

The Relationships
of the Pedionomidae
(Aves: Charadriiformes)

STORRS L. OLSON
and
DAVID W. STEADMAN

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ABSTRACT

Olson, Storrs L., and David W. Steadman. The Relationships of the Pedionomidae (Aves: Charadriiformes). *Smithsonian Contributions to Zoology*, number 337, 25 pages, 13 figures, 1981.—Since 1893, the Australian Plains-wanderer, *Pedionomus torquatus*, has been placed in a monotypic family and has been thought to be related to the button quails, Turnicidae, presently included in the order Gruiformes. Our examination of the osteology of *Pedionomus* shows that this bird is a typical member of the Charadriiformes and has no significant characters in common with the Turnicidae. The evidence used previously by Gadow (1891) to classify *Pedionomus* is better explained by a charadriiform origin for the genus. The diastataxic condition of the secondaries, the thigh muscle formula, the condition of the carotid arteries, the presence of the hallux, and the pyriform shape of the eggs are among the known non-osteological characters of *Pedionomus* that differ from the Turnicidae and that corroborate its placement in the Charadriiformes. Within the Charadriiformes, *Pedionomus* shares the most similarities with the South American seedsnipes of the family Thinocoridae, the next most similar group being the coursers of the family Glareolidae. *Pedionomus* tends to bridge the gap between the aberrant seedsnipes and the more typical Charadriiformes, although it is sufficiently distinct to merit its own family. In any sequential listing, the Pedionomidae should be placed in the order Charadriiformes, immediately preceding the Thinocoridae.

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Introduction

Since its discovery, the singular Plains-wanderer, *Pedionomus torquatus*, endemic to the interior of southeastern Australia, has been considered a relative of the so-called button quails, or hemipodes, of the family Turnicidae. Hence, through a series of taxonomic adversities, it has come to rest with the Turnicidae in the order Gruiformes. *Pedionomus* has a somewhat quail-like appearance and the females are larger and more brightly colored than the males, as in the Turnicidae. The chief external feature used to distinguish *Pedionomus* from its presumed relatives has been the presence of a well-developed hallux, this digit being altogether absent in the Turnicidae.

Only two anatomical studies have dealt with the systematic position of *Pedionomus*. The first of these was an admittedly preliminary investigation by Gadow (1891), mostly of various soft parts preserved in two spirit specimens sent to the Cambridge University Museum of Zoology (these specimens have subsequently been lost; C. W. Benson, in litt., 27 October 1978). The second

was a valuable but inconclusive osteological study by Bock and McEvey (1969).

Gadow (1891) started with the assumption that *Pedionomus* was probably related to the Turnicidae and his comparisons were made only with the Turnicidae and the Galliformes. He concluded that the characters he examined referred "*Pedionomus* to the Turnices as their lowest most Rallo-Galline members [sic]" (page 211). That Gadow was prejudiced towards such a conclusion is clearly demonstrated by his seeing similarities to turnicids in such elements as the sternum and pelvis of *Pedionomus*, which, in fact, are completely unlike those of *Turnix* (Bock and McEvey, 1969; this study). Gadow (1893) later elevated *Pedionomus* to the rank of a monotypic family allied to the Turnicidae, a position it has occupied to this day.

Bock and McEvey (1969) made extensive comparisons of the osteology of *Pedionomus*, *Turnix*, and *Ortyxelos*, the last being an aberrant African genus currently placed in the Turnicidae. Curiously, they did not attempt comparisons with other groups, but they did succeed in showing that *Pedionomus* differs enormously from the Turnicidae in most aspects of the skeleton. They supported the continued recognition of the family Pedionomidae and amply demonstrated that *Pe-*

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dionomus "is not simply a *Turnix* with a hallux" (page 206).

After perusal of Bock and McEvey's illustrations it became evident to us that the skeleton of *Pedionomus* appeared to be quite typically charadriiform. Subsequent examination of skeletal material has fully substantiated our original impressions and in the following account we shall justify the removal of the Pedionomidae from their place near the Turnicidae in the Gruiformes to the vicinity of the Thinocoridae in the Charadriiformes.

ACKNOWLEDGMENTS.—We are especially indebted to Allan R. McEvey, National Museum of Victoria, Melbourne, for lending the skeletons of *Pedionomus* that made this study possible. Walter J. Bock kindly permitted us to use some of the illustrations of skulls that appeared originally in Bock and McEvey (1969). Peter Ballmann and Richard L. Zusi examined skeletons of *Pedionomus* with us and pointed out additional charadriiform characters that we had overlooked. We are also grateful to Shane Parker, George R. Zug, and Richard L. Zusi for their comments and criticisms of the manuscript. The photographs are by Victor E. Krantz and the illustrations of the skull of *Thinocorus* are by Irene Jewett. We are obliged to Jean Smith for her careful typing of the manuscript.

Review of Gadow's Characters

If *Pedionomus* is a member of the Charadriiformes, as we shall show on the basis of its osteology, we need to account for the characters that led Gadow (1891) to conclude that *Pedionomus* was allied with the Turnicidae. These he conveniently summarized in a table (reproduced herein as Table 1) comparing *Pedionomus* with the Turnices and the Rasores (= Galliformes). It was this analysis that led to *Pedionomus* being placed in the wrong order for the past 90 years.

Gadow's study is a classic case of choosing the better of two wrong answers, and is quite similar to the history of classification of flamingos (Phoenicopteridae), which were once thought to

TABLE 1.—Characters comparing *Pedionomus* with the Turnicidae (Turnices) and the Galliformes (Rasores), reproduced from the table in Gadow (1891), including misspellings, with characters numbered to facilitate reference to our text

Characters of <i>Pedionomus</i>	Turnices	Rasores	Neither
1. Number of Primary remiges	*	*	...
2. Number of Secondary remiges	...	*	...
3. Absence of fifth secondary	0
4. Aftershaft structure	*
5. Number of rectrices	*
6. Pterylosis	*
7. Oilgland	*	*	...
8. Nasal operculum	*	*	...
9. Scutillation of Feet	*
10. Hallux	...	*	...
11. Second, third, fourth toes	*
12. Must. caud-ilio-femoralis	...	*	...
13. Carotids	...	*	0
14. Syrinx	*
15. Absence of Crop	*
16. Liver, three lobes	*	*	...
17. Liver, situation of right lobe	*
18. Intestinal convolutions	0
19. Number of cervical vertebrae	*
20. Brachial plexus	0
21. Number of sternal ribs	0
22. Spina communis sterni	*
23. Absence of Proc-obliquus sterni	*
24. Furcula	*
25. Pelvis	*
26. Nasal bones	*

be mosaics between storks and ducks but which are related to neither—they too are Charadriiformes (Olson and Feduccia, 1980). Our analysis of Gadow's characters is as follows.

1. "Number of Primary remiges"—There are 10 primaries in *Pedionomus*, Turnicidae, and Galliformes. The Charadriiformes and most other orders of birds also have 10 primaries.

2. "Number of Secondary remiges"—There are 11 secondaries in *Pedionomus*, a condition Gadow (1891) attributed to the Galliformes but not the Turnicidae. The Charadriiformes also have 11 secondaries.

3. "Absence of fifth secondary"—This is the

so-called diastataxic or aquincubital condition, found in neither the Turnicidae nor the Galliformes, both of which are eutaxic. The Charadriiformes, however, are diastataxic, like *Pedionomus*.

4. "Aftershaft structure"—Gadow (1891:207) likened *Pedionomus* to the Turnicidae in having the aftershaft "very thin and delicate, but much longer than in the Rasores [= Galliformes]." The aftershaft is of variable length in the Charadriiformes. We found that the aftershaft in *Thinocorus* (Charadriiformes), however, is very similar to that in *Pedionomus*, whereas in *Turnix*, the aftershaft is longer and considerably denser than in *Pedionomus*.

5. "Number of rectrices"—Gadow (1891) found 12 rectrices in *Pedionomus*. The same number is found in the Turnicidae, whereas Gadow remarked that most Galliformes have more. The number of rectrices in the Charadriiformes is variable between and within families. In the Thinocoridae, for example, *Attagis* has 14, whereas *Thinocorus* has 12, like *Pedionomus*.

6. "Pterylosis"—Gadow's (1891:207) statement that in *Pedionomus* "the whole distribution and shape of the feather tracts closely resemble that of the Turnices" cannot be accepted without confirmation and without comparison with the Charadriiformes. He made similar statements about the sternum and pelvis of *Pedionomus* and erred considerably in doing so. We did not have a spirit specimen of *Pedionomus* available for study.

7. "Oilgland"—The oil gland is tufted in *Pedionomus*, Turnicidae, and Galliformes. It is also tufted in the Charadriiformes and in many other orders.

8. "Nasal operculum"—*Pedionomus* has a nasal operculum, a character that Gadow (1891) listed as being like both the Turnicidae and the Galliformes. A nasal operculum is also found in various Charadriiformes.

9. "Scutillation [sic] of Feet"—The tarsus in *Pedionomus* has a single row of scutes in front and a single row behind, like the Turnicidae and unlike Galliformes, in which there are usually two rows of scutes on the plantar surface of the tarsus.

A *Pedionomus*-like condition also occurs in many Charadriiformes.

10. "Hallux"—The hallux is present in *Pedionomus*, as in Galliformes, but is invariably absent in the Turnicidae. The hallux is present in the majority of Charadriiformes, though it has been lost or reduced in numerous instances.

11. "Second, third, fourth toes"—The unenlightening text of Gadow's (1891:207-208) remarks on the toes of *Pedionomus* is as follows:

The number of toes is four, the hallux being weak but functional; all the toes are furnished with very short nails. But for the bare distal portion of the leg, and the presence of the hallux, the whole foot of *Pedionomus* closely resembles that of the Turnices and differs from that of the Rasores although its intermediate position between a *pes cursorius* and a *pes radens* is obvious.

The bare tibia ("distal portion of the leg") is a typical charadriiform character. The slender claws of *Pedionomus* are unlike the more robust ones of *Turnix*; overall, we find more similarity to the foot in certain of the Charadrii than to that of the Turnicidae.

12. "Must. [sic] caud-ilio-femoralis"—The caudal and iliac portions of *M. caudo-iliofemoralis* are designated in thigh muscle formulae as "A" and "B" respectively; *M. flexor cruris lateralis* (= semitendinosus) and its accessory part are designated "X" and "Y," respectively. The formula in the Turnicidae is AXY whereas in the Galliformes it is BXY. All four muscles are present in *Pedionomus* (ABXY) but Gadow (1891:208) found the "A" muscle to be

an extremely thin and feeble slip . . . and if the reduction of A were continued, *Pedionomus* would have the same symbolic formula as *Pavo*, *Meleagris*, viz. BXY. Certainly there is no resemblance between *Pedionomus* and *Turnix* in this respect, but it would be very rash to conclude that *Pedionomus* is allied to the Rasores because of this formula.

The thigh muscle formula in the Charadrii is also ABXY and part "A" may occasionally be lost (see Olson and Feduccia, 1980:26-27). Thus, in this respect *Pedionomus* is more like the Charadrii than either the Turnicidae or Galliformes.

13. "Carotids"—Gadow (1891:209) found *Pedionomus* to have the bicarotid condition (type

A-1 of Glenny, 1955) which differs from the derived B-4-s condition in the Turnicidae (Glenny, 1955) and agrees with some, but not all Galliformes. Gadow recognized that this was not an indication of affinity between *Pedionomus* and Galliformes and that it is an "old, unchanged feature, which persists in most birds." The A-1 carotid condition also occurs in all Charadriiformes except flamingos.

14. "Syrinx"—Although Gadow (1891:209) stated that "the Syrinx exhibits no specially remarkable features," he continued to say that it seemed more similar to that of the Turnicidae than that of Galliformes. Without a syrinx of *Pedionomus* on hand for examination, we are unable to evaluate this character. In the absence of comparisons with the Charadriiformes, it cannot be relied upon.

15. "Absence of Crop"—Gadow (1891) stated that the crop was absent in *Pedionomus*, which he took as an indication of affinity with *Turnix*, as opposed to the Galliformes, which have a well developed crop. Nevertheless, he later stated that "the crop is less marked or only temporary in the Birds-of-Prey, the Cassowary, the Hummingbirds, in Mormon [= *Fratercula*], *Pedionomus*, and *Panurus*" (Gadow, in Newton, 1896:113). He does not say which account we are supposed to believe. The crop is generally absent in the Charadriiformes but is present in the Thinocoridae (Gadow, *ibid.*; pers. obs.) and in *Pluvianellus* (Jehl, 1975).

16. "Liver, three lobes"—According to Gadow (1891:210),

The liver of *Pedionomus* consists apparently of three almost equally sized lobes, owing to the left original lobe being split in half. In this respect *Pedionomus* agrees only with the Turnices and with the Rasores, it differs however from the latter and agrees with the former by the small size of the right lobe, which is scarcely half the size of the double left lobe.

We dissected a specimen of *Attagis malouinus* (Thinocoridae) and found that the left lobe of the liver was double and somewhat larger than the right (Figure 1A), as in *Pedionomus*. We have not attempted to determine the distribution of this

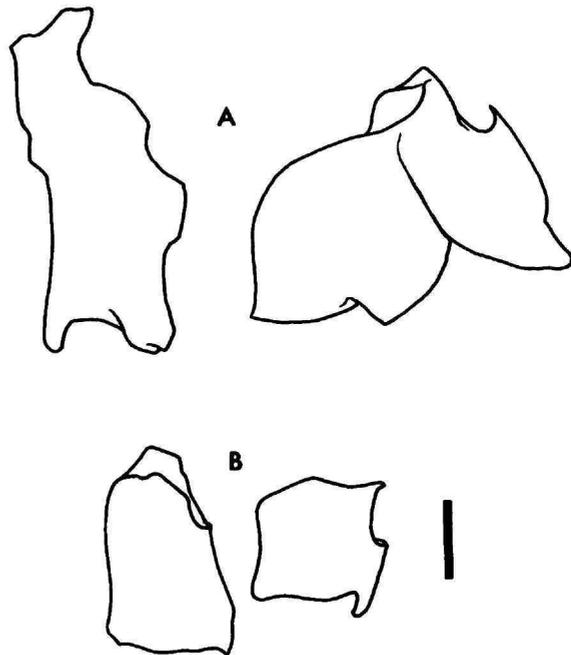


FIGURE 1.—Livers in ventral view: A, *Attagis malouinus* (Thinocoridae); B, *Charadrius falklandicus* (Charadriidae). The large bifurcated left lobe in *Attagis* is similar to that reported by Gadow (1891) for *Pedionomus*. (Scale = 1 cm.)

condition in the Charadriiformes, although in one example of *Charadrius falklandicus* (Figure 1B), we found that the right lobe was much larger than the left and that the left was undivided, as apparently is the case in many birds.

17. "Liver, situation of right lobe"—See character 16 above.

18. "Intestinal convolutions"—According to Gadow (1891:210), "The intestinal convolutions of *Pedionomus* are certainly different from those of either Turnices or Rasores." This statement is compatible with *Pedionomus* being allied to some other group.

19. "Number of cervical vertebrae"—*Pedionomus* and *Turnix* have 15 cervical vertebrae, whereas the Galliformes have 16. All Charadriiformes have 15 cervical vertebrae except the Burhinidae and Jacanidae, which have 16, and the Phoenicopteridae, which have 18 or 19. Thus,

Pedionomus also agrees with the majority of Charadriiformes in this character.

20. "Brachial plexus"—The brachial nerve plexus in *Pedionomus* is formed by spinal nerves 12 through 15, unlike either the Turnicidae or the Galliformes. This pattern did not occur in the few species of Charadriiformes examined by Fürbringer (1888:240), but in one specimen of *Attagis malouinus* (Thinocoridae) that we dissected, the brachial plexus was composed of nerves 12 through 15, as in *Pedionomus*.

21. "Number of sternal ribs"—Gadow (1891:210) found "five, almost six ribs . . . attached to the sternum" in *Pedionomus*, whereas there are fewer in *Turnix* and the Galliformes. He recognized this as a primitive "Ralline" condition. It is also typical of many Charadriiformes.

22. "Spina communis sterni"—See character 23 below.

23. "Absence of Proc-obliquus sterni"—These are characters that will separate *Pedionomus* from the Galliformes but not from numerous other birds, including Charadriiformes, and are not indicative of relationship to the Turnicidae. The sternum of *Pedionomus* has no similarity whatever to that of *Turnix* but is almost inseparable from that of the Thinocoridae (Figure 3).

24. "Furcula"—Gadow (1891) thought the furcula of *Pedionomus* to be more like that of *Turnix* than that of the Galliformes, but, as with the sternum, there is little similarity. The furcula of *Pedionomus* is charadriiform in nature (Figure 5).

25. "Pelvis"—Gadow (1891:211) stated that in *Pedionomus* "the configuration of the pelvis closely resembles that of the Turnices." This assertion is utterly erroneous. The pelvis of *Pedionomus* bears not the slightest resemblance to that of *Turnix* (Figure 10) and is typically charadriiform in structure.

26. "Nasal bones"—*Pedionomus* and *Turnix* are both schizorhinal, whereas the Galliformes are holorhinal. All Charadriiformes except *Pluvianus*, *Burhinus*, and flamingos, are also schizorhinal.

In his analysis of the characters of *Pedionomus*, Gadow (1891:211) concluded:

To settle the affinities of *Pedionomus* simply by the numerical majority of coincidences of these characters would be a not unprecedented but utterly fallacious mode of investigation. *The quality not the quantity of these "taxonomic characters" refers Pedionomus to the Turnices as their lowest most Rallo-Galline members* [italics Gadow's].

Neither the quality nor the quantity of such characters can be revealing when comparisons are made with the wrong groups. As we have seen, all of the verifiable characters of *Pedionomus* in Gadow's list can also be found in the Charadriiformes, including all of those that occur in neither the Turnicidae nor the Galliformes. Thus, there never has been any valid anatomical evidence to link *Pedionomus* with the Turnicidae.

Life History and Behavior

Relatively little is known of the habits of *Pedionomus*, the most valuable accounts being those of Legge (1869), North (1913), Purnell (1915), D'Ombrain (1926), Souter (1938), Llewellyn (1975), Frith (1976), and Parker (1978). *Pedionomus* lives in flat, grassy plains in southeastern Australia, where in recent years it is thought to have become quite scarce through habitat destruction and through depredations of introduced mammals (North, 1913; D'Ombrain, 1926; Frith, 1976), although Llewellyn (1975) and Parker (1978) are more sanguine about its status.

Unlike the Turnicidae, *Pedionomus* never occurs in coveys and is characteristically very reluctant to fly, to the extent that birds have often been captured by hand. The flight has been described as "dipping" and "fluttery . . . reminding one somewhat of a young lark" (Legge, 1869:237), which contrasts markedly with *Turnix*, in which the flight is rapid and straight, as in Galliformes. An interesting trait of *Pedionomus* is the habit of standing on tiptoe with the body very erect and the head held high, as if looking intently about (Legge, 1869, D'Ombrain, 1926; photograph in Purnell, 1915:142). A similar very erect peering stance is commonly reported for the glareolid *Cursorius cursor* (e.g., Dement'ev and Gladkov, 1969). Austin (1961:126) refers to coursers (Glar-

colidae) as having "a peculiar habit of stretching upward on tiptoe with necks outstretched to peer around the horizon."

The nest of *Pedionomus* is a scrape in the ground, lined with grass and usually placed at the base of a shrub or clump of grass. The eggs are four in number, greenish in ground color and blotched with darker shades. Their placement in the nest, with the sharper end toward the center (Souter, 1938), is typical of the Charadriiformes. In their distinctly pyriform shape, the eggs of *Pedionomus* differ markedly from those of the Turnicidae, and numerous authors have remarked that they appear similar to those of Charadriiformes (Legge, 1869; Frith, 1976; Parker, 1978; illustrated in Campbell, 1913, and North, 1913). This fact, combined with the non-turnicid aspects of its behavior and the anatomical differences noted by Gadow (1891), induced North (1913) to erect a new suborder, Pedionomi, for *Pedionomus*, though he retained it in an order Hemipodii along with the Turnicidae. This subordinal designation was omitted from the synonymies of higher taxonomic categories given by Brodkorb (1967).

Plumage

The females of *Pedionomus* are larger and more distinctively colored than the males, which on first consideration seems to be an indication of affinity with the Turnicidae. "Reversal" of the sexes, however, is a well known phenomenon in the Charadriiformes as well. In the Phalaropodidae, for example, the males are duller colored and assume all the nesting duties. Females are larger than males in the Jacanidae, and are larger and more brightly colored than the males in the Rostratulidae. Within the Scolopacidae there is considerable variation in the roles of the sexes, and in a number of species the males are smaller than females and assume some or all of the nesting duties. This is not true, however, of the Thincoridae, in which there is no appreciable sexual dimorphism in size (Blake, 1977). The males of *Thinocorus* are more distinctively colored and are less involved with nesting than females (Maclean,

1969), whereas the sexes in *Attagis* are monomorphic. Reversal of plumage between the sexes in *Pedionomus* is not incompatible with a hypothesis of charadriiform relationships.

The growth and development of plumages in *Pedionomus* is discussed by Crome and Rushton (1975), who also describe and illustrate the downy young. Their illustration does not permit detailed comparisons with the downy young of other birds, but does indicate that the pattern in *Pedionomus* is indistinct, consisting of a light venter and darker dorsum with diffuse blackish spots. Such a pattern roughly resembles that found in the Thincoridae and Glareolidae and is unlike the distinctively patterned young of many other Charadriiformes (Jehl, 1968), or those of *Turnix*, which are boldly striped with white, black, and brown (Fjeldså, 1977).

Comparative Osteology

When moving a family from one order to another, considerable documentation is expected. Were it not for this fact, the following comparisons could be regarded as superfluous, because the osteology of *Pedionomus* is so obviously that of a charadriiform. The figures and their legends alone should prove quite sufficient to establish this. Had skeletons of *Pedionomus* been more widely available to various researchers in the past, its affinities would no doubt have been recognized long ago.

The following specimens were used in the comparisons. A representative of at least one genus in each family of Charadriiformes was included. The comparisons assume that the taxa examined are representative of the osteology of their entire family. Except for *Pedionomus*, all catalog numbers refer to specimens in the collections of the National Museum of Natural History, Smithsonian Institution. Specimens marked with an asterisk were used in the photographs but not in the comparisons.

Turnicidae: *Turnix maculatus* (344363, 344365), *Turnix suscitator* (343207, 347288). Pedionomidae: *Pedionomus torquatus* (National Museum of Victoria

B8818, B8872, W6084). Jacanidae: *Actophilornis africanus* (432028), *Hydrophasianus chirurgus* (343226), *Jacana jacana* (345811). Rostratulidae: *Rostratula benghalensis* (343516), *Nycticryphes semicollaris* (*227770). Haematopodidae: *Haematopus ater* (490221). Charadriidae: *Hoplopterus armatus* (430389), *Charadrius vociferus* (499440). Scolopaciidae: *Tringa solitaria* (499231), *Numenius phaeopus* (431526). Phalaropodidae: *Steganopus tricolor* (499659). Recurvirostridae: *Recurvirostra avocetta* (429086), *Ibidorhynchus struthersi* (292766). Phoenicopteridae: *Phoeniconaias minor* (488729). Dromadidae: *Dromas ardeola* (321489). Burhinidae: *Burhinus vermiculatus* (488870). Glareolidae: *Glareola maldivarum* (19580), *Rhinoptilus cinctus* (431520), *Pluvianus aegyptius* (500294). Thinocoridae: *Thinocorus orbignyianus* (*290109, *290111), *Thinocorus rumicivorus* (227504, *227772, *343099), *Attagis malouinus* (490853). Chionidae: *Chionis alba* (490989). Stercorariidae: *Stercorarius pomarinus* (17766). Laridae: *Larus philadelphia* (501257), *Sterna dougallii* (488053). Rynchopidae: *Rynchops niger* (499470). Alcidae: *Cerorhinca monocerata* (347759).

Because Bock and McEvey (1969) described the osteology of *Pedionomus* in some detail and have already established that *Pedionomus* differs greatly from *Turnix*, we have attempted to keep the following analysis brief, making it purely comparative in order to show the similarities of *Pedionomus* with the Charadriiformes. An asterisk (*) indicates a character that was discussed by Bock and McEvey when their description agrees with our observations. Exceptions are discussed individually.

SKULL

FIGURE 2

1. Occipital condyle.—*Pedionomus*: large. *Turnix*: small. Charadriiformes: large in all except *Tringa*, *Steganopus*, and *Thinocorus* (small).

2. Interorbital bridge.—*Pedionomus*: narrow. *Turnix*: broad. Charadriiformes: extremely variable in width, ranging from narrow (*Rostratula*,

Tringa, *Steganopus*, *Attagis*, *Thinocorus*) to as wide or wider than in *Turnix* (*Actophilornis*, *Jacana*, *Hoplopterus*, *Charadrius*, *Burhinus*, *Pluvianus*, *Chionis*, *Rynchops*).

3. Median furrow on the dorsal surface of interorbital bridge.—*Pedionomus*: deep. *Turnix*: shallow. Charadriiformes: extremely variable, ranging from absent (*Haematopus*, *Dromas*, *Chionis*, *Stercorarius*) to as shallow as in *Turnix* (*Hydrophasianus*, *Steganopus*, *Recurvirostra*, *Larus*, *Sterna*, *Rynchops*, *Cerorhinca*), to relatively deeper than in *Pedionomus* (*Hoplopterus*, *Charadrius*, *Burhinus*, *Pluvianus*), with other forms intermediate; *Rostratula*, *Tringa*, *Rhinoptilus*, and *Attagis* are very similar to *Pedionomus*.

4. * Ectethmoid plate.—*Pedionomus*: small and flattened. *Turnix*: greatly inflated, extending anteriorly to occupy most of the space between the two branches of the nasals. Charadriiformes: small and flattened in all but *Phoeniconaias* (inflated).

5. * Medial condyle of quadrate.—*Pedionomus*: small. *Turnix*: large. Charadriiformes: small in all but *Dromas*, *Glareola*, *Chionis*, *Attagis*, *Stercorarius*, and *Rynchops* (large).

6. Posterior condyle of quadrate.—Bock and McEvey (1969:195) report the posterior condyle of the quadrate to be larger in *Pedionomus* than in *Turnix*, but we see no appreciable differences.

7. Quadrate groove.—Bock and McEvey (1969:195) mention a distinct groove separating the lateral and medial condyles of the quadrate in *Turnix*, which they reported to be absent in *Pedionomus*. We found this groove in both forms. Its presence is seemingly exaggerated by the large size of the medial condyle in *Turnix* (see character 5).

8. * Orbit.—*Pedionomus*: large. *Turnix*: small. Charadriiformes: large in all except *Actophilornis*, *Hydrophasianus*, *Jacana*, *Tringa*, and *Steganopus* (small).

9. * Frontals.—*Pedionomus*: slope down sharply to join the nasals rather abruptly. *Turnix*: slope down gently to join the nasals rather gradually. Charadriiformes: slope down sharply to join the nasals abruptly in all except *Haematopus*, *Numenius*, *Steganopus*, *Ibidorhynchus*, *Recurvirostra*, *Dromas*, *Glare-*

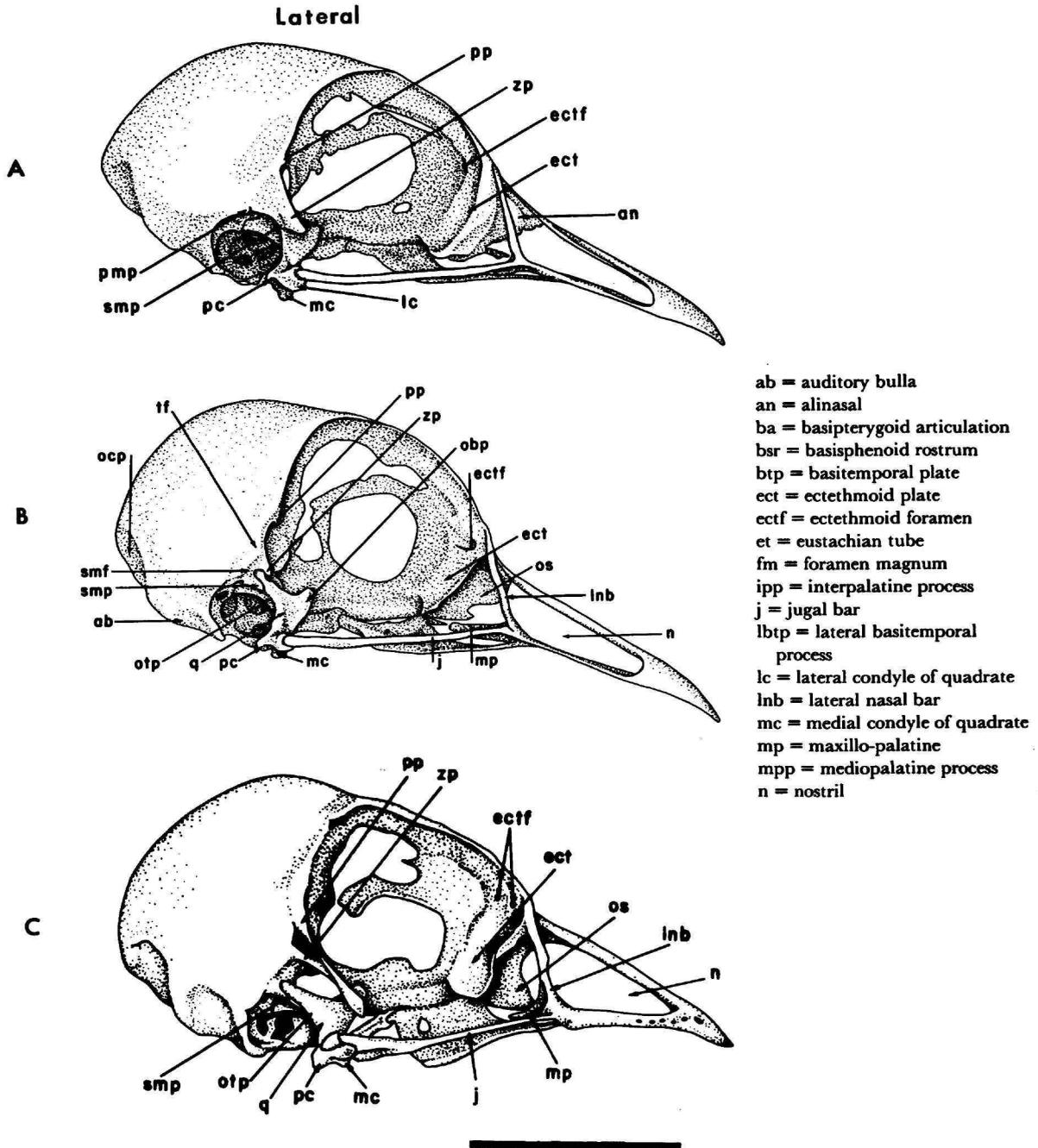
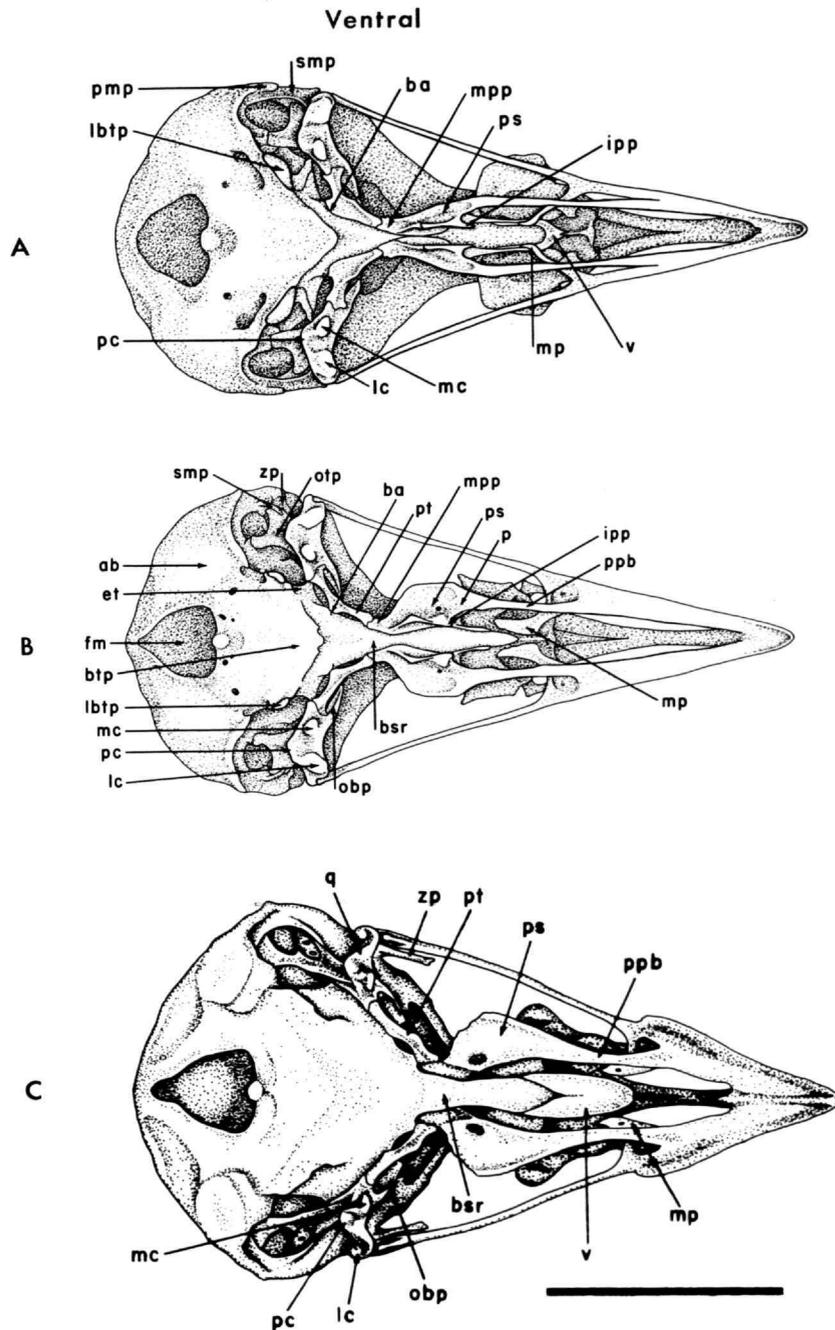


FIGURE 2.—Skulls in lateral and ventral views: A, *Turnix nigricollis* (Turnicidae); B, *Pedionomus torquatus* (Pedionomidae); C, *Thinocorus rumicivorus* (Thinocoridae). Although the skull of *Thinocorus* is distinctive in its own right, it shows more similarities in common with *Pedionomus* than the latter shows with *Turnix*. Note particularly the expanded palatines in *Pedionomus* and *Thinocorus*,



obp = orbital process of quadrate
ocp = occipital plate
os = orbital septum
otp = otic process of quadrate
p = palatine
pc = posterior condyle of quadrate
pmp = posterior meatic process
pp = postorbital process
ppb = prepalatine bar
ps = palatine shelf
pt = pterygoid
q = quadrate
smf = suprimeatic fossa
smp = suprimeatic process
tf = temporal fossa
v = vomer
zp = zygomatic process

as opposed to the very different palatal structure in *Turnix*. (Vomer omitted from ventral view of *Pedionomus*; parts A and B and all abbreviations from Bock and McEvey (1969)—we make no claim for consistency or appropriateness in the labelling of these figures; scale = 1 cm.)

eola, *Larus*, *Sterna*, *Stercorarius*, and *Cerorhinca*; *Actophilornis* and *Jacana* are intermediate.

10. * Ossified alinasal.—*Pedionomus*: absent. *Turnix*: present. Charadriiformes: absent.

11. * Braincase.—*Pedionomus*: high, wide, and short. *Turnix*: low, narrow, and long. Charadriiformes: high, wide, and short in all except *Actophilornis*, *Hydrophasianus*, *Jacana*, *Tringa*, *Steganopus*, and *Ibidorhynchus*.

12. Nasal bar.—*Pedionomus*: stout. *Turnix*: extremely thin. Charadriiformes: variable in thickness, but always stouter than in *Turnix*.

13. * Maxillo-palatines.—*Pedionomus*: broad. *Turnix*: narrow. Charadriiformes: broad.

14. * Palatines.—*Pedionomus*: large. *Turnix*: small. Charadriiformes: large.

15. Posterolateral corner of palatines.—Bock and McEvey (1969:195) state that "the palatines differ [from *Pedionomus*], with this bone . . . having a sloping posterolateral corner in *Turnix*." Both *Turnix* and *Pedionomus* have a "sloping posterolateral corner," but it is more truncate in *Pedionomus*, as in Charadriiformes.

16. * Pterygoid.—*Pedionomus*: less massive, with an indistinct bend at the basipterygoid articulation. *Turnix*: slightly more massive, with a distinct bend at the basipterygoid articulation. These differences are extremely slight. Charadriiformes: resemble *Pedionomus* and *Turnix* in all except *Dromas*, *Burhinus*, *Phoeniconaias*, *Pluvianus*, *Rhinoptilus*, *Glareola*, *Thinocorus*, *Attagis*, *Chionis*, *Larus*, *Sterna*, *Stercorarius*, *Rynchops*, and *Cerorhinca*.

17. Vomer.—Bock and McEvey (1969:193) state that the vomer of *Turnix* "is basically similar to the vomer of *Pedionomus* except that the anterior plate is shorter." We would stress the high degree of variability in gross morphology of the vomer within the genus *Turnix*, and even within the species *T. sylvatica*, as demonstrated in figure 7 of Bock and McEvey (1969). This reveals the limited value of the vomer as a taxonomic tool in this instance. Among Charadriiformes the vomer is roughly similar to that of *Pedionomus* in *Steganopus*, *Ibidorhynchus*, *Rhinoptilus*, *Thinocorus*, and *Attagis*.

18. * Postorbital process.—*Pedionomus*: present, but small. *Turnix*: absent. Charadriiformes: pres-

ent, but longer than in *Pedionomus* in all except *Rhinoptilus*, which is similar to *Pedionomus*.

19. Zygomatic process.—Bock and McEvey (1969:195) say that *Pedionomus* "lacks the large zygomatic process and has only a small hollow on the postorbital wall as opposed to the larger hollow in *Turnix*." We are unable to detect any significant differences, as the zygomatic process is so reduced in both genera.

20. Ectethmoid foramen.—Bock and McEvey (1969:195) report the ectethmoid foramen to be larger in *Pedionomus* than in *Turnix*. We see no consistent difference between *Pedionomus* and *Turnix* in the size of this foramen, which, however, is located more medially in *Turnix*.

MANDIBLE

1. * Size and shape.—*Pedionomus*: stout, straight. *Turnix*: thin, more decurved. Charadriiformes: extremely variable, but the mandibles of *Charadrius* and *Rhinoptilus* are very similar to that of *Pedionomus*.

2. Retroarticular and internal process.—Bock and McEvey (1969:195) state that "the retroarticular and internal processes in *Turnix* are longer [than in *Pedionomus*] and narrow without a posterior wall connecting them," which is true, although the differences are very slight. *Pedionomus* resembles all Charadriiformes in these characters except for certain forms with more specialized mandibles and resultant longer retroarticular processes (*Haematopus*, *Numenius*, *Steganopus*, *Recurvirostra*, *Phoeniconaias*, *Glareola* and *Chionis*).

3. Articular surfaces.—Bock and McEvey (1969:195) state that "the lateral portion of the articular surfaces in *Turnix* flares out beyond the edge of the ramus," but this condition also occurs in *Pedionomus* and all Charadriiformes.

STERNUM

FIGURE 3

1. * Shape, in dorsal view.—*Pedionomus*: broad, short. *Turnix*: narrow, elongated. Charadri-

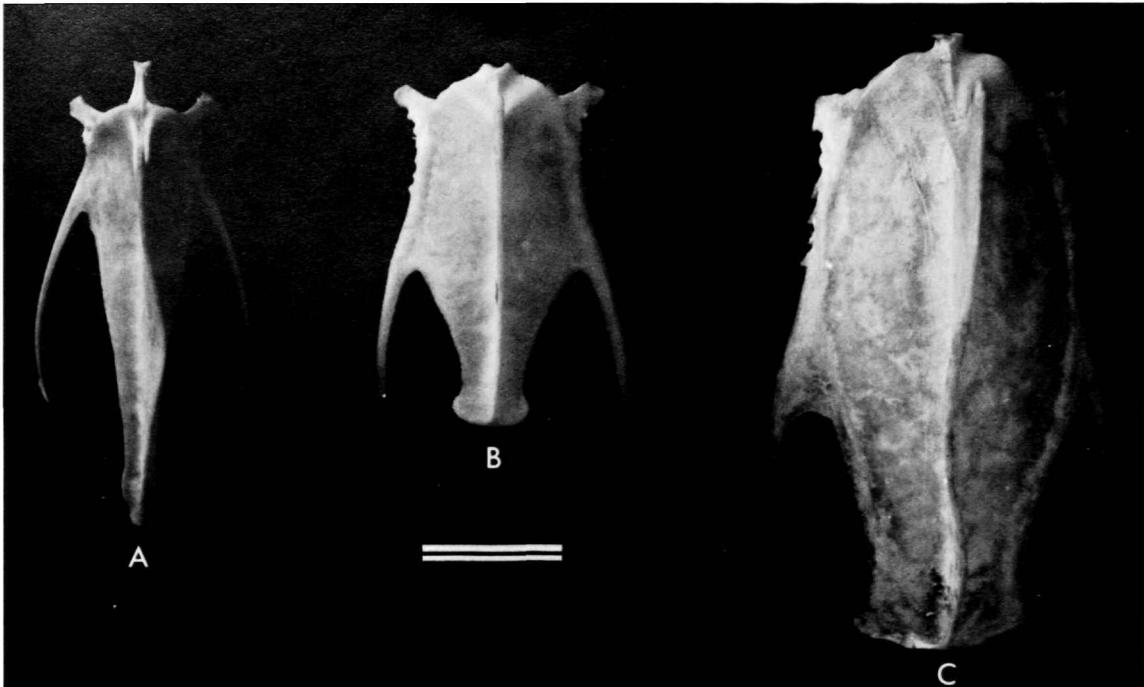


FIGURE 3.—Sterna in ventral view: A, *Turnix suscitator*; B, *Pedionomus torquatus*; C, *Thinocorus orbignyianus*. The sternum of *Pedionomus* is utterly unlike that of *Turnix* in lacking the prominent manubrial spine, the slender elongated xiphium, and the deep sternal notches; however, apart from the different angle of the sternocoracoidal processes, it is very similar to *Thinocorus*. (Scale = 1 cm.)

iformes: generally intermediate, with none as narrow as in *Turnix*; only *Glareola*, *Thinocorus*, *Attagis*, and *Rynchops* are as broad (or nearly so) as *Pedionomus*.

2. * Manubrium.—*Pedionomus*: short, stout. *Turnix*: long, slender. Charadriiformes: short, stout.

3. * Sterno-coracoidal process.—*Pedionomus*: stout, directed mainly laterally, and only slightly anteriorly. *Turnix*: slender, directed mainly anteriorly, and only slightly laterally. Charadriiformes: stout, although often reduced in overall size, except in *Cerorhinca* (narrow); directed mainly laterally, and only slightly or not at all anteriorly.

4. Xiphial margin.—*Pedionomus*: more or less straight. *Turnix*: pointed. Charadriiformes: more

or less straight, except in *Haematopus*, *Recurvirostra*, *Glareola*, *Stercorarius*, *Rynchops*, and *Cerorhinca* (pointed to rounded).

5. * Sternal notches.—*Pedionomus*: two, shallow. *Turnix*: two, deep. Charadriiformes: two, shallow in *Rostratula*, *Phoeniconaias*, *Attagis*, *Thinocorus*, and some *Stercorarius*; two, slightly deeper in *Actophilornis*, *Hydrophasianus*, *Jacana*; four notches, two of which may be closed to form fenestrae, in all others.

6. Posterior lateral process.—*Pedionomus*: stout. *Turnix*: very narrow. Charadriiformes: stout, varying from not quite as stout as in *Pedionomus* to occasionally stouter.

The sternum of *Pedionomus* is obviously charadriiform in its overall aspect, while bearing no resemblance to that of *Turnix*. The total dissimi-

larity of the sternum in these taxa makes us doubtful if Gadow really examined them, despite his statement (1891:210) that "the sternum of *Pedionomus* is decidedly like that of the Turnices. . . ." Two sterna of volant birds could scarcely be more different from each other than are those of *Pedionomus* and *Turnix*.

CORACOID

FIGURE 4

1. Furcular facet in internal view.—*Pedionomus*: very broad, protruding well beyond the line formed by the ventral surface of the shaft. *Turnix*: narrow, not extending beyond the line formed by the surface of the shaft. Charadriiformes: very broad and protrudent.

2. Procoracoid and scapular facet.—*Pedionomus*: not particularly close to the humeral end. *Turnix*: extremely close to the humeral end, but the procoracoid is not fused to the brachial tuberosity as stated by Bock and McEvey (1969). Charadriiformes: not particularly close to the humeral end.

3. *Excavation of dorsal surface of the shaft.—*Pedionomus*: not deeply excavated. *Turnix*: deeply excavated along the sternal two-thirds of its length. Charadriiformes: not deeply excavated.

4. Sterno-coracoidal process.—*Pedionomus*: large, pointed. *Turnix*: small, not sharply pointed. Charadriiformes: large, pointed in all except *Phoeniconaias* (not sharply pointed).

5. Lateral extent of sternal facet.—*Pedionomus*: large. *Turnix*: small. Charadriiformes: large.

6. Inward curvature of sternal facet in dorsal view.—*Pedionomus*: strong. *Turnix*: slight. Charadriiformes: either strong or moderate in all except *Hydrophasianus*, *Ibidorhynchus*, *Recurvirostra*, *Phoeniconaias*, *Burhinus*, *Pluvianus*, *Rhinoptilus*, *Stercorarius*, *Larus*, and *Sterna* (slight).

SCAPULA

1. Furcular articulation in dorsal view.—*Pedionomus*: small, barely extending anterior to the

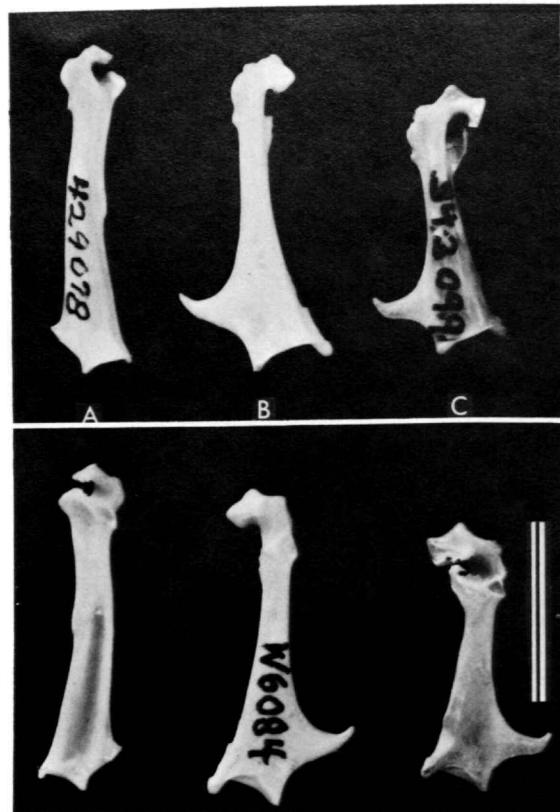


FIGURE 4.—Coracoids in ventral view (top row) and dorsal view (bottom row): A, *Turnix sylvatica*; B, *Pedionomus torquatus*; C, *Thinocorus rumicivorus*. The configuration of the coracoid of *Pedionomus*, with its large uncinatc sternocoracoidal process and overhanging furcular facet, is typical of the Charadriiformes and bears no resemblance whatever to the peculiar coracoid of *Turnix*. (Scale = 1 cm.)

coracoidal articulation. *Turnix*: large, more pointed. Charadriiformes: small, barely extending anterior to the coracoidal articulation in all except *Steganopus* and *Phoeniconais* (large, more pointed) and *Pluvianus* and *Glareola* (intermediate).

FURCULA

FIGURE 5

1. * Interclavicular width in anterior view.—*Pedionomus*: broad. *Turnix*: narrow. Charadriiformes: broad.

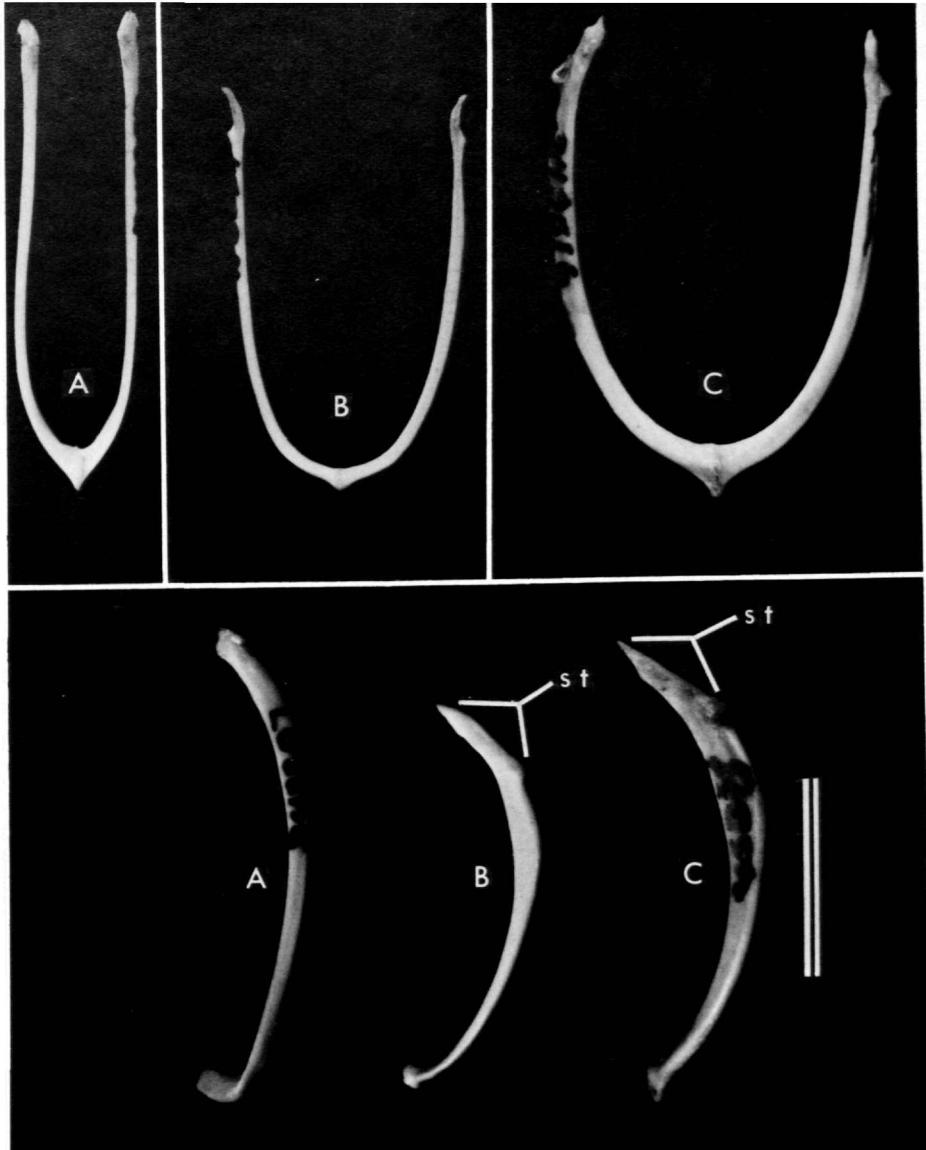


FIGURE 5.—Furculae in dorsal view (top row) and lateral view (bottom row): A, *Turnix suscitator*; B, *Pedionomus torquatus*; C, *Rostratula benghalensis* (Rostratulidae). In the long, pointed scapular tuberosity (st), which is nearly absent in *Turnix*, and the lack of a prominent hypocleidium, *Pedionomus* clearly resembles the Charadriiformes and differs from *Turnix*. (Scale = 1 cm.)

2. Scapular tuberosity.—*Pedionomus*: long, slender, well-defined. *Turnix*: short, broad, indistinct. Charadriiformes: long, slender, well-defined.

3. Coracoidal facet.—*Pedionomus*: conspicuous, well delimited from the shaft. *Turnix*: small, almost completely obliterated. Charadriiformes: conspicuous, well delimited from the shaft in all except *Hoplopterus*, *Recurvirostra*, *Burhinus*, and *Chionis* (intermediate).

4. Shaft.—*Pedionomus*: slender. *Turnix*: slender. Charadriiformes: stout, with only *Jacana* approaching *Pedionomus* or *Turnix* in slenderness.

5. Shaft, in lateral view.—*Pedionomus*: very curved. *Turnix*: slightly curved. Charadriiformes: very curved.

6. Hypocleidium.—*Pedionomus*: small. *Turnix*: large. Charadriiformes: extremely variable, ranging from small (*Actophilornis*, *Hydrophasianus*, *Jacana*, *Numenius*, *Rostratula*, *Chionis*, *Cerorhinca*) to large (*Charadrius*, *Tringa*, *Steganopus*, *Burhinus*, *Rhinoptilus*, *Glareola*, *Stercorarius*, *Larus*, *Sterna*, *Rynchops*), with other forms being intermediate.

HUMERUS

FIGURE 6

1. * General proportions.—*Pedionomus*: long, slender. *Turnix*: shorter, stouter. Charadriiformes: long, slender in *Dromas* and *Rhinoptilus*; less so in all others.

2. * Head in anconal view.—*Pedionomus*: pointed. *Turnix*: rounded. Charadriiformes: quite variable, ranging from as pointed as in *Pedionomus* (*Rhinoptilus*, *Thinocorus*) to as rounded as in *Turnix* (*Jacana*, *Haematopus*, *Burhinus*, *Attagis*, *Rynchops*, *Cerorhinca*), with other forms being intermediate.

3. Internal tuberosity.—*Pedionomus*: very prominent in its anconal protrusion. *Turnix*: not prominent. This disagrees with the findings of Bock and McEvey (1969), who report a smaller internal tuberosity in *Pedionomus* than in *Turnix*. Charadriiformes: very prominent.

4. Scar for attachment of M. proscapulohumeralis at medial end of capital groove ("medial knob" of Bock and McEvey, 1969:210).—*Pedio-*

nomus: absent. *Turnix*: present. Charadriiformes: absent.

5. * External tuberosity and pectoral attachment.—*Pedionomus*: small. *Turnix*: large. Charadriiformes: small in all except *Tringa*, *Steganopus*, *Rostratula*, and *Pluvianus* (intermediate), and *Attagis* and *Cerorhinca* (large).

6. * Tricipital fossa ("pneumatic fossa" of Bock and McEvey, 1969:210).—*Pedionomus*: small. *Turnix*: extremely large and deep, resembling only penguins among living birds. Charadriiformes: small to intermediate in size, being largest in *Actophilornis*, *Hydrophasianus*, and *Jacana*.

7. * Ligamental furrow.—*Pedionomus*: well developed. *Turnix*: inconspicuous. Charadriiformes: well developed in all except *Phoeniconaias* (intermediate).

8. * Bicipital crest.—*Pedionomus*: small. *Turnix*: large. Charadriiformes: large in all except *Numenius* (small) with several other forms intermediate.

9. Partly closed canal for nervus coracobrachialis cranialis.—*Pedionomus*: present. *Turnix*: absent. Charadriiformes: present in most forms, but absent in other orders of birds (Ballmann and Adrover, 1970). When present, this feature appears to be diagnostic of the Charadriiformes.

10. Deltoid crest.—Bock and McEvey (1969: 199) report a "lack of a medial overhang on the deltoid crest" in *Pedionomus* whereas this overhang was said to be present in *Turnix*. This distinction is not apparent to us.

11. * Olecranal fossa.—*Pedionomus*: narrow, deep. *Turnix*: wide, shallow. Charadriiformes: narrow, deep in all except *Actophilornis*, *Ibidorhynchus*, *Phoeniconaias*, *Burhinus*, *Chionis*, and *Cerorhinca* (intermediate).

12. * Internal condyle.—*Pedionomus*: small, projecting less distad. *Turnix*: large, projecting more distad. Charadriiformes: projects less distad in all forms; small in *Tringa*, *Rostratula*, *Pluvianus*, *Glareola*, *Attagis*, and *Thinocorus*; large in *Charadrius*, *Steganopus*, and *Rhinoptilus*; difficult to determine in other genera because of great differences in size.

13. Entepicondyle.—*Pedionomus*: flares less laterad. *Turnix*: flares more laterad. Charadri-



iformes: flares less laterad in all except *Hydrophasianus*, *Jacana*, *Haematopus*, *Burhinus*, *Pluvianus*, and *Chionis* (intermediate or resemble *Turnix*).

14. Ectepicondylar spur.—Bock and McEvey (1969:200) report a smaller ectepicondylar spur in *Pedionomus* than in *Turnix*. These spurs are actually about the same size in *Pedionomus* and *Turnix*, but are shaped differently, with *Pedionomus* resembling the Charadriiformes and differing from *Turnix* in having this spur extending distally as a ridge that reaches the external condyle.

15. Intercondylar furrow.—Bock and McEvey (1969:200) report a shallower, wider intercondylar furrow in *Pedionomus* than in *Turnix*, but this is not apparent to us.

ULNA

FIGURE 7

1. * Olecranon.—*Pedionomus*: short. *Turnix*: long. Charadriiformes: short.

2. * Internal cotyla.—*Pedionomus*: small, faces proximad. *Turnix*: large, faces largely palmar. Charadriiformes: small to intermediate in size, oriented as in *Pedionomus* or intermediately.

3. * External cotyla.—*Pedionomus*: small, inconspicuous; located only slightly distad to internal cotyla. *Turnix*: large, conspicuous; located largely distad to internal cotyla. Charadriiformes: small, inconspicuous; located only slightly distad to internal cotyla in all except *Actophilornis*, *Hydrophasianus*, *Jacana*, *Burhinus*, and *Rynchops* (intermediate in size and position). This character appears to separate all Charadriiformes from all Gruiformes, as well as from *Turnix*.

FIGURE 6.—Humeri in anconal view (top row) and palmar view (bottom row): A, *Turnix suscitator*; B, *Pedionomus torquatus*; C, *Nycticryphes semicollaris* (Rostratulidae). The humerus of *Pedionomus* possesses a small ectepicondylar spur and lacks the greatly excavated tricipital fossa and distally protruding entepicondyle of *Turnix*. Its conformation is typically charadriiform apart from the long, slender shaft, which is one of the diagnostic features of the Pedionomidae, being shared only with the *Rhinoptilus* (Glareolidae) and the Dromadidae among Charadriiformes. (Scale = 1 cm.)

4. * Shaft, in internal view.—*Pedionomus*: straight; slender. *Turnix*: curved; stout. Charadriiformes: straight; extremely variable in relative stoutness, ranging from those stouter than in *Turnix* (*Actophilomis*, *Hydrophasianus*, *Charadrius*, *Attagis*, *Thinocorus*, *Chionis*, *Cerorhinca*) to those as slender as in *Pedionomus* (*Phoeniconaias*, *Dromas*,



FIGURE 7.—Ulnae in dorsal view (top row) and proximal ends in internal view (bottom row): A, *Turnix suscitator*; B, *Pedionomus torquatus*; C, *Rhinoptilus africanus* (Glareolidae). The ulna of *Pedionomus* is typically charadriiform in lacking the short, curved shaft and the prominent olecranon (o) and external cotyla (e) of *Turnix*. (Scale = 1 cm.)

Burhinus, *Stercorarius*), with other forms intermediate.

5. Proximal portion of shaft.—*Pedionomus*: palmo-anconally compressed and laterally expanded. *Turnix*: somewhat palmo-anconally expanded and laterally compressed. Charadriiformes: as in *Pedionomus* in all except *Cerorhinca*, which resembles *Turnix*.

6. Area between ligamental attachment of carpal tuberosity and internal condyle.—*Pedionomus*: slightly notched. *Turnix*: with abrupt, deep notch. Charadriiformes: slightly notched or intermediate.

RADIUS

FIGURE 8

1. * Shape of shaft.—*Pedionomus*: straight. *Turnix*: distal end strongly inflected palmad. Char-

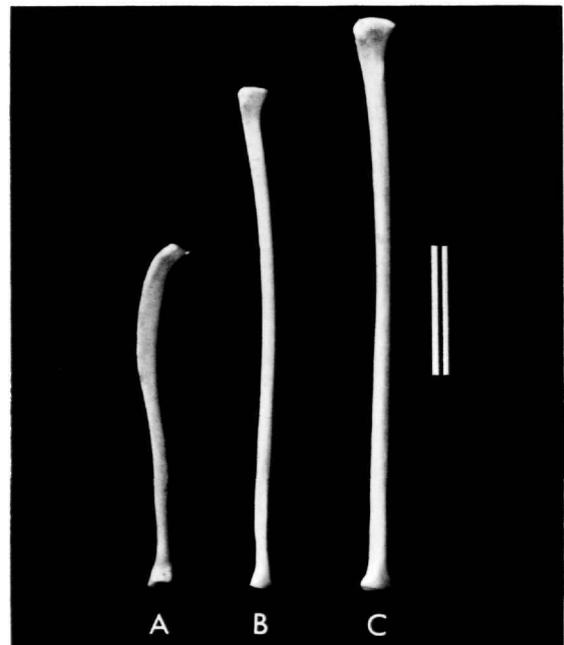


FIGURE 8.—Radii in palmar view: A, *Turnix suscitator*; B, *Pedionomus torquatus*; C, *Rostratula benghalensis*. The long, straight, unflattened shaft in *Pedionomus* does not differ from that in Charadriiformes and is utterly unlike that of *Turnix*. (Scale = 1 cm.)

adriiformes: straight in all except *Hydrophasianus* and *Jacana* (intermediate) and *Actophilornis* (very inflected palmad as part of the modification for use as a combative organ).

2. * Proportions of shaft.—*Pedionomus*: slender. *Turnix*: stout. Charadriiformes: stout or intermediate in all except *Steganopus*, *Recurvirostra*, *Phoeniconaias*, *Burhinus*, *Dromas*, *Rhinoptilus*, *Glareola*, *Thinocorus*, *Sterna*, *Stercorarius*, and *Rynchops* (slender).

3. Distal half of shaft.—*Pedionomus*: only slightly expanded laterally and compressed palmo-anconally. *Turnix*: strongly laterally expanded and palmo-anconally compressed. Charadriiformes: as in *Pedionomus* except in *Jacana* (intermediate) and *Actophilornis* (laterally expanded more than in *Turnix*).

CARPOMETACARPUS

FIGURE 9

1. * Shape.—*Pedionomus*: straight, slender. *Turnix*: less straight, stouter. Charadriiformes: quite

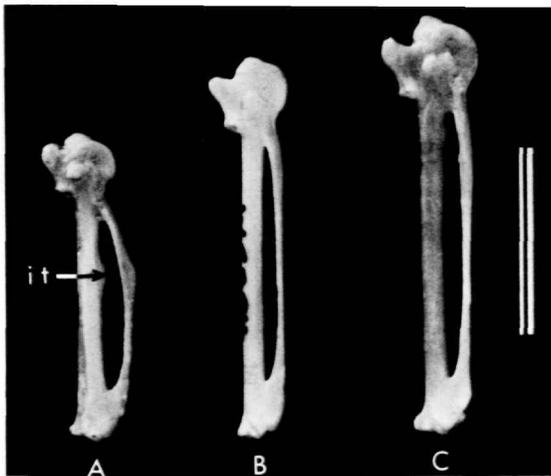


FIGURE 9.—Carpometacarpus in internal view: A, *Turnix suscitator*; B, *Pedionomus torquatus*; C, *Tringa solitaria* (Scolopaciidae). The narrow intermetacarpal space and lack of an intermetacarpal tuberosity (it), among other characters, easily distinguishes the carpometacarpus of *Pedionomus* from that of *Turnix*, whereas it differs in no major way from that of most Charadriiformes. (Scale = 1 cm.)

variable, ranging from as stout as in *Turnix* (*Cerorhinca*) through intermediate forms (*Jacana*, *Haematopus*, *Chionis*), to as slender as in *Pedionomus* (all other forms); straight in all Charadriiformes.

2. Extensor process.—Bock and McEvey (1969:200) state that in *Pedionomus* this is higher than in *Turnix* and does not project proximally. These differences may exist, but are extremely minor and difficult to detect.

3. Intermetacarpal tuberosity.—*Pedionomus*: barely detectable. *Turnix*: well developed. Charadriiformes: barely detectable.

PELVIS

FIGURE 10

1. * Width.—*Pedionomus*: very broad, caused largely by the lateral extension of the prelumbar parapophyses. *Turnix*: narrow. Charadriiformes: quite variable, ranging from as narrow as in *Turnix* (*Actophilornis*, *Hydrophasianus*, *Jacana*, *Haematopus*, *Hoplopterus*, *Dromas*, *Cerorhinca*) to as broad as in *Pedionomus* (*Attagis*), with *Charadrius* and *Thinocorus* nearly as broad as in *Pedionomus*; other forms are intermediate.

2. Interparapophyseal area of the preacetabular sacrum.—*Pedionomus*: largely unossified, forming large openings. *Turnix*: extensively ossified, almost completely roofing over the entire dorsal surface of the sacrum. Charadriiformes: largely unossified in all except *Jacana*, which somewhat resembles *Turnix*.

3. Posterior iliac crest.—Bock and McEvey (1969:200) state that in *Pedionomus* this is not as sharp as in *Turnix* and lacks the "heavy process found in *Turnix*." This is not apparent to us.

4. * Antitrochanter.—*Pedionomus*: small. *Turnix*: large. Charadriiformes: large or intermediate in all except *Thinocorus*, *Sterna*, and *Rynchops* (small).

5. * Pectineal process.—*Pedionomus*: small. *Turnix*: large. Charadriiformes: large or intermediate in all except *Recurvirostra*, *Phoeniconaias*, *Dromas*, *Rostratula*, *Rhinoptilus*, *Glareola*, *Attagis*, and *Thinocorus* (small).

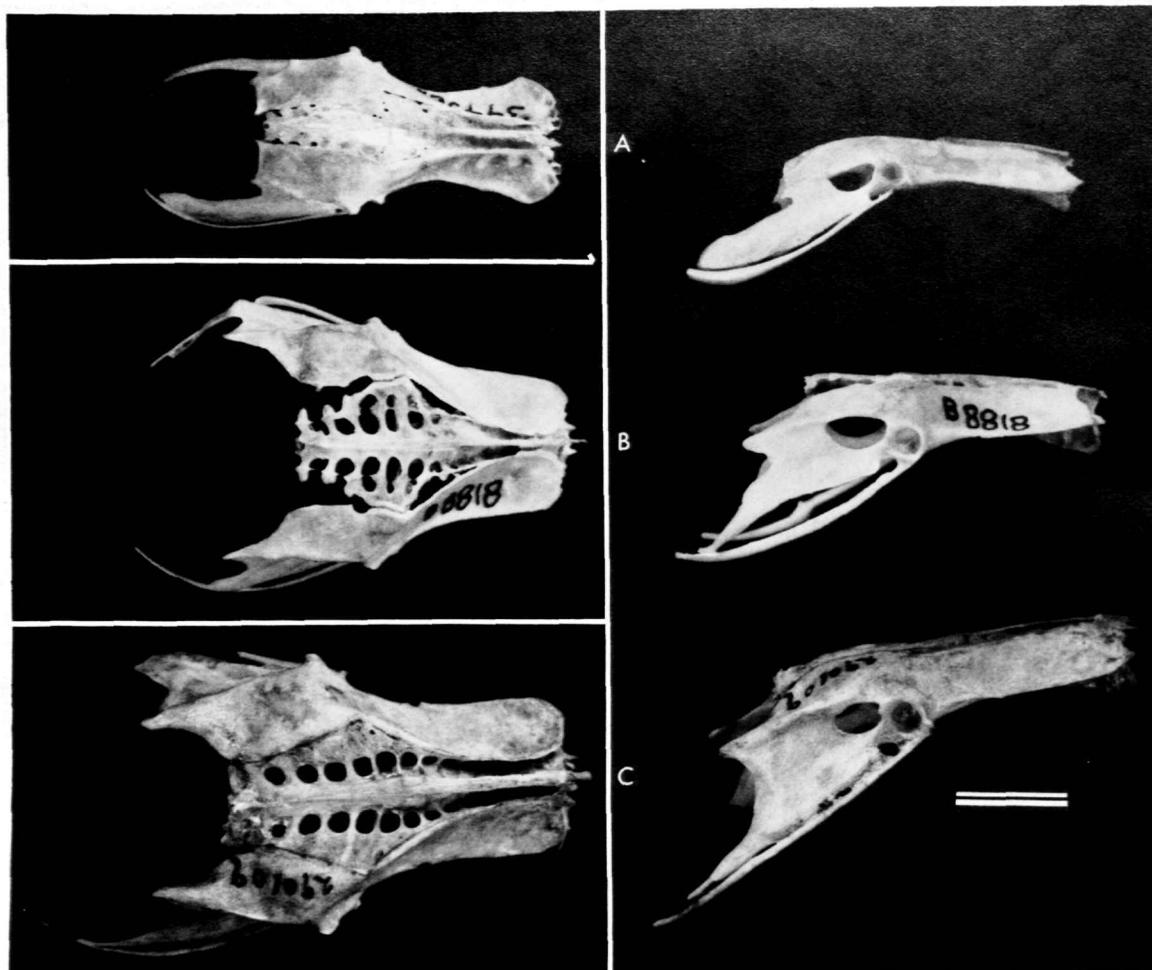


FIGURE 10.—Pelves in dorsal view (left row) and lateral view (right row): A, *Turnix maculatus*; B, *Pedionomus torquatus*; C, *Thinocorus orbignyianus*. The striking dissimilarity of *Pedionomus* and *Turnix* is obvious. The relatively greater width of the pelvis in *Pedionomus* is a character shared with the *Thinocoridae*, as opposed to other *Charadriiformes*. (Scale = 1 cm.)

6. * Posterior extension of the ilium.—*Pedionomus*: well beyond the posterior end of the sacral caudal vertebrae, forming a large, pointed projection at its most posterior extent. *Turnix*: barely beyond the posterior end of the sacral caudal vertebrae, forming a very small projection at its most posterior point. *Charadriiformes*: as in *Pedionomus*, the prominence at the posterior end is well developed in *Actophilornis*, *Hydrophasianus*, *Ja-*

cana, *Steganopus*, *Recurvirostra*, *Phoeniconaias*, *Stercorarius*, and *Larus*.

7. Shape of ischium.—*Pedionomus*: tapers continuously, forming a point at the posterior end; shorter than pubis. *Turnix*: remains about the same width throughout its length, rounded at the end; as long as pubis. *Charadriiformes*: as in *Pedionomus* in all except *Phoeniconaias* and *Burhinus* (wide, rounded).

FEMUR

FIGURE 11

1. Shaft.—*Pedionomus*: stout. *Turnix*: slender. Charadriiformes: stout, often even stouter than in *Pedionomus*. In addition, Bock and McEvey (1969:201) report the shaft in *Turnix* to be straighter than in *Pedionomus*. We cannot see this distinction.

2. Neck.—*Pedionomus*: short. *Turnix*: long. Charadriiformes: short to intermediate.

3. External condyle.—*Pedionomus*: large. *Turnix*: small. Charadriiformes: large.

TIBIOTARSUS

FIGURE 12

1. Inner cnemial crest.—*Pedionomus*: large, especially in its distal portion. *Turnix*: small. Charadriiformes: large, especially in its distal portion,



FIGURE 11.—Femora in anterior view: A, *Turnix maculatus*; B, *Pedionomus torquatus*; C, *Attagis malouinus* (Thinocoridae). The stout shaft and neck are among several characters that separate the femur of *Pedionomus* from that of *Turnix* and show affinity to the Charadriiformes. (Scale = 1 cm.)

in all except *Ibidorhynchus*, *Rostratula*, *Rynchops*, and *Cerorhinca* (small).

2. Amount of internal protrusion from the shaft in the internal condyle.—*Pedionomus*: much. *Turnix*: little. Charadriiformes: extremely variable, ranging from little (*Actophilornis*, *Jacana*, *Hoplopterus*, *Tringa*, *Steganopus*, *Burhinus*, *Rhinoptilus*, *Glareola*, *Rynchops*) to as much or more than in *Pedionomus* (*Rostratula*, *Haematopus*, *Charadrius*, *Nuneniensis*, *Ibidorhynchus*, *Recurvirostra*, *Phoeniconaias*, *Attagis*, *Thinocorus*, *Chionis*, *Larus*, *Sterna*, *Cerorhinca*), with other forms intermediate.

3. Distal projection on the internal condyle.—Bock and McEvey (1969:201) report this to be smaller in *Turnix* than *Pedionomus*, but we see no such difference.

TARSOMETATARSUS

FIGURE 13

1. Shaft.—*Pedionomus*: stout. *Turnix*: slender. Charadriiformes: extremely variable, ranging from more slender than in *Turnix* (*Actophilornis*, *Hydrophasianus*, *Jacana*, *Rostratula*, *Hoplopterus*, *Charadrius*, *Tringa*, *Steganopus*, *Recurvirostra*, *Dromas*, *Burhinus*, *Pluvianus*, *Rhinoptilus*, *Glareola*) to more stout than in *Pedionomus* (*Chionis*, *Sterna*, *Rynchops*, *Cer-*

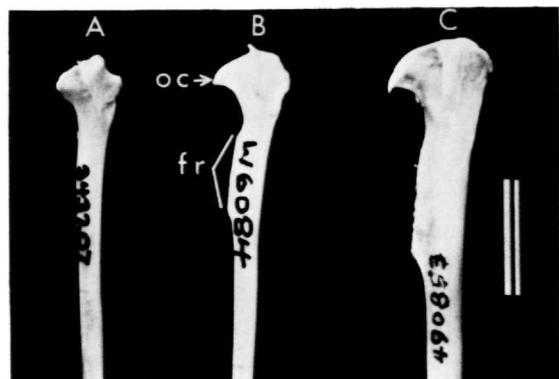


FIGURE 12.—Proximal ends of tibiotalars in anterior view: A, *Turnix suscitator*; B, *Pedionomus torquatus*; C, *Attagis malouinus*. The prominent, decurved outer cnemial crest (oc) and the distinct fibular ridge (fr) separate *Pedionomus* from *Turnix* and show close similarity to the Charadriiformes. (Scale = 1 cm.)

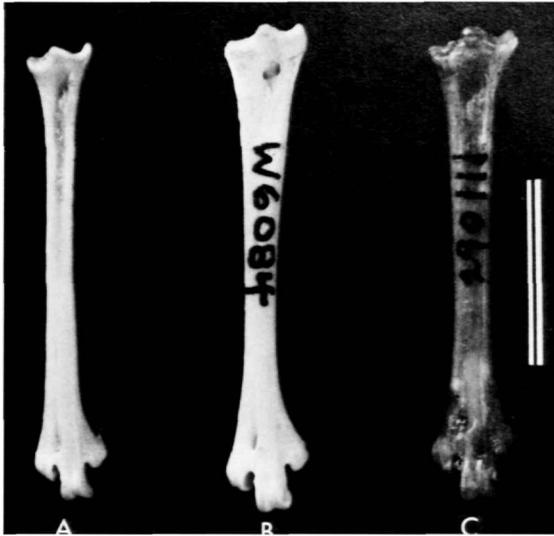


FIGURE 13.—Tarsometatarsi in anterior view: A, *Turnix maculatus*; B, *Pedionomus torquatus*; C, *Thinocorus orbignyianus*. Note the more slender shaft in *Turnix*, as opposed to the two Charadriiformes. (Scale = 1 cm.)

orhinca), with other forms intermediate.

2. Plantar protrusion of the hypotarsus, in proximal view.—*Pedionomus*: little. *Turnix*: conspicuous. Charadriiformes: quite variable, ranging from little (*Haematopus*, *Numenius*, *Steganopus*, *Ibidorhynchus*, *Glareola*, *Attagis*, *Thinocorus*, *Chionis*) to those exceeding *Turnix* (*Actophilornis*, *Hydrophasianus*, *Jacana*, *Hoplopterus*, *Charadrius*, *Tringa*, *Recurvirostra*, *Phoeniconaias*, *Dromas*, *Burhinus*, *Pluvianus*, *Rhinoptilus*, *Larus*, *Stercorarius*), with other forms intermediate.

3. Facet for metatarsal I.—Bock and McEvey (1969:202) report this to be present in *Pedionomus* and absent in *Turnix*, correlated with the loss of the hallux in the latter. It is, however, very indistinct in *Pedionomus* and in all other Charadriiformes except *Actophilornis*, *Hydrophasianus*, *Jacana*, *Rostratula*, *Numenius*, and *Tringa*, in which it is distinct.

4. Distal foramen.—*Pedionomus*: large. *Turnix*: small. Charadriiformes: large in all except *Ibidorhynchus*, *Recurvirostra*, *Phoeniconaias*, *Burhinus*, *Rhinoptilus*, and *Rynchops* (small or intermediate).

5. Trochleae.—*Pedionomus*: large. *Turnix*: small. Charadriiformes: extremely variable, ranging from smaller than in *Turnix* (*Tringa*, *Steganopus*, *Rhinoptilus*, *Glareola*) to larger than or equal to *Pedionomus* (*Hydrophasianus*, *Haematopus*, *Numenius*, *Ibidorhynchus*, *Rostratula*, *Attagis*, *Thinocorus*, *Chionis*, *Larus*, *Sterna*, *Rynchops*, *Cerorhinca*), with other forms intermediate.

6. Inner trochlea.—*Pedionomus*: rotated more plantad. *Turnix*: less plantad rotation. Charadriiformes: rotated as in *Pedionomus* in all except *Recurvirostra* (more plantad) and *Actophilornis*, *Hydrophasianus*, *Jacana*, *Burhinus*, *Rhinoptilus*, *Attagis*, *Rynchops*, *Stercorarius*, and *Sterna* (less plantad).

7. Length.—Bock and McEvey (1969:202) report the tarsometatarsus of *Turnix* to be slightly shorter than that of *Pedionomus*, but this depends on the individual specimen of *Turnix*, some of which equal *Pedionomus* in size.

Osteological Diagnoses

Below, we have summarized the osteological characters by which the Charadriiformes may be diagnosed to include *Pedionomus* and to exclude the Turnicidae and Gruiformes. Because *Pedionomus* is distinct enough to justify continuing to maintain it in a monotypic family, we have also provided a brief osteological diagnosis for the Pedionomidae.

Order CHARADRIIFORMES

DIAGNOSIS.—*Pedionomus* shares the following unique combination of characters with other members of the Charadriiformes: (1) absence of an ossified alinasal; (2) broad maxillo-palatines; (3) large palatines; (4) presence of postorbital process; (5) sternal manubrium short and stout; (6) posterior lateral process of sternum stout; (7) sterno-coracoidal process of sternum directed mainly laterally and only slightly anteriorly; (8) furcular facet of coracoid broad and protrudent; (9) dorsal surface of coracoidal shaft not deeply excavated; (10) interclavicular width great; (11) scapular tuberosity of furcula long and slender;

(12) shaft of furcula highly curved in lateral view; (13) internal tuberosity of humerus prominent; (14) absence of a distinct scar for attachment of *M. proscapulohumeralis brevis* at medial end of capital groove; (15) presence of a partly closed canal for nervus coracobrachialis cranialis on humerus; (16) olecranon short; (17) external cotyla of ulna small and inconspicuous; (18) shaft of ulna quite straight in internal view; (19) intermetacarpal tuberosity poorly developed; (20) femur stout; (21) neck of femur rather short; (22) external condyle of femur large.

Family PEDIONOMIDAE

DIAGNOSIS.—Medium-sized Charadriiformes distinguished from other families of the order by the following unique combination of characters: (1) postorbital process of skull smaller than all except *Rhinoptilus* (Glareolidae); (2) sternum relatively broader and shorter than all except Thinocoridae, Rynchopidae, and *Glareola* (Glareolidae); (3) two sternal notches (found also in Jacanidae, Rostratulidae, Phoenicopteridae, Thinocoridae, and some Stercorariidae); (4) furcular shaft more slender; (5) humerus relatively longer and more slender than all except Dromadidae and *Rhinoptilus* (Glareolidae); (6) head of humerus in anconal view more pointed than all except *Rhinoptilus* (Glareolidae) and *Thinocorus* (Thinocoridae); (7) bicipital crest of humerus relatively smaller than all except *Numenius* (Scolopacidae); (8) pelvis relatively wider than all except *Attagis* (Thinocoridae); (9) antitrochanter of pelvis smaller than all except *Thinocorus* (Thinocoridae), *Sterna* (Laridae), and Rynchopidae; (10) pectineal process of pelvis smaller than all except *Recurvirostra* (Recurvirostridae), Phoenicopteridae, Dromadidae, Rostratulidae, Glareolidae, and Thinocoridae.

Discussion

On the basis of its osteology, *Pedionomus* belongs in the order Charadriiformes, within which it is not nearly so aberrant as, for example, the Jacan-

idae. It has no features that can be interpreted as showing tendencies towards the Gruiformes or any other order of birds, and it has no affinity with the Turnicidae. The long association of *Pedionomus* with *Turnix* is a historical accident that can be traced back to the influence of Gadow (1891, 1893) and would surely have been corrected before now were it not for the failure of Bock and McEvey (1969) to make outgroup comparisons in their osteological study of *Pedionomus*.

The few known non-osteological characters of *Pedionomus* also support its removal from the vicinity of the Turnicidae and its placement in the Charadriiformes. These include the diastataxic condition of the secondaries, the thigh muscle formula, the configuration of the carotid arteries, the liver morphology, the nature of the brachial nerve plexus, the presence of the hallux, and the shape and nature of the eggs. The little that is known of the life history and behavior of *Pedionomus* does not contradict this conclusion.

The hypothetical discussions of Bock and McEvey (1969:202–204) concerning the functional morphology and taxonomic position of *Pedionomus* with respect to *Turnix* may now be disregarded. Although we agree with Bock and McEvey (1969:204) that there is “little evidence . . . to support the inclusion of the Turnices in the Gruiformes,” the statement that “*Turnix* and *Pedionomus* are more closely related to one another than to other gruiform birds” is meaningless. Neither *Pedionomus*, nor *Turnix* in our opinion, is closely related to the Gruiformes and they are likewise not closely related to each other.

Although Huxley (1868) removed the Turnicidae from the Galliformes and placed them in their own order, most early anatomists detected similarities between the Turnicidae and the Galliformes (see Sibley and Ahlquist, 1972), and even Gadow (1893) placed the Turnicidae (along with the Pedionomidae) in that order. Lowe (1923) declared in a convoluted and ambiguous paper that the Turnicidae were not galliform, but he did not state the group to which he believed the Turnicidae to be related. His paper marked the beginning of the modern disassociation of the

Turnicidae from the Galliformes. By default, one assumes, Wetmore (1930) included the Turnicidae, with their baggage of the Pedionomidae along as usual, in his order Gruiformes. This was done merely in a list and no evidence was offered then or subsequently for a gruiform relationship for the Turnicidae. While the true affinities of the Turnicidae are at present quite uncertain, for *Pedionomus* there remains only the problem of determining its position within the Charadriiformes.

Among the suborders of Charadriiformes as recognized by Wetmore (1960), *Pedionomus* is referable to the Charadrii; it possesses none of the characters that define the Lari (gulls and terns) or Alcae (auks). Recently, however, Strauch (1978) has put forth a different subordinal classification of the Charadriiformes, based mainly on osteological characters. He proposed the following suborders: Scolopaci, for the Jacanidae, Rostratulidae, Scolopacidae, Phalaropodidae, and Thinocoridae; Alcae for the Alcidae; and Charadrii for all the remaining families, including the gulls and terns. We have studied Strauch's paper and are not entirely convinced of the validity of some of his conclusions, partly because his major divisions hinge on a few seemingly very minor characters. The collection of families included in his "Scolopaci" is about as diverse as any possible combination of Charadriiformes, yet these are united only by the following three characters (Strauch, 1978:334): (1) absence of maxillo-palatine strut A; (2) absence of a coracoidal foramen; (3) presence of a ridge in the capital groove of the humerus. The ossified connective tissue that constitutes the various "maxillo-palatine struts" presents problems of homology and this character we find difficult to discern or evaluate in many species, including *Pedionomus*. The two remaining characters attributed to the Scolopaci are definitely possessed by *Pedionomus*. Therefore, if one were to follow Strauch's classification, the Pedionomidae would be placed in the suborder Scolopaci. This conclusion is supported by the similarities shared between *Pedionomus* and the Thinocoridae, a family that

Strauch placed in the Scolopaci.

A compilation of the characters discussed in the comparative osteology section shows that *Pedionomus* agrees with the Thinocoridae in 66 characters, more than with any other family of Charadriiformes. The Thinocoridae are followed by the Glareolidae (62 shared characters), Scolopacidae (60), and Rostratulidae (58). Other charadriiform families share less than 50 of these characters with *Pedionomus*. These characters would be more useful if their "polarity" (i.e., primitive or derived) could be determined, but appropriate information on this is more often lacking than not. One of our major criticisms of Strauch's (1978) study is that he often assigned "polarities" to character states with insufficient justification and sometimes probably erroneously.

There is only one unique, shared osteological character (pelvic width) that unites *Pedionomus* with the Thinocoridae as opposed to all other families of Charadriiformes. Even this distinction is somewhat clouded by the rather similar pelvic morphology of *Charadrius*. *Pedionomus* shares but one other character uniquely with a single genus of Charadriiformes, namely the small postorbital process in common with *Rhinoptilus* (Glareolidae). Three more osteological characters are shared between *Pedionomus* and only two other genera. These are (1) the long, slender humerus shared with *Dromas* and *Rhinoptilus*; (2) the pointed head of the humerus shared with *Rhinoptilus* and *Thinocorus*; and (3) the stout, straight mandible shared with *Charadrius* and *Rhinoptilus*.

Rather than any single character pointing to the affinities of *Pedionomus*, consideration should be given to how combinations of characters are distributed with regard to related groups. The more consistent similarity of the skeletal elements of *Pedionomus* to either *Thinocorus* or *Attagis*, or both, suggests that the Thinocoridae are the most probable close relatives of the Pedionomidae. The similarity between *Pedionomus* and the Thinocoridae may be particularly appreciated in the broad, two-notched sternum (Figure 3) and the broad pelvis (Figure 10.) Whereas the Thinocoridae once appeared to stand significantly apart from

other Charadriiformes, *Pedionomus* now provides a form somewhat intermediate between this aberrant group and the more typical members of the order. We suggest that in any sequential listing of the families of Charadriiformes, the Pedionomidae should be placed immediately preceding the Thinocoridae.

Pedionomus lives in open, grassy regions of southeastern Australia; the Thinocoridae are ground-dwelling birds confined to open areas of western and southern South America. If these families are in fact each other's closest relative, then they could be viewed as providing a far more satisfying instance of possible dispersal through Antarctica

than any of the avian examples hitherto offered (cf. Cracraft, 1973; Rich, 1975). On the other hand, it could be argued that these families are relicts of a group that was once more widely distributed and which has been replaced by other taxa in northern regions. The fossil record of the Thinocoridae and Pedionomidae consists entirely of Quaternary specimens referable to extant genera (Campbell, 1976, 1979; Rich and McEvey, 1980). Therefore, in the absence of any information on the pre-Pleistocene paleontology of these groups, their biogeographic history, as with all other suggested examples of southern hemisphere dispersal in birds, remains entirely hypothetical.

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A few points of style: (1) Do not use periods after such abbreviations as "mm, ft, yds, USNM, NNE, AM, BC." (2) Use hyphens in spelled-out fractions: "two-thirds." (3) Spell out numbers "one" through "nine" in expository text, but use numerals in all other cases if possible. (4) Use the metric system of measurement, where possible, instead of the English system. (5) Use the decimal system, where possible, in place of fractions. (6) Use day/month/year sequence for dates: "9 April 1976." (7) For months in tabular listings or data sections, use three-letter abbreviations with no periods: "Jan, Mar, Jun," etc.

Arrange and paginate sequentially EVERY sheet of manuscript—including ALL front matter and ALL legends, etc., at the back of the text—in the following order: (1) title page, (2) abstract, (3) table of contents, (4) foreword and/or preface, (5) text, (6) appendixes, (7) notes, (8) glossary, (9) bibliography, (10) index, (11) legends.

