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Functional anatomy of the reproductive system of the caenogastropod of genus *Cleopatra,* (Troschel, 1857), Family Paludomidae, in Qena Province, Egypt

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ABSTRACT

Genus *Cleopatra* belonging to Caenogastropda is dioecious. The mature male and female cannot be differentiated externally, but often the removal of shell and differentiation between the two sexes can be achieved by the difference in colour of gonads. The gonads are deep yellow in the male and yellowish-white in the female, the complete reproductive organs of each sex, and commonly formed of the gonad, the gonoduct, and the accessory glands. The male has a well-developed testis found in the spire of the visceral mass, a thin vas deferens and a glandular pallial gonoduct. The latter can be differentiated into a closed prostate gland, a finger-like blind vesicula seminalis, and an opened anterior vas deferens. The sperms are of two types which can be discerned by SEM according to the outline of the head and the length of the flagellum. The female reproductive system is made up of the ovary, having a location corresponding to that of the testis, two main ovarian ductules, the oviduct and the pallial glandular gonoduct. The latter consists of five regions, the receptaculum seminis, albumen gland, capsule gland, uterus and open spermatophore chamber. There is an internal groove in the mantle wall, just anterior to the male or the female slit, to be apparently used for the transfer of the gametes either to the exterior or to the interior.

INTRODUCTION

The Paludomidae Stoliczka, 1868 is currently understood as representing taxa with a general distribution including most of tropical sub-Saharan Africa and Madagascar as well as South and Southeast Asia (see Neiber and Glaubrecht 2019 who summarize the results of phylogenetic analyses presented by West and Michel 2000; Michel 2004; Wilson *et. al.*, 2004; Glaubrecht and Strong 2007; Strong *et. al*. 2011; for a recent compilation on the diversity of family-group names available for this group and recent classifications, see also Bouchet and Rocroi 2005; Bouchet *et. al*. 2017).

Species in this family of freshwater cerithioideans show a high diversity with regard to shell shape and ornamentation. The endemic paludomids of Lake Tanganyika have especially attracted much attention by taxonomists, early bio-geographers, and evolutionary biologists because of their thalassoid (Bourguignat 1885) appearance, i.e. their resemblance to various marine gastropod families (Glaubrecht 1996, 2008, 2009 and

2011). A large number of names have been introduced for Tanganyikan paludomids by the French malacologists Bourguignat, the head of the so called ‘Nouvelle École’ (Dance 1970), on the basis of differences of the shell that are often hardly perceptible (Bourguignat 1885 and 1888). However, being among the first to work on the gastropod fauna of the lake, several names first introduced by this author are still in use to this day, although the far greater number certainly represent individual variations that do not merit to be accepted and are thus to a large extent a burden today for taxonomists, biogeographers, and evolutionary biologists working on the paludomid fauna of Lake Tanganyika.

Although several synoptical works covering the regional diversity of Paludomidae in Africa or Asia have been published (e.g. Preston 1915; Pilsbry and Bequaert 1927; Leloup 1953; Brown 1994; West *et. al*. 2003;. Strong & Gargominy 2008; Neiber & Glaubrecht, 2019), Bolotov *et. al,* (2021)

The basic prerequisite of any taxonomic work on a specific group of organisms is the historical perspective of what is already known, or from a nomenclatural point of view, which names have already been proposed for the group in question. However, a comprehensive annotated list of paludomid names is currently unavailable. Therefore, the nomenclature presented here aims at filling this gap by providing information on all names for recent and fossil family-, genus-, and species-group taxa introduced for Paludomidae. In addition, the present contribution is intended to facilitate future taxonomic work on Paludomidae by providing direct internet links to many important older taxonomic publications following the general outlines of the nomenclators of other groups of freshwater snails presented by Haszprunar (2014) on valvatids and Neubauer (2016) on melanopsids

A review of available investigation on the reproductive system of the family paludomidae reveals that they are nearly few, bright and incomplete of those, one can mention the work of Marcus &Marcus (1963); Aboul-Elaa and Beddiny (1969); Berry *et. al.,* (1973); Starmühlner, (1974, 1977 and 1979); Houbrick, (1973, 1974, 1980, 1981a, b, c); Beddiny& Hamada,(1983); Houston, (1983), Moustafa, (1987), Strong (2005); Strong & Frest, (2007); Bouchet & Jean- Rocroi, (2005); Amarasinghe & Krishnarajah (2009).

Although it seems that the general plan of organization of the reproductive system of Thiaridae (now pludomidae) is known from the previous publication, yet the details of its structure and function are still somewhat incomplete and superfacial. Also, the details of varations in its structure which are able to occure in different genera and species of the family, are still poorly studies. Such variations may be taxonomically importance as they may offer valuble criteria upon which the differentiation between those genera and species is based. Therefore, the present work deal with the functional morphology of the reproductive system of a valuable freshwater (Paludomidae) Cleopatrinnae of genus Cleopatra in Upper Egypt.

MATERIALS AND METHODS

The present study was carried out in the faculty of Science at Qena city, South Valley University, Egypt. The specimens of *Cleopatra,* used in the present investigation were regularly collected in great numbers (300 specimens each time) from certain freshwater courses as River Nile; Elkalabia drainage and irrigation canals in Qena Governorate, Upper Egypt. The physical factors were recorded where the water temperature ranged from 16 to 28.5 C°, pH ranged from 6.75 to 7.8, dissolved Oxygen ranged from 5.5 to 7.6 ppm, conductivity ranged from 0.22 to 0.98 mS and TDS ranged from 150 to 890 mg/L. The samples of *Cleopatra* snails were collected monthly throughout a period of one year (from January 2016 till December 2016) and reared in the laboratory.

Cleopatra snails were found in Egypt in three different colors, most commonly crawling on the bottom of small ponds and slow running parts of the river Nile and its branches. Some specimens were also found embedded, either partially or completely, in mud along the bank of freshwater courses. In nature, the snails were found in common association with one or more other molluscan genera such as *Physa, Bellamya, Melanoides, Lanistes, Bulinus, Neritina, Mutela* and rarely *Lymnaea. c*ollected specimens were taken to the laboratory in separate containers with labels indicating the locality and date. The snails of *Cleopatra* were sorted out, cleaned and reared in large plastic aquaria provided with dechlorinated tap water and some water plants as *Ceratophyllum demersum.* The snails were fed on fresh lettuce leaves which were added to the aquaria after the removal of excess food and faeces during changing water at the end of suitable intervals of four or seven days. The snails were daily observed and dead specimens were removed. This method was found to be adequate to avoid water pollution that may cause the death of snails.

Full grown male and female specimens used in the present investigation for dissection, examination and drawing, ranged between 13.3±0.092 and 13.5±0.077 mm. in the average shell height, respectively. All measurements given in the following description are normal to these sizes and were taken by an eye piece micrometer.

Drawings of the soft parts of the snails were done with the help of camera Lucida. The terms ‘’proximal’’ and ‘’distal’’ used in this text designate the relatively position of the part concerned with respect to the head region of snail, i.e. the proximal part is the nearest one to the latter region. For dissection of the soft parts, the body whorls of the shell were carefully broken, the columellar muscle was dislodged and the soft parts were gently twisted out of the remaining nuclear whorls.

It is worth mentioning in this regard that fresh *Cleopatra* specimens were more suitable for the dissection and examination of the soft parts than of the preserved ones. This is because the preservation in 70% alcohol or 10% formalin solutions makes the colour of the soft parts pale and causes their rigidity. Gross anatomy of the external features and digestive system (buccal mass) was carried out under a binocular dissecting microscope.

Genus *Cleopatra* belongs to Subfamily: Cleopatrinae, Family: Paludomidae, Superfamily: Cerithioidea, Order: Caenogastropoda, Class: Gastropoda and Phylum: Mollusca

RESULTS

The mature male and female cannot be differentiated externally (Fig.1), but after the removal of shell, differentiation between the two sexes can be achieved by the different in gonads colour.

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Figure (1): Different morphs of the Egyptian freshwater of genus *Cleopatra*

The plan of organisation of the male and female genitalia of the available and common sp. of genus *Cleopatra* is nearly similar to that of other caenogastropoda.

The male reproductive system consists mainly of the following organs: the testis, non-glandular vas deferens, lying in the spire and the glandular pallial gonduct .

(A) - The male reproductive system

1 - The testis:

The testis lies as a nearly curved flat thin triangular follicular deep yellow pale, on the non-collumellar aspects of an intermediate pint gland of the spire of the visceral mass, just beneath the mantle wall and covering the digestive gland in this area. It is commonly found in about two of the apical whorls of the visceral mass other than a part of the penultimate whorls. In the average sized adult specimens, the unfolded testis measures about 5.0 mm in length and 2.3 mm in its maximum width at its proximal end (Figs. 2-4).

2- The vasa efferentia and the thin nonglandular vas deferens:

Macroanatomy reveals that each group of adjacent seminiferous tubules leads into a fine ductule forming the vas efference, which extends towards the collumellar side of the whorls of the visceral mass, penetrating the digestive gland tubules and inclining toward each other to become connected with common relatively wide duct forming the thin nonglandular vas deferens (Figs.2 - 4)

3 – The pallial glandular gonoduct:

On reaching the mantle cavity, the thin nonglandular vas deferens enters it at the posterior part of its left side to open into the distal end of the pallial glandular gonoduct at subterminal points on as its right side. Then the pallial gonoduct extends within the roof of the mantle cavity in an antero-oblique direction along the right side of the rectum, to end during inactivity, just posterior to the right part of the mantle collar. It is pale yellow in colour and easily differentiated in macro-anatomy into a main conical bulky part and a blind finger like thin lateral one, projecting from the dorsal side of the former at a point a little nearer to its distal end (Figs. 2 - 4).

This region correspond in its position and glandular nature to the portal gland of some other caenogastroda e.g. *Paludestrina ventrosa* (Robson, 1922), *Mysorella costigera* (Seshaiya, 1930), *Pirenella conica* (Demain *et. al.,* 1963), *Modulus moclulus*, *Diastome melanoides* and *componile symbolicum* (Houbrick, 1980, 1981 b, c). The structure and section of this region in the present material favours its designation as a prostate gland.

The proximal region of the main pallial gonoduct is laterally compressed glandular duct with a narrow dorsal margin about 0.30 mm thick. It is relatively broad left and right sides and narrow gradually toward the free end to be 4.0 mm wide. Careful examination of its ventral margin in macro - anatomy shows a longitudinal slit-like orifice extending along a fraction of its ventral margin from a posterior point about 2.5 mm from its distal end till the tip of its free end. This slit, which is about 1.4 mm long, connects the lumen of the male gonoduct to the exterior. The glandular nature of this anterior region of the main pallial gonoduct shows that it is reasonable to refer to it as the glandular opened vas deference.

The finger-like blind part originating from the glandular appeared vas deferens bends forward after about 0.400 mm from its point of emergence. It is slightly curved ventrally as it possess anteriorly within the connective tissue of the mantle wall. Consequently, this finger like blind glandular part may be considered as a vesicular seminalis for the storage and preservation of surviving sperms before they are released to the anterior (Figs. 2 – 4).

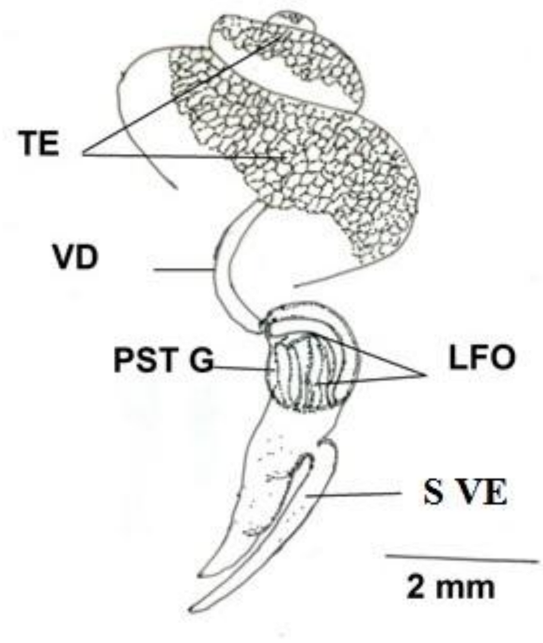

Fig. (2)

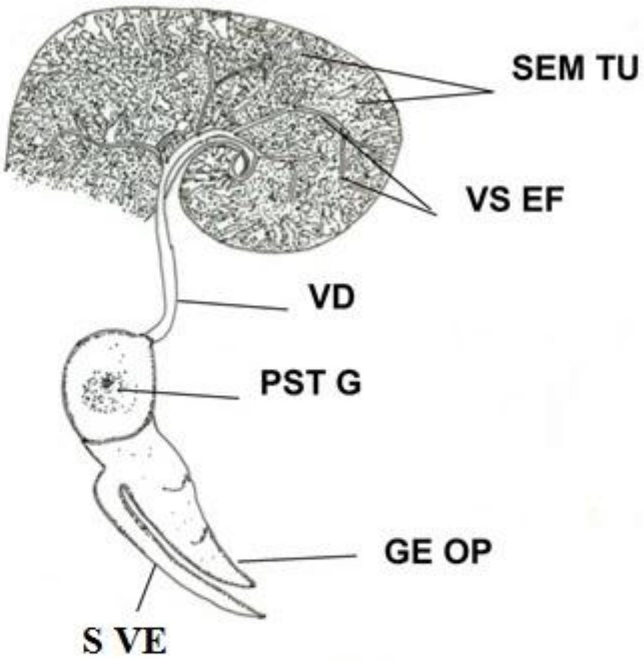

Fig. (3)

Figure (2): A Camera lucida drawing of the right aspect of the mature male genital system in situ. TE – testis, VD – vas deferens, PST G – prostate gland, LFO- lateral folds, SVE – seminal vesicle

Figure (3): A Camera lucida drawing of the left aspect of the mature male genital system in situ. SEM TU seminiferous tubules, VS EF – vas efferens, VD – vas deferens, PST G – prostate gland, GE OP – genital opening , SVE –seminal Vesicle

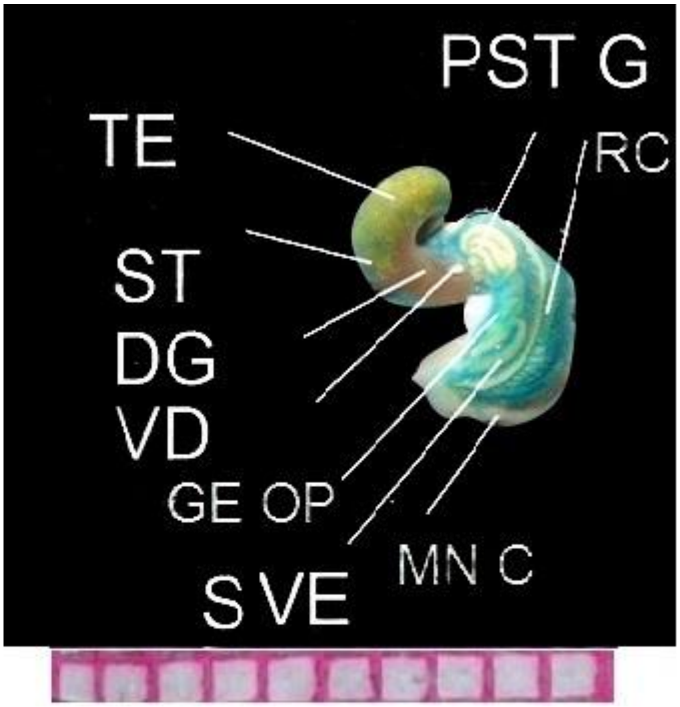

Figure (4): A photograph of the dorsolateral aspect of the mature male genital system in situ. TE – testis, ST- seminiferous tubules, DG-digestive gland, VD – vas deferens, GE OP- genital opening, S VE – seminal vesicle, MN C– mantle collar, PST G – prostate gland, RC- Rectum.

(B) - The female reproductive system:

The female reproductive system of the species under investigation, like that of any other mesogatropod, consists mainly of the ovary, the common oviduct and the pallial glandular gonoduct.

1 - The Ovary:

The ovary of the present species is a flattened, thin triangular follicular yellowish white organ on the non - columellar aspect of the spire of the visceral mass. It lies just below the mantle wall, close to the underlying digestive gland tubules and occupying the same location and number of whorls of the visceral mass, as the testis in the mature specimens. In the average sized adult female, the unfolded ovary measures about 6 mm in length and 2 mm, in maximum width at the broad proximal end (Figs. 5 - 7).

2 - The ovarian ductule and the common oviduct:

Macroanatomy of the ovary of the present species shows that the connected ovarian follicles lead into two relatively thin ductules. The two ovarian ductules begin to appear nearly at the end of the apical third of the length of the ovary and extend, converging toward each other, within the ovarian follicles till about the end of its median third where they become united forming the common oviduct. The latter passes interiorly within the connective tissue of the middle of the columellar edge of the visceral mass till it enters the mantle cavity. At the upper or posterior limit of the right side of the mantle cavity, the common oviduct bends posteriorly to acquire a U - shape before joining the glandular pallial gonoduct at a point on its ventral posterior or distal extremity. The common oviduct is a narrow elongated whitish duct, about 3.5 mm in length, (Figs. 5 - 7).

3 - The pallial glandular gonoduct:

The pallial glandular gonoduct extends obliquely forwards within the right dorsolateral part of the roof of the mantle cavity, on the outer ventero-lateral side of the rectum to end a little posterior to the right dorsal partof the mantle collar. In macro-anatomy, the pallial glanular gonoduct is a compact massive laterally compressed structure which is conical in outline; about 4.2 mm long with laterally broad posterior or distal part, about 1.3 mm. wide and an anterior or proximal narrow end about 0.2 mm. in lateral width. It has a dorsal convex surface and a ventral concave one, and its thickness decreases gradually from the distal region, which is 2 mm. thick, towards its proximal end which is about 1 mm thick. In macro-anatomy, the whole pallial gonoduct can be superficially differentiated, from its right side under the binocular microscope, into three regions. The first distal region which joins the common oviduct is a pear - shaped whitish sac about 0.8 mm long with a distal tapering narrow part at its connection with the common oviduct, and a broad proximal one about 0.3 mm. in the lateral width. The second region is a globular broad glandular structure, having an oval looped shape, in the right side view, with two adherent distal and proximal limbs only separated by pigmented connective tissue. This latter region is adjacent to the dorsal proximal part of the first region. From the left side, the proximal lower limb 0f the second region is covered by the proximal part of the first region. From a nearly mid-dorsal point on the second region, a third glandular yellowish white laterally compressed region passes anteriorly till the end of the pallial gonoduct. This third region is elongated and ventrally concave with a narrow distal end and tapering proximal one; being about 3.1 mm in length and 0.35 mm. in maximum lateral width. (Figs. 5 - 7).

On careful examination of the female pallial gonoduct, from the left side, one can hardly discern the fourth region which is translucent sac - like structure extending from the proximal end of the first region anteriorly to end close to the anterior or proximal free tip of the third region. This sac-like structure, which overlaps a ventral part of the left side region, has a distal broad part; about 0.3 mm. in maximum lateral width which narrows gradually towards the anterior or proximal tip, (Figs. 5 & 6).

In a trial to elucidate the nature of these regions and the mode of connection between them, hand, transverse sections were made at five levels along the pallial gonoduct (Fig. 8). The first section (A) passes through the first and second region and reveals that the two are glandular structure having irregularly thich walls and irregular lumina. The first region is clearly smaller in cross section than the second, and the two are roughly triangular in outline, (Fig.9). Section (B) shows the first region and the two limbs of the second region. The dorsal limb of the latter has a thick inverted U - shaped part of the wall which is completed by a relatively thin one to peripheral slit - like cavity shifted to the left side of the pallial gonoduct and connected with a somewhat median narrow lumen. The ventral limb of this region is shifted to the right side and appears to the end blindly, (Fig. 10). In section (C) the four regions of the pallial gonoduct can be seen. The third region lays middorsally with a high thick wall and a slit-like vertical lumen, connected with that of the proximal end of the first region. On the right side of this connection, there is a cross separate section through the proximal part of the second region which appears to have a wall of nearly equal thickness and a central slit - like lumen. But on the left side of this connection, there is an oval vertically located closed section through the fourth region, showing its relatively thin wall and a slit-like lumen, (Fig. 11). Section (D) passes only through the third and fourth regions showing the enlargement in the lumen of the former which is bordered by a wall of a variable thickness. This wall is relatively thick at its dorsal and right aspects, while its left side, which is close to section of the fourth region, is thin, (Fig. 12). Section (E) passes through the proximal part of each of the third and fourth regions, showing the opening of the latter into the mantle cavity at the ventral aspect of the left side of the anterior part of the pallial gonoduct, (Fig. 13)

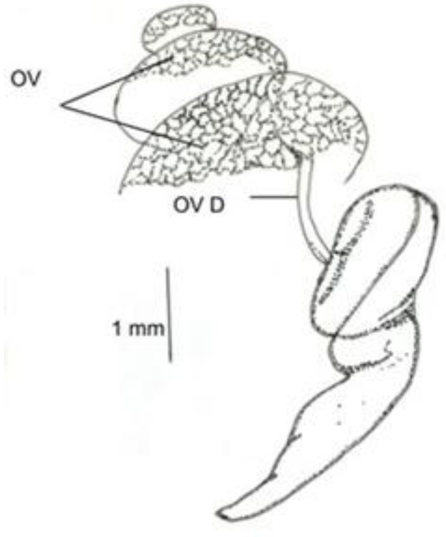

Fig. (5)

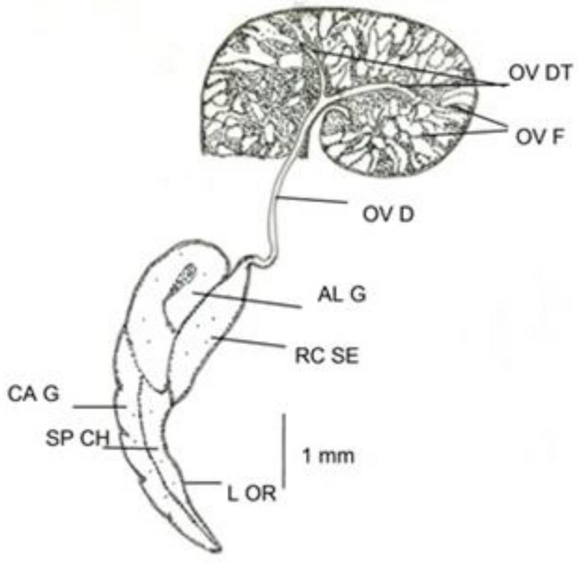

Fig. (6)

Figure (5)*:* A camera lucida drawing of the dorsolateral aspect of the reproductive system of a mature female in situ. OV – ovary; OV D - oviduct

Figure (6): A camera lucida drawing of the left side of the reproductive system of a mature female in situ.

OV DT – ovarian ductules; OV F – ovarian follicules; OV D – oviduct; AL G – albumen gland; RC SE – receptaculum seminalis; L OR – lateral orifice; CA G – capsules gland; SP CH – spermatophore chamber

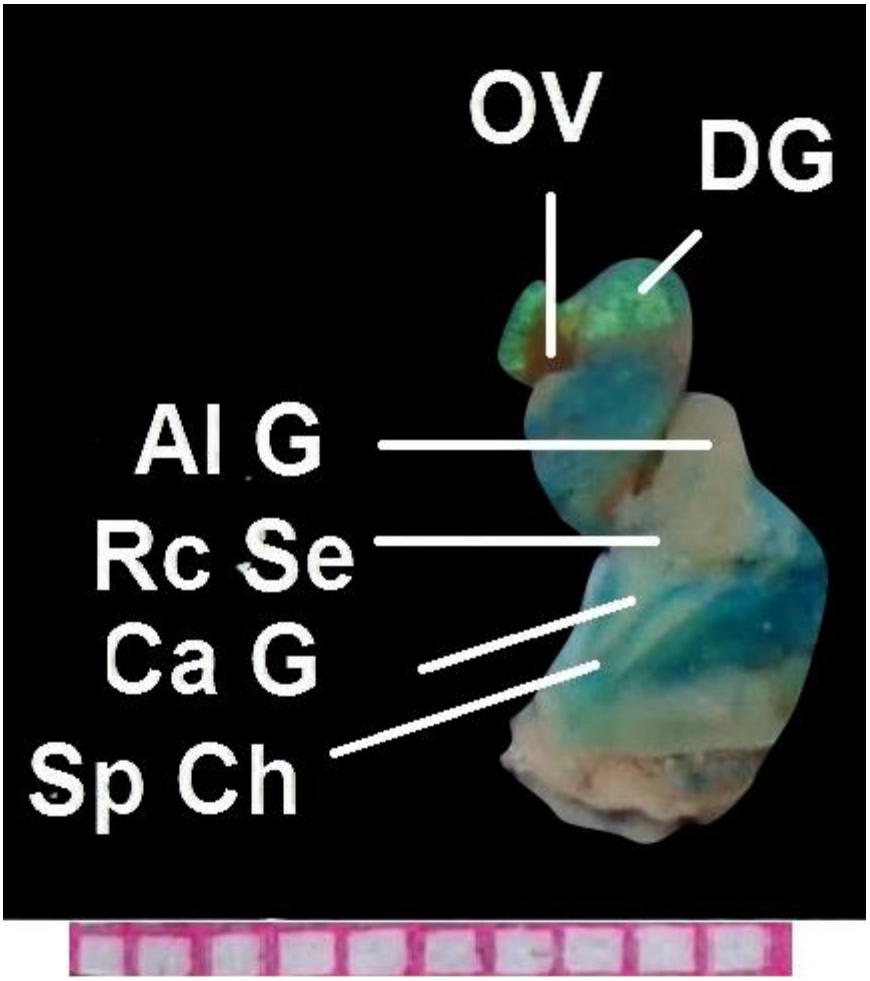

Figure (7): A photograph of the dorsolateral aspect of the reproductive system of a mature female in situ. OV – ovary; OV D – oviduct; DG – digestive gland – Al G – albumin gland – RC SE – receptacle seminal – CA G – capsule gland; Sp Ch- Spermatophore Chamber.

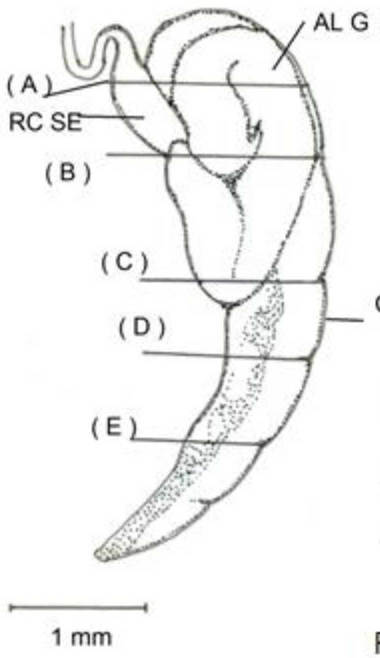

Fig. (8)

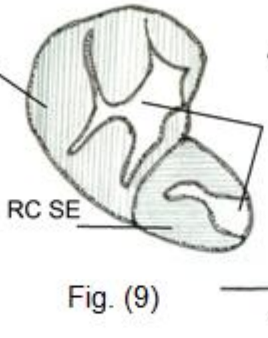

Fig. (9)

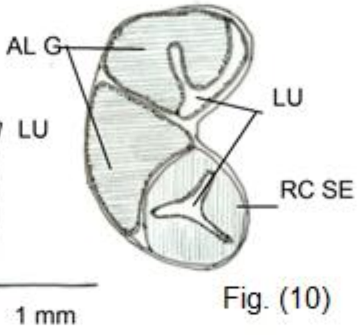

Fig. (10)

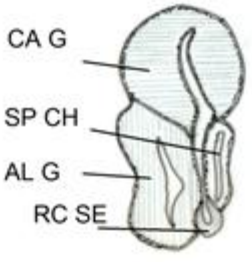

Fig. (11)

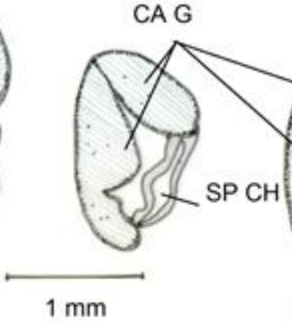

Fig. (12)

Fig. (13)

Figure (8): A camera lucida drawing of the right side view of the pallial glandular to reveal its constituents. Al G – albumin gland; RC SE – receptacle seminal; CA G capsule gland

Figure (9): A camera lucida drawing of the anterior view of a hand transverse section of the female pallial glandular gonoduct at the level (A) of figure (7) passing through the receptaculum seminis and the albumin gland. Al G – albumin gland – RC SE – receptacle seminal

Figure (10): A camera lucida drawing of the anterior view of a hand transverse section of the female pallial glandular gonoduct at the level (B) of figure (7) passing through the receptaculum seminis and the albumin gland. Al G – albumin gland; RC SE – receptacle seminal; LU - lumen

Figure (11): A camera lucida drawing of the anterior view of a hand transverse section of the female pallial glandular gonoduct at the level (C) of figure (7) passing through the albumin gland, the spermatophore chamber and the receptaculum seminis opening into the capsule gland.

Al G – albumin gland; RC SE – receptacle seminal; CA G – capsule gland; SP CH – spermatophore chamber.

Figure (12): A camera lucida drawing of the anterior view of a hand transverse section of the female pallial glandular gonoduct at the level (D) of figure (7) passing through the capsule gland and spermatophore chamber. CA G – capsule gland; SP CH – spermatophore chamber.

Figure (13): A camera lucida drawing of the anterior view of a hand transverse section of the female pallial glandular gonoduct at the level (E) of figure (7) to show the opening of the spermatophore chamber to the mantle cavity. CA G – capsule gland.

DISCUSSION

The reproductive system of genus *Cleopatra* in Upper Egypt shows the generalized scheme of the reproduction tract of many other members of the superfamily (Seshaiya, 1934; Binder, 1959; StarmÜhlner, 1969; Houbrick, 1969, 1971, 1973, 1974, 1980, 1981a, b, c and Houston, 1985). This scheme is based on its construction of the gonad and gonadal duct and the pallial glandular gonoduct. Genus *Cleopatra* in Egypt as those in occidental African snails (Binder, 1959) and other *Cleopatra* sp. In Madagascar (StarmÜhlner, 1969), has a pallial gonoduct with a distal or anterior small groove. Houston (1985) has stated that the reproductive system in the cerithiacea are either open or closed pallial ducts and that in the letter case, the females may have a reduced sperm groove or not. Accordingly the previously mentioned *Cleopatra* snails belong to the latter type. It is worthwhile mentioning that the open condition of the pallial glandular oviduct within the Cerithiacea ranges from an extreme form when the opening extends along its entire length except for the posterior most region as in *Certhium* and *Liocerithium* to an intermediate one in which there is, in addition to the anterior copulatory aperture, a slit - like opening along the mid-ventral surface of the oviducal gland as in *Seila* (Houstin, 1985).

The prostate gland of genus *Cleopatra*, which is nearly Cerithoid in position (Starmuhlner, 1969 and Houbrick, 1980), has no direct connexion with the exterior as it is the case in some other cerithiaceans such as *Seila assimilata* and *Triphora conterast* (Houstin, 1985). But it differs from the opened prostate gland of *Pirenella conica* (Demian et al., 1963), *Cymatium* (Houbrick and Fretter, 1969) and *Cerithium maculosum* (Houston, 1985).

The finger - like glandular blind structure emerging from the opened glandular vas deferens of the present investigated species, it correspond to the vesicula seminalis of other mesogastropd. It is worth mentioning in this regard, that no corresponding finger - like structure has been observed before in the male pallial gonoduct of any thiarids even in that of the same species in the Occidental Africa (Binder, 1959) or in that of other three *Cleopatra* species of Madagascar (Starmuhlner, 1969). Binder (1959) has only reported that in the male sex, the pallial spermduct of *Cleopatra bulimoides* is a simple closed tube. But, however Moore (1898) referred briefly to a curious finger - like outgrowth from the male gonoduct of the thiarid snail *Typhobia horei* as an interovertible penis (p.191, fig. 54). He recorded that the latter extends into the mantle and contains a muscular mass. Although this structure corresponds in its outline and origin to the vesicula seminalis of *C. bulimoides*, yet its structure is quite different from that of the latter (Moore, 1898). also differentiated an enlargement with about six singular parallel inner folds at the anterior part of the male duct. This enlargement appears to correspond in its macroanatomy to the prostate gland of the present species.

The present investigation of the female reproductive system of the morphs of *Cleopatra bulimoides* has elucidated that it consists of the ovary, oviductules, common oviduct and pallial gladular gonoduct. The latter can be differentiated into the receptaculum semins, the albumen gland, capsule gland, uterus and spermatophore chamber which opens into the mantle cavity by a mid - ventral anterior slit - like orifice. It is noticeable that no gonopericardial connexion was found during this study.

The results of this work, as well as those of similar researches on the reproductive system of other Caenogastropoda (mesogastropods) (Aboul- Ela & Beddiny, 1969, Beddiny & Hamada1983), support Fretter (1946) statement that the pallial oviduct of mesogastropod and stenoglossan is elaborated for the reception and storage of sperm and for production of secretions both nutritive and protective, in which the eggs are embedded before they leave the genital duct. Fretter (1946) add that the glandular elements are fairly constant in their disposition and the gland surrounding the posterior end of the pallial oviduct constitute as albumin gland, whilist, anteriorly around the greater length of the duct, they form either a jelly gland, as in *Littorina* and *Lacuna*, which embed their eggs in a gelatinous secretion, or a capsule gland as in the majority of mesogastropds and in the stenoglossa, all of which Produce egg capsule. In spite of this generalization in the structure and function of the pallial oviduct in mesogastropods, yet its outline, relative arrangement and connection of its constituents vary greatly within the different genera, even between those belonging to the same family. For instance, the female pallial gonoduct of *C. bulimoides* differs in such points from the corresponding ducts of certain other thiarid genera such as *Paludomus* (Seshaiya, 1934) and *Thiara* (starmuhlner, 1969). Also, the previous points together with the detailed structure of the pallial oviduct show specific variation within the same genus, as those between the pallial gonoduct of *C. colbeaui* (Starmuhlner, 1969) and that of the present species C. bulimoides. It is noticeable, however, that Starmuhlner, (1969) had differentiated the female pallial gonoduct of *C. colbeaui* into a receptaculum semins, " drusiger ovidukt" or an uterus and a vagina, without referring to certain other constituents of the posterior and anterior edges of the duct (p.196, fig. 259). In his study on the anatomy and systematics of melaniens of occidental Africa, Binder (1959) had concisely described the female genital system of *C. bulimoides*, recording that the pallial oviduct is closed, forming a tube with a horseshoe - shaped lumen. He added that it consists of two channels; the left is glandular and ciliated and the right is only ciliated and it opens into the pallial cavity by a long oblique orifice. He had further supposed that there are two communicating channels, namely the receptaculum seminis and the oviduct proper, and a separate simple bursa copulatrix without villosities or muscular coat and he gave a photomicrograph of a section passing through these parts, (p. 752, fig. 11). The absence of a groove on the external surface of the foot opposite to the genital pathway of the female *C. bulimoides* recorded by Binder, (1959) coincides with the present finding.

But his statement that there is the same place a deep dimple lined with mucous cells can be accepted, as a temporary depression in the pedal integument occurring during the passage of the inhalant and exhalant water currents. It worth mentioning that Moore (1898) reported that in the thiarid *Typhobia horei*, there is a lower expansion of the oviduct forming a very thin sac which functions as a brood chamber or uterus. Such structure corresponds in position only to the pallial glandular gonoduct of the female *Cleopatra bulimoides* under investigation

Recently, genus *Cleopatra* was transferred from family Thiaridae to family Paludomidae Stoliczka, 1868. Bouchet & Rocroi (2005) and Neiber & Glaubrecht (2019) stated that:

Paludomus huberi **Thach, 2020** syn. nov.

=*Paludomus andersoniana* Nevill (1877): 35.

=*Paludomus huberi* Thach (2020a): 23; pl. 5, figs 67–68; pl. 6, 69–74.

Holotype: NCSM 113633 (North Carolina Museum of Natural Sciences, Raleigh, North Carolina, United States of America). Type locality: Inle Lake, Myanmar [approx. 20.55°N, 96.92°E, Salween River basin].

Comments: In the original diagnosis, this nominal taxon was compared with *Paludomus siamensis* Blanford, 1903. Regrettably, however, the author overlooked several *Paludomus* taxa described from Myanmar (Benson 1856; Nevill 1877; Annandale (1918b). *Paludomus huberi* is conspecific with *P. andersoniana* Nevill, 1877 based on the identical shell shape, similar size, and the same coloration patterns (Nevill 1877). Neiber & Glaubrecht (2018) used the terminology used to describe the radula (radula formula) follows Glaubrecht (1996, 2008): cusp/denticle formula is given as follows: (1) rachidian (number of left side cusps/ median denticle(s)/number of right side cusps), (2) lateral teeth (inner cusps/pronounced denticle/ outer cusps), (3) marginal teeth (number of cusps on inner marginal tooth plus number of cusps on outer marginal tooth). Left and right in descriptions of opercula refer to the relative positions of features of a closed shell in apertural view with the spire pointing upwards. On the other hand Systematic Account; the family-group taxonomy follows Bouchet *et al.* (2017). Paludomidae Stoliczka, 1868, Paludominae Stoliczka, 1868, Genus *Paludomus* Swainson, 1840.

Remarks

The numerous nominal paludomid taxa described from Asia and the Indo-Australian Archipelago are traditionally either assigned to a single genus, *Paludomus*

Swainson, 1840, that is further subdivided on the basis of differences in the structure of the operculum and the shell by some authors into four subgenera: *Paludomus* s. str., *Tanalia* Gray, 1847, *Philopotamis* Layard, 1855, and *Stomatodon* Benson, 1862 (e.g., Starmühlner (1974, 1977, 1979; Subba Rao, 1989), or these subgenera have been regarded as distinct genera (e.g., Brot, 1880). *Paludomus* s. str. 1840 *Paludomus* Swainson (1840: 198–201, 210, 340); type species: *Melania conica* Gray, 1833, in Griffith & Pidgeon (1833– 1834) by subsequent designation (Gray, 1847: 155). 1840 *Hemimitra* Swainson (1840: 199–200, 202, 340) as a subgenus of *Paludomus*; type species: *Paludomus* (*Hemimitra*) *retusa* Swainson, 1840, by monotypy. 1851 *Rivulina* I. Lea & H. C. Lea (1851: 196–197); *Melania modicella* I. Lea & H. C. Lea, 1851.

Remarks

Paludomus s. str. is characterized within Paludominae by a corneous, sub-triangularly ovate, concentrically striated operculum with a sinistral, paucispiral nucleus that is slightly displaced to the left (Layard, 1855; H. Adams & A. Adams, 1854–1858; Brot, 1880; Starmühlner, 1977). Swainson (1840) separated shells, in which “the general form of *Paludomus* is preserved, but the whorls are coronated by spines” (p. 199) in the subgenus *Hemimitra* of his genus *Paludomus* and introduced simultaneously the

Species-group name *Paludomus* (*Hemimitra*) *retusa* (*non Melania retusa* Gray, 1833, in Griffith & Pidgeon, 1833–1834: pl. 14, fig. 9) for such specimens from India (p. 340). Type material of *Paludomus* (*Hemimitra*) *retusa* Swainson, 1840, could not be found in the collections of the Manchester Museum and the National Museum of New Zealand, where parts of the collections of W. Swainson are said to be housed (McMillian, 1980). Some specimens may have been sold at auctions or given to other institutions without adequate documentation or labelling, and some may have been thrown away as rubbish (Nicholson, 1913; McMillian, 1980). Several species currently classified in *Paludomus* conform to the diagnosis of *Hemimitra* by Swainson (1840). Since the brief description provided by Swainson (1840) does not allow an unambiguous identification of the taxon with one of the paludomid species with coronated whorls, and to clarify the taxonomic position of the genus-group name *Hemimitra* Swainson, 1840, objectively, in our opinion a neotype designation for the nominal taxon *Paludomus* (*Hemimitra*) *retusa* Swainson, 1840, is necessary under ICZN *Code* Art. 75 (ICZN, 1999). The nominal taxon *Melania stephanus* Benson, 1836 (Fig. 1A, B), described from the northeast frontier of Bengal (Benson, 1836a, b), more precisely given as Sylhet by Nevill (1884: 297), can easily be separated from all other Asian Paludomidae by the relatively widely. Neiber & Glaubrecht (2019), separate Cleopatrinae Pilsbry & Bequaert, 1927; where Original reference. Pilsbry and Bequaert (1927: 249).

Original spelling. Cleopatrinæ Pilsbry & Bequaert, 1927.

Type genus. *Cleopatra* Troschel, 1857.

Remarks

Elevated to family rank by Germain (1933: 30), and Paludominae Stoliczka**,** 1868, Original reference. Stoliczka (1868: 206–207). Type genus**.** *Paludomus* Swainson, 1840, Remarks. Elevated to family rank by Pilsbry and Bequaert (1927: 248); used as the name of a tribe (with the suffix –eae) by Wenz (1939: 703). So, when comparing the structure of the shell, radula and the position of the reproductive system of different morphs of with the abovementioned Paludomidae, the present authors prefer to elevate this genus to family Cleopatrinae

It is clear from this discussion that further detailed knowledge on the functional morphology of the reproductive systems in different groups of the super family Cerithiacea is needed, in order to elucidate the accurate specific and generic characters of these group and their phylogeny.

REFERENCES

Aboul-Ela, I. A. and Beddiny, E. A. (1969). Morphological and histological studies on the genitalia of lanistes boltini chemitz, 1768. Ain Shams Sci. Bull., Cairo. No. **13**:145-167.

Adams, H. and Adams, A. (1853). The genera of recent Mollusca; arranged according to their organization. In three volumes – Vol. I. Van Voorst, London, 484 pp. https://biodiversitylibrary.org/page/3782650

Adams, H. and Adams, A. (1854). The genera of recent Mollusca; arranged according to their organization. In three volumes. Vol. I. Part X. Van Voorst, London.

Adams, H. and Adams, A. (1858). The genera of recent Mollusca; arranged according to their organization. In three volumes.–Plates. Van Voorst, London, 138 pp. [138 pls] https://doi.org/10.5962/bhl.title.4772

Amarasinghe, A. A. T. and Krishnarajah, S. R. (2009). Distribution patterns of the genus *Paludomus* (Gastropoda: Thiaridae: Paludominae) in Mahaweli, Kelani, Kalu, Gin and Maha-Oya river basins of Sri Lanka. *Taprobanica*, **1**: 130–134.

Annandale, N. (1918). Aquatic molluscs of the Inle Lake and connected waters. *Records of the Indian Museum*, **14**: 103–182, pls. 10–19.

Beddiny, E. A. M. and Hamada, M. I. (1983). Morphological and histological studies on the reproductive system of the viviparid snail *Bellamya unicolor* (Olivi, 1804-) Assiut. Vet. Med. J., **11**(21): 127-137.

Benson, W. H. (1836). Descriptive catalogue of a collection of land and fresh-water shells, chiefly contained in the Museum of the Asiatic Society. Part 2 – Fluviatile Shells. Journal of the Asiatic Society of Bengal **5**: 741–750. https://biodiversitylibrary.org/page/37188918

Benson, W. H. (1856). Descriptions of three new species of *Paludomus* from Burmah, and of some forms of *Stenothyra* (*Nematura*) from Penang, Mergui, &c. The Annals and Magazine of Natural History (2) **17**: 494–501. https://doi.org/10.1080/00222935608697559

Benson, W. H. (1862). Description of a singular shell from southern India, allied to *Tanalia*; with remarks on a Travancore *Batissa*, and on the Himalayan form *Tricula*. The Annals and Magazine of Natural History (3) **10**: 414–416. https://doi.org/ 10.1080/00222936208681351

Binder, E. (1959). Anatomie at systematique des melaniens d'Afrique Occidental (Moll. Gastropoda). Revue Suisse de Zoologic **66**(32): 735-759.

Blanford, W. T. (1903). Notes on Mr. W. M. Daly's collections of land and fresh-water Mollusca from Siam. Proceedings of the Malacological Society of London **5**: 274–284. [pl. 8]. https://doi.org/10.1093/oxfordjournals.mollus.a065982

Bolotov, I. N.; Konopleva, E. S.; Vikhrev, I. V.; Gofarov, M. Y.; lopes-lima, M.; Bogan, A. E.; lunn, Z.; Chan, N.; Win, T.; Aksenova, O. V.; Tomilova, A. A.; Tanmuangpak, K.; Tumpeesuwan, S. and Kondakov, A. V. (2021). Nominal taxa of freshwater Mollusca from Southeast Asia described by Dr. Nguyen N. Thach: A brief overview with new synonyms and fixation of a publication date, *Ecologica Montenegrina* **41**: 73-83. http://dx.doi.org/10.37828/em.2021.41.11

Bouchet P. and Rocroi, J. P. (2005). Part 1. Nomenclator of gastropod family-group names. In: Bouchet P, Rocroi J-P (Eds) Classification and nomenclator of gastropod families. Malacologia **47**: 5–239. https://doi.org/10.4002/040.052.0201

Bouchet, P.; Rocroi, J. P.; Hausdorf, B.; Kaim, A.; Kano, Y.; Nützel, A. ; Parkhaev, P. M.; Schr◌dl, M. and Strong, E. E. (2017). Revised classification, nomenclator and typification of gastropod and monoplacophoran families. Malacologia **61**: 1–526. https://doi.org/10.4002/040.061.0201

Bourguignat, J. R. (1855). Aménités malacologiques. Revue et Magasin de Zoologie pure et appliquée, **7** (2): 317–334. [pls 7–8] https://biodiversitylibrary.org/page/2281180

Bourguignat, J. R. (1888). Iconographie malacologique des animaux mollusques fluviatiles du Lac Tanganika. Imprimerie Crété, Corbeil, 82 pp. [35 pls] https://doi.org/10.5962/bhl.title.12884

Brot, A. (1880). Die Gattung *Paludomus* auct. (*Tanalia*, *Stomatodon*, *Philopotamis*, *Paludomus*) (Melaniaceen). Systematisches Conchylien-Cabinet von Martini und Chemnitz **1**(25): 1–52. [pls 3–8] https://doi.org/10.5962/bhl.title.124338

Brown, D. S. (1994). Freshwater snails of Africa and their medical importance. Revised 2nd edition. Taylor & Francis, London, Bristol, 608 pp.

Dance, S. P. (1970). Non-marine molluscs of Borneo 1. Streptaxacea: Streptaxidae. *Journal of Conchology*. 27: 149-162. page(s): 151-152; pl. 6, figs 3-4; text fig. 2 (p. 160).

Demian, E. S.; Yousif, F. and Rifaat, M. A. (1963). Morphological studies on Pirenella conica (Blainville), the snail vector of Heterophyiasis in Egypt. Ain Shams, Sci. Bull., **9**:273-347.

Fretter, V. (1984). Prosobranchs. In: Tompa AS, Verdonk NH, van den Biggelaar JAM (Eds) The Mollusca. Volume 7. Reproduction. Academic Press, Orlando-London, 1–45.

Germain, L. (1933). Mollusques terrestres et fluviلtiles de l’Afrique Occidentale Française. Bulletin du Comité d’ةtudes Historiques et Scientifiques de l’Afrique Occidentale Française **16**: 1–68. https://doi.org/10.5962/bhl.title.12885.

Glaubrecht, M. (1996). Evolutions oclogie und Systematik am Beispiel von Sü; - und Brackwasserschnecken (Mollusca: Caenogastropoda: Cerithioidea): Ontogenese-Strategien, palنontologische Befunde und historische Zoogeographie. Backhuys Publishers, Leiden, 4 + 16 +499 pp, 25 pls.

Glaubrecht, M. (2008). Adaptive radiation of thalassoid gastropods in Lake Tanganyika, East Africa: morphology and systematization of a paludomid species flock in an ancient lake. Zoosystematics and Evolution **84**: 71–122. https://doi.org/10.1002/zoos.200700016

Glaubrecht, M. (2009). On ‘‘Darwinian mysteries’’ or molluscs as models in evolutionary biology: from local speciation to global radiation. American Malacological Bulletin **27**: 3–23. https://doi.org/10.4003/006.027.0202

Glaubrecht, M. (2011). Towards solving Darwin’s “mystery”: speciation and radiation in lacustrine and riverine freshwater gastropods. American Malacological Bulletin **29**: 187–216. https://doi.org/10.4003/006.029.0211

Glaubrecht, M. and Strong, E. E. (2007). Ancestry to an endemic radiation in Lake Tanganyika? Evolution of the viviparous gastropod *Potadomoides* Leloup, 1953 in the Congo River system (Caenogastropoda, Cerithioidea, Paludomidae). Biological Journal of the Linnean Society **92**: 367–401. https://doi.org/10.1111/j.1095-8312.2007.00867.x

Gray, J. E. (1847). A list of genera of Recent Mollusca, their synonyma and types. Proceedings of the Zoological Society of London **15**: 129–182. https://biodiversitylibrary.org/page/12862913

Griffith, E. and Pidgeon, E. (1833–1834). The Mollusca and Radiata. Arranged by the Baron Cuvier,with supplementary Additions to each Order. In: Griffith E (Ed.) The Animal Kingdom arranged in conformity with its Organization, by the Baron Cuvier, Member of the Institute of France, &c. &c. &c. with supplementary Additions to each Order. Volume the Twelfth. Whittaker and Co., London, 1–8, 1–601, pls 1–40, 1–20. https://doi.org/10.5962/bhl.title.10154

Haszprunar, G. (2014). A nomenclator of extant and fossil taxa of the Valvatidae (Gastropoda, Ectobranchia). ZooKeys 377: 1–172. https://doi.org/10.3897/zookeys.377.6032 Heer O (1861) Recherches sur le climat et la végétation du pays tertiaire. Jean Wurster & Comp., Winterthur, 6 + 220 + 22 pp. [2 pls] https://books.google.de/books?id=2qL7UYq PXvkC&printsec=frontcover

Houbrick, R. S. (1973). Studies on the reproductive biology of the genus *Cerithium* (Gastropoda-Prosobranchia) in the western Atlantic. Bull. Mar. Sci., Vol. **23** (4): 875-904.

Houbrick, R. S. (1974). The genus Cerithium in the western Atlanta (Cerithiidae-Prosobranchia). Johnsonia Vol. **5**(50): 33-84.

Houbrick, R. S. (1980). Observation on the anatomy and life history of *Modulus modulus* (prosobranchia-Modulidae). Malacogia, **20** (1): 117-142.

Houbrick, R. S. (1981a). Anatomy and systematics of *Gourmya gounmi* (Prosobranchia-Cerithidae), Atethyan relict from the Southwest pacific. The Nautilus, **95** (1): 1-11.

Houbrick, R. S. (1981b). anatomy of *Diastoma melanoides* (Reeve) (1849), with remarks on the systematic position of the family Diastomatidae (Prosobranchia – Gastropoda). Proc. Biol. Soc. Wash., **94** (2): 598-621.

Houbrick, R. S. (1981c). Anatomy, biology and systematics of *Campanill symbolicum* with reference to adabtive radiation of the cerithiacea (Gastropoda- Prosobranchia) Malacologia, **21** (1-2): 263-289.

Houbrick, R. S. and Fretter, V. (1969). Some aspects of the functional anatomy and biology of *Crmatium* and *Bursa*. Proc. Malac. Soc. Lond., **38**: 415-429.

Houston, R. S. (1958). Genital ducts of the Cerithiacea (Gastropoda- Prosobranchia) from the Gulf of California. J. Mollusc. Stud., **51**: 183-189.

ICZN (International Commission on Zoological Nomenclature) (1999). International Code of Zoological Nomenclature.International Trust for Zoological Nomenclature, London, 306 pp. https://doi.org/10.5962/bhl.title.50608

Layard, E. L. (1855). Observations on the genus *Paludomus* of Swainson, with descrpitions of several new species, and the description of a new species of *Anculotus*. Proceedings of the Zoological Society of London **22**: 87–94. https://doi.org/10.1111/j.1469-7998.1854.tb07237.x

Lea, I. and Lea, H. C. (1851). Description of a new genus of the family Melaniana, and of many new species of the genus *Melania*, chiefly collected by Hugh Cuming, Esq., during his zoological voyage in the East, and now first described. Proceedings of the Zoological Society of London **18**: 179–197. https://doi.org/10.1111/j.1096-3642.1851.tb01137.x

Leloup, E. (1953). Exploration hydrobiologique du Lac Tanganika (1946–1947). Resultats scientifiques. Gasteropodes. Institut Royal des Sciences Naturelles de Belgique, Bruxelles, 273 pp. [13 pls] https://doi.org/10.1126/science.118.3076.727

Marcus, E. and Marcus, E. (1963). Mesogastropoden von der kueste Sao Paulos. Abh. Math.-Naturwiss. KI., Jg. 1963, **1**: 1-105.

McMillian, N. F. (1980). Wiliam Swainson (1789-1855) and his shell collections. Journal of the Society for the Bibliography of Natural Histroy, **9**:427-434.

Michel, E. (2004). Vinundu, a new genus of gastropod (cerithioidea: 'thiaridae') with two species from Lake Tanganyika, east africa, and its molecular phylogenetic relationships. Journsal of molluscan studies, **70**: 1–19.

Moore, J. E. S. (1898d). On the hypothesis that Lake Tanganyika represents an old Jurassic sea. Quarterly Journal of Microscopical Science. New Series **41**: 303–321. [pl. 23] https://doi.org/10.5962/bhl.part.1223

Moore, J. E. S. (1898a). On the zoological evidence for the connection of Lake Tanganyika with the Sea. Proceedings of the Royal Society of London **62**: 451–458. https://biodiversitylibrary.org/page/43453285

Moore, J. E. S. (1898b). The molluscs of the Great African Lakes. I. Distribution. Quarterly Journal of Microscopical Science. New Series **41**: 159–180. https://biodiversitylibrary.org/page/13773897

Moore, J. E. S. (1898c). The molluscs of the Great African Lakes. – II. The anatomy of the Typhobias, with a description of the new genus (*Batanalia*). Quarterly Journal of Microscopical Science. New Series **41**: 181–204. [pls 11–14] https://biodiversitylibrary.org/page/13773919

Moore, J. E. S. (1898e). Descriptions of the genera *Bathanalia* and *Bythoceras*, from Lake Tanganyika. Proceedings of the Malacological Society of London **3**: 92–93. https://doi.org/10.1093/oxfordjournals.mollus.a065153

Moustafa, A .S. (1987). Functional morphology of the freshwater snails "*Cleopatra bulimoides*". M. Sc .thesis Zoology Department, Faculty of Science, Assiut University. Egypt.

Neiber, M. T. and Glaubrecht, M. (2018). NomenclaTure of genus-group names of RECENT Asian Paludomidae (Gastropoda: Cerithioidea), WITH a revision of *Paludomus* (*Odontochasma*) *stomatodon* (Benson, 1862) from the Western Ghats, India, MALACOLOGIA, **62**(2):1-16.

Neiber, M. T. and Glaubrecht, M. (2019a). Nomenclature of genus-group names of recent Asian Paludomidae (Gastropoda: Cerithioidea), with a revision of *Paludomus*

(*Odontochasma*) *stomatodon* (Benson, 1862) from the Western Ghats, India. Malacologia **62**: 329–344. https://doi.org/10.4002/040.062.0209

Neiber, M. T. and Glaubrecht, M. (2019b). Paludomidae Stoliczka, 1868. In: Lydeard C, Cummings KS (Eds) Freshwater Mollusks of the World – A Distribution Atlas. Johns Hopkins University Press, 68–73.

Nevill, G. (1877). List of the Mollusca brought back by Dr. J. Anderson from Yunnan and Upper Burma, with descriptions of new species. Journal of the Asiatic Society of Bengal **46**: 14–41. https://biodiversitylibrary.org/page/35548100

Nevill, G. (1884). Hand list of Mollusca in the Indian Museum, Calcutta. Part II. *Gastropoda.Prosobranchia-Neurobranchia (contd.).* Trustees of the Indian Museum Calcutta, Calcutta, 10 + 306 pp.

Nicholson, F. (1913). The old Manchester Natural History Society and its museum. *Memoirs and Proceedings of the Manchester Literary and Philosophical Society*, **58**: 1–15.

Pilsbry, H. A. and Bequaert, J. (1927). The aquatic mollusks of the Belgian Congo, with a geographical and ecological account of Congo malacology. Bulletin of the American Museum of Natural History, **53** (2): 69–602.

Pilsbry, H. A. and Bequart, J. (1927). The aquatic mollusks of the Belgian Congo, with a geographical and ecological account of Congo malacology. Bull. Am. Mus. Nat. Hist. **53**:69-602.

Preston, H. B. (1915b). The fauna of British India, including Ceylon and Burma. Mollusca (Freshwater Gastropoda & Pelycypoda). Taylor & Francis, London, 244 pp.

Robson, G. C. (1922). On the anatomy and affinities of paludestrina ventrosa, Montague. Quart. J. Microsc. Sci., LXVI: 161-185.

Seshaiya, R. V. (1934a). A further note on the style sac of gastropods. Rec. Ind. Mus., Vol. **36**: 179-183.

Seshaiya, R. V. (1934b). Anatomy of *paludomus tanschaurica* (Gmelin). Rec. Ind. MUs., Vol. **36**: 185-211.

Starmühlner, F. (1969). Die Gastropoden der madagassischen Binnengewasser. Malacolo, **8**(12): 434 -569 figs.

Starmühlner, F. (1974). Results of the Austerian - Ceylonese hydrobiological mission 1970 of the 1st Zoological institute University of Vienna (Austeria) and the department of Zoology of the University of Ceylon, Part IV: The freshwater gastropods of Ceylon. Bull. Fish. Res. Stn. Seri Lanka (Ceylon), **25**(1& 2): 97 - 181.

Starmühlner, F. (1977). The genus *Paludomus* in Ceylon. Malacologia 16: 261–264. https://biodiversitylibrary.org/page/13131340

Starmühlner, F. (1979). Distribution of freshwater mollusks in mountain streams of tropical Indo-Pacific islands (Madagascar, Ceylon, New Caledonia). Malacologia **18**: 245–255. https://biodiversitylibrary.org/page/13095212

Stoliczka, F. (1868). Cretaceous fauna of southern India. Palوontologia Indica, being figures and descriptions of the organic remains procured during the progress of the Geological Survey of India. The Gastropoda. Memoirs of the Geological Survey of India **2**(5): 205–244. https://doi.org/10.5962/bhl.title.51904

Strong, E. E.; Colgan, D. J.; Healy, J. M.; Lydeard, C.; Ponder. W. F. and Glaubrecht, M. (2011). Phylogeny of the gastropod superfamily Cerithioidea using morphology and molecules. Zoological Journal of the Linnean Society **162**: 43–89. https://doi.org/10.1111/j.1096-3642.2010.00670.x

Strong, E. E. (2005). A morphological reanalysis of Pleurocera acuta Rafinesque, 1831, and Elimia livescens (Menke, 1830) (Gastropoda: Cerithioidea: Pleuroceridae). Nautilus **119**, 119–132.

Strong, E. E. and Frest, T. J. (2007). On the anatomy and systematics of Juga from western North America (Gastropoda: Cerithioidea: Pleuroceridae). Nautilus **121**, 43–65.

Strong, E. E.; Gargominy, O.; Ponder, W. F. and Bouchet, P. (2008). Global diversity of gastropods (Gastropoda; Mollusca) in freshwater. Hydrobiologia **595**, 149–166.

Subba Rao, N. V. (1989). Handbook, Freshwater Molluscs of India. Zoological Survey Swainson W (1840) A Treatise on Malacology: or the natural classification of shells and shell-fish. Longman, Orme, Brown, Green & Longmans, London, 419 pp. https://doi.oorg/10.5962/bhl.title.8027

Swainson, W. (1840). A Treatise on Malacology: or the natural classification of shells and shell-fish. Longman, Orme, Brown, Green & Longmans, London, 419 pp. https://doi.org/10.5962/bhl.title.8027

Thach, N. N. (2020). New Shells of South Asia. Volume 2. Sea Shells, Freshwater & Land Snails. With one new genus and 140 new species and subspecies, reply to comments made in error. 48HrBooks Company, Akron, 190pp.

Troschel, F. H. (1856–1857). Das Gebiss der Schnecken, zur Begründung einer natürlichen Classification. Nicolai, Berlin, 252 pp. [20 pls] https://doi.org/10.5962/bhl.title.11262

Wenz, W. (1939). Teil 1: Allgemeiner Teil und Prosobranchier. Lieferung 4. In: Schindewolf OH (Ed.) Handbuch der Palنozoologie. Band 6. Gastropoda. Borntraeger, Berlin, 481–720. https://doi.org/10.1017/s0016756800072459

West, K.; Michel, E.; Todd, J.; Brown, D. and Clabaugh, J. (2003). The gastropods of Lake Tanganyika: Diagnostic key and taxonomic classification with notes on the fauna.

Centre for African Wetlands, Ghana, on behalf of the International Association of Theoretical and Applied Limnology, Chapel Hill, 132 pp.

West, K. and Michel, E. (2000). The dynamics of endemic diversification: Molecular phylogeny suggests an explosive origin of the thiarid gastropods of Lake Tanganyika. In: Rossiter A, Kawanabe H (Eds) Advances in Ecological Research, 31, Biology of Ancient Lakes: Biodiversity, Ecology and Evolution. Academic Press, London, 331–354. https://doi.org/10.1016/S0065-2504(00)31018-2

Wilson, A. B.; Glaubrecht, M. and Meyer, A. (2004). Ancient lakes as evolutionary reservoirs: evidence from the thalassoid gastropods of Lake Tanganyika. Proceedings of the Royal Society London B **271**: 529–536. https://doi.org/10.1098/rspb.2003.2624