

***Thiornis sociata* NAVÁS, a nearly complete miocene Grebe (Aves: Podicipedidae)**

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Abstract

Thiornis sociata NAVÁS (1922), described from a complete postcranial skeleton from the Middle Miocene at Libros, Teruel, Spain, was originally inferred to be a gallinule in the family Rallidae. The holotype was reprepared and is shown to be a medium-sized grebe (Podicipedidae), the best-preserved Tertiary fossil yet known for the family. Although it has some features similar to the genus *Tachybaptus*, these are considered likely to be primitive and the species is tentatively referred to the genus *Podiceps* as *P. sociatus*.

Key words: *Thiornis sociata*; *Podiceps*; Podicipedidae; Miocene; Spain; Grebes.

Kurzfassung

Thiornis sociata NAVÁS 1922, beschrieben nach einem vollständigen postcranialen Skelett aus dem Mittel-Miozän von Libros, Teruel, Spanien, wurde ursprünglich für einen Vertreter der Rallidae gehalten. Nun aber erwies sich der nachpräparierte Holotypus als ein mittelgroßer Lappentaucher (Podicipedidae), er ist das besterhaltene bekannte tertiäre Fossil dieser Familie. Zwar hat er einige Merkmale mit der Gattung *Tachybaptus* gemeinsam, die aber für symplesiomorph gehalten werden. Deshalb wird die Art vorerst als *P. sociatus* in die Gattung *Podiceps* gestellt.

Schlagwörter: *Thiornis sociata*; *Podiceps*; Podicipedidae; Miozän; Spanien; Lappentaucher.

Introduction

The Reverendo Padre LONGINOS NAVÁS was a pious Jesuit priest and prolific naturalist at the Colegio del Salvador in Zaragoza, Spain. His publications, both religious and scientific, number in the hundreds (GREGORIO & SALA, 1928). Those dealing with natural history span the period from 1900 to 1936, at which time NAVÁS would have been 78 years of age. The end of NAVÁS' mortal days is unknown, as he was apparently among the desaparecidos of the Spanish Civil War (OLIVER FLINT, pers. comm.). Of his many scientific contributions, mostly in entomology, only a

handful concerned fossils, and only once did he venture into avian paleontology, when he described a new genus and species of bird, *Thiornis sociata*, from Miocene deposits at Libros, Teruel, Spain, along with several other vertebrates and invertebrates (NAVÁS, 1922). NAVÁS provisionally referred *Thiornis* to the order of "zancudas" (wading birds), in the family and tribe of the gallinules, for which reason subsequent authors (e.g. LAMBRECHT, 1933; BRODKORB, 1967) placed it in the family Rallidae (Gruiformes).

CRACRAFT's (1973) remarks on *Thiornis* were largely irrelevant because the specimen in the British Museum on which he based most of his observations is

not the holotype (see OLSON, 1977: 373). This specimen was referred to *Thiornis*, perhaps by LAMBRECHT (1933), probably because it is from the same locality. LAMBRECHT illustrated the specimen, but did not regard it as the type. BRODKORB (1967) also erroneously regarded the type to be in the British Museum. I examined the British Museum specimen (A/1620) in July 1992. From what I could determine of the morphology of the humerus and coracoid, this bird definitely did not belong to the same family as *Thiornis sociata*. The skull and bill are preserved in this specimen and with further preparation it might prove to be of considerable interest in its own right. ANTONIO SÁNCHEZ MARCO (in litt.) informs me that there is another fossil from Libros in Madrid that was identified by NAVÁS as *Thiornis*, the identity of which may also be questioned until further study.

Although the true whereabouts of the holotype of *Thiornis sociata* were not generally known, the specimen had in fact long been in the ancient, dusty, public exhibit halls of the Paris Museum, where it had been on view at least since 1930 (OLSON, 1977: 373). Because NAVÁS' (1922) original measurements of *T. sociata* showed that its proportions are quite unlike those in the Rallidae (CRACRAFT, 1973; OLSON, 1977), a reassessment of the relationships of this fossil has long been needed. I was able to obtain the holotype on loan and to have part of it reprepared for more detailed study. Even before repreparation, however, it was easy to ascertain that this excellent specimen, consisting of a complete postcranial skeleton plus feather impressions, was a grebe, so that it only remained to determine its affinities within the Podicipedidae.

Material examined

I examined modern osteological specimens of all extant species of grebes, except *Tachybaptus pelzelni* of Madagascar, from the collections of the USNM, UMMZ, MVZ, ROM, and FMNH (see Acknowledgments for identity of museum acronyms): Nomenclature follows STORER (1979). Measurements in Table 1 are based on the following number of specimens (M = male, F = female, ? = unsexed): *Rollandia rolland chilensis* (4M, 1F, 1?), *Rollandia microptera* (2M, 1F, 1?), *Tachybaptus novaehollandiae* (3M, 2F, 1?), *Tachybaptus ruficollis* (5M 5F), *Tachybaptus rufolavatus* (1M, 2F), *Tachybaptus dominicus* (7M, 2F), *Podilymbus podiceps* (measurements from STORER, 1976; those for the coracoid and tibiotarsus were corrected for differences in measuring technique), *Podilymbus gigas* (1M, 3F), *Poliiocephalus poliocephalus* (2M, 2F), *Poliiocephalus rufopectus* (1F), *Podiceps major* (2M,

5F, 3?), *Podiceps auritus* (4M, 4F), *Podiceps g. holboelli* (8M, 7F), *Podiceps g. grisegena* (1M, 1F, 3?), *Podiceps cristatus* (4M, 4F, 2?), *Podiceps nigricollis* (4M, 4F), *Podiceps occipitalis* (4M, 2F), *Podiceps taczanowskii* (1M, 1F), *Podiceps gallardoi* (1M, 1M trunk), *Aechmophorus occidentalis/clarkii* (4M, 4F).

Systematic Paleontology

Order Podicipediformes FÜRBRINGER, 1888

Family Podicipedidae BONAPARTE, 1831

The holotype of *Thiornis sociata* is easily recognized as a highly specialized diving bird by the long narrow pelvis; short, robust femur; highly developed patella and inner cnemial crest of the tibiotarsus; and the laterally compressed tarsometatarsus, with an elevated, and posteriorly rotated inner trochlea. It is much more specialized for foot-propelled diving than any Cenozoic birds except loons (Gaviidae) and grebes. It differs from the Gaviidae in having a large, unfused patella in addition to the enlarged inner cnemial crest, and in the characteristic laterally flattened pedal phalanges and broad, flattened unguis phalanges. These and all other visible aspects of the skeleton agree with the highly distinctive morphology of the Podicipedidae.

Genus *Podiceps* LATHAM, 1787

Podiceps sociatus (NAVÁS, 1922), new combination (Figs. 1-4)

Holotype: Virtually complete skeleton with feather impressions, lacking only the skull and some cervical vertebrae, and some of the distal phalanges of the right pes, MNHN 1930-1.

Locality and horizon: Described from near the town of Libros, province of Teruel, northeastern Spain. The specimen is preserved in a slab of laminated oil-shale (mudstone) that formed as part of the Libros-Minas Gypsum in a lake in Vallesian times (early late Miocene) in the Libros Basin (ANADÓN et al., 1989). The deposits thus fall within biochronological zone MN 9 or MN 10 (BRUIJN et al., 1992). The waters of this lake were suggested to have been alkaline and fresh to slightly saline, based on preserved diatoms (MARGALEF, 1978).

Preservation and preparation of holotype: The specimen was originally preserved in two thin slabs, with most of the bones split in half longitudinally. Carbonized feather impressions, especially of the wing

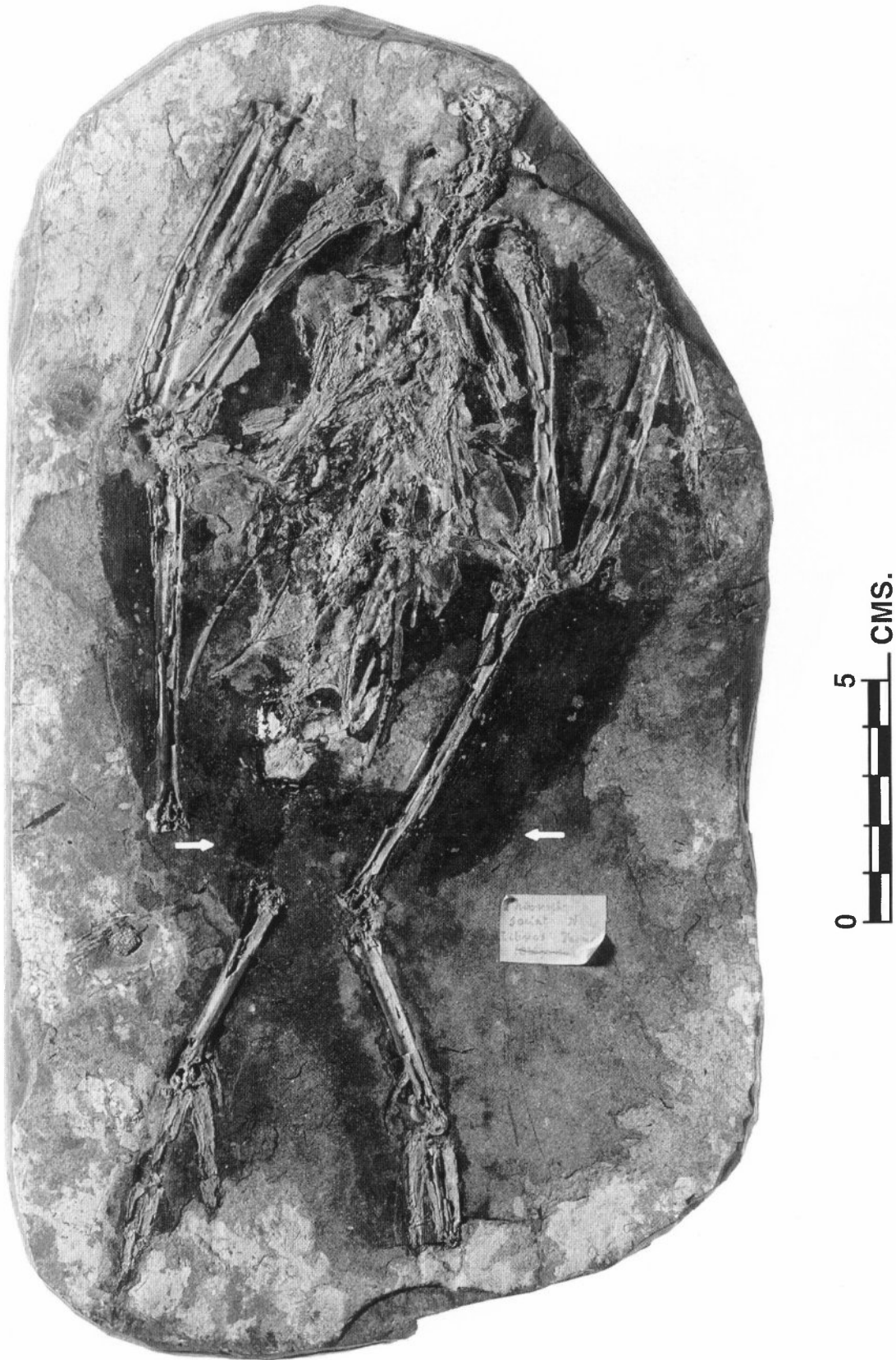


Fig. 1: Holotype of *Thiornis sociata* (MNHN 1930-1). Original slab before preparation. Note the outlines of the remiges and rectrices (arrows).

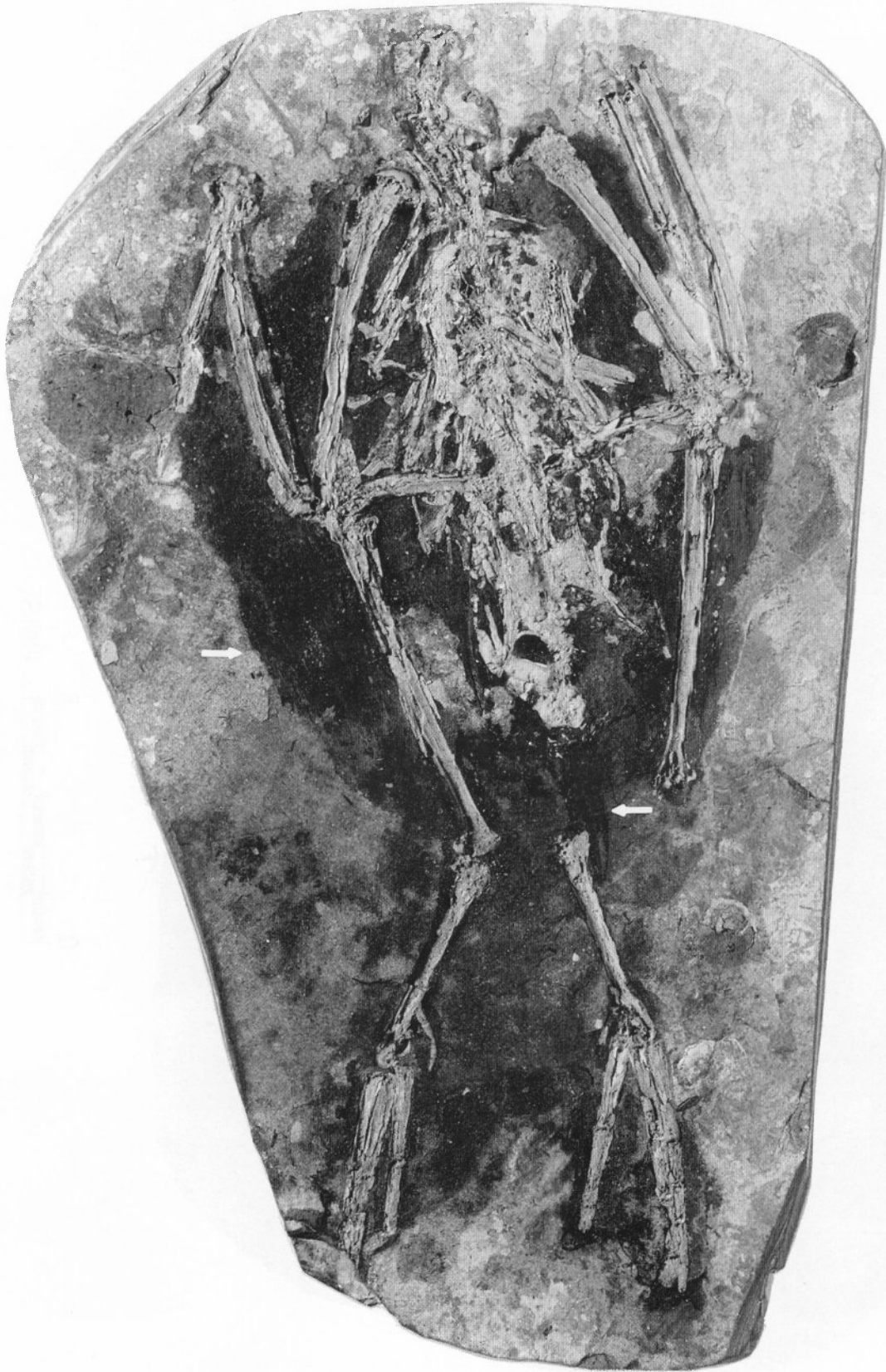


Fig. 2: Holotype of *Thiornis sociata* (MNHN 1930-1). Counterslab. Note again the outlines of the remiges and rectrices (arrows).

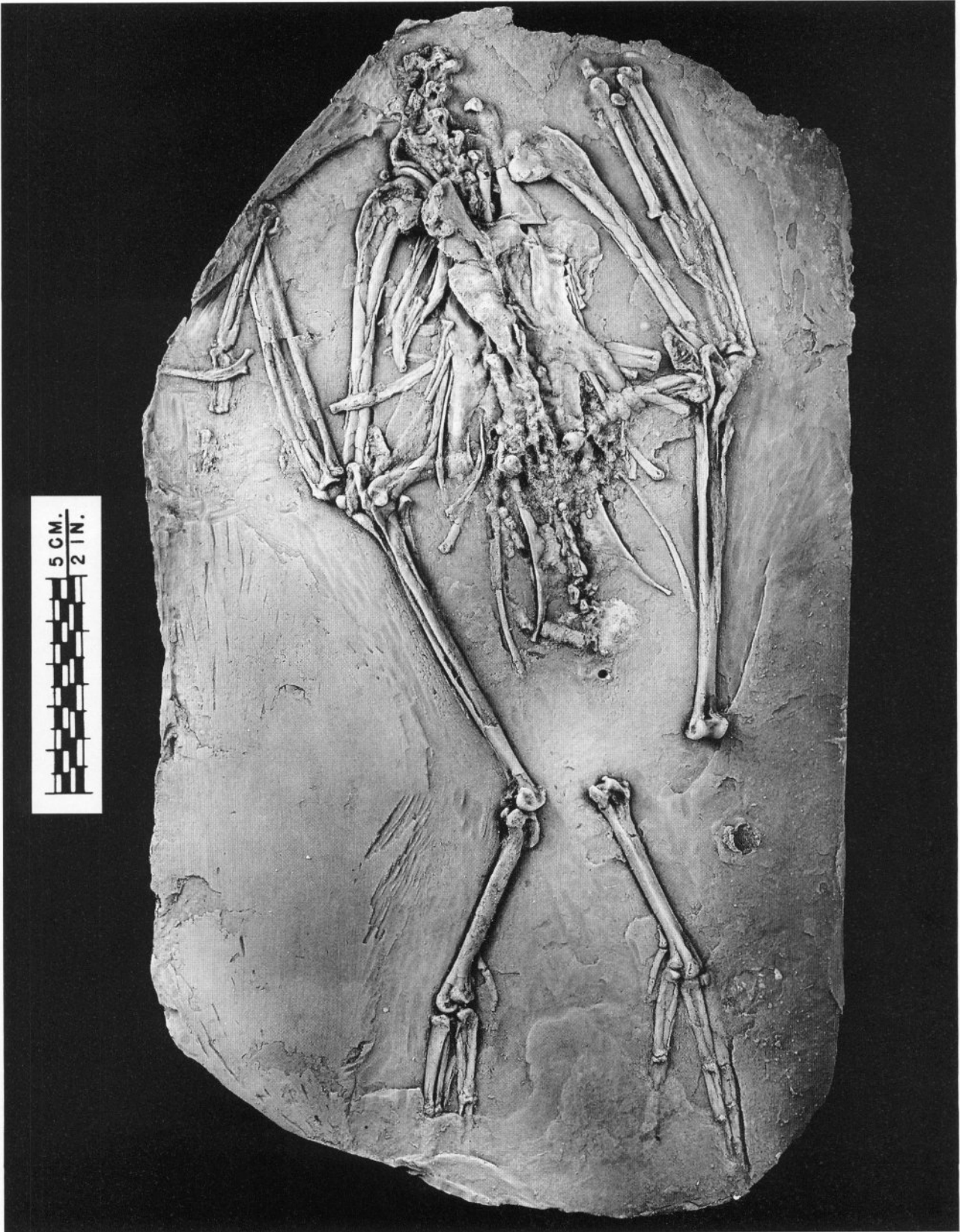


Fig. 3: Holotype of *Thiornis sociata* (MNHN 1930-1). Original slab after preparation by imbedding in epoxy resin and removing the matrix from the opposite side. Specimen coated with ammonium chloride to enhance detail.

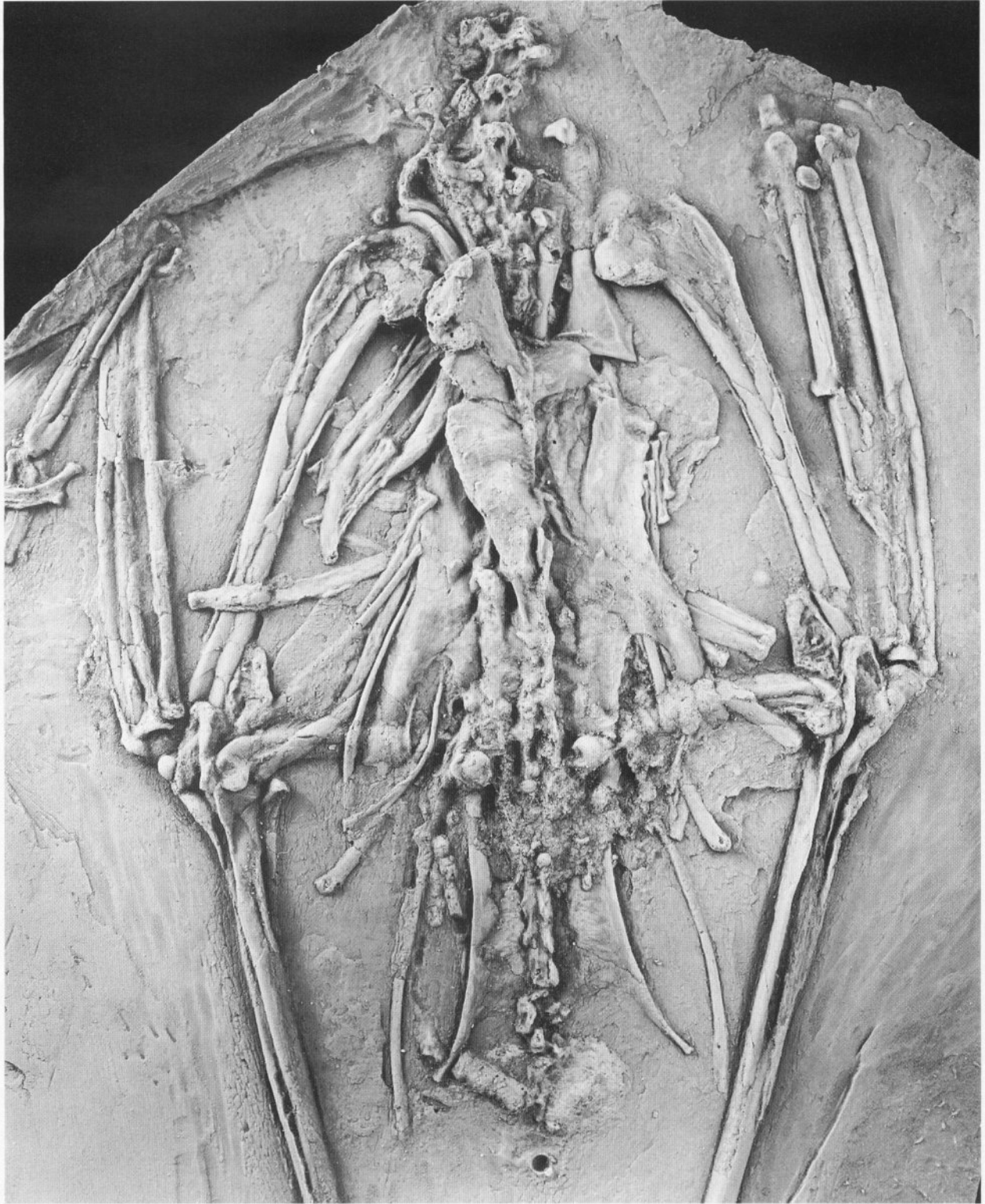


Fig. 4: Holotype of *Thiornis sociata* (MNHN 1930-1). Enlarged view of anterior portion of specimen as shown in Fig. 3. Specimen coated with ammonium chloride to enhance detail.

and tail, are clearly visible as darker images against the lighter matrix. Because of subsequent warping of the slabs, it was no longer possible to fit the two halves together. In order to observe details of the outer surface of the bones, one of the slabs was embedded in epoxy resin and the overlying matrix was removed from the opposite side (Figs. 3, 4). This revealed the skeleton essentially in ventral view, with the sternum uppermost, the wing elements shown in palmar aspect, the left leg more or less in anterior view and the right leg in medial view.

Measurements (mm) of holotype: Coracoid: length from head to external sternal angle, 33.4; width of sternal end, 13.5. Furcula: length, 37.0. Sternum: approximate width at posterior costal facet, 29. Humerus: length, 75.7; proximal width, 15.4; distal width, ca. 8. Ulna: length, 73.5. Radius: length, 68.6. Carpometacarpus: length, 36.5. Major alar digit: length phalanx 1, 14.8; length phalanx 2, 9.9. Femur: length, 34.7. Patella: length, 12.8. Tibiotarsus: total length including inner cnemial crest, 89.8; length from proximal articular surface, 76.8; distal width, 8.1. Tarsometatarsus: length, 48.7; proximal width, 9.0. Metatarsal 1: length, 5.3. Pedal digit 1: total length, 10.8; length phalanx 1, 7.7; length phalanx 2, 3.0. Pedal digit II: total length, 43.8; length phalanx 1, 20.4; length phalanx 2, 17.4; length phalanx 3, 6.3. Pedal digit III: total length, 52.7; length phalanx 1, 21.0; length phalanx 2, 12.9; length phalanx 3, 12.0; length phalanx 4, 7.0. Pedal digit IV: total length, 53.9; length phalanx 1, 21.9; length phalanx 2, 9.2; length phalanx 3, 8.4; length phalanx 4, 9.4; length phalanx 5, 5.2.

The distance between the heads of the femora, which are articulated in their natural positions, is 10.2 mm. No further useful measurements were possible for the pelvis.

Comparisons: Although I examined skeletons of virtually all modern grebes (see Material examined), the following taxa were selected for the comparisons below either for their resemblance in size (*Podilymbus podiceps*, *Podiceps auritus*, *P. nigricollis*) or in certain qualitative features (*Podiceps occipitalis*, *Tachybaptus ruficollis*, *Poliocephalus novaehollandiae*, *Rollandia rolland*).

Coracoid: In the fossil, the head does not project as far ventrally as in most grebes and is thus more similar to *Tachybaptus* and *Poliocephalus*.

Furcula: The clavicle in lateral view is much less curved than in typical grebes, being more similar to *Tachybaptus* and *Poliocephalus* in this respect but the shaft is more robust in the fossil than in any modern forms.

Sternum: A deep lateral notch can be discerned on either side, although the xiphial area is obscured. The carina appears to project rather far anteriorly but this

has doubtless been affected to some extent by crushing. There are no trenchant differences in the sternum between the fossil and modern grebes as far as can be told.

Humerus: The pectoral crest in the fossil is more expanded and rounded, rather than somewhat incised as in modern grebes.

Ulna: The shaft is more robust than in *Podiceps*.

Carpometacarpus: This has the form typical of all modern grebes, in which the bone is straight, slender, with a very narrow intermetacarpal space.

Pelvis: The posterior portion of the pelvis in the fossil is comparatively broad, with the ilia flaring outward. The ischia are very long and narrow and extend posteriorly well beyond the sacrum and the dorsoposterior point of the ilium. This is the condition that obtains in *Tachybaptus* and *Poliocephalus*, whereas in other genera the pelvis is more laterally compressed and the ischia are much shorter, about equal to the dorsoposterior point of the ilium in extent and separated from it by only a shallow notch. There is some variation; for example, the posterior portion of the pelvis in *Podiceps occipitalis* is broader than in other species of that genus, but not so much as in *Tachybaptus* and the fossil.

Femur: Most details of the femora are obscure but this bone is definitely not as slender and elongate as in *Podilymbus* and is like most other grebes in this respect.

Tibiotarsus: The cnemial crest is enlarged, as typical of grebes, but is relatively short and wide, being least like *Podiceps*, in which genus this crest is the most slender and elongate. There is a well-developed, broad patella, similar to modern grebes.

Tarsometatarsus: The shaft is not as slender and laterally compressed as in *Podiceps* and more closely resembles that of *Tachybaptus*, *Podilymbus*, etc.

Size: The general size of all modern grebes may be assessed from Table 1. Interestingly, the length measurements of the major elements of *Thiornis sociata* can consistently be matched by only a single species, *Podiceps auritus*. The pectoral elements are also similar to those of *Podilymbus podiceps* and some of those of *P. gigas*, due to the reduced flight capability of the latter, but the leg elements do not agree in size with that genus, except that the tibiotarsus barely falls in the range of *P. gigas*. The next most similar species in size is *Podiceps nigricollis*, which, however, is invariably smaller. This strong agreement in size between *Thiornis sociata* and *P. auritus* and no other modern species of grebe is very suggestive.

Proportions: The proportions of *Thiornis sociata* differ from those of modern species of similar size. In a specimen of *Podiceps auritus* in which the lengths of the coracoid, femur, and postacetabular pelvis are essentially identical with *Thiornis*, the humerus is

	Coracoid	Humerus	Ulna	Carpus	Femur	Tibiotarsus	Tarsus
<i>Tachybaptus dominicus</i>	20.3-24.2	45.7-54.2	43.3-51.4	20.0-23.4	25.2-29.7	54.1-64.0	30.4-34.1
<i>Tachybaptus rufolavatus</i>	20.6-20.8	47.9-52.1	42.8-46.7	21.3-23.0	28.3-31.2	61.2-65.9	34.3-35.8
<i>Tachybaptus novaehollandiae</i>	24.1-25.3	53.8-58.4	50.4-53.9	21.1-26.4	28.0-30.2	61.8-67.5	33.8-37.3
<i>Tachybaptus ruficollis</i>	22.5-26.9	51.4-58.1	46.6-53.4	22.8-26.2	27.6-33.1	61.2-68.8	32.3-38.6
<i>Rollandia rolland chilensis</i>	23.7-26.6	48.9-58.2	47.5-53.2	21.0-25.5	29.7-33.0	65.1-71.3	33.1-36.7
<i>Poliocephalus poliocephalus</i>	25.6-27.0	55.9-61.8	52.6-56.0	26.7-28.6	28.7-31.0	65.0-70.5	36.6-39.5
<i>Poliocephalus rufopectus</i>	26.0	60.5	54.5	26.7	33.1	75.4	41.9
<i>Podiceps occipitalis</i>	25.4-26.9	65.0-67.2	59.4-61.3	27.8-30.1	31.8-35.6	73.1-77.5	38.0-41.9
<i>Podiceps nigricollis</i>	26.8-30.3	62.6-72.7	58.6-66.2	27.6-32.7	30.5-34.0	73.2-84.1	38.7-43.6
<i>Podiceps auritus</i>	29.7-33.6	72.4-83.5	63.9-74.6	31.6-36.8	31.4-35.5	81.2-93.8	42.2-49.9
<i>Podilymbus podiceps</i>	31.8-35.9	65.6-81.2	61.6-76.4	29.2-37.6	35.2-42.7	72.0-87.0	39.0-44.2
<i>Podiceps taczanowskii</i>	28.0-28.9	67.9-69.2	61.8-62.4	29.6-30.0	35.4-36.1	83.3-86.2	44.2-46.9
<i>Podiceps gallardoi</i>	32.7-33.3	80.2	73.2	37.4	39.1-40.7	93.5	48.4
<i>Podilymbus gigas</i>	33.4-37.5	78.4-85.8	70.0-76.5	30.3-36.8	43.7-46.1	88.2-96.0	43.6-45.5
<i>Podiceps g. grisegena</i>	35.4-38.4	91.8-95.7	84.0-88.1	40.0-43.1	39.1-41.6	99.1-107.9	51.8-56.1
<i>Podiceps cristatus</i>	39.3-44.7	100.6-116.5	91.1-106.6	42.7-49.2	41.0-45.9	118.9-129.6	61.3-67.7
<i>Rollandia microptera</i>	29.1-34.4	64.2-74.3	49.0-56.4	25.8-30.1	41.5-46.5	95.7-112.8	49.0-56.1
<i>Aechmophorus occidentalis/clarkii</i>	41.7-49.8	103.2-120.2	89.9-107.9	44.8-53.0	39.7-49.2	123.6-147.2	68.2-77.8
<i>Podiceps g. holboelli</i>	43.2-48.8	106.0-119.4	96.0-110.6	45.9-52.3	42.7-50.9	120.6-137.3	60.1-68.7
<i>Podiceps major</i>	39.1-49.3	102.0-125.2	90.2-108.5	43.9-54.8	42.4-52.8	120.4-151.1	60.5-76.4

Tab. 1: Minimum and maximum measurements of lengths of major postcranial elements of grebes (Podicipedidae). The measurements for *Thiornis sociata* fall within the ranges indicated in boldface. For numbers of specimens, see Material examined. The general arrangement is by increasing size of the femur, with some adjustments. Proportional differences between taxa that make the measurements of certain elements fall "out of sequence" are the reduced pectoral apparatus in the three presumed flightless species (*Podiceps taczanowskii*, *Podilymbus gigas*, and *Rollandia microptera*) and the proportionately longer femur in the genus *Podilymbus*. *Podiceps occipitalis* also seems to have a proportionately long femur for its size, and its position in the table, as with the species of *Podilymbus*, has been adjusted. Length measurement of the coracoid is the greatest diameter of the bone; that of the tibiotarsus includes the cnemial crest.

slightly longer, but the ulna slightly shorter, and carpometacarpus about equal to that of the fossil. The tibiotarsus, tarsometatarsus, and preacetabular pelvis are all shorter than in the fossil.

Discussion

Although there are 6 genera currently recognized in the Podicipedidae (STORER, 1979), these are defined mainly by characters of courtship behavior (STORER, 1963). Two tribes were recognized by STORER (1963) on the basis of the number of canals in the hypotarsus, although this appears to be individually variable in at least some instances (an accessory canal was present in 1 of 4 specimens of *Podiceps major* examined at ROM, pers. obs.). Otherwise, the grebes are osteologically rather homogeneous, with few trenchant adaptations to differentiate the genera. *Podilymbus* is perhaps the most distinctive in its relatively longer femur and in the feeding adaptations of the head and neck (ZUSI & STORER, 1969).

Diving adaptations (e.g. lateral compression of the pelvis and tarsometatarsus, lengthened cnemial crest) are less pronounced in the small dabchicks (*Tachybaptus*, *Poliiocephalus*) than in other grebes, such as *Podiceps*, although within *Podiceps* there is some variation, as *P. occipitalis*, for example, appears less specialized than the more typical species such as *P. cristatus*, *P. auritus*, or *P. nigricollis*.

In its general morphology, particularly the pelvis and hindlimb, *Thiornis sociata* is decidedly more similar to *Tachybaptus* than to modern species of *Podiceps*. Yet in size it is much larger than any known forms of *Tachybaptus* and consistently falls within the range only of *Podiceps auritus* (Table 1), one the commonest and most widespread grebes in the Northern Hemisphere.

Several interpretations of the relationships of *Thiornis sociata* are possible. It could represent an extinct lineage of large species within *Tachybaptus*, or an extant lineage that has become much smaller since the Miocene. Conversely, it may be representative of the general state of evolution of grebes in the Miocene and thus be a primitive form of *Podiceps*, perhaps ancestral to some modern lineage such as *P. auritus*. We know very little about the morphology of Miocene grebes. The characters of *T. sociata* that appear similar to *Tachybaptus* are, in fact, probably primitive. The earliest known grebe, *Miobaptus walteri*, from the early Miocene (Aquitainian) of Czechoslovakia (SVEC, 1982, 1984), was a smaller form that was also described as being most similar to *Tachybaptus*. There is certainly nothing about the morphology of *Thiornis* to merit retaining it as a genus separate from all modern grebes. I therefore recommend that it be

carried in the nomenclaturally oldest and most widespread genus *Podiceps*, as *Podiceps sociatus*, until such time as further knowledge of Neogene grebes should either confirm or refute this assignment.

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