

# The Species of Moas (Aves: Dinornithidae)

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## ABSTRACT

In order to provide a basis for future studies on the functional morphology and evolutionary history of the New Zealand moas, the species-level systematics of the family is reviewed. Based on a study of museum collections and an analysis of intraspecific variability, only 13 species are considered to be valid: *Anomalopteryx didiformis*, *A. oweni*, *Megalapteryx didinus*, *M. benhami*, *Pachyornis elephantopus*, *P. mappini*, *Euryapteryx curtus*, *E. geranoides*, *Emeus crassus*, *Dinornis struthoides*, *D. torosus*, *D. novaezealandiae*, and *D. giganteus*. The taxa accepted as valid in this paper probably fit the biological species concept more closely than do those of previous classifications, in which as many as 29 species have been recognized. The "species-pairs," *Pachyornis mappini*-*P. septentrionalis*, *Euryapteryx curtus*-*E. exilis*, *E. geranoides*-*E. gravis*, and *Emeus crassus*-*E. huttonii* probably represent examples of sexual size dimorphism.

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## Introduction

Birds provide a number of classic examples of insular adaptive radiations, the best known being the Hawaiian honeycreepers (Drepanididae) and the Galapagos finches (Geospizinae). A unique radiation of this sort is also found in the New Zealand moas (Dinornithidae)—unique because a spectacular radiation took place not only in feeding mechanisms, but also in body size and proportions, in contrast to the well-known passerine radiations. This occurred within a group that was completely flightless, and indeed it is probable that being flightless enhanced selective pressures toward divergence in cranial morphology and body size.

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Moas are primitive ratite birds whose closest living relatives are probably the kiwis (Cracraft, 1974). I have postulated elsewhere that the common ancestor of the kiwis and moas probably had a distribution in the Cretaceous that included western Antarctica and parts of South America and that moas and kiwis were isolated on New Zealand following northward continental drift of that landmass beginning in the Late Cretaceous (Cracraft, 1973a; 1974). If this is so, then the radiation of moas probably began in the Tertiary, but it is my opinion that the taxonomic and morphological diversity observed in the Holocene assemblages of moas is the result of a relatively recent, probably Pleistocene, episode of speciation (Cracraft, in prep.). Thus, species formation within moas probably involved repeated cycles of isolation and sympatry among populations of the two major islands and among populations that very likely were isolated in forest refugia at glacial maxima. It is within such a model of their evolution that I have considered the species-level systematics of moas.

Despite the fact that hundreds of papers have been written about moas (see summaries in Lambrecht, 1933; Oliver, 1949), there is comparatively little known about their functional morphology or evolutionary history. Upon initiating such studies, it quickly became clear that the complexities and confusion of presently accepted species-level systematics would hinder any advances in morphological or evolutionary investigations. It thus became necessary to review the status of the various species of moas, and this paper presents the results of that study.

The species-level systematics of moas has suffered from a century of typological thinking and a lack of application of modern concepts of population biology. No less than 60 specific names have been applied to a group that almost certainly con-

tains fewer than 20 biological species (see Brodkorb, 1963, for citations to the taxonomic literature). Each variant, each newly discovered bone in some cases, was frequently given a new specific name. Unfortunately, the taxonomic philosophy of certain influential recent workers, rather than clarifying the systematics of these birds, merely confounded matters further. Oliver (1949:132–134), for example, believed that “it is the work of the systematist . . . to define the units that make up [a series of continuous sizes between extreme forms],” and that “in dealing with fossil species we should not hesitate to give specific names to forms that differ only slightly from one another . . .” (1949:164). It was this philosophical approach that enabled Oliver as late as 1949 to describe one new genus and six new species of moas, all of which were based on a small number of isolated bones. As will be seen, none of these taxa appears to be valid.

It is my purpose here to propose species-limits within moas which it is hoped will reflect the biological structure of those species. I have attempted to obtain some estimate of intraspecific variability and to apply this to recognizing species-limits. Species based on isolated bones or on inadequate material are critically evaluated for validity; likewise, geographic representatives on separate islands, previously given separate species names, are here considered conspecific unless there is good evidence to the contrary. Species-limits of moas undoubtedly will remain a matter of personal opinion for some time to come, and I make no pretense at having arrived at a definitive picture. There is a need for additional studies, and the systematics of these birds would benefit especially from a comprehensive numerical-multivariate approach. I do believe, however, that the species-limits proposed in this paper considerably clarify moa taxonomy and facilitate more interesting studies of their evolution.

**MATERIALS AND METHODS.**—I have studied material of moas in the following museums (abbreviations used in the text follow in parentheses): British Museum (Natural History) (BM); American Museum of Natural History; Field Museum of Natural History; Canterbury Museum, Christchurch; Otago Museum, Dunedin; and National Museum of New Zealand (formerly Dominion Museum) (DM), Wellington. During this study the

only major collection I was unable to examine was that at the Auckland Museum (AM), Auckland. Fortunately, Archey's (1941) valuable monograph on the moas is based almost entirely on the Auckland collection and I was, therefore, able to incorporate much information on that material into this study.

Of the species recognized by Oliver (1949) I have examined material of all except *Pachyornis murihiku*, *Anomalopteryx antiquus*, *Megalapteryx hectori*, and *M. benhami*. All of these were described from isolated bones and it is probable that none represents a valid species, with the possible exception of *M. benhami*. Thus, I was able to study the majority of taxa in need of critical evaluation.

In addition to using standard univariate statistical procedures, I have employed several multivariate morphometric techniques in order to characterize patterns of intra- and interspecific variability in more detail. The theory and methodology of multivariate approaches and their application to biological problems are discussed by Blackith and Reyment (1971) and Oxnard (1973). Basically, these techniques describe patterns of variation or degrees of similarity (or difference) for many variables taken simultaneously over many taxa. I have used two techniques: (1) principal components analysis (BMDO1M; Dixon, 1970) in order to examine the structure of variation within groups, primarily to investigate problems of sexual dimorphism in size and shape within a species; (2) discriminant function-canonical analysis (BMDO7M; Dixon, 1970), in order to examine the patterns of variation among groups that are defined prior to the analysis. I employed this approach to examine the nature of the separations among the presumed species of a genus to evaluate species distinctness and the presence of sexual dimorphism. Part of the output of BMDO7M is a posterior probability classification which allows one to discover whether individuals assigned to one group prior to the analysis are in fact closer to the means of another group.

In all examples employing multivariate techniques, I undertook the analysis of each hindlimb element based either on my own data or that in Archey (1941) and Oliver (1949) using the following four variables: bone length, breadth of proximal end, breadth of shaft at midpoint, and breadth of distal end.

ACKNOWLEDGMENTS.—It is with pleasure that I dedicate this paper to Dr. Alexander Wetmore in honor of his ninetieth birthday, his many contributions to avian paleontology and ornithology, and especially for the affection he has shown us all.

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### Intraspecific Variability

The relative variability of one species of kiwi and four species of moas, all of which are believed to represent "good" biological species, are examined here. By gaining some understanding of the degree of variability within species recognized to be valid by nearly all previous workers, a basis of comparison can thereby be provided for assessing species-limits among the more controversial taxa considered in the following section. For reasons to be discussed below, these assessments of variability within "good" species cannot be used as absolute limits or criteria of species variability, but they can serve as guidelines.

### CAUSES OF VARIABILITY IN MOAS

It has been known for 100 years or more that moas are highly variable. Moreover, some workers have seemed to appreciate the fact—although they seldom stated so explicitly—that this variation is complex in nature and cannot be attributed to any

single factor. The main obstacle to understanding this variation is that of dealing with fossil (perhaps more correctly, subfossil) populations and their well-known problems of sampling in space and time. Some workers have sought to solve these problems either by ignoring them or by naming new species for each variant and thereby eliminating the necessity of delimiting or explaining intra-specific variability (note comments by Oliver cited above).

At this time it is not possible to make quantitative estimates of the separate factors contributing to patterns of variability within species of moas. Sample sizes for some species over their entire range, or for local populations of most species, are usually too small; stratigraphic control is lacking for all but a few of the moa specimens collected so far. Consequently, one is forced to estimate intuitively the relative importance of temporal, geographic, and individual components of variation. Within most fossil populations, particularly of moas, the following five factors seem important.

INTRAPOPULATIONAL VARIATION.—This is the variation observed in individuals of the same local interbreeding populations. We might expect the amount of such variation to be relatively low compared to those samples in which the influences of geographic or temporal variation are also present. Most of the samples discussed in this section do not represent single local populations; such samples probably do exist for certain species, but restrictions of time while in New Zealand did not permit me to study this aspect of variation in detail. Certain samples of *Apteryx australis* and *Euryapteryx curtus* (including *E. exilis*) might provide examples of this type of variation, and these are discussed below.

SEXUAL DIMORPHISM.—Since sexual size dimorphism is common in other ratites (with either males or females being larger), one would expect moas to show sexual size dimorphism also. Unfortunately, sample sizes are usually inadequate to lend support to this, although evidence is presented below of four probable examples of sexual size dimorphism in moas. The question of how much size difference to expect between sexes must be considered when dealing with fossil populations: if there were too great a difference between two particular samples, then we might be inclined to recognize two species rather than two sexes. But

## ANALYSIS OF SPECIES

what is "too great" a difference? Almost no quantitative information has been published about dimorphism in other ratites. In one study of the Emu (*Dromiceius novaehollandiae*), data gathered by Long (1965) show that coefficients of variation (CV) of combined male-female samples range from 3.5 for bill length to 19.14 for body weight. Coefficients of variation for lengths of a few skeletal elements range from 4.77 for the tarsometatarsus to 5.28 for the tibiotarsus. These CVs for the skeletal elements are generally less than those calculated for the expanded species of moas discussed in the next section.

**GEOGRAPHIC VARIATION.**—The major factor in this type of variation in moas is probably inter-island differentiation. It has previously been noted that the bones of North Island forms tend to be shorter and less stout than those of comparable taxa from the South Island (Archey, 1941:62, 71; Scarlett, 1972:20; Oliver, 1949:164). In addition, some intra-island differentiation may have occurred, but samples are too limited to confirm this. I believe geographic differentiation contributes greatly to the large variability in the samples of certain species discussed below.

**TEMPORAL VARIATION.**—It is difficult to assess the importance of temporal variation in affecting variability within moas. The chronology of natural moa deposits is not well known. One can be reasonably certain that these assemblages are no older than 7000–8000 years, and most are undoubtedly much younger, apparently less than 4000 years old (Fleming, 1962). Hence, it may be that temporal variation contributes relatively little to the variability of the available samples of moas.

**VARIATION AND RECENCY OF SYMPATRY.**—If speciation in moas has resulted from isolation in forest refugia during glacial maxima, then it is reasonable to assume that variability would have increased as a result of this isolation, thus providing an example of intra-island geographic variation. Many samples of moas probably are composed of different populations that had come in contact following the last glaciation. Thus, we may be sampling birds that had recently diverged morphologically, and some of the variation observed may be the result of recent character displacement in size following this contact.

Basic statistical data for the femora, tibiotarsi, and tarsometatarsi of *Apteryx australis* and four species of moas are given in Table 1. Of particular importance for the discussions that follow are the coefficients of variation (CV), which are measures of relative variability independent of size.

*Apteryx australis*: This sample (housed in the National Museum of New Zealand) of 24–32 individuals referable to the modern Brown Kiwi, comes from the Castle Rocks cave deposit on the South Island. It is evident from Table 1 that *A. australis*, with CVs ranging from 4.68 to 7.6, exhibits less variability than any of the moas. I attribute this to the relative lack of geographic and temporal influences since the sample comes from a single locality and was probably deposited over a relatively short span of time. Of the species studied, this sample of *A. australis* possibly comes closest to representing only intrapopulational variation. The degree of variability in this sample is similar to that shown by fossil populations of some species of gruiforms (Cracraft, 1973b). In *A. australis*, measurements of length are less variable than those of breadth.

*Megalapteryx didinus*: This sample is taken from many localities in the South Island (data from Archey, 1941; Oliver, 1949). In a later section I synonymize *M. hectori* with *M. didinus*, but specimens assigned to the former are not included in this sample. This species may be one of the more variable of moas in that the lowest CV is 5.79 while the highest is 12.04. Most of this variability is probably attributable to geographic variation. As with *A. australis*, measurements of length are less variable than those of breadth.

*Anomalopteryx didiformis*: The analysis of this species is based on a large sample collected from sites on both islands. Included in this series by Archey (1941, table A) are a few specimens that might be assigned to Oliver's (1949) species *A. parvus*. Few workers accept *A. parvus* as a distinct species (see below) and my analysis is based on all the specimens listed by Archey. This species also shows a fairly high degree of variability, with CVs ranging from 6.79 to 9.3. Again, lengths are less variable than other measurements. The variability of this sample is probably influenced substantially by geographic and intrapopulational variation.

TABLE 1.—Statistics for *Apteryx australis* and four species of moas (measurements in mm)

| Character               | <i>Apteryx<br/>australis</i> | <i>Megalapteryx<br/>didinus</i> | <i>Anomalopteryx<br/>didiformis</i> | <i>Dinornis<br/>torosus</i> | <i>Pachyornis<br/>elephantopus</i> |
|-------------------------|------------------------------|---------------------------------|-------------------------------------|-----------------------------|------------------------------------|
| <b>FEMUR</b>            |                              |                                 |                                     |                             |                                    |
| <b>Length</b>           |                              |                                 |                                     |                             |                                    |
| n .....                 | 24                           | 16                              | 38                                  | 16                          | 21                                 |
| $\bar{x}$ .....         | 89.45                        | 245.69                          | 238.45                              | 295.38                      | 308.86                             |
| SD .....                | 4.43                         | 15.29                           | 16.2                                | 17.73                       | 15.54                              |
| CV .....                | 4.96                         | 6.22                            | 6.79                                | 6                           | 5.03                               |
| <b>Proximal breadth</b> |                              |                                 |                                     |                             |                                    |
| n .....                 | 24                           | 13                              | 37                                  | 12                          | 20                                 |
| $\bar{x}$ .....         | 20.1                         | 71.62                           | 82.27                               | 108.83                      | 129.55                             |
| SD .....                | 1.53                         | 6.19                            | 7.65                                | 10.21                       | 12.11                              |
| CV .....                | 7.6                          | 8.64                            | 9.3                                 | 9.38                        | 9.35                               |
| <b>Distal breadth</b>   |                              |                                 |                                     |                             |                                    |
| n .....                 | 24                           | 15                              | 38                                  | 12                          | 21                                 |
| $\bar{x}$ .....         | 21.45                        | 75.73                           | 85.53                               | 117.58                      | 145.57                             |
| SD .....                | 1.13                         | 7.72                            | 7.89                                | 11.75                       | 8.84                               |
| CV .....                | 5.25                         | 10.2                            | 9.26                                | 9.99                        | 6.07                               |
| <b>TIBIOTARSUS</b>      |                              |                                 |                                     |                             |                                    |
| <b>Length</b>           |                              |                                 |                                     |                             |                                    |
| n .....                 | 32                           | 15                              | 39                                  | 14                          | 27                                 |
| $\bar{x}$ .....         | 129.93                       | 385.33                          | 377.21                              | 588.36                      | 542.93                             |
| SD .....                | 6.08                         | 22.3                            | 27.33                               | 36.77                       | 37.97                              |
| CV .....                | 4.68                         | 5.79                            | 7.25                                | 6.25                        | 6.99                               |
| <b>Proximal breadth</b> |                              |                                 |                                     |                             |                                    |
| n .....                 | 32                           | 12                              | 33                                  | 10                          | 19                                 |
| $\bar{x}$ .....         | 17.31                        | 85.58                           | 101.27                              | 139.7                       | 167.42                             |
| SD .....                | 1.06                         | 7.75                            | 8.9                                 | 8.34                        | 14.32                              |
| CV .....                | 6.11                         | 9.06                            | 8.79                                | 5.97                        | 8.56                               |
| <b>Distal breadth</b>   |                              |                                 |                                     |                             |                                    |
| n .....                 | 32                           | 15                              | 38                                  | 13                          | 27                                 |
| $\bar{x}$ .....         | 15.71                        | 51.93                           | 56.71                               | 82.07                       | 97.33                              |
| SD .....                | 0.88                         | 6.25                            | 4.89                                | 6.86                        | 9                                  |
| CV .....                | 5.59                         | 12.04                           | 8.62                                | 8.36                        | 9.25                               |
| <b>TARSOMETATARSUS</b>  |                              |                                 |                                     |                             |                                    |
| <b>Length</b>           |                              |                                 |                                     |                             |                                    |
| n .....                 | 30                           | 18                              | 43                                  | 16                          | 29                                 |
| $\bar{x}$ .....         | 64.85                        | 179.39                          | 179.02                              | 303.13                      | 230.55                             |
| SD .....                | 3.3                          | 10.9                            | 13.96                               | 22.75                       | 15.75                              |
| CV .....                | 5.09                         | 6.07                            | 7.8                                 | 7.51                        | 6.83                               |
| <b>Proximal breadth</b> |                              |                                 |                                     |                             |                                    |
| n .....                 | 29                           | 16                              | 41                                  | 13                          | 27                                 |
| $\bar{x}$ .....         | 17.17                        | 53.25                           | 59.15                               | 88.54                       | 105.85                             |
| SD .....                | 0.98                         | 5.04                            | 5.34                                | 5.08                        | 10.25                              |
| CV .....                | 5.73                         | 9.46                            | 9.03                                | 5.73                        | 9.68                               |
| <b>Distal breadth</b>   |                              |                                 |                                     |                             |                                    |
| n .....                 | 30                           | 17                              | 42                                  | 14                          | 29                                 |
| $\bar{x}$ .....         | 21.05                        | 72.41                           | 77.43                               | 112.71                      | 134.52                             |
| SD .....                | 1.11                         | 7.4                             | 6.26                                | 7.62                        | 12.06                              |
| CV .....                | 5.29                         | 10.22                           | 8.08                                | 6.76                        | 8.97                               |

*Dinornis torosus*: The data for this species are based on a small sample collected from many sites in the South Island (Archey, 1941; Oliver, 1949). Variability is fairly high, with CVs ranging from 5.73 to 9.99. This is the only species in which lengths tend to be more variable than breadths. Variability in this sample is probably affected by geographic and temporal components.

*Pachyornis elephantopus*: This sample is from various sites on the South Island (Archey, 1941; Oliver, 1949; and measurements by the author). Coefficients of variation are comparable to those of *A. didiformis* and *D. torosus*, ranging from 5.03 to 9.68. Once again, length measurements are less variable than those of breadth. Intra-island components probably contribute substantially to variability in this species.

#### SUMMARY

Variability within individual species of moas appears somewhat higher than is found in most other birds so far studied. For example, in six fossil species of gruiforms, CVs for hindlimb elements averaged 6–7 (Cracraft, 1973b:97–107). Simpson (1946) presented data for the King Penguin (*Aptenodytes patagonicus*) and Goodge (1951) analyzed variability in the Common Murre (*Uria aalge*); both workers found low CVs, averaging 2–4, in these extant species.

Data for *A. didiformis*, *D. torosus*, and *P. elephantopus* would seem to suggest that in moas CVs generally fall in the range of 6–10, but if the sample of *M. didinus* were used as a standard, then CVs as high as 10–12 might be expected within a single species. Indeed, estimates based on the above samples may be conservative in that they possibly include only individuals of a single sex, specimens of the other sex previously having been considered as forming a distinct species.

During growth, the length of long bones apparently reaches its maximum value before maximum body weight is obtained (Cock, 1963). Bone breadths of adults, on the other hand, probably reflect final body weight since they have a mechanical relationship to the amount of weight that can be supported. It can thus be expected that breadth measurements will tend to be more variable than those for length, since the former depend upon variation in body weight at the termination of

growth. Estimates of variation in length might be preferred over those for breadth as a more precise, and more conservative, measure of intraspecific variability. For this reason the comparisons in the following section will be based on measurements of length.

#### Systematics

In this section I have attempted to formulate species limits based on information from univariate and multivariate analyses of variation, personal examination and comparison of many complete and partial skeletons, and an evaluation of previously published opinions on moa systematics. Detailed discussions of morphology (particularly at the generic level and higher), natural history, and taxonomic synonymies can be found in Archey (1941), Oliver (1949), Brodkorb (1963), or papers cited therein, and are not included here unless they bear directly on the subject of species limits.

#### Family DINORNITHIDAE

##### Subfamily ANOMALOPTERYGINAE

##### *Anomalopteryx* Reichenbach, 1852

SUMMARY.—Two species of *Anomalopteryx* are tentatively admitted here—a larger form, *A. didiformis*, found on both North and South islands, and a smaller, less common form, *A. oweni*, found only on the North Island.

##### *Anomalopteryx didiformis* (Owen, 1844)

SYNONYMS.—*Anomalopteryx parvus* (Owen, 1883), *Anomalopteryx antiquus* Hutton, 1892.

Of the two species of the genus recognized here, this was the more common and occurred on both the North and South islands. Archey's (1941:14–29) discussion, although not employing statistical methods, amply demonstrated the great variation present within this species.

*Anomalopteryx parvus*, based on fairly extensive material from both islands, is included in this species, following Archey (1941), Brodkorb (1963), and Scarlett (1972). This is contrary to Oliver (1949:138), who maintained *A. parvus* as distinct. Oliver (1949:144–145, figs. 115–116) pictured bones

of the two species for comparative purposes, and indeed these appear quite different in size. Oliver's method of analysis and argumentation, however, was to compare the extremes in size or shape, thus magnifying the differences. There is a continuity in size and morphology in specimens assigned to these two species (Archey, 1941:18); thus, unlike examples to be described below in other genera, it is not possible to recognize two size groups within *A. didiformis* that could represent sexual size dimorphism.

According to Scarlett (1972:22), *A. antiquus* is now considered to come from lower Pleistocene deposits rather than being Miocene or Pliocene in age as previously thought. Scarlett further indicated that *A. antiquus* is "doubtfully distinct from *didiformis*" and that there are no significant morphological differences between them. Likewise, Archey (1941:29) noted close similarities between the two species. I did not locate the type during my stay at the Canterbury Museum. At present I believe that compelling evidence is lacking to maintain *A. antiquus* as a separate species.

#### *Anomalopteryx oweni* (Haast, 1885)

There has been some controversy about the generic assignment of this species. As did all other early workers, Haast (1885, 1886) placed this species in *Dinornis*. Shortly thereafter, Lydekker (1891:280) put *oweni* in *Anomalopteryx* on the basis of its skull morphology. Archey (1941:44) transferred the species to *Pachyornis* without comment; Brodkorb (1963:211) followed Archey. Oliver (1949:134–135) returned *oweni* to *Anomalopteryx*, claiming that the type cranium illustrated by Haast (1886) shows the diagnostic features of *Anomalopteryx*, as does the associated premaxilla, and that most of the skeletal material assigned to *oweni* by Archey belongs to *Pachyornis septentrionalis* (= *P. mappini* of this paper).

Although I was unable to examine the type-material of *A. oweni* in the Auckland Museum, several comments on the species can still be made. The cranium and premaxilla illustrated by Haast do appear to be more similar to *Anomalopteryx* than to *Pachyornis*, although the rounded anterior border of the temporal fossa in dorsal view and the markedly sloping nasal region in lateral view do not resemble species of either genus. Some of the

hindlimb elements listed by Archey as belonging to *oweni* are within the size range of *Pachyornis mappini* (including *P. septentrionalis*), whereas others appear to be too small to be referred to that species. Thus, until the systematics of *oweni* can be clarified by restudy of the type and comparison with other material, I tentatively include it as a valid species in the genus *Anomalopteryx*.

#### *Megalapteryx* Haast, 1886

SUMMARY.—Two species of *Megalapteryx* are accepted here—a small one, *M. didinus*, and a larger one, *M. benhami*. Both are known from the South Island, the alleged presence of *M. didinus* in the North Island being doubtful.

#### *Megalapteryx didinus* (Owen, 1883)

SYNONYM.—*Megalapteryx hectori* Haast, 1886.

*Megalapteryx didinus* is known from a moderate number of bones from the South Island, few of which were found in association. The presence of this species on the North Island is suspect (Oliver, 1949:151–152).

Archey (1941) synonymized *M. hectori* with *M. didinus* without comment, but Oliver (1949:149) maintained the species. Brodkorb (1963) and Scarlett (1972) followed Archey. I also believe there is insufficient evidence to justify recognition of *M. hectori*. Only a few limb bones are presumably applicable to this species (I did not examine the type, which is in the Nelson Museum), and their size, although somewhat smaller than typical bones of *M. didinus*, probably falls within the limits of variability for that species. For example, CVs for the lengths of the hindlimb elements for the combined sample of *M. didinus* and *M. hectori* are comparable to CVs of the other moas listed in Table 1: e.g., femur, 8.45; tibiotarsus, 6.76; and tarsometatarsus, 7.40. I therefore follow the authors cited above in synonymizing *hectori* with *didinus*.

#### *Megalapteryx benhami* Archey, 1941

This species was described on the basis of a femur and a tibiotarsus, not positively associated, from the Mt. Arthur region, South Island. Oliver (1949) also lists a femur from Wairanga, South Island.

The bones were placed in *Megalapteryx* on the basis of several morphological characters associated with the rotular groove and muscle scars (Archey, 1941:35), and it would be important for future workers to confirm the validity of these characters in distinguishing genera. As many authors have noted, there is great variability in the form of the femur and it is frequently difficult to identify this element to genus unless found in association with more diagnostic bones. As it now stands, the species *M. benhami* can be tentatively accepted, as its larger size (mean femur length of 296.5 mm; length of tibiotarsus, 454 mm) is very probably outside the range of variation for *M. didinus*. Future workers need to restudy the material of this species in order to verify its validity and generic assignment.

### *Pachyornis* Lydekker, 1891

SUMMARY.—Two species of *Pachyornis* are recognized here. The larger, *P. elephantopus*, is known only from the South Island. A smaller species, *P. mappini*, showing what appears to be pronounced sexual dimorphism in size, was restricted to the North Island.

### *Pachyornis elephantopus* (Owen, 1856)

SYNONYMS.—*Pachyornis murihiku* Oliver, 1949; *Pachyornis australis* Oliver, 1949.

*Pachyornis elephantopus* was restricted to the South Island and was the larger of the two species of the genus recognized here. It was also one of the more common species of moas and is represented by a number of complete skeletons from the Pyramid Valley Swamp.

Oliver (1949:67) described *P. murihiku* for a single skeleton said to be from a "full-grown but not quite mature" individual from Southland, South Island. The type was supposedly in the Southland Museum, Invercargill, but according to Scarlett (1972:21) it cannot now be found. Both Brodkorb (1963) and Scarlett (1972) accepted *P. murihiku* as a distinct species. The measurements of *P. murihiku* indicate that it was only slightly smaller than *P. elephantopus* (Oliver, 1949:59, 86–87); furthermore, if the measurements of the limb bones of *P. murihiku* are included in the

sample of *P. elephantopus* in Table 1, the CVs of bone length are not appreciably increased; viz. femur, 6.52; tibiotarsus, 8.04; and tarsometatarsus, 7.67. Oliver (1949:68–70) listed the following characters as distinguishing *P. murihiku* from *P. elephantopus*: (1) culmen rises at a higher angle, (2) the "front of the body [of the sternum] is not bent upwards so far as to bring it to a right angle with the rest of the body," and (3) the ischia and pubes are widely diverging. It is difficult to evaluate these features in terms of species differences, especially since the type of *P. murihiku* is from an immature individual. In the absence of additional material it may be questioned whether the above differences should be accepted as being consistent between the two species. There is a great deal of variation in skeletons of *P. elephantopus*, and I believe that the above features of *P. murihiku* must be verified by additional specimens before this species is accepted as valid.

Oliver (1949:70) described another species of *Pachyornis*, *P. australis*, from a single well-preserved cranium from Takaka River, South Island. Both Brodkorb (1963) and Scarlett (1972) accepted *P. australis* as a distinct species, although Scarlett indicated that it may be a variant of *P. elephantopus*. I have compared the type (DM 26) with a large series of skulls of *P. elephantopus* and can find no significant differences that can be regarded as being of specific value. Even though the skull of *P. australis* is at the lower end of the size range for *P. elephantopus*, several skulls assigned to the latter species by Oliver himself (1949:84) are of comparable size (e.g., DM 95, DM 198, DM 333). Crania of *P. elephantopus* exhibit considerable variability in shape and in the development of processes and muscle scars. For example, within a series of skulls of *P. elephantopus* in the National Museum of New Zealand it was possible to find the following characters attributed to "*P. australis*" by Oliver (1949:70–72): (1) skull wider in proportion to length, (2) evenly rounded cranium, (3) wide space between lambdoidal and temporal ridges, and (4) narrow temporal fossa. Furthermore, there are similarities in rostral shape and considerable variation in the development of the transverse process of the basisphenoid rostrum. Therefore, it does not seem prudent to accept *P. australis* as a valid species.



***Pachyornis mappini* Archey, 1941**

SYNONYM.—*Pachyornis septentrionalis* Oliver, 1949.

Archey (1941:41) proposed this species for a small North Island form of *Pachyornis*. The type (AM 124) is an almost complete skeleton. Most of the remaining material assigned to *P. mappini* consists of isolated elements and many of those in the National Museum of New Zealand have been acquired recently and are as yet undescribed.

Oliver (1949:61) described a new species, *P. septentrionalis*, for a partial skeleton (DM 129), also from the North Island. He included in this species those bones from the lower end of the series that Archey (1941) placed in *P. mappini*. Oliver (1949:61) stated that bones of *P. septentrionalis*, in addition to being smaller, are also more slender than those of *P. mappini*. Brodkorb (1963) accepted both species, while Scarlett (1972) suggested that the two might be conspecific.

An analysis of the skeletal measurements of these nominal species (Archey, 1941:139; Oliver, 1949: 86; measurements by the author) indicates that two separable populations do appear to exist, the major difference between them being in size (Table 2). Using principal components analysis of each element of the hindlimb (Figure 1), a moderately well-defined separation between the two forms can be demonstrated along the first principal component, which in this case is a size axis. The second component is a shape axis, mainly defining

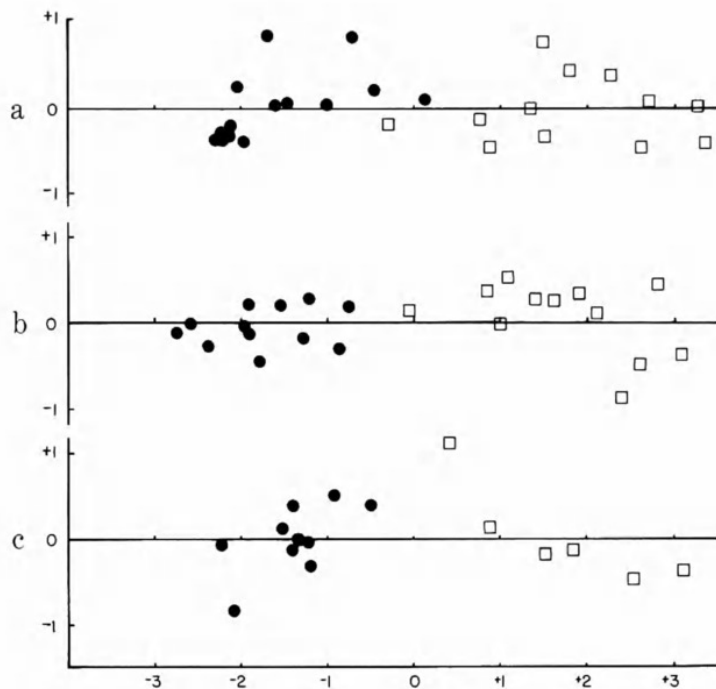


FIGURE 1.—Principal components analyses of logarithmically transformed measurements of the femur (a), tibiotarsus (b), and tarsometatarsus (c) of *Pachyornis septentrionalis* (dark circles) and *P. mappini* (open squares). The first principal component of each analysis is graphed along the abscissa and is a size axis; the second principal component is graphed along the ordinate and is a shape axis, primarily indicating relative robustness. (Note that the two taxa are separated by size but not by shape. See text for details.)

relative robustness, and it is evident that the two populations do not differ significantly in this respect. Thus, Oliver's (1949:61) claim that bones of *P. septentrionalis* are more slender than those of *P.*

TABLE 2.—Statistics for *Pachyornis mappini* and *P. septentrionalis* (measurements in mm)

| Character                        | <i>P. mappini</i> | <i>P. septentrionalis</i> | <i>P. mappini</i> +<br><i>P. septentrionalis</i> |
|----------------------------------|-------------------|---------------------------|--|
| <b>Length of femur</b>           |                   |                           |  |
| n .....                          | 12                | 14                        | 26   |
| $\bar{x}$ .....                  | 206.25            | 174.07                    | 188.92   |
| SD .....                         | 12.88             | 11.63                     | 20.27  |
| CV .....                         | 6.24              | 6.68                      | 10.73  |
| <b>Length of tibiotarsus</b>     |                   |                           |  |
| n .....                          | 12                | 12                        | 24   |
| $\bar{x}$ .....                  | 365.5             | 291.67                    | 328.58   |
| SD .....                         | 30.44             | 14.79                     | 44.38  |
| CV .....                         | 8.33              | 5.07                      | 13.51  |
| <b>Length of tarsometatarsus</b> |                   |                           |  |
| n .....                          | 7                 | 10                        | 17   |
| $\bar{x}$ .....                  | 156.29            | 133                       | 142.59   |
| SD .....                         | 12.57             | 3.71                      | 14.37  |
| CV .....                         | 8.04              | 2.79                      | 10.08  |

TABLE 3.—Posterior probability classification of stepwise discriminate function analysis for bones assigned to *Pachyornis mappini* and *P. septentrionalis*

| Character                       | <i>P.</i><br><i>mappini</i> | <i>P.</i><br><i>septentrionalis</i> | <i>n</i> | Percent<br>misclassified |
|---------------------------------|-----------------------------|-------------------------------------|----------|--------------------------|
| <b>Femur</b>                    |                             |                                     |          |                          |
| <i>P. mappini</i> .....         | 11                          | 1                                   | 12       | 8.3                      |
| <i>P. septentrionalis</i> ..... | 1                           | 13                                  | 14       | 7.1                      |
| <b>Tibiotarsus</b>              |                             |                                     |          |                          |
| <i>P. mappini</i> .....         | 12                          | 0                                   | 12       | 0                        |
| <i>P. septentrionalis</i> ..... | 0                           | 12                                  | 12       | 0                        |
| <b>Tarsometatarsus</b>          |                             |                                     |          |                          |
| <i>P. mappini</i> .....         | 7                           | 0                                   | 7        | 0                        |
| <i>P. septentrionalis</i> ..... | 0                           | 10                                  | 10       | 0                        |

*mappini* is not substantiated. In order to examine further the distinction between the two forms, I analyzed the data using a step-wise discriminate function-canonical analysis. The distinctness of the two groups was further verified and few of the elements were misclassified (Table 3).

What is the meaning of these differences? If, in fact, the two taxa do not represent distinct species, then very likely we are dealing with sexual size differences. Table 2 presents some basic statistical data for lengths of the hindlimb bones. The combined sample of measurements for the lengths of the femur and tarsometatarsus do not show CVs much higher than those for *P. mappini* alone, or for those of other moas (Table 1). It can be noted also that the CV of 2.79 for the tarsometatarsus length of *P. septentrionalis* (Table 2) is suspiciously low compared to CVs of other moas. It is my belief that these two skeletal populations probably represent different sexes and that Oliver's (1949) description of a new species was unwarranted. I therefore synonymize *septentrionalis* with *mappini* until firm evidence can be offered that they are distinct.

#### *Euryapteryx* Haast, 1874

SYNONYM.—*Zelornis* Oliver, 1949.

Oliver (1949:117–128) created the genus *Zelornis* for the species *Euryapteryx exilis* Hutton (the genotype) and *Emeus haasti* Rothschild. Archey (1941) considered the former to be a valid species in the genus *Euryapteryx*, while the latter he treated as a synonym of *Euryapteryx gravis* (p. 54). The diagnostic feature separating *Zelornis* from *Euryapteryx* was said to be the high arched culmen.

Oliver (1949:110) admitted that there were no differences in the shape of the postcranial elements. The type-specimen of *Z. exilis* is a skeleton from Wangaehu in the Wanganui Museum. The skull was figured by Oliver (1949, figs. 92–94) where it is readily apparent that the premaxilla is considerably broken and abraded. The premaxilla of *Z. exilis* does not appear to differ in shape from those referred to *Z. haasti*. I have examined nearly all of the cranial material assigned to *Zelornis haasti* by Oliver (1949:127) and can find no important differences in size or shape that will distinguish it at the generic level from *Euryapteryx*. To my knowledge Scarlett (1972) is the only recent author to synonymize *Zelornis* with *Euryapteryx*, and I concur with his decision.

SUMMARY.—Two sexually dimorphic species are recognized here—a moderately large form, *E. geranoides*, present on both North and South islands, and a small species, *E. curtus*, confined to North Island.

#### *Euryapteryx curtus* (Owen, 1846)

SYNONYMS.—*Euryapteryx exilis* Hutton, 1897; *Euryapteryx tane* Oliver, 1949.

*Euryapteryx curtus* was a small species of moa, apparently confined to the North Island. The only morphological difference between *E. curtus* and *E. exilis* is in size (Archey, 1941:60), *E. exilis* being slightly larger (Table 4). In order to assess the morphological similarities in size and shape in *Euryapteryx*, I analyzed the measurements of the femur, tibiotarsus, and tarsometatarsus given by Archey (1941) and Oliver (1949), using principal components and canonical analyses. Figure 2 plots

TABLE 4.—Statistics for species of *Euryapteryx* (measurements in mm)

| Character                        | <i>E. tane</i> | <i>E. curtus</i> | <i>E. exilis</i> | <i>E. exilis</i> +<br><i>E. curtus</i> | <i>E. geranoides</i> | <i>E. gravis</i> | <i>E. gravis</i> +<br><i>E. geranoides</i> |
|----------------------------------|----------------|------------------|------------------|--|----------------------|------------------|--|
| <b>Length of Femur</b>           |                |                  |                  |  |                      |                  |  |
| n .....                          | 3              | 15               | 18               | 33                                     | 8                    | 13               | 21   |
| $\bar{x}$ .....                  | 190.67         | 167.6            | 198.17           | 184.27                                 | 236.63               | 280.15           | 263.57                                     |
| SD .....                         | 9.29           | 12.82            | 10.89            | 18.24                                  | 12.53                | 10.89            | 24.4                                       |
| CV .....                         | 4.87           | 7.65             | 5.5              | 9.9                                    | 5.3                  | 3.89             | 9.26                                       |
| <b>Length of tibiotarsus</b>     |                |                  |                  |  |                      |                  |  |
| n .....                          | 3              | 20               | 17               | 37                                     | 5                    | 12               | 17   |
| $\bar{x}$ .....                  | 328            | 268.8            | 331.65           | 297.68                                 | 387.6                | 475.17           | 449.41                                     |
| SD .....                         | 9              | 16.5             | 12.67            | 34.97                                  | 17.99                | 21.57            | 45.74                                      |
| CV .....                         | 2.74           | 6.14             | 3.82             | 11.75                                  | 4.64                 | 4.54             | 10.18                                      |
| <b>Length of tarsometatarsus</b> |                |                  |                  |  |                      |                  |  |
| n .....                          | 3              | 19               | 15               | 34                                     | 9                    | 13               | 22   |
| $\bar{x}$ .....                  | 149            | 124.74           | 148.4            | 135.12                                 | 174.78               | 209.62           | 195.36                                     |
| SD .....                         | 7.55           | 8.29             | 4.39             | 13.64                                  | 12.34                | 16.16            | 22.68                                      |
| CV .....                         | 5.07           | 6.65             | 2.96             | 10.09                                  | 7.06                 | 7.71             | 11.61                                      |

group centroids for the first two canonical axes. The multivariate analysis substantiates the separation of *E. exilis* and *E. curtus*, but the centroids themselves as projected onto the first axis are only about two and a half SD units from each other (except for the tibiotarsus where they are almost four units apart). If one examines the statistics of the combined sample (Table 4), the population *E. exilis* + *E. curtus* has CVs of about 10–12 for bone lengths. This variability is comparable to that of *Pachyornis mappini*, and I believe it is likely that the difference between *E. exilis* and *E. curtus* is one of sexual size dimorphism. Most of the specimens in Archey's series of these two forms (1941, tables H, I) come from Doubtless Bay, North Island.

Oliver (1949:105) described a separate species, *E. tane*, for a small number of specimens that were larger than those of *E. curtus*. He (1949:123) noted that some of the leg bones of *E. tane* possibly belonged to what he called *Zelornis exilis*. It is readily apparent that the samples of *E. tane* and *E. exilis* are virtually identical (Table 4; Figure 2). There is little question, therefore, that *E. tane* should be synonymized with *E. curtus* as defined here.

#### *Euryapteryx geranoides* (Owen, 1848)

SYNONYMS.—*Euryapteryx gravis* (Owen, 1870), *Zelornis haasti* (Rothschild, 1907).

The type-material of *E. geranoides* consists of a

cranium, premaxilla, and mandible collected at Te Rangatapu, North Island, and housed in the British Museum (Natural History). According to Oliver (1949:106) the mandible belongs to *Anomalopteryx didiformis*, and the cranium and premaxilla, which may or may not be associated, belong to *Euryapteryx*. To my knowledge a lectotype has not yet been designated, but the cranium (BM 21687) would be a logical choice. The type cranium and premaxilla are smaller than most of the material attributed to *E. gravis* but larger than in *E. curtus*. Therefore, *E. geranoides* has been accepted as a distinct species of intermediate size by Archey (1941), Oliver, (1949), and Brodkorb (1963). It should be pointed out that there is apparently no postcranial material directly associated with cranial material attributable to *E. geranoides* (*sensu stricto*).

Material assigned to the large form known as *E. gravis* is abundant in South Island localities (the type-skeleton in the British Museum is from Kakanui) but very rare on the North Island (Archey, 1941:54–56; Oliver, 1949:108–112). Statistics presented in Table 4 and the results of the canonical analyses shown in Figure 2 confirm the intermediate position of *E. geranoides* between "*E. exilis*" (= *E. curtus*) and *E. gravis*. The question is whether *E. geranoides* is a distinct species, and if not, to which species—the larger *E. gravis* or the smaller *E. curtus*—this skeletal population belongs. Recently, Scarlett (1972:21) suggested that *E. gera-*

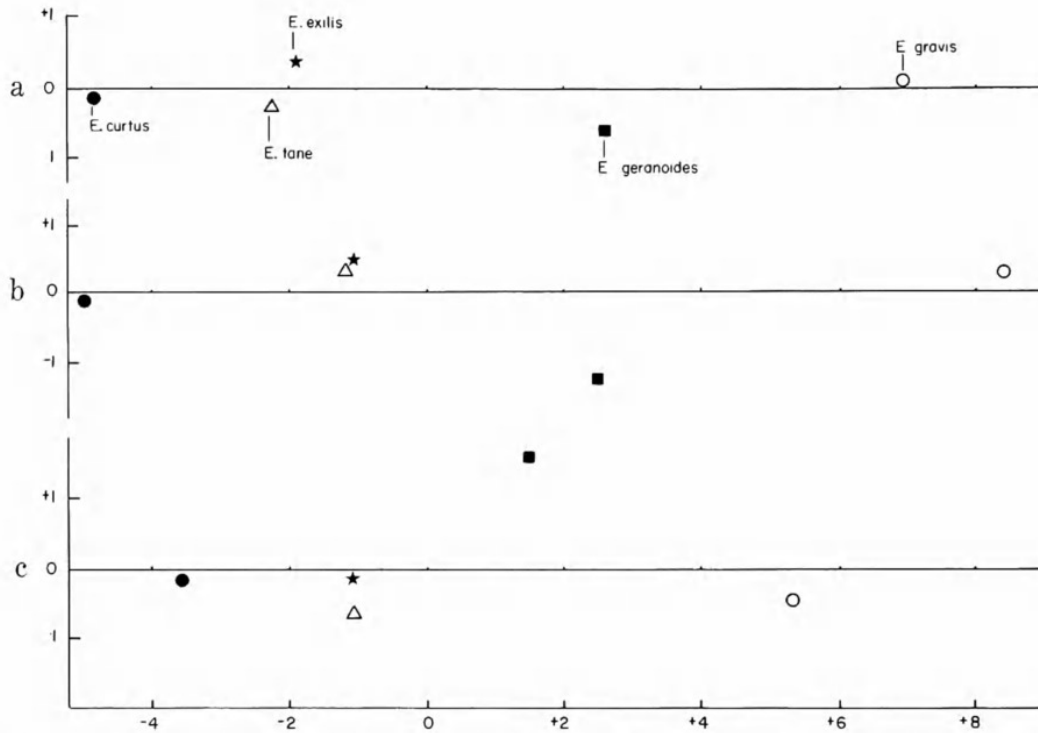


FIGURE 2.—Group centroids of five nominal taxa of *Euryapteryx* plotted against the first (abscissa) and second (ordinate) canonical axes for logarithmically transformed measurements of the femur (a), tibiotarsus (b), and tarsometatarsus (c). Scales are in standard deviation units. Note the closeness of group centroids of *E. tane* and *E. exilis*, the closeness of *E. curtus* to *E. tane*–*E. exilis*, and the intermediate position of *E. geranoides* between *E. gravis* and the smaller forms. (See text for details.)

*noides* might be united with *E. curtus* once the gaps were eliminated.

I would like to suggest here that *E. geranoides* is conspecific with *E. gravis* and that these forms represent another case of sexual size dimorphism. The evidence is two-fold. First, measurements of the combined sample exhibit CVs very similar to those seen in *P. mappini*–*P. septentrionalis* and *E. curtus*–*E. exilis*, the two other presumed examples of sexual size dimorphism (Table 4). Secondly, bones attributed to *E. geranoides* and *E. gravis* occur on both North and South islands. If *E. geranoides* were conspecific with *E. curtus* (or with *E. exilis*, if this form were distinct from *E. curtus*), then the absence of *E. curtus* from the South Island is unexplained. If *E. geranoides* and *E. exilis* represented different sexes, then both should be present on the South Island. Present evidence, therefore, is more consistent with the hypothesis that *E. curtus*–*E. exilis* constitute one sexually dimorphic species and *E. geranoides*–*E. gravis* another. In the case of the latter, the older name, *geranoides*, has priority.

As noted above, the cranial material of *Zelornis haasti* is very similar to that of *E. geranoides*. The femur and tibiotarsus of the one skeleton of *Z. haasti* are somewhat larger than typical “*E. gravis*” (Oliver, 1949:128; see also Table 4), but the associated tarsometatarsus is easily within the size range of that form. Hence, it is likely that the few bones assigned to *Z. haasti* are large, perhaps aberrant bones of *E. geranoides*, and I follow Archey (1941) in synonymizing *haasti*.

### *Emeus* Reichenbach, 1852

#### *Emeus crassus* (Owen, 1846)

SYNONYM.—*E. huttonii* (Owen, 1879).

There has been little difference of opinion about species-limits within *Emeus*. Most recent authors (Archey, 1941; Oliver, 1949; Brodkorb, 1963) have accepted two species, the large *crassus* and the smaller *huttonii*. Only Scarlett (1972:22) has combined the two species, stating that several specimens from Pyramid Valley are intermediate in

TABLE 5.—Statistics for species of *Emeus* (measurements in mm)

| Character                        | <i>E. crassus</i> | <i>E. huttonii</i> | <i>E. crassus</i> +<br><i>E. huttonii</i> |
|----------------------------------|-------------------|--------------------|---|
| <b>Length of femur</b>           |                   |                    |   |
| n .....                          | 21                | 10                 | 31  |
| $\bar{x}$ .....                  | 272.81            | 238.4              | 261.71                                    |
| SD .....                         | 12.23             | 11.92              | 20.24                                     |
| CV .....                         | 4.48              | 5                  | 7.73                                      |
| <b>Length of tibiotarsus</b>     |                   |                    |   |
| n .....                          | 21                | 11                 | 32  |
| $\bar{x}$ .....                  | 464.24            | 386.64             | 437.56                                    |
| SD .....                         | 23.08             | 19.01              | 43.16                                     |
| CV .....                         | 4.97              | 4.92               | 9.86                                      |
| <b>Length of tarsometatarsus</b> |                   |                    |   |
| n .....                          | 22                | 10                 | 32  |
| $\bar{x}$ .....                  | 213.55            | 184.4              | 204.44                                    |
| SD .....                         | 11.58             | 13.46              | 18.22                                     |
| CV .....                         | 5.42              | 7.3                | 8.91                                      |

size. Both forms occurred in the South Island and are known primarily from the Canterbury and Otago districts. Although according to Archey (1941:51) several bones referable to *Emeus* have allegedly been found at Martinborough and Te Aute on the North Island, Yaldwyn (1956) does not list *Emeus* from the Martinborough Caves, nor did Oliver (1949) make note of *Emeus* on the North Island. On the South Island *E. crassus* has been reported as moderately common, whereas *E. huttonii* was apparently less so.

Statistics presented in Table 5 show that the bones assigned to *E. crassus* and *E. huttonii* by Archey (1941) and Oliver (1949) comprise two distinct populations. Multivariate analysis of the hindlimb measurements verifies the univariate re-

sults, and in the posterior probability classification of the discriminate function analysis, few bones are misclassified (Table 6).

The two forms of *Emeus* could represent two species, or alternatively, they might represent sexual dimorphism within a single species. It is my opinion that the latter hypothesis is more probable. First, the combined sample of the two populations does not exhibit variability that could be considered outside the limits for a single species of moa, all CVs being fairly low (Table 5: femur length, 7.73; tibiotarsus length, 9.86; tarsometatarsus length, 8.91). Secondly, the two forms appear to have been broadly sympatric, both occurring together in the larger fossil deposits. To my knowledge there is no good evidence that one had a distribution exclusive of the other. If the two forms represent dimorphic sexes, then the larger form, *crassus*, would appear to have been the female, as an egg was found preserved in association with a skeleton of this form at Pyramid Valley (Falla, 1941). I therefore follow Scarlett (1972) in tentatively synonymizing *E. huttonii* with *E. crassus*.

**Subfamily DINORNITHINAE**

***Dinornis* Owen, 1843**

SUMMARY.—Four species of *Dinornis* are recognized here. The smallest, *D. struthoides*, was confined to the North Island. A second species, *D. torosus*, was only slightly larger than *D. struthoides* and was restricted to the South Island. A larger form, *D. novaezealandiae*, and the largest species of moa, *D. giganteus*, were both found on the North and South islands.

TABLE 6.—Posterior probability classification of stepwise discriminate function analysis for bones assigned to *Emeus crassus* and *E. huttonii*

|                          | <i>E. crassus</i> | <i>E. huttonii</i> | <i>n</i> | Percent misclassified |
|--------------------------|-------------------|--------------------|----------|-----------------------|
| <b>Femur</b>             |                   |                    |          |                       |
| <i>E. crassus</i> .....  | 18                | 1                  | 19       | 5.3                   |
| <i>E. huttonii</i> ..... | 0                 | 10                 | 10       | 0                     |
| <b>Tibiotarsus</b>       |                   |                    |          |                       |
| <i>E. crassus</i> .....  | 20                | 0                  | 20       | 0                     |
| <i>E. huttonii</i> ..... | 0                 | 10                 | 10       | 0                     |
| <b>Tarsometatarsus</b>   |                   |                    |          |                       |
| <i>E. crassus</i> .....  | 21                | 1                  | 22       | 4.5                   |
| <i>E. huttonii</i> ..... | 1                 | 10                 | 11       | 9.1                   |

*Dinornis struthoides* Owen, 1844

SYNONYM.—*Dinornis gazella* Oliver, 1949.

Because of a decision by the International Commission of Zoological Nomenclature (Hemming, 1954), the name *D. struthoides* refers to all those specimens included under the name *D. novaezealandiae* in Archey (1941), Oliver (1949), and Brodkorb (1963). This species was the smallest of the genus and was found on the North Island. Oliver (1949:170) recorded two bones from the South Island which he assigned to this species, noting that some of these bones were "indistinguishable in size and proportions" from those of the North Island. Neither Archey (1941), Brodkorb (1963), nor Scarlett (1972) listed this species from the South Island and it may be that Oliver's specimens are referable to small individuals of *D. torosus*. Thus, the presence of *D. struthoides* on the South Island needs to be verified (unfortunately, I did not examine the relevant material while in New Zealand). In any case, if *D. struthoides* were present on the South Island, it was evidently uncommon.

Oliver (1949:166) described a new species from the North Island, *D. gazella*, based on a pelvis and some referred bones that are smaller than those typical of *D. struthoides* (Table 7). The size differences are slight, however, and the variation exhibited by the combined sample of *struthoides* and *gazella* is easily within the range of a single

species (Table 8). I compared a series of bones (DM 108: 5 tarsometatarsi, 3 tibiotarsi from Te Aute) referred by Oliver to *D. gazella* with bones of *D. struthoides* and found that those of the former had thinner shafts although the two samples were nearly equal in length. The differences appear to be entirely related to age, as the bones referred to *D. gazella* are those of immature individuals. Therefore, I suggest that *D. gazella* be merged with *D. struthoides*.

*Dinornis torosus* Hutton, 1891

This species is only slightly larger than *D. struthoides* and has been considered the South Island counterpart of that species (e.g., Archey, 1941:62; Oliver, 1930). Indeed, I would be inclined to merge *D. torosus* with *D. struthoides* if it were not for some significant differences that apparently exist in cranial structure.

As I will detail in subsequent papers on evolutionary relationships and cranial morphology, *D. torosus* appears to be more advanced in cranial structure than *D. struthoides* but in certain other respects is more primitive than the two larger species *D. novaezealandiae* and *D. giganteus*. The skull of *D. torosus* differs from that of *D. struthoides* in having the basisphenoid rostrum moderately inflated, and the mandible stouter and less deflected ventrally. The most important and consistent difference seems to be in the nature of the

TABLE 7.—Statistics for species of *Dinornis* (measurements in mm)

| Character                 | <i>D. struthoides</i> | <i>D. gazella</i> | <i>D. torosus</i> | <i>D. novaezealandiae</i> | <i>D. robustus</i> | <i>D. hercules</i> | <i>D. maximus</i> | <i>D. giganteus</i> |
|---------------------------|-----------------------|-------------------|-------------------|---------------------------|--------------------|--------------------|-------------------|---------------------|
| Length of femur           |                       |                   |                   |                           |                    |                    |                   |                     |
| n .....                   | 12                    | 1                 | 15                | 15                        | 12                 | 1                  | 23                | 8                   |
| $\bar{x}$ .....           | 265                   | 231               | 295.33            | 340.53                    | 354.5              | 353                | 406.13            | 390.88              |
| SD .....                  | 17.41                 | —                 | 18.35             | 13.14                     | 15.47              | —                  | 20.73             | 22.2                |
| CV .....                  | 6.57                  | —                 | 6.21              | 3.86                      | 4.36               | —                  | 5.1               | 5.68                |
| Length of tibiotarsus     |                       |                   |                   |                           |                    |                    |                   |                     |
| n .....                   | 9                     | 3                 | 14                | 21                        | 15                 | 5                  | 32                | 10                  |
| $\bar{x}$ .....           | 520.67                | 469.67            | 588.36            | 701.67                    | 718.6              | 779.8              | 866.63            | 875.2               |
| SD .....                  | 29.08                 | —                 | 36.77             | 40.87                     | 22.8               | 37.99              | 46.54             | 71.57               |
| CV .....                  | 5.59                  | —                 | 6.25              | 5.82                      | 3.17               | 4.87               | 5.37              | 8.18                |
| Length of tarsometatarsus |                       |                   |                   |                           |                    |                    |                   |                     |
| n .....                   | 15                    | 5                 | 16                | 13                        | 14                 | 3                  | 29                | 10                  |
| $\bar{x}$ .....           | 282.2                 | 259               | 303.13            | 368.08                    | 382.64             | 420.33             | 463.41            | 486.1               |
| SD .....                  | 19.27                 | 12.43             | 22.75             | 30.54                     | 17.72              | —                  | 38.78             | 30.08               |
| CV .....                  | 6.83                  | 4.8               | 7.51              | 8.3                       | 4.63               | —                  | 8.37              | 6.19                |

TABLE 8.—Statistics for combined species of *Dinornis* (measurements in mm)

| Character                 | <i>D. struthoides</i> + | <i>D. novaezealandiae</i> +                |  |
|---------------------------|-------------------------|--|--|
|                           | <i>D. gazella</i>       | <i>D. robustus</i> +<br><i>D. hercules</i> | <i>D. giganteus</i> +<br><i>D. maximus</i> |
| Length of femur .....     |                         |  |  |
| n .....                   | 13                      | 28   | 31   |
| $\bar{x}$ .....           | 262.38                  | 346.96                                     | 402.19                                     |
| SD .....                  | 19.15                   | 15.38                                      | 21.82                                      |
| CV .....                  | 7.3                     | 4.43                                       | 5.42                                       |
| Length of tibiotarsus     |                         |  |  |
| n .....                   | 12                      | 41   | 43   |
| $\bar{x}$ .....           | 507.92                  | 717.39                                     | 866.91                                     |
| SD .....                  | 34.43                   | 42.17                                      | 53.32                                      |
| CV .....                  | 6.78                    | 5.88                                       | 6.15                                       |
| Length of tarsometatarsus |                         |  |  |
| n .....                   | 20                      | 30   | 39   |
| $\bar{x}$ .....           | 276.4                   | 380.1                                      | 469.23                                     |
| SD .....                  | 20.3                    | 27.79                                      | 37.73                                      |
| CV .....                  | 7.35                    | 7.31                                       | 8.04                                       |

basisphenoid rostrum. In *D. giganteus*, and to a lesser extent in *D. novaezealandiae*, there is a marked inflation of the basisphenoid rostrum as compared to the condition seen in *D. torosus*. Based on the comparative series I was able to examine, these differences are consistent between species.

***Dinornis novaezealandiae* Owen, 1843**

SYNONYMS.—*Dinornis ingens* Owen, 1844; *D. robustus* Owen, 1846; *D. hercules* Oliver, 1949.

As a result of the above-mentioned decision of the International Commission of Zoological Nomenclature (Hemming, 1954), *D. ingens* now becomes a synonym of *D. novaezealandiae*. Consequently, the latter name belongs to those forms of *Dinornis* that were larger than *D. struthoides* and *D. torosus* but smaller than *D. giganteus*. Bones referred to *D. novaezealandiae* (= *D. ingens* of Archey, Oliver, and Brodkorb) are known from both the North and South islands, although they were apparently less common in the latter. I include *D. robustus* in this species because it appears to be little more than the South Island representative of *D. novaezealandiae*. Bones referred to the two species overlap considerably in length (Table 7), but those included under the name *D. robustus* are somewhat stouter than those assigned to *D. novaezealandiae* (Archey, 1941:71, Oliver, 1949:171).

Oliver (1949:174) described an additional species, *D. hercules*, from a few limb bones from the North Island. The type tibiotarsus (DM 217) is about the same length as some tibiotarsi of *D. novaezealandiae* but has the shaft more curved; in general, bones assigned to *D. hercules* by Oliver are slightly larger than those of *D. novaezealandiae* (Table 7). Scarlett (1972:21) suggested that *D. hercules* may be a "bow-legged variant" of *D. giganteus*, but I believe most of the specimens assigned to *D. hercules* are closer to *D. novaezealandiae* in size and I here include it with that species. I was able to compare the type of *D. hercules* with other species of *Dinornis* and in my opinion the differences in stoutness and the curvature of the shaft of the type are attributable to individual variation.

The combined sample of bones of *D. novaezealandiae*, *D. robustus*, and *D. hercules* exhibits very little variation, all CVs being less than 7.50 (Table 8). This variability is well within that for a single species of moa.

***Dinornis giganteus* Owen, 1844**

SYNONYM.—*Dinornis maximus* Owen, 1867.

*Dinornis giganteus* is the North Island representative of the largest species of moa and *D. maximus* is its South Island form. Bones of the latter are somewhat stouter, but measurements of the two overlap greatly (Table 7). I can see little

value in considering these minor variations to be indicative of species differences. The combined samples show a relatively small amount of variability, certainly within the limits of a single species (Table 8). Judging from the available collections, the North Island form was less common than the South Island form.

### Conclusions

In contrast to the 20 species recognized by Archey (1941) and 29 species recognized by Oliver (1949), I here accept only 13 species as being valid. The present arrangement is actually fairly similar in parts to Archey's, but combines several North and South islands counterparts, while several "species-pairs" are regarded as examples of sexual size dimorphism. Further study may show that *Anomalopteryx oweni* and *Megalapteryx benhami*, which are based on somewhat dubious material, perhaps do not deserve recognition. Certainly the acceptance of the large number of species advocated by Oliver is untenable.

The systematic results of this paper can be summarized by the following classification:

#### Family DINORNITHIDAE

##### Subfamily ANOMALOPTERYGINAE

Genus *Anomalopteryx* Reichenbach, 1852

*A. didiformis* (Owen, 1844)

*A. oweni* (Haast, 1885)

Genus *Megalapteryx* Haast, 1886

*M. didinus* (Owen, 1883)

*M. benhami* Archey, 1941

Genus *Pachyornis* Lydekker, 1891

*P. elephantopus* (Owen, 1856)

*P. mappini* Archey, 1941

Genus *Euryapteryx* Haast, 1874

*E. curtus* (Owen, 1846)

*E. geranoides* (Owen, 1848)

Genus *Emeus* Reichenbach, 1852

*E. crassus* (Owen, 1846)

##### Subfamily DINORNITHINAE

Genus *Dinornis* Owen, 1843

*D. struthoides* Owen, 1844

*D. torosus* Hutton, 1891

*D. novaezealandiae* Owen, 1843

*D. giganteus* Owen, 1844

The 13 species recognized here appear to have been distributed as follows:

| NORTH ISLAND                     | SOUTH ISLAND                    |
|----------------------------------|---------------------------------|
| <i>Anomalopteryx didiformis</i>  | <i>Anomalopteryx didiformis</i> |
| <i>A. oweni</i>                  |                                 |
|                                  | <i>Megalapteryx didinus</i>     |
|                                  | <i>M. benhami</i>               |
| <i>Pachyornis mappini</i>        | <i>Pachyornis elephantopus</i>  |
| <i>Euryapteryx geranoides</i>    | <i>Euryapteryx geranoides</i>   |
| <i>E. curtus</i>                 |                                 |
| <i>Emeus crassus</i> (uncertain) | <i>Emeus crassus</i>            |
| <i>Dinornis struthoides</i>      | <i>Dinornis struthoides</i>     |
|                                  | (uncertain)                     |
| <i>D. novaezealandiae</i>        | <i>D. novaezealandiae</i>       |
| <i>D. giganteus</i>              | <i>D. giganteus</i>             |
|                                  | <i>D. torosus</i>               |

It is of interest to note that the smaller and topographically less diverse North Island had fewer species than the South Island. Also, many of the North Island forms appear to have been smaller than their South Island counterparts.

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