The Relationships of the Pedionomidae
(Aves: Charadriiformes)

STORRS L. OLSON
and
DAVID W. STEADMAN

SMITHSONIAN CONTRIBUTIONS TO ZOOLOGY • NUMBER 337
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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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The Relationships of the Pedionomidae (Aves: Charadriiformes)

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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-
"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 Turnicidae and the 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 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 *Thinocorvus* (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 *Thinocorvus* 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. “Oil gland”—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, Melangris*, 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 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.


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-
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 Thinoecoridae, 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 Thinoecoridae 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
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**

3. Median furrow on the dorsal surface of interorbital bridge.—*Pedionomus*: deep. *Turnix*: shallow. Charadriiformes: extremely variable, ranging from absent (Haematopodidae, Dromadidae, Glareolidae) to as shallow as in *Turnix* (Hydrophasianus, Steganopus, Recurvirostra, Larus, Sterna, Rynchops, Certhia), to relatively deeper than in *Pedionomus* (Hoplopterus, Charadrius, Burhinus, Pluvianus), with other forms intermediate; Rostratula, Tringa, Rhinoptilus, and Attagis are very similar to *Pedionomus*.
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).
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 Haematopodidae, Numenius, Steganopus, Ibidorhynchus, Recurvirostra, Dromas, Glar-
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.
as opposed to the very different palatal structure in *Tumix*. (Vomer omitted from ventral view of *Pedionamus*; 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; Actophilosornis and Jacana are intermediate.


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: present, 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, Recurvisstra, 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. Charadrii-
FIGURE 3.—Sternal in ventral view: A, Turnix suscitator; B, Pedionomus torquatus; C, Thinocorus orbignyanus. 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, Attacis, and Rynchops are as broad (or nearly so) as Pedionomus.


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, Attacis, 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.


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.


**SCAPULA**

1. Furcular articulation in dorsal view.—*Pedionomus*: small, barely extending anterior to the coracoidal articulation. *Turnix*: large, more pointed. Charadriiformes: small, barely extending anterior to the coracoidal articulation in all except Steganopus and Phoeniconaias (large, more pointed) and Pluvianus and Glareola (intermediate).
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 hypoleidium, Pedionomus clearly resembles the Charadriiformes and differs from Turnix. (Scale = 1 cm.)

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).


HUMERUS


2. * Head in anconal view.—Pedionomus: pointed. Turnix: rounded. Charadriiformes: quite variable, ranging from as pointed as in Pedionomus (Rhinoptilus, Thinorhynchus) to as rounded as in Turnix (Jacana, Haematopus, Burhinus, Attagis, Rynchops, Cerorhinchus), 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.


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.


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 Thinorhynchus; 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. Charadrii-
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**

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, Nycticryptes 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 (Glaricolidae) 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* (Actophilornis, Hydrophasianus, Charadrius, Attagis, Thinocorus, Chionis, Cerorhinca) to those as slender as in *Pedionomus* (Phoeniconaias, Dromas, Burhinus, Stercorarius), with other forms intermediate.


**Radius**

**Figure 8**

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


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 variable, ranging from as stout as in Turnix (Cerorhina) 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.


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, Holoptyerus, Dromas, Cerorhina) 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.


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, Jacana, 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.


**Tibiotarsus**

**Figure 12**

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


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**

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) sternum short and stout; (6) posterior lateral process of sternum stout; (7) sterno-coracoidal process of sternum directed mainly laterally and only slightly anteriorly; (8) furcilar 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 (Scopacidae); (8) pelvis relatively wider than all except Attagis (Thinocoridae); (9) antitrochanter 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 Jacanidae. 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 Gadon (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 Gadon (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 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.

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