J. Helminthol. Soc. Wash.
66(2), 1999 pp. 123–132

A Taxonomic Reconsideration of the Genus *Plagiorhynchus* s. lat. (Acanthocephala: Plagiorhynchidae), with Descriptions of South African *Plagiorhynchus* (*Prosthorhynchus*) *cylindraceus* from Shore Birds and *P.* (*P.*) *malayensis*, and a Key to the Species of the Subgenus *Prosthorhynchus*

OMAR M. AMIN,[1,4] ALBERT G. CANARIS,[2] AND J. MICHAEL KINSELLA[3]

[1] Institute of Parasitic Diseases, P.O. Box 28372, Tempe, Arizona 85285 and Department of Zoology, Arizona State University, Tempe, Arizona 85287 U.S.A. (e-mail: omaramin@aol.com),
[2] P.O. Box 1479, Hamilton, Montana 59840-1479 U.S.A. (e-mail: acanaris@bitterroot.net), and
[3] 2108 Hilda Avenue, Missoula, Montana 59801 U.S.A. (e-mail: wormdwb@aol.com)

ABSTRACT: A population of *Plagiorhynchus* (*Prosthorhynchus*) *cylindraceus* (Goeze) Schmidt and Kuntz is described from 4 species of shore birds in South Africa. Specimens of 3 supposed synonyms of *P.* (*P.*) *cylindraceus*, namely *P.* (*P.*) *formosus* Van Cleave, *P.* (*P.*) *taiwanensis* Schmidt and Kuntz, and *P.* (*P.*) *transversus* (Rudolphi) Travassos, were studied and this synonymy was verified. The taxonomic status of *Plagiorhynchus* s. str. and of *Prosthorhynchus* was reconsidered, and both were retained as subgenera. Females of *Plagiorhynchus* (*Prosthorhynchus*) *malayensis* (Tubangui) Schmidt and Kuntz (*nec malayense*) are described for the first time; males are redescribed. A key to species of the subgenus *Prosthorhynchus* is provided.

KEY WORDS: Acanthocephala, *Plagiorhynchus* (*Prosthorhynchus*) *cylindraceus*, description, South Africa, shore birds, Aves, subgenera *Plagiorhynchus* s. str. and *Prosthorhynchus*, *Plagiorhynchus* (*Prosthorhynchus*) *malayensis*, taxonomic key.

A collection of acanthocephalans was made by one of us (A.G.C.) from 7 species of shore birds in South Africa in 1981. All 7 species yielded a new centrorhynchid acanthocephalan, *Neolacunisoma geraldschmidti* Amin and Canaris, 1997. Additionally, 5 of these 7 host species harbored 2 species of plagiorhynchid acanthocephalans.

One unidentified species of *Plagiorhynchus* infected 1 host species, and the other 4 host species were infected with *Plagiorhynchus* (*Prosthorhynchus*) *cylindraceus* (Goeze, 1782) Schmidt and Kuntz, 1966. The study of the latter species, a number of its synonyms, and various plagiorhynchid species prompted reconsideration of the generic–subgeneric status of *Plagiorhynchus* and *Prosthorhynchus* and the construction of a key to species of the latter subgenus. Among the acanthocephalans borrowed for this study were a few specimens of *Plagiorhynchus* (*Prosthorhynchus*) *malayensis* (Tubangui, 1935) Schmidt and Kuntz, 1966 (*nec malayense*), that were sufficiently informative to describe females for the first time and redescribe males. This paper reports on these findings.

[4] Corresponding author.

Materials and Methods

Twenty-eight individuals (12 males and 16 females) of *P.* (*P.*) *cylindraceus* were recovered from 4 species of shore birds (Charadriiformes) collected by one of us (A.G.C.) from the Berg River, Cape Province, South Africa, between 24 May and 31 July 1981. The host species were the curlew sandpiper (*Calidris ferruginea* (Pontoppidan, 1763), 1 individual infected with 25 acanthocephalans); Kittlitz' plover (*Charadrius pecuarius* (Temminck, 1823), 1 of 4 individuals infected with 1 acanthocephalan); triple-banded plover (*Charadrius tricollaris* (Vieillot, 1818), 1 of 5 individuals infected with 1 acanthocephalan); and blacksmith plover (*Holopterus armatus* (Burchell, 1822), 1 of 7 individuals infected with 1 acanthocephalan). In addition, 26 unidentifiable plagiorhynchid acanthocephalans were collected by A.G.C. from 2 white-fronted sand plovers (*Charadrius marginatus* Vieillot, 1818) and 10 uninformative plagiorhynchid acanthocephalans from the stilt (*Himantopus himantopus* (Linnaeus, 1758)), *H. armatus*, *Charadrius pallidus* Strickland, 1852, and *C. pecuarius*. These unidentified specimens are in the collection of M. Kinsella, Missoula, Montana.

Specimens were processed by the late Gerald D. Schmidt. We do not know the processing method used. Measurements, made using an ocular micrometer and conversion table, are in micrometers unless otherwise stated. Width measurements refer to maximum width. Most specimens were deposited in the United States National Parasite Collection (USNPC), Beltsville, Maryland, and a few were retained in the collection of the first author (O.M.A.). A few study specimens were

loaned from USNPC, but most were from the Harold W. Manter Laboratory Collection (HWMLC), University of Nebraska State Museum, Lincoln, Nebraska. We report the results of examination of the specimens collected from the South African shore birds.

Results and Discussion

Plagiorhynchus (*Plagiorhynchus*) sp.

The 26 specimens of *Plagiorhynchus* (*Plagiorhynchus*) sp. collected from *C. marginatus* were slender, with the proboscis wider near its middle, long lemnisci and uterus, a near-terminal female gonopore, elliptical eggs with polar prolongation of the fertilization membrane, and cement glands of unequal length and altogether about as long as the 2 testes. The specimens were not sufficiently informative to make a specific designation.

Plagiorhynchus (*Prosthorhynchus*) *cylindraceus* (Goeze, 1782) Schmidt and Kuntz, 1966

Except for 1 female in the ovarian ball stage, all 13 other female and 11 male *P.* (*P.*) *cylindraceus* collected from the single curlew sandpiper examined were sexually mature adults with ripe eggs and sperm, respectively. Of the other 3 host species examined, 1 individual of each was infected with 1 immature female. The curlew sandpiper appears to be the natural host of *P.* (*P.*) *cylindraceus* in South Africa.

Our South African specimens were diagnosed as *P.* (*P.*) *cylindraceus* based on their close similarities with that species and taxa now synonymized with it, as listed in Amin (1985) and compared herein (Table 1). Measurements of the 1 available female *Plagiorynchus* (*Prosthorhynchus*) *transversus* (Rudolphi, 1819) Travassos, 1926, the other supposed synonym (USNPC #65269) agreed with those listed in the table. Some of the specimens examined, and particularly European *P.* (*P.*) *cylindraceus,* however, appeared less robust and more slender, and females as long as 40 mm were reported (Golvan, 1956, Fig. 1). Another difference was related to the roots of the middle proboscis hooks, which were longer than the blades in European *P.* (*P.*) *cylindraceus* (see Golvan, 1956, pl. 1A). This was also observed in some but not all *P.* (*P.*) *cylindraceus* from Long Island, New York, and New Hampshire, U.S.A. (HWMLC 33444–33452), but not in specimens from Israel (HWMLC 34871). Golvan's specimens reached lengths of 15 mm in males and 40 mm in females and had as many as 24 longitudinal rows of proboscis hooks. In all other respects, the synonymy of *P.* (*P.*) *cylindraceus, P.* (*P.*) *transversus, Plagiorhynchus* (*Prosthorhynchus*) *formosus* Van Cleave, 1918, and *Plagiorhynchus* (*Prosthorhynchus*) *taiwanensis* Schmidt and Kuntz, 1966, was upheld.

Description of South African *Plagiorhynchus* (*Prosthorhynchus*) *cylindraceus*

GENERAL: Specimens robust and bluntly pointed, females not much longer but more plump than males. Subdermal nuclei discoidal, in shallow ameboid branched interconnected vesicles, appearing rod-shaped in profile, with vertical orientation at almost regular intervals from anterior end of trunk to short distance from posterior end. Secondary lacunar vessels transverse throughout trunk. Proboscis hooks in straight longitudinal rows, without dorsoventral or any other differentiation. Blades generally similar in length, but becoming slightly shorter abruptly anteriorly and more gradually posteriorly (Table 1). Hook roots simple, posteriorly directed, and usually about as long as or slightly shorter than blades. Posterior 2 hooks of each row spiniform, second to last hook with short root which may be further reduced to large knob; last hook rootless and invariably with small knob instead. Lemnisci long and slender, much longer than proboscis receptacle, nucleated, subequal, sometimes branched or multiple, may extend past posterior end of posterior testis. Testes ovoid, contiguous, usually in anterior half of trunk. Four cement glands in 2 sets of 2 each, originating at various levels beginning anteriorly near posterior end of posterior testis. Four separate cement gland ducts originating anteriorly at level of anterior end of Saefttigen's pouch and joining pouch at its posterior end. Gonopore near-terminal in adult males but distinctly subterminal in adult females, vagina usually curved anteriad in a 90 degree angle. Ripe eggs mostly elliptical with concentric shell and no polar prolongation of fertilization membrane. Fertilization membrane of a few eggs in gravid females (5–15%) may exhibit unipolar or, less frequently, bipolar prolongation.

SPECIMENS DEPOSITED: USNPC 88031 (10 males and 10 females on 10 slides from *Calidris ferruginea* in the Berg River, Cape Province, South Africa).

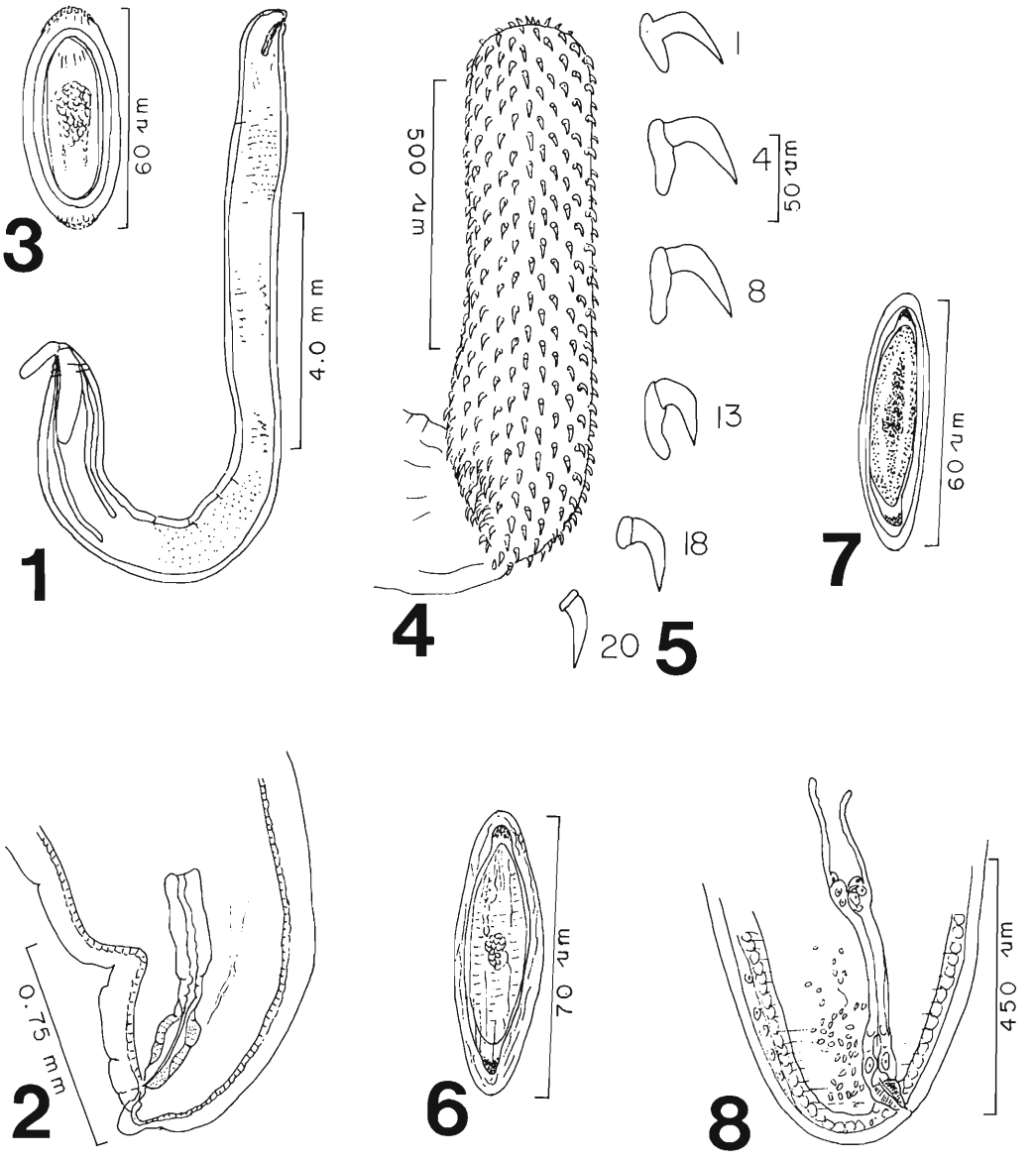
Table 1. Comparison between the South African *Plagiorhynchus* (*Prosthorhynchus*) *cylindraceus* and synonyms as reported by others or measured (this paper) in selected diagnostic characteristics.

	P. cylindraceus			*P. formosus*		*P. taiwanensis*	
	South Africa, this paper (n = 23)	Golvan, 1956 (n = ?)	This paper (n = 20)	Van Cleave, 1918, 1942; Schmidt and Olsen, 1964 (n = ?)	This paper (n = 20)	Schmidt and Kuntz, 1966 (n = 60)	This paper (n = 8)
Trunk (mm)							
Males	7.79–0.15 × 1.67–1.88	10–15 ×	4.545–10.45 × 0.61–1.82	8–13 × 1.5–2.5	5.61–12.42 × 1.24–2.45	10.0–14.0 × 1.75–2.75	8.03–11.21 × 1.57–2.30
Females	8.97–11.06 × 2.06–2.55	20–40 ×	5.15–12.12 × 0.45–2.818	9–15 × 2–3	8.03–13.32 × 1.33–2.88	13.0–16.0 × 2.5–3.0	9.09–15.0 × 1.88–3.18
Proboscis (mm)							
Males	1.15–1.21 × 0.21–0.24	—	0.88–1.03 × 0.24–0.33	0.80–1.10 × 0.25–0.33	0.94–1.12 × 0.24–0.30	—	0.88–1.06 × 0.24–0.26
Females	1.24–1.39 × 0.24–0.27	—	0.97–1.15 × 0.27–0.33	0.80–1.10 × 0.25–0.33	1.00–1.21 × 0.21–0.36	—	1.00–1.33 × 0.29–0.35
Proboscis hooks							
Rows (no.)	14–17	14–20, up to 24	16–17	15–18	13–17	14–16	16–17
Hooks/row	15–18	10–18	13–15	11–15	13–15	11–15	13–16
Proboscis hooks (mean length from anterior)							
	M (11)*	F (12)*	M	F	M (8)	F (12)	V.C.	S.&O.	M (10)	F (10)	M (?)†	F (?)†	M (3)	F (5)
	59	56	NG‡	NG	53	55	71	60	56	59	62	67	59	69
	62	66	NG	NG	66	67	77	79	56	64	65	73	62	76
	64	69	NG	NG	67	66	83	79	62	72	65	76	67	72
	68	69	NG	NG	66	72	83	79	70	77	67	85	67	74
	68	69	NG	NG	70	73	83	79	72	78	67	85	67	77
	71	73	NG	NG	70	79	83	79	73	79	70	85	69	78
	70	75	NG	NG	69	79	83	79	77	81	70	85	69	76
	71	76	NG	NG	74	78	83	79	77	81	73	85	69	76
	69	76	NG	NG	71	82	83	79	75	77	73	85	62	78
	72	73	NG	NG	67	80	77	79	73	78	67	85	60	82
	71	73	NG	NG	71	75	77	79	75	74	59	85	56	77
	69	73	NG	NG	71	72	77	79	69	73	59	88	57	78
	68	69	NG	NG	66	64	65	79	66	68	56	91	57	73
	62	66	NG	NG	66	63	—	60	63	64	56	88	56	70
	59	62	NG	NG	56	61	—	60	60	57	—	73	52	64
	56	60	NG	NG	—	—	—	—	—	—	—	—	—	—
	53	60	NG	NG	—	—	—	—	—	—	—	—	—	—
Eggs	64–78 × 25–28	80 × 30	42–70 × 12–34	40–75+ × 18–30+	56–73 × 25–31	65–75 × 24–27	53–73 × 22–28							

* Numbers in parentheses indicate the numbers of specimens used for determination.

† ?, Number of specimens examined not given.

‡ NG, not given.



Figures 1–8. Species of *Plagiorhynchus* (*Prosthorhynchus*) and *P.* (*Plagiorhynchus*). 1–5. *Plagiorhynchus* (*Prosthorhynchus*) *malayensis*, female. 1. Lateral view of whole specimen. 2. Posterior end and reproductive system. 3. Egg from the body cavity. 4. Proboscis. 5. Proboscis hook numbers 1, 4, 8, 13, 18, 20 of 1 row. 6. *Plagiorhynchus* (*Prosthorhynchus*) *bullocki,* egg from the body cavity of a gravid female. 7, 8. *Plagiorhynchus* (*Plagiorhynchus*) *paulus*. 7. Egg from the body cavity of a gravid female. 8. Posterior end and reproductive system of a female, showing the subterminal position of the gonopore.

SPECIMENS EXAMINED: *P.* (*P.*) *cylindraceus* adults: HWMLC 33443–33449, 33451, 35658, 36785 (Nebraska, New Hampshire, New York, U.S.A.); 34871, 34882 (Israel). *P.* (*P.*) *formosus* adults: USNPC 4598 (syntypes), 60023; HWMLC 30539, 30978, 30983, 30987, 31037, 33877, 33938–33941, 34480, 34652, 35005 (Colorado, Oregon, and Kansas, U.S.A.), many slides of larvae from various intermediate hosts. HWMLC 30975, 30978, 30983, 30987, 31037, 31037, 31061 labeled "*Plagiorhynchus formosus* ex. *Sturnus vulgaris,* intestine; Kansas"

were clearly misidentified and placed in the wrong genus as judged by their thin body form and small size, proboscis size and armature, and eggs; some had spiny trunks. *P.* (*P.*) *taiwanensis* adults: USNPC 60718 (paratypes). HWMLC 34124–34126 (paratypes). *P.* (*P.*) *transversus* adult: USNPC 65269.

The examined specimens provided additional data that are not included in Table 1: 1 *P.* (*P.*) *transversus* female (USNPC 65269) had hook roots that were considerably longer than the blades and eggs with concentric membranes, with no more than 5% having polar prolongation of the fertilization membrane. The position of the gonopore was obscured. The *P.* (*P.*) *formosus* specimens had proboscides with only up to 15 hooks per row. The roots of the middle proboscis hooks were longer than the blades in some specimens. Gravid females had up to 10% of their ripe eggs showing some polar prolongation of the fertilization membrane. The female gonopore was invariably and definitively subterminal. The *P.* (*P.*) *taiwanensis* specimens were robust and almost identical to *P.* (*P.*) *formosus*. Distinct differences in lemniscal length, which were used to justify the designation of *P.* (*P.*) *taiwanensis* as a separate species (Schmidt and Kuntz, 1966), were not observed in this study, in agreement with later observations by Schmidt (1981). The proboscis had only up to 15 hooks per row. The roots of the middle proboscis hooks were invariably slightly shorter than the blades. Up to 15% of the ripe eggs had some polar prolongation of the fertilization membrane. The female gonopore was definitively subterminal.

Plagiorhynchus (*Prosthorhynchus*) *malayensis* (Tubangui, 1935) Schmidt and Kuntz, 1966 (Figs. 1–5)

GENERAL: Tubangui (1935) originally described this species from 1 male specimen obtained from the gruiform bird, the banded landrail *Gallirallus* (=*Hypotaenidia*) *philippensis* Linnaeus, 1766, in Luzon, Philippines, as *Oligoterorhynchus malayensis*. It was later transferred to the genus *Prosthorhynchus* by Yamaguti (1963) because of its cylindrical proboscis. Schmidt and Kuntz (1966) redescribed the males based on 2 new specimens (USNPC 60730) collected from 2 other species of gruiform birds from Taiwan (the white-breasted water hen, *Amaurornis phoenicurus chinensis* (Boddaert, 1783) and the banded crake, *Rallina eurozonoides formosana* Seebohm, 1894) and on the original description. The female remained unknown. Eleven specimens (6 males and 5 females on 8 slides) of the same species, all from the G. D. Schmidt collection, became available for this study (10 specimens from HWMLC, 1 from USNPC). Seven of the 8 slides were dated 1965; the remaining slide (1 male specimen) was dated 1972. One of the 2 males described by Schmidt and Kuntz (1966) (USNPC 60730) was also dated 1965. The 5 female specimens in this collection were adequate for description. The 6 male specimens in the same collection also provided additional new information.

FEMALE: Trunk elongate, slender, cylindrical (Fig. 1), 11.5–18.2 ($\bar{x}$ = 15.1) mm long by 1.12–1.37 (1.23) mm wide. Proboscis cylindrical, rounded anteriorly 1.06–1.30 (1.18) mm long by 0.26–0.30 (0.28) mm wide (Fig. 4), with 19 hook rows, each with 20–21 hooks. All hooks similar in shape, except basal hooks spiniform. Hooks increasing in size posteriorly to hooks 4–8, then gradually decreasing to hooks 20, 21, reaching size of anterior hooks. Lengths of 1 row of hooks of 1 female (Figs. 1, 4, 5) from anterior 48, 53, 56, 56, 62, 62, 62, 64, 62, 62, 62, 59, 56, 56, 56, 56, 56, 53, 53, 50, 50. Roots of posterior 4 hooks in each row greatly and more progressively reduced posteriorly, well developed in all other hooks, and with anterior manubria in anterior 4–6 hooks; manubria most developed anteriorly (Fig. 5). Neck of same female 303 long by 333 wide. Proboscis receptacle 1.97–2.03 (2.00) mm long by 0.27–0.48 (0.37) mm wide. Lemnisci narrow and much longer than proboscis receptacle, 4.30–5.45 (4.74) mm long by 0.12 mm wide. Reproductive system short, robust with well-developed vagina, very short uterus, and comparatively large uterine bell, 757 long (5% of trunk length). Gonopore decidedly subterminal (Fig. 2). Eggs elongate ovoid, 53–84 (64) long by 22–31 (28) wide; external shell sculptured with elevated ridges and grooves particularly at poles, all shells concentric (Fig. 3) with less than 5% of ripe eggs showing mild to moderate polar prolongation of fertilization membrane.

FEMALE (Fig. 1): HWMLC 36329.

OTHER FEMALES: HWMLC 33878, 36327, 36328.

HOST: *Amaurornis phoenicurus* (Boddaert, 1783).

SITE OF INFECTION: Intestine.

LOCALITY: Borneo, Indonesia; Taiwan.

MALE: Trunk slender, cylindrical, 10.0–13.0 (11.5) mm long by 0.82–1.42 (1.09) mm wide. Proboscis cylindrical with rounded anterior end, 1.00–1.21 (1.11) mm long by 0.20–0.24 (0.23) mm wide. Proboscis with 16–21 longitudinal rows of 20–22 hooks each. Differences between anterior, middle, and posterior hook sizes and shape and size of roots comparable to females. Lengths of hooks from anterior 42 (42), 48–56 (52), 53–56 (54), 53–59 (56), 50–59 (54), 50–62 (57), 50–56 (54), 48–59 (54), 48–64 (57), 48–56 (53), 45–56 (52), 45–59 (53), 48–56 (53), 48–56 (53), 48–56 (53), 45–56 (51), 45–56 (50), 45–56 (51), 45–53 (49), 45–50 (47), 42–48 (45). Neck 151–242 (181) long by 212–333 (273) wide. Proboscis receptacle 1.88–2.12 (1.98) mm long by 0.30–0.42 (0.34) mm wide. Lemnisci narrow and markedly longer than proboscis receptacle, 2.36–3.33 (2.82) mm long. Testes ovoid, contiguous, at middle of trunk. Anterior testis 0.94–1.15 (1.05) mm long by 0.45–0.70 (0.52) mm wide. Posterior testis 0.91–1.88 (1.14) mm long by 0.45–0.73 (0.55) mm wide. Four tubular cement glands, 2.12–4.24 (3.14) mm long by 0.09–0.30 (0.18) mm wide; cement glands begin at posterior end of posterior testis and join into 2 cement ducts posteriorly at level of anterior end of Saefftigen's pouch, which they join at its posterior end. Saefftigen's pouch 1.21–1.36 (1.29) mm long by 0.45–0.48 (0.47) mm wide. Bursa 0.94–1.36 (1.15) mm long by 0.97–1.21 (1.09) mm wide.

SPECIMENS EXAMINED: USNPC 60730; HWMLC 33878, 36327, 36328, 36329.

Other species of the 2 *Plagiorhynchus* subgenera were studied to help with the construction of the following key. This study produced the following unexpected information, which demonstrated the wide variability within the genus *Plagiorhynchus* and provided a context against which its taxonomic complexity could be evaluated.

Plagiorhynchus (*Prosthorhynchus*) *bullocki* Schmidt and Kuntz, 1966

The specimens (5 males and 4 females from the Formosan hill partridge, *Arborophilia crudigularis* (Swinhoe, 1864) from Taiwan) were in general agreement with the original description, except that proboscis hooks numbered 17–18 in each of 14–16 longitudinal rows (instead of 16–17, 16) and most ripe eggs (at least 80%) showed mild to strong polar prolongation of the fertilization membrane (Fig. 6). Schmidt and Kuntz (1966) did not refer to a polar prolongation of the fertilization membrane, and their figure 11 shows none. The gonopore of both sexes is decidedly subterminal. The above 2 traits are in conflict with the traditional criteria for the subgenus *Prosthorhynchus* (females with subterminal gonopore and eggs with concentric shells) or the subgenus *Plagiorhynchus* (females with terminal gonopore and eggs with polar prolongation of fertilization membrane). See Remarks following.

SPECIMENS EXAMINED: HWMLC 34074, 34133.

Plagiorhynchus (*Prosthorhynchus*) *gracilis* (Petrochenko, 1958) Schmidt and Kuntz, 1966

One male from the intestine of the masked lapwing, *Vanellus miles* (Boddaert, 1783), in Tasmania was slender and somewhat robust anteriorly, with lemnisci about as long as the proboscis receptacle. The proboscis had 21 rows of more than 15 hooks each and 6 tubular cement glands. All of Petrochenko's (1958) male specimens were "wrinkled," and the resulting "corrugation" affected the "subsequent distribution of internal organs." His males had 20 proboscis hook rows, each with 16 hooks and only 3 tubular cement glands (Petrochenko, 1958, p. 182).

SPECIMEN EXAMINED: HWMLC 39385.

Plagiorhynchus (*Prosthorhynchus*) *golvani* Schmidt and Kuntz, 1966

Observations on 1 male from the intestine of a collared bush-robin, *Tarsiger* (=*Erithacus*) *johnstoniae* (Ogilvie-Grant, 1906) (Turdidae), in Taiwan were in agreement with the original description.

SPECIMEN EXAMINED: HWMLC 34299.

Plagiorhynchus (*Plagiorhynchus*) *charadrii* (Yamaguti, 1939) Van Cleave, 1951

The specimens (9 males and 12 females on 10 slides), dated 1965 to 1978 and collected from shore birds in Taiwan, Hawaii, and Tasmania, generally agreed with the descriptions of Yamaguti (1939) and Schmidt and Kuntz (1966). The proboscides had 17–18 rows of 14–15 hooks each. The gonopore was terminal in both sexes, but eggs varied considerably in size and

degree of polar prolongation of the middle membrane, if any. For example, females collected from the Kentish plover, *Charadrius alexandrinus* Deignan, 1941, and the golden plover *Pluvialis dominica* Gmelin, 1789, in Taiwan and Hawaii had eggs up to 85 × 28 and 132 × 50, respectively. These eggs mostly had a polar prolongation of the middle membrane as described by Yamaguti (1939) and Schmidt and Kuntz (1966), whose specimens' eggs measured 105–120 × 30–45. Some females from the red-capped plover, *Charadrius (Alexandrinus) ruficapillus* Temminck, 1822, in Tasmania had larger eggs, up to 168 × 67, that mostly had no visible prolongation of the fertilization membrane. In most other females examined, however, about 80% of the eggs normally had no polar prolongation. This extreme variation in the polar swelling of the fertilization membrane poses taxonomic problems and is clearly not related to egg size or maturity. It may be associated with host species or with unknown geographical factors.

SPECIMENS EXAMINED: HWMLC 34128, 34747, 39347, 39374.

Plagiorhynchus (*Plagiorhynchus*) *paulus* Van Cleave and Williams, 1951

Measurements of 2 males and 2 females from the varied thrush, *Zoothera* (=*Ixoreus*) *naevius* (Gmelin, 1784), in the State of Washington, U.S.A., did not agree with the original description. For example, testes were longer (anterior 0.848 × 0.364 mm, posterior 0.666 × 0.364 mm), proboscis receptacle 1.060 × 0.212 mm in 1 male and 1.394 × 0.273 mm in 1 female, cement glands 0.697 × 0.106 mm to 1.515 × 0.121 mm and eggs 50–76 (66) × 14–28 (19) (n = 8). A few (5–10%) of the eggs showed no polar prolongation of the fertilization membrane, but most did (Fig. 7). The female gonopore was, however, not terminal as would be expected in a species placed in *Plagiorhynchus*. The female gonopore was actually subterminal (Fig. 8). No reference to the position of the female gonopore was made in the original description (Van Cleave and Williams, 1951) or in subsequent accounts by other authors (e.g., Petrochenko, 1958). Based on this character alone, this species would be assigned to *Prosthorhynchus*. However, the polar prolongation of the egg fertilization membrane, among other factors discussed below, further complicates the issue. No reassignment is made at this time.

SPECIMEN EXAMINED: HWMLC 34333.

Inclusion of species in the key

Amin (1985) listed 19 species in the subgenus *Prosthorhynchus,* and Golvan (1994) listed 27, while Hoklova (1986) listed 11 species from land vertebrates. Part of this discrepancy is because of synonyms not acknowledged by Golvan (1994) or Hoklova (1986) and hence not included in the key. The following species are not recognized as valid: *P.* (*P.*) *formosus, P.* (*P.*) *taiwanensis,* and *P.* (*P.*) *transversus* (synonyms of *P.* (*P.*) *cylindraceus*, see this paper; Schmidt, 1981; Amin, 1985). Other synonyms of *P.* (*P.*) *cylindraceus* noted by Golvan (1994) are *P.* (*P.*) *rosai* (Porta, 1910) Meyer, 1932, and *P.* (*P.*) *upupae* Lopez-Neyra, 1946. *Rhadinorhynchus asturi* Gupta and Lata, 1967, was erroneously named *Prosthorhynchus asturi* by Golvan (1994); this species, with a spinose trunk, is clearly a rhadinorhynchid. Golvan (1956) proposed other synonymies that he later retracted (Golvan, 1994). *Plagiorhynchus* (*Prosthorhynchus*) *pupa* (von Linstow, 1905) Meyer, 1931, is a synonym of *Polymorphus pupa* (von Linstow, 1905) Kostylev, 1922 (see Amin, 1992). Golvan (1994) removed *Prosthorhynchus* (*Prosthorhynchus*) *limnobaeni* Tubangui, 1933, to the subgenus *Plagiorhynchus* despite the fact that this species is known from only 2 males. This reassignment to *Plagiorhynchus* is unjustified, and the species is retained in the subgenus *Prosthorhynchus*. It is not, however, included in the key because of controversy regarding the only usable diagnostic trait, the proboscis armature. Tubangui (1933) indicated that proboscis hooks are "in forty-three alternating anteroposterior rows of eight hooks each," but his Plate 5, Figure 1 shows a proboscis with about 18–20 longitudinal rows, each with 30 hooks. Golvan (1956) accepted the 43 × 8 formula and Petrochenko (1958, after Meyer, 1932–1933) indicated 16 longitudinal rows of 17 hooks each. Yamaguti (1963) quoted both figures, 43 × 8 and 16 × 17. Both Petrochenko (1958) and Yamaguti (1963) retained the species in *Prosthorhynchus* as originally described. Golvan (1956, 1994) synonymized *P.* (*Prosthorhynchus*) *rectus* Sphern, 1942 *nec* Linton, 1892, with "*Prosthorhynchus schmidti* nom. nov." This entity, originally described as *Echinorhynchus rectus*

Linton, 1892, was declared incertae sedis by Schmidt and Kuntz (1966) and is not recognized here. Golvan (1956, 1994) removed *P. (Prosthorhynchus) reticulatus* (Westrumb, 1821) Schmidt and Kuntz, 1966, to the subgenus *Plagiorhynchus* without any justification. The reassignment is not accepted, and the species is included in the key. *Plagiorhynchus (Prosthorhynchus) rostratum* (de Marval, 1902) Meyer, 1932, was considered incertae sedis by Amin (1985) and is not included in the key. Golvan (1994) also listed "*Prosthorhynchus luehei* Travassos, 1916" (=*Echinorhynchus spirula* Rudolphi, 1819; *E. spirula* Linstow, 1878, 1897; *Gigantorhynchus spirula* Porta, 1908, 1909; *Prosthenorchis luhei* Travassos, 1916; *Prosthorhynchus spiralis* (Rudolphi, 1809) Schmidt and Kuntz, 1966). The species is considered incertae sedis (Schmidt and Kuntz, 1966) and is not included in the key because its inadequate description does not allow its placement in either of the 2 subgenera of *Plagiorhynchus.* Another species, *Plagiorhynchus kuntzi* Gupta and Fatma, 1988, is not included in the key because it is not assignable to either subgenus. The position of the female gonopore was described as "terminal or subterminal"; the description was based on only 1 female and 1 male (Gupta and Fatma, 1988). Petrochenko (1958) and Yamaguti (1963) listed 22 and 21 species of *Prosthorhynchus,* respectively, but the taxonomic status and assignment of many of these species also has been changed since.

Based on the above account, 21 species are considered valid and are included in the following key. Petrochenko's (1958) key is outdated and did not include newer taxa and recent concepts as outlined in our present work. The shorter key by Hoklova (1986) addressed only species from the former U.S.S.R., some of which are synonyms.

Key to Species of the Subgenus *Prosthorhynchus*

1. Proboscis with 30 rows of hooks; eggs small (40 × 20); trunk pigmented ..... *P. (P.) pigmentatus* (Marval, 1902) Meyer, 1932
   Proboscis with 8–21 rows of hooks; eggs larger; trunk not pigmented 2
2. All proboscis hooks of almost uniform size (50–54 long), with rectangular well-developed roots ..... *P. (P.) limnobaeni* (Tubangui, 1933) Golvan, 1956
   Posterior 1–8 hooks smaller, spine-like, with underdeveloped, rudimentary, or no roots .. 3
3. Proboscis with 7–8 spine-like hooks posteriorly 4
   Proboscis with 1–7 spine-like hooks posteriorly 5
4. Spine-like hooks rootless ..... *P. (P.) varispinus,* Wang 1966
   Spine-like hooks with laterally split roots and manubrium ..... *P. (P.) golvani* Schmidt and Kuntz, 1966
5. Proboscis with 5–7 rootless spine-like hooks ..... *P. (P.) bullocki* Schmidt and Kuntz, 1966
   Proboscis with 1–4 spine-like hooks 6
6. Proboscis with 3–4 spine-like hooks having greatly reduced but definite roots ..... *P. (P.) malayensis* (Tubangui, 1935) Schmidt and Kuntz, 1966
   Proboscis with 1–3 spine-like hooks having underdeveloped, rudimentary, or no roots .. 7
7. Adults very long (males 45 mm, females 60 mm) ..... *P. (P.) scolopacidis* (Kostylev, 1915) Schmidt and Kuntz, 1966
   Adults shorter (males up to 30 mm, females up to 40 mm long) 8
8. Eggs large, 125–130 × 45–50 ..... *P. (P.) pittarum* (Tubangui, 1935) Schmidt and Kuntz, 1966
   Eggs smaller than 125–130 × 45–50 9
9. Proboscis with 8 rows of hooks, posterior hooks with very short roots; most eggs with polar prolongation of fertilization membrane ..... *P. (P.) russelli* (Tadros, 1970) Golvan, 1994
   Proboscis with 14 or more rows of hooks, posterior hooks with greatly reduced, rudimentary, or no roots; most eggs with concentric shells 10
10. Vaginal sphincter strongly developed on 1 side ..... *P. (P.) asymmetricus* Belopolskaja, 1983
    Vaginal sphincter symmetrical 11
11. Lemnisci considerably shorter than proboscis receptacle; proboscis with 18 rows, each with 20 hooks ..... *P. (P.) angerense* (Travassos, 1926) Schmidt and Kuntz, 1966
    Lemnisci slightly or considerably longer than proboscis receptacle; proboscis with 14–20 rows, each with 10–22 hooks 12
12. Ventral surface of female gonopore with elevated papilla ..... *P. (P.) genitopapillosus* Lundstrom, 1942
    No papilla at female gonopore 13
13. Proboscis small, 640–770 × 190–230, with 18 rows of hooks ..... *P. (P.) ogati* (Fukui and Morisita, 1936) Schmidt and Kuntz, 1966
    Proboscis larger, with 14–20 rows of hooks 14
14. Proboscis less than 1.0 mm long 15
    Proboscis 1.0 mm long, or longer 16
15. Proboscis 800–900 × 200 with 16–18 rows of 15–18 hooks each, hooks very small, middle and posterior hooks 23 and 4 long; females 17 mm long; eggs 70 × 10 ..... *P. (P.) rheae* (Marval, 1902) Schmidt and Kuntz, 1966
    Proboscis 957 × 65 with 16–18 rows of 20–22 hooks each, middle and posterior hooks

39 and 13 long; females 4.6 mm long; eggs 44–46 × 26–28 ..... *P. (P.) rossicus* (Kostylev, 1915) Schmidt and Kuntz, 1966

16. Proboscis consistently longer than 1.0 mm ... 17
Proboscis length averaging about 1.0 mm 20
17. Proboscis with 18–20 rows of hooks 18
Proboscis with 14–16 rows of hooks 19
18. Proboscis 1.25–1.44 × 0.33 mm with 18–20 rows of 15 hooks each, middle hooks 58–59 long, posterior 3 hooks rootless ..... *P. (P.) gallinagi* (Schachtachtinskaia, 1953) Schmidt and Kuntz, 1966

Proboscis 1.18 × 0.260–0.033 mm with 20 rows of 16 hooks each, middle hooks 71–77 long, posterior 3 hooks with underdeveloped but definite roots ..... *P. (P.) gracilis* (Petrochenko, 1958) Schmidt and Kuntz, 1966

19. Proboscis 1.0–1.3 mm long with 16–17 hooks per row, 1–3 basal hooks with broadened base but no definite root; females 12–15 mm long; eggs 80 × 40 ..... *P. (P.) reticulatus* (Westrumb, 1821) Golvan, 1956

Proboscis 1.1 × 0.3 mm with 14–15 hooks per row, posterior hooks spiniform and rootless; females 7.0–8.5 mm long; eggs 70 × 35 .... *P. (P.) nicobarensis* (Soota and Kansal, 1970) Zafar and Farooqi, 1981

20. Proboscis 0.96–1.1 × 0.19–0.22 mm with 20 rows of 19–20 hooks each, most posterior hooks rootless; proboscis receptacle 1.8 mm long; males 7 × 1.1 mm, females 8 × 1.1 mm ..... *P. (P.) longirostris* (Travassos, 1927) Amin, 1985

Proboscis 0.8–1.3 × 0.2–0.36 mm with 14–20 (usually 14–18) rows of 10–18 (usually 13–18) hooks each, posterior 1–3 spiniform hooks with greatly reduced or no roots; proboscis receptacle 2.0–2.5 mm long; males 4.5–30 × 0.6–2.4 mm, females 5–40 × 0.4–3.2 mm ..... *P. (P.) cylindraceus* (Goeze, 1782) Schmidt and Kuntz, 1966

Remarks

Plagiorhynchinae was established by Meyer (1931) as a subfamily of Polymorphidae, within which he included the genera *Plagiorhynchus* Lühe, 1911, and *Prosthorhynchus* Kostylew 1915, as well as *Sphaerechinorhynchus* Johnston and Deland, 1929, and *Porrorchis* Fukui, 1929. Golvan (1956, 1960) erected 2 new subfamilies, Porrorchinae and Sphaerechinorhynchinae, to accommodate forms with short spheroid proboscides. This left only 2 genera, *Plagiorhynchus* and *Prosthorhynchus,* in the Plagiorhynchinae. Petrochenko (1956) established the family Prosthorhynchidae to contain *Prosthorhynchus,* among other genera, that infect terrestrial vertebrates as adults and terrestrial insects as larvae and that have eggs with concentric shells and no polar prolongations. Yamaguti (1963) placed Plagiorhynchidae Golvan, 1960 emend. in Echinorhynchidea Southwell and Macfie, 1925, in which adult and larval worms infected aquatic vertebrates and crustaceans, respectively, and eggs had a polar prolongation of the middle membrane. Schmidt and Kuntz (1966) synonymized *Prosthorhynchus* with *Plagiorhynchus* and reduced the 2 genera to subgenera of the genus *Plagiorhynchus* s. lat. Schmidt and Kuntz (1966) observed that the only 2 consistent morphological differences between the 2 taxa, the position of the female genital pore and the presence or absence of polar swelling in the egg fertilization membrane, were "not invariable." Amin (1982, 1985) accepted Schmidt and Kuntz's (1966) classification, and additional documentation was produced by this study. Hoklova (1986) and Golvan (1994), however, preferred to retain the original independent status of the 2 genera in Polymorphidae.

In the present work, an examination of many specimens and a review of relevant literature provided additional documentation and justification of Schmidt and Kuntz's (1966) decision to reduce *Plagiorhynchus* s. str. and *Prosthorhynchus* to subgenera of the genus *Plagiorhynchus* s. lat. All characteristics examined were found to vary considerably within each taxon, and to overlap between the 2 taxa. Characters found with some degree of variation and with very little but evident overlap include hosts, egg membranes, and female gonopore. Species of the subgenus *Plagiorhynchus* s. str. normally infect shore and aquatic arthropods (crustaceans and insects) as larvae, have a terminal gonopore in the female, and have eggs with polar prolongation of the fertilization membrane. Species of subgenus *Prosthorhynchus* normally infect terrestrial birds and occasionally mammals as adults and terrestrial arthropods as larvae, have a subterminal gonopore in the female, and have eggs with concentric shells showing no prolongation of any membrane. Despite Golvan's (1994) assertions and Hoklova's (1986) reservations, we have found exceptions to each of these 3 more stable characteristics, constituting an overlap between the concept of *Plagiorhynchus* s. str. and that of *Prosthorhynchus.* Our *P. (Prosthorhynchus) cylindraceus* specimens from South Africa were collected from 5 species of shore birds, suggesting an aquatic life cycle in the definitive and intermediate hosts. The same specimens and many others reported as syno-

nyms of the same species included females having up to 15% of their eggs with polar prolongation of the fertilization membrane. Most eggs (at least 80%) of the *P.* (*Prosthorhynchus*) *bullocki* female specimens examined also had polar prolongation of the fertilization membrane. Females of *P.* (*Prosthorhynchus*) *bullocki* have a definite subterminal gonopore; thus, this taxon remains in limbo between the 2 subgenera. Similarly, females of *P.* (*Plagiorhynchus*) *paulus* with eggs mostly having prolongation of the fertilization membrane have a subterminal gonopore. Because the eggs vary in size, shape, and the presence and degree of polar prolongation and because host ecological parameters are not consistent within each subgenus, the position of the female gonopore becomes the only remaining reliable trait distinguishing the 2 subgenera. Examples of the limitations to sole use of this characteristic include that of *P.* (*P.*) *paulus* and the fact that males cannot be keyed out. Variability within and between the 2 subgenera in all 3 characteristics (host, female gonopore, eggs) should be considered in toto while considering the limitations inherent in each.

Despite the above documented variations and limitations, no new subgeneric diagnoses are given or believed necessary; those provided by Schmidt and Kuntz (1966) are considered adequate.

Literature Cited

Amin, O. M. 1982. Acanthocephala. Pages 933–941 *in* S. P. Parker, ed. Synopsis and Classification of Living Organisms. McGraw-Hill Book Company, New York.

———. 1985. Classification. Pages 27–72 *in* D. W. T. Crompton and B. B. Nickol, eds. Biology of the Acanthocephala. Cambridge University Press, London.

———. 1992. Review of the genus *Polymorphus* Lühe, 1911 (Acanthocephala: Polymorphidae), with the synonymization of *Hexaglandula* Petrochenko, 1950, and *Subcorynozoma* Hoklova, 1967, and a key to the species. Qatar University Science Journal 12:115–123.

Golvan, Y. J. 1956. Acanthocèphales d'oiseaux. Troisième note. Revision des espèces Européennes de la sous-famille de Plagiorhynchinae A. Meyer 1931 (Polymorphidae). Annales de Parasitologie Humaine et Comparée 31:351–384.

———. 1960. Le phylum des Acanthocephala. Troisième note. La classe de Palaeacanthocephala (Meyer 1931). Annales de Parasitologie Humaine et Comparée 35:350–386.

———. 1994. Nomenclature of the Acanthocephala. Research and Reviews in Parasitology 54:35–205.

Gupta, V. and S. Fatma. 1988. On four acanthocephalan parasites of vertebrates from Uttar Pradesh and Tamil Nadu. Indian Journal of Helminthology (1987) 39:128–142.

Hoklova, I. G. 1986. The Acanthocephalan Fauna of Terrestial Vertebrates of S.S.S.R. Nauka Press, Moscow. 276 pp.

Meyer, A. 1931. Neue Acanthocephalen aus dem Berliner Museum. Begrundung eines neuen Acanthocephalensystems auf Grund einer Untersuchung der Berliner Sammlung. Zoologische Jahrbucher, Abteilung für Systematik, Ökologie und Geographie der Tiere 62:53–108.

———. 1932–1933. Acanthocephala. Pages 1–582 *in* Dr. H. G. Bronn's Klassen und Ordnungen des Tier-Reichs. Vol. 4. Akademisch Verlagsgesellschaft MBH, Leipzig.

Petrochenko, V. I. 1956. Acanthocephala of Domestic and Wild Animals. Vol. 1. Izdatel'stvo Academii Nauk S.S.S.R., Moscow. 465 pp. (English translation by Israel Program for Scientific Translations Ltd., 1971)

———. 1958. Acanthocephala of Domestic and Wild Animals. Vol. 2. Izdatel'stvo Akademii Nauk S.S.S.R., Moscow. 478 pp. (English translation by Israel Program for Scientific Translations Ltd., 1971)

Schmidt, G. D. 1981. *Plagiorhynchus formosus* Van Cleave, 1918, a synonym of *Plagiorhynchus cylindraceus* (Goeze, 1782) Schmidt and Kuntz, 1966. Journal of Parasitology 67:597–598.

———, **and R. E. Kuntz.** 1966. New and little-known plagiorhynchid Acanthocephala from Taiwan and the Pescadores Islands. Journal of Parasitology 52: 520–527.

———, **and O. W. Olsen.** 1964. Life cycle and development of *Prosthorhynchus formosus* (Van Cleave, 1918) Travassos, 1926, an acanthocephalan parasite of birds. Journal of Parasitology 50: 721–730.

Tubangui, M. A. 1933. Notes on Acanthocephala in the Philippines. Philippine Journal of Science 50: 115–128, 6 plates.

———. 1935. Additional notes on Philippine Acanthocephala. Philippine Journal of Science 56:13–17, 2 plates.

Van Cleave, H. J. 1918. The Acanthocephala of North American birds. Transactions of the American Microscopical Society 37:19–47.

———. 1942. A reconsideration of *Plagiorhynchus formosus* and observations of Acanthocephala with atypical lemnisci. Transactions of the American Microscopical Society 61:206–210.

Yamaguti, S. 1939. Studies on the helminth fauna of Japan. Part 29. Acanthocephala, II. Japanese Journal of Zoology 13:317–351.

———. 1963. Systema Helminthum. Vol. 5. Acanthocephala. Interscience Publishers, New York. 423 pp.