The global freshwater bivalve checklist’s extension: Freshwater occurrences and phylogenetic position of *Galatea* clams from West Africa (Venerida: Donacidae)

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**Abstract**

The bivalve genus *Galatea* Bruguière, 1797 (Venerida: Donacidae) was thought to contain exclusively brackish-water clams, the ranges of which are confined to estuaries and lower tidal parts of large rivers in West Africa. This genus was therefore included to the global freshwater bivalve checklists (Bogan 2013; Graf 2013) as a largely estuarine group. Conversely, a review of published data alongside our field surveys indicate that at least three populations of *Galatea* spp. largely occur in freshwater environment, i.e. those from the Sanaga (Cameroon), Niger (Nigeria), and Volta (Ghana) rivers. The systematic placement of these populations is unclear, as are the taxonomic status and validity of numerous nominal taxa described in this genus from a variety of localities throughout the Atlantic Coast of Africa (Angola to Senegal). We tentatively assign the populations from Niger and Volta to *Galatea paradoxa* (Born, 1778), while the Sanaga’s population is considered here as *Galatea schwabi* (Clench, 1929). However, these taxa do not share clear morphological differences and may belong to a single widespread species. In this study, we present the first DNA sequence data for a *Galatea* member, i.e. *G. schwabi*. Our COI phylogeny supports its placement within the family Donacidae suggesting sister relationships between *Galatea* and *Donax* Linnaeus, 1758. Most *Galatea* populations play a vital role for local riparian communities in West Africa as an intensively exploited food source. Furthermore, the clams are heavily threaten by anthropogenic impacts such as dam construction, riverbed substrate mining, and river pollution. The fishing loads and habitat degradation altogether lead to the rapid decreasing of *Galatea* populations in several water bodies, e.g. the Volta River in Ghana. It is impossible to develop conservation and management plans for these clams due to the lack of reliable species-level taxonomic concept of the genus. It is clear that the *Galatea* taxonomy and ecology need a thorough revision in the future based on DNA sequences of newly collected samples from all West African rivers, in which these remarkable clams occur.

**Key words:** Bivalvia, freshwater animals, West Africa, Sanaga River, Niger River, Volta River, phylogeny, systematics, conservation.
Introduction

Freshwater bivalves are a diverse ecological group, which contains representatives of different families (Graf 2013). The order Unionida with six families represents the most species-rich monophyletic radiation of bivalves in fresh water (Graf & Cummings 2007; Bogan 2008, 2013). The family Sphaeriidae is another example of a large and widespread freshwater group (Cooley & Foighil 2000; Korniushin & Gaubrecht 2002). Conversely, primary marine bivalve families can also contain secondary freshwater members, e.g. Cyrenidae, Phairidae, Pholadidae, Teredinidae, and Donacidae (Brandt 1974; Graf 2013; Bolotov et al. 2018a, b; Shipway et al. 2019). Most freshwater and estuarine representatives in these groups are poorly known both taxonomically and ecologically, including members of the family Donacidae (Daget 1998). This family belongs to the superfamily Tellinoidea placed among the order Venerida (Bouchet et al. 2010).

The genus Galatea Bruguière, 1797 (=Egeria Roissly, 1805) is a group of brackish-water donacid bivalves with 10–11 species, which were described chiefly from the estuaries of West African rivers from Angola to Senegal (Bernardi 1860; Daget 1998; Mienis 2000; Huber 2010; Graf 2013). Pilsbry and Bequaert (1927) published the most comprehensive overview of the taxonomy and biology of Donacidae in West Africa up to that time, although this work was based largely on samples from the Congo Basin. Clench (1929) listed two genera of Donacidae, i.e. Iphigenia and Egeria, as freshwater taxa, and described E. schwabi Clench, 1929. Purcheon (1963) discussed and illustrated the anatomy and biology of Egeria in detail. Later, Bogan (2008) listed two genera and two species of Donacidae as freshwater bivalves, and noted that other species are known to occur in brackish-water habitats. Huber (2010) briefly discussed the synonymy of Galatea based on conchological variability of available nominal taxa. Olayemi et al. (2012) studied the anatomy of the nominal taxon Egeria radiata Lamarck, 1804 from West Africa. Graf (2013) listed Galatea as a solely brackish genus but no mention was made on freshwater taxa. Iphigenia was assigned as a typically brackish-water group with seven species but two species of Iphigenia, i.e. Iphigenia centralis (Germain, 1904) and I. laevigata (Gmelin, 1791), were listed as freshwater bivalves (Graf 2013).

Bivalve molluscs represent a nutritious and low-impact (i.e. having a low environmental footprint) protein source for local communities throughout tropical countries (Willer & Aldridge 2020). The Galatea clams are harvested intensively in many West African regions, e.g. Ghana, Nigeria, Cameroon, and Congo (Pilsbry & Bequaert 1927; Lawson 1963; Purchon 1963; Etim 1996; Etim et al. 1997; Mienis 2000). The clam’s soft body is characterized by high nutritional qualities (Ifon & Umoh 1987). They can accumulate several pollutants such as heavy metals but were considered suitable for human consumption based on the WHO Safety Reference Standards (Obirikorang et al. 2009, 2010). Galatea spp. attract a full attention of local scientists due to commercial importance of these clams. A large body of regional literature describes Galatea’s life cycle and population dynamics (Etim 1996; Adjei-Boateng & Wilson 2012), biochemistry (Ifon & Umoh 1987), growth and age patterns (Etim & Brey 1994; Etim et al. 1997; Adjei-Boateng & Wilson 2013; Akinjogunla & Moruf 2019), parasites (Adyemo et al. 2013), and habitats (Obirikorang et al. 2013). Several applied issues such as practices and economy of local fisheries (Lawson 1963; Purchon 1963), and aquaculture techniques (Amoah & Ofori 2013) were also taken into account.

Conversely, the systematics of Galatea clams is still poorly known, and only a few taxonomic reviews on this genus or selected species groups are available (Bernardi 1860; Pilsbry & Bequaert 1927; Clench 1929; Daget 1998; Huber 2010). The DNA sequences of Galatea taxa were lacking until recently, while the genetic polymorphism of G. paradoxus (Born, 1778) population from Nigeria was recovered using an inter-simple sequence repeat (ISSR)-PCR approach (Henry et al. 2018).

This study (1) revises environmental preferences of Galatea clams based on newly collected data and published occurrences from Cameroon, Nigeria, and Ghana; (2) estimates the phylogenetic position of a Galatea species from Cameroon using new molecular sequences of the mitochondrial cytochrome c oxidase subunit I (COI) gene; and (3) discusses several taxonomic and biogeographic issues regarding this genus.

Material and Methods

Data collection
The new samples of Galatea clams were collected by wading at appropriate localities in Cameroon and Nigeria (collectors Oleg S. Pokrovsky and Abiona J. Adesanya, respectively) (Tables 1-2). Small tissue snips from Cameroon’s samples for DNA analyses were placed in 96% ethanol immediately after collecting. In
contrast, only dry shells were collected for specimens from Nigeria (soft body was removed by Abiona J. Adesanya for another project). The shell and tissue samples were deposited in the Russian Museum of Biodiversity Hotspots [RMBH], N. Laverov Federal Center for Integrated Arctic Research of the Ural Branch of the Russian Academy of Sciences, Arkhangelsk, Russia.

Table 1. Geographic localities and shell dimensions of *Galatea schwabi* samples from Sanaga River, Cameroon.

| Specimen          | Locality                                             | Length  | Height  | Width  | Shell elongation index (SEI) | Shell convexity index (SCI) | Approximate distance from the river mouth (km) |
|-------------------|------------------------------------------------------|---------|---------|--------|-----------------------------|-----------------------------|---------------------------------|
| Topotype RMBH biv800/1 | Sanaga River near Mouanko (lower reaches, slightly brackish section) | 63.90   | 48.47   | 29.53  | 75.85                       | 46.21                       | 24                              |
| Topotype RMBH biv800/2 | Sanaga River near Mouanko (lower reaches, slightly brackish section) | 92.55   | 63.53   | 37.33  | 68.64                       | 40.33                       | 24                              |
| Specimen RMBH biv801/1 | Sanaga River at Monatélé (middle reaches, freshwater section) | 67.32   | 51.62   | 32.47  | 76.68                       | 48.23                       | 200                             |
| Specimen RMBH biv801/2 | Sanaga River at Monatélé (middle reaches, freshwater section) | 103.49  | 76.65   | 42.64  | 74.07                       | 41.20                       | 200                             |

Shell elongation index (SEI = height/length ratio × 100) and the shell convexity index (SCI = width/length ratio × 100).

**Morphological study**

Each sample was studied using morphological characters such as shell shape, umbo position, structure of pseudocardinal and lateral teeth, shape of muscle attachment scars (Bolotov et al. 2018a, b), and was compared with the original descriptions of nominal taxa. Shell length, shell height, and shell width were measured using a digital caliper (Digimatic Coolant Proof, Mitutoyo, Japan). Two morphometric indexes were calculated with these measurements: (1) shell convexity index (SCI = width/length ratio × 100), and (2) shell elongation index (SEI = height/length ratio × 100) (Kondakov et al. 2020).

**DNA extraction and sequencing**

The present study includes new molecular data for four *Galatea schwabi* specimens (Table 3). Total genomic DNA was extracted from ethanol-preserved samples using the NucleoSpin® Tissue Kit (Macherey-Nagel GmbH & Co. KG, Germany), following the manufacturer protocol. In the present study, we used data inferred from the *COI* gene, a fragment of which (657 bp) was amplified using LoboF1 and LoboR1 primer pairs (Lobo et al. 2013). The PCR mix contained approximately 100 ng of total cellular DNA, 10 pmol of each primer, 200 μmol of each dNTP, 2.5 μl of PCR buffer (with 10×2 mmol MgCl₂), 0.8 units of Taq DNA polymerase (SibEnzyme Ltd., Russia), and H₂O, which was added up to a final volume of 25 μl. Thermocycling included one cycle at 95°C (4 min), followed by 34-36 cycles of 95°C (50 sec), 48°C (50 sec), and 72°C (50 sec), with a final extension at 72°C (5 min). Forward and reverse sequencing was performed on an automatic sequencer (ABI PRISM 3730, Applied Biosystems, USA) using the ABI PRISM BigDye Terminator v. 3.1 reagent kit. The resulting sequences were checked using a sequence alignment editor BioEdit v. 7.2.5 (Hall 1999).

**Sequence alignment and phylogenetic analyses**

The in-group of our *COI* dataset was based on 31 sequences of taxa from the orders Venerida and Adapedonta (Table 3). We used 4 new sequences of *Galatea schwabi* samples, and 27 additional sequences from the NCBI’s GenBank. Two representatives of the family Lucinidae (order Lucinida) were used as outgroup, i.e. *Myrtea spinifera* (Montagu, 1803) and *Lucina pensylvanica* (Linnaeus, 1758) (Table 3). The sequences were aligned through the MUSCLE algorithm in MEGA7 (Kumar et al. 2016). Maximum likelihood phylogenetic analysis was performed using the server for IQ-TREE (W-IQ-TREE) with GTR+G evolutionary model (Trifinopoulos et al. 2016) and ultrafast bootstrap algorithm (UFBoot) with 5,000 replicates (Hoang et al. 2017).
Table 2. Occurrences of *Galatea* species from freshwater and slightly brackish environments in West Africa.

| No. | Species    | Country | River | Locality | Latitude | Longitude | Year of finding | Reference               |
|-----|------------|---------|-------|----------|----------|-----------|-----------------|-------------------------|
| 1   | *G. schwabi* | Cameroon | Sanaga | Lobetal  | 3.6322   | 9.7704    | 1929            | Clench (1929)           |
| 2   | *G. schwabi* | Cameroon | Sanaga | Mouanko  | 3.6360   | 9.8100    | 2019            | This study              |
| 3   | *G. schwabi* | Cameroon | Sanaga | Montatélé | 4.2710   | 11.1990   | 2019            | This study              |
| 4   | *G. paradoxa* | Nigeria  | Niger  | Yenagoo  | 4.9173   | 6.2635    | 2017            | This study              |
| 5   | *G. paradoxa* | Nigeria  | Niger  | Oporoma  | 4.8000   | 6.0833    | 2012            | Adeyemo et al. (2013)   |
| 6   | *G. paradoxa* | Nigeria  | Niger  | Eniwarl  | 4.1466   | 6.1305    | 2012            | Adeyemo et al. (2013)   |
| 7   | *G. paradoxa* | Nigeria  | Cross  | Itu      | 5.1833   | 7.9718    | 1989            | Etim (1996); Etim et al. (1997) |
| 8   | *G. paradoxa* | Ghana    | Volta  | Sogankope | 5.9973   | 0.5861    | 1963            | Purchon (1963)          |
| 9   | *G. paradoxa* | Ghana    | Volta  | Torgome  | 6.1124   | 0.1348    | 1954            | Lawson (1963)           |
| 10  | *G. paradoxa* | Ghana    | Volta  | Asuchari | 6.0957   | 0.1952    | 1954            | Lawson (1963)           |
| 11  | *G. paradoxa* | Ghana    | Volta  | Aleboke  | 6.1083   | 0.2345    | 1954            | Lawson (1963)           |
| 12  | *G. paradoxa* | Ghana    | Volta  | Volivoe  | 6.0988   | 0.2597    | 1954            | Lawson (1963)           |
| 13  | *G. paradoxa* | Ghana    | Volta  | Duffor   | 6.0914   | 0.2833    | 1954            | Lawson (1963)           |
| 14  | *G. paradoxa* | Ghana    | Volta  | Aveyime  | 6.0408   | 0.3769    | 1954            | Lawson (1963)           |
| 15  | *G. paradoxa* | Ghana    | Volta  | Addiome  | 6.0626   | 0.4901    | 1954            | Lawson (1963)           |
| 16  | *G. paradoxa* | Ghana    | Volta  | Ada      | 5.8194   | 0.6439    | 2010            | Adeji-Boateng & Wilson (2012) |
| 17  | *G. paradoxa* | Ghana    | Volta  | Aveglo   | 5.8817   | 0.6486    | 2010            | Adeji-Boateng & Wilson (2012) |

**Distribution mapping**

Occurrences of *Galatea paradoxa* and *G. schwabi* were sampled based on original data and published references (Table 2). The map was created using ESRI ArcGIS 10 software (https://www.esri.com/arcgis). The topographic base of the map was compiled with free open sources such as Natural Earth Free Vector and Raster Map Data (https://www.naturalearthdata.com), Global Self-consistent Hierarchical High-resolution Geography, GSHHG v2.3.7 (https://www.soest.hawaii.edu/wessel/gshhg), and HydroSHEDS (https://www.hydrosheds.org).

**Results**

Our results indicate that no less than two *Galatea* species are widely distributed in freshwater environments in West Africa (Figs 1-2 and Table 2). In particular, *Galatea schwabi* was recorded in the middle reaches of the Sanaga River (approximately 200 km upstream of the mouth), while *G. paradoxa* is known to occur in freshwater and slightly brackish sites of the Niger, Cross, and Volta rivers (Fig. 1 and Table 2).

Both species share similar conchological features such as a triangular shell shape with elevated umbo, massive hinge plate, and well-developed muscle attachment scars (Figs. 3-4). Structure and number of pseudocardinal and lateral teeth are identical in individuals of the two species. One more common specific trait is purplish rays impregnated into prismatic layer, covering the shell from the umbo to ventral margin. The coloration of shells can be variable. Shells of *Galatea schwabi* are greenish yellow in young individuals to dark brown in adults. The periostracum of *Galatea paradoxa* from Nigeria is darker even in young clams, and shares a number of somewhat brown flecks, which are usually located in the umbo area. The nacre is whitish, without shining. The umbo cavity is rather developed in both taxa, although in the case of *Galatea paradoxa* it is deeper, most likely due to the higher beaks. In summary, *Galatea schwabi* from Cameroon and *G. paradoxa* from Nigeria are almost undistinguishable from each other conchologically except the morphology of periostracum and a degree of beak development (Figs. 3-4). The shell convexity index and shell elongation index for *Galatea schwabi* (Table 1) indicate that the shell proportions share high intraspecific variability even based on a limited number of specimens.
| Family          | Species                          | Locality                                                                 | Specimen Voucher No.* | COI GenBank acc. nos. | References                        |
|-----------------|----------------------------------|---------------------------------------------------------------------------|-----------------------|----------------------|-----------------------------------|
| **IN-GROUP**    |                                  |                                                                           |                       |                      |                                   |
| Donacidae       | *Galatea schwabi* (Clench, 1929) | Cameroon: Sanaga River near Mouanko (lower reaches, slightly brackish section) | RMBH biv800/1 [topotype] | MW000251 | This study                                      |
| Donacidae       | *G. schwabi* (Clench, 1929)      | Cameroon: Sanaga River near Mouanko (lower reaches, slightly brackish section) | RMBH biv800/2 [topotype] | MW000252 | This study                                      |
| Donacidae       | *G. schwabi* (Clench, 1929)      | Cameroon: Sanaga River near Mouanko (lower reaches, slightly brackish section) | RMBH biv800/3 [topotype] | MW000253 | This study                                      |
| Donacidae       | *G. schwabi* (Clench, 1929)      | Cameroon: Sanaga River at Monatelé (middle reaches, freshwater section)    | RMBH biv801           | MW000254 | This study                                      |
| Donacidae       | Donax variegatus (Gmelin, 1791)   | Portugal: Monte Gordo                                                      | Dvar COI Hap1         | MF668378  | Fernandez-Perez et al. (2017)                  |
| Donacidae       | *D. trunculus* Linnaeus, 1758     | Spain: Catalonia                                                           | BivAToL-132          | KC429143  | Sharma et al. (2017)                         |
| Semelidae       | Scrobicularia plana (da Costa, 1778) | UK: Wales                                                               | BivAToL-20           | KX713497  | Combes et al. (2017)                        |
| Tellinidae      | Limecola balbica (Linnaeus, 1758) | UK: England                                                               | BivAToL-286          | KC429141  | Sharma et al. (2013)                        |
| Semelidae       | Semele scabra (Hanley, 1843)     | China: Lingao, Hainan Province                                             | SESC-0121            | JN398365  | Yuan et al. (2012)                         |
| Tellinidae      | Iridona iridescens (Benson, 1842) | China: Leqing, Zhejiang Province                                          | MOIR-0101            | JN398362  | Yuan et al. (2012)                         |
| Tellinidae      | Scissula similis (J. Sowerby, 1806) | USA: Florida Keys                                                        | BivAToL-7            | KC429142  | Sharma et al. (2013)                        |
| Cardiidae       | Cerastoderma edule (Linnaeus, 1758) | UK: England                                                               | BivAToL-21           | KC429134  | Sharma et al. (2013)                        |
| Cardiidae       | Dallocardia maricata (Linnaeus, 1758) | USA: South Carolina                                                      | BivAToL-207          | KX713457  | Combes et al. (2017)                        |
| Sphaeriidae     | Masculium indicum (Deshayes, 1854) | Nepal: Bagmati                                                           | 17488                | KF483411  | Clewing et al. (2013)                       |
| Sphaeriidae     | Pisidium costulossom Connolly, 1931 | South Africa: Mpubulanga                                                 | 15815                | KF483422  | Clewing et al. (2013)                       |
| Sphaeriidae     | P. viridarium Kuiper, 1956        | Lesotho: Thaba-Tseka                                                    | 15834                | KF483397  | Clewing et al. (2013)                       |
| Cyreniidae      | Corbicula flumea (O. F. Müller, 1774) | Russia: Arkhangelsk, Yuras River                                       | MCorb14              | KX192354  | Bespalaya et al. (2018)                     |
| Cyreniidae      | Polymsoda caroliniana (Bosc, 1801) | USA: Florida, Lower Florida Keys                                          | UMMZ 265499          | AF196276  | Sirippattawan et al. (2000)                  |
| Cyrenoididae    | Cyrenoida floridana (Dall, 1896)  | USA: Florida Keys                                                        | BivAToL-27           | KC429123  | Sharma et al. (2013)                        |
| Arcticidae      | Arctica islandica (Linnaeus, 1767) | UK: Scotland                                                             | BivAToL-191          | KC713445  | Combes et al. (2017)                        |
| Dreissenidae    | Dreissenia polymorpha (Pallas, 1771) | Croatia: Zagreb, Jarun Lake                                             | Drpo1                | JX099437  | Bilandzija et al. (2013)                    |
| Dreissenidae    | Mytilopsis leucophaeata (Conrad, 1831) | USA: Florida Keys                                                      | BivAToL-9            | KX713485  | Combes et al. (2017)                        |
| Mactridae       | Macra violacea (Gmelin, 1791)     | China: Hong Kong                                                        | BivAToL-430          | KC713475  | Combes et al. (2017)                        |
| Mactridae       | Meropestia nicobarica (Gmelin, 1791) | China: Hong Kong                                                    | BivAToL-429          | KC713478  | Combes et al. (2017)                        |
| Mactridae       | Mulinia lateralis (Say, 1822)     | USA, Florida                                                             | BivAToL-246          | KC713480  | Combes et al. (2017)                        |
| Veneridae       | Chamelea striatula (da Costa, 1778) | Spain: Ponteveledra                                                      | CSTPon01             | KY547747  | García-Souto et al. (2017)                  |
| Veneridae       | Mercenaria mercenaria (Linnaeus, 1758) | USA: South Carolina                                                      | BivAToL-208          | KX713477  | Combes et al. (2017)                        |

...continued on the next page
The description of *Galatea schwabi* presented by Clench (1929) is very similar to that of *G. paradoxa hermaphroditasensu* Clench, 1929 non Gmelin, 1791. Clench (1929) marked that *Galatea schwabi* differs from the latter taxon by having a darker periostracum, thinner shell, and smaller hinge plate, while the general shell outlines and a few specific traits such as purplish rays on the nacre were similar for both species. The Clench’s samples of both taxa were collected from the same locality, the main channel of the Sanaga River at Lobetal. Based on the Gmelin’s (1791) protologue, *Egeria paradoxa hermaphroditas* has a triangular shell with smooth and olive-colored periostracum, white and cerulean stripes on the inner side of the valve, and crenate pseudocardinal teeth. Nevertheless, the image of this species published in Martini & Chemnitz (1782: pl. 32, fig. 336) can hardly be compared with *Galatea schwabi*, as it seems to be more similar conchologically to a *Corbicula* clam.

**Figure 1.** Occurrences of *Galatea schwabi* (red stars) and *Galatea paradoxa* (light green stars). The locality data is given in Table 2. Freshwater basins are colored as follows: Sanaga (1), Cross (2), Niger (3), and Volta (4). The red dash indicates the Edea Hydroelectric Power Station’s dam on the Sanaga River. (Map: Mikhail Y. Gofarov).
Our COI gene phylogeny indicated that *Galatea schwabi* from Cameroon belongs to the marine family Donacidae, and, at first glance, sisters to the genus *Donax* Linnaeus, 1758 (Fig. 5).

A taxonomic review of two *Galatea* species occurring in freshwater habitats is presented below, including a non-exhaustive synonymy, data on the type specimen and type locality, examined materials, habitats, and distribution. For *Galatea schwabi*, a brief conchological re-description is provided as well.

**Taxonomic Account**

Order Venerida Gray, 1854  
Superfamily Tellinoidea Blainville, 1814  
Family Donacidae Fleming, 1828

Genus *Galatea* Bruguière, 1797

*Galatea schwabi* (Clench, 1929)  
= *Egeria schwabi* Clench (1929): 122, pl. 1, figs. 1-2; Purchon (1963): 251; Daget (1998): 227.  
= *Egeria paradoxa hermaphrodita* Clench (1929): 121 [non Gmelin (1791): 3278].  
= *Galatea schwabi* Huber (2010): 692.

Figs. 1-3, Table 1.

Type: Holotype MCZ 78.072 [Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts, USA].
Type locality: “Lobetal, lower Sanaga River” [CAMEROON: Sanaga River at Lobetal (lower reaches, slightly brackish section), 3.6322°N, 9.7704°E, altitude 5-6 m a.s.l., Littoral Province] (Clench 1929).

Topotypes examined: CAMEROON: Sanaga River near Mouanko (lower reaches, slightly brackish section), 3.6360°N, 9.8100°E, altitude 5-6 m a.s.l., Littoral Province, 19-21.iii.2019, 5 specimens [RMBH biv800: 2 shells; 5 ethanol-preserved tissue snips], Oleg Pokrovsky leg. The topotypes were collected 4 km east (upstream) of the type locality.

Other material examined: CAMEROON: Sanaga River at Monatélé (middle reaches, freshwater section), 4.2710°N, 11.1990°E, altitude 380 m a.s.l., Central Province, 19-21.iii.2019, 2 specimens [RMBH biv801: 2 shells; one ethanol-preserved tissue snip], Oleg Pokrovsky leg.

Conchological re-description: Shell triangular, rather thick and strong. Specific trait is radial rays running from the umbones to the ventral margin, which can vary in number and width on both valves. These rays are purplish and impregnated into prismatic layer, visible also in the inner side of the shell, but mainly along the margin, especially in the ventral and anterior edges. Umbones high, almost in the center of the shell, eroded. Periostracum smooth, thin, have a propensity for scaling off. Nacre whitish, not shining; muscle scars and basal areas of pseudocardinal teeth can be tinted in purple. Young specimens with greenish yellow coloration, which turning to dark brown or black in adult individuals. Hinge plate strong and well-developed. The right valve with one median, dissected pseudocardinal tooth and short, flat lateral tooth; tubercular tooth-like structure is also above anterior muscle scar. The left valve with three pseudocardinal teeth, intermediate tooth usually smaller than the other two, and serves to articulate into hollow space of dissected teeth from the right valve. Umbo cavity very deep. Muscle attachment scars are well-developed, anterior scar oval-shaped, posterior scar more circular.

Figure 3. Shells of Galatea schwabi from Sanaga River, Cameroon. (A-B) Topotypes RMBH biv800, Mouanko (lower reaches, slightly brackish section). (C-D) Specimens RMBH biv801, Monatélé (middle reaches, freshwater section). Red arrows show well-developed muscle attachment scars. Scale bar = 10 mm. (Photos: Artem A. Lyubas).
Habitats: This species inhabits freshwater and slightly brackish sections of a large river (see Fig. 2 for a freshwater section). Its type locality is situated approximately 20 km upstream of the river mouth, “just beyond tide water” (Clench 1929) but we recorded Galatea schwabi from the middle reaches of the Sanaga River at altitude 380 m a.s.l. The Edea Hydroelectric Power Station’s dam separates this part of its population from the downstream stock (Fig. 1).

Distribution: Sanaga River in Cameroon (Fig. 1 and Table 2).

Comments: This species may represent a separate taxon or a local population of the widespread Galatea paradoxa. DNA sequences of Galatea paradoxa samples from Ghana and Nigeria are urgently needed to produce a final solution on the status of these taxa.

*Galatea paradoxa* (Born, 1778)

=Venus paradoxa Born (1778): 53.
=Galathea radiata Lamarck (1804): 433.
=Egeria paradoxa Daget (1998): 224.
=Galatea paradoxa Germain (1918): 133; Huber (2010): 322 (compendium), 692 (special remarks).

Figs 1 and 4.
Type: Holotype in the Natural History Museum Vienna, Vienna, Austria (fide Daget 1998).

Type locality: Unknown.

Material examined: NIGERIA: Niger River at Yenagoa, 4.9173°N, 6.2635°E, Bayelsa State, 01.ii.2017, 9 shells [RMBH biv1086], Abiona J. Adesanya leg.

Habitats: This species prefers slightly brackish and freshwater habitats in the downstream sections of large rivers (Lawson 1963; Purchon 1963; Etim & Brey 1994; Etim 1996; Etim et al. 1997; Adeyemo et al. 2013; this study).

Distribution: Volta, Niger, and Cross rivers in West Africa (Fig. 1 and Table 2).

Comments: The type locality of *Venus paradoxa* Born, 1778 is unknown, and there is still not much evidence that the species we are discussing on belongs to this nominal taxon. Multiple authors applied the name *radiata* Lamarck, 1804 to *Galatea* populations from the Volta, Niger, and Cross rivers (e.g. Bernardi 1860; Lawson 1963; Purchon 1963; Etim & Brey 1994; Etim 1996; Etim et al. 1997) but it was synonymized with *paradoxa* Born, 1778 (e.g. Germain 1918; Daget 1998). Germain (1918: figs 18-19) illustrated the holotype of *Galatea radiata* Lamarck.

![Figure 5. Maximum likelihood (IQ-TREE) phylogeny of Bivalvia (Venerida and Adapedonta) based on the COI gene sequences (Table 1). A *Galatea* member is dark red. Scale bar indicates the branch lengths (substitutions per site). Black numbers near nodes indicate the ultrafast bootstrap support (BS) values.](image)

**Discussion**

**Diversity of freshwater bivalves in Africa**

Most African freshwater bivalve taxa belong to the order Unionida (Bogan 2008; Graf 2013). Members of several families such as the Unionidae, Margaritiferidae, Etheriidae, and Iridinidae are known to occur on this continent (Graf & Cummings 2007; Bogan 2008). In its turn, the taxonomic richness of non-Unionida freshwater bivalve assemblage in Africa is lower, with a few species of Cyrenidae (*Corbicula*) and Donacidae, and a larger radiation of the Sphaeriidae being reported (Daget 1998). Three species from the family Donacidae can be considered freshwater animals with some tolerance to brackish environments, i.e. *Profischeria centralis* (Germain, 1904) [Niger Basin], *P. delessertii* (Bernardi, 1860) [Angola to Côte d'Ivoire; a freshwater population in Lake Togo, Togo (Mienis 2016)], and *Iphigenia laevigata* (Gmelin, 1791) [Congo to Senegal] (Graf 2013; Mienis 2016). Conversely, the first species is known from the single
type specimen with a vague type locality (“le Moyen Niger et le Bani”) that was probably transferred from a brackish coastal site to the inland region by humans (Daget 1998).

Here, we present evidence that *Galatea schwabi* must also be included to the global checklist of freshwater bivalves as an euryhaline animal, a population of which also occurs in freshwater environment in the middle section of the Sanaga River. Additionally, it was found that *Galatea paradoxa* did not occur in the 30-km-long lowermost section of the Volta River in Ghana, most likely due to saline and brackish environments, which are prevailed throughout this part of the watercourse (Purchon 1963). The lower boundary of its occurrence in the Volta River corresponded with the upper limit of penetration of saline waters into the river. Hence, the Volta’s species should be considered a freshwater bivalve, which has some tolerance to brackish waters (Lawson 1963; Purchon 1963; Amoah & Ofori-Danson 2012). Currently, its beds between the Volta dams (Akosombo and Kpong) and Sogankope were largely disappeared due to habitat degradation and overfishing (Adjei-Boateng & Wilson 2012; Amoah & Ofori-Danson 2012).

Furthermore, *Galatea paradoxa* occurs in freshwater sections of the Niger and Cross rivers in Nigeria (Etim & Brey 1994; Etim 1996; Etim et al. 1997; Adeyemo et al. 2013; this study). These findings indicate that the concept of *Galatea* as an exclusively estuarine group of bivalves (Thiele 1935; Daget 1998; Graf 2013) is misleading because of insufficient and fragmentary ecological and occurrence data on these aquatic animals.

**Taxonomic and biogeographic issues**

Currently, the species-level taxonomy of the genus *Galatea* is poorly understood but it is thought to contain 10-11 species (Huber 2010; Graf 2013). Several *Galatea* taxa seem to have restricted ranges, e.g. *G. schwabi* from the Sanaga River, *G. congica* Boettger, 1885, *G. tenuicula* Philippi, 1848 and *G. nux* (Pilsbry & Bequaert, 1927) from the Congo Estuary, and *G. bengoensis* Dunker, 1849 from Angola (Pilsbry & Bequaert 1927; Daget 1998). However, these taxa were introduced based on conchological features alone, and their validity needs to be confirmed using a comparative DNA-based approach.

Clench (1929) listed two nominal taxa from the same locality (Lobetal) of the lower Sanaga River, i.e. *Egeria schwabi* and *E. paradoxa hermaphroditina*. Our morphological and phylogenetic analyses indicated that Clench (1929) described conchological varieties of a single species as two separate taxa. Hence, *Egeria paradoxa hermaphroditina* sensu Clench, 1929 non Gmelin, 1791 must be considered a synonym of *Galatea schwabi*. Conversely, the taxonomic placement of *Galatea* populations from the Sanaga, Volta, and Niger rivers is unclear, and needs future DNA-based research. If these populations belong to a single species, *Galatea schwabi* will become a junior synonym of an older nominal taxon (e.g. *G. paradoxa*).

The Ponto-Caspian clams *Monodacna colorata* (Eichwald, 1829) (Cardiidae) and *Dreissena bugensis* (Andrusov, 1897) (Dreissenidae) are additional examples of bivalve species distributed in both brackish and freshwater environments, e.g. the Caspian Sea and the Volga River (Kurina 2020; Son et al. 2020). In tropical Asia, the freshwater bivalve genus *Novaculina* Benson, 1830 (Pharidae) seem to represent an ecological relative of the African *Galatea* taxa. This Asian genus is a marine-derived, secondary freshwater group, which contains four species with strictly allopatric ranges (Bolotov et al. 2018b). These species are known to occur in lower and middle sections of large and medium-sized rivers, and can tolerate slightly brackish water (Brandt 1974; Liu & Zhang 1979; Sayenko et al. 2017; Bolotov et al. 2018b). At first glance, *Galatea* appear to share a higher salinity tolerance compared with that of *Novaculina*, as the majority of the nominal taxa in the first genus were described from estuarine parts of rivers (Pilsbry & Bequaert 1927; Daget 1998). However, an easier accessibility of collecting localities in the downstream river sections during the historical period of XVIII – beginning of XX centuries can bias this pattern, as it was the probable case for *Galatea schwabi*.

**Conclusion**

Recently, unexpected freshwater representatives of primary marine groups of bivalves were discovered, e.g. the shipworm *Lithoredo abatanica* Shipway, Distel & Rosenberg, 2019 (Teredinidae) in the Philippines (Shipway et al. 2019), and the piddock *Lignopholas fluminalis* (Blanford, 1867) (Pholadidae) in Myanmar (Bolotov et al. 2018a). These findings indicate how large gaps occur in our current knowledge on aquatic invertebrates from the downstream freshwater sections of rivers, especially in tropical areas. The genus *Galatea*, which was thought to be a group of exclusively brackish-water bivalves endemic to the Atlantic Coast of Africa (Thiele 1935; Daget 1998; Graf 2013), can also be considered a little known taxon.
While ecological research on this genus is in its initial stage for now, our findings demonstrate that at least two *Galatea* species – *G. schwabi* and *G. paradoxa* – are freshwater molluscs, which largely occur in freshwater sections of rivers (Lawson 1963; Purchon 1963; Etim & Brey 1994; this study). We can expect that some other species of this genus were considered to be entirely brackish-water animals due to the lack of reliable occurrence data (e.g. those from the Congo Estuary: Pilsbry & Bequaert 1927), and that more *Galatea* taxa could be found in freshwater environments in the future.

Finally, *Galatea* nominal taxa need a thorough taxonomic revision based on an integrative approach. At first glance, we could assume that one endemic species of this group allopatrically evolved in each large freshwater drainage of the West African Coast, as did *Novaculina* species, their putative ecological relatives, in several largest rivers of Asia (Bolotov et al. 2018b). However, the presence of widespread *Galatea* species with broad ranges covering a variety of freshwater basins throughout West Africa and reflecting Late Quaternary rearrangements of river network cannot be excluded. This genus seems to be a perspective model group to reconstruct ancient connections between largest rivers in West Africa and to understand general patterns of marine animals’ expansion into freshwater environments.

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