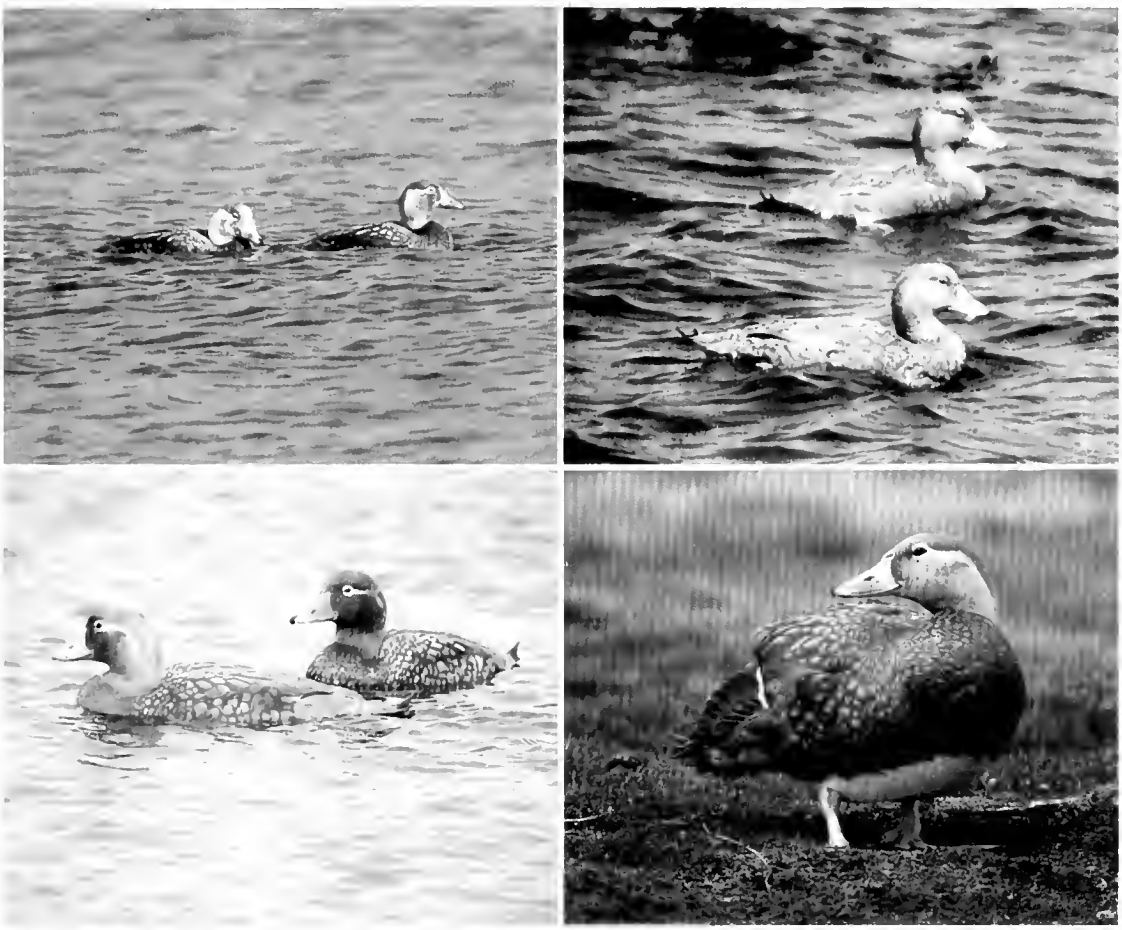
Taxonomy and Identification of

STEAMER-DUCKS

(Anatidae: *Tachyeres*)



Bradley C. Livezey and Philip S. Humphrey

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Front Cover. The four species of Steamer-ducks as follows. Upper left. White-headed Flightless Steamer-ducks (Photograph by R. Straneck); Upper right. Magellanic Flightless Steamer-ducks (Photograph by D. Zimmerman); Lower left. Falkland Flightless Steamer-ducks (Photograph by B. C. Livezey); and Lower right. Flying Steamer-duck (Photograph by G. L. Vaechterlein).

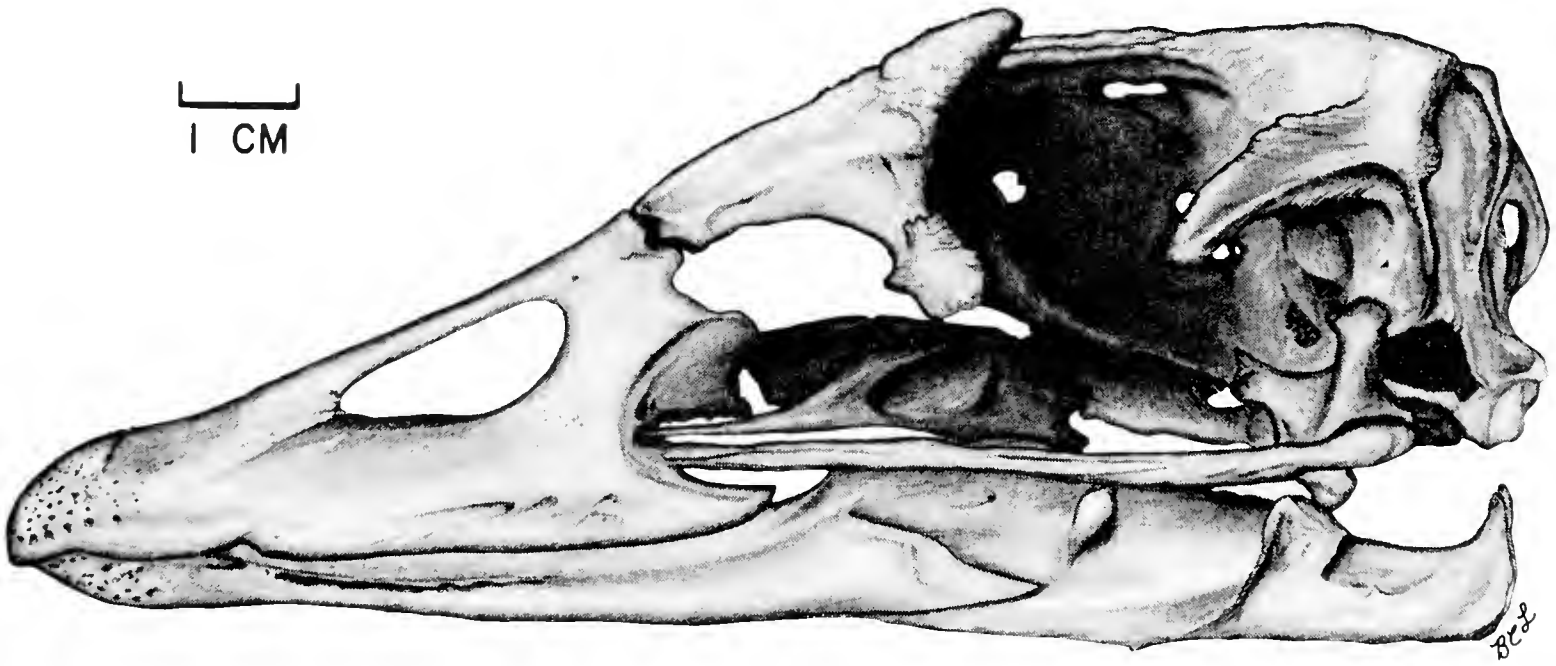

Fig. 1. Skull of male *Tachyeres pteneres* (KU 79842), lateral view.

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INTRODUCTION

During our ten-year study of the steamer-ducks (*Tachyeres*), a moderately specialized South American genus of shelducks (Tadorninae: Livezey 1986a), our primary interests have been the morphological bases and adaptive significance of flightlessness, geographic variation, sexual dimorphism, and phylogenetic relationships of the four species. As these investigations progressed, however, it became apparent that basic taxonomic issues, including alpha-taxonomy and the designation of types, and the data and techniques associated with identification of specimens, required attention. Taxonomic difficulties have plagued the study of steamer-ducks since their discovery in the late sixteenth century, and certain of the present-day problems in systematics of the genus have their origins in this history of controversy. This state of affairs is in part due to the three most salient characteristics of the genus *Tachyeres*: (1) large size, which exacerbated the difficulties of collection and study of specimens; (2) widespread flightlessness, an often conspicuous characteristic that principally created taxonomic confusion; and (3) drab gray-and-white plumage, which offered few clues to the recognition and diagnosis of species. The taxonomy of *Tachyeres* also has been prone to oversimplification ("lumping of species"), apparently because of the traditional view that species of waterfowl should be readily distinguishable using plumage characters, even under field conditions.

The present paper has six major objectives: (1) to present a history of the study of the genus, which in turn will provide an insight into the complicated taxonomy that has been applied to its members; (2) to provide generic and specific synonymies and species accounts; (3) to present the available information on the molts and plumages of *Tachyeres*; (4) to compare the diagnostic characters of the four species and to construct keys to the identification of specimens; (5) to summarize information on field identification and aviculture of steamer-ducks; and (6) to present a subject-indexed bibliography of the considerable but scattered literature on steamer-ducks. Our hope is that the work will enable ornithologists, some of whom have shared with us their concerns, to identify steamer-ducks in the hand and (under good conditions) in the field. Should this endeavor prove successful, we anticipate that these unique birds will receive the continuing study that they deserve.

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M. Sallaberry A., A. Veloso, J. Ballasteros C., and the Gibson Family. Specimens were made available by the Field Museum of Natural History (Chicago), British Museum of Natural History (Tring), American Museum of Natural History (New York), San Diego Museum of Natural History, Peabody Museum of Natural History (Yale University), Museum of Comparative Zoology (Harvard University), Museum of Zoology (University of Michigan), and U. S. National Museum of Natural History. R. Straneck (Laboratorio de Sonidos Naturales, Museo Argentino de Ciencias Naturales, Buenos Aires) provided field recordings of vocalizations of steamer-ducks, and J. W. Hardy (Florida State Museum, Gainesville) prepared sonograms of selected recordings. Unpublished observations of steamer-ducks incorporated into the distribution maps were provided by P. Canevari, J. C. Chebez, X. Ferrer, O. Kühnemann, T. Narosky, M. Nores, and R. Straneck. We also thank R. Mengel, M. Jenkinson, and their colleagues for preparation of specimens; P. Rasmussen for executing Figure 9; and K. McManness, K. Corbin, and M. Schmalz for typing.

METHODOLOGICAL NOTES

Specimens

Much of our work on steamer-ducks has been based on observations made and specimens collected during our field work. We made five trips during 1979–84 (the first with Max C. Thompson), gained first-hand experience with all four species of Tachyeres, and for all but *T. leucocephalus* we studied each at several localities. By species and locality, these were: *T. patachonicus*—Puerto Melo, Lago Fontana, and lagos Futalaufquen and Krügger, Chubut, Argentina; Puerto Deseado, Lago Argentino, and lagos in Parque Nacional Perito Moreno, Santa Cruz, Argentina; Ushuaia and Lapataia, Tierra del Fuego, Argentina; Bahía de Ancud, and nearby lagos Llanquihue and Rupanco, Region X, Chile; *T. brachypterus*—Lively Island and Port Stanley, Falkland Islands; *T. leucocephalus*—Puerto Melo, Chubut, Argentina; *T. pteneres*—Ushuaia and Lapataia, Tierra del Fuego, Argentina; and Bahía de Ancud, Chile. These specimens and associated data were augmented by specimens studied at other institutions, which contributed greatly to the localities represented. A complete listing of the specimens examined is given in a later section.

Molts and Plumages

Description of plumage patterns used the color scheme of Palmer (1962). Downy young were assigned to age classes using standard criteria detailed in Humphrey and Livezey (1985:945).

Measurements

Masses were measured within 12 hours of collection of the birds using spring scales. Most skin measurements used are standard (Baldwin *et al.* 1931), although a few comments are needed. Sample sizes for tail lengths are comparatively small because we collected this datum only in the latter half of the field work, and because of a relatively high frequency of specimens with worn or missing rectrices. Lamellar counts were the total number of lamellae (regardless of size) on one side of the upper bill of a fresh bird; counts in dried skins may not be reliable because of reduced visibility and shrinkage of lamellae. Wing areas were estimated by doubling the area (using planimeter) of the tracing of an extended wing.

Skeletal measurements are largely self-explanatory, but a few warrant description. These include some of the skull measurements: cranial height maximal distance from dorsal surface to ventral surface of braincase; cranial length—distance along midline from frontonasal suture to posterior of braincase; postorbital width—maximal width of cranium, measured on the lateral processes of quadratojugal bones; antorbital width maximal distance across the antorbital processes of the lacrymal bones; frontonasal width—distance across rostrum at frontonasal suture; skeletal height, length, and width of bill—measured as on skin but base of bill defined as frontonasal suture. Head width of the humerus is the maximal breadth of the element at its proximal end. Head

width of the femur is the width of the proximal end with the head of the bone oriented perpendicularly to the caliper surface. Tibiotarsus length includes that of cnemial crest. Least widths at midpoints (LWMs) were measured on six major limb elements.

Osteological nomenclature follows Baumel *et al.* (1979) with alternate terminology of Howard (1929) given in parentheses.

Statistical Analyses

Univariate comparisons were made using two-way analysis of variance (ANOVA). Except for masses, areas, and ratios, which were log-transformed for analysis, all statistics were based on raw data.

Discriminant functions and canonical analyses were used to contrast species using suites of measurements (Pimentel 1979). Analyses were performed on raw data; analyses based on log-transformed (base *e*) data produced virtually identical results and affected no inferences or interpretations. For multivariate analyses of skeletons, we used a program for estimation of data missing because of bilateral breakage or deformity; these estimates composed less than 1% of any data set analyzed.

All programs used were part of the Biomedical Computer Programs (Dixon 1988).

ORNITHOLOGICAL HISTORY OF THE STEAMER-DUCKS

Early Descriptions

In 1582, Pedro Sarmiento de Gamboa observed an unfamiliar duck in the Straits of Magellan, which inspired the following description (1895:53; translation of Sarmiento de Gamboa 1768): "In the water they cannot rise but by their feet, using their pinions as oars. They thus go through the water with great velocity, and they leave a track like that of a boat when propelled by oars. Their velocity is so great that a good boat under sail, with a fair wind, cannot overtake them." Eighteen years later in the Straits, O. Van Noort (1926:48) noted as common a flightless "goose" in Goose Bay. During passage of Captain Wood through the Straits in 1669, Hacke (1699:60) observed "...great Blue-Ducks, which are not very shy."

A number of subsequent voyagers to the Straits and the Falkland Islands wrote of these large waterfowl and their characteristic, spray-producing method of surface locomotion, most referring to them as "race-horses" or "loggerheads" (Pernety 1769:570; Byron 1773:50; Hawkesworth 1773:411–412; Penrose 1775:35; Clayton 1774:40, 1776:104; Cook 1777:186, 1778:27; Elliott and Pickersgill 1984:39). Whether the name "loggerhead" was based on the physical appearance of the birds or their pugnacious behavior is not clear. Byron (1773:50–51) described them as "...a bird much larger than a goose, which we called the racehorse, from the velocity with which it moved upon the surface of the water, in a sort of half flying, half running motion." Most early accounts were distinctly culinary in perspective. Penrose (1775:35–36) wrote: "One kind of duck however we had, which was by no means a delicacy; we called it the loggerhead, for an obvious reason; and it seemed to be a large species of the Muscovy [*Cairina moschata*] sort, only its wings resembled those of the penguin; as these ducks...were utterly unable to fly, our method was to drive a large team of them together into some defile, and then to knock down as many as we had occasion for. The use we put their flesh to was to boil it well in the copper, and then to give it to our pigs,...and though this mode of fattening may appear rather indelicate to some people, yet it is astonishing how the hogs thrived with it." Clayton (1776:104) reported similar exploits: "But here is a species of ducks, called the loggerhead, from its large head. They have short wings, are unable to fly, and only swim and flap along on the water at an extraordinary rate. When driven ashore with boats they run fast, but soon squat down and are easily caught; they are eatable, but are but indifferent food; they are of a dark brown dirty colour." Cook (1777:186) also described the locomotor behavior of the birds: "Here is a kind of duck, called by our people race-horses, on account of the great swiftness with which they run on the water; for they cannot fly,

the wings being too short to support the body in the air." Cook, evidently without the benefit of personal experience, was less critical of the palatability of the ducks, writing (p. 205): "We shot some [race-horses], and found them to weigh twenty-nine or thirty pounds; those who eat of them said they were very good."

Molina (1782:239) may have referred to this duck (known locally as the "quethu") from Chiloe Island (Chile). Murphy (1936) justifiably doubted the relevance of the binomial name used by Molina (*Diomedea chilocusis*), one based on an inadequate description and suggesting a relationship with the tubenoses (Procellariiformes). The authors of two of the earliest global faunal compilations referred to the bird only by the vernacular names used by voyaging naturalists (Latham 1785:439; Buffon 1798:159). Beginning with naming of the "loggerhead" as *Anas cinerea* by Gmelin (1788:506), a species name later rejected as unavailable by Murphy (1936), the species, as then construed, was given six different binomial names before its monotypy was questioned. Latham (1790:834) applied the first species name to be found available by later taxonomists—*Anas brachyptera*.

King (1828:100) initially named specimens of the group as *Oidemia patachonica*, describing the birds as forty inches long, predominantly gray with white specula and abdomens, having yellow-orange bills with black nails, yellow legs, and wings with a blunt spur at the bend. King (1831:15) later distinguished another species, *Micropterus patachonicus*, that was more red-colored on the throat and scapulars, had a greenish-black bill, and was smaller than its congener *M. brachyptero* [*sic*], evidently referring to *Anas brachyptera* Latham (1790:834), mentioned by Quoy and Gaimard (1824:347). King (1839:36) was not enthusiastic about their palatability, writing: "The flavor of their flesh is so strong and fishy, that at first we killed them solely for specimens. Five or six months, however, on salt provisions taught many to think such food palatable, and the seamen never lost an opportunity of eating them. I have preferred these ducks to salt beef, as a preventive against scurvy rather than from liking their taste." King (1839:542) also clarified the taxonomic distinction, listing *Oidemia patachonica* as a synonym for flightless *Micropterus brachypterus*, and added to his description of the smaller species (*M. patachonicus*) its ability to fly. The reapplication of the name *patachonicus* to the two species recognized by King, an action with important nomenclatural implications (Livezey 1989b), evidently stemmed from his partiality to a name appropriate for a bird "Patagonian in stature...as well as in station..." (King 1828:100). This taxonomic decision marked the beginning of a century-long ornithological controversy concerning the existence of both flying and flightless species of steamer-duck, so named by King (1839:35) because of their resemblance to paddle-wheel steamships when "steaming" across the water surface.

Flighted and Flightless Species

During the period from 1830 to 1861, most naturalists, some familiar with steamer-ducks in the field, mentioned only the flightless taxon in their works (Darwin 1839a:190, 1839b:257; Gray 1840:74, 1849:623; Forster 1844:338; Gray 1844:140; Gould 1841:136, 1859:96; Strickland 1841:39; Hartlaub 1846:19; Des Murs 1847:457; Lichtenstein 1854:100; Boeck 1855:511; Bonaparte 1856:651; Germain 1860:315; Sclater 1860:389, 1861a:367). Eyton (1838:144) listed both species, but stated, without reference: "Both are destitute of the powers of flight, merely using their wings to flapper over the surface of the sea." He also admitted to having "considerable doubts" as to the validity of recognizing two species. Darwin (1839a:257–258) observed steamer-ducks in the Falkland Islands during his voyage on the 'Beagle' and wrote: "In these islands a great loggerheaded duck or goose (*Anas brachyptera*), which sometimes weighs twenty-two pounds, is very abundant. These birds were in former days called, from their extraordinary manner of paddling and splashing upon the water, race-horses; but now they are named, much more appropriately, steamers. Their wings are too small and weak to allow of flight, but by their aid, partly swimming and partly flapping the surface of the water, they move very quickly. The manner is something like that by which the common house-duck escapes

when pursued by a dog; but I am nearly sure that the steamer moves its wings alternately, instead of both together, as in other birds. These clumsy, loggerheaded ducks make such a noise and splashing, that the effect is exceedingly curious....The steamer is able to dive only to a very short distance. It feeds entirely on shell-fish from the kelp and tidal rocks; hence the beak and head, for the purpose of breaking them, are surprisingly heavy and strong; the head is so strong [see Fig. 1] that I have scarcely been able to fracture it with my geological hammer; and all our sportsmen soon discovered how tenacious these birds were of life." Two decades later, in *The Origin of Species*, Darwin (1859:206) described the "logger-headed duck (*Micropterus* of Eyton)" as using their wings "solely as flappers," implying that all steamer-ducks were flightless.

However, Abbott (1861:162) defended the specific distinction between flying and flightless steamer-ducks made by King (1831:15), based on experience with both forms in the Falkland Islands. This prompted at least one brief, if apologetic, mention by Sclater (1861b:46) that there might be two species of steamer-duck. Abbott (1861:162) also reported a nest of the flying species, an observation that was to be disregarded by most subsequent workers. Cox (1863:174, 235) added to this evidence through his observations of flightless steamer-ducks on the seacoast and numerous flying steamer-ducks on freshwater lakes, but did not distinguish the forms taxonomically.

In the summer of 1866, A. Newton persuaded R. O. Cunningham, during his forthcoming trip to the Straits, to ascertain whether or not two species of steamer-duck existed (Cunningham 1871a:493). During the trip, Cunningham (1868a:127; 1868b:491) observed that some individuals of *Micropterus cinereus* could fly whereas the heavy weight of others precluded flight. However, mention of flighted steamer-ducks was conspicuously absent from most other published discussions of the genus for the next eight years (Pelzeln 1865:139; Schlegel 1866:13, 118; 1872:274; Sclater 1867:335, 340; 1868:529; Giglioli 1868:498; Philippi 1868:283, 309; Sclater and Salvin 1868:189; 1870:499; Gray 1871:88).

Ultimately Cunningham (1871a:493–494; 1871b:94–95; 1871c:262) postulated that there was only one species of steamer-duck, and that flying individuals were but adolescents that with maturity would become too heavy for flight. Cunningham based this conclusion on the relative ossification of eight specimens: two partial skeletons and two crania of "adult" (presumably flightless) individuals; two skeletons of "immature" flying birds; and two crania of unfledged young. He noted that his specimens of "adult" birds were gray with orange-yellow bills, whereas "younger" birds (his *patachonicus*) were smaller, more red-colored on the throat and scapulars, and had greenish-black bills. Cunningham (1871a:493–494) concluded from an examination of this material: "My principal reasons for this conclusion are, that the flying and flightless birds associate together, that the former are smaller in size than the latter, and that I have invariably found the skeletons of the volant individuals to present unequivocal traces of immaturity, while, on the other hand, those of the non-volant were constantly found to be fully ossified. I believe, therefore, that as the bird increases in size and weight, owing to the deposition of an increased amount of mineral matter in the bones and various other causes, it gradually abandons the habit of flight, finding that the speed with which it can progress through the water by means of the rapid movements of its wings, together with its diving-powers, are sufficient to preserve it from threatened danger." However, even Cunningham unintentionally revealed some lingering doubts, or at least confusion. In a description of the sternum of flightless steamer-ducks he (1871a:498) wrote: "...In *adult species* the posterior border is more deeply excavated than in adolescent (flying) birds [emphasis added]."

The hypothesis proposed by Cunningham was received fairly well, (Sclater and Salvin 1876:403, 1878:437; Sclater 1881:107, 108; Vinciguerra 1883:58; Sharpe 1891:309; Martens 1900:25; Evans 1909:121), although thereafter until the early 1900's most proponents of his one-species hypothesis did not cite his explanation, but simply continued to exclude mention of the flying form from their works (e.g., Thomson 1877:205; Spry 1879:293; Reichenow 1882a:48; Hyades 1883:1343; Tristram 1889:47; Moseley 1892:480;

Lataste 1893:122; Gadow 1902:169; Oates 1902:184; Nicoll 1904:49; Pycraft 1906:401; Reed 1907:105; Cobb 1910:66; Beck 1918:8). The one-species view was solidified substantially by the endorsement given it by Owen (1875:254, 266) in his replacement of the (monotypic) generic name *Micropterus* (erected by Lesson 1828:416) with the currently used *Tachyeres* (from the Greek, Ταχυηρης meaning 'swift rower'), because of the previous application of *Micropterus* to the North American freshwater basses. This change of genus was adopted by Sharpe (1899a). Although Owen (1875:254) used the binomial taxon *Tachyeres brachypterus* in erecting the genus, most taxonomists of the 'one-species' school from 1876 until the early 1900's instead used the name *Tachyeres cinereus* to refer to the group.

Despite widespread acceptance during this period of the view that there was but one species of steamer-duck, field observers, convinced of the existence of both flying and flightless species, published their views with increasing frequency. Giglioli (1875:934) was persuaded that two species existed, and even suggested another, but contradictory, binomial name for the flying form—*Micropterus macropterus*. Coppinger (1883:61–62) observed flying steamer-ducks mostly on freshwater lakes and flightless birds on saltwater, and noted that color of plumage and bill distinguished young flightless birds from the flying form, in opposition to the model presented by Cunningham. Although not discussed in the literature, two poorly ossified skeletons of juvenile flightless steamer-ducks, which alone could have disproved the development-related hypothesis of flightlessness, were collected in 1888 on the "Albatross Expedition" and deposited in the U. S. National Museum of Natural History.

Oustalet (1891:B212–232), prompted by field observations and specimens collected near Cape Horn, including osteological comparisons, refuted the view of Cunningham and treated the flying and flightless forms as distinct species, devoting sixteen pages to the description of the former; Oustalet included, however, several medium-sized, relatively short-winged birds from the Falklands in his *M. patachonicus* (see table on p. 215). In addition to arguments based on anatomical differences, distributions, and locomotion, Oustalet (pp. 213-214) pointed out that the frequent association of the two forms in flocks is not relevant to the question of their possible conspecificity.

Several museum taxonomists and anatomists also showed less than complete acceptance of the theory of Cunningham. In an exhaustive synonymy of the genus, Salvadori (1895:375) recognized only one species (*Tachyeres cinereus*) but acknowledged the observation of Cox (1863:235) of numerous flying *Micropterus cinereus* on the Andean lakes. Schalow (1898:672–674) reviewed the taxonomic debate and considered the plumage characters given by Oustalet (1891) to be inadequate for diagnosis; like Salvadori (1895), Schalow listed only *T. cinereus*. Beddard (1898:457), although evidently accepting the basic thesis of Cunningham, found no greater density of bone in flightless steamer-ducks than in other waterfowl. Newton (1893) stopped short of complete endorsement of the theory proposed by Cunningham, and he (1893:597) even suggested the unprecedented notion that the flightlessness of *Tachyeres* was related to the molt of the remiges.

After the turn of the century, the controversy became more pointed. Dabbene (1902:403) considered the one-species hypothesis of Cunningham (1871a), but rejected it based on the discovery of a fully ossified steamer-duck specimen that differed anatomically from flightless birds and "corresponded perfectly" with the flying *Micropterus patachonicus* described by Oustalet (1891). Dabbene (1902:404–405) went so far as to consider the flying and flightless forms to be generically distinct—*Micropterus patachonicus* and *Tachyeres cinereus*, respectively.

Crawshay (1907:110–115) treated flying and flightless steamer-ducks of Tierra del Fuego as a single species (*Tachyeres cinereus*), concluding that (pp. 110–111): "The question of whether one or two species are to be admitted has been finally determined in favour of one in the opinion of the majority.... I do not think I came across one [sheepman] who had definitely arrived at the knowledge that the power of flight could be possessed by some individuals and lacking in others." Nicoll (1908:171–172) supported the view advanced by Cunningham, offering the following rationales:

"All the examples we obtained, and all those I have examined in the British Museum, undoubtedly belong to one species only; and if I may venture to give an opinion, I should say that Professor Cunningham's is undoubtedly the right solution, as it would surely be an almost unprecedented thing to find two very nearly allied species living together, one able to fly and the other unable to do so. At the same time, it is somewhat remarkable that, although we saw examples of this duck of all ages and in all stages of development, we met with but one which was able to fly. It may be that this species is gradually becoming entirely flightless, and that the volant individuals met with are survivals of a former stage in a state of transition, and have not as yet lost the full power of flight." Paessler (1909:103) also believed that steamer-ducks comprised a single species, although he had seen some individuals fly for 500–1000 meters when pursued. Scott and Sharpe (1912:492), after an examination of specimens of steamer-ducks in the British Museum and the Museum of the Jardin des Plantes, including those identified by Oustalet (1891) as flying *Micropterus patachonicus*, concluded, as had Cunningham, that flying individuals are the young members of a single species of steamer-duck, the adults of which are flightless. They (p. 492) also described plumage patterns and soft parts of these "immature" birds, thereby hypothesizing a molt sequence to account for the plumages described by Oustalet (1891) for *T. patachonicus*.

Blaauw (1912a:46–49), in a narrative of his voyage through the Straits of Magellan in 1911, became the leading proponent of the two-species view during the first two decades of the twentieth century. In two papers about this expedition, he (1912a:46–49, 1916:488–492) established several important points that contradicted the traditional one-species hypothesis: (1) flightless steamer-ducks are distinctly larger than the flying species; (2) young of the flightless *T. cinereus* are as flightless as the adults; (3) flightless steamer-ducks are confined to the sea whereas the flying species frequent both fresh and salt water; (4) sexual dichromatism is much less pronounced in the flightless species, in which the adults of both sexes have gray heads and orange-yellow bills, than in flying birds, in which adult males have gray heads and orange-yellow bills but females have brown heads and dark-colored bills; (5) the flying species is much smaller and browner in plumage than the flightless form, although both species have a white speculum; (6) members of the flying species also "steam" across the water like the flightless birds, but do so more buoyantly.

Brooks (1917:155–157) attempted to reconcile these observations with his own of steamer-ducks in the Falkland Islands, but had little success. He reported that (p. 156): "Among many hundreds of these ducks seen in the Falklands, all, except perhaps in size (Mr. Blaauw gives no measurements) answer absolutely his description of what he diagnoses as *T. patachonicus*. No birds of dark plumage, the females, even [*sic*] had yellow bills, and no females were seen in anything that could possibly be referred to as a gray plumage. And out of many hundreds seen none took flight, although I do not doubt for an instant that a small percentage can fly." Brooks (1917:155) concluded: "There is no doubt in my mind that there are both flying and non-flying steamer ducks, but how they are to be satisfactorily separated and diagnosed remains a task as yet unaccomplished." Sclater (1917:620), then editor of *The Ibis*, commented on the "vexed question" debated by Blaauw and Brooks, and concluded that "...the whole matter still remains obscure."

In that same year, Phillips (1917:117–118) quoted at length from a letter (dated 14 August 1916) in which Brooks went further (p. 118; emphasis in original):

"*We are worse off than ever.* His *T. patachonicus* agrees in appearance with the only birds (perhaps thousands) that I saw on the Falklands. His *T. cinereus*, with orange-yellow bill in both sexes, perhaps does not exist at all. Is it not very rare in Ducks sexually unlike in colour to both have the yellow bill which so often characterizes the male?

"I rather doubt if these birds can ever be satisfactorily differentiated, for it seems to me that this species is in the midst of its transition from a flying to a non-flying form, as in the Falklands it certainly exhibits every stage from mere flapping to flights from nest to the water, probably not greatly exceeding half a mile. It would surprise me if a

satisfactory line could be drawn anywhere. Obviously the flying birds are greatly in the minority throughout its range, and if more exist in Tierra del Fuego and southern Patagonia, it may be because it has become necessary in a region where for ages they have had primitive man and other natural enemies to contend with."

Phillips (1917:118–119) followed this excerpt with his own opinions, based only on the reports and specimens of others:

"First, then, I should think that the theory of Dr. Cunningham, which connects volant power with adolescence, must certainly go by the board.

"Second. Volant steamer ducks appear to be more common on the mainland and on Tierra del Fuego than on the Falklands.

"Third. The power of flight may be associated with a different size and different plumage, but this fact has not been clearly demonstrated.

"Fourth. The Falkland Island Steamer Ducks are well differentiated as to sex. The males are large and light coloured (apparently getting lighter with age) and have yellow bills (at least in the breeding-season). The females are smaller, browner, and have dark bills.

"Fifth. The species seems to be on the borderland as concerns its power of flight. Even in non-flying birds there is a marked variation in the ability to use the wings."

Blaauw (1917:274–276) replied to these criticisms with equal confidence, reaffirming the validity of his diagnoses and questioning the basis for the doubts expressed by Brooks and Phillips. He wrote (pp. 274–275):

"It seems evident that Mr. Phillips' collector, Mr. Brooks, has only seen *one* species of steamer-duck and that *Tachyeres patachonicus*.

"Mr. Phillips has therefore experience of *one* species only, and accordingly it may perhaps be doubted if he can reasonably talk with authority about *two*! Mr. Phillip's collector has only been to the Falkland Islands, which are a stronghold of *Tachyeres patachonicus*....

"That Mr. Brooks has not seen *T. patachonicus* fly and could not make them fly although he has seen "thousands," notwithstanding that those birds were, judging from his description, really *T. patachonicus*, only tends to prove that Mr. Brooks has either exceptionally bad luck or was not able to identify those birds when seen on the wing."

Evidently, it occurred to neither Blaauw nor Phillips that a population of flightless, sexually dichromatic steamer-ducks similar in aspect to *T. patachonicus* inhabited the Falklands.

Mogensen (1917:84–85), independently of Blaauw, was convinced that two anatomically distinguishable species of steamer-ducks occurred on the continent. He noted that both sexes of the flightless species have grey heads and yellow-orange bills; whereas in the flying species only the male is so colored, the female being darker in the head and bill. Mogensen also observed that the flightless species is limited to sea coasts, but the flying species can occur in both fresh and salt water, and in the latter both species often occurred together. He even provided measurements to demonstrate that the wings of flying *T. patachonicus* were longer (34–36 cm) than those of heavier, flightless *T. cinereus* (26–28 cm).

Qualified support for the two-species view also was forthcoming from observers in the Falkland Islands. Wace (1921:201) reviewed the literature on the controversy and, although he went so far as to treat the flying form as a taxonomic variety *patachonicus* of the single species *T. cinereus*, he concluded by reviving the idea that flying birds are the lighter-bodied adolescents of the flightless species. Vallentin (1924:322–328) concluded that (p. 324): "According to my observations there are two species of *Micropterus* to be found in the Falklands, and those accurate observers, Captains King and Abbott, were absolutely correct in their brief diagnoses." Vallentin (1924) explicitly listed only *T. cinereus* for the Falklands (p. 322), as in his previous works (Vallentin 1901:350; 1904:33); however, he referred (p. 325) to "the 'Flying Loggerhead', *M. patachonicus* (King)" in the text, reported having flushed several flying steamer-ducks from nests located well inland, and noted that they had proportionately longer wings and more oval eggs than the flightless form.

The situation in the Falkland Islands was clarified significantly by the observations of Bennett (1924, 1926), although evidently his contribution largely was ignored by subsequent workers. Bennett (1924:280–282) provided mensural com-

parisons of the common "logger-head" (*T. cinereus*) and the "canvas-back duck" (*T. patachonicus*), including total length, wing length, four dimensions of the bill, wing-spread, and lengths of tarsus and middle digit. He also noted interspecific differences in bill lamellae, bill shape, wing-spurs, coloration of primaries, sternal shape, size of supraorbital gland, intestinal color, size of testicles, and habitat. However, Bennett (1926:327) cautioned that, despite these distinctions, the plumage pattern of the flying species is almost identical to that of its flightless relative.

Phillips (1925:287–297), in his classic four-volume work *A Natural History of the Ducks*, had become much less certain of his taxonomic conclusions on steamer-ducks. He stated in the first paragraph of his description (p. 287), "I regard the question of two races as yet unresolved but think we may go so far as to say that the findings cannot all be explained on the basis of one natural species." He still retained *Tachyeres cinereus* as the single species in the group, but repeatedly admitted in the text that more than one species might be recognized. In his diagnoses Phillips compromised by separately describing a "gray phase, *Tachyeres cinereus?*" (p. 287) which corresponded to the Patagonian flightless form discussed by Blaauw (1916, 1917); a "red phase, *Tachyeres patachonicus?*" (p. 288) which agreed with the flying form of Blaauw and others; and an "intermediate type" (p. 289) comprising the large, possibly flightless birds from the Falkland Islands, described by Brooks (1917) and Phillips (1917), that resembles in plumage and soft parts the flying birds of the continent. He provisionally concluded that these "phases" represented age-classes, which presumed that steamer-ducks require up to three years to reach maturity. Phillips (pp. 290–291) acknowledged several problems with this treatment: (1) there were known to exist large flightless steamer-ducks (on the continent) in which both sexes have yellow bills, the young of which being flightless from birth, but that have wings that are absolutely (not relatively) shorter than those of the smaller, "red" flying form; (2) some "red-type" birds were known to be reproductively mature, and appeared to be fully developed in plumage and wing spurs; (3) apparent abundance of flying birds varied inexplicably even in the same locality, e.g., R. M. Beck found at Chiloé Island that flying birds were common during May-June but, during December-February, W. Percy did not see a single steamer-duck fly, even when pursued; (4) in the Falklands it appeared that males of the large "gray-type" mate with "red-type" females, but the young produced from such parents were unknown. The apparent mixing of "types" and diagnostic characters in the Falklands seems to have been primarily responsible for the reluctance of Phillips to elevate his gray and red "phases" to full species.

Phillips (1925) was not alone in his quandary. Snouckaert van Schauberg (1926:150–151) reviewed the differing views about the genus, but offered no opinion of his own. Wetmore (1926:418) listed only one species, *T. cinereus*, but commented: "The question of specific entity among the flying and non-flying steamer ducks is one that is far from settlement." Stresemann (1927:47) reviewed briefly the controversy, and concluded by quoting a letter from Phillips (dated 14 December 1926) that "...the presence of one species will not explain the story of the steamer duck." Stenhouse (1929:185–186), in a catalog of several of the first specimens of steamer-ducks stored at the Scottish Museum, acknowledged the taxonomic debate, but judged that (p. 186), "The balance of opinion, especially among field naturalists, is in favour of there being two [species]." Mogensen (1930:207), however, adopted a weaker position, relegating flying *patachonicus* to a subspecies of a single species *T. cinereus*. In his *Checklist of Birds of the World*, Peters (1931:176) listed only a single species of steamer-duck, *T. brachypterus*, but footnoted that the question concerning the number of species to recognize in the genus was "...still an open one." Conversely, Hellmayr (1932:335–337) described both *T. brachypterus* and *T. patachonicus* for Chile, but similarly stated (p. 337) that "...the question whether the flying individuals really constitute a different species is far from being settled." Reynolds (1932:35) went further, stating: "It is quite incomprehensible to me that the huge series of skins in the States has not established definitely the fact that in Tierra del Fuego—at all events—two species must be acknowledged." Dabbene (1932) reviewed the published controversy con-

cerning the systematics of *Tachyeres*, including the three "phases" discussed by Phillips (1925), and provided accounts for two species—flightless *T. cinereus* and flighted *T. patachonicus*. Casares (1933:146) tallied two species of steamer-duck for Argentina (including the Falklands), but listed no binomina or distributional limits.

At this late date, a curious, almost Lamarckian variant of the 'adolescence' hypothesis of Cunningham was proposed by Chapman (1926:120; 1933:361–362), a naturalist with substantial field experience with both flying and flightless steamer-ducks on the coasts and mountain lakes of southern Chile. Chapman observed that flying individuals occurred on the coast in winter but evidently not in summer, when they were seen on inland lakes, and flightless birds occurred year-round on the sea coasts, accompanied by obviously young birds in summer. He attempted to reconcile this apparent seasonality of flightlessness by suggesting that there was only one species of steamer-duck in which all young birds (until their first winter) could fly, but that birds nesting on saltwater later became flightless, whereas birds nesting on freshwater must travel between their nests and coastal feeding grounds and hence retained the power of flight throughout life. Palmer (1934) also cited the 'adolescence' hyothesis as the explanation for flighted and flightless steamer-ducks.

Finally Lowe (1934:467–495), armed with study skins, eggs, embryos, and detailed field notes on both flying and flightless steamer-ducks collected by P. W. Reynolds in Tierra del Fuego, as well as single spirit specimens of both the flying (from Reynolds in Tierra del Fuego) and flightless forms (from W. Percy at Chiloé), established beyond doubt the existence of both flying (*T. patachonicus*) and flightless (*T. brachypterus*) species of steamer-duck in continental South America. Lowe and Reynolds documented a number of differences: habitat and locomotion; plumage pattern and soft parts; tracheal and syringeal morphology; egg size and thickness of shells; weights, dimensions, muscle weights, and plumage pattern of well-developed embryos; and dimensions of cranial and postcranial skeletons. They even listed the different names given the two species by the local Yahgan and Ona tribes. Reynolds and Lowe lacked specimens from the Falkland Islands, but Reynolds (*in* Lowe 1934:470) asserted: "In the Falkland Islands the case, if not identical, is similar; possibly the forms found there may require subspecific separation from the corresponding categories of Tierra del Fuego. I have heard this belief expressed, and Mr. Bennett's remarks (Ibis, 1926, p. 327) do not altogether fit my Tierra del Fuego specimens."

Lowe (1934) also specifically addressed the hypothesis of developmental loss of flight proposed by Cunningham. Based on an examination of skeletal specimens then available, he wrote (p. 488–489): "...At this distance of time we may, too, have little or no hesitation in stressing the opinion that Cunningham had a very inadequate idea of the complexity of the problem which lay before him. We may, too, feel confident that the birds he collected with their cranial sutures still unfused were juvenile specimens, which may well have belonged to either the flying or non-flying species. Be this as it may, however, there does not seem to be a scrap of evidence for Cunningham's theory that the flying Steamer Ducks are only the juveniles of the non-flying. The osteological specimens collected by Mr. Reynolds, as well as those in the British Museum, so far as one can place reliance on them, disprove it." With this statement, Lowe finally laid to rest the hypothesis of Cunningham, although the idea remained in the popular literature for decades (e.g., Neilson *et al.* 1960:2466).

Not surprisingly, Reynolds (1934:350–351; 1935:84–85) promptly employed Lowe's new taxonomy in his own works. However, Percy (1934:867–868), having provided Lowe with the important spirit specimen of the (continental) flightless form, was not enthusiastic about some of Lowe's conclusions. Percy (1934:867) denied having stated anywhere (as averred by Lowe [1934:468]) that he was convinced of the validity of the 'one-species' view, but then went on to point out "undoubted facts" on steamer-ducks which he felt were not considered by Lowe (1934). These points were: (1) flying birds are absent from the coast of central Chile during December-February when downy young are present; and (2) during May and June the "same flock" contains a mixture of flying, flightless, and "inter-

mediate" steamer-ducks, contrary to the claim of Lowe (1934:468) that the flightless birds in coastal Chile keep to themselves.

Boubier (1934), evidently independently of Lowe (1934), included *Tachyeres* in a brief review of avian flightlessness. Citing the works of Blaauw (1916), Wace (1921), and Bennett (1924, 1926), Boubier (1934) recognized two species of steamer-duck and noted that the flying species (*T. patachonicus*) was characterized by smaller total length (662 mm) but longer wings (285 mm) than the respective dimensions (720 mm, 270 mm) of the flightless species (*T. cinereus*, considered to inhabit both the continent and Falkland Islands). Boubier (1934) also mentioned the interspecific differences in bill color and patterns of secondary remiges described by Bennett (1924).

Unfortunately, significant errors in taxonomy were soon to follow the landmark work by Lowe (1934). Zotta (1935:180) listed both of the taxa recognized by Lowe (1934), but provided inexplicably inaccurate distributions for both species. Zotta (1935; reprinted in 1944) limited the distributional range of flying *T. patachonicus* to Isla Chiloé, the Straits of Magellan, Tierra del Fuego, Isla de los Estados, and Santa Cruz, whereas he included in that for flightless *T. brachypterus* a much larger region (Valdivia to the Straits on the Pacific coast, the Falkland Islands, and the Argentine provinces of Neuquen, Río Negro, Chubut, Santa Cruz, and Tierra del Fuego), one that postulated the presence of the flightless form on inland, freshwater lakes. This discrepancy cannot be attributed to a simple reversal of distributional description between the two taxa, in that the opposite arrangement would exclude the Falkland Islands from the range of the flightless species. It is likely that the erroneous distributional descriptions given by Zotta (1935) contributed to the errors made subsequently by Reed (1939) and Junge (1939), both of whom included the land-locked Argentine province of Neuquen within the distributional ranges of taxa described as flightless.

A Second Flightless Species

Eventually, a taxonomic analysis that encompassed flying and flightless steamer-ducks from both continental and Falkland localities was contributed by Murphy (1936:951–972) in his classic work, *The Oceanic Birds of South America*. From an examination of 106 skin specimens and a number of eggs and downy young, Murphy distinguished three species: (1) Falkland Flightless Steamer Duck (*Tachyeres brachypterus*), limited to the Falklands, earlier assumed by Lowe (1934) to be conspecific with the continental flightless species; (2) Flying Steamer Duck (*T. patachonicus*), occurring throughout southern South America and the Falkland Islands; and (3) Magellanic Flightless Steamer Duck (*T. pteneres*) of the coasts of southern Chile, Tierra del Fuego, and Staten Island. Murphy (1936:954) dismissed the name *cinereus* (first applied to steamer-ducks by Gmelin [1788:506]) as unavailable for any of the species of *Tachyeres* because it had been applied previously to the Gadwall (*Anas strepera*) by Gmelin (1774:249), a conclusion reached earlier by Collin (1927:54). He characterized the three species using standard skin measurements and plumage descriptions, as well as detailed comparisons of downy young, egg size, life histories, locomotor behavior, and body proportions (especially the ratio of tarsus length to wing length). His studies, augmented by the field notes of R. M. Beck, also revealed (p. 953) that in some respects the Falkland Flightless Steamer-Duck more closely resembled the Flying Steamer-Duck than it did the Magellanic Flightless Steamer Duck. Stoner (1942:17–18) later reported the finding of J. E. Hamilton of the Falklands that whereas flightless *T. brachypterus* was considerably heavier than *T. patachonicus*, it had wings of "identical" length.

The three-species taxonomy proposed by Murphy (1936), with few exceptions (e.g., Schmidt 1943:55; Berlioz 1950:881), was adopted by ornithologists during the next four decades (e.g., Hellmayr and Conover 1948:374–377; Goodall *et al.* 1951:162–167; Delacour 1954:296–278; Meyer de Schauensee 1966:40; Weller 1976:45). One taxonomic error, however, is noteworthy because of its perpetuation by subsequent authors. In accordance with the taxonomy of the day, Hellmayr (1932:335) listed *T. brachypterus* as the flightless species found in coastal Chile. The taxonomic implications of Murphy (1936) for Chilean orni-

thology were clarified by Reed and Philippi B. (1938:13), who pointed out that flightless *Tachyeres* on the Pacific coast were *T. pteneres*, not *T. brachypterus*. Evidently unaware of Murphy (1936) or Reed and Philippi B. (1938), probably misled by Zotta (1935), and perhaps attempting to follow Lowe (1934), three authors—Reed (1939:34–36), Housse (1942:177, 1948:329) and Behn (1942:121)—misclassified the flightless birds of Chile, *T. pteneres*, as *T. brachypterus*, a name applied by Murphy (1936) to the Falkland endemic. Housse (1942:177, 1948:329) even explicitly listed the Falkland endemic as *T. pteneres*, and later he (1945:91–92) worsened the distributional confusion by listing all three taxa for Chile. Housse (1945:91) explained that *T. brachypterus* was a resident of the Falklands but that, although flightless, its rapid swimming enabled it to visit southernmost Argentina, Chile and adjacent islands. Another naturalist, Barros V. (1945:200; 1948:52), repeated the error by listing *T. brachypterus* as the flightless steamer-duck of coastal Chile. Perhaps in response to these errors, Philippi B. (1945) noted the new name applied by Murphy (1936) to the flightless steamer-duck of Chile.

A Fourth Species

Substantive difficulties with the taxonomic and distributional conclusions of Murphy (1936) began to appear by the late 1950's. Steamer-ducks were known to occur on the Atlantic coast of Patagonia as far north as Puerto Deseado, Santa Cruz Province (48° S) since Burmeister (1888:248). Murphy (1936:969) gave this as the northern limit for *T. patachonicus* on the Atlantic coast, evidently unaware of the specimen of *T. patachonicus* reported by Scott and Sharpe (1912:487) farther north in Río Negro Province (41° S). Much later, Bo (1958:39) reported an adult male *T. patachonicus* taken in Bahía Solano, Chubut Province (46° S). These distributional revisions soon were incorporated into regional avifaunal works (Olrog 1959:71, 1963:100, 1968a:111, 1979:50; Meyer de Schauensee 1966:40).

Observations of apparently flightless steamer-ducks on the Atlantic coast of Patagonia also challenged the information given by Murphy (1936:958), who stated that the continental flightless species (*T. pteneres*) was limited in distribution to coastal environments from Corral, Chile to the islands of Cape Horn and Staten Island; an earlier description of the range of *T. pteneres* by Murphy (1936:179), however, left some doubt as to the possible infrequent occurrence of the species in coastal Santa Cruz, Argentina. It is clear from the route taken by R. M. Beck (Murphy 1936:182), the exceptionally industrious collector working for Murphy, that Beck made no collections of birds in coastal Chubut. Without presenting supportive specimens or sight records, Olrog (1959:70, 1963:100) described the Atlantic distribution of *T. pteneres* as seacoasts from Tierra del Fuego to Chubut. He (1968a:111) later limited the Atlantic breeding distribution of *T. pteneres* to Tierra del Fuego, but stated that the species ranged farther north during winter. In three of his later works, Olrog (1959:70, 1963:100, 1968a:111) described the Falkland Flightless Steamer-Duck (*T. brachypterus*) as limited entirely to the Falklands. One decade later, however, Olrog (1979:50) extended the range of *T. brachypterus* "eventualmente" to the coast of Chubut, while maintaining the view that *T. pteneres* also occurs on the coasts of Santa Cruz and Chubut. In his last work, Olrog (1984:269) continued to include the Atlantic coast of Santa Cruz and Chubut (to Golfo San Jose) within the distributional range of *T. pteneres*. Meyer de Schauensee (1966:40; 1970:33) also included the provinces of Chubut and Santa Cruz within the distributional limits of *T. pteneres*. The idea that *T. pteneres* seasonally extended its distributional range northward along the Argentine coast was amplified by a distributional map in Johnsgard (1978:137), which depicted a winter range for this species encompassing the coasts of Santa Cruz and Chubut (to Península Valdés).

The diagnostic characters given by Murphy (1936), based almost entirely on museum skin specimens, were of little help in field identification of steamer-ducks on saltwater, and difficulties in identification of specimens continued. A skin (held at American Museum) of a male steamer-duck, collected on the coast of Chubut in 1886 by J. Young, was labeled as *M. cinereus* and later as *T.*

pteneres, probably on the basis of the locality and its moderately large size; the skin was entered into the catalog of the American Museum in pencil as "*pteneres*?". Apparently, this specimen was available for study (perhaps cataloged) by R. C. Murphy, but was never mentioned in a publication and evidently was overlooked by all subsequent investigators. On 7 November 1960, P. S. Humphrey collected a female steamer-duck (skin specimen at Peabody Museum, Yale University) on Isla Blanca, near Camarones, Chubut, which he identified by locality as *T. patachonicus*. Three skin specimens collected by C. Kovacs—a male from Punta Tombo (Chubut) on 19 April 1968 and a male and female from Camarones on 10 July 1970—were originally identified as *T. pteneres* and are held at the Museum of Natural Science, Louisiana State University. C. Kovacs also collected and prepared as skins two male steamer-ducks (now at the Museo Argentino de Ciencias Naturales, Buenos Aires), collected on 16 November 1971 and 5 February 1972 in the Bahía de Camarones, Chubut; these were identified as *T. patachonicus*. In November 1971, M. Gochfeld collected a male steamer-duck found dead on the beach at Punta Tombo which was prepared as a skeleton and identified as *T. pteneres* (now at American Museum of Natural History, New York). On 10 June 1972, C. Kovacs collected another pair of steamer-ducks at Camarones, Chubut, which were donated as mounted specimens to the Museo Argentino; the specimens remained uncatalogued and unidentified until 1989. On 25 August 1972, J. R. Jehl, Jr. collected one male and one female steamer-duck in Bahía Concepción, Chubut; the male was prepared as a study skin and the female as a skeleton (both deposited at the San Diego Museum of Natural History) and both initially were labeled as *T. pteneres*, then re-identified as *T. patachonicus*.

Boswall and Prytherch (1972:125) found steamer-ducks nesting at Punta Tombo, Chubut, which they initially identified as *T. pteneres* because of the apparent flightlessness of the birds. Later they were persuaded by Olrog (based on presumed breeding ranges) and J. Delacour and P. Scott (from their examination of a photograph of three birds) that the species involved was *T. patachonicus*. Boswall and his colleagues only saw a bird "fly" once in five days of observation, and this was a very short, weak, downhill passage of a female from nest to water. Evident flightlessness of the birds was attributed to wing-molt, which seemed to be indicated in the photographed birds (p. 78), a condition confirmed later by M. W. Weller and O. S. Pettingill (Boswall 1973a:35). Boswall (1973a:35) stated that the wing length of a drake found dead also supported the identification. Boswall (1973a:35) and Boswall and MacIver (1979:75) also reported the measurements and weights of six eggs from a nest at Punta Tombo, which were larger than measurements for *T. patachonicus* presented by Murphy (1936:969) and agreed most closely with those for *T. brachypterus*. Boswall and MacIver (1979:75) speculated that the small means given by Murphy (1936) for *T. patachonicus* may have resulted from misidentifications of large *T. patachonicus* eggs as those of *T. brachypterus*. Similarly, Daciuk (1976:27–29, 1977:363) identified by locality the steamer-ducks nesting on Isla Quintano, Golfo San Jorge, Chubut as *T. patachonicus*, despite the apparent flightlessness of the birds and their unusually large eggs.

Todd (1979:160) reported the suspicion of M. Rumboll, an Argentine ornithologist, that flightless steamer-ducks on the Atlantic coast of Argentina were either *T. brachypterus*, or an undescribed species or subspecies. Rumboll and F. Erize persuaded P. S. Humphrey and M. C. Thompson to collect specimens of the steamer-ducks in coastal Chubut during an expedition to Patagonia in 1979. Based on these specimens, collected from Puerto Melo (Chubut), Puerto Deseado (Santa Cruz), and Ushuaia (Tierra del Fuego), as well as skins examined in Argentine museums, Humphrey and Thompson (1980) provisionally recognized (but did not formally describe) four new species of steamer-duck: "white-headed steamer duck," flightless, of coastal Chubut; "masked steamer duck," also flightless and from coastal Chubut; "lesser flying steamer duck" of southern coastal Patagonia; and "pygmy flying steamer duck," based on a single skin specimen from Lago San Martin (Santa Cruz). Additional specimens collected by Humphrey and B. C. Livezey in marine and freshwater localities during the next two years permitted a formal de-

scription of the White-headed Flightless Steamer-Duck (*T. leucocephalus*; Humphrey and Thompson 1981). Upon subsequent examination, the specimens collected earlier in Chubut by Young, Humphrey, Kovacs, Gochfeld, and Jehl also proved to be *T. leucocephalus*. Humphrey, however, did not describe the other three putative taxa. The "masked" form was found to be a collection of small individuals of *T. leucocephalus* in alternate plumage. A larger sample of flying steamer ducks revealed that the "lesser" form was an artificial collection of small specimens from the osteologically variable and geographically differentiated *T. patachonicus* (Humphrey and Livezey 1982a, Livezey 1986b). The single specimen of the "pygmy" form was determined to be a juvenile of freshwater-nesting *T. patachonicus*.

Overview

Throughout the taxonomic history of steamer-ducks, there were repeated, protracted, and often imaginative attempts to reconcile contemporary views with new, distinctly contradictory information. There also was a stubborn reluctance to admit the existence of two closely related sympatric species of duck that appeared to differ principally in the ability to fly. Indeed, ornithologists for several decades preferred the improbable notion advanced by Cunningham that flight in steamer-ducks was a function of immaturity, a conclusion based on a small, unfortunate sample in which the flightless species (*T. pteneres*) was represented by adult specimens and the flying species by incompletely ossified juveniles or subadults. The taxonomy proposed by Murphy (1936) had a profound influence on subsequent workers who endeavored to make their observations and interpretations conform to his scheme. Taxonomic progress undoubtedly was impeded also by the overall similarity in size and appearance of the species, a problem exacerbated by the occurrence of three molts and plumages per annual cycle in some or all of the species of *Tachyeres* (Humphrey and Livezey 1982a). Difficulties of collecting and preparing specimens of these heavy, toughly built, and difficult-to-kill birds, as well as the remote distributional range of the genus, further limited the numbers of specimens available for study.

Remarkably, the history of the taxonomic consensus for *Tachyeres* mirrors a current phylogenetic hypothesis for the genus (Fig. 2; Livezey

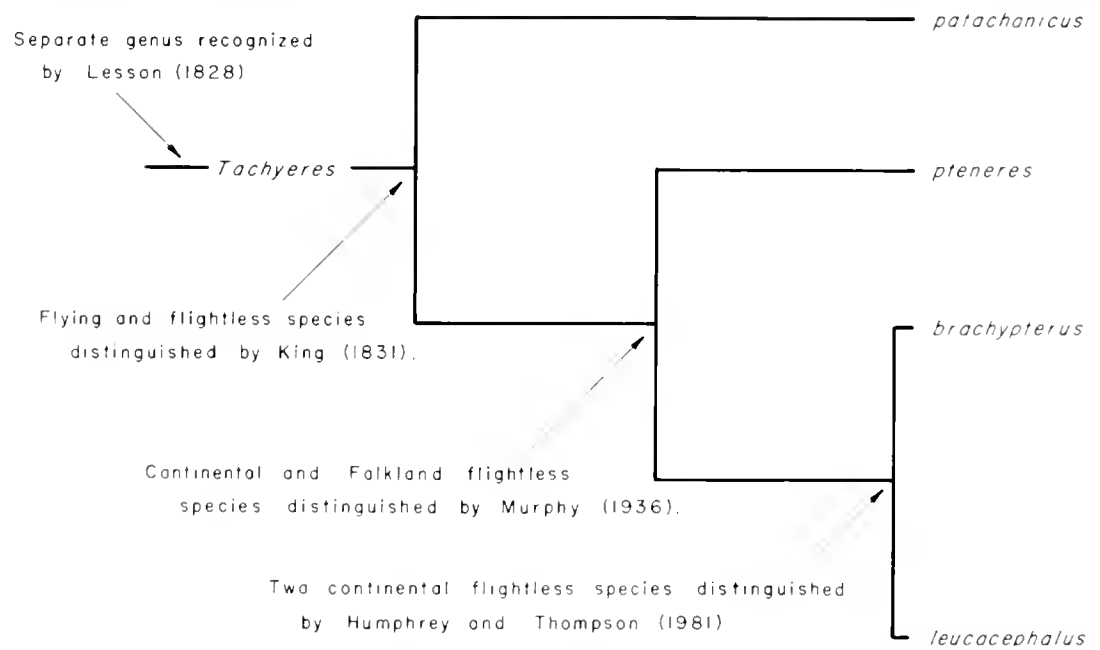

Fig. 2. Phylogenetic tree for *Tachyeres*, based on Livezey (1986c) and Corbin *et al.* (1988), and annotation of the chronological coincidence of key diagnoses of species by taxonomists.

1986c, Corbin *et al.* 1988). The ornithological community first recognized a single taxon ('representing' the ancestor of the genus), and later distinguished the flighted lineage from the collective flightless (mirrored by the first branching in the tree). Next, Magellanic *T. pteneres* was distinguished taxonomically from Falkland *T. brachypterus*, which corresponds to the second hypothesized vicariance event and associated speciation. Finally, the recent recognition of *T. leucocephalus* parallels the last glaciation-related vicariance event presumed to have isolated *T. leucocephalus* of Chubut from its sister-species *T. brachypterus*. This congruence of taxonomic history with phylogeny is particularly noteworthy because of the poor correspondence, inferred earlier by Murphy (1936), between similarity of plumage aspect and phylogenetic relationship.

Variation in flying ability in *Tachyeres* has preoccupied most taxonomists, and the impact of flightlessness on the classification of the genus has been profound. Ironically, in light of current knowledge, ability to fly is at best an unreliable, composite character that is difficult to determine and is the result of a number of anatomical, behavioral, and environmental conditions. Pereyra (1950:196) was one of the last authorities to recognize but a single species of *Tachyeres* although he (1943:227) listed two species in an earlier work; he explained the variation in flying ability in the genus as strictly the result of sexual differences in body weight, the massive males being flightless but the lighter females being capable of low flight. It is known now that an appreciable proportion of male Flying Steamer-Ducks (*T. patachonicus*) at some marine localities are permanently flightless (Humphrey and Livezey 1982b). Such locomotion-independent determinations, however, required systematic methods that were not available until recently.

SYSTEMATIC REVIEW

Relationships of *Tachyeres*

Of all the ornithologists recognizing more than one species of steamer-duck, only Dabbene (1902) did not consider them congeneric; the assignment of flightless steamer-ducks to *Tachyeres* and the flighted species to *Micropterus* by Dabbene (1902), however, may have resulted as much from the taxonomic confusion that reigned at the turn of the century as from a perception of relationships. Most other systematists placed all steamer-ducks together in their own genus; the older name *Micropterus* Lesson, 1828, being preoccupied in Pisces, was replaced by *Tachyeres* Owen, 1875, although the former was used infrequently into the twentieth century.

Exceptions to this separate-genus treatment included assignments of steamer-ducks to the generalized Linnaean taxa *Anser* (for 'geese') and *Anas* (for 'ducks') by early taxonomists (e.g., Gmelin 1788, Latham 1790). Another view of the generic relationships of steamer-ducks was indicated by several nineteenth-century ornithologists who included the steamer-ducks in already recognized genera of diving ducks: *Oidemia* (currently included in *Melanitta*, scoters; King 1828), *Fuligula* (currently *Aythya*, pochards; Schlegel 1866), and *Camptolaimus* (currently *Camptorhynchus*, Labrador Duck; Gray 1871).

The perception of a relationship between *Tachyeres* and largely northern-hemisphere diving ducks was shared by a number of other taxonomists who, although they assigned the steamer-ducks to their own genus, indicated this view by their subfamilial classifications. These higher-level affiliations with diving ducks involved sea-ducks (*Polysticta*, *Somateria*, *Melanitta*, and *Bucephala*) and pochards (Aythyini), and were inferred primarily on the basis of shared diving habits and diving-related anatomical characters (e.g., Scott and Sharpe 1912; Peters 1931; Delacour 1936; Boetticher 1939, 1942; Hellmayr and Conover 1948; Verheyen 1953a, b, 1955, 1961; Simonetta 1963; Markham 1971). This 'alliance' between largely northern-hemisphere genera of diving duck and the austral steamer-ducks necessarily influenced early biogeographic surveys of waterfowl (e.g., Sclater and Salvin 1876, Sclater 1880a, Sclater and Hudson 1889, Casares 1940).

On the basis of the behavior, external morphology, and syringeal anatomy of steamer-ducks, Delacour and Mayr (1945) concluded that the resemblance of *Tachyeres* to the eiders was superficial and that steamer-ducks were most closely related to the shelducks (their Tribe Tadornini). This treatment was followed by most taxonomic discussions involving *Tachyeres* during the next three decades, but most authorities chose to emphasize the distinctiveness of the genus by placing it in a separate tribe allied with the shelducks (Boetticher 1952; Delacour 1954; Gilliard 1958; Moynihan 1958; Johnsgard 1960, 1961a, b, 1963, 1965, 1968, 1978; Lack 1974; Brush 1976; Winkler and Walters 1983; Kolbe 1984).

An osteological study of waterfowl led Woolfenden (1961) to recommend that *Tachyeres* be moved from the Tadornini to the dabbling ducks, tribe Anatini. Previously suggested by Ripley (1957), this 'affinity' between the dabbling ducks and *Tachyeres* did not prove influential for subsequent writers in that none adopted this classification. Several writers, however, subsequently retreated from a firm assignment of *Tachyeres* to the Tadornini, either listing the genus between the shelducks and the dabbling ducks (Meyer de Schauensee 1966, 1970; Blake 1977; Johnsgard 1979) or stating that the intrafamilial relationships of *Tachyeres* were unclear (Austin 1961; Delacour 1964, Weller 1976). One series of investigations did provide some equivocal phenetic support for the 'affinity' between *Tachyeres* and the dabbling ducks; biochemical comparisons of uropygial secretions by Jacob (1977, 1980, 1982) and Jacob and Ziswiler (1982) revealed similarities between those of steamer-ducks and those of *Anas* and the eiders (*Somateria*).

A phylogenetic analysis of Recent genera of waterfowl based on morphological characters confirmed the inclusion of *Tachyeres* within the Tadorninae (Livezey 1986a), with a less well supported hypothesis of close relationship between *Tachyeres* and two other 'aberrant' genera—the neotropical Torrent Duck (*Merganetta armata*) and the New Zealand Blue Duck (*Hymenolaimus malacorhynchus*). The corresponding classification of *Tachyeres*—subtribe Merganetteae of the tribe Tadornini in the anatid subfamily Tadorninae—is followed here. Relationships within the genus *Tachyeres* were inferred using morphological (Livezey 1986c) and electrophoretic data (Corbin *et al.* 1988). These studies indicated that the comparatively primitive but variable *T. patachonicus* is the sister-species to the three flightless species, and, of the latter, the medium-sized Atlantic species (*T. leucocephalus* and *T. brachypterus*) are closest relatives.

Sibley and Monroe (1990:32) considered the three flightless species as constituting a superspecies, but incorrectly considered *pteneres* to be the senior included specific taxon. More surprising was the inclusion of *Tachyeres* in an enlarged Tribe Anserini, an eclectic group comprising the true geese, sheldgeese and shelducks, and the 'perching ducks' (Sibley and Monroe 1990); no empirical support for this arrangement was cited.

Synonymies for *Tachyeres*

Members of the genus *Tachyeres* have been given 25 different binomial (and trinomial) names (excluding apparent misspellings) involving seven genera. Most of the oldest taxa were ambiguous with respect to the four currently recognized species. Many provided no distinguishing characters or described broad distributional ranges, and are presumed to have referred to the entire known genus. Others provided localities of observation, which in some cases exclude certain flightless species from further consideration on distributional grounds, but the information given does not permit a confident identification of species. The determination of whether the birds were *T. patachonicus* or members of a flightless species presents particular difficulties, and is often impossible for birds described from coastal habitats (see discussion of identification beyond). For example, the numerous early accounts of birds seen on saltwater in the Falkland Islands (e.g., Lesson 1826, Darwin 1839a, b) described birds of large size and apparently incapable of flight. Unfortunately for purposes of identification, both characteristics can apply to both *T. patachonicus* and *T. brachypterus*, and the species are virtually indistinguishable in the field.

Unfortunately, for decades following the description of *T. patachonicus* by King (1831, 1839), most writers made no mention of a second species of steamer-duck (e.g., Darwin 1839a, b). Lesson (1837, 1838) was one of the first to accept the existence of a second species of *Tachyeres*, but interpreted the discovery to mean that the large flightless species was found in the Falklands (which he had visited) and the smaller *T. patachonicus* was found in the Straits of Magellan. The taxonomy of Eyton (1838, 1869a) presents a special problem, in which he recognized two species—*brachypterus* and *patachonicus*—but stated that both species were flightless and he provided suspiciously similar measurements for the two forms. Most 19th-century ornithologists, however, followed their prominent British colleagues—notably Sclater, Cunningham, and Owen—in treating *Tachyeres* as monotypic. During this period, proponents of the one-species view varied in the distributional limits applied to steamer-ducks; e.g., through the 1870s, Sclater and his co-workers listed only collections and records of steamer-ducks from the Falkland Islands, but subsequently extended the distributional limits of the genus to the continent. Salvadori (1895:373) wrote that steamer-ducks were "Confined to Straits of Magellan and Falklands." Reed (1939) was one of the last authors to recognize but two species of steamer-duck—*Tachyeres brachypterus* and *T. patachonicus*—and was alone in listing both for the inland, mountainous Argentine province of Neuquen! Similarly, Junge (1939) included mountain lakes among the habitats of the single taxon he recognized for southern Chile, *T. patachonicus*, a species he described as flightless. Both authorities may have been misled by the inexplicably inaccurate species distributions given by Zotta (1935:180).

Consequently, we list under the generic account the following classes of references: (1) references which explicitly or are presumed to include the entire genus *Tachyeres* under a single taxon; (2) references to apparently flightless steamer-ducks, generally with locality information, but with descriptions inadequate for exclusion of *T. patachonicus*; and (3) references to steamer-ducks, presumed flightless or otherwise, in which the distributional limits given include the ranges of two or more species of flightless *Tachyeres*. For these nonspecific citations we include a single-letter designation (in brackets) to indicate the geographic region concerned, thereby defining the subset of species that may have been included. These designations are:

G general; referred to entire genus (often considered to be monotypic), or the region poorly defined or included entire distributional range of genus.

F Falkland Islands; *T. brachypterus* and/or *T. patachonicus* involved.

T Tierra del Fuego (including Isla de los Estados); *T. pteneres* and/or *T. patachonicus* involved.

A Atlantic coast of Patagonia (coastal Argentina north of Tierra del Fuego); involved *T. patachonicus* and/or possibly *T. leucocephalus*.

P Pacific coast of Patagonia (Chilean coast north of Tierra del Fuego); involved *T. pteneres* and/or *T. patachonicus*.

Sources *clearly* referring to flightless forms but as distinct only from the flying form (i.e., there was no diagnostic or distributional information by which to determine which flightless form was intended), are included under the flightless species included in the distributional ranges described (annotated as "in part"). References to currently recognized species (based on examination of listed specimens, descriptions, illustrations, observations of birds in flight or on inland lakes, inability to fly in captivity, and/or distributional information) are listed under the corresponding current taxa.

Pages listed include all references to the taxon in the works. Apparent misspellings also are included (indicated by asterisks), as are errors in gender, if the erroneous taxa were used consistently in the works. Other taxonomic complications are annotated following the individual citations. Etymology of species names was described by Gotch (1981). Published vernacular names are listed by language and are followed by the earliest references to each name. Suprageneric classification follows Livezey (1986a).

Order Anseriformes (Wagler, 1831)
Suborder Anseres Wagler, 1831
Family Anatidae Vigors, 1825
Subfamily Tadorninae Reichenbach, 1852
Tribe Tadornini Delacour and Mayr, 1945
Subtribe Merganetteae Bonaparte, 1853

Genus *Tachyeres* Owen, 1875
Steamer-Ducks

?Diomedea chiloensis.—Molina (1782:239) [P]; considered synonymous with "*Micropterus cinereus* Gray" by Philippi (1867:793) but not by Deautier and Steullet (1930:474).

Anas cinerea.—Gmelin (1788:506 [F,T]); Garnot (1826:59 [F]); Brehm (1831:903 [G]); Merrem (1841:29 [G]); Giebel (1872:347 [G]); Frauscher (1894a:174 [T]).

Anas brachyptera.—Latham (1790:834 [F]); Quoy and Gaimard (1824:347 [G]); Garnot (1826:59 [F]); Reichenbach (1836:entry 394 [G]); Darwin (1839a:257 [F]; 1839b:190 [F]).

Anser cinereus.—Bonnaterre (1790:112 [F]).

Anser brachypterus.—Vieillot (1818:344 [F]); Dumeril (1825:470 [G]).

Anas brachyptera et *cinerea*.—Lesson (1826:227–228 [G]; 1831:630 [F]; 1837:533 [F]; 1838:720 [F]).

Micropterus brachypterus.—Lesson (1828:416 [F], gender of species not given); Gould (1841:136 [F]); Lichtenstein (1854:100 [P]); Wood (1862:735 [G]); Hubbard (1907:217 [G]).

Micropterus cinerea.—Reichenbach (1845:t. 77, illus. 894 [G]).

Micropterus cinereus.—G. R. Gray (1840:74 [G]; 1844:623 [G]); J. E. Gray (1844:140 [G]); Strickland (1841:39 [G]); Hartlaub (1846:19 [F]); Des Murs (1847:457 [P,T]); Reichenbach (1852: plate VIII, table VII [G]); Boeck (1855:511 [P]); Bonaparte (1856:651 [G]); Germain (1860:315 [P]); Sclater (1860:389 [F]; 1867:335, 340 [P]); Pelzeln (1865:139 [P]); Cunningham (1868:127 [F,T]; 1871c:262 [F,T]; Giglioli (1868:498 [T]); Philippi (1867:793 [P]; 1868:283, 309 [P]); Sclater and Salvin (1868:189 [T]; 1873:130 [T]); Thomson (1877:205 [F,T]); Vinciguerra (1883:58 [T]); Lataste (1893:122 [T]); Paessler (1909:103 [F,T,P]).

*[*Anas*] *pteneros*.—Attributed erroneously to Forster (1844:338) by Bonaparte (1856:651), Salvadori (1895:374), Scott and Sharpe (1912:489), and Phillips (1925:288).

Fuligula cinerea.—Schlegel (1866:13, 118 [F]; 1872:274 [G]); Sundevall (1872:149 [G]).

Camptolaimus [subgenus indeterminate] *cinereus*.—Gray (1871:88 [G]).

Tachyeres brachypterus.—Owen (1875:254, 258, 266, 272 [G]; 1879:366 [G]); Coffin (1927:54 [G]); Peters (1931:76 [G]); Pereyra (1950:196 [T,F,P]).

Tachyeres cinereus.—Sclater and Salvin (1876:402 [G]; 1878:437 [T]); Sclater (1879b:310 [T]; 1881:150 [T]); Sharpe (1891:309 [F]; 1899b:224 [G]); Reichenow (1882a:48 [G]; 1882b:17 [G]); Coppinger (1883:56, 61–62 [T]); Stejneger (1885:149 [G]); MacFarlane (1887:202 [F,T]); Burmeister (1888:248 [A]); Ridgway (1889:138 [T]); Sclater and Hudson (1889:137 [F,T]); Tristram (1889:47 [T]); Lucas (1891:130 [T]); James (1892:10 [P]); Gadow (1893:154 [T]; 1902:169 [G]); Newton (1894:518 [F,T]; 1895:597 [F,T]; 1896:737 [F,T]; 1899:518, 597 [F,T]); Salvadori (1895:326, 373 [G]; 1900:633 [G]); Lane (1897:195 [P]); Beddard (1898:456, 460, 466, 468 [G]); Martens (1900:25 [G]); Dabbene (1914:296 [G]); Oates (1902:184 [F,T]); Nicoll (1904:49 [T]); Vallentin (1904:33 [F]); Hubbard (1907:217 [G]; Reed (1907:105 [P]); Wilton *et al.* (1908:6, 62 [F]); Evans (1909:121 [G]); Knowlton and Ridgway (1909:195 [G]); Townsend (1909:242 [T]; 1910:6 [T]); Cobb (1910:66 [F]; 1933:80 [F]); Quijada-B. (1910:339 [G]); Mitchell (1911:514 [G]); Paessler (1911:128 [T]; 1913:41, 43, 48 [T]; 1914:272 [T]; 1915:60 [T]); Brabourne and Chubb (1912:57 [T,F]); Scott and Sharpe (1912:487, 489–492, 498 [G]); Bertoni (1913:76 [G]); Shufeldt (1913:210–215, 217–220 [G]); Brooks (1917:155 [F]); Brooks *in* Phillips (1917:117–118 [F, T]); Anonymous (1918:205 [F]); Finn (1924:138 [G]); Lynch Arribalzaga (1924:270 [A,T]); Chapman (1926:120 [P]); Heinroth (1929:532 [G]); Palmer (1934:4096 [G]); Schmidt (1943:55 [G]); Hamilton (1946:131 [F]); Glegg (1947:433 [F]); Meunier (1959:453 [G]); Neilson *et al.* (1960:2466 [G]).

Anser cinerea.—Milne-Edwards (1882:42 [G]).
Anas (*Micropterus*) *cinereus*.—Frauscher (1894b: 205 [T]).
Tachyeres cinerea.—Beddard (1897:467 [G]); Böker (1935:202 [G]).
Trachyeres cinereus.—Vallentin (1901:350 [F]).
Tachyeres brachyptera.—Peters (1931:176 [G]); Boetticher (1939:434 [G]); Berlioz (1950:881 [G]); Simonetta (1963:127 [G]).

Vernacular Names

English
Race-horse.—Byron (1773:50); Hawkesworth (1773:411); Cook (1777:186); Forster (1777:492); Buffon (1798:159; 1812:369).
Loggerhead.—Penrose (1775:35); Clayton (1776:104).
Loggerhead goose.—Penrose (1775:35); Latham (1785:439).
Loggerhead duck.—Forster (1777:493).
Steamer-duck.—King (1839:35).
Sea-horse.—Blaauw (1916:448).

Spanish
Quethu.—Molina (1782:239).
Quetu.—Des Murs (1847:457).
Cagues.—Des Murs (1847:457).
Quetru.—Germain (1860:315).
Quetra.—Giebel (1872:347).
Pato quetru.—James (1892:10).
Quetar.—Lane (1897:195).
Quaitar.—Lane (1897:195).
Pato vapor.—Blaauw (1912:67).
Quetro.—Phillips (1925:287).
Quettro.—Chapman (1933:361).
Pato vapor grande no volador.—Pereyra (1950:196).

Dutch
Stoomboot-eend.—Schlegel (1872:274).

German
Kurzflugelente.—Reichenbach (1836:entry 394).
Patagonische Riesenente.—Reichenow (1882a:48).
Dampfergans.—Frauscher (1894a:174).
Quetra der Patagonier.—Frauscher (1894a:174).
Grauen Tauchente.—Cobb (1910:20–21).
Dampfschiffente.— Agostini (1924:114).

French
Oye grise.—Pernety (1769:576).
Oye du plein.—Pernety (1769:576).
Canard-lourdaut.—Cook (1778:285).
Canard aux ailes courtes.—Quoy and Gaimard (1824:139).
Oie du plain.—Lesson (1826:228).
Canard-lourdaud.—Lesson (1826:228).
Canard à ailes courtes.—Reichenbach (1836:entry 394).
Canard microptère.—Oustalet (1891:B212).
Canard (a) vapeur.—Oustalet (1891:B212).
Canard cendre.—Cobb (1910:20–21).
Canard géant.—Boubier (1934:85).
Macreuse australe.—Housse (1942:329).
Canard plongeur de Patagonie.—Berlioz (1950:881).

Italian
Pato a vapor.—Agostini (1924:114).
Anitra a vapore.—Agostini (1955:74).

Czechoslovak
Kachyně.—Kolbe (1984:170).

Russian
Утки-пароход.—Kolbe (1984:170).

Japanese
フナガモ属.—Yamashina (1986:70).

Fuegian: (tribe not given)
Karawus-poug.—Coppinger (1883:122).

Content

Tachyeres comprises four species, one comparatively widespread, geographically variable, and (largely) flighted species, and three mutually allopatric, marine-coastal, flightless species: Flying Steamer-Duck (*T. patachonicus*), first described by King (1831) and decisively diagnosed by Lowe (1934); Falkland Flightless Steamer-Duck (*T. brachypterus*), segregated from the continental flightless species by Murphy (1936); Magellanic

Flightless Steamer-Duck (*T. pteneres*), a comparatively distinct species that was the first to be distinguished from the flying form, and formally diagnosed by Murphy (1936); and White-headed Flightless Steamer-Duck (*T. leucocephalus*), an overlooked or misidentified endemic of coastal Chubut, Argentina, described by Humphrey and Thompson (1981).

Type Species

The type species of the genus *Tachyeres* is, by monotypy, *Anas brachyptera* Latham 1790, i.e., the species name was that to which Owen (1875) referred in naming the genus *Tachyeres*. A neotype for *T. brachypterus* is designated below. Fortunately, this species (as currently delimited) is representative of the genus for several reasons: (1) *T. brachypterus* shares all the diagnostic characters of the genus; (2) the species is flightless (a distinctive character rare among the Anatidae but shared by *T. pteneres*, *T. leucocephalus*, and some males of *T. patachonicus*), of moderate size, and its plumage pattern is very similar to those of its congeners (with the possible exception of the unique *T. pteneres*); (3) *T. brachypterus* is the species most frequently kept in captivity; and (4) this species was of historical importance, and references to this form occur in the writings of most early explorers and naturalists (e.g., Lesson 1831; Darwin 1839a, b; Gould 1841; Sclater 1861a).

Brief Description

Steamer-ducks are medium to large Fuego-Patagonian marine-littoral (all species) and freshwater (one species) ducks, are predominantly battleship gray with lower breast, belly, and most secondaries white, show variable pattern and coloration of the head, and have moderately elongate, recurved central rectrices. Members of the genus lack any metallic coloration and are sexually dichromatic in some definitive plumages. Males are larger and more robust (bull-necked) than females. Bills of adult males are largely bright orange. Except in juveniles and subadults, the feet are bright yellow-orange.

Distribution

Members of the genus are limited in distribution to marine coasts and (in *T. patachonicus*) freshwater, primarily mountain lakes, throughout southern Argentina, Chile, and in the Falkland Islands (Fig. 3). The northern limit of the continental range of the genus can be approximated by a line connecting Concepción, Chile with Viedma, Argentina. The marine-littoral range of the flighted species overlaps, at least seasonally, those of each of the three, mutually allopatric flightless species.

Tachyeres patachonicus (King, 1831) Flying Steamer-Duck

Micropterus patachonicus.—King (1831:15; 1839:542); Lesson (1837:533; 1838:720); Eyton (1838:143; 1869a:100–101); Abbott (1861:162); Sclater (1861b:46); Giglioli (1875:934); Oustalet (1891:212–216, 218, 220–222, 224–226, 227–231, plate 5, in part); Sclater (1892:173–174); Dabbene (1902:403–404).

Micropter(o)us patachonichus.—Eyton (1838:50; 1869b; plate 18, reprinting of figure from 1838 work with misspelling).

Micropterus patachonica.—Eyton (1856:348).

Micropterus cinereus.—Cox (1863:235, in part); Sclater and Salvin (1870:499); Cunningham (1871a:493, in part); Paessler (1909:103, in part).

[*Micropterus macropterus*.—Giglioli (1875:934), parenthetical suggestion of alternate name.]

Micropterus brachypterus.—Moreno (1879:[165, 173]).

Micropterus brachipterus.—Boxe (1883:13).

Micropterus pathachonicus.—Vinciguerra (1883:58).

Micropterus patagonicus.—Carbajal (1900:282).

Tachyeres cinereus.—Sclater (1881:107, in part); Sharpe (1881:13, in part); Crawshay (1907:110, in part); Nicoll (1908:163, in part); Skottsberg (1911:47); Scott and Sharpe (1912:487, in part); Phillips (1925:134, 287–288, in part); Wetmore (1926:418).

Tachyeres patachonicus.—Holmberg (1895: [221]); Dabbene (1910:233; 1932:205–206); Sclater (1913:315); Blaauw (1916:488–489,

Fig. 3. Approximate distributional limits of the four species of *Tachyeres*. Range of *T. patachonicus* (excluding vagrants) is enclosed by diagonal barring (includes coastal and inland areas), and the coastal ranges of the three (mutually allopatric) flightless species are shown in stipple.

491; 1917:274–276; 1921:58); Mogensen (1917:85); Anonymous (1920:77); Bennett (1924:280–282; 1926:327); Vallentin (1924: 325); Snouckaert van Schauberg (1926:150–151); Stresemann (1927:47); Hellmayr (1932: 336–337); Boubier (1934:85–86); Lowe (1934:449–482, 484–487, 489–493; 1935:426); Reynolds (1934:351); Reynolds *in* Lowe (1934:470–472, 477–479); Reynolds (1935:85); Zotta (1935:180; 1944:30); Bullock (1936:137); Murphy (1936:199, 208, 953–956, 958, 964–965, 968–969); Steullet and Deautier (1936:364, 366–367); Junge (1939:166, in part); Laubmann (1940:18–20); Morrison (1940:254); Housse (1942:177; 1945:92; 1948:329); Stonor (1942:17–18); Pereyra (1943:227); Trimble (1943:420); Delacour and Mayr (1945:15, 38; 1949:42, 63); Parques Nacional Argentina (1947:39); Hellmayr and Conover (1948:374–377); Olrog (1948:473; 1950:518; 1959:70; 1963:100; 1968a:111; 1968b:plate 11; 1979:50; 1984:92, 269); Yañez (1948:154; 1949:8–10); Ripley (1950:5; 1957:225); Goodall *et al.* (1951:162–163); Boetticher (1952:23, 68–69, 91); Pergolani de Costa (1953:36; 1970:35); Verheyen (1953a:384, 410, 434–435; 1953b:463, 486–487; 1955:2,15); Delacour (1954:271, 276–277; 1964:335); Philippi-B. *et al.* (1954:29); Scott (1954:61; 1972:48); Agostini (1955:74); Holgersen (1957:59); Tour (1957:162); Bo (1958:39); Moynihan (1958:183, 200–201); Van Tyne and Berger (1959:234); Cawkell *et al.* (1960:216); O. S. Pettingill (1960:606); Schönwetter (1960:131); Cawkell and Hamilton (1961:15); Johnsgard (1961b:64; 1962:140; 1965:94; 1968:105; 1978:135; 1979:453); Berndt and Meise (1962:192); Godoy (1963:31); Philippi-B. (1964:46); Bernath (1965:98); Carlquist (1965:232); Johnson (1965:195–196; 1969:5; 1970:2); McKinney (1965:195); Pettingill (1965:71); Smith (1965:56); Johansen (1966:231); Meyer de Schauensee (1966:40; 1970:33; 1982:33); Stresemann and Stresemann (1966:305); Zapata (1967:364); Lack (1968:347); Weller (1968:200; 1969:128; 1972:26, 37; 1975a:295; 1975b:87; 1975c:110; 1976:45; 1980:26); Humphrey *et al.* (1970:129–130, 135–139); Markham (1970:46; 1971:48); Sibley and Ahlquist (1972:93); Strange (1972a:256); Bock (1973:208); Boswall (1973b:248); Duguy (1973:6; possibly included *T. leucocephalus*); Jehl (1973:129); Jehl *et al.* (1973:61, may have included *T. leucocephalus*); Vigil (1973:69–70); Jory *et al.* (1974:132); Lack (1974:85); MacLean (1974:193); Merne (1974:34, 78); Schlatter (1974:2; 1976a:14; 1976b:137, 140; 1979:163); Morony *et al.* (1975:21); Woods (1975:123; 1982:50); Gruson (1976:11); Jehl and Rumboll (1976:146); Kühnemann (1976:157); Venegas C. (1976:177–178, 183); Wolters (1976:98); Blake (1977:227); Daciuk (1977:363, 371; probably included in *T. leucocephalus*); Jacob (1977:52, 54–58; 1982:87); Navas (1977:35,86); Reed (1977:27); Navas and Bo (1977:79); Clements (1978:27); De la Peña (1978:57; 1986:79; 1987:39); Soothill and Whitehead (1978:280–281); Blandamer and Burton (1979:132); Goodall (1979:76); Todd (1979:160); Hillgarth and Kear (1979:142); Venegas C. and Jory H. (1979:73); Contreras *et al.* (1980:45); Howard and Moore (1980:71; 1984:71); Erize *et al.* (1981:131, 178, 199); Gotch (1981:83); Humphrey and Thompson (1981:1, 3, 5–6, 8); Storer (1981:53; 1984:637); Venegas C. (1981:217; 1986:11, 61); Araya (1982:5); Humphrey and Livezey (1982a:1–2, 10, 12, 15, 21–22; 1982b:368, 370, 371; 1985:944–951); Jacob and Ziswiler (1982:274, 276); Livezey and Humphrey (1982:12–16; 1983:485–486; 1984a:257; 1984b:368–376; 1985:154–156; 1986:540–553, 556); Scherer and Hilsberg (1982:360, 373); Corbin (1983:216); Carpi (1984:116); Daciuk and Heber (1984:174); Kolbe (1984:170, 172); Walters (1984:18); Edwards (1985:21); Fjeldsa (1985:111); Harrison (1985:665); Livezey *et al.* (1985:18–19; 1986:445–450); Murray (1985:567); Narosky *et al.* (1985:11); Nuechterlein and Storer (1985a:87; 1985a:568); Raikow (1985:82, 86–87); Araya M. *et al.* (1986:116); Clark (1986:100); Livezey (1986b:511–512, 515–523; 1986c:458, 460–466, 467; 1989a:1, 3, 6–15, 17, 20–26, 28–28, 31–33, 40; 1989b:181–182; 1989c:428; 1990:661); McGowan (1986:306; 1989:538,

542); Yamashina (1986:70); Dunning (1987:23); Humphrey *et al.* (1987:68–69); Narosky and Fiameni (1987:16); Narosky and Yzurieta (1987:79); Wolsey (1987:39); Cabal (1988:25); Gauthier (1988:113); Madge and Burn (1988:58, 180); Ryan *et al.* (1988:29, 32, 33); Buitron and Nuechterlein (1989:18); Fjeldsâ and Krabbe (1990:120, 712, 718); Sibley and Monroe (1990:32).

Tachyeres cinereus var. [*Tachyeres patachonicus*].—Wace (1921:201).

Tachyeres cinereus patachonicus.—Mogensen (1930:207).

Tachyeres macropterus.—Anonymous (1933:230); evidently based on informal suggestion of alternate name *Micropterus macropterus* by Giglioli (1875:934).

Tachyeres brachypterus.—Zotta (1935:180, in part [?]); Pereyra (1950:196, in part); Gollan (1951:286).

**Tachyeres patagonicus*.—Reed (1939:34); Behn (1942:121); Pisano V. (1973:33); Daciuk (1975:172).

**Tachyres patachonicus*.—Krieg (1940:161; 1951:159).

**Tachyeros patachonicus*.—Zapata (1969:23).

**Tachyeres patachonichus*.—Raikow (1970:570).

**Tachyeres pataghonicus*.—Barros (1971:172).

**Tachyertes patachonicus*.—Adams and Templeton (1979:39).

**T[achyeres] patachonicus*.—McGowan (1982: 215).

Tachyeres pteneres.—De la Peña (1987:40).

Vernacular Names

English

Patagonian micropterus.—Eyton (1838:143).

Flying loggerhead.—Abbott (1861:162).

Lesser Steamer Duck.—Blaauw (1912a:54).

Canvas-back(ed) (duck).—Bennett (1924:280).

Lake logger.—Bennett (1924:281).

Flying Steamer-Duck.—Bennett (1926:327).

Flying loggerhead duck.—Bridges (1948:64).

Spanish

Pato silvon.—Bove (1883:13).

Pato real.—Reynolds *in* Lowe (1934:470).

Pato vapor que vuela.—Bullock (1936:137).

Pato quetru volador.—Housse (1945:92).

Pato vapor volador.—Delacour and Mayr (1949:63).

Pato vapor grande volador.—Pergolani de Costa (1953:36).

Pata vapor gran volador.—Zapata (1969:23).

Pato vapor de agua dulce.—Vigil (1973:69).

Pato volador.—Kühnemann (1976:157).

Pato azul.—Kühnemann (1976:157).

German

Fliegende Dampfschiffente.—Johansen (1966:231).

Langflugel-Dampfschiffente.—Berndt and Meise (1962:192), Wolters (1976:98).

French

Microptère de la Patagonie.—Lesson (1837:533; 1838:720).

Canard-vapeur volant.—Johnsgard (1978:135).

Czechoslovak

Kachyně patagonská.—Kolbe (1984:172).

Russian

Патагонская утки-пароходм.—Kolbe (1984: 172).

Japanese

トビフナガモ.—Yamashina (1986:70).

Fuegian (Yahgan)

Tachka.—Phillips (1925:288).

Dusca.—Reynolds *in* Lowe (1934:471).

Tushca.—Bridges (1948:435).

Fuegian (Ona)

Tari.—Reynolds *in* Lowe (1934:471).

Original Description and Type

First distinguished from regionally sympatric flightless congener(s) by King (1831); an earlier application of the species name to *T. pteneres*, in the binomen *Oidemia patachonica* King, 1828, has been suppressed by the International Commission of Zoological Nomenclature (1991) and placed on the Official Index of Rejected and Invalid Spe-

cific Names in Zoology (Livezey 1989b). The original description by King (1831:15) included the reddish throat and scapulars and comparatively small size of the species; King (1839:542) later included the capacity for flight among its diagnostic characters. Substantial geographic variation exists in *T. patachonicus*, and the species may best be considered a superspecies (Humphrey and Livezey 1982a, b; Livezey 1986b, c).

No type material of *T. patachonicus* is known to be extant. Accordingly, we designate as neotype the following skin specimen, held at the Subdepartment of Ornithology, British Museum (Natural History), Tring, Hertfordshire, England:

Specimen no. 1928·4·21·1—Male; collected on Estancia Viamonte, Isla Grande, Tierra del Fuego, Argentina; on 1 September 1927; by P. W. Reynolds.

Standard Measurements
(mean ± standard deviation, range, *n*)

Total weight (g).—Males: 2958 ± 296, 2100–3600, 54. Females: 2347 ± 295, 1665–3118, 51.

Wing length (arc, mm).—Males: 304 ± 11, 282–325, 62. Females: 287 ± 10, 265–312, 64.

Culmen length (mm).—Males: 53.9 ± 2.6, 48–60, 67. Females: 52.3 ± 2.3, 47–58, 67.

Nail width (mm).—Males: 11.6 ± 0.9, 10–14, 66. Females: 10.8 ± 0.8, 9–12, 67.

Tarsus length (mm).—Males 60.0 ± 3.0, 53–66, 65. Females: 56.3 ± 3.1, 50–66, 67.

Tail length (arc, mm).—Males: 111 ± 6, 93–119, 31. Females: 104 ± 6, 91–117, 30.

Measurements (mm) of Eggs (*n* = 40)

Length.—mean = 77.1, range 73–84.
Width.—mean = 52.2, range 51–55.

Brief Description

This species is the smallest of the steamer-ducks, but the mean length of wing (arc) is greater, sex for sex, than in the three larger, flightless species. Body is predominantly battleship gray in aspect with considerable chestnut on scapulars, sides, and flanks; lower breast, belly, and most secondaries are white (Fig. 4). Recurved central tail feathers are longer, bill proportionately longer and more delicate in profile, and the body and neck are more slender than in the flightless species. Males are larger and more robust than females. Bill color of adult males is bright yellow-orange, duller during the prebasic molt; bill is darker in adult females and subadults and juveniles of both sexes.

The species (at least Atlantic-coastal populations) is characterized by three molts and plumages per cycle, the prebasic molt replacing the whole feather coat, the other molts replacing only the feathers of the head and neck. The definitive alternate and supplemental plumages are sexually dichromatic.

Juvenal and basic plumages: head and neck (both sexes) are dark brown with a faint whitish postocular streak in the juvenal plumage.

Definitive alternate plumage: male—gray crown, brown cheek, white postocular streak; female—head and neck dark brown with interrupted postocular streak.

Definitive supplemental plumage: male—head and neck white (crown pale gray in some individuals) with small patch of chestnut on throat; female—head and neck medium brown with short whitish postocular streak.

Class-I downy differs from downies of all other *Tachyeres* in having very narrow, continuous supraloral and supraocular patches which are separated from (not continuous with) the postocular streak.

Distribution

Flying Steamer-Ducks occur throughout the distributional range of the genus (Fig. 5). Murphy (1936) was overly conservative in his delimitation of the inland, freshwater distribution of this species, as were Johnsgard (1978:134), Kolbe (1984:171), and Madge and Burn (1988:58). *T. patachonicus* breeds on many freshwater lakes (in low densities) from Isla Grande north to Lago Nahuel Huapi, Neuquen, Argentina; the species is also known to breed on Isla de los Estados, Tierra del Fuego (P. Angle, pers. comm.) and on islands in the Beagle Channel (Humphrey *et al.* 1970). Olrog (1984:269) inexplicably extended the distributional range of *T. patachonicus* on the coast of

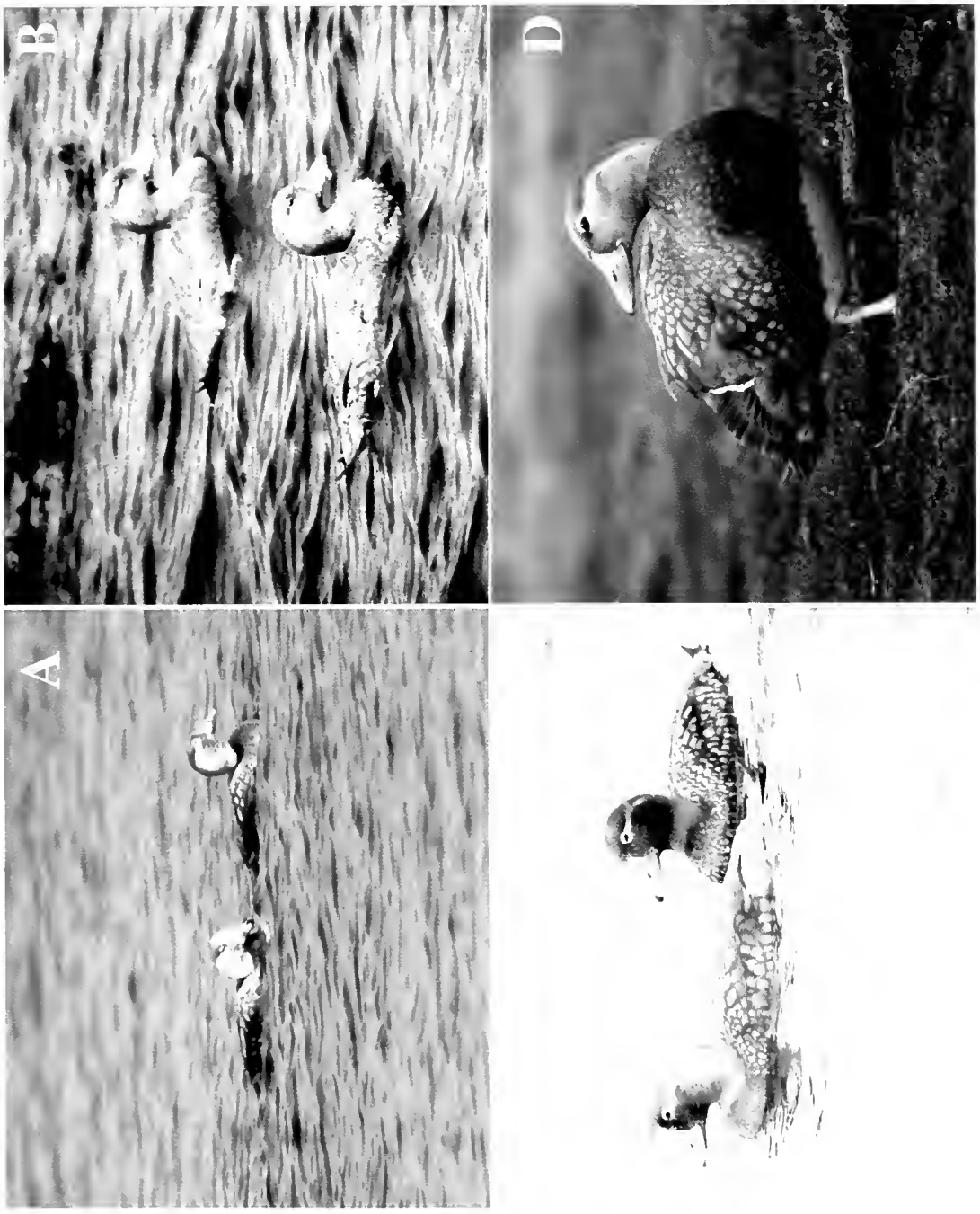

Fig. 4. Photographs of the four species of *Tachyeres* in the field. A *T. leucocephalus*, male (left) and female (right), by R. Straneck (Punta Tombo, Chubut, Argentina, October 1977); B — *T. pteneres*, male (front) and female (rear), by D. Zimmerman (Ushuaia, Tierra del Fuego, Argentina, December 1983); C — *T. brachypterus*, male (left) and female (right), by B. C. Livezey (Port Stanley, Falkland Islands, January 1984); D — *T. patachonicus*, male, by G. L. Nuechterlein (Laguna Nevada, Santa Cruz, Argentina, January 1982).

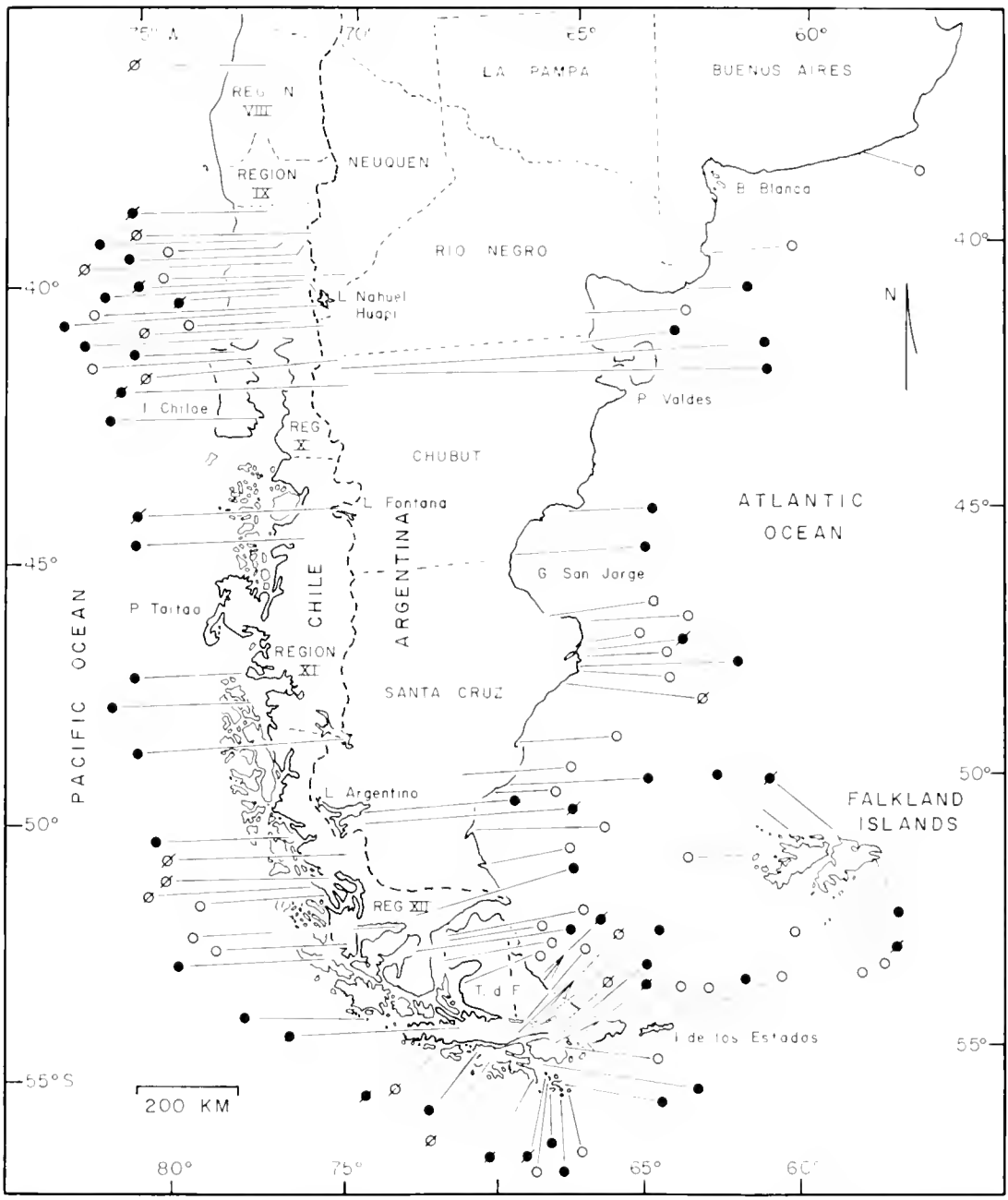

Fig. 5. Detailed map of the distribution of *I. patachonicus* based on specimens, published records, and adequately documented, unpublished observations. Specimens are shown as solid circles, sight records as open circles; evidence of breeding (nests, broods) is indicated by diagonal slashes.

Chile north to the vicinity of Santiago (33° S); this species occurs at least infrequently as far north as 39° S in Chile (M. Christie, unpublished inventory for Parques Nacionales de Argentina) or the Provincee of Ñuble (Araya M. *et al.* 1986). Goodall *et al.* (1951:163) gave its northern limits in Chile as Bahia de Talcahuano on the coast and Ñuble inland. Fjeldsa and Krabbe (1990:120)

described *T. patachonicus* as: "Common at 700–1200 m on barren upland plateaus of inland Sta Cruz and on the Somuncura plateau of Rio Negro, Arg., and in Ñuble ascends to 1800 m." The northernmost Atlantic specimen of *T. patachonicus* from Río Negro Province, Argentina (Scott and Sharpe 1904), and sight records from Bahía San Blas, Buenos Aires Province (M. Nores, pers. comm.), and Costa Bonita, Buenos Aires Province (Narosky *et al.* 1985, Narosky and Fiameni 1987) probably pertain to casual, nonbreeding vagrants.

Although inland records of Flying Steamer-Ducks are most frequently made on high-altitude lakes, the species also has been reported on low-altitude lakes in Santa Cruz, Argentina and in riverine habitats near Lago Viedma, Santa Cruz, Argentina. It is believed widely that *T. patachonicus* on the Falklands breeds only on freshwater lakes (Weller 1972, 1976), and that the species is uncommon throughout the archipelago (Strange 1972b:206). It is likely that birds breeding on freshwater, both on the continent and the Falklands, move to marine coasts for the winter. Reynolds (*in* Lowe 1934:475) wrote of *T. patachonicus* in Isla Grande, Tierra del Fuego: "In winter it is restricted to the coast, where in summer many breed; but others penetrate far inland, spreading wherever there is water from the sea to the mountains." However, Finn (1924:139), who recognized but a single species of *Tachyeres*, wrote: "...In Tierra del Fuego they [steamer-ducks] are found on fresh water also, and when this freezes in winter, often die in trying to find other quarters." This remark may stem from the statement of Crawshay (1907:114–115): "Frequently I found these birds [steamer-ducks] lying dead inland, starved to death apparently, through the freezing of their waters." In contrast, but without documentary evidence or references, Soothill and Whitehead (1978:280) stated that the species: "In winter, flies less often and can be found resting or sleeping on frozen inland waters, but in Isla Grande (Tierra del Fuego) it is restricted to the coast during winter months."

TACHYERES BRACHYPTERUS (LATHAM, 1790) FALKLAND FLIGHTLESS STEAMER-DUCK

Anas brachyptera.—Latham (1790:834; listed in generic synonymy, may have included *T. patachonicus*).

Micropterus brachypterus.—Eyton (1838:144, in part; 1869a:101, in part).

**Micropterus brachyterus*.—Eyton (1856:348, in part).

Micropterus cinereus.—Gould (1859:96); Abbott (1861:150, 161); Sclater (1861a:367; 1868:529; 1872:256; 1877:337); Cunningham (1871a:493, in part).

Tachyeres cinereus.—Sclater (1879a:376; 1880b:529; 1881:107, in part; 1882:792; 1883:442; 1896:450); Holmberg (1895:[221], in part); Dabbene (1902:403–404, in part); Ramsay (1915:211); Wace (1921:201); Bennett (1924:280–282; 1926:327, in part); Vallentin (1924:322); Phillips (1925:134, 287–288, in part); Snouckaert van Schauberg (1926:150–151, in part); Seth-Smith (1927:245); Smyth (1927:12); Stresemann (1927:47, in part); Boubier (1934:85–86, in part).

Micropterus patachonicus.—Oustalet (1891:212–216, 218, 220–222, 224–226, 227–231, plate 5, in part).

Tachyeres brachypterus.—Lowe (1934:479–488, 490–493, in part); Reynolds *in* Lowe (1934:470–472, 474–477, in part); Zotta (1935:180, in part; 1944:30, in part); Murphy (1936:199, 208, 953–956, 958, 961–962, 964–965, 968–969); Steullet and Deautier (1936:365–367, in part); Reed (1939:34–35, in part); Laubmann (1940:19); Boetticher (1942:42; 1952:23, 68, 91); Stonor (1942:17–18); Delacour and Mayr (1945:15, 38; 1949:42, 63); Hellmayr and Conover (1948:374–376); Goodall *et al.* (1951:162); Anonymous (1952:49); Sladen (1952:222); Pergolani de Costa (1953:36; 1970:35); Delacour (1954:273, 276); Moynihan (1958:183); Olrog (1959:70; 1963:100; 1968a:110; 1968b:plate 11; 1979:50; 1984:92, 269); Van Tyne and Berger (1959:233–234; 1976:397); Cawkell *et al.* (1960:217); E. R. Pettingill (1960:195); O. S. Pettingill (1960:606;

1965:71; 1982:920); Schönwetter (1960:131); Cawkell and Hamilton (1961:13, 15); Berndt and Meise (1962:192); Johnsgard (1962:131; 1965:93; 1968:105; 1978:138; 1979:452); Prince Philip (1962:54); Godoy (1963:31); Carlquist (1965:231–233, in part); McKinney (1965:212); Smith (1965:55); Johansen (1966:231); Meyer de Schauensee (1966:40); Stresemann and Stresemann (1966:305); Gewalt (1968:188–189); Griswold (1968:32); Johnstone (1968:127); Lack (1968:347); Schmidt (1969:125); Raikow (1970:570; 1985:82); Woods (1970:18–19, 1975:118; 1980:49); Weller (1971:108; 1972:26, 44, plate 1; 1975a:295; 1975c:110; 1976:45); Scott (1972:48); Strange (1972a:256); Bock (1973:208); Lack (1974:85); Merne (1974:34, 80); Daciuk (1975:172; 1976:27); Morony *et al.* (1975:12); Welty (1975:239, 458; 1982:282, 543); Brush (1976:482); Wolters (1976:98); Jacob (1977:52); Navas (1977:35–36); Navas and Bo (1977:79); Clements (1978:28); De la Peña (1978:58; 1986:81); Kear (1978:61); Soothill and Whitehead (1978:281); Blandamer and Burton (1979:132); Boswall and MacIver (1979:75–76); Todd (1979:160, 162); Howard and Moore (1980:71; 1984:71); Tonni (1980:11, 14); Warham (1980:98); Gotch (1981:82); Humphrey and Thompson (1981:1, 3–6, 19); Humphrey and Livezey (1982a:1–2, 21–22; 1982b:368, 371; 1985:944–951); Mlíkovsky (1982:728); Carpi (1984:116); Livezey and Humphrey (1982:12; 1983:485–486; 1984a: 257–259; 1984b:368, 375–376; 1985:154–156; 1986:540–549, 551–556); Scherer and Hilsberg (1982:360); Daciuk and Heber (1984:174); Kolbe (1984:66, 170–172); Mendall *et al.* (1984:306); Walters (1984:18); Edwards (1985:21); Harrison (1985:655); Nuechterlein and Storer (1985:87); Livezey (1986b:512; 1986c:458, 460–463, 465; 1989a:1–3, 5–7, 9–16, 20–22, 24–28, 31–33, 40; 1989b:182); Livezey *et al.* (1986:445–448, 450); McGowan (1986:305, 306); Yamashina (1986:70); Narosky and Yzurieta (1987:79); Cabal (1988:24); Gauthier (1988:113); Madge and Burn (1988:58, 183); Ryan *et al.* (1988:29); Sibley and Monroe (1990:32).

Tachyeres pteneres.—Housse (1945:91; 1948:329).

Tachyeres brachypterus.—Anonymous (1951: 34).

Tachyeres branchyptera.—Kendeigh (1952:187); Cott (1953a:414; 1953b:651).

Tachyeres brachyapterus.—Gruson (1976:11).

Tachyertes brachypterus.—Adams and Templeton (1979:38).

Tachyeres patachonicus.—Wittenberger and Tilson (1980:211).

Tachyeres brachytterus.—Provine (1983:19; 1984:453).

Tachyceres brachypterus.—McGowan (1982: 215).

Vernacular Names

English

Logger-head.—Bennett (1924:280–282).

Sea logger.—Bennett (1924:281).

Logger (duck).—Bennett (1926:327).

Falkland Flightless Steamer Duck.—Murphy (1936:954).

Falkland Steamer Duck.—Clements (1978:28).

Spanish

Remero veloz, cortas alas.—Housse (1945:91).

Pato vapor de Malvinas.—Delacour and Mayr (1949:63).

Pato vapor de las Malvinas.—Pergolani de Costa (1953:36).

Pato-vapor malvinero.—MacDonagh (1941:45).

German

Mitteldampfschiffente.—Berndt and Meise (1962:192).

Falkland-Dampfschiffente.—Bock (1973:208); Wolters (1976:98).

French

Canard aux ailes courtes.—Lesson (1837:533; 1838:720).

Canard-vapeur des Iles Falkland.—Johnsgard (1978:138).

Czechoslovak

Kachyně krátkokokřídla.—Kolbe (1984:171).

Russian

Фолклендская утки-пароход —Kolbe (1984: 171).

Japanese

フナガモ —Yamashina (1986:70).

Original Description and Type

This species, and the Magellanic *T. pteneres* (below), were collectively differentiated from the smaller, flighted *T. patachonicus* by numerous workers since King (1831). Although many of the early accounts of steamer-ducks were based on observations of apparently flightless birds in the Falkland Islands (e.g., Lesson 1826, Darwin 1839b), comparatively few authorities included specimens from the Falkland Islands in their comparisons; exceptions included Abbott (1861), Bennett (1924, 1926), and Phillips (1925, in part). The original description by Latham (1790:834) included as diagnostic characters of the species its orange bill, gray body, short wings, white wing patches, and large size (between that of a goose and a swan). In his 1790 work, Latham gave the range of the species as the Falkland Islands, whereas in his earlier work he (1785:439) included Staten Island (Isla de los Estados). This species was diagnosed as specifically distinct from continental flightless steamer-ducks by Murphy (1936).

No types were designated and no type material is known. Accordingly, we designate as neotype the following skin specimen, held at the American Museum of Natural History, New York:

Specimen no. 443786—Male; collected at Port Stanley, East Falkland Islands; on 27 October 1915; by R. H. Beck.

Standard Measurements of Adults
(mean ± standard deviation, range, *n*)

Total weight (g).—Males: 4228 ± 443, 3300–4800, 12. Females: 3519 ± 336, 2900–4196, 11.

Wing length (arc, mm).—Males: 276 ± 13, 238–296, 24. Females: 268 ± 12, 245–292, 15.

Culmen length (mm).—Males: 56.8 ± 2.2, 53–61, 25. Females: 57.2 ± 2.1, 53–60, 15.

Nail width (mm).—Males: 13.5 ± 0.8, 11–15, 25. Females: 12.5 ± 0.8, 11–14, 15.

Tarsus length (mm).—Males: 67.8 ± 3.1, 60–72, 25. Females: 63.8 ± 2.5, 58–67, 15.

Tail length (arc, mm).—Males: 102 ± 5, 92–110, 15. Females: 96 ± 7, 76–103, 12.

Measurements (mm) of Eggs (*N* = 11)

Length.—mean = 81.8, range 77–86.
Width.—mean = 56.6, range 56–57.

Brief Description

The body is predominantly battleship gray in aspect with considerable chestnut on scapulars, sides, and flanks; lower breast, belly, and most secondaries are white (Fig. 4). Central tail feathers are elongate and recurved. Males are larger and more robust than females. Bill color of adult males is bright yellow-orange; bill is largely orange in adult females, and darker in subadults and juveniles of both sexes.

There are three molts and plumages per cycle, the prebasic molt replacing the whole feather coat, the other molts replacing only the feathers of the head and neck. The definitive alternate plumage is sexually dichromatic; the definitive supplemental plumage is also probably sexually dichromatic.

Juvenal and basic plumages: head and neck (both sexes) dark brown with a faint whitish postocular streak in the juvenal plumage.

Definitive alternate plumage: male—gray crown, brown cheek, white postocular streak; female—head and neck dark brown with white postocular streak.

Definitive supplemental plumage: male—head and neck white (crown pale gray in some individuals) with small patch of chestnut on throat; female—unknown.

Class-I downy differs from downies of all other *Tachyeres* in having the postocular streak undivided and the supraloral and supraocular patches narrow and continuous with the postocular streak.

Distribution

Endemic to and abundant throughout the Falkland Islands on marine coasts and nearby ponds; unfortunately, available records provide an inadequate representation of the distribution and

breeding range of the species (Fig. 6). The presence of *T. brachypterus* on the Jason Islands is likely but unconfirmed, but the species evidently does not inhabit Beauchene Island. Cawkell and Hamilton (1961:13) reported that individual birds have been observed three miles from shore.

Tachyeres pteneres (Forster, 1844) Magellanic Flightless Steamer-Duck

Oidemia patachonica.—King (1828:100); synonymized with *Micropterus brachypterus* (currently segregated as *T. pteneres*) by King (1839:35, 542), Strickland (1841:39), Gibson (1877:136), and Stenhouse (1929:185; 1930:274). Kuroda (1942:41) mistakenly stated that Gibson (1877) synonymized *Oidemia patachonica* King with *Anas cristata* Gmelin. As detailed by Herman *et al.* (1990:13), *Oidemia patachonica* was suppressed and placed on the Official Index of Rejected and Invalid Specific Names in Zoology *via* Livezey (1989b) and International Commission on Zoological Nomenclature (1991).

**Micropterus brachyptero*.—King (1831:15).

Micropterus brachypterus.—Eyton (1838:144, in part; 1869a:101, in part); King (1839:542).

Anas pteneres.—Forster (1844:338).

Micropterus cinereus.—Cox (1863:235, in part); Newton (1870:504); Cunningham (1871a:493, in part); Giglioli (1875:933–943, 963); Oustalet (1891:212–216, 220–222, 224–226, 228–231, plate 4); Selater (1892:173–174); Carbajal (1900:282); Agostini (1955:216).

Tachyeres cinereus.—Selater (1881:107, in part); Sharpe (1881:13, in part); Holmberg (1895:[221], in part); Schalow (1898:672–673); Dabbene (1902:403–404, in part; 1910:233); Crawshay (1907:110, in part); Nicoll (1908:163, in part); Blaauw (1912a:47–48; 1912b:7; 1916:488–492, plate XIV; 1917:275–276; 1921:57–58); Selater (1913:315); Mogensen (1917:85; 1930:207); Anonymous (1920:77); Phillips (1925:134, 287–288, in part); Bennett (1926:327, in part); Snouckaert von Schauberg (1926:150–151, in part); Stresemann (1927:47, in part); Stenhouse (1929:185; 1930:274); Dabbene (1932:205–206); Reynolds (1932:35); Boubier (1934:85–86, in part).

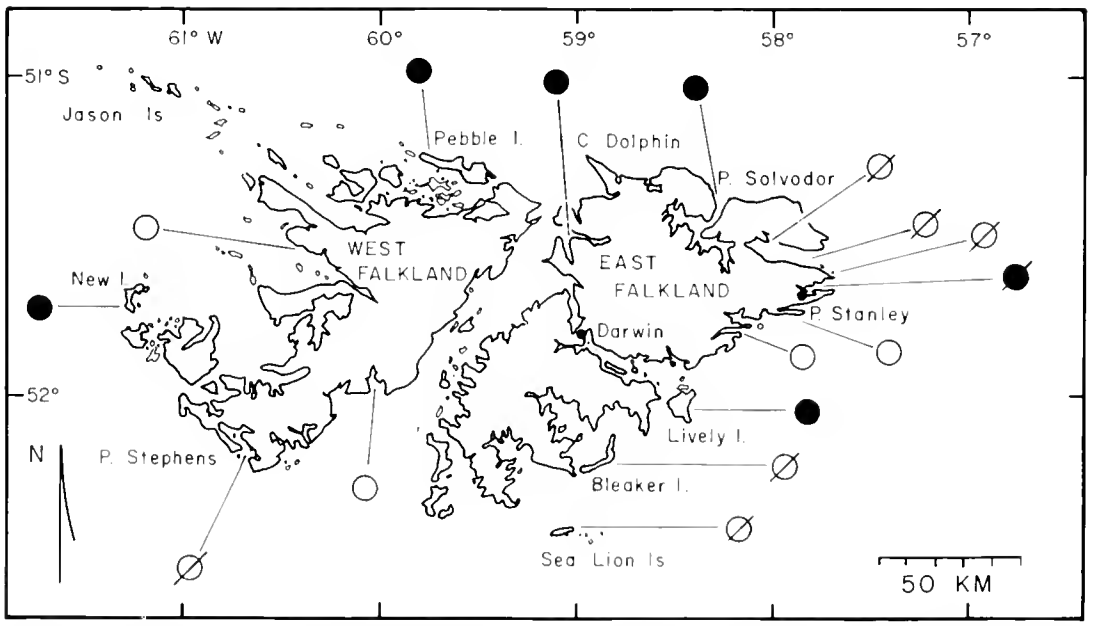

Fig. 6. Detailed map of the distribution of *T. brachypterus* based on specimens, published records, and adequately documented, unpublished observations. Specimens are shown as solid circles, sight records as open circles, and evidence of breeding (nests, broods) is indicated by diagonal slashes.

Tachyeres brachypterus.—Hellmayr (1932:335, 337); Lowe (1934:479–488, 490–493, in part; 1935:424); Reynolds (1934:350–351; 1935:84); Reynolds *in* Lowe (1934:470–472, 474–477, in part); Castellanos (1935:36); Steullet and Deautier (1935:365–367, in part); Zotta (1935:180, in part; 1944:30, in part); Junge (1939:161, in part); Reed (1939:34–35, in part); Behn (1942:121); Housse (1942:177; 1948:329); Pereyra (1943:227); Barros V. (1945:200; 1948:52); Carlquist (1965:231–233, in part).

Tachyeres brachyptera.—Anonymous (1935:129).

Tachyeres pteneres.—Murphy (1936:199, 953–958, 964–965, 968–969); Bullock (1936:137); Steullet and Deautier (1936:367); Reed and Philippi B. (1938:13); Laubmann (1940:19–20); Anonymous (1942:310; 1950:44); Housse (1945:92); Trimble (1943:419); Delacour and Mayr (1945:15, 38; 1949:40, 42, 63); Philippi B. (1945:144; 1964:47, in part); Hellmayr and Conover (1948:374–376); Olrog (1948:473; 1950:518; 1959:70; 1963:100; 1968a:111; 1968b:plate 11; 1979:500; 1984:92, 269; the last five references evidently included both *T. pteneres* and *T. leucocephalus*); Yañez (1948:153; 1949:8, 10); Goodall *et al.* (1951:162, 165, 167); Boetticher (1952:23, 68, 91); Pergolani de Costa (1953:36; 1970:35); Verheyen (1953a:384, 435; 1953b:463, 486–487; 1955:2, 15; 1958:9); Delacour (1954:270–271, 274); Scott (1954:61; 1972:48); Philippi-B. *et al.* (1954:29); Holgersen (1957:59); Moynihan (1958:183, 201); Lysaght (1959:289, 312); Van Tyne and Berger (1959:233; 1976:397); Woolfenden (1961:4); Schönwetter (1960:132); Berndt and Meise (1962:192); Godoy (1963:31); Humphrey and Clark (1964:186); Bernath (1965:98); Johnsgard (1965:94; 1968:105; 1978:136, in part; 1979:452, in part); Johnson (1965:195); Pettingill (1965:71); Smith (1965:55); Johansen (1966:231); Meyer de Schauensee (1966:40, in part; 1970:32, in part; 1982:32, in part); Stresemann and Stresemann (1966:305); Gewalt (1968:188); Griswold (1968:32); Lack (1968:347; 1974:85); Schmidt (1969:125); Weller (1969:128; 1975b:86; 1975c:110; 1976:45); Humphrey *et al.* (1970:129–137); Markham (1970:45, 48; 1971:22); Raikow (1970:570; 1985:82); Barros V. (1971:172); Bock (1973:208–209); Jehl (1973:129; 1975:596); Pisano V. (1973:42); Texera (1973:295–297); Vigil (1973:69, 71, in part); MacLean (1973:24; 1974:193); Merne (1974:34, 79); Morony *et al.* (1975:12); Woods (1975:122); Brush (1976:482, 485); Gruson (1976:11); Jehl and Rumboll (1976:146); Kühnemann (1976:157); Venegas C. (1976:177–180, 183; 1981:216–217; 1986:11, 61); Wolters (1976:98); Blake (1977:227, in part); Daskam (1977); Jacob (1977:52–58; 1982:87); Navas (1977:35–36); Navas and Bo (1977:79); Reed (1977:27); Sielfeld K. (1977:285, 294); Clements (1978:28); De la Peña (1978:58; 1986:80, in part); Soothill and Whitehead (1978:281); Boswall and MacIver (1979:75); Goodall (1979:76); Todd (1979:160); Venegas C. and Jory H. (1979:72); Clark (1984:212–213; 1986:100, in part); Howard and Moore (1980:71; 1984:71); Erize *et al.* (1981:178); Gotch (1981:83); Humphrey and Thompson (1981:1, 3, 5–6, 10); Araya (1982:5); Humphrey and Livezey (1982a:1–2, 21–22; 1982b:368, 370–371; 1985:944–951); Jacob and Ziswili (1982:274, 276); Livezey and Humphrey (1982:12–16; 1983:485–486; 1984a:257; 1984b:368–373; 1985:154–155; 1986:540–549, 552, 556); Mlíkovský (1982:728); Scherer and Hilsberg (1982:360); Carpi (1984:116, in part); Daciuk and Heber (1984:174, in part); Kolbe (1984:66, 170–172); Mendall *et al.* (1984:306); Walters (1984:18); Edwards (1985:21); Araya M. *et al.* (1986:116, in part); Livezey (1986b: 512; 1986c:458, 460–466; 1989a:1, 3, 6–15, 20–22, 24–27, 31–33, 41; 1989b:182); Livezey *et al.* (1986:445–448, 450); McGowan (1986: 305); Yamashina (1986:70); Narosky and Yzurieta (1987:79); Wolsey (1987:39); Chebez (1988:26); Gauthier (1988:113); Madge and Burn (1988:58, 181); Ryan *et al.* (1988:29, 31, 33); Sibley and Monroe (1990:32).

Tachyeres patachonicus.—Junge (1939:166, in part).

**Iacheres pteneres*.—Vera (1974:1).

†*Tachyertes pteneres*.—Adams and Templeton (1979:38).

Vernacular Names

English
Short-winged micropterus.—Eyton (1838:144).
Common Steamer.—Finn (1924:139).
Magellanic Flightless Steamer Duck.—Murphy (1936:954).
Flapping loggerhead.—Bridges (1948:97).
Flightless Steamer-Duck.—Narosky and Yzurieta (1987:79).

Spanish
Pato vapor que no vuela.—Bullock(1936:137).
Pato quetro.—Barros V. (1945:200).
Pato quetru.—Housse (1945:92).
Remero veloz sin alas.—Housse (1945:92).
Pato vapor magellanico.—Delacour and Mayr (1949:63).
Pato quetru no volador.—Goodall *et al.* (1951:165).
Pato vapor no volador de Cabo de Hornos.—Pergolani de Costa (1953:36).
Pato vapor comun.—Olrog (1959:70).
Pato motor.—Barros V. (1971:172).
Pato vapor grande.—Vigil (1973:69, 71).
Pato vapor de mar.—Vigil (1973:69).
Pato-vapor austral.—Narosky and Yzurieta (1987:79).

Dutch
Stoombooteenden.—Blaauw (1912b:7).

German
Rersendampfschiffente.—Berndt and Meise (1962:192).
Fluglose Dampfschiffente.—Johansen (1966:231).
Magellan-Dampfschiffente.—Gewalt (1968:188); Wolters (1976:98).

French
Micropière cendre.—Oustalet (1891:229).
Canard-vapeur de Patagonie. Johnsgard (1978:136).

Czechoslovak
Kachyně parníková.—Kolbe (1984:170).

Russian
Магелланова утки пароход.—Kolbe(1984: 170).

Japanese
オオフナガモ.—Yamashina (1986:70).

Fuegian (Yahgan)
Alakuch.—Phillips (1925:288).
Alacush.—Reynolds *in* Lowe (1939:471).

Fuegian (Ona)
Aloksh.—Reynolds *in* Lowe (1934:471).

Fuegian (Yamana)
Alakush.—Barros V. (1971:172).

Original Description and Type

This species was probably the species first observed by European explorers (Sarmiento de Gamboa in 1582), contrary to the claim by Sclater and Salvin (1876:402) that the genus was discovered by Europeans in the Falkland Islands, and it was this distinctive flightless form against which the flighted form was compared and ultimately distinguished as specifically distinct (e.g., King 1831, Oustalet 1891, Blaauw 1917, Lowe 1934). This species was segregated from its Falkland flightless congener by Murphy (1936). The original description by Forster (1844:338–340) was exceptionally detailed, including mention of its flightlessness, descriptions of plumage patterns, colors of soft parts, anatomical details of the bill and feet, counts of rectrices and remiges, its Magellanic distributional range, and a variety of measurements, including an (unfortunately exaggerated) body weight (16 libras, 7–8 kg).

No holotype for *L. pteneres* was designated. Purported co-type material for suppressed *Oidemia patachonica* was cited by Stenhouse (1929, 1930), Warren (1966), and Warren and Harrison (1973). Consequently, we designate as neotype the following skin specimen, held at the American Museum of Natural History, New York:

Specimen no. 443669—Male; collected at Isla Chiloe, Chile; on 19 May 1914; by R. H. Beck.

Standard Measurements of Adults
(mean ± standard deviation, range, *n*)

Total weight (g).—Males: 5394 ± 392, 4950–6500, 16. Females: 4184 ± 463, 3400–5000, 17.

Wing length (arc, mm).—Males: 273 ± 12, 243–294, 38. Females: 262 ± 11, 235–282, 28.

Culmen length (mm).—Males: 59.4 ± 3.8, 54–70, 37. Females: 58.4 ± 3.4, 50–63, 30.

Nail width (mm).—Males: 16.1 ± 0.9, 14–18, 37. Females: 15.3 ± 0.8, 13–17, 30.

Tarsus length (mm).—Males: 71.4 ± 3.8, 65–79, 37. Females: 67.5 ± 3.2, 62–75, 30.

Tail length (arc, mm).—Males: 98 ± 8, 83–112, 14. Females: 87 ± 7, 73–106, 27.

Measurements (mm) of Eggs (n = 32)

Length.—mean = 82.7, range 78–88.
Width.—mean = 56.5, range 52–61.

Brief Description

This species is the largest of the steamer-ducks. The body is predominantly battleship gray in aspect, and differs from *T. patachonicus*, *T. leucocephalus*, and *T. brachypterus* in lacking extensive chestnut on scapulars, sides, and flanks. The lower breast, belly, and most secondaries are white. The central tail feathers are slightly elongate and recurved (Fig. 4). Males are larger and more robust than females. Bill color of adults of both sexes is bright yellow-orange; bill is dark in subadults and juveniles of both sexes.

There are two molts and plumages per cycle, the prebasic molt replacing the whole feather coat, the prealternate molt replacing only the feathers of the head and neck. The definitive basic and alternate plumages are sexually dichromatic. The definitive basic plumages of the head and neck of neither sex resemble the juvenal plumage. Juvenal plumage of head and neck (both sexes) is medium to dark gray, lighter ventrally; there is a small patch of brownish chestnut on the throat.

Definitive basic plumage: male—dark gray crown, light gray cheek, indistinct postocular streak, small indistinct chestnut throat patch; female—head and neck medium-dark gray, short faint postocular streak, small indistinct patch of chestnut on throat.

Definitive alternate plumage: male—light gray crown, rest of head and neck pale gray to white with indistinct patch of pale cinnamon on throat; female—crown dark gray, cheeks medium gray, short pale gray to whitish postocular streak, chestnut patch on throat.

The class-I downy differs from downies of all other *Tachyeres* in having the postocular streak divided, and the supraloral and supraocular patches are very small (and separate) or lacking entirely.

Distribution

Resident on marine coasts and islands from immediately north of Isla de Chiloé, Chile south to Tierra del Fuego, including Isla de los Estados, Argentina, where H. M. Cadot, Jr. (pers. comm., 1971) found them to be the most common duck (Fig. 7). Olrog (1963:100) stated that the species ranges north to Concepción, Chile, during winter, but confirmatory specimens are lacking. Olrog (1948:473) suggested that *T. pteneres* nested also on Lago Fagnano, a large inland freshwater lake on Isla Grande, Tierra del Fuego, but no documentary evidence was provided and Olrog deleted this idea from his subsequent works. Contrary to the statements of Olrog (1959, 1963, 1968, 1979, 1984), Philippi-B. (1964:47), Smith (1965:55), Meyer de Schauensee (1966:40; 1970:33), Vigil (1973:69), Woods (1975:122), Blake (1977:227), De la Peña (1978:58; 1986:80; 1987:40), Johnsgard (1978:137; 1979:452), Carpi (1984:117), Daciuk and Heber (1984:174), Clark (1986:100), and Araya M. *et al.* (1986:61), there is no specimen to document that *T. pteneres* occurs, even during winter, on the Atlantic coast north of Rio Grande, Isla Grande, Tierra del Fuego. The idea that *T. pteneres* occurs on the Atlantic coast of Patagonia may represent, in part, confusion (in Chubut) with flightless *T. leucocephalus* or the reluctance of many *T. patachonicus* to take flight, but it appears to have had its origin in the vague, partially incorrect delimitation of its range given by Murphy (1936:199): "The distribution of the mainland Flightless and Flying species *largely coincides throughout* a range extending from Puerto Deseado on the Atlantic, southward to Cape Horn.... The Flightless species...is *normally* absent from the whole eastern part of Tierra del Fuego and the Atlantic coast of Patagonia. *Most* of the steamer ducks in these districts represent the Flying species [emphasis added]."

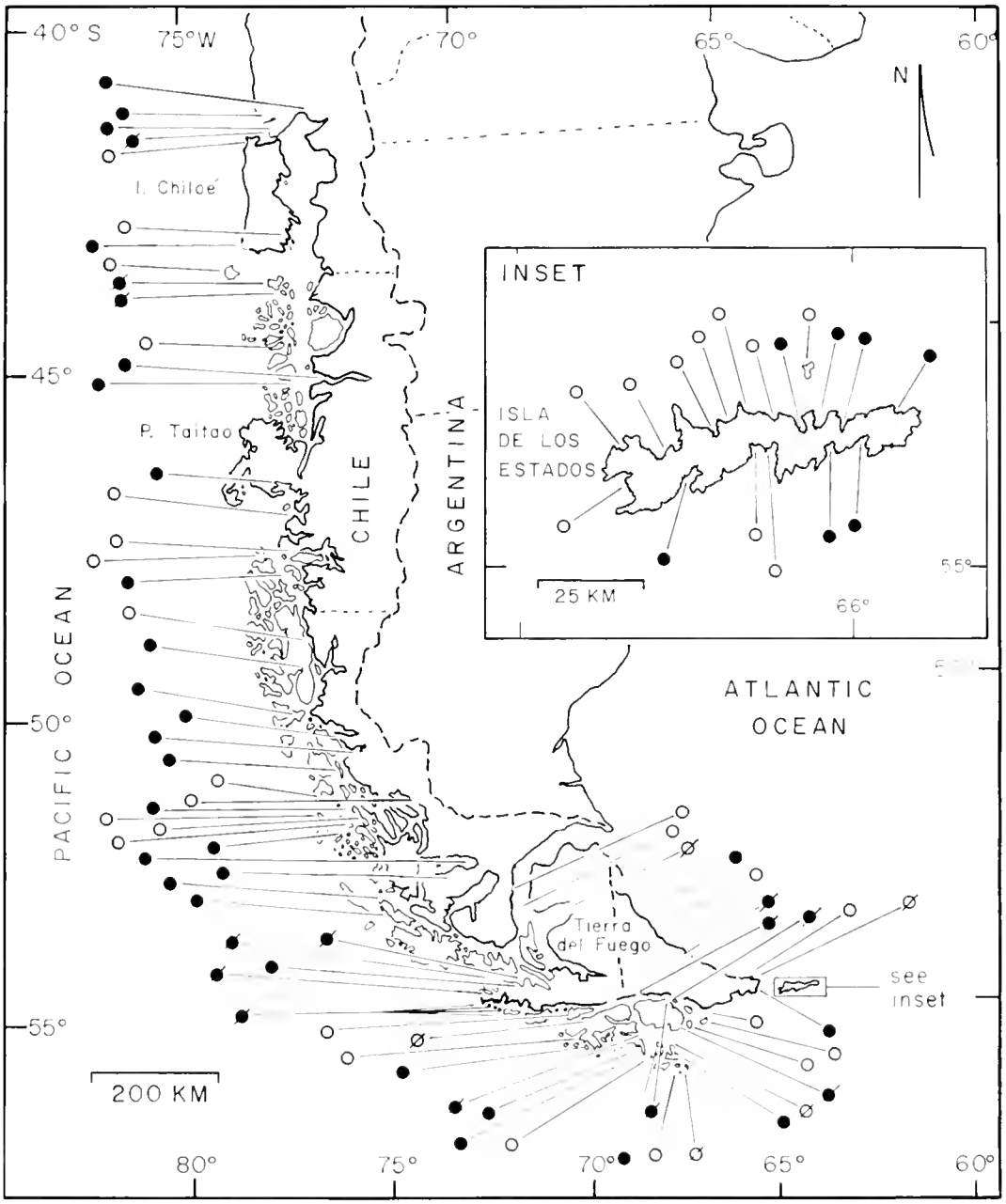

Fig. 7. Detailed map of the distribution of *L. ptenices* based on specimens, published records, and adequately documented, unpublished observations. Specimens are shown as solid circles, sight records as open circles; evidence of breeding (nests, broods) is indicated by diagonal slashes.

Tachyeres leucocephalus Humphrey and Thompson 1981
White-headed Flightless Steamer-Duck

Tachyeres pteneres.—Olrog (1959:70; 1963:100; 1968:111; 1979:500; 1984:92, 269; in part, see under *T. pteneres*); Meyer de Schauensee (1966:40, in part; 1970:32, in part); Vigil (1973:69, in part); Johnsgard (1978:136, in part); Carpi (1984:116, in part); Daciuk and Heber (1984:174, in part); Araya M. *et al.* (1986:61, in part); De la Peña (1986:80, in part).

**Tachieres patachonicus*.—Korschenewski (1969:52; may have included *T. patachonicus*).

Tachyeres patachonicus.—Boswall and Prytherch (1972:125); Boswall (1973a:35); Jehl *et al.* (1973:58, 61, in part); Daciuk (1976:27–29; 1977:363, 371, in part, probably included *T. patachonicus*); Boswall and MacIver (1979:75–76, 78).

Tachyeres brachypterus.—Olrog (1979:50, in part).

Tachyeres leucocephalus.—Humphrey and Thompson (1981:3–6, 8,10); Humphrey and Livezey (1982a:1, 21, 22; 1982b:368, 37; 1983:4; 1985:944–951); Livezey and Humphrey (1982:12–16; 1984a:257; 1984b:368–369, 371, 375–376; 1985:154–156; 1986:540–552, 554); Meyer de Schauensee and Mack (1982:431, 438); Straneck *et al.* (1982:256); Howard and Moore (1984:71); Edwards (1985:21); Livezey *et al.* (1985:18–19; 1986:445–450); Raikow (1985:82); Livezey (1986b:512; 1986c:458, 460–463, 465–466; 1989a:1, 3, 6–7, 9–15, 20–23, 25, 28, 31–33, 41); Humphrey *et al.* (1987: 68–69); Narosky and Yzurieta (1987:79); Madge and Burn (1988:58, 182); McGowan (1989:538–540, 542); Sibley and Monroe (1990:32).

Tachyeres leucocephala.—Corbin (1983:216); Kolbe (1984:170, 171).

Vernacular Names

English

White-headed Flightless Steamer-Duck.—Humphrey and Thompson (1981:3).

Chubut Steamer-Duck.—Narosky and Yzurieta (1987:79).

White-face(d) Steamerduck.—McGowan (1989:538–539).

Spanish

Pato vapor nor-patagónico.—Erize *et al.* (1981:148).

Pato vapor no volador de cabeza blanca.—Humphrey and Livezey (1985:944).

Pato-vapor cabeza blanca.—Narosky and Yzurieta (1987:79).

Original Description and Type

This species was recognized as specifically distinct only in 1980 (Humphrey and Thompson 1980) and described by Humphrey and Thompson (1981), although specimens of this form were observed and collected infrequently during the 1960s and 1970s; a single skin specimen was taken as early as 1886. Humphrey and Thompson (1981) diagnosed the species using a combination of its intermediate external measurements (body mass, wing-loadings, and lengths of the culmen, tarsus, and middle toe), two qualitative osteological characters (robustness of the humerus and caudal breadth of the sternal basin), the largely white head of adult males in alternate plumage, and the comparatively broad white postocular stripe of adult females in alternate plumage.

The holotype (skin specimen) was designated by Humphrey and Thompson (1981) and deposited at the Museo Argentino de Ciencias Naturales, Buenos Aires, Argentina:

Specimen no. 52694—Male; collected at Puerto Melo, Chubut, Argentina; on 24 September 1979; by M. C. Thompson and P. S. Humphrey.

Standard Measurements of Adults
(mean ± standard deviation, range, *n*)

Total weight (g).—Males: 3808 ± 491, 2600–4400, 19. Females: 3013 ± 295, 2450–3550, 16.

Wing length (arc, mm).—Males: 281 ± 10, 262–295, 14. Females: 273 ± 10, 255–290, 13.

Culmen length (mm).—Males: 55.9 ± 2.9, 51–63, 16. Females: 55.8 ± 1.5, 54–59, 13.

Nail width (mm).—Males: 12.4 ± 0.8, 11–14, 16. Females: 11.8 ± 0.8, 10–13, 13.

Tarsus length (mm).—Males: 64.8 ± 1.9, 61–69, 16. Females: 62.5 ± 2.3, 59–66, 13.

Tail length (mm).—Males: 97 ± 10, 78–109, 7. Females: 94 ± 6, 83–101, 7.

Measurements (mm) of Eggs (n = 15)

Length.—mean = 81.2, range 72–86.
Width.—mean = 54.2, range 51–56.

Brief Description

The body is predominantly battleship gray in aspect with considerable dusky brown on scapulars, sides, and flanks; lower breast, belly, and most secondaries are white (Fig. 4). Central tail feathers are slightly elongate and recurved. Males are larger and more robust than females. Bill color of adult males is bright yellow-orange; it is darker yellow-orange in adult females and subadults and juveniles of both sexes.

There are two molts and plumages per cycle, the prebasic molt replacing the whole feather coat, the prealternate molt replacing only the feathers of the head and neck. The definitive basic and alternate plumages are sexually dichromatic.

Juvenal plumage: head and neck (both sexes) is dark brown.

Definitive basic plumage: male—crown dark gray, cheeks reddish-brown, broad white postocular streak, large cinnamon patch on throat; female—head and neck dark brown with small, white postocular streak.

Definitive alternate plumage: male—head and neck predominantly white; crown, lores, and anterior cheek gray in some individuals, with small patch of cinnamon on throat; female—crown gray, cheeks brown; long, uninterrupted, prominent white postocular streak.

Class-I downy differs from downies of all other *Tachyeres* in having the supraloral and supraocular patches wide and continuous with the wide postocular streak.

Distribution

T. leucocephalus is limited in distribution to coastal Chubut, Argentina, from Península Valdes south through the Bahía de Camarones and Bahía de Concepción to the northernmost regions of the Golfo San Jorge (Fig. 8). Within this limited range, at least during the breeding season, this species is by far the most abundant species of *Tachyeres*; it may be that the very similar *T. patachonicus* occurs in this area only as a (non-breeding) straggler during the breeding season, or during winter.

MOLTS AND PLUMAGES

History of Study

General Knowledge of Anatid Plumages

The early explorers of southernmost South America and the Falkland Islands during the 17th and 18th centuries were not trained ornithologists. Nevertheless, they contributed a great deal to early understanding of the distribution and habits of steamer-ducks. Many of those who worked on steamer-ducks in the 19th and early 20th centuries—whether in the field or with museum specimens—were ornithologists by training or experience, or, at the very least, naturalists. Therefore, it is useful to assess the state of knowledge of molts and plumages of waterfowl in the 19th and early 20th centuries and how this might have influenced the assumptions, preconceptions, and conclusions of ornithologists of the period about the molts and plumages of steamer-ducks.

Newton (1895), in his classic *Dictionary of Birds*, stated that knowledge of molts and plumages of a great many species of European waterfowl was moderately advanced by the 19th century even though, as he pointed out (1895:595): "The literature relating to this branch of ornithology...[was] very small." Nevertheless there must have been considerable knowledge about the molts and plumages of those species of European waterfowl that had been hunted for centuries for

Fig. 8. Detailed map of the distribution of *T. leucocephalus* based on specimens, published records, and adequately documented, unpublished observations. Specimens are shown as solid circles, photographs as heavy rings, and sight records as open circles; evidence of breeding (nests, broods) is indicated by diagonal slashes.

food or sport. The flightless condition of waterfowl during the summer following the nesting season was well known as early as the 12th century and laws prohibiting the hunting of waterfowl during the nesting and molting seasons were passed in England as early as the 16th century (cf. Newton 1895:597). Popular and scientific knowledge about molts and plumages of many species of European

waterfowl during the 19th century was considerable, and it was known that many species:

(1) Are sexually dichromatic;

(2) Exhibit seasonal differences in appearance, viz., males of sexually dichromatic species have a bright plumage worn most of the year and assume a brief, dull eclipse plumage during the flightless period following the breeding season;

(3) Take two or three years before attaining adult (definitive) plumage; and

(4) Have male 'eclipse' (basic) and female plumages that are similar to or identical to the juvenal plumage.

The controversy that most affected early understanding of molts and plumages in *Tachyeres* was the debate concerning recognition of one or two species of steamer-duck. Most workers on steamer-ducks during the 19th and early 20th centuries were preoccupied with this taxonomic problem and not with interpretation of molts and plumages *per se*. In addition, most of them knew little or nothing about the molts and plumages of waterfowl and ignored the subject except insofar as descriptive data concerning plumage aspects appeared relevant to the taxonomic question.

There were, however, a few workers (e.g., Oustalet, Blaauw, Phillips, Chapman, Lowe, Murphy) who presumably were knowledgeable about the molts and plumages of European and other northern-hemisphere waterfowl. Their interpretations of the molts and plumages of steamer-ducks, however, either did not take this knowledge into account or were based on certain preconceptions concerning southern-hemisphere waterfowl. Because sexual dichromatism is weak or lacking in several southern-hemisphere species, these workers may have assumed that all southern-hemisphere waterfowl had only a single molt and one sexually monochromatic plumage per year. These workers, too, were preoccupied with the problematic taxonomy of steamer-ducks.

Even with good series of specimens of known age, a resource not available to ornithologists in the 19th and early 20th centuries, understanding the variation in plumage pattern of any species of waterfowl is difficult. Furthermore, until review of the genus by Murphy (1936), the whole problem was confounded by substantial taxonomic uncertainties. In what follows, we examine the growth of knowledge and interpretation of plumages and soft parts of steamer-ducks in three eras: (1) Era of Exploration, (2) Era of Taxonomic Controversy, and (3) Era of Murphy.

Era of Exploration

From the 16th into the 19th century, steamer-ducks were treated as a single species and descriptions of their plumages were typological. Three important points characterized this period: (1) descriptions of steamer-duck plumages were not associated with any taxonomic controversy; (2) steamer-ducks were universally understood to be flightless; and (3) it apparently did not occur to any of these early workers that steamer-ducks might have more than one plumage a year.

The explorers and naturalists of this period variously observed and collected specimens of steamer-ducks in the Magellanic region of southernmost South America and the Falkland Islands, and the cabinet naturalists of the day examined specimens collected in these regions and took account of the notes made by the collectors. Although some of the resulting descriptions of steamer-ducks were more detailed than others, all of them captured the essential generic features of a steamer-duck, namely that they were large, gray ducks with underparts and secondaries white, and yellow or orange bill and feet. Some accounts mentioned the orange wing-spurs (Forster 1777), and iris color as red brown (Forster 1777) or orange (Latham 1785).

The description by Forster (1844) of the plumage pattern of *Tachyeres (Anas) pteneres* was an exceedingly detailed account that, in its carefulness and attention to detail, was a century ahead of its time. His account of the structure and coloration of the bill and feet was exceptionally thorough. In addition, Forster described the white on the secondaries in great detail on a feather by feather basis, and he was the first to have noted that the lower breast, abdomen, and under tail coverts are yellowish-white (ochroleuca), an evanescent color not preserved in museum specimens. Forster also was exceptional because he specified the sexes of the specimens he described. He characterized

the head of the male as lutescenti-album with the eye region white and the upper neck silky white (sericeo-albus); he stated that the head and neck of the female are cinereous and the eye region is white.

Other descriptions of the plumage and soft parts of steamer-ducks by early explorers and naturalists were few in number and typically not sex-specific (e.g., Forster 1777, Latham 1785, Bonnaterre 1790, Buffon 1812, Quoy and Gaimard 1824, King 1828). Quoy and Gaimard (1824) visited the Falkland Islands in February, March, and April, and their account was the only one that mentioned red on the throat and breast; their description evidently concerned *T. brachypterus*, which, although indistinguishable from *T. patachonicus* in color pattern, was the species most frequently encountered in the coastal waters of the Falkland Islands. None of the early explorers and naturalists mentioned downy young steamer-ducks and juveniles, and none indicated any differences between the sexes in soft part colors.

Era of Taxonomic Controversy

Accounts of the molts and plumages of steamer-ducks from the early 19th century until 1936 included considerable new information about definitive, immature, and downy plumages, sexual dimorphism, and interspecific differences in plumage coloration and pattern of adults. Although a great many specimens of steamer-ducks were collected during this era and many descriptions of their plumages were detailed, the consensus continued to be that steamer-ducks had but a single plumage per year.

Interest in the taxonomic issue led several naturalists of the time to characterize phenotypic differences more enthusiastically than they might have otherwise. Because *T. patachonicus* and *T. brachypterus* are virtually indistinguishable in the field and difficult to tell apart as skin specimens, our discussion here will focus primarily on findings related to the continent, i.e., comparisons of *T. patachonicus* with *T. pteneres*. Whether interpreted as taxonomic or age-related differences, many of the characteristics of *T. patachonicus* and *T. pteneres* were included in these early descriptions.

Characteristics of Adult *T. patachonicus*

Adult *T. patachonicus* was described by various authors (under the names *brachypterus* and *cinereus*) as differing from adult *T. pteneres* in being smaller, having redder feathers on throat and scapulars (King 1831, 1839; Lesson 1837; Cunningham 1871b; Phillips 1925) and in having feathers of back, breast and flanks, scaly in appearance because of their dark borders and silvery centers (Oustalet 1891). Cunningham (1871b:95) wrote that "...Younger individuals (*M. Patachonicus*) are chiefly distinguished by...their greenish-black bills...." Cunningham, of course, believed that there was but a single species of steamer-duck of which younger individuals (called by other authors *patachonicus*) were capable of flight.

Oustalet (1891) observed no differences in bill color between male and female *T. patachonicus*; he noted only that in *T. patachonicus* the coloration of the beak is generally less lively and more uniform than in *T. pteneres*. Although Oustalet (1891) presented six comparative statements concerning the differences between *T. pteneres* and *T. patachonicus* (using older generic and specific names), Blaauw (1912, 1916, 1921) was the first to succinctly compare adults of *T. pteneres* (his *cinereus*) and *T. patachonicus* and describe sexual dimorphism in the two species. For *T. patachonicus*, Blaauw (1912a:47–48) wrote that "...both sexes are much *smaller* than the preceding one [*T. pteneres*] and the female is much smaller than the male. The *female* is also coloured quite differently. The male...is clear grey with a white breast and clear yellow bill....The female is much smaller than the male. The head is brown and the rest of the body of a beautiful *wine* colour with white breast." Blaauw (1916:491) noted later that the female "...is of a beautiful dark wine-colour, with grey centres to the feathers of the upperside and sides. The bill...is brown or black." He (1916:491) also stated that "...A pair [*T. patachonicus*] invariably consisted of a large clear grey bird with a yellow bill, and a much smaller brown one with dark bill."

Scott and Sharpe (1912:492) recognized only one species of *Tachyeres* and considered *T. patachonicus* the immature of the flightless species (*T. pteneres*) "...which seems not to attain full

adult plumage until at least the second and perhaps the third year of its life; moreover, the first breeding is probably accomplished in the phase of plumage called by Dr. Oustalet *M. patachonicus*." Scott and Sharpe provided a detailed description of a male specimen, now in the collections of the Field Museum of Natural History, which was collected at the mouth of the Río Negro in February 1898. Based on our examination of this specimen, the bird was undergoing prebasic molt and the remiges had not attained their full growth. Scott and Sharpe (1912) described the colors of the soft parts as follows: "Bill: Horn-color, shaded with blue and green, the nail abruptly black....The feet and legs are dull greenish brown, strongly shaded with orange." This description and that of the feather coat indicate that this specimen was molting into definitive basic plumage. Although predicated on a mistaken concept of phylogenetic relationships, Scott and Sharpe (1912:492) insightfully commented that: "The change of color to orange or cadmium-yellow in the breeding season is to be looked for, as similar changes in the colors of the bill occur in other allied sea-ducks." As far as we can tell, this is the first recognition of the fact that colors of the bill and feet in definitive male *T. patachonicus* become duller during the prebasic molt.

Phillips (1925) was aware of the problematic taxonomy of steamer-ducks and divided his descriptions of adult birds into those pertaining to three "phases" corresponding to the three species to be recognized later by Murphy (1936). Phillips (1925:288) described adult red-phase specimens (*Tachyeres patachonicus*) as follows: "Many of these birds (I have studied some forty-three specimens) do not suggest youth. They are mostly uniform in coloring, with adult tail-feathers, and in many cases the carpal spur is well developed. There are no apparent sex differences....Bill, in life yellowish above, and bluish or greenish below nostril, nail black. In dried skins nearly always dark lead-color all over culmen, sometimes slightly yellowish towards base, but never yellow all over as in *Tachyeres cinereus*....Legs and feet yellowish, very nearly, if not quite the same as in *Tachyeres cinereus*." Because Phillips noted no sexual differences, we judge that most of the males in his series of specimens must have been in basic plumage.

Chapman (1933:361) noted that "On January 24, 1924, on a fresh water pond in northern Tierra del Fuego, I saw a pair of adult Quettros (the male with the head and neck white) accompanied by one young about a week old, both of which adults, when flushed, took wing easily and flew out of sight toward the sea." This is probably the first description of a male *T. patachonicus* in supplemental plumage.

Characteristics of *T. pteneres*

Cunningham (1871b:95) described the plumage of *T. pteneres*, which he considered to be the adults of a single species of steamer-duck, as "...The bill is orange-yellow, with the unguis black. The head is cinereous, becoming gradually paler as the individual increases in age, with a small patch beneath the eye, and a streak above it, nearly white. The whole of the upper surface, the throat, the superior part of the breast, with the exception of a white speculum, are lead-gray. The lower part of the breast and abdomen vary from a tint verging on primrose-yellow to pale yellowish-white; and the legs and feet are dark yellow." This description is notable because: (1) Cunningham apparently did not consider the species to be sexually dichromatic; (2) he attributed variation in color of the head to variations in the ages of adult birds; and (3) he noticed the evanescent yellow bloom on the lower breast and belly.

Oustalet (1891) examined ten specimens of what he called *Micropterus cinereus*, all of which, from their localities, were *T. pteneres*. These specimens were described as having gray to bluish gray heads and that the rest of the body except for the lower breast and belly was gray, paler on the sides and flanks, and darker on the back, and without any trace of red. Bills of both sexes were yellow-orange with nail black. Comparing *T. pteneres* with *T. patachonicus*, Oustalet noted that the fundamental colors of the plumage of the adult are the same. He considered the colors of *T. pteneres* as generally less distinct than in *T. patachonicus* and that the gray color of the plumage of *T. pteneres* is not as dark as in *T. patachonicus* and the feathers of the back, breast, and flanks lack the scaly appearance found in *T. patachonicus*. Finally, Oustalet

noted that the red or reddish tint of the throat and breast of *T. patachonicus* is almost always lacking in *T. pteneres*.

Subsequent descriptions by Salvadori (1895), Nicoll (1904), Blaauw (1912, 1916, 1921), Mogensen (1917), and Phillips (1925) provided in varying detail the same descriptive information as did Cunningham (1871) and Oustalet (1891).

Sexual Differences of Adult *T. patachonicus*

Presumably because of the small amount of material available to them, King (1831, 1839) and Cunningham (1871b) did not remark upon the sexual dichromatism of *T. patachonicus*. Oustalet (1891) presented descriptions of six specimens of *T. patachonicus* including one adult female and one adult male. Although his descriptions indicate that the beak of the female was black becoming greenish-brown at the base of the upper mandible and that of the male was light orange-yellow, he made no note about sexual dichromatism in the species.

The sexual dichromatism of adult *T. patachonicus* was clearly described by several authors (Blaauw 1912, 1916, 1921; Mogensen 1917; Lowe 1934). Blaauw (1916:491) noted that: "A pair invariably consisted of a large clear grey bird with a yellow bill, and a much smaller brown one with a dark bill." Blaauw (1921:58) described the sexual dichromatism of adult *T. patachonicus* as follows: "The male is clear gray with a white breast and a clear yellow bill....The female has a brown head, and the rest of the body is of a beautiful vinaceous color, with a white breast. The bill is brown."

Sexual Differences of Adult *T. pteneres*

Most early descriptions of plumage pattern and soft part colors of *T. pteneres* did not address sexual dichromatism (Des Murs 1847, Cunningham 1871b). Oustalet (1891) examined ten specimens of *T. pteneres*, five of which were determined to be females and one a male. He described both sexes as having yellow or yellow-orange bills with black tips and feet yellow or yellow-orange variably mottled with gray.

Salvadori (1895) described an adult male in some detail, including colors of bill and feet, but noted (p. 375) of the female only that it was "Similar to the male, but somewhat smaller." Nicoll (1904) and Evans (1909) described both sexes of *T. pteneres* (under *T. cinereus*) as having orange or orange-yellow bill and feet, respectively.

Blaauw (1912, 1916, 1921) was the first to indicate details of sexual dichromatism in *T. pteneres*, noting (1921:57) that "...both sexes are gray; the male has a pale or pearl-gray head and neck, and a bright yellow bill. In the female the gray is duller, so that the head is not strikingly paler than the rest of the body. The bill is also yellow but not so clear in color." He did not mention any difference in size between the sexes.

Mogensen (1917) described male *T. pteneres* as being somewhat lighter than the female especially on the head, but did not mention any differences in bill color. Phillips (1925:288) noted of adult female *T. pteneres*: "Size somewhat smaller; color same as in male....Bill yellow or yellowish but not such a clear or brilliant yellow as in the male." Lowe (1934) stated that the adult female has "head and neck grey, not much darker than."

Juvenal Plumage of *T. patachonicus*

There was no mention of the juvenal plumage of steamer-ducks until the statement by Selater (1881:108) that "In all the immature birds the bill is uniform black." Oustalet (1891) described two "young" specimens which he identified as *T. patachonicus*. One of these, for which sex was not given, had the plumage mixed with tufts of down on the back and on the wings but still showing the principal colors of the adult plumage and the red tinge of the sides of the head and breast. The other specimen, which he determined to be female and younger than the first, was collected on 9 February 1883. The specimen had dark gray plumage with blackish brown on the borders of the feathers, the head was uniform gray without a white streak in the vicinity of the eye, and there was no white band on the wing; the last observation indicates that the growing juvenal remiges were still quite short.

Lowe (1934:476) stated that "When able to fly, and for some time afterwards, young *T. patachonicus* of both sexes are scarcely distin-

guishable from the adult females. In the immature, however, the transocular stripe, although apparently longer, lacks sharp contrast with the contiguous plumage and is not clearly defined." Evidently the "immature" plumage referred to by Lowe encompassed the post-juvenal, pre-definitive plumages of the head and neck.

Juvenal Plumage of *T. pteneres*

Nicoll (1904) collected in southern Chile west of the Straits of Magellan three specimens of what surely must have been *T. pteneres* (the adult male and female both had orange bills). One of the specimens was a juvenile with dark brown bill and feet. Blaauw (1921:57) noted that "In the young birds [of *T. pteneres*]...the plumage is tinged in some parts with brownish gray, but not enough to obscure the generally gray aspect. The bill color of such young birds is mixed with a dark greenish tint, and their legs are dark. These birds were evidently young of the year, since they were under the guidance of a pair of adults."

Phillips (1925:288) stated that: "We know that there are individuals which do not pass through any red or reddish-tinted phase. Whether these are exclusively the young of the gray phase (*Tachyeres cinereus*) we do not know. A specimen in juvenal plumage from Cape Horn with the primaries not yet fully developed...is gray all over the upper side and without the prominent wine-colored edges to the feathers on the breast, sides, and flanks. Abdomen white as in the adult; whole head and neck gray with some rust color on the cheeks and lower side of neck, but not nearly so dark or so ruddy as in most examples of the red phase (*Tachyeres patachonicus*). In other words, this young bird does not look as though he were going to pass through the extreme dark and ruddy phase...." He noted further (p. 288) that the bill in this specimen was "probably dark greenish on the culmen and lighter below. Legs and feet yellow...tarsus 63 (rather large for the red type)."

Downy Young of *T. patachonicus*

Oustalet (1891) evidently had obtained specimens of downies of both *T. patachonicus* and *T. pteneres* but apparently was unaware of the diagnostic features of the patterns of the head, and it is not clear how he identified his specimens of downy steamer-ducks. Oustalet (1891) described a downy steamer-duck which he identified as *T. patachonicus* but his description could pertain to either *T. patachonicus* or *T. pteneres*. The bird was a very young female (chick) still in down brought in alive by the Fuegians at Orange Bay on 11 February 1883. The iris was light brown; the beak was black, becoming reddish on the posterior upper mandible and light horn at the tip, which still had the egg tooth. The membrane between the lower mandibles was yellowish; the tarsi were dark greenish olive becoming blackish; the down already showed the distribution of colors of the plumage of the adult, notably the white streaks on the sides of the head behind the eyes.

Oustalet described two other downies, collected on 10 February 1883, which he had identified as *T. cinereus* which, from his description, possibly were *T. patachonicus*. The specimens had beak and feet blackish, head and body covered with down but already showing the dominant colors of the plumage of the adult, and a large white superciliary streak extended a little posteriorly along the neck. He described yet another downy, a very young female brought in alive by the Fuegians on 26 January 1883, which was identified as *T. cinereus* (but which also probably was *T. patachonicus*). The head and body were entirely covered with down which was brown above with white on the chin and abdomen, above and behind the eyes, and on the sides of the neck where there was a large recurved band joining the light color of the chin. Two even younger females were brought in alive by the Fuegians on 12 January 1883. Here again, Oustalet identified them as *T. cinereus* but, from his description, they probably were *T. patachonicus* because they each had a wide, white postocular streak.

Lowe (1934) was the first to present an absolutely diagnostic description of the downy young of *T. patachonicus*. He (p. 481) described the "Supraorbital stripe and postocular patches" as being "White, broad, more diffuse and continuous down sides of neck. In two chicks a few days old the patches were separated by a very narrow line of brown."

Downy Young of *T. pteneres*

Cunningham (1871b:97) described a downy young, clearly that of *T. pteneres*, as follows: "...the entire upper surface of the body, the sides of the head, and a gorget around the lower part of the neck, were covered with a greyish-black down, while the under surface and a spot placed obliquely above and behind the eye were white."

Oustalet (1891) stated that he could identify with certainty as *M. cinereus* (i.e., *T. pteneres*) a number of young individuals. Based on his text, it is clear that his certainty was misplaced since the patterns he described for the heads of these downies all pertained to *T. patachonicus* except for one young male killed on 6 February 1883. The last specimen had the head and body still covered in large part by down. The upper parts were brown, the breast brownish gray, the belly white, the sides of the head brownish gray with a very lightly marked postocular streak, wings reduced stumps but showing a small white transverse band. The beak and feet were blackish brown with some yellowish spots on the sides of the toes.

Salvadori (1895:375) described downy young steamer-ducks as having: "Head, neck, breast, upper parts, sides, and flanks dusky gray; abdomen and undertail coverts white; two white spots on the sides of the head, one behind the eye on the temporal region, and another lower down behind the ear-coverts ...." From his description, the downy young in question was without question a specimen of *T. pteneres*. Scott and Sharpe (1912:492) described young birds in down as having "...head, breast and upper parts, as well as the sides and flanks, dull slaty gray, with a brownish tone; the abdomen and under parts and two spots on the head behind the eye on either side are white or creamy white." The specimens examined by Scott and Sharpe clearly pertained to *T. pteneres*.

Blaauw (1916) described the downy of *T. pteneres* but his description was not diagnostic for the species. Phillips (1925:289) described downy young *Tachyeres* as having "lores and cheeks light buffy brown shading to almost white on sides of neck, while above, behind, and below the eye are indefinite whitish streaks forming, with a slightly darker streak between the bill and eye, a definite 'face pattern.' " The downies Phillips described were clearly those of *T. pteneres*. Lowe (1934) was the first to compare unequivocally identified, prehatching embryos; he stated (p. 481) that downy *T. pteneres* had "No supraorbital stripe, postocular patches white, not so broad or so diffuse, and interrupted by a conspicuous belt of the general dark coloration of the crown."

Ornithologists during the era of taxonomic controversy made several significant contributions to knowledge of the plumages of Fuego-Patagonian steamer-ducks. These included description of the differences between adults of *T. patachonicus* and *T. pteneres* by several authors, regardless of whether they considered them one or two species. In addition, several authors described the sexual dichromatism of *T. patachonicus* and the relative lack of it in *T. pteneres*. Finally, Lowe (1934) contributed substantially to the later taxonomic resolution by Murphy (1936) by, among other things, definitively describing the differences in the head patterns of downy young *T. patachonicus* and *T. pteneres*.

Era of Murphy

This era started with the publication of the classic two-volume work *Oceanic Birds of South America* by Murphy (1936), which included a landmark analysis of the taxonomy of steamer-ducks. In addition to bringing the era of taxonomic controversy about steamer-ducks to a close, Murphy presented detailed descriptions of adult and downy plumages of three species of *Tachyeres* based on an examination of a large series of specimens and a synthesis of published and unpublished information concerning the natural history of each of the species. Subsequent ornithological works were characterized by acceptance of the conclusions presented by Murphy (1936) concerning the taxonomy, plumages, and distributions of steamer-ducks. A number of problems remained, however, and several of his conclusions (some incorrect) profoundly influenced later workers.

Number of Molts per Cycle

Murphy (1936:941) wrote that "Males of no South American duck have an eclipse plumage which is so characteristic among northern-hemi-

sphere species." Although the nature of the so-called 'eclipse' plumage was not understood at the time of his writing, a likely implication of this passage is that *Tachyeres* have but one molt per year. Johnsgard (1962:146) listed *Tachyeres* as not having an "Eclipse plumage present in males..." but listed the genus as having "Two molts of body feathers per year." Weller (1968:206) observed that "Most southern-hemisphere ducks have plumage cycles which differ from northern forms by the absence of the 'eclipse' plumage....Some species lack sexual dimorphism, others have sexual dimorphism all year, and some possess the first nonnuptial (basic) plumage strongly developed." It is not clear from this passage whether Weller believed that most southern-hemisphere ducks have but one molt and plumage per cycle. Nevertheless, with respect to *Tachyeres*, Weller (1976) concluded that variation in patterns of the head and neck of male steamer-ducks is a function of age rather than the result of different plumages in a given cycle, clearly implying that steamer-ducks have but one plumage and molt per cycle.

Intraspecific Variation Attributed to Age

Cunningham (1871b:95) noted for the "adult" steamer-duck that "The head is cinereous, becoming gradually paler as the individual increases in age...." Although Murphy (1936:957) did not explicitly state this principle of variation with age, he noted of the reddish spot on the throat of *T. pteneres* that "...Fledglings and young adults...show less of it than thoroughly mature birds." Delacour (1954) also acknowledged age-related, seasonal, and individual variation in *T. pteneres*.

Woods (1975:118), in his description of *T. brachypterus*, stated that "Old males have an almost completely white head, while younger males have a grey head with white round the eye continuing in a curve down the side of the neck...From the second year, an immature male gradually gains more grey on the head and more orange on the bill." Weller (1976:47) stated that: "In Flying Steamer Ducks and Falkland Flightless Steamer Ducks, mature males are white headed...." He also stated (p. 49) that "On the basis of plumage colour and behaviour of Falkland Island birds, I suspect that there are at least four age classes: yearlings in large flocks, birds two years or older in smaller groups or roving pairs, still older non-breeding birds with some white on the head of males resident on suboptimal territories, and white-headed males that are successful breeders. I have too few observations to judge whether this pattern also is true of Flying Steamer Ducks, but variation in head and bill color of males suggests this possibility." Weller (1976:46) also noted that adult males of the Flying Steamer-Duck and Falkland Island Flightless Steamer-Duck have the head: "Whitish; younger males with greyish or brownish face; white eye stripe." For the Magellanic Flightless Steamer-Duck, he stated (p. 46) that the head of the adult male is: "Uniform gray; whitish crown in older males."

Navas (1977) noted of *T. patachonicus* that the oldest males are less rusty in general and have the head and neck lighter gray or partially or totally white. Johnsgard (1978:138) stated of *T. brachypterus* that "*Adult males* have a head that is predominantly gray and white (nearly pure white in old males)...." Curiously, the only authors to attribute intraspecific variation in head coloration of males to season are Chileans. Goodall et al. (1951) noted of *T. patachonicus* that the male during certain seasons of the year has a white head. They noted also for *T. pteneres* that the color of the head varies a great deal by season being at times completely whitish. Araya and Holman (1986) noted of *T. patachonicus* that the male may have a white head in certain seasons of the year.

Molt of Remiges

Murphy (1936:961) wrote that "Most of the adults [*T. pteneres*] taken by Beck at Chiloé in May were in worn and molting plumage....In these and other examples some of the remiges had become frayed practically down to the shaft as a result of their frequent battering against the water. Among most such birds the two outer-most primaries were new, the inner ones at the point of being shed in sequence." In his discussion about *T. patachonicus*, Murphy (1936:971) noted that "At Ushuaia on April 1...adults in the vicinity had lost most of their rectrices, while the remiges were in

the midst of moult, old worn primaries standing in juxtaposition with fresh ones."

In contrast, Stresemann and Stresemann (1966) found that in all three species of *Tachyeres* the primaries are shed simultaneously. Of all the specimens of *Tachyeres* we have examined in wing molt, we have seen only one individual, perhaps diseased, in which the remiges were not being replaced simultaneously (*T. brachypterus*, male, collected on Lively Island, 12 February 1984; KU 80521). Simultaneous replacement of the remiges is the rule in the family Anatidae; however, the Ruddy-headed Sheldgeese (*Chloephaga rubidiceps*) in Chile and Argentina typically undergo sequential replacement of the remiges (Summers 1982). Other cases of non-simultaneous replacement such as the one *T. brachypterus* we examined must be considered anomalous.

Development of Fledglings

Murphy (1936:971) stated that "Fledglings of the flying species, no less than those of the flightless, acquire their wing quills very slowly, so that they only have barely sprouted primaries for a considerable period after the down has entirely disappeared. Three of the flying species in this stage were taken at Ushuaia on April 1." Soothill and Whitehead (1978:280), writing about *T. patachonicus*, stated that "The fledglings, just like those of the flightless species, acquire their wing quills very slowly. Even when the down has disappeared entirely, there is a considerable period of time during which the primaries have only barely sprouted." From the way in which this was stated, we suspect that Soothill and Whitehead rephrased the statement by Murphy (1936) and that their comments were not based on original observations.

Unpublished notes by Abby Goodall (pers. comm., January 1981) concerning the early development of a downy *T. pteneres* hatched from an egg found at Harberton corroborate the idea that fledgling steamer-ducks acquire their remiges very slowly. Dated photographs of this bird, which hatched on 5 January 1977, during the ensuing weeks show that from 5 January to 5 March the young steamer-duck continued to be completely covered with down and had developed no contour feathers whatsoever. Later in March the young bird began to develop contour feathers and by 1 April its head, neck, upper back, sides and flanks were completely covered with juvenal feathers; there was still considerable down on the lower back. By 1 April the primary remiges were quite long but it cannot be determined whether they were fully grown. This record indicates that the young *T. pteneres*, reportedly well fed, remained 'downy' for two months after hatching, did not start to develop contour feathers until it was more than two months old, and that the remiges probably were not fully grown until the bird was about three months of age. This inference contrasts with that for most North American ducks, in which age at first flight varies from 37 to 77 days and for most species it is less than two months (Pettingill 1970).

Resemblance of First-year Males to Adult Females

Lowe (1934:476) was the first to note that "...young *T. patachonicus* of both sexes are scarcely distinguishable from the adult females." Murphy (1936:964) noted for *T. brachypterus* that: "Younger males exactly resemble females...." Murphy also stated (p. 968) for *T. patachonicus* that: "Younger males resemble females in the extension of reddish coloration to the sides of the head or even to the forehead and crown. The color of their bills also resembles that of females." Delacour (1954) also noted that young males resemble females in both *T. patachonicus* and *T. brachypterus*.

Several other authors (Navas 1977, Johnsgard 1978, Soothill and Whitehead 1978) noted that immature males of *T. patachonicus* resemble the female. Navas (1977) observed that immatures resemble females, as do the youngest adult males. Johnsgard (1978:138), in his description of *T. brachypterus*, wrote that "*Juveniles* and first-year birds resemble females but usually lack the white streak behind the eyes, and second-year males gradually acquire a grayish head and orange bill." Woods (1982:49), also writing about *T. brachypterus*, stated that "First year birds resemble the female but usually lack the white head streak."

Golden Collar of *T. brachypterus*

Murphy (1936:955) stated that "An unique character of *T. brachypterus* is the more or less distinct ring of glossy golden feathers around the neck. It is usually evident in females to a greater extent than in males, but no old Falkland birds seem to be without a trace of it." In his description of *T. brachypterus*, Murphy (p. 964) went on to say that, in the adult male, "...neck with a distinct silken yellowish or golden sheen never present in *pteneres*...." He (pp. 964–965) also stated of adult females "...base of neck showing a glossy, golden yellow ring, somewhat indefinite in extent, but more pronounced than the same feature in males, and peculiar to this species...."

Subsequent to Murphy, the descriptions of *T. brachypterus* by several authors (Delacour 1954, Olrog 1959, Pettingill 1965, Johnsgard 1978, Soothill and Whitehead 1978) mentioned the "golden collar." Johnsgard (1978:138) stated that "*In the field*, this species can be separated from the flying steamer-duck by...a golden-yellowish collar at the base of the neck." Soothill and Whitehead (1978:281) wrote concerning *T. brachypterus* that males have "...more yellow around the neck than *T. pteneres*" and noted of the female that "...the yellow neck collar more pronounced."

We are puzzled by the alleged "golden collar" of Falkland Flightless Steamer-Ducks. We have examined the series of skin specimens of this species available to Murphy at the American Museum of Natural History and have observed hundreds of individuals of this species at close range in the Falkland Islands, including examination of some 20 freshly collected specimens of adults and subadults of both sexes, without having discerned a pronounced golden yellow collar in either sex of adults. It is noteworthy that several authors (Cawkell and Hamilton 1961; Woods 1975, 1982; Weller 1976), familiar with Falkland Flightless Steamer-Ducks in the field, have not included the "golden collar" in their descriptions of the species.

Comments on Descriptions

Our studies of the plumages and molts of steamer-ducks and our protocols for collecting data on molt and plumage in the field were limited and, in retrospect, unsatisfactory for two reasons. First, molt and plumage studies initially were a low priority in our field work. Second, our preconceptions concerning molts and plumages of southern-hemisphere waterfowl, and steamer-ducks in particular, prevented us from posing appropriate hypotheses and designing efficient methodologies for collection of data. These deficiencies have limited our knowledge of the molts and plumages most seriously for *T. pteneres* and *T. leucocephalus*. Fortunately, by 1982 we had worked out many of these problems so that when we had an opportunity to visit the Falkland Islands we were able to collect a limited series of specimens of *T. brachypterus* in a way that enabled us to provide preliminary documentation of the sequence of molts and plumages in that species.

The preconceptions that impeded our studies of molts and plumages in steamer-ducks during 1979–1981 were the following:

(1) "Males of no South American duck have an eclipse plumage, which is so characteristic among northern-hemisphere species" (Murphy 1936:941).

(2) Variation in pattern or aspect of the plumages of the head and neck of male steamer-ducks is a function of age (Weller 1976) rather than the result of different plumages in a given cycle.

(3) Waterfowl of the southern hemisphere in general have "simple" rather than "complex" patterns of plumage succession as implied by Weller (1968:209): "...fairly typical northern hemisphere patterns (of plumage sequence) are apparent in southern Cinnamon Teal [*Anas cyanoptera* subspp.] and Argentine Ruddies [*Oxyura vittata*], suggesting that these are recent arrivals to South America."

For example, Humphrey and Thompson collected several adult male Flying Steamer-Ducks in November 1979 which had scattered white feathers in the crown which they attributed to a leucisticism when, in fact, they were the first few white feathers of an unrecognized supplemental plumage. It was not until field work in late 1980 and early 1981 that we considered the possibility that Flying Steamer-Ducks might have three molts and plumages per cycle.

A breakthrough in our understanding of the molts and plumages of Atlantic-coastal and Fuegian

Flying Steamer-Ducks followed our organization of photographs, head pelts, and skins by sex, age group, and season. We were then able to determine that definitive males go through a clear sequence of three molts and plumages per cycle, the three plumages being worn at distinctly different seasons of the year and having very different aspects. There is nothing subtle about it: the plumages of the head and neck of adult male Flying Steamer-Ducks from Atlantic coastal Patagonia and Ushuaia are distinctly different and easily recognizable. The white-headed supplemental plumage was readily explained as being attained by a presupplemental molt during the austral spring. As we noted previously (Humphrey and Livezey 1982a:6), "specimens of adult male Flying Steamer-Ducks in supplemental plumage are practically non-existent in museum collections, which accounts for the statement by Murphy (1936:968) that 'the oldest males...have clear gray heads, except for the white postocular stripe and the reddish throat patch.' "

In 1982 and 1983 we collected a limited series of *T. patachonicus* in the Andean lakes of Argentina and the southern lakes and coast of Chile and discovered that the sequence of molts and plumages of adult males from those populations was not readily interpretable in terms of what we had learned from Fuego-Patagonian coastal populations. Flying Steamer-Ducks from the Andean lakes of Argentina and from southern Chile (Region X) may have either two or three molts and plumages of the head and neck per cycle (see discussion of plumages and molts for *T. patachonicus* beyond).

During field work in the Falkland Islands, we collected 20 Falkland Flightless Steamer-Ducks and were able to obtain specimens of definitive males representing three distinct plumages of the head and neck along with hundreds of photographs of birds in various plumages. During field work at Puerto Melo (coastal Chubut), we obtained specimens and photographs of *T. leucocephalus* that indicate that the species has only two molts and plumages per cycle. Material available to us representing the Magellanic Flightless Steamer-Duck (*T. pteneres*) also suggests that the species has only two molts and plumages per cycle.

In summary, our current understanding of the molts and plumages of steamer-ducks is as follows:

(1) The Falkland Flightless Steamer-Duck and coastal Fuego-Patagonian Flying Steamer-Ducks have three molts and plumages per cycle. We hypothesize that Flying Steamer-Ducks from the Andean lakes of Argentina and Region X of Chile also have three molts and plumages per cycle but it is also possible that they have but two.

(2) The White-headed Flightless Steamer-Duck and the Magellanic Flightless Steamer-Duck each have two molts and plumages per cycle.

(3) The basic plumage of the head and neck in both *T. brachypterus* and *T. patachonicus* is sexually monochromatic and similar to the juvenal plumage. The definitive basic plumage of the head and neck of *T. leucocephalus* is sexually dichromatic and that of the definitive female is like the juvenal plumage. The plumages of *T. pteneres* are least well known, but basic plumages of both sexes are similar to the juvenal, and alternate plumages are lighter and only weakly sexually dichromatic.

(4) Definitive plumages are attained during molt II in Fuego-Patagonian coastal *T. patachonicus* and probably also in *T. brachypterus*. The definitive alternate plumage of the head and neck in male *T. leucocephalus* may not be attained prior to prealternate molt IV or later.

Unfortunately, molts and plumages have been studied for very few species in the tribe Tadornini (Livezey 1986a). *Tachyeres* is exceptional for the comparatively detailed information on molts and plumages that is available; virtually nothing is known about the molts and plumages of *Hymenolaimus* and *Merganetta*, genera of possibly close relationship to *Tachyeres* (Livezey 1986a). Some species of Tadornini are known to have two molts and plumages per cycle but we do not know whether this is consistently the case for all species within the tribe. We can only speculate, therefore, that the hypothetical ancestor of *Tachyeres* had two molts and plumages per cycle; the plesiomorphic state may be a single molt per annual cycle. We feel it most unlikely that the ancestral condition comprised three molts and plumages per cycle because of the extreme rarity of this pattern in the Anatidae. Assuming that the

ancestral sequence of molts and plumages for *Tachyeres* is two molts and plumages per cycle, then the sequence of three molts and plumages per cycle evolved independently twice in the genus, once in part or all of *T. patachonicus* and once in *T. brachypterus*, assuming that the phylogenetic hypothesis of Livezey (1986c) and Corbin *et al.* (1988) for the species of *Tachyeres* is correct. Alternatively, the three-plumaged condition may have evolved in ancestral *Tachyeres*, was retained in *T. patachonicus* and *T. brachypterus*, and the supplemental plumage secondarily lost independently in both *T. leucocephalus* and *T. pteneres*.

We have been unable to identify life-historical, behavioral, or environmental characteristics held in common by *T. patachonicus* and *T. brachypterus* that distinguish both of those species from *T. leucocephalus* and *T. pteneres* and account for the (possibly independent) evolution of the sequence of three molts and plumages per cycle in the former. Nevertheless, in *T. patachonicus* and *T. brachypterus*, the sequence, timing, and aspects of plumages are virtually identical and the two species cannot be reliably distinguished in the field where they co-occur in the Falkland Islands.

We have examined specimens of downy young of the four recognized species of steamer-duck (Humphrey and Livezey 1985). The specimen of the Flying Steamer-Duck (age class I) examined was from Chilean Tierra del Fuego and collected by G. Watson (USNM 485600). Additional specimens of class-I downy Flying Steamer-Duck collected by M. W. Weller in the Falkland Islands were examined subsequent to our 1985 publication. From the meager specimens and data available, we cannot determine whether there is any significant geographic variation in patterns or aspect of class-I downy Flying Steamer-Duck. We have not examined class-I downy specimens of *T. patachonicus* from populations breeding on mountain lakes of Argentina or Chile.

The plumage of very young (age class I) downy steamer-ducks is the only plumage which is absolutely diagnostic for each of the four species of steamer-duck. The diagnostic differences among the four species in the class-I downy plumage consist principally of variations in the pattern of the head, comprising specifically color of the upper and lower eyelid and distribution of white in front of, above, and behind the eye.

The juvenal plumages of the four species of steamer-duck are not sexually dichromatic and are virtually identical among the four described species. Head and neck of all four species in juvenal plumage are unicolor dark brown or dusky gray with the crown slightly darker and an indistinct chestnut patch on the throat. Juveniles of *T. patachonicus* and *T. brachypterus* have very faint, narrow, indistinct whitish postocular streaks. Because of their great similarity, we judge that juveniles of the four species would be impossible to distinguish in the field.

Our data on predefinitive plumages in all four species of steamer-duck are meager and difficult to interpret. Based on the size of the bursa of Fabricius, we judge that the majority of definitive plumages in all species of steamer-duck are attained by molt II. A possible exception is the definitive alternate plumage of male *T. leucocephalus* which may be attained by prealternate molt IV.

Tachyeres patachonicus

Humphrey and Livezey (1982a) published an account of the molts and plumages of Flying Steamer-Ducks based principally on fresh, sexed specimens with information concerning condition or absence of the bursa of Fabricius. In that study we concluded that Flying Steamer-Ducks have three molts and plumages per cycle and that definitive plumages may be attained starting with the second prebasic molt when birds are about one year of age.

Subsequent to the completion of our 1982 study we learned that Flying Steamer-Ducks exhibit considerable geographic variation. Our early descriptions of plumages of Flying Steamer-Ducks may not apply in detail to freshwater populations in Chile (Region X), the Andean lakes of Argentina, and the Falkland Islands. Unfortunately, samples of fully documented specimens of Flying Steamer-Ducks (including data on sex, gonad measurements, condition of bursa of Fabricius) from these populations are inadequate to interpret their sequences of molts and plumages. Our (1982)

descriptions of the molts and plumages of Flying Steamer-Ducks thus apply in detail only to marine coastal populations from southern Patagonia and Tierra del Fuego.

The sequence of molts and plumages of adult male Atlantic coastal and Fuegian Flying Steamer-Ducks comprises (Fig. 9): (1) a prebasic molt which results in a briefly-worn juvenal-like dark head and neck and which also replaces remiges, rectrices, and the entire feather coat of the body; (2) a prealternate molt during the growth of new remiges which results in a head with dark cap, brown cheeks, and white postocular streak, worn about nine months until mid or late spring; and (3) a presupplemental molt which results in a predominantly white head and neck worn for one or two months from mid to late spring until the early austral summer. Thus, except for feathers of the head and neck which are replaced three times a cycle, the body feathers of adult Flying Steamer-Ducks appear to be replaced but once per cycle by means of a prebasic molt which usually occurs during a relatively brief time in the austral summer.

The same sequence of molts and plumages is also true for adult females in which: (1) the basic plumage of the head and neck is dark and almost unicolor; (2) the alternate plumage comprises a dark gray cap, white postocular streak, and dark brown cheeks; and (3) the supplemental plumage of the head and neck has a dark brown cap, dark reddish-brown cheeks and has no postocular streak or only a very slight one.

Adult females from coastal Patagonia and Tierra del Fuego appear to undergo the presupplemental molt somewhat earlier than males. In addition, from the small sample available to us, the presupplemental molt in adult males from Tierra del Fuego may occur as much as a month later than in Puerto Deseado.

In Atlantic-coastal and Fuegian Flying Steamer-Ducks of both sexes the definitive basic plumage of the head and neck is acquired immediately prior to and during the onset of the prebasic molt of the wing and closely resembles the juvenal plumage. This is replaced during prebasic molt of the wings by the alternate plumage of the head and neck which exhibits moderate sexual dichromatism, differs in aspect from the juvenal plumage, and is worn for approximately nine months. The definitive supplemental plumage of the head and neck is strongly sexually dimorphic and is worn relatively briefly.

The following descriptions apply to marine coastal populations from Patagonia and Tierra del Fuego and include, when possible, notes on plumages of other populations, all of which we assume but cannot demonstrate to have three molts and plumages per cycle. Flying Steamer-Ducks probably attain definitive plumages with the second prebasic molt when they are about one year old.

Definitive Plumages of Males

Basic Plumage

Head and neck.—Vary from brown, dark brown, to dark purplish gray with crown slightly darker and posterior cheeks and side of neck slightly lighter in some specimens; variation (termed "phases" by Humphrey and Livezey 1982*a*) is not age-related. Throat dark cinnamon bordered laterally by medium to dark gray. Some specimens have a very short trace of a whitish postocular streak.

Lower breast, belly, under tail coverts.—White.

Upper back.—Fresh feathers medium gray with narrow dark gray margins anteriorly becoming browner (dusky brown) more posteriorly as the feathers become more extensively light silvery gray.

Scapulars.—Light silvery gray broadly margined with sepia.

Lower back, rump, and upper tail coverts.—Medium to dark gray; feathers with faintly darker margins.

Upper breast and sides.—Fresh upper breast feathers cinnamon becoming slightly more reddish distally and broadly tipped with blackish brown with a subterminal patch of light silvery gray. Laterally, the feathers are less cinnamon and medium gray until on the upper sides there is no cinnamon. Also the more anterior upper breast feathers are darker cinnamon. There is considerable individual variation in the extent and shade of cinnamon on feathers of the upper breast and upper sides and in the distribution of feathers with

cinnamon bases. Some individuals have very little cinnamon on the bases of the upper breast feathers. This variation is not due to wear and fading; we have no evidence that there is more than one molt of upper breast and sides per cycle.

Sides and flanks.— Light silvery gray, feathers with wide chestnut margins. Margins of worn feathers become narrow and brownish olive and eventually fade to buffy brown with much narrower tips. We could detect no differences among males from the Falklands, Atlantic coast of Patagonia, Tierra del Fuego, the Argentine lakes, and the lakes of Region X, Chile, in appearance of fresh definitive basic sides and flanks.

Alternate Plumage

As far as we can determine, only the feathering of the head and neck is replaced during the prealternate molt.

Head and neck.—Crown medium to dark gray; lores and cheeks medium dull grayish-brown; long white postocular streak partly occluded in auricular region; throat medium cinnamon.

The limited series of specimens available to us from the Andean lakes of Argentina and the lakes and coasts of Region X, Chile, does not enable us to demonstrate conclusively that adult males in these populations have three molts and plumages on the head and neck per cycle. From the material available we can formulate two hypotheses concerning the sequence of molts and plumages of the head and neck of Flying Steamer-Ducks from the Andean Lake District of Argentina and Region X, Chile:

Hypothesis 1: Adult males have but two plumages of the head and neck per cycle comprising (1) an all dark basic plumage and (2) an alternate plumage comprising gray cap, reddish cheeks, and long white postocular streak, similar to the alternate plumage of coastal populations from southern Patagonia and Tierra del Fuego. This hypothesis postulates the lack of a supplemental plumage.

Hypothesis 2: Adult males have three plumages of the head and neck per cycle comprising (1) an all dark basic plumage; (2) an hypothetical alternate plumage comprising gray cap, reddish cheeks, and white postocular streak; and (3) a definitive supplemental plumage of the head and neck that comprises either: (a) gray cap, reddish cheeks, and long white postocular streak, or (b) head and neck entirely white (as in coastal Patagonian and Fuegian birds). We have collected no specimens of birds in this latter plumage (3b) in the Andean lakes of Argentina and Region X, Chile.

We tentatively conclude that it is most likely that Chilean and Andean males have three molts and plumages (hypothesis 2) and that we have neither seen nor collected birds in what we presume to be alternate plumage. Possibly the alternate and supplemental plumages are indistinguishable.

Supplemental Plumage

As far as we can determine, only the feathering of the head and neck is replaced during the presupplemental molt.

Head and neck.—White with pale gray wash on cheeks, darker on lores; throat medium cinnamon bordered with pale gray. The amount and distribution of gray on the head and neck of coastal Patagonian and Fuegian males varies considerably from: (1) cap, cheeks, and lores light brownish-gray; to (2) head and upper neck light or medium gray with a short, narrow white postocular streak. Some individuals may have completely white head and neck except for a cinnamon patch on the throat.

It is possible that the definitive supplemental plumage of the head and neck of males from the Andean lakes of Argentina and Region X, Chile also is white, but we have no specimens to document this. The few specimens of adult males available to us (bursa of Fabricius vestigial or lacking) starting prebasic molt of the head and neck have medium gray cap and nape, forehead slightly lighter and nape slightly darker; lores and cheeks light fuscous with faint smoke-gray tips, becoming grayer and slightly lighter posteriorly. The base of the neck is white, the chin is light medium brownish-gray, and the throat medium reddish chestnut. There is a prominent white postocular streak.

A highly worn January specimen (KU 79854) from near Puerto Montt, Chile, had faded head and neck with new dark basic feathers coming in on the

forehead. The crown and nape of this bird were faded gray and the cheeks and lores light gray with posterior cheeks and base of the neck white. The lower cheek was slightly darker and the throat was medium reddish chestnut. In the bright sun this bird would look white-headed in the field.

It is possible that the supplemental plumage of the head and neck of adult males from the Andean lakes of Argentina and the southern lakes of Chile becomes increasingly white in older birds. However, there is stronger evidence to suggest that, if these populations have three molts and plumages per cycle, the definitive supplemental plumage has gray cap, fuscous cheeks and a prominent white postocular streak, and resembles the alternate plumage of coastal birds from southern Patagonia and Tierra del Fuego.

Definitive Plumages of Females

Basic Plumage

Head and neck.—Dark chocolate brown; cap darker in some individuals; neck medium brown in some individuals; throat dark cinnamon; eye lids white; white postocular streak short or (possibly) absent.

Lower breast, belly, under tail coverts—White.

Upper back.—As in definitive white male except that feather margins are sepia to brownish-olive and wider.

Lower back, rump, and upper tail coverts.—Dark gray; feathers of the lower back and rump are faintly silvery and have narrow, indistinctly darker edges.

Upper breast and sides.—As in definitive male.

Sides and flanks.—Slightly darker than those of definitive males, although the difference is not a reliable character for determining sex. Sides appear to be replaced only once per cycle. The first basic sides and flanks are identical with those of subsequent basic plumages except the chestnut margins appear to be slightly narrower.

Alternate Plumage

Head and neck.—Forehead and crown dark gray; lores and cheeks dark brown; white postocular streak occluded posteriorly by medium brown becoming a whitish patch on sides of neck; throat dark cinnamon, neck medium brown with paler, almost whitish collar.

Supplemental Plumage

Head and neck.—Crown medium gray with brownish cast to dark grayish-brown; lores and cheeks fuscous chestnut to dark reddish brown, grading to dark grayish brown and then darkish medium gray on the neck; throat medium chestnut. The white postocular streak is short. While similar to the alternate, the supplemental plumage differs in lacking the white collar, and in having a very short postocular streak and a pronounced reddish cast in the lores.

Predefinitive Plumages (Both Sexes)

Juvenal Plumage

The following account describes a specimen (KU 79211), one of two males collected on 20 January 1981 at Puerto Deseado from a family group of five juveniles accompanied by a pair of adults; the two males collected were identical in aspect. Although we have examined no females in juvenal plumage we presume they are identical in aspect to males of similar age.

Head and neck.—Dark brown, crown slightly darker, patch on throat chestnut. Upper and lower eyelids white; narrow, ill-defined pale buffy postocular streak extending the length of the cheek.

Lower breast, belly, under tail coverts.—White.

Upper back.—Feathers silvery gray with dark, almost blackish gray margins, giving a scalloped effect.

Scapulars.—Silvery gray with darker blackish margins.

Lower back, rump, and upper tail coverts—Medium gray.

Upper breast and sides.—Feathers pale silvery gray with dark almost blackish gray margins. No chestnut at the bases of any of the feathers of the upper breast and sides except for the last rows of feathers just before white feathers of the upper breast.


PATACHONICUS
BRACHYPTERUS
LEUCOCEPHALUS
PTENERES
♂ DEFINITIVE SUPPLEMENTAL
♂ DEFINITIVE ALTERNATE
♂ DEFINITIVE BASIC
JUVENAL

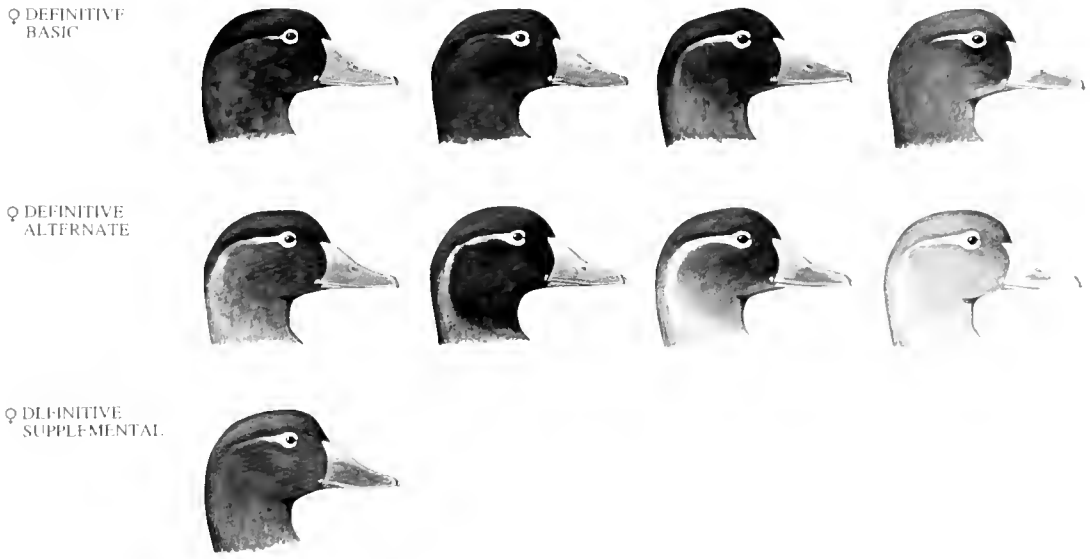

Fig. 9. Portraits of heads of *Tachyeres* arranged by species, sex, and plumage. The definitive supplemental plumage of female *T. brachypterus* is unknown.

Sides and flanks.—Feathers silvery gray with blackish gray margins; the flank feathers are medium gray with very narrow, washed out brownish or chestnut margins.

Downy Plumage

The following description is based on three specimens from Chile: USNM 485600 (class-I, female, 1 February 1964), FMNH 120521 (class-II, female, 28 January 1940), FMNH 120522 (class-II, 28 January 1940).

Head and neck.—Upper eyelid dark brownish olive; lower eyelid whitish. Cheeks, lores, forehead, crown and nape dark brownish olive. Supraocular and supraloral patches are whitish and very narrow, becoming even narrower anteriorly; they are widely separated from the postocular streak which is broad and whitish.

Upperparts.—Yoke light fuscous; lower back and rump dark brownish-olive.

Underparts.—Upperbreast brownish-olive; lower breast and belly white.

Tachyeres brachypterus

Series of specimens of the Falkland Flightless Steamer-Duck collected in February 1984 demonstrate conclusively that this species, like the Flying Steamer-Duck, has three molts and plumages per cycle (Fig. 9). Definitive plumages of both sexes are indistinguishable from those of Atlantic Coastal and Falkland populations of the Flying Steamer-Duck and seasonal occurrence of the three definitive plumages appears to be approximately the same in the two species. Our understanding of aspects and timing of predefinitive plumages is very limited, but we suspect that definitive plumages are attained during molt II.

Definitive Plumages of Males

Basic Plumage

Head and neck.—Lores dusky brown, grading to dark chestnut posteriorly, medium chestnut on the cheeks and slightly lighter on the sides of the neck, grayish more posteriorly and on the hind neck; narrow, rather short white postocular streak. Chin medium dusky brown; throat chestnut. Forehead dark chestnut mixed with light gray feathers; crown chestnut, darker on the nape.

The prebasic molt of the head and neck has just begun in an adult male (KU 80525) collected on 14 February 1984; the specimen had no bursa of Fabricius. In this specimen dark blackish brown feathers are replacing the supplemental white feathers of the forehead, lores, and anterior cheeks. Two adult males (KU 80515 and KU 80520) collected on 9 and 10 February (neither with bursa of Fabricius) are in full basic plumage of the head and neck except for the crown, which is molting into the light to medium gray of the alternate plumage.

Lower breast, belly, under tail coverts.—White.

Upper back.—Feathers medium gray, the more posterior ones with broad blackish brown margins and a silvery gray wash.

Scapulars.—Silvery gray with broad, dark chestnut margins.

Lower back, rump, and upper tail coverts.—Medium gray becoming somewhat lighter posteriorly.

Upper breast and sides.—Upper breast dark brown with faint margins of pale grayish. The individual feathers are medium chestnut with broad dark brown terminal band and, in the more posterior feathers, a narrow subterminal band of pale gray. With wear the upper breast becomes increasingly chestnut in appearance. The feathers of the sides are silvery gray with wide blackish brown margins.

Sides and flanks.—Feathers light gray with dark brown margins which become wider and dark chestnut in the long flank feathers.

Remiges and rectrices.— Blackish brown with varying amounts of silvery gray on their dorsal surfaces.

Alternate Plumage

As far as we can determine, only the feathering of the head and neck is replaced during the prealternate molt.

Head and neck.— Crown medium gray; lores dusky brown becoming medium gray posteriorly; cheeks duffish brown becoming somewhat lighter

and grayer posteriorly. Hind neck and sides of neck pale to light gray, darker and more brownish in some individuals. Chin medium gray, throat and ventral neck chestnut. Long, white postocular streak, more prominent in some individuals than others. One specimen (KU 80517) is in heavy prealternate molt of the head and neck and in very heavy prebasic molt of the body; the old worn remiges were still firmly attached. Prealternate molt of the head and neck may occur as late as February and as early as October or November. Color slides provided us by O. S. Pettingill, Jr., M. W. Weller, and T. Narosky show bright-billed, presumably definitive birds in alternate plumage in November, December, and January. We photographed and collected definitive males in alternate plumage in January and February.

Supplemental Plumage

Head and neck.—The definitive supplemental plumage of males has the throat medium to dark chestnut and the rest of the head white. It appears that some individuals have completely white crowns and napes, while others have crown and nape pale to medium gray. We have seen no specimens in presupplemental molt or in fresh definitive supplemental plumage of the head and neck. All specimens we have examined are in worn supplemental plumage with the head and neck predominantly white except for dark incoming basic feathers in the lores, forehead, anterior crown and anterior cheeks. We have examined specimens and photographs of definitive males with varying amounts of white supplemental plumage on the head and neck indicating that the presupplemental molt may start as early as October and as late as December or January.

Definitive Plumages of Females

Basic Plumage

Comparison of specimens shows that, except for plumages of the head and neck, the basic plumages of definitive males and females are identical.

Head and neck.—The heads and necks of four females without bursa of Fabricius collected in February all appear to be mostly in definitive basic plumage with varying amounts of new alternate plumage. All four specimens (KU 80516, KU 80532, KU 80513, KU 80518) have fresh, unworn, new remiges. In these four specimens the lores and anterior cheeks are dusky to blackish brown becoming chestnut more posteriorly. The forehead, crown, nape and hind neck are dusky brown becoming lighter and somewhat grayer posteriorly. The throat and ventral neck are dark chestnut. The eyelids are white and some individuals have a very short white postocular streak.

Alternate Plumage

Head and neck.—We have not examined any specimens in full alternate plumage of the head and neck. Photographs indicate that the definitive alternate plumage of the head and neck of females is similar in aspect to that of the Atlantic-coastal populations of Flying Steamer-Duck. The crown is medium to dark gray; lores and cheeks medium dull grayish-brown; long white postocular streak; throat chestnut.

Supplemental Plumage

Head and neck.—Unknown.

Predefinitive Plumages (Both Sexes)

Juvenal Plumage

Slides taken by T. Narosky in December 1978 (file no. 2692) and February 1978 (file no. 2685) at Port Stanley show two individuals in full juvenal plumage. The remiges on both individuals in each photograph are partially grown in that the white secondaries are barely visible beyond their coverts and the tips of the primaries are not evident. We assume that, as in other species of steamer-duck, there is no sexual dichromatism of the juvenal plumage in this species.

Head and neck.—Unicolor dark brown; upper and lower eyelids white; narrow, pale buffy postocular streak extends for about a centimeter posterior to the eye and then becomes broader

and very faint, curving ventrally posterior to the cheek.

Lower breast, belly, under tail coverts.—White.

Upper back.—Feathers medium gray with dusky brown margins.

Scapulars.—Medium gray, broadly margined with dusky brown.

Lower back, rump, and upper tail coverts.—Medium gray, each feather with narrow dusky brown margin.

Upper breast and sides.—While the ventral upper breast is not visible in the photographs, the feathers of the sides of the upper breast are medium gray, broadly margined with dusky brown.

Sides and flanks.—Feathers medium gray with broad dusky brown margins. In one individual, the elongate flank feathers are light to medium dusky brown with darker margins.

Downy Plumage

The following description is based on five unsexed, class-I specimens from the Falkland Islands: AMNH 419160 (7 December 1915), MCZ 70521 (15 December 1915), MCZ 70522 (figured in Murphy 1936), BM 1930.12.18.1, BM (no number, 29 November 1936).

Head and neck.—Upper eyelid medium fuscous; lower eyelid whitish to pale fuscous. Cheeks, lores, forehead, crown, and nape medium fuscous. The very pale (almost whitish) smoke gray supraocular and supraloral patches are uninterrupted, very narrow and even narrower at the junctions of the supraloral and supraocular patches and the supraocular patch and postocular streak. The ventral margin of the supraocular patch above the upper eyelid is dark dusky brown. The supraocular patch is continuous with the postocular streak which is very pale smoke gray and continuous.

Upperparts.—Yoke light fuscous; lower back and rump medium to dark fuscous.

Underparts.—Upper breast fuscous; lower breast and belly white.

Tachyeres pteneres

The Magellanic Flightless Steamer-Duck has two molts and plumages per cycle. As in all other species of steamer-duck, the prealternate molt apparently involves only feathers of the head and neck (Fig. 9). We have found no evidence that feathers of other pterylae are replaced more than once per cycle.

The definitive basic plumage of the head and neck of male *T. pteneres* does not resemble the juvenal plumage. Thus there is sexual dichromatism of the definitive basic plumages of the Magellanic Flightless Steamer-Duck; the females have definitive basic plumage of the head and neck unicolor medium gray whereas the definitive basic plumage of the head and neck of males has a medium gray cap and lores, light gray cheeks and neck, and pale gray to whitish, rather short postocular streak. The Magellanic Flightless Steamer-Duck is unique in the genus in that the definitive basic plumages of the head and neck of neither sex resemble the juvenal plumage.

We have examined specimens of male Magellanic Flightless Steamer-Ducks in definitive alternate plumage collected in November, December, and January, many of them in the early stages of prebasic molt of the head and neck. In addition, we have examined four specimens from the American Museum of Natural History, collected by Beck near Chiloe Island, also in definitive alternate plumage of the head and neck. We have seen two specimens (taken in December and January) in definitive basic plumage of the head and neck. Nine additional specimens (taken during April-July) are in definitive basic plumage of the head and neck and one of them (AMNH 443670) still in prebasic molt of the head and neck.

From the limited data at our disposal, we speculate that the majority of adult male Magellanic Flightless Steamer-Duck are in alternate plumage of the head and neck during the late spring and summer and wear the basic plumage of the head and neck during the balance of the year for perhaps 8 to 10 months. Assuming a relationship between the occurrence of the definitive alternate plumage in males and nesting, the occurrence of four males collected in May in definitive alternate plumage of the head and neck would indicate that at least some Magellanic Flightless Steamer-Duck nest during the austral winter; this would appear to be especially likely in the lower latitudes around Chiloé Island and farther to the north.

Definitive Plumages of Males

Basic Plumage

Head and neck.—An adult male (AMNH 443707) collected on 31 July in the Beagle Channel is in fresh plumage, wings unworn and apparently quite new. Forehead, crown, and lores medium to darkish gray becoming darker anteriorly. Feathers of forehead and crown with narrow dark chestnut shaft streaks. Nape medium gray becoming lighter on dorsal neck. Cheeks light gray becoming darker anteriorly and broadly mottled darker elsewhere. Chin medium gray. Indistinct, diffuse, light-medium chestnut thumb-sized throat patch. Neck light gray, darker dorsally. Indistinct, pale gray (mottled slightly darker) postocular streak.

An adult male (USNM 536348) collected on 24 April in Argentine Tierra del Fuego has crown and lores medium gray, forehead slightly paler, anterior cheeks light-medium gray becoming paler posteriorly and grading into light gray in the neck. Chin light to medium gray becoming paler posteriorly. Throat faintly brownish gray, grading into light gray on the ventral neck. No feathers on the head and neck were molting.

Lower breast, belly, under tail coverts.—White.

Upper back.—Feathers dark gray, the more posterior ones with a patch of light silvery gray along the rachis.

Scapulars.—Feathers dark gray with patch of light silvery gray along the rachis.

Lower back, rump, and upper tail coverts.—Feathers medium to dark gray with slightly darker margins.

Upper breast and sides.—Feathers of the upper breast are banded with a very narrow pale slightly worn smoky gray tip; a subterminal band that is blackish-brown and is broader anteriorly and narrower posteriorly; the next band is variable in shape and size and color, being cinnamon in more anterior feathers and becoming faded cinnamon posteriorly and finally becoming medium gray in the more posterior and lateral feathers including those of the upper sides.

Sides and flanks.—Feathers light silvery-gray with medium blackish-brown margins. Sides and flanks are moderately worn in a specimen taken in November and the dark margins, especially anteriorly, are narrower and the feather tips frayed and light smoke gray.

Remiges and rectrices.—Black or blackish-brown with varying amounts of silvery-gray on their dorsal surfaces.

Alternate Plumage

Head and neck.—An adult male (AMNH 443669) collected on 19 May at Chiloé Island has crown and lores light gray becoming slightly darker anteriorly; cheeks pale gray becoming whitish posteriorly. White postocular streak present, and chin pale gray. Throat with very small patch of pale chestnut becoming paler and grayish/whitish at its margins. Neck pale gray dorsally grading to whitish ventrally. Other adult male specimens in alternate plumage of the head and neck from Chiloé Island are AMNH 443661 (12 May) and AMNH 443671 (19 May).

In addition, an adult male (AMNH 733418) collected on 27 November at Frutillar (near Puerto Montt) Chile was in quite worn plumage with old, frayed wings. The head and neck appear to be in worn alternate plumage. The forehead is light faintly buffy gray becoming darker on the crown which is medium gray. The lores are medium gray. Cheeks light smoky gray becoming whitish posteriorly. Chin pale smoky gray. Throat with diffuse light-medium chestnut patch. Neck worn and whitish.

The definitive alternate plumage of males is, except for light gray crown, brownish-gray lores and pale gray neck, all white with an indistinct patch of pale cinnamon on the throat. A November specimen from Tierra del Fuego (KU 77969) and a December Chilean bird (KU 79842) are in this gray-capped alternate plumage in which the rest of the head and neck is white.

Definitive Plumages of Females

Basic Plumage

Comparison of series of specimens of definitive males and females at the American Museum of Natural History reveals that, other than the head

and neck, the definitive basic plumages of the two sexes are identical.

Head and neck.—Forehead, crown, and lores medium darkish gray; feathers of forehead with faint, paler margins (from wear and fading). Cheeks medium gray or medium smoke gray becoming darker anteriorly. Chin and neck medium gray. Indistinct thumb-sized patch of medium chestnut on throat. Faint, ill-defined, short postocular streak light gray, mottled darker.

Examination of specimens taken during December (KU 79835) and November (KU 77967) indicated that the definitive basic head and neck is unicolor gray with no white or whitish postocular streak. The first specimen had dropped its remiges and was in heavy prebasic molt of the head which was about three-quarters complete. The second specimen was in high basic plumage of the head and neck and is starting the prealternate molt; of particular note in the specimen are the obviously growing, white postocular feathers.

Alternate Plumage

Head and neck.—Crown and forehead dark gray, becoming paler on the nape; lores dark gray becoming medium gray on cheeks and fading to light gray and then pale gray—almost whitish—at base of neck. Short pale gray to whitish postocular streak. Chin medium gray; throat varies from smallish patch of pale cinnamon or reddish brown to a more extensive patch of dull chestnut. Wear and fading may account for some of this variation. One December bird (KU 79839) was beginning prealternate molt of the head and neck and already had a pale gray postocular streak.

Predefinitive Plumages (Both Sexes)

Alternate Plumage

Head and neck.—Two males collected in November had crown, forehead, nape, lores, and chin medium gray. Cheeks light gray. Throat faintly marked pale cinnamon. The extent and strength of the cinnamon on the throat varies from practically indiscernible to a distinct pale patch.

Juvenal Plumage

Examination of nine specimens of Magellanic Flightless Steamer-Duck in full juvenal plumage, collected at various localities in March, April, May, and July, revealed that males and females are identical in this plumage. Observations by N. and J. Goodall (pers. comm.) indicate that the prejuvenal molt in *T. pteneres* may not begin until the young birds exceed 60 days of age. It is not known how long the juvenal plumage is worn nor the age at which the first prebasic molt begins. From the ten specimens (one unsexed) at hand we suspect that the onset of the first prebasic molt in Magellanic Flightless Steamer-Ducks is much delayed compared to most other tadornine and anatine waterfowl.

Head and neck.—Forehead, crown, nape, lores dark (purplish) gray; neck medium dusky gray, lighter ventrally. Cheeks medium to darkish dusky gray becoming dark anteriorly and in the lores. Chin medium dusky gray. Thumb-sized patch of medium brownish chestnut on throat.

Lower breast, belly, undertail coverts.—White.

Upper back.—Medium dusky grayish-brown. Posteriorly the feathers have dark dusky-brown margins giving a faintly scalloped appearance.

Scapulars.—Medium grayish-brown with dark dusky-brown margins.

Lower back, rump, and upper tail covets.—Medium to dark grayish or dusky brown.

Upper breast and sides.—Feathers medium dusky gray, more or less heavily tipped dark blackish-brown becoming less heavily marked on upper sides and paler and less distinct posteriorly. Feather bases are pale smoky gray.

Sides and flanks.—Medium dusky brown, feathers darker toward tips and becoming slightly brownish posteriorly. Some feathers of sides with faint traces of pearly gray along distal rachis.

Remiges and rectrices.—Blackish brown with slight wash of silvery gray on dorsal surface near rachis. Primaries and greater upper primary coverts dark dusky brown with blackish brown shafts. Secondaries white. Axillaries and central part of wing lining white; balance of under wing coverts medium dusky brown, the greater under primary coverts paler. Retrices medium blackish-brown

with black shaft and very faint mesial wash of silvery gray.

Downy Plumage

The following description is based on eight class-I specimens from Chile: AMNH 443684 (male, 3 December 1914), AMNH 443685 (male, 4 December 1914), AMNH 443687 (female, 19 January 1915), AMNH 443689 (male, 30 November 1914), AMNH 443704, 443705, 443706, 443708 (3 males, 1 female, 11 January 1915).

Head and neck.—Upper eyelid blackish-brown; lower eyelid whitish. Cheeks, lores, forehead, crown, and nape dark brownish-olive becoming lighter on the anterior forehead. Supraloral patch very small or absent; supraocular region blackish brown except for a whitish patch which may be absent, faint, or small but when present is always separated from the postocular patch and from the supraloral patch when it is present. Postocular streak whitish and divided into separate anterior and posterior parts.

Upperparts.—Yoke medium brownish-olive; rest of upper parts dark brownish-olive.

Underparts.—Upper breast brownish-olive; lower breast and belly white.

TACHYERES LEUCOCEPHALUS

In their description of *Tachyeres leucocephalus*, Humphrey and Thompson (1981:8) stated that "from examination of specimens and photographs of *T. leucocephalus*, we judge that adult birds of both sexes go through a complete prebasic molt in summer (February), shedding the remiges simultaneously and then without interruption undergo a partial molt involving the head and neck and possibly other parts of the body. Adult males collected in September were white-headed as were those with worn wings collected in February before they had initiated the prebasic molt. The limited data at our disposal suggest that either adult males wear a white alternate plumage of the head and neck most of the year or that, if there is a supplemental plumage, it too is white...we tentatively assume a two plumage cycle since we have no evidence to the contrary."

Since that was written, we have examined many additional specimens of the White-headed Flightless Steamer Duck and have found no evidence for three molts and plumages per cycle in *T. leucocephalus*; nevertheless, a supplemental plumage may remain undetected. Although the hypothesized pattern of two molts and plumages per cycle for this species best explains the limited data at our disposal, study of specimens representing all sex and age classes throughout the year will be needed before a full understanding of the plumages and molts in this species will be possible. Some of the puzzling data that need explanation include: (1) May and September-October specimens undergoing body molt in certain tracts other than head and neck; (2) female specimens undergoing molt in sides, flanks and other body tracts (other than head and neck) in September-October but not males; and (3) definitive alternate plumage of the head and neck of males apparently not attained until the third or later prebasic molt in contrast to coastal Flying Steamer-Ducks wherein the definitive alternate plumage apparently is attained by the second prealternate and molt.

Since molts and plumages of steamer-ducks appear to be tightly linked to their reproductive cycles, some of the apparent variability in seasonal occurrence of birds in molt and various plumage states may be attributable to individual variation in breeding activities. Although it is evident that the majority of White-headed Flightless Steamer-Ducks nest during the austral spring and summer, there may be substantial variation in extreme dates.

Based on available data, we hypothesize the following sequence of molts and definitive plumages for male White-headed Flightless Steamer-Ducks (Fig. 9): (1) a prebasic molt which results in gray cap, red-brown cheek, and white postocular streak on the head and neck and which also replaces remiges, rectrices, and the entire feather coat of the rest of the body; (2) a prealternate molt which results in an alternate plumage of the head and neck which is predominantly white and which is acquired during the fourth and subsequent prealternate molts. As far as we can determine, except for feathers of the head and neck which are replaced two times a cycle, the body feathers of

adult White-headed Flightless Steamer-Ducks are replaced but once a cycle by means of a prebasic molt which usually occurs during a relatively brief time in the austral summer.

The same sequence of molts and plumages is also true for adult females in which the basic plumage of the head and neck is unicolor dark brown with a small, white postocular streak. The definitive alternate plumage of females comprises a dark gray crown, reddish-brown cheeks, and a long, uninterrupted relatively broad, white postocular streak.

In contrast to *T. brachypterus* and *T. patachonicus*, in which the definitive basic plumages are dark and unicolor and essentially indistinguishable from those of females, the definitive basic plumage of male *T. leucocephalus* differs from that of females and has gray cap, dark cheek, and white postocular streak. Except for bill color, basic plumages of the head of male and female *T. brachypterus* and *T. patachonicus* show little sexual dichromatism and resemble the juvenal plumage. The only way we can account for gray-capped, darkish-cheeked males molting into another gray-capped, darkish-cheeked plumage is by hypothesizing that the predefinitive alternate plumage of the head and neck is similar or identical to the basic plumage.

We can find no evidence that the sides, flanks, and possibly other tracts (apart from the head and neck) molt more than once per cycle. Nevertheless, we have examined specimens of both sexes molting or in fresh sides and flanks in May, and of females molting or with fresh sides and flanks in September and October. We could detect no differences in the latter case between fresh sides and flanks of September-October birds and those of birds collected in February.

Predefinitive, i.e., first basic and first alternate plumages of the White-headed Flightless Steamer-Duck are either unknown or poorly understood.

Definitive Plumages of Males

Basic Plumage

Head and neck.—Forehead, crown, and nape dark gray; cheeks and lores medium reddish-brown; broad white postocular streak; sides of throat and chin medium gray; extensive patch on throat medium cinnamon; white collar at base of neck. For birds that nest in the late spring or early summer it appears that this plumage of the head and neck is attained during the prebasic molt which follows nesting and is worn until early austral spring (September-October). We collected a male in December, one of a pair with very small downies; the bird was in high, white alternate plumage with a very few dark basic feathers growing in on the cheeks and anterior forehead. The wings of this bird were old and worn. We believe that Humphrey and Thompson (1981:8) were incorrect in their judgment "that following the complete prebasic molt in summer, both sexes...then without interruption undergo a partial molt involving the head and neck and possibly other parts of the body." Examination of additional specimens and photographs indicates that the definitive basic plumage of the head and neck of males is worn for seven to nine months before being replaced during the early spring by the alternate plumage.

Lower breast, belly, under tail coverts.—White.

Upper back.—Feathers light silvery gray with narrow dusky-brown margins; anteriorly, the silvery-gray becomes reduced in extent and the feathers are medium gray with narrow, darker margins.

Scapulars.—Light silvery gray with narrow, dusky brown margins.

Lower back, rump, and upper tail coverts.—Medium gray.

Upper breast and sides.—Six adult males collected in February have fresh, unworn upper sides and upper breasts with varying amounts of molt. Upper breast feathers have reddish-cinnamon bases with narrow blackish-brown tips with silvery-gray subterminal band. The silvery-gray becomes more extensive in the more lateral feathers and upper sides. Feathers of the upper breast and sides are very worn in a December adult male and less so in two September specimens. In the two September specimens the upper breast feathers are medium reddish-cinnamon with narrow blackish-brown subterminal bands and very narrow, frayed, faded smoke-gray tips. Laterally, the cinnamon is replaced by light to medium-gray. In the December specimen, reddish-cinnamon occurs in a wider

expanse of feathers laterally and many of the feathers have a small subterminal white spot. Wear on the upper breast has eliminated most or all of the subterminal dark band so that many of the feathers are faded cinnamon with frayed paler tips.

Sides and flanks.—Light silvery-gray with dusky-brown tips. In some specimens the feathers are somewhat darker silvery-gray and may have less silvery sheen. Posteriorly, the flank feathers have broader dusky-brown tips than those in the sides. Three September specimens and one collected in December have worn and faded sides and flanks in which the tips have become lighter and browner. In the December specimen wear has made the dark feather tips narrower and with pale frayed edges. It appears that the sides and flanks of definitive males are replaced only once a cycle during the prebasic molt, usually in the austral summer. Thus, males are wearing worn sides and flanks when the heads and necks are in fresh alternate plumage.

Remiges and rectrices.—Black or blackish-brown with varying amounts of silvery-gray on their dorsal surfaces. Primaries and greater upper primary coverts dark dusky-brown with blackish-brown shafts; rest of upper wing medium fuscous. Secondaries white, the inner vane of the innermost ones medium blackish-brown; tertials medium dusky brown. Axillaries and central part of wing lining white; balance of under wing coverts medium dusky-brown, the greater under primary coverts paler. Rectrices dark blackish-brown, with black shaft and faint mesial wash of white silvery-gray.

Alternate Plumage

As far as we can determine, only the feathering of the head and neck is replaced during the prealternate molt.

Head and neck.—Predominantly white. Some individuals have a medium gray cap of varying extent (size and extent possibly varies with age); in others, the forehead and crown is white. There are varying amounts of pale smoky-gray in the lores and anterior cheeks. The chin is pale smoke-gray grading posteriorly into a relatively narrow patch of light brownish-red or light cinnamon on the throat. The prealternate molt apparently is limited to the head and neck and occurs, as far as we can determine, in September and October. This plumage is worn until the complete prebasic molt which usually occurs in the austral summer following the nesting season.

Definitive Plumages of Females

Basic Plumage

Head and neck.—Unicolor dark brown, neck slightly paler; small, white postocular streak.

Lower breast, belly, undertail coverts.—White.

Upper back.—As in definitive males except that feather margins are wider and are sepia to brownish-olive in color.

Scapulars.—As in definitive male except that the feather margins are wider and sepia to brownish-olive in color.

Lower back, rump, and upper tail coverts.—Dark gray, feathers of the lower back and rump faintly silvery with narrow, indistinct darker edges. In worn birds (several February specimens), the feather edges are frayed and broadly tipped with buffy brown and worn smoke gray tips.

Upper breast and sides.—As in definitive male. A specimen collected in September had fresh upper breast and sides with a very few new feathers still growing. It is puzzling that some females were molting or were in fresh upper breast, sides, and flanks in September.

Sides and flanks.—Light silvery gray (as in definitive males) with feather margins broadly chestnut. Sides and flanks of definitive females in fresh plumage have much richer reddish and wider feather margins than males; this gives the sides and flanks of definitive females a more heavily scalloped appearance than in males. Sides and flanks of a definitive bird collected in September were identical in appearance to new feathers in February specimens. We are uncertain about number and timing of molts of sides and flanks in definitive females. We have found extensive molt in definitive females in both September and February but the feathers are identical. We have found no evidence of molt during September of sides and flanks in definitive males.

A leucistic female *T. leucocephalus* (SW 3531

= KU 77936) was collected at Puerto Melo, Chubut on 28 September 1979; the bird was evidently an adult (ovary 20 x 20 mm, body mass 2850 g), and was conspicuously lighter than nearby conspecifics, even at a distance. The leucisticism affected all pterylae.

Alternate Plumage

Head and neck.—Crown gray, cheeks reddish-brown becoming light grayish-brown posteriorly, long, uninterrupted, white postocular streak.

Predefinitive Plumages of Males

Basic Plumage

Head and neck.—A specimen (KU 79243) collected in February from a family group comprising two adults and four or five young had wings only partly grown with the primaries about 10 cm out of their sheaths. This specimen has slight molt on the head and neck which we interpret to be the end of the first prebasic molt.

A male (KU 79235) collected on 11 February had a vestigial bursa of Fabricius and had just completed most of what we consider to have been its third prebasic molt. However, this prebasic molt of the head and neck was still underway and the alternate plumage being replaced on the head had darkish cap, cheek and white postocular streak, suggesting that the predefinitive alternate plumage of the head and neck (second alternate) is similar in aspect to the definitive basic plumage. Another male (KU 79236) with vestigial bursa collected 8 February had growing remiges, primaries about 10 cm long and secondaries about 15 cm, and was in heavy molt in all regions of the body. The retained, worn, presumably second alternate feathers of the head and neck were comparable in aspect to the definitive basic plumage. We hypothesize that the definitive alternate plumage of the head and neck of males does not occur until three years of age, i.e., before the third or subsequent prealternate molts.

Sides and flanks.—New first basic feathers growing in on a September male with many retained juvenal feathers are like the definitive basic feathers of the sides and flanks.

Predefinitive Plumages of Females

Basic Plumage

Upper back.—Compared to the definitive female, feathers of the first basic female upper back have less intense silvery gray and narrower margins that are dark gray.

Scapulars.—Compared to definitive females, the scapulars of the first basic female are less intense silvery gray and have narrower margins that are brownish-olive. The first basic plumage is less "contrasty" silver versus rich brown than is the definitive basic plumage of females.

Lower back, rump, and upper tail coverts.—A female collected in September had lower back and rump as in definitive female.

Upper breast and sides.—Upper breast and sides of two females collected in February with large bursae (in first basic plumage) were like definitive basic upper breast and sides.

Sides and flanks.—A presumably subadult female collected in September (ovary 25 X 15 mm) had unworn sides and flanks light silvery gray (more extensive on each feather than in definitive birds) and with narrower chestnut margins which were less richly chestnut than in definitive birds. A female taken in February with vestigial bursa had fresh sides and flanks mixed with more light silvery gray on each feather and narrower browner margins than in the definitive specimens.

Juvenal and Downy Plumages (Both Sexes)

Juvenal Plumage

We collected three specimens (two males, one female) in complete juvenal plumage (KU 7924, KU 79243, and KU 79244). All three specimens were collected from family groups in February 1981 at Puerto Melo. Remiges on each of the specimens were only partly grown, having developed 5–10 cm out of their sheaths. Based on these specimens, there is no sexual dimorphism in the juvenal plumage and birds of both sexes are identical at this stage of development except that males are somewhat larger than females.

Head and neck.—Unicolor dark brown, neck paler; indistinct pale buffy postocular streak.

Lower breast, belly, undertail coverts.—White.

Upper back.—Feathers medium gray but slightly darker than those on the upper breast and sides. Each feather has a dark, blackish-gray terminal band 3–4 mm wide.

Scapulars.—Outer webs medium gray; inner webs medium brownish-gray. Each feather has a blackish-brown margin; some feathers have a faint tan tip which may be a vestige of the formerly attached down.

Lower back, rump, and upper tail coverts.—Medium gray.

Upper breast and sides.—Feathers dull medium gray or brownish-gray for most of their lengths, with a blackish-brown subterminal band about 2–3 mm wide and a terminal band of light brown. A few feathers at the junction of the upper breast with the white lower breast have a trace of medium cinnamon just proximal to the dark terminal band.

Sides and flanks.—Medium brownish-gray, each of the feathers with a faint wash of pale pearly gray and a medium-brown margin, becoming slightly lighter at the tip.

Downy Plumage

The following description is based on five class-1 specimens from Chubut, Argentina, collected during 12–14 December 1981: MACN 52698 (male), KU 79624, 79625 (unsexed anatomical specimens), KU 79501 (female), and KU 79502 (male).

Head and neck.—Upper and lower eyelids whitish to pale pearl gray. Cheeks light to medium grayish brown becoming paler ventrally and posteriorly in some individuals. There is a dark grayish-brown streak through the eye along the dorsal margin of the cheeks and lores. Lores light to medium grayish-brown. Supraloral patch broad and continuous with the supraocular patch and postocular streak, all being whitish or pearl gray.

Upperparts.—Yoke light grayish-brown; rest of upper parts dark grayish-fuscous.

Underparts.—Upper breast medium grayish-brown; lower breast and belly white.

DIAGNOSTIC CHARACTERS

Generic Characters

External Characters

Steamer-ducks of all species are readily distinguishable from other waterfowl by the combination of large size (2–6+ kg), white wing specula, predominantly gray body color with white underparts, heavy bill, dull reddish throat patch, bright orange feet (in adults), variably developed wing-knobs, and (in most plumages) light postocular streaks, and the absence of metallic hues or contrastingly pale fore-patches on the dorsal surfaces of the wings. The three flightless species of *Tachyeres* are the only large (exceeding 1 kg in body mass) extant anseriforms that are permanently incapable of flight. Within their natural distributional range, steamer-ducks conceivably could be confused only with the much smaller Crested Duck (*Lophonetta specularioides*) or any of the three sympatric species of sheldgeese (*Chloephaga*); both of these genera are readily distinguishable from *Tachyeres* by their metallic wing specula, dark bills, variably patterned but non-gray body plumage, and (in *Chloephaga*) white forewings.

Skeletal Characters

Less obvious are the diagnostic skeletal characters of *Tachyeres*, five of which are derived and evidently unique among Anseriformes (Livezey 1986a). Femora of steamer-ducks possess well developed intermuscular lines on their caudal surfaces, lines which characteristically are produced into irregular, folded ridges proximally (Fig. 10A). Carpometacarpi of *Tachyeres* are characterized by deep, ovoid cuneiform fossae (Fig. 10B). The scapulae of steamer-ducks possess unusually bulbous, ventrally protrusive coracoidal facets (Fig. 10C). The robust, heavily armored skulls of

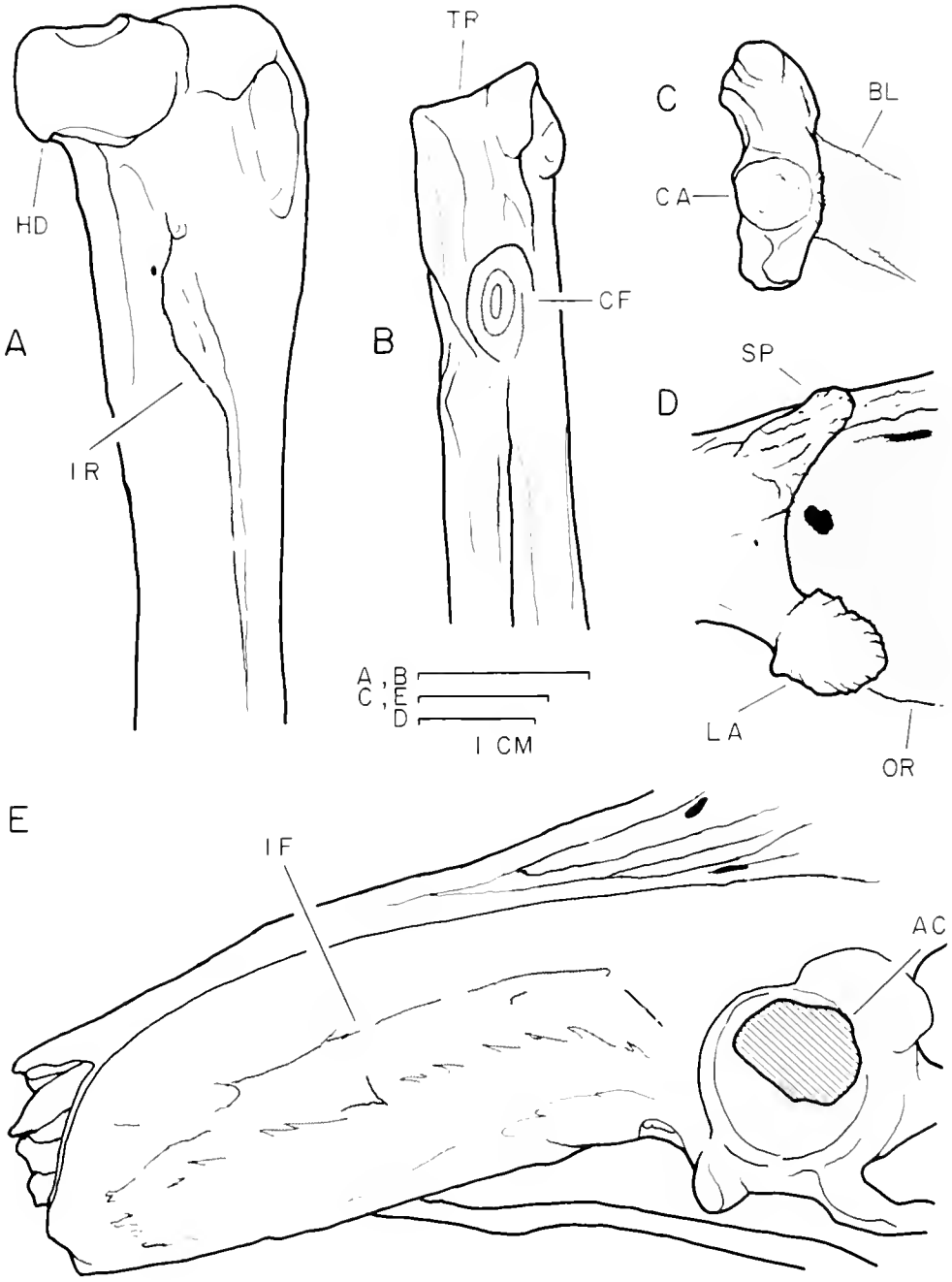

Fig. 10. Unique skeletal characters of *Iachyeres* (drawn from *I. pteneres*, KU 79842): A—caudal view of proximal end of femur (HD = head) showing prominent intermuscular ridge (IR); B—caudal view of proximal end of carpometacarpus (TR = trochlea) showing deep, ovoid cuneiform fossa (CF); C—proximal end of scapula (BL = blade) showing bulbous, ventrally protrusive coracoidal articulation (CA); D—lateral view of preorbital region of skull (LA = lacrymal process, OR = orbit) showing prominent, dorsolaterally projecting, knobby supraorbital process (SP); E—lateral view of cranial (preacetabular) portion of pelvis (AC = acetabulum) showing variably deep, irregular depression in iliac fossa (IF).

steamer-ducks are quite distinctive (Fig. 1), and mature birds possess supraorbital processes which are unique among Anseriformes in the combination of dorsolateral orientation and thick, rugose structure (Fig. 10D). Finally, members of the genus have pelves featuring variably deep, irregular depressions in the (preacetabular) iliac fossae (Fig. 10E).

Determination of Age

Unfortunately for purposes of identification, the distinctiveness of the genus *Tachyeres* is matched by the difficulty of distinguishing the four member species. The majority of the qualitative and mensural differences among species reliably apply only to adult (at least fully ossified, fledged) specimens, and therefore our review of species diagnoses is preceded by a consideration of techniques for determination of age of specimens.

Plumage and Soft Parts

Downy steamer-ducks are not likely to be confused with adult birds; identifying characters were discussed by Humphrey and Livezey (1985) and are summarized beyond. Juvenile steamer-ducks (no longer downy) usually can be separated from older birds by a combination of several external characteristics. Juveniles not yet fledged can be singled out in the field by their small size (body mass often 1 kg less than accompanying adults), the presence of incompletely grown (sheathed) primary remiges (also occur in adults in prebasic molt), and the aggregation of birds into groups larger than two. Plumages of juveniles of all species are darker, sex for sex, than the respective adult plumages, are almost devoid of white (including the postocular region), are distinctly more brown than gray in the general color of the head and neck, and the reddish throat patch is very faint. Juvenal rectrices differ from those of subsequent plumages in having distinctive terminal notches. Juvenal plumages were described earlier for *T. leucocephalus* (Humphrey and Thompson 1981) and *T. patachonicus* (Humphrey and Livezey 1982a).

Bills of juvenile *Tachyeres* of both sexes virtually lack orange coloration, and typically are dark bluish or greenish black. With increasing age, bills of males (both sexes of *T. pteneres*), become progressively more orange until the dark tones are limited to small areas beneath the nostrils, although this trend is complicated by a seasonal darkening of bills of males during prebasic molt (Humphrey and Livezey 1982a). Foot color shows a parallel developmental trend, being dull tan with comparatively prominent "knuckle" marks in many older predefinitive specimens (Humphrey and Livezey 1982a). As with the coloration of the bill, the feet of definitive males become less orange during wing molt.

Wing spurs are generally well developed in adult *Tachyeres* but there is substantial individual, age–related, and sexual variation in this structure. Juvenile birds and some yearlings show little or no enlargement of the spurs, and the overlying skin is relatively thin, fully feathered, and dull grayish flesh in color. Spurs of older birds typically become much enlarged, covered with bare orange skin, and often are equipped with a thick cornified knob; the degree of this development varies among individuals, evidently because of differences between birds in the frequency of wing–assisted combat. The structure is useless for identification of species.

Skeletal Development

Fledgling *Tachyeres* often retain signs of immaturity in certain skeletal structures, the juvenility of which is indicated by incomplete ossification and/or thickness. Incompletely ossified elements remain comparatively pliable when fresh and, after cleaning and drying, often become somewhat chalky or easily warped. Several skeletal structures are prone to such late development in *Tachyeres*, notably the caudal margins (margo caudalis) and carina of the sternum, the antorbital processes of the skull, and the distal–most limb elements, especially the phalanges. Also, the cranium becomes progressively thicker and more rugose during the first few years of life; those of juveniles appear comparatively smooth, and suture lines between cranial elements remain distinct in very young birds.

Bursa and Gonads

As in waterfowl generally (Hochbaum 1942, Shortt 1943, Elder 1946, Davis 1947, Hanson 1962), the bursa of Fabricius (cloacal bursa) in *Tachyeres* shrinks with age. In juvenile steamer-ducks the bursa is large and glandular, shrinks to modest size in yearling birds, and becomes vestigial or disappears entirely in older specimens (Humphrey and Livezey 1982a). Despite significant interspecific differences in body mass, an inverse association between sizes of bursae and gonads is demonstrated in both sexes, even if species are pooled (Figs. 11, 12). There is, however, considerable variation in this overall relationship due in large part to seasonal variation in size of gonads. The precise age at sexual maturity in *Tachyeres* is not known and may vary among the species; it appears that most paired birds on territories are "adults," i.e., have no bursa or bursa of vestigial size, and are estimated to have attained a minimum age of two years (Humphrey and Livezey 1982a).

Although specimens of Anatidae are most frequently classified to sex on the basis of gonads, the syrinx provides another means for Tadorninae and Anatinae, wherein the syrinx is enlarged into an asymmetrical bulla in males. This criterion is particularly useful for skeletal specimens and freshly collected downy young (Beer 1962).

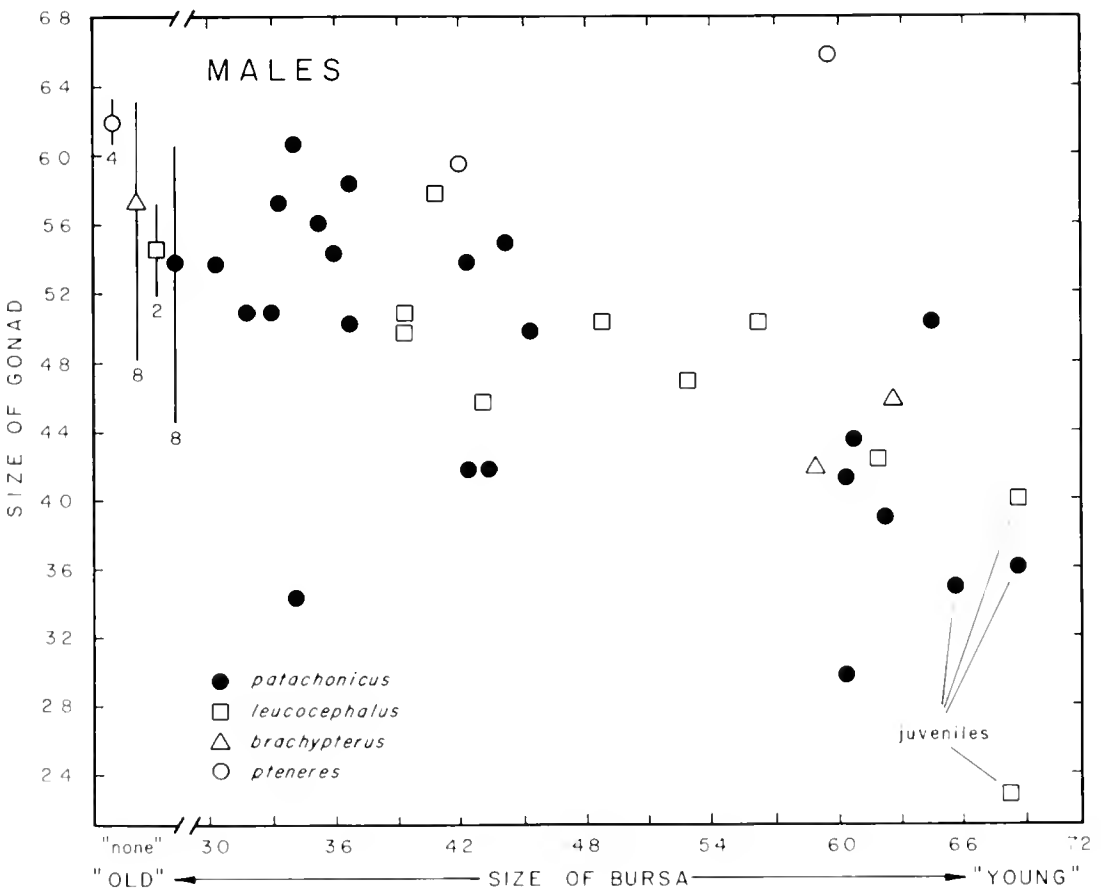

Fig. 11. Logarithmic plot of sizes (products of maximal lengths and widths) of testes and cloacal bursae for males of four species of *Tachyeres*. Means, ranges, and sample sizes of testicular areas are depicted for specimens lacking bursae.

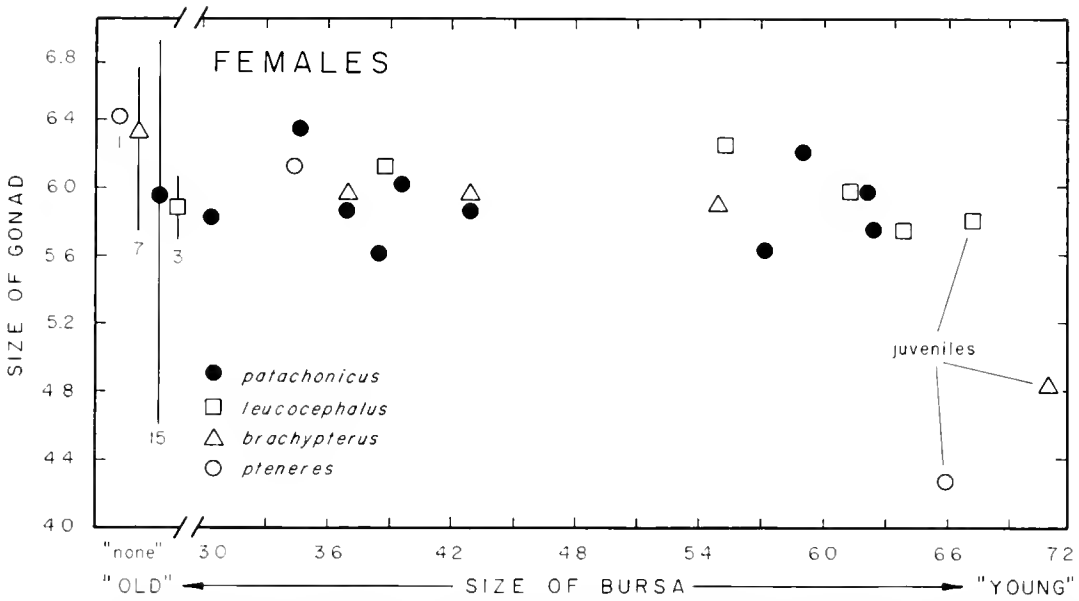

Fig. 12. Logarithmic plot of sizes (products of maximal lengths and widths) of ovaries and cloacal bursae for females of four species of *Tachyeres*. Means, ranges, and sample sizes of ovarian areas are depicted for specimens lacking bursae.

Qualitative Characters of Species

External Differences

Except for variations in the amount of reddish-brown on scapulars, sides, and flanks, all steamer-ducks have essentially the same aspect from the neck down, i.e., body battleship gray with white lower breast and belly. Coloration of the head and neck is extremely variable both within and among species. In its first two years of life, a steamer-duck, depending on the species, may wear five (*T. pteneres*, *T. leucocephalus*) or seven (*T. brachypterus*, *T. patachonicus*) plumages (Fig. 9). Moreover, because steamer-ducks may nest any month of the year (most nest in the austral spring and summer, i.e., October–January) there may be considerable variation in the chronology of molts. The situation is simplified (or complicated) by the fact that most of the plumages are so similar that they cannot be distinguished from superficial examination and many of them (first-year plumages) are still unknown.

T. patachonicus and *T. brachypterus* have three molts and plumages per year (Fig. 9). In definitive males, the supplemental ("breeding") plumage of the head and neck is predominantly white and from a distance the birds look completely white-headed in that plumage. The supplemental plumage in most individuals is worn for a month or two, usually during October–January. The supplemental plumage is followed by a basic plumage in which the head is unicolor dark brown. This is worn for a few weeks at the most and is followed by an alternate plumage in which the males have a dark gray crown, darkish cheeks, and a broad, white postocular streak.

T. leucocephalus and *T. pteneres* have, as far as is known, two molts and plumages per cycle (Fig. 9). Males in definitive alternate plumage appear white-headed but, in the hand, *T. leucocephalus* may have varying amounts of light to medium gray on the forehead and *T. pteneres* may have the whole head and neck pale gray to white. Female *T. leucocephalus* in definitive alternate plumage has a broad, white postocular streak, dark cap, and somewhat lighter cheeks. Female *T. pteneres* in definitive alternate plumage has medium gray head and neck, cap somewhat darker, and differs from alternate females of the three other species in

having an orange bill and lacking a conspicuous white postocular streak. Comparative summaries of the definitive plumages of all species of steamer-ducks are set forth in Tables 1 and 2.

Of the four species of *Tachyeres*, adults of only one can be identified confidently using characters of plumage pattern and soft parts. This unique species is *T. pteneres*, the adults of which differ from those of their congeners in lacking significant sexual dichromatism, both sexes having entirely orange bills (except the black nails) and predominantly gray heads and necks; the species also is unique in virtual absence of chestnut hues in the scapulars, sides, and flanks (Figs. 4, 9). Adult female *T. leucocephalus* in alternate plumage differs, less obviously, from females of other *Tachyeres* in having comparatively broad postocular streaks (Fig. 9). Murphy (1936) made reference to a "golden collar" of feathers at the base of the necks of some *T. brachypterus*, a character offered as an aid in separating *T. brachypterus* from the smaller, sympatric *T. patachonicus*. We have been unable to distinguish this character in *T. brachypterus*, either on study skins or in the field. In other respects, adults of the three sexually dichromatic species—*T. patachonicus*, *T. leucocephalus*, and *T. brachypterus*—are not distinguishable using qualitative features of plumages and soft parts.

Murphy (1936:955), evidently stimulated by the descriptions and counts of remiges in *T. pteneres* given by Forster (1844) and Bennett (1924), studied differences between *T. pteneres* and *T. patachonicus* in the patterns and amount of white on the secondary remiges: "In both species the outermost one or two secondaries have a slight and variable dark subterminal spotting. If we disregard this, and count the secondaries inward, we find that in *patachonicus* the first ten, eleven, or twelve quills are white, the first dark marks appearing on the inner web of the eleventh, twelfth, or thirteenth feather. In most instances the next succeeding feather is entirely dark. In *pteneres*, only six, seven, or eight secondaries from the outermost are white, the gray markings usually beginning on the inner web of the eighth or ninth, succeeding quills after the first spotted one being more or less dark on both webs or entirely dark."

We tested this distinction by sketching on standard forms the color patterns of the secondary remiges of all birds collected. Selected diagrams of each species and sex are depicted in Figs. 13–17. Counts of "white" feathers were difficult to make because of the spectrum of degree of spotting observed. Murphy (1936) chose to disregard the "slight and variable dark subterminal spotting" he observed in the "outermost one or two secondaries." We found it difficult to determine the amount of spotting that should be considered "slight," and the extent of spotting that should be classified as "subterminal." Further problems resulted from the variable basal shading noted in many birds, and the continuum of shades from white through gray to black that was observed.

Whatever rules one adopts, the shading patterns in secondary remiges of *T. pteneres* and *T. patachonicus* appear to be quite similar, and any difference in "modal" condition would be unreliable for species diagnosis. We found that *T. patachonicus* almost never has 12 largely white secondaries; this was true of all the other species as well. Specimens of all four species typically had 10 to 11 "largely white" secondaries, although there was a tendency for *T. pteneres* to have more heavily marked secondaries, prompting us to count only nine "white" secondaries in some specimens. We never found a specimen with only six or seven of what we would judge to be white secondaries. Wing patterns of *T. brachypterus* and *T. leucocephalus* were indistinguishable from those of *T. patachonicus*.

Sexual dichromatism in shading patterns may further complicate these patterns. In the *T. brachypterus* we collected, we found a dark terminal spot on the outermost (first) secondary in nine of ten females, but this mark was absent in all 11 males. Lastly, we doubt that this technique could be attempted effectively with dried skin specimens, because of reduced access to the secondary remiges.

Fresh downy young are identifiable to species using characters of the head patterns of the natal plumage. These differences were assessed by Humphrey and Livezey (1985), work based in turn on the earlier diagnoses presented by Lowe (1934) and Murphy (1936). Briefly, downy young of *T. l*

Table 1. Analysis of diagnostic characters of adult steamer-ducks, by region of sympatry (on saltwater), of potential utility in the field. Key characters within each region are shown in boldface.

Region	Species	Sex	Bill Color	Bill Shape	Neck	Wing & Tail Lengths	Body Color	Generalized Head Pattern
CHILE, TIERRA DEL FUEGO	*T. patachonicus*	M	orange	**slender**	heavy	**long**	**brownish** gray	**All white, or brownish with gray cap & white streak.**
		F	**darkish**	**slender**	**slender**	**long**	**brownish** gray	**Dark brown with white postocular streak.**
	T. pteneres	M	orange	**stocky**	**very** heavy	**short**	**silvery** gray	**Uniform pale gray.**
		F	**orange**	**stocky**	**heavy**	**short**	**silvery** gray	**Uniform medium gray.**
CHUBUT	*T. patachonicus*	M	orange	**slender**	heavy	**long**	brownish gray	All white, or brownish with graycap & white streak.
		F	darkish	**slender**	**slender**	**long**	brownish gray	Dark brown with **narrow** white post-ocular streak.
	T. leucocephalus	M	orange	**stocky**	**very** heavy	**short**	brownish gray	All white, or brownish with gray cap and white streak.
		F	darkish	**stocky**	**heavy**	**short**	brownish gray	Dark brown with **broad** white post-ocular streak.
FALKLAND	*T. patachonicus*	M	orange	**slender**	heavy	**long**	brownish gray	All white, or brownish with gray cap and white streak.
		F	darkish	**slender**	**slender**	**long**	brownish gray	Dark brown with narrow white post-ocular streak.
	T. brachypterus	M	orange	**stocky**	**very** heavy	**short**	brownish gray	All white, or brownish with gray cap and white streak.
		F	darkish	**stocky**	**heavy**	**short**	brownish gray	Dark brown with narrow white post-ocular streak.

Table 2. Summary of generalized aspects of heads and necks of *Tachyeres* in definitive plumages, by sex and species.

Sex	Species	Plumage of head and neck		
		Basic	Alternate	Supplemental
Male	*T. patachonicus*	Unicolor dark brown	Gray cap, brown cheek, *white postocular streak*	Largely white
	T. brachypterus	Unicolor dark brown	Gray cap, brown cheek, white postocular streak	Largely white
	T. leucocephalus	Dark cap, brown cheek white postocular streak	Largely white	—[a]
	T. pteneres	Dark cap, gray cheek	Pale gray to white	—[a]
Female	*T. patachonicus*	Unicolor dark brown	Dark cap, brown cheek, white postocular streak interrupted in middle	Cap gray, cheeks brown, short white postocular streak
	T. brachypterus	Unicolor dark brown	Dark cap, brown cheek, white postocular streak long, narrow, unbroken	Same as alternate
	T. leucocephalus	Unicolor dark brown postocular streak short	Dark cap, brown cheek, white postocular streak long, wide, unbroken	—[a]
	T. pteneres	Dark gray cap, medium gray cheek	Dark gray cap, medium gray cheek, short pale gray postocular streak	—[a]

[a]Plumage not documented.

leucocephalus differ from those of other *Tachyeres* in having whitish (not dark) upper eyelids and the crown being darker than the cheeks. Downy *T. pteneres* are distinguishable from the downies of other *Tachyeres* by their divided (two-parted) postocular streaks and by their very small (or absent) supraloral and supraocular patches. Downy specimens of *T. patachonicus* differ from those of *T. leucocephalus* in color of eyelid, relative darkness of crown, and by having narrow supraloral and supraocular patches which are separate from the postocular streak; from downies of *T. pteneres* in having a continuous (not two-parted) postocular streak; and from those of *T. brachypterus* in having the postocular streak separated from the supraloral and supraocular patches. Downies of *T. brachypterus* differ from those of *T. leucocephalus* in eyelid color and the narrowness of the supraloral and supraocular patches; from downies of *T. pteneres* in having a continuous (not two-parted) postocular streak; and from the young of *T. patachonicus* in having the supraloral and supraocular patches continuous with the postocular streak.

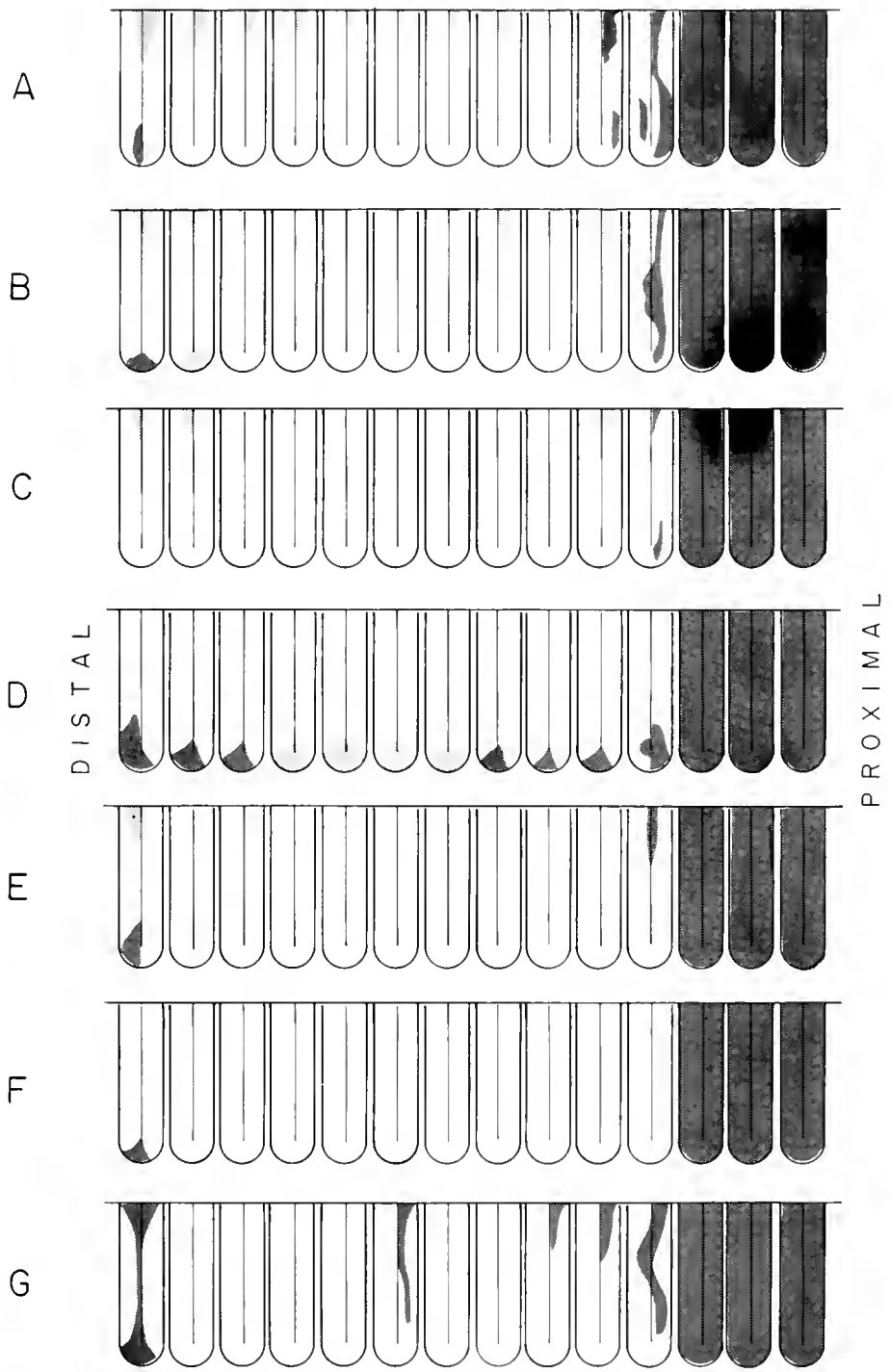

Fig. 13. Diagrams of shading patterns of secondary remiges (wing specula) of selected *T. patachonicus* from maritime coastal sites of Argentina: A—male, Ushuaia (KU 79203); B—male, Puerto Deseado (KU 79215); C—male, Puerto Deseado (KU 79219); D—female, Ushuaia (KU 79190); E—female, Ushuaia (KU 79192); F—female, Puerto Deseado (KU 79209); G—female, Puerto Deseado (KU 79212).

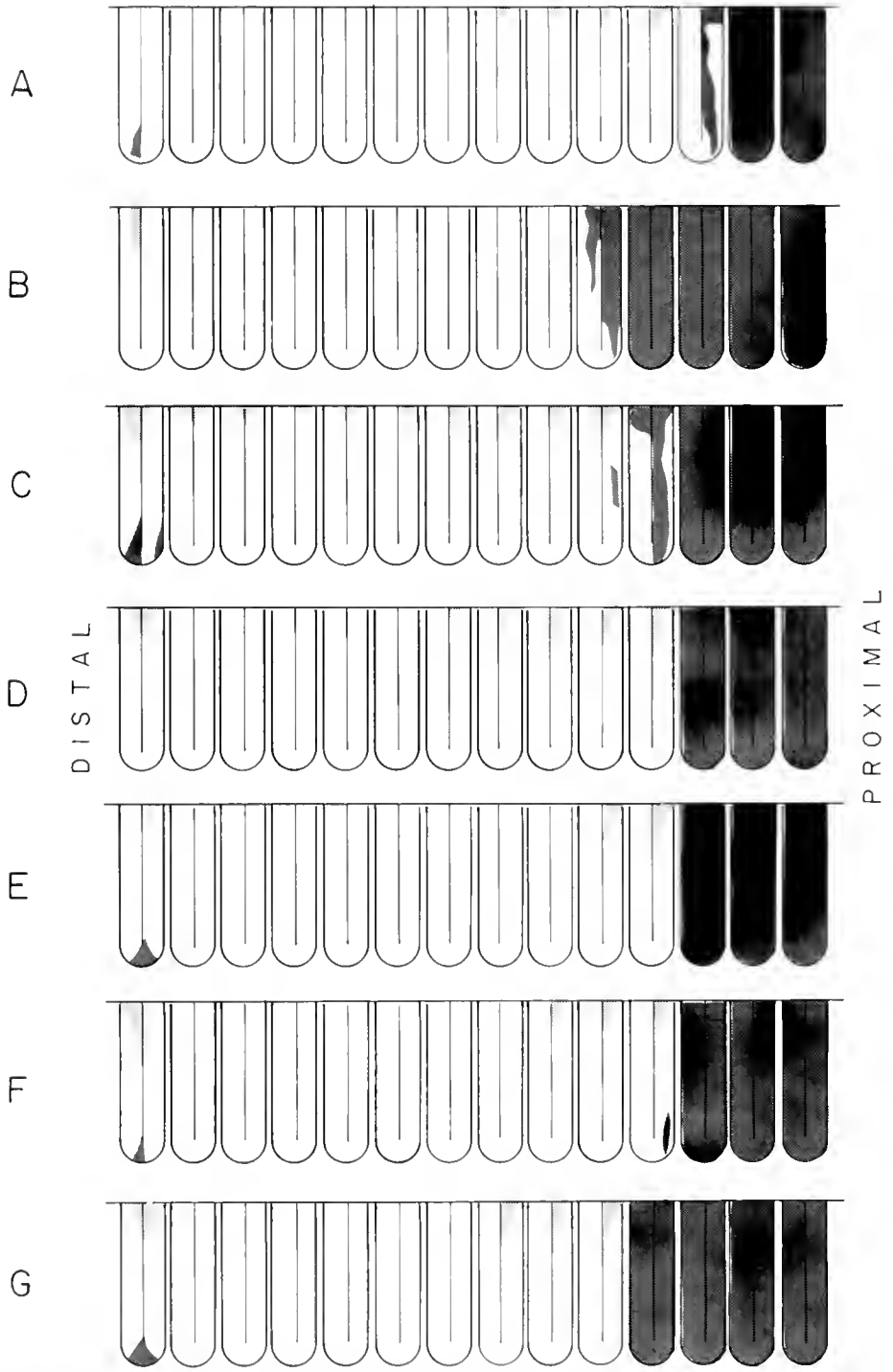

Fig. 14. Diagrams of shading patterns of secondary remiges (wing speculа) of selected *T. patachonicus* from Andean lakes (Argentina and Chile) and the coast of central Chile (Ens. Hunto, Region X): A—male, Lago Fontana (KU 79471); B—male, Lago Roca (KU 79460); C—male, Lago Rupanco (KU 79856); D—male, Ens. Hunto (KU 79854); E—female, Perito Moreno (KU 79465); F—female, Lago Rupanco (KU 79855); G—female, Lago Futalaufquen (KU 79476).

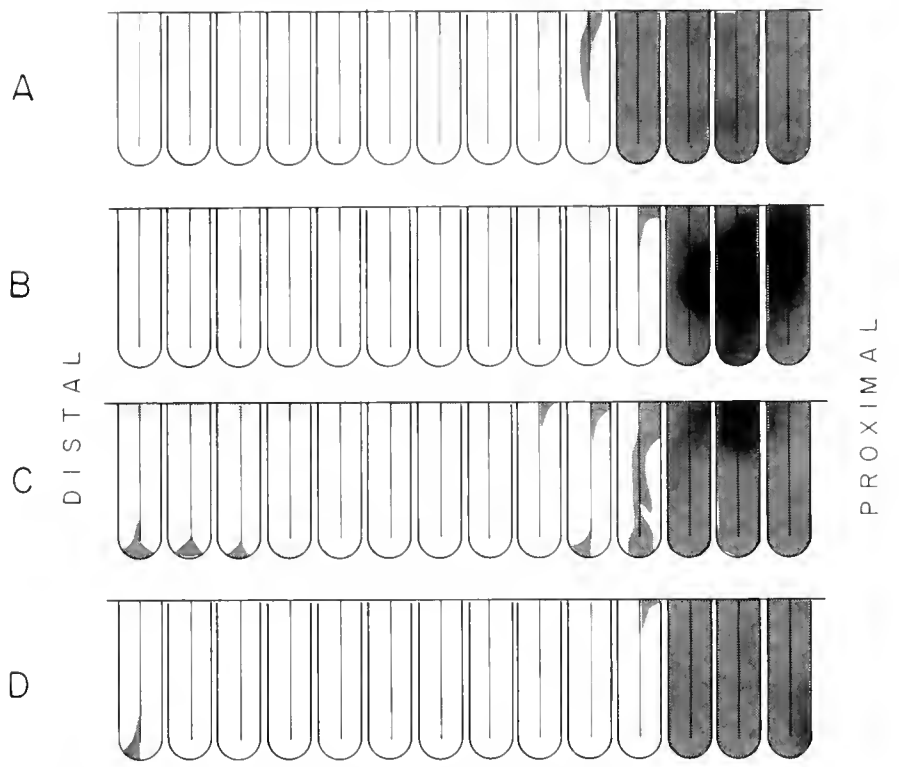

Fig. 15. Diagrams of shading patterns of secondary remiges (wing speculæ) of selected *T. brachypterus* from Lively Island, east Falkland Islands; A—male (KU 80515); B—male (KU 80530); C—female (KU 80529); D—female (KU 80524).

Skeletal Differences

Osteological comparisons played a crucial role in the conclusive diagnosis of flighted and flightless steamer-ducks by Lowe (1934); the relative lengths of selected elements, notably the illustrations of humeri and sterna of *T. patachonicus* and *T. pteneres* (his *brachypterus*), added a new dimension to the problematic interspecific differences in size and plumage. However, like the relative thickness of limb elements and sternal conformation of *T. leucocephalus* illustrated by Humphrey and Thompson (1981), such skeletal proportions are treated more effectively as quantitative, statistically comparable characters (see below).

As part of a phylogenetic analysis of the genus *Tachyeres*, Livezey (1986c) listed nine qualitative characters which varied within the genus. Despite moderate intraspecific variation in several of these features, these characters can provide additional aids to identification of skeletal remains of *Tachyeres* (e.g., weathered carcasses), clues that are independent of the more traditional comparisons of plumages and measurements. Anatomical terminology used in the following descriptions follows Baumel *et al.* (1979).

Two characters of the skull—one involving the occipital condyle and the other the *processus mandibulae medialis* of the mandible—vary among species of *Tachyeres*. In *T. pteneres*, the occipital condyle is produced ventrad to the plane of the basioccipital plate, whereas in other *Tachyeres* the condyle is more dorsal in position (Fig. 18). The *processus mandibulae medialis* has three qualitatively distinguishable conditions in the genus (Fig. 19); in *T. patachonicus* the process is almost without medial inflection; in the sister-species *T. brachypterus* and *T. leucocephalus* there is moderate inflection; and in *T. pteneres* the medial inflection is pronounced (state for *T. pteneres* incorrectly given in Table 1 of Livezey 1986c).

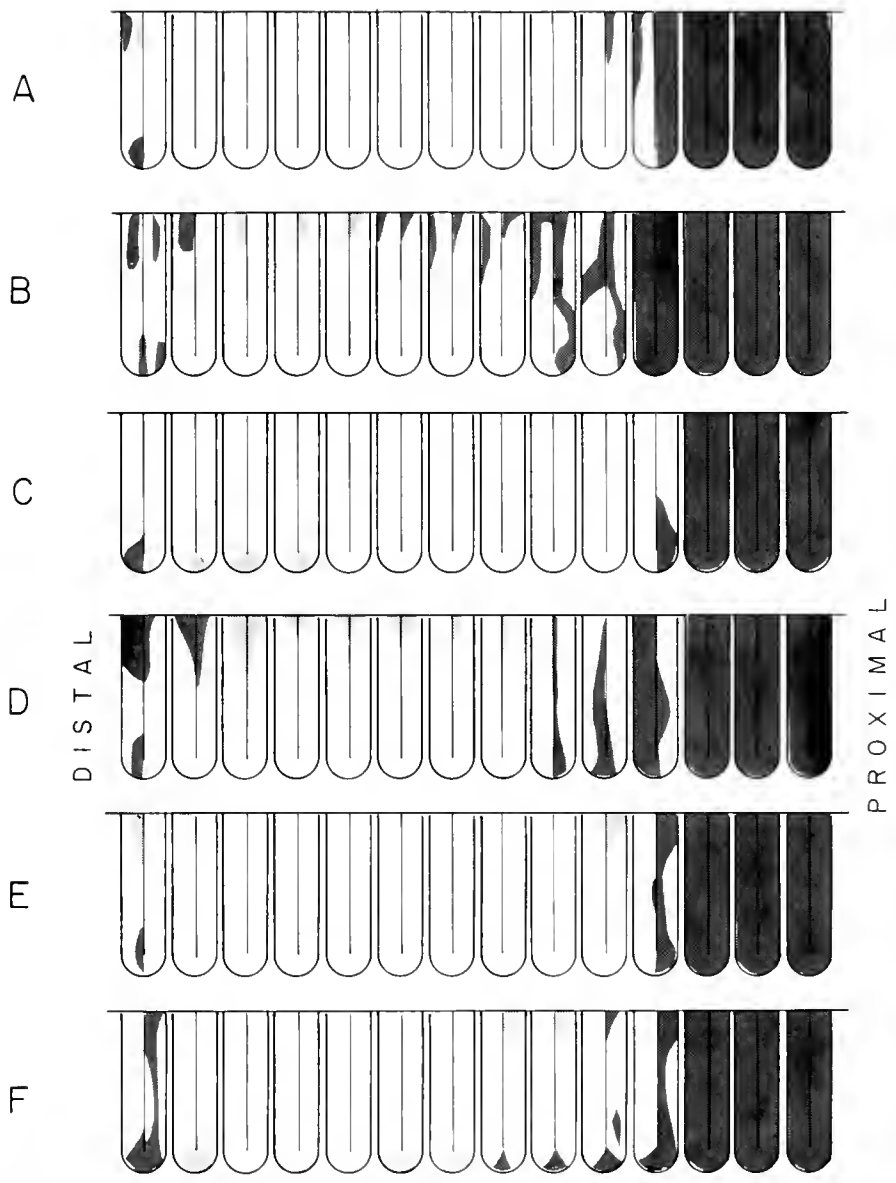

Fig. 16. Diagrams of shading patterns of secondary remiges (wing specula) of selected *T. pteneres*: A—male, Ushuaia (KU 79178); B—male, Ushuaia (KU 79179); C—female, Ushuaia (KU 79181); D—female, Ushuaia (KU 79194); E—male, Ens. Codihue, Chile (KU 79842); F—female, Ens. Codihue (KU 79843).

The carpometacarpus has four qualitative characters useful for distinguishing species–subgroups of *Tachyeres*. The attachment site or 'scar' of *M. extensor metacarpi ulnaris* is proximal to the *synostium metacarpi proximalis* (proximal metacarpal fornix) in flightless species, but is coincident with it in *T. patachonicus* (Fig. 20). The *trochlea carpalis ventralis* (internal rim of carpal trochlea) extends caudally beyond the *os metacarpale minus* (metacarpal III) in *T. pteneres*, whereas in other species of *Tachyeres* the former approximates the latter in caudal extension (Fig. 20). A small (unnamed) tuberosity on the proximocaudal surface of *os metacarpale minus*

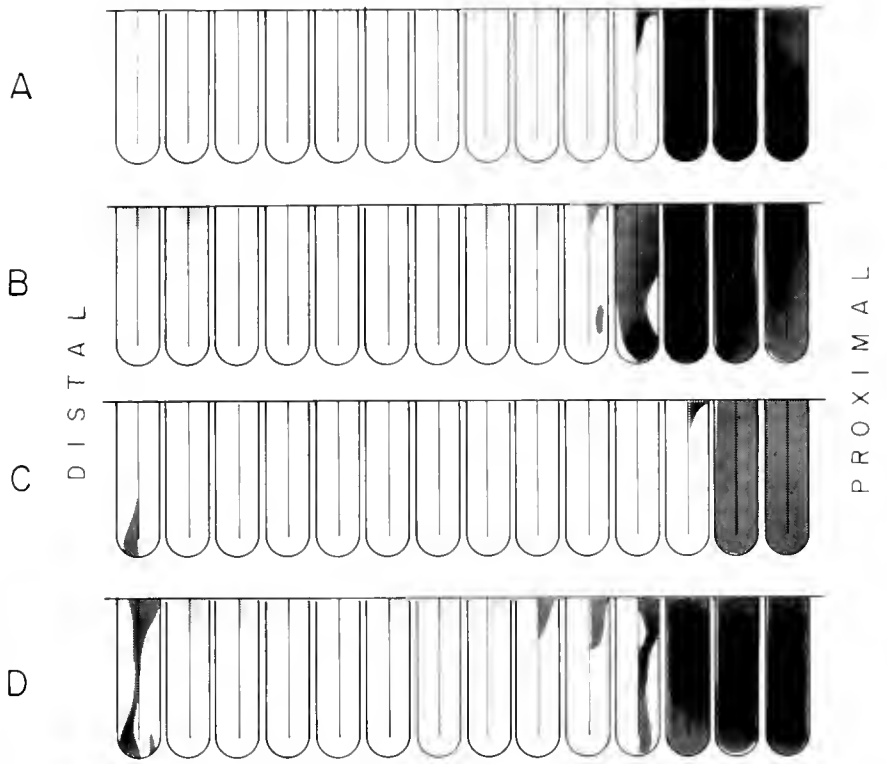

Fig. 17. Diagrams of shading patterns of secondary remiges (wing specula) of selected *T. leucocephalus* from Puerto Melo: A—male (KU 79246); B—male (KU 79235); C—female (KU 79457); D—female (KU 79240).

(metacarpal III) is separable into three size classes: indistinctly developed in most *T. patachonicus*; moderately developed in *T. brachypterus* and *T. pteneres*; and comparatively conspicuous in *T. leucocephalus* (Fig. 20). Finally, the distal terminus of the *sulcus tendineus* assumes two distinct conformations: an open, indistinctly ridged channel in *T. patachonicus* and *T. pteneres*; and a proximo–distally abbreviated passage surrounded by prominent, typically pointed, and sometimes joined 'lips' in *T. brachypterus* and *T. leucocephalus* (Fig. 21).

Three other elements of the pectoral limb provide useful qualitative characters in *Tachyeres*—the radius, coracoid, and scapula. The radius of *T. leucocephalus* is distinguishable from those of its congeners by the proximally appressed scapholunar facet (Fig. 22). The coracoids of flightless species of *Tachyeres* differ from that of *T. patachonicus* by the two–layered aspect of the *facies articularis sternalis ventralis* (ventral sternal facet). The degree of torsion of the *corpus scapulae* (scapular blade) also distinguishes *T. patachonicus* from flightless steamer-ducks, being (variably) greater in the latter.

Given the flightless condition of three species of *Tachyeres*, it might be expected that there would be interspecific differences in the sternum, especially in the development of the carina (keel). Livezey and Humphrey (1986) documented significant statistical differences among species in *relative* (but not absolute) depth of the sternal carina, but variation in this structure and large interspecific differences in sternal size render non–mensural appraisal of sternal differences problematic.

Quantitative Characters of Species

External Measurements

All external measurements, including the standard dimensions given in the species accounts,

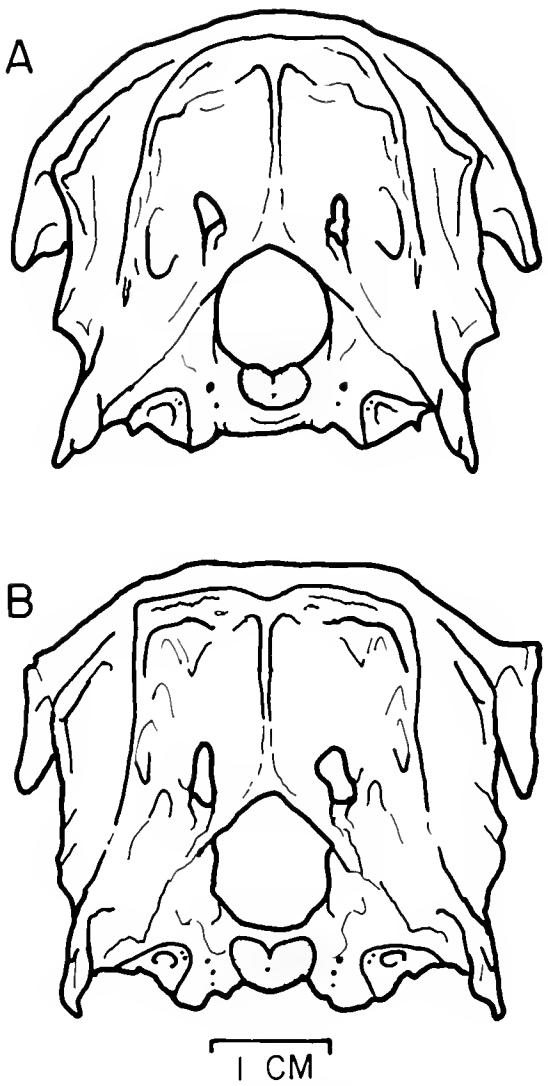

Fig. 18. Occipital condyles (stippled) of *Tachyeres*, showing the comparatively ventral position of that in *T. pteneres*: A—*T. brachypterus* (KU 80527); B—*T. pteneres* (KU 79842).

differed significantly among species ($P < 0.001$). Most measurements also differed between the sexes, the only exceptions being culmen length and lamellar count (Table 3). All but lamellar count, wing length, and tail length ranked species in accordance with total body mass: *T. pteneres* largest, followed by *T. brachypterus*, *T. leucocephalus*, and *T. patachonicus*. Although there is overlap among species in most measurements, study of suites of measurements, especially of combinations of size-correlated and size-opposed measurements, provided effective species diagnoses in most cases (Table 3).

Lengths of the primary remiges (flight feathers) provide similar information for species identification. We collected and measured two remiges—the ninth (longest) primary and the first (outermost) secondary from each specimen collected during 1980–84 that was not in wing molt. In all dimensions recorded—total length, length of vane, calamus length (from umbilicus), and calamus width (at umbilicus)—*T. patachonicus* exceeded its more massive, flightless congeners (Table 4; Livezey and Humphrey 1986). Of the flightless species, *T. leucocephalus* and *T. brachypterus* had longer remiges than the larger *T. pteneres* (Table 4); this ranking of total lengths largely reflects the longer vanes of *T. leucocephalus* and *T. brachypterus*, in that the calami of *T. pteneres* exceed in length those of the two smaller, flightless species (Table 4); widths of calami (not tabulated) followed lengths of calami in interspecific and intersexual rankings. These interspecific differences in lengths and proportions of primary and secondary remiges can be useful aids to identification of *Tachyeres*, especially for separation of *T. patachonicus* from its flightless congeners (Fig. 23). For purposes of identification, however, care must be taken to exclude from comparisons specimens with significantly worn remiges, a frequent condition in all species of *Tachyeres*, especially the flightless species. Also, juvenile birds (i.e., specimens with juvenal remiges) have remiges which are shorter, sex for sex, than those of older birds (Humphrey and Livezey 1982a, Livezey and Humphrey 1986); juvenal primaries of yearling birds are roughly 1.5–2 cm shorter than those of older birds, and juvenal secondary remiges are 1–1.5 cm shorter than basic secondaries, depending on species and sex. Microstructure of remiges of *Tachyeres* does not differ between flighted and flightless species (McGowan 1989).

Several simple ratios have proven especially useful for distinguishing flightless *Tachyeres* from *T. patachonicus*. This is generally the diagnosis of greatest interest because the three flightless spe-

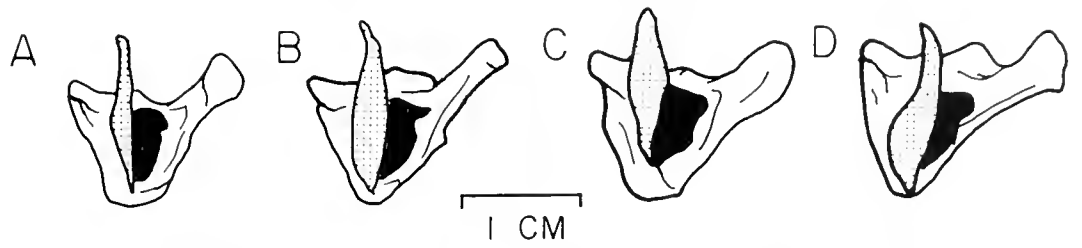

Fig. 19. Caudal views of left mandibular rami of *Tachyeres*, illustrating the variable medial inflection of the *processus mandibulae medialis* (stippled): A—essentially uninflected process in *T. patachonicus* (KU 79205); B, C—moderately inflected processes of *T. brachypterus* (KU 80519) and *T. leucocephalus* (KU 77931), respectively; D—pronounced medial inflection of process of *T. pteneres* (KU 79842).

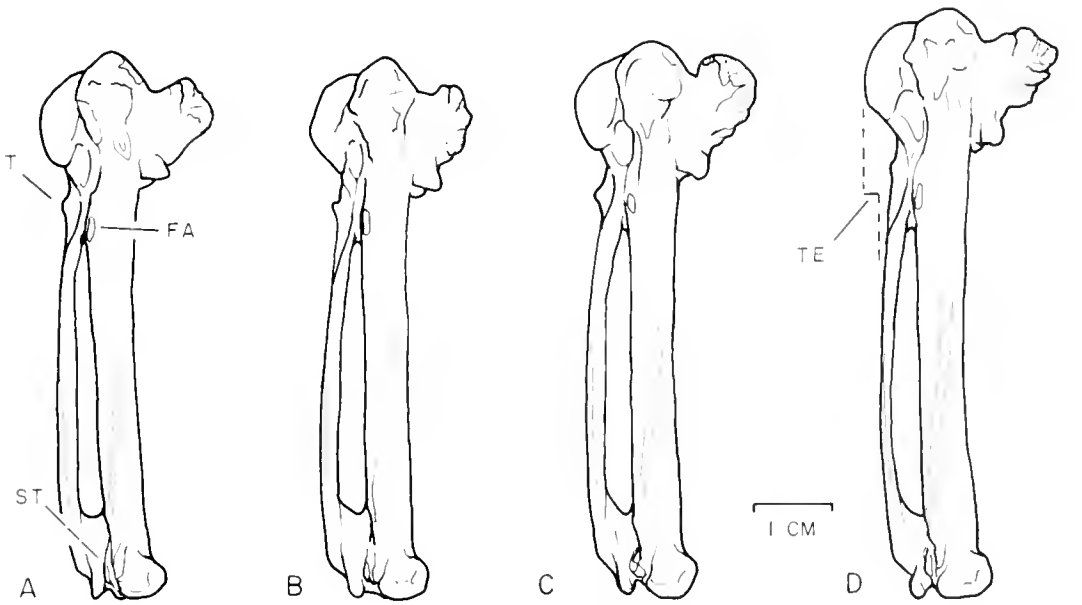

Fig. 20. Carpometacarpi of *Tachyeres*, lateral surfaces: A—*T. patachonicus* (KU 79205), B—*T. brachypterus* (KU 80527), C—*T. leucocephalus* (KU 77925), D—*T. pteneres* (KU 79842). Structures indicated: T—tuberosity, disproportionately large in *T. brachypterus* and *T. leucocephalus*; FA—the attachment site of *M. extensor metacarpi ulnaris* (the "flexor" of Woolfenden 1961), progressively proximad to fornix in A—D; ST—the *sulcus tendineus*, with pointed or bridged margins in *T. brachypterus* and *T. leucocephalus*; and TE—the comparatively great caudal extent of the trochlea in *T. pteneres*.

cies are mutually allopatric and each may co-occur with *T. patachonicus* in marine littoral environments. Lamellar density, the ratio of lamellar count over bill length, ranks species and sexes *inversely* with respect to body mass, and hence facilitates separation of *T. patachonicus* from flightless *Tachyeres* (Table 5), especially if used in combination with a measure of size (e.g., tarsus length or total mass). Except for relatively rare instances of flightless marine *T. patachonicus* (Humphrey and Livezey 1982b), wing-loadings (g body mass • cm^{-2} wing area) are informative: *T. patachonicus* typically has wing loadings less than 2.5; specimens of flightless taxa exceed this value (Table 5). The ratio of wing length to tarsus length provides similar separation of the two groups (Table

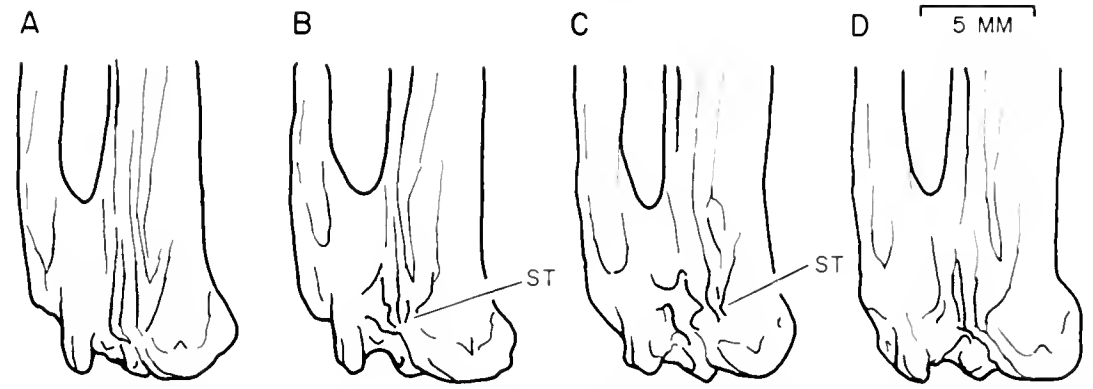

Fig. 21. Distal ends of carpometacarpi of *Tachyeres*, lateral surfaces, showing the pointed margins of the *sulcus tendineus* (ST; stippled) in *T. brachypterus* and *T. leucocephalus*: A—*T. patachonicus* (KU 79205), B—*T. brachypterus* (KU 80527), C—*T. leucocephalus* (KU 77925), and D—*T. pteneres* (KU 79842).

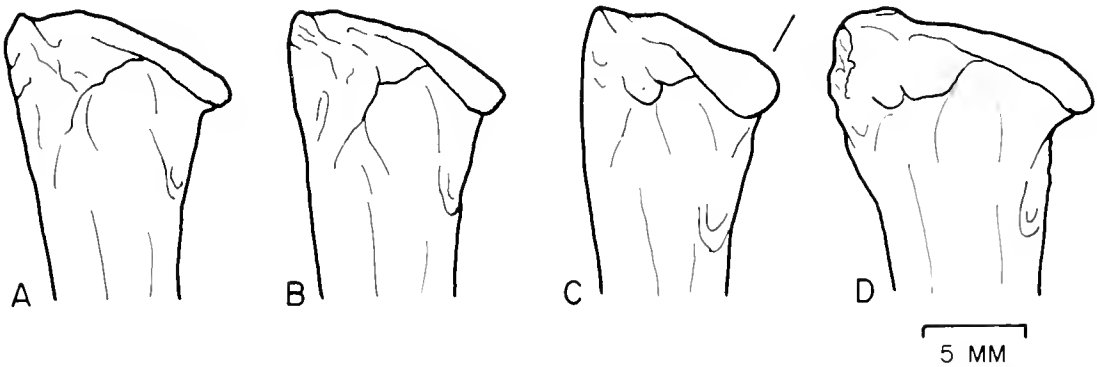

Fig. 22. Distal ends of radii of *Tachyeres*, showing the comparatively large, appressed scapholunar facet (stippled) of *T. leucocephalus*: A—*T. patachonicus* (KU 79205), B—*T. brachypterus* (KU 80527), C—*T. leucocephalus* (KU 77938), D—*T. pteneres* (KU 79842).

5, Fig. 24), is measured more easily, and can be used with study skins. Roughly, the wings of *T. patachonicus* are five times as long as their tarsi, whereas the ratios of the flightless species average four; sexual differences were insignificant. Murphy (1936) gave the means for the reciprocal of this ratio as: *T. pteneres*, 0.26; *T. brachypterus*, 0.24; and *T. patachonicus*, 0.20.

Multivariate analysis of a suite of external measurements provides the most reliable discrimination of species and sexes (Appendix). Using the four most commonly available skin measurements (culmen length, nail width, tarsus length, and wing length) in a stepwise discriminant analysis, 71.4% of 245 specimens were correctly (jackknifed) classified to species and sex (Fig. 25); this compares favorably to the 12.5% expected for random assignments. If sex is known, species identifications using the same data achieved 91.5% success for males ($n = 130$) and 90.4% for females ($n = 115$), as compared to the random expectations of 25%. This indicates that, for these characters, knowing the sex of the specimen improves accuracy of identification by almost 20%. Inclusion of total weight in the analyses reduced the sample sizes and only slightly improved the success of species–sex classifications (79.4% success, $n = 131$). Classification functions incorporating the four external measurements are given in the Appendix.

Table 3. Summary statistics[a] for selected external measurements of steamer-ducks, by species and sex. Units of measurement are mm (linear), cm^2 (areal), and g (masses).

Character[b]	*T. patachonicus*		*T. leucocephalus*		*T. brachypterus*		*T. pteneres*	
	Males	Females	Males	Females	Males	Females	Males	Females
Culmen length[6,0]	53.9 ± 2.6 (67)	52.3 ± 2.3 (67)	55.9 ± 2.3 (16)	55.8 ± 1.5 (13)	56.8 ± 2.2 (25)	57.2 ± 2.1 (15)	59.5 ± 3.8 (37)	58.4 ± 3.4 (30)
Nail width[6,6]	11.6 ± 0.9 (66)	10.8 ± 0.8 (67)	12.4 ± 0.8 (16)	11.8 ± 0.8 (13)	13.5 ± 0.8 (25)	12.5 ± 0.8 (15)	16.1 ± 0.9 (37)	15.3 ± 0.9 (30)
Tarsus length[6,6]	60.0 ± 3.0 (65)	56.3 ± 3.1 (67)	64.8 ± 1.9 (16)	62.5 ± 2.3 (13)	67.8 ± 3.1 (25)	63.8 ± 2.5 (15)	71.4 ± 3.8 (37)	67.5 ± 3.2 (30)
Digit-III length[6,6]	84.8 ± 5.5 (66)	78.3 ± 5.1 (65)	87.6 ± 2.8 (16)	84.7 ± 5.5 (13)	91.6 ± 3.2 (25)	85.1 ± 3.7 (15)	96.8 ± 5.5 (37)	90.6 ± 5.8 (30)
Wing (arc) length[6,6]	303 ± 11 (62)	287 ± 10 (64)	281 ± 10 (14)	273 ± 10 (13)	276 ± 13 (24)	268 ± 12 (15)	273 ± 12 (38)	262 ± 11 (28)
Tail length[6,6]	111 ± 5.9 (31)	104 ± 6.3 (30)	97 ± 10.2 (7)	94 ± 5.9 (7)	102 ± 5.0 (15)	96 ± 7.1 (12)	98 ± 7.7 (14)	87 ± 6.7 (27)
Total mass[6,6]	2958 ± 296 (54)	2349 ± 295 (51)	3808 ± 491 (19)	3013 ± 295 (16)	4228 ± 443 (12)	3518 ± 336 (11)	5394 ± 392 (16)	4184 ± 463 (17)
Wing area[6,4]	1296 ± 108 (41)	1223 ± 80 (35)	1161 ± 84 (12)	1109 ± 81 (12)	1109 ± 78 (10)	1063 ± 61 (10)	1086 ± 76 (11)	1006 ± 85 (7)
Number of bill lamellae[6,0]	45.6 ± 2.5 (35)	46.5 ± 2.7 (30)	42.5 ± 2.6 (10)	44.0 ± 1.7 (9)	41.3 ± 2.6 (9)	41.6 ± 2.3 (10)	40.3 ± 2.9 (6)	41.2 ± 1.3 (6)

[a]Mean ± standard deviation (*n*).

[b]Superscripts reflect the level of significance of interspecific and intersexual differences, respectively, in two-way ANOVAs: 0 — not significant, $P > 0.05$; 4 — $P < 0.001$; 6 — $P < 0.0001$. Tests of areas and masses were based on log-transformed data, although these data are tabulated untransformed.

Table 4. Summary statistics (mean ± standard deviation) for selected measurements of ninth (longest) primary and first (outermost) secondary remiges of steamer ducks, by species and sex (excluding birds less than one year of age).

	T. patachonicus		*T. leucocephalus*		*T. brachypterus*		*T. pteneres*	
Character[a]	Males	Females	Males	Females	Males	Females	Males	Females
Ninth primary remex (*n*)	22	23	3	6	8	9	5	3
calamus length	48.5 ± 2.2	46.8 ± 2.5	39.3 ± 4.7	41.3 ± 3.8	43.9 ± 2.2	43.3 ± 1.7	44.6 ± 2.1	45.0 ± 1.0
vane length[1,0]	177.8 ± 6.9	169.8 ± 5.3	157.3 ± 8.5	155.5 ± 7.1	151.0 ± 6.6	147.9 ± 7.7	147.6 ± 1.8	141.0 ± 1.7
total length[6,2]	226.2 ± 7.3	216.5 ± 6.8	198.3 ± 9.9	196.8 ± 5.0	194.9 ± 5.7	191.2 ± 7.7	192.2 ± 2.3	186.0 ± 2.6
First secondary remex (*n*)	22	23	4	6	7	9	5	3
calamus length[0,0]	32.3 ± 1.6	30.7 ± 1.7	29.8 ± 1.0	27.5 ± 0.5	30.4 ± 2.2	29.9 ± 1.6	30.8 ± 1.3	30.0 ± 1.0
vane length[0,0]	128.0 ± 4.3	122.0 ± 3.7	114.8 ± 4.1	109.0 ± 4.8	109.4 ± 2.0	105.9 ± 4.7	108.8 ± 1.6	104.7 ± 3.5
total length[6,6]	160.3 ± 5.2	152.7 ± 4.0	144.5 ± 4.8	136.5 ± 5.1	139.9 ± 4.1	135.8 ± 5.4	139.6 ± 2.4	134.7 ± 4.0

[a]Significance levels of interspecific and intersexual differences, respectively, in two-way ANOVA: 0 — not significant, 1 — $P < 0.05$, 2 — $P < 0.01$, 6 — $P < 0.0001$.

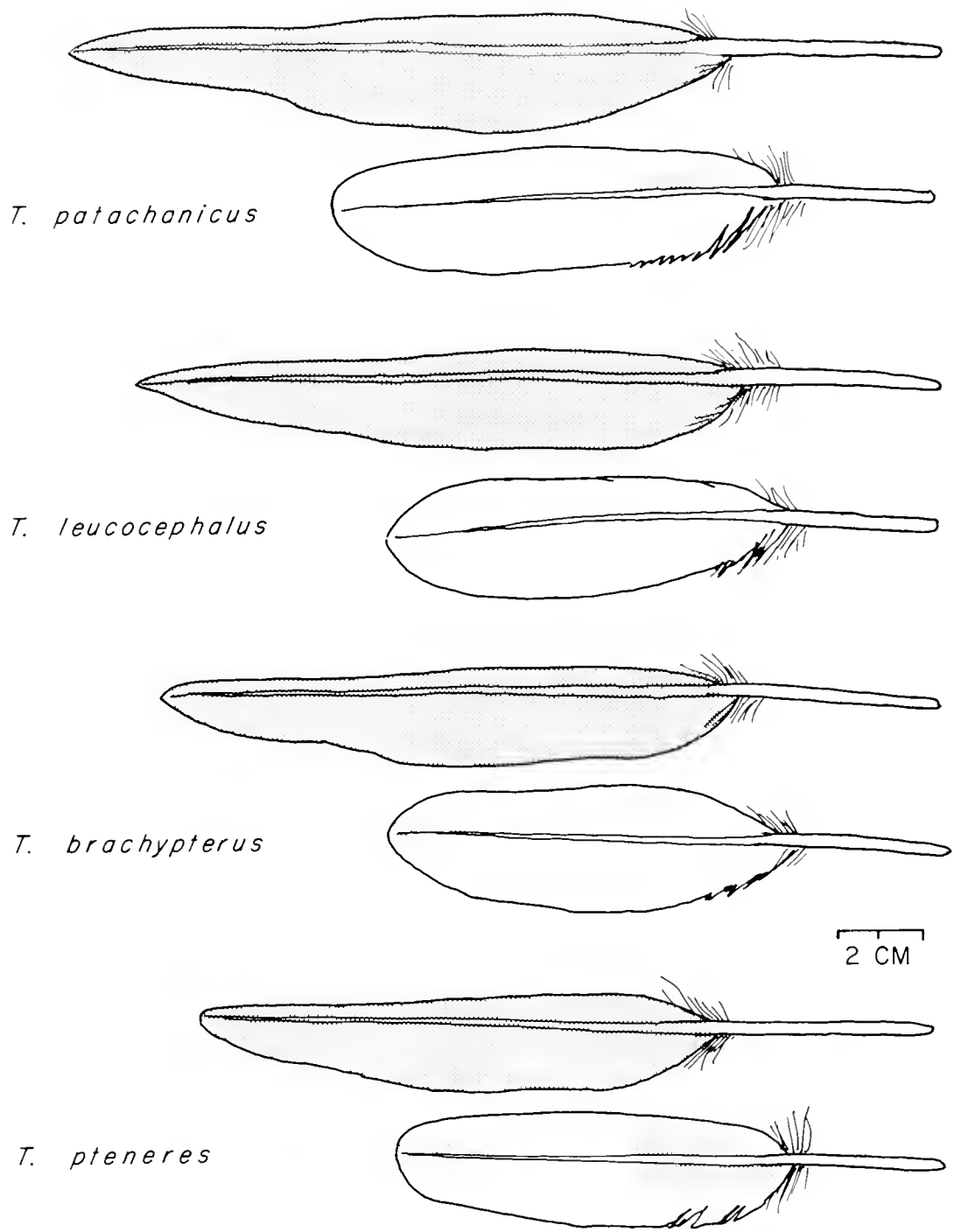

Fig. 23. Diagrams of longest (ninth) primary and outermost (first) secondary remiges of *Tachyeres*, illustrating the longer, broader flight feathers of *T. patachonicus*. A—*T. patachonicus*, male (KU 79461); B—*T. leucocephalus*, male (KU 79246); C—*T. brachypterus*, male (KU 80525); D—*T. pteneres*, male (KU 79182).

Table 5. Summary statistics[a] for selected ratios of external characters of steamer-ducks, by species and sex. Units of measurements are mm (linear), cm^2 (area), and g (masses).

Character[b]	*T. patachonicus*		*T. leucocephalus*		*T. brachypterus*		*T. pteneres*	
	Males	Females	Males	Females	Males	Females	Males	Females
Lamellae/bill length[6,6]	0.70 ± 0.04	0.75 ± 0.04	0.64 ± 0.03	0.70 ± 0.03	0.58 ± 0.04	0.60 ± 0.02	0.54 ± 0.05	0.58 ± 0.02
	(35)	(30)	(10)	(9)	(9)	(10)	(6)	(6)
Wing loading[6,6]	2.3 ± 0.2	1.9 ± 0.2	3.2 ± 0.4	2.6 ± 0.3	3.8 ± 0.4	3.2 ± 0.2	5.0 ± 0.6	4.3 ± 0.5
(total mass/wing area)	(41)	(35)	(12)	(11)	(10)	(10)	(11)	(7)
Wing length/tarsus length[6,1]	5.1 ± 0.2	5.1 ± 0.3	4.3 ± 0.2	4.4 ± 0.2	4.1 ± 0.3	4.2 ± 0.2	3.8 ± 0.2	3.9 ± 0.2
	(57)	(61)	(13)	(13)	(24)	(15)	(36)	(26)

[a]Mean ± standard deviation (*n*).

[b]Significance levels of interspecific and intersexual differences, respectively, in two-way ANOVA: 1 — $P < 0.05$, 6 — $P < 0.0001$. Tests performed on log-transformed ratios, but statistics based on untransformed ratios are tabulated.

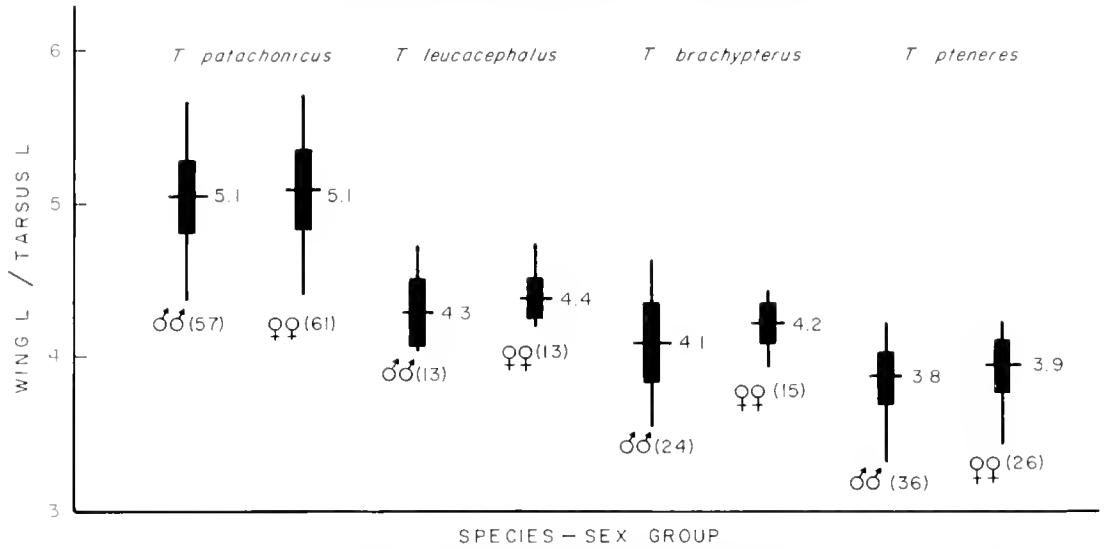

Fig. 24. Graphs of means (horizontal lines), standard deviations (wide vertical bars), ranges (narrow vertical bars), and sample sizes (n) for ratios of wing length over tarsus length for eight species-sex groups of *Tachyeres*.

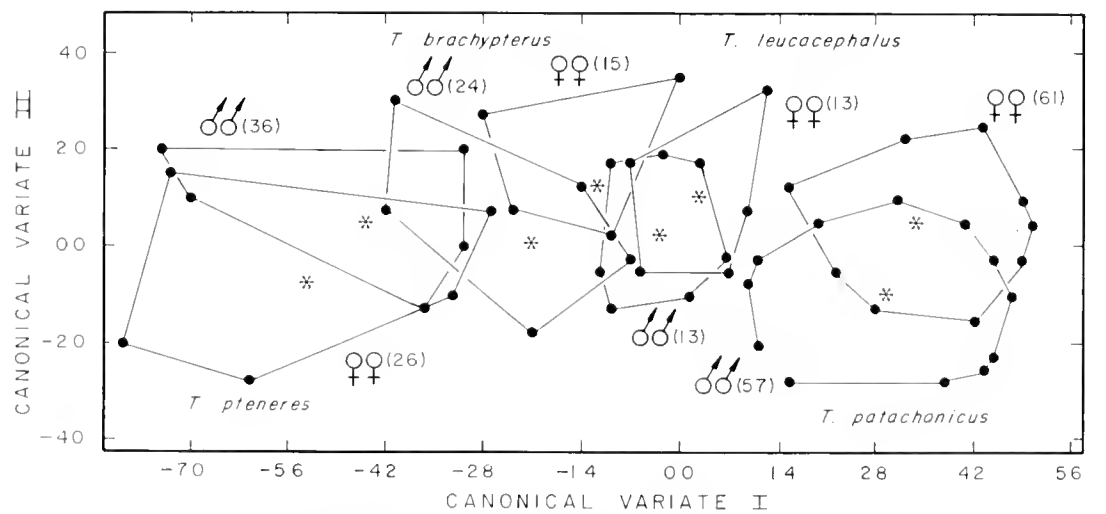

Fig. 25. Plot of eight species-sex groups of *Tachyeres* on first two canonical variates of four external measurements; only extreme individuals (delimiting polygons) and means (asterisks) are plotted.

Skeletal Measurements

Two-way ANOVAs of 36 skeletal dimensions (Table 6) demonstrated significant differences among species ($P < 0.0001$) in all but sternal keel depth ($P > 0.10$); intersexual differences were found in all measurements, males exceeding females in all ($P < 0.0001$). Except for lengths of a few wing elements and widths of limb elements, interspecific differences paralleled the size rankings of species produced by total body weight, although magnitudes of the differences varied among measurements. Wing elements were much more similar in their lengths than would be predicted by overall body size, evidently related to flightlessness in three of the species. Actual reversal in interspe-

Table 6. Summary statistics[a] for selected skeletal measurements (mm) of steamer-ducks, by species and sex. Least width at midpoint is abbreviated LWM

Character[b]	*T. patachonicus*		*T. leucocephalus*		*T. brachypterus*		*T. pteneres*	
	Males	Females	Males	Females	Males	Females	Males	Females
Humerus length	124.1 ± 4.4 (55)	118.2 ± 4.3 (46)	122.5 ± 3.5 (20)	115.8 ± 2.3 (17)	124.1 ± 3.7 (14)	117.1 ± 3.9 (12)	132.6 ± 4.0 (18)	125.1 ± 3.4 (16)
Head width	27.4 ± 1.1 (54)	25.7 ± 1.0 (48)	28.9 ± 1.0 (19)	27.6 ± 0.5 (17)	28.5 ± 0.8 (14)	26.4 ± 0.9 (12)	30.2 ± 1.0 (19)	29.0 ± 1.0 (16)
LWM	7.8 ± 0.3 (54)	7.2 ± 0.3 (46)	8.5 ± 0.4 (19)	8.1 ± 0.3 (17)	8.1 ± 0.3 (14)	7.5 ± 0.5 (12)	8.7 ± 0.3 (18)	8.2 ± 0.3 (16)
Ulna length	102.8 ± 3.7 (49)	98.5 ± 3.9 (39)	100.4 ± 3.3 (15)	95.7 ± 1.8 (14)	98.2 ± 2.5 (14)	94.1 ± 2.9 (12)	101.7 ± 3.2 (16)	96.3 ± 2.8 (16)
LWM	6.3 ± 0.3 (49)	5.8 ± 0.3 (40)	7.1 ± 0.3 (15)	6.8 ± 0.2 (14)	6.4 ± 0.3 (14)	6.0 ± 0.3 (12)	7.2 ± 0.2 (16)	6.6 ± 0.3 (16)
Radius length	96.2 ± 3.8 (49)	91.7 ± 3.8 (40)	94.4 ± 3.1 (15)	90.2 ± 2.0 (14)	91.7 ± 2.6 (14)	87.7 ± 2.9 (12)	95.5 ± 3.0 (16)	90.2 ± 3.4 (15)
LWM	4.1 ± 0.3 (49)	3.7 ± 0.2 (42)	4.7 ± 0.5 (15)	4.2 ± 0.2 (14)	4.3 ± 0.3 (14)	4.1 ± 0.2 (12)	4.9 ± 0.2 (16)	4.3 ± 0.3 (16)
Carpometacarpus length	67.2 ± 2.7 (49)	63.5 ± 2.4 (42)	66.3 ± 2.0 (15)	62.4 ± 1.4 (14)	66.0 ± 1.9 (14)	62.4 ± 2.0 (12)	68.9 ± 2.1 (16)	64.6 ± 2.3 (16)
Digit-II length	50.0 ± 1.9 (49)	47.4 ± 2.0 (42)	50.6 ± 1.5 (15)	47.1 ± 1.3 (14)	51.0 ± 1.6 (14)	48.0 ± 1.3 (12)	52.5 ± 1.6 (16)	49.0 ± 1.8 (16)
Skeletal wing length	344.1 ± 12.3 (49)	327.6 ± 12.3 (39)	340.0 ± 10.5 (15)	321.1 ± 6.3 (14)	339.2 ± 9.0 (14)	321.6 ± 9.4 (12)	356.3 ± 9.9 (16)	335.8 ± 9.9 (16)
Femur length	73.7 ± 2.9 (54)	70.0 ± 2.4 (48)	80.0 ± 2.2 (19)	76.3 ± 1.1 (17)	82.2 ± 2.2 (14)	76.5 ± 2.0 (12)	90.5 ± 1.8 (19)	85.2 ± 1.9 (16)
Head width	15.3 ± 0.8 (54)	14.7 ± 0.7 (48)	17.1 ± 0.7 (19)	16.5 ± 0.6 (17)	17.2 ± 0.4 (14)	16.3 ± 0.5 (12)	18.8 ± 0.5 (19)	18.0 ± 0.5 (16)
LWM	6.3 ± 0.3 (54)	6.0 ± 0.3 (48)	7.1 ± 0.3 (19)	6.9 ± 0.1 (17)	7.1 ± 0.2 (14)	6.5 ± 0.2 (12)	7.8 ± 0.3 (19)	7.3 ± 0.2 (16)
Tibiotarsus length	125.6 ± 5.0 (49)	119.4 ± 4.5 (42)	134.4 ± 3.5 (15)	128.3 ± 2.1 (14)	137.6 ± 3.7 (14)	129.1 ± 3.8 (12)	150.7 ± 4.1 (16)	141.4 ± 3.5 (16)
LWM	5.3 ± 0.4 (54)	5.0 ± 0.3 (46)	6.3 ± 0.4 (15)	5.9 ± 0.2 (14)	6.1 ± 0.2 (14)	5.6 ± 0.2 (12)	6.7 ± 0.3 (16)	6.3 ± 0.3 (16)

Table 6. Continued on page 85

Table 6. Continued.

Character[b]	*T. patachonicus*		*T. leucocephalus*		*T. brachypterus*		*T. pteneres*	
	Males	Females	Males	Females	Males	Females	Males	Females
Tarsometatarsus length	61.8 ± 2.9 (49)	58.2 ± 2.1 (42)	65.5 ± 2.7 (15)	63.3 ± 1.3 (14)	69.4 ± 1.7 (14)	64.4 ± 1.7 (11)	74.6 ± 2.3 (16)	68.9 ± 1.4 (16)
LWM	5.3 ± 0.3 (49)	5.0 ± 0.3 (42)	6.2 ± 0.4 (15)	5.9 ± 0.2 (14)	5.9 ± 0.2 (14)	5.5 ± 0.2 (11)	6.7 ± 0.3 (16)	6.2 ± 0.3 (16)
Digit-III length	74.8 ± 6.3 (49)	67.6 ± 5.5 (42)	83.1 ± 3.3 (15)	78.7 ± 2.0 (14)	86.8 ± 4.8 (14)	82.6 ± 2.4 (11)	94.1 ± 2.9 (16)	86.2 ± 1.9 (16)
Sternum keel length	129.9 ± 5.9 (54)	119.0 ± 4.7 (48)	130.2 ± 6.3 (19)	121.9 ± 2.9 (17)	136.7 ± 3.8 (14)	124.5 ± 4.7 (12)	146.4 ± 5.1 (19)	135.9 ± 4.4 (15)
Basin length	110.4 ± 4.9 (54)	102.4 ± 3.5 (48)	112.3 ± 4.8 (19)	106.3 ± 2.0 (17)	118.2 ± 3.4 (14)	108.9 ± 3.2 (12)	125.7 ± 3.5 (19)	118.1 ± 4.5 (15)
Least width	55.0 ± 2.5 (54)	51.8 ± 1.8 (48)	59.0 ± 2.1 (19)	56.6 ± 1.2 (17)	61.3 ± 1.2 (14)	58.3 ± 1.8 (12)	65.7 ± 2.1 (19)	64.2 ± 2.3 (16)
Posterior width	74.9 ± 3.6 (54)	69.0 ± 3.4 (48)	83.6 ± 6.6 (19)	80.3 ± 2.5 (17)	79.4 ± 3.4 (14)	73.7 ± 3.5 (12)	85.3 ± 3.4 (19)	78.0 ± 4.6 (14)
Keel depth	30.4 ± 1.5 (54)	28.9 ± 1.7 (48)	30.5 ± 1.4 (19)	29.1 ± 1.2 (17)	29.9 ± 1.6 (14)	28.3 ± 1.5 (12)	30.9 ± 1.2 (19)	29.1 ± 1.2 (15)
Coracoid length	65.3 ± 2.6 (54)	60.6 ± 2.3 (48)	69.4 ± 2.1 (19)	64.3 ± 1.4 (17)	69.4 ± 1.3 (14)	64.6 ± 1.9 (12)	74.7 ± 2.5 (19)	70.5 ± 2.1 (16)
Basal width	30.1 ± 1.4 (54)	27.4 ± 1.0 (48)	32.8 ± 1.3 (19)	30.7 ± 0.7 (17)	32.7 ± 0.7 (14)	29.6 ± 1.1 (12)	34.0 ± 0.9 (19)	31.9 ± 1.2 (16)
Scapula length	99.4 ± 3.7 (54)	94.3 ± 2.9 (48)	104.4 ± 3.7 (19)	99.9 ± 2.4 (17)	105.1 ± 2.1 (14)	99.9 ± 2.7 (12)	113.7 ± 3.4 (19)	109.0 ± 3.3 (16)
Interacetabular width	32.8 ± 1.9 (54)	30.7 ± 1.6 (48)	36.0 ± 1.3 (16)	34.7 ± 1.2 (16)	36.0 ± 1.0 (14)	33.0 ± 1.1 (12)	39.5 ± 1.4 (19)	37.2 ± 1.5 (16)
Cranial height	30.4 ± 0.7 (46)	29.0 ± 0.8 (38)	32.3 ± 0.9 (12)	30.7 ± 0.5 (13)	32.5 ± 0.7 (14)	31.4 ± 0.6 (10)	34.1 ± 0.7 (16)	32.5 ± 0.5 (14)
Length	70.0 ± 1.9 (46)	66.1 ± 2.0 (38)	73.7 ± 1.8 (11)	70.0 ± 1.0 (13)	74.8 ± 1.5 (14)	71.2 ± 1.4 (10)	79.1 ± 1.1 (16)	75.2 ± 1.3 (14)

Table 6. Continued on page 86

Table 6. Continued

Character[b]	*T. patachonicus*		*T. leucocephalus*		*T. brachypterus*		*T. pteneres*	
	Males	Females	Males	Females	Males	Females	Males	Females
Interorbital width	9.9 ± 1.0 (46)	8.7 ± 0.6 (38)	10.5 ± 0.7 (12)	9.3 ± 0.7 (13)	10.9 ± 0.8 (14)	9.7 ± 0.8 (10)	12.0 ± 0.9 (16)	11.0 ± 0.6 (14)
Postorbital width	38.3 ± 1.5 (46)	36.5 ± 1.3 (38)	41.7 ± 1.4 (12)	40.1 ± 1.1 (12)	43.9 ± 1.0 (14)	41.4 ± 1.1 (10)	45.3 ± 1.4 (16)	43.3 ± 1.0 (13)
Antorbital width	25.4 ± 1.5 (44)	23.1 ± 1.9 (35)	29.1 ± 2.0 (10)	24.1 ± 0.9 (12)	29.1 ± 1.8 (13)	25.5 ± 1.2 (10)	32.1 ± 1.5 (16)	27.8 ± 1.2 (13)
Frontonasal hinge width	17.2 ± 1.2 (46)	15.8 ± 1.1 (38)	19.4 ± 1.7 (11)	17.5 ± 0.8 (13)	19.2 ± 1.6 (14)	17.9 ± 0.6 (10)	22.5 ± 1.3 (16)	19.7 ± 1.0 (14)
Internarial width	6.0 ± 0.4 (45)	5.5 ± 0.4 (38)	6.5 ± 0.5 (11)	6.2 ± 0.2 (12)	6.8 ± 0.4 (14)	6.5 ± 0.5 (10)	7.2 ± 0.4 (16)	6.8 ± 0.5 (14)
Bill height	23.2 ± 1.1 (46)	21.3 ± 0.8 (38)	25.0 ± 0.4 (11)	23.0 ± 0.7 (13)	25.6 ± 0.7 (14)	24.2 ± 0.6 (10)	27.4 ± 0.9 (16)	25.6 ± 0.6 (14)
Length	55.3 ± 2.1 (46)	53.0 ± 2.4 (38)	56.4 ± 1.6 (11)	54.2 ± 1.4 (13)	59.2 ± 1.9 (14)	57.8 ± 1.4 (10)	60.7 ± 1.9 (16)	58.5 ± 1.7 (14)
Width	25.2 ± 1.0 (46)	23.8 ± 1.0 (38)	26.9 ± 1.2 (11)	25.9 ± 0.7 (13)	27.7 ± 1.0 (14)	25.9 ± 0.7 (10)	30.8 ± 1.2 (16)	28.7 ± 1.0 (14)

[a]Statistics tabulated are mean ± standard deviation (*n*).

[b]All interspecific and intersexual differences, except interspecific differences in sternal keel depth, were significant in two-way ANOVAs ($P < 0.0001$). Interaction effects were insignificant in all measurements.

cific rankings, wherein small *T. patachonicus* had greater mean measurements than the larger flightless species, occurs in lengths of the ulna and radius. As a result, simultaneous consideration of such wing element lengths and a more size-related element (e.g., sternum, femur) is effective for distinguishing *T. patachonicus* from the flightless species. Lowe (1934) illustrated the difference in relative lengths of the humerus and sternum between *T. patachonicus* and *T. pteneres* (his *brachypterus*). Another anomaly occurs in widths of limb elements, in that *T. leucocephalus* has consistently wider, more robust limb bones than its larger relative *T. brachypterus* (Table 6). Overlap exists between species in all measurements, but selected combinations of characters—e.g., ulna length, femur length, and humerus head width—would be effective for species identification in many cases. A few of the measurements are less reliable because they are influenced somewhat by age, even after fledging: sternal keel length, sternal keel depth, and antorbital and interorbital widths of the skull.

A particularly effective criterion for distinguishing *T. patachonicus* from the three flightless species is the ratio of humerus length to femur length (Fig. 26). Flightless *Tachyeres* have ratios below 1.6 and ratios for *T. patachonicus* lie above this value; only 1 skeleton in 198 violated this rule (a male *T. leucocephalus* had a value of exactly 1.61). Mean values for this ratio are as follows: *T. patachonicus*, 1.69; *T. leucocephalus*, 1.53; *T. brachypterus*, 1.52; *T. pteneres*, 1.47; sexual differences within species were not significant ($0.08 \leq P \leq 0.71$).

The relatively robust limb bones of *T. leucocephalus* are most clearly shown by the ratio of the least width at the midpoint of the shaft divided by the length of the element; limb bones of *T. leucocephalus* are either the most robust in the genus (humerus, femur, tarsometatarsus) or equaled only by those of *T. pteneres* (radius, ulna, tibiotarsus). Except for the radius and ulna, these 'ratios of robustness' are made more useful by the lack of significant intersexual differences within species ($P > 0.15$; Table 7).

Another ratio useful for distinguishing *T. leucocephalus* from other *Tachyeres* is posterior sternal width divided by sternal basin length, 'sternal flaring' (Table 7). Interspecific differences in this ratio (log-transformed for ANOVA) were highly significant ($P < 0.0001$); intersexual differences were nonexistent ($P > 0.75$). The comparatively great sternal 'flaring' in *T. leucocephalus* was noted qualitatively and illustrated in the description of the species (Humphrey and Thompson 1981). Overlap between *T. leucocephalus* and the three other species is minimal. Using 0.72 as

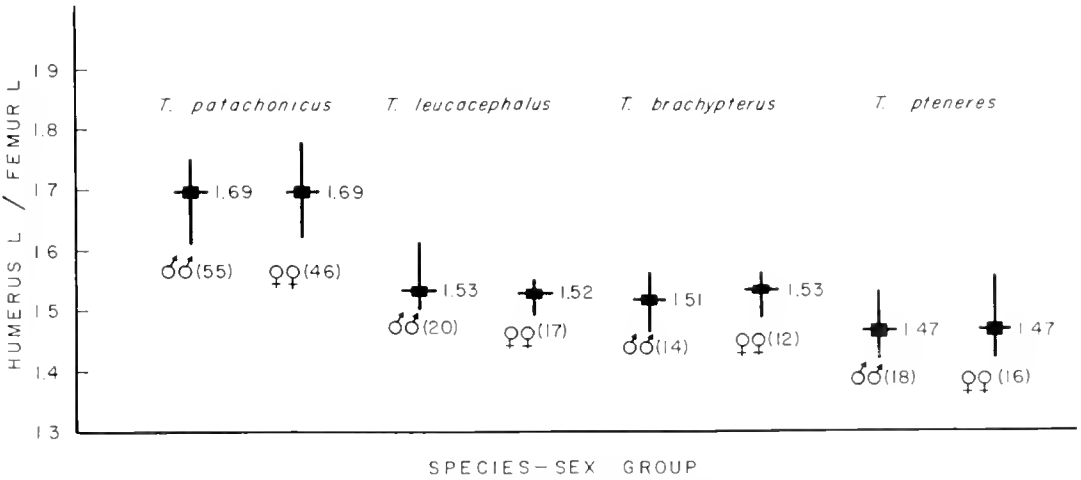

Fig. 26. Graphs of means (horizontal lines), standard deviations (wide vertical bars), ranges (narrow vertical bars), and sample sizes (*n*) for ratios of humerus length over femur length for eight species-sex groups of *Tachyeres*.

Table 7. Summary statistics[a] for selected ratios (relative widths expressed as percentages) of skeletal measurements of steamer-ducks, by species and sex

Character[b]	*T. patachonicus* Males	*T. patachonicus* Females	*T. leucocephalus* Males	*T. leucocephalus* Females	*T. brachypterus* Males	*T. brachypterus* Females	*T. pteneres* Males	*T. pteneres* Females
Relative width[c]								
Humerus[6,0]	6.3 ± 0.3 (55)	6.1 ± 0.2 (46)	6.9 ± 0.2 (20)	7.0 ± 0.2 (17)	6.5 ± 0.3 (14)	6.4 ± 0.3 (12)	6.6 ± 0.3 (18)	6.6 ± 0.3 (16)
Ulna[6,2]	6.1 ± 0.3 (49)	5.9 ± 0.2 (34)	7.0 ± 0.2 (15)	7.1 ± 0.2 (14)	6.6 ± 0.3 (14)	6.4 ± 0.2 (12)	7.1 ± 0.3 (16)	6.8 ± 0.3 (16)
Radius[6,6]	4.3 ± 0.3 (49)	4.0 ± 0.3 (40)	5.0 ± 0.5 (15)	4.7 ± 0.3 (14)	4.7 ± 0.5 (14)	4.6 ± 0.2 (12)	5.1 ± 0.3 (16)	4.8 ± 0.5 (15)
Femur[6,0]	8.5 ± 0.3 (54)	8.5 ± 0.3 (48)	8.9 ± 0.4 (19)	9.0 ± 0.1 (17)	8.6 ± 0.2 (14)	8.5 ± 0.3 (12)	8.6 ± 0.3 (19)	8.6 ± 0.3 (16)
Tibiotarsus[6,0]	4.7 ± 0.2 (49)	4.2 ± 0.1 (42)	4.6 ± 0.2 (15)	4.6 ± 0.2 (14)	4.4 ± 0.1 (14)	4.3 ± 0.1 (12)	4.4 ± 0.2 (16)	4.5 ± 0.2 (16)
Tarsometatarsus[6,0]	8.6 ± 0.4 (49)	8.6 ± 0.5 (42)	9.4 ± 0.5 (15)	9.4 ± 0.3 (14)	8.5 ± 0.3 (14)	8.5 ± 0.2 (11)	8.9 ± 0.3 (16)	9.0 ± 0.4 (16)
Sternal flaring[6,0,d]	0.69 ± 0.03 (54)	0.67 ± 0.03 (48)	0.74 ± 0.05 (19)	0.76 ± 0.03 (17)	0.67 ± 0.02 (14)	0.68 ± 0.03 (12)	0.68 ± 0.03 (19)	0.66 ± 0.04 (14)
Humerus length/ Femur length[6,0]	1.69 ± 0.03 (55)	1.69 ± 0.03 (46)	1.53 ± 0.03 (20)	1.52 ± 0.01 (17)	1.51 ± 0.03 (14)	1.53 ± 0.03 (12)	1.47 ± 0.03 (18)	1.47 ± 0.04 (16)

[a]Mean ± standard deviation (*n*), in percentages for relative widths.

[b]Superscripts reflect the level of significance of interspecific and intersexual differences, respectively, in two-way ANOVAs: 0 — not significant, $P > 0.05$; 2 — $P < 0.01$; 6 — $P < 0.0001$. Tests were based on log-transformed data, but ratios are tabulated untransformed.

[c]Relative widths are the least widths at midpoint of shaft divided by total length of element.

[d]Sternal flaring is the maximal posterior width divided by basin length.

a dividing value for the ratio (sexes pooled), only 4 of 36 (11%) *T. leucocephalus* fall below this value, whereas only 5 of 102 (5%) *T. patachonicus*, 2 of 26 (8%) *T. brachypterus*, and 1 of 33 (3%) *T. pteneres* fall above it.

Multivariate discrimination of complete skeletons is extremely powerful (Fig. 27). Stepwise canonical analysis, using 19 of 36 skeletal measurements, correctly identified the species *and* sex of 98.8% of 165 complete skeletons in jackknifed classifications; the two errors in classification were small missexed specimens of *T. patachonicus* and *T. brachypterus*. Variables and classification coefficients are given in the Appendix. Far fewer measurements are needed to achieve classification percentages approaching those for these "optimal" models (Fig. 28). Classification percentages of complete skeletons to species and sex exceeded 90% using only six measurements and reached 95% incorporating 10 variables. If sex is specified, species identifications using optimal models were completely successful for both males (n = 90, 19 variables used) and females (n = 75, 10 variables used). Limiting the analyses to single sexes permitted greater reductions in the number of variables needed to classify. For males, species classifications were 97.8% correct using only two measurements (lengths of the femur and ulna); species identification of complete skeletons of females reached 94.7% success using two measurements (least sternal width and width of ulna at midpoint).

Partial skeletons, which typically result from preparation of study skins or the salvage of damaged carcasses, lack skulls and distal limb elements and are less successfully identified. Identification of 199 partial skeletons using 10 of the 13 available measurements was 91.7% correct. Classification functions are given in the Appendix. If sex is known, successful identifications of species increased to 96.3% for males (n = 108, 9 variables incorporated into model) and 100% for females (n = 91, 7 variables). As for complete skeletons, much simpler combinations of variables are necessary to achieve reliable classification of partial skeletons of known sex. Determination of species for males exceeded 90% using only three variables, and surpassed 95% based on five measurements (Fig. 28). In partial skeletons, only two measurements (femur length and posterior sternal width) were needed to achieve 95.6% success in species classification (Fig. 28).

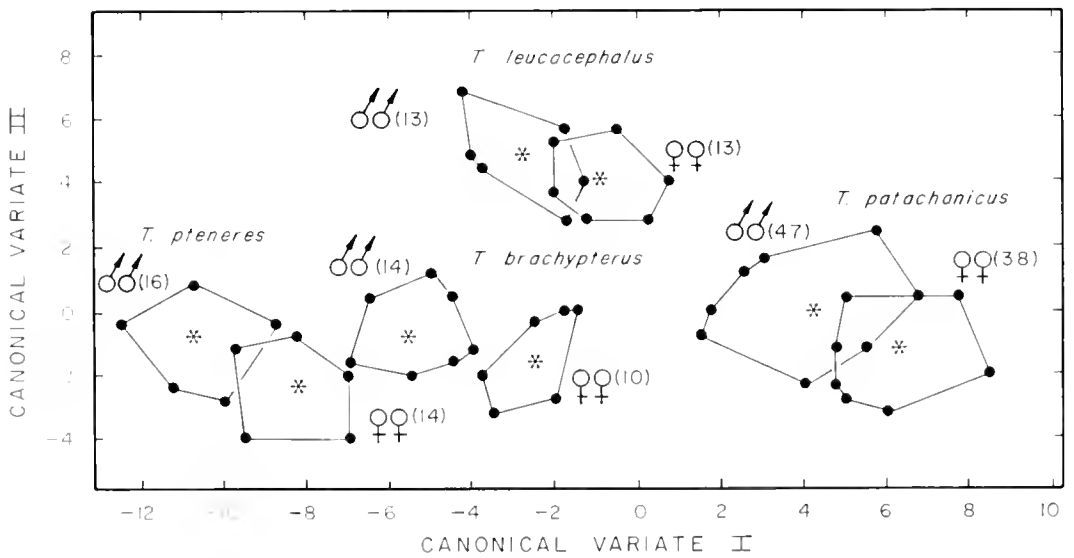

Fig. 27. Plot of eight species-sex groups of *Tachyeres* on first two canonical variates of 19 skeletal measurements; only extreme individuals (delimiting polygons) and means (asterisks) are plotted.

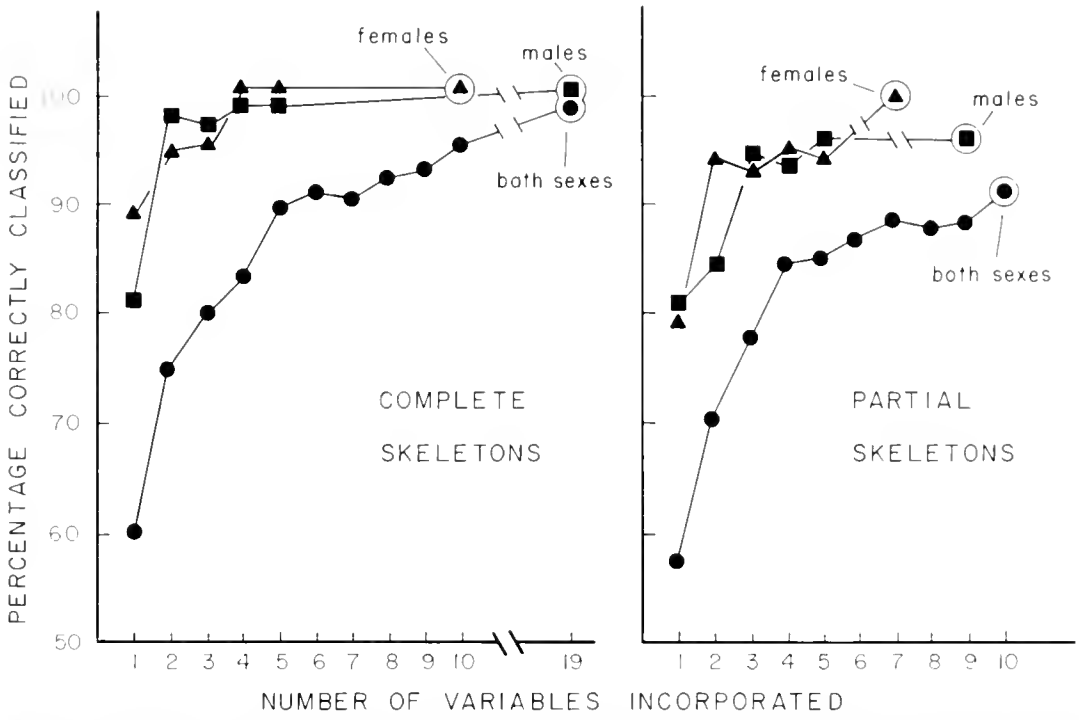

Fig. 28. Classification percentages for increasing numbers of measurements available for complete and partial skeletons; analyses of males, females, and sexes combined are plotted separately, and terminal (circled) points of each curve represent optimal, backstep-selected models.

KEYS TO IDENTIFICATION OF SPECIMENS

Skins

Downy Young

The following key, after that given by Humphrey and Livezey (1985), is applicable to class–I downies and, perhaps, to early class–II downies retaining clear head patterns. Characteristic head patterns of the four species were illustrated by Humphrey and Livezey (1985).

1a. Upper eyelid whitish; crown darker than cheeks; supraloral and supraocular patches wide and continuous with wide postocular streak ..... *I. leucocephalus*

1b. Upper eyelid dark; crown not darker than cheeks 2

2a. Postocular streak divided; supraloral and supraocular patches very small or absent, and separate when present ..... *I. pteneres*

2b. Postocular streak undivided; supraloral and supraocular patches present 3

3a. Supraloral and supraocular patches very narrow (almost occluded anteriorly), continuous, and separated from postocular streak ..... *I. patachonicus*

3b. Supraloral and supraocular patches narrow and continuous with postocular streak ..... *I. brachypterus*

Fledged Birds

Age-related changes in body mass, colors of soft parts, and plumage pattern preclude the presentation of qualitative and mensural diagnostic keys for skins

of fledged specimens of all species of *Tachyeres*. Accordingly, qualitative characters in the key given below are representative only of adults in definitive plumages, whereas mensural characters apply to birds of at least one year of age and not in wing molt.

1a. Ratio of wing length to tarsus length generally exceeds 4.5; wing–loading usually less than 2.5 g • cm $^{-2}$; *males* typically with body mass less than 3500 g, wing length greater than 290 mm, and tail length greater than 105 mm; *females* typically with body mass less than 2750 g, wing length greater than 280 mm, and tail length greater than 100 mm; most males and all females capable of flight; occurs throughout Fuego–Patagonia and Falkland Islands, including freshwater and coastal localities ..... *T. patachonicus*

1b. Ratio of wing length to tarsus length generally less than 4.5; wing–loading greater than 2.5 g • cm^{-2}; *males* typically with body mass greater than 3500 g, wing length less than 290 mm, and tail length less than 105 mm; *females* typically with body mass greater than 2750 g, wing length less than 280 mm, and tail length less than 100 mm; both sexes incapable of flight; limited to marine coastal habitats 2

2a. Adults essentially without sexual dichromatism, *both sexes* having a bright orange bill, gray head and neck, faint postocular streak, and lacking extensive chestnut coloration on scapulars, sides and flanks; ratio of wing length to tarsus length generally less than 4.0; *males* typically with body mass greater than 5 kg and nail width frequently exceeding 15 mm; *females* typically with body mass greater than 4 kg and nail width frequently exceeding 14 mm; occurs in marine coastal habitats from central Chile south and east to Isla de los Estados, Argentina ..... *T. pteneres*

2b. Adults showing sexual dichromatism, males having distinctly lighter (often virtually white) heads and more orange bills than females; both sexes have comparatively distinct whitish postocular streaks; adults with substantial amounts of chestnut coloration on scapulars, sides, and flanks; ratio of wing length to tarsus length generally greater than 4.0; *males* typically with body mass less than 5 kg and nail width usually less than 15 mm; *females* typically with body mass less than 4 kg and nail width usually 14 mm or less; limited to coastal environments of Chubut, Argentina or the Falkland Islands 3

3a. *Males* indistinguishable externally from 3b; *females* with postocular streak becoming indistinct posteriorly; endemic to the marine coasts of the Falkland Islands ..... *T. brachypterus*

3b. *Males* indistinguishable externally from 3a; *females* with postocular streak typically broad posteriorly to whitish collar; endemic to marine coastal Chubut, Argentina ..... *T. leucocephalus*

Skeletons

1a. Ratio of humerus length to femur length greater than 1.6; additional *modal* characters are medially uninflected processus mandibulae medialis of mandible and attachment site of M. extensor metacarpi ulnaris on carpometacarpus opposite proximal fornix of intermetacarpal space; occurs in both coastal and inland localities throughout Fuego–Patagonia and the Falkland Islands ..... *T. patachonicus*

1b. Ratio of humerus length to femur length less than 1.6; additional *modal* characters are medially inflected processus mandibulae medialis of mandible and the attachment site of M. extensor metacarpi ulnaris on carpometacarpus proximad to proximal fornix of intermetacarpal space; limited in distribution to marine coasts of Fuego–Patagonia and the Falkland Islands 2

2a. Occipital condyle usually extends ventrad to basioccipital plate; carpal trochlea extends caudad to metacarpal III; sulcus tendineus of carpometacarpus with straight, parallel lips; *males* generally with femur lengths greater than 87 mm, *females* with femur lengths greater than 82 mm; limited in distribution to coasts of central Chile south and east to Isla de los Estados ..... *T. pteneres*

2b. Occipital condyle usually dorsad to basioccipital plate; carpal trochlea does not extend caudad to metacarpal III; sulcus tendineus of carpometacarpus typically with short, pointed, often bridging borders; *males* generally with femur lengths less than 87 mm, *females* with femur lengths less than 82 mm 3

3a. Ratio of sternal caudal width to sternal least

width usually exceeds 0.72; scapholunar facet of radius relatively large, appressed to shaft; endemic to coastal Chubut, Argentina .... *T. leucocephalus*

3b. Ratio of sternal caudal width to sternal least width usually less than 0.72; scapholunar facet of radius not expanded; endemic to coastal environments of the Falkland Islands ... *T. brachypterus*

FIELD IDENTIFICATION

Introductory Comments

The species of steamer–duck are so similar to one another and have such a complicated array of molts and plumages that it remains very difficult to definitively characterize any one of the species using only field marks or external characters. Historically this caused a great deal of trouble for museum taxonomists and continues to be a problem for field ornithologists who wish to make identifications without collecting specimens. These difficulties have troubled a number of ornithologists who have felt that it was inappropriate to describe a new species of flightless steamer–duck (*T. leucocephalus*) which, it was felt, might more appropriately have been considered simply a subspecies of another population of flightless steamer–duck (e.g., *T. pteneres* or *T. brachypterus*); evidently the notion was, we judge, that 'big' birds that look alike and have allopatric distributions cannot be distinct species.

In many respects, the cryptic species of *Tachyeres* are comparable in difficulty to the *Empidonax* flycatchers of North America, wherein identification is best considered a specimen–based, not a field, exercise. We suspect that there are several other genera of large birds (e.g., *Phalacrocorax*, *Anas*, *Branta*) that include undescribed or unrecognized species that are osteologically separable, reproductively isolated, and biochemically distinct, but so similar that, with museum skin specimens and for purposes of field identification, the majority of ornithological taxonomists are unwilling to recognize them as species. Why this should be so for large birds and not small ones like *Empidonax*, *Vireo*, *Anthus*, and many others (principally passerines) is not clear.

Given the close similarities of the four recognized species of steamer–duck, the best approach to their field identification is a geographic one. The only serious problems with field identification are in regions where two species may co–occur. For the most part this is the case in marine littoral environments but may also be true in freshwater ponds near the seashore in Tierra del Fuego, the southernmost regions of the continent, and the Falkland Islands. Several references include illustrations of steamer-ducks (Delacour 1954; Olrog 1959, 1984; Scott 1972; Harrison 1983; Narosky and Yzurieta 1987), but the most detailed and up–to–date are those provided by Madge and Burn (1988). Fine illustrations of both sexes, a bird in flight, and downy young for *T. patachonicus* are given by Fjeldså and Krabbe (1990; plates V, VIII). However, before discussing field identification of steamer-ducks by region, there are several general problems to consider, i.e., ecological segregation, size and overall proportions, and flightlessness as aids in field identification.

Ecological Segregation

Flightless steamer-ducks are limited to marine coasts, except for infrequent, short walks they may make to brackish and freshwater bodies near the coast. The vast majority of flightless *Tachyeres* are encountered on the shores of bays and exposed headlands, and are especially abundant at river mouths and around offshore islands. Of the three flightless species, only *T. leucocephalus* is commonly found on beaches with extensive tide flats. Murphy (1936:199) observed that an "avoidance" of extensive tide flats by flightless *T. pteneres* underlies its absence on the Atlantic coast north of Tierra del Fuego. Rocky, rugged headlands, occasionally interspersed with sandy and stony beaches, and flanked by bunch grass and brush, are more typical habitats of *Tachyeres* (De la Peña 1982:44; pers. obs.). Breeding adults are seen most frequently in pairs along well defined and defended segments of shore (Murphy 1936, McWhan 1952, Weller 1976, Livezey and Humphrey 1985a). Intensive territoriality, both intraspecific and toward other species, is

characteristic of *Tachyeres*, the evolutionary implications of which remain controversial (Livezey and Humphrey 1985a, b; Nuechterlein and Storer 1985a, b; Murray 1985, 1986; Livezey 1987a); MacDonagh (1941) presented an early discussion of territoriality in flighted and flightless *Tachyeres*. Nonbreeding adults and subadult birds frequently are encountered in large, often quarrelsome flocks near shorelines not occupied by territorial pairs. All species of *Tachyeres* frequently dive for food (Weller 1964a, Livezey 1988a), and all typically nest on the ground (Weller 1964b), although members of several species have nested in natural or human-made cavities (Humphrey and Livezey 1985).

Flying Steamer-ducks are more varied in habitat than their flightless congeners. On marine coasts of Tierra del Fuego and Chile, *T. patachonicus* occurs more frequently on open beaches than *T. pteneres*, which instead frequents rocky shores (Livezey 1988a). In coastal Chubut, our few records of *T. patachonicus* were made in habitats heavily used by the much more common *T. leucocephalus*; the two species infrequently occur in mixed flocks. In the Falkland Islands, *T. patachonicus* co-occurs occasionally with abundant *T. brachypterus* on saltwater, especially in winter, but is believed to inhabit freshwater ponds during the nesting season (Weller 1972, 1976). In addition, *T. patachonicus* occurs on freshwater lakes, at least during the nesting season, from Tierra del Fuego north to mountain lakes in Neuquen, Argentina, and Region X, Chile. Fjeldsá and Krabbe (1990) reported the presence of flocks of nonbreeding *T. patachonicus* on large, often turbid, sometimes alkaline lakes.

General Appearance

All species of *Tachyeres* are comparatively bulky and thick-necked, and have heavy bills, largely gray backs and sides, white bellies, and orange-yellow, conspicuously large feet. The upper breast and sides show variable amounts of brown. Both sexes have a white speculum, which contrasts with the dark gray of the rest of the wing, and a short or, in *T. patachonicus*, moderately long, recurved tail. During the breeding season, heads of adult males are substantially lighter than their backs (largely white in all but *T. pteneres*), and are markedly lighter than those of their female consorts.

In good light and at medium or short range, the greater bulk, relatively shorter wings, and shorter, straighter tails of the flightless species should distinguish each from the smaller, slimmer *T. patachonicus*. Pairs of adult *T. pteneres* can be identified immediately by the orange bills of *both male and female*; bills of females of other species in the genus are much darker than those of their mates, with yellow-orange being absent or limited to a small area near the base. During the breeding season, adult male *T. pteneres* are unique in having a silver-gray head plumage, whereas the heads of breeding adult males of the other three species are largely white with gray cap and cheeks. The head and neck plumages of female *T. pteneres* are decidedly more gray than corresponding plumages of females of the other three species, and the postocular streak of *T. pteneres* is typically less conspicuous. If comparison with other waterfowl is possible—e.g., sheldgeese (*Chloephaga* spp.) or dabbling ducks (*Anas* spp.)—the substantial size of *T. pteneres* is readily apparent. Even in Tierra del Fuego, where only *T. pteneres* occurs with *T. patachonicus*, species identification in the field can be challenging, and we encourage observers to follow Earnshaw (1973:208) in reporting sightings of steamer-ducks as simply "*Tachyeres* sp." if conditions do not permit confident identification to species.

Distinguishing *T. patachonicus* from *T. leucocephalus* (coastal Chubut) or *T. brachypterus* (Falkland Islands) in the field is much more difficult. The shorter wings of the flightless species sometimes may be distinguished at close range, especially if the wings are stretched or flapped. The more slender neck and longer tail of *T. patachonicus* can be evident under good field conditions, particularly if the birds adopt the 'alert' posture in which the back is arched and neck extended. Unfortunately, contrary to the belief of a number of local amateurs, *T. patachonicus* is indistinguishable from *T. brachypterus* on saltwater, unless the former is seen in flight (Matthews 1977; pers. obs.).

Behavior

Only *T. patachonicus* is capable of genuine sustained flight, although some males of this species are permanently flightless in some marine localities

(Humphrey and Livezey 1982b). Momentary ascent or short, descending, flapping passages can be accomplished by all three flightless species, especially if aided by a strong head-wind (Livezey and Humphrey 1982). Wind conditions significantly affect the ease of attaining flight in *T. patachonicus* as well, even when the birds are pursued. Obviously, steamer-ducks of all species cannot fly when in wing molt, an event that typically occurs during middle to late (austral) summer (Humphrey and Livezey 1982a).

All species of *Tachyeres* 'steam,' the characteristic, turbulent method of surface locomotion for which the group was named (Livezey and Humphrey 1983). In typical steaming, the head and neck are drawn up and back, not extended forward as in a take-off run of *T. patachonicus*; Flying Steamer-ducks sometimes begin by steaming but later adopt a take-off posture and take flight. Generally, the three flightless species appear heavier than *T. patachonicus* while steaming and evidently are less able to raise the breast above the water surface. However, the larger species can steam quite rapidly, and for 1 km or more without rest, and we have observed very buoyant steaming by *T. brachypterus*. Giai (1951:256) likened the surface locomotion of downy Brazilian Mergansers (*Mergus octosetaceus*) to the steaming of *Tachyeres*, but we doubt that this comparison is valid in detail.

Steamer-ducks also swim and dive proficiently, the latter being a commonly employed (and effective) escape behavior (Livezey and Humphrey 1982); steamer-ducks use wing-strokes at submergence but typically do not use their wings for propulsion under water (Johnsgard 1962, Livezey and Humphrey 1984a). Terrestrial locomotion of steamer-ducks often appears rather awkward; the birds are often observed waddling slowly from a loafing site toward water upon approach by an observer. When pressed, however, steamer-ducks are capable of surprisingly rapid running for short distances, especially down inclined shorelines toward the safety of water, which typically is followed by steaming, diving, or (in *T. patachonicus*) flight. Sometimes *T. patachonicus* takes flight directly from shore, particularly if the birds launch from an incline and are aided by a head-wind. Contrary to the conclusion of Hebard (1959), at least *T. pteneres* occasionally employs 'injury-feigning' (Livezey and Humphrey 1982).

Vocalizations

The vocal behavior of steamer-ducks has received a moderate amount of study, at least in comparison to other anatids, probably because of the association of most vocalizations with territoriality in *Tachyeres*. Cunningham (1871b:96) first noted sexual differences in vocalizations of steamer-ducks (species not given), describing that of the male as "a sort of mew rapidly repeated" and that of the female as "a kind of deep growl." Moynihan (1958) described the calls of female *T. patachonicus* as "Grunts," short, moderately loud, and deep vocalizations given singly or repeated in variably long series. Moynihan (1958) divided the higher, more whistle-like calls of male *T. patachonicus* into three types, in order of increasing aggressiveness: "Sibilant Grunts," "Ticking Grunts," and "Rasping Grunts." Vocalizations of both sexes of *T. patachonicus* were heard by Moynihan (1958) most frequently in territorial encounters between pairs, during which the birds performed other "hostile" displays such as "False Drinking," "Stretches," "Short-high-and-broad Postures," "Submerged Sneaks," and "Head-flagging." Moynihan (1958:201) also reported that *T. pteneres* produced a similar diversity of vocalizations under similar sociobehavioral circumstances, but that both sexes of *T. pteneres* "...uttered more complex Grunting as well."

Woods (1975:121) described three types of calls of male *T. brachypterus*: a "loud vibratory...'cheeroo,'... [a] more conversational...'cheeoo,'... [and] a rapid sharp 'kek-kek-kek.'" The calls of female *T. brachypterus* as "...a short, guttural quacking note" and "...a peculiar low creaking note."

Weller (1976:50) rendered one call of male *T. brachypterus* as "...a clear, high-pitched, rasping whistle...syllabylized as '*pe-ough*' or '*pe e ough.*'" Weller contrasted the homologous call of male *T. pteneres* as "more slurred" and regularly seeming to have an extra syllable (syllabylized as "*pse e ough*" or "*pse e-e-ough*"), and that of male *T. patachonicus* as "similar but higher pitched." Weller noted that males of all three species also uttered more intense series of short notes, syllabylized as "*pew pew pew.*" He described only the calls of females for *T. brachypterus*, which he termed "croaking grunts" and rendered as

"*gurr–r*," "*gurrk*," "*gurrk–gurrk–gurrk*," and "*gronk–groink–groink*;" he also attributed a concurrent "clicking sound" to the female. Weller noted that paired *T. brachypterus* vocalized synchronously during territorial defense, the males intensifying their calls in tandem as hostilities escalated. Neuchterlein and Storer (1985) described such territorial "duetting" between mated *T. patachonicus*, and presented the first sonogram of vocalizations for the genus; this sonogram depicted "Groans" and "Grunts" by a female, and "Rasping Grunts" and an extended bout of "Ticking" by a male.

Fjeldså and Krabbe (1990:120) described the vocalizations of territorial male *T. patachonicus* as "...long series *tutidididi...*, *huirr hurr hurr...*, *br–br–br...* and engine–like toc–toc–toc...alternating with loud whistled *bzheeo*. Also low cackling *mrr* and *kek kek*. Calls *bzee*."

Vocalizations of all four species of *Tachyeres* were recorded in the field by Roberto Straneck, copies of which he generously gave to us. Concisely summarized, most vocalizations of steamer-ducks are associated with territorial disputes and therefore are agonistic in nature. In all four species (Fig. 29): (1) males give "Rasping Grunts," descending, rasping calls which are comparatively lower in frequency and prolonged in *T. pteneres*; (2) males often follow "Rasping Grunts" with bouts of "Ticking;" (3) females often duet with males (particularly during bouts of "Ticking") with deeper "Grunts," often preceded by a few deep, more prolonged "Groans" (Nuechterlein and Storer 1985). The vocalizations of *Tachyeres* deserve special attention by future workers, particularly with respect to behavioral ecology and interspecific differences.

STEAMER–DUCKS IN CAPTIVITY

Steamer-ducks are rarely kept in captivity, not only because of their limited and comparatively isolated distributional ranges, but also because of their aggressive behavior toward a diversity of other species. Livezey and Humphrey (1985a) compiled a number of records of such interspecific attacks by steamer-ducks; additional targets of aggression by captive *Tachyeres* include a Rhea (species not given), Demoiselle Cranes (*Anthropoides virgo*), Tasmanian Native–hens (*Tribonyx mortierii*), and Crested Screamers (*Chauna torquata*) (Griswold 1968, Schmidt 1969). Todd (1979:162) recommended: "Under no circumstances can these hostile ducks be mixed with any wildfowl (or most other birds), as they would kill them instantly, regardless of size." He (p. 162) added, however, that "...in spite of their obvious temperamental shortcomings, most captive steamer ducks that I am familiar with were extremely endearing." In addition to their aggressive temperament, steamer-ducks do moderately poorly in captivity, suffering significantly from disease and proving difficult to breed (Hillgarth and Kear 1979).

The first record of a captive steamer-duck was one *T. brachypterus* presented by Captain T. E. L. Moore to the Menagerie of the London Zoological Society on 5 September 1861 (Sclater 1861, 1872, 1877, 1879, 1880b, 1883); this individual of unspecified sex evidently lived for more than 20 years in captivity. Nine more *T. brachypterus* were captured during the expedition by Captain Lecomte to the Falklands during June 1867, but unfortunately none of the birds survived a stormy passage between Port Stanley and Montevideo (Sclater 1868). An additional live specimen of *T. brachypterus* was presented to the Menagerie in London by F. E. Cobb on 12 June 1882 (Sclater 1882, 1883). A third and evidently final specimen of *T. brachypterus* donated to the Menagerie was presented by A. McCall on 23 June 1888 (Sclater 1896); based on the report by Hubbard (1907), this individual survived for almost 20 years. These two instances of long–lived steamer-ducks indicate that the datum on longevity tabulated by Mitchell (1911:514) for *Tachyeres*—15 months—was a substantial underestimate.

The Falkland endemic continued to be the most frequently acquired *Tachyeres* into the twentieth century. S. Kemp and A. G. Bennett arranged for four specimens of *T. brachypterus*, captured during the 'Discovery' expedition, to be given to the London Zoological Gardens (Seth–Smith 1927). Heinroth (1929) noted the presence of "*Tachyeres*

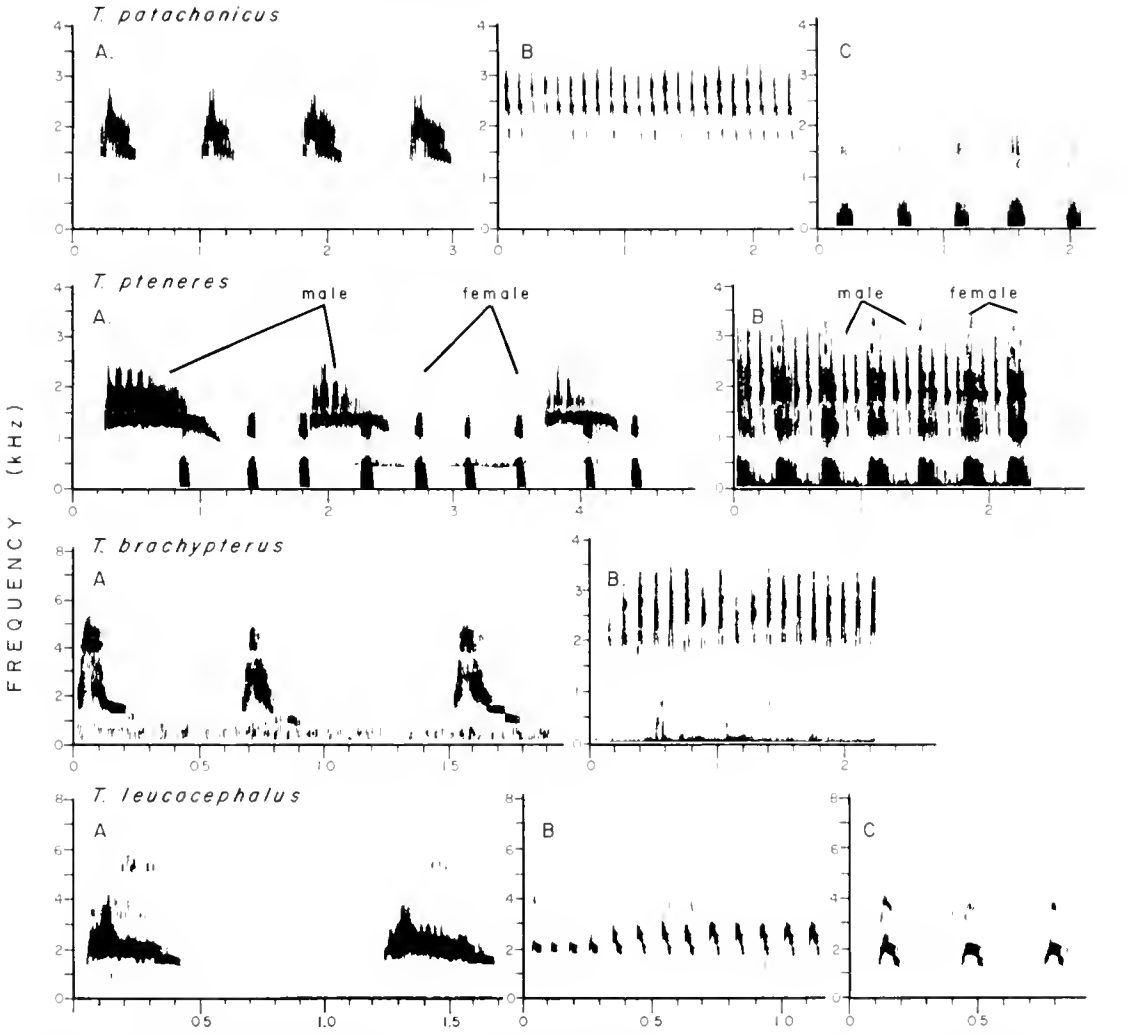

Fig. 29. Sonograms of *Tachyeres* based on recordings made in the field by R. Straneck: *T. patachonicus*—(A) "Rasping Grunts" by male (Bahia Lapataia, Tierra del Fuego, Argentina, January 1981), (B) "Ticking" by male (Laguna los Escarchados, Santa Cruz, Argentina, November 1981), (C) "Grunts" by female (Laguna la Nevada, Santa Cruz, Argentina, November 1981); *T. pteneres* (Bahia Lapataia, Tierra del Fuego, Argentina, January 1981)—(A) duetted "Rasping Grunts" by male and "Grunts" by female, (B) duetted "Ticking" by male and "Grunts" by female; *T. brachypterus* (Carcass Island, Falkland Islands, December 1978)—(A) "Rasping Grunts" by male, (B) "Ticking" by male; *T. leucocephalus* (Punta Tombo, Chubut, Argentina, November 1982)—(A) "Rasping Grunts" by male, (B) "Ticking" by male, (C) "Grunts" by female (in distance).

cinereus" at the London Zoo, and Delacour (1954) reported that three pairs of *T. brachypterus* reached England in 1928, one of which was sent to the aviary at Cleres, France, by S. Lewis and where the birds lived for seven years. Another female *T. brachypterus* was brought to the Wildfowl Trust, Slimbridge, England, by W. J. L. Sladen (Anonymous 1950, 1952), but it did not survive (Anonymous 1951, Sladen 1952). Specimens of *T. brachypterus* acquired during the next decade (e.g., Anonymous 1957, Johnstone 1968) led to successful breeding in captivity at zoos in Duisburg, Germany (Gewalt 1968), Zurich, Switzerland (Schmidt 1969), and the Wildfowl Trust, England (Johnstone, pers. comm.

[1968] *fide* Schmidt 1969; Johnstone 1970). The ducklings hatched at the Zurich Zoo were thought to be possible hybrids between *T. pteneres* and *T. brachypterus*, but errors in the plates by Scott in Delacour (1954) appear to have caused the confusion (Schmidt 1969); no hybrids among species of *Tachyeres* are known (Scherer and Hilsberg 1982). Efforts to breed *T. brachypterus* have continued at the Wildfowl Trust for more than a decade since, with variable success (Anonymous 1973, 1974, 1978, 1982, 1983, 1984, 1985, 1986, 1987, 1988; Kear 1974, 1976, 1978; Lubbock 1979, 1980, 1981). A female *T. brachypterus* held at Sea World, San Diego, California (Todd 1979), was the subject of study of diving behavior in *Tachyeres* (Livezey and Humphrey 1984a) and appeared in a program on flightless birds entitled "Birds of Paradox" produced by the British Broadcasting Corporation.

The Magellanic Flightless Steamer–Duck has occurred even less frequently in avicultural collections, although *T. pteneres* were kept in captivity for use as decoys by Fuegian natives (Bridges 1948:103). Morrison (1940:249) mentioned his involvement with a "collection of live Kelp–Geese [*Chloephaga hybrida*], Steamer-Ducks, and Penguins" during a visit to southern Chile. *T. pteneres* was listed as a "needed" species at the Wildfowl Trust during the 1950s (Anonymous 1950, 1958). Delacour (1954) reported that two *T. pteneres* were brought to his aviary at Cleres in 1939 by A. Morrison from southern Chile (see Morrison 1940); one died soon after arrival and the other "...was in excellent condition until the invasion of June 1940" (Delacour 1954:273). In July 1962, the Philadelphia Zoo received an "immature" male *T. pteneres*, and an "adult" female of the same species was acquired in January 1964; these birds were successfully bred in 1967 (Anonymous 1967, Griswold 1968). Additional live specimens of steamer-ducks identified as *T. pteneres* were acquired by the Wüppertaler Zoo, Berlin (Bock 1973), the Wildfowl Trust (Kear 1977; Anonymous 1978, 1983, 1985, 1986, 1987; Lubbock 1979, 1980), Sylvan Heights Waterfowl, Scotland Head, North Carolina (J. Ballance, pers. comm.), and the Detroit Zoo, Michigan (T. Schneider, pers. comm.). There is some doubt about the species identity of the captive "*T. pteneres*" in American collections; photographs of the birds in North Carolina indicate that they are instead *T. brachypterus*.

Not surprisingly, the recently described *T. leucocephalus* of coastal Chubut, to our knowledge, has not been kept in captivity. It is more noteworthy, however, that the most widespread member of the genus, *T. patachonicus*, also has never been acquired for avicultural collections (Delacour 1954), although the statement of Hillgarth and Kear (1979:142) that "...*Tachyeres patachonicus* has not bred [in captivity]..." suggests otherwise. The greater mobility of the Flying Steamer–Duck probably has enabled it to elude capture more easily. It also seems likely that the absence of *T. patachonicus* from aviaries, especially during the early collecting expeditions to the Falklands in the late nineteenth century, contributed to the widespread reluctance by taxonomists to accept the existence of a flighted species of *Tachyeres*.

PROSPECTS FOR THE FUTURE

At the time of this writing, populations of all four species of *Tachyeres* appear to be secure. *T. pteneres* and *T. brachypterus* are particularly numerous throughout much of their respective ranges, although the former has become uncommon in the northernmost parts of its range (Chiloé and northern Bahía de Ancud). The comparatively widespread *T. patachonicus* is decidedly less common than its flightless congeners in areas of sympatry, and the status of *T. patachonicus* in the Falkland Islands is inadequately known. In one respect, the broad distributional range of *T. patachonicus* renders it less vulnerable to threats to its continued existence. However, until the population structure and possibly underappreciated taxonomic complexities of *T. patachonicus* are better understood (Livezey 1986b, Corbin *et al.* 1988), the possible threats to its differentiated, possibly reproductively isolated components cannot be assessed.

The species of steamer–duck deserving the most vigilant monitoring is *T. leucocephalus*. This species is not only the most recently described member of the Anseriformes, it also has one of the most restricted distributional ranges of any continental

species of waterfowl. The vulnerability of *T. leucocephalus* is magnified by its flightlessness, non-migratory habits, and strictly coastal distribution. At present, the population of *T. leucocephalus* appears stable and, at least locally, the species is abundant. Shipping and coastal oil refineries, however, are increasingly common activities in coastal Patagonia, and the threat of oil spills to coastal birds is substantial. In fact, oiled seabirds and significant associated mortality already have been observed in Chubut (Jehl 1975; pers. obs.). A single major oil spill in Chubut could directly threaten a significant proportion of the total population of *T. leucocephalus* and endanger its benthic food supply.

A number of compelling problems remain concerning the ecology and evolutionary morphology of steamer-ducks. Basic data are lacking on the migration, winter distributions, and possible reproductive isolation of *T. patachonicus* breeding on freshwater lakes. Even less well known are the *T. patachonicus* of the Falkland Islands; the few available specimens and geographic isolation suggest that this insular population has differentiated morphologically from its continental counterparts and may be deserving of species rank. Although some headway has been made in the study of the molts and plumages of steamer-ducks, much remains unknown; particularly poorly understood are the predefinitive plumages of all species (particularly of *T. pteneres*) and the evident geographic variation in the aspects and possible number of definitive plumages of *T. patachonicus*. Our understanding of flightlessness in *Tachyeres* would be improved significantly by a quantitative study of the ontogeny of the body and pectoral girdle in young of known age in both flighted and flightless steamer-ducks.

The extreme territoriality of steamer-ducks provides an unusually promising opportunity for the study of this ecologically important behavioral phenomenon, the implications of which remain controversial (Livezey and Humphrey 1985a, b; Murray 1985, 1986; Neuchterlein and Storer 1985a, b; Livezey 1987). Particularly intriguing questions concern the temporal and spatial stability of territories (especially in tidal habitats and near islands with high nest-densities), the ecological and evolutionary implications of interspecific aggression, the ontogeny, sexuality, and seasonality of territoriality, and the impact of territoriality on population densities and dispersion. The open habitat, low mobility, extreme pugnacity, and conspicuousness of steamer-ducks, especially flightless species, and sexual and age-related differences in plumage aspect, make steamer-ducks particularly appropriate subjects for the study of territoriality. The tameness and abundance of *T. brachypterus*, and the likely ease with which both sexes could be attracted into live traps for marking by playbacks of calls (Weller 1976) or decoys, qualify this species as probably the optimal member of the Anseriformes for the study of territoriality.

SUMMARY

A systematic review of the four species of steamer-duck (*Tachyeres*), a genus of benthic-diving tadornine waterfowl limited in distribution to southern South America, is presented. Four species are recognized: Flying Steamer-Duck (*T. patachonicus*), Falkland Flightless Steamer-Duck (*T. brachypterus*), Magellanic Flightless Steamer-Duck (*T. pteneres*), and White-headed Flightless Steamer-Duck (*T. leucocephalus*). The monograph has six major objectives: (1) to present a history of study of the genus; (2) to provide generic and specific synonymies and species accounts; (3) to describe the molts and plumages of steamer-ducks; (4) to present diagnostic characters and keys for identification; (5) to summarize information on field identification and aviculture of *Tachyeres*; and (6) to present an indexed bibliography for the genus.

The ornithological history of the steamer-ducks spans four centuries, and is divisible into four major periods: (1) early descriptions by explorers and naturalists (*ca.* 1582–1830); (2) debate concerning the existence of flying and flightless species in the genus (1831–1935); (3) recognition of two (continental and Falkland) flightless species and a flying species (1936–1979); and (4) discovery of a second continental flightless species (1980 to present). The taxonomic history of the genus reflects, in part, these changing perceptions, further complicated by de-

bate concerning the placement of *Tachyeres* within the family and nomenclatural confusion (involving 25 different binomina in seven genera, excluding misspellings). Complete synonymies are given for the genus and included species, with concise descriptions of diagnostic characters and distributional limits and designation of types. Common names in 12 languages are also given.

Knowledge of the molts and plumages of steamer-ducks remains far from complete. History of study of molts and plumages of *Tachyeres* is divisible into three eras, closely associated with changing perceptions of the systematics of the genus: (1) era of exploration (prior to 1830); (2) era of taxonomic controversy (1830–1935); and (3) era of Murphy (1936 to present).

We interpret available information as supportive of several important findings: (1) *T. brachypterus* and coastal Fuego–Patagonian *T. patachonicus* (and probably other populations of the latter) have three molts and plumages per annual cycle, whereas, *T. pteneres* and *T. leucocephalus* have only two; (2) basic plumages of the head and neck in *T. brachypterus* and *T. patachonicus* (and probably *T. pteneres*) are sexually monochromatic and resemble the juvenal plumage, and that of *T. leucocephalus* is sexually dichromatic wherein the female resembles the juvenal plumage; (3) definitive plumages are attained during molt II in Atlantic–coastal *T. patachonicus* and (probably) *T. brachypterus*, those of *T. leucocephalus* may not be attained until molt IV, and the age at attainment of definitive plumage in *T. pteneres* is unknown. Detailed descriptions of natal, juvenal, and definitive plumages are given for both sexes and all four species of *Tachyeres*, emphasizing topics for which information and specimens are inadequate for confident interpretation.

Diagnostic characters of steamer-ducks include massive body proportions, colors of plumage and soft parts, and five skeletal characters. Species of *Tachyeres* are distinguishable by a variety of characters of plumage pattern and skeleton, most notably by selected ratios of external and skeletal dimensions (e.g., ratio of wing length to tarsus length, or ratio of humerus length to femur length). Multivariate discrimination of species and sexes is possible using discriminant functions based on suites of external or skeletal measurements. Keys to species of *Tachyeres* are presented, but identification of skin specimens of subadult birds of unknown sex and/or locality may be problematic.

Problems of field identification of steamer-ducks essentially reduce to distinguishing the smaller, widespread *T. patachonicus* from each of the mutually allopatric, marine–coastal, flightless species that also occur on inland lakes (more than 1 km from the coast). In coastal Chile and Tierra del Fuego, (adult) *T. pteneres* are unique in their large size and the orange color of the bills of *both sexes*. Distinguishing *T. patachonicus* in the field from the two intermediate flightless species—*T. brachypterus* (Falklands) or *T. leucocephalus* (coastal Chubut)—is difficult; distinguishing *T. patachonicus* from *T. brachypterus* on marine coasts of the Falklands is probably not possible under most field conditions.

Steamer-ducks have been kept in captivity infrequently, but cause difficulties in aviaries because of their pugnacious behavior toward other waterfowl and have proven moderately difficult to breed. The most frequently held species, both historically and at present, is *T. brachypterus*.

Wild populations of all four species of *Tachyeres* appear secure, although local declines in numbers and threat posed by oil spills to marine populations (particularly *T. leucocephalus*) justify efforts to monitor and protect selected populations. Important subjects for future study include: the dynamics, migration, and possible genetic fragmentation of populations of *T. patachonicus* (especially the Falkland population); basic information concerning the molts and plumages of freshwater *T. patachonicus*, *T. leucocephalus*, and (especially) *T. pteneres*; and the evolutionary implications of the extreme territoriality of the members of the genus.

The published literature on the genus—one that spans four centuries and comprises over 550 references—is summarized in a subject–indexed bibliography.

RESUMEN

Se presenta una revisión sistematica de las cuatro especies de pato vapor (*Tachyeres*), un género de aves acuáticas, conocidos como tadorninos buceadores benticos cuya distribucion esta

restringida al extremo sur de América del Sur. Se reconocen cuatro especies: El pato vapor volador (*T. patachonicus*), el pato vapor no volador de Falkland, (*T. brachypterus*), el pato vapor no volador magallanico (*T. pteneres*), y el pato vapor no volador de cabeza blanca (*T. leucocephalus*). Esta monografía tiene seis objetivos principales: (1) presentar la historia del estudio de este género; (2) proveer sinonimias genéricas y específicas y sumarios informativos de las especies; (3) describir las mudas y plumajes de los patos vapores; (4) presentar caracteres diagnósticos y claves para la identificación y avicultura de *Tachyeres*; y (6) presentar un indice bibliográfico del género.

La historia ornitológica de los patos vapores se extiende por cuatro siglos, y se la puede dividir en cuatro periodos principales: (1) las primeras descripciones de exploradores y naturalistas (cerca a 1582–1830); (2) el debate concerniente a la existencia de especies voladoras y no voladoras en el género (1832–1935); (3) el reconocimiento de dos (continental y de las islas Falkland [Malvinas]) especies no voladoras y una especie voladora (1936–1979); y (4) el descubrimiento de una segunda especie continental no voladora (1980–presente). La historia taxonomica del género refleja, en parte, este panorama cambiante que es complicado aun mas por el debate sobre la asignacion de *Tachyeres* dentro de la famila y confusiones de nomenclatura (relacionadas a 25 binomiales diferentes en 7 géneros, excluidos los errores de escritura). Se presentan sinonimias completas para el genero y especies incluidas, con descripciones concisas de los caracteres diagnósticos, limites distribucionales y designacion de tipos. Se proveen nombres comunes en 12 idiomas. El conocimiento de las mudas y plumajes de los patos vapores dista todavía de ser completo.

La historia del estudio de mudas y plumaje de *Tachyeres* se la puede dividir en 3 eras, cercanamente asociadas con las percepciones cambiantes de la sitematica del genero: (1) era de exploracion (previa a 1830); (2) era de controversia taxonomica (1830–1935); y (3) era de Murphy (1936–presente).

La informacion disponible la interpretamos como soporte de algunos importantes hallazgos: (1) *T. brachypterus* y *T. patachonicus* de las costas de Tierra del Fuego y de la Patagonia Argentina (y probablemente otras poblaciones de este ultimo) tienen 3 mudas y plumajes por ciclo anual, mientras, *T. pteneres* y *T. leucocephalus* tienen solamente dos; (2) los plumajes básicos de la cabeza y el cuello en *T. brachypterus* y *T. patachonicus* (y probablemente *T. pteneres*) son sexualmente monocromáticos y se parecen el plumaje juvenil, y aquel de *T. leucocephalus* es sexualmente dicromático y en el que el plumaje de la hembra se parece al plumaje juvenil; (3) plumajes definitivos se logran en la muda II en *T. patachonicus* de la costa atlántica y (probablemente) *T. brachypterus*, aquellos de *T. leucocephalus* tal vez no se logren hasta la muda IV, y la edad a la que *T. pteneres* alcanza el plumaje definitivo es desconocida.

Descripciones detalladas de plumajes natales, juveniles, y definitivos se dan para ambos sexos y para las cuatro especies de *Tachyeres*, y se enfatizan aspectos para los cuales informacion y especimenes son inadecuados para interpretaciones correctas.

Los carateres disagnosticos de los patos vapores incluyen proporciones del cuerpo grandes, colores del plumaje y partes suaves y cinco caracteres del esqueleto. Las especies de *Tachyeres* son distinguibles por una variedad de caracteres de patron plumaje y esqueleto, más notablemente por proporciones seleccionadas de dimensiones externas y del esqueleto (e.g., proporcion de la longitud del ala sobre la longitud del tarso, o proporcion de la longitud del humero sobre la longitud del femur). Discriminacion multivariada de las especies y sexos es posible con el uso de funciones discriminantes basadas en un conjunto de medidas del esqueleto y externas. Se presentan claves para la identificacion de las especies de *Tachyeres*, pero la identificacion de pieles de especimenes de aves subadultas de sexo o localidad desconocida puede ser problemática.

Los problemas de identificacion de los patos vapores se reducen a distinguir al pequeño y ampliamente distribuido *T. patachonicus* de cada una de las mutuamente alopatricas especies no voladoras de la costa marina que también ocurren en lagos tierra adentro (mas de 1 km de la costa). En las costas de Chile y de Tierra del Fuego, (adultos) *T. pteneres* son unicos por su tamaño grande y el color naranja de los picos en ambos sexos. La distinción en el campo de *T. patachonicus* de las dos especies

no voladoras intermedias—*T. brachypterus* (islas Falkland [Malvinas]) o *T. leucocephalus* (Chubut de la costa)—es difícil; y distinguir *T. patachonicus* de *T. brachypterus* en las costas marinas de las islas Falkland (Malvinas) probablemente no es posible en la mayoría de condiciones de campo.

Los patos vapores no han sido mantenidos en cautiverio con frecuencia, pues presentan dificultades en los aviarios debido a su comportamiento belicoso hacia otras aves acuáticas y al parecer su reproducción es difícil. La especie mantenida con mayor frecuencia, históricamente y al presente, es *T. brachypterus*.

Poblaciones salvajes de las cuatro especies de *Tachyeres* al parecer están seguras, a pesar de que declinaciones locales en números y la amenaza latente por derramamientos de petróleo a las poblaciones marinas (particularmente *T. leucocephalus*) justifican esfuerzos para monitorear y proteger a las poblaciones. Aspectos importantes para estudios futuros incluyen: la dinámica, migración, y posible fragmentación genética de las poblaciones de *T. patachonicus* (en especial la población de islas Falkland [Malvinas]); información básica concerniente a la muda y plumajes de *T. patachonicus*, *T. leucocephalus*, y especialmente *T. pteneres*; y las implicaciones evolutivas de la extrema territorialidad de los miembros del género.

La literatura publicada sobre el género—que se extiende por cuatro siglos y comprende más de 550 referencias—se resume en un índice bibliográfico temático.

SPECIMENS EXAMINED

Specimens examined in this research, which numbered almost 500, are of several types (SN = study skin, SK = skeleton, SK* = skeleton for which external data were recorded, SN/SK = skin and partial skeleton, AN = anatomical or spirit specimen); when determined, sexes are indicated (M = male, F = female); sexes given in brackets were determined by measurements and/or plumage. Downy young are marked by "d" and birds in juvenal plumage are indicated by "j."

Institutions holding the specimens are indicated by abbreviations immediately preceding the corresponding specimen number(s), and are as follows: AM = American Museum of Natural History, New York; BK = Museum of Vertebrate Zoology, University of California, Berkeley, California; BM = British Museum (Natural History), Tring, Hertfordshire, England; CM = Carnegie Museum of Natural History, Pittsburgh, Pennsylvania; CR = Universitets Zoologiske Museum, Copenhagen; FD = Field Museum of Natural History, Chicago, Illinois; HA = Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts; IS = Iowa State University, Ames, Iowa; KU = Museum of Natural History, University of Kansas, Lawrence, Kansas; LA = Los Angeles County Museum of Natural History, Los Angeles, California; MI = Museum of Zoology, University of Michigan, Ann Arbor, Michigan; MA = Museo Argentino de Ciencias Naturales, Buenos Aires, Argentina; NM = National Museum of Natural History, Smithsonian Institution, Washington, D. C.; PH = Philadelphia Academy of Sciences, Philadelphia, Pennsylvania; RO = Royal Ontario Museum of Natural History, Ontario, Canada; RS = Royal Museum of Scotland, Edinburgh; SD = San Diego Museum of Natural History, San Diego, California; SW = Southwestern College, Winfield, Kansas; YA = Peabody Museum of Natural History, Yale University, New Haven, Connecticut.

TACHYERES PATACHONICUS (222)

ARGENTINA

Río Negro.— BM 99.1.27.10 (SN, M), FD (originally Princeton) "8847" (SN, M).

Neuquen.— Lago Nahuel Huapi: BM 99.1–27.10 (SN, M), MA 1478a (SN, M), MA 31523 (SN), MA 36363 (SN, M). Lago Lolog: MA 35051 (SN, F). Zapala, Laguna Blanca: MA 49987 (SN, F).

Chubut.— Puerto Melo: SW 3532/KU 77940 (SN/SK, M), KU 79450 (SK, M), KU 79479 (SK, F). Río Pico, Lago No. 3: MA 52486 (SN, F). Lago Fontana: KU 79468 (SN/SK, M), KU 79469 (SN/SK, F), KU 79470 (SK*, F), KU 79471 (SK*, M), KU 79472 (SK*, F), KU 79473 (SK*, F), KU 79475 (SK*, M), KU 79476 (SK*, F), KU 79477 (SN/SK),

KU 79478 (SK*, M), BK 42829 (SN, M), BK 42830 (SN, F), BK 42831 (SN, F). Lago Krügger: KU 79474 (SK*, M). Arroyo Verde: FD "2404" (SN, F), FD "2405" (SN, M), FD "2406" (SN, M). Cholila: MA (uncataloged, Kovacs No. 77) (SN, M).

Santa Cruz.— Puerto Deseado: SW 3535/KU 77944 (SN/SK, M), SW 3536/KU 77945 (SN/SK, F), SW 3537/KU 77946 (SN/SK, M), KU 77947 (SK, F), KU 77948 (SK, M), KU 77949 (SK, F), KU 77950 (SK, F), SW 3538/KU 77951 (SN/SK, F), KU 77952 (SK, M), KU 77953 (SK, F), SW 3539/KU 77954 (SN/SK, M), SW 3540/KU 77955 (SN/SK, F), KU 77956 (SK, F), KU 77957 (SK, M), KU 77958 (SK, M), KU 79209 (SK*, F), KU 79210 (SK*, M), KU 79211 (SK*, M, j), KU 79212 (SK*, F), KU 79213 (SK*, F), KU 79214 (SK*, M), KU 79215 (SK*, M), KU 79216 (SK*, M), KU 79217 (SK*, F), KU 79218 (SK*, F), KU 79219 (SK*, M), KU 79220 (SK*, M), KU 79221 (SK*, F), KU 79222 (SK*, F), KU 79227 (SK*, F), KU 79228 (SK*, M), KU 79229 (SK*, F), KU 79230 (SK*, M), KU 79231 (SK*, M), KU 79232 (SK*, F), KU 79233 (SK*, M), MI 157719 (SK, M), NM 534266 (SN, M), YA 6400 (SK, M), YA 82326 (SN, F), YA 82327 (SN, F). Río Santa Cruz: MA 52297 (SN, M). Bahía de los Nodales: SD 38353 (SK, F). Rio Gallegos: FD "4697" (SN, M), PH 81103 (SN, M). Laguna de los Escarchados: CP791 (SK, M), MI 220945 (SK, F?, d). Lago San Martin: MA 4288a (SN, j). Lago Roca: KU 79459 (SK*, M), KU 79460 (SK*, M), KU 79461 (SK*, M), KU 79462 (SK*, F), KU 79463 (SK*, M). Perito Moreno: KU 79464 (SK*, M), KU 79465 (SK*, F), KU 79466 (SK*, F), KU 79467 (SK*, M).

Tierra del Fuego — Beagle Channel: AM 443720 (SN, F), AM 443721 (SN, F), AM 443718 (SN, M), AM 443717 (SN, M), AM 443719 (SN, M). Cabo Peñas: BM 1929.6.14.3 (SN, F), SD 37540 (SN, F). Rio Grande: SD 38645 (SK, M), YA 11772 (SN, F), YA 11773 (SN, F), BM 1932.7.12.11 (SN, M, j); RO (1 uncataloged frozen adult male, to be anatomical specimen, from lake 114 km south of Rio Grande). Ushuaia: AM 443729 (SN, M), AM 443727 (SN, F), AM 443728 (SN, F), MA 5780 (SN, M), MA 10006 (SN, M), KU 77959 (SK, M), SW 3541/KU 77960 (SN/SK, M), SW 3542/KU 77961 (SN/SK, F), KU 77962 (SK, F), KU 77963 (SK, M), KU 77972 (SK, M), KU 77973 (SK, F) KU 79183 (SK, M), KU 79190 (SK, F), KU 79191 (SK, F), KU 79192 (SK, F) KU 79198 (SK, F), KU 79199 (SK, M), KU 79200 (SK, F), KU 79201 (SK, M), KU 79203 (SK, M), KU 79204 (SK, F), KU 79205 (SK, M), KU 79207 (SK, F), KU 79208 (SK, M), YA 82322 (SN), YA 82323 (SN), YA 82324 (SN), YA 82325 (SN), YA 82330 (SN, F), YA 82331 (SN, F), YA 82332 (SN, M), YA 82333 (SN, F), YA 6485 (SK, M), YA 6845 (SK, M), YA 8246 (SK, F), MI 15720 (SK, F). Viamonte: BM 1932.7.12.13 (SN, M, j), BM 1928.4.21.1 (SN, M), BM 1928.7.21.2 (SN, F), BM 1932.7.12.12 (SN, M). Isla de los Estados (Staten Island): NM 491013 (SK*, M), NM 491014 (SK*, F), NM 511771 (A), NM 511772 (A, F), NM 536349 (SN, F), NM 536350 (SN, M), NM 536351 (SN/SK, F).

Chile

Region X.— Corral: BM 96.12.31.7 (SN, F). Valdivia: MA 4883a (SN, F). Chiloé and Bahia de Ancud: AM 443741 (SN, M), AM 443743 (SN, M), AM 443744 (SN, M), AM 443749 (SN, F), AM 443766 (SN, F), AM 443755 (SN, F), AM 443753 (SN, F), AM 443754 (SN, F), AM 443759 (SN, F), AM 443762 (SN, F), AM 443763 (SN, F), AM 443740 (SN, M), AM 443742 (SN, M), AM 443745 (SN, M), AM 443746 (SN, M), AM 443447 (SN, M), AM 443748 (SN, M), AM 443751 (SN, F), AM 443756 (SN, F), AM 443757 (SN, F), AM 443758 (SN, F), AM 443760 (SN, F), AM 443761 (SN, F), AM 443764 (SN, F), AM 443765 (SN, M), RO 35404 (SN, [F]), PH 81097 (SN, M), FD "3888" (SN, M). Codihue: KU 79840 (SK*, M), KU 79844 (SK*, M). Ensenada Huito: KU 79852 (SK*, F), KU 79853 (SK*, F), KU 79854 (SK*, M). Lago Llanquihue: KU 79849 (SK*, M). Lago Rupanco: KU 79855 (SK*, F), KU 79856 (SK*, M), KU 79857 (SK*, M), KU 79858 (SK*, F), KU 79859 (SK*, M).

Region XI.— Puerto Aisen (intersection of Rio Simpson and Rio Mañhuales): FD "2407" (SN, M).

Region XII.— Río Ciaike: FD 104109 (SK, M), FD 14774 (SN, F), FD 120519 (SN, F); FD 120521 (SN, F, d), FD 120522 (SN, d). San Agostini Sound: CM 120774 (SN, F), CM 120776 (SN, M), CM 120777 (SN, F), CM 120778 (SN, d), CM 120779 (SN, d). Puerto Churrucha: BM 80.11.18.565 (SN,

F). Elizabeth Island: BM 79.9.3.28 (SN, F). Puerto Bueno: BM 79.9.3.29 (SN, F). Bertrand Island: PH 81105 (SN, F). Wollaston Island: AM 443737 (SN, F). Navarino Island: AM 443738 (SN, M). Straits of Magellan: BM 80.11.18.565 (SN, F).

FALKLAND ISLANDS

East Falklands.—Cape Dolphin: BM 1940.12.6–36 (SN, [F]), BM 1940.12.6–36 (SN, M), BM 1940.12.6–34 (SN, F), BM 1940.12.6–35 (SN, F), BM "86" (SN, d). Bleaker Island: AM 443785 (SN, M), AM 443729 (SN, M). Fitzroy (Swan Pond): IS 1434 (SN, M, d), IS 1451 (SN, M, d), IS 1452 (SN, F, d), IS 1453 (SN, F, d), IS 1474 (Sn, F). Unspecified: BM 1930.12.18.1 (SN, d), BM 1962.1.160 (SK, [F]).

Unspecified.— BM 1928.7.21.18 (SN, d).

TACHYERES BRACHYPTERUS (69)

FALKLAND ISLANDS

East Falklands.— Port Stanley: AM 443791 (SN, F), AM 443782 (SN, M), AM 443785 (SN, M), AM 443788 (SN, M), AM 443784 (SN, M), AM 443786 (SN, M), AM 443783 (SN, M), AM 445783 (SM, M), AM 443789 (SN, F). Diamond Cove: BM 1932.7.2.41 (SN, d). Fitzroy: IS 1435 (SN, M, d), IS 1439 (SN, M, d), IS 1454 (SN, M, d). Lively Island: KU 80513 (SK*, F), KU 80514 (SK*, F), KU 80515 (SK*, M), KU 80516 (SK*, F), KU 80517 (SK*, M), KU 80518 (SK*, F), KU 80519 (SK*, M), KU 80520 (SK*, M), KU 80521 (SK*, F), KU 80522 (SK*, F), KU 80523 (SK*, M), KU 80524 (SK*, F), KU 80525 (SK*, M), KU 80526 (SK*, M), KU 80527 (SK*, M), KU 80528 (SK*, F), KU 80529 (SK*, F), KU 80530 (SK*, M), KU 80531 (SK*, F), KU 80532 (SK*, F), KU 80604 (SK, M), KU 80605 (SK, M). Sea Lion Island: AM 443771 (SN, M). San Salvador: BM 44.1.18.66 (SN). San Carlos: HA 2204 (SK, F). Mare Harbour (East[?] Falklands): BM 1920.2.74 (SN). Unspecified: AM 443773 (SN, M), AM 443775 (SN, F).

West Falklands.— Pebble Island: BM 1940.12.6.33 (SN, F). New Island: MI 136206 (SK, M), MI 135895 (SN, M), MI 135897 (SN, M), MI 135896 (SN, F). Unspecified: HA 2206 (SK, M).

Unspecified.— BM 1940.12.7.26 (SN, M), BM 1940.12.7.27 (SN), BM 1949.52.38 (SK, M), BM 1930.12.18.1 (SN), BM 1900.11.30.1 (SN, d), BM 1900.11.30.2 (SN, d), BM 1900.11.30.3 (SN, d), BM 1900.11.30.4 (SN, d), BM "725" (SN, M, j), PH 55809 (SN, M), PH 5581D (SN, F), AM 419160 (SN), HA 70521 (SN), HA 70522 (SN); RS 1913.237.82 (SN), RS 1921.143.122 (SN), RS 1921.143.123 (SN), RS 1958.71 (SNs, 5 specimens).

TACHYERES PTENERES (132)

ARGENTINA

Tierra del Fuego.— Beagle Channel: BM 1929.614.2 (SN, F), AM 443707 (SN, M). Gable Island: AM 443714 (SN, F, j). Ushuaia: AM 443711 (SN, M), AM 443713 (SN, F), KU 77964 (SN, F), SW 3543/KU 77965 (SN/SK, M), KU 77966 (SN/SK, M), KU 77967 (SK, F), KU 77968 (SK*, F), KU 77969 (SK*, M), KU 77970 (SK*, M), KU 77971 (SK*, M), KU 79178 (SK*, M), KU 79179 (SK*, M), KU 79180 (SK*, M), KU 79181 (SK*, M), KU 79182 (SK*, M), KU 79194 (SK*, F), KU 79195 (SK*, M), KU 790206 (SK*, F), MI 157721 (SK, M), SD 40490 (SK, F), YA 6486 (SK, M), YA 6487 (SK, M), YA 82235 (SN, M), YA 82236 (SN, F), YA 82237 (SN, M), YA 82238 (SN, F), YA 82240 (SN, F, d), YA 82241 (SN, F, d), YA 82243 (SN, F, d), YA 82244 (SN, F, d), YA 82245 (SN, M, d), YA 82335 (SN, F), YA 82336 (SN, F). Bahía Buen Suceso: NM 536348 (SN, M). Lapataia: SD 38646 (SK, M). Harberton: BM 1932.12.14 (SN, M), BM 1932.12.20.1 (SN, d). Isla de los Estados: MA 4144a (SN, M), NM 490930 (SK, M), NM 490937 (SK), NM 490939 (SK, M), NM 490942 (SK, F), NM 490943 (SK, F), NM 511767 (A), NM 511768 (A, F), NM 511769 (A, F), NM 5411770 (A), NM 536349 (SN, F).

CHILE

Region X.— Chiloe and Bahía de Ancud: AM 424579 (SN, M), AM 351200 (SN, M), AM 424578 (SN, M), AM 424580 (SN, F), AM 443661 (SN, M), AM 443663 (SN, F), AM 443664 (SN, F), AM 443665 (SN, F), AM 443667 (SN, M), AM 443668 (SN, M), AM 443669 (SN, M), AM 443671 (SN,

M), AM 443673 (SN, M), AM 443674 (SN, F), AM 443675 (SN, F), AM 443676 (SN, F), NM 443677 (SN, F), AM 443678 (SN, F), AM 443680 (SN, F), AM 443715 (SN, F), PH 81099 (SN, M), LA 24902 (SN, F, d), FD "2399" (SN, F), FD "2400" (SN, F), FD "2401" (SN, M), FD "2402" (SN, F), FD 62419 (SN, M, d), KU 79835 (SK*, F). Ensenada Codihue: KU 79839 (SK*, F), KU 70842 (SK*, M), KU 79843 (SK*, F). Islas Guaitecas: CM 123555 (SN, F, d), CM 123556 (SN, M, d), FD "2763" (SN, M, d).

Region XI.— Puerto Aisen: PH 16978 (SN, [F]). Punta Lagunas: CM 120850 (SN, F).

Region XII.— Mintiroso Bay: CM 123470 (SN, M, d). Almirante Bay: CM 123461 (SN, M, d). Isla Hermite: FD "4695" (SN, M, j), FD "4696" (SN, M, j), MA 42241 (SN, M). Isla Carolina: AM 443716 (SN, M). Falso Cabo de Hornos: AM 446796 (SN, M). Cabo de Hornos: AM 443683 (SN, M). Bahía Orange: AM 733420 (SN, M). Isla London: AM 443694 (SN, M), PH 81095 (SN, F, d), 3 unnumbered downy young at AM. Isla Wollaston: AM 443686 (SN, M). Isla Navarino: NM 488291 (SK), PH 81102 (SN, [F]). San Agostini Sound: CM 120775 (SN, M). Bahía Eden: BM 1903.12.30.199 (SN, F), PH 120816 (SN), PH 120816 (SN, M). Puerto Bueno: PH 120795 (SN, M). Bahía Wide: PH 120813 (SN, M). Isla Newton: SD 37539 (SN, M), SD 37582 (SK, F). Isla Harbour: NM 18484 (SK, j). Caleta Latitud: NM 18553 (SK, j). Bahía Tom: BM 80.11.18.563 (SN, F), BM 80.11.18.561 (SN, d), BM 80.8.3.25 (SN, M, d). Straits of Magellan: BM 80.11.18.564 (SN, M), BM 42.736 (SN, [F]), RO 35406 (SN, [F]). Walney Sound: BM 79.9.3.30 (SN, M). Grays Harbor, Smythe Channel: BM 1903.12.30.200 (SN, M). Canal Messier: BM 80.11.18.562 (SN, F). Bahía Churruca: BM 1903.12.30.202 (SN, F). "Magallanes I.": YA 22796 (SN, M, j). Unnumbered downy young at AM from Isla Timbales, Isla Brecknock (2), Isla Stewart, and "Beagle Channel."

Unspecified.—NM 18484 (SK), NM 18553 (SK), AM 1222 (SK, F).

Tachyeres leucocephalus (61)

Argentina

Chubut.— Bahía Concepción: SD 38277 (SN, M), SD 38352 (SK, F). Punta Tombo: AM 8513 (SK, M). Punta Tafor: RO 146919 (SK, [M]). Bahía de Huevos (Egg Harbour): AM 733415 (SN, M). Camarones: MA 52194 (SN, M), MA 52195 (SN, M), MA (uncataloged, Kovacs No. 75) (SN, M), MA (uncataloged, Kovacs No. 76) (SN, F), YA 82328 (SN, F), YA 82334 (SN, M, d); RO—2 uncataloged, frozen birds (M, F) to be preserved as anatomical specimens. Puerto Melo: MA 52694/KU 77932 (SN/SK, M, holotype), MA 52698 (SN, M, d); MA—3 unaccessioned skeletons given by P. S. Humphrey in 1984; KU 77925 (SK*, M), SW 3527/KU 77926 (SN/SK, F), KU 77927 (SK*, F), KU 77928 (SK*, M), KU 77929 (SK*, F), SW 3528/KU 77930 (SN/SK, M), KU 77931 (SK*, M), KU 77933 (SK*, M), SW 3530/KU 77934 (SN/SK, F), KU 77935 (SK*, M), SW 3531/KU 77936 (SN/SK, F), KU 77937 (SK*, F), KU 77938 (SK*, M), KU 77939 (SK*, F), KU 77941 (SK*, F), SW 3533/KU 77942 (SN/SK, M), SW 3534/KU 77943 (SN/SK, M), KU 79234 (SK*, M), KU 79235 (SK*, M), KU 79236 (SK*, M), KU 79237 (SK*, M), KU 79238 (SK*, F), KU 79239 (SK*, F), KU 79240 (SK*, F), KU 79241 (SK*, F), KU 79243 (SK*, M, j), KU 79244 (SK*, M), KU 79245 (SK, M), KU 79246 (SK*, M), KU 79247 (SK*, F), KU 79248 (SK*, M), KU 79249 (SK*, F), KU 79455 (SN/SK, F), KU 79456 (SN/SK, M), KU 79624 (A, d), KU 79625 (A, d), KU 79626 (A, d), KU 79501 (SN, F, d), KU 79502 (SN, M, d), KU 79457 (SK*, F), MA 53329 (SN, F), MA 53330 (SN, M).

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Sources containing references to steamer-ducks are indexed by subject using combinations of one or more single-letter designations; these follow the references and are enclosed in square brackets. The 12 designations and their meanings are as follows:

A	anatomy
B	behavior
C	captive birds
D	distributional data
E	exploitation by humans
F	feeding habits
H	habitat
L	locomotion
M	minimal mention
N	nesting
P	predation
T	taxonomy

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APPENDIX

Multivariate Identification of Specimens

Bivariate Canonical Plots

Skin specimens. A reasonably precise classification of study skins to species can be achieved by calculating the scores of each on the first two canonical variates shown in Fig. 25. These scores are based on three of the four basic skin measurements taken for most specimens in this study—nail width, tarsus length (cranial surface), and wing length (arc length of straightened wing, from wrist). Scores on each axis are calculated by multiplying each measurement (mm) by the corresponding coefficient in Table A1, then summing the three resultant products with the 'constant' term for that axis. After this is done for each axis, the point can be plotted on Fig. 25 and its position indicates its likely group membership.

Table A1. Coefficients (non-standardized) and constants for first two canonical variates for external measurements (plotted in Fig. 25) separating the eight species-sex groups of *Tachyeres*.

	Coefficients for Variate	
Term	I	II
Nail width	-0.853	-0.373
Tarsus length	-0.207	-0.026
Wing length	0.067	-0.074
Constant	5.070	27.233

Complete skeletons. An analogous method of identification can be performed using the coefficients for the 19 skeletal measurements incorporated in the canonical axes depicted in Fig. 27. As described for external measurements, scores for a specimen on each axis are calculated by summing the 'constant' term with the products of each measurement (mm) with its corresponding coefficient; coefficients and constants for canonical axes I and II for skeletons are given in Table A2. Because of the greater precision and dimensionality of the skeletal model, the resultant species-sex classifications are significantly more reliable than those based on external measurements.

Table A2. Coefficients (non-standardized) and constants for first two canonical variates for skeletal measurements (plotted in Fig. 27) separating eight species-sex groups of *Tachyeres*.

	Coefficients for Variate	
Term	I	II
Humerus length	-0.294	-0.341
Ulna length	0.752	0.247
LWM	-0.158	2.114
Femur head width	-0.025	-0.035
Tibiotarsus length	-0.117	-0.015
Tarsometatarsus length	-0.049	0.009
LWM	-0.634	0.005
Digit-III length	-0.050	0.030
Sternum keel length	0.051	-0.116
least width	-0.215	-0.278
posterior width	-0.027	0.179
Coracoid length	-0.147	0.300
basal width	-0.194	0.521
Interacetabular width	-0.097	0.039
Interorbital width	-0.012	-0.104
Postorbital width	-0.024	-0.030
Antorbital width	-0.011	-0.019
Bill height	-0.145	-0.124
length	-0.039	-0.121
Constant	22.260	-4.232

Classification Functions

General methodology. More powerful for *pairwise* discrimination among species-sex groups, but much more tedious to use, are classification functions. These functions are presented as coef-

ficients (for the same variables incorporated in the associated canonical analyses) for *each group* considered in the analysis. Initially, one must choose the two groups to compare with respect to the specimen at hand; this choice may be based on information on sex, locality, plumage pattern, or a preliminary plotting on the canonical axes described above. The specimen is then compared against the two groups simultaneously by calculating the score of the specimen using as coefficients the *differences* between corresponding coefficients for the two groups concerned. The resultant score is then compared to those derived using the mean measurements for the groups being compared (Tables 3 and 6); the group with the score most similar to that of the specimen is the group into which the specimen is tentatively classified. In theory, all such pairwise comparisons can be performed, and the closest match indicates the optimal classification for the specimen. For a *Tachyeres* of unknown sex, this would require 28 pairwise comparisons for optimal discrimination among the eight species-sex groups. In practice, however, without the aid of a complete data set for *Tachyeres* specimens and appropriate computer support, most classifications will be based on discrimination between a smaller subset of the groups delimited by ancillary data associated with the specimens to be identified.

Skin specimens. Coefficients of classification functions are given for skin specimens of unknown sex in Table A3, and for skin specimens of known sex in Table A4. For example, assume one wishes to classify a skin specimen of a male steamer-duck from coastal Chubut using classification functions. Assume that the specimen has a nail width of 14 mm, tarsus length of 63 mm, and a wing length of 292 mm. Given that the specimen is known to be a male, the coefficients to use are those for males only. (Table A4, in part.) Given the locality, only two species need to be considered—*T. leucocephalus* and *T. patachonicus*. Therefore the coefficients of interest are the *differences* between those given for these two species; i.e., the coefficient for nail width is 7.418 – 5.926 = 1.492, that for tarsus length is 4.239 – 3.485 = 0.754, that for wing length is 1.493 – 1.761 = –0.268, and the constant term is –395.204 – (–408.367) = 13.163. The score of the specimen is simply the sum of the products of these coefficients with the corresponding measurements; for this specimen the score is (1.492)(14) + (0.754)(63) + (–0.268)(292) + 13.163 = 3.297. Performing similar calculations for the corresponding mean values given in Table 6, the 'standard scores' are –5.494 for male *T. patachonicus* and 5.215 for male *T. leucocephalus*. By comparison of the signs of the scores, it is clear that the specimen is to be classified as *T. leucocephalus*.

Skeletal specimens. Coefficients of classification functions for *complete* skeletons are presented in Table A5 for the eight species-sex groups; because these functions achieve relatively high classification percentages, functions based on separate sex analyses are not presented. Information on locality or simple ratios should be used to exclude from consideration some of the species-sex classes for the skeleton at hand. In addition, the syrinx is preserved in many skeletal specimens of *Tachyeres*, and the presence of an asymmetrically inflated bulla demonstrates unequivocally that the specimen is a male. *Partial* skeletons, those lacking skulls and distal limb elements, can be classified using coefficients given in Table A6.

Table A3. Coefficients for classification functions using external measurements for eight species-sex groups of *Tachyeres*.

	T. patachonicus		*T. leucocephalus*		*T. brachypterus*		*T. pteneres*	
Term	Male	Female	Male	Female	Male	Female	Male	Female
Nail width	6.640	5.972	8.303	7.588	9.937	8.710	13.662	13.050
Tarsus length	3.267	3.013	4.126	3.947	4.488	4.137	4.909	4.533
Wing length	1.920	1.828	1.612	1.581	1.500	1.500	1.342	1.315
Constant	-430.870	-381.512	-414.392	-386.060	-428.514	-398.447	-469.698	-426.871

Table A4. Coefficients for classification functions using external measurements for *Tachyeres* of known sex.

Term	*T. patachonicus*	*T. leucocephalus*	*T. brachypterus*	*T. pteneres*
Males				
Nail width	5.926	7.418	8.881	12.216
Tarsus width	3.485	4.239	4.565	4.948
Wing length	1.761	1.493	1.397	1.261
Constant	-408.367	-395.204	-409.078	-447.730
Females				
Culmen length	4.963	5.562	5.767	5.616
Nail width	3.283	4.703	5.846	10.961
Tarsus length	2.472	3.540	3.759	4.221
Wing length	1.799	1.465	1.355	1.141
Constant	-476.579	-494.759	-504.379	-540.353

Table A5. Coefficients for classification functions using measurements from complete skeletons for eight species-sex groups of *Tachyeres*.

	T. patachonicus		*T. leucocephalus*		*T. brachypterus*		*T. pteneres*	
Term	Male	Female	Male	Female	Male	Female	Male	Female
Humerus length	1.011	0.445	1.179	0.373	2.528	1.552	6.371	5.290
Ulna length	-0.676	0.527	-4.684	-3.533	-7.006	-4.992	-12.586	-10.985
LWM	45.064	40.186	52.843	53.282	39.723	37.872	47.630	40.670
Femur head width	-5.647	-3.032	-3.644	-3.110	-5.640	-3.009	-4.143	-2.661
Tibiotarsus length	-0.012	0.205	1.004	1.034	0.976	0.979	1.938	2.050
Tarsometatarsus length	5.099	4.529	4.805	5.288	6.343	5.478	5.597	4.737
LWM	-56.826	-51.032	-49.567	-42.782	-51.078	-48.691	-46.087	-38.622
Digit-III length	1.868	1.556	2.279	2.030	2.370	2.268	2.530	2.136
Sternum keel length	-1.039	-1.107	-2.212	-2.073	-1.600	-1.740	-1.739	-1.663
Least width	4.343	4.452	4.544	5.015	6.580	6.804	7.570	8.241
Posterior width	0.504	0.159	1.469	1.226	0.448	0.131	0.832	0.375
Coracoid length	2.745	1.646	5.489	3.641	3.807	3.094	4.355	3.621
Basal width	9.569	7.423	12.830	11.249	11.766	9.589	11.359	9.393
Interacetabular width	-0.534	-0.577	-0.007	0.721	-0.043	-0.845	1.182	1.090
Interorbital width	-1.212	-2.119	-2.424	-2.386	-2.748	-3.302	-1.256	-0.484
Postorbital width	6.856	8.074	7.459	9.017	9.871	10.253	6.505	7.954
Antorbital width	-0.603	-1.094	0.073	-2.862	-0.150	-0.938	-0.079	-2.079
Bill height	5.490	2.838	4.911	2.154	5.553	4.431	7.369	5.051
Length	6.458	6.913	6.392	7.010	7.753	8.502	6.778	7.544
Constant	-860.925	-754.260	-1001.131	-916.414	-1068.150	-956.253	-1222.408	-1081.227

Table A6. Coefficients for classification functions using measurements from partial skeletons for eight species-sex groups of *Tachyeres*.

	T. patachonicus		*T. leucocephalus*		*T. brachypterus*		*T. pteneres*	
Term	Male	Female	Male	Female	Male	Female	Male	Female
Humerus head width	4.358	4.143	2.896	3.324	1.831	1.469	1.118	2.324
Femur length	7.055	7.151	7.684	7.702	8.887	8.240	10.350	9.768
Head width	-5.231	-3.828	-3.169	-1.692	-2.818	-0.542	-1.522	-0.277
LWM	-5.135	-3.762	5.782	5.575	-0.066	-2.168	3.371	-0.301
Sternum keel length	-1.675	-1.775	-2.842	-2.764	-1.819	-1.936	-1.758	-1.779
Least width	3.070	3.237	3.017	3.382	4.468	4.909	4.988	5.823
Posterior width	1.179	1.014	1.878	1.829	1.173	1.063	1.274	0.921
Keel depth	5.168	5.193	5.044	4.628	3.748	3.887	2.910	2.727
Coracoid length	4.051	3.305	4.707	3.474	3.119	2.898	2.790	2.285
Basal width	12.128	10.347	14.309	12.891	12.857	10.929	11.967	10.316
Constant	-678.879	-596.675	-802.351	-726.005	-802.952	-697.345	-928.294	-834.136

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