

The Relationships of the Seed-snipe (Thinocoridae) as Indicated by Their Egg White Proteins and Hemoglobins

By CHARLES G. SIBLEY, KENDALL W. CORBIN, and JON E. AHLQUIST

Department of Biology and Peabody Museum of Natural History, Yale University,
New Haven, Connecticut, USA

Introduction

The seed-snipe are small to medium-sized ground-dwelling, seed-eating birds with long, pointed wings, short tails and legs, and a stout, conical or fowl-like bill. The plumage tends to be cryptically colored above, as in many ground-dwelling birds, with white, gray, or rufous underparts. Two species have black markings on the throat.

The two genera, *Thinocorus* (Escholtz, 1829) and *Attagis* Geoffroy Saint-Hilaire and Lesson (1830), each contain two species: *T. orbignyianus* and *rumicivorus*, *A. gayi* and *malouinus*.

The diagnostic characters of this group are as follows (modified from Sibley, 1955):

1. Palate aegithognathous (Sharpe, 1896, called it schizognathous and Gadow, 1893, "incompletely aegithognathous".)
2. Nares pseudo-holorhinal; impervious.
3. Basisphenoidal rostrum thick and long.
4. Vomer broad and fused posteriorly.
5. No basipterygoid processes or occipital fontanelles.
6. Supraorbital glands present.
7. Lacrimals reduced, partially free (Lowe, 1931 b).
8. Hallux present.
9. Flexor tendons of Type 1.
10. Syrinx tracheobronchial.
11. A crop, strong gizzard, and long caeca present.
12. Oil gland feathered.
13. Apterium with thick black down.
14. Nostrils covered by an operculum.
15. Muscle formula ABXY +.
16. Coracoids not overlapping.

The four species of seed-snipe occur from Ecuador to Chile and Argentina and in Tierra del Fuego. The type of *Attagis malouinus* came from the Falkland Islands, but the species is apparently only a straggler there. Most of the populations of seed-snipe occur in the high Andes or at lower elevations near the southern tip of the continent, but some races of *Thinocorus rumicivorus* live in the arid coastal lowlands of south-western Ecuador, Peru, and northern Chile.

Accounts of the habits of the seed-snipe have been published by Sclater and Hudson (1889), Lane (1897), Crawshaw (1907), Wetmore (1926), Hellmayr (1932), Goodall (1964), and Johnson (1965). Dr. Gordon Maclean (pers. comm.) has recently completed a field study of the group.

Seed-snipe were first described in 1783 by Boddaert who named the species *Tetrao malouinus*. Lesson (1831) placed the thinocorids and *Chionis* in the same family which he thought was related to the gallinaceous birds. The superficial resemblance to gallinaceous birds influenced a number of subsequent workers. When the pterylography of *Thinocorus rumicivorus* was studied (Nitzsch and Burmeister, 1840; English translation by Sclater, 1867), Nitzsch was inclined to place *Thinocorus* near the Alektorides, a diverse assemblage composed of *Palamedea* (= *Anhima*), *Otis*, *Dicholophus* (= *Cariama*), *Psophia*, and *Grus*. In completing and editing the work after Nitzsch's death, Burmeister found that the pterylosis of *Thinocorus* was most like that of *Glareola* and *Tachydromus* (= *Stiltia isabella*) and differed only in minor ways from that of *Charadrius*. On the basis of external morphology Gray (1849) concluded that the Thinocoridae have gallinaceous affinities and are most closely allied to the sheath-bills (*Chionis*), which he also placed with the galliform birds. His arrangement was as follows:

Order Gallinae

Family Cracidae

Family Megapodidae

Family Phasianidae

Family Tetraonidae

Family Chionididae

Subfamily Thinocorinae

Subfamily Chionidinae

Family Tinamidae

Bonaparte (1853) followed a similar scheme, but placed the Thinocoridae in a separate family next to the Pteroclididae. In Lilljeborg's (1866) system the seed-snipe, sand-grouse, and sheath-bills were united in a single family Pteroclididae which was placed in an order Gallinae like that of Gray. From a study of osteology Eyton (1867) suggested the following sequence:

Order Littores

Family Otidae

Subfamily Otinae

Subfamily Tinaminae

Family Chionidae

Subfamily Chioninae

Subfamily Thinocorinae

Family Charadriidae

Carus (1868) also believed that the seed-snipe were related to the shore-birds and placed *Thinocorus* in the Chionidae of his order Grallae, which

contained both charadriiform and gruiform groups. The classification of Sundevall (1872) was like that of Lilljeborg, but Sclater and Salvin (1873) preferred to recognize the *Thinocoridae* as a family in their order *Limicolae* along with the *Oedicnemidae* (= *Burhinidae*), *Parridae* (= *Jacanidae*), *Charadriidae*, *Chionididae*, and *Scolopacidae*. Sclater (1880) also followed this arrangement.

Garrod (1877) made a thorough anatomical study of *Thinocorus* and *Attagis*. He confirmed that their pterylosis was most like that of shorebirds and pointed out several differences between thinocorids and the *Turnicidae*. In his opinion the closest allies of seed-snipe are *Cursorius* and *Glareola*. As evidence for this he cited the following:

1. Absence of a pterygoid articulation to the basisphenoid rostrum.
2. Absence of supra-occipital foramina.
3. Similarity of palatal structure.
4. Similarity of myology.

Parker (1878) on the other hand enumerated similarities between the thinocorids and turnicids. He was inclined to place them near the *Geranomorphae* (= Wetmore's *Gruiformes*).

Reichenow (1882) proposed a suborder *Deserticolae* to contain the *Thinocoridae*, *Turnicidae*, and *Pteroclididae*. He thought that the nearest relatives of this group were the *Calamocoelae* (= *Rallidae*, *Eurypygidae*), *Arvicolae* (= *Otididae*, *Gruidae*), and *Limicolae*. Stejneger (1885) united the *Thinocoridae* and *Chionididae* in a superfamily closest to several other shorebird groups.

Fürbringer (1888; p. 1224—1225; 1902) reviewed in detail the taxonomic allocations of the *Thinocoridae* and concluded that they belonged in the shorebird assemblage. He proposed the following sequence:

Order Charadriornithes

Suborder Charadriiformes

Gens sensu lato Laro-Limicolae

Gens sensu stricto Charadrii

Family Charadriidae

Family Glareolidae

Family Dromadidae

Family Chionididae

Family Laridae

Family Alcidae

Family Thinocoridae

Gens sensu lato Parrae

Family Parridae

Gens sensu lato Otides

Family Oedictnemidae

Family Otidae

From a study of osteology Seebohm (1888: 431) suggested that "*Dromas* and *Chionis* might be regarded as Gaviae [gulls], and *Glareola*, *Cursorius*, *Pluvianus*, and *Oedictnemus* as Limicolae, whilst *Thinocorus* might be regarded as an archaic survivor of the common ancestors of both..." Seebohm (1890) recognized the family Cursoriidae with subfamilies Cursoriinae, Chionidinae, and Thinocorinae. Sharpe (1891) included the same groups in his Charadriiformes as did Fürbringer but split his suborder Attagides into the families Thinocoridae and Attagidae.

Gadow (1892, 1893) used 40 characters from geographic distribution, biology, myology, osteology, and internal and external anatomy as an index to relationships among avian groups. He defined the Thinocoridae as Neotropical Charadriiformes, with schizorhinal (tending to holorhinal) nares; with no basipterygoid processes; phytophagous, with a globular crop. His arrangement of the order is as follows:

Order Charadriiformes

Suborder Limicolae

Family Charadriidae

Family Chionididae

Family Glareolidae

Family Thinocoridae

Family Oedictnemidae

Family Parridae

Suborder Lari

Family Laridae

Family Alcidae

Suborder Pterocles

Suborder Columbae

Mitchell (1901) found essentially the same configuration of the intestinal tract in *Thinocorus* as in *Glareola* and the Charadriidae. Mitchell (1905) also compared the myology of the families of Gadow's Limicolae and noted that *Thinocorus* differed in no important ways from the others. Although Shufeldt (1903) placed the seed-snipe beside the Chionididae and Glareolidae in the suborder Cursorae of his Charadriiformes, he mentions no details on thinocorids, and from his analysis of characters of the Limicolae it seems clear that he did not examine this group.

Mathews and Iredale (1921) were impressed by the general similarity of the *Thinocoridae* to game birds and placed them in their order Galli. Without explanation they state (p. 217), "The internal characters cited in favour of a Charadriiform alliance were obviously misunderstood."

Lowe (1922) provisionally excluded the *Thinocoridae* from his Charadriiformes and later (1923: 277) thought "that they together with the families *Turnicidae* and *Pteroclididae*, should be regarded as the still-surviving blind-alley offshoots of an ancient generalised and basal group (now extinct), from which group sprang the Schizomorphs or the now dominant Plovers, Pigeons, and Fowls." The structure of the quadrate convinced Lowe (1926) that the seed-snipe are charadriiform rather than galliform. He (1931a) included them in his suborder Laro-Limicolae along with the *Glareolidae*, *Chionididae*, *Dromadidae*, and *Laridae*, but then (1931b) changed his opinion. He interpreted the color pattern of the downy young, pterylosis, and myology to be more limicoline than gruine. However, he listed (p. 731) several points in their osteology which are "far from typically limicoline", and chose to erect a separate order, the Grui-Limicolae between his Grues and Limicolae, for them. In his opinion (p. 716) they "do not seem to have a single larine character."

Low (1931) placed the *Thinocoridae* in his suborder Lari-Limicolae beside the *Dromadidae*, *Glareolidae*, and *Chionididae*, but Stresemann (1927—1934) was not convinced of any proposed alliance and maintained ordinal status for the group. Most later authors gave the seed-snipe superfamilial rank within the Charadriiformes (Peters, 1934; Hellmayr and Conover, 1948; Wetmore, 1930, 1951, 1960; Storer, 1960) or at least placed them in a separate family (Berlioz, 1950; Mayr and Amadon, 1951). Judin (1965) included the *Thinocoridae* and *Chionididae* in his superfamily Chionidoidea.

Glenny (1948, 1952, 1955) described the arrangement of carotid arteries in thinocorids. Like other Charadriiformes the carotids are A—1, coracoid ligamentum botalli, is present. A common root from the common carotid artery Type A, and thoracic artery Type 1. The ligamentum aortae, but no ligamentum botalli, is present. A common root from the common carotid may be shared by the superficial cervicals and vertebrales. In *Thinocorus*, but apparently not in *Attagis*, an accessory esophageal artery arises from the base of the superficial cervical.

Hanke and Niethammer (1955) compared the structure of the esophagus of *Thinocorus orbignyianus* to that of *Pterocles* and several shorebirds. Their results agreed with the inclusion of the seed-snipe in the Charadriiformes.

Verheyen (1958) concluded from a study of osteology that the *Thinocoridae* are New World representatives of the *Pterocletes*. He placed both groups in his order Turniciformes with the *Turnicidae* and *Mesoenatidae* but later (1961) changed his opinion and included them in his Columbiiformes.

Stresemann (1959) again emphasized the lack of convincing evidence for their affinities by keeping the seed-snipe in a separate order. Subsequently the Stresemanns (1966: 212) found that the molt of the *Thinocoridae* begins in an ascending fashion with primary 10, but after the eighth or seventh primary is lost, an inner one may be dropped out, and the replacement proceeds irregularly. Although this pattern differs from that of other shorebirds, in which the molt is regularly ascending, other aspects of molt, the form of the wing, and the number of secondaries and rectrices are the same. The Stresemanns hold the opinion (p. 222) that the *Thinocoridae* seem to be closely allied to the *Charadriidae* and *Scolopacidae*.

Four groups, representing four orders in Wetmore's (1960) system, have been proposed as the nearest relatives of the seed-snipe. A possible alliance to the *Charadriiformes*, especially to the *Chionididae*, stems as much from repetition of Lesson's (1831) and Gray's (1849) classifications as it does from sound anatomical evidence. The *Tetraonidae* of the *Galliformes*, *Turnicidae* of the *Gruiformes*, and *Pteroclididae* of the *Columbiformes* were thought to be related to seed-snipe because they share adaptations to an open terrestrial environment (foot structure, cryptic coloration) and phytophagous habits (shape of bill, possession of large caeca). The *Thinocoridae* may be related to one or more of these groups or to some other avian group. One cannot choose among these alternatives because the evidence is conflicting and the probability of convergence is high.

To obtain new data relevant to this problem we have compared the starch-gel electrophoretic patterns of the egg white proteins and hemoglobins of seed-snipe to those of several possibly related groups. The rationale behind using the characteristics of protein molecules in systematics is well documented (Sibley, 1960, 1962, 1964, 1965, 1967, in press; Sibley and Ahlquist, in press; Zuckerkandl and Pauling, 1965a, b; Fitch and Margoliash, 1967).

Methods and Materials

Egg white was collected from unincubated eggs and stored at 4° C. Prior to electrophoresis each sample was diluted 1:6 (v/v) with starch-gel buffer.

Blood was collected using 10% (w/v) ethylenediamine tetraacetate disodium salt (EDTA) as an anticoagulant. To separate the erythrocytes from the plasma, whole blood was centrifuged at 1000 rpm for five minutes. The plasma was decanted, and the red cells were suspended in 1% (w/v) NaCl and centrifuged. After five repetitions of the washing procedure the cells were lysed in two times their volume of distilled water. Following centrifugation at 4000 rpm to remove cellular debris, the supernatant containing the hemoglobin was decanted, saturated with carbon monoxide,

frozen, and stored at -75°C . Prior to electrophoresis a small sample was thawed and diluted with starch-gel buffer.

Starch-gel electrophoresis (Smithies, 1955, 1959a, b) with a discontinuous buffer system (Poulik, 1957), modified according to Sibley, Corbin, and Haavie (in press), was used. The starch buffer was composed of 0.046 M Tris(hydroxymethyl)aminomethane, 0.007 M citric acid, 0.005 M lithium hydroxide, and 0.019 M boric acid at pH 7.95. The bridge buffer consisted of 0.05 M lithium hydroxide and 0.19 M boric acid, pH 7.98. Electrophoresis was effected by a constant current of 35 ma (hence voltage varied from 400—600 V) until a bromphenol blue dye marker moved 8 cm from the application slot (about 4—5 hours). The gel was removed, sliced, and stained for total protein with amido black 10 B. Gels were destained by successive washings with 2.5 % (v/v) acetic acid and photographed.

Results

The interpretation of electrophoretic patterns is discussed elsewhere (Sibley, in press; Sibley and Ahlquist, in press).

The principal components of an egg white pattern of a non-passerine bird are diagrammed in Figure 1. Figure 2 shows the egg white patterns

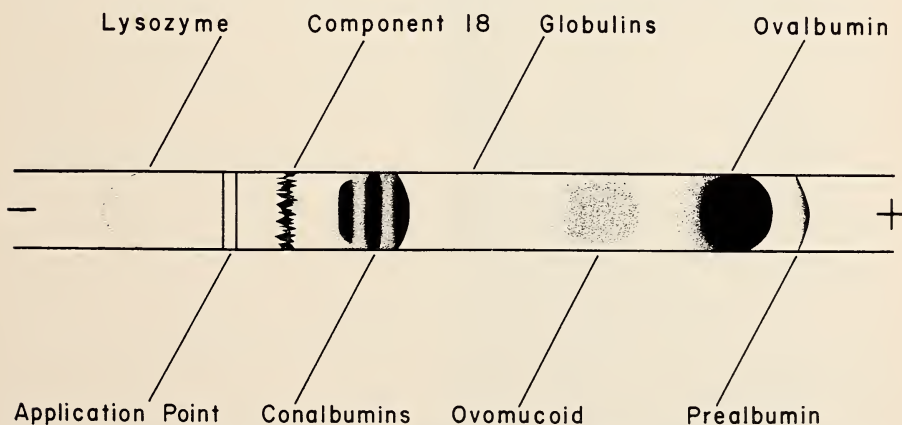


Figure 1. Diagram of the starch-gel electrophoretic pattern of the egg white proteins of a non-passerine bird. The (+) indicates the anodal direction; the (—) the cathodal direction.

of *Thinocorus orbignyianus* and *Attagis gayi* along with 13 other genera representing 11 of the families recognized by Wetmore (1960). The patterns of *Thinocorus* and *Attagis* have ovalbumins of identical mobilities and differ but slightly in the mobilities of the ovomucoids. *Attagis* has two of its three

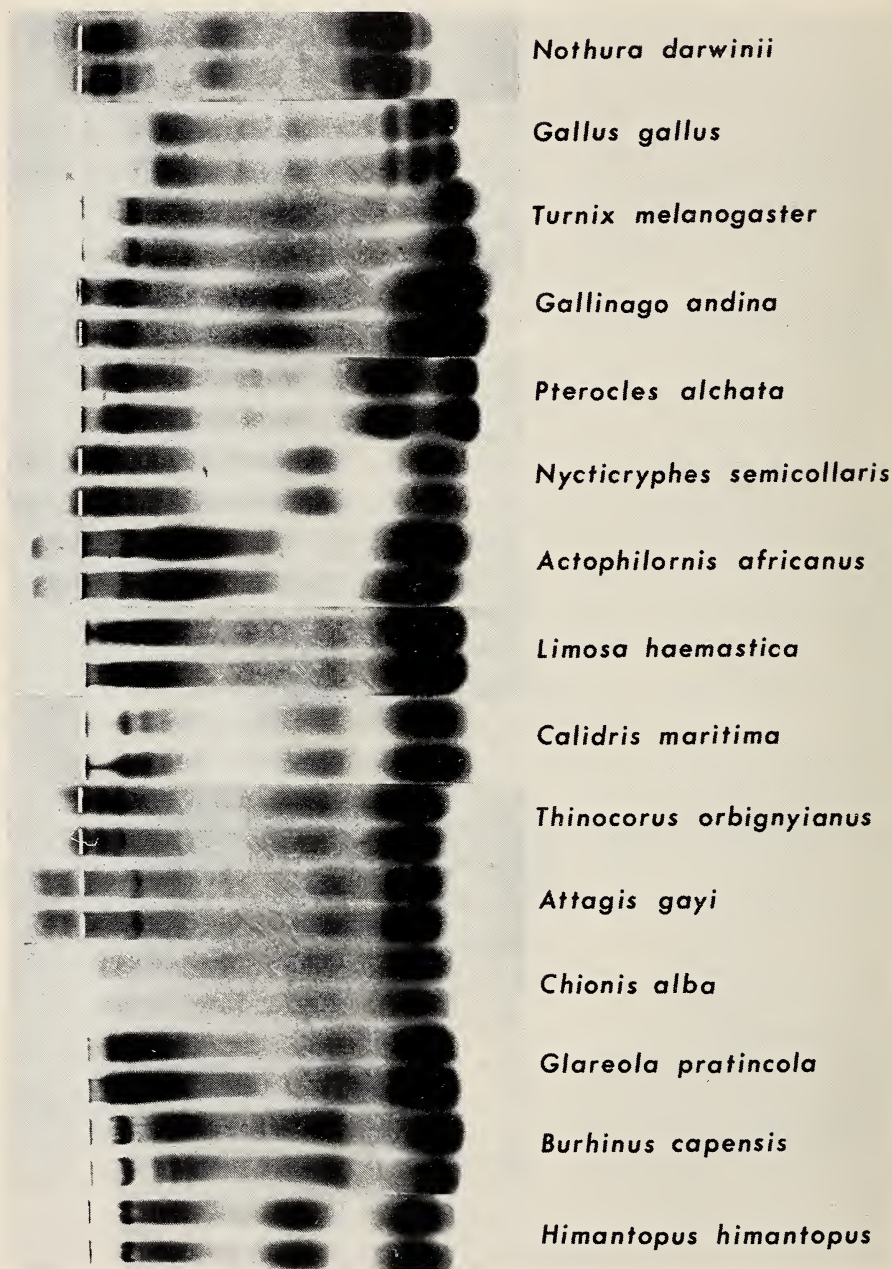


Figure 2. Starch-gel electrophoretic patterns of the egg white proteins of some species of *Thinocoridae* and groups proposed as allies.

conalbumin bands migrating cathodally; only one conalbumin band does so in *Thinocorus*. This presumably represents an insignificant difference since the conalbumins are close to their iso-electric points.

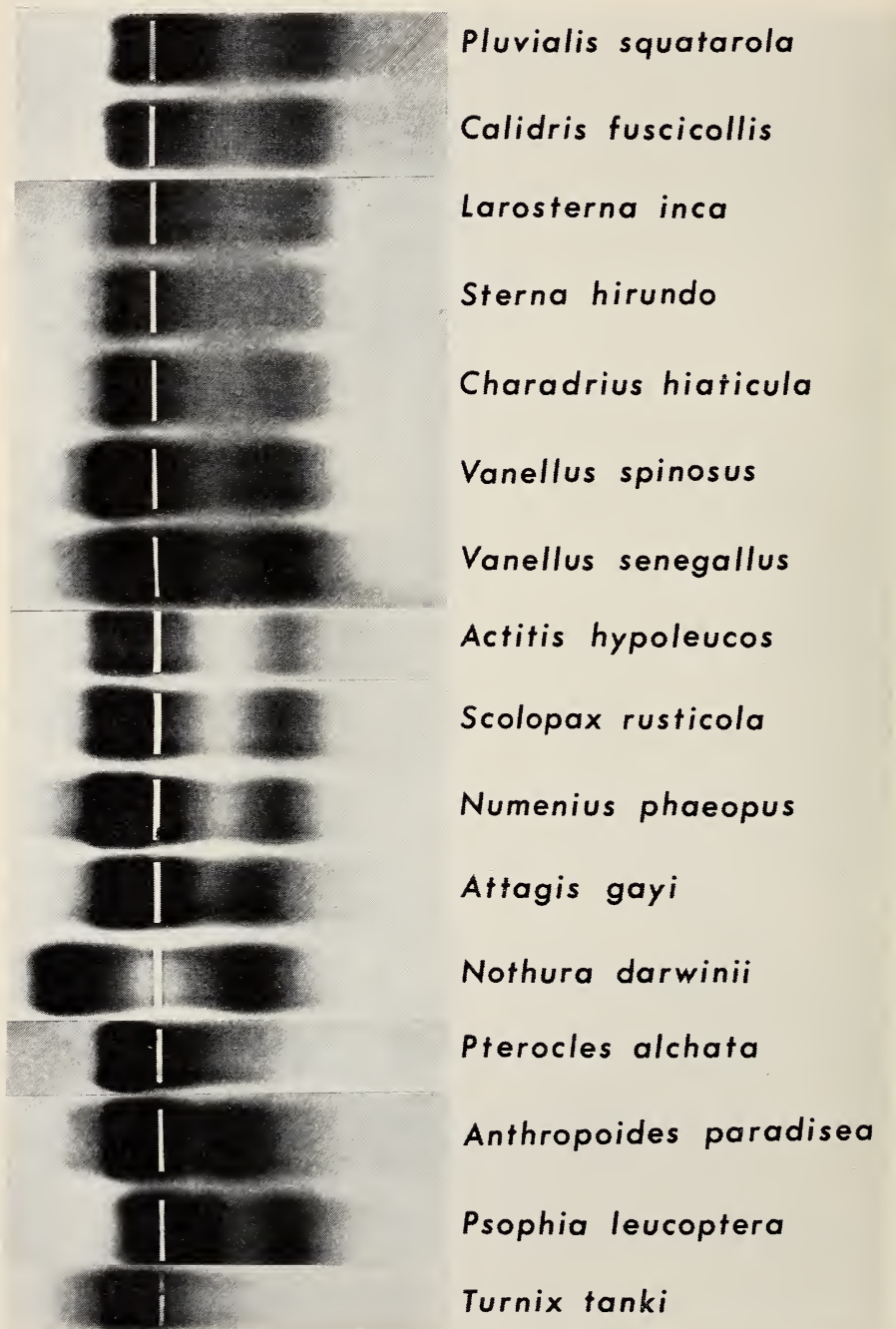
The pattern of *Gallus* with three ovalbumin components, a small ovomucoid fraction, and conalbumins of faster mobilities is unlike those of the seed-snipe. The pattern of *Turnix* differs from those of the thinocorids in having conalbumins which migrate ahead of Component 18, a broad diffuse ovomucoid in the middle region of the pattern, and an almost circular ovalbumin of higher relative mobility. In the distinctive pattern of the sand-grouse (*Pterocles*) the ovalbumin has a higher mobility than that of the seed-snipe, and immediately cathodal to it is a broader band of ovomucoid.

The patterns most similar to those of *Thinocorus* and *Attagis* in the number, arrangement, and mobility of components are those of the Charadriiformes. The pattern of *Thinocorus* is a good match for those of *Chionis* and *Glareola* and differs but slightly from that of *Calidris maritima*. The patterns of *Himantopus* and *Nycticryphes* also are like those of seed-snipe.

The starch-gel electrophoretic patterns of the hemoglobins are shown in Figure 3. The Charadriiformes show three main components, one on each side of the application point and a third farther toward the anode. The patterns of ten charadriiform species representing three families are alike, and the pattern of *Attagis gayi* is almost identical to them. The tinamou *Nothura* differs in having two main components, the cathodal one migrating more rapidly than in *Attagis*. *Pterocles* and *Turnix* lack the anodal fraction which is present in the patterns of *Attagis* and the shorebirds. The pattern of *Attagis* is less like those of the crane *Anthropoides* and the trumpeter *Psophia* than those of the shorebirds.

Summary and Conclusions

Previous writers have believed that the closest relatives of the seed-snipe (Thinocoridae) are either the grouse (Tetraonidae), the button-quails (Turnicidae), sand-grouse (Pteroclididae), or the sheath-bills (Chionididae). The starch-gel electrophoretic patterns of the egg white proteins of *Thinocorus orbignyianus* and *Attagis gayi* and of the hemoglobins of *A. gayi* are more like those of the Charadriiformes than of any other group. We conclude that the evidence available from all sources indicates that the Thinocoridae are charadriiform, but it is not possible from the electrophoretic data to suggest which other group of shorebirds may be closest to the seed-snipe. More detailed comparative studies of the structures of single proteins can be expected to answer this question.



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Figure 3. Starch-gel electrophoretic patterns of the hemoglobins of *Attagis gayi* (Thinocoridae) and representative species of groups which have been proposed as possible allies.

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