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Cranes of the World: 1. Classification and Evolution

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Classification and Evolution

Cranes and their relatives the limpkins and trumpeters are fairly closely related members of the order of birds (Gruiformes) that also includes rails, gallinules, coots, and other marsh-adapted birds. Cranes, limpkins, and trumpeters are usually included within a superfamily, Gruoidea, although at least one recent authority (Cracraft, 1973) has suggested that the three groups all be included within a single family, Gruidae. However, traditionally only the cranes have been included within the Gruidae, and only the cranes will be dealt with in detail in this book. Nevertheless, the limpkins and trumpeters must be considered if the evolution of cranes is to be discussed, and thus it is perhaps desirable to define each of these three groups in a semiformal way, so that their similarities and differences are at once apparent.

Cranes can be defined as large, long-legged and long-necked members of the Gruiformes, with a small and elevated hind toe, an elongated and tapering bill that is often longer than the head, and nostrils that are oval or nearly linear and are open (pervious) from side to side. In most species the upper half of the head is nearly naked in adults, exposing colorful skin areas. The toes are not webbed, but are connected at the base by a membrane, and are moderately long. The wings are rounded in profile and have 10 functional primaries (and a vestigial eleventh in most), with the seventh or eighth primary the longest. The wing molt is relatively simultaneous, so that in most species at least the birds may be flightless for a time. There are from 18 to 25 secondaries, with the inner ones longer and curved, often even longer than the primaries, and usually with noncoherent vanes that break up into airy plumes. The tail is moderately long and is composed of 12 feathers (rectrices). There are 17 to 20 cervical vertebrae, 6 or 7 complete ribs, and the trachea is usually looped back to touch or even invade the keel of the sternum, sometimes coiling extensively within it. The sexes are alike in plumage, and all species are monogamous but usually are gregarious outside the breeding season. Their calls are loud and often resonant. From one to four spotted buffy or pale bluish eggs are laid in nests that are located on dry land or in marshy vegetation. Both sexes incubate and care for the young, which are mostly cinnamon brown and require two to three months to fledge. Most species are probably predominantly vegetarian, but all to some degree eat animal materials. There are fourteen species (fifteen if the crowned cranes are considered as two species), and cranes are found in all continents except South America and the Antarctic.

Limpkins are medium-sized, long-legged and long-necked members of the Gruiformes, having a large hind toe that is placed at the same level as the anterior toes, an elongated bill that is much longer than the head, and nostrils that are elongated and pervious. The head is entirely feathered, and the toes lack webbing at their bases and are relatively long and slender. The wings are strongly rounded, with the sixth and seventh primaries the longest. The secondaries are progressively longer inwardly, with the inner ones as long as the longest primaries, but their vanes are coherent. The wing molt is apparently gradual, so that the birds are never flightless. There are 12 rectrices in the long and rounded tail. There are 16 cervical vertebrae, and 6 or 7 complete ribs. The trachea is doubly looped in the lower neck of adult males but is not in contact with the keel of the sternum. The sexes are alike in plumage, and the single species is rather solitary, forming monogamous pairs. Limpkin calls are loud, and are reminiscent of human crying or wailing. Four to eight pale buffy eggs spotted with brown are laid in nests located among marsh vegetation, on bushes or vines, or in low trees (Kale, 1978). Incubation is by both sexes, and the downy young are almost uniformly brown and rather crane-like in appearance (Harrison, 1978). The young are cared for by both sexes, and continue to be fed for an

extended period, even after they have fledged. Both adults and young feed to some degree on aquatic insects and amphibians, but they forage mainly on freshwater snails (*Pomacea*), to which their bills are highly adapted (Snyder and Snyder, 1969). The single species occurs from Florida through the West Indies and Mexico to southern South America.

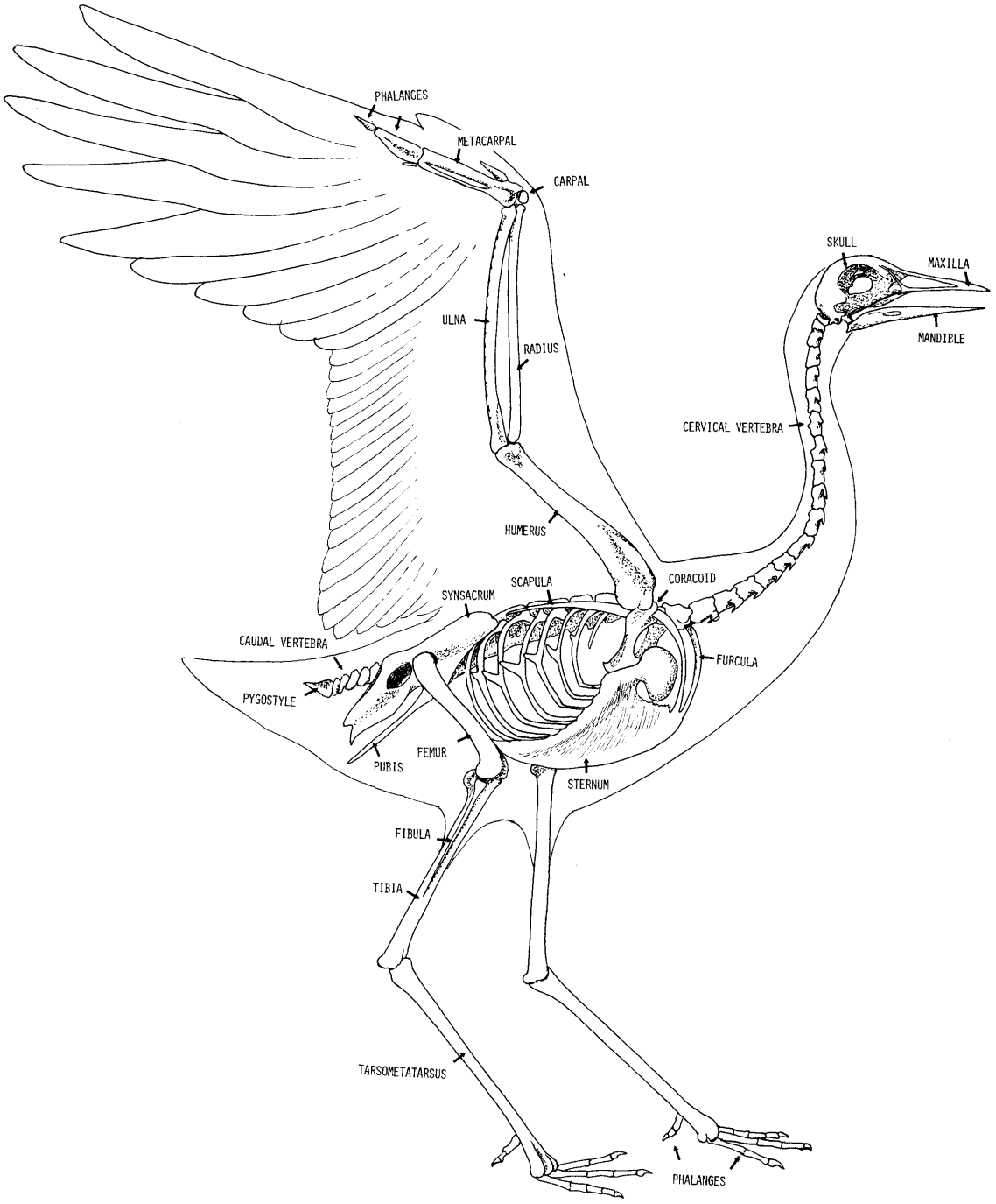
Trumpeters are medium-sized members of the Gruiformes, with legs and neck of medium length, a small and elevated hind toe, a short and decurved bill, and nostrils that are somewhat oval and pervious. The head is entirely covered with feathers, and the toes are relatively short and unwebbed. The wings are strongly rounded, with 10 primaries (no vestigial eleventh), and the 16 secondaries are relatively long. Together with some of the longer scapulars, the secondaries are conspicuously tipped in each of the three species with green, gray, or white, forming a distinctive patch. The tail is fairly short and has 12 rectrices. There are 17 or 18 cervical vertebrae and 8 complete ribs. The trachea has been reported to form a long subcutaneous loop extending back nearly to the vent. However, this tracheal condition has been reported lacking in some specimens, suggesting that it might be limited to adult males. The sexes are alike in plumage, and adult trumpeters produce an extremely low-pitched booming or rumbling call, probably because of the specialized tracheal condition. "Singing" by groups is often performed from tree roosts at night. The birds are gregarious, but adults establish monogamous pairs and perform crane-like dancing displays during courtship (Sick, 1972). Six to ten rough white or pale greenish eggs are laid in ground nests, in tree holes, or in the crowns of palms. Nesting evidently occurs in small colonies, with five or six nests in adjoining trees. Incubation may be performed by the female alone (observations in captivity) or by both sexes (reported in the wild). The downy young are grayish to blackish, uniquely patterned with cinnamon lines on the back and brownish on the crown and wings. The young evidently grow very slowly, with chicks two months old still largely downy. The birds are mostly vegetarians, but about a fifth of their diet may be of insects (Beebe, Hartley, and Howes, 1917). There are three very similar species, all of which are confined to tropical South American forests.

In their general skeletal structure (fig. 1) cranes and limpkins have much in common; indeed, the two groups might be considered part of a common family on skeletal grounds (Beddard, 1898). In cranes, as in the limpkin, the skull has small gaps, or fontanels, in the occipital area, and the septum that separates the orbits has large "windows," or fenestrae. Trumpeters lack occipital fontanels, and have smaller interorbital fenestrae. Further, the skull of trumpeters has a group of about five small supraorbital bones, a condition otherwise found in only a few other "primitive" groups of birds. Finally, the maxillopalatine bones are convex, rather than concave as in cranes (fig. 2).

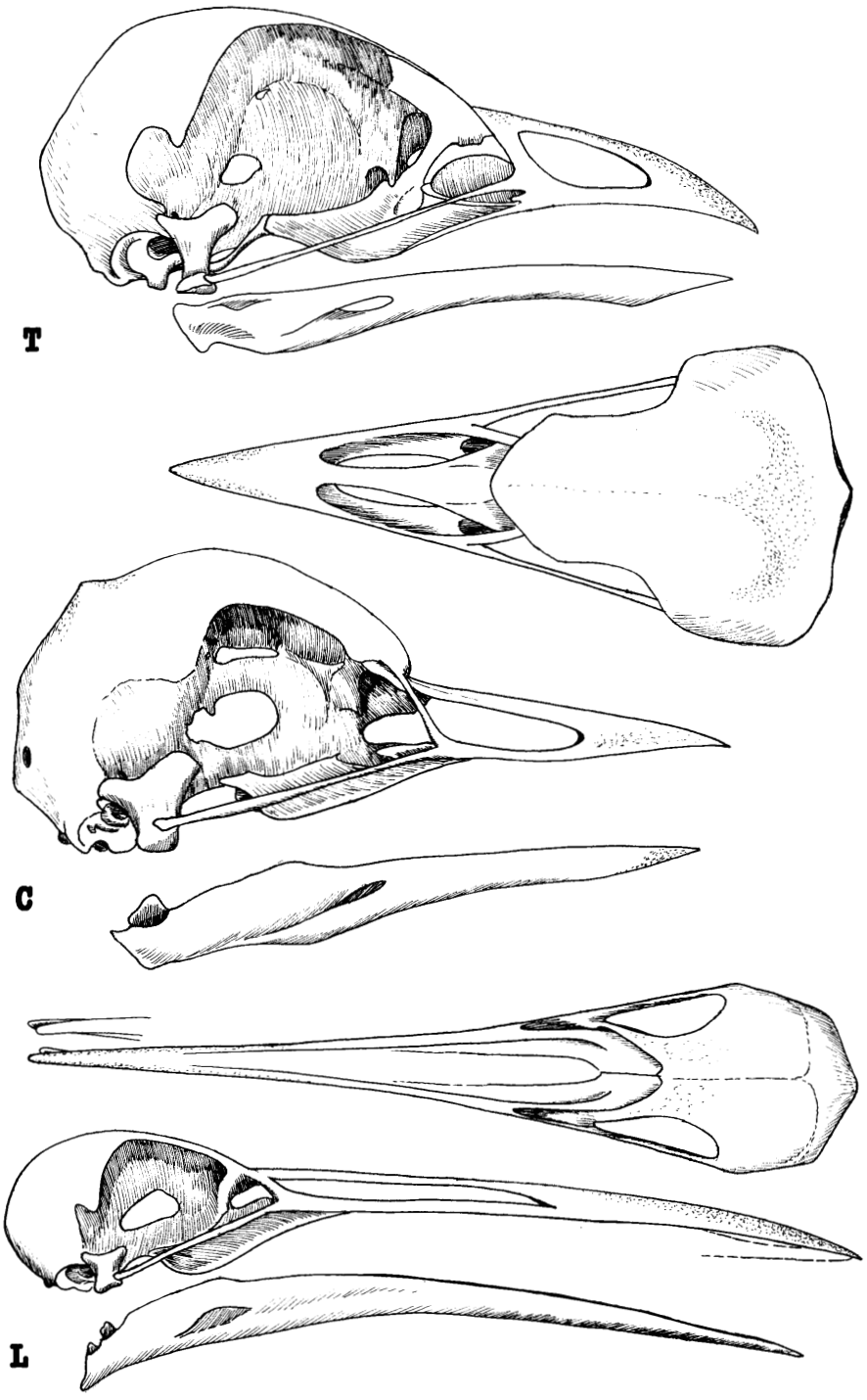
By contrast, the skull of the limpkin is remarkably similar to that of a typical crane, although the bill is much more elongated. Two other unusual features of the limpkin bill include the fact that the lower mandible is typically slightly twisted to the right, which enables the bird to reach into the aperture of a snail and around the bend of the shell to cut the columellar muscle. There is also a slight gap remaining between the mandibles a short distance back from the tip, a condition that may be useful for grasping snails and for carrying them in the bill (Snyder and Snyder, 1969) (fig. 2).

In the rest of its skeleton, the crane's only remarkable characteristic is the fact that in all the species of *Grus* the trachea is extensively convoluted within the keel of the sternum. The acoustic significance of this feature will be discussed in the chapter on vocalizations, but at this point it need only be noted that the sternum of the limpkin approaches the condition exhibited in the crowned cranes. In both of these groups the furcula (or "wishbone") does not reach the keel of the sternum, and the trachea passes through its opening toward the lungs in an essentially direct fashion. Yet, in both of these groups there is an indentation in the upper portion of the keel, the apparent homolog of the extensively excavated opening found in the keel among species of the genus *Grus* (fig. 3). In Beddard's (1902) view this condition suggests that in these forms the trachea was once coiled in front of the sternum. As noted earlier, the trachea of the male limpkin does exhibit coiling, but it occurs in the lower portion of the neck, well anterior to the sternum (Wetmore, 1965; Rüppell, 1933).

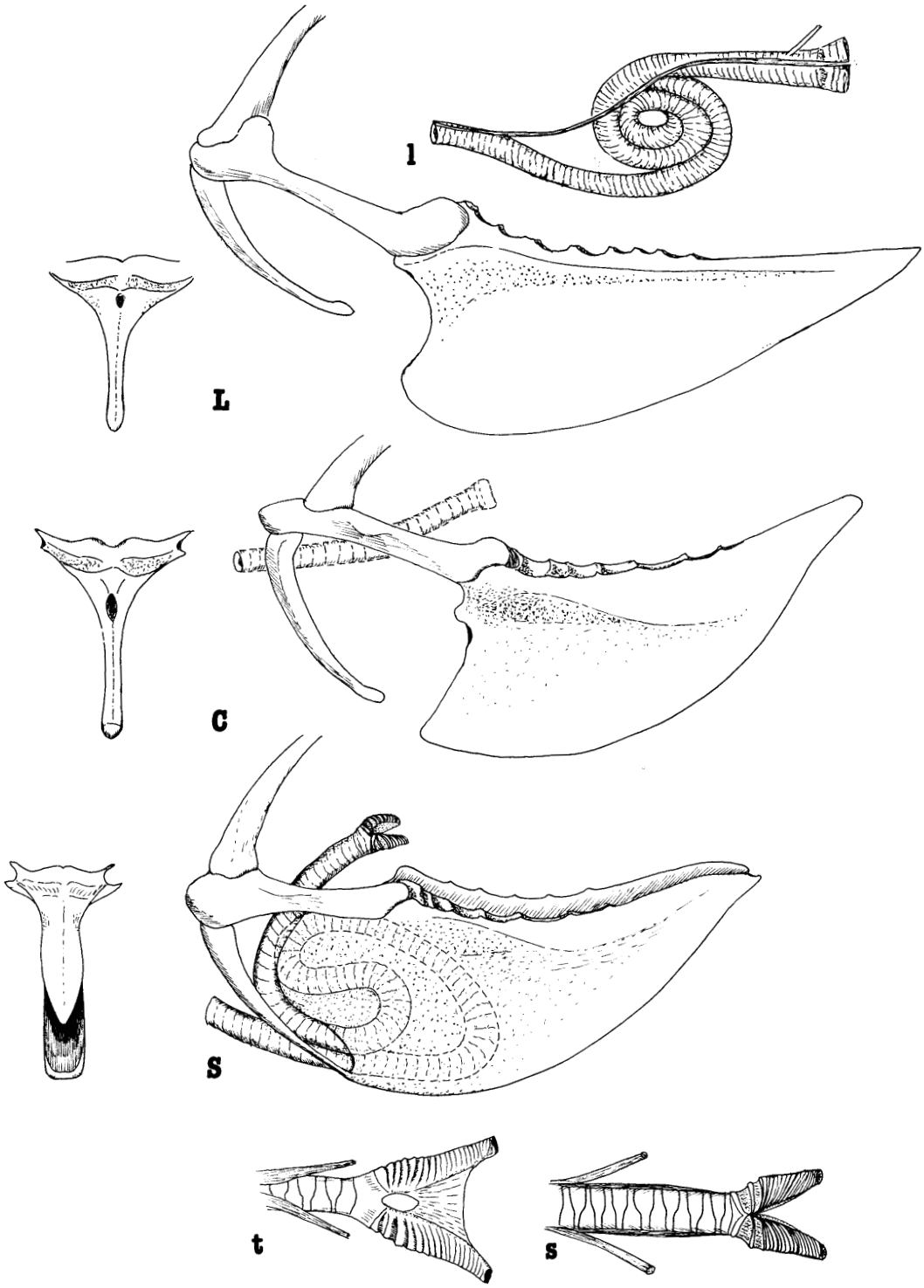
In the genus *Grus*, the furcula is extended to fuse with the keel of the sternum, and the entire keel is both widened and extensively excavated to receive the trachea, which coils within it for varying distances according to the species. The syringeal anatomy of the limpkin has not yet been carefully described, but another major difference that separates cranes from the trumpeter seems to be present in the syrinx and bronchi. Judging from the illustration of Beddard (1890), the bronchi of the trumpeter appear to be connected by a thin membrane, which probably effectively eliminates acoustical contribution by internal tympaniform membranes. This limits vocal activity to the external tympaniform membranes, which appear to be relatively poorly developed. On the other hand, in the genera *Grus* and *Bugeranus* at least, the internal tympaniform membranes are very large and triangular, and extend from the first bronchial semiring nearly to the lungs. Additionally in *Grus* and *Bugeranus* the paired intrinsic tracheal muscles extend back along the sides of the



1. Skeletal anatomy of a *Grus* crane.



2. Lateral view of a trumpeter skull (T), dorsal and lateral views of a crowned crane skull (C), and dorsal and lateral views of a limpkin skull (L). Tip of limpkin bill is also shown in ventral view, to illustrate asymmetry.



3. Sternum and pectoral girdle of limpkin (L), crowned crane (C), and sandhill crane (S) in lateral and frontal view, and ventral views of the tracheae of the limpkin (l), trumpeter (t), and sandhill crane (s). In part after Beddard (1890, 1902) and Rüppell (1923).

trachea to reach the first bronchial semirings, while in *Balearica* they terminate about 14 rings anterior to the end of the trachea (fig. 3). Evidently the latter condition also prevails in *Psophia* (Beddard, 1890, 1891).

The evolutionary and fossil history of the cranes and their relatives is still surprisingly unsettled, in spite of a rather large number of known fossil forms. As an example of this uncertainty, one might consider the divergent methods of crane classification that have appeared in the last few decades. Thus, in Wetmore's (1960) classification of the birds of the world, the crane-like forms are classified as follows:

Superfamily Gruoidea
[Family Geranoididae (fossil)]
[Family Eogruidae (fossil)]
Family Gruidae
Family Aramidae
Family Psophiidae

Not many years later, in cataloging fossil bird groups, Brodkorb (1967) provided an arrangement that took a rather different form:

Family Gruidae
[Subfamily Geranoidinae (fossil)]
Subfamily Balearicinae
[Subfamily Eogruinae (fossil)]
Subfamily Gruinae
[Family Ergilornithidae (fossil)]
Family Aramidae
Family Psophiidae

In a similar review of fossil material, Cracraft (1973) proposed a classification that differs considerably from these two, and also from other recent groups, especially in the inclusion of both the trumpeters and the limpkins within the crane family:

Superfamily Geranoidea
[Family Geranoididae (fossil)]
[Family Bathornithidae (fossil)]
Superfamily Gruoidea
[Family Eogruidae (fossil)]
Family Gruidae
Subfamily Gruinae
Subfamily Psophiinae
Tribe Psophiini
Tribe Aramini

It is thus apparent that there is still no complete agreement as to the phylogeny and relationships of the crane-like birds. Cracraft judged that the crane-like birds (infraorder Grui) evolved during the Cenozoic period (that is, in the last 60 million years), and developed along two distinct phyletic lines. One of these lineages (the superfamily Geranoidea) subsequently died out, while the other (superfamily Gruoidea) gave rise to the contemporary groups that include the present-day cranes, trumpeters, and limpkin. In Cracraft's view, both of these major lineages had a common ancestor with the typical rails (Rallidae) during Cretaceous times. Jacob, Plawer, and Rosenfeldt (1979) also suggest a close relationship between cranes and rails.

As a group, the Gruiformes show a good deal of anatomical similarity to the shorebird order Charadriiformes, and it is very probable that these two major orders evolved from common ancestral stock (Beddard, 1891; Lowe, 1931; Howard, 1950; Feduccia, 1980). Thus, not only do some gruiform birds show characteristics in common with the Charadriiformes, such as the sunbitterns and the bustards, but also some charadriiform groups such as the jacanas have distinct similarities to the Gruiformes (Johnsgard, 1981).

Cracraft (1973) believed that the trumpeters are more closely related to the limpkin than to typical cranes, and that within the aramid-psophiid lineage the trumpeters' characteristics are relatively primitive. Although there is no fossil record of the trumpeters, Cracraft thought it likely that they arose about the same time as did the aramids, in the late Eocene or early Oligocene. Sibley (1960) believed that on the basis of egg-white proteins the trumpeters might be considered somewhat intermediate between cranes and rails, and later (Sibley and Ahlquist, 1972) noted a strong resemblance to rails in the egg-white characteristics of trumpeters, with a less striking similarity to *Balearica*. Cranes, trumpeters, and gallinules are also very similar in chromosome characteristics (Sasaki and Takagi, 1981).

Likewise the aramids are believed by Cracraft to be clearly closer to the cranes than to the rails, and in particular their skeletal features show strong similarities to such primitive cranes as *Balearica*. Fossil evidence indicates that the limpkin group goes back at least to the middle of the Oligocene, and perhaps originated as early as the late Eocene. Yet, some features of the aramids are distinctly raillike, and several writers (Fürbinger, 1888; Shufeldt, 1915) have commented on the intermediacy of the limpkin between the cranes and the rails. However, Beddard (1902) emphasized the strong skeletal similarities between the limpkin and cranes, as did also Mitchell (1915), while Garrod (1876) judged the limpkin to be most closely affiliated with the cranes, but more distantly similar to trumpeters and other gruiform groups.

A somewhat different view of crane evolution has been presented by Stegmann (1978), who judged that the cranes are closest to the bustards (Otididae) in their wing morphology, but have become more specialized for long flights. He imagined the sequence of evolution to proceed from the rails through the bustards to the cranes. He also thought that the trumpeters might be more closely related to the galliform birds than to the Gruiformes, or perhaps are nearest the cariamids, an

obscure South American group usually placed close to the bustard family. Cracraft (1973) also believed that the cariamids might offer the nearest phylogenetic group to the trumpeters, but he did not extend his own studies to include this group.

However the cranes evolved, it is clear that by Eocene times they were well established in the Old World (genus *Paleogrus*, three species from England and Europe; *Geranopsis*, one species from England), while in North America the primitive and divergent crane-like *Geranoides* was present (Cracraft, 1969). Fragmentary remains of a questionable form, *Eubalearica tugarinovi*, have also been described from the Eocene of Usbek Soviet Socialist Republic. Both *Paleogrus* and *Geranopsis* more closely approach *Balearica* than *Grus* in their skeletal characteristics, and in some respects are hardly separable from that genus, suggesting that forms resembling the modern crowned cranes were already present in Eocene times. By late Oligocene and early Miocene times the genus *Probalearica* was present in both the Old World (France) and the New World (Florida). This also was a *Balearica*-like crane, and likewise distinctly similar to *Paleogrus*. Finally, by Pliocene times the genus *Pliogrus* was present in Europe. It evidently closely approached *Grus* in at least some of its characteristics, but *Pliogrus* is still only very poorly documented (Cracraft, 1973). A summary of fossil crane species is provided in table 1.

Most fossil cranes are known but from a few fragmentary and poorly preserved remains. Yet, a veritable treasure of fossil cranes has recently been unearthed in late Miocene deposits of northern Nebraska, among beds of volcanic ash nearly 10 million years old. Upwards of thirty crane specimens, some of them nearly complete, have been discovered in association with a rich assortment of rhinos, horses, and other fauna similar to that of a present-day African savanna community (Voorhies, 1981). Although these cranes have yet to be carefully studied and named, it is obvious that they are very close in skeletal features to the modern *Balearica* forms, with a simple sternum and a relatively straight trachea. This adds additional evidence to the view that the crowned crane type was once a widespread form and probably preceded *Grus* as a major crane type. It should perhaps also be noted that a Miocene crane fossil from Nebraska that has been estimated as of about the same age (Upper Snake Creek) has a humeral structure identical to the modern sandhill crane (Wetmore, 1928). As such, this would represent the oldest known fossil evidence of any bird species still surviving. However, a close comparison of this specimen with the newly discovered Nebraska form that was essentially contemporaneous with it will have to be made to eliminate the possibility that they are members of the same genus, and that both genera occurred in central North America at that time. In the same paper, Wetmore (1928) described a fossil *Aramus*, also from the Upper Snake Creek beds, that closely approaches the modern limpkin. The fossil *Grus* described by Wetmore is considered by Skinner, Skinner and Gooris (1977) to

TABLE 1

Synopsis of Fossil Gruidae of the World*

Geologic Period	*Balearicinae (of Brodkorb, 1967)*	*Gruinae (of Brodkorb, 1967)*
Pleistocene & Recent		*Grus bohatshevi* (Asia)
		Grus melitensis (Europe)
		Baeopteryx latipes (North America)
		Baeopteryx cubensis (Cuba)
Pliocene	*Pliogrus pentelici* (Europe)	*Grus nannodes* (North America)
	Pliogrus germanicus (Europe)	*Grus conferta* (North America)
Miocene	*Probalearica crataegensis* (North America)	*Grus ?canadensis* (North America)
	Paleogrus excelsus (Europe)	*Grus miocenicus* (Europe)
	Probalearica problematica (Europe)	
Eocene	*Eubalearica tugarinovi* (Asia)†	
	Geranopsis hastingsi (Europe)	
	Paleogrus hordweilliensis (Europe)	
	Paleogrus princeps (Europe)‡	
	Paleogrus geiseltalensis (Europe)	

*After Brodkorb (1967) and Cracraft (1973), but excluding neospecies from prehistoric or Pleistocene sites, and those forms removed from Brodkorb's list of Gruidae by Cracraft. *Grus miocenicus* (Grigorescu and Kessler, 1977) added.

†Of questionable gruiform status, according to Cracraft.

‡*Ornitocnemus robustus* of Brodkorb (1967).

be part of the type fauna of the Snake Creek formation, and of Late Clarendonian age, or of the same age as the *Balearica*-like fossils recently found by Voorhies.

The present-day species of the cranes of the world have generally been placed in 4 genera and 14 species, at least since the publication of Peters's (1934) widely adopted system. He recognized a single species of *Balearica*, two of *Anthropoides*, one of *Bugeranus*, and ten of *Grus*. Previously, Blaauw (1897) had recognized 16 species in three genera (*Grus*, *Anthropoides*, and *Balearica*), and Blyth and Tegetmeier (1881) had accepted 16 species in 2 genera (*Grus* and *Balearica*). By comparison, Sharpe (1894) recognized 9 genera (6 of which were monotypic) and 19 species. Archibald (1975, 1976) reevaluated the Gruidae from a behavioral standpoint and proposed a classification very similar to that of Peters's, except that two species of *Balearica* were recognized and the Siberian crane was shifted from *Grus* to *Bugeranus*. The same sequence of genera proposed by Peters was followed. Wood (1979) came to very similar conclusions after a phenetic study of the morphology of cranes, and in particular judged that the Siberian crane might be considered congeneric with *Bugeranus carunculatus*. He did not deal directly with the question of the number of acceptable species of *Balearica*, but recently Dowsett and Dowsett-Lemaire (1980) judged that the crowned cranes should be considered conspecific, and also believed that the wattled cranes might be included in the genus *Grus*, as earlier treated by Snow (1978). I agree that the crowned cranes have not yet been proven to consist of two species, but I have followed Archibald and Wood in recognizing two species of *Bugeranus*. Beyond that, I have adopted Archibald's views on the relationships within the genus *Grus*, and the sequence of species and genera used in this book is derived from his conclusions, except that *Balearica* is used to begin the sequence rather than to terminate it, to conform to the weight of evidence suggesting that the crowned cranes are the most primitive of the living Gruidae.