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REVIEW OF THE GENUS *POLYMORPHUS* LUHE, 1911 (ACANTHOCEPHALA:POLYMORPHIDAE), WITH THE SYNONYMIZATION OF *HEXAGLANDULA* PETROCHENKO, 1950, AND *SUBCORYNOSOMA* HOKLOVA, 1967, AND A KEY TO THE SPECIES

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مراجعـــة جنس بوليمورفاس لوهي ١٩١١ (شوكيات الرأس : بوليمورفيدي) ووضع الجنسين هيكساجلانديولا بتروشينكو ١٩٥٠ وسابكورينوسوما هوكلوفا ١٩٦٧ كمترادفين ومفتاح للأنواع

عمـــر أمـــين

لقد تم في هذا البحث تقييم وضع ومفهوم ومكونات جنس **بوليمورفاس** (= **بروفيليكوليس** ماير ١٩٣١ ، **فالسيفيكوليس** وبستر ١٩٤٨ ، **بارافيليكوليس** بتروشينكو ١٩٥٠ ، **سابفيليكوليس** هوكلوفا ١٩٦٧) بدقة . كذلك تم تقديم وصف جديد لهذا الجنس على اعتبار الجنسين هيكساجلانديولا بتروشينكو ١٩٥٠ وسابكورينوسوما هوكلوفا ١٩٦٧ مترادفين في مرتبة أدنى .

ومن بين ما قدم من تغييرات تصنيفية إعادة **بوليمورفاس بريفيس** (**أريثمورينكاس بريفيس**) إلى جنس **بوليمورفاس** ، واعتبار **بوليمورفاس ماجانس** و**بوليمورفاس مينيوتاس** مترادفين ، وتأكيد وضع النوع **بوليمورفاس بيوبا** ، والتشكك في وضع النوع **بوليمورفاس تروكاس** فان كليف ١٩٤٥ كما قدمته هوكلوفا . وقد تم الاعتراف بتحت جنسين فقط هما **بوليمورفاس** لوهي ١٩١١ ويضم ٣٦ نوعاً ، و**بروفيليكوليس** ماير ١٩٣١ ويضم ١٠ أنواع ، كما تم تقديم مفتاح للتعرف على هذه الأنواع .

Key Words: Acanthocephala, *Polymorphus,* Review, *Profilicollis, Falsifilicollis, Parafilicollis, Subfilicollis, Subcorynosoma, Hexaglandula,* Key to species.

ABSTRACT

The position, concept and composition of the genus *Polymorphus* (= *Profilicollis* Meyer, 1931; *Falsifilicollis* Webster, 1948; *Parafilicollis* Petrochenko, 1950; *Subfilicollis* Hoklova, 1967) are critically evaluated and a new diagnosis of the genus is proposed based on the designation of *Hexaglandula* Petrochenko, 1950 and *Subcorynosoma* Hoklova, 1967 as junior synonyms. Other taxonomic changes proposed include the reassignment of *Polymorphus brevis* (= *Arhythmorhynchus brevis*) back to *Polymorphus*, the synonymization of *Polymorphus magnus* with *Polymorphus minutus*, the recognition of *Polymorphus pupa* and of the questionable status of *Polymorphus trochus* Van Cleave, 1945 sensu Hoklova, 1966. Hoklova's subgenera are reviewed and rejected. Only two subgenera are recognized, *Polymorphus* Luhe, 1911 with 36 species and *Profilicollis* Meyer, 1931 with 10 species. A key to species of the genus is provided.

INTRODUCTION

The discovery of *Polymorphus spindlatus* by Amin and Heckmann (1991) brought into focus the present confused taxonomic state of the genus *Polymorphus* Luhe, 1911. The concept of the genus changed considerably since Luhe first erected it for *Polymorphus minutus* (Goeze, 1782) Luhe, 1911. Some diagnoses are barely recognizable as of *Polymorphus*. A number of species of *Polymorphus* were assigned to *Profilicollis* Meyer, 1931; *Falsifilicollis* Webster, 1948; *Parafilicollis* Petrochenko, 1956; *Subfilicollis* Hoklova, 1967; *Arhythmorhynchus* Luhe 1911; *Filicollis* Luhe, 1911 and *Plagiorhynchus* Luhe, 1911 (= *Prosthorhynchus* Kostylev, 1915) that were placed in various families and subfamilies. One or more of these genera/subgenera were later either synonymized with, or reduced to, subgenera of *Polymorphus*. The erection of *Hexaglandula* by Petrochenko (1950) for forms with 6 cement glands caused more confusion and was not consistent with other decidedly *Polymorphus* species which also have 6 cement glands, e.g., *Polymorphus cetaceum* (Johnston and Best, 1942) Schmidt and Dailey, 1971, and *Polymorphus arctocephali* Smales, 1986. The relationship between *Polymorphus* and related genera, particularly *Arhythmorhynchus,* need clearer definition. The relationship between *Polymorphus* and *Profilicollis* also needs to be more clearly elucidated since certain species of *Polymorphus* have the type of egg characteristic of *Profilicollis*. The different subgeneric assignments to *Polymorphus,* see for example Amin (1985) and Hoklova (1986), are assessed and certain synonymies and new assignments are made.

It is hoped that this study will provide the necessary definition to clarify the taxonomic status of this complex genus. The work is presented in a historic context in order to relate the evaluation of the concept of *Polymorphus* to its present status and composition as conceived by various authors.

THE POSITION, CONCEPT, AND COMPOSITION OF *POLYMORPHUS*

The characteristic generic of features of *Polymorphus*, erected for only one species, *P. minutus* (Goeze, 1782), by Luhe (1911) included small body size, body wall nuclei, grid-like lacunar system, trunk spines anterior to constriction, radially symmetrical proboscis hooks which decreases in size anteriorly and posteriorly, double-walled proboscis receptacle with brain near its posterior end, long neck, moderately long lemnisci, testes behind one another, tubular cement glands, genital opening terminal without spines, and eggs with polar prolongation of middle membrane. Except for features like the long neck or the position of the testes and possibly the distribution of the body wall nuclei, the above diagnosis remains largely valid today. As the number of species included in the genus increased, the generic concept continued to expand to accommodate them. Many of the diagnostic features added by various authors were too restrictive to be of generic value as the interspecific variability within *Polymorphus* continued to increase with the discovery of more species. These restrictive diagnostic features are noted in the following few paragraphs.

Southwell and MacFie (1925), who discussed only *P. minutus*, diagnosed the body as thickened anteriorly and the proboscis as subcylindrical. Travassos (1926) recognized *Polymorphus* under subfamily Centrorhynchinae (Van Cleave, 1916) of family Echinorhynchidae Cobbold, 1879 but Thapar (1927) included it in his new family Acanthogyridae and order Acanthogyridea. The inconsistencies in Travassos's (1926) system, based on the use of insufficiently constant characters, were not satisfactorily eliminated in Thapar's (1927) scheme which recognized separate families as composites.

In Meyer's (1931) system, *Polymorphus* was correctly placed in his family Polymorphidae and order (Class) Palaeacanthocephala, and included 14 species (Meyer, 1932) all of which are presently recognized members of the genus except *P. magnus* which is here synonymized with *P. minutus* (following section). In his brief diagnosis, Meyer (1932) restrictively referred to short compact bodies cylindrical or weakly ovoid proboscides, trunk spines anterior to mid constriction, tubular cement glands, string-like lemnisci, and numerous small nuclei in the body wall. Meyer (1931) also established a new genus, *Profilicollis*, for two long-necked species *Polymorphus botulus* and *Polymorphus arcticus* (=*Filicollis botulus* Van Cleave, 1916 and *Filicollis arcticus* Van Cleave, 1920) with eggs with concentric membranes, but kept *Filicollis* Lühe, 1911 for *Filicollis anatis* (Schrank, 1788) and *Filicollis sphaerocephalus* (Bremser in Rudolphi, 1819). *Profilicollis* raised considerable controversy. Witenberg (1932) and later Van Cleave (1937, 1939, 1947) synonymized it with *Polymorphus* and Van Cleave (1937) reassigned *F. botulus* and *F. arcticus* as well as *F. sphaerocephalus* and *Filicollis altmani* Perry, 1942 to *Polymorphus* (see Van Cleave, 1947).

Webster (1948) recognized the diversity within *Polymorphus* and erected a new subgenus, *Falsifilicollis* for forms with greatly inflated and spheroidal proboscis and slender elongate neck previously included in *Filicollis*. These included *Polymorphus sphaerocephalus, Polymorphus altmani, Polymorphus kenti* Van Cleave, 1947 and *Polymorphus texensis* Webster, 1948. As Schmidt and Kuntz (1967) correctly pointed out, *Profilicollis* Meyer, 1931 has priority for the concept of *Falsifilicollis* Webster, 1948.

Petrochenko (1956) erected Filicollidae for *Filicollis* Lühe, 1911 including only *F. anatis* (Schrank, 1788) Lühe, 1911, and *Parafilicollis* Petrochenko 1956 including *P. major, P. altmani, P. kenti* and *P. sphaerocephalus*. His three major diagnostic features of *Parafilicollis* were the long neck, spheroidal proboscis and eggs without polar prolongation of middle membrane. Additional features included unpronounced sexual dimorphism, anterior trunk spines not well defined in young females, and 4-6 tubular cement glands. Petrochenko (1956) placed *Parafilicollis* in Gigantorhynchidae Southwell and MacFie, 1925 based primarily on the egg shape. Schmidt and Kuntz (1967) declared *Parafilicollis* as without status because Meyer (1931) erected *Profilicollis* for the same concept. The shape of eggs was clearly shown to be of no diagnostic value at the generic level in Polymorphidae by Van Cleave (1939), Schmidt and Kuntz (1966, 1967) and Amin (this paper).

Golvan (1960-61) accepted *Profilicollis* (=*Falsifilicollis* Webster, 1948) as a subgenus diagnosed with spheroidal proboscis and long slender neck, and included the same four species listed by Webster (1948), but without indicating a subgenus for the other species of the genus. Yamaguti (1963) synonymized *Profilicollis* with *Polymorphus*, and *Parafilicollis* with Webster's, 1948 *Falsifilicollis* which he amended and elevated to the generic status. Yamaguti's (1963) diagnosis of *Falsifilicollis* was essentially the same as that of Petrochenko's (1956) of *Parafilicollis* except for his reference to proboscis armature (16-30 longitudinal rows of 7-12 hooks each), 4-8 tubular cement glands, and tandem testes. Yamaguti (1963) included *Falsifilicollis* and *Filicollis* in Filicollidae Petrochenko, 1956 which he correctly transferred to Echinorhynchidea Southwell and MacFie, 1925. Clearly *Falsifilicollis* and *Parafilicollis* occupy the same concept for which Meyer (1931) originally erected *Profilicollis*. These three taxa are also clearly synonymous with *Polymorphus* since the subgenus *Profilicollis* was erected by Golvan (1961) for Webster's (1948) original subgenus *Falsifilicollis*. It is thus logical to assign subgeneric status to *Polymorphus* Webster, 1948 and to *Profilicollis* (Meyer, 1931) Golvan, 1961 as Schmidt and Kuntz (1967) correctly proposed.

While the above subgeneric controversies were going on, the diagnosis of the genus *Polymorphus* was undergoing changes of its own. Even though with the erection of *Hexaglandula* Petrochenko, 1950, which is here synonymized with *Polymorphus* (see status of *Hexaglandula* following), Petrochenko (1958) removed part of the inconsistencies from his generic diagnosis of *Polymorphus*, the latter still contained considerable restrictive constraints. These did not cover the present membership of *Polymorphus* or even the 23 species he assigned to that genus. His diagnostic characters restrictively included spindle-shaped body; considerable part of massive anterior region covered with spines which extend further from midbody on one side than the other; separated by constriction; cylindrical or ovate proboscis, proboscis hooks nearly equal in size; posterior hooks smaller and rootless; three cement glands in *Polymorphus contortus*; eggs spindle shaped and middle membrane with corrugated protrusions at poles (Petrochenko, 1958).

Golvan (1960-61) accepted *Hexaglandula* and its four species listed by Petrochenko (1958), erected *Profilicollis* with four species (*P. botulus, P. arcticus, P. altmani, P. texensis*) and recognized 26 species in *Polymorphus*. These included *P. kenti*

and *P. major*, which, however, perfectly fit Golvan's (1960-1961) own concept of *Profilicollis; Polymorphus* remained without an assigned subgenus. His diagnosis of *Polymorphus* was rather similar to that by Lühe (1911) but included the following restrictive features: proboscis short cylindroid or ovoid; basal proboscis hooks with rudimentary roots; neck short; brain at middle of proboscis receptacle; lemnisci digitiform, longer than proboscis receptacle; testes always contiguous; three tubular cement glands; eggs with polar prolongation of middle membrane.

Yamaguti's (1963) diagnosis of *Polymorphus* was essentially a hybrid between Lühe's (1911) and Golvan's (1960-61) and considerably more conservative than Petrochenko's (1958). However, it still contained restrictive features of little utility even with his deletion of the concept of *Profilicollis* from the generic concept of *Polymorphus* by the amendation and elevation of Webster's (1948) subgenus *Falsifilicollis* to the generic level which he included in Filicollidae. Such features included: body plump; anterior trunk shallowly constricted; proboscis cylindrical or somewhat ovoid; posterior proboscis hooks with reduced roots; neck distinct; three tubular cement glands; eggs with prominent polar prolongation of middle shell (Yamaguti, 1963).

Like Yamaguti (1963), Hoklova accepted *Hexaglandula*, and recognized *Profilicollis* (=Yamaguti's elevated *Falsifilicollis*), as an independent genus with seven species, in Filicollidae (see Hoklova, 1974). She did not, however, include *P. arcticus* (Van Cleave, 1920) Van Cleave, 1937 in her concept of *Profilicollis* but placed it in *Polymorphus* (*Polymorphus*) (see Hoklova, 1971, 1986). Her most complete diagnosis of *Polymorphus* was more encompassing of the wide diversity within the genus but still suffered from some of the restrictive characterizations stated by earlier observers. These included: body spindle-shaped less often pear-shaped; anterior trunk spines arranged in a chessboard-like pattern; hypodermic nuclei small and numerous; proboscis rounded, oval or cylindrical; roots of posterior hooks reduced; brain in the middle of the double walled proboscis receptacle; testes tandem; four tubular cement glands; eggs spindle-shaped with polar prolongation of middle membrane (Hoklova, 1986).

Hoklova also established two subgenera in *Polymorphus*, *Subfilicollis* Hoklova, 1967 with three species [*Polymorphus pupa* (Linstow, 1905) Kostylev, 1922; *Polymorphus phippsi* Kostylev, 1922; *Polymorphus gavii* Hoklova, 1965] and *Subcorynosoma* Hoklova, 1967 with three species [*Polymorphus corynoides* Skrjabin, 1913; *Polymorphus strumosoides* Lundstrom, 1942; *P. swartzi* Schmidt, 1965], and retained 21 other species in her "standard" subgenus *Polymorphus* (see Hoklova, 1971a). Her subgeneric concepts were stated to be based on "morphological and ecological peculiarities" (Hoklova, 1986), but no ecological information was included in her subgeneric diagnoses. Species in her subgenus *Polymorphus* presumably have oval or ovoid proboscis; well defined trunk constriction; identical extension of trunk spines over dorsal and ventral sides; and eggs with oval polar prolongation of middle membrane. There are exceptions to each of those characteristics in many of the species included in that subgenus as follows: the proboscis of *Polymorphus cincli* Belopolskaya, 1959, *Polymorphus striatus* (Goeze, 1782) Lühe, 1911, *Polymorphus biziurae* Johnston and Edmonds, 1948 and *Polymorphus mathevossianae* Petrochenko, 1949 is cylindrical. The proboscis of *Polymorphus crassus* Van Cleave, 1924 is unusually enlarged anteriorly and that of *Polymorphus trochus* Van Cleave, 1945 is pyriform in females (see status of *P. trochus* following). The trunk of *Polymorphus marchii* (Porta, 1901) Meyer, 1932, *P. cincli, P. striatus* and *P. contortus* (Bremser in Westrumb, 1821) Travassos, 1926 has no constriction. Anterior trunk spines are not equally extended on the dorsal and ventral sides of *Polymorphus acutis* Van Cleave and Starrett, 1940 and *Polymorphus marilis* Van Cleave, 1939. The eggs of *P. biziurae* Johnston and Edmonds, 1948 have three concentric membranes without any prolongation of the middle one. For further discussion on the significance of egg structure in polymorphid classification see Van Cleave (1939), Schmidt and Kuntz (1966, 1967) and Amin (this paper; above). Species in Hoklova's (1986) subgenus *Subfilicollis* presumably have rounded, almost spherical proboscides; trunk spines small and in narrow strips of identical width both at the ventral and dorsal sides; long cylindrical necks and weakly defined polar prolongation of middle membrane of eggs. The considerable overlap in all these characteristics with those listed for Hoklova's subgenus *Polymorphus* makes it impossible to make unquestionable species assignments. For example, the proboscis of *Polymorphus meyeri* Lundstrom, 1942 is also ovoid, the neck of *P. acutis* and *Polymorphus actuganensis* Petrochenko, 1949 is also long and cylindrical and the extent of definition of the polar prolongation of the middle membrane of eggs varies considerably within the genus and with the extent of egg development. Hoklova's subgenus *Subfilicollis* has been correctly considered synonymous to *Polymorphus* by various authors, including Amin (1982, 1985). In the diagnosis of her subgenus *Subcorynosoma*, Hoklova (1986) used some of the same characteristics that were rendered inoperative in her two other subgenera (above). Other characters were not used dichotomously, e.g., body form and neck length and shape (above), and are thus useless for comparison. Members of *Subcorynosoma* were diagnosed as having a narrow cylindrical proboscis, trunk spines large and extending significantly farther ventrally than dorsally, and middle membrane of eggs forming a long stretched polar prolongation. While this subgenus appears to be better defined and descriptive of its three designated member species, it still suffered from the same pitfalls noted in Hoklova's (1986) two other subgenera. For example, the proboscis of *P. corynoides* is ovoid-elongate and that of *P. swartzi* is enlarged proximally and trunk spines of *P. corynoides* do not appear to extend farther ventrally than dorsally. Other species of *Polymorphus* also have long and cylindrical proboscides, e.g., *P. biziurae, P. cincli* and *P. mathevossianae* and trunk spines longer than 30 or 36 μm (the maximum length in *P. strumosoides* and *P. swartzi*) are also known in other species, e.g., *Polymorphus cucullatus* Van Cleave and Starrett, 1940. Hoklova's (1986) use of "differences" in egg structure is most inadequate for distinguishing her subgenera (see above). The above discussion makes it clear that none of the diagnostic characteristics used by Hoklova (1971a, 1986) is sufficiently adequate or consistent to support her subgeneric diagnoses and assignments. Accordingly, *Subcorynosoma* Hoklova, 1967 is declared a junior synonym of *Polymorphus* Luhe, 1911.

Diagnosis of Polymorphus

Synonymies:

Profilicollis Meyer, 1931
Fasifilicollis Webster, 1948
Hexaglandula Petrochenko, 1950

Parafilicollis Petrochenko, 1956
Subfilicollis Hoklova, 1967
Subcorynosoma Hoklova, 1967

The following diagnosis is based on the acceptance of *Profilicollis* Meyer, 1931; *Falsifilicollis* Webster, 1948; *Parafilicollis* Petrochenko, 1956 and *Subfilicollis* Hoklova, 1967 as junior synonyms of *Polymorphus* Luhe, 1911 (see Amin, 1982, 1985) and the additional synonymization of *Hexaglandula* Petrochenko, 1950 and *Subcorynosoma* Hoklova, 1967 with it (Amin, this paper).

Generic diagnosis — Polymorphidae, Polymorphinae: Body usually small, plump, and anteriorly expanded, with pronounced, shallow or no constriction, or cylindroid or pyriform; anterior part of trunk with spines which may occasionally extend ventrally farther than dorsally. Main Lacunar canals lateral with reticular anastomoses. Proboscis cylindrical, ovoid, spindle-or pear-shaped with a short or long neck, or spheroid with very long neck. Proboscis hooks gradually decrease in size toward anterior and posterior ends; roots of anterior hooks simple and well developed, those of posterior hooks reduced, rudimentary or absent. Proboscis receptacle double-walled and inserted at base of proboscis; brain near base or middle of receptacle. Lemnisci digitiform or clavate. Testes usually spheroid, contiguous, and in anterior half of trunk; tandem; oblique or opposite. Cement glands four or six, usually tubular, occasionally clavate. Genital orifice terminal in both sexes, not spined. Eggs fusiform with variably pronounced polar prolongation of middle membrane or ovoid with all membranes concentric and lacking any prolongation. Parasites of aquatic and shore birds or occasionally of aquatic mammals and fish.

Type Species: *Polymorphus minutus* (Goeze, 1782) Luhe, 1911

Genus Hexaglandula Petrochenko, 1950

The subgenus *Hexaglandula* was erected by Petrochenko (1950) for 2 species of *Polymorphus* with 6 cement glands each, *Polymorphus mutabilis* (Rudolphi, 1819) Travassos, 1926 and *Polymorphus corynosoma* Travassos, 1915, then elevated to the generic status by Petrochenko (1958). In all other respects the generic diagnosis (Petrochenko, 1958) was not unlike that of *Polymorphus*. Golvan (1960-61) and Yamaguti (1963) accepted *Hexaglandula* with an additional 2 redesignated *Polymorphus* species included in Petrochenko (1958), *Polymorphus inermis* Travassos, 1923 and *Polymorphus paucihamatus* Heinzer, 1936. Amin (1982, 1985) also accepted *Hexaglandula* in the absence of critical taxonomic studies of the genus. I now propose the designation of the genus *Hexaglandula* as a junior synonym of the genus *Polymorphus* for the following reasons. The number and/or shape of cement glands do not appear to be valid taxonomic traits in many acanthocephalan genera and/or families. Variability in these structures has not been seriously considered by Petrochenko (1950, 1956, 1958). Two decidedly *Polymorphus* species: *P. arctocephali* and *P. cetaceum* have 6 claviform elongate cement glands each; the other *Polymorphus* species have 4 tubular glands each. Petrochenko (1956, 1958) and Golvan (1960-61) have overemphasized the importance of cement glands in acanthocephalan taxonomy (Amin 1985). Petrochenko's (1956) splitting of other genera, e.g., *Echinorhynchus* Muller, 1776, based on cement gland pattern was shown to be in error (Amin and Redlin, 1980). Southwell and MacFie (1925) objected to the use of cement glands' shape and number in taxonomic considerations, and Thapar (1927) indicated that they are too variable and only express an "artificial basis" for classification. Van Cleave's (1949) use of cement glands to characterize Eoacanthocephala, Archiacanthocephala and Palaeacanthocephala was primarily based on their anatomical structure and not their number or shape. The Palaeacanthocephalan family Rhadinorhynchidae has the same number of cement glands as Archiacanthocephala (8) but the gland's cortical granular zone bears many nuclear fragments like those in other Palaeacanthocephalan families (Van Cleave, 1949). Schmidt (1965) indicated that *Hexaglandula* is "insufficiently differentiated from *Polymorphus* ... to warrant splitting ... species from *Polymorphus*" even though he later included it in his key to the genera of Polymorphidae (Schmidt, 1973).

Accepting the above arguments, the 6 species previously included in *Hexaglandula* are now reassigned to *Polymorphus* as follows:

Polymorphus mutabilis (Rudolphi, 1819) Travassos, 1926 [= *Hexaglandula mutabilis* (Rudolphi, 1819) Petrochenko, 1950]

Polymorphus corynosoma Travassos, 1915 [= *Hexaglandula corynosoma* (Travassos, 1915) Petrochenko, 1958]

Polymorphus inermis Travassos, 1923 [= *Hexaglandula inermis* (Travassos, 1923) Petrochenko, 1958]

Polymorphus paucihamatus Heinze, 1936 [= *Hexaglandula paucihamatus* (Heinze, 1936) Petrochenko, 1958]

Polymorphus ariusis (Bilquees, 1971) comb. n. (= *Hexaglandula ariusis* Bilquees, 1971)

Polymorphus karachiensis (Bilquees, 1971) comb. n. (= *Hexaglandula karachiensis* Bilquees, 1971)

Subgenus *Subcorynosoma* Hoklova, 1967

The subgenus *Subcorynosoma* Hoklova, 1961 (established for *P. corynoides* Skrjabin, 1913; *P. strumosoides* Lundstrom, 1942 and *P. swartzi* Schmidt, 1965) is designated as a junior synonym of *Polymorphus* Lühe, 1911. Hoklova's subgenera were not dichotomously distinguished (Hoklova, 1986). Species in *Subcorynosoma* were diagnosed as having a narrow cylindrical proboscis and large trunk spines extending farther ventrally than dorsally. However, the proboscides of *P. corynosoma* and *P. swartzi* and trunk spines of *P. corynoides* do not fit the subgeneric diagnosis. This diagnosis is actually more descriptive, in part, of other species of *Polymorphus*: (see the above section on "the position, concept and composition of *Polymorphus*").

Polymorphus brevis (Van Cleave, 1916) Travassos, 1926

This species was originally described as *Arhythmorhynchus brevis*, based on already prepared museum specimens, by Van Cleave (1916). Travassos (1926) assigned the species to genus *Polymorphus* and Meyer (1932) accepted this generic assignment. Van Cleave (1945) re-examined the status of the species from additional collections and re-assigned the species back to *Arhythmorhynchus* based on his "belief that ... the species is in agreement with the accepted concepts of the genus *Arhythmorhynchus*" and that Meyer's (1932) relegation, "apparently" based on his interpretation of the proboscis as "either weakly ovoidal or possibly approaching cylindrical form", was in error. He did not refer to the reasons for the re-assignment by Travassos (1926). In the diagnosis of the genus *Arhythmorhynchus*, Meyer (1932), among others, indicated that the proboscis

is enlarged in the middle and with few greatly enlarged ventral hooks; "*A. brevis*" has no such enlarged hooks. Petrochenko (1958), Golvan (1960-61), and Yamaguti (1963) subsequently recognized the species under *Arhythmorhynchus*, but Petrochenko indicated that this assignment is "doubtful." In their generic diagnosis of *Arhythmorhynchus*, these three authors described the trunk as filiform with a short anterior enlargement, and the proboscis as being wider at the middle where ventral hooks are greatly enlarged. Subsequently, forms without enlarged anterior trunk, or proboscis, or greatly enlarged ventral proboscis hooks, but with cylindrical filiform bodies were included in *Anhythmorhynchus* by Schmidt (1973). This naturally erodes some of the classical criteria which were traditionally used to distinguish *Arhythmorhynchus* from closely related genera particularly *Polymorphus*. *Arhythmorhynchus* clearly needs to be revised. The presence of large subcuticular nulcei only in the anterior expanded part of *Arhythmorhnychus frassoni* (Molin, 1858) Luhe, 1911, the type and only species on which Lühe (1911) based his diagnosis of the genus *Arhythmorhynchus*, has not been recognized by Petrochenko (1958) as a generic trait and has not been described in a number of species of *Arhythmorhynchus*. The posterior trunk of *P. brevis* also lacks subcuticular nuclei (Van Cleave, 1916). In *Polymorphus*, the posterior unexpanded portion of the trunk is supposed to contain hyperdermal nuclei; see Schmidt's (1973) key. In the first diagnosis of *Polymorphus* based on only one species, *P. minutus*, Lühe (1911), and later Meyer (1932), refer to numerous small nuclei in the body wall. This trait was not recognized by Southwell and MacFie (1925), Petrochenko (1958), Golvan (1960-61) or Yamaguti (1963), was not reported in most species of *Polymorphus*, and thus not routinely used for species assignment. Three well recognized species of *Polymorphus*, *P. contortus* (Bremser in Westrumb, 1821) Travassos, 1926, *P. marilis* Van Cleave, 1939, and *Polymorphus paradoxus* Connell and Corner, 1957, do not appear to have hypodermal nuclei in the posterior trunk wall; (see Denny 1969, Figs. 9a, b, c). Describing *Arhythmorhynchus petrochenkoi* under *Polymorphus* by Schmidt (1969) soley for having hypodermal nuclei with posterior trunk distribution, and later on assigning it to *Arhythmorhynchus* by Atrashkevic (1979), indicates that the character of hypodermal nuclei alone is not sufficiently adequate to differentiate the two genera. Based on the above, "*A. brevis*" is again relegated to the genus and subgenus *Polymorphus* in agreement with the earlier re-assignment by Travassos (1926) and Meyer (1932).

Polymorphus chasmagnathi
(Holcman-Spector, Mané-Carzon and Dei-Cas, 1977) Amin, 1985

This species was originally described as *Falsifilicollis chasmagnathi* from an experimental infection of guinea pigs with immatures by Holcman-Spector *et al.* (1977). Amin (1985) placed it in the genus *Polymorphus* (=*Falsifilicollis* Webster, 1948) under the subgenus *Polymorphus* Lühe, 1911. Considering the very long neck and spheroid proboscis of this species, it's re-assignment to the subgenus *Profilicollis* Meyer, 1931 is recognized in agreement with Vizcaino (1989) who described adults for the first time from natural definitive hosts in Argentina.

Polymorphus magnus Skrjabin, 1913

Since the original description of this species from *Netta rufina* in Kazakhastan by Skrjabin's (1913), it has been accepted by many parasitologists. The very close similarities between it and *P. minutus* have also been recognized by various observers and some have suggested that the two species are practically inseparable, e.g. Bykovskaya (1948), Bezubik (1957) and McDonald (1988). Bykovskaya (1948) examined collections from which Skrjabin obtained his material and which varied from his description, that brought the two species closer together. She indicated that "*P. magnus*" differs from *P. minutus* only by larger dimensions. Petrochenko (1958) contended that Bykovskaya (1948) compared Skrjabin's (1913) description of *P. magnus* with Lühe's (1911) "incorrect" description of *P. minutus* which included 10mm long females; a length also cited by Meyer (1932). The "wide range of variability" exhibited by *P. minutus* was also observed by Van Cleave and Starrett (1940) and Schmidt (1965), among others. The differences between *P. minutus Sensu* Goeze (1782), Bykovskaya (1948) and Bezubik (1956), and *P. magnus sensu* Skrjabin (1913) and Petrochenko (1950), were reduced to differences in body length and in the fact that 3.0-3.5mm long female *P. minutus* have eggs while 6.0-7.0 mm long female "*P. magnus*" do not (Bezubik, 1957). The curve of male and female body length of Bezubik's (1957) had intermediate forms (3.94-9.5 mm) only one peak, making it impossible to differentiate the two species. Egg production by females of different sizes was attributed to the physiological state of worms (Bezubik, 1957). Petrochenko's (1950) "*P. minutus*" was apparently *P. contortus* and the variable egg measurements reported by various authors were apparently an expression of the widely fluctuating egg size "most frequently in the same individuals, both in the short ... and ... the long specimens' (Bezubik, 1957). Ecological parameters such as host species and season are known to affect acanthocephalan size, reproductive activity, and egg production: see for example Amin (1987a) and Amin and Redlin (1980). The above arguments are sufficiently convincing to propose the designation of *Polymorphus magnus* Skrjabin, 1913 as a junior synonym of *Polymorphus minutus* (Goeze, 1782) Luhe, 1911.

Polymorphus pupa (Linstow, 1905) Kostylev, 1922

Since the inadequate description of this species as *Echinorhynchus pupa* by Linstow (1905), it has been assigned to *Polymorphus* by Kostylev (1922), to *Filicollis* by Travassos (1926) and to *Plagiorhynchus* (*Prosthorhynchus*) by Meyer (1931), regarded as unrecognizable by Van Cleave and Rausch (1951), and as *incerta sedis* by Yamaguti (1963) and Schmidt (1965). Other authors e.g., Petrochenko (1958), Hoklova (1986), McDonald (1988) and Amin (this paper) regard the species as a recognizable member of the genus *Polymorphus*. The material reported by Hoklova (1971b, 1986), and others quoted therein, restores provisional confidence in the identity of that species pending the examination of type and other material. The species is included in the following key even though it is not formally resurrected at this time.

Polymorphus trochus Van Cleave, 1945

Since its original description in 1945, *P. trochus* was most commonly found in the American coot, *Fulica americana*, but rarely in North American ducks (Priebe, 1952, Podesta and Holmes, 1970, and McDonald, 1988). The species is peculiar in that its proboscis shows distinct sexual dimorphism; pyriform with the terminal portion narrowing into a bluntly pointed tip in females but essentially cylindroid in males. Hoklova (1966a, b, 1986) described a polymorphid acanthocephalan from a number

of bird species, mostly ducks, *Anas*, that she named *P. trochus* Van Cleave, 1945 which is, however, clearly distinct from that species. McDonald (1988) also noted the difference between these two forms. In Hoklova's species, the basically stout cylindroid proboscis does not significantly differ between sexes. Proboscis armature, body size and shape, position of testes and egg size, among other characteristics, also vary from Van Cleave's (1945) description. Based on the above anatomic and host differences, it is proposed that *Polymorphus trochus sensu* Hoklova is a different species from *Polymorphus trochus* Van Cleave, 1945. It may well be a new species. The correct status of this species can only be ascertained upon the independent examination of representative specimens and the designation of type material of this acanthocephalan if it is new.

Subgeneric diagnosis

Considering the above treatment, only two subgenera of the genus *Polymorphus: Polymorphus* Lühe, 1911 and *Profilicollis* Meyer, 1931, are recognized. These are diagnosed below.

The subgenus *Polymorphus* - Polymorphidae, Polymorphinae, *Polymorphus*: trunk usually anteriorly expanded, sometimes elongate, with one, or occasionally two or no constrictions. Proboscis cylindrical, ovoid to ovoid-elongate, pyriform or spindle-shaped. Neck long or short. Mature eggs usually with polar prolongation of middle membrane.
Type species: *Polymorphus* (*Polymorphus*) *minutus* (Goeze, 1782) Lühe, 1911.

The subgenus *Profilicollis* - Polymorphidae, Polymorphinae, *Polymorphus*: trunk usually cylindroid without an anterior expansion, may occasionally be constricted. Proboscis ovoid to spheroid. Neck very long. Mature eggs usually with no prolongation of middle membrane.
Type species: *Polymorphus* (*Profilicollis*) *botulus* (Van Cleave, 1916) Witenberg, 1932.

Key to species of Polymorphus

The subgenus *Polymorphus* Lühe, 1911, includes 36 species, six of which were formerly included in *Hexaglandula*. The key does not include *P. trochus* of Hoklova (1966) (see status of *P. trochus*, above) or *P. magnus* (=*P. minutus*, this paper) but includes *P. brevis* and *P. pupa*. The second subgenus, *Profilicollis* Meyer, 1931, has 10 species that include *P. chasmagnathi*. In the key, the exclusive use in individual couplets of single traits which might show considerable variability with geographical, host or developmental factors is avoided; for example, see Van Cleave (1916, 1939, 1945), Bezubik (1957), Schmidt (1965), Schmidt and Kuntz (1966, 1967), Amin (1986, 1987b), Amin and Redlin (1980) and Ching (1989).

1. Proboscis cylindrical, ovoid to ovoid-elongate, pyriform or spindle-shaped; neck long or short; mature eggs usually with polar prolongation of middle membrane ..... subgenus *Polymorphus* Luhe, 1911 2
   Proboscis ovoid to spheroid; neck very long; mature eggs usually with no polar prolongation of middle membrane ... subgenus *Profilicollis* (Meyer, 1931) Golvan, 1961 36

2. With 6 cement glands; in birds, mammals or fish 3
   With 4 cement glands; in birds or mammals 10

3. In mammals; trunk anteriorly expanded into a bulb or disc; proboscis cylindrical 4
   In birds or fish; trunk not so expanded; proboscis variable 5

4. Proboscis more than 1.0 mm long; largest proboscis hooks 80 μm; largest trunk spines 90 μm; in seals; Australia *P. arctocephali* Smales, 1986
   Proboscis less than 1.0 mm long; largest proboscis hook 75 μm; largest trunk spines 50 μm; in dolphins; Australia ..... *P. cetaceum* (Johnston and Best, 1942) Schmidt and Dailey, 1971

5. In birds; trunk may be expanded anteriorly, or medially, or with constriction 6
   In fish; trunk elongated without expansion or constriction 9

6. Proboscis with 6 hooks per row 7
   Proboscis with 13 to 18 hooks per row 8

7. Trunk 8.0-8.5 x 1.8-2.25 mm; proboscis ovoid-elongate with 12 longitudinal rows of hooks; in gulls; Europe ..... *P. paucihamatus* Heinze, 1936
   Trunk 15.0-25.0 x 1.5-2.5 mm; proboscis fusiform with 16 longitudinal rows of hooks; in herons; Brazil ..... *P. inermis* Travassos, 1923

8. Trunk elongate with faint anterior constriction, 6.0-10.0 x 1.0-1.4 mm; proboscis elongate cylindrical with 16-18 hooks per row; eggs with polar prolongation of middle membrane; in tern, cormorant, kingfisher, egret, roseate, spoonbill, limpkin; South America ..... *P. mutabilis* (Rudolphi, 1819) Travassos, 1926
   Trunk broadened anteriorly, no constriction, 4.0-7.0 x 1.0-2.0 mm; proboscis elongate pyriform with 13 hooks per row; eggs with no polar prolongation of middle membrane; in herons; Puerto Rico, Brazil ..... *P. corynosoma* Travassos, 1915

9. Trunk elongated cylindrical; proboscis long-cylindrical, 1.8 x 0.25 mm with 18 rows of hooks; testes 300-500 μm wide; in catfish; Karachi coast ..... *P. karachiensis* (Bilquees, 1971) comb. n.
   Trunk elongated fusiform; proboscis cylindrical but swollen anteriorly, 1.0-1.4 x 0.3-0.4 mm with 16 rows of hooks; testes 670-850 μm wide; in catfish; Karachi coast ..... *P. ariusis* ..... (Bilquees, 1971) comb. n.

10. In aquatic rodents and waterfowl; Canada; trunk with two constrictions; proboscis ovoid-elongate ..... *P. paradoxus* Connell and Corner, 1957
    In birds; trunk with one or no constrictions; proboscis variable 11

11. Proboscis protruding from an orifice in flattened anterior extremity, large: 1.7 x 0.76 mm at apex, abruptly truncated anteriorly, largest hooks reaching 190 μm; in wood ibis; United States ..... *P. crassus* Van Cleave, 1924
    Proboscis not so shaped or inserted and markedly smaller, largest hooks shorter than 110 μm 12

12. Proboscis sexually dimorphic, pyriform and more strongly swollen at base in females; in coot, mallard duck; North America ..... *P. trochus* Van Cleave, 1945
    Proboscis with no sexual dimorphism 13

13. Proboscis cylindrical, may be expanded distally proximally or at middle 14

Proboscis ovoid or ovoid elongate 21

14. Proboscis expanded at middle 15
Proboscis not expanded at middle 16

15. Proboscis spindle-shaped with 18-20 longitudinal rows of 11-13 hooks each, largest hooks 54-70 μm; trunk ovoid anteriorly; eggs 93-120 x 26-35 μm; in black crowned night heron; Peru ..... *P. spindlatus* Amin and Heckmann, 1991
Proboscis and trunk markedly more slender; proboscis with 18 longitudinal rows of 13-16 (usually 15) hooks each, largest hooks 41-47 μm; eggs 76-100 x 24-30 μm; in osprey, bittern, great blue heron, black crowned night heron; North America ..... *P. brevis* (Van Cleave, 1916) ..... Travassos, 1926

16. Proboscis anteriorly enlarged, with 12-16 hooks per row; in herons, bittern, eagle, swan, duck, egret, merganser; Europe ..... *P. striatus* (Goeze, 1782) Luhe, 1911
Proboscis not anteriorly enlarged, with up to 12 hooks per row 17

17. Proboscis with proximal swelling, hooks in 18 rows; eggs 78-86 x 15-16 μm; in Barrow's golden eye; Alaska .... *P. swartzi* Schmidt 1965
Proboscis without swelling proximally or elsewhere, hook rows >20 or ≤18; eggs larger or smaller 18

18. Large, males 6-9 mm, females 11-18 mm long; 21-22 proboscis hook rows; eggs small 58-65 x 29-34 μm without polar prolongation of middle membrane; in musk ducks; Australia ..... *P. biziurae* Johnston and Edmonds, 1947
Small, less than 5.5 mm long; proboscis hook rows 20 or less; eggs longer than 100 μm with polar prolongation of middle membrane 19

19. Sexes of equal size, 2.6-4.5 mm long; proboscis with 20 hooks rows, largest hooks 31-49 μm long; in ducks; Russia ..... *P. mathevossianae* Petrochenko, 1949
Males and females of unequal size; proboscis with fewer than 20 hook rows, largest hooks longer than 49 μm 20

20. Males, 2.8-5 mm long, shorter than females, 5-5.5 mm; 16-18 roboscis hook rows with 11-14 hooks each, largest hooks 46-52 μm long; in common golden eye duck; Sweden ..... *P. strumosoides* Lundstrom, 1942 .....
Males, 2.8 mm long, longer than females, 1-1.2 mm; 12-14 proboscis hook rows with 9-10 hooks each, largest hooks reaching 64 μm; in dipper; Russia ..... *P. cincli* Belopolskaia, 1959

21. Proboscis ovoid 22
Proboscis ovoid-elongate 25

22. Large, males 13-20 mm and females 20-25 mm long; proboscis with 18-20 hook rows; in eider ducks; arctic Asia ..... *P. pupa* (Linstow, 1905) Kostylev, 1922
Males and females smaller, not exceeding 10 and 15 mm in length; proboscis with fewer than 18 hook rows 23

23. Proboscis with 13 or 14 hook rows, largest hooks 96-110 μm long; in loons; Russia ..... *P. gavii* Hoklova, 1965
Proboscis with more than 14 hook rows, largest hooks not exceeding 71 μm 24

24. Proboscis 300-400 μm long, with 16 or 17 hook rows, largest hooks 45-66 μm long; in mallards, tufted ducks; Sweden ..... *P. meyeri* Lundstrom, 1942
Proboscis larger, 470-700 μm long, with 14-18 (usually 15-16) hook rows, largest hooks 68-71 μm long; in eider, ducks, grebes; Russia ..... *P. phippsi* Kostylev, 1922

25. Trunk less than 3 mm long 26
Trunk more than 3 mm long 28

26. Proboscis 100-200 μm long, with 8 rows of hooks; in water rail; Italy ..... D. *P. marchii* (Porta, 1910) Meyer, 1932
Proboscis longer than 200 μm, with 10 or more rows of hooks 27

27. Proboscis 200-400 μm long with 14-18 (usually 16) rows of 6-8 (usually 8) hooks each; testes oblique; in ducks, bittern, shrike; Europea, USA .... *P. contortus* (Bremser, 1821) Travassos, 1926
Proboscis 400-700 μm long with 10 rows of 10-12 hooks each; testes tandem; in mallard duck; Russia .... *P. corynoides* Skrjabin, 1913

28. Proboscis 950 μm long, with 22 rows of hooks; in hooded merganser; North America .... *P. cucullatus* Van Cleave and Starrett, 1940
Proboscis less than 700 μm in length, with up to 18 rows of hooks 29

29. Trunk uniformlly cylindrical with spiny area extending past constriction; proboscis 400 μm long or less, with 16-18 rows of 6-8 hooks each 30
Trunk not so shaped or spined; proboscis longer than 400 μm, with 13-18 rows usually of 8 or more hooks each 31

30. Trunk 10.3 mm long; proboscis 370 x 250 μm, with 6-8 hooks per row; in ducks; South America .... *P. miniatus* (Linstow, 1896) Meyer, 1933
Trunk 8-14 mm long; proboscis 400 x 200-280 μm with 7-8 hooks per row; in ducks, cormorants, sandpiper; North America, Russia ..... *P. marilis* Van Cleave, 1939

31. Proboscis 450 x 150 μm, with 11-12 hooks per row; largest hooks 40-45 μm long; in ducks, grebe, gull, coot, godwit; North America, Siberia .... *P. acutis* Van Cleave and Starrett, 1940
Proboscis larger (400-700 x 200-400 μm), with less than 11 hooks per row; largest hooks longer than 50 μm 32

32. Proboscis with 18 rows of hooks; proboscis receptacle 1516 x 258 μm; in puddle ducks; Kazakhstan, Sakhalin .... *P. actuganensis* Petrochenko, 1949
Proboscis usually with 14 or 16 rows of hooks; proboscis receptacle shorter than 1300 μm 33

33. Trunk widest posterior to constriction where testes are located; testes tandem; ovoid-elongate, large 770-1500 x 560-770 μm; in water turkey, heron, ducks, merganser; North America ..... *P. obtusus* Van Cleave, 1918
Trunk widest anterior to constriction; testes at or anterior to constriction, oblique or opposite, round, smaller 200-980 x 300-680 μm 34

34. Males and females of equal length 3.8-4.3 mm; largest proboscis hooks 53-71 μm; testes opposite, 364-311 μm; in puddle ducks, sea ducks, velvet scoter duck; Kazakhstan .. .. *P. kostylewi* Petrochenko, 1949
Females larger than males; largest proboscis hooks longer,

68-79 μm; testes oblique 35

35. Males 4.6-5.4, females 5.7-6.0 mm long; proboscis with 13-16 (usually 14) rows of 6-9 (usually 7-8) hooks each; testes 500-640 x 200-300 μm; in ducks; Sweden .... *P. diploinflatus* Lundstrom, 1942
Males 3.0-8.0, females 3.5-12.2 mm long; proboscis with 14-18 (usually 16) rows of 7-10 hooks each; testes 500-980 x 300-680 μm; in ducks, swans, chicken, gull, murre, gallinule, rail, merganser, geese, crow, shorebirds, fulmar, wren, thrush, quillemot, white wagtail, dovekie, tern, starling; Europe, Asia, North America .... *P. minutus* (Goeze, 1782) Luhe, 1911

36. Proboscis 2.3-2.5 mm in diameter, largest hooks up to 150 μm long; proboscis receptacle 6-8 mm long; males with 6 cement glands; in kelp gull, silver gull, other gulls, yellow-crowned night heron, wood rails, scarlet ibis, oystercatcher; Brazil, South Australia, Montevideo ..... *P. sphaerocephalus* (Bremser in Rudolphi, 1819) Van Cleave, 1947
Proboscis less than 2.0 mm in diameter, largest hooks less than 120 μm long; proboscis receptacle less than 6 mm long; males with 4 cement glands 37

37. Proboscis spheroid, with 25-30 rows of 9-12 hooks each 38
Proboscis spheroid or ovoid, with less than 25 rows of 7-10 hooks each 39

38. Proboscis 1.5 mm in diamter, with 27 rows of 10-11 hooks each, largest hooks 53-58 μm long; proboscis receptacle 5.0 mm long; in herring gull; Canada ....*P. kenti* Van Cleave, 1947
Proboscis 500-960 μm in diameter, with 25-30 rows of 9-12 hooks each, largest hooks 50-70 μm long; proboscis receptacle 1.7-2.75 mm long; in eider ducks, scoters; North America ..... *P. altmani* (Perry, 1942) Van Cleave, 1947

39. Trunk cylindroid; proboscis spheroid, 1-2 mm in diameter 40
Trunk spindle or bottle-shaped; proboscis ovoid, less than 1 mm in diameter 42

40. Largest proboscis hooks 71-92 μm long; proboscis receptacle 4.5-5.4 mm long..... 41
Largest proboscis hooks 33-51 μm long; proboscis receptacle 2.95-3.56 mm long; in sanderling; USA .... *P. texensis* Webster, 1948

41. Males 10-16, females 11 mm long; proboscis slightly wider than long; posterior testis large, 1.05-1.93 x 0.79-1.47 mm; in sheathbills; South Shetlands .... *P. antarcticus* Zdzitowiecki, 1985
Males 2.5-14.3, females 3.9-28.6 mm long; proboscis slightly longer than wide; posterior testis smaller, 0.91-1.15 x 0.62-0.65 mm; in guinea pigs (exper.), coot, grebe, ibis; Uruguay, Argentina .... *P. chasmagnathi* Holcman-Spector, Mane-Carzon, Dei-Cas, 1977

42. Proboscis with 22 rows of hooks; eggs 126-155 x 30-41 μm, may show polar prolongation of middle membrane; in eider ducks; Canada, Russia .... *P. arcticus* (Van Cleave, 1920) Van Cleave, 1937
Proboscis with up to 20 rows of hooks; eggs shorter than 110 μm, no polar prolongation of middle membrane 43

43. Proboscis with 12-15 rows of hooks; lemnisci 3.0-5.2 mm long; eggs small, 62-65 x 23 μm; in domestic duck; Taiwan ..... *P. formosus* Schmidt and Kuntz, 1967
Proboscis with 16-20 rows of hooks; lemnisci 1.3-3.6 mm long; eggs larger, 68-108 x 24-40 μm 44

44. Trunk spindle-shaped with constriction at level of posterior end of lemnisci, males 16-22 mm, females 21-40 mm long; largest proboscis hooks 99-108 μm long; in sea and bay ducks; Europe ..... *P. major* Lundstrom, 1942
Trunk bottle-shaped with constriction well behind level of posterior end of lemnisci; males 13-16 mm, females 16.5-20 mm long; largest proboscis hooks 80-96 μm long; in eider ducks, golden eye, greater scaup, oldsquaw, other sea ducks; North America, Eurasia .... *P. botulus* (Van Cleave, 1916) Witenberg, 1932

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