

## THE PATTERNS OF DOWNY GREBES

ROBERT W. STORER

The striking patterns of downy grebes have long been known, but little use of interspecific differences in these patterns has been made in systematic studies. Mayr (1945) demonstrated a considerable difference between the patterns of young of *Tachybaptus ruficollis* and *T. novaehollandiae* and used this as evidence for the specific distinctness of these two forms. Wetmore and Parkes (1954), in discussing the systematic position of the Great Grebe (*Podiceps major*), stated that the young of this species resembled those of other species of *Podiceps* and differed from young of the Western Grebe (*Aechmophorus occidentalis*) in being striped. Recently Niethammer (1964) published a study of the pigmentation and color pattern of downy Great Crested Grebes (*Podiceps cristatus*). In addition, he illustrated and described briefly the patterns of *P. auritus* and *P. nigricollis* and compared these species with the figures of the two species of *Tachybaptus* published by Mayr.

The downy plumages of several species of grebes have not been described, and a comparative study of the downy plumages on a family-wide basis has not hitherto been attempted. I have been fortunate in having examined enough material (more than 150 specimens and all but four of the species or semispecies) to attempt such a comparative study. The aims of this paper are thus to describe the major types of plumage patterns found in young grebes, to discuss their phylogenetic significance, and to point out where further studies and collecting are desirable.

### DESCRIPTION OF SPECIMENS

Some young grebes have a bare patch on the crown, and most have bare patches in the loreal area when hatched. The skin of the crown patch of downy Western Grebes (*Aechmophorus occidentalis*) has been reported to change from orange to scarlet "if the chick is disturbed or irritated" (Nero, in Palmer, 1962:95), a fact which I have been able to verify. A similar color change has been noted (Palmer, 1962:80) in young of the Eared Grebe (*Podiceps nigricollis*) and probably occurs in all grebes having such crown spots. Although the function of this spot is unknown, it may act in stimulating a parent to feed the young. If the degree of excitement of the young, and hence the depth of color of the spot, were related to hunger, the parent might tend to feed the young which had been unfed the longest time. An experimental approach could easily be applied to checking this hypothesis. It is possible that the bare spots on or near the lores change color like the crown spot. The bill and loreal spots are boldly marked in many species.

The pattern of light and dark down on the head varies considerably from species to species, and to a lesser extent among individuals of the same species; not infrequently the patterns on the two sides of the head of the same individual differ. One rule which seems to apply throughout the family is that when light and dark stripes are present on the back and neck, the mid-dorsal stripe is always dark. The most frequent pattern of striping on the neck is that of dark mid-dorsal and mid-ventral stripes separated by three light and two dark stripes on each side. When loss of dark stripes occurs, it is the ventral ones which disappear. The dark mid-ventral neck stripe is often formed by the fusion of a pair of stripes which run anteriorly and medially on the breast; but in some young these stripes do not meet but run forward on the neck leaving a white mid-ventral stripe.

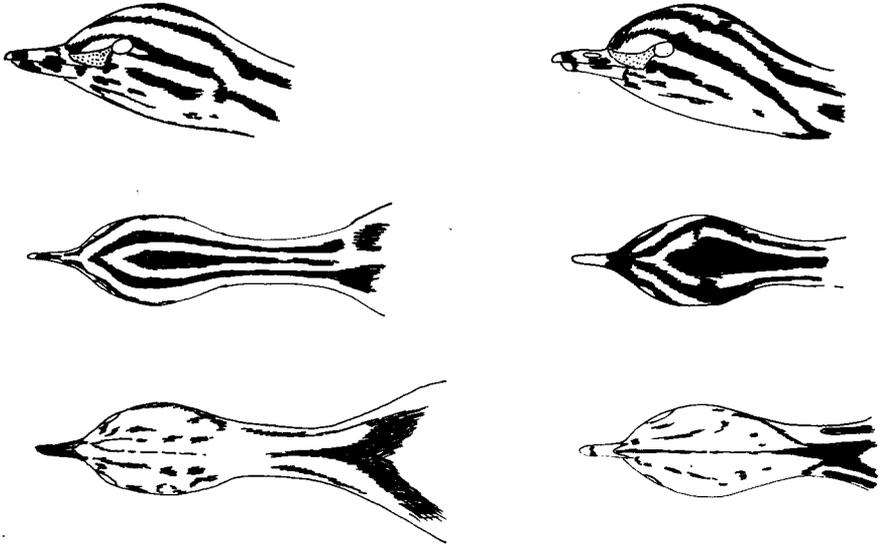


Figure 1. Lateral, dorsal, and ventral aspects (top to bottom) of the head and neck of the downy young of *Rollandia rolland chilensis*. BM 1946.49.71 (left) and *R. r. rolland*. BM 59.7.6.13 (right).

*Rollandia* and "Centropelma." The downy young of *Rollandia rolland chilensis* was described by Dabbene (1916:190) and the young of the nominate race more briefly by Brooks (1917:136). In spite of the abundance and wide distribution of this species in temperate South America, specimens of the downy young are rare in collections. Through the courtesy of J. D. Macdonald of the British Museum, I have had the good fortune to examine one downy young each of *R. r. rolland* and *R. r. chilensis*, and a half-grown young of the former was made available to me through the kindness of R. A. Paynter, Jr., of the Museum of Comparative Zoology at Harvard University.

Dorsally, the partly grown young of *chilensis* is marked with black and light rufous. The mid-dorsal black stripe is broad on the crown, becoming narrow on the neck and tapering to a point on the hind neck (fig. 1). The two dorsolateral black stripes join at the forehead and run posteriorly until they are lost in the complex pattern of the back. It is not possible with the material at hand to determine accurately this back pattern, which appears to be a mixture of longitudinal stripes and chevrons. The smaller young of the nominate race is in general similar to the young of *chilensis* except that a dark bar joins the mid-dorsal crown stripe with the two lateral ones. The larger young of *rolland* has lost nearly all the light markings on the back, but the pattern of the head and neck is much like that of the small young. In the juvenal plumage of *chilensis*, the remains of the striped pattern are confined to the sides of the head and the throat. The downy young of this species appears to be unique among grebes in having neither a bare area nor a well-marked spot of rufous down on the crown.

A young of "*Centropelma*" *micropteron* several days old (75 g) has a pattern most like that of *Rollandia rolland* (fig. 2). The rufous is largely confined to the light longitudinal stripes of the crown. The margins of these stripes are irregular,

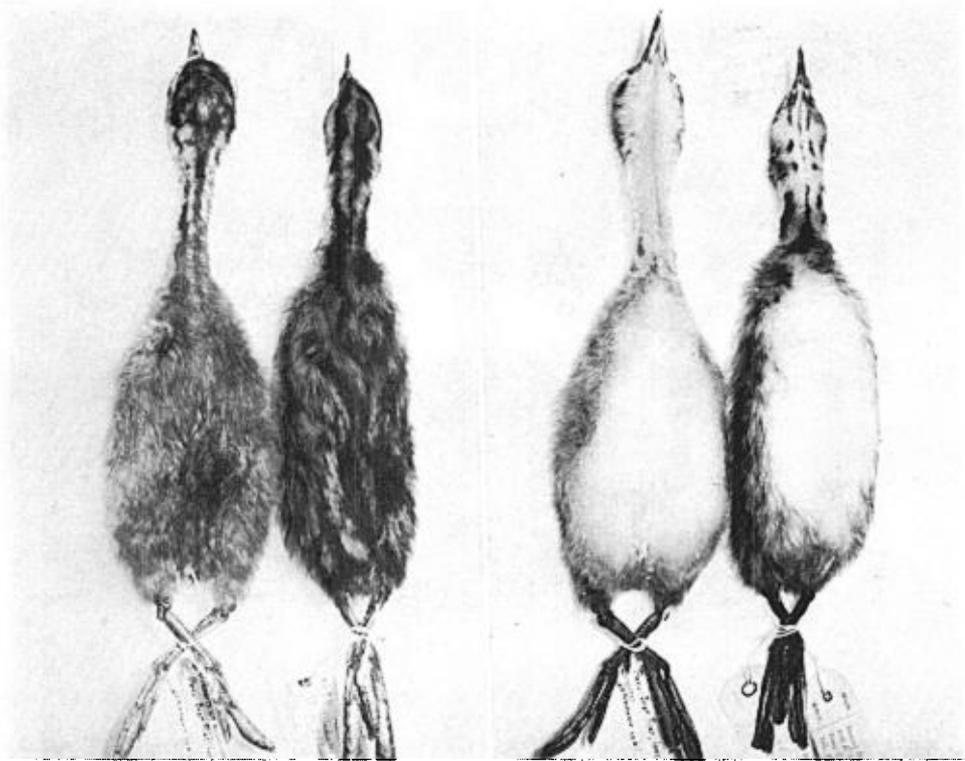


Figure 2. At the left in each pair: the downy young of *Rollandia micropteron* (UMMZ 157,239); at the right in each pair: *R. rolland chilensis* (BM 1946.49.71) from above and from below. Photographs by Joseph R. Jehl, Jr.

and the stripes are broken by dark blotches. The dark mid-dorsal stripe contains a pale, diffuse spot near its anterior end on the crown. The dark dorsolateral neck stripes are broken near the nape, but, like the unbroken mid-dorsal stripe, extend back into the dark of the back, which is brownish gray obscurely marked with grayish white. The pattern of the back is strongest on the posterior half, where there are three blackish longitudinal stripes. A slightly smaller specimen from the collections of the American Museum of Natural History is essentially similar but shows a slightly stronger back pattern in which the light markings are tinged with pale rufous. This suggests that the pattern may be even better defined in newly hatched young. These specimens and three older examples from the American Museum show considerable individual variation in the pattern of rufous and black on the crown. Ventrally, the young of *micropteron* is pale and little marked. The dark ventrolateral neck stripe is broken or reduced to blotches, and the mid-ventral stripe appears as a few pale blotches in a V on the upper part of the breast.

*Podilymbus*. In downy Pied-billed Grebes (*P. podiceps*), the bare crown spot disappears "in a few days" (Palmer, 1962:105), being replaced by down, at least some of which is rufous. The characteristic pattern of young of this species includes one to four rufous patches on the crown and nape (fig. 3). These are the triangular (rarely diamond-shaped) crown patches already mentioned, a nearly transverse bar

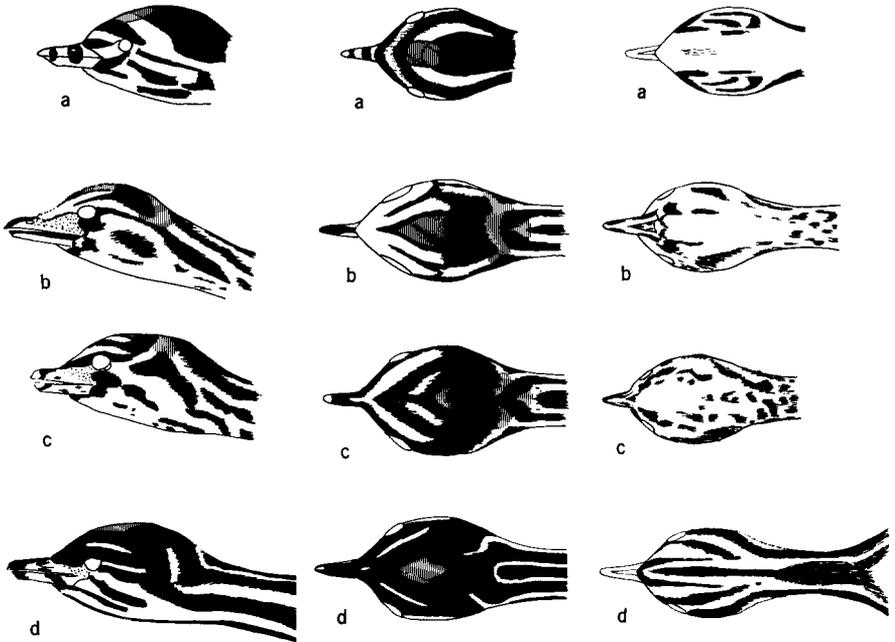


Figure 3. Lateral, dorsal, and ventral aspects (left to right) of the head and neck of the downy young of: a. *Tachybaptus pelzelni* (BM 1931.8.18.3709); b. and c. *Podilymbus podiceps* (UMMZ 72,414 and 84,622); and d. *Podiceps dominicus* (UMMZ 114,970). Vertical hatching indicates extent of rufous down.

on each side of the nape, and a chevron-shaped spot capping the anterior end of the black median neck stripe like an arrowhead. Variations include an almost complete loss of the crown spot, a joining of the lateral bars in the midline and their extension forward toward the eye so that the mark becomes a sprawling M shape, and the chevron-shaped patch being extended forward from its apex to meet the joined transverse bars. The mid-dorsal and dorsolateral black stripes on the neck are present and broad. The ventrolateral stripes are usually broken and the mid-ventral stripe missing. Ventrally on the lower neck and upper part of the breast there is an area of dense black spotting which stops sharply where the white of the belly begins but continues along the sides and flanks. This spotting gradually becomes less densely marked anteriorly. The back is marked with five broad black stripes separated by narrow whitish ones. The middle black stripe is the narrowest and the outermost, the broadest and least well defined, often blending into the dark, mottled sides as the white stripe on its outer margin fades out or becomes broken into blotches. The black and white pattern of the head is complex and variable. Dorsally, a white V forms two superciliary lines which meet at the base of the culmen, and two white lines parallel these superciliaries and lie between them and the crown patch. The latter lines ordinarily do not meet anteriorly although they may join the superciliaries. The pattern of the side of the head consists of four more-or-less broken stripes, as shown in figure 3.

Bowes (1965:15) describes unhatched chicks of the Giant Pied-bill (*P. gigas*) "close to hatching" as being "almost black with 3 or 4 longitudinal stripes of white running down the back, from head to tail. Belly is lighter brown and streaked. Pied

mark is distinct on a stubby whitish bill. Lores are pink." One of these specimens, which she kindly donated to the University of Michigan Museum of Zoology, does not differ significantly from young of *P. podiceps*. Down encroaches on the bare crown spot. Some of the down on the anterior edge of this spot is rufous, as is the down which forms the transverse bars on the nape (in this case nearly meeting at the midline) and the more posterior chevron. The lower neck and upper part of the breast are dark, presumably heavily marked, the rest of the breast and abdomen are white, and the mid-dorsal stripe is black.

*Tachybaptus*. I have examined small downy young of *T. ruficollis* and larger young of *ruficollis*, *novaehollandiae*, and *pelzelni*. The young of *rufolavatus* is apparently unknown. Young of the first three species resemble those of *Podilymbus* in having a rufous crown patch. The young of *ruficollis* and *novaehollandiae* have a patch of long, silvery white, hairlike down on the forehead. This is most conspicuous in the very small young, in which the rufous crown patch may be small or absent, and it becomes less noticeable as the young grow and the crown patch becomes better developed. Mayr's figures (1945:232) clearly show the differences in the patterns of the head and neck between *ruficollis* and *novaehollandiae*. Figure 3 shows the head pattern in a half-grown young of *T. pelzelni*. (The down of the neck of this specimen is soiled and matted so that the neck pattern could not be discerned.)

As Mayr (1945:233) has pointed out, the small young of *T. r. ruficollis* are very dark, black above with light rufous stripes on the back. In older young, the back is lighter and the stripes are more diffuse. The most dorsal pair of light stripes converge and run together for a short distance near the anterior end of the body, diverging again at the base of the neck. I was not able to determine if this is also true of young of *novaehollandiae* and *pelzelni*. Young of the latter differ conspicuously from those of *ruficollis* in having pure white stripes on the back and more white on the face and throat, as well as in the pattern of the crown.

"*Podiceps*" *dominicus*. The downy young of this species appear most like those of *Tachybaptus ruficollis* and *Podilymbus* but differ from the former chiefly in lacking rufous in the light stripes on the back and in details of the striping on the sides of the head and the throat and from the latter in lacking spotting on the lower neck and sides and in having but one rufous patch on the crown.

The pattern of *dominicus* is shown in figure 3. There is a median crown patch of rufous, varying in shape from triangular through diamond-shaped to roughly trident-shaped. Anterior to it or connected with it is a small white spot. The dark mid-ventral stripe starts at the chin and runs posteriorly, becoming wider on the neck and dividing near the upper part of the breast to continue along the sides and flanks. In the juvenal plumage, the median stripe on the throat and neck is lost, but the gray on the chest, sides, and flanks remains. The light stripes on the back and sides are narrow and white like those of *Podilymbus*. Four pairs of these are usually present, and a fifth can be seen on some individuals. These stripes disappear before the juvenal feathers come in, as do all but the anterior parts of the white neck stripes. A remnant of the rufous crown patch can also be seen in at least some juveniles, while the bold pattern on the sides of the head is fully retained.

"*Podiceps*" *poliocephalus* and "*P.*" *rufopectus*. The only description of the downy young of *poliocephalus* which I have found is that given by McGilp (1923:239), who says: "The young are dusky brown, covered with down with a few grey spots here and there." The young of *rufopectus* is described and figured by Oliver (1955:91-92), but even this description is not sufficiently detailed for a good comparison with

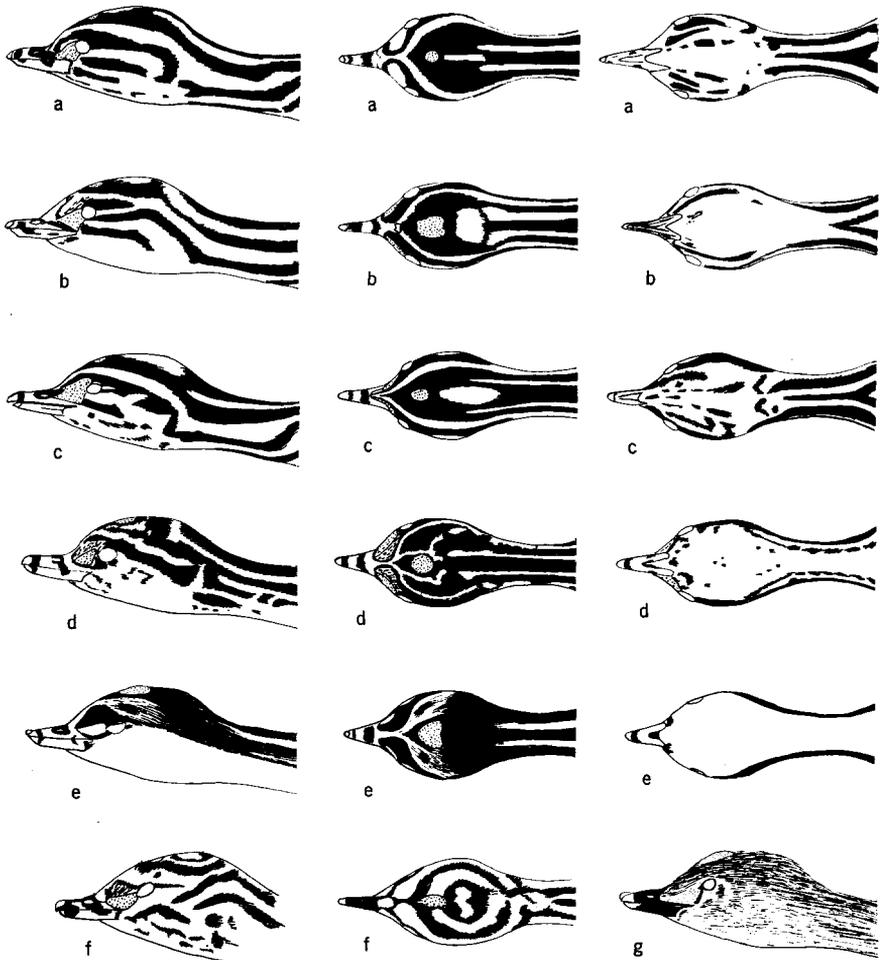


Figure 4. Lateral, dorsal, and ventral aspects (left to right) of the head and neck of the downy young of: a. *Podiceps grisegena holboellii* (UMMZ 108,007); b. *P. cristatus infuscatus* (UMMZ 156,910); c. *P. auritus cornutus* (UMMZ 154,528); d. *P. nigricollis californicus* (UMMZ field no. 4728); e. *P. o. occipitalis* (UMMZ, embryo nearly ready to hatch); f. *P. major* (left BM 92.2.10.324; center BM 92.2.10.322); and g. *Aechmophorus o. occidentalis* (UMMZ field no. 4709). The bare crown spot is stippled.

the species that I have examined, and the figure, a side view of the head, does not show the pattern of the crown and neck. Oliver's mention of rufous on the crown suggests similarity with young of *Podilymbus*, *Tachybaptus*, and "*Podiceps*" *dominicus*.

*Podiceps (sensu stricto)*. As I have pointed out earlier (1963a:563), the nucleus of the genus *Podiceps* consists of six closely related species: *grisegena*, *cristatus*, *auritus*, *nigricollis*, *occipitalis*, and *taczanowskii*. I have examined small young of all but the last and have found that their patterns are basically similar. On the other hand, young of these five species differ from each other, largely in the accentuation or loss of parts of the basic pattern.

The patterns of the young of these five species are shown in figure 4. The bare

crown spot is conspicuous in all, and it is even quite evident in a young *grisegena* weighing 114 g and in a half-grown young of *cristatus*. The basic pattern on the body consists of nine dark stripes on the back and sides. Of these, the central one is the narrowest. The most lateral (and ventral) one on each side may be broken up into spots or blotches, and the next two on each side may be broken by irregular, transverse bars of white. The breast and belly are white. The young of *grisegena* tend to have the stripes on the flanks broken up into many spots; this tendency is found to a lesser degree in young of *auritus*. In *grisegena* and *cristatus* the light stripes on the back are washed with pale brownish whereas they are nearly white in the three smaller species. These stripes gradually become obliterated as the birds grow. The young of *nigricollis* and *occipitalis* have the narrowest light stripes on the back and the most solidly black flanks. This pattern, with the reduction of white markings on the head and black markings on the throat and underpart of the neck, makes the young of these species appear nearly black above and white below in contrast to the more striped appearance of those of the other three species.

The basic pattern of the neck consists of seven dark stripes, one mid-dorsal and three pairs of lateral stripes. The most ventral pair of lateral stripes is the most variable: they may fuse into a single mid-ventral stripe anteriorly (fig. 4a and c), they may meet in a V (fig. 4b), they may be joined by a crossbar, or they may not meet (fig. 4d). The young of *grisegena*, *cristatus*, and *auritus* vary considerably in this character; those of *nigricollis* and *occipitalis* show no fusion of these stripes, although in a few examples of the former there may be an additional short, thin stripe on the midsection of the neck. The young of *nigricollis* also differ from those of related species in frequently having the lateral and ventrolateral neck stripes broken up into spots or blotches.

The crown pattern of *grisegena*, *cristatus*, and *auritus* is characterized by a central white stripe or spot behind the bare crown spot. This lies between or anterior to the ends of the white neck stripes which form the borders of the dark mid-dorsal stripe. The next lateral white stripes on the neck run forward, diverging as they reach the crown and then converging to join on the forehead. The central white patch on the crown is narrowest in *grisegena* and broadest in *cristatus*. In addition to lacking this patch, young of *nigricollis* and *occipitalis* differ from those of their close relatives in having two white stripes on each side of the crown. The more median of the two appears to be an isolated segment of the most dorsal pair of white neck stripes and fuses with the more lateral stripe above or anterior to the eye. There is considerable variation in this pattern in young of *nigricollis*. For example, the two lateral crown stripes on each side may fuse to form a V, the apex of which does not extend forward to meet its fellow on the midline. The extent of striping on the nape, neck, and back is also variable, the stripes being almost completely lost in some individuals. In several unhatched young of *occipitalis*, the two crown stripes on each side are broadly and diffusely joined, and all connection with the light neck stripes is lost.

The complex patterns on the sides of the head are shown in figure 4. The dark stripe, more or less broken, which reaches forward to and above the eye, is evidently a forward extension of the mid-lateral neck stripe. One or more rows of streaks and spots may represent extensions of the lowest pair of lateral neck stripes. Of all the complex patterning of the downy young, only that on the head may be carried into the juvenal plumage. Juveniles of the two larger species, *grisegena* and *cristatus*, retain much of this streaking, *auritus* considerably less, and *nigricollis* none. In young

of *occipitalis* (and probably *taczanowskii*) there is no streaking on the cheeks and throat.

A one-third to one-half-grown young of *taczanowskii* in the collections of the American Museum of Natural History is covered with medium-gray down above and white down below in much the same pattern as that of the adult. The bare crown patch has been greatly reduced. The crown is blackish with the remains of white forehead and crown stripes like those of *nigricollis* or *occipitalis*. Neither this bird nor two full-grown juveniles show any indication of facial stripes. The small downy young of this species has not been described. But, because the juvenal and adult plumages of this species closely resemble those of *P. o. occipitalis*, the downy young of the two species will probably also prove similar.

*Podiceps major*. Scott and Sharpe (1904:76) give a brief description of the downy young of this species, mentioning the bare crown patch, the black and white striping of the neck and back, and the presence of a distinct pattern on the crown and sides of the head. They depict a bird in juvenal plumage, showing remnants of the pattern of the downy young on the head. Their description was based on specimens in the British Museum, evidently the same which I have examined.

The downy young of *P. major* are the most boldly patterned of all grebes. The back is marked with seven longitudinal black stripes, separated by white stripes, which are broader than those of *Podiceps (sensu stricto)*. The most ventral stripe on each side is broken into blotches, and there are blackish blotches on the posterior part of the belly. The dark stripes on the neck consist of two pairs of lateral ones, a ventral one formed by the fusion of two lateral ones, and a dorsal one which ends before it reaches the nape or divides into two branches which merge with the first lateral stripes. There is a bull's-eye pattern on the crown, which, however, does not center on the bare spot but posterior to it. The sides of the head are complexly marked, as shown in figure 4.

*Aechmophorus occidentalis*. The supposed lack of pattern on young of the Western Grebe has frequently been mentioned. For example, Bent (1919:6) states: "The downy young of the western grebe is entirely different from the young of any other American grebe; its plain, unspotted coat suggests a closer relationship with the loons than with the other grebes." And Wetmore and Parkes (1954:127) write that the downy young of this species are "a uniform gray, completely unlike any other grebe." This is not strictly true. The difference between the gray of the back and the white of the belly is mentioned by Bent (*loc. cit.*) and by Palmer (1962:95). But the facts that the extent of the white on the underparts is similar to that in young of the Red-necked Grebe and several other species and that the bare spot on the crown is similar to that in many species of *Podiceps* have not been emphasized. Most remarkable is the presence of a very faint but clearly demonstrable pattern on the head of downy Western Grebes. A large area surrounding the bare spot on the crown and extending forward nearly to the base of the bill is dark, as is a broad band extending posteriorly from the gape. Below this there is another dark band, which turns dorsad and borders a pale cheek patch. A dark vertical bar extends from the nape partway down the side of the neck. A broad pale patch surrounds the eye and extends forward above the bare lores to the base of the bill. This pattern is shown, somewhat exaggerated in contrast, in figure 4g. This pattern can be seen in skins of young, but is more easily studied in young preserved in formalin or alcohol.

## DISCUSSION

Evidence from the pattern of the downy young supports several conclusions which I drew earlier (1963a) regarding the phylogeny of the grebes. The close relationship of the six species of the genus *Podiceps* which perform Discovery Ceremonies (*griseogena*, *cristatus*, *auritus*, *nigricollis*, *occipitalis*, and *taczanowskii*) is borne out by the basic similarity of their downy young. The pattern of the young of *occipitalis* is the simplest known within the genus. What pattern there is resembles that of young *nigricollis*. This similarity supports the conclusions based on behavioral, ecological, and morphological evidence that *occipitalis* and its very recent offshoot, *taczanowskii*, are geographical representatives of *nigricollis*.

Downy young of *major* and *occidentalis* resemble those of the above six species of *Podiceps* and of no other grebes in having a bare crown patch. Aside from this, the downy young of *major* bear little resemblance to those of *Aechmophorus occidentalis*, as mentioned by Wetmore and Parkes (1954:127). On the other hand, the young of *major* differ in several respects (the bull's-eye pattern of the crown, the pattern on the sides of the head, and the seven versus nine stripes on the body) from those of *Podiceps* (*sensu stricto*). This supports my conclusions (1963b:288), based on behavioral evidence, that *major* "may be more closely related to the large species of *Podiceps* than to *Aechmophorus* but it is not very close to either." At present it seems best to place *major* in *Podiceps* with the understanding that, should that genus be subdivided, *major* would be separated from the core species. The near obliteration of pattern in young of *occidentalis* is unique among grebes and supports the conclusion that the genus *Aechmophorus* should be maintained for this species.

The downy young of *rolland* are quite distinct in their pattern but resemble those of *micropteryx* more closely than those of any other species. This is in accord with maintaining the genus *Rollandia* for these species (Storer, 1963a).

The remaining species all have rufous down in one or more patches on the crown. This supports the view that the dabchicks (*Tachybaptus*) are closer to the pied-bills (*Podilymbus*) than to the core species of *Podiceps*. The young of *dominicus*, *rufopectus*, and *poliocephalus* appear more like those of *Tachybaptus* and *Podilymbus* than those of *Podiceps* (*sensu stricto*). This finding suggests that they do not belong in *Podiceps*, but more behavioral and morphological data are needed before their proper generic allocation can be made.

Apart from the purely phylogenetic aspect of this subject, there are several matters that merit further investigation. In at least some species there is considerable individual variation in the patterns of the young. The significance of this variation remains to be studied, as does the significance of differences between the patterns of young of such closely related sympatric species as *Tachybaptus ruficollis* and *T. novaehollandiae* in the East Indies, *T. ruficollis*, *T. rufolavatus*, and *T. pelzelni* on Madagascar, and the large species of *Podiceps* in the Northern Hemisphere. The adaptive value of the reduction or near loss of pattern in young of *Aechmophorus occidentalis*, *Podiceps occipitalis*, and probably *P. taczanowskii* is not clear but may be associated with these birds spending much time on large, open bodies of water. Yet, paradoxically, the most boldly marked young of all grebes are those of *Podiceps major*, which also frequent large lakes. Perhaps most interesting of all would be investigations of the significance of the various parts of the pattern in the parent-young relationships.

## SUMMARY

The patterns of downy young grebes may be divided into three groups: those with a bare crown spot, those with one or more rufous patches of down on the top of the head, and those in which the crown is striped with black and rufous buff. The first group contains eight species, which are best placed in two genera, *Podiceps* (seven species) and *Aechmophorus* (monotypic). The third group consists of two species, *rolland* and *micropterum*, which are placed in the genus *Rollandia*. The remaining species belong in the second group, which consists of the genera *Podilymbus* (two species) and *Tachybaptus* (three or four species), plus three species, *dominicus*, *rufopectus*, and (presumably) *poliocephalus*, whose relationships are not clear.

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*Museum of Zoology, University of Michigan, Ann Arbor, Michigan 48104, 4 October 1966.*