyagoda & Kottelat 1994).

Lepidopygopsis Raj, 1941 was found to be closely related to *Hypselobarbus* species and thus part of the Torini in two molecular phylogenetic studies, based on the same cytochrome *b* sequences (Dahanukar *et al.* 2013, Yang *et al.* 2015). It resembles schizothoracines in having a sheath of enlarged scales covering the belly and the base of the anal fin, a serrated last unbranched dorsal-fin ray and a lateral line that is distinctly curved in the caudal region (Dahanukar *et al.* 2013). Because of its striking morphological dissimilarity to other Torini the phylogenetic position and evolutionary origin of *Lepidopygopsis* should be reappraised using independent data (i.e. specimens identified and analysed independently).

Phylogenetic interpretation and evolution of Torini. Torini originated in Asia (Saitoh *et al*. 2011) and colonised Africa via the Middle East. This is also evident from the fact that the African and Middle Eastern Torini cluster within the Indomalayan Torini (Yang *et al.* 2015, Figure 1). The African and Middle Eastern Torini (Figure 1: 1) are characterised by being hexaploid (Arai 2011, Tsigenopoulos *et al.* 2010, Berrebi *et al.* 2014). They share the possession of a smooth last unbranched dorsal-fin ray and large scales with numerous parallel radii with the related tetraploid Asian genera of Torini. Hexaploidy might result from hybridisation of tetraploid Torini and *Cyprinion*-like cyprinids (Yang *et al.* 2015). This hybridisation event probably occurred in the Middle East during the westward range extension of the Torini, because no hexaploid Torini are known from Indomalaya.

The split between *Pterocapoeta*, the African hexaploids and the Middle Eastern hexaploids (Figure 1: 2) is unresolved. *Pterocapoeta* is the relict of an early colonisation of Morocco by freshwater fishes from sub-Saharan Africa.

The relationship between *Arabibarbus*, *Carasobarbus* and *Mesopotamichthys* (Figure 1: 3a+b) is unresolved. These genera probably split during the late Miocene or Pliocene (Tsigenopoulos *et al.* 2010, Borkenhagen 2014).

Morocco was colonised by Torini for a second time. This time *Carasobarbus* species (and probably the ancestor of *'L.' reinii*) came from the Middle East along the southern margin of the Mediterranean Sea, possibly during the 'Lago Mare' phase of the Messinian salinity crisis (5.5 to 5.33 MA bp; Krijgsman *et al.* 1999). This lead to the split between the eastern and western group of *Carasobarbus* (Figure 1: 4). The reasons for the split between *C. fritschii* and *C. harterti* (Figure 1: 5) are unclear. These two species occur sympatrically in part of their range (Borkenhagen & Krupp 2013) and both, sympatric speciation and allopatric speciation with secondary contact, seem possible.

The split between *C. kosswigi* and *C. sublimus* on the one hand and the rest of the eastern group of *Carasobarbus* on the other hand (Figure 1: 6) might be attributed to ecological factors. In contrast to other *Carasobarbus* species *C. kosswigi* and *C. sublimus* have a specialised mouth shape and are adapted to fast flowing waters (Borkenhagen *et al.* 2011, Borkenhagen & Krupp 2013).

The Jordan River was connected to the Tigris–Euphrates system, which is evident by the presence of faunal elements of the Jordan and the Euphrates in the Damascus oasis and the Al-Azraq oasis (Por 1989, Heller 2007). The end of the connection between Jordan and Euphrates separated the ancestors of *C. canis* from the lineage that gave rise to *C. apoensis*, *C. chantrei*, *C. exulatus* and *C. luteus* (Figure 1: 7).

The Arabian Peninsula was colonised from the Tigris–Euphrates system in the east, probably during the Pliocene (Borkenhagen 2014). The Wādī ar Rimah / Wādī al Bāţin or other ancient Arabian wadi systems are possible pathways (Beineke 2006, Borkenhagen 2014). This event gave rise to *A. arabicus*, *A. hadhrami* and *C. exulatus* (Figure 1: 8a+b).

Part of the present Orontes River was connected to the Tigris–Euphrates system. The termination of this connection gave rise to *C. chantrei* (Figure 1: 9).

Carasobarbus luteus is divided into two lineages. Lineage I contains sequences from the entire range of the species, whereas lineage II contains two sequences from the Khabur River in Syria, where it occurs sympatrically with lineage I. The same effect was already described and discussed in an earlier paper, based on a restricted number of nucleotides (Borkenhagen *et al.* 2011). It is probably a case of retained ancient polymorphism (Borkenhagen *et al.* 2011). The event that gave rise to *C. luteus* lineage II (Figure 1: 10) remains unknown.

The separation between *C. luteus* lineage I and *C. apoensis* (Figure 1: 11) occurred recently as the genetic difference between them is low.

In several of the species with a wide range of distribution (e.g. *C. fritschii* and *L. intermedius* (Rüppell, 1835)) there is some degree of intraspecific genetic variability, which reflects the different river drainage basins (supplementary material S3-6).

Conclusions

The hexaploid Torini from Africa and the Middle East originated in the Indomalayan realm and form a well-supported monophyletic group. The morphologically defined genera *Arabibarbus*, *Carasobarbus*, *Labeobarbus*, *Mesopotamichthys* and *Pterocapoeta* are recovered as monophyletic groups in the molecular phylogenetic analysis, the genus *Varicorhinus* is not and is a synonym of *Labeobarbus*, as proposed by Tsigenopoulos *et al.* (2010), Berrebi *et al.* (2014) and Vreven *et al.* (2016). The (generic) status of '*Labeobarbus' reinii*, '*L.*' *habereri* and '*L.*' *bynni occidentalis* is unclear and a revision is necessary. The Maghreb was colonised by Torini during two independent events via different routes. The Tigris–Euphrates system played an important role in colonisation of the Middle East by freshwater fishes. The Jordan River lost its connection to the Tigris–Euphrates system earlier than the Orontes and the Arabian Peninsula was colonised from the Tigris–Euphrates system in the east via ancient wadi systems.

Acknowledgements

In memory of Horst Zetzsche, who provided invaluable support during my work at Senckenberg.

I thank Nisreen Alwan, Zuhair Amr, Abdelhamid Azeroual, Mehrgan Ebrahimi, Hamid Reza Esmaeili, Jörg Freyhof, Christiane Frosch, Mehdi Ghanbari-Fardi, Zeinab Gholami, Abbas Kazemi, Friedhelm Krupp, Masoumeh Malek, Nadia Manasfi, Majid Moradmand, Hossein Parsa, Sobhan Rahimi, Hassan Rahimian, Bettina Reichenbacher, Hassan Salehi, Alireza Sari, Adwan Shehab, Azad Teimori, Florian Wicker and for help with organising and participating in fieldwork in Iran, Jordan, Morocco, Saudi Arabia and Syria.

Friedhelm Krupp, Edouard Lavergne, Matthias Schneider, Wolfgang Schneider and Uwe Zajonz conducted fieldwork in Yemen and generously provided specimens and tissue samples.

I am grateful to Jörg Freyhof, Stéphane Ostrowski and Johannes Els for providing additional specimens and finclips. Amer Al-Shamma'a collected, Nashat Hamidan shipped and Florian Wicker sequenced the samples of *M. sharpeyi*.

Heike Kappes and Barbara Herte helped with the laboratory analyses. I acknowledge the Grunelius-Möllgaard Laboratory at SMF for lab support.

Tilman Alpermann, , Friedhelm Krupp and Florian Wicker offered valuable comments on the manuscript.

Part of the fieldwork was funded by the German Academic Exchange Service (DAAD), in the framework of the project "Establishment of a Middle Eastern Biodiversity Network". Field work in Yemen was supported by the Coastal Zone Management Pilot Project of the Environment Protection Authority Yemen and the World Bank and received financial support from grant TF 023492 of the Global Environment Facility.

References

Arai, R. (2011) *Fish Karyotypes: A Check List*. Springer, Tokyo, 348 pp.

Arunachalam, M., Chinnaraja, S., Chandran, A. & Mayden, R.L. (2014) On the identities of *Cyprinus* (=*Hypselobarbus*) *curmuca* Hamilton, *Barbus* (=*Hypselobarbus*) *kolus* Sykes, and *Hypselobarbus kurali* Menon and Rema Devi (Cypriniformes: Cyprinidae), with descriptions of three new species of *Hypselobarbus* from peninsular India. *Species*, 11, 72–94.

Arunachalam, M., Raja, M., Muralidharan, M. & Mayden, R.L. (2012) Phylogenetic Relationships of Species of *Hypselobarbus* (Cypriniformes: Cyprinidae): An Enigmatic Clade Endemic to Aquatic Systems of India. *Zootaxa*, 3499, 63–73.

Beineke, J. (2006) *Spät-Quartäre Paläogeographie der Arabischen Halbinsel*. Paderborn University, Paderborn, 201 pp.

Berrebi, P., Chenuil, A., Kotlík, P., Machordom, A. & Tsigenopoulos, C.S. (2014) Disentangling the evolutionary history of the genus *Barbus sensu lato*, a twenty years adventure. *In*: Alves, M.J., Cartaxana, A., Correia, A.M. & Lopes, L.F. (Eds.), *Professor Carlos Almaça (1934–2010). Estado da Arte em Áreas Cientícas que Desenvolveu.* Museu Nacional de História Natural e da Ciência, Lisboa, pp. 29–55.

Beshera, K.A., Harris, P.M. & Mayden, R.L. (2016) Novel evolutionary lineages in *Labeobarbus* (Cypriniformes; Cyprinidae) based on phylogenetic analyses of mtDNA sequences. *Zootaxa*, 4093 (3), 363–381.
https://doi.org/10.11646/zootaxa.4093.3.4

Borkenhagen, K. (2014) A new genus and species of cyprinid fish (Actinopterygii, Cyprinidae) from the Arabian Peninsula, and its phylogenetic and zoogeographic affinities. *Environmental Biology of Fishes*, 97, 1179–1195.
https://doi.org/10.1007/s10641-014-0315-y

Borkenhagen, K., Esmaeili, H.R., Mohsenzadeh, S., Shahryari, F. & Gholamifard, A. (2011) The molecular systematics of the *Carasobarbus* species from Iran and adjacent areas, with comments on *Carasobarbus albus* (Heckel, 1843). *Environmental Biology of Fishes*, 91, 327–335.
https://doi.org/10.1007/s10641-011-9787-1

Borkenhagen, K. & Krupp, F. (2013) Taxonomic revision of the genus *Carasobarbus* Karaman, 1971 (Actinopterygii, Cyprinidae). *ZooKeys*, 339, 1–53.
https://doi.org/10.3897/zookeys.339.4903

Boulenger, G.A. (1909) *Catalogue of the fresh-water fishes of Africa in the British Museum (Natural History)*. Taylor & Francis, London, xi + 373 pp.

Briolay, J., Galtier, N., Brito, R.M. & Bouvet, Y. (1998) Molecular phylogeny of Cyprinidae inferred from cytochrome b DNA sequences. *Molecular Phylogenetics and Evolution*, 9, 100–108.
https://doi.org/10.1006/mpev.1997.0441

Cavender, T.M. (1991) The fossil record of Cyprinidae. *In:* Winfield, I.J. & Nelson, J.S. (Eds.), *Cyprinid Fishes. Systematics, biology and exploitation.* Springer, Dordrecht, pp. 34–54.
https://doi.org/10.1007/978-94-011-3092-9_2

Coad, B.W. (2015) Freshwater Fishes of Iran. Available from: http://www.briancoad.com/Species%20Accounts/Contents%20new.htm (accessed 3 August 2015)

Couvering, J.A.H. van (1977) Early Records of Freshwater Fishes in Africa. *Copeia*, 1977, 163.
https://doi.org/10.2307/1443521

Dahanukar, N., Philip, S., Krishnakumar, K., Ali, A. & Raghavan, R. (2013) The phylogenetic position of *Lepidopygopsis typus* (Teleostei: Cyprinidae), a monotypic freshwater fish endemic to the Western Ghats of India. *Zootaxa*, 3700 (1), 113–139.
https://doi.org/10.11646/zootaxa.3700.1.4

Darriba, D., Taboada, G.L., Doallo, R. & Posada, D. (2012) jModelTest 2: more models, new heuristics and parallel computing. *Nature Methods*, 9, 772.
https://doi.org/10.1038/nmeth.2109

Eschmeyer, W.N. (2015) Catalog of Fishes: Genera, Species, References. Electronic version. Available from: http://research.calacademy.org/research/ichthyology/catalog/fishcatmain.asp (accessed 1 March 2015)

Guindon, S. & Gascuel, O. (2003) A Simple, Fast, and Accurate Algorithm to Estimate Large Phylogenies by Maximum Likelihood. *Systematic Biology*, 52, 696–704.
https://doi.org/10.1080/10635150390235520

Harzhauser, M., Kroh, A., Mandic, O., Piller, W.E., Göhlich, U., Reuter, M. & Berning, B. (2007) Biogeographic responses to geodynamics: A key study all around the Oligo–Miocene Tethyan Seaway. *Zoologischer Anzeiger - A Journal of Comparative Zoology*, 246, 241–256.
https://doi.org/10.1016/j.jcz.2007.05.001

Heller, J. (2007) A historic biogeography of the aquatic fauna of the Levant. *Biological Journal of the Linnean Society*, 92, 625–639.
https://doi.org/10.1111/j.1095-8312.2007.00850.x

Hoàng, H.Đ., Phạm, H.M., Durand, J.D., Trần, N.T. & Phan, P.Đ. (2015) Mahseers genera *Tor* and *Neolissochilus* (Teleostei: Cyprinidae) from southern Vietnam. *Zootaxa*, 4006 (3), 551–568.
https://doi.org/10.11646/zootaxa.4006.3.8

Karaman, M.S. (1971) Süßwasserfische der Türkei. 8. Teil. *Mitteilungen aus dem Hamburgischen Zoologischen Museum und Institut*, 67, 175–254.

Khaironizam, M.Z., Akaria-Ismail, M. & Armbruster, J.W. (2015) Cyprinid fishes of the genus *Neolissochilus* in Peninsular Malaysia. *Zootaxa*, 3962 (1), 139–157.
https://doi.org/10.11646/zootaxa.3962.1.7

Khare, P., Mohindra, V., Barman, A.S., Singh, R.K. & Lal, K.K. (2014) Molecular evidence to reconcile taxonomic instability in mahseer species (Pisces: Cyprinidae) of India. *Organisms Diversity & Evolution*, 14, 307–326. https://doi.org/10.1007/s13127-014-0172-8

Knight, J.D.M., Rai, A. & D'souza, R.K.P. (2013) On the identities of *Barbus mussullah* Sykes and *Cyprinus curmuca* Hamilton with notes on the status of *Gobio canarensis* Jerdon (Teleostei: Cyprinidae). *Zootaxa*, 3750 (3), 201–215. https://doi.org/10.11646/zootaxa.3750.3.1

Knight, J.D.M., Rai, A. & D'souza, R.K.P. (2014) A further note on the identity of *Barbus mussullah* Sykes (Teleostei: Cyprinidae). *Zootaxa*, 3821 (2), 280–284. https://doi.org/10.11646/zootaxa.3821.2.8

Krijgsman, W., Hilgen, F.J., Raffi, I., Sierro, F.J. & Wilson, D.S. (1999) Chronology, causes and progression of the Messinian salinity crisis. *Nature*, 400, 652–655. https://doi.org/10.1038/23231

Laskar, B.A., Bhattacharjee, M.J., Dhar, B., Mahadani, P., Kundu, S., Ghosh, S.K. & Laudet, V. (2013) The Species Dilemma of Northeast Indian Mahseer (Actinopterygii: Cyprinidae): DNA Barcoding in Clarifying the Riddle. *PLoS ONE*, 8, e53704. https://doi.org/10.1371/journal.pone.0053704

Levin, B.A. (2012) New data on morphology of the African scraping feeder *Varicorhinus beso* (Osteichthyes: Cyprinidae) with the special reference to specialized traits. *Journal of Ichthyology*, 52, 908–923. https://doi.org/10.1134/S0032945212110069

Levin, B.A., Golubtsov, A.S., Dgebuadze, Y.Y. & Mugue, N.S. (2013) New evidence of homoplasy within the African genus *Varicorhinus* (Cyprinidae): an independent origin of specialized scraping forms in the adjacent drainage systems of Ethiopia inferred from mtDNA analysis. *African Zoology*, 48, 400–406. https://doi.org/10.1080/15627020.2013.11407609

Mayden, R.L., Chen, W.J., Bart, H.L., Doosey, M.H., Simons, A.M., Tang, K.L., Wood, R.M., Agnew, M.K., Yang, L., Hirt, M.V., Clements, M.D., Saitoh, K., Sado, T., Miya, M. & Nishida, M. (2009) Reconstructing the phylogenetic relationships of the earth's most diverse clade of freshwater fishes-order Cypriniformes (Actinopterygii: Ostariophysi): A case study using multiple nuclear loci and the mitochondrial genome. *Molecular Phylogenetics and Evolution*, 51, 500–514. https://doi.org/10.1016/j.ympev.2008.12.015

Mayden, R.L., Tang, K.L., Wood, R.M., Chen, W.-J., Agnew, M.K., Conway, K.W., Yang, L., Simons, A.M., Bart, H.L., Harris, P.M., Li, J., Wang, X., Saitoh, K., He, S., Liu, H., Chen, Y., Nishida, M. & Miya, M. (2008) Inferring the Tree of Life of the order Cypriniformes, the earth's most diverse clade of freshwater fishes: Implications of varied taxon and character sampling. *Journal of Systematics and Evolution*, 46, 424–438.

Miya, M., Saitoh, K., Wood, R., Nishida, M. & Mayden, R.L. (2006) New primers for amplifying and sequencing the mitochondrial ND4/ND5 gene region of the Cypriniformes (Actinopterygii : Ostariophysi). *Ichthyological Research*, 53, 75–81. https://doi.org/10.1007/s10228-005-0303-5

Nelson, J.S. (2006) *Fishes of the world*. John Wiley, Hoboken N.J., xix + 601 pp.

Otero, O. (2001) The oldest-known cyprinid fish of the Afro-Arabic Plate, and its paleobiogeographical implications. *Journal of Vertebrate Paleontology*, 21, 386–388. http://dx.doi.org/10.1671/0272-4634(2001)021[0386:TOKCFO]2.0.CO;2

Pasco-Viel, E., Yang, L., Veran, M., Balter, V., Mayden, R.L., Laudet, V. & Viriot, L. (2014) Stability versus diversity of the dentition during evolutionary radiation in cyprinine fish. *Proceedings of the Royal Society B: Biological Sciences*, 281 (1780), 1–9. https://doi.org/10.1098/rspb.2013.2688

Pethiyagoda, R. & Kottelat, M. (1994) Three new species of fishes of the genera *Osteochilichthys* (Cyprinidae), *Travancoria* (Balitoridae) and *Horabagrus* (Bagridae) from Chalakudy River, Kerala, India. *Journal of South Asian Natural History*, 1, 97–116.

Por, F.D. (1989) *The Legacy of Tethys. An Aquatic Biogeography of the Levant*. Kluwer, Dordrecht, 214 pp.

Rainboth, W.J. (1985) *Neolissochilus*, a new genus of South Asian cyprinid fishes. *Beaufortia*, 35, 25–35.

Rambaut, A. & Drummond, A.J. (2009) Tracer v1.5. Available from http://beast.bio.ed.ac.uk/Tracer (Accessed 22 Feb. 2017)

Roberts, T.R. (1999) Fishes of the cyprinid genus *Tor* in the Nam Theun watershed (Mekong Basin) of Laos, with description of a new species. *Raffles Bulletin of Zoology*, 47, 225–236.

Ronquist, F. & Huelsenbeck, J.P. (2003) MrBayes 3: Bayesian phylogenetic inference under mixed models. *Bioinformatics*, 19, 1572–1574. https://doi.org/10.1093/bioinformatics/btg180

Saitoh, K., Sado, T., Doosey, M.H., Bart, H.L., Inoue, J.G., Nishida, M., Mayden, R.L. & Miya, M. (2011) Evidence from mitochondrial genomics supports the lower Mesozoic of South Asia as the time and place of basal divergence of cypriniform fishes (Actinopterygii: Ostariophysi). *Zoological Journal of the Linnean Society*, 161, 633–662. https://doi.org/10.1111/j.1096-3642.2010.00651.x

Saitoh, K., Sado, T., Mayden, R.L., Hanzawa, N., Nakamura, K., Nishida, M. & Miya, M. (2006) Mitogenomic evolution and interrelationships of the Cypriniformes (Actinopterygii: Ostariophysi): the first evidence toward resolution of higher-level relationships of the world's largest freshwater fish clade based on 59 whole mitogenome sequences. *Journal of Molecular*

Evolution, 63, 826–841.
https://doi.org/10.1007/s00239-005-0293-y

Stiassny, M.L.J. & Getahun, A. (2007) An overview of labeonin relationships and the phylogenetic placement of the Afro-Asian genus *Garra* Hamilton, 1922 (Teleostei : Cyprinidae), with the description of five new species of *Garra* from Ethiopia, and a key to all African species. *Zoological Journal of the Linnean Society*, 150, 41–83.
https://doi.org/10.1111/j.1096-3642.2007.00281.x

Tamura, K., Stecher, G., Peterson, D., Filipski, A. & Kumar, S. (2013) MEGA6: Molecular Evolutionary Genetics Analysis version 6.0. *Molecular biology and evolution*, 30, 2725–2729.
https://doi.org/10.1093/molbev/mst197

Tang, Q., Getahun, A. & Liu, H. (2009) Multiple in-to-Africa dispersals of labeonin fishes (Teleostei: Cyprinidae) revealed by molecular phylogenetic analysis. *Hydrobiologia*, 632, 261–271.
https://doi.org/10.1007/s10750-009-9848-z

Tsigenopoulos, C.S., Kasapidis, P. & Berrebi, P. (2010) Phylogenetic relationships of hexaploid large-sized barbs (genus *Labeobarbus*, Cyprinidae) based on mtDNA data. *Molecular Phylogenetics and Evolution*, 56, 851–856.
https://doi.org/10.1016/j.ympev.2010.02.006

Tsigenopoulos, C.S., Ráb, P., Naran, D. & Berrebi, P. (2002) Multiple origins of polyploidy in the phylogeny of southern African barbs (Cyprinidae) as inferred from mtDNA markers. *Heredity*, 88, 466–473.
https://doi.org/10.1038/sj.hdy.6800080

Tweddle, D. & Skelton, P.H. (1998) Two new species of *Varicorhinus* (Teleostei: Cyprinidae) from the Ruo River, Malawi, Africa, with a review of other southern African *Varicorhinus* species. *Ichthyological Exploration of Freshwaters*, 8, 369–384.

Vreven, E.J.W.M.N., Musschoot, T., Snoeks, J. & Schliewen, U.K. (2016) The African hexaploid Torini (Cypriniformes: Cyprinidae): review of a tumultuous history. *Zoological Journal of the Linnean Society*, 177 (2), 231–305.
https://doi.org/10.1111/zoj.12366

Yang, L., Hirt, M.V., Sado, T., Arunachalam, M., Manickam, R., Tang, K.L., Simons, A.M., Wu, H.-H., Mayden, R.L. & Miya, M. (2012) Phylogenetic placements of the barbin genera *Discherodontus*, *Chagunius*, and *Hypselobarbus* in the subfamily Cyprininae (Teleostei: Cypriniformes) and their relationships with other barbins. *Zootaxa*, 3586, 26–40.

Yang, L., Mayden, R.L., Sado, T., He, S., Saitoh, K. & Miya, M. (2010) Molecular phylogeny of the fishes traditionally referred to Cyprinini *sensu stricto* (Teleostei: Cypriniformes). *Zoologica Scripta*, 39, 527–550.
https://doi.org/10.1111/j.1463-6409.2010.00443.x

Yang, L., Sado, T., Vincent Hirt, M., Pasco-Viel, E., Arunachalam, M., Li, J., Wang, X., Freyhof, J., Saitoh, K., Simons, A.M., Miya, M., He, S. & Mayden, R.L. (2015) Phylogeny and polyploidy: Resolving the classification of cyprinine fishes (Teleostei: Cypriniformes). *Molecular Phylogenetics and Evolution*, 85, 97–116.
https://doi.org/10.1016/j.ympev.2015.01.014

Supplementary material

S1—Excel-Table with list of material used in the present study
S2—Nexus file with alignment and MrBayes command blocks
S3—PDF-file with phylogram from unpartitioned dataset
S4—Text-file with phylogram from unpartitioned dataset in Newick format
S5—PDF-file with phylogram from partitioned dataset
S6—Text-file with phylogram from partitioned dataset in Newick format

Acknowledgements

I am grateful to Prof. Dr. Michael Türkay, who was my supervisor until his much too early death.

I thank Prof. Dr. Sven Klimpel for unhesitantly taking over the supervision of my PhD project.

I thank Dr. Friedhelm ‘Fareed’ Krupp for his patient supervision and mentoring. Without his constant support this whole project would not have been possible. He always had an open ear and mind and he always found the time to comment on manuscripts and to discuss results and ideas.

In memory of Horst Zetzsche, who provided invaluable support during my work at the Senckenberg Museum. Without him I would have been lost from the start.

I am grateful to my parents Hille and Peter Borkenhagen and my sister Katrin Mendel for their unconditional love, encouragement and support.

I thank my colleagues and friends in Frankfurt, Florian Wicker, Tilman Alperman, Matze Schneider, Hannes Pulch, Edouard Lavergne, Nadia Manasfi, Nisreen Alwan, Eva Feltkamp, Uwe Zajonz, Susanne Dorow, Jennifer Steppler, Daniela Henkel, Maren Ziegler, Carola Becker, Christiane Frosch, Nina Stiehr, Jeannette Fabis, Sebastian Steinke, Reka Gyulay and Wolfgang Schneider. Daniela Henkel and Matthias Schneider read the manuscript and provided valuable feedback.

I thank my colleagues and friends from the workgroup Marine Animal Ecology at the Research and Technology Centre, University of Kiel, especially to Prof. Dr. Stefan Garthe for his support and encouragement to further pursue my PhD project. Leonie Enners read the manuscript and provided valuable feedback.

I thank Nisreen Alwan, Zuhair Amr, Abdelhamid Azeroual, Mehrgan Ebrahimi, Hamid Reza Esmaeili, Jörg Freyhof, Christiane Frosch, Mehdi Ghanbari-Fardi, Zeinab Gholami, Abbas Kazemi, Friedhelm Krupp, Masoumeh Malek, Majid Moradmand, Hossein Parsa, Sobhan Rahimi, Hassan Rahimian, Bettina Reichenbacher, Hassan Salehi, Alireza Sari, Adwan Shehab, Azad Teimori and Florian Wicker for help with organising and participating in fieldwork in Iran, Jordan, Morocco, Saudi Arabia and Syria.

I thank Jörg Freyhof, Stéphane Ostrowski and Johannes Els for providing additional specimens and finclips. Amer Al-Shamma'a collected, Nashat Hamidan shipped and Florian Wicker sequenced the samples of *M. sharpeyi*.

I thank James Maclaine, Oliver Crimmen and Patrick Campbell (BMNH); Hamid Reza Esmaeili (CBSU); Guy Duhamel, Romain Causse, Patrice Pruvost, Claude Ferrara and Zora Gabsi (MNHN); Ernst Mikschi, Helmut Wellendorf, Christa Prenner and Matthias Reithofer (NMW) for making the collections under their care available for study.