

***Didogobius lanceolatus* sp. nov.,  
a new goby species from Mauritania,  
with diagnoses for two new gobiine genera**

(Teleostei, Gobiidae, Gobiinae)

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*Didogobius lanceolatus* sp. nov. is described from a single specimen collected from the southern Banc d'Arguin, Mauritania. The species differs from all currently described congeners, as well as from all species of the closely related species of the genera *Chromogobius* and *Gammogobius*, by the combination of the following characters: (1) lanceolate caudal fin; (2) small (reduced) vs. large eyes; (3) 27 vertebrae; (4) D2I, 13, AI, 11; (5) predorsal region in front of first dorsal fin D1 naked; (6) body squamation reduced, with only few areas on flank covered by externally visible cycloid scales behind pectoral origin and on caudal peduncle; (7) anterior oculoscapular canal present, with only pores  $\sigma, \kappa, \alpha, \rho$ ; (8) posterior oculoscapular and preopercular head canal absent; (9) suborbital row 7 close to pore  $\alpha$  with more than five papillae; (10) suborbital rows 2 and 4 close to orbit; (11) interorbital papillae absent. The new species appears most closely related to the type species of *Didogobius* Miller 1966, *D. bentuvii* Miller, 1966, as it shares a set of apparently derived morphological characters, such as the lanceolate caudal fin, minute eyes and the anterior oculoscapular canal with only pores  $\sigma, \kappa, \alpha, \rho$  present. Phylogenetic analysis of COI-barcoding data further suggests a close relationship with two other species of the genus *Didogobius* exclusively sharing with the new species and *D. bentuvii* elevated unpaired fin ray counts, i. e., D2 branched rays  $\geq 12$  (vs.  $\leq 11$  in all other species) and A branched rays  $\geq 11$  (vs.  $\leq 10$  in all other species); these two species are *D. kochi* Van Tassell, 1988 and *D. schlieweni* Miller, 1992. Based on the description of new *Didogobius* species obviously closely related to the type species of *Didogobius*, on re-examination of the single type specimen of *D. bentuvii* and on the new DNA barcoding data we restrict and re-diagnose the genus *Didogobius* to include only the aforementioned four species. The other former *Didogobius* species are placed in two new genera, each unambiguously diagnosable on previously established morphological data: *Marcelogobius* gen. nov. with *M. splechnai*, *M. helena* and *M. janetorum*, and *Peter* gen. nov. with the two shrimp-associated species *P. amicuscaridis* and *P. wirtzi*.

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## Introduction

With slightly more than 2000 valid species gobies (Teleostei: Gobiiformes: Gobiidae, incl. Kraemeriidae and Microdesmidae) belong to the most-species-rich vertebrate groups (Fricke et al. 2023). Most species are small or even miniature, rarely exceeding 10 cm total length. As with many predominantly marine and brackish-water taxa, the highest species richness is found in the Indo-Pacific region (Fricke et al. 2023). Nevertheless, a substantial part belonging to only two phylogenetic lineages, the *Pomatoschistus*-lineage and the *Gobius*-lineage (sensu Agorreta et al. 2013) is endemic to the eastern Atlantic (including the South African Cape), the Mediterranean and the Ponto-Caspian regions (Kovačić & Patzner 2011, Schliewen 2011). In addition, the Western Indian Ocean genus *Coryogalops* Smith, 1958 belongs to the *Gobius*-lineage (Agorreta et al. 2013). The diversity of the *Gobius*-lineage currently falls into approx. 30 genera, with approximately 150 described and undescribed species (Kovačić & Patzner 2011, Schliewen 2011, Schliewen, pers. obs.). Based on the phylogenetic analysis of Agorreta et al. (2013), the *Gobius*-lineage comprises several well-defined major clades, whose interrelationships remain poorly resolved. One of these clades is represented by members of the genera *Didogobius* Miller, 1966 and *Chromogobius* de Buen, 1930 with eleven valid and at least five undescribed species (including the one described below) distributed from the islands in the tropical eastern Atlantic, Portugal, the Mediterranean and, with one species, in the Black Sea. As far as their life history is known, all species are truly cryptobenthic (sensu Kovačić et al. 2012), i. e. they always live underneath the bottom surface, in rock crevices or within biocover surface (Kovačić et al. 2012). It is thus unsurprising that before targeted sampling of cryptobenthic habitats using SCUBA diving and anaesthetics started at around the 1970's the knowledge about the diversity of cryptobenthic gobies had remained limited mainly to few species occurring in the intertidal or which had been collected sporadically in deeper habitats.

One species of the *Gobius*-lineages collected accidentally is *Didogobius bentuvii* Miller, 1966, the type species of the genus *Didogobius*. It was apparently collected only because a small-meshed beam-trawl, designed to collect epibenthic fishes, had unintentionally been driven deep into the clay-and-silt bot-

tom off the River Rubin estuary (Israel) at a depth of about 36 m. The single specimen was similar to the genus *Chromogobius* and to the Caspian genus *Asra* Iljin, 1941 (now included in *Benthophiloides* Beling & Iljin 1927), but differed from all described members of these genera known at that time by a combination of characters of the head lateral line system, the vertebrae count, caudal fin shape, and eye size (Miller 1966). Mainly these multiple differences provided the original diagnosis of the new monotypic genus Miller (1966). Subsequently, more species were described, which shared the head lateral line character states, but which differed in several other characters. The first species, *D. kochi* van Tassel, 1988 (distributed in the Canary Islands, Madeira and Senegal) differed, e.g., substantially from the type species, but nevertheless was placed in *Didogobius* because of similarities of the head lateral line system; thus, its inclusion in *Didogobius* necessitated a revised diagnosis of the genus *Didogobius*. This was necessary for virtually all subsequent descriptions of new *Didogobius* species, i. e. *D. splechnai* Ahnelt & Patzner 1995 (Mediterranean), *D. schlieweni* Miller, 1993 (Mediterranean), *D. amicuscaridis* Schliewen & Kovačić, 2008 (São Tomé und Príncipe), *D. wirtzi* Schliewen & Kovačić, 2008 (Cape Verde), *D. helenae* Van Tassel & Kramer, 2014 (Canary islands) and *D. janetarum* Schliewen et al., 2018 (Cape Verde). To assign all *Didogobius* species in a single genus despite substantial morphologically heterogeneity the latest re-diagnosis of the genus differentiates it from *Chromogobius* on the basis of only two disputed head lateral line characters despite the study reiterates previous findings, that multiple other character states would allow for the delineation of new genera within the *Didogobius* species complex (Schliewen et al. 2018). It was cautioned that a formal generic reassessment necessitates the critical examination of new data of the highly divergent type species *D. bentuvii*, known to date only from the holotype.

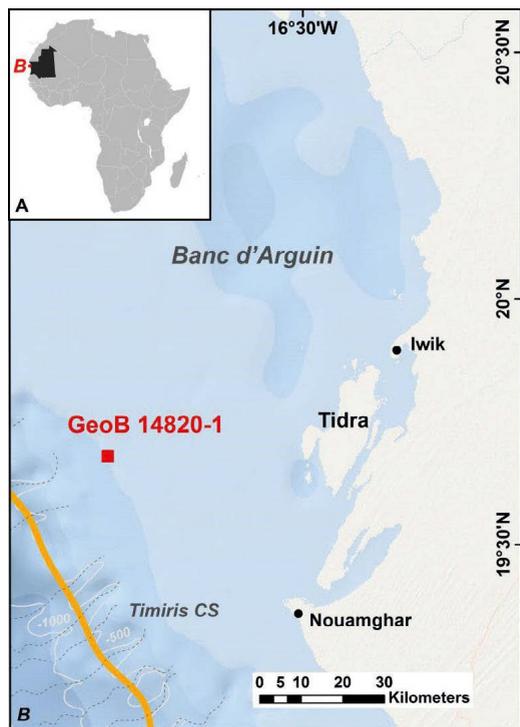
In 2010 an unknown goby was accidentally collected at 30 m water depth in the southern Banc d'Arguin off the island Tidra, Mauritania, via grab sampling mud and silty mud. This specimen revealed to be phenotypically similar to *D. bentuvii* and it was collected from a similar muddy habitat and depth. Nevertheless, a comparison showed that it is clearly a different species, despite sharing multiple character states previously believed to be unique to the type

species of *Didogobius*. The description of the new species, re-examination of the single type specimen of *D. bentuvii*, new DNA barcoding data including the new species closely related to the type species and the re-assessment of previously established morphological data allowed for the re-diagnosis of *Didogobius* and to establish diagnoses for two new genera, formerly placed in *Didogobius*.

The Banc d'Arguin is located along the coast of northern Mauritania and is characterized as a coastal wetland with shallow water, tidal flats and large sea grass beds (Schaffmeister et al. 2006), along with mudflats, channels, sand banks, and islands of variable sizes (Araujo & Campredon 2016). The Banc d'Arguin covers an area of around 10 000 km<sup>2</sup> (Wolff et al. 1993). Generally, the species composition of the Banc d'Arguin varies along with the different habitat features (Compain 2021). Its fish fauna is characterized by temperate, sub-tropical as well as tropical elements (Jager 1993). Additionally, the shallow areas of the Banc d'Arguin are known as a nursery for many fish species, providing a rich source of food for many seabirds (Camphuysen & van der Meer 2005). A study by Gushchin & Fall (2012) identified 91 fish species in the littoral area of the Golfe d'Arguin, while van Etten (2002) already identified 23 fish species with most of them belonging to the family Gobiidae, despite only a very small area near Zira island (19.86°, -16.29°) was sampled.

## Material and methods

The specimen was collected during the RV Maria S. Merian cruise MSM 16/3 "PHAETON" – Paleoceanographic and paleoclimatic record on the Mauritania Shelf (Westphal et al. 2014) in the southern Banc d'Arguin 19.682450° and -16.922700° in 30 m water depth via grab sampling (station GeoB: 14820-1, see Fig. 1). The holotype was documented with a Nikon D700 camera and a digital light microscope (Keyence VHX-1000D) for detailed observation and further description. It was preserved in ethanol, denatured ≥ 96% plus 1% MEK, for morphological and genetic analyses. A fin-clip of the left pectoral was taken thereafter. Distance measurement methods followed definitions provided in Schliewen & Kovačić (2008) and were taken with a Mitutoyo 505-732 dial calliper (accuracy 0.01 mm) or, in order to avoid specimen damage, in some cases from variously enlarged digital x-rays or specimen photos with a 10.0 mm size standard. Meristic counts were taken following definitions provided in Schliewen et al. (2018). Terminology of lateral line system follows Miller (1986), a modification for suborbital row terminology in Schliewen et al. (2018), and they are based on Sanzo (1911). The specimen was reversibly stained in 2% solution of Cyanine Blue in distilled water (Saruwatari et al. 1997) for studying scales and sensory papillae



**Fig. 1.** A. Overview map of Africa indicating Mauritania (■) and the study area (B, ■). B. Study area with MSM 16/3 'PHAETON' sample location (red square) and the deep-water coral ecosystem (orange line) along the slope of Mauritania and inside the Canyon Systems (CS). Basemap from ESRI (2019) ([www.esri.com](http://www.esri.com)) and contours from GEBCO (2019) ([www.gebco.net](http://www.gebco.net)), deep-water scleractinian framework distribution, canyon positions and names from Sanz et al. (2017).

rows. X-rays were prepared using the default autoexposure settings of the UltraFocus Digital Radiography System (Faxitron Bioptics, Arizona, USA).

For assessing the phylogenetic position of the new species described herein, DNA extraction was performed at the biome-id laboratories (Wilhelmshaven, Germany). The genomic DNA of *D. lanceolatus* sp. nov. was extracted using the NucleoSpin® Tissue Kit (Macherey Nagel, Düren, Germany). A fragment of the mitochondrial Cytochrome-c-Oxidase (COI) was amplified with a fish-specific primer cocktail (Ivanova et al. 2007). Additional M13 forward and reverse tails were added to the primers for Sanger sequencing. The PCR product was amplified using One Taq 2x Master Mix (New England Biolabs, Frankfurt am Main). The PCR thermal conditions included an initial denaturation at 94°C (3 min), followed by 35 cycles at 94°C (denaturation, 20 s), 48°C (annealing, 30 s), 68°C (extension, 45 s), and a final extension at 68°C (5 min). The PCR product was visualized via electrophoresis on a 1.5% agarose gel stained with

GelRed (Biotium Inc., Fremont, CA, USA) and 10  $\mu$ L of the amplicon was purified using 2.5  $\mu$ L of ExoSap Mix (10 Unit Exonuclease I und 2 Unit FastAP Thermosensitive Alkaline Phosphatase). All PCR reactions were conducted using an Eppendorf Mastercycler Pro system (Eppendorf, Hamburg, Germany). Forward and reverse sequencing was conducted on an AB3730XL (Thermo Fisher Scientific, Waltham, MA, USA) MacroGen Europe (Amsterdam, The Netherlands). Additional COI sequences were generated using the lab protocol described in Kovačić et al. (2017). Sequences were first manually edited using Sequencer v5.4. (Gene Codes, Ann Arbor, MI, USA) and imported as fasta files into BioEdit v. 7.2.5 (Hall 1999), then aligned with default settings and adjusted by eye; finally, the alignment was trimmed to equal fragment length of 572 base pairs. To infer mtDNA-based phylogenetic relationships the new data were combined with published (Genbank) or newly sequenced COI-data from related species. BOLD or Genbank accession numbers are based on species names in the phylogenetic analyses results presented below, except for the 15 newly generated COI-haplotypes deposited under the following GenBank accession-numbers and BOLD-ID numbers: *Didogobius lanceolatus* sp. nov. (BOLD-ID: DNGLB01; SMF 39647; ZSM tissue voucher PIS-GO-2348); OQ672514: *Marcelogobius janetarium* comb. nov. (ZSM tissue voucher PIS-GO-1801); OQ672516: *Marcelogobius splechnai* comb. nov. (ZSM tissue voucher PIS-GO-1878); OQ672509, OQ672512, OQ672513: *Didogobius kochi* "Cape Verde Islands" (ZSM tissue vouchers PIS-GO-1016, PIS-GO-1216, PIS-GO-1217); OQ672518: *Didogobius schlieveni* (PMR VP4629; ZSM tissue voucher ZSM-PIS-GO-2123); OQ672510, OQ672515: *Chromogobius quadrivittatus* (ZSM tissue vouchers PIS-GO-1070, PIS-GO-1085); OQ672506-OQ672508, OQ672511 and OQ672517: *Chromogobius* cf. *zebratus* (ZSM tissue vouchers PIS-GO-561, PIS-GO-918, PIS-GO-1091, PIS-GO-1175, PIS-GO-891, PIS-GO-1091). A Maximum Likelihood tree hypothesis (ML) was calculated with the software package MEGA7.02.6 (Kumar et al. 2016), using the HKY + Gamma + I model (Gamma with five discrete categories). HKY + Gamma + I was chosen from 24 nucleotide substitution models based on the lowest Bayesian Information Criterion (BIS) values after running the "Model Selection" tool in MEGA7. *Gorogobius nigrinctus* was selected as outgroup taxon based on Agorreta et al. (2013). Statistical node support was assessed using nonparametric bootstrap analysis with 1000 pseudoreplicates. All specimens used in the present study are deposited in the Senckenberg Museum, Frankfurt (SMF), the SNSB-Bavarian State Collection of Zoology, Munich, Germany (ZSM) or in the Natural History Museum Rijeka, Croatia (PMR).

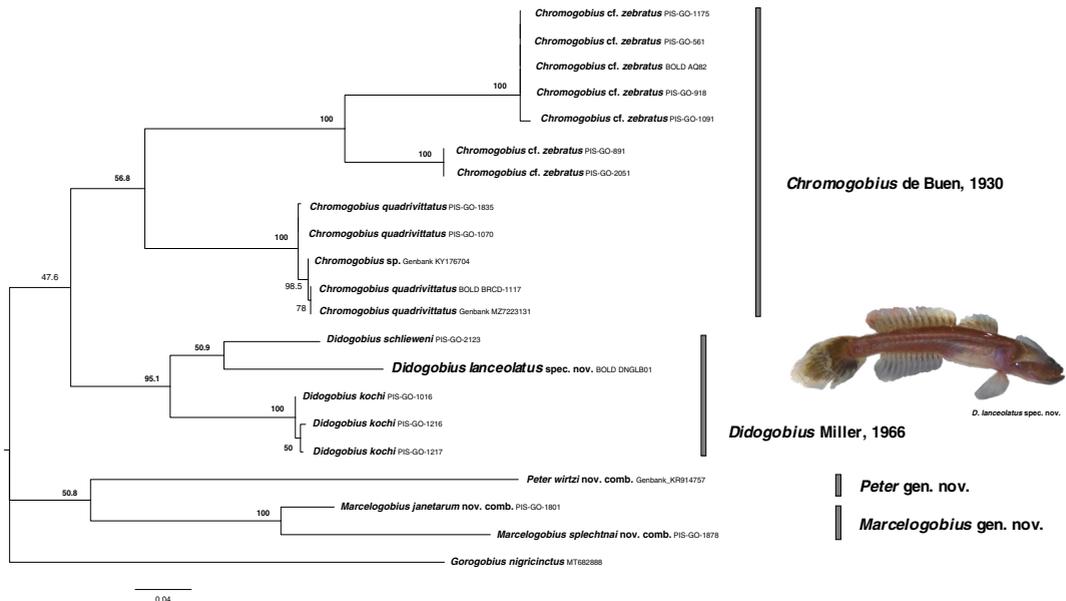
### Generic identification and phylogenetic position

Generic identification would be consistent with the most recently modified diagnosis of the genus *Didogobius* Miller, 1966 in Schliewen et al. (2018):

"*Didogobius* are Gobiinae sensu Pezold (1993) with the following characters shared by all currently valid members of the genus: (1) suborbital papillae without row a; (2) six suborbital transverse rows, row 3 missing, last row 7 represented by a single papilla or several papillae near pore  $\alpha$ , or, if the head canal is absent it is near replacement large papilla; (3) suborbital row 5 long, from near eye to near row d; (4) paired rows of interorbital transversal papillae absent, if head canal absent, individual large replacement papillae are present but not a pair of transversal rows. (5) Head naked, predorsal area naked or scaled posteriorly (scaled up to six rows of cycloid scales in middorsal and up to approx.  $\frac{1}{4}$  of predorsal area length); (6) no mental barbels; (7) pelvic disc complete with fully developed anterior membrane (frenum); (8) head canals variably reduced from anterior oculoscapular and preopercular canals present and posterior oculoscapular canal absent to complete absence of head canals." However, as discussed already in Schliewen et al. (2018), and as now supported with new DNA barcoding data conflicting molecular phylogenetic and morphological evidence implies that *Didogobius*, as defined in Schliewen et al. (2018), is paraphyletic with respect to *Chromogobius*. We therefore restrict *Didogobius* to the type species and those three species sharing with the type species elevated second dorsal fin (D2) and anal fin ray counts and whose mitochondrial DNA barcoding (COI) haplotypes from a well-supported clade within all investigated members of the *Chromogobius-Didogobius* species complex. Based on morphological data compiled in Schliewen & Kovačić (2008), Van Tassell & Kramer (2014), Schliewen et al. (2018) and including the confirmation of osteological data previously published by Miller (1966) for the holotype of *D. bentuvii* (BMNH 1965.2.1.1) the revised diagnosis of *Didogobius* is presented here.

### Revised diagnosis of *Didogobius*:

Gobiinae sensu Pezold (1993) with the following characters shared by all currently valid members of the genus: (1) suborbital papillae without row a; (2) six suborbital transverse rows, row 3 missing, last row 7 represented by a single papilla or several papillae near pore  $\alpha$ ; (3) suborbital row 5 long, from near eye to near row d; (4) paired rows of interorbital transversal papillae absent; (5) head naked, predorsal area naked; (6) no mental barbels; (7) pelvic disc complete with fully developed anterior membrane (frenum); (8) anterior oculoscapular canal present but variably reduced with either only pores  $\sigma$ ,  $\kappa$ ,  $\alpha$ ,  $\beta$ ,  $\rho$  present or pores  $\sigma$ ,  $\lambda$ ,  $\kappa$ ,  $\omega$ ,  $\alpha$ ,  $\beta$ ,  $\rho$  present; preopercular canals present or absent, and posterior



**Fig. 2.** Maximum likelihood phylogeny of COI-barcode haplotypes (572 bp) of all available sequences of *Didogobius* species and members of the related genera *Chromogobius*, *Marcelogobius* gen. nov. and *Peter* gen. nov. The tree was rooted with *Gorogobius nigricinctus* based on Agorreta et al. (2013). Numbers on branches are bootstrap support values (%) for the maximum likelihood analysis. Tip labels include the ZSM-PIS-GO goby tissue collection number (if newly sequenced in this study), GenBank accession or Barcode of Life Data System (BOLD) numbers. Inserted: Photo of the live holotype of *D. lanceolatus* sp. nov. (photo: A. Freiwald and L. Beuck).

oculoscapular canal absent; (9) D2 branched rays  $\geq 12$  and A branched rays  $\geq 11$ ; (10) first D1 ray not the longest; (11) posterior nostril tubular.

Support for the generic identification comes from the phylogenetic analysis of mitochondrial COI-barcoding data. A hypothesis for phylogenetic relationships of DNA-haplotypes places the new species in a statistically strongly supported clade (BS 95.1) with *Didogobius kochi* and *D. schlieveni*, two species matching the revised diagnosis of *Didogobius* as given above (Fig. 2). Since the type species of *Didogobius*, *D. bentuvii*, shares multiple unique character states with the new Mauritanian species described herein, we infer that those two are closely related, although COI-barcoding data are not available for *D. bentuvii*, known only from the holotype. Thus, under the revised diagnosis given above, *Didogobius* now is restricted to the type species *D. bentuvii*, the highly similar *D. lanceolatus* spec. nov., *D. schlieveni* and *D. kochi*.

With the restriction of *Didogobius* to this diagnosis, several species are now excluded from *Didogobius* and thus in need of generic reassignment, i. e. (i) the two shrimp-associated species *D. amicuscaridis* and *D. wirtzi*, and (ii) the banded species *D. splechnai*, *D. helenae* and *D. janetarum*. Since both are unambigu-

ously diagnosable on the basis of multiple previously established characters we provide diagnoses for these two species groups and formally assign them to two new genera (see below). Together with the three described *Chromogobius* species, the *Chromogobius-Didogobius* complex thus comprises four genera.

### Species identification

Apart from the type species of the genus *Didogobius*, *D. bentuvii* Miller, 1966, the new species differs from all remaining species of the *Chromogobius-Didogobius* species complex by the following characters: a lanceolate vs. rounded caudal fin, the anterior oculoscapular canal with only pores  $\sigma$ ,  $\kappa$ ,  $\alpha$ ,  $\rho$  present, and small (reduced) vs. large eyes; from *Didogobius bentuvii*, *D. kochi* Van Tassell, 1988, *D. schlieveni* Miller, 1992, *Marcelogobius helenae*, *M. splechnai*, *M. janetarum*, and *Chromogobius britoi* it differs by having more than one papilla (six or seven) in sub-orbital row 7; from *D. kochi*, *D. schlieveni* Miller, 1993, *Peter amicuscaridis* Schlieven & Kovačić, 2008 and *P. wirtzi* Schlieven & Kovačić, 2008 by having only 10 vs. 11–14 D2 soft rays; from *M. helenae* by having anterior oculoscapular head canal present

vs. absent; from *M. janetarum* Schliewen, Wirtz & Kovačić, 2018 and *D. kochi* specimens from the Canary Islands by a naked predorsal region vs. posterior quarter of predorsal region in front of first dorsal fin origin with several rows of cycloid scales; from *C. zebratus*, *C. britoi*, *C. quadrivittatus*, *D. kochi*, *D. schlieveni*, *M. splechtnei*, *P. amicuscaridis* and *P. wirtzi* by preopercular canal absent vs. present. For a comprehensive comparison see character compilations in Schliewen & Kovačić (2008: table 2), Van Tassell & Kramer (2014: table 2), and Schliewen et al. (2018), Kovačić et al. (2019).

Class Osteichthyes Huxley, 1880  
Order Gobiiformes Günther, 1880  
Family Gobiidae Cuvier, 1816  
Genus *Didogobius* Miller, 1966

***Didogobius lanceolatus* Schliewen,  
Knorrn & Böhmer, 2023 sp. nov.**

Figs 3–7

**Types.** Holotype: SMF 39647, male, 65.1 + 20.6 mm, Mauritania, southern Banc d'Arguin off Tidra (19.682450°, -16.922700°), in 30 m depth collected with olive-coloured mud (surface) and dark greenish grey-coloured silty mud (bulk), 4<sup>th</sup> of November 2010 at 15:28 UTC, MSM 16/3 grab sample, sta. no. GeoB 14820-1.

**Diagnosis.** *Didogobius lanceolatus* sp. nov. differs from all currently described members of the genera *Didogobius*, *Chromogobius*, *Marcelogobius* gen. nov. and *Peter* gen. nov. by the combination of the following characters: (1) lanceolate caudal fin; (2) small (reduced) vs. large eyes; (3) 27 vertebrae; (4) D2I+13, AI+11; (5) predorsal region in front of D1 naked; (6) body squamation reduced, with only a few cycloid scales anteriorly and in tail region; (7) anterior oculoscapular canal present, with only pores  $\sigma$ ,  $\kappa$ ,  $\alpha$ ,  $\varrho$ ; (8) posterior oculoscapular and preopercular head canal absent; (9) suborbital row 7 with more than five papillae; (10) suborbital rows 2 and 4 close to orbit.

### Description

General morphology. Body proportions and meristics of the holotype are given in Table 1. For a general view see Figs 3, 4. Body elongate and laterally compressed, head moderately depressed; interorbital space broad (more than three times of eye diameter), dorso-laterally positioned eyes. Mouth oblique (~35° from horizontal), lower jaw slightly projecting, posterior angle of jaws slightly behind rear margin

of pupil. Snout longer than eye and rounded in dorsal view. Anterior nostril tubular (longer than diameter), without process from rim, reaching but not overlapping the upper lip; posterior nostril with slightly erected rim, but not tubular. Upper lips about as thin anteriorly as laterally. Branchiostegal membrane attached along entire lateral margin; posterior margin of operculum almost reaching frontal edge of pectoral fin base. Cranial roof covered by dorsal axial musculature. Pectoral girdle without dermal flaps on anterior edge.

Fins. D1 VI; D2 I/13 (last bifid); A (left/right) I/11; P (21,21); V (left/right) I/5+5/I; C (branched/segmented rays) 17/17; upper and lower procurrent rays: 7/7; total caudal rays: 31. Fin lengths and proportions are given in Table 1. First D1 slightly shorter than second spine, third to sixth spines becoming progressively shorter; interdorsal space not distinct (fin folded without fin membrane, thus membrane connection between D1 and D2 not discernible without damaging specimen); longest D2 rays not reaching base of uppermost caudal fin rays. A originates posterior of vertical through D2 origin; C lanceolate, longer than head length; uppermost rays of P not free of membrane, P not reaching D2; V complete and elliptical with ray 1 to ray 5 becoming progressively shorter, and a well-developed anterior pelvic membrane (frenum), its height in midline approx. half of V spine length and at its lateral margins approx. 3/4 of V spine length (ventral fin membrane slit along midline).

Scales. Body squamation apparently strongly reduced. Head, predorsal, prepectoral, breast and abdominal area without externally visible scales. Flanks without externally visible scales except for a patch of thin cycloid scales behind P origin and on dorsal, caudal and ventral areas of caudal peduncle. On the photograph of the freshly collected specimen, however, darkly pigmented areas are visible on the flanks, which most likely correspond to scales deeply embedded into the flank skin, remnant “empty” scale pouches after scale loss due to sampling, or just relict pigments patches after regressive evolution of scale cover. In the preserved holotype no clearly discernible scale pouches were visible despite clearly discernible flank neuromast rows.

Teeth. Teeth in lower jaw in two rows. Outer row with five (left side) or six (right side) comparatively large-sized anterior teeth frontally on each side, caniniform, pointing slightly backwards. Inner anterior teeth smaller and conical, numerous, more or less in one row in anterior position; the three or four innermost of inner row large, caniniform. Teeth in upper jaw in three rows. Outer row with approximately ten teeth of about equal size on each side, the anterior three ones on each side large and

caniniform, the posterior-lateral ones medium to small, decreasing in size posteriorly; second row a rather broad band of small conical teeth; innermost third row consisting of only three large strongly recurved canine teeth across dorsal midline (one visible on left, two on right side).

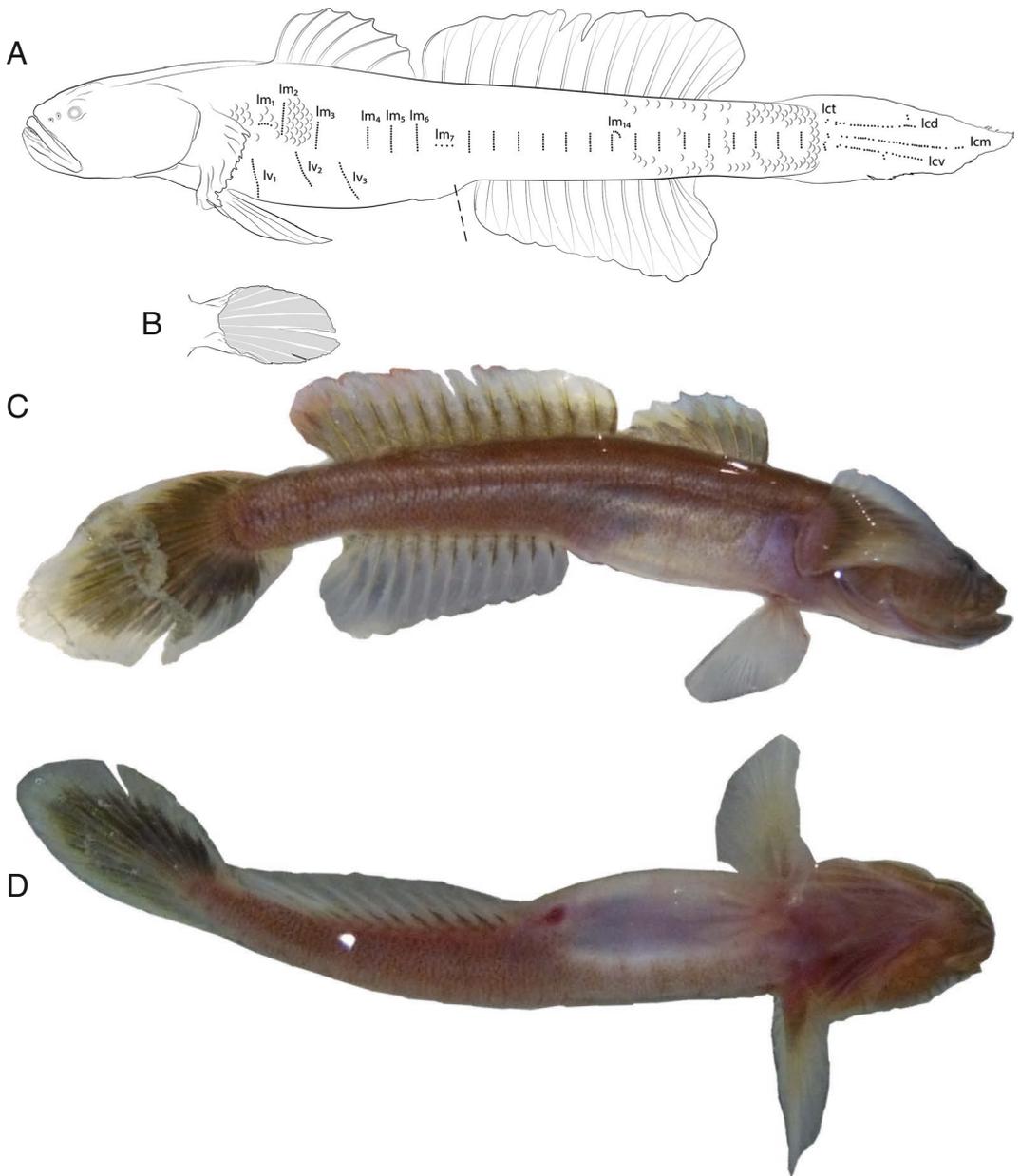
Osteology. Vertebral column and pterygiophore insertion pattern (pty) (Fig. 5). 10 precaudal and 17 caudal vertebrae (including urostyle), total count: 27. Pty 3-22110; two pterygiophores anterior to the first haemal spine. Number of C rays total branched rays: 17, upper procurent rays: 7, lower procurent rays: 7.

Lateral line system (Figs 3, 5, 6). Head with anterior oculoscapular canal with pores  $\sigma$ ,  $\kappa$  (merely visible),  $\alpha$ ,  $\rho$ . Posterior oculoscapular canal and preopercular canal absent. Rows and number of

sensory papillae, counted on left and right side of holotype are: (I) Preorbital: snout with four rows in median preorbital series. Row r (9,9) median to pore  $\sigma$ . Upper row  $s_1$  (11,6) transversal near posterior nostril, lower  $s_2$  (6,4) near anterior nostril, and  $s_3$  longitudinal above upper lip (8,8). Lateral series c in four parts: superior  $c_2$  as two rows, internal row between posterior and anterior nostrils (4,4), external row (8,7); middle transversal  $c_1$  (6,5) below anterior nostril; inferior upper  $c_2$  (7,8) and lower  $c_1$  (4,4) as two rows between lips and row 1. (II) Suborbital: six transverse and two longitudinal rows of sensory papillae on cheek. Rows 1, 2, 4 and 5 before longitudinal row b; row 6 divided by row b in superior (6s) and inferior sections (6i); row 7 near pore  $\alpha$ . Row 1 (12,13) slightly in front of eye orbit. Rows 2 (15,17) below center of orbit, row 4

**Table 1.** Morphometric measurements and meristic counts of *Didogobius lanceolatus* sp. nov. following Schliewen & Kovačić (2008).

	Holotype		
	mm	% of SL	% of HL
Total length (TL)	86.55	-	-
Standard length (SL)	67.78	-	-
Head length (HL)	16.56	24.4	-
Snout length	4.71	6.9	28.4
Eye (horizontal diameter)	1.58	2.3	9.5
Eye (vertical diameter)	1.26	1.9	7.6
Interorbital distance	4.62	6.8	27.9
Pre-anal length	32.94	48.6	-
Pectoral fin length	11.50	17.0	-
Pectoral fin height	7.44	11.0	-
Pelvic fin length	11.71	17.3	-
1st dorsal fin length	10.50	15.5	-
2nd dorsal fin length	26.62	38.3	-
Pre-1st-dorsal fin length	22.85	33.7	-
Pre-2nd-dorsal fin length	34.23	50.5	-
Anal fin length	17.99	26.5	-
Caudal fin length	18.77	27.7	-
Body height at anus	10.27	15.2	62.0
Body height at pectoral-fin base level	10.19	15.0	-
Caudal peduncle length	9.16	13.5	-
Caudal peduncle height	6.38	9.4	-
<b>Meristics</b>			
First dorsal fin (D1) spines	VI		
Second dorsal fin spine and rays	I,13		
Anal fin rays	I,11		
Pectoral fin rays	21,21		
Pelvic fin rays	I,5		
Branched/Segmented caudal fin rays	17/17		
Upper/Lower procurent rays	7/7		
Vertebrae	10 + 17 = 27		



**Fig. 3.** *Didogobius lanceolatus* sp. nov. (SMF 39647, male, 65.1 + 20.6 mm, Mauritania, southern Banc d'Arguin, holotype). **A.** Schematic drawing of fins, trunk squamation, trunk lateral line system sensory papillae, left lateral view (abbreviations and nomenclature of lateral line system based on Sanzo (1911) and Miller (1986)); **B.** pelvic fin disc, ventral view (drawing by R. Böhmer); **C.** right lateral view; **D.** ventro-lateral view; images of live specimen in seawater (photos: A. Freiwald and L. Beuck).

(16,15) slightly anterior to rear margin orbit, row 5 (21,21) starting slightly posterior to rear margin of orbit, row 6 starting with row 6s (15,12) well behind rear margin of orbit and ending ventrally

below level of row d with lower extension of row 6i (12 + 7, 13 + 6), row 7 with more than one single papilla (6,5). Longitudinal row b (14,15). Longitudinal row d subdivided into anterior section d1 (11,10),

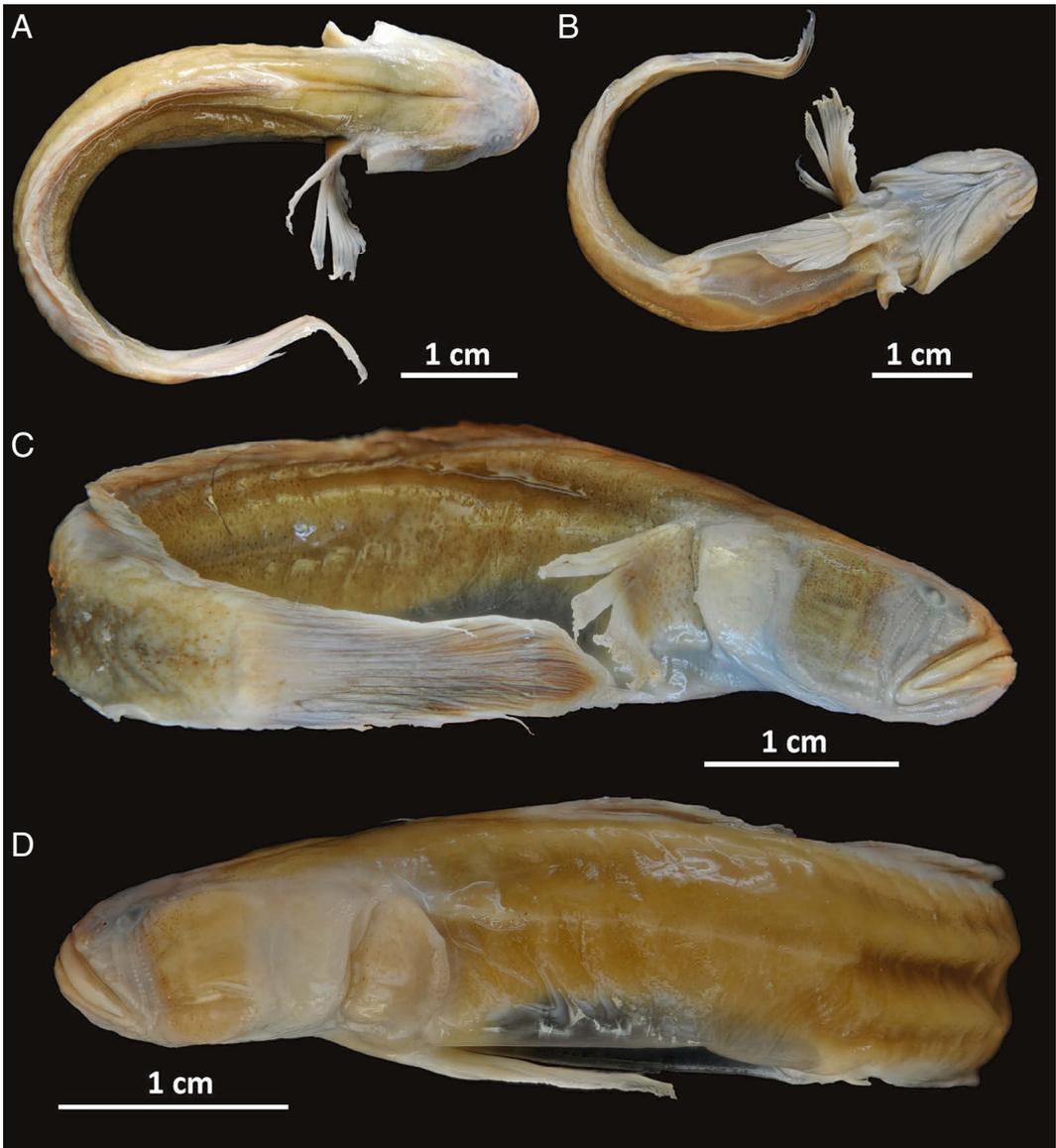
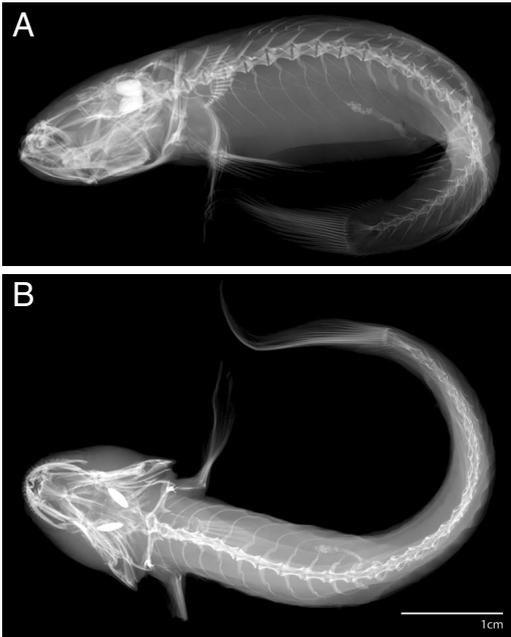


Fig. 4. *Didogobius lanceolatus* sp. nov. (SMF 39647, male, 65.1+20.6 mm, Mauritania, southern Banc d'Arguin, preserved holotype). A. Dorsal view; B. ventral view; C. right lateral view; D. left lateral view, blueish hue on breast and head are an artefact after cyan blue staining (photos: N. Mahnken and A. Knorrn).

starting parallel to upper lip starting anterior to row 1 and ending at end of row 2; middle section d2 (9,6) between end of row 2 and end of row 5; and posterior section d3 (4,4) between end of row 5 and mid of row 6i. (III) Preoperculo-mandibular: external row e slightly separated into an anterior section e1 (32,30) and a posterior section e2 (25,27); internal row i continuous 18 (21 incl. paired papil-

lae), 19 (24 incl. paired or tripled papillae); papillae 1, 9, 15 being paired on left side and papillae 1, 9, 18 and papilla 19 tripled on right side, row f longitudinal long (17,16) with anterior 10 papillae arranged in oblique paired order and posterior papillae linear. (IV) Oculoscapular: anterior longitudinal row  $x_1$  (19,17), located between rows n and tr; posterior longitudinal row  $x_2$  (5,5) above transversal

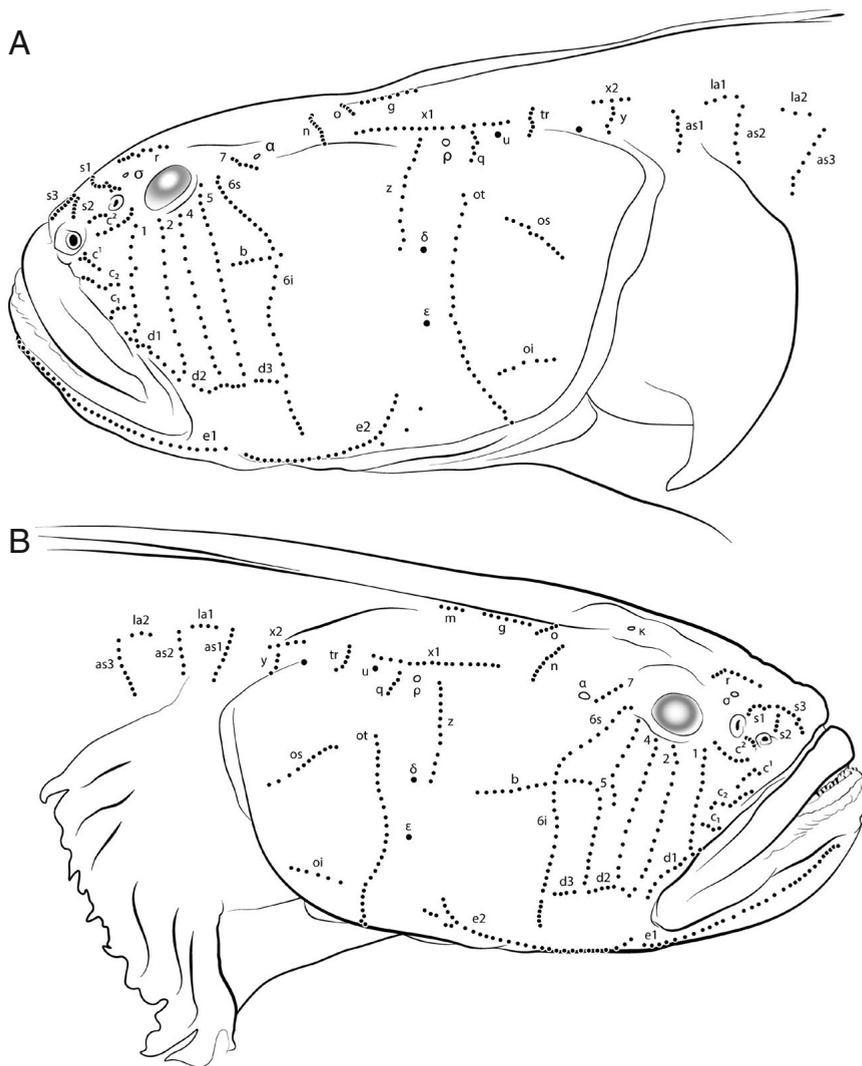


**Fig. 5.** *Didogobius lanceolatus* sp. nov. (SMF 39647, male, 65.1+20.6 mm, Mauritania, southern Banc d'Arguin, radiograph of the holotype). **A.** Left lateral view; **B.** ventral view (X-rays: U. Schliewen).

row *y* (5,4) which is directly below center of row *x*<sub>2</sub> and not separated from it; transversal row *z* (13,13) originating dorsally before pore *q* and descending to level of row *b* but separated from posterior end of latter; transversal row *q* (6,5) behind pore *q*; row *u* as one large papilla behind row *q*; transversal row *tr* (7,6) slightly distant from posterior end of row *x*<sub>1</sub>; a single large papilla below anterior part of row *x*<sub>2</sub>. Axillary papillae transversal axillary rows *as*<sub>1</sub> (7,9), *as*<sub>2</sub> (7,-6), *as*<sub>3</sub> (9,9) present, and longitudinal rows *la*<sub>1</sub> (4,4) between *as*<sub>1</sub> and *as*<sub>1</sub> and *la*<sub>2</sub> (3,3) between *as*<sub>2</sub> and *as*<sub>3</sub>. (V) Opercular: transverse row *ot* (28,-27); superior longitudinal row *os* (11,-11); and inferior longitudinal row *oi* (7,6); two large papillae present on the place of absent preopercular canal pores *ε* and *δ*. (VI) Anterior dorsal: transversal row *n* (11,10) long, posterior to interspace between pores *α* and *κ*; transversal rows *o* (5,5) divided from each other; longitudinal row *g* (8,7) ends posteriorly to center of row *o*, longitudinal row *m* behind row *g* (/4, i. e. counted on right side only), longitudinal row *h* not continuous (5+4,5+4 extending anteriorly from origin of D1. (VII) Interorbital papillae absent. (VIII) Trunk: *lm* series in 22 (left) or 21 (right) predominantly transverse rows along midline from behind pectoral fin origin to before caudal fin origin; only *lm*<sub>1</sub> and *lm*<sub>7</sub> longitudinal; *lm* neuromast

counts (starting anteriorly): *lm*<sub>1</sub> (5,6), *lm*<sub>2</sub> (13,13), *lm*<sub>3</sub> (11,8), *lm*<sub>4</sub> (9,9), *lm*<sub>5</sub> (11,10), *lm*<sub>6</sub> (11,11), *lm*<sub>7</sub> (4 or 5,4), *lm*<sub>8</sub> (9,9), *lm*<sub>9</sub> (8,8), *lm*<sub>10</sub> (8,8), *lm*<sub>11</sub> (7,8), *lm*<sub>12</sub> (8,8), *lm*<sub>13</sub> (8,8), *lm*<sub>14</sub> (7+8), *lm*<sub>15</sub> (8,7+5), *lm*<sub>16</sub> (7,8), *lm*<sub>17</sub> (7,8), *lm*<sub>18</sub> (6,7), *lm*<sub>19</sub> (7,6), *lm*<sub>20</sub> (7,7), *lm*<sub>21</sub> (7,7), *lm*<sub>22</sub> (7, n/a); rows *lm*<sub>14</sub> (left side) and *lm*<sub>15</sub> (right side dorso-caudally prolonged into a curved series of 5 papillae and dorsally extended after a gap with additional two neuromasts; *lv* series in three transverse rows: *lv*<sub>1</sub> (15,14), *lv*<sub>2</sub> (15,12) and *lv*<sub>3</sub> (15,15). (IX) Caudal fin: three longitudinal rows *lc* on caudal fin: *lcd* (22, the first two neuromasts arranged transversally; two additional neuromasts dorsally of terminal part of *lcd*); *lcm* (33); *lcv* (23) two additional neuromasts ventrally of middle section of *lcv* at about half caudal fin length); one transverse row *lct* (8).

**Coloration.** In life (based on photographs of holotype exposed to seawater (Fig. 2) shortly after capture). Flank ground coloration pale rosy with a dusky-grey hue, with superficial neuromast (rows *lm* and *lv*) clearly distinguishable as tiny black papillae rows, and each presumable scale (or scale pocket) with as a grey little spot. Basal two thirds of D1 and D2 greyish-beige opaque with spines and rays and their immediate surroundings distinguishable as greyish-black vertical lines; outer third of D1 and D2 white. Basal third of A beige-opaque with rays distinguishable as narrow greyish-black vertical lines; outer two thirds whitish-opaque with areas of rays dusky-grey. Base of C pale rosy as flank, central area blackish-grey becoming beige-grey more caudally, outer quarter of C as a broad white caudal fin margin. Abdomen whitish-translucent with the silvery shining peritoneum visible through skin in lateral view; ventral abdomen, breast and isthmus translucent, rendering the abdomen light grey, the breast reddish and the isthmus whitish-grey. Pelvic disc and pectorals opaque whitish-grey, central area of pectoral with a yellowish-beige tinge closing basally with a dark grey area around pectoral fin base. Head coloration light beige with snout, jaws and branchiostegal rays dark grey; head neuromasts visible as black dots and dot rows. Preserved in ethanol (based on photographs of holotype (Fig. 3)). Body and head beige with scattered melanophores visible on flanks, predorsal head region and pectoral fin base. Fins, operculum, suborbital and ventral head region opaque whitish. Belly translucent. Iris dark. First dorsal fin with oblique dark band in middle. Second dorsal fin with widely scattered dots and narrow dark upper margin. Anal fin lightly pigmented. Caudal fin transparent. Pectoral fins transparent, few melanophores visible. Pelvic fins transparent with a few melanophores on spines.



**Fig. 6.** *Didogobius lanceolatus* sp. nov. (SMF 39647, male, 65.1+20.6 mm, Mauritania, southern Banc d'Arguin, head lateral line neuromasts and canal pores, holotype). **A.** Left lateral view; **B.** right lateral view (abbreviations and nomenclature of lateral line system based on Sanzo (1911), Miller (1986) and Schliewen et al. (2018); drawings by R. Böhmer).

**Etymology.** Latin for “with a little lance”, derived from Latin *lanceola*, a diminutive term of *lancea*, meaning “lance”, i.e. a small lance. An adjective referring to the lance-shaped caudal fin of the new species, a character shared in the *Chromogobius-Didogobius* species complex only shared with the type species of the genus *Didogobius*, *D. bentuvii*.

**Distribution.** The location, where the only individual of the new species of *Didogobius* described herein was detected, is situated at a shallow, muddy area adjacent to the continental slope of Mauritania.

There, the waters are characterized by the large Canary Upwelling System (12–43°N), causing a massive production of phytoplankton, which fuels species richness and abundance, especially the one of fish (Carlier et al. 2015).

**Ecology.** As known for other members of the subfamily Gobiinae, such as, e.g. *Lesueurigobius* species (Malm, 1874) (Rice & Johnstone 1972) and also presumed for the congener *Didogobius bentuvii* based on morphological similarities with unrelated burrowing goby genera (see Miller 1966), we suppose for *Dido-*

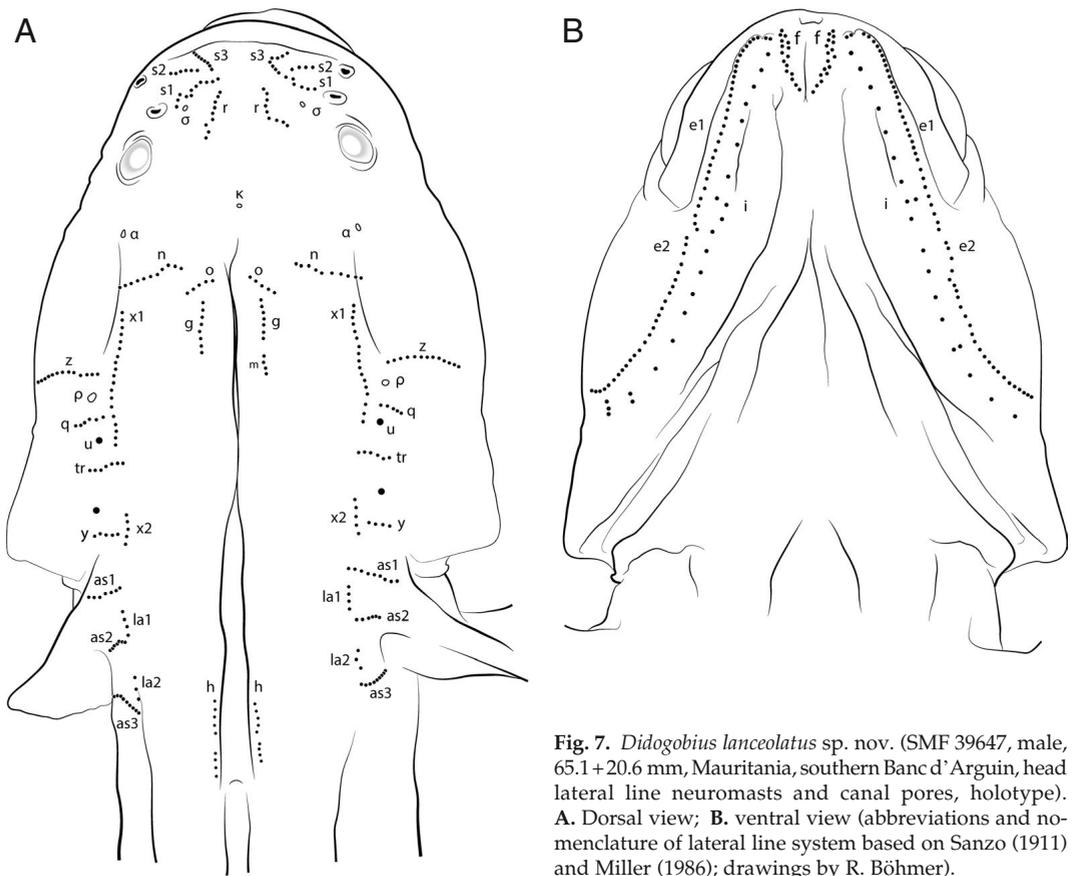


Fig. 7. *Didogobius lanceolatus* sp. nov. (SMF 39647, male, 65.1 + 20.6 mm, Mauritania, southern Banc d'Arguin, head lateral line neuromasts and canal pores, holotype). **A.** Dorsal view; **B.** ventral view (abbreviations and nomenclature of lateral line system based on Sanzo (1911) and Miller (1986); drawings by R. Böhmer).

*gobius lanceolatus* sp. nov. a cryptobenthic lifestyle, living at least temporarily sheltered in soft sediment burrows. This species had remained undescribed and just was an accidental finding collected with (silty) mud where the individual could not be documented on the grab sample surface but was found during post-processing/sieving process. Indeed, its inconspicuous body and fin coloration resembling the habitat substrate, its relatively small eye diameter, elongate body, lanceolate caudal fin and squamation with numerous minute cycloid scales and the large sensory papillae on head further support this burrowing ecology hypothesis. The sediment sample contained agglutinated worm tubes and shells of *Atrina chaoutardi*. Live associated fauna comprised a second unidentified fish species and beyond abundant polychaetes, gastropods, bivalves, amphipods and shrimps. A potential burrow-dwelling lifestyle might provide shelter against predators on this relatively flat seafloor lacking any hard substrates. In addition, it should be mentioned that the presumed crypto-benthic lifestyle of *D. lanceolatus* sp. nov. is

supported by the fact that no other individual of this species has been found so far. This may also be the case with *D. bentuvii*, who seems to display a similar burrowing lifestyle (Miller 1966) of which only the holotype is currently accessible to scientists.

#### Generic reassignment taxa excluded from *Didogobius*

As mentioned above, with the restriction of *Didogobius* to the new species, *D. bentuvii*, *D. schlieweni* and *D. kochi*, several species are now excluded from *Didogobius* and thus in need generic reassignment, i. e. (i) the two shrimp-associated species *D. amicuscaridis* and *D. wirtzi*, and (ii) the banded species *D. splechnai*, *D. helenae* and *D. janetarum*. Since both these species-groups are unambiguously diagnosable on the basis of multiple previously established characters (see character compilations in Van Tassell & Kramer 2004, Schliewen & Kovačić 2008, Schliewen et al. 2018) the following diagnoses are provided for these

two species groups and they are formally assigned to two new genera, *Marcelogobius* gen. nov. and *Peter* gen. nov., respectively:

### *Marcelogobius* Schliewen gen. nov.

**Type species:** *Didogobius splechnai* Ahnelt & Patzner, 1995 based on the holotype (NMW 92804, 22.7 mm SL) and six paratypes (19.4 to 27.8 mm SL), collected by R.A. Patzner near Portinatx, Ibiza island, Balearic Islands, Spain, in submarine caves between 7 to 11 m in September 1991 and 1992.

**Diagnosis of *Marcelogobius* gen. nov.:** Gobiinae sensu Pezold (1993) with the following characters shared by all currently valid members of the genus: (1) suborbital papillae without row a; (2) six suborbital transverse rows, row 3 missing, last row 7 represented by a single papilla near pore  $\alpha$ ; (3) suborbital row 5 long, from near eye to near row d; (4) paired rows of interorbital transversal papillae absent; (5) head naked, predorsal area naked or scaled in front of D1 origin; (6) no mental barbels; (7) pelvic disc complete with fully developed anterior membrane (frenum); (8) anterior oculoscapular canal present with pores  $\sigma$ ,  $\lambda$ ,  $\kappa$ ,  $\omega$ ,  $\alpha$ ,  $\beta$ ,  $\varrho$ ; preopercular canals present or absent, posterior oculoscapular canal absent; (9) D2 branched rays  $\leq 11$  and A branched rays  $\leq 10$ ; (10) first D1 ray longest; (11) posterior nostril tubular.

**Etymology.** The generic name *Marcelogobius* gen. nov. honours the Croatian biologist, Marcelo Kovačić, who is the leading active goby expert for the Eastern Atlantic, Mediterranean and Ponto-Caspian region.

**Included species:** The type species, *M. splechnai* (Ahnelt & Patzner, 1995) comb. nov., *M. helenae* (Van Tassell & Kramer, 2014) comb. nov., and *M. janetorum* Schliewen, Wirtz & Kovačić 2018 comb. nov.

### *Peter* Schliewen gen. nov.

**Type species:** *Didogobius wirtzi* Schliewen & Kovačić, 2008 based on the holotype (ZSM 36566, 30.5 mm SL) and the paratype (SMNS 26370, 26.6 mm SL), collected by P. Wirtz at Bay of Tarrafal, Santiago Island, Cape Verde Islands over mixed sand and coral rubble bottom in 16 m depth in August 2007.

**Diagnosis of *Peter* gen. nov.:** Gobiinae sensu Pezold (1993) with the following characters shared by all currently valid members of the genus: (1) suborbital papillae without row a; (2) six suborbital transverse rows, row 3 missing, last row 7 represented by more than three papillae near pore  $\alpha$ ; (3) suborbital row 5

long, from near eye to near row d; (4) paired rows of interorbital transversal papillae absent; (5) head naked, predorsal area naked or scaled in front of D1 origin; (6) no mental barbels; (7) pelvic disc complete with fully developed anterior membrane (frenum); (8) anterior oculoscapular canal present with pores  $\sigma$ ,  $\lambda$ ,  $\kappa$ ,  $\omega$ ,  $\alpha$ ,  $\beta$ ,  $\varrho$ ; preopercular canals present, posterior oculoscapular canal absent; (9) D2 branched rays  $\leq 11$  and A branched rays  $\leq 10$ ; (10) second D1 ray longest or as long as first D1 ray; (11) posterior nostril flat; (12) flank coloration of with brown bands and broad white interspaces.

**Etymology.** The generic name *Peter* gen. nov. refers to the same first name of two outstanding goby enthusiasts at the same time, i. e. first Peter J. Miller, the British goby systematicist, who has contributed particularly to the knowledge of European and African gobies more than any other goby scientist; and second, Peter Wirtz, the tirelessly diving German naturalist and biologist, who discovered dozens of new animal species in the marine waters of the eastern tropical Atlantic, including the two shrimp-associated goby species *Peter amicuscaridis* comb. nov. and *Peter wirtzi* comb. nov. Gender masculine.

**Included species:** The type species, *P. wirtzi* (Schliewen & Kovačić, 2008) comb. nov. and *P. amicuscaridis* (Schliewen & Kovačić, 2008) comb. nov.

### Discussion

The type species of *Didogobius*, *D. bentuvii*, is known from a single specimen collected in the southeastern Mediterranean Sea close to the entry of the Suez Canal, and its phylogenetic relationships were difficult to determine at the time of description of *Didogobius* (Miller 1966). Albeit deemed unlikely, a relationship with Indo-Pacific goby genera rather than with other Eastern Atlantic, Mediterranean or Ponto-Caspian ones could not be excluded with certainty (Miller 1966). Later, more newly described goby species shared character states with the *D. bentuvii*, but several character states remained unique for *D. bentuvii* (Miller 1992, Ahnelt & Patzner 1995, Van Tassell 1988, Schliewen & Kovačić 2008, Van Tassel & Kramer 2014, Schliewen et al. 2018). The discovery of a first *Didogobius* species sharing most of these unique characters with the *Didogobius* type species, e. g., the minute eyes, lanceolate fin and pale coloration in combination with its eastern Atlantic distribution and with its molecularly relationships with eastern Atlantic and Mediterranean *Didogobius* and *Chromogobius* species supports Miller's preferred hypothesis that the type species is rather not a Lessepsian immigrant but a specialized goby with

Eastern Atlantic-Mediterranean relationships. However, the clade combining *Didogobius*, *Marcelogobius* gen. nov., *Peter* gen. nov. and *Chromogobius* species does not appear to form the sistergroup to the Ponto-Caspian benthophiline gobies but rather represents an ancient Atlanto-Mediterranean lineage within the *Gobius*-lineage (Agorreta et al. 2013, COI-data presented herein), living in subtropical shallow-water and with a presumed cryptobenthic lifestyle. Thus, Miller's alternatively proposed relationship of the type species of *Didogobius* with benthophiline gobies of the Ponto-Caspian, particularly with *Benthophiloides turcomanus* (Iljin, 1941), appears rather based on eco-phenotypic convergence than on phylogenetic relationships. Nevertheless, more data with more goby taxa are needed to consolidate the phylogenetic placement of the *Didogobius*-*Chromogobius* species complex.

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